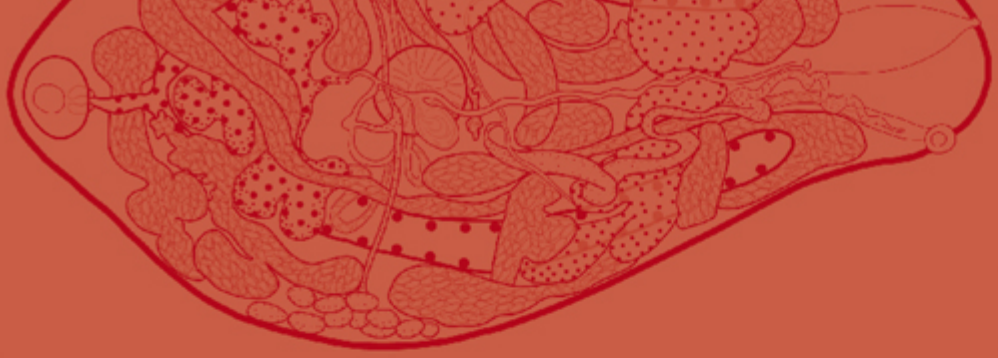
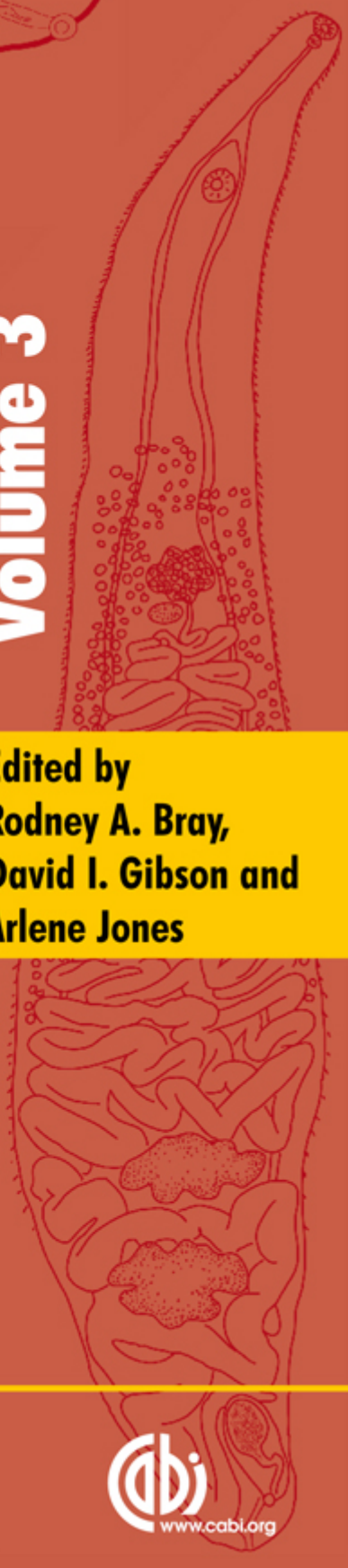


# KEYS TO THE TREMATODA

Volume 3

Edited by
Rodney A. Bray,
David I. Gibson and
Arlene Jones



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# Keys to the Trematoda
## Volume 3

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**Rodney A. Bray, David I. Gibson and Arlene Jones**

*Natural History Museum, London, UK*

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# General Introduction

This is the third of three volumes of *Keys to the Trematoda*, a series on the systematics and identification of the Class Trematoda Rudolphi, 1808 of the Phylum Platyhelminthes. It presents some of the taxa in the Order Plagiorchiida and one family of the Order Strigeida omitted from Volume 1. The volume includes five plagiorchiidan superfamilies, the Opisthorchioidea, Gorgoderoidea, Monorchioidea, Plagiorchioidea and Microphalloidea plus the strigeidan family Didymozoidae. The organization of this volume is discussed further in Chapter 1.

As with Volumes 1 and 2, invited specialists were given a basic classification of the Trematoda and a list of nominal genera in their groups taken from the Host–Parasite Catalogue and Database maintained in the Parasitic Worms Division, Department of Zoology, Natural History Museum, London. The editors provided guidance for the preparation of chapters, but did not restrict authors in their approach to their group, except where it affected the basic classification or the work of other authors. Consequently, contributions do vary in, for example, the detail that authors consider necessary to diagnose taxa within their group and the style of the illustrations.

We have continued to treat the superfamily as the basic unit of classification and, in Chapter 1, a cumulative key is provided to the superfamilies in the three volumes. Each superfamily and family group is generally treated as a separate chapter. As in the first two volumes, the key to the superfamilies is likely to be the weakest link in the chain. Each chapter has an introduction outlining the history of the group and recent or current changes within it, followed by keys and diagnoses for suprageneric groups and genera; characters common to the members of a family group tend not to be repeated at lower levels in the classification. At least one illustration for a representative of each genus considered valid is included.

The projected glossary is not included due to the volume size restrictions.

We have continued to apply the Principle of Coordination in the *International Code of Zoological Nomenclature* (1999, Article 36) and have, therefore, treated family-group names as coordinate taxa with the same authority, so that some of the authorities given here will be different from those elsewhere in the literature.

This volume has an index to taxa and a bibliography covering all the chapters in the volume.

Rodney A. Bray, David I. Gibson and Arlene Jones
*Natural History Museum, London, UK*



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# 1 Introduction and Key to Superfamilies

R.A. Bray

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## Introduction

This, the third and final volume of the *Keys to the Trematoda*, includes five superfamilies and one family that was omitted from Volume 1, the Didymozoidae Monticelli, 1888. During the production of these volumes, the molecular phylogeny of the Digenea has been progressing, but relatively slowly and based on a limited range of genes and sequences (Cribb *et al.*, 2001b; Olson *et al.*, 2003). Nevertheless, a consensus of the general outline is emerging. The five superfamilies treated in this volume are based mainly on these molecular results, particularly Olson *et al.* (2003) and, for the plagiorchioid and microphalloid taxa, the papers by Tkach and his colleagues (Tkach *et al.*, 1999, 2000a, 2001a, b, 2003). As the molecular phylogeny of the Digenea has been in progress during the production of these volumes, there will, inevitably, be some misplaced families, but we hope that the primary objective of the volumes, as an aid to identification, is not too badly compromised.

The Trematoda as recognized in these three volumes comprises two subclasses. The subclass Aspidogastrea, treated in Volume 1, comprises four families with 12 genera and about 80 species. The other subclass, the Digenea, is much larger and is treated in all three volumes of this series. It comprises 25 superfamilies, 148 families and nearly 2800 nominal genera. We estimate that about 18,000 nominal species have been described. Sixty of the digenean families include fish parasites, of which 38 families are exclusively fish parasites. The equivalent figures for the other vertebrate groups are: Mammalia 55 and 25; Aves 41 and 15; Reptilia 50 and 19; and Amphibia 19 and 2. Thus 99 (67%) of the families are found in a single vertebrate group. The remaining 49 families are found in more than one vertebrate group, but only in the case of the Microphallidae Ward, 1901 is a family reported from all five vertebrate groups.

In this volume we have included a key to all the superfamilies of the Digenea, indicating in which volume the detailed treatment is to be found.

The problems encountered in devising keys to the families and genera are compounded in devising keys to superfamilies. The superfamilies treated in this volume and, to a lesser extent, in the other volumes include a wide morphological variation, which overlaps that of other

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superfamilies, superficially at least. Hard-and-fast morphological key characters do not exist for many taxa and, therefore, a strict dichotomous key can be very misleading. We have developed the following key, but the user should be very aware of the difficulties in devising the key and the many exceptions. In several cases the reader will be directed to more than one superfamily. As intimated above, the following classification is based on phylogenies inferred from molecular data, as we have as far as possible attempted to reflect a natural system, but, as many of the taxa are not based on morphology, they have no unequivocal non-homoplasious apomorphies.

## Key to the superfamilies of the Digenea

**1a.** Parasitic in alimentary canal and associated cavities and organs (body-cavity, gall-bladder, urinary system, mouth, nasal cavity, branchial cavity, lungs) ..... 4.
**1b.** Not parasitic in alimentary canal and associated cavities and organs ..... 2.

**2a.** Parasitic under scales of fishes in warmer waters ..... Transversotrematoidea Witenberg, 1944. (Volume 1)
**2b.** Parasitic in tissues of body ..... 3.

**3a.** Parasitic in blood system (including heart, branchial, mesenteric and urinary bladder vessels, etc.) ..... Schistosomatoidea Stiles & Hassall, 1898. (Volume 1)
**3b.** Parasitic in body tissues (connective tissue, associated with muscles and other organs, eyes, ovary, branchial region, etc.) of marine (one exception) (especially scombroid) fishes ..... Didymozoidae Monticelli, 1888. (This volume, Chapter 65)

**4a.** Mouth well apart from anterior extremity; caecum single, elongate to saccular; ventral sucker absent; genital pore close to posterior extremity ..... Bucephaloidea Poche, 1907. (Volume 1)
**4b.** Mouth at or close to anterior extremity ..... 5.

**5a.** Oral sucker and ventral sucker usually present; mouth usually opens through oral sucker; parasitic in fishes and other vertebrate groups ..... 6.
**5b.** Oral and ventral suckers absent; mouth opens through pharynx (although this does resemble oral sucker); parasitic in teleost fish (mainly tropical marine, occasionally freshwater) ..... Bivesiculoidea Yamaguti, 1934. (Volume 1)

**6a.** Male and female terminal ducts unite to form hermaphroditic duct; prepharynx absent; testes normally pre-ovarian; excretory vesicle Y-shaped ..... 7.
**6b.** Male and female ducts open separately into genital atrium, rarely forming hermaphroditic duct, or through common genital pore; prepharynx present or absent; testes pre- or post-ovarian; excretory vesicle I-, Y- or V-shaped ..... 8.

**7a.** Hermaphroditic duct usually enclosed in sinus-sac; cirrus-sac absent; vitellarium variable, tubular to compact masses (usually two, occasionally seven or more, rarely one; follicular only in Ptychogonimidae); mainly in fishes, occasionally in amphibians and reptiles ..... Hemiuroidea Looss, 1899. (Volume 1)

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**7b. Hermaphroditic duct not enclosed in sinus-sac; cirrus-sac absent, but prostatic sac encloses seminal vesicle and pars prostatica; vitellarium follicular; testes postovarian (except in Leuceruthrinae); in freshwater and marine fishes ..... Azygioidea Lühe, 1909. (Volume 1)**

**8a. Cirrus-sac present or absent; prepharynx present or absent; vitellarium follicular; excretory vesicle I-, Y- or V-shaped; mainly in higher vertebrates ..... 9.**
**8b. Cirrus-sac present; prepharynx absent; vitellarium tubular, branched; excretory vesicle Y-shaped; extremely large forms from marine teleosts ..... ..... Hemiuroidea Looss, 1899 in part (Hirudinellidae Dollfus, 1932). (Volume 1)**

**9a. Body with specialized holdfast organ situated posterior to ventral sucker; body often bipartite, with broad cup-shaped anterior region; body unspined ..... ..... Diplostomoidea Poirier, 1886. (Volume 1)**
**9b. Body lacking specialized holdfast organ; body not normally distinctly bipartite; body may or may not be spined over at least part of its surface ..... 10.**

**l0a. Excretory pore at level of pharynx; testes extremely elongate, extending to most of body-length; vitellarium forms two extremely elongate bands that extend close to posterior extremity; in lungs and trachea of Nearctic and Neotropical freshwater turtles ..... ..... Heronimoidea Ward, 1917. (Volume 2)**
**10b. Excretory pore always far more posterior, usually at or close to posterior extremity; testes usually not elongate; vitellarium usually follicular; host distribution wider and, if in turtles, occupies sites in gut ..... 11.**

**11a. Ventral sucker absent or at least poorly developed ..... 12.**
**11b. Ventral sucker present ..... 14.**

**12a. Ventral sucker absent or at least poorly developed; oral sucker usually absent or at least poorly developed (occasionally present in Eucotylidae); caeca usually form cyclocoel; usually in nasal sinuses, air sacs, trachea, abdominal cavities, orbit and urinary tubules of birds (especially) and reptiles ..... Cyclocoeloidea Stossich, 1902. (Volume 1)**
**12b. Ventral sucker absent; oral sucker present or absent; in various sites in teleost fishes, reptiles, birds and mammals ..... 13.**

**13a. Cirrus-sac absent; pharynx present, functionally replacing oral sucker; excretory system entirely or partly reticulate; metraterm absent or poorly developed; in gut of marine and freshwater teleost fishes and reptiles ..... Microscaphidioidea Looss, 1900. (Volume 2)**
**13b. Cirrus-sac present; pharynx absent but oral sucker present; excretory system not reticulate, with V- or Y-shaped vesicle; metraterm usually distinct; various sites in teleosts, reptiles (chelonians and iguanids), birds and mammals ..... ..... Pronocephaloidea Looss, 1899. (Volume 2)**

**14a. Oral sucker absent, functionally replaced by pharynx ..... 15.**
**14b. Oral sucker usually or always present; pharynx typically present, very rarely absent or rudimentary ..... 16.**

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15a. Ventral sucker close to posterior extremity or not; cirrus-sac present; prostatic gland-cells external to cirrus-sac; in marine fishes ..... Lepocreadioidea Odhner, 1905 in part (Gyliauchenidae Fukui, 1929). (Volume 2)

15b. Ventral sucker always at or close to posterior extremity; cirrus-sac present or absent; if cirrus-sac present, prostatic gland cells internal to cirrus-sac; in (mainly) freshwater fishes and all other vertebrate groups, especially herbivorous mammals ..... Paramphistomoidea Fischoeder, 1901. (Volume 2)

16a. Hermaphroditic sac present ..... Haploporoidea Nicoll, 1914. (Volume 2)

16b. Hermaphroditic sac absent ..... 17.

17a. Pharynx usually absent; genital pore posterior to middle of hindbody; adults in oesophagus or buccal cavity of piscivorous birds, occasionally reptiles, rarely amphibians and mammals ..... Clinostomoidea Lühe, 1901. (Volume 1)

17b. Pharynx usually present; genital pore in forebody, anterior to middle of body or posterior to middle of body; in various hosts and sites ..... 18.

18a. Intestine with single caecum; testis usually single, rarely double; excretory vesicle Y-shaped; cirrus-sac usually absent, rarely present; in marine, estuarine and freshwater fishes ..... Haplosplanchnoidea Poche, 1926. (Volume 2)

18b. Intestine with two caeca; testes usually two, rarely multiple, single or absent ..... 19.

19a. Vitelline fields relatively small, with relatively few follicles or paired masses ..... 20.

19b. Vitelline fields extensive, many follicles ..... 23.

20a. Cirrus-sac absent ..... 21.

20b. Cirrus-sac present ..... 22.

21a. Caeca short, saccular; oral sucker larger than ventral; in birds, rarely mammals ..... Gymnophalloidea Odhner, 1905 (Gymnophallidae Odhner, 1905). (Volume 1)

21b. Caeca usually elongate; oral sucker not usually smaller than ventral; in various hosts .... Opisthorchioidea Looss, 1899. (This volume, Chapter 2)
Gorgoderoidea Looss, 1899 (in part). (This volume, Chapter 9)
Microphalloidea Ward, 1901 (in part). (This Volume, Chapter 46)

22a. In teleost fishes only ..... Monorchioidea Odhner, 1911. (This volume, Chapter 6)

22b. In a variety of hosts ..... Gymnophalloidea Odhner, 1905 (in part). (Volume 1)
Gorgoderoidea Looss, 1899 (in part). (This volume, Chapter 9)
Microphalloidea Ward, 1901 (in part). (This volume, Chapter 46)

23a. Genital pore in hindbody ..... 24.

23b. Genital pore in forebody or at level of ventral sucker ..... 25.

24a. Gonads close to posterior extremity; genital pore usually in posterior hindbody; in birds and mammals (occasionally reptiles and amphibians) ..... Brachylaimoidea Joyeux & Foley, 1930. (Volume 1)

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**24b. Gonads separated from posterior extremity; genital pore in anterior hindbody or close to posterior extremity (Urotrematidae Poche, 1926); in freshwater fishes, reptiles, rodents and bats ..... Plagiorchioidea Lühe, 1901 (in part). (This volume, Chapter 22)**

**25a. Tegument always lacks large areas of spine; in marine and freshwater fishes, rarely in amphibians and reptiles ..... Allocreadioidea Looss, 1902. (Volume 2)**
**25b. Tegument usually covered extensively by spines, but easily lost; in wide variety of hosts ..... 26.**

**26a. In wide variety of hosts ..... Echinostomatoidea Looss, 1899. (Volume 2)**
**..... Plagiorchioidea Lühe, 1901 (in part). (This volume, Chapter 22)**
**..... Opisthorchioidea Looss, 1899. (This volume, Chapter 2)**
**..... Gorgoderoidea Looss, 1899 (in part). (This volume, Chapter 9)**
**26b. In fishes only ..... Lepocreadioidea Odhner, 1905 (in part). (Volume 2)**

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# 2 Superfamily Opisthorchioidea Looss, 1899

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The Opisthorchioidea Looss, 1899 is one of the most firmly established higher taxa within the Digenea, comprising three fairly well-studied families with similar morphology and life-cycles. They are parasites of piscivorous teleosts, reptiles, birds and mammals. The simple-tailed cercariae, some with a finfold, are produced in rediae within gastropods and emerge to penetrate fish (rarely amphibians), in which the metacercariae develop. The definitive host becomes infected by ingestion of the second intermediate host. The miracidium remains in the egg until swallowed by a snail intermediate host.

The superfamily was first recognized by Faust (1929) as the 'Opisthorchoidea', including only the family Opisthorchiidae Looss, 1899. The same year Witenberg (1929) also erected a superfamily under the same name to include the families Opisthorchiidae and Heterophyidae Leiper, 1909. The following year Witenberg (1930) conceded priority to Faust, but retained the Heterophyidae in the Opisthorchioidea. Ciurea (1933) recognized the Cryptogonimidae Ward, 1917 at the family level and Price (1940) included it in the Opisthorchioidea, along with the Acanthostomidae Poche, 1926, now considered a synonym of the Cryptogonimidae (see Miller & Cribb, Chapter 4, this volume). Subsequent authors have continued to recognize the superfamily (e.g. La Rue, 1957), the validity of which has been supported by molecular results (Cribb *et al.*, 2001b; Olson *et al.*, 2003). The phylogenetic relationships between the families are not yet resolved (Olson *et al.*, 2003).

## Superfamily Opisthorchioidea Looss, 1899

(Syns Opisthorchoidea Faust, 1929; Heterophyoidea Faust, 1929; Opisthorchoidea Witenberg, 1929)

**Diagnosis:** Body-shape variable, oval, lanceolate, fusiform, cylindrical, elongate or extremely elongate. Tegument armed with spines (sometimes scale-like), occasionally unarmed. Eye-spot pigment usually present. Oral sucker subterminal or terminal, round to distinctly funnel-shaped, sometimes reduced or rudimentary, with or without dorsal ridge, dorsal lobe, posterior prolongation or circumoral spines. Ventral sucker always present, sometimes asymmetrical, may have cavity reduced or absent, with reduced musculature, may be armed with spines or sclerites or be embedded in

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ventrogenital sac. Prepharynx present or absent. Pharynx well developed. Oesophagus short or long. Intestinal bifurcation usually in forebody, rarely posterior to ventral sucker. Caeca two, long or short, rarely with anterior diverticula, usually terminate blindly, rare variations include atrophied or single caeca, cyclocoel, uroproct, separate ani at posterior extremity or single caecum with anus at posterior extremity and single blind caecum. Testes usually two, occasionally single, multiple or follicular, tandem, diagonal or symmetrical, entire or lobed, usually in hindbody, rarely entirely in forebody or extending into forebody. Seminal vesicle in forebody, rarely equatorial or in hindbody, tubular, coiled, undivided or uni-, bi- or tripartite (distal chamber may be thick-walled expulsor); male duct may unite with uterus usually dorsal to ventral sucker to form hermaphroditic duct. Pars prostatica often inconspicuous. Cirrus and cirrus-sac absent. Genital or ventrogenital sac may be present (Heterophyidae), rarely armed with spines or sclerites. Gonotyl present or absent, single, double or occasionally multiple, may have narrow pockets, in form of distinct muscular sucker-like or lobed structure immediately anterior to ventral sucker, rarely posterior to common genital pore, rarely armed with spines, occasionally with distinct non-muscular lobes of tegument. Genital pore in forebody, at level of ventral sucker or in anterior hindbody, rarely with separate male and female pores; in Heterophyidae pore may open on wall of ventrogenital sac, on gonotyl, on wall of genital sac, rarely in ventral sucker. Ovary in hindbody, entire or lobate, median or submedian, usually pretesticular, rarely between or posterior to testes. Seminal receptacle typically canalicular, rarely uterine. Laurer's canal probably always present. Uterus with many coils, usually entirely in hindbody, occasionally developed significantly in forebody. Eggs probably typically operculate, rarely with single distinct spine, filament or abopercular knob. Vitellarium follicular; follicles form two lateral bands, usually extracaecal and in hindbody, sometimes reaching posterior extremity or into forebody, may be restricted, rarely extensive throughout body. Excretory vesicle Y-shaped, saccate, tubular or V-shaped; pore terminal or subterminal. In bursa Fabricii, intestine, liver, bile-ducts, gall-bladder, body-cavity, pancreas, renal ureter and ureter of marine and freshwater fish, reptiles, mammals and birds, rarely amphibians; cosmopolitan. Type-genus *Opisthorchis* Blanchard, 1895.

## Key to families

**1a. Genital or ventrogenital sac present; in intestine of fish- and frog-eating birds and mammals, and occasionally freshwater siluroid fish ..... Heterophyidae Leiper, 1909.**
**1b. Genital or ventrogenital sac absent ..... 2.**

**2a. Testes usually near posterior extremity; uterus mostly or entirely pretesticular; gonotyl never present; in liver, bile-ducts and gall-bladder of birds and mammals, or digestive tracts of reptiles and teleost fishes ..... Opisthorchiidae Looss, 1899.**
**2b. Testes usually distant from posterior extremity; uterus often extensive posterior to testes, sometimes mainly pretesticular; gonotyl may be present; in intestine (rarely body-cavity or gall-bladder) of marine and freshwater fishes and reptiles, rarely amphibians ..... ..... Cryptogonimidae Ward, 1917.**

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# 3 Family Opisthorchiidae Looss, 1899

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Opisthorchiids are small to medium-sized flukes, the majority parasitic in the liver, bile-ducts and gall-bladder of birds and mammals, with some species found in the digestive tracts of reptiles and teleost fish. Together with the closely related Heterophyidae Leiper, 1909 and Cryptogonimidae Ward, 1917, they form the superfamily Opisthorchioidea Looss, 1899 of the monotypic suborder Opisthorchiata La Rue, 1957 (Olson *et al*., 2003). Within the Plagiorchiida La Rue, 1957, opisthorchioid trematodes represent neither the basal nor the most derived group. Looss (1899) erected this taxon as a subfamily and Braun (1901b) raised it to family level.

The Opisthorchiidae Looss, 1899 is characterized by the absence of a cirrus-sac. The terminal (distal) part of the vas deferens is enlarged to form a thin-walled, mostly tubular seminal vesicle, which is sinuous or coiled and opens through the common genital pore in a usually small, shallow genital atrium anterior to the ventral sucker. Many opisthorchiids have a lanceolate or elongate body, which is smooth or covered with tegumental spines, and their vitelline follicles form two bands along the lateral margins of the body. However, there are several exceptions from this body-plan. The excretory vesicle is Y-shaped, with a sigmoid, sinuous or straight stem that usually bifurcates at the pretesticular level.

Opisthorchiids have a three-host life-cycle. The eggs are numerous, small and operculate and contain formed miracidia. The egg must be eaten by the molluscan host, a prosobranchiate gastropod. The simple-tailed (pleurolophocercous) cercariae have the flame-cell formula 2 [(n + n) + (n + n + n)], with n = 3–6 (Filimonova, 2000). They are produced in rediae and emerge to penetrate fish and occasionally amphibians, which serve as second intermediate hosts, with the metacercariae encysting in the muscles (Yamaguti, 1975; Cribb *et al*., 2003). However, the life-cycles of some species maturing in non-piscivorous birds and mammals, such as species of *Euamphimerus* Yamaguti, 1941 and *Pachytrema* Looss, 1907, may be modified.

*Clonorchis sinensis* (Cobbold, 1875), *Opisthorchis felineus* (Rivolta, 1884) and *O. viverrini* (Poirier, 1886) are causative agents of the human infections clonorchiasis and opisthorchiasis, respectively. It is estimated that over 30 million people worldwide are infected (Roberts & Janovy, 1996; Mas-Coma & Bargues, 1997; Crompton, 1999), with a further 290 million at risk in regions where raw or undercooked fish are consumed, particularly in South-east Asia and circumpolar parts of Eurasia and North America (Rim *et al*., 1994; Muller, 2002; Chai *et al*., 2005).

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The taxonomy of some genera and subfamilies of the Opisthorchiidae have been dealt with by several authors, e.g. Looss (1899), Lühe (1908), Barker (1911), Poche (1926), Morgan (1927), Verma (1927), Price (1940), Baer (1944), Bisseru (1957), Yamaguti (1958b, 1971) and Filimonova (1998, 2000). The most comprehensive, but now outdated, monograph of the group was published by Skrjabin & Petrov (1950), but the phylogenetic relationships of opisthorchiids have never been assessed (Cribb *et al.*, 2001b; King & Scholz, 2001). The present key is largely based on morphological characters used by previous authors. It was impossible to sample sufficient material of a representative number of genera and subfamilies to assess their relationships inferred from phylogenetic analysis of morphological, life-cycle and molecular data. It is, therefore, possible that subsequent studies will better clarify relationships of opisthorchiid genera and their natural grouping.

Diagnoses of all genera ever placed in the Opisthorchiidae have been revised on the basis of a critical evaluation of extensive material of type- and voucher specimens of most opisthorchiid genera (preferentially, type-species were examined). Comparative material of several genera, especially those described from India, was not available for study despite several attempts to borrow type-specimens from collections where they have had to be deposited (Department of Zoology, Shibli Graduate College, Azamgarh; Department of Zoology, Ranchi University, Ranchi; Professor S.P. Gupta's Helminthological Collection, University of Lucknow, Lucknow; etc.). This means that the data from the original descriptions had to be compiled without the critical assessment of material. About 50 genera, comprising dozens of species, have been assigned to the family but the actual number of valid genera is apparently much lower because of numerous synonymies and homonymies (King & Scholz, 2001).

Yamaguti (1958b) divided opisthorchiids into the following subfamilies, many of them monotypic (marked with an asterisk): Opisthorchiinae Looss, 1899; Allogomtiotrematinae Yamaguti, 1958; *Delphinicolinae Yamaguti, 1933; *Diasiellinae Yamaguti, 1958; Metorchiinae Lühe, 1909; *Oesophagicolinae Yamaguti, 1933; *Pachytrematinae Railliet, 1919; *Plotnikoviinae Skrjabin, 1945; Pseudamphimerinae Skrjabin & Petrov, 1950; Pseudamphistominae Yamaguti, 1958; *Ratziinae Dollfus, 1929; *Tubangorchiinae Yamaguti, 1958; Aphallinae Yamaguti, 1958; Phocitreminae Yamaguti, 1933; and Pholeterinae Yamaguti, 1958.

The latter three subfamilies, i.e. the Aphallinae, Phocitreminae and Pholeterinae, are not considered here, because they belong to the Heterophyidae Leiper, 1909 and are treated elsewhere (see Pearson, Chapter 5, this volume).

Filimonova (2000) proposed two other monotypic subfamilies, namely the Holometrinae Filimonova, 2000 (type-genus *Holometra* Looss, 1899) and Microtrematinae Filimonova, 2000 (type-genus *Microtrema* Kobayashi, 1915).

In the present chapter, the classification to subfamilies of Yamaguti (1958b, 1971) is followed with several modifications. Several opisthorchiid genera are so markedly distinct that their placement in separate subfamilies seems to be well justified. In addition, classification to the subfamily level may facilitate the identification of individual genera. It should, however, be emphasized that the present classification, which includes a large number of monotypic subfamilies, is tentative and may not reflect the phylogenetic relationships of opisthorchiid genera.

## Subfamily Opisthorchiinae Looss, 1899

The Opisthorchiinae contains by far the largest number of opisthorchiid genera and species. Despite the morphological variation of individual genera, most taxa share a similar body-plan, such as the distribution of the uterine loops (usually intercaecal), the vitelline follicles (mostly in

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two bands along the lateral margins of the body but with different anterior and posterior extents), the position of the testes (often tandem, near the posterior extremity), the relative positions of the ovary, seminal receptacle and testes, and the shape of the body (usually lanceolate or elongate).

Assignation of many opisthorchiid genera, such as *Agrawalotrema* Sahay & Sahay, 1988, *Amphimerus* Barker, 1911, *Clonorchis* Blanchard, 1895, *Evranorchis* Skrjabin, 1944, *Gomtia* Thapar, 1930, *Hepatiarius* Feizullaev, 1961, *Nigerina* Baugh, 1958, *Paropisthorchis* Stephens, 1912, *Thaparotrema* Gupta, 1955 and *Trionychotrema* Jin & Zhang, 1981, to the Opisthorchiinae has been accepted by most authors. The subfamilial classification of a few genera, however, has been more problematic and they have appeared within different subfamilies.

*Cladocystis* Poche, 1926 was considered an opisthorchiine by Yamaguti (1958b, 1971) but it is included in the Metorchiinae here, following Skrjabin & Petrov (1950), mainly because of the presence of uterine loops anterior to the ventral sucker and lateral to the intestinal caeca, the symmetrical testes and the spination of the body-surface.

*Cyclorchis* Lühe, 1908 was also considered to be a member of the Opisthorchiinae by Yamaguti (1958b, 1971) but was placed in the Ratziinae (considered here as an opisthorchiid subfamily) by Skrjabin & Petrov (1950). It is unique among opisthorchiines in having uterine loops that are largely extracaecal (versus mostly intercaecal, with some loops ventral to the caeca in other opisthorchiine genera). However, in all other characteristics, *Cyclorchis* corresponds to the general body-plan of opisthorchiines and is retained in this subfamily.

The most complicated taxonomic situation exists regarding opisthorchiids from birds that possess a markedly narrowed or attenuated anterior part of the body and partly or completely reduced suckers, especially the oral sucker, i.e. *Pseudamphimerus* Gower, 1940, *Erschoviorchis* Skrjabin, 1945 and *Euamphimerus*, which were placed in the Pseudamphimerinae by Yamaguti (1971), and *Plotnikovia* Skrjabin, 1945 of the monotypic Plotnikoviinae (see the different classifications presented by Skrjabin, 1945a; Skrjabin & Petrov, 1950; Yamaguti, 1958b, 1971; Filimonova, 2000).

The shape of the body may represent an important taxonomic character (except for members of *Opisthorchis* and *Amphimerus* – see below), as may the development of the suckers. However, in the case of the genera previously placed in the Pseudamphimerinae, their morphology entirely corresponds in all other characteristics with that of the opisthorchiines, especially members of *Amphimerus*, i.e. the elongate body that is slightly widened posteriorly, the well-developed pharynx and oesophagus, the long, often slightly sinuous, intestinal caeca almost reaching the posterior extremity, vitelline follicles along the lateral margins of the body and almost reaching the posterior extremity, the simple genital pore immediately anterior to the ventral sucker, the uterus formed by tightly looped coils filling the space between the ventral sucker and the ovary and between the caeca or lateral to them, the voluminous, postovarian seminal receptacle, the sinuous stem of the excretory vesicle, passing between the testes, etc.

Filimonova (2000) suppressed the Pseudamphimerinae and placed its genera, namely *Pseudamphimerus, Erschoviorchis* and *Euamphimerus*, as well as *Diasiella* Travassos, 1949 of the Diasiellinae, in the Plotnikoviinae. In contrast, in this chapter the pseudamphimerine genera are assigned to the Opisthorchiinae, based on the arguments listed in the previous paragraph. *Euamphimerus* had previously been assigned to this subfamily by Yamaguti (1941) and, together with *Erschoviorchis*, also by Skrjabin & Petrov (1950). Therefore, the Pseudamphimerinae is also suppressed here, but becomes a synonym of the Opisthorchiinae, not the Plotnikoviinae as proposed by Filimonova (2000).

The type-genus, *Opisthorchis* Blanchard, 1895, *sensu* Skrjabin & Petrov (1950) and Yamaguti (1958b, 1971), contains trematodes of markedly distinct morphology, reported from a wide

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spectrum of definitive hosts (mammals, birds and teleosts) and sites of infection (liver, bile-ducts and intestine), which casts doubts upon the correctness of their recognition of only one genus. Most artificial seems to be the placement of species from freshwater fish, as they possess a spined, elongate body rather than a smooth (unspined), lanceolate body, typical of the species from mammals and birds. Because of marked differences in morphology, site of infection and spectrum of definitive hosts, a narrowing of the concept of *Opisthorchis* is proposed here, retaining only species with a smooth, medium-sized, usually lanceolate body that occur in the liver, gall-bladder and bile-ducts of mammals and birds. Those species previously placed in *Opisthorchis* that possess a small, elongate to fusiform body covered with simple tegumental spines and occur in the intestine and gall-bladder of freshwater teleosts in Asia and Africa are transferred to *Thaparotrema* (see below).

*Agrawalotrema* Sahay & Sahay, 1988 was erected for a new species, *A. ritai* Sahay & Sahay, 1988, from the intestine of the siluriform fish *Rita rita* at Patna, Bihar, in India (Sahay & Sahay, 1988). However, it is morphologically indistinguishable from and thus synonymous with *Opisthorchis pedicellata* Verma, 1927 (= *Thaparotrema pedicellatum*) found also in *Rita* from the same river at Allahabad (Verma, 1927; Figs 3.24, 3.25). *Agrawalotrema* therefore becomes a junior synonym of *Thaparotrema*.

*Amphimerus* Barker, 1911 is closely related to *Opisthorchis*, differing only in the postovarian extent of the vitelline follicles. It contains a number of taxa that differ markedly from each other in body-shape, from lanceolate with a wide posterior end (similar to *Opisthorchis felineus*) in most species from mammals, such as *A. costarricensis* Lamothe-Argumedo & Brenes Madrigal, 1984, *A. guayaquilensis* (Rodriguez, Gomez & Montalván, 1948), *A. lancea* (Diesing, 1850), *A. pricei* (Foster, 1939) and *A. pseudofelineus* (Ward, 1901), to long, almost cylindrical in species from birds, such as *A. anatis* (Yamaguti, 1933), *A. arcticus* Kontrimavitschus & Bakhmeteva, 1960 and *A. elongatus* Gower, 1938, but also in *A. neotropicalis* Caballero & Montero, 1963 from mammals (opossum). Some species of *Amphimerus* have also been reported as spined (e.g. *A. arcticus* and *A. ovalis* Barker, 1911), whereas others are unarmed (Barker, 1911; Filimonova, 2000). This morphological heterogeneity indicates that the genus may not be a natural assemblage. However, until a revision is carried out, it is considered premature to propose a taxonomic rearrangement.

*Clonorchis* Looss, 1907 is monotypic and its validity has been questioned, among others, by Morgan (1927) and Price (1940), as it very closely resembles *Opisthorchis*. The only reliable characters in which the genera differ are the shape and the lateral extent of the testes, which are dendritic and extend extracaecally in *C. sinensis* but are entire or lobed and intercaecal or ventral to the caeca in species of *Opisthorchis* (the testes are dendritic in *O. dendriticus* Morgan, 1927 but they do not cross the intestinal caeca laterally). A slight difference also exists in the more anterior extent of the vitelline follicles in *Clonorchis* (anterior to the ventral sucker or starting slightly posterior to it) compared with the more posterior position, starting at a distance posterior to the ventral sucker, in all species of *Opisthorchis*, including *O. dendriticus*. However, there appears to be intraspecific variation in the anterior and posterior extent of the vitellarium in *C. sinensis* and species of *Opisthorchis* (see Barker, 1907; Looss, 1907a). The course and shape of the stem of the excretory vesicle (allegedly straight and dorsal to the testes in *Clonorchis* versus sigmoid and passing between the testes in *Opisthorchis*) are not suitably diagnostic. In fact, the stem of the excretory vesicle of *C. sinensis* is slightly sigmoid, passing around the central parts of the testes and being situated dorsal to the lateral branches of the testes (see Fig. 3.31), similar to that found in some species of *Opisthorchis* that possess large, lobate or dendritic testes (*O. asiaticus* (Skrjabin, 1913) and *O. dendriticus*). The validity of *Clonorchis* should be confirmed using phylogenetic analyses, especially those inferred from molecular data, because its closeness to *Opisthorchis* is obvious and

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its distinguishing characters may represent interspecific variation, considering the morphological heterogeneity of species of the latter genus.

*Erschoviorchis* was characterized mainly by the absence of an oral sucker (Skrjabin & Petrov, 1950; Yamaguti, 1958b, 1971). However, examination of several specimens, including the paratype of the type-species, *E. lintoni* (Gower, 1939), has shown that the sucker is actually present, but it is rudimentary (see Fig. 3.5). Dollfus (1946b) suppressed *Erschoviorchis* as a synonym of *Amphimerus* because both taxa possess pre- and postovarian vitelline follicles, but this has not been accepted by later authors and is not followed here.

*Evranorchis* Skrjabin, 1944 was erected by Skrjabin (1944) for *Opisthorchis ophidiarum* Tubangui & Masiluñgan, 1935. Although the species was described from only a single specimen found in the intestine of a sea-snake in the Philippines (?accidental infection due to the consumption of fish), the genus has been widely accepted. *E. ophidiarum* resembles species of *Gomtia* that also possess a well-developed prepharynx, a spined body and a straight excretory stem that passes dorsally to the testes. *Evranorchis* differs from *Gomtia* in possessing a much longer (> 8 mm) body with parallel sides (*Gomtia* is shorter, < 3 mm long, and narrows at both ends) and shorter vitelline fields (reaching ovarian level in *Evranorchis*, but postovarian and reaching testicular level or close to the posterior extremity in *Gomtia*) (see Tubangui & Masiluñgan, 1935; Gupta, 1955). These differences are minor and may represent only interspecific variation. Nevertheless, *Evranorchis* is provisionally retained until new material is available for more detailed comparison of its morphology with that of other opisthorchiids. Susmita & Sahay (1990) described *E. hemidactyli* Susmita & Sahay, 1990, from India, which indicates that species of *Evranorchis* may be confined to reptiles. However, the description is incomplete and contains several errors, including the presence of a cirrus-sac (!). The very schematic illustration clearly demonstrates that the new species was based on only one deformed and damaged specimen. The deposition of *E. hemidactyli* specimen(s) was also not mentioned by Susmita & Sahay (1990) and it seems almost certain that type-material does not exist. Therefore, the validity of *E. hemidactyli* and its assignation to *Evranorchis* needs confirmation on the basis of new material.

*Gomtia* Thapar, 1930 was established for trematodes in the intestine of an unidentified siluriform fish at Lucknow, India (Thapar, 1930). Its validity was questioned by Mehra (1941) but supported by Skrjabin & Petrov (1950), Gupta (1955) and Yamaguti (1958b, 1971). The most important characters differentiating its species from those of *Opisthorchis* from fish (here transferred to *Thaparotrema*) and *Agrawalotrema ritai* (syn. of *Thaparotrema pedicellatum*) are the morphology of the excretory vesicle (with a straight stem passing dorsally to the testes versus sigmoid and passing around the testes in species of *Thaparotrema*) and the presence of a relatively long prepharynx (prepharynx absent in *Thaparotrema*). In addition, most species now transferred to *Thaparotrema* have vitelline follicles reaching the ventral sucker or anterior to it and their testes are slightly diagonal, whereas species of *Gomtia* have follicles starting far posterior to the ventral sucker and their testes are tandem. Dayal (1949) described two new species of *Gomtia* found in the intestine of siluriform fish at Lucknow, India, *G. gagatia* Dayal, 1949 from *Gagatia cenia* and *Gomtia lucknowia* Dayal, 1949 from *Bagarius yarrellii*. They were distinguished from *G. piscicola* Thapar, 1930 by negligible and dubious differences in the relative sizes of the suckers (sucker ratio 1.1:1 in *G. piscicola*, 1:1 in *G. lucknowia* and 0.9:1 in *G. gagatia*), the size of the seminal vesicle, the relative size of the prepharynx, pharynx and other unspecified organs, and the shape of the testes (in fact, almost identical in all three taxa). The only true difference between these three taxa is in the presence of pre-ovarian vitelline follicles in the intercaecal region in *G. gagatia*; in *G. piscicola* and *G. lucknowia*, the follicles are ventral to the intestinal caeca and do not extend medially (Thapar, 1930; Dayal, 1949). Therefore, *G. lucknowia* is synonymized with *G. piscicola*,

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whereas *G. gagatia* is provisionally retained as a valid taxon, although its type-material, if it exists, could not be examined.

*Hepatiarius* Feizullaev, 1961 was established to include *Opisthorchis longissimus* (Linstow, 1883) (syn. *Distomum longissimum* Linstow, 1883) from herons and ducks as the type-species and *H. sudarikovi* Feizullaev, 1961 from the bile-ducts of *Egretta garzetta* in Azerbaijan. The genus was differentiated from the most closely related *Opisthorchis* in having the anterior part of the body widened (Feizullaev, 1961). However, the body is widened between the suckers in three species of *Opisthorchis*, namely *O. altaevi* Saidov, 1954, *O. asiaticus* (Skrjabin, 1913) and *O. dendriticus* Morgan, 1927 (see Skrjabin, 1913; Filimonova, 2000). Body-shape does not seem to be a reliable generic feature in *Opisthorchis* and *Amphimerus* because of their highly variable shape. This comment also applies to *H. longissimus*, because the anterior part of the specimen illustrated in the original description of *Distomum longissimum* by Linstow (1883, fig. 50) is not enlarged. The shape of the body also largely depends on the state of contraction and the fixation method used. Consequently, *Hepatiarius* is suppressed as a junior synonym of *Opisthorchis*. In fact, Filimonova (2000) also invalidated *Hepatiarius*, transferring *H. longissimus* to *Opisthorchis* and proposing *H. sudarikovi* Feizullaev, 1961 as the new type-species of *Hepatiarius*. This taxonomic action is, however, not acceptable according to the rules of the International Code of Zoological Nomenclature and *Hepatiarius* is suppressed by the invalidity of its type-species.

*Neometorchis* Bilqees, Shabbir & Parveen, 2003 was erected to accommodate *N. lobatum* [*sic*] Bilqees, Shabbir & Parveen, 2003 from the liver (the intestine was reported as the site of infection in the species description) of a duck (*Anas* sp.) from Pakistan (Bilqees *et al.*, 2003a). The authors ignored the subfamily Opisthorchiinae, to which their trematodes apparently belong. Instead, they considered *Neometorchis* to be a member of the Metorchiinae despite marked differences in the course of the uterus and distribution of the vitelline follicles. It is clear from the morphology of *N. lobatum* that it is a species of *Opisthorchis*. Therefore, *Neometorchis* is synonymized with *Opisthorchis* and *N. lobatum* becomes *O. lobatus* (Bilqees, Shabbir & Parveen, 2003) n. comb. (Fig. 3.30).

*Nigerina* Baugh, 1958 was monotypic, including only *N. hardoiensis* Baugh, 1958, found in the gall-bladder and liver of *Phalacrocorax niger* in India (Baugh, 1958). It is most similar to *Amphimerus* in possessing, *inter alia*, vitelline follicles in the postovarian region, a short seminal duct reaching only slightly posterior to the ventral sucker, a short oesophagus and a posterolateral seminal receptacle. Baugh (1958) did not differentiate it from *Amphimerus* explicitly, but distinguished it from other opisthorchiine genera in having the margins of the hindbody ruffled, forming conical lateral projections that have a stratified nature (Baugh, 1958). It was considered valid by Yamaguti (1971) and is also accepted here. *A. interruptus* (Braun, 1901), described from the intestine (?) of fish-eating birds in North and South America, also has ruffled lateral margins with conical projections (see Braun, 1901b; Barker, 1911; Fig. 3.15), as in *N. hardoiensis*. Therefore, it is transferred to *Nigerina*, becoming *N. interrupta* (Braun, 1901) n. comb.

Skrjabin (1913) erected *Notaulus* for *N. asiaticus* Skrjabin, 1913. It differs from species of *Opisthorchis* in the more elongate shape of the body. Another species, *O. dendriticus* Morgan, 1927, was also placed in *Notaulus* because of its elongate body (Skrjabin & Petrov, 1950). It appears that this body-shape causes the stem of the excretory vesicle to pass dorsal to the testes as opposed to sinuously passing around them as is typical for other species of *Opisthorchis*. However, body-shape is variable in *Opisthorchis* and *Amphimerus* and cannot be used to distinguish genera. Therefore, *Notaulus* is considered a synonym of *Opisthorchis* in accordance with most previous authors, including Yamaguti (1958b, 1971) and several Russian authors who considered *Notaulus* a subgenus of *Opisthorchis* (e.g. Filimonova, 2000).

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The validity of *Paropisthorchis* Stephens, 1912, a monotypic genus proposed for *Opisthorchis caninus* Barker, 1911 from dogs in India by Stephens (1912) to accommodate liver-flukes with an armed body and a peduncle bearing both the ventral sucker and the genital pore, was questioned by Leiper (1913) and Morgan (1927), who considered the presence of a peduncle to be a consequence of differences in processing. Gupta & Pande (1963) also considered *Paropisthorchis* invalid, and a junior synonym of *Opisthorchis*, but found the peduncle to be a constant feature of *O. caninus*, thus supporting the validity of this species. In contrast, *Paropisthorchis* was treated as valid by Yamaguti (1958b, 1971). A study of *P. caninus* specimens from dogs from India and Pakistan, including unmounted 'cotypes' in a vial (USNPC 50453), shows that the peduncle is invariably present (Figs 3.21 and 3.22). If it is not protruded, it can easily be recognized, being separated from the body by a deep groove. Such a peduncle was never observed in any of the numerous specimens of different species of *Opisthorchis* studied. Therefore, *Paropisthorchis* is here considered to be valid because of the presence of the peduncle and the complete spination of the body, in contrast to species of *Opisthorchis* from birds and mammals.

*Pseudamphimerus* was placed in the monotypic Pseudamphimerinae because of the presence of a gonotyl, a character unique among opisthorchiids (but common in the closely related Heterophyidae – see Pearson, 1973, and Chapter 5, this volume). In the paratype of *P. sterni* (USNPC 9290), the genital pore opens on a papilla-like structure surrounded by circular musculature and (supposedly) gland-cells. This structure, however, does not resemble a true gonotyl, i.e. a muscular pad-like structure separated from the genital pore proper as found in many heterophyid genera (Pearson, 2002), but it is similar to structures surrounding the genital pore in other opisthorchiid genera, such as *Allogomtiotrema* Yamaguti, 1958, *Ratzia* Poche, 1926 or *Satyapalia* Hafeezullah, 1974. Examination of the *P. sterni* paratype also shows that the oral sucker is not completely absent as stated in the original description (Gower, 1940, pp. 163, 165). A small, spherical sucker is actually present around the oral opening, but it is strongly reduced and its margins are indistinct.

*Pseudogomtiotrema* Gupta & Jain, 1991 was proposed for *P. caranxi* Gupta & Jain, 1991, from the intestine of a marine fish, *Caranx malabaricus*, from the Bay of Bengal in India (Gupta & Jain, 1991). That the original description was based on deformed worms is obvious from the unnatural shape of the body, especially the almost filiform anterior part, the deformed pre-ovarian region, upwardly [*sic*] directed tegumental spines, the artificially everted ventral sucker, and other features. In addition, the illustration is a schematic sketch rather than a scientific illustration, which prevents an assessment of the morphology of the trematodes. Taking into account the poor quality of the description, the morphological data provided by Gupta & Jain (1991) should be considered with caution. The type-material, although requested by the present author, has not been available and doubts remain whether it actually exists. As far as it is possible to assess from the original description, *Pseudogomtiotrema* possesses several characteristics typical of *Gomtia* Gupta, 1955, with its long prepharynx, the straight stem of the excretory vesicle dorsal to the testes, the position of the testes close to the posterior extremity, the vitelline follicles starting far posterior to the ventral sucker, a long, slightly winding seminal vesicle and the body covered with tegumental spines. *P. caranxi* differs from species of *Gomtia* in the more posterior extension of the vitelline fields, the alleged absence of a seminal receptacle (?) and a more elongate, almost filiform anterior part of the body, which appears to be caused by the artificial elongation of the worms; these differences are considered to be of specific importance only. Therefore, *P. caranxi* is transferred to *Gomtia* as *G. caranxi* (Gupta & Jain, 1991) n. comb. and *Pseudogomtiotrema* becomes a synonym of *Gomtia*. The definitive host of *G. caranxi* also causes suspicion as it is the first record of an opisthorchiid in a marine host. The poor condition of the worms described by Gupta & Jain (1991) may indicate that *Caranx* was an accidental host.

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*Thaparotrema* Gupta, 1955 was erected for *T. vittalani* Gupta, 1955 from the intestine of the bagrid catfish, *Rita rita*, in India (Gupta, 1955). It was accepted by Yamaguti (1958b, 1971) and is also considered valid here, although no material has been studied. Considering the heterogeneity of *Opisthorchis* in shape, size and spination of the body, site of infection and spectrum of definitive hosts (see comments above), species previously placed in this genus but with a small, elongate or fusiform body covered with tegumental spines, no prepharynx and with a sinuous excretory stem are transferred to *Thaparotrema*, despite slight differences between them and *T. vittalani* in body-shape and the anterior extent of the vitellarium. Therefore, the following new combinations are proposed (voucher specimens of the former two taxa only have been available): *T. piscicola* (Odhner, 1902) n. comb., *T. pedicellatum* (Verma, 1927) n. comb., *T. mehrai* (Agarwal, 1959) n. comb., *T. parasiluri* (Long & Lee, 1958) n. comb. and *T. thaparae* (Agarwal, 1959) n. comb.

The description of *Trionychotrema* Jin & Zhang, 1981 and its type- and only species, *T. taenioidea* Jin & Zhang, 1981, was very brief (Jin & Zhang, 1981). This genus is very similar in its morphology, including the presence of acinous groups of vitelline follicles posterior to the ovary, to *Amphimerus*, whose type-species, *A. ovalis* Barker, 1911, was also found in the bile-ducts of a soft-shelled turtle of the genus *Trionyx* in North America (Barker, 1911; see above). However, these genera can be distinguished by the anterior extent of the vitellarium (anterior to the ventral sucker in *Trionychotrema* but distinctly posterior in *Amphimerus*) and the shape of the body (elongate with almost parallel sides and a truncate posterior end in *Trionychotrema* compared with other shapes in *Amphimerus* – even species with an elongate body from birds lack a truncate posterior end). For these reasons, *Trionychotrema* is tentatively considered to be valid, even though type- or voucher-specimens of its only species have not been available to the present author.

## Subfamily Allogomtiotrematinae Yamaguti, 1958

The Allogomtiotrematinae includes only two genera (Yamaguti, 1971), which are unique among opisthorchiids in possessing a wide oesophagus with a single or double sac-like diverticulum posteriorly. It is also typified by combinations of the following characters: (i) the genital pore lies at a distance from the ventral sucker (usually about halfway between its anterior margin and the intestinal bifurcation); (ii) the large, subventral oral sucker; (iii) the seminal receptacle anterolateral or lateral to the ovary; and (iv) the stem of the excretory vesicle is straight and passes dorsally to the testes. Species of this subfamily are intestinal parasites of freshwater fish in India. In contrast to other opisthorchiid genera from teleosts in South-east Asia (*Gomtia* and *Thaparotrema*), the Allogomtiotrematinae allegedly lack tegumental spines.

Gupta (1955) erected both the extant genera of the Allogomtiotrematinae, but both names were pre-occupied. Consequently, Yamaguti (1958b) proposed *Allogomtiotrema* as a replacement name for *Gomtiotrema* Gupta, 1955 *nec* Sinha, 1934 and *Gomtiotrema attu* Gupta, 1955 became *A. attu* (Gupta, 1955), the type-species of the genus. The original subfamily name, Gomtiotrematinae Gupta, 1955, accordingly had to be changed to Allogomtiotrematinae Yamaguti, 1958. *Assamia* Gupta, 1955 was pre-occupied by *Assamia* Sorensen, 1884 (Arachnida) and *Assamia* Buckton, 1896 (Insecta). Lakshminarayana & Hafeezullah (1974) proposed the replacement name *Satyapalia*, with *A. gauhatiensis* Gupta, 1955 becoming the type-species as *S. gauhatiensis* (Gupta, 1955). Although no specimens of any species of the Allogomtiotrematinae have been available to the present author, several unique characteristics justify the validity of the subfamily and both its genera, which differ markedly from each other.

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Lokhande (1990) described *Allogomtiotrema vidarbhasi* Lokhande, 1990 from the intestine of *Wallagonia attu* in the Morna and Katepurna Rivers in the Akola district of Maharashtra. It was differentiated from *A. attu*, found in the same host species, by a shorter, non-lobulate body, the ventral sucker larger than the oral sucker, a larger pharynx, a shorter oesophagus, a slightly more anterior extent of the vitelline fields and the position of the ovary ('ovary is close just away anterior testis in new form'). It is obvious from the very schematic illustration of the apparently flattened and deformed specimens of *A. vidarbhasi* in Lokhande's (1990) paper that the description was based on relatively young specimen(s), with a very short uterus containing few eggs. Nevertheless, the conspecificity of *A. vidarbhasi* with *A. attu* is obvious because the differential characters are negligible or even incorrect, e.g. the ventral sucker in the former taxon is actually smaller than the oral one, not larger as stated by Lokhande (1990). Consequently, *A. vidarbhasi* is synonymized with *A. attu*.

## Subfamily Delphinicolinae Yamaguti, 1933

The Delphinicolinae consists of a monotypic genus, which is so markedly different from all other genera of the Opisthorchiidae (see below) that its placement in a separate subfamily is unquestionable. So unique are the characteristics of *Delphinicola* Yamaguti, 1933, and thus the Delphinicolinae, it may even justify a separate family within the Opisthorchioidea. The most typical features of *Delphinicola* (see Yamaguti, 1933) are as follows: (i) the presence of a uterine seminal receptacle; (ii) a highly developed vitellarium filling about three-quarters of the body-length from the region posterior to the ventral sucker as far as the posterior extremity and surrounding the gonads; (iii) a sac-shaped, symmetrical vitelline reservoir with parallel main collecting ducts, forming an H-shaped structure; and (iv) a ventral sucker close to the anterior extremity. A study of the holotype and paratypes of *Delphinicola tenuis* Yamaguti, 1933 (MPM No. 22712) revealed another important characteristic overlooked by previous authors, including Yamaguti (1933). The intestinal caeca of *D. tenuis* were reported to end blindly near the posterior extremity, as in all other genera of the Opisthorchiidae. In fact, they open externally close to the excretory pore (Fig. 3.36). A similar character, i.e. ani at or near the posterior extremity, has also been found in some acanthostomines (now in the family Cryptogonimidae Ward, 1917) (see Miller & Cribb, Chapter 4, this volume).

## Subfamily Diasiellinae Yamaguti, 1958

The Diasiellinae is a small subfamily, proposed by Yamaguti (1958b) to accommodate the type- and only genus, *Diasiella* Travassos, 1949 (syn. *Diasia* Travassos, 1922, pre-occupied), which is also monotypic, with its type-species, *D. diasi* (Travassos, 1922), found in the pancreas of darters (*Anhinga*) in Brazil (Travassos, 1922). Yamaguti (1958b) characterized the subfamily and genus as possessing a flattened, fusiform body with reduced suckers (the oral is absent or rudimentary and the ventral very small) and symmetrical testes, overlapping the intestinal caeca ventrally near their ends. However, Skrjabin & Petrov (1950) did not consider *Diasiella* (as *Diasia*, apparently unaware of its name change) to merit subfamilial status, placing it in the Pachytrematidae Railliet, 1919 on the basis of the short excretory stem, which bifurcates posteriorly to the gonads (in fact it bifurcates anterior to the testes in *Diasiella*), symmetrical testes in the posterior part of the body and overlapping the caeca medially, asterisk-like bunches of vitelline follicles, weakly developed suckers and

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numerous uterine loops. There is some resemblance between *Pachytrema* and *Diasiella*, especially in the arrangement of the vitelline follicles and the symmetrical position of the testes. However, other characters (the development and position of the suckers, the morphology of the digestive system, especially anteriorly, the pre-ovarian position of the seminal receptacle in *Diasiella* and its absence in *Pachytrema*, the shape and position of the seminal vesicle, etc.), as well as the site of infection (gall-bladder versus pancreas), indicate that the genera are not closely related and their assignment to different subfamilies is justified. Consequently, *Diasiella* is considered to be a member of the Diasiellinae, as proposed by Yamaguti (1958b, 1971). Filimonova (2000) suppressed the Diasiellinae, placing *Diasiella* in the Plotnikoviinae Skrjabin, 1945, with all members of the Pseudamphimerinae Yamaguti, 1958 (*Pseudamphimerus, Erschoviorchis* and *Euamphimerus*). She argued that all these genera possess a reduced or completely atrophied oral sucker, a weakly developed ventral sucker and vitelline fields reaching the testicular level or as far as the posterior extremity, and occur in the pancreas, in the mesenteries or under the epithelium of the gall-bladder of birds. Despite the similarity between these subfamilies, *Diasiella* is considered here to be unrelated to members of the Plotnikoviinae and Pseudamphimerinae, particularly because of the extent of the uterus anterior to the ventral sucker, the different positions of the testes (symmetrical), seminal vesicle (anterior to the ventral sucker) and seminal receptacle (pre-ovarian), and the shape of the body (fusiform, often with a wider anterior part and with plicated ('ruffled') lateral margins).

## Subfamily Metorchiinae Lühe, 1909

The Metorchiinae is composed of four genera typified by the uterus reaching anterior to the ventral sucker, with loops extending extracaecally. All its genera have a spined, usually pyriform or fusiform body (never elongate, cylindrical or with an attenuate, filiform anterior region), and their vitelline follicles are confined to the anterior (pre-equatorial) or mid-region of the body (except for *Cladocystis* Poche, 1926 with follicles reaching the posterior third of the body).

The position of *Cladocystis* among the metorchiine genera has become unstable following its inclusion by Yamaguti (1958b, 1971) in the Opisthorchiinae. However, *Cladocystis* has, unlike all but one opisthorchiine genera (*Cyclorchis*), the uterus anterior to the ventral sucker and passing extracaecally, and symmetrical testes (versus tandem or diagonal in all opisthorchiine genera recognized here). Here, the generic concept of Skrjabin & Petrov (1950) is followed, especially because of the extent of the uterine loops (anterior to the ventral sucker and often extracaecal), the body covered with tegumental spines and the symmetrical testes. However, *Cladocystis* is markedly different from other metorchiine genera and future studies may provide arguments for a position outside the Metorchiinae.

Baer (1944) established *Allometorchis* Baer, 1944 for *Parametorchis intermedius* Price, 1929 (type-species), *P. canadensis* (Price, 1929) and *P. manitobensis* (Allen & Wardle, 1934). He was apparently unaware of the paper by Morozov (1939), who described *P. skrjabini* Morozov, 1939 and placed it in a newly proposed subgenus *Metametorchis* that was differentiated by possession of a simple uterus not forming a rosette. Skrjabin & Petrov (1950) raised *Metametorchis* to generic level, with *M. skrjabini* (Morozov, 1939) as the type-species. They also transferred the three species previously described in *Parametorchis* to this genus. However, these three North American species have the uterus surrounding the ventral sucker with numerous loops, thus resembling the rosette-like uterus of *Parametorchis*. Indeed, Yamaguti (1958b, p. 860) synonymized *Metametorchis* Morozov, 1939 with *Parametorchis*. Kennedy (1983), who revised *Parametorchis* and related taxa, also considered *Allometorchis* (= *Metametorchis*) to be a synonym of *Parametorchis*. Yamaguti

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(1971) resurrected *Metametorchis* and distinguished it from *Parametorchis* in having a uterus that does not form a rosette and the excretory stem running dorsally to the testes (versus passing between the testes in *Parametorchis*). However, in *P. canadensis, P. intermedius* and *P. manitobensis* the excretory stem passes between the testes and, since their uterine loops also form a rosette, they apparently belong to *Parametorchis*, as concluded by Kennedy (1983). The type-species of *Metametorchis* has not been available to the present author but its morphology does not justify an independent genus, especially given how vague the definition of a rosette-like uterus is and taking into account the variability in uterine morphology in opisthorchiids. Therefore, *Metametorchis* (and *Allometorchis* as its junior synonym) is considered a synonym of *Parametorchis*, in agreement with the conclusions of Yamaguti (1958b) and Kennedy (1983).

Filimonova (2000) proposed a new, monotypic subfamily, the Holometrinae Filimonova, 2000, to accommodate *Holometra* Looss, 1899. She justified this based on two differences between *Holometra* and members of the Metorchiinae: (i) the vitelline fields lie laterally to the oesophagus (they also lie along the anterior part of the caeca) and do not reach posteriorly as far as the ventral sucker in *Holometra* (versus between the postbifurcal region and the ovary, i.e. also posterior to the ventral sucker, in the Metorchiinae); and (ii) uterine loops separate the testes from the ovary in the former genus, but not in the Metorchiinae. The former character clearly distinguishes *Holometra* from other metorchiines, but the latter is also present in *Cladocystis*. Therefore, *Holometra* is here considered to be a member of the Metorchiinae and the Holometrinae is suppressed as its junior synonym.

*Holometra* was reported (Skrjabin & Petrov, 1950; Yamaguti, 1958b, 1971) to contain two species, *H. exigua* (Mühling, 1898) (syn. *Distomum exiguum* Mühling, 1898) from the bile-ducts of *Circus rufus*, found originally in East Prussia (now Russia – Kaliningrad region), and *H. aegyptiaca* Lühe, 1908. The latter was proposed by Lühe (1908) for trematodes found by A. Looss in the bile-ducts of *C. rufus* from Egypt. *H. aegyptiaca* (syn. *H. exigua* of Looss (1899) *nec* Mühling (1898)) differs in the more anterior position of the vitelline fields (between the oral sucker and the anterior part of the intestinal caeca, not reaching the level of the ventral sucker – plate 24, fig. 4 in Looss, 1899; redrawn as fig. 1364 by Yamaguti, 1971) than *H. exigua*, in which the follicles start at the level of the intestinal bifurcation and reach posteriorly almost as far as the ventral sucker (fig. 11 in Mühling, 1898). The examination of *Holometra* specimens collected by A. Looss in Egypt (USNPC 9642) has shown variation in the extent of the vitelline follicles. For example, dorsally situated follicles start at the pharyngeal level in one specimen, thus resembling the trematode figured by Looss (1899), but ventral follicles reach anteriorly just to the level of the intestinal bifurcation, as in the *H. exigua* specimen illustrated by Mühling in his fig. 11; posteriorly, dorsal and ventral follicles reach the ventral sucker. In another specimen collected by Looss (Fig. 3.40), follicles start at the level of the intestinal bifurcation and do not reach as far as the ventral sucker. Because of this variability, the two taxa described from the same definitive host are considered to be synonymous; *Holometra* thus becomes monotypic.

## Subfamily Microtrematinae Filimonova, 2000

*Microtrema* Kobayashi, 1915 was erected by Kobayashi (1915; English version published in 1920) for trematodes from the liver of the domestic pig in Japan and Formosa (now Taiwan) designated as *M. truncatum* Kobayashi, 1915. Skrjabin & Petrov (1950) placed it in the Pachytrematidae Baer, 1944 because of the short excretory stem, which bifurcates posteriorly to the gonads, the symmetrical testes in the posterior part of the body and in contact with the caeca, the asterisk-like bunches of

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vitelline follicles, the weakly developed suckers and an extensive uterus. Yamaguti (1958b, 1971), in contrast, placed *Microtrema* in the Pseudamphistominae Yamaguti, 1958, based on the truncated shape of the posterior end of the body, the short or absent oesophagus, the uterine loops reaching laterally to the caeca, the symmetrical or diagonal testes and parasitism of the biliary system of mammals. However, *Microtrema* differs from all other opisthorchiid genera in several characters that justify placement in a separate subfamily: (i) the uterus is almost completely anterior to the ventral sucker; (ii) the posterior (postequatorial) position of the ventral sucker; and (iii) the intertesticular position of the seminal receptacle. The Microtrematinae also differs from most opisthorchiid subfamilies in possessing a seminal vesicle anterior to the ventral sucker, an excretory vesicle bifurcating posteriorly to the symmetrical testes and a body truncated posteriorly.

The subfamily was proposed by Filimonova (2000) in her paper on the Opisthorchiinae and Plotnikoviinae. However, she neither provided any argument for this proposal nor mentioned which genera other than *Microtrema*, if any, should be placed in the new subfamily. Despite these deficiences, I agree with her proposal and *Microtrema* is considered here to be the sole member of the Microtrematinae.

## Subfamily Oesophagicolinae Yamaguti, 1933

Yamaguti (1933) described *Oesophagicola laticaudae* Yamaguti, 1933 and proposed the monotypic subfamily Oesophagicolinae for it. Subsequent authors have agreed (e.g. Skrjabin & Petrov, 1950; Yamaguti, 1958b, 1971). No material of *Oesophagicola laticaudae* has been available for this study (type-specimens are not available in the Meguro Parasitological Museum, Tokyo, Japan – J. Araki, personal communication). Nevertheless, the subfamily status has been accepted because of the following morphological characters: (i) the stem of the excretory vesicle is long and straight and bifurcates posterior to the ventral sucker and its wide and long arms reach alongside the oral sucker to near the anterior extremity; (ii) the vitellarium is dendritic (composed of tubular lobes) and occupies most of the lateral space between the region posterior to the ventral sucker and the posterior extremity, with numerous follicles reaching intercaecally or even to the median line of the body; (iii) the uterine loops almost completely fill the space ventral to the caeca between the ventral sucker and the anterior margin of the posterior testis; and (iv) the genital atrium is wide and opens via a slit-like aperture.

## Subfamily Pachytrematinae Railliet, 1919

The Pachytrematinae, although monotypic, is so distinct from other opisthorchiid subfamilies in its morphology that some authors, e.g. Baer (1944) and Skrjabin & Petrov (1950), have raised it to family rank. It is treated here as a subfamily of the Opisthorchiidae, although a higher taxonomic status cannot be excluded. It contains only *Pachytrema* Looss, 1907, which was erected for *P. calculus* Looss, 1907 from the gall-bladder of larids in Italy (Looss, 1907b). Currently, it contains several species from Eurasia and the Americas, but the validity of some requires confirmation. All species are characterized by a widely oval, elliptical body, a post- or intertesticular ovary, symmetrical testes near the lateral margins of the body, the ventral sucker close to the anterior extremity, a very short or absent oesophagus, and the vitellarium formed of grape-like bunches of small follicles near the lateral margins of the body along most of the caecal length; a seminal receptacle is allegedly absent (Looss, 1907b).

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Two genera previously described for species from the gall-bladder of birds in North America and India, respectively, are synonyms of *Pachymetra. Minuthorchis* Linton, 1928 was established by Linton (1928) for his new species, *M. sanguineus* Linton, 1928, from the gall-bladder of *Larus atricilla* and *Thalasseus maximus* in the USA. However, it was synonymized with *Pachytrema* by Yamaguti (1958b, 1971) because of the lack of substantial differences. Based on a study of Linton's (1928) description of *Minuthorchis*, I consider this synonymy to be correct. *Multivitellaria* Phadke & Gulati, 1929 (type-species *M. hewletti* Phadke & Gulati, 1929 from the gall-bladder of *Corvus splendens* in India) was first synonymized with *Pachytrema* by Purvis (1937). This synonymy was accepted by Skrjabin & Petrov (1950) and Yamaguti (1958b, 1971) because there are no characteristics that would justify the validity of the genus. I concur with this opinion.

## Subfamily Plotnikoviinae Skrjabin, 1945

*Plotnikovia* Skrjabin, 1945, based on *Diasia podilymbae* Olsen, 1938, was placed by Olsen (1938) in the Pachytrematinae; it differs from other opisthorchiid genera, including *Diasiella* Travassos, 1949, in the following characteristics or their combination: (i) reduced suckers, with the oral sucker being terminal; (ii) an elongate body, with almost parallel sides and an obtuse posterior end; (iii) a bipartite seminal vesicle anterior to the ventral sucker; (iv) a genital pore distinctly anterior to the ventral sucker; and (v) wide caeca that reach the posterior extremity. The probable absence of Laurer's canal (Olsen, 1938) may represent another differential character of the subfamily. These features justify the placement of *Plotnikovia* in a separate subfamily, as proposed by Skrjabin (1945a) and accepted by subsequent authors (Skrjabin & Petrov, 1950; Yamaguti, 1958b, 1971).

Filimonova (2000) included members of two opisthorchiid subfamilies, namely the Diasiellinae (with *Diasiella*) and Pseudamphimerinae Skrjabin & Petrov, 1950 (with *Pseudamphimerus, Erschoviorchis* and *Euamphimerus*), in the Plotnikoviinae. She based her proposal on: (i) a reduced or completely atrophied oral sucker; (ii) the weakly developed ventral sucker; (iii) the vitelline fields reaching posteriorly beyond the testes or to the posterior extremity; and (iv) parasitism of the pancreas or the mesenteries or under the epithelium of the gall-bladder of birds. On the other hand, members of these three subfamilies differ markedly in morphology, as discussed above (e.g. in the structure of the digestive system, the position of the testes, seminal receptacle and seminal vesicle, the anterior extent of the uterus, body-shape, etc.). Therefore, the taxonomic arrangement of Filimonova (2000) is not followed here and the Diasiellinae and Plotnikoviinae are retained as valid, both subfamilies being monotypic. In agreement with Filimonova (2000), the Pseudamphimerinae is suppressed, but its members are placed in the Opisthorchiinae, rather than in the Plotnikoviinae *sensu* Filimonova (2000).

In the illustration of the dorsal view of *Diasia podilymbae* (= *Plotnikovia podilymbae*), Olsen (1938, fig. 1) did not figure the ventral sucker, which apparently led subsequent authors to consider it absent ('atrophied' – Yamaguti, 1971). The ventral sucker is present, but reduced in size, as is obvious from Olsen's (1938, fig. 6) illustration of the anterior end (see Fig. 3.51).

## Subfamily Pseudamphistominae Yamaguti, 1958

Skrjabin & Petrov (1950) placed *Pseudamphistomum* Lühe, 1908 in the Metorchiinae because of the presence of uterine loops anterior to the ventral sucker. However, Yamaguti (1958b) proposed a new subfamily, the Pseudamphistominae, for it and *Microtrema* Kobayashi, 1915. Comparing

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*Pseudamphistomum* with *Microtrema*, I incline to the opinion that their resemblance, based mainly on a roughly similar body-shape, is only superficial. They differ so markedly in a number of important morphological characters (the position of the testes, seminal vesicle and uterine loops, morphology of the excretory vesicle, distribution of the vitellarium, morphology of the genital pore, etc.) that they should be in different subfamilies, following the subfamilial concept of Yamaguti (1958b, 1971), which is largely accepted in this chapter. *Microtrema* is therefore excluded from the Pseudamphistominae, which becomes monotypic, as proposed by Filimonova (2000).

The Pseudamphistominae is characterized mainly by three features, unique among the Opisthorchiidae: (i) the posterior end of the body forms a sucker-like depression, at the base of which the excretory vesicle opens; (ii) the genital pore and deeply embedded ventral sucker open at the top of a muscular pad formed by two large anterolateral muscular lobes; and (iii) the terminal part of the seminal vesicle is thick-walled and strongly muscular.

## Subfamily Ratziinae Poche, 1926

The subfamily Ratziinae was proposed by Poche (1926) because of the unavailability of the previous subfamily name Brachymetrinae Railliet, 1919, since *Brachymetra* Stossich, 1904 was preoccupied by *Brachymetra* Mayr, 1865 (Insecta). Poche (1926) erected *Ratzia* to accommodate *B. parva* (Stossich, 1904), which became the type-species of the new subfamily. Baer (1944) raised the Ratziinae to family level and added another opisthorchiid genus from reptiles, namely *Cyclorchis* Lühe, 1908. Skrjabin & Petrov (1950) accepted this and treated the Ratziidae as a separate family in the 'Opisthorchioidea Braun, 1901'. By way of contrast, Yamaguti (1958b, 1971) included the group as a subfamily of the Opisthorchiidae, with *Cyclorchis* placed separately within the Opisthorchiinae. This concept is followed here.

*Ratzia*, the type- and only genus of the subfamily, is morphologically similar to members of the Opisthorchiinae but differs in the following characters: (i) the caeca are short, reaching to the anterior testis only (in the third quarter of the body-length); (ii) the vitelline fields extend along the entire length of the caeca, both extra- and intercaecally, and are almost confluent anteriorly; (iii) the uterus is confined to a relatively small region between the seminal receptacle and the ventral sucker; (iv) the deeply embedded ventral sucker and genital pore open into a large atrium at the top of a muscular papilla surrounded by gland-cells; (v) the long oesophagus; and (vi) the short, thick-walled seminal vesicle.

## Subfamily Tubangorchiinae Yamaguti, 1958

The Tubangorchiinae is monotypic. *Tubangorchis caintaensis* (Tubangui, 1928) was originally described as *Metorchis caintaensis* Tubangui, 1928 from the intestine of the gruiform bird *Hypotaenidia philippensis* (= *Rallus owstoni*) in Luzon, Philippines (Tubangui, 1928). The subfamily differs from other opisthorchiid subfamilies in the form and position of the ventral sucker and the genital pore, which are at the level of the intestinal bifurcation, close to the pharynx. The ventral sucker is reduced and embedded within a large atrium opening through a large, transversely oval aperture surrounded by a circle of large tegumental spines. The genital pore is small, transversely oval and submedian and opens at the anterior margin of the ventral sucker.

The atrium of *Tubangorchis* Skrjabin, 1944, enclosing a reduced ventral sucker and genital pore, resembles the ventrogenital sac of trematodes of the closely related families Heterophyidae

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and Cryptogonimidae (see Pearson, Chapter 5, and Miller & Cribb, Chapter 4, this volume). However, it is tentatively retained in the Opisthorchiidae until phylogenetic analyses determine its actual position among the opisthorchioid families, i.e. Opisthorchiidae, Heterophyidae and Cryptogonimidae (Olson *et al*., 2003).

## Subfamily Witenbergiinae n. subfam.

A new subfamily, the Witenbergiinae, is proposed to accommodate the type- and only genus *Witenbergia* Vaz, 1932. *Witenbergia* is unique among opisthorchiids in possessing uterine loops reaching beyond the testes to the posterior extremity. The absence of post-testicular uterine loops in two vouchers recently collected in Brazil (see Fig. 3.62) may be accounted for by incomplete development of these specimens with relatively few eggs compared with those of the type-series. A post-testicular uterus is also present in *Pachytrema* (Pachytrematinae), but this is due to the anterior, pre-ovarian position of the testes in this genus, in which the uterine loops do not reach the posterior extremity. Other characteristic features of *Witenbergia* are the presence of a very long prepharynx, the length of which is about one-quarter of the total body-length, the pre-ovarian seminal receptacle (present only in *Allogomtiotrema* from fish in India and *Diasiella* from birds in South America) and a cup-shaped, terminal oral sucker. *Witenbergia* therefore differs so markedly from other opisthorchiid genera that it merits the erection of a separate subfamily. The original description (Vaz, 1932) of the type- and only species, *W. witenbergi* Vaz, 1932, was incomplete in that the course and posterior extent of the caeca were not described and the morphology of the excretory vesicle and the position of the excretory pore were not mentioned. Examination of two vouchers collected in 2004 in Brazil (IOC 36564a, b) confirmed most of the characteristics presented in the original description (with the exception of the post-testicular uterus – see above) but also made it possible to supplement this description with the morphology of the caeca and excretory vesicle. Skrjabin (1945b) proposed that *Witenbergia* be placed in the Phocitrematinae Skrjabin, 1945 and Opisthorchiidae, because of the 'analogous structure of their digestive organs and similar topographic relations between their ovaries and spermathecae'. However, *Phocitrema* is a member of the Heterophyidae (see Pearson & Courtney, 1977) and thus not related to *Witenbergia*. Similarly, the placement of *Witenbergia* in the Aphallinae Yamaguti, 1958, as a subfamily of the Opisthorchiidae, proposed by Yamaguti (1971), is not accepted here because this subfamily is currently recognized as a member of the Heterophyidae (Pearson, Chapter 5, this volume).

## Family Opisthorchiidae Braun, 1901

(Syns Pachytrematidae Railliet, 1919; Ratziidae Poche, 1926)

**Diagnosis:** Body small to medium-sized, lanceolate, elongate, fusiform or cylindrical, usually tapered anteriorly. Tegument unspined or spined. Oral sucker subterminal or terminal, sometimes reduced or rudimentary. Ventral sucker usually pre-equatorial, exceptionally reduced. Prepharynx present or absent. Pharynx present, well developed. Oesophagus short or long. Intestinal bifurcation in anterior third of body (slightly pre-equatorial in *Witenbergia*). Caeca long, straight or sinuous, blind in all genera but one (*Delphinicola*), reaching testicular level or posterior extremity. Testes two, tandem, diagonal or symmetrical, in posterior part of body. Seminal vesicle usually tubular, coiled, in forebody, rarely equatorial or in hindbody. Cirrus-sac absent. Genital pore in forebody. Ovary entire or lobate, median or submedian, mostly pretesticular. Sacciform seminal

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receptacle postovarian, rarely pre-ovarian or absent, seminal vesicle occasionally uterine. Laurer's canal usually present, opening on dorsal surface. Uterus forms numerous loops, usually intercaecal or ventral to caeca, with extracaecal loops in some genera, mostly pre-ovarian and in hindbody, rarely in forebody and exceptionally postovarian. Eggs operculate. Vitellarium well developed; vitelline follicles form two lateral bands, largely extracaecal and in hindbody, sometimes reaching posterior extremity. Excretory vesicle Y-shaped, with sigmoid or straight stem usually bifurcating at pretesticular level; pore terminal or subterminal. Life-cycle includes two intermediate hosts; pleurolophocercous cercariae develop in prosobranchiate snails and metacercariae in flesh of fishes. Adults in liver, bile-ducts, gall-bladder and pancreas of mammals and birds, rarely in intestine of fish and reptiles; cosmopolitan. Type-genus *Opisthorchis* Blanchard, 1895.

## Key to subfamilies

**1a.** Ventral sucker and genital pore bifurcal, close to oral sucker; ventral sucker reduced, deeply embedded within sac with its opening lined by large tegumental spines; in intestine of birds ..... Tubangorchiinae Yamaguti, 1958.

**1b.** Ventral sucker postbifurcal, not deeply embedded within sac lined with large tegumental spines ..... 2.

**2a.** Oesophagus wide, with one or two small posterior diverticula; genital pore far anterior to ventral sucker (about halfway between its anterior margin and intestinal bifurcation); in intestine of freshwater fish ..... Allogomtiotrematinae Yamaguti, 1958.

**2b.** Oesophagus tubular, without posterior diverticula; genital pore immediately anterior to ventral sucker ..... 3.

**3a.** Vitelline follicles filling three-quarters of body-length from ovary to posterior extremity, continuous medially in dorsal and ventral planes; caeca open via ani near posterior extremity; uterine seminal vesicle present; in bile-ducts of dolphins ..... ..... Delphinicolinae Yamaguti, 1933.

**3b.** Vitelline follicles less extensively developed; caeca end blindly; uterine seminal receptacle absent ..... 4.

**4a.** Uterus reaches beyond testes to posterior extremity; prepharynx very long, about one-quarter of body-length; seminal receptacle pre-ovarian; in intestine of freshwater fish ..... ..... Witenbergiinae n. subfam.

**4b.** Uterus not reaching posterior extremity, almost always pretesticular; prepharynx absent or short; seminal receptacle postovarian or absent ..... 5.

**5a.** Body widely oval, elliptical; ovary post- or intertesticular; ventral sucker very near anterior extremity; in gall-bladder of birds, exceptionally mammals ..... ..... Pachytrematinae Railliet, 1919.

**5b.** Body of different shape (usually much more elongate); ovary pretesticular; ventral sucker more posterior ..... 6.

**6a.** Posterior end of body with sucker-like depression .... Pseudamphistominae Yamaguti, 1958.

**6b.** Posterior end of body without sucker-like depression ..... 7.

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**7a. Stem of excretory vesicle wide and very long, bifurcates posterior to ventral sucker, with arms reaching close to anterior extremity; vitellarium of tubular lobes that fill most dorsolateral space posterior to ventral sucker and reach posterior extremity; genital atrium wide and genital pore transverse slit-like; in oesophagus of sea snakes ..... Oesophagicolinae Yamaguti, 1933.**

**7b. Excretory vesicle of different shape, without stem reaching to ventral sucker and arms to anterior extremity; vitellarium follicular, with different distribution; genital atrium and genital pore not as above; not in oesophagus of sea snakes ..... 8.**

**8a. Uterus almost completely anterior to ventral sucker; ventral sucker postequatorial; in liver of mammals ..... Microtrematinae Filimonova, 2000.**

**8b. Uterus largely posterior to ventral sucker; ventral sucker in anterior half of body; in various sites of birds, mammals, fish and reptiles ..... 9.**

**9a. Seminal receptacle pre-ovarian; seminal vesicle anterior to ventral sucker; oral sucker absent or rudimentary; testes symmetrical, near posterior extremity; body fusiform; in pancreas of birds ..... Diasiellinae Yamaguti, 1958.**

**9b. Seminal receptacle postovarian; seminal vesicle posterior to ventral sucker (partly anterior in *Cyclorchis*); oral sucker well developed (if absent or reduced, then body elongate, with attenuated anterior part); testes diagonal or tandem (symmetrical in *Cladocystis*); in various sites of birds, mammals, fish and reptiles ..... 10.**

**10a. Uterine loops reach into forebody; vitelline follicles usually in anterior (pre-equatorial) or mid-region of body; tegument spined ..... Metorchiinae Lühe, 1909.**

**10b. Uterus posterior to ventral sucker; vitelline follicles usually in posterior or mid-region of body; tegument unspined or spined ..... 11.**

**11a. Caeca short, terminating in third quarter of body-length; vitelline follicles along entire length of caeca, both extra- and intercaecal, almost confluent anteriorly; in intestine of snakes ..... Ratziinae Poche, 1926.**

**11b. Intestinal caeca long; vitelline follicles largely extracaecal or overlapping caeca; in various sites of birds, mammals, fish and reptiles ..... 12.**

**12a. Body elongate, with almost parallel sides and obtuse posterior end; seminal vesicle anterior to ventral sucker; intestinal caeca very wide; in (?) mesenteries of birds ..... Plotnikoviinae Skrjabin, 1945.**

**12b. Body of different shape; seminal vesicle posterior to ventral sucker; intestinal caeca narrow; in liver, biliary system and intestine of birds, mammals, fish and reptiles ..... Opisthorchiinae Looss, 1899.**

## Subfamily Opisthorchiinae Looss, 1899

(Syn. Pseudamphimerinae Skrjabin & Petrov, 1950)

**Diagnosis:** Body small to medium-sized, of variable shape, often lanceolate, elongate or cylindrical, tapered anteriorly. Tegument unspined or spined. Oral sucker usually subterminal, reduced or rudimentary in some genera. Ventral sucker usually small, pre-equatorial. Prepharynx absent or

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present. Pharynx well developed. Oesophagus usually short. Intestinal bifurcation in anterior quarter of body, usually near anterior extremity, closely posterior to pharynx. Caeca narrow, occasionally wide, and long and blind, reach testes or posterior extremity. Testes tandem or diagonal, in posterior third of body. Seminal vesicle tubular, looped, posterior to ventral sucker. Genital pore immediately anterior to ventral sucker. Ovary entire or lobate, submedian to median, pretesticular. Seminal receptacle usually postovarian. Laurer's canal usually present. Uterus entirely intercaecal or ventral to caeca (with extracaecal loops in *Cyclorchis*), pre-ovarian and posterior to ventral sucker. Vitellarium forms two lateral bands of follicles, largely extracaecal, between ventral sucker and ovary or reaches posterior extremity. Excretory vesicle Y-shaped, with sigmoid stem running between testes or straight stem dorsal to testes, bifurcates at pretesticular level; pore terminal or subterminal. In liver, biliary system and intestine of mammals, birds, fish and reptiles; cosmopolitan. Type-genus *Opisthorchis* Blanchard, 1895.

## Key to genera

**1a. Prepharynx well developed ..... 2.**
**1b. Prepharynx absent or very short ..... 3.**

**2a. Vitelline fields end at ovarian level; body cylindrical, with parallel sides ..... ..... *Evranorchis* Skrjabin, 1944. (Fig. 3.1)**

**Diagnosis:** Body long, slender, nearly parallel-sided. Tegument spined. Oral sucker subterminal, well developed. Ventral sucker small, near anterior extremity. Prepharynx long. Oesophagus short. Intestinal bifurcation near anterior extremity. Caeca reach posterior extremity. Testes oval, tandem, near posterior extremity. Seminal vesicle narrow, strongly winding posterior to ventral sucker. Ovary submedian, pretesticular. Seminal receptacle between ovary and anterior testis. Uterus intercaecal, between ovary and ventral sucker. Vitelline follicles extend along caeca between posterior end of seminal vesicle and ovary. Excretory vesicle with straight stem dorsal to testes, bifurcates at postovarian level; pore terminal. In intestine of snakes and geckos (?); Asia (Philippines and possibly India). Type-species *E. ophidiarum* (Tubangui & Masiluñgan, 1935) Skrjabin, 1944.

**2b. Vitelline follicles reach posteriorly to beyond ovary and to level of testes or posterior extremity; body elongate, tapers anteriorly ..... *Gomtia* Thapar, 1930. (Figs 3.2, 3.3)**
(Syn. *Pseudogomtiotrema* Gupta & Jain, 1991)

**Diagnosis:** Body small. Tegument spined. Oral sucker subterminal. Ventral sucker in anterior third of body. Prepharynx well developed. Pharynx oval. Oesophagus short. Caeca narrow, reach posterior testis. Intestinal bifurcation in anterior quarter of body, closely posterior to pharynx. Testes tandem, unlobed or weakly lobed, near posterior extremity. Ovary median. Uterus almost exclusively intercaecal, forms numerous loops between ovary and ventral sucker. Vitellarium forms two lateral fields of follicles, starting far posterior to ventral sucker and extending to anterior testis or, exceptionally, to posterior extremity; follicles ventrolateral to caeca or may extend medially in pre-ovarian region. Excretory vesicle with long, straight stem, dorsal to testes, branches at ovarian level; pore terminal. In intestine of siluriform fishes; Asia (India). Type-species *G. piscicola* Thapar, 1930.

**3a. Vitelline follicles extend alongside ovary to level of posterior testis or to posterior extremity ..... 4.**

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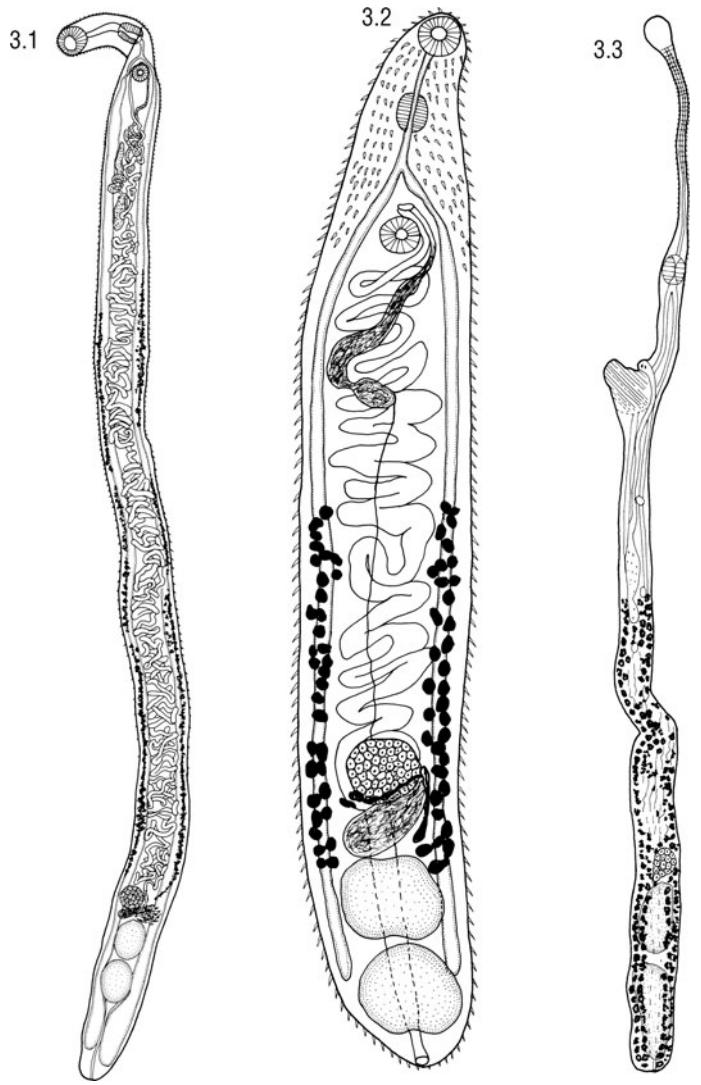



**Fig. 3.1.** *Evranorchis ophidiarum* (Tubangui & Masiluñgan, 1935). After Tubangui & Masiluñgan (1935).
**Fig. 3.2.** *Gomtia piscicola* Thapar, 1930. After Thapar (1930). Tegumental spines are apparently enlarged compared to their actual size.
**Fig. 3.3.** *Gomtia caranxi* (Gupta & Jain, 1991) n. comb. After Gupta & Jain (1991).

**3b. Vitelline follicles limited to pre-ovarian region or reach posteriorly only to anterior margin of anterior testis ..... 9.**

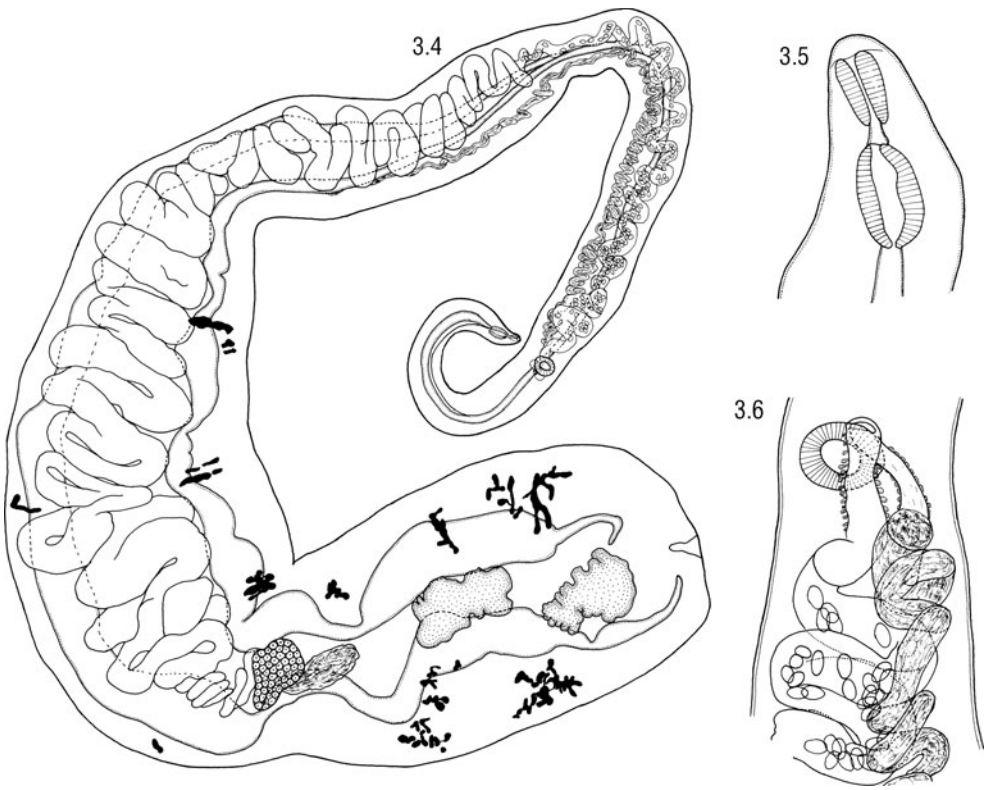
**4a. Anterior part of body attenuate, tapering to sharp point; oral sucker reduced or atrophied ..... 5.**
**4b. Anterior part of body not attenuate; oral sucker well developed ..... 7.**

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**5a. Vitellarium composed of a few asterisk-like bunches of follicles, limited to postequatorial part of body ..... *Erschoviorchis* Skrjabin, 1945. (Figs 3.4–3.6)**

**Diagnosis:** Body long, tapered anteriorly, almost filiform. Tegument unspined. Oral sucker reported as absent, actually present, but strongly reduced (atrophied), elongate. Ventral sucker in anterior sixth of body. Prepharynx very short. Pharynx elongate. Oesophagus longer than prepharynx. Intestinal bifurcation very near anterior extremity. Caeca reach to posterior extremity. Testes lobed, tandem or slightly diagonal, near posterior extremity. Vas deferens very long, winding, not forming definite seminal vesicle. Ovary in posterior quarter of body. Seminal receptacle posterolateral to ovary. Laurer's canal present. Uterus strongly coiled, largely intercaecal, with some loops reaching extracaecally. Vitellarium composed of few separate acinous bunches of follicles, largely extracaecal, postequatorial, reaches posterior testis. Excretory vesicle with sinuous stem between testes; pore terminal. In pancreas of fish-eating birds; Holarctic Region. Type-species *E. lintoni* (Gower, 1939) Skrjabin, 1945.

**5b. Vitellarium composed of numerous follicles forming two lateral bands along caeca, starting at postbifurcal level or posterior to ventral sucker ..... 6.**




**Figs 3.4–3.6.** *Erschoviorchis lintoni* (Gower, 1939). Paratypes from pancreas of *Gavia immer*, USA, USNPC 7916. Original. 3.4. Ventral view. 3.5. Anterior extremity (note reduced, but distinct oral sucker), ventrally. 3.6. Ventral sucker region, dorsally.

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**6a. Oral sucker strongly reduced, atrophied, with indistinct margins; vitelline follicles extend into forebody ..... *Pseudamphimerus* Gower, 1940. (Figs 3.7–3.9)**

**Diagnosis:** Body elongate, tapered anteriorly from region of ventral sucker to sharp point; posterior end rounded. Tegument unspined. Oral sucker atrophied, with indistinct borders; aperture subterminal. Ventral sucker small, in second quarter of body. Prepharynx short. Pharynx spherical, large. Oesophagus long. Intestinal bifurcation in anterior fifth of body. Caeca slightly sinuous, reach posterior extremity. Testes slightly indented, almost tandem, in posterior quarter of body. Genital pore at apex of muscular papilla (erroneously considered gonotyl by Gower (1940) and subsequent authors). Ovary multilobate, submedian, pretesticular. Seminal receptacle voluminous. Laurer's canal present. Uterus almost entirely intercaecal, between ovary and ventral sucker. Vitelline follicles numerous, mostly extracaecal, between caecal ends and region posterior to intestinal bifurcation; follicles absent at ovarian level and almost confluent anterior to ventral sucker. Excretory vesicle with sigmoid stem winding between testes, bifurcates between testis and seminal receptacle; pore terminal. In gall-bladder and bile-ducts of terns (Laridae); North America. Type-species *P. sterni* Gower, 1940.

**6b. Oral sucker small but distinct; vitelline follicles confined to hindbody ..... ..... *Euamphimerus* Yamaguti, 1941. (Figs 3.10, 3.11)**

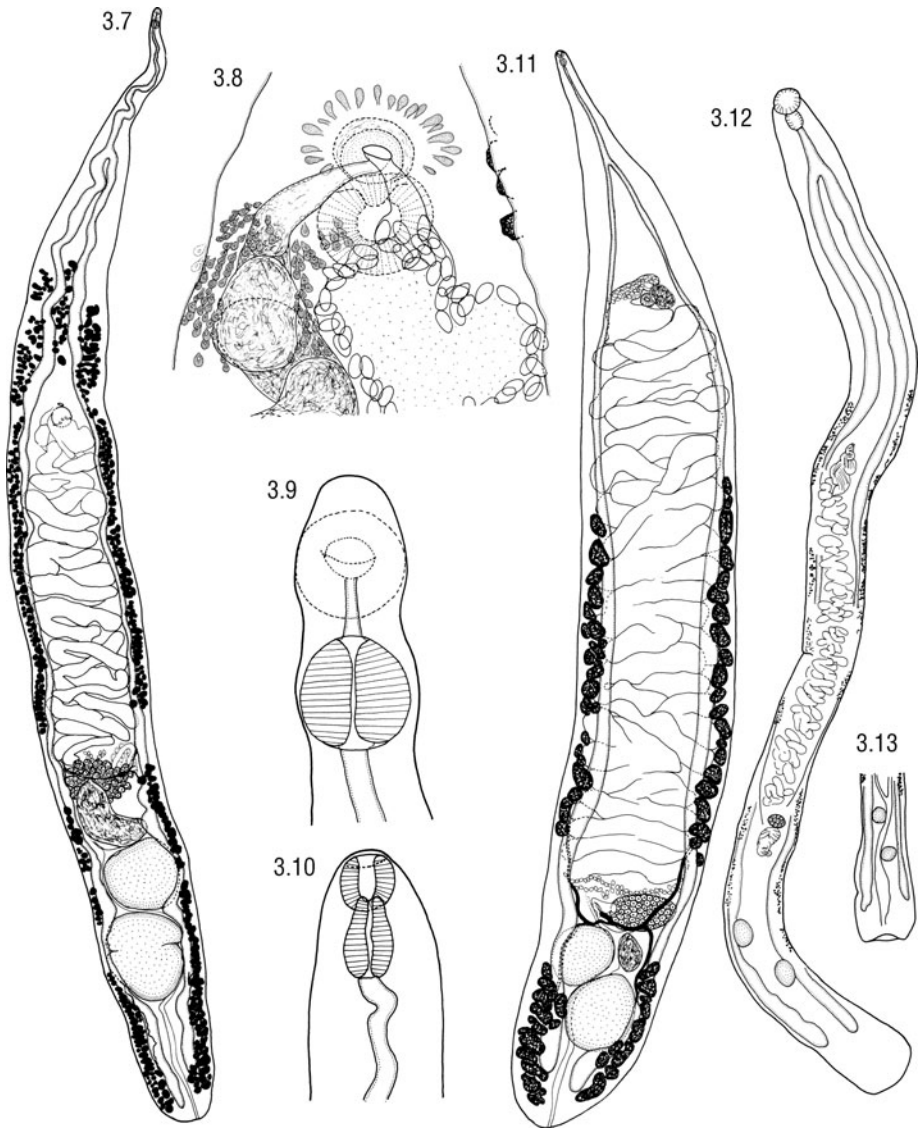
**Diagnosis:** Body slender, tapers anteriorly. Tegument unspined. Oral sucker very small. Ventral sucker small, but larger than oral sucker, in anterior third of body. Prepharynx absent or very short. Pharynx elongate, longer than oral sucker. Oesophagus long. Intestinal bifurcation in anterior sixth of body. Caeca reach close to posterior extremity. Testes diagonal, unlobed, near posterior extremity. Ovary submedian. Laurer's canal absent. Uterus forms numerous transverse loops between ovary and genital pore, largely intercaecal, with loops overlapping caeca laterally. Vitelline follicles extracaecal or slightly overlap caeca, form two lateral bands interrupted in ovarian region; anterior follicles start far posterior to ventral sucker, do not reach ovary; posterior vitelline follicles start at testicular level and reach close to posterior extremity, posterior to caecal ends. Excretory vesicle with sigmoid stem passing between testes, bifurcates anterolateral to testes; pore terminal. In intestine and pancreas of birds; Eurasia. Type-species *E. nipponicus* Yamaguti, 1941.

**7a. Vitelline follicles reach anterior to ventral sucker; body elongate, with almost parallel sides and truncated (obtuse) posterior end ..... ..... *Trionychotrema* Jin & Zhang, 1981. (Figs 3.12, 3.13)**

**Diagnosis:** Body elongate, with almost parallel sides and obtuse or slightly concave posterior end. Tegument with fine longitudinal wrinkles. Oral sucker subterminal. Ventral sucker preequatorial, smaller than oral sucker. Prepharynx absent. Oesophagus short. Intestinal bifurcation near anterior extremity. Caeca wide, end close to posterior extremity. Testes oval, diagonal or almost tandem, in posterior quarter of body. Ovary entire, submedian, distant from anterior testis. Laurer's canal present. Uterus intercaecal, between ovary and ventral sucker. Vitelline follicles form relatively few separate groups (acini) between region anterior to ventral sucker to anterior or posterior testis. Excretory vesicle with stem passing between testes and bifurcating just anterior to testes; pore probably terminal (not described and not obvious from figure 2 of Jin & Zhang, 1981). In gall-bladder and liver of turtles; Asia (China). Type-species *T. taenioidea* Jin & Zhang, 1981.

**7b. Vitelline follicles posterior to ventral sucker; shape of body different, without truncated (obtuse) posterior end ..... 8.**

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**Figs 3.7–3.9.** *Pseudamphimerus sterni* Gower, 1940. Paratype from gall-bladder of *Sterna hirundo*, USA, USNPC 9290. Original. 3.7. Dorsal view. 3.8. Ventral sucker region, dorsally. 3.9. Anterior end (note vestige of oral sucker with indistinct margins), dorsal view.

**Figs 3.10, 3.11.** *Euamphimerus pancreaticus* Baer, 1960. Paratype from pancreas of *Turdus merula*, Switzerland, MHNG INVE T8/12. Original. 3.10. Anterior end (note small, but distinct oral sucker), dorsal view. 3.11. Dorsal view.

**Figs 3.12, 3.13.** *Trionychotrema taenioidea* Jin & Zhang, 1981. After Jin & Zhang (1981). 3.12. Total view (ventral sucker, at level of seminal vesicle, not illustrated in the original description – fig. 2 of Jin & Zhang, 1981). 3.13. Posterior end with stem of excretory vesicle.

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**8a. Lateral margins of body ruffled, forming conical lateral projections ..... ..... *Nigerina* Baugh, 1958. (Figs 3.14, 3.15)**

**Diagnosis:** Body elongate, slightly widened posteriorly, with ruffled lateral margins forming conical lateral projections with concentration of muscle fibres. Tegument unspined. Oral sucker well developed, terminal or subterminal. Ventral sucker smaller than oral sucker, in anterior third of body. Prepharynx absent. Oesophagus short. Intestinal bifurcation near anterior extremity. Caeca reach posterior extremity. Testes round, diagonal, near posterior extremity. Ovary median, oval, pretesticular. Seminal receptacle posterolateral to ovary. Laurer's canal present. Uterus intercaecal, between ovary and ventral sucker. Vitellarium poorly developed; follicles in lateral fields of hindbody (postequatorial), reach posteriorly as far as to posterior testis. Excretory vesicle with sigmoid stem, passes between testes; pore terminal. In gall-bladder, liver and intestine of piscivorous birds; Asia (India) and the Americas. Type-species *N. hardoiensis* Baugh, 1958.

**8b. Lateral margins of body not ruffled, without conical lateral projections ..... ..... *Amphimerus* Barker, 1911. (Figs 3.16–3.18)**

**Diagnosis:** Body variable in shape, from lanceolate, tapered anteriorly, to elongate or cylindrical. Tegument spined or smooth. Oral sucker subterminal, well developed. Ventral sucker pre-equatorial, usually in anterior third or quarter of body. Prepharynx absent. Pharynx oval. Oesophagus short. Intestinal bifurcation near anterior extremity. Caeca long, reach close to posterior extremity. Testes entire or lobed, tandem or slightly diagonal, in posterior third of body. Seminal vesicle tubular, convoluted. Ovary median or slightly submedian, pretesticular. Seminal receptacle posterolateral to ovary. Laurer's canal present. Uterus forms numerous coils between ovary and ventral sucker, largely intercaecal, with some loops ventral to caeca, exceptionally reach lateral to caeca. Vitellarium almost entirely extracaecal; fields usually separated into two groups at ovarian level; anterior group between region posterior to ventral sucker (very far posterior in many species) and ovary; posterior group extend to posterior testis or posterior extremity. Excretory vesicle with sigmoid stem passing between testes, bifurcates between anterior testis and ovary; pore terminal. In bile-ducts of mammals and birds (type-species found in turtles); cosmopolitan. Type-species *A. ovalis* Barker, 1911.

**9a. Uterus with numerous extracaecal loops ..... *Cyclorchis* Lühe, 1908. (Figs 3.19, 3.20)**

**Diagnosis:** Body fusiform, with anterior part narrower. Tegument unspined. Oral sucker subterminal. Ventral sucker larger than oral sucker, pre-equatorial. Prepharynx absent. Oesophagus long. Intestinal bifurcation in anterior quarter of body. Caeca reach testes or close to posterior extremity. Testes diagonal or symmetrical. Seminal vesicle long, with distal part anterior to ventral sucker. Ovary median. Seminal receptacle large, posterolateral to ovary. Laurer's canal present. Uterus winds strongly between ovary and ventral sucker, extends extracaecally. Vitellarium extracaecal, limited to lateral fields of hindbody from equatorial to ovarian or testicular level. Excretory vesicle Y-shaped, with stem sigmoid or straight, passes between testes and bifurcates between anterior testis and seminal receptacle; pore terminal or subterminal. In bile-ducts of reptiles (snakes and monitor lizards); Africa. Type-species *C. amphileucus* (Looss, 1896) Lühe, 1908.

**9b. Uterus intercaecal or extends ventral to caeca ..... 10.**

**10a. Tegument spined ..... 11.**
**10b. Tegument unspined, smooth ..... 12.**

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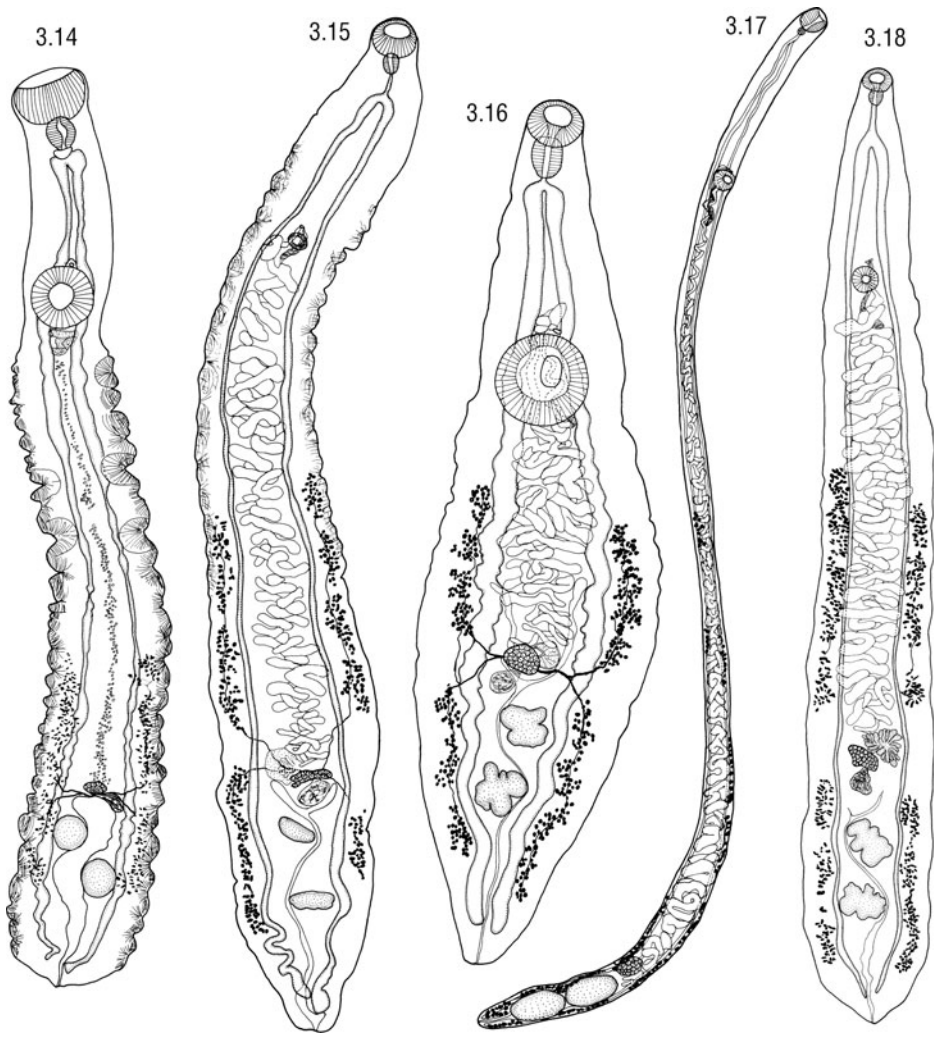
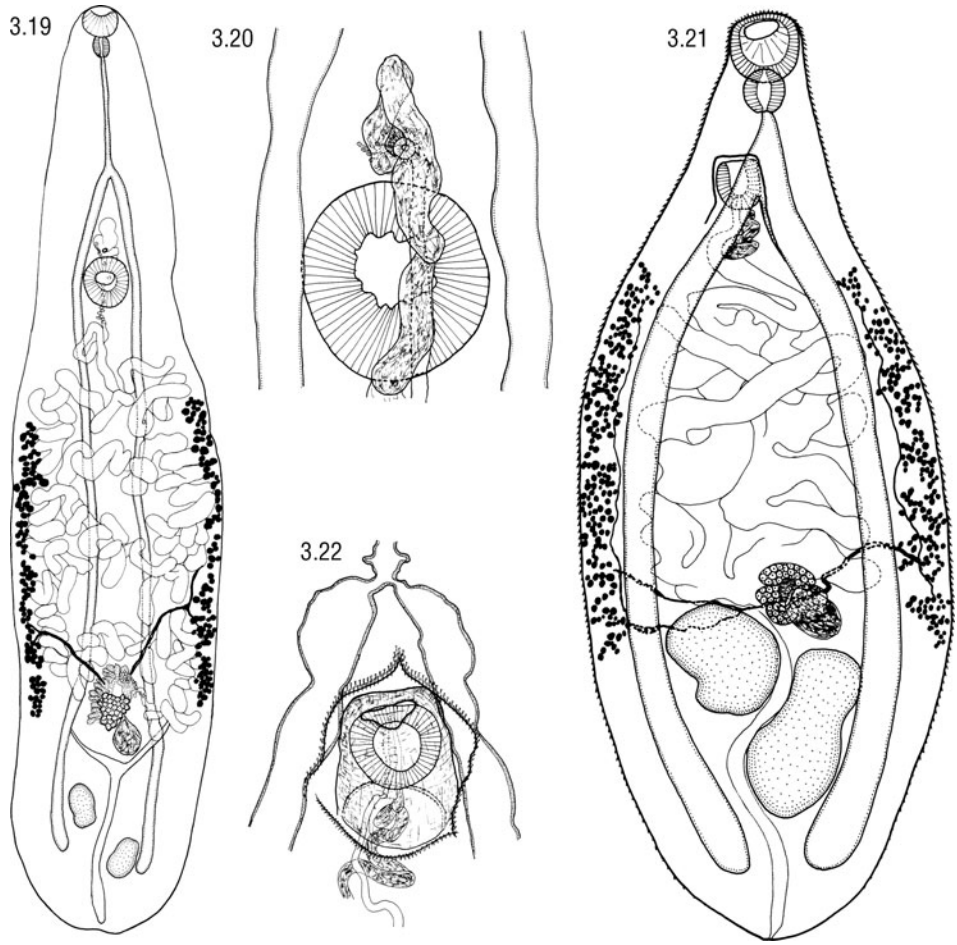



**Fig. 3.14.** *Nigerina hardoiensis* Baugh, 1958. After Baugh (1958).
**Fig. 3.15.** *Nigerina interrupta* (Braun, 1901) n. comb. From intestine of *Casmerodius albus*, Mexico, CNHE 1380. Original. Dorsal view.
**Fig. 3.16.** *Amphimerus lancea* (Diesing, 1850). From liver of *Sotalia fluviatilis*, Brazil, BMNH 1980.2.13. 1–3. Original. Ventral view.
**Fig. 3.17.** *Amphimerus arcticus* Kontrimavitschus & Bakhmet'eva, 1960. From intestine of *Gavia immer*, Canada, USNPC 87041. Original. Ventral view.
**Fig. 3.18.** *Amphimerus costarricensis* Lamothe-Argumedo & Brenes Madrigal, 1984. Paratype from bile-ducts of *Felis catus*, Costa Rica, CNHE 704. Original. Ventral view.

**11a. Ventral sucker and genital pore open on muscular peduncle; body broadly lanceolate .... ..... *Paropisthorchis* Stephens, 1912. (Figs 3.21, 3.22)**

**Diagnosis:** Body widely lanceolate, tapers slightly anteriorly. Tegument covered with simple spines. Oral sucker subterminal, larger than ventral sucker. Ventral sucker in anterior quarter or fifth of body, on prominent muscular peduncle. Prepharynx absent or very short. Oesophagus short.

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**Figs 3.19, 3.20.** *Cyclorchis amphileucus* (Looss, 1896). From bile-duct of *Naja haje*, Egypt, USNPC 9606 (3.19) and NHMB 4621 (3.20 – syntype). Original. 3.19. Ventral view. 3.20. Ventral sucker region, dorsal view. **Figs 3.21, 3.22.** *Paropisthorchis caninus* (Barker, 1911). From liver of domestic dog, India, BMNH 1923.11.10.8 (3.21) and 1968.2.27.174–223 (3.22). Original. 3.21. Dorsal view 3.22. Peduncle with ventral sucker and terminal genitalia, ventral view.

Intestinal bifurcation closely posterior to pharynx. Caeca wide, reach to near posterior extremity. Testes entire or slightly lobed, diagonal, in posterior third of body. Ovary lobate, slightly submedian. Seminal receptacle lateral or posterolateral to ovary. Uterus largely intercaecal, with several loops ventral to intestinal caeca, between ovary and genital pore. Vitellarium forms two extracaecal bands of follicles, often in bunches, from postpeduncular region to anterior testis. Excretory vesicle with sigmoid stem passing between testes and bifurcating at ovarian level; pore terminal. In liver of carnivorous mammals; Asia (India). Type-species *P. caninus* (Barker, 1911) Stephens, 1912.

**11b. Muscular peduncle absent; body elongate or fusiform** ..... ..... ***Thaparotrema*** **Gupta, 1955. (Figs 3.23–3.27)**
(Syn. *Agrawalotrema* Sahay & Sahay, 1988)

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**Diagnosis:** Body elongate or fusiform. Tegument spined. Oral sucker subterminal. Ventral sucker well developed, pre-equatorial. Prepharynx short or absent. Pharynx oval. Oesophagus short. Intestinal bifurcation near anterior extremity. Caeca reach close to posterior extremity. Testes tandem or diagonal, near caecal ends. Ovary submedian, anterolateral to anterior testis. Seminal receptacle usually posteromedian to ovary. Laurer's canal present. Uterine coils almost entirely intercaecal, between ovary and ventral sucker. Vitelline follicles in lateral, largely extracaecal, fields from postbifurcal level in some species (*T. vittalani* and *T. parasiluri*), but posterior to ventral sucker in others, to level of ovary or anterior testis. Excretory vesicle with sigmoid stem; pore terminal or subterminal. In gall-bladder and intestine of freshwater fish; Asia and Africa. Type-species *T. vittalani* Gupta, 1955.

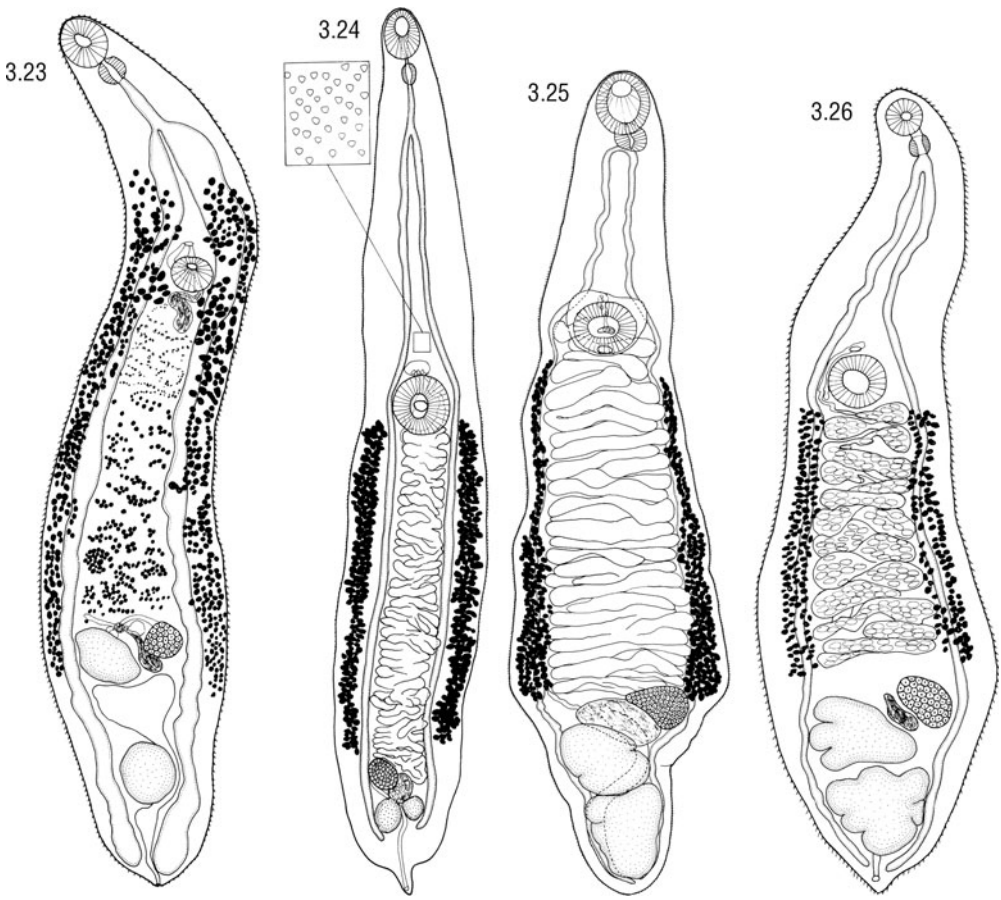



**Fig. 3.23.** *Thaparotrema vittalani* Gupta, 1955. After Gupta (1955).
**Fig. 3.24.** *Thaparotrema pedicellatum* (Verma, 1927) n. comb. From intestine of *Hemibagrus nemurus*, Thailand, BMNH 1983.8.8.79–91. Original. Ventral view. Inset – scale-like tegumental spines.
**Fig. 3.25.** *Thaparotrema pedicellatum* (Verma, 1927) n. comb. From intestine of *Rita buchanani* (fish name not found in FishBase), India, BMNH 1954.9.14.323–347. Original. Ventral view.
**Fig. 3.26.** *Thaparotrema pedicellatum* (Verma, 1927) n. comb. (syn. *Agrawalotrema ritai* Sahay & Sahay, 1988). After Sahay & Sahay (1988).

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**12a. Testes lobed or entire (dendritic in *O. dendriticus*), intercaecal or with lateral margins ventral to caeca; vitelline fields start at distance posterior to ventral sucker ..... ..... *Opisthorchis* Blanchard, 1895. (Figs 3.28–3.30)**

(Syns *Notaulus* Skrjabin, 1913; *Hepatiarius* Feizullaev, 1961; *Neometorchis* Bilqees, Shabbir & Parveen, 2003)

**Diagnosis:** Body lanceolate, fusiform or cylindrical. Tegument unspined (except for *O. noverca* Braun, 1903). Oral sucker subterminal. Ventral sucker pre-equatorial. Prepharynx absent. Pharynx oval.

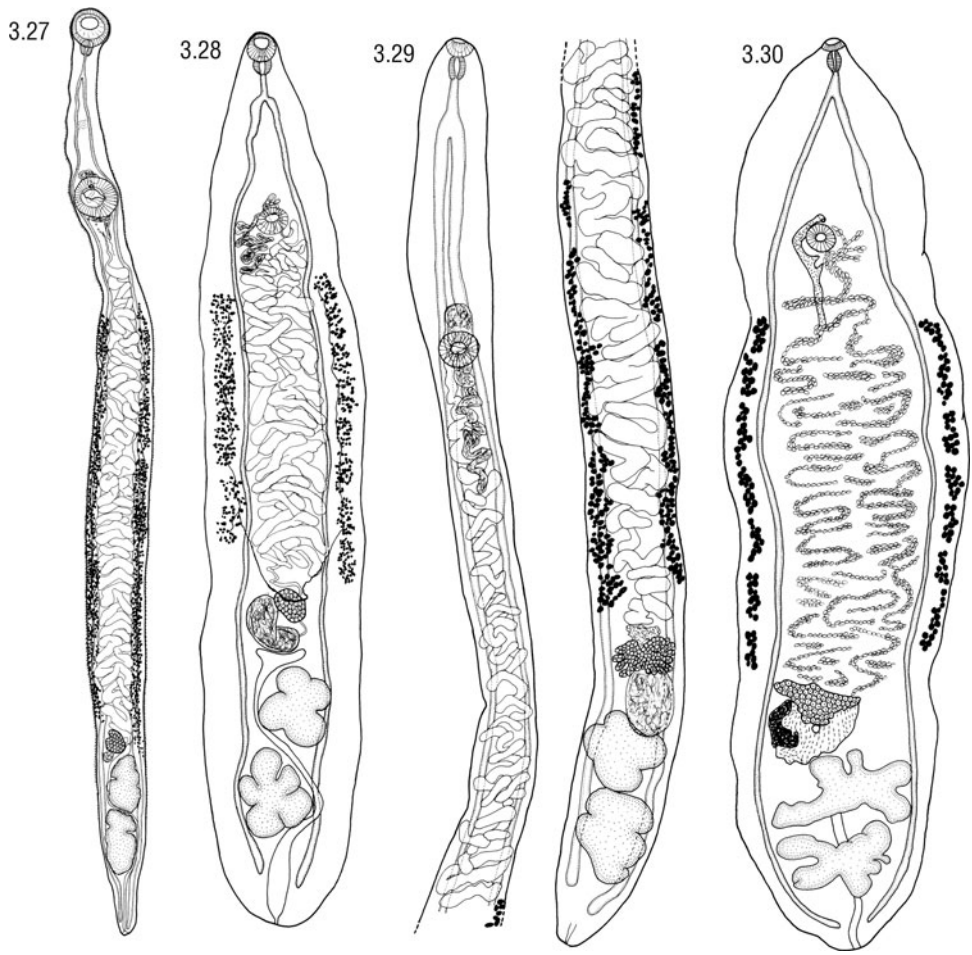



**Fig. 3.27.** *Thaparotrema piscicola* (Odhner, 1902) n. comb. From gall-bladder of *Gymnarchus niloticus*, Africa, BMNH 1973.12.14.1–7. Original. Ventral view. Tegumental spines illustrated in anterior postbifurcal region.

**Fig. 3.28.** *Opisthorchis felineus* (Rivolta, 1884). From liver of domestic cat, Russia, BMNH 1927.8.12. 1–2. Original. Ventral view.

**Fig. 3.29.** *Opisthorchis longissimus* (Linstow, 1883). From liver of *Botaurus stellaris*, Azerbaijan, GELAN 55/8. Original. Ventral view.

**Fig. 3.30.** *Opisthorchis lobatus* (Bilqees, Shabbir & Parveen, 2003) n. comb. After Bilqees *et al.* (2003a).

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Oesophagus short. Intestinal bifurcation near anterior extremity. Caeca narrow, reaching posteriorly beyond testes, close to posterior extremity. Testes diagonal to almost tandem, entire, lobed or dendritic (*O. dendriticus*), in posterior third of body. Ovary simple or lobate, median or submedian. Seminal receptacle posterolateral to ovary. Laurer's canal present. Uterus almost entirely intercaecal, rarely with a few loops ventral to caeca or extracaecal, between ovary and ventral sucker. Vitellarium usually extracaecal, forms two lateral bands between region posterior to seminal vesicle and ovary. Excretory vesicle with slightly sigmoid stem passing between testes or dorsal to lateral branches of testes, bifurcating between seminal receptacle and anterior testis; pore terminal. In liver and biliary system of mammals, including man, and birds; cosmopolitan. Type-species *O. felineus* (Rivolta, 1884) Blanchard, 1895.

**12b. Testes dendritic, extend extracaecally; vitelline follicles may reach to ventral sucker ..... ..... *Clonorchis* Looss, 1907 (Fig. 3.31)**

**Diagnosis:** Body lanceolate, tapered anteriorly. Tegument unspined. Oral sucker subterminal. Ventral sucker smaller than oral sucker, in anterior third of body. Prepharynx absent. Oesophagus short. Intestinal bifurcation very near anterior extremity. Caeca reach close to posterior extremity. Testes tandem, dendritic, overlap caeca laterally, in posterior third of body. Ovary lobate, slightly submedian, pretesticular. Seminal receptacle voluminous, posteromedian to ovary. Laurer's canal present. Uterine loops almost entirely intercaecal, between ovary and ventral sucker. Vitellarium forms two extracaecal, uninterrupted bands of follicles between level of ventral sucker (anterior or slightly posterior to ventral sucker) and anterior testis. Excretory vesicle with sinuous stem, passes around dorsal bodies of testes, bifurcates between anterior testis and seminal receptacle; pore terminal. In liver of mammals, including man; South-east Asia. Type-species *C. sinensis* (Cobbold, 1875) Looss, 1907.

## Subfamily Allogomtiotrematinae Yamaguti, 1958

(Syn. Gomtiotrematinae Gupta, 1955[1])

**Diagnosis:** Body elongate, with round extremities or fusiform. Tegument unspined. Oral sucker large, subventral (at distance from anterior extremity). Ventral sucker well developed, preequatorial. Prepharynx absent. Pharynx small. Oesophagus wide, with single or double sac-like pouch posteriorly. Intestinal bifurcation near pharynx. Caeca sinuous, end near posterior extremity. Testes symmetrical or diagonal, in posterior half of body, postovarian. Seminal vesicle tubular or saccular, anterior to ventral sucker. Genital pore about halfway between oesophageal pouch and ventral sucker, with circular sphincter. Ovary small, submedian, pretesticular. Seminal receptacle present. Laurer's canal present. Uterus intercaecal, between ovary and genital pore. Vitelline follicles largely postequatorial, extracaecal and ventral to caeca or exclusively intercaecal, may reach to caecal ends or to posterior extremity. Excretory vesicle Y-shaped, with long, straight stem bifurcating posterior to ovary; pore terminal or subterminal. In intestine of siluriform and mastacembelid fish; India. Type-genus *Allogomtiotrema* Yamaguti, 1958.

## Key to genera

**1a. Vitelline follicles in two bands near lateral margins of body, extracaecal or ventral to caeca, reach far anterior to testes; uterus long; ovary very far posterior to ventral sucker ..... ..... *Allogomtiotrema* Yamaguti, 1958. (Fig. 3.32)**
(Syn. *Gomtiotrema* Gupta, 1955 *nec* Sinha, 1934)

[1]This synonymy is due to the unavailability of the generic name because of its homonymy with *Gomtiotrema* Sinha, 1934.

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**Diagnosis:** Body with round extremities. Oral sucker large. Ventral sucker slightly smaller than oral sucker, in anterior quarter of body. Oesophagus sac-like, projecting backward from intestinal bifurcation in two small pouches, surrounded by gland-cells. Testes diagonal, in posterior third of body. Seminal vesicle narrow, tubular, strongly coiled. Genital pore between oesophageal pouches and ventral sucker. Ovary immediately anterolateral to anterior testis. Seminal receptacle anterolateral to ovary. Vitelline follicles almost entirely postequatorial but extend far anterior to testes, extracaecal or ventral to caeca, reach to caecal ends. Uterus long. Excretory pore subterminal or terminal. In intestine of siluriform and mastacembelid fishes; India. Type-species *A. attu* (Gupta, 1955) Yamaguti, 1958.

**1b. Vitelline follicles entirely intercaecal, post-testicular; uterus very short; ovary just posterior to ventral sucker ..... *Satyapalia* Lakshminarayana & Hafeezullah, 1974. (Fig. 3.33)**
(Syn. *Assamia* Gupta, 1955 *nec* Sorensen, 1884)

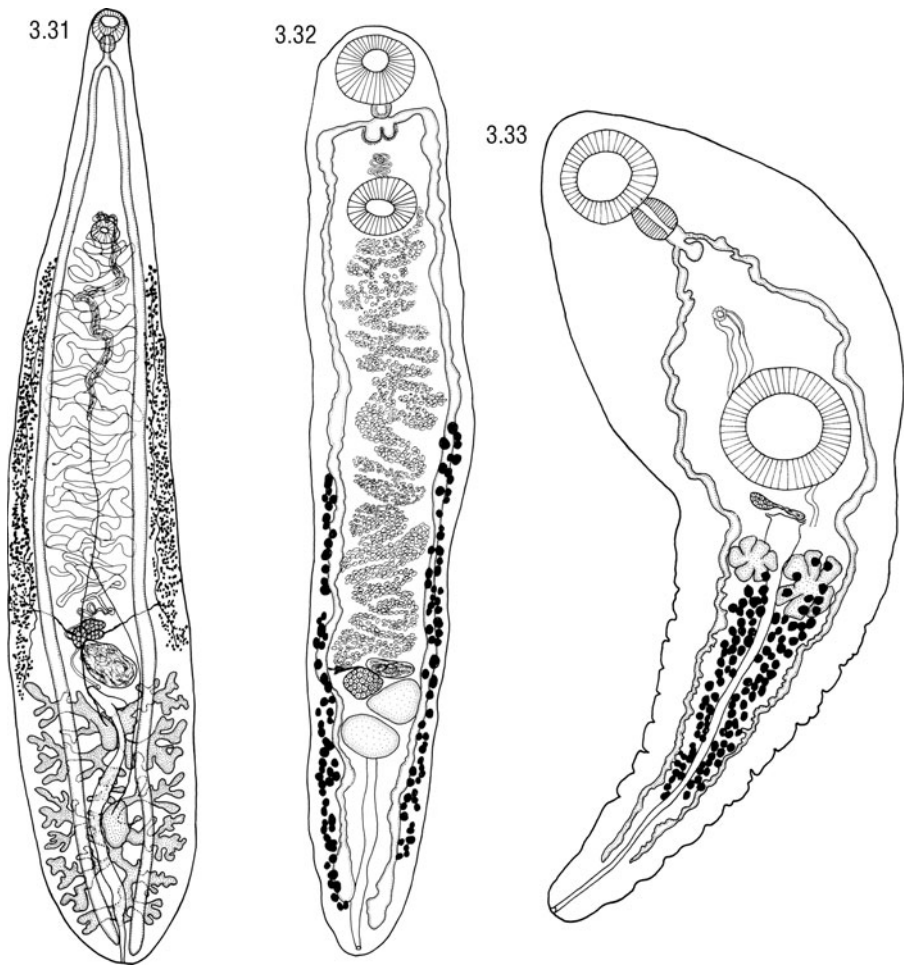



**Fig. 3.31.** *Clonorchis sinensis* (Cobbold, 1875). Specimen from liver of man, BMNH 1976.4.9.85–87. Original. Dorsal view.
**Fig. 3.32.** *Allogomtiotrema attu* (Gupta, 1955). After Gupta (1955).
**Fig. 3.33.** *Satyapalia gauhatiensis* (Gupta, 1955). After Gupta (1955).

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**Diagnosis:** Body fusiform. Ventral sucker slightly pre-equatorial. Oesophagus with posterior pouch. Testes lobate or entire, symmetrical or slightly diagonal, not far posterior to ventral sucker. Seminal vesicle tubular or saccular. Genital pore muscular, median, halfway between intestinal bifurcation and ventral sucker. Ovary closer to ventral sucker than to testes. Seminal receptacle lateral or posterolateral to ovary. Uterus short, forms few coils between testes and genital pore. Vitelline follicles exclusively intercaecal, usually start at testicular level, reach near to caecal ends or close to posterior extremity. Excretory pore terminal. In intestine of freshwater fish (Siluriformes); India. Type-species *S. gauhatiensis* (Gupta, 1955) Lakshminarayana & Hafeezullah, 1974.

## Subfamily Delphinicolinae Yamaguti, 1933

**Diagnosis:** Body cylindrical, long, narrow. Tegument entirely spined. Oral sucker large, terminal. Ventral sucker smaller than oral sucker, close to anterior extremity. Prepharynx short, wide. Pharynx elongate. Oesophagus short. Intestinal bifurcation near anterior extremity. Caeca simple, reach posterior extremity and open via two ani. Testes tandem, postequatorial, far from posterior extremity. Seminal vesicle tubular, posterior to ventral sucker. Genital pore anterior to ventral sucker, submedian. Ovary median, oval, pretesticular. Uterine seminal receptacle present, pre-ovarian. Laurer's canal present. Uterus completely intercaecal, pre-ovarian. Vitelline follicles very extensive, form one uninterrupted band extending full width of body, start slightly posterior to seminal vesicle and reach posterior extremity, extracaecal anterior to ovary and continuous medially both ventrally and dorsally posterior to ovary. Vitelline reservoir sac-shaped, symmetrical, with parallel anterior and posterior main collecting ducts, forming H-shape. Excretory vesicle with long, narrow, straight stem passing dorsal to testes and bifurcating at ovarian level; pore terminal. In bile-ducts of marine mammals (*Delphinus*); off Japan. Type-genus *Delphinicola* Yamaguti, 1933.

### Genus *Delphinicola* Yamaguti, 1933 (Figs 3.34–3.36)

**Diagnosis:** With characters of subfamily. Type-species *D. tenuis* Yamaguti, 1933.

## Subfamily Diasiellinae Yamaguti, 1958

**Diagnosis:** Body fusiform, with rounded anterior end and often with transverse tegumental thickenings giving appearance of plicated ('ruffled') lateral margins or with transverse annulations, especially in posterior part of body. Oral sucker absent, but mouth opening forms terminally situated, circular atrium with feebly muscular margin. Ventral sucker very small, pre-equatorial. Prepharynx very short or absent. Pharynx oval, well developed. Oesophagus much longer than prepharynx. Intestinal bifurcation near anterior extremity. Caeca end near posterior extremity. Testes lobed or entire, symmetrical, overlap caeca ventrally near their ends. Seminal vesicle coiled, anterior to ventral sucker. Genital pore just anterior to ventral sucker. Ovary lobate, median, pretesticular. Seminal receptacle anterodorsal to ovary. Laurer's canal not observed. Uterus largely intercaecal or ventral to caeca, between ovary and ventral sucker, with terminal (distal) loops anterior to ventral sucker. Vitellarium formed by extracaecal bunches of follicles between

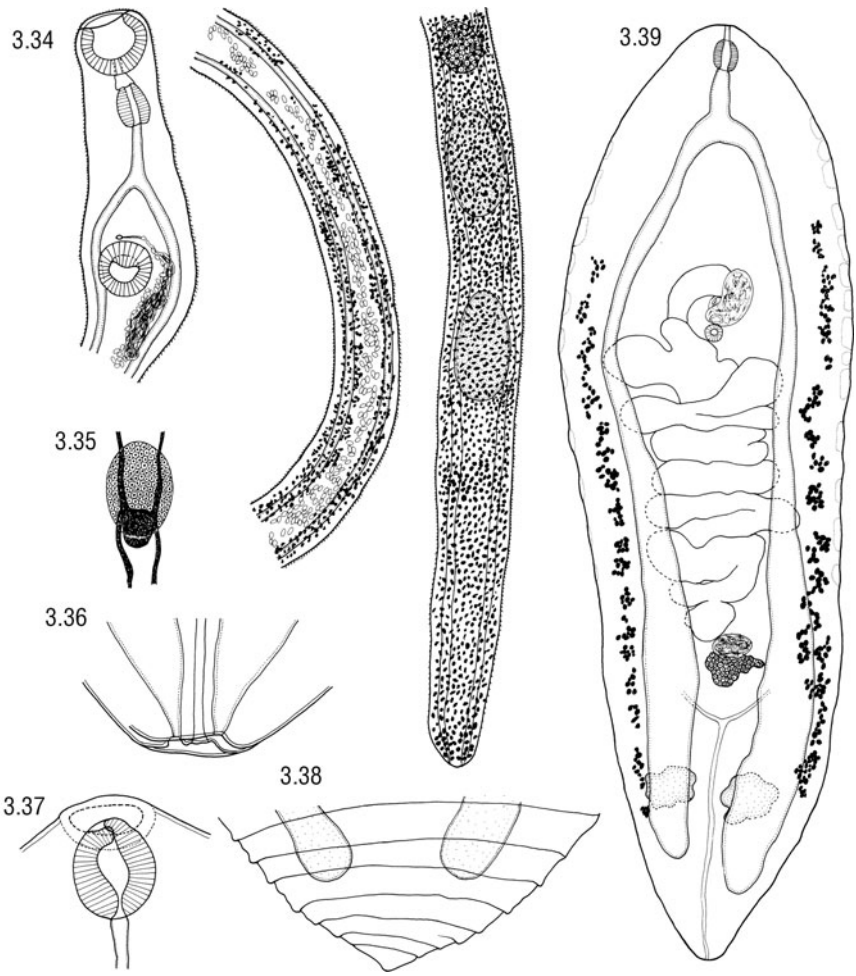
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level anterior to ventral sucker and testes or slightly posterior. Excretory vesicle with straight stem passing between testes and branching in postovarian region; pore terminal. In pancreas of fish-eating birds (darters, herons); South and North America. Type-genus *Diasiella* Travassos, 1949.

## Genus *Diasiella* Travassos, 1949 (Figs 3.37–3.39)

(Syn. *Diasia* Travassos, 1922 *nec* Lilljeberg, 1853)

**Diagnosis:** With characters of subfamily. Type-species *D. diasi* (Travassos, 1922) Travassos, 1949.




**Figs 3.34–3.36.** *Delphinicola tenuis* Yamaguti, 1933. Paratype from bile-duct of *Delphinus dussumieri*, Japan, MPM 22712. Original. 3.34. Ventral view. 3.35. Vitelline reservoir, ventral view. 3.36. Posterior end of body with external openings of intestinal caeca (ani).

**Figs 3.37–3.39.** *Diasiella diasi* (Travassos, 1922). From pancreas of *Anhinga anhinga*, Brazil. Original. 3.37. IOC 3926. Anterior end, dorsal view. 3.38. IOC 3926. Posterior end, dorsal view. 3.39. IOC 3929. Dorsal view.

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## Subfamily Metorchiinae Lühe, 1909

(Syn. Holometrinae Filimonova, 2000)

**Diagnosis:** Body small to medium-sized, often slightly tapered anteriorly. Tegument covered with simple or scale-like tegumental spines. Oral sucker subterminal. Ventral sucker pre-equatorial, smaller than or as large as oral sucker. Prepharynx absent or very short. Pharynx oval or elongate. Oesophagus usually short. Intestinal bifurcation in anterior quarter of body. Caeca reach testicular level or close to posterior extremity. Testes entire to lobed, tandem, diagonal or symmetrical, post-equatorial, often near posterior extremity. Seminal vesicle tubular, more or less coiled. Genital pore immediately anterior to ventral sucker. Ovary median to submedian, pretesticular. Seminal receptacle voluminous, posterolateral to ovary. Laurer's canal present (not observed in *Cladocystis*). Uterus extensive, surrounds ventral sucker, intercaecal, ventral to caeca or extracaecal, pretesticular. Vitelline follicles in anterior or mid-region of body, largely extracaecal. Excretory vesicle with sinuous or sigmoid stem; pore terminal or ventral to posterior testis. In gall-bladder, biliary duct and liver of birds and mammals (*Cladocystis* in intestine of fish); cosmopolitan. Type-genus *Metorchis* Looss, 1899.

### Key to genera

**1a. Uterus reaches posteriorly beyond ovary, usually lateral to caeca; testes symmetrical or slightly diagonal ..... 2.**

**1b. Uterus entirely pre-ovarian, intercaecal or with few extracaecal loops; testes tandem or diagonal ..... 3.**

**2a. Vitelline follicles entirely anterior to ventral sucker, between pharynx and ventral sucker, usually form one group, uninterrupted medially ..... *Holometra* Looss, 1899. (Fig. 3.40)**

**Diagnosis:** Body small, fusiform. Ventral sucker smaller than oral sucker. Prepharynx absent. Pharynx elongate. Oesophagus short. Intestinal bifurcation in mid-forebody. Caeca reach testes. Testes entire, slightly diagonal, near posterior extremity. Seminal vesicle forms several loops. Ovary oval, submedian, postequatorial. Seminal receptacle posterolateral to ovary. Uterus occupies most of space between ventral sucker and testes, with loops reaching lateral to caeca (extracaecal) in region posterior to ventral sucker; distal loops anterior to ventral sucker. Vitelline follicles between pharynx and ventral sucker, usually form one group, uninterrupted medially. Excretory vesicle with wide, slightly sinuous stem that passes between testes; pore terminal. In bile-ducts of birds of prey; Europe, North Africa (Egypt). Type-species *H. exigua* (Mühling, 1898) Looss, 1899.

**2b. Vitelline follicles entirely posterior to ventral sucker, in lateral bands along intestinal caeca, reach anterior margin of testes ..... *Cladocystis* Poche, 1926. (Figs 3.41–3.44)**

**Diagnosis:** Body fusiform, small. Oral sucker small. Ventral sucker smaller than or of similar size to oral sucker, pre-equatorial. Prepharynx short. Pharynx well developed, only slightly shorter than oral sucker diameter. Oesophagus much longer than prepharynx. Caeca reach testes. Testes large, entire or slightly lobed, usually longitudinally elongate, symmetrical, near posterior extremity. Seminal vesicle forms several loops. Ovary submedian, usually trilobed. Laurer's canal not observed. Uterus fills most of space between just posterior to bifurcal level and testicular level. Vitelline follicles form two lateral fields between just posterior to ventral sucker and anterior margin of testes, largely or entirely extracaecal. Excretory vesicle with anterior arms reaching oral sucker, with short lateral branches; pore subterminal. In intestine of fish, probably accidentally in oesophagus of fish-eating birds (herons); South and North America, Africa. Type-species *C. trifolium* (Braun, 1901) Poche, 1926.

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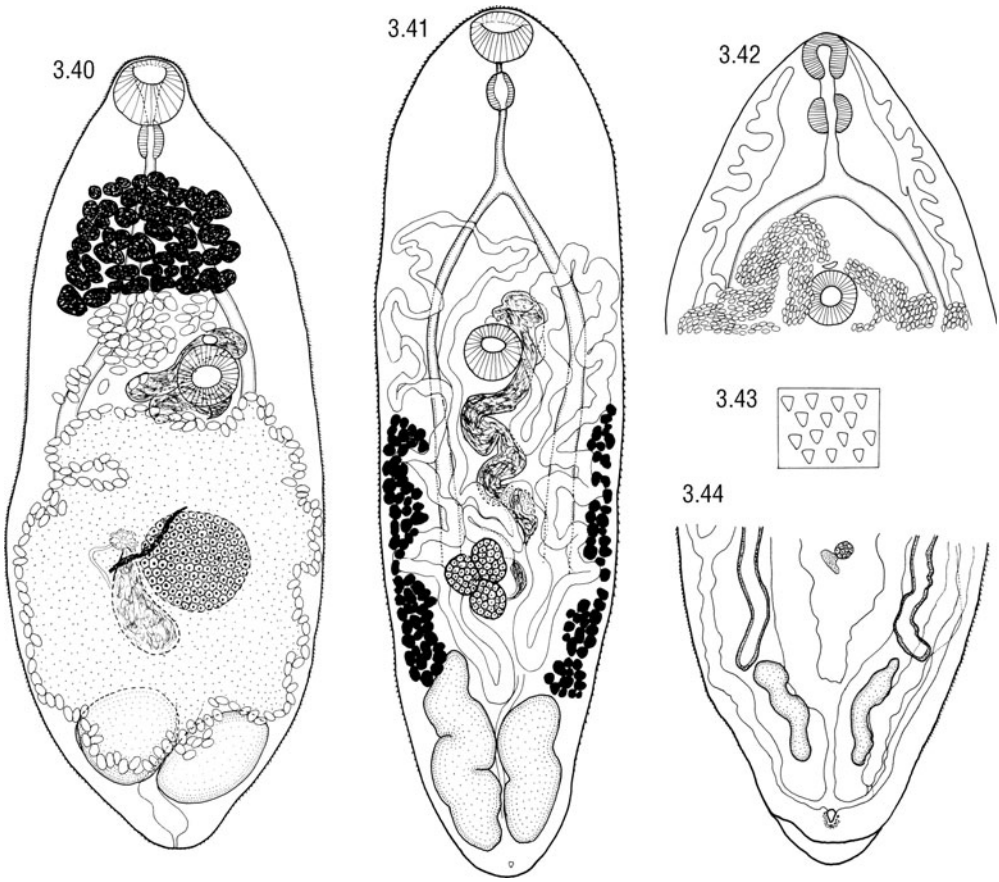



**Fig. 3.40.** *Holometra exigua* (Mühling, 1898). From bile-ducts of *Circus rufus*, Egypt, USNPC 9642. Original. Ventral view.

**Figs 3.41–3.44.** *Cladocystis trifolium* (Braun, 1901). Adult from trachea of *Casmerodius albus*, Mexico, CNHE 1415 (3.41) and metacercaria from gills of *Cichlasoma fenestratum*, Mexico, CNHE 1732 (3.43–3.44). Original. 3.41. Ventral view. 3.42. Anterior end of body with lateral arms of excretory system. After Braun (1902). 3.43. Tegumental spines of ventral sucker region. 3.44. Posterior end of body (note branching of excretory system). Dorsal view.

**3a. Excretory pore ventral to posterior testis, far anterior to posterior extremity; excretory vesicle bifurcates ventral to testes; testes oblique; vitelline follicles and uterus reach into post-equatorial region ..... *Metorchis* Looss, 1899. (Fig. 3.45)**

**Diagnosis:** Body small to medium-sized, tapered anteriorly, with widely rounded posterior end. Tegument with simple spines. Oral sucker well developed. Ventral sucker slightly pre-equatorial, smaller than or as large as oral sucker. Prepharynx absent. Pharynx oval. Oesophagus short. Intestinal bifurcation in anterior fifth of body. Caeca usually wide, long, curved medially near posterior extremity of body. Testes entire or lobed, diagonal, near caecal ends. Seminal vesicle tubular, coiled. Ovary slightly submedian or median. Vitellarium forms two lateral, largely extracaecal fields between intestinal bifurcation or anterior postbifurcal region to ovarian level.

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Uterus intercaecal and ventral to caeca, exceptionally loops reach lateral to caeca, between anterior postbifurcal region and ovary. Excretory vesicle bifurcates ventral to testes; pore ventral to posterior testis, distant from posterior extremity. In gall-bladder of mammals and birds; cosmopolitan. Type-species *M. albidus* (Braun, 1893) Looss, 1899.

**3b. Excretory pore terminal; excretory vesicle bifurcates at pretesticular level; testes tandem; vitelline follicles and uterus almost entirely pre-equatorial ..... ..... *Parametorchis* Skrjabin, 1913. (Fig. 3.46)**
(Syns *Metametorchis* Morozov, 1939; *Allometorchis* Baer, 1944)

**Diagnosis:** Body elongate, attenuate anteriorly and rounded posteriorly. Oral sucker small. Ventral sucker in anterior third of body. Prepharynx absent. Pharynx well developed. Oesophagus very short or absent. Intestinal bifurcation near anterior extremity. Caeca usually sinuous, reach near to posterior extremity. Testes lobed or entire, tandem or slightly diagonal, in posterior half of body. Ovary entire or lobed, median or slightly submedian, near middle of body. Uterus strongly coiled, between anterior postbifurcal region and ovary; loops intercaecal or ventral to caeca, exceptionally extracaecal. Vitellarium pre-equatorial, forming two largely extracaecal bands of follicles, sometimes confluent in anterior postbifurcal region. Excretory vesicle with sigmoid stem, passing between or dorsal to testes, bifurcates between seminal receptacle and anterior testis; pore terminal. In liver and biliary system of mammals; Holarctic. Type-species *P. complexus* (Stiles & Hassall, 1894) Skrjabin, 1913.

## Subfamily Microtrematinae Filimonova, 2000

**Diagnosis:** Body medium-sized, tapered anteriorly and truncated posteriorly. Tegument densely spined. Oral sucker subterminal. Ventral sucker smaller than oral sucker, postequatorial. Prepharynx reported to be short in original description but not illustrated. Pharynx well developed. Oesophagus short. Intestinal bifurcation near anterior extremity. Caeca simple, reach near posterior extremity, slightly curved medially near their ends. Testes symmetrical, posterior to ventral sucker, intercaecal or medioventral to caeca. Seminal vesicle spindle-shaped, anterior to ventral sucker. Genital pore at short distance anterior to ventral sucker. Ovary lobulate, near ventral sucker, anteromedian to testes. Seminal receptacle postovarian, intertesticular. Laurer's canal present. Uterus almost exclusively anterior to ventral sucker, with few loops in hindbody or extracaecal. Vitellarium consists of lateral bands of clustered follicles (acini), extending along most of length of caeca from anterior postbifurcal region to post-testicular level, not reaching caecal ends. Excretory vesicle with short, slightly sinuous stem, bifurcates posterior to testes; long arms pass medially and parallel to caeca into anterior postbifurcal region; pore terminal. In liver of mammals (domestic pig, dog and cat); eastern Asia (Japan, Taiwan, China). Type-genus *Microtrema* Kobayashi, 1915.

### Genus *Microtrema* Kobayashi, 1915 (Fig. 3.47)

**Diagnosis:** With characters of subfamily. Type-species *M. truncatum* Kobayashi, 1915.

## Subfamily Oesophagicolinae Yamaguti, 1933

**Diagnosis:** Body robust, spindle-shaped, with rounded ends. Tegument covered with very small spines. Oral sucker large, subterminal. Ventral sucker much smaller than oral sucker, at

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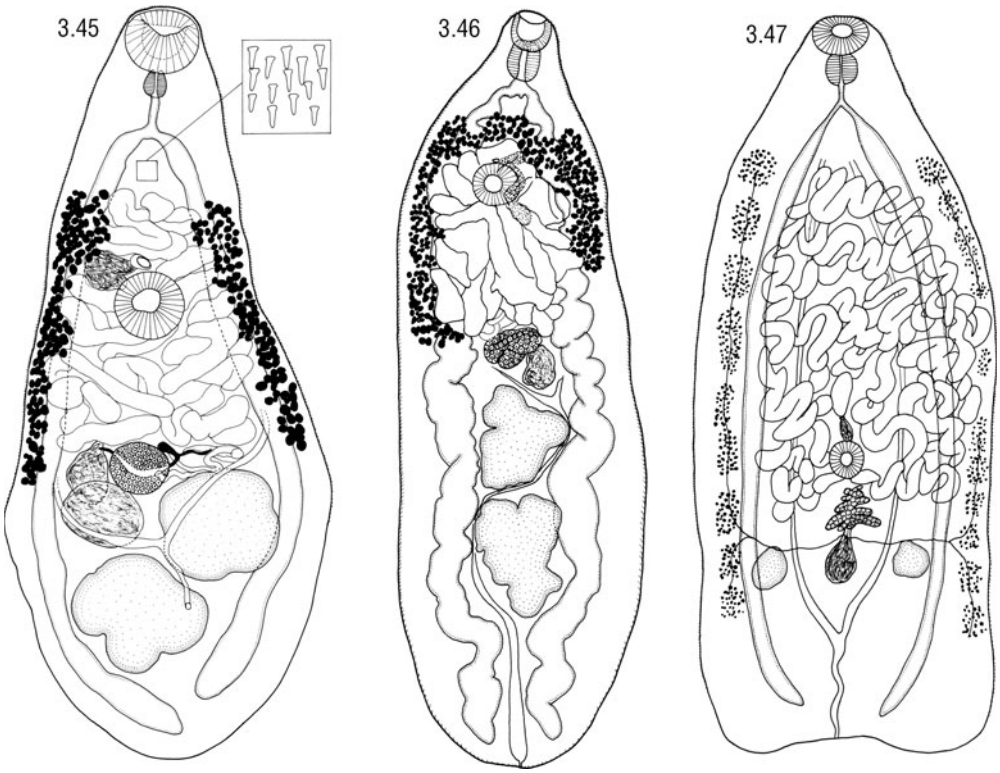



**Fig. 3.45.** *Metorchis albidus* (Braun, 1893). From gall-bladder of domestic cat, Switzerland, MHNG D/068. Original. Ventral view. Inset: tegumental spines from postbifurcal region.
**Fig. 3.46.** *Parametorchis complexus* (Stiles & Hassall, 1894). Co-type from gall-bladder of domestic cat, USA, USNPC 8. Original. Ventral view.
**Fig. 3.47.** *Microtrema truncatum* Kobayashi, 1915. After Kobayashi (1915, 1920).

about one-third of body-length. Prepharynx very short. Pharynx spherical, well developed. Unicellular glands along pharynx. Oesophagus very short, directed dorsally. Caeca wide, slightly sinuous, reach to posterior extremity. Testes irregularly indented, tandem, intercaecal, near posterior extremity. Seminal vesicle tubular, sigmoid, posterodorsal to ventral sucker. Genital atrium wide, with transverse slit-like aperture, just anterior to ventral sucker. Ovary submedian, postequatorial, pretesticular. Seminal receptacle pyriform, posteromedian to ovary. Laurer's canal present. Uterus extensive, with coils filling most of body ventral to caeca between ventral sucker and posterior testis. Vitellarium extensive, composed of dendritic tubular lobes, occupies most of lateral regions of hindbody, with some lobes reaching median line of body. Excretory vesicle with long, wide stem dorsal to uterus and ventral to testes and ovary, bifurcates posterior to ventral sucker; arms long, wide, reach oral sucker; pore terminal. In lower part of oesophagus and occasionally stomach of marine snakes (Elapidae); off Japan. Type-genus *Oesophagicola* Yamaguti, 1933.

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## Genus *Oesophagicola* Yamaguti, 1933 (Fig. 3.48)

**Diagnosis:** With characters of subfamily. Type-species *O. laticaudae* Yamaguti, 1933.

## Subfamily Pachytrematinae Railliet, 1919

**Diagnosis:** Body broadly oval to elliptical. Tegument unspined. Oral sucker small. Ventral sucker small, close to oral sucker. Prepharynx absent. Pharynx small. Oesophagus very short or absent. Intestinal bifurcation very near anterior extremity. Caeca wide, curved along lateral margins of body, reach close to posterior extremity. Testes small, oval, symmetrical, intercaecal or ventral to caeca, near posterior third of body. Seminal vesicle saccular. Genital pore immediately anterior to ventral sucker. Ovary small, median, post-testicular or almost intertesticular. Seminal receptacle absent. Laurer's canal present. Uterus coiled, between ovary and intestinal bifurcation, usually intercaecal; some loops may overlap caeca laterally. Vitellarium forms separate acinous bunches of small follicles, extracaecal or ventral to caeca, extends from level of ventral sucker to near caecal ends. Excretory vesicle with straight, narrow stem that bifurcates posterior to ovary; pore subterminal. In gall-bladder of birds, exceptionally in mammals (rodents); in Eurasia, North and South America. Type-genus *Pachytrema* Looss, 1907.

## Genus *Pachytrema* Looss, 1907 (Fig. 3.49)

(Syns *Minuthorchis* Linton, 1928; *Multivitellaria* Phadke & Gulati, 1929)

**Diagnosis:** With characters of subfamily. Type-species *P. calculus* Looss, 1907.

## Subfamily Plotnikoviinae Skrjabin, 1945

**Diagnosis:** Body elongate, with parallel sides, gradually narrows anteriorly from level of ventral sucker, truncate at posterior end. Tegument unspined. Oral sucker terminal, reduced. Ventral sucker reduced, near posterior end of anterior quarter of body. Prepharynx very short. Pharynx well developed, larger than oral sucker. Oesophagus relatively short. Intestinal bifurcation near anterior extremity. Caeca wide, slightly sinuous, reach posterior extremity. Testes small, tandem, near posterior extremity. Seminal vesicle saccular, divided into larger, thin-walled proximal chamber and smaller, thick-walled distal chamber, anterior to ventral sucker. Genital pore at short distance anterior to ventral sucker. Ovary submedian, lobulate, pretesticular, in posterior quarter of body. Seminal receptacle posteromedian to ovary. Laurer's canal probably absent (not seen in whole-mounts and sections). Uterine coils intercaecal, between ovary and genital pore. Vitellarium follicular; lateral fields extracaecal or overlap caeca lateroventrally, between level posterior to ventral sucker and posterior extremity. Excretory vesicle with wide and straight stem ventral to testes, bifurcates at ovarian level; pore subterminal, ventral. In mesenteries (?) of birds (grebes); North America. Type-genus *Plotnikovia* Skrjabin, 1945.

## Genus *Plotnikovia* Skrjabin, 1945 (Figs 3.50–3.52)

**Diagnosis:** With characters of subfamily. Type-species *P. podilymbae* (Olsen, 1938) Skrjabin, 1945.

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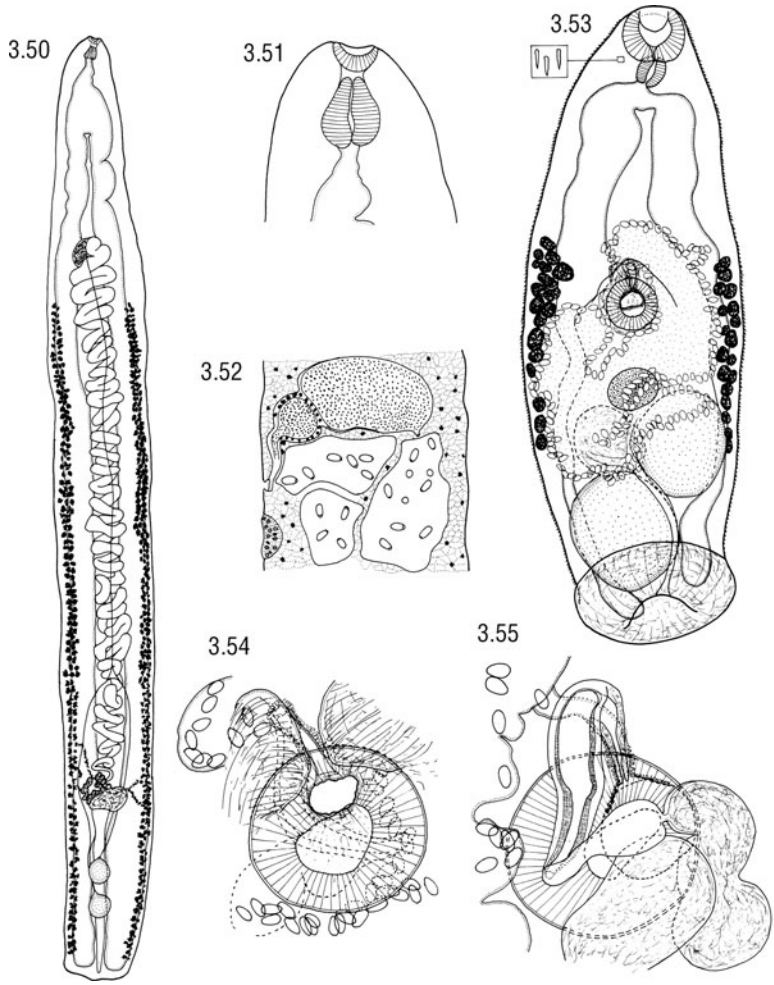



**Fig. 3.48.** *Oesophagicola laticaudae* Yamaguti, 1933. After Yamaguti (1933). Neither very small tegumental spines nor the stem of the excretory vesicle, reported to be ventral to the testes and ovary, were illustrated in the original description (Yamaguti, 1934 – fig. 34).
**Fig. 3.49.** *Pachytrema calculus* Looss, 1907. From gall-bladder of *Larus fuscus*, UK, BMNH 1973.7.2. 1–2. Original. Ventral view.

## Subfamily Pseudamphistominae Yamaguti, 1958

**Diagnosis:** Body elongate-oval; posterior end truncated with sucker-like terminal depression. Tegument covered with simple spines. Oral sucker subterminal. Ventral sucker slightly pre-equatorial, embedded. Prepharynx absent. Pharynx oval. Oesophagus absent or very short. Intestinal bifurcation just posterior to pharynx. Caeca wide, slightly sinuous, reach close to posterior extremity. Testes entire, diagonal or almost symmetrical, near caecal ends. Seminal vesicle convoluted, with thick-walled terminal (distal) part (*pars musculosa* of the ejaculatory duct – see fig. 5 in Lühe, 1908). Genital pore just anterior to aperture of ventral sucker, surrounded by two muscular, posterolateral lobes. Ovary median or submedian, pretesticular. Seminal receptacle voluminous, posterolateral to ovary. Uterus strongly coiled, extends laterally over caeca, between

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**Figs 3.50–3.52.** *Plotnikovia podilymbae* (Olsen, 1938). After Olsen (1938). 3.50. Dorsal view. 3.51. Anterior end. 3.52. Sagittal section of ventral sucker region (note shape and position of bipartite seminal vesicle).

**Figs 3.53–3.55.** *Pseudamphistomum truncatum* (Rudolphi, 1819). From liver of *Lutra lutra*, Sweden, BMNH 1991.4.24.1–3 (3.53) and *Larus leucopterus*, Germany, MHNG C/30–31 (3.54, 3.55). Original. 3.53. Ventral view. 3.54. Ventral sucker region, ventrally. 3.55. The same, more dorsally. Note thick-walled ejaculatory duct.

seminal receptacle and region anterior to ventral sucker. Vitellarium consists of relatively few large follicles, extracaecal or overlapping caeca lateroventrally, between region anterior to ventral sucker and testes. Excretory vesicle with sinuous stem passing between testes, bifurcates between anterior testis and seminal receptacle; pore at base of sucker-like posterior depression. In bile-ducts and gall-bladder of mammals, occasionally man; Eurasia and Africa. Type-genus *Pseudamphistomum* Lühe, 1908.

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## Genus *Pseudamphistomum* Lühe, 1908 (Figs 3.53–3.55)

**Diagnosis:** With characters of subfamily. Type-species *P. truncatum* (Rudolphi, 1819) Lühe, 1908.

## Subfamily Ratziinae Poche, 1926

**Diagnosis:** Body elongate, fusiform. Tegument of anterior part covered with scale-like spines. Oral sucker subterminal. Ventral sucker slightly pre-equatorial, smaller than oral sucker, far posterior to intestinal bifurcation, embedded, opens into large atrium on muscular papilla surrounded by gland-cells. Prepharynx very short. Pharynx small. Oesophagus long. Intestinal bifurcation in anterior third of body. Caeca short, terminate at three-quarters of body-length. Testes diagonal, entire or slightly lobed, at distance from posterior extremity. Seminal vesicle short, thick-walled. Genital pore large, transversely oval, opens anterior to aperture of ventral sucker into atrium. Ovary submedian, pretesticular. Seminal receptacle voluminous, posterior to ovary. Laurer's canal present. Uterus completely intercaecal, limited to small area between seminal receptacle and genital pore. Vitelline follicles form two lateral fields along entire length of caeca, extra- and intercaecal, almost confluent near intestinal bifurcation; posterior follicles may reach posterior to testes. Excretory vesicle with wide, slightly sigmoid stem passing between testes, bifurcates between anterior testis and seminal receptacle; pore subterminal. In intestine of reptiles (colubrid snakes); progenetic metacercariae encysted on surface of muscles of amphibians (frogs); Europe (Mediterranean) and North Africa. Type-genus *Ratzia* Poche, 1926.

## Genus *Ratzia* Poche, 1926 (Figs 3.56–3.58)

(Syn. *Brachymetra* Stossich, 1904 nec *Brachymetra* Mayr, 1865)

**Diagnosis:** With characters of subfamily. Type-species *R. parva* (Stossich, 1904) Poche, 1926.

## Subfamily Tubangorchiinae Yamaguti, 1958

**Diagnosis:** Body foliate, with narrow anterior end. Tegument spined. Oral sucker subterminal. Ventral sucker pad-like, at bifurcal level, smaller than oral sucker, deeply embedded within large atrium. Aperture of atrium transversely oval, surrounded by large tegumental spines. Prepharynx absent. Pharynx oval. Oesophagus very short or absent. Intestinal bifurcation close to pharynx. Caeca reach close to posterior extremity. Testes large, indented, irregular in shape, slightly diagonal (almost tandem), postequatorial, intercaecal. Seminal vesicle tubular, convoluted. Genital pore at anterolateral margin of ventral sucker. Ovary slightly submedian, pretesticular. Seminal receptacle voluminous, postovarian and pretesticular. Laurer's canal present. Uterus occupies most of intercaecal field between anterior testis and intestinal bifurcation, with few eggs ventral to caeca. Vitelline follicles almost entirely extracaecal, between intestinal bifurcation and posterior extremity, almost confluent posteriorly. Excretory vesicle with slightly sinuous stem passing between testes, bifurcates between anterior testis and seminal receptacle; pore terminal. In intestine of birds (Gruiformes: Rallidae); Philippines. Type-genus *Tubangorchis* Skrjabin, 1944.

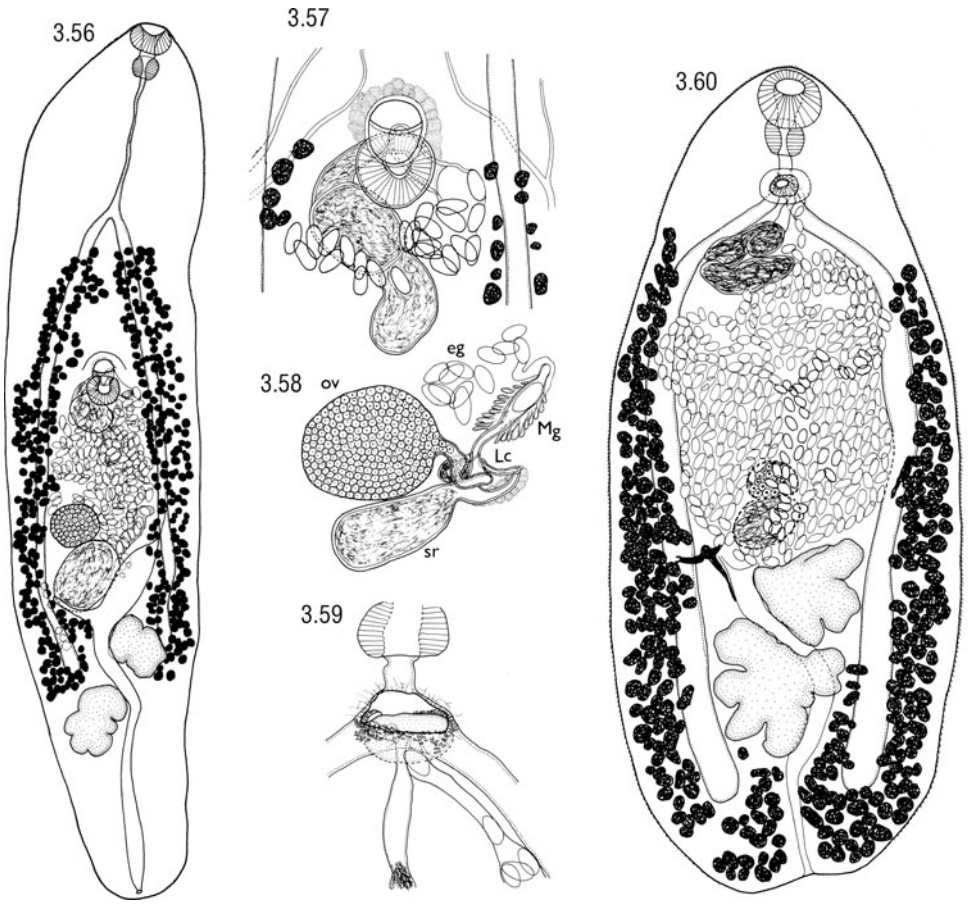
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## Genus *Tubangorchis* Skrjabin, 1944 (Figs 3.59, 3.60)

**Diagnosis:** With characters of subfamily. Type-species *T. caintaensis* (Tubangui, 1928) Skrjabin, 1944.

## Subfamily Witenbergiinae n. subfam.

**Diagnosis:** Body long, widened posteriorly, with rounded posterior end. Tegument unspined. Oral sucker cup-shaped, terminal. Ventral sucker slightly postequatorial. Prepharynx very long, as long as oesophagus, about quarter of body-length. Pharynx large, elongate. Oesophagus long. Intestinal bifurcation closely anterior to ventral sucker. Intestinal caeca reach anterior margin of anterior



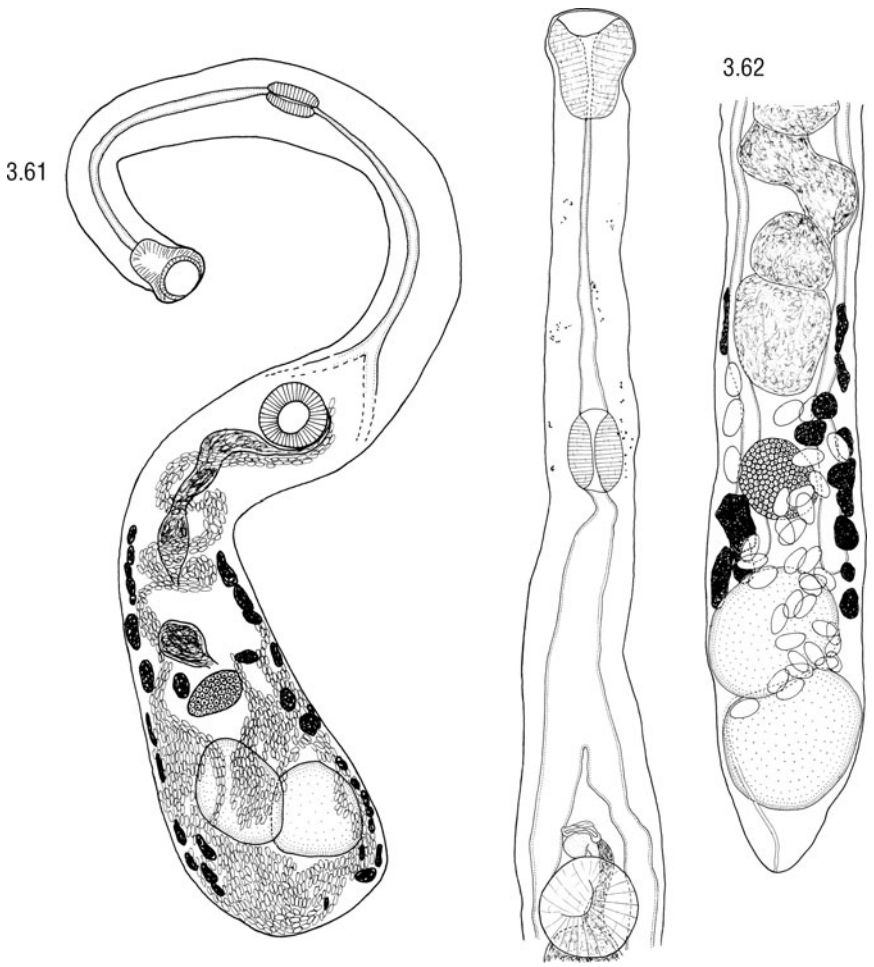

**Figs 3.56–3.58.** *Ratzia parva* (Stossich, 1904). From intestine of *Natrix maura*, Morocco, BMNH 1976.1.19.23–34. Original. 3.56. Ventral view. 3.57. Ventral sucker region with terminal genitalia. 3.58. Ovarian complex: eg – eggs; Lc – Laurer's canal; Mg – Mehlis' glands; ov – ovary; sr – seminal receptacle.
**Figs 3.59, 3.60.** *Tubangorchis caintaensis* (Tubangui, 1928). From intestine of *Gallirallus philippinensis* (3.59) and *Gallinula chloropus* (3.60), Philippines, CVMP 50a & 77-31. Original. 3.59. Ventral sucker region with terminal genitalia. 3.60. Ventral view.

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testis. Testes diagonal or almost tandem, partly overlapping each other, near posterior extremity. Seminal vesicle voluminous, sinuous, posterior to ventral sucker. Genital pore transversely slit-like, between intestinal bifurcation and ventral sucker. Ovary median, pretesticular. Seminal receptacle saccular, pre-ovarian. Uterus inter- and extracaecal, between ventral sucker and posterior extremity, with numerous loops posterior to ovary and at testicular level. Vitelline follicles sparse, large, in lateral fields from posterior end of seminal vesicle to anterior testis or even up to posterior extremity. Excretory vesicle Y-shaped, with narrow stem sinuous between testes; pore terminal. In intestine of pimelodid catfish (Siluriformes); South America (Brazil). Type-genus *Witenbergia* Vaz, 1932.

## Genus *Witenbergia* Vaz, 1932 (Figs 3.61, 3.62)

**Diagnosis:** With characters of subfamily. Type-species *W. witenbergi* Vaz, 1932.




**Figs 3.61, 3.62.** *Witenbergia witenbergi* Vaz, 1932. 3.61. After Vaz (1932). 3.62. From *Pseudoplatystoma fasciatum*, Brazil, IOC 36564a. Original. Ventral view.

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# 4 Family Cryptogonimidae Ward, 1917

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## Introduction

The Cryptogonimidae Ward, 1917 is a large family found globally in the intestine or pyloric caeca of marine and freshwater teleosts, reptiles and, rarely, amphibians. Virtually all cryptogonimids have three-host life-cycles utilizing gastropods as first and fish as second intermediate hosts. Rarely, sexual maturity is reached in the second intermediate host (e.g. species of *Aphalloides* Dollfus, Chabaud & Golvan, 1957 and *Neochasmus* Van Cleave & Mueller, 1932). The family includes over 200 species, and 64 genera are recognized here. The taxonomic status and utility of subfamilies within the Cryptogonimidae are presently unsatisfactory and, as a result, no subfamilies are recognized here.

The family-group concept was established by Ward (1917), who erected the subfamily Cryptogoniminae for *Cryptogonimus* Osborn, 1903 and placed it in the Heterophyidae Leiper, 1909. The Cryptogonimidae was first recognized by Ciurea (1933), who placed it in the 'Heterophyoidea Faust, 1929' (now Opisthorchioidea Looss, 1899). Price (1940) revised the Opisthorchioidea and distinguished the Heterophyidae from the Cryptogonimidae primarily on the extent of the excretory vesicle which, in heterophyids, generally extends only close to the level of the ovary or ventral sucker, whereas in cryptogonimids it generally extends to near the level of the pharynx. The Siphoderidae Linton, 1910 was proposed by Linton (1910) as a new family for *Siphodera vinaledwardsii* (Linton, 1901) Linton, 1910. Manter (1934) transferred it, as the subfamily 'Siphoderinae Manter, 1934', to the Heterophyidae, but it is now considered a cryptogonimid. Although the Siphoderidae pre-dates the Cryptogonimidae, following Article 35.5 of the International Code of Zoological Nomenclature (1999), the Cryptogonimidae Ward, 1917 is retained as the valid family name because of prevailing usage.

Brooks (1980), following the suggestion of Cable & Hunninen (1942) that the presence of a gonotyl may be the only difference between the Acanthostomidae Poche, 1926 and the Cryptogonimidae, revised the subfamily Acanthostominae Poche, 1926, and placed it in the Cryptogonimidae, effectively synonymizing the two families. The Acanthostomidae was distinguished from the Cryptogonimidae by Yamaguti (1971) primarily because the uterus was confined to the area anterior to the testes and did not extend into the post-testicular region. Although

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Brooks's classification has not been universally accepted, there is no compelling reason to recognize separate families and we agree with his classification.

The Cryptogonimidae belongs in the Opisthorchioidea, which also includes the Heterophyidae and Opisthorchiidae Looss, 1899, two families that commonly infect birds and mammals as definitive hosts, although both have representatives in fishes. The relationships of the Cryptogonimidae within both the superfamily and the Digenea have been studied using ssrDNA and lsrDNA genes for three species (*Mitotrema anthostomatum* Manter, 1963, *Siphodera vinaledwardsii* and *Caecincola parvulus* Marshall & Gilbert, 1905) by Olson *et al.* (2003). The three genera formed a clade, but additional phylogenetic analysis is needed to resolve generic and subfamilial relationships and to test the monophyly of the family as a whole.

Cryptogonimids are not readily recognizable by any one character, but by a combination of characters. They usually have a spiny tegument (rarely smooth), a well-developed oral sucker, pharynx and ventral sucker, a ventral sucker almost always equivalent to or smaller than the oral sucker, a common genital pore that opens immediately anterior to the ventral sucker, the lack of a cirrus and cirrus-sac, the presence or absence of a muscular gonotyl, relatively numerous small darkly pigmented eggs and a Y-shaped excretory vesicle (although in some squat species it appears V-shaped) that extends well anterior to the mid-body, often to pharyngeal level. The oral sucker ranges from small to extremely large and from round to funnel-shaped and may have a crown of oral spines. The digestive system consists of a prepharynx, a well-developed muscular pharynx, an oesophagus and an intestine of variable structure. Most species have two blind caeca, but a few have caeca that open at ani or form a uroproct, have one caecum ending blindly and one opening at an anus, or have one short or atrophied caecum. The excretory vesicle is usually Y-shaped with the arms reaching anteriorly beyond the ventral sucker to the level of the intestinal bifurcation or pharynx (rarely shorter). The male reproductive system usually comprises two testes (rarely one, and multiple or follicular testes are present in a few genera) and a simple seminal vesicle that connects with the uterus just distal to the common genital pore. A ventrogenital sac is often present when the ventral sucker is retracted into the body and may have a muscular gonotyl or distinct folding of the tegument associated with it. The gonotyl, as recognized here, generally consists of a distinct muscular sucker-like or lobed structure usually anterior to the ventral sucker. Multiple gonotyls are present in some genera. Gonotyls presumably facilitate sperm transfer, but the role in copulation is not understood. The female reproductive system consists of a single ovary, smooth or slightly to highly lobed, a seminal receptacle and a Laurer's canal, which is probably always present, although not always reported. The uterus is mostly restricted to the hindbody (occasionally extending well into the forebody), often in tight coils and usually packed with numerous relatively small darkly pigmented eggs. The distribution of the vitelline follicles varies dramatically and is often important in distinguishing genera.

The life-cycle has been documented for at least 25 species (Cribb *et al.*, 2001a). Cryptogonimids typically have a three-host life-cycle in which the sexually reproducing adult inhabits the intestine or pyloric caeca of the definitive host. Eggs passed in the faeces are ingested by gastropods, in which miracidia emerge and penetrate the gut wall. Two asexually reproducing generations of mother sporocyst and redia are followed by typically 'opisthorchioid' cercariae, nearly always with a prominent finfold on the dorsal surface of the unforked tail, and with eye-spots that usually persist as dispersed pigment in the forebody of the adults. The flame-cell pattern is most commonly $2[(2 + 2) + (2 + 2)] = 16$, but other patterns are known (Ostrowski de Núñez, 1974). Cercarial body pigmentation is rare. Fully developed cercariae emerge from the gastropod to penetrate and encyst in the fins or tissue of fish and form metacercariae, which generally resemble sexually mature adults, except for the development of the vitellarium and egg production. In

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*Aphalloides coelomicola* Dollfus, Chabaud & Golvan, 1957, the metacercaria is progenetic and the second intermediate host may serve as the definitive host (Pampoulie *et al*., 2000). Usually, the second intermediate host is eaten by the definitive host. All known first intermediate hosts are from the gastropod superfamilies Cerithioidea and Rissooidea (see Cribb *et al*., 2001a).

## Subfamily classification

The subfamily classifications and characters are unsatisfactory (Cribb, 1985, 1986; Bartoli & Bray, 1987; Bartoli & Gibson, 1995). We exclude from the family the monogeneric subfamilies Acetodextrinae Morozov, 1952, Pseudexorchiinae Yamaguti, 1958 (both are heterophyids: see Pearson, Chapter 5, this volume) and the Tubanguiinae Yamaguti, 1958 (*Tubanguia* Srivastava, 1935 is here considered a genus *incertae sedis* – see below). After Brooks (1980) synonymized the Acanthostomidae with the Cryptogonimidae, the number of subfamilies based on Yamaguti (1971) (excluding the Acetodextrinae, Pseudexorchiinae and Tubanguiinae) is 23, of which 16 are monogeneric. Except for the revision of the Acanthostominae by Brooks (1980) and Brooks & Holcman (1993) and the accompanying phylogenetic analysis, little systematic work has been done on relationships of genera within the family. The large number of monogeneric subfamilies does not aid identification of individual genera, especially as many subfamilies are separated by only a few characters, some of which are trivial.

We found no convincing morphological characters justifying subfamily-level division. There are some distinct groups that are probably closely related based on shared ecological and host preference. For example, in genera from the freshwater perciform families Centrarchidae and Moronidae, there is a complex of species that are probably related. Many of these genera have funnel-shaped oral suckers and some form of a muscular gonotyl. One, *Multigonotylus* Premvati, 1967, has multiple gonotyls; it resembles *Polycryptocylix* Lamothe-Argumedo, 1973, from a marine lutjanid, which also has multiple gonotyls, but the two genera are probably not closely related. Homoplasy is probably rife and future subfamily classifications will need to consider both ecological and host preference as well as morphology. Groups that may deserve subfamily status include: genera found in marine Lutjanidae and Haemulidae (although differing dramatically in morphology, they are probably more closely related to each other than to genera parasitizing other host groups); the three genera from the lateolabracid *Lateolabrax japonicus*; genera from reptiles and some fish (Acanthostominae of Brooks, 1980); genera from marine uranoscopids; genera from freshwater cichlids; and some genera from freshwater centrarchids and moronids. Although these groups represent good candidates for subfamily status, many genera do not fit into these schemes.

Until phylogenetic analyses are used to identify evolutionary lineages of genera, current subfamily classifications are of little diagnostic use. We have, therefore, not recognized subfamilies. The phylogenetic analyses by Brooks (1980) and Miller & Cribb (2007a) are good examples (and the only ones to determine intergeneric relationships) of the kind of analyses needed with other cryptogonimids to help resolve this problem.

## Characters used in diagnosing cryptogonimid genera

Although a few cryptogonimid genera have unique defining characters, most are diagnosed by a suite of characters.

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*Body-shape*. This varies from nearly spherical in *Stegopa* Linton, 1910 to extremely elongate in *Mitotrema* Manter, 1963. The most common body-shape is oval to elongate-oval. Body-shape is not generally used alone for generic diagnosis but, in combination with other characters, is informative.

*Tegument*. It is nearly always covered in minute spines or scale-like spines and is rarely used to distinguish genera. *Caimanicola* Freitas & Lent, 1938 has distinctly enlarged tegumental spines in the forebody, which are diagnostic. Species of *Aphalloides*, from the body-cavities of their definitive hosts, lack spines (Bakke, 1980). Species of *Polyorchitrema* Srivastava, 1939 also lack spines.

*Oral sucker*. Oral sucker morphology varies widely and is important in generic recognition. The shape ranges from nearly round, the most common, to the distinctly funnel-shaped suckers of *Diplopharyngotrema* Yamaguti, 1958 and *Claribulla* Overstreet, 1969 and to the relatively enormous sucker of *Stegopa*.

Oral spines occur in 25 genera. They are usually in a single row, but *Acanthocollaritrema* Travassos, Freitas & Bührnheim, 1965, *Acanthostomoides* Szidat, 1954 and *Novemtestis* Yamaguti, 1942 have two rows. Spine size and number vary dramatically and mainly help distinguish species rather than genera. Some taxa can retract the oral spines into tegumental pockets or folds in the tegument, e.g. *Proctocaecum* Baugh, 1957 (Tkach & Snyder, 2003), *Stemmatostoma* Cribb, 1986 and *Telogaster* Macfarlane, 1945 (Cribb, 1986), and this is probably common in forms with oral spines.

*Mitotrema* is unique in having six muscular lobes (two ventral, two lateral and two dorsal). *Orientodiploproctodaeum* Bhutta & Khan, 1970 has a distinctive anterior collar around the oral sucker.

*Ventral sucker*. The ventral sucker is smaller than the oral sucker except in *Centrovarium* Stafford, 1904, *Neometadena* Hafeezullah & Siddiqi, 1970, *Polyorchitrema* and *Pseudometadena* Yamaguti, 1952, almost always round and rarely specialized. Retraction of the ventral sucker often gives the appearance of a 'ventrogenital sac', which incorporates the common genital pore, ventral sucker and sometimes a gonotyl. Pearson (1973), in his revision of the heterophyid subfamily Haplorchinae Looss, 1899, described a tegumental invagination that included the genital pore and gonotyl but not the ventral sucker as a 'genital sac', and an invagination that included the ventral sucker, genital pore and gonotyl as a 'ventrogenital sac'. Because the gonotyl of many cryptogonimids is not embedded in the tegument with the ventral sucker and genital pore, we use the term 'ventrogenital sac' in this chapter to broadly define cases where the ventral sucker and genital pore (and gonotyl if applicable) are obviously embedded in an invagination in the tegument.

*Gonotyl*. Although the diversity and complexity of cryptogonimid gonotyls and their associated ventrogenital complexes do not rival those of the heterophyids, there are still numerous gonotyl types and configurations. Generally, gonotyls are distinctly muscular, often shaped like a reduced ventral sucker (e.g. *Cryptogonimus chili* Osborn, 1903) or a muscular lobe (e.g. *Allacanthochasmus varius* Van Cleave, 1922 and *Bolbogonotylus corkumi* Font, 1987). A muscular pad or sucker-like structure is diagnostic of *Neochasmus* and *Proctocaecum*. Multiple gonotyls are seen in *Multigonotylus, Oligogonotylus* Watson, 1976 and *Polycryptocylix*.

Most gonotyls are immediately anterior to the ventral sucker and common genital pore. Notable exceptions are the species of *Neochasmus*, in which the gonotyl is immediately posterior to the genital pore and can be at the level of or posterior to the ventral sucker, and *Orientodiploproctodaeum diacanthi* Bhutta & Khan, 1970 and *Retrobulla angelae* Cribb, 1985, which have a muscular lobe-like gonotyl immediately posterior to the ventral sucker.

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Many cryptogonimids have been described as having a gonotyl that is a non-muscular fold in the tegument immediately anterior or posterior to the ventral sucker. Whether this is an artefact resulting from retraction of the ventral sucker into the body, leaving a fold around the ventrogenital sac, or if this structure actually functions in the same manner as a muscular gonotyl and warrants the term 'gonotyl' is unclear. We here arbitrarily define a gonotyl as consisting of a distinctly muscular pad, lobe or sucker-like structure, or distinctly large lobes or folding of tegument (but not distinctly large lobes or folding of tegument resulting from the ventral sucker being retracted deeply into the body or from flattening of the specimen during preparation).

*Gut*. The length of the prepharynx is rarely diagnostic at the generic level. The pharynx is not useful at generic level. Oesophageal length is generally not informative, but the position of the intestinal bifurcation relative to the ventral sucker is diagnostic for *Turgecaecum* Sullivan, 1975.

The relative length and termination of the caeca are useful characters. Usually, they end blindly, but there may be separate ani, a uroproct, a cyclocoel, one caecum ending blindly and one opening at an anus, one atrophied caecum, or only a single caecum that ends blindly or at an anus. Most of this diversity occurs within the acanthostomines (*sensu* Brooks, 1980) and their relatives, which have all of the above-mentioned configurations. Lamothe-Argumedo & Ponciano-Rodríguez (1985) revised the Acanthostominae largely on caecal conformation, although there are disagreements between investigators as to the best characters to utilize in the classification of this group.

Where the caeca end blindly, their length and termination point relative to other organs is important. Some genera have relatively short caeca that end anterior to the testes (e.g. *Caecincola* Marshall & Gilbert, 1905 and *Campechetrema* Lamothe-Argumedo, Salgado-Maldonado & Pineda-López, 1997), whereas in many they end near the posterior extremity. *Anisocladium* Looss, 1902 and *Anisocoelium* Lühe, 1900 have distinctly unequal caeca.

*Excretory vesicle*. It is generally Y-shaped. Its extent is only informative at the generic level for *Acanthostomoides* and *Aphalloides*, where it does not extend anterior to the ventral sucker.

*Testes*. The number, arrangement and location of the testes vary widely. *Retrobulla* Cribb, 1985 has only one. *Acanthosiphodera* Madhavi, 1976, *Lobosorchis* Miller & Cribb, 2005, *Novemtestis, Polyorchitrema* and *Siphodera* Linton, 1910 are all distinguished partly by having multiple or follicular testes.

The position of the testes relative to the ovary is important for species in which the testes extend into the forebody or where the ovary is distinctly posterior to the testes, as in *Acanthocollaritrema, Retrovarium* Miller & Cribb, 2007 and *Allometadena* Madhavi, 1976.

*Ovary*. Its shape and location vary widely. It ranges from compact and entire, to compact and slightly lobed, to compact and deeply lobed, to deeply lobed and almost follicular, to deeply lobed and seemingly divided into two approximately symmetrical halves. It is usually median (dextral in *Andritrema* Zhang & Yang, 1993) and usually anterior to the testes, but in some genera is at the level of the testes, or slightly to distinctly posterior to them.

*Seminal receptacle*. Its position is diagnostic of *Timoniella* Rebecq, 1960, in which it is distinctly pre-ovarian.

*Uterus*. The uterus is diagnostic if confined to the region between the testes and ventral sucker, or developed extensively in the forebody or has an extraordinary extent or distribution.

*Eggs. Mehrailla* Srivastava, 1939 is partly diagnosed by triangular eggs with a distinct anopercular filament. *Cryptogonimus* eggs may have distinct curved anopercular spines.

*Vitellarium*. The restriction or extent of the vitelline follicles is often used to diagnose genera.

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## Notes on genera

Below is a brief overview of many of the genera currently recognized within the Cryptogonimidae. The most significant proposal is the synonymy of what was formerly the largest genus, *Paracryptogonimus* Yamaguti, 1934, with *Siphoderina* Manter, 1934 (see *Siphoderina* below).

## Genus *Acanthocollaritrema* Travassos, Freitas & Bührnheim, 1965

This monotypic genus was proposed by Travassos *et al*. (1965) for *A. umbilicatum* Travassos, Freitas & Bührnheim, 1965 from *Centropomus undecimalis* off the coast of Brazil. A new family, the Acanthocollaritrematidae Travassos, Freitas & Bührnheim, 1965, was erected for it and distinguished by the posterior location of the ventral sucker, the testes in the forebody and the ovary in the hindbody. Robaldo & Padovan (1998) redescribed this species and considered that the lack of a gonotyl and genital atrium justified the separate family. Despite this, it generally resembles other cryptogonimids (spinous tegument, small darkly pigmented eggs, no cirrus-sac, genital pore immediately anterior to the ventral sucker and excretory vesicle arms extending to the intestinal bifurcation). A number of other cryptogonimid genera are also found in centropomids. Also, two other genera, *Allometadena* and *Retrovarium*, are distinguished by having a post-testicular ovary and the testes extending slightly into the forebody. Thus, we consider the Acanthocollaritrematidae a synonym of the Cryptogonimidae.

## Genus *Acanthosiphodera* Madhavi, 1976

This monotypic genus was proposed by Madhavi (1976) for *A. bengalensis* Madhavi, 1976 (emend.) from *Lutjanus malabaricus. Acanthosiphodera* was originally proposed by Madhavi (1974b) in an abstract, but the correct date of the authority should be 1976 based on International Code of Zoological Nomenclature (ICZN) rules. It closely resembles *Siphodera* in having multiple or follicular testes, a follicular ovary and a virtually identical vitelline follicle distribution, but differs in having circumoral spines.

## Genus *Acanthostomoides* Szidat, 1956

This monotypic genus proposed by Szidat (1956) for *A. apophalliformis* Szidat, 1956 from the freshwater fish *Percichthys truca* in Argentina, shares 11 of the 13 characters used by Brooks (1980) to define the Acanthostominae, but differs by having two rows of circumoral spines and vitelline follicles confluent dorsally and ventrally. A redescription and complete life-history was given by Ostrowski de Núñez *et al*. (1999). Shimazu *et al*. (2000) also redescribed it. The excretory vesicle extends only to the level of the ovary, a common heterophyid characteristic, but rare among cryptogonimids.

## Genus *Acanthostomum* Looss, 1899

The type-species, *A. spiniceps* (Looss, 1896) Looss, 1899, was described by Looss (1896) as *Distomum spiniceps* Looss, 1896 from the siluriform fish *Bagrus bajad* in the Nile in Egypt. Our

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concept of the genus follows that of Brooks (1980) and Brooks & Holcman (1993). It currently contains 20 species. Brooks & Caira (1982) synonymized the monotypic *Ateuchocephala* Coil & Kuntz, 1960 and *Paracanthostomum* Fischthal & Kuntz, 1965 with *Atrophecaecum* Bhalerao, 1940 (now considered a subgenus of *Acanthostomum*) because they considered the lack of oral spines in those species to represent secondary losses.

## Genus *Allacanthochasmus* Van Cleave, 1922

This was proposed by Van Cleave (1922) for *A. varius* Van Cleave, 1922 from the freshwater moronid *Morone chrysops* in North America. Mueller & Van Cleave (1932) described *A. artus* Mueller & Van Cleave, 1932 from the same host and locality. It differs from *A. varius* in the more elongate body, the testes are strongly oblique and the gonotyl consists of a cylindrical stalk-like structure with approximately five small projections at the distal end. Despite these morphological differences, they appear closely related and we recognize their congeneric status. Saoud *et al.* (1988) described a third species, *A. lutjani* Saoud, Ramadan & Al-Kawari, 1988, from *Lutjanus fulviflamma* in the Arabian Gulf. Its gonotyl is a muscular, stalked protrusion with an apical crown of spines; their SEM micrograph shows it protruding with a crown of spines. In their comparison of *A. lutjani*, Saoud *et al.* (1988) did not mention its resemblance to the monotypic *Gonacanthella* Sogandares-Bernal, 1959, also from a lutjanid and having a similarly spined gonotyl. These two species are probably closely related. *G. lutjani* Sogandares-Bernal, 1959 was described from only a single intact specimen and it is possible the oral spines were lost (see discussion below on *Neometadena*), so these species may be congeneric. The host affinity (marine fish in the Lutjanidae) and general morphology of *A. lutjani* suggests it is more closely related to the *Siphoderina*/*Gonacanthella* group of cryptogonimids which share the same host-group. We therefore propose the new combination *Siphoderina lutjani* (Saoud *et al.*, 1988) n. comb., pending further characterization of the ventrogenital structure. *Allacanthochasmus* is thus restricted to freshwater fish of the Moronidae.

## Genus *Andrincola* Zhang & Yang, 1993

This was proposed by Zhang & Yang (1993) for *A. mabianensis* Zhang & Yang, 1993 from the Chinese giant salamander *Andrias davidianus*. *Neoandrincola* Zhang & Yang, 1997 was later proposed by Zhang & Yang (1997) for *N. muchuanensis* Zhang & Yang, 1997 from the intestine of the same host at the same locality. *Neoandrincola* was distinguished from *Andrincola* by having a second gonotyl posterior to the ventral sucker; a similar structure has been reported for *Bolbogonotylus* Font, 1987. We were unable to examine type-material for *N. muchuanensis*, but we saw that of *B. corkumi* Font, 1987. Below (see *Bolbogonotylus*), we discuss the lobe-like structure posterior to the ventral sucker and choose not to use it for generic diagnosis. It appears to be an artefact of the tegument folding on itself, as the ventral sucker is retracted. Zhang & Yang (1997) do not discuss the structure of the 'gonotyl' posterior to the ventral sucker but, in their figure, it appears nearly identical to the structure observed in *B. corkumi*, and we do not recognize it here as diagnostic at generic level. Consequently, *Neoandrincola* is a junior synonym of *Andrincola* and we transfer *N. muchuanensis* to *Andrincola* as *A. muchuanensis* (Zhang & Yang, 1997) n. comb. *Andrincola* and the monotypic *Andritrema* Zhang & Yang, 1993 are both from the same host, and are the only two genera in the family reported from amphibians.

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## Genus *Andritrema* Zhang & Yang, 1993

This monotypic genus was proposed by Zhang & Yang (1993) for *A. ellipticum* Zhang & Yang, 1993 (emend.) from the amphibian *Andrias davidianus* and distinguished primarily by the distinctly dextral ovary. Zhang & Yang (1993) stated that *A. ellipticum* possessed an atrial recess, but their figure is not easy to interpret and, without access to type-material, it is difficult to ascertain whether this is indeed an atrial recess, some form of muscular gonotyl or a folding of the tegument over the ventral sucker and genital pore.

## Genus *Anisocladium* Looss, 1902

This was proposed for *A. fallax* (Rudolphi, 1819) Looss, 1902, originally described as *Distoma fallax* by Rudolphi (1819) from *Uranoscopus scaber*. Looss (1901a) provided the first good description and proposed the generic name *Anisogaster* to include *A. fallax* and a second species, *A. gracile* (Looss, 1901) Looss, 1902, which he described from the same host; Looss (1902) later renamed the genus *Anisocladium* because *Anisogaster* was pre-occupied. *Anisocladium fallax* and *A. gracile* were synonymized by Dawes (1946), Morozov (1955a) and Radukovic *et al*. (1989), but Bartoli & Gibson (2000) concluded that both species were valid.

## Genus *Anisocoelium* Lühe, 1900

This monotypic genus was proposed by Lühe (1900a) for *A. capitellatum* (Rudolphi, 1819) Lühe, 1900, originally described by Rudolphi (1819) as *Distomum capitellatum* Rudolphi, 1819 from *Uranoscopus scaber*. This species is unique in the family because its principal site of infection is the gall-bladder, although Nikolaeva & Solonchenko (1970) reported specimens from both intestine and gall-bladder. Bartoli & Gibson (2000) discussed probable errors in reports of this species from other hosts, and questioned a report of it from *Mullus barbatus* by Hristovski & Jardas (1983, 1991) and Paradiznik (1992), which could be a misidentification of the hemiuroid *Derogenes latus* Janiszewska, 1953.

## Genus *Anoiktostoma* Stossich, 1899

This was proposed by Stossich (1899) for *Distomum coronatum* Wagener, 1852 from the rectum of the sciaenid *Sciaena umbra* in the Mediterranean. The morphologically similar *Ryjikovia* Gaevskaya & Aljoshkina, 1985 proposed (Gaevskaya & Aljoshkina, 1985) for three species from the sciaenid *Umbrina canariensis* was distinguished from *Siphoderina* and *Neochasmus* by the anterior extent of the vitelline follicles and uterus, without reference to *Anoiktostoma*. Bartoli & Gibson (1995) redescribed *A. coronatum* and distinguished it from *Paracryptogonimus* (now *Siphoderina*) by the relatively large oral spines, the entire to slightly lobed ovary and the uterus extending well into the forebody. Specimens recovered by Bartoli & Gibson (1995) also have slightly elongate testes. The only differences between *Ryjikovia* and *Anoiktostoma* are that the ovary is more highly lobed in the former, and the testes may be more elongate and may have slight lobation (possibly an artefact of fixation) in the former. We therefore do not recognize *Ryjikovia* and transfer its species to *Anoiktostoma* as *A. formosum*

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(Gaevskaya & Aljoshkina, 1985) n. comb., *A. elongatum* (Gaevskaya & Aljoshkina, 1985) n. comb. and *A. ovale* (Gaevskaya & Aljoshkina, 1985) n. comb.

## Genus *Aphalloides* Dollfus, Chabaud & Golvan, 1957

This was proposed by Dollfus *et al*. (1957) for *A. coelomicola* Dollfus, Chabaud & Golvan, 1957 from the goby *Pomatoschistus microps* on the Mediterranean coast of France. A second species, *A. timmi* Reimer, 1970, was described from the same host in the Baltic Sea (Reimer, 1970). Both occur as adults in the body-cavity. The life-cycle of *A. timmi* is unusual for a cryptogonimid in that the second intermediate host also serves as the definitive host (Maillard, 1973; Bakke, 1980). Pampoulie *et al*. (2000) suggested that the death of the goby was probably necessary for transmission. Both species are consistent morphologically with cryptogonimids, except for the lack of a spined tegument and the short excretory vesicle. We retain the genus in the Cryptogonimidae, but further study is needed to determine its systematic relationship within the Opisthorchioidea.

## Genus *Biovarium* Yamaguti, 1934

This was proposed by Yamaguti (1934) for *B. cryptocotyle* Yamaguti, 1934 from *Lateolabrax japonicus* off Japan and is distinguished by an ovary divided into two distinct asymmetrical lobes between the ventral sucker and testes. It forms an interesting species complex with a closely related genus also from *L. japonicus, Diplopharyngotrema* Yamaguti, 1958. Yamaguti (1958a) proposed *Diplopharyngotrema* for *D. lateolabracis* Yamaguti, 1958, which he described from two specimens, and distinguished it by the funnel-shaped oral sucker, 'bi-partite' pharynx and tandem, separated testes. We examined his three voucher specimens in the Harold W. Manter Laboratory of Parasitology (HWML 666) and saw no evidence of a 'bi-partite' pharynx. We do not consider this character reliable to distinguish *Diplopharyngotrema*. The only differences between the two genera are that species of *Diplopharyngotrema* have a funnel-shaped oral sucker, do not have a 'bi-lobed' ovary and the testes are usually separated by more than one testis diameter. Future analysis may warrant the synonymy of these obviously closely related genera, but for now we retain both. We recognize seven species, *B. cryptocotyle, B. cheni* Pan, 1984, *B. heterovale* Pan, 1984, *B. lateolabracis* Yamaguti, 1958, *B. lobiorchium* Pan, 1984, *B. tsingtaoense* Gu & Shen, 1978 (emend.) and, tentatively, *B. pomadasydis* Shen & Tong, 1985. *B. pomadasydis* was described from a haemulid and is generally similar to the other six species of *Biovarium*, but differs in having well-separated testes and vitelline follicles that do not enter the forebody.

## Genus *Bolbogonotylus* Font, 1987

This monotypic genus was proposed by Font (1987) for *B. corkumi* Font, 1987 from the freshwater bass *Micropterus dolomieu* in Wisconsin, USA. Font (1987) described it as having a 'bi-lobed' gonotyl with one lobe anterior and one lobe posterior to the ventral sucker. We examined the holotype and a paratype (USNPC 78726-78727) and observed the posterior lobe, which appears to be non-muscular and may be part of the tegument folding on itself, as the ventral sucker is retracted, or actually function as a rudimentary gonotyl. The diagnostic value of this

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character is questionable. We do not incorporate the posterior lobe in the diagnosis, believing that this character is not significant at the generic level. Regardless of the presence of the posterior lobe, *B. corkumi* differs from the morphologically similar and monotypic *Textrema* Dronen, Underwood & Suderman, 1977, also from species of *Micropterus*, in having a funnel-shaped oral sucker, vitelline follicles confined to the hindbody, a gonotyl lacking spine- or rod-like structures and tandem testes well anterior to the posterior end of the body.

## Genus *Centrovarium* Stafford, 1904

This was proposed by Stafford (1904) for *C. lobotes* (McCallum, 1895), originally described as *Distomum lobotes* MacCallum, 1895 from the freshwater fishes *Esox lucius* and *Stizostedion vitreum* (now *Sander vitreus*) from North America. Two other species, *C. marinum* Hafeezullah & Siddiqi, 1970 from the marine *Lutjanus fulviflamma* off India, and *C. matlai* Dutta & Manna, 1993 from an Indian freshwater/brackish fish *Nandus nandus*, have been described. We question the placement of *C. marinum*. The only distinctions between this species and *C. lobotes* were the sucker-ratio and the position of the seminal vesicle (Hafeezullah & Siddiqi, 1970a). They did not mention the extent of the caeca in *C. marinum*. Based on the morphology and host affinity of this species, which agrees with *Metadena* Linton, 1910, we transfer *C. marinum* to *Metadena* as *M. marina* (Hafeezullah & Siddiqi, 1970) n. comb. We tentatively retain *C. matlai* in *Centrovarium* despite the few distinct differences this species has relative to *C. lobotes; C. matlai* has a smaller ventral sucker, an ovary divided into only three to five lobes, caeca that extend to the level of the testes rather than the ovary, and vitelline follicles that do not enter the forebody.

## Genus *Cicesetrema* Pérez-Ponce de León, Castillo-Sanchez & Rosales-Casián, 1999

This monotypic genus was proposed by Pérez-Ponce de León *et al*. (1999) for *C. unami* Pérez-Ponce de León, Castillo-Sanchez & Rosales-Casián, 1999 from the Pacific halibut *Paralichthys californicus* off Baja, Mexico. We examined two paratypes (USNPC 88955; HWML 15017). The ventral sucker is deeply retracted into the body and the 'gonotyl' appears to be formed by the tegument being folded over the entire ventral sucker, leaving a small opening. There does appear to be some muscular structure associated with the small opening in the tegument, but its structure is unclear and we recognize it only tentatively as a gonotyl in the diagnosis and key.

## Genus *Cryptogonimus* Osborn, 1903

The type-genus for the family was proposed by Osborn (1903) for *C. chili* Osborn, 1903 from the freshwater centrarchid *Micropterus dolomieu* in North America. The ovary of *C. chili* was not described well and appears entire in the original figure. We examined a voucher specimen deposited by Osborn (USNPC 51550) and two others (USNPC 60414 and 76696) and their ovaries are distinctly lobed. The genus currently contains *C. chili, C. diaphanus* (Stafford, 1904) Miller, 1941 and *C. spinovum* Greer & Corkum, 1979, all from centrarchids. *C. diaphanus* was described by Stafford (1904) as *Protenteron diaphanus* and transferred by Miller (1941) to *Cryptogonimus* based

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on a single specimen from Stafford's collection (the type-material could not be located). It has not been reported since and may be a synonym of *C. chili. C. spinovum* has a curved spine at the anopercular end of its eggs and caeca that extend beyond the testes (Greer & Corkum, 1979). Despite these differences, the host affinity and other morphological characters, such as the gonotyl structure, funnel-shaped oral sucker and trilobed ovary, suggest a close relationship between these two species. The only other cryptogonimid with spinous or filamented eggs is the marine species *Mehrailla ovocaudatum* Srivastava, 1939.

## Genus *Diplopharyngotrema* Yamaguti, 1958

This was proposed by Yamaguti (1958a) for *D. lateolabracis* Yamaguti, 1958 from the lateolabracid *Lateolabrax japonicus* off Japan. The 'bi-partite' pharynx used by Yamaguti (1958a) to distinguish it from *Biovarium* (which also infects *L. japonicus*, see above) is not a reliable character and, as already discussed, we do not recognize it in the diagnosis of this genus.

*Biovarium xiamenense* Liu, 1996 described by Liu (1996) in *L. japonicus* off Fujian Province, China, was not compared with *Diplopharyngotrema*, but it agrees with our concept of the genus and we transfer it as *D. xiamenense* (Liu, 1996) n. comb.

Gu & Shen (1978) proposed a new genus and species, *Sacculoesophagipora bipapillosa* Gu & Shen, 1978 from *L. japonicus* off China, described as having a cirrus and cirrus-sac, distinctly non-cryptogonimid characters. Wang P.-q. (1982a) transferred *S. bipapillosa* to *Diplopharyngotrema*. We could not obtain type-material and only tentatively recognize it as valid, as the original description is poor. If a cirrus and cirrus-sac are present, the systematic placement of this species must be reassessed. Gu & Shen (1978) proposed another new genus and species, *Terminoisocoelium laterolecithale* Gu & Shen, 1978, also from *L. japonicus*, which appears to differ from *D. lateolabracis* only by a more elongate body and vitelline follicles that extend from the ventral sucker to posterior to the testes. They did not compare it with *Diplopharyngotrema*, from which these differences do not warrant separation; we transfer *T. laterolecithale* as *D. laterolecithale* (Gu & Shen, 1978) n. comb. *B. schistolecithale* Gu & Shen, 1978, also proposed by Gu & Shen (1978), agrees better with *Diplopharyngotrema* than with *Biovarium*, although its testes are contiguous, possibly representing a form intermediate between these closely related genera. We transfer it to *Diplopharyngotrema* as *D. schistolecithale* (Gu & Shen, 1978) n. comb.

*Pseudoisocoelium* Pan, 1984 proposed by Pan (1984c) for *P. bigonopori* Pan, 1984, also from *Lateolabrax japonicus* off China, was characterized as having two separate genital pores that open anterior to the ventral sucker. The sagittal section figures by Pan (1984c) are unclear and do not conclusively show two separate pores. It clearly resembles members of *Diplopharyngotrema*, which are found in the same host and locality. We synonymize *Pseudoisocoelium* with *Diplopharyngotrema* and propose *D. bigonopori* (Pan, 1984) n. comb.

## Genus *Exorchis* Kobayashi, 1921

Kobayashi (1921) erected this for *E. oviformis* Kobayashi, 1921 from the freshwater siluriform *Silurus* (now *Parasilurus) asotus* in Japan. Three other species have been described from the same host, *E. dongtinghuensis* Zhang, Zuo, Liu, & Zhou, 1993, *E. multivitellarius* Pan, 1984 and *E. ovariolobularis* Hua, 1990. *Parametadena* Pan, 1984 was erected by Pan (1984a) for *P. macrobursae* Pan, 1984 from the freshwater siluriform *Pelteobagrus fulvidraco* in China. The

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main distinction from *Exorchis* was that the testes are not entirely extracaecal but overlap the caeca (also seen in *E. ovariolobularis*, although not mentioned by Pan). The host affinity (freshwater siluriforms), biogeographical affinity (Japan and China) and morphological similarities suggest that these species are closely related and there is insufficient evidence to recognize *Parametadena*. We synonymize it with *Exorchis* and transfer *P. macrobursae* to *Exorchis* as *E. macrobursae* (Pan, 1984) n. comb. *Exorchis* now contains five species, all restricted to freshwater siluriforms in Asia.

## Genus *Gonacanthella* Sogandares-Bernal, 1959

This monotypic genus was proposed by Sogandares-Bernal (1959a) for *G. lutjani* Sogandares-Bernal, 1959 from *Lutjanus jordani* off the Pacific coast of Panama. One of the main diagnostic characters, according to Sogandares-Bernal (1959a), was an entire ovary. We examined the holotype (USNPC 38873) and found the ovary barely discernible. This species was described from two specimens and the paratype was not deposited, so we tentatively recognize the species as having an entire ovary.

## Genus *Isocoelioides* Zhukov, 1971

This monotypic genus proposed by Zhukov (1971) for *I. orientalis* Zhukov, 1971 from *Lateolabrax japonicus* near Japan is closely related to the *Biovarium*/*Diplopharyngotrema* group from the same host (see above), but appears distinct in some important features. The posterior testis is well separated from the anterior testis and is at the posterior extremity, the ovary is not divided into asymmetrical lobes and the vitelline follicles appear to form transversely elongate bands across the entire width of the body from slightly anterior to the ovary to the anterior margin of the posterior testis. The ventroterminal slit figured by Zhukov (1971) may be tegument folded over the oral sucker due to it being retracted into the body (several species can retract the oral sucker deeply into the tegument). We were unable to examine type-material, so whether this slit is a stable morphological character or just a tegumental folding is unclear. We recognize *Isocoelioides*, but redescription of the type-species, with emphasis on the form of the oral sucker and vitellarium, is needed.

## Genus *Mehrailla* Srivastava, 1939

This monotypic genus was originally proposed in an abstract by Srivastava (1937) as *Mehracola ovocaudatum* Srivastava, 1937 from the marine fish *Stromateus cinereus* (now *Pampus cinereus*) near India. He later (Srivastava, 1939b) published a complete description but changed the generic name to *Mehrailla. Mehracola* Srivastava, 1937 is a *nomen nudum*, as it was not properly described or illustrated. *Mehrailla* resembles species of *Metadena* (primarily found in lutjanids), but differs in the lobation of testes and the filamented egg. Literature records of this genus from species of *Lutjanus* (Hafeezullah & Siddiqi, 1970a; Zaidi & Khan, 1977; Hafeezullah & Dutta, 1980; Bilqees, 1981; Leong & Wong, 1989) are doubtful, because none mentions filamented eggs and, if figures are present, they are of distorted specimens.

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## Genus *Metadena* Linton, 1910

This is one of the oldest and, as recognized here, one of the largest, cryptogonimid genera, incorporating about 20 species, all of which are marine and most are found in the closely related Lutjanidae and Haemulidae. They share a rather generalized cryptogonimid morphology that is not particularly distinctive, and many appear closely related to *Siphoderina* (also predominantly in lutjanids), differing only in the lack of oral spines. *Metadena* was proposed by Linton (1910) for *M. crassulata* Linton, 1910 from *Neomaenis* (now *Lutjanus*) *analis* off Florida, USA. *Pseudosiphoderoides* Yamaguti, 1958 and *Siphoderoides* Manter, 1940, also found in lutjanids and haemulids, are here considered synonyms of *Metadena*.

*Pseudosiphoderoides* was proposed for *P. hapalogenyos* Yamaguti, 1958, from *Hapalogenys* sp. (Haemulidae), and distinguished primarily by a smooth tegument, having a 'medium sized' body, lacking oral spines and a gonotyl, the seminal vesicle being tubular and sinuous instead of a large undivided sac, and the ventral sucker being covered by a circular fold of tegument. Yamaguti (1970) described *P. opakapaka* Yamaguti, 1970 and *P. rooseveltiae* Yamaguti, 1970, and later (Yamaguti, 1971) included *P. apharei* (Yamaguti, 1942) (originally described as *Siphoderina apharei*, but transferred to *Metadena* by Yamaguti (1953b) and then *Pseudosiphoderoides* by Yamaguti (1971),[1] *P. longus* (Oshmarin, Mamaev & Parukhin, 1961), *P. lutiani* (Yamaguti, 1942) and *P. sargusi* (Nagaty & Abdel-Aal, 1961). Yamaguti (1942b) mentioned that the tegument of *P. apharei* has exceedingly small spines, and the tegument of *P. lutiani* is apparently armed with minute spines, although they were not distinct due to post-mortem maceration. We examined the holotypes of *P. opakapaka* (USNPC 63745) and *P. rooseveltiae* (USNPC 63746), and observed tiny tegumental spines. The only apparent morphological difference between *Pseudosiphoderoides* and *Metadena* is the size of the worms (species in *Pseudosiphoderoides* tend to be larger than those in *Metadena*), which we consider interspecific rather than intergeneric variation. Finally, we do not consider the difference in the form of the seminal vesicle, as used by Yamaguti (1958a), to be informative at generic level. The host affinity and general morphology suggest that these species are closely related, and we synonymize *Pseudosiphoderoides* with *Metadena* with the following new combinations: *M. hapalogenyos* (Yamaguti, 1958) n. comb., *M. longa* (Oshmarin, Mamaev & Parukhin, 1961) n. comb., *M. lutiani* (Yamaguti, 1942) n. comb., *M. opakapaka* (Yamaguti, 1970) n. comb., *M. rooseveltiae* (Yamaguti, 1970) n. comb. and *M. rotivarijera* (Shen, 1986) n. comb. The last species is unique in being reported as having an entire ovary and is thus recognized only tentatively. We exclude *P. sargusi* (originally the type-species of *Mahrosa* Nagaty & Abdel-Aal, 1961, here considered a genus *inquirendum*, see below), from this genus, as a species *inquirenda*, because it was inadequately described. *P. xishaensis* Gu & Shen, 1983 was described by Gu & Shen (1983) from *Caesio erythrogaster* (now *Caesio cuning*). It is distinct in having tandem, highly lobed testes and appears to be intermediate between *Metadena* and *Siphodera* Linton, 1910. Another species from a caesionid, *S. gurukun* Machida, 1986, resembles *P. xishaensis*, differing only in that the testes are distinctly multiple or follicular in the former as opposed to two, distinctly separate and lobed in the latter. These species are obviously closely related, but we

[1] The transfer of *Siphoderina apharei* Yamaguti, 1942 to *Paracryptogonimus* by Velasquez (1961) is not recognized here because the host reported by Velasquez (1961) was not adequately identified. We prefer to recognize *Metadena apharei* (Yamaguti, 1942) and *Siphoderina apharei* (Yamaguti, 1970) n. comb. (formerly *Paracryptogonimus apharei*) as separate until further study of material from the type-localities is undertaken.

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consider *P. xishaensis* a species *incertae sedis* until its relationship with species in the *Metadena/ Siphodera* group can be critically assessed.

*Siphoderoides* Manter, 1940 proposed by Manter (1940) for *S. vancleavei* Manter, 1940 from the haemulid *Orthostoechus* (now *Haemulon) maculicauda* off the Pacific coast of Colombia, was described from a single specimen and the genus was distinguished primarily on the presence of a muscular gonotyl posterior to the ventral sucker. We examined the holotype (USNPC 9362) and determined that the structure is an artefact of flattening and is the creased, folded tegument rather than a distinct muscular structure. Therefore, this does not distinguish *Siphoderoides* from *Metadena*. The host affinity (Haemulidae are closely related to Lutjanidae) also indicates no distinction from *Metadena*, so we synonymize these genera and transfer *S. vancleavei* Manter, 1940 as *M. vancleavei* (Manter, 1940) n. comb. Shen (1990) proposed *S. lutiani* Shen, 1990 from *Lutjanus erythropterus*, but it lacks the 'gonotyl' described by Manter (1940) and warrants transfer to *Metadena*. A new combination would be pre-occupied by *M. lutiani* (Yamaguti, 1942) n. comb., so we propose *M. sheni* nom. nov. for this species. Recently, Al-Bassel (2002) proposed *Palaeocryptogonimus alexandrinus* Al-Bassel, 2002 from a goatfish *Mullus surmuletus* off Egypt. This record is unlikely because species of *Palaeocryptogonimus* Szidat, 1954 are otherwise restricted to freshwater doradids and cichlids from Mexico and South America. The morphology and host ecology (marine) suggest that it belongs to *Metadena* and we propose *M. alexandrinus* (Al-Bassel, 2002) n. comb.

## Genus *Neochasmus* Van Cleave & Mueller, 1932

*Neochasmus* was proposed by Van Cleave & Mueller (1932) for *N. umbellus* Van Cleave & Mueller, 1932 from the freshwater fish *Micropterus salmoides* in North America. Seven further species have been described: *N. labeosus* Bennett, 1935 from the water snake *Natrix rhombifera* in North America; *N. ictaluri* Sogandares-Bernal, 1955 from the freshwater siluriform *Ictalurus furcatus* in North America; *N. sogandaresi* Overstreet, 1971 from *Morone saxatilis* in North America; *N. ackerti* Watson, 1976 from a haemulid in Central America; *N. magnus* Winter, 1958 from a lutjanid off the Pacific coast of Mexico; *N. microvatus* (Tubangui, 1928) Tubangui & Masiluñgan, 1944 from a gobiid and haemulid off the Philippines; and *N. olmecus* Lamothe-Argumedo, Pineda-López & Salas, 1989 from a centropomid near Tabasco, Mexico. Some obvious inconsistencies between species in gonotyl morphology and host distribution need to be addressed. We examined the 'co-type' of *N. umbellus* deposited by Mueller (USNPC 8572) and some voucher specimens (USNPC 77975). We also examined the holotype and some paratypes of *N. ictaluri* (USNPC 37483) (HWML 675, 22140 and 22680), syntypes of *N. labeosus* (USNPC 50397 and 51732), a voucher of *N. microvatus* (USNPC 39078) and the holotype and a paratype of *N. sogandaresi* (USNPC 71655 and 71656). Four species, *N. umbellus* (the type-species), *N. ictaluri, N. labeosus* and *N. sogandaresi*, all from freshwater hosts, have a muscular gonotyl or lobed protrusions posterior to the genital pore. They all have a highly lobed to follicular, transversely elongate ovary, and a similar vitelline follicle distribution and host ecology, and form the concept of the genus as recognized here.

The other four species all show greater affinity with *Siphoderina*. *N. ackerti* and *N. microvatus* lack gonotyls (Watson, 1976) and their host distribution (Gobiidae, Haemulidae and Lutjanidae) suggests they are species of *Siphoderina*, which occur predominantly in lutjanids and haemulids. *N. olmecus* differs from typical species of *Neochasmus* in not having a gonotyl posterior to the common genital pore, having a compact ovary and having a double rather than single crown of oral spines. The gonotyl was not described or figured well by Lamothe-Argumedo *et al.* (1989) and may be an artefact of the tegument folding over the ventral sucker. Three other species of

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*Siphoderina* are known from centropomids. *N. magnus* Winter, 1958 was described from *Lutjanus colorado* off Mexico (Winter, 1958). Its gonotyl was not characterized properly and, if present, is not posterior to the genital pore. The general morphology and host affinity of these species suggest a close relationship with *Siphoderina*. We transfer them as *S. ackerti* (Watson, 1976) n. comb., *S. olmecus* (Lamothe-Argumedo, Pineda-López & Salas, 1989) n. comb., *S. microvata* (Tubangui, 1928) n. comb. and *S. magna* (Winter, 1958) n. comb.

## Genus *Neocladocystis* Manter & Pritchard, 1969

This was proposed by Manter & Pritchard (1969) for *Cladocystis tanganyikae* Prudhoe, 1951 (type-species) from several unidentified cichlid species and *Lamprichthys tanganicanus* from Africa, *C. intestinalis* Vaz, 1932 from a characid in South America and *N. congoensis* Manter & Pritchard, 1969 from the bagrid *Parauchenoglanis guttatus* in Africa. They distinguished it from *Cladocystis* by the presence of tegumental spines, unbranched arms of the excretory vesicle and an entire ovary. It is restricted to freshwater fishes and resembles *Brientrema*, also found in Africa, but lacking oral spines and a gonotyl. *Cladocystis* Poche, 1926 is an opisthorchiid genus (see Scholz, Chapter 3, this volume).

## Genus *Neometadena* Hafeezullah & Siddiqi, 1970

Proposed by Hafeezullah & Siddiqi (1970a) for *N. lutiani* Hafeezullah & Siddiqi, 1970 from *Lutjanus johnii* and *L. fulviflamma* off India. This species is virtually identical to the type-species of *Neoparacryptogonimus* Hafeezullah, 1975, *N. ovatus* (Yamaguti, 1952) Hafeezullah, 1975. Yamaguti (1952) had described *N. ovatus* from an unknown fish as a species of *Paracryptogonimus*, but it was reported by Madhavi (1976), Leong & Wong (1989), Shen (1990) and Nahhas *et al.* (2003) from haemulid, lutjanid and chirocentrid fishes. Hafeezullah (1975) proposed *Neoparacryptogonimus* for it based on differences in the distribution of the vitelline follicles. *N. lutiani* and *N. ovatus* resemble each other in body-shape, in the conspicuously thick tegument and in the distribution of the vitelline follicles. The only difference is the absence of oral spines in *N. lutiani*. Hafeezullah (1975) discussed the possibility of oral spines being lost in other species and the difficulty of finding scars marking where they had been. We find that oral spines are easily lost in specimens that have been dead for only a short time. Notably, Hafeezullah & Siddiqi (1970a) reported *Paracryptogonimus americanus* Manter, 1940 as having lost nearly its entire row of oral spines, and Hafeezullah (1975) described *P. sootai* Hafeezullah, 1975 from a *Lutjanus* sp. as also having lost most of its oral spines. We conclude that the two specimens described as *Neometadena lutiani* have simply lost their oral spines and, as there are no other differences between them, we synonymize *Neometadena lutiani* with *Neoparacryptogonimus ovatus*. *Neometadena* is the senior synonym, so we propose *N. ovata* (Yamaguti, 1952) n. comb.

Fischthal & Kuntz (1964a) described a third similar species, *Paracryptogonimus orientalis* Fischthal & Kuntz, 1964, from a single flattened specimen from *L. fulviflamma* off the Philippines, distinguishing it from *Neoparacryptogonimus ovatus* on the sucker-ratio and oral spine length. Hafeezullah (1975) transferred it to *Neoparacryptogonimus*. Nahhas *et al.* (2003) suggested synonymizing *N. orientalis* with *N. ovatus* based on variation in the sucker-ratio of specimens of *N. ovatus*, but stated that the oral spine length should be investigated first. We collected this species from *Lutjanus* spp. from the Great Barrier Reef, observed slight intraspecific variation in oral

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spine length and agree with Nahhas *et al.* (2003); *N. orientalis* is a junior synonym of *Neometadena ovata* n. comb. *P. rostratus* Nagaty & Abdel-Aal, 1961, proposed by Nagaty & Abdel-Aal (1961) for a single specimen from the lethrinid *Lethrinus rostratus* (now *L. olivaceus*), also lacks spines; it resembles *N. ovata* n. comb., was considered a probable synonym of *Neoparacryptogonimus ovatus* by Manter (1963) and was formally synonymized by Nahhas *et al.* (2003).

Two other species have been combined with *Neoparacryptogonimus. Paracryptogonimus saccatus* Manter, 1963, proposed by Manter (1963) from an unknown fish off Fiji, was transferred to *Neoparacryptogonimus* by Hafeezullah (1975). Nahhas *et al.* (1998) described *N. sphericus* Nahhas, Sey & Nishimoto, 1998, from *Lutjanus coccineus* (now *L. gibbus*) and a batrachoidid, *Batrichthys* (now *Allenbatrachus) grunniens*, off the Kuwaiti coast of the Persian Gulf. They differ significantly from the concept of *Neometadena* and were transferred to *Retrovarium* by Miller & Cribb (2007a).

## Genus *Olmeca* Lamothe-Argumedo & Pineda-López, 1990

This monotypic genus was proposed for *O. laurae* Lamothe-Argumedo & Pineda-López, 1990 by Lamothe-Argumedo & Pineda-López (1990) from the centropomid fish *Centropomus parallelus* at Tabasco, Mexico. This species resembles *Tabascotrema verai* Lamothe-Argumedo & Pineda-López, 1990, described from a cichlid in the same locality in the same paper (Lamothe-Argumedo & Pineda-López, 1990). These two species share a broadly similar morphology, but differ in that the caeca of *T. verai* extend only to the level of the testes and the ovary of *T. verai* separates the testes rather than just overlapping the anterior testis. The host groups are also quite different. We tentatively recognize both genera.

## Genus *Palaeocryptogonimus* Szidat, 1954

*Palaeocryptogonimus* was proposed by Szidat (1954) for *P. claviformis* Szidat, 1954 from the siluriform fish *Rhinodoras dorbignyi* in Argentina. In his description and whole-mount figure, the ventral sucker appears to be covered by a muscular gonotyl, termed 'Szidat's gonotyl' by Yamaguti (1971). In the sagittal section figure, it appears to be only the tegument folding over the ventral sucker rather than an actual muscular gonotyl, so we do not recognize this structure as a gonotyl in the generic diagnosis. *P. claviformis* is morphologically similar to the only species of *Pseudocaecincola* Lamothe-Argumedo, Salgado-Maldonado & Pineda-López, 1991, *P. batallae* Lamothe-Argumedo, Salgado-Maldonado & Pineda-López, 1991, from the cichlid *Petenia splendida* in Mexico. These two species have a similar body-shape, oral sucker shape, prepharyngeal and oesophageal length, caeca that end slightly posterior to the testes, ventral sucker position (ventral to or slightly posterior to the intestinal bifurcation), testicular position, ovarian shape and position and vitelline distribution (extends from slightly posterior to slightly anterior to the ventral sucker). *P. claviformis* is larger than *Pseudocaecincola batallae*, and the uterus does not extend to the posterior extremity. Lamothe-Argumedo *et al.* (1991) described *P. batallae* as having a bilobed gonotyl, which, from the description and figure provided, appears to be a non-muscular folding of the tegument over the ventral sucker and not a strong character. Although the two species have different host families (Doradidae and Cichlidae), both are from fresh water and have only slight differences in morphology, which we interpret as intra- rather than intergeneric variation. Thus, we synonymize *Pseudocaecincola* with *Palaeocryptogonimus* and propose *Palaeocryptogonimus batallae* (Lamothe-Argumedo, Salgado-Maldonado & Pineda-López, 1991) n. comb.

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## Genus *Paraisocoelium* Ozaki, 1932

This monotypic genus was proposed by Ozaki (1932) for *P. exorchis* Ozaki, 1932 from *Uranoscopus japonicus* off Japan. It is characterized by the subterminal spineless oral sucker, elongate body, extracaecal testes, highly lobed ovary, uterus that does not extend posteriorly beyond the testes and vitelline follicles that do not extend posteriorly beyond the level of the testes. The most similar genus, *Isocoelium* (from the same host and locality), differs from *Paraisocoelium* in the distribution of the vitelline follicles (filling the majority of the space between the ovary and the anterior testis and not entering the forebody), and having elongate intercaecal testes at the posterior extremity. Shen (1989) described *P. platycephali* Shen, 1989 from a platycephalid, *Platycephalus indicus*, off China, but it differs sufficiently from *Paraisocoelium exorchis* to warrant the proposal of a new genus (see *Perlevilobus* below).

## Genus *Parspina* Pearse, 1920

This was proposed by Pearse (1920) for *P. bagre* Pearse, 1920 from the freshwater siluriform fish *Pimelodella metae* in Venezuela, but not assigned to a family. Szidat (1954) later proposed *Proneochasmus* Szidat, 1954 for *P. argentinensis* Szidat, 1954 from the freshwater siluriform *Pimelodus clarius* (now *Pimelodus blochii*) in Argentina, and assigned it to the Cryptogonimidae. Szidat (1954) did not discuss *Parspina* when comparing *Proneochasmus* with other genera. Sogandares-Bernal (1959a) recognized their similarities and synonymized *Proneochasmus* with *Parspina*. Yamaguti (1971) re-examined the holotype of *P. bagre*, which he described and figured as having a 'thin-walled cirrus pouch' enclosing the seminal vesicle, small pars prostatica and short ejaculatory duct. This thin membrane should not be considered a true cirrus-sac, but we mention it as a diagnostic character to highlight its presence and emphasize that further work is needed to fully characterize this structure.

## Genus *Perlevilobus* n. g.

This genus is proposed for *P. platycephali* (Shen, 1989) n. comb., originally described by Shen (1989) as *Paraisocoelium platycephali* Shen, 1989 from *Platycephalus indicus* off China (see *Paraisocoelium*). It differs from the type and only species of *Paraisocoelium, P. exorchis*, in having the ovary only slightly lobed to entire (not distinctly deeply lobed to follicular as in *P. exorchis*), the uterus extending well posterior to the testes, the testes not being distinctly extracaecal and the oral sucker being round to funnel-shaped. We have collected specimens of *P. platycephali* from *P. indicus* off the east coast of Australia, and they agree with the description of Shen (1989), who did not describe the oral sucker or the ovary shape, which we find varies from most often slightly lobed to rarely deeply lobed or apparently entire. Shen (1989) described the ovary as elliptical, but in his figure it appears slightly lobed. Most of our specimens have a slightly to distinctly funnel-shaped oral sucker, but occasionally it appears round. This species differs substantially enough from other cryptogonimid genera lacking oral spines, in both morphology and host ecology, to warrant a separate genus. The name *Perlevilobus* is derived from the Latin *perlevis* meaning very slight and *lobus* meaning lobe. It is proposed in recognition of the slightly lobed or entire ovary of species in the genus and is to be treated as masculine. Voucher specimens were deposited in the Queensland Museum, Brisbane, Australia under the accession numbers G227687–G227691.

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## Genus *Polycryptocylix* Lamothe-Argumedo, 1970

This was proposed by Lamothe-Argumedo (1970) for *P. leonilae* Lamothe-Argumedo, 1970 from *Lutjanus guttatus* off Oaxaca, Mexico. *Paracryptogonimus muscularis* Yamaguti, 1970, described by Yamaguti (1970) from the lutjanid *Aphareus furca* off Hawaii, is the only species of *Paracryptogonimus* (now *Siphoderina*) with multiple gonotyls. It resembles *Polycryptocylix leonilae*, but differs in having lobed rather than sucker-like (as in *P. leonilae*) gonotyls anterior to the ventral sucker. The host affinity and general morphology suggest these two species are related and we here propose *Polycryptocylix muscularis* (Yamaguti, 1970) n. comb.

## Genus *Pseudallacanthochasmus* Velasquez, 1961

*Pseudallacanthochasmus* was proposed by Velasquez (1961) for *P. grandispinus* Velasquez, 1961 from an unidentified species of *Lutjanus* off the Philippines. It was subsequently reported from the haemulid *Pomadasys hasta* by Hafeezullah & Siddiqi (1970a), and from *Hoplias malabaricus* by Fortes *et al*. (1996) (the latter record is not credible because the host is a freshwater characiform from Brazil). *Pseudallacanthochasmus plectorhynchi* Mamaev, 1970 was described by Mamaev (1970) based on a distorted specimen from the haemulid *Plectorhinchus cinctus* and differs from *Pseudallacanthochasmus grandispinus* in having symmetrical testes and an intertesticular ovary. This species was transferred to *Beluesca* Miller & Cribb, 2007 by Miller & Cribb (2007c). *Pseudoacanthostomum magnivesiculum* Gaevskaya & Aljoshkina, 1985 was described by Gaevskaya & Aljoshkina (1985) from the sparid *Dentex canariensis* in the eastern Atlantic. The type and only other species of *Pseudoacanthostomum* Caballero, Bravo-Hollis & Grocott, 1953 has a uroproct and is found in siluriforms, whereas *P. magnivesiculum* has blind caeca and is found in sparids. *P. magnivesiculum* agrees morphologically with the concept of *Pseudallacanthochasmus*, and the sparid host is more closely related to lutjanids than siluriforms, so we propose *Pseudallacanthochasmus magnivesiculum* (Gaevskaya & Aljoshkina, 1985) n. comb.

## Genus *Pseudocryptogonimus* Yamaguti, 1958 *nec* Khan & Bilqees, 1990

This monotypic genus was proposed by Yamaguti (1958b) for *Cryptogonimus cirrhiti* Bravo-Hollis, 1953, from a marine cirrhitid, *Cirrhitus rivulatus* off the Pacific coast of Mexico. *Pseudocryptogonimus* was also proposed as new by Khan & Bilqees (1990) for *P. pakistanensis* Khan & Bilqees, 1990 from a single specimen from *Labeo rohita* (this host is at best surprising because it is a herbivorous cypriniform). The description and accompanying figure by Khan & Bilqees (1990) are inadequate so we consider *Pseudocryptogonimus pakistanensis* Khan & Bilqees, 1990 a species *inquirenda*.

## Genus *Siphoderina* Manter, 1934

*Siphoderina* is the largest genus in the family, with over 30 species. It was proposed by Manter (1934) for *S. brotulae* Manter, 1934 from *Brotula barbata* (Ophidiidae) off Florida, USA and originally diagnosed as lacking oral spines. It was transferred to *Metadena* by Manter (1947), but Durio & Manter (1969) restudied serial sections of a paratype of *S. brotulae* and discovered that oral spines were present, although lost in the holotype. They reinstated *Siphoderina*, amended the generic

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diagnosis to include oral spines and described a new species, *S. paracatalae* Durio & Manter, 1969, from an unknown species of *Lutjanus*. Given that *Siphoderina* does possess oral spines, the only difference between it and *Paracryptogonimus* is the supposed presence of the non-muscular gonotyl in the former. We examined the holotypes and some paratypes of *S. brotulae* (holotype USNPC 8760, paratype HWML 406) and *S. paracatalae* (holotype USNPC 63324, paratypes HWML 625 and 2108) and determined that the 'gonotyl' is actually just a small, non-muscular fold of tegument over the ventral sucker, possibly an artefact of flattening the specimen; it is not a convincing character to distinguish *Siphoderina*. There are no substantial morphological characters that separate these genera and we synonymize them. *Paracryptogonimus* was proposed in the same year as *Siphoderina* by Yamaguti (1934) for *P. acanthostomus* Yamaguti, 1934 from *Lutjanus vitta* near Japan. The month of publication of Yamaguti's (1934) work could not be determined, but a list of monographs published by the Carnegie Institution of Washington lists Manter's (1934) work as being issued on 16 January 1934. It is doubtful that Yamaguti's publication was issued before then, so, according to the International Code of Zoological Nomenclature (1999), *Siphoderina* is the senior name and is recognized here as valid. *Lappogonimus* Oshmarin, Mamaev & Parukhin, 1961, which includes *L. echinostomus* Oshmarin, Mamaev & Parukhin, 1961 and *L. morosovi* Parukhin, 1965, both with distinctly lobed testes, was synonymized with *Paracryptogonimus* by Yamaguti (1971). We tentatively accept this view, as this could be considered as intra- rather than intergeneric variation. We transfer the species of *Paracryptogonimus* to *Siphoderina* as *S. acanthostomus* (Yamaguti, 1934) n. comb., *S. aloysiae* (Stossich, 1885) n. comb., *S. americanus* (Manter, 1940) n. comb., *S. apharei* (Yamaguti, 1970) n. comb., *S. brevicaeca* (Nahhas, Tran & Nguyen, 2003) n. comb., *S. catalae* (Durio & Manter, 1969) n. comb., *S. centropomi* (Siddiqi & Cable, 1960) n. comb., *S. echinostomus* (Oshmarin, Mamaev & Parukhin, 1961) n. comb., *S. elongata* (Gu & Shen, 1979) n. comb., *S. ghanensis* (Fischthal & Thomas, 1968) n. comb., *S. hirastricta* (Manter, 1963) n. comb., *S. leilae* (Nagaty, 1957) n. comb., *S. longitestis* (Durio & Manter, 1969) n. comb., *S. lutiani* (Wang, 1991) n. comb. (we only tentatively recognize this species, as it was described as having an entire ovary), *S. macrospinus* (Caballero, Hidalgo & Grocott, 1956) n. comb., *S. manilensis* (Velasquez, 1961) n. comb., *S. mexicanus* (Bravo-Hollis, 1953) n. comb., *S. morosovi* (Parukhin, 1965) n. comb., *S. neoamericanus* (Siddiqi & Cable, 1960) n. comb., *S. onaga* (Yamaguti, 1970) n. comb., *S. provitellosus* (Durio & Manter, 1969) n. comb., *S. ramadani* (Nahhas, Sey & Nishimoto, 1998) n. comb., *S. sootai* (Hafeezullah, 1975) n. comb., *S. testitactus* (Durio & Manter, 1969) n. comb., *S. ulaula* (Yamaguti, 1970) n. comb., *S. xiamenensis* (Liu, 1996) n. comb. and *S. yamagutii* (Lamothe-Argumedo, 1969) n. comb.

Gu & Shen (1979) described *Siphoderina asiatica* Gu & Shen, 1979 from two species of *Lutjanus* off China.

*Siphoderina hardayali* Pandey & Tiwari, 1982 proposed by Pandey & Tiwari (1982) from an unknown host from a fish market was inadequately described and probably belongs to the Tandanicolidae. We exclude it as a species *incertae sedis*.

With the inclusion of the one species transferred to *Siphoderina* from *Allacanthochasmus* (see above), four from *Neochasmus* (see above), and species of *Paracryptogonimus*, the number of species included here in *Siphoderina* is 35. More than 70% of them infect marine lutjanids.

## Genus *Stegopa* Linton, 1910

This was proposed by Linton (1910) for *S. globosa* Linton, 1910 from *Neomaenis* (now *Lutjanus*) *griseus* off Florida, USA. Manter (1947) redescribed it based on specimens from the same host and

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locality and transferred it to *Metadena*. Yamaguti (1971) proposed *Lopastoma* for *Metadena lopastoma* Winter, 1958 from the lutjanid *Hoplopagrus guentherii* off the Pacific coast of Mexico (Winter, 1958). These two species are remarkably similar. Both have a squat body, a relatively large oral sucker occupying over half of the body-width, vitelline follicles mainly in the forebody, the ovary at the level of the testes and sometimes extending slightly posterior to them, and a uterus occupying nearly all available body-space from the posterior extremity to the oral sucker. Yamaguti (1971) did not discuss the similarities between them and did not mention the morphologically similar *M. magdalenae* Arai, 1963, proposed by Arai (1963) for specimens from *Paralichthys californicus* off the Pacific coast of Mexico, which shares the characters of the two above species. These three species merit a separate genus. We recognize *Stegopa* with *S. globosa* Linton, 1910 as the type-species, and propose *S. lopastoma* (Winter, 1958) n. comb. and *S. magdalenae* (Arai, 1963) n. comb.

## Genus *Timoniella* Rebecq, 1960

*Timoniella* was proposed by Rebecq (1960) for *T. atherinae* Rebecq, 1960 based on metacercariae from *Atherina mochon* (now *A. boyeri*) in the Mediterranean. Maillard (1974) described its life-cycle and discovered, when feeding metacercariae to *Morone* (now *Dicentrarchus*) *labrax* (Moronidae), that they developed into *Acanthostomum praeterita* Looss, 1901. He proposed the combination *T. praeteritum* (Looss, 1901) Maillard, 1974, now the senior synonym of the type-species of the genus. Brooks (1980) reviewed *Timoniella*, described a new species, *T. incognita* Brooks, 1980, and transferred *A. unami* Peláez & Cruz, 1953, *A. loossi* Pérez Vigueras, 1957 and *A. imbutiformis* (Molin, 1859) to this genus. Two other species are *T. absita* Blair, Brooks, Purdie & Melville, 1988 and *T. ostrowskiae* Brooks & Holcman, 1993. *A. balthicum* Reimer, Hildebrand, Scharberth & Walter, 1996 was described by Reimer *et al*. (1996) from the syngnathid *Syngnathus typhle* in the Baltic Sea and compared with *A*. (now *Timoniella) imbutiformis* (Molin, 1859), which has been reported from the Adriatic, Black and Mediterranean Seas. *A. balthicum* has the distinctly pre-ovarian seminal receptacle characteristic of *Timoniella*, so we transfer it to *Timoniella* as *T. balthicum* (Reimer, Hildebrand, Scharberth & Walter, 1996) n. comb., bringing the number of species in the genus to eight.

## Genera *inquirenda*

## Genus *Megamonostomella* Rahemo & Al-Naemi, 1998

*Megamonostomella* Rahemo & Al-Naemi, 1998 is invalid as no species were ascribed to it. The same applies to the Megamonostomatinae Rahemo & Al-Naemi, 1998.

## Genus *Mahrosa* Nagaty & Abdel-Aal, 1961

Proposed by Nagaty & Abdel-Aal (1961) for *M. sargusi* Nagaty & Abdel-Aal, 1961, based on a single specimen from *Sargus* (now *Diplodus*) *noct* (Sparidae), both genus and species were inadequately described and illustrated. Yamaguti (1971) synonymized it with *Pseudosiphoderoides*, but we consider it a genus *inquirendum*.

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## Genus *Paracryptogonimoides* Nagaty & Abdel-Aal, 1961

This was proposed by Nagaty & Abdel-Aal (1961) for *P. nocti* Nagaty & Abdel-Aal, 1961 from a single specimen from *Sargus* (now *Diplodus) noct* (Sparidae) in the Red Sea. The description is inadequate.

## Genus *Pseudoanisocoelium* Gupta & Tandon, 1984

This was proposed by Gupta & Tandon (1984) for *P. dorabi* Gupta & Tandon, 1984 from three specimens from the chirocentrid *Chirocentrus dorab* off India. The description is inadequate.

## Genus *Pseudocryptogonimus* Khan & Bilqees 1990 *nec* Yamaguti, 1958

See discussion above on *Pseudocryptogonimus* Yamaguti, 1958. The description of *P. pakistanensis* Khan & Bilqees, 1990 is inadequate.

## Genera and species *incertae sedis*

## Genus *Tubanguia* Srivastava, 1935

This monotypic genus was proposed by Srivastava (1935b), without a diagnosis, for *Haplorchis anguillarum* Tubangui, 1933 from *Anguilla mauritiana* (now *A. marmorata*) in the Philippines, which differed from *Haplorchis* Looss, 1899 mainly in having two rather than a single testis. A diagnosis was first provided by Yamaguti (1958b), who placed *Tubanguia* along with the heterophyid genus *Haplorchoides* Chen, 1949 in a new subfamily, the Tubanguiinae Yamaguti, 1958, within the Cryptogonimidae. *T. anguillarum* was described as having a distinctly reduced or absent ventral sucker similar to that of *Haplorchoides* Chen, 1949 (now considered a heterophyid, see Pearson, Chapter 5, this volume), and the extent of the excretory vesicle is unknown. Although this species may be a heterophyid, we consider the genus and species as *incertae sedis*, pending a redescription of this species and a critical review accenting the ventrogenital complex.

## *Metadena bagarii* Moravec & Sey, 1989

Moravec & Sey (1989a) proposed this for a single specimen recovered from the freshwater siluriform *Bagarius bagarius* in Vietnam. They tentatively placed it in *Metadena* and discussed its relationship to *Exorchis*, also found in freshwater siluriforms from Asia. We agree that its position needs to be verified and, rather than recognizing it in *Metadena*, we consider it a species *incertae sedis*.

## *Pseudosiphoderoides xishaensis* Gu & Shen, 1983

See discussion in section on *Metadena* on this species.

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## *Lopastoma markevichi* Kurochkin & Korotaeva, 1982

Kurochkin & Korotaeva (1982) described this from the cheilodactylid *Nemadactylus valenciennesi* off southern Australia. We collected it from *Dactylophora nigricans*, also a cheilodactylid, which feeds primarily on benthic invertebrates, off Western Australia. The large cirrus-sac and the genital pore on the lateral margin of the body suggest that this species is a zoogonid, not a cryptogonimid.

## Family Cryptogonimidae Ward, 1917

(Syns Acanthocollaritrematidae Travassos, Freitas & Bührnheim, 1965; Acanthostomidae Poche, 1926; Isocoelidae Pan, 1984; Siphoderidae Linton, 1910[2])

**Diagnosis:** Body spherical to extremely elongate, often oval. Cercarial eye-spot pigment usually present. Tegument with small to minute spines or scale-like spines, rarely unspined. Oral sucker nearly round to distinctly funnel-shaped, occasionally with distinct lobes on margin, usually opening nearly terminally, occasionally ventroterminally; circumoral spines present or absent. Ventral sucker at mid-body or in anterior half of body, rarely in posterior half of body, unspecialized and round, usually smaller than oral sucker, rarely larger, often embedded in ventrogenital sac. Prepharynx very short to long. Pharynx present, usually well developed, unspecialized. Oesophagus very short to long. Intestinal bifurcation usually in forebody, rarely posterior to ventral sucker. Caeca two, rarely atrophied or single, usually blind, long or distinctly short, rarely form cyclocoel, uroproct, open via separate ani at posterior extremity or one caecum opens at anus at posterior extremity and one caecum blind. Testes usually in hindbody, rarely entirely in forebody or overlapping into forebody, usually two, occasionally single, multiple or follicular, rarely distinctly elongate, symmetrical to strongly oblique or distinctly tandem. Cirrus and cirrus-sac absent. Seminal vesicle present, may be tubular, saccular or tubulosaccular, occasionally distinctly bipartite, unites with uterus usually dorsal to ventral sucker to form hermaphroditic duct; pars prostatica often inconspicuous. Gonotyl present or absent, single, or occasionally multiple, may be present as distinct muscular sucker-like or lobed structure immediately anterior to ventral sucker, rarely posterior to common genital pore, rarely armed with spines, occasionally distinct non-muscular lobes of tegument. Common genital pore medial, immediately anterior to ventral sucker. Ovary in hindbody, usually anterior to testes, occasionally at level of testes, rarely entirely posterior to testes, entire to distinctly trilobed to highly lobed. Laurer's canal probably always present. Canalicular seminal receptacle present. Uterus with many coils, usually entirely in hindbody, occasionally developed significantly in forebody. Eggs relatively small, lightly to darkly pigmented, probably typically operculate, rarely with single distinct spine or filament. Vitellarium always follicular; follicles usually distinctly restricted, rarely extensive throughout body. Excretory vesicle Y-shaped; arms usually extend well into forebody, rarely terminate posterior to or at level of ventral sucker; pore terminal. In intestine (rarely body-cavity or gall-bladder) of marine and freshwater fishes and reptiles, rarely amphibians, rarely progenetic in second intermediate hosts; cosmopolitan. Type-genus *Cryptogonimus* Osborn, 1903.

[2] Article 35.5 of the International Code of Zoological Nomenclature (1999) gives precedence to Cryptogonimidae Ward, 1917 over Siphoderidae Linton, 1910 as the valid family name because of prevailing usage.

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## Key to genera

**1a. Circumoral crown of spines absent ..... 2.**
**1b. Circumoral crown of spines present ..... 40.**

**2a. One testis only ..... *Retrobulla* Cribb, 1985. (Fig. 4.1)**
**Diagnosis:** Body elongate; length:width ratio *c.* 5. Oral sucker slightly wider than long, without enlarged oral spines, opens nearly terminally. Ventral sucker unspecialized, embedded deeply in ventrogenital sac. Sucker-width ratio[3] *c.* 2. Forebody *c.* 33% of body-length. Prepharynx short. Oesophagus distinctly longer than prepharynx. Intestinal bifurcation in mid-forebody. Caeca blind, short, end just posterior to ventral sucker, near mid-body. Testis single, with two sperm ducts, in mid-hindbody. Seminal vesicle tubulosaccular. Gonotyl a simple lobe arising from posterior wall of ventrogenital sac. Ovary entire, just posterior to mid-body, overlapping testis. Uterus in hindbody, extends close to posterior extremity. Vitelline follicles in two lateral groups in region between ventral sucker and anterior margin of testis. Arms of excretory vesicle extend to midway between ventral sucker and pharynx. In freshwater fishes (Terapontidae); Australia. Type- and only species *R. angelae* Cribb, 1985.

**2b. Two or more testes ..... 3.**

**3a. More than two testes ..... 4.**
**3b. Two testes ..... 6.**

**4a. Ventral sucker larger than oral sucker; testes 8–50 small follicles in posterior part of body; ovary entire to slightly lobed ..... *Polyorchitrema* Srivastava, 1939. (Fig. 4.2)**
**Diagnosis:** Body oval, length:width ratio *c.* 2.5–3. Tegument lacks spines. Oral sucker nearly round, without enlarged oral spines, opens subterminally. Ventral sucker unspecialized, larger than oral sucker, embedded in ventrogenital sac. Sucker-width ratio *c.* 0.4–0.8. Forebody *c.* 25% of body-length. Prepharynx very short. Oesophagus very short. Intestinal bifurcation in posterior forebody. Caeca blind, end close to posterior extremity. Testes 8–50 follicles in posterior hindbody. Seminal vesicle tubulosaccular. Gonotyl may be present immediately anterior to ventral sucker. Ovary entire to slightly lobed, immediately anterior to testes. Uterus between testes and ventral sucker. Vitelline follicles in two lateral groups, in hindbody, from posterior extremity to slightly posterior to ventral sucker. Arms of excretory vesicle reach level of pharynx. In marine and freshwater fishes (Schilbeidae, Sparidae); India. Type-species *P. piscicola* Srivastava, 1939.

**4b. Ventral sucker smaller than oral sucker; testes usually nine, not consisting of numerous small follicles; ovary deeply lobed ..... 5.**

**5a. Uterus does not extend posteriorly beyond anteriormost testes; vitelline follicles from pharynx to posterior extremity ..... *Iheringtrema* Travassos, 1947. (Fig. 4.3)**
**Diagnosis:** Body elongate-oval; length:width ratio *c.* 3. Oral sucker almost round, without enlarged oral spines, opens subterminally. Ventral sucker unspecialized, not obviously embedded in ventrogenital sac. Sucker-width ratio *c.* 2–2.5. Forebody *c.* 20% of body-length. Prepharynx very short. Oesophagus very short. Intestinal bifurcation in mid-forebody. Caeca blind, end close

[3] Sucker-width ratios in the diagnoses throughout this chapter refer to the oral sucker width divided by the ventral sucker width.

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to posterior extremity. Testes nine, irregular, in posterior hindbody. Seminal vesicle tubular. Gonotyl absent. Ovary deeply lobed, median, immediately anterior to testes. Uterus between gonads and ventral sucker. Vitelline follicles in two lateral groups, confluent posteriorly, from posterior extremity to pharynx. Excretory vesicle extent not known. In freshwater fishes (Pimelodidae); Brazil. Type- and only species *I. iheringi* Travassos, 1947.

**5b. Uterus extends posteriorly beyond testes; vitelline follicles in anterior hindbody ..... ..... *Siphodera* Linton, 1910. (Fig. 4.4)**

**Diagnosis:** Body oval to elongate-oval; length:width ratio *c.* 2–3.5. Oral sucker nearly round, without enlarged oral spines, opens almost terminally. Ventral sucker unspecialized, usually smaller, rarely larger than oral sucker, embedded in ventrogenital sac. Sucker-width ratio *c.* 1–2.5. Forebody *c.* 20–33% of body-length. Prepharynx short. Oesophagus short. Intestinal bifurcation in mid-forebody. Caeca blind, end close to posterior extremity. Testes usually nine, in two lateral groups or one large group in hindbody. Seminal vesicle tubulosaccular. Gonotyl absent. Ovary deeply lobed, immediately anterior to testes. Uterus in hindbody, extends close to posterior extremity. Vitelline follicles in two lateral groups, may extend from level of testes into forebody.

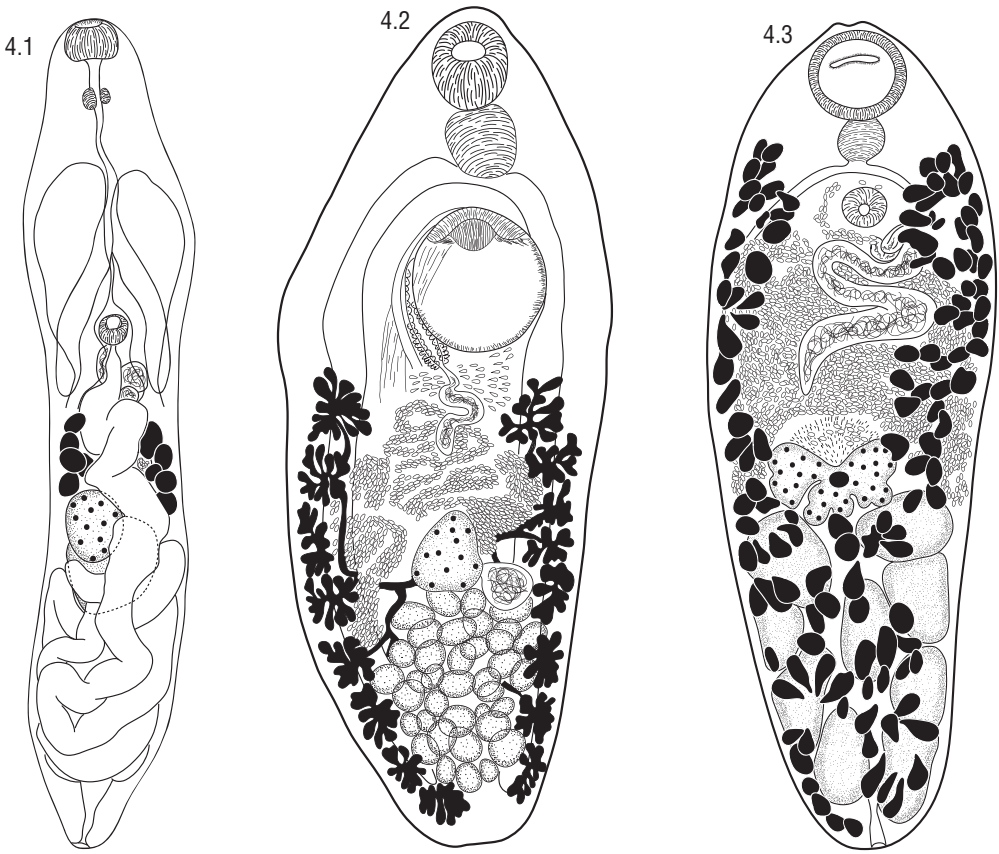



**Fig. 4.1.** *Retrobulla angelae* Cribb, 1985. After Cribb (1985).
**Fig. 4.2.** *Polyorchitrema piscicola* Srivastava, 1939. After Yamaguti (1971).
**Fig. 4.3.** *Iheringtrema iheringi* Travassos, 1947. After Yamaguti (1971).

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Arms of excretory vesicle reach level of pharynx. In marine fishes (many families; primarily Lutjanidae); Atlantic, Indian and Pacific Oceans. Type-species *S. vinaledwardsii* (Linton, 1901) Linton, 1910.

**6a. Caeca open at separate ani or via uroproct at posterior extremity ..... 7.**
**6b. Caeca blind ..... 8.**

7a. **Oral sucker infundibuliform with six muscular lobes; body exceptionally elongate; caeca open via uroproct at posterior extremity ..... *Mitotrema* Manter, 1963. (Fig. 4.5)**
**Diagnosis:** Body exceptionally elongate; length:width ratio *c.* > 20. Oral sucker infundibuliform with six muscular lobes, two ventral, two lateral and two dorsal, opens terminally. Sucker-width ratio *c.* 1.5–2.5. Forebody *c.* < 10% of body-length. Prepharynx very long. Oesophagus very short. Intestinal bifurcation dorsal to ventral sucker. Caeca open via uroproct at posterior extremity. Testes two, tandem, separated, close to posterior extremity. Seminal vesicle tubular. Gonotyl absent. Ovary entire, anterior to and well separated from anterior testis. Uterus in hindbody, extends to just short of posterior extremity. Arms of excretory vesicle extend to between pharynx and oral sucker. Vitelline follicles in two lateral groups, form

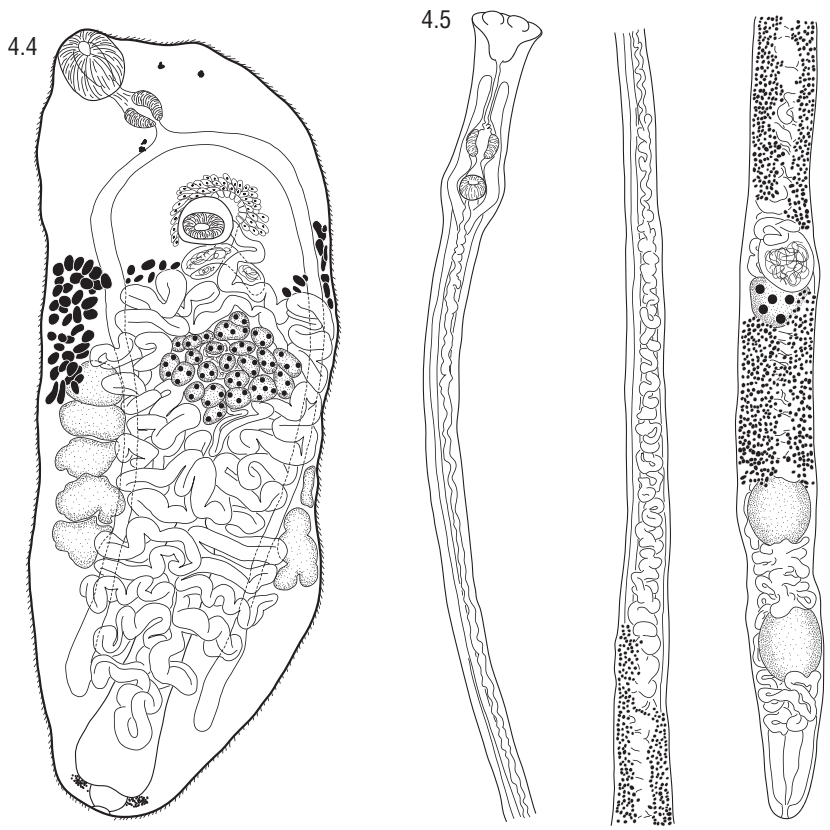



**Fig. 4.4.** *Siphodera vinaledwardsii* (Linton, 1901) Linton, 1910. After Yamaguti (1971).
**Fig. 4.5.** *Mitotrema anthostomatum* Manter, 1963. After Cribb *et al.* (1996).

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bands anterior to ovary and between ovary and anterior testis, sometimes confluent in midline. In marine fishes (Serranidae); Pacific Ocean. Type- and only species *M. anthostomatum* Manter, 1963.

**7b. Oral sucker margin entire, surrounded by large collar; body not exceptionally elongate; caeca open via separate ani at posterior extremity ..... *Orientodiploproctodaeum* Bhutta & Khan, 1970. (Fig. 4.6)**

(Syns *Anterodiscus* Bilqees, 1974; *Cryptocollaritrema* Madhavi, 1974; *Folliculovarium* Singh & Sinha, 1981; *Harutrema* Mehra & Kharoo, 1975; *Multiovarium* Bilqees, 1974)

**Diagnosis:** Body oval to elongate-oval; length:width ratio *c.* 2–3. Oral sucker with entire margin, surrounded by large collar, slightly wider than long to almost round, without enlarged oral spines, opens terminally. Ventral sucker unspecialized, embedded in ventrogenital sac. Sucker-width ratio *c.* 2–3. Forebody *c.* 33% of body-length. Prepharynx very short. Oesophagus very short. Intestinal bifurcation immediately posterior to pharynx. Caeca open via separate ani at posterior extremity. Testes two, intercaecal, oblique, in mid-hindbody. Seminal vesicle tubular. Gonotyl absent or present as muscular lobe-like structure immediately posterior to ventral sucker. Ovary deeply lobed, between ventral sucker and testes. Uterus in hindbody; coils mainly intercaecal, from close to posterior extremity to ventral sucker. Vitelline follicles in two lateral groups, extracaecal, from close to posterior extremity to slightly anterior to ventral sucker. Arms of excretory vesicle almost reach pharynx. In marine and euryhaline fishes (Lutjanidae, Sciaenidae and Scombridae); Indian Ocean and adjacent rivers. Type-species *O. diacanthi* Bhutta & Khan, 1970.

**8a. Multiple gonotyls on ventral surface between oral and ventral suckers ..... 9.**
**8b. Gonotyl single or absent ..... 10.**

**9a. Vitelline follicles restricted to hindbody; oral sucker unspecialized ..... *Oligogonotylus* Watson, 1976. (Fig. 4.7)**

**Diagnosis:** Body oval to elongate-oval; length:width ratio *c.* 2.5–3.5. Oral sucker almost round, without enlarged oral spines, opens subterminally. Ventral sucker unspecialized, not obviously embedded in ventrogenital sac. Sucker-width ratio *c.* 1–1.5. Forebody *c.* 30–40% of body-length. Prepharynx short. Oesophagus short. Intestinal bifurcation immediately anterior to ventral sucker. Caeca blind, end close to posterior extremity. Testes two, tandem, contiguous, in mid- to posterior hindbody. Seminal vesicle tubulosaccular. Multiple gonotyls (*c.* 5–8) present as sucker-like muscular pads, from immediately anterior to ventral sucker to level of pharynx. Ovary deeply lobed, between ventral sucker and anterior testis. Uterus in hindbody, extends close to posterior extremity. Vitelline follicles in two lateral groups, from posterior testis to slightly anterior to ventral sucker. Arms of excretory vesicle almost reach pharynx. In freshwater fishes (Cichlidae, Characidae); Mexico and Central America. Type- and only species *O. manteri* Watson, 1976.

**9b. Vitelline follicles mainly or entirely in forebody; oral sucker funnel-shaped ..... *Multigonotylus* Premvati, 1967. (Fig. 4.8)**

**Diagnosis:** Body elongate; length:width ratio *c.* 6. Oral sucker funnel-shaped, wider than long, without enlarged oral spines, opens nearly terminally. Ventral sucker unspecialized, embedded in ventrogenital sac. Sucker-width ratio *c.* 3. Forebody *c.* 50% of body-length. Prepharynx short.

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Oesophagus short. Intestinal bifurcation in anterior half of forebody. Caeca blind, end posteriorly to testes. Testes two, strongly oblique to nearly tandem, in mid-hindbody. Seminal vesicle saccular, tripartite. Multiple gonotyls present as transverse muscular bands immediately anterior to ventral sucker to immediately posterior to intestinal bifurcation. Ovary tri- to deeply lobed, in mid-hindbody, slightly anterior to testes or overlapping. Uterus in hindbody, extends close to posterior extremity. Vitelline follicles in two lateral groups, between ventral sucker and pharynx. Arms of excretory vesicle reach pharynx. In freshwater fishes (Centrarchidae); North America. Type- and only species *M. micropteri* Premvati, 1967.

**10a. Body squat, almost round; uterus extensive in forebody ..... 11.**
**10b. Body oval to elongate; uterus not extensive in forebody ..... 12.**

**11a. Oral sucker relatively large, > 50% of body-width; vitelline follicles form transverse band in forebody or at level of ventral sucker; ovary between or slightly posterior to testes; testes reach intercaecally ..... *Stegopa* Linton, 1910. (Fig. 4.9)**
(Syn. *Lopastoma* Yamaguti, 1971)

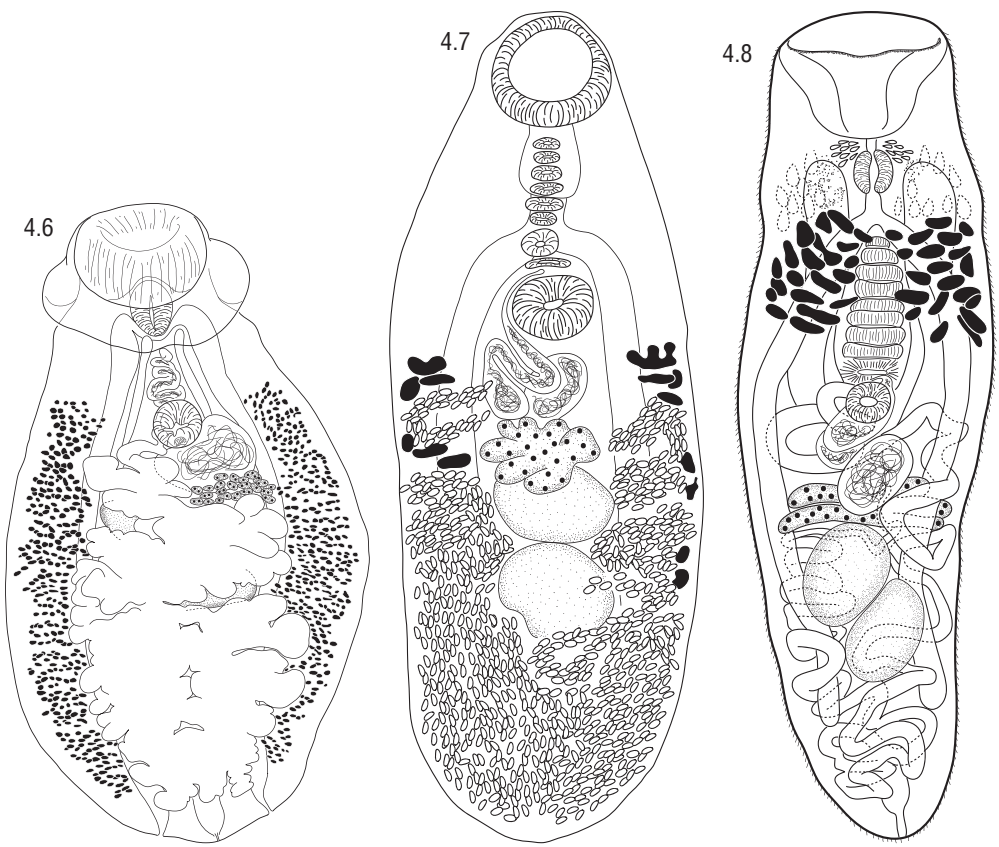



**Fig. 4.6.** *Orientodiploproctodaeum diacanthi* Bhutta & Khan, 1970. After Bray (1987c).
**Fig. 4.7.** *Oligogonotylus manteri* Watson, 1976. After Watson (1976).
**Fig. 4.8.** *Multigonotylus micropteri* Premvati, 1967. After Yamaguti (1971).

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**Diagnosis:** Body squat, almost round; length:width ratio *c.* 1–1.3. Oral sucker relatively large, occupies almost full body-width, much wider than long. Ventral sucker unspecialized, not obviously embedded in ventrogenital sac. Sucker-width ratio *c.* 3–6. Forebody *c.* 25–50% of body-length. Prepharynx very short. Oesophagus very short. Intestinal bifurcation immediately anterior to or dorsal to ventral sucker. Caeca blind, end close to posterior extremity. Testes two, symmetrical, posterior to and overlapping ventral sucker. Seminal vesicle saccular. Gonotyl absent. Ovary deeply lobed, an almost transverse band at level of testes or slightly posterior. Uterine coils extend from posterior extremity to well into forebody to level of oral sucker. Vitelline follicles form almost complete transverse band across body immediately anterior to or at level of ventral sucker. Excretory vesicle extent unknown. In marine fishes (Lutjanidae, Haemulidae, Paralichthyidae); eastern Pacific and western Atlantic. Type-species *S. globosa* Linton, 1910.

**11b. Oral sucker < 50% of body-width; vitelline follicles extend from posterior extremity to ventral sucker; ovary forms non-compact follicular band mainly posterior to testes; testes distinctly extracaecal ..... *Allometadena* Madhavi, 1976.[4] (Fig. 4.10)**

**Diagnosis:** Body squat, may be wider than long; length:width ratio *c.* 1. Oral sucker slightly wider than long, without enlarged oral spines, opening subterminally. Ventral sucker unspecialized, not obviously embedded in ventrogenital sac. Sucker-width ratio *c.* 3. Forebody *c.* 50% of body-length. Prepharynx very short. Oesophagus very short. Intestinal bifurcation immediately posterior to pharynx. Caeca blind, end close to posterior extremity. Testes two, symmetrical, lateral to caeca in anterior hindbody, may extend just into forebody. Seminal vesicle tubulosaccular, partly in forebody. Gonotyl absent. Ovary follicular, in band across mid-hindbody, extends posterior to testes. Uterus extensive in fore- and hindbody. Vitelline follicles distributed erratically across hindbody and extend between posterior extremity and posterior forebody close to ventral sucker. Excretory vesicle extent not known. In marine fishes (Lutjanidae); Indian Ocean. Type- and only species *A. rotundum* Madhavi, 1976.

**12a. Gonotyl protruding, stalk-like with crown of spines ..... ..... *Gonacanthella* Sogandares-Bernal, 1959. (Fig. 4.11)**

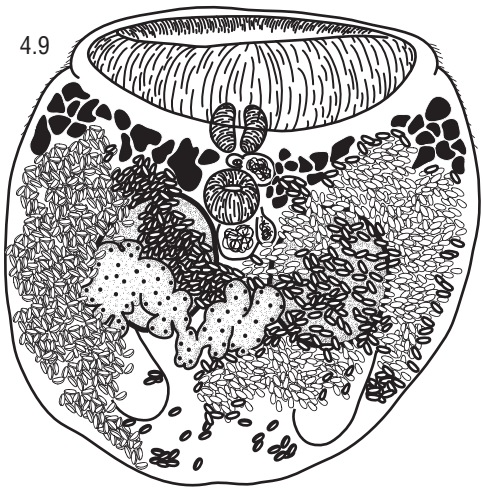
**Diagnosis:** Body oval; length:width ratio *c.* 1.5. Oral sucker almost round, without enlarged oral spines, opens subterminally. Ventral sucker unspecialized, embedded in ventrogenital sac. Sucker-width ratio *c.* 3. Forebody *c.* 33% of body-length. Prepharynx very short. Oesophagus longer than prepharynx. Intestinal bifurcation immediately anterior to ventral sucker. Caeca blind, end subterminally. Testes two, symmetrical, in mid-hindbody. Seminal vesicle tubular, loops into forebody. Gonotyl a protruding stalk-like structure immediately anterior or ventral to ventral sucker, with crown of spines up to 16 µm long. Ovary entire (?), between testes. Uterus in hindbody, extends close to posterior extremity. Vitelline follicles in two groups, nearly confluent in midline, between gonads and ventral sucker. Excretory vesicle extent unknown. In marine fishes (Lutjanidae); Western Atlantic. Type- and only species *G. lutjani* Sogandares-Bernal, 1959.

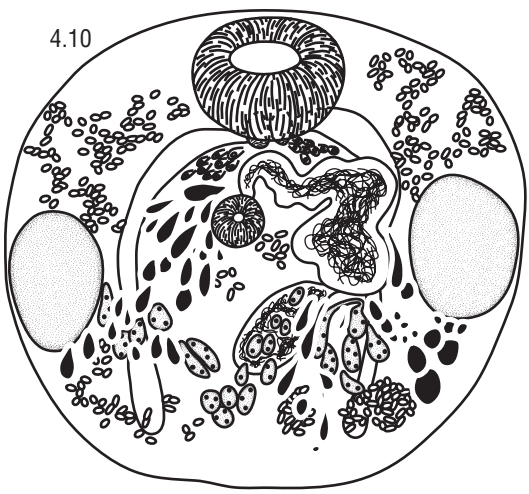
**12b. Gonotyl absent or not protruding and stalk-like with crown of spines ..... 13.**

**13a. Ovary entire ..... 14.**
**13b. Ovary with slight or deep lobes ..... 15.**

[4] See Addendum.

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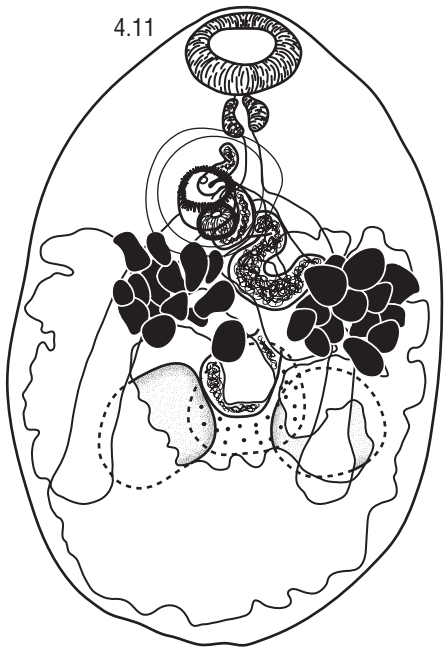




**Fig. 4.9.** *Stegopa lopastoma* (Winter, 1958) n. comb. After Yamaguti (1971).
**Fig. 4.10.** *Allometadena rotundum* Madhavi, 1976. After Madhavi (1976).
**Fig. 4.11.** *Gonacanthella lutjani* Sogandares-Bernal, 1959. Holotype USNPC 38873. Original.

**14a. Testes strongly oblique to tandem; oral sucker funnel- or cup-shaped; vitelline follicles between gonads and ventral sucker; in marine fishes ..... ..... *Claribulla* Overstreet, 1969. (Fig. 4.12)**

**Diagnosis:** Body elongate with distinct constriction immediately posterior to oral sucker; length: width ratio *c*. 6. Oral sucker funnel- or cup-shaped, without enlarged oral spines, opens almost terminally. Ventral sucker unspecialized, deeply embedded in ventrogenital sac. Sucker-width ratio *c*. 2.5. Forebody *c*. 40% of body-length. Prepharynx very short. Oesophagus short. Intestinal bifurcation in anterior forebody. Caeca blind, end posteriorly to testes. Testes two, strongly oblique to tandem, in mid-hindbody. Seminal vesicle tubulosaccular, in forebody. Gonotyl absent. Ovary entire, immediately anterosinistral to anterior testis. Uterus in hindbody, extends close to posterior extremity. Vitelline follicles in two restricted lateral groups between ventral sucker and gonads. Arms of excretory vesicle reach pharynx. In marine fishes (Albulidae, Sphyraenidae); Florida. Type- and only species *C. longula* Overstreet, 1969.

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**14b. Testes symmetrical to slightly oblique; oral sucker almost round; vitelline follicles extend from well anterior to ovary to level of testes; in freshwater fishes ..... ..... *Neocladocystis* Manter & Pritchard, 1969. (Fig. 4.13)**

**Diagnosis:** Body oval; length:width ratio *c.* 1–2. Oral sucker almost round, without enlarged oral spines, opens subterminally. Ventral sucker unspecialized, not obviously embedded in ventrogenital sac. Sucker-width ratio *c.* 1.5. Forebody *c.* 25–33% of body-length. Prepharynx short. Oesophagus short. Intestinal bifurcation immediately anterior to ventral sucker. Caeca blind, end at level of testes. Testes two, symmetrical to slightly oblique at posterior extremity. Seminal vesicle tubular. Gonotyl absent. Ovary entire, immediately anterior to testes. Uterus in hindbody between testes and ventral sucker. Vitelline follicles in two lateral groups, in hindbody, from level of testes to mid-body. Arms of excretory vesicle may almost reach level of pharynx, sometimes do not exceed intestinal bifurcation. In freshwater fishes (Cichlidae, Characidae, Bagridae); Africa and South America. Type-species *N. tanganyikae* (Prudhoe, 1951) Manter & Pritchard, 1969.

**15a. Uterus reaches no further posteriorly than testicular zone ..... 16.**
**15b. Uterus extends well into post-testicular zone ..... 18.**

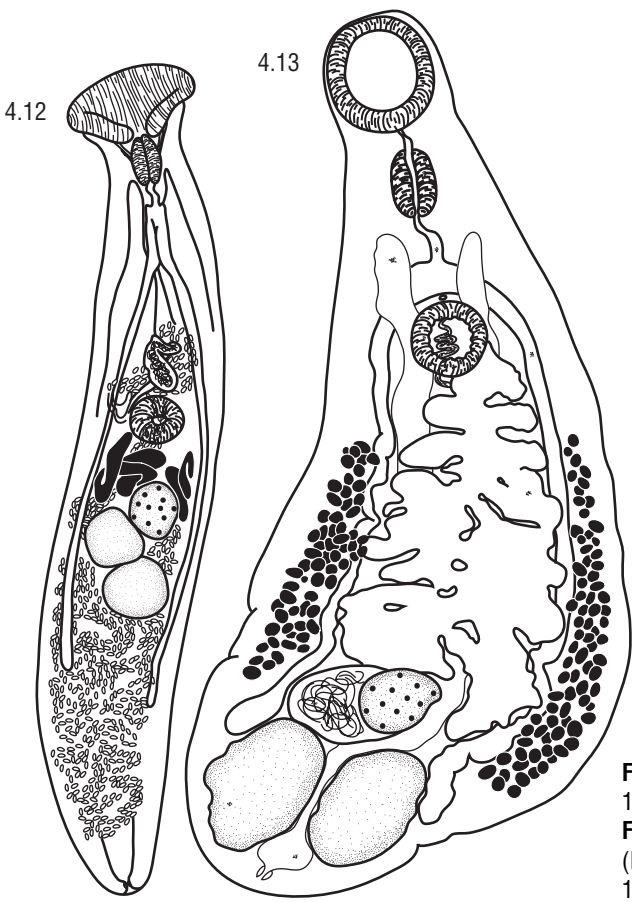



**Fig. 4.12.** *Claribulla longula* Overstreet, 1969. After Overstreet (1969).
**Fig. 4.13.** *Neocladocystis tanganyikae* (Prudhoe, 1951) Manter & Pritchard, 1969. After Prudhoe (1951).

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**16a. Tegumental spines absent; excretory vesicle extends to midway between ovary and ventral sucker; in body-cavity of marine fishes (Gobiidae) ..... ..... *Aphalloides* Dollfus, Chabaud & Golvan, 1957. (Fig. 4.14)**

**Diagnosis:** Body oval to elongate-oval; length:width ratio *c.* 3–4. Tegument lacks spines. Oral sucker almost round, without enlarged oral spines, opens subterminally. Ventral sucker unspecialized, embedded in ventrogenital sac. Sucker-width ratio *c.* 1–1.5. Forebody *c.* 20% of body-length. Prepharynx very short. Oesophagus long, distinctly longer than prepharynx. Intestinal bifurcation in mid-forebody. Caeca blind, end near anterior margin of testes. Testes two, symmetrical to slightly oblique, at posterior extremity and largely posterior to caecal ends. Seminal vesicle tubular. Gonotyl absent. Ovary deeply lobed, anterior to and often well separated from testes. Uterus in hindbody, not passing posteriorly beyond testes. Vitelline follicles in two lateral groups, in hindbody, not extending posteriorly beyond testes. Arms of excretory vesicle extend anteriorly to midway between ovary and ventral sucker. In body-cavity of marine fishes (Gobiidae); Mediterranean, Baltic and north-east Atlantic. Type-species *A. coelomicola* Dollfus, Chabaud & Golvan, 1957.

**16b. Tegumental spines present; excretory vesicle reaches pharynx; in intestine of fishes ..... 17.**

**17a. Testes elongate, mainly intercaecal; vitelline follicles in two groups, one between anterior testis and ovary and other between ovary and ventral sucker ..... ..... *Isocoelium* Ozaki, 1927. (Fig. 4.15)**

**Diagnosis:** Body very elongate; length:width ratio *c.* 11–16. Oral sucker longer than wide, without enlarged oral spines, opens subterminally. Ventral sucker unspecialized, not obviously embedded in ventrogenital sac. Sucker-width ratio *c.* 2. Forebody *c.* 20–25% of body-length. Prepharynx short. Oesophagus long. Intestinal bifurcation in posterior forebody. Caeca blind, end close to posterior extremity. Testes two, mostly intercaecal, distinctly elongate, strongly oblique to slightly tandem because of position on opposite sides of excretory vesicle. Seminal vesicle tubular. Gonotyl absent. Ovary deeply lobed, well separated from anterior testis, occupies full width of body in mid-hindbody. Uterus in hindbody, does not extend posteriorly beyond anterior testis. Vitelline follicles in two bands occupying full body-width, from midway between ventral sucker and ovary to ovary, and between ovary and anterior testis. Arms of excretory vesicle reach pharynx. In marine fishes (Uranoscopidae); off Japan. Type- and only species *I. mediolecithale* Ozaki, 1927.

**17b. Testes not elongate, extracaecal; vitelline follicles extend from slightly posterior to ovary to ventral sucker ..... *Paraisocoelium* Ozaki, 1932. (Fig. 4.16)**

**Diagnosis:** Body elongate; length:width ratio *c.* 6. Oral sucker longer than wide, without enlarged oral spines, opens subterminally. Ventral sucker unspecialized, not obviously embedded in ventrogenital sac. Sucker-width ratio *c.* 2. Forebody *c.* 25% of body-length. Prepharynx short. Oesophagus long, longer than prepharynx. Intestinal bifurcation in mid-forebody. Caeca blind, end between testes and posterior extremity. Testes two, not elongate, extracaecal, oblique in posterior hindbody. Seminal vesicle tubular. Gonotyl absent. Ovary deeply lobed, between ventral sucker and testes. Uterus in hindbody, not reaching posteriorly beyond anterior testis. Vitelline follicles in two lateral groups, from slightly posterior to ovary to ventral sucker. Arms of excretory vesicle almost reach pharynx. In marine fishes (Uranoscopidae); off Japan. Type- and only species *P. exorchis* Ozaki, 1932.

**18a. Testes tandem ..... 19.**

**18b. Testes symmetrical to slightly oblique ..... 25.**

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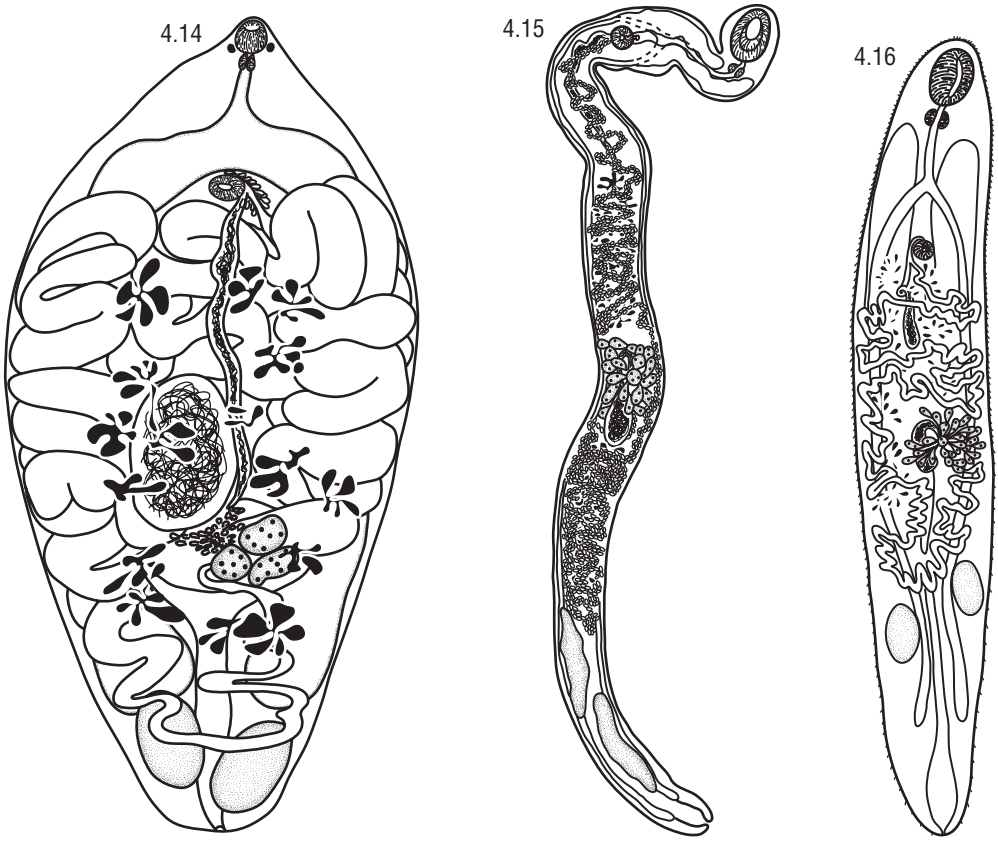



**Fig. 4.14.** *Aphalloides coelomicola* Dollfus, Chabaud & Golvan, 1957. After Naidenova (1970).
**Fig. 4.15.** *Isocoelium mediolecithale* Ozaki, 1927. After Ozaki (1927).
**Fig. 4.16.** *Paraisocoelium exorchis* Ozaki, 1932. After Yamaguti (1971).

**19a. Gonotyl present ..... 20.**
**19b. Gonotyl absent ..... 21.**

**20a. Gonotyl with spine- or rod-like structures, arising from anterior wall of ventrogenital sac; testes in posterior hindbody; vitelline follicles restricted predominantly to forebody ..... ..... *Textrema* Dronen, Underwood & Suderman, 1977. (Fig. 4.17)**

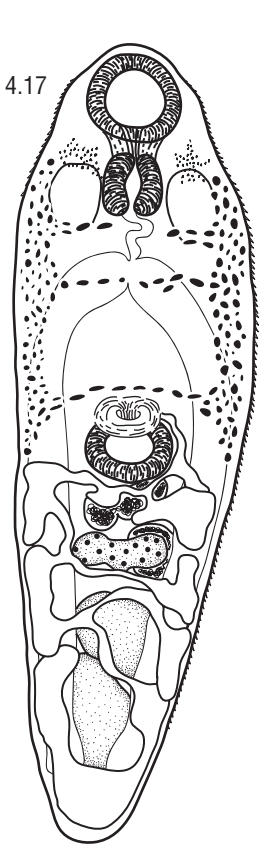
**Diagnosis:** Body elongate-oval; length:width ratio *c.* 3–4. Oral sucker almost round, without enlarged oral spines, opens subterminally. Ventral sucker unspecialized, embedded in ventrogenital sac. Sucker-width ratio *c.* 1. Forebody *c.* 40–45% of body-length. Prepharynx short. Oesophagus short. Intestinal bifurcation in mid-forebody. Caeca blind, end close to posterior extremity. Testes two, tandem, contiguous, in posterior hindbody. Seminal vesicle tubulosaccular. Gonotyl present as muscular lobe with spine- or rod-like structures arising from anterior wall of ventrogenital sac. Ovary slightly lobed, median, immediately pretesticular. Uterus in hindbody, extends close to posterior extremity. Vitelline follicles in two lateral groups predominantly in forebody, from level of ventral sucker to pharynx. Eggs with small anopercular knob. Arms of excretory vesicle reach

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level of pharynx. In freshwater fishes (Centrarchidae); North America. Type- and only species *T. hopkinsi* Dronen, Underwood & Suderman, 1977.

**20b. Gonotyl without spine-like structures, immediately anterior to common genital pore; testes well separated from posterior extremity; vitelline follicles between ovary and ventral sucker** ..... ***Bolbogonotylus*** **Font, 1987. (Fig. 4.18)**

**Diagnosis:** Body elongate; length:width ratio *c.* 10. Oral sucker funnel-shaped, approximately as long as wide, without enlarged oral spines, opens nearly terminally. Ventral sucker unspecialized, embedded in ventrogenital sac. Sucker-width ratio *c.* 2.5–3. Forebody *c.* 25% of body-length. Prepharynx short. Oesophagus short. Intestinal bifurcation in mid-forebody. Caeca blind, end close to posterior extremity. Testes two, tandem, contiguous, in mid-hindbody well separated from posterior extremity. Seminal vesicle bipartite. Gonotyl present as large muscular lobe immediately anterior to common genital pore, without spine-like structures. Ovary large, transversely extended, lobed, occupies almost full body-width immediately anterior to anterior testis. Uterus in hindbody, extends close to posterior extremity. Vitelline follicles in two lateral groups, extend anteriorly from ovary to just posterior to ventral sucker. Arms of excretory vesicle reach mid-forebody. In freshwater fishes (Centrarchidae); North America. Type- and only species *B. corkumi* Font, 1987.



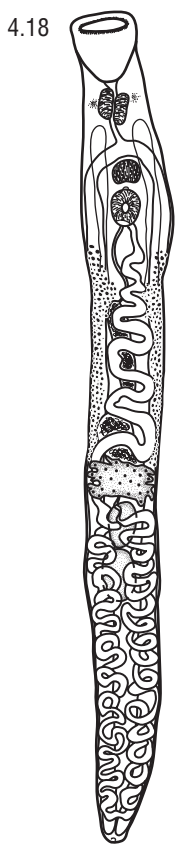




**Fig. 4.17.** *Textrema hopkinsi* Dronen, Underwood & Suderman, 1977. After Dronen *et al.* (1977).
**Fig. 4.18.** *Bolbogonotylus corkumi* Font, 1987. After Font (1987).

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**21a. Ovary deeply lobed and almost completely divided into two lateral masses ..... ..... *Biovarium* Yamaguti, 1934. (Fig. 4.19)**

**Diagnosis:** Body elongate-oval; length:width ratio *c.* 4–9. Oral sucker almost round, without enlarged oral spines, opens subterminally. Ventral sucker unspecialized, embedded in ventrogenital sac. Sucker-width ratio *c.* 1.5–3. Forebody *c.* 17–50% of body-length. Prepharynx short. Oesophagus short, similar in length to prepharynx. Intestinal bifurcation in anterior forebody. Caeca blind, end close to posterior extremity. Testes two, tandem, usually contiguous, rarely separate, in mid-hindbody. Seminal vesicle tubulosaccular. Gonotyl absent. Ovary deeply lobed and almost completely divided into two lateral masses, immediately anterior to anterior testis. Uterus in hindbody, extends close to posterior extremity. Vitelline follicles in two lateral groups, sometimes confluent in forebody, from mid-forebody to mid-hindbody. Arms of excretory vesicle reach pharynx. In marine fishes (Lateolabracidae, rarely Haemulidae); off Japan and China. Type-species *B. cryptocotyle* Yamaguti, 1934.

**21b. Ovary not divided into dextral and sinistral portions ..... 22.**

**22a. Vitelline follicles in three transverse bands occupying entire width of body; posterior testis close to posterior extremity and well separated from anterior testis; oral sucker opens via ventro-subterminal slit ..... *Isocoelioides* Zhukov, 1971. (Fig. 4.20)**

**Diagnosis:** Body elongate; length:width ratio *c.* 8. Oral sucker almost round, without enlarged oral spines, opens via ventro-subterminal slit. Ventral sucker unspecialized, not obviously embedded in ventrogenital sac. Sucker-width ratio *c.* 2.5. Forebody *c.* 25% of body-length. Prepharynx short. Oesophagus short. Intestinal bifurcation in mid-forebody. Caeca presumably blind, extend at least to level of ovary; posterior extent unknown. Testes two, tandem, well separated in hindbody; posterior testis close to posterior extremity. Seminal vesicle tubular. Gonotyl absent. Ovary deeply lobed, occupies full width of body. Uterus in hindbody, extends close to posterior extremity. Vitelline follicles in three bands occupy full width of body, immediately anterior to ovary and seminal receptacle, between ovary and anterior testis and between testes. Excretory vesicle extent unknown. In marine fishes (Lateolabracidae); off Japan and Yellow Sea. Type- and only species *I. orientalis* Zhukov, 1971.

**22b. Vitelline follicles in two lateral groups; testes well anterior to posterior extremity; oral sucker not opening via ventro-subterminal slit ..... 23.**

**23a. Oral sucker relatively large and funnel-shaped; testes usually well separated ..... ..... *Diplopharyngotrema* Yamaguti, 1958. (Fig. 4.21)**

(Syns *Pseudoisocoelium* Pan, 1984; *Sacculoesophagipora* Gu & Shen, 1978; *Terminoisocoelium* Gu & Shen, 1978)

**Diagnosis:** Body elongate; length:width ratio *c.* 6–22. Oral sucker relatively large and funnel-shaped, slightly wider than long, without enlarged oral spines, opens terminally. Ventral sucker unspecialized, embedded in ventrogenital sac. Sucker width ratio *c.* 1.5–3.5. Forebody *c.* 20–30% of body-length. Prepharynx long. Oesophagus short. Intestinal bifurcation in mid- to posterior forebody. Caeca blind, end close to posterior extremity. Testes two, tandem, usually well separated, rarely contiguous, in hindbody. Seminal vesicle tubular. Gonotyl absent. Ovary irregularly multilobed, anterior to and separated from anterior testis. Uterus in hindbody, extends close to posterior extremity. Vitelline follicles in two lateral groups, may extend from posterior forebody to posterior to testes. Excretory vesicle extent unknown. In marine fishes (Lateolabracidae); off China and Japan. Type-species *D. lateolabracis* Yamaguti, 1958.

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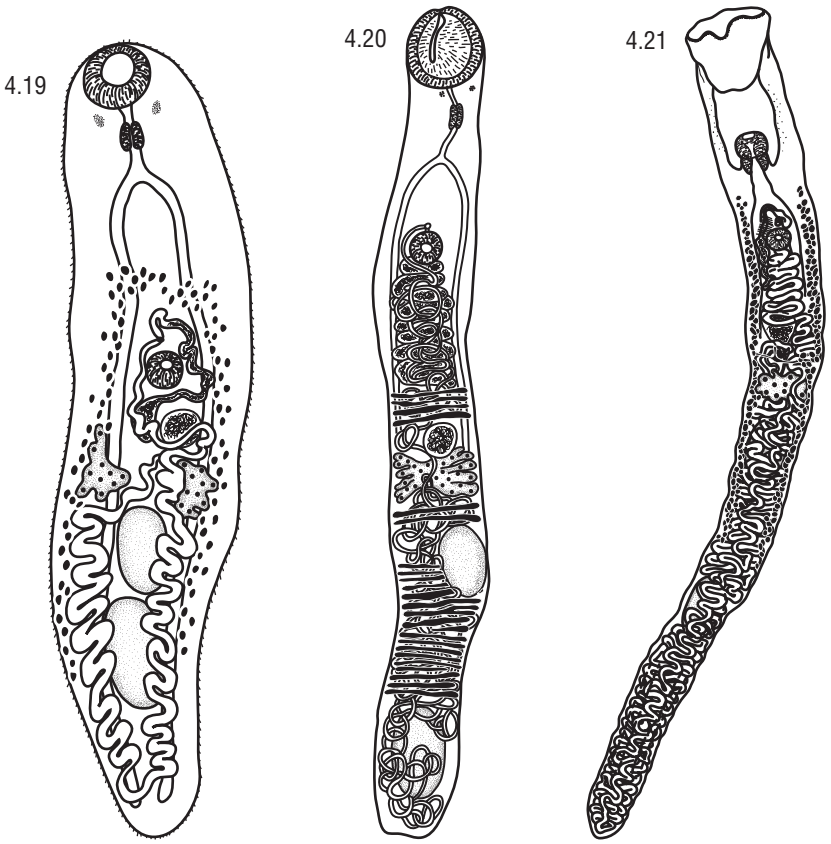



**Fig. 4.19.** *Biovarium cryptocotyle* Yamaguti, 1934. After Shen & Qiu (1995).
**Fig. 4.20.** *Isocoelioides orientalis* Zhukov, 1971. After Zhukov (1971).
**Fig. 4.21.** *Diplopharyngotrema lateolabracis* Yamaguti, 1958. After Yamaguti (1971).

**23b. Oral sucker not relatively large and funnel-shaped; testes contiguous or slightly separated ..... 24.**

**24a. Oral sucker round; ventral sucker near intestinal bifurcation; vitelline follicles extend to posterior testis or well into posterior end of body; in Sparidae ..... ..... *Aphallus* Poche, 1926. (Fig. 4.22)**
(Syn. *Santeria* Bray, 1986)

**Diagnosis:** Body elongate; length:width ratio *c.* 4–6. Oral sucker round, without enlarged oral spines, opens subterminally; exudate from frontal glands may resemble enlarged oral spines. Ventral sucker unspecialized, not obviously embedded in ventrogenital sac. Sucker-width ratio *c.* 1. Forebody *c.* 20–25% of body-length. Prepharynx short. Oesophagus long, distinctly longer than prepharynx. Intestinal bifurcation immediately anterior to or dorsal to ventral sucker. Caeca blind, end close to posterior extremity. Testes two, tandem, in mid-hindbody. Seminal vesicle tubular. Gonotyl absent. Ovary slightly to deeply lobed, immediately anterior to anterior testis. Uterus in hindbody, extends close to posterior extremity. Vitelline follicles in two lateral groups, from between ventral sucker and ovary to at least posterior margin of posterior testis and often

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close to posterior extremity. Arms of excretory vesicle reach mid-forebody. In marine fishes (Sparidae); Mediterranean Sea and Indian Ocean. Type-species *A. tubarium* (Rudolphi, 1819) Poche, 1926.

**24b. Oral sucker round to funnel-shaped; ventral sucker well posterior to intestinal bifurcation; vitelline follicles extend from ovary to slightly anterior to ventral sucker; in Platycephalidae ..... *Perlevilobus* n.g. (Figs 4.23, 4.24)**

**Diagnosis:** Body elongate; length:width ratio *c.* 9. Oral sucker round to funnel-shaped, without enlarged oral spines, opens nearly terminally. Ventral sucker unspecialized, not obviously embedded in ventrogenital sac, well posterior to intestinal bifurcation. Sucker-width ratio *c.* 1.5. Forebody *c.* 40% of body-length. Prepharynx short. Oesophagus long, longer than prepharynx. Intestinal bifurcation in mid-forebody. Caeca blind, end close to posterior extremity. Testes two, strongly oblique to tandem, in mid-hindbody. Seminal vesicle tubular. Gonotyl absent. Ovary slightly to distinctly lobed, rarely entire, anterior to testes, in mid-hindbody. Uterus in hindbody, extends close to posterior extremity. Vitelline follicles in two lateral groups, from ovary to slightly anterior to ventral sucker. Arms of excretory vesicle reach level of pharynx. In marine fishes (Platycephalidae); Indo-Pacific. Type- and only species *P. platycephali* (Shen, 1989) n. comb.

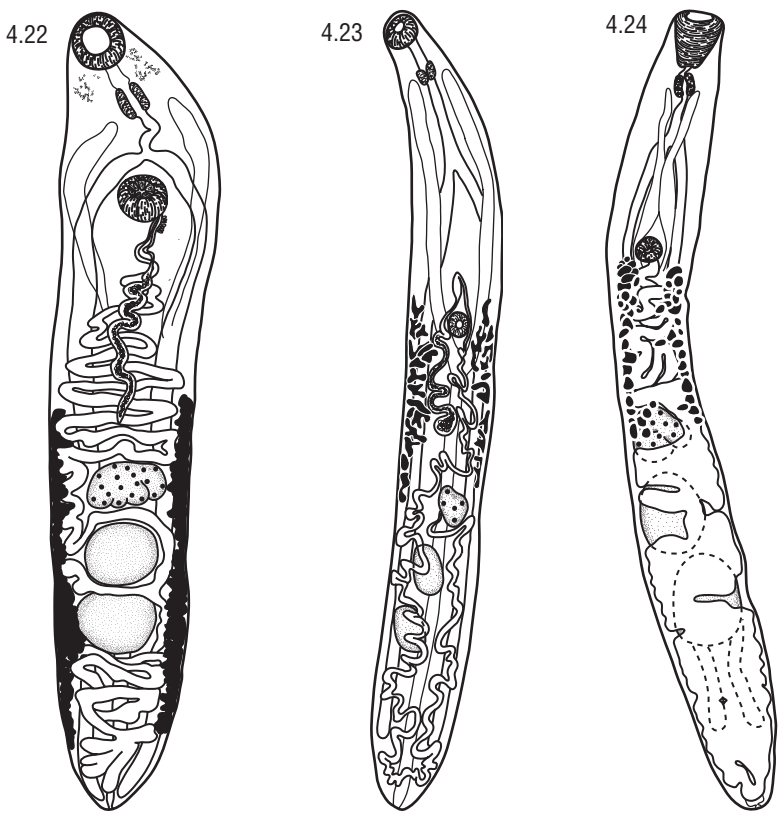



**Fig. 4.22.** *Aphallus tubarium* (Rudolphi, 1819) Poche, 1926. After Bartoli & Bray (1987).
**Figs 4.23, 4.24.** 4.23. *Perlevilobus platycephali* (Shen, 1989). After Shen (1989). 4.24. *P. platycephali* from Moreton Bay, Australia. Original.

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**25a. Gonotyl distinctly muscular, anterior to or ventral to ventral sucker ..... 26.**
**25b. Gonotyl absent, or if present, not distinctly muscular ..... 29.**

**26a. Intestinal bifurcation posterior to ventral sucker ..... ..... *Turgecaecum* Sullivan, 1975. (Fig. 4.25)**

**Diagnosis:** Body elongate-oval; length:width ratio *c.* 4. Oral sucker funnel-shaped, almost as long as wide, without enlarged oral spines, opens terminally. Ventral sucker unspecialized, embedded in ventrogenital sac. Sucker-width ratio *c.* 3. Forebody *c.* 33% of body-length. Prepharynx short. Oesophagus long, longer than prepharynx. Intestinal bifurcation well posterior to ventral sucker, dorsal to ovary. Caeca blind, end well short of posterior extremity at anterior margin of testes. Testes two, symmetrical, in posterior half of hindbody. Seminal vesicle bipartite. Gonotyl large, muscular, sucker-like, immediately posterior to ventral sucker. Ovary distinctly trilobed, in anterior hindbody. Uterus in hindbody, extends close to posterior extremity. Vitelline follicles in two lateral groups, in forebody. Arms of excretory vesicle reach level of ventral sucker. In freshwater fishes (Centrarchidae); North America. Type- and only species *T. longifauces* Sullivan, 1975.

**26b. Intestinal bifurcation dorsal to or anterior to ventral sucker ..... 27.**

**27a. Ovary intertesticular; oesophagus longer than prepharynx; vitelline follicles reach level of oral sucker; in amphibians ..... *Andrincola* Zhang & Yang, 1993. (Fig. 4.26)**
(Syn. *Neoandrincola* Zhang & Yang, 1997)

**Diagnosis:** Body elongate-oval; length:width ratio *c.* 3–5. Oral sucker almost round, slightly wider than long, without enlarged oral spines, opens subterminally to nearly terminally. Ventral sucker unspecialized, embedded in ventrogenital sac. Sucker-width ratio *c.* 2–2.5. Forebody *c.* 25–33% of body-length. Prepharynx very short. Oesophagus long, distinctly longer than prepharynx. Intestinal bifurcation dorsal to ventral sucker. Caeca blind, end close to posterior extremity. Testes two, symmetrical, in anterior hindbody. Seminal vesicle bipartite. Gonotyl a sucker-like muscular pad, immediately anterior to common genital pore. Ovary divided into three lobed branches, between testes. Uterus extensive in hindbody; loops may extend slightly into posterior forebody. Vitelline follicles may extend from gonads in anterior hindbody to oral sucker. Excretory vesicle extent unknown. In amphibians (Cryptobranchidae); China. Type-species *A. mabianensis* Zhang & Yang, 1993.

**27b. Ovary anterior to testes; oesophagus not longer than prepharynx; vitelline follicles do not reach oral sucker; in fishes ..... 28.**

**28a. Gonotyl relatively large, often resembling second ventral sucker, immediately anterior to ventral sucker; vitelline follicles do not extend posteriorly beyond testes but may enter forebody; ovary trilobed or has few lobes; in freshwater Perciformes ..... ..... *Cryptogonimus* Osborn, 1903. (Figs 4.27, 4.28)**
(Syn. *Protenteron* Stafford, 1904)

**Diagnosis:** Body elongate; length:width ratio *c.* 3–5. Oral sucker funnel-shaped, longer than wide, without enlarged oral spines, opens nearly terminally. Ventral sucker unspecialized, deeply embedded in ventrogenital sac. Sucker-width ratio *c.* 2–3. Forebody *c.* 30% of body-length. Prepharynx short. Oesophagus short. Intestinal bifurcation immediately anterior to ventral sucker. Caeca blind, variable, may end in anterior hindbody, anterior to testes or may extend to near

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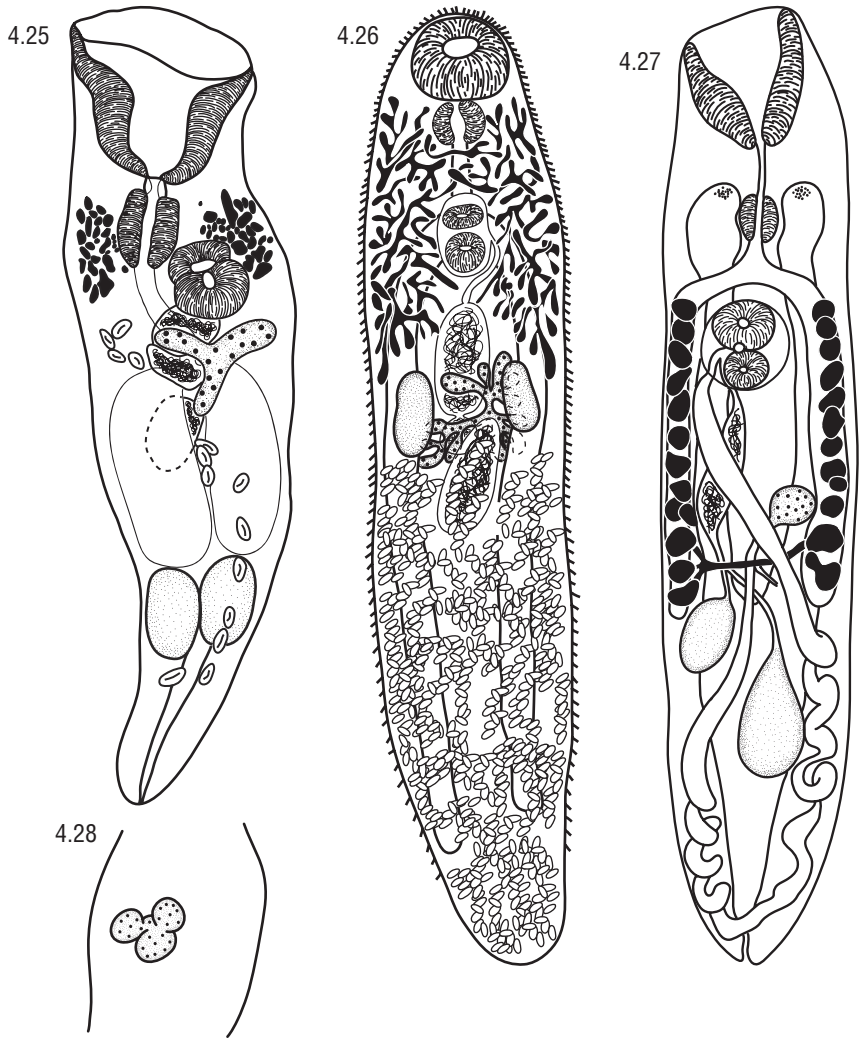



**Fig. 4.25.** *Turgecaecum longifauces* Sullivan, 1975. After Sullivan (1975).
**Fig. 4.26.** *Andrincola mabianensis* Zhang & Yang, 1993. After Zhang & Yang (1993).
**Figs 4.27, 4.28.** 4.27. *Cryptogonimus chili* Osborn, 1903. After Osborn (1903). 4.28. *C. chili* ovary. Voucher HWML 24964. Original.

posterior extremity. Testes two, strongly oblique to symmetrical, in mid-hindbody. Seminal vesicle tubular. Gonotyl present as muscular sucker-like pad immediately anterior to common genital pore. Ovary slightly to deeply lobed, anterior to and close to or somewhat separated from testes. Uterus in hindbody, extends close to posterior extremity. Eggs may have distinct curved anopercular spine. Vitelline follicles in two lateral groups from mid-forebody to level of gonads. Arms of excretory vesicle reach pharynx. In freshwater fishes (Centrarchidae and other families); North America. Type-species *C. chili* Osborn, 1903.

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**28b. Gonotyl ventral to or at anterior margin of ventral sucker, smaller than ventral sucker; vitelline follicles may extend posteriorly beyond testes but do not enter forebody; ovary deeply lobed; in marine Pleuronectiformes ..... *Cicesetrema* Pérez-Ponce de León, Castillo-Sanchez & Rosales-Casián, 1999. (Fig. 4.29)**

**Diagnosis:** Body elongate-oval, broadest at level of oral sucker; length:width ratio *c.* 2.5. Oral sucker very large, distinctly wider than long, without enlarged oral spines, opens terminally. Ventral sucker unspecialized, deeply embedded in ventrogenital sac. Sucker-width ratio *c.* 2. Forebody *c.* 25% of body-length. Prepharynx very short. Oesophagus very short. Intestinal bifurcation in posterior forebody. Caeca blind, end in posterior hindbody well short of extremity. Testes two, oblique, in anterior hindbody. Seminal vesicle tubulosaccular. Gonotyl muscular, ventral to, overlapping and smaller than ventral sucker; anatomy not completely understood. Ovary deeply lobed, between ventral sucker and anterior testis. Uterus in hindbody, almost reaches posterior extremity. Vitelline follicles in two lateral groups, from ovary to just posterior to testes. Arms of excretory vesicle reach pharynx. In marine fishes (Paralichthyidae); Pacific off Mexico. Type- and only species *C. unami* Pérez-Ponce de León, Castillo-Sanchez & Rosales-Casián, 1999.

**29a. Caeca end anterior to or at level of testes ..... 30.**
**29b. Caeca end posterior to testes ..... 33.**

**30a. Oral sucker funnel-shaped; vitelline follicles predominantly confined to forebody ..... *Caecincola* Marshall & Gilbert, 1905. (Fig. 4.30)**

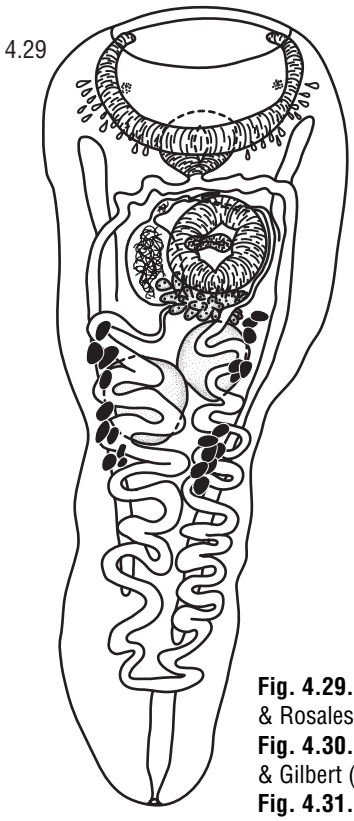
**Diagnosis:** Body elongate-oval, often with constriction immediately posterior to oral sucker; length:width ratio *c.* 2–3. Oral sucker funnel-shaped, wider than long, without enlarged oral spines, opens almost terminally. Ventral sucker unspecialized, embedded in ventrogenital sac. Sucker-width ratio *c.* 3–3.5. Forebody *c.* 33–50% of body-length. Prepharynx short. Oesophagus short. Intestinal bifurcation immediately anterior to or dorsal to ventral sucker. Caeca blind, end in anterior hindbody, not extending posteriorly beyond testes. Testes two, symmetrical to slightly oblique, in mid-hindbody. Seminal vesicle bipartite. Gonotyl absent. Ovary distinctly bi- or trilobed, immediately anterior to or ventral to testes. Uterus in hindbody, extends close to posterior extremity. Vitelline follicles in two lateral groups, mainly in forebody, may reach posterior margin of ventral sucker. Arms of excretory vesicle reach mid-forebody. In freshwater fishes (Centrarchidae); North America. Type-species *C. parvulus* Marshall & Gilbert, 1905.

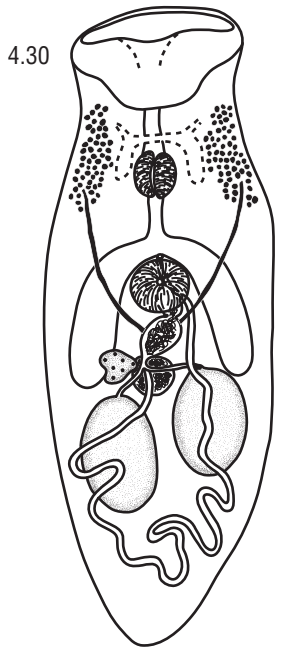
**30b. Oral sucker not funnel-shaped; vitelline follicles mainly in forebody or not ..... 31.**

**31a. Ovary distinctly transversely elongate, intertesticular; anterior testis may extend anterior to ovary ..... *Tabascotrema* Lamothe-Argumedo & Pineda-López, 1990. (Fig. 4.31)**

**Diagnosis:** Body elongate-oval; length:width ratio *c.* 2.5. Oral sucker nearly round, without enlarged oral spines, opens almost terminally. Ventral sucker unspecialized, not obviously embedded in ventrogenital sac. Sucker-width ratio *c.* 1. Forebody *c.* 40% of body-length. Prepharynx short. Oesophagus short. Intestinal bifurcation in mid-forebody. Caeca blind, end in mid-hindbody at level of testes. Testes two, oblique, in mid-hindbody. Seminal vesicle saccular, extends well into forebody. Gonotyl absent. Ovary intertesticular, a deeply lobed transverse band, occupies more than half of body-width, at level of anterior testis and separating testes. Uterus in hindbody, extends close to posterior extremity. Vitelline follicles in two lateral groups, from posterior

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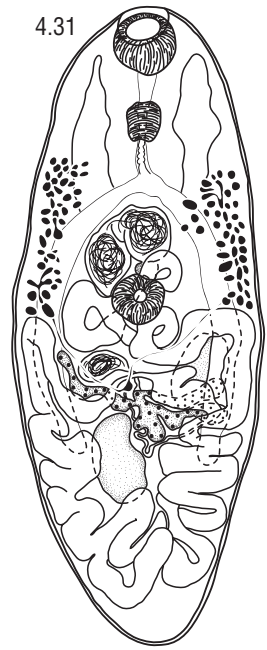




**Fig. 4.29.** *Cicesetrema unami* Pérez-Ponce de León, Castillo-Sanchez & Rosales-Casián, 1999. After Pérez-Ponce de León *et al.* (1999).
**Fig. 4.30.** *Caecincola parvulus* Marshall & Gilbert, 1905. After Marshall & Gilbert (1905).
**Fig. 4.31.** *Tabascotrema verai* Lamothe-Argumedo & Pineda-López, 1990. After Lamothe-Argumedo & Pineda-López (1990).

margin of ventral sucker to level of oesophagus. Arms of excretory vesicle reach level of oral sucker. In freshwater fishes (Cichlidae); Mexico. Type- and only species *T. verai* Lamothe-Argumedo & Pineda-López, 1990.

**31b. Ovary compact or transversely elongate, anterior to testes ..... 32.**

**32a. Ovary transversely elongate; testes in mid-body; vitelline follicles anterior to ovary; in Cichlidae ..... *Campechetrema* Lamothe-Argumedo, Salgado-Maldonado & Pineda-López, 1997. (Fig. 4.32)**

**Diagnosis:** Body elongate-oval; length:width ratio *c.* 2.5. Oral sucker slightly wider than long, without enlarged oral spines, opens subterminally. Ventral sucker unspecialized, embedded deeply in ventrogenital sac. Sucker-width ratio *c.* 3. Forebody *c.* 25% of body-length. Prepharynx very short. Oesophagus very short. Intestinal bifurcation in mid-forebody. Caeca blind, short, end at level of ovary. Testes two, symmetrical to slightly oblique in mid-body. Seminal vesicle saccular. Gonotyl apparently present; anatomy not understood. Ovary deeply lobed, transversely elongate, anterior to testes. Uterus in hindbody, extends close to posterior extremity. Vitelline follicles in two lateral groups, from ovary to mid-forebody. Arms of excretory vesicle reach oral sucker. In freshwater fishes (Cichlidae); Mexico. Type- and only species *C. herrerai* Lamothe-Argumedo, Salgado-Maldonado & Pineda-López, 1997.

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**32b. Ovary compact; testes in posterior half of body; vitelline follicles may extend posteriorly beyond ovary; in freshwater Esociformes and Perciformes ..... ..... *Centrovarium* Stafford, 1904. (Fig. 4.33)**

**Diagnosis:** Body elongate-oval; length:width ratio *c.* 2.5–5. Oral sucker nearly round, without enlarged oral spines, opens almost terminally. Ventral sucker unspecialized, not obviously embedded in ventrogenital sac. Sucker-width ratio *c.* 1–2. Forebody *c.* 25–30% of body-length. Prepharynx short. Oesophagus usually longer than prepharynx, sometimes short. Intestinal bifurcation in mid-forebody. Caeca blind, end at level of ovary or testes. Testes two, symmetrical to slightly oblique, in mid-hindbody. Seminal vesicle tubulosaccular to bipartite. Gonotyl absent. Ovary deeply lobed, median, anterior to and separate from testes. Uterus in hindbody, extends close to posterior extremity. Vitelline follicles in two lateral groups, may be partly confluent medially, from mid-forebody to mid-hindbody. Arms of excretory vesicle reach pharynx. In freshwater fishes (numerous families); North America and India. Type-species *C. lobotes* (McCallum, 1895) Stafford, 1904.

**33a. Eggs triangular with distinct polar filament; in Stromateidae ..... ..... *Mehrailla* Srivastava, 1939. (Fig. 4.34)**

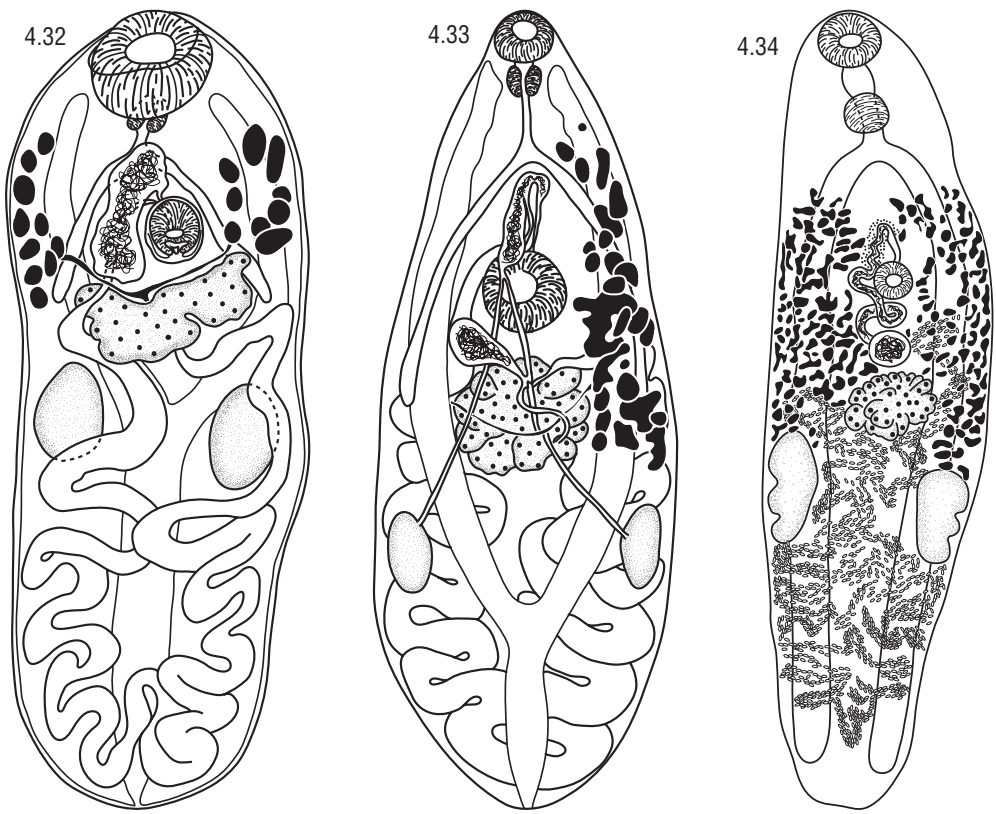



**Fig. 4.32.** *Campechetrema herrerai* Lamothe-Argumedo, Salgado-Maldonado & Pineda-López, 1997. After Lamothe-Argumedo *et al.* (1997).
**Fig. 4.33.** *Centrovarium lobotes* (McCallum, 1895) Stafford, 1904. After Yamaguti (1971).
**Fig. 4.34.** *Mehrailla ovocaudatum* Srivastava, 1939. After Yamaguti (1971).

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**Diagnosis:** Body elongate-oval; length:width ratio *c.* 3.5. Oral sucker slightly wider than long, without enlarged oral spines, opens subterminally. Ventral sucker unspecialized, not obviously embedded in ventrogenital sac. Sucker-width ratio *c.* 1.5. Forebody *c.* 33% body-length. Prepharynx short. Oesophagus short. Intestinal bifurcation in mid-forebody. Caeca blind, end close to posterior extremity. Testes two, symmetrical, with three distinct lobes on external face of testes, in mid-hindbody. Seminal vesicle tubular. Gonotyl absent. Ovary deeply lobed, anterior to and between testes. Uterus in hindbody, postovarian, extends slightly anterior to ventral sucker. Vitelline follicles in two lateral groups, from anterior margin of testes to mid-forebody. Eggs triangular with distinct anopercular filament. Excretory vesicle extent unknown. In marine fishes (Stromateidae); Indian Ocean. Type- and only species *M. ovocaudatum* Srivastava, 1939.

**33b. Eggs without distinct polar filament; not in Stromateidae ..... 34.**

**34a. Ovary dextral at mid-body; uterine loops predominantly in lateral fields; in amphibians ..... *Andritrema* Zhang & Yang, 1993. (Fig. 4.35)**

**Diagnosis:** Body oval; length:width ratio *c.* 2–2.5. Oral sucker slightly wider than long, without enlarged oral spines, opens subterminally. Ventral sucker unspecialized, embedded in ventrogenital sac. Sucker-width ratio *c.* 2. Forebody *c.* 33% of body-length. Prepharynx very short. Oesophagus long, distinctly longer than prepharynx. Intestinal bifurcation immediately anterior to ventral sucker. Caeca blind, end in mid-hindbody. Testes two, oblique, in mid-hindbody. Seminal vesicle bipartite. Gonotyl absent. Ovary deeply lobed, dextral at level of anterior testes. Uterine coils restricted to hindbody, descending and ascending in lateral fields. Vitelline follicles in two lateral groups, from slightly posterior to ventral sucker to pharynx. Arms of excretory vesicle reach pharynx. In amphibians (Cryptobranchidae); China. Type- and only species *A. ellipticum* Zhang & Yang, 1993 (emend.).

**34b. Ovary median; uterine loops extensive throughout hindbody; in fishes ..... 35.**

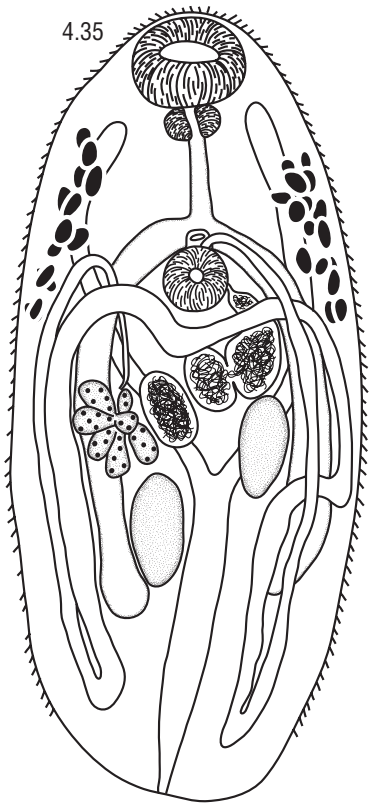
**35a. Anterior margin of testes at level of or anterior to ventral sucker; testes usually extracaecal or overlap caeca laterally; body squat ..... *Exorchis* Kobayashi, 1921. (Fig. 4.36)**
(Syn. *Parametadena* Pan, 1984)

**Diagnosis:** Body squat; length:width ratio *c.* 1–1.5. Oral sucker slightly wider than long, without enlarged oral spines, opens subterminally. Ventral sucker unspecialized, not obviously embedded in ventrogenital sac. Sucker-width ratio *c.* 1–2. Forebody *c.* 15–40% of body-length. Prepharynx very short. Oesophagus very short. Intestinal bifurcation in mid-forebody. Caeca blind, end close to posterior extremity. Testes two, predominantly extracaecal, near level of ventral sucker, may extend into forebody. Seminal vesicle tubulosaccular. Gonotyl absent. Ovary slightly to deeply lobed, close to and may slightly overlap ventral sucker. Uterus in hindbody, extends close to posterior extremity. Vitelline follicles in two lateral groups or confluent medially, always extend anterior to testes and usually at least partly anterior to ventral sucker. Arms of excretory vesicle may reach level of pharynx. In freshwater Siluriformes; China and Japan. Type-species *E. oviformis* Kobayashi, 1921.

**35b. Anterior margin of testes does not enter forebody; testes not distinctly extracaecal; body oval to elongate-oval ..... 36.**

**36a. Oral sucker large, funnel-shaped, *c.* 70% of body-width ..... ..... *Pseudocryptogonimus* Yamaguti, 1958. (Fig. 4.37)**

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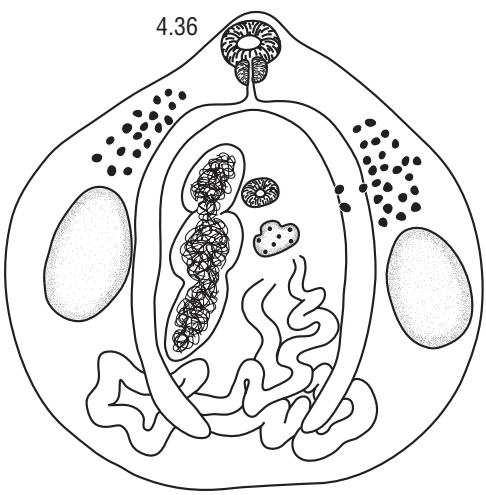







**Fig. 4.35.** *Andritrema ellipticum* Zhang & Yang, 1993 (emend.). After Zhang & Yang (1993).
**Fig. 4.36.** *Exorchis oviformis* Kobayashi, 1921. After Kobayashi (1921).
**Fig. 4.37.** *Pseudocryptogonimus cirrhiti* (Bravo-Hollis, 1953) Yamaguti, 1958. After Yamaguti (1971).

**Diagnosis:** Body elongate-oval; length:width ratio *c.* 3. Oral sucker funnel-shaped, slightly wider than long, *c.* 70% of body-width, without enlarged oral spines, opens nearly terminally. Ventral sucker unspecialized, embedded in ventrogenital sac. Sucker-width ratio *c.* 3. Forebody *c.* 33% of body-length. Prepharynx short. Oesophagus short. Intestinal bifurcation immediately anterior to

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ventral sucker. Caeca blind, end midway between testes and posterior extremity. Testes two, symmetrical to oblique, in mid-hindbody. Seminal vesicle tubular. Gonotyl absent. Ovary deeply lobed, immediately anterior to testes. Uterus in hindbody, extends close to posterior extremity. Vitelline follicles in two lateral groups or confluent in midline, extend from posterior margin of ovary to posterior margin of ventral sucker. Arms of excretory vesicle reach level of pharynx. In marine fishes (Cirrhitidae); off Pacific coast of Mexico. Type- and only species *P. cirrhiti* (Bravo-Hollis, 1953) Yamaguti, 1958.

**36b. Oral sucker nearly round, < 70% of body-width ..... 37.**

**37a. Forebody *c.* 50% of body-length; vitelline follicles confined to forebody; in freshwater Centropomidae ..... *Olmeca* Lamothe-Argumedo & Pineda-López, 1990. (Fig. 4.38)**

**Diagnosis:** Body elongate-oval; length:width ratio *c.* 2–2.5. Oral sucker nearly round in outline, without enlarged oral spines, opens almost terminally. Ventral sucker unspecialized, not embedded in ventrogenital sac. Sucker-width ratio *c.* 1. Forebody *c.* 50% of body-length. Prepharynx short. Oesophagus very short. Intestinal bifurcation in anterior half of forebody. Caeca blind, end close to posterior extremity. Testes two, oblique in mid-hindbody. Seminal vesicle saccular, extends into forebody. Gonotyl absent. Ovary a deeply lobed transverse band, occupies more than half of body-width, at level of anterior testis. Uterus in hindbody; may extend slightly into posterior forebody. Vitelline follicles in two lateral groups, sometimes confluent in forebody, from ventral sucker to mid-forebody. Arms of excretory vesicle reach level of oral sucker. In freshwater fishes (Centropomidae); Mexico. Type- and only species *O. laurae* Lamothe-Argumedo & Pineda-López, 1990.

**37b. Forebody < 45% of body-length; vitelline follicles may not be confined to forebody; not in Centropomidae ..... 38.**

**38a. Ventral sucker slightly larger than oral sucker; uterus predominantly posterior to ovary and testes; vitelline follicles between posterior extremity and testes ..... ..... *Pseudometadena* Yamaguti, 1952. (Fig. 4.39)**

**Diagnosis:** Body oval; length:width ratio *c.* 1.5–2. Oral sucker nearly round, without enlarged oral spines, opens almost terminally. Ventral sucker slightly larger than oral sucker, unspecialized, not obviously embedded in ventrogenital sac. Sucker-width ratio *c.* < 1. Forebody *c.* 25% of body-length. Prepharynx short. Oesophagus long, distinctly longer than prepharynx. Intestinal bifurcation immediately anterior to or dorsal to ventral sucker. Caeca blind, end close to posterior extremity. Testes two, symmetrical, in anterior hindbody near posterior margin of ventral sucker. Seminal vesicle saccular, bipartite. Gonotyl absent. Ovary deeply lobed, between testes in anterior hindbody. Uterus in hindbody, predominantly posterior to ovary and testes, extending to posterior extremity. Vitelline follicles in two lateral groups, between posterior extremity and testes. Arms of excretory vesicle reach level of pharynx. In euryhaline and marine fishes (Serranidae); Indo-Pacific. Type- and only species *P. celebesensis* Yamaguti, 1952.

**38b. Ventral sucker smaller than oral sucker; uterus extensive anterior to ovary; vitelline follicles do not extend posteriorly beyond posterior margin of testes ..... 39.**

**39a. Caeca end slightly posterior to testes; vitelline follicles confined to region slightly anterior and slightly posterior to ventral sucker; in freshwater fishes ..... ..... *Palaeocryptogonimus* Szidat, 1954. (Fig. 4.40)**

(Syn. *Pseudocaecincola* Lamothe-Argumedo, Salgado-Maldonado & Pineda-López, 1991)

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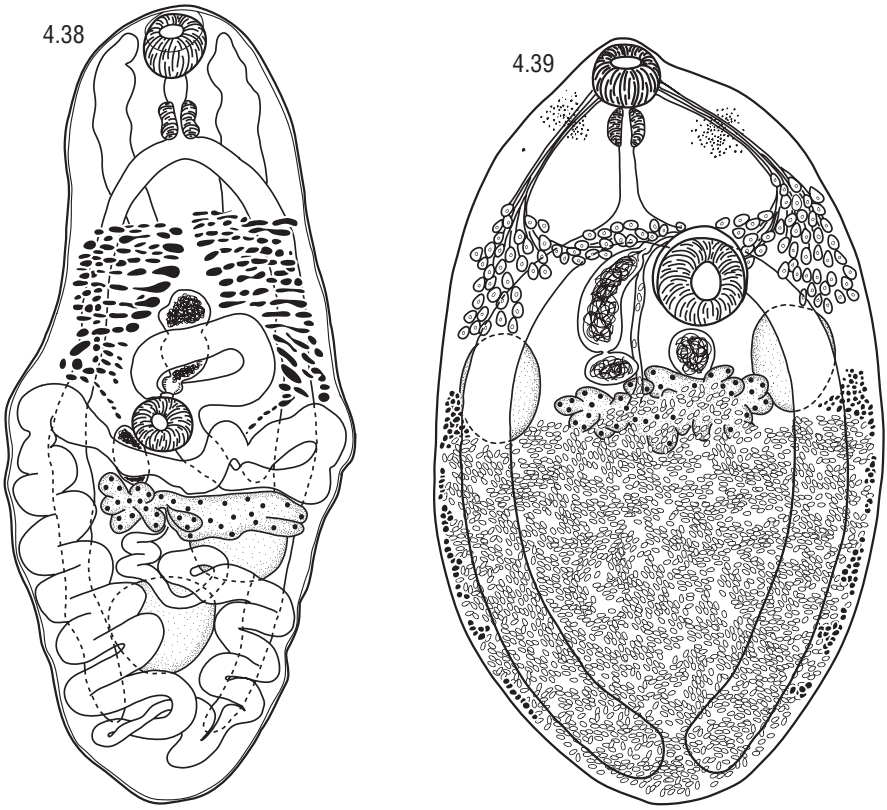


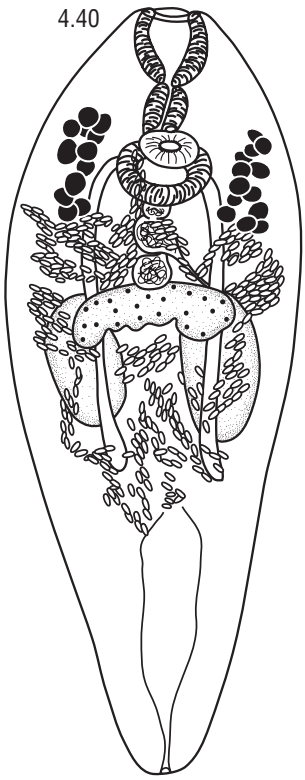

**Fig. 4.38.** *Olmeca laurae* Lamothe-Argumedo & Pineda-López, 1990. After Lamothe-Argumedo & Pineda-López (1990).
**Fig. 4.39.** *Pseudometadena celebesensis* Yamaguti, 1952. After Yamaguti (1952).

**Diagnosis:** Body oval to elongate-oval; length:width ratio *c.* 2–3. Oral sucker nearly round, may be shorter or longer than wide, without enlarged oral spines, opens terminally. Ventral sucker unspecialized, embedded in ventrogenital sac. Sucker-width ratio *c.* 1–2. Forebody *c.* 15–25% of body-length. Prepharynx very short. Oesophagus very short. Intestinal bifurcation immediately anterior to or dorsal to ventral sucker. Caeca blind, end in mid-hindbody slightly posterior to testes. Testes two, symmetrical, in mid- to anterior hindbody. Seminal vesicle saccular. Gonotyl absent. Ovary deeply lobed, slightly anterior to or overlaps testes in anterior hindbody. Uterus in hindbody, may reach posterior extremity. Vitelline follicles in region slightly anterior and slightly posterior to ventral sucker. Arms of excretory vesicle reach into forebody. In freshwater fishes (Doradidae, Cichlidae); Mexico and South America. Type-species *P. claviformis* Szidat, 1954.

**39b. Caeca end well posterior to testes; vitelline follicles may extend from slightly posterior to testes to level of pharynx; in marine fishes ..... *Metadena* Linton, 1910. (Fig. 4.41)**
(Syns *Achoerus* Vlassenko, 1931; *Disacanthus* Oshmarin, Mamaev & Parukhin, 1961; *Pseudosiphoderoides* Yamaguti, 1958; *Siphoderoides* Manter, 1940)

**Diagnosis:** Body oval to elongate-oval; length:width ratio *c.* 1–6. Oral sucker nearly round, without enlarged oral spines, opens subterminally or almost terminally. Ventral sucker unspecialized,

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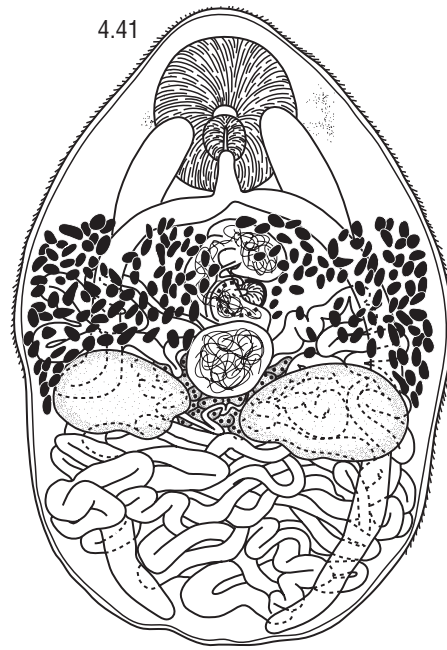




**Fig. 4.40.** *Palaeocryptogonimus claviformis* Szidat, 1954. After Szidat (1954).
**Fig. 4.41.** *Metadena crassulata* Linton, 1910. After Yamaguti (1971).

embedded in ventrogenital sac. Sucker-width ratio *c.* 1.5–3.5. Forebody *c.* 20–45% of body-length. Prepharynx short. Oesophagus short. Intestinal bifurcation immediately anterior to or dorsal to ventral sucker or in mid-forebody. Caeca blind, end close to posterior extremity. Testes two, symmetrical to oblique, in mid- to anterior hindbody. Seminal vesicle tubulosaccular. Gonotyl absent or present as non-muscular lobe anterior to ventral sucker. Ovary deeply lobed, between to slightly anterior to or well separate from testes. Uterus mainly in hindbody; loops may extend into forebody and close to posterior extremity. Vitelline follicles in two lateral groups or form a transverse band, may extend from slightly posterior to testes to level of pharynx, rarely restricted to forebody, sometimes nearly confluent in midline. Arms of excretory vesicle reach pharynx. In marine fishes (many families, predominantly Lutjanidae); cosmopolitan. Type-species *M. crassulata* Linton, 1910.

**40a. Testes multiple or follicular ..... 41.**
**40b. Testes two ..... 43.**

**41a. Oral sucker exceptionally large, with width *c.* five times that of ventral sucker; caeca open at separate ani ..... *Novemtestis* Yamaguti, 1942. (Fig. 4.42)**
**Diagnosis:** Body oval; length:width ratio *c.* 1.5. Oral sucker distinctly wider than long, with enlarged oral spines, opens nearly terminally. Ventral sucker unspecialized, embedded in ventrogenital sac. Sucker-width ratio *c.* 5. Forebody *c.* 30% of body-length. Prepharynx very short.

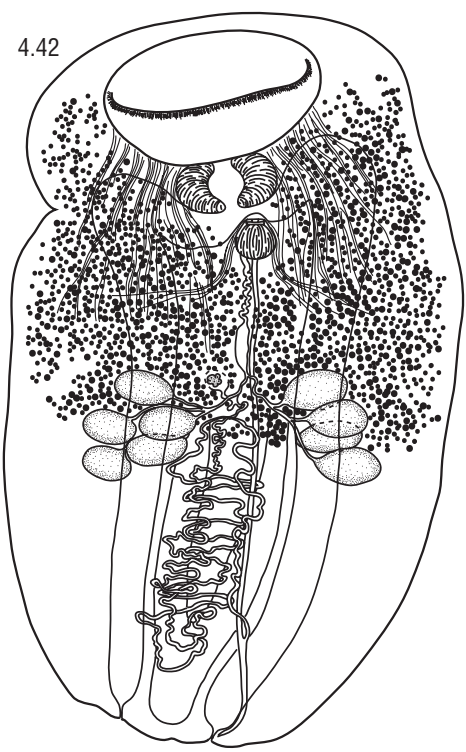
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Oesophagus very short. Intestinal bifurcation immediately anterior to ventral sucker. Caeca open at separate ani at posterior extremity. Testes nine, in groups of four and five each at mid-body. Seminal vesicle tubular. Gonotyl absent. Ovary presumed entire, immediately anterior to testes. Uterus in hindbody posterior to ovary. Vitelline follicles confluent dorsally and ventrally from level of testes to oral sucker. Arms of excretory vesicle extend to near pharynx. In marine fishes as metacercariae (Mullidae); adult unknown; western Pacific. Type- and only species *N. armatus* Yamaguti, 1942.

**41b. Oral sucker not exceptionally large, width less than four times width of ventral sucker; caeca blind ..... 42.**

**42a. Oral sucker opens terminally; vitelline follicles in forebody; ovary deeply lobed but compact ..... *Lobosorchis* Miller & Cribb, 2005. (Fig. 4.43)**

**Diagnosis:** Body oval; length:width ratio *c.* 1.5. Oral sucker distinctly wider than long, with enlarged oral spines, opening nearly terminally. Ventral sucker unspecialized, embedded in ventrogenital sac. Sucker-width ratio *c.* 2.5. Forebody *c.* 40% of body-length. Prepharynx short. Oesophagus short, similar in length to prepharynx. Intestinal bifurcation immediately anterior to ventral sucker. Caeca blind, end close to posterior extremity. Testes in two symmetrical groups of four to five deeply divided follicles, in mid-hindbody. Seminal vesicle saccular. Gonotyl a simple



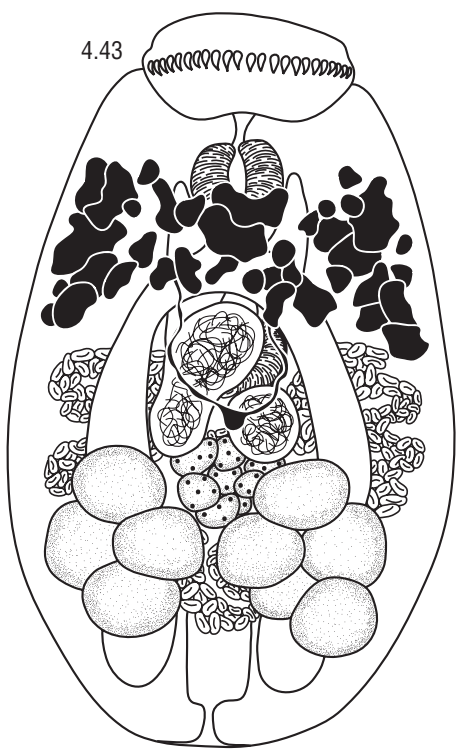




**Fig. 4.42.** *Novemtestis armatus* Yamaguti, 1942. After Yamaguti (1942a).
**Fig. 4.43.** *Lobosorchis tibaldiae* Miller & Cribb, 2005. After Miller & Cribb (2005).

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lobe arising from anterior wall of ventrogenital sac. Ovary deeply lobed, compact, median, in mid-hindbody. Uterus in hindbody, extends close to posterior extremity. Vitelline follicles in transverse band in forebody from level of pharynx to ventral sucker. Arms of excretory vesicle reach pharynx. In marine fishes (Lutjanidae); tropical Indo-Pacific. Type- and only species *L. tibaldiae* Miller & Cribb, 2005.

**42b. Oral sucker opens subterminally; vitelline follicles from posterior to ventral sucker to level of ovary; ovary deeply lobed, almost follicular ..... ..... *Acanthosiphodera* Madhavi, 1976. (Fig. 4.44)**

**Diagnosis:** Body elongate-oval; length:width ratio *c.* 2.5. Oral sucker slightly wider than long, with enlarged oral spines, opens subterminally. Ventral sucker unspecialized, not obviously embedded in ventrogenital sac. Sucker-width ratio *c.* 1.3. Forebody occupies *c.* 25% of body-length. Prepharynx short. Oesophagus short, similar in length to prepharynx. Intestinal bifurcation in mid-forebody. Caeca blind, end close to posterior extremity. Testes nine, scattered in mid-hindbody. Seminal vesicle tubulosaccular. Gonotyl absent. Ovary deeply lobed, almost follicular, median, in anterior hindbody. Uterus in hindbody, extends close to posterior extremity. Vitelline follicles in two lateral groups, posterior to ventral sucker and anterior testis. Arms of excretory vesicle reach level of oral sucker. In marine fishes (Lutjanidae); Indian Ocean. Type- and only species *A. bengalensis* Madhavi, 1976 (emend.).

**43a. Multiple gonotyls present ..... *Polycryptocylix* Lamothe-Argumedo, 1970. (Fig. 4.45)**

**Diagnosis:** Body elongate-oval; length:width ratio *c.* 2.5–3.5. Oral sucker nearly round, with enlarged oral spines, opens terminally. Ventral sucker unspecialized, embedded in ventrogenital sac. Sucker-width ratio *c.* 1.5–2. Forebody *c.* 30–40% of body-length. Prepharynx short. Oesophagus short. Intestinal bifurcation in mid-forebody. Caeca blind, end close to posterior extremity. Testes two, oblique, in mid-hindbody. Seminal vesicle tubulosaccular. Muscular gonotyls present from immediately anterior to ventral sucker to bifurca1 level. Ovary deeply lobed, immediately anterior to testes. Uterus in hindbody, extends close to posterior extremity. Vitelline follicles in two lateral groups between level of ovary to just inside forebody. Arms of excretory vesicle reach pharynx. In marine fishes (Lutjanidae); Pacific coast of Mexico and Hawaii. Type-species *P. leonilae* Lamothe-Argumedo, 1970.

**43b. Gonotyl single or absent ..... 44.**

**44a. Ovary entirely posterior to or extends distinctly posterior to testes; testes intrude into or completely in forebody ..... 45.**

**44b. Ovary anterior to or at level of testes; testes well posterior to ventral sucker ..... 46.**

**45a. Ventral sucker in posterior third of body; testes well anterior to ventral sucker; ovary posterior to ventral sucker; vitelline follicles entirely anterior to testes ..... ..... *Acanthocollaritrema* Travassos, Freitas & Bührnheim, 1965. (Fig. 4.46)**

**Diagnosis:** Body elongate-oval; length:width ratio *c.* 3–3.5. Oral sucker nearly round, with two rows of enlarged oral spines, opens almost terminally. Ventral sucker unspecialized, embedded in ventrogenital sac in posterior third of body. Sucker-width ratio *c.* 1.25–1.5. Forebody *c.* 75% of body-length. Prepharynx short. Oesophagus short. Intestinal bifurcation in anterior forebody. Caeca blind, end close to posterior extremity. Testes two, almost symmetrical, in mid-forebody. Seminal vesicle bipartite, saccular. Gonotyl absent. Ovary a deeply lobed transverse band, immediately posterior to or slightly overlapping ventral sucker. Uterus extensive in fore- and

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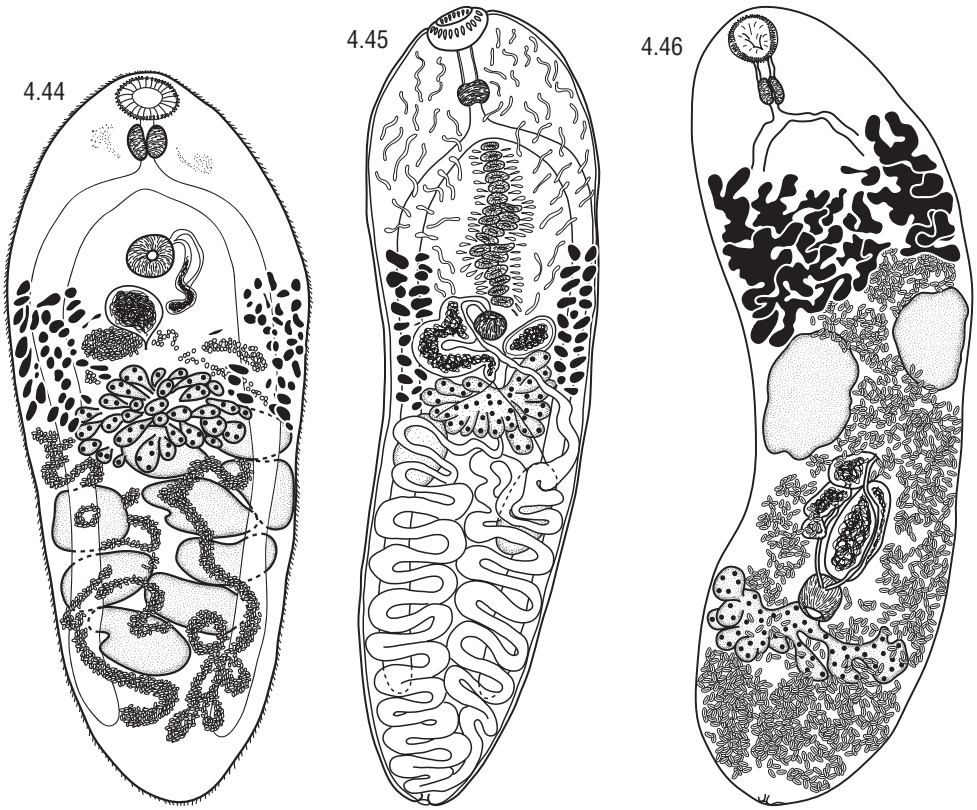



**Fig. 4.44.** *Acanthosiphodera bengalensis* Madhavi, 1976 (emend.). After Madhavi (1976).
**Fig. 4.45.** *Polycryptocylix leonilae* Lamothe-Argumedo, 1970. After Lamothe-Argumedo (1970).
**Fig. 4.46.** *Acanthocollaritrema umbilicatum* Travassos, Freitas & Bührnheim, 1965. After Robaldo & Padovan (1998).

hindbody, extends from slightly anterior to testes to posterior extremity. Vitelline follicles confluent dorsally, from anterior margin of testes to intestinal bifurcation. Arms of excretory vesicle reach bifurcal level. In marine fishes (Centropomidae); off Brazil. Type- and only species *A. umbilicatum* Travassos, Freitas & Bührnheim, 1965.

**45b. Ventral sucker not in posterior third of body; anterior half of testes at level of or extending anterior to ventral sucker; ovary post-testicular; vitelline follicles extend posterior to testes ..... *Retrovarium* Miller & Cribb, 2007. (Fig. 4.47)**

**Diagnosis:** Body squat, almost round to ovoid, rarely extremely squat; length:width ratio *c*. 0.8–1.7. Tegument with small to minute spines. Oral sucker almost round, with enlarged oral spines, opens subterminally to terminally. Ventral sucker unspecialized, embedded in ventrogenital sac. Sucker-width ratio *c*. 1.5–5. Forebody occupies *c*. 25–35% of body-length. Prepharynx very short. Oesophagus very short. Intestinal bifurcation immediately anterior to ventral sucker. Caeca blind, end close to posterior end of body. Testes two, symmetrical; anterior half of testes commonly at level of ventral sucker, may extend into forebody. Seminal vesicle bipartite. Common genital pore immediately anterior to ventral sucker. Gonotyl absent. Ovary deeply lobed, posterior to testes in

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mid-hindbody. Uterus mainly in hindbody; loops may swell into tightly packed 'uterine sac' on dextral or sinistral side of the body, extend close to posterior end of body. Vitelline follicles in two lateral groups, from posterior to ovary to forebody. Arms of excretory vesicle reach bifurcal or pharyngeal level. In marine fishes (Lutjanidae, Haemulidae); tropical Indo-West Pacific. Type-species *R. gardneri* Miller & Cribb, 2007.

**46a. Uterus loops far into forebody, reaches well anteriorly to intestinal bifurcation ..... 47.**
**46b. Uterus does not loop far into forebody, not distinctly anterior to intestinal bifurcation ..... 48.**

**47a. Caeca short, end near anterior half of testes; vitelline follicles in hindbody; in freshwater fishes ..... *Stemmatostoma* Cribb, 1986. (Fig. 4.48)**

**Diagnosis:** Body elongate; length:width ratio *c.* 5. Oral sucker funnel-shaped, longer than wide, with enlarged oral spines, opens terminally. Ventral sucker unspecialized, embedded in ventrogenital sac. Sucker-width ratio *c.* 1.5. Forebody *c.* 50% of body-length. Prepharynx long. Oesophagus long. Intestinal bifurcation immediately anterior to or at level of ventral sucker. Caeca blind, end in anterior half of hindbody. Testes two, oblique, in mid-hindbody. Seminal vesicle bipartite. Gonotyl a simple lobe arising from anterior wall of ventrogenital sac. Ovary trilobed, in mid-hindbody overlapping testes. Uterus in fore- and hindbody, extends close to posterior extremity; anterior loops enter posterior forebody. Vitelline follicles in two lateral groups, between ventral sucker and anterior testis. Arms of excretory vesicle almost reach pharynx. In freshwater fishes (Terapontidae); Australia. Type- and only species *S. pearsoni* Cribb, 1986.

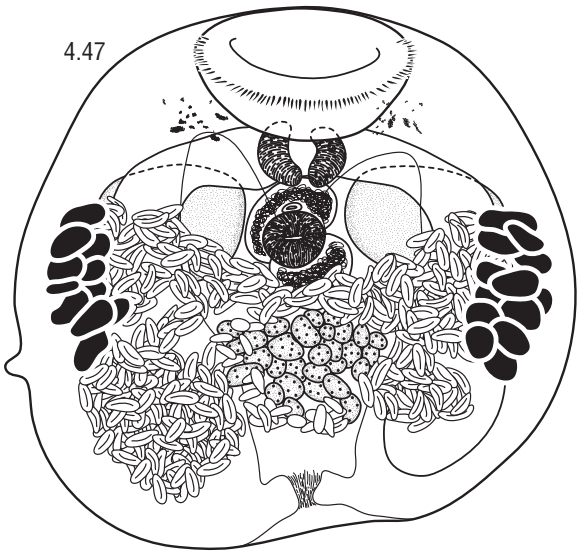
**47b. Caeca long, end well posterior to testes; vitelline follicles extensive in fore- and hindbody; in marine fishes ..... *Anoiktostoma* Stossich, 1899. (Fig. 4.49)**
(Syn. *Ryjikovia* Gaevskaya & Aljoshkina, 1985)

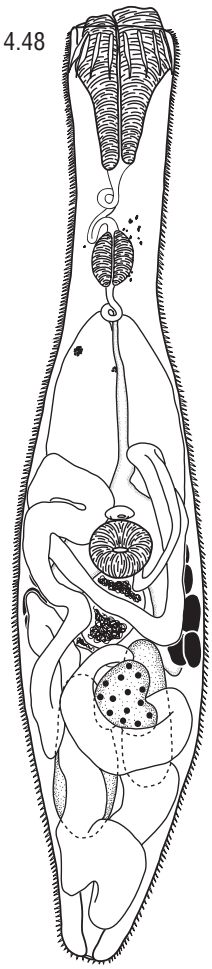
**Diagnosis**: Body oval to fusiform; length:width ratio *c.* 2–4. Oral sucker slightly wider than long, with enlarged oral spines, opens nearly terminally. Ventral sucker unspecialized, not obviously embedded in ventrogenital sac. Sucker-width ratio *c.* 1.5–2.5. Forebody *c.* 30–45% of body-length. Prepharynx very short. Oesophagus long. Intestinal bifurcation immediately anterior to ventral sucker, or in mid-forebody. Caeca long, blind, end well posterior to testes. Testes two, symmetrical to oblique, in hindbody, may be elongate or slightly lobed. Seminal vesicle bipartite. Gonotyl absent. Ovary entire to slightly lobed, sometimes deeply lobed, at level of or immediately anterior to testes. Uterus extensive in fore- and hindbody, may extend close to posterior extremity. Vitelline follicles in two lateral groups, from bifurcation to anterior testis, sometimes confluent in midline. Arms of excretory vesicle almost reach pharynx. In marine fishes (Sciaenidae); Mediterranean Sea and eastern Atlantic. Type-species *A. coronatum* (Wagener, 1852) Stossich, 1899.

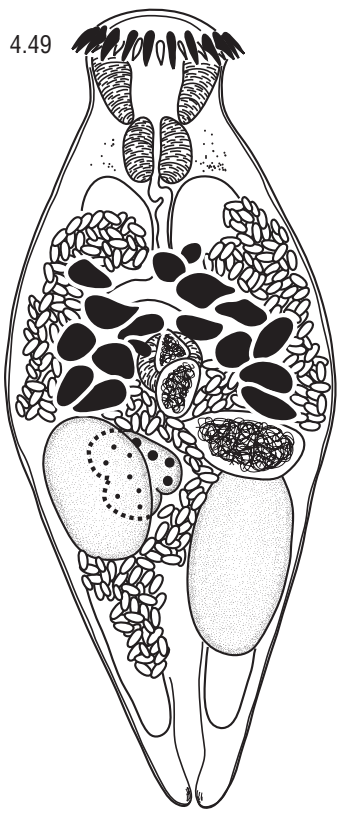
**48a. Intestinal bifurcation well posterior to ventral sucker, in mid-hindbody ..... *Telogaster* Macfarlane, 1945. (Fig. 4.50)**

**Diagnosis:** Body fusiform; length:width ratio *c.* 3.5. Oral sucker nearly round, with enlarged oral spines, opens terminally. Ventral sucker unspecialized, not obviously embedded in ventrogenital sac. Sucker-width ratio *c.* 1. Forebody *c.* 33% of body-length. Prepharynx short. Oesophagus very long. Intestinal bifurcation in mid-hindbody. Caeca blind, end at anterior margin of ovary. Testes two, symmetrical, elongate, at posterior extremity. Seminal vesicle tubulosaccular. Gonotyl absent. Ovary slightly lobed, median, immediately anterior to testes. Uterus in hindbody, not extending

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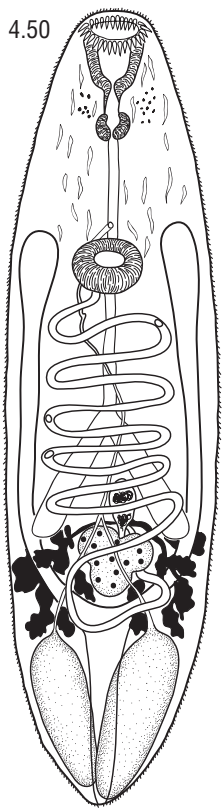




**Fig. 4.47.** *Retrovarium gardneri* Miller & Cribb, 2007. After Miller & Cribb (2007a).
**Fig. 4.48.** *Stemmatostoma pearsoni* Cribb, 1986. After Cribb (1986).
**Fig. 4.49.** *Anoiktostoma coronatum* (Wagener, 1852) Stossich, 1899. After Bartoli & Gibson (1995).
**Fig. 4.50.** *Telogaster opisthorchis* Macfarlane, 1945. After Macfarlane (1945).

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posteriorly beyond anterior margin of testes. Vitelline follicles in two lateral groups in area between anterior margin of testes and anterior margin of ovary. Arms of excretory vesicle reach level of ventral sucker. In freshwater fishes (Anguillidae); Australia and New Zealand. Type- and only species *T. opisthorchis* Macfarlane, 1945.

**48b. Intestinal bifurcation dorsal or well anterior to ventral sucker ..... 49.**

**49a. Ovary entire ..... 50.**[5]
**49b. Ovary slightly to highly lobed ..... 57.**

**50a. Uterus extends well posterior to ovary; one caecum ends well short of other ..... ..... *Anisocladium* Looss, 1902. (Fig. 4.51)**
(Syn. *Anisogaster* Looss, 1901 *nec* Deyrolle, 1862)

**Diagnosis:** Body very elongate; length:width ratio > 20. Oral sucker funnel-shaped, longer than wide, with enlarged oral spines or several wart-like tubercles on margin of sucker, opens nearly terminally. Ventral sucker unspecialized, partly embedded in ventrogenital sac. Sucker-width ratio *c.* 1.25–3. Forebody *c.* 3–20% of body-length. Prepharynx short. Oesophagus short to very short relative to body-length. Intestinal bifurcation immediately anterior to ventral sucker. Caeca blind, unequal; shorter caecum not extending posteriorly beyond posterior testis; longer caecum ends midway between posterior testis and posterior extremity. Testes two, tandem, separate, in hindbody. Seminal vesicle tubular. Gonotyl absent or present as 'small fold' immediately anterior to common genital pore. Ovary entire, anterior to and separated from testes, in posterior half of hindbody. Uterus in hindbody, most profuse posterior to ovary. Vitelline follicles extend from just anterior to ovary to no more than halfway between ovary and ventral sucker. Arms of excretory vesicle extend into forebody. In marine fishes (Uranoscopidae); Mediterranean. Type-species *A. fallax* (Rudolphi, 1819) Looss, 1902.

**50b. Uterus mainly between ovary and ventral sucker; caeca of nearly equal length ..... 51.**

**51a. Testes symmetrical to slightly oblique, close to posterior extremity ..... ..... *Brientrema* Dollfus, 1950. (Fig. 4.52)**

**Diagnosis:** Body fusiform; length:width ratio *c.* 2–2.5. Oral sucker nearly round, with enlarged oral spines, opens terminally. Ventral sucker unspecialized, embedded in ventrogenital sac. Sucker-width ratio *c.* 1.5–2.5. Forebody *c.* 20–25% of body-length. Prepharynx and oesophagus very short. Intestinal bifurcation immediately anterior to or dorsal to ventral sucker. Caeca blind, end close to posterior extremity. Testes two, symmetrical to slightly oblique close to posterior extremity. Seminal vesicle tubulosaccular. Gonotyl a spined muscular structure immediately anterior to ventral sucker. Ovary entire, anterior to testes in posterior hindbody. Uterus in hindbody between ovary and ventral sucker. Vitelline follicles in two lateral groups, in hindbody, from posterior extremity to slightly anterior to ovary. Arms of excretory vesicle reach pharynx. In freshwater fishes (Malapteruridae, Citharinidae) and pelicans (probable pseudoparasitism); Africa. Type-species *B. pelecani* Dollfus, 1950.

**51b. Testes tandem to distinctly oblique in mid-hindbody to posterior extremity ..... 52.**

**52a. Double crown of oral spines present ..... *Acanthostomoides* Szidat, 1956. (Fig. 4.53)**

[5] See Addendum.

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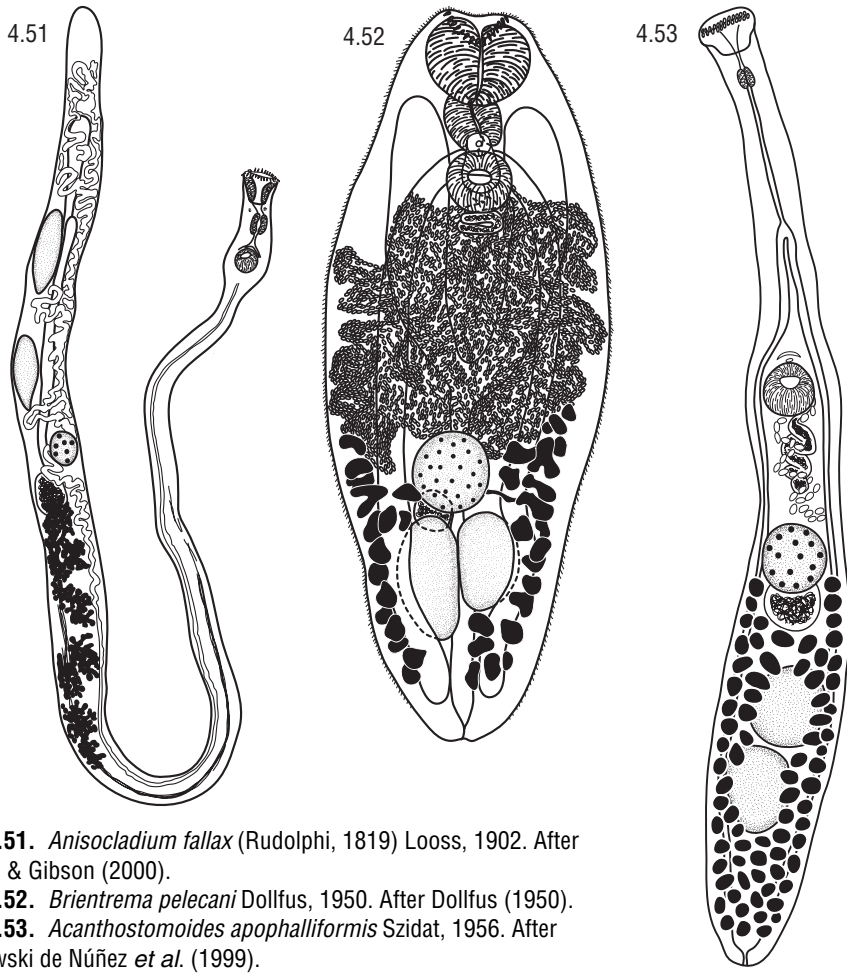



**Fig. 4.51.** *Anisocladium fallax* (Rudolphi, 1819) Looss, 1902. After Bartoli & Gibson (2000).
**Fig. 4.52.** *Brientrema pelecani* Dollfus, 1950. After Dollfus (1950).
**Fig. 4.53.** *Acanthostomoides apophalliformis* Szidat, 1956. After Ostrowski de Núñez *et al.* (1999).

**Diagnosis:** Body elongate, noticeably wider in hindbody; length:width ratio *c.* 4–8. Oral sucker funnel-shaped to almost round, wider than long, with two rows of enlarged oral spines, opens terminally. Ventral sucker unspecialized, embedded in ventrogenital sac. Sucker-width ratio *c.* 1–1.5. Forebody *c.* 35–40% of body-length. Prepharynx short. Oesophagus longer than prepharynx. Intestinal bifurcation in mid-forebody. Caeca blind, end close to posterior extremity. Testes two, tandem to strongly oblique in mid- to posterior hindbody. Seminal vesicle tubulosaccular. Gonotyl absent. Ovary entire, anterior to and separated from testes in anterior half of hindbody. Uterus in hindbody between ovary and ventral sucker. Vitelline follicles confluent dorsally and ventrally from posterior margin of ovary to posterior extremity. Arms of excretory vesicle extend only to ovary. In freshwater fishes (Percichthyidae, Salmonidae); southern South America. Type- and only species *A. apophalliformis* Szidat, 1956.

**52b. Single crown of oral spines present ..... 53.**

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**53a. Gonotyl present ..... 54.**
**53b. Gonotyl absent ..... 55.**

**54a. Gonotyl present as solid muscular pad, immediately anterior to ventral sucker; caeca open via ani close to posterior extremity ..... *Proctocaecum* Baugh, 1957. (Fig. 4.54)**

**Diagnosis:** Body elongate; length:width ratio *c*. 6–15. Oral sucker funnel-shaped, longer than wide, with enlarged oral spines, opens nearly terminally. Ventral sucker unspecialized, embedded in ventrogenital sac. Sucker-width ratio *c*. 1–2.5. Forebody *c*. < 33% of body-length. Prepharynx long, often longer than oesophagus. Oesophagus short. Intestinal bifurcation immediately anterior to ventral sucker. Caeca open at separate ani close to posterior extremity. Testes two, tandem, contiguous or close, in posterior hindbody. Seminal vesicle tubular. Gonotyl present as solid muscular pad, immediately anterior to ventral sucker. Ovary entire, anterior to and separated from testes, in posterior hindbody. Uterus in hindbody, between ovary and ventral sucker. Vitelline follicles in two lateral groups, in hindbody, from level of anterior testis to slightly posterior to ventral sucker. Arms of excretory vesicle reach level of pharynx. In crocodilians and chelonians; Neotropical. Type-species *P. coronarium* (Cobbold, 1861) Baugh, 1957.

**54b. Gonotyl a muscular sucker-like structure immediately anterior to ventral sucker; one caecum ends blindly, other opens via anus close to posterior extremity ..... ..... *Gymnatrema* Morozov, 1955. (Fig. 4.55)**

**Diagnosis:** Body elongate; length:width ratio *c*. 7. Oral sucker funnel-shaped, approximately as long as wide, with enlarged oral spines, opens nearly terminally. Ventral sucker unspecialized, not obviously embedded in ventrogenital sac. Post-ventral sucker pit present. Sucker-width ratio *c*. 3.5. Forebody *c*. 33% of body-length. Prepharynx long. Oesophagus short. Intestinal bifurcation midway between pharynx and ventral sucker. Caeca extend close to posterior extremity, one blind, other opens laterally close to posterior extremity. Testes two, tandem, in posterior hindbody. Seminal vesicle tubular. Gonotyl muscular, sucker-like, immediately anterior to ventral sucker. Ovary entire, anterior to and separated from testes, in hindbody. Uterus in hindbody between ovary and ventral sucker. Vitelline follicles extend from posterior extremity to mid-hindbody, confluent in midline posteriorly. Arms of excretory vesicle reach pharynx. In freshwater fishes (Gymnarchidae); Africa. Type- and only species *G. gymnarchi* (Dollfus, 1950) Morozov, 1955.

**55a. Seminal receptacle pre-ovarian; caeca may open via uroproct or separate ani or end blindly close to posterior extremity ..... *Timoniella* Rebecq, 1960. (Fig. 4.56)**
(Syn. *Pelaezia* Lamothe-Argumedo & Ponciano-Rodríguez, 1986)

**Diagnosis:** Body elongate; length:width ratio *c*. 3–9. Oral sucker funnel-shaped, longer than wide, with enlarged oral spines, opens terminally. Ventral sucker unspecialized, not obviously embedded in ventrogenital sac. Sucker-width ratio *c*. 1–3.5. Forebody *c*. 25–50% of body-length. Prepharynx long, distinctly longer than oesophagus. Oesophagus short. Intestinal bifurcation immediately anterior to ventral sucker. Caeca blind, form cyclocoel or uroproct or open via separate ani close to posterior extremity. Testes two, tandem, contiguous, in posterior hindbody. Seminal vesicle tubular. Simple gonotyl absent or sometimes present. Ovary entire, immediately anterior to testes in posterior hindbody. Seminal receptacle thick-walled, pre-ovarian. Uterus in hindbody, may extend from posterior testis to ventral sucker. Vitelline follicles in two lateral groups, in hindbody, from level of anterior testis to slightly posterior to ventral sucker. Excretory

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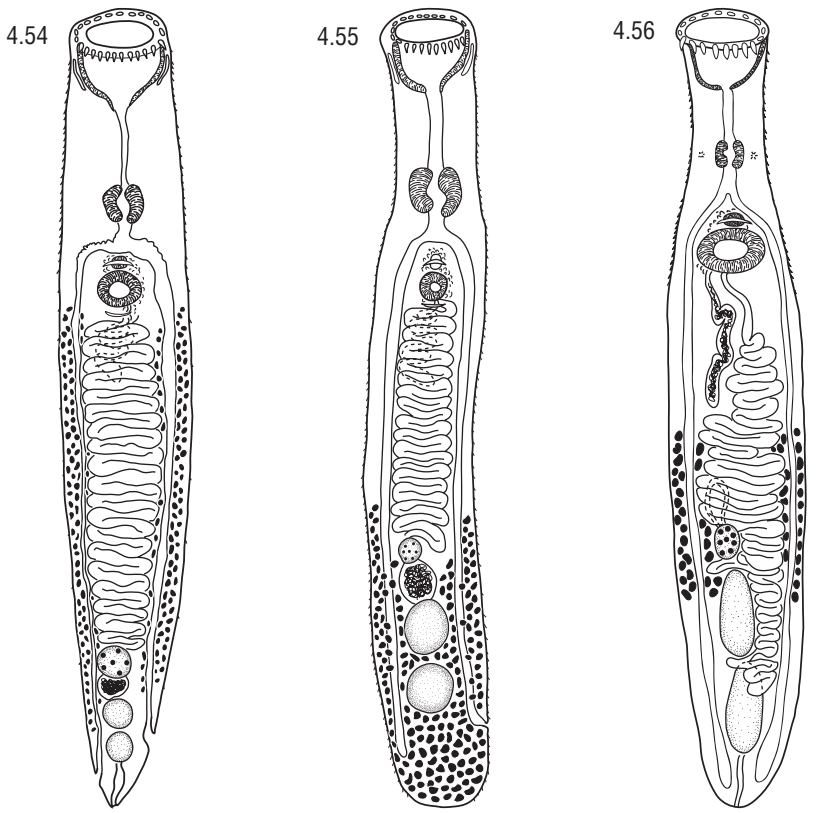



**Fig. 4.54.** *Proctocaecum coronarium* (Cobbold, 1861) Baugh, 1957. After Brooks (1980).
**Fig. 4.55.** *Gymnatrema gymnarchi* (Dollfus, 1950) Morozov, 1955. After Brooks (1980).
**Fig. 4.56.** *Timoniella praeterita* (Looss, 1901) Maillard, 1974. After Brooks (1980).

vesicle extent unknown. In fishes and reptiles; Mediterranean, Caspian, Black Seas and northeast Atlantic. Type-species *T. praeterita* (Looss, 1901) Maillard, 1974, syn. *T. atherinae* Rebecq, 1960.

**55b. Seminal receptacle postovarian; caeca open via ani close to posterior extremity, or may be atrophied or one caecum may be lost ..... 56.**

**56a. Tegumental spines distinctly enlarged in forebody; caeca open separately at same level close to posterior extremity ..... *Caimanicola* Freitas & Lent, 1938. (Fig. 4.57)**

**Diagnosis:** Body elongate; length:width ratio *c.* 5. Tegumental spines unusually robust in forebody. Oral sucker funnel-shaped, nearly as long as wide, with enlarged oral spines, opens nearly terminally. Ventral sucker unspecialized, not obviously embedded in ventrogenital sac. Sucker-width ratio *c.* 2.5. Forebody *c.* 33% of body-length. Prepharynx short. Oesophagus usually distinct, sometimes very short. Intestinal bifurcation in posterior forebody. Caeca open via separate ani at same level close to posterior extremity. Testes two, tandem, in posterior hindbody. Seminal

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vesicle tubular. Gonotyl absent. Ovary entire, immediately anterior to anterior testis. Uterus in hindbody, anterior to ovary. Vitelline follicles in two lateral groups, from level of gonads to midway between ovary and ventral sucker. Excretory vesicle extent unknown. In crocodilians and chelonians; Neotropical. Type-species C. *marajoara* Freitas & Lent, 1938.

**56b. Tegumental spines not distinctly enlarged in forebody; caeca usually open separately close to posterior extremity, but may be atrophied or one caecum may be lost ..... ..... *Acanthostomum* Looss, 1899. (Fig. 4.58)**

(Syns *Acanthochasmus* Looss, 1901; *Atrophecaecum* Bhalerao, 1940; *Ateuchocephala* Coil & Kuntz, 1960; *Haplocaecum* Simha, 1958; *Paracanthostomum* Fischthal & Kuntz, 1965; *Stunkardiella* Lamothe-Argumedo & Ponciano-Rodríguez, 1986)

**Diagnosis:** Body elongate-oval to distinctly elongate; length:width ratio *c*. 2-3.5. Oral sucker funnel-shaped, with enlarged oral spines (rarely without spines), opens terminally. Ventral sucker unspecialized, not obviously embedded in ventrogenital sac. Sucker–width ratio *c*. 1–2.5. Forebody *c*. 5–40% of body-length. Prepharynx short. Oesophagus short. Intestinal bifurcation just anterior to ventral sucker. Caeca open via separate ani close to posterior extremity at same level; one may be atrophied or there may only be one caecum. Testes two, tandem, contiguous or nearly so, in posterior hindbody. Seminal vesicle tubular. Gonotyl absent. Ovary entire, immediately anterior to anterior testis in posterior hindbody. Uterus in hindbody, between ovary and ventral sucker. Vitelline follicles in two lateral groups, in hindbody, may extend from level of anterior testis to

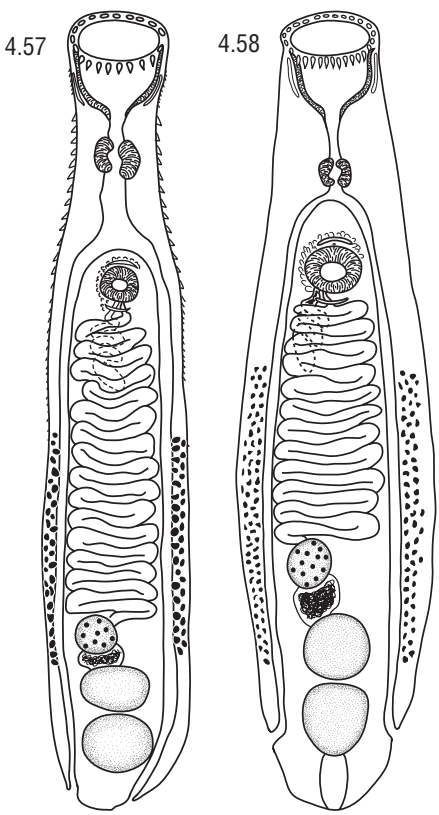


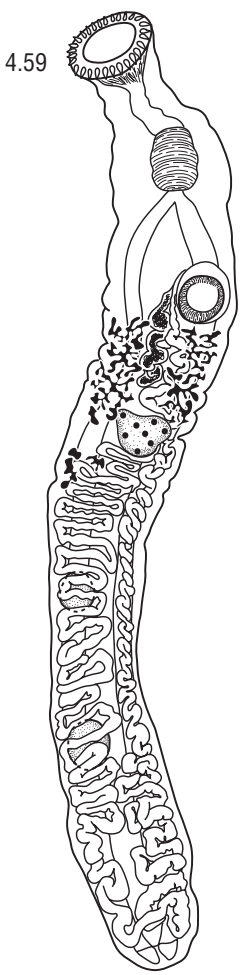

**Fig. 4.57.** *Caimanicola marajoara* Freitas & Lent, 1938. After Brooks (1980).
**Fig. 4.58.** *Acanthostomum spiniceps* Looss, 1899. After Brooks (1980).

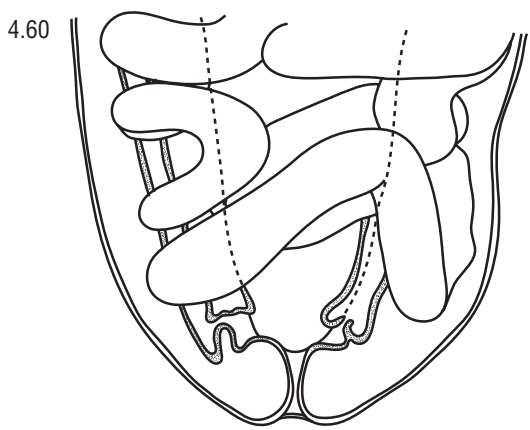
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slightly posterior to ventral sucker. Arms of excretory vesicle reach pharynx. In fishes and reptiles; cosmopolitan. Type-species *A. spiniceps* Looss, 1899.

**57a. Caeca open via uroproct at posterior extremity .....**
**..... *Pseudoacanthostomum* Caballero, Bravo-Hollis & Grocott, 1953. (Figs 4.59, 4.60)**

**Diagnosis:** Body elongate-oval; length:width ratio *c*. 3.5–7.5. Oral sucker funnel-shaped, about as long as wide, with enlarged oral spines, opens terminally. Ventral sucker unspecialized, embedded in ventrogenital sac. Sucker-width ratio *c*. 2. Forebody *c*. 20–33% of body-length. Prepharynx short. Oesophagus short. Intestinal bifurcation in mid-forebody. Caeca open via uroproct at posterior extremity. Testes two, tandem, separate or contiguous, in mid-hindbody. Seminal vesicle tubulosaccular. Gonotyl absent. Ovary slightly lobed, about midway between ventral sucker and testes. Uterus in hindbody, most profuse from ovary to posterior extremity. Vitelline follicles in two lateral groups in hindbody, between level of anterior testis and ventral sucker. Arms of excretory vesicle reach pharynx. In marine siluriforms (Ariidae); eastern Pacific and western Atlantic. Type- and only species *P. panamense* Caballero, Bravo-Hollis & Grocott, 1953.




**Figs 4.59, 4.60.** *Pseudoacanthostomum panamense* Caballero, Bravo-Hollis & Grocott, 1953. 4.59. After Yamaguti (1971). 4.60. Uroproct. After Scholz *et al.* (1999).

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**57b. Caeca end blindly ..... 58.**

**58a. Thin-walled membrane surrounds seminal vesicle, pars prostatica and short ejaculatory duct ..... *Parspina* Pearse, 1920. (Fig. 4.61)**
(Syn. *Proneochasmus* Szidat, 1954)

**Diagnosis:** Body oval; length:width ratio *c.* 1.5–2.5. Oral sucker nearly round in outline to slightly funnel-shaped, longer than wide, with enlarged oral spines, opens terminally. Ventral sucker unspecialized, embedded in ventrogenital sac. Sucker-width ratio *c.* 1–1.5. Forebody *c.* 25–33% of body-length. Prepharynx very short. Oesophagus very short. Intestinal bifurcation immediately anterior to ventral sucker. Caeca blind, end close to posterior extremity. Testes two, symmetrical to slightly oblique in mid-hindbody. Seminal vesicle, small pars prostatica and ejaculatory duct enclosed in thin-walled membrane. Gonotyl absent. Ovary slightly lobed, transversely elongate, immediately anterior to testes. Uterus in hindbody, extends close to posterior extremity. Vitelline follicles in two lateral groups, from level of testes to mid-forebody. Arms of excretory vesicle reach pharynx. In freshwater siluriforms (Heptapteridae and Pimelodidae); South America. Type-species *P. bagre* Pearse, 1920.

**58b. Thin-walled membrane surrounding seminal vesicle, pars prostatica and short ejaculatory duct absent ..... 59.**

**59a. Gonotyl present as muscular pad, as sucker-like structure or as non-muscular lobes posterior to common genital pore ..... *Neochasmus* Van Cleave & Mueller, 1932. (Fig. 4.62)**

**Diagnosis:** Body oval to elongate-oval; length:width ratio *c.*2–3.5. Oral sucker nearly round or distinctly wider than long, with enlarged oral spines, opens nearly terminally. Ventral sucker unspecialized, embedded in ventrogenital sac. Sucker-width ratio *c.* 1–2. Forebody *c.* 15–25% of body-length. Prepharynx short. Oesophagus short. Intestinal bifurcation immediately anterior to or dorsal to ventral sucker. Caeca blind, end immediately posterior to testes or midway between testes and posterior extremity. Testes two, symmetrical, in mid-hindbody. Seminal vesicle tubulosaccular. Gonotyl present as solid spined or unspined muscular pad, sucker-like structure or non-muscular lobes of tegument immediately posterior to ventral sucker or common genital pore. Ovary deeply divided to distinctly follicular, forms transverse band occupying nearly entire width of body immediately anterior to testes. Uterus in hindbody, not developed extensively anterior to ovary. Vitelline follicles in two lateral groups, from level of testes to ventral sucker. Arms of excretory vesicle reach pharynx. In freshwater fishes (Moronidae, Centrarchidae, Ictaluridae, Percidae) and reptiles (Colubridae); North America. Type-species *N. umbellus* Van Cleave & Mueller, 1932.

**59b. Gonotyl absent or, if present, not posterior to common genital pore ..... 60.**

**60a. One caecum distinctly shorter than other; longer caecum ends well short of posterior extremity; uterus does not extend posterior to longer caecum ..... ..... *Anisocoelium* Lühe, 1900. (Fig. 4.63)**

**Diagnosis:** Body elongate to fusiform; length:width ratio *c.* 6–7. Oral sucker slightly wider than long, with enlarged oral spines, opens nearly terminally. Ventral sucker unspecialized, embedded in ventrogenital sac. Sucker-width ratio *c.* 2. Forebody *c.* 20–25% of body-length. Prepharynx short. Oesophagus short. Intestinal bifurcation in mid-forebody. Caeca blind, distinctly unequal, longer caecum ends well short of posterior extremity. Testes two, tandem to highly oblique, in anterior hindbody. Seminal vesicle tubular. Gonotyl absent. Ovary deeply lobed, median, ventral and overlaps anterior testis. Uterine coils mainly in hindbody, not extending posteriorly beyond

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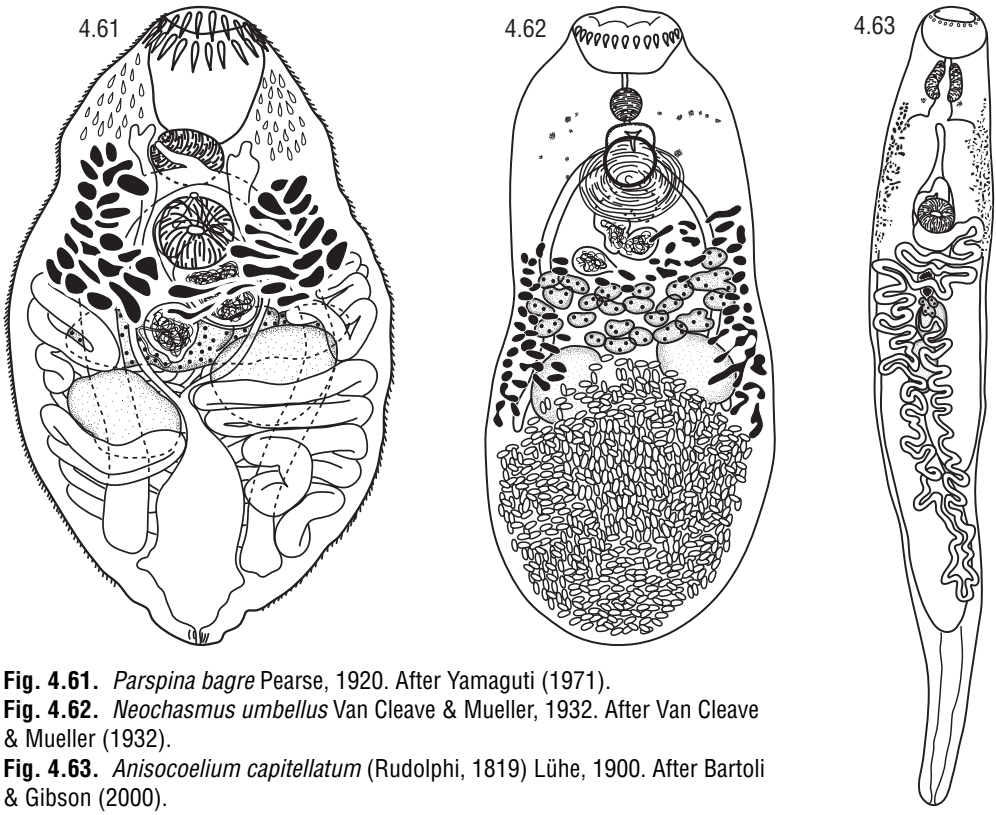



**Fig. 4.61.** *Parspina bagre* Pearse, 1920. After Yamaguti (1971).
**Fig. 4.62.** *Neochasmus umbellus* Van Cleave & Mueller, 1932. After Van Cleave & Mueller (1932).
**Fig. 4.63.** *Anisocoelium capitellatum* (Rudolphi, 1819) Lühe, 1900. After Bartoli & Gibson (2000).

end of longer caecum. Vitelline follicles in two lateral groups, from slightly posterior to ventral sucker to pharynx. Arms of excretory vesicle reach pharynx. In marine fishes (Uranoscopidae); Mediterranean. Type- and only species *A. capitellatum* (Rudolphi, 1819) Lühe, 1900.

**60b. Caeca of nearly equal length; uterus extends close to posterior extremity ..... 61.**

**61a. Testes tandem ..... *Pseudallacanthochasmus* Velasquez, 1961.[6] (Fig. 4.64)**
**Diagnosis:** Body elongate-oval to elongate; length:width ratio *c*. 3.5–8. Oral sucker funnel-shaped, approximately as long as wide, with enlarged oral spines, opens terminally. Ventral sucker unspecialized, embedded in ventrogenital sac. Sucker-width ratio *c*. 1.5–2. Forebody *c*. 25–33% of body-length. Prepharynx short. Oesophagus short. Intestinal bifurcation in mid-forebody or immediately anterior to ventral sucker. Caeca blind, end close to posterior extremity. Testes two, tandem, separated or contiguous, in posterior hindbody. Seminal vesicle tubulosaccular. Gonotyl absent. Ovary slightly lobed, anterior to testes in mid-hindbody. Uterus in hindbody, extends close to posterior extremity. Vitelline follicles in two lateral groups sometimes confluent in midline, may extend from level of anterior testes to bifurcation. Arms of excretory vesicle reach

[6] See Addendum.

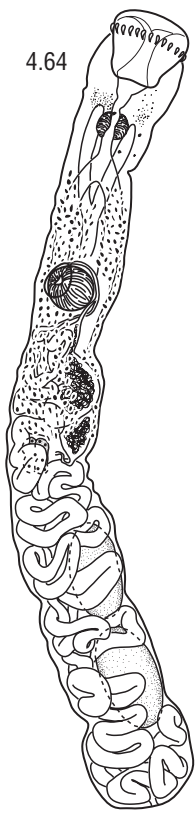
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pharynx. In marine fishes (Lutjanidae and Sparidae); eastern Atlantic and Indo-Pacific. Type-species *P. grandispinus* Velasquez, 1961.

**61b. Testes symmetrical to distinctly oblique ..... 62.**

**62a. Ventral sucker similar in size or slightly larger than oral sucker; tegument distinctly thick in anterior half of body; vitelline follicles extend well posteriorly beyond testes ..... ..... *Neometadena* Hafeezullah & Siddiqi, 1970. (Fig. 4.65)**
(Syn. *Neoparacryptogonimus* Hafeezullah, 1975)

**Diagnosis:** Body oval; length:width ratio *c.* 1.5. Tegument distinctly thick in anterior half of body. Oral sucker nearly round in outline, with enlarged oral spines, opens terminally. Ventral sucker unspecialized, not obviously embedded in ventrogenital sac, similar in size to or slightly larger than oral sucker. Sucker-width ratio *c.* 0.8–1.5. Forebody *c.* 25% of body-length. Prepharynx very short. Oesophagus very short. Intestinal bifurcation immediately anterior to or dorsal to ventral sucker. Caeca blind, end close to posterior extremity. Testes two, symmetrical, intercaecal, in mid-hindbody. Seminal vesicle tubulosaccular. Gonotyl absent. Ovary forms three to four large lobes immediately anterior to or slightly overlapping testes. Uterus in hindbody, extends close to posterior extremity. Vitelline follicles in two predominantly extracaecal lateral groups, from posterior extremity to ventral sucker. Arms of excretory vesicle reach pharynx. In marine fishes (numerous families, primarily Lutjanidae); Indo-Pacific. Type- and only species *N. ovata* (Yamaguti, 1952) n. comb., syn. of *N. lutiani* Hafeezullah & Siddiqi, 1970.



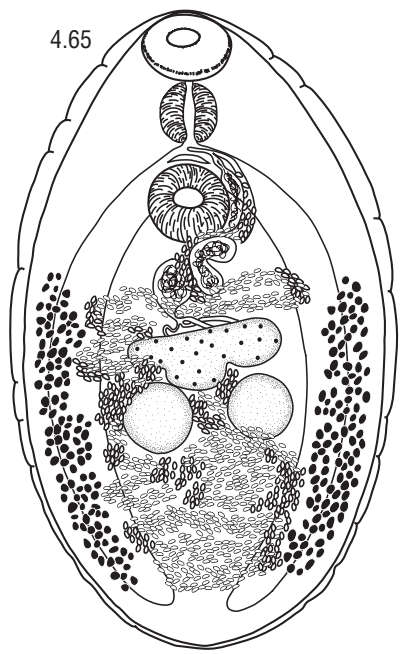




**Fig. 4.64.** *Pseudallacanthochasmus grandispinus* Velasquez, 1961. After Yamaguti (1971).
**Fig. 4.65.** *Neometadena ovata* (Yamaguti, 1952) n. comb. After Yamaguti (1952).

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**62b. Ventral sucker smaller than oral sucker; tegument not distinctly thick in anterior half of body; vitelline follicles do not extend noticeably posterior beyond testes ..... 63.**

**63a. Gonotyl present as distinctly muscular lobe or cylindrical stalk-like structure, immediately anterior to common genital pore; ovary forms distinct transverse deeply lobed band, occupies nearly entire body-width; in freshwater Perciformes ..... ..... *Allacanthochasmus* Van Cleave, 1922. (Fig. 4.66)**

**Diagnosis:** Body elongate-oval; length:width ratio *c.* 2–5. Oral sucker slightly wider than long to slightly funnel-shaped, with enlarged oral spines, opens nearly terminally. Ventral sucker unspecialized, embedded in ventrogenital sac. Sucker-width ratio *c.* 1.5–2.5. Forebody *c.* 45% of body-length. Prepharynx short. Oesophagus short. Intestinal bifurcation in mid- to anterior forebody. Caeca blind, end midway between testes and posterior extremity or close to it. Testes two, symmetrical to highly oblique, in mid- to anterior hindbody. Seminal vesicle tubulosaccular, may extend well into forebody. Gonotyl present as muscular lobe or cylindrical stalk-like structure with five small projections at distal end, immediately anterior to common genital pore. Ovary deeply lobed, forms transverse band, occupies nearly entire body-width, midway between testes and ventral sucker. Uterus in hindbody, extends close to posterior extremity. Vitelline follicles in two lateral groups, from level of ovary to mid-forebody. Arms of excretory vesicle reach pharynx. In freshwater Perciformes (Moronidae); North America. Type-species *A. varius* Van Cleave, 1922.

**63b. Gonotyl absent or if present, not as above, but a non-muscular lobe or folding of tegument; ovary relatively compact; in marine Perciformes ..... ..... *Siphoderina* Manter, 1934.[7] (Figs 4.67, 4.68)**

(Syns *Lappogonimus* Oshmarin, Mamaev, & Parukhin, 1961; *Paracryptogonimus* Yamaguti, 1934)

**Diagnosis:** Body oval to elongate-oval; length:width ratio *c.* 1–9. Oral sucker usually almost round, may be shorter or longer than wide, with enlarged oral spines, opens subterminally to terminally. Ventral sucker unspecialized, embedded in ventrogenital sac. Sucker-width ratio *c.* 1–5. Forebody *c.* 15–50% of body-length. Prepharynx short. Oesophagus short. Intestinal bifurcation immediately anterior to or dorsal to ventral sucker or in mid-forebody. Caeca blind, end close to posterior extremity, rarely at level of testes. Testes two, symmetrical to distinctly oblique, entire to deeply lobed, in mid-hindbody. Seminal vesicle tubulosaccular. Gonotyl absent or present as nonmuscular 'small fold' of tegument immediately anterior to common genital pore. Ovary deeply lobed, slightly overlaps or well separated from testes in mid- to anterior hindbody. Uterus in hindbody, extends close to posterior extremity. Vitelline follicles in two lateral groups, may be partly confluent medially, from level of testes to well into forebody; follicles not extending posteriorly beyond posterior margin of testes. Arms of excretory vesicle reach pharynx. In marine and euryhaline fishes (numerous families, primarily Lutjanidae); cosmopolitan. Type-species *S. brotulae* Manter, 1934.

## Addendum

*Caulanus* Miller & Cribb, 2007, based on *C. thomasi* Miller & Cribb, 2007 from *Lutjanus bohar* from the Great Barrier Reef and the Maldives, is closest to *Pseudallacanthochasmus*, but differs in having ani and a uterus that is extensive in both fore- and hindbodies (Miller & Cribb, 2007b).

[7] See Addendum.

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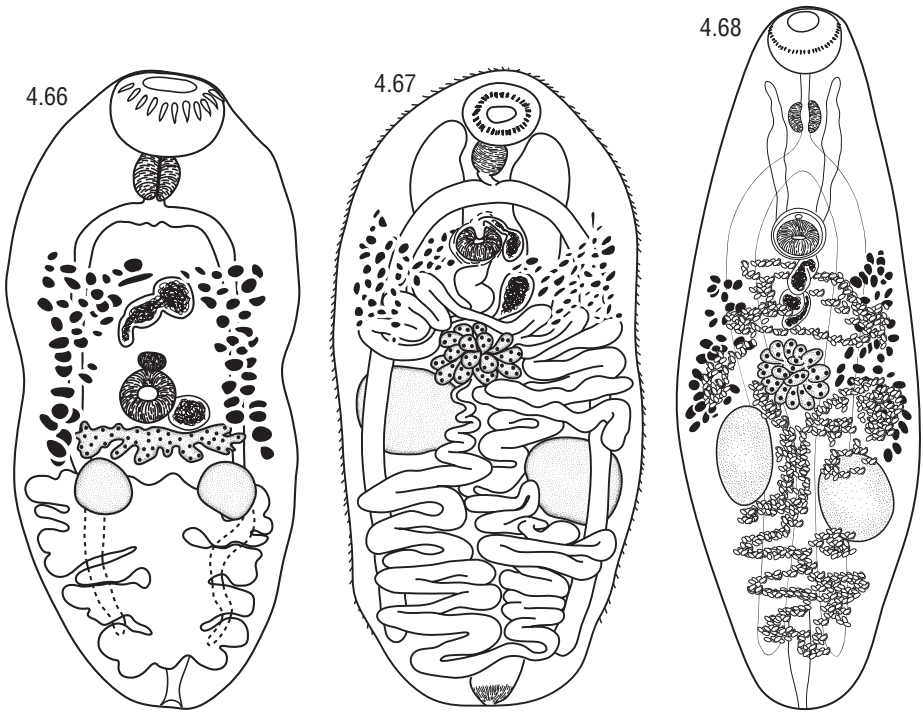



**Fig. 4.66.** *Allacanthochasmus varius* Van Cleave, 1922. After Van Cleave (1922).
**Figs 4.67, 4.68.** 4.67. *Siphoderina paracatalae* Durio & Manter, 1969. After Durio & Manter (1969). 4.68. *S. acanthostomus* (Yamaguti, 1934) n. comb. After Yamaguti (1934).

*Latuterus* Miller & Cribb, 2007, based on two species from *Lutjanus bohar* from the Great Barrier Reef and the Maldives differs from *Allometadena* in having the vitellarium in the forebody and having intercaecal testes (Miller & Cribb, 2007b).

*Beluesca* Miller & Cribb, 2007, based on two species from *Plectorhinchus gibbosus*, from the Great Barrier Reef, differs from other cryptogonimids in the combination of an elongate body, the funnel-shaped oral sucker, relatively few oral spines, a highly lobed ovary, the symmetrical to oblique testes, the uterus restricted to the hindbody and the vitellarium reaching anteriorly from the ovary into the forebody (Miller & Cribb, 2007c).

*Cheladiadema* Miller & Cribb, 2007, based on *C. marjoriae* Miller & Cribb, 2007 from haemulid fishes on the Great Barrier Reef, differs from other cryptogonimids in the combination of the lanceolate body, the relatively few oral spines, an entire ovary, a prepharynx longer than the oesophagus, tandem testes, the uterus restricted to the hindbody and reaching into the post-testicular region and vitelline fields reaching from the ovary to the pharynx (Miller & Cribb, 2007c).

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# 5 Family Heterophyidae Leiper, 1909

John Pearson

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## Introduction

Notable essays in defining the family Heterophyidae Leiper, 1909[1] are those of Ransom (1920) and Witenberg (1929), following on from the careful anatomical studies of Looss (1894) on *Heterophyes* Cobbold, 1886 and Jägerskiöld (1896, 1899, 1903) on *Galactosomum* Looss, 1899, *Cryptocotyle* Lühe, 1899 and *Scaphanocephalus* Jägerskiöld, 1903, together with the dismembering of the behemoths *Distomum* Retzius, 1786 and *Monostomum* Rudolphi, 1809. Witenberg (1929) introduced the neutral term gonotyl, which is free of implications of form to which the earlier term genital sucker was prone. Witenberg (1929, 1953) and others, including Price (1940), Martin (1950a, b, 1951, 1958) and Yamaguti (1971), failed to distinguish between the gonotyl and the ventral sucker when the latter had changed shape and acquired spines or sclerites. They almost invariably called the modified sucker a gonotyl, and, by default, the gonotyl a reduced ventral sucker. This confusion appears to stem from Witenberg's employing his new term, gonotyl, first for *Heterophyes*, in which it is armed and the ventral sucker unmodified, and later in the same paper identifying as gonotyls the armed, un-sucker-like bodies in *Stictodora* Looss, 1899, *Haplorchis* Looss, 1899 and *Adleriella* Witenberg, 1930.

Chen (1936) correctly identified the armed ventral sucker of *Haplorchis* and stated in his diagnosis of the family that the ventral sucker is present and a gonotyl is often present; but he offered no argument. Chaos was made cosmos for *Stictodora* and *Galactosomum* by Cable *et al.* (1960), who pointed out that the ventral sucker is identified by its encapsulating muscular septum, to which Rees (1978) added a limiting membrane. Rees also reiterated the view of Cable & Hunninen (1942) that genital and ventrogenital sacs are distinct from the genital atrium.

Pearson (2002) dissected Witenberg's gonotyl into three, non-homologous anatomies, namely: a variously modified and armed ventral sucker that is identifiable by its capsule with

[1] Leiper (1909) first used the name Heterophyinae in a report 'presented to both UK Houses of Parliament by command of His Majesty. March, 1909'. Later in the same year (May), Nicoll (1909) also used this subfamily name. According to the 'Principle of Coordination' (ICZN, 1999, Art. 36.1), Leiper, 1909 is the correct authorship for the family Heterophyidae.

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limiting membrane and possession of nuclei; a modified genital atrium enclosed by a pseudocapsule composed of an open meshwork of muscle fibres; and a gonotyl that is largely muscular and defined by its unbounded origin from the wall of the ventrogenital sac and the absence of nuclei. A fourth anatomy is a copulatory organ in the form of an eversible, tubular invagination of the wall of the ventrogenital sac dorsally. These definitions inform the present key.

Subfamilies are not recognized here because their usefulness must await revision to be refined by molecular studies, particularly in reference to the systematic value of the ventrogenital complex.

Cable *et al*. (1960) elevated the subfamily Tetracladiinae Yamaguti, 1958 to family status for *Tetracladium* Kulachkova, 1954 and their new genus *Opisthovarium* Cable, Connor & Balling, 1960, but, as described herein, there is no justification for this elevation.

The following subjective synonyms are proposed: *Opisthovarium*, synonym of *Tetracladium* Kulachkova, 1954; *Metagonimoides* Price, 1931, synonym of *Metagonimus* Katsurada, 1912; *Massaliatrema* Dollfus & Timon-David, 1960, synonym of *Cryptocotyle* Lühe, 1899; *Caiguiria* Nasir & Diaz, 1971, synonym of *Pygidiopsis* Looss, 1901; *Pricetrema* Ciurea, 1933 and *Apophalloides* Yamaguti, 1971, synonyms of *Apophallus* Lühe, 1909; *Sobolephya* Morozov, 1950, synonym of *Stictodora* Looss, 1899; *Parastictodora* Martin, 1950, synonym of *Acanthotrema* Travassos, 1928; and *Allocercarioides* Yamaguti, 1971, synonym of *Galactosomum* Looss, 1899.

All but two of the nine generic synonymies proposed in the key are based on the examination of specimens of the type-species, which exhibited congruence of structure of the ventrogenital complex and absence of significant differences in other characters. The exceptions are: *Sobolephya* Morozov, 1950, for which no specimens could be borrowed, but which appears to differ from *Stictodora* only in the position of the ovary, seemingly the result of death and attenuation of the body before fixing; and *Apophalloides* Yamaguti, 1971, known from a single specimen, which is most probably a macerated and distorted member of *Apophallus* Lühe, 1909.

Accepting the synonymy of *Sobolephya* and *Stictodora*, local material of the type-species of *Sobolephya* is given the appellation *Stictodora oshmarini* (Morozov, 1952) n. comb.

Comparison of a paratype of *Heterophyopsis niemongolis* Qiu, Zhang & Lie, 1984 with locally collected specimens of a species of *Heterotestophyes* Leonov, 1957 confirmed that the specimens were conspecific, but revealed that the paratype had the oral sucker diagnostic of *Heterotestophyes*; hence the appellation *Heterotestophyes niemongolis* (Qiu, Zhang & Lie, 1984) n. comb. is used here.

*Pseudexorchis* Yamaguti, 1938 is included here, as its cercaria is not cryptogonimid but heterophyid.

Characters of prime importance in identification are, *pace* Witenberg (1929) and Yamaguti (1971), those of the terminal genital ducts, ventral sucker and their adnexae, collectively the ventrogenital complex, the elements of which are discussed by Pearson (1964, pp. 602ff., 670, 1973). The adnexae comprise one or two gonotyls and an invagination of the ventral body-wall. The gonotyl is a projection, typically muscular, unarmed, anucleate and not sucker-like, arising from the wall of the ventrogenital sac, and overhanging or bearing the genital pore; it is not a discrete organ, and in this is distinct from the ventral sucker, which has a muscular capsule, a limiting and stainable membrane and nuclei, whether sucker-like or modified in shape and armed, or even non-muscular (Rees, 1978). The invagination of the body-wall includes the genital pore, forming a genital sac, as in the first five genera in the key; or it also includes the ventral sucker and gonotyl, if present, forming a ventrogenital sac, as in all other genera. The ventrogenital sac is typically permanent; but may be facultative, that is, the ventral sucker may be flush with the ventral surface or withdrawn into the sac.

Details of the complicated and three-dimensional ventrogenital complex can be studied with ease and accuracy only in unflattened specimens mounted ventral surface up. Methods for preparing good whole-mounts are given by Pearson & Ow-Yang (1982).

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The distribution of vitelline follicles and the course of the uterus are as illustrated, unless otherwise stated in the definition.

The following genera may be heterophyids but are at present unrecognizable and treated as *incertae sedis: Ophiohaplorchis* Yamaguti, 1971, *Ponticotrema* Issaitschikow, 1927, *Tauridiana* Issaitschikow, 1924 and *Tubanguia* Srivastava, 1935.

## Family Heterophyidae Leiper, 1909

(Syns Coenogoniminae Looss, 1899 (superseded – ICZN Art 40.2); Adleriellinae Witenberg, 1930; Apophallinae Ciurea, 1924; Ascocotylinae Yamaguti, 1958; Centrocestinae Looss, 1899; Cercarioidinae Witenberg, 1929; Cotylogoniminae Pratt, 1902; Cryptocotylinae Lühe, 1909; Diplotrematidae Connor, 1957; Euryhelminthinae Morozov, 1950; Galactosominae Ciurea, 1933; Haplorchinae Looss, 1899; Irinaiinae Yamaguti, 1971; Knipowitschetrematinae Morozov, 1950; Metagoniminae Morozov, 1950; Monorchotreminae Nishigori, 1924; Ophiohaplorchiinae Yamaguti, 1971; Opisthometrinae Yamaguti, 1958; Phagicolinae Faust, 1920; Pygidiopsinae Yamaguti, 1958; Scaphanocephalinae Yamaguti, 1958; Stellantschasminae Price, 1939; Stictodoridae Poche, 1926; Tetracladiinae Yamaguti, 1958)

**Diagnosis:** Body-shape various, with average lengths 900–2300 μm (range 200–7000 μm). Tegument of forebody armed with ctenoid scales, less often spines; scales become spines on hindbody. Scattered cercarial pigment granules usually occur in forebody. Oral sucker with or without dorsal ridge, dorsal lobe, posterior prolongation or circles of spines. Ventral sucker always present and nucleate, unmodified and with axis of symmetry dorsoventral, or modified, with axis inclined, and one or more of: cavity reduced or absent, asymmetry, reduced musculature, armature of spines or sclerites. Prepharynx usually short. Pharynx present. Oesophagus long or short. Caeca two, long or short, rarely with anterior diverticula, terminate blindly. Testes one or two, usually symmetrical, entire or lobed. Cirrus and cirrus-sac absent. Seminal vesicle undivided or bi- or tripartite or chambered; distal chamber may be a thick-walled expulsor. Genital or ventrogenital sac present, rarely armed with spines or sclerites. Gonotyl present or absent, one or two, some with narrow pockets, spined only in *Procerovum*. Genital atrium typically short, rarely spined. Genital pore, rarely separate male and female pores, close to and anterior, anterosinistral, posterosinistral, posterodextral or posterior to ventral sucker, opening on wall of ventrogenital sac or on gonotyl, on wall of genital sac, rarely in ventral sucker. Ovary entire or lobed, usually anterior to testes, rarely between or posterior to testes. Seminal receptacle typically canalicular, rarely uterine. Laurer's canal present. Eggs operculate, thick-shelled, with or without abopercular knob, partly or fully embryonated, 22–57 μm long. Vitellarium follicular, typically in hindbody, may extend into forebody. Excretory vesicle saccate, tubular, V- or Y-shaped, with or without additional arms, slender or inflated, rarely passing ventral sucker; pore terminal or nearly so. In fish- and frog-eating birds and mammals, and freshwater siluroid fish. Type-genus *Heterophyes* Cobbold, 1886.

## Key to genera

**1a. Genital sac present, distinctly separate from ventral sucker; genital pore not close against ventral sucker; gonotyl absent (Fig. 5.1) ..... 2.**

**1b. Ventrogenital sac present, facultative or permanent; genital pore close against ventral sucker; gonotyl present or absent (Figs 5.18, 5.66) ..... 6.**

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**2a. Genital sac posterodextral to ventral sucker, small; genital atrium largely eversible, heavily spined, opens simply into genital sac ..... *Protoheterophyes* Pearson, 2002. (Figs 5.1–5.3)**

**Diagnosis:** Body subclavate, 0.9–1.32 mm long, forebody shorter than hindbody. Tegument scaly. Seminal vesicle thin-walled, bipartite. Genital atrium eversible, armed with stout, curved spines in distal two-thirds, joined by radial muscle fibres to open network of criss-crossing, primarily meridional muscle fibres that form globular pseudocapsule with parenchymatous medulla and no limiting membrane, opens simply into genital sac. Gonotyl absent. Genital sac posterodextral to ventral sucker, small. Genital pore not close against ventral sucker. Testes oblique. Seminal receptacle canalicular, small. Coils of uterus often full of sperm. Eggs 29–35 × 16–19 µm. In birds; Australia. Type-species *P. spuriocirrus* Pearson, 2002.

**2b. Genital sac posterosinistral to ventral sucker, large; genital atrium lightly spined or spineless, opens on half papilla on large, protractile, slightly eversible protrusion armed with one or two circles of cteniform sclerites ..... 3.**

**3a. Oral sucker with dorsal transverse muscular ridge separated by parenchyma from main body of sucker; arms of excretory vesicle exceed ovary ..... ..... *Heterotestophyes* Leonov, 1957. (Figs 5.4, 5.5)**

**Diagnosis:** Body elongate; forebody longer than hindbody, 1.3–2.0 mm long. Oral sucker with dorsal transverse muscular ridge separated by parenchyma from main body of sucker. Seminal vesicle thin-walled, bipartite. Genital sac present, distinctly separate from ventral sucker. Protrusion with pseudocapsule, armed with single, uninterrupted circle of 70–120 sclerites, encloses spined genital atrium, which enters dorsally and enlarges to open ventrally on an excentric half-papilla. Genital pore not close against ventral sucker. Gonotyl absent. Seminal receptacle uterine. Eggs 24–32 × 14–20 µm. Arms of excretory vesicle extend anteriorly beyond ovary. In terns and gulls (Laridae); Eurasia, Australasia. Type-species *H. sobolevi* Leonov, 1957.

**3b. Oral sucker unmodified; arms of excretory vesicle do not exceed ovary ..... 4.**

**4a. Testes tandem; uterus extends posterior to testes ..... ..... *Heterophyopsis* Tubangui & Africa, 1938. (Figs 5.6–5.8)**
(Syn. *Pseudoheterophyes* Yamaguti, 1939)

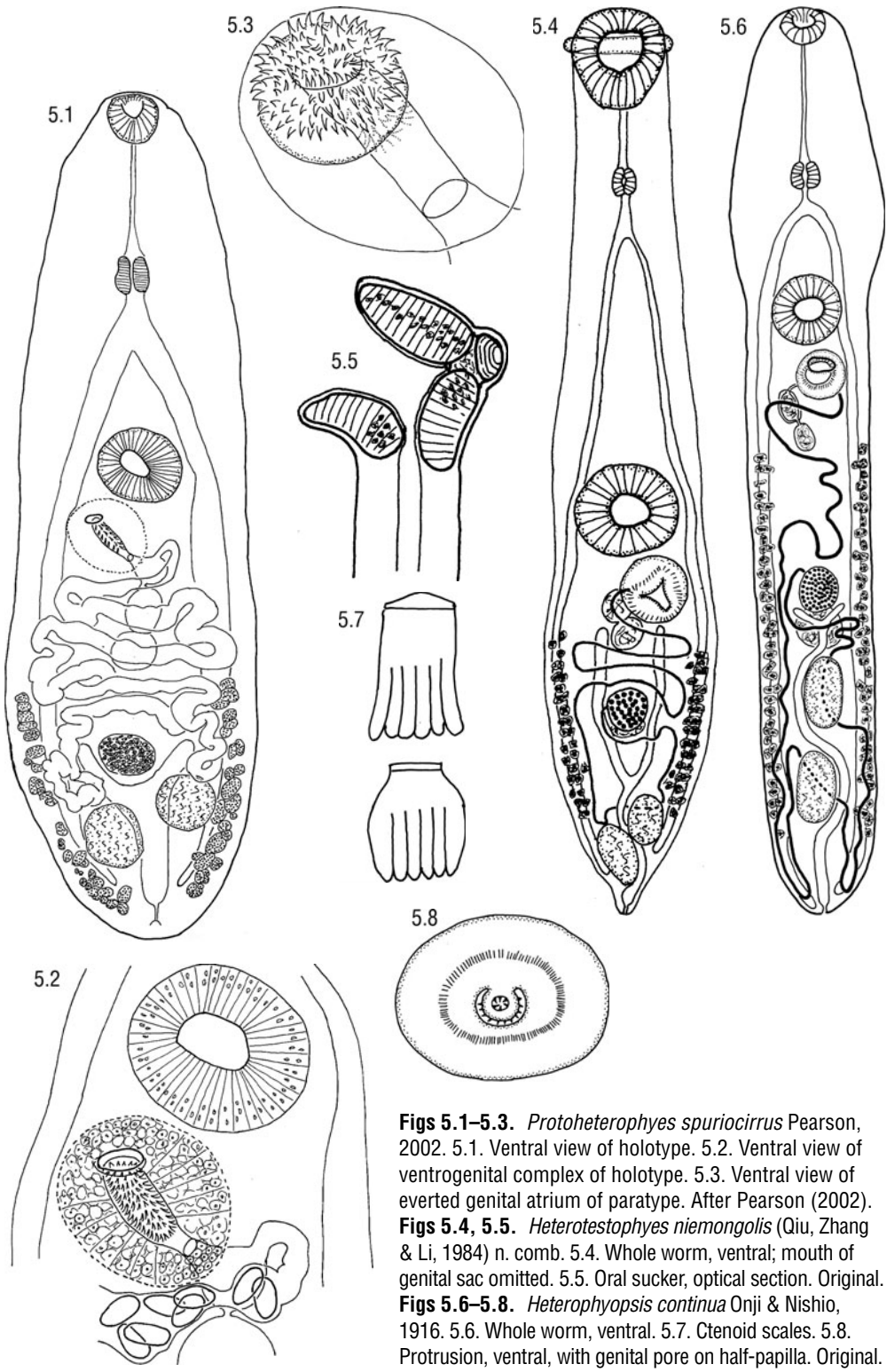
**Diagnosis:** Body elongate, 1.0–2.0 mm long, hindbody about twice as long as forebody. Tegument scaly. Oral sucker unmodified. Testes tandem. Seminal vesicle bipartite; proximal part slightly muscular; distal part a thick-walled expulsor. Protrusion and pseudocapsule as in *Protoheterophyes*. Protrusion armed with continuous or interrupted circle of 90–125 sclerites. Genital atrium and half-papilla spined. Gonotyl absent. Seminal receptacle canalicular. Uterus extends posteriorly to testes. Eggs 23–27 × 14–17 µm. Arms of excretory vesicle do not pass ovary. In birds; Far East, Australasia. Type-species *H. continus* (Onji & Nishio, 1916).

**4b. Testes opposite or oblique; uterus not extending posterior to testes ..... 5.**

**5a. Ventral sucker close to intestinal bifurcation; seminal vesicle composed of two thin-walled chambers at acute angle; seminal receptacle canalicular; uterus approaches genital atrium sinistrally ..... *Heterophyes* Cobbold, 1886. (Figs 5.9, 5.10)**
(Syns *Coenogonimus* Looss, 1899; *Cotylogonimus* Lühe, 1899)

**Diagnosis:** Body 0.8–2.0 mm long. Tegument scaly. Oral sucker unmodified. Ventral sucker close to intestinal bifurcation. Testes opposite or oblique. Seminal vesicle composed of two thin-walled

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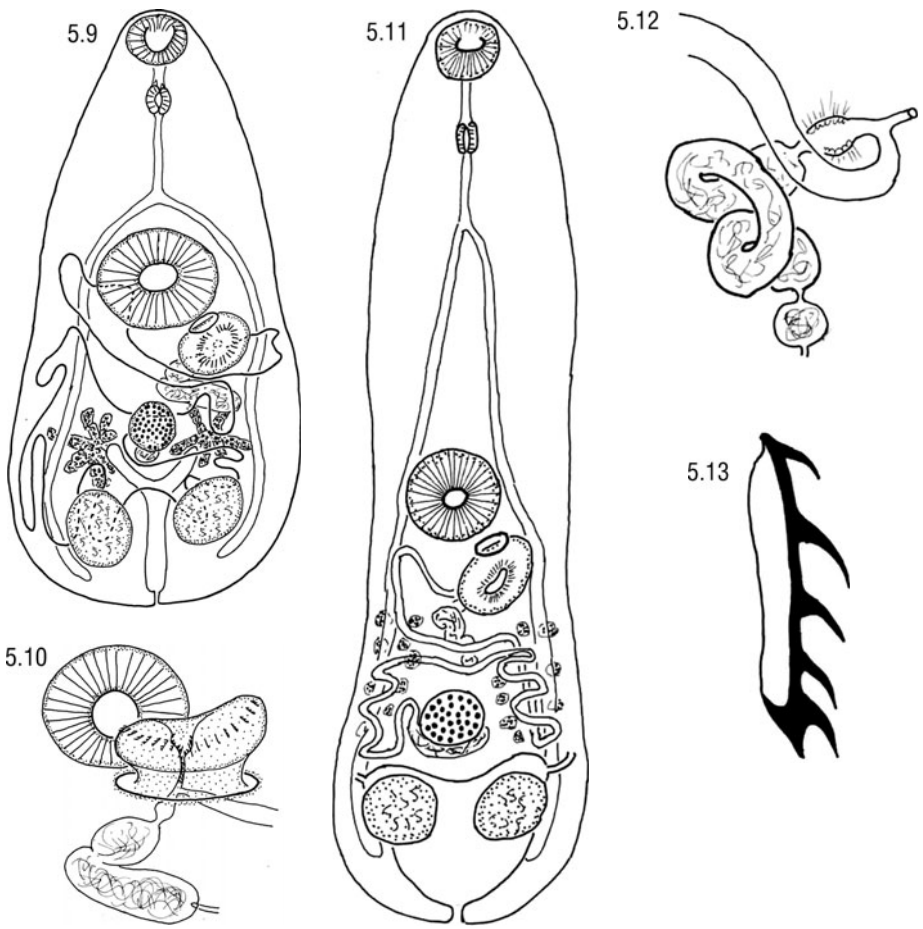

**Figs 5.1–5.3.** *Protoheterophyes spuriocirrus* Pearson, 2002. 5.1. Ventral view of holotype. 5.2. Ventral view of ventrogenital complex of holotype. 5.3. Ventral view of everted genital atrium of paratype. After Pearson (2002). **Figs 5.4, 5.5.** *Heterotestophyes niemongolis* (Qiu, Zhang & Li, 1984) n. comb. 5.4. Whole worm, ventral; mouth of genital sac omitted. 5.5. Oral sucker, optical section. Original. **Figs 5.6–5.8.** *Heterophyopsis continua* Onji & Nishio, 1916. 5.6. Whole worm, ventral. 5.7. Ctenoid scales. 5.8. Protrusion, ventral, with genital pore on half-papilla. Original.

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chambers at acute angle. Protrusion and pseudocapsule as in *Protoheterophyes*, with interrupted circle of ten to 90 sclerites. Genital atrium spined. Seminal receptacle canalicular. Uterus not extending posterior to testes, approaches genital atrium sinistrally. Eggs 20–30 × 12–16 µm. Arms of excretory vesicle do not exceed ovary. In birds and mammals; Africa, Eurasia, Australasia. Type-species *H. heterophyes* (von Siebold, 1852).

**5b. Ventral sucker well postbifurcal; seminal vesicle composed of two tandem chambers, proximal thin-walled and rounded, distal thicker-walled and elongate; seminal receptacle uterine; uterus approaches genital atrium dextrally ..... ..... *Alloheterophyes* Pearson, 1999. (Figs 5.11–5.13)**

**Diagnosis:** Body 0.8–2.6 mm long. Tegument scaly. Oral sucker unmodified. Ventral sucker well postbifurcal. Testes opposite or oblique. Seminal vesicle composed of two tandem chambers




**Figs 5.9, 5.10.** *Heterophyes nocens* Onji & Nishio, 1916. 5.9. Whole worm, ventral. 5.10. Protrusion protracted and partly everted. After Waikagul & Pearson (1989).
**Figs 5.11–5.13.** *Alloheterophyes chini* (Pearson & Pearson, 1983). 5.11. Whole worm, ventral, from holotype. 5.12. Seminal vesicle, from holotype. 5.13. Sclerite from protrusion. After Pearson (1999).

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proximal thin-walled and rounded, distal thicker-walled and elongate. Protrusion and pseudocapsule as in *Protoheterophyes*, with either one interrupted circle of 78–92 sclerites, or with an outer complete circle of 142–168 sclerites and inner U-shaped band of 43–56 sclerites. Genital atrium without spines. Seminal receptacle uterine. Uterus not extending posterior to testes, approaches genital atrium dextrally. Eggs 24–30 × 14–18 μm. Excretory vesicle V- or Y-shaped, or campanulate, arms do not exceed ovary. In egret (Ardeidae), terns (Laridae), kingfishers (Alcedinidae); Australasia, Far East. Type-species *A. chini* (Pearson & Pearson, 1983).

**6a. Caeca with branch lateral to pharynx; gravid adults *in copula* ..... ..... *Tetracladium* Kulachkova, 1954. (Figs 5.14–5.16)**
(Syns *Opisthovarium* Cable, Connor & Balling, 1960, new synonym; *Diplotrema* Connor, 1957)

**Diagnosis:** Body cylindrical, 3–6 mm long. Tegument spined. Gravid adults *in copula*. Oral sucker elliptical; mouth an anteroventral slit. Ventral sucker very small; axis of symmetry dorsoventral or inclined posteriorly; cavity reduced and bearing large unguiculate sclerite with free margin bearing knobs and crenellations marginally or spines dorsally. Caeca with branch lateral to pharynx. Ventrogenital sac permanent, shallow over genital pore and ventral sucker, deeper sinistrally; mouth of sac with large, semicircular, posterosinistral overhang for reception of thumbnail sclerite of partner. Seminal vesicle bipartite; distal part smaller. Gonotyl absent. Genital pore between ventral sucker and deep sinistral cup of ventrogenital sac. Gonads tandem; ovary anterior to, between or posterior to testes. Seminal receptacle canalicular. Eggs 21–35 × 12–17 μm. In large intestine and cloaca of terns and gulls (Laridae), gannets (Sulidae), penguins (Spheniscidae); Australia, Eurasia, Caribbean. Type-species *T. sternae* Kulachkova, 1954.

**6b. Caeca simple; adults rarely *in copula* ..... 7.**

**7a. Ventrogenital sac strongly dextral; testes two ..... 8.**
**7b. Ventrogenital sac median or slightly dextral; testes one or two ..... 9.**

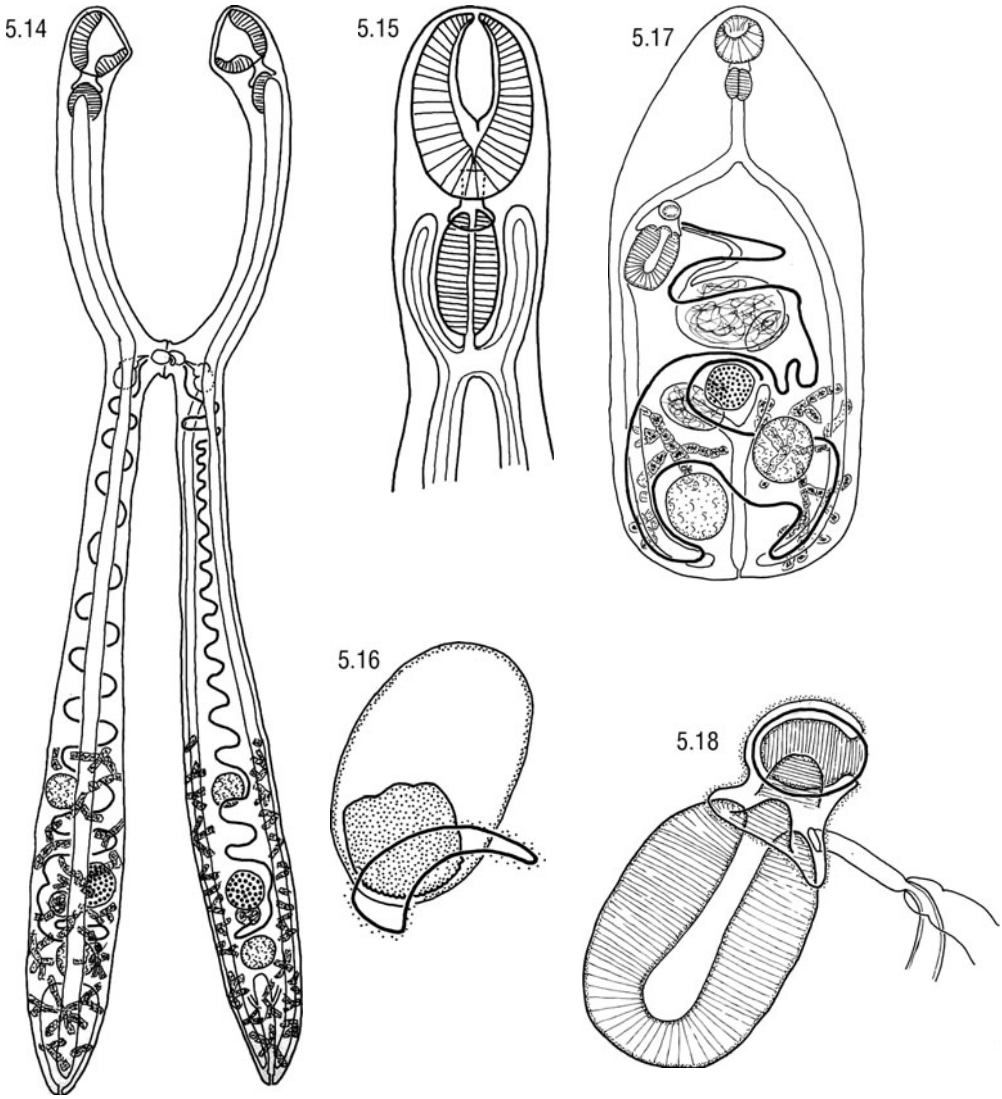
**8a. Gonotyls two, one typical and dorsal, other ventral; in birds and mammals ..... ..... *Metagonimus* Katsurada, 1912. (Figs 5.17, 5.18)**
(Syns *Loxotrema* Kobayashi, 1912; *Yokogawa* Leiper, 1913; *Loossia* Ciurea, 1915; *Dexiogonimus* Witenberg, 1929; *Loxotremuna* Strand, 1942; *Metagonimoides* Price, 1931, new synonym)

**Diagnosis:** Body 0.3–1.5 mm long. Tegument scaly. Ventral sucker large, with projecting midventral lobe on lip; axis inclined horizontally and anterosinistrally. Testes two. Ventrogenital sac permanent, strongly dextral. Gonotyls two, one typical ventral, other dorsal, muscular. Seminal vesicle thin-walled, bipartite; proximal chamber small, distal large. Testes opposite or oblique. Seminal receptacle canalicular. Vitelline follicles in hindbody, rarely extend into forebody. Eggs 21–35 × 12–20 μm. In birds and mammals; Eurasia, North America. Type-species *M. yokogawai* Katsurada, 1912.

**8b. Copulatory organ a partly eversible invagination; in fish ..... ..... *Acetodextra* Pearse, 1924. (Figs 5.19–5.21)**

**Diagnosis:** Body linguiform or fusiform, flattened, 2–4 mm long. Tegument spined. Ventral sucker large; axis inclined anterosinistrally. Testes two. Seminal vesicle undivided, long. Ventrogenital sac permanent, strongly dextral. Copulatory organ a deep, tubular, thick-walled,

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**Figs 5.14–5.16.** *Tetracladium sternae* Kulachkova, 1954. 5.14. Pair *in copula*, lateral, hindbody ventral in dextral member. 5.15. Anterior end, ventral. 5.16. Ventral sucker and mouth of ventrogenital sac. Original.
**Figs 5.17, 5.18.** *Metagonimus takahashi* Suzuki, 1930. 5.17. Whole worm, ventral. 5.18. Ventrogenital complex, ventral. Original.

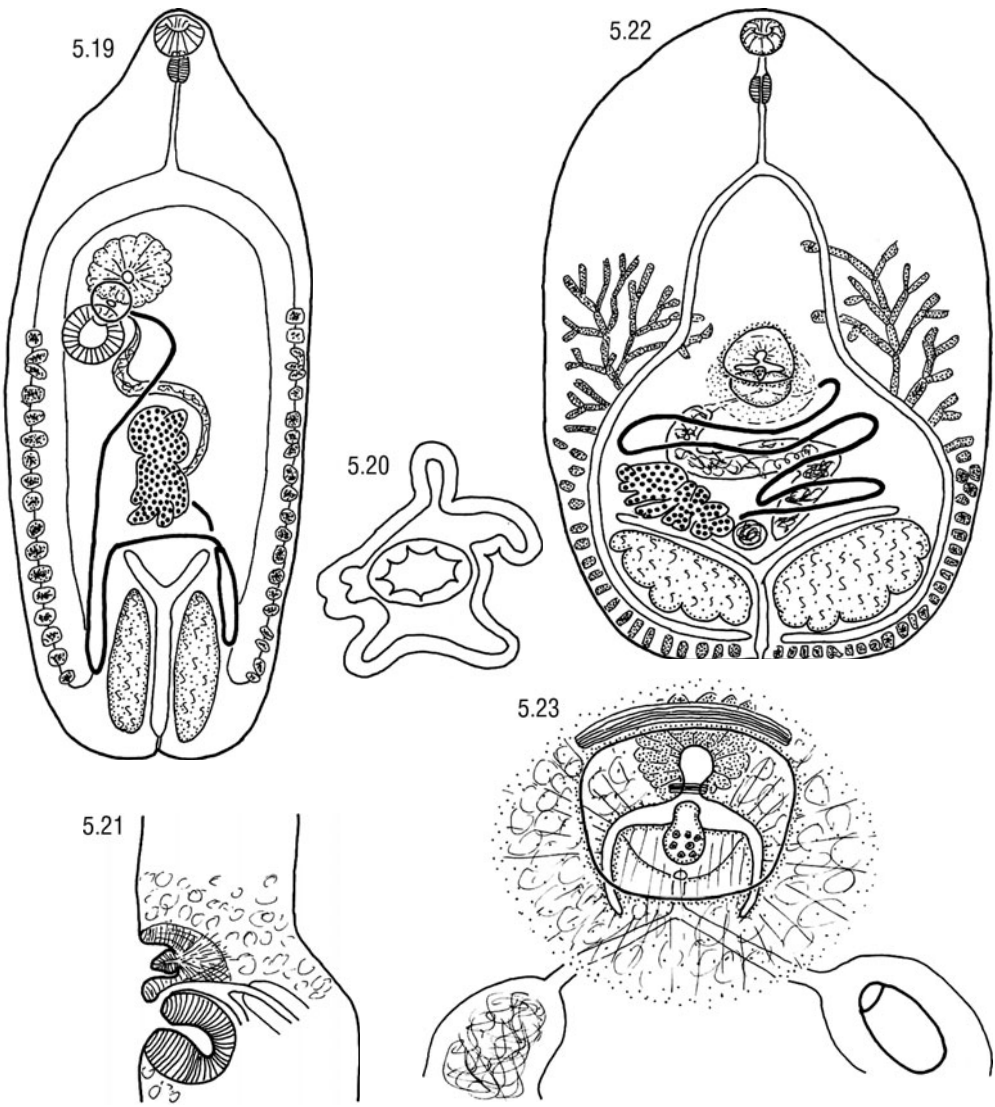
dorsal invagination of dorsal wall of ventrogenital sac, wider and irregular at inner end, surrounded by large aureole of glandulo-muscular appearance, partly eversible. Seminal receptacle canalicular. Eggs 41–45 × 22–24 µm. In ovary and swim-bladder of freshwater siluroid fishes; North America. Type-species *A. amiuri* (Stafford, 1900) Pearse, 1924.

**9a. Ventral sucker a nucleated parenchymatous knob; anterior pocket sucker-like ..... 10.**
**9b. Ventral sucker well developed, muscular; anterior or other pocket not sucker-like .... 11.**

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**10a. Body elliptical, pentagonal or ligulate ..... *Cryptocotyle* Lühe, 1899. (Figs 5.22, 5.23)**
(Syns *Tocotrema* Looss, 1899; *Dermocystis* Stafford, 1905; *Hallum* Wigdor, 1918; *Ciureana* Skrjabin, 1923; *Massaliatrema* Dollfus & Timon-David, 1960, new synonym)

**Diagnosis:** Body elliptical, pentagonal or ligulate, 0.6–2.0 mm long. Tegument scaly. Ventral sucker about as large as cavity of anterior pocket, borne on large, protractile bulge of posterior




**Figs 5.19–5.21.** *Acetodextra amiuri* (Stafford, 1900). 5.19. Whole worm, ventral. Original. 5.20. Optical sections of mouth and depths of invaginated copulatory organ, ventral. Original. 5.21. Sagittal section of ventrogenital complex showing partially everted copulatory organ. After Mueller & Van Cleave (1932).
**Figs 5.22, 5.23.** *Cryptocotyle concava* (Creplin, 1825). 5.22. Whole worm, ventral. 5.23. Ventrogenital complex, ventral. Original.

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wall of ventrogenital sac. Gonotyl absent. Testes opposite, oblique or tandem, lobed or entire. Seminal vesicle thin-walled, undivided and sinuous or bipartite, with proximal thin-walled and distal thick-walled expulsor. Ventrogenital sac permanent, with prominent transverse band of muscle fibres just anterior to mouth of ventrogenital sac, with anterior pocket that lacks continuous capsule and outer limiting membrane, with strong transverse band of muscle fibres forming hemisphincter ventral to entrance of pocket into ventrogenital sac proper. Genital pore, or separate male and female pores, open dorsal to bulge. Seminal receptacle canalicular. Eggs 34 × 18 μm. In birds and mammals; cosmopolitan. Type-species *C. concava* (Creplin, 1825) Lühe, 1899.

**10b. Body elongate and flared anteriorly ..... *Scaphanocephalus* Jägerskiöld, 1903. (Fig. 5.24)**
**Diagnosis:** Body elongate and flared anteriorly, 3–5 mm long. Tegument scaly. Ventrogenital complex as in *Cryptocotyle*. Testes slightly or deeply lobed. Seminal receptacle canalicular. Eggs 27–29 × 16–20 μm. Excretory vesicle Y-shaped; arms extend anteriorly beyond ventrogenital complex, stem with two blind branches. In birds (Pandionidae, Accipitridae); Eurasia, Australia, Philippines, North America. Type-species *S. expansus* (Creplin, 1842) Jägerskiöld, 1903.

**11a. Genital pore in ventral sucker ..... *Pseudopygidiopsis* Yamaguti, 1971. (Figs 5.25, 5.26)**
**Diagnosis:** Body obovate to pyriform, 320–530 μm long. Tegument scaly. Prepharynx very short. Ventrogenital sac permanent, deep, campanulate in lateral view, inserted on rim of ventral sucker; mouth of sac small and with sphincter. Ventral sucker unmodified except for dorsal entrance of genital atrium. Seminal vesicle bipartite; proximal chamber small, thin-walled, joined to distal chamber by long, slender duct; distal chamber larger, with thicker, muscular wall. Gonotyl absent. Genital atrium projects into cavity of ventral sucker. Genital pore in ventral sucker. Laurer's canal and seminal receptacle unknown. Uterus fills hindbody dorsally and ventrally from ventral sucker to posterior end. Eggs 22 × 12 μm. In Pelicanidae; Africa. Type-species. *P. congolensis* (Baer, 1959) Yamaguti, 1971.

**11b. Genital pore not in ventral sucker ..... 12.**

**12a. With at least one of the following: (i) oral sucker with one or two circles of spines; (ii) gonotyl with pockets; (iii) oral sucker prolonged posterior to junction with prepharynx ..... 13.**
**12b. With none of the above ..... 20.**

**13a. Testis single ..... *Pygidiopsoides* Martin, 1951. (Fig. 5.27)**
**Diagnosis:** Body 220–480 μm long, fusiform to ovoid. Tegument spined. Oral sucker with single circle of 14 spines. Ventral sucker unmodified. Testis single. Seminal vesicle bipartite. Ventrogenital sac permanent, eversible. Gonotyls two, muscular, symmetrical, lateral. Genital atrium long; proximal part with thick sphincter ('common genital ejector' of Martin, 1951). Genital pore probably close to ventral sucker and between gonotyls. Uterus fills most of hindbody. Seminal receptacle canalicular. Eggs 28 × 14 μm. Excretory vesicle saccate or tubular. Experimentally in birds and mammals; California, USA. Type-species *P. spindalis* Martin, 1951.

**13b. Testes two ..... 14.**

**14a. Testes tandem ..... 15.**
**14b. Testes opposite ..... 16.**

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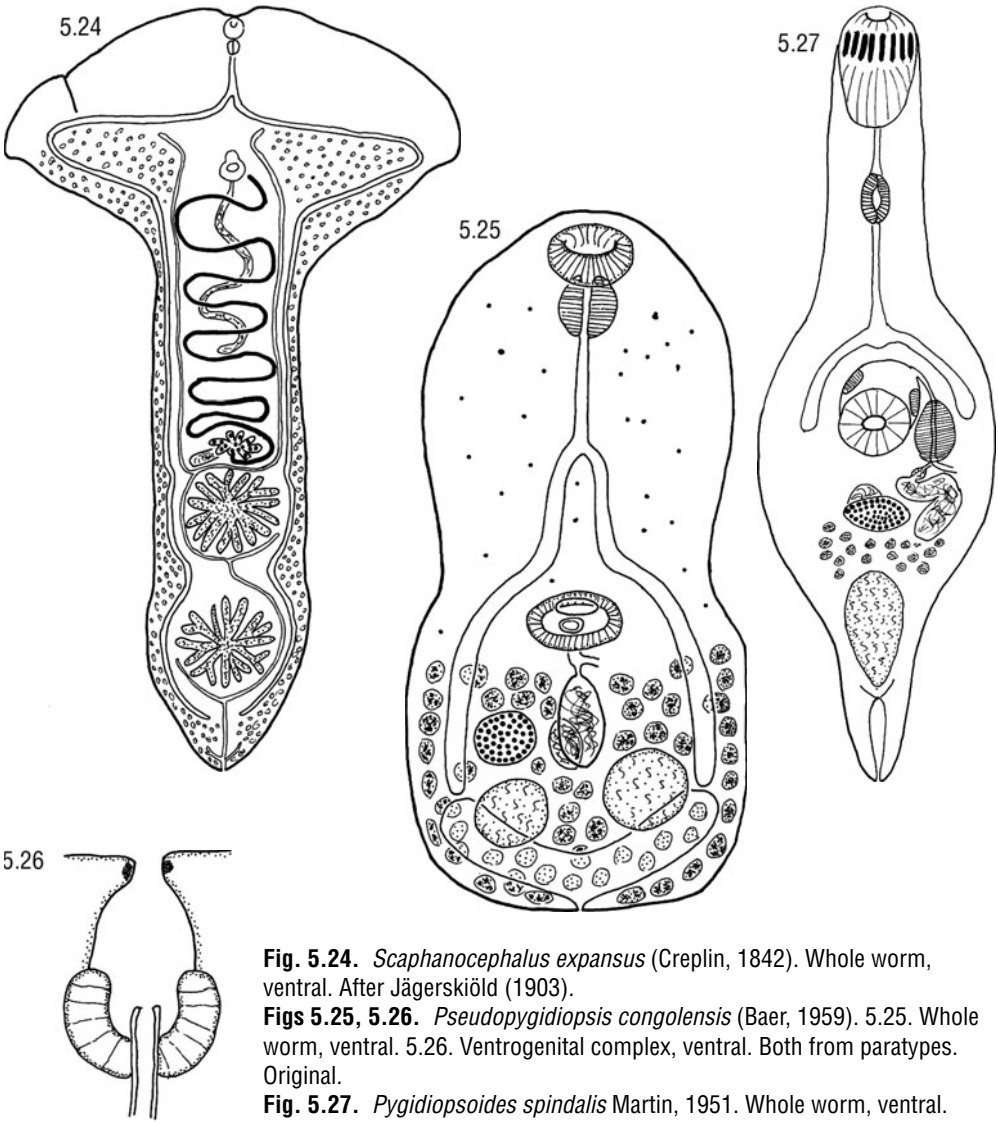



**Fig. 5.24.** *Scaphanocephalus expansus* (Creplin, 1842). Whole worm, ventral. After Jägerskiöld (1903).
**Figs 5.25, 5.26.** *Pseudopygidiopsis congolensis* (Baer, 1959). 5.25. Whole worm, ventral. 5.26. Ventrogenital complex, ventral. Both from paratypes. Original.
**Fig. 5.27.** *Pygidiopsoides spindalis* Martin, 1951. Whole worm, ventral. After Martin (1951).

**15a. Uterus extends to posterior extremity; vitellarium pre-ovarian ..... ..... *Opisthometra* Poche, 1926. (Figs 5.28, 5.29)**
(Syn. *Lacerdaia* Travassos, 1931)

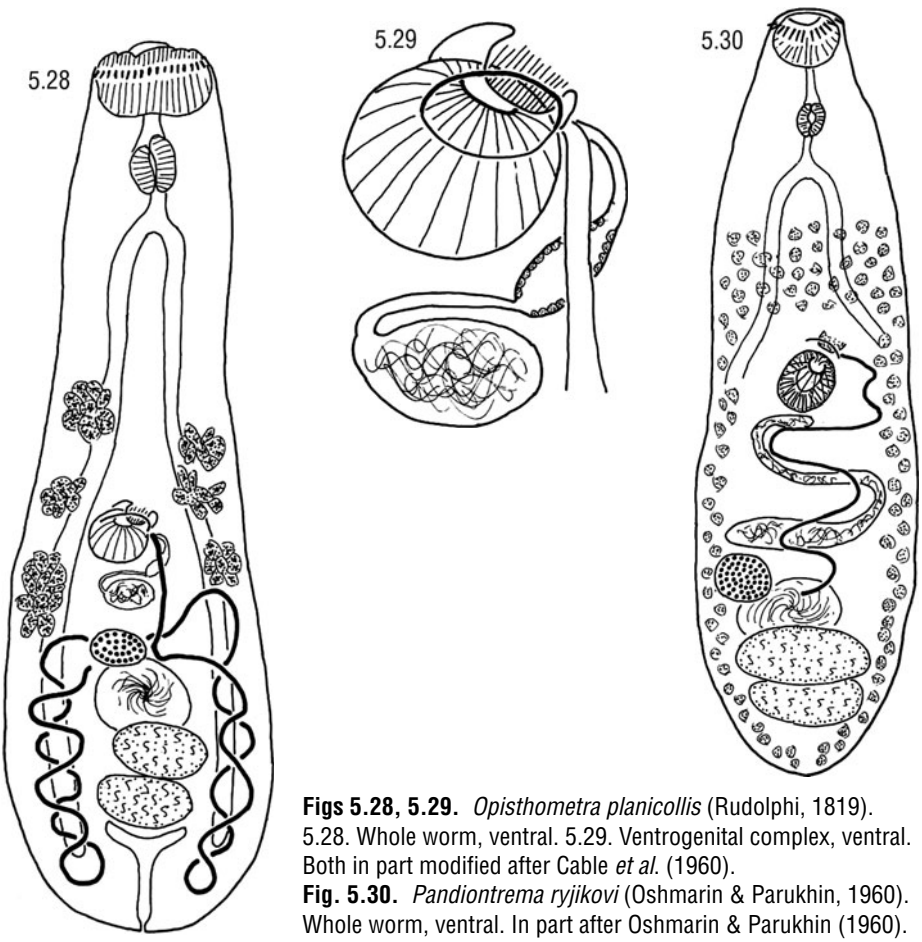
**Diagnosis:** Body 1.0–1.5 mm long. Tegument spined. Oral sucker with single circle of 26–36 blunt spines. Ventral sucker with axis inclined anterosinistrally. Testes two, tandem. Seminal vesicle undivided, short. Ventrogenital sac permanent. Gonotyl muscular, arises anterosinistrally, overlaps margin of ventral sucker. Genital pore overhung by ventral sucker and gonotyl. Seminal receptacle canalicular. Uterus extends to posterior extremity. Eggs 20–22 × 9–14 µm. Vitellarium pre-ovarian. In gannets (Sulidae); Caribbean, South America. Type-species *O. planicollis* (Rudolphi, 1819).

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**15b. Uterus pretesticular; vitellarium reaches posterior end** ..... ..... ***Pandiontrema*** **Oshmarin, 1963. (Fig. 5.30)**
(Syn. *Acanthotrema* Oshmarin & Parukhin, 1960 *nec* Travassos, 1928)
**Diagnosis:** Body 1.0 mm long. Oral sucker with single circle of 31 spines. Testes two, tandem. Ventrogenital complex as in *Opisthometra*. Seminal vesicle undivided, long, sinuous. Seminal receptacle canalicular. Uterus pretesticular. Eggs 30 × 20 µm. Vitellarium reaches posterior end. Excretory vesicle unknown. In osprey (Pandionidae); Florida, Sea of Japan. Type-species *P. ryjikovi* (Oshmarin & Parukhin, 1960) Oshmarin, 1963.

**16a. Gonotyl absent** ..... **17.**
**16b. Gonotyl present** ..... **18.**

**17a. Body > 1.5 mm long; ovary lobed** ..... ***Pholeter*** **Odhner, 1914. (Figs 5.31, 5.32)**
**Diagnosis:** Body 2–3.5 mm long, stoutly fusiform to truncate-ovoid or cuneiform. Tegument scaly. Oral sucker with one or two circles of small spines, with or without dorsal lip demarcated by inner transverse groove. Ventral sucker with axis inclined anterosinistrally. Testes two, opposite.

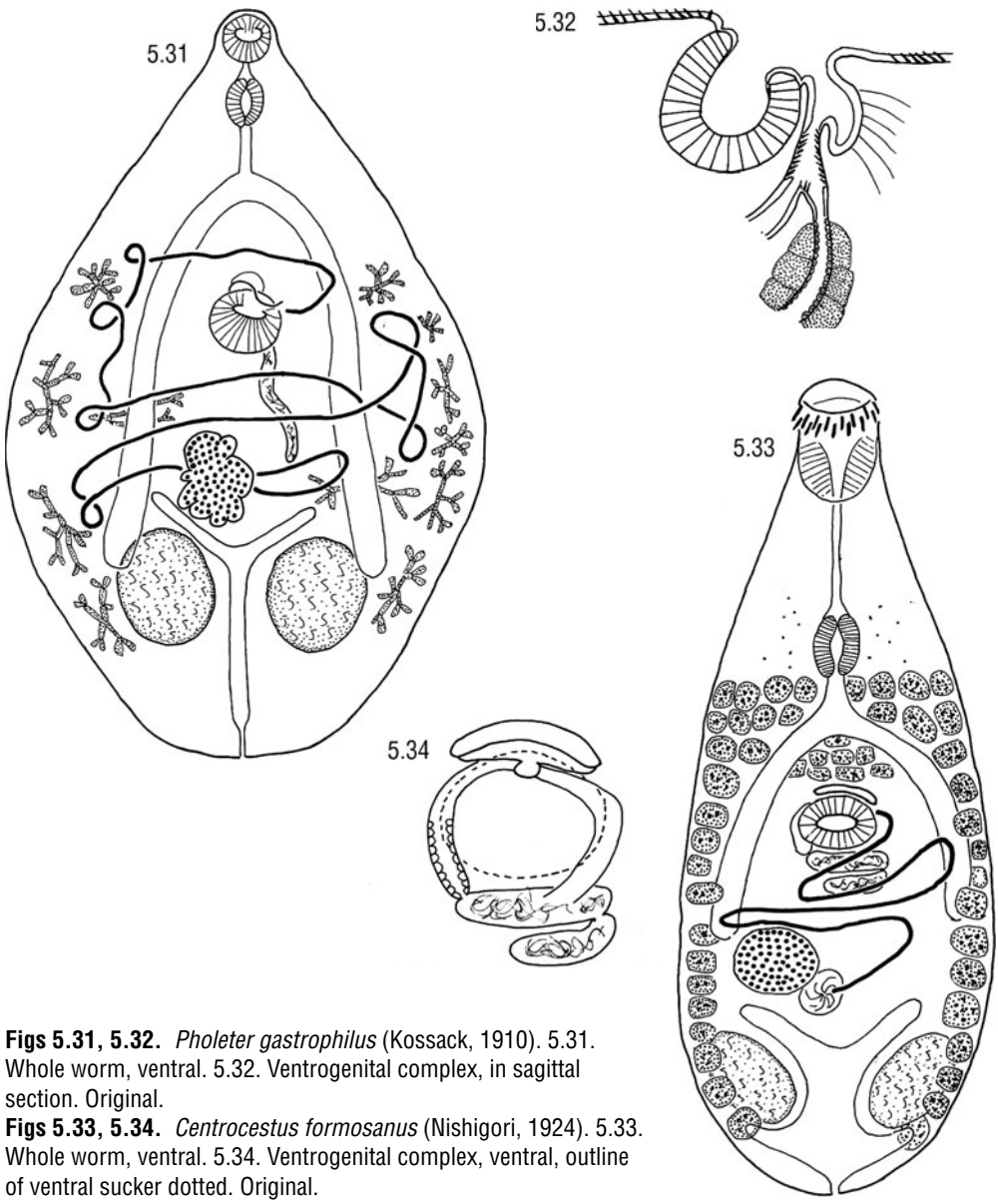



**Figs 5.28, 5.29.** *Opisthometra planicollis* (Rudolphi, 1819). 5.28. Whole worm, ventral. 5.29. Ventrogenital complex, ventral. Both in part modified after Cable *et al.* (1960).
**Fig. 5.30.** *Pandiontrema ryjikovi* (Oshmarin & Parukhin, 1960). Whole worm, ventral. In part after Oshmarin & Parukhin (1960).

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Seminal vesicle undivided, elongate, sinuous. Gonotyl absent. Ventrogenital sac facultative, shallow. Genital atrium with villous lining. Ovary lobed. Seminal receptacle canalicular, dorsal to ovary. Eggs 19–24 × 11–13 μm. In pairs in cystic cavities in wall of stomach of dolphin (Delphinidae) and porpoise (Phocoenidae) and of intestine of pelican (Pelicanidae) and cormorant (Phalacrocoracidae); cosmopolitan. Type-species *P. gastrophilus* (Kossack, 1910) Odhner, 1914.

**17b. Body < 1.0 mm long; ovary entire ..... *Centrocestus* Looss, 1899. (Figs 5.33, 5.34)**
(Syns. *Stephanopirumus* Onji & Nishio, 1916; *Stamnosoma* Tanabe, 1922)




**Figs 5.31, 5.32.** *Pholeter gastrophilus* (Kossack, 1910). 5.31. Whole worm, ventral. 5.32. Ventrogenital complex, in sagittal section. Original.
**Figs 5.33, 5.34.** *Centrocestus formosanus* (Nishigori, 1924). 5.33. Whole worm, ventral. 5.34. Ventrogenital complex, ventral, outline of ventral sucker dotted. Original.

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**Diagnosis:** Body scaly, < 1.00 mm long. Oral sucker with dorsal lip demarcated by inner transverse groove, with two circles of spines. Ventral sucker with axis dorsoventral or inclined anteriorly. Testes two, opposite. Seminal vesicle bipartite. Gonotyl absent. Ventrogenital sac facultative; genital part thick-walled and eversible. Ovary entire. Seminal receptacle canalicular. Eggs 30–40 × 15–19 μm. In birds and mammals; Africa, Eurasia, Indonesia, Philippines, Japan, Hawaii. Type-species *C. cuspidatus* (Looss, 1896) Looss, 1899.

**18a. Dorsal lip of oral sucker unmodified ..... *Pygidiopsis* Looss, 1907. (Figs 5.35, 5.36)**
(Syn. *Caiguiria* Nasir & Diaz, 1971, new synonym)

**Diagnosis:** Body 300–900 μm long. Tegument scaly. Oral sucker with or without complete circle of minute spines and posterior row of four spines dorsally, dorsal lip unmodified. Ventral sucker retractile; axis dorsoventral. Testes two, opposite. Seminal vesicle bipartite. Ventrogenital sac facultative or permanent. Gonotyl anterosinistral or sinistral to ventral sucker, of one or two raised, long-elliptical, muscular, protrusible pads with row or groups of parallel, narrow pockets with or without spicule-like deposit basally. Seminal receptacle canalicular. Uterine coils in hindbody, rarely extend well into forebody. Eggs 19–23 × 11–12 μm. In birds and mammals; cosmopolitan. Type-species *P. genata* Looss, 1907.

**18b. Dorsal lip of oral sucker protractile, demarcated by inner transverse groove ..... 19.**

**19a. Oral sucker wall prolonged posteriorly beyond junction with prepharynx as tapering appendage ..... *Ascocotyle* Looss, 1899. (Fig. 5.37)**
(Syns *Phagicola* Faust, 1920; *Parascocotyle* Stunkard & Haviland, 1924; *Metascocotyle* Ciurea, 1933; *Pseudascocotyle* Sogandares-Bernal & Bridgman, 1960; *Leighia* Sogandares-Bernal & Lumsden, 1963)

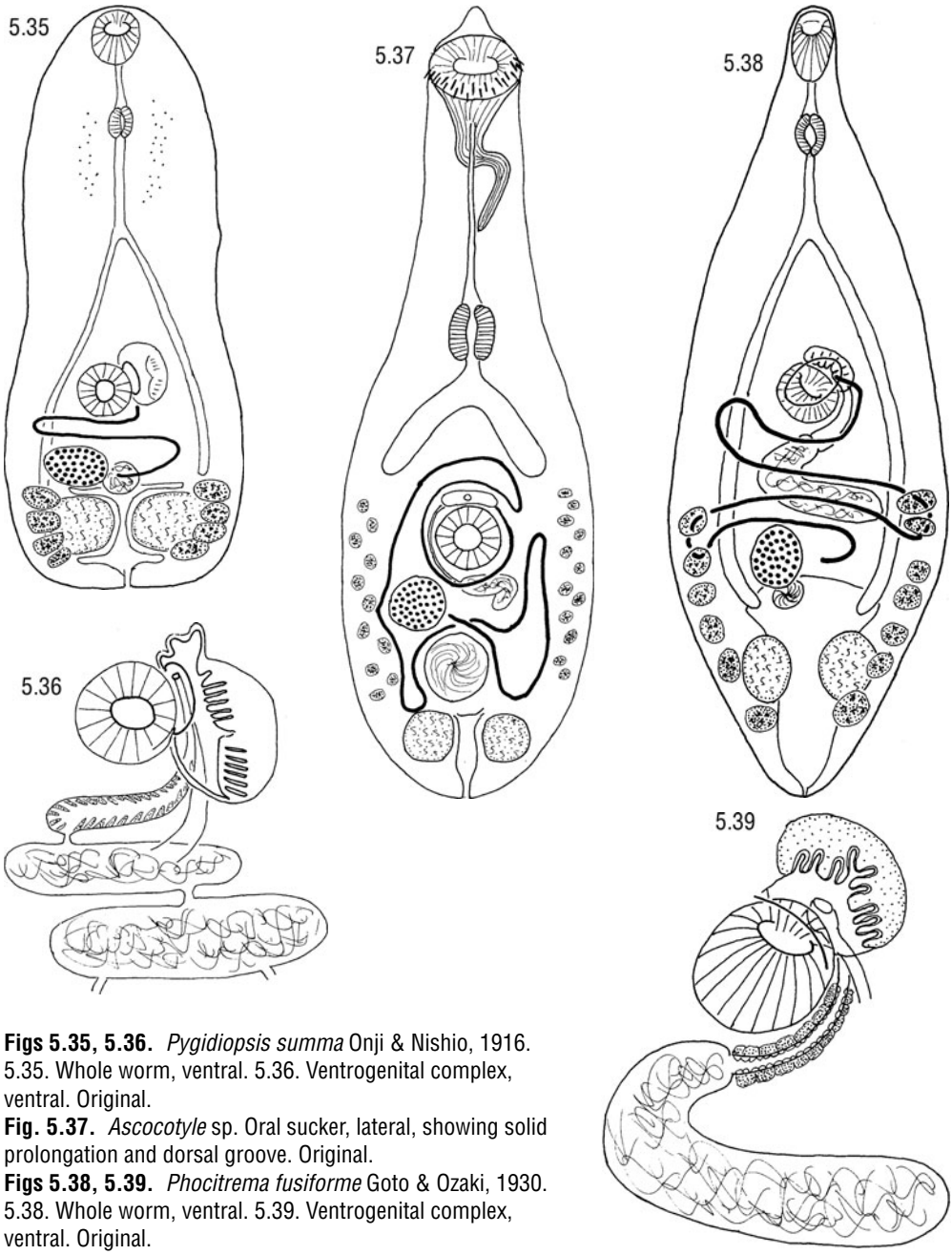
**Diagnosis:** Body 0.2–1.0 mm long. Tegument spiny. Oral sucker with solid, tapering, muscular, extensible prolongation dorsal to prepharynx and two circles of spines; anterior circle complete; posterior circle complete, incomplete ventrally and laterally, or absent, dorsal lip protractile, demarcated by inner transverse groove. Ventral sucker with axis dorsoventral or inclined (even horizontal) anterosinistrally. Testes two, opposite. Seminal vesicle J-shaped, undivided or bipartite. Ventrogenital sac facultative or permanent. Gonotyl as in *Pygidiopsis*. Seminal receptacle canalicular. Uterine coils as in *Pygidiopsis*. Vitelline follicles in hindbody, rarely extend well into forebody. Eggs mostly about 20 × 10 μm, less often 30 × 15 μm. In birds and mammals; cosmopolitan. Type-species *A. coleostoma* (Looss, 1896) Looss, 1899.

**19b. Oral sucker not prolonged posteriorly as tapering appendage ..... ..... *Phocitrema* Goto & Ozaki, 1930. (Figs 5.38, 5.39)**

**Diagnosis:** Body 1.0–1.5 mm long. Tegument scaly. Oral sucker ovate, not prolonged posteriorly, without circle of spines, dorsal lip protractile, demarcated by inner transverse groove. Ventral sucker with axis inclined anterosinistrally. Testes two, opposite. Seminal vesicle undivided. Ventrogenital sac facultative. Gonotyl as in *Pygidiopsis*, with single row of about ten pockets. Seminal receptacle canalicular. Eggs 23–28 × 13–15 μm. Excretory vesicle T- or Y-shaped, or inflated. In seals, sea otter and Arctic fox; northern Pacific. Type-species *P. fusiforme* Goto & Ozaki, 1930.

**20a. Genital pore anteromedian to ventral sucker ..... 21.**
**20b. Genital pore sinistral or posterior to ventral sucker ..... 24.**

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**Figs 5.35, 5.36.** *Pygidiopsis summa* Onji & Nishio, 1916. 5.35. Whole worm, ventral. 5.36. Ventrogenital complex, ventral. Original.
**Fig. 5.37.** *Ascocotyle* sp. Oral sucker, lateral, showing solid prolongation and dorsal groove. Original.
**Figs 5.38, 5.39.** *Phocitrema fusiforme* Goto & Ozaki, 1930. 5.38. Whole worm, ventral. 5.39. Ventrogenital complex, ventral. Original.

**21a. Testis single; gonotyl absent ..... *Phocitremoides* Martin, 1950. (Fig. 5.40)**
**Diagnosis:** Body 220–270 µm, oval to pyriform. Tegument scaly. Ventrogenital sac facultative, with or without two rows of enlarged spines on ventral surface of body posterior to mouth of sac; genital portion of sac thick-walled. Testis single. Seminal vesicle bipartite. Gonotyl absent. Genital pore anteromedian to ventral sucker. Seminal receptacle canalicular. Uterine convolutions largely

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intercaecal, extend from just anterior to ventral sucker to posterior end. Eggs 26 × 16 µm. In herons and egrets (Ardeidae) and experimentally in chick and rat; California and Puerto Rico, USA. Type-species *P. ovalis* Martin, 1950.

**21b. Testes one or two; gonotyl(s) or copulatory invagination present ..... 22.**

**22a. Gonotyl single or copulatory invagination median ..... 23.**

**22b. Gonotyls two, lateral and opposite ..... *Apophallus* Lühe, 1909. (Fig. 5.41)**
(Syns *Rossicotrema* Skrjabin & Lindtrop, 1919; *Cotylophallus* Ransom, 1920; *Pricetrema* Ciurea, 1933, new synonym; *Apophalloides* Yamaguti, 1971, new synonym)

**Diagnosis:** Body 0.5–1.9 mm long, ovoid-pyriform to elongate. Tegument scaly. Ventral sucker with axis inclined anteriorly. Testes two, tandem. Seminal vesicle elongate, S-shaped, undivided but may be constricted. Ventrogenital sac permanent. Gonotyls two, lateral and opposite, arise dorsally close against ventral sucker, clavate in lateral aspect, rounded in ventral aspect, overhang ventral sucker ventrally. Genital pore anteromedian to ventral sucker. Seminal receptacle canalicular. Vitelline follicles from posterior end to level of ventral sucker or beyond to intestinal bifurcation. Eggs about 33 × 25 µm. In birds and mammals; Eurasia, North America. Type-species *A. muehlingi* (Jägerskiöld, 1899) Lühe, 1909.

**23a. Copulatory organ an eversible invagination; in fish ..... ..... *Pseudexorchis* Yamaguti, 1938. (Figs 5.42–5.44)**

**Diagnosis:** Body *c.* 0.5 mm long, broad ellipsoid to subrectangular. Tegument spined. Ventral sucker with axis inclined anteriorly. Testes two, opposite. Ventrogenital sac facultative, shallow, typically with mouth of sac agape and copulatory organ inverted. Copulatory organ thick-walled (cf. *Acetodextra*), an eversible invagination. Genital pore anteromedian to ventral sucker. Seminal receptacle canalicular. Eggs 50–57 × 26–29 µm. In freshwater siluroid fishes; Japan. Type-species *P. major* (Hasegawa, 1934) Yamaguti, 1938.

**23b. Copulatory organ a gonotyl; in mammals ..... *Euryhelmis* Poche, 1926. (Figs 5.45, 5.46)**
(Syn. *Eurysoma* Dujardin, 1845 *nec* Oberleitner in Dejean, 1831)

**Diagnosis:** Body 0.3–1.9 mm long, strongly flattened, wider than long and rectangular to pentangular or longer than wide and ovoid. Tegument spined. Ventral sucker with axis inclined anteriorly. Testes one or two. Seminal vesicle elongate, with or without one or two constrictions. Ventrogenital sac permanent. Gonotyl elliptical to reniform, largely parenchymatous, overhangs genital pore. Genital pore anteromedian to ventral sucker. Seminal receptacle canalicular. Uterus confined to left side, or extends full width of body. Eggs 28–34 × 13–15 µm. In frog- and salamander-eating mammals; Eurasia, North and Central America. Type-species *E. squamula* (Rudolphi, 1819) Poche, 1926.

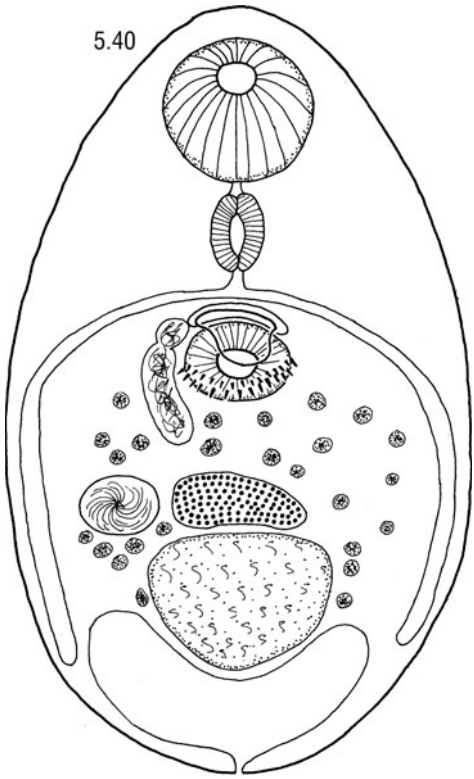
**24a. Body < 1.0 mm long; uterus of three descending primary loops ..... 25.**

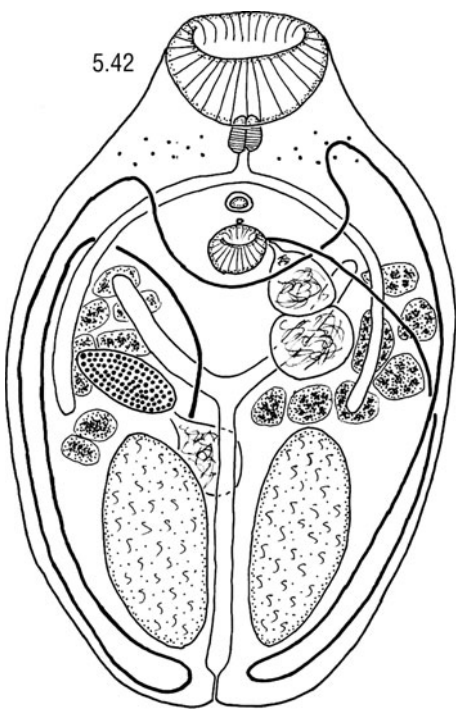
**24b. Body typically > 1.0 mm long; uterus of one or two descending primary loops ..... 28.**

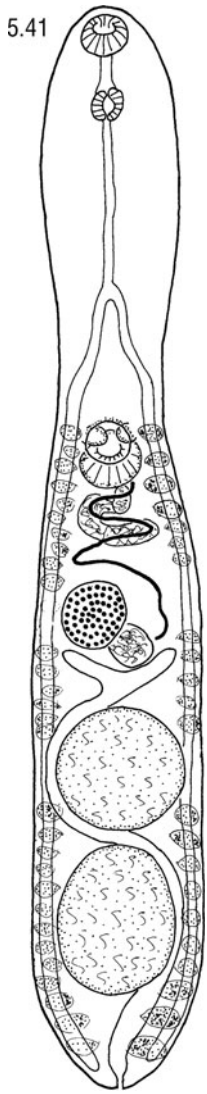
**25a. Ventral sucker sucker-like; testes one or two; distal chamber of seminal vesicle an expulsor ..... 26.**

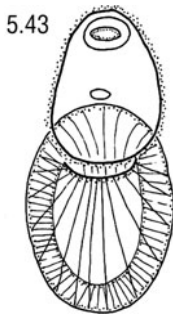
**25b. Ventral sucker not sucker-like; testis single; distal chamber of seminal vesicle thin-walled ..... 27.**

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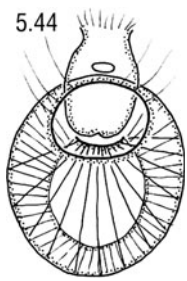
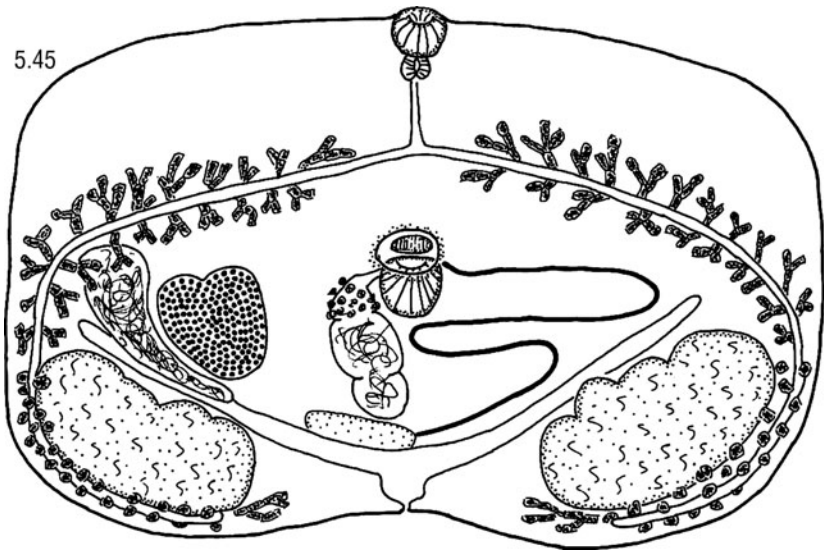



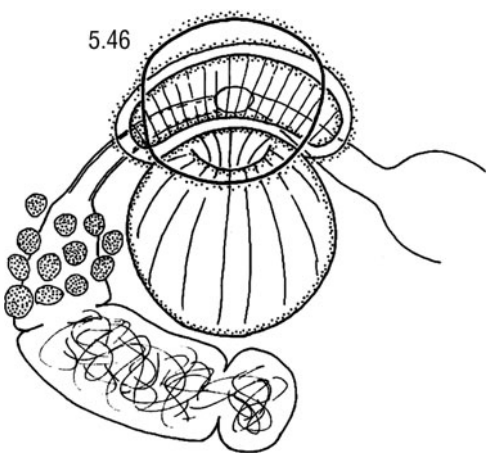

**Fig. 5.40.** *Phocitremoides ovalis* Martin, 1950. Whole worm, ventral. After Martin (1950b).
**Fig. 5.41.** *Apophallus muehlingi* (Jägerskiöld, 1899). Whole worm, ventral. Original.
**Figs 5.42–5.44.** *Pseudexorchis major* (Hasegawa, 1934). 5.42. Whole worm, ventral. 5.43. Ventrogenital complex, ventral, copulatory organ largely inverted. 5.44. Copulatory organ everted. Original.

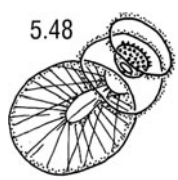
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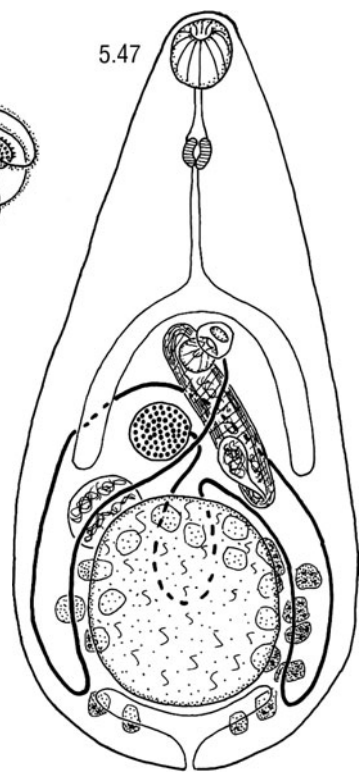
**26a. Ventral sucker unarmed; gonotyl spined, bears genital pore; testis single** ..... ..... *Procerovum* **Onji & Nishio, 1916. (Figs 5.47, 5.48)**

**Diagnosis:** Body elongate-ovoid. Tegument scaly. Ventral sucker sucker-like, unarmed, with axis inclined anterosinistrally. Testis single. Distal chamber of seminal vesicle an expulsor. Ventrogenital




**Figs 5.45, 5.46.** *Euryhelmis squamula* (Rudolphi, 1819). 5.45. Whole worm, ventral. 5.46. Ventrogenital complex, ventral. Original.

**Figs 5.47, 5.48.** *Procerovum varium* Onji & Nishio, 1916. 5.47. Whole worm, ventral. 5.48. Ventrogenital complex, ventral. Original.

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sac permanent. Gonotyl spined, bears genital pore. Seminal receptacle canalicular. Uterus of three descending primary loops. Eggs 26 × 13 µm. In birds and mammals; South-east Asia, western Pacific, Australasia. Type-species *P. varium* Onji & Nishio, 1916.

**26b. Ventral sucker armed or not; male and female pores separate, not on unspined gonotyl; testes one or two ..... *Stellantchasmus* Onji & Nishio, 1916. (Figs 5.49–5.51)**
(Syn. *Diorchitrema* Witenberg, 1929)

**Diagnosis:** Body pyriform. Tegument scaly. Ventral sucker sucker-like with axis inclined anterosinistrally, unarmed or armed with minute spines or single sclerite. Distal chamber of seminal vesicle an expulsor. Gonotyl unarmed. Male and female pores separate, not on gonotyl. Testes two and symmetrical or tandem; or one and sinistral. Ventrogenital sac permanent. Seminal receptacle canalicular. Eggs 23 × 12 µm. In birds and mammals; Eurasia, Australasia, Hawaii. Type-species *S. falcatus* Onji & Nishio, 1916.

**27a. Gonotyl present; dorsal pocket of ventrogenital sac absent; seminal receptacle posterodorsal to testis ..... *Euhaplorchis* Martin, 1950. (Figs 5.52, 5.53)**

**Diagnosis:** Body 230–300 µm long, fusiform. Tegument spined. Ventral sucker pyriform, with axis inclined anterosinistrally, with rounded parenchymatous base and conical anucleate apex, with eversible cavity lined with eight rows each of six spines borne on slender rod-like base. Testis single. Seminal vesicle ellipsoidal, thin-walled. Ventrogenital sac permanent, with no dorsal pocket. Gonotyl small, rounded, overlaps genital pore and apex of ventral sucker. Seminal receptacle canalicular, posterodorsal to testis. Uterus postcaecal, loops mostly anteroposterior. Eggs 28 × 16 µm. Experimental in chick; California, USA. Type-species *E. californiensis* Martin, 1950.

**27b. Gonotyl absent; dorsal pocket present; seminal receptacle dextral to ovary ..... ..... *Haplorchis* Looss, 1899. (Figs 5.54, 5.55)**
(Syns *Monorchotrema* Nishigori 1924; *Kasr* Khalil, 1932)

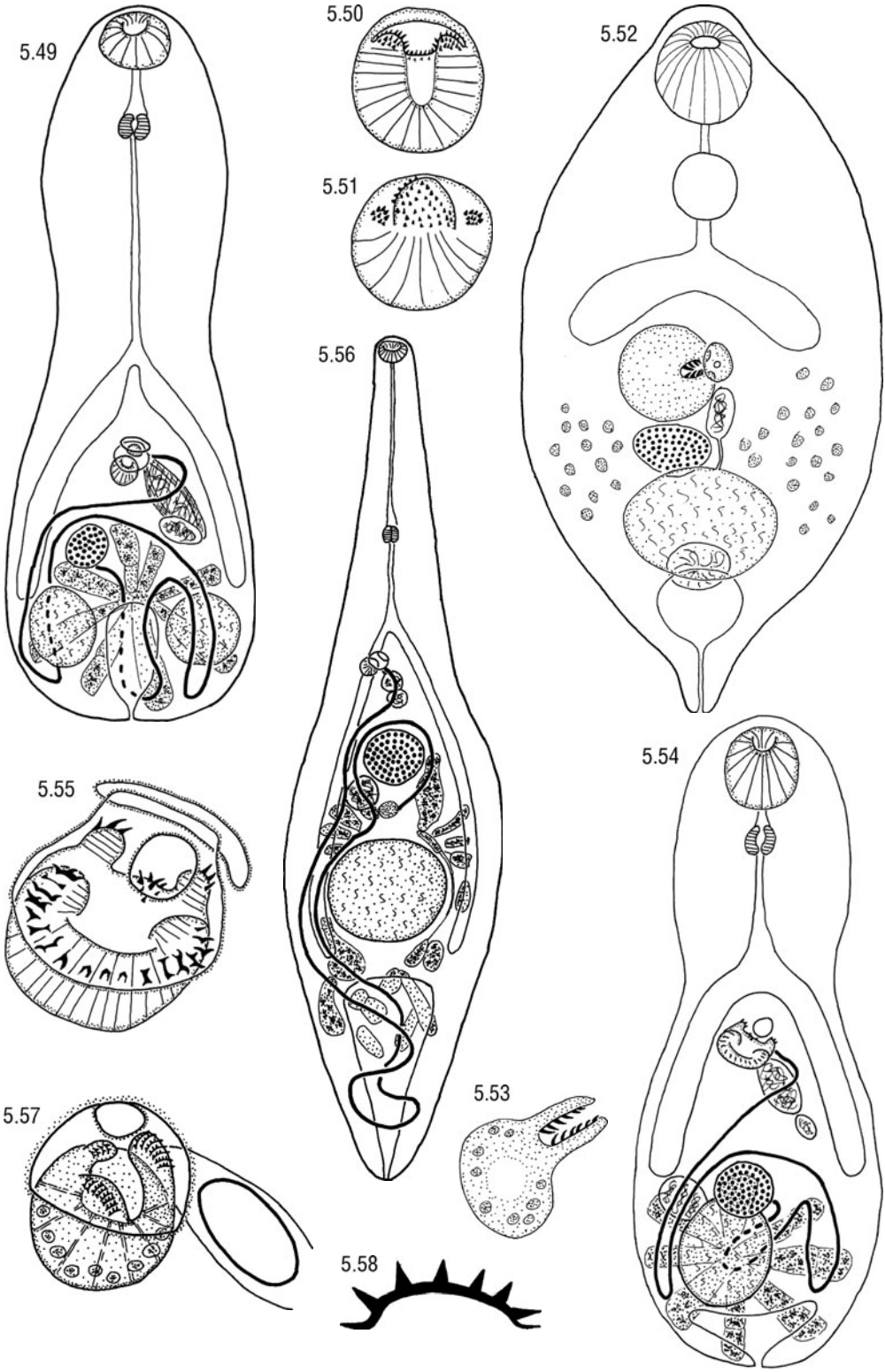
**Diagnosis:** Body pyriform. Tegument scaly. Ventral sucker with reduced cavity, with axis inclined anterosinistrally, bilaterally symmetrical or asymmetrical, armed with spines or toothed sclerites. Testis single. Ventrogenital sac permanent; dorsal pocket unarmed or armed with spines and spiny plates. Gonotyle absent. Seminal vesicle bi- or tripartite, thin-walled. Seminal receptacle canalicular, dextral to ovary. Eggs 24–30 × 13–16 µm. In birds and mammals; Africa, Eurasia, Australasia, Hawaii. Type-species *H. pumilio* (Looss, 1896) Looss, 1899.

**28a. Testis single ..... 29.**
**28b. Testes two ..... 30.**

**29a. Ventral sucker armed with cteniform sclerites or spines; in fish ..... ..... *Haplorchoides* Chen, 1949. (Figs 5.56–5.58)**
(Syn. *Pseudohaplorchis* Dayal, 1949)

**Diagnosis:** Body 0.7–1.3 mm long. Tegument scaly. Ventral sucker bipartite; base rounded, nucleate, embedded, with parenchymatous medulla; apex asymmetrical, anucleate, projects into ventrogenital sac, with reduced cavity of apex whose rim is produced into sinistral thumb ventral to genital pore, armed with one, two or three groups of cteniform sclerites or spines. Testis single. Seminal vesicle bipartite. Ventrogenital sac permanent, medial or dextral, without dorsal pocket. Gonotyl absent. Seminal receptacle canalicular. Eggs 28–38 × 16–20 µm. In freshwater siluroid fish; Africa, India, South-east Asia, Indonesia, Philippines. Type-species *H. cahirinus* (Looss, 1896) Chen, 1949.

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**29b. Ventral sucker armed with two elongate pointed sclerites; in mammals ..... ..... *Adleriella* Witenberg, 1930. (Figs 5.59, 5.60)**
(Syn. *Adleria* Witenberg, 1929)

**Diagnosis:** Body 270–470 µm long. Tegument spined. Ventral sucker spheroidal, with shallow cavity bearing two forcipulate sclerites. Testis single. Seminal vesicle bipartite. Ventrogenital sac permanent. Gonotyl large, dextral to ventral sucker. Ovary and seminal receptacle posterior to testis. Uterus fills hindbody. Eggs 24 × 13 µm. Excretory vesicle unknown. In dogs and cats; Israel. Type-species *A. minutissima* (Witenberg, 1929) Witenberg, 1930.

**30a. Gonotyl elongate, sinuous; uterus with two descending primary loops ..... ..... *Irinaia* Caballero y C. & Bravo Hollis, 1966. (Figs 5.61, 5.62)**

**Diagnosis:** Body 4.0–4.5 mm long. Tegument spined. Ventral sucker with axis inclined anterosinistrally. Testes two. Seminal vesicle elongate, tubular, constricted, thick-walled. Ventrogenital sac permanent. Gonotyl elongate, sinuous. Seminal receptacle canalicular. Uterus with two descending primary loops. Eggs 21 × 13 µm. Excretory vesicle Y-shaped. Habitus reminiscent of *Acetodextra*. In Ardeidae or Cochleariidae; Nicaragua. Type-species *I. brenes* Caballero y C. & Bravo Hollis, 1966.

**30b. Gonotyl, when present, compact and simple; uterus with one descending primary loop ..... 31.**

**31a. Gonotyl present ..... 32.**
**31b. Gonotyl absent ..... 34.**

**32a. Ventral sucker armed with fewer than ten large sclerites ..... ..... *Acanthotrema* Travassos, 1928 *nec* Oshmarin & Parukhin, 1960. (Figs 5.63, 5.64)**
(Syn. *Parastictodora* Martin, 1950, new synonym)

**Diagnosis**: Body 0.3–1.5 mm long, pyriform to ligulate. Tegument scaly. Ventral sucker rounded; axis inclined sinistrally; medulla parenchymatous; reduced cavity bears two to eight projecting, elongate, hollow, spined or unspined sclerites united or not basally. Seminal vesicle bipartite, thin-walled. Ventrogenital sac permanent, without sinistral pocket. Gonotyl present. Genital atrium short. Seminal receptacle canalicular. uterus with one descending primary loop. Eggs 20–24 × 11–13 µm. Excretory vesicle saccate, tubular, or V- or Y-shaped. In birds and mammals; cosmopolitan. Type-species *A. acanthotrema* Travassos, 1928.

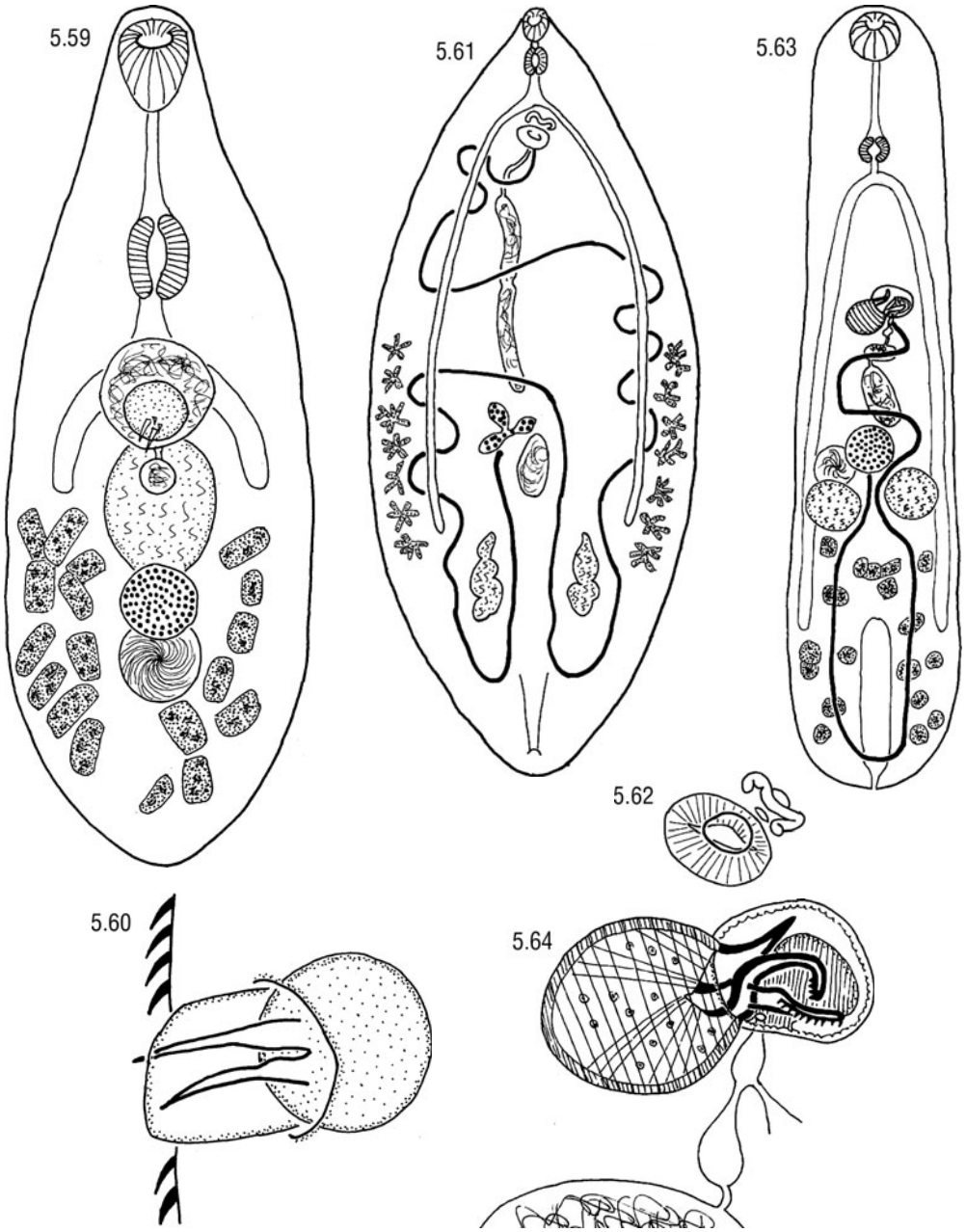
**32b. Ventral sucker armed with more than ten small spines, rarely unspined ..... 33.**

**33a. Ventral sucker rounded, with one or two spined eversible cavities; expulsor absent; prostatic bulb present ..... *Stictodora* Looss, 1899. (Figs 5.65–5.73)**
(Syns *Cornatrium* Onji & Nishio, 1916; *Sobolephya* Morozov, 1950, new synonym)

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**Figs 5.49–5.51.** (*Opposite*) *Stellantchasmus falcatus* Onji & Nishio, 1916. 5.49. Whole worm, ventral. 5.50. Ventral sucker, cavity inverted. 5.51. Ventral sucker, cavity everted. Original.
**Figs 5.52, 5.53.** (*Opposite*) *Euhaplorchis californiensis* Martin, 1950. 5.52. Whole worm, ventral. 5.53. Ventral sucker, cavity inverted. After Martin (1950a).
**Figs 5.54, 5.55.** (*Opposite*) *Haplorchis pumilio* (Looss, 1896). 5.54. Whole worm, ventral. 5.55. Ventrogenital sac, mouth of dorsal pocket, and apex of ventral sucker, ventral. Original.
**Figs 5.56–5.58.** (*Opposite*) *Haplorchoides cahirinus* (Looss, 1896). 5.56. Whole worm, ventral. 5.57. Ventrogenital complex, ventral. 5.58. Sclerite from ventral sucker. Original.

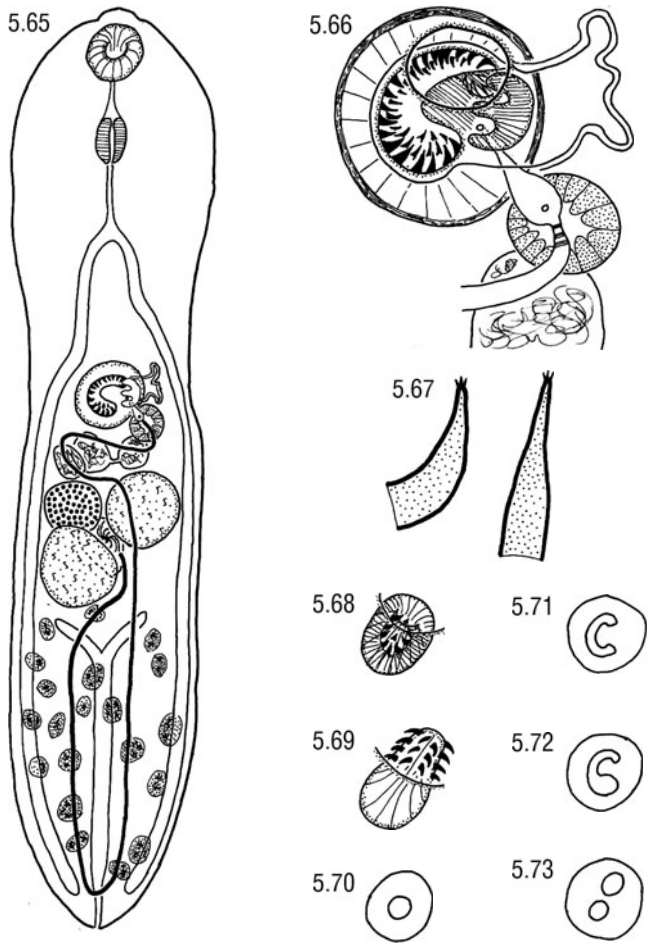
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**Figs 5.59, 5.60.** *Adleriella minutissima* (Witenberg, 1929). 5.59. Whole worm, ventral. After Witenberg (1929). 5.60. Ventral sucker and gonotyl. From syntype. Original.
**Figs 5.61, 5.62.** *Irinaia brenesi* Caballero y C. & Bravo-Hollis, 1966. 5.61. Whole worm, ventral. 5.62. Ventral sucker, gonotyl and mouth of ventrogenital sac, ventral. After Caballero y C. & Bravo-Hollis (1966).
**Figs 5.63, 5.64.** *Acanthotrema acanthotrema* Travassos, 1928. 5.63. Whole worm, ventral. 5.64. Ventrogenital complex, ventral. Both from a syntype. Original.

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**Diagnosis:** Body 0.6–1.4 mm long, elongate-pyriform, or forebody wider than hindbody. Tegument scaly. Ventral sucker rounded, sucker-like, with one crescentic or two rounded spined eversible cavities; spines hollow, with trifid or single tips, numbering 12–140. Testes two. Seminal vesicle bi- or tripartite; expulsor absent. Pars prostatica spherical, largely filled by in-bulging ends of ducts of prostatic gland-cells. Ventrogenital sac permanent, with pocket sinistral to gonotyl; wall thick and muscular. Gonotyl small, U- or E-shaped. Genital pore between arms of gonotyl.




**Figs 5.65–5.67.** *Stictodora lari* Yamaguti, 1939. 5.65. Whole worm, ventral. 5.66. Ventrogenital complex, ventral. 5.67. Spines from ventral sucker. Original.
**Figs 5.68, 5.69.** *Stictodora sawakinensis* Looss, 1899. 5.68. Cavity of ventral sucker inverted. 5.69. Cavity everted. Original.
**Fig. 5.70.** Ventral aspect of cavity of ventral sucker of *Stictodora sawakinensis* and *S. manilensis* Africa & Garcia, 1935. Original.
**Fig. 5.71.** Cavity of ventral sucker of *Stictodora oshmarini* (Morozov, 1952) n. comb. Original.
**Fig. 5.72.** Cavity of ventral sucker of *Stictodora lari* and *S. guerreroi* Garcia & Refuerzo, 1936. Original.
**Fig. 5.73.** Twin cavities of ventral sucker of *S. diplacantha* Johnston, 1942. Original.

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Genital atrium short. Seminal receptacle canalicular. Eggs 28–34 × 16–19 µm. In birds and mammals; Eurasia, Australasia, Pacific coast of North America, Africa. Type-species *S. sawakinensis* Looss, 1899.

**33b. Ventral sucker rounded, oval, pyriform or asymmetrical, with most spines external to reduced cavity; expulsor present; prostatic bulb absent ..... *Galactosomum* Looss, 1899. (Figs 5.74, 5.75)**

(Syns *Microlistrum* Braun, 1901; *Knipowitschiatrema* Isaichikov, 1927; *Retevitellus* Cable, Connor & Balling, 1960; *Galactosomoides* Cable, Connor & Balling, 1960; *Allocercarioides* Yamaguti, 1971, new synonym)

**Diagnosis:** Body 0.8–7.0 mm long; shape various, ovoid-ellipsoid, elongate with or without narrow waist, with forebody wider or narrower than hindbody. Tegument scaly or spined. Ventral sucker rounded, oval, pyriform or asymmetrical, with most spines external to reduced cavity, with axis inclined anterosinistrally, rarely unspined; reduced cavity may be spined and eversible; apex protractile. Testes two. Seminal vesicle two-chambered (separated by distinct constriction) or bipartite (broadly joined, distal part with circular muscle fibres, proximal with diagonal muscle fibres), rarely unconstricted; expulsor present. Prostatic bulb absent. Ventrogenital sac permanent, median or slightly dextral, rarely spined, with or without sinistral pocket. Gonotyl may bear genital pore. Genital atrium short. Seminal receptacle canalicular. Uterus rarely reaches anteriorly beyond ventral sucker. Eggs 21–36 × 12–19 µm. Excretory vesicle tubular, extends to between ovary and halfway between posterior testis and posterior extremity. In intestine, ureter or bursa Fabricii of birds and intestine of mammals; cosmopolitan. Type-species *G. lacteum* (Jägerskiöld, 1896) Looss, 1899.

**34a. Ventral sucker distinctly bipartite, with apex dorsal to base; genital atrium long, thick-walled ..... *Neostictodora* Sogandares-Bernal, 1959. (Figs 5.76, 5.77)**

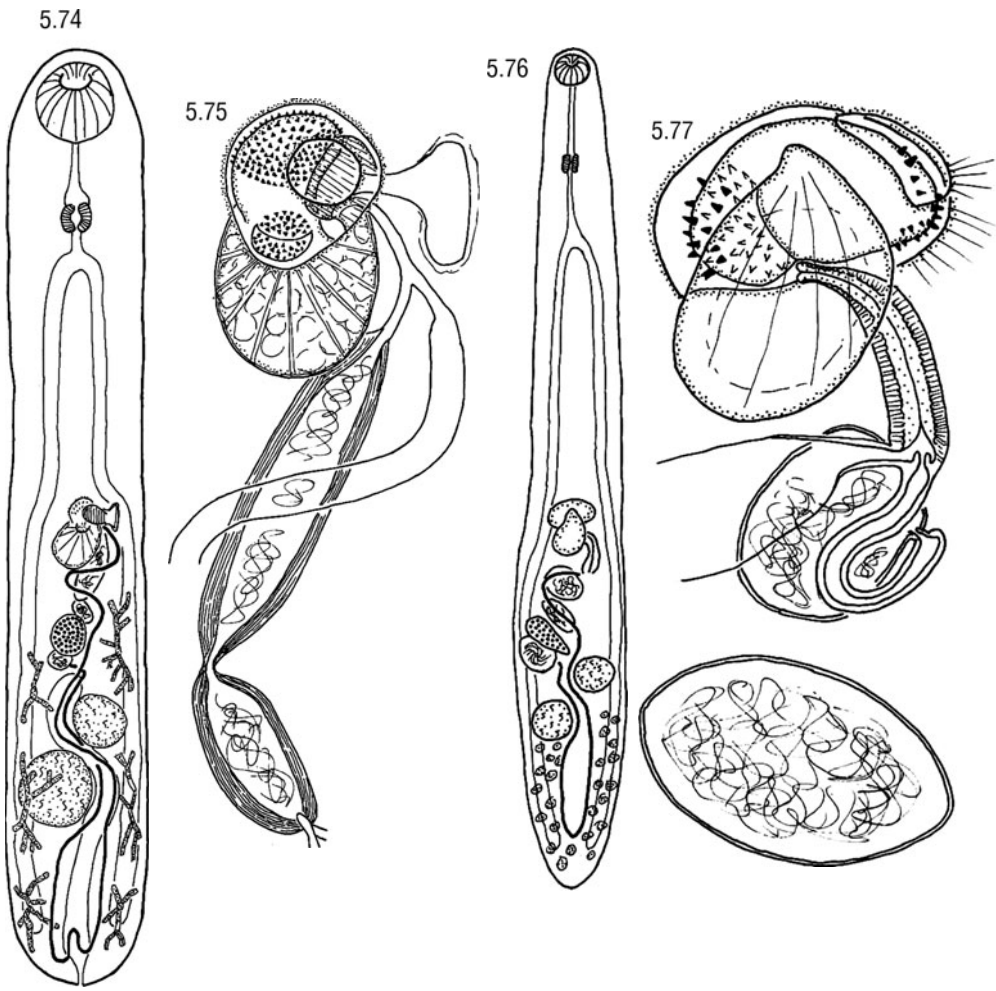
**Diagnosis:** Body about 1.6 mm long. Tegument scaly. Ventral sucker large, bipartite; axis inclined anteriorly; base ovoid and with parenchymatous medulla; apex reniform, dorsal to base, armed laterally with two groups of short, stout spines with single or bifid tips; dextral group larger than sinistral. Testes two. Seminal vesicle bipartite; wall muscular. Ventrogenital sac permanent; sinistral pocket absent; mouth of sac sinistral. Genital atrium long, with thick muscular wall and thicker lining. Gonotyl absent. Seminal receptacle canalicular. Eggs 22–25 × 12–13 µm. Excretory vesicle not known. In skimmers (Rhynchopidae); Florida, USA. Type-species *N. huttoni* Sogandares-Bernal, 1959.

**34b. Ventral sucker rounded; genital atrium short, thin-walled ..... 35.**

**35a. Body distinctly and permanently divided into wide forebody overlapping narrower hindbody ..... *Cercarioides* Witenberg, 1929. (Figs 5.78, 5.79)**

**Diagnosis:** Body 1.7–7.0 mm long, permanently divided into wide forebody, which overlaps narrow hindbody. Tegument spined. Testes two. Ventral sucker small, rounded; axis inclined posteriorly; medulla parenchymatous, with eversible crescentic cavity armed with stout spines and spined knobs. Testes two. Seminal vesicle bipartite or undivided. Ventrogenital sac permanent; sinistral pocket absent. Genital atrium short, thin-walled. Genital pore posterior to ventral sucker. Gonotyl absent. Seminal receptacle canalicular. Vitelline fields intra- or extracaecal. Eggs 34–43 × 19–25 µm. In birds; Africa, Eurasia, Australasia. Type-species *C. aharonii* Witenberg, 1929.

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**Figs 5.74, 5.75.** *Galactosomum phalacrocoracis* Yamaguti, 1939. 5.74. Whole worm, ventral. 5.75. Ventrogenital complex, ventral. Original.
**Figs 5.76, 5.77.** *Neostictodora huttoni* Sogandares-Bernal, 1959. 5.76. Whole worm, ventral. After Sogandares-Bernal (1959b). 5.77. Ventrogenital complex, ventral, duct joining chambers of seminal vesicle not seen. From holotype. Original.

**35b. Body undivided, subcylindrical** ..... ..... *Condylocotyla* **Pearson & Prévot, 1985. (Figs 5.80–5.82)**

**Diagnosis:** Body 2.3–3.2 mm long, undivided, subcylindrical. Tegument spined. Ventral sucker with axis inclined posterosinistrally; cavity spined, eversible, armed with three pairs of spiny or tuberculate knobs with thickened tegument. Testes two. Seminal vesicle thin-walled, bipartite; proximal chamber elongate and sinuous, distal spherical. Ventrogenital sac permanent, with narrow-mouthed sinistral pocket with villous lining. Genital atrium short, thin-walled. Genital pore posterosinistral to ventral sucker. Gonotyl absent. Seminal receptacle

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canalicular. Eggs 32 × 17 μm. In gulls (Laridae); Mediterranean, Black Sea. Type-species *P. pilodora* Pearson & Prévot, 1985.

## Genera *incertae sedis*

### *Macrotestophyes* Varenov, 1963 (Figs 5.83, 5.84)

**Diagnosis:** Body 1.0 mm long. Tegument spined. Ventral sucker smaller than gonotyl, not included in 'genital sinus' (= genital sac). Ventrogenital complex obscure. Genital pore appears to open on gonotyl. In muskrat; Russia. Type-species *M. ondatrae* Varenov, 1963.

### *Sonkulitrema* Ablasov & Chibichenko, 1960 (Fig. 5.85)

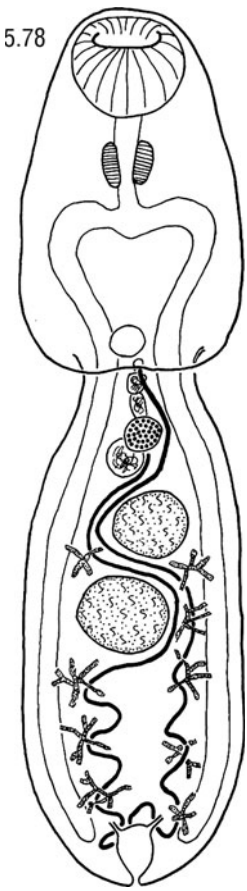
**Diagnosis:** Body 700 μm long. Seminal vesicle thin-walled, undivided. Genital sac unknown. Gonotyl sucker-like; cavity overhung by clavate projection of lip dextrally, armed with U-shaped row of about 20 spines. Genital pore unknown. In terns (Laridae); Kyrgyzia. Type-species *S. sternae* Ablasov & Chibichenko, 1960.

## Addendum

*Neoheterophyes* Khotenovskii, 1970 currently includes six species found exclusively in Asian bats. The most prominent feature of the genus is the presence of a highly muscular tubular organ (termed 'accessory sucker' or 'accessory appendages' by Matskási, 1973a, b) associated with the ventral sucker that appears on total mounts as several accessory suckers. The function of this organ is presently unknown, although Khotenovskii (1970a) suggested that it is connected to the seminal receptacle. The type-species *Neoheterophyes bychowskyi* Khotenovskii, 1970 was described by Khotenovskii (1970a) from the far east of Russia. Since then, five more species, namely *N. topali* Matskási, 1973, *N. brevicorpus* Matskási, 1973, *N. huynhi* Matskási, 1973, *N. sawadai* (Kifune, 1980) and *N. yamato* Kifune, 2000, have been described in Vietnam, India and Japan (Matskási, 1973a, b; Kifune, 1980, 2000). Some of these species, especially *N. topali* Matskási 1973 and *N. sawadai* Kifune, 1980, substantially differed from *N. bychowskyi* in body shape, length of caeca and arrangement of some internal organs, particularly the vitellarium and ovary. It should be mentioned that *N. brevicorpus* and *N. huynhi* only slightly differ from each other in body shape and *N. sawadai* differs from *N. topali* only in sucker ratio. However, any definitive conclusion on possible identity of these pairs of species can be made only upon examination of additional materials and/or molecular comparison.

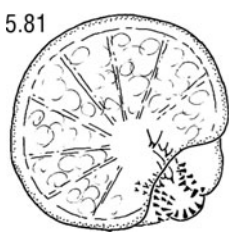
**Figs 5.78, 5.79.** (*Opposite*) *Cercarioides aharonii* Witenberg, 1929. 5.78. Whole worm, ventral. 5.79. Ventrogenital complex, ventral, uterus omitted. Original, from holotype.
**Figs 5.80–5.82**. (*Opposite*) *Condylocotyla pilodora* Pearson & Prévot, 1985. 5.80. Whole worm, ventral. 5.81. Ventral sucker, ventral, with spined cavity everted. 5.82. Ventrogenital complex, ventral. Original.
**Figs 5.83, 5.84.** (*Opposite*) *Macrotestophyes ondatrae* Varenov, 1963. 5.83. Whole worm, ventral. 5.84. Ventrogenital complex, ventral. After Varenov (1963).
**Fig. 5.85.** (*Opposite*) *Sonkulitrema sternae* Ablasov & Chibichenko, 1960. Whole worm, ventral. After Belopol'skaya (1963).

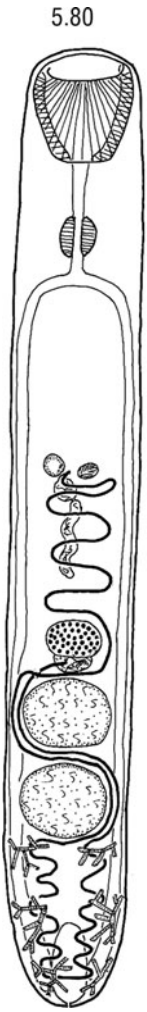
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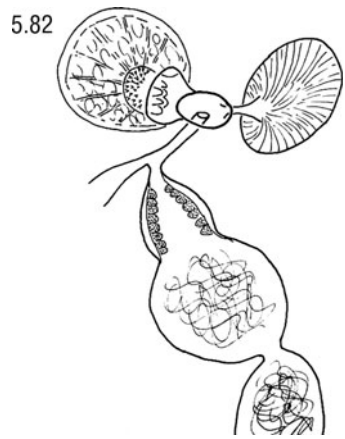


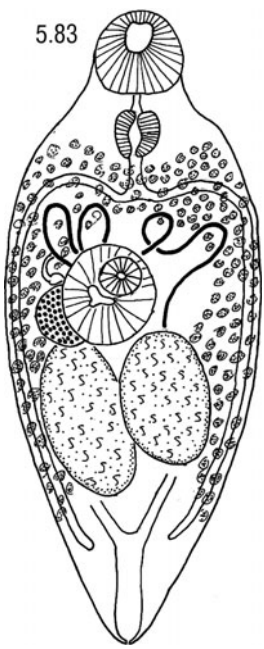


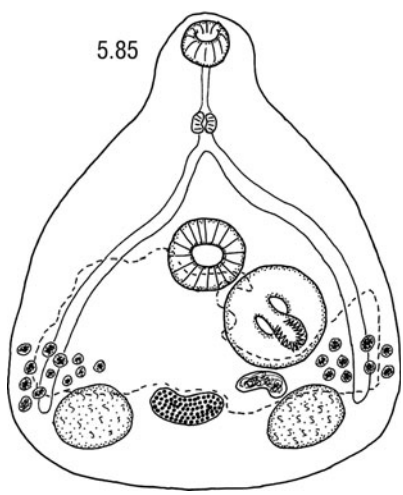


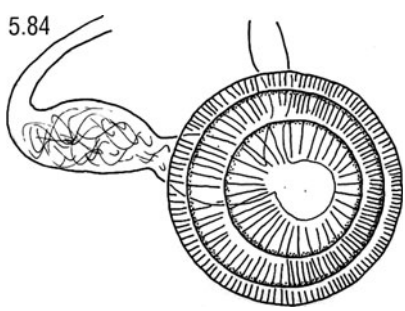



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## *Neoheterophyes* Khotenovskii, 1970 (*incertae sedis*) (Figs 5.86–5.88)
(Syn. *Duboisitrema* Kifune, 1980)

**Diagnosis:** Body small, rounded, pyriform or elongate. Tegument armed with small spines. Oral sucker subterminal. Ventral sucker smaller than, similar in size to or larger than oral sucker, in anterior half of body; extends into muscular accessory sac which may appear as several additional suckers. Prepharynx short or indistinct. Pharynx small. Oesophagus indistinct to relatively long. Caeca very short or extending into hindbody, but always terminating anterior to testes. Testes oval or rounded, symmetrical or oblique, may be situated anterior to ventral sucker, at level of ventral sucker or posterior to it. Seminal vesicle claviform or convoluted, thick-walled in the region of ventral sucker. Genital pore in forebody. Ovary rounded or irregularly shaped, usually between ventral sucker and one testis and may overlap both testes. Seminal receptacle present.

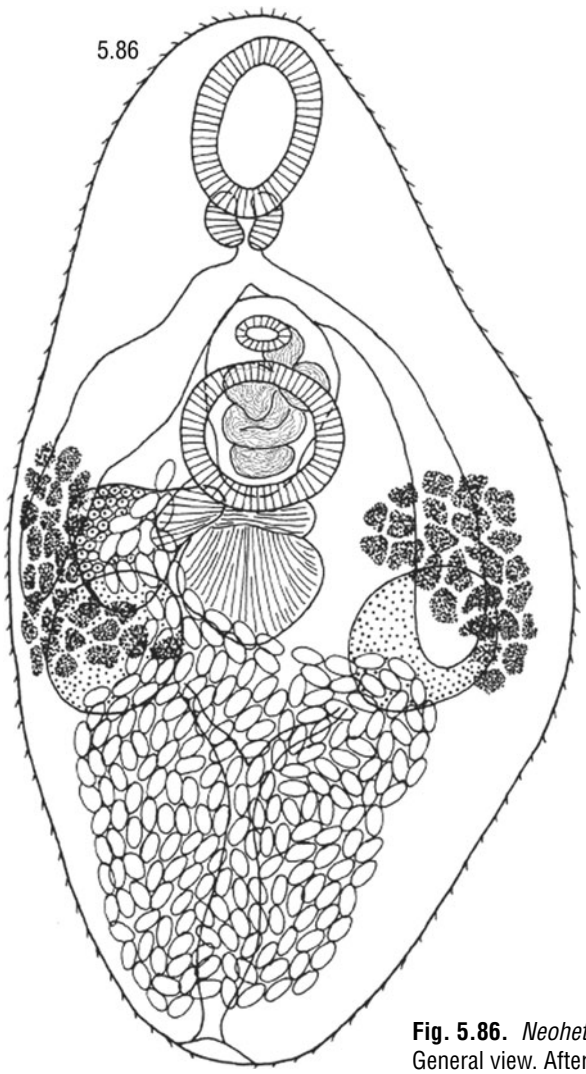
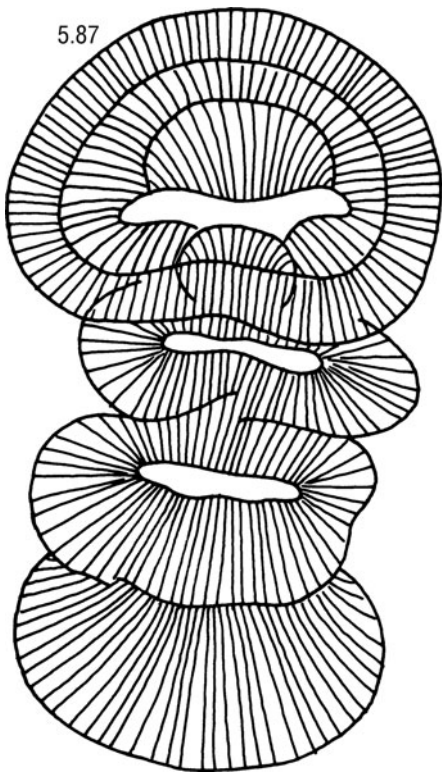



**Fig. 5.86.** *Neoheterophyes bychowskyi* Khotenovskii, 1970. General view. After Khotenovskii (1970a).

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Uterus occupies most of hindbody. Metraterm not pronounced. Eggs numerous. Vitellarium in two bunches or elongated groups of numerous follicles situated symmetrically on either side of body close to ends of caeca; may be in shoulder region or in middle of body posterior to ventral sucker; posterior margin of vitelline groups may overlap anterior margin of testes. Excretory pore terminal; excretory vesicle Y-shaped with long stem bifurcating just posterior to testes. In intestine of Chiroptera; Palaearctic and Indo-Malayan regions. Type-species *N. bychowskyi* Khotenovskii, 1970.

*V.V. Tkach*



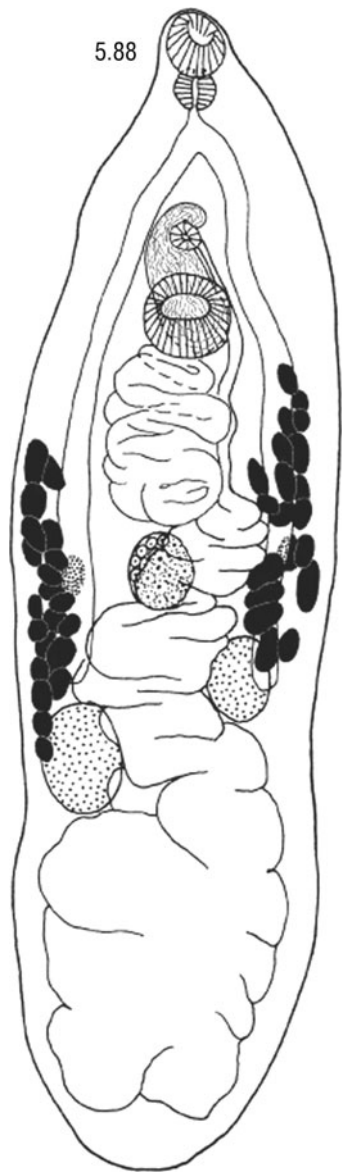




**Fig. 5.87.** *Neoheterophyes bychowskyi* Khotenovskii, 1970. Ventral sucker with accessory organ. After Khotenovskii (1970a).
**Fig. 5.88.** *Neoheterophyes sawadai* (Kifune, 1980). After Kifune (1980).

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# 6 Superfamily Monorchioidea Odhner, 1911

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## Introduction

The superfamily Monorchioidea Odhner, 1911 unites two generally unspecialized families of trematodes, the Monorchiidae Odhner, 1911 and the Lissorchiidae Magath, 1917, found as sexual adults in the intestine of mainly marine and freshwater fishes, respectively. Only with the advent of molecular approaches has it become apparent that the group is worthy of superfamily status; this taxon was originally used at this level by Olson *et al*. (2003), who found molecular support for it to contain the lissorchiids in addition to the monorchiids. The group was also considered to be distinct at the subordinal level, i.e. forming the Monorchiata Olson, Cribb, Tkach, Bray & Littlewood, 2003. As discussed by Bray in Chapter 8 of this volume on the Lissorchiidae, Shimazu (1992) gave a clear summary of the features of the two families, which are readily separable (although their members were long combined together in the Monorchiidae) and have strikingly different life-cycles. Monorchiid sporocysts infect bivalves, from which oculate cercariae emerge, whereas lissorchiid rediae infect gastropods, from which non-oculate cercariae emerge.

## Superfamily Monorchioidea Odhner, 1911

**Diagnosis:** Body small or medium-sized, oval to elongate or long and slender. Eye-spot pigment present or not. Tegument usually spined. Oral sucker subterminal, round or funnel-shaped, rarely with ring of spines. Ventral sucker usually pre-equatorial. Prepharynx present or absent, of variable size. Pharynx well developed. Oesophagus of variable length. Intestinal bifurcation usually in forebody. Caeca short to long, blind. Testis single or double, rarely eight, symmetrical, oblique or tandem when double, usually in hindbody, exceptionally in forebody. Cirrus-sac claviform, extends posterodorsally to ventral sucker or into anterior hindbody. Seminal vesicle internal, bipartite, unipartite or tubular. Pars prostatica often vesicular, variable. Ejaculatory duct capable of forming cirrus; cirrus usually armed. Genital atrium distinct, small or apparently absent, may be spined. Genital pore median or submedian, in fore- or hindbody or lateral to ventrally sublateral at level of ventral sucker. Ovary entire or lobed, in fore- or hindbody, median or dextral,

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pretesticular. Seminal receptacle uterine; canalicular seminal receptacle may be present but small and functionless. Mehlis' gland and Laurer's canal present. Uterus usually with numerous coils, occupies entire hindbody, may extend into forebody. Terminal organ (sac-like structure associated with terminal part of uterus) present or absent. Eggs oval, operculate, may have polar filament. Vitellarium usually in form of symmetrical bunches of follicular or tubular acini, rarely as compact masses in various regions of body, extensive or limited. Excretory vesicle tubular, I-, V- or Y-shaped; pore terminal. In gastro-intestinal tract of marine or freshwater fishes; cosmopolitan. Type-genus *Monorchis* Looss, 1902.

## Key to families

**1a. Genital pore median in forebody; metraterm with distinct terminal organ; in marine, occasionally freshwater, fishes ..... Monorchiidae Odhner 1911.**

**1b. Genital pore lateral or sublateral; metraterm simple, may be spined, but lacks terminal organ; in freshwater fishes ..... Lissorchiidae Magath, 1917.**

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# 7 Family Monorchiidae Odhner, 1911

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## Introduction

Members of the family Monorchiidae Odhner, 1911 are characterized by the possession of a spiny tegument, complex terminal genitalia armed with recurved spines, restricted fields of vitelline follicles and well-developed uterine coils. They occur in the gastro-intestinal tract of marine fishes throughout the world. Information available on the life-cycles of monorchiids indicates that cercariae with or without eye-spots develop in marine bivalve molluscs, encyst in a wide range of marine invertebrates as metacercariae and develop into adult flukes in marine fishes (Lloyd & Guberlet, 1932; Martin, 1940; De Martini & Pratt, 1964; Bartoli, 1965, 1966; Prévot, 1967; Stunkard, 1981a, b; Bartoli *et al*., 2000). Taking into consideration the cercarial features and the pattern of the life-cycle, La Rue (1957) placed the Monorchiidae in the suborder Plagiorchiata La Rue, 1857 and the superfamily Allocreadioidea Looss, 1902. However, Olson *et al*. (2003), based on Bayesian inference of DNA sequences, erected a new suborder Monorchiata to include the superfamily Monorchioidea Odhner, 1911, in which are included the families Monorchiidae and Lissorchiidae Poche, 1926.

Established by Odhner (1911a) for *Monorchis monorchis* (Stossich, 1890) Looss, 1902, the family now includes more than 290 nominal species in 58 genera (Nahhas & Grewal, 1999). The family was considered polyphyletic (Brooks *et al*., 1989) because of the great diversity exhibited by its members in body organization, especially in the number of testes, extent of the vitellarium and uterus and shape of the excretory vesicle, which may be saccular, V- or Y-shaped. The most striking distinguishing feature of the family is the presence of a sac-like structure associated with the terminal genitalia and a continuation of the uterus, termed variously the metraterm, metraterm sac, vaginal sac, Looss' organ or terminal organ. Several authors expressed the view that details of the terminal genitalia, including the shape of the terminal organ (unipartite or bipartite), the point where the uterus joins it, together with the shape of the seminal vesicle and the pattern of spination of the cirrus, genital atrium and terminal organ, should form the basis for the differentiation of genera, while features such as the extent of the caeca and the distribution of the vitelline follicles have little taxonomic significance (Nahhas & Powell, 1965; Sey & Nahhas, 1997; Dove & Cribb, 1998). The structure of the terminal organ varies considerably. It may be a simple

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thick-walled, sac-like structure that is a continuation of the uterus proper. In many monorchiids, it is a bipartite structure consisting of a posterior vesicle and an anterior tubular part that is usually spiny and the uterus joins it at the junction between the two parts or more anteriorly. In the descriptions given for the terminal organ by various authors, it is seen that there is no uniformity in designating its proximal and distal ends. I propose here that the part of the terminal organ that opens into the genital atrium be considered as the proximal end and the blind opposite end as the distal end, and that the two parts of the bipartite terminal organ be designated as the anterior tubular and the posterior vesicular parts.

The three major reports dealing with the division of the monorchiids into subfamilies are those of Manter & Pritchard (1961), Mamaev (1968b) and Yamaguti (1971). Manter & Pritchard included all the genera reported to that date in five subfamilies: the Monorchiinae Odhner 1911, Asymphylodorinae Szidat, 1943, Hurleytrematinae Yamaguti, 1958, Opisthomonorchiinae Yamaguti, 1952 and Octotestiinae Yamaguti, 1958. Mamaev (1968b) recognized the same five subfamilies. Yamaguti (1971) divided the monorchiids into 12 subfamilies, many of which have not been recognized by subsequent authors. Wang (1985) recognized all these subfamilies as valid and added one more, the Macrostominae Wang, 1985, whose members are now considered lissorchiids (Bray, Chapter 8, this volume). In the present account, the system proposed by Manter & Pritchard has mainly been followed but the addition of many new genera over the years has necessitated some changes. A comprehensive revision of subfamily structure is clearly needed, but existing knowledge on the biology of the group is inadequate. Based on the available information, some changes to the system of Manter & Pritchard (1961) are proposed here.

The subfamily Asymphylodorinae, originally included in the Monorchiidae, has now been moved to the Lissorchiidae (see Shimazu, 1992; Bray, Chapter 8, this volume).

Among the other subfamilies, the Monorchiinae is the largest. The wide variation exhibited in the morphology of its various genera, especially in the number of testes, distribution of the vitelline follicles, structure of the terminal genitalia and shape of the excretory vesicle, indicates that it is probably a heterogeneous assemblage of genera and needs a thorough revision. Three genera included, i.e. *Opisthomonorcheides* Parukhin, 1966, *Opisthodiplomonorchis* Madhavi, 1974 and *Neolasiotocus* Ahmad, 1991, stand distinct from the others in having very long, slender bodies, testes close to the posterior extremity and vitelline follicles extended over a fairly extensive area, occupying the dorsal and lateral regions of the body. The subfamily Opisthomonorcheidinae Yamaguti, 1971 is here considered to include these three genera.

Three of the six subfamilies regarded here as valid are characterized by the occurrence of filamentous eggs and are distinguished by the genital pore being in the forebody in the Hurleytrematinae, in the hindbody in the Opisthomonorchiinae and in the forebody in combination with the disposition of the gonads in the forebody in the Anamonorchiinae Yamaguti, 1970. The Octotestiinae is also included here as a subfamily of the Monorchiidae, although Yamaguti (1971) gave it full family status.

*Elliptobursa* Wu, Lu & Zhu, 1996, erected by Wu *et al.* (1996) based on *E. singlorchis* Wu, Lu & Zhu, 1996 from *Mugil cephalus*, and *Allomonorchis* Lu, Wu & Chen (1999), erected by Lu *et al.* (1999) for *A. huangfuensis* Lu, Wu & Chen, 1999 from *M. macrolepis*, are undoubtedly haploporids, as evidenced by the presence of a single testis, a long external seminal vesicle, a well-developed prostatic complex and a long hermaphroditic duct wrongly interpreted as a cirrus. Similarly, *Pseudopalaeorchis* Kamegai, 1970, reported as a monorchiid, has clearly defined zoogonid characters such as a spined tegument, a lateral genital pore and a bipartite seminal vesicle. *Cestrahelmins* Fischthal, 1957, reported from freshwater fishes and included in the Monorchiidae, apparently shows affinities with the Macroderoididae McMullen, 1937.

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*Micromonorchis* Khoche, 1969 has only briefly been described and has not been figured. It appears to be related to the heterophyid genus *Haplorchoides* Chen, 1949, many species of which have been recorded from freshwater fishes. The descriptions of *Sphericomonorchis* Thatcher, 1996 from freshwater fishes and *Polylecithus* Wang & Wang, 1993 from marine fishes lack many details. These three genera are treated here as genera *inquirenda. Lenolopa* Lu & Wu, 1996, characterized by the presence of a long external seminal vesicle, extensive vitelline fields and lacking a terminal organ, may not belong in the Monorchiidae. Data available on the genus for the precise determination of its family assignment are inadequate and it must be considered as *incertae sedis*. Another genus whose validity is to be questioned is *Paraproctotrematoides* Nagaty & Abdel-Aal, 1972. The description lacks details of the terminal genitalia and vitelline distribution. It is most probably a haploporid.

*Alloproctotrema* Machida, 1973 is here synonymized with *Postmonorchis* Hopkins, 1943, with which it was not compared by Machida (1973). *Bathymonorchis* Bray & Gaevskaya, 1993 is congeneric with *Monorchis* Looss, 1902, considering that the characters used for the separation of these two genera, the distribution of uterine coils and the location of the testis are of no more than specific value.

Madhavi (1977) erected two new genera, *Retractomonorchis* Madhavi, 1977 and *Caballerotrematoides* Madhavi, 1977. The former was differentiated from *Opisthomonorcheides* Parukhin, 1966 by the position of the genital pore in the forebody and the presence of a thin-walled genital atrium that can be detected only when filled with eggs. Presuming that a thin-walled genital atrium also exists in *Opisthomonorcheides* but was overlooked, Hafeezullah (1984) synonymized *Retractomonorchis* with it. Accordingly, the generic diagnosis of *Opisthomonorcheides* is to be amended to state 'genital pore is in the forebody'. Another synonym of this genus appears to be *Longimonorchis* Mamaev, 1970, erected by Mamaev (1970) to include *L. ovacutus* Mamaev, 1970 from the stromateid fish *Formio niger*. Both of these genera agree in almost all details of their structure. *Tritesticulum* Bilqees, 1971, based on three specimens collected from *Stromateus* sp. off the Karachi coast, is similar to *Opisthomonorcheides*, but its description is inadequate and probably erroneous, and its inclusion within the Allocreadiidae Looss, 1902 was a grave error.

*Leiomonorchis* Mamaev, 1970 and *Caballerotrematoides* Madhavi, 1977 exhibit similarities in their morphological details as well as their hosts. In the absence of major differences, *Caballerotrematoides* is here considered a synonym of *Leiomonorchis*. Since the single species *C. leiognathi* Madhavi, 1977 would become a secondary homonym of *L. leiognathi* Mamaev, 1970, this specific name is here modified to *L. mamaevi* nom. nov. (syn. *C. leiognathi* Madhavi, 1977).

A new genus, *Neotimonia* n.g., is proposed here for *Timonia caballeroi* Madhavi, 1977, which differs from the other species of *Timonia* Bartoli & Prevot, 1966 by the bipartite terminal organ, vitellarium in the forebody and uterine coils descending into the post-testicular space. These features clearly warrant the erection of a new genus. *N. caballeroi* (Madhavi, 1977) n. comb. is the type-species of the new genus.

*Ametrodaptes* Bravo-Hollis, 1956, *Huridostomum* Mamaev, 1970 and *Neopisthomonorchis* Varma, 1982 are characterized by the presence of a ring of spines on the oral sucker. Except for slight differences in the location of the gonads and the distribution of the vitelline follicles, *Neopisthomonorchis* is similar to *Ametrodaptes* and the differences cited do not justify a distinct genus. I consider them synonyms. *Huridostomum* differs from *Ametrodaptes* in the distribution of the vitelline fields in the region of the ventral sucker rather than in the region of the gonads and in the very long, sinuous cirrus-sac, almost extending to the level of the ovary. Triveni Lakshmi & Madhavi (2008) erected a new genus *Pseudametrodaptes* Triveni Lakshmi & Madhavi, 2008 to include the four Indian species of *Ametrodaptes*, and differentiated the new genus by the structure of terminal genitalia including the absence of spines in the genital atrium, a unipartite rather than

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bipartite terminal organ and the uterus joining the posterior part rather than the anterior part of the terminal organ.

*Opisthodiplomonorchis* Madhavi, 1974, synonymized with the deropristid *Skrjabinopsolus* Ivanov in Ivanov & Murygin, 1937 by Hafeezullah (1984), was resurrected as valid by Choudhury & Dick (1998) and is recognized here.

The original description of *Ancylocoelium* Nicoll, 1912 is brief and lacked details of the terminal genitalia, such that the relationships of this genus with other monorchiid genera remained enigmatic. However, the recent redescription of the type-species, *A. typicum* Nicoll, 1912, by Bartoli & Bray (2004), based on specimens collected from the type-host and type-locality, suggested that *Ancylocoelium* is a synonym of *Lasiotocus* Looss in Odhner (1911). *A. typicum* became *L. typicus* (Nicoll, 1912). Another genus that closely resembles *Lasiotocus* is *Chrisomon* Manter & Pritchard, 1961, erected by Manter & Pritchard (1961) for *Telolecithus tropicus* Manter, 1940. The two genera were separated by the configuration and extent of the vitellarium, composed in *Chrisomon* of star-shaped clusters of tubular acini rather than the follicular vitellarium characteristic of *Lasiotocus*. However, Bartoli & Bray (2004) showed that *C. tropicum* has a follicular vitellarium and synonymized *Chrisomon* with *Lasiotocus*. They further suggested that other nominal species of *Chrisomon*, with a vitellarium in the form of star-shaped clusters of tubular acini, may belong to a new genus. Other than the type-species, eight species were reported in *Chrisomon* (see Dove & Cribb, 1998). Considering that they all have a vitellarium in the form of star-shaped tubular acini occupying a more extensive area than in *Lasiotocus* spp., a new genus, *Parachrisomon* n.g., is here proposed for them, with *P. decapteri* (Nahhas & Cable, 1964) n. comb. as the type-species. The other species are: *P. albulae* (Overstreet, 1969) n. comb., *P. delicatus* (Manter & Pritchard, 1964) n. comb., *P. ulua* (Yamaguti, 1970) n. comb., *P. weke* (Yamaguti, 1970) n. comb., *P. israelensis* (Fischthal, 1980) n. comb., *P. brotulidorum* (Toman, 1973) n. comb. and *P. gaigai* (Dove & Cribb, 1998) n. comb.

*Physochoerus* Poche, 1926 is undoubtedly a monorchiid, but, in view of the limited and inadequate description, it is not included in this account and is considered a genus *inquirendum. Infundibulostomum* Siddiqi & Cable, 1960, included in the Fellodistomidae Nicoll, 1909, resembles a monorchiid in its basic structure, but features such as the absence of a terminal organ, an unarmed cirrus and the presence of a canalicular seminal receptacle preclude its inclusion in the Monorchiidae. It may be a fellodistomid, but was not treated as such by Bray (2002b).

The most problematic genera are those belonging to the monorchiine group represented by *Genolopa* Linton, 1910, *Proctotrema* Odhner, 1911, *Lasiotocus, Paraproctotrema* Yamaguti, 1934, *Proctotrematoides* Yamaguti, 1938, *Bupharynx* Yamaguti, 1971 and *Monorchicestrahelmins* Yamaguti, 1971. Their validity is controversial (Thomas, 1959; Manter & Pritchard, 1961; Bartoli & Prévot, 1966; Prévot & Bartoli, 1967; Dove & Cribb, 1998). They are now separated based on differences in the organization of the terminal genitalia. For instance, *Genolopa, Paraproctotrema, Bupharynx* and *Monorchicestrahelmins* differ from the others in the group in having spines in the genital atrium. In *Genolopa* and *Paraproctotrema*, the terminal organ is bipartite, in contrast to *Bupharynx* and *Monorchicestrahelmins*, where it is unipartite. *Paraproctotrema* is characterized by the presence of a distinct bulb-like sphincter at the distal end of the uterus. *Bupharynx* is here regarded as a synonym of *Monorchicestrahelmins*: the only feature separating the two, the size of the pharynx, is only of specific significance. The genital atrium is unspined in *Proctotrema, Lasiotocus, Parachrisomon* and *Proctrotrematoides*. In *Proctotrema* the terminal organ is unipartite whereas in the other three genera it is bipartite. *Proctotrematoides* is characterized by the presence of a distinct spiny diverticulum in the genital atrium. *Lasiotocus* and *Parachrisomon* are very similar but can be distinguished by the nature and extent of the development of the vitellarium.

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A close similarity is seen between the putative opecoelid genus *Helicometroides* Yamaguti, 1934 and the monorchiid *Hysterorchis* Durio & Manter, 1968. Morphologically they are identical. Apparently misled by the well-developed vitelline follicles and presence of filamented eggs, Yamaguti (1934) placed *Helicometroides* in the Opecoelidae Ozaki, 1925, but the presence of a spined tegument and a spined cirrus rather suggest an affinity with the Monorchiidae. Based on these features, *Helicometroides* is here treated as a monorchiid. In the absence of any major differences, *Hysterorchis* is considered a synonym of *Helicometroides*. The two species *Hysterorchis vitellosus* Durio & Manter, 1968 and *Hysterorchis leiperi* Ahmad, 1981 become *Helicometroides vitellosus* (Durio & Manter, 1968) n. comb and *Helicometroides leiperi* (Ahmad, 1981) n. comb.

The validity of some monorchiid genera possessing two testes is questionable. Overstreet (1969) considered *Diplomonorcheides* Thomas, 1959 as a synonym of *Diplomonorchis* Hopkins, 1941. Another synonym of this genus appears to be *Zhukovtrema* Sey & Nahhas, 1997 (syn. *Pseudomonorcheides* Zhukov, 1983 *nec* Wang, 1982).

Some apparently monorchiid genera have erroneously been allocated to other digenean families. One such is *Allobacciger* Hafeezullah & Siddiqi, 1970, originally placed in the family Fellodistomidae. It has a well-developed terminal organ and closely resembles *Pseudomonorcheides* Wang, 1982, except for the absence of spines on the tegument and in the terminal genitalia, which were probably lost due to poor preservation. Cribb *et al.* (1999a) collected specimens of the type-species, *A. macrorchis* Hafeezullah & Siddiqi, 1970, or 'a very similar species', and found clear spines in the terminal genitalia and considered the genus consistent with the Monorchiidae. Machida & Uchida (2001) described a second species, *A. centropygis* Machida & Uchida, 2001, as a monorchiid. *Pseudomonorcheides* is here regarded as synonymous with *Allobacciger. P. ditrematis* Wang, 1982 becomes *A. ditrematis* (Wang, 1982) n. comb.

Resulting from this revision, the family Monorchiidae is left with 40 valid genera distributed among six subfamilies. Keys for separation of these various subfamilies and genera and their diagnostic features are presented below.

## Family Monorchiidae Odhner, 1911

**Diagnosis:** Body small or medium-sized, oval to elongate or long and slender. Eye-spot pigment may be present. Tegument usually spined. Oral sucker subterminal, round or funnel-shaped, rarely with ring of spines. Ventral sucker usually pre-equatorial. Prepharynx present or absent, of variable size. Pharynx well developed. Oesophagus of variable length. Intestinal bifurcation in forebody. Caeca long, narrow, end blindly between testicular level and posterior extremity. Testis single or double, rarely eight, symmetrical or tandem when double, usually in hindbody, exceptionally in forebody. External seminal vesicle rarely present. Cirrus-sac well developed, in forebody or curving round ventral sucker, sometimes entirely in hindbody, encloses simple, bipartite or tubular seminal vesicle, pars prostatica with numerous prostatic cells and spined cirrus. Genital atrium well developed, may be spined. Genital pore median or submedian, in fore- or hindbody. Ovary spherical or lobed, in fore- or hindbody, median or dextral, pretesticular, contiguous with testis or separated by uterine coils. Mehlis' gland and Laurer's canal present. Seminal receptacle uterine. Uterus usually with numerous coils, occupies entire hindbody, may extend into forebody, opens through tubular metraterm into distal or middle part of terminal organ. Terminal organ simple or bipartite, entirely spined or only in anterior part, occasionally absent. Eggs oval, operculate, may have polar filament. Vitellarium usually forms symmetrical bunches of follicular or tubular acini, rarely compact masses in various regions of body, extensive or limited. Excretory vesicle usually saccular, sometimes

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tubular, V- or Y-shaped; pore terminal. In gastro-intestinal tract of marine fishes (occasionally freshwater fishes); cosmopolitan. Type-genus *Monorchis* Looss, 1902.

## Key to subfamilies

**1a. Testes one or two ..... 2.**
**1b. Testes eight or more ..... Octotestiinae Yamaguti, 1958.**

**2a. Eggs without filament ..... 3.**
**2b. Eggs with long polar filament ..... 4.**

**3a. Body long, slender; testes near posterior extremity; vitelline follicles fairly numerous ..... ..... Opisthomonorcheidinae Yamaguti, 1971.**
**3b. Body small, oval or elongate; position of testes variable; vitellarium, few follicles or small acinous bunch ..... Monorchiinae Odhner, 1911.**

**4a. Genital pore in forebody ..... 5.**
**4b. Genital pore in hindbody ..... Opisthomonorchiinae Yamaguti, 1952.**

**5a. Gonads in forebody ..... Anamonorchiinae Yamaguti, 1970.**
**5b. Gonads in hindbody ..... Hurleytrematinae Yamaguti, 1958.**

## Subfamily Monorchiinae Odhner, 1911

(Syns Ancylocoeliinae Skrjabin & Koval, 1957; Lasiotocinae Yamaguti, 1958; Postmonorcheidinae Yamaguti, 1958; Pseudoproctotrematinae Yamaguti, 1958; Telolecithinae Yamaguti, 1958)

**Diagnosis:** Body small, oval or elongate. Tegument spined. Oral sucker circular or funnel-shaped, rarely with ring of spines. Caeca long or short. Testis single or double, symmetrical or oblique or tandem when double, usually in hindbody, rarely in forebody. Cirrus-sac extending into hindbody or not, encloses oval or tubular seminal vesicle, prostatic complex and spined cirrus. External seminal vesicle rarely present. Genital atrium spined or not. Genital pore median, postbifurcal. Ovary submedian, smooth or lobed. Terminal organ present. Eggs small, oval; polar filament absent. Vitellarium of few follicles or tubular acini or compact masses, in lateral fields of forebody or hindbody. Excretory vesicle saccular, tubular, I-, V- or Y-shaped. In intestine of marine fishes. Type-genus *Monorchis* Looss, 1902.

## Key to genera

**1a. Testis single ..... 2.**
**1b. Testes two ..... 17.**

**2a. Vitellarium follicular, in 'shoulder' region (i.e. forebody) ..... 3.**
**2b. Vitellarium follicular or compact masses in lateral fields at level of ventral sucker or in hindbody ..... 4.**

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**3a. External seminal vesicle absent; cirrus-sac extends well into hindbody .....**
**..... *Monorchis* Looss, 1902. (Fig. 7.1)**
(Syn. *Bathymonorchis* Bray & Gaevskaya, 1993)

**Diagnosis:** Body small, oval or rounded. Oral sucker subterminal. Ventral sucker equatorial or postequatorial. Prepharynx short. Pharynx oval. Oesophagus distinct, Intestinal bifurcation in mid-forebody. Caeca long, reach posterior extremity. Testis single, submedian, in posterior half of body. External seminal vesicle absent. Cirrus-sac curves around ventral sucker into hindbody, encloses oval seminal vesicle, numerous prostatic cells and spined cirrus. Genital atrium unarmed. Genital pore median, postbifurcal. Ovary entire to distinctly lobed, pretesticular. Uterus fills most of hindbody, joins middle part of terminal organ. Terminal organ with spined anterior and unspined posterior parts. Vitelline follicles form bunches in shoulder region. Excretory vesicle V- or Y-shaped. In intestine of marine fishes; Mediterranean, Atlantic, Gulf of Mexico, Bay of Bengal, Mozambique Gulf. Type-species *M. monorchis* (Stossich, 1890) Looss, 1902.

**3b. External seminal vesicle present; cirrus-sac in forebody .....**
**..... *Allolasiotocus* Yamaguti, 1959. (Fig. 7.2)**

**Diagnosis:** Body small, fusiform, delicate. Oral sucker subterminal. Ventral sucker in anterior half of body. Prepharynx absent. Pharynx small. Oesophagus short. Intestinal bifurcation well anterior

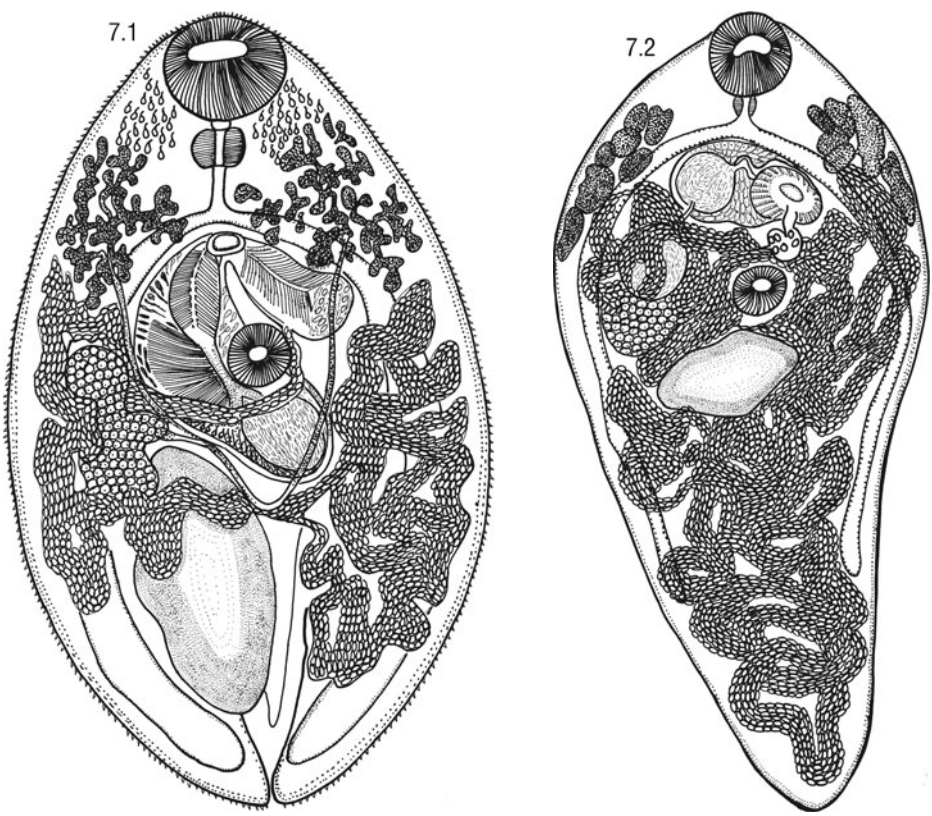



**Fig. 7.1.** *Monorchis monorchis* (Stossich, 1890) Looss, 1902. Ventral view. After Yamaguti (1971).
**Fig. 7.2.** *Allolasiotocus nibeae* Yamaguti, 1959. Ventral view. After Yamaguti (1959).

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to ventral sucker. Caeca not reaching posterior extremity. Testis single, in anterior half of hindbody, close to ventral sucker. External seminal vesicle present. Cirrus-sac club-shaped, in forebody, postbifurcal, encloses large internal seminal vesicle, well-developed prostatic complex and armed cirrus. Genital atrium densely spined. Genital opening submedian, postbifurcal. Ovary dextral at level of ventral sucker or in anterior hindbody. Uterus occupies most of body posterior to genital pore. Terminal organ saccular, lined with acicular spines. Vitelline follicles in bunches in 'shoulder' region. In intestine of marine fishes; off China and Japan. Type-species *A. nibeae* Yamaguti, 1959.

**4a. Ovary in forebody ..... *Pseudoproctotrema* Yamaguti, 1942. (Figs 7.3, 7.4)**
**Diagnosis:** Body small, elliptical, delicate. Oral sucker discoid. Ventral sucker small, postequatorial. Prepharynx long. Pharynx small. Oesophagus long. Intestinal bifurcation in anterior forebody. Caeca long, narrow, reach middle of hindbody. Testis single, median, dorsal or posterodorsal to ventral sucker. Cirrus-sac in forebody, recurved, encloses seminal vesicle, well-developed prostatic complex and spinous cirrus. Genital pore immediately anterior to ventral sucker. Ovary in forebody, submedian, dextral to base of cirrus-sac. Uterus occupies most of hindbody as well as posterior part of forebody, opens into terminal organ near its distal end. Terminal organ elliptical, unspined, situated longitudinally in median field, with its base directed anteriorly. Eggs small. Vitelline masses anterolateral to testis. Excretory vesicle fusiform. In mullid fishes; off Japan. Type-species *P. parupenei* Yamaguti, 1942.

**4b. Ovary in hindbody ..... 5.**

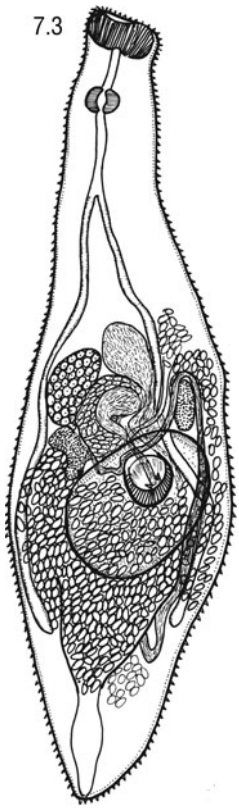
**5a. Vitellarium in symmetrical bunches, posterolateral to testis ..... ..... *Telolecithus* Lloyd & Guberlet, 1932. (Fig. 7.5)**
**Diagnosis:** Body oval. Oral sucker subterminal. Ventral sucker pre-equatorial. Oesophagus short. Intestinal bifurcation midway between suckers. Caeca long, reach posterior region of body. Testis slightly indented, in middle of hindbody. Cirrus-sac claviform, extends well posteriorly beyond ventral sucker, contains oval seminal vesicle, prostatic complex and spined cirrus. Genital pore median, postbifurcal. Ovary lobed, pretesticular. Uterine coils chiefly in post-testicular region; uterus opens into spined portion of bipartite terminal organ. Vitelline follicles form symmetrical bunches in lateral fields posterolateral to testis. Excretory vesicle saccular. In intestine of marine fishes; north-eastern Pacific. Type-species *T. pugetensis* Lloyd & Guberlet, 1932.

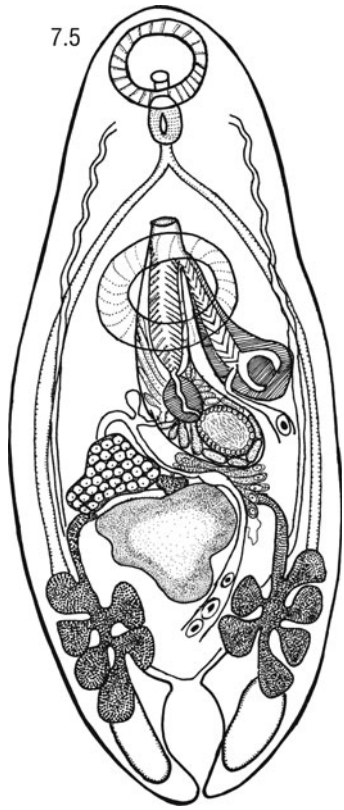
**5b. Vitellarium at level of ventral sucker or testis ..... 6.**

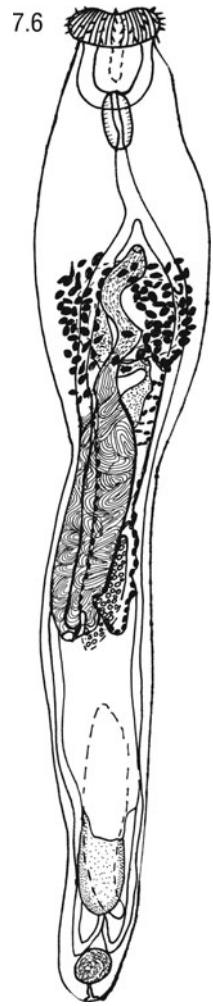
**6a. Oral sucker with ring of enlarged spines ..... 7.**
**6b. Oral sucker without ring of spines ..... 9.**

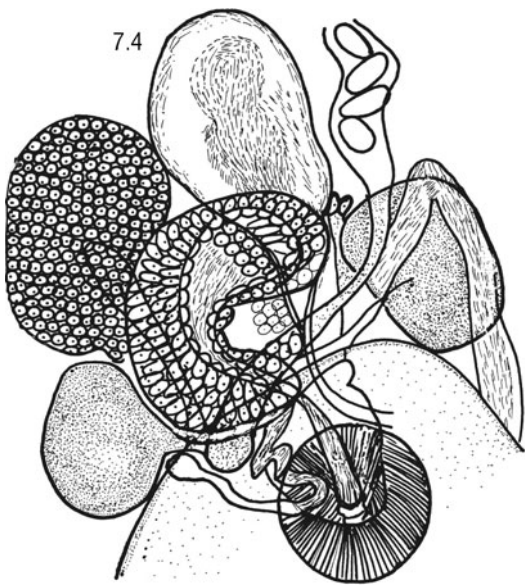
**7a. Cirrus-sac long, sinuous; vitelline follicles form band at level of ventral sucker ..... ..... *Huridostomum* Mamaev, 1970. (Fig. 7.6)**
**Diagnosis:** Body elongate. Oral sucker cup-shaped, with ring of enlarged spines. Ventral sucker poorly developed, in anterior third of body. Pharynx small. Oesophagus long. Intestinal bifurcation in mid-forebody. Caeca long, reaching close to posterior extremity. Testis single, elliptical, in posterior quarter of body. Cirrus-sac very long, sinuous, extends well posterior to ventral sucker, reaches level of testis, encloses a long seminal vesicle, few prostatic cells and long spined eversible ejaculatory duct. Genital atrium without spines. Genital pore median, in forebody. Ovary elliptical, indented, pretesticular, separated from testis by uterine coils. Uterus occupies most of pretesticular region. Terminal organ simple, sac-like, armed with spines; uterus joins its distal part. Vitelline

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**Figs 7.3, 7.4.** *Pseudoproctotrema parupenei* Yamaguti, 1942. 7.3. Ventral view. After Yamaguti (1942b). 7.4. Enlarged view of genitalia. After Yamaguti (1942b).
**Fig. 7.5.** *Telolecithus pugetensis* Lloyd & Guberlet, 1932. Ventral view. After Lloyd & Guberlet (1932).
**Fig. 7.6.** *Huridostomum formionis* Mamaev, 1970. Dorsal view. After Mamaev (1970).

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follicles small, form single band in region of ventral sucker. Excretory vesicle tubular. In intestine of stromateid fishes; Gulf of Tonkin, Bay of Bengal. Type-species *H. formionis* Mamaev, 1970.

**7b. Cirrus-sac claviform; vitelline follicles in lateral fields of ovariotesticular zone ..... 8.**

**8a. Terminal organ bipartite ..... *Ametrodaptes* Bravo-Hollis, 1956. (Fig. 7.7)**
(Syn. *Neopisthomonorchis* Varma, 1982)

**Diagnosis:** Body elongate. Oral sucker large, with alternating rows of spines dorsally. Prepharynx as long as pharynx. Intestinal bifurcation in posterior forebody. Caeca extend to posterior end of body. Testis single, elliptical, in posterior third of body. Cirrus-sac claviform, contains saccular seminal vesicle, prostatic complex and spined cirrus. Genital atrium with diverticulum bearing numerous spines. Genital pore immediately anterior to ventral sucker. Ovary pretesticular. Uterus occupies greater part of hindbody; metraterm with distinct sphincter, opens into proximal part of terminal organ. Terminal organ bipartite; proximal portion finely spinous. Vitelline follicles in lateral fields in gonadal region. Excretory vesicle tubular, reaches ovary. In marine fishes; Pacific coast of Mexico and USA, India. Type-species *A. mexicanus* Bravo-Hollis, 1956.

**8b. Terminal organ unipartite ..... *Pseudametrodaptes* Triveni Lakshmi & Madhavi, 2008 (Figs 7.8, 7.9)**

**Diagnosis:** Body elongate. Oral sucker funnel-shaped, weakly muscular, with ring of spines, arranged in two rows dorsally and single row ventrally. Ventral sucker in anterior third of body. Prepharynx long. Pharynx elliptical. Oesophagus short. Intestinal bifurcation immediately anterior to ventral sucker. Caeca long, end near posterior extremity of body. Testis single, elliptical, equatorial or postequatorial. Cirrus-sac slender, claviform, extends well into hindbody. Seminal vesicle bipartite or saccular. Prostatic complex well developed. Cirrus spined. Genital atrium tubular, thin-walled, unarmed. Genital pore median, in forebody. Ovary spherical or indented, pretesticular. Uterus fills most of hindbody, opens into distal end of terminal organ. Terminal organ small, unipartite, spined. Eggs not filamented. Vitelline follicles in lateral fields in ovariotesticular zone or just anteriorly. Excretory vesicle not described. In marine teleosts; northern Indian Ocean. Type-species *P. secundus* (Madhavi, 1977) Triveni Lakshmi & Madhavi, 2008.

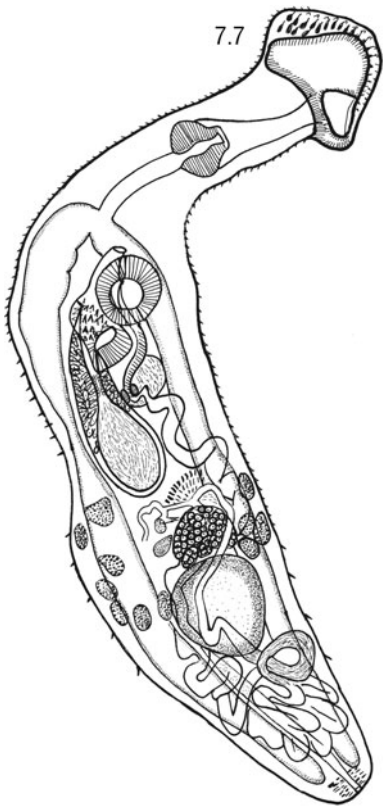
**9a. Testis near posterior extremity; uterine coils not extending posteriorly beyond testis ..... 10.**

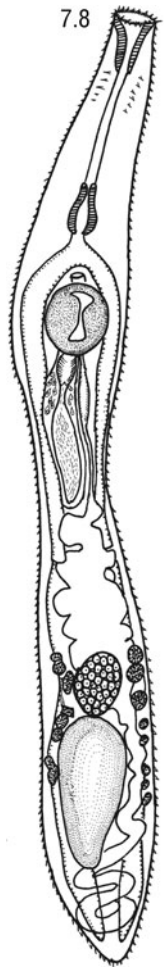
**9b. Testis in middle third of body; uterine coils fill pre- and post-testicular regions ..... 11.**

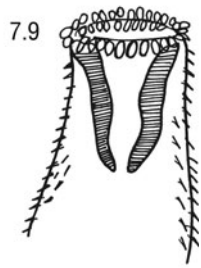
**10a. Body broadly pyriform; vitellarium forms small clusters of follicles on either side of testis or ovary ..... *Postmonorchis* Hopkins, 1941. (Fig. 7.10)**
(Syn. *Alloproctotrema* Machida, 1973)

**Diagnosis:** Body round or oval. Oral sucker terminal. Ventral sucker in middle third of body. Prepharynx short. Pharynx small. Oesophagus distinct. Intestinal bifurcation at mid-body between suckers. Caeca long, terminate close to posterior extremity. Testis near posterior extremity. Cirrus-sac long, extends well into hindbody, encloses oval seminal vesicle, prostatic complex and short spined cirrus. Genital atrium spinous. Genital pore median, anterior to ventral sucker. Ovary rounded, pretesticular. Uterus forms compact coils in extracaecal fields from level of bifurcation to near posterior end, but not beyond testis. Metraterm opens into spiny proximal portion of bipartite terminal organ. Vitellarium consists of two compact extracaecal groups of follicles at level of ovary or just anterior. Excretory vesicle saccular. In intestine of marine fishes; Atlantic coast of USA, Pacific coast of Japan. Type-species *P. orthopristis* Hopkins, 1941.

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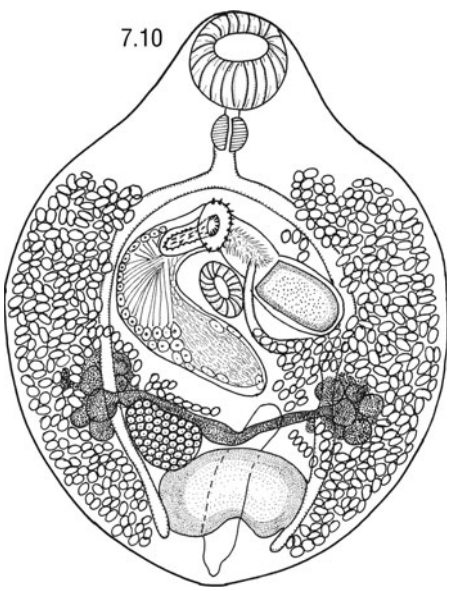




**Fig. 7.7.** *Ametrodaptes mexicanus* Bravo-Hollis, 1956. Ventral view. After Bravo-Hollis (1956).
**Figs 7.8, 7.9.** *Pseudametrodaptes secundus* (Madhavi, 1977). 7.8. Ventral view. After Madhavi (1977). 7.9. Enlarged view of anterior end. After Madhavi (1977).
**Fig. 7.10.** *Postmonorchis orthopristis* Hopkins, 1941. Ventral view. After Hopkins (1941).

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**10b. Body elongate; vitellarium forms groups of acinous tubules in ovariotesticular zone ..... ..... *Leiomonorchis* Mamaev, 1970. (Figs 7.11, 7.12)**
(Syn. *Caballerotrematoides* Madhavi, 1977)

**Diagnosis:** Body elongate. Suckers well developed, forebody short. Suckers well developed. Prepharynx small. Pharynx globular. Oesophagus long, slender. Intestinal bifurcation in posterior forebody. Caeca long. Testis single, oval, median, near posterior end of body. Cirrus-sac long, claviform, contains oval seminal vesicle, prostatic complex and armed cirrus. Genital atrium unarmed. Genital pore median, anterior to ventral sucker. Ovary lobed, pretesticular, separated from testis by uterine coils. Uterine coils fill space between testis and ventral sucker, not extending posteriorly beyond testis. Metraterm joins spinous anterior part of bipartite terminal organ. Vitellarium acinous, forming star-shaped clusters in lateral fields of middle third of body. Excretory vesicle tubular. In intestine of leiognathid fishes; Bay of Tonkin, Bay of Bengal. Type-species *L. leiognathi* Mamaev, 1970.

**11a. Genital atrium spined ..... 12.**
**11b. Genital atrium not spined ..... 14.**

**12a. Terminal organ unipartite ..... 13.**
**12b. Terminal organ bipartite ..... *Genolopa* Linton, 1910. (Fig. 7.13)**

**Diagnosis:** Body fusiform, spinulate. Oral sucker subterminal. Ventral sucker pre-equatorial. Prepharynx short. Oesophagus distinct. Intestinal bifurcation in forebody. Caeca long, terminate just short of posterior extremity. Testis submedian, postequatorial. Cirrus-sac large, extends well into hindbody, contains oval seminal vesicle, numerous prostatic cells and eversible spined cirrus. Genital atrium spined. Genital pore median, postbifurcal. Ovary compact or lobed, pretesticular, dextral. Uterus occupies all available space in hindbody, with sphincter at proximal end of metraterm, opens into base of spined proximal portion of bipartite terminal organ. Vitelline follicles form bunches in ovarian zone. Excretory vesicle small, saccular. In intestine of marine teleosts; Gulf of Mexico, Pacific Ocean, Bay of Bengal. Type-species *G. ampullacea* Linton, 1910.

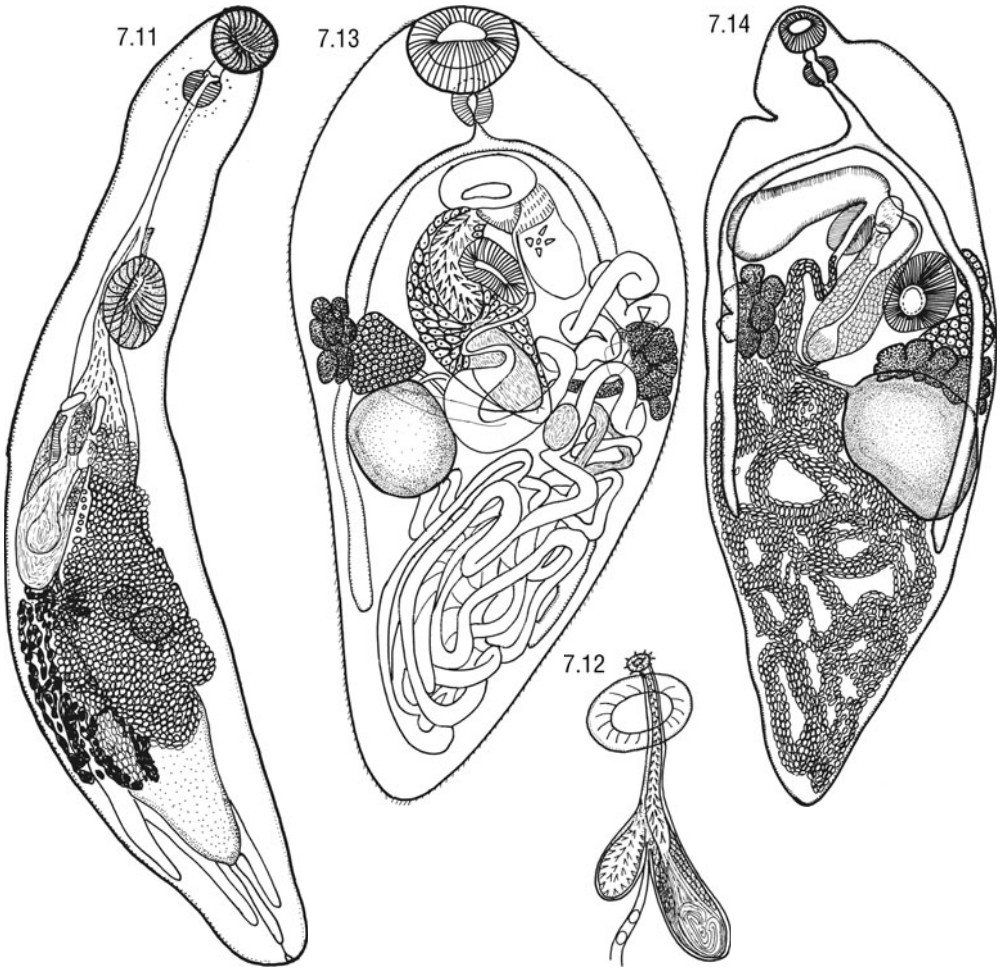
**13a. Metraterm with prominent muscular bulb ..... ..... *Paraproctotrema* Yamaguti, 1934. (Fig. 7.14)**

**Diagnosis:** Body fusiform. Oral sucker subterminal. Ventral sucker pre-equatorial. Prepharynx distinct. Oesophagus short or long. Intestinal bifurcation in mid-forebody. Caeca narrow, terminate in middle of hindbody. Testis median or submedian, in anterior half of hindbody. Cirrus-sac extends into hindbody, encloses oval seminal vesicle, prostatic complex with numerous prostatic cells and spined cirrus. Genital atrium spined. Genital pore median, anterior to ventral sucker. Ovary lobed, posterolateral to ventral sucker and anterior to testis. Uterus occupies entire posttesticular region. Metraterm with muscular bulb distally, opens into proximal end of terminal organ. Terminal organ club-shaped, lined with prominent spines. Vitelline fields lateral, in ovariotesticular zone; follicles large, compact. In intestine of marine fishes; off Japan. Type-species *P. fusiforme* Yamaguti, 1934.

**13b. Metraterm without bulb ..... *Monorchicestrahelmins* Yamaguti, 1971. (Fig. 7.15)**
(Syn. *Bupharynx* Yamaguti, 1971)

**Diagnosis:** Body elongate. Oral sucker ventro-subterminal. Ventral sucker in middle third of body. Pharynx small or very large and muscular. Oesophagus short or long. Intestinal bifurcation in mid-forebody. Caeca long. Testis single, ovoid, in middle of body. Cirrus-sac claviform, curved

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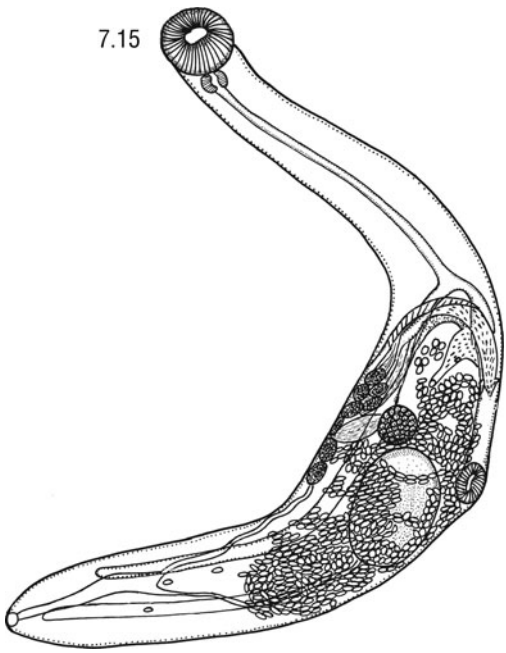



**Figs 7.11, 7.12.** *Leiomonorchis leiognathi* Mamaev, 1970. 7.11. Ventral view. After Mamaev (1970). 7.12. Enlarged view of terminal genitalia. After Mamaev (1970).
**Fig. 7.13.** *Genolopa ampullacea* Linton, 1910. Ventral view. After Yamaguti (1971).
**Fig. 7.14.** *Paraproctotrema fusiforme* Yamaguti, 1934. Dorsal view. After Yamaguti (1934).

anteriorly, encloses saccular seminal vesicle, well-developed prostatic complex and spined cirrus. Genital atrium spined, opening anterior to ventral sucker. Genital pore median, anterior to ventral sucker. Ovary round, anterodextral to testis. Uterus occupies greater part of post-testicular region. Metraterm without bulb. Terminal organ unipartite covered inside with acicular spines. Vitelline follicles form symmetrical extracaecal bunches in ovariotesticular region. Excretory vesicle I-shaped. In intestine of marine fishes; off Celebes and Mexico. Type-species *M. lethrini* (Yamaguti, 1953) Yamaguti, 1971.

**14a. Terminal organ unipartite ..... *Proctotrema* Odhner, 1911. (Fig. 7.16)**
**Diagnosis:** Body elongate. Oral sucker funnel-shaped. Ventral sucker small, pre-equatorial. Intestinal bifurcation in mid-forebody. Caeca not reaching posterior extremity. Testis in middle or

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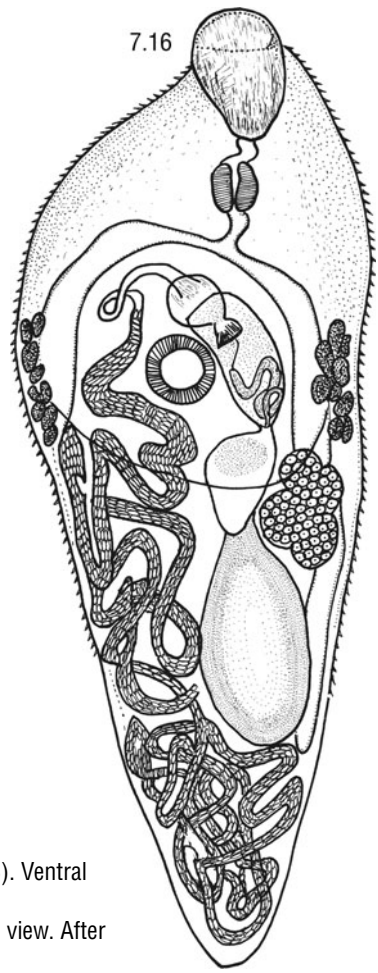




**Fig. 7.15.** *Monorchicestrahelmins lethrini* (Yamaguti, 1953). Ventral view. After Yamaguti (1953a).
**Fig. 7.16.** *Proctotrema bacillovatum* Odhner, 1911. Ventral view. After Bartoli & Prévot (1966).

posterior third of body. Cirrus-sac curves round ventral sucker, encloses tubular seminal vesicle, prostatic complex and armed cirrus. Genital atrium unarmed. Genital pore median, postbifurcal. Ovary lobed or not, anterodextral to testis. Uterus occupies most of hindbody, joins terminal organ distally. Terminal organ oval, undivided, spined. Eggs numerous, oval. Vitellarium forms symmetrical bunches of follicles lateral to ovary and ventral sucker. Excretory vesicle I-shaped, almost reaches ventral sucker. In marine teleost fishes; Mediterranean, Bay of Bengal, off Ghana. Type-species *P. bacillovatum* Odhner, 1911.

**14b. Terminal organ bipartite ..... 15.**

**15a. Genital atrium with spiny diverticulum .....**
**..... *Proctotrematoides* Yamaguti, 1938. (Fig. 7.17)**

**Diagnosis:** Body elongate. Eye-spot pigment present or absent. Oral sucker cup-shaped. Ventral sucker globular, pre-equatorial. Prepharynx short. Pharynx elongate. Oesophagus long. Intestinal bifurcation in mid-forebody. Caeca long, extend to posterior extremity. Testis in middle of hind-

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body. Cirrus-sac extends well into hindbody, encloses oval seminal vesicle, prostatic complex and armed cirrus. Genital atrium with thick, spiny posterior diverticulum. Genital pore median, anterior to ventral sucker. Ovary smooth or lobed, dextral. Uterine coils fill most of hindbody. Terminal organ bipartite, with spines in anterior part, and uterus joins it at junction of two parts. Eggs numerous. Vitelline follicles in two lateral longitudinal fields extend from level of ventral sucker to near posterior margin of testis. Excretory vesicle I-shaped, extends to near intestinal bifurcation. In gastro-intestinal tract of marine teleosts; off Japan, Ghana, Bay of Bengal, Jamaica. Type-species *P. pisodontophidis* Yamaguti, 1938.

**15b. Genital atrium without spiny diverticulum ..... 16.**

**16a. Vitellarium follicular, in ovariotesticular zone or at level of ventral sucker .....**
**..... *Lasiotocus* Looss in Odhner, 1911. (Figs 7.18, 7.19)**
(Syns *Ancylocoelium* Nicoll, 1912; *Chrisomon* Manter & Pritchard, 1961)

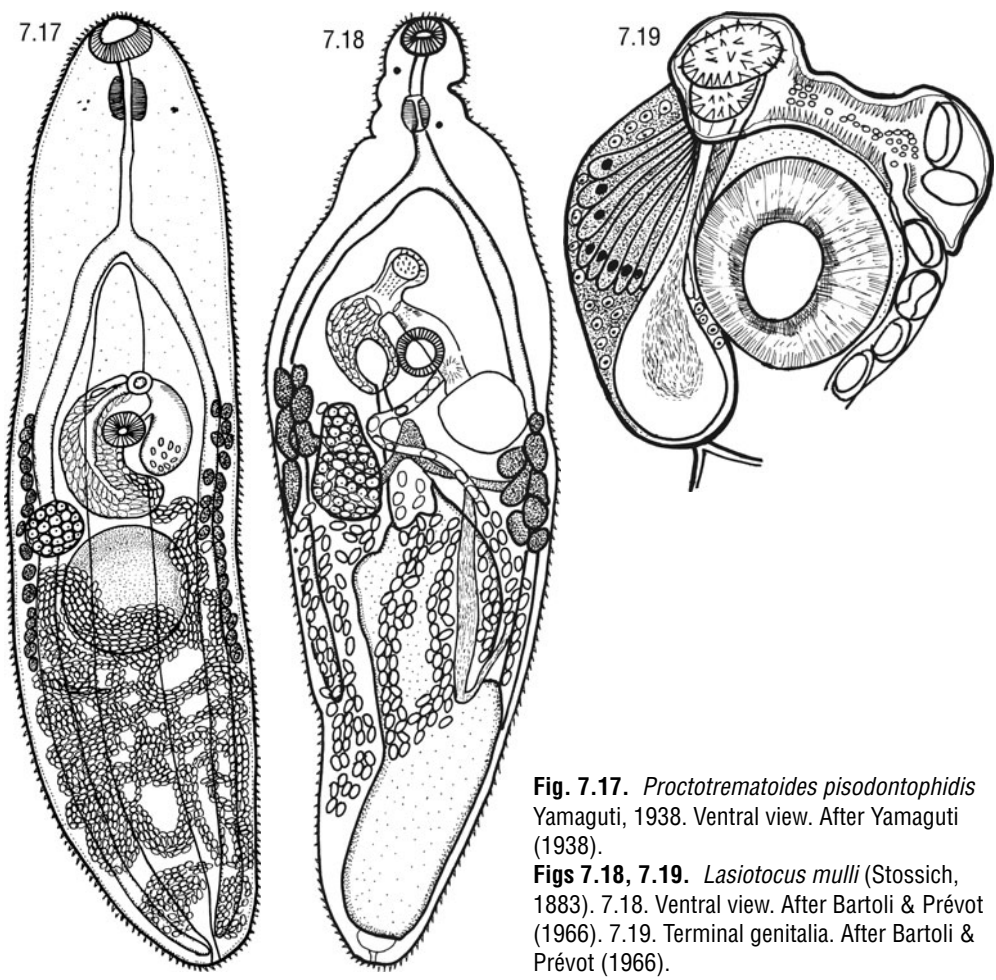



**Fig. 7.17.** *Proctotrematoides pisodontophidis* Yamaguti, 1938. Ventral view. After Yamaguti (1938).
**Figs 7.18, 7.19.** *Lasiotocus mulli* (Stossich, 1883). 7.18. Ventral view. After Bartoli & Prévot (1966). 7.19. Terminal genitalia. After Bartoli & Prévot (1966).

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**Diagnosis:** Body plump or elongate. Eye-spot pigment present or absent. Oral sucker cup- or funnel-shaped. Ventral sucker small, pre-equatorial. Intestinal bifurcation in forebody. Caeca long, slender, of variable length. Testis in middle or posterior third of body. Cirrus-sac extends posteriorly beyond ventral sucker, encloses saccular seminal vesicle, prostatic complex and spined cirrus. Genital atrium unarmed. Genital pore anterior to ventral sucker, median. Ovary pretesticular. Uterus occupies most of hindbody. Terminal organ bipartite, with posterior unarmed vesicle and spined anterior part; latter with sphincter at its distal end and receives uterus part-way along its length. Vitellarium forms symmetrical bunches of follicles at level of ventral sucker, testis and/or ovary. Excretory vesicle saccular to tubular. In marine teleost fishes; Mediterranean, Indian Ocean, Pacific Ocean off Ghana. Type-species *L. mulli* (Stossich, 1883) Looss in Odhner, 1911.

**16b. Vitellarium in form of tubular acini, in lateral fields of hindbody, may rarely extend into forebody ..... *Parachrisomon* n.g. (Fig. 7.20)**

**Diagnosis:** Body elongate. Tegument spinous. Oral sucker subterminal. Ventral sucker in middle third of body. Prepharynx present. Pharynx elongate to transversely oval. Intestinal bifurcation in posterior forebody. Caeca long, reach posteriorly beyond testis. Testis single, large, elongate, near posterior end of body. Cirrus-sac clavate to elongate, extends well posterior to ventral sucker, encloses saccular seminal vesicle, prostatic complex and spined cirrus. Genital atrium short, unarmed. Genital pore median, anterior to ventral sucker. Ovary lobed or not, anterior to testis. Uterine seminal receptacle present. Uterus fills most of hindbody, opens into distal part of spined terminal organ. Terminal organ bipartite; anterior part spined, posterior part vesicular. Eggs unfilamented. Vitellarium of tubular acini forming star-shaped bunches in hindbody, rarely extending into forebody. Excretory vesicle Y-shaped or saccular; pore terminal. In marine fishes; Pacific and Indian Ocean, Gulf of Mexico. Type-species *P. decapteri* (Nahhas & Cable, 1964) n. comb.

**17a. Testes symmetrical ..... 18.**
**17b. Testes oblique ..... 22.**

**18a. Testes in middle of hindbody; uterus extends well posteriorly beyond testes ..... 19.**
**18b. Testes close to posterior extremity; uterus not extending posteriorly beyond testes ..... ..... *Monorcheides* Odhner, 1905. (Fig. 7.21)**

**Diagnosis:** Body oval. Oral sucker terminal. Ventral sucker small, pre-equatorial. Intestinal bifurcation in forebody. Caeca long, reach beyond testes. Testes two, symmetrical; one on each side close to posterior end of body. Cirrus-sac small or large, extends, or not, posteriorly beyond ventral sucker, encloses simple seminal vesicle, prostatic complex and spined cirrus. Genital pore median, just postbifurcal. Ovary deeply lobed, submedian, pretesticular. Uterus fills hindbody, not extending posteriorly beyond testes, opens into terminal organ at its base. Terminal organ simple, spined. Vitellarium follicular, two symmetrical bunches at level of ventral sucker or in forebody, usually on each side of ventral sucker. Excretory vesicle Y-shaped. In intestine of marine fishes; Mediterranean, northern Pacific, Hawaii, Barents Sea, Bay of Bengal. Type-species *M. diplorchis* Odhner, 1905.

**19a. Caeca short; vitellarium forms two lateral clusters on either side of pharynx ..... ..... *Allobacciger* Hafeezullah & Siddiqi, 1970. (Fig. 7.22)**
(Syn. *Pseudomonorcheides* Wang, 1982)

**Diagnosis:** Body small, plump. Oral sucker subterminal, large. Ventral sucker small, in mid-region of body. Pharynx small. Oesophagus short. Intestinal bifurcation in mid-forebody. Caeca short, inflated, end in anterior half of body. Testes two, symmetrical, immediately posterior to

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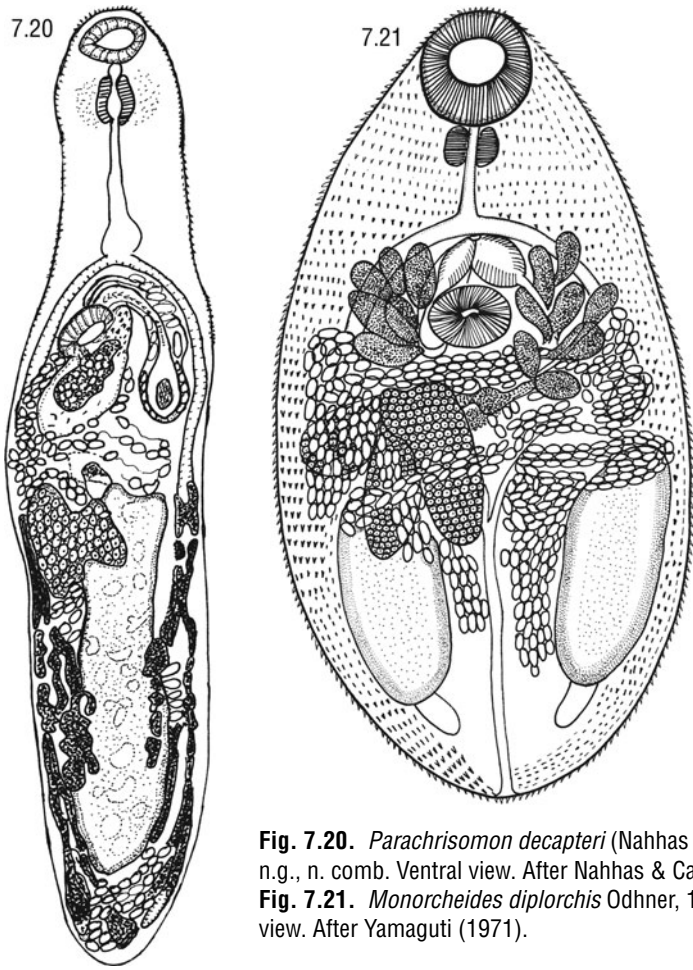


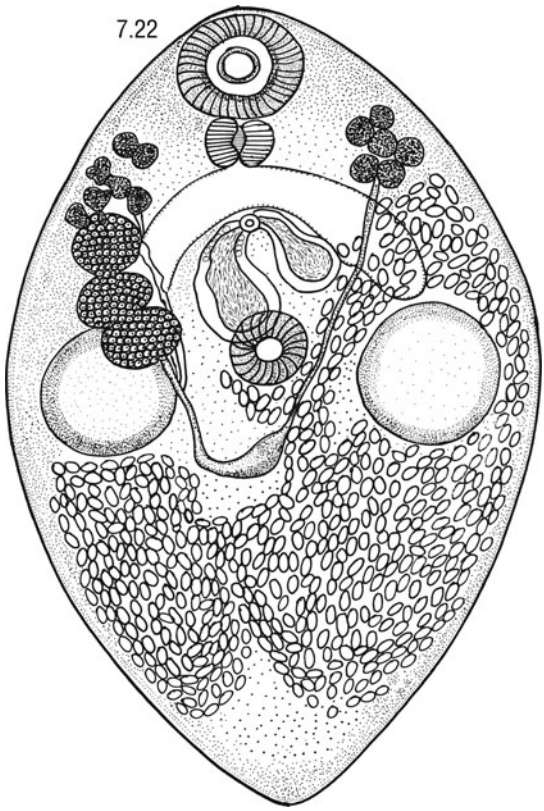

**Fig. 7.20.** *Parachrisomon decapteri* (Nahhas & Cable, 1964) n.g., n. comb. Ventral view. After Nahhas & Cable (1964).
**Fig. 7.21.** *Monorcheides diplorchis* Odhner, 1905. Ventral view. After Yamaguti (1971).

caecal ends. Cirrus-sac claviform, contains saccular seminal vesicle, prostatic complex and armed cirrus. Genital atrium small. Genital pore just postbifurcal. Ovary deeply lobed, dextral to ventral sucker. Uterus fills most of post-testicular space and region to left of cirrus-sac. Terminal organ saccular. Vitelline follicles form symmetrical bunches on either side of pharynx. Excretory vesicle V-shaped; pore terminal. In intestine of marine teleost fishes; off China, India, Japan. Type-species *A. macrorchis* Hafeezullah & Siddiqi, 1970.

**19b. Caeca long, extend to testes and beyond; vitellarium not reaching pharynx ..... 20.**

**20a. Testes closely posterior to ventral sucker; vitelline follicles between ventral sucker and testes ..... 21.**
**20b. Testes far posterior to ventral sucker; vitelline follicles chiefly in gonadal zone ..... ..... *Diplomonorchis* Hopkins, 1941. (Fig. 7.23)**
(Syns *Diplomonorcheides* Thomas, 1959; *Pseudomonorcheides* Zhukov, 1983 *nec* Wang,1982; *Zhukovtrema* Sey & Nahhas, 1997)

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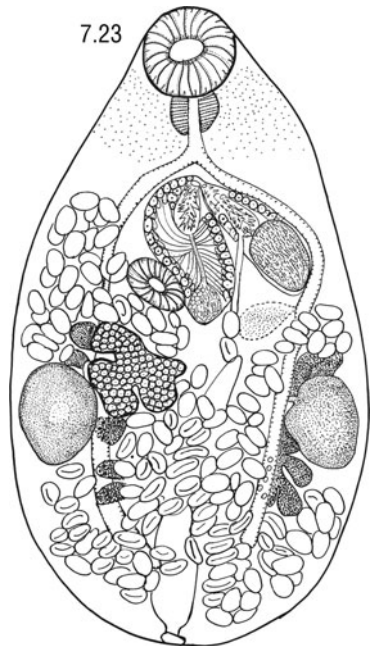




**Fig. 7.22.** *Allobacciger ditrematis* (Wang, 1982) n. comb. Dorsal view. After Wang P.-q. (1982b).
**Fig. 7.23.** *Diplomonorchis leiostomi* Hopkins, 1941. Ventral view. After Hopkins (1941).

**Diagnosis:** Body small, oval. Oral sucker subterminal. Ventral sucker in middle third of body. Pharynx moderately developed. Intestinal bifurcation midway between suckers. Caeca long, end posteriorly to testes. Testes two, spherical, symmetrical or oblique, near middle of hindbody, far posterior to ventral sucker. Cirrus-sac extends just posteriorly beyond ventral sucker, encloses oval seminal vesicle, narrow pars prostatica with numerous prostatic cells and spined cirrus. Genital pore median, in forebody, just postbifurcal. Ovary compact or lobed, dextral, pretesticular. Uterine coils occupy entire hindbody, may extend into forebody. Metraterm joins terminal organ at base of its anterior spined portion. Terminal organ bipartite, consists of unspined posterior and spined anterior portions. Vitelline follicles chiefly in gonadal region, extend just anteriorly or posteriorly to testes. Excretory vesicle I-shaped. In intestine of marine fishes; Atlantic and Pacific Oceans off USA. Type-species *D. leiostomi* Hopkins, 1941.

**21a. Cirrus unusually long; terminal organ unipartite .....**
**..... *Ovipusillus* Dove & Cribb, 1998. (Fig. 7.24)**
**Diagnosis:** Body oval. Oral sucker globular. Ventral sucker in middle third of body. Intestinal bifurcation in mid-forebody. Caeca short, end in mid-body. Testes two, symmetrical or oblique,

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largely anterior to ovary, may overlap ventral sucker zone. Cirrus-sac very large, encloses round seminal vesicle, long pars prostatica and unusually long coiled, spiny, eversible cirrus. Genital atrium unspined. Genital pore median, anterior to ventral sucker. Ovary deeply lobed, median, in hindbody. Uterus forms compact coils in hindbody. Terminal organ unipartite, evenly spined, receives uterus at its distal end. Eggs small. Vitellarium in two lateral fields, in posterior forebody, may overlap ventral sucker region. Excretory vesicle V- or Y-shaped. In intestine of marine fishes; Pacific off Australia. Type-species *O. mayu* Dove & Cribb, 1998.

**21b. Cirrus not long; terminal organ bipartite ..... ..... *Paramonorcheides* Yamaguti, 1938. (Fig. 7.25)**

**Diagnosis:** Body elongate. Oral sucker subterminal. Ventral sucker pre-equatorial. Intestinal bifurcation in forebody. Caeca end some distance anterior to posterior extremity. Testes two, longitudinally elongate, symmetrical or not. Cirrus-sac extends posteriorly past ventral sucker, contains oval seminal vesicle, well-developed prostatic cells and armed eversible cirrus. Genital atrium small. Genital pore median, anterior to ventral sucker. Ovary lobed, pre- or intertesticular. Uterus occupies all available space in hindbody. Metraterm opens into terminal organ at junction of two portions. Distal part of bipartite terminal organ saccular; proximal part with spines. Vitellarium in two lateral groups of follicles in region between ventral sucker and testis. Excretory vesicle saccular. In intestine of marine fishes; Pacific Ocean. Type-species *P. awatati* Yamaguti 1938.

**22a. Uterus not extending posteriorly beyond testes ..... 23.**
**22b. Uterus extends well posteriorly beyond testes ..... 24.**

**23a. Testes large, ovoid, overlap each other, close to posterior end; uterus not separating testes ..... *Postmonorcheides* Szidat, 1950. (Fig. 7.26)**

**Diagnosis:** Body linguiform. Suckers large. Oral sucker rounded. Ventral sucker in anterior third of body, smaller than oral sucker. Intestinal bifurcation in forebody. Caeca terminate in testicular zone. Testes large, ovoid, obliquely juxtaposed, overlap each other in median line, near posterior extremity. Cirrus-sac elliptical, not extending into hindbody, contains oval seminal vesicle, poorly developed prostatic complex and short spined cirrus. Genital pore median, anterior to ventral sucker. Ovary trilobed, overlaps anterior testis. Uterus extends into forebody but not posteriorly beyond or between testes. Terminal organ unipartite, spined, receives uterus at its distal end. Vitellarium forms stellate clusters of large acini, anterolateral to ovary. Excretory vesicle unknown. In pyloric caeca of marine fishes; off Tierra del Fuego. Type-species *P. maclovini* Szidat, 1950.

**23b. Testes elliptical, oblique, separated by uterus, in posterior half of body ..... ..... *Timonia* Bartoli & Prévot, 1966. (Fig. 7.27)**

**Diagnosis:** Body elongate. Suckers small. Ventral sucker pre-equatorial. Pharynx small. Oesophagus long. Intestinal bifurcation midway between suckers. Caeca long, terminate close to posterior extremity. Testes two, elliptical, oblique, in posterior half of body, separated by uterus. Cirrus-sac of variable size, may or may not extend posteriorly to ventral sucker, encloses oval seminal vesicle, prostatic complex and spined cirrus. Genital pore median, anterior to ventral sucker. Ovary massive, lobed or not, pretesticular, separated from testes by uterine coils. Uterus fills space between ventral sucker and testes, not extending posteriorly beyond testes. Terminal organ oval, spined, receives uterus laterally. Vitelline follicles in lateral fields between cirrus-sac and postovarian region. Excretory vesicle ampulliform. In gastro-intestinal tract of marine fishes; Mediterranean. Type-species *T. mediterranea* Bartoli & Prévot, 1966.

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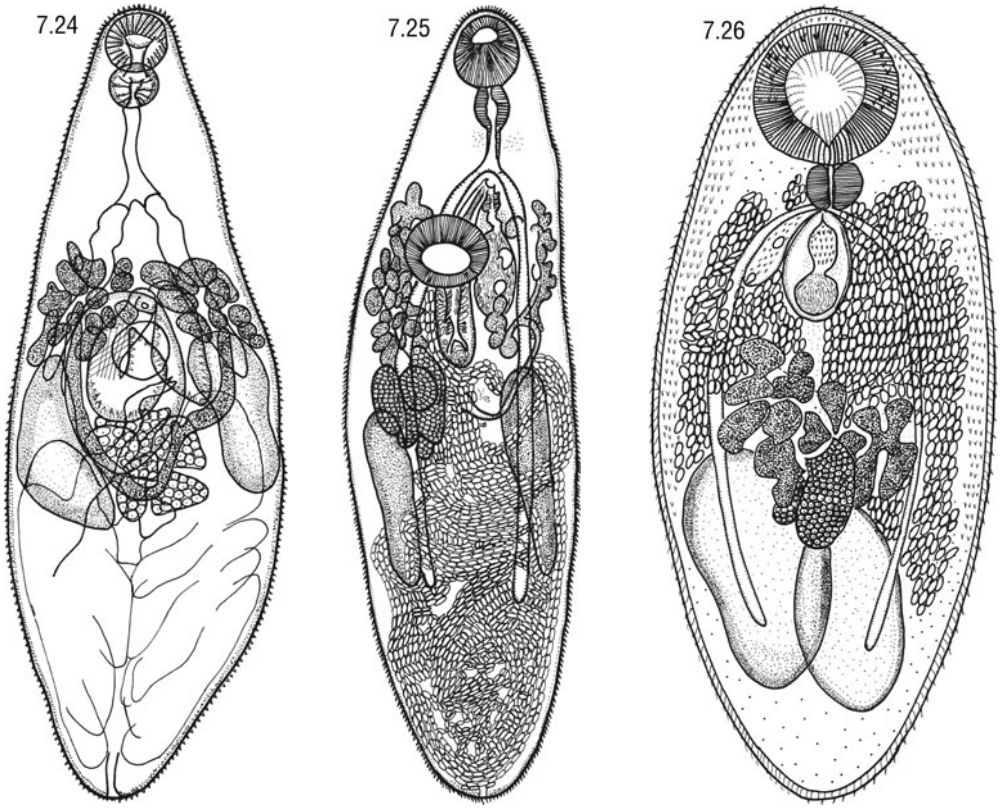



**Fig. 7.24.** *Ovipusillus mayu* Dove & Cribb, 1998. Ventral view. After Dove & Cribb (1998).
**Fig. 7.25.** *Paramonorcheides awatati* Yamaguti, 1938. Ventral view. After Yamaguti (1938).
**Fig. 7.26.** *Postmonorcheides maclovini* Szidat, 1950. Dorsal view. After Szidat (1950).

**24a. Vitellarium forms two compact masses anteriorly to or at level of ovary ..... ..... *Paratimonia* Prévot & Bartoli, 1967. (Fig. 7.28)**

**Diagnosis:** Body elongate. Ventral sucker in anterior third of body. Intestinal bifurcation in mid-forebody. Caeca long, narrow, terminate in testicular region. Testes two, oblique, intercaecal, in posterior part of hindbody. Cirrus-sac well developed, curved, encloses oval seminal vesicle, pars prostatica and long spined cirrus. Genital atrium small. Genital pore median, in forebody, just postbifurcal. Ovary trilobed, dextral, pretesticular. Uterus occupies entire hindbody, extends to pharynx. Terminal organ bipartite; proximal part spinous. Vitellarium two compact masses, anterior to or at level of ovary. Excretory vesicle sac-like. In intestine of marine fishes; Mediterranean Sea. Type-species *P. gobii* Prévot & Bartoli, 1967.

**24b. Vitellarium consisting of irregularly shaped follicles in two groups at level of ventral sucker ..... *Neotimonia* n.g. (Fig. 7.29)**

**Diagnosis:** Body elliptical. Suckers small, subequal. Ventral sucker pre-equatorial. Prepharynx small. Pharynx globular. Oesophagus moderately long. Intestinal bifurcation in forebody. Caeca

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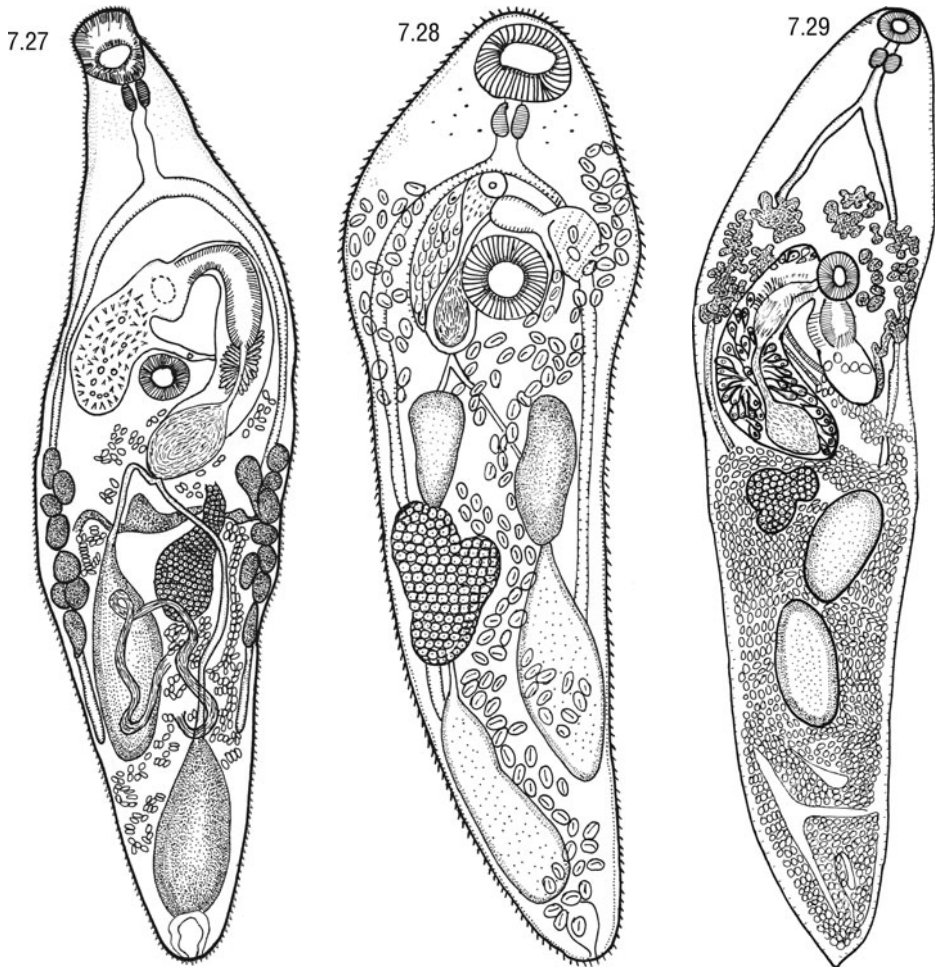



**Fig. 7.27.** *Timonia mediterranea* Bartoli & Prévot, 1966. Dorsal view. After Bartoli & Prévot (1966).
**Fig. 7.28.** *Paratimonia gobii* Prévot & Bartoli, 1967. Ventral view. After Prévot & Bartoli (1967).
**Fig. 7.29.** *Neotimonia caballeroi* (Madhavi, 1977) n.g., n. comb. Ventral view. After Madhavi (1977).

long, narrow, terminate at level of testes. Testes two, elliptical, obliquely tandem, in middle third of hindbody. Cirrus-sac arcuate, extends well into hindbody, encloses oval seminal vesicle, well-developed prostatic complex and spined cirrus. Genital atrium short, unarmed. Genital pore median, just anterior to ventral sucker. Ovary lobed, to right of anterior testis. Uterine coils extensive, fill entire hindbody except for region occupied by gonads and cirrus-sac. Metraterm opens into proximal region of terminal organ. Terminal organ well developed, bipartite; posterior part unarmed; anterior part with triangular spines. Eggs not filamented. Vitellarium consists of many irregularly shaped follicles in two groups at level of ventral sucker. Excretory vesicle and pore unknown. In intestine of marine fishes; northern Indian Ocean. Type-species *N. caballeroi* (Madhavi, 1977) n. comb.

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## Subfamily Anamonorchiinae Yamaguti, 1970

**Diagnosis:** Body fusiform. Tegument spined. Oral and ventral suckers weakly developed; latter in posterior third of body. Prepharynx small. Pharynx well developed. Oesophagus long. Intestinal bifurcation in anterior forebody. Caeca long, narrow, end at level of ventral sucker. All genitalia except vitellarium in forebody. Testis single, submedian, in anterior half of forebody. Cirrus-sac cylindrical, inverted, in forebody, contains oval seminal vesicle, numerous prostatic cells and broad cirrus bearing acicular spines. Genital atrium unarmed. Genital pore anterior to ventral sucker. Ovary submedian, between testis and cirrus-sac. Uterine coils occupy most of forebody. Terminal organ thin-walled, saccular, lined with acicular spines, adjacent to cirrus-sac. Eggs thick-shelled, with long polar filament. Vitellarium forms bunches of follicles on either side of ventral sucker. Excretory vesicle I-shaped; pore terminal. In stomach, intestine and pyloric caeca of marine fishes; Pacific Ocean off Hawaii. Type-genus *Anamonorchis* Yamaguti, 1970.

### Genus *Anamonorchis* Yamaguti, 1970 (Fig. 7.30)

**Diagnosis:** With characters of subfamily. Type-species *A. ulua* Yamaguti, 1970.

## Subfamily Hurleytrematinae Yamaguti, 1958

**Diagnosis:** Body oval, elongate or long and slender. Tegument spined. Eye-spot pigment present or absent. Oral sucker small. Ventral sucker pre-equatorial. Prepharynx present or absent. Pharynx globular. Oesophagus long. Intestinal bifurcation in forebody. Caeca long. Testes single or double, oval, symmetrical, oblique or tandem when double, in middle or posterior third of hindbody. Cirrus-sac contains saccular or bipartite seminal vesicle, numerous prostatic cells surrounding narrow pars prostatica and usually heavily and rarely moderately spined cirrus. Genital atrium small. Genital pore anterior to ventral sucker, usually median, rarely submedian. Ovary pretesticular, entire or lobed. Uterus fills most of hindbody. Terminal organ present or not, unipartite or bipartite when present, armed with spines. Eggs filamented. Vitellarium forms symmetrical bunches of follicles or tubular acini of variable extent. Excretory vesicle saccular or tubular. In intestine of marine fishes; cosmopolitan. Type-genus *Hurleytrema* Srivastava, 1939.

## Key to genera

**1a. Testis single** ..... **2.**
**1b. Testes two** ..... **6.**

**2a. Terminal organ unipartite** ..... **3.**
**2b. Terminal organ bipartite** ..... **5.**

**3a. Seminal vesicle bipartite** ..... ***Hurleytrematoides* Yamaguti, 1954. (Figs 7.31, 7.32)**
**Diagnosis:** Body elongate. Eye-spot pigment in forebody. Suckers small. Ventral sucker in anterior third of body. Caeca long, extend close to posterior end of body. Testis single, in middle of

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hindbody. Cirrus-sac small, clavate, encloses bipartite seminal vesicle, weakly developed prostatic complex and spined cirrus. Genital pore median, just anterior to ventral sucker. Ovary globular or lobed, pretesticular. Uterus fills entire hindbody, opens into terminal organ near its distal end. Terminal organ unipartite, spined. Vitelline follicles in lateral fields between ovary and cirrus-sac. In intestine of marine teleosts; Gulf of Mexico, Pacific Ocean, Bay of Bengal. Type-species *H. chaetodoni* (Manter, 1942) Yamaguti, 1954.

**3b. Seminal vesicle undivided** ..... **4.**

**4a. Vitelline follicles small, in hindbody** ..... ***Hurleytrema*** **Srivastava, 1939. (Fig. 7.33)**

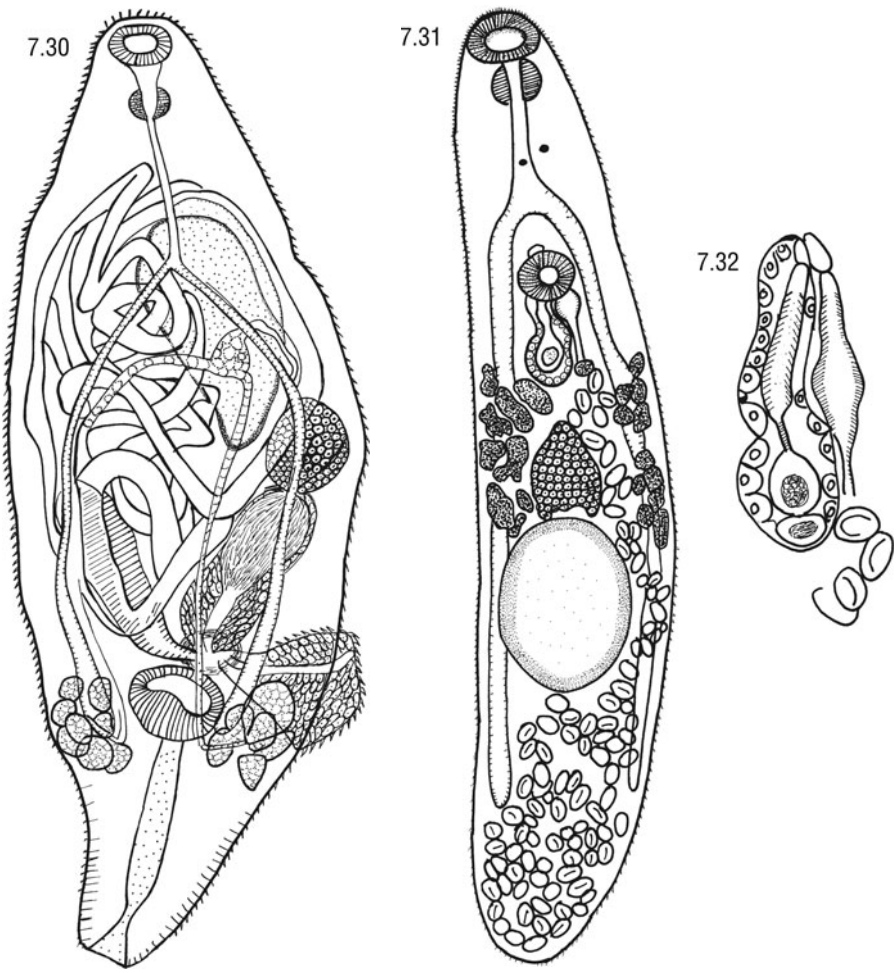



**Fig. 7.30.** *Anamonorchis ulua* Yamaguti, 1970. Dorsal view. After Yamaguti (1970).
**Figs 7.31, 7.32.** *Hurleytrematoides curacaensis* Nahhas & Cable, 1964. 7.31. Ventral view. After Nahhas & Cable (1964). 7.32. Terminal genitalia. After Nahhas & Cable (1964).

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**Diagnosis:** Body slender, elongate. Suckers weakly developed. Ventral sucker in anterior third of body. Caeca end close to posterior extremity. Testis single, in posterior half of body. Cirrus-sac elongate, encloses oval seminal vesicle, prostatic complex and armed cirrus. Genital pore to left of midline. Ovary trilobed, pretesticular. Uterus occupies entire intercaecal field of hindbody. Terminal organ unipartite, lined with minute spines, receives metraterm distally. Eggs triangular. Vitellarium acinous, lateral, small follicles, divided into pre- and post-testicular groups, extends from level of ventral sucker to near posterior extremity. Excretory vesicle Y-shaped. In intestine of marine fishes; Arabian Sea, off Mexico. Type-species *H. ovocaudatus* Srivastava, 1939.

**4b. Vitelline follicles large, form two groups anterior to ventral sucker ..... ..... *Provitellus* Dove & Cribb, 1998. (Fig. 7.34)**

**Diagnosis:** Body small, elongate-oval. Suckers small. Ventral sucker in middle third of body. Caeca short, terminate at level of ventral sucker. Testis single, in mid-hindbody. Cirrus-sac elongate, encloses spherical seminal vesicle, short pars prostatica and spiny eversible cirrus. Genital pore median, just anterior to ventral sucker. Ovary entire, slightly pretesticular. Uterus fills entire hindbody. Terminal organ unipartite, spinous; uterus enters at distal end. Eggs fairly large. Vitellarium composed of large lobed follicles in two lateral fields anterior to ventral sucker. Excretory vesicle saccular. In intestine of marine fishes; off Queensland, Australia. Type-species *P. turrum* Dove & Cribb, 1998.

**5a. Seminal vesicle bipartite ..... *Parahurleytrema* Nahhas & Powell, 1965. (Figs 7.35, 7.36)**

**Diagnosis:** Body pyriform or elongate, spined. Suckers small. Pharynx well developed. Oesophagus long. Intestinal bifurcation midway between suckers. Caeca long, reach beyond testis. Testis single, median, in middle of hindbody. Cirrus-sac arcuate, contains bipartite seminal vesicle, short tubular pars prostatica, well-developed prostatic cells and spined eversible cirrus. Genital pore anterior to ventral sucker. Ovary pretesticular. Uterus fills most of post-testicular space. Terminal organ bipartite; posterior chamber unarmed; anterior part spinous. Vitellarium follicular; follicles form two lateral groups, chiefly at level of ventral sucker and testis. Excretory vesicle saccular. In intestine of marine fishes; off West Africa, Gulf of Mexico. Type-species *P. trachinoti* (Thomas, 1959) Nahhas & Powell, 1965.

**5b. Seminal vesicle simple ..... *Pseudohurleytrema* Yamaguti, 1954. (Fig. 7.37)**

**Diagnosis:** Body small, elongate. Suckers well developed. Ventral sucker in anterior third of body. Caeca blind, terminate at level of testis. Testis single, median, in posterior third of body. Cirrus-sac long, reaches ovary, contains saccular seminal vesicle, tubular pars prostatica surrounded by prostatic cells and weakly spined cirrus. Genital atrium unspined. Genital pore immediately anterior to ventral sucker. Ovary lobed, pretesticular. Uterus reaches close to posterior extremity. Metraterm well differentiated, opens into proximal portion of terminal organ. Terminal organ bipartite; distal portion unspined, proximal portion heavily spined. Vitelline follicles in two lateral groups at level of ovary. Excretory vesicle saccular. In intestine of marine fishes; Gulf of Mexico, off Philippines, off Brazil. Type-species *P. eucinostomi* (Manter, 1942) Yamaguti, 1954.

**6a. Body long, slender; testes tandem; vitellarium comprises tubular acini in between ovary and ventral sucker ..... *Diplolasiotocus* Yamaguti, 1952. (Fig. 7.38)**

**Diagnosis:** Body long, slender. Oral sucker terminal. Ventral sucker small, at mid-body. Pharynx small. Oesophagus fairly long. Caeca long, terminate at level of anterior testis. Testes two, tandem, contiguous, in posterior third of body. Cirrus-sac elongate, contains bipartite seminal vesicle, prostatic complex and densely spined cirrus. Genital pore immediately anterior to ventral sucker.

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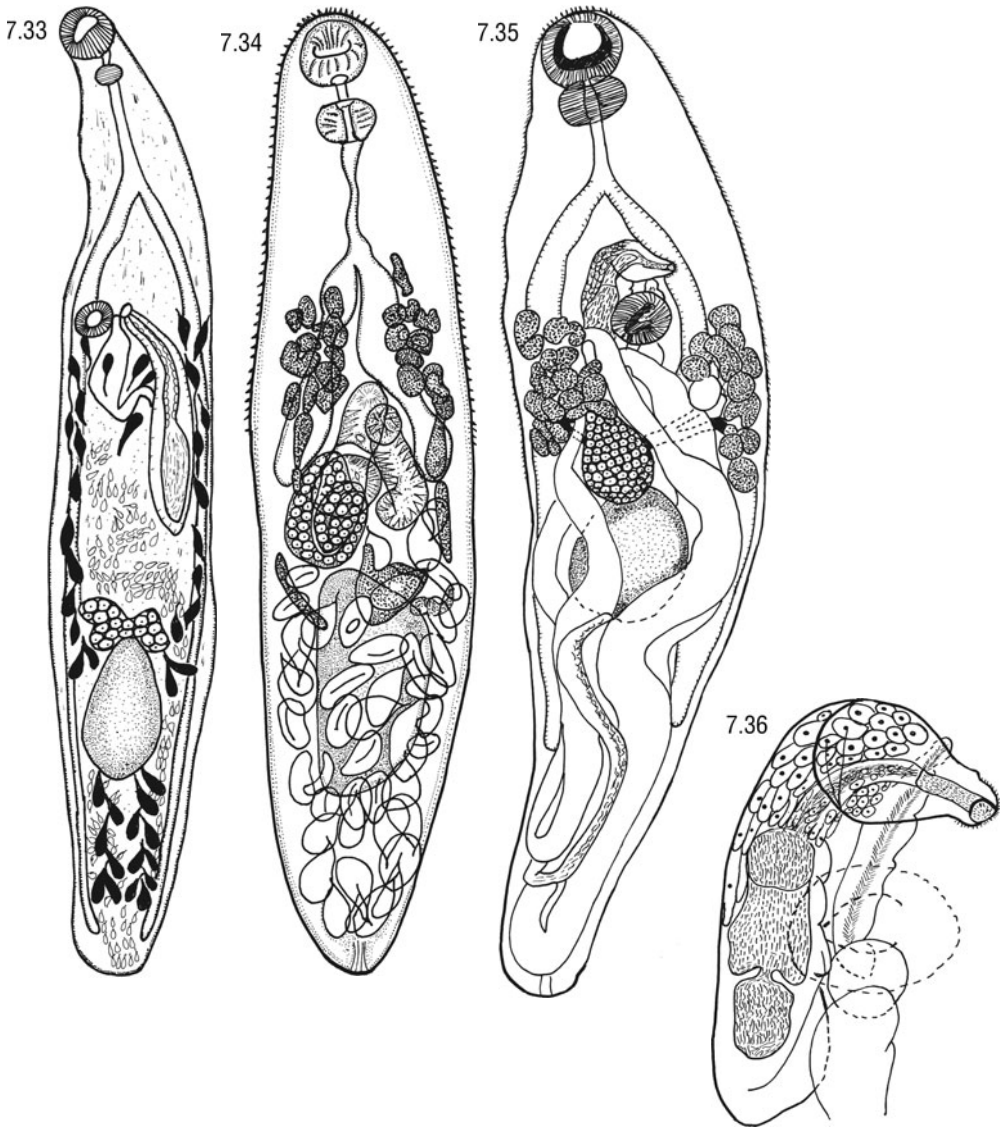



**Fig. 7.33.** *Hurleytrema ovocaudatus* Srivastava, 1939. Ventral view. After Srivastava (1939c).
**Fig. 7.34.** *Provitellus turrum* Dove & Cribb, 1998. Ventral view. After Dove & Cribb (1998).
**Figs 7.35, 7.36.** *Parahurleytrema coronatum* (Manter & Pritchard, 1961). 7.35. Ventral view. After Manter & Pritchard (1961). 7.36. Terminal genitalia. After Manter & Pritchard (1961).

Ovary pretesticular, submedian. Uterine coils occupy entire hindbody. Terminal organ simple, lined by spines. Vitellarium comprises tubular acini, in lateral fields between ventral sucker and ovary. Excretory vesicle tubular, reaches posterior testis. In intestine of marine fishes; Pacific Ocean. Type-species *D. chaetodontis* Yamaguti, 1952.

**6b. Body oval or elongate; testes symmetrical or oblique; vitelline follicles numerous in fore- and hindbodies** ..... 7.

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7a. **Testes symmetrical, close to posterior extremity; uterus not extending posteriorly beyond testes** ..... ***Helicometroides*** **Yamaguti, 1934. (Fig. 7.39)**
(Syn. *Hysterorchis* Durio & Manter, 1968)

**Diagnosis:** Body elongate, spined. Forebody with eye-spot pigment. Oral sucker terminal. Ventral sucker pre-equatorial. Oesophagus long. Intestinal bifurcation just anterior to ventral sucker. Caeca long. Testes two, elongate, symmetrical, close to posterior extremity. Cirrus-sac claviform, curved around ventral sucker, contains bipartite seminal vesicle, few prostatic cells and spined cirrus. Genital pore submedian, anterosinistral to ventral sucker. Ovary lobed, anterior to right testis. Uterus intercaecal, between testes and ventral sucker. Terminal organ cylindrical, unspined. Vitelline follicles comparatively large, from level of oesophagus to anterior part of testis, confluent

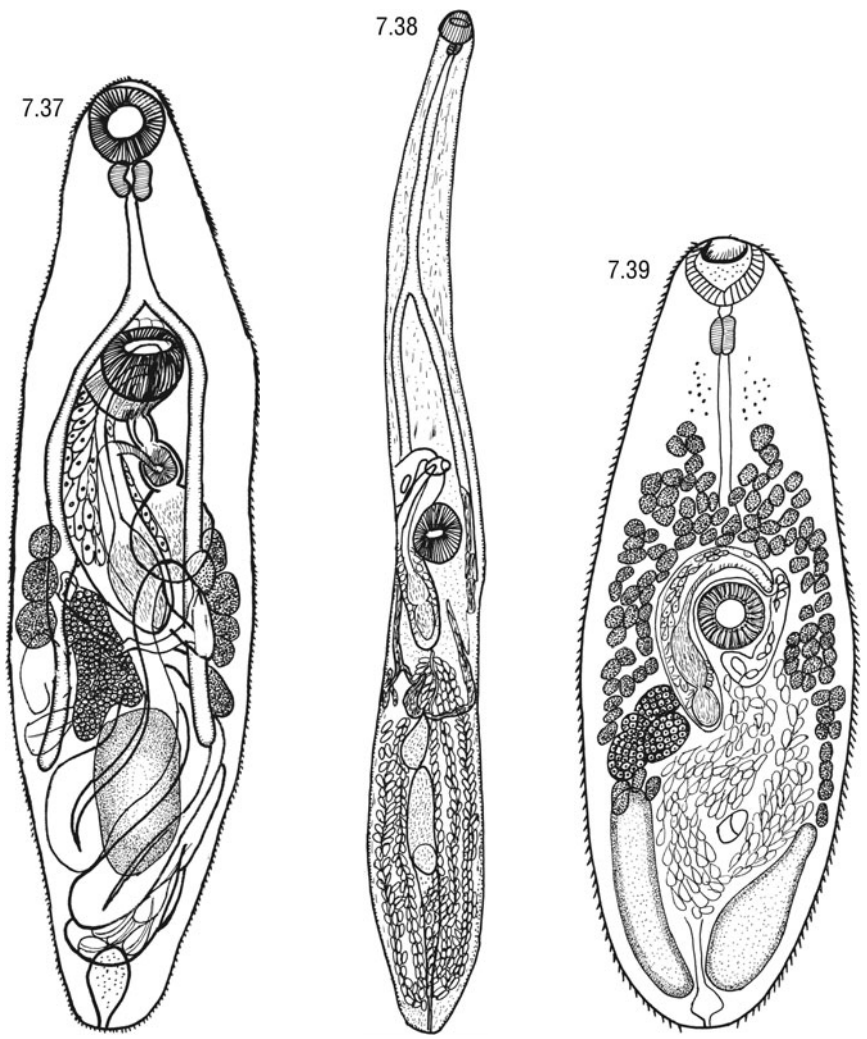



**Fig. 7.37.** *Pseudohurleytrema eucinostomi* (Manter, 1942). Ventral view. After Yamaguti (1971).
**Fig. 7.38.** *Diplolasiotocus chaetodontis* Yamaguti, 1952. Ventral view. After Yamaguti (1952).
**Fig. 7.39.** *Helicometroides longicollis* Yamaguti, 1934. Ventral view. After Yamaguti (1934).

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anteriorly. Excretory vesicle tubular. In intestine of marine fishes; western Pacific, Bay of Bengal. Type-species *H. longicollis* Yamaguti, 1934.

**7b. Testes oblique in middle of hindbody; uterus fills post-testicular space ..... ..... *Diplohurleytrema* Nahhas & Cable, 1964. (Fig. 7.40)**

**Diagnosis:** Body fusiform. Suckers well developed. Oral sucker terminal. Ventral sucker pre-equatorial. Caeca short, terminate just posterior to ventral sucker. Testes diagonal, in middle of hindbody. Cirrus-sac long, claviform, encloses bipartite seminal vesicle, well-developed prostatic complex and spined cirrus. Genital pore median, anterior to ventral sucker. Ovary entire, dextral, posterodorsal to ventral sucker. Uterus in testicular and post-testicular regions, fills post-testicular space. Metraterm well differentiated, tubular, spined. No terminal organ. Vitelline follicles extend laterally between level of pharynx and level of ovary. Excretory vesicle tubular. In intestine of marine fishes; off north Atlantic coast of South America. Type-species *D. brevicaecum* Nahhas & Cable, 1964.

## Subfamily Octotestiinae Yamaguti, 1958

**Diagnosis:** Body fairly large, flat, elliptical. Tegument smooth. Oral and ventral suckers well developed. Ventral sucker at junction of anterior and middle thirds of body. Pharynx present. Oesophagus short. Intestinal bifurcation in forebody. Caeca long, sinuous, end close to posterior extremity. Testes eight to 11, in two longitudinal rows, occupy entire postovarian intercaecal field. Cirrus-sac rounded, thin-walled, contains round seminal vesicle, well-developed prostatic complex and eversible cirrus armed with spines. Genital pore median, postbifurcal. Ovary multilobate, submedian, just posterior to ventral sucker. Uterine coils extend into submedian area enclosed by two rows of testes. Terminal organ lined with acicular spines, surrounded by gland-cells. Eggs oval, thin-shelled, not filamented. Vitellarium forms series of grape-like bunches in extracaecal fields for considerable distance. Excretory vesicle tubular. In body-cavity of marine and freshwater teleost fishes; Japan, China. Type-genus *Octotestis* Yamaguti, 1951.

### Genus *Octotestis* Yamaguti, 1951 (Fig. 7.41)

(Syn. *Paradecemtestis* Wang, 1963)

**Diagnosis:** With characters of subfamily. Type-species *O. iseensis* Yamaguti, 1951.

## Subfamily Opisthomonorchiinae Yamaguti, 1952

**Diagnosis:** Body elongate. Tegument spined. Oral sucker subterminal. Ventral sucker in middle third of body. Prepharynx small. Pharynx oval. Oesophagus fairly long. Intestinal bifurcation in anterior forebody. Caeca long, reaching to or beyond testis. Testis single, in posterior third of body. Cirrus-sac globular or elongate, extends from posterior border of ventral sucker to level of ovary, encloses oval or sinuous seminal vesicle, numerous prostatic cells and short unarmed or armed cirrus. Genital atrium spined. Genital pore median, in hindbody, near posterior border of ventral sucker. Ovary submedian, pretesticular. Uterus occupies most of post-testicular area. Terminal organ absent. Eggs with filament at anopercular end. Vitelline follicles few, form two lateral groups between level of ventral sucker and ovarian region or in forebody. Excretory vesicle tubular. In intestine of carangid fishes. Type-genus *Opisthomonorchis* Yamaguti, 1952.

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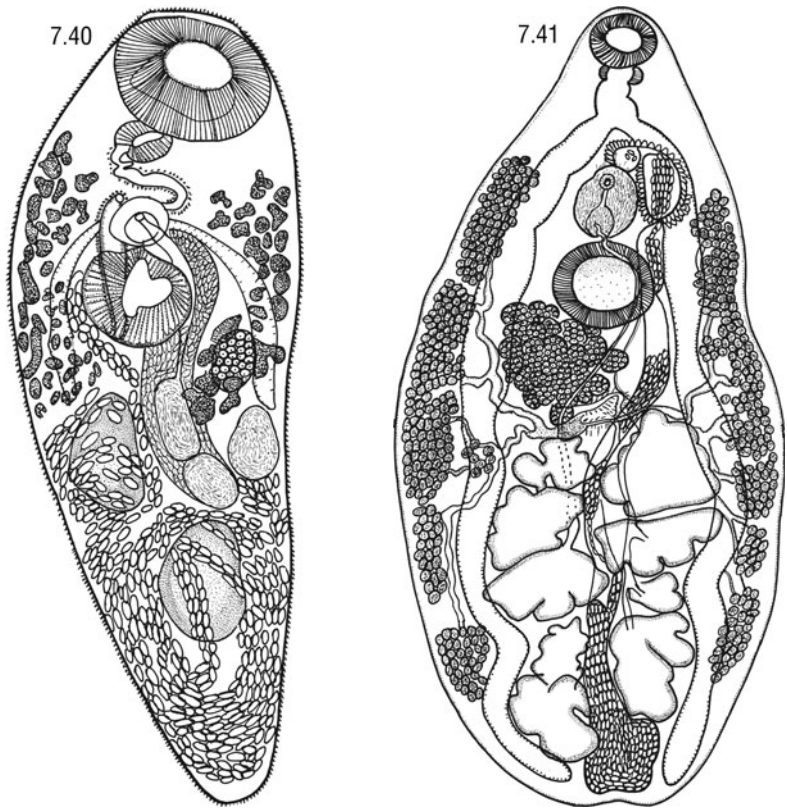



**Fig. 7.40.** *Diplohurleytrema brevicaecum* Nahhas & Cable, 1964. Ventral view. After Nahhas & Cable (1964).
**Fig. 7.41.** *Octotestis iseensis* Yamaguti, 1951. Ventral view. After Yamaguti (1951).

## Key to genera

**1a. Cirrus-sac elongate; vitellarium forms two lateral groups between ventral sucker and ovary ..... *Opisthomonorchis* Yamaguti, 1952. (Fig. 7.42)**

**Diagnosis:** Body elongate. Eye-spot pigment present. Caeca long, reaching beyond testis. Cirrus-sac elongate, extends to level of ovary, contains seminal vesicle, numerous prostatic cells and armed cirrus. Genital atrium spined. Genital pore median, close to posterior border of ventral sucker. Ovary submedian. Uterus occupies most of post-testicular area. Metraterm and terminal organ not differentiated. Vitelline follicles in two lateral groups between ventral sucker and ovary. Excretory vesicle tubular. In carangid fishes; off Japan. Type-species *O. carangis* Yamaguti, 1952.

**1b. Cirrus-sac globular; vitelline follicles form transverse band in forebody ..... ..... *Pseudopisthomonorchis* Madhavi, 1974. (Figs 7.43, 7.44)**

**Diagnosis:** Body elongate. Eye-spot pigment present. Suckers small. Ventral sucker in middle third of body; its aperture bears minute spines. Caeca long, reaching level of testis. Cirrus-sac globular, in hindbody, contains oval seminal vesicle, well-developed prostatic complex and short

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unarmed cirrus. Genital atrium armed with rows of minute spines. Genital pore in hindbody, median, just posterior to ventral sucker. Ovary pretesticular, dextral. Uterus occupies entire post-testicular region. Vitelline follicles large, lobed, form transverse band anterior to ventral sucker. In carangid fishes; Bay of Bengal. Type-species *P. carangi* Madhavi, 1974.

## Subfamily Opisthomonorcheidinae Yamaguti, 1971

**Diagnosis:** Body long, slender, delicate. Tegument spined. Forebody short, hindbody long. Suckers poorly developed. Ventral sucker in anterior quarter of body. Intestinal bifurcation in forebody. Caeca long, terminate near posterior extremity of body or some way short. Testes single

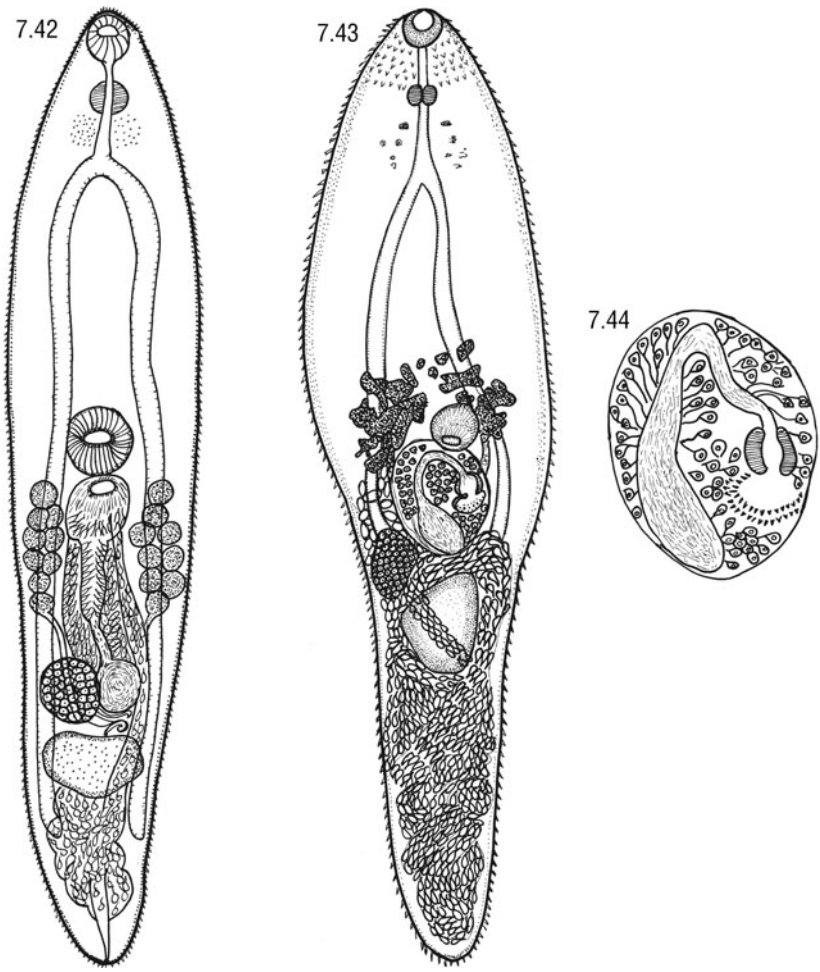



**Fig. 7.42.** *Opisthomonorchis carangis* Yamaguti, 1952. Ventral view. After Yamaguti (1952).
**Figs 7.43, 7.44.** *Pseudopisthomonorchis carangi* Madhavi, 1974. 7.43. Ventral view. After Madhavi (1974a). 7.44. Terminal genitalia. After Madhavi (1974a).

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or double, close to posterior extremity. Cirrus-sac small, extends into hindbody, encloses oval seminal vesicle, prostatic complex and spined cirrus. Genital atrium long, tubular or short, thin-walled. Genital pore median, in posterior forebody. Ovary pretesticular, separated from testis by uterine coils. Uterus fills intercaecal space between ovary and cirrus-sac, may extend into post-testicular space, joins terminal organ at its proximal or distal end. Terminal organ oval or bipartite. Eggs oval, numerous, not filamented. Vitellarium follicular; follicles small, in space between testis and cirrus-sac. Excretory vesicle I-shaped. In intestine of marine fishes; Indian Ocean. Type-genus *Opisthomonorcheides* Parukhin, 1966.

## Key to genera

**1a. Testis single ..... *Opisthomonorcheides* Parukhin, 1966. (Figs 7.45, 7.46)**
(Syns *Retractomonorchis* Madhavi, 1977; *Longimonorchis* Mamaev, 1970; *Tritesticulum* Bilqees, 1971)

**Diagnosis:** Body long, slender, delicate. Forebody short; hindbody long. Suckers small. Prepharynx long. Oesophagus short. Caeca long, terminate close to posterior extremity. Testis single, large, elliptical, near posterior extremity. Cirrus-sac small, elongate, contains oval seminal vesicle, prostatic complex and spined cirrus. Genital atrium tubular, thin-walled, passes dorsally to ventral sucker. Genital pore median, just anterior to ventral sucker. Ovary lobed, anterior to testis, separated from it by uterine coils. Uterine coils occupy space between posterior extremity and cirrus-sac, including post-testicular space. Metraterm joins distal end of terminal organ. Terminal organ small, armed with triangular spines. Eggs small, oval. Vitelline follicles small, numerous, dorsal, between testis and posterior part of cirrus-sac. Excretory vesicle tubular. In intestine of carangid and stromateid fishes; northern Indian Ocean. Type-species *O. decapteri* Parukhin, 1966.

**1b. Two testes present ..... 2.**

**2a. Testes close to posterior extremity; uterus pretesticular; terminal organ simple ..... ..... *Opisthodiplomonorchis* Madhavi, 1974. (Fig. 7.47)**

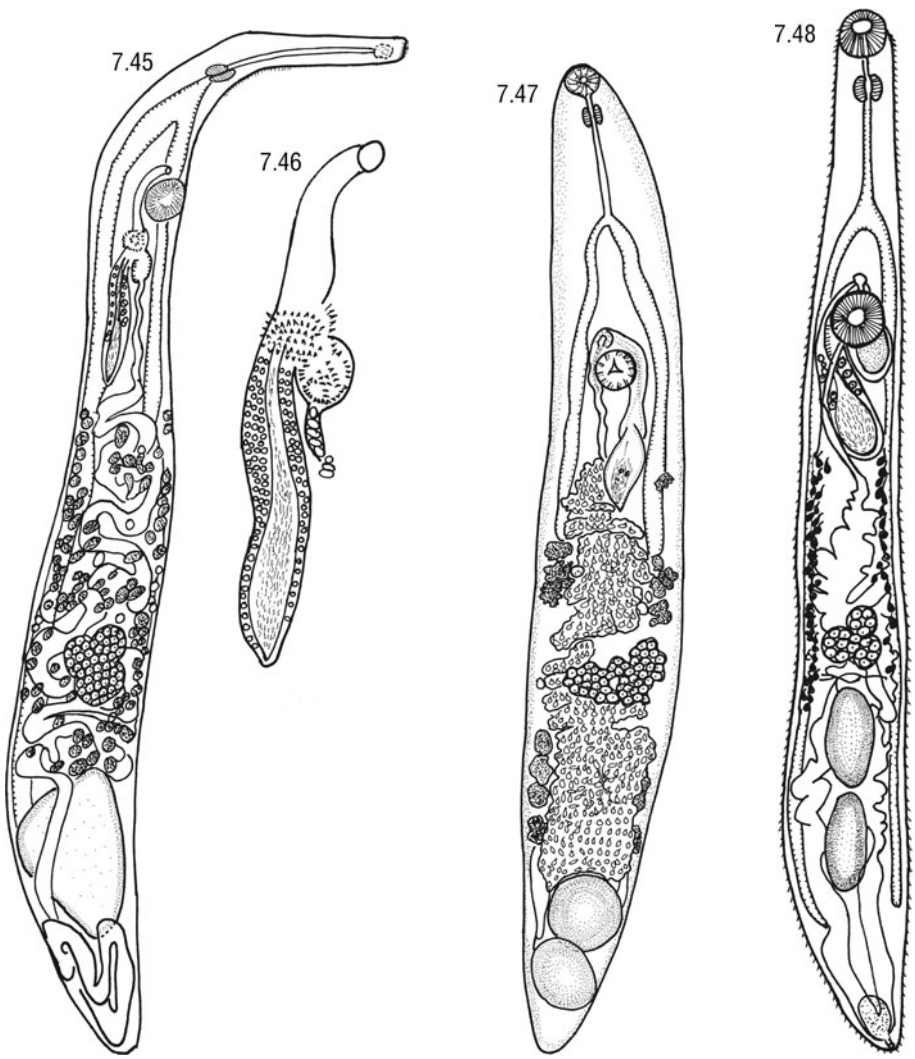
**Diagnosis:** Body elongate. Ventral sucker in anterior third of body. Caeca do not extend to posterior end. Testes two, oval, tandem near posterior extremity. Cirrus-sac small, encloses oval seminal vesicle, prostatic complex and spined cirrus. Genital atrium not spined. Genital pore median, just anterior to ventral sucker. Ovary multilobed, pretesticular, separated from testes by uterine coils. Uterus pretesticular, not extending posteriorly beyond testis. Terminal organ simple, sac-like, lined by triangular spines; metraterm joins its distal end. Vitelline follicles in lateral fields between cirrus-sac and testis, in two lateral groups of pre- and postovarian follicles. Excretory vesicle tubular, extends anteriorly to level of ventral sucker or beyond. In intestine of polynemid and psettodid fishes; Bay of Bengal. Type-species *O. elongatus* Madhavi, 1974.

**2b. Testes slightly separated from posterior end; uterus extends into post-testicular space; terminal organ bipartite ..... *Neolasiotocus* Ahmad, 1991. (Fig. 7.48)**

**Diagnosis:** Body long, slender. Suckers subequal. Ventral sucker in anterior third of body. Intestinal bifurcation in posterior forebody. Caeca long, reach beyond testes. Testes two, elliptical, tandem, slightly separated from posterior end. Cirrus-sac curves around ventral sucker, encloses

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oval seminal vesicle, prostatic complex and spined cirrus. Genital atrium unarmed. Genital pore median, in forebody. Ovary lobed, pretesticular. Uterus occupies intercaecal space posteriorly to cirrus-sac, fills post-testicular space and intrudes between ovary and testis, joins bipartite terminal organ at junction of vesicular posterior and spined anterior part. Vitelline follicles in lateral fields between cirrus-sac and anterior testis. Excretory vesicle saccular. In marine fishes; Arabian Sea. Type-species *N. brayi* Ahmad, 1991.




**Figs 7.45, 7.46.** *Opisthomonorcheides delicatus* (Madhavi, 1977). 7.45. Ventral view. After Madhavi (1977). 7.46. Terminal genitalia. After Madhavi (1977).
**Fig. 7.47.** *Opisthodiplomonorchis elongatus* Madhavi, 1974. Ventral view. After Choudhury & Dick (1998).
**Fig. 7.48.** *Neolasiotocus brayi* Ahmad, 1991. Ventral view. After Ahmad (1991).

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# 8 Family Lissorchiidae Magath, 1917

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## Introduction

Lissorchiids are parasites of freshwater fishes, mainly Cypriniformes, and are reported only from North America, the Palaearctic region, India and South-east Asia. They are usually characterized by a spinous tegument, spines in the ejaculatory duct and metraterm, a lateral genital pore and a restricted follicular vitellarium. Many species have a single testis, but with two vasa efferentia clearly indicating a reduction from two.

Magath (1917) erected the subfamily Lissorchiinae for his new genus *Lissorchis*. He considered that it either belonged in a modified Plagiorchiidae Lühe, 1901 or should have full family status. Shimazu (1992) gave a clear summary of the features distinguishing members of this family from members of the Monorchiidae Odhner, 1911, a family in which several of the genera defined here have been placed by various authors (e.g. Yamaguti, 1971). These distinguishing features are: (i) mainly freshwater (probably entirely), not marine. (ii) the non-oculate cercariaea (but a chaetomicrocercous cercaria in *Neopaleorchis* Schell, 1973) in rediae in snails (as opposed to oculate cercariae in sporocysts in clams); (iii) the stenostomate excretory system, rather than mesostomate, with a distinctive flame-cell formula; (iv) the lateral or sublateral genital pore, rather than median in the forebody; and (v) the metraterm is simple, in that, although it may be spined, it lacks a terminal organ. Magath (1917) described the life-cycle of the type-species of *Lissorchis, L. fairporti* Magath, 1917, as having a caudate xiphidiocercaria in a sporocyst in a planorbid snail, but subsequent work has thrown doubt on this, such that Shimazu (1992) reckoned that Magath had mistakenly described a plagiorchiid cercaria. Unfortunately, it appears that the genuine life-cycle of *L. fairporti* has not been elucidated. The general recognition of this family as including such monorchiid-like genera as *Asymphylodora* Looss, 1899 and *Palaeorchis* Szidat, 1943 has developed fairly slowly. Mehra (1966) placed the Lissorchiinae 'n. subf.' as a subfamily of the A**s**ymphylodoridae 'Mehra, 1962' and Brahamputrotrematinae 'n. subf.' as a subfamily of the Monorchiidae, but Yamaguti (1971) considered asymphylodorines as monorchiids and distinct from lissorchiids. Yamaguti (1971) included the subfamily Complexobursinae Yamaguti, 1971 in the Lissorchiidae, but molecular evidence in Hall *et al.* (1999) and an examination of specimens of the type-species, *C. vjetnamensis* Oshmarin & Mamaev, 1963, prompted Bray (2002b) to recognize *Complexobursa* Oshmarin & Mamaev, 1963 as a valid fellodistomid genus.

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The details of the female proximal system have often not been well described, but a small (?functionless) canalicular seminal receptacle and a uterine seminal receptacle are often reported (Shimazu, 1992). According to Yamaguti (1971) a seminal receptacle is absent in the Lissorchiidae.

*Anarhichotrema* Shimazu, 1973 and *Neolissorchis* Machida, 1985 were both originally placed in the Lissorchiidae (see Shimazu, 1973; Machida, 1985), but in this volume they are considered to belong in the family Zoogonidae, and they are also considered synonymous (Bray, Chapter 64, this volume).

*Anapalaeorchis* Fujino & Kifune, 1991 is, as suggested by Shimazu (1992), very similar to *Asymphylotrema* Dvorjadkin & Besprozvanych, 1985, differing only in the tandem rather than oblique testes and the caeca reaching the middle rather than the posterior margin of the posterior testis. In view of the variation found in this group, both genuinely phenotypic and fixation effects, these genera are considered synonymous in this study. The type-species of *Anapalaeorchis*, therefore, becomes *Asymphylotrema hamajimai* (Fujino & Kifune, 1991) n. comb. *Alloplagiorchis garricki* Simer, 1929 is superficially similar to *Asymphylotrema* and, therefore, *Alloplagiorchis* Simer, 1929 might be considered the oldest available name for this genus. This action has not been taken, however, as Barnhart & Powell (1979), in describing *Lissorchis kritskyi* Barnhart & Powell, 1979 from the same host species, considered the description of *A. garricki* to be 'superficial' and based on only three specimens. They were unsuccessful in obtaining specimens. The original figure (Simer, 1929) gives the impression of considerable contraction and it is thought possible that *L. kritskyi* is the same species but based on better specimens.

The description by Dayal & Gupta (1953) of their new genus *Brahamputrotrema* is most perfunctory and this taxon cannot be recognized from this date, but should be dated from Gupta (1955). The genus has often been erroneously spelled as *Brahmputrotrema*. Goodman & Panesar (1976) distinguished *Brahamputrotrema* and *Parasymphylodora* Szidat, 1943 (considered herein a synonym of *Asymphylodora*, see below) by the recurved (or not) nature of the cirrus-sac and whether the genital pore lies posteriorly or anteriorly to the cirrus-sac. In this study, these are considered minor features that do not distinguish genera. Here, *Brahamputrotrema* is distinguished from *Asymphylodora* by the lack of armament in the ejaculatory duct and metraterm and by the tendency of the vitellarium to extend into the forebody. *A. punctatusi* Gupta & Verma, 1976, described from the same host-species as the type-species of *Brahamputrotrema*, lacks armament of the ejaculatory duct and metraterm and has the vitellarium reaching into the forebody, indicating that it is a member of the latter genus (see Gupta & Verma, 1976). *Brahmputrotrema* [*sic*] *batesia* Dwivedi, 1970 has a submedian genital pore and vitelline follicles extending to the posterior extremity (Dwivedi, 1970). The eggs are large, 110–140 µm long, and few (three in the illustration). This species is considered *incertae sedis*. *Parasymphylodora manteri* Goodman & Panesar, 1976, reported as an adult from a freshwater pulmonate snail in Uganda, has an unarmed cirrus and metraterm and the vitellarium reaches into the forebody (Goodman & Panesar, 1976); therefore, it is closer to *Brahamputrotrema* than to *Asymphylodora*. The opposite can be said for *P. parasquamosa* Kulakova, 1972 (see Kulakova, 1972).

Many descriptions of *Lissorchis* consider the ejaculatory duct to be unarmed, or do not discuss this point. Choudhury & Nelson (1998) examined serial sections of the type-species, *L. fairporti* Magath, 1917, and found the cirrus to be spined. They also observed cirrus-spines on re-examination of other species where none had been described (*L. simeri* (Mueller & Van Cleave, 1932), *L. polylobatus* (Haderlie, 1950) and *L. crassicrurus* (Haderlie, 1954)) and considered these a plesiomorphic feature for lissorchiids. It is clear from several descriptions of *Lissorchis* spp. that the canalicular seminal receptacle is reduced (Mueller, 1934; Wallace, 1941; Fischthal, 1942; Barnhart & Powell, 1979; Choudhury & Nelson, 1998). Mueller (1934) found that the seminal receptacle of *L. simeri*, 'though small . . . contains sperm, whereas in *attenuatum* it was found to be empty'.

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*Wangxiyunia* nom. nov. is proposed for *Macrostomum* Wang, 1985, pre-occupied by *Macrostomum* Schmidt, 1848, an acoelomorphan 'turbellarian'. This genus was erected by Wang (1985) for *Orientotrema cyprini* Wang, 1982, based on the very large, 'trumpet-shaped' oral sucker. The shape of the oral sucker and the discrepancy between the sizes of the suckers serves to distinguish this genus from *Asymphylodora*. Three nominal species appear to belong in this genus, all reported from *Cyprinus carpio*. These are the type-species, *W. cyprini* (Wang, 1982) n. comb., *W. sinensis* (Wang & Pan, 1964) n. comb. (formerly in *Orientotrema*) and *W. borealis* (Qir & Wang, 1995) n. comb. (formerly in *Macrostomum*) (Chen & Li, 1973; Wang H.-y., 1982; Qir & Wang, 1995).

*Micromonorchis* Khoche, 1969 is considered a *nomen nudum*, but, as it was reported from a freshwater host (Khoche, 1969), it is probably a lissorchiid.

*Neopaleorchis* Schell, 1973 and *Anapalaeorchis* Fujino & Kifune, 1991 are very similar, differing in a single transverse vitelline field in *Neopaleorchis* and the separate lateral fields in *Anapalaeorchis*. There is, however, some indication that vitelline follicles spread across the dorsal plane in *A. hamajimae* Fujino & Kifune, 1991, as illustrated in his figure 15 by Shimazu (1992). *Neopaleorchis* also differs from other lissorchiids for which the life-cycle has been described in having a chaetomicrocercous cercaria in a redia.

*Orientotrema* Tang, 1962 was erected by Tang (1962) for *Asymphylodora japonicum* Yamaguti, 1938 and *A. macrostoma* Ozaki, 1925 based on the 'sinuous tube-shape' of the excretory vesicle rather than the 'sac-like' excretory vesicle of the type-species of *Asymphylodora, A. tincae* (Modeer, 1790). A similar distinction was one of the characters used by Szidat (1943) to validate his new genus *Parasymphylodora*, but Shimazu (1992) considered this distinction insufficient to distinguish either genus from *Asymphylodora*. In the absence of stronger distinguishing features and in view of the variability found in the genus, Shimazu's synonym is accepted here. Mehra (1966) pointed out that several earlier authors have also considered *Parasymphylodora* a synonym of *Asymphylodora*.

*Palaeorchis* Szidat, 1943 is a well-established genus of, mainly, Palaearctic species. Two forms described in China, *P. lobiovaris* Zhang, 1988 and *P. panjionghuai* Pan *et al.*, 1987, may be distinct enough, with their deeply lobate ovary and the vitellarium almost entirely in the forebody, to represent a distinct genus (Pan *et al.*, 1987; Zhang, 1988). Other species with unusual characters at present recognized as members of *Palaeorchis* include *P. postovaris* Zhang, 1988, with a post-testicular ovary and tiny caeca (Zhang, 1988), and *P. sinensis* Wang, 1983, with long caeca, more or less tandem testes and a small vitellarium at the level of the ventral sucker (Wang, 1983). *P. senegalensis* Fischthal & Thomas, 1972, reported from a marine fish, and based on a single, dextrolaterally mounted specimen (Fischthal & Thomas, 1972b), has not been considered in deriving the definition of *Palaeorchis*.

*Prosovitellina* Wang, 1985 and *Prostholecithum* Wang in Wang, Sun, Zhao, Zhang & Wang, 1985 were both erected during 1985. *Prostholecithum* was erected as a subgenus of *Asymphylodora* by Wang *et al.* (1985), including *A. (P.) elopichthydis* Wang in Wang, Sun, Zhao, Zhang & Wang, 1985 and *A. (P.) indica* Srivastava, 1936. The date of Wang *et al.* (1985) is 'Dec. 1985'. Presumably, *Prosovitellina* was erected earlier; the date is not given by Wang (1985), but the article is part 2 of the volume, rather than the part 5 of Wang *et al.* (1985). Both Pan *et al.* (1990) and Zhang *et al.* (1999) clearly give priority to *Prosovitellina*, although, in discussion, Pan *et al.* (1990) used *Prostholecithum* as a full generic name. The type-species of the subgenus *Prostholecithum, Asymphylodora (P.) elopichthydis*, has been included in the formation of the diagnosis, but is unusual in that the ovary lies sinistrally beside the testis (Wang *et al.*, 1985). Zhang *et al.* (1999) placed this species within *Prosovitellina. Asymphylodora (Prostholecithum) indica* Srivastava, 1936 is not considered a member of this genus as the bulk of the vitellarium

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lies posteriorly to the anterior margin of the ventral sucker. In fact, the vitellarium reaches the ovary, and has a distribution similar to that of *A. macrostoma* Ozaki, 1925 (see Shimazu, 1992). *A. indica* has also been placed in *Parasymphylodora* by Szidat (1943) and in *Brahamputrotrema* by Goodman & Panesar (1976). Other *Asymphylodora* species with a vitellarium that just intrudes into the forebody are *A. ritai* Gupta & Agrawal, 1967 and *A. punctatusi* Gupta & Verma, 1976, but in both cases the vitellarium also extends well into the hindbody, reaching the ovary (Gupta & Agrawal, 1967; Gupta & Verma, 1976). *A. macrostoma* and *A. ritai* have been considered synonyms of *A. tincae* by Rai (1972).

*Tigrotrema* was erected by Bhadauria & Dandotia (1984) for *T. gwaliorense* Bhadauria & Dandotia, 1984 (emend.), from *Channa punctatus* in India, and placed in the family Lissorchiidae. The genital pore is described as median, the ovary lies posteriorly to the testis and the vitellarium is very extensive. These are unusual characteristics for the Lissorchiidae and there is considerable doubt as to whether this form is a lissorchiid. *T. gwaliorense* is very similar to *Brahamputrotrema channa* Bhadauria & Dandotia, 1988 from the same host and locality (Bhadauria & Dandotia, 1988), in which the ovary is described as anterior to the testis. *Tigrotrema* is treated here as a genus *incertae sedis*.

## Family Lissorchiidae Magath, 1917

(Syns Asymphylodorinae Szidat, 1943; Asymphylodoridae Mehra, 1963)

**Diagnosis:** Body small to medium-sized, elongate-oval to fusiform. Tegument usually spinous. Oral sucker subterminal. Ventral sucker equatorial or more anterior. Prepharynx short. Pharynx well developed. Oesophagus short. Intestinal bifurcation usually in forebody. Caeca short to long, blind. Testes single or double, in posterior half of body; if two, tandem, oblique or symmetrical. Cirrus-sac claviform, extends posterodorsally to ventral sucker or into anterior hindbody. Seminal vesicle bipartite, unipartite or occasionally tubular. Pars prostatica often vesicular, variable. Ejaculatory duct capable of forming cirrus, armed or not. Genital atrium small to apparently absent. Genital pore lateral or ventrally sublateral at level of ventral sucker. Ovary entire or lobed, often trilobed, median or submedian, anterior to anterior testis. Canalicular seminal receptacle absent or small (?functionless). Laurer's canal present. Uterine seminal receptacle present. Uterus long, coiled; uterine field extending throughout most of hindbody, encircling gonads, often with distinct post-testicular zone. Metraterm well developed, spinous or not. Eggs numerous, small, usually operculate, embryonated. Vitellarium follicular, in small lateral fields, occasionally confluent dorsally. Excretory vesicle tubular, I-shaped; pore terminal. In freshwater teleosts; Holarctic. Type-genus *Lissorchis* Magath, 1917.

## Key to subfamilies

**1a. Testis single ..... Asymphylodorinae Szidat, 1943.**
**1b. Testes double ..... Lissorchiinae Magath, 1917.**

## Subfamily Lissorchiinae Magath, 1917

**Diagnosis:** With characters of family. Testes two. Type-genus *Lissorchis* Magath, 1917.

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## Key to genera

**1a. Testes tandem or oblique; caeca tubular, reach at least to level of testes ..... 2.**
**1b. Testes symmetrical or nearly so; caeca saccular, barely or not reaching ovary .....**
**..... *Palaeorchis* Szidat, 1943. (Fig. 8.1)**
(Syn. *Laterocreadium* Macy & Berntzen, 1970)

**Diagnosis:** Body oval. Tegument spinous. Ventral sucker rounded, pre-equatorial, of similar size to oral sucker. Pharynx oval, small. Oesophagus distinct. Intestinal bifurcation in posterior forebody or just overlapping ventral sucker. Intestinal caeca short, saccular, divergent, usually extending only to mid-level of body or level of ovary. Testes symmetrical or nearly so. Cirrus-sac claviform, reaching into hindbody. Internal seminal vesicle bipartite or unipartite. Pars prostatica short, vesicular. Ejaculatory duct long, thick-walled, spined. Genital pore sinistral, sublateral, at level of ventral sucker or anterior hindbody. Ovary oval to reniform, or distinctly lobed, usually mainly pretesticular. Canalicular seminal receptacle small, empty or containing spermatozoa and/or oöcytes. Uterus usually extensive in hindbody, with significant fraction posterior to testes. Metraterm distinct, thick-walled, spined. Eggs tanned, operculate. Vitelline follicles few, in lateral fields in hindbody or forebody. Excretory vesicle not reaching testes. In freshwater teleosts; Holarctic. Type-species *P. diplorchis* (Yamaguti, 1936) Szidat, 1943.

**2a. Caeca long, reaching beyond testes ..... *Lissorchis* Magath, 1917. (Fig. 8.2)**
(Syns *Triganodistomum* Simer, 1929; *Alloplagiorchis* Simer, 1929)

**Diagnosis:** Body elongate-oval to fusiform. Tegument spinous. Ventral sucker larger than or similar in size to oral, pre-equatorial. Intestinal bifurcation in mid- to posterior forebody or dorsal to ventral sucker. Caeca long, reaching beyond testes close to posterior extremity. Testes tandem, in mid-hindbody, entire or slightly lobed. Cirrus-sac claviform, extending into anterior hindbody. Internal seminal vesicle bipartite or unipartite. Pars prostatica short. Ejaculatory duct unarmed or armed with minute spines. Genital pore sinistral, lateral, at level of ventral sucker. Ovary lobed to multilobed, median or submedian, closely anterior to anterior testis. Small canalicular seminal receptacle present. Uterus long, coiled; uterine field extends throughout most of hindbody, encircles gonads, often with large post-testicular zone. Metraterm unarmed. Eggs numerous, small, operculate. Vitelline fields lateral; follicles numerous, small, lateral to caeca, between ventral sucker and anterior part of post-testicular field. Excretory vesicle reaches ovary. In intestine of catastomid (and occasionally other cypriniform) freshwater teleosts; Nearctic. Type-species *L. fairporti* Magath, 1917.

**2b. Caeca not reaching into post-testicular region ..... 3.**

**3a. Vitellarium forms separate lateral fields .....**
**..... *Asymphylotrema* Dvorjadkin & Besprozvanych, 1985. (Fig. 8.3)**
(Syn. *Anapalaeorchis* Fujino & Kifune, 1991)

**Diagnosis:** Body oval to pyriform. Tegument spinous. Ventral sucker rounded, larger than oral sucker, just pre-equatorial. Pharynx oval. Oesophagus long. Intestinal bifurcation dorsal to ventral sucker or in posterior forebody. Caeca extend to posterior testis. Testes two, entire or irregularly oval, tandem or oblique, in mid-hindbody. Cirrus-sac claviform, diagonal, in anterior hindbody or dorsal to ventral sucker. Internal seminal vesicle bipartite. Pars prostatica small, round. Ejaculatory duct fairly long, heavily spined, protrusible. Genital pore lateral to sublateral, sinistral, at level of ventral sucker. Ovary trilobed, anterodextral to anterior testis. Canalicular seminal

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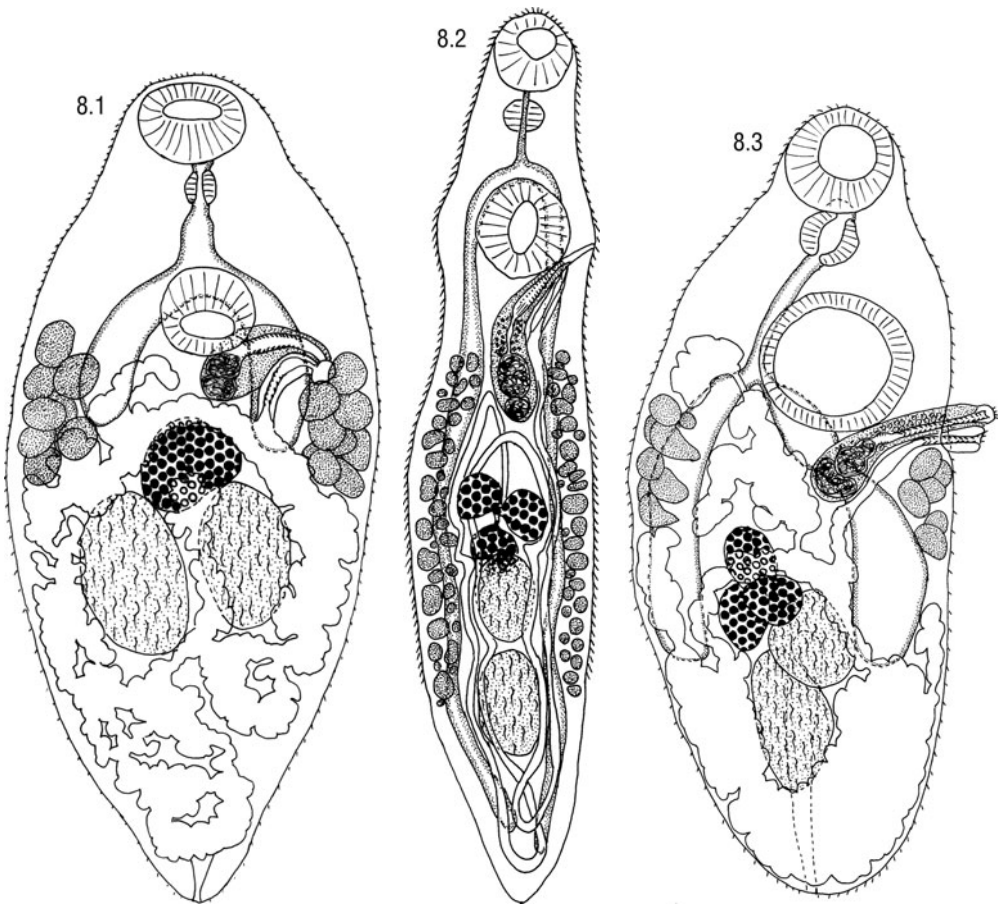



**Fig. 8.1.** *Palaeorchis diplorchis* (Yamaguti, 1936). After Shimazu (1992).
**Fig. 8.2.** *Lissorchis hypentelii* (Fischthal, 1942). After Fischthal (1942).
**Fig. 8.3.** *Asymphylotrema hamajimai* (Fujino & Kifune, 1991) n. comb. After Shimazu (1992).

receptacle small, empty or with few spermatozoa. Uterus confined to hindbody. Eggs small, operculate. Metraterm well developed, spined. Vitelline follicles few, in separate lateral fields mainly in anterior hindbody. Excretory vesicle extends to mid-level of anterior testis. In freshwater fishes; eastern Palaearctic. Type-species *A. macracetabulum* (Belous in Sobolev, 1955) Dvorjadkin & Besprozvanych, 1985.

**3b. Vitellarium confined to area around testes, confluent dorsally .....**
**..... *Neopaleorchis* Schell, 1973. (Fig. 8.4)**

**Diagnosis:** Body oval. Tegument spinous. Ventral sucker oval, pre-equatorial. Pharynx subglobular, small. Oesophagus long. Intestinal bifurcation dorsal to posterior part of ventral sucker. Caeca reach mid-testicular zone. Testes oval, entire, tandem, in mid-hindbody. Cirrus-sac claviform, recurved. Internal seminal vesicle folded ('not bipartite'). Pars prostatica small, vesicular. Ejaculatory duct short, spinous. Genital pore sinistral, sublateral, at level of ventral sucker. Ovary lobed, mainly

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pretesticular. Canalicular seminal receptacle absent. Laurer's canal 'not observed'. Uterus fills most of available space in hindbody, including significant fraction in post-testicular region. Eggs tanned, operculate. Metraterm distinct (unarmed?). Vitellarium follicular, in single field crossing body dorsally in testicular region. Excretory vesicle reaches testes. Cercaria chaetomicrocercous. Adult in freshwater fish (*Catostomus*); Nearctic. Type-species *N. catostomi* Schell, 1973.

## Subfamily Asymphylodorinae Szidat, 1943

**Diagnosis:** With characters of family. Testis single. Type-genus *Asymphylodora* Looss, 1899.

## Key to genera

**1a. Vitellarium mostly in forebody, not reaching into hindbody ..... ..... *Prosovitellina* Wang, 1985. (Fig. 8.5)**

(Syns *Asymphylodora (Prostholecithum*) Wang in Wang, Sun, Zhao, Zhang & Wang, 1985; *Prostholecithum* Wang in Wang, Sun, Zhao, Zhang & Wang, 1985)

**Diagnosis:** Body pyriform to oval. Tegument unarmed. Ventral sucker oval to rounded, of similar size to oral sucker, just pre-equatorial. Pharynx oval, small. Oesophagus distinct. Intestinal bifurcation in posterior forebody. Caeca reach just beyond testis. Testis oval, entire, in mid-hindbody. Cirrus-sac claviform, reaches into hindbody. Internal seminal vesicle unipartite. Pars prostatica? Ejaculatory duct heavily spined. Genital pore sublateral, sinistral, at level of ventral sucker. Ovary oval, entire, anterodextral or sinistral to testis. Seminal receptacle? Laurer's canal? Uterus reaches into post-testicular zone, restricted to hindbody. Metraterm heavily spined. Eggs yellowish brown. Vitelline follicles few; fields mainly restricted to forebody. Excretory vesicle sac-like. In freshwater fishes (Cyprinidae); China. Type-species *P. rhinogobii* (Wang, 1982) Wang, 1985.

**1b. At least some part of vitellarium in hindbody ..... 2.**

**2a. Ejaculatory duct and metraterm unarmed; vitellarium usually reaching into forebody ..... ..... *Brahamputrotrema* Gupta, 1955. (Fig. 8.6)**

**Diagnosis:** Body pyriform. Tegument spinous. Oral sucker subglobular, subterminal. Ventral sucker rounded, just pre-equatorial. Pharynx oval. Oesophagus long. Intestinal bifurcation in posterior forebody. Caeca reach mid-testicular level. Testis in posterior half of hindbody. Cirrus-sac broadly claviform. Internal seminal vesicle unipartite. Pars prostatica small. Ejaculatory duct of medium length, unarmed. Genital pore dextral, sublateral, at level of ventral sucker. Ovary irregularly rounded, pretesticular, median. Seminal receptacle? Laurer's canal? Uterus extensive, from intestinal bifurcation to posterior extremity. Metraterm unarmed. Eggs tiny, non-operculate. Vitelline fields reach from pharynx to mid-ovary. Excretory vesicle reaches ovary. In freshwater teleosts (*Ophiocephalus*); India. Type-species *B. punctatum* Gupta, 1955 (emend.).

**2b. Ejaculatory duct and metraterm armed with spines; vitellarium usually restricted to hindbody ..... 3.**

**3a. Oral sucker smaller than or of similar size to ventral sucker ..... ..... *Asymphylodora* Looss, 1899. (Fig. 8.7)**

(Syns *Orientotrema* Tang, 1962; *Parasymphylodora* Szidat, 1943)

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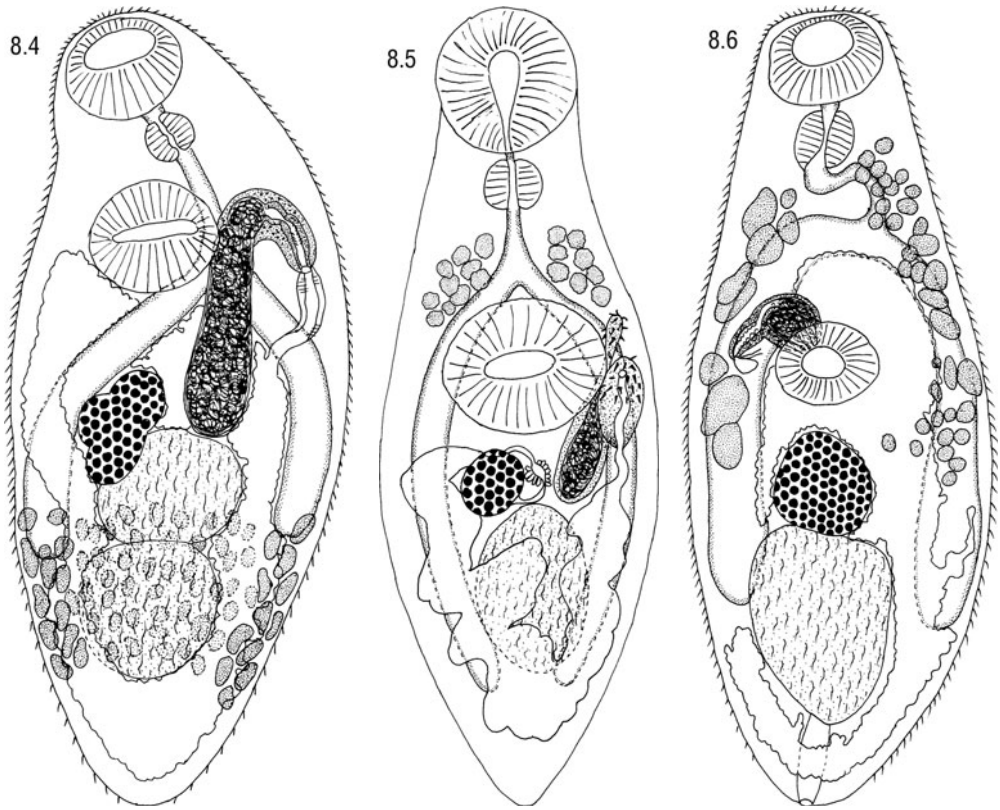



**Fig. 8.4.** *Neopaleorchis catostomi* Schell, 1973. After Schell (1973).
**Fig. 8.5.** *Prosovitellina rhinogobii* (Wang, 1982). After Wang H.-y. (1982).
**Fig. 8.6.** *Brahamputrotrema punctatum* Gupta, 1955. After Gupta (1955).

**Diagnosis:** Body pyriform, small. Tegument spinous. Oral sucker subglobular, subterminal, smaller than or of similar size to ventral sucker. Ventral sucker rounded, pre-equatorial or equatorial. Prepharynx short. Pharynx oval, small. Oesophagus distinct. Intestinal bifurcation dorsal to ventral sucker or in posterior forebody. Caeca reach ovary, testis or slightly more posteriorly. Testis in mid- to posterior hindbody. Cirrus-sac claviform, may reach ovary. Internal seminal vesicle bipartite or unipartite. Pars prostatica usually short. Ejaculatory duct medium to long, spined. Genital pore sublateral, sinistral, at about level of ventral sucker. Ovary oval, occasionally lobed, pretesticular. Both uterine and canalicular seminal receptacles described. Laurer's canal present. Uterus fills much of hindbody, extends to posterior extremity. Metraterm spined. Eggs operculate. Vitelline follicles in small lateral fields, usually entirely in hindbody. Excretory vesicle I-shaped or saccular. In freshwater teleosts; Holarctic. Type-species *A. tincae* (Modeer, 1790) Looss, 1899.

**3b. Oral sucker massive, infundibuliform, distinctly larger than ventral** ..... ..... ***Wangxiyunia*** **nom. nov. (Fig. 8.8)**
(Syn. *Macrostomum* Wang, 1985 *nec* Schmidt, 1848)

**Diagnosis:** Body small, widest at oral or ventral sucker level, with narrow neck. Tegument spinous. Oral sucker massive, infundibuliform, flared. Ventral sucker rounded, more or less equatorial, much

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smaller than oral. Prepharynx absent? Pharynx oval, small. Oesophagus short, distinct. Intestinal bifurcation in mid- to posterior forebody. Caeca reach into post-testicular zone. Testis oval, in mid-hindbody. Cirrus-sac claviform, lies diagonally in anterior hindbody. Internal seminal vesicle unipartite or bipartite. Pars prostatica narrow, short. Ejaculatory duct of moderate length, spined. Genital pore sublateral, sinistral at level of ventral sucker. Ovary oval, entire or irregular, dextral, mainly or entirely pretesticular, in anterior hindbody or overlapping ventral sucker. Seminal receptacle? Laurer's canal? Uterus extensive between intestinal bifurcation or ventral sucker and postcaecal region. Metraterm spined. Vitelline follicles in small lateral fields in anterior and mid-hindbody. In freshwater fishes (mainly *Cyprinus*); China. Type-species *W. cyprini* (Wang, 1982) n. comb.

## Genus *incertae sedis*

### *Tigrotrema* Bhadauria & Dandotia, 1984 (Fig. 8.9)

**Diagnosis:** Body elongate-oval. Tegumental armament? Oral sucker large, subglobular, subterminal. Ventral sucker rounded, pre-equatorial. Prepharynx absent. Pharynx oval, small. Oesophagus

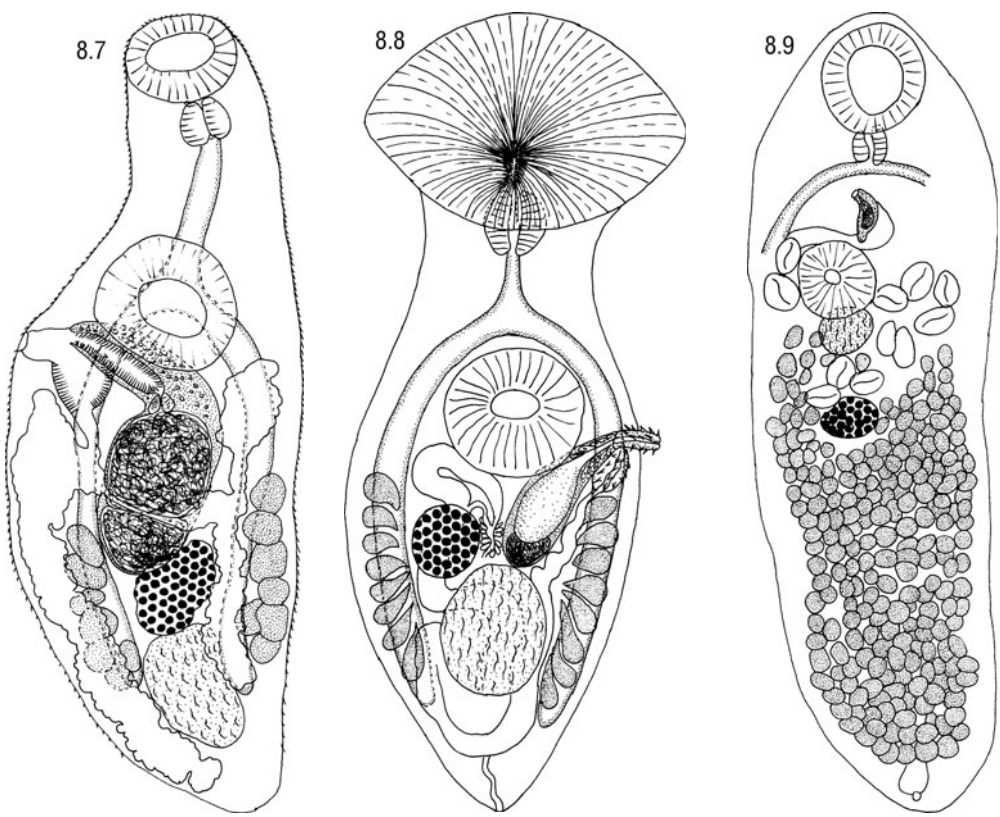



**Fig. 8.7.** *Asymphylodora tincae* (Modeer, 1790) from *Tinca tinca*, Czechoslovakia (BMNH 1971.6.4.4). Original.
**Fig. 8.8.** *Wangxiyunia cyprini* (Wang, 1982) n. comb. After Wang H.-y. (1982).
**Fig. 8.9.** *Tigrotrema gwaliorense* Bhadauria & Dandotia, 1984. After Bhadauria & Dandotia (1984).

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short. Intestinal bifurcation in mid-forebody. Caeca reach close to posterior extremity. Testis single, in anterior hindbody. Cirrus-sac in forebody. Internal seminal vesicle saccular. Pars prostatica? Ejaculatory duct muscular (presumably unarmed). Genital pore median, just postbifurcal. Ovary rounded, post-testicular. Seminal receptacle absent? Laurer's canal? Uterus pre-ovarian? Metraterm? Eggs? Vitellarium occupies most of postovarian zone. Excretory vesicle I-shaped; pore terminal. In freshwater fish (*Channa*); India. Type-species *T. gwaliorense* Bhadauria & Dandotia, 1984 (emend.).

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# 9 Superfamily Gorgoderoidea Looss, 1899

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## Introduction

There are no outstanding morphological autapomorphies for this superfamily. As can be seen from the diagnosis below, many characters vary greatly between the families and some within families. Thus, it is not possible to summarize the morphology of the group in a short, succinct fashion. Similarly, the hosts and sites of infection vary greatly within the group, gorgoderoids being found in virtually all vertebrate groups from elasmobranchs to mammals. More detailed studies will tell whether the superfamily will survive in anything like its current form.

As far as we are aware, this taxon was first recognized at the superfamily level by Odening (1960d) as '*Gorgoderoidea* nom. n.'. Reference to Odening (1974) shows that this superfamily contained only the family Gorgoderidae Looss, 1899. Brooks *et al*. (1985) also considered that the superfamily contained just the nominate family, as did Brooks & McLennan (1993) and, apparently, Tkach *et al*. (2000a). In the molecular and combined evidence trees produced by Cribb *et al*. (2001b), the families Gorgoderidae Looss, 1899, Dicrocoeliidae Looss, 1899 and Orchipedidae Skrjabin, 1913 formed a monophylum, but no nomenclatural decisions were taken. The Gorgoderoidea, as recognized here, is based, therefore, on the concept developed by Olson *et al*. (2003) using molecular phylogenies based on rRNA genes. They recovered a clade including the three families mentioned above, plus the Haploporidae Nicoll, 1914 + Atractotrematidae Yamaguti, 1939, Paragonimidae Dollfus, 1939, Troglotrematidae Odhner, 1914, Callodistomidae Odhner, 1910 and Encyclometridae Mehra, 1931. Of these families, the Haploporidae, Atractotrematidae, Callodistomidae and Encyclometridae have been treated elsewhere in these volumes (Bray, 2002a; Overstreet & Curran, 2005a, b; Tkach, Chapter 29, this volume). For convenience of identification, some families not treated by Olson *et al*. (2003) are included in this key based on their morphological similarities to the families recognized by molecular studies. These are the Anchitrematidae Mehra, 1935, Brachycoeliidae Looss, 1899, Braunotrematidae Yamaguti, 1958, Collyriclidae Ward, 1917, Cortrematidae Yamaguti, 1958, Mesocoeliidae Dollfus, 1929 and Prouterinidae Foreyt, Schell & Beyer, 1996. Molecular results (Tkach *et al*., 2000a, 2001b; Curran *et al*., 2006; Razo-Mendivil *et al*., 2006; Choudhury *et al*., 2007) indicate that the Brachycoeliidae and Mesocoeliidae may be members of the Plagiorchioidea.

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## Superfamily Gorgoderoidea Looss, 1899

(Syn. Orchipedoidea Skrjabin, 1913)

**Diagnosis:** Body small to large, flattened or thick, circular, oval, conical, pyriform, fusiform or elongate, or divided into distinctively narrower forebody and wider hindbody, may have paired pulvinate bolsters dorsolaterally at anterior extremity, may be almost spherical. Tegument smooth or armed with spines, sometimes papillate or wrinkled. Oral sucker well developed. Ventral sucker usually well developed, sessile or protuberant, usually in anterior half of body, occasionally absent. Prepharynx present or absent. Pharynx muscular or absent. Oesophagus usually present, may be absent. Intestinal bifurcation in forebody. Caeca two, occasionally one, simple, long or short, rarely diverticulate, sometimes sinuous, may unite posteriorly. Testes entire to deeply lobed, in hindbody or at level of ventral sucker, inter- or extracaecal, or overlapping caeca, symmetrical to tandem, two or more in number. Cirrus-sac present or absent; pseudosinus-sac rarely present. Internal or external seminal vesicle present. Pars prostatica usually present. Genital pore median to submedian, usually in forebody between level of pharynx and ventral sucker, occasionally at anterior end of body or at level of ventral sucker or in anterior hindbody, may be on distinct papilla; occasionally, male and female pores apparently separate, occasionally at posterior extremity. Ovary submedian or median, intercaecal, pretesticular, post-testicular or paratesticular, in hindbody or occasionally in forebody. Canalicular seminal receptacle present or absent; oviducal or uterine seminal receptacle occasionally reported. Laurer's canal present or not observed. Uterus usually in hindbody, may extend into forebody, occasionally restricted to forebody, usually extensive. Eggs small or large. Vitellarium follicular or dendritic, of variable distribution, usually limited in extent, or in two masses, often lobed or compact, pre-ovarian in hindbody. Excretory vesicle I-, Y-, V-, T- or H-shaped; pore terminal; or occasionally on mid-ventral surface or sublateral. In intestine, gall-bladder, bile-ducts, pancreatic ducts, body-cavity, urinary-bladder, ureters, swim-bladder, nasal and paranasal sinuses, lungs, brain, tissues or encysted in skin and in wall of digestive tract. In elasmobranchs, teleosts, amphibians, reptiles, birds and mammals; cosmopolitan in terrestrial, freshwater and marine environments. Type-genus *Gorgodera* Looss, 1899.

## Key to families

**1a. Testes two ..... 3.**
**1b. Testes numerous ..... 2.**

**2a. Vitellarium compact or follicular and restricted; in body-cavity of elasmobranchs or urinary bladder of amphibians and teleosts ..... Gorgoderidae Looss, 1899 (in part).**
**2b. Vitellarium follicular, extensive; in cavities of respiratory tract or adjacent tissues and cavities of birds and mammals ..... Orchipedidae Skrjabin, 1913.**

**3a. Body with paired pulvinate bolsters dorsolaterally at anterior extremity; in intestine of chelonians ..... Braunotrematidae Yamaguti, 1958.**
**3b. Body lacking paired pulvinate bolsters dorsolaterally at anterior extremity; not in chelonians ..... 4.**

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**4a. Uterus restricted to forebody; in nasal and paranasal sinuses, lungs and brain of bears .... ..... Prouterinidae Foreyt, Schell & Beyer, 1996.**
**4b. Uterus partly in hindbody; not in nasal and paranasal sinuses and brain of bears ..... 5.**

**5a. Ventral sucker absent ..... Collyriclidae Ward, 1917 (in part).**
**5b. Ventral sucker present ..... 6.**

**6a. Genital pore at level of ventral sucker or in hindbody ..... 7.**
**6b. Genital pore in forebody ..... 10.**

**7a. Genital pore at level of ventral sucker or in anterior hindbody ..... 8.**
**7b. Genital pore at posterior extremity ..... Cortrematidae Yamaguti, 1958.**

**8a. Caeca long, distinctly sinuous; cirrus-sac absent; vitellarium dendritic; testes and ovary extremely deeply lobate; in capsules within lungs (usually) of mammals ..... ..... Paragonimidae Dollfus, 1939.**
**8b. Caeca variable in length, not distinctly sinuous; cirrus-sac present or absent; vitellarium follicular; testes and ovary usually entire or moderately lobate, not encapsulated in lungs of mammals ..... 9.**

**9a. Genital pore usually in middle third of body immediately posterior to ventral sucker, exceptionally just anterior to ventral sucker or at anterior extremity; Laurer's canal relatively short; uterus variable in extent, usually rather short and intercaecal or postcaecal, and posterior to genital pore; in tissue, body-sinus or digestive tract of mammals and birds ..... ..... Troglotrematidae Odhner, 1914 (in part).**
**9b. Genital pore(s) close to median line in middle of body; Laurer's canal very long, runs in posterodorsal direction, ends blindly or opens on dorsal body-surface; uterus in posterior half of body only, or may occupy most of body; encysted in skin and in wall of digestive tract of birds and mammals ..... Collyriclidae Ward, 1917 (in part).**

**10a. Testes extracaecal ..... 11.**
**10b. Testes intercaecal ..... 12.**

**11a. In intestine of reptiles and bats ..... Anchitrematidae Mehra, 1935.**
**11b. In urinary-bladder or body-cavity of fishes, amphibians or reptiles ..... ..... Gorgoderidae Looss, 1899 (in part).**

**12a. Ovary pretesticular ..... 13.**
**12b. Ovary post-testicular ..... 15.**

**13a. In urinary-bladder or body-cavity of fishes, amphibians or reptiles ..... ..... Gorgoderidae Looss, 1899 (in part).**
**13b. In intestine or liver of amphibians, reptiles or mammals ..... 14.**

**14a. In intestine of amphibians, reptiles and, rarely, mammals; caeca terminate well before posterior extremity ..... Brachycoeliidae Looss, 1899.**

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**14b. In small intestine and liver of mammals; caeca reach posterior extremity ..... ..... Troglotrematidae Odhner, 1914 (in part).**

**15a. Vitellarium mainly in forebody; in intestine of amphibians and reptiles, exceptionally fish ..... Mesocoeliidae Dollfus, 1929.**
**15b. Vitellarium mainly in hindbody; usually in bile-ducts or gall-bladder of birds, mammals and, rarely, reptiles ..... Dicrocoeliidae Looss, 1899.**

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# 10 Family Gorgoderidae Looss, 1899

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## Introduction

Members of the family Gorgoderidae Looss, 1899 are well known as small to large endoparasites of amphibians, fishes and reptiles. Many species inhabit the urinary bladder of their hosts but, more rarely, other locations, such as the swim-bladder, coelom (elasmobranchs), gall-bladder or intestine, are utilized. Important characteristics are: the non-spinous tegument; the thin body musculature; well-developed suckers; the flattened body, which is usually broader posteriorly to the ventral sucker; the subterminal oral sucker, which is smaller than the ventral sucker; the presence or absence of a pharynx; simple elongate caeca, which may be branched or united posteriorly; a pre-equatorial ventral sucker; the genital pore in the forebody close to the intestinal bifurcation; the separate genital ducts leading to the genital atrium; the simple male genital terminalia with an external seminal vesicle, a weakly developed pars prostatica and an ejaculatory duct; the weakly developed or absent genital atrium; the gonads in the hindbody; either two testes or multiple testicular follicles; a pretesticular ovary; the presence or absence of a seminal receptacle and Laurer's canal; the pre-ovarian vitellarium in two masses that are compact or dendritic; the uterus extending far into the hindbody, rarely forming loops anteriorly to the ventral sucker; and the small and non-operculate eggs.

The first life-cycles were elucidated by Sinitsin (1905) for *Gorgodera cygnoides* (Zeder, 1800), *G. pagenstecheri* Sinitsin, 1905 and *G. varsoviensis* Sinitsin, 1905. Cercariae of the cystocercous type, produced by daughter-sporocysts attached to the gills of freshwater bivalve molluscs, emerge and become metacercariae in larvae of aquatic insects such as odonatan naiads, snails, crayfish, *Mesocyclops* (cyclopodids), tadpoles or larval urodeles (see Lutz, 1926; Joyeux & Baer, 1934; Krull, 1935; Odlaug, 1937; Rankin, 1939; Prudhoe & Bray, 1982). Active gorgoderid cercariae are caught by predatory aquatic insects, whereas inactive ones are eaten by tadpoles or snails. Following ingestion of the metacercariae, the worms migrate to the kidneys as juveniles and become adults in the urinary bladder of frogs (*Rana, Hyla*, etc.), toads (*Bufo*) and salamanders (*Amblystoma*). Cercariae produced in the life cycles of gorgoderids are now known to include types other than those of the cystocercous or macrocercous type, indicating a diversity not necessarily reflected by the morphology of the adults (Coil, 1960; Cribb, 1987b). Life-cycles of various gorgoderids are

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known from freshwater species, but Manter (1970) speculated that those of marine species are probably similar (see Bott & Cribb, 2005a). Exceptions to the three-host life-cycle have been demonstrated by Wanson & Larson (1972) and Orecchia *et al*. (1975) for species of *Phyllodistomum* Braun, 1899, which become adults in fish from larvae that completed their development in clams (*Sphaerium, Anodonta*), thus requiring no second intermediate host. Mitchell & Mason (1980) suggested that encystment of cercariae within daughter-sporocysts freed from the gills of the intermediate host (*Pisidium*) might result in the evolution of a new species by involving different hosts in the life-cycle. Maguza (1972) studied intraspecific variations, i.e. mirror-image forms, of adult worms and considered the variations as possible evidence leading to speciation. The importance of observed variability of morphological features for the systematics of gorgoderids has been noted and subjected to morphometric analysis by Kudinova (1979), resulting in the conclusion that, in some instances, variations were sufficient to synonymize genera and subfamilies (Koval, 1971; Brooks & Mattis, 1978).

Several exceptions to the simple terminal genitalia characteristic of most gorgoderids, i.e. the absence of a cirrus-sac, internal seminal vesicle and cirrus, are now known. A cirrus-sac with an internal seminal vesicle, a pars prostatica and an ejaculatory duct are clearly present in serial sections of *Degeneria* Campbell, 1977. A cirrus-sac was described for *Dendrorchis* Travassos, 1926, but declared absent by Brooks & MacDonald (1986) following the examination of syntypes. *Chelatrema* Gupta & Kumari, 1973, if described correctly, possesses a cirrus-sac and cirrus. In *Xystretrum* Linton, 1910, the genital ducts are enclosed within a 'pseudosinus sac' (see *X. hawaiiense* Yamaguti, 1970) within an eversible genital papilla, termed a cirrus by several authors, including Hanson (1955), who also showed that the cirrus of *X. pulchrum* (Travassos, 1921) has papillae.

Zeder (1800) was the first to describe a trematode, *Distomum cygnoides*, from the urinary bladder of frogs and later Braun (1899) erected *Phyllodistomum* for *Distomum folium* Olfers, 1816 from the urinary bladder of fishes. Looss (1899) proposed *Gorgodera* Looss, 1899 for *D. cygnoides* Zeder, 1800, and later *D. vitellilobum* Olsson, 1876 from the frog, *Rana temporaria*, was placed in *Gorgoderina* Looss, 1902 by Looss (1902).

Looss (1901b) proposed the Gorgoderidae with two subfamilies, the Gorgoderinae Looss, 1899 and the Anaporrhutinae Looss, 1901. Looss (1902) included *Gorgodera, Gorgoderina* and *Catoptroides* Odhner, 1902 in the Gorgoderinae. Several other genera were subsequently added to the subfamily: *Xystretrum* Linton, 1910; *Macia* Travassos, 1920; *Microlecithus* Ozaki, 1926; *Vitellarinus* Zmeev, 1936; *Gorgotrema* Dayal, 1938; *Phyllochorus* Dayal, 1938; and *Plesiodistomum* Dayal, 1942. Lewis (1935), Bhalerao (1937a), Wu (1938), Kaw (1950) and Yamaguti (1958b, 1971) considered *Catoptroides* a synonym of *Phyllodistomum* and both Yamaguti (1934) and Bhalerao (1937a) also regarded *Microlecithus* as a synonym of *Phyllodistomum*. Yamaguti (1958b, 1971) considered *Vitellarinus* and *Plesiodistomum* synonyms of *Phyllodistomum* and *Macia* a synonym of *Xystretrum*. Pande (1937) included *Gorgoderina* and Kaw (1950) and Yamaguti (1958b, 1971) included *Phyllochorus* as synonyms of *Phyllodistomum*. However, Pigulevsky (1952, 1953) retained *Catoptroides, Microlecithus* and *Vitellarinus* as subgenera of *Phyllodistomum* and placed the genera *Dendrorchis, Gorgoderina* and *Phyllochorus* along with *Phyllodistomum* in a separate subfamily, i.e. the Phyllodistomatinae [*sic*], previously erected at the family level as the Phyllodistomidae Nybelin, 1926 by Nybelin (1926). Yamaguti (1971) did not recognize these subgenera because of the variability in the characters.

The Anaporrhutinae originally included only *Anaporrhutum* Brandes in Ofenheim, 1900, and to this Looss (1901b) added *Plesiochorus* Looss, 1901 and *Probolitrema* Looss, 1901. Among the genera that have been added to the subfamily are: *Petalodistomum* Johnston, 1913; *Dendrorchis*

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Travassos, 1926; *Staphylorchis* Travassos, 1922; *Nagmia* Nagaty, 1930; and *Plesiodistomum* Dayal, 1949. Nagaty (1930) reviewed the subfamily Anaporrhutinae and synonymized *Dendrorchis* with *Phyllodistomum. Dendrorchis* was retained by Yamaguti (1971) in the Phyllodistominae despite the reported presence of a cirrus-sac. Although *Dendrorchis* lacks a pharynx, it appeared closest to *Degeneria* Campbell, 1977, which is pharyngeate and was presumed to share the characteristics of the uterus extending into the forebody and presence of a cirrus-sac, until Brooks & MacDonald (1986) examined syntypes of *Dendrorchis neivai* Travassos, 1926 and found that no cirrus-sac was present. The generic diagnosis of *Dendrorchis* here has been amended accordingly. Manter (1962) considered *Cylindrorchis* Southwell, 1913 a gorgoderid and a possible member of the Anaporrhutinae, but later authors (e.g. Gibson & Bray, 1979; Gibson, 2002b) have considered it a hemiuroid of the family Dictysarcidae Skrjabin & Guschanskaja, 1955.

Travassos (1923a) differentiated the Gorgoderinae and Anaporrhutinae on the form and arrangement of the vitellarium and position of the testes. According to Travassos, the vitellarium of the Gorgoderinae is lobed or rounded and the testes are intercaecal, in contrast to the branched vitellarium and inter- or extracaecal testes in the Anaporrhutinae. Ward (1918), Loewen (1929) and Nagaty (1930) used the presence or absence of a muscular pharynx and seminal receptacle as differentiating characters for these two subfamilies. Variability, for both species and genera, in the form of the vitellarium, testicular number, position and arrangement, and the inconsistent presence of the seminal receptacle stirred much controversy among helminthologists in defining the Anaporrhutinae, Gorgoderinae and subfamilies added later. Kaw (1950) regarded the presence of a muscular pharynx in the Anaporrhutinae and its absence in the Gorgoderinae as the only reliable diagnostic character for division of the Gorgoderidae into two subfamilies.

Pigulevsky (1952, 1953) retained the genera synonymized by previous authors by the erection of new subfamilies and subgenera. Pigulevsky (1952) divided the gorgoderids into a number of subgenera. For the subfamily Gorgoderinae, he proposed that *Gorgodera* Looss, 1899 be subdivided into five subgenera (*Gorgodera* Looss, 1899, *Antodera* Pigulevsky, 1952, *Extremodera* Pigulevsky, 1952, *Mediodera* Pigulevsky, 1952 and *Postodera* Pigulevsky, 1952) based upon rather subjective specific differences. This was rejected by Yamaguti (1971). For the Anaporrhutinae, Pigulevsky (1952) divided *Petalodistomum* into the subgenera *Petalodistomum* and *Staphylorchis* Travassos, 1922 and *Probolitrema* into the subgenera *Probolitrema* and *Reduxotrema* Pigulevsky, 1952. He erected two new subfamilies: the Plesiorchinae Pigulevsky, 1952 for two genera known from reptiles at that time, *Plesiochorus* Looss, 1901 and *Bicornuata* Pearse, 1949; and in the subfamily 'Phyllodistomatinae [*sic*] Pigulevsky, 1952' he recognized *Phyllodistomum* with four subgenera (*Phyllodistomum, Catoptroides, Microlecithus* and *Vitellarinus*) and *Gorgoderina*, comprised of two subgenera (*Gorgoderina* and *Gorgorimma* Pigulevsky, 1952).

*Gorgoderina* (syn. *Microlecithus* Ozaki, 1926) was considered a synonym of *Phyllodistomum* by Pande (1937) and Kaw (1950), but retained as distinct by subsequent authors. Fernandes (1958) provided a tabular comparison of 14 spp. of the subgenus *Gorgoderina. Gorgoderina* was split by Pereira & Cuocolo (1940) into the subgenera *Gorgoderina* and *Neogorgoderina* but this was necessarily suppressed, as the designated type of *Neogorgoderina, G. simplex* (Looss, 1899), is the type-species of *Gorgoderina*. Pigulevsky's (1952) subgenus *Gorgorimma* was merged with *Gorgoderina* by Yamaguti (1971), who also suppressed *Metagorgoderina* Fernandes, 1958 for lack of a designated type.

Yamaguti (1958b) recognized Gorgoderinae, Anaporrhutinae and Plesiochorinae and added three subfamilies: the Phyllodistominae Nybelin, 1926, with three genera (*Phyllodistomum, Dendrorchis* and *Gorgotrema*); the Probolitrematinae Yamaguti, 1958 for *Probolitrema* Looss, 1902; and the Xystretrinae Yamaguti, 1958 for *Xystretrum* Linton, 1910. Yamaguti (1971)

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recognized the division of the Gorgoderidae into six subfamilies, the Gorgoderinae, Anaporrhutinae, Phyllodistominae, Plesiochorinae, Probolitrematinae and Xystretrinae, but did not recognize the 'Phyllodistomatinae' as proposed by Pigulevsky (1952), nor did he consider his subgeneric divisions of *Phyllodistomum* or *Gorgodera* sufficiently distinctive as proposed. In addition, the published figures in Pigulevsky (1952) do not appear to agree with the subgeneric distinctions, i.e. the symmetry of the testes in *Postodera* Pigulevsky, 1952 and *Mediodera* Pigulevsky, 1952. Yamaguti (1971) also differed from Pigulevsky (1952, 1953) in the placement of *Gorgoderina* in the Gorgoderinae instead of the Phyllodistominae. *Cetiotrema* Manter, 1970, which Manter (1970) considered a member of the Gorgoderinae along with *Phyllodistomum*, was moved by Yamaguti (1971) to the Phyllodistominae without explanation and despite the fact that the body of *Cetiotrema* is not divided into the two dissimilar regions characteristic of the members of the Phyllodistominae. Serial sections of one of Manter's specimens have provided some further details of *Cetiotrema*. Yamaguti (1971) divided his keys by host group: from fishes, the Gorgoderinae, Xystretrinae, Phyllodistominae, Anaporrhutinae and Probolitrematinae; from amphibians, the Gorgoderinae and Phyllodistominae; and from reptiles the Plesiochorinae. However, the shared morphological features of species from fish and amphibians do not indicate such a distinction.

Gibson (1976) was of the opinion that the anaporrhutine genera found in the body-cavity of elasmobranchs were poorly distinguished and might well be synonymous. In this chapter they are reduced to three genera, *Probolitrema* Looss, 1902, *Anaporrhutum* Brandes in Ofenheim, 1900 and *Petalodistomum* Johnston, 1913, although two others are recognized at the subgeneric level. *Winteria* Lamothe-Argumedo, 1969 (pre-occupied by the fish genus *Winteria* Brauer, 1901) was originally described as having numerous small diverticula of the caeca. The photograph and drawing in Lamothe-Argumedo (1969), however, show undulating caeca with irregular outlines, rather than diverticula. This condition is similar to that found in *Anaporrhutum* (*Staphylorchis*) Travassos, 1922, with which *Winteria* is here synonymized. The diverticulate caeca of *Petalodistomum* are used to distinguish it from *Anaporrhutum* in this key, but the descriptions of this feature vary somewhat and its validity is questionable. Curran *et al.* (2003) recognized five genera, the three genera recognized here plus *Nagmia* and *Staphylorchis*, which have here been treated as subgenera.

Brooks & MacDonald (1986) discussed the relationships in the Gorgoderidae based upon a cladistic analysis of 19 morphological characters of the adults and placed all genera in two subfamilies, the Gorgoderinae and the Anaporrhutinae. This was accompanied by a key to the genera. However, several couplets of the key are not in parallel and several genera were omitted. The possession of a cirrus-sac in gorgoderids was noted by Brooks & MacDonald (1986) in a cladistic analysis of the family and considered ancestral (plesiomorphic) and its absence a loss (apomorphic), making *Degeneria* basal within the family. They suggested that *Phyllodistomum* had no special traits to support it being considered a monophyletic group, probably because adult gorgoderines lack a series of easily discerned apomorphic characters reflecting their phylogenetic history (Cribb, 1987a). Cribb (1987a) proposed that as many as five distinct phylogenetic units may have been grouped under *Phyllodistomum* based upon life-cycle data and proposed that strikingly different life-cycles and cercarial morphology are not associated with indistinguishable adult morphology. Cribb (1987a) pointed to the importance of cercarial anatomy in reflecting phylogenetic history in the gorgoderines, because it combines many adult features with all the structures related to their role in the life-cycle. Most likely, Cribb's axiom is applicable to an accurate phylogenetic treatment of the entire family.

Eleven new genera have been proposed as additions to the family since the synopsis by Yamaguti (1971). *Winteria* was proposed by Lamothe-Argumedo (1969), along with a key to the genera of the Anaporrhutinae. *Nagmioides* Dollfus, 1971 was considered a junior synonym of *Nagmia* by Brooks & Mattis (1978), because the only distinction was the configuration of the

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vitellarium. *Chelatrema* Gupta & Kumari, 1973 was described by Gupta & Kumari (1973) as a hemiurid possessing a pharynx, a single compact vitellarium and a cirrus-sac. *Chelatrema* (Fig. 10.1) appears to be a gorgoderid intestinal fish parasite but should be considered a genus *inquirendum*, in agreement with Gibson & Bray (1979) and Gibson (2002a), until it can be re-examined. *Progorgodera* Brooks & Buckner, 1976, as noted by Prudhoe & Bray (1982), bears 'a very strong morphological resemblance to *Gorgodera*', and undistorted specimens should be collected and examined. The type- and only specimen of *Phyllodistomoides* Brooks, 1977 is distorted, broken and the sac-like genitalia obscured, making details of its true identity questionable. *Degeneria* Campbell, 1977 was described from both living and preserved specimens and the presence of a cirrus-sac confirmed by the examination of serial sections (Fig. 10.20). *Amazonadistoma* Thatcher, 1979 has been retained, although no specimens were available for examination. A paratype of *Pseudophyllodistomum johnstoni* Cribb, 1987 has been illustrated (Fig. 10.12), showing how inconspicuous folding of the lateral margins of the hindbody alters the appearance of the true foliate hindbody form. *Gigantogorgoderina* Machida & Kuramochi, 1994 is a synonym of the hemiuroid *Gonocerca* Manter, 1925 (see Machida & Kamegai, 1997). Most recently, Moravec & Nie (2002) erected the new genus *Neophyllodistomum* Moravec & Nie, 2002 for *Phyllodistomum serrispatula* Chin, 1963 on the basis of the serrate margins of the hindbody, which 'were observed to be permanently present in live trematodes moving freely in physiological saline'. Similar body margins are reported from *Amazonadistoma* Thatcher, 1979, but this genus lacks the coiling of the uterus in the forebody.

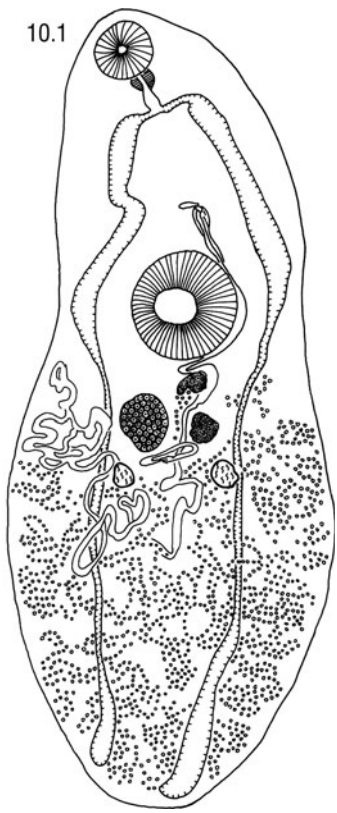



**Fig. 10.1.** *Chelatrema smythi* Gupta & Kumari, 1973, genus *inquirendum*. After Gupta & Kumari (1973).

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## Cladistic analysis

Gorgoderid genera were coded using *Plagiorchis* as the outgroup in an extension of the analysis presented by Brooks & MacDonald (1986). The list of characters used was rechecked from specimens whenever possible and has been modified and extended.

Characters:

**1.** Pharynx present (0); absent (1).
**2.** Form of testes. Compact, paired (0); follicular, dispersed (1); follicular, compact (2).
**3.** Number of testes. Two testes (0), < 10 large follicles (1), > 20 small follicles (2).
**4.** Position of testes. Intercaecal (0); lateral to caeca (1); overlapping caeca (2).
**5.** Structure of vitellarium. Follicular, compact (0); follicular, dendritic, elongate (1); compact, paired (2).
**6.** Position of vitellarium. Lateral to caecal wall (0); extend extracaecally (1).
**7.** Laurer's canal. Present (0); absent (1).
**8.** Cirrus-sac. Present (0); absent (1).
**9.** Caecal structure. Paired, simple (0); cyclocoel (1); paired with diverticula (2).
**10.** Body-shape. Pyriform, foliate (0); elongate, tapered posteriorly (1); elongate, truncate posteriorly (2).
**11.** Uterine configuration. Loops extend extracaecally (0); loops into forebody (1); loops intercaecal only (2).
**12.** Seminal receptacle. Present (0); absent (1).
**13.** Excretory vesicle shape. Y-shaped (0); I-shaped (1); H-shaped (2).
**14.** Hindbody margin. Smooth (0); scalloped (1); either (2).
**15.** Hindbody delineation. Folds absent (0); separated by distinct lateral folds (1).
**16.** Ventral surface of hindbody. Smooth (0); with transverse corrugations (1).
**17.** Pseudosinus-sac. Absent (0); present (1).
**18.** Eversible intromittent organ. Present (0); absent (1).

The plesiomorphic condition is indicated by (0) and derived states by either (1) or (2). Binary characters of Brooks & MacDonald (1986) for testes, vitellarium, caecal structure, body-shape, uterine configuration and shape of the excretory vesicle were treated as single multistate characters. Multistate characters were unordered. The character matrix (see p. 213) consisting of 18 total characters was analysed for 21 genera using PAUP version 4.0b10. A heuristic search resulted in 110 equally parsimonious trees 42 steps in length. The resulting tree was relatively well resolved, revealing two distinct groups distinguished by the presence or absence of a pharynx, position of testes and presence or absence of Laurer's canal, seminal receptacle and cirrus-sac. The results of the cladistic analysis revealed two groups corresponding to and supporting the classical separation of gorgoderids into the subfamilies Gorgoderinae and Anaporrhutinae. The more recently added genera *Phyllodistomoides, Progorgodera, Cetiotrema, Neophyllodistomum, Pseudophyllodistomum* and *Amazonadistoma* cluster with *Gorgodera, Gorgoderina, Gorgotrema, Phyllodistomum, Xystretrum* and *Dendrorchis*, classically included in the Gorgoderinae. *Degeneria* is basal to the remainder of Anaporrhutinae. The distinctions between *Anaporrhutum* and *Staphylorchis* as well as *Petalodistomum* and *Nagmia* are not well resolved, and they are considered distinct only at the subgeneric level.

Additional characters are needed to more completely refine the analysis of the relationships among the gorgoderids. SEM has revealed significant differences in the arrangement of papillae

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on the tegument and ventral sucker, which are deemed useful in generic separation of species of *Gorgoderina* and *Phyllodistomum*. The most acceptable fixation methods for gorgoderid taxonomy were discussed by Bakke (1988) and recommended to be: (i) 10% hot buffered formalin saline; or (ii) Berland's fluid if heat is not available.

Specimens were examined from the collections of the US National Parasite Collection, the British Museum (Natural History) Collection, Manter Laboratory of Parasitology Collection at the University of Nebraska State Museum and the Collecion Autónoma de México. Some specimens were sectioned in paraffin wax to determine internal anatomical details. Many species were redrawn from the literature.

## Glossary

The following terms used in this chapter are defined as follows:

**Pseudosinus-sac**, also **pseudohermaphroditic pouch** *sensu* Yamaguti (1971), a sac-like ending of the genital terminalia in *Xystretrum* (Gorgoderidae), in which the uterine metraterm penetrates but does not unite with the male duct, as in the case of the terminalia of hemiuroid trematodes.

**Fertilization chamber**, 'Befruchlungsraum' of Fuhrmann (1928), a small spindle-shaped expansion of the oviduct, called a seminal receptacle by authors for some species of the Gorgoderinae, i.e. *Gorgodera japonica* Yamaguti, 1934 and *Phyllodistomum* (syn. (*Gorgoderina*) *tanneri* Olson, 1937), but it is always found in the Anaporrhutinae.

**Genital papilla**, part of the terminal genitalia; an eversible muscular structure resembling a cirrus but containing a hermaphroditic duct or separate terminal portions of the male and female ducts; see *Xystretrum*.

## Family Gorgoderidae Looss, 1899

(Syn. Phyllodistomidae Nybelin, 1926)

**Diagnosis:** Body small to large, often flattened, oval, narrow and uniform, or may be divided into distinctively narrower forebody and wider hindbody. Tegument smooth, rarely with scattered spines, sometimes papillate. Suckers well developed. Oral sucker rounded, subterminal. Ventral sucker usually projecting prominently. Prepharynx present or absent. Muscular pharynx present or absent. Oesophagus usually distinct. Intestinal bifurcation in forebody. Caeca simple, rarely diverticulate, sometimes sinuous, reaching near posterior extremity, may unite posteriorly. Testes in hindbody, inter- or extracaecal, or overlapping caeca, symmetrical or asymmetrical, two or more in number. Cirrus-sac or pseudosinus-sac rarely present. Seminal vesicle and pars prostatica usually weakly developed. Genital pore median, between intestinal bifurcation and ventral sucker. Ovary submedian or nearly median, intercaecal, pretesticular, paratesticular or occasionally slightly post-testicular. Seminal receptacle and Laurer's canal present or absent. Uterus in hindbody; first loops descend into hindbody then ascend to genital pore; loops may over-reach caeca or remain confined to intercaecal area. Eggs small, not operculate. Vitellarium in two masses, often lobed or compact, pre-ovarian in hindbody, intercaecal, occasionally extracaecal and pretesticular (*Probolitrema*). Excretory vesicle I-, Y- or sometimes H-shaped; pore terminal or subterminal. In intestine, gall-bladder, body-cavity, urinary-bladder, ureters, swim-bladder of elasmobranchs, teleosts, amphibians and reptiles; cosmopolitan in freshwater and marine environments. Type-genus *Gorgodera* Looss, 1899.

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## Key to subfamilies

**1a. Testes intercaecal; pharynx present or absent; seminal receptacle and cirrus-sac absent; Laurer's canal present or absent ..... Gorgoderinae Looss, 1899.**
**1b. Testes overlap and extend laterally to caeca; pharynx present; seminal receptacle present or absent; cirrus-sac present or absent; Laurer's canal absent ..... ..... Anaporrhutinae Looss, 1901.**

## Subfamily Gorgoderinae Looss, 1899

(Syn. Xystretrinae Yamaguti, 1958)

**Diagnosis:** Body elongate to pyriform or divided into narrow anterior region and foliate hindbody. Suckers in anterior part of body. Oral sucker terminal or subterminal. Ventral sucker smaller than oral sucker or large and protruding from body-surface. Pharynx absent in all except *Phyllodistomoides*. Oesophagus often short. Caeca usually slender, not sinuous, reaching close to posterior extremity, diverticulate in *Amazonadistoma*, unite to form cyclocoel in *Xystretrum*. Gonads intercaecal. Testes two or divided into tandem rows of large follicles. Cirrus-sac absent; pseudosinus-sac present in *Xystretrum*. Ovary pretesticular or paratesticular. Laurer's canal present or absent. Seminal receptacle absent. Uterine loops numerous and usually extend extracaecally, rarely anterior to ventral sucker (*Dendrorchis, Pseudophyllodistomum*). Vitelline masses intercaecal, pre-ovarian, but postovarian in *Amazonadistoma*. Primarily in urinary system of marine and freshwater fish and amphibians; cosmopolitan. Type-genus *Gorgodera* Looss, 1899.

## Key to genera

**1a. Uterine loops in fore- and hindbody ..... 2.**
**1b. Uterine loops entirely in hindbody ..... 5.**

**2a. Pharynx present ..... *Phyllodistomoides* Brooks, 1977. (Fig. 10.2)**
**Diagnosis:** Body pyriform. Oral sucker terminal. Ventral sucker pre-equatorial. Pharynx present. Oesophagus relatively long; caeca end near posterior end of body. Testes two, compact, in hindbody, intercaecal. Cirrus-sac absent (?). Ovary pretesticular, in hindbody, submedian. Seminal receptacle absent. Laurer's canal not observed. Uterus sinuous, with extracaecal loops in hindbody and extending into forebody. Eggs small. Vitellarium in form of two lobed masses, immediately posterior to ventral sucker. Excretory vesicle I-shaped; pore terminal. In swim-bladder of freshwater Neotropical teleost fishes; Colombia. Type-species *P. duncani* Brooks, 1977.

**2b. Pharynx absent ..... 3.**

**3a. Hindbody with distinctly serrate margins ..... ..... *Neophyllodistomum* Moravec & Nie, 2002. (Fig. 10.3)**
**Diagnosis:** Body elongate; forebody narrower than hindbody; hindbody margins with distinct serrate outgrowths. Oral sucker ventral, subterminal. Ventral sucker smaller than oral sucker. Pharynx absent. Intestinal bifurcation in mid-forebody. Caeca terminate blindly near posterior extremity. Testes two, diagonal, irregularly lobed. Cirrus-sac absent. Seminal vesicle present. Genital pore median, just postbifurcal. Ovary submedian, pretesticular, on same side as posterior testis. Uterus mostly intercaecal,

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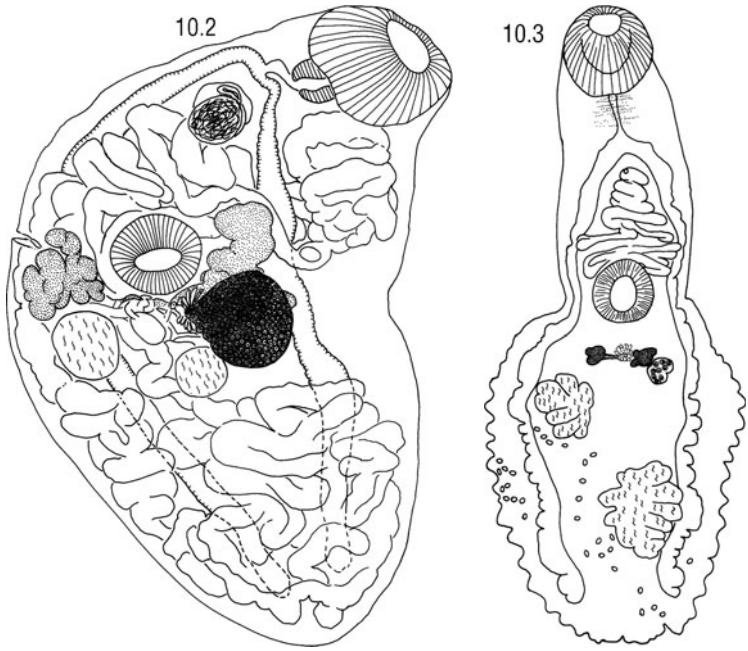



**Fig. 10.2.** *Phyllodistomoides duncani* Brooks, 1977, holotype. Original.
**Fig. 10.3.** *Neophyllodistomum serrispatula* (Chin, 1963). After Chin (1963).

coils in hindbody and forebody. Vitelline masses lobed, paired, between ventral sucker and ovary and anterior testis. Excretory vesicle I-shaped, pore terminal. In ureters of freshwater fish (*Monopterus albus*); China. Type-species *N. serrispatula* (Chin, 1963) Moravec & Nie, 2002.

**3b. Hindbody with smooth margins** ..... **4.**

**4a. Hindbody broad, foliate; uterus extends extracaecally into forebody** ..... ..... ***Dendrorchis* Travassos, 1926. (Fig. 10.4)**

**Diagnosis:** Body pyriform, with smooth margins, flattened; forebody markedly tapered as in *Phyllodistomum*, hindbody broad, foliate. Oral sucker ventral, subterminal. Ventral sucker subequal to oral sucker. Pharynx absent. Intestinal bifurcation closer to oral than to ventral sucker. Caeca approach each other and terminate blindly near posterior extremity. Testes two, diagonal, branched. Cirrus-sac absent; seminal vesicle present. Genital pore submedian, approximately midway between intestinal bifurcation and ventral sucker. Ovary submedian, almost opposite anterior testis. Seminal receptacle absent. Laurer's canal present. Uterus extends into intercaecal and extracaecal fields of hindbody and forebody. Vitelline masses compact, paired, transversely elongate, between ventral sucker and ovary and/or anterior testis. Excretory vesicle I-shaped; pore terminal. In swim-bladder of Neotropical fish (*Brycon lundi*); Brazil. Type-species *D. neivai* Travassos, 1926.

**4b. Hindbody elongate with parallel sides; uterine coils intercaecal, protrude into forebody** ..... ***Cetiotrema* Manter, 1970. (Fig.10.5)**

**Diagnosis:** Body large with almost parallel sides and rounded ends; hindbody elongate, tapered, sides of body thin but remainder of body may be highly muscular, minutely papillose ventrally. Suckers equal or subequal. Oral sucker subterminal. Ventral sucker in anterior fifth of body.

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Pharynx absent. Oesophagus short. Intestinal bifurcation slightly anterior to midway between suckers. Caeca simple, straight, terminate near posterior extremity. Testes two, ovoid, diagonal, intercaecal. Cirrus-sac absent. Seminal vesicle partly anterior to genital pore. Genital pore median, posterior to intestinal bifurcation, approximately midway between suckers. Ovary pretesticular, dextral. Seminal receptacle absent. Laurer's canal not observed. Uterus with narrow coils, mostly intercaecal, occasional loops extend lateral to caeca in postovarian region; several loops intrude into forebody. Eggs with embryos only partly developed. Vitellarium slightly preovarian, intercaecal, divided into two tridigitate clusters of claviform, sometimes branching, lobes united by narrow isthmus. Excretory vesicle Y-shaped; stem extends to level of testes; arms short; pore dorsal, submarginal near posterior extremity. In urinary-bladder or ureters of pelagic marine fishes; off South Australia, Indonesia and Florida, USA. Type-species *C. crassum* Manter, 1970.

**5a. Testes two ..... 6.**
**5b. Testes in form of numerous follicles or seven to nine distinct bodies ..... 10.**

**6a. Intestinal caeca form cyclocoel; pseudosinus-sac present; hindbody corrugated and demarcated by folds ..... *Xystretrum* Linton, 1910. (Figs 10.6–10.10)**
(Syn. *Macia* Travassos, 1921)

**Diagnosis:** Forebody tapered anteriorly; hindbody oval in outline, folded or corrugated. Oral sucker terminal. Ventral sucker medium-sized, pre-equatorial. Pharynx absent. Oesophagus short.

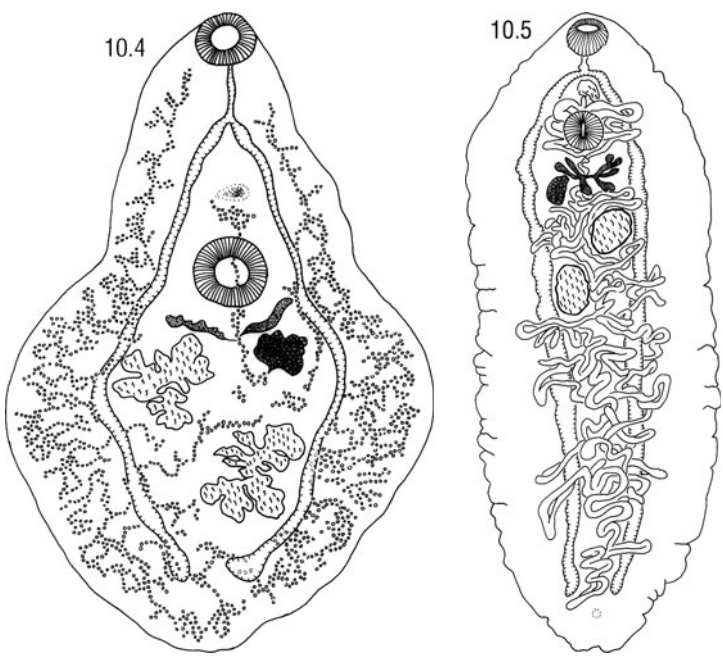



**Fig. 10.4.** *Dendrorchis neivai* Travassos, 1926. After Pigulevsky (1953).
**Fig. 10.5.** *Cetiotrema crassum* Manter, 1970. After Manter (1970).

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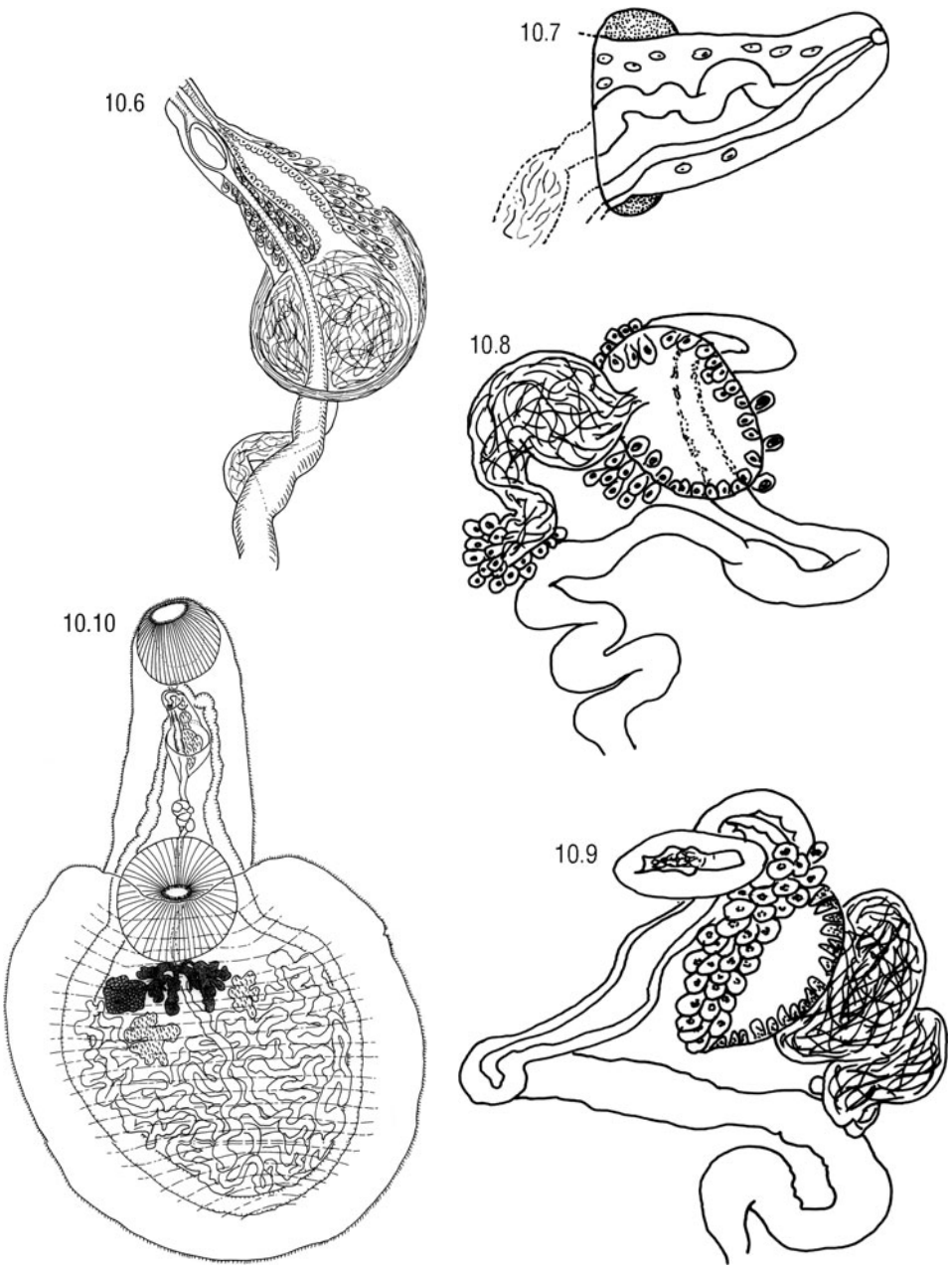



**Fig. 10.6.** Pseudosinus sac of *Xystretrum hawaiiense* Yamaguti, 1970. After Yamaguti (1970).
**Fig. 10.7.** 'Cirrus' of *Xystretrum pulchrum* (Travassos, 1921). After Manter (1970).
**Fig. 10.8.** *Xystretrum moretonense* Manter, 1972. Dorsal view of external seminal vesicle and prostatic vesicle. After Manter (1972).
**Fig. 10.9.** *Xystretrum moretonense* Manter, 1972. Genital pore, metraterm and male terminal genitalia. After Manter (1972).
**Fig. 10.10.** *Xystretrum solidum* Linton, 1910, holotype. Original.

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Caeca united posteriorly forming cyclocoel. Testes two, intercaecal, nearly symmetrical, in broadest part of hindbody. Seminal vesicle tubular. Pseudosinus-sac present. Male duct and uterus enter pseudosinus-sac but do not unite. Cirrus-sac absent; intromittent organ present. Genital pore postbifurcal. Ovary immediately anterior to right testis. Seminal receptacle absent. Uterus confined to intercaecal area of hindbody. Vitelline masses divided into digitiform lobes, paired, between ventral sucker and testes. Excretory vesicle I-shaped; pore dorsal. In urinary bladder of tropical and subtropical marine teleosts; Bermuda, Florida, USA, Mexico, Hawaii, Australia. Type-species *X. solidum* Linton, 1910.

**6b. Intestinal caeca not united posteriorly; pseudosinus-sac absent; hindbody not as above ..... 7.**

**7a. Hindbody margin corrugated, finely scalloped; caeca diverticulate; uterus complex, with coils extending lateral to caeca ..... *Amazonadistoma* Thatcher, 1979. (Fig. 10.11)**

**Diagnosis:** Body cylindrical, becoming slender anteriorly, rounded and flattened posteriorly. Hindbody margins corrugated, finely scalloped. Oral sucker large, subterminal. Ventral sucker large, pre-equatorial. Pharynx absent. Intestinal bifurcation near posterior margin of oral sucker. Caeca long, diverticulate. Testes two, postequatorial, symmetrical or diagonal. Cirrus-sac absent. Seminal vesicle small, sinuous. Genital pore median, between suckers. Genital sucker present. Ovary pretesticular, lateral to midline. Seminal receptacle absent. Mehlis' gland dorsal to vitelline glands. Laurer's canal present. Uterus confined to hindbody, sinuous, complex, with intercaecal and extracaecal loops. Eggs small, numerous. Vitellarium pretesticular, forms two compact symmetrical masses. Excretory vesicle I-shaped, long; pore terminal. In intestine of freshwater fishes; Neotropical region. Type-species *A. negrense* Thatcher, 1979 (emend.).

**7b. Hindbody without corrugated scalloped margin; caeca diverticulate or not; uterus complex or simple, coils intercaecal or extracaecal ..... 8.**

**8a. Uterus simple, with coils intercaecal; excretory vesicle saccular ..... ..... *Pseudophyllodistomum* Cribb, 1987. (Fig. 10.12)**

**Diagnosis:** Body flattened, spatulate, frequently with lateral undulations on hindbody. Ventral sucker equal to or larger than oral sucker. Pharynx absent. Oesophagus present. Caeca reach close to posterior extremity. Testes two, intercaecal, diagonal, margins entire or prominently lobed. Cirrus-sac absent. Seminal vesicle saccular or bipartite, directly dorsal to genital atrium. Ejaculatory duct elongate, convoluted. Genital pore just postbifurcal. Ovary submedian, margins entire or distinctly lobed. Laurer's canal present. Seminal receptacle absent. Uterus intercaecal, consisting of single descending and ascending loop and few secondary loops. Eggs large, embryonated. Vitellarium two compact masses, immediately pre-ovarian, margins entire or slightly lobed. Excretory vesicle I-shaped, saccular, reaching ovarian level; flame-cell formula, $2[(3 + 3 + 3) + (3 + 3 + 3)] = 36$; pore terminal. Cercariae with long tails not enclosing cercarial body, produced in sporocysts in corbiculid bivalves. Metacercariae large, with genitalia often fully developed, in decapod crustaceans. Adults in urinary-bladder of freshwater fishes; Australasia. Type-species *P. johnstoni* Cribb, 1987.

**8b. Uterus complex, with coils extending laterally to caeca; excretory vesicle slender, I-shaped ..... 9.**

**9a. Hindbody slender elongate ..... *Gorgoderina* Looss, 1902. (Fig. 10.13)**
(Syns *Microlecithus* Ozaki, 1926; *Neogorgoderina* Pereira & Cuocola, 1940; *Gorgorimma* Pigulevsky, 1952)

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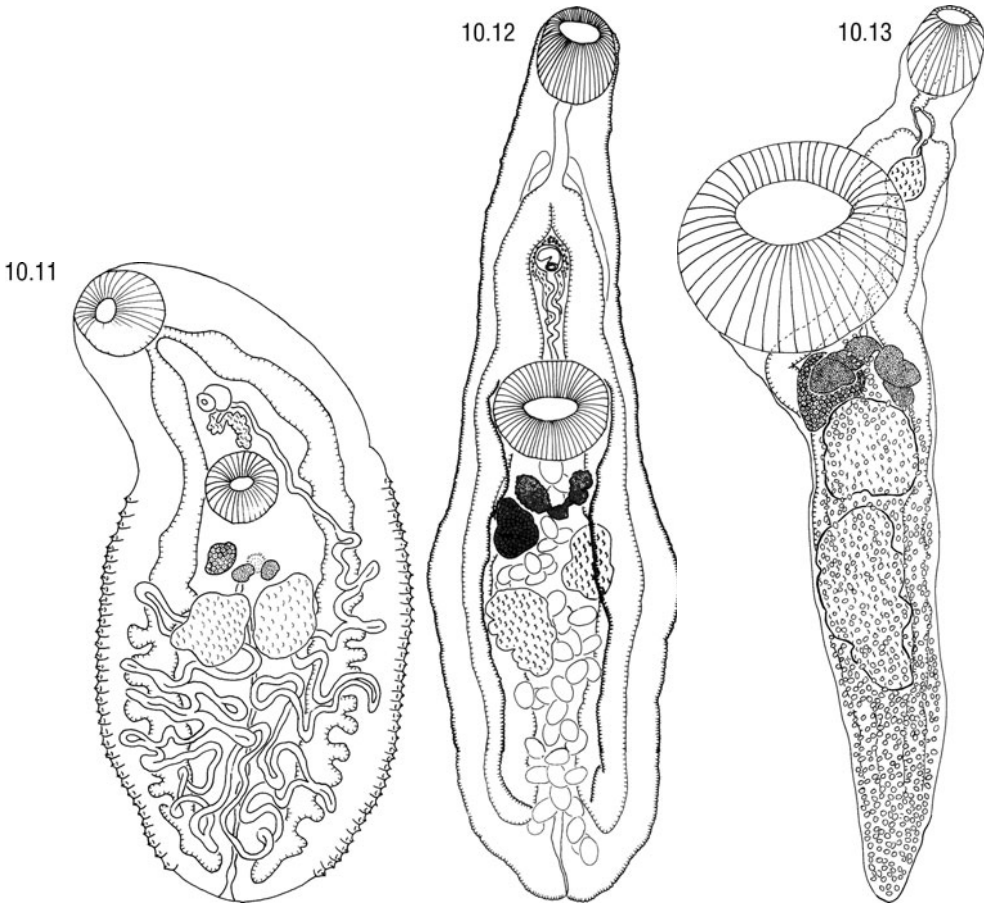


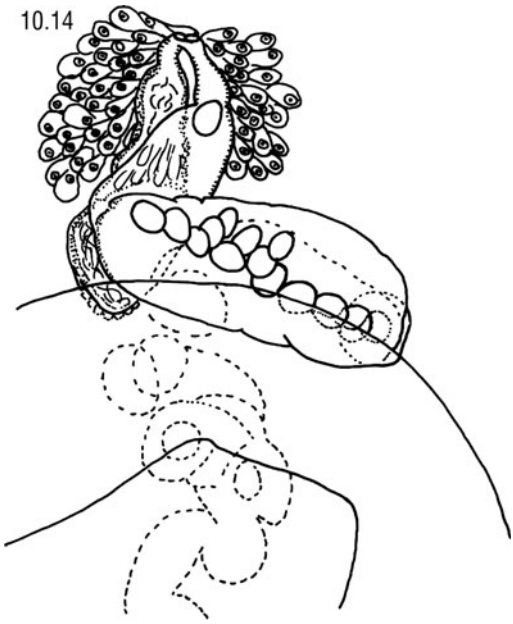

**Fig. 10.11.** *Amazonadistoma negrense* Thatcher, 1979. After Thatcher (1979).
**Fig. 10.12.** *Pseudophyllodistomum johnstoni* Cribb, 1987, paratype. Original.
**Fig. 10.13.** *Gorgoderina attenuata* (Stafford, 1902), syntype. Original.

**Diagnosis:** Body elongate; hindbody slender, elongate. Oral sucker subterminal. Ventral sucker prominent in anterior third of body. Pharynx absent. Oesophagus short. Caeca simple, terminate near posterior extremity. Testes two, intercaecal, postovarian, slightly diagonal. Cirrus-sac absent. Seminal vesicle in forebody. Genital pore median or submedian, immediately postbifurcal. Ovary in middle third of body, submedian. Seminal receptacle absent. Uterine complex, coils occupy most of hindbody, extend lateral to caeca. Eggs embryonated. Vitelline masses compact, smooth or lobed, paired, pre-ovarian. Excretory vesicle slender, I-shaped; pore terminal. In urinary-bladder of amphibians; cosmopolitan. Type-species *G. simplex* (Looss, 1899) Looss, 1902.

**9b. Hindbody broad, foliate ..... *Phyllodistomum* Braun, 1899. (Figs 10.14, 10.15)**
(Syns *Spathidium* Looss, 1899; *Catoptroides* Odhner, 1902; *Vitellarinus* Zmeev, 1936; *Phyllochorus*, Dayal, 1938; *Plesiodistomum* Dayal, 1942)

**Diagnosis:** Forebody tapered; hindbody broad, foliate, with more or less crenulate margin. Oral sucker terminal; mouth ventral. Ventral sucker pre-equatorial. Pharynx absent. Caeca simple,

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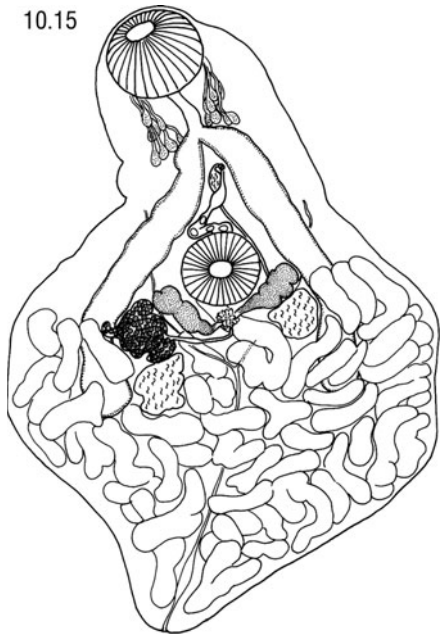




**Fig. 10.14.** Genital terminalia of *Phyllodistomum americanum* Osborn, 1903. After Tiekotter & Coggins (1982).
**Fig. 10.15.** *Phyllodistomum folium* (Olfers, 1816). After Yamaguti (1971).

sinuous, terminate near posterior extremity. Testes two, intercaecal, diagonal or symmetrical, in widest part of hindbody. Cirrus-sac absent. Seminal vesicle submedian, saccate. Genital pore median, between ventral sucker and intestinal bifurcation. Ovary posterior to ventral sucker, submedian, pretesticular. Seminal receptacle absent. Uterus occupies most of available space in hindbody, extends into extracaecal area. Vitellarium masses two, variously lobed. Excretory vesicle slender, I-shaped; pore terminal or subterminal. In urinary-bladder of amphibians and both freshwater and marine fishes, rarely in intestine or body-cavity; cosmopolitan. Type-species *P. folium* (Olfers, 1816) Braun, 1899.

**10a. Testes in form of numerous small follicles dispersed intercaecally ..... ..... *Gorgotrema* Dayal, 1938. (Fig. 10.16)**

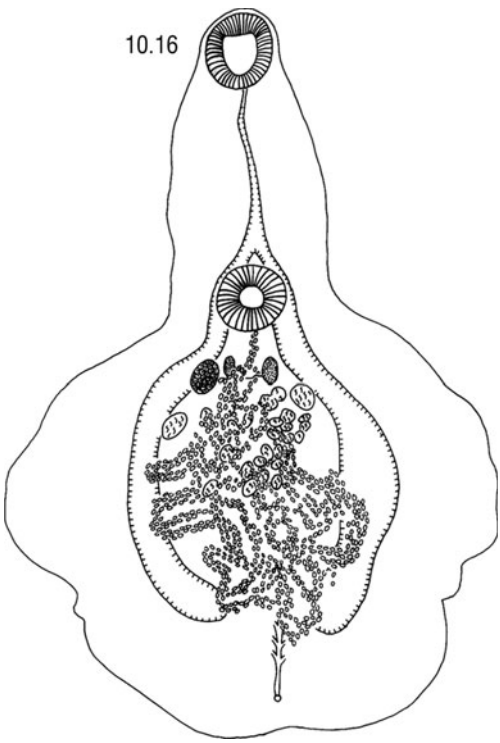
**Diagnosis:** Body flat, divided into anterior elongate, neck-like portion and posterior expanded portion covered with minute scattered spines. Oral sucker terminal, with funnel-shaped cavity. Ventral sucker pre-equatorial. Prepharynx and pharynx absent. Oesophagus long. Caeca simple, wide, terminate short of posterior extremity. Testes numerous, intercaecal, follicular, scattered in anterior half of hindbody. Cirrus-sac absent. Seminal vesicle present. Genital atrium present. Genital pore prebifurcal. Ovary dextral, intercaecal between ventral sucker and testes. Seminal receptacle absent. Laurer's canal not described. Uterine coils intercaecal, post-testicular. Eggs thin-shelled. Vitellarium two unbranched compact symmetrical masses, median, in hindbody, at level of ovary. Excretory vesicle I-shaped with lateral branches, reaches to posterior testes; pore subterminal. In urinary system of teleosts; India. Type-species *G. barbius* Dayal, 1938.

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**10b. Testes in form of seven to nine large bodies ..... 11.**

**11a. Seven testes present; hindbody foliate .....**
**..... *Progorgodera* Brooks & Buckner, 1976. (Figs 10.17, 10.18)**

**Diagnosis:** Forebody tapered anteriorly; hindbody foliate. Oral sucker terminal with subventral aperture. Ventral sucker pre-equatorial. Pharynx absent. Caeca simple, may be sinuous, terminate near posterior end of body. Testes seven, in hindbody, intercaecal, in two longitudinal rows. Seminal vesicle saccate. Cirrus-sac and cirrus absent. Genital pore median, postbifurcal. Ovary



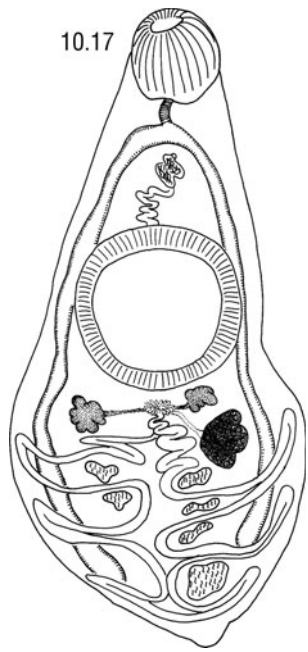







**Fig. 10.16.** *Gorgotrema barbius* Dayal, 1938. After Pigulevsky (1953).
**Figs 10.17, 10.18.** *Progorgodera foliata* Brooks & Buckner, 1976. 10.17. General view. After Brooks & Buckner (1976). 10.18. detail of form of vitelline gland from paratype. Original.

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submedian, pretesticular. Seminal receptacle absent. Laurer's canal present. Uterus occupies most of available space in hindbody. Eggs embryonated. Vitellarium two lobed masses, in hindbody. Excretory vesicle I-shaped; pore terminal. In urinary bladder of amphibians (*Siren*); Illinois, USA. Type-species *P. foliata* Brooks & Buckner, 1976.

**11b. Nine testes present; hindbody elongate ..... *Gorgodera* Looss, 1899. (Fig. 10.19)**
**Diagnosis:** Forebody relatively short; hindbody elongate; lateral margins smooth. Oral sucker subterminal. Ventral sucker prominent, in anterior third of body. Pharynx absent. Oesophagus slender. Caeca simple, terminate at or near posterior extremity. Testes nine, postovarian, intercaecal, round or irregular, in two longitudinal rows or in zigzag row. Cirrus-sac absent. Seminal vesicle in forebody, relatively small. Genital pore median, between ventral sucker and intestinal bifurcation. Ovary median or submedian, near mid-body. Laurer's canal present. Seminal receptacle absent. Uterus in hindbody. Vitellarium two compact or lobed, symmetrical masses, intercaecal, anterior to level of ovary. Excretory vesicle I-shaped; pore terminal. In urinary bladder of amphibians; Eurasia, North America, Africa, Japan, Australia. Type-species *G. cygnoides* (Zeder, 1800) Looss, 1899.

## Subfamily Anaporrhutinae Looss, 1901

(Syns Plesiorchinae Pigulevsky, 1952; Probolitrematinae Yamaguti, 1958)

**Diagnosis:** Body usually rounded (*Anaporrhutum*), rarely elongate (*Bicornuata*) or narrow (*Plesiochorus*), may be divided into narrow anterior region and foliate hindbody (*Degeneria*). Suckers in anterior part of body. Oral sucker ventro-subterminal. Ventral sucker often larger than oral sucker but not voluminous projection from body-surface. Prepharynx very short or absent. Pharynx present. Oesophagus short. Caeca long, often sinuous, enlarged or diverticulate, rarely slender and straight (*Plesiochorus*), reach close to posterior extremity. Gonads not restricted to intercaecal space. Testes two, variously lobed, over-reaching caeca ventrally or divided into numerous follicles distributed partly or entirely laterally to caeca. Cirrus-sac absent in all except *Degeneria*; pseudosinus-sac not reported. Ovary pretesticular, between testes or slightly post-testicular. Laurer's canal absent. Seminal receptacle present or absent. Uterus usually confined to intercaecal space, with few or numerous loops, rarely overlaps caeca laterally or extends anterior to ventral sucker (*Degeneria*). Vitellarium two multilobed to digitiform masses, intercaecal, overlapping caeca or completely lateral to caeca, pre-ovarian in all except *Neoanaporrhutum*. In urinary system of marine fish, body-cavity of selachians and gall-bladder or urinary-bladder of marine turtles; cosmopolitan. Type-genus *Anaporrhutum* Ofenheim, 1900.

## Key to genera

**1a. Cirrus-sac present; uterine loops in forebody, extracaecal ..... ..... *Degeneria* Campbell, 1977. (Figs 10.20, 10.21)**
**Diagnosis:** Body flat; forebody broadly tapered; hindbody foliate. Pre-oral papilla present. Oral sucker ventroterminal, with funnel-shaped cavity. Ventral sucker equatorial, protuberant. Prepharynx undetermined. Pharynx present. Oesophagus short. Caeca simple, terminate near posterior extremity. Testes two, in mid-region of hindbody, symmetrical, lobed, overlap caeca. Cirrus-sac present in forebody, containing seminal vesicle, prostatic cells and short ejaculatory duct. Genital pore postbifurcal. Ovary submedian, pretesticular. Seminal receptacle large, inter-

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testicular. Uterine loops occupy all available space in hindbody and extend laterally beyond caeca to various levels in forebody. Eggs large, embryonated. Vitellarium intercaecal, paired masses, symmetrical, lobed, immediately posterior to ventral sucker. Excretory vesicle Y-shaped, bifurcates between testes; arms short; pore terminal. In urinary system of deep-water marine teleosts (*Halosauropsis*); North Atlantic Ocean. Type-species *D. halosauri* (Bell, 1887) Campbell, 1977.

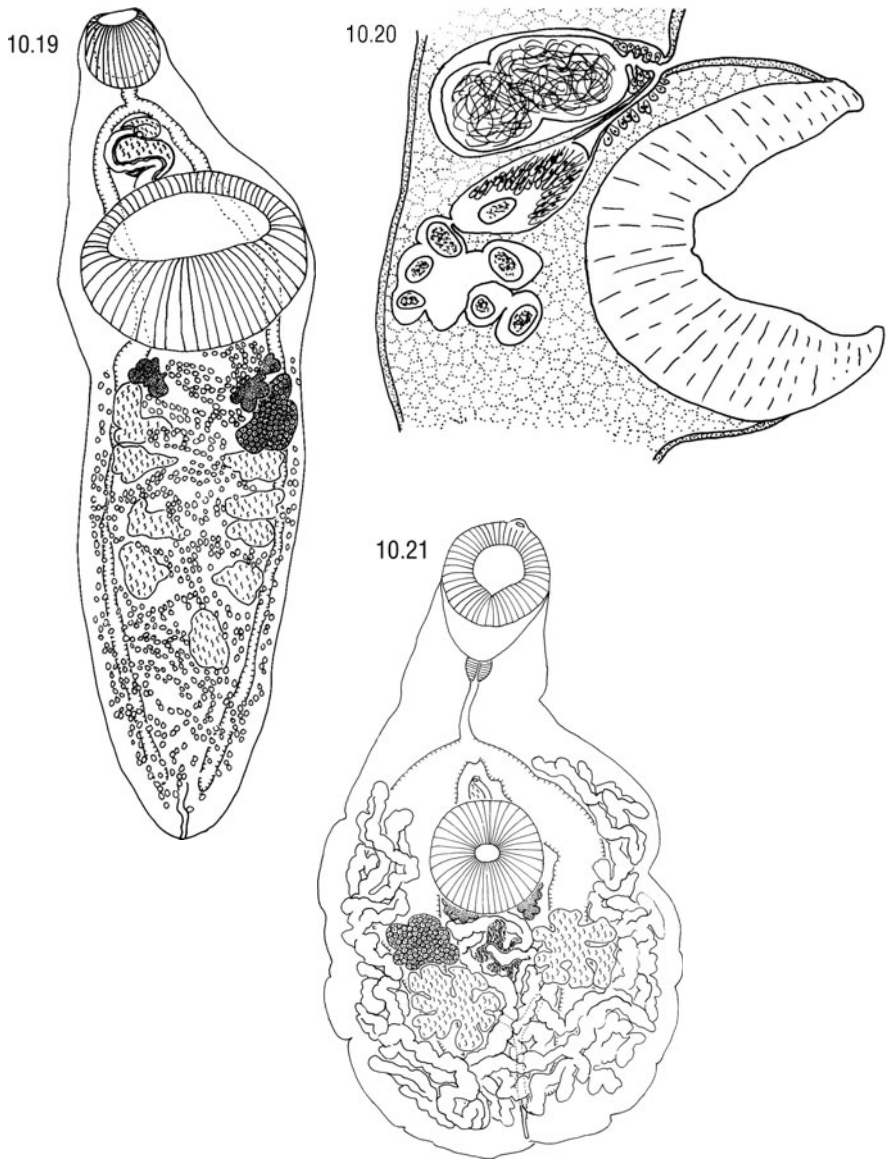



**Fig. 10.19.** *Gorgodera amplicava* Looss, 1899, syntype. Original.
**Fig. 10.20.** Cirrus-sac in sagittal section of *Degeneria halosauri* Campbell, 1977. After Campbell (1977).
**Fig. 10.21.** *Degeneria halosauri* Campbell, 1977. After Campbell (1977).

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**1b. Cirrus-sac absent; uterine loops in hindbody, intercaecal ..... 2.**

**2a. Vitellarium extends extracaecally ..... 3.**
**2b. Vitellarium does not extend extracaecally ..... 5.**

**3a. Body truncate posteriorly, bearing two large posterolateral papillae ..... ..... *Bicornuata* Pearse, 1949. (Fig. 10.22)**

**Diagnosis:** Body stout, truncate posteriorly, with two large finger-like posterolateral papillae. Oral sucker large. Ventral sucker pre-equatorial, relatively large, with two lateral papillae on internal margin of rim. Prepharynx short. Pharynx present. Oesophagus short. Caeca almost reach posterior extremity. Testes two, in mid-hindbody, branched, symmetrical, overlap caeca and extend extracaecally. Seminal vesicle tubular, winding, dorsal to ventral sucker. Cirrus-sac absent. Genital pore median, immediately anterior to ventral sucker. Ovary immediately posterior to ventral sucker, lobate, sinistral. Uterus mostly intercaecal; loops cross caeca when gravid and extend to near posterior end. Eggs ellipsoidal, small. Vitellarium two symmetrical lobed masses immediately posterolateral to ventral sucker, extends extracaecally. Excretory vesicle tubular, I-shaped; pore terminal. In gall-bladder of marine turtles; western North Atlantic Ocean. Type-species *B. caretta* Pearse, 1949.

**3b. Body not truncate posteriorly, lacks posterolateral papillae ..... 4.**

**4a. Body broadly oval; testes form two large groups of follicles; uterus intercaecal ..... ..... *Probolitrema* Looss, 1902. (Fig. 10.23)**

**Diagnosis:** Body large, rounded to lanceolate, flat or somewhat concave ventrally and convex dorsally, pointed anteriorly, broad and rounded posteriorly. Oral sucker large. Ventral sucker pre-equatorial. Prepharynx undetermined. Pharynx present. Oesophagus present. Caeca with or without diverticula, terminate near posterior extremity. Testes two, subdivided into numerous follicles forming longitudinal bands in extracaecal areas of hindbody. Cirrus-sac absent. Seminal vesicle median, between ventral sucker and intestinal bifurcation; anterior region surrounded by prostatic cells. Genital pore just postbifurcal. Ovary in hindbody, submedian, compact. Seminal receptacle present. Uterine loops occupy bulk of intercaecal space in hindbody. Vitellarium two dendritic masses, branches may anastomose, pretesticular, extracaecal. Excretory pore subterminal. Excretory vesicle Y-shaped. In body-cavity of sharks and rays; cosmopolitan. Type-species *P. richiardii* (Lopez, 1888) Looss, 1902.

**4b. Body elongate, slender anteriorly, hindbody wider and tapering; testes two; uterine coils extend laterally to caeca ..... *Plesiochorus* Looss, 1901. (Fig. 10.24)**

**Diagnosis:** Body elongate; forebody narrow; hindbody broader and tapered; maximum width at mid-hindbody. Oral sucker large. Ventral sucker large, at junction of two body-regions. Prepharynx undetermined. Pharynx present. Oesophagus short. Caeca simple, reach close to posterior extremity. Testes two, lobate, symmetrical, in anterior part of hindbody, overlap and extend lateral to caeca ventrally. Cirrus-sac absent. Seminal vesicle convoluted, anterodorsal to ventral sucker. Pars prostatica delimited. Ovary lobate, between ventral sucker and right or left testis. Seminal receptacle present. Uterine coils occupy inter- and pretesticular regions, extend beyond caeca laterally. Vitellarium two compact masses, lobed or not, symmetrical, pretesticular, posterolateral to ventral sucker, extends extracaecally. Excretory pore subterminal. Excretory vesicle Y-shaped; stem bifur-

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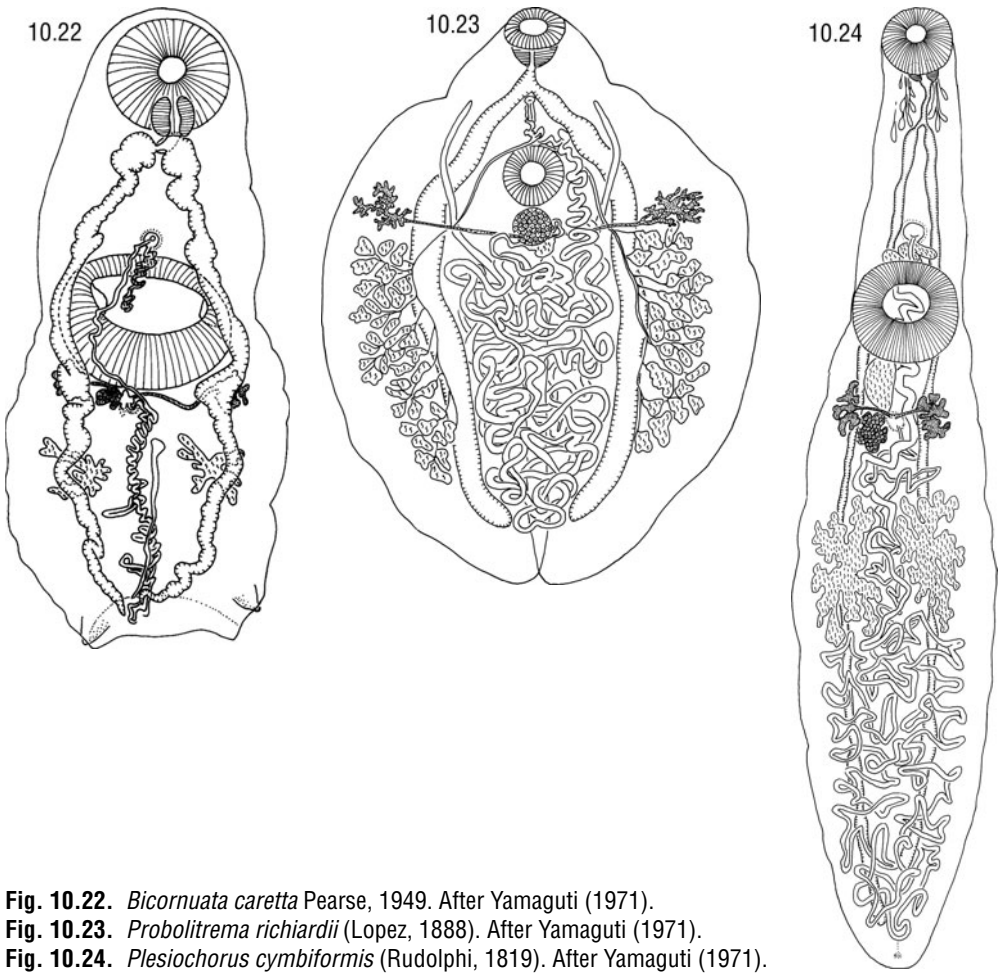



**Fig. 10.22.** *Bicornuata caretta* Pearse, 1949. After Yamaguti (1971).
**Fig. 10.23.** *Probolitrema richiardii* (Lopez, 1888). After Yamaguti (1971).
**Fig. 10.24.** *Plesiochorus cymbiformis* (Rudolphi, 1819). After Yamaguti (1971).

cates between testes; arms extend to level of pharynx or oral sucker; pore subterminal. In urinary-bladder of marine turtles; mid-Atlantic, Pacific and Mediterranean. Type-species *P. cymbiformis* (Rudolphi, 1819) Looss, 1901.

**5a. Caeca without diverticula** ..... ..... ***Anaporrhutum* Brandes in Ofenheim, 1900. (Figs 10.25–10.27)**

(Syns *Staphylorchis* Travassos, 1922; *Winteria* Lamothe-Argumedo, 1969 *nec* Brauer, 1901)

**Diagnosis:** Body large; hindbody broad, rounded posteriorly. Oral sucker large. Ventral sucker comparatively large, near anterior extremity. Prepharynx short. Pharynx muscular. Oesophagus short. Intestinal caeca sinuous, without diverticula. Testes in two groups of spherical follicles distributed partly intercaecally and partly extracaecally, or extracaecally in hindbody. Cirrus-sac absent. Seminal vesicle in forebody, conspicuous, sinuous. Genital pore median near intestinal bifurcation and/or pharynx. Ovary submedian, anterior to testes. Seminal receptacle large. Uterus intercaecal. Vitelline glands follicular or dendritic, ventral and intracaecal. Excretory vesicle with

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long lateral branches resembling mesostomate H-shape, or I-shaped; pore terminal. In pericardium and body-cavity of elasmobranch fishes; Indo-Pacific and Red Sea. Type-species *A. albidum* Brandes in Ofenheim, 1900.

## Key to subgenera

**1a. Caeca slightly sinuous; testes in form of numerous small follicles distributed across both intercaecal and extracaecal space ..... ..... *A.* (*Anaporrhutum*) Brandes in Ofenheim, 1900 (Fig. 10.25).**

**Diagnosis:** Body broadly oval, but somewhat constricted and conical anteriorly. Caeca slightly sinuous. Testes distributed inter- and extracaecally in anterior half of hindbody. Type-species *A. (Anaporrhutum) albidum* Brandes in Ofenheim, 1900.

**1b. Caeca strongly sinuous; testes in form of numerous small follicles distributed in extracaecal space ..... *A.* (*Staphylorchis*) Travassos, 1922.[1] (Figs 10.26, 10.27)**
(Syn. *Winteria* Lamothe-Argumedo, 1969)

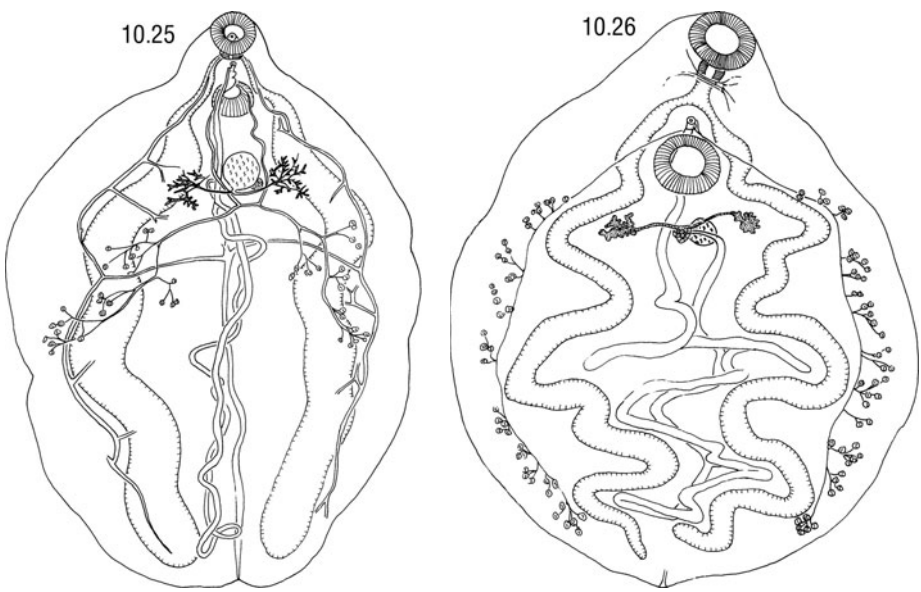



**Fig. 10.25.** *Anaporrhutum (Anaporrhutum) albidum* Brandes in Ofenheim, 1900. After Pigulevsky (1953).
**Fig. 10.26.** *Anaporrhutum (Staphylorchis) cymatodes* (Johnston, 1913). After Pigulevsky (1953).

[1] *Staphylorchis* was considered a subgenus of *Petalodistomum* by Pigulevsky (1952); it is retained here as a subgenus of *Anaporrhutum* in agreement with Brooks & MacDonald (1986).

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**Diagnosis:** Body broadly oval. Caeca strongly sinuous. Testes distributed extracaecally throughout entire length of hindbody. Type-species *A. (Staphylorchis) cymatodes* (Johnston, 1913) Travassos, 1922.

**5b. Caeca with numerous short diverticula ..... ..... *Petalodistomum* Johnston, 1913. (Figs 10.28–10.30)**
(Syns *Nagmia* Nagaty, 1930; *Pernagmia* Nagaty & Abdel-Aal, 1961; *Nagmioides* Dollfus, 1971; *Neoanaporrhutum* Gupta & Tiwari, 1985)

**Diagnosis:** Body broad, flattened. Oral sucker smaller than ventral sucker. Ventral sucker preequatorial. Prepharynx lacking. Pharynx present. Oesophagus short. Caeca with numerous irregular branches, terminate near posterior extremity. Testes in two follicular masses, extracaecal or mainly extracaecal, in widest part of hindbody. Seminal vesicle present. Cirrus-sac absent. Genital pore immediately postbifurcal. Ovary submedian, posterodorsal to ventral sucker. Seminal receptacle large. Uterus intercaecal. Vitellarium multilobed, in two follicular, paired, masses, intercaecal or mainly intercaecal, at or just posterior to ovarian level. Excretory vesicle I-shaped; pore terminal. In body-cavity of rays; off Australia and Mexico and in Arabian Sea. Type-species *P. polycladum* Johnston, 1913.

## Key to subgenera

**1a. Testes divided into several large masses, may be lobed ..... ..... *P.* (*Petalodistomum*) Johnston, 1913. (Fig. 10.28)**

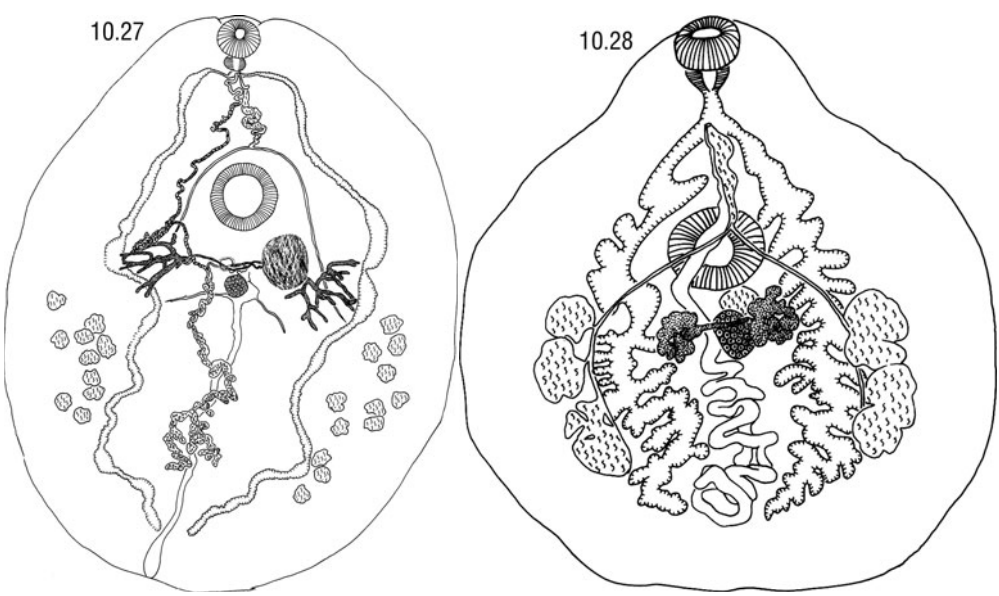


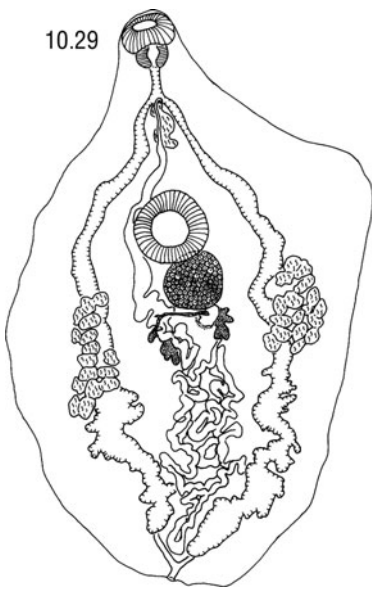

**Fig. 10.27.** *Anaporrhutum (Staphylorchis) pacificum* (Caballero, 1945) n. comb. paratype. Original.
**Fig. 10.28.** *Petalodistomum (Petalodistomum) polycladum* Johnston, 1913. After Yamaguti (1971).

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**Diagnosis:** Testicular follicles massive, may be lobed, in tandem pairs. Type-species *P. (Petalodistomum) polycladum* Johnston, 1913.

**1b. Testes divided into numerous small follicles in form of two condensed grape-like clusters ..... *P.* (*Nagmia*) Nagaty, 1930.**[2] **(Fig. 10.30)**
(Syns *Pernagmia* Nagaty & Abdel-Aal, 1961; *Nagmioides* Dollfus, 1971; *Neoanaporrhutum* Gupta & Tiwari, 1985)

**Diagnosis:** Testes form grape-like clusters of irregular small follicles joined by branching ducts. Type-species *P.* (*Nagmia*) *yorkei* Nagaty, 1930.



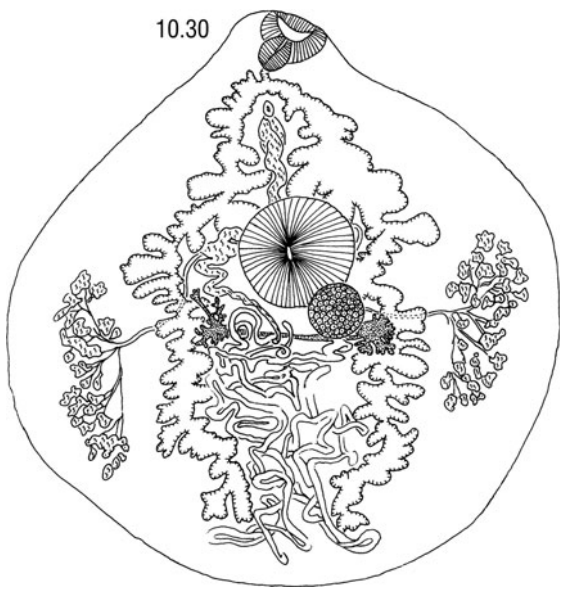




**Fig. 10.29.** *Petalodistomum* (*Nagmia*) *hanumanthai* (Gupta & Tiwari, 1983) n. comb. After Gupta & Tiwari (1983).
**Fig. 10.30.** *Petalodistomum* (*Nagmia*) *yorkei* (Nagaty, 1930) Johnston, 1934. After Yamaguti (1971).

[2] Considered a subgenus of *Petalodistomum* following Brooks & MacDonald (1986).

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## Appendix 10.1.

Matrix of morphological characters for the Gorgoderidae. Codes: 0, the plesiomorphic or primitive state; 1, 2 and 3 identify derived traits; ? = not known.

| | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 | 15 | 16 | 17 | 18 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Ancestor* | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Phyllodistomoides* | 0 | 0 | 0 | 0 | 0 | 0 | ? | 1 | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 1 |
| *Neophyllodistomum* | 1 | 0 | 0 | 0 | 2 | 0 | ? | 1 | 0 | 0 | 1 | ? | 1 | 1 | 0 | 0 | 0 | 1 |
| *Dendrorchis* | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 1 |
| *Xystretrum* | 1 | 0 | 0 | 0 | 2 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 1 | 0 | 1 | 1 | 1 | 0 |
| *Gorgotrema* | 1 | 1 | 2 | 0 | 2 | 0 | ? | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 1 |
| *Phyllodistomum* | 1 | 0 | 0 | 0 | 2 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 1 | 2 | 0 | 0 | 0 | 1 |
| *Progorgodera* | 1 | 0 | 1 | 0 | 2 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 1 |
| *Gorgodera* | 1 | 0 | 2 | 0 | 2 | 0 | 0 | 1 | 0 | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 1 |
| *Gorgoderina* | 1 | 0 | 0 | 0 | 2 | 0 | 0 | 1 | 0 | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 1 |
| *Degeneria* | 0 | 0 | 0 | 2 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 |
| *Plesiochorus* | 0 | 0 | 0 | 2 | 0 | 1 | 1 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 |
| *Bicornuata* | 0 | 0 | 0 | 1 | 0 | 1 | 1 | 1 | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 |
| *Probolitrema* | 0 | 2 | 2 | 1 | 1 | 1 | 1 | 1 | 0 | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 1 |
| *Anaporrhutum* | 0 | 2 | 2 | 2 | 1 | 0 | 1 | 1 | 0 | 0 | 2 | 0 | 2 | 0 | 0 | 0 | 0 | 1 |
| *Staphylorchis* | 0 | 2 | 2 | 1 | 1 | 0 | 1 | 1 | 0 | 0 | 2 | 0 | 2 | 0 | 0 | 0 | 0 | 1 |
| *Petalodistomum* | 0 | 2 | 2 | 1 | 1 | 0 | 1 | 1 | 2 | 0 | 2 | 0 | 1 | 0 | 0 | 0 | 0 | 1 |
| *Nagmia* | 0 | 2 | 2 | 1 | 1 | 0 | 1 | 1 | 2 | 0 | 2 | 0 | 1 | 0 | 0 | 0 | 0 | 1 |
| *Pseudophyllodistomum* | 1 | 0 | 0 | 0 | 2 | 0 | 0 | 1 | 2 | 0 | 2 | 1 | 1 | 0 | 0 | 0 | 0 | 1 |
| *Cetiotrema* | 1 | 0 | 0 | 0 | 2 | 0 | ? | 1 | 0 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 1 |
| *Amazonadistoma* | 1 | 0 | 0 | 0 | 2 | 0 | 0 | 1 | 2 | 0 | 0 | 1 | 1 | 1 | 0 | 1 | 0 | 1 |

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# 11 Family Anchitrematidae Mehra, 1935

T. Pojmańska

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## Introduction

The family Anchitrematidae Mehra, 1935 includes two genera, *Anchitrema* Looss, 1899 and *Mujibia* Bilqees & Kaikobad, 1972, with few species, from the intestine of reptiles and bats in Asia and Africa. These genera resemble the Dicrocoeliidae Looss, 1899 in the general pattern of their adult morphology, but differ mainly by the extracaecal or postcaecal position of the testes, the poor development of the cirrus-sac and the structure of the excretory system.

The first family-group name, erected for *Anchitrema*, was the subfamily Anchitreminae Mehra, 1935, created by Mehra (1935) and placed in the family Dicrocoeliidae. This subfamily was suppressed by Skarbilovich (1948), who transferred *Anchitrema* to the subfamily Lecithodendriinae Looss, 1902 in the family Lecithodendriidae Looss, 1902. Yamaguti (1958b) returned to the concept of Mehra, placing *Anchitrema* in a separate subfamily within the Dicrocoeliidae and emending the subfamily name to Anchitrematinae. Caballero y C. (1961b) raised this to family level, as the Anchitremidae, based on the original name Anchitreminae. Skrjabin (1966b) accepted the separate family status for *Anchitrema*, with the name Anchitrematidae. This name, also adopted by Odening (1968b, 1971) and Yamaguti (1971), is that currently used in the literature.

## Family Anchitrematidae Mehra, 1935

**Diagnosis:** Body stout, elongate. Suckers in anterior third of body, relatively small, oral slightly larger than ventral. Pharynx muscular. Oesophagus very short or absent. Intestinal bifurcation in anterior forebody. Caecal length varies. Testes longitudinally oval, just posterior to ventral sucker, symmetrical, lateral. Cirrus-sac small, anterior to ventral sucker, enclosing convoluted seminal vesicle. Genital pore median, between ventral sucker and intestinal bifurcation. Ovary median, posterior to testes. Canalicular seminal receptacle. Laurer's canal present. Uterus with both descending and ascending limbs strongly coiled, occupies hindbody posterior to testes. Eggs small, numerous. Vitellarium composed of fine follicles in two narrow lateral bands, descending from

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level of posterior margin of testes and not reaching posterior extremity. Excretory vesicle Y-shaped, with long arms; flame-cell formula (known for *Anchitrema* only): 2[(3 + 3 + 3) + (3 + 3 + 3)] = 36. Development not known. In intestine of reptiles and bats; Asia (India, Pakistan, Philippines) and northern and equatorial Africa (Congo, Egypt, Tunisia). Type-genus *Anchitrema* Looss, 1899.

## Key to genera

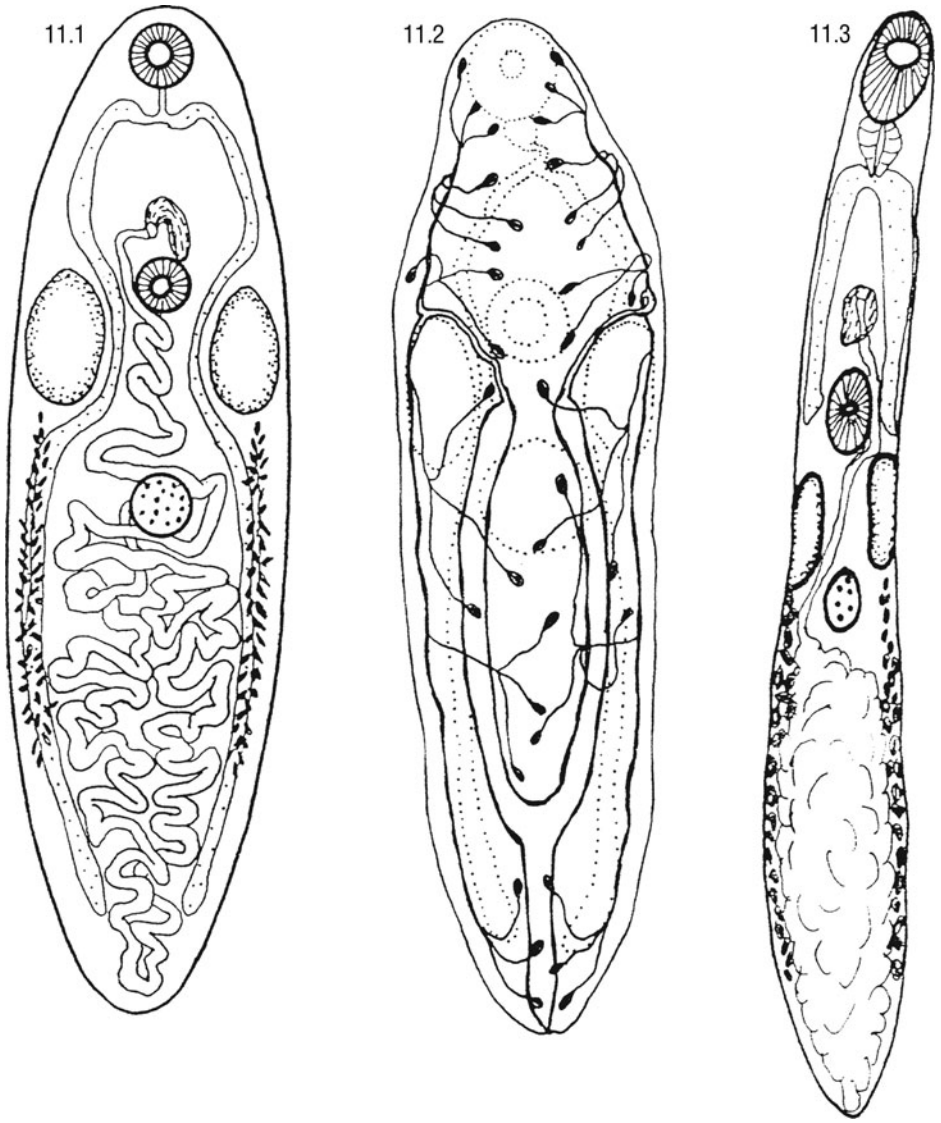
**1a. Caeca long; testes extracaecal** ..... ***Anchitrema* Looss, 1899. (Figs 11.1, 11.2)**
(Syn. *Exorchocoelium* Thapar, 1931)

**Diagnosis**: Body armed with spines. Oesophagus very short or absent. Caeca long, reach close to posterior extremity. Testes entirely or partly extracaecal. Ovary entire, rounded. Vitelline fields extracaecal, or overlapping caeca, not reaching caecal ends. In intestine of reptiles and bats; Asia (India, Philippines) and north and equatorial Africa (Egypt, Congo,Tunisia). Type-species *A. sanguineum* (Sonsino, 1894) Looss, 1899.

**1b. Caeca short; testes posterior to caecal ends** ..... ***Mujibia* Bilqees & Kaikobad, 1972. (Fig. 11.3)**

**Diagnosis:** Body unarmed. Oesophagus absent. Caeca short, terminate at level of ventral sucker. Testes posterior to caecal ends, in extreme lateral position. Ovary longitudinally oval. Vitelline fields do not reach posterior extremity. In intestine of reptiles; Asia (Pakistan). Type-species *M. elongata* Bilqees & Kaikobad, 1972 (emend.).

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**Figs 11.1, 11.2.** *Anchitrema sanguineum* (Sonsino, 1894). 11.1. General view. After Yamaguti (1971). 11.2. Excretory system. After Odening (1968b).
**Fig. 11.3.** *Mujibia elongata* Bilqees & Kaikobad, 1972. After Bilqees & Kaikobad (1972).

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# 12 Family Brachycoeliidae Looss, 1899

T. Pojmańska

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## Introduction

Brachycoeliids are a widespread group found in the intestine, bile-ducts and gall-bladder of amphibians, reptiles and, rarely, mammals. They are generally characterized by short caeca, a pretesticular ovary and small vitelline fields mainly in the forebody or the anterior hindbody. On the occasions where the caeca are relatively long, they do not reach the posterior extremity. The subgeneric name *Brachycoelium* was established by Dujardin (1845) for *Distomum crassicolle* Rudolphi, 1809 (a synonym of *B. salamandrae* (Frölich, 1789)) and raised to full generic status by Stiles & Hassall (1898). Looss (1899) created a new subfamily, the Brachycoeliinae Looss, 1899, for this genus and three other genera, which was placed by Odhner (1910) in the family Dicrocoeliidae Looss, 1899. Johnston (1912) raised the Brachycoeliinae to family status. Over the next few years, some authors accepted the status of subfamily in the Dicrocoeliidae for this group (Travassos, 1921; Fuhrmann, 1928) or Lepodermatidae Looss, 1899 (= Plagiorchiidae Lühe, 1901) (see Cort, 1919; Baer, 1924), while others (Johnston, 1912; Dollfus, 1929, 1930; Faust, 1929, 1932; Cheng, 1960) recognized its family rank. Each of these authors had his own ideas about the set of genera to be included in this family or subfamily. The greatest number of genera (nine) was included by Travassos (1921a), but most were then redistributed into different families by other authors. Dollfus (1930) recognized two subfamilies in the Brachycoeliidae Looss, 1899: the Brachycoeliinae and the Cymatocarpinae Baer, 1924. The latter was raised by Odening (1959b) to family status as the Cymatocarpidae Baer, 1924. Earlier, Dollfus (1929) had removed *Mesocoelium* Odhner 1910 from the Brachycoeliinae and established a separate subfamily, the Mesocoeliinae Dollfus, 1929, for it within the Dicrocoeliidae. Dollfus (1933) also separated the mesocoeliids from the dicrocoeliids, raising the Mesocoeliinae to the status of family. This was accepted by Skrjabin (1963), who recognized three separate families, the Brachycoeliidae, Dicrocoeliidae and Mesocoeliidae, but not by Yamaguti (1958b, 1971), who recognized two subfamilies within the Brachycoeliidae: the Brachycoeliinae and the Mesocoeliinae. On the other hand, Skrjabin (1963) did not accept the creation of a separate family or even subfamily for *Cymatocarpus* Looss, 1899 and affiliated it with the Brachycoeliidae, which he did not subdivide into subfamilies.

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Here, the concept of Skrjabin (1963) is adopted. The mesocoeliids are not included in the Brachycoeliidae, because the features distinguishing these two groups, such as the position of the ovary in relation to the testes, the position of the genital pore, the extent of the vitelline bands and the flame-cell formula (although known for *Brachycoelium* only), are considered family-level characters. No subfamilies are distinguished in the family, as the general plan of morphology is similar for all five genera, and our knowledge of their biology is rather poor.

*Robertdigenea* Caballero & Caballero, 1970, for which Caballero & Caballero (1970) established the separate subfamily Robertdigeninae Caballero & Caballero, 1970 in the Dicrocoeliidae, is included in the Brachycoeliidae on the basis of the position of the ovary in relation to the testes and the size of the cirrus-sac.

## Family Brachycoeliidae Looss, 1899

(Syns Cymatocarpidae Baer, 1924; Cymatocarpinae Baer, 1924; Robertdigeninae Caballero & Caballero, 1970; Brachycoeliinae Looss, 1899)

**Diagnosis:** Body elongate or wide, usually armed. Suckers in anterior third of body, relatively small; ventral usually slightly smaller than oral. Pharynx muscular. Oesophagus present. Intestinal bifurcation in forebody. Caeca usually short, not passing level of gonads, but longer in some species. Gonads posterior to, or (in some *Brachycoelium* species) in region of, ventral sucker, with ovary anterior to testes. Testes symmetrical or diagonal. Cirrus-sac well developed, large, usually passing around ventral sucker on one side, rarely entirely anterior to it, encloses seminal vesicle and pars prostatica. Genital pore posterior to intestinal bifurcation, median or submedian. Ovary submedian, anterior to testes. Laurer's canal and seminal receptacle present. Uterus with strongly coiled descending and ascending limbs, occupies whole hindbody posterior to testes. Eggs numerous, operculate. Vitelline follicles in two lateral bands or clusters in anterior part of body. Excretory vesicle long, I- or Y-shaped with long stem and short arms; pore terminal to subterminal. Flame-cell formula (known for *Brachycoelium* only): $2[3 + 3 + 3) + (3 + 3 + 3)] = 36$. In intestine, bileducts and gall-bladder of amphibians, reptiles and, rarely, mammals; cosmopolitan. Type-genus *Brachycoelium* Dujardin, 1845.

## Key to genera

**1a. Body wide; caeca terminate posterior to testes ..... 4.**
**1b. Body elongate; caeca terminate anterior to or in testicular zone ..... 2.**

**2a. Caeca short, not passing level of ventral sucker; vitelline fields reach level of ovary; distance between ovary and testes small ..... 3.**
**2b. Caeca reach level of testes; vitelline fields reach level of testes; distance between testes and ovary quite large ..... *Tremiorchis* Mehra & Negi, 1926. (Figs 12.1, 12. 2)**
(Syn. *Centrovitus* Bhalerao, 1926)

**Diagnosis:** Body elliptical to lanceolate. Suckers of similar size, or ventral slightly smaller than oral. Oesophagus shorter than caeca. Caeca reach or pass level of anterior testis. Gonads in middle third of body. Testes large, diagonal, distant from ventral sucker and separated from ovary. Cirrus-sac large, falciform, passing around ventral sucker on one side and extending posterior to it. Genital pore

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median or submedian, just anterior to ventral sucker. Ovary submedian. Vitelline follicles form two lateral bands, extending from intestinal bifurcation to caecal ends. Eggs small, numerous. Excretory vesicle Y-shaped, with short arms; stem almost reaches level of ovary. Development unknown. In amphibians and reptiles; Asia (India). Type-species *T. ranarum* Mehra & Negi, 1926.

**3a. Excretory vesicle reaches level of testes; oesophagus relatively short; vitellarium reaches close to oral sucker ..... *Brachycoelium* Dujardin, 1845. (Figs 12.3–12.5)**

**Diagnosis**: Body elongate or fusiform. Oral sucker generally larger than ventral. Pharynx small. Oesophagus may be shorter or longer than caeca. Caeca short, in form of inverted V, anterior to ventral sucker in most species, sometimes reaching its level but never surpassing it. Gonads in anterior half of body. Testes symmetrical or slightly diagonal, in most cases posterior to ventral sucker, sometimes overlapping it. Cirrus-sac relatively small, anterior to or overlapping ventral sucker. Genital pore between intestinal bifurcation and ventral sucker. Ovary submedian, anterior to one testis, usually at level of ventral sucker, rarely anterior or posterior to it. Vitelline follicles forming two wide lateral bands or clusters, sometimes almost confluent in midline, extending from level of pharynx to level of ovary. Size and number of eggs vary. Excretory vesicle with long stem reaching level of testes, sometimes with short arms; main collecting canals arise subapically from stem or from apices of arms. In known life-cycles, two intermediate hosts are involved, both terrestrial molluscs. Cercaria of xiphidiocercaria type, tailless or with stumpy tail; metacercaria unencysted, in body-cavity of second intermediate host. In amphibians and reptiles; Europe, North Africa (Egypt), North America (USA, Canada). Type-species *B. salamandrae* (Frölich, 1789) Lühe, 1909.

**3b. Excretory vesicle reaches level of pharynx; oesophagus long; vitellarium distant from oral sucker ..... *Cymatocarpus* Looss, 1899. (Figs 12.6, 12.7)**

**Diagnosis:** Body linguiform. Suckers of similar size or oral slightly larger than ventral; ventral sucker almost equatorial. Pharynx small. Oesophagus long. Caeca short, sacciform, divergent, not reaching level of ventral sucker. Gonads posterior to ventral sucker. Testes slightly diagonal. Cirrus-sac large, falciform, passes ventral sucker on one side, reaching well posterior to it; cirrus stout, armed with spines. Genital pore median, anterior to ventral sucker. Ovary lateral, on same side as posterior testis, distant from ventral sucker. Vitelline bands extend from middle of oesophagus to level of ovary. Uterus strongly coiled, descending on ovarian side and ascending on opposite side of body; terminal part forms large metraterm. Eggs small, numerous. Excretory vesicle I-shaped, very long, reaching level of pharynx; main collecting ducts arise at level of testes. Metacercaria known from crabs (*Pagurus*). In reptiles (turtles); Egypt and New Guinea. Type-species *C. undulatus* Looss, 1899.

**4a. Caecal ends distant from posterior extremity; genital pore posterior to ventral sucker; vitellarium anterior to intestinal bifurcation ..... ..... *Iquitos* Mañé-Garzón & Gil, 1963. (Fig. 12.8)**

**Diagnosis:** Body broad, flattened. Suckers well developed, of about equal size. Pharynx muscular. Oesophagus short. Caeca reach into posterior half of body but terminate well short of posterior extremity. Testes symmetrical, between caecal ends. Cirrus-sac very large, falciform, with both extremities posterior to ventral sucker, tending to curve around it. Genital pore submedian, posterior to ventral sucker. Ovary submedian, just anterior to one testis. Vitelline follicles form two lateral, extracaecal clusters, anterior to ventral sucker. Laurer's canal not observed. Uterus strongly coiled, descending on ovarian side and ascending on opposite side of body, occupies hindbody posterior to testes. Excretory vesicle Y-shaped, with short arms. In intestine of frogs; Peru. Type-species *I. ceii* Mañé-Garzón & Gil, 1963.

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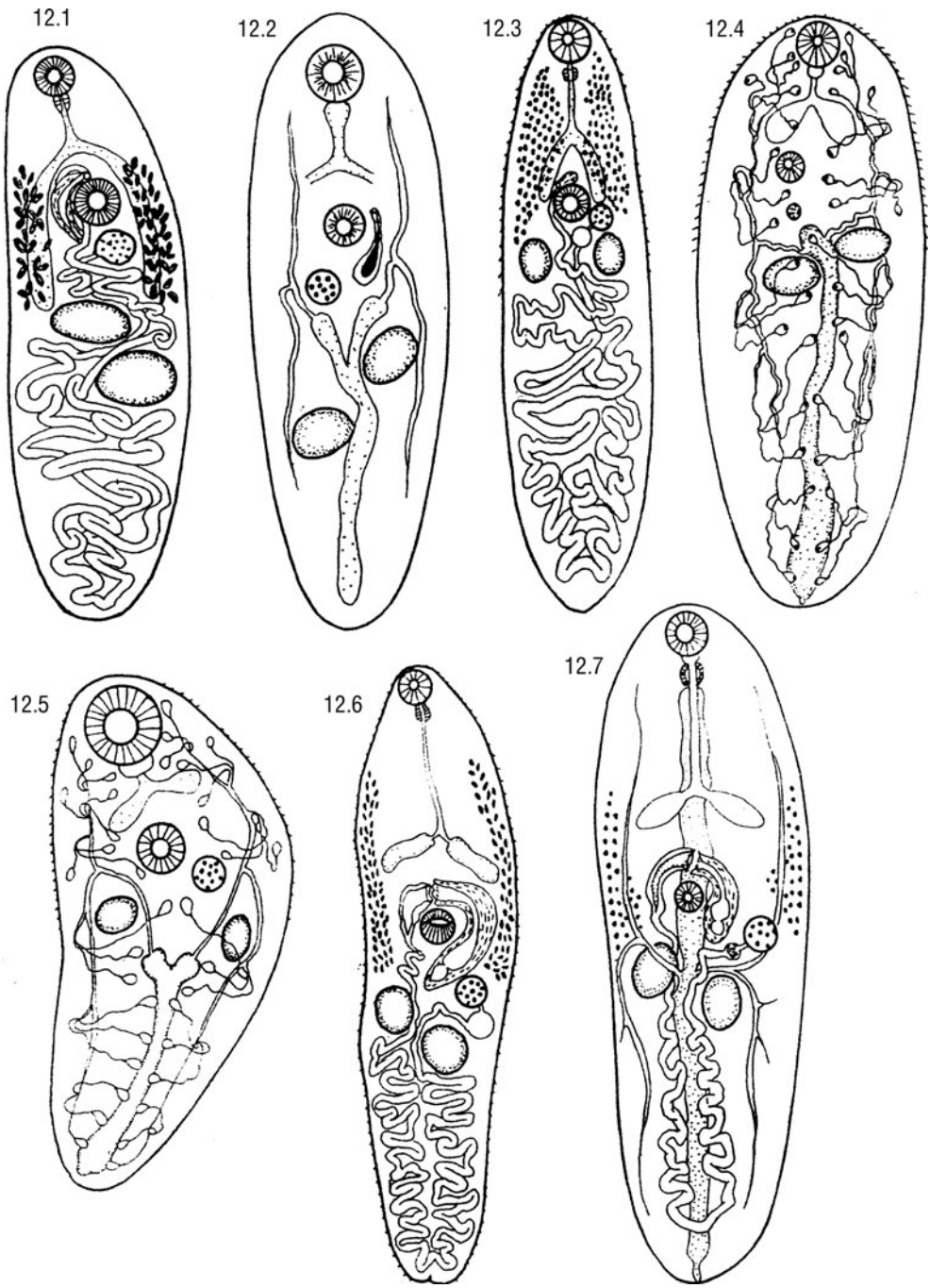



**Fig. 12.1.** *Tremiorchis ranarum* Mehra & Negi, 1926. Ventral view. After Mehra & Negi (1926).
**Fig. 12.2.** *Tremiorchis varanum* Verma, 1930. Excretory system; note main collecting ducts arising from the apices of arms of excretory vesicle. After Verma (1930).
**Fig. 12.3.** *Brachycoelium salamandrae* (Frölich, 1789). General view; note the length of caeca. After Lühe (1909) and Yamaguti (1971).

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**4b. Caeca terminate well into post-testicular region; genital pore anterior to ventral sucker; vitellarium at level of ventral sucker ..... ..... *Robertdigenea* Caballero & Caballero, 1970. (Fig. 12.9)**

**Diagnosis:** Body almost round, unspined. Suckers relatively small, of equal size. Pharynx muscular. Oesophagus relatively long. Caeca long, reaching well into post-testicular region. Testes symmetrical, large, reniform, slightly lobed, posterior to ventral sucker. Cirrus-sac very large, S-shaped, reaches posterior extremity of ventral sucker; cirrus with digitiform papilla. Genital pore submedian, between ventral sucker and intestinal bifurcation. Ovary smaller than testes, submedian, at level of ventral sucker. Vitelline follicles form two extracaecal clusters, at level of ovary and anterior region of testes. Uterus with numerous inter- and extracaecal coils in hindbody. Excretory vesicle V-shaped (? according to original diagnosis of genus, but on the figure of *R. dollfusi* it seems to have a stem). In bile-ducts and gall-bladder of rodents; Central America (Costa Rica). Type-species *R. dollfusi* Caballero & Caballero, 1970.

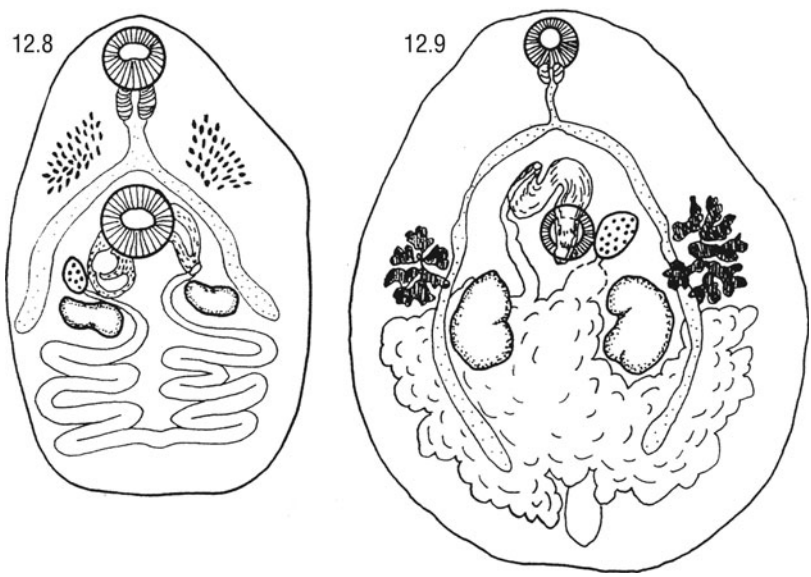



**Fig. 12.8.** *Iquitos ceii* Mañé-Garzón & Gil, 1963. After Mañé-Garzón & Gil (1963).
**Fig. 12.9.** *Robertdigenea dollfusi* Caballero & Caballero, 1970. After Caballero & Caballero (1970).

**Fig. 12.4.** (*Opposite*) *Brachylecithum mesorchium* Byrd, 1937. Excretory system; note the excretory vesicle without arms and main collecting ducts arising near its apex; note also short caeca. After Byrd (1937).
**Fig. 12.5.** (*Opposite*) *Brachycoelium trituri* (Holl, 1958). Excretory system; note the excretory vesicle with short arms and main collecting canals arising from their apices. After Byrd (1937).
**Fig. 12.6.** (*Opposite*) *Cymatocarpus undulatus* Looss, 1899. After Looss (1899) and Yamaguti (1971).
**Fig. 12.7.** (*Opposite*) *Cymatocarpus undulatus* Looss, 1899 metacercaria. Note extent of excretory vesicle and the points of origin of the main collecting ducts. After Dollfus (1927) and Skrjabin (1963).

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# 13 Family Braunotrematidae Yamaguti, 1958

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## Introduction

The Braunotrematidae Yamaguti, 1958 is monotypic. *Braunotrema pulvinatum* (Braun, 1899) Price, 1930 (emend.) is an intestinal parasite of chelonians in Brazil, characterized by paired pulvinate bolsters dorsolaterally at the anterior extremity. Its generic name and systematic position have been changed on several occasions. Odhner (1910) established a new genus, *Thaumatocotyle* Odhner, 1910, for this species, described originally as *Distomum pulvinatum* Braun, 1899. Travassos (1923b) found that the generic name *Thaumatocotyle* was pre-occupied and changed it to *Thaumarhocotyle*. Price (1930a), overlooking the work of Travassos, and for the same reason, replaced the name *Thaumatocotyle* with *Braunotrema*. Regarding the familial affiliation of this genus, Travassos (1923b) attributed it to the family Gorgoderidae Looss, 1901. However, Poche (1926) removed it (using Odhner's designation *Thaumatocotyle*), together with three other genera, from the family Gorgoderidae, to a new family, the Callodistomidae Poche, 1926. This familial affiliation for *Braunotrema* was maintained by Yamaguti (1958b), who separated it in a new subfamily, the Braunotrematinae Yamaguti, 1958. Skrjabin (1959) also placed this genus in the family Callodistomidae (as the Callodistomatidae) but not in a separate subfamily. Later, Yamaguti (1971) raised the Braunotrematinae to full family status (provisionally, because of a lack of information on the biology of these parasites).

According to the principle of priority (ICZN, 1999), the generic name *Thaumarhocotyle* Travassos, 1923 should be re-established, but this appellation appears to have passed unnoticed and has never been used in the parasitological literature. In view of this and to avoid confusion, the name *Braunotrema* Price 1930 is retained here on the grounds of its common usage and the existing familial designation.

## Family Braunotrematidae Yamaguti, 1958

**Diagnosis:** Body elongate, unarmed, with characteristic paired pulvinate bolsters dorsolaterally at anterior extremity. Suckers quite large, of similar size, in anterior half of body. Prepharynx not

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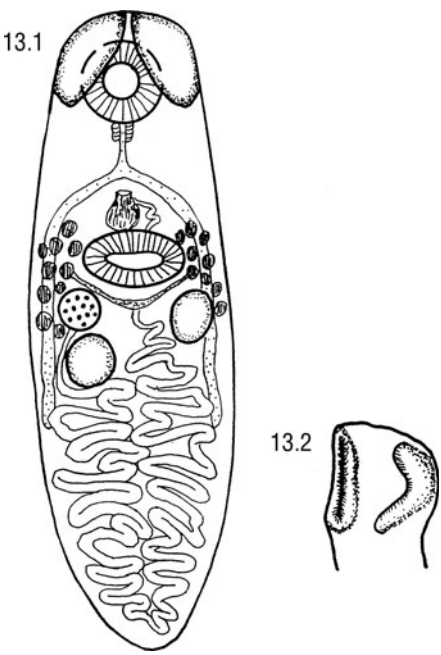

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observed. Pharynx rather small, muscular. Oesophagus distinct. Intestinal bifurcation in mid-forebody. Caeca extend slightly beyond middle of body. Gonads posterior to ventral sucker, with ovary. Testes two, posterior to ventral sucker, diagonal, well separated, intercaecal. Cirrus-sac between ventral sucker and intestinal bifurcation, enclosing seminal vesicle and pars prostatica. Cirrus short. Genital pore median, just posterior to intestinal bifurcation. Ovary submedian on same side and anterior to posterior testis. Seminal receptacle absent. Laurer's canal not observed. Uterus with coiled descending and ascending limbs, occupies hindbody posterior to testes. Eggs small, numerous. Vitellarium composed of few large follicles in two short lateral bands that overlap caeca, from level of anterior margin of ventral sucker to posterior margin of ovary. Excretory vesicle long, I-shaped, reaches testes; pore terminal. Development not known. In intestine of chelonians; Brazil. Type-genus *Braunotrema* Price, 1930.

## ***Braunotrema*** **Price, 1930** (Figs 13.1, 13.2)

(Syns *Thaumatocotyle* Odhner, 1910 *nec* Scott, 1904; *Thaumarhocotyle* Travassos, 1923)

**Diagnosis:** With characters of family. Type-species *B. pulvinatum* (Braun, 1899) Price, 1930 (emend.).




**Figs 13.1, 13.2.** *Braunotrema pulvinatum* (Braun, 1899). 13.1. Dorsal view. 13.2. Anterior extremity, lateral view. After Braun (1901a) and Yamaguti (1971).

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# 14 Family Collyriclidae Ward, 1917

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## Introduction

Collyriclids are distinguished from other members of the Gorgoderoidea Looss, 1899 by the habitat of the adults, i.e. cysts in the skin or intestinal wall of birds and mammals. The two genera included in this family, *Collyriclum* Kossack, 1911 and *Collyricloides* Vaucher, 1969, are also distinctive in the possession of an extraordinarily long Laurer's canal. However, there are some striking differences between these genera, including the presence or absence of a ventral sucker and the excretory pore opening midventrally or terminally. Despite this, the similarities between them, their tissue-dwelling habit, body-shape and size and general arrangement of the internal organs, are such that their inclusion in the same family has never been questioned.

*Collyriclum* was established by Kossack (1911) for *Monostomum faba* Bremser, 1831, which occurs, usually in pairs, in cysts in the skin of birds. It was included by Odhner (1914) in his new family Troglotrematidae Odhner, 1914 along with four other genera: *Troglotrema* Odhner, 1914, *Pholeter* Odhner, 1914, *Renicola* Cohn, 1904 and *Paragonimus* Braun, 1899. Although Ward (1917) proposed a distinct family, the Collyriclidae Ward, 1917, for *Collyriclum*, most taxonomists for the subsequent 20 years or more preferred to retain it in the Troglotrematidae. Dollfus (1939) demonstrated that the Troglotrematidae required redefining and splitting (see Blair *et al*., Chapter 21, this volume). Thereafter, the Collyriclidae was generally accepted as valid and distinct (except by Yamaguti (1958b), who reduced it to subfamily status in the Troglotrematidae).

Vaucher (1969) described *Collyricloides massanae* Vaucher, 1969 from cysts in the intestinal wall of rodents in France. It was subsequently reported from starlings (genus *Sturnus*) in the Netherlands by Borgsteede & Smit (1980). Vaucher regarded his new genus as closest to *Collyriclum* and placed it in the Collyriclidae, requiring the concept of this family to be broadened considerably. The two genera are similar in the general arrangement of organs, in possessing a very long Laurer's canal and in their cyst-dwelling habit. However, unlike *Collyriclum, Collyricloides* possesses both a well-developed cirrus-sac and a ventral sucker. Uniquely, it also possesses a midventral papilla on which open (separately) both the common genital pore and the excretory pore.

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In life, this papilla extends into the opening connecting the worm cyst with the lumen of the intestine (Jourdane & Triquell, 1973).

## Family Collyriclidae Ward, 1917

**Diagnosis:** Body small to medium-sized, hemispherical and flattened ventrally but convex dorsally, or almost spherical. Body-surface bears spines. Oral sucker terminal or subterminal ventral. Ventral sucker present or absent; if present, slightly anterior to equator. Prepharynx absent. Pharynx present. Oesophagus short. Intestinal bifurcation in anterior part of body. Caeca simple, blind, very wide, smooth-walled, not reaching posterior extremity. Testes two, symmetrical, in middle third or third quarter of body, dorsal or lateral to caeca. Cirrus-sac strongly or very weakly developed, contains seminal vesicle and pars prostatica. Genital pore(s) close to median line and to equator, open together or separately on variably developed nipple-like structure. Ovary large, strongly lobed, slightly submedian, largely or entirely pretesticular. Mehlis' gland present. Seminal receptacle present, associated with Laurer's canal or not. Laurer's canal very long, runs in posterodorsal direction, blind or opens on dorsal body-surface. Uterine loops in posterior half of body only, or may occupy most of body. Terminal portion of uterus dilated or not. Eggs small, numerous. Vitellarium follicular, in several lateral or sublateral clusters on each side largely or entirely anterior to testes and may almost reach anterior end of body. Excretory vesicle large, saccate or pyriform; pore terminal or close to genital pore on midventral papilla. Encysted in skin and in wall of digestive tract of birds and mammals; Nearctic, Neotropical, Europe, northern Asia. Type-genus *Collyriclum* Kossack, 1911.

## Key to genera

**1a. Ventral sucker absent ..... *Collyriclum* Kossack, 1911. (Fig. 14.1)**
**Diagnosis:** Body weakly muscled, hemispherical, flat or concave ventrally and convex dorsally, slightly broader than long; breadth increases with age. Tegument covered with regularly spaced clusters of spines. Oral sucker small, terminal or ventro-subterminal. Ventral sucker absent. Intestinal bifurcation in anterior part of body. Caeca sublateral, follow curve of body, terminate about one-quarter of body-length from posterior end. Testes ovoid to pyriform, sometimes irregularly lobed, symmetrical, sublateral, slightly postequatorial, dorsal to caeca. Cirrus-sac small, very weakly developed (sometimes said to be absent), contains small seminal vesicle, pars prostatica and short ejaculatory duct. Separate genital pores almost median, slightly anterior to equator, just posterior to intestinal bifurcation, adjacent to one another on small nipple. Ovary to right of genital pore and mostly or completely anterior to right testis. Mehlis' gland median at level of genital pore. Seminal receptacle formed by one or more outpocketings of Laurer's canal. Laurer's canal extends to about level of posterior edges of testes, where it ends blindly in older specimens. Uterus extensively coiled in posterior half of body; terminal portion expanded and full of eggs. Vitelline follicles grouped anterolateral to each testis into five to nine distinct but adjacent clusters. Excretory vesicle pyriform, voluminous, extends anteriorly to level of ovary; pore terminal, apparently located on flexible nipple. Encysted, usually in pairs, in skin

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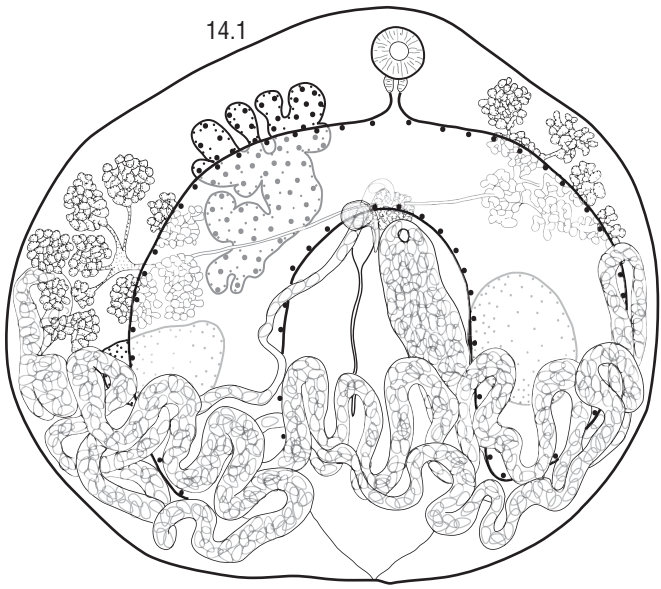
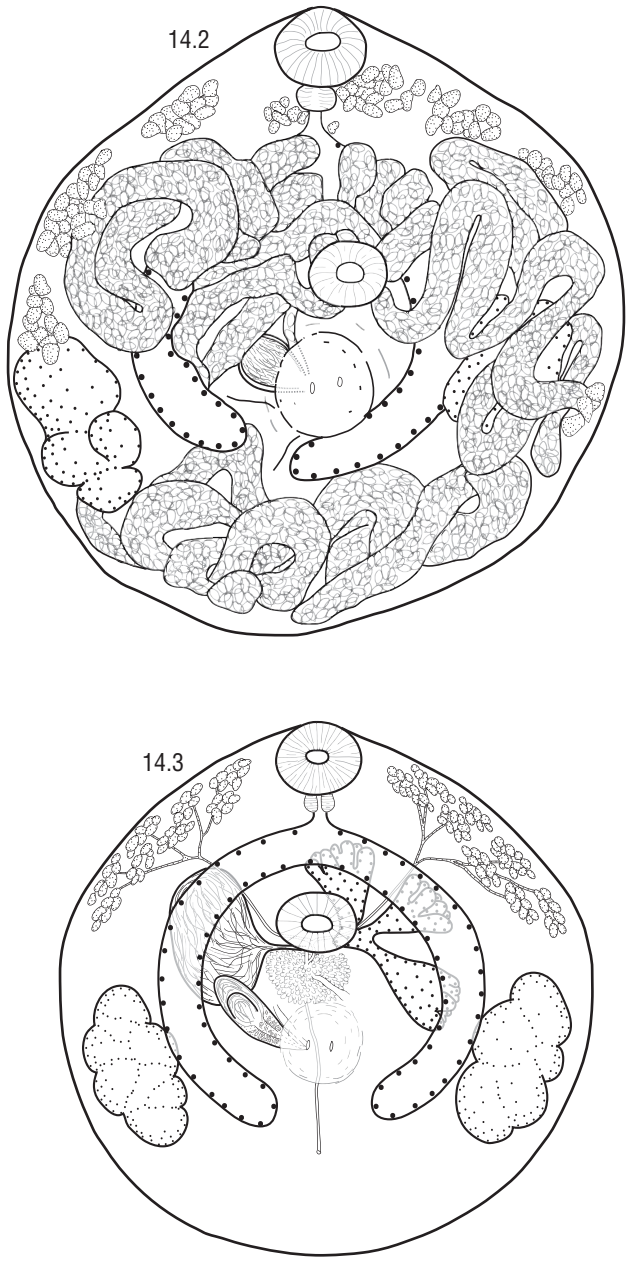



**Fig. 14.1.** *Collyriclum faba* (Bremser in Schmalz, 1831), ventral view. Composite based on figures in Bykhovskaya-Pavlovskaya & Khotenovsky (1964).

(rarely other sites) of birds (many Passeriformes and domestic Galliformes); Nearctic, Neotropical, Europe, northern Asia. Type-species *C. faba* (Bremser in Schmalz, 1831) Kossack, 1911.

**1b. Ventral sucker present ..... *Collyricloides* Vaucher, 1969. (Figs 14.2, 14.3)**
**Diagnosis:** Body almost spherical. Tegument bears spines and, especially near excretory and genital pores, irregular protuberances. Oral sucker apparently ventro-subterminal. Ventral sucker slightly anterior to equator, slightly smaller than oral sucker. Intestinal bifurcation in forebody. Caeca sublateral following curve of body, terminate at about one-quarter of body-length from posterior end. Testes large, lobed, lateral, mainly in third quarter of body, posterior to level of ventral sucker and largely lateral to caeca. Cirrus-sac long but narrow, in dorsoventral plane or somewhat oblique, contains large internal seminal vesicle, pars prostatica and ejaculatory duct. Common genital pore just submedian, slightly posterior to ventral sucker on distinct papilla. Ovary to left of median line, with base dorsal to ventral sucker. Seminal receptacle very large, to right of median line at level of ovary, apparently not associated with Laurer's canal. Mehlis' gland median, posterodorsal to ventral sucker. Laurer's canal opens dorsally posterior to level of caecal ends. Uterus winds extensively in body; short metraterm present. Vitelline follicles mostly anterolateral in body, six to eight clusters on each side. Excretory vesicle large, saccate; pore on ventral papilla, slightly to left of genital pore. Singly in cysts projecting from serosal surface of intestine of rodents and passerine birds; western Europe. Type-species *C. massanae* Vaucher, 1969.

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**Figs 14.2, 14.3.** *Collyricloides massanae* Vaucher, 1969, ventral views. 14.2. Entire specimen. 14.3. Reconstruction from serial sections with uterus omitted. Both redrawn after Vaucher (1969).

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# 15 Family Cortrematidae Yamaguti, 1958

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## Introduction

The family Cortrematidae Yamaguti, 1958 contains only a single genus, *Cortrema* Tang, 1951, from the digestive tract of passerine birds in the Palaearctic region and Africa. In *Cortrema*, a ventral sucker is present but a cirrus-sac is not. The genital pore is close to the posterior end of the body near the excretory pore. Laurer's canal is extremely long, extending to at least midway between the ventral sucker and the posterior end of the body. This suite of characters separates the family from other members of the Gorgoderoidea Looss, 1899.

Tang (1951) proposed the genus and species *Cortrema corti* Tang, 1951 for worms from the bursa Fabricii of passerine birds in China. Worms were apparently not encysted or encapsulated in the wall of this organ, but free in the lumen. Tang placed his new genus in the Troglotrematidae Odhner, 1914 and regarded it as close to *Collyriclum* Ward, 1917 because of the general similarity of some organs, especially the ovary and testes. Yamaguti (1958b) erected the Cortrematidae Yamaguti, 1958 for *Cortrema*. Khotenovskiĭ (1961) transferred to *Cortrema* two species described by Bykhovskaya-Pavlovskaya (1950, 1953), *Renicola magnicaudata* Bykhovskaya-Pavlovskaya, 1950 (original record from the kidney of a swallow, but Khotenovskiĭ questioned this site) and *Leyogonimus testilobatus* Bykhovskaya-Pavlovskaya, 1953 (from the posterior intestine of jays). Although very similar to *C. corti* in most respects, they have a shorter Laurer's canal that does not reach the posterior end of the body. His reasons for this transfer are convincing. Khotenovskiĭ (1961) reduced the Cortrematidae to subfamily status within the Lecithodendriidae Lühe, 1901.

Tang & Tang (1981) experimentally infected freshwater pulmonate snails using embryonated eggs from *Cortrema corti*. They compared cercarial and adult morphology with those of lecithodendriids and concluded that *Cortrema* should not be placed in the Lecithodendriidae and that the Cortrematidae was a suitable receptacle for it. We have accepted this view.

## Cortrematidae Yamaguti, 1958

**Diagnosis:** Body small to medium in size, typically pyriform, somewhat attenuated posteriorly, flat or concave ventrally and convex dorsally. Tegument bears spines. Oral sucker terminal or

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subterminal, ventral. Ventral sucker close to equator or somewhat anterior to this, similar in size to oral sucker. Prepharynx absent. Pharynx small. Oesophagus short. Intestinal bifurcation in anterior forebody. Caeca simple, blind, not extending far into last quarter of body. Testes two, symmetrical, large, irregular in shape or deeply lobed, lateral and dorsal to caeca in middle third of body but may extend posterior to this. Seminal vesicle very long, follows somewhat irregular course alongside uterus to small genital atrium, which opens at submedian to sublateral pore at posterior end of body. Cirrus-sac absent; pars prostatica and ejaculatory duct not reported. Ovary large, median, in forebody, deeply lobed. Laurer's canal very long, extending to at least midway between ventral sucker and posterior end of body, contains sperm and gives off dilated seminal receptacle near its base. Uterus extensively looped from level of pharynx to beyond caecal extremities; terminal portion a muscular metraterm running alongside seminal vesicle. Eggs small, operculate, numerous. Vitelline follicles lateral at level of ovary and extending to level of posterior edge of ventral sucker. Excretory vesicle broad, tubular, extending anteriorly between caecal ends sometimes almost as far as ventral sucker; pore sublateral at posterior extremity on side opposite genital opening. In bursa Fabricii, caeca and other parts of intestine of passeriform birds; China, Russia, Africa, Europe. Type-genus *Cortrema* Tang, 1951.

## *Cortrema* Tang, 1951 (Fig. 15.1)

**Diagnosis:** With characters of family. Type-species *C. corti* Tang, 1951.

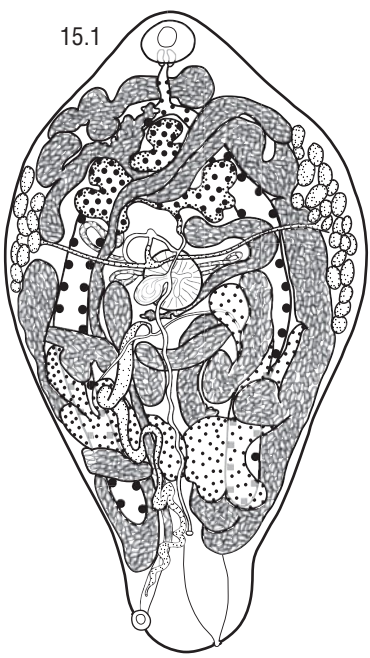



**Fig. 15.1.** *Cortrema corti* Tang, 1951. Dorsal view. Redrawn after Tang & Tang (1981).

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# 16 Family Dicrocoeliidae Looss, 1899

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## Introduction

The Dicrocoeliidae Looss, 1899 constitutes a large family, comprising over 400 species, which express great variability of body-shape and size and topography of the internal organs. Arranging so much material into a clear system is not easy. In the literature, there are several systems for the family, the most important of which are those proposed by Shtrom (1940), Travassos (1944), Skrjabin & Evranova (1952), Yamaguti (1958b, 1971), Odening (1964a) and Panin (1981, 1984). A comparison of these systems shows great differences in the affiliation of genera to the higher taxa (subfamilies, tribes), as well as in the assessment of the validity of some genera.

The subfamily Dicrocoeliinae Looss, 1899 was established by Looss (1899), who included four genera: *Dicrocoelium* Dujardin, 1845, *Anchitrema* Looss, 1899, *Athesmia* Looss, 1899 and *Lyperosomum* Looss, 1899. Looss (1907b) added two more genera: *Eurytrema* Looss, 1907 and *Platynosomum* Looss, 1907. All species in these genera, except *Anchitrema*, which is an intestinal parasite, inhabited the bile-ducts of terrestrial vertebrates. Odhner (1910) raised this subfamily to family status, adding *Mesocoelium* Odhner, 1910 and *Hoploderma* Cohn, 1903 (renamed by Poche (1926) as *Pintneria* Poche, 1926, because the name *Hoploderma* was pre-occupied), both intestinal parasites of vertebrates. Fuhrmann (1928) distinguished two subfamilies, the Dicrocoeliinae (already comprising 19 genera) and the Brachycoeliinae Looss, 1899 (with four genera), and Dollfus (1929) added a third subfamily, the Mesocoeliinae Dollfus, 1929. Dollfus (1930) excluded the subfamily Brachycoeliinae from the Dicrocoeliidae, raising it to family status, and arranged the remaining genera of dicrocoeliids in the Dicrocoeliinae and Mesocoeliinae. Later, Dollfus (1933) also separated mesocoeliines from the Dicrocoeliidae, raising the Mesocoeliinae to family status.

The concept of Dollfus (1933) was accepted by Skrjabin & Evranova (1952), Skrjabin & Morozov (1959), Odening (1964a), Skrjabin (1970) and Panin (1981, 1984). On the other hand, the mesocoeliids were retained as a subfamily in the Dicrocoeliidae by Travassos (1944), whereas Yamaguti (1958b, 1971) retained them in the Brachycoeliidae Looss, 1899. The systems for the Dicrocoeliidae adopted by the above authors differed also in the number of subfamilies they comprised. Travassos (1944) recognized three: the Dicrocoeliinae, Mesocoeliinae and a new subfamily, the Infidinae Travassos, 1944. Skrjabin & Evranova (1952) retained only two: the Dicrocoeliinae

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and Infidinae. Yamaguti (1958b) included four: the Anchitrematinae, Dicrocoeliinae and two new subfamilies, the Leipertrematinae Yamaguti, 1958 and Stromitrematinae Yamaguti, 1958. Odening (1964a), who included four subfamilies, retained the Dicrocoeliinae, Leipertrematinae and Stromitrematinae and added a new one, the Proacetabulorchiinae Odening, 1964. Yamaguti (1971) recognized six subfamilies, the Dicrocoeliinae, Leipertrematinae, Stromitrematinae, Proacetabulorchiinae and two new subfamilies, the Platynotrematinae Yamaguti, 1971 and Prosolecithinae Yamaguti, 1971. He removed the Anchitrematinae, which had earlier been raised by Caballero (1961b) to the rank of family, from the Dicrocoeliidae. Panin (1981, 1984) recognized four subfamilies, but adopted only three under their previous names (Dicrocoeliinae, Infidinae and Proacetabulorchiinae). He renamed the Leipertrematinae as the Eurytrematinae Panin, 1981 (as, according to him, the genus *Leipertrema* Sandosham, 1951 is not characteristic of this group of dicrocoeliids with its symmetrical testes) and proposed *Eurytrema* Looss, 1907 as the type-genus of this subfamily. He also followed the view of Bykhovskaya-Pavlovskaya & Kulakova (1978) that the retention of the ventral sucker (although rudimentary) in representatives of the subfamily Stromitrematinae is sufficient to invalidate its independent status, and transferred the three genera in this subfamily to the Eurytrematinae.

The species richness of the dicrocoeliids, as well as the variety of patterns of their morphology, presents difficulties for the construction of generic keys. For this reason Yamaguti (1958b) distinguished tribes within the Dicrocoeliinae and Leipertrematinae, thus grouping fewer genera. The idea of tribes was maintained by him (Yamaguti, 1971) and was adapted by Odening (1964a), although there were some differences between them in the affiliation of some genera to particular tribes. Panin (1984) did not distinguish these taxa in his system.

All the systems proposed were based on morphological similarities of the adults, arbitrarily chosen by the individual authors. Some authors (Tokobayev & Logacheva, 1963; Panin, 1971) suggested basing the systematics on the type of life-cycles of these digeneans, Panin (1971) distinguishing the following three types of life-cycle for the dicrocoeliids:

**1.** Dicrocoeliid-type: with two intermediate hosts (terrestrial mollusc and arthropod) and long-tailed xiphidiocercariae, which leave the first intermediate host in mucoid balls (characteristic for *Dicrocoelium* Dujardin, 1845, *Brachylecithum* Shtrom, 1940, *Lutztrema* Travassos, 1941).
**2.** Eurytrema-type: also with two intermediate hosts (terrestrial mollusc and arthropod) and xiphidiocercariae with a rudimentary tail (microcerci), which leave the first intermediate host enclosed in daughter-sporocysts (characteristic for *Eurytrema* Looss, 1907, *Concinnum* Bhalerao, 1936, *Conspicuum* Bhalerao, 1936, *Paradistomum* Kossack, 1910, *Zonorchis* Travassos, 1944 (now a synonym of *Skrjabinus* Bhalerao, 1936)).
**3.** Platynosomum-type: with two intermediate and one paratenic hosts (terrestrial mollusc, arthropod and amphibian or reptile, respectively) and xiphidiocercariae with a rudimentary tail, which leave the first intermediate host enclosed and often encysted inside the daughter-sporocyst; in the paratenic host, the non-encysted metacercariae inhabit the bile-ducts of liver (characteristic for *Platynosomum* Looss, 1907). It has to be stressed that, according to Maldonado (1945) and Eckerlin & Leigh (1962), amphibians or reptiles are the obligatory third intermediate hosts in the life-cycles of some dicrocoeliids.

Baer (1970, 1971) thought that the number of known life-cycles of dicrocoeliids is too small to construct the systematics of this group on this basis. This is still true, although some consistency within the subfamilies can be observed.

Here, none of the systems mentioned above is accepted in its original form. The taxonomy of the dicrocoeliids has had to be modified, as new species have been described, new genera and

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subfamilies have been erected, and new information on the morphology and biology of some species has been gathered. The taxonomy proposed is closest to the concept of Odening (1964a), although some ideas of Yamaguti (1958b, 1971) and Panin (1984) are also adopted. The main difference between the present classification and that of Odening (1964a) is that taxa at tribe level are not distinguished.

In this system, the Dicrocoeliidae comprises species developing exclusively in the terrestrial environment. Four subfamilies are recognized: the Dicrocoeliinae, Leipertrematinae, Proacetabulorchiinae and Prosolecithinae.

The Robertdigeninae Caballero & Caballero, 1970, established by Caballero & Caballero (1970), is suppressed and its only genus, *Robertdigenea* Caballero & Caballero, 1970, is transferred to the Brachycoeliidae on the basis of the position of the ovary anterior to the testes, the position of the genital pore and the size and position of the cirrus-sac.

The Stromitrematinae Yamaguti, 1958 is suppressed following Bykhovskaya-Pavlovskaya & Kulakova (1978), a stance supported by Panin (1984), and its genera are transferred to the Leipertrematinae.

The Neodicrocoeliinae Agrawal & Sharma, 1990, established by Agrawal & Sharma (1990a), is suppressed, as its only genus, *Neodicrocoelium* Agrawal & Sharma, 1990, is considered here as *incertae sedis* within the superfamily Plagiorchioidea (see Chapter 66, this volume).

The proposal of Panin (1981, 1984) to replace the name Leipertrematinae by Eurytrematinae is not accepted, as there is no justification for this action. Following the concept of Odening (1964a), *Leipertrema* Sandosham, 1951 is considered as the type-genus of the subfamily.

*Allocorrigia* Turner & Corkum, 1977 and *Neodicrocoelium* Agrawal & Sharma, 1990 are excluded from the Dicrocoeliidae because they have morphological features that do not fit this family, and because they involve aquatic hosts in their life-cycle; they are treated as genera *incertae sedis* in the superfamily Plagiorchioidea (see Chapter 66, this volume).

*Corvotrema* Sahay & Sahay, 1978 and *Paradictinogryptus* Agrawal & Sharma 1989 are treated here as *nomina nuda*, as the descriptions given by Sahay & Sahay (1978) and Agrawal & Sharma (1989), respectively, are very poor and no figures exist.

All of the taxa at the subgeneric level are suppressed, as in many cases the analysis of morphology of some species exhibited the features of more than one subgenus.

Subfamilies are differentiated by such features as the general topography of the testes, vitellarium and uterus. For distinguishing genera in particular subfamilies, the following features are considered: the position of the testes in relation to the ventral sucker and to the caeca, the position of the vitellarium in relation to the testes or the ovary, the structure of the vitellarium, the position of the genital pore, the length of the caeca and the position of the uterine coils.

To make the diagnoses of the taxa more comparable at particular levels, the same characters of digenean morphology are considered. Therefore, although they are based on the diagnoses published by various authors, all are amended. All the figures are modified or reconstructed from published images.

## Family Dicrocoeliidae Looss, 1899

**Diagnosis:** Body of various shapes, flattened, rarely subglobular. Tegument armed with spines or unspined, sometimes with conical papillae on surface. Suckers usually well developed. Oral sucker subterminal. Ventral sucker in anterior half of body. Prepharynx usually lacking. Pharynx muscular. Oesophagus generally short, sometimes practically absent. Intestinal bifurcation almost always

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in forebody. Caeca usually two (exceptionally one); length varies. Testes usually in anterior half of body. Cirrus-sac well developed, anterior to ventral sucker, usually encloses seminal vesicle, pars prostatica and unarmed cirrus. Genital pore median or submedian, in region of intestinal bifurcation or pharynx. Ovary usually in anterior half of body, posterior to testes. Seminal receptacle usually present. Mehlis' gland and Laurer's canal present. Uterus with descending and ascending limbs forming numerous coils, occupies most of hindbody; its terminal section always runs between testes. Eggs numerous, operculate, contain miracidium when deposited. Vitellarium follicular, usually limited in extent, forms two lateral bands or clusters; rarely, only one band exists. Excretory system with I-, Y- or T-shaped vesicle and flame-cell formula: 2[(2 + 2 + 2) + (2 + 2 + 2)] = 24; pore terminal or subterminal. Cercaria with stylet (xiphidiocercaria), long-tailed (*Vitrinocercaria longicauda*) or with rudimentary tail (*V. brevicauda*). Life-cycles completed in terrestrial environment, in most cases with two intermediate hosts: snails (mainly Pulmonata) and arthropods (mainly insects); in some cycles paratenic (or third intermediate) host is involved (amphibians or reptiles). In bile-ducts and gall-bladder (more rarely pancreatic ducts or intestine) of birds and mammals and, rarely, reptiles and marsupials; cosmopolitan. Type-genus *Dicrocoelium* Dujardin, 1845.

## Key to subfamilies

**1a. Testes tandem or oblique ..... 2.**
**1b. Testes symmetrical or almost so ..... 3.**

**2a. Testes anterior to ventral sucker ..... Proacetabulorchiinae Odening, 1964.**
**2b. At least one testis posterior to ventral sucker ..... Dicrocoeliinae Looss, 1899.**

**3a. Vitellarium at least partly posterior to ovary; uterine coils occupy entire hindbody ..... ..... Leipertrematinae Yamaguti, 1958.**
**3b. Vitellarium anterior to ovary; uterine coils generally limited to middle of body ..... ..... Prosolecithinae Yamaguti, 1971.**

## Subfamily Dicrocoeliinae Looss, 1899

**Diagnosis:** Body delicate, from broadly oval to more or less elongate. Tegument unarmed or with spines, or with conical papillae on surface. Suckers of medium size, subequal or ventral larger than oral; both usually in anterior third of body. Pharynx muscular or of medium length. Oesophagus generally short, sometimes practically absent. Intestinal bifurcation in forebody. Caeca usually two (exceptionally one), long, extending close to posterior extremity or shorter, in most cases reaching beyond middle of body. Both testes usually posterior to ventral sucker, tandem or diagonal (never symmetrical), may be lobed. Cirrus-sac rather small, may reach anterior border of ventral sucker. Genital pore usually at level of intestinal bifurcation. Ovary median or submedian. Mehlis' gland weakly developed. Uterus mainly intercaecal, may cross caeca laterally. Vitellarium usually forms two lateral groups of follicles, posterior to testes; in several genera, only one lateral group occurs. Known life-cycles of dicrocoeliid-type, with long-tailed xiphidiocercaria developed in terrestrial snails, and insects as second intermediate hosts. In birds and mammals, exceptionally in marsupials; cosmopolitan. Type-genus *Dicrocoelium* Dujardin, 1845.

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## Key to genera

**1a. Only one testis posterior to ventral sucker ..... *Controrchis* Price, 1928. (Fig. 16.1)**
**Diagnosis:** Body oval. Tegument with anterior region covered with spines. Both suckers in anterior third of body; oral smaller than ventral. Oesophagus short. Caecal ends distant from posterior extremity but distinctly beyond middle of body. Testes in tandem, one anterior to and second posterior to ventral sucker. Cirrus-sac reaches region of anterior testis. Genital pore submedian, anterior to intestinal bifurcation. Ovary distinctly smaller than testes, submedian, just posterior to posterior testis. Uterus intercaecal, occupies most of hindbody. Vitellarium forms two lateral clusters posterior to posterior testis. Excretory vesicle simple, long, reaches level of vitellarium. In gall-bladder of mammals; Central America (Costa Rica). Type-species *C. biliophilus* Price, 1928.

**1b. Both testes posterior to ventral sucker ..... 2.**

**2a. Vitellarium forms two bands or clusters ..... 3.**
**2b. Vitellarium forms only one lateral band or cluster, on opposite side to ovary ..... 14.**

**3a. Anterior extremity of vitellarium anterior to ovary ..... 4.**
**3b. Anterior extremity of vitellarium at level of ovary or more posteriorly ..... 7.**

**4a. Testes close to ventral sucker; vitelline bands relatively short; caeca not reaching posterior extremity ..... 5.**
**4b. Testes distant from ventral sucker; vitelline bands long; caeca reach close to posterior extremity ..... *Megacetabulum* Oshmarin, 1964. (Fig. 16.2)**
**Diagnosis:** Body long, slender; forebody short. Suckers close one to another; oral small, with prominent pre-oral lobe; ventral very large, protruded. Pharynx small. Oesophagus short. Caeca long, reach close to posterior extremity. Testes diagonal, distant from ventral sucker, separated from each other and from ovary by uterine coils. Cirrus-sac elongate, reaches anterior border of ventral sucker. Genital pore at level of intestinal bifurcation. Ovary submedian. Uterine coils intercaecal, occupy entire hindbody. Vitellarium in two bands, narrow, long, composed of numerous small follicles, pass alongside caeca, beginning anterior to anterior testis and terminating far posterior to ovary. Excretory system not observed. In intestine of birds; Asia (Vietnam) and New Zealand. Type-species *M. microrchum* Oshmarin, 1964.

**5a. Suckers subequal or oral larger than ventral; ovary close to posterior testis; genital pore posterior to intestinal bifurcation ..... 6.**
**5b. Ventral sucker larger than oral; ovary distant from posterior testis; genital pore usually anterior to intestinal bifurcation ..... *Lyperosomum* Looss, 1899. (Figs 16.3, 16.4)**
(Syns *Oswaldoia* Travassos, 1919; *Dicrocoelioides* Dollfus, 1954; *Paralutztrema* Faust, 1967; subgenus *Lyperosomoides* Yamaguti, 1971)
**Diagnosis:** Body elongate fusiform, or more slender. Tegument unspined. Oral sucker usually much smaller than ventral. Pharynx small. Oesophagus varies in length. Caeca terminate well away from posterior extremity, often asymmetrical. Testes diagonal, sometimes almost tandem, usually close to ventral sucker. Cirrus-sac large, entirely anterior to ventral sucker. Genital pore median or submedian, anterior to ventral sucker, usually also anterior to intestinal bifurcation. Ovary round, submedian, posterior to and distant from posterior testis. Uterus forms many coils

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in hindbody. Vitellarium in two narrow bands, relatively long, in middle third of body, beginning at level of testes and not reaching caecal ends. Excretory vesicle I-shaped; its extent not determined. In bile-ducts and gall-bladder of birds, rarely of mammals; Europe, Asia, Africa, North and South America. Type-species *L. longicauda* (Rudolphi, 1809) Braun, 1902.

**6a. Body unspined;[1] excretory vesicle I- or Y-shaped** .....
..... ***Dicrocoelium* Dujardin, 1845. (Fig. 16.5)**
(Syn. subgenus *Mediorchis* Panin, 1971)

**Diagnosis:** Body elongate, lanceolate or fusiform. Tegument unspined. Oral sucker usually slightly larger than ventral. Pharynx small. Oesophagus relatively long. Caeca do not reach posterior extremity. Testes large, immediately posterior to ventral sucker, diagonal, may be lobed. Cirrus-sac elongate, may reach anterior border of ventral sucker. Genital pore median, just posterior to intestinal bifurcation. Ovary smaller than testes, close to posterior testis. Uterus occupies

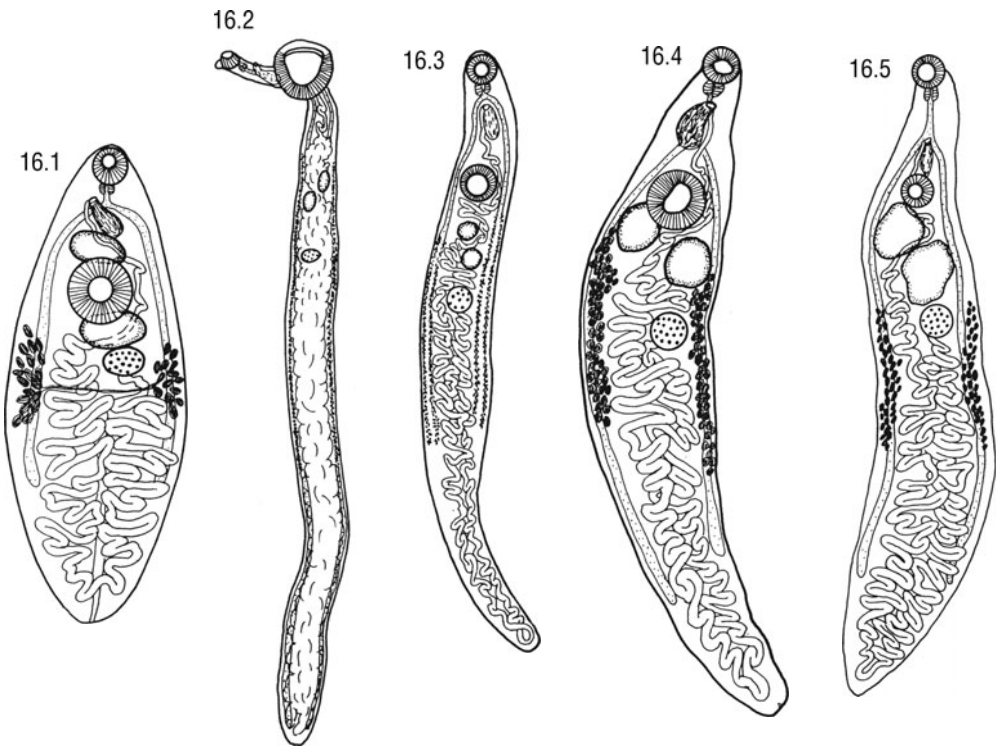



**Fig. 16.1.** *Controrchis biliophilus* Price, 1928. After Yamaguti (1971).
**Fig. 16.2.** *Megacetabulum microrchum* Oshmarin, 1964. After Yamaguti (1971).
**Fig. 16.3.** *Lyperosomum longicauda* (Rudolphi, 1809). Note short oesophagus and position of genital pore posterior to intestinal bifurcation. After Skrjabin & Evranova (1952).
**Fig. 16.4.** *Lyperosomum armenicum* Shcherbakova, 1942. Note relatively long oesophagus and position of genital pore anterior to intestinal bifurcation. After Skrjabin & Evranova (1952).
**Fig. 16.5.** *Dicrocoelium dendriticum* (Rudolphi, 1809). After Skrjabin & Evranova (1952).

[1] In well-fixed specimens a very dense covering of extremely minute spine-like structures may be visible.

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entire hindbody, intercaecal. Vitellarium in two bands composed of small follicles, limited to middle third of body. Excretory vesicle I- or Y-shaped; stem may reach close to ovary; pore terminal. In bile-ducts and gall-bladder of birds and mammals; cosmopolitan. Type-species *D. dendriticum* (Rudolphi, 1819) Dujardin, 1845.

**6b. Body spined; excretory vesicle V-shaped ..... *Pseudoparadistomum* Roca, 2003. (Fig. 16.6)**
**Diagnosis.** Body elongate, rounded in both extremities. Tegument spined. Oral sucker much larger than ventral. Prepharynx lacking. Pharynx small. Oesophagus relatively long. Caeca not reaching posterior extremity, asymmetrical. Testes diagonal; anterior testis immediately posterior to ventral sucker. Cirrus-sac pyriform, may reach level of intestinal bifurcation. Genital pore median or submedian, at the level of intestinal bifurcation. Ovary smaller than testes, lateral, post-testicular. Uterus occupies entire hindbody, intercaecal. Vitellarium in two bands composed of small follicles limited to middle third of body, commencing at level of posterior testis or ovary. Eggs large. Excretory vesicle V-shaped. In small intestine of lizards; Canary Islands, Spain. Type-species *P. yaizaiense* Roca, 2003 (emend.).

**7a. Intestine with single caecum ..... *Lutztrema* Travassos, 1941. (Fig. 16.7)**
**Diagnosis:** Body elongate. Tegument unspined. Oral sucker smaller than ventral. Pharynx small. Oesophagus continues as single long, convoluted caecum, not reaching posterior extremity. Testes large, tandem or diagonal, may be lobed. Cirrus-sac elongate. Genital pore about halfway between suckers. Ovary smaller than testes, submedian, close to posterior testis. Uterus strongly coiled, occupies entire hindbody. Vitellarium composed of several large follicles, posterior to ovary, forms two short lateral bands or clusters, sometimes united anteriorly. Excretory vesicle tubular, long, may reach close to ovary. In bile-ducts and gall-bladder of birds; Europe (Great Britain, Poland, former Czechoslovakia), Asia (China, India), North America (Canada, USA), South America (Brazil), Australia. Type-species *L. obliquum* (Travassos, 1917) Travassos, 1941.

**7b. Intestine with two caeca ..... 8.**

**8a. Body relatively short; vitelline bands in posterior half of body ..... 9.**
**8b. Body elongate, to filiform; vitelline bands in middle third of body ..... 11.**

**9a. Genital pore in region of intestinal bifurcation; ovary close to testes ..... 10.**
**9b. Genital pore clearly anterior to intestinal bifurcation; ovary distant from testes .....**
**..... *Opistholecithum* Baer, 1970. (Fig. 16.8)**
**Diagnosis:** Body lanceolate with attenuated anterior extremity. Oral sucker small. Pharynx relatively large, muscular. Oesophagus relatively long. Caeca long, convoluted, almost reach posterior extremity. Testes large, slightly diagonal, close to ventral sucker; anterior overlaps ventral sucker. Cirrus-sac elongate. Genital pore slightly posterior to pharynx. Ovary median, distant from testes, in posterior third of body. Uterus intercaecal, with descending limb reaching posterior extremity and ascending limb coiled in median line of body. Vitellarium in two short bands, composed of several large follicles, posterior to ovary, close to posterior extremity. Excretory vesicle with stem reaching level of ovary. In gall-bladder of mammals (insectivores); Africa (Ivory Coast). Type-species. *O. margaritae* Baer, 1970.

**10a. Body lanceolate; testes diagonal ..... *Metadelphis* Travassos, 1944. (Fig. 16.9)**
**Diagnosis:** Body lanceolate, broadest posteriorly. Tegument unspined, sometimes covered with conical papillae. Suckers subequal. Oesophagus distinct. Caecal extent not determined. Testes

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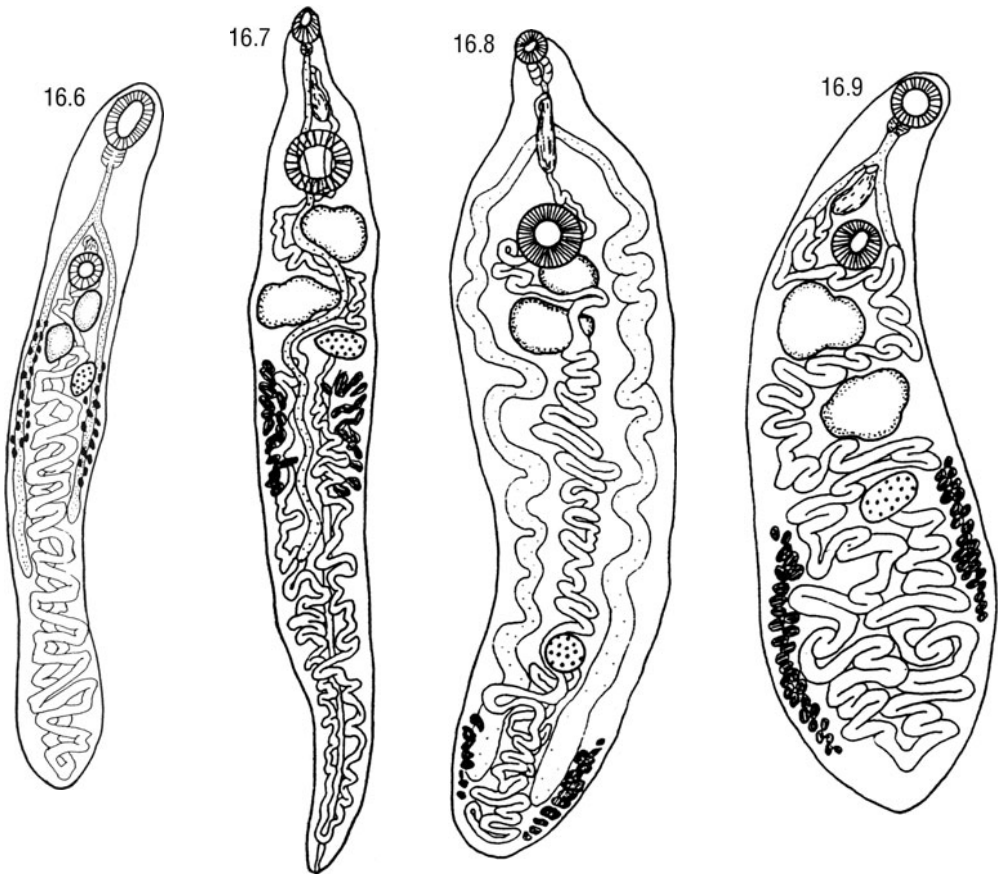



**Fig. 16.6.** *Pseudoparadistomum yaizaiense* Roca, 2003. After Roca (2003). (The legend for Figure 1 in Roca (2003) is: *Pseudoparadistomum yazai*.)
**Fig. 16.7.** *Lutztrema monenteron* (Price & McIntosh, 1935). After Price & McIntosh (1935).
**Fig. 16.8.** *Opistholecithum margaritae* Baer, 1970. After Baer (1970).
**Fig. 16.9.** *Metadelphis evandroi* Travassos, 1944. After Travassos (1944).

large, diagonal, in anterior half of body, may be weakly lobed. Cirrus-sac elongate, between intestinal bifurcation and ventral sucker. Genital pore close to intestinal bifurcation. Ovary smaller than testes, submedian, fairly close to posterior testis, in posterior half of body. Strongly coiled uterus fills entire body, apart from space occupied by gonads. Vitelline follicles form two narrow postovarian bands, in posterior half of body. Excretory system not observed. In gall-bladder of marsupials; Brazil. Type-species *M. evandroi* Travassos, 1944.

**10b. Body elongate, narrow; testes smooth, almost tandem .....**
**..... *Opisthobrachylecithum* Yamaguti, 1971. (Fig. 16.10)**

**Diagnosis:** Body narrow, elongate. Oral sucker relatively large, but smaller than ventral. Pharynx small. Oesophagus distinct. Caeca long, terminating near posterior extremity. Testes smooth, in middle third of body, almost tandem, separated one from another and from ovary by uterine coils. Cirrus-sac saccular, between intestinal bifurcation and ventral sucker. Genital pore at level of

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intestinal bifurcation. Ovary round, median, in posterior half of body. Uterus intercaecal. Vitellarium in two bands composed of several follicles, begins at level of ovary and terminates near caecal ends. Excretory system not observed. In birds; Asia (Russia). Type-species *O. belopolskiae* (Zueva & Belogurov, 1965) Yamaguti, 1971.

**11a. Vitellarium composed of few large follicles ..... 12.**
**11b. Vitellarium composed of many small follicles ..... 13.**

**12a. Suckers subequal ..... *Brachylecithum* Shtrom, 1940. (Figs 16.11, 16.12)**
(Syns Subgenus *Brachylecithum* Shtrom, 1940; *Eugenia* Oshmarin, 1948; *Orthorchis* Travassos, 1944; subgenus *Brachylecithoides* Yamaguti, 1971)

**Diagnosis:** Body long, slender, flattened or cylindrical. Tegument unspined or covered with spines or conical papillae. Suckers in anterior third of body; ventral sucker may be slightly larger than oral. Pharynx rather small. Oesophagus short. Caeca terminate far from posterior extremity. Testes tandem or somewhat diagonal, distant from or close to one another. Cirrus-sac elongate, may reach anterior border of ventral sucker. Genital pore median, usually at level of intestinal bifurcation, sometimes anterior or posterior to it. Ovary median, usually separated by uterine coils from posterior testis. Uterine coils occupy entire hindbody, also extracaecal. Vitellarium in two relatively short bands, composed of few large follicles, in middle third of body. Excretory vesicle Y-shaped, with long stem, which may reach close to level of vitellarium. In bile-ducts and gall-bladder of birds and mammals; cosmopolitan. Type-species *B. filum* (Dujardin, 1845) Shtrom, 1940.

**12b. Ventral sucker much larger than oral ..... ..... *Brachydistomum* Travassos, 1944. (Figs 16.13–16.15)**
(Syns *Olssoniella* Travassos, 1944; *Globostomum* Oshmarin 1970)

**Diagnosis:** Body lanceolate, with tapered, short forebody. Oral sucker relatively small; ventral prominent, much larger than oral; both in anterior third of body. Pharynx small. Oesophagus short. Caeca long. Testes diagonal or tandem, close to ventral sucker and to one another. Cirrus-sac elongate, may reach anterior border of ventral sucker. Genital pore median or submedian, at level of intestinal bifurcation or slightly more anterior. Ovary submedian, close to posterior testis. Uterine coils occupy whole hindbody, also extracaecal. Vitellarium short, sometimes broad, composed of few large follicles forming two bands or clusters in middle third of body. Excretory system not observed. In bile-ducts and gall-bladder of birds; Europe, Asia, Australia. Type-species *B. microscelis* (Yamaguti, 1933) Travassos, 1944.

**13a. Body elongate but not filiform; testes relatively close to ventral sucker; vitelline bands long ..... *Corrigia* Shtrom, 1940. (Fig. 16.16)**

**Diagnosis:** Body elongate, not filiform, slender. Tegument unspined. Both suckers in anterior quarter of body. Pharynx small. Oesophagus short (sometimes practically absent). Caeca long, reach close to posterior extremity. Testes relatively close to ventral sucker and each other, tandem. Cirrus-sac small, between intestinal bifurcation and ventral sucker. Genital pore at level of intestinal bifurcation or immediately posterior to it. Ovary small, median, far from posterior testis. Uterus generally intercaecal. Vitelline follicles small, form relatively long, narrow bands beginning at level of ovary or posterior to it, in middle third of body. Excretory system not observed. In intestine or pancreas of birds and mammals; Holarctic. Type-species *C. corrigia* (Braun, 1901) Shtrom, 1940.

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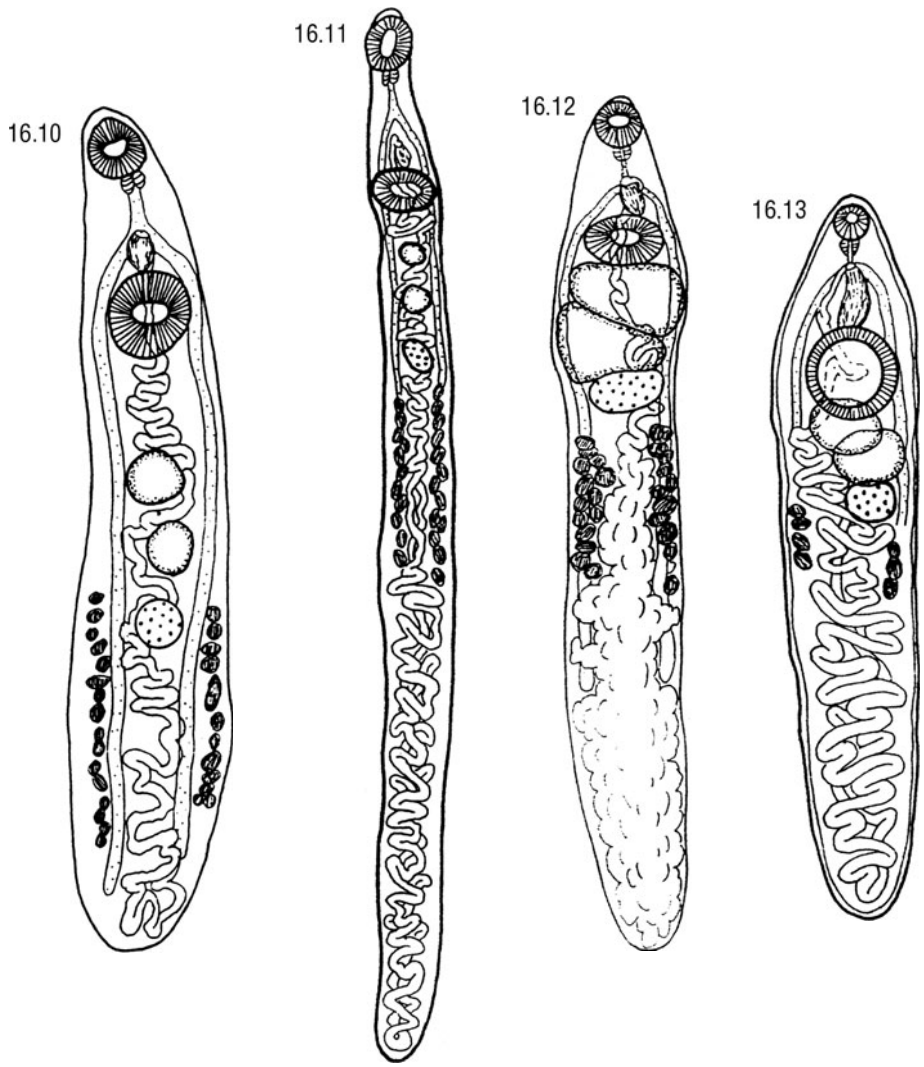



**Fig. 16.10.** *Opisthobrachylecitum belopolskiae* (Zueva & Belogurov, 1965). After Yamaguti (1971).
**Fig. 16.11.** *Brachylecithum filum* (Dujardin, 1845). Note position of genital pore posterior to intestinal bifurcation. After Yamaguti (1971).
**Fig. 16.12.** *Brachylecithum mosquensae* (Skrjabin & Isaichikov, 1927). Note position of genital pore at the level of intestinal bifurcation. After Yamaguti (1971).
**Fig. 16.13.** *Brachydistomum olssoni* (Railliet, 1900). Note testes arranged diagonally and narrow vitelline bands. After Travassos (1944).

**13b. Body filiform; testes distant from ventral sucker; vitelline bands very short ..... ..... *Skrjabinosomum* Evranova, 1944. (Fig. 16.17)**

**Diagnosis:** Body filiform, unspined, with very long hindbody. Oral sucker small. Ventral sucker larger, short distance from oral sucker. Pharynx small. Oesophagus short. Caeca long. Testes longitudinally oval, tandem, distant from ventral sucker and from one another. Cirrus-sac small,

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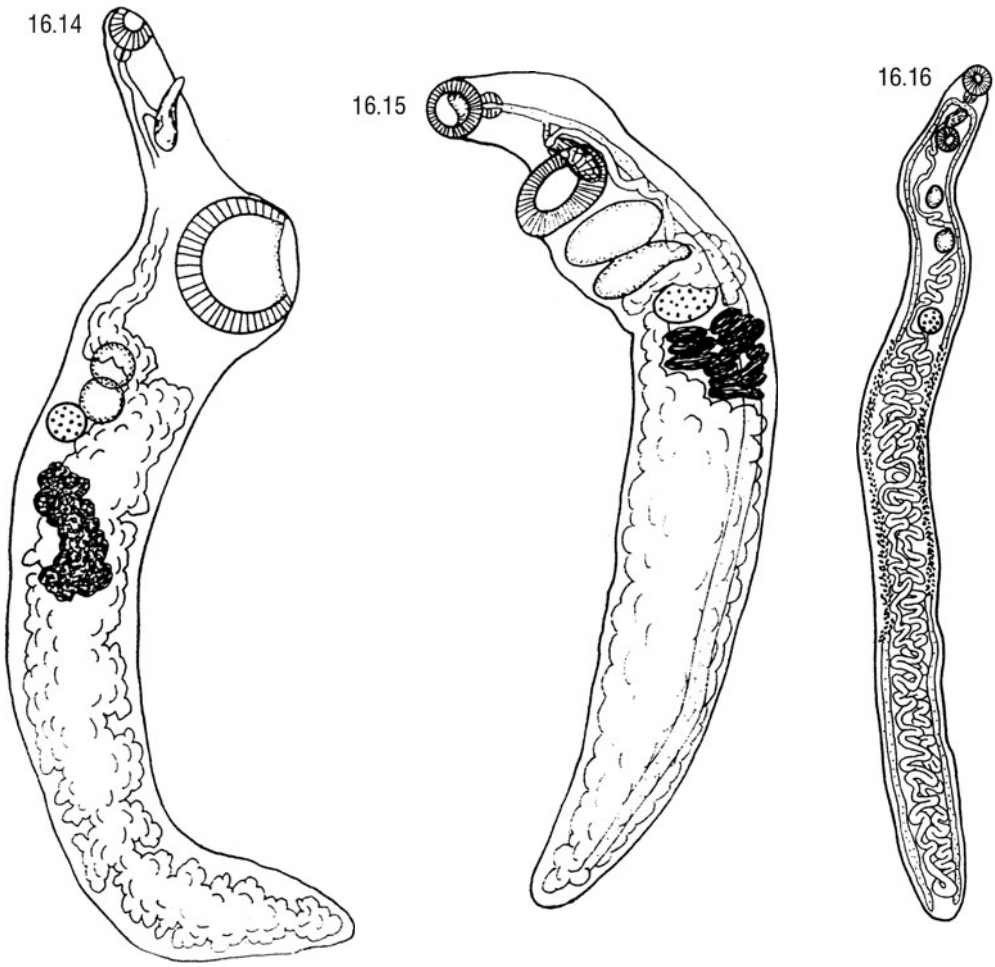



**Fig. 16.14.** *Brachydistomum microscelis* (Yamaguti, 1933). Note testes arranged in tandem. After Skrjabin & Evranova (1952).
**Fig. 16.15.** *Brachydistomum gracupicae* (Oshmarin, 1970). Note broad vitelline clusters. After Oshmarin (1970).
**Fig. 16.16.** *Corrigia vitta* (Dujardin, 1845). After Travassos (1944).

immediately anterior to ventral sucker. Genital pore median, anterior to ventral sucker. Ovary round, distant from posterior testis. Uterus with very long, coiled descending and ascending limbs. Vitellarium in two short bands, composed of small follicles, distinctly posterior to ovary. Excretory system not observed. In intestine and liver of birds; Australia, New Guinea. Type-species *S. porrectum* (Braun, 1899) Evranova, 1944.

**14a. Vitellarium forms single band ..... 15.**
**14b. Vitellarium forms single cluster ..... *Pseudathesmia* Travassos, 1942. (Fig. 16.18)**

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**Diagnosis:** Body flattened, fusiform. Tegument with conical papillae. Suckers small, in first third of body. Pharynx muscular. Oesophagus short. Caeca terminate in posterior half of body, but distant from posterior extremity. Testes weakly lobed, diagonal; anterior testis close to ventral sucker. Cirrus-sac anterior to ventral sucker. Genital pore median, posterior to intestinal bifurcation. Ovary clearly submedian, smaller than testes, may be weakly lobed. Uterus not reaching posterior extremity, intercaecal. Single vitelline cluster beginning at level of ovary and not reaching level of caecal ends. Excretory vesicle I-shaped, may reach close to level of anterior extent of vitellarium. In bile-ducts and gall-bladder of mammals; South America (Brazil). Type-species *P. paradoxa* Travassos, 1942.

**15a. Ovary distant from testes; vitelline band in posterior half of body ..... ..... *Unilaterilecithum* Oshmarin, 1952. (Fig. 16.19)**

**Diagnosis:** Body long, slender. Spines not mentioned. Suckers of medium size; ventral slightly smaller than oral. Pharynx muscular. Oesophagus short. Extent of caeca not determined. Testes smooth, diagonal, in anterior half of body. Cirrus-sac reaches anterior border of ventral sucker. Genital pore median, posterior to intestinal bifurcation. Ovary round, submedian, in posterior half of body, distant from testes. Uterus fills entire hindbody. Single vitelline band composed of relatively large follicles, in posterior half of body, reaches near posterior extremity. Excretory system not described. In liver of birds; Europe (Russia). Type-species *U. beloussi* Oshmarin, 1952.

**15b. Ovary close to testes; vitelline band mostly in middle third of body ..... 16.**

**16a. Caecum single; testes usually diagonal ..... ..... *Athesmioides* Cribb & Spratt, 1992. (Figs 16.20–16.22)**

**Diagnosis:** Body of extremely variable shape, from long, filiform to short, lanceolate. Tegument unarmed. Ventral sucker larger than oral, in anterior third of body. Pharynx small. Oesophagus opens into single caecum terminating in posterior half of body. Testes usually diagonal, or almost tandem in relaxed specimens. Cirrus-sac large, partly dorsal to ventral sucker. Genital pore median, between pharynx and ventral sucker. Ovary posterior to posterior testis, submedian or median. Uterus strongly coiled in hindbody. Single vitelline band posterior to ovary, terminates at level of caecal end. Excretory vesicle I-shaped, reaches close to level of anterior extent of vitellarium. In bile-ducts and gall-bladder of rodents; Australia. Type-species *A. aiolos* Cribb & Spratt, 1992.

**16b. Caeca double; testes tandem or slightly diagonal ..... 17.**

**17a. Caeca extend into posterior half of body ..... *Athesmia* Looss, 1899. (Fig. 16.23)**
(Syns *Lyperotrema* Travassos, 1919; *Hepatotrema* Stunkard, 1923)

**Diagnosis:** Body slender, long. Tegument unspined. Suckers of subequal sizes, in anterior quarter of body. Pharynx small. Oesophagus relatively long. Caeca terminate in posterior half of body, but distant from posterior extremity. Testes usually slightly lobed, tandem or nearly so, in anterior half of body, separate from one another and from ventral sucker. Cirrus-sac elongate, small. Genital pore at level of intestinal bifurcation. Ovary submedian, separated from posterior testis. Uterus strongly coiled posterior to ovary, intercaecal. Single vitelline band composed of fine follicles, begins posterior to ovary and terminates near caecal extremities. Excretory vesicle I- or Y-shaped; stem may reach close to level of anterior extent of vitellarium. In bile-ducts and gall-bladder of birds and mammals; Europe, Africa, Madagascar, Asia, North, Central and South America. Type-species *A. heterolecithoides* (Braun, 1899) Looss, 1899.

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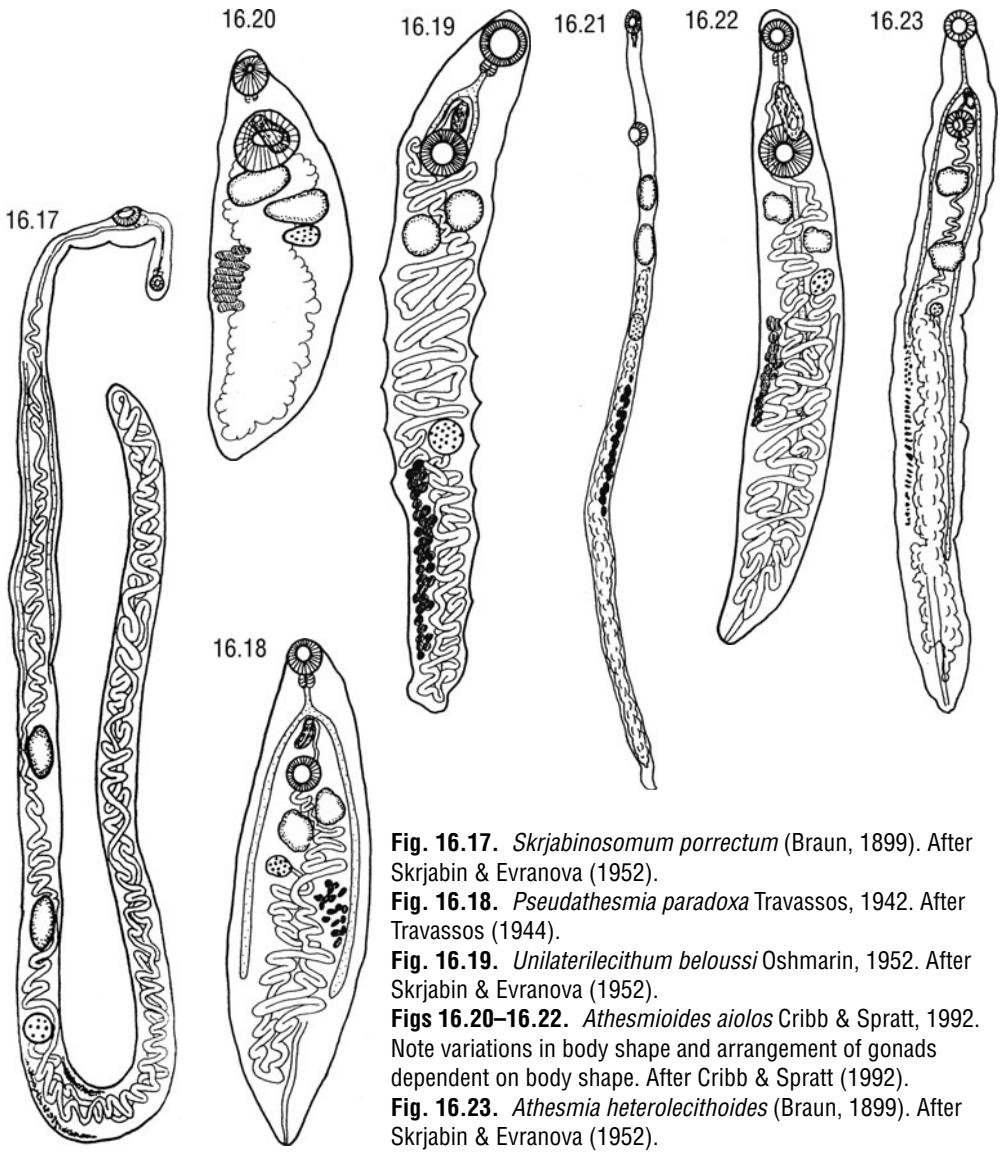



**Fig. 16.17.** *Skrjabinosomum porrectum* (Braun, 1899). After Skrjabin & Evranova (1952).
**Fig. 16.18.** *Pseudathesmia paradoxa* Travassos, 1942. After Travassos (1944).
**Fig. 16.19.** *Unilaterilecithum beloussi* Oshmarin, 1952. After Skrjabin & Evranova (1952).
**Figs 16.20–16.22.** *Athesmioides aiolos* Cribb & Spratt, 1992. Note variations in body shape and arrangement of gonads dependent on body shape. After Cribb & Spratt (1992).
**Fig. 16.23.** *Athesmia heterolecithoides* (Braun, 1899). After Skrjabin & Evranova (1952).

**17b. Caeca very short, terminate in anterior region of body ..... ..... *Caballerolecythus* Lamothe-Argumedo, Falcón-Ordaz, García-Prieto & Fernández-Fernández, 2005. (Fig. 16.24)**

**Diagnosis:** Body strongly elongate, slender. Tegument with papillae. Oral sucker slightly larger than ventral. Prepharynx absent. Pharynx small. Oesophagus relatively long. Caeca very short, terminate in anterior region of body at level of ovary. Testes ovoid, in tandem, in anterior half of body, separate from one another and from ventral sucker. Cirrus-sac elongate, long, between intestinal bifurcation and ventral sucker. Genital pore at level of intestinal bifurcation. Ovary

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median, separate from posterior testis. Uterus strongly coiled posterior to ovary. Single vitelline band on left margin of body, entirely dorsal to caeca and ovary, not reaching posterior extremity. Eggs small, numerous. Excretory vesicle Y-shaped. In bile-ducts of rodents; Mexico. Type-species *C. ibunami* Lamothe-Argumedo, Falcón-Ordaz, García-Prieto & Fernández-Fernández, 2005.

## Subfamily Leipertrematinae Yamaguti, 1958

(Syns Stromitrematinae Yamaguti, 1958; Eurytrematinae Panin, 1981)

**Diagnosis:** Body usually broad, rarely slender. Tegument covered with spines or unarmed. Suckers in anterior half of body; ventral may be near middle of body-length. Pharynx relatively small, muscular. Oesophagus short. Intestinal bifurcation usually in forebody, occasionally dorsal to ventral sucker. Caeca of various lengths. Testes symmetrical, or almost so, at level of ventral sucker (either on each side or slightly anterior or posterior to it). Genital pore median or submedian, at level of intestinal bifurcation or anterior to it. Ovary posterior to or between testes. Uterus with numerous coils with descending and ascending limbs, often extending extracaecally. Vitelline follicles form two clusters or two lateral bands; bands often short, sometimes longer, entirely or at least partly posterior to ovary. Known life-cycles of eurytrema- or platynosomum-type, with short-tailed xiphidiocercaria. In mammals, birds and reptiles. Type-genus *Leipertrema* Sandosham, 1951.

## Key to genera

**1a. Ventral sucker well developed ..... 2.**
**1b. Ventral sucker weak, sometimes undetectable ..... 22.**

**2a. Caeca short, terminate in anterior half of body or just beyond middle of body; genital pore near pharynx ..... 3.**
**2b. Caeca long, reach far beyond middle of body; genital pore in various positions ..... 6.**

**3a. Caeca short but distinct; oesophagus short; vitelline bands usually relatively short ..... 4.**
**3b. Caeca rudimentary; oesophagus long; vitelline bands relatively long ..... ..... *Lutziella* Rohde, 1966.[2] (Fig. 16.25)**

**Diagnosis:** Body fusiform, flat, broadest in region of ventral sucker. Tegument unspined. Oral sucker larger than ventral. Pharynx small. Oesophagus very long, reaches level of posterior margin of ventral sucker. Intestinal bifurcation dorsal to ventral sucker. Caeca rudimentary, sacciform. Testes lateral to ventral sucker. Cirrus-sac small. Genital pore submedian, posterior to pharynx. Ovary as large as testes, submedian, just posterior to intestinal bifurcation. Uterus with numerous coils occupying most of hindbody (but not reaching posterior extremity) and forebody. Vitellarium composed of relatively few, fairly large follicles, forms two relatively long lateral bands in middle third of body, beginning at level of testes. Excretory vesicle I-shaped; pore terminal. In gall-bladder of bats; Malaysia. Type-species *L. microacetabularis* Rohde, 1966.

**4a. Caeca reach middle of body; testes intercaecal; vitellarium not passing caecal extremities ..... 5.**

[2] Erected by Rohde (1966) as a subgenus of *Lutztrema*.

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**4b. Caeca not reaching middle of body; testes partly extracaecal; vitellarium posterior to caecal ends ..... *Leipertrema* Sandosham, 1951. (Fig. 16.26)**

**Diagnosis:** Body lanceolate to fusiform, broadest in region of ventral sucker and testes. Tegument armed with spines. Suckers subequal. Pharynx very small. Oesophagus short. Intestinal bifurcation in forebody. Caeca short, extend just beyond testes, not reaching middle of body. Testes longitudinally oval, large, posterolateral to ventral sucker, mostly extracaecal. Cirrus-sac elongate, of medium size, reaches anterior border of ventral sucker. Genital pore median, just posterior to pharynx. Ovary small, median, between posterior edges of testes. Uterine coils reach posterior extremity. Vitellarium composed of several large follicles forming two clusters posterior to ovary and between caecal ends. Excretory vesicle I-shaped; pore terminal. In pancreas of primates; Asia (Borneo, Malaysia). Type-species *L. rewelli* Sandosham, 1951.

**5a. Lateral margins of body distinctly serrate in vitelline region; vitellarium forms lateral bands ..... *Brodenia* Gedoelst, 1913. (Fig. 16.27)**

**Diagnosis:** Body elongate, unarmed, distinctly enlarged and serrate laterally in ovariovitelline region. Suckers subequal, in first third of body. Pharynx small. Oesophagus short. Caeca terminate

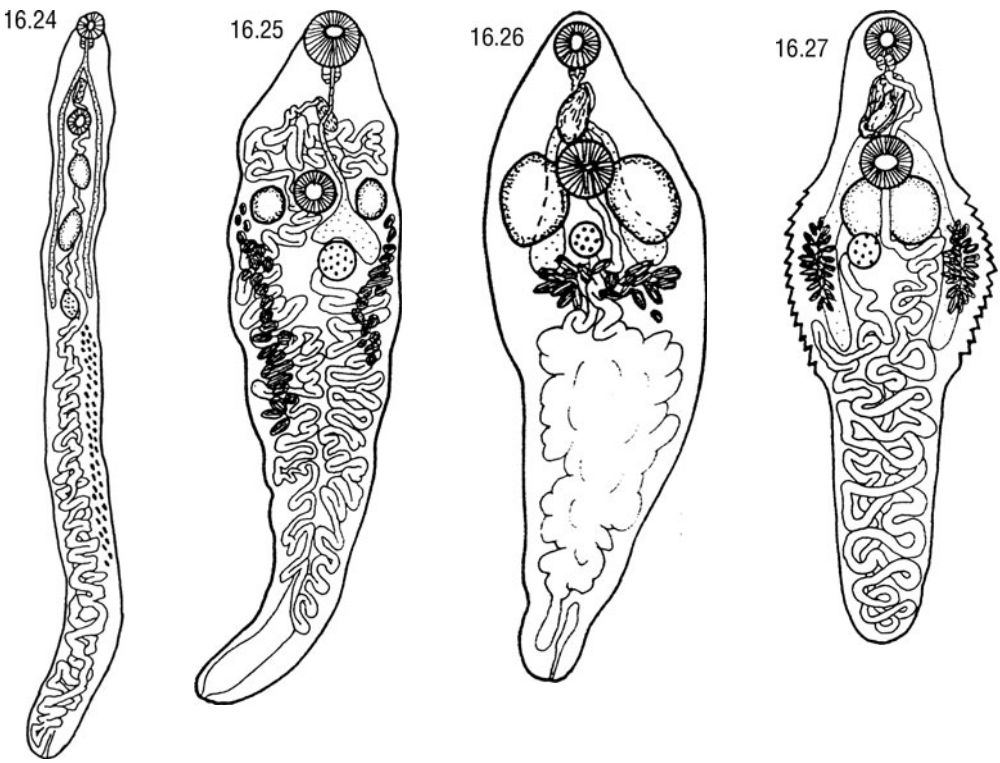



**Fig. 16.24.** *Caballerolecythus ibunami* Lamothe-Argumedo, Falcón-Ordaz, García-Prieto, Fernández-Fernández, 2005. After Lamothe-Argumedo *et al.* (2005).
**Fig. 16.25.** *Lutziella microacetabularis* (Rohde, 1966). After Rohde (1966).
**Fig. 16.26.** *Leipertrema rewelli* Sandosham, 1951. After Yamaguti (1971).
**Fig. 16.27.** *Brodenia serrata* Gedoelst, 1913. After Yamaguti (1971).

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at about middle of body. Intestinal bifurcation in forebody. Testes longitudinally oval, posterior to ventral sucker, may partly overlap caeca. Cirrus-sac large, reaches anterior border of ventral sucker. Genital pore just posterior to pharynx. Ovary smaller than testes, submedian, just posterior to one of testes. Laurer's canal not observed. Uterine coils occupy most of hindbody and reach posterior extremity. Vitellarium forms short lateral bands between testes and caecal ends. Excretory system not described. In pancreas of primates; Africa (Guinea, Congo). Type-species *B. serrata* Gedoelst, 1913.

**5b. Lateral margins of body smooth; vitellarium forms lateral clusters ..... ..... *Manidicola* Graber & Gevrey, 1981. (Fig. 16.28)**

**Diagnosis:** Body fusiform, with conical anterior extremity, broadest in vitelline region, lateral margins smooth. Tegument unspined. Suckers subequal; ventral, near middle of body. Pharynx small. Oesophagus relatively long. Intestinal bifurcation in forebody. Caeca reach slightly beyond ovary. Testes longitudinally oval, large, in region of ventral sucker, intercaecal. Cirrus-sac elongate, of medium size, between pharynx and intestinal bifurcation. Genital pore median, just posterior to pharynx. Ovary small, submedian, separate from testes. Uterine coils occupy hindbody. Vitellarium forms two lateral clusters at level of ovary; clusters do not extend beyond caeca. Excretory vesicle I-shaped, long; extent not determined. In intestine of mammals; Africa (Congo). Type-species *M. congolensis* Graber & Gevrey, 1981.

**6a. Testes posterior or posterolateral to ventral sucker ..... 7.**
**6b. Testes anterior or anterolateral to ventral sucker ..... 19.**

**7a. Genital pore distinctly submedian; ovary at least partly between testes ..... ..... *Infidum* Travassos, 1916. (Figs 16.29, 16.30)**

**Diagnosis:** Body flattened, broadly oval. Tegument armed with spines or not. Suckers subequal. Pharynx small. Oesophagus short. Intestinal bifurcation in forebody. Caeca quite long, but not reaching posterior extremity. Testes posterolateral to ventral sucker, may be lobed. Cirrus-sac reaches or even partly overlaps ventral sucker. Genital pore strongly submedian, at level of oesophagus or intestinal bifurcation. Ovary median or submedian, entirely or partly between testes. Uterine coils generally intercaecal. Vitellarium composed of fine follicles, forms two lateral, mostly extracaecal, bands of differing lengths and beginning anterior to testes. Excretory vesicle I- or Y-shaped; its stem reaches close to ovary; pore terminal. In gall-bladder of reptiles; South America (Brazil, Galapagos). Type-species *I. infidum* (Gomes de Faria, 1910) Travassos, 1916.

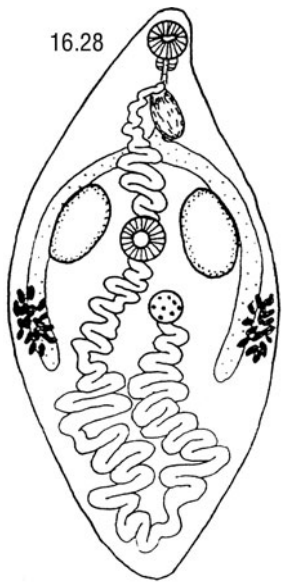
**7b. Genital pore more or less median; ovary posterior to testes ..... 8.**

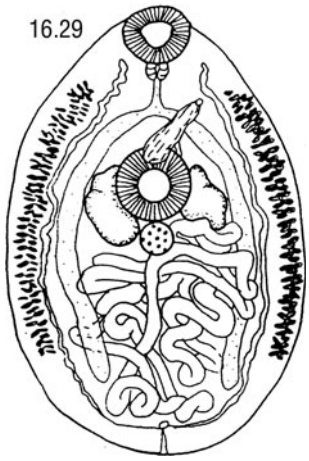
**8a. Caeca wide, straight, not reaching posterior extremity ..... 9.**
**8b. Caeca narrow, length variable ..... 10.**

**9a. Genital pore at level of intestinal bifurcation or anterior to it; caeca terminate close to posterior extremity; vitelline bands posterior to testes ..... ..... *Paradistomum* Kossack, 1910. (Figs 16.31, 16.32)**
(Syn. *Paradistomoides* Travassos, 1944)

**Diagnosis:** Body usually oval with rounded extremities or more elongate. Tegument unspined. Suckers large, subequal. Pharynx quite large. Oesophagus short. Intestinal bifurcation in forebody. Caeca wide, straight, end close to posterior extremity. Testes symmetrical or almost so, smooth or

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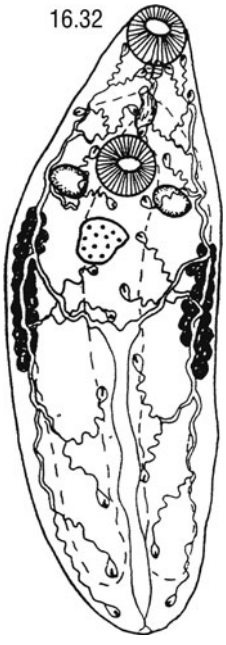




**Fig. 16.28.** *Manidicola congolensis* Graber & Gevrey, 1981. Drawn from photographs of Graber & Gevrey (1981).
**Fig. 16.29.** *Infidum infidum* (Gomes de Faria, 1910). Note long vitelline bands. After Yamaguti (1971).
**Fig. 16.30.** *Infidum similis* Travassos, 1916. Note short vitelline bands. After Travassos (1944).
**Fig. 16.31.** *Paradistomum mutabile* (Molin, 1859). After Travassos (1944).
**Fig. 16.32.** *Paradistomum samoensis* Byrd, 1949. Note the extent of excretory vesicle. After Byrd (1949).

lobed, posterior or posterolateral to ventral sucker, overlapping caeca or entirely extracaecal. Cirrus-sac elongate, usually reaches anterior margin of ventral sucker. Genital pore median or slightly submedian, anterior to or at level of intestinal bifurcation. Ovary median to submedian, posterior to ventral sucker, may be lobed. Uterus occupies entire hindbody, extends extracaecally. Vitellarium composed of few large follicles, forms two short bands or clusters posterior to testes. Excretory vesicle tubular, long, almost reaches level of ovary; pore terminal. Life-cycle of eurytrema-type. In gall-bladder and bile-ducts or, rarely, intestine of reptiles; Europe, South-east Asia, Madagascar, South America (Brazil), Australia. Type-species *P. robusculum* Kossack, 1910.

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**9b. Genital pore posterior to intestinal bifurcation; caeca terminate distant from posterior extremity; vitelline bands begin at level of pharynx ..... ..... *Paradistomoidella* Brooks & Palmieri, 1981. (Fig. 16.33)**

**Diagnosis:** Body oval, with rounded extremities. Tegument unspined. Suckers well developed; ventral smaller than oral. Pharynx large, muscular. Oesophagus practically absent. Intestinal bifurcation in forebody. Caeca wide, straight, extend beyond level of ovary but end distant from posterior extremity. Testes symmetrical or slightly diagonal, posterolateral to ventral sucker. Cirrus-sac dorsal to ventral sucker, contains bipartite seminal vesicle. Genital pore immediately anterior to ventral sucker, posterior to intestinal bifurcation. Ovary median, just posterior to testes, may be lobed. Uterus with coiled descending and ascending limbs posterior to ovary. Vitellarium forms two lateral bands from level of pharynx that extend along caeca. Excretory vesicle I-shaped; pore terminal. In intestine of reptiles; Malaysia. Type-species *P. cerberi* Brooks & Palmieri, 1981.

**10a. Vitellarium forms clusters of follicles ..... 11.**
**10b. Vitellarium forms bands of follicles ..... 12.**

**11a. Ventral sucker larger than oral; vitelline clusters at level of ovary ..... ..... *Concinnum* Bhalerao, 1936. (Figs 16.34, 16.35)**

**Diagnosis:** Body oval, elliptical or fusiform. Tegument armed or not. Suckers well developed; ventral in anterior half of body, larger than oral. Pharynx rather small. Oesophagus present. Intestinal bifurcation in forebody. Caeca narrow, terminate well short of posterior extremity. Testes usually intercaecal, but may overlap caeca or be extracaecal, posterolateral to ventral sucker. Cirrus-sac elongate. Genital pore usually anterior to intestinal bifurcation. Ovary submedian, smaller than testes, posterior to or partly between testes. Uterus coiled in entire hindbody, extends extracaecally. Eggs small to medium in size. Vitelline follicles form two clusters at level of ovary. Excretory vesicle I- or Y-shaped; stem reaches close to level of caecal ends; pore terminal. Known life-cycles of eurytrema-type. In bile-ducts and gall-bladder of mammals and birds; Africa (Congo), North America (USA), South America (Brazil) and Asia (India, Japan, Sumatra). Type-species *C. concinnum* (Braun, 1910) Bhalerao, 1936.

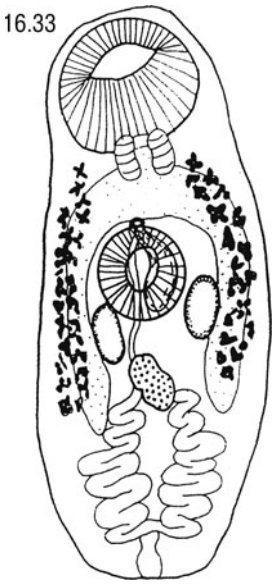
**11b. Suckers subequal; vitelline clusters posterior to ovary ..... ..... *Parametadelphis* Travassos, 1955. (Fig. 16.36)**

**Diagnosis:** Body fusiform. Tegument with papillae on surface. Suckers well developed, subequal. Pharynx small. Oesophagus short. Intestinal bifurcation in forebody. Extent of caeca not determined (according to Travassos (1955), rather short, perhaps to level of vitellarium). Testes symmetrical, posterolateral to ventral sucker, slightly lobed. Cirrus-sac elongate, situated diagonally between ventral sucker and intestinal bifurcation. Genital pore slightly submedian, at level of intestinal bifurcation. Ovary submedian, separated from testes by uterine coils. Uterine coils occupy entire area between intestinal bifurcation and posterior extremity, also extracaecal. Vitelline clusters clearly posterior to ovary. Excretory system not described. In gall-bladder of mammals; South America (Brazil). Type-species *P. compactus* Travassos, 1955.

**12a. Genital pore anterior to intestinal bifurcation ..... 13.**
**12b. Genital pore at level of intestinal bifurcation ..... 17.**

**13a. Vitelline bands begin at level of testes ..... 14.**
**13b. Vitelline bands begin at level of ventral sucker ..... 15.**

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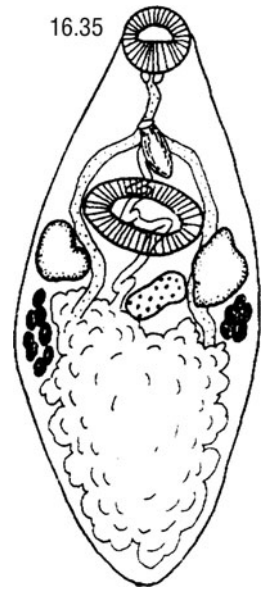



**Fig. 16.33.** *Paradistomoidella cerberi* Brooks & Palmieri, 1981. After Brooks & Palmieri (1981).
**Fig. 16.34.** *Concinnum concinnum* (Braun, 1901). Note intercaecal position of testes. After Travassos (1944).
**Fig. 16.35.** *Concinnum ellipticum* Travassos, 1941. Note extracaecal position of testes. After Travassos (1944).

**14a. Ventral sucker close to intestinal bifurcation, in anterior third of body; vitellarium usually in middle third of body ..... *Skrjabinus* Bhalerao, 1936. (Fig. 16.37)**
(Syn. *Zonorchis* Travassos, 1944)

**Diagnosis:** Body elongate, elliptical or fusiform. Tegument unspined. Both suckers in anterior third of body; ventral subequal or larger than oral, close to intestinal bifurcation in anterior third of body. Pharynx well developed. Oesophagus short or very short. Intestinal bifurcation in forebody. Caeca usually terminate near posterior extremity, sometimes almost reach it. Testes just posterior or posterolateral to ventral sucker. Cirrus-sac usually extends beyond intestinal bifurcation. Genital pore anterior to intestinal bifurcation, even at level of pharynx. Ovary rounded, submedian, separated from testes by uterine coils. Uterine coils intercaecal, occupy entire hindbody. Vitelline bands of different length, composed of fine follicles, usually in middle third of body, sometimes much longer, begin at level of posterior margin of testes. Excretory vesicle I- or Y-shaped, with long stem that can reach level of vitellarium. Known life-cycles of eurytrema-type. In gall-bladder and bile-ducts of birds and mammals; cosmopolitan. Type-species *S. skrjabini* (Issaitschikow, 1920) Bhalerao, 1936.

**14b. Ventral sucker distant from intestinal bifurcation, near middle of body; vitellarium in posterior half of body ..... *Conspicuum* Bhalerao, 1936. (Fig. 16.38)**

**Diagnosis:** Body fusiform, with maximum width posterior to testes. Tegument unspined. Oral sucker smaller than ventral; ventral near middle of body, distant from intestinal bifurcation. Pharynx well developed. Oesophagus present. Intestinal bifurcation in forebody. Caeca long, end near posterior extremity. Testes posterior or posterolateral to ventral sucker, may be lobed. Cirrus-sac elongate or oval, between pharynx and intestinal bifurcation. Genital pore submedian, anterior to intestinal bifurcation, often at level of pharynx. Ovary submedian, usually just posterior to one testis, sometimes more posterior. Uterine coils intercaecal. Vitelline bands of medium length, beginning at level of testes, in

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posterior half of body. Excretory vesicle Y-shaped, with long stem and rudimentary arms; stem terminates well apart from ovary. Known life-cycles of eurytrema-type. In gall-bladder of birds, rarely of mammals; Europe, Asia (Kamchatka, India), Africa (Congo), North America, Central America (Cuba), South America (Brazil). Type-species *C. conspicuum* (Gomes de Faria, 1912) Bhalerao, 1936.

**15a. Suckers subequal ..... 16.**
**15b. Ventral sucker much larger than oral ..... *Canaania* Travassos, 1944. (Fig. 16.39)**
**Diagnosis:** Body oval, broad, with more or less pointed posterior extremity. Tegument unspined. Oral sucker relatively small. Ventral sucker near middle of body-length, much larger than oral sucker. Pharynx well developed. Oesophagus short. Intestinal bifurcation in forebody. Caeca long, extend to near posterior extremity. Testes posterior to ventral sucker, may overlap caeca. Cirrus-sac elongate, anterior to ventral sucker and separated from it. Genital pore at level of pharynx. Ovary submedian, posterior to testes or partly at their level. Uterine coils usually intercaecal, occupy both forebody and hindbody but do not reach posterior extremity. Eggs small, numerous. Vitelline follicles form two relatively long bands extending along caeca from level of anterior border of ventral sucker, or more anteriorly, to beyond ovary. Excretory vesicle tubular, almost reaches level of ovary; pore terminal. In bile-ducts of mammals; South America (Brazil). Type-species *C. obesa* Travassos, 1944.

**16a. Body oval; cirrus-sac small; ovary as large as testes ..... ..... *Lubens* Travassos, 1919. (Fig. 16.40)**
**Diagnosis:** Body broadly oval. Suckers equal or subequal, in first quarter of body. Pharynx small. Oesophagus very short. Intestinal bifurcation in forebody. Caeca long, almost reach posterior extremity. Testes relatively small, posterior to ventral sucker. Cirrus-sac small, at level of intestinal bifurcation. Genital pore at level of pharynx. Ovary submedian, distant from testes, as large as or may be larger than testes. Uterine coils occupy entire hindbody, also present extracaecally. Vitelline bands narrow, of various lengths, usually begin at level of ventral sucker or anterior borders of testes and extend along caeca far beyond ovary. Eggs small. Excretory vesicle Y-shaped, with long stem and arms reaching to anterior half of body; pore subterminal. In gall-bladder of birds; Asia (India, Philippines), North America (USA), Central America (Costa Rica) and South America (Brazil). Type-species *L. lubens* (Braun, 1901) Travassos, 1919.

**16b. Body elongate; cirrus-sac large; ovary smaller than testes ..... ..... *Platynosomoides* Yamaguti, 1971. (Fig. 16.41)**
**Diagnosis:** Body fusiform, with long hindbody. Tegument unspined. Oral sucker slightly smaller than ventral; latter in first quarter of body. Pharynx large. Oesophagus short. Intestinal bifurcation in forebody. Caeca end near posterior extremity. Testes large, immediately posterior to ventral sucker. Cirrus-sac elongate, quite large. Genital pore at level of pharynx. Ovary submedian, smaller than testes, posterior to left testis. Uterine coils intercaecal, occupy entire hindbody. Vitelline bands quite long, extend along caeca from level of ventral sucker to far beyond ovary. Excretory system not observed. In liver of mammals, especially rodents; Asia (Armenia, Dagestan, Malaysia) and Africa (Congo). Type-species *P. muris* (Shcherbakova, 1942) Yamaguti, 1971.

**17a. Vitelline bands very long, beginning at level of pharynx ..... ..... *Dictyonograptus* Travassos, 1919. (Fig. 16.42)**
**Diagnosis:** Body broadly fusiform. Tegument unspined. Suckers subequal, in first quarter of body. Pharynx small. Oesophagus short. Intestinal bifurcation in forebody. Caeca long but not reaching posterior extremity. Testes oval, just posterior to ventral sucker. Cirrus-sac small, may

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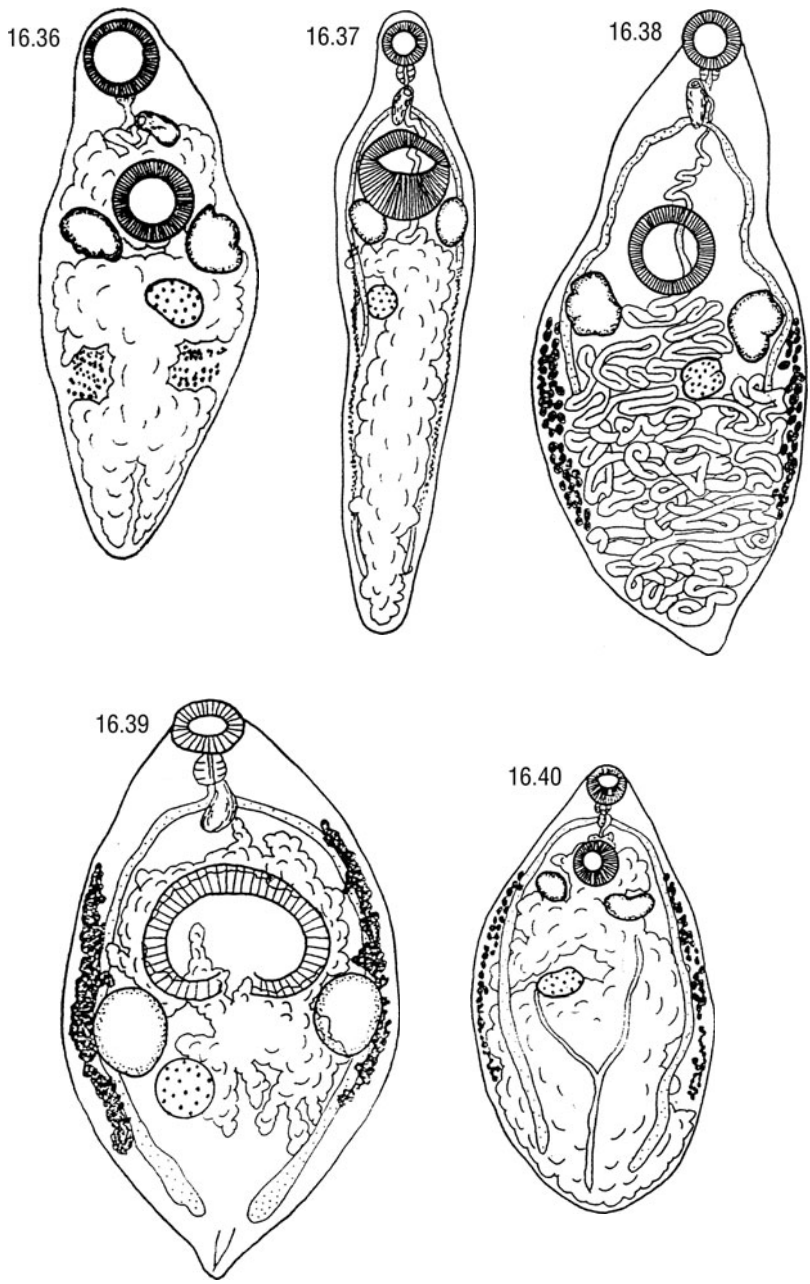



**Fig. 16.36.** *Parametadelphis compactus* Travassos, 1955. After Travassos (1955).
**Fig. 16.37.** *Skrjabinus similis* Shtrom, 1940. After Shtrom (1940).
**Fig. 16.38.** *Conspicuum conspicuum* (Gomes de Faria, 1912). After Skrjabin & Evranova (1952).
**Fig. 16.39.** *Canaania obesa* Travassos, 1944. After Travassos (1944).
**Fig. 16.40.** *Lubens lubens* (Braun, 1901). Note the shape of excretory vesicle. After Travassos (1944).

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reach anterior border of ventral sucker. Genital pore median, just posterior to intestinal bifurcation. Ovary small, submedian, partly between testes. Uterine coils occupy entire hindbody. Eggs very numerous, of medium size. Vitelline bands long, extend from level of pharynx to caecal ends. Excretory system not described. In pancreas and gall-bladder of mammals; Asia (Vietnam) and South America (Brazil). Type-species *D. dictyonograptus* Travassos, 1919.

**17b. Vitelline bands short, beginning posterior to testes or at their level ..... 18.**

**18a. Genital pore at level of intestinal bifurcation; cirrus-sac relatively small ..... ..... *Platynosomum* Looss, 1907. (Fig. 16.43)**

**Diagnosis:** Body usually elongate, with long hindbody. Tegument with or without spines. Suckers in anterior quarter of body, subequal or ventral larger than oral. Pharynx small. Oesophagus short but distinct. Intestinal bifurcation in forebody. Caecal termination distant from posterior extremity. Testes large, usually lobed, just posterior or posterolateral to ventral sucker. Cirrus-sac relatively small, may reach anterior border of ventral sucker. Genital pore slightly submedian, usually just anterior to intestinal bifurcation. Ovary smaller than testes, immediately posterior to one of them, submedian, may be lobed. Uterine coils occupy entire hindbody. Vitelline bands in middle third of body, usually begin at level of ovary, posterior to ventral sucker. Excretory vesicle tubular, may reach close to Mehlis' gland. Known life-cycles of platynosomum-type, with terrestrial molluscs as first, arthropods as second and lizards as paratenic (or third intermediate) hosts. In liver, gall-bladder and pancreas of birds and mammals; Europe, Africa, Asia, North, Central and South America. Type-species *P. semifuscum* Looss, 1907.

**18b. Genital pore posterior to intestinal bifurcation; cirrus-sac large, elongate ..... ..... *Eurytrema* Looss, 1907. (Fig. 16.44)**

(Syn. subgenus *Pancreaticum* Bhalerao, 1936)

**Diagnosis:** Body broadly oval or fusiform. Tegument armed or not. Suckers subequal; ventral usually slightly smaller, distant from oral, sometimes in middle of body-length. Pharynx well developed. Oesophagus very short. Intestinal bifurcation in forebody. Caeca usually long but terminate distant from posterior extremity. Testes posterolateral to ventral sucker, may overlap caeca, may be lobed. Cirrus-sac large, elongate, between intestinal bifurcation and ventral sucker, may reach ventral sucker. Genital pore posterior to intestinal bifurcation. Ovary submedian, clearly posterior to testes, may be lobed. Uterine coils intercaecal. Vitelline bands rather short, wide, with follicles sometimes forming clusters, posterior to testes. Excretory vesicle T-shaped; stem long, reaches close to ovary; pore terminal. Known life-cycles of eurytrema-type. In bile-ducts, gall-bladder, pancreatic ducts and intestine of mammals; Europe, Madagascar, Asia and South America (Brazil). Type-species *E. pancreaticum* (Janson, 1889) Looss, 1907.

**19a. Body almost discoid; uterine coils reach level of oral sucker; vitelline bands reach caecal ends ..... *Euparadistomum* Tubangui, 1931. (Figs 16.45, 16.46)**

(Syn. *Evandrocotyle* Jansen, 1941)

**Diagnosis:** Body broadly oval to discoid. Tegument unspined. Suckers relatively large, subequal; ventral in about middle of body. Pharynx oval. Oesophagus short. Intestinal bifurcation in forebody. Caeca usually wide, reach close to posterior extremity. Testes entirely anterior or anterolateral to ventral sucker. Cirrus-sac very small. Genital pore median or submedian, at level of intestinal bifurcation or posterior to it. Ovary median or submedian, posterior to ventral sucker, may overlap its posterior border. Uterus forms numerous coils, inter- and extracaecal, reaches level of oral sucker. Vitelline bands composed of fine follicles, narrow, usually long, between intestinal bifurcation and caecal ends (sometimes slightly shorter). Excretory vesicle Y-shaped, with long stem reaching close to

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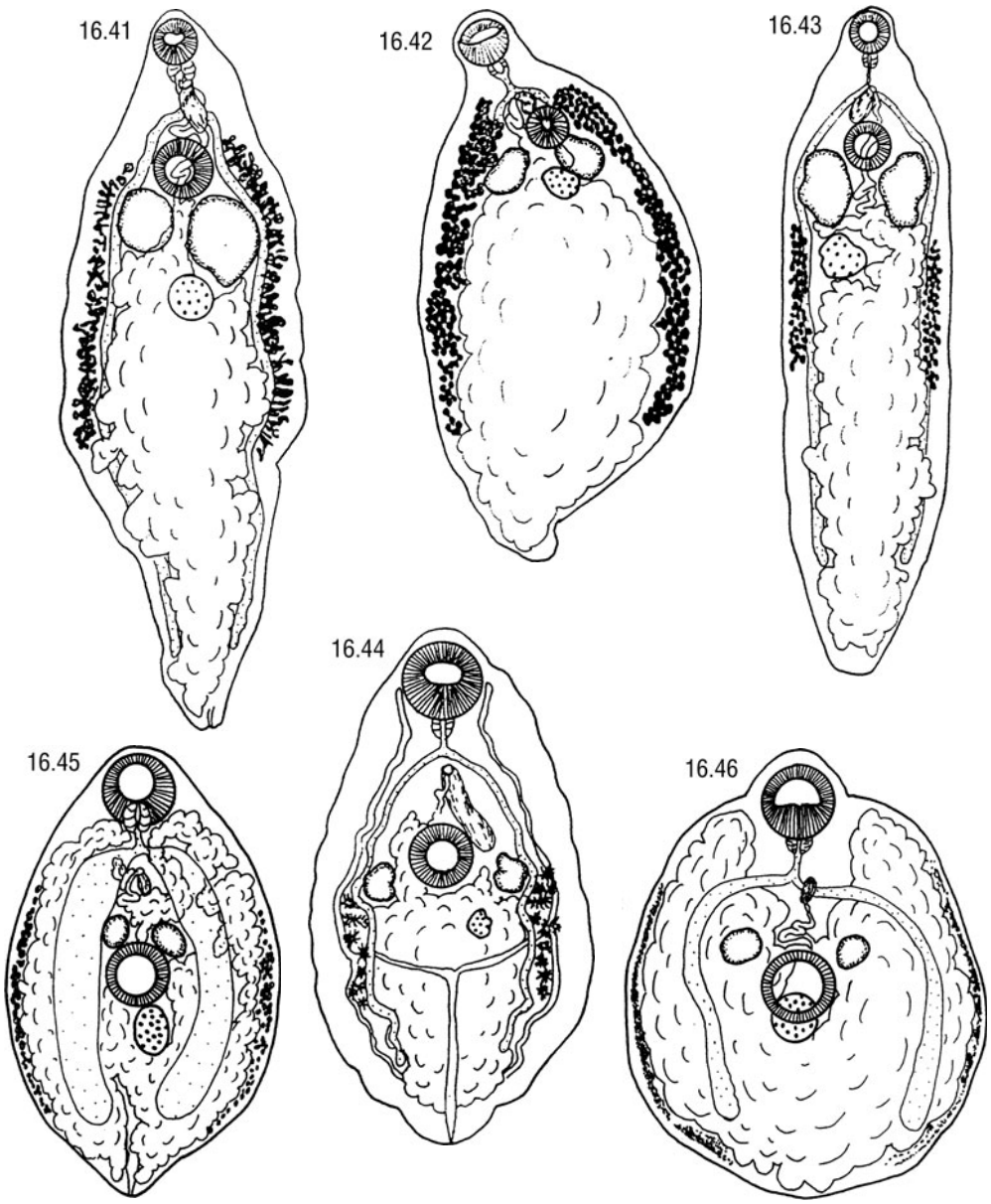



**Fig. 16.41.** *Platynosomoides muris* (Shcherbakova, 1916). After Skrjabin & Evranova (1952).
**Fig. 16.42.** *Dictyonograptus dictyonograptus* Travassos, 1919. After Travassos (1944).
**Fig. 16.43.** *Platynosomum semifuscum* Looss, 1907. After Skrjabin & Evranova (1952).
**Fig. 16.44.** *Eurytrema pancreaticum* (Janson, 1889). After Travassos (1944).
**Fig. 16.45.** *Euparadistomum varani* Tubangui, 1931. Note the median position of genital pore, posterior to intestinal bifurcation. After Travassos (1944).
**Fig. 16.46.** *Euparadistomum pipistrelli* (Sandground, 1937). Note the discoid body-shape and the position of the genital pore at the level of intestinal bifurcation. After Travassos (1944).

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Mehlis' gland; pore terminal. In gall-bladder or intestine of reptiles and mammals; Africa, Madagascar, Asia, South America (Brazil), New Guinea and Fiji. Type-species *E. varani* Tubangui, 1931.

**19b. Body broadly oval; uterine coils not reaching anteriorly to intestinal bifurcation; vitelline bands not reaching caecal ends ..... 20.**

**20a. Vitellarium of fine follicles, forming bands in region of ventral sucker ..... ..... *Platynotrema* Nicoll, 1914. (Fig. 16.47)**
(Syn. *Praeorchitrema* Oshmarin, 1952)

**Diagnosis:** Body broadly oval. Tegument armed or not. Suckers relatively large; ventral in about middle of body, larger than oral. Pharynx small. Oesophagus short. Intestinal bifurcation in forebody. Caeca long, reach to near posterior extremity. Testes lobed, anterolateral to ventral sucker. Cirrus-sac elongate. Genital pore at level of intestinal bifurcation or more anterior. Ovary smaller than testes, submedian, close to posterior border of ventral sucker or separated from it by uterine coils. Uterine coils mainly in hindbody, extracaecal. Vitelline bands composed of fine follicles, extracaecal, short, extend from zone of ventral sucker more or less posterior to ovary, do not reach caecal ends. Excretory vesicle tubular, reaches close to ovary; pore subterminal. In bile-ducts or gall-bladder of birds; Asia, Australia. Type-species *P. biliosum* Nicoll, 1914.

**20b. Vitellarium of large follicles forming two clusters just posterior to ventral sucker ... 21.**

**21a. Vitellarium forms large inter- and extracaecal clusters, reaching beyond ovary; caeca reach posterior extremity ..... *Ugandalubens* Goodman, 1988. (Fig. 16.48)**

**Diagnosis:** Body flattened, very broad in middle third. Tegument unspined. Suckers relatively small, subequal; ventral situated in about middle of body. Pharynx large. Oesophagus short. Intestinal bifurcation in forebody. Caeca very long, convoluted, reach posterior extremity. Testes transversely oval, anterolateral to ventral sucker. Cirrus-sac elongate, extends posterior to intestinal bifurcation. Genital pore median, at level of pharynx. Ovary distant from ventral sucker, submedian. Uterus usually intercaecal; its ascending limb strongly coiled at level of ventral sucker. Vitelline clusters occupy large zones extra- and intercaecally, extending from level of ventral sucker to posterior quarter of body. Excretory vesicle tubular, reaches third quarter of body; pore subterminal. In gall-bladder of birds; Africa (Uganda). Type-species *U. banagei* Goodman, 1988.

**21b. Vitellarium forms short extracaecal clusters at level of ovary; caeca do not reach posterior extremity ..... *Paraconcinnum* Vassiliadès & Richard, 1970. (Fig. 16.49)**

**Diagnosis:** Body fusiform, very broad in middle, posterior to ventral sucker. Tegument unspined. Suckers relatively small; ventral in anterior half of body, slightly larger than oral. Pharynx large. Oesophagus short. Intestinal bifurcation in forebody. Caeca terminate in middle third of body. Testes large, slightly lobed, anterolateral to ventral sucker. Cirrus-sac sacciform, reaches intestinal bifurcation. Genital pore at level of pharynx. Ovary much smaller than testes, submedian, separated from ventral sucker. Uterine coils loosely arranged, mainly in hindbody, inter- and extracaecal. Vitellarium composed of several large follicles, forming two extracaecal clusters at level of ovary. Excretory vesicle tubular, reaches level of caecal ends; pore subterminal. In pancreatic ducts of mammals (Muridae); Africa (Congo). Type-species *P. hylomysci* Vassiliadès & Richard, 1970.

**22a. Ovary lobed; vitellarium forms two bands at level of ovary ..... ..... *Stromitrema* Skrjabin, 1944. (Fig. 16.50)**

**Diagnosis:** Body oval or fusiform. Suckers quite large, subequal; oral muscular; ventral weakly muscled and hardly detectable. Pharynx small. Oesophagus short, practically absent. Intestinal

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bifurcation in forebody. Caeca not reaching posterior extremity. Testes in anterior half of body, lateral to ventral sucker, overlap caeca. Cirrus-sac large, elongate. Genital pore median, just posterior to intestinal bifurcation. Ovary strongly lobed, median or submedian, posterior to ventral sucker. Vitelline bands short, broad, posterior to testes, at level of ovary in middle third of body. Uterus strongly coiled in both hindbody and forebody, extends extracaecally. Excretory system not described. In gall-bladder of birds; Europe (Russia, Czech Republic). Type-species *S. koshewnikowi* (Skrjabin & Massino, 1925) Skrjabin, 1944.

**22b. Ovary unlobed; vitellarium forms two clusters in posterior half of body ..... 23.**

**23a. Testes smaller than ovary, in middle third of body .....**
**..... *Pancreatrema* Oshmarin, 1952. (Fig. 16.51)**

**Diagnosis:** Body fusiform, with conical posterior extremity. Oral sucker of medium size. Ventral sucker rudimentary, very indistinct. Pharynx small. Oesophagus short. Intestinal bifurcation in forebody. Caecal ends not observed. Testes smaller than ovary, round, in middle third of body. Cirrus-sac small, rounded. Genital pore posterior to intestinal bifurcation. Ovary entire, submedian, in posterior half of body. Uterus occupies most of body posterior to intestinal bifurcation. Vitelline follicles form two clusters posterior to ovary. Excretory system not described. In pancreas of birds; Europe (Russia) and Australia. Type-species *P. disacetabulum* Oshmarin, 1952.

**23b. Testes larger than ovary, in anterior third of body .....**
**..... *Bravotrema* Groschaft, 1970. (Fig. 16.52)**

**Diagnosis:** Body fusiform, with conical posterior extremity. Tegument unspined. Suckers in anterior third of body. Oral sucker small. Ventral larger than oral, but weakly developed. Pharynx small. Oesophagus short. Intestinal bifurcation in forebody. Caeca end distant from posterior extremity. Testes smooth, larger than ovary, in anterior third of body anterolateral to ventral sucker, overlap caeca. Cirrus-sac quite large, sacciform. Genital pore submedian, at level of intestinal bifurcation. Ovary smaller than testes, submedian, in posterior half of body, far posterior to ventral sucker. Uterus occupies most of body, intercaecal. Vitelline follicles large, form clusters posterior to ovary. Excretory vesicle Y-shaped, with short stem and arms. In liver of birds; Central America (Cuba). Type-species *B. hollisae* Groschaft, 1970.

## Subfamily Proacetabulorchiinae Odening, 1964

**Diagnosis:** Body slim, elongate, with prominent ventral sucker. Tegument unspined. Distance between oral and ventral suckers large. Pharynx muscular. Oesophagus relatively long. Intestinal bifurcation in forebody. Caeca long, reach close to posterior extremity. Testes tandem between intestinal bifurcation and ventral sucker. Cirrus-sac variable in size. Genital pore anterior to intestinal bifurcation. Ovary posterior to ventral sucker, median. Uterus intercaecal, occupies entire hindbody. Vitellarium forms two lateral bands. Excretory system not described. Life-cycle not known. In intestine or liver of birds; Asia. Type-genus *Proacetabulorchis* Gogate, 1940.

## Key to genera

**1a. Ventral sucker in anterior third of body; vitelline bands in middle third of body .....**
**..... *Proacetabulorchis* Gogate, 1940. (Fig. 16.53)**

**Diagnosis:** Hindbody much longer than forebody. Ventral sucker in anterior third of body. Cirrus-sac small. Testes larger than ovary. Ovary not far from ventral sucker. Vitellarium forms

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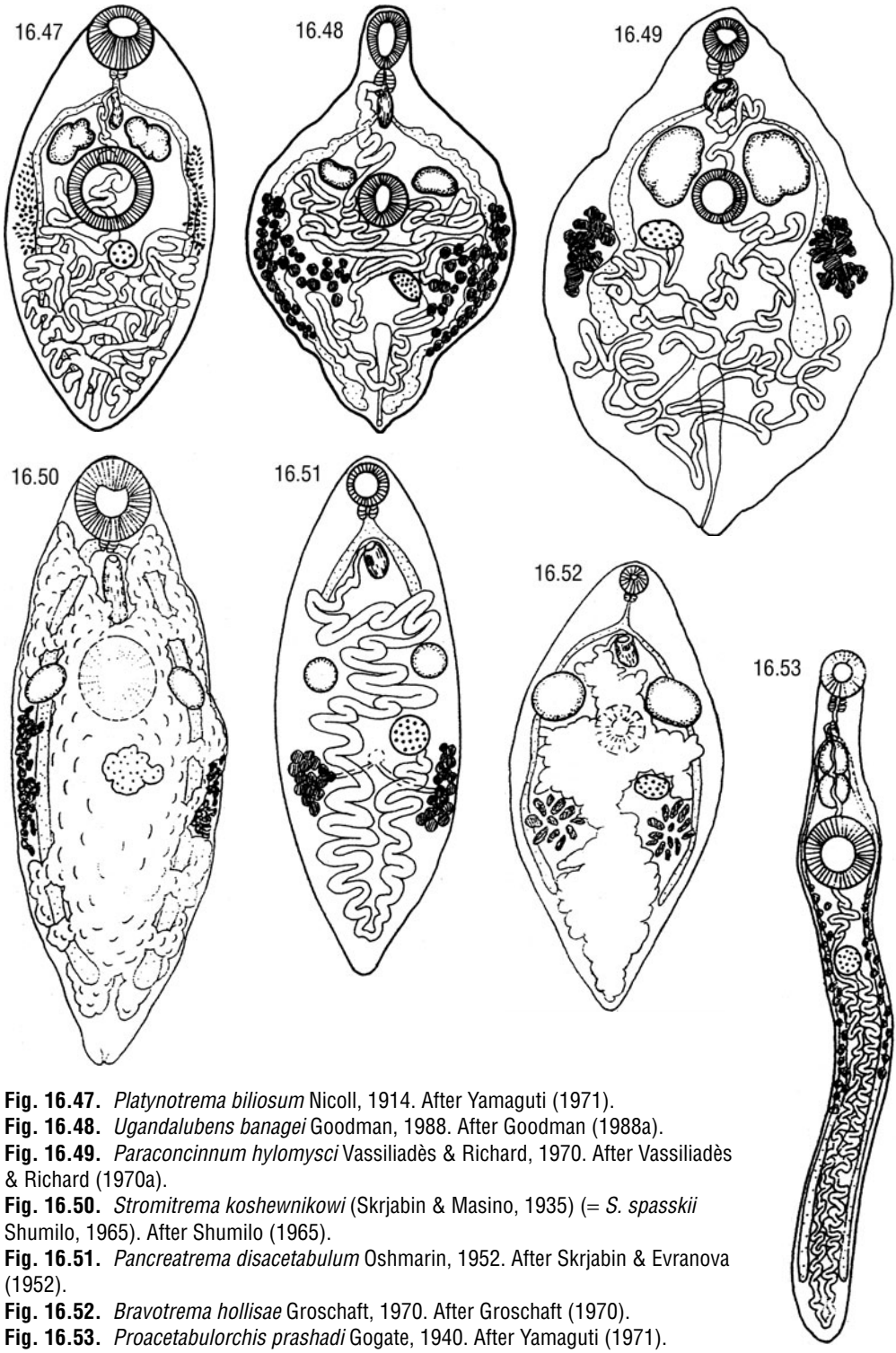



**Fig. 16.47.** *Platynotrema biliosum* Nicoll, 1914. After Yamaguti (1971).
**Fig. 16.48.** *Ugandalubens banagei* Goodman, 1988. After Goodman (1988a).
**Fig. 16.49.** *Paraconcinnum hylomysci* Vassiliadès & Richard, 1970. After Vassiliadès & Richard (1970a).
**Fig. 16.50.** *Stromitrema koshewnikowi* (Skrjabin & Masino, 1935) (= *S. spasskii* Shumilo, 1965). After Shumilo (1965).
**Fig. 16.51.** *Pancreatrema disacetabulum* Oshmarin, 1952. After Skrjabin & Evranova (1952).
**Fig. 16.52.** *Bravotrema hollisae* Groschaft, 1970. After Groschaft (1970).
**Fig. 16.53.** *Proacetabulorchis prashadi* Gogate, 1940. After Yamaguti (1971).

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lateral bands in middle third of body, beginning just posterior to ventral sucker and extending far posterior to ovary. In intestine of birds; Asia (Japan). Type-species *P. prashadi* Gogate, 1940.

**1b. Ventral sucker in middle of body; vitelline bands in last third of body, reaching posterior extremity ..... *Proacetabulorchoides* Oshmarin, 1970. (Fig. 16.54)**

**Diagnosis:** Hindbody as long as forebody. Ventral sucker in middle of body. Cirrus-sac large. Testes and ovary of similar sizes. Ovary about midway between ventral sucker and posterior extremity. Vitellarium forms lateral bands, which begin at level of ovary and extend to posterior extremity. In liver of birds; Asia (Vietnam). Type-species *P. anatis* Oshmarin, 1970.

## Subfamily Prosolecithinae Yamaguti, 1971

**Diagnosis:** Body fusiform, broadest at level of ventral sucker, with narrowed extremities. Tegument unspined. Suckers quite large, in anterior half of body; ventral distant from oral. Pharynx large, muscular. Oesophagus short. Intestinal bifurcation in forebody. Caeca long. Testes oval, symmetrical to slightly diagonal, anterior or posterior to ventral sucker. Cirrus-sac of medium size. Genital pore anterior to intestinal bifurcation. Ovary submedian, posterior to testes and ventral sucker. Uterus coiled in mid-region of body, rarely descending far posteriorly beyond ovary. Vitelline follicles not numerous, in two extracaecal bands between intestinal bifurcation and ovary. Excretory vesicle I-shaped, almost reaches ovary; pore terminal. Life-cycle not known. In liver or biliary system of small mammals; Africa, South America, Europe. Type-genus *Prosolecithus* Yamaguti, 1971.

## Key to genera

**1a. Testes anterior to ventral sucker; oral sucker smaller than ventral; vitellarium reaches ovarian level ..... *Hemixenotrema* Baer, 1971. (Fig. 16.55)**

**Diagnosis**. Body broadest at level of ventral sucker. Ventral sucker very large. Pharynx quite large. Oesophagus short. Caeca long but not reaching posterior extremity. Testes intercaecal, symmetrical or slightly diagonal, anterior to ventral sucker, may overlap anterior margin posteriorly. Cirrus-sac elongate, reaches level of anterior margins of testes. Genital pore median, at level of pharynx. Ovary submedian, separated from ventral sucker. Uterus descends only slightly posterior to ovary. Vitelline bands mostly extracaecal, extend from level of anterior margin of ventral sucker to ovary. In gall-bladder of rodents; Africa (Ivory Coast). Type-species *H. hunkeleri* Baer, 1971.

**1b. Testes posterior to ventral sucker; oral sucker almost equal to ventral sucker; vitellarium not reaching ovarian level ..... 2.**

**2a. Testes just posterior to ventral sucker; gonads in anterior half of body; genital pore median ..... *Yungasicola* Gardner & Pérez-Ponce de Léon, 2002. (Fig. 16.56)**

**Diagnosis:** Body broadest in middle of body. Oral sucker slightly larger than ventral. Oesophagus very short. Caeca long but not reaching posterior extremity. Testes symmetrical, just posterior to ventral sucker, may overlap its posterior margin. Cirrus-sac elongate, in median line, mostly intercaecal. Genital pore median, at level of pharynx or oesophagus. Gonads in anterior half of body. Ovary much smaller than testes and just posterior to one of them. Uterus coiled intercaecally, in middle part of body, only slightly posterior to ovary. Vitelline bands extracaecal, extend from level of anterior margin of ventral sucker to posterior margin of testes. In gall-bladder and bile-ducts of rodents; South America (Bolivia). Type-species *Y. travassosi* Gardner & Pérez-Ponce de Léon, 2002.

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**2b. Testes distant from ventral sucker; gonads in posterior half of body; genital pore submedian ..... *Prosolecithus* Yamaguti, 1971. (Figs 16.57, 16.58)**

**Diagnosis**. Body delicate, transparent, distinctly widened in middle region. Oesophagus relatively long. Caeca very long, reach posterior extremity, sometimes even convoluted. Testes separated from ventral sucker, slightly diagonal. Cirrus-sac extends beyond intestinal bifurcation. Genital pore submedian, halfway between pharynx and intestinal bifurcation. Gonads in posterior half of body. Ovary smaller than testes and posterior to one of them. Vitelline follicles extend from level of ventral sucker to posterior margin of testes. Uterus may reach far posterior to ovary. In liver of insectivores; Europe (Poland, Ukraine). Type-species *P. pellucidus* (Pojmańska, 1957) Yamaguti, 1971.

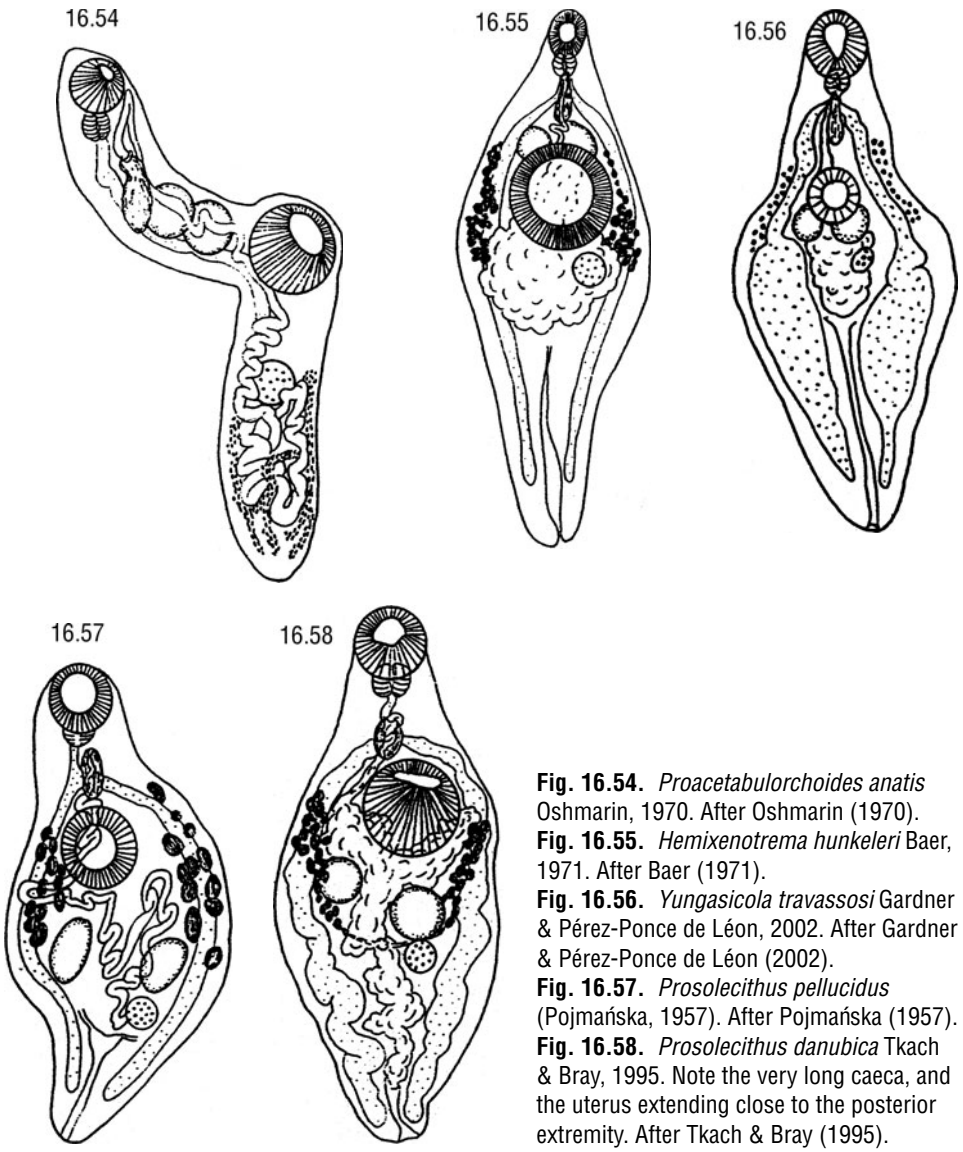



**Fig. 16.54.** *Proacetabulorchoides anatis* Oshmarin, 1970. After Oshmarin (1970).
**Fig. 16.55.** *Hemixenotrema hunkeleri* Baer, 1971. After Baer (1971).
**Fig. 16.56.** *Yungasicola travassosi* Gardner & Pérez-Ponce de Léon, 2002. After Gardner & Pérez-Ponce de Léon (2002).
**Fig. 16.57.** *Prosolecithus pellucidus* (Pojmańska, 1957). After Pojmańska (1957).
**Fig. 16.58.** *Prosolecithus danubica* Tkach & Bray, 1995. Note the very long caeca, and the uterus extending close to the posterior extremity. After Tkach & Bray (1995).

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# 17 Family Mesocoeliidae Dollfus, 1929

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## Introduction

Mesocoeliids are widespread parasites of amphibians and reptiles, exceptionally fish, characterized by a post-testicular ovary, caeca that do not reach close to the posterior extremity and a vitellarium mainly in the forebody. *Mesocoelium* Odhner, 1910 was established by Odhner (1910) and placed in the family Dicrocoeliidae Looss, 1899, subfamily Dicrocoeliinae Looss, 1899, with the type-species *M. sociale* (Lühe, 1901) (treated previously by Braun (1901a) as *Dicrocoelium sociale* (Lühe, 1901)). Johnston (1912) placed the genus in the subfamily Brachycoeliinae Looss 1899 within the Dicrocoeliidae. Cort (1919) transferred the Brachycoeliinae to the Lepodermatidae Odhner, 1910 (= Plagiorchiidae Lühe, 1901). At the same time, Travassos (1919), taking into account the post-testicular position of the ovary, transferred *Mesocoelium* from the brachycoeliids back to the Dicrocoeliinae. This was accepted by Sewell (1920), although he believed that *Mesocoelium* occupied an intermediate position between the Dicrocoeliinae and Brachycoeliinae, and also by Dollfus (1922). Dollfus (1929) established a separate subfamily, the Mesocoeliinae Dollfus, 1929, with *Mesocoelium* and *Pintneria* Poche, 1926, which comprised intestinal parasites of amphibians and reptiles, in contrast to the Dicrocoeliinae from the gallbladder of birds and mammals. Finally, Dollfus (1933) raised the Mesocoeliinae to family status, which was accepted by Skrjabin & Morozov (1959) and Odening (1971), but not by Yamaguti (1958b, 1971), who included the subfamily in the Brachycoeliidae Looss, 1899. He also removed *Pintneria* from the Mesocoeliinae, affiliating it to the Dicrocoeliidae (subfamily Dicrocoeliinae, tribe Pintnerini Yamaguti, 1958).

Here, the system of Dollfus (1933) is adopted, not only because of the biological features he mentioned (host-specificity, site in host), but also on the basis of some morphological characters that differ distinctly between the Mesocoeliidae and both the Brachycoeliidae and the Dicrocoeliidae (the position of the ovary in relation to the testes, the position of the genital pore, the extent of the vitelline bands). Both genera included in the Mesocoeliidae by Dollfus (1933) are retained; nevertheless, more information is needed on the morphology and biology of *Pintneria*.

The mesocoeliids resemble the Dicrocoeliidae in general appearance, but differ in the flame-cell formula and the position of the terminal part of the uterus.

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## Family Mesocoeliidae Dollfus, 1929

**Diagnosis:** Body elongate. Tegument armed with spines. Suckers well developed, in anterior half of body. Prepharynx present, although difficult to detect in some species. Pharynx muscular. Oesophagus present. Intestinal bifurcation in forebody. Caeca usually reach or extend beyond equatorial level (rarely shorter). Testes two, intercaecal, in region of ventral sucker. Cirrus-sac well developed, anterior to ventral sucker, may overlap its anterior margin, encloses seminal vesicle and pars prostatica. Genital pore at level of intestinal bifurcation or slightly anterior to it (see below). Ovary posterior to testes. Seminal receptacle and Laurer's canal present. Uterus with strongly coiled descending and ascending limbs, occupies entire area posterior to gonads; terminal section of ascending limb runs laterally to testis on opposite side of body to ovary. Vitellarium composed of numerous follicles, in two lateral bands, along caeca, beginning at level of pharynx or even more anteriorly. Excretory vesicle Y-shaped, with poorly developed arms, or I-shaped, not reaching level of gonads; pore terminal. Development poorly known. In intestine of amphibians and reptiles, exceptionally fish; Africa, Madagascar, North America, Central America, South America, Asia, Australia. Type-genus *Mesocoelium* Odhner 1910.

## Key to genera

**1a. Testes symmetrical or slightly diagonal ..... *Mesocoelium* Odhner, 1910. (Figs 17.1–17.3)**
**Diagnosis:** Body usually with tapered posterior extremity. Suckers relatively large; oral larger than ventral. Pharynx well developed. Length of oesophagus varies. Caeca short, in most species extending posteriorly beyond ventral sucker and middle of body, sometimes shorter, not reaching level of ventral sucker. Testes symmetrical or slightly diagonal, at level of ventral sucker, or slightly anterior or posterior to it. Cirrus-sac usually large, falciform, between intestinal bifurcation and ventral sucker, sometimes overlapping its anterior margin. Genital pore median or submedian, at level of intestinal bifurcation or slightly anterior to it. Ovary submedian, posterior to one testis, close to or separated from it, usually posterior to ventral sucker or at its level (if testes are situated anterior to ventral sucker). Uterus very long with strongly coiled descending and ascending limbs. Eggs small, operculate, numerous. Vitelline bands wide at anterior extremity (sometimes almost confluent), narrower posteriorly, usually extend from level of pharynx to caecal ends, sometimes reach level of oral sucker anteriorly. Excretory vesicle Y-shaped, with poorly developed arms; flame-cell formula: $2[(3 + 3 + 3) + (3 + 3 + 3)] = 36$; pore terminal. Life-cycle (partly known for several species only; see Ochi, 1930, Thomas, 1965) comprises two generations of sporocysts, tailless cercaria (cercariaeum) and metacercaria encysted within daughter-sporocyst or in second intermediate host, terrestrial molluscs and insects (ants). In intestine of amphibians and reptiles, rarely fish; Africa, Madagascar, North America (USA), Central America, South America (Brazil), Asia, Australia. Type-species *M. sociale* (Lühe, 1901) Odhner, 1910.

**1b. Testes in tandem ..... *Pintneria* Poche, 1907. (Figs 17.4, 17.5)**
(Syn. *Hoploderma* Cohn, 1903 *nec* Michael, 1898)
**Diagnosis:** Body oval, widening towards posterior extremity. Suckers in first third of body. Pharynx small. Caeca reach into posterior half of body. Testes tandem, median, one slightly

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anterior to ventral sucker, other dorsal to ventral sucker. Cirrus-sac anterior to ventral sucker. Genital pore between pharynx and ventral sucker, median. Ovary submedian, close to posterior testis. Coils of descending and ascending limbs of uterus occupy entire hindbody. Eggs small, numerous. Vitelline bands quite long, from level of oral sucker to caecal ends. Excretory vesicle I-shaped; flame-cell formula not known; pore terminal. In intestine of reptiles; Java. Type-species *P. mesocoelium* (Cohn, 1903) Poche, 1907.

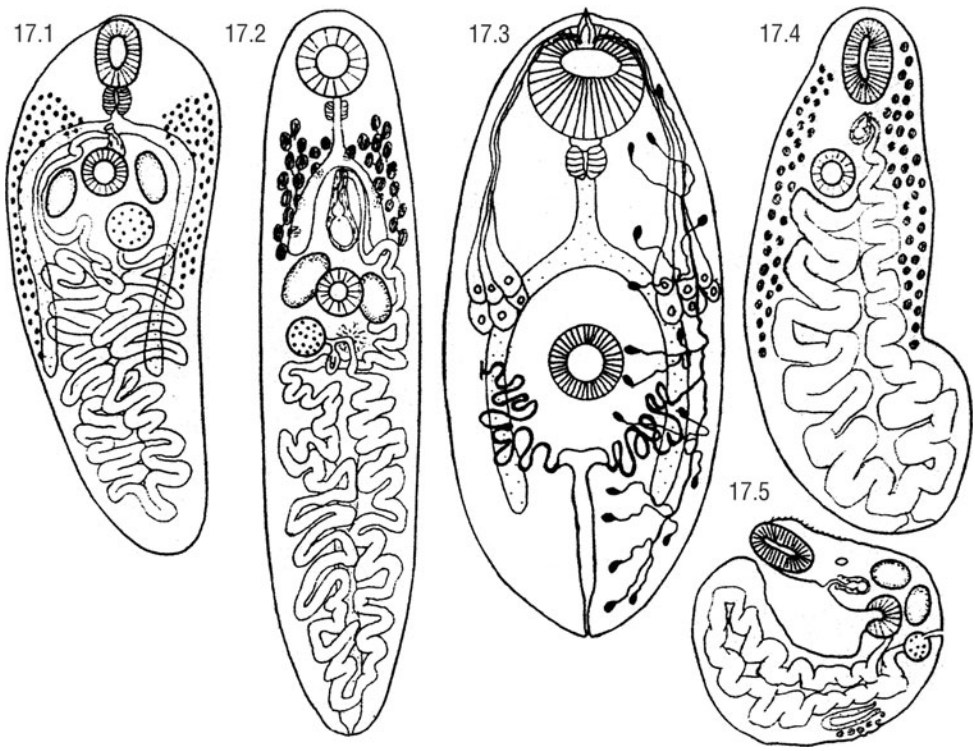



**Fig. 17.1.** *Mesocoelium sociale* (Lühe, 1901). Note relatively long caeca. After Yamaguti (1971).
**Fig. 17.2.** *Mesocoelium elongatum* Goto & Ozaki, 1929. Note short caeca. After Goto & Ozaki (1929).
**Fig. 17.3.** *Mesocoelium monodi* Dollfus, 1929. Excretory system. After Thomas (1965).
**Figs 17.4, 17.5.** *Pintneria mesocoelium* (Cohn, 1903). 17.4. Ventral view. 17.5. Lateral view. After Skrjabin & Morozov (1959).

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# 18 Family Orchipedidae Skrjabin, 1913

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## Introduction

The family Orchipedidae Skrjabin, 1913 is a small family of gorgoderoids distinguished by having the testes in the form of numerous follicles largely or entirely in the hindbody and the terminal genitalia free in the parenchyma. Members of this family inhabit the respiratory tract and adjacent tissues of mammals and birds.

Braun (1901b) proposed *Orchipedum* Braun, 1901 for trematodes from the trachea of a duck and noted that it seemed close to *Psilostomum* Looss, 1899. Odhner (1913), in proposing the new family Psilostomidae Looss, 1900, considered that *Orchipedum* should not be placed in this family. Skrjabin (1913), however, erected the subfamily Orchipedinae Skrjabin, 1913 within the Psilostomidae. Skrjabin (1925) recognized this taxon at the family level, a status retained by most subsequent workers.

A second genus, *Mammorchipedum* Skrjabin, 1947, was erected by Skrjabin (1947b) for *Orchipedum isostoma* (Rudolphi, 1819) Dollfus, Callot & Desportes, 1935. Rudolphi (1819) had applied the name *Distoma isostoma* Rudolphi, 1819 to an unencysted metacercaria from freshwater crayfish in Europe. Dollfus *et al*. (1935) obtained their adult worms from the nasal cavities of various mammals experimentally fed with similar metacercariae. Whether *Mammorchipedum* should be regarded as distinct from *Orchipedum* has been debated. Skrjabin (1947b) distinguished them as follows: the frequent presence of a transverse constriction around the body at about the level of the ventral sucker in *Orchipedum* (absent from *Mammorchipedum*); the relatively more anterior position of the ventral sucker in *Orchipedum*; the genital pore at the level of the intestinal bifurcation in *Orchipedum* (slightly more posterior in *Mammorchipedum*); and the presence of vitelline follicles between the caeca in the hindbody in *Orchipedum* (not present in *Mammorchipedum*). Zarnowski (1956) pointed out that most *Orchipedum* species lack the transverse constriction and that some have genital pore(s) in the same location as that stated to be diagnostic for *Mammorchipedum*. Zarnowksi retained *Mammorchipedum* but accepted only the relative lengths of the pretesticular portion of the body and the presence or absence of vitelline follicles between the caeca in the hindbody as differential characters. Schell (1967) regarded *Mammorchipedum* as a synonym of *Orchipedum*. Ryzhikhov *et al*. (1985a, b) regarded the former

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genus as valid but distinguished it from *Orchipedum* only by the absence of vitelline follicles between the caeca in the hindbody and by host-specificity and location. We follow Ryzhikov *et al.* (1985a, b) in recognizing *Mammorchipedum*.

The remaining species in the family have, until now, usually been placed in the Achillurbainiidae Dollfus, 1939. Dollfus (1939) reported a curious new fluke from an abscess associated with the orbit in a leopard, *Felis pardus* L., imported into France from Malaysia. He named it *Achillurbainia nouveli* Dollfus, 1939 and erected a new family, the Achillurbainiidae, for it. Fain & Vandepitte (1957) described a new genus and species, *Poikilorchis congolensis* Fain & Vandepitte, 1957, based on a worm from a subcutaneous cyst behind the ear of an inhabitant of the then Belgian Congo. Testicular follicles in *Achillurbainia* Dollfus, 1939 extend well anterior to the ventral sucker, whereas in *Poikilorchis* Fain & Vandepitte, 1957 they are entirely posterior to the ventral sucker. Beaver *et al.* (1977, citing a personal communication from Dollfus) regarded the two genera as synonyms, as did Miyazaki (1991), and we have accepted this view. Apart from the more anterior margin of the testicular field and the apparently more strongly undulating caeca in *Achillurbainia*, there is little to separate them. Figure 10 of Chen (1965) shows a worm identified as *A. nouveli* from a cyst behind the ear of a girl in China, in which the testicular follicles extend to the anterior edge of the ventral sucker, a situation intermediate between those seen in other members of *Achillurbainia* and in *Poikilorchis*. Apart from the two cases mentioned above, eggs with the flattened opercular pole and raised opercular rim, characteristic of both nominal genera, have been recovered on several occasions from cysts behind the ears of humans in Africa and Asia (reviewed by Miyazaki, 1991). In none of these cases was an adult worm found. Eggs of slightly different morphology have been recovered from the peritoneal cavity of humans in South America and might be those of *A. recondita* Travassos, 1942 (see Beaver *et al.*, 1977).

Mehra (1962) stated emphatically that the Achillurbainiidae is a junior synonym of the Orchipedidae, and we accept this, noting that many of the features shared between these nominal families are unusual in digeneans. Members of both live in the upper respiratory tract or in the tissues of the head (rare instances also from other sites). Spines are absent from the body-surface. The numerous testicular follicles occur largely in the hindbody, the ovary lies slightly posterior to the ventral sucker, and the uterus is largely or entirely anterior to the ovary. The terminal genitalia are free in the parenchyma and open at a pore anterior to the ventral sucker (sometimes at about the level of the intestinal bifurcation). The excretory vesicle is a long tube, bifurcating just posterior to the ovary. Shimizu (1979) appears to be the only other person to have noted a similarity between the Achillurbainidae and the Orchipedidae. Mehra (1962) 'erected' the superfamily Orchipedioidea to contain only the family Orchipedidae.

## Family Orchipedidae Skrjabin, 1913

(Syn. Achillurbainiidae Dollfus, 1939)

**Diagnosis:** Body medium-sized to large, flat, elongate, rounded anteriorly and rounded or tapered posteriorly. Tegument unarmed. More or less distinct transverse constriction sometimes present at level of ventral sucker. Posterior end of body sometimes both strongly tapered and annulated. Oral sucker terminal or subterminal ventral, smaller than ventral sucker. Ventral sucker large, pre-equatorial. Prepharynx absent. Pharynx present. Oesophagus very short and often flexed dorsally, or apparently absent. Intestinal bifurcation in anterior forebody. Caeca simple, blind, sublateral for most of their course, vary from strongly sinuous to almost straight, terminate close to posterior extremity. Testes in

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form of numerous (*c.* 25 to > 700) rounded or irregular follicles, usually intercaecal (sometimes also lateral to caeca) posterior to ovary but may not reach as far posteriorly as caecal ends and may extend laterally into forebody. Cirrus-sac absent. Seminal vesicle probably always present, coiled, free in parenchyma. Prostatic cells surround terminal male duct in some species. Genital pore(s) sometimes apparently separate but adjacent, between levels of pharynx and ventral sucker, median or almost so. Ovary spherical or elliptical, submedian, slightly posterior to ventral sucker. Mehlis' gland, where reported, median, posterior to ovary. Seminal receptacle and Laurer's canal present. Uterus intercaecal between anterior limit of intercaecal testes and genital pore. Eggs rather large, numerous. Vitelline follicles abundant along body-margins lateral to caeca, reach or almost reach posterior extremity, extend into forebody or not, where often confluent in median line, present or not in hindbody between caeca. Excretory vesicle tubular, long, divides into two transverse arms (sometimes not apparent), just posterior to ovary; pore terminal. In cavities of respiratory tract and adjacent tissues and cavities of birds and mammals; cosmopolitan. Type-genus *Orchipedum* Braun, 1901.

## Key to genera

**1a. Vitelline follicles not present between caeca in hindbody ..... ..... *Mammorchipedum* Skrjabin, 1947. (Fig. 18.1)**

**Diagnosis:** Body of medium size, moderately elongate, rounded at each end, broadest in region of ventral sucker. Ventral sucker large, in second quarter of body. Caeca sublateral, follow slightly sinuous course. Testicular follicles (*c.* 55–80) restricted to intercaecal region posterior to ovary. Seminal vesicle present. Prostatic cells occur around terminal male duct. Genital pore(s) median, sometimes said to be separate and adjacent, slightly closer to ventral sucker than to intestinal bifurcation. Vitelline follicles mainly lateral from level of pharynx to posterior end of body, confluent in median line in forebody but absent between caeca posterior to ventral sucker. In nasal cavities of mammals (mustelids, canids, felids); Europe, Russia, northern Asia. Type-species *M. isostoma* (Rudolphi, 1819) Skrjabin, 1947.

**1b. Vitelline follicles present between caeca in hindbody ..... 2.**

**2a. Ventral sucker in second quarter of body; testicular follicles intercaecal and lateral to caeca, often extend into forebody and anterior to ovary; posterior end of body broadly rounded; caeca follow undulating course to greater or lesser extent ..... ..... *Achillurbainia* Dollfus, 1939. (Fig. 18.2)**
(Syn. *Poikilorchis* Fain & Vandepitte, 1957)

**Diagnosis:** Body large, flattened, somewhat foliate, broadest at about equator or slightly posterior to this. Ventral sucker in second quarter of body or at junction between first and second quarters. Caeca follow moderately to strongly sinuous course. Testicular follicles (*c.* 75 to *c.* 700) intercaecal and extracaecal posterior to level of ovary, mostly lateral if present anterior to this: anterior limit of testicular field varies from level of posterior edge of ventral sucker to slightly posterior to intestinal bifurcation. Seminal vesicle present, sometimes surrounded by prostatic cells. Genital pore median or just submedian, close to intestinal bifurcation or a short distance posterior to this. Vitelline follicles numerous, present from level of pharynx to posterior extremity, extracaecal and intercaecal where not displaced by other organs. In cavities of respiratory system and adjacent tissues of mammals (didelphids, felids, humans, rodents, viverrids, mustelids, tupaiids); Africa, Asia, South America. Type-species *A. nouveli* Dollfus, 1939.

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**2b. Ventral sucker usually in first quarter of body (if posterior to this, vitelline follicles present only in hindbody); testicular follicles entirely intercaecal and not occurring anterior to ovary; posterior end of body attenuated, not rounded; caeca more or less straight ..... *Orchipedum* Braun, 1901. (Fig. 18.3)**

**Diagnosis:** Body large, elongate, broadest at level of ventral sucker or somewhat posterior to this, rounded anteriorly and gradually tapering posteriorly; attenuated posterior end may bear transverse annuli. More or less distinct transverse constriction sometimes present at level of ventral sucker. Ventral sucker pre-equatorial, usually in anterior quarter or fifth of body. Caeca more or less straight. Testicular follicles (*c*. 25 to *c*. 400) fill intercaecal space posterior to ovary, do

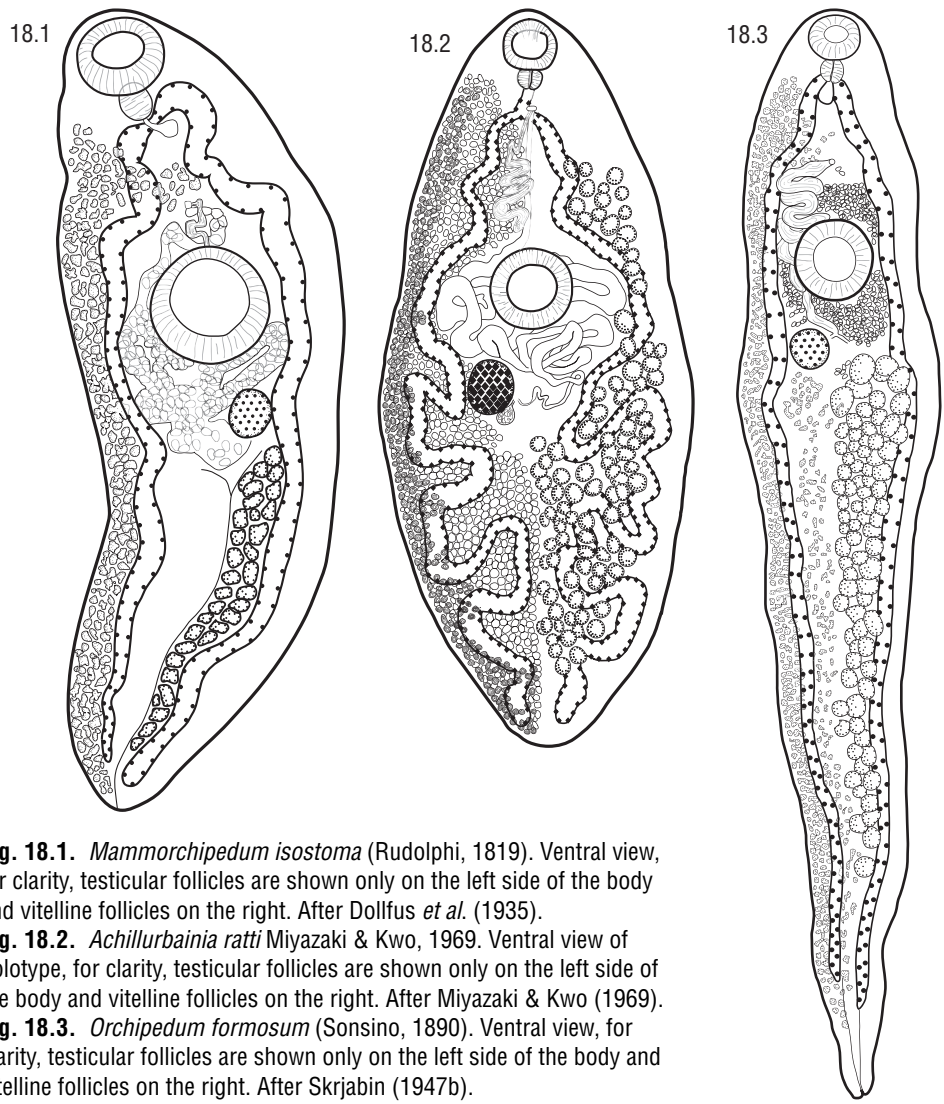



**Fig. 18.1.** *Mammorchipedum isostoma* (Rudolphi, 1819). Ventral view, for clarity, testicular follicles are shown only on the left side of the body and vitelline follicles on the right. After Dollfus *et al*. (1935).
**Fig. 18.2.** *Achillurbainia ratti* Miyazaki & Kwo, 1969. Ventral view of holotype, for clarity, testicular follicles are shown only on the left side of the body and vitelline follicles on the right. After Miyazaki & Kwo (1969).
**Fig. 18.3.** *Orchipedum formosum* (Sonsino, 1890). Ventral view, for clarity, testicular follicles are shown only on the left side of the body and vitelline follicles on the right. After Skrjabin (1947b).

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not extend to ends of caeca. Seminal vesicle probably always present, sometimes surrounded by prostatic cells. Genital pore midway between ventral sucker and intestinal bifurcation, or closer to latter. Vitelline follicles most numerous along body-margins lateral to caeca, extend into forebody or not, also intercaecal in hindbody dorsal to testes. In trachea of birds (Anseriformes, Charadriiformes, Ciconiiformes, Gruiformes, Passeriformes, Pelecaniformes, Phoenicopteriformes, Podicipediformes); probably in all temperate and tropical regions. Type-species *O. tracheicola* Braun, 1901.

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# 19 Family Paragonimidae Dollfus, 1939

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## Introduction

Adult paragonimids are large, fleshy trematodes occurring in pairs in capsules within the lungs (usually) of mammals. They differ from other members of the Gorgoderoidea Looss, 1899 by a suite of characters, including the absence of a cirrus-sac, extensive dendritic vitellarium and the habit of encysting in pairs in the lungs of mammals.

Kerbert (1878) described as *Distoma westermanii*[1] Kerbert, 1878 worms from the lungs of a tiger that had died in Amsterdam Zoological Gardens. Braun (1899) made *D. westermanii* the type of his new genus *Paragonimus* Braun, 1899. Shortly afterwards, Looss (1899) placed it in his new genus *Polysarcus* Looss, 1899, which must fall as a synonym (and was in any case pre-occupied). Parasitologists at that time (e.g. Stiles & Hassall, 1900) assigned *Paragonimus* to the Fasciolidae Railliet, 1895, whereas Odhner (1914) placed it in the Troglotrematidae Odhner, 1914. Dollfus (1939) erected the family Paragonimidae Dollfus, 1939 for it. However, some later authors (e.g. Dawes, 1946; Baer & Joyeux, 1961) continued to place it in the Troglotrematidae.

Within *Paragonimus*, Chen (1963, cited in Chen, 1964a, b) recognized three subgenera (*Paragonimus* Braun, 1899, *Rodentigonimus* Chen, 1963 and *Megagonimus* Chen, 1963); Chen's subgeneric names have seldom been used since and are not recognized here. Chen (1963, cited in Chen, 1964a, b) erected a new genus, *Pagumogonimus*, which he distinguished from *Paragonimus* primarily because the metacercaria of the former possessed 72 flame-cells (60 in *Paragonimus*). Later, it became apparent that this was not a valid basis for separating the genera, and Chen (1977) placed more emphasis on adult characters, in particular the elongate body-shape and the location of the ventral sucker in the anterior third of the body. A molecular study by Blair *et al.* (1999a) showed that the type-species of *Pagumogonimus, P. skrjabini* (Chen, 1959), is very close to *Paragonimus miyazakii* Kamo, Nishida, Hatsushika & Tomimura, 1961, a species with a body-shape more typical of *Paragonimus* species as recognized by Chen. Blair *et al.* (2005) reduced

[1] Stiles & Hassall (1900, p. 567) discussed the spelling of the trivial name and stated a preference for retaining Kerbert's original spelling. However, for many years the form '*westermani*' has been used universally.

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*P. miyazakii* to a subspecies within *Paragonimus skrjabini* Chen, 1959. A recently published morphometric analysis of lungflukes (Zhan *et al*., 1997) failed to recover monophyly of nominal *Pagumogonimus* species. *Pagumogonimus* is here regarded as a synonym of *Paragonimus*.

Another genus erected by Chen (1962), *Euparagonimus* Chen 1962, has a distinctive morphology. The excretory vesicle in both adults and metacercariae does not extend anteriorly beyond the ventral sucker (it extends to the intestinal bifurcation in *Paragonimus*). In adults, the testes are somewhat star-shaped and lie ventral to the caeca, a condition slightly different from that in *Paragonimus* species. However, the molecular study by Blair *et al*. (1999a) showed that *Euparagonimus* was nested among *Paragonimus* species. The morphometric study by Zhan *et al*. (1997) similarly nested *Euparagonimus cenocopiosus* Chen, 1962 among *Paragonimus* species. Consequently, the former genus must fall as a synonym and the subfamily Euparagoniminae Chen, 1963 is not recognized.

The major taxonomic treatments of the family are by Chen (1985, in Chinese) and Kurochkin (1987, in Russian). A review of current knowledge is given by Blair *et al*. (1999b).

## Family Paragonimidae Dollfus, 1939

(Syn. Euparagoniminae Chen 1963)

**Diagnosis:** Body medium to large, oval to subspherical. Tegument spined. Oral sucker terminal or almost so, usually similar in size to ventral sucker. Ventral sucker pre-equatorial, sometimes distinctly so. Pharynx present. Oesophagus very short. Intestinal bifurcation in anterior forebody. Caeca undulating, terminate blindly near posterior end. Testes large, opposite or almost so, in posterior half of body, usually in form of several club-shaped lobes joined at their bases. Cirrus-sac and cirrus absent. Male terminal duct slightly expanded to form straight or curved seminal vesicle, then narrows to enter short pars prostatica, from which ejaculatory duct passes to common genital pore near posterior margin of ventral sucker. Ovary variably lobed and subdivided, submedian, on either side of body, close to ventral sucker. Laurer's canal present. Seminal receptacle in form of saccate diverticulum near base of Laurer's canal. Uterus mostly in middle third of body, most extensive on side opposite ovary, terminates in short metraterm. Eggs large. Vitelline follicles dendritic, dense, surround caeca and extend almost to midline, especially dorsally, along most of body-length. Excretory vesicle long, tubular, median, almost reaches intestinal bifurcation; pore terminal or subterminal. Adults in capsules within lungs, rarely other sites, of (usually) mammals of many orders (primates, rodents, carnivores, etc.); Asia, Africa, North and South America. Type-genus *Paragonimus* Braun, 1899.

## Genus *Paragonimus* Braun, 1899 (Fig. 19.1)

(Syns *Polysarcus* Looss, 1899; *Euparagonimus* Chen, 1962; *Pagumogonimus* Chen, 1963; *Rodentigonimus* Chen, 1963; *Megagonimus* Chen, 1963)

**Diagnosis:** With characters of family. Type-species *P. westermani* (Kerbert, 1878) Braun, 1899.

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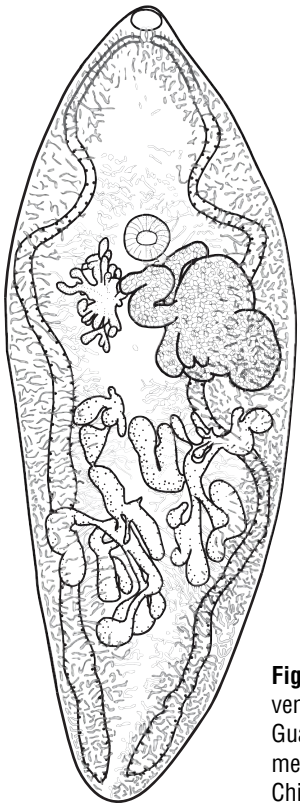


**Fig. 19.1.** *Paragonimus skrjabini* Chen, 1959. Strongly compressed adult in ventral view. Specimen from collection of Zhong Shan Medical University, Guangzhou, China, experimentally raised in a dog (428 days) infected with metacercariae from a freshwater crab from Weiyuan, Sichuan Province, China. Original.

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# 20 Family Prouterinidae Foreyt, Schell & Beyer, 1996

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## Introduction

The Prouterinidae Foreyt, Schell & Beyer, 1996 was erected for *Prouterina wescotti* Foreyt, Schell & Beyer, 1996, a species found in the nasal and paranasal sinuses of a single black bear (*Ursus americanus*) from Idaho, USA (Foreyt *et al*., 1996). Specimens were also detected in the lungs and brain. No additional hosts or localities are known (Foreyt *et al*., 1999).

In *Prouterina* Foreyt, Schell & Beyer, 1996, the uterus occupies the forebody, the suckers are well developed, the genital pore is posterior to the ventral sucker, the testes are tandem, the caeca are long, a cirrus-sac is present and the vitelline follicles fill most of the lateral regions of the body. This suite of characters is diagnostic of the Prouterinidae, but the affinities of the family are rather obscure. Foreyt *et al*. (1996) considered *Prouterina* to resemble the renicolids in body-shape but not in many internal anatomical features. Here, the family has been placed in the Gorgoderoidea Looss, 1899 (see Bray & Blair, Chapter 9, this volume).

## Family Prouterinidae Foreyt, Schell & Beyer, 1996

**Diagnosis:** Body small to medium in size, conical, with broad, rounded anterior end, widest at ventral sucker, tapers gradually towards narrow posterior end. Tegument armed. Oral sucker terminal. Ventral sucker similar in size to oral sucker, slightly pre-equatorial. Prepharynx absent. Pharynx present. Oesophagus short. Intestinal bifurcation in forebody. Caeca long, simple, sublateral, terminate near posterior extremity. Testes two, oval or somewhat lobed, tandem, in third quarter of body in relaxed specimens, largely ventral to plane of caeca. Cirrus-sac present, ovoid, dorsal to ventral sucker, contains 'looped prostate canal, cirrus, and some prostate cells'. Genital pore slightly posterior to ventral sucker. Ovary spherical or ovoid, dextral, anterodorsal to anterior testis or lateral to ventral sucker. Mehlis' gland, Laurer's canal and seminal receptacle not known. Uterus restricted to and extensively coiled in forebody; metraterm present. Eggs large, moderately abundant. Vitellarium follicular; follicles abundant laterally from level of pharynx to posterior end of body, confluent dorsally in and posterior to testicular zone. Excretory system mostly

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unknown; pore terminal. In nasal and paranasal sinuses, lungs and brain of black bear; North America, Idaho. Type-genus *Prouterina* Foreyt, Schell & Beyer, 1996.

## Genus *Prouterina* Foreyt, Schell & Beyer, 1996 (Fig. 20.1)

**Diagnosi**s: With characters of family. Type-species *P. wescotti* Foreyt, Schell & Beyer, 1996.

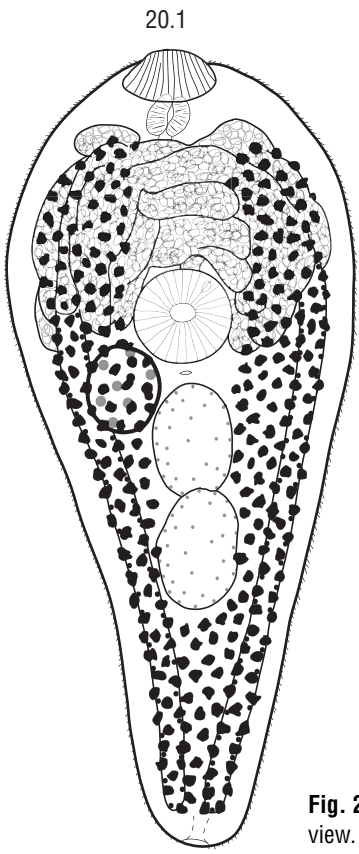



**Fig. 20.1.** *Prouterina wescotti* Foreyt, Schell & Beyer, 1996. Ventral view. After Foreyt *et al.* (1996).

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# 21 Family Troglotrematidae Odhner, 1914

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## Introduction

Troglotrematids are small to medium-sized gorgoderoids found in the lumen of the intestine, cavities of the upper respiratory tract, kidneys or liver of mammals and seabirds. Distinctive morphological features uniting all genera in the family are few, perhaps indicating that the family is not a natural taxon. All members have oral and ventral suckers, a pair of symmetrical testes and caeca that are not markedly sinuous. The uterus is mostly or entirely in the hindbody, the seminal vesicle is commonly bipartite and the genital pore is typically just posterior to the ventral sucker. Included in the family are the important genera *Nanophyetus* Chapin, 1927 (vector of a rickettsial disease of dogs in North America and common parasites of humans in East Siberia) and *Troglotrema* Odhner, 1914 (associated with skull lesions in mustelids).

The Troglotrematidae Odhner, 1914, Nanophyetidae Wallace, 1935 and Paragonimidae Dollfus, 1939 have a complicated, shared history. At times, a single family, the Troglotrematidae, has been accepted, often subdivided in various ways. Recently, the three nominal families have been generally regarded as distinct entities. Here, we do not recognize the Nanophyetidae as distinct and place its genera within the Troglotrematidae.

Odhner (1914) proposed the Troglotrematidae (as Troglotremidae) to contain five genera: *Pholeter* Odhner, 1914, *Collyriclum* Kossack, 1911, *Troglotrema, Paragonimus* Braun, 1899 and *Renicola* Cohn, 1904 (the last added in an addendum). They all live in cysts in tissues or in cavities in the body other than the lumen of the digestive tract.

Odhner figured and described the type-species, *T. acutum* (Leuckart, 1842), as possessing a caudal projection or cone. Baer (1931a) stated such a projection to be absent from numerous specimens he examined and implied that it might have been a fixation artefact in Odhner's specimen. Other authors have generally not remarked on its presence. Andreiko (1973) stated it to be present in *T. srebarni* Genov, 1964, although Genov (1964) apparently did not mention it. Unfortunately, Odhner's drawing of a presumably atypical specimen of *T. acutum* has been reproduced frequently (e.g. Fuhrmann, 1928; Yamaguti, 1971).

Baer (1931b) added to the Troglotrematidae the new subfamily Nephrotrematinae Baer, 1931 to house *Nephrotrema* Baer, 1931 from the kidneys of mammals. Wallace (1935) added the

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intestinal parasites *Nanophyetus* Chapin, 1927 and his new genus *Sellacotyle* Wallace, 1935 in a new subfamily, the Nanophyetinae Wallace, 1935.

Dollfus (1939) considered the Troglotrematidae, as then constituted, to be an unnatural group and proposed that its genera, listed above, could be distributed among six families: Paragonimidae; Collyriclidae Ward, 1917; Pholeteridae Dollfus, 1939; Renicolidae Dollfus, 1939; Nanophyetidae (presumably containing only *Nanophyetus* and *Sellacotyle*); and Troglotrematidae (containing only *Troglotrema* and *Nephrotrema*). Dollfus' arrangement offered a simple means of distinguishing between the nominal families Troglotrematidae and Nanophyetidae. Genera included by him in the former family have a Y-shaped excretory vesicle and live in sites distant from the intestine; those in the latter have a more-or-less saccate excretory vesicle and occur in the intestine. This convenient distinction has become less clear as additional genera have been added to the families. Some genera with a bifurcate excretory vesicle live in the intestine (e.g. *Macroorchis* Ando, 1919 (first placed tentatively in a family, the Troglotrematidae, by Witenberg, 1932); *Paragono* Pearse, 1930 (placed by its author in the Troglotrematidae); and *Xiphidiotrema* Senger, 1953 (placed by its author in the Troglotrematidae)). Further evidence that these two nominal families are not distinct from one another comes from cercarial morphology and from molecular sequences (see below).

Cercariae are known for one or more species of *Nephrotrema, Troglotrema, Skrjabinophyetus* Dimitrova & Genov, 1967, *Nanophyetus* and *Sellacotyle*. In each case, the cercaria has a cluster of gland-cells arranged radially around a ventral opening near the posterior end of the body (discussed and figured by Vogel & Voelker, 1978). This is a unique feature uniting this group and distinguishing it from *Paragonimus*, the sole genus in the Paragonimidae (see Blair, Chapter 19, this volume). Furthermore, Bayssade-Dufour & Jourdane (1976) noted similarities in cercarial chaetotaxy between *Nephrotrema* (Troglotrematidae *sensu* Dollfus) and *Skrjabinophyetus* (Nanophyetidae *sensu* Dollfus) consistent with them belonging to the same family.

We also have molecular evidence favouring synonymy of the Troglotrematidae and Nanophyetidae. Relevant sequences are from the nuclear 28S rRNA gene of *Nephrotrema truncatum* (Leuckart, 1842), *S. neomydis* Dimitrova & Genov, 1967, *Nanophyetus salmincola* (Chapin, 1926) and three species of *Paragonimus*. All other available sequences from members of the Gorgoderoidea (see fig. 6 in Olson *et al*., 2003) were included in the analysis. In the phylogenetic tree (Fig. 21.1, details of methods in caption), *Nephrotrema truncatum* (Troglotrematidae) and *S. neomydis* (Nanophyetidae) appear as sisters with *Nanophyetus salmincola* (Nanophyetidae), sister to these two in turn. The three species of *Paragonimus* form a sister clade to this. Branch lengths between all genera, including *Paragonimus*, are no greater than between genera of several well-established families on the tree (e.g. Dicrocoeliidae Looss, 1899) and less than among, for example, genera of the Gorgoderidae Looss, 1899. This shows that the troglotrematids and nanophyetids are scarcely diverged enough to merit separate family status. We shall retain *Paragonimus* in a separate, but sister, family, the Paragonimidae, in this volume (see Blair, Chapter 19, this volume). Despite the blurred line separating the Troglotrematidae and the Nanophyetidae, many authors have retained both as distinct families (e.g. Baer & Joyeux 1961; Yamaguti, 1971).

The validity of *Nanophyetus, Sellacotyle, Pseudotroglotrema* Yamaguti, 1971 and *Skrjabinophyetus*, and their species, needs careful consideration. Chapin (1926) described *Nanophyes salmincola* Chapin, 1926 from the intestines of dogs. The generic name *Nanophyes* was subsequently found to be pre-occupied and was replaced by *Nanophyetus* in 1927 (Chapin, 1927). Chapin placed his genus in the Heterophyidae Leiper, 1909. Although some later authors (e.g. Skrjabin & Podjapolskaja, 1931) agreed with this placement, Witenberg (1932) pointed out the similarity between *Nanophyetus* and *Troglotrema* and regarded the former as a junior synonym of the latter.

Wallace (1933), in an abstract, coined the name *Troglotrema mustelae* Wallace, 1933 for a worm from the intestine of mustelids in the USA. He did not provide a description until 1935,

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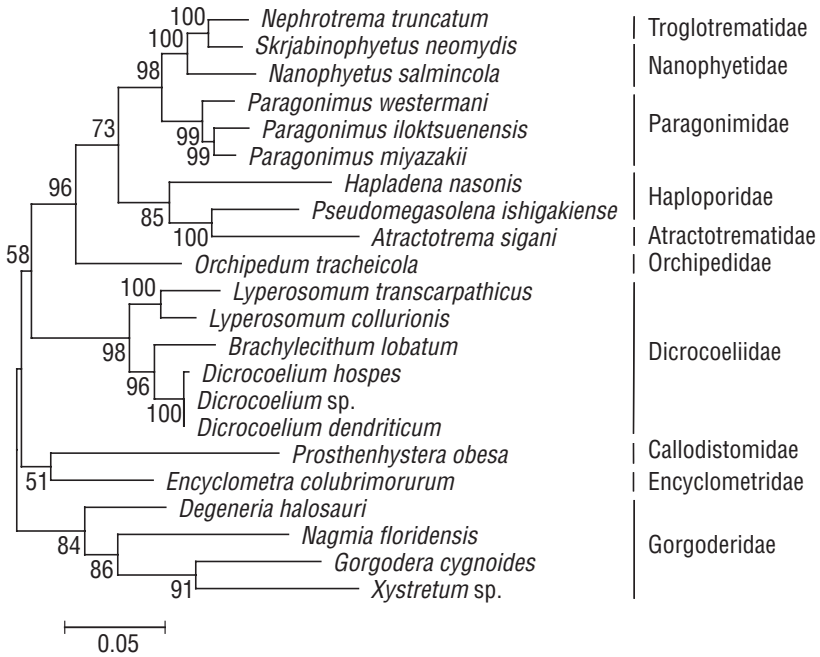



**Fig. 21.1.** Midpoint-rooted maximum-likelihood tree inferred from partial 28S ribosomal RNA sequences from all available members of the Gorgoderoidea (*sensu* Olson *et al.*, 2003). Sequences were aligned using ClustalW. All sites with gaps in any sequence were subsequently removed, leaving 1169 sites for analysis. TREE-PUZZLE 5.2 (Schmidt *et al.*, 2002) was used to find the tree. This program estimates a number of parameters from the data as follows: number of constant sites 673 (= 57.6% of all sites); most appropriate model of substitution is HKY (Hasegawa *et al.*, 1985); transition/transversion parameter (estimated from data set) is 2.61 (SE 0.21). All sequences passed the test for similar base composition. Numbers on branches indicate the percentage of (1000) puzzling steps in which that bipartition was found.

at which time he (Wallace, 1935) erected *Sellacotyle* to contain it. A second species of *Sellacotyle, S. vitellosa* Sogandares-Bernal, 1961, was described from mustelids in Louisiana by Sogandares-Bernal (1961). *Sellacotyle* and *Nanophyetus* are very similar. Wallace (1935) separated them on the basis of body-size, the presence of a cirrus-sac in the latter (absent in the former, the bipartite seminal vesicle lying free in the parenchyma) and the length of the caeca (extending at most to the posterior edge of the ventral sucker in the former genus but posterior to this in the latter). Of these three features, the first and last seem hardly of generic significance, leaving only the presence or absence of a cirrus-sac to distinguish between the genera. Wallace (1935) had apparently overlooked the description of *N. schikhobalowi* Skrjabin & Podjapolskaja, 1931 by Skrjabin & Podjapolskaja (1931), which implied that a cirrus-sac was absent from this species. Witenberg (1932) considered Skrjabin & Podjapolskaja (1931) to have been in error in this regard. Later Russian authors (e.g. Filimonova, 1965) reported a cirrus-sac in *N. schikhobalowi*. It seems that the presence or absence of a cirrus-sac is a valid means of separating these genera.

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*Pseudotroglotrema* Yamaguti, 1971 was erected for *P. asadai* Yamaguti, 1971, found in the intestine of a stray dog near Tokyo. Yamaguti (1971) implied that *Pseudotroglotrema* can be distinguished from *Nanophyetus* in that the base of the cirrus-sac of the latter is anterior to the genital pore. This does not always seem to be the situation (e.g. fig. 1 in Skrjabin & Podjapolskaja, 1931). Another feature used to distinguish between them was the length of the caeca, extending posterior to the testes in *Pseudotroglotrema*, whereas in *Nanophyetus* they do not reach the posterior margin of the testes. However, in *N. japonensis* Saito, Saito, Yamashita, Watanabe & Sekikawa, 1982 as redescribed by Saito (1985), the caeca extend almost to the posterior end of the body. The shape of the excretory vesicle is not known for *P. asadai*. From the published information, *P. asadai* can hardly be distinguished from *N. japonensis* except in body-size. We regard *Pseudotroglotrema* as a synonym of *Nanophyetus. P. asadai* was said to lack spines (Yamaguti, 1971), which is an unusual feature for a troglotrematid if correct: some species of *Paragono* also apparently lack spines.

*Skrjabinophyetus* Dimitrova & Genov, 1967 was erected for a small worm, *S. neomydis*, from the intestine of soricids in Bulgaria. The species was subsequently described from southern France (Euzet & Jourdane, 1970) and Germany (Brendow, 1970). Brendow (1970) questioned the name of the type-species, preferring *S. repens* (Bregenzer, 1916). He based this on the similarity between *Cercaria repens* Bregenzer, 1916 and the cercaria he demonstrated to be that of a *Skrjabinophyetus* species. Subsequent workers have not followed this suggestion, and we shall not do so here. Jourdane (1977) pointed out that Brendow (1970) included features of cercariae of both *S. neomydis* and *Nephrotrema truncatum* in his description. A striking feature of *S. neomydis* is the large oral sucker, the diameter of which is about three times that of the ventral sucker. Jourdane (1973a) described a second species, *S. soricis* Jourdane, 1973, from southern France. This species differs markedly from the type-species in being much smaller, in having ventral and oral suckers of near-equal size and in the anterior extent of the vitelline follicles, which occur up to the level of the oral sucker. We consider that *S. soricis* can hardly be distinguished from members of *Nanophyetus* and refer it to that genus as *N. soricis* n. comb. Jourdane (1977) described the cercariae of both nominal species of *Skrjabinophyetus*. These differ from each other, and from those of *Nanophyetus* and *Sellacotyle* species, in details of numbers of penetration gland-cells and in flame-cell formulae. The taxonomic significance of these differences is hard to evaluate. Bayssade-Dufour & Jourdane (1976) and Jourdane (1977) relied on cercarial chaetotaxy (based on the distribution of sensory endings on the tegument) for evidence that the two nominal *Skrjabinophyetus* species were congeners. However, they only had comparative data for one other troglotrematid, *Nephrotrema truncatum*, making a definitive statement on relationships impossible.

Three genera included here were first noted as metacercariae in freshwater crustaceans from eastern Asia. In each case, rudiments of the gonads and associated organs were sufficiently developed to indicate adult morphology clearly, and in two cases adults were raised in experimentally infected mammals. *Macroorchis* Ando, 1919 was erected by Ando (1919 – in a published abstract from the ninth meeting of the Japanese Pathology Society) based on specimens developing experimentally in the intestines of various mammals fed metacercariae from freshwater crabs. Yamaguti (1958b) placed *Macroorchis* in his new nanophyetid subfamily, Macroorchiinae Yamaguti, 1958. The early Japanese literature on this genus was summarized by Dollfus (1925).

Nakagawa (1917) briefly described and figured, from crabs in Taiwan, various developmental stages of metacercariae he regarded as belonging to *Paragonimus westermani* (Kerbert, 1878). Subsequently, he (Nakagawa, 1918) named a new genus and species for these, *Stephanolecithus parvus* Nakagawa, 1918. A brief mention in English is given in Nakagawa (1919). Adults were obtained from the liver and gall-bladder of experimentally infected mammals. A fuller description, including a figure, was given by Nakagawa (1958, details in English from Yamaguti, 1975). In the title of this paper, he appeared to ascribe authorship of the genus and species names to

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Goto. However, this was apparently because he had sought advice from Goto as to an appropriate name: Nakagawa remains the appropriate author. Nakagawa (1958) compared his genus with *Prosthogonimus* Lühe, 1899 (Prosthogonimidae Lühe, 1909) but regarded it as very distinct. Yamaguti (1958b), at that time unaware of Nakagawa's (1958) paper, placed the genus in the Opisthorchiidae Looss, 1899, subfamily Stephanolecithinae Yamaguti, 1958. Subsequently, Yamaguti (1971) transferred *Stephanolecithus* Nakagawa, 1918 and the Stephanolecithinae to the Troglotrematidae. Lee (1965), also apparently unaware of Nakagawa's work, described two species of his new genus *Beaveria* Lee, 1965 from the liver and small intestine of Malaysian rats and assigned the genus to the Troglotrematidae in his new subfamily Beaveriinae Lee, 1965. Yamaguti (1971) pointed out that *Beaveria* is clearly a synonym of *Stephanolecithus*. Betterton & Lim (1975) questioned the troglotrematid affinities of *Stephanolecithus* (as *Beaveria*) and also suggested, independently of Nakagawa (1958), that it might belong close to *Prosthogonimus*.

Pearse (1930) described *Paragono kelloggi* Pearse, 1930 based on encysted metacercariae with a Y-shaped excretory vesicle from estuarine crabs in China. Pearse placed it in the Troglotrematidae. Yamaguti (1971) erected for it the subfamily Paragoninae Yamaguti, 1971 and suggested that the definitive host for *Paragono* might be crab-eating mammals. However, adults of two species clearly belonging to *Paragono* were described by Zhang *et al*. (1984) from the intestine of seabirds in China. *Paragono* is the only troglotrematid genus to occur in birds.

Type-species of all remaining genera were based on adult specimens. *Xiphidiotrema lockerae* Senger, 1953 was described by Senger (1953) from adult worms in the intestine of shrews in the USA. Senger noted the similarity of his new genus with *Nephrotrema*. However, because in size and habitat it more closely resembled *Sellacotyle* and *Nanophyetus*, he placed it closer to the other two genera (in the Nanophyetinae). Yamaguti (1958b, 1971) preferred to ally it with *Nephrotrema*, presumably on the basis of its bifurcate excretory vesicle. Chin & Gu (1980) agreed, and went one step further, proposing that the Nephrotrematinae be raised to family rank to contain *Nephrotrema* and *Xiphidiotrema*.

*Soricitrema baeri* Bykhovskaya-Pavlovskaya, Vysotzkaya & Kulakova, 1970 was described from the kidneys of shrews in Russia (Bykhovskaya-Pavlovskaya *et al*., 1970). Jourdane (1971) pointed out that the reported differences between this nominal species and *N. truncatum* were not sufficient even to recognize it as a separate species, let alone merit the erection of a new genus. *Soricitrema* is therefore regarded as a synonym of *Nephrotrema*.

The two genera that fit least well into the Troglotrematidae are *Paragono* and *Stephanolecithus*. Both are included here provisionally. *Paragono* is atypical in having the genital pore anterior to the ventral sucker and a branched or dendritic ovary. *Stephanolecithus* has the genital pore near the anterior end of the body and a more extensive uterus than is usually seen in troglotrematids.

Of the seven different subfamilies among which Yamaguti (1971) distributed the genera discussed here, only two contained more than one genus. We remain uncertain about the relationships between the genera, even those, such as *Nephrotrema* and *Xiphidiotrema*, placed in the same subfamily by Yamaguti (1971). Consequently, we prefer not to recognize any subfamilies.

## Family Troglotrematidae Odhner, 1914

(Syns Troglotremidae [*sic*] Odhner, 1914; Nephrotrematinae Baer, 1931; Nanophyetinae Wallace, 1935; Stephanolecithinae Yamaguti, 1958; Macroorchiinae Yamaguti, 1958; Sellacotylinae Yamaguti, 1958; Beaveriinae Lee, 1965; Paragoninae Yamaguti, 1971)

**Diagnosis:** Body small to medium-sized, pyriform, fusiform or flattened, may be attenuated or rounded at either end. Tegument almost always armed. Oral sucker subterminal. Ventral sucker

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equatorial or pre-equatorial, usually similar in size to oral sucker. Prepharynx very short or absent. Pharynx present. Oesophagus short or long, or not apparent. Intestinal bifurcation at various levels between oral sucker and about one-third of body-length. Caeca two, simple, variable in length, sometimes not extending beyond ventral sucker. Testes two, often large and longer than wide, symmetrical or subsymmetrical, anterior or posterior (usually) to ventral sucker, often overlap it, rarely at posterior end of body, usually entire. Cirrus-sac present or absent; if absent, bipartite seminal vesicle free in parenchyma; if present, cirrus-sac may contain bipartite seminal vesicle. Genital pore usually in middle third of body immediately posterior to ventral sucker, exceptionally just anterior to ventral sucker or at anterior of body. Ovary median or submedian in middle third of body (rarely anterior to this), pre-, inter- or post-testicular, usually entire, rarely lobed. Laurer's canal usually present. Seminal receptacle often present, in form of expansion of oviduct, blind diverticulum from oviduct, canalicular or uterine. Uterus variable in extent, usually rather short and intercaecal or postcaecal and posterior to genital pore. Eggs small to large, numerous or few. Vitelline follicles variably distributed, typically extensive but sometimes very restricted. Excretory vesicle Y-, V- or I-shaped, or saccate; pore terminal. In tissue, body sinus or digestive tract of mammals and birds; cosmopolitan. Type-genus *Troglotrema* Odhner, 1914.

## Key to genera

**1a. Genital pore anterior or lateral to ventral sucker; posterior median indentation of body often present ..... 2.**

**1b. Genital pore posterior to ventral sucker; posterior median indentation of body absent ..... 3.**

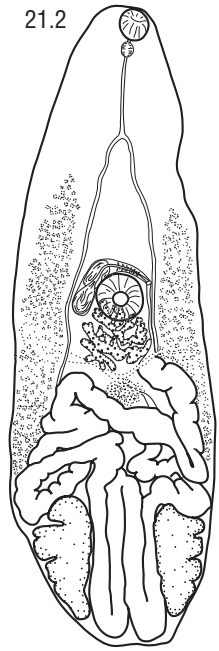
**2a. Testes at posterior extremity; genital pore just anterior or anterolateral to ventral sucker ..... *Paragono* Pearse, 1931. (Fig. 21.2)**

**Diagnosis:** Body small, flattened, tapered anteriorly, rounded posteriorly, often with median indentation at posterior end. Tegument spined or not. Oral sucker small, subterminal. Ventral sucker equal to or larger than oral sucker, equatorial or slightly anterior to this. Oesophagus long, narrow. Intestinal bifurcation about midway between suckers. Caeca simple, narrow, terminate laterally close to anterior edges of testes. Testes large, symmetrical, lateral at posterior end, irregularly lobed. Cirrus-sac present, transverse, curved around anterior edge of, or dorsal to, ventral sucker, apparently contains bipartite seminal vesicle. Genital pore at, or just anterior to, left margin of ventral sucker. Ovary irregularly and deeply lobed, median, just posterior or posterodorsal to ventral sucker. Mehlis' gland posterior to ovary. Laurer's canal and seminal receptacle not known. Uterus extensive in postovarian region with loops passing to posterior end of body between testes. Eggs small, probably numerous. Vitelline follicles in lateral extracaecal fields anterior to testes in second and third quarters of body. Excretory vesicle apparently Y-shaped; pore terminal, opens into posterior median indentation if present. In intestine of seabirds (Charadriiformes); coastal China. Type-species *P. kelloggi* Pearse, 1930.

**2b. Testes in mid-body, separated from posterior end by ends of caeca and vitelline follicles; genital pore beside oral sucker or pharynx ..... *Stephanolecithus* Nakagawa, 1918. (Fig. 21.3)**

(Syn. *Beaveria* Lee, 1965)

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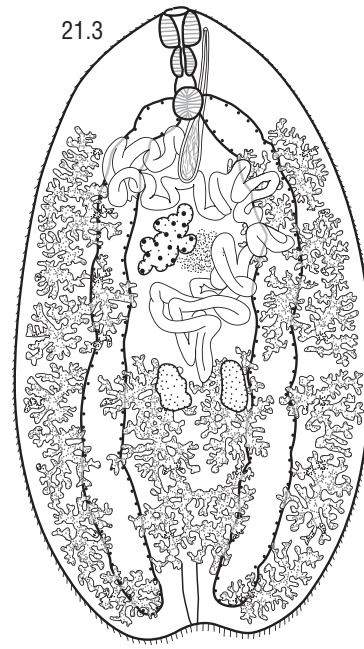




**Fig. 21.2.** *Paragono numenii* Zhang, Qiu & Li, 1984. Ventral view. After Zhang *et al.* (1984).
**Fig. 21.3.** *Stephanolecithus* as *Beaveria beaveri* Lee, 1965. Ventral view. After Lee (1965).

**Diagnosis:** Body small to medium-sized, flat, oval in ventral view, rounded posteriorly, where usually with conspicuous median indentation. Tegument spined. Oral sucker small, subterminal. Ventral sucker slightly smaller or larger than oral sucker, in anterior quarter of body. Oesophagus short. Caeca simple, sometimes follow slightly sinuous course, terminate close to posterior end. Testes symmetrical, intercaecal, entire or lobed, in mid-body. Cirrus-sac elongate, close to median line, with base dorsal or posterior to ventral sucker, tapers towards genital pore at left side of oral sucker or pharynx, contains elongate seminal vesicle, pars prostatica and ejaculatory duct from which cirrus may form. Ovary lobed or not, just dextrally submedian, between testes and ventral sucker. Mehlis' gland median to ovary. Laurer's canal present. Seminal receptacle present or absent, when present apparently a blind diverticulum from oviduct. Uterine loops mostly intercaecal between testes and ventral sucker, intrude into intertesticular region and may extend lateral to caeca. Metraterm short, dorsal to cirrus-sac. Eggs of medium size, numerous. Vitelline follicles extensive laterally and dorsolaterally, overlap caeca, may not extend anterior to ventral sucker and always absent from immediate vicinity of oral sucker and pharynx, often approach or reach median line posterior to testes. Excretory vesicle Y-shaped, with long stem bifurcating between testes; pore opens into terminal indentation if present. In small intestine and liver (probably gall-bladder and bile-ducts) of mammals (Rodentia), also in cats and dogs experimentally; China, Taiwan, Malaysia, Indonesia. Type-species *S. parvus* Nakagawa, 1918.

**3a. Oesophagus much longer than caeca; caeca very short, not extending posterior to ventral sucker ..... *Baiohelmins* Cribb & Pearson, 1988. (Figs 21.4, 21.5)**
**Diagnosis:** Body minute, fusiform. Tegument spined. Oral sucker aperture just subterminal. Ventral sucker at about equator, similar in size to oral sucker. Oesophagus long. Intestinal bifurca-

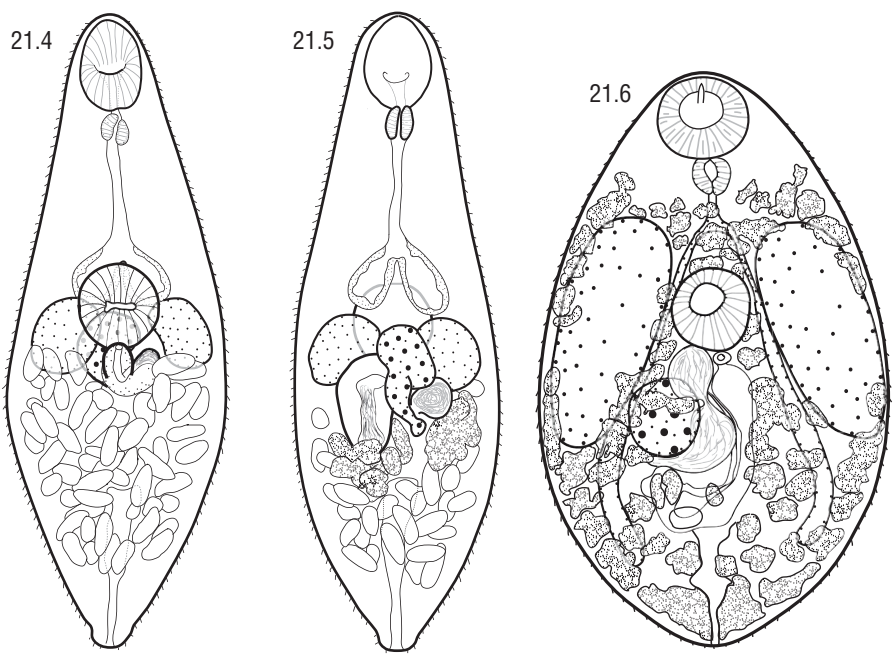
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tion close to ventral sucker. Caeca very short and broad, not extending posterior to ventral sucker. Testes entire, symmetrical, posterolateral to ventral sucker, abut ends of caeca. Cirrus-sac S-shaped in lateral view, posterior to ventral sucker, contains internal seminal vesicle, pars prostatica and ejaculatory duct, from which cirrus may form. Genital pore median, immediately posterior to ventral sucker. Ovary entire, median, between and dorsal to testes, overlaps ventral sucker. Laurer's canal and saccate seminal receptacle present. Uterus occupies most of hindbody. Eggs small, moderately numerous. Vitelline follicles in two small dorsolateral groups posterior to testes, ovary and cirrus-sac. Excretory vesicle tubular, I-shaped or, if contracted, saccate; pore terminal. In intestine of mammals (Rodentia); Australia. Type-species *B. elegans* Cribb & Pearson, 1988.

**3b. Oesophagus much shorter than caeca; caeca terminate at various levels between ventral sucker and posterior end of body ..... 4.**

**4a. Ovary posterior or largely posterior to testes ..... 5.**
**4b. Ovary anterior to testes ..... 7.**

**5a. Cirrus-sac absent ..... *Macroorchis* Ando, 1919. (Fig. 21.6)**
**Diagnosis:** Body small to medium in size, oval, pyriform, rarely elongate and attenuated posteriorly. Tegument spined. Oral sucker subterminal, may contain stylet. Ventral sucker usually slightly pre-equatorial, sometimes much closer to anterior end, similar in size to oral sucker. Oesophagus short to medium length. Caeca simple, narrow, terminate in posterior quarter or




**Figs 21.4, 21.5.** *Baiohelmins elegans* Cribb & Pearson, 1988. 21.4. Ventral view. 21.5. Dorsal view. After Cribb & Pearson (1988).
**Fig. 21.6.** *Macroorchis spinulosus* Ando, 1919. After Chai *et al.* (1996).

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third of body. Testes large to very large, entire, much longer than broad, symmetrical, extracaecal, at level of ventral sucker or slightly posterior to this. Cirrus-sac absent. Seminal vesicle large, bipartite, free in parenchyma posterior to ventral sucker, opens via possible short prostatic region and ejaculatory duct at median genital pore immediately posterior to ventral sucker. Ovary usually rounded, median or slightly submedian to either side, between posterior ends of testes or slightly posterior to this. Laurer's canal present. Uterine seminal vesicle present. Uterus intercaecal, initially runs posteriorly, often reaches anterior edge of excretory vesicle and may extend beyond ends of caeca. Metraterm apparently not differentiated. Eggs of medium size, few to numerous. Vitelline follicles from level of intestinal bifurcation to posterior end, most abundant laterally but may reach median line, especially posterior to ventral sucker. Excretory vesicle somewhat elongate, broadest between ends of caeca and variously described as Y- or V-shaped; pore terminal. In intestine of mammals (Insectivora, Rodentia, Carnivora); Japan, Korea. Type-species *M. spinulosus* Ando, 1919.

**5b. Cirrus-sac present ..... 6.**

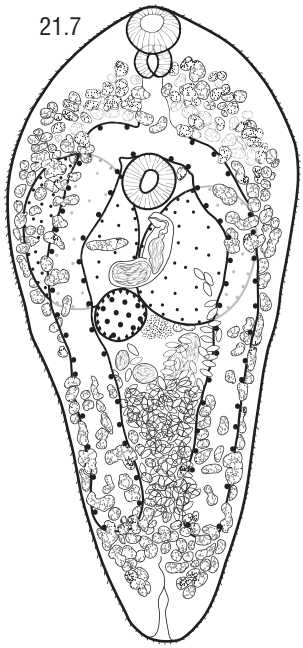
**6a. Vitelline follicles in fore- and hindbody ..... *Nephrotrema* Baer, 1931. (Fig. 21.7)**
(Syn. *Soricitrema* Bykhovskaya-Pavlovskaya, Vysotzkaya & Kulakova, 1970)

**Diagnosis:** Body of medium size, plump, pyriform, widest at level of ventral sucker and attenuated posteriorly. Tegument armed with spines. Oral sucker subterminal. Ventral sucker at about one-third from anterior end, similar in size to oral sucker. Oesophagus short. Caeca moderately broad, reach close to posterior extremity. Testes large to very large, longer than wide, entire, symmetrical or somewhat diagonal, sometimes contiguous medially, at level of ventral sucker or anterior or posterior to this, intercaecal and/or dorsal to caeca. Cirrus-sac elongate, close to ventral sucker and sometimes dorsal or lateral to it, contains small, usually bipartite seminal vesicle, well-differentiated pars prostatica and short ejaculatory duct. Genital pore median, slightly posterior to ventral sucker. Ovary entire, submedian, posterior or posterodorsal to right testis. Laurer's canal present. Seminal receptacle possibly present. Uterus posterior to ventral sucker, largely in second third or third quarter of body, intercaecal. Metraterm short. Eggs large, moderately numerous. Vitelline follicles distributed along entire length of body, most abundant laterally but may reach median line, especially posterior to ventral sucker. Excretory vesicle Y-shaped; main stem bifurcates posterior to uterus; pore terminal. In kidney of mammals (Insectivora); Europe. Type-species *N. truncatum* (Leuckart, 1842) Baer, 1931.

**6b. Vitelline follicles in hindbody only ..... *Xiphidiotrema* Senger, 1953. (Fig. 21.8)**

**Diagnosis:** Body small, pyriform or fusiform, rounded anteriorly and pointed posteriorly. Tegument spinous. Oral sucker large, subterminal; small stylet sometimes present in dorsal wall. Ventral sucker equatorial or slightly anterior to this, smaller than, or equal to, oral sucker. Oesophagus short. Caeca simple, terminate close to posterior end of body or somewhat anterior to this. Testes large, symmetrical, sometimes much longer than wide, immediately anterolateral to ventral sucker, ventral to caeca or extracaecal. Cirrus-sac elongate-pyriform, posterolateral to ventral sucker, contains seminal vesicle, pars prostatica and ejaculatory duct, from which short cirrus may form. Genital pore median, slightly posterior to ventral sucker. Ovary just posterior to ventral sucker, dextrally submedian. Seminal receptacle and Laurer's canal not reported. Uterus intercaecal posterior to ventral sucker, with few moderately large eggs. Vitelline follicles entirely posterior to ventral sucker, extensive but sometimes absent from midline in region of ovary and cirrus-sac. Excretory vesicle V- or Y-shaped; pore terminal. In intestine of mammals (Insectivora); USA, China. Type-species *X. lockerae* Senger, 1953.

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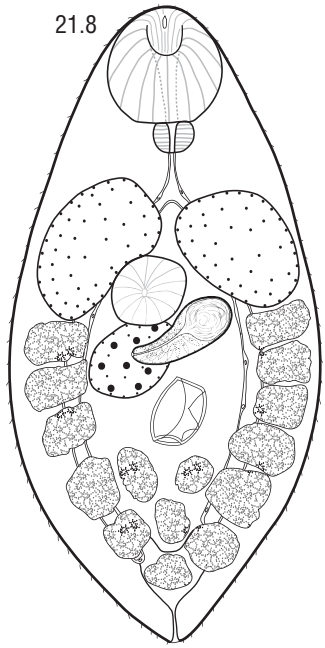




**Fig. 21.7.** *Nephrotrema truncatum* (Leuckart) as *Soricitrema baeri* Bykhovskaya-Pavlovskaya, Vysotzkaya & Kulova, 1970. Ventral view. After Bykhovskaya-Pavlovskaya *et al.* (1970).
**Fig. 21.8.** *Xiphidiotrema lockerae* Senger, 1953. Ventral view. After Senger (1953).

**7a. Excretory vesicle small, saccate ..... 8.**
**7b. Excretory vesicle Y-shaped with long stem ..... *Troglotrema* Odhner, 1914. (Fig. 21.9)**
**Diagnosis:** Body small to medium in size, rounded or pyriform, slightly attenuated posteriorly, where caudal projection sometimes reported. Tegument spinous. Oral sucker subterminal. Ventral sucker slightly pre-equatorial, similar in size to oral sucker. Oesophagus rather short, may be folded in sagittal plane. Caeca long, simple, may be slightly sinuous, sometimes locally dilate or constricted, terminate near posterior end. Testes large to very large, usually entire, almost symmetrical, usually posterior to level of ventral sucker but may overlap this level. Cirrus-sac quite large, median or submedian, largely posterior to ventral sucker or curled dorsally over sucker, contains bipartite seminal vesicle, prostatic complex and short unarmed cirrus. Genital pore median or just submedian, immediately posterior to ventral sucker. Ovary submedian, rounded to pyriform, anterior to or overlapping level of either testis, usually overlaps level of ventral sucker. Laurer's canal present. Seminal receptacle probably rudimentary. Uterus largely confined to region bounded by testes, cirrus-sac and ovary but may extend slightly posterior to testes. Eggs large and moderately numerous. Vitelline follicles extensive from level of oral sucker to posterior end of body, mostly close to caeca, approach median line dorsally and at each end of body. Excretory vesicle Y-shaped, dividing posterior to testes into two long arms extending anterior to ventral sucker; pore terminal. In frontal, ethmoidal and maxillary sinuses, gall-bladder and cysts attached to small intestine of mammals (Rodentia, Carnivora); Europe, southern Asia and probably Central Africa. Type-species *T. acutum* (Leuckart, 1842) Odhner, 1914.

**8a. Diameter of oral sucker much less than twice that of ventral sucker ..... 9.**
**8b. Diameter of oral sucker much greater than twice that of ventral sucker ..... ..... *Skrjabinophyetus* Dimitrova & Genov, 1967. (Fig. 21.10)**

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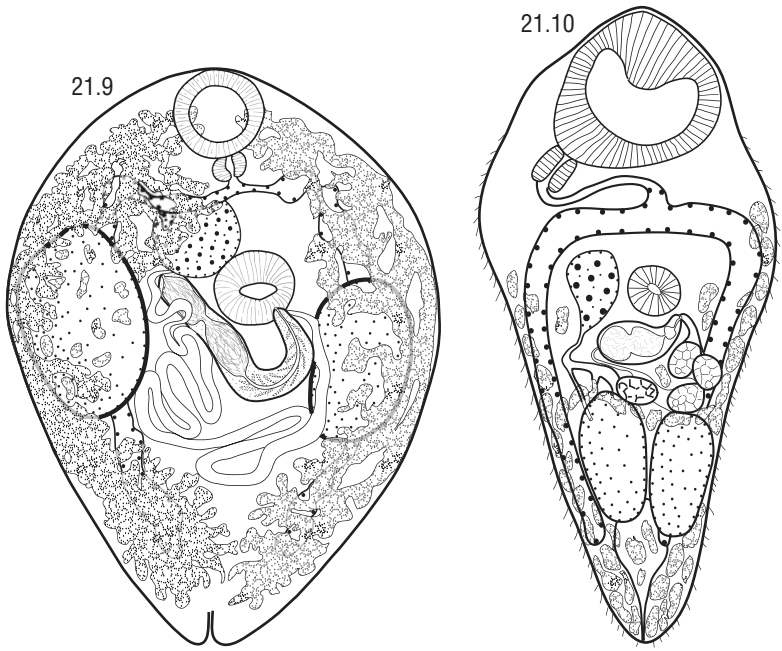



**Fig. 21.9.** *Troglotrema acutum* (Leuckart, 1842) Odhner, 1914. Ventral view. After Baer (1931a).
**Fig. 21.10.** *Skrjabinophyetus neomydis* Dimitrova & Genov, 1967. Ventral view. After Brendow (1970).

**Diagnosis:** Body small, pyriform or fusiform, with shape and disposition of internal organs varying considerably according to method of preparation. Tegument spined. Oral sucker subterminal, very large, much greater than twice the size of ventral sucker. Ventral sucker equatorial or slightly anterior to this, much smaller than oral. Oesophagus short to long, sometimes not apparent. Caeca simple, almost reach posterior end. Testes symmetrical or almost so, large, entire, longer than wide; position highly variable but typically posterior to ventral sucker. Cirrus-sac transversely and/or dorsoventrally oriented just posterior to ventral sucker or curled around dorsal or lateral margins of sucker, contains bipartite seminal vesicle, pars prostatica and ejaculatory duct, from which cirrus may form. Genital pore median, just posterior to ventral sucker. Ovary entire, pyriform, ovoid or spherical, submedian, just anterior to either testis. Laurer's canal present. Seminal receptacle absent. Uterus short, forms loop between testes and may extend well posterior to these, may extend anteriorly as far as intestinal bifurcation. Eggs of medium size, not numerous. Vitelline follicles numerous, especially dorsally, occupy posterior two-thirds of body but rarely extend anteriorly as far as intestinal bifurcation. Excretory vesicle saccate; pore terminal. In intestine of mammals (Insectivora); Europe. Type-species *S. neomydis* Dimitrova & Genov, 1967.

**9a. Cirrus-sac present ..... *Nanophyetus* Chapin, 1927. (Fig. 21.11)**
(Syns *Nanophyes* Chapin, 1926 *nec* Schoenherr 1838; *Pseudotroglotrema* Yamaguti, 1971)
**Diagnosis:** Body very small, variable in shape but typically oval to pyriform. Tegument spined. Oral sucker subterminal, moderately large. Ventral sucker equatorial or slightly anterior to this, generally slightly smaller than oral sucker. Oesophagus short, sometimes apparently absent. Caeca simple, usually terminate in middle third of body dorsal to anterior ends of testes but may almost

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reach posterior end of body. Testes large, oval, longer than wide, symmetrical, sometimes oblique, lateral at about middle of hindbody, may overlap level of ventral sucker. Cirrus-sac transverse or oblique, close to ventral sucker and generally opposite ovary, with base typically anterior to genital pore, contains bipartite seminal vesicle and pars prostatica; formation of cirrus from ejaculatory duct disputed. Genital pore midventral, slightly posterior to ventral sucker. Ovary spherical or oval, submedian, pretesticular, adjacent to ventral sucker. Laurer's canal present. Presence of seminal receptacle disputed; sperm reported in dilatation of oviduct between ovary and base of Laurer's canal (i.e. oviducal seminal receptacle). Uterus forms single or double loop in sagittal plane between testes; metraterm receives terminal male duct shortly before genital pore. Eggs large, few. Vitelline follicles occupy much of dorsal and lateral regions of body except anterior end. Excretory vesicle saccate, small; pore terminal. In intestine of mammals (Carnivora, Insectivora) including man, also many experimental hosts; North America, Europe, Asia. Type-species *N. salmincola* (Chapin, 1926) Chapin, 1927.

**9b. Cirrus-sac absent ..... *Sellacotyle* Wallace 1935. (Fig. 21.12)**
**Diagnosis:** Body very small, pyriform. Tegument spinous. Oral sucker large, subterminal. Ventral sucker, in middle third of body, slightly larger than oral sucker. Oesophagus short. Caeca simple, terminate close to posterior edge of ventral sucker. Testes large, oval, longer than wide, symmetrical, lateral, occupy much of body posterior to ventral sucker. Seminal vesicle bipartite, free in parenchyma posterodorsal to ventral sucker or between this and right testis, continues into short pars prostatica. Cirrus-sac absent. Genital pore median, just posterior to ventral sucker. Ovary

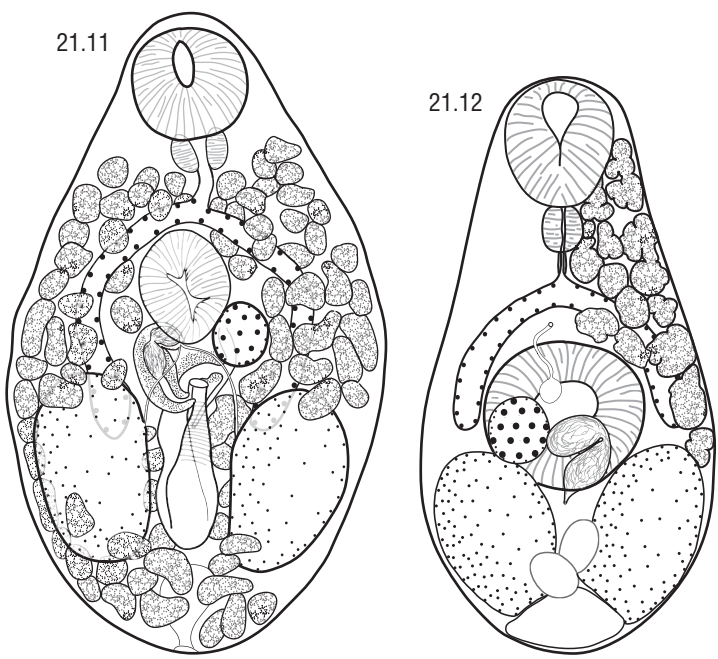



**Fig. 21.11.** *Nanophyetus salmincola* (Chapin, 1926). Ventral view. After Yamaguti (1971).
**Fig. 21.12.** *Sellacotyle mustelae* Wallace, 1935. Dorsal view with vitelline follicles omitted from left side. After Wallace (1935).

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round, median or submedian, pretesticular or between anterior edges of testes, often partly dorsal to ventral sucker. Laurer's canal present. Seminal receptacle present. Uterus short, between testes; metraterm receives terminal male duct shortly before opening via genital pore. Eggs moderately large, few in number. Vitelline follicles lateral between levels of oral sucker and testes, sometimes reaching posterior end of body, occur towards midline dorsally in region of oesophagus and near posterior end. Excretory vesicle saccate; pore terminal. In intestine of mammals (Carnivora, Rodentia); North America. Type-species *S. mustelae* Wallace 1935.

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# 22 Superfamily Plagiorchioidea Lühe, 1901

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## Introduction

The superfamily Plagiorchioidea Lühe, 1901, as recognized here, is based mainly on molecular phylogenies (Tkach *et al.*, 2000a, 2001b; Cribb *et al.*, 2001b; Olson *et al.*, 2003), but considerations of ease of identification have also been taken into account. The families Plagiorchiidae Lühe, 1901, Auridistomidae Stunkard, 1924, Cephalogonimidae Looss, 1899, Choanocotylidae Jue Sue & Platt, 1998, Glypthelminthidae Cheng, 1959, Haematoloechidae Freitas & Lent, 1939, Leptophallidae Dayal, 1938, Macroderoididae McMullen, 1937, Omphalometridae Looss, 1899 and Telorchiidae Looss, 1899 are included as a result of these studies. Other families, the Dolichoperoididae Johnston & Angel, 1940, Echinoporidae Krasnolobova & Timofeeva, 1965, Encyclometridae Mehra, 1931, Gekkonotrematidae Yamaguti, 1971, Meristocotylidae Fischthal & Kuntz, 1964, Mesotretidae Poche, 1926, Ocadiatrematidae Fischthal & Kuntz, 1981, Opisthogonimidae Travassos, 1928, Orientocreadiidae Yamaguti, 1958, Reniferidae Pratt, 1902, Styphlotrematidae Baer, 1924, Thrinascotrematidae Jue Sue & Platt, 1999 and Urotrematidae Poche, 1926, have been included based on morphological and, in a few cases, life-cycle characters. As pointed out by Tkach (Chapter 29, this volume), recent molecular studies (Tkach *et al.*, 2001b; Olson *et al.*, 2003; Bray *et al.*, 2005; Curran *et al.*, 2006; Choudhury *et al.*, 2007) have indicated that the Encyclometridae may be more closely related to the Gorgoderoidea Looss, 1899, but for convenience of identification it is retained in the plagiorchioid key. Similarly, the families Brachycoeliidae Looss, 1899 and Mesocoeliidae Dollfus, 1929 are retained in the superfamily Gorgoderoidea (Bray & Blair, Chapter 9, this volume), although molecular results (Tkach *et al.*, 2000a, 2001b; Curran *et al.*, 2006; Razo-Mendivil *et al.*, 2006; Choudhury *et al.*, 2007) indicate that they may belong in the Plagiorchioidea. There is no doubt that the arrangement of families in the superfamilies in this series of volumes, and particularly this volume, will change as more molecular and life-cycle data become available.

The key for this superfamily has been difficult to design. The family Plagiorchiidae is clearly paraphyletic or polyphyletic and is almost certainly a temporary repository for a number of genera that will be placed elsewhere as our knowledge increases. In view of the fact that members currently assigned to this family exhibit such a variety of characteristics, great care should be taken in the use of this key.

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## Superfamily Plagiorchioidea Lühe, 1901

**Diagnosis**: Body tiny to large, elongate, elliptical, cylindrical, fusiform, lanceolate or pyriform, slender or plump, exceptionally with sleeve-like lateral projections posterior to ventral sucker. Tegument armed with spines or not. On rare occasions numerous elevated glands present on ventral surface posterior to ventral sucker. Oral sucker subterminal, oval, rounded or infundibuliform, occasionally with enlarged circumoral spines, may bear paired papilla-like armed or unarmed lateral or ventrolateral lappets. Ventral sucker usually in anterior half of body, sometimes equatorial or postequatorial, occasionally divided into two parts by septum. Prepharynx usually present, sometimes apparently absent. Pharynx present. Oesophagus of varying length, sometimes indistinct. Intestinal bifurcation usually distinctly in forebody. Caeca two, usually extend into second half of body, usually terminate posterior to testes, occasionally form cyclocoel. Testes two, in hindbody, occasionally at posterior extremity, postovarian, oblique, tandem or symmetrical. External seminal vesicle occasionally present. Cirrus-sac usually relatively large, in fore- or hindbody, contains bipartite or convoluted undivided tubular seminal vesicle, prostatic complex and protrusible armed or unarmed cirrus. Genital atrium usually present, small to large. Genital pore in forebody or hindbody, between anterior and posterior extremity, median to lateral, occasionally armed. Ovary median or submedian, pretesticular, posterior, posterolateral to or overlapping ventral sucker. Canalicular or uterine seminal receptacle present or absent. Juel's organ-like structure occasionally present. Laurer's canal present or absent. Uterus usually passes between testes and reaches to, or close to, posterior extremity, or uterus is entirely pretesticular. Eggs usually operculate, large or small. Vitellarium follicular, usually forms lateral fields or clusters of follicles, mostly in hindbody, often extends into forebody, rarely forms single median field; lateral vitelline fields may be confluent in hindbody or forebody. Excretory vesicle in adults I-, Y- or V-shaped, with short or long arms, occasionally branches arise from base of vesicle, occasionally stem with short diverticula; pore usually terminal. In digestive or respiratory tract or urogenital system of fishes or tetrapods, occasionally oviparous in invertebrates; cosmopolitan. Type-genus *Plagiorchis* Lühe, 1899.

## Key to families

**1a. Genital pore in forebody or at level of ventral sucker ..... 7.**
**1b. Genital pore in hindbody ..... 2.**

**2a. Genital pore in anterior hindbody ..... 3.**
**2b. Genital pore at or close to posterior extremity ..... Urotrematidae Poche, 1926.**

**3a. Oral sucker ornamented with lappets, spines and/or incisions ..... 4.**
**3b. Oral sucker not ornamented ..... 5.**

**4a. Oral sucker flared or infundibuliform, with lappets and/or ventral incision, without distinct crown of spines; prepharynx long; oesophagus short; intestinal bifurcation in anterior forebody; caeca extend almost to posterior extremity of body; in freshwater turtles, Australia ..... Choanocotylidae Jue Sue & Platt, 1998.**
**4b. Oral sucker small, with crown of small spines and lateral lobes; prepharynx short; oesophagus long; intestinal bifurcation just inside posterior half of forebody; caeca extend to about**

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**middle of post-testicular region; in freshwater turtles, Taiwan ..... ..... Ocadiatrematidae Fischthal & Kuntz, 1981.**

**5a. Ovary pretesticular; in reptiles ..... 6.**
**5b. Ovary just post-testicular; in Palaearctic and Indo-Malayan bats ..... ..... Mesotretidae Poche, 1926.**

**6a. Rudimentary Juel's organ-like feature (Fischthal's organ) present; uterus pretesticular; in gekkonid lizards, New Hebrides ..... Gekkonotrematidae Yamaguti, 1971.**
**6b. Rudimentary Juel's organ-like feature absent; uterus reaches posterior extremity; in Neotropical snakes ..... Opisthogonimidae Travassos, 1928.**

**7a. Oral sucker with lateral muscular papillae or lappets ..... ..... Auridistomidae Stunkard, 1924, Telorchiidae Looss, 1899 (Allotelorchiinae Goodman, 1988) and Plagiorchiidae Lühe, 1901 (*Eustomos* MacCallum, 1921, *Longigula* Qiu, Zhang & Li, 1983 and *Parallopharynx* Caballero, 1946).**
**7b. Oral sucker lacks lateral muscular papillae or lappets ..... 8.**

**8a. Genital pore at or near anterior extremity ..... Cephalogonimidae Looss, 1899.**
**8b. Genital pore further posterior ..... 9.**

**9a. Genital pore median, at level of oral sucker, pharynx or oesophagus ..... 10.**
**9b. Genital pore further posterior ..... 12.**

**10a. Ventral sucker undivided; in anurans or snakes ..... 11.**
**10b. Ventral sucker distinctly divided into two parts, each with its own lumen; in gastrointestinal system and lungs of varanid lizards ..... ..... Meristocotylidae Fischthal & Kuntz, 1964.**

**11a. Forebody short; ventral sucker weakly developed or absent; vitelline follicles usually clumped in rosettes; in lungs of anuran amphibians ..... ..... Haematoloechidae Freitas & Lent, 1939.**
**11b. Forebody long; ventral sucker well developed; vitelline follicles in continuous fields; in lungs, trachea and oesophagus of snakes ..... ..... Dolichoperoididae Johnston & Angel, 1940.**

**12a. Uterus mainly or totally pretesticular ..... 13.**
**12b. Bulk or much of uterus reaches into post-testicular region ..... 14.**

**13a. Testes in about mid-hindbody; in intestine and gall-bladder of mammals ..... ..... Omphalometridae Looss, 1899.**
**13b. Testes at posterior extremity; in intestine or oviduct of amphibians and reptiles ..... ..... Telorchiidae Looss, 1899.**

**14a. External seminal vesicle present ..... 15.**
**14b. External seminal vesicle absent ..... 16.**

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15a. Prepharynx usually not observed; canalicular seminal receptacle present or apparently absent; in digestive tract and lungs of snakes ..... Leptophallidae Dayal, 1938.
15b. Prepharynx distinct; uterine seminal receptacle present; in freshwater fishes and reptiles ..... Orientocreadiidae Yamaguti, 1958.

16a. Excretory vesicle with two branches arising from base of stem; main stem of vesicle branches between testes and ventral sucker with numerous shallow diverticula; in marine turtles and marine fish ..... Styphlotrematidae Baer, 1924.
16b. Excretory vesicle lacks branches at base ..... 17.

17a. Excretory vesicle almost reaches anterior extremity; in stomach of Australian freshwater turtles ..... Thrinascotrematidae Jue Sue & Platt, 1999.
17b. Excretory vesicle shorter ..... 18.

18a. Genital pore armed with acicular spines ..... ..... Echinoporidae Krasnolobova & Timofeeva, 1965.
18b. Genital pore unarmed ..... 19.

19a. In tetrapods ..... 20.
19b. In intestine of freshwater heterotherms, usually fishes, exceptionally in freshwater crustaceans or leeches, and marine fishes; North America, South America, Europe, Asia, Atlantic Ocean ..... Macroderoididae McMullen, 1937.

20a. Excretory vesicle I-shaped; in amphibians ..... Glypthelminthidae Cheng, 1959.
20b. Excretory vesicle usually Y-shaped; in tetrapods ..... 21.

21a. Excretory vesicle Y-shaped, with short arms, or occasionally I-shaped; in digestive tract, exceptionally urogenital system, of tetrapods ..... 22.
21a. Excretory vesicle Y-shaped, with long stem and arms encircling ventral sucker; in digestive and respiratory tracts, exceptionally in reproductive organs, of snakes; Nearctic and Neotropical regions ..... Reniferidae Pratt, 1902.

22a. Excretory vesicle Y-shaped, with short arms, or rarely I-shaped; in digestive tract, exceptionally urogenital system, of tetrapods; cosmopolitan ..... Plagiorchiidae Lühe, 1901.
22b. Excretory vesicle Y-shaped, with very long, wide stem and short or very short branches; stem may have numerous lateral diverticula; in oesophagus, stomach and intestine of snakes and freshwater turtles; Eurasia ..... Encyclometridae Mehra, 1931.

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# 23 Family Plagiorchiidae Lühe, 1901

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## Introduction

This is a very large group of digeneans parasitic in tetrapod hosts worldwide. Plagiorchiids can be found in all parts of the digestive tract of their hosts, including the mouth and cloaca, and also in the bile-ducts, gall-bladder, liver, lungs, ureters and kidney. Arguably, this is the family with the most complex taxonomic history and most controversial content of all digeneans. At different times, about 150 genera have been included in the Plagiorchiidae Lühe, 1901, the majority of them subsequently being either synonymized or transferred to other families. The literature on the plagiorchiids and the genera that have been included in this family is enormous, and it is impossible to provide here even a superficial account of the different views on the system of the family. It has been summarized at different times by Baer (1924), Mehra (1937), Skrjabin & Antipin (1958a, 1960, 1961) and Sharpilo & Iskova (1989). Some of the most substantial contributions to the systematics of the Plagiorchiidae were made by Looss (1899), Lühe (1899, 1909), Baer (1924), McMullen (1937), Mehra (1937), Olsen (1937), Byrd *et al.* (1940a), Skrjabin & Antipin (1958a, 1960, 1961), Yamaguti (1958b, 1971), Odening (1959b, 1964c), Prudhoe & Bray (1982) and Sharpilo & Iskova (1989); this list could be expanded many times. Some of the systematic opinions expressed by these and other workers are discussed elsewhere in this volume.

Some of the controversies associated with plagiorchiid taxonomy concern its type-genus, *Plagiorchis* Lühe, 1899, and the type-species of *Plagiorchis*, namely *P. vespertilionis* (Müller, 1780). Two synonymous genera, *Plagiorchis* Lühe, 1899 and *Lepoderma* Looss, 1899, were published in the same year and even on the same day, which led to decades of arguing in the literature regarding the issue of priority, with different researchers considering one or other genus the senior synonym. However, as shown by Poche (1926), Braun (1900a) had already noticed that the issue No. 604 of *Zoologischer Anzeiger*, containing the erection of *Plagiorchis* Lühe, 1899, was published on 28 December 1899 and sent to subscribers on 29 December while the issue of *Zoologischer Jahrbücher* containing the erection of *Lepoderma* Looss, 1899 was also published on 28 December 1899 but was sent to subscribers on 30 December. This small advantage was considered by Poche (1926), Skrjabin & Antipin (1958a) and the majority of other researchers as sufficient to recognize the priority of *Plagiorchis* Lühe, 1899. This opinion is also accepted here.

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There has also long been a misunderstanding regarding the morphology of *Plagiorchis vespertilionis* (Müller, 1780), a parasite of bats, which led to numerous misidentifications of *Plagiorchis* from bats around the world. This problem was considered in detail by Sharpilo & Tkach (1992) and Tkach *et al*. (2000b). These authors clarified the question of the morphological identity of *P. vespertilionis*, redescribed this species and provided a key for the differentiation of *Plagiorchis* species parasitic in bats in Europe.

There has never been complete agreement on the composition of the Plagiorchiidae between any two authors and the whole system of the family has frequently been reshuffled. Among the main reasons of such a situation is the extremely high morphological diversity of these digeneans, on one hand, and the lack of agreement on characters that should be used to differentiate these genera, on the other. Poor descriptions and illustrations, inaccessible type-material and lack of knowledge on life-cycles of many plagiorchiid genera have added to this confusion. All previous systems split the Plagiorchiidae into several or numerous subfamilies. At the same time, there was permanent disagreement between different authors regarding the content of the subfamilies. In fact, the use of subfamilies was mainly counterproductive, brought even more instability into the systematics of the family and made identification of genera more difficult. In this key, we drop all subfamilies, except for those that were raised to the rank of family. Currently, there are not enough data to confidently separate the remaining genera in the Plagiorchiidae into monophyletic lineages.

In my opinion, the family Plagiorchiidae (*sensu stricto*) should include only digeneans from tetrapods possessing a well-defined cirrus-sac containing a bipartite seminal vesicle, a uterus that passes between the testes or partly overlaps them, a Y-shaped excretory vesicle with short arms, a protonephridial formula of $2[(3 + 3 + 3) + (3 + 3 + 3)] = 36$, and arthropods as intermediate hosts. This strict definition could not be followed in this chapter for numerous reasons. First of all, there are insufficient available data on the morphology of many genera, in particular details of the organization of the excretory system and copulatory apparatus. Some of the specimens available for examination in museum collections are in such poor condition that it is not possible to see essential features, while specimens of many taxa, including many type-specimens, are not accessible. Life-cycle data on many genera, particularly those from tropical regions, are lacking. As a result, the Plagiorchiidae, as presented here, may potentially contain members of at least five or six families. Thus, this chapter should by no means be considered as a taxonomic revision of the Plagiorchiidae but merely as an aid for the identification of genera. As a part of ongoing revisionary work, a number of genera from the previously over-inflated Plagiorchiidae have been separated in this volume into their own families, e.g. the Leptophallidae Dayal, 1938, Haematoloechidae Freitas & Lent, 1939, Glypthelminthidae Cheng, 1959, Omphalometridae Looss, 1899, Encyclometridae Mehra, 1931, Opisthogonimidae Travassos, 1928, Reniferidae Travassos, 1928 and Styphlotrematidae Baer, 1924 (see introductions in corresponding chapters). On most occasions, such groupings have already been proposed as separate families or subfamilies in the past. Nevertheless, the genera preserved within the Plagiorchiidae in this chapter are still clearly non-monophyletic.

Despite some success in efforts to collect as many representatives of the Plagiorchiidae as possible for molecular phylogenetic study, it has proved to be impossible so far to obtain critically important taxa from Africa, India and South America. It is hoped that a combined molecular and morphological approach will help to clarify some of the remaining questions of plagiorchiid systematics in the near future.

Only new synonymies, new systematic allocations and a new genus are briefly discussed below in alphabetical order. Otherwise, previously proposed synonymies are accepted here.

It should be emphasized that some morphological features, such as coiled versus bipartite seminal vesicle, presence/absence of seminal receptacle, etc., may not be readily seen or can be

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seen only in properly fixed adult specimens. Nevertheless, these characters seem to be stable within a genus of plagiorchiids and very useful in differenting genera. The shape of the excretory vesicle is widely used in the systematics of the Plagiorchioidea Lühe, 1901, and, although a very important character, this strongly depends on fixation and, in some cases, the age of the parasite (for a good discussion on this issue, see Prudhoe & Bray, 1982); therefore, it is not used in this key as one of the discriminative morphological features.

Nicoll (1914) mistakenly stated that *Aptorchis aequalis* Nicoll, 1914, the type-species of the genus, lacks a seminal receptacle and its caeca are short and terminate just posterior to the ventral sucker. Both these attributes were included in the generic diagnosis of Yamaguti (1971) and the latter featured in his keys. As shown in several recent works on *Aptorchis* Nicoll, 1914 (see Jue Sue & Platt, 1999a; Platt & Jensen, 2002; Tkach & Snyder, 2007a, 2008), caeca in all known members of this genus reach the posterior end of the body and all species of *Aptorchis* possess a seminal receptacle, and thus these particular characters cannot be used to differentiate between *Aptorchis* and the genera included by Yamaguti (1971) in the Plagiorchiinae.

*Astiotrema* Looss, 1900 has been considered a member of the Plagiorchiidae by almost all authors. Very unusually, representatives of this genus have been described from fish, snakes, turtles and caudate amphibians. In the molecular phylogenetic studies of Tkach *et al*. (2001b) and Olson *et al*. (2003), a parasite of snakes, *A. monticelli* Stossich, 1904, was found to be not closely related to *Plagiorchis* and other plagiorchioid digeneans. Earlier, Prudhoe & Bray (1982) suggested that:

> in the concept presented by Yamaguti (1971) *Astiotrema* would appear to represent a composite group of genera, not yet recognized, and is in need of a very careful revision based on an understanding of the systematics of the family Plagiorchiidae. Even a superficial comparison of the descriptions of *Astiotrema reniferum, A. monticelli* and *A. trituri* will throw some doubt on their being congeneric.

Our recent unpublished molecular phylogenetic results, using a wider representation of *Astiotrema*, have demonstrated that three species of *Astiotrema* from European snakes, African fishes and turtles from South-east Asia form a monophyletic clade closest to the heterophyids, while *A. trituri* Grabda, 1959, a parasite of newts, is very close to *Plagiorchis*. Members of *Astiotrema* from snakes, fish and turtles possess an undivided sac-like seminal vesicle, while *A. trituri* possesses a typically plagiorchiid-like bipartite seminal vesicle. Furthermore, *A. trituri* has a typical plagiorchiid life-cycle, with cercariae developing in sporocysts and aquatic arthropods (cladoceran crustaceans) serving as intermediate hosts (Grabda, 1959b). Very little is known about the life-cycle and development of *Astiotrema* from other hosts; however, it is known that *A. monticelli* utilizes amphibians as second intermediate hosts and, more importantly, the cercariae develop in rediae (Shevchenko & Vergun, 1960). This is in agreement with the placement of *Astiotrema* among the opisthorchioid digeneans in molecular phylogenetic analyses. Thus, *A. trituri* should be removed from *Astiotrema*. Although it is very similar in general morphology to members of *Plagiorchis*, it has a unique morphological feature that allows easy differentiation from members of this genus and other plagiorchiids, namely the position of the right testis posterior to the right caecum while the left testis is intercaecal and separated from the right testes by numerous uterine coils. Therefore, a new genus, *Neoastiotrema* n.g. is established here with *Neoastiotrema trituri* (Grabda, 1959) n. comb. as the type- and only species. The original description of *N. trituri* can be found in Grabda (1959a) and additional descriptions have been published by several authors (e.g. Grabda 1959b; Sharpilo & Iskova, 1989). Consequently, *Astiotrema* Looss, 1900 is hereby removed from the Plagiorchiidae and is temporarily considered as *incertae sedis*.

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*Choledocystus* Pereira & Cuocolo, 1941 was established for *C. eucharis* Pereira & Cuocolo, 1941, but was later considered a synonym of *Glypthelmins* Stafford, 1905 (e.g. by Yamaguti, 1971). On the basis of a morphological examination of numerous specimens, SEM data and molecular phylogenetic analysis, Razo-Mendivil *et al*. (2006) resurrected *Choledocystus* and suggested that it should include five to seven species previously included in *Glypthelmins*. Among other features, they demonstrated that species of *Choledocystus* have a Y-shaped excretory vesicle, versus I-shaped in *Glypthelmins*. In their phylogenetic analysis, *Choledocystus hepaticus* (Lutz, 1928) clustered basal to the reniferid clade. Until more is known about the phylogenetic affinities of *Choledocystus*, and particularly its type-species, this genus is allocated in this volume to the polyphyletic Plagiorchiidae.

The description of *Neomicroderma elongata* Park, 1940, the type-species of *Neomicroderma* Park, 1940, was clearly based on very poor specimens. The drawing provided and the description almost perfectly conform with the diagnosis of *Allopharynx* Strom, 1928, except for the testes being situated somewhat further from the ovary than in a typical *Allopharynx*. In my opinion, this can be considered as a species-level character only. Park (1940) was obviously unaware of the description of *Allopharynx* and did not compare his species with that genus. *N. elongata* was recovered from the gall-bladder and intestine of a snake, which are normal sites of *Allopharynx*. Therefore, *Neomicroderma* is here considered a synonym of *Allopharynx*.

*Ostioloides* Odening, 1960 was included in the Haematoloechidae Freitas & Lent, 1939 (or Haematoloechinae, depending on systematic views) by most authors. However, it does not conform to the diagnosis of the Haematoloechidae and is here allocated to the Plagiorchiidae (see Tkach, Chapter 32, this volume).

*Plagiorchis luehei* Travassos, 1927 does not belong to *Microderma* Mehra, 1931, as suggested by Yamaguti (1971), because of substantial anatomical differences. Among other features, *P. luehei* has a coiled seminal vesicle, whereas that of *Microderma* is described as bipartite. In addition, these species are parasitic in very different groups of hosts, namely turtles and snakes, on different continents. On the other hand, *P. luehei* is very close to *Glossidioides* Yamaguti, 1958 and exhibits only species-level differences compared with *G. loossi* (Travassos, 1927).

In my opinion, *Sarumitrema* Beverley-Barton, 1963 was correctly allocated among the Telorchiidae by Prudhoe & Bray (1982), but it is included here in the Plagiorchiidae until further revision is made or more data are available on the phylogenetic affinities of this genus.

The systematic position of *Styphlodora* Looss, 1899, as well as its content and the synonymy of its species, has been the subject of numerous publications, including large reviews (e.g. Baer, 1924; Mehra, 1931, 1937; Byrd & Denton, 1938a; Byrd *et al*., 1940a, b; Dawes, 1942; Skrjabin & Antipin, 1961). *Platymetra* Mehra, 1931 was established for *S. bascanienis* Goldberger, 1911 based on some differences in the structure and position of the cirrus-sac, a blindly terminating Laurer's canal, its development, the configuration of the vitellarium and the appearance of the excretory vesicle. Byrd *et al*. (1940a) refuted this genus, stating that the excretory system in *S. bascaniensis* and other *Styphlodora* species is not sufficiently known. This opinion was supported by Skrjabin & Antipin (1961). *Platymetra* is considered a synonym of *Styphlodora* in the present chapter; however, it should be noted that the majority of species identified as *Styphlodora* in North America actually differ from typical *Styphlodora*, especially in the configuration, position and level of development of the vitellarium. Thus, the possibility cannot be excluded that these forms represent a phylogenetic lineage deserving generic status. However, additional data on the anatomy of the excretory system, and probably molecular phylogenetic studies, are needed to corroborate or refute this hypothesis. On the other hand, as correctly recognized by Dawes (1942), forms described by Byrd *et al*. (1940b) as belonging to a new genus, *Paurophyllum* Byrd, Parker &

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Reiber, 1940, show no differences from typical *Styphlodora*. Skrjabin & Antipin (1961) did not accept this synonymy, but the viewpoint of Dawes (1942) is supported here and *Paurophyllum* is placed into synonymy with *Styphlodora*.

*Symmetritesticulata* Krasnolobova, 1977 was proposed by Krasnolobova (1977) to include two species, *S. symmetrica* (Schaldybin, 1958) (a parasite of bats) and *S. macrobursatum* (Tschertkova & Rodonaja, 1965) (a parasite of moles), both originally included in *Plagiorchis*. In my opinion, this genus is invalid because the descriptions of both these species are inadequate. *S. symmetrica* is reminiscent of a pleurogenid and *S. macrobursatum* is almost certainly an omphalometrid belonging to the genus *Neoglyphe* Shaldybin, 1953.

*Zeferinella* Artigas & Paulino, 1988 shows no essential morphological differences from *Haplometroides* Odhner, 1910. Therefore, *Zeferinella* is placed into synonymy with *Haplometroides* and *Z. vazi* Artigas & Paulino, 1988 is considered a synonym of *H. buccicola* Odhner, 1910.

## Family Plagiorchiidae Lühe, 1901

(Syns Alloglyptinae Yamaguti, 1958; Aptorchinae Yamaguti, 1958; Bieriinae Freitas, 1956; Chamaeleophilinae Yamaguti, 1971; Enodiotrematinae Baer, 1924; Glossidiellinae Yamaguti, 1971; Haplometrinae Pratt, 1902; Lepodermatidae Odhner, 1910; Maederiinae Bourgat & Combes, 1979; Natrioderinae Yamaguti, 1958; Oistosomatinae Yamaguti, 1958; Sigmaperidae Hughes, Higginbotham & Clary, 1942; Sigmaperinae Poche, 1926; Sticholecithinae Freitas, 1956; Stomatrematinae Yamaguti, 1958; Styphlodorinae Dollfus, 1937; Travtrematinae Goodman, 1954)

**Diagnosis**: Body elongate, elliptical, cylindrical, fusiform, lanceolate or pyriform; slender or plump; exceptionally (*Oistosomum*) sleeve-like lateral projections are present posterior to ventral sucker. Tegument usually covered with spines. Exceptionally (*Aptorchis*) numerous elevated glands present on ventral surface posterior to ventral sucker. Suckers well apart from each other. Oral sucker subterminal; exceptionally, papilla-like lateral or ventrolateral lappets may be present on both sides. Ventral sucker usually in anterior half of body, sometimes equatorial or immediately postequatorial. Prepharynx usually present, sometimes indistinct. Pharynx present. Oesophagus of varying length, sometimes indistinct. Intestinal bifurcation usually distinctly in forebody. Caeca usually extend into second half of body, almost always terminate posterior to testes. Testes two, in hindbody, postovarian, oblique, tandem or symmetrical. Cirrus-sac usually relatively large, in region of or extends posterior to ventral sucker; contains straight bipartite or convoluted undivided tubular seminal vesicle, prostatic complex and protrusible cirrus; cirrus unarmed or armed with small or large spines. Genital pore median, submedian or sublateral, exceptionally lateral (*Bieria*), between intestinal bifurcation and ventral sucker, exceptionally lateral to ventral sucker (*Cheloniotrema*). Ovary median or submedian, pretesticular, posterior, posterolateral to or overlapping ventral sucker. Seminal receptacle present or absent. Laurer's canal present. Uterus usually passes between testes and reaches to, or close to, posterior extremity; exceptionally, uterine loops are entirely pretesticular. Vitellarium follicular, usually forming lateral fields or clusters of follicles, mostly in hindbody, often extending into forebody; exceptionally, vitelline follicles form single median field extending from pharynx to testes (*Sticholecitha*) or two rather compact clusters in shoulder region (*Stomatrema*); sometimes, lateral vitelline fields may be confluent in hindbody or forebody. Excretory vesicle in adults usually Y-shaped with short arms, rarely I-shaped; pore usually terminal. In digestive tract, exceptionally urogenital or respiratory system, of tetrapods; cosmopolitan. Type-genus *Plagiorchis* Lühe, 1899.

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## Key to genera

**1a. Body with sleeve-like lateral projections posterior to ventral sucker ..... ..... *Oistosomum* Odhner, 1902. (Fig. 23.1)**

**Diagnosis:** Body elongate, with sleeve or ear-like triangular expansions on each side of body at level of testes. Tegument spined. Suckers approximately equal in size. Oral sucker oval, subterminal. Ventral sucker small, near anterior end of body. Prepharynx indistinct. Pharynx comparatively large. Oesophagus very short. Intestinal bifurcation in mid-forebody. Caeca terminate near posterior extremity. Testes large, symmetrical, in anterior hindbody, may be notched. Cirrus-sac elongate, pyriform, overlaps ventral sucker. Genital pore median, postbifurcal. Ovary submedian, between ventral sucker and dextral testis. Seminal receptacle large, between ovary and dextral testis. Uterus passes between testes and occupies intercaecal post-testicular space, extending somewhat posteriorly to ends of caeca. Vitellarium extends in lateral fields from posterior to pharynx to level of testes. Excretory system unknown. Parasites of crocodiles; Africa. Type-species *O. caduceus* Odhner, 1902.

**1b. Body without sleeve-like lateral projections ..... 2.**

**2a. Vitellarium in median field extending from pharynx to testes ..... ..... *Sticholecitha* Prudhoe, 1949. (Fig. 23.2)**

**Diagnosis:** Body elongate. Tegument spined. Oral sucker subterminal, larger than ventral sucker. Ventral sucker about one-third of body length from anterior extremity. Prepharynx very short. Oesophagus short. Intestinal bifurcation midway between suckers. Caeca reach middle of post-testicular region. Testes oblique or nearly tandem, intercaecal, in middle third of body. Cirrus-sac club-shaped, extends transversely from anterior margin of ventral sucker, contains convoluted tubular seminal vesicle, prostatic complex and unarmed cirrus. Genital pore sublateral, between left caecum and margin of body. Ovary median, immediately posterior to ventral sucker. Seminal receptacle small. Laurer's canal present. Uterine coils mainly inter- and postcaecal, reach to posterior extremity. Eggs numerous. Vitelline follicles disposed dorsally in elongate group along median line, extending from intestinal bifurcation to region of posterior testis. Excretory vesicle Y-shaped with long stem bifurcating posterior to ovary into very short arms. In oesophagus of snakes; neotropics. Type-species *S. serpentis* Prudhoe, 1949.

**2b. Vitellarium not as above ..... 3.**

**3a. Vitellarium in two groups of follicles in shoulder region of forebody, posterior extent variable ..... 4.**

**3b. Vitellarium not as above ..... 5.**

**4a. Lateral groups of vitelline follicles almost entirely in forebody; uterine loops almost completely occupy post-testicular space; testes symmetrical; genital pore median, in forebody; ventral sucker larger than oral sucker; in mouth of snakes ..... ..... *Stomatrema* Guberlet, 1928. (Fig. 23.3)**

**Diagnosis:** Body oval, plump. Tegument spined. Both suckers large and very muscular. Oral sucker subterminal. Ventral sucker large, pre-equatorial. Prepharynx indistinct. Pharynx large. Oesophagus indistinct. Intestinal bifurcation in forebody. Caeca terminate near posterior extremity. Testes symmetrical or slightly oblique, in middle third of body, in hindbody. Cirrus-sac elongate, curved or winding, overlaps ventral sucker posteriorly, containing bipartite seminal

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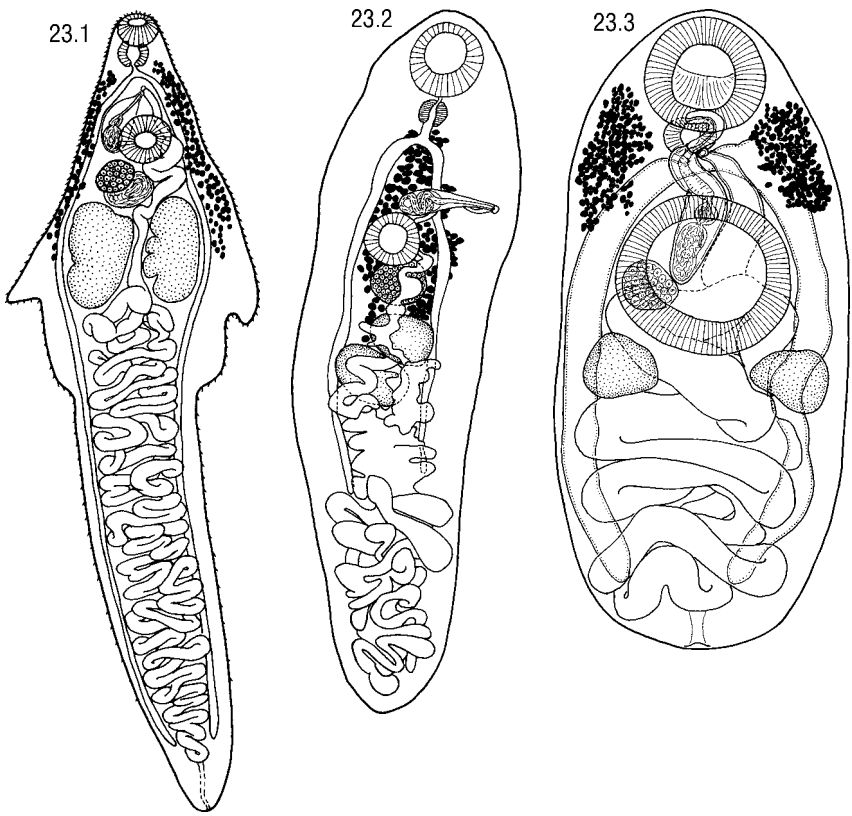



**Fig. 23.1.** *Oistosomum caduceus* Odhner, 1902. After Yamaguti (1971).
**Fig. 23.2.** *Sticholecitha serpentis* Prudhoe, 1949. After Prudhoe (1949).
**Fig. 23.3.** *Stomatrema pusilla* Guberlet, 1928. Original.

vesicle, prostatic complex and cirrus. Genital pore median or submedian, ventral to intestinal bifurcation or immediately postbifurcal. Ovary to right of median line, overlaps ventral sucker. Seminal receptacle present. Uterus passes between testes and reaches posterior extremity. Vitellarium in two mostly extracaecal masses in shoulder region. Excretory vesicle Y-shaped, with long arms. In mouth or oesophagus of snakes; North America. Type-species *S. pusilla* Guberlet, 1928.

**4b. Lateral groups of vitelline follicles extend from oral sucker to level of posterior margin of ovary; very few uterine loops posterior to testes; testes oblique; genital pore lateral to ventral sucker; ventral sucker smaller than oral sucker; in digestive tract of freshwater turtles ..... *Cheloniotrema* Caballero, Cerecero & Grocott, 1957. (Fig. 23.4)**

**Diagnosis:** Body elongate, fusiform. Tegument spined. Oral sucker subterminal, larger than ventral sucker. Ventral sucker just postbifurcal, approximately at border between anterior and middle thirds of body. Prepharynx apparently absent. Pharynx strongly developed. Oesophagus very short. Intestinal bifurcation at level of anterior part of ventral sucker. Caeca terminate near posterior extremity. Testes oblique, postequatorial. Cirrus-sac small, overlaps left part of

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ventral sucker, contains winding tubular seminal vesicle, prostatic complex and short unarmed cirrus. Genital pore sinistrolateral to ventral sucker, ventral to beginning of left caecum. Ovary immediately posterodextral to ventral sucker. Seminal receptacle and Laurer's canal present. Uterine coils extend into post-testicular region and into extracaecal spaces of middle third of body but do not reach ends of caeca. Eggs numerous. Vitellarium in two non-merging lateral fields extending from posterior to oral sucker to level of posterior end of ovary. Excretory vesicle Y-shaped, divided into short arms anterior to anterior testis. In digestive tract or bile-duct of freshwater turtles; Mexico, Panama. Type-species *C. tropicum* Caballero, Cerecero & Grocott, 1957.

**5a. Vitellarium in two lateral groups of large follicles extending along caeca posterior to testes ..... *Enodiotrema* Looss, 1900. (Figs 23.5, 23.6)**
(Syn. *Enodia* Looss, 1899 *nec* Huebner, 1819 or Dahlbom, 1844)

**Diagnosis:** Body elongate, subcylindrical. Tegument spined. Suckers approximately equal in size. Ventral sucker about one-third of body length from anterior end of body. Prepharynx indistinct. Oesophagus short. Intestinal bifurcation in forebody. Caeca terminate shortly beyond vitellarium, at substantial distance from posterior extremity. Testes oblique, in equatorial region. Cirrus-sac short and thick, oval, in forebody, encloses winding tubular seminal vesicle, prostatic complex and spined cirrus. Genital pore submedian, dextral, in forebody. Ovary submedian, immediately posterolateral to ventral sucker. Seminal receptacle small, posterior to ovary. Uterus inter- and postcaecal, reaches posterior extremity. Vitellarium consists of relatively few large follicles, arranged in two elongate supracaecal groups extending along post-testicular part of caeca. Excretory vesicle Y-shaped, bifurcates between ovary and testes; arms terminate immediately posterior to intestinal bifurcation; stem and arms with numerous lateral branches. In intestine of sea turtles; cosmopolitan. Type-species *E. megachondrus* (Looss, 1899) Looss, 1901.

**5b. Vitellarium not as above ..... 6.**

**6a. Papilla-like lateral or ventrolateral lappets on both sides of oral sucker present ..... 7.**
**6b. Papilla-like lateral or ventrolateral lappets on both sides of oral sucker absent ..... 9.**

**7a. Body small, moderately elongate with wider rounded anterior end and blunt posterior end; ovary adjacent to distal portion of cirrus-sac ..... *Eustomos* MacCallum, 1921. (Fig. 23.7)**

**Diagnosis:** Body elongate, widened anteriorly, with rounded anterior end and blunt posterior end. Tegument armed with spines. Oral sucker much larger than ventral sucker, with pair of ventrolateral lappets or papillae. Ventral sucker just pre-equatorial. Prepharynx short. Pharynx small. Oesophagus short, of approximately same length as prepharynx. Intestinal bifurcation midway between suckers. Caeca almost reach posterior extremity. Testes small, oblique, in posterior third of body. Cirrus-sac well developed, contains bipartite seminal vesicle, well-developed pars prostatica and cirrus. Genital pore median, in forebody. Ovary submedian, just posterior to ventral sucker. Uterus passes between testes and fills most of post-testicular space. Vitellarium follicular, in two lateral fields extending from level of ovary to level just posterior to testes. Excretory vesicle Y-shaped; pore opens into funnel-like structure at posterior extremity. In intestine of freshwater turtles; North America. Type-species *E. chelydrae* MacCallum, 1921.

**7b. Body very elongate, narrow or tapering at both ends; ovary distant from cirrus-sac ... 8.**

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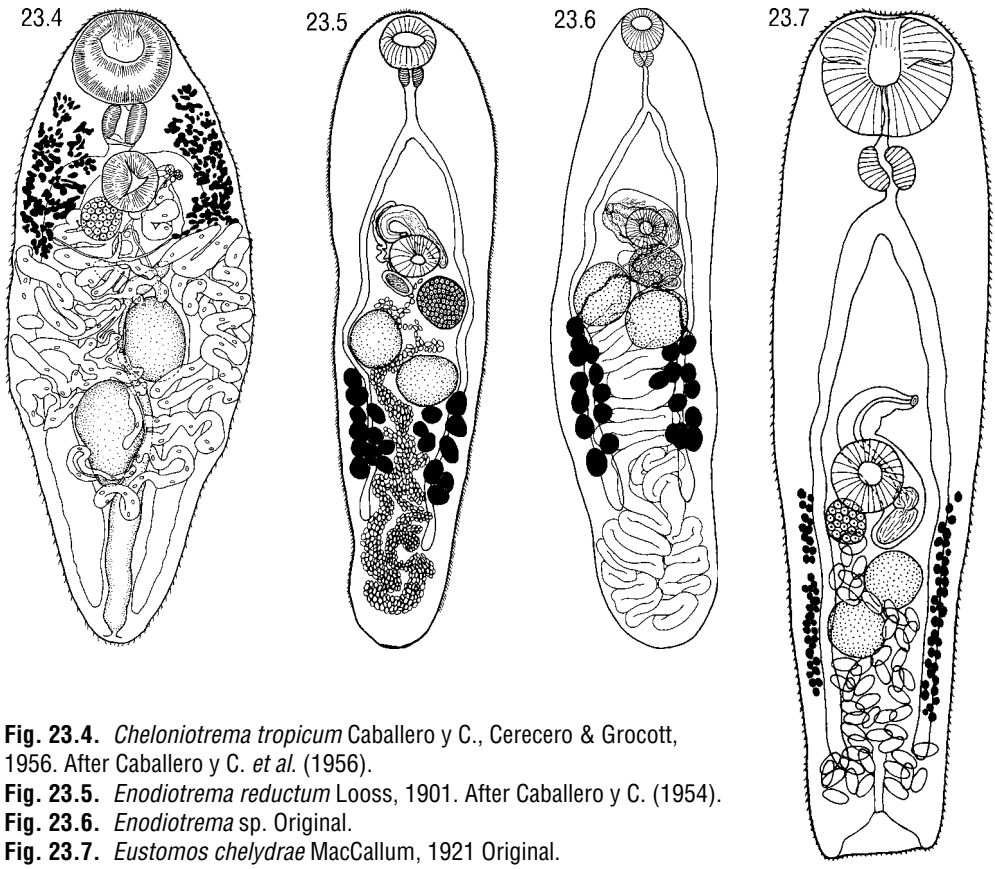



**Fig. 23.4.** *Cheloniotrema tropicum* Caballero y C., Cerecero & Grocott, 1956. After Caballero y C. *et al.* (1956).
**Fig. 23.5.** *Enodiotrema reductum* Looss, 1901. After Caballero y C. (1954).
**Fig. 23.6.** *Enodiotrema* sp. Original.
**Fig. 23.7.** *Eustomos chelydrae* MacCallum, 1921 Original.

**8a. Oesophagus long; oral sucker with lappets armed with five or six large spines; in turtles, Asia ..... *Longigula* Qiu, Zhang & Li, 1983. (Figs 23.8, 23.9)**

**Diagnosis:** Body very elongate. Tegument armed with spines. Oral sucker equal to or smaller than ventral sucker; with pair of lateral lobes or lappets each armed with five or six spines substantially larger than regular tegumental spines. Ventral sucker at border between anterior and middle thirds of body. Prepharynx indistinct. Pharynx small. Oesophagus long. Intestinal bifurcation in posterior forebody. Caeca terminate near posterior extremity. Testes tandem, equivalent to one testicular distance from each other in last quarter of body. Cirrus-sac extends distinctly posterior to ventral sucker. Genital pore median, in forebody. Ovary equatorial or postequatorial. Seminal receptacle present. Uterus intercaecal, reaches posterior extremity. Metraterm present. Vitelline follicles extracaecal, clustered in several groups confined to hindbody, but not extending posteriorly beyond posterior testis. Excretory vesicle Y-shaped, long, divided into two lateral branches between anterior testis and ovary, branches extend to oral sucker. In intestine of freshwater turtles; China. Type-species *L. auris* Qiu, Zhang & Li, 1983.

**8b. Oesophagus indistinct or very short; oral sucker with lappets lacking large spines; in Neotropical iguanid lizards ..... *Parallopharynx* Caballero, 1946. (Figs 23.10–23.13)**

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**Diagnosis:** Body slender, very elongate, flattened cylindrical. Tegument spined. Oral sucker ventrosubterminal, larger or equal to ventral sucker, with pair of unarmed anterolateral auricular lappets. Ventral sucker small, in anterior third of body. Prepharynx present. Pharynx relatively large. Oesophagus indistinct. Intestinal bifurcation in anterior forebody. Caeca reach posterior extremity. Testes slightly oblique to tandem, in about middle of posterior half of body, separated by several uterine coils. Cirrus-sac very elongate, extends posteriorly far beyond ventral sucker, contains winding seminal vesicle and well-developed pars prostatica. Genital pore median or slightly submedian, somewhat anterior to ventral sucker. Ovary median, closer to anterior testis than to ventral sucker, but separated from both by numerous uterine coils. Seminal receptacle postovarian. Laurer's canal present. Uterus mostly in transverse coils, passes between testes and almost reaches end of caeca but not posterior extremity. Metraterm shorter than cirrus-sac. Vitelline follicles extending in long lateral extra- and supracaecal fields in hindbody; posterior extent may reach level of posterior testis or beyond; fields may be interrupted at levels of ovary and testes. In intestine of iguanid lizards; neotropics. Type-species *P. arctus* Caballero, 1946.

**9a. Distal portions of male and female ducts fuse together to form short hermaphroditic duct before opening to outside through genital pore ..... *Alloglyptus* Byrd 1950. (Fig. 23.14)**

**Diagnosis:** Body linguiform or spatulate, with broadly rounded extremities and almost parallel sides. Tegument unspined. Oral sucker subterminal, larger than ventral sucker. Ventral sucker very small, in anterior fifth of body. Prepharynx very short or absent. Oesophagus short. Intestinal bifurcation in mid-forebody. Caeca terminate at about quarter of body length from posterior extremity. Testes symmetrical or nearly so, at about border between first and second quarters of body. Cirrus-sac small, arcuate, on right side of ventral sucker, contains seminal vesicle, small pars prostatica and small cirrus. Male and female ducts united to form short hermaphroditic duct. Genital pore median, immediately anterior to ventral sucker. Ovary submedian, posterolateral to or overlapping ventral sucker. Seminal receptacle median. Laurer's canal present. Uterine coils filling all post-testicular space. Eggs numerous. Vitelline follicles extend in two lateral fields extending along whole length of caeca. Excretory vesicle I-shaped, reaches to near level of testes. Flame-cell formula: $2 \times 6 \times 3 = 36$. In lizards; North and Central America. Type-species *A. crenshawi* Byrd 1950.

**9b. Hermaphroditic duct absent ..... 10.**

**10a. Both caeca or at least one caecum extends posteriorly beyond anterior testis or both testes ..... 15.**

**10b. Caeca terminate anterior to testes or lateral to testes but not reaching their posterior margin ..... 11.**

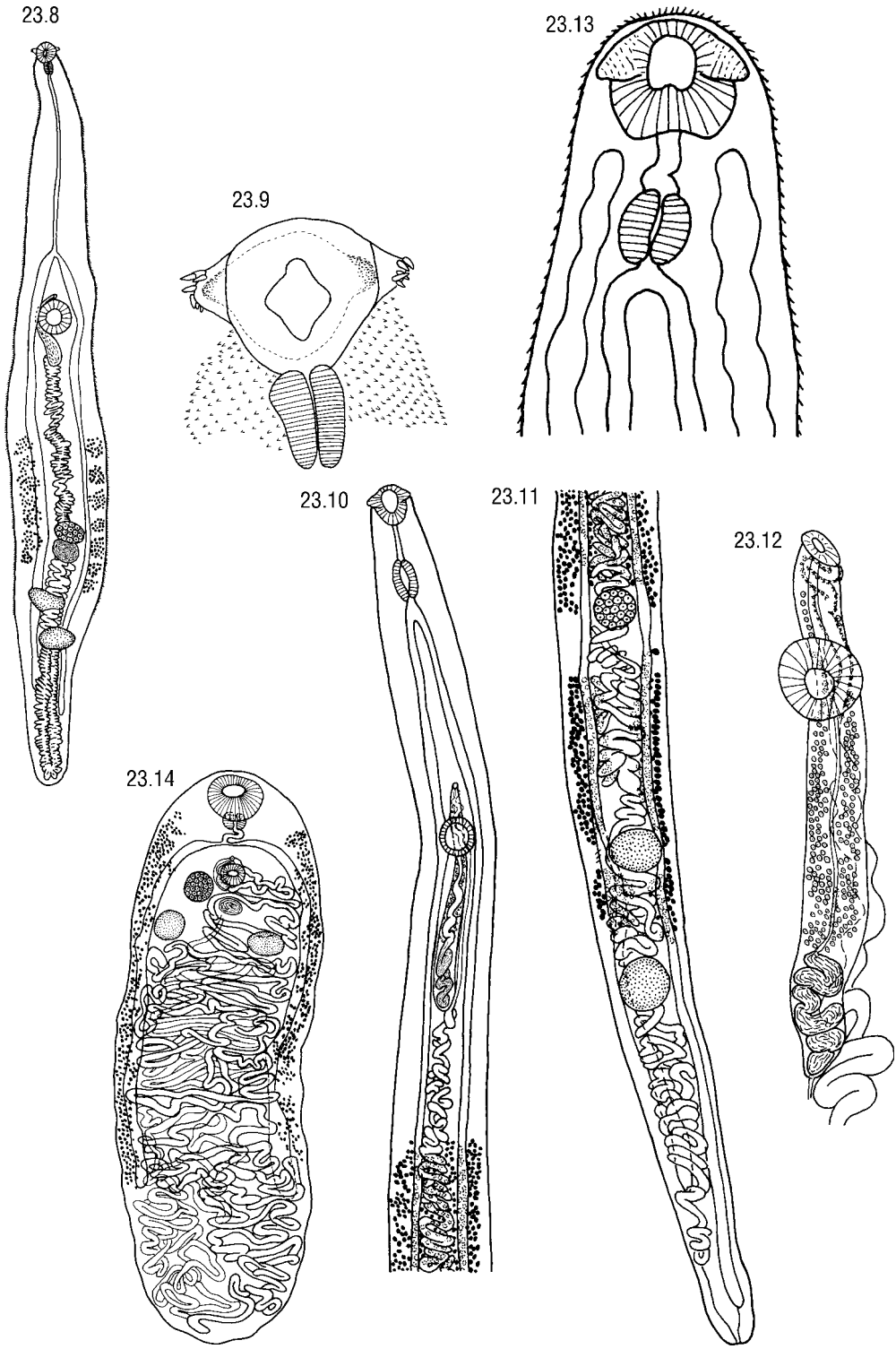
**Figs 23.8, 23.9.** (*Opposite*) *Longigula auris* Qiu, Zhang & Li, 1983. 23.8. General view. 23.9. Oral sucker with lappets. After Qiu *et al.* (1983).

**Figs 23.10–23.12.** (*Opposite*) *Parallopharynx matternae* Zamparo, Brooks, Tkach & Rodriguez, 2004. 23.10. Anterior part of body. 23.11. Posterior part of body. 23.12. Terminal genitalia and ventral sucker. After Zamparo *et al.* (2004).

**Fig. 23.13.** (*Opposite*) *Parallopharynx arctus* Caballero, 1946. After Thatcher (1963).

**Fig. 23.14.** (*Opposite*) *Alloglyptus crenshawi* Byrd 1950. After Byrd (1950).

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**11a. Body greatly elongated; ovary distant from ventral sucker; vitelline follicles in two compact lateral fields between ovary and testes; in snakes ..... ..... *Natriodera* Mehra, 1937. (Fig. 23.15)**

**Diagnosis:** Body very elongated. Tegument spined. Oral sucker subterminal, larger than ventral sucker. Ventral sucker in anterior half of body. Prepharynx very short or indistinct. Pharynx small. Oesophagus very long. Intestinal bifurcation dorsal to ventral sucker. Caeca terminate just anterior to testes, approximately at border between middle and posterior thirds of body. Testes oblique, just posterior to ends of caeca. Cirrus-sac long, extends posteriorly far beyond ventral sucker; contains winding, tubular seminal vesicle. Genital pore submedian, in forebody, dextral to distal part of oesophagus. Ovary median, approximately halfway between base of cirrus-sac and anterior testis. Vitellarium forms two lateral extra- and supracaecal groups of acinous clusters of follicles between ovary and anterior testis. Uterus passes between testes and reaches posterior extremity. Excretory vesicle unknown. In lungs of snakes; North America. Type-species *N. verlata* (Talbot, 1934) Mehra, 1937.

**11b. Body elliptical, moderately elongated; ovary immediately posterior to ventral sucker; vitelline follicles in two longer lateral fields that may or may not merge in forebody or hindbody; in amphibians or lizards ..... 12.**

**12a. Vitelline fields extend from level of ventral sucker to midway between ventral sucker and testes; uterus entirely pretesticular; genital pore extracaecal ..... ..... *Sarumitrema* Beverley-Burton, 1963. (Fig. 23.16)**

**Diagnosis:** Body elongate, lanceolate. Tegument armed with spines. Oral sucker subterminal, somewhat larger than ventral sucker. Ventral sucker in anterior half of body. Prepharynx short. Oesophagus present. Intestinal bifurcation in mid-forebody. Caeca terminate in posterior quarter of body, at anterior margins of testes. Testes symmetrical or slightly oblique, near posterior extremity, immediately posterior to caeca. Cirrus-sac anterior to ventral sucker, with base just anterior to ventral sucker and distal end extracaecal; contains coiled seminal vesicle, pars prostatica and short unarmed cirrus. Genital pore submedian or sublateral and extracaecal at bifurcal level. Ovary submedian, just posterior to ventral sucker. Seminal receptacle posterior to ovary. Uterus with very numerous coils, entirely pretesticular and occupies most of space between ovary and testes. Vitellarium follicular, in two lateral extracaecal fields in middle third or second quarter of body. Excretory vesicle Y-shaped. In intestine of amphibians; Africa. Type-species *S. histatorchis* Beverley-Burton, 1963.

**12b. Posterior margins of vitelline fields reach testes or somewhat beyond; uterus passes between testes and has at least several post-testicular loops; genital pore between ventral sucker and intestinal bifurcation ..... 13.**

**13a. Vitelline fields extend into post-testicular region and almost reach posterior extremity; vitelline fields confluent in forebody and, usually, in hindbody ..... ..... *Maederia* Bourgat & Combes, 1979. (Fig. 23.17)**

(Syn. *Phrynobatrachotrema* Goodman, 1986)

**Diagnosis:** Body elongate-oval. Tegument spined. Suckers more or less similar in size. Prepharynx short or indistinct. Oesophagus present, of varying length. Intestinal bifurcation in posterior forebody. Caeca relatively short, terminate at short distance anterior to testes and at substantial distance from posterior extremity. Testes rounded, symmetrical or slightly oblique, posterior to intestinal caeca. Genital pore median, immediately anterior to ventral sucker. Cirrus-sac small,

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claviform, overlaps ventral sucker or curves around its edge, contains winding seminal vesicle. Ovary rounded, submedian, just posterior to ventral sucker and may partly overlap it. Seminal receptacle postovarian. Vitelline follicles small, widely distributed over area between pharynx and posterior extremity except for rather small area posterior to ventral sucker. Uterine coils pass between testes and reach posterior extremity. Excretory vesicle Y-shaped. In intestine of anuran amphibians; Africa. Type-species *M. eburnensis* (Maeder, 1969) Bourgat & Combes, 1979 (emend.).

**13b. Vitelline fields extending posteriorly only to level of anterior or posterior margin of testes; vitelline fields not confluent ..... 14.**

**14a. Vitelline fields extend beyond ends of caeca and reach posterior margins of testes; caeca terminate lateral to testes not reaching their posterior margin ..... ..... *Chamaeleophilus* Yamaguti, 1971. (Fig. 23.18)**

**Diagnosis:** Body small to moderately large, almost parallel-sided, rounded at both ends. Tegument smooth. Oral sucker subterminal. Ventral sucker somewhat larger than oral sucker, just pre-

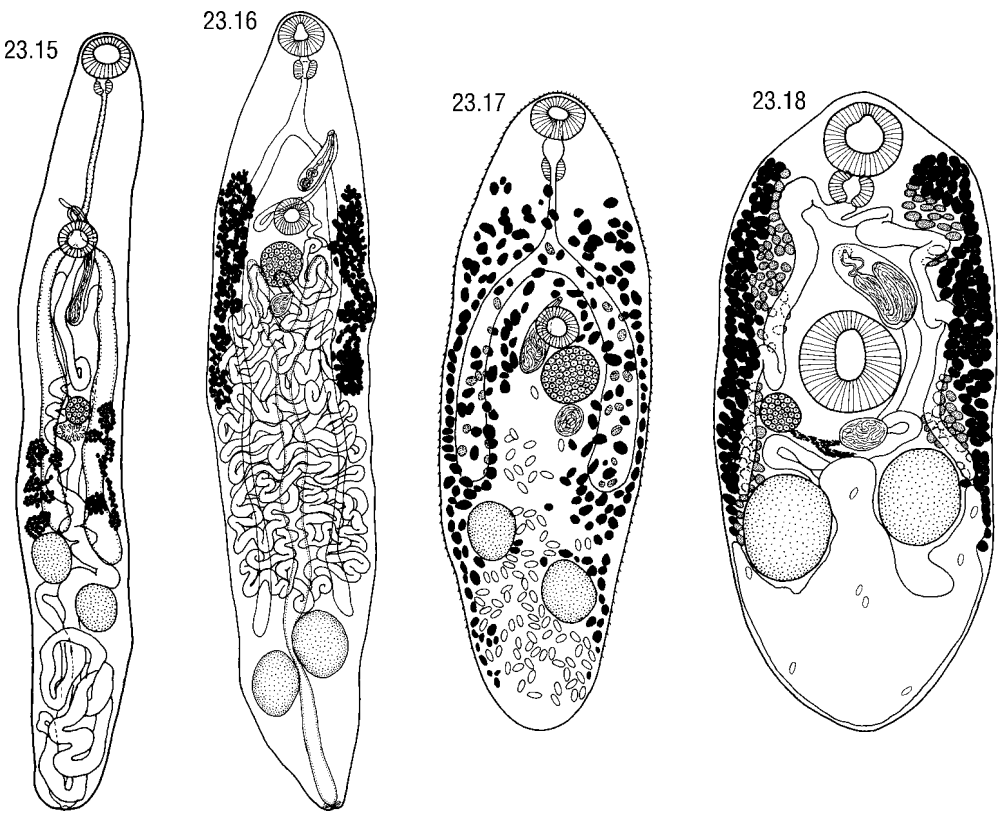



**Fig. 23.15.** *Natriodera verlata* (Talbot, 1934). After Yamaguti (1971).
**Fig. 23.16.** *Sarumitrema histatorchis* Beverley-Barton, 1963. Original.
**Fig. 23.17.** *Maederia eburnensis* (Maeder, 1969). After Bourgat & Combes (1979).
**Fig. 23.18.** *Chamaeleophilus sanneri* (Deblock, Capron & Brygoo, 1962). After Yamaguti (1971).

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equatorial. Prepharynx absent. Pharynx well developed. Oesophagus very short. Intestinal bifurcation in mid-forebody. Caeca irregularly wind, terminate anterolateral or lateral to testes. Testes round, slightly oblique or almost symmetrical. Cirrus-sac oval, positioned obliquely between ventral sucker and intestinal bifurcation, contains convoluted tubular seminal vesicle, pars prostatica and short cirrus. Genital pore median, postbifurcal. Ovary posterolateral to ventral sucker, anterior to right testis. Seminal receptacle median, in hindbody. Uterus occupies entire inter- and post-testicular space. Eggs numerous. Vitelline follicles arranged in two lateral, mostly extracaecal fields extending from level of pharynx or oral sucker to level of testes. Excretory system unknown. In lungs of chameleons; Africa. Type-species *C. sanneri* (Deblock, Capron & Brygoo, 1962) Yamaguti, 1971.

**14b. Vitelline fields reach only to ends of caeca and anterior margins of testes; caeca terminate just anterior to testes ..... *Manodistomum* Stafford, 1905. (Fig. 23.19)**
(Syn. *Plagitura* Holl, 1928)

**Diagnosis:** Body elongate, flattened elliptical. Tegument spined. Oral sucker subterminal. Ventral sucker usually pre-equatorial, similar in size to or larger than oral sucker. Prepharynx short. Pharynx well-developed. Oesophagus of varying length. Intestinal bifurcation in mid-forebody. Caeca terminate at anterior margins of testes. Testes symmetrical, close to posterior extremity and just posterior to ends of caeca. Cirrus-sac may overlap ventral sucker. Genital pore median, postbifurcal or bifurcal. Ovary submedian, overlapping or immediately posterior to ventral sucker. Vitelline fields extend along whole length of caeca. Uterus intercaecal, inter- and post-testicular, reaching close to posterior extremity. Excretory vesicle Y-shaped. In digestive tract of amphibians; North America. Type-species *M. occultum* Stafford, 1905.

**15a. Right caecum terminates just anterior to right testis; left caecum terminates posterior to left testis (occasionally vice versa) ..... *Neoastiotrema* n.g. (Fig. 23.20)**

**Diagnosis:** Body elliptical. Tegument armed with spines. Suckers are of approximately same size. Oral sucker oval, subterminal. Ventral sucker in anterior third of body, similar in size to oral sucker. Prepharynx present. Pharynx small. Oesophagus present. Intestinal bifurcation about midway between suckers. Right caecum terminates just anterior to right testis, left caecum terminates posterior to left testis (occasionally vice versa). Testes in posterior half of body, oblique, well separated by numerous uterine coils. Cirrus-sac claviform, arching around right margin of ventral sucker, with base between ovary and ventral sucker; contains bipartite seminal vesicle, pars prostatica and small unarmed cirrus. Genital pore median, immediately anterior to ventral sucker. Ovary posterodextral to ventral sucker, near base of cirrus-sac. Seminal receptacle present. Laurer's canal present. Uterus occupies most of hindbody, passing between testes and reaching posterior extremity. Eggs numerous. Vitellarium follicular, anterior margins of fields at level of anterior margin of ventral sucker; posterior margins between testes, usually at level of end of long caecum; fields not confluent. Excretory vesicle Y-shaped with long stem passing between testes and short arms; pore terminal. In intestine of amphibians; Palaearctic. Type-species *N. trituri* (Grabda, 1959) n. comb.

**15b. Both caeca extend posteriorly beyond anterior testis or both testes ..... 16.**

**16a. Both caeca terminate between anterior and posterior testis ..... ..... *Pneumotrema* Bhalerao, 1937. (Fig. 23.21)**

**Diagnosis:** Body very elongate, attenuated posteriorly. Tegument spined. Oral sucker subterminal. Ventral sucker much larger than oral sucker, in anterior third of body. Prepharynx present or indistinct. Pharynx well developed. Oesophagus very short. Intestinal bifurcation in anterior fore-

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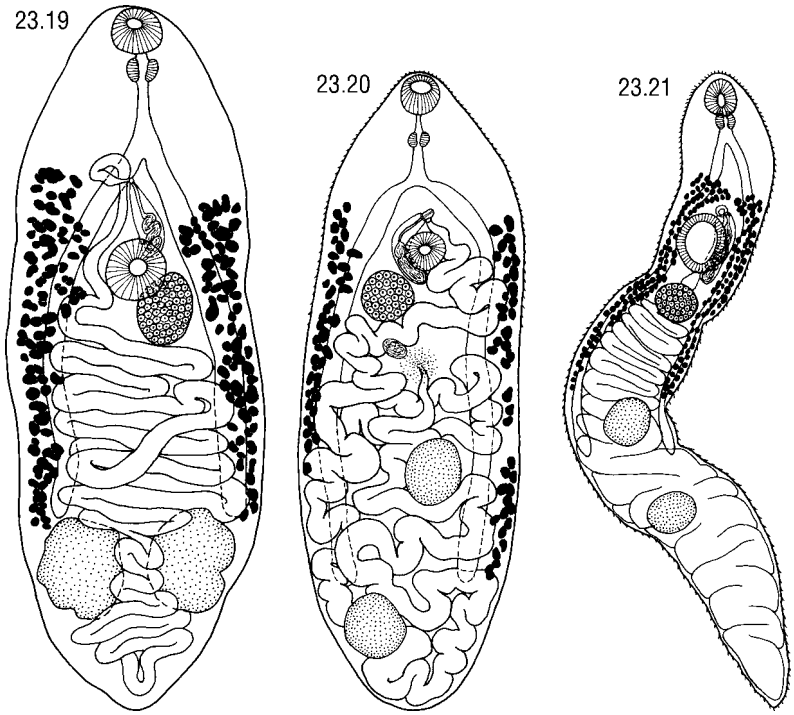



**Fig. 23.19.** *Manodistomum parvum* (Stunkard, 1933). After Prudhoe & Bray (1982).
**Fig. 23.20.** *Neoastiotrema trituri* (Grabda, 1959). After Grabda (1959a).
**Fig. 23.21.** *Pneumotrema travassosi* Bhalerao, 1937. After Bhalerao (1937b).

body. Caeca terminate at level of posterior margin of anterior testis or slightly posterior. Testes entire, rounded, tandem or nearly so; anterior testis between caecal extremities, posterior testis postcaecal. Cirrus-sac cylindrical, along margin of ventral sucker or partly overlapping, containing slightly winding tubular seminal vesicle, pars prostatica and cirrus. Genital pore submedian at anterosinistral margin of ventral sucker. Ovary round, median, just posterior to ventral sucker. Seminal receptacle absent. Laurer's canal present. Uterus occupies most of postovarian space and reaches posterior extremity. Eggs numerous. Vitellarium follicular, circumcaecal, extending from forebody to near ends of caeca. Excretory vesicle Y-shaped, with long stem. In lungs of lizards; neotropics. Type-species *P. travassosi* Bhalerao, 1937.

**16b. Both caeca or at least one caecum extends into post-testicular region ..... 17.**

**17a. Body distinctly divided into two parts; thin tapering anterior portion contains both suckers and copulatory apparatus and widened posterior part contains gonads and uterus ... ..... *Xenopodistomum* Macnae, Rock & Makowski, 1973. (Fig. 23.22)**

**Diagnosis:** Body delicate, broadly pyriform, tapered at anterior end and broadly rounded at posterior end, divided into narrow forebody and expanded hindbody. Oral sucker subterminal, similar in size to or slightly larger than ventral sucker. Ventral sucker in anterior quarter of body, in or at posterior extremity of narrow anterior part of body. Prepharynx absent. Pharynx well

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developed. Oesophagus long. Intestinal bifurcation in forebody. Caeca terminate short of posterior extremity. Testes symmetrical in anterior region of hindbody, overlap caeca. Cirrus-sac thin-walled, contains bipartite seminal vesicle, pars prostatica and short cirrus. Genital pore submedian, ventral to left caecum. Ovary small, median, closely anterior to testes. Seminal receptacle very large, immediately postovarian. Uterus arranged in mostly transverse and mainly intracaecal slings occupying much of hindbody. Vitellarium in two mostly extracaecal rows of rosette-like clusters of follicles, extending from level of ventral sucker to about ends of caeca. Excretory vesicle Y-shaped. In gall-bladder of anuran amphibians; southern Africa. Type-species *X. xenopodis* Macnae, Rock & Makowski, 1973.

**17b. Body not distinctly divided into two parts ..... 18.**

**18a. Genital pore extracaecal; parasites of amphibians, lizards or snakes ..... 19.**
**18b. Genital pore not distinctly extracaecal, but may be extracaecal in parasites of Australian freshwater turtles ..... 22.**

**19a. Genital pore marginal; body very elongate, narrow; ovary at great distance from ventral sucker; in lungs of snakes ..... *Bieria* Leão, 1946. (Fig. 23.23)**
**Diagnosis:** Body slender, very elongate, with almost parallel margins for most of its length, but enlarged in region of ventral sucker. Tegument spined. Oral sucker subterminal. Ventral sucker larger than oral sucker, near anterior end of body. Prepharynx very short. Oesophagus short. Intestinal bifurcation in forebody. Caeca terminate some distance short of posterior extremity, approximately halfway between posterior testis and end of body, may be of somewhat unequal length. Testes entire, oval, tandem, sometimes oblique, in middle third of body. Cirrus-sac situated transversely between intestinal bifurcation and ventral sucker, with base just anterior to ventral sucker; contains winding tubular seminal vesicle and unarmed cirrus. Genital pore lateral, in forebody, bifurcal or somewhat postbifurcal. Ovary median, at long distance posterior to ventral sucker and at short distance from anterior testis. Seminal receptacle and Laurer's canal present. Uterus passes between testes and may reach into extracaecal space and extends to posterior extremity. Eggs numerous. Vitellarium in form of numerous bunch-like clusters of small follicles, intercaecal, caecal and extracaecal, extends from pre-ovarian zone to ends of caeca or somewhat beyond. Excretory vesicle Y-shaped, with arms of unequal length. In lungs of snakes; neotropics. Type-species *B. artigasi* Leão, 1946.

**19b. Genital pore submedian or sublateral; body moderately elongate, elliptical; ovary immediately posterior to ventral sucker or at short distance from it; in amphibians or lizards ..... 20.**

**20a. Lateral vitelline fields extend from level of intestinal bifurcation to ends of caeca; caeca terminate approximately at junction of middle and posterior thirds of body ..... ..... *Ostioloides* Odening, 1960. (Fig. 23.24)**
**Diagnosis:** Body elongate, elliptical. Tegument spined. Oral sucker small, subterminal or terminal. Ventral sucker in anterior half of body, similar in size to oral sucker. Prepharynx indistinct. Pharynx small. Oesophagus present. Intestinal bifurcation in mid-forebody. Caeca terminate at considerable distance from posterior extremity. Testes round, entire, symmetrical or almost, intercaecal, pre-equatorial. Cirrus-sac claviform, near intestinal bifurcation, crosses caecum, with base not reaching ventral sucker, contains bipartite seminal vesicle, short pars prostatica and long smooth cirrus. Genital pore lateral to oesophagus. Ovary median or submedian, immediately posterior to ventral sucker. Seminal receptacle and Laurer's canal present. Uterus strongly coiled,

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occupies most of inter- and postcaecal space. Vitellarium forms lateral extra- and supracaecal fields, consists of small follicles that sometimes have tendency to form distinct groups; fields extend along almost entire length of caeca. Excretory vesicle Y-shaped, with long stem and short arms. In intestine of amphibians; Africa. Type-species *0. rappiae* (Szidat, 1932) Odening, 1960.

**20b. Lateral vitelline fields begin at level of ventral sucker and reach either anterior or posterior testis, thus terminating far from caeca extremities; caeca terminate near posterior extremity ..... 21.**

**21a. Vitelline fields consist of relatively few large follicles, which reach posterior testis; in anuran amphibians in Africa ..... *Laiogonimus* Vercammen-Grandjean, 1960. (Fig. 23.25)**
(Syn. *Astiotrema (Biguetrema)* Deblock & Capron, 1962)

**Diagnosis:** Body small, elongate, usually tapering posteriorly. Tegument spined. Suckers well developed, subequal. Oral sucker subterminal. Ventral sucker in anterior half of body. Prepharynx short. Oesophagus short. Intestinal bifurcation in forebody. Caeca reach almost to posterior

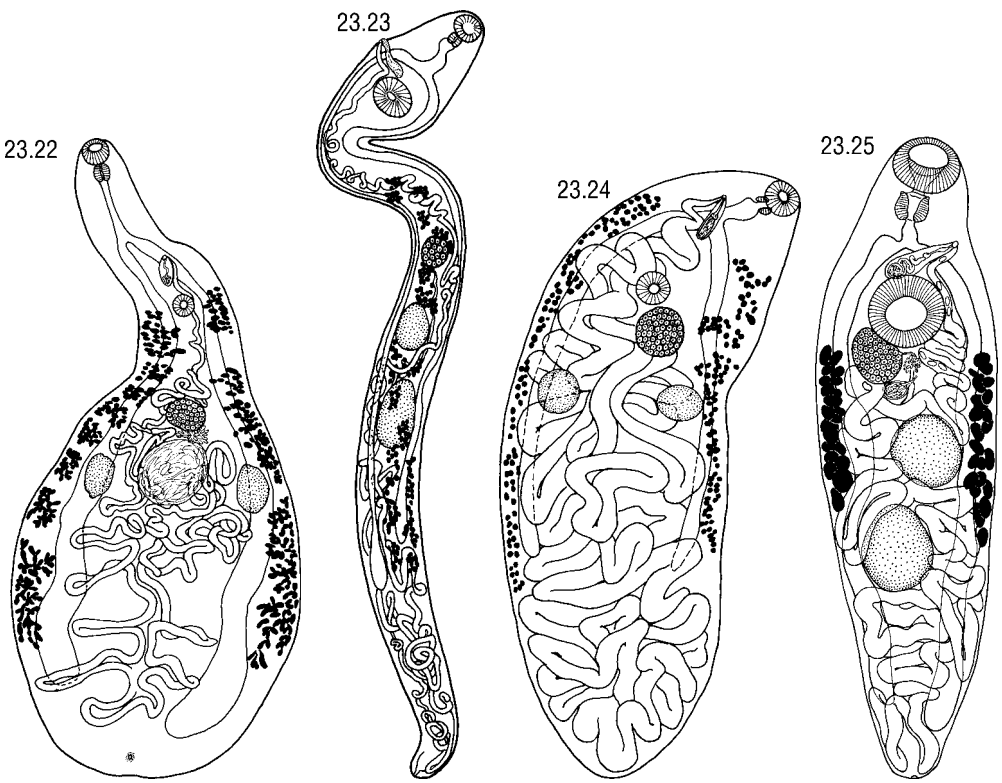



**Fig. 23.22.** *Xenopodistomum xenopodis* Macnae, Rock & Makowski, 1973. After Prudhoe & Bray (1982).
**Fig. 23.23.** *Bieria artigasi* Leão, 1946. After Yamaguti (1971).
**Fig. 23.24.** *0stioloides rappiae* (Szidat, 1932). After Prudhoe & Bray (1982).
**Fig. 23.25.** *Laiogonimus vercammengrandjeani* Meskal, 1970. Original.

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extremity. Testes oblique, postequatorial. Cirrus-sac club-shaped, extends obliquely from anterior margin of ventral sucker; contains winding seminal vesicle, pars prostatica and smooth cirrus. Genital pore sinistral, bifurcal or at level of oesophagus. Ovary submedian, just posterior to ventral sucker. Seminal receptacle present. Uterus occupies entire postovarian space, passing between testes. Eggs numerous. Vitellarium consists of large follicles disposed in two lateral, mostly extracaecal groups of six to 18 follicles, extending along caeca between ventral sucker and posterior testis. Excretory vesicle Y-shaped with long stem and short branches. In intestine of anuran amphibians; Africa. Type-species *L. mariavirginiae* Vercammen-Grandjean, 1960.

**21b. Vitelline fields consist of small follicles which do not reach posterior testis; in lizards of Central and South America ..... *Parahaplometroides* Thatcher, 1963. (Fig. 23.26)**

**Diagnosis:** Body elongate. Tegument densely covered with spines. Oral sucker subterminal. Ventral sucker at about one-third of body length from anterior end of body, similar in size to oral sucker. Prepharynx short. Oesophagus short. Intestinal bifurcation in mid-forebody. Caeca almost reach posterior extremity. Testes oblique, postequatorial. Cirrus-sac claviform, extending obliquely from anterior margin of ventral sucker; contains coiled tubular seminal vesicle, small pars prostatica and cirrus. Genital pore dextral, at level of oesophagus or extracaecal at intestinal bifurcation. Ovary entire, submedian, posterosinistral to ventral sucker and may be separated from it by few uterine coils. Seminal receptacle small. Laurer's canal present. Uterine coils pass between testes and reach posterior extremity. Metraterm well differentiated. Vitellarium in form of two short lateral fields of small follicles, extending from level of ventral sucker to level of anterior testis. Excretory vesicle Y-shaped. In mouth of iguanid lizards; neotropics. Type-species *P. basiliscae* Thatcher, 1963.

**22a. Uterus entirely pretesticular; parasites of freshwater turtles ..... ..... *Sigmapera* Nicoll, 1918. (Fig. 23.27)**

**Diagnosis:** Body small, elongate, delicate. Tegument spined. Oral sucker smaller than ventral sucker. Ventral sucker equatorial or just pre- or postequatorial, musculature poorly developed, surface densely covered with minute spines. Prepharynx well developed, somewhat longer than pharynx. Oesophagus long. Intestinal bifurcation halfway between oral and ventral suckers. Caeca reach posterior extremity. Testes oval, just anterior to caecal extremities. Cirrus-sac large, with base extending posteriorly far beyond ventral sucker; contains bipartite seminal vesicle, very strongly developed glandular pars prostatica and short thick cirrus armed with spines. Genital pore median, submedian or sublateral, may be extracaecal, at some distance anterior to ventral sucker or at level of its anterior margin. Ovary submedian, in posterior third of body halfway between testes and ventral sucker. Seminal receptacle postovarian. Laurer's canal opens at posterior margin of dorsal protuberance. Uterus short, entirely pretesticular. Eggs not very numerous. Vitelline fields lateral, mostly in hindbody, may or may not be confluent in forebody; at posterior end vitelline fields are separated only by stem of excretory vesicle. Excretory vesicle Y-shaped, with short stem and short arms; pore terminal. In digestive tract of freshwater turtles; Australia. Type-species *S. cincta* Nicoll, 1918.

**22b. Uterus extends into post-testicular space ..... 23.**

**23a. Lateral vitelline fields consist of small follicles distributed in anterior half of body extending from anterior end of body to level of testes, usually confluent anteriorly; caeca almost reach posterior extremity ..... *Xenopharynx* Nicoll, 1912. (Fig. 23.28)**

(Syns *Bhaleraopharynx* Skrjabin & Antipin, 1958; *Neopisthorchis* Chatterji & Kruidenier, 1961)

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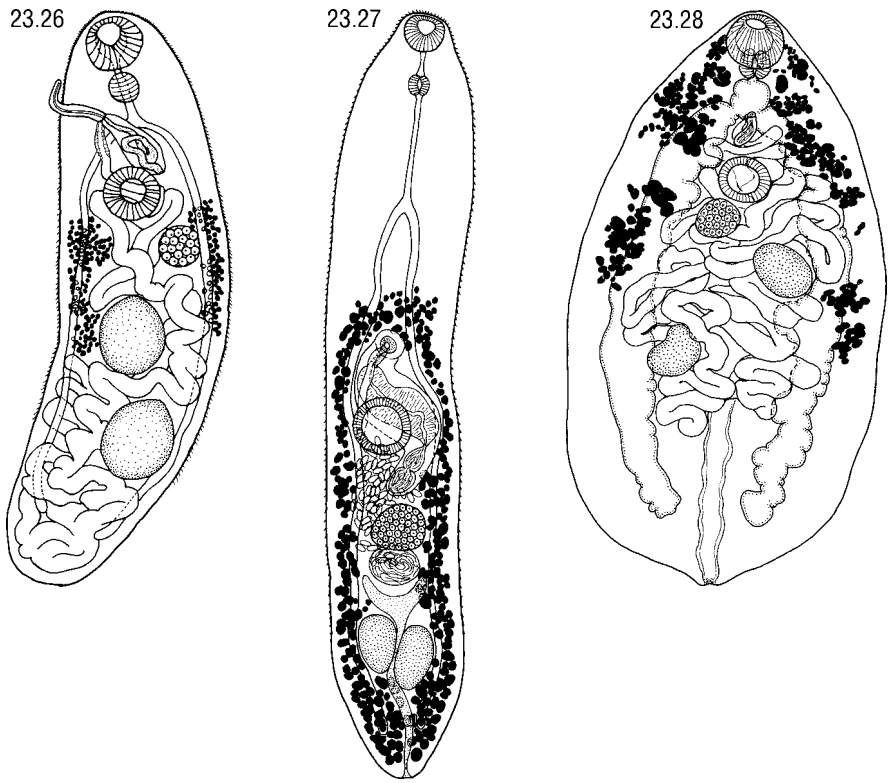



**Fig. 23.26.** *Parahaplometroides basiliscae* Thatcher, 1963. After Thatcher (1963).
**Fig. 23.27.** *Sigmapera cincta* Nicoll, 1918. Original.
**Fig. 23.28.** *Xenopharynx solus* Nicoll, 1912. Original.

**Diagnosis:** Body strongly flattened, elliptical. Tegument smooth. Oral sucker subterminal. Ventral sucker in anterior third of body, similar in size to oral sucker. Prepharynx absent. Oesophagus short. Intestinal bifurcation in mid-forebody. Caeca terminate at or near posterior extremity. Testes oblique in middle third of body, separated by several coils of uterus. Cirrus-sac very small, immediately postbifurcal, not reaching ventral sucker. Genital pore ventral to intestinal bifurcation or close to it. Ovary median or submedian, either immediately posterior to ventral sucker or at short distance from it. Seminal receptacle present. Laurer's canal not observed. Uterus somewhat posterior to testes, but not reaching posterior end of caeca. Eggs numerous. Vitellarium in lateral fields consisting of small follicles distributed in anterior half of body and extending from anterior extremity to level of testes, usually confluent anteriorly. Excretory vesicle Y-shaped, with long stem and short arms. In gall-bladder of snakes; India, Malaya. Type-species *X. solus* Nicoll, 1912.

**23b. Vitelline fields not as above ..... 24.**

**24a. True seminal receptacle present ..... 30.**
**24b. True seminal receptacle absent or at least not apparent ..... 25.**

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**25a. Proximal part, at least, of seminal vesicle coiled ..... 26.**
**25b. Seminal vesicle bipartite, with saccular proximal part ..... 28.**

**26a. Testes tandem; uterine limbs pass ventrally and dorsally to testes; in lungs of amphibians ..... *Haplometra* Looss, 1899. (Fig. 23.29)**

**Diagnosis:** Body elongate, almost cylindrical. Tegument spined. Oral sucker larger than ventral sucker, subterminal. Ventral sucker small, in anterior half of body. Prepharynx very short or indistinct. Oesophagus short. Intestinal bifurcation in forebody. Caeca terminate close to posterior extremity. Testes tandem or nearly so, equatorial or postequatorial. Cirrus-sac arches around margin of ventral sucker or may partly overlap with it; contains coiled seminal vesicle, distinct pars prostatica and stout cirrus. Genital pore median, immediately anterior to ventral sucker. Ovary submedian, posterolateral to ventral sucker. Seminal receptacle absent. Uterus occupies most of hindbody, passing dorsally and ventrally to testes. Vitellarium forms bunches of follicles extending from level of intestinal bifurcation along most of caecal length; may be confluent in forebody. Excretory vesicle Y-shaped, with long stem and short arms. In lungs of amphibians; Eurasia, northern Africa. Type-species *H. cylindracea* (Zeder, 1800) Looss, 1899.

**26b. Testes oblique or nearly symmetrical; uterine limbs pass between testes; parasites of intestine or gall-bladder of turtles ..... 27.**

**27a. Body very elongate; testes oblique; ovary at mid-distance between ventral sucker and anterior testis ..... *Microderma* Mehra, 1931. (Fig. 23.30)**

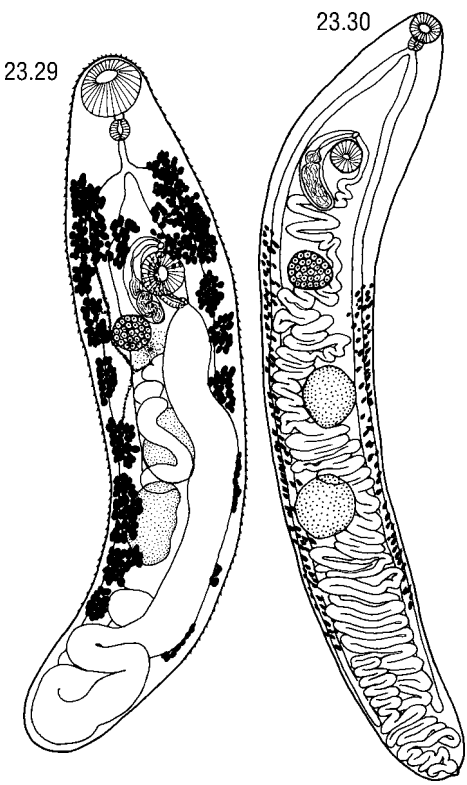



**Fig. 23.29.** *Haplometra cylindracea* (Zeder, 1800). After Sharpilo & Iskova (1989).
**Fig. 23.30.** *Microderma elingue* Mehra, 1931. After Mehra (1937).

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**Diagnosis:** Body very elongate. Tegument spined. Suckers relatively small, similar in size. Oral sucker subterminal. Ventral sucker in anterior third of body. Prepharynx and oesophagus indistinct. Pharynx small. Intestinal bifurcation in anterior forebody. Caeca terminate near posterior extremity. Testes oblique; anterior testis equatorial or immediately postequatorial. Cirrus-sac claviform, extends posteriorly well beyond ventral sucker; contains bipartite seminal vesicle and well-developed pars prostatica. Genital pore median, immediately anterior to ventral sucker. Ovary median or slightly submedian, nearly halfway between ventral sucker and anterior testis. Seminal receptacle absent. Uterus passing between testes and reaching posterior extremity. Vitellarium forms lateral fields consisting of bunch-like groups of follicles extending from level just anterior to ovary to near ends of caeca. Excretory vesicle Y-shaped with arms reaching to near oral sucker; pore terminal. In intestine of freshwater turtles; India. Type-species *M. elingue* Mehra, 1931.

**27b. Body moderately elongated or elliptical; testes symmetrical or nearly so; ovary closely adjacent to ventral sucker ..... *Bilorchis* Mehra, 1937. (Fig. 23.31)**

**Diagnosis:** Body moderately elongated. Tegument covered with very fine spines. Oral sucker subterminal. Ventral sucker pre-equatorial. Prepharynx short. Pharynx oval. Oesophagus very short. Intestinal bifurcation in mid-forebody. Caeca reach posterior extremity. Testes intercaecal, symmetrical, equatorial or just postequatorial. Cirrus-sac short, median, situated along the middle axis of body, with base overlapping ventral sucker. Cirrus-sac contains coiled seminal vesicle, pars prostatica with well-developed prostatic gland-cells and short, unarmed cirrus. Genital pore slightly submedian, close to intestinal bifurcation or about midway between it and ventral sucker. Ovary rounded, entire, posterosinistral to ventral sucker. Seminal receptacle absent. Uterus filling most of hindbody, passing between testes. Metraterm short. Eggs numerous. Vitelline fields consist of small follicles, band-like, extracaecal, extend from intestinal bifurcation to near ends of caeca. Excretory vesicle unknown. In gall-bladder of freshwater turtles; India. Type-species *B. indicus* Mehra, 1937 (emend.).

**28a. Testes oblique; in intestine of birds and mammals, accidentally of amphibians and reptiles ..... *Plagiorchis* Lühe, 1899. (Figs 23.32, 23.33)**

(Syns *Lepoderma* Looss, l899; *Cercolecithos* Perkins, 1928; *Multiglandularis* Schulz & Skvortsov, 1931; *Neolepoderma* Mehra, 1937; *Plagiorchoides* Olsen, 1937; *Choristogonoporus* Stunkard, 1938; *Paralepidauchen* Brinkmann, 1956; *Metaplagiorchis* Timofeeva, 1962)

**Diagnosis:** Body oval to fusiform, elliptical or somewhat more elongate. Tegument covered with spines. Oral sucker subterminal. Ventral sucker one-third of body length or more from anterior body end; sucker size-ratio variable, although ventral sucker usually smaller than oral sucker. Prepharynx present or apparently absent. Pharynx present. Oesophagus present or absent. Intestinal bifurcation in forebody. Caeca terminate at or near posterior extremity. Testes oblique, usually in middle, rarely in posterior, third of body. Cirrus-sac usually, but not always, extends posteriorly beyond ventral sucker; contains bipartite seminal vesicle, pars prostatica and smooth cirrus. Genital pore immediately anterior to ventral sucker, median or slightly submedian. Ovary posterior or posterolateral to ventral sucker or near base of cirrus-sac. Seminal receptacle absent. Laurer's canal present. Uterus passing between ovary and anterior testis as well as between testes, reaching or nearly reaching posterior extremity. Eggs numerous. Vitellarium forms fields reaching from level of intestinal bifurcation into hindbody, usually extending to posterior extremity or terminating somewhat anterior to it, usually confluent in post-testicular region and may be confluent

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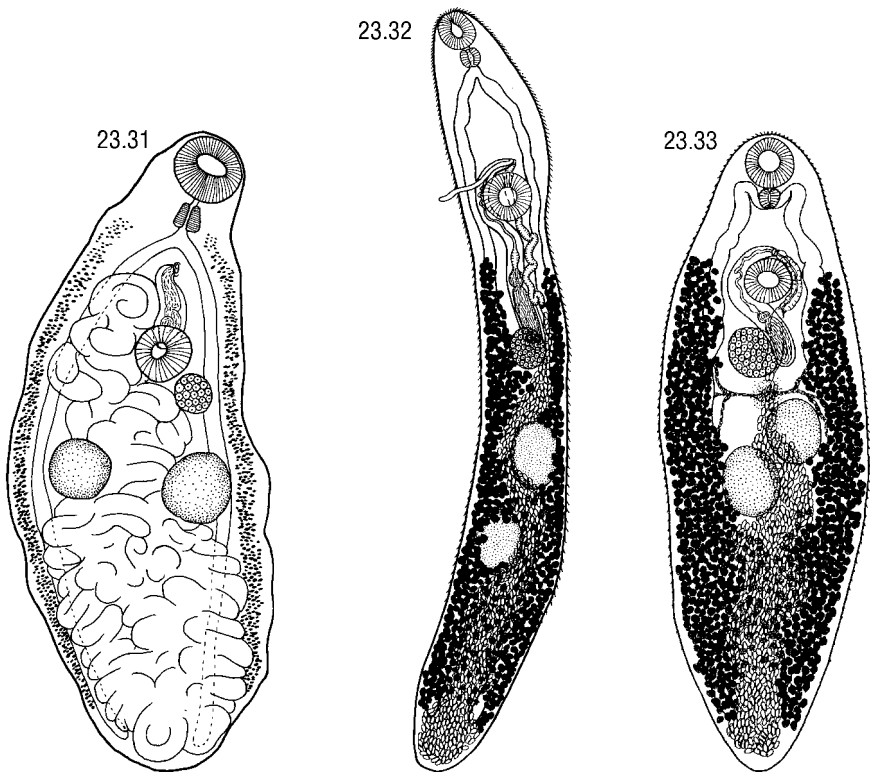



**Fig. 23.31.** *Bilorchis indicus* Mehra, 1937. After Mehra (1937).
**Fig. 23.32.** *Plagiorchis vespertilionis* (Müller, 1780). After Sharpilo & Tkach (1992).
**Fig. 23.33.** *Plagiorchis muelleri* Tkach & Sharpilo, 1990. After Tkach *et al.* (2000b).

in forebody. Excretory vesicle Y-shaped, bifurcates between ovary and anterior testis. In intestine of tetrapods; cosmopolitan. Type-species *Plagiorchis lima* (Rudolphi, 1809) Lühe, 1899 (junior synonym of *P. vespertilionis* (Müller, 1780) Braun, 1900).

**28b. Testes symmetrical or slightly oblique; in gall-bladder, bile-ducts, liver or intestine of amphibians or mammals ..... 29.**

**29a. Vitelline fields very broad, extending from oral sucker to posterior extremity, confluent in forebody and posteriorly to testes; ovary lateral or anterolateral to ventral sucker; parasites of gall-bladder, liver and small intestine of Palaearctic mammals ..... ..... *Skrjabinoplagiorchis* Petrov & Merkusheva, 1963. (Fig. 23.34)**

**Diagnosis:** Body oval, may be almost rounded. Tegument covered with spines. Suckers of similar size with small variations. Oral sucker rounded, subtermimal. Ventral sucker immediately pre-equatorial. Prepharynx present or absent. Pharynx present. Oesophagus present or absent. Intestinal bifurcation in mid-forebody. Caeca terminate at or near posterior extremity. Testes symmetrical, immediately postequatorial. Cirrus-sac anterior to ventral sucker; cirrus unarmed. Genital pore submedian, anterolateral to ventral sucker. Ovary lateral or anterolateral to ventral

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sucker. Seminal receptacle absent. Laurer's canal present. Uterine coils mainly in testicular region, overlap testes. Eggs numerous. Vitelline fields very strongly developed, extend from anterior to posterior extremities of body, confluent in fore- and hindbody. Excretory vesicle Y-shaped, with short stem. In gall-bladder, liver and small intestine of small mammals; Palaearctic. Type-species *S. polonicus* (Soltys, 1957) Petrov & Merkusheva, 1963.

**29b. Vitelline fields moderately developed, not confluent, extending from level of intestinal bifurcation to post-testicular region, but never reach posterior extremity; ovary posterior or posterolateral to ventral sucker; parasites of Neotropical anuran amphibians ..... ..... *Choledocystus* Pereira & Cuocolo, 1941. (Fig. 23.35)**

**Diagnosis:** Body rounded-oval to fusiform. Tegument spined. Oral sucker subterminal, larger than or equal to ventral sucker. Ventral sucker closely pre-equatorial. Prepharynx indistinct. Pharynx well developed. Oesophagus short. Intestinal bifurcation in mid-forebody. Caeca extend to near posterior extremity. Testes entire, more or less rounded, arranged symmetrically or somewhat obliquely in middle of body. Cirrus-sac relatively large, arcuate; contains bipartite seminal vesicle, well-developed pars prostatica and unarmed cirrus. Genital pore submedian, close to intestinal bifurcation. Ovary submedian, immediately posterior to ventral sucker. Seminal receptacle absent. Vitelline follicles lateral to intestinal caeca or partly overlap them, extend from intestinal bifurcation to level of posterior margins of testes or caecal ends. Excretory vesicle more or less Y-shaped, with very short limbs. In gall-bladder, bile-ducts and liver of anuran amphibians; neotropics. Type-species *C. elegans* (Travassos, 1926) Pereira & Cuocolo, 1941.

**30a. Vitellarium very strongly developed, with fields extending from level of intestinal bifurcation to posterior extremity and confluent anterior to ventral sucker and posterior to uterus, thus surrounding all other internal organs and completely overlapping ends of**

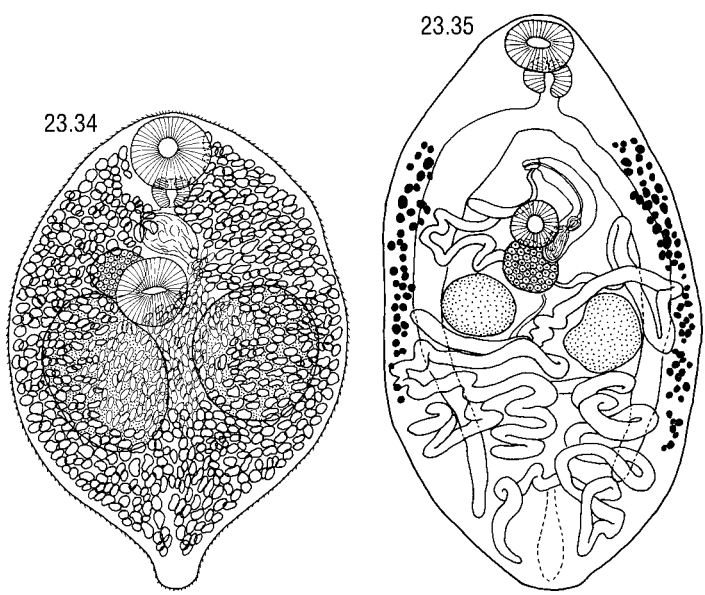



**Fig. 23.34.** *Skrjabinoplagiorchis polonicus* (Soltys, 1957). After Sharpilo & Iskova (1989).
**Fig. 23.35.** *Choledocystus elegans* (Travassos, 1926). After Prudhoe & Bray (1982).

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**caeca; cirrus-sac very small, entirely anterior to ventral sucker ..... ..... *Rudolphitrema* Travassos, 1926. (Fig. 23.36)**
(Syn. *Rudolphiella* Travassos, 1924 *nec* Fuhrmann, 1916)

**Diagnosis:** Body small, oval. Oral sucker larger than ventral sucker. Ventral sucker at border between anterior and middle thirds of body. Prepharynx absent. Pharynx small. Oesophagus about twice length of pharynx. Intestinal bifurcation in mid-forebody. Caeca extend to posterior extremity. Testes rounded, widely separated by uterine loops, lying somewhat obliquely in posterior third of body. Cirrus-sac very small, anterior to ventral sucker; contains convoluted seminal vesicle. Genital pore slightly submedian, immediately anterior to ventral sucker. Ovary rounded, situated posterolaterally near ventral sucker. Seminal receptacle small, but distinct, immediately posterior to ovary. Uterine coils extending posteriorly beyond testes. Vitelline fields envelop intestinal caeca, extend from intestinal bifurcation to ends of caeca, confluent in median line anteriorly to ventral sucker and posteriorly to uterus. Excretory system unknown. In intestine of anuran amphibians; neotropics. Type-species *R. rudolphi* (Travassos, 1924) Travassos, 1926.

**30b. Combination of form of vitellarium and cirrus-sac size and position not as above ..... 31.**

**31a. Seminal vesicle tubular, coiled in proximal part of cirrus-sac ..... 33.**
**31b. Seminal vesicle bipartite ..... 32.**

**32a. Vitelline fields not extending posteriorly beyond testes; caeca relatively short, terminate just posterior to posterior testis, at border between middle and posterior thirds of body; parasites of mouth and oesophagus of Neotropical snakes ..... ..... *Haplometroides* Odhner, 1910. (Fig. 23.37)**
(Syn. *Zeferinella* Artigas & Paulino, 1988)

**Diagnosis:** Body elongated, with rounded ends. Tegument covered with spines. Oral sucker larger than ventral sucker. Ventral sucker small, one-third to one-quarter of body length from anterior end. Prepharynx indistinct. Pharynx present. Oesophagus of moderate length. Intestinal bifurcation about halfway between pharynx and ventral sucker. Caeca terminate just posterior to testes, at considerable distance from posterior extremity. Testes oblique, in middle third of body. Cirrus-sac relatively small, largely anterior to ventral sucker; contains bipartite seminal vesicle, pars prostatica and cirrus. Genital pore anterosinistral to ventral sucker. Ovary submedian, immediately posterior to ventral sucker. Seminal receptacle present. Vitelline fields extend along caeca from level of ventral sucker to posterior testis. Uterus passes between testes and occupies most of post-testicular space. Excretory vesicle Y-shaped, with long stem and short arms. Parasitic in mouth or oesophagus of snakes; neotropics. Type-species *H. buccicola* Odhner, 1910.

**32b. Vitelline fields extend posteriorly well beyond testes; caeca long, terminate near posterior extremity; in intestine of turtles ..... *Aptorchis* Nicoll, 1914. (Figs 23.38–23.42)**
(Syn. *Dingularis* Jue Sue & Platt, 1999)

**Diagnosis:** Body elongate. Tegument armed with spines. Exceptionally (*A. glandularis*) ventral surface posterior to ventral sucker may have large glands arranged in three longitudinal rows. Oral sucker of similar size to or smaller than ventral sucker. Ventral sucker in anterior half of body. Prepharynx of variable length. Pharynx larger or smaller than oral sucker. Oesophagus usually short. Intestinal bifurcation in forebody. Anterior caecal diverticula present or absent. Caeca extend almost to posterior extremity. Testes entire, intercaecal, in posterior third of body, symmetrical, oblique or tandem. Cirrus-sac large, sinuous or tortuous, may form a complete loop, extends well posterior to ventral sucker; contains bipartite seminal vesicle, glandular pars prostatica and unarmed cirrus. Genital pore in forebody or at level of

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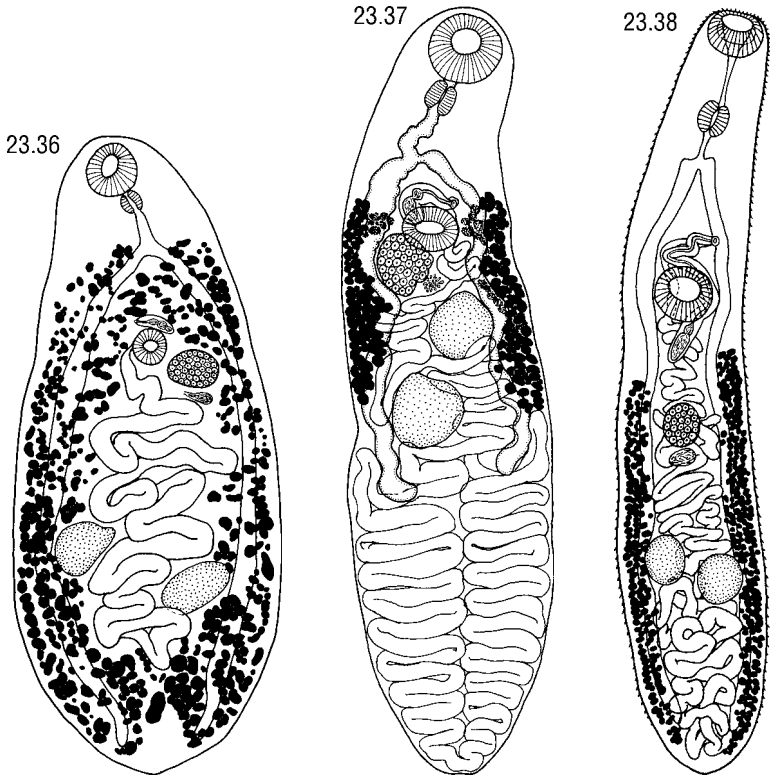



**Fig. 23.36.** *Rudolphitrema rudolphi* (Travassos, 1924). After Prudhoe & Bray (1982).
**Fig. 23.37.** *Haplometroides buccicola* Odhner, 1910. Original.
**Fig. 23.38.** *Aptorchis aequalis* Nicoll, 1914. Original.

anterior margin of ventral sucker, submedian or sublateral, may be extracaecal. Ovary median or submedian, in posterior half of body, between testes and ventral sucker. Seminal receptacle usually posterodorsal, sometimes lateral to ovary. Laurer's canal present. Uterus inter- and postcaecal, extends to posterior extremity. Vitelline follicles large or small, extend in ventrolateral extracaecal fields from posterior level of cirrus-sac almost to ends of caeca or to posterior extremity; in latter case fields may be confluent posteriorly. Excretory vesicle in adult worms Y-shaped, with very long stem and short arms; pore subterminal. In digestive tract of freshwater turtles; Australia. Type-species *A. aequalis* Nicoll, 1914.

**33a. Vitelline fields extend along much of body reaching or almost reaching ends of intestinal caeca, either in uninterrupted fields consisting of numerous small follicles or interrupted fields consisting of numerous bunch-like clusters of follicles ..... 35.**
**33b. Vitellarium in form of two compact lateral clusters of follicles or relatively short vitelline fields; in latter case these fields are confined to middle third of body ..... 34.**

**34a. Body oval, plump; both suckers very strongly developed; ventral sucker equatorial or slightly pre-equatorial; cirrus-sac powerful, anterior to ventral sucker; cirrus armed with**

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**large spines; metraterm exceptionally strongly developed with thick muscular walls ..... ..... *Travtrema* Pereira, 1929. (Figs 23.43, 23.44)**
(Syn. *Leptophyllum* Cohn, 1902 *nec* Klemm, 1883 and Verhoeff, 1895)

**Diagnosis:** Body small, stout, thick. Tegument smooth. Suckers powerful. Oral sucker subterminal, large. Ventral sucker very large, transversely elongated, pre-equatorial or nearly equatorial, usually larger than oral sucker. Prepharynx short. Pharynx relatively large. Oesophagus very short or indistinct. Intestinal bifurcation in mid-forebody. Caeca terminate some distance short of posterior extremity. Testes symmetrical or nearly so, intercaecal, entire or with irregular edges, at about border between middle and posterior thirds of body. Cirrus-sac powerful, entirely or mostly anterior to ventral sucker; contains winding seminal vesicle, well-developed prostatic complex and large cirrus armed with prominent large spines. Genital pore submedian, usually ventral to right caecum between intestinal bifurcation and ventral sucker. Ovary small, submedian, between ventral sucker and left testis. Seminal receptacle well developed, rounded or elongate, posterior or lateral to ovary. Uterus occupies most of post-testicular region. Metraterm exceptionally muscular and long, reaches posterior margin of ventral sucker or beyond it. Eggs numerous. Vitellarium forms two mostly extracaecal bunch-like groups of large follicles on either side of gonads. Excretory vesicle Y-shaped. In intestine, cloaca or ureter of snakes; Nearctic and Neotropical regions. Type-species *T. stenocotyle* (Cohn, 1902) Pereira, 1929.

**34b. Body moderately elongate; both suckers in anterior third of body; cirrus-sac powerful, anterior to ventral sucker; cirrus apparently unarmed; metraterm weakly developed ..... ..... *Styphlodora* Looss, 1899. (Figs 23.45–23.47)**
(Syns *Platymetra* Mehra, 1931; *Paurophyllum* Byrd, Parker & Reiber, 1940)

**Diagnosis:** Body elongate to oval. Tegument spined. Sucker ratio variable. Oral sucker subterminal, usually small. Ventral sucker in anterior third of body. Prepharynx indistinct. Oesophagus present, of variable length. Intestinal bifurcation in forebody. Caeca almost reach posterior extremity or terminate at some distance from it. Testes oblique, sometimes almost symmetrical, in middle third of body posterior to ventral sucker. Cirrus-sac more or less overlaps ventral sucker and may extend posteriorly beyond it; contains winding seminal vesicle, pars prostatica and unarmed cirrus. Genital pore median or submedian, anterior to ventral sucker or postbifurcal. Ovary submedian, posterodextral to ventral sucker, usually at short distance from it. Seminal receptacle present. Uterus inter- and postcaecal, reaches posterior extremity. Vitellarium forms single bunch of follicles in ventral sucker–testicular zone, or field consisting of several bunches on each side, beginning at level of ventral sucker and extending posteriorly beyond testes. Excretory stem with numerous side branches or diverticula. In intestine, gall-bladder, kidney or ureter of snakes and varanid lizards; widespread. Type-species *S. serrata* Looss, 1899.

**35a. Ovary well separated from base of cirrus-sac by several to numerous uterine coils ..... 38.**

**Figs 23.39–23.41.** (*Opposite*) *Aptorchis glandularis* Tkach & Snyder, 2008. 23.39. General view. 23.40. General view showing distribution of ventral glands. 23.41. Young specimen showing shape of excretory vesicle. After Tkach & Snyder (2008).

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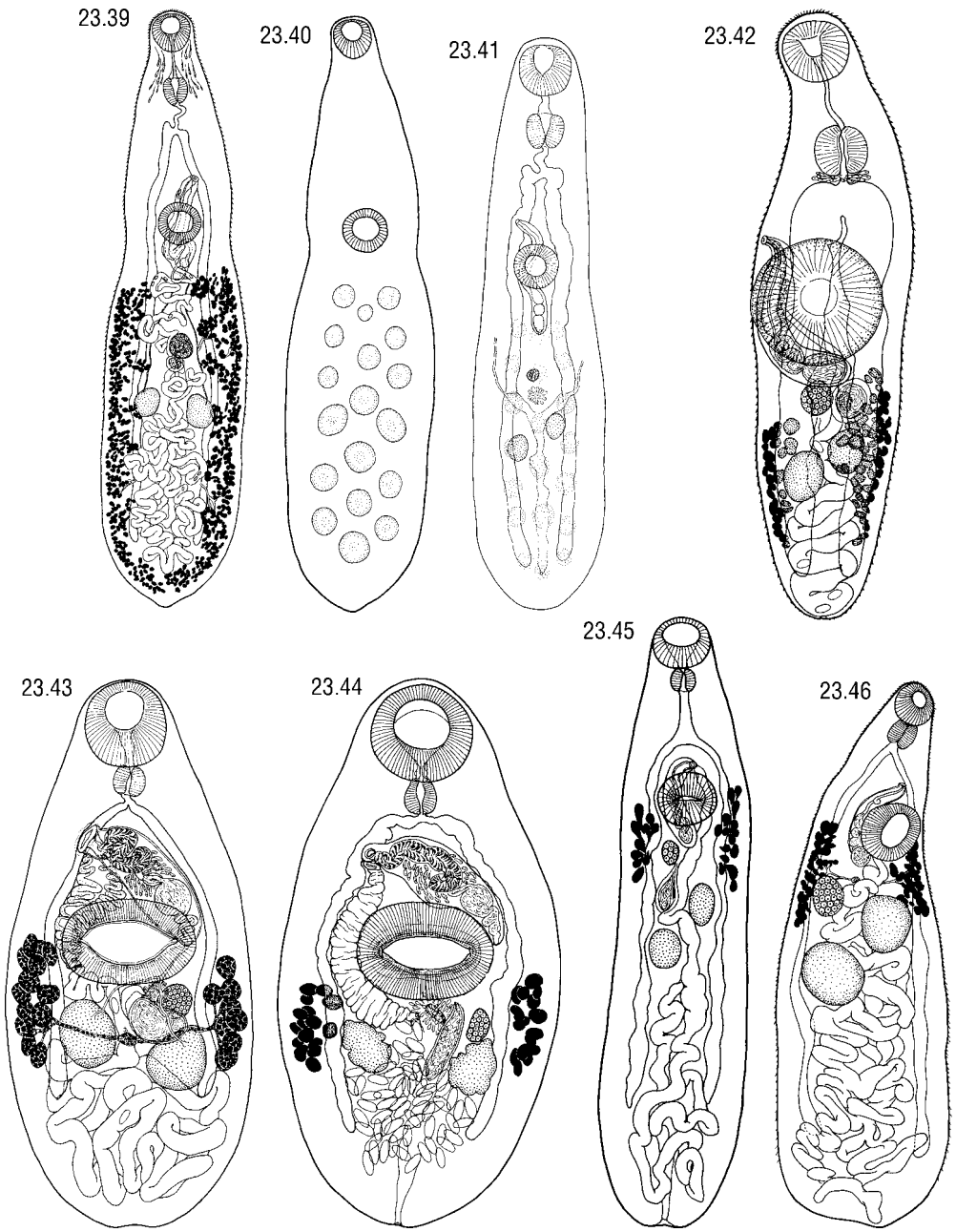



**Fig. 23.42.** *Aptorchis megacetabulus* Tkach & Snyder, 2007. After Tkach & Snyder (2007a).
**Fig. 23.43.** *Travtrema ovale* (Byrd & Roudabush, 1939). Original.
**Fig. 23.44.** *Travtrema tamiamiensis* (McIntosh, 1939). Original.
**Fig. 23.45.** *Styphlodora simplexa* (Byrd, Parker & Reiber, 1940). Original.
**Fig. 23.46.** *Styphlodora renalis* Tubangui, 1933. Original.

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**35b. Ovary very close to cirrus-sac, not separated from it by uterine coils or separated by only single coil ..... 36.**

**36a. Vitelline fields begin well anterior to ovary; oesophagus distinct; in intestine of freshwater turtles in India ..... *Glossimetra* Mehra, 1937. (Fig. 23.48)**

**Diagnosis:** Body elongate. Tegument armed with spines. Oral sucker smaller than ventral sucker. Ventral sucker in anterior third of body. Prepharynx short or indistinct. Oesophagus present. Intestinal bifurcation in mid-forebody. Caeca reach posterior extremity. Testes oblique, entire, elliptical or transversely oval, post-equatorial. Cirrus-sac very large, parallel to median body axis, extends posteriorly far beyond ventral sucker; contains coiled seminal vesicle proximally, long pars prostatica and muscular cirrus armed with minute chitinous scales. Genital pore median, immediately anterior to ventral sucker. Ovary rounded, entire, dextrolateral to base of cirrus-sac, at about mid-distance between ventral sucker and anterior testis. Uterus passes between testes and occupies most of post-testicular space. Vitelline fields lateral, extracaecal, extend from about halfway between ventral sucker and ovary to near ends of caeca. Excretory vesicle Y-shaped with long stem bifurcating into long arms reaching oral sucker; pore subterminal, dorsal. In intestine of freshwater turtles; India. Type-species *G. orientalis* Mehra, 1937.

**36b. Vitelline fields begin at level of ovary or posterior to it; oesophagus indistinct; in lungs of Neotropical snakes ..... 37.**

**37a. Forebody distinctly enlarged; caeca winding anteriorly; vitellarium in form of numerous bunch-like clusters on either side of body, beginning posterior to ovary ..... ..... *Glossidiella* Travassos, 1927. (Fig. 23.49)**

**Diagnosis:** Body elongate, slender, tapering posteriorly and markedly enlarged in forebody. Oral sucker subterminal, somewhat larger than ventral sucker. Ventral sucker in anterior third of body. Prepharynx present. Oesophagus indistinct. Intestinal bifurcation in mid-forebody. Caeca winding anteriorly, terminate at posterior extremity. Testes rounded, entire, oblique, in middle third of body. Cirrus-sac long, with base reaching ovary; contains tubular, coiled seminal vesicle, proximally. Genital pore immediately anterosinistral to ventral sucker. Ovary rounded, entire, submedian, near base of cirrus-sac and somewhat posterior to ventral sucker. Uterus intra- and extracaecal, passes between testes and occupies most of postovarian part of hindbody. Vitelline follicles form numerous bunch-like clusters, extending along caeca from ovary to near caecal extremities. Excretory system unknown. In lungs of snakes; neotropics. Type-species *G. ornata* Travassos, 1927.

**37b. Forebody not distinctly enlarged; caeca not winding anteriorly; vitelline fields begin at ovarian level, narrow, interrupted by spaces but not forming distinct bunch-like clusters ..... *Glossidioides* Yamaguti, 1958. (Fig. 23.50)**

**Diagnosis:** Body fusiform, pointed posteriorly. Oral sucker subterminal. Ventral sucker one-third to one-quarter of body length from anterior end of body. Prepharynx present, wide. Oesophagus indistinct. Intestinal bifurcation in mid-forebody. Caeca terminate at some distance short of posterior extremity. Testes large, oblique, close to each other in middle third of body. Cirrus-sac large, claviform, lies transversely between ventral sucker and intestinal bifurcation, with its base just anterior to ovary; contains convoluted tubular seminal vesicle, bulbous pars prostatica and long ejaculatory duct. Genital pore anterodextral to ventral sucker. Ovary round, entire, posterolateral to ventral sucker. Uterus intra- and extracaecal, occupies most of hindbody between ovary and end of caeca but does not reach posterior extremity. Eggs numerous. Vitelline

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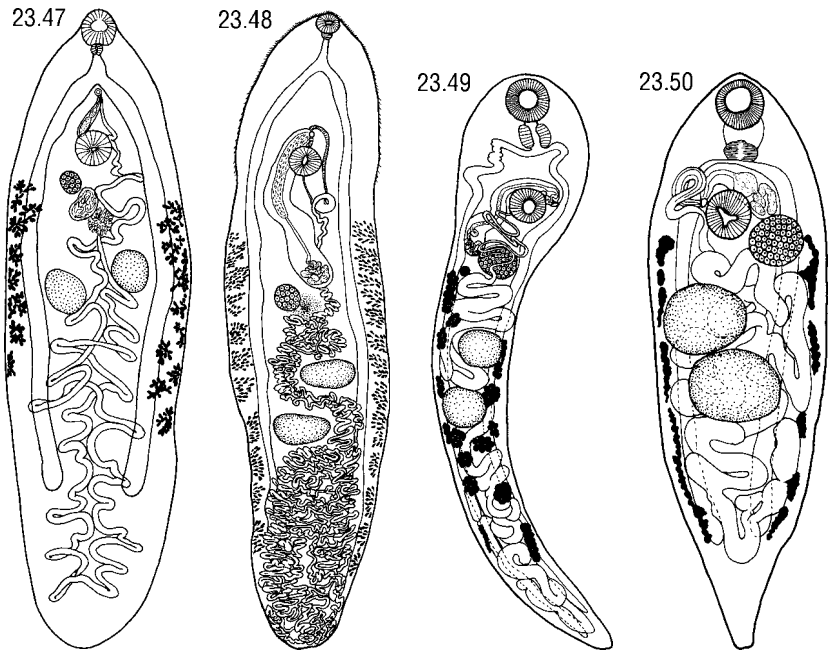



**Fig. 23.47.** *Styphlodora magna* Byrd & Denton, 1938. Original.
**Fig. 23.48.** *Glossimetra orientalis* Mehra, 1937. After Mehra (1937).
**Fig. 23.49.** *Glossidiella ornata* Travassos, 1927. After Travassos (1928b).
**Fig. 23.50.** *Glossidioides loossi* (Travassos, 1927). After Travassos (1928b).

fields narrow, interrupted in some places, extend from ovarian level to caecal extremities. Excretory system Y-shaped. In lungs of snakes; neotropics. Type-species *G. loossi* (Travassos, 1927) Yamaguti, 1958.

**38a. Ovary close to base of cirrus-sac and separated from it by few uterine coils; vitellarium begins slightly anterior to ovary; cirrus heavily armed with spines** ..... ..... ***Spinometra*** **Mehra, 1931. (Fig. 23.51)**

**Diagnosis:** Body greatly elongated, tapers anteriorly. Tegument covered with spines. Oral sucker very small. Ventral sucker small, but substantially larger than oral sucker, close to oral sucker, at about one-sixth of body length from anterior end of body. Prepharynx indistinct. Oesophagus long, narrow. Intestinal bifurcation in anterior forebody. Caeca almost reach posterior extremity. Testes oblique or nearly tandem, large, elliptical or ovoid, transversely elongate, in middle third of body, equatorial or just postequatorial. Cirrus-sac very large, club-shaped, highly muscular, somewhat conical, oriented along median axis of body and extending posteriorly far beyond ventral sucker, with base close to ovary but separated from it by several uterine coils; contains convoluted seminal vesicle in basal region, long tubular pars prostatica with well-developed prostate gland cells and long, stout cirrus armed with spines. Genital pore immediately anterosinistral to ventral sucker. Ovary median or submedian, just posterior to base of cirrus-sac. Seminal receptacle and Laurer's canal present. Uterus passes between testes and occupies most of hindbody posterior to ovary. Metraterm well developed, with thick muscular

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folded wall. Vitellarium in form of numerous extra- or supracaecal bunch-like clusters of follicles extending from level slightly posterior to ovary to near end of caeca. Excretory vesicle Y-shaped with long stem provided with somewhat ramified lateral branches and dividing near anterior testis into two arms. In intestine of freshwater turtles; India. Type-species *S. kachugae* Mehra, 1931.

**38b. Ovary distant from base of cirrus-sac and separated from it by numerous uterine loops; vitellarium begins far anterior to ovary; cirrus unspined ..... ..... *Allopharynx* Strom, 1928. (Figs 23.52–23.54)**

(Syns *Megacustis* Bennett, 1933; *Ophiorchis* Mehra, 1937; *Ptyasiorchis* Mehra, 1937; *Neomicroderma* Park, 1940)

**Diagnosis:** Body spatulate, with more or less pointed ends. Suckers small, close to each other. Oral sucker subterminal. Prepharynx short or indistinct. Oesophagus of variable length. Intestinal bifurcation in about mid-forebody. Caeca terminate near posterior extremity. Testes oblique, or almost tandem, pre- or postequatorial in middle third of body. Cirrus-sac elongate, more or less overlaps ventral sucker, usually extends posteriorly beyond it, contains winding seminal vesicle, short pars prostatica and short ejaculatory duct. Genital pore median, between ventral sucker and

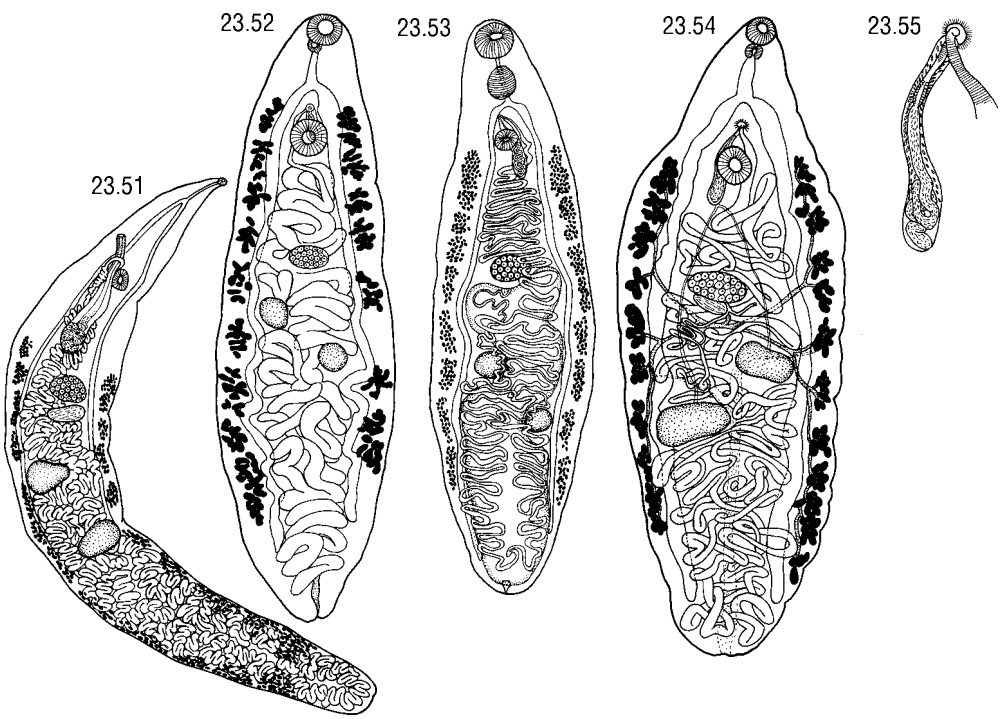



**Fig. 23.51.** *Spinometra kachugae* Mehra, 1931. After Mehra (1931).
**Fig. 23.52.** *Allopharynx amudariensis* Strom, 1928. After Sharpilo (1976).
**Fig. 23.53.** *Allopharynx multispinosus* (Bennett, 1935). After Bennett (1935).
**Figs 23.54, 23.55.** *Allopharynx tropidonoti* (MacCallum, 1919). 23.54. General view. 23.55. Terminal parts of reproductive system. After Yamaguti (1971).

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intestinal bifurcation. Ovary median or submedian, pre-equatorial, far from ventral sucker and cirrus-sac, and separated from them by numerous uterine coils. Uterus intercaecal, reaches posterior extremity, exceptionally does not reach ends of caeca. Vitellarium bunch-like, extends in lateral fields from level of ventral sucker or somewhat posterior to it, to near posterior ends of caeca but never reaching them; exceptionally, vitellarium ends at third of distance between ovary and posterior extremity. Excretory system Y-shaped, with long stem and short arms. In gall-bladder of snakes and intestine of lizards; widespread. Type-species *A. amudariensis* Strom, 1928.

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# 24 Family Auridistomidae Stunkard, 1924

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## Introduction

Auridistomids are intestinal parasites of North American, European and African turtles. They possess auricular projections on the lateral margins of the oral sucker. A pharynx is present, followed by a short oesophagus, and the caeca terminate near the posterior extremity. Tandem or diagonal testes are located in the middle third of the body. A well-developed cirrus-sac is located mainly anterior to the ventral sucker, only occasionally overlapping its posterior margin. Uterine coils pass between the ovary and testes. The anterior extent of the follicular vitellarium is variable, but the follicles fill the body posterior to the ovary, terminating near the posterior extremity.

Stunkard & Franz (1977) provided a detailed description of the convoluted taxonomic history of the family Auridistomidae Stunkard, 1924, a group first erected as a subfamily by Stunkard (1924) and recognized at the family level by Fuhrmann (1928), and reviewed previous opinions on its relationship to the Telorchiidae Looss, 1899. Ultimately, Stunkard & Franz (1977) regarded the Auridistominae Stunkard, 1924 as one of four subfamilies that they included within the Telorchiidae. Yamaguti (1971), however, considered the Auridistomidae and Telorchiidae to be separate, although he (Yamaguti, 1975) pointed out that similarities in the life-cycle patterns of these parasites indicated a close relationship between them. In addition to the type-genus, *Auridistomum* Stafford, 1905, from the snapping turtle *Chelydra serpentina*, only one other genus, *Patagium* Heymann, 1905, is currently assigned to the family. The synonymy of *Pterygotomaschalos* Stunkard, 1923 and *Tetrapapillatrema* Ralph 1938 with *Auridistomum* was first proposed by Wharton (1940) and subsequently accepted by Yamaguti (1971) and Stunkard & Franz (1977).

Support for the close relationship of the Auridistomidae and Telorchiidae comes not only from similarities in life-cycle patterns, but also from the occurrence of muscular oral papillae (*sensu* Freidenfelds *et al.*, 1994), also called auricular projections or lappets, on all species of Auridistomidae and on several species of the Telorchiidae. Among the telorchiids, although the oral sucker usually lacks muscular papillae, these structures are present on all species in the telorchiid subfamily Allotelorchiinae Goodman, 1988 and two species of *Telorchis* Lühe, 1899 in the Telorchiinae Looss, 1899. The phylogenetic analysis of *Telorchis* by MacDonald & Brooks (1989b) provided an excellent initial step in understanding the evolutionary history and taxonomic

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significance of these papillae and, when this type of analysis is extended to other genera of papillose telorchiids and both genera of auridistomatids, additional insight into the classification of these taxa will be gained.

Because the occurrence of muscular oral papillae is not restricted to the Auridistomidae, this character alone is insufficient to distinguish the two families. A distinction, however, can be made by comparing the placement of testes. Auridistomids are always papillose and have testes in the middle third of the body. The vast majority of telorchiids are non-papillose. The posterior testis is always in the posterior third of the body, typically near the posterior extremity, and the anterior testis is most often nearly contiguous with the posterior testis in the hindbody; exceptionally, the testes may be widely separated.

## Family Auridistomidae Stunkard, 1924

**Diagnosis:** Body elongate, slender. Tegument spined or not. Oral sucker subterminal, with two pairs of lateral muscular papillae. Ventral sucker round, median, in anterior third of body. Prepharynx apparently present or absent. Pharynx present. Oesophagus short to long. Intestinal bifurcation in forebody. Caeca elongate, terminate blindly near posterior extremity. Testes two, tandem to diagonal, in middle third of body. Cirrus-sac mostly anterior to ventral sucker, contains coiled tubular seminal vesicle and distinct pars prostatica. Ejaculatory duct and cirrus present. Genital atrium absent. Genital pore median, near or posterior to intestinal bifurcation. Ovary pretesticular, median to submedian, posterior to ventral sucker. Seminal receptacle present. Laurer's canal present in *Auridistomum*. Uterus forms descending and ascending coils between ovary and anterior or posterior testis. Metraterm absent. Eggs small. Vitellarium follicular, in lateral fields extending from intestinal bifurcation or ovary to near posterior extremity. Excretory vesicle Y-shaped with long stem; pore terminal. In intestine of turtles; North America, Europe. Type-genus *Auridistomum* Stafford, 1905.

## Key to genera

**1a. Vitellarium extends from ovary to near posterior extremity; genital pore just postbifurcal ..... *Auridistomum* Stafford, 1905. (Fig. 24.1)**

(Syns *Pterygotomaschalos* Stunkard, 1923; *Tetrapapillatrema* Ralph, 1938)

**Diagnosis:** Body elongate. Tegument spinous. Oral sucker large, subterminal. Ventral sucker small, round, median, in anterior third of body. Prepharynx short. Oesophagus short. Caeca slender, elongate. Testes tandem to slightly diagonal, round, in middle third of body. Cirrus-sac elongate, robust, extends from intestinal bifurcation to slightly past posterior margin of ventral sucker, contains coiled, tubular seminal vesicle. Prostatic cells surround ejaculatory duct; cirrus present. Genital pore just postbifurcal. Ovary round. Uterus coils between ovary and anterior testis and anterior to ovary. Vitelline follicles in lateral fields between ovary and posterior extremity. Excretory vesicle Y-shaped, with long stem and short branches at level of ovary. Ciliated dorsal pouch (*sensu* Yamaguti, 1971) dorsal to excretory vesicle. In intestine of turtles; North America. Type-species *A. chelydrae* (Stafford, 1900) Stafford, 1905.

**1b. Vitellarium extends from intestinal bifurcation to posterior extremity; genital pore midway between intestinal bifurcation and ventral sucker ..... *Patagium* Heymann, 1905. (Fig. 24.2)**

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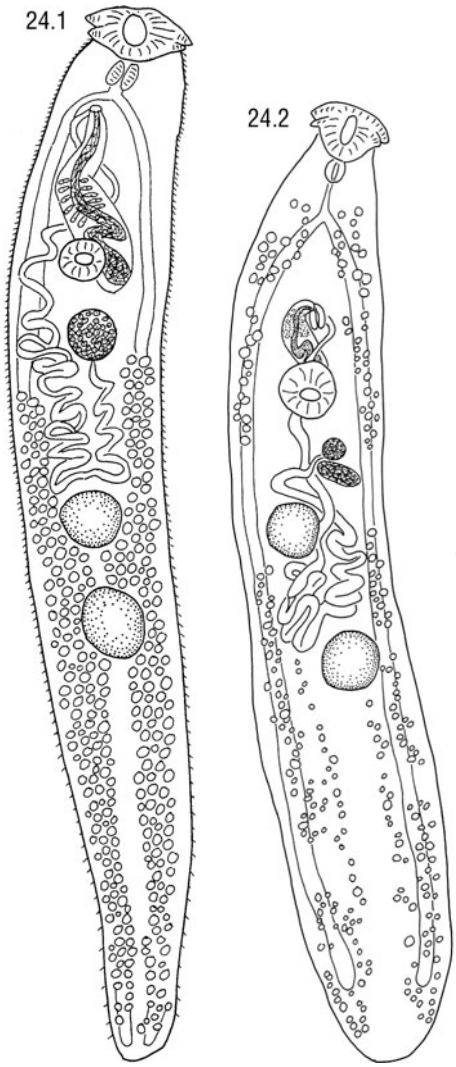



**Fig. 24.1.** *Auridistomum chelydrae* (Stafford, 1900). Voucher USNPC 59144. Original.
**Fig. 24.2.** *Patagium pellucidum* (Coil & Kuntz, 1958). Holotype USNPC 38280. Original.

**Diagnosis:** Body spatulate. Tegumental spines not reported. Ventral sucker round, median, in anterior third of body. Prepharynx absent. Oesophagus present. Caeca elongate, slender. Testes round, diagonal, in middle third of body. Cirrus-sac relatively small, contains coiled, tubular seminal vesicle. Pars prostatica, ejaculatory duct and cirrus present. Genital pore midway between intestinal bifurcation and ventral sucker. Ovary round, submedian, midway between ventral sucker and anterior testis. Uterus winds between ovary and posterior testis; coils separate testes. Vitelline follicles in lateral fields from intestinal bifurcation to posterior extremity. Excretory vesicle Y-shaped, with long stem and long arms, branching near testes and extending to pharynx. In intestine of turtles; Europe. Type-species *P. brachydelphium* Heymann, 1905.

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# 25 Family Cephalogonimidae Looss, 1899

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## Introduction

The Cephalogonimidae Looss, 1899 is a small family of small, spinous digeneans parasitic in the gastro-intestinal tract of fishes, amphibians and reptiles. Its major differential characters include the position of the genital pore at the anterior extremity and the presence, in some taxa, of lateral branches of the excretory vesicle. Its history is closely associated with that of the Prosthogonimidae Lühe, 1909 (see Jones, Chapter 59, this volume). Cephalogonimids are parasites of lower vertebrates, while prosthogonimids occur in birds and mammals. They are treated as distinct families here because large and small subunit ribosomal RNA gene sequence analysis (Olson *et al*., 2003) has indicated that they are not as closely related as the similarities in their morphology would appear to suggest (see Jones, Chapter 59, this volume).

The family-group name was first established at subfamily level by Looss (1899), who erected the Cephalogoniminae Looss, 1899 for *Cephalogonimus* Poirier, 1886 and *Leptalea* Looss, 1899 (preoccupied, later renamed *Emoleptalea* Looss, 1900). The first use of the name at family level was apparently by Nicoll (1914), in a paper in which he placed *Prosthogonimus* Lühe, 1899 in the Cephalogonimidae. Later, Nicoll (1924) reversed this position by placing *Cephalogonimus* in the Prosthogonimidae, but then (Nicoll, 1926) he treated the families as synonymous, with the Prosthogonimidae as the senior synonym. Ward (1917) included *Cephalogonimus* in the Prosthogoniminae Lühe, 1909, but Poche (1926) accepted the Cephalogonimidae for *Cephalogonimus* and *Emoleptalea*. Of various species added to *Cephalogonimus, C. ovatus* (Rudolphi, 1803) and *C. pellucidus* (von Linstow, 1873) have long been recognized as species of *Prosthogonimus*. Following a comparison of the characters of the Cephalogonimidae and Lepodermatidae Odhner, 1910 (within which Odhner (1910) and Poche (1926) had put *Prosthogonimus*), Pande (1932) reduced the former to a synonym of the latter.

Caballero y C. & Sokoloff (1936) followed Pande (1932) in placing *Cephalogonimus* in the Lepodermatidae and Cephalogoniminae, as did Mehra (1937), who included both *Cephalogonimus* and *Emoleptalea* (syn. *Leptalea*). Mehra distinguished the Cephalogoniminae and Prosthogoniminae by a suite of morphological characters and by the occurrence of cephalogonimines in the gut of fishes, amphibians and reptiles, but of prosthogonimines in the bursa Fabricii and oviduct of birds

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and the liver of microtine rodents. In the light of subsequent additions to each group, some of the characters (body-shape, position of the genital pore, size of the cirrus-sac, ovary entire or lobed, distribution of the uterine coils) are no longer entirely distinctive at the family or subfamily levels.

Yamaguti (1971) recognized both the Cephalogonimidae and the Prosthogonimidae and also erected a new subfamily, the Paracephalogoniminae Yamaguti, 1971, for *Paracephalogonimus* Skrjabin, 1950, established for *P. minutus* (Mehra, 1937) from *Lissemys punctatus* in India by Skrjabin (1950). He distinguished it from the cephalogonimines by its rounded body-shape, the distribution of the vitelline follicles in the 'shoulder' region of the forebody and the encroachment of the uterine coils into the forebody. Subfamilies have not been adopted here as there is no logistic reason to do so.

Subsequent additions are *Oudhia* Gupta, 1955 (but see the discussion on the family Maseniidae Chatterji, 1933 below) for a single specimen from the intestine of an Indian freshwater fish, *Heteropneustes fossilis* (see Gupta, 1955, who originally classified it as a reniferid) and *Cephalogonimoides* Brooks & Buckner, 1976, based on *C. sireni* (Premvati, 1969) from an amphibian, *Siren lacertina*, in Florida. Brooks & Buckner (1976) diagnosed *Cephalogonimoides* on the basis of its symmetrical testes, lobed ovary, ventral sucker much larger than the oral sucker, caeca extending to the posterior end of the body, muscular prepharynx and absence of a seminal receptacle (said to be present by Premvati, 1969). Premvati (1969) considered her species to combine the prosthogonimid characters of symmetrical testes and a lobed ovary with the cephalogonimid characters of (typically) elongate-oval body-shape, genital pore terminal to the oral sucker and an amphibian host. She stated that there are three to six rows of spines on the oral sucker, but Brooks & Buckner (1976) did not mention them.

Another small family of digeneans from African and Asian freshwater fishes appears morphologically close to the Cephalogonimidae. The Maseniidae Chatterji, 1933 was erected as a subfamily by Chatterji (1933) and subsequently raised to family rank independently by Yamaguti (1953a) and Gupta (1955); its history was summarized by Ramadan *et al.* (1987). Unfortunately, there appear to be no sequence data available for maseniids. Beverley-Burton (1962) pointed out the striking similarity of *Oudhia* to *Masenia* Chatterji, 1933, and Fischthal & Thomas (1972a) noted that that *Masenia*, *Eumasenia* Srivastava, 1951, *Oudhia* and *Emoleptalea* Looss, 1900 appeared to be 'closely related'. It is, indeed, striking that pairs of species in different genera, but from the same host-species or genus, are so similar. Rai & Pande (1967) suggested that there was only one Indian species of *Eumasenia*, synonymizing several species with *E. moradabadensis* Srivastava, 1951. As a result, this broadly conceived species was then harboured by several siluriform species, i.e. *Heteropneustes fossilis, Rita rita, Clarias batrachus* and *Mystus vittatus*. Each of these host-species is reported to harbour other very similar species. *H. fossilis* also hosts *Cephalogonimus heteropneustes* Gupta, 1951, *Oudhia horai* Gupta, 1955, *Emoleptalea loossi* Srivastava, 1960 and *E. dollfusi* Srivastava, 1960. Furthermore, *Clarias batrachus* also harbours *Masenia collata* Chatterji, 1933 and *M. dayali* Gupta, 1955, and other *Clarias* spp. harbour *Eumasenia bangweulensis* Beverley-Burton, 1962, *Eumasenia* (originally *Emoleptalea*) *proteropora* (Thomas, 1958) and *Pseudomasenia kwangtungensis* Pan, 1984. *Mystus vittatus* also harbours *Masenia vittatusi* Agrawal, 1963, *M. gomtia* Agrawal, 1963 and *Oudhia hardayali* Kumar & Agarwal, 1980. *R. rita* also harbours *O. kanungoi* Agrawal & Agarwal, 1985. In addition, the similar species *Emoleptalea synodontidos* Dollfus, 1950, *Eumasenia synodontis* Khalil & Thurston, 1973 and *Paramasenia rifaati* Ramadan, Saoud & Taha, 1987 are found in African *Synodontis* spp.

Beverley-Burton (1962) pointed out the similarity of *Oudhia* to *Masenia* and considered it a likely synonym, but, having compared it with *Emoleptalea*, this is not adopted here. Rather, *Oudhia* is synonymized with *Emoleptalea*, with the following new combinations: *E. horai* (Gupta, 1955) n. comb. for *O. horai* Gupta, 1955; *E. kanungoi* (Agrawal & Agarwal, 1985) n. comb. for

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*O. kanungoi* Agrawal & Agarwal, 1985; and *E. hardayali* (Kumar & Agarwal, 1980) n. comb. for *O. hardayali* Kumar & Agarwal, 1980. None of the species of *Oudhia* has the crown of circumoral spines characteristic of *Masenia* (see Chatterji, 1933; Gupta, 1955; Kumar & Agarwal, 1980; Agrawal & Agarwal, 1985).

In erecting *Eumasenia*, Srivastava (1951) used four characters to distinguish it from *Masenia*, a 'mid-dorsal chasm' of the crown of oral spines, the anterior location of the genital atrium, the distinct diverticulum at the base of the pars prostatica and the large eggs. The latter three distinctions have been invalidated by the variation found in the species described subsequently. The former character appears too minor to sustain a generic distinction and, therefore, in this key we consider *Eumasenia* a synonym of *Masenia*.

According to Pan (1984b), *Pseudomasenia* Pan, 1984 differs from *Masenia* in its interrupted collar of spines and from *Eumasenia* by the lack of a prostatic diverticulum and the shape of the excretory vesicle. Beverley-Burton (1962) redefined *Eumasenia* to include species with or without the prostatic diverticulum. Subsequent descriptions of *Eumasenia* species (e.g. *E. synodontis* Khalil & Thurston, 1973) did not mention a prostatic diverticulum, so it appears to be absent in most cases. Srivastava (1951) and Khalil & Thurston (1973) described the excretory vesicle as Y-shaped, with branches extending laterally to the testes in *E. moradabadensis* Srivastava, 1951 and *E. synodontis* Khalil & Thurston, 1973, respectively, whereas Beverley-Burton (1962) described the excretory vesicle as tubular in *E. bangweulensis*. Specimens of the latter species have a broad vesicle that reaches the testes, as do specimens of *E. synodontis*. It appears likely that the stems of the excretory system reaching laterally to the testes may occasionally dilate, or the anterior margin of the vesicle may be forced laterally to the testes by contraction. In either case, it appears that the condition described for the type-species of *Eumasenia* and *E. synodontis* is not materially distinct from that of *E. bangweulensis* or *Pseudomasenia kwangtungensis* Pan, 1984, and that *Pseudomasenia* is indistinguishable from *Eumasenia*, which is here considered a synonym of *Masenia. P. kwangtungensis* becomes *M. kwangtungensis* (Pan, 1984) n. comb.

Ramadan *et al*. (1987) gave a key to the family, mentioning only the lack of circumoral spines as a differentiating character of *Paramasenia* Ramadan, Saoud & Taha, 1987. In their abstract, they cited the position of the genital pore and the extent of the vitellarium as other features. The genital pore was said to be lateral or dorsal to the oral sucker and the vitellarium to be confined to the ventral sucker zone, neither of which appears to be a strong difference. Possibly, the circumoral spines might have been lost in preparation, but 25 specimens were studied and the tegumental spines were present. There appears to be no clear difference between this genus and *Emoleptalea*, with which it is here synonymized, resulting in the formation of *E. rifaati* (Ramadan, Saoud & Taha, 1987) n. comb. for *P. rifaati* Ramadan, Saoud & Taha, 1987.

## Family Cephalogonimidae Looss, 1899

(Syns Cephalogoniminae Looss, 1899; Maseniidae Chatterji, 1933; Paracephalogoniminae Yamaguti, 1971)

**Diagnosis:** Body very small to medium-sized, dorsoventrally flattened, spinous; shape varies from subcylindrical or linguiform to (rarely) rounded. Circumoral spines present or absent. Oral sucker subterminal; size relative to ventral sucker variable. Ventral sucker usually small, usually in anterior half of body. Prepharynx usually said to be present. Pharynx small. Oesophagus short to absent. Intestinal bifurcation in forebody. Caeca simple, blind; extent variable. Testes variable in relative position, intercaecal, in anterior part of hindbody. Cirrus-sac long (reaches ventral sucker

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or not, or may extend further posteriorly), claviform, contains seminal vesicle, pars prostatica and long ejaculatory duct. Prostatic vesicle present or absent. Genital pore at or near anterior extremity, median or submedian. Ovary submedian, often in hindbody but may be lateral or posterolateral to ventral sucker, pretesticular. Seminal receptacle large, occasionally said to be absent. Laurer's canal and Mehlis' gland present. Uterus coiled mainly in post-testicular region or more extensive anteriorly. Eggs small, numerous, operculate. Vitelline follicles usually in lateral fields, confined to hindbody or not, not extensive. Excretory vesicle Y-shaped, may have numerous lateral branches; pore terminal or subterminal. In gut of freshwater fishes, amphibians and reptiles; Africa, Asia, North and South America. Type-genus *Cephalogonimus* Poirier, 1886.

## Key to genera

**1a. Testes symmetrical; ovary indented or slightly lobed; caeca almost reach posterior extremity of body ..... *Cephalogonimoides* Brooks & Buckner, 1976. (Fig. 25.1)**

**Diagnosis:** Body oval. Circumoral spines in three to six rows apparently present. Ventral sucker equatorial, larger than oral sucker. Prepharynx muscular. Pharynx present. Oesophagus very short or absent. Intestinal bifurcation in anterior third of body, clearly anterior to ventral sucker. Caeca extend close to posterior end of body. Testes close to ventral sucker, symmetrical. Cirrus-sac reaches ventral sucker or not, encloses tubular seminal vesicle, well-developed pars prostatica and long ejaculatory duct. Genital pore terminal, anterior to oral sucker. Ovary submedian, posterolateral or lateral to ventral sucker, lobed. Seminal receptacle absent (said to be present by Premvati, 1969). Uterine coils occupy most of available space in hindbody. Vitelline fields variable, mainly extend from bifurcal level to testicular zone. Excretory vesicle Y-shaped with lateral diverticula; pore terminal. In intestine of amphibians (*Siren lacertina*); North America (Florida). Type- and only species *C. sireni* (Premvati, 1969) Brooks & Buckner, 1976.

**1b. Testes variable in relative position; ovary entire; caecal ends usually clearly short of posterior extremity ..... 2.**

**2a. Vitelline follicles in restricted lateral fields anterior to level of ventral sucker ..... ..... *Paracephalogonimus* Skrjabin, 1950. (Fig. 25.2)**

**Diagnosis:** Body < 1 mm long, 0.52–0.63 mm, almost round. Circumoral spines not described. Oral sucker slightly larger than ventral sucker. Ventral sucker just pre-equatorial. Prepharynx said to be present but not illustrated. Pharynx well developed. Oesophagus absent (according to Mehra, 1937), or extremely short? Intestinal bifurcation almost immediately posterior to pharynx. Caecal ends (not figured in Fig. 25.2) extend slightly posterior to posterior testis (Mehra, 1937). Testes entire, oval, oblique; anterior testis adjacent to and posterolateral to ventral sucker; posterior testis virtually median. Cirrus-sac large, elongate, curved, claviform, narrow distally, contains bipartite seminal vesicle, well-developed pars prostatica and ejaculatory duct, curves anterior to and overlaps ventral sucker; proximal end approaches level of ovary. Genital pore at anterior extremity. Ovary almost oval, submedian, dextral or sinistral at about level of ventral sucker, opposite anterior testis. Mehlis' gland medial to ovary. Uterus occupies most of hindbody and encroaches slightly into forebody up to posterior limits of vitelline fields. Vitelline follicles in two restricted lateral extracaecal groups between level of mid-region of oral sucker and about anterior margin of ventral sucker. Excretory pore and vesicle not mentioned by Mehra. In small intestine of *Lissemys punctatus*; India. Type- and only species *P. minutus* (Mehra, 1937) Skrjabin, 1950.

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**2b. Vitelline fields lateral at level of ventral sucker or more extensive anteriorly and posteriorly, but not entirely in forebody ..... 3.**

**3a. Genital pore submedian at level of prepharynx, pharynx or oral sucker; in freshwater fishes ..... 4.**

**3b. Genital pore at or near anterior extremity; in amphibians and reptiles ..... ..... *Cephalogonimus* Poirier, 1886. (Fig. 25.3)**

**Diagnosis:** Body elongate-oval, usually medium-sized (*c.* 5 mm long or less); extremities usually rounded. Tegument armed; spines more numerous anteriorly than posteriorly. Circumoral spines absent. Oral sucker equal to or slightly larger or smaller than ventral sucker. Ventral sucker in anterior half of body, may be almost equatorial. Prepharynx present in at least some species, short. Pharynx present. Oesophagus short to absent. Intestinal bifurcation in anterior third or quarter of body, far anterior to ventral sucker. Caeca of variable length, end in post-testicular region, often reaching close to (but not reaching) posterior extremity. Testes entire, rounded to irregular, oblique to obliquely or directly tandem, in anterior half of hindbody. Cirrus-sac large, elongate, claviform, obliquely oriented, usually reaches or overlaps level of ventral sucker, contains seminal vesicle, well-developed pars prostatica and narrow ejaculatory duct. Genital pore at or close to anterior extremity. Ovary entire, rounded or oval, submedian and usually obliquely anterior to anterior testis, posterolateral or occasionally almost lateral to ventral sucker. Mehlis' gland complex usually medial to ovary, or occasionally lateral to it. Seminal receptacle posterior or posteromedial to ovary, pyriform or ovoid. Laurer's canal opens mid-dorsally at level of anterior testis in at least some species. Uterus with descending and ascending limbs; coils occupy most of hindbody, extend to or near to posterior extremity, often overlie caeca. Metraterm reported as present or absent. Vitelline follicles in two fairly restricted lateral fields, usually between level of ventral sucker and somewhat posteriorly to posterior testis, but may extend further anteriorly and posteriorly and may overlap caeca. Excretory vesicle Y-shaped with additional lateral branches (rarely reported as vesicular); pore terminal or subterminal. In intestine of amphibians and reptiles; North and South America, India. Type-species *C. lenoiri* Poirier, 1886.

**4a. Enlarged circumoral spines absent; vitelline follicles form lateral bunches at level of ventral sucker ..... *Emoleptalea* Looss, 1900. (Fig. 25.4)**

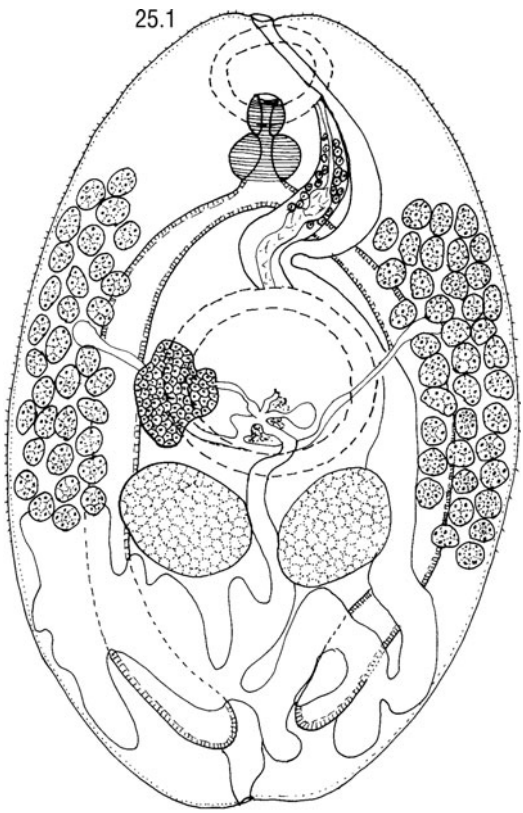
(Syns *Leptalea* Looss, 1899, pre-occupied; *Oudhia* Gupta, 1955; *Paramasenia* Ramadan, Saoud & Taha, 1987)

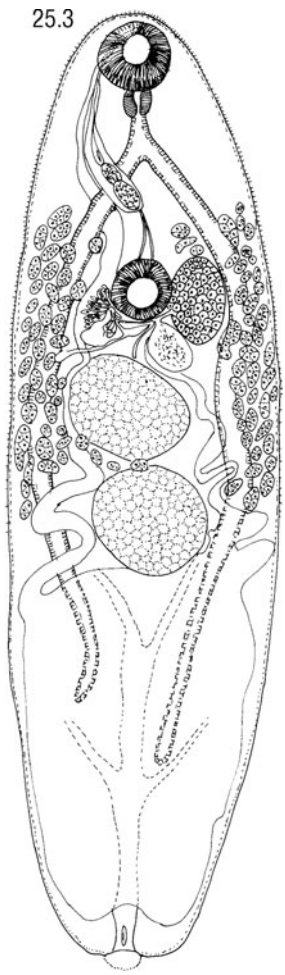
**Diagnosis:** Body small, elongate, delicate, spinous anteriorly. Enlarged circumoral spines absent. Oral sucker comparatively large. Ventral sucker small, pre-equatorial. Prepharynx present. Pharynx small. Oesophagus and caeca slender. Intestinal bifurcation in forebody. Caecal ends reach level of ovary or testes. Testes tandem, oblique or symmetrical, postequatorial. Cirrus-sac elongate-claviform, sigmoid, extends through forebody to level of ventral sucker, contains bipartite internal seminal vesicle, small pars prostatica and ejaculatory duct. Genital pore submedian at level of oral sucker. Ovary slightly submedian on opposite side to genital pore, between ventral sucker and anterior testis. Seminal receptacle postovarian. Uterus descends on right to posterior extremity, then ascends on left, occupying most of hindbody. Vitelline follicles few, form bunch on each side of ventral sucker and in anterior region of hindbody. Excretory vesicle Y-shaped with long stem; pore terminal. In intestine of freshwater fishes; Africa, India. Type-species *E. exilis* (Looss, 1899) Looss, 1900.

**4b. Enlarged circumoral spines present; vitelline follicles mainly in hindbody, from level of ventral sucker to level of testes ..... *Masenia* Chatterji, 1933. (Fig. 25.5)**

(Syn. *Eumasenia* Srivastava, 1951)

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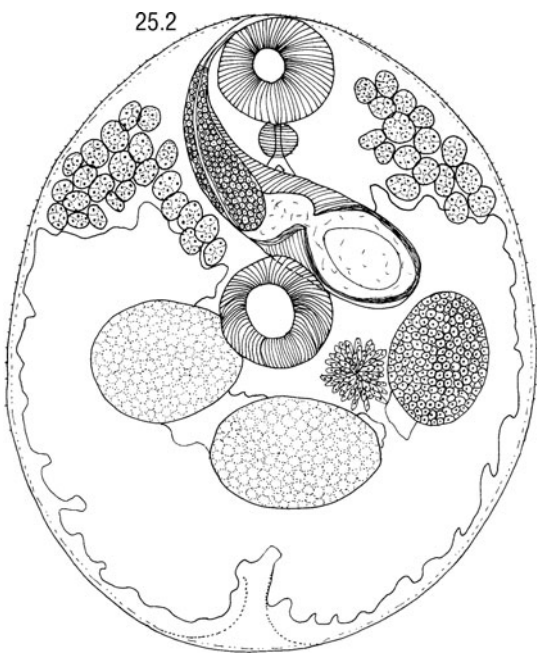




**Fig. 25.1.** *Cephalogonimoides sireni* (Premvati, 1969) Brooks & Buckner, 1976. Dorsal view. After Premvati (1969).
**Fig. 25.2.** *Paracephalogonimus minutus* (Mehra, 1937) Skrjabin, 1950. Uterus in outline only; caeca obscured. After Skrjabin (1950).
**Fig. 25.3.** *Cephalogonimus americanus* Stafford, 1902. Uterus in outline only. After Lamothe-Argumedo (1965).

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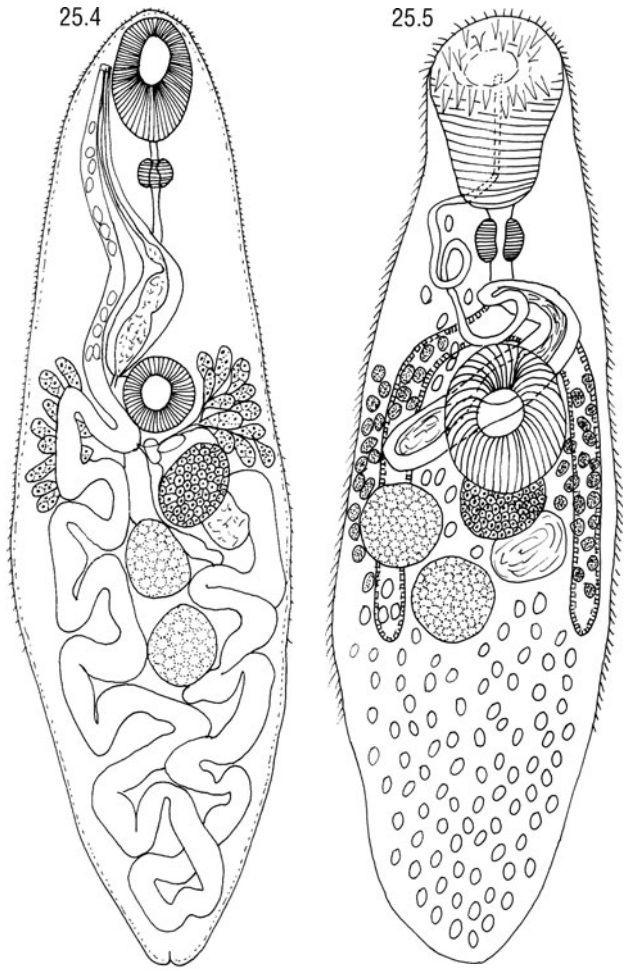



**Fig. 25.4.** *Emoleptalea exilis* (Looss, 1899) Looss, 1900. Caeca not shown. After Skrjabin (1950).
**Fig. 25.5.** *Masenia collata* Chatterji, 1933. Modified after Chatterji (1933).

**Diagnosis:** Body small, elongate, rounded anteriorly and posteriorly, spinous. Circumoral spines present, may have dorsal hiatus. Oral sucker infundibuliform, longer than ventral sucker. Ventral sucker in anterior half of body. Prepharynx present. Pharynx small, muscular. Oesophagus short. Intestinal bifurcation close to pharynx. Caeca end at level of ovary or testes. Testes ovoid, postovarian, oblique, overlap each other. Cirrus-sac elongate-claviform, reaches ventral sucker. Internal seminal vesicle bipartite. Pars prostatica long, narrow, occasionally with diverticulum. Ejaculatory duct long, narrow. Genital pore close to anterior extremity, dorsal, lateral or ventral to oral sucker. Ovary irregularly oval, in hindbody, pretesticular, submedian. Canalicular seminal receptacle present. Uterus fills most of hindbody not occupied by gonads. Metraterm weakly developed. Eggs numerous, operculate or not. Vitellarium follicular, two small symmetrical fields lateral to ventral sucker and gonads. Excretory vesicle saccular or Y-shaped with short, broad arms, reaching into testicular region or to level of ventral sucker; pore terminal or dorso-subterminal. In intestine of freshwater fishes; India, Africa. Type-species *M. collata* Chatterji, 1933.

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# 26 Family Choanocotylidae Jue Sue & Platt, 1998

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## Introduction

The Choanocotylidae Jue Sue & Platt, 1998 is a small family presently including only two genera and six species, so far found exclusively in Australian freshwater turtles of the genera *Chelodina* and *Emydura*. The life-cycles and morphology of the larval stages of two species, *Choanocotyle elegans* Jue Sue & Platt, 1998 and *C. nematoides* Jue Sue & Platt, 1998, have been described in detail by Jue Sue & Platt (1998b). Platt (2003) established a new genus, *Auriculotrema* Platt, 2003, for *Auriculotrema lechneri* Platt, 2003. Platt & Tkach (2003) described two additional *Choanocotyle* species, *C. hobbsi* Platt & Tkach, 2003 and *C. juesuei* Platt & Tkach, 2003, using morphological and molecular criteria. Recently, Tkach & Snyder (2007b) described *Choanocotyle platti* Tkach & Snyder, 2007, also based on morphological and molecular characteristics. The members of this family are obviously plagiorchioids due to the presence of true xiphidiocercariae. A unique combination of several morphological characters in the adults and/or cercariae, such as the arrangement of the reproductive organs and position of the genital pore (Figs 26.1–26.4), the unusual morphology of the anterior extremity and the organization of the excretory system, make the phylogenetic affinities of this family unclear. Jue Sue & Platt (1998b) could not confidently allocate it to any of the major plagiorchioid lineages, although they suggested that it might be closely related to the Telorchiidae Looss, 1899 and Auridistomidae Stunkard, 1924. In the molecular phylogenetic analysis by Olson *et al*. (2003), the Choanocotylidae was always placed among families belonging to the Plagiorchioidea Lühe, 1901, and, in analyses performed using different algorithms, they were closest to either the Auridistomidae, the Telorchiidae or the Plagiorchiidae Lühe, 1901. At present it is not possible, however, to establish their phylogenetic affinities more precisely.

## Family Choanocotylidae Jue Sue & Platt, 1998

**Diagnosis:** Body elongate, cylindrical. Tegument spined; spination may reach posterior end of body. Oral sucker medium to large, wider than remainder of forebody, with or without one pair

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of muscular, anteroventral lappets, with complete or incomplete ventral incision, retractable or not, but, if retractable, funnel-shaped when withdrawn, flared when protracted. Ventral sucker small, armed with concentric circles of small spines. Prepharynx longer than oesophagus, folded or not. Oesophagus very short. Intestinal bifurcation in anterior forebody. Caeca extend almost to posterior extremity. Testes two, subspherical, entire, tandem, closely adjacent or at some distance from each other. Cirrus-sac relatively large, reflexed anteriorly, may have a median loop, extends well into hindbody, contains bipartite seminal vesicle, long pars prostatica and unarmed cirrus. Genital pore immediately posterior to ventral sucker. Ovary subspherical, postequatorial, pretesticular, usually median. Mehlis' gland posteroventral to ovary. Oötype thick-walled. Seminal receptacle thick-walled, smaller than ovary. Laurer's canal long, thick-walled, opens on anterior margin of protuberance on median dorsal surface posterior to ovary. Uterus mainly intercaecal, with ascending and descending limbs, opens into genital atrium anteroventrally to male pore. Eggs numerous. Vitellarium follicular; follicles large or small, scattered or compact, extending from level of ovary or slightly anterior to it, to posterior extremity. Excretory vesicle I-shaped, elongate, somewhat inflated and notched anteriorly, reaches ovarian complex; pore terminal. In intestine of freshwater turtles; Australia. Type-genus *Choanocotyle* Jue Sue & Platt, 1998.

## Key to genera

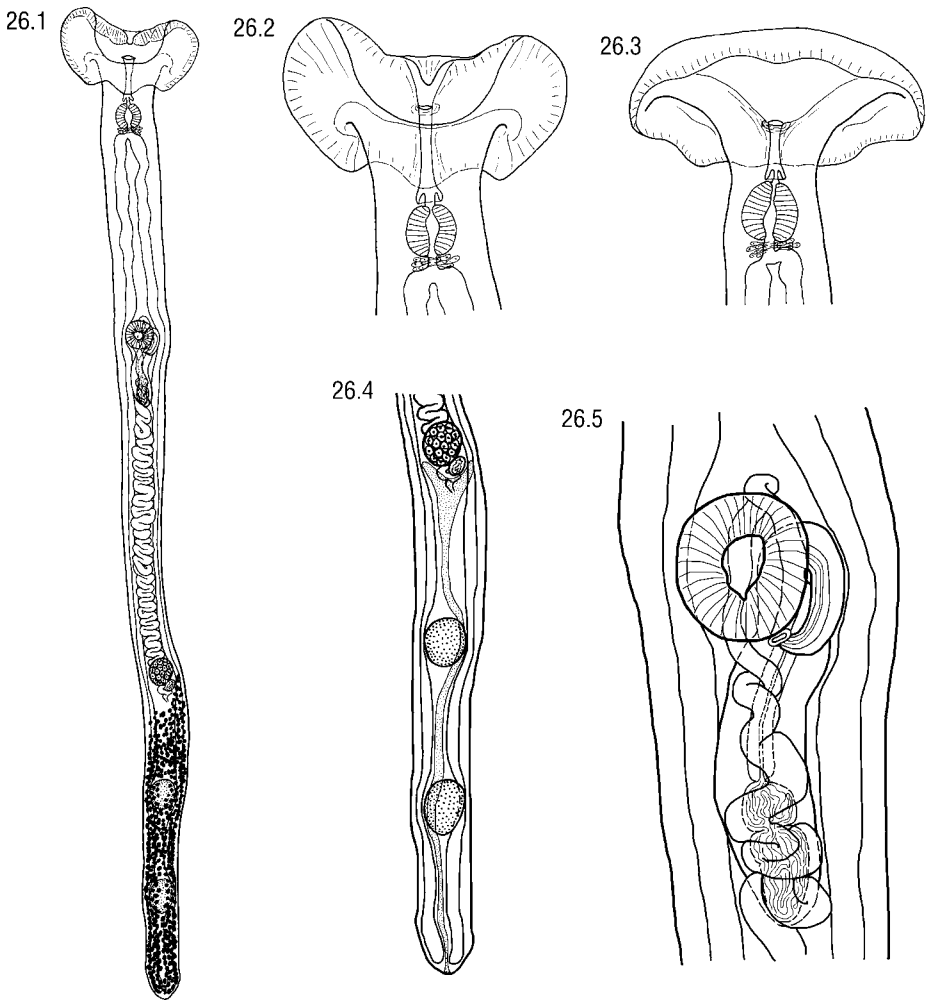
**1. Oral sucker without muscular, anteroventral lappets, with complete ventral incision, funnel-shaped when withdrawn, flared when protracted; testes at some distance from each other ..... *Choanocotyle* Jue Sue & Platt, 1998. (Figs 26.1–26.6)**

**Diagnosis:** Body elongate to very elongate. Oral sucker usually much wider than remainder of forebody, completely ventrally incised, without lappets, funnel-shaped when withdrawn and flared when protracted. Prepharynx may be folded. Cirrus-sac may have median loop in some species. Testes at some distance from each other, usually separated by vitelline follicles. Vitellarium does not extend anteriorly beyond level of posterior margin of ovary. In intestine of freshwater turtles; Australia. Type-species *C. elegans* Jue Sue & Platt, 1998.

**2. Oral sucker with pair of muscular, anteroventral lappets, with incomplete ventral incision, non-retractable; testes closely adjacent to each other ..... ..... *Auriculotrema* Platt, 2003. (Figs 26.7–26.10)**

**Diagnosis:** Body elongate. Oral sucker about as wide as remainder of forebody, with pair of muscular, anteroventral lappets, partly ventrally incised, non-retractable. Prepharynx not folded. Cirrus-sac with medial loop. Testes closely adjacent to each other. Vitellarium extends anteriorly somewhat beyond ovary. In intestine of freshwater turtles; Australia. Type-species *A. lechneri* Platt, 2003.

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**Figs 26.1–26.5.** *Choanocotyle platti* Tkach & Snyder, 2007. 26.1. Adult. 26.2, 26.3. Fully everted oral suckers. 26.4. Posterior end of the body with vitellarium not shown. 26.5. Distal parts of male and female reproductive system and ventral sucker. After Tkach & Snyder (2007b).

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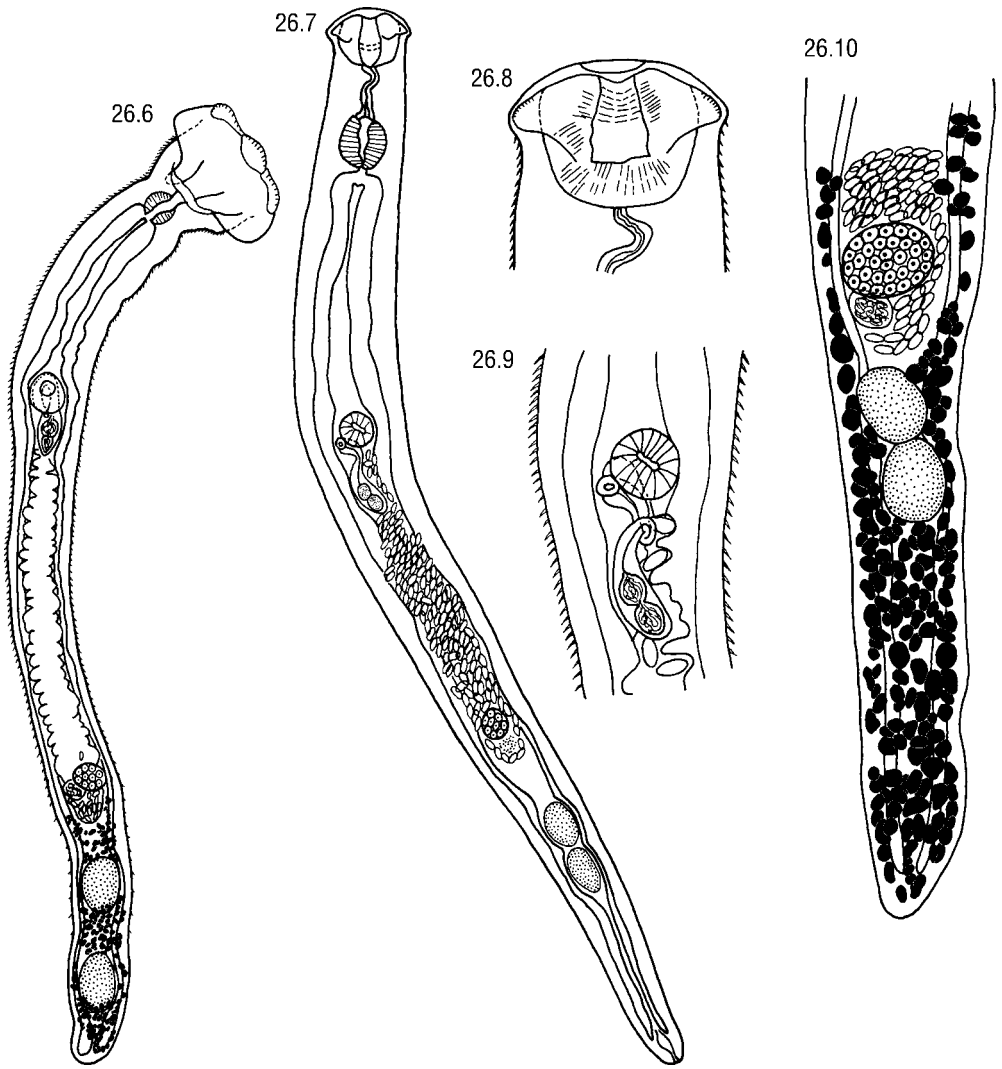



**Fig. 26.6.** *Choanocotyle juesuei* Platt & Tkach, 2003. After Platt & Tkach (2003).
**Figs 26.7–26.10.** *Auriculotrema lechneri* Platt, 2003. 26.7. Adult with vitellarium not shown. 26.8. Oral sucker. 26.9. Cirrus-sac. 26.10. Posterior end showing distribution of vitelline follicles. After Platt (2003).

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# 27 Family Dolichoperoididae Johnston & Angel, 1940

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## Introduction

The Dolichoperidae Yamaguti, 1971 was erected without comment by Yamaguti (1971) for *Dolichopera* Nicoll, 1914 (type-genus) and *Dolichoperoides* Johnston & Angel, 1940 digeneans with a 'plagiorchioid life cycle' from the lungs, trachea, oesophagus and ?intestine[1] of Australian snakes. The family contains only two species. Yamaguti took this step knowing that a family-group name, i.e. Dolichoperoidinae Johnston & Angel, 1940 (type-genus *Dolichoperoides* Johnston & Angel, 1940), already existed. In this work, the oldest family-group name is used. Within the family, Yamaguti recognized two subfamilies, the Dolichoperinae and the Dolichoperoidinae, each with a single genus: both genera had been included in the Dolichoperoidinae by Johnston & Angel (1940). The two groups differ essentially in that the uterus of *Dolichopera* is coiled mainly in the forebody, but it is mainly in the hindbody of *Dolichoperoides*; there are also smaller differences, such as in cirrus-sac size and the position of the symmetrical testes.

The two species of this family were initially assigned to the Lepodermatidae Odhner, 1910 (a synonym of the Plagiorchiidae Lühe, 1901) by Nicoll (1914). Baer (1924) listed *Dolichopera* as a member of the Reniferidae Pratt, 1902 (also a synonym of the Plagiorchiidae), Mehra (1931, 1937) placed it in the subfamily Reniferinae (family Lepodermatidae/Plagiorchiidae) and Perkins (1928) included it in the Telorchiinae Looss, 1899 (family ?Plagiorchiidae). Johnston & Angel (1940) placed the Dolichoperoidinae in the Reniferidae and Yamaguti (1958b) allocated it to the Plagiorchiidae. Skrjabin & Antipin (1958b) included both genera in the Ochetosomatidae Leão, 1945 (syn. Reniferidae) within the Plagiorchioidea. As indicated above, Yamaguti (1971) raised this group to family status.

[1] Yamaguti (1971) stated that the site was usually the intestine. However, Nicoll (1914) indicated the site of *Dolichopera parvula* as 'intestine and lungs(?)', but on the reprint in the collection of the Natural History Museum, London, he changed this by hand to 'oesophagus and lungs', which agrees with the sites given by Johnston & Angel (1940) for the Dolichoperoidinae.

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## Family Dolichoperoididae Johnston & Angel, 1940

(Syn. Dolichoperidae Yamaguti, 1971)

**Diagnosis:** Body small, elongate-fusiform. Tegument covered with small spines. Oral sucker ventroterminal. Ventral sucker slightly smaller than oral sucker, just inside posterior half of body. Prepharynx short. Pharynx relatively small. Oesophagus short. Intestinal bifurcation in anterior forebody. Caeca two, long, pass directly posteriorly to end blindly close to posterior extremity. Testes two, entire, symmetrical or almost so, separate, in anterior or posterior half of hindbody. Cirrus-sac large or small, in forebody, contains saccular or bipartite seminal vesicle, short pars prostatica and long or short ejaculatory duct, which may form cirrus. Genital pore ventrally sublateral on either side of body, at level of oral sucker. Ovary subglobular, smaller than testes, submedial, closely posterior to ventral sucker, anterior to and separated from testes by uterine loops. Laurer's canal present. Canalicular seminal receptacle posterolateral to ovary. Uterus long, convoluted, loops in hindbody between testes and ventral sucker, may or may not wind considerably in forebody; loops reach extracaecally; metraterm narrow, runs alongside cirrus-sac to open via genital pore. Eggs operculate, tanned, small to medium-sized. Vitellarium follicular; follicles small, in restricted lateral fields between about level of ventral sucker and level of testes, absent in post-testicular region, mainly extracaecal, not confluent. Excretory vesicle Y-shaped, tubular, reaches level between ovary and testes; arms reach just into forebody; pore terminal. In lungs, trachea and oesophagus of snakes; Australia. Type-genus *Dolichoperoides* Johnston & Angel, 1940.

### Key to genera

1. **Uterus coiled mainly in hindbody; cirrus-sac large, extends back into posterior forebody; testes in posterior half of hindbody** ..... ..... *Dolichoperoides* **Johnston & Angel, 1940. (Fig. 27.1)**

**Diagnosis:** Ventral sucker close to middle of body. Testes in posterior half of hindbody. Cirrus-sac large, extends back into posterior forebody. Uterus coiled mainly in hindbody. Type-species *D. macalpini* (Nicoll, 1914) Johnston & Angel, 1940.

2. **Uterus coiled mainly in forebody; cirrus-sac small, in anterior forebody; testes in anterior half of hindbody** ..... *Dolichopera* **Nicoll, 1914. (Fig. 27.2)**

**Diagnosis:** Ventral sucker well posterior to middle of body. Testes in anterior half of hindbody. Cirrus-sac small, in anterior forebody. Uterus coiled mainly in forebody. Type-species *D. parvula* Nicoll, 1914.

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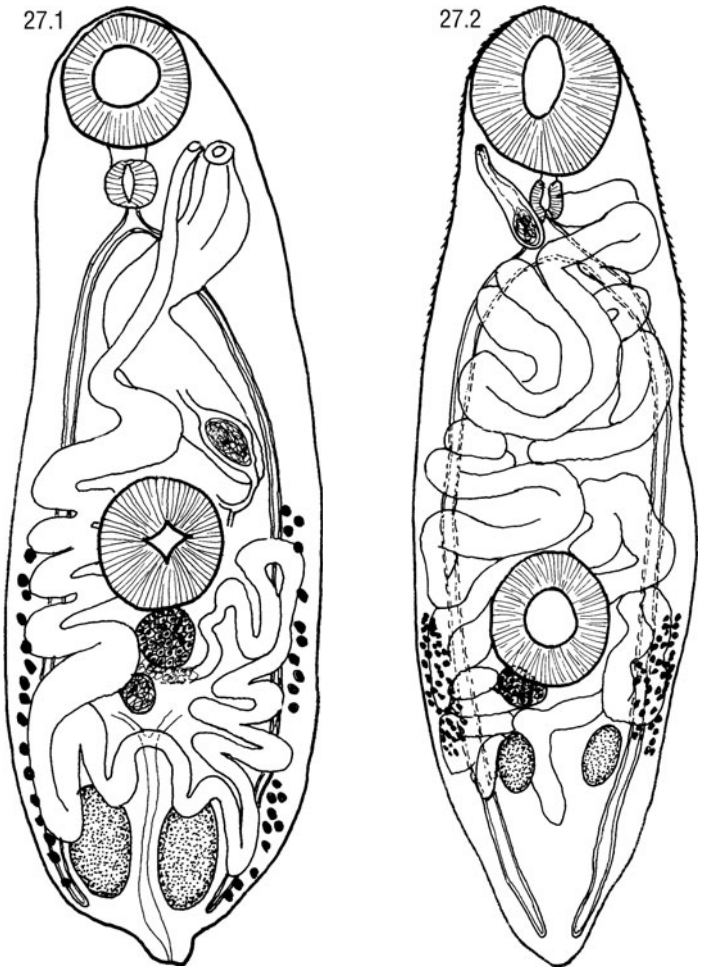



**Fig. 27.1.** *Dolichoperoides macalpini* (Nicoll, 1914). After Johnston & Angel (1940).
**Fig. 27.2.** *Dolichopera parvula* Nicoll, 1914. After Nicoll (1914).

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# 28 Family Echinoporidae Krasnolobova & Timofeeva, 1965

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## Introduction

The apparently monotypic family Echinoporidae Krasnolobova & Timofeeva, 1965 was erected by Krasnolobova & Timofeeva (1965) for the species *Echinoporus megacetabulus* Oshmarin, 1963. This species appears to have been recorded only twice, both times in accipitrid birds of prey, originally by Oshmarin (1963) from *Circus cyaneus* in the far east of Russia and subsequently by Krasnolobova & Timofeeva (1965) from *Milvus korschun* (now *M. migrans*) in the Republic of Tuva in Asiatic Russia. The latter authors also noted a close similarity between this form and 'Trematoda Digenea gen. sp.' of Odening (1962b), found in a pelican *Pelecanus philippensis* of Indian origin in Berlin Zoo, which they considered a synonym, despite apparent differences in host diet, although there is some overlap, and implications for the parasite's life-cycle.

The family is recognized mainly from the arrangement of the gonads, with the ovary situated between two symmetrical testes and the presence of long, acicular spines associated with the genital pore. Originally, Oshmarin (1963), when erecting *Echinoporus*, considered it to be a microphallid, but Krasnolobova & Timofeeva (1965) indicated links with the Heterophyidae Leiper, 1909, an opisthorchioid group, and the Dicrocoeliidae Looss, 1899, a plagiorchioid group. Yamaguti (1971) stated that the family was probably valid and related to the Plagiorchiidae Lühe, 1901.

## Family Echinoporidae Krasnolobova & Timofeeva, 1965

**Diagnosis:** Body elongate-oval, slightly more tapered anteriorly and rounded posteriorly. Tegument armed? Oral sucker relatively large, ventrally subterminal. Ventral sucker globular, stout, larger than oral sucker, almost entirely inside anterior half of body. Prepharynx apparently absent. Pharynx large. Oesophagus virtually absent. Intestinal bifurcation at level of posterior margin of pharynx, well anterior to ventral sucker. Caeca two, variable in width, pass back dorsomedial to testes, end blindly in middle of post-testicular region. Testes two, large,

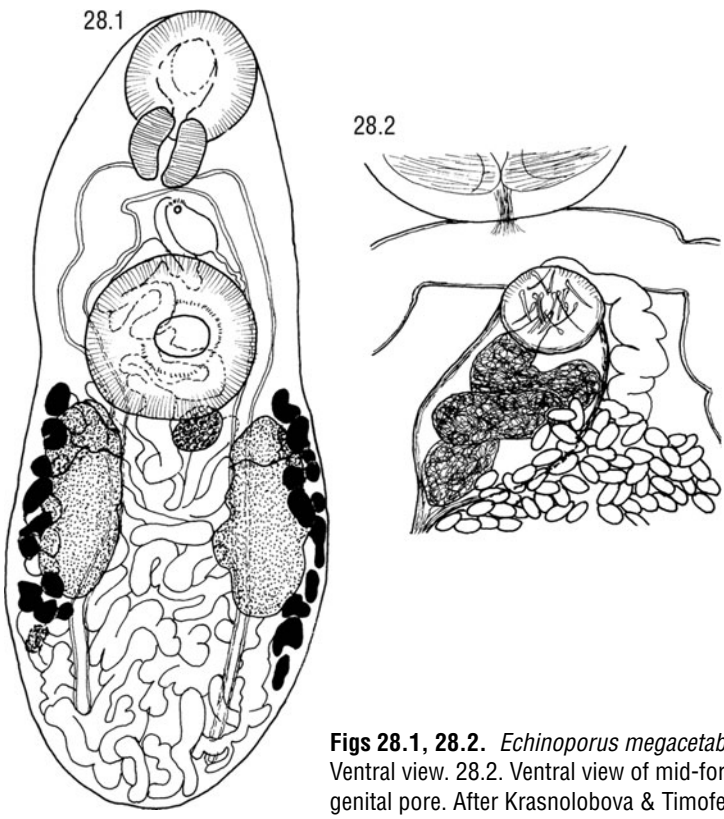
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longitudinally suboval, symmetrical, in anterior hindbody. Cirrus-sac present, submedial in posterior forebody, relatively small, oval, contains long, winding seminal vesicle and short pars prostatica. Genital atrium ?absent, or small. Genital pore midventral, closely postbifurcal, armed with small number of acicular spines. Ovary submedial, in anterior hindbody or posterodorsal to ventral sucker, close to level of anterior testicular margins, subglobular, smaller than testes. Seminal receptacle present (in Odening's specimen). Uterine coils fill much of hindbody, absent lateral to testes, pass forward mid-dorsally to ventral sucker. Metraterm present. Eggs relatively small (*c*. 30 μm). Vitellarium follicular; follicles relatively large and few in number, present in lateral fields from level of ventral sucker well into post-testicular region. Excretory system not known. In intestine of accipitrid and pelecanid birds; Asian Russia and ?India. Type-genus *Echinoporus* Oshmarin, 1963.

## Genus *Echinoporus* Oshmarin, 1963 (Figs 28.1, 28.2)

**Diagnosis:** With characters of family. Type-species *E. megacetabulus* Oshmarin, 1963.




**Figs 28.1, 28.2.** *Echinoporus megacetabulus* Oshmarin, 1963. 28.1. Ventral view. 28.2. Ventral view of mid-forebody showing armature of genital pore. After Krasnolobova & Timofeeva (1965).

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# 29 Family Encyclometridae Mehra, 1931

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## Introduction

The taxonomic history of *Encyclometra* Baylis & Cannon, 1924, a genus of gut parasites of snakes, is extremely complex. In the years 1924–1925 alone, the same taxon was described under four different generic names, namely *Encyclometra* Baylis & Cannon, 1924, *Odhneria* Baer 1924, *Paraplagiorchis* Dollfus, 1924 and *Orthorchis* Mödlinger 1925 (see Baylis & Cannon, 1924; Baer, 1924; Dollfus, 1924; Mödlinger 1925; for a detailed discussion see Skrjabin & Antipin, 1960). Although the paper by Baer (1924) was published several days earlier than that of Baylis & Cannon (1924), the generic name *Odhneria* was pre-occupied by the microphallid *Odhneria* Travassos, 1921; therefore, *Encyclometra* remained the earliest valid name for this genus. Later, it appeared that all four species described by the above authors in 1924–1925, as well as several other forms described prior to 1924, were synonymous with *Distoma colubrimurorum* Rudolphi 1819, which, as a result, acquired the name *Encyclometra colubrimurorum* (Rudolphi, 1819). According to different authors, the number of recognized species of *Encyclometra* varies from two to several (see Yeh, 1958; Skrjabin & Antipin, 1960; Sharpilo, 1976).

Many authors have emphasized that the morphological peculiarities of *Encyclometra* made its phylogenetic affinities unclear and systematic allocation problematic. Nevertheless, the majority (e.g. Baer, 1924; Mehra, 1931, 1937; Yeh, 1958; Skrjabin & Antipin, 1960; Yamaguti, 1971) allocated this genus to the Plagiorchiidae Lühe, 1901, usually within its own subfamily, the Encyclometrinae Mehra, 1931, which had been erected by Mehra (1931). Odening (1960a, 1968a) studied the excretory system of *E. colubrimurorum* and discovered that it has a very dilate excretory vesicle and a large number of protonephridia (adult protonephridial formula $2[(2 \times 7 + 2 \times 7) + (2 \times 7 + 2 \times 7 + 2 \times 7)] = 140$). The number of protonephridial cells is much greater and their arrangement is very different in *E. colubrimurorum* compared with members of the Plagiorchiidae; therefore, the Encyclometrinae was elevated by Odening to full family level. This opinion is supported here.

Sinha (1949) described a new genus and species, *Encyclobrephus robustus* Sinha, 1949, from the turtle *Hardella thurgi* in India. Because of its close morphological similarity to members of *Encyclometra*, he placed *Encyclobrephus* Sinha, 1949 in the subfamily Encyclometrinae. Skrjabin & Antipin (1960) agreed with the systematic arrangement proposed by Sinha (1949), whereas

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Yamaguti (1971) considered *Encyclobrephus* a plagiorchiine. However, I agree with Sinha (1949), because the two genera do share many features, including the topology of the reproductive organs, tandem testes, cirrus-sac in the forebody containing a tubular convoluted seminal vesicle, and the shape of the excretory vesicle. As the protonephridial formula and life-cycle of *Encyclobrephus* are not known, it seems to me reasonable to keep *Encyclobrephus* in the Encyclometridae, at least until more morphological, life-cycle and/or molecular data are available.

Recent molecular studies (Tkach *et al.* 2001b; Olson *et al.*, 2003; Bray *et al.*, 2005; Curran *et al.*, 2006; Choudhury *et al.*, 2007) indicated possible close phylogenetic affinities between *Encyclometra* and members of the Gorgoderoidea Looss, 1899. However, the lack of complete information on the life-cycle and morphology of cercariae prevents more exact systematic allocation of the Encyclometridae at this point. Additional molecular and life-cycle studies should shed more light on the phylogenetic affinities of this presently enigmatic group.

## Family Encyclometridae Mehra, 1931

**Diagnosis:** Body elongate, flattened, fusiform to lanceolate. Tegument with or without spines. Oral sucker subterminal, well developed. Ventral sucker well developed, larger or smaller than oral sucker. Prepharynx present, but may be indistinct. Pharynx well developed. Oesophagus short, may be indistinct. Intestinal bifurcation in forebody. Caeca usually terminate near posterior end of body; exceptionally with one caecum distinctly shorter than other. Testes two, spherical or subspherical, entire or slightly lobed, tandem, closely adjacent or at some distance from each other in middle of hindbody. Cirrus-sac well developed, with thick muscular wall, transverse or oblique, just anterior to ventral sucker, contains winding tubular seminal vesicle, pars prostatica and unarmed cirrus. Genital atrium present. Genital pore close to anterior margin of ventral sucker, anterolateral or slightly submedian, usually sinistral. Ovary spherical or subspherical, submedian or median, pretesticular, immediately posterior to ventral sucker or partly overlapping it. Elongate or tubular seminal receptacle and Laurer's canal present. Oötype and Mehlis' gland immediately postovarian. Uterus mainly intercaecal, fills most of hindbody, with many loops in well-developed ascending and descending limbs; ascending and descending limbs may be relatively well separated or overlapping. Eggs numerous. Vitellarium consists of small follicles in two lateral fields; posteriorly, fields may extend to posterior end of body or end slightly posterior to testes; anteriorly, fields may extend to midway between testes and ovary or to intestinal bifurcation; fields usually merge posteriorly. Excretory vesicle Y-shaped, with very long, wide stem and short or very short branches; stem may have numerous lateral diverticula; pore terminal. In oesophagus, stomach and intestine of snakes and freshwater turtles; Eurasia. Type-genus *Encyclometra* Baylis & Cannon, 1924.

## Key to genera

1. **Tegument without spines; oral sucker smaller than or similar in size to ventral sucker; cirrus-sac oriented transversely; vitelline fields reach posterior end of body, but do not extend anteriorly beyond level of posterior margin of ventral sucker** ..... ***Encyclometra* Baylis & Cannon, 1924. (Fig. 29.1)**
(Syns *Odhneria* Baer 1924 *nec* Travassos, 1921; *Paraplagiorchis* Dollfus, 1924; *Orthorchis* Mödlinger, 1925)

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**Diagnosis:** Body elongate, fusiform to lanceolate. Tegument unspined. Oral sucker smaller than ventral sucker or suckers of similar size. Intestinal caeca usually terminate near posterior end of body; exceptionally, one caecum distinctly shorter than other. Testes two, spherical or subspherical, entire or slightly lobed, tandem, closely adjacent or at some distance from each other, in middle of hindbody. Cirrus-sac oriented transversely, occasionally somewhat diagonal. Genital pore anterolateral to ventral sucker. Vitelline fields reach posterior end of body, but do not extend anteriorly beyond level of posterior margin of ventral sucker. Stem of excretory vesicle with numerous lateral diverticula. In oesophagus, stomach or intestine of snakes; Eurasia. Type-species *E. colubrimurorum* (Rudolphi, 1819) Baylis & Cannon, 1924.

**2. Tegument with small spines; oral sucker larger than ventral sucker; cirrus-sac oriented diagonally; vitelline fields extend from the level somewhat posterior to testes to level of intestinal bifurcation ..... *Encyclobrephus* Sinha, 1949. (Fig. 29.2)**

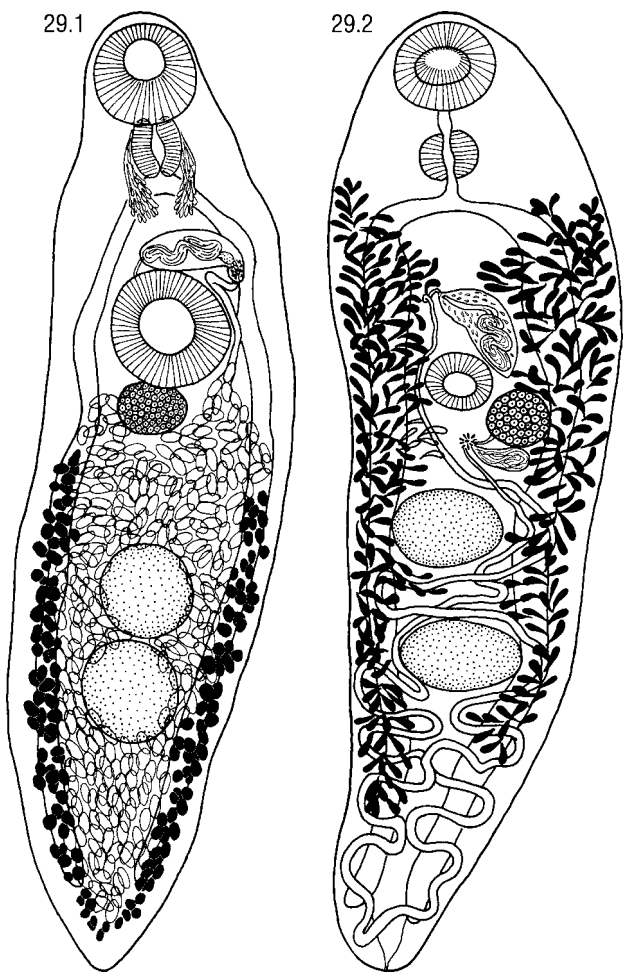



**Fig. 29.1.** *Encyclometra colubrimurorum* (Rudolphi, 1819). After Sharpilo (1976).
**Fig. 29.2.** *Encyclobrephus robustus* Sinha, 1949. After Sinha (1949).

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**Diagnosis:** Body elongate. Tegument spinous. Oral sucker larger than ventral sucker. Intestinal caeca terminate near posterior end of body. Testes two, entire, tandem, slightly elongate transversely, in middle of hindbody. Cirrus-sac oriented diagonally. Genital pore anterior to ventral sucker, submedian. Vitelline fields extend from level somewhat posterior to testes, to level of intestinal bifurcation. In intestine of freshwater turtles; Eurasia. Type-species *E. robustus* Sinha, 1949.

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# 30 Family Gekkonotrematidae Yamaguti, 1971

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## Introduction

The monotypic family Gekkonotrematidae Yamaguti, 1971 was erected without comment by Yamaguti (1971) for *Gekkonotrema postporum* Fischthal & Kuntz, 1967, a species and genus recorded only once from the intestine and gall-bladder of the gekkonid lizards *Lepidodactylus lugubris* and *Gymnodactylus pelagicus* on an island in the New Hebrides, south-west Pacific. Fischthal & Kuntz (1967) considered it to be an allocreadiid. Yamaguti (1971) also suggested that the family is related to the Allocreadiidae Looss, 1902, despite the presence of a spined tegument. The one unusual feature of the group is that the genital pore occurs in the hindbody just posterior to the ventral sucker. In some features, such as the spined tegument, follicular vitellarium and genital pore in the anterior part of the hindbody, it resembles the Mesotretidae Poche, 1926. The diet (insects) of the hosts of the two groups (gekkonid lizards and bats) is also similar, suggesting the likelihood of a similar life-cycle. Consequently, the Gekkonotrematidae is here treated with the plagiorchioids. In aspects of its morphology, it resembles two genera in South American snakes, the macroderid *Liophistrema* Artigas, Ruiz & Leão, 1943 (from the lungs) and the plagiorchiid *Opisthogonimus* Lühe, 1900 (from the mouth and oesophagus, sometimes intestine), especially in the position of the genital pore, but in these genera the uterus is mainly postovarian rather than mainly pre-ovarian. Until more information is available concerning a range of plagiorchioid groups, it seems pragmatic to retain the Gekkonotrematidae as a family within the Plagiorchioidea Lühe, 1901.

## Family Gekkonotrematidae Yamaguti, 1971

**Diagnosis:** Body medium-sized, elongate-fusiform, with gland-cells in parenchyma. Tegument covered with small spines. Oral sucker ventroterminal. Ventral sucker much smaller than oral sucker, at about 25–30% of body-length. Prepharynx and pharynx well developed and oesophagus very short, all surrounded by gland-cells. Intestinal bifurcation in about middle of forebody. Caeca two, long, pass directly posteriorly to end blindly very close to posterior extremity. Testes

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two, slightly obliquely tandem, contiguous or almost so, at about five-sixths of body-length, globular to oval. Cirrus-sac relatively small, curved, almost entirely in hindbody but may partly loop into region of ventral sucker, contains tubular or slightly saccular seminal vesicle, which may be somewhat bipartite, pars prostatica and small, protrusible cirrus. Genital atrium small, indistinct. Genital pore median, immediately posterior to ventral sucker. Ovary median to submedian, anterior to testes, at about two-thirds of body-length, globular to oval, smaller than testes. Laurer's canal present. Canalicular seminal receptacle present posterior to ovary. Rudimentary Juel's organ-like feature present (Yamaguti, 1971, called it Fischthal's organ). Uterus long, winds laterally between anterior testis and ventral sucker, crossing caeca; metraterm short, narrow, surrounded by gland-cells. Eggs operculate, reasonably large. Vitellarium follicular; follicles small, numerous (rod-shaped according to Yamaguti), in lateral fields between about middle of body and posterior extremity; fields confluent in post-testicular region and sometimes dorsally to testes (Yamaguti also says anterior to ovary), may be interrupted on one side at level of gonads. Excretory vesicle tubular, I-shaped, reaching testes (Yamaguti says to ovary, where it is enlarged); pore terminal. In intestine and gall-bladder of gekkonid lizards; New Hebrides. Type-genus *Gekkonotrema* Fischthal & Kuntz, 1967.

## Genus *Gekkonotrema* Fischthal & Kuntz, 1967 (Fig. 30.1)

**Diagnosis:** With characters of family. Type-species *G. postporum* Fischthal & Kuntz, 1967.

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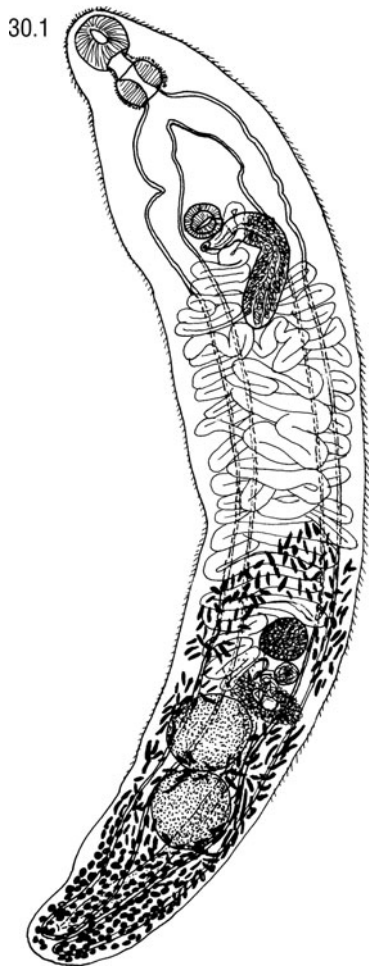



**Fig. 30.1.** *Gekkonotrema postporum* Fischthal & Kuntz, 1967. After Fischthal & Kuntz (1967) and Yamaguti (1971).

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# 31 Family Glypthelminthidae Cheng, 1959

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## Introduction

The Glypthelminthidae Cheng, 1959 currently includes one large genus, *Glypthelmins* Stafford, 1905, all members of which are intestinal parasites of amphibians. It was erected at subfamily level by Cheng (1959) and is here raised to full family status. The systematic position of *Glypthelmins* has always been unstable. It has been included in several different subfamilies of the Plagiorchiidae Lühe, 1901 (Baer, 1924; Mehra, 1937; Olsen, 1937; Skrjabin & Antipin, 1958a; Prudhoe & Bray, 1982), the Macroderoididae McMullen, 1937 (Odening, 1964c; Sullivan & Byrd, 1970; Yamaguti, 1971) or the Brachycoeliidae Looss, 1899 (Caballero, 1938; Dollfus, 1950; Cheng, 1959). The taxonomic history and both nomenclatural and systematic problems associated with the genus have been described by many authors (e.g. Skrjabin & Antipin, 1958a; Byrd & Maples, 1963; Prudhoe & Bray, 1982; Razo-Mendivil *et al.*, 2006). Although the general morphology of *Glypthelmins* spp. is similar to that of typical plagiorchiids, some features of its organization and life-cycle suggest that they do not belong to the Plagiorchiidae. Unlike plagiorchiids, *Glypthelmins* possesses an I-shaped excretory vesicle. At the same time, the topology of the internal organs and host range separate this genus from the Macroderoididae. *Glypthelmins* spp. are characterized by a rather unique life-cycle. Their metacercariae encyst beneath the skin epidermis of their amphibian hosts and infection occurs when amphibians ingest cast skin. A series of recent molecular phylogenetic studies (Tkach *et al.*, 2001c; Olson *et al.*, 2003; Razo-Mendivil *et al.*, 2006) have clearly demonstrated that *Glypthelmins* is not closely related to typical plagiorchiids, macroderoidids or brachycoeliids and represents a separate clade closest to the Haematoloechidae Freitas & Lent, 1939. *Glypthelmins* spp. differ substantially from the Haematoloechidae, however, in the position of the genital pore, the shape of the excretory vesicle, the organization of the terminal parts of the male reproductive system and the life-cycle (members of the Haematoloechidae use aquatic arthropods as intermediate hosts). All this suggests that *Glypthelmins* represents an independent family-level lineage within the Plagiorchioidea. Razo-Mendivil *et al.* (2006) have, however, stressed that it is unclear whether all currently recognized species of *Glypthelmins* form a monophyletic group.

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*Choledocystis* Pereira & Cuocolo, 1941 was established for *C. eucharis* Pereira & Cuocolo, 1941, but was later considered as a synonym of *Glypthelmins* (e.g. Yamaguti, 1971). On the basis of the morphological examination of numerous specimens, SEM data and molecular phylogenetic analysis, Razo-Mendivil *et al*. (2006) have resurrected *Choledocystis* and suggested that it should include between five and seven species previously attributed to *Glypthelmins*. Among other features, they demonstrated that species of *Choledocystis* have a Y-shaped excretory vesicle. In their phylogenetic analysis, *C. hepaticus* (Lutz, 1928) clustered basally to the reniferid clade. Until more is known about the phylogenetic affinities of *Choledocystis* and particularly its type-species, the genus is here allocated to the polyphyletic Plagiorchiidae.

*Haplometrana* Lucker, 1931 has been considered an independent genus by many authors (e.g. Olsen, 1937; Waitz, 1959; Yamaguti, 1971), but was synonymized with *Glypthelmins* by O'Grady (1987). In the molecular phylogenetic study of Razo-Mendivil *et al*. (2006), *G. intestinalis* (Lucker, 1931), the type-species of *Haplometrana*, is nested among other *Glypthelmins*, thus confirming the opinion of O'Grady (1987), which is also accepted here.

*Hylotrema* Sullivan in Schell, 1985 was proposed in a PhD dissertation (Sullivan, 1973) with *H. pennsylvaniensis* [*sic*] (Cheng, 1961) as the type-species, but was not formally published until it was included in Schell's (1985) book. No other workers have recognized this genus. The molecular phylogenetic analysis of Razo-Mendivil *et al*. (2006) placed *G. pennsylvaniensis* among the typical *Glypthelmins* species. Thus, *Hylotrema* is considered here a synonym of *Glypthelmins*.

*Margeana* Cort, 1919 was considered by Miller (1930) to be a synonym of *Glypthelmins*, but was later reinstated as a separate genus by Cheng (1959), only to be synonymized again by Byrd & Maples (1963). This latter action was supported by subsequent authors (Yamaguti, 1971; Sullivan, 1976) and is accepted in this volume.

*Rauschiella* Babero, 1951 was established for *R. tineri* Babero, 1951 on the basis of several morphological characters, among them a Y-shaped excretory vesicle (Babero, 1951). While most authors considered *Rauschiella* as a separate genus, Brooks & McLennan (1993) placed it in synonymy with *Glypthelmins*. Razo-Mendivil *et al*. (2006) resurrected it based on morphological and molecular evidence, and provisionally included 12 to 14 species in this genus. The validity of *Rauschiella* is supported here; on the other hand, its familial allocation remains unclear. In this volume it is included in the Macroderoididae (see Font & Lotz, Chapter 34, this volume).

*Reynoldstrema* Cheng, 1959 was established for *Glypthelmins africana* Dollfus, 1950 by Cheng (1959). This species shares many morphological features, such as the body shape, the distribution of the vitelline follicles, the relative position of the reproductive organs, the shape of the seminal vesicle and the presence of a seminal receptacle, with both *Glypthelmins* and *Plagiorchis* Lühe, 1899, being somewhat closer to the latter. Unfortunately, available descriptions of *G. africana* do not provide information about the shape of the excretory vesicle. Yamaguti (1971) placed it among synonyms of *Plagiorchis*. However, the host range of *G. africana* (anuran amphibians) is highly atypical for *Plagiorchis*. Therefore, we consider *Reynoldstrema* a synonym of *Glypthelmins* until data on the excretory system and/or biology of *G. africana* are available.

*Repandum* Byrd & Maples, 1964 was synonymized with *Glypthelmins* by Yamaguti (1971), who concluded that the diagnoses of the two genera are essentially the same. However, earlier, Babero (1951) transferred *G. repandum* (Rudolphi, 1819) to his newly created genus *Rauschiella* and Cheng (1959) to *Margeana* (see above). Sullivan (1977) supported Babero's taxonomic decision, which is followed here. Hence, *Repandum* is considered here a synonym of *Rauschiella* rather than of *Glypthelmins* (see Font & Lotz, Chapter 34, this volume).

The family-group name was first proposed by Cheng (1959) as Glypthelminae Cheng, 1959, which was subsequently corrected by Yamaguti (1971) to Glypthelminthinae.

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## Family Glypthelminthidae Cheng, 1959

(Syns Glypthelminae Cheng, 1959; Glypthelminthinae Yamaguti, 1971)

**Diagnosis**: Body elongate or cylindrical. Tegument armed with small, serrate, scale-like spines extending from anterior end to varying levels of hindbody. Oral sucker subterminal, larger than ventral sucker. Ventral sucker in anterior or middle third of body. Prepharynx short. Pharynx well developed, sometimes wider than ventral sucker. Median glands around pharynx and oesophagus. Pharyngeal glands present or absent. Intestinal bifurcation about halfway between pharynx and ventral sucker. Caeca extend to near posterior end of body, but do not reach it. Testes in hindbody, intercaecal or sometimes overlapping caeca, spherical to oval, entire, usually symmetrical or oblique, occasionally tandem. Cirrus-sac straight or curved, usually extending posteriorly beyond ventral sucker, contains bipartite seminal vesicle and coiled cirrus. Genital pore median, in forebody. Ovary submedian, spherical to oval, entire, sinistral and anterior to testes, sometimes close to or overlapping ventral sucker. Seminal receptacle small, usually situated posterior to ovary. Oötype, Laurer's canal and Mehlis' gland present. Uterus extends to posterior end of body, completely filling postcaecal space; transverse uterine loops usually intercaecal, occasionally overlapping caeca or expanding into extracaecal space; occasionally, uterine loops occupy pretesticular region. Metraterm muscular, approximately as long as cirrus-sac, dorsal to cirrus-sac. Eggs operculate. Vitellarium consists of numerous follicles forming extracaecal fields, sometimes expanding into intercaecal space; anterior margin of vitelline fields at different levels between ovary and pharynx; posteriorly vitelline follicles usually extend beyond posterior margin of testes, but do not reach posterior end of body; fields confluent or not dorsal to intestinal bifurcation, cirrus-sac and testes. Excretory vesicle I-shaped, reaches posterior margin of testes; pore terminal. Protonephridial formula 2 [(3 + 3 + 3) + (3 + 3 + 3)] = 36. In intestine of amphibians; Palaearctic, Oriental, Ethiopian, Nearctic and Neotropical regions. Type-genus *Glypthelmins* Stafford, 1905.

### Genus *Glypthelmins* Stafford, 1905 (Figs 31.1–31.4)

(Syns *Margeana* Cort, 1919; *Haplometrana* Lucker, 1931; *Reynoldstrema* Cheng, 1959; *Hylotrema* Sullivan in Schell, 1985)

**Diagnosis:** With characters of the family. Type-species *Glypthelmins quieta* (Stafford, 1900).

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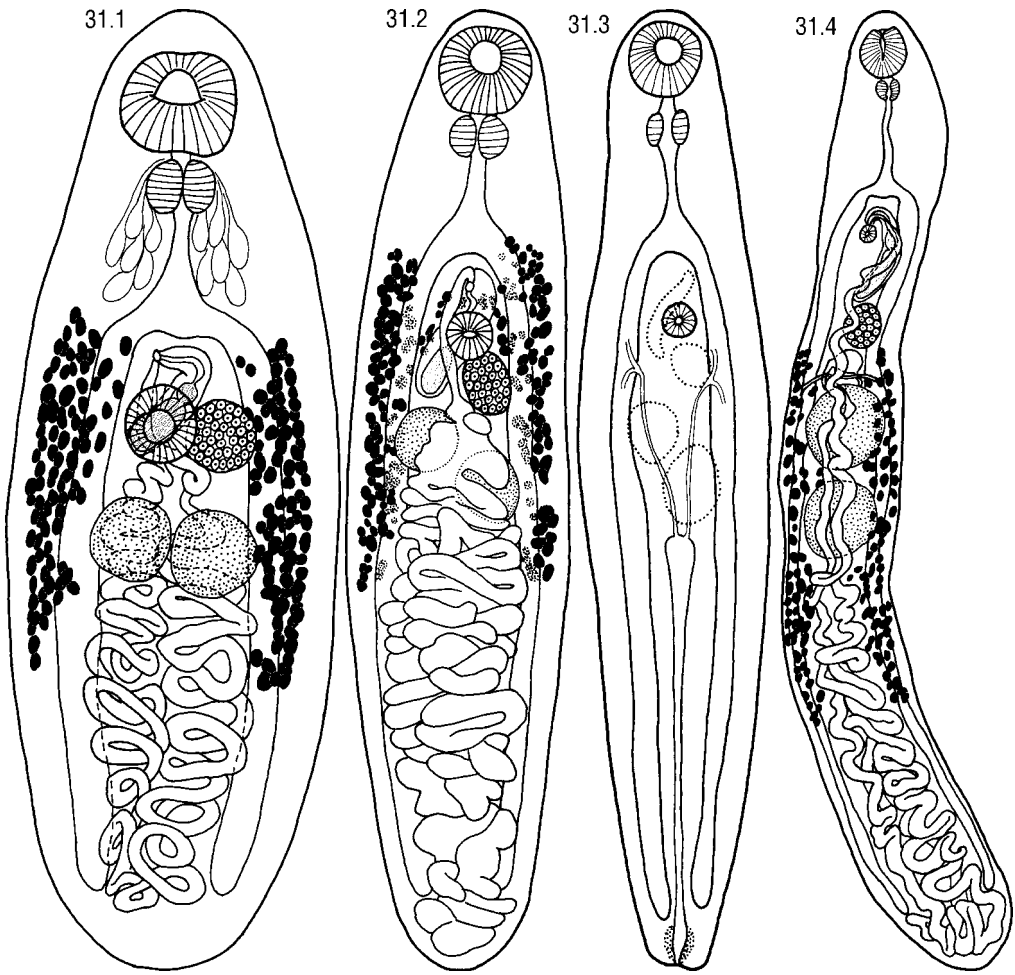



**Fig. 31.1.** *Glypthelmins quieta* (Stafford, 1900). After Prudhoe & Bray (1982).
**Fig. 31.2.** *Glypthelmins tuxtlasensis* Razo-Mendivil, Leon-Regagnon & Pérez-Ponce de León, 2006. After Razo-Mendivil *et al.* (2006).
**Fig. 31.3.** *Glypthelmins facioi* Brenes Madrigal, Arroyo Sancho, Jimenez-Quiros & Delgado Flores, 1959, ventral view showing the shape of excretory vesicle. After Sullivan (1976).
**Fig. 31.4.** *Glypthelmins intestinalis* (Lucker, 1931) After Prudhoe & Bray (1982).

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# 32 Family Haematoloechidae Freitas & Lent, 1939

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## Introduction

The Haematoloechidae Freitas & Lent, 1939[1] is a compact, but cosmopolitan, family of digeneans, which is quite well characterized both by its morphological features (e.g. the median genital pore at the level of the pharynx or oesophagus, the vitelline follicles usually arranged in rosettes or grape-like clusters) and by its site of infection and definitive hosts, the lungs of anuran amphibians. It has received great attention in the literature and has a complex taxonomic history. The first formally named member of the family was *Distomum variegatum* Rudolphi, 1819 (now *Haematoloechus variegatus*). The correct name of the type-genus of the family has been controversial. Looss (1899) established the genus *Haematoloechus* Looss, 1899 for *D. variegatum*, which he split into three species; later, however, he (Looss, 1902) decided to substitute the name, which he believed was pre-occupied by *Haematoloecha* Stäl, 1814, with *Pneumonoeces* Looss, 1902. Since then, some authors have agreed with this name change, while the majority have continued to use the name *Haematoloechus*. Ingles (1932) discussed this problem and decided that the existing International Rules of Zoological Nomenclature (which later became the International Code of Zoological Nomenclature) supported the use of the original generic name of *Haematoloechus*. Although, even after that, some authors (e.g. Skrjabin & Antipin, 1962a) have still used the name *Pneumonoeces*, I feel that nomenclatural stability would be best served by using the name *Haematoloechus*, and this is consistent with recent versions of the ICZN.

The family-group name was first proposed by Mehra (1937) as the subfamily Pneumonoecinae Mehra, 1937 with the type-genus *Pneumonoeces* (= *Haematoloechus*). This was renamed Haematoloecinae [*sic*] Freitas & Lent, 1939 by Freitas & Lent (1939). By applying ICZN Article 40.2.1, the name Haematoloechidae Freitas & Lent, 1939, is used here, as I consider that it has had 'prevailing usage'. The genera included in the Haematoloechidae in this chapter have been

[1] Recommendation (40A) of the IZCN is that, in cases where the family-group name has been replaced, the date of its priority should be given in parentheses, i.e. in this case, Haematoloechidae Freitas & Lent, 1939 (1937). Although we note this priority here, it is believed that its inclusion would be confusing to most users.

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placed in various subfamilies of the Plagiorchiidae Lühe, 1901 by various authors, e.g. Pneumonoecinae (see Mehra, 1937; Skrjabin & Antipin, 1962a) or Saphederatinae Baer, 1924 (see Baer, 1924). In the more recent literature, however, it is commonly accepted that this group represents a separate family within the Plagiorchioidea Lühe, 1901 (see Odening, 1964c; Yamaguti, 1971; Sharpilo & Iskova, 1989). This viewpoint is supported by molecular phylogenetic analysis based on ribosomal DNA sequences (Tkach *et al*., 2000a, 2001b).

The taxonomy of almost all genera included in this group, either now or in the past, has been a subject of disagreement between researchers. Some of these problems are addressed below.

*Pneumobites* Ward, 1917 was erected by Ward (1917) for two North American species, *P. longiplexus* (Stafford, 1902) and *P. breviplexus* (Stafford, 1902). However, the morphological criteria used for separation of this genus were clearly inadequate and it has not been recognized by subsequent authors.

*Ostiolum* Pratt, 1903 was erected by Pratt (1903) to encompass haematoloechids lacking extracaecal uterine loops. The majority of haematoloechids possess extracaecal uterine loops that pass from the posterior end part of the way along the lateral margins of the body, remaining close to and running parallel to the lateral margin and laterally to the caeca. Since then, *Ostiolum* has been recognized as a separate genus by some authors (e.g. Travassos & Darriba, 1930; Sudarikov, 1950; Odening, 1960b; Skrjabin & Antipin, 1962a) or regarded as a synonym of *Haematoloechus* by others (e.g. Yamaguti, 1971; Kennedy, 1981). Alternatively, it has also been considered a subgenus of *Haematoloechus* (e.g. Mehra, 1937; Odening, 1958). Recent molecular phylogenetic studies (Snyder & Tkach, 2001; León-Règagnon & Brooks, 2003) have confirmed the views of those authors who did not recognize it. Molecular analysis has convincingly demonstrated that, for instance, *H. complexus* (Seely, 1906) and *H. medioplexus* Stafford, 1902, which both lack extracaecal uterine loops, belong to different evolutionary lineages within *Haematoloechus*, each containing species with and without extracaecal uterine loops. These lineages differ in their intermediate host-ranges and the way in which cercariae penetrate the second intermediate hosts. Thus, the presence or absence of the extracaecal uterine loops can be considered as a good character for distinguishing species of haematoloechids but is not valid as a diagnostic feature at the generic level. Therefore, *Ostiolum* is here considered a synonym of *Haematoloechus*.

The subgenus *Anomolecithus* Odening, 1958 was erected by Odening (1958) for two species, *Haematoloechus asper* Looss, 1899 and *H. nanchangensis* Hsiung, 1934. Skrjabin & Antipin (1962a) considered the criteria used by Odening (1958) for the recognition of this subgenus, particularly the egg-size and shape of the vitelline follicles, insufficient and thus did not recognize it. The recent molecular phylogenetic analysis by Snyder & Tkach (2001) included *H. asper* within *Haematoloechus*, corroborating the view of Skrjabin & Antipin (1962a); hence, *Anomolecithus* is considered here as a synonym of *Haematoloechus*.

*Ostioloides* Odening, 1960 was erected by Odening (1960b) for *Haplometroides rappiae* Szidat, 1932 described from an African frog, *Rappia concolor*. It was included in *Haematoloechus* by Yamaguti (1958b). Skrjabin & Antipin (1962a) rejected Odening's views and considered the original generic allocation by Szidat (1932) to be correct. Later, Fischthal & Thomas (1968) recognized the validity of *Ostioloides*, but included it in the Plagiorchiidae; at the same time, they recognized the Haematoloechidae as a separate family. The validity of *Ostioloides* and its position within the Haematoloechidae was supported by Yamaguti (1971). I agree with the authors who considered *Ostioloides* a valid genus, as *O. rappiae* differs from *Haplometroides* Odhner, 1911 in some morphological features, host-range and geographical distribution. However, placing *Ostioloides* in the Haematoloechidae cannot be accepted. It differs from members of that family in several important morphological features, such as the relatively short caeca, vitelline follicles

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arranged in almost uninterrupted lateral fields (in haematoloechids the follicles tend to be in clusters), a typical plagiorchiid cirrus-sac, and the position of the genital pore at a substantial distance from the pharynx. None of these characters is found in haematoloechids. Thus, I agree with Fischthal & Thomas (1968) and *Ostioloides* is considered here a member of the Plagiorchiidae.

*Metahaematoloechus* Yamaguti, 1971 was established by Yamaguti (1971) for *Haematoloechus exoterorchis* Rees, 1964 on the basis of the unusual extracaecal position of the testes. Recent molecular analysis by León-Règagnon & Brooks (2003) has supported Yamaguti (1971), and thus it is here considered as valid. Maeder (1973) also established a new genus, *Parahaematoloechus* Maeder 1973, for *H. exoterorchis*, apparently being unaware of Yamaguti's (1971) actions. Thus, *Parahaematoloechus* becomes a junior synonym of *Metahaematoloechus*.

*Skrjabinoeces* Sudarikov, 1950 was established for forms in which the vitelline follicles do not extend posteriorly beyond the level of the testes or the anterior limit of the extracaecal uterine loops (Sudarikov, 1950). Some authors (e.g. Skrjabin & Antipin, 1962a; Sharpilo & Iskova, 1989) have considered *Skrjabinoeces* a separate genus, while others (Odening, 1958; Yamaguti, 1971) have placed it in *Haematoloechus* as a subgenus. However, besides the unusual distribution of the vitelline follicles, *Skrjabinoeces* differs substantially from members of *Haematoloechus* in cercarial characters, such as the shape of the stylet (straight without widening at the anterior end) and, more significantly, the lack of a tail finfold, which is present in all *Haematoloechus* cercariae described so far. Moreover, available (unpublished) molecular data place *Skrjabinoeces* on a branch separate from numerous members of *Haematoloechus* and thus support its status as a valid genus.

*Neohaematoloechus* Odening 1960 includes forms from South America that lack a ventral sucker as adults (Odening, 1960b). It should be noted that the ventral sucker in several *Haematoloechus* species is extremely weakly developed and almost indistinguishable in adult worms. Members of *Neohaematoloechus* do not possess any additional characters that differentiate them from *Haematoloechus*. Thus, I anticipate that, when representatives of *Neohaematoloechus* are included in a molecular phylogenetic analysis, this genus may well be synonymized with *Haematoloechus*. At this point, however, the generic status of *Neohaematoloechus* is preserved until its systematic position can be verified using additional evidence.

## Family Haematoloechidae Freitas & Lent, 1939

(Syns Pneumonoecidae Mehra, 1937; Haematoloechidae Odening, 1964)

**Diagnosis:** Body elongate or elongate-oval, somewhat tapered anteriorly. Tegument armed with spines or not. Oral sucker well developed, subterminal. Ventral sucker pre-equatorial, equatorial or absent. Prepharynx usually indistinct. Pharynx well developed, sometimes relatively large. Oesophagus short or apparently absent. Intestinal bifurcation in anterior forebody. Caeca long, blind, reaching close to posterior end of body. Testes two, entire or lobed, postequatorial, usually diagonal, more rarely almost symmetrical or tandem; usually intercaecal, exceptionally extracaecal. Cirrus-sac narrow, median, cylindrical, may be very long, frequently winding, reaches level of posterior part of ventral sucker or beyond. Genital pore median, at level of pharynx or oesophagus. Ovary entire or lobed, near ventral sucker, pretesticular, slightly separated from testes. Seminal receptacle large, may be much larger than ovary. Laurer's canal absent. Uterine loops fill entire hindbody; descending and ascending limbs pass between testes; several loops extend into forebody; extracaecal uterine loops present or absent. Eggs very numerous, embryonated. Vitellarium follicular, follicles usually arranged in rosettes or grape-like clusters along caeca for greater part of length, or entire length; exceptionally may be confined to pretesticular region. Excretory vesicle

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Y-shaped; arms at least as long as stem; excretory flame-cell formula 2[(3 + 3 + 3) + (3 + 3 + 3)] = 36; pore terminal. In lungs of anuran amphibians; cosmopolitan. Type-genus *Haematoloechus* Looss, 1899.

## Key to genera

**1a. Vitellarium extends into post-testicular region ..... 2.**
**1b. Vitellarium does not extend into post-testicular region .....**
**..... *Skrjabinoeces* Sudarikov, 1950. (Fig. 32.1)**

**Diagnosis:** Ventral sucker smaller than oral sucker, in posterior part of anterior half of body. Testes diagonal or nearly symmetrical, intercaecal. Ovary overlapping ventral sucker or lateral to it. Uterus with extracaecal loops that do not extend anteriorly beyond posterior margin of anterior testis. Vitellarium consists of large follicles, not forming isolated bunches, not extending into post-testicular region; fields may be confluent anterior to ventral sucker. Europe, Asia. Type-species *S. similis* (Looss, 1899) Sudarikov, 1950.

**2a. Testes intercaecal, entire or somewhat lobed ..... 3.**
**2b. Testes extracaecal, deeply lobed ..... *Metahaematoloechus* Yamaguti, 1971. (Fig. 32.2)**
(Syn. *Parahaematoloechus* Maeder, 1973)

**Diagnosis:** Ventral sucker slightly larger than oral. Testes elongate and deeply lobed, symmetrical or slightly oblique, extracaecal in mid-region of body. Ovary more or less median, overlaps ventral sucker; posterior margin of ovary at level of anterior margin of testes. Uterus with pair of short anteriorly directed extracaecal loops reaching posterior groups of vitelline follicles on either side of the body. Vitelline follicles in three paired, lateral, extracaecal groups of rosettes, two anterior and one posterior; anterior groups arranged symmetrically and dorsally to intestinal caeca, extend from about level of intestinal bifurcation to level of ovary; posterior group just posterior to testes. Africa. Type-species *M. exoterorchis* (Rees, 1964) Yamaguti, 1971.

**3a. Ventral sucker present in adults ..... *Haematoloechus* Looss, 1899. (Figs 32.3–32.5)**
(Syns *Pneumonoeces* Looss, 1902; *Ostiolum* Pratt, 1903; *Pneumobites* Ward, 1917; *Anomolecithus* Odening, 1958)

**Diagnosis:** Body elongate or elongate-oval. Tegument spinous or not. Oral sucker subterminal, usually larger than ventral. Ventral sucker in anterior or middle third of body. Testes oblique or nearly symmetrical, intercaecal, in middle region of body or just posterior. Ovary near to, or overlapped by, ventral sucker. Vitelline follicles in form of rosettes, grape-like clusters or in irregular pattern, extend posteriorly past level of testes. Uterine loops occupy most of hindbody and intercaecal space in forebody; extracaecal loops present or absent. Vitelline follicles in the form of rosettes, or in grape-like clusters or in irregular pattern, extend posteriorly beyond level of testes. Cosmopolitan. Type-species *H. variegatus* (Rudolphi, 1819) Looss, 1899.

**3b. Ventral sucker absent in adults ..... *Neohaematoloechus* Odening 1960. (Fig. 32.6)**

**Diagnosis:** Ventral sucker absent in adults. Testes intercaecal, oblique or nearly symmetrical, in mid-region of body. Ovary at border between anterior and middle thirds of body. Extracaecal uterine loops present. Vitelline follicles form grape-like clusters or irregular in pattern, dispersed between intestinal bifurcation and posterior end of body; lateral fields may be confluent in preovarian and post-testicular regions. South America. Type-species *N. neivai* (Travassos & Artigas, 1927) Odening, 1960.

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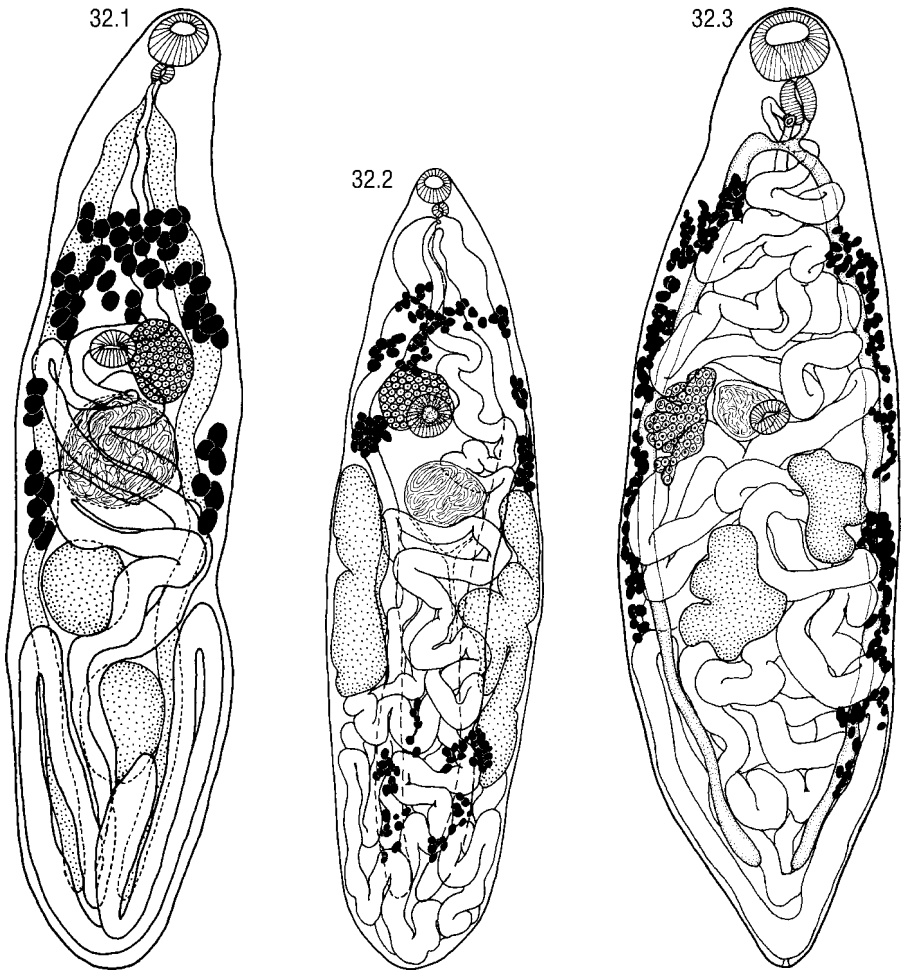



**Fig. 32.1.** *Skrjabinoeces similis* (Looss, 1899). After Sharpilo & Iskova (1989).
**Fig. 32.2.** *Metahaematoloechus exoterorchis* (Rees, 1964). Original.
**Fig. 32.3.** *Haematoloechus johnsoni* Bourgat, 1977. Original.

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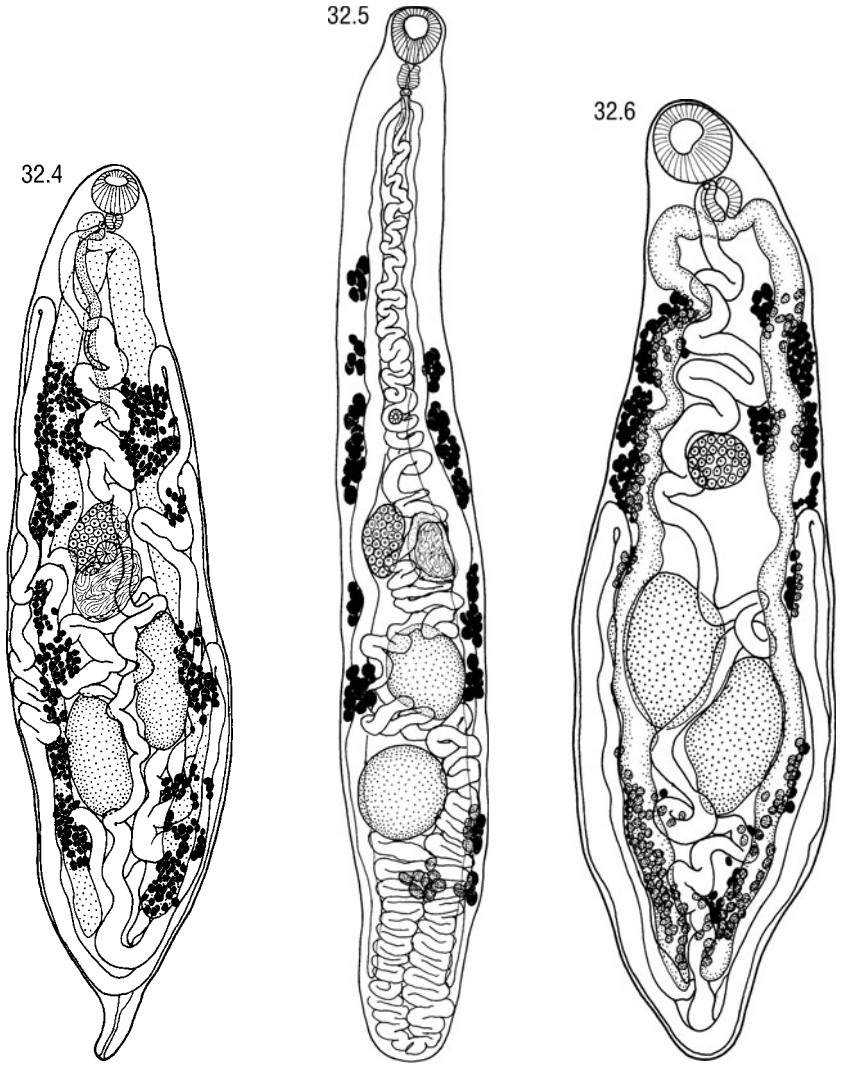



**Fig. 32.4.** *Haematoloechus micrurus* Rees, 1964. Original.
**Fig. 32.5.** *Haematoloechus medioplexus* (Stafford, 1902). Original.
**Fig. 32.6.** *Neohaematoloechus neivai* (Travassos & Artigas, 1927). Original.

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# 33 Family Leptophallidae Dayal, 1938

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## Introduction

This is a small group of plagiorchioid digeneans uniting several genera found as adults only in snakes and possessing an external seminal vesicle. The four genera included here in the family Leptophallidae Dayal, 1938 have not been considered in the literature to be close relatives and have been frequently allocated to different families or even superfamilies. Species of *Leptophallus* Lühe, 1909, *Metaleptophallus* Yamaguti, 1958 and *Paralepoderma* Dollfus, 1950, all parasites of different parts of the digestive tract of snakes, have traditionally been considered by most authors as a distinct group of closely related genera belonging to the family Plagiorchiidae Lühe, 1901and subfamily Leptophallinae Dayal, 1938 (see Skrjabin, 1971; Sharpilo & Iskova, 1989) or as a tribe, the Leptophallini Dayal, 1938, of the subfamily Plagiorchiinae Lühe, 1901 (see Odening, 1960c, 1964b). *Paralepoderma* has also been allocated by Yamaguti (1971) to the subfamily Styphlodorinae Dollfus, 1937. Contrary to the above situation, *Macrodera* Looss, 1899, which includes lung parasites of snakes, is a taxon with unclear phylogenetic relationships and, consequently, has had a highly unstable systematic position. During recent decades, different authors have allocated it to the family Ochetosomatidae Leão, 1944, as the type-genus of the subfamily Macroderinae Goodman, 1952 (see Goodman, 1952, 1959; Odening, 1964b; Dobrovol'ski, 1971; Sharpilo & Iskova, 1989), which was raised to full family status with four subfamilies by Yamaguti (1971).

Molecular analyses and comparisons of cercarial morphology by Tkach *et al.* (1999, 2000a, 2001b) have, however, demonstrated that these four genera are very closely related and form a compact and distinct family-group within the Plagiorchioidea Lühe, 1901. Moreover, in a comparative study of cercarial chaetotaxy, Grabda-Kazubska & Bayssade-Dufour (1999) demonstrated a great similarity in the distribution of sensilla in all species of these four genera that have been examined, which suggests a close affinity between them. A most striking morphological feature of the adult stages, uniting all four genera and strongly suggesting their close relationship, is the presence of an external seminal vesicle (Figs 33.1–33.8), a feature that has probably evolved independently in several groups of digeneans. Thus, separation of these genera into different families cannot be accepted and they are considered here as a single family, the Leptophallidae. This name was first proposed by Dayal (1938) for the subfamily Leptophallinae within the Plagiorchiidae, based

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primarily on the presence of the external seminal vesicle. Along with *Leptophallus*, Dayal (1938) included in the Leptophallinae three other, obviously unrelated, genera, namely *Nizamia* Dayal, 1938, *Ganada* Chatterji, 1933 and *Neoganada* Dayal, 1938 (all three were later synonymized with the orientocreadiid genus *Orientocreadium* Tubangui, 1931; see Jones & Bray, Chapter 40, this volume). Dayal (1938) did not designate a type-genus for this subfamily, but it must be *Leptophallus*. The name Leptophallinae Dayal, 1938 clearly has priority over the Macroderinae Goodman, 1952, which, along with the Macroderidae Goodman, 1952, becomes a synonym of the Leptophallidae. Consequently, the systematic position of all the other taxa included by Yamaguti (1971) in the Macroderidae needs to be revised; in this volume, most of them are considered to be members of the Plagiorchiidae. New morphological, life-cycle and molecular data are necessary to adequately address these problems. Some of the digeneans (particularly *Bieria* Leão, 1946) from the lungs of South American snakes are very similar to *Macrodera* in their general body-plan. Therefore, I anticipate that in future the Leptophallidae may be expanded, but at present there are not enough data to justify such taxonomic decisions.

Species of *Leptophallus* and *Metaleptophallus* inhabiting the oesophagus and mouth of snakes are so similar to each other in size and general morphology that this has led some researchers to propose their synonymy (Fischthal & Kuntz, 1963; Sharpilo & Iskova, 1989; Tkach *et al*., 1999). At present, however, I prefer to consider them as independent genera on the basis of the good morphological characters used to differentiate them. *Paralepoderma* differs from other members of the Leptophallidae in having a compact body and very muscular suckers, somewhat similar to some other completely unrelated digenean taxa parasitic in the cloaca of snakes and birds, such as *Leucochloridium* Carus, 1835 and *Travtrema* Pereira, 1929. Thus, these features are probably determined by the site in the definitive host. Conversely, *Macrodera*, which is a lung parasite, has a very elongate slender body with both suckers in its anterior region, followed by a 'neck' and enlarged posterior part of the body mainly filled by the uterus and possessing a weak musculature. The number of protonephridia in such a relatively large worm as *Macrodera* remains the same as in the small representatives of the other three genera. Thus, this family represents an excellent example of radiation associated with colonization of different sites within a host.

*Paralepoderma rameswaramensis* Chattopadhyaya, 1970 was described from the intestine of a marine turtle *Chelone mydas* in India (Chattopadhyaya, 1970b). In my opinion, this species does not belong to *Paralepoderma* due to some substantial morphological discrepancies, such as the lack of an external seminal vesicle, and the presence of short caeca and of a muscular, spined cirrus, which are not leptophallid features. The host and site of *P. rameswaramensis* also make its close affinity with *Paralepoderma* highly unlikely. It is considered here to be *incertae sedis*.

## Family Leptophallidae Dayal, 1938

(Syns Leptophallinae Dayal, 1938; Macroderinae Goodman, 1952; Macroderidae Goodman, 1952)

**Diagnosis:** Body oval, elongate or very elongate. Tegument covered with spines. Oral sucker subterminal. Ventral sucker usually in mid-region of body, occasionally in anterior region of body close to oral sucker. Both suckers relatively large. Prepharynx usually not observed. Pharynx present, relatively small. Oesophagus relatively short, sometimes almost indistinct. Intestinal bifurcation in forebody. Caeca blind, may terminate at different levels, from just posterior to ventral sucker to almost reaching posterior extremity of body. Testes two, posterior to ventral sucker, symmetrical or diagonal. External seminal vesicle present, may be short to very long, extending

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almost twice diameter of ventral sucker into hindbody. Cirrus-sac in forebody, contains internal seminal vesicle and prostatic glands. Genital pore median or slightly submedian, at or short distance from anterior margin of ventral sucker, always postbifurcal. Ovary round or oval, pretesticular, near lateral or posterior margin of ventral sucker, but may be distant from ventral sucker, in middle of body. Seminal receptacle present or apparently absent. Laurer's canal present. Uterus almost entirely filling hindbody. Eggs numerous. Vitellarium forms two lateral groups of follicles in shoulder region, at ventral sucker level or just posterior to ventral sucker, alternatively in two narrow interrupted marginal groups on both sides of hindbody. Excretory vesicle Y-shaped; pore terminal. In digestive tract and lungs of snakes; Europe, Asia, North Africa. Type-genus *Leptophallus* Lühe, 1909.

## Key to genera

**1a. Body oval or slightly elongate; ovary close to ventral sucker ..... 2.**
**1b. Body very elongate; ovary at substantial distance posterior to ventral sucker ..... ..... *Macrodera* Looss, 1899 (Figs 33.1, 33.2)**
(Syn. *Saphedera* Looss, 1902)

**Diagnosis:** Body very elongate, with suckers close to each other in slightly widened oval anterior region followed by narrow region and cylindrical hindbody. Oral sucker larger or smaller than ventral sucker. Oesophagus short or indistinct. Caeca reach close to posterior extremity of body. Testes almost tandem at two-thirds of body-length. External seminal vesicle extends deep into hindbody. Ovary distant from ventral sucker, in middle of body. Seminal receptacle apparently absent. Uterus extensive, entirely filling hindbody. Vitellarium in two narrow, interrupted marginal fields on either side of mid-region of hindbody. In lungs of snakes; Europe, Asia. Type-species *M. longicollis* (Abildgaard, 1788) Looss, 1899.

**2a. Vitellarium in two lateral fields of follicles (may be confluent) in forebody ..... ..... *Leptophallus* Lühe, 1909. (Figs 33.3, 33.4)**

**Diagnosis:** Body small, oval or slightly elongate. Oral sucker somewhat larger than ventral sucker. Ventral sucker in middle of body. Oesophagus very short. Caeca terminate somewhat posteriorly to testes, far from posterior extremity. Testes symmetrical, just posterior to ventral sucker. External seminal vesicle not extending posteriorly further than middle of ventral sucker. Ovary dextral at level of ventral sucker or slightly anterolateral or posterolateral to it. Seminal receptacle present. Uterus almost entirely fills hindbody. Vitellarium in two lateral fields of follicles (may be confluent) in forebody. In oesophagus and mouth cavity of snakes; Europe, Asia and Africa. Type-species *L. nigrovenosus* (Bellingham, 1844) Lühe, 1909.

**2b. Vitellarium in two compact lateral clusters of follicles at level of or just posterior to ventral sucker ..... 3.**

**3a. Vitellarium in two compact lateral clusters on either side of ventral sucker; testes symmetrical or sub-symmetrical; caeca reach posterior extremity ..... ..... *Paralepoderma* Dollfus, 1950. (Figs 33.5, 33.6)**

**Diagnosis:** Body small, oval. Suckers relatively large and very muscular. Oral sucker somewhat larger than ventral sucker. Ventral sucker in middle of body. Oesophagus indistinct or very short. Caeca reach posterior extremity. Testes symmetrical or sub-symmetrical. External seminal vesicle

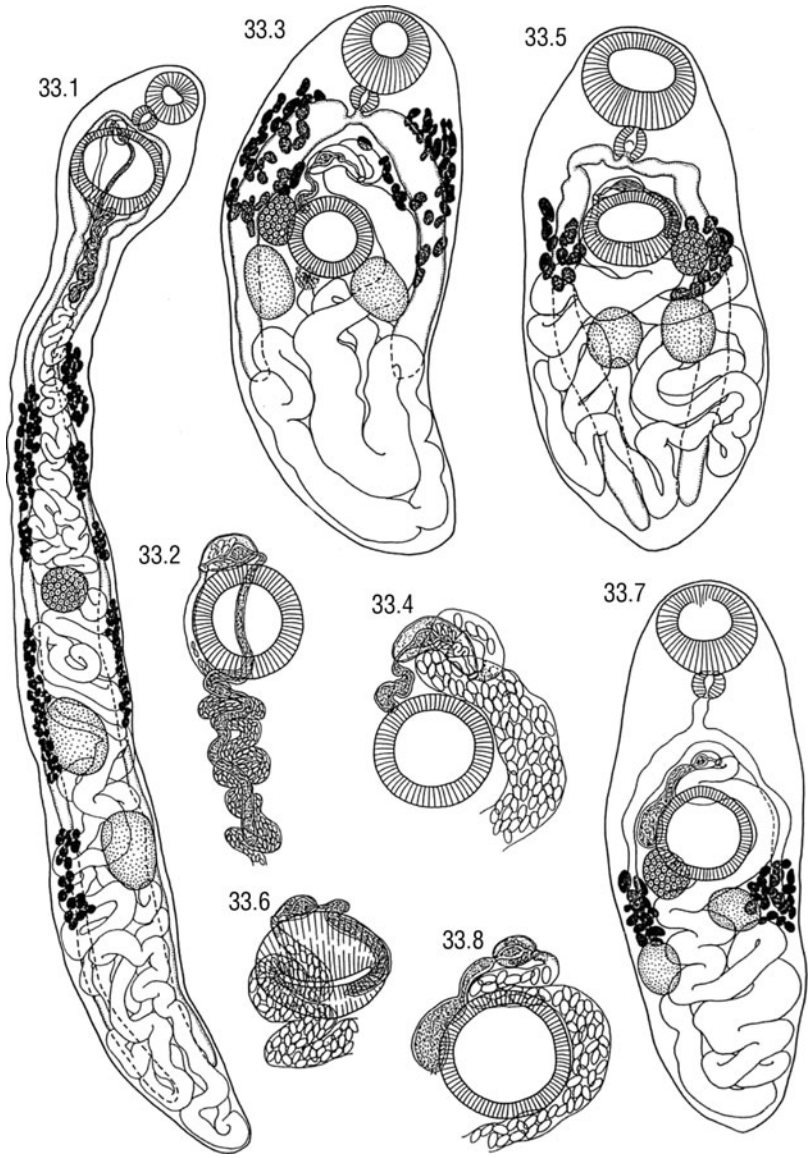
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does not extend into hindbody. Genital pore submedian. Ovary just posterolateral to ventral sucker. Seminal receptacle apparently absent. Uterus almost entirely fills hindbody. Vitellarium in two compact lateral clusters on either side of ventral sucker. In cloaca of snakes; Europe, Asia and Africa. Type-species *P. cloacicola* (Lühe, 1909) Dollfus, 1950.

**3b. Vitellarium in two compact lateral clusters posterior to ventral sucker; testes diagonal; caeca terminate at considerable distance from posterior extremity, not extending posteriorly beyond vitellarium ..... *Metaleptophallus* Yamaguti, 1958. (Figs 33.7, 33.8)**

**Diagnosis:** Body small, slightly elongate. Suckers almost equal in size or oral sucker slightly larger. Oesophagus short. Caeca terminate at considerable distance from posterior extremity, not extending posteriorly beyond vitellarium. Testes diagonal. External seminal vesicle does not extend into hindbody. Genital pore median or slightly submedian. Ovary just posterolateral to ventral sucker. Seminal receptacle apparently absent. Uterus almost entirely fills hindbody. Vitellarium in two compact lateral clusters posterior to ventral sucker. In oesophagus and buccal cavity of snakes; Europe. Type-species *M. gracillimus* (Lühe, 1909) Yamaguti, 1958.

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**Figs 33.1, 33.2.** *Macrodera longicollis* (Abildgaard, 1788). 33.1. Ventral view. 33.2. Terminal genitalia. After Tkach *et al.* (1999).
**Figs 33.3, 33.4.** *Leptophallus nigrovenosus* (Bellingham, 1844). 33.3. Ventral view. 33.4. Terminal genitalia. After Tkach *et al.* (1999).
**Figs 33.5, 33.6.** *Paralepoderma cloacicola* (Lühe, 1909). 33.5. Ventral view. 33.6. Terminal genitalia. After Tkach *et al.* (1999).
**Figs 33.7, 33.8.** *Metaleptophallus gracillimus* (Lühe, 1909). 33.7. Ventral view. 33.8. Terminal genitalia. After Tkach *et al.* (1999).

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# 34 Family Macroderoididae McMullen, 1937

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## Introduction

The family Macroderoididae McMullen, 1937 was erected by McMullen (1937) for flukes that were intestinal parasites of freshwater fishes, but the group now includes forms that mature in crustaceans, leeches and marine fishes. In addition to the type-genus, *Macroderoides* Pearse, 1924, McMullen also assigned *Alloglossidium* Simer, 1929 to the family. He chose, as his principal character for the family diagnosis, the I-shaped excretory vesicle of the adult and cercaria of both genera, using it to distinguish his family from the Plagiorchiidae Lühe, 1901, which he characterized as having a Y-shaped vesicle and a broader range of hosts, i.e. 'parasitic in the digestive tract of vertebrates'. Careful examination of McMullen's diagnoses reveals no other characters by which these families can be distinguished. Unfortunately, this choice of characters has been the source of great confusion and controversy in the subsequent assignment of genera to these families. Complete life-histories, including descriptions of cercariae, are known for only a minority of macroderoidids and plagiorchiids. Illustration of the shape of the adult excretory vesicle is lacking in the descriptions of many genera assigned to these families. Examination of type-specimens is usually of little value, because the shape of the excretory vesicle cannot usually be determined in preserved material.

Yamaguti (1958b) did not recognize the Macroderoididae; instead, he placed *Macroderoides* in the Allocreadiidae Looss, 1902 and *Alloglossidium* in the Plagiorchiidae. However, Yamaguti (1971) greatly modified his treatment of these taxa. Disregarding McMullen's distinction between the Macroderoididae and the Plagiorchiidae, he included, in his diagnosis of the Macroderoididae, excretory vesicles that were either tubular (I-shaped) or Y-shaped and extended the host-range from freshwater fishes (nine genera) to include marine fishes (two genera), as well as amphibians (six genera) and reptiles (five genera). Subsequently, no other author has followed Yamaguti's (1971) taxonomic recommendations. For example, Prudhoe & Bray (1982) not only criticized the family diagnosis of McMullen (1937), pointing out the inconstancy in the shape of the excretory vesicle, but placed most of the amphibian genera assigned by Yamaguti to the Macroderoididae in the Plagiorchiidae. Gibson (1996) was equally sceptical of the usefulness of the characters defining the Macroderoididae, and further reduced its scope by excluding Yamaguti's (1958b) subfamily Walliniinae Yamaguti, 1958, to which genera parasitizing marine fishes had been assigned (Yamaguti,

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1958b, 1971). Choudhury *et al.* (2002), however, reached a different conclusion when assigning their new species, *Wallinia chavarriae* Choudhury, Daverdin & Brooks, 2002, to the Macroderoididae and Walliniinae, although they recognized and discussed their controversial taxonomic history. *Wallinia* Pearse, 1920 is included in the Allocreadiidae by Tkach (Chapter 66, this volume). Moravec & Salgado-Maldonado (2002) provisionally placed *Perezitrema* Baruš & Moravec, 1967 in the Macroderoididae, but pointed out problems with *P. bychowskyi* (Caballero & Caballero, 1975), which has an anus and cyclocoel, and has features similar to lepocreadioid families.

The following genera were assigned to us by the editors for our treatment of the Macroderoididae: *Alloglossidium* Simer, 1929, *Alloglossoides* Corkum & Turner, 1977, *Biguetrema* Deblock & Capron, 1962, *Caudouterina* Martin, 1966, *Cirkennedya* Gibson & Bray, 1979, *Gauhatiana* Gupta, 1955, *Macroderoides* Pearse, 1924, *Magnivitellinum* Kloss, 1966, *Paramacroderoides* Venard, 1941, *Perezitrema* Baruš & Moravec, 1967 and *Rauschiella* Babero, 1951. Because there is no consensus regarding the diagnosis of the Macroderoididae or what genera should be assigned to the family, we accept them as assigned, except for *Caudouterina* for reasons stated below. We provide a key for the identification of these genera, and believe that it is the perogative of other workers to treat the higher taxonomy of these genera as they deem appropriate. Lacking agreement by recent authors on characters distinguishing the Macroderoididae and Plagiorchiidae, we return to the original distinction based on the I-shaped vesicle of the former family and the Y-shaped vesicle of the latter family, as established by McMullen (1937) when erecting the Macroderoididae. Until consensus is reached regarding separation of these families, the assignment of genera such as *Gauhatiana* Gupta, 1953 and *Rauschiella* Babero, 1951, both of which possess Y-shaped vesicles, to Macroderoididae must be considered provisional.

*Macroderoides* Pearse, 1924, the type-genus, is an intestinal parasite of freshwater fishes in North America, especially of primitive holosteans such as *Lepisosteus* and *Amia*. Pulmonate snails serve as first intermediate hosts of *Macroderoides* and all other members of the family with known life-cycles. Xiphidiocercariae produced in daughter-sporocysts emerge and encyst as metacercariae in small fishes that are subsequently eaten by piscivorous definitive hosts (Leigh, 1956).

*Alloglossidium* Simer, 1929 has been the subject of numerous life-history and phylogenetic studies. The ancestral life-cycle of members of the genus is typified by *A. corti* (Lamont, 1921), first studied by McCoy (1928). Xiphidocercariae penetrate and encyst in a wide variety of invertebrates, and catfishes become infected through ingestion of metacercariae in hosts such as dragonflies and crayfishes. Adults are intestinal lumen-dwellers, releasing eggs with host faeces; these eggs infect pulmonate snails (McCoy, 1928; McMullen, 1935; Crawford, 1937). Most species of *Alloglossidium* are progenetic and produce eggs in leeches or crustaceans, eliminating the requirement of a vertebrate definitive host. Progenetic species are derived from ancestors with cycles similar to that of *A. corti* (see Font, 1980; Carney & Brooks, 1991). Phylogenetic analysis of *Alloglossidium* (see Smythe & Font, 2001) and related genera indicated that *Alloglossoides* Corkum & Turner, 1977 and *Hirudicolotrema* Fish & Vande Vusse, 1976 are its junior synonyms. *Parastiotrema* Miller, 1940 was also considered a synonym of *Alloglossidium* by Gibson (1996), and this is accepted here.

A revision of *Rauschiella* Babero, 1951, which uses frogs as hosts in Central and South America, was provided by Sullivan (1977). Its uterine configuration and location of testes differ markedly from all other macroderoidids. Life-cycle studies have not been published. *Biguetrema* Deblock & Capron, 1962, described from frog hosts in Madagascar, was designated a junior synonym of *Laiogonimus* Vercammen-Grandjean, 1960 by Yamaguti (1971). *Gauhatiana* Gupta, 1955 is represented by a single species, *G. batrachii* (Dayal & Gupta, 1954), parasitizing the freshwater fish *Clarias batrachus* in India. Yeh & Fotedar (1958) considered *Gauhatiana* a synonym of *Astiotrema* Looss, 1900. *Magnivitellinum simplex* Kloss, 1966, the type- and only species of its genus, was reported from a

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freshwater fish, *Astyanax bimaculatus*, in Brazil. Another monotypic genus that has been considered a macroderoidid is *Caudouterina* Martin, 1966, represented by *C. rhyacotriton* Martin, 1966 from the Olympic salamander in the north-western USA. Unlike most macroderoidids, it has a thickened tegument devoid of spines, a characteristic that supports the assignment of the genus to the Allocreadiidae Looss, 1902 by Prudhoe & Bray (1982), which is supported by Caira & Bogéa (2005).

With regard to host and habitat, the most unusual species assigned to the family is *Cirkennedya porlockensis* Gibson & Bray, 1979. The assignment of this species by Gibson & Bray (1979) to the Macroderoididae was made on the basis of morphological similarity to diagnostic characters for the family, but with full recognition that, because of obvious ecological differences, these characters might be convergent. They also provided a cogent summary of taxonomic problems associated with the family.

## Family Macroderoididae McMullen, 1937

**Diagnosis:** Body elongate, typically bearing tegumental spines. Oral sucker round, subterminal, rarely funnel-shaped, terminal. Ventral sucker round, typically in anterior half of body. Prepharynx present or absent. Pharynx present. Oesophagus short. Intestinal bifurcation in forebody. Caeca elongate, usually extending to near posterior extremity, blind, exceptionally forming cyclocoel. Testes two, tandem or diagonal, typically entire, usually in hindbody. Cirrus-sac present, entirely anterior to or overlapping ventral sucker. Seminal vesicle internal, often bipartite. Cirrus weakly developed to robust. Genital pore median or submedian, immediately anterior to ventral sucker. Ovary median or submedian, between ventral sucker and testes. Mehlis' gland and Laurer's canal usually present. Seminal receptacle usually uterine. Uterus usually with ascending and descending coils passing between testes, exceptionally otherwise. Metraterm usually absent. Eggs numerous, small, operculate. Vitellarium follicular, forming symmetrical lateral fields of variable extent, typically from intestinal bifurcation to posterior testis. Excretory vesicle usually I-shaped, exceptionally Y-shaped; pore terminal. In intestine of freshwater heterotherms, exceptionally in freshwater crustaceans or leeches, and marine fishes; North America, South America, Europe, Asia, Atlantic Ocean. Type-genus *Macroderoides* Pearse, 1924.

## Key to genera

**1a. Oral sucker funnel-shaped, with terminal aperture ..... 2.**
**1b. Oral sucker nearly spherical, with subterminal aperture ..... 3.**

**2a. Oral sucker with rows of enlarged circumoral spines; caeca blind .....**
**..... *Paramacroderoides* Venard, 1941. (Fig. 34.1)**
(Syn. *Pseudoparamacroderoides* Gupta & Agrawal, 1968)

**Diagnosis:** Body small, subcylindrical, covered with coarse spines. Oral sucker terminal, large, funnel-shaped, with rows of circumoral spines larger than body-spines. Ventral sucker smaller than oral sucker, median, in anterior third of body. Prepharynx present. Caeca blind, terminate close to posterior extremity. Testes in middle third of body. Cirrus-sac overlaps ventral sucker, contains bipartite seminal vesicle and unspined cirrus. Genital pore median, in posterior forebody. Ovary contiguous with or adjacent to posterior end of cirrus-sac. Canalicular seminal receptacle ovoid, saccular, postovarian. Coils of uterus descend to near posterior end. Metraterm absent. Vitelline follicles lateral, extend from ovary to middle of post-testicular region. Excretory vesicle I-shaped; pore terminal. In intestine of freshwater fishes; North America, India. Type-species *P. echinus* Venard, 1941.

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**2b. Oral sucker without enlarged spines; caeca unite and form anus ..... ..... *Perezitrema* Baruš & Moravec, 1967. (Fig. 34.2)**
(Syns *Neotropicotrema* Caballero & Caballero, 1975; *Allomacroderoides* Watson, 1976)
**Diagnosis:** Body elongate, cylindrical, spinous. Oral sucker terminal, very large, funnel-shaped, lacks rows of large, circumoral spines. Ventral sucker much smaller than oral sucker, in mid-body. Prepharynx short. Caeca unite near posterior extremity, form cyclocoel, which opens via anus. Testes rounded, tandem to oblique, in hindbody. Cirrus-sac robust, overlaps ventral sucker, contains bipartite seminal vesicle, prostatic cells and unspined cirrus. Genital pore median. Ovary round, median to submedian, posterior to ventral sucker, anterior to testes. Uterus reaches posterior extremity. Metraterm absent. Vitelline follicles in lateral fields extending from ventral sucker to posterior testis. Excretory vesicle I-shaped; pore dorsal to anus. In intestine of freshwater and brackish water fishes; Central America, Caribbean region. Type-species *P. viguerasi* Baruš & Moravec, 1967.

**3a. Ventral sucker small, pad-like, without lumen, probably not functional as attachment organ ..... *Cirkennedya* Gibson & Bray, 1979. (Fig. 34.3)**
**Diagnosis:** Body large, fusiform. Tegumental spines minute. Oral sucker subterminal, globular. Ventral sucker small, weakly muscular, pad-like, without lumen, in anterior third of body. Prepharynx well developed. Caeca wide, extend into post-testicular region; ends obscured by uterus. Testes large, oval to fusiform, tandem, in mid-hindbody, contiguous. Elongate cirrus-sac extends into hindbody. Seminal vesicle bipartite; anterior portion small, tear-shaped; posterior portion large, elongate. Pars prostatica ill-defined, tubular, straight, with few gland-cells. Spinous cirrus usually protruded. Genital atrium absent. Genital pore median in posterior forebody; male and female pores side by side. Ovary oval, anterior to testes. Mehlis' gland postovarian. Laurer's canal and uterine seminal receptacle present. Uterine coils fill most of body posterior to ventral sucker and extend to posterior extremity, not passing between testes. Metraterm muscular. Vitelline follicles in symmetrical lateral fields from intestinal bifurcation past posterior margin of testes. Excretory vesicle I-shaped, extending to ovary; pore terminal. In intestine of *Mola*; north-eastern Atlantic Ocean. Type-species *C. porlockensis* Gibson & Bray, 1979.

**3b. Ventral sucker muscular, cup-shaped, with lumen, functional as holdfast organ ..... 4.**

**4a. Testes in anterior half of body ..... *Rauschiella* Babero, 1951. (Fig. 34.4)**
(Syn. *Repandum* Byrd & Maples, 1963)
**Diagnosis:** Body elongate, with almost parallel sides, spinous. Oral sucker oval, subterminal. Ventral sucker oval. Prepharynx short. Caeca terminate near posterior extremity. Testes in anterior hindbody only slightly diagonal, nearly symmetrical. Cirrus-sac elongate, overlaps ventral sucker, containing coiled seminal vesicle, elongate pars prostatica and smooth ejaculatory duct. Genital pore median, in posterior forebody. Ovary subspherical, submedian, overlaps ventral sucker. Uterine seminal receptacle present. Laurer's canal present. Mehlis' gland present. Uterus entirely intercaecal, with short descending coils on one side of midline and ascending coils on other side. Metraterm absent. Vitelline follicles very small, tightly packed, extracaecal, extend from pharynx to posterior quarter of body. Excretory vesicle Y-shaped; pore terminal. In intestine of amphibians and reptiles; Central and South America. Type-species *R. tineri* Babero, 1951.

**4b. Testes in posterior half of body ..... 5.**

**5a. Cirrus-sac completely anterior to ventral sucker ..... ..... *Magnivitellinum* Kloss, 1966. (Fig. 34.5)**
**Diagnosis:** Body elongate, spined anteriorly. Oral sucker subterminal, comparatively small, oval. Ventral sucker median. Prepharynx short. Oesophagus distinct. Intestinal bifurcation in

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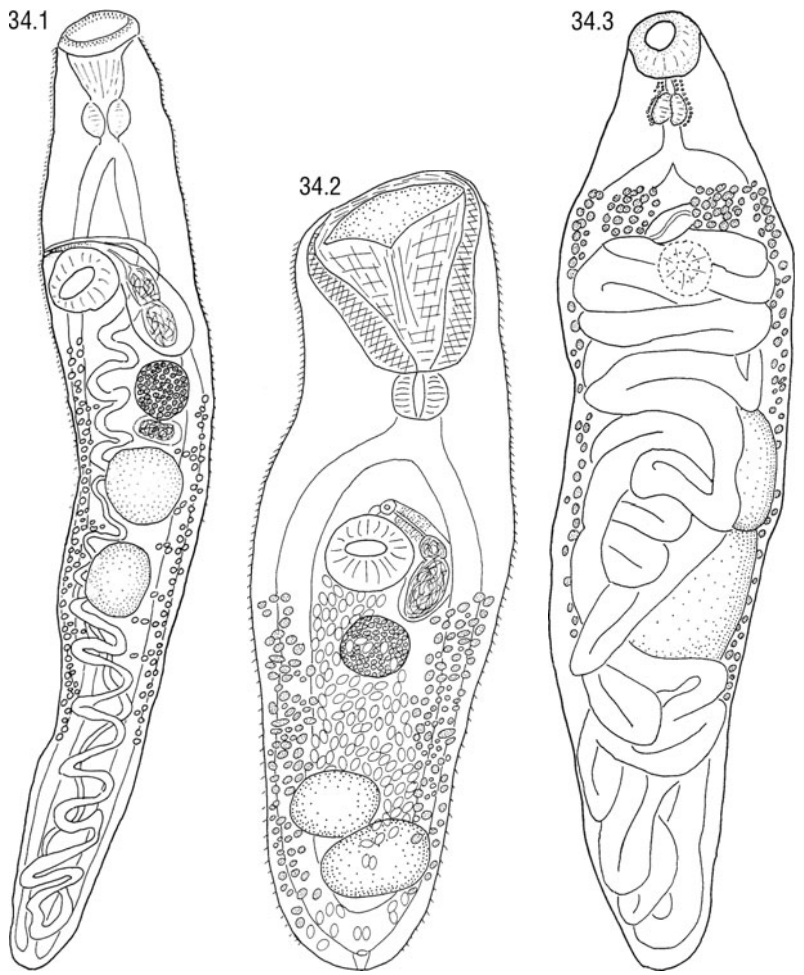



**Fig. 34.1.** *Paramacroderoides echinus* Venard, 1941. Paratype, forebody is turned laterally. Original.
**Fig. 34.2.** *Perezitrema bychowskyi* (Caballero & Caballero, 1975). After Moravec & Salgado-Maldonado (2002).
**Fig. 34.3.** *Cirkennedya porlockensis* Gibson & Bray, 1979. Holotype. Original.

mid-forebody. Caeca reach to testes or about halfway along post-testicular region. Testes in middle third of body, overlap caeca. Cirrus-sac very small and strongly recurved, in forebody; containing tubular seminal vesicle, pars prostatica and ejaculatory duct. Genital pore submedian in posterior forebody. Ovary submedian. Seminal receptacle uterine (?). Vitelline follicles few, very large, from caecal bifurcation to posterior testis. Excretory vesicle not known; pore terminal. In intestine of freshwater fish (*Astyanax bimaculatus*); Brazil. Type-species *M. simplex* Kloss, 1966.

**5b. Cirrus-sac not completely anterior to ventral sucker ..... 6.**

**6a. Vitelline follicles in two clusters in lateral fields ..... *Gauhatiana* Gupta, 1955. (Fig. 34.6)**

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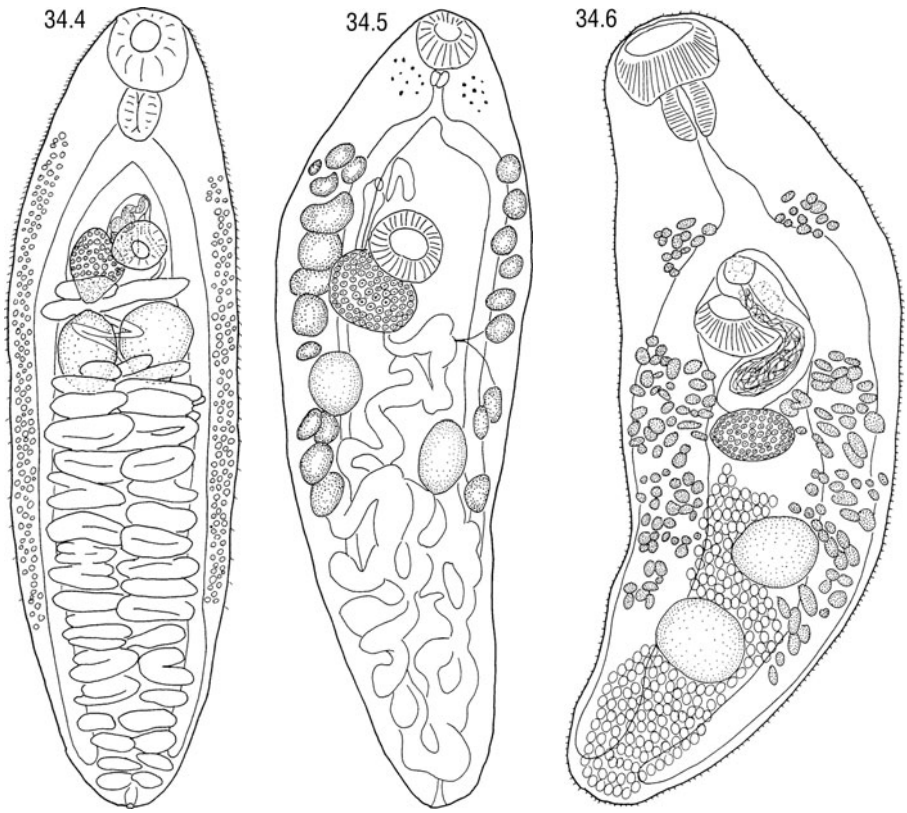



**Fig. 34.4.** *Rauschiella palmides* (Lutz, 1928). Ex *Leptodactylus bolivianus*, Venezuela. Original.
**Fig. 34.5.** *Magnivitellinum simplex* Kloss, 1966. After Kloss (1966).
**Fig. 34.6.** *Gauhatiana batrachii* Gupta, 1955. After Gupta (1955).

**Diagnosis:** Body spined, tapered at extremities. Oral sucker comparatively large, subterminal, oval. Ventral sucker median. Prepharynx apparently absent. Pharynx large. Caeca terminate near posterior extremity. Testes diagonal, separated by uterus, in middle third of hindbody. Cirrus-sac large, overlaps ventral sucker. Genital pore submedian. Ovary ovoid, submedian. Seminal receptacle large, postovarian, presumably canalicular. Laurer's canal present. Mehlis' gland not observed. Uterus extends to posterior extremity. Vitelline follicles form two distinct clusters, in lateral fields on each side of body. Excretory vesicle Y-shaped; pore dorso-terminal. In intestine of freshwater fish; India. Type-species *G. batrachii* (Dayal & Gupta, 1954) Gupta, 1955.

**6b. Vitelline follicles form continuous lateral fields** ..... 7.

**7a. Vitelline follicles extend anteriorly beyond level of ventral sucker; cirrus small, poorly developed** ..... ***Alloglossidium* Simer, 1929. (Fig. 34.7)**
(Syns *Parastiotrema* Miller, 1940; *Hirudicolotrema* Fish & Vande Vusse, 1976; *Alloglossoides* Corkum & Turner, 1977)

**Diagnosis:** Body spined, fusiform to very elongate. Oral sucker subterminal to terminal, rounded. Ventral sucker in anterior half of body. Caeca moderately short to long, terminate from just

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posterior to mid-body to near posterior extremity. Testes spherical to elongate, tandem, diagonal or symmetrical. Cirrus-sac claviform, overlaps ventral sucker. Cirrus small, poorly developed. Genital pore in forebody. Ovary spherical, scalloped or elongate. Uterus extends to posterior extremity. Vitelline follicles in continuous lateral fields; anterior extent between close to pharynx and near ovary; posterior extent testicular level. Excretory vesicle I-shaped, extends to level of posterior testis or ovary; pore terminal. In intestine of freshwater fishes and leeches, and viscera of freshwater crustaceans; North America, Afghanistan. Type-species *A. kenti* Simer, 1929.

**7b. Vitelline follicles not extending anteriorly as far as level of ventral sucker; cirrus large, robust ..... *Macroderoides* Pearse, 1924. (Fig. 34.8)**[1]
(Syn. *Plesiocreadium* Winfield, 1929)

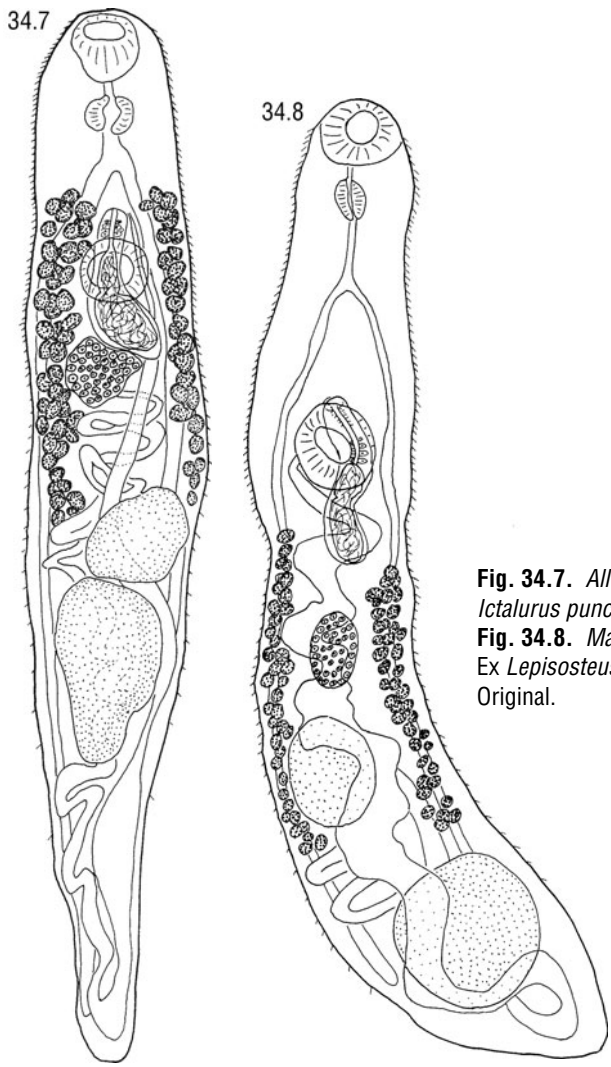



**Fig. 34.7.** *Alloglossidium kenti* Simer, 1929. Ex *Ictalurus punctatus*, Mississippi, USA. Original.
**Fig. 34.8.** *Macroderoides spinifer* Pearse, 1924. Type. Ex *Lepisosteus osseus*, New York Aquarium, USA. Original.

[1] See Addendum.

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**Diagnosis:** Body heavily spined, elongate. Oral sucker nearly terminal, oval. Ventral sucker in anterior half of body. Prepharynx short. Oesophagus long. Intestinal bifurcation in mid-forebody. Caeca terminate between level of posterior testis and posterior extremity. Testes diagonal to tandem. Cirrus-sac greatly overlaps ventral sucker. Cirrus large, robust. Genital pore median, in posterior forebody. Ovary median to submedian. Uterus extends to posterior extremity. Vitelline follicles in continuous lateral fields, begin posteriorly to ventral sucker and extend to testes. Excretory vesicle I-shaped, short; pore terminal. In intestine of freshwater fishes; North America, Europe. Type-species *M. spinifer* Pearse, 1924.

## Addendum

The genus *Malawitrema* Bray & Hendrix, 2007 is similar to *Macroderoides*, but differs in the length of the caeca, the extent of the vitelline fields and the symmetrical testes (Bray & Hendrix, 2007).

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# 35 Family Meristocotylidae Fischthal & Kuntz, 1964

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## Introduction

This group was erected as the subfamily Meristocotylinae Fischthal & Kuntz, 1964 of unknown relationships by Fischthal & Kuntz (1964c) for *Meristocotyle varani*, a new species and genus they described from a lizard, *Varanus salvator*, in the Philippines. They recorded the presence of two specimens, an adult in the stomach and a juvenile in the lungs, but suggested that the position of the adult might have been the result of post-mortem migration. This species has not been reported since, but Yamaguti (1971) re-examined and figured the holotype. The most obvious and unusual feature of this taxon is the presence of a horizontally divided ventral sucker with two lumina. Recently, a second species of the genus, *M. provitellaria* Liu, Li, Shih & Qiu, 2002, has been described by Liu *et al*. (2002) from the gastro-intestinal tract (mainly) and lungs of the same host in China.

Yamaguti (1971) raised the subfamily to full family status without comment and defined it and the genus in detail. Similarly, Liu *et al*. (2002) also defined the family (their diagnosis is almost identical to Yamaguti's) and redefined the genus but, like Yamaguti, did not comment on the relationships of the group. The presence of some specimens in the lungs perhaps suggests an affinity with the Leptophallidae Dayal, 1938 (see Tkach, Chapter 33, this volume), and there are some similarities in the distribution of organs, such as the gonads and uterus, but *Meristocotyle* differs in the distribution of the vitellarium, the unarmed tegument and the unusual bipartite nature of the ventral sucker.

## Family Meristocotylidae Fischthal & Kuntz, 1964

**Diagnosis:** Medium-sized worms with stout, fusiform body, dorsoventrally flattened, with rounded anterior extremity and more tapered, conical hindbody. Tegument unarmed. Forebody almost half length of worm, broad, ventrally concave. Pre-oral lobe distinct. Oral sucker ventrally subterminal, well developed. Ventral sucker large, just inside posterior half of body or almost so, mounted on distinct eminence, longitudinally elongate and distinctly divided into two parts, each

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with its own lumen. Prepharynx present. Pharynx well developed. Oesophagus short. Intestinal bifurcation in anterior forebody, distant from ventral sucker. Caeca two, blind, extend just into hindbody or almost so, end anteriorly to bulk of uterus. Testes two, globular to oval, symmetrical and well separated or obliquely tandem and contiguous, at level of posterior ventral sucker or in anterior hindbody. Cirrus-sac long, elongate-fusiform, reaches from level of anterior margin of ventral sucker to level of pharynx, contains small, convoluted seminal vesicle, long pars prostatica surrounded by thick layer of prostatic cells and short, muscular ejaculatory duct, which may evert through genital pore, forming cirrus. Genital atrium ?absent. Genital pore sinistro-submedial at level of pharynx. Ovary entire, subglobular, sublateral (left or right), just anterior or anterodorsal to ventral sucker. Seminal receptacle and Laurer's canal present. Main mass of uterine coils postcaecal, fill much of hindbody, extend between posterior extremity and ventral sucker; uterus narrow in forebody where it passes directly towards genital pore. Eggs numerous, operculate, large. Vitellarium follicular; follicles numerous, in lateral fields; fields fill much of forebody, often confluent dorsally, reach from level of oral sucker or intestinal bifurcation to level of ventral sucker or into anterior half of hindbody; when fields extend into hindbody, gap occurs at level of ventral sucker. In gastro-intestinal system and lungs of varanid lizards (water monitors); China and Southeast Asia (Philippines). Type-genus *Meristocotyle* Fischthal & Kuntz, 1964.

## Genus *Meristocotyle* Fischthal & Kuntz, 1964 (Fig. 35.1)

**Diagnosis:** With characters of family. Type-species *M. varani* Fischthal & Kuntz, 1964.

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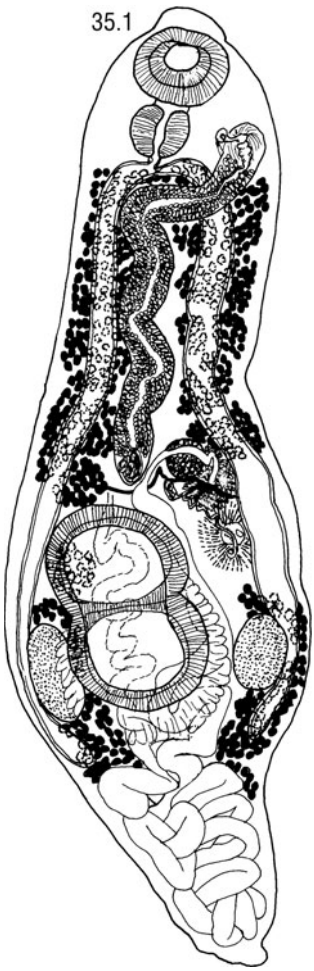



**Fig. 35.1.** *Meristocotyle varani* Fischthal & Kuntz, 1964. After Yamaguti (1971).

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# 36 Family Mesotretidae Poche, 1926

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## Introduction

The Mesotretidae Poche, 1926 is a small family of plagiorchioid digeneans comprising only one genus and three species. These worms are parasitic in the intestine of bats, primarily belonging to the family Rhinolophidae, in several European countries (*Mesotretes peregrinus* (Braun, 1900)) and China (*M. orientalis* Sun & Jiang, 1987 and *M. hangzhouensis* Sun, Jiang & Yan, 1988). The type-species of *Mesotretes* Braun, 1900, namely *M. peregrinus*, was described by Braun (1900a) as *Distomum peregrinum* Braun, 1900; yet, later in the same year, he (Braun, 1900b) established the new genus *Mesotretes* for this species. The family-group name was proposed by Poche (1926). The members of the Mesotretidae can be readily distinguished from other plagiorchioids by a combination of such distinct characters as the position of the genital pore in the hindbody and the post-testicular ovary. The life-cycle of *Mesotretes* is not known; neither are the phylogenetic affinities of this quite enigmatic family.

## Family Mesotretidae Poche, 1926

**Diagnosis:** Body elongate. Tegumentary spination almost reaches posterior extremity. Oral sucker subterminal. Ventral sucker somewhat larger than or similar in size to oral sucker, in anterior third of body. Prepharynx absent. Pharynx present. Oesophagus indistinct to long. Intestinal bifurcation in forebody. Caeca end blindly close to posterior extremity. Testes sausage-shaped or oval, tandem, in mid-hindbody. Cirrus-sac claviform, longitudinal, between ventral sucker and anterior testis, contains bipartite seminal vesicle. Genital pore median, posterior to ventral sucker. Ovary oval or round, just posterior to testes, median or slightly submedian. Seminal receptacle posterior to ovary. Uterus consists of descending and ascending limbs, usually passing between testes and filling post-testicular part of hindbody. Eggs numerous. Vitellarium consists of numerous small vitelline follicles in two lateral fields, confluent posterior to testes, which reach posterior extremity; anteriorly, vitelline fields reach level of ventral sucker or somewhat anterior to it;

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especially well developed dorsally. In intestine of Chiroptera; Europe, China. Type-genus *Mesotretes* Braun, 1900.

## Genus *Mesotretes* Braun, 1900 (Figs 36.1, 36.2)

**Diagnosis:** With characters of family. Type-species *M. peregrinus* (Braun, 1900) Braun, 1900.

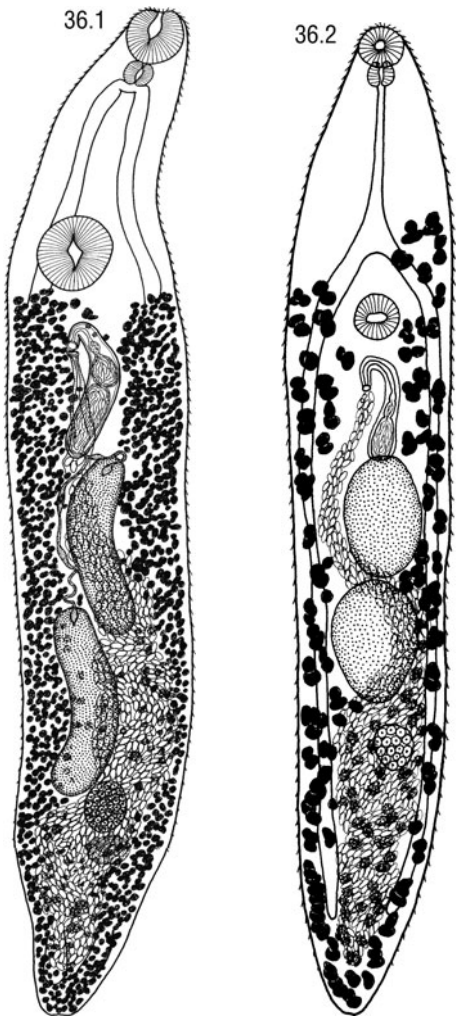



**Fig. 36.1.** *Mesotretes peregrinus* (Braun, 1900). Ventral view. Original.
**Fig. 36.2.** *Mesotretes hangzhouensis* Sun, Jiang & Yan, 1988. After Sun *et al.* (1988).

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# 37 Family Ocadiatrematidae Fischthal & Kuntz, 1981

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## Introduction

The monotypic family Ocadiatrematidae Fischthal & Kuntz, 1981 was erected by Fischthal & Kuntz (1981a) for a new genus and species, *Ocadiatrema taiwanense* Fischthal & Kuntz, 1981, which they described on the basis of three worms from the small intestine of the Chinese freshwater stripe-necked turtle, *Ocadia sinensis*, on Taiwan. This species does not appear to have been recorded subsequently. Fischthal & Kuntz erected the family after keying down the worms in Yamaguti (1971) to the Auridistomidae Stunkard, 1924, another group of intestinal parasites of turtles. However, they considered that it was differentiated by, among other features, the absence of muscular oral lobes, the presence of a crown of spines on the oral sucker, testes in the posterior third of the body, a cirrus-sac and genital pore in the hindbody, and a uterus extending to the posterior extremity. However, in the type-specimens there appear to be two pairs of oral lobes (Figure 37.2), just as in auridistomids (these were interpreted as glandular by Fischthal & Kuntz (1981a), but they also look muscular), and the so-called crown of spines is very indistinct. Nevertheless, the other differences do appear to be valid. *O. taiwanense* also bears a superficial resemblance to the spirorchiid genus *Hapalorhynchus* Stunkard, 1922, species of which are frequently recorded from *Ocadia sinensis*, but it clearly has a pharynx and a pretesticular rather than intertesticular ovary. The position of the genital pore just posterior to the ventral sucker suggests a link with the Gekkonotrematidae Yamaguti, 1971, but the pretesticular uterus of the latter group would appear to preclude a close link, and there are differences in the oesophageal and caecal lengths. In some aspects of its morphology, such as the position of the genital pore, it resembles the opisthogonimid genus *Liophistrema* Artigas, Ruiz & Leão, 1943 from the lungs of a South American snake and *Opisthogonimus* Lühe, 1900 from the mouth and oesophagus of South American snakes (the latter two genera are very similar).

## Family Ocadiatrematidae Fischthal & Kuntz, 1981

**Diagnosis:** Body large, elongate, fusiform. Tegument covered with small, broad, scale-like spines. Oral sucker small, ventroterminal, with ?irregular crown of small spines. Two pairs of small,

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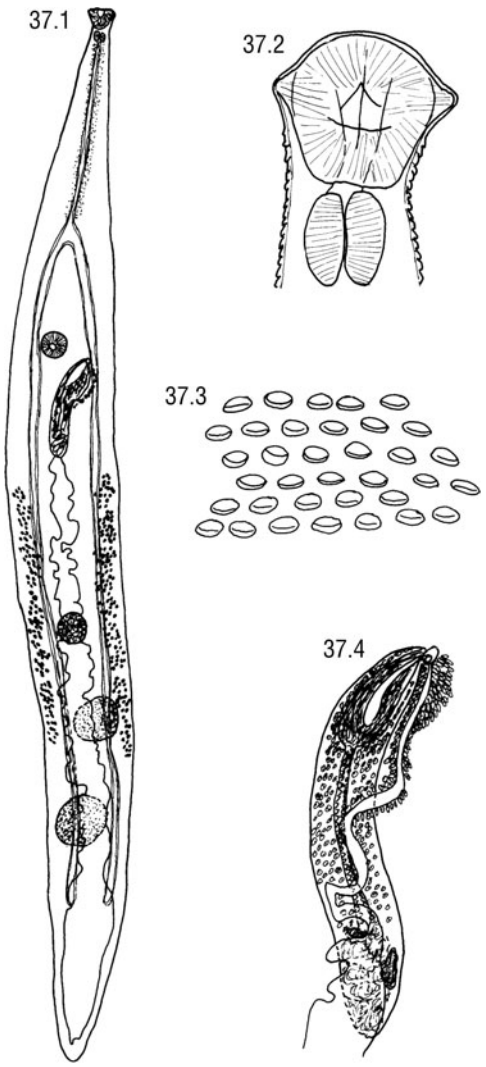

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glandular/muscular conical projections/lobes present laterally at level of oral sucker. Ventral sucker small but larger than oral sucker, just inside anterior third of body. Prepharynx short. Pharynx small. Oesophagus very long, surrounded by gland-cells. Intestinal bifurcation just inside posterior half of forebody. Caeca two, long, pass directly posteriorly to end blindly in about middle of post-testicular region. Testes two, slightly obliquely tandem, well separated, in about third quarter of hindbody, subglobular. Cirrus-sac well developed, thick-walled, curved, in anterior hindbody, extends anteromedially from about 40% of distance between ventral sucker and ovary to sinistro-submedial position just posterior to ventral sucker, contains coiled seminal vesicle, long, straight pars prostatica and well-developed, muscular ejaculatory duct, which forms protrusible cirrus. Genital atrium small, indistinct. Genital pore sinistro-submedial, closely posterior to ventral sucker. Ovary median to submedian, well anterior to testes, in about middle of hindbody, globular to oval, smaller than testes. Laurer's canal present. Canalicular seminal receptacle present posterior to ovary. Uterus long, winds mainly intercaecally (often overlaps caeca in postovarian region) between posterior extremity and posterior end of cirrus-sac; metraterm sinuous, narrow, runs alongside cirrus-sac, surrounded by gland-cells. Eggs operculate, tanned, small. Vitellarium follicular; follicles small, numerous, in acinous groups, mainly extracaecal, in lateral fields between about level just posterior to cirrus-sac and about level of intertesticular region; fields not confluent. Excretory vesicle tubular, Y-shaped, bifurcating between anterior testis and ovary; arms reach level of posterior end of cirrus-sac; pore terminal. In intestine of freshwater turtle; Taiwan. Type-genus *Ocadiatrema* Fischthal & Kuntz, 1981.

## Genus *Ocadiatrema* Fischthal & Kuntz, 1981 (Figs 37.1–37.4)

**Diagnosis:** With characters of family. Type-species *O. taiwanense* Fischthal & Kuntz, 1981.

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**Figs 37.1–37.4.** *Ocadiatrema taiwanense* Fischthal & Kuntz, 1981. 37.1. Entire worm. After Fischthal & Kuntz (1981a). 37.2. Anterior extremity, only one pair of oral lobes visible (type-material, USNPC 075615.00). Original. 37.3. Spines on forebody (type-material, USNPC 075615.00). Original. 37.4. Terminal genitalia; uterus obscures seminal vesicle. After Fischthal & Kuntz (1981a).

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# 38 Family Omphalometridae Looss, 1899

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## Introduction

This is a small group of plagiorchioid digeneans uniting several genera found as adults only in insectivores and is characterized morphologically by the uterus, which never extends into the post-testicular region of the body and usually not beyond the anterior testis. Opinions of different authors on the systematic rank and content of this group have varied ever since Looss (1899) erected the subfamily Omphalometrinae Looss, 1899 and the genus *Omphalometra* Looss, 1899 for *Distomum flexuosum* Rudolphi 1809. Odhner (1911b) included the Omphalometrinae within the Lepodermatidae Looss, 1899 (= Plagiorchiidae Lühe, 1901) and considered *Omphalometra* to be closely related to *Opisthioglyphe* Looss, 1899. Dollfus (1949) established *Rubenstrema* Dollfus, 1949, which he included as a subgenus of *Opisthioglyphe*. Shaldybin (1953) erected a further subgenus, *Neoglyphe* Shaldybin, 1953, within *Opisthioglyphe*. Yamaguti (1958b) again considered this group as a subfamily, including seven genera, *Omphalometra, Opisthioglyphe, Dolichosaccus* Johnston, 1912, *Rudolphitrema* Travassos, 1926, *Neoglyphe, Sigmapera* Nicoll, 1918 and *Kaurma* Chatterji, 1936; they included parasites of amphibians, reptiles and mammals. Odening (1959b) placed *Skrjabinomerus* Sobolev, Mashkov & Mashkov, 1939 into synonymy with *Omphalometra* and established the family Omphalometridae Looss, 1899, containing only the type-genus. Later, Skrjabin (1966c) expanded it to five genera, exclusively parasites of the Insectivora: *Omphalometra, Skrjabinomerus, Neoglyphe, Rutshurutrema* Baer 1959 and *Rubenstrema*. Yamaguti (1971) changed his earlier opinion and considered the Omphalometridae as a separate family, containing several genera of digeneans parasitic in different groups of vertebrates. In contrast, Sharpilo & Iskova (1989) included this group within the Opisthioglyphinae Dollfus, 1949. Bayssade-Dufour & Grabda-Kazubska (1993) studied cercarial chaetotaxy of *Omphalometra* and *Neoglyphe* and showed that these two genera are not close relatives of *Opisthioglyphe*. Based on combined morphological and molecular evidence (for details see Tkach *et al*., 2000a, 2001b), *Opisthioglyphe* belongs to the Telorchiidae Looss, 1899, where it is treated in this volume (Font & Lotz, Chapter 43, this volume). Tkach *et al*. (2001a) suggested that the Omphalometrinae should be considered as a subfamily of the Plagiorchiidae. However, taking into account the morphological features differentiating this group from other lineages and the highly complicated situation of the taxonomic

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content of the Plagiorchiidae (many life-cycles are completely unknown and many genera are still unavailable for molecular analysis), the Omphalometridae is treated here as a separate family.

One of the most prominent morphological features of this group is the uterus, which never extends into post-testicular region of the body and, in all but one genus, does not extend beyond the anterior testis. Omphalometrids may be found in the stomach, intestine, gall-bladder and even the uterus and vagina of shrews, moles and desmans. The latter two sites of infection appear to be secondary for this group. To the best of my knowledge, the original finding of *Neoglyphe hinoi* (Ozaki, 1931) Yamaguti, 1958 in the uterus and vagina of shrews (Ozaki, 1931) has not been confirmed by any other author. A number of the genera included in the Omphalometridae by Yamaguti (1971) are considered here to be outside this family or invalid, while some others are placed into synonymy (see details below).

*Dolichosaccus* Johnston, 1912 and *Opisthioglyphe* Looss, 1899 were considered by Yamaguti (1971) in the Omphalometridae, but are included in the Telorchiidae in this volume based on available morphological, developmental and molecular evidence (see Font & Lotz, Chapter 43, this volume).

*Dolichosacculus* Johnston, 1943 was described from an immature specimen found in the intestine of a cormorant in New South Wales, Australia (Johnston, 1943). At the time, it was placed in the Omphalometridae; however, Yamaguti (1971) suggested that it was an accidental record of a parasite from a recently swallowed frog and that the digenean found by Johnston (1943) most probably belongs to *Dolichosaccus*. Although the description and drawing provided by Johnston (1943) allow for more than one potential generic allocation, I agree with Yamaguti (1971) and consider *Dolichosacculus* a synonym of *Dolichosaccus* (see above).

*Kaurma* Chatterji, 1936 was established for *K. longicirra* Chatterji, 1936 described from a turtle in Burma (now Myanmar) (Chatterji, 1936). The genus was initially included in the Allocreadiidae Stossich, 1904 and later transferred to the Omphalometridae by Yamaguti (1971). The description and drawing by Chatterji (1936), as well as a detailed morphological re-examination of *K. intermedia* Rohde, 1963 deposited in the Natural History Museum, London (BMNH 1962.7.4.1), showed that the organization of the cirrus-sac in this species is very different from that in members of the Omphalometridae and the Plagiorchiidae. Unfortunately, at this point it is impossible to confidently allocate this genus into any known family and it is considered here as a genus *incertae sedis*.

*Maicuru* Freitas, 1960 was originally described from a toad, *Bufo granulosus*, in Brazil as a member of the Plagiorchiidae (see Freitas, 1960b). Yamaguti (1971) considered it within the Omphalometridae, while Prudhoe & Bray (1982) included it in the Allocreadiidae. Most recently, *Maicuru* was considered by Caira & Bogéa (2005) as a genus *incertae sedis* in Chapter 40 of Volume 2 of this series. They did not mention or depict the lateral body lobes of this species as mentioned and illustrated in the original description. According to Dr Stephen Curran (Gulf Coast Research Laboratory, Ocean Springs, Mississippi; personal communication), these lobes/projections are real morphological structures, observed in live specimens of an as yet undescribed species of *Maicuru* found in fishes in Peru. Based on his observations and analysis of high-quality microphotographs of the holotype, he is confident that this is an allocreadiid genus.

*Ophiotreminoides* Coil & Kuntz 1960 was described from a sea-snake and originally placed by Coil & Kuntz (1960) in the Acanthocolpidae Lühe, 1909, but later transferred by Yamaguti (1971) to the Omphalometridae. Recently, it was listed by Bray *et al*. (2005) among equivocal acanthocolpids in need of further study. Both morphology (the uroproct; the simple internal seminal vesicle versus the bipartite vesicle in omphalometrids; etc.) and host-specificity of these digeneans suggest that they are not closely related to omphalometrids. Therefore, this genus is considered here as a genus *incertae sedis*.

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*Rhacophotrema* Uchida, Itagaki & Inoue, 1980 was originally included in the Omphalometridae (see Uchida *et al.*, 1980). However, several morphological features, such as the smooth tegument, position of the genital pore and organization of the cirrus-sac, as well as host-specificity, suggest that it belongs to the Batrachotrematidae Dollfus & Williams, 1966, where it was placed by Zhang & Sha (1985) and Cribb (2005).

*Rudolphitrema* has been commonly included in the Plagiorchiidae, but was transferred by Yamaguti (1971) into the Omphalometridae without comment. In this volume, it is considered among the Plagiorchiidae. This is a poorly known taxon and I anticipate that its systematic position may change when more data, especially DNA sequences, become available.

*Rutshurutrema* was described from the gall-bladder of the shrew *Crocidura occidentalis* in the Belgian Congo (now Democratic Republic of Congo) (Baer, 1959). It was placed in synonymy with *Neoglyphe* by Yamaguti (1971) without comment. I disagree and consider *Rutshurutrema* a separate genus because of several essential morphological characters differentiating these two genera. Among them is the difference in the relative position of the testes (tandem, transversely elongate in all members of *Neoglyphe* versus diagonal, longitudinally elongate in *Rutshurutrema*), much greater number of eggs and much smaller cirrus-sac in *Rutshurutrema*. The localization of *Rutshurutrema* in the gall-bladder instead of the gastro-intestinal tract is additional evidence of substantial biological differences between these genera.

*Sarumitrema* Beverley-Burton, 1963 was included by Beverley-Burton (1963) and several other authors in the Plagiorchiidae, but transferred by Yamaguti (1971) to the Omphalometridae without comment. In this volume, it is treated as a plagiorchiid because some of its morphological characteristics, among them the distribution of the vitelline fields and the organization of the cirrus-sac, distinguish it from the Omphalometridae.

The systematic position of *Sigmapera* Nicoll, 1918 has always been controversial. The genus has usually been considered a plagiorchiid with unclear phylogenetic affinities (for a historical account and extensive discussion see Jue Sue & Platt, 1998a). Because of the superficial similarity between *Sigmapera* and some heterophyids, Poche (1926) allocated it to the Heterophyidae Odhner, 1914 as the sole member of the subfamily Sigmaperinae Poche, 1926. This viewpoint was obviously erroneous and was not accepted by subsequent authors. Yamaguti (1958b, 1971) included this genus first in the subfamily Omphalometrinae within the Plagiorchiidae, and then in the Omphalometridae when considered as a separate family. Jue Sue & Platt (1998a) provided a detailed redescription of the type-species, *S. cincta* Nicoll, 1918, based on the types and new specimens, and an excellent description of all stages of its life-cycle. I have also re-examined the type-specimen of *S. cincta* as well as a large number of freshly collected specimens. Adult *Sigmapera* indeed bear a substantial similarity to some members of the Omphalometridae: in particular, in the pretesticular uterus, the arrangement of the vitelline follicles, the presence of a well-developed cirrus-sac and the general shape of the excretory vesicle in adults. On the other hand, there are substantial differences separating *Sigmapera* from omphalometrids. Among them are differences in the number of penetration glands in the cercariae – three glands on one side and four on the other, as against eight pairs in some members of the Omphalometridae. An additional substantial difference is the number of protonephridia; the protonephridial formula of omphalometrids is $2[(3 + 3 + 3) + (3 + 3 + 3)] = 36$, while in *Sigmapera* it is $2[(2 + 2 + 2) + (2 + 2 + 2)] = 24$. Adult *Sigmapera* possess a characteristic dorsal protuberance associated with the exit of Laurer's canal, whereas no omphalometrid has such a structure. *Sigmapera* uses amphibians or snails as second intermediate hosts while all omphalometrids studied so far use arthropods. Finally, adult *Sigmapera* parasitize Australian freshwater turtles, while all 'typical' omphalometrids are parasites of insectivores, a group of

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mammals completely lacking in Australia. Thus, *Sigmapera* is considered here within the Plagiorchiidae, although this systematic arrangement is most probably temporary.

*Skrjabinomerus* Sobolev, Mashkov & Mashkov, 1939 was considered a synonym of *Omphalometra* by Odening (1959b). Yamaguti (1971) resurrected it, however, based on differences in the extent of the vitellarium (confined to the hindbody in *Skrjabinomerus*, but extending well into the forebody in *Omphalometra*). This feature alone cannot be considered substantial enough to separate two genera in this particular group of digeneans. For example, in *Rubenstrema exasperatum* (Rudolphi, 1819), the vitellarium reaches into the forebody while in *R. opisthovitellinum* (Soltys, 1954) it does not. Otherwise, the latter two species are very similar morphologically and extremely close genetically (Tkach *et al*., 2001a). Due to lack of other important differentiating morphological features, *Skrjabinomerus* is considered here as a synonym of *Omphalometra*.

I support Andreiko (1970) and Genov (1984), who considered *Sorexeglyphe* Sadovskaja, 1954 a synonym of *Neoglyphe* Shaldybin, 1953.

*Plagioglyphe* Krasnolobova, 1973 was established for *Plagiorchis fastuosus* Szidat, 1924, *P. morosovi* Sobolev, 1946, *P. obtusus* Strom, 1940 and *Opisthioglyphe megastomus* Baer, 1943 based on the fact that in all these species the uterus does not extend posteriorly beyond the posterior testis. The first three species, all parasites of shorebirds, do not conform to the diagnosis of *Plagiorchis* Lühe, 1899 and might be grouped in a separate genus, although it should be noticed that all available descriptions and drawings of these three species are poor and based on deformed and/or young specimens; therefore, additional studies are necessary to clarify their morphology. *Plagioglyphe* was included in the Plagiorchiinae, Plagiorchiidae by Krasnolobova (1973) and in the Opisthioglyphinae, Plagiorchiidae by Sharpilo & Iskova (1989). Although members of *Plagioglyphe* are superficially similar to omphalometrids, the knowledge of these three species is so limited that I refrain from including it in either the Omphalometridae or Plagiorchiidae and consider it as a genus *incertae sedis*. On the other hand, *Opisthioglyphe megastomus* Baer, 1943 is a parasite of shrews and is distinct in that the testes in this species are not separated by the uterus. Based on this morphological feature and host-specificity, a new genus, *Neoplagioglyphe* n.g., is established here for *Plagioglyphe megastomus* (Baer, 1943) (see diagnosis below). According to Vaucher (1971), the excretory vesicle is Y-shaped and the protonephridial formula is $2[(3 + 3 + 3) + (3 + 3 + 3)] = 36$.

## Family Omphalometridae Looss, 1899

**Diagnosis:** Body elongate or plump, sometimes very thin dorsoventrally, almost leaf-like. Tegument spined. Oral sucker subterminal. Ventral sucker in anterior half or middle third of body. Prepharynx usually present, sometimes indistinct. Pharynx well developed. Oesophagus short to moderately long. Intestinal bifurcation in forebody. Caeca may terminate at or near posterior end of body or at least at level of posterior margin of posterior testis. Testes elongate longitudinally or transversely, tandem or diagonal, intercaecal, in posterior half of body. Cirrus-sac may be relatively straight with curved distal end or comma-shaped, may be entirely in forebody or overlap ventral sucker, with proximal part of cirrus-sac at level of posterior margin of sucker or extending some distance into hindbody, sometimes reaching anterior testis, contains bipartite seminal vesicle, prostatic complex and eversible cirrus usually densely covered with very small spines. Genital pore median or slightly submedian, posterior to or at level of intestinal bifurcation. Ovary submedian, at or posterior to level of ventral sucker. Canalicular seminal receptacle present. Laurer's canal present. Uterus intercaecal, sometimes overlapping caeca, may extend into

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intertesticular space, but never into post-testicular space. Eggs numerous or relatively few. Vitellarium follicular, in lateral fields in hindbody, or into forebody to variable extent, may or may not be confluent anteriorly and posteriorly. Excretory vesicle Y-shaped, with arms reaching level of ventral sucker or even anterior to it; flame-cell formula 2[(3 + 3 + 3) + (3 + 3 + 3)] = 36; pore terminal. In intestine and gall-bladder of mammals; Eurasia, Africa, North America. Type-genus *Omphalometra* Looss, 1899.

## Key to genera

**1a. Body oval to elliptical; uterus pretesticular or extending into testicular zone ..... 2.**
**1b. Body very elongate; uterus entirely pretesticular .....**
**..... *Omphalometra* Looss, 1899. (Fig. 38.1)**
(Syn. *Skrjabinomerus* Sobolev, Mashkov & Mashkov, 1939)

**Diagnosis:** Body very elongate. Suckers relatively small, either equal in size or oral sucker larger than ventral sucker. Ventral sucker just pre-equatorial. Prepharynx short or indistinct. Pharynx well developed. Oesophagus short or indistinct. Intestinal bifurcation very close to anterior extremity, distant from ventral sucker. Caeca terminate near posterior extremity. Testes two, deeply lobed, tandem, in hindbody. Cirrus-sac well defined, claviform, extending posteriorly well beyond ventral sucker; contains bipartite seminal vesicle with proximal part substantially larger than distal part. Genital pore median or slightly submedian, immediately anterior to ventral sucker. Ovary median, in mid-region of body. Uterus intercaecal between anterior testis and genital pore. Metraterm short. Eggs numerous. Vitellarium strongly developed; numerous small follicles form lateral fields that may or may not be confluent posterior to testes and anterior to ventral sucker; anterior margin of vitelline fields at level of ventral sucker or midway between ventral sucker and anterior end of body. Excretory vesicle Y-shaped, bifurcates posterior to posterior testis; arms extend some distance anterior to ventral sucker. In intestine of insectivores; Eurasia. Type-species *O. flexuosa* (Rudolphi, 1809) Looss, 1899.

**2a. In stomach or intestine of shrews ..... 3.**
**2b. In gall-bladder of shrews ..... *Rutshurutrema* Baer, 1959. (Figs 38.2, 38.3)**

**Diagnosis:** Body oval or elongate; in latter case tapering posteriorly. Tegument covered with numerous thin spines. Suckers approximately equal in size or ventral sucker larger than oral sucker. Ventral sucker in anterior third of body. Prepharynx indistinct. Pharynx well developed. Oesophagus very short or indistinct. Intestinal bifurcation in forebody. Caeca terminate near posterior extremity or in last quarter of body. Testes two, moderately to strongly lobed, diagonal, in middle or posterior third of body. Cirrus-sac claviform, overlaps ventral sucker and slightly extends into hindbody. Genital pore median, between ventral sucker and intestinal bifurcation. Ovary median, pretesticular, immediately posterolateral to ventral sucker. Uterus intercaecal between posterior testis and genital pore. Eggs numerous. Vitellarium consisting of numerous small follicles forming lateral fields extending from level of pharynx to posterior body end, confluent posterior to testes. In gall-bladder of shrews; Africa, Eurasia. Type-species *R. acanthodes* Baer, 1959.

**3a. Very small, slender; cirrus-sac extends posteriorly beyond posterior margin of ventral sucker; suckers similar in size or oral sucker larger than ventral sucker; testes not separated by uterus ..... 4.**

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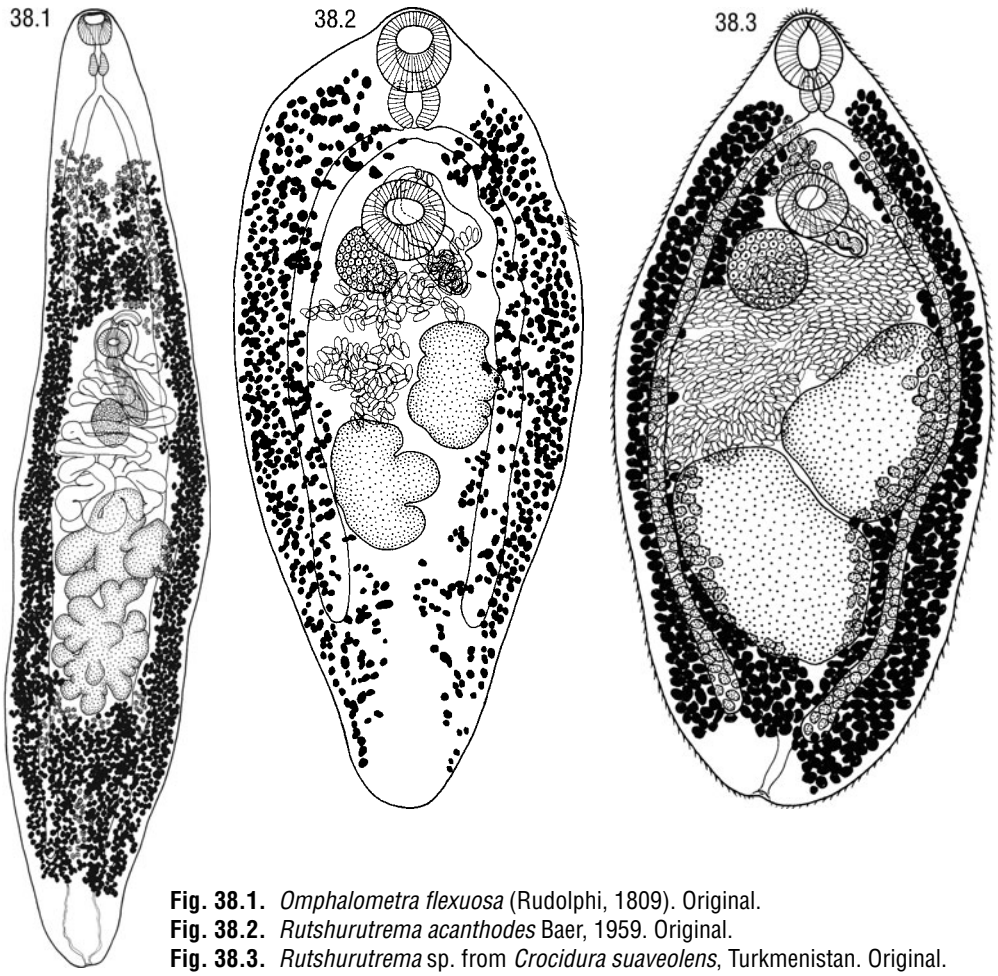



**Fig. 38.1.** *Omphalometra flexuosa* (Rudolphi, 1809). Original.
**Fig. 38.2.** *Rutshurutrema acanthodes* Baer, 1959. Original.
**Fig. 38.3.** *Rutshurutrema* sp. from *Crocidura suaveolens*, Turkmenistan. Original.

**3b. Relatively large, very muscular and thick-bodied; cirrus-sac entirely in forebody; suckers very powerful, ventral sucker larger than oral sucker; testes separated by uterus ..... ..... *Rubenstrema* Dollfus, 1949. (Figs 38.4, 38.5)**

**Diagnosis:** Body elongate. Tegument spined. Suckers very muscular. Ventral sucker in anterior half of body, larger than oral sucker. Prepharynx indistinct. Pharynx well developed. Oesophagus indistinct. Caeca reaching posterior extremity. Testes diagonal, just postequatorial, entire or lobed, separated by uterus. Cirrus-sac claviform, entirely in forebody, encloses bipartite seminal vesicle, well-developed prostatic complex and ejaculatory duct. Genital pore usually just in forebody. Ovary immediately posterolateral to ventral sucker. Uterus between ventral sucker and posterior testis, extends into intertesticular space. Eggs numerous. Vitellarium well developed, consisting of numerous small follicles, confluent in post-testicular region; anterior extent at level of middle of ventral sucker or pharynx; when reaching pharynx, vitelline fields interrupted on both sides at level of ventral sucker. Excretory vesicle bifurcates between testes. In intestine of insectivores; Eurasia. Type-species *R. exasperatum* (Rudolphi, 1819) Dollfus, 1949.

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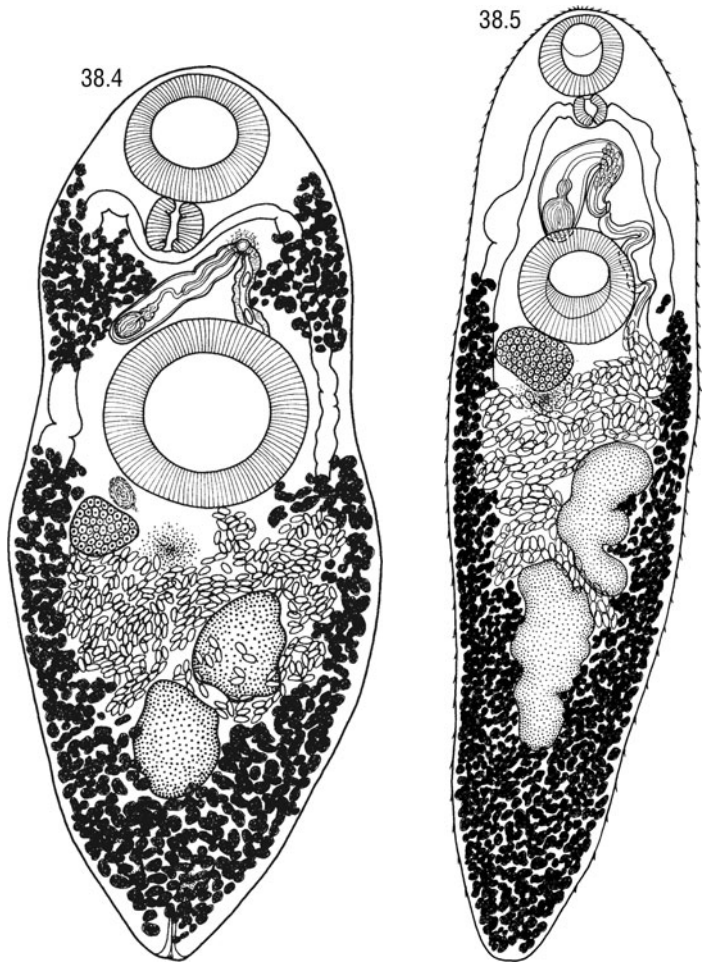



**Fig. 38.4.** *Rubenstrema exasperatum* (Rudolphi, 1819). Original.
**Fig. 38.5.** *Rubenstrema opisthovitellina* (Soltys, 1953). Original.

**4a. Body pear-shaped or oval, extremely flattened dorsoventrally; testes always tandem and strongly transversely elongate; suckers approximately similar in size or oral sucker slightly larger than ventral; uterus entirely pretesticular** ..... ***Neoglyphe* Shaldybin, 1953. (Figs 38.6, 38.7)**
(Syn. *Sorexeglyphe* Sadovskaja, 1954)

**Diagnosis:** Body pear-shaped or oval, extremely flattened dorsoventrally. Tegument densely covered with spines. Suckers approximately similar in size or oral sucker slightly larger than ventral. Ventral sucker usually at border between first and second third of body. Prepharynx very short, but distinct. Pharynx well developed. Oesophagus short. Intestinal bifurcation in mid-forebody. Caeca terminate posterior to testes, near posterior extremity. Testes tandem, contiguous, in posterior half, usually posterior third, of body, irregularly shaped, frequently lobed, always transversely elongate. Cirrus-sac claviform, curved, reaches well into hindbody, to left of ovary, sometimes

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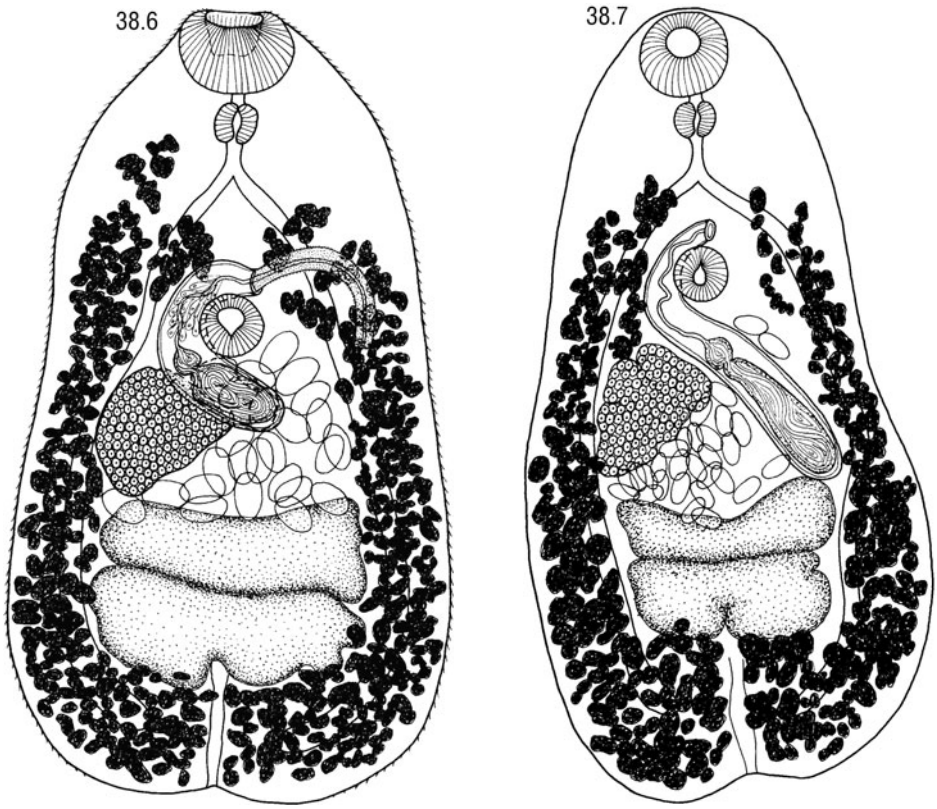



**Fig. 38.6.** *Neoglyphe locellus* (Kossack, 1910). Original.
**Fig. 38.7.** *Neoglyphe sobolevi* (Shaldybin, 1953). Original.

reaches anterior testis, contains bipartite seminal vesicle, prostatic complex and ejaculatory duct. Proximal part of seminal vesicle much longer than distal. Cirrus covered with very small spines. Genital pore in forebody, median. Ovary posterolateral to ventral sucker. Uterus entirely pretesticular. Eggs relatively few. Metraterm well defined. Vitellarium consists of numerous follicles forming lateral fields confluent posterior to testes and extending anteriorly to level of intestinal bifurcation or pharynx. In intestine of mammals; Eurasia, North America. Type-species *N. locellus* (Kossack, 1910) Shaldybin, 1953.

**4b. Body elongate or oval, narrows at posterior end; testes tandem or diagonal, spherical or rounded; oral sucker much larger than ventral; uterus may reach posterior testis ..... ..... *Neoplagioglyphe* n.g. (Fig. 38.8)**

**Diagnosis:** Body elongate or oval, narrows at posterior end. Tegument spined. Oral sucker much larger than ventral sucker. Ventral sucker usually at border between first and second third of body. Prepharynx very short or indistinct. Pharynx well developed. Oesophagus indistinct. Caeca terminate close to posterior extremity. Testes entire, rounded or spherical, contiguous, diagonal or tandem, in posterior half of body. Cirrus-sac claviform, curved, reaches well into hindbody to left of ovary, sometimes reaching anterior testis, contains bipartite seminal vesicle, prostatic complex and

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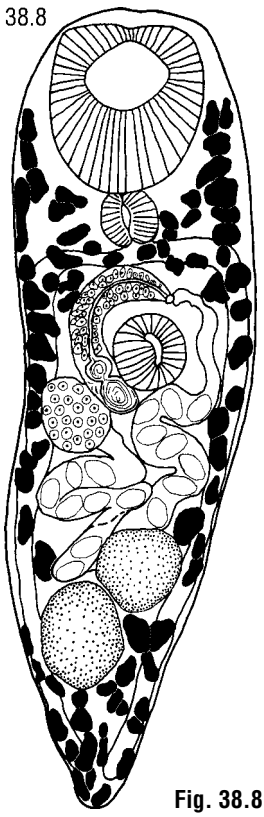



**Fig. 38.8.** *Neoplagioglyphe megastomus* (Baer, 1943) n. comb. After Baer (1944).

ejaculatory duct. Proximal part of seminal vesicle longer than distal. Cirrus unspined. Genital pore in forebody, median or submedian. Ovary posterolateral or lateral to ventral sucker. Uterus between genital pore and posterior testis, not between testes. Eggs not very numerous. Vitellarium consists of numerous large follicles forming lateral fields confluent posterior to testes and anterior to ventral sucker, extends anteriorly to level of pharynx. Excretory vesicle Y-shaped. In intestine of mammals; Europe. Type-species *N. megastomus* (Baer, 1943) n. comb.

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# 39 Family Opisthogonimidae Travassos, 1928

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## Introduction

The Opisthogonimidae Travassos, 1928 is a small group of plagiorchioid digeneans currently comprising three genera reported as adults only from snakes in the neotropics. It was originally proposed as a subfamily by Travassos (1928b) for *Opisthogonimus* Lühe, 1900 because of several peculiar morphological features of this genus, most notably the position of the genital pore in the hindbody. It should be noted that the species *O. lecithonotus* Lühe, 1900, the type-species, was for a long time considered a junior synonym of *O. phylodriadum* (West, 1896), which was thus looked upon by some authors as the type-species for several decades. Artigas *et al.* (1943) studied this question and proved that the two species are different, and, therefore, *O. lecithonotus* was re-established as the type-species of *Opisthogonimus*. Mehra (1937) considered the Opisthogoniminae Travassos, 1928 as a subfamily of the Plagiorchiidae Lühe, 1901. Later, Artigas *et al.* (1942) proposed another plagiorchiid subfamily, the Liophistrematinae Artigas, Ruiz & Leão, 1942. However, Freitas (1956) raised the Opisthogoniminae to full family status and included within this family the Liophistrematinae. According to Freitas (1956), the Opisthogonimidae included four subfamilies, the Opisthogoniminae (with *Opisthogonimus* Lühe, 1900 and *Westella* Artigas, Ruiz & Leão, 1942), the Sticholecithinae Freitas, 1956 (with *Sticholecitha* Prudhoe, 1949), the Liophistrematinae (with *Liophistrema* Artigas, Ruiz & Leão, 1942) and the Bieriinae Freitas, 1956 (with *Bieria* Leão, 1946).

Skrjabin & Antipin (1958a) included both *Liophistrema* and *Bieria* in the Liophistrematinae but, in the same year, Yamaguti (1958b) placed *Opisthogonimus, Westella* and *Liophistrema* in the Opisthoginiminae within the Plagiorchiidae. Skrjabin & Antipin (1962b) made further changes in the classification of the Opisthogonimidae by accepting the system proposed by Freitas (1956), with the exception of the subfamily Bieriinae. They recognized three subfamilies, the Opisthogoniminae (*Opisthogonimus* and *Westella*), Sticholecithinae (*Sticholecitha*) and Liophistrematinae (*Liophistrema* and *Bieria*).

Artigas & Perez (1969) revised the known species of the Opisthogonimidae and convincingly demonstrated that *Opisthogenes* Nicoll, 1914, established for digeneans from a South American snake in the London Zoological Gardens, should be considered a synonym of *Opisthogonimus*. These authors removed *Sticholecitha* and *Bieria* from the Opisthogonimidae and accommodated

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them in the family 'Bieriidae Artigas & Perez, 1969' (i.e. in effect, they raised the Bieriinae Freitas, 1956 to full family status). I agree that the latter two genera should not be included in the Opisthogonimidae because of the presence of the genital pore in the forebody and other morphological features that do not conform with the remainder of the opisthogonimids. At the same time, the recognition of a separate family for them seems to be premature and not well grounded; therefore, in the present volume, they are included in the obviously polyphyletic Plagiorchiidae.

Yamaguti (1971) considered *Westella* a subgenus of *Opisthogonimus*. However, I can see few morphological differences between these forms that justify the recognition of subgenera and thus consider it a synonym of *Opisthogonimus*.

The most recent addition to the Opisthogonimidae, *Paracotyletrema* Volonterio, Baletta & Meneghel, 2006, possesses a very large curved cirrus-sac and a genital pore in the hindbody, and it is characterized by a smaller body than that of other opisthogonimids (Volonterio *et al*., 2006).

The position of the genital pore in the hindbody is known in a few other plagiorchioids, such as Choanocotylidae Jue Sue & Platt, 1998 and Gekkonotrematidae Yamaguti, 1971. However, substantial morphological differences between these three groups suggest the absence of a close evolutionary relationship. Unfortunately, their affinities cannot be examined at present using either life-cycles or DNA, because such data are presently available only for the Choanocotylidae.

Based on a combination of morphological features, in the present keys I recognize the Opisthogonimidae as a separate family including three genera, namely *Opisthogonimus, Paracotyletrema* and *Liophistrema*. Yamaguti (1971) placed *Liophistrema* into the clearly polyphyletic Macroderidae Goodman, 1952, which contained members of at least three different families. This genus may potentially not belong to the Opisthogonimidae; however, current data are not adequate for further clarifying its systematic position.

## Family Opisthogonimidae Travassos, 1928

(Syns Liophistrematinae Artigas, Ruiz & Leão, 1942; Opisthogonimidae Freitas, 1956)

**Diagnosis:** Body usually elongate, rarely oval. Tegumental spines present. Oral sucker subterminal. Ventral sucker of similar size to oral sucker or smaller. Prepharynx present, although may be very short. Pharynx oval. Oesophagus short. Caeca terminate near posterior extremity or some distance short of it. Testes diagonal or almost symmetrical. Cirrus-sac large or, rarely, small, contains convoluted seminal vesicle, curved, between ventral sucker and ovary or overlaps posterior or middle region of ventral sucker. Genital pore submedian, in hindbody. Ovary submedian, pretesticular, posterior to ventral sucker or partly overlapping it. Seminal receptacle present. Laurer's canal present. Uterus reaches posterior end of body. Eggs numerous. Vitellarium follicular, forming lateral extra- or intracaecal fields in middle portion of body, or irregularly dispersed as individual small follicles or bunches of follicles in middle third of body. Excretory vesicle Y-shaped, with long stem and short arms; pore terminal. In mouth, oesophagus, lungs and intestine of snakes; Neotropical region. Type-genus *Opisthogonimus* Lühe, 1900.

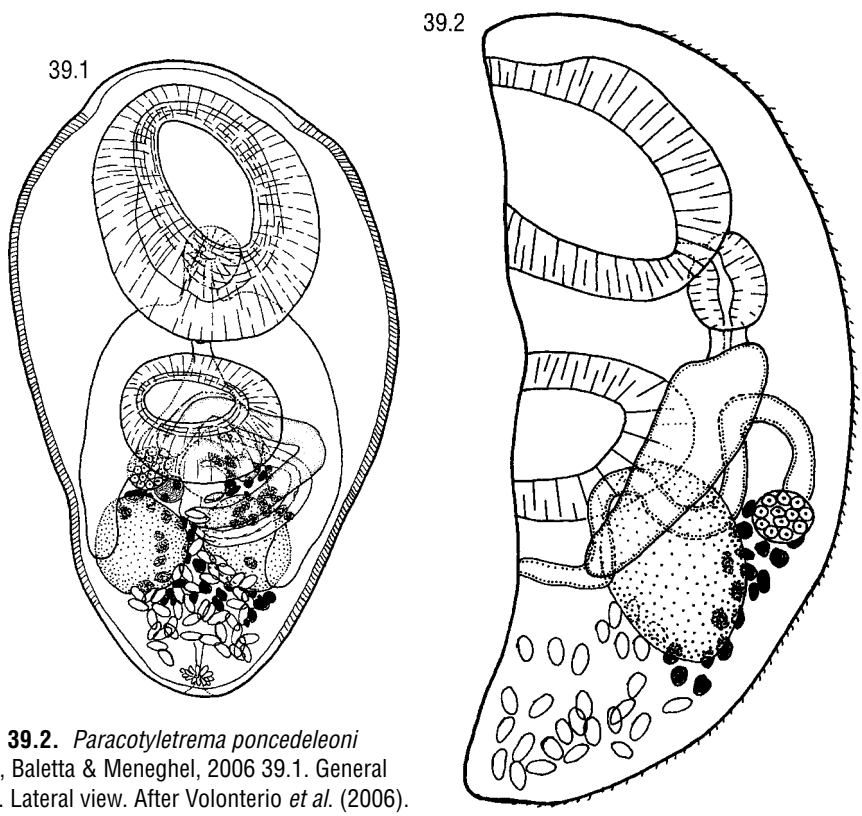
## Key to genera

**1a. Body elongate; oral sucker in adult worms with diameter less than one-fifth of body-length; ventral sucker well separated from oral sucker and usually at, or close to, border between first and second thirds of body; testes well posterior to ventral sucker; caeca extend posteriorly far beyond level of testes ..... 2.**

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**1b. Body very compact, irregularly oval; oral sucker very large, with diameter of one-third to almost one-half of body-length; suckers close together, with ventral sucker in middle of body; testes immediately posterior to, or overlap, ventral sucker; caeca end at level of posterior margin of testes or slightly beyond ..... ..... *Paracotyletrema* Volonterio, Baletta & Meneghel, 2006. (Figs 39.1, 39.2)**

**Diagnosis**: Body small, with maximum width at level of posterior end of oral sucker. Oral sucker powerful, with diameter of more than quarter body-length, larger than ventral sucker. Ventral sucker equatorial to slightly pre-equatorial, at distance of about diameter of pharynx from oral sucker. Prepharynx short. Pharynx small. Oesophagus short. Intestinal caeca end at level of posterior margin of testes or slightly beyond but never reach posterior end of body. Genital pore in testicular zone of anterior hindbody, median or sinistrally submedian. Cirrus-sac long, more than half body-length, contorted. Testes symmetrical, immediately posterior to ventral sucker, postequatorial, spherical or ovoid. Ovary spherical to ovoid, smaller than testes, overlaps ventral sucker, dextral. Seminal receptacle, Laurer's canal and Mehlis' gland present. Uterus caecal and intercaecal, extends to posterior end of body. Well-defined metraterm initially passes laterally, then curves posteriorly and runs parallel to descending portion of cirrus-sac. Vitellarium dorsal, mostly intercaecal, consisting of numerous follicles in two partly merged fields, somewhat overlapping testes, ventral sucker and ovary. Excretory vesicle not known; pore terminal. In mouth and oesophagus of snakes; Neotropical region. Type-species *P. poncedeleoni* Volonterio, Baletta & Meneghel, 2006.




**Figs 39.1, 39.2.** *Paracotyletrema poncedeleoni* Volonterio, Baletta & Meneghel, 2006 39.1. General view. 39.2. Lateral view. After Volonterio *et al.* (2006).

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**2a. Cirrus-sac strongly curved, usually question mark-shaped and usually overlaps ventral sucker, with its distal part curved posteriorly ..... ..... *Opisthogonimus* Lühe, 1900. (Figs 39.3–39.5)**

(Syns *Opisthogenes* Nicoll, 1914; *Westella* Artigas, Ruiz & Leão, 1942)

**Diagnosis**: Body elongate, fusiform, spatulate, claviform or subcylindrical. Oral sucker subterminal. Ventral sucker at about third of body-length from anterior body end. Prepharynx present. Oesophagus short. Caeca terminate near posterior extremity or at some distance short of it. Testes diagonal or sub-symmetrical, in middle third of body. Cirrus-sac usually question mark-shaped with distal region oriented posteriorly, usually large, rarely small, between ventral sucker and ovary or overlapping ventral sucker, contains convoluted seminal vesicle. Genital pore submedian, in hindbody. Ovary submedian, pretesticular, more or less separated from ventral sucker. Seminal receptacle present. Uterus reaches to, or close to, posterior extremity. Vitelline follicles either lateral in extra- or intracaecal fields of middle portion of body, or dispersed as individual small follicles or bunches of follicles in middle third of body. Excretory vesicle Y-shaped, with numerous fine anastomosing branches; pore terminal. In mouth and intestine of snakes; Neotropical region. Type-species *O. lecithonotus* Lühe, 1900.

**2b. Cirrus-sac only slightly curved, entirely in hindbody, its distal part slightly curved anteriorly ..... *Liophistrema* Artigas, Ruiz & Leão, 1942. (Fig. 39.6)**

**Diagnosis:** Body elongate, relatively large. Oral sucker subterminal, larger than ventral sucker. Ventral sucker at border between first and second thirds of body. Prepharynx short but distinct. Pharynx small. Oesophagus very short. Caeca extend into posterior third of body but do not reach posterior extremity. Testes rounded, intercaecal, diagonal, in middle third of body. Cirrus-sac small, between ventral sucker and ovary, contains more or less convoluted seminal vesicle and armed cirrus. Genital pore submedian, in hindbody. Ovary spherical, submedian, between anterior testes and cirrus-sac. Seminal receptacle immediately postovarian. Uterus with numerous coils, occupies most of hindbody and reaches posterior extremity. Metraterm well differentiated, narrow. Eggs numerous. Vitellarium consists of several bunches of small follicles forming irregular field extending from cirrus-sac to some distance posterior to testes. Excretory vesicle Y-shaped, with very short stem; pore terminal. In lungs of snakes; Neotropical region. Type-species *L. pulmonale* Artigas, Ruiz & Leão, 1942 (emend.).

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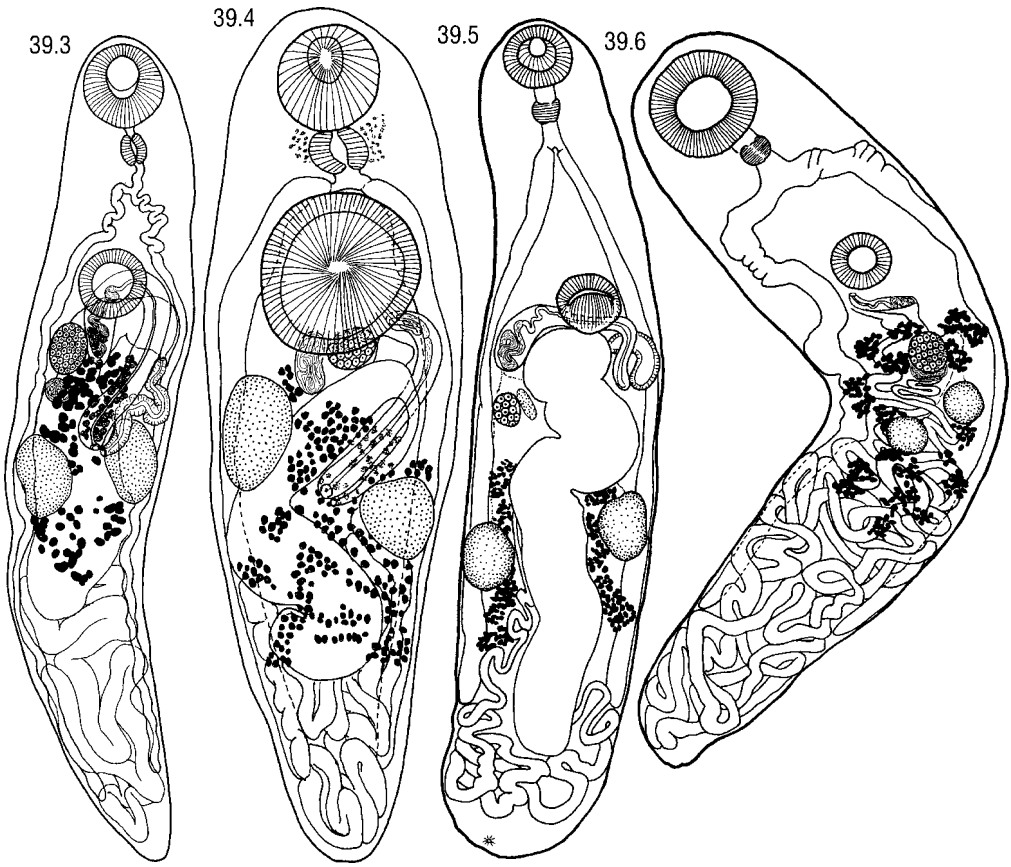



**Fig. 39.3.** *Opisthogonimus lecithonotus* Lühe, 1900. Original.
**Fig. 39.4.** *Opisthogonimus megabothrium* Pereira, 1928. After Skrjabin & Antipin (1962b).
**Fig. 39.5.** *Opisthogonimus sulina* (Artigas, Ruiz & Leão, 1942). After Artigas *et al.* (1942).
**Fig. 39.6.** *Liophistrema pulmonale* Artigas, Ruiz & Leão, 1942. After Artigas *et al.* (1942).

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# 40 Family Orientocreadiidae Yamaguti, 1958

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## Introduction

The Orientocreadiidae Yamaguti, 1958 is a small family of fish and reptile parasites from the Palaearctic and Ethiopian regions. It is characterized by its spiny tegument (sometimes reported as smooth), the uterus filling most of the hindbody, a fairly restricted follicular vitellarium, presence of both external and internal seminal vesicles and a uterine seminal receptacle. It was erected as the subfamily Orientocreadiinae Yamaguti, 1958 in the Allocreadiidae Looss, 1902 by Yamaguti (1958b) for *Orientocreadium* Tubangui, 1931 and *Macrotrema* Gupta, 1951, considered a family in the Lepocreadioidea Odhner, 1905 by Skrjabin & Koval (1960), and reviewed by Skrjabin & Koval (1963). *Orientocreadium* was reviewed by Fischthal & Kuntz (1963) and Shimazu (1990). The extensive uterus, reaching the posterior extremity, spined tegument and follicular vitellarium indicate that, until other evidence is available, the superfamily Plagiorchioidea Lühe, 1901 is the most appropriate venue for this family.

Yamaguti (1953b) treated *Ganada* Chatterji, 1933, *Neoganada* Dayal, 1938 and *Nizamia* Dayal, 1938 as synonyms of *Orientocreadium*. Later (Yamaguti, 1958b), he added *Ganadotrema* Dayal, 1949 and *Paratormopsolus* Bychowsky & Dubinina, 1954 as synonyms and then *Macrotrema* in 1971 (Yamaguti, 1971). Beverley-Burton (1962) considered that only three *Orientocreadium* species were valid, and included in that observation species originally placed in *Ganada, Neoganada* and *Ganadotrema*. Fischthal & Kuntz (1963) regarded *Paratormopsolus* as a synonym of *Orientocreadium*, and *Neoganada*, *Nizamia*, *Ganadotrema* and *Macrotrema* as synonyms of *Ganada*. *Ganada* and *Orientocreadium* were distinguished by the Y-shaped excretory vesicle in the former. Shimazu (1990) also considered *Paratormopsolus* a synonym of *Orientocreadium*, but followed Fischthal & Kuntz's (1963) system 'for the time being'. He pointed out, however, that Tang & Lin (1973) and Besprozvannykh (1984) found the excretory vesicle of the cercaria of *Orientocreadium* spp. to be Y-shaped. He quoted Tubangui (1931), Yamaguti (1934), Beverley-Burton (1962) and Fischthal & Kuntz (1963) as describing an I-shaped excretory vesicle, but was unable to confirm that himself. Nevertheless, he retained distinct genera based on this feature. El-Naggar *et al*. (1993) redescribed *O. batrachoides* Tubangui, 1931 in some detail, but described the excretory vesicle just as 'saccular'. Most recently, Dutta (1995) considered all these genera

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synonymous with *Orientocreadium*. R.A. Bray examined the specimens of *Orientocreadium* in the BMNH collection but was unable to detect the nature of the excretory system in any of these variously fixed specimens. Whilst bearing in mind that careful examination of live specimens might indicate that this feature has some systematic value, it is not considered here to be a practical differentiating character.

The nature of the seminal receptacle has been the subject of some debate in orientocreadiids. Fischthal & Kuntz (1963), summarizing the information to that date, stated that in *Orientocreadium* a 'true' seminal receptacle was lacking, but a uterine seminal receptacle was present. They said that in *Ganada* a 'true' seminal receptacle was sometimes present along with the uterine seminal receptacle. Tang & Lin (1973) illustrated an expanded proximal part of Laurer's canal containing sperm in *O. batrachoides*. Shimazu (1990) stated that there was no seminal receptacle in orientocreadiids, but that the proximal uterus served as a seminal receptacle. However, in the two species he described he reported that the proximal part of Laurer's canal and the distal part of the oviduct were expanded and sometimes contained a few sperm. El-Naggar *et al*. (1993) also found no seminal receptacle but reported seeing moving sperm in the oötype and Laurer's canal. Kim & Rim (1995) found no seminal receptacle, but reported sperm in the uterus in two *Orientocreadium* spp. Observations on the specimens in the BMNH collection confirm the usual presence of the uterine seminal receptacle, but sperm was not seen elsewhere in the female system.

Most good descriptions of orientocreadiids describe spines on the tegument and the strong suspicion is that, when they are reported as missing, this is due to post-mortem loss.

Agrawal & Sharma (1990b) erected a new subgenus, *Pseudoorientocreadium* Agrawal & Sharma, 1990, within *Orientocreadium*, which is differentiated from the nominate subgenus by having 'numerous rows of circum oral spines'. From the illustrations of the type- and only species, *O. (P.) tori* Agrawal & Sharma, 1990, these spines appear to be rather small. Our present knowledge of this form indicates that this taxon, if recognized, should be retained as a subgenus.

## Family Orientocreadiidae Yamaguti, 1958

**Diagnosis:** Body elongate to fusiform. Tegument spinous or reportedly not. Oral sucker subglobular, subterminal. Ventral sucker in anterior half of body, rounded. Prepharynx distinct. Pharynx oval. Oesophagus usually short, may be long. Intestinal bifurcation in posterior forebody. Caeca terminate blindly near posterior extremity. Testes two, entire or lobate, median, tandem or oblique, in posterior half of body. External seminal vesicle present. Cirrus-sac claviform. Internal seminal vesicle oval. Pars prostatica narrow. Ejaculatory duct spined or not. Genital atrium shallow. Genital pore median, immediately anterior to ventral sucker. Ovary entire or trilobed, submedian, pretesticular. Sperm may accumulate in distal oviduct and proximal Laurer's canal. Mehlis' gland usually postovarian. Uterine seminal receptacle present. Uterus extends to, or near to, posterior extremity, reaching extracaecally. Metraterm well developed, spined or not. Eggs operculate, small, numerous, segmented, fully embryonated or not. Vitellarium follicular, in lateral fields in hindbody; fields continuous or interrupted, usually reaching posterior extremity, may or may not unite to form lattice in young worms. Excretory vesicle I- or Y-shaped, reaching posterior testis; pore terminal or subterminal. In freshwater fishes and reptiles; Palaearctic and Ethiopian regions. Type-genus *Orientocreadium* Tubangui, 1931.

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## Genus *Orientocreadium* Tubangui, 1931 (Fig. 40.1)

(Syns *Ganada* Chatterji, 1933; *Ganadotrema* Dayal, 1949; *Macrotrema* Gupta, 1951 *nec* Regan, 1912; *Neoganada* Dayal, 1938; *Nizamia* Dayal, 1938; *Paratormopsolus* Bychowsky & Dubinina, 1954)

**Diagnosis:** With characters of family. Type-species *O. batrachoides* Tubangui, 1931.

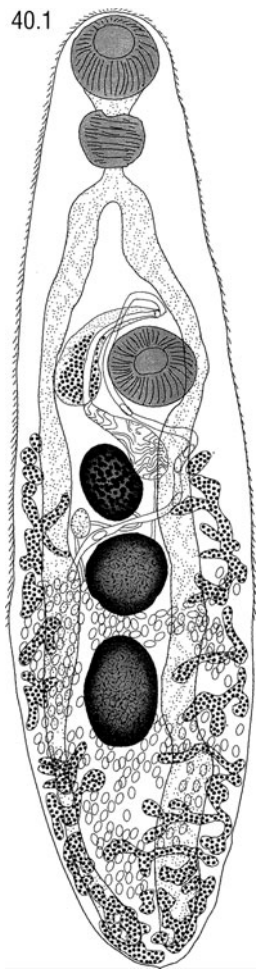



**Fig. 40.1.** *Orientocreadium batrachoides* Tubangui, 1931. After Tubangui (1931).

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# 41 Family Reniferidae Pratt, 1902

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## Introduction

This family includes plagiorchioid digeneans parasitic in Nearctic and Neotropical snakes and is characterized, among other features, by its Y-shaped excretory vesicle with a long stem and long arms encircling the ventral sucker, the lack of a seminal receptacle and a life-cycle involving amphibians as second intermediate hosts. The group has had a highly complicated taxonomic history since Pratt (1902a) proposed the subfamily Reniferinae Pratt, 1902 within the Plagiorchiidae Lühe, 1901 to include *Renifer* Pratt, 1902, *Ochetosoma* Braun, 1902, *Styphlodora* Looss, 1899, *Astiotrema* Looss, 1900 and *Oistosomum* Odhner, 1902. *Renifer* and *Ochetosoma* have been shown to be synonymous (Leão, 1945), while the remaining four genera have been allocated to different families. However, Baer (1924) raised the Reniferinae to the rank of family, a decision not accepted by all subsequent authors. Those not agreeing with this designation usually included the taxon as a subfamily within the Plagiorchiidae, apart from Yamaguti (1971), who considered it a tribe, the Ochetosomatini Leão, 1945, within the plagiorchiid subfamily Styphlodorinae Dollfus, 1937. Many authors have proposed systems for this group, with the most important contributions being made by Baer (1924), Mehra (1931, 1937), Talbot (1934), Byrd & Denton (1938a), Kagan (1947), Skrjabin & Antipin (1957) and Dubois & Mahon (1959). Among these schemes, the system and diagnosis of the group and its constituent genera proposed by Byrd & Denton (1938a), and generally followed by Skrjabin & Antipin (1957), seem to me to be the best grounded.

Leão (1945) convincingly argued that *Renifer* and *Ochetosoma* are synonymous and provided evidence that *Ochetosoma* is older than *Renifer*. Skrjabin & Antipin (1957) and some other authors accepted this viewpoint and used the name Ochetosomatidae Leão, 1945 as the family name. However, during the course of work on this chapter, it was discovered that the name *Ochetosoma* is pre-occupied by the much older *Ochetosoma* Leuckart & Rüppell, 1828, used for a genus of the Echiuridae Quatrefages, 1847, phylum Echiura Newby, 1940. Therefore, the generic name *Renifer* Pratt, 1902 is recognized as valid here and, accordingly, the family name Reniferidae Pratt, 1902 is used.

In some cases, systematic rearrangements have been made with no or very little justification. For instance, Skrjabin & Antipin (1957) accepted a family diagnosis proposed by Byrd & Denton (1938a), but a year later the same authors (Skrjabin & Antipin, 1958b), without any explanation,

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added six more genera to the family, none of them strictly fitting the diagnoses provided by Skrjabin & Antipin (1957). At different times, at least 29 genera have been included in the Reniferidae (or Reniferinae), namely *Aptorchis* Nicoll, 1914, *Astiotrema* Looss, 1900, *Bhaleraopharynx* Skrjabin & Antipin, 1958, *Bilorchis* Mehra, 1937, *Caudorchis* Talbot, 1933, *Dasymetra* Nicoll, 1911, *Dolichopera* Nicoll, 1914, *Heterocoelium* Travassos, 1921, *Lechriorchis* Stafford, 1905, *Macrodera* Looss, 1899, *Manodistomum* Stafford, 1905, *Mediorima*, Nicoll, 1914, *Neochetosoma* Caballero, 1949, *Neorenifer* Byrd & Denton, 1938, *Natriodera* Mehra, 1937, *Ochetosoma* Braun, 1902, *Ochetosomoides* Wang, 1982, *Oistosomum* Odhner, 1902, *Ophiorchis* Mehra, 1937, *Oudhia* Gupta, 1953, *Plagitura* Holl, 1928, *Platymetra* Mehra, 1931, *Pneumatophilus* Odhner, 1910, *Ptyasiorchis* Mehra, 1937, *Renifer* Pratt 1902, *Stomatrema* Guberlet, 1928, *Styphlodora* Looss, 1899, *Xenopharynx* Nicoll, 1912 and *Zeugorchis* Stafford, 1905. Some of these genera have been synonymized (see the discussion and key below), whereas others have been transferred to other families, such as the Plagiorchiidae, Leptophallidae Dayal, 1938 and Dolichoperoididae Johnston & Angel, 1940 (see discussions and diagnoses in Tkach, Chapter 23, Tkach, Chapter 33, and Gibson, Chapter 27, this volume). In the present key, I include in the Reniferidae only *Renifer, Dasymetra, Pneumatophilus, Lechriorchis, Paralechriorchis* and *Zeugorchis*, which share the set of distinctive features mentioned at the beginning of this introduction. None of the remaining genera appears to possess all of these features.

Very detailed accounts of the taxonomic history of the group and reasons for the various rearrangements can be found in Byrd & Denton (1938a) and Skrjabin & Antipin (1957); hence, only a few systematic issues are addressed below.

*Neorenifer* Byrd & Denton 1938 was established for members of *Renifer* with a genital pore situated anteriorly to the intestinal bifurcation, i.e. in the region of the pharynx and oral sucker, while, according to Byrd & Denton (1938a), members of *Renifer* have the genital pore at the level of the intestinal bifurcation. Kagan (1947) rejected *Neorenifer* on the basis of the substantial variability observed in the position of the genital pore among species attributed to *Renifer* and *Neorenifer*. Skrjabin & Antipin (1957) agreed with this, and I also concur. Accordingly, all species possessing a lateral (extracaecal) genital pore situated at a level between the intestinal bifurcation and the oral sucker belong to *Renifer*.

*Natriodera* Mehra, 1937 was created for the species *Macrodera verlatum* Talbot, 1934 because of the substantial differences between this species and *M. longicollis* (Abildgaard, 1788), the type-species of *Macrodera* Looss, 1899. Mehra (1937) and a majority of other authors placed *Natriodera* in the Reniferinae. Subsequently, it has been included in the Reniferidae except by Yamaguti (1958b, 1971), who created the subfamily Natrioderinae Yamaguti, 1958 within the Plagiorchiidae for it, and Goodman (1959), who allocated it to the Macroderinae Goodman, 1959, also within the Plagiorchiidae. The genus resembles reniferids in the general topology of its organs, the absence of a seminal receptacle and the shape of the seminal vesicle; however, as shown by Goodman (1959), it differs substantially in the nature of the excretory vesicle, which has short branches not reaching the ventral sucker. Therefore, it is considered here within the polyphyletic Plagiorchiidae.

*Paralechriorchis* Byrd & Denton, 1938 was established for species that differ from *Lechriorchis* mainly in the relative length of the metraterm and cirrus-sac and in the shape of the uterine loops. Some authors placed this genus among synonyms of either *Lechriorchis* or *Manodistomum* (see discussion below). The systematic importance of the above characters is not quite clear, and, therefore, *Paralechriorchis* is considered here as a separate genus until more is known of the phylogenetic interrelationships among reniferids. *P. bosci* (Cobbold, 1859), allocated to *Paralechriorchis* by Byrd & Denton (1938a), is provisionally considered here to belong to *Zeugorchis* because of substantial differences between this and other species of *Paralechriorchis*, especially in the much

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longer intestinal caeca, the position of the testes near the posterior end of body and, to a lesser extent, the long oesophagus. Unfortunately, the very brief original description and poor illustrations of *P. bosci* do not permit a more definitive allocation.

*Stomatrema* Guberlet, 1928 is small genus including three or four species specific to the mud snake *Farancia abacura* in North America. The majority of authors have allocated this genus to the Plagiorchiinae, whereas Yamaguti (1971) created the subfamily Stomatrematinae Yamaguti, 1971 for it. These digeneans share with typical reniferids the peculiar shape of the excretory vesicle with long arms encircling the ventral sucker, parasitism in the mouth of snakes and the life-cycle pattern. However, in species of *Stomatrema* the stem of the excretory vesicle is shorter and they have a well-defined seminal receptacle. Details of the organization of the seminal vesicle are not mentioned in any of the available descriptions, but it is usually illustrated as bipartite. Unfortunately, the poor quality of the museum specimens examined by the author and Dr Rodney Bray did not allow for accurate assessment of this and other morphological features of *Stomatrema*. Taking into account the above differences, I include *Stomatrema* in the Plagiorchiidae, although it cannot be excluded that this genus may be eventually returned to the Reniferidae.

*Caudorchis* Talbot, 1933 was considered by several authors (Price, 1935; Byrd & Denton, 1938a; Skrjabin & Antipin, 1957) to be a synonym of *Zeugorchis*. I agree.

On the other hand, Harwood (1932) and Yamaguti (1971) considered *Zeugorchis* and *Plagitura* among the synonyms of *Manodistomum* Stafford, 1905, and Yamaguti (1971) added also *Paralechriorchis* to this list. The taxonomic history of these synonymies is rather complicated. Stafford (1905) described, without illustrations, *Manodistomum occultum* Stafford, 1905 based on an immature specimen found in a newt (site of infection unknown) and a metacercaria from frog muscles. Stafford thought that these two forms were identical and noticed their similarity to his new genus *Zeugorchis* described in the same paper. It is almost certain that the immature digenean described by Stafford from the intestine of the newt did not belong to the same species as the metacercaria described by him from frog muscles. The former was congeneric with the form later described within *Plagitura* Holl, 1928, while the latter was one of the reniferid metacercarial forms commonly found in frogs in that part of the world. Later, Holl (1928) erected *Plagitura* Holl, 1928 for *P. salamandra* Holl, 1928 found in the same newt species as Stafford's *M. occultum*. Price (1930b) correctly synonymized *Plagitura* with *Manodistomum*. The synonymy of *Zeugorchis* and *Manodistomum* by Harwood (1932) was based on the superficial similarity of these forms and cannot be accepted. *Manodistomum* ( = *Plagitura*) is characterized by the presence of a seminal receptacle and a much shorter excretory vesicle with arms not reaching the ventral sucker. Furthermore, the stem of the excretory vesicle in *Manodistomum* is heavily pocketed, whereas in reniferids it is rather smooth. Therefore, *Manodistomum* is here placed provisionally in the Plagiorchiidae.

Rabalais & Gibson (1972) considered *Zeugorchis* a synomym of *Lechriorchis* based on the wide morphological variability of species belonging to both genera. This action, as well as some of the synonymies of species proposed by these authors, appears somewhat premature and I retain *Zeugorchis* as a separate genus until the interrelationships among reniferids and the relative systematic value of the morphological characters of this group are better understood.

*Oudhia* Gupta, 1953 was included in the Ochetosomatidae (= Reniferidae) by Skrjabin & Antipin (1957) without comment. Yamaguti (1971) transferred it to the Cephalogonimidae Looss, 1899, where it is treated in this volume (Jones & Bray, Chapter 25). In any case, it is clear that *Oudhia* cannot belong to the Reniferidae because it differs in the presence of a large seminal receptacle, a clearly bipartite seminal vesicle, short arms of the excretory vesicle and parasitism in fish.

*Ochetosomoides* Wang, 1982 was erected by Wang P.-q. (1982a) for *O. scomberomori* Wang, 1982 found in Indo-Pacific king mackerel. The latter species and genus cannot be included in the

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Reniferidae because of several substantial morphological differences, among which are the entirely pretesticular uterus (in adult specimens of reniferids part of the uterus is post-testicular) and the large external seminal vesicle (this is absent in all members of the Reniferidae). The description of *O. scomberomori* lacked details of organization of the reproductive and excretory systems. It was placed 'for convenience' in the Lepocreadiidae Odhner, 1905 by Bray (2005a).

Although some authors described reniferids without tegumental spines, I am certain that all members of this family do possess spines. It is well known that tegumental spines can be easily lost if the digeneans are not fixed properly or quickly enough after the death of the worm. Among very numerous specimens, both from my own collection and museum loans, only specimens known to be collected from frozen hosts or those in poor condition (i.e. inadequately fixed) lacked spines.

The content of this family as well as the arrangement of its genera and species may, and almost certainly will, change when more data on the morphology of adult and larval stages, life-history and phylogenetic interrelationships of plagiorchioidean digeneans are available. Due to the highly unstable and variable nature of the majority of the morphological characters used in the current classification of the Reniferidae, it may be anticipated that all of the presently recognized genera may collapse into just two, *Renifer* and *Pneumatophilus*. At this point, however, such dramatic systematic changes are premature. The future inclusion of the current and provisional members of the Reniferidae in molecular phylogenetic analyses will help to assess the systematic value of certain morphological characters, such as the presence or absence of the seminal receptacle, the shape of the seminal and excretory vesicles, and other features.

## Family Reniferidae Pratt, 1902

(Syns Reniferinae Pratt, 1902; Ochetosomatidae Leão 1945)

**Diagnosis:** Body elongate-oval, usually with rounded extremities. Tegument armed with spines. Oral sucker subterminal. Ventral sucker pre-equatorial. Prepharynx usually present. Pharynx present, rounded. Oesophagus usually present. Intestinal bifurcation in forebody. Caeca variable in length, ending blindly at or beyond middle of body. Testes two, smooth or lobate, symmetrical or oblique, in middle or posterior third of body. Cirrus-sac well developed, rarely extends posteriorly beyond ventral sucker, contains coiled seminal vesicle. Genital pore between suckers, median, submedian or marginal. Ovary pretesticular, posterior to or somewhat overlapping ventral sucker, smooth or lobed. Laurer's canal present. Seminal receptacle absent. Uterus well developed, descends and ascends between testes, reaching to posterior end of body, may have numerous loops or just one descending and one large ascending loop. Metraterm present, variable in length and degree of development. Eggs numerous. Vitelline follicles usually arranged in two lateral extra- or supracaecal fields, rarely extending into intracaecal space, usually situated in middle third of body, sometimes extending into posterior third. Excretory vesicle Y-shaped, with long stem and arms encircling ventral sucker; pore terminal. In digestive tract and respiratory tracts, exceptionally in reproductive organs, of snakes; Nearctic and Neotropical regions. Type-genus *Renifer* Pratt, 1902.

## Key to genera

**1a. Genital pore median or submedian, post-bifurcal ..... 2.**

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**1b. Genital pore marginal or submarginal, pre-bifurcal .....**
**..... *Renifer* Pratt, 1902. (Figs 41.1–41.4)**
(Syns *Ochetosoma* Braun, 1901 *nec* Leuckart & Rüppell, 1828; *Pseudorenifer* Price 1935; *Neorenifer* Byrd & Denton, 1938; *Neochetosoma* Caballero, 1949)

**Diagnosis:** Body oval to elongate. Caeca variable in length, may or may not be directed towards midline of body between testes. Testes symmetrical or nearly so. Cirrus-sac large, muscular, entirely in forebody or somewhat overlapping ventral sucker. Genital pore marginal or submarginal between levels of pharynx and intestinal bifurcation. Ovary submedian, near posterior margin of ventral sucker or lateral to it. Metraterm variable in length, usually well developed and muscular. Vitelline fields may be separated by space into two fields on each side of body. In upper digestive tract of snakes. Type-species *R. ellipticus* Pratt, 1902.

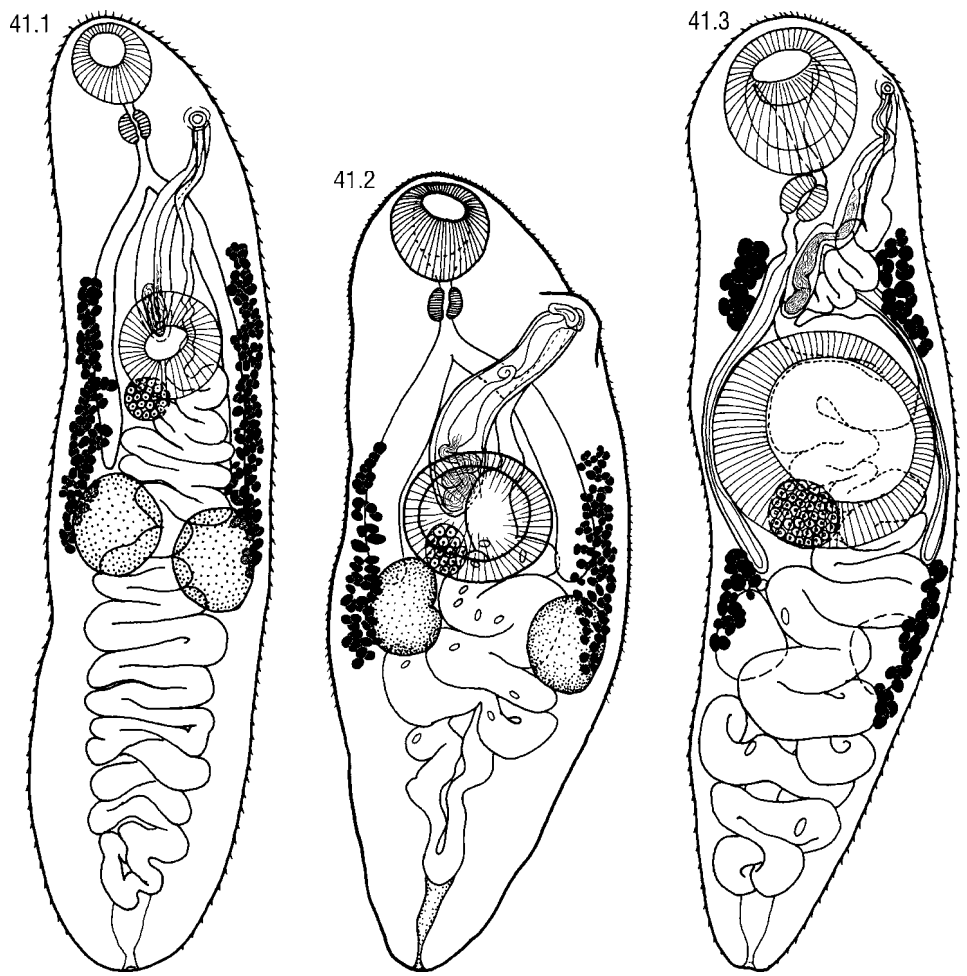



**Fig. 41.1.** *Renifer ellipticus* Pratt 1902. Original.
**Fig. 41.2.** *Renifer heterocoelium* (Travassos, 1921). Original.
**Fig. 41.3.** *Renifer aniarum* (Leidy, 1890). Original.

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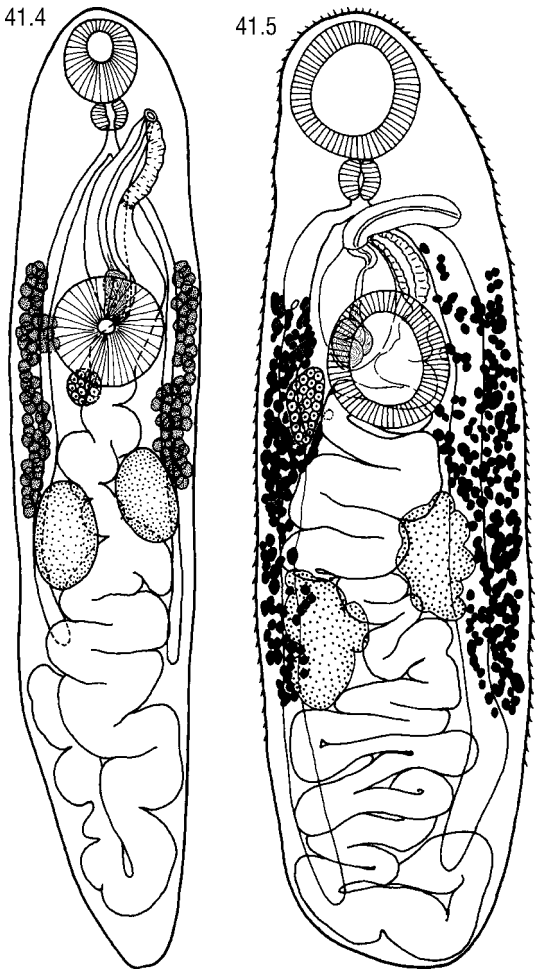



**Fig. 41.4.** *Renifer validum* (Nicoll, 1911). Original.
**Fig. 41.5.** *Dasymetra conferta* Nicoll, 1911. Original.

**2a. Testes symmetrical or almost so** ..... **3.**
**2b. Testes distinctly diagonal** ..... ***Dasymetra* Nicoll, 1911. (Fig. 41.5)**
**Diagnosis:** Body rather stout and muscular. Prepharynx and oesophagus present. Caeca long, almost reaching posterior end of body. Testes clearly diagonal, entire or slightly lobed, oval or irregular in shape. Cirrus-sac large, may or may not extend posteriorly beyond ventral sucker. Genital pore median or slightly submedian, at level of intestinal bifurcation or somewhat posterior to it. Ovary submedian, close to posterior margin of ventral sucker, on same side of body as cirrus-sac. Uterus forms characteristic knot-like loop at posterior end of body. Metraterm very muscular, about half length of cirrus-sac. Vitelline fields dendritic in appearance, overlap caeca; lateral fields may merge in region of ovary. In upper digestive tract of snakes. Type-species *D. conferta* Nicoll, 1911.

**3a. Testes at or just posterior to middle of body** ..... **4.**
**3b. Testes in posterior quarter of body** ..... ***Zeugorchis* Stafford, 1905. (Fig. 41.6)**
(Syn. *Caudorchis* Talbot, 1933)

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**Diagnosis:** Body oval. Caeca reach to testicular level. Testes symmetrical, in posterior quarter of body, posterior to caeca and close to posterior extremity. Cirrus-sac muscular, may or may not extend into hindbody. Genital pore median or slightly submedian between ventral sucker and intestinal bifurcation. Ovary median or submedian, at posterior margin of ventral sucker. Uterus slightly post-testicular, mainly between testes and ovary. Metraterm muscular, about half length of cirrus-sac. Lateral vitelline fields may overlap caeca and extend into intercaecal space. In digestive and respiratory tracts of snakes. Type-species *Z. aequatus* Stafford, 1905.

**4a. Body elongate, usually elliptical; testes entire or somewhat irregular in shape ..... 5.**
**4b. Body strongly flattened, pyriform, widest at level of testes; testes usually strongly lobed, rarely oval ..... *Pneumatophilus* Odhner, 1910. (Fig. 41.7)**

**Diagnosis:** Body strongly flattened, with anterior end somewhat attenuated and caudal end broadly rounded. Ventral sucker larger than oral sucker. Caeca relatively short, not extending posteriorly beyond testes and usually terminate at level of anterior margin of testes. Testes symmetrical, not greatly separated from ovary, deeply lobed or smooth. Cirrus-sac muscular, not extending posteriorly beyond ventral sucker. Genital pore median or slightly submedian, at level

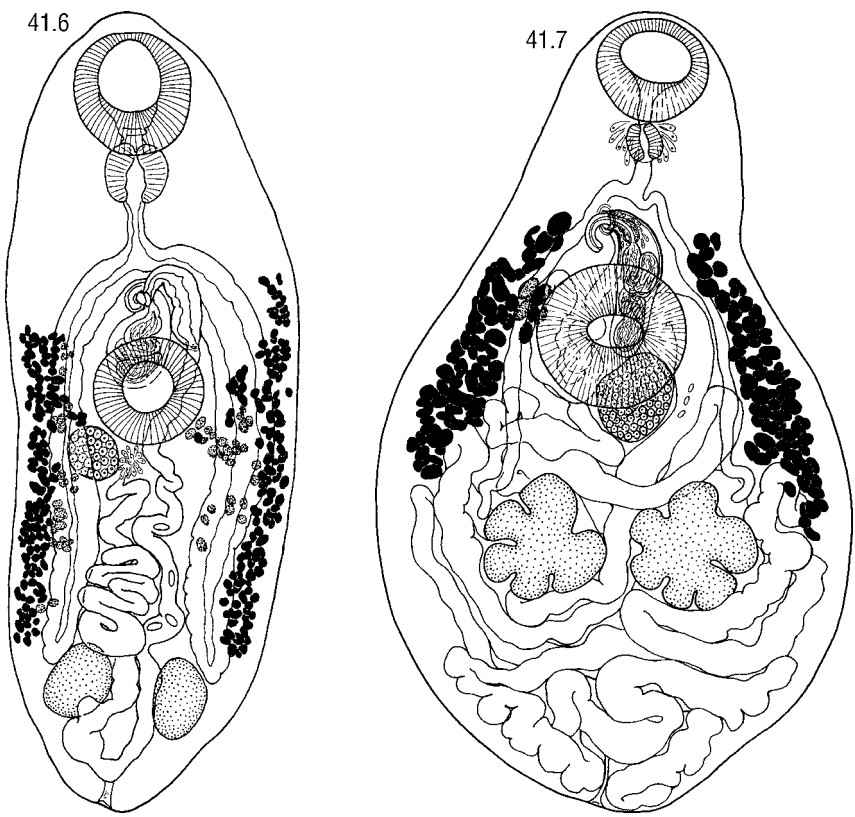



**Fig. 41.6.** *Zeugorchis eurinus* (Talbot, 1933). Original.
**Fig. 41.7.** *Pneumatophilus leidyi* Byrd & Denton, 1937. Original.

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of intestinal bifurcation or slightly posterior to it. Ovary submedian, at posterior margin of ventral sucker. Uterus forms numerous transverse and vertical loops in hindbody. Metraterm muscular, about two-thirds of cirrus-sac length. Vitelline fields mostly extracaecal, extending from level of anterior margins of testes to level of intestinal bifurcation. In respiratory tract of snakes. Type-species *P. variabilis* (Leidy, 1856).

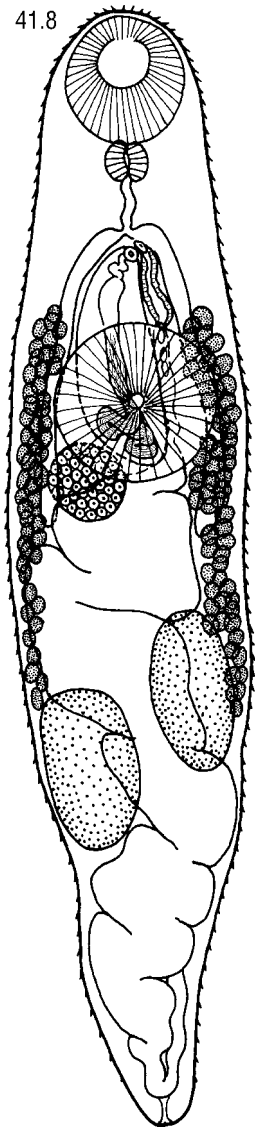
**5a. Cirrus-sac long; metraterm one-third to half length of cirrus-sac; uterus consists of two longitudinal loops; ascending loop is strongly inflated when filled with eggs ..... ..... *Lechriorchis* Stafford, 1905. (Fig. 41.8)**
(Syn. *Mediorima* Nicoll, 1914)

**Diagnosis:** Ventral sucker larger than oral sucker. Prepharynx short. Oesophagus present. Testes symmetrical or slightly diagonal. Cirrus-sac long, muscular, does not extend posterior to middle of ventral sucker. Genital pore median or slightly submedian, between intestinal bifurcation and ventral sucker. Ovary submedian, at posterior margin of ventral sucker. Uterus consists of two longitudinal loops; ascending loop is strongly inflated when filled with eggs. Metraterm well developed, muscular, about one-third to half length of cirrus-sac. Vitelline fields usually in middle of body, but may extend anteriorly to level of intestinal bifurcation and posteriorly to level of posterior margins of testes. In respiratory and digestive tracts of snakes. Type-species *L. primus* Stafford, 1905.

**5b. Cirrus-sac middle-sized; metraterm about equal in length to cirrus-sac; uterus consists of several transverse folds ..... *Paralechriorchis* Byrd & Denton, 1938. (Fig. 41.9)**

**Diagnosis:** Prepharynx very short. Oesophagus as long as pharynx or somewhat longer. Caeca do not extend posteriorly beyond testes. Testes symmetrical, oval or irregular in shape, usually at border between middle and posterior thirds of body. Cirrus-sac middle-sized, muscular, does not extend posterior to middle of ventral sucker. Genital pore median or slightly submedian, at or just posterior to intestinal bifurcation. Ovary submedian, at posterior margin of ventral sucker. Uterus with several transverse folds. Metraterm well developed, muscular, approximately as long as cirrus-sac. Anterior limit of vitelline fields between levels of ventral sucker and intestinal bifurcation; posterior limit at level of anterior or posterior margins of testes. In digestive and reproductive tracts of snakes. Type-species *P. syntomentera* (Sumwalt, 1926).

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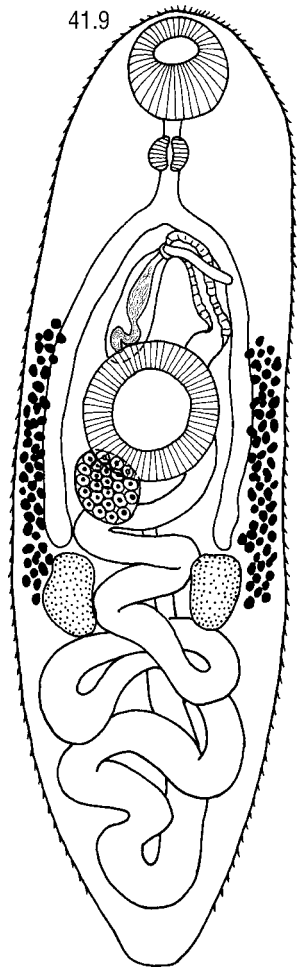




**Fig. 41.8.** *Lechriorchis tygarti* Talbot, 1933. Original.
**Fig. 41.9.** *Paralechriorchis syntomentera* (Sumwalt, 1926). After Schell (1985).

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# 42 Family Styphlotrematidae Baer, 1924

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## Introduction

The Styphlotrematidae Baer, 1924 is an enigmatic family of plagiorchioid digeneans containing the single genus *Styphlotrema* Odhner, 1911. This genus has a highly complex taxonomic history with systematic arrangements changed in almost every paper on the subject. It is described in numerous publications, the most detailed being Skrjabin & Antipin (1961). The type- and only species of the genus, *S. solitaria* Looss, 1899 was first described by Looss (1899) from the sea turtle *Thalassochelys corticata* (now *Caretta caretta*) in Egypt within *Styphlodora* Looss, 1899. Odhner (1911b) established *Styphlotrema* for this species and Baer (1924) created the subfamily Styphlotrematinae within his new family Reniferidae Baer, 1924.

The taxonomic composition of this family has always been controversial. For instance, Baer (1924) included *Styphlotrema* and *Pachypsolus* Looss, 1901 in the Styphlotrematinae, whereas Mehra (1931) expanded the subfamily to seven genera by adding *Styphlodora* Looss, 1899, *Glossidium* Looss, 1899, *Glossidiella* Travassos, 1928, *Aptorchis* Nicoll, 1914 and *Spinometra* Mehra, 1931. Later, Mehra (1937) removed *Aptorchis* from this subfamily, but added *Glossimetra* Mehra 1937. Byrd & Denton (1938b) reshuffled the system again and moved *Styphlotrema* and *Pachypsolus* to the Enodiotrematinae Baer, 1924 within the Plagiorchiidae. Byrd *et al*. (1940a) concluded that the highly unusual organization of the excretory vesicle of *Styphlotrema*, featuring two additional lateral arms arising from the base of an otherwise Y-shaped vesicle, substantially differentiates it from *Styphlodora* and other plagiorchiids. Thus, they recognized it as a subfamily including only the type-genus. However, Yamaguti (1958b) transferred *Styphlotrema* to the Styphlodorinae Dollfus, 1937, a decision reversed by Skrjabin & Antipin (1961), who resurrected the Styphlotrematinae, to include a single genus. Later, Yamaguti (1971) proposed a tribe, the Styphlotrematini, with five genera, within the subfamily Styphlodorinae. However, most genera included by Yamaguti within this tribe are obviously not closely related to *Styphlotrema*. Therefore, in the present work, I support the viewpoint of both Byrd *et al*. (1940a) and Skrjabin & Antipin (1961). Furthermore, *Styphlotrema* is considered here within its own family, and I, therefore, raise the subfamily to full family status as the Styphlotrematidae Baer, 1924, since no other members of the obviously polyphyletic Plagiorchiidae possess an excretory vesicle with a similar structure.

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This arrangement will somewhat reduce the extreme morphological diversity among the Plagiorchiidae as it is presently recognized.

Kohn & Fernandes (1982) described a second species, *S. artigasi* Kohn & Fernandes, 1982, from a marine fish. Despite a general morphological similarity, *S. artigasi* differs somewhat from *S. solitaria* in the structure of seminal vesicle and vitellarium, and no information on the organization of the excretory vesicle was provided. Thus, I anticipate that the systematic position of *S. artigasi* will change once the missing morphological data are obtained.

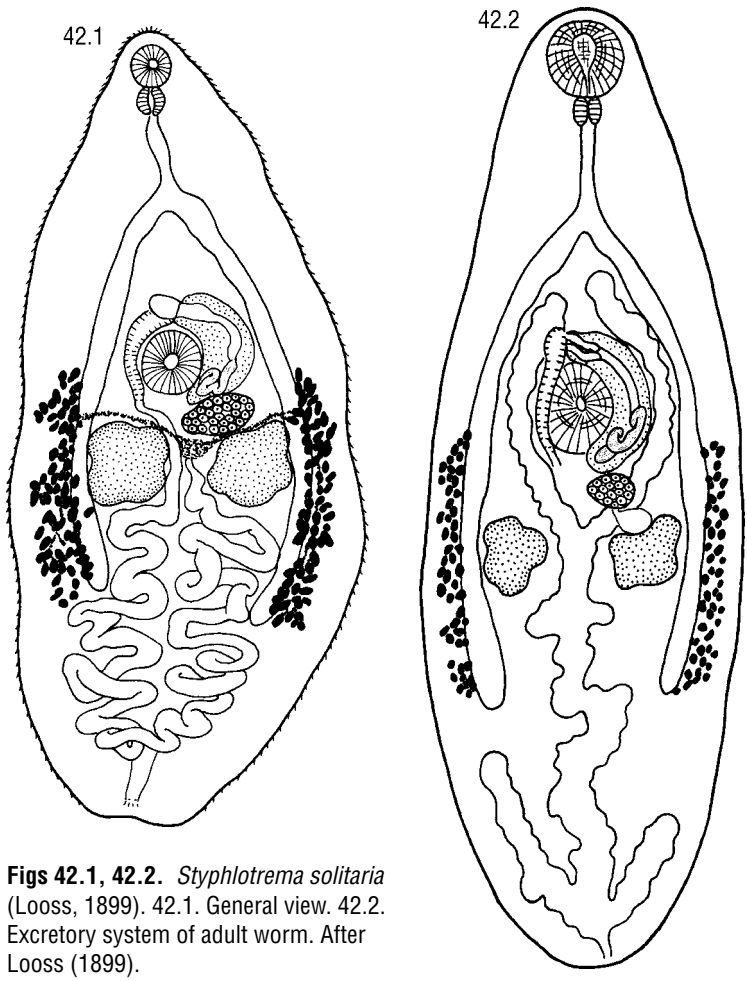
## Family Styphlotrematidae Baer, 1924

**Diagnosis:** Small digeneans with elongate-oval body. Tegumentary spination almost reaches posterior end of body. Oral sucker subterminal. Ventral sucker pre-equatorial, somewhat larger than oral sucker. Prepharynx indistinct. Oesophagus three to four times longer than pharynx. Intestinal bifurcation approximately midway between suckers. Caeca terminate at level of posterior margin of vitelline fields at about halfway between ventral sucker and posterior extremity. Testes irregularly symmetrical in middle of body, somewhat posterior to ventral sucker. Cirrus-sac claviform, longitudinal, curved around left side of ventral sucker, contains coiled seminal vesicle, pars prostatica and short eversible cirrus. Genital pore median or slightly submedian, immediately anterior to ventral sucker. Ovary oval or pyriform, between ventral sucker and left testis, just posterior to testes, median or slightly submedian. Small seminal receptacle between, or overlapped by, ovary and left testis. Laurer's canal present. Uterus well developed, inter- and postcaecal, occupies most of hindbody. Metraterm well defined. Eggs numerous. Vitellarium consists of numerous small follicles in two lateral fields occupying extracaecal space in middle third of body, from level of posterior margin of ventral sucker to ends of caeca. Excretory vesicle has two branches arising from its base, while main stem of vesicle branches between testes and ventral sucker into two long arms embracing ventral sucker and almost reaching intestinal bifurcation; stem with numerous shallow diverticula; pore subterminal. In intestine of marine turtles and marine fish; Mediterranean Sea and western Atlantic Ocean. Type-genus *Styphlotrema* Odhner, 1911.

## Genus *Styphlotrema* Odhner, 1911 (Figs 42.1, 42.2)

**Diagnosis:** With characters of family. Type-species *S. solitaria* (Looss, 1899).

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**Figs 42.1, 42.2.** *Styphlotrema solitaria* (Looss, 1899). 42.1. General view. 42.2. Excretory system of adult worm. After Looss (1899).

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# 43 Family Telorchiidae Looss, 1899

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## Introduction

The family Telorchiidae Looss, 1899 consists of intestinal parasites of turtles, other reptiles and amphibians. The distinguishing morphological characteristics of these spinous worms include tandem, usually almost contiguous, testes, typically located near the posterior extremity in genera with elongate bodies; exceptionally in more broadly ovoid worms, the testes may be diagonal. The ovary is pretesticular, usually just posterior to the ventral sucker and separated from the anterior testis by uterine coils. The most common uterine configuration is a series of submedian descending coils and a similar, often symmetrical series of ascending coils on the other side of the midline. A cirrus-sac is always present and typically overlaps the ventral sucker, but may be entirely anterior to it.

*Telorchis* was erected twice in the same year by Lühe (1899) and Looss (1899), and, according to Perkins (1928), on the same day, 28 December. Lühe (1900b) renamed Looss' genus *Cercorchis* Lühe, 1900 and this can be considered the action of the 'first reviser', giving *Telorchis* Lühe, 1899 priority, a stance that has been almost uniformly adopted since. *Cercorchis* is now considered a synonym of *Telorchis* Lühe, 1899. The subfamily Telorchiinae Looss, 1899 was erected by Looss (1899), in the paper where he erected the junior homonym, and accepted by Lühe (1900b). Stunkard (1924) recognized this taxon at the family level, when erecting *Pterygotomaschalos attenuatus* Stunkard, 1924, a species that has subsequently been assigned to the Auridistomidae Stunkard, 1924 and was considered by Yamaguti (1971) to be a synonym of *Auridistomum chelydrae* (Stafford, 1900).

Various classifications have been proposed, beginning with that of Stunkard (1924), who divided the family into two subfamilies, the Telorchiinae Looss, 1899 and the Auridistominae Stunkard, 1924. Yamaguti (1971) recognized three subfamilies, the Telorchiinae, Loefgreniinae Yamaguti, 1958 and Orchidasmatinae Dollfus, 1937. However, he considered the Opisthioglyphinae Dollfus, 1949 a junior synonym of the Omphalometrinae Looss, 1899 in the family Omphalometridae Looss, 1899, whereas more recent workers (Allison & Blair, 1987; Barton, 1994) included the Opisthioglyphinae in the Telorchiidae. Because their arguments are cogent, we include the Opisthioglyphinae, along with the Telorchiinae, Loefgreniinae and Orchidasmatinae, in the Telorchiidae. Additional support for inclusion of the Opisthioglyphinae in the

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Telorchiidae is provided by Tkach *et al.* (2001c), based on 28S rDNA sequences of *Telorchis assula* (Dujardin, 1845) Dollfus, 1957 and *Opisthioglyphe ranae* (Frölich, 1791) Looss, 1907. Lastly, Goodman (1988b) erected the Allotelorchiinae Goodman, 1988 for two auriculate genera of telorchiids.

Genera assigned to us by the editors for consideration as telorchiids were: *Allotelorchis* Goodman, 1988, *Anadasmus* Looss, 1899, *Auritelorchis* Stunkard, 1979, *Cercorchis* Lühe, 1900, *Divitelluses* Cai & Li, 1993, *Dolichosaccus* Johnson, 1912, *Loefgrenia* Travassos, 1920, *Oligolecithus* Vercammen-Grandjean 1960, *Orchidasma* Looss, 1900, *Paracercorchis* Mehra & Bokhari, 1932, *Paratelorchis* Mehra & Bokhari, 1932, *Paratelorchis* Stunkard & Franz, 1977, *Protenes* Barker & Covey, 1911, *Pseudotelorchis* Yamaguti, 1971 and *Telorchis* Lühe, 1899. To these, we add *Opisthioglyphe* Looss, 1899, the type-genus of the Opisthioglyphinae.

Within the Telorchiinae, members of *Telorchis* are intestinal parasites of turtles, snakes and salamanders. Pulmonate snails serve as first intermediate hosts, in which xiphidiocercariae are produced in daughter-sporocysts. Tadpoles and snails are the most common second intermediate hosts of the encysted metacercariae, and parasites attain sexual maturity in amphibians and reptiles that ingest infected tadpoles and snails (see Yamaguti, 1975, for a review of life-history studies). A taxonomic revision and phylogenetic analysis of *Telorchis* (see MacDonald & Brooks, 1989b) resulted in numerous synonymies, recognized phylogenetically important morphological characters and demonstrated instances of both co-speciation and host-switching in the evolutionary history of the genus. Radke *et al.* (2002) employed the methodology of researchers studying phytophagous insect–plant systems to track resource utilization of North American species of *Telorchis*, providing further insight into their evolutionary history. Two genera are considered junior synonyms of *Telorchis*. Much controversy is associated with *Cercorchis* Lühe, 1900; over many decades, various workers have considered it valid, whereas others have relegated it to synonymy (see Prudhoe & Bray, 1982). In the most recent revision of *Telorchis* by MacDonald & Brooks (1989b), *Cercorchis* was regarded as a junior synonym of *Telorchis*. We agree, as we have been unable to find characters to distinguish the two genera. Yamaguti (1971) regarded *Paracercorchis* Mehra & Bokhari, 1932 as a junior synonym of *Telorchis*. After examining the description of *Paracercorchis*, we support this. As detailed by Stunkard (1979), D.I. Gibson informed him that *Paratelorchis* Mehra & Bokhari, 1932 has precedence over *Paratelorchis* Stunkard & Franz, 1977. However, Gibson further remarked that *Paratelorchis* Mehra & Bokhari, 1932, while designated as a new genus, was not accompanied by a description. Mehra (1937) said, '*Paratelorchis* n.g. appeared as an error in place of *Paracercorchis* n.g. in the footnote on page 48 of our paper': therefore this should be a synonym of *Telorchis*. We, therefore, are unable to consider *Paratelorchis* Mehra & Bokhari, 1932 in our treatment of the Telorchiidae.

In contrast to the species-rich *Telorchis*, most other genera include few species and these have not been the subjects of life-history studies. Most telorchiids are assigned to the Telorchiinae. *Pseudotelorchis* was erected by Yamaguti (1971) for a single species, *P. compactus* (Cable & Sanborn, 1970), because of its unique pattern of uterine coils, diagonal testes and extra-intestinal habitat (oviduct) within the turtle host. MacDonald & Brooks (1987) confirmed that *P. compactus* is monophyletic and regarded it as a basal species within the family. *Protenes* Barker & Covey, 1911, which parasitizes turtles in North America, differs from other genera in having a dorsolateral rather than median genital pore. The brief description and rather inadequate drawing of *Divitelluses cantonensis* Cai & Li, 1993 makes treatment of this genus problematic (Cai & Li, 1993). If not an artefact, the large gap in the lateral vitelline fields at the testicular level provides a useful character to distinguish this genus from all other telorchiids. We tentatively regard this character as real until shown otherwise and, therefore, include *Divitelluses* in our treatment of the family. Species of *Oligolecithus* Vercammen-Grandjean, 1960 parasitize

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African amphibians. They can be distinguished from other genera in the subfamily by a retort-shaped cirrus-sac that is mostly, or entirely, in the forebody.

Stunkard (1979) proposed *Auritelorchis* for *Paratelorchis* Stunkard & Franz, 1977, which is pre-occupied by *Paratelorchis* Mehra & Bokhari, 1932. *A. dollfusi* (Stunkard & Franz, 1977) differs from most previously described telorchiids in having an oral sucker with dorsal and ventral ear-like lobes on the anterolateral faces of the sucker. However, additional auriculate telorchiids were described by Goodman (1988b). *Allotelorchis* Goodman, 1988 was erected for *A. thomasi* (Dollfus, 1950), originally described from an African tortoise as *Auridistomum thomasi* Dollfus, 1950. Goodman (1988b, figure 2) included the ear-like lappets of the oral sucker in his figure of *Auritelorchis harwoodi* Goodman, 1988, but the lappets cannot be seen on the stained whole-mount of the holotype of *A. harwoodi* that we used for our illustration of the genus (Fig. 43.7). Goodman (1988b) distinguished these two auriculate genera by the short uterus of *Allotelorchis* versus the long uterus extending into the hindbody of *Auritelorchis*, and erected the Allotelorchiinae to accommodate them. Although the apparent possession of oral lappets is a common character of these two genera, large differences in the cirrus-sac, uterine configuration and extent of the vitellarium indicate that these oral lappets may be convergent. MacDonald & Brooks (1989b) regarded them as an apomorphic character and placed *Auritelorchis dollfusi* in *Telorchis*. Additional insight with regard to the anatomy of these oral projections, such as the study by Freidenfelds *et al.* (1994), who used the term 'muscular papillae' for these structures, and their evolutionary history within the Telorchiidae may result in further taxonomic revisions in the future, possibly including a consideration of the Auridistomidae.

All other genera of telorchiids are distinct enough to warrant placement in subfamilies other than the Telorchiinae and the Allotelorchiinae. The Loefgreniinae Yamaguti, 1958 is monotypic, containing only *Loefgrenia loefgreni* Travassos, 1920, described from a South American turtle. *Loefgrenia* Travassos, 1920 is distinguished by its long, crenulate forebody and the crescentic muscular thickening of the region of the ventral sucker.

The Orchidasmatinae Dollfus, 1937 is also monotypic, containing only *Orchidasma amphiorchis* (Braun, 1899), a parasite of marine turtles. This species is readily distinguished from other telorchiids in having testes widely separated from one another by a large expanse of uterine coils. Yamaguti (1971) regarded the pre-occupied name *Anadasmus* Looss, 1899 as a junior synonym of *Orchidasma* Looss, 1900.

One can sympathize both with those authors, including Prudhoe & Bray (1982), Allison & Blair (1987), Barton (1994) and Tkach *et al.* (2001c), who place the Opisthioglyphinae Dollfus, 1949 within the Telorchiidae and those (Yamaguti, 1971) who ally it with other taxonomic groups. On one hand, the two genera that we consider within the Opisthioglyphinae, *Opisthioglyphe* Looss, 1899 and *Dolichosaccus* Johnson, 1912, share morphological characters with other telorchiids, and analysis of ribosomal DNA has revealed other similarities (Tkach *et al.*, 2001c). On the other hand, they are the most morphologically distinct of all members of the family; the uterus is composed of relatively few coils, situated between the ovary and anterior testis, and the vitelline follicles extend to near the posterior extremity. Despite these atypical characteristics, we were compelled by the persuasive arguments of Allison & Blair (1987) and Barton (1994) to include both genera in the Telorchiidae. Species of *Opisthioglyphe* parasitize a taxonomically diverse spectrum of amphibians over a broad geographical range encompassing Europe, Asia and Africa. They possess a cirrus-sac more weakly developed and more anteriorly located than that of most telorchiid genera. The morphological variability of species of *Dolichosaccus* has led some authors to recognize several subgenera and others to propose that these subgenera be raised to generic level. A common feature of species of *Dolichosaccus* is the possession of a large cirrus-sac mostly, or totally, in the forebody. However, we believe

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that additional morphological studies are required before the limits of extant subgenera can be fully understood or before the genus can be split into multiple genera. Therefore, we shall take a taxonomically conservative approach and treat the genus in its broadest sense.

## Family Telorchiidae Looss, 1899

**Diagnosis:** Body typically elongate, exceptionally ovoid, bears minute tegumental spines. Oral sucker rounded, subterminal, exceptionally with ear-like lappets (= papillae *sensu* Freidenfelds *et al*., 1994). Ventral sucker round, median, in anterior half of body. Prepharynx small or absent. Pharynx present. Oesophagus typically long, rarely short, may be absent. Intestinal bifurcation in forebody. Caeca elongate, terminate blindly near posterior extremity. Testes two, usually smooth, exceptionally slightly lobed, usually tandem, almost contiguous near posterior extremity of elongate taxa, exceptionally diagonal in some ovoid specimens. Cirrus-sac variable in size and position, extremely robust with very spinous cirrus to weak and retort-shaped, overlapping or entirely anterior to ventral sucker. Internal seminal vesicle typically saccular, unipartite. Genital atrium absent. Genital pore usually median, occasionally submedian, at level of or posterior to intestinal bifurcation. Ovary pretesticular, in forebody or mid-body, median to submedian, usually separated from anterior testis by uterine coils (except in *Orchidasma*). Mehlis' gland usually inconspicuous. Canalicular seminal receptacle present or absent. Laurer's canal present. Uterine configuration typically consists of numerous, tightly packed descending coils from ovary to anterior testis and similar, often symmetrical, ascending coils to genital pore; exceptionally, uterus with few transverse coils. Metraterm muscular and robust to absent. Eggs small or large, numerous or few, operculate. Vitellarium follicular; follicles usually small, lateral, typically occupy middle third of body, occasionally extend from intestinal bifurcation to near posterior extremity. Excretory vesicle usually Y-shaped with long stem; pore usually terminal. In intestine (or oviduct in *Pseudotelorchis*) of amphibians and reptiles, especially turtles; mainly freshwater, exceptionally marine, cosmopolitan. Type-genus *Telorchis* Lühe, 1899.

## Key to subfamilies

**1a. Anterior and posterior testes separated by numerous uterine coils ..... Orchidasmatinae Dollfus, 1937.**

**1b. Anterior and posterior testes not separated by numerous uterine coils ..... 2.**

**2a. Forebody very long and crenulate; semilunar muscular thickening in region of ventral sucker ..... Loefgreniinae Yamaguti, 1958.**

**2b. Forebody relatively short, with smooth margin; ventral sucker lacks semilunar muscular thickening ..... 3.**

**3a. Oral sucker with lateral ear-like muscular lappets (= papillae) ..... Allotelorchiinae Goodman, 1988.**

**3b. Oral sucker lacking lateral ear-like muscular lappets ..... 4.**

**4a. Vitelline follicles extend to near posterior extremity, typically confluent medially near posterior extremity ..... Opisthioglyphinae Dollfus, 1949.**

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**4b. Vitelline follicles do not extend to near posterior extremity, never confluent medially ..... ..... Telorchiinae Looss, 1899.**

## Subfamily Telorchiinae Looss, 1899

**Diagnosis:** Body elongate with near-parallel sides to oval. Oral sucker round, subterminal. Ventral sucker small to large. Prepharynx present or absent. Oesophagus typically short. Caeca usually slender. Testes smooth, round to oval, exceptionally slightly lobed, tandem to diagonal, contiguous or nearly so, near posterior extremity. Cirrus-sac very elongate to small, extends far posterior to ventral sucker or almost entirely anterior to sucker, contains saccular seminal vesicle; pars prostatica and ejaculatory duct present, typically elongate; prostatic cells surround ejaculatory duct. Genital pore median or submedian, just anterior to ventral sucker or near intestinal bifurcation. Ovary round or oval, median or submedian, contiguous with ventral sucker or widely separated, typically pre-equatorial, occasionally in mid-body. Uterus often forms descending and ascending, near symmetrical, lateral, tightly packed coils between ovary and anterior testis; occasionally, descending and ascending coils not symmetrical. Metraterm robust and elongate or absent. Eggs small, numerous. Vitelline follicles in lateral fields typically most extensive in middle third of body; fields never extend close to posterior extremity, rarely extend anteriorly to or beyond level of ventral sucker; follicles typically very small and abundant, exceptionally large, few. Excretory vesicle Y-shaped; pore usually terminal. In intestine, rarely oviduct, of amphibians and reptiles (especially turtles); North America, South America, Europe, Asia. Type-genus *Telorchis* Lühe, 1899.

## Key to genera

**1a. Testes diagonal ..... 2.**
**1b. Testes tandem ..... 3.**

**2a. Vitellarium with few large follicles ..... ..... *Oligolecithus* Vercammen-Grandjean, 1960. (Fig. 43.1)**
**Diagnosis:** Body linguiform. Ventral sucker larger than oral sucker. Prepharynx present or absent. Oesophagus short. Testes rounded with slightly irregular margins, diagonal, almost contiguous. Cirrus-sac almost completely anterior to ventral sucker, flask-shaped, diagonal, contains saccular seminal vesicle, short pars prostatica and ejaculatory duct. Genital pore midway between caecum and lateral body margin. Ovary round, posterolateral to ventral sucker, nearly contiguous with sucker. Seminal receptacle may be hidden by uterus. Uterus forms descending and ascending coils between ovary and testes; ascending and descending coils overlap and do not form regular transverse folds. Metraterm about half as long as cirrus-sac. Vitelline follicles few, large, in lateral fields in middle third of body. Excretory vesicle Y-shaped, with bulbous or sinuous stem. In intestine of amphibians; Africa. Type-species *O. elianae* Vercammen-Grandjean, 1960.

**2b. Vitellarium with many small follicles ..... *Pseudotelorchis* Yamaguti, 1971. (Fig. 43.2)**
**Diagnosis:** Body bluntly oval. Ventral sucker, round, median, larger than oral sucker, pre-equatorial. Prepharynx absent. Oesophagus very short. Testes diagonal, contiguous, with scalloped margins. Cirrus-sac mostly in forebody, with distinct lateral flexure; seminal vesicle sacculate. Genital pore submedian. Ovary nearly round, posterolateral to and contiguous with ventral sucker. Uterine

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seminal receptacle present. Uterus forms descending and ascending irregular transverse coils between ovary and testes. Vitelline follicles pyriform, small, numerous, in small lateral clusters in middle third of body. Excretory vesicle not known. In oviduct of *Emydoides blandingi*; North America. Type-species *P. compactus* (Cable & Sandborn, 1970) Yamaguti, 1971.

**3a. Genital pore dorsolateral ..... *Protenes* Barker & Covey, 1911 (Fig. 43.3)**
**Diagnosis:** Body elongate, with nearly parallel margins. Oral sucker small. Ventral sucker small, round median, pre-equatorial. Prepharynx present. Testes round, tandem, nearly contiguous. Cirrus-sac elongate, sinuous, contains sacculate seminal vesicle; cirrus often formed. Genital pore dorsolateral. Ovary almost median, round. Canalicular seminal receptacle absent. Uterus forms descending and ascending symmetrical, transverse, tightly packed coils between ovary and anterior

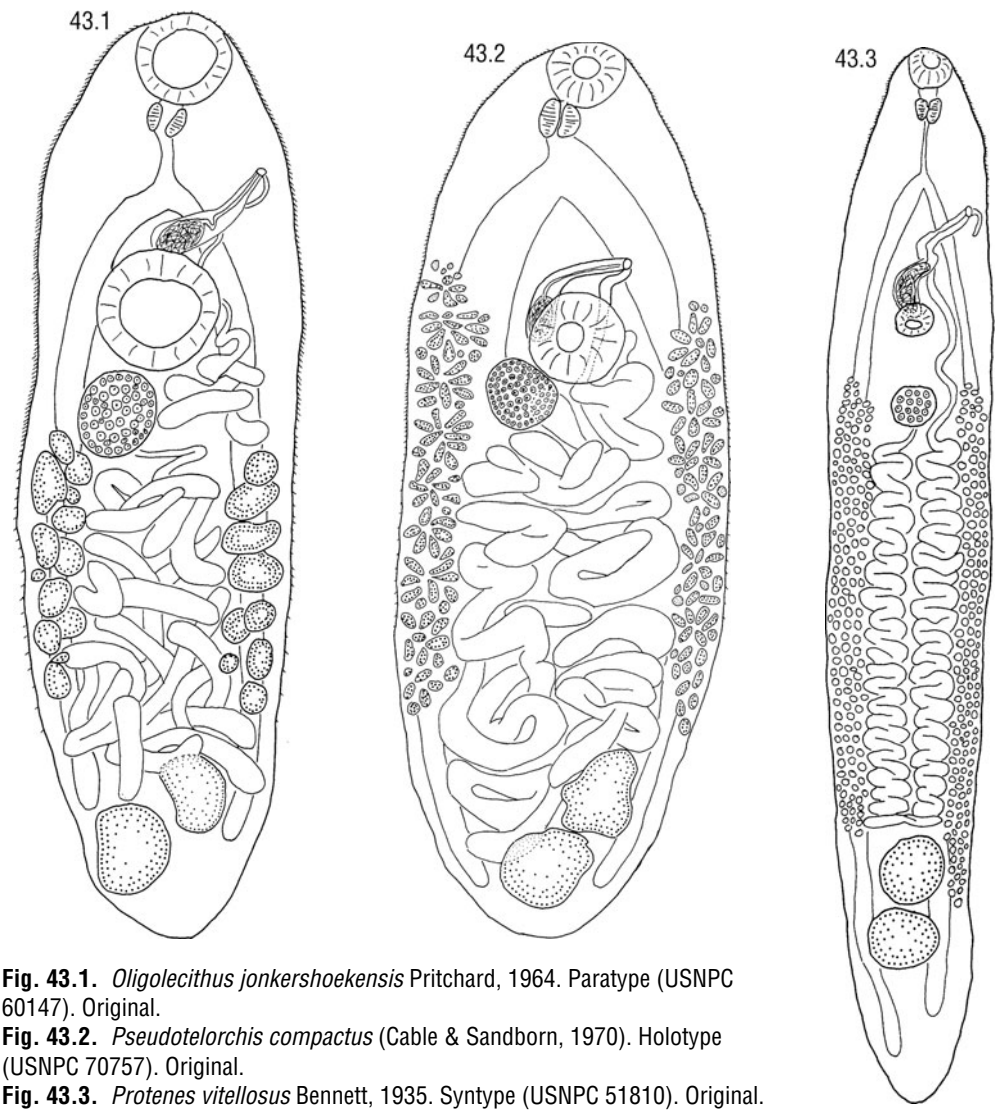



**Fig. 43.1.** *Oligolecithus jonkershoekensis* Pritchard, 1964. Paratype (USNPC 60147). Original.
**Fig. 43.2.** *Pseudotelorchis compactus* (Cable & Sandborn, 1970). Holotype (USNPC 70757). Original.
**Fig. 43.3.** *Protenes vitellosus* Bennett, 1935. Syntype (USNPC 51810). Original.

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testis. Vitellarium in lateral fields in middle third of body from ovary to anterior testis; follicles small, numerous. Excretory vesicle Y-shaped; pore terminal. In intestine of turtles; North America. Type-species *P. angustus* (Stafford, 1900) Barker & Covey, 1911.

**3b. Genital pore median or submedian ..... 4.**

**4a. Each lateral vitelline field one contiguous cluster of follicles ..... ..... *Telorchis* Lühe, 1899 *nec* Looss, 1899. (Fig. 43.4)**
(Syns *Telorchis* Looss, 1899 *nec* Lühe, 1899; *Cercorchis* Lühe, 1900; *Paracercorchis* Mehra & Bokhari, 1932; *Paratelorchis* Mehra & Bokhari, 1932 *nec* Stunkard & Franz, 1977, *lapsus*)

**Diagnosis:** Body elongate with parallel margins to linguiform. Prepharynx present or absent. Oesophagus short to moderately long. Caeca slender. Testes round or oval, tandem, nearly contiguous. Cirrus-sac large, elongate, straight or sinuous, mainly posterior to ventral sucker, contains sacculate seminal vesicle, elongate ejaculatory duct lined with prostatic cells; cirrus often protruded. Genital pore median or submedian; in posterior forebody. Ovary at various distances posterior to ventral sucker, round to oval, median or submedian. Uterus forms descending and ascending symmetrical, tightly packed transverse coils between ovary and anterior testis. Metraterm typically robust, muscular, elongate. Vitellarium forms contiguous lateral fields of small follicles in middle third of body. Excretory vesicle Y-shaped; pore terminal. In intestine of amphibians and reptiles, especially turtles; North and South America, Europe, Asia. Type-species *T. clava* (Diesing, 1850) Lühe, 1899.

**4b. Each lateral vitelline field in two lateral clusters of follicles, with follicles absent at level of testes ..... *Divitelluses* Cai & Li, 1993. (Fig. 43.5)**

**Diagnosis:** Body linguiform. Oral sucker small. Ventral sucker round, median, larger than oral sucker, pre-equatorial. Prepharynx absent (?). Pharynx small. Oesophagus distinct. Caeca slender. Testes irregularly oval, nearly contiguous. Cirrus-sac small, overlaps ventral sucker. Genital pore median. Ovary small, round, submedian, in anterior hindbody. Uterus forms descending and ascending coils between ovary and anterior testis. Vitellarium comprised of two divided lateral fields of small follicles; anterior field between level of ovary and short distance anterior to anterior testis; posterior field smaller, between posterior testis and posterior extremity; follicles absent from testicular region. Excretory vesicle Y-shaped. In intestine of turtles; China. Type-species *D. cantonensis* Cai & Li, 1993.

## Subfamily Allotelorchiinae Goodman, 1988

**Diagnosis:** Body elongate, slender. Oral sucker, round, subterminal, with lateral auricular lappets. Ventral sucker smaller than oral sucker. Prepharynx present or absent. Pharynx small. Oesophagus present or absent. Intestinal bifurcation in forebody. Caeca slender to inflated. Testes round, tandem, near posterior extremity or in anterior half of hindbody. Cirrus-sac elongate, slender, overlapping ventral sucker, or small, ovoid, entirely anterior to ventral sucker. Genital pore median, in posterior forebody. Ovary small, round, median or submedian, in anterior hindbody. Uterus short, restricted to area between anterior testis and genital pore, or extensive, consists of symmetrical ascending and descending coils between ovary and testes. Eggs few or very numerous, large or small. Vitelline follicles extend from base of cirrus-sac to level between just anterior to anterior testis and close to posterior extremity. Excretory vesicle stem elongate, arms short, surround ovary in *Auritelorchis*; pore terminal. In intestine of turtles, snakes; Africa, North America. Type-genus *Allotelorchis* Goodman, 1988.

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## Key to genera

**1a. Vitellarium terminates near posterior extremity; uterus short, between anterior testis and genital pore ..... *Allotelorchis* Goodman, 1988. (Fig. 43.6)**

**Diagnosis:** Body spination uncertain. Prepharynx absent. Oesophagus short. Caeca long, undulating. Testes oval, located some distance from posterior extremity, separated by vitelline follicles. Cirrus-sac oval, in forebody. Genital pore median, in posterior forebody. Ovary ovoid, submedian, in hindbody. Canalicular seminal receptacle present. Uterus short, restricted to area between anterior testis and genital pore. Eggs large, few. Vitellarium with large follicles in scattered clusters

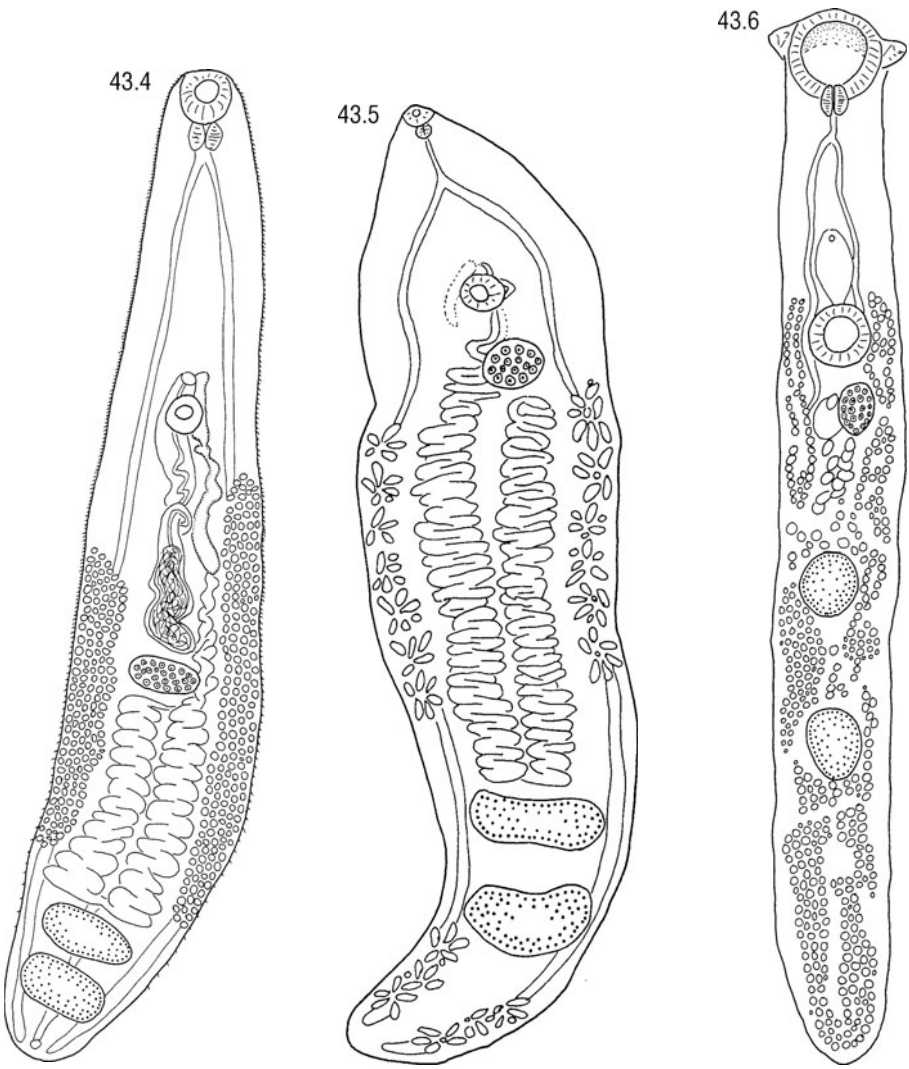



**Fig. 43.4.** *Telorchis robustus* Goldberger, 1911. Voucher specimen (USNPC 71419). Original.
**Fig. 43.5.** *Divitelluses cantonensis* Cai & Li, 1993. After Cai & Li (1993).
**Fig. 43.6.** *Allotelorchis thomasi* (Dollfus, 1950). After Goodman (1988b).

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between ventral sucker and posterior extremity and from lateral margins across mid-line of body. Excretory vesicle not known. In freshwater turtles; Africa. Type-species *A. thomasi* (Dollfus, 1950) Goodman, 1988.

**1b. Vitellarium terminates anterior to testes; uterus forms multiple descending and ascending coils between ovary and testes ..... *Auritelorchis* Stunkard, 1979. (Fig. 43.7)**
(Syn. *Paratelorchis* Stunkard & Franz, 1977 *nec* Mehra & Bokhari, 1932)

**Diagnosis:** Body spination absent, may be lost. Oral sucker with dorsal and ventral ear-like lobes on anterolateral faces (not shown in figure). Prepharynx short. Testes round to oval, tandem, near posterior extremity. Cirrus-sac long, slightly coiled, contains saccular seminal vesicle. Genital pore in forebody, median (but appears lateral in holotype due to twisting of body). Ovary median, near mid-body. Seminal receptacle absent. Mehlis' gland postovarian. Uterus with symmetrical descending and ascending transverse coils between ovary and testes. Metraterm elongate, muscular. Eggs numerous, small. Vitellarium forms lateral fields of small follicles between base of metraterm and anterior testis. Excretory vesicle Y-shaped with long stem. In intestine of snakes; Florida. Type-species *A. dollfusi* (Stunkard & Franz, 1977) Stunkard, 1979.

## Subfamily Loefgreniinae Yamaguti, 1958

**Diagnosis:** Body very elongate with crenulate, subcylindrical forebody and flattened hindbody. Semilunar muscular thickening in region of ventral sucker. Oral sucker round, subterminal. Ventral sucker round, median, pre-equatorial. Prepharynx, pharynx and oesophagus inconspicuous. Caeca slender. Testes lobed, diagonal, near posterior extremity. Cirrus-sac small, partly overlaps ventral sucker, contains sacculate seminal vesicle and withdrawn cirrus (i.e. ejaculatory duct). Genital pore median, in posterior forebody, covered by semilunar muscular thickening. Ovary small, round, median, in hindbody. Seminal receptacle small, rounded, postovarian. Uterus forms asymmetrical descending and ascending coils between ovary and testes. Metraterm well developed, between ovary and genital pore. Eggs numerous. Vitelline follicles extremely small, in lateral fields from level of ovary to level of testes. Excretory system not known. In intestine of reptiles; Brazil. Type-genus *Loefgrenia* Travassos, 1920.

### Genus *Loefgrenia* Travassos, 1920 (Fig. 43.8)

**Diagnosis:** With characters of subfamily. Type-species *L. loefgreni* Travassos, 1920.

## Subfamily Opisthioglyphinae Dollfus, 1949

**Diagnosis:** Body broadly oval to elongate, spinous. Oral sucker round, subterminal. Ventral sucker round, median, pre-equatorial. Prepharynx present. Pharynx present. Oesophagus length variable. Intestinal bifurcation in mid-forebody. Caeca reach into posterior part of body. Testes round, nearly contiguous, tandem to diagonal, in hindbody. Cirrus-sac mainly anterior to, or overlaps, ventral sucker, contains coiled tubular or saccate seminal vesicle. Genital pore median, postbifurcal. Ovary round, submedian. Seminal receptacle round to oval, posterior or lateral to ovary. Uterus typically with relatively few lateral coils either between testes and ovary or entirely anterior to ovary. Eggs

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small, numerous. Vitellarium consists of extensive follicles extending from intestinal bifurcation to near posterior extremity; lateral fields may be confluent in midline in hindbody. Excretory vesicle Y-shaped, with long stem; pore terminal. In intestine of amphibians; Europe, Asia, Africa, South America, Australia, New Zealand. Type-genus *Opisthioglyphe* Looss, 1899.

## Key to genera

**1a. Uterine coils mainly between ovary and anterior testis; cirrus-sac contains winding, tubular seminal vesicle ..... *Opisthioglyphe* Looss, 1899. (Fig. 43.9)**

**Diagnosis:** Body oval, flattened. Oesophagus short to moderately long. Testes round, diagonal or tandem; in mid-hindbody. Cirrus-sac mostly anterior to ventral sucker, contains winding, tubular seminal vesicle; prostatic cells surround short ejaculatory duct. Ovary round, lateral or posterolateral to ventral sucker. Seminal receptacle round to ovoid, opposite or posterior to ovary. Uterus forms lateral coils between ovary and anterior testis, never posterior to testes. Eggs small, numerous. Vitelline follicles fill entire extracaecal space from intestinal bifurcation to close to posterior extremity; lateral fields typically confluent near posterior extremity. Excretory vesicle Y-shaped. In intestine of amphibians; Europe, Asia, Africa. Type-species *O. ranae* (Frölich, 1791) Looss, 1899.

**1b. Uterine coils typically pre-ovarian, but may extend posterior to testes; cirrus-sac contains saccular seminal vesicle ..... *Dolichosaccus* Johnson, 1912. (Fig. 43.10)**
(Syn. *Lecithopyge* Perkins, 1928; *Dolichosacculus* Johnston, 1943)

**Diagnosis:** Body ovoid to elongate. Oesophagus short to moderately long. Caeca slender. Testes round, diagonal or tandem, near posterior extremity. Cirrus-sac small to large, often mostly anterior to ventral sucker, but may overlap sucker, contains saccular unipartite or bipartite seminal vesicle; prostatic cells surround ejaculatory duct, often prominent. Ovary round to oval, submedian, occasionally median, may overlap ventral sucker or may be widely separated from sucker by uterine coils, pre-equatorial. Seminal receptacle postovarian. Laurer's canal elongate. Uterus variable in extent, may form few lateral coils between anterior margin of ovary and ventral sucker or coil between ovary and testes. Eggs small, numerous. Vitelline follicles fill entire extracaecal area and often become confluent in hindbody and occasionally in forebody. Excretory vesicle Y-shaped. In intestine of amphibians; Australia, New Zealand, South America. Type-species *D. trypherus* Johnston, 1912.

## Subfamily Orchidasmatinae Dollfus, 1937

**Diagnosis:** Body elongate; sides nearly parallel except near extremities; hindbody crenulate. Oral sucker round, subterminal, larger than ventral sucker. Ventral sucker round, median, pre-equatorial. Prepharynx small. Pharynx large. Oesophagus present. Intestinal bifurcation in mid-forebody. Caeca slender, reach close to posterior extremity. Anterior testis immediately posterior to ovary; posterior testis near posterior extremity; testes separated by numerous lateral uterine coils. Cirrus-sac very long, extremely robust, contains saccular seminal vesicle, narrow pars prostatica and spinous ejaculatory duct; formed cirrus large, muscular, spinous. Genital pore median, immediately anterior to ventral sucker. Ovary very small, round, midway between base of cirrus-sac and anterior testis. Seminal receptacle small, ovoid, immediately postovarian. Uterus forms ascending and descending coils between testes and ascending coils to base of

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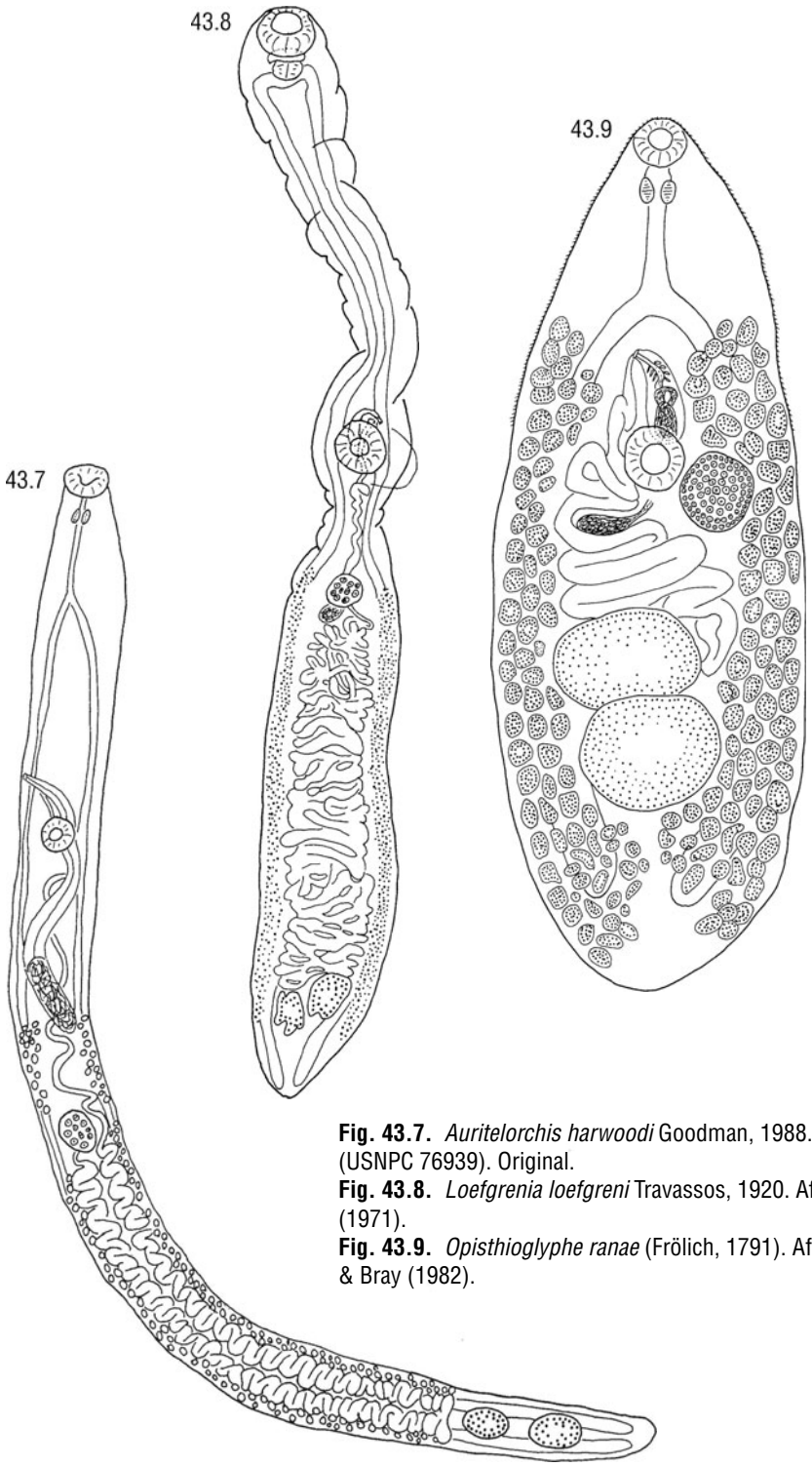



**Fig. 43.7.** *Auritelorchis harwoodi* Goodman, 1988. Holotype (USNPC 76939). Original.
**Fig. 43.8.** *Loefgrenia loefgreni* Travassos, 1920. After Yamaguti (1971).
**Fig. 43.9.** *Opisthioglyphe ranae* (Frölich, 1791). After Prudhoe & Bray (1982).

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cirrus-sac. Metraterm very robust, muscular, spinous. Eggs very thick-walled. Vitelline follicles small, in lateral fields, fill middle third of body from base of cirrus-sac to terminate anteriorly to posterior testis. Excretory system I-shaped; pore terminal. In intestine of marine turtles; Pacific Ocean, Atlantic Ocean, Gulf of Mexico, Indian Ocean, Mediterranean Sea, Red Sea. Type-genus *Orchidasma* Looss, 1900.

## Genus *Orchidasma* Looss, 1900. (Fig. 43.11)

(Syn. *Anadasmus* Looss, 1899 *nec* Walsingham, 1897)

**Diagnosis:** With characters of subfamily. Type-species *O. amphiorchis* (Braun, 1899) Looss, 1900.

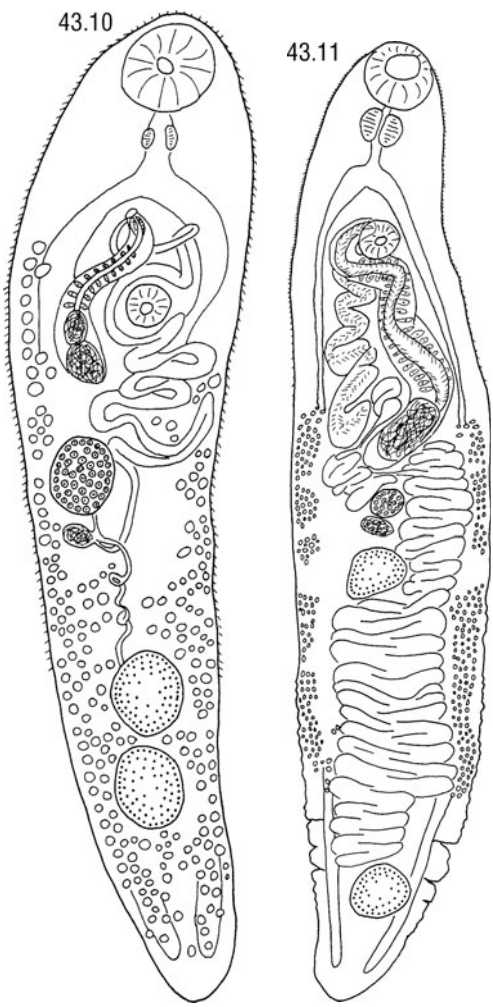



**Fig. 43.10.** *Dolichosaccus trypherus* Johnston, 1912. After Prudhoe & Bray (1982).
**Fig. 43.11.** *Orchidasma amphiorchis* Looss, 1900. Voucher specimen (USNPC 84871). Original.

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# 44 Family Thrinascotrematidae Jue Sue & Platt, 1999

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## Introduction

The Thrinascotrematidae Jue Sue & Platt, 1999 presently includes only one genus of digeneans parasitic in Australian freshwater turtles. The life-cycle and morphology of adult and larval stages of the single known species, *Thrinascotrema brisbanicum* Jue Sue & Platt, 1999 (emend.), have been described in detail by Jue Sue & Platt (1999b). This is an obviously plagiorchiid digenean due to the presence of a true xiphidiocercaria. However, a unique combination of several morphological characters observed in the adults and/or cercariae of *T. brisbanicum*, such as the unusually long tubular excretory vesicle almost reaching the anterior extremity and the very high number of flame-cells (formula 2[(12 + 12 + 12) + (12 + 12 + 12)] = 144), separates this genus from members of the Plagiorchiidae Lühe, 1901 and other known plagiorchioid families. Jue Sue & Platt (1999b) mentioned that the arrangement of the excretory ducts in the cercaria resembles that described in metacercariae of *Encyclometra colubrimurorum* (Rudolphi, 1819), another species traditionally included in the Plagiorchiidae, but then allocated to a separate family, mainly due to the organization of the excretory system and the high number of flame-cells (see Tkach, Chapter 29, this volume). Members of the Plagiorchiidae and the whole superfamily Plagiorchioidea Lühe, 1901, as circumscribed by Odening (1964c), are characterized by a much smaller number and different arrangement of flame-cells (formula 2[(3 + 3 + 3) + (3 + 3 + 3)] = 36. Recent molecular phylogenetic analyses (Tkach *et al*., 2001b; Olson *et al*., 2003) have confirmed that *Encyclometra* Baylis & Cannon, 1924 does not belong to the Plagiorchioidea. Lack of molecular data on *Thrinascotrema* Jue Sue & Platt, 1999 does not allow clarification of the phylogenetic interrelationships between this genus and *Encyclometra*; hence, the Thrinascotrematidae is considered here as a separate family. The family diagnosis follows Jue Sue & Platt (1999b), with minor modifications.

## Family Thrinascotrematidae Jue Sue & Platt, 1999

**Diagnosis:** Body plump; ends bluntly rounded. Tegument armed with spines extending to posterior end. Oral sucker large. Ventral sucker spined, equal to or slightly larger than oral sucker, in

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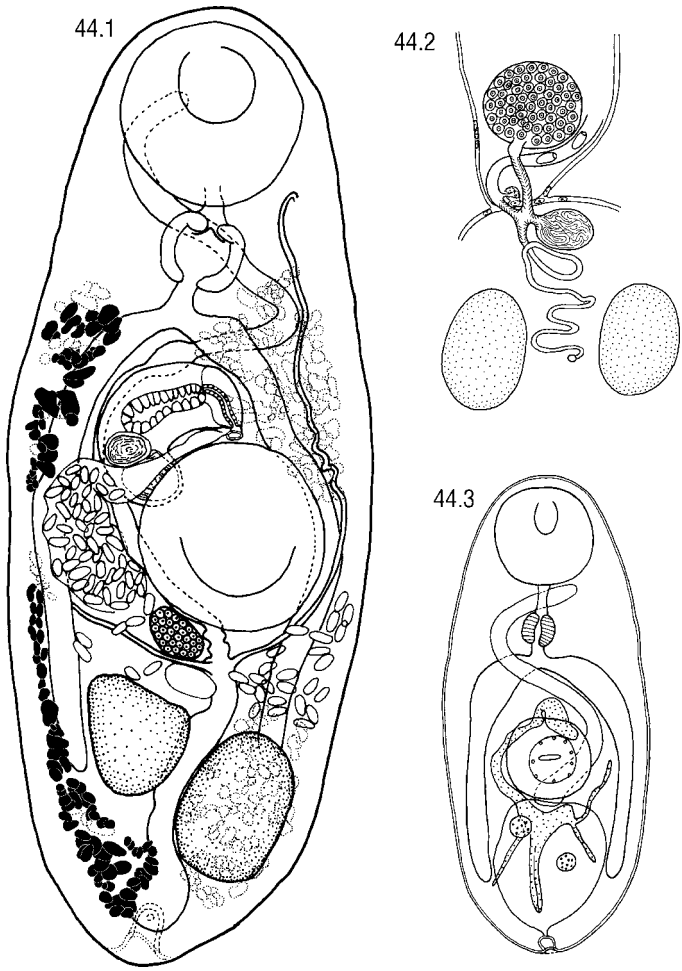

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middle third of body. Prepharynx short. Pharynx well developed. Oesophagus short. Intestinal bifurcation mid-way between oral and ventral suckers. Caeca simple, reach level of anterior margin of posterior testis. Testes large, in posterior third of body; shape and relative position variable. Cirrus-sac short, contains bipartite seminal vesicle, pars prostatica and cirrus; proximal end slightly overlaps ventral sucker, never extends posterior to ventral sucker. Genital atrium small. Genital pore median, immediately anterior to ventral sucker. Ovary median or submedian, between anterior testis and ventral sucker. Seminal receptacle saccate, posterior or lateral to ovary. Laurer's canal long, convoluted, opens through dorsal pore between testes. Mehlis' gland prominent. Uterus convoluted, occupies most of hindbody when gravid. Eggs numerous. Vitellarium in two fields extending from pharynx to posterior end on either side of body, at level of ventral sucker. Excretory vesicle long, tubular, extends almost to anterior end, terminates blindly dorsal to oral sucker; excretory ducts stenostomate; primary collecting ducts arise ventrolaterally from vesicle, posterior to ventral sucker; subterminal dorsal or ventral. In stomach of freshwater turtles; Australia. Type- and only genus *Thrinascotrema* Jue Sue & Platt, 1999.

## Genus *Thrinascotrema* Jue Sue & Platt, 1999 (Figs 44.1–44.3)

**Diagnosis:** With characters of the family. Type- and only species *T. brisbanicum* Jue Sue & Platt, 1999 (emend.).

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**Figs 44.1–44.3.** *T. brisbanicum* Jue Sue & Platt, 1999. 44.1. Adult. 44.2. Female reproductive system. 44.3. Metacercaria. After Jue Sue & Platt (1999b).

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# 45 Family Urotrematidae Poche, 1926

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## Introduction

Until recently, the Urotrematidae Poche, 1926 contained only two genera, *Urotrema* Braun, 1900 and *Urotrematulum* Macy, 1933. Urotrematids are mostly parasites of insectivorous bats, although they have occasionally been reported from some rodents and lizards. The cirrus-sac and the genital pore are at the posterior extremity. The ovary is anterior to the testes and all uterine coils are posterior to the ovary, passing between the two tandem testes in the hindbody. The excretory vesicle is V-shaped. Although the life-histories of urotrematids are unknown, the trophic ecology of the known definitive hosts indicates that insects are likely to be the second intermediate hosts. Species occur in North, Central and South America and in Africa.

Bray *et al.* (1999) re-examined type-specimens of two genera from freshwater fishes, previously assigned to the family Sinineobucephalidae Zhang, Pan & Li, 1987 [*sic*], which had been created for them (Zhang *et al.*, 1987). From analysis of the morphological characteristics of *Sinineobucephalopsis* Zhang, Pan & Li, 1987 and *Sinogastromyzontrema* Li, Zhang & Li, 1988, they concluded that both could be accommodated in the Urotrematidae by extending the family diagnosis to include specimens with a Y-shaped excretory vesicle. They considered some species of these genera synonymous with those placed in *Urotrema* and *Urotrematulum* by Chinese workers (Wang P.-q., 1986; Zhang, 1992; Zhang & Yang, 1992). The caeca in most urotrematids other than *Urotrema wardi* Vigueras, 1940 extend to near the posterior extremity but, in some specimens from Chinese freshwater fishes, they terminate well short of this. Although these four genera can be unified in one family by shared morphological features, Bray *et al.* (1999) noted disparities in host utilization and in the biogeography of genera newly assigned to the Urotrematidae, when compared with previously recognized genera. They pointed out that doubt exists regarding 'the confamilial status of these forms'. We agree with their assessment that sole reliance on morphological characteristics may artificially unite groups of species that are not closely related. Nonetheless, until other relevant biological criteria, such as life-history data, are acquired for these genera, their unification into a single family is warranted.

As yet unresolved is the position of the Urotrematidae within the Digenea. Most, but not all, authors place it in the suborder Plagiorchiata La Rue, 1975. Affiliation with the superfamily Telorchioidea Looss, 1899 was recommended by Brooks *et al.* (1985), based on their cladistic

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analysis of morphological characters. However, MacDonald & Brooks (1989a) added a caution that the utilization of tadpoles as second intermediate hosts by other telorchioids and the presumed use of insects as second intermediate hosts by urotrematids lend some uncertainty to these relationships. On the other hand, the molecular phylogeny of Olson *et al*. (2003) indicated that all digeneans in their analysis (which omitted urotrematids) with a posterior genital pore (apart from the Bucephalidae) were included in the group Diplostomida.

Of the four genera currently assigned to the Urotrematidae, *Urotrema* is the most speciose and geographically widespread. The type-species, *U. scabridum* Braun, 1900, parasitizes several genera of insectivorous bats, ranging from North America to South America and Africa. Most other species of *Urotrema* also parasitize bats, but have also been reported from muskrats and *Anolis* lizards. See Bray *et al*. (1999) for details of the host and geographical distributions. Members of the genus possess an ovary just posterior to the ventral sucker and tandem, round testes in the hindbody. The anterior extent of the vitellarium is at the level of the ventral sucker.

*Urotrematulum* is readily distinguished from *Urotrema* by the position of the ovary, which is located a considerable distance posterior to the ventral sucker. The testes are lobed. The vitellarium does not extend anteriorly as far as the level of the ventral sucker. The genus is monotypic, containing only *Urotrematulum attenuatum* Macy, 1933 described from the bat *Lasionycteris noctivagans* in Minnesota, USA.

In addition to biological characteristics involving host utilization and geographical distribution, *Sinineobucephalopsis* and *Sinogastromyzontrema* can be distinguished from the above genera on the basis of morphological characteristics. In *Sinineobucephalopsis*, the testes are contiguous, are in the anterior to mid-hindbody and may be oblique or tandem, and the caeca end far short of the posterior extremity. Four species have been described, all in the intestine of freshwater fishes in China. In *Sinogastromyzontrema*, the testes are symmetrical to obliquely symmetrical and not contiguous, the caeca end just posterior to the testes and all uterine coils are entirely post-testicular. A single species, *S. guangxiense* Li, Zhang & Li, 1988 (emend.), has been described from several cypriniform fishes in China.

## Family Urotrematidae Poche, 1926

(Syn. Sinineobucephalidae Zhang, Pan & Li, 1987)

**Diagnosis:** Body elongate and small to elongate-oval and large. Tegument spinous. Oral sucker rounded, subterminal. Prepharynx short or apparently absent. Pharynx small, subglobular to oval. Oesophagus elongate. Intestinal bifurcation in forebody. Caeca terminate blindly near posterior extremity or in anterior part of hindbody. Testes two, tandem to obliquely symmetrical to symmetrical, unlobed or lobed, rounded to oval, contiguous or not; may be separated by uterine coils, in mid-, anterior or posterior hindbody. Cirrus-sac claviform, at posterior extremity. Internal seminal vesicle winding, tubular. Pars prostatica present. Small genital atrium present. Genital pore near posterior extremity. Ovary in anterior hindbody, median or slightly dextral, round to oval, lobed or unlobed. Seminal receptacle small, postovarian. Laurer's canal present. Mehlis' gland present. Uterine coils entirely posterior to ovary, pass between testes or not, descend through hindbody to open into genital atrium. Eggs small, numerous, operculate. Vitellarium follicular, in non-confluent elongate, lateral fields, or shorter fields that overlap medially. Excretory vesicle V- or Y-shaped; pore terminal. In intestines of insectivorous bats, rodents, *Anolis* lizards and freshwater fishes; North, Central and South America, Africa and China. Type-genus *Urotrema* Braun, 1900.

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## Key to genera

**1a. Testes tandem in posterior half of hindbody, widely separated from ovary by extensive uterine coils; caeca end in posterior hindbody; in mammals or reptiles, the Americas and Africa ..... 2.**

**1b. Testes tandem, oblique or symmetrical in mid- to anterior hindbody, separated from ovary by few uterine coils, or adjacent to ovary; caeca end far from posterior extremity; in freshwater fishes, China ..... 3.**

**2a. Ovary and testes unlobed; ovary slightly posterior to ventral sucker; vitellarium extends to level of ventral sucker ..... *Urotrema* Braun, 1900. (Fig. 45.1)**

**Diagnosis:** Body elongate. Oral sucker small. Ventral sucker nearly equal in size to oral sucker, in forebody. Prepharynx present. Oesophagus elongate. Caeca reach into posterior half of hindbody. Testes large, round, tandem, in mid- to posterior hindbody, distant from ovary. Cirrus-sac contains large seminal vesicle; cirrus short, unarmed. Genital pore subterminal and ventral, situated at base of cirrus-sac. Ovary rounded, slightly posterior to ventral sucker, median or slightly dextral. Uterus extensively coiled between ovary and anterior testis and between testes, forms well-defined metraterm. Vitellarium with numerous small follicles in lateral fields extending from level of ventral sucker to anterior testis. Excretory vesicle V-shaped. In intestine of bats, rodents, lizards; North, Central and South America, Africa. Type-species *U. scabridum* Braun, 1900.

**2b. Ovary and testes lobed; ovary far posterior to ventral sucker; anterior extent of vitellarium not near ventral sucker ..... *Urotrematulum* Macy, 1933. (Fig. 45.2)**

**Diagnosis:** Body elongate, narrowed at anterior end, bluntly rounded posteriorly. Oral sucker small. Ventral sucker equal in size to oral sucker. Pharynx present. Oesophagus elongate, narrow. Caeca reach close to posterior extremity. Testes with five to eight lobes, tandem, median, in posterior hindbody. Cirrus-sac pyriform. Ovary lobed, median, far posterior to ventral sucker. Uterus extensively coiled, with numerous loops between ovary and testes and several loops between testes. Vitellarium with numerous small follicles beginning just anterior to ovary and terminating in anterior hindbody. Excretory vesicle V-shaped. In intestine of bats; USA. Type-species *U. attenuatum* Macy, 1933.

**3a. Testes tandem to oblique; testes large compared to body-width; uterus passes around or between testes and coils laterally in post-testicular region ..... ..... *Sinineobucephalopsis* Zhang, Pan & Li, 1987. (Fig. 45.3)**

**Diagnosis:** Body elongate-oval. Oral sucker small, slightly transversely oval. Prepharynx short, within posterior concavity of oral sucker. Pharynx small, subglobular. Oesophagus long, narrow. Caeca reach to about middle of post-testicular region or just beyond. Testes two, tandem to oblique, round to oval, contiguous, anterior to mid-body. Cirrus-sac claviform. Internal seminal vesicle, tubular, coiled. Pars prostatica narrow; ejaculatory duct may form cirrus. Genital pore sinistroterminal. Ovary oval to subglobular, anterodextral or anterior to anterior testis, posterodextral to ventral sucker. Uterus passes around or between testes and coils laterally in post-testicular region. Metraterm not observed. Vitelline follicles in band across body in region of ventral sucker, may be separated into lateral fields or bands in hindbody. Excretory vesicle with only short I-shaped posterior part seen. In intestine of freshwater fishes; China. Type-species *S. macrocirrus* Zhang, Pan & Li, 1987.

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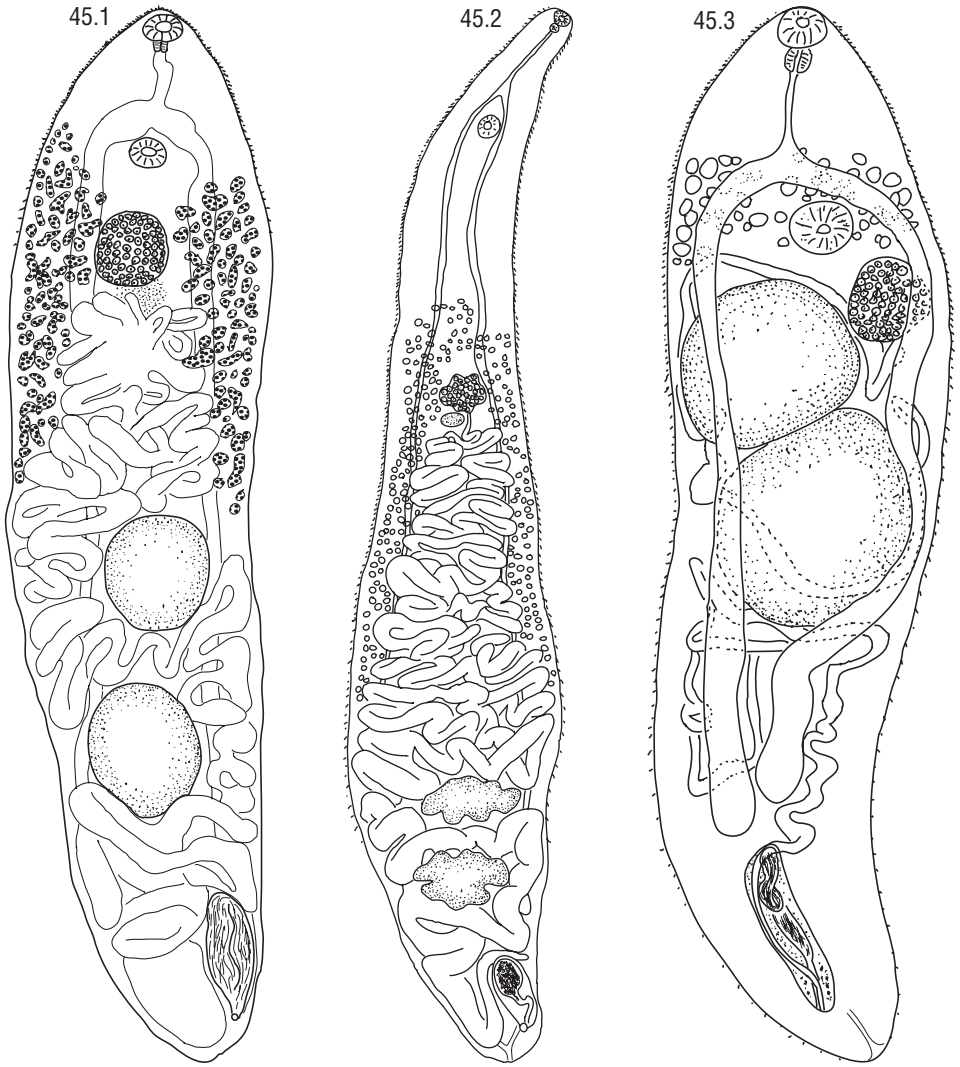



**Fig. 45.1.** *Urotrema lasiurense* Macy, 1933 (emend.). After Macy (1933).
**Fig. 45.2.** *Urotrematulum attenuatum* Macy, 1933. After Yamaguti (1971).
**Fig. 45.3.** *Sinineobucephalopsis macrocirrus* Zhang, Pan & Li, 1987. After Bray *et al.* (1999).

**3b. Testes symmetrical to obliquely symmetrical; testes small compared to body-width; uterine coils fill hindbody in post-testicular region** ..... ..... *Sinogastromyzontrema* **Li, Zhang & Li, 1988. (Fig. 45.4)**

**Diagnosis:** Body large, elongate-oval. Oral sucker round. Ventral sucker round, about third of body-length from anterior end. Prepharynx short. Pharynx oval. Oesophagus elongate. Caeca terminate just posterior to testes. Testes symmetrical to obliquely symmetrical, separate, in anterior hindbody, small in comparison to body-width, oval, entire or irregular. Cirrus-sac small, claviform. Internal seminal vesicle coiled, tubular. Pars prostatica and ejaculatory duct tubular. Genital pore opens sinistroventrally near posterior end. Ovary entire, round, just anterior to right testis,

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in anterior hindbody. Seminal receptacle subglobular, just posterior to ovary. Laurer's canal present. Uterus passes posteriorly from Mehlis' gland, with discrete lateral coils filling hindbody posterior to testes. Metraterm dorsal to cirrus-sac. Vitelline follicles elongate, in two lateral fields in rosettes, between level of ventral sucker and just posterior to testes. Excretory vesicle extends to at least middle of post-testicular field; originally described as Y-shaped. In intestine of freshwater fish; China. Type-species *S. guangxiense* Li, Zhang & Li, 1988 (emend.).

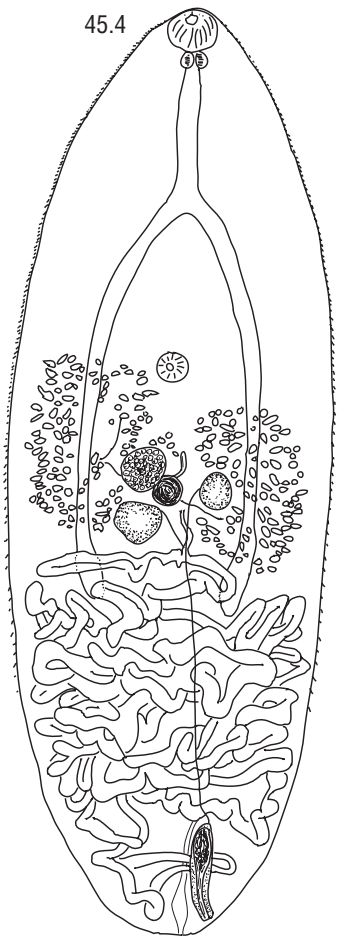



**Fig. 45.4.** *Sinogastromyzontrema guangxiense* Li, Zhang & Li, 1988 (emend.). After Bray *et al.* (1999).

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# 46 Superfamily Microphalloidea Ward, 1901

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## Introduction

The Microphalloidea Ward, 1901 was first established at this level by Morozov (1955b) and, as outlined by Tkach *et al.* (2003), contained a wide variety of constituents. The suite of families considered members of this group in the current volume is based on recent molecular findings (Tkach *et al.*, 2000a, 2001b, 2003; Cribb *et al.*, 2001b; Olson *et al.*, 2003; Bray *et al.*, 2005), along with a consideration that the virgulate taxa (see Lotz & Font, Chapter 54, this volume) comprise a paraphyletic group of 'lecithodendriid-like' taxa. These molecular results have established that the families Microphallidae Ward, 1901, Eucotylidae Cohn, 1904, Faustulidae Poche, 1926, Lecithodendriidae Lühe, 1901, Pachypsolidae Yamaguti, 1958, Pleurogenidae Looss, 1899, Prosthogonimidae Lühe, 1909, Renicolidae Dollfus, 1939 and Zoogonidae Odhner, 1902 form a monophylum now known as the Microphalloidea. All of these families except the Eucotylidae, which was treated in Volume 1 of this series (Kanev *et al.*, 2002b), are included here, along with other families that are related morphologically and in some cases share the virgulate cercaria with the lecithodendriids and pleurogenids (i.e. Gyrabascidae Macy 1935, Leyogonimidae Dollfus, 1951 and Phaneropsolidae Mehra, 1935). The families recognized as microphalloids on morphological grounds only are the Anenterotrematidae Yamaguti, 1958, Diplangidae Yamaguti, 1971, Eumegacetidae Travassos, 1922, Exotidendriidae Mehra, 1935, Renschetrematidae Yamaguti, 1971, Stomylotrematidae Poche, 1925 and Taiwantrematidae Fischthal & Kuntz, 1981.

The superfamily is, therefore, not defined on morphological grounds and it is difficult to detect morphological synapomorphies. This key, in line with the philosophy of all these volumes, is primarily a tool for identification, rather than a phylogenetic text, but we have also attempted to produce our keys in line with the latest ideas on phylogeny. As many of the families recognized here are based on molecular findings and contain a wide variety of morphologies, it has not been possible to develop an entirely reliable key. We have in some cases resorted to host relationships, which do appear to be of some phylogenetic value, judging by the results of Tkach *et al.* (2003). Nevertheless, the warnings about the fallibility of keys, which should accompany every one, are particularly relevant with this superfamily. In one case, we have not been able to suggest a

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satisfactory morphological distinction between all the members of two families and the reader should compare their forms with the keys to the members of both families mentioned.

## Superfamily Microphalloidea Ward, 1901

**Diagnosis:** Body tiny to medium-sized; shape variable. Tegument spinous or not. Suckers generally two. Oral sucker subterminal, occasionally ornamented. Ventral sucker poorly to well developed, may be retracted into body, rarely absent. Digestive tract usually present, rarely absent. Prepharynx, pharynx and oesophagus usually present. Intestinal bifurcation in forebody. Caeca paired, of variable length, blind, occasionally atrophied or absent. Testes two; shape and position variable. Cirrus-sac present or not; when present, usually contains seminal vesicle, pars prostatica and ejaculatory duct. Cirrus often formed, may be heavily spined. Genital atrium usually present, may have complicated accessory organs. Genital pore ventral or marginal, occasionally dorsal, in fore- or hindbody, occasionally close to anterior extremity, occasionally with separate male and female pores. Ovary pre-, para- or post-testicular. Canalicular seminal receptacle present or absent. Laurer's canal present. Uterus variable, short to long. Eggs numerous or few. Metraterm usually present, may be heavily spined. Vitellarium follicular; fields relatively small, usually in two symmetrical clusters, ribbon-like or otherwise, variously situated. Excretory system V-, Y- or I-shaped in post- or intertesticular position; pore terminal or subterminal. In many organ systems of all vertebrate classes; cosmopolitan. Type-genus *Microphallus* Ward, 1901.

## Key to families

**1a. Genital pore well inside hindbody; cirrus-sac with proximal extremity oriented anteriorly; ovary lobed, in forebody ..... Leyogonimidae Dollfus, 1951.**
**1b. Genital pore in forebody, at level of ventral sucker, or in anterior hindbody; cirrus-sac or naked terminal male ducts oriented transversely or with proximal extremity oriented posteriorly; ovary usually entire, usually in hindbody ..... 2.**

**2a. Cirrus-sac present ..... 3.**
**2b. Cirrus-sac absent ..... 19.**

**3a. Alimentary tract absent or greatly reduced; in bats ... Anenterotrematidae Yamaguti, 1958.**
**3b. Alimentary tract distinct (gut occasionally atrophied in *Microphallus* Ward, 1901, Microphallidae Ward, 1901) ..... 4.**

**4a. Ejaculatory duct and metraterm armed with massive spines ..... ..... Exotidendriidae Mehra, 1935.**
**4b. Ejaculatory duct and metraterm unarmed or armed with minute spines ..... 5.**

**5a. Testes in forebody or, if ventral sucker absent, situated anteriorly ..... 6.**
**5b. Testes in hindbody or at level of ventral sucker ..... 10.**

**6a. In tetrapods ..... 7.**
**6b. In fishes ..... 9.**

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**7a. In birds ..... 8.**
**7b. In amphibians and occasionally reptiles ..... Pleurogenidae Looss, 1899 (in part).**

**8a. Genital pore median ..... Eumegacetidae Travassos, 1921.**
**8b. Genital pore marginal ..... Stomylotrematidae Poche, 1925 (in part).**

**9a. Genital pore marginal ..... ..... Zoogonidae Odhner, 1902 (*Panopula* Overstreet & Pritchard, 1977).**
**9b. Genital pore median ..... Faustulidae Poche, 1926 (*Antorchis* Linton, 1911).**

**10a. Genital pore close to anterior extremity ..... Prosthogonimidae Lühe, 1909.**
**10b. Genital pore usually distant from anterior extremity ..... 11.**

**11a. In tetrapods ..... 12.**
**11b. In fishes ..... 17.**

**12a. Caeca with two or three anteriorly or laterally directed projections on each side at level of pharynx or between pharynx and ventral sucker ..... Pachypsolidae Yamaguti, 1958.**
**12b. Caeca simple ..... 13.**

**13a. Testis single ..... Taiwantrematidae Fischthal & Kuntz, 1981.**
**13b. Two testes ..... 14.**

**14a. Terminal genitalia complex; genital atrium may have complex diverticula; genital pore usually sinistral at level of ventral sucker ..... Microphallidae Ward, 1901 (in part).**
**14b. Normal cirrus-sac present; genital atrium small or insignificant; genital pore median to marginal ..... 15.**

**15a. Genital pore usually marginal or submarginal ..... 16.**
**15b. Genital pore usually median or submedian; in mammals and birds ..... ..... Phaneropsolidae Mehra, 1935 (in part).**

**16a. In amphibians and occasionally reptiles ..... Pleurogenidae Looss, 1899.**
**16b. In the intestinal tract, especially caecum, bursa Fabricii or cloaca of birds ..... ..... Stomylotrematidae Poche, 1925 (*Laterotrema* Semenov, 1928).**

**17a. Genital pore marginal ..... Zoogonidae Odhner, 1901.**
**17b. Genital pore not marginal ..... 18.**

**18a. Genital pore near lateral edge of ventral sucker ... Microphallidae Ward, 1901 (in part).**
**18b. Genital pore median ..... Faustulidae Poche, 1926.**

**19a. Ovoid accessory sac containing dart-like body associated with male terminal genitalia; male and female genital pores open separately on body-surface ..... ..... Renschetrematidae Yamaguti, 1971.**
**19b. Accessory sac as above lacking; male and female systems usually open through common genital pore ..... 20.**

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**20a. Genital pore marginal ..... Gyrabascidae Macy, 1935.**
**20b. Genital pore not marginal ..... 21.**

**21a. Terminal genitalia complex; genital atrium may have complex diverticula; genital pore usually sinistral at level of ventral sucker ..... Microphallidae Ward, 1901 (in part).**
**21b. Terminal genitalia simple; genital pore median to submedian ..... 22.**

**22a. In tetrapods ..... 23.**
**22b. In fish ..... 24.**

**23a. In kidneys and ureters of aquatic birds ..... Renicolidae Dollfus, 1939.**
**23b. In intestine of birds, mammals or rarely reptiles ..... ..... Lecithodendriidae Lühe, 1901 and Phaneropsolidae Mehra, 1935 (in part).**

**24a. Tegument unarmed ..... Diplangidae Yamaguti, 1971.**
**24b. Tegument armed with spines ..... Faustulidae Poche, 1926 (in part).**

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# 47 Family Microphallidae Ward, 1901

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## Introduction

The Microphallidae Ward, 1901 is a large family of small worms found in the intestine of most vertebrate classes, but mainly birds, acquired by the consumption of crustaceans. A common characteristic of all the species of the family is the flame-cell formula 2[(2 + 2) + (2 + 2)] = 16 solenocytes, which is present at every stage of the sexual generation (cercaria, metacercaria and adult). The general morphology of the adults exhibits a few constant characters, such as small body size (rarely more than 1 mm), well-separated subequal and small suckers, a short digestive tract with short divergent caeca that rarely extend posteriorly beyond the level of the ventral sucker, an ovary that is always pretesticular on the opposite side to the genital pore, a 'genital pouch' anterior to the ventral sucker between the ovary and genital pore and a short excretory vesicle. Great variation, however, occurs in the configuration of the male duct between the vas deferens and the copulatory organ, the genital atrium and in the arrangement of the vitellarium. Every combination of characters seems possible. With our ignorance concerning the hierarchy of the taxonomic value of these characters, the exact affiliation of species is enigmatic and hypothetical.

General literature compilations on the Microphallidae include, in chronological order, those of Belopol'skaya (1952), Yamaguti (1958b), Belopol'skaya (1963), Yamaguti (1971) and Deblock (1971); the latter presented dichotomous keys to about 160 species in 28 genera described before 1971. Initially, the Microphallinae Ward, 1901 was considered a subfamily of the Heterophyidae Odhner, 1914; it was raised to full family rank by Travassos (1921b) to contain three genera: *Microphallus* Ward, 1901, *Maritrema* Nicoll, 1907 and *Levinseniella* Stiles & Hassall, 1901. Baer (1944) recognized the family Maritrematidae Nicoll, 1907 for species with a true cirrus-sac. Bayssade-Dufour *et al.* (1993) agreed with this proposition and demonstrated, by means of the cercarial chaetotaxy, that *Maritrema* is primitive compared with the two other genera studied, namely *Megalophallus* Cable, Connor & Balling, 1960 (slightly more evolved than *Maritrema*) and *Gynaecotyla* Yamaguti, 1939 (distinctly more evolved). In addition, chaetotaxy demonstrated a connection between these genera and the Lecithodendriidae Odhner, 1910. The dismembering of the family Microphallidae according to the rate of evolution of its constituent genera can now be discussed. I choose to retain all the microphallids together under their original collective name,

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with a division into four supersubfamilies[1] (Maritrematidi Nicoll, 1907, Promicrophallidi Fischthal & Kuntz, 1981, Gynaecotylidi Guschanskaja, 1952 and Microphallidi Ward, 1901). This classification (derived from classical data) has not been the subject of major critical discussion, and it constitutes the basis for these keys to the generic level. The keys strive to respect a theoretical phylogeny of the group, based on the complexity of the anatomical characteristics of the genital ducts of adult forms. Much unknown data limit the proposed classification and a number of enigmatic taxa are monotypic. Several genera of the Maritrematinae Nicoll, 1907, which are dissimilar and not closely related, are assembled in the artificial group 'Vitello-racemina' for convenience. The hierarchy of taxa in the family of Microphallidae is summarized in Table 47.1; the new names are justified by the existence of genera with characteristics too distinctive to fall within the diagnoses of the sister taxa, which are already well defined and homogeneous.

The phenetic analysis of Microphallidae by Bayssade-Dufour *et al*. (1993) based on cercarial chaetotaxy suggests a partition of the family into two distinct groups, the 'archaic' 'Maritrematidae', related to the Lecithodendriidae Lühe, 1901 and Renicolidae Dollfus, 1939, and the 'more evolved' Microphallidae, with the Microphallinae and Gynaecotylinae Guschanskaja, 1952.

## Comments on generic synonymies

*Allomicrophalloides* Ke & Liang, 1982 and *Multivitellus* Ke & Liang, 1982, from the same host in the same geographical region, may represent two morphological forms of a more or less extended single species, but are retained as separate here.

**Table 47.1.** Organization of the family Microphallidae Travassos, 1920.

| Supersubfamilies | Subfamilies | Tribes |
|---|---|---|
| Maritrematidi | Pseudolevinseniellinae | |
| | Maritrematinae | Maritrematini |
| | | Odhneriini |
| | | 'Vitello-racemina' |
| Promicrophallidi | Promicrophallinae | |
| Gynaecotylidi | Gynaecotylinae | |
| | Basantisiinae | Plenosominoidini |
| | | Basantisiini |
| | | Labidotrematini |
| | Androcotylinae | |
| | Sphairiotrematinae | |
| Microphallidi | Endocotylinae | |
| | Microphallinae | Microphallini |
| | | Atriotrematini |
| | Levinseniellinae | Thulakiotrematini |
| | | Ascorhytini |
| | | Levinseniellini |

[1] The use of this taxonomic category is at the insistence of the author; it does not represent the views of the editors.

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*Allopseudolevinseniella* Yamaguti, 1971 is a junior synonym of *Pseudolevinseniella* Tsai, 1955. The partial or total loss of the digestive tract is accidental, is peculiar to one species and, according to Baer (1944), is not of generic importance. This phenomenon is sporadically observed in five genera of microphallids.

*Apharyngolevinseniella* Yamaguti, 1975 is here considered a junior synonym of *Levinseniella* (*Monarrhenos*) Deblock & Pearson, 1970. See the preceding remark concerning the lack of a digestive tract.

*Austromicrophallus* Szidat, 1964 is a junior synonym of *Levinseniella* Stiles & Hassall, 1901 according to Deblock (1978), who redescribed the type and included it in the subgenus *Levinseniella* (*Monarrhenos*) Deblock & Pearson, 1970. For a discussion on the lack of a digestive tract, see the comments on *Allopseudolevinseniella* above.

*Belopolskiella* Oshmarin, 1963 is a junior synonym of *Basantisia* Pande, 1938, according to Deblock (1975), who redescribed the type-species, *Belopolskiella prolecithum* Oshmarin, 1963, and compared it with *Basantisia halcyonae* Oshmarin, Alekseev & Smetanina, 1969 and *B. longa* Oshmarin, Alekseev & Smetanina, 1969. The three species are congeneric and *B. halcyonae* and *B. longa* are junior synonyms.

*Bulbovitellus* Yamaguti, 1971 is a junior synonym of *Microphallus* according to Montoliu *et al.* (1992), who redescribed the type-material of *M. fusiformis* Reimer, 1963 and compared it with new Spanish specimens of this species.

*Carneophallus* Cable & Kuns, 1951 is a junior synonym of *Microphallus* according to Capron *et al.* (1958). The multiple anatomical variations of the phallus of the numerous species in *Microphallus*, i.e. size, shape, absence or presence of accessory basal or distal lobes (with number, position, form and size), form and position of the ejaculatory duct, surface ornamentations, etc., defy classification and cannot have generic significance.

*Cornucopula* Rankin, 1939 is a junior synonym of *Gynaecotyla* Yamaguti, 1939, according to Rankin (1940).

*Feminacopula* Ke, Liang & Yu, 1987 is a junior synonym of *Microphallus*. The type-species, *F. numenia* Ke, Liang & Yu, 1987, is morphologically identical and synonymous with *M. vaginosus* Deblock & Pearson, 1969. The four projecting stripes of the cirrus are superficial ornaments without generic value. The multiple but simple folds of the enlarged metraterm cannot be considered identical with atrial pockets.

*Heardlevinseniella* Yamaguti, 1971 is a junior synonym of *Levinseniella* (*Monarrhenos*) Deblock & Pearson, 1970, according to Overstreet & Perry (1972).

*Macrostomtrema* Chiu, 1961 is a junior synonym of *Basantisia* Pande, 1938, according to Deblock & Pearson (1968).

*Maritreminoides* Rankin, 1939 is a synonym of *Maritrema* according to Deblock (1973), because of the lack of correspondence between the definition of the genus by Rankin (1939) and its type-species, a true *Maritrema*. The different species of *Maritreminoides* have been distributed into the genera *Maritrema* (*Atriospinosum*) Deblock, 1973, *Maritremopsis* Deblock, 1973, *Quasimaritrema* Deblock, 1973 and *Quasimaritremopsis* Deblock, 1973.

*Maritremopsis* Deblock, 1973 is considered a junior synonym of *Metamaritrema* Yamaguti, 1971 in the present work, as the genera have the same diagnosis.

*Mecynophallus* Cable, Connor & Balling, 1960 is a junior synonym of *Probolocryphe* according to Yamaguti (1971).

*Megalatriotrema* Rao, 1969 is the senior synonym of *Bengaliniella* and *Allomicrophallus*, because of the synonymy of the type-species, *M. hispidum* Rao, 1969, with *Microphallus dicaecus* Mukherjee & Ghosh, 1967 (type-species of *Bengaliniella*) and with *M. indicus* Mukherjee & Ghosh, 1967 (type-species of *Allomicrophallus*) according to Deblock *et al.* (1970).

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*Microphallus garciai* Ibanez, 1973 is a senior synonym of *Megalophalloides apanhorayi* Ching & Ibanez, 1976 (unpublished personal data), and is transferred to *Megalophalloides* as *M. garciai* (Ibanez, 1973) n. comb.

*Mehraformis* Bhardwaj, 1963 is an aberrant genus of the Maritrematinae, poorly drawn, misinterpreted and inadequately described (Bhardwaj, 1963). According to Deblock *et al*. (1970), the type-species cannot be recognized. The illustration evokes *Megalatriotrema*. I consider it a *nomen nudum*.

*Monocaecum* Stafford, 1903 is a junior synonym of *Microphallus* according to Baer (1944). The rudimentary caeca are not of generic value. (See comments above on *Allopseudolevinseniella*.)

*Ornithotrema* Caballero, Brenes & Arroyo, 1963, considered by the original authors (Caballero *et al*., 1963) as a member of the Maritrematinae, is a problematic microphallid. The type-species, *O. momoti* Caballero, Brenes & Arroyo, 1963, appears identical with *Metamaritrema* Yamaguti, 1971, except for the exact median position of the genital pore, just anterior to the ventral sucker (the ventral sucker is distinct) and the greater number of vitelline follicles. At the distal extremity of the cirrus-sac are two unarmed accessory sacs with a common pore (unpublished personal data). Knowledge of the excretory formula of the species should confirm its position either among the microphallids, or in a distinct family (Ornithotrematidae Skrjabin, 1966), as proposed by Skrjabin (1966a). *O. longibursatus* Caballero & Brenes, 1964 is a species of *Metamaritrema* according to Deblock (1971), and so this second species is no help in solving the taxonomic problem posed by the type-species of this enigmatic genus. The genus is treated here as *incertae sedis*.

*Oschmarinotrema* Yamaguti, 1971 is a junior synonym of *Levinseniella* (*Levinseniella*) Stiles & Hassall, 1901 according to Deblock's (1975) assessment of the type-species, *O. acanthophalla* (Oshmarin, 1963). The unusual genital morphology of the type-species results from an erroneous interpretation by the author of a typical genital atrium of *Levinseniella* protruded through the genital pore with its accessory sacs, the folds of which simulate an armature. The classically club-shaped phallus is enormous.

*Paraheterophyes* Afanassief, 1941 is a junior synonym of *Microphallus* according to Belopol'skaya (1952).

*Paraspelotrema* Wang, 1982, imperfectly figured and interpreted, is probably a junior synonym of *Gynaecotyla* Yamaguti, 1939 according to Deblock & Bartoli (1988).

*Pseudocarneophallus* Yamaguti, 1971 is considered a synonym of *Microphallus* Ward, 1901 for the same reason evoked for *Carneophallus* (variations in the development of the phallus) and because the class of the vertebrate host cannot be a generic character. Encysted microphallid metacercariae become mature after a few hours in the digestive tract of any vertebrate. The apparent specificity is trophic, linked to ingestion of crustacean intermediate hosts. Consequently, host-specificity is not strict.

*Pseudomegalophallus* Yamaguti, 1971 is considered a junior synonym of *Megalophallus* Cable, Connor & Balling, 1960. The absence of the gut and the specificity of microphallids for their vertebrate hosts have no generic value, either separately or in combination (see *Allopseudolevinseniella* and *Pseudocarneophallus*).

*Renschetrema* Rohde, 1964 (Renschetrematinae Yamaguti, 1971) is too distinct in its morphology to be classified among the Microphallidae (separate male and female dorsal genital pores; special and complex male copulatory apparatus) (see Deblock, Chapter 61, this volume). A description of the excretory formula should confirm the family position of this enigmatic genus. In addition, the infection of Chiroptera via a crustacean second intermediate host does not seem credible.

*Sagittotrema* Bondarenko, 1966 is characterized by the presence, in the anterior region of the body, of linear tegumentary swellings on either side of the oral sucker, with loss of spines and

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histological modification. This aspect seems a priori to be more accidental than dependent on some genetic characteristic. The study of the type led Deblock (1971) to consider the genus as a junior synonym of *Pseudospelotrema* Yamaguti, 1939.

*Spelophallus* Jägerskiöld, 1908, accepted by Baer (1944), has been proposed as a subgenus of *Microphallus* Ward, 1901 by Deblock (1971) for some obvious anatomical disparities, which were well described by Jägerskiöld (1908), i.e. the metraterm insertion at the margin of the genital pore, creating a false genital atrium (or 'phallus pouch'), and by Biguet *et al.* (1958), i.e. the existence of a vestigial vesiculoprostatic pouch in material of *M. canchei* Biguet, Deblock & Capron, 1958, a synonym of *S. primas* Jägerskiöld, 1908, according to Reimer (1963) and Deblock & Ky (1966).

*Spelotrema* Jägerskiöld, 1901 is a junior synonym of *Microphallus* according to Baer (1944) and Stunkard (1951).

*Streptovitella* Swales, 1933 is a junior synonym of *Maritrema* Nicoll, 1907, according to Ciurea (1933).

## Genus *incertae sedis*

*Aspalacitrema* Deblock & Rausch, 1965 is a problematic genus. The diagnosis indicates that it belongs in the Maritrematidi, but does not suggest to which tribe it should be ascribed. The status of the genus will be questionable as long as its flame-cell formula is unknown.

## Glossary

**Accessory sac:** Hollow organ of variable morphology opening into the cavity of the genital atrium and so called after an analogy with the atrial accessory sac of *Echinocotyle* Blanchard, 1891 (Cestoda: Hymenolepididae). Four morphological types of sac are described in the different genera of the microphallid subfamily Levinseniellinae (see below 'Atrial accessory sacs' for the four definitions of types).

**Accolade:** Derived from a typographic term referring to a double curve joining several words, letters, lines, etc., horizontally or vertically. Used for the vitellarium of some maritrematines, in which it forms two short, horizontal arches anteriorly to the testes.

**Atrial accessory sacs:** Four types are found in the genital atrium complex of the microphallid subfamily Levinseniellinae:

**Type I.** Diverticula or sacs generally multiple (one to 12 or more) and all similar, rather small, regularly ovoid, hollow, with thick wall, generally unarmed but sometimes armed inside with sclerotized plates, teeth or hooks. These sacs are inserted on the sinistral wall of the genital atrium in one or two rows forming a semicircle; they are enveloped in parenchymatous tissue, which is slightly different from the general parenchyma. These sacs are occasionally able to protrude all together through the genital pore. They were originally called 'male pockets' by Jägerskiöld (1907).

**Type II.** A single diverticulum much longer and bigger than Type I, like a purse with a thick, deformable wall, exceptionally sclerotized, and attached to the dextral side of the genital atrium, partly situated dorsally to the ventral sucker. This sac was originally called a 'female pocket' by Jägerskiöld (1907).

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**Type III.** A single purse-like diverticulum, of medium size, with a deformable wall; similar to Type II, but appended from the posterior wall of atrium; it is not associated with the ventral sucker.

**Type IV.** A single large diverticulum (similar in size to the testes), on the sinistral side of the genital atrium and enveloping either a thin sclerotinized spatula or an ovoid, movable, thick muscular mass. These masses, spatulate or muscular, are apparently able to protrude through the genital pore.

**Atrial scale:** A muscular, semicircular protuberance of the atrial margin associated with the ventral sucker and parallel to the longitudinal axis of the body.

**Cirrus:** As it relates to the copulatory organ characteristic of the microphallid subfamily Maritrematinae. It invaginates within the genital pouch and is a continuation of the proximal ejaculatory duct and the prostatic chamber. It is not atrial. It is evaginable, like the finger of a glove turned inside out, through the genital atrium and the genital pore. The evaginated cirrus exhibits many kinds of morphology (filiform, cylindrical, straight, crescentic, etc.) with a tegument that may be glabrous, spinous or verrucous, all aspects of which are found on an invaginated cirrus. The extremity of the cirrus, partly projected through the genital pore, is incorrectly called a male 'papilla' in the literature.

**Cornucotyle:** The muscular and fleshy crescent-shaped hermaphroditic atrial organ characteristic of the microphallid tribe Gynaecotylini; the muscular, fleshy aspect resembles the phallus of the genus *Microphallus*. It is associated with the genital pouch and receives the uteroterm.

**Elasmocotyle:** The non-fleshy hermaphroditic atrial organ characteristic of the microphallid subfamily Basantisiinae, with several partly sclerotized parietal protuberances, originating from the internal and atrial wall of the genital pouch. It contains a short hermaphroditic canal.

**Genital atrium complex:** The genital atrium with at least one accessory sac; if several sacs exist, they may be morphologically identical or different (see 'Accessory sacs').

**Genital atrium simple:** Genital atrium without accessory sac.

**Genital horseshoe pouch:** Horseshoe-shaped genital pouch, with its aperture directed posteriorly, typical of the Basantisiinae.

**Genital musculature:** Muscular bundles specialized for the motion of the genital pouch and of the pieces forming the cornucotyles and elasmocotyles. The number and power of the bundles vary according to their function in the genus or species considered: (i) they curve outside the genital pouch as extrinsic muscles of this organ; (ii) they move one or other piece of the elasmocotyle; (iii) as adductors, they move the branches of the genital horseshoe pouch; and these branches actively serve as tongs during copulation. This apparatus is typical of the Basantisiinae.

**Genital pouch** (so-called *in lit*. 'male genital pouch' or 'false cirrus-sac'): General term for a sac-like structure enclosing the seminal vesicle, prostatic gland and pars prostatica, but lacking an evaginable cirrus.

**Hermaphroditic atrial copulatory organ:** Organ typical of the Basantisiinae, with a single, short hermaphroditic canal formed by the confluence of the distal male and female genital ducts inside the elasmocotyle; consequently, the genital opening of the elasmocotyle is unique (see 'Uteroterm').

**Papilla** (or male papilla): Inappropriate term for cirrus and phallus.

**Phallosphere:** A regularly spherical cyst with a smooth and refractile, sclerotized wall containing a tubular and partly muscular, fleshy male copulatory organ. It is characteristic of *Sphairiotrema*. Devoid of a metraterm aperture, the phallosphere has no value as a genital atrium. It is a 'phallus pouch'.

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**Phallus:** Fleshy male copulatory organ, often muscular, characteristic of *Microphallus* and other microphallines. Situated inside the genital atrium (or exceptionally in a true phallus pouch), it is able to project through the genital pore. It does not invaginate.

**Phallus pouch:** The pouch enveloping the male copulatory organ but not joined by the metraterm. Only situated on the male tract, this pouch cannot be considered as a true genital atrium, which is classically defined as hermaphroditic. It is consequently a real 'phallus pouch'. It is found in such genera as *Sphairiotrema*, *Microphallus* (*Spelophallus*), *Atriotrema* and *Spiculotrema*. Also known as a pseudogenital atrium.

**Plate Pl 2:** A partly or totally sclerotized structure attached to the ventral face of the genital pouch at the posterior level of the seminal vesicle, facing the elasmocotyle of the Basantisiinae.

**Pseudogenital atrium:** See 'Phallus pouch'.

**Rhyncostome:** Terminal buccal formation, annular but not sucker-like, with a more or less elongate dorsal piece that eventually folds up ventrally on itself. It resembles a small rostellum. It is a characteristic of *Rhyncostophallus*.

**Spinous atrio-acetabular plate:** Local modification of the atrial wall near the ventral sucker, bearing numerous minute spines. This special plate is described in a few genera (*Maritrema* (*Atriospinosum*), *Quasimaritrema*, *Endocotyle*).

**Uteroterm:** Distal differentiation of the uterine canal without a copulatory function, joining not to the genital atrium but to either the male ejaculatory duct or the cornucotyle, depending on the genus. This confluence constitutes a genital hermaphroditic ending. A sphincter is present at the level of the uteroterm. It is a characteristic of the Gynaecotylinae and Basantisiinae.

**Vesiculoprostatic (or vesicular and prostatic) pouch:** Terms synonymous with 'false cirrus-sac' or 'genital pouch' (see above).

## Genus *Aspalacitrema* Deblock & Rausch, 1965 (*incertae sedis*)

**Diagnosis:** Body linguiform or elliptical and small (300–400 µm); tegument with small spines. Suckers well separated. Oral sucker slightly larger than ventral. Glandular ducts present dorsal to oral sucker. Ventral sucker pre-equatorial. Digestive tract short, in forebody. Caeca very divergent ending submarginally. Testes large, lateral, symmetrical, immediately posterolateral to ovary. Cirrus-sac present, thin-walled, cylindrical, transversely J-shaped, half-surrounding ventral sucker. Seminal vesicle short, bipartite. Prostatic chamber ovoid, voluminous with granular cells. Ejaculatory duct long, more or less folded, often protrudes through genital pore without forming true cirrus of rigid type. Genital atrium simple and reduced. Genital pore dextral or sinistral to equator of ventral sucker. Ovary lateral, dextral or sinistral to ventral sucker, on opposite side to genital pore. Seminal receptacle present. Uterine coils posterior to ventral sucker and testes, but not encircling testes. Metraterm elongate and well differentiated, opening into genital atrium on ventral sucker side. Eggs 36–42 µm, not numerous. Vitellarium a single mass of follicles in hindbody, median, between testes; vitelline ducts not described. Excretory vesicle and solenocytes not described. In intestine of mammals; North America. Type-species *A. aspalacis* (Rausch, 1962) Deblock & Rausch, 1965.

## Family Microphallidae Ward, 1901

Syn. Maritrematidae Nicoll, 1907

**Diagnosis:** Adults tiny, 500 ± 300 µm, rarely more than 1000 µm. Body flattened dorsoventrally and usually thin, longer than broad, linguiform, pyriform or fusiform, rarely triangular or globular

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due to contraction. Tegument spinous; spination decreasing from anterior to posterior; spines squamous. Suckers generally two, medium-sized, equal or not, well separated (Gynaecotylini with two ventral suckers). Oral sucker ventrally subterminal, occasionally atypical. Ventral sucker embedded in parenchyma, small, generally postequatorial, rarely absent. Digestive tract present with rare exceptions. Prepharynx short. Pharynx present. Oesophagus present. Caeca widely divergent, generally not extending beyond ventral sucker or level of ovary, with few exceptions, occasionally atrophied or absent. Testes two, lateral, symmetrical, postovarian, well separated by uterine coils. Male terminal genitalia intercaecal, anterior to ventral sucker, enclosed in pouch or free in parenchyma; when present, pouch contains evaginable cirrus or not; when cirrus absent, genital atrium contains copulatory organ of various types (either plump, muscular phallus and cornucotyle, or complex and partly sclerotized elasmocotyle). Phallus pouch (or pseudogenital atrium) occasionally present. Genital atrium either simple, more or less large, or complex (atrial walls complicated with diverticula, or 'accessory sacs', of various types). Genital pore ventral, near lateral edge of ventral sucker, more often sinistral than dextral. Ovary postcaecal, pretesticular, on opposite side of body to genital pore, at level of ventral sucker, median, submedian or lateral. Seminal receptacle absent. Laurer's canal present. Oötype and Mehlis' gland equidistant from all three gonads. Numerous postcaecal uterine coils in hindbody; extratesticular uterine coils often present, from which precaecal loops may arise. Metraterm usually present, opens deeply or laterally on wall of genital atrium, or more rarely on sinistral margin of genital pore; other arrangements (uteroterm and hermaphroditic canal) more rarely seen. Eggs numerous (except in tiny species), small ($20 \pm 5$ µm), unembryonated *in utero*. Vitellarium follicular, always in two symmetrical clusters, ribbon-like or otherwise, and variously situated, more often postcaecal than precaecal. Vitelline ducts short or long according to position of vitelline clusters and to medial or distal site of insertion of main ducts; vitelloduct unpaired in hindbody at level of ventral sucker. Excretory system always with 16 flame-cells with formula 2 [(2 + 2) + (2 + 2)] = 16; vesicle with short arms V-, Y- or I-shaped in post- or intertesticular position; pore median, terminal. Life-cycle with three hosts (prosobranch mollusc, crustacean, vertebrate); crustacean host omitted from some abridged cycles. Xiphidiocercaria monostome, anenteric, leptocercous with 16 flame-cells; formula persists in metacercarial and adult stages. Metacercaria encysted, identical to adult when mature. Life-cycle takes place in brackish, marine or fresh waters, in decreasing order of frequency. Adult chiefly in intestine of vertebrates; rarely in other sites. No strict specificity; final host depends on trophic habits of predators (chiefly birds) for crustacean or, occasionally, molluscan hosts of infective larvae; cosmopolitan. Type-genus *Microphallus* Ward, 1901.

## Key to supersubfamilies[2]

**1a. Male genital pouch present (commonly called 'cirrus pocket'), with cirrus or fleshy phallus inside ..... 2.**
**1b. No male genital pouch (seminal vesicle and prostate free in parenchyma) ..... ..... Microphallidi Ward, 1901 (status amend.).**

**2a. Evaginable cirrus present ..... Maritrematidi Nicoll, 1907 (status amend.).**
**2b. Protrusible fleshy phallus present (instead of evaginable cirrus) ..... ..... Promicrophallidi Fischthal & Kuntz, 1981 (status amend.).**

[2] The order of the taxa in the key does not follow that used in the other chapters, at the insistence of the author.

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**2c. Male genital pouch without cirrus or fleshy phallus inside, so-called 'vesiculo-prostatic pouch' present ..... Gynaecotylidi Guschanskaya, 1952 (status amend.).**

## Supersubfamily Maritrematidi Nicoll, 1907 (status amend.)

**Diagnosis:** Male genital pouch present as standard cirrus-sac, with seminal vesicle, prostatic gland, ejaculatory duct, invaginated cirrus and commonly prostatic chamber; genital atrium generally reduced (exception: Pseudolevinseniellinae), simple, empty. Cirrus evaginable through genital pore. In digestive tract of vertebrates; cosmopolitan. Type-genus *Maritrema* Nicoll, 1907.

## Key to subfamilies

**1a. Genital atrium a wide, simple, broad, deep ventral invagination of spinous body tegument ..... Pseudolevinseniellinae Tsai, 1955.**

**1b. Genital atrium a small, simple, superficial and ventral cavity, delimited by thin membranous wall (more or less perceptible) ..... Maritrematinae Nicoll, 1907.**

## Subfamily Pseudolevinseniellinae Tsai, 1955

**Diagnosis:** Body elongate (400–500 μm), rather plump. Two suckers. Digestive tract present or not; when present, oesophagus short, caeca short, widely divergent in forebody, anterior to vitellarium. Testes symmetrical in posterior quarter of body. Cirrus-sac in forebody, transverse, short, broad; seminal vesicle present; two prostatic glands: proximal cirrus-sac with large, clear cells of main prostatic gland; distal cirrus-sac with dense, small cells of secondary prostatic gland. Prostatic chamber present. Ejaculatory duct short. Invaginated cirrus short, voluminous, with broad spinous duct armed with numerous spines. Genital atrium sinistral to ventral sucker, simple, large and deep, capping distal extremity of cirrus-sac. Genital pore sinistral to ventral sucker, rather large. Ovary at level of ventral sucker, dextral. Uterus occupies hindbody, without marginal extratesticular loops. Metraterm present, opens into dorsal base of genital atrium. Vitellarium in forebody, in symmetrical clusters on each side of cirrus-sac, and postcaecal when caeca present; clusters of about ten rounded follicles; vitelline ducts long, U-shaped. Excretory vesicle V-shaped, short, between testes. In digestive tract of vertebrates; southern China, Australia. Type-genus *Pseudolevinseniella* Tsai, 1955.

### Genus *Pseudolevinseniella* Tsai, 1955 (Figs 47.1, 47.2)

(Syn. *Allopseudolevinseniella* Yamaguti, 1971)

**Diagnosis:** With characters of subfamily. Type-species *P. cheni* Tsai, 1955.

## Subfamily Maritrematinae Nicoll, 1907

**Diagnosis:** Cirrus-sac present. Genital atrium superficial, ventral, small, simple, delimited by thin, membranous wall, with metraterm opening on its sinistral margin (rare exceptions). In digestive tract (very few exceptions) of vertebrates; cosmopolitan. Type-genus *Maritrema* Nicoll, 1907.

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## Key to tribes

**1a. Vitellarium disposed along anterior edges of testes; short T-shaped vitelline ducts ..... ..... Maritrematini Nicoll, 1907 (status amend.).**
**1b. Vitellarium not disposed along anterior edges of testes ..... 2.**

**2a. Vitellarium symmetrical or subsymmetrical, not in files but forms two postcaecal clusters of about ten rounded follicles, situated laterally in ovariotesticular region; vitelline ducts transverse, medium-sized, inserted in centre of clusters; organs of cirrus-sac in straight line ..... Odhneriini Deblock, 1971.**
**2b. Lacking above characters of vitellarium; follicles in compact pre- or postcaecal clusters; vitelline ducts medium or long, not T-shaped; organs of cirrus-sac more or less convoluted ..... Artificial group of 'Vitello-racemina'.**

## Tribe Maritrematini Nicoll, 1907 (status amend.)

**Diagnosis:** Vitellarium along anterior edges of testes, in hindbody (with rare exceptions), forms two symmetrical files of follicles, either small and numerous, or larger and few (length of files inversely proportional to volume of follicles); short files form two pretesticular symmetrical arches; long files form two ribbons, first pretesticular, then marginal, encircling uterine coils either completely (annular vitellarium) or partly (horseshoe vitellarium); vitelline ducts generally short, T-shaped, terminal (inserted on extremity of ribbons closest to ventral sucker); more rarely long, not T-shaped, inserted submedially on ribbons; distal extremities of ribbons anterior to caeca in few genera. In intestine of vertebrates; cosmopolitan. Type-genus *Maritrema* Nicoll, 1907.

## Key to genera

**1a. Uterine coils entirely postcaecal ..... 2.**
**1b. Uterine coils not entirely postcaecal, extended anteriorly by two precaecal loops ..... 7.**

**2a. Ventral sucker lacking ..... *Anacetabulitrema* Deblock & Rosé, 1964. (Fig. 47.3)**
**Diagnosis**: General morphology similar to *Maritrema* (see semicouplet 5a) except male and female terminal ducts precaecal and sinistral. Body medium-sized (350 µm). Ventral sucker lacking. Oesophagus short. Caeca end at ovarian level. Testes postovarian, lateral, symmetrical. Cirrus-sac long, thin-walled, mainly postcaecal, transverse and oblique; ejaculatory duct long, convoluted. Genital atrium simple, superficial and small with metraterm opening on posterior margin. Genital pore precaecal and sinistral. Ovary dextrally submedian, intercaecal. Uterus postcaecal with coils around testes. Vitellarium annular; vitelline ducts short, T-shaped, as in *Maritrema*. Excretory vesicle short, post-testicular, V-shaped. In intestine of Anseriformes; western Palaearctic (Europe). Type-species *A. samarae* Deblock & Rosé, 1964.

**2b. Ventral sucker present ..... 3.**

**3a. Vitellarium of numerous small follicles forming ring or sinuous chain of two long, symmetrical ribbons, opened or closed posteriorly ..... 4.**

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**3b. Vitellarium with few, large follicles, in equatorial and testicular areas, symmetrical or not ... 6.**

**4a. Vitellarium resembles open, symmetrical ribbons but follows sinuous course: each branch curves around internal and upper margins of each testis; anterior extremity of ribbons overlaps caeca or not (characteristic type of vitelline gland, in form of 'ring clasp') ..... ..... *Pseudomaritrema* Belopol'skaya, 1952. (Fig. 47.4)**

**Diagnosis**: Morphology similar to *Maritrema* (semicouplet 5a) except for vitelline arrangement. Body small or medium-sized (350–600 μm). Ventral sucker present. Digestive tract of short or medium length. Caeca in forebody. Testes postovarian, lateral, symmetrical. Cirrus-sac postcaecal, transverse, thin-walled; ejaculatory duct long or very long, sigmoid, prolonged by long duct of invaginated cirrus. Genital atrium reduced. Genital pore sinistral to ventral sucker. Ovary median. Uterus postcaecal in hindbody; coils surround testes. Vitellarium with anterior extremities of ribbons pretesticular or overlapping caeca; vitelline ducts short, T-shaped, in hindbody, posterior to ovary with submedial insertions at ribbons. Excretory vesicle short, post-testicular, V-shaped. In intestine of Charadriiformes; northern and eastern Siberia. Type-species *P. posterolecithale* Belopol'skaya, 1952.

**4b. Vitellarium in symmetrical ribbons reach close to margins of hindbody, surrounding uterine coils and testes, horseshoe-shaped with posteriorly directed opening, or complete ring ..... 5.**

**5a. Genital pore simple, superficial, slightly differentiated, unarmed ..... ..... *Maritrema* (*Maritrema*) Nicoll, 1907. (Figs 47.5, 47.6)**

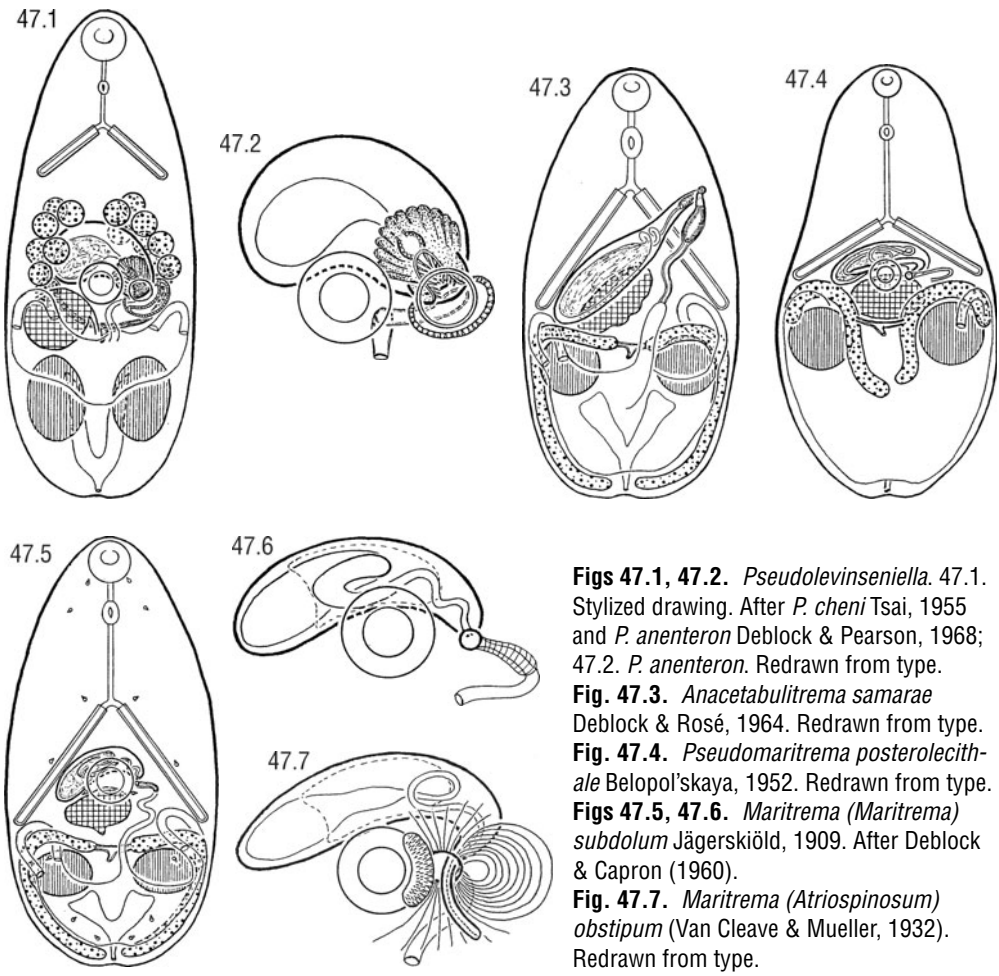
(Syn. *Streptovitella* Swales, 1933)

**Diagnosis**: Body linguiform, occasionally fusiform, or almost rounded when contracted, small or medium-sized (300–600 μm), rarely large. Suckers usually subequal. Oesophagus short or medium-sized. Caeca of variable length, usually reach ventral sucker, but from very short (anterior to cirrus-sac) to semi-long (reach testicular level). Testes postovarian, lateral, symmetrical. Cirrus-sac intercaecal, thin- or thick-walled, either short, arcuate and transverse, or long and inverted J-shaped with proximal end reaching right margin of body, and distal end at level of genital pore; ejaculatory duct generally curled, with distinct or indistinct prostatic chamber. Invaginated cirrus slightly or strongly developed; evaginated cirrus of various sizes, diameters and shapes, filiform, cylindrical, crescent-shaped, with tegument partly or entirely glabrous, spinous or verrucous. Genital atrium reduced. Genital pore sinistrolateral to ventral sucker, simple, superficial, slightly differentiated, unarmed. Ovary at level of ventral sucker, median to dextral, entire or slightly lobed. Uterus postcaecal, with lateral and extratesticular coils generally present, occasionally absent. Metraterm size commensurate with evaginated cirrus. Vitellarium in symmetrical ribbons reaching close to margins of hindbody, surrounding uterine coils and testes, horseshoe-shaped with posteriorly directed opening, or ring-shaped; vitelline ducts median, very short, T-shaped, inserted at proximal extremities of vitelline ribbons. Excretory vesicle short, V- or Y-shaped, post-testicular. In intestine of vertebrates, mainly birds (Charadriiformes, Lariformes, Anseriformes, etc.); cosmopolitan. Type-species *M. gratiosum* Nicoll, 1907.

**5b. Genital pore modified, provided on one side with superficial, spinous atrio-acetabular plate and, on other side, with numerous, thin, concentric and subtegumentary muscular rings ..... *Maritrema* (*Atriospinosum*) Deblock, 1973. (Fig. 47.7)**

**Diagnosis**: Morphology similar to *Maritrema* (*Maritrema*) (semicouplet 5a). Genital pore modified, provided on one side with superficial, spinous atrio-acetabular plate, and on other side

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**Figs 47.1, 47.2.** *Pseudolevinseniella*. 47.1. Stylized drawing. After *P. cheni* Tsai, 1955 and *P. anenteron* Deblock & Pearson, 1968; 47.2. *P. anenteron*. Redrawn from type.
**Fig. 47.3.** *Anacetabulitrema samarae* Deblock & Rosé, 1964. Redrawn from type.
**Fig. 47.4.** *Pseudomaritrema posterolecithale* Belopol'skaya, 1952. Redrawn from type.
**Figs 47.5, 47.6.** *Maritrema (Maritrema) subdolum* Jägerskiöld, 1909. After Deblock & Capron (1960).
**Fig. 47.7.** *Maritrema (Atriospinosum) obstipum* (Van Cleave & Mueller, 1932). Redrawn from type.

associated with numerous thin, subtegumentary concentric muscular rings. In intestine of freshwater fishes and birds (Anseriformes, Ralliformes); cosmopolitan. Type-species *M.* (*A.*) *obstipum* (Van Cleave & Mueller, 1932) Mueller, 1934.

**6a. Vitelline follicles in wide ribbons, symmetrical or not (made asymmetrical by marginal extremities, haphazardly passing anteriorly or posteriorly on either side); posterior uterine coils in several regular, radiating festoons ..... ..... *Paramaritremopsis* Deblock & Bush, 1985. (Fig. 47.8)**

**Diagnosis**: Morphology *Maritrema*-like (semicouplet 5a), except in vitelline and uterine configurations. Caeca in forebody, short, divergent. Cirrus-sac an inverted J-shape, long, with muscular wall. Male duct long, sigmoid, without prostatic chamber; cirrus unarmed. Genital pore and genital atrium reduced, sinistrolateral to ventral sucker. Ovary median. Uterine loops lateral extratesticular; anterior loops penetrating more or less deeply into region between caecum and cirrus-sac, mainly on poral side; posterior loops form radiating festoons. Pretesticular vitellarium of variable morphology, with few, large follicles, and distal extremities of ribbons passing contingently on either side anteriorly or posteriorly; vitelline ducts median, short, T-shaped. Excretory

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vesicle short, post-testicular, V-shaped. In intestine of Charadriiformes; Nearctic. Type-species *P. stunkardi* Deblock & Bush, 1985.

**6b. Vitellarium of large follicles in two short, pretesticular symmetrical arches; posterior uterine coils without festoons ..... *Metamaritrema* Yamaguti, 1971. (Fig. 47.9)**
(Syn. *Maritremopsis* Deblock, 1973)

**Diagnosis**: General morphology *Maritrema*-like (semicouplet 5a) except in vitelline configuration. Body form variable. Vitellarium with two short transverse, symmetrical and pretesticular arches of few large follicles. Posterior uterine coils without festoons. In various sites of hosts, mainly intestine, or bile-ducts, kidneys of mammals and birds; cosmopolitan. Type-species *M. prolixum* (Caballero & Montero-Gei, 1961) Yamaguti, 1971.

**7a. Vitellarium symmetrical, entirely postcaecal; oral sucker of normal construction ..... 8.**

**7b. Vitellarium long, symmetrical and annular as in *Maritrema*, but partly postcaecal and partly in forebody, encircles ovary, cirrus-sac and caeca, reaches level of oesophagus and pharynx; oral sucker modified with minute anterior rostellum ..... ..... *Probolocoryphe* Otagaki, 1958. (Fig. 47.10)**
(Syns *Macrophallus* Otagaki, 1958 *nec* Mueller, 1922; *Mecynophallus* Cable, Connor & Balling, 1960)

**Diagnosis**: Body medium-sized, fusiform. Oral sucker longer than ventral, with short anterodorsal rostellum. Digestive tract short, in forebody, anterior to cirrus-sac. Testes symmetrical, postovarian, postvitelline, in mid-hindbody. Cirrus-sac thin-walled, arcuate, transverse, anterior to ventral sucker; evaginated cirrus filiform, unarmed. Genital atrium minute. Genital pore sinistrolateral to ventral sucker. Ovary dextral to ventral sucker. Anterior region of uterus with two dorsal symmetrical coils, anterior to caeca, ascending to level of pharynx; posterior coils surround testes in hindbody. Metraterm distinct. Vitellarium semi-annular, long, partly postcaecal and partly precaecal, partly marginal, encircles ovary, cirrus-sac and caeca, reaches level of oesophagus or pharynx, not enclosing testes and posterior uterine coils; vitelline ducts median, short, T-shaped. Excretory vesicle short, V- or Y-shaped. In intestine of birds (Charadriiformes, Ralliformes); eastern Palaearctic, Nearctic and Neotropical. Type-species *P. asadai* (Otagaki, 1958) Otagaki, 1958.

**8a. Vitelline follicles few, large, in two short pretesticular arches ..... ..... *Quasimaritremopsis* Deblock, 1973. (Fig. 47.11)**

**Diagnosis**: General morphology *Quasimaritrema*-like (semicouplet 9a). Body oval, medium-sized. Digestive tract short; oesophagus short. Caeca short in forebody. Testes postovarian, symmetrical, lateral in hindbody. Cirrus-sac thin-walled, medium-sized, postcaecal, in forebody. Genital atrium minute; genital pore sinistrolateral to ventral sucker. Ovary submedian dextral. Uterus mainly postcaecal apart from two lateral and ascending precaecal loops. Metraterm present but not distinct. Vitelline follicles few, large, in two short pretesticular arches, not passing marginally posterior to testes; vitelloducts not described (probably short, T-shaped). Excretory vesicle short V-shaped, post-testicular. In intestine of freshwater fishes; Nearctic. Type-species *Q. medius* (Van Cleave & Mueller, 1932) Deblock, 1973.

**8b. Vitelline follicles in two long marginal ribbons encircling uterine coils and testes, forming almost closed ring ..... 9.**

**9a. Genital pore modified, with lateral, superficial, spinous atrio-acetabular plate ..... ..... *Quasimaritrema* Deblock, 1973. (Fig. 47.12)**

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**Diagnosis**: General morphology *Maritrema* (*Atriospinosum*)-like (semicouplet 5b). Body medium-sized (about 400 μm). Oesophagus short. Caeca short, divergent, in forebody. Cirrus-sac transverse, arcuate and medium-sized, postcaecal in forebody. Genital atrium minute. Genital pore sinistrolateral to ventral sucker, with lateral, superficial, spinous, atrio-acetabular plate. Subtegumentary concentric annular musculature at poral level not described. Ovary not described (probably submedian, dextral). Uterus mainly postcaecal, with two lateral, ascending coils reaching precaecal and oesophageal areas. Metraterm present, not distinct. Vitelline follicles in two long marginal ribbons encircling uterine coils and testes, forming almost closed ring; vitelloducts short, T-shaped. Excretory vesicle short, V-shaped, posterior to testes. Vertebrate host unknown; eastern Palaearctic. Type-species *Q. caridinae* (Yamaguti & Nishimura, 1944) Deblock, 1973.

**9b. Genital pore without spinous plate of above type ..... ..... *Floridatrema* Kinsella & Deblock, 1994. (Fig. 47.13)**

**Diagnosis**: General morphology *Quasimaritrema*-like (semicouplet 9a). Body medium-sized (400 μm). Oesophagus short. Caeca divergent, terminate at level of ventral sucker. Testes postovarian, symmetrical, lateral in hindbody. Cirrus-sac in forebody, large, arcuate, J-shaped; proximal ejaculatory duct coiled with long, cylindrical spermatic chamber; cirrus stout, spinous. Genital atrium minute. Genital pore sinistrolateral to ventral sucker without spinous atrio-acetabular plate. Ovary submedian dextral. Anterior part of uterus with symmetrical dorsal coils, ascending anterior to caeca to level of oesophagus. Metraterm long, well-differentiated, ensheathed by gland-cells. Vitellarium in hindbody, in form of symmetrical horseshoe-shaped ribbons; vitelline ducts short, T-shaped. Excretory vesicle short, Y-shaped. In intestine of mammals; Nearctic. Type-species *F. heardi* Kinsella & Deblock, 1994.

## Tribe Odhneriini Deblock, 1971

**Diagnosis:** Cirrus-sac cylindrical; all organs aligned along axis. Genital pore sublateral, sinistral to ventral sucker, or more posterior. Uterus postcaecal. Vitellarium symmetrical or sub-symmetrical, not in files but forming two postcaecal clusters of about ten rounded follicles, situated laterally in ovariotesticular region. Vitelline ducts transverse, medium-sized, inserted in centre of vitelline clusters. In intestine of birds; cosmopolitan. Type-genus *Odhneria* Travassos, 1921.

## Key to genera

**1a. Genital pore sinistral to ventral sucker, at equator ..... 2.**

**1b. Genital pore sinistral, displaced posteriorly to testicular level ..... ..... *Testiculoporus* Kinsella & Deblock, 1997. (Fig. 47.14)**

**Diagnosis**: Body fusiform, narrow, elongate (500 μm). Oral sucker slightly wider than ventral sucker. Ventral sucker postequatorial. Oesophagus rather long. Caeca short, divergent, terminate at level of ventral sucker. Testes oval, symmetrical, posterolateral, submarginal. Cirrus-sac cylindrical, inverted J-shaped, partly encroaching on anterior half of ventral sucker and reaching poral testis; pars prostatica present; invaginated cirrus short. Genital atrium simple, reduced, superficial. Genital pore sinistral, displaced posteriorly, at testicular level. Ovary dextral to ventral sucker. Uterus postcaecal, occupies hindbody, with extratesticular loops. Metraterm short with ventral opening joining anterior margin of genital pore. Vitellarium with two symmetrical clusters of about ten rounded follicles at ovariotesticular level, partly marginal; vitelline ducts transverse,

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pretesticular. Excretory vesicle unknown. In intestine of Charadriiformes; Nearctic. Type-species *T. cedarkeyensis* Kinsella & Deblock, 1997.

**2a. Uterine coils without extratesticular and lateral loops; testes oval, with oblique axis; vitellarium marginal, slightly asymmetrical, with poral cluster posterior to level of genital pore, slightly more posterior and shorter than aporal cluster ..... ..... *Odhneria* Travassos, 1921. (Figs 47.15, 47.16)**

**Diagnosis**: Body fusiform, narrow, elongate (850 ±150 μm), with characteristic appearance. Suckers subequal. Ventral sucker postequatorial. Oesophagus rather long. Caeca short, divergent, at level of ventral sucker. Testes oval, symmetrical, marginal, with oblique long axis, rather posterior in hindbody and partly posterior to vitellarium. Cirrus-sac in forebody short, arcuate, transverse; pars prostatica present; invaginated cirrus short, with thick striated wall; thin down-like covering on evaginated cirrus, rarely observed. Genital atrium simple, reduced, superficial. Genital pore sublateral, equatorial. Ovary dextral to ventral sucker. Uterus postcaecal, occupies hindbody; extratesticular ascending loops absent. Metraterm long, muscular, dorsal to cirrus-sac and pre-atrial loop, joins sinistral margin of atrial pore ventrally. Vitelline follicles in two marginal groups at ovariotesticular level, slightly asymmetrical, more linear on aporal side than on poral; vitelline ducts transverse, pretesticular. Excretory vesicle short V- or Y-shaped, reaches testes. In intestine of birds (Ciconiiformes, Charadriiformes); cosmopolitan. Type-species *O. odhneri* Travassos, 1921.

**2b. Lateral, extratesticular uterine loops present, reaching caecal ends ventrally, partly covering both testes and vitellarium; testes oval with transverse axis; vitellarium forms symmetrical clusters at ovariotesticular level ..... *Pseudospelotrema* Yamaguti, 1939. (Fig. 47.17)**

(Syn. *Sagittotrema* Bondarenko, 1966)

**Diagnosis**: Resembles *Odhneria*. Body elongate (900 μm), fusiform. Ventral sucker postequatorial, slightly larger than oral sucker. Oesophagus rather long. Caeca short, divergent, at level of ventral sucker. Testes symmetrical, submarginal, in hindbody, with transverse axis, partly covered by uterine coils and vitellarium. Cirrus-sac postcaecal in forebody, relatively short, arcuate, transverse; pars prostatica present; invaginated cirrus 100 μm long, unstriated (but not precisely described). Genital atrium simple, reduced, superficial. Genital pore on left edge of ventral sucker. Ovary dextral to ventral sucker. Uterine coils mainly postcaecal with ascending, ventral, marginal loops up to level of ventral sucker. Metraterm muscular, well defined, not forming dorsal loop before reaching sinistral margin of genital atrium. Vitellarium forms two symmetrical clusters of follicles at ovariotesticular level; vitelline ducts transverse, pretesticular. Excretory vesicle V-shaped. In intestine of birds (Alciformes, Anseriformes, Charadriiformes); shores of Pacific Ocean. Type-species *P. japonicum* Yamaguti, 1939.

## 'Vitello-racemina' group

**Definition:** Artificial group of Maritrematidae (cirrus-sac present), with morphology not congruent with Maritrematini and Odhneriini.

## Key to genera

**1a. Vitellarium symmetrical, precaecal (or 'extracaecal'), composed of two bulky clusters of pre- or postcaecal follicles ..... 2.**

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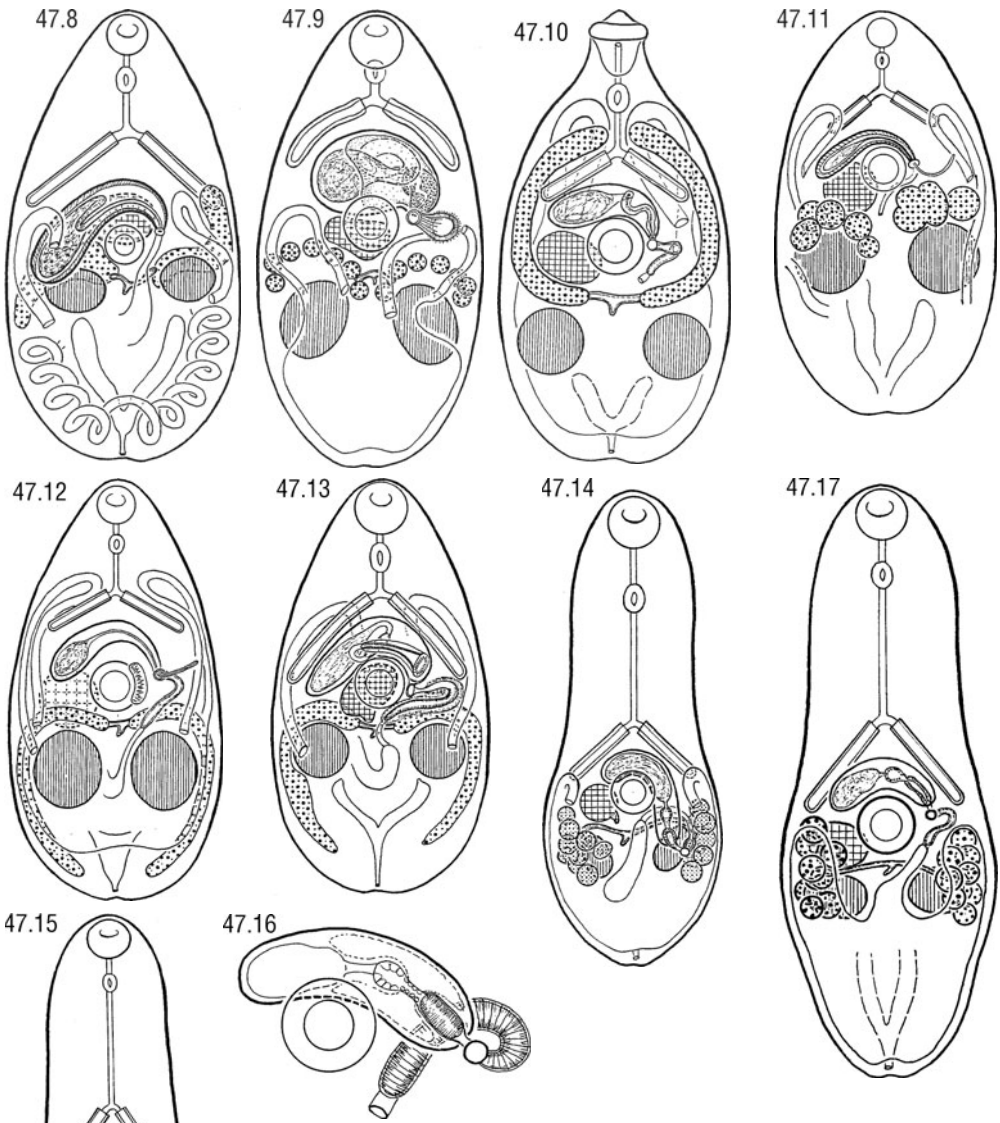



**Fig. 47.8.** *Paramaritremopsis stunkardi* Deblock & Bush, 1985. Redrawn from type.
**Fig. 47.9.** *Metamaritrema prolixum* (Caballero & Montero Gei, 1961). Redrawn from type.
**Fig. 47.10.** *Probolocoryphe asadai* (Otagaki, 1958). Redrawn.
**Fig. 47.11.** *Quasimaritremopsis medius* (Van Cleave & Mueller, 1932). Redrawn from type.
**Fig. 47.12.** *Quasimaritrema caridinae* (Yamaguti & Nishimura, 1944). Redrawn from type.
**Fig. 47.13.** *Floridatrema heardi* Kinsella & Deblock, 1994. Redrawn from type.
**Fig. 47.14.** *Testiculoporus cedarkeyensis* Kinsella & Deblock, 1997. Redrawn from type.
**Figs 47.15, 47.16**. *Odhneria odhneri* Travassos, 1921. Redrawn from type.
**Fig. 47.17.** *Pseudospelotrema japonicum* Yamaguti, 1939. Redrawn from type.

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**1b. Vitellarium symmetrical, postcaecal, composed of either bulky clusters of follicles or non-bulky files of follicles ..... 4.**

**2a. Uterine loops entirely postcaecal or in hindbody ..... 3.**
**2b. Uterus postcaecal, with two uterine loops lateral and symmetrical ascending to pharyngeal level ..... *Plenosoma* Ching, 1960. (Fig. 47.18)**
**Diagnosis**: Body small (220 μm), pyriform. Oral sucker slightly larger than ventral sucker. Digestive tract short, anterior to cirrus-sac and ventral sucker. Testes postovarian, symmetrical, marginal, partly covered by uterine coils. Cirrus-sac inverted J-shape, stout, surrounds anterior half of ventral sucker; proximal ejaculatory duct short; prostatic chamber rather voluminous; invaginated cirrus short, broad with stout spines. Genital atrium simple, reduced. Genital pore sinistral to ventral sucker. Ovary dextral to ventral sucker. Uterus in hindbody, reduced, with two lateral precaecal loops reaching pharyngeal level; voluminous enigmatic hyalin structure at site of metraterm. Vitellarium precaecal, ventral and lateral, forms clusters of small follicles; vitelline ducts long, U-shaped. Excretory vesicle short, V-shaped. In intestine of birds (Charadriiformes); Nearctic. Type-species *P. minimum* Ching, 1960.

**3a. Vitellarium marginal, relatively short, at level of ventral sucker; caeca short ..... ..... *Allomicrophalloides* Ke & Liang, 1982. (Fig. 47.19)**
**Diagnosis**: Body oval, medium-sized (560 μm). Oesophagus medium-sized. Caeca short, reach ovarian level. Testes symmetrical posterolateral, close to posterior extremity. Cirrus-sac short, inverted J-shape, surrounding anterior half of ventral sucker; prostatic chamber not known; evaginated cirrus long, cylindrical, unarmed. Genital atrium simple. Genital pore sinistral to ventral sucker. Ovary mainly in hindbody, median. Uterus confined to ovariotesticular space, without extratesticular marginal loops. Metraterm unknown. Vitellarium composed of short, marginal, symmetrical clusters, external to caeca, in mid-body, at level of cirrus-sac; vitelline ducts long, U-shaped. Excretory system unknown. In digestive tract of Charadriiformes; eastern Palaearctic. Type-species *A. opisthorchis* Ke & Liang, 1982.

**3b. Vitellarium marginal, relatively long, from level of cirrus-sac to anterior margin of testes; caeca very long ..... *Multivitellus* Ke & Liang, 1982. (Fig. 47. 20)**
**Diagnosis**: As for *Allomicrophalloides* (semicouplet 3a), except oesophagus short. Caeca very long, reach anterior margins of testes. Vitelline clusters marginal, long, between level of anterior part of cirrus-sac and anterior edge of testes; vitelline ducts transverse, medium-sized. In digestive tract of Charadriiformes; eastern Palaearctic. Type-species *M. longintestinus* Ke & Liang, 1982.

**4a. Vitellarium of bulky clusters of follicles, in mid-body or in hindbody (post-testicular) ..... 5.**
**4b. Vitellarium not bulky, but in linear files of follicles ..... 7.**

**5a. Vitellarium in mid-body, at ovariotesticular level ..... ..... *Pseudospelotrematoides* Baer, 1944. (Fig. 47.21)**
**Diagnosis**: Body fusiform, large (1 mm), plump, with characteristic appearance. Ventral sucker pre-equatorial, larger than oral sucker. Oesophagus short. Caeca short, in forebody. Testes symmetrical, marginal, with longitudinal axis, not covered by uterine coils. Cirrus-sac medium-sized, inverted J-shape, anterior to ventral sucker and intercaecal, with proximal end not reaching right margin of body; seminal vesicle retort-shaped, reflexed anterior to prostatic chamber; ejaculatory duct (?invaginated cirrus) short, narrow. Genital atrium simple, reduced, superficial. Genital pore

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anterosinistral at level of ventral sucker. Ovary dextral to ventral sucker. Uterus postcaecal, post-testicular, without extratesticular loops. Metraterm rectilinear, not distinct. Vitellarium in two dense groups of numerous small follicles, postcaecal, caps testes and partly overlaps ovary; vitelline ducts transverse, pretesticular, of medium size. Excretory vesicle and flame-cell formula unknown (?true microphallid). In intestine of Cinclidae (Passeriformes); eastern Palaearctic. Type-species *P. cincli* (Yamaguti, 1939) Baer, 1944.

**5b. Vitellarium post-testicular, on either side of excretory vesicle ..... 6.**

**6a. Uterus in hindbody; no obvious muscle fibres in forebody .....**
**..... *Vitellatus* Ke, 1979. (Fig. 47.22)**

**Diagnosis**: Body of medium size (650 µm), linguiform. No obvious muscle fibres in forebody. Oral sucker wider than ventral sucker. Oesophagus short. Caeca short, divergent, in forebody. Testes postovarian, symmetrical, marginal, partly covered with uterine coils. Cirrus-sac in forebody, inverted U-curved in long arc, with broad spermatic canal along axis; terminal of genital ducts not known. Genital atrium simple. Genital pore sinistral to ventral sucker. Ovary at level of ventral sucker, dextral. Uterus in hindbody, with two short, lateral, extratesticular postcaecal ascending loops. Metraterm unknown. Vitellarium composed of two compact masses of follicles, post-testicular in hindbody; vitelline ducts and excretory system unknown. In intestine of Charadriiformes; eastern Palaearctic. Type-species *V. compactus* Ke, 1979.

**6b. Uterus mainly in hindbody, with single loop ascending aporally and laterally, in form of transverse sling anterior or posterior to cirrus-sac; numerous longitudinal muscle fibres obvious in forebody ..... *Numeniotrema* Belopol'skaya, 1952. (Figs 47.23, 47.24)**

**Diagnosis**: Body linguiform, long or very long (resulting from frequent stretching of forebody); longitudinal muscle fibres numerous and obvious in forebody, and characteristic. Oral sucker smaller than ventral sucker. Ventral sucker postequatorial. Oesophagus often long. Caeca short, at level of ventral sucker or in forebody. Testes postovarian, symmetrical, marginal, partly covered by uterine coils. Cirrus-sac in forebody, short, arcuate, transverse; prostatic chamber unknown; short, broad, sclerotized, rigid tube replaces ejaculatory duct. Genital atrium simple, reduced, superficial. Genital pore sinistral to ventral sucker margin. Ovary dextral to ventral sucker. Uterus mainly in hindbody, with coils around testes; aporal extratesticular ascending loop passes level of ovary or cirrus-sac to form transverse sling posteriorly to caeca. Metraterm muscular, short, distinct. Vitellarium in hindbody, post-testicular; vitelline ducts medium-sized, arcuate, post-testicular. Excretory vesicle short, V-shaped, post-testicular. In intestine of Charadriiformes; cosmopolitan. Type-species *N. musculosum* Belopol'skaya, 1952.

**7a. Vitellarium composed of two marginal ribbons of few round, rather large follicles .....**
**..... *Longiductotrema* Deblock & Heard, 1969. (Fig. 47.25)**

**Diagnosis**: Body linguiform to pyriform, medium-sized (450 µm). Digestive tract in forebody. Oesophagus medium-sized. Caeca short. Testes symmetrical, posterolateral, not close to posterior extremity. Cirrus-sac in forebody, intercaecal, short, arcuate, transverse; prostatic chamber present; invaginated cirrus short, glabrous. Genital atrium simple. Genital pore sinistral to ventral sucker. Ovary dextral to ventral sucker. Uterus postcaecal; ascending extratesticular marginal loops present. Metraterm long, ensheathed by gland-cells. Vitellarium postcaecal, marginal, composed of two ribbons of about ten large round follicles, not surrounding testes; vitelline ducts very long, inserted in middle of each ribbon, looping anterior to testes. Excretory vesicle post-testicular,

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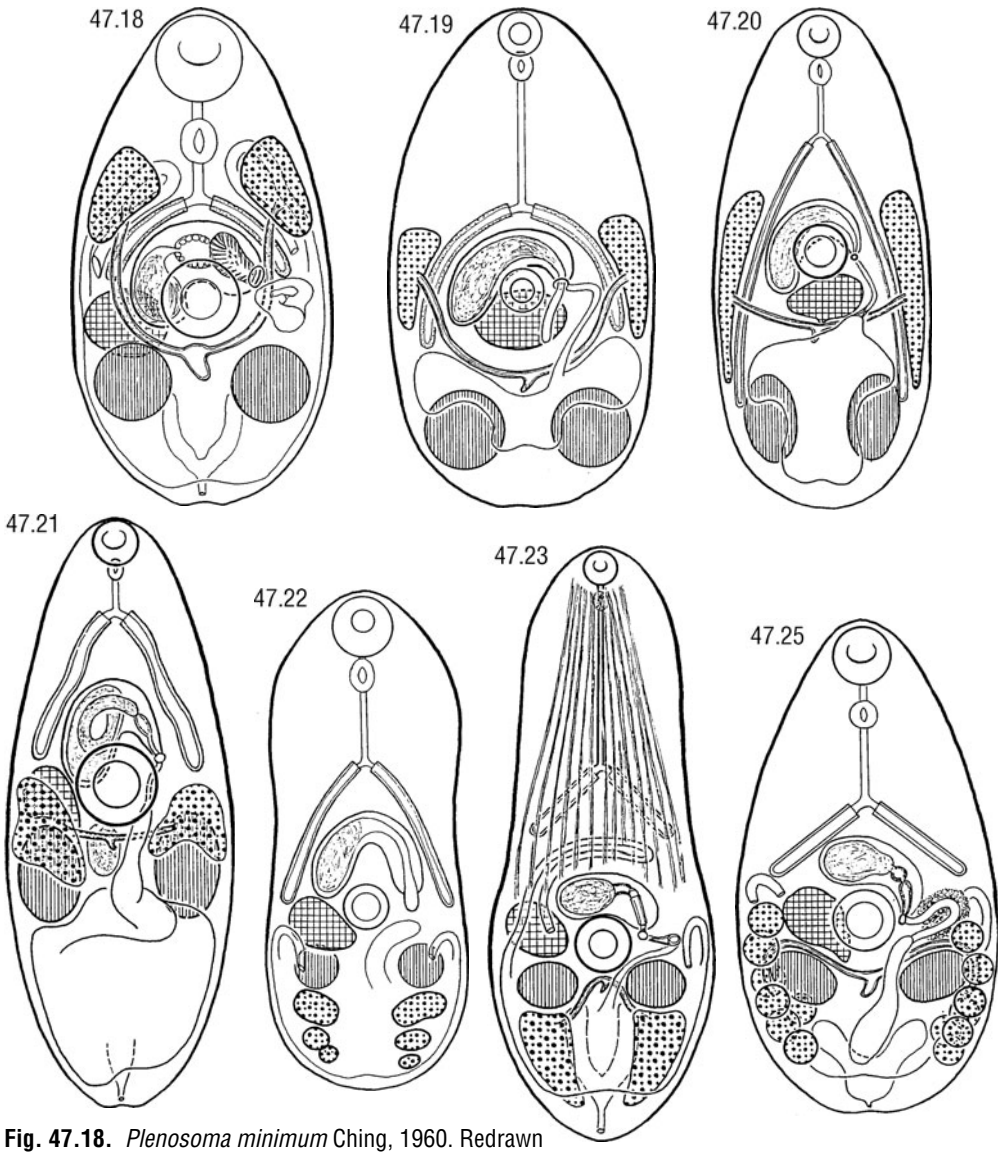
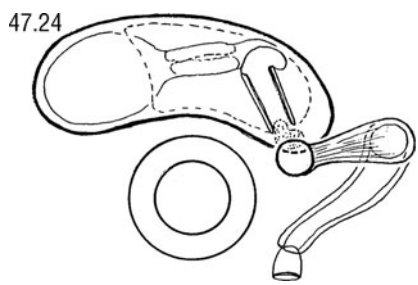



**Fig. 47.18.** *Plenosoma minimum* Ching, 1960. Redrawn from type.
**Fig. 47.19.** *Allomicrophalloides opisthorchis* Ke & Liang, 1982. After Ke & Liang (1982).
**Fig. 47.20.** *Multivitellus longintestinus* Ke & Liang, 1982. After Ke & Liang (1982).
**Fig. 47.21.** *Pseudospelotrematoides cincli* (Yamaguti, 1939). After Yamaguti (1939).
**Fig. 47.22.** *Vitellatus compactus* Ke, 1979. After Ke (1979).
**Figs 47.23, 47.24.** *Numeniotrema musculosum* Belopol'skaya, 1952. Redrawn from type.
**Fig. 47.25.** *Longiductotrema floridense* Deblock & Heard, 1969. Redrawn from type.




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V-shaped. In intestine of birds (Ralliformes, Lariformes); Nearctic and Mediterranean Palaearctic. Type-species *L. floridense* Deblock & Heard, 1969 (emend.).

**7b. Vitellarium of two submarginal, long, relatively broad, ribbons of numerous follicles of various sizes ..... *Sogandaritrema* Deblock, 1971. (Fig. 47.26)**

**Diagnosis**: Body oval, flat, large (1–1.5 mm). Ventral sucker mainly pre-equatorial. Digestive tract very short, atrophied. Pharynx lacking. Caeca short, rudimentary, terminate far from margins of body. Testes symmetrical, not marginal, just postovarian. Cirrus-sac minute, arcuate, transverse, in forebody; ejaculatory duct sigmoid; prostatic chamber absent; invaginated cirrus not distinguished from distal ejaculatory duct. Genital atrium minute, simple. Genital pore sinistral to ventral sucker. Ovary dextral, not marginal, at level of ventral sucker. Uterus ventral, with extratesticular marginal loops at level of ventral sucker; posterior coils not occupying entire hindbody. Vitellarium dorsal, submarginal, composed of two symmetrical clusters of very numerous follicles of various sizes, forming two long, relatively large ribbons, not surrounding testes or uterine coils, extending from anterior edges of testes to approximately posterior extremity; vitelline ducts long, arcuate, not pretesticular, insertion subcentral (not terminal) on ribbons. Excretory vesicle Y-shaped, mainly post-testicular. Vertebrate host unknown, may not exist (Lotz & Corkum, 1983); Nearctic. Type-species *S. progeneticum* (Sogandares-Bernal, 1962) Deblock, 1971 (emend.).

## Supersubfamily Promicrophallidi Fischthal & Kuntz, 1981 (status amend.)[3]

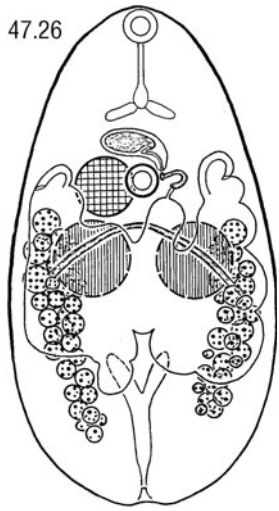
**Diagnosis:** Male genital pouch present as poorly developed 'cirrus-sac', with seminal vesicle, prostatic gland, pars prostatica, non-evaginable cirrus but protrusible fleshy phallus of *Microphallus*-type. Genital atrium present, simple. In digestive tract of vertebrates (Aves); South-east Palaearctic (Taiwan). Type-genus *Promicrophallus* Fischthal & Kuntz, 1981.

## Genus *Promicrophallus* Fischthal & Kuntz, 1981 (Fig. 47.27)

**Diagnosis**: With characters of supersubfamily. Body linguiform, flattened, small (250–300 μm). Oral sucker ventro-subterminal. Ventral sucker lacking. Pharynx present. Oesophagus medium-sized. Caeca short, divergent, at level of mid-body. Testes two, postovarian, symmetrical, lateral in hindbody. Vesiculoprostatic pouch present, thin-walled, inverted U-shaped, in intercaecal region of mid-body, with ovoid seminal vesicle enveloped by prostatic gland; prostatic chamber tubular; phallus long (25–50 μm × 20–30 μm), pyriform, fleshy, muscular, with axial ejaculatory duct. Genital atrium simple, relatively large, submedian, empty, close to anterolateral margin of left testis. Genital pore rather large, with muscular fibres radiating superficially in subtegument. Ovary dextral, immediately postcaecal, pretesticular. Uterus postcaecal in hindbody, with short lateral and pretesticular coils. Size of metraterm commensurate with large, protrusible phallus, thick-walled, muscular, opens into posterior wall of genital atrium. Vitellarium two symmetrical compact masses of follicles, post-testicular in hindbody; vitelline ducts unknown. Excretory vesicle long, Y-shaped; arms extend to cirrus-sac. In intestine of Galliformes; South-east Palaearctic (Taiwan). Type-species *P. taiwanensis* Fischthal & Kuntz, 1981.

[3] Originally designated as subfamily by Fischthal & Kuntz (1981b)

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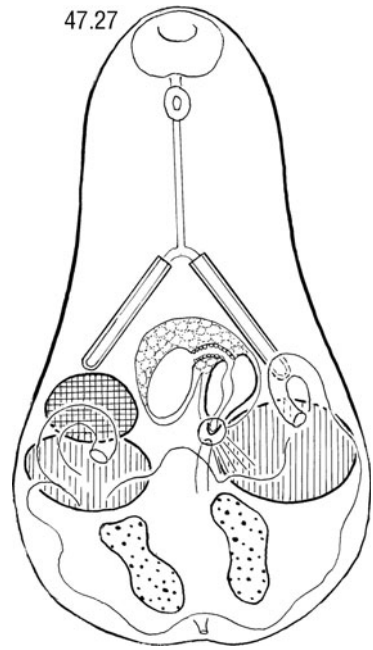




**Fig. 47.26.** *Sogandaritrema progeneticum* (Sogandares-Bernal, 1962). Redrawn from type.
**Fig. 47.27.** *Promicrophallus taiwanensis* Fischthal & Kuntz, 1981. Redrawn from authors.

## Supersubfamily Gynaecotylidi Guschanskaja, 1952 (status amend.)

**Diagnosis**: Male genital pouch without cirrus; so-called 'vesiculoprostatic pouch', morphologically similar to true cirrus-sac or not ('false cirrus-sac'). Absent cirrus is replaced by atrial organ with various morphologies characteristic of subfamilies (either fleshy and named 'cornucotyle' or sclerotized and named 'elasmocotyle', more rarely phallus of microphalloid type); all organs as voluminous as adjacent ventral sucker. Mainly in intestine of birds, also mammals; cosmopolitan. Type-genus *Gynaecotyla* Yamaguti, 1939.

## Key to subfamilies

**1a. One or two suckers; shape and position of vesiculoprostatic pouch similar to true cirrus-sac; male copulatory organ present as either atrial phallus similar to those of Microphallini, or not atrial but enclosed in cyst; metraterm present ..... 2.**

**1b. Two or three suckers; vesiculoprostatic pouch either medium-sized, thin-walled, transverse, arcuate, in forebody, or long and horseshoe-shaped anterior to ventral sucker, or more frequently around it; hermaphroditic atrial copulatory organ of several types, muscular and fleshy or not; metraterm absent ..... 3.**

**2a. Genital atrium present, simple, receiving metraterm and enclosing muscular, fleshy, non-invaginable phallus ..... Androcotylinae Deblock & Heard, 1970.**

**2b. Genital atrium not apparent, reduced to genital pore with margin receiving metraterm; phallus muscular, fleshy, enclosed in regular, rounded thick-walled cyst (or 'phallosphere') ..... Sphairiotrematinae Deblock & Ky, 1966.**

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**3a. Two symmetrical ventral suckers; vesiculoprostatic pouch transverse; copulatory organ fleshy ..... Gynaecotylinae Guschanskaja, 1952.**

**3b. One ventral sucker; vesiculoprostatic pouch horseshoe-shaped; copulatory organ usually not fleshy (one exception), with separate sclerotized pieces ..... ..... Basantisiinae Yamaguti, 1958.**

## Subfamily Androcotylinae Deblock & Heard, 1970

**Diagnosis**: Body medium-sized (300–500 μm). Resembles *Microphallus*. Suckers two, subequal. Oesophagus medium length. Caeca short, divergent, ends at level of ventral sucker. Testes postovarian, symmetrical, lateral. Vesiculoprostatic pouch fusiform, muscular, thick-walled, transverse, slightly curved, in intercaecal space anterior to ventral sucker; seminal vesicle fusiform; prostatic gland surrounds distal ejaculatory duct, long, rectilinear; prostatic chamber outside vesiculoprostatic pouch, inserted distally in long ejaculatory duct of phallus. Phallus complex, voluminous, muscular, fleshy, at distal extremity of genital pouch, circular, with large ventral dome covering two conical accessory lobes; aperture of ejaculatory duct deeply situated, laterodorsally. Extrinsic genital musculature of phallus complex, with numerous powerful muscular bundles inserted dorsally. Genital atrium large. Genital pore sinistral to ventral sucker. Ovary dextral to ventral sucker. Uterus postcaecal, surrounding testes. Metraterm distinct, with widened aperture, joins sinistral wall of genital atrium. Vitellarium as in *Microphallus*; two symmetrical clusters of few follicles in testicular region, not exclusively marginal; vitelline ducts long, arcuate. Excretory vesicle short, post-testicular, V-shaped. In intestine of Charadriiformes; Nearctic. Type-genus *Androcotyle* Deblock & Heard, 1970.

### Genus *Androcotyla* Deblock & Heard, 1970 (Figs 47.28, 47.29)

**Diagnosis**: With characters of subfamily. Type-species *A. arenariae* Deblock & Heard, 1970.

## Subfamily Sphairiotrematinae Deblock & Ky, 1966

**Diagnosis:** Body medium-sized (360 μm). Suckers two, subequal. Oesophagus of medium length. Caeca short, divergent, at level of ventral sucker. Testes symmetrical, postovarian, lateral. Vesiculoprostatic pouch thick-walled, muscular, fusiform, longer than adjacent caecum, terminates near margin, resembles true cirrus-sac in *Maritrema*. Seminal vesicle long, fusiform. Prostatic gland reduced. Ejaculatory duct rectilinear without distinct prostatic chamber. Special phallus pouch or phallosphere, cyst-like, rounded, thick-walled, sclerotized, with diameter larger than ventral sucker, dorsal to genital pore, at distal extremity of vesiculoprostatic pouch. Phallus long, tubular, coiled in phallosphere; muscularity or fleshiness incompletely known; evaginated aspect unknown. Genital musculature absent. Genital atrium not apparent, reduced to genital pore, sinistral to ventral sucker. Ovary submedian, dextral, at level of ventral sucker. Uterus postcaecal, in hindbody and surrounding testes. Metraterm simple, thin-walled, looping around phallosphere to ventrosinistral margin of genital pore. Vitellarium as in *Microphallus*, with two symmetrical clusters of few follicles in ovariotesticular region. Vitelline ducts undescribed. Excretory vesicle short, post-testicular, V-shaped. In intestine of Charadriiformes; western Europe. Type-genus *Sphairiotrema* Deblock & Ky, 1966.

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## Genus *Sphairiotrema* Deblock & Ky, 1966 (Figs 47.30, 47.31)

**Diagnosis:** With characters of subfamily. Type-species *S. prudhoei* Deblock & Ky, 1966.

## Subfamily Gynaecotylinae Guschanskaya, 1952

**Diagnosis**: Body medium to large (400 to > 1000 μm), linguiform, with three suckers (one oral and two symmetrical ventral suckers of equal size or almost so). Genital pore dextral or sinistral, near lateral margin of furthest sucker from ovary. Vesiculoprostatic pouch in intercaecal region, thin-walled and not muscular, medium-sized, arcuate, transverse, anterior to two ventral suckers, contains seminal vesicle, prostatic gland and pars prostatica. Atrial copulatory organ rounded (or 'cornucotyle'), rather voluminous, with diameter subequal to ventral suckers, at distal extremity of genital pouch, composed of one or two crescent-shaped pieces, fleshy, muscular (as in phallus of *Microphallus*). Genital musculature present but not greatly developed. Sclerotized single plate joined to ventral face of seminal vesicle absent (see Basantisiini). Male ejaculatory duct and uteroterm (terminal part of distal uterus lacks copulatory function) may converge on cornucotyle. Ovary at ventral sucker level. Uterine coils numerous, surrounding testes or not. Vitellarium symmetrical, in various positions in hindbody. Excretory vesicle short, I- or V-shaped. In intestine of Charadriiformes; cosmopolitan. Type-genus *Gynaecotyla* Yamaguti, 1939.

## Key to genera

**1a. Genital pore dextral to ventral sucker furthest from ovary; ovary sinistral, at level of ventral suckers; caeca of medium length, end at ventral sucker level, marginal and not curved anteriorly to testes; vitellarium two symmetrical clusters of follicles posterior to testes; atrial cornucotyle voluminous, composed of two unequal fleshy crescents, with concavity of greater and more external crescent enveloping half smaller and more dorsal ..... ..... *Gynaecotyla* Yamaguti, 1939. (Figs 47.32, 47.33)**

(Syns *Cornucopula* Rankin, 1939; ? *Paraspelotrema* Wang, 1982)

**Diagnosis**: Body linguiform, medium-sized to large (600 ± 300 μm). Suckers three (oral and two ventral). Ventral suckers subequal or not. Oesophagus short to medium-sized. Caeca not curved, terminating marginally at ovariotesticular level. Testes surrounded by uterine coils or not. Vesiculoprostatic pouch in intercaecal region, thin-walled and not muscular, short, arcuate, transverse, anterior to two ventral suckers. Atrial cornucotyle voluminous, composed of two unequal fleshy crescents, with concavity of greater and more external crescent enveloping half smaller and more dorsal. Sclerotized apparatus may be present, moved by several specialized genital muscles inserted on vesiculoprostatic pouch and between the two crescents of cornucotyle. Genital atrium present, simple. Genital pore dextral near ventral sucker furthest from ovary. Ovary sinistral, at level of ventral suckers. Uterus postcaecal; uteroterm inserted dorsally to genital atrium in cornucotyle. Vitellarium two symmetrical clusters of follicles posterior to testes; vitelline ducts long, arcuate. Excretory vesicle short, I-shaped, post-testicular. In intestine of Charadriiformes; cosmopolitan. Type-species *G. squatarolae* (Yamaguti, 1934) Yamaguti, 1939.

**1b. Genital pore sinistral to ventral sucker furthest from ovary; ovary dextral, at level of ventral suckers; caeca long, curved towards each other anteriorly to testes; vitellarium two**

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**symmetrical clusters of follicles, marginal, extracaecal, extending along sides of body at ovariotesticular level; atrial cornucotyle composed of single fleshy crescent ..... ..... *Diacetabulum* Belopol'skaya, 1952. (Figs 47.34, 47.35)**
(Syn. *Derytrema* Rebecq, 1962)

**Diagnosis**: Body linguiform, medium-sized to large (500–1500 μm). Suckers three (oral and two ventral). Ventral suckers subequal or not. Oesophagus short or medium-sized. Caeca long, curved towards each other anteriorly to testes. Testes symmetrical, postcaecal, submarginal. Vesiculoprostatic pouch in intercaecal region, thin-walled and not muscular, arcuate, transverse, anterior to two ventral suckers. Atrial cornucotyle sinistral, of similar diameter to ventral sucker, composed of one curved piece, with concavity opposite to adjacent sucker; surfaces partly ornamented with numerous short, irregularly distributed conical tubercles. Several sclerotized, complex, small pieces at level of concavity, articulated and moved by specialized, narrow genital muscles inserted on vesiculoprostatic pouch. Genital atrium simple. Genital pore sinistral, close to ventral sucker furthest from ovary. Ovary dextral, in curve of caecum. Uterus postcaecal, without uterine loops lateral to testes. Metraterm absent; uteroterm opens dorsally under cornucotyle. Vitellarium two symmetrical clusters of follicles, either massed together immediately anterolateral to testes, or extended along margin at ovariotesticular level. Vitelline ducts long, transverse, pretesticular. Excretory vesicle short, Y-shaped, post-testicular. In intestine of Charadriiformes; cosmopolitan. Type-species *D. curvicolon* Belopol'skaya, 1952.

## Subfamily Basantisiinae Yamaguti, 1958

**Diagnosis**: Single ventral sucker, superficial or eventually embedded in parenchyma. Vesiculoprostatic pouch present, long, horseshoe-shaped, aperture directed posteriorly, thin-walled and not muscular, surrounding ventral sucker or sometimes anterior to it. Atrial copulatory organ rather voluminous at poral extremity of vesiculoprostatic pouch, generally with three separate sclerotized pieces (so-called 'elasmocotyle'; except in *Plenosominoides* with two fleshy pieces) projected into genital atrium; elasmocotyle contains single short genital hermaphroditic duct. Genital musculature powerful, with several specialized muscle bundles attached to either vesiculoprostatic pouch or to one or other piece of atrial apparatus. Single sclerotized piece plate (Pl 2) attached to ventral face of genital pouch, at level of seminal vesicle facing atrial apparatus (generally characteristic of subfamily, but absent in Labidotrematini). Genital pore dextral or sinistral to ventral sucker. Various positions of testes, ovary, vitellarium and uterine coils. Uteroterm present. In intestine of birds, rodents or not known; south-eastern Asia, Australia. Type-genus *Basantisia* Pande, 1938.

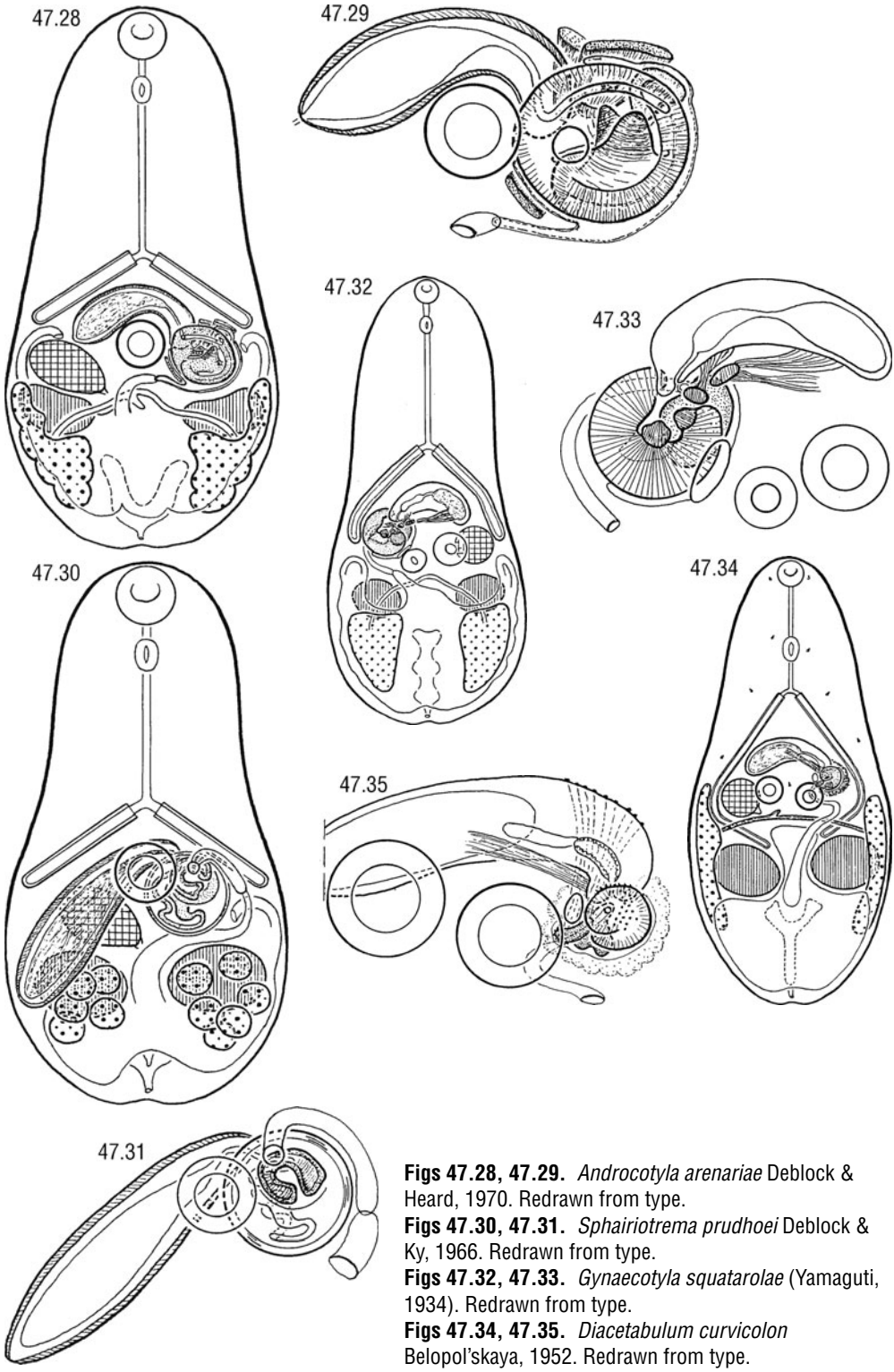
## Key to tribes

**1a. Seminal plate Pl 2 present; elasmocotyle present or not (in this case replaced by fleshy organ); branches of horseshoe-shaped pouch of equal lengths ..... 2.**

**1b. Seminal plate Pl 2 absent; elasmocotyle present; branches of horseshoe-shaped pouch of unequal lengths ..... Labidotrematini n. tribe.**

**2a. Elasmocotyle present; vitellarium pre- or postcaecal ..... ..... Basantisiini Yamaguti, 1958 (status amend.)**

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**Figs 47.28, 47.29.** *Androcotyla arenariae* Deblock & Heard, 1970. Redrawn from type.
**Figs 47.30, 47.31.** *Sphairiotrema prudhoei* Deblock & Ky, 1966. Redrawn from type.
**Figs 47.32, 47.33.** *Gynaecotyla squatarolae* (Yamaguti, 1934). Redrawn from type.
**Figs 47.34, 47.35.** *Diacetabulum curvicolon* Belopol'skaya, 1952. Redrawn from type.

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**2b. Elasmocotyle absent, replaced by two parallel, rectilinear fleshy pieces, evoking unrolled cornucotyle of Gynaecotylinae (not crescent-shaped); vitellarium precaecal ..... ..... Plenosominoidini n. tribe.**

## Tribe Basantisiini Yamaguti, 1958 (status amend.)

**Diagnosis:** Body medium-sized to large (400–900 μm), often fusiform but pyriform or dumpy when contracted. Oral and ventral suckers present. Ventral sucker more or less embedded in parenchyma. Digestive tract short, in forebody. Testes postovarian, symmetrical or subsymmetrical. Vesiculoprostatic pouch thin-walled, horseshoe-shaped, generally encircling ventral sucker, more rarely anterior, with two branches of equal lengths, generally devoid of diverticula. Atrial elasmocotyle generally composed of three well-separated sclerotized parts: two pieces ventral, superficial, tandem, more or less prominent on either side of hermaphroditic duct, and third piece dorsal, flattened or not, short or long. Seminal plate Pl 2 opposite hermaphroditic aperture. Genital musculature specialized, more or less powerful. Genital atrium present, simple. Genital pore dextral, near margin of ventral sucker. Ovary sinistral at level of ventral sucker, near vesiculoprostatic pouch. Uterus postcaecal, surrounds testes. Uteroterm joins male ejaculatory duct to form hermaphroditic canal inside distal part of vesiculoprostatic pouch between three pieces of elasmocotyle. Vitellarium symmetrical, pre- or postcaecal, generally comprised of ten rounded follicles. Excretory vesicle short, V- or I-shaped, post- or intertesticular. In intestine of birds and rodents; Asia, Australia. Type-genus *Basantisia* Pande, 1938.

## Key to genera

**1a. Vesiculoprostatic pouch partly encircles ventral sucker ..... 2.**
**1b. Vesiculoprostatic pouch more anterior in forebody, not encircling ventral sucker ..... 3.**

**2a. Vitellarium pretesticular in hindbody ..... *Basantisia* Pande, 1938. (Figs 47.36, 47.37)**
(Syns *Macrostomtrema* Chiu, 1961; *Belopolskiella* Oshmarin, 1963)

**Diagnosis**: Body fusiform, linguiform or pyriform if contracted; medium-sized to large (300–1000 μm). Oral sucker generally larger than ventral. Ventral sucker embedded in parenchyma or not. Oesophagus short or medium-sized. Caeca short and in forebody, or medium and at level of ventral sucker, more or less divergent, partly marginal or not; deep prominent gastrodermis may occur. Testes in mid-hindbody, slightly asymmetrical. Vesiculoprostatic pouch horseshoe-shaped, encircling ventral sucker or not; seminal Pl 2 plate present. Elasmocotyle with three rather voluminous pieces, more or less sclerotized; dorsal piece short. Genital musculature more or less developed. Genital atrium dextral, simple, present. Genital pore dextrally posterolateral to ventral sucker. Ovary sinistral to ventral sucker, slightly posterior to vesiculoprostatic pouch. Uterine coils postcaecal with extratesticular loops or not. Uteroterm present. Vitellarium composed of two clusters of about ten rounded follicles, postcaecal, anterior to testes, not marginal; vitelline ducts pretesticular, transverse, medium-sized. Excretory vesicle short, intertesticular, I-shaped. In intestine of birds (mainly Coraciiformes); Indian area, eastern Asia, Australia. Type-species *B. ramai* Pande, 1938.

**2b. Vitellarium in forebody, precaecal, marginal ..... ..... *Queenslandisia* Pearson & Deblock, 1987. (Figs 47.38, 47.39)**

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**Diagnosis**: Body small or medium-sized (250–450 μm), fusiform, or linguiform when contracted. Suckers subequal, medium-sized. Ventral sucker embedded in parenchyma. Oesophagus medium-sized. Caeca in forebody, short, divergent. Testes postovarian, symmetrical, marginal in hindbody. Vesiculoprostatic pouch median, horseshoe-shaped, encircles ventral sucker; seminal plate Pl 2 present. Elasmocotyle with two moderately developed, pedunculate, dorsal sclerotized pieces; no dorsal lever. Genital musculature present. Genital atrium present, simple. Genital pore at level of ventral sucker, dextral. Ovary sinistral in anterior hindbody. Uterus in hindbody, looped around testes. Uteroterm present. Vitellarium symmetrical, from body margin to anterior edge of caeca, composed of two clusters of about ten rounded follicles; vitelline ducts long, U-shaped. Excretory vesicle short, post-testicular, Y-shaped. In intestine of rodents and probably also of birds; Australia. Type-species *Q. australiensis* (Deblock & Pearson, 1968) Pearson & Deblock, 1987.

**3a. Vitellarium pretesticular, in hindbody ..... ..... *Mochliscotrema* Deblock & Pearson, 1986. (Figs 47.40, 47.41)**

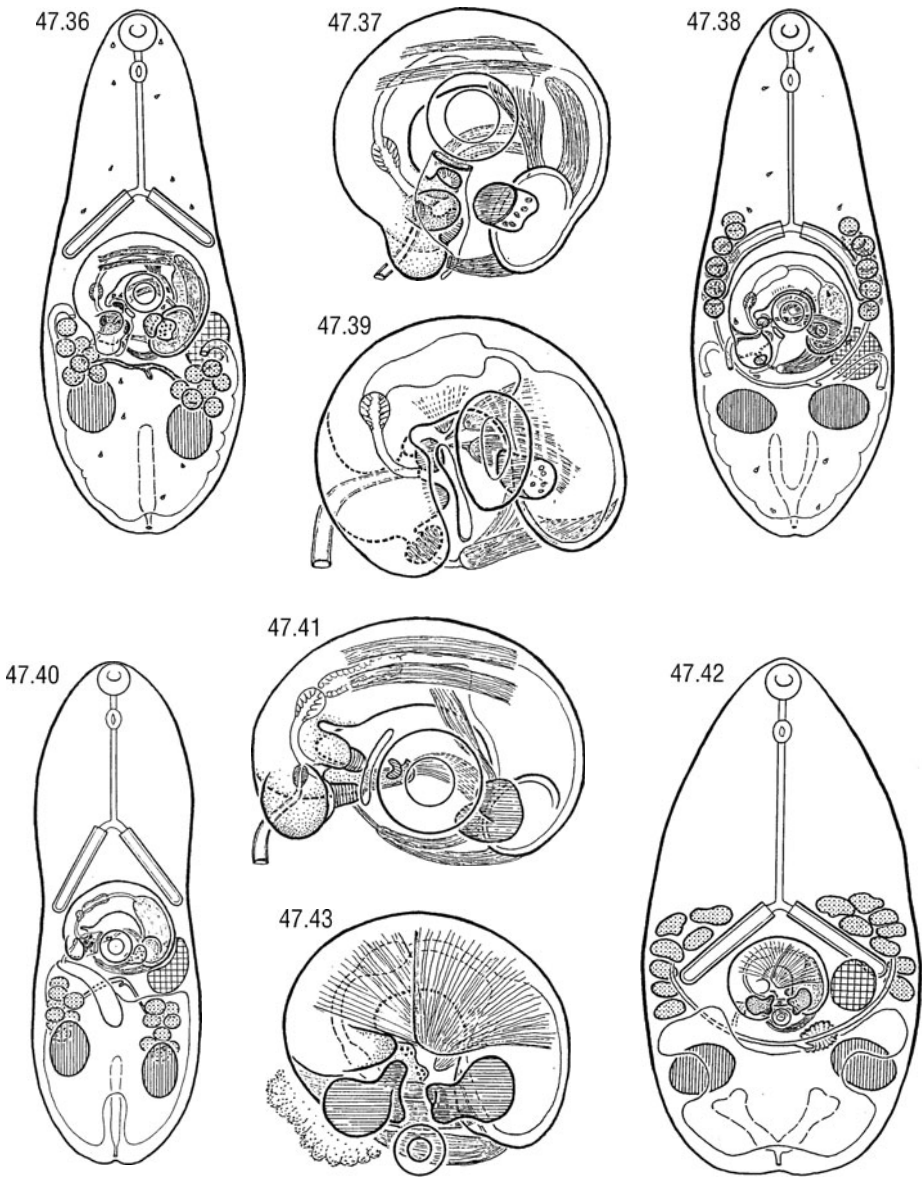
**Diagnosis**: Body generally long (600–700 μm), slender, shorter and pyriform when contracted. Ventral sucker superficial or embedded in parenchyma. Oesophagus medium-sized. Caeca rather short, more or less divergent; deep prominent gastrodermis may occur. Testes postovarian in mid-hindbody, slightly asymmetrical. Vesiculoprostatic pouch horseshoe-shaped, partly encircling ventral sucker; poral branch of vesiculoprostatic pouch may have diverticulum; seminal vesicle, prostatic gland and pars prostatica present; seminal plate Pl 2 present. Elasmocotyle with two ventral sclerotized pieces, somewhat elongate, side by side, resembling beak; dorsal piece elongate, forming transverse lever. Genital musculature present; one bundle acts as dorsal transverse lever. Genital pore anterolateral, dextral to ventral sucker. Ovary sinistral to ventral sucker, slightly posterolateral to vesiculoprostatic pouch. Uterus postcaecal in hindbody, with extratesticular loops, or not. Uteroterm present. Vitellarium composed of two clusters of about ten rounded follicles, postcaecal, anterior to testes. Vitelline ducts medium-sized, arched, pretesticular. Excretory vesicle intertesticular, I-shaped, short or long. In intestine of birds (Alcedinidae, Laridae, Accipitridae); southern Asia, Australia. Type-species *M. queenslandense* (Deblock & Pearson, 1968) Deblock & Pearson, 1986 (emend.).

**3b. Vitellarium in forebody, precaecal, lateral ..... 4.**

**4a. Vitellarium with two symmetrical clusters of about 12 separate and irregular follicles; body linguiform ..... *Microphalloides* Yoshida, 1938. (Figs 47.42, 47.43)**

**Diagnosis**: Body linguiform, elliptical when contracted, medium-sized or large (600–900 μm). Two suckers; ventral smaller than oral. Ventral sucker embedded in parenchyma and posterior to vesiculoprostatic pouch. Oesophagus medium-sized. Caeca in forebody, short, divergent. Testes postovarian, symmetrical, marginal, in hindbody. Vesiculoprostatic pouch median, in forebody, horseshoe-shaped; seminal vesicle, prostatic gland and pars prostatica present; seminal plate Pl 2 sclerotized, powerful. Elasmocotyle with powerful sclerotized ventral piece. Genital musculature powerful, diversified, with strong fan-shaped bundles at centre of horseshoe. Genital atrium simple, anterodextral to ventral sucker. Genital pore not observed. Ovary sinistral to ventral sucker at level of vesiculoprostatic pouch. Uterine coils in hindbody, not looped around testes. Uteroterm present. Vitellarium in forebody, symmetrical, from body margin to anterior margins of caeca, comprised of about 12 contiguous and irregular follicles; vitelline ducts long, U-shaped. Excretory vesicle short, post-testicular, V-shaped. In intestine of birds; Japan, southern China. Type-species *M. japonicus* (Osborn, 1919) Yoshida, 1938.

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**Figs 47.36, 47.37.** *Basantisia* Pande, 1938. From a theoretical reconstitution of the genus according to Deblock & Pearson (1986). (Note: The illustration of *B. ramai* Pande, 1938 is not typical of the complexity of the genital ducts of the genus; also, it is uncertain that *B. ramai sensu* Oshmarin *et al.*, 1969 is identical with *B. ramai* Pande, 1938.)
**Figs 47.38, 47.39.** *Queenslandisia australiensis* (Deblock & Pearson, 1968). Redrawn from type.
**Figs 47.40, 47.41.** *Mochliscotrema queenslandense* (Deblock & Pearson, 1968). Redrawn from type.
**Figs 47.42, 47.43.** *Microphalloides japonicus* (Osborn, 1919). Redrawn after author's and Bridgman *et al.*'s (1972) Japanese specimens.

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**4b. Vitellarium bulky and comprised of two symmetrical circular clumps of numerous small follicles; body tranversely oval ..... ..... *Transversohelmins* Fischthal & Kuntz, 1973. (Figs 47.44, 47.45)**

**Diagnosis**: Body medium-sized (350–400 μm) transversely oval. Oral sucker smaller than ventral. Oesophagus medium-sized. Caeca in forebody, short, divergent. Testes symmetrical, marginal, slightly postovarian. Vesiculoprostatic pouch horseshoe-shaped, slightly dextral, partly anterior to ventral sucker; seminal vesicle, prostatic gland and pars prostatica present; seminal plate Pl 2 present. Elasmocotyle lightly sclerotized with large, ovoid, verrucous anterodorsal piece; posterior and ventral pieces absent. Powerful genital musculature present, with two antagonistic bundles moving seminal plate Pl 2. Genital atrium present, simple. Genital pore not observed. Ovary sinistral at level of vesiculoprostatic pouch, immediately posterior to left caecum. Uterine coils postcaecal, encircle testes except laterally. Uteroterm present. Vitellarium marginal, precaecal, composed of two symmetrical circular clumps of numerous small follicles; vitelline ducts long, V-shaped. Excretory vesicle not observed. In intestine of Charadriiformes; South-east Asia. Type-species *T. borneoensis* Fischthal & Kuntz, 1973.

## Tribe Plenosominoidini n. tribe

**Diagnosis**: Body medium-sized to large (500–1000 μm), more or less pyriform or linguiform. Suckers subequal. Ventral sucker equatorial, superficial, with contour altered by encroachment of sinistral genital pore. Oesophagus short. Caeca long, pretesticular, ends submarginal at ovariotesticular level. Testes in mid-hindbody, symmetrical. Vesiculoprostatic pouch horseshoe-shaped, intercaecal, in forebody; seminal vesicle, prostatic gland and pars prostatica present; seminal plate Pl 2 present. Atrial copulatory organ pedunculate, dextral to vesiculoprostatic pouch, composed of two parallel fleshy, muscular pieces, not crescent-shaped, not sclerotized, resembling cornucotyle of Gynaecotylinae. Genital musculature powerful, well diversified, with strong ventral fan-shaped mass of bundles at centre of horseshoe, also some transverse bundles. Genital atrium simple, anterosinistral to ventral sucker. Ovary dextral, at level of ventral sucker. Uterine coils numerous, but absent posterior to testes and in extratesticular space, with two ascending extracaecal loops reaching pharyngeal level. Uteroterm opens dorsally between two pieces of atrial organ. Vitellarium symmetrical, extracaecal and marginal in forebody, from pharyngeal level to level of ventral sucker; follicles numerous, small; vitelline ducts long, U-shaped. Excretory vesicle short, post-testicular, V-shaped, diverticulate. In intestine of dog (exp.); natural vertebrate host not known; South-east Asia. Type-genus *Plenosominoides* Ke & Liang, 1984.

## Genus *Plenosominoides* Ke & Liang, 1984 (Figs 47.46, 47.47)

**Diagnosis:** With characters of tribe. Type-species *P. yangshanensis* Ke & Liang, 1984.

## Tribe Labidotrematini n. tribe

**Diagnosis**: Body fusiform, long (750 ±100 μm). Ventral sucker superficial or embedded in parenchyma. Oesophagus medium-sized. Caeca in forebody, short, more or less divergent. Testes postovarian, in mid-hindbody, symmetrical. Vesiculoprostatic pouch arched asymmetri-

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cally, with several digitiform or ampullar diverticula and appendices from proximal and distal branches; proximal branch shorter sinistrally, prolonged posteriorly as voluminous ovoid muscular mass, inserted in peculiar atrium; vesiculoprostatic pouch and muscular mass encircle ventral sucker; seminal plate Pl 2 lacking. Distal branch with elasmocotyle large, composed of three parts, partly sclerotized, with anatomically simple or complex pieces. Genital musculature powerful with several specialized muscular bundles. Genital atrium simple dextral; genital pore dextrally posterolateral to ventral sucker. Ovary sinistral to ventral sucker. Uterus in hindbody, looped around testes. Uteroterm present. Vitellarium in forebody, composed of two extracaecal clusters of about ten rounded follicles; vitelline ducts long, U-shaped. Excretory vesicle V-shaped post-testicular. In intestine of Coraciiformes; South-east Asia. Type-genus *Labidotrema* Pearson & Deblock, 1986.

## Genus *Labidotrema* Pearson & Deblock, 1986 (Figs 47.48, 47.49)

**Diagnosis:** With characters of tribe. Type-species *L. dittolepum* Pearson & Deblock, 1986.

## Supersubfamily Microphallidi Ward, 1901 (status amend.)

**Diagnosis:** Male genital pouch absent; seminal vesicle and prostatic gland embedded in parenchyma. Male copulatory organ muscular, with fleshy phallus in simple or complex genital atrium, rarely protruding through genital pore. Mainly in intestine of birds, also in other vertebrate groups; cosmopolitan. Type-genus *Microphallus* Ward, 1901.

## Key to subfamilies

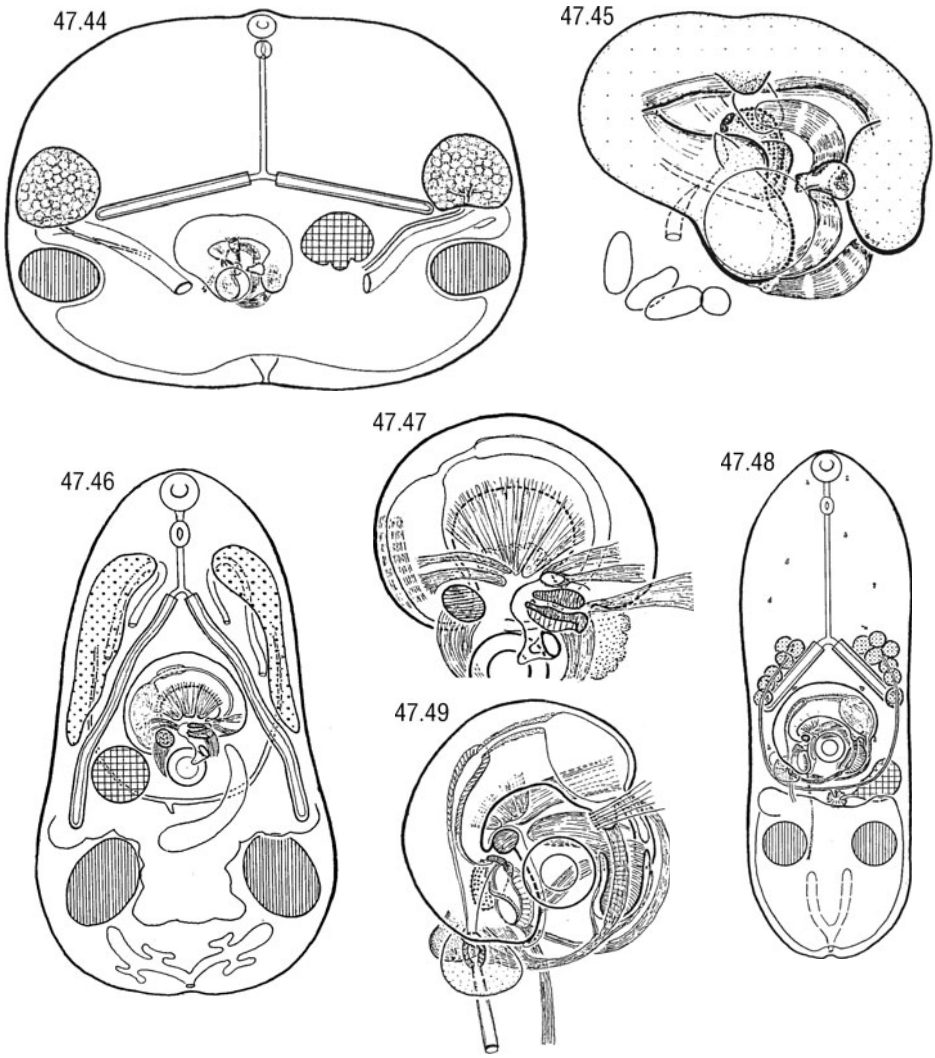
**1a. Genital atrium simple (without accessory sac) ..... 2.**
**1b. Genital atrium complex, with one or several accessory sacs, which are anatomically similar or different (so-called male and female pockets) ..... ..... Levinseniellinae Stiles & Hassall, 1901.**

**2a. Genital atrium closely enveloping phallus and not affecting shape of ventral sucker ..... ..... Microphallinae Ward, 1901.**
**2b. Genital atrium very small (smaller than diameter of pharynx), close to ventral sucker; shape of ventral sucker margin altered, such that cavity of sucker is connected with genital pore by narrow passage ..... Endocotylinae Belopol'skaya, 1952.**

## Subfamily Microphallinae Ward, 1901

**Diagnosis:** Male genital pouch absent. Phallus fleshy, muscular, not club-shaped, of 'microphalloid'-type (referred to as 'male papilla' in literature), more or less voluminous, morphologically simple or complex. Genital atrium not affecting shape of ventral sucker, closely enveloping phallus. Mainly in intestine of birds, also other vertebrate groups; cosmopolitan. Type-genus *Microphallus* Ward, 1901.

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**Figs 47.44, 47.45.** *Transversohelmins borneoensis* Fischthal & Kuntz, 1973. Redrawn from type.
**Figs 47.46, 47.47.** *Plenosominoides vajrasthirae* (Waikagul, 1983). Redrawn from types.
**Figs 47.48, 47.49.** *Labidotrema dittolepum* Pearson & Deblock, 1986. Redrawn from type.

## Key to tribes

**1a. Phallus fleshy and muscular, of so-called 'microphalloid'-type, of various sizes, in form of massive organ, sometimes lobed, filling genital atrium; metraterm aperture usually broad, widens towards sinistral wall of genital atrium ..... Microphallini Ward, 1901 (status amend.)**

**1b. Phallus fleshy and muscular, long and cylindrical, coiled in proper phallus pouch; metraterm aperture narrow, superficially joining ventrosinistral margin of genital pore ..... Atriotrematini n. tribe.**

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## Tribe Microphallini Ward, 1901 (status amend.)

**Diagnosis:** Phallus fleshy, muscular, of so-called 'microphalloid'-type, of various sizes, in form of massive organ, sometimes lobed, filling genital atrium. Metraterm aperture usually broad, widening towards sinistral wall of genital atrium. Mainly in intestine of birds, also other vertebrate groups; cosmopolitan. Type-genus *Microphallus* Ward, 1901.

## Key to genera

**1a. Oral sucker typical, ventrally subterminal, muscular, cup-shaped ..... 2.**
**1b. Oral sucker replaced by terminal 'rhynchostome', not muscular or cup-shaped, composed of peri-oral ring prolonged anteriorly by small cylindrical, conical tongue ..... ..... *Rhyncostophallus* Deblock & Canaris, 1997. (Fig. 47.50)**

**Diagnosis:** Body linguiform, medium-sized (360 µm), flattened. Resembles *Microphallus*. Oral sucker replaced by terminal 'rhynchostome', not muscular or cup-shaped, composed of peri-oral ring prolonged anteriorly by small cylindrical, conical tongue. Ventral sucker postequatorial, may be closed by superficial veil. Oesophagus medium-sized. Caeca short, divergent, in forebody. Testes postovarian, symmetrical, posterolateral, in hindbody. Male genital pouch absent. Seminal vesicle and ejaculatory duct as in *Microphallus*. Phallus of 'microphalloid'-type, fleshy, muscular, massive, spherical. Genital atrium simple, enveloping phallus. Genital pore sinistral to ventral sucker. Ovary dextral to ventral sucker. Uterus postcaecal, coiled around testes. Metraterm indistinct with enlarged opening, joins sinistral wall of genital atrium. Vitellarium symmetrical in hindbody, composed of two paratesticular and post-testicular clusters of few follicles; vitelline ducts transverse, medium, arcuate, post-testicular. Excretory vesicle unknown. In intestine of Charadriiformes; Australia. Type-species *R. insularegii* Deblock & Canaris, 1997.

**2a. Male genital duct tubular, simple, straight beyond seminal vesicle, with prostatic chamber situated along duct or at distal extremity ..... 3.**
**2b. Male genital duct complicated, with voluminous formation acting as prostatic chamber, situated along proximal ejaculatory duct or at its distal extremity ..... 6.**

**3a. Prostatic chamber extended along middle of ejaculatory duct; prostatic gland well apart from distal seminal vesicle and ejaculatory duct, or surrounds them ..... 4.**
**3b. Prostatic chamber at distal extremity of ejaculatory duct, inside small dome sunk into base of phallus; prostatic gland around distal seminal vesicle and proximal ejaculatory duct ..... 5.**

**4a. Prostatic gland reduced, well apart from seminal vesicle, surrounds ejaculatory duct; metraterm distinct, opens into base of genital atrium dorsally, near base of phallus ..... ..... *Megalophalloides* Ching & Ibañez, 1976. (Figs 47.51, 47.52)**

**Diagnosis:** Body medium-sized (450 µm), flattened. Resembles *Microphallus*. Oral sucker slightly large than ventral sucker. Ventral sucker postequatorial. Oesophagus medium-sized. Caeca short, divergent, at level of ventral sucker. Testes symmetrical, lateral, in hindbody. Male genital pouch absent. Seminal vesicle in forebody in intercaecal space; prostatic gland reduced, well apart from seminal vesicle; prostatic chamber not apparent. Phallus large, flattened, with double line of stout

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basal spines laterally on each side, at level of short ejaculatory duct, which passes through thickness of proximal phallus. Genital atrium simple, envelops phallus. Genital pore sinistral to ventral sucker. Ovary dextral to ventral sucker. Uterus postcaecal in hindbody, coiled around testes. Metraterm dorsal with narrow opening deep in genital atrium, near ejaculatory duct. Vitellarium post-testicular, composed of two lateral clusters of about ten follicles; vitelline ducts medium-sized, arched. Excretory vesicle post-testicular, V-shaped. In intestine of crab-eating vertebrates; Neotropical. Type-species *M. apanhorayi* Ching & Ibañez, 1976 (syn. of *M. garciai* (Ibañez, 1973) n. comb.).

**4b. Prostatic gland well apart from seminal vesicle and proximal ejaculatory duct, and more or less extended (may overlap caeca anteriorly); metraterm with villous lining, well developed, opens on sinistral margin of genital pore ventrally; phallus voluminous, ornamented with various structures (buttons, nipples, ribbons, etc.) ..... ..... *Megalophallus* Cable, Connor & Balling, 1960. (Fig. 47.53)**
(Syn. *Pseudomegalophallus* Yamaguti, 1971)

**Diagnosis:** Body medium to large (400–1000 μm). Resembles *Microphallus*, except for position of prostatic gland well apart from seminal vesicle and ejaculatory duct. Oral sucker smaller than ventral sucker. Caeca short, divergent, anterior to ventral sucker, or atrophied (oesophagus ends as small pouch, more or less bifid). Testes postovarian, symmetrical, lateral in mid-hindbody. Male genital pouch absent. Prostatic gland well apart from seminal vesicle and proximal ejaculatory duct, and more or less extended (may overlap caeca anteriorly); proximal ejaculatory duct forms loop anterior to tubular prostatic chamber. Phallus smaller than or equal in diameter to ventral sucker; shape simple or not (digitate); surface ornamented with various prominent structures. Genital atrium simple, envelops phallus, resembles phallus pouch. Genital pore sinistral to ventral sucker. Ovary dextral to ventral sucker. Uterus postcaecal in hindbody, coiled around testes. Metraterm with villous lining, well developed, opens ventrally to sinistral margin of genital pore. Vitellarium symmetrical, at testicular and post-testicular level in hindbody, formed of two clusters of about ten follicles; vitelline ducts long, arcuate. Excretory vesicle V-shaped, short, post-testicular. In intestine of marine fishes or birds (Charadriiformes, Lariformes); North America, western Europe. Type-species *M. pentadactylus* Cable, Connor & Balling, 1960.

**5a. Metraterm of similar size to phallus, with widened opening into sinistral wall of genital atrium ..... *Microphallus* (*Microphallus*) Ward, 1901. (Figs 47.54, 47.55)**
(Syns *Spelotrema* Jägerskiöld, 1901; *Monocaecum* Stafford, 1903; *Paraheterophyes* Afanassief, 1941; *Carneophallus* Cable & Kuns, 1951; *Pseudocarneophallus* Yamaguti, 1971; *Bulbovitellus* Yamaguti, 1971; *Feminacopula* Ke, Liang & Yu, 1987)

**Diagnosis:** Body linguiform, flattened, small to large (400 ± 300 μm). Ventral sucker postequatorial, without superficial veil. Oesophagus short or medium-sized. Caeca short, divergent, at level of ventral sucker or just anterior; digestive tract occasionally atrophied. Testes postovarian, symmetrical, lateral. Male genital pouch absent. Seminal vesicle ovoid, in intercaecal space anterior to ventral sucker; prostatic gland envelops distal part of seminal vesicle and surrounds short ejaculatory duct; prostatic chamber small, usually in base of cupola-like phallus. Phallus atrial, muscular, fleshy; size varies from same size as pharynx to that of ventral sucker, or much larger; may be turgid or not, spherical, tubular, cup-shaped, etc., or provided with accessory basal lobe (conical, or more complex, eventually spoon-like), single or not, or with distal lobe generally reduced; superficial ornamentation rare. Genital atrium simple, enveloping phallus closely. Genital pore sinistral to ventral sucker. Ovary dextral to ventral sucker. Uterus postcaecal, coiled around testes. Metraterm of similar size to phallus, with widened pore opening into sinistral wall of genital

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atrium. Vitellarium formed of two clusters of about ten follicles, paratesticular and post-testicular in hindbody; vitelline ducts medium-sized, arched. Excretory vesicle short, post-testicular, V-shaped. In intestine of warm-blooded vertebrates (mainly birds, also mammals) and rarely fishes; cosmopolitan. Type-species *M. opacus* (Ward, 1894) Ward, 1901.

**5b. Metraterm aperture narrow, joins ventrosinistral margin of genital pore; phallus pouch present; vesiculoprostatic pouch vestigial (very thin) ..... ..... *Microphallus* (*Spelophallus*) Jägerskiöld, 1908. (Fig. 47.56)**
(Syn. *Spelophallus* Jägerskiöld, 1908)

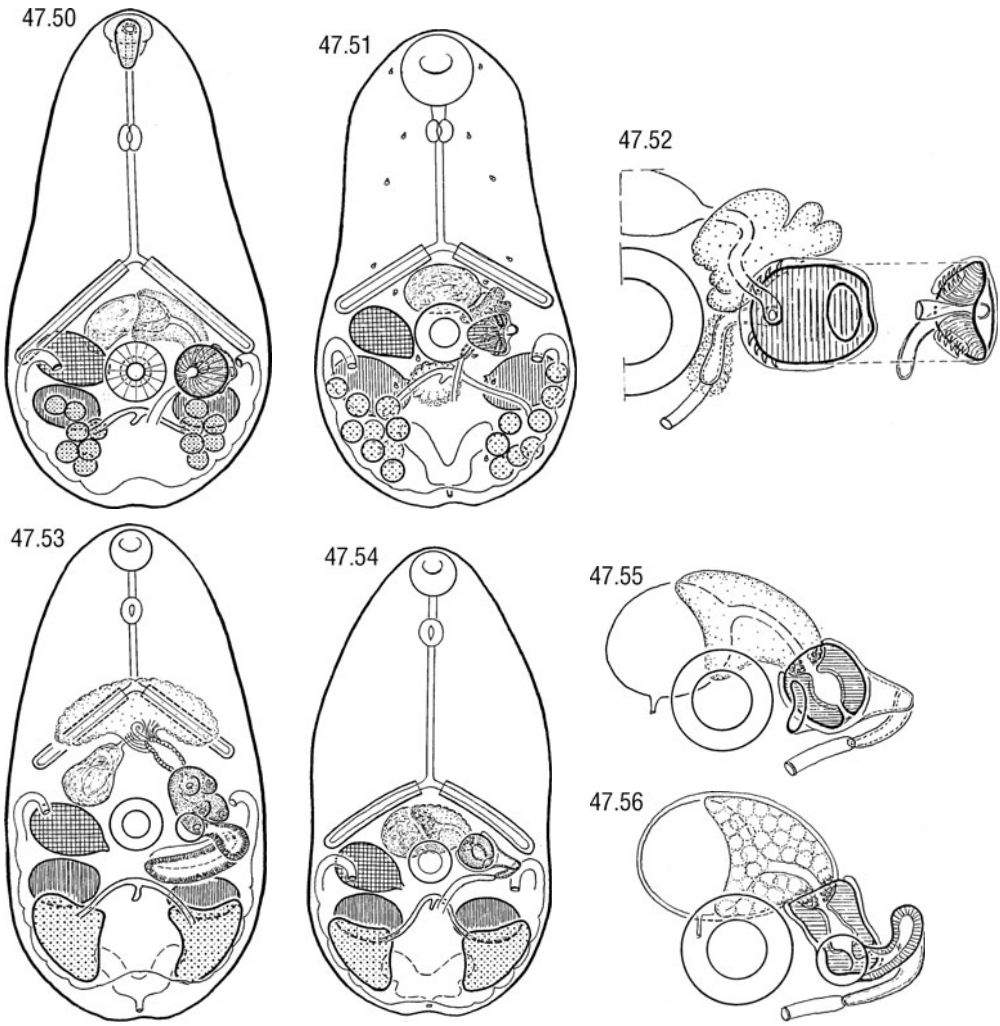



**Fig. 47.50.** *Rhyncostophallus insularegii* Deblock & Canaris, 1997. Redrawn from type.
**Figs 47.51, 47.52.** *Megalophalloides garciai* (Ibañez, 1973) n. comb. Redrawn from type and paratypes; syn. *M. apanhorayi* Ching & Ibañez, 1976.
**Fig. 47.53.** *Megalophallus pentadactylus* Cable, Connor & Balling, 1960. Redrawn from type.
**Figs 47.54, 47.55.** *Microphallus (Microphallus)* Ward, 1901. Redrawn from standardized pattern.
**Fig. 47.56.** *Microphallus (Spelophallus) primas* (Jägerskiöld, 1908). Redrawn after Biguet *et al.* (1958). (Note: *M. canchei* is syn. of *M. (S.) primas.*)

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**Diagnosis:** Body linguiform, flattened, large (800 ± 200 μm). Ventral sucker postequatorial without superficial veil. Oesophagus medium-sized. Caeca short, divergent, at level of ventral sucker. Testes postovarian, symmetrical, lateral. Vesiculoprostatic pouch vestigial (very thin); seminal vesicle ovoid, intercaecal, anterior to ventral sucker; prostatic gland envelops distal part of seminal vesicle and surrounds short ejaculatory duct; prostatic chamber small, in base of cupola-like phallus. Phallus fleshy, muscular, provided with reduced accessory distal lobe. Phallus pouch present, envelops phallus closely. Genital pore sinistral to ventral sucker. Ovary dextral to ventral sucker. Uterus postcaecal, coiled around testes. Metraterm obvious, heterogeneous, villous proximally, muscular distally, with aperture joining ventrosinistral margin of genital pore. Vitellarium formed of two clusters of about ten follicles, paratesticular and post-testicular in hindbody. Vitelline ducts medium-sized, arched, post-testicular. Excretory vesicle short, post-testicular, V-shaped. In intestine of crab-eating marine birds (Lariformes, Anseriformes); northern and western Europe. Type-species *M.* (*Spelophallus*) *primas* (Jägerskiöld, 1908) Stunkard, 1951.

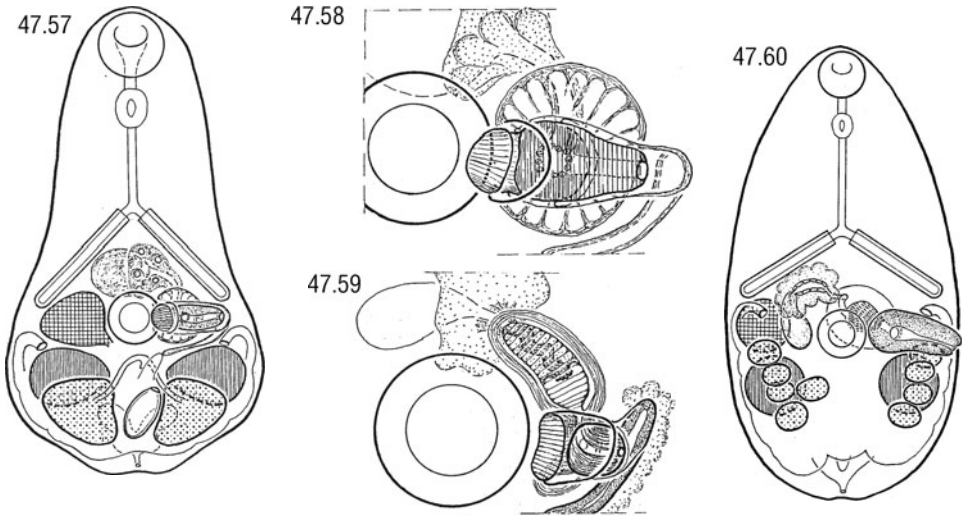
**6a. Proximal ejaculatory duct very long, supported by envelope acting as large prostatic chamber, either: (i) subcircular with diameter of ventral sucker, dorsal to genital atrium (formation described as 'phallophorus' (apparently 'bearing phallus')) and with long prostatic ducts opening on periphery of male duct inside phallus; or (ii) cylindrical, muscular, fibrous, elongate, between seminal vesicle and genital atrium, adjacent to margin of ventral sucker; with bundle of long prostatic ducts entering mid-part of cylindrical prostatic chamber (and not inside phallus) ..... *Atriophallophorus* Deblock & Rosé, 1964. (Figs 47.57–47.59)**

**Diagnosis:** Body linguiform or triangular, small (150–200 μm). Resembles *Microphallus*. Ventral sucker postequatorial. Oesophagus medium or short. Caeca short, divergent, in mid-body. Testes symmetrical in hindbody. Male genital pouch absent. Seminal vesicle intercaecal in mid-body, ovoid; prostatic gland caps distal part of seminal vesicle; proximal ejaculatory ducts very long, supported by envelope acting as large prostatic chamber, either: (i) subcircular with diameter of ventral sucker, dorsal to genital atrium (formation described as 'phallophorus' (apparently bearing phallus)) and with long prostatic ducts running through to periphery of male duct inside phallus; or (ii) cylindrical, fibrous, elongate between seminal vesicle and genital atrium, adjacent to margin of ventral sucker; bundle of long prostatic ducts enter as far as mid-part of cylindrical prostatic chamber (not inside phallus). Phallus of 'microphalloid'-type, more or less turgid, with ejaculatory duct in axis. Genital atrium present, envelops phallus with enormous dextral parietal atrial scale; genital pore sinistral to ventral sucker. Ovary dextral to ventral sucker. Uterus postcaecal, with few coils around testes. Metraterm long, with widened opening into sinistral wall of genital atrium. Eggs not numerous, relatively large. Vitellarium formed of two clusters of follicles, paratesticular and post-testicular in hindbody; vitelline ducts short, arched, post-testicular. Excretory vesicle short, V-shaped, post-testicular. In intestine of birds (Anseriformes, Charadriiformes); cosmopolitan. Type-species *A. minutus* (Price, 1934) Deblock & Rosé, 1964.

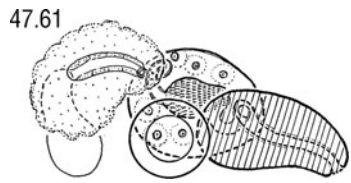
**6b. Proximal ejaculatory duct straight, short; large dilatation of distal, long, spinous ejaculatory duct present in voluminous ovoid chamber ..... ..... *Megistospermaticus* Deblock & Canaris, 1992. (Figs 47.60, 47.61)**

**Diagnosis:** Body linguiform, medium-sized (430 μm). Resembles *Microphallus*. Ventral sucker postequatorial. Oesophagus medium. Caeca short, divergent, in forebody. Testes symmetrical, posterolateral in hindbody. Male genital pouch absent. Seminal vesicle pyriform or ovoid, between ovary and ventral sucker; prostatic gland caps distal part of seminal vesicle and surrounds proximal

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**Figs 47.57, 47.58.** *Atriophallophorus minutus* (Price, 1934). Redrawn from original specimens and new French specimens from Deblock & Rosé (1964).
**Fig. 47.59.** *Atriophallophorus coxiellae* Smith, 1974. Redrawn from type and paratypes from various hosts from Tasmania (adults from anseriform and charadriiform birds and metacercariae from the mollusc *Coxiella badgerensis*).
**Figs 47.60, 47.61.** *Megistospermaticus kasmatospinosus* Deblock & Canaris, 1992. Redrawn from type.




long and cylindrical prostatic chamber; additional large ovoid chamber, delimited by thin, sclerotized membrane, around long distal region of ejaculatory duct, filled with large, round, clear cells; ejaculatory duct with dilate, spinous duct related to large phallus of 'microphalloid'-type, ovoid or not. Genital atrium reduced, simple; no dextral parietal atrial scale. Genital pore sinistral to ventral sucker. Ovary dextral to ventral sucker. Uterus postcaecal with coils around testes. Metraterm loops around ejaculatory duct chamber on left, and joins sinistral margin of genital atrium. Vitellarium composed of two symmetrical clusters of few large follicles, lateral at ovariotesticular level; vitelline ducts medium-sized, transverse. Excretory vesicle short, V-shaped, post-testicular. In intestine of Charadriiformes; Africa. Type-species *M. kasmatospinosus* Deblock & Canaris, 1992.

## Tribe Atriotrematini n. tribe

**Diagnosis:** Body medium-sized (350–400 μm), ovoid, flattened. Oral sucker larger than ventral sucker. Ventral sucker equatorial or slightly postequatorial. Oesophagus short. Caeca short, divergent, in forebody. Testes symmetrical, lateral, in mid-hindbody. Male genital pouch absent. Seminal vesicle ovoid or pyriform, partly dorsal to ventral sucker; prostatic gland well apart from seminal vesicle, encircles well-developed, long, cylindrical prostatic chamber. Phallus elongate, cylindrical, fleshy, wall entirely covered with numerous, thin tubercles, coiled in phallus pouch. Phallus pouch larger than ventral sucker, envelops phallus closely. Genital pore ventral, opening sinistrally to ventral sucker. Ovary dextral to ventral sucker. Uterus postcaecal, post-testicular,

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coiled around testes. Metraterm long, distinct, loops around phallus pouch, with narrow opening at ventrosinistral margin of genital pore. Vitellarium formed of few large follicles in two submarginal clusters at ovariotesticular level; vitelline ducts medium, transverse, pretesticular. Excretory vesicle unknown. In intestine of Charadriiformes; eastern Europe. Type-genus *Atriotrema* Belopol'skaya, 1958.

### Genus *Atriotrema* Belopol'skaya, 1958 (Figs 47.62, 47.63)

**Diagnosis:** With characters of tribe. Type-species *A. lecitholaterale* Belopol'skaya, 1958.

## Subfamily Endocotylinae Deblock, 1971

**Diagnosis:** Body small to medium-sized (400 ± 200 μm), linguiform, flattened. Two suckers; ventral sucker postequatorial, with crescent-shaped margin and aperture pointing sinistrally; shape of margin altered, such that cavity of sucker is connected with genital pore by narrow passage. Oesophagus short to medium in length. Caeca short, at level of ventral sucker, divergent. Testes symmetrical, lateral and posterior to ends of caeca, well separated by uterine coils and posterior extensions of vitelline fields. Male genital pouch absent. Seminal vesicle and prostatic gland free in parenchyma, in intercaecal space anterior to ventral sucker; long ejaculatory duct sinuous, intraprostatic, with small, terminal prostatic chamber; no cirrus or phallus; ejaculatory duct forms small boss in genital atrium. Genital atrium simple, very small. Genital pore apparently within sinistral equatorial margin of sucker, at level of small, spinous atrio-acetabular plate. Ovary submedian, dextral, just pretesticular. Uterus mainly postcaecal; posterior uterine coils sometimes in radiating, regular loops; extratesticular coils absent or not; two lateral and pretesticular loops extend dorsally toward caeca, or between caeca and male complex. Metraterm indistinct, with narrow opening at base of genital atrium. Eggs numerous. Vitellarium composed of numerous, small follicles forming two sinuous ribbons, initially precaecal and marginal in forebody, then intertesticular as in *Pseudospelotrema* (vitellarium a 'ring clasp'); vitelline ducts, short, T-shaped, in hindbody, with subterminal insertions at ribbons. Excretory vesicle V-shaped, with long marginal, lateral, well-separated, post-testicular arms. In intestine of Charadriiformes; cosmopolitan. Type-genus *Endocotyle* Belopol'skaya, 1952.

### Genus *Endocotyle* Belopol'skaya, 1952 (Figs 47.64, 47.65)

**Diagnosis:** With characters of subfamily. Type-species *E. incana* Belopol'skaya, 1952.

## Subfamily Levinseniellinae Stiles & Hassall, 1901

**Diagnosis:** Genital atrium complex, diverticulate, with one or several anatomically identical or different accessory sacs.[4] Atrial phallus present, unarmed, fleshy but not muscular, club-shaped

[4] The four types of 'atrial accessory sacs' are defined in the Glossary, p. 455.

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(and so-called 'phallus of levinsenielloid type'); occasionally, phallus fleshy and muscular of 'microphalloid-type'. Mainly in intestine of birds, also amphibians and reptiles, or not known; cosmopolitan. Type-genus *Levinseniella* Stiles & Hassall, 1901.

## Key to tribes

**1a. Genital atrium with accessory sacs of Type I, with or without accessory sac of Type II ... ..... Levinseniellini Stiles & Hassall,1901 (status amend.).**
**1b. Genital atrium with accessory sac of Type III ..... Thulakiotrematini n. tribe.**
**1c. Genital atrium with accessory sacs of Type IV, accompanied or not by accessory sac of Type II ..... Ascorhytini Deblock, 1971.**

## Tribe Levinseniellini Stiles & Hassall, 1901 (status amend.)

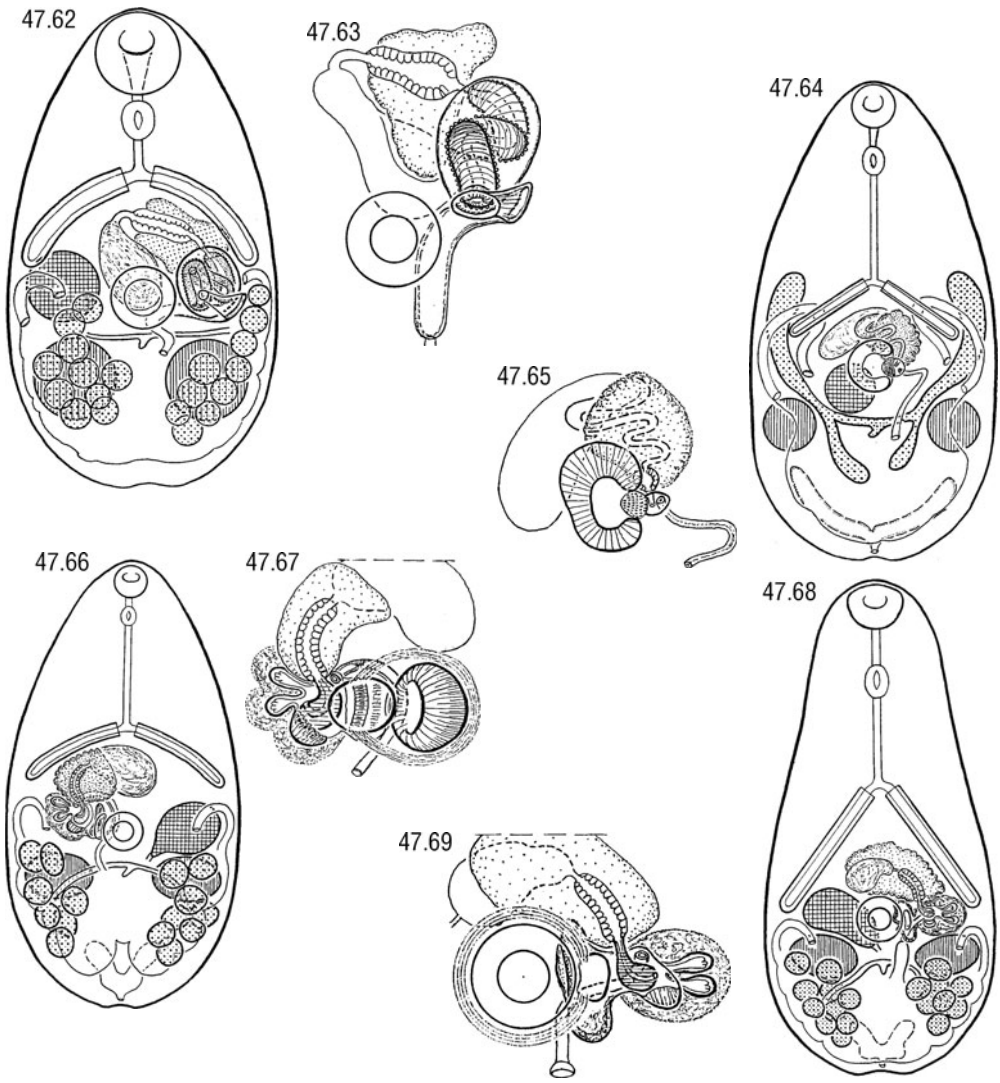
**Diagnosis:** Atrial accessory sac Type I: like fingers of glove, armed or unarmed, with one to 12 or more sacs and disposed in one or two superimposed semicircles; and possibly Type II: large, single, purse-like diverticulum, partly dorsal to ventral sucker. Type-genus *Levinseniella* Stiles & Hassall, 1901.

## Key to genera

**1a. Genital pore sinistral ..... 2.**
**1b. Genital pore dextral ..... *Megalatriotrema* Rao, 1969. (Figs 47.66, 47.67)**
(Syns *Bengaliniella* Deblock, Mukherjee & Ghosh, 1970; *Allomicrophallus* Yamaguti, 1971)
**Diagnosis:** Body linguiform, flattened, large (1200 µm). Suckers subequal. Ventral sucker slightly postequatorial. Oesophagus medium-sized. Caeca divergent, short, at level of ventral sucker. Testes postovarian, symmetrical, lateral in hindbody. Seminal vesicle pyriform in forebody, intercaecal. Male genital pouch absent. Prostatic gland envelops distal part of seminal vesicle, then surrounds rather long cylindrical prostatic chamber (as in *Levinseniella*). Phallus of 'Levinseniella type' (not muscular but fleshy, club-shaped). Genital atrium dextral, polysaccular as in *Levinseniella* (2 + 1 Type I accessory sacs, dextral), associated with longitudinal undulation of atrial sinistral bottom. Genital pore dextral to ventral sucker. Ovary sinistral to ventral sucker. Uterus postcaecal, with coils around testes. Metraterm differentiated, passes dorsally over genital atrium, with narrow pore sinistrodorsal to base of phallus. Vitellarium formed of two symmetrical clusters of about ten follicles at testicular and post-testicular level; vitelline ducts long, arched, at testicular level. Excretory vesicle short, V-shaped, post-testicular. In intestine of amphibians and reptiles; southern Asia. Type-species *M. hispidum* Rao, 1969.

**2a. Presence of one or several accessory atrial sacs of Type I associated with one sac of Type II ..... *Levinseniella* (*Levinseniella*) Stiles & Hassall, 1901. (Figs 47.68, 47.69)**
(Syn. *Levinsenia* Stossich, 1899)
**Diagnosis:** Body medium to large (500–1200 µm), flattened, linguiform, rather elongate. Oral sucker slightly more robust than ventral sucker, sometimes with pair of symmetrical, small, lateral auricles. Ventral sucker distinctly postequatorial, surrounded with annular, subtegumentary and fine muscle fibres, more or less obvious according to species. Oesophagus rather long. Caeca

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**Figs 47.62, 47.63.** *Atriotrema lecitholaterale* Belopol'skaya, 1958. Redrawn from type.
**Figs 47.64, 47.65.** *Endocotyle incana* Belopol'skaya, 1952. Redrawn after Belopol'skaya (1952) and personal specimens.
**Figs 47.66, 47.67.** *Megalatriotrema hispidum* Rao, 1969. Redrawn from type.
**Figs 47.68, 47.69.** *Levinseniella (Levinseniella) brachysomum* (Creplin, 1837). Redrawn after Deblock *et al.* (1958) (*L. tridigitata* (Creplin, 1837), syn. of *L. brachysomum*).

slightly divergent, medium-sized, at level of ventral sucker. Testes postovarian, symmetrical, lateral in hindbody. Male genital pouch absent. Seminal vesicle pyriform, intercaecal in forebody; prostatic gland envelops distal part of seminal vesicle, then surrounds rather long cylindrical prostatic chamber, obvious and characteristic of tribe. Phallus typical, club-shaped (bent, fleshy and not muscular). Genital atrium sinistral, polysaccular (two to 12 or more sinistral accessory sacs of

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Type I, associated with one dextral sac of Type II). Genital pore sinistral to ventral sucker. Ovary dextral to ventral sucker. Uterus postcaecal, in hindbody, coiled around testes. Metraterm slightly differentiated, passes dorsally to base of genital atrium; narrow pore opens on sinistrodorsal side of phallus base (between phallus and first accessory sac of Type I). Vitellarium in hindbody, formed of two symmetrical clusters of about ten large follicles at testicular and post-testicular level; vitelline ducts long, arched, post-testicular. Excretory vesicle, short, post-testicular, V-shaped. In intestine of birds (Charadriiformes, Anseriformes, Lariformes); cosmopolitan. Type-species *L. brachysomum* (Creplin, 1837) Stiles & Hassall, 1901.

**2b. Atrial accessory sacs of Type I present only ..... ..... *Levinseniella* (*Monarrhenos*) Deblock & Pearson, 1970. (Fig. 47.70)**
(Syns *Austromicrophallus* Szidat, 1964; *Heardlevinseniella* Yamaguti, 1971; *Oschmarinotrema* Yamaguti, 1971; *Apharyngolevinseniella* Yamaguti, 1975)

**Diagnosis:** Atrial accessory sacs of Type I only present. Otherwise as for *Levinseniella* (*Levinseniella*). In intestine of birds (Charadriiformes, Anseriformes, Lariformes); cosmopolitan. Type-species *L. (M.) monodactyla* Deblock & Pearson, 1970.

## Tribe Thulakiotrematini n. tribe.

**Diagnosis:** Body large (1300 μm), rather elongate. Resembles *Levinseniella*. Suckers subequal. Ventral sucker distinctly postequatorial. Oesophagus medium in length. Caeca elongate, slightly divergent, at level of ventral sucker. Testes postovarian, symmetrical, lateral in hindbody. Male genital pouch absent. Seminal vesicle pyriform, in mid-body, intercaecal; prostatic gland double with first group of cells enveloping distal part of seminal vesicle around proximal ejaculatory duct, and second group of more anterior cells more extensive, mainly in intercaecal area; long, cylindrical and obvious prostatic chamber. Phallus subspherical, fleshy and muscular, of *Microphallus*-type. Genital atrium complex, mono-diverticulate with only one accessory sac of Type III, as large as phallus. Genital pore sinistral to ventral sucker. Ovary dextral to ventral sucker. Uterus postcaecal, coiled around testes. Metraterm differentiated, passes dorsally to genital atrium, with widened aperture, opens through sinistral wall of genital atrium. Vitellarium and vitelline ducts as in *Levinseniella*. Excretory vesicle short, post-testicular, V-shaped. Metacercaria in marine crustaceans; vertebrate host unknown; Australia. Type-genus *Thulakiotrema* Deblock, Williams & Evans, 1990.

## Genus *Thulakiotrema* Deblock, Williams & Evans, 1990 (Figs 47.71, 47.72)

**Diagnosis:** With characters of tribe. Type-species *T. genitale* Deblock, Williams & Evans, 1990.

## Tribe Ascorhytini Deblock, 1971

**Diagnosis:** Atrial accessory sac of Type IV: single, large, enclosing either thin sclerotized plate, or ovoid and voluminous muscular mass; and possible accessory sac of Type II. In intestine of birds; Holarctic. Type-genus *Ascorhytis* Ching, 1965.

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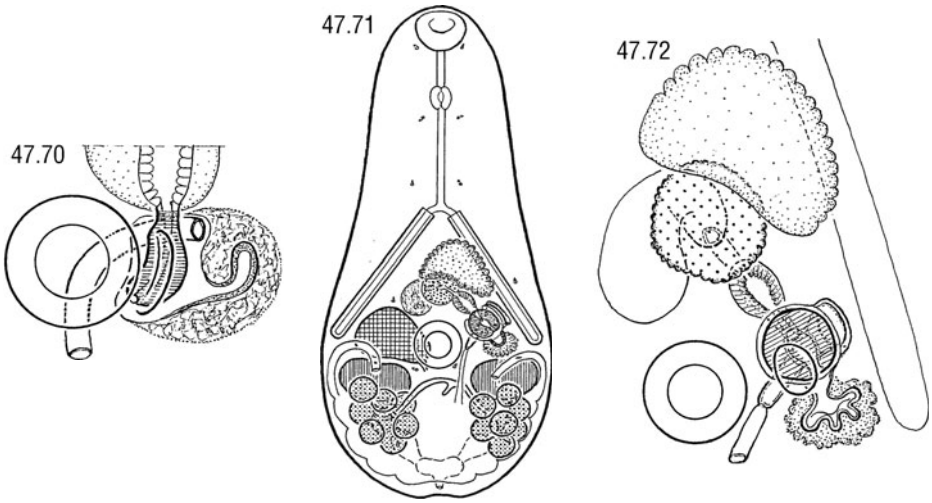



**Fig. 47.70.** *Levinseniella (Monarrhenos) monodactyla* Deblock & Pearson, 1970. Redrawn from type.
**Figs 47.71, 47.72.** *Thulakiotrema genitale* Deblock, Williams & Evans, 1990. Redrawn from type.

## Key to genera

**1a. Atrial accessory sac only of Type IV, with large sclerotized plate, pyriform in dorsoventral view, and long spicule-like in profile, movable with specialized genital muscles ..... ..... *Spiculotrema* Belopol'skaya, 1949. (Figs 47.73, 47.74)**

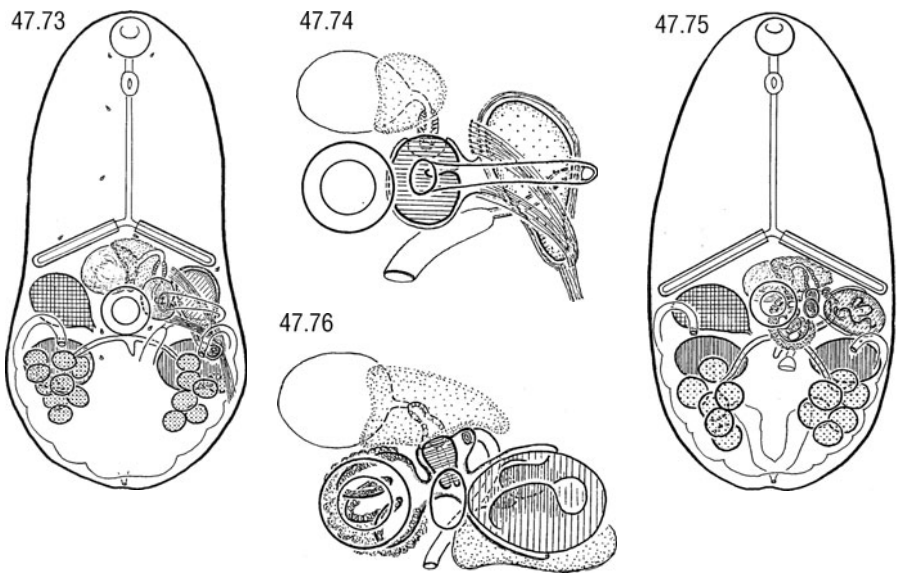
**Diagnosis:** Body rather large (700–800 μm), linguiform, flattened. Resembles *Microphallus*. Suckers subequal; ventral sucker postequatorial. Caeca short, divergent in mid-body. Testes postovarian, symmetrical, lateral. Male genital pouch absent. Seminal vesicle intercaecal, partly dorsal to ventral sucker; prostatic gland enveloping distal part of seminal vesicle; ejaculatory duct short; prostatic chamber distinct, elongate, contiguous with phallus. Phallus spheroidal of microphalloid-type, as large as ventral sucker, in membranous phallus pouch. Atrial accessory sac only of Type IV, linked to phallus pouch, and containing large sclerotized plate, pyriform in dorsoventral view, long and spicule-like in profile, movable with specialized genital muscles. Genital pore sinistral to ventral sucker linked to phallus pouch. Ovary dextral to ventral sucker. Vitellarium formed of two clusters of few large follicles, at ovariotesticular level; vitelline ducts long, arched, at testicular level. Uterus postcaecal, coiled around testes. Metraterm not well differentiated, passes dorsally, then around accessory sac to open at sinistral margin of genital pore. Excretory vesicle not known. In digestive tract of birds (Charadriiformes); eastern Siberia. Type-species *S. littorale* Belopol'skaya, 1949 (emend.).

**1b. Genital atrium with two accessory sacs: one of Type II and one of Type IV enclosing ovoid, muscular mass ..... *Ascorhytis* Ching, 1965. (Figs 47.75, 47.76)**

**Diagnosis:** Body of medium size (450–600 μm), linguiform, flattened. Resembles *Microphallus*. Suckers subequal; ventral sucker postequatorial. Caeca short, divergent, at level of ventral sucker. Testes postovarian, symmetrical, lateral. Male genital pouch absent. Seminal vesicle intercaecal partly dorsal to ventral sucker; prostatic gland enveloping distal part of seminal vesicle; ejaculatory duct short; prostatic chamber distinct, elongate, contiguous with phallus. Phallus cylindrical of

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microphalloid-type, not as large as ventral sucker. Genital atrium complex, vast, with two accessory sacs diametrically opposite: (i) dextral, pocket-like, associated with ventral sucker; (ii) sinistral, with muscular mass, voluminous, of ovoid outline, but variable in shape; specialized genital muscles absent. Genital pore sinistral to ventral sucker. Ovary dextral to ventral sucker. Uterus postcaecal, coiled around testes. Metraterm differentiated, passing dorsally to base of genital atrium between the two accessory sacs, with narrow aperture sinistral to base of phallus (as in *Levinseniella*). Vitellarium symmetrical composed of two clusters of few post-testicular follicles; vitelline ducts long, arched, post-testicular. Excretory vesicle short, post-testicular, V-shaped. In intestine of birds; North America. Type-species *A. charadriiformis* (Young, 1949) Ching, 1965.




**Figs 47.73, 47.74.** *Spiculotrema littorale* Belopol'skaya, 1949. Redrawn from type and paratypes.
**Figs 47.75, 47.76.** *Ascorhytis charadriiformis* (Young, 1949). Redrawn from type and H.L. Ching's specimens.

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# 48 Family Anenterotrematidae Yamaguti, 1958

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## Introduction

Members of the family Anenterotrematidae Yamaguti, 1958 are very unusual digeneans in that they lack any sign of an alimentary canal. They are parasites of the small intestine, and occasionally gall-bladder, of bats in the Neotropical region. *Anenterotrema* Stunkard, 1938 was erected by Stunkard (1938) for two new species of intestinal parasites, *A. auritum* Stunkard, 1938 (the type-species, which was redrawn by Yamaguti, 1971) and *A. singulare* Stunkard, 1938, from bats in the Yucatan region of Mexico. Zdzitowiecki & Rutkowska (1980) also reported and described *A. auritum* from other chiropteran hosts in Cuba.

The taxonomic history of the group was reviewed by Santos & Gibson (1998). Stunkard (1938) gave no generic diagnosis or indication of the diagnostic criteria for *Anenterotrema*, but suggested that it may be lecithodendriid or allocreadiid in affiliation. Skarbilovich (1948), who considered the genus to belong to the Lecithodendriidae Lühe, 1901, produced a diagnosis based on Stunkard's (1938) descriptions and used the absence of an alimentary canal as the diagnostic feature. Yamaguti (1958b) used this character and the presence of a head-collar (a feature not mentioned by Skarbilovich in his generic diagnosis) and symmetrical, post-testicular vitelline fields as the key features for the erection of the family Anenterotrematidae for this genus. Later, Yamaguti (1971) amended the family diagnosis, referring to the vitellarium as comprising unilateral groups of relatively large follicles posterior to the gonads. The family was assigned to the Microphalloidea Ward, 1901 by Odening (1964a), but was not recognized by Thatcher (1993), who retained *Anenterotrema* in the Lecithodendriidae.

Another species, *A. stunkardi* Caballero y C. & Grocott, 1960, from Panamanian bats, was added by Caballero y C. & Grocott (1960), and a second genus, *Edcaballerotrema* Freitas, 1960, was included by Freitas (1960a) for *E. eduardocaballeroi* Freitas, 1960 from Brazilian bats. This genus was distinguished mainly by the position of the vitellarium anterior to the ventral sucker. The type-species was redescribed by Freitas & Dobbin (1962). However, Caballero y C. (1961a) had already transferred it to *Anenterotrema*, as *A. eduardocaballeroi* (Freitas, 1960), and synonymized *Edcaballerotrema* with *Anenterotrema*. Santos & Gibson (1998) examined the holotype of *A. eduardocaballeroi* (CHIOC no. 23.655-a) and found that the vitellarium comprised a bunch

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of small sinistrolateral follicles hidden among coils of uterus in the hindbody. They also confirmed an observation by Yamaguti (1971) that the anterior position of the vitellarium in the forebody, indicated by both Freitas (1960a) and Freitas & Dobbin (1962), was caused by a misinterpretation of parenchymal cells as vitelline follicles. Caballero y C. (1964) described *A. freitasi* Caballero y C., 1964 from a Costa Rican bat and transferred *Paralecithodendrium liliputianum* Travassos, 1928, from a Brazilian bat, to *Anenterotrema*. This species, as *Edcaballerotrema liliputianum*, had also been described by Freitas (1961) and Freitas & Dobbin (1962). Yamaguti (1971) indicated that the position of the vitellarium in the forebody of this species, reported by Travassos (1928a) and Freitas & Dobbin (1962), was also a misinterpretation of parenchymal cells as vitelline follicles, and an examination of the holotype (CHIOC 33.657) by Santos & Gibson (1998) confirmed that it is not possible to see the vitellarium due to the large number of eggs in the uterus.

Marshall & Miller (1979) added another genus, *Apharyngotrema* Marshall & Miller, 1979, to the family for their new species, *A. apharyngotrema* Marshall & Miller, 1979, from an Ecuadorian bat. They distinguished it from *Anenterotrema* by its greater size, 'differences also in size relationship and ratios of internal organs and body length', small differences in the vitelline and uterine distribution and the absence of a head-collar. They appeared to be unaware of the species of *Anenterotrema* recognized subsequent to the work of Stunkard (1938) and, in the same work, erected another new species, *Anenterotrema mesolecitha* Marshall & Miller, 1979, from a bat in Ecuador, which lacks a head-collar, and for which they amended the generic diagnosis. Santos & Gibson (1998) added another species, *Apharyngotrema lenti* Santos & Gibson, 1998, to *Apharyngotrema* and described an un-named species of *Anenterotrema*, both from Brazilian bats.

At first sight, there would seem little justification in recognizing *Apharyngotrema* as distinct from *Anenterotrema*. However, Santos & Gibson (1998) maintained that the members of the family fall into two groups:

> [*Anenterotrema*:] small, oval-pyriform worms of less then 1 mm in length, with the vitellarium usually restricted to a single field which may be unilateral or extend across the body; occasionally the vitellarium, which is often obscured by loops of the uterus, appears to form two groups of follicles, but these tend not to be symmetrical and are not as laterally situated as in *Apharyngotrema*.
> [*Apharyngotrema*:] larger, more elongate, fusiform worms of 1–5 mm in length, with the vitellarium in two separate and almost symmetrical lateral fields.

In this work, these two genera are recognized on this basis and the family is treated as a component of the wide conception of the Microphalloidea used in this volume.

## Family Anenterotrematidae Yamaguti, 1958

**Diagnosis:** Body small to medium-sized, oval, pyriform, tear-shaped (more tapered anteriorly) or fusiform. Tegument unarmed. Oral sucker well developed, ventrally subterminal; circumoral muscular head-collar with associated papillae present or absent. Ventral sucker well developed, may be slightly larger or smaller than oral sucker, well inside anterior half of worm or close to middle. Alimentary canal (pharynx, oesophagus and caeca) absent. Testes two, symmetrical or almost so (usually) to oblique, usually well separated, in anterior hindbody (or even either side of ventral sucker), subspherical, entire or irregularly lobed. Cirrus-sac present, small to medium-sized, tear-shaped to fusiform, in posterior half of forebody, contains coiled, tubular seminal vesicle, short, tubular pars prostatica and short, tubular ejaculatory duct, which forms muscular,

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unarmed, protrusible cirrus. Genital atrium small. Genital pore ventromedian in mid-forebody. Ovary post-testicular (occasionally intertesticular), lateral (dextral or sinistral) or submedian in anterior half of hindbody, irregularly oval to spherical. Seminal receptacle and Laurer's canal present (usually obscured by eggs). Uterine coils fill much of hindbody and sometimes extend into posterolateral regions of forebody, often obscure other features, extend into posterior hindbody; no distinct metraterm. Eggs very numerous, small, thin-shelled, operculate, may be embryonated in distal uterus. Vitellarium follicular; follicles relatively few, in irregular field or two subsymmetrical groups posterior to ovary, often obscured by uterus, may appear to coalesce into irregular mass(es). Excretory vesicle saccular, not reaching level of ovary (where known); pore terminal. In small intestine and occasionally gall-bladder of Chiroptera; Neotropical. Type-genus *Anenterotrema* Stunkard, 1938.

## Key to genera

**1a. Small, oval, pyriform or tear-shaped, < 1 mm long, with vitellarium usually restricted to a single field, which may be unilateral or extend across body ..... ..... *Anenterotrema* Stunkard, 1938. (Fig. 48.1)**
(Syn. *Edcaballerotrema* Freitas, 1960)

**Diagnosis:** Body very small (< 1 mm long), stout, oval, pyriform or tear-shaped. May have muscular head-collar with associated papillae surrounding oral sucker. Testes large, subsymmetrical, in middle third of body. Ovary dorsolateral to submedian, closely or occasionally far posterior to testes, or between testes. Vitelline follicles form single field either on one side of body or extending across it. Type-species *A. auritum* Stunkard, 1938.

**1b. Larger, more elongate, fusiform, 1–5 mm long, with vitellarium in two separate and almost symmetrical lateral fields ..... *Apharyngotrema* Marshall & Miller, 1979. (Fig. 48.2)**

**Diagnosis:** Body medium-sized (1–5 mm long), fusiform. Head-collar absent. Testes subsymmetrical to oblique, in anterior half of worm or almost so. Ovary dextrally or sinistrally submedian, post-testicular. Vitelline follicles in two subsymmetrical, widely separated groups, well posterior to testes. Type-species *A. apharyngotrema* Marshall & Miller, 1979.

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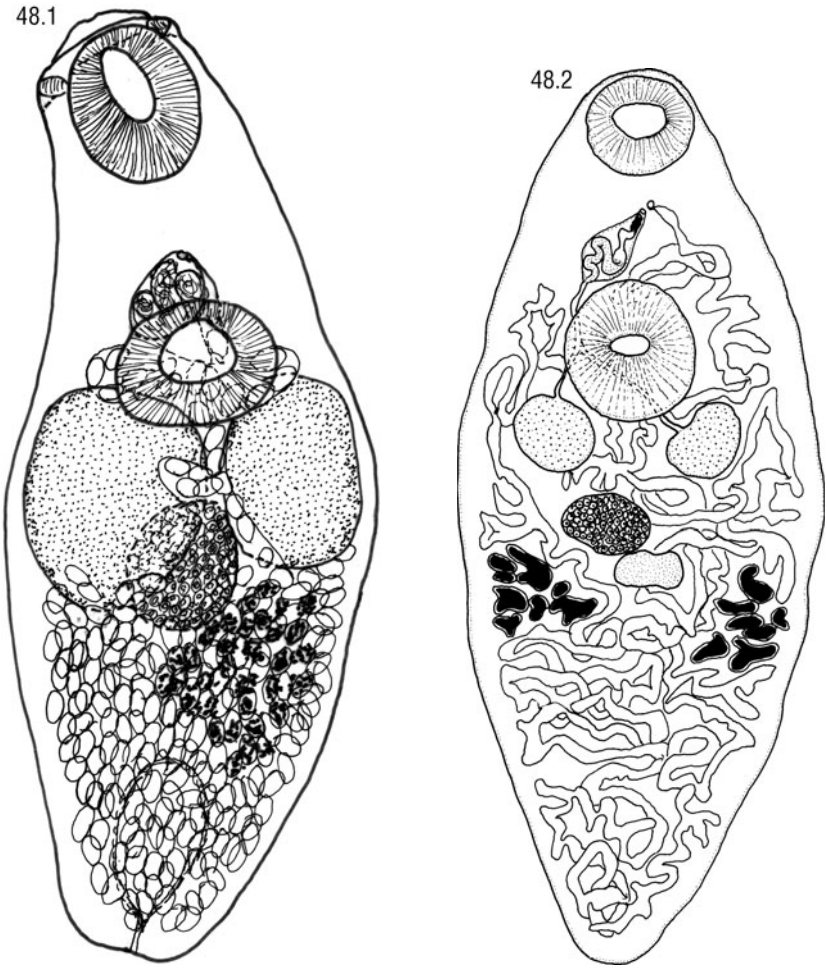



**Fig. 48.1.** *Anenterotrema auritum* Stunkard, 1938. After Yamaguti (1971).
**Fig. 48.2.** *Apharyngotrema apharyngotrema* Marshall & Miller, 1979. After Marshall & Miller (1979).

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# 49 Family Diplangidae Yamaguti, 1971

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## Introduction

The Diplangidae Yamaguti, 1971 is a small family containing two genera, one of which is known only from a single specimen. Diplangids are reported in marine teleosts of a variety of families, but with distinct evidence of a predilection for the Haemulidae (Amato, 1982). They are characterized by a restricted follicular vitellarium, an unarmed tegument and the lack (or perhaps great reduction) of a cirrus-sac. The family is mainly distributed in the Gulf of Mexico region of the Atlantic and off the Pacific coast of Mexico and the USA.

The Diplangidae is not well established. *Diplangus* Linton, 1910 has been considered a zoogonid (Price, 1934), a steganodermatid (Skrjabin, 1957) and a callodistomid (Yamaguti, 1953b), but lacks the major zoogonid/steganodermatid features, such as a lateral genital pore and an armed tegument. There are conflicting reports of the presence of a cirrus-sac, which is said to be absent in *Diplangus* (see Yamaguti, 1971) but in the second genus, *Pseudodiplangus* Yamaguti, 1971, is described as 'very delicate, thin-walled' (Siddiqi & Cable, 1960) or 'membranous, practically lacking' (Yamaguti, 1971). Examination of the holotype of *P. anoplosus* (Siddiqi & Cable, 1960) (USNPC 82519 – the only known specimen) indicates that Yamaguti's (1971) description is apt. If a cirrus-sac does indeed exist, it is extremely thin-walled and not clearly distinguishable from other connective tissues in the body of the worm. This distinguishes the family from both the zoogonid/steganodermatid group and the Callodistomidae Odhner, 1910. The latter occur in the gall-bladder of African and South American freshwater chondrosteans and teleosts, whereas diplangids are marine intestinal parasites.

Overstreet (1969) reduced the type-species of *Bilecithaster* Siddiqi & Cable, 1960 to synonymy with *Diplangus parvus* Manter, 1947.

Yamaguti (1971) re-illustrated the only known specimen of *Pseudodiplangus* to show a Y-shaped excretory vesicle and defined it as such, in contrast to Siddiqi & Cable (1960), who described it as I-shaped. In the holotype of *P. anoplosus*, the uterus obscures all but the extreme posterior part of the excretory vesicle, so it has not been possible to decide between these conflicting statements. Yamaguti (1971) stated that Laurer's canal was not observed, but Siddiqi & Cable (1960) reported its presence and it is traceable in the holotype.

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## Family Diplangidae Yamaguti, 1971

**Diagnosis:** Body fusiform. Tegument unarmed. Oral sucker subterminal, subglobular. Ventral sucker large, protuberant or not, in middle or anterior half of body, may be deeply retracted into body. Prepharynx short. Pharynx small, oval. Oesophagus short. Intestinal bifurcation in mid-forebody. Caeca reach to about level of testes or just into post-testicular region. Testes tandem to oblique, entire, in anterior to mid-hindbody. Cirrus-sac absent or membranous and indistinct. Seminal vesicle bipartite, saccular to sigmoid. Pars prostatica vesicular. Ejaculatory duct short, narrow. Genital pore median or submedian, at level of oesophagus or pharynx. Ovary pretesticular, median in anterior hindbody, entire. Canalicular seminal receptacle present. Laurer's canal may be present. Uterus reaches posteriorly beyond testes. Eggs numerous. Vitellarium follicular; fields small, lateral in anterior hindbody, at level of ventral sucker or in forebody. Excretory vesicle I-shaped, possibly also Y-shaped; pore terminal. In intestine of marine teleosts; Gulf of Mexico and Pacific Ocean off California and Mexico. Type-genus *Diplangus* Linton, 1910.

## Key to genera

**1a. Vitellarium in hindbody or at level of ventral sucker ..... ..... *Diplangus* Linton, 1910. (Fig. 49.1)**
(Syn. *Bilecithaster* Siddiqi & Cable, 1960)

**Diagnosis:** Ventral sucker large, protuberant or not, in middle or anterior half of body, may be deeply retracted into body. Caeca reach to about level of testes or just into post-testicular region. Testes tandem in mid-hindbody. Cirrus-sac absent. Seminal vesicle bipartite, saccular to sigmoid. Pars prostatica vesicular. Ejaculatory duct short, narrow. Genital pore median or submedian, at level of oesophagus or pharynx. Laurer's canal not observed. Canalicular seminal receptacle present. Vitellarium in hindbody or at level of ventral sucker. Excretory vesicle I-shaped, reaches ovary. In marine teleosts (mainly haemulids); Gulf of Mexico and off California. Type-species *D. paxillus* Linton, 1910.

**1b. Vitellarium in forebody ..... *Pseudodiplangus* Yamaguti, 1971. (Fig. 49.2)**
**Diagnosis:** Ventral sucker large, at base of deep ventral fold. Caeca reach testicular level. Testes oblique, in anterior hindbody. Cirrus-sac practically absent. Seminal vesicle bipartite. Pars prostatica vesicular. Genital pore submedian, at pharyngeal level. Seminal receptacle small? Laurer's canal present. Vitelline fields fairly small, lateral, in forebody. Excretory vesicle shape uncertain. In marine fishes (*Ocyurus*); off Puerto Rico. Type-species *P. anoplosus* (Siddiqi & Cable, 1960) Yamaguti, 1971.

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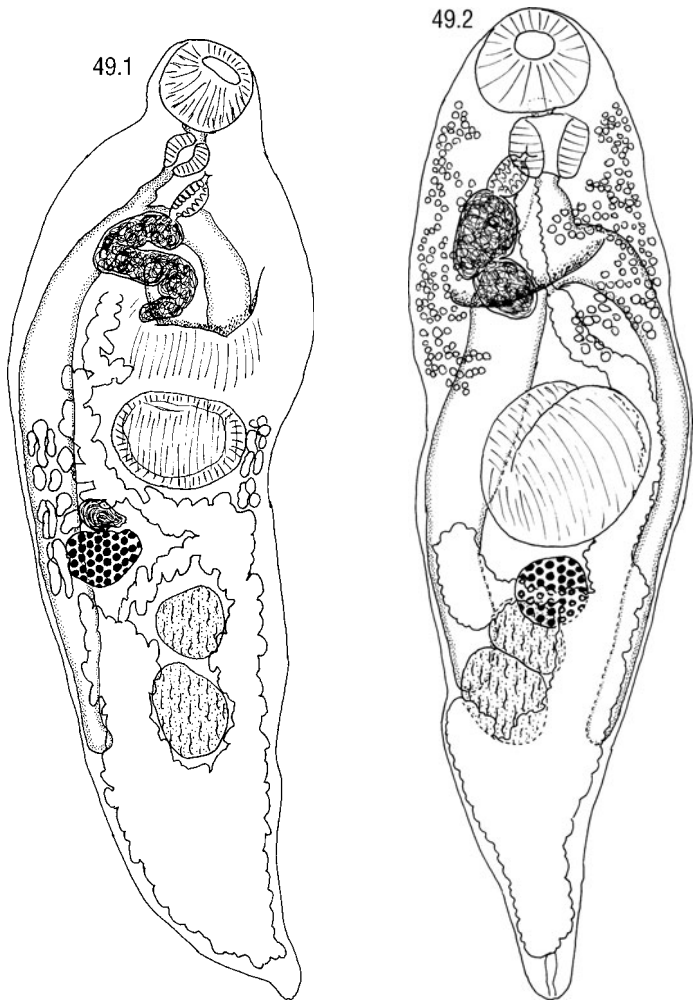



**Fig. 49.1.** *Diplangus paxillus* Linton, 1910. After Manter (1947).
**Fig. 49.2.** *Pseudodiplangus anoplosus* (Siddiqi & Cable, 1960). Ventral view of holotype, uterus in outline (USNPC 39321). Original.

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# 50 Family Eumegacetidae Travassos, 1922

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## Introduction

The Eumegacetidae Travassos, 1922 is a small family of bird parasites, characterized by anteriorly situated testes, which lie symmetrically in the forebody when the ventral sucker is present and well anterior when the ventral sucker is absent. Travassos (1922) erected the family for *Eumegacetes* Looss, 1900, and Oshmarin (1964) added *Papillatrema* Oshmarin, 1964. Khotenovskii (1966) allocated the species of *Eumegacetes* between two genera, *Eumegacetes* and *Posthovitellum* Khotenovskii, 1966, based on the distribution of the vitelline follicles. He further subdivided *Eumegacetes* into two subgenera, *Eumegacetes* and *Anterovitellum* Khotenovskii, 1966, also on the basis of the distribution of the vitelline follicles. Jaiswal & Humayun (1973) reduced *Posthovitellum* to subgeneric level and thereby brought consistency to recognition of subgenera of *Eumegacetes* using vitelline distribution. *Orthetrotrema* Macy & Basch, 1972 was transferred from the Lecithodendriidae Lühe, 1901 to the Eumegacetidae by Madhavi & Kumari (1995) because ofthe similarity between the life-cycle stages of *O. monostomum* Macy & Basch, 1972 and *Eumegacetes artamii* Mehra, 1935. Therefore, at present, there are three genera in the family, *Eumegacetes, Papillatrema* and *Orthetrotrema*.

## Family Eumegacetidae Travassos, 1922

**Diagnosis:** Body 2–8 mm in length, elongate oval. Tegument spinous or smooth. Oral sucker well developed, subterminal. Ventral sucker present or absent; if present, well developed, round, medial, equatorial to postequatorial. Prepharynx short to absent. Pharynx well developed. Oesophagus short to absent. Caeca paired, extend into posterior half of body, often to near posterior extremity. Testes paired, entire, symmetrical, in anterior third of body, at or near level of cirrus-sac. Cirrus-sac present, oriented anteriorly, medial, in anterior third of body. Genital pore median, in anterior third of body at level of pharynx or oral sucker. Ovary median, in posterior third of body, entire to lobed. Seminal receptacle and Laurer's canal present or unreported. Uterus mainly in posterior half of body, but extends into anterior half. Eggs operculate, small, numerous.

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Vitellarium follicular, in lateral fields of body, varying in extent. Excretory vesicle V- to Y-shaped. In intestinal tract, especially rectum, cloaca and renal system of birds (Coraciiformes, Cuculiformes, Passeriformes, Piciformes, Charadriiformes), progenetic in haemocoel of dragonflies (Odonata); cosmopolitan. Type-genus *Eumegacetes* Looss, 1900.

## Key to genera

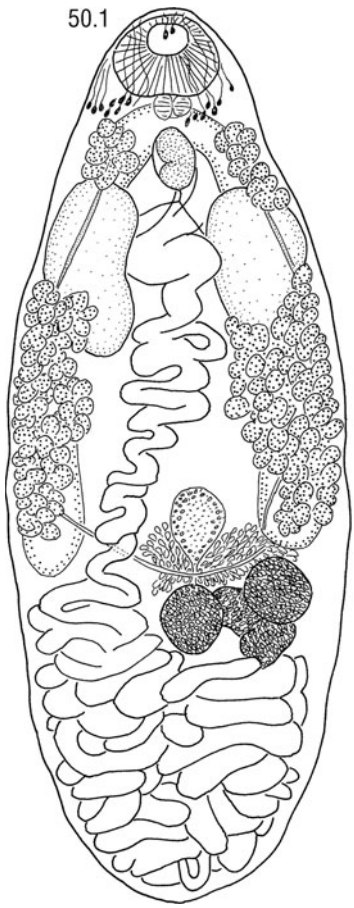
**1a. Ventral sucker absent ..... *Orthetrotrema* Macy & Basch, 1972. (Fig. 50.1)**
**Diagnosis:** Body 3–8 mm in length, oval elongate. Tegument without spines. Oral sucker subterminal. Ventral sucker absent. Prepharynx absent. Pharynx present. Oesophagus short to absent. Intestinal bifurcation close to or adjacent to pharynx. Caeca extend past mid-body. Testes entire to irregular, in anterior third of body. Cirrus-sac immediately posterior to intestinal bifurcation, contains compact seminal vesicle, small pars prostatica and ejaculatory duct. Cirrus present. Genital pore near intestinal bifurcation. Ovary lobed, submedian, in posterior third of body. Seminal receptacle and Laurer's canal present. Uterus fills posterior third of body. Metraterm small, thick-walled. Eggs small, operculate, numerous. Vitellarium in lateral fields, mostly between testes and ovary. Excretory vesicle V-shaped. Progenetic in haemocoel of dragonflies (Odonata); southern and south-eastern Asia. Type-species *O. monostomum* Macy & Basch, 1972.

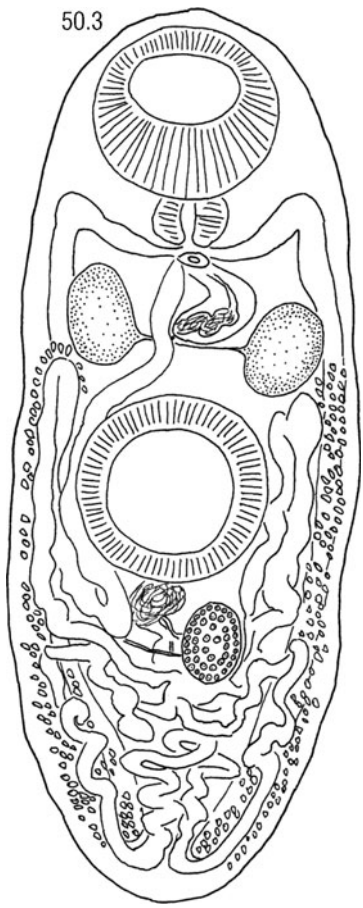
**1b. Ventral sucker present ..... 2.**

**2a. Tegument heavily spined; body with conspicuous posterior papilla; cirrus-sac region may project prominently in form of cone, at tip of which opens genital pore ..... ..... *Papillatrema* Oshmarin, 1964. (Fig. 50.2)**
**Diagnosis:** Body 2–3 mm long, oval elongate, with conspicuous papilla at posterior end. Tegument heavily spined. Oral sucker well developed, subterminal. Ventral sucker well developed, postequatorial. Prepharynx absent. Pharynx well developed. Oesophagus short to absent. Intestinal bifurcation in forebody. Caeca extend to near posterior end of body. Testes entire, in anterior third of body, mostly in forebody. Cirrus-sac well developed, median, in forebody, contains seminal vesicle, well-developed pars prostatica and short ejaculatory duct. Ventral region of body surrounding cirrus-sac may project ventrally in form of prominent cone. Genital pore opens at tip of prominent ventral cone, near oral sucker. Ovary oval, submedial, in posterior third of body, mostly in hindbody. Seminal receptacle well developed. Laurer's canal unreported. Uterus fills hindbody, extends anteriorly on either side of ventral sucker. Metraterm present. Eggs small, operculate, numerous. Vitellarium follicular, in lateral fields that extend along caeca for most of their length. Excretory vesicle unreported. In intestine of birds (Passeriformes); south-eastern Asia. Type-species *P. echinatum* Oshmarin, 1966.

**2b. Tegument not heavily spined; body without posterior papilla; cirrus-sac region not projecting ventrally in form of cone ..... *Eumegacetes* Looss, 1900. (Fig. 50.3)**
(Syns *Megacetes* Looss, 1899 *nec* Thomson, 1859; *Posthovitellum* Khotenovskii, 1966)
**Diagnosis:** Body 2–6 mm long, oval elongate. Tegument spinous or not. Oral sucker well developed, subterminal. Ventral sucker well developed, equatorial to postequatorial. Prepharynx absent. Pharynx well developed. Oesophagus short to absent. Intestinal bifurcation in forebody. Caeca extend to near posterior end of body. Testes entire, in anterior third of body, mostly in forebody. Cirrus-sac well developed, median to submedian, in forebody, contains seminal vesicle, well-developed pars prostatica and ejaculatory duct. Genital pore median near level of intestinal

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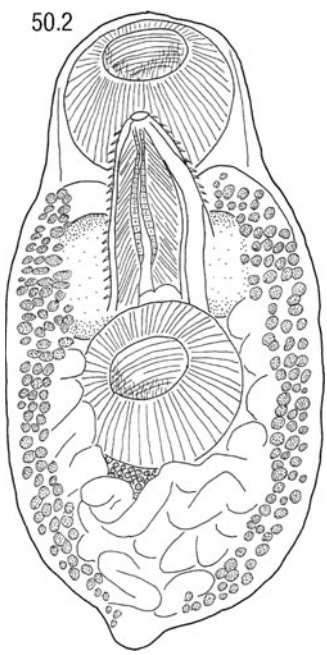




**Fig. 50.1.** *Orthetrotrema monostomum* Macy & Basch, 1972. After Macy & Basch (1972).
**Fig. 50.2.** *Papillatrema echinatum* Oshmarin, 1964. After Yamaguti (1971).
**Fig. 50.3.** *Eumegacetes triangularis* (Looss, 1899) Looss, 1900. After Yamaguti (1971).

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bifurcation or pharynx. Ovary oval to pyriform, median to submedian, in posterior third of body, mostly in hindbody. Seminal receptacle well developed. Laurer's canal unreported. Uterus fills hindbody, extends anteriorly on either side of ventral sucker. Metraterm present. Eggs small, operculate, numerous. Vitellarium follicular, in lateral fields of hindbody or extending into forebody. Excretory vesicle V-shaped. In intestine, including rectum, cloaca and renal system of birds (Coraciiformes, Cuculiformes, Passeriformes, Piciformes, Charadriiformes); the Americas, Eurasia. Type-species *E. triangularis* (Looss, 1899) Looss, 1900.

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# 51 Family Exotidendriidae Mehra, 1935

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## Introduction

The family Exotidendriidae Mehra, 1935 contains intestinal and renal parasites of reptiles characterized by very heavy spination of the cirrus and metraterm. Three genera are recognized, *Exotidendrium* Mehra, 1935, *Simhatrema* Chattopadhyaya, 1970 and *Renivermis* Blair, Purdie & Melville, 1989. Mehra (1935) erected the subfamily Exotidendriinae for *Exotidendrium* and Srivastava (1981) elevated it to family level. Chattopadhyaya (1970a) erected *Simhatrema* for *S. simhai* Chattopadhyaya, 1970, and Srivastava (1981) and Holmes (1989) provided valuable reviews of the genus. Blair *et al*. (1989) added *Renivermis* and provided an important appraisal of the family with a key to the genera, upon which the key below is based.

## Family Exotidendriidae Mehra, 1935

**Diagnosis:** Body 1–3 mm long. Tegument spinous. Gland-cells present in parenchyma. Oral sucker subterminal. Ventral sucker median, pre-equatorial to postequatorial. Prepharynx short. Pharynx present. Oesophagus short to elongate. Intestinal bifurcation in forebody. Caeca paired, short to long. Testes paired, symmetrical to nearly tandem, entire, postcaecal, from equatorial to near posterior end of body. Cirrus-sac long, well developed, contains seminal vesicle, extensive pars prostatica and ejaculatory duct; ejaculatory duct forms long cirrus with heavy spines. Genital pore median to submedian, in forebody, posterior to intestinal bifurcation. Ovary lateral or median, entire, in hindbody. Seminal receptacle and Laurer's canal present or not reported. Uterus in hindbody or forebody. Metraterm large, with heavy spines. Eggs operculate, small, numerous. Vitellarium composed of large follicles, in hindbody, variable in extent. Excretory vesicle V- or Y-shaped; terminal to dorso-subterminal. In intestine and renal systems of Crocodilia and Squamata; Africa, southern Asia, Australia. Type-genus *Exotidendrium* Mehra, 1935.

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## Key to genera

**1a. Ventral sucker in posterior third of body ..... ..... *Renivermis* Blair, Purdie & Melville, 1989. (Fig. 51.1)**

**Diagnosis:** Body 1–3 mm long, subcylindrical. Tegument spinous only around ventral sucker. Gland-cells in parenchyma. Oral sucker subterminal. Ventral sucker large, in posterior third of body. Prepharynx short. Pharynx well developed. Oesophagus short to absent. Intestinal bifurcation in anterior forebody. Caeca long, extend to near posterior end of body. Testes symmetrical, entire, posterior to ventral sucker near posterior end of body. Cirrus-sac long, well developed, arcuate, anterior to ventral sucker, contains seminal vesicle, pars prostatica and ejaculatory duct forming cirrus with heavy spines. Genital pore median, equatorial to postequatorial. Ovary median, near posterior end of body, entire, intertesticular. Seminal receptacle and Laurer's canal present. Uterus extensive in forebody, mostly between genital pore and pharynx. Eggs small, operculate, numerous. Vitelline follicles few, large, clustered near posterior end of body, mostly posterior to ventral sucker. Excretory vesicle Y-shaped; stem small; arms extend to near oral sucker; pore dorso-subterminal. In kidney of brackish-water Crocodilia; Australia. Type-species *R. crocodyli* Blair, Purdie & Melville, 1989.

**1b. Ventral sucker equatorial or pre-equatorial ..... 2.**

**2a. Ovary post-testicular; vitelline follicles mostly post-testicular; filament on abopercular end of egg ..... *Exotidendrium* Mehra, 1935 (Fig. 51.2)**

**Diagnosis:** Body 1–2 mm in length, elongate oval. Tegument spinous. Gland-cells in parenchyma. Oral sucker small, subterminal. Ventral sucker small, pre-equatorial. Prepharynx present. Pharynx present. Oesophagus elongate. Intestinal bifurcation in mid-forebody. Caeca short, terminate in anterior half of body. Testes symmetrical or oblique to nearly tandem, entire, equatorial, anterior to ovary. Cirrus-sac long, sinuous, extends from near ovary to intestinal bifurcation, contains seminal vesicle, pars prostatica and ejaculatory duct, which forms cirrus with heavy spines. Genital pore median to submedian, posterior to intestinal bifurcation. Ovary entire, median to submedian, typically post-testicular in posterior third of body. Seminal receptacle present; Laurer's canal not reported. Uterus in hindbody, mostly posterior to testes. Metraterm large, well developed, with heavy spines. Eggs small, operculate, numerous; filament at abopercular pole. Vitelline follicles large, scattered throughout hindbody. Excretory vesicle Y-shaped; pore dorsally subterminal. In cloaca of Crocodilia; Africa, southern Asia. Type-species *E. gharialii* Mehra, 1935.

**2b. Ovary pretesticular; vitelline follicles pretesticular; no filament on abopercular end of egg ..... *Simhatrema* Chattopadhyaya, 1970. (Fig. 51.3)**

**Diagnosis:** Body 1–3 mm long, oval to elongate. Tegument spinous. Gland-cells in parenchyma of forebody. Oral sucker well developed, subterminal. Ventral sucker well developed, pre-equatorial. Prepharynx present. Pharynx well developed. Oesophagus present. Intestinal bifurcation in mid-forebody. Caeca long, extend to testicular zone. Testes oval, symmetrical, subequal, entire, posterior to ventral sucker, in posterior third of body. Cirrus-sac long, arcuate, extends from hindbody to forebody, contains seminal vesicle, pars prostatica and ejaculatory duct, which forms cirrus with spines. Genital pore median, in hindbody, postbifurcal. Ovary entire, lateral, mostly pretesticular. Seminal receptacle and Laurer's canal not reported. Uterus extensive in hindbody. Metraterm well developed, muscular, with thick spines. Eggs small, operculate, numerous. Vitelline follicles large, in band across body from testes to level of ventral sucker. Excretory vesicle V- to Y-shaped; pore terminal. In large intestine of marine Squamata, may be contained in fibrous cysts; Bay of Bengal, waters off Malaysia, northern Australia. Type-species *S. simhai* Chattopadhyaya, 1970.

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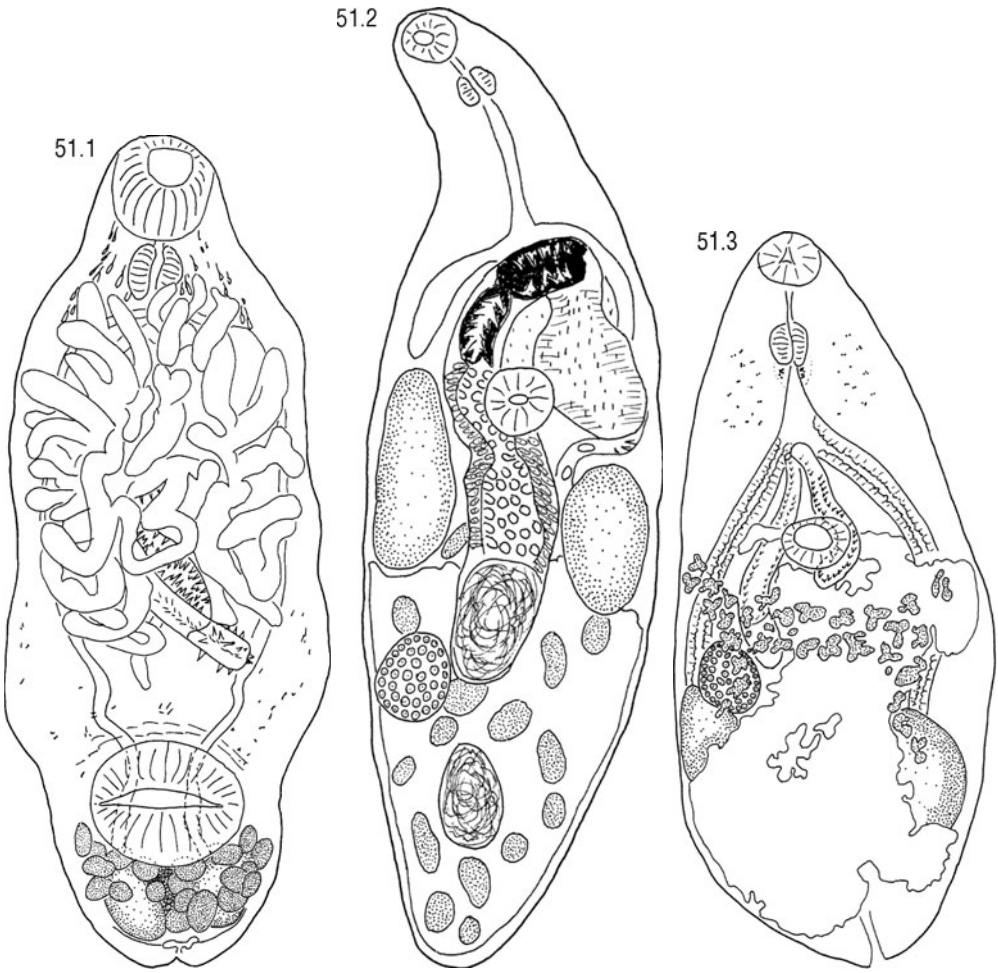



**Fig. 51.1.** *Renivermis crocodyli* Blair, Purdie & Melville, 1989. After Blair *et al.* (1989).
**Fig. 51.2.** *Exotidendrium gharialii* Mehra, 1935. After Yamaguti (1971).
**Fig. 51.3.** *Simhatrema simhai* Chattopadhyaya, 1970. After Holmes (1989).

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# 52 Family Faustulidae Poche, 1926

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## Introduction

The family Faustulidae Poche, 1926 has only recently been widely recognized, due mainly to molecular phylogenetic results, which have shown that it is not closely related to the Fellodistomidae Nicoll, 1909 but is, in fact, close to the Zoogonidae Odhner, 1902 (Hall *et al.*, 1999; Cribb *et al.*, 2001b; Olson *et al.*, 2003). Members of the family are found mainly in the intestine of marine teleosts, but occasionally in fresh water. They are generally characterized by a spinous tegument, a cirrus-sac, a restricted follicular vitellarium, a canalicular seminal receptacle, a posteriorly placed opening of Laurer's canal and a median genital pore.

*Faustula* Poche, 1926 was erected by Poche (1926) as a replacement name for *Eurema* MacCallum, 1919, based on *E. keksooni* MacCallum, 1919 from the 'gills' of a 'ray' from off Singapore. In fact, as MacCallum (1919) pointed out, 'it was found at the bottom of the dish after washing the gills and may have come from the gullet or mouth'. Poche (1926) took MacCallum's (1919) description at face value and, because paired lateral vaginae in the forebody were described, erected a new 'supersuperfamilie', the Faustulida Poche, 1926 and the new family Faustulidae for it. As recently as 1993, Thatcher (1993) repeated this error and erected the order Faustuliformes Thatcher, 1993 for it. However, the family name Faustulidae has been recognized as the oldest available for the taxon generally known as the Baccigerinae Yamaguti, 1958, which has recently (Hall *et al.*, 1999) been raised to family status. The morphology of the holotype of the type-species is now well known due to redescriptions by Price (1938) and Zhukov (1978). Price (1938) tentatively assigned it to the Fellodistomidae and Zhukov (1978) agreed with Yamaguti's (1971) placement in the Baccigerinae. Members of this genus exhibit the usual characters associated with baccigerines, with the multilobate ovary being a distinguishing feature. According to Srivastava (1935a) and Hafeezullah & Siddiqi (1970b), the seminal receptacle is uterine. Price (1938), however, found 'seminal receptacle apparently absent, although the oviduct is widened at the point where Laurer's canal is given off and this dilation apparently functions as a seminal receptacle', with Laurer's canal opening close to posterior limit of the uterus. This can be clearly seen in the specimen (USNPC 36451). Rizvi's (1971) description of *F. hilsai* Rizvi, 1971 shows a very similar situation, but with Laurer's canal opening very close to the posterior extremity. Observations of

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two sets of sections of poorly preserved specimens (BMNH 1977.3.28.127–128) reinforce this view. Several further species of *Faustula* have been described and it is now clear that they are primarily parasites of migratory and marine clupeids in the northern Indian Ocean. The synonymy of *Faustula* and *Orientophorus* Srivastava, 1935 was recognized by Yamaguti (1958b). Three specimens of *Faustula* have been examined, the holotype of *F. keksooni*, the holotype of *F. basiri* Hafeezullah & Siddiqi, 1970 (USNPC 63209) and a voucher of *F. gangetica* (Srivastava, 1935) (USNPC 63210). Concentric rings of muscle bundles form a circle reaching from about the genital pore to the ventral sucker (Figure 52.8) in *F. basiri*. A similar feature, although less well defined, can be seen in the other two flattened specimens. *F. gasterostei* Schell, 1973 is probably a member of *Pronoprymna* Poche, 1926. *F. qikouensis* Qiu & Li in Shen & Qiu, 1995 is probably a member of *Bacciger* Nicoll, 1924.

The spinous tegument of *Allofellodistomum* Yamaguti, 1971 indicates that this genus probably belongs in the Faustulidae, but our knowledge of other important diagnostic features, e.g. the cirrus-sac contents and the position of the opening of Laurer's canal, does not allow us to confirm this.

*Antorchis* Linton, 1911 was a replacement name for *Mesorchis* Linton, 1910 *nec* Dietz, 1909. Machida (1975) sank *Parantorchis* Yamaguti, 1934 and *Neoparantorchis* Hafeezullah & Siddiqi, 1971 into it, and redescribed the type of *Parantorchis*, correcting several points. *Jonesiella* Hafeezullah & Siddiqi, 1970 is a pre-occupied name, replaced by *Neoparantorchis*, which is considered to have a bipartite seminal vesicle (Hafeezullah & Siddiqi, 1970b).

The concept of *Bacciger* used here is based mainly on that of Bray & Gibson (1980), who thought that *Ovotrema* Pigulewsky, 1938 was a 'questionable synonym' of this genus. Cribb *et al.* (1999a) considered *Bacciger* lacking in the 'specialisations seen in the other genera'; however, some nominal species clearly do not fit into the genus as defined here. These include *B. lizae* Shen in Shen & Qiu, 1995, with its pregonadal uterus and vitellarium at the posterior end of the body, and *B. mugilis* Shen, 1987, with testes at the posterior extremity, pretesticular uterus, vitellarium in the hindbody and intestinal bifurcation in the hindbody. *Steringotrema microacetabularis* Suriano & Martorelli, 1983 also appears to be a faustulid, probably belonging to *Bacciger*.

There are two descriptions of the type-species of *Baccigeroides* Dutta, 1995, i.e. *B. hafeezullai* Dutta, 1995, that attempt to erect the new genus, i.e. Dutta (1995) and Manna & Datta (1996). The latter paper lacked a figure, but on the reprint distributed by the authors a drawing is appended, which is clearly the same as the figure in Dutta (1995). Its distinctive features are the anteriorly situated cirrus-sac and genital pore, the saccular internal seminal vesicle and unarmed tegument. The second species recognized, *B. cochinensis* (Hafeezullah & Siddiqi, 1970), is extremely similar to the type-species and may be a senior synonym.

Dronen *et al.* (1994) erected the subfamily Echinobrevicecinae Dronen, Blend & McEachran, 1994 for *Echinobreviceca* Dronen, Blend & McEachran, 1994, based on an I-shaped excretory vesicle, densely spined tegument and pretesticular ovary. As pointed out by Cribb *et al.* (1999a), this subfamily cannot be sustained as the spined tegument and pretesticular ovary are fairly common in baccigerines, and the excretory vesicle in many baccigerines is saccular, similar to that found in *Echinobreviceca* (see, for example, the drawings of *Paradiscogaster eniwetokensis* Martin & Hammerich, 1970 in Bray *et al.* (1994, figs 15–25)).

*Gissutrema* Machida & Kamegai, 1997 has been recognized, *pro tempore*, as a member of the Acanthocolpidae Lühe, 1906 (see Bray, 2005b).

*Neobenthotrema* Wang, 1991 was described from *Triacanthus brevirostris* off China (Wang, 1991). Given its morphology and host, it is almost certainly a synonym of *Paradiscogaster indicus* (Srivastava, 1939), reported from *T. brevirostris* and *T. strigilifer* in the Bay of Bengal by Madhavi (1975). *Neobenthotrema* is described as having a very small ventral sucker, unlike the distinct one

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found in *Paradiscogaster*, but it seems likely that the sucker remained attached to the gut mucosa and was torn from the worms (five were described) when they were removed from the host. In view of these observations, *Neobenthotrema* is considered a synonym of *Paradiscogaster*. Other synonymies and the status of *Paradiscogaster* Yamaguti, 1934 have been discussed recently by Cribb *et al*. (1999a).

The status of *Pronoprymna* Poche, 1926 was discussed by Bray & Gibson (1980), who considered *Pentagramma* Chulkova, 1939 and *Pseudopentagramma* Yamaguti, 1971 to be its synonyms. They also pointed out the similarity of *Walliniella* Yamaguti, 1971, which was based on poorly preserved specimens from a common host of the type-species of *Pronoprymna*. They were reluctant to synonymize this genus with *Pronoprymna* because of the postovarian testes. *Walliniella* is poorly known and should be considered a genus *inquirendum*. Machida & Kuramochi (2003) extended the definition to include *P. mijun* Machida & Kuramochi, 2003, which has oblique to almost tandem testes and vitelline follicles not as tightly packed as in other species.

*Pseudobacciger* Nahhas & Cable, 1964 has recently been reviewed by Dimitrov *et al*. (1999) and Rahimian & Thulin (2003).

The type- and only species of *Pseudosellacotyla* Yamaguti, 1953, *P. lutzi* (Freitas, 1941), was originally placed in the nanophyetid genus *Sellacotyle* Wallace, 1935. Yamaguti (1953b) erected *Pseudosellacotyla* Yamaguti, 1953, which was placed in the Heterophyidae Leiper, 1909. Later, Yamaguti (1958b) erected the subfamily Pseudosellacotylinae Yamaguti, 1958 in the Microphallidae Ward, 1901. S. Deblock (personal communication) has pointed out its similarity to *Bacciger* and *Pseudobacciger*. The lack of a cirrus-sac indicates a close relationship with the latter genus.

*Yamagutia* Srivastava, 1937 was not properly described until the work of Srivastava (1939a). The almost lateral genital pore looks rather zoogonid-like, but it lacks spines, i.e. it comfortably fits neither Faustulidae nor Zoogonidae. The true state of the seminal receptacle is not clear, but it is probably canalicular. Cribb *et al*. (1999b) stated:

> *Yamagutia* Srivastava, 1939 contains a single species, *Y. lateroporus* Srivastava, 1939. In general appearance this species resembles *Paradiscogaster* except that the genital pore is figured as being lateral and the ventral sucker appears unspecialised. We suspect that the position of the genital pore is an artefact of flattening and that it will prove to be median in undistorted specimens. Should the sucker be unspecialised then this species would agree with *Bacciger* which would be broadly consistent with its host, *Chatoessus* (now *Dorosoma*) *nasus* which is a clupeid as are many of the hosts of species of *Bacciger*. We note, however, that the ventral sucker is considerably larger than is typical within *Bacciger*. Should the ventral sucker prove to be specialised then *Y. lateroporus* would probably be best considered a species of *Paradiscogaster*. For the present we think it best to continue to recognise *Yamagutia*.

*Pseudofellodistomum* Wang, 1989 is difficult to place. The armed tegument suggests that it may be a faustulid, but other characteristics are somewhat distinct, particularly the posteriorly situated testes. Nothing is known of the contents of the cirrus-sac, the proximal female system or the excretory system. It is considered a genus *incertae sedis*.

## Family Faustulidae Poche, 1926

(Syns Discogasteroididae Srivastava, 1939; Baccigeridae Yamaguti, 1958; Discogasteroidinae Srivastava, 1939; Antorchinae Skrjabin & Koval, 1957; Antorchiinae Yamaguti, 1958; Baccigerinae Yamaguti, 1958; Parantorchiinae Yamaguti, 1958; Pentagramminae Yamaguti, 1958; Pseudosellacotylinae Yamaguti, 1958; Echinobrevicecinae Dronen, Blend & McEachran, 1994)

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**Diagnosis:** Body small, oval to fusiform. Tegument usually spined, occasionally unarmed. Oral sucker subterminal, smaller to larger than ventral sucker. Ventral sucker variable in size and position, usually about equatorial. Prepharynx short. Pharynx small, globular to oval. Oesophagus distinct, short to long, occasionally with lateral outgrowths. Intestinal bifurcation in forebody. Caeca often short, divergent, may reach testicular region or just beyond, blind. Testes two, symmetrical to slightly oblique, usually in anterior hindbody. Cirrus-sac thin-walled or occasionally absent, usually in forebody, occasionally in hindbody. Seminal vesicle bipartite or saccular, enclosed in cirrus-sac when latter present. Pars prostatica long, strongly invested with gland-cells or apparently absent or short tubular with few external gland-cells. Ejaculatory duct short, narrow, may evert to form small cirrus. Genital atrium deep, narrow. Genital pore usually median or submedian in forebody. Ovary oval to lobed, pre-, inter- or post-testicular. Laurer's canal present, long, usually opening at or near posterior extremity; proximal region dilated to form canalicular seminal receptacle. Uterine seminal receptacle absent. Uterus usually almost entirely post-testicular, extensive. Eggs numerous, usually small, operculate, shells smooth, without spines or filaments. Vitellarium in two fields, each with one or several compact clusters of small follicles; fields symmetrical in lateral regions of forebody or anterior hindbody. Excretory vesicle V- or Y-shaped with short stem; arms reach into forebody; pore terminal or subterminal. In intestine and stomach of marine, brackish-water and freshwater teleosts; cosmopolitan. Type-genus *Faustula* Poche, 1926.

## Key to genera

**1a. Cirrus-sac absent ..... 2.**
**1b. Cirrus-sac present ..... 3.**

**2a. Seminal vesicle bipartite, dorsal to ventral sucker or in anterior hindbody; excretory arms long; in marine teleosts ..... *Pseudobacciger* Nahhas & Cable, 1964. (Fig. 52.1)**
**Diagnosis:** Body oval. Tegument armed. Oral sucker subglobular, subterminal. Ventral sucker rounded in middle third of body. Prepharynx absent or short. Pharynx subglobular. Oesophagus short to distinct. Intestinal bifurcation in posterior forebody. Caeca divergent, reach just posteriorly to testes. Testes symmetrical, irregular, in anterior hindbody. Cirrus-sac absent. Seminal vesicle indistinctly bipartite, dorsal to ventral sucker or reaching into anterior hindbody. Pars prostatica indistinct. Ejaculatory duct not observed. Genital pore median, bifurcal. Ovary irregular to lobed, median, posterior to or between testes. Canalicular seminal receptacle small. Laurer's canal opens near posterior extremity. Uterus extensive, mainly post-testicular. Vitellarium in two bunches of few follicles, extracaecal, at level of ventral sucker. Excretory vesicle V-shaped; arms reach oesophageal level; pore subterminal. Parthenitae in clams. Metacercariae in shrimps. Adults in marine teleosts (mainly clupeiforms); Atlantic, Pacific and Indian Oceans. Type-species *P. harengulae* (Yamaguti, 1938) Nahhas & Cable, 1964.

**2b. Seminal vesicle broadly tubular, curved, may reach well into hindbody; excretory arms short; in freshwater teleosts ..... *Pseudosellacotyla* Yamaguti, 1953. (Fig. 52.2)**
**Diagnosis:** Body small, pyriform. Tegument armed. Oral sucker subglobular, subterminal. Ventral sucker rounded, in mid-body. Prepharynx short. Pharynx oval. Oesophagus short. Intestinal bifurcation in posterior forebody. Caeca short, saccular, highly divergent, reach level of ventral sucker. Testes large, oval, entire, symmetrical, in hindbody. Cirrus-sac absent.

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Seminal vesicle broadly tubular, curved, may reach well into hindbody. Pars prostatica and ejaculatory duct not described. Genital pore median, immediately anterior to ventral sucker. Ovary rounded or irregular, intertesticular. Canalicular seminal receptacle present. Laurer's canal not seen. Uterus fills most of hindbody. Vitellarium follicular, in two small lateral fields, between level of oral sucker or pharynx and caeca. Excretory vesicle V-shaped; arms short, wide; pore terminal. In freshwater teleosts (*Hoplias*); South America. Type-species *P. lutzi* (Freitas, 1941) Yamaguti, 1953.

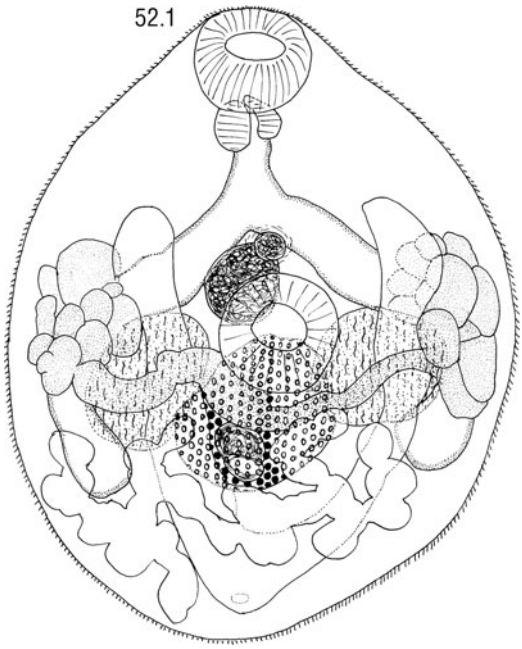
**3a. Genital pore median or submedian** ..... **4.**
**3b. Genital pore marginal** ..... ***Yamagutia* Srivastava, 1937. (Fig. 52.3)**
**Diagnosis:** Body fusiform. Tegument unarmed. Oral sucker subglobular, subterminal. Ventral sucker transversely oval, in mid-body. Prepharynx small. Pharynx subglobular. Oesophagus long. Intestinal bifurcation in mid-forebody. Caeca short, saccular, divergent, terminate in forebody. Testes oval, entire, oblique, fairly near posterior extremity. Cirrus-sac oval, transverse, in forebody. Internal seminal vesicle bipartite. Pars prostatica elongate, ensheathed in many gland-cells. Ejaculatory duct fairly long. Genital pore dextrally submarginal, postbifurcal in posterior forebody. Ovary subglobular, pre-testicular, sinistral to posterior part of ventral sucker. Seminal receptacle oval. Laurer's canal present. Uterus occupies much of hindbody, reaches posterior extremity. Vitellarium follicular; lateral fields bifurcal to level of middle of ventral sucker, better developed on poral side. Excretory vesicle Y-shaped, with short stem; extent of arms not given; pore subterminal. In marine teleosts (*Chatoessus* (= *Dorosoma, Nematalosa*)); Arabian Sea. Type-species *Y. lateroporus* Srivastava, 1937.

**4a. Body oval to rounded** ..... **5.**
**4b. Body conical, with lateral margins folded ventrally and truncate posterior margin** ..... ***Trigonocryptus* Martin, 1958. (Fig. 52.4)**
**Diagnosis:** Body conical, with lateral folds separate posteriorly and converging anteriorly; posterior extremity truncate. Tegument armed. Oral sucker subterminal, with ventrolateral extensions. Ventral sucker large, transversely elongate, dumb-bell-shaped, ridged, indented anteriorly and posteriorly, in posterior half of body. Prepharynx short. Pharynx oval to globular. Oesophagus short. Intestinal bifurcation in mid-forebody. Caeca short, saccular, divergent, overlap ventral sucker. Testes symmetrical, at posterior extremity, oval, entire. Cirrus-sac oval, anterior to or just overlapping ventral sucker. Internal seminal vesicle bipartite. Pars prostatica well developed with narrow lumen, ensheathed in many gland-cells. Ejaculatory duct short. Genital pore median, bifurcal. Ovary oval, entire, median, mainly pretesticular. Canalicular seminal receptacle present. Laurer's canal opens dorsally on protuberance close to posterior extremity. Uterus intertesticular and pretesticular, not post-testicular, mainly dorsal to ventral sucker. Eggs numerous, tanned, operculate. Vitellarium follicular, in symmetrical lateral fields between mid-level of oral sucker and overlapping ventral sucker. Excretory vesicle V-shaped; arms short (apparently reach only to testes); pore terminal or ventrally subterminal. In marine teleosts (Tetraodontidae); Pacific Ocean off Hawaii, Japan and Australia. Type-species *T. conus* Martin, 1958.

**5a. Testes and/or ovary in forebody or partly so** ..... **6.**
**5b. Gonads in hindbody or overlapping ventral sucker** ..... **7.**

**6a. Testes mainly in hindbody; ovary in forebody; caeca long, reach close to posterior extremity** ..... ***Allofellodistomum* Yamaguti, 1971. (Fig. 52.5)**

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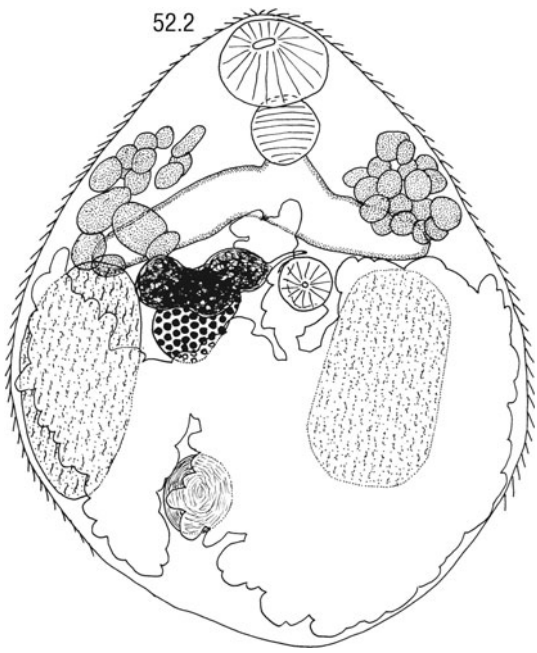
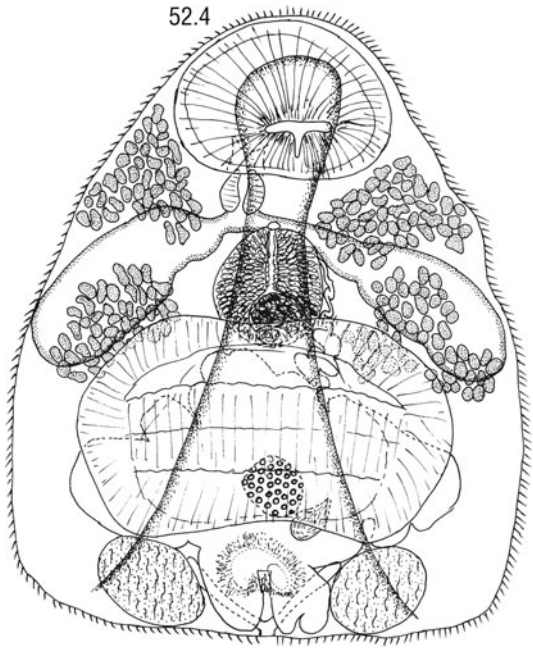



**Fig. 52.1.** *Pseudobacciger harengulae* (Yamaguti, 1938). After Dimitrov *et al.* (1999).
**Fig. 52.2.** *Pseudosellacotyle lutzi* (Freitas, 1941). After Kohn *et al.* (1985).
**Fig. 52.3.** *Yamagutia lateroporus* Srivastava, 1937. After Srivastava (1939a).

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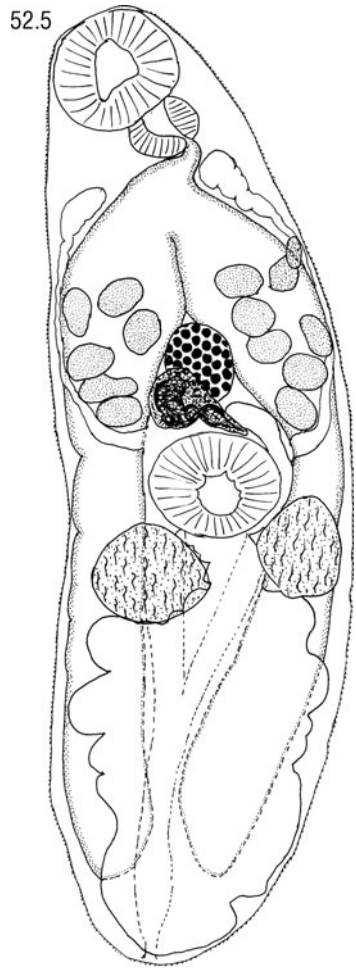




**Fig. 52.4.** *Trigonocryptus conus* Martin, 1958. After Yamaguti (1971).
**Fig. 52.5.** *Allofellodistomum preovaricum* (Caballero, Bravo-Hollis & Grocott, 1952). After Caballero y C. *et al.* (1952).

**Diagnosis:** Body elongate oval. Tegument spinous. Oral sucker subterminal. Ventral sucker in mid-body. Prepharynx apparently absent. Pharynx oval. Oesophagus short. Intestinal bifurcation in mid-forebody. Caeca wide, long, reach close to posterior extremity. Testes symmetrical, in anterior hindbody, oval, entire. Cirrus-sac broadly claviform, immediately anterior to ventral sucker. Internal seminal vesicle saccular. Pars prostatica? Ejaculatory duct? Genital pore submedian, immediately anterior to ventral sucker. Ovary in posterior forebody, median, oval, entire. Seminal receptacle absent? Laurer's canal? Uterus occupies much of post-testicular space. Eggs elongate reniform, large. Vitellarium in two lateral fields of few oval follicles; fields reach from ventral sucker to intestinal bifurcation. Excretory vesicle Y-shaped; arms reach oesophagus; pore terminal. In marine teleosts (*Arius* (= *Galeichthys*)); Pacific Ocean off Panama. Type-species *A. preovaricum* (Caballero, Bravo-Hollis & Grocott, 1952) Yamaguti, 1971.

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**6b. Testes in forebody or partly so; ovary in posterior forebody, dorsal to ventral sucker or, occasionally, in anterior hindbody; caeca short, saccular, divergent ..... ..... *Antorchis* Linton, 1911. (Fig. 52.6)**

(Syns *Jonesiella* Hafeezullah & Siddiqi, 1970 *nec* Brady, 1880; *Mesorchis* Linton, 1910 *nec* Dietz, 1909; *Neoparantorchis* Hafeezullah & Siddiqi, 1971; *Parantorchis* Yamaguti, 1934)

**Diagnosis:** Body plump, fusiform to pyriform. Tegument armed with small spines. Dorsal pouch in mid-hindbody. Oral sucker terminal to subterminal. Ventral sucker rounded in mid- to posterior body. Prepharynx short. Pharynx oval. Oesophagus distinct. Intestinal bifurcation in mid-forebody. Caeca short, saccular, divergent, reach posterior forebody or anterior hindbody. Testes symmetrical, in forebody or partly so. Cirrus-sac oval, often recurved. Internal seminal vesicle coiled, tubular, bipartite or oval. Pars prostatica long, distinct, lumen relatively narrow, surrounded by wide layer of gland-cells. Ejaculatory duct short, straight. Cirrus may form, has been described as spined. Genital pore median, in mid- to posterior forebody. Ovary oval, in posterior forebody or dorsal to ventral sucker, occasionally in anterior hindbody. Canalicular seminal receptacle present. Laurer's canal opens in hindbody, may be close to posterior extremity. Uterus fills most of hindbody and reaches into forebody laterally. Vitellarium in lateral fields of few follicles in mid-forebody. Excretory vesicle V- or Y-shaped with short stem; arms reach testes; pore terminal. In marine and freshwater teleosts; in warm waters of all oceans. Type-species *A. urna* (Linton, 1910) Linton, 1911.

**7a. Uterus usually reaches posteriorly beyond testes, mainly in hindbody; ventral sucker not close to posterior extremity ..... 8.**

**7b. Uterus pretesticular, almost entirely in forebody; ventral sucker in posterior third of body ..... *Parayamagutia* Machida, 1971. (Fig. 52.7)**

**Diagnosis:** Body oval. Tegument spinous. Oral sucker subterminal, oval. Ventral sucker oval, in posterior third of body. Prepharynx short. Pharynx oval. Oesophagus long. Intestinal bifurcation in anterior half of body. Caeca short, saccular, divergent, reach into posterior forebody. Testes symmetrical to subsymmetrical, in anterior hindbody and overlapping ventral sucker, close to posterior extremity, oval, entire. Cirrus-sac oval, in mid-body. Internal seminal vesicle bipartite. Pars prostatica present. Genital pore dextrally submedian, bifurcal or more anterior. Ovary ovoid, intertesticular, at posterior margin of ventral sucker. Canalicular seminal receptacle present. Laurer's canal opens posteriorly to seminal receptacle. Uterus pretesticular, extensive, almost entirely in forebody, reaches lateral margins and pharynx. Vitellarium follicular, in two lateral fields at anterior extremity, reaching almost to mid-body laterally to uterus. Excretory vesicle Y-shaped; stem short; pore terminal. In marine teleosts (*Ostracion*); Pacific Ocean off Japan and Australia. Type-species *P. ostracionis* Machida, 1971.

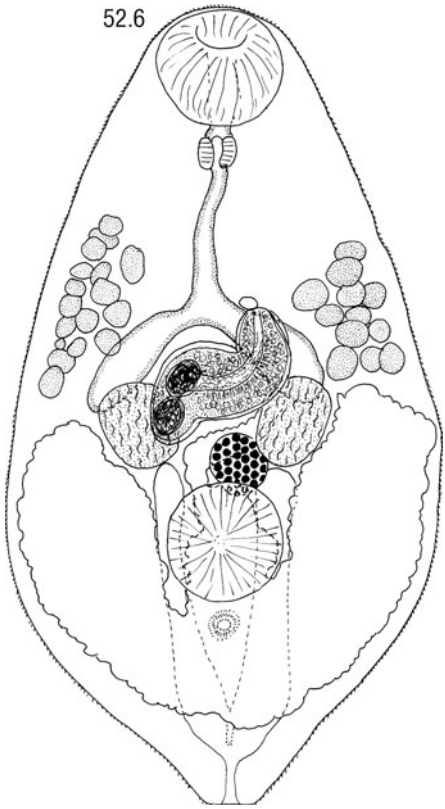
**8a. Ovary entire or with few lobes ..... 9.**

**8b. Ovary multilobed, acinous ..... *Faustula* Poche, 1926. (Fig. 52.8)**

(Syns *Eurema* MacCallum, 1918 *nec* Hübner, 1820; *Orientophorus* Srivastava, 1935)

**Diagnosis:** Body oval to pyriform. Tegument armed. Concentric rings of muscles form circle ventrally in posterior forebody. Oral sucker subglobular to cup-shaped, terminal to subterminal. Ventral sucker rounded, in mid-body. Prepharynx short. Pharynx oval. Oesophagus long. Intestinal bifurcation in posterior forebody. Caeca reach into anterior hindbody. Testes two, symmetrical at ventral sucker level or in anterior hindbody. Cirrus-sac claviform, in forebody or overlapping

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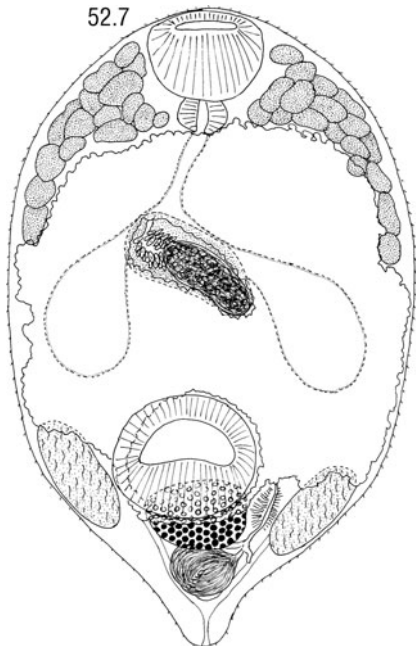




**Fig. 52.6.** *Antorchis pomacanthi* (Hafeezullah & Siddiqi, 1970). Specimen from *Pomacanthus semicircularis*, Heron Island (BMNH 1998.8.5.31–34). Original.
**Fig. 52.7.** *Parayamagutia ostracionis* Machida, 1971. After Machida (1971).

ventral sucker. Internal seminal vesicle elongate, tubular, undulating. Pars prostatica not distinctly differentiated. Internal male duct ensheathed by double layer of gland-cells. Ejaculatory duct short. Genital pore median, bifurcal or postbifurcal. Ovary post-testicular, acinous, multilobate. Seminal receptacle canalicular, may appear as dilatation of oviduct. Laurer's canal opens close to posterior extremity. Uterus fills most of hindbody. Vitellarium follicular, in lateral fields in region between mid-oesophagus and anterior hindbody. Excretory vesicle V-shaped; arms reach anteriorly beyond intestinal bifurcation; pore terminal. In freshwater, brackish-water and marine teleosts (? accidentally in rays); India, northern Indian Ocean and Pacific Ocean off Japan and China. Type-species *F. keksooni* (MacCallum, 1918) Poche, 1926.

**9a. Ventral sucker not greatly larger or smaller than oral sucker, of normal acetabulum-like structure ..... 10.**

**9b. Ventral sucker distinctly larger than oral sucker, usually strongly developed with muscular ridges, patterning or lobes, may be flat, not acetabulum-like ..... ..... *Paradiscogaster* Yamaguti, 1934. (Fig. 52.9)**

(Syns *Discogaster* Yamaguti, 1934 *nec* Burmeister, 1835; *Discogastroides* Strand, 1934; *Odontocotyle* Hafeezullah & Siddiqi, 1971; *Odontotrema* Hafeezullah & Siddiqi, 1970 *nec* Lindholm, 1927; *Pseudodiscogasteroides* Gupta, 1953; *Neobenthotrema* Wang, 1991)

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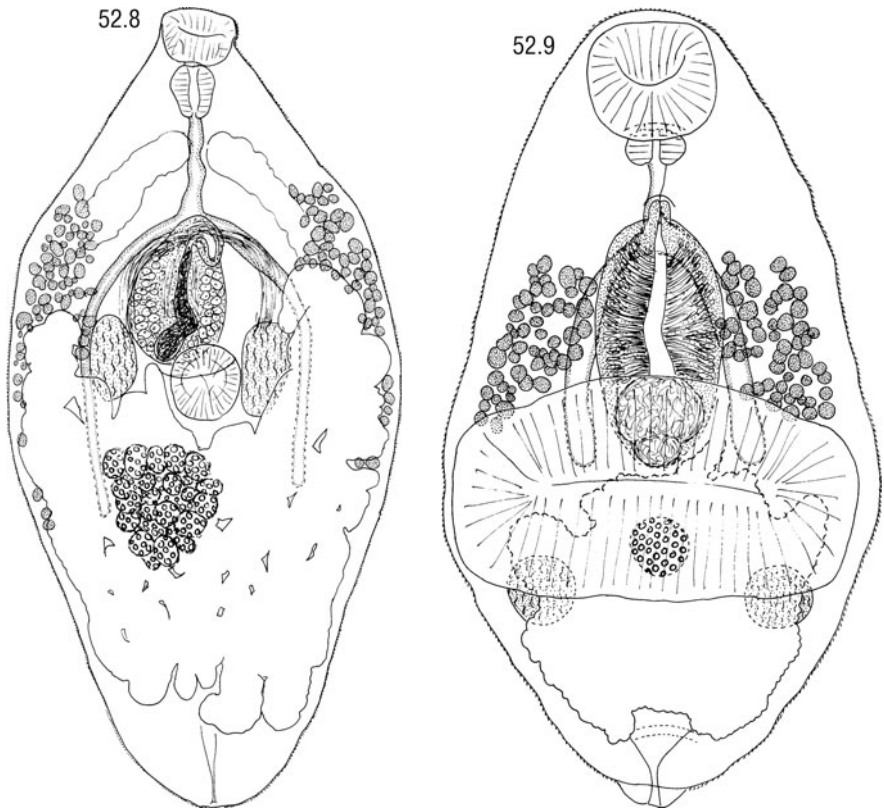



**Fig. 52.8.** *Faustula basiri* Hafeezullah & Siddiqi, 1970. Holotype (USNPC 63209). Original.
**Fig. 52.9.** *Paradiscogaster machidai* Cribb, Anderson & Bray, 1999. Paratype (BMNH 1998.8.5.30). Original.

**Diagnosis:** Body pyriform to oval, often plump. Tegument spinous; spines small. Dorsal tegumental ridges and glandular pits often present in hindbody. Oral sucker subglobular, subterminal. Ventral sucker large, equatorial to postequatorial, usually strongly developed with muscular ridges, patterning or lobes, may be flat, not acetabulum-like. Prepharynx short. Pharynx rounded, small. Oesophagus short to long. Intestinal bifurcation in mid- to posterior forebody. Caeca short, saccular, divergent, reach ventral sucker or not, do not reach into hindbody. Testes symmetrical or symmetrically oblique, in anterior hindbody or overlap ventral sucker. Cirrus-sac oval, overlaps ventral sucker. Internal seminal vesicle bipartite. Pars prostatica rectilinear, with narrow lumen, ensheathed in dense gland-cell mass. Ejaculatory duct short. Genital pore median, bifurcal to postbifurcal. Ovary rounded, pretesticular or intertesticular. Canalicular seminal receptacle present. Laurer's canal present. Uterus fills much of hindbody, including ventrally to gonads. Vitellarium follicular, forms two lateral fields of few follicles, in forebody or overlapping ventral sucker. Excretory vesicle Y-shaped, but stem often wide and arms very short or practically absent, resulting in claviform vesicle, confined to posterior hindbody; pore terminal or dorsoterminal. In marine teleosts; Indo-West Pacific region. Type-species *P. pyriformis* Yamaguti, 1934.

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**10a. Vitellarium two groups of distinct follicles; ovary pre- or intertesticular, oval to trilobed ..... 11.**

**10b. Vitelline follicles usually condensed into two compact groups (follicles occasionally separated); ovary post-testicular, trilobed ..... *Pronoprymna* Poche, 1926. (Fig. 52.10)**

(Syns *Pentagramma* Chulkova, 1939 *nec* Van Duzee, 1897; *Pseudopentagramma* Yamaguti, 1971)

**Diagnosis:** Body fusiform. Tegument unarmed. Oral sucker cup-shaped or subglobular, terminal or subterminal. Ventral sucker rounded, in anterior half of body. Prepharynx short. Pharynx globular to oval. Oesophagus distinct. Intestinal bifurcation in posterior forebody. Caeca reach just beyond testes. Testes oval to lobed, symmetrical to almost tandem, in anterior hindbody. Cirrus-sac elongate oval, thin-walled, overlaps ventral sucker. Internal seminal vesicle bipartite. Pars prostatica short, with few gland-cells. Ejaculatory duct short. Genital atrium deep, narrow. Genital pore median, bifurcal. Ovary trilobed, median, post-testicular. Canalicular seminal receptacle formed in proximal Laurer's canal. Laurer's canal opens fairly close to posterior extremity. Uterus extensive, mainly post-testicular. Vitellarium forms two symmetrical masses of tightly packed (occasionally separated) follicles, lateral or just posterior to ventral sucker; diagonal vitelline collecting duct prominent. Excretory vesicle V- or Y-shaped, with very short stem; arms reach oesophagus; pore terminal. In marine teleosts (mainly clupeiforms); northern hemisphere. Type-species *P. ventricosa* (Rudolphi, 1819) Poche, 1926.

**11a. Hindbody relatively short; testes close to posterior extremity; bulk or all of uterus pretesticular ..... *Echinobreviceca* Dronen, Blend & McEachran, 1994. (Fig. 52.11)**

**Diagnosis:** Body pyriform; hindbody relatively short. Tegument armed to posterior extremity. Oral sucker subglobular, subterminal. Ventral sucker large, rounded, in mid-body. Prepharynx short. Pharynx oval. Oesophagus short. Intestinal bifurcation in posterior forebody. Caeca short, saccular, divergent, overlap anterior margin of ventral sucker. Testes two, symmetrical, large, fill much of hindbody, not quite to posterior extremity, oval, entire. Cirrus-sac oval. Internal seminal vesicle bipartite. Pars prostatica straight, surrounded by numerous gland-cells. Ejaculatory duct short. Genital pore median, mid-way between suckers. Ovary oval, entire, anterior to left testis. Canalicular seminal receptacle present. Laurer's canal opens close to posterior extremity, close to or at distinct tegumental ridge. Uterus mainly pretesticular, may overlap testes. Metraterm not distinct. Vitellarium follicular, forms lateral fields of relatively few follicles at level of cirrus-sac, reaches pharynx. Excretory vesicle saccular, reaches testes, pore terminal. In deep-water marine teleosts (*Caelorinchus*); north-western Atlantic Ocean and Gulf of Mexico. Type-species *E. coelorhynchae* Dronen, Blend & McEachran, 1994.

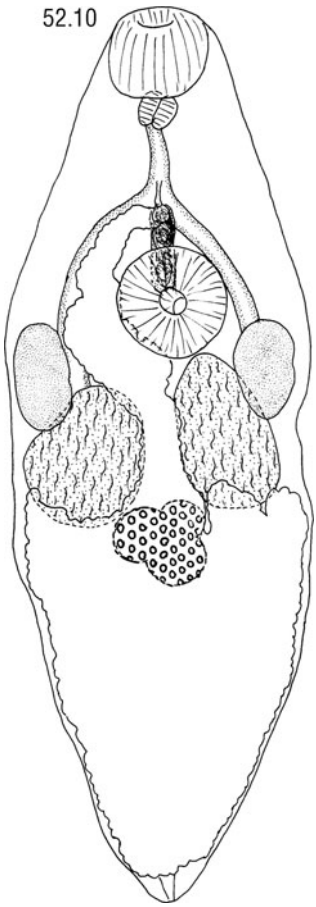
**11b. Hindbody relatively long; testes in anterior hindbody; bulk or all of uterus post-testicular ..... 12.**

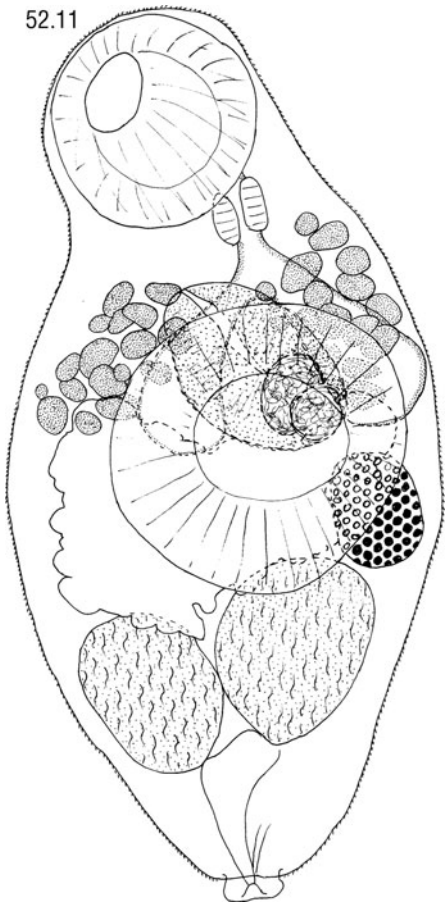
**12a. Genital pore immediately anterior to ventral sucker, median; seminal vesicle bipartite ..... *Bacciger* Nicoll, 1924. (Fig. 52.12)**

(Syn. ?*Ovotrema* Pigulewsky, 1938)

**Diagnosis:** Body oval. Tegument armed with small spines. Oral sucker subterminal to terminal, oval to infundibuliform. Ventral sucker in anterior to mid-body. Prepharynx short. Pharynx oval. Oesophagus distinct. Intestinal bifurcation in posterior forebody. Caeca short, divergent, reach ventral sucker or testes. Testes two, symmetrical, in anterior hindbody, may overlap ventral sucker. Cirrus-sac oval. Internal seminal vesicle bipartite. Pars prostatica short to long, with indistinct

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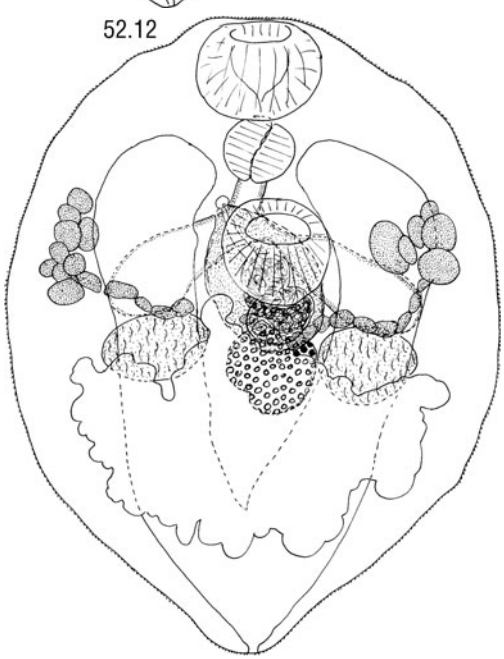




**Fig. 52.10.** *Pronoprymna ventricosa* (Rudolphi, 1919). Specimen from *Alosa alosa*, Celtic Sea (BMNH 1978.2.22.1–2). Original.
**Fig. 52.11.** *Echinobreviceca coelorhynchae* Dronen, Blend & McEachran, 1994. Composite drawing from paratypes (BMNH 1992.11.11. 1–3). Original.
**Fig. 52.12.** *Bacciger israelensis* Fischthal, 1980. Specimen from *Boops boops*, Varvara, Black Sea (BMNH 1992.8.21.1). Original.

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to distinct glandular sheath. Ejaculatory duct narrow, short. Genital pore median, in posterior forebody. Ovary oval to lobate. Canalicular seminal receptacle present. Laurer's canal opens near posterior extremity. Uterus fills bulk of post-testicular region. Vitellarium follicular, forms two lateral fields of few follicles, in forebody and overlapping ventral sucker. Excretory vesicle V- to Y-shaped; arms reach into forebody; pore terminal. In marine and freshwater teleosts; cosmopolitan. Type-species *B. bacciger* (Rudolphi, 1919) Nicoll, 1924.

**12b. Genital pore submedian, at level of anterior part of oesophagus or pharynx; seminal vesicle saccular ..... *Baccigeroides* Dutta, 1995. (Fig. 52.13)**
(Syn. *Baccigeroides* Manna & Datta, 1996)

**Diagnosis:** Body oval. Tegumental spines not reported. Oral sucker subterminal, subglobular. Ventral sucker rounded, small, in anterior half of body. Prepharynx short. Pharynx small, subglobular. Oesophagus long. Intestinal bifurcation in mid- to posterior forebody. Caeca short, divergent, reach to about testicular level. Testes symmetrical to subsymmetrical, in anterior hindbody. Cirrus-sac short, claviform, entirely in forebody. Internal seminal vesicle saccular. Pars prostatica narrow, with distinct gland-cells. Ejaculatory duct short, straight. Genital pore submedian, at level of anterior part of oesophagus or pharynx. Ovary in anterior hindbody between and overlapping anterior margin of testes, oval, entire. Canalicular seminal receptacle present. Laurer's canal? Uterus extensive posteriorly to gonads, may be extensive or not anteriorly to gonads. Metraterm undifferentiated. Vitellarium follicular, forms two lateral patches of few (six to eight) follicles lateral to ventral sucker and overlapping into fore- and hindbody. Excretory vesicle Y-shaped; arms reach oesophagus; pore terminal. In marine teleosts; Indian Ocean. Type-species *B. hafeezullai* Dutta, 1995.

## Genus *incertae sedis*

### *Pseudofellodistomum* Wang, 1989 (Fig. 52.14)

**Diagnosis:** Body elongate, fusiform. Tegument armed. Oral sucker subglobular, subterminal. Ventral sucker rounded in anterior half of body. Prepharynx short. Pharynx oval. Oesophagus distinct. Intestinal bifurcation in mid-forebody. Caeca reach about half-way along hindbody, between ovary and testes. Testes oval, entire, oblique, close to posterior extremity. Cirrus-sac oval, in forebody. Internal seminal vesicle saccular? Pars prostatica? Ejaculatory duct? Genital pore median, slightly postbifurcal. Ovary subglobular, said to be sinistral (dextral in figure), about mid-way between ventral sucker and testes. Seminal receptacle? Laurer's canal? Uterus extensive, pretesticular, intercaecal, encroaching between testes and ovary and between ovary and ventral sucker. Eggs numerous, small. Metraterm? Vitellarium follicular, forms two lateral fields of few (eight) large follicles between anterior edge of ventral sucker and just anterior to testes. Excretory vesicle and pore? In marine teleost (*Eleutheronema*); off China. Type-species *P. plagiorchis* Wang, 1989.

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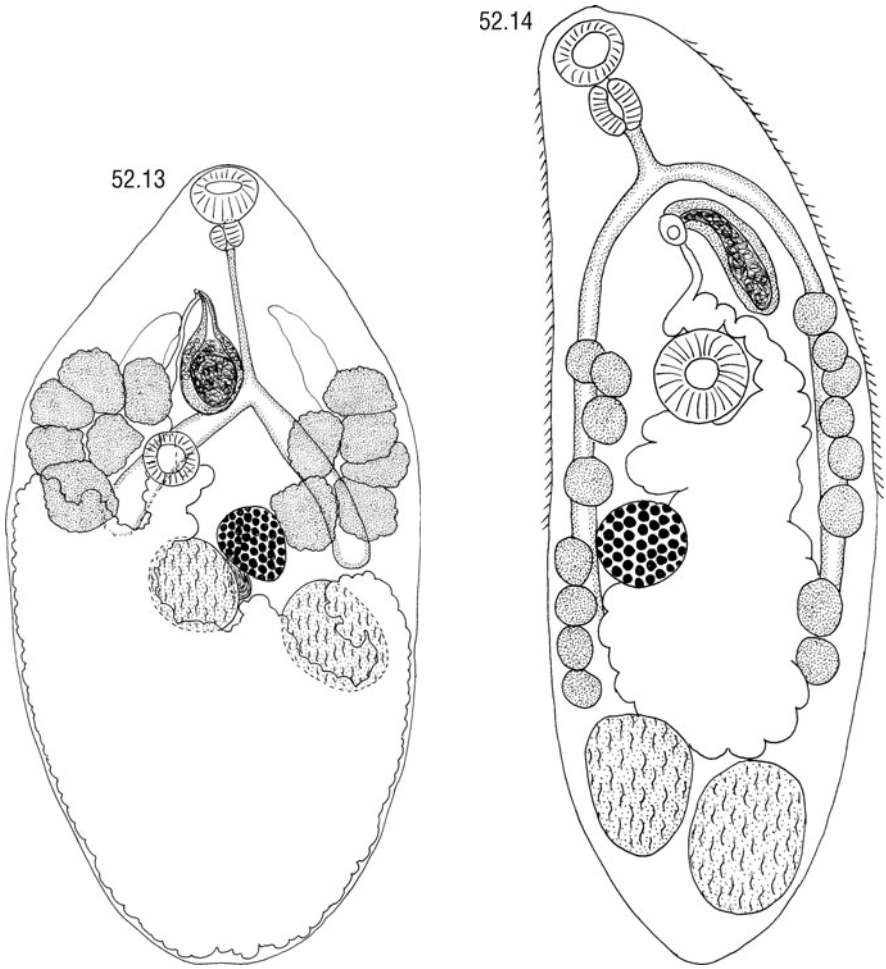



**Fig. 52.13.** *Baccigeroides cochinensis* (Hafeezullah & Siddiqi, 1970). Holotype (USNPC 63215). Original.
**Fig. 52.14.** *Pseudofellodistomum plagiorchis* Wang, 1989. After Wang (1989).

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# 53 Family Gyrabascidae Macy, 1935

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## Introduction

These parasites of bats and rodents (and experimentally in carnivores) are characterized by the lack of a pars prostatica, cirrus and cirrus-sac, with the seminal vesicle lying free in the parenchyma. Macy (1935) described *Gyrabascus brevigastrus* Macy, 1935 from the little brown bat *Myotis lucifugus* collected in Wisconsin, USA, and erected the subfamily Gyrabascinae Macy, 1935 for it. Olivier (1938) described *Allassogonoporus marginale* Olivier, 1938 from the muskrat *Ondatra zibethica* collected in Michigan, USA. Skarbilovich (1948) erected the subfamily Allassogonoporinae Skarbilovich, 1948 for it and Odening (1964c) raised it to family level. Based on an examination of the type-material of *G. brevigastrus*, Tkach *et al.* (2002) concluded that it was conspecific with *Allassogonoporus marginale*, and, therefore, *Gyrabascus* and the Gyrabascidae Macy, 1935, which is here raised to family status, have priority. Tkach *et al.* (2001b, 2002) suggested a close relationship between *Gyrabascus* and *Parabascus* Looss, 1907. If this is true, then the Gyrabascidae may ultimately prove to be synonymous with the Phaneropsolidae Mehra, 1935 (see Lotz & Font, Chapter 57, this volume).

## Family Gyrabascidae Macy, 1935

(Syn. Allassogonoporidae Skarbilovich, 1948)

**Diagnosis:** Body ovate to broadly oval. Tegument heavily spined. Oral sucker subterminal. Ventral sucker in anterior half of body, approximately equal in size to oral sucker. Prepharynx short. Pharynx present, small. Oesophagus elongate. Intestinal bifurcation immediately anterior to ventral sucker. Caeca terminate anterior to testes or extend into hindbody. Testes paired, symmetrical in middle of body, entire. Cirrus and cirrus-sac absent. Seminal vesicle elongate, free in parenchyma; pars prostatica absent. Genital atrium present, duct-like. Genital pore marginal; at level of ventral sucker, very slightly in hindbody or in forebody. Ovary anterior to or overlapping testes, submedian, near level of ventral sucker, entire or lobed. Seminal receptacle and Laurer's canal present. Uterus mostly posterior to ventral sucker. Metraterm poorly developed. Vitellarium

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follicular, caecal to precaecal, confluent across body or in paired groups of follicles. Excretory vesicle I-shaped; pore terminal. In intestine of mammals; North and South America, Europe, Asia. Type-genus *Gyrabascus* Macy, 1935.

## Key to genera

**1a. Vitellarium a single confluent mass in forebody; caeca extend to near posterior extremity; genital pore marginal in region of ventral sucker, not anterior to vitellarium ..... ..... *Gyrabascus* Macy, 1935. (Fig. 53.1)**

(Syns *Allassogonoporus* Olivier, 1938; *Myotitrema* Macy, 1940; *Moedlingeria* Yamaguti, 1958)

**Diagnosis:** Body broadly oval, nearly as wide as long. Oral sucker terminal to subterminal. Ventral sucker in anterior half of body, slightly larger than oral sucker. Prepharynx very short. Testes in middle third of body. Seminal vesicle lying transversely in region of ventral sucker. Genital pore on either left or right margin of body, in region of ventral sucker, not anterior to vitellarium. Ovary entire to lobed, extending anterior to testes. Uterus comprised of overlapping coils filling posterior half of body. Eggs small, numerous. Vitellarium a single confluent cluster forming extensive field in forebody. In bats and rodents; North America, Europe, Asia. Type-species *G. brevigastru*s Macy, 1935.

**1b. Vitelline fields in mid-body, not confluent; caeca terminate near mid-body; genital pore marginal at level of pharynx, anterior to ventral sucker and vitellarium ..... ..... *Cephalophallus* Macy & Moore, 1954. (Fig. 53.2)**

**Diagnosis:** Body small, oval to elongate, tapered at posterior end, longer than wide. Oral sucker subterminal, relatively large. Ventral sucker present, relatively large, in middle third of body. Caeca short, terminate at mid-body, not extending posterior to testes. Testes in region of ventral sucker. Seminal vesicle diagonal. Genital pore on left margin of body at level of pharynx anterior to ventral sucker and vitellarium. Ovary entire, submedial in ventral sucker region. Uterus not extensive, in posterior half of body. Eggs < 100. Vitellarium in two discrete non-confluent clusters at caecal ends in mid-body. In *Mustella vison* (exp.); Oregon, USA. Type-species *C. obscurus* Macy & Moore, 1954.

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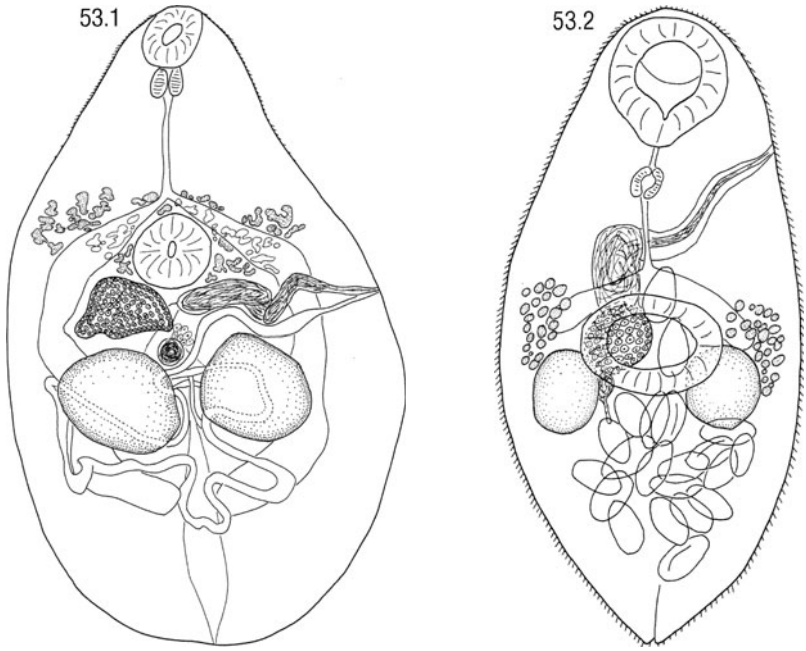



**Fig. 53.1.** *Gyrabascus brevigastrus* Macy, 1935. Paratype, forebody twisted laterally. Original.
**Fig. 53.2.** *Cephalophallus obscurus* Moore & Macy, 1954. After Macy & Moore (1954).

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# 54 Family Lecithodendriidae Lühe, 1901

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## Introduction

Lecithodendriids are parasites of bats, and occasionally birds, characterized by a median genital pore and the lack of a true cirrus-sac and cirrus. Lühe (1901) erected the subfamily Lecithodendrinae [*sic*] Lühe, 1901 and Odhner (1910) elevated it to family status, considering it to include 'brachycoelid' digeneans, i.e. those with short caeca. He divided the Lecithodendriidae Lühe, 1901 into two subfamilies, the Lecithodendriinae, for parasites of mammals with a median or submedian genital pore, comprising *Lecithodendrium* Looss, 1896, *Phaneropsolus*, Looss, 1899, *Pycnoporus* Looss, 1899, and the subfamily Pleurogeninae Looss, 1899, for parasites of amphibians with a lateral or sublateral genital pore, comprising *Pleurogenes* Looss, 1896 and *Prosotocus* Looss, 1899. He also included the genera *Anchitrema* Looss, 1899 and *Eumegacetes*, Looss, 1900. By 1935, a number of other genera had been added to the family and Mehra (1935) divided it into six subfamilies, the Eumegacetinae Travassos, 1922, Anchitreminae Mehra, 1935, Phaneropsolinae Mehra 1935 and Exotidendriinae Mehra, 1935, as well as the Lecithodendriinae and the Pleurogeninae. Mehra used the presence or absence of a cirrus-sac and cirrus, the length of the caeca and the position of the genital pore to distinguish them.

Skarbilovich (1948) characterized subfamilies by the position of the genital pore and recognized only four subfamilies, the Lecithodendriinae for species with the median genital pore anterior to the ventral sucker, the Gyrabascinae Macy, 1935 for those with the genital pore median but posterior to the ventral sucker, the Allassogonoporinae Skarbilovich, 1948 for those with a lateral genital pore posterior to the ventral sucker, and the Pleurogeninae for those with a lateral genital pore anterior to the ventral sucker.

Odening (1959b) recognized the importance of the presence or absence of the cirrus and cirrus-sac for distinguishing pleurogenids from lecithodendriids and elevated the Pleurogeninae to family rank. Later, Odening (1964c) elevated the Allassogonoporinae to family level based on the shape of the excretory vesicle, the lateral position of the genital pore and seminal vesicle and the absence of a cirrus-sac.

Khotenovskii (1970) accepted the Pleurogenidae Looss, 1899 and viewed the presence of the cirrus-sac as important. He divided it into two subfamilies, the Pleurogeninae for amphibian

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parasites possessing a well-developed cirrus and cirrus-sac with the genital pore opening laterally or sublaterally and the Parabascinae Yamaguti, 1958 (= Phaneropsolidae Mehra, 1935) for mammalian parasites possessing a cirrus and cirrus-sac with the genital pore opening medially or submedially.

In our view, the presence or absence of the cirrus and cirrus-sac, the position of the genital pore and the host group are important for determining the familial groupings of 'lecithodendriid-like' species. We are of the opinion that the virgula organ is an important characteristic that identifies 'lecithodendriid-like' species as a natural group, the 'virgulate digeneans'. The virgula organ occurs as a pair of structures in the oral sucker of the cercaria (Kruidener, 1951). They are reservoirs containing mucoid secretions from gland-cells in the body. In fact, they are residual ducts of the mucoid body gland-cells and the ducts remain after the gland-cell bodies degenerate. The ducts are markedly enlarged and appear as paired comma-shaped reservoirs, hence the name virgula. The virgula organs open to the exterior and, during penetration of the second intermediate host, release material that forms a pseudocyst around the cercarial body to attach it to the host as penetration occurs (Kruidener, 1951; Burns, 1961). By the term 'lecithodendriid-like', we mean to imply the 'virgulate digeneans', that is the five families Pleurogenidae Looss, 1899, Lecithodendriidae Lühe, 1901, Gyrabascidae Macy 1935, Phaneropsolidae Mehra, 1935 and Leyogonimidae Dollfus, 1951. All have members for which at least one cercarial stage has been described. All have been found to have a virgulate xiphidocercaria. Only *Ganeo* Klein, 1905, traditionally included in the Pleurogenidae, is known to have a non-virgulate xiphidocercaria (Bhutta & Khan, 1974). In addition, it parasitizes a pulmonate snail as a first intermediate host. For those reasons, it should be removed from the Pleurogenidae or any of the other 'lecithodendriid-like' groups (Bhutta & Khan, 1974). On the other hand, the family Eumegacetidae Travassos, 1922 has two members for which the life-cycles are known, *Eumegacetes artamii* Mehra, 1935 and *Orthetrotrema monostomum* Macy & Basch, 1972. In both cases the cercaria is a non-virgulate xiphidiocercaria; however, the cercariae share many characters with members of the microphallid 'ubiquita group' and the prosthogonimid 'microcotyla group' (Kumari & Madhavi, 1994; Madhavi & Kumari, 1995). The combination of a xiphidocercaria, a caenogastropod snail first intermediate host and an arthropod second intermediate host supports the view that the virgulate digeneans are related to the microphallids, prosthogonimids and eumegacetids. Additional families conventionally allied with the virgulate digeneans for which no cercarial stage is known include the Stomylotrematidae Poche, 1926, the Exotidendriidae Mehra, 1935 and the Anenterotrematidae Yamaguti, 1958.

According to phylogenetic analyses, the Microphalloidea is a clade and comprises the virgulate digeneans along with the microphallids and the prosthogonimids (Brooks *et al.*, 1985, 1989; Tkach *et al.*, 2000a, 2001b, 2002, 2003; Olson *et al.*, 2003). Brooks *et al.* (1985, 1989) considered that the virgulate digeneans are a monophyletic group, the Lecithodendriidae (*sensu lato*). If so, the virgula organ is a synapomorphy for the 'lecithodendriid-like' groups. However, molecular phylogenetic analyses indicate that the virgulate digeneans are a paraphyletic group and that the microphallids and the prosthogonimids have secondarily and independently lost the virgula. However, a much larger set of morphological, life-history and molecular characters from more species will be needed before either of the two hypotheses can be confidently supported (Zamparo *et al.*, 2003a).

The term 'hermaphroditic organ' refers to the protrusible, bulbous structure formed around the hermaphroditic duct in *Caprimulgorchis* Jha 1943. 'Pseudogonotyl' refers to the thickened cuticle, bulbous when everted, pouch-like when inverted, which can sometimes be detected in *Ochoterenatrema* Caballero y C., 1943.

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## Family Lecithodendriidae Luhe, 1901

**Diagnosis:** Cercaria virgulate. Body small, ovoid. Tegument typically with spines. Oral sucker round, usually subterminal. Ventral sucker round, median, in anterior half of body. Prepharynx short, may be absent. Pharynx small. Oesophagus short. Intestinal bifurcation in forebody. Caeca two, short, end in anterior half of body. Testes two, symmetrical, entire or rarely lobed, in mid-body. Seminal vesicle in thin-walled pseudocirrus-sac or free in parenchyma. Pars prostatica well developed or absent. Cirrus-sac absent; pseudocirrus-sac present. Cirrus absent, but occasionally eversible hermaphroditic duct is present, which resembles cirrus. Genital pore median, in fore- or hindbody. Ovary submedian in mid-body. Canalicular seminal receptacle present. Laurer's canal opens dorsally. Uterus fills posterior half of body. Eggs operculate, small, numerous. Vitellarium follicular, in anterior or mid-body. Excretory vesicle V- to Y-shaped; pore terminal or subterminal. In intestine of bats, occasionally birds; cosmopolitan. Type-genus *Lecithodendrium* Looss, 1896.

### Key to genera

**1a. Ventral sucker modified into circular depression bounded anteriorly and posteriorly by muscular ridges that extend on each side as sucker-like pouches ..... ..... *Vesperugidendrium* Pande, 1937. (Fig. 54.1)**

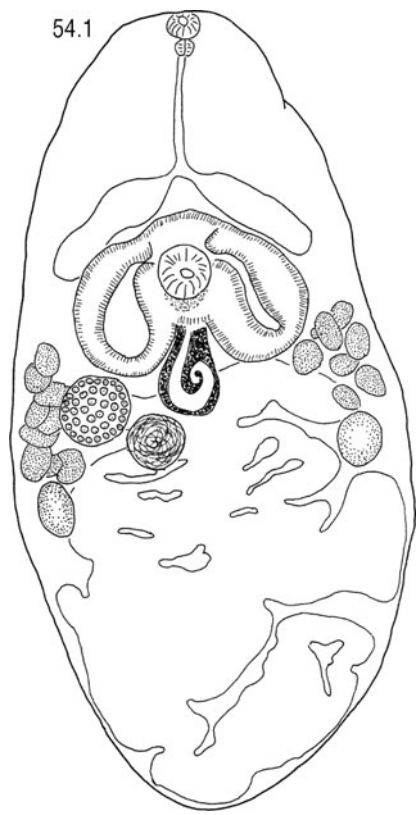



**Fig. 54.1.** *Vesperugidendrium pandei* Gupta & Mehrotra, 1970. After Gupta & Mehrotra (1970).

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**Diagnosis:** Body small, elongate-oval. Tegument aspinose. Oral sucker very small, subterminal. Ventral sucker pre-equatorial, modified as circular depression bounded anteriorly and posteriorly by muscular ridges, provided with one sucker-like pouch on each side. Prepharynx very short. Oesophagus long. Caeca widely divergent, short, end at level of ventral sucker. Testes entire, postequatorial. Pseudocirrus-sac present, thin-walled, elongate, median, between two lateral ventral sucker pouches, contains seminal vesicle and pars prostatica. Male and female pores empty into genital atrium. Genital pore median, opens in centre of ventral sucker depression. Ovary posterior to ventral sucker complex, entire, extends anteriorly to testes. Seminal receptacle prominent. Uterus fills posterior half of body. Eggs small, numerous. Vitellarium follicular, in two clusters largely anterior to testes and posterior to ventral sucker complex. Excretory vesicle V-shaped. In bats; India. Type-species *V. indicum* Pande, 1937.

**1b. Ventral sucker not modified ..... 2.**

**2a. Seminal vesicle free in parenchyma ..... 3.**
**2b. Seminal vesicle enclosed in thin-walled pseudocirrus-sac ..... 4.**

**3a. Prominent pars prostatica present; genital pore in forebody .....**
**..... *Castroia* Travassos, 1928. (Fig. 54.2)**

**Diagnosis:** Body reniform, wider than long. Tegument aspinose. Oral sucker small, terminal. Ventral sucker in anterior half of body, contained in acetabulo-genital sac. Prepharynx very short. Oesophagus elongate. Caeca widely divergent, nearly transverse, extend to and occasionally overlap testes. Testes entire, just posterior to caecal ends. Seminal vesicle free in parenchyma, coiled adjacent to ventral sucker. Pars prostatica present, well developed. Genital atrium small. Genital pore median or submedian, anterior to ventral sucker. Ovary lobed, extends anterior to testes. Uterus comprises overlapping transverse coils filling posterior half of body. Metraterm present. Eggs small, numerous. Vitellarium follicular in two clusters anterior to or overlapping caecal ends. Excretory vesicle V- to Y-shaped; pore subterminal. In bats; South America, Asia. Type-species *C. silvai* Travassos, 1928.

**3b. Pars prostatica absent; genital pore in hindbody ..... *Ophiosacculus* Macy, 1935. (Fig. 54.3)**
(Syn. *Retortosacculus* Yamaguti, 1958)

**Diagnosis:** Body small, elliptical. Tegument spinous. Oral sucker subterminal. Ventral sucker smaller than oral sucker, equatorial or pre-equatorial. Prepharynx absent. Oesophagus present, short. Caeca short, extend to anterior margin of testes. Testes entire, just posterior to caecal ends, in ventral sucker zone. Seminal vesicle free in parenchyma, long; proximal part bulky, extends into hindbody; distal part slender, extends into forebody. Genital pore median or submedian, in hindbody. Ovary entire, anterior to ventral sucker or rarely lateral. Uterus occupies most of post-testicular region. Eggs small, numerous. Vitellarium in two lateral clusters of follicles in anterior of body, at level of pharynx and caeca, usually overlap caeca and reach anterior margins of testes. Excretory vesicle V- shaped. In bats; Eurasia. Type-species *O. mehelyi* (Modlinger, 1930) Macy, 1935.

**4a. Acetabulo-genital sac encloses ventral sucker and genital pores .....**
**..... *Gymnoacetabulum* Lunaschi & Drago, 2007. (Fig. 54.4)**
(Syn. *Suttonia* Lunaschi, 2001 *nec* Smith, 1953)

**Diagnosis:** Body small, nearly circular, flattened. Tegument spinous. Oral sucker subterminal. Ventral sucker equatorial, weakly developed, contained in small sac that connects to acetabulo-genital sac

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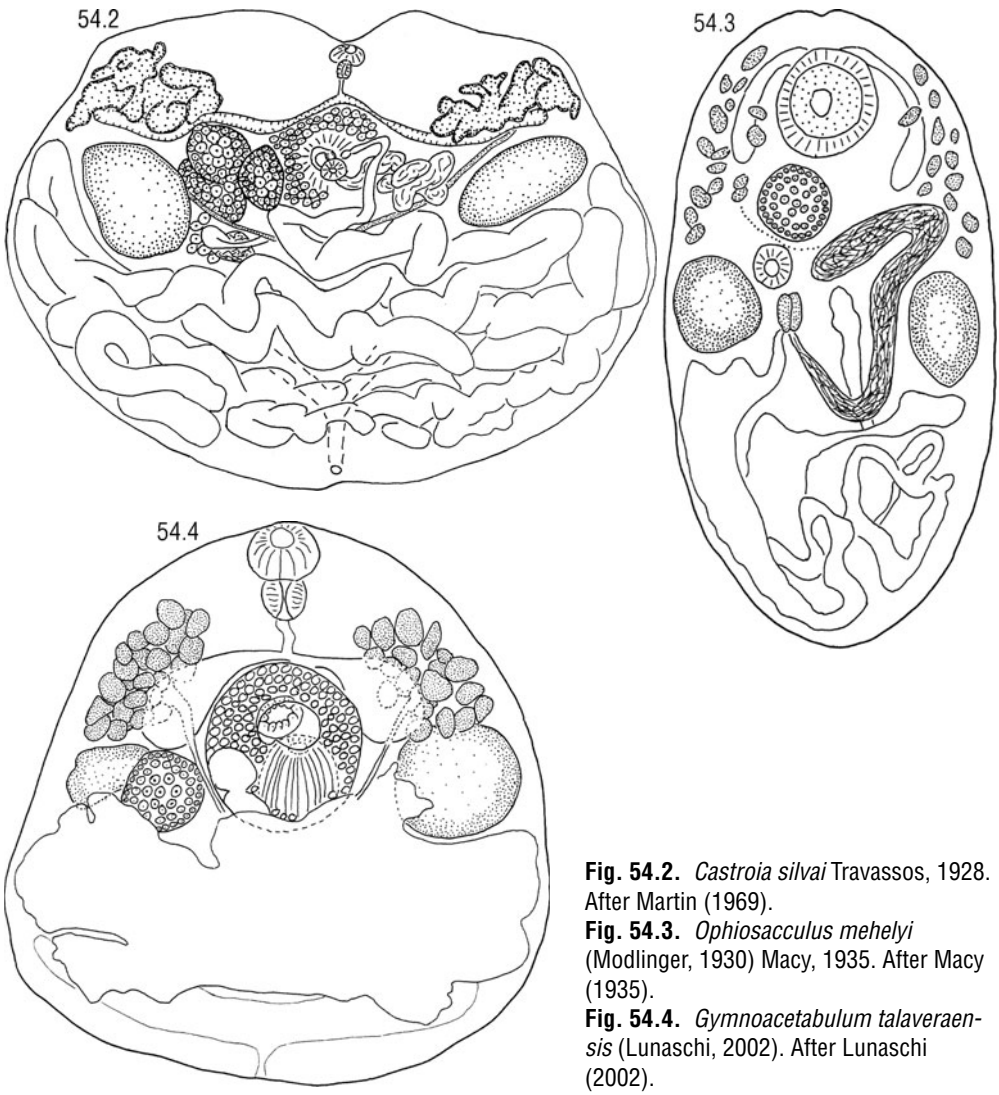



**Fig. 54.2.** *Castroia silvai* Travassos, 1928. After Martin (1969).
**Fig. 54.3.** *Ophiosacculus mehelyi* (Modlinger, 1930) Macy, 1935. After Macy (1935).
**Fig. 54.4.** *Gymnoacetabulum talaveraensis* (Lunaschi, 2002). After Lunaschi (2002).

through opening near posterior margin of acetabulo-genital sac. Acetabulo-genital sac contains ventral sucker and genital pore. Prepharynx absent. Oesophagus short. Caeca short, reach anterior margin of testes. Testes equatorial, lateral to ventral sucker, postcaecal. Pseudocirrus-sac well developed, median, intercaecal and dorsal to ventral sucker, contains compact mass of prostatic cells surrounding seminal vesicle. Pars prostatica well developed. Ejaculatory duct short, connects to male genital pore on right side of acetabulo-genital sac. Genital pores open separately into acetabulo-genital sac, submedian and anterior to ventral sucker, with female pore sinistral. Ovary median or submedian and intertesticular. Mehlis' gland and Laurer's canal present. Uterus fills hindbody. Eggs small. Vitellarium follicular; follicles in clusters in precaecal to caecal region. Excretory vesicle V-shaped; pore terminal. In bats; Argentina. Type-species *G. talaveraensis* (Lunaschi, 2001) Lunaschi & Drago, 2007.

**4b. Acetabulo-genital sac absent ..... 5.**

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**5a. Genital atrium enlarged ..... 6.**
**5b. Genital atrium not enlarged, forming hermaphroditic duct ..... 7.**

**6a. Expanded genital atrium lined with distinct spines .....**
**..... *Acanthatrium* Faust, 1919. (Fig. 54.5)**
(Syn. *Mesothatrium* Skarbilovich, 1948)

**Diagnosis:** Body small, ovoid. Tegument typically spinous. Oral sucker subterminal. Ventral sucker typically smaller than oral sucker, equatorial or pre-equatorial. Prepharynx short or absent. Oesophagus short to elongate. Caeca short, extend to anterior margin of testes. Testes entire, just posterior to caecal ends, in forebody or at level of ventral sucker. Pseudocirrus-sac present, thin-walled, spherical to oval, median, largely between intestinal bifurcation and ventral sucker, contains seminal vesicle and pars prostatica. Genital atrium present, enlarged, with distinct spines. Genital pore median, in forebody. Ovary entire to lobed, in forebody or at level of ventral sucker. Uterus occupies most of post-testicular region. Eggs small, numerous. Vitellarium follicular, typically in two lateral clusters of follicles, precaecal, caecal or postcaecal. Excretory vesicle V-shaped; pore terminal. In bats; cosmopolitan. Type-species *A. nycteridis* Faust, 1919.

**6b. Expanded genital atrium lacks spines, contains one or more prominent papillae .....**
**..... *Papillatrium* Richard, 1966. (Fig. 54.6)**

**Diagnosis:** Body small, oval, round or pyriform. Tegument apparently unspined. Oral sucker subterminal. Ventral sucker typically smaller than oral sucker, equatorial or pre-equatorial. Prepharynx short or absent. Oesophagus short. Caeca short, extend to anterior margin of testes. Testes entire, just posterior to caecal ends, in ventral sucker zone. Pseudocirrus-sac present, thin-walled, spherical to oval, median, largely between intestinal bifurcation and ventral sucker, contains seminal vesicle and pars prostatica. Genital atrium enlarged, unarmed, contains one or more distinct papillae. Genital pore in forebody. Ovary entire, in ventral sucker zone. Uterus forms overlapping coils filling posterior half of body. Eggs numerous, small. Vitellarium follicular; follicles may be numerous and small or fewer and larger, precaecal or postcaecal. Excretory vesicle V-shaped; pore terminal. In bats; Africa and Asia. Type-species *P. inversum* Richard, 1966.

**7a. Oral sucker with lateral papillae; hermaphroditic duct eversible, bearing numerous spines**
**..... *Glyptoporus* Macy 1936. (Fig. 54.7)**
(Syn. *Ototrema* Font, 1978)

**Diagnosis:** Body small, oval, round or pyriform. Tegument apparently unspined. Oral sucker subterminal. Ventral sucker typically smaller than oral sucker, equatorial or pre-equatorial. Prepharynx short or absent. Oesophagus short. Caeca short, extend to anterior margin of testes. Testes entire, just posterior to caecal ends, in ventral sucker zone. Pseudocirrus-sac thin-walled, median, extends from ventral sucker into forebody, elongate, curved, not spherical or oval, contains seminal vesicle and pars prostatica. Genital atrium forms armed, eversible hermaphroditic duct, easily mistaken for cirrus. Genital pore anterior to ventral sucker. Ovary entire, in ventral sucker zone. Uterus forms overlapping coils filling posterior half of body. Eggs numerous, small. Vitellarium follicular, in two lateral groups, precaecal to caecal. Excretory vesicle V-shaped; pore terminal. In bats; North America. Type-species *G. noctophilus* Macy, 1936.

**7b. Oral sucker without lateral papillae; hermaphroditic duct not eversible, unarmed ..... 8.**

**8a. Genital atrium surrounded by distinct hermaphroditic organ .....**
**..... *Caprimulgorchis* Jha 1943. (Fig. 54.8)**
(Syn *Fontius* Lotz & Palmieri, 1985)

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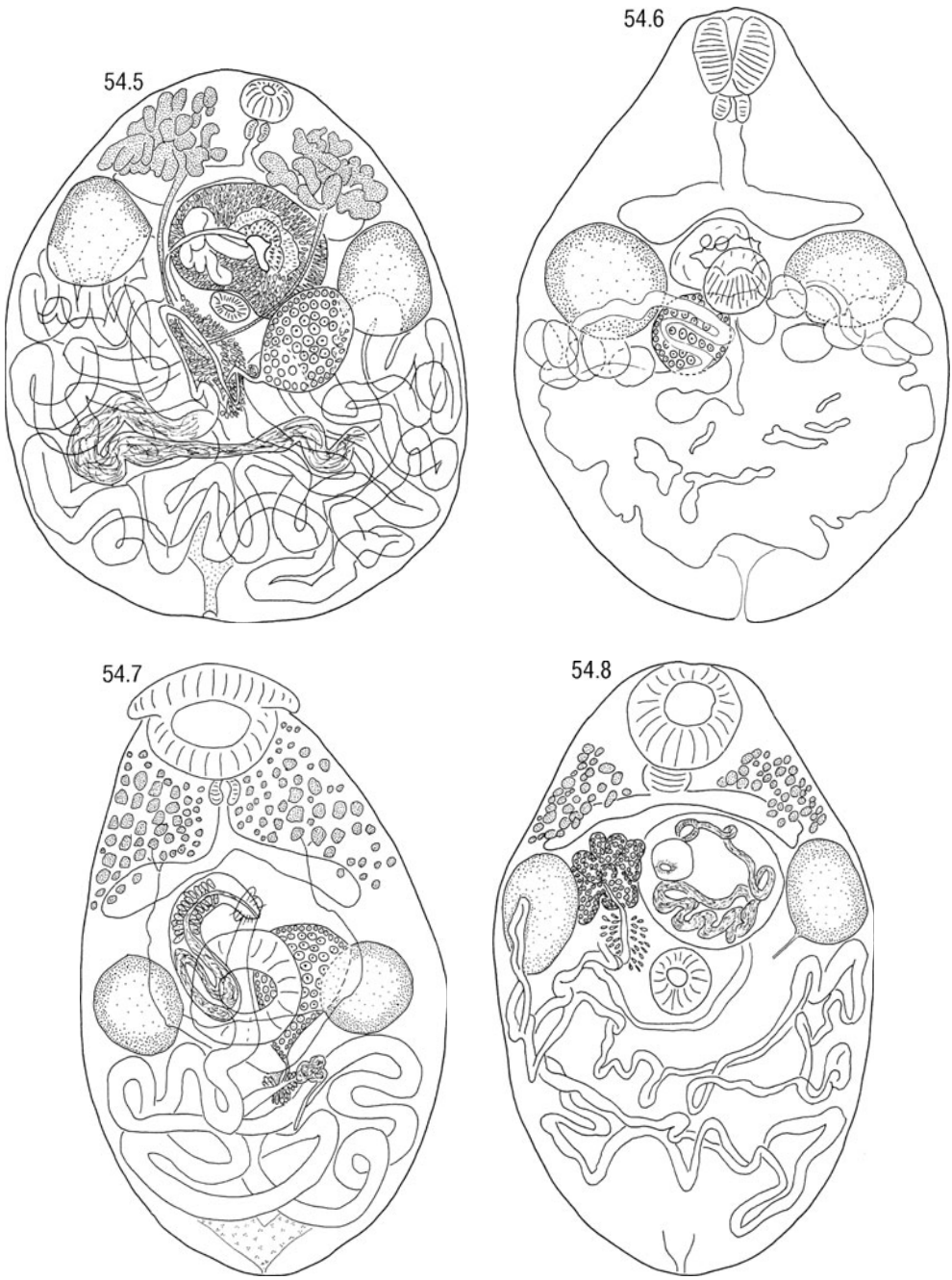



**Fig. 54.5.** *Acanthatrium nycteridis* Faust, 1919. After Yamaguti (1971).
**Fig. 54.6.** *Papillatrium inversum* Richard, 1966. After Yamaguti (1971).
**Fig. 54.7.** *Glyptoporus noctophilus* Macy, 1936. Modified after Font (1978).
**Fig. 54.8.** *Caprimulgorchis karchanii* Jha, 1943. After Yamaguti (1971).

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**Diagnosis:** Body small, oval to pyriform. Tegument spinous. Oral sucker subterminal. Ventral sucker equatorial or pre-equatorial. Prepharynx short or absent. Oesophagus short. Caeca short, extend to anterior margin of testes. Testes entire, just posterior to caecal ends, in forebody or ventral sucker zone. Pseudocirrus-sac thin-walled, spherical to oval, median, largely between intestinal bifurcation and ventral sucker, contains seminal vesicle and pars prostatica. Genital atrium forms hermaphroditic duct surrounded by protrusible, bulbous hermaphroditic organ. Genital pore in forebody. Ovary entire or lobed in forebody or ventral sucker zone. Uterus forms overlapping coils filling posterior half of body. Eggs numerous, small. Vitellarium follicular, in two lateral groups, precaecal to caecal. Excretory vesicle V-shaped; pore terminal. In bats, occasionally birds; Asia. Type-species *C. karchanii* Jha, 1943.

**8b. Hermaphroditic organ absent ..... 9.**

**9a. Pseudogonotyl present, lateral to ventral sucker ..... ..... *Ochoterenatrema* Caballero y C., 1943. (Fig. 54.9)**

**Diagnosis:** Body small, ovoid to pyriform. Tegument apparently without spines. Oral sucker subterminal. Ventral sucker equal to or smaller than oral sucker, equatorial to pre-equatorial, at level of testes. Prepharynx short or absent. Oesophagus short to elongate. Caeca short, divergent, extend to anterior margin of testes. Pseudogonotyl at left of ventral sucker, consists of thickened cuticle, bulbous when everted, pouch-like when inverted, may be conspicuous or not easily seen. Testes entire, just posterior to caecal ends, at level of ventral sucker. Pseudocirrus-sac present, thin-walled, spherical to oval, median, largely between intestinal bifurcation and ventral sucker, contains seminal vesicle and pars prostatica. Genital atrium forms hermaphroditic duct. Genital pore median, in forebody. Ovary entire to lobed, submedian, in forebody to ventral sucker region. Uterus occupies most of post-testicular region. Eggs small, numerous. Vitellarium follicular, typically in two lateral clusters of follicles, precaecal, caecal or postcaecal. Excretory vesicle V-shaped; pore terminal. In bats; western hemisphere. Type-species *O. labda* Caballero y C., 1943.

**9b. Pseudogonotyl absent ..... 10.**

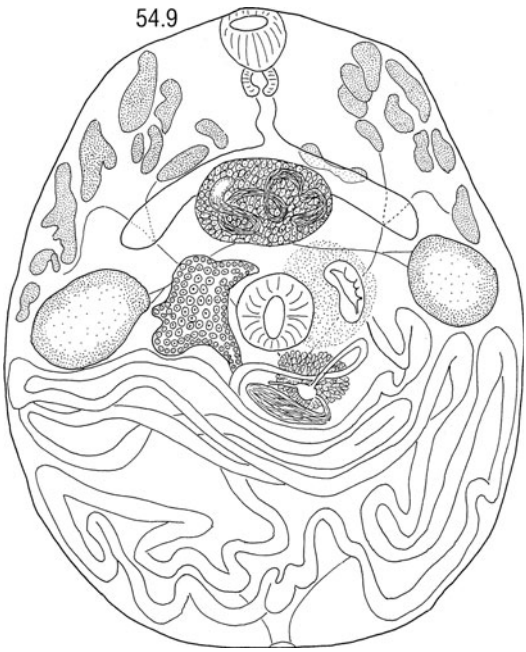
**10a. Vitellarium largely post-testicular, occasionally overlaps posterior margin of testes ..... ..... *Lecithodendrium* Looss, 1896. (Fig. 54.10)**

(Syns *Mesodendrium* Faust, 1919; *Glirotrema* Kirshenblat, 1941; *Mesodendroides* Skarbilovich, 1948)

**Diagnosis:** Body small, ovoid, pyriform or elongate. Tegument apparently without spines or spinous. Oral sucker subterminal. Ventral sucker equatorial to pre-equatorial. Prepharynx short or absent. Oesophagus short to elongate. Caeca short, divergent. Testes entire, posterior to caeca, typically at level of ventral sucker. Pseudocirrus-sac present, thin-walled, spherical to oval, median, largely between intestinal bifurcation and ventral sucker, contains seminal vesicle and pars prostatica. Genital atrium forms hermaphroditic duct. Genital pore median, in forebody. Ovary entire to irregular, oval to pyriform, submedian, anterior or posterior to or at level of ventral sucker, typically post-testicular or posterior to middle of testicular region. Uterus occupies most of post-testicular region. Eggs small, numerous. Vitellarium follicular, typically in two lateral clusters of follicles, wholly or rarely largely posterior to testes. Excretory vesicle V-shaped; pore terminal. In bats; cosmopolitan. Type-species *L. linstowi* Dollfus, 1931.[1]

[1] No type-species was originally designated. For an explanation of why this species is now recognized as the type-species see Dollfus (1931, 1937) and Sogandares-Bernal (1956).

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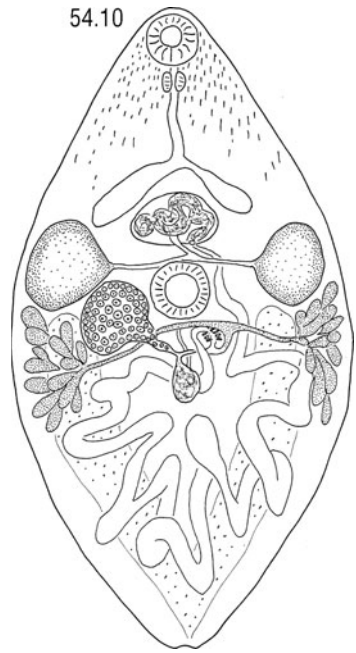




**Fig. 54.9.** *Ochoterenatrema labda* Caballero y C.,1943. After Caballero y C. (1943).
**Fig. 54.10.** *Lecithodendrium linstowi* Dollfus, 1931. After Yamaguti (1971).

**10b. Vitellarium testicular or pretesticular ..... 11.**

**11a. Testes in hindbody, some distance from caecal ends .....**
**..... *Pycnoporus* Looss, 1899. (Fig. 54.11)**
(Syn. *Lecithoporus* Mehra, 1935)

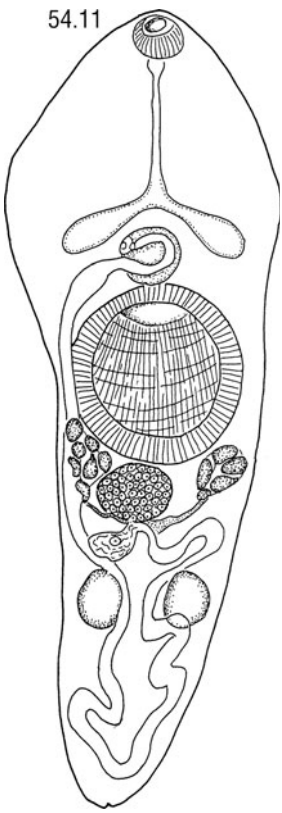
**Diagnosis:** Body small ovoid, pyriform or elongate. Tegument spinous or apparently without spines. Oral sucker subterminal. Ventral sucker equatorial to pre-equatorial. Prepharynx short or absent. Oesophagus short to elongate. Caeca short, divergent. Testes entire, posterior to ventral sucker, some distance from caecal ends. Pseudocirrus-sac present, thin-walled, spherical to oval, median, largely between intestinal bifurcation and ventral sucker, contains seminal vesicle and pars prostatica. Genital atrium forms hermaphroditic duct. Genital pore median, in forebody. Ovary entire to irregular, oval to pyriform, submedian, anterior or posterior to or at level of ventral sucker. Uterus occupies most of hindbody. Eggs small, numerous. Vitellarium follicular, typically in two lateral clusters of follicles, wholly or rarely largely anterior to testes, posterior to caeca. Excretory vesicle V-shaped; pore terminal. In bats; cosmopolitan. Type-species *P. heteroporus* (Dujardin, 1845) Looss, 1899.

**11b. Testes in ventral sucker zone close to caecal ends .....**
**..... *Paralecithodendrium* Travassos, 1921. (Fig. 54.12)**
(Syns *Prosthodendrium* Dollfus, 1931; *Travassodendrium* Skarbilovich, 1943; *Chiroptodendrium* Skarbilovich, 1943; *Skrjabinodendrium* Skarbilovich, 1943; *Longitrema* Chen, 1954)

**Diagnosis:** Body small, ovoid, pyriform or elongate. Tegument spinous. Oral sucker subterminal. Ventral sucker pre-equatorial to postequatorial. Prepharynx short or absent. Oesophagus short to

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elongate. Caeca short, divergent, typically extend to testes. Testes entire, in ventral sucker zone close to caecal ends. Pseudocirrus-sac present, thin-walled, spherical to oval, median, largely between intestinal bifurcation and ventral sucker, contains seminal vesicle and pars prostatica. Genital atrium forms hermaphroditic duct. Genital pore median, in forebody. Ovary entire to lobed, oval to pyriform, submedian, typically in testicular and ventral sucker zones. Uterus occupies most of post-testicular region. Eggs small, numerous. Vitellarium follicular, typically in two lateral clusters of follicles, anterior to testes, overlaps caeca or anterior to caeca. Excretory vesicle V-shaped; pore terminal. In bats; cosmopolitan. Type-species *P. anticum* (Stafford, 1905) Travassos, 1921.



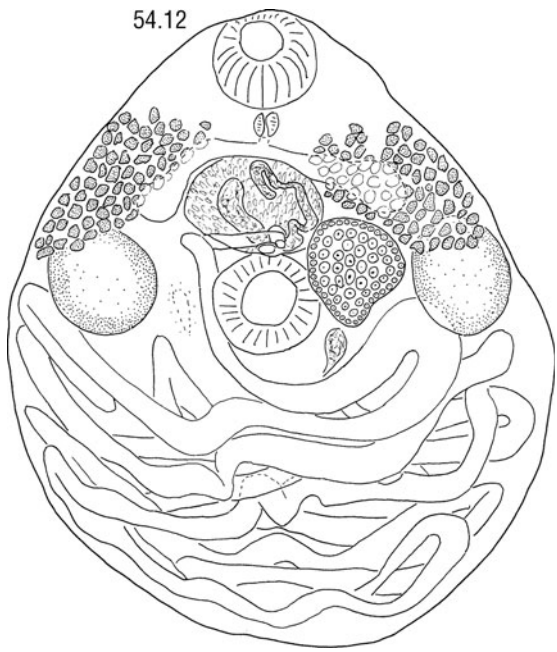




**Fig. 54.11.** *Pycnoporus heteroporus* (Dujardin, 1845) Looss, 1899. After Yamaguti (1971).
**Fig. 54.12.** *Paralecithodendrium swansoni* Macy, 1936. After Byrd & Macy (1942).

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# 55 Family Leyogonimidae Dollfus, 1951

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## Introduction

Members of the family Leyogonimidae Dollfus, 1951 are parasites of the intestine, mesenteries or hepatic system of birds and mammals, where they may be histolytic or encysted. They are characterized by the posterior position of the genital pore, which is in the hindbody and sometimes quite close to the posterior extremity. The pretesticular ovary is in the forebody and is distinctly lobate. Dollfus (1951) erected the subfamily Leyogoniminae Dollfus, 1951 for *Leyogonimus* Ginetsinskaya, 1948. Subsequently, the Leyogoniminae has been treated as a subfamily of either the Stomylotrematidae Poche, 1925, e.g. Skrjabin (1947a) and Khotenovskii (1971), or the Lecithodendriidae Lühe, 1901, e.g. Vaucher (1968) and Yamaguti (1971), and either position can be justified. It also shares characteristics with the Prosthogonimidae Lühe, 1909. The recent discovery that *L. polyoon* (Braun, 1902) has a virgulate cercaria (R. Cole, S. Taft and T.C. Huspeni, personal communication) suggests a closer relationship with the Phaneropsolidae Mehra, 1935 than with the Prosthogonimidae or Stomylotrematidae. Until further phylogenetic analyses clarify the relationships among the Stomylotrematidae, Leyogoniminae, Phaneropsolidae and Prosthogonimidae, we prefer to elevate the subfamily Leyogoniminae to family rank. In addition to *Leyogonimus*, we include the genera *Posterocirrus* Andreiko & Khotenovskii, 1964 and *Metoliophilus* Macy & Bell, 1968.

Odening (1964b) added *Laterotrema* Semenov, 1928 to the Leyogoniminae and erected the subgenus *Lecithodollfusia* Dollfus, 1964 for the species *Laterotrema arenula*. Khotenovskii (1971) raised *Lecithodollfusia* to full generic level but transferred it to the Pleurogenidae Looss, 1899. We agree with his removal of *Lecithodollfusia* from the Leyogoniminae, but prefer to place this genus in the family Phaneropsolidae (see Lotz & Font, Chapter 57, this volume). Following most workers, we keep *Laterotrema* in the Stomylotrematidae (see Lotz & Font, Chapter 62, this volume).

*Cortrema* Tang, 1951 has been placed variously in the Troglotrematidae Odhner, 1914, the Leyogonimidae or the Cortrematidae Yamaguti, 1959. Tang & Tang (1981) reported that the life-cycle of *C. corti* Tang, 1951 included a pulmonate snail as first intermediate host and a non-virgulate xiphidiocercaria. This suggests that *Cortrema* does not belong among the lecithodendriids and it is treated in this volume in its own family within the Gorgoderoidea Looss, 1899 (Blair & Barton, Chapter 15, this volume).

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Andreiko & Khotenovskii (1964) established *Posterocirrus* Andreiko & Khotenovskii, 1964 for *P. clethrionomi* Andreiko & Khotenovskii, 1964 from a bank vole and placed it in the Lecithodendriidae. Vaucher (1968) erected *Paraleyogonimus* Vaucher, 1968 for *P. baeri* Vaucher, 1968, also from a bank vole, without citing Andreiko & Khotenovskii (1964) and, therefore, failed to differentiate *Paraleyogonimus* and *Posterocirrus*. It is very likely that *Paraleyogonimus baeri* is a junior synonym of *Posterocirrus clethrionomi* and certainly *Paraleyogonimus* is a junior synonym of *Posterocirrus*.

Filimonova (1973) erected *Lobogonimus* Filimonova, 1973 for *L. skrjabini* Filimonova, 1973 from a grebe and placed it in the Leyogoniminae. She cited neither Andreiko & Khotenovskii (1964) nor Vaucher (1968) in her paper. *L. skrjabini* can be distinguished from *Posterocirrus clethrionomi* by the absence of a metraterm in *L. skrjabini*. Although this difference may distinguish species, in our opinion it does not distinguish genera.

Macy & Bell (1968) differentiated *Metoliophilus* Macy & Bell, 1968 from members of the Leyogoniminae by the lack of a genital atrium and the median genital pores. In our opinion, this genus shares enough characters with other leyogonimids to warrant inclusion in this family. These characters include the cirrus-sac orientation, the median, lobed ovary, the scale-like tegumental spination, the I-shaped excretory vesicle and the ability to invade tissue.

## Family Leyogonimidae Dollfus, 1951

**Diagnosis:** Virgulate digeneans. Body 1–4 mm long, broadly oval, pyriform to elongate. Tegument spinous, typically scale-like. Oral sucker round, terminal to subterminal. Ventral sucker round, median, equatorial to pre-equatorial. Prepharynx short to absent. Pharynx well developed. Oesophagus short to elongate. Intestinal bifurcation in mid-forebody. Caeca paired, extend to middle of body, terminate in hindbody beyond testes. Testes paired, symmetrical, entire or irregularly lobed, typically in middle third of body, occasionally further posterior. Cirrus-sac present, oriented posteriorly, contains seminal vesicle, pars prostatica and ejaculatory duct. Genital atrium present or absent. Genital pore (or pores) marginal, rarely submedian, in hindbody, typically posttesticular, opens posterior to proximal end of cirrus-sac. Ovary median, lobed, in forebody or mostly in forebody, pretesticular. Canalicular seminal receptacle present. Laurer's canal well developed. Uterus variable, may fill only posterior half of body or may extend from near posterior end of body to near pharynx. Eggs operculate, small, usually numerous. Vitellarium follicular, in forebody. Excretory vesicle I-shaped or Y-shaped with long, expanded unpaired stem; pore terminal. In intestine, mesenteries or hepatic system of birds and mammals, may be histolytic or encysted; Eurasia, North America. Type-genus *Leyogonimus* Ginetsinskaya, 1948.

## Key to genera

**1a. Uterus not restricted to posterior half of body, extends anterior to ovary to near pharynx ..... *Posterocirrus* Andreiko & Khotenovskii, 1964. (Fig. 55.1)**
(Syns *Paraleyogonimus* Vaucher, 1968; *Lobogonimus* Filimonova, 1973)

**Diagnosis:** Body thick, 2–4 mm long, somewhat longer than wide. Tegument with scale-like spines. Oral sucker subterminal. Ventral sucker equatorial to pre-equatorial. Prepharynx short. Pharynx well developed. Oesophagus short. Caeca long, extend posterior to testes. Testes large, irregularly lobed, mostly in hindbody. Cirrus-sac in hindbody, strongly oriented posteriorly, contains seminal vesicle, pars prostatica and ejaculatory duct. Genital pore opens near posterior end

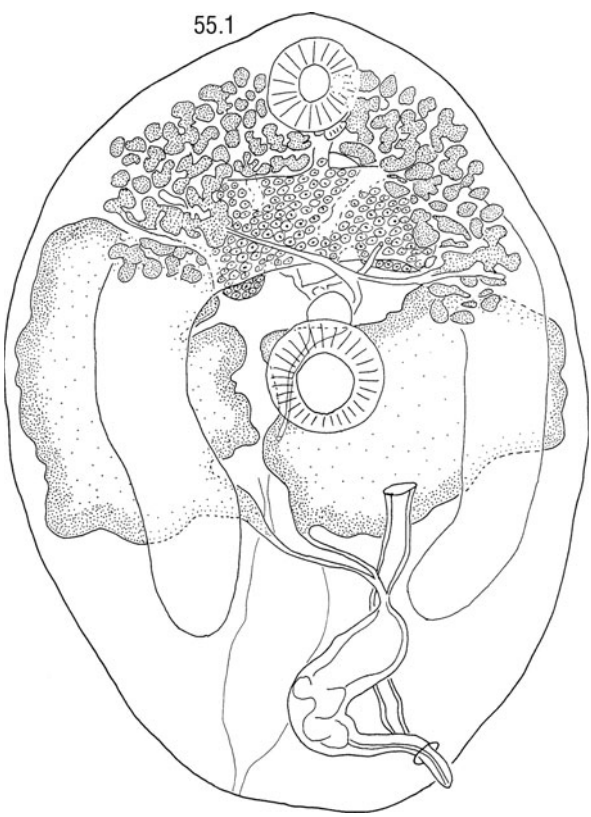
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of body, lateral to excretory vesicle. Ovary deeply lobed, medial, in forebody or mostly in forebody. Uterus fills most of body, extends from near pharynx to posterior margin of testes. Eggs numerous. Vitellarium in forebody, extends from oral sucker or pharynx to intestinal bifurcation. Excretory vesicle I- to Y-shaped with long unpaired stem. In intestine and hepatic system or encysted in mesenteries and liver of mammals (Rodentia) and birds (Passeriformes); Eurasia. Type-species *P. clethrionomi* Andreiko & Khotenovskii, 1964.

**1b. Uterus restricted to posterior half of body, never anterior to ovary ..... 2.**

**2a. Genital pores submedial; male and female pores open separately .....**
**..... *Metoliophilus* Macy & Bell, 1968. (Fig. 55.2)**

**Diagnosis:** Body 2–3 mm long, elongate. Tegument with scale-like spines. Oral sucker subterminal. Ventral sucker equatorial. Prepharynx short. Pharynx present. Oesophagus moderate. Caeca long, extend well posterior to testes. Testes entire, in region of ventral sucker. Cirrus-sac arcuate, mostly in forebody, directed posteriorly, extends from near ovary into hindbody; contains seminal vesicle, pars prostatica and ejaculatory duct. Genital atrium absent. Male pore opens



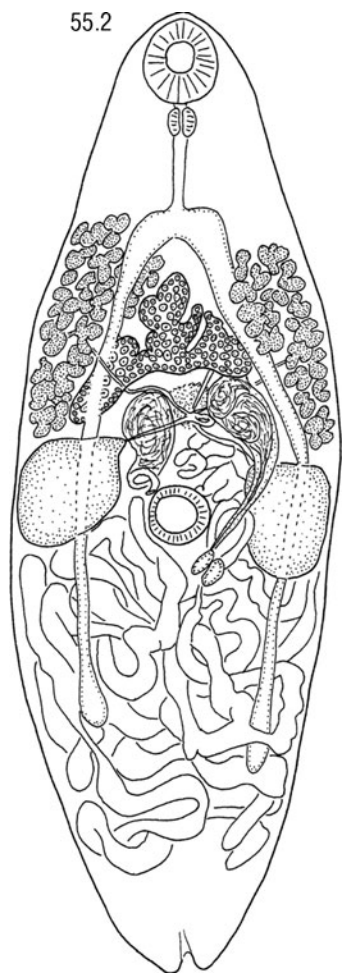




**Fig. 55.1.** *Posterocirrus clethrionomi* Andreiko & Khotenovskii, 1964. After Andreiko & Khotenovskii (1964).
**Fig. 55.2.** *Metoliophilus uvaticus* Macy & Bell, 1968. After Macy & Bell (1968).

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submedially, in hindbody; female pore opens immediately posterior to male pore. Ovary deeply lobed, medial. Seminal receptacle large. Uterus in hindbody, mostly posterior to testes. Metraterm present, extends anteriorly from female genital pore, recurves towards pore. Eggs numerous. Vitellarium in forebody, extends from intestinal bifurcation to anterior margin of testes. Excretory vesicle I-shaped, extends to level of ventral sucker. In intestine of birds (Passeriformes, Galliformes (experimental)), may be histolytic; North America. Type-species *M. uvaticus* Macy & Bell, 1968.

**2b. Genital pore marginal, male and female pores open into genital atrium ..... ..... *Leyogonimus* Ginetsinskaya, 1948. (Fig. 55.3)**
(Syn. *Macyella* Neiland, 1951)

**Diagnosis:** Body *c.* 1 mm long, pyriform to elongate. Tegument spinous. Oral sucker terminal to subterminal. Ventral sucker equatorial to pre-equatorial. Prepharynx short. Pharynx well developed. Oesophagus long. Caeca long, terminate in hindbody, may extend posteriorly beyond testes. Testes entire, in region of ventral sucker or in hindbody. Cirrus-sac straight to arcuate, in hindbody, directed posteriorly, extends from testes to open marginally posterior to testes, contains seminal vesicle, pars prostatica and ejaculatory duct. Genital atrium present. Genital pore opens on lateral margin of body in posterior third of body. Ovary median, lobed. Uterus mostly in hindbody, may encircle testes. Eggs not numerous. Vitellarium in forebody, or at level of ventral sucker. Excretory vesicle I-shaped. In intestine of birds (Gruiformes, Passeriformes), may be histolytic; Eurasia, North America. Type-species *L. polyoon* (Braun, 1902) Ginetsinskaya, 1948.

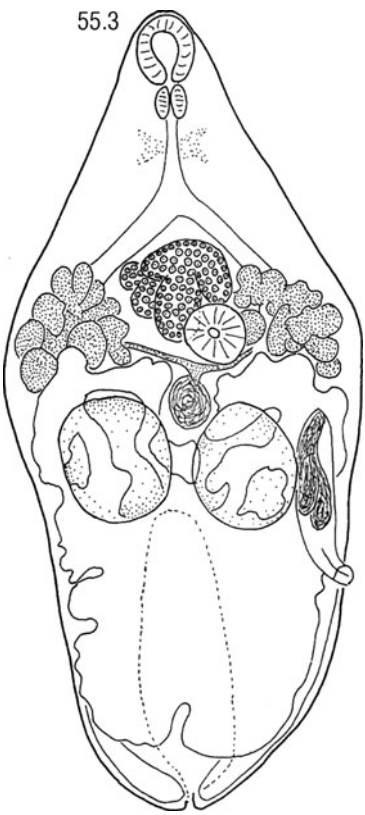



**Fig. 55.3.** *Leyogonimus polyoon* (von Linstow, 1887). After Yamaguti (1971).

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# 56 Family Pachypsolidae Yamaguti, 1958

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## Introduction

Pachypsolidae Yamaguti, 1958 contains only the type-genus, within which are a few species found in the digestive tract of marine chelonians and freshwater crocodilians. It is characterized by the presence of four to six anteriorly or laterally directed diverticula arising from the anterior portions of the caeca. Rudolphi (1819) described *Distoma irroratum* Rudolphi, 1819 from a sea turtle, identified as *Testudo midas*, from the Adriatic Sea (see Blair & Limpus, 1982). Looss (1901b) placed the species within his new genus *Pachypsolus* Looss, 1901. Pratt (1902b) placed *Pachypsolus* as one of several 'related genera' close to members of his 'new' subfamily Plagiorchiinae Looss, 1901 in the family Fasciolidae Railliet, 1895. Many subsequent authors have accepted that *Pachypsolus* has plagiorchiid affinities, although there was not always agreement on which family and subfamily were most appropriate for the genus.

Baer (1924) erected the subfamily Styphlotrematinae Baer, 1924 to include *Pachypsolus* and *Styphlotrema* Odhner, 1911. He placed this subfamily within his new family Reniferidae Baer, 1924, along with a number of genera formerly in the Lepodermatidae Odhner 1911. Fuhrmann (1928) did not accept the splits proposed by Baer and placed *Pachypsolus* in Plagiorchiidae Lühe, 1901 (syn. Lepodermatidae Looss, 1899) without recognition of any subfamilies. Thereafter, the genus was generally left in the Styphlotrematinae and Plagiorchiidae. One exception was the work by Byrd & Denton (1938b), who placed it in the Enodiotrematinae Baer, 1924. Yamaguti (1958b) erected the family Pachypsolidae Yamaguti, 1958 without explanation or comment. Travassos *et al.* (1969) proposed the monotypic subfamily Pachypsolinae as the sole subfamily within the Pachypsolidae, and Gomes & Pinto (1978) have, in contravention of the Principle of Coordination, ascribed authority for Pachypsolinae to Travassos *et al.* (1969). The phylogeny inferred by Olson *et al.* (2003), using rDNA sequences, placed the Pachypsolidae in the superfamily Microphalloidea Ward, 1901, as sister to the Renicolidae + Eucotylidae.

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## Family Pachypsolidae Yamaguti, 1958

**Diagnosis:** Body of medium size, elongate, rounded at each end (posterior end sometimes truncate); margins parallel or body slightly tapered towards anterior. Tegument with or without spines. Oral sucker large, with subterminal opening, ventral. Ventral sucker conspicuous in middle third of body close to equator, smaller, equal to or larger than oral sucker. Prepharynx absent. Pharynx large, immediately posterodorsal to oral sucker. Oesophagus very short or absent. Intestinal bifurcation mid-forebody. Caeca inflated anteriorly, often with two or three anteriorly or laterally directed projections on each side at level of pharynx or between pharynx and ventral sucker; remainder of each caecum simple, almost straight, close to body margins, terminating blindly at posterior end of body. Testes two, often large or medium-sized, spherical or subspherical, opposite or somewhat oblique, in middle third of body posterior to ventral sucker. Cirrus-sac very variable, generally banana-shaped and dorsal or lateral to ventral sucker, contains coiled internal seminal vesicle within proximal quarter, prostatic region and eversible ejaculatory duct (cirrus); posterior end at any level from testes to anterior region of ventral sucker. Genital pore sinistrally submedian, generally closer to ventral than to oral sucker. Ovary spherical to ovoid, submedian, usually immediately anterodorsal to right testis and may overlap ventral sucker. Mehlis' gland posteromedial to ovary. Laurer's canal present. Seminal receptacle, where reported, canalicular. Uterus extensively looped throughout entire body posterior to testes, overlaps caeca; ascending limb narrows dorsal to ventral sucker and becomes thick-walled metraterm alongside cirrus-sac. Vitellarium follicular; fields lateral, confined to posterior half of body or may extend from slightly posterior to level of testes to pharyngeal region and somewhat towards dorsal mid-line anterior to ventral sucker. Excretory vesicle I-shaped, reaches level of ovary; pore terminal. In stomach and intestine of marine chelonians; probably throughout their range; and cloaca and large intestine of freshwater crocodilians; South America. Type- and only genus *Pachypsolus* Looss, 1901.

## Genus *Pachypsolus* Looss, 1901 (Fig. 56.1)

**Diagnosis:** With characters of family. Type-species *P. irroratus* (Rudolphi, 1819) Looss, 1902.

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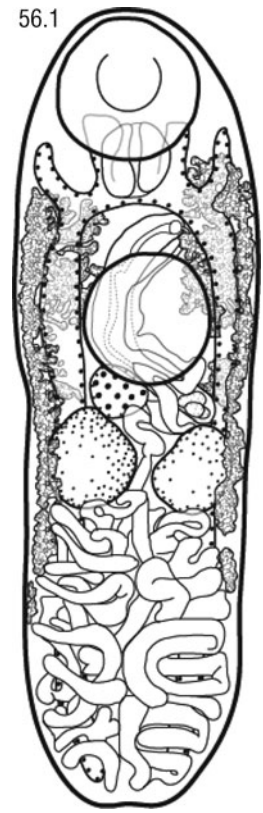



**Fig. 56.1.** *Pachypsolus irroratus* (Rudolphi, 1819) Looss, 1902. Ventral view. After Blair & Limpus (1982).

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# 57 Family Phaneropsolidae Mehra, 1935

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## Introduction

Mehra (1935) erected the subfamily Phaneropsolinae Mehra, 1935 within the Lecithodendriidae Lühe, 1901 to include only *Phaneropsolus* Looss, 1899, based on the presence of a well-developed cirrus-sac and the median position of the genital pore. Khotenovskii (1970) recognized the taxon as a subfamily of the Pleurogenidae, but under the name Parabascinae Yamaguti, 1958 (considered a junior synonym of Phaneropsolinae Mehra, 1935 here). The Parabascinae (= Phaneropsolinae) was for mammalian parasites with a genital pore opening medially or submedially, whereas the Pleurogeninae included those amphibian parasites possessing a genital pore opening laterally or sublaterally. We accept both of these taxa at the family level (see also Lotz & Font, Chapter 58, this volume).

Yamaguti (1971) examined the holotype and several paratypes of *Odeningotrema bivesicularis* Rohde, 1962 and concluded that no cirrus-sac was present.

*Pithecotrema* was erected by Tang & Tang (1982) for a species described from one specimen taken from a rhesus monkey. It resembles the pleurogenid genus *Pseudosonsinotrema*; however, until further studies clarify its position, we prefer to place it in the Phaneropsolidae with other lecithodendriid-like parasites of primates.

Jourdane (1973b) determined that *Pseudocephalotrema pyrenicum* has a virgulate cercaria, confirming that the genus is related to the lecithodendriids.

Odening (1964a) erected the subgenus *Lecithodollfusia* for the species *Laterotrema arenula* (Creplin, 1825) Dollfus 1956 and included the genus in the Leygonimidae. Khotenovskii (1970) raised *Lecithodollfusia* to genus and moved it to the Pleurogenidae. There is a very close morphological relationship between the genera *Lecithodollfusia* and *Postorchigenes* and the two may in fact by synonyms. Therefore we prefer to include *Lecithodollfusia* in the Phaneropsolidae rather than the Pleurogenidae.

Baer (1944) erected the genus *Cephalotrema* for *C. minutum* from a shrew collected in Europe. Brendow (1970) described the life-cycle of *Cercaria elasticum* Bregenzer, 1916 and found that the adult developing from the cercaria was identical to *C. minutum*. As the cercaria of *C. elasticum* figured by Brendow (1970) has a virgula, the species of *Cephalotrema* should be placed in the Phaneropsolidae rather than the Prosthogonimidae.

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## Family Phaneropsolidae Mehra, 1935

(Syn. Parabascinae Yamaguti, 1958)

**Diagnosis:** Body small, ovoid, typically with tegumental spines. Oral sucker round, terminal to subterminal. Ventral sucker round, median, equatorial, pre- or postequatorial. Prepharynx short or absent. Pharynx small. Oesophagus short or absent. Intestinal bifurcation in forebody. Caeca paired, short to long. Testes two, symmetrical, entire or irregularly lobed, typically in middle third of body, occasionally more posterior. Cirrus-sac present or absent. Genital atrium prominent or not. Genital pore median to sublateral, occasionally marginal, at level of ventral sucker, or more anterior or posterior; occasionally dorsal. Ovary submedian in mid-body, entire to irregularly lobed. Seminal receptacle usually present. Laurer's canal opens dorsally. Uterus fills posterior half of body; loops may extend into forebody. Eggs operculate, typically small, typically numerous. Vitellarium follicular, typically in forebody but occasionally extends into hindbody. Excretory vesicle V- to Y-shaped, rarely I-shaped; pore terminal. Cercaria virgulate. In intestine of mammals, birds, rarely reptiles; cosmopolitan. Type-genus *Phaneropsolus* Looss, 1899.

### Key to genera

**1a. Cirrus-sac absent or reduced to thin membrane enclosing seminal vesicle ..... 2.**

**1b. Cirrus-sac present, well developed, encloses seminal vesicle, pars prostatica and ejaculatory duct ..... 5.**

**2a. Vitellarium extends from anterior to caeca to posterior to testes ..... ..... *Odeningotrema* Rohde, 1962. (Fig. 57.1)**

**Diagnosis:** Body < 1 mm long, oval to pyriform. Tegument spinous. Oral sucker subterminal. Ventral sucker pre-equatorial, larger than oral sucker. Prepharynx short. Pharynx small. Oesophagus about as long as caeca. Caeca short, end at level of ventral sucker. Testes symmetrical, entire to irregular, posterior to ventral sucker. Cirrus-sac absent (see Yamaguti, 1971). Bipartite seminal vesicle, pars prostatica and ejaculatory duct just anterior to ventral sucker or may somewhat overlap ventral sucker. Genital pore opens at anterolateral margin of ventral sucker or more laterally. Ovary entire to irregular, pretesticular, at level of ventral sucker. Seminal receptacle present. Uterus mostly in hindbody. Eggs not numerous. Vitellarium in forebody and hindbody, extends from pharynx to posterior to testes. Excretory vesicle Y-shaped. In intestine of mammals (Primates, Insectivora, Chiroptera); South-east Asia. Type-species *O. bivesiculare* Rohde, 1962 (emend.).

**2b. Vitellarium does not extend from anterior to caeca to posterior to testes ..... 3.**

**3a. Vitellarium restricted to posterior to testes, does not extend anterior to testes ..... ..... *Passeritrema* Sitko, 2004. (Fig. 57.2)**

**Diagnosis:** Body 1–2 mm long, elongate-oval. Tegument spinous. Oral sucker subterminal. Ventral sucker equatorial. Prepharynx short. Pharynx small. Oesophagus about as long as caeca. Caeca short, end anterior to or at level of ventral sucker. Testes symmetrical, entire, at level of ventral sucker, extend posterior to ventral sucker. Cirrus-sac absent, may be reduced to fine membrane. Seminal vesicle prominent, mostly anterior to ventral sucker. Cirrus absent. Genital pore lateral to ventral sucker. Ovary lateral, entire, mostly pretesticular. Seminal receptacle present. Uterus mostly

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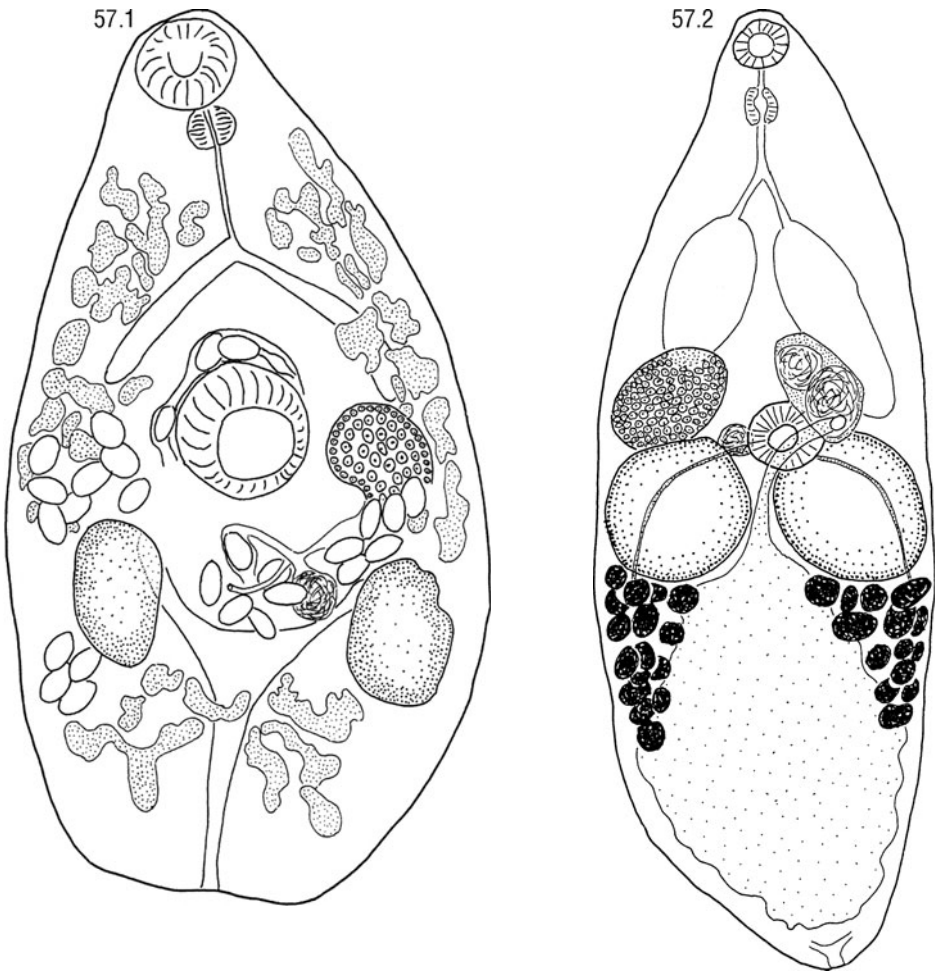



**Fig. 57.1.** *Odeningotrema bivesicularis* Rohde, 1962. After Rohde (1962).
**Fig. 57.2.** *Passeritrema rysavyi* Sitko, 2004. After Sitko (2004).

in hindbody, post-testicular. Eggs numerous. Vitellarium comprises two lateral groups of follicles, restricted to hindbody, mostly posterior to testes and lateral to uterus. Excretory vesicle V-shaped. In intestine of birds (Passeriformes); central Europe. Type-species *P. rysavyi* Sitko, 2004.

**3b. Vitellarium restricted to anterior to testes, usually precaecal** ..... **4.**

**4a. Genital pore in forebody** ..... ***Pleuropsoloides*** **Goodman, 1990. (Fig. 57.3)**
**Diagnosis:** Body < 1 mm long, oval. Tegument spinous. Oral sucker subterminal. Ventral sucker equatorial. Prepharynx short. Pharynx well developed. Oesophagus shorter than caeca. Caeca short, end anterior to testes. Testes symmetrical, entire, at level of ventral sucker. Cirrus-sac absent. Bipartite seminal vesicle prominent, mostly anterior to ventral sucker. Ejaculatory duct surrounded by prostatic cells. Genital pore anterior to ventral sucker, immediately posterior to intestinal bifurcation. Ovary oval, submedial, between testes, entire, mostly pretesticular. Seminal

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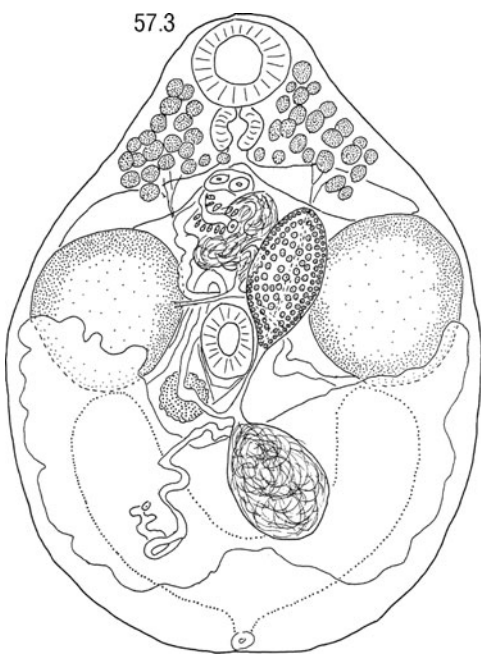
receptacle well developed. Uterus occupies most of hindbody posterior to testes. Eggs numerous. Vitellarium comprises two lateral groups of follicles, mostly anterior to caeca, reaches level of pharynx and oral sucker. Excretory vesicle V-shaped. In intestine of birds (Passeriformes); Africa. Type-species *P. peirci* Goodman, 1990.

**4b. Genital pore in hindbody ..... *Echinuscodendrium* Skarbilovich, 1943. (Fig. 57.4)**
**Diagnosis:** Body *c.* 1 mm long, pyriform. Tegument spinous. Oral sucker subterminal. Ventral sucker equatorial. Prepharynx short or absent. Pharynx well developed. Oesophagus nearly as long as caeca. Caeca short, end posterior to ventral sucker, partly overlap testes. Testes symmetrical, entire, mostly posterior to ventral sucker, embedded among uterine loops. Cirrus-sac absent. Seminal vesicle small; pars prostatica absent; ejaculatory duct present. Cirrus absent. Genital pore median, posterior to ventral sucker, in zone of testes. Ovary lobed, pretesticular, at level of ventral sucker. Seminal receptacle present. Uterus occupies most of hindbody, overlaps testes. Metraterm short. Eggs numerous, with abopercular spine. Vitellarium in two dense masses of follicles on each side of oesophagus, mostly anterior to caeca and posterior to pharynx. Excretory vesicle I-shaped. Encysted in intestine of birds (Passeriformes); North America. Type-species *E. echinus* (McIntosh, 1936) Skarbilovich, 1943.

**5a. Caeca short, do not extend beyond middle of testes, usually terminate anterior to testes .... 6.**
**5b. Caeca long, extend beyond middle of testes and usually further posterior ..... 18.**

**6a. Genital pore median to submedian, within vertical zone of ventral sucker ..... 7.**
**6b. Genital pore not median, outside vertical zone of ventral sucker ..... 8.**

**7a. Male and female genital pores open into genital atrium; common genital pore at level of or anterior to pharynx ..... *Phaneropsolus* Looss, 1899. (Fig. 57.5)**



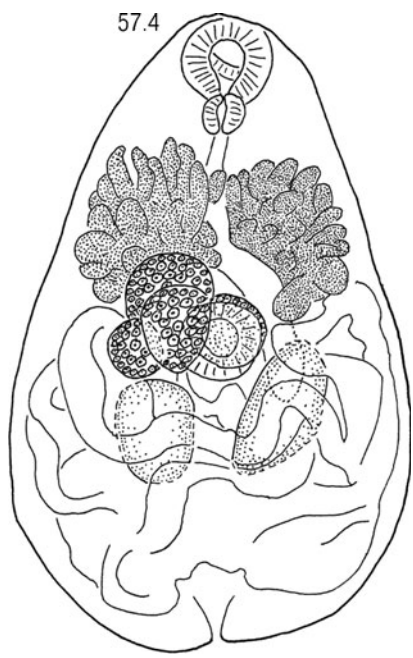




**Fig. 57.3.** *Pleuropsoloides peirci* Goodman, 1990. After Goodman (1990).
**Fig. 57.4.** *Echinuscodendrium echinus* (McIntosh, 1936). After McIntosh (1936b).

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**Diagnosis:** Body from 0.5 to > 2 mm long, oval to elongate. Tegument spinous. Oral sucker well developed, subterminal. Ventral sucker equatorial to pre-equatorial. Prepharynx short or absent. Pharynx small. Oesophagus short to absent. Caeca short, end at level of ventral sucker. Testes symmetrical, entire, equatorial or pre-equatorial. Cirrus-sac well developed, straight or curved, intercaecal, oriented anteriorly from near ventral sucker to genital atrium, contains well-developed seminal vesicle, pars prostatica and ejaculatory duct; ejaculatory duct long, surrounded by gland-cells. Cirrus short, often armed with spines or tubercles. Genital pore medial at level of pharynx or oral sucker. Ovary entire occasionally irregular, typically post-testicular, occasionally testicular to pretesticular. Seminal receptacle present. Uterus mostly in hindbody, posterior to testes; uterine loop may extend anterior to testes. Eggs numerous. Vitellarium in two lateral groups of follicles, mostly pre-caecal. Excretory vesicle V-shaped. In intestine of reptiles (Squamata), birds (Charadriiformes, Passeriformes, Caprimulgiformes), mammals (Primates); cosmopolitan. Type-species *P. micrococcus* (Rudolphi, 1819) Looss, 1899.

7b. **Male and female pores widely separated; male pore posterior to pharynx at level of intestinal bifurcation** ..... ***Tremajoannes*** **Saoud, 1964. (Fig. 57.6)**

**Diagnosis:** Body *c.* 1 mm long, fusiform to oval. Tegument spinous. Oral sucker well developed, subterminal. Ventral sucker equatorial. Prepharynx short or absent. Pharynx well

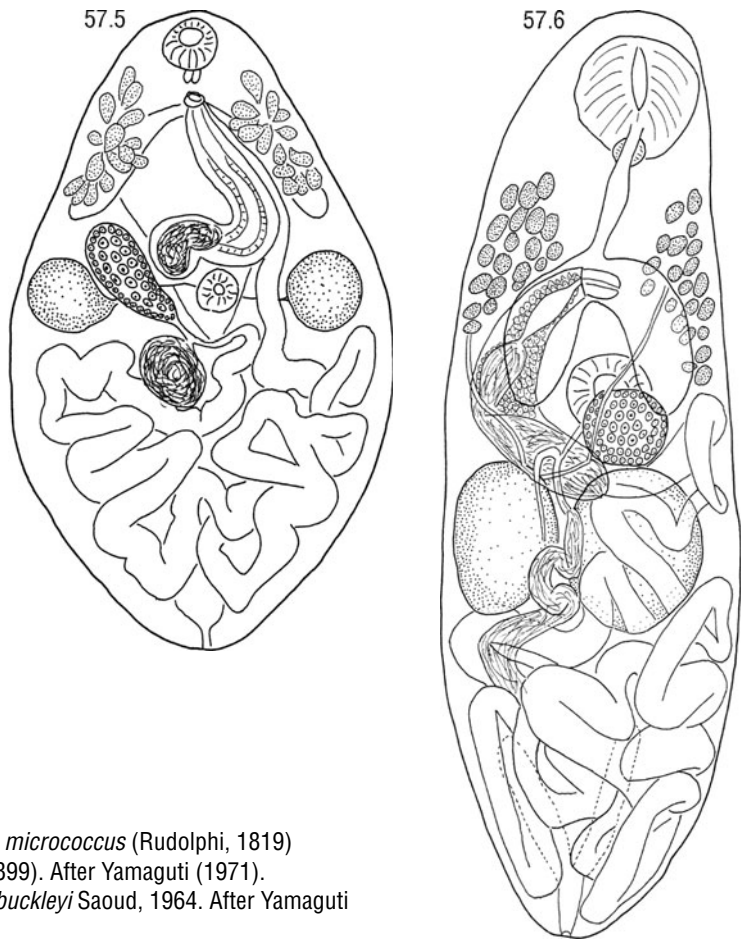



**Fig. 57.5.** *Phaneropsolus micrococcus* (Rudolphi, 1819) (= *P. sigmoideus* Looss, 1899). After Yamaguti (1971).
**Fig. 57.6.** *Tremajoannes buckleyi* Saoud, 1964. After Yamaguti (1971).

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developed. Oesophagus short, about as long as caecum. Caeca short, end at level of ventral sucker. Testes symmetrical, entire, in hindbody. Cirrus-sac well developed, to left of ventral sucker, extending into forebody to open at male pore near left caecum. Seminal vesicle, pars prostatica and ejaculatory duct well developed; all contained in cirrus-sac. Ovary entire, anterior to right testis, near level of ventral sucker. Seminal receptacle not evident. Uterus extensive, fills most of hindbody, joins metraterm near posterior end of cirrus-sac. Metraterm extends laterally to open at female pore near anterior margin of left testis. Eggs numerous. Vitellarium in forebody, lateral to caeca and oesophagus or overlaps caeca posteriorly. Excretory vesicle Y- or V-shaped; pore terminal. In intestine of mammals (Chiroptera); North and South America. Type-species *T. buckleyi* Saoud, 1964.

**8a. Cirrus-sac oriented posteriorly; male genital pore posterior to proximal part of cirrus-sac ..... *Limatulum* Travassos, 1921. (Fig. 57.7)**

**Diagnosis:** Body < 1 mm long, fusiform to nearly oval. Tegument spinous. Oral sucker well developed, subterminal. Prepharynx short or absent. Pharynx well developed. Oesophagus short or absent. Caeca short, end at level of ventral sucker, anterior to testes. Ventral sucker equatorial. Testes paired, opposite, symmetrical, entire to somewhat irregular, at level of ventral sucker. Cirrus-sac well developed, to left of ventral sucker, curved, oriented posteriorly. Cirrus-sac contains well-developed seminal vesicle, pars prostatica and ejaculatory duct. Male genital pore opening posterolateral to ventral sucker, separate from, but near, female genital pore. Ovary entire to irregular, anterior to testes, at or anterior to level of ventral sucker. Seminal receptacle present. Vitellarium in forebody, lateral to caeca and oesophagus or overlaps caeca posteriorly. Uterus extensive, filling most of hindbody. Metraterm present, opens at female pore posterolateral to ventral sucker near male pore. Eggs numerous. Excretory vesicle V-shaped. In stomach and intestine of mammals (Chiroptera); North and South America. Type-species *L. oklahomense* Macy, 1931.

**8b. Cirrus-sac oriented transversely or anteriorly; genital pore anterior to or at level of proximal part of cirrus-sac ..... 9.**

**9a. Genital pore on lateral margin of body; muscular metraterm extends anterior to cirrus-sac ..... *Pithecotrema* Tang & Tang, 1982. (Fig. 57.8)**

**Diagnosis:** Body *c.* 2 mm long, pyriform. Oral sucker well developed, subterminal. Prepharynx short or absent. Pharynx small. Oesophagus shorter than caecum. Caeca short. Ventral sucker preequatorial. Testes paired, opposite, symmetrical, entire, at level of ventral sucker or more posterior. Cirrus-sac well developed, claviform, curved, mostly anterior to ventral sucker, oriented transversely. Cirrus-sac contains well-developed winding seminal vesicle, pars prostatica and ejaculatory duct. Male genital pore opening on lateral margin of body, in forebody, at level of intestinal bifurcation. Ovary irregularly lobed, anterior to testes, in or anterior to acetabular zone. Seminal receptacle not observed. Vitellarium mostly in forebody, between pharynx and testes, overlaps anterior margin of testes. Uterus extensive, fills most of hindbody, mostly posterior to testes. Metraterm muscular, anterior to cirrus-sac, opens through female pore anterior to male pore. Eggs numerous. Intestine of mammals (Primates); China. Type-species *P. kelloggi* Tang & Tang, 1982.

**9b. Genital pore not on lateral margin of body ..... 10.**

**10a. Vitellarium extends into hindbody and posterior to testes ..... ..... *Pseudocryptotropa* Yamaguti, 1958. (Fig. 57.9)**
(Syn. *Novetrema* Rohde, 1962)

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**Diagnosis:** Body < 1 mm long, oval to pyriform. Tegument spinous. Oral sucker well developed, subterminal. Prepharynx short or absent. Pharynx well developed. Oesophagus about as long as caecum. Caeca short, mostly anterior to ventral sucker. Ventral sucker equatorial. Testes paired, opposite, symmetrical, entire, in posterior third of body, within uterine zone. Cirrus-sac claviform, transverse, curved, in forebody. Cirrus-sac contains tubular seminal vesicle, pars prostatica and ejaculatory duct; attenuated distal portion of seminal vesicle muscular, surrounded by prostatic cells. Ovary entire, overlapping posterior margin of ventral sucker. Seminal receptacle present. Uterus mostly in hindbody, posterior to testes; uterine loops extend anterior to testes. Genital pore mid-lateral, anterior to ventral sucker, near one of caeca. Eggs not numerous. Vitellarium extends in lateral fields from level of pharynx to near posterior extremity. Excretory vesicle Y-shaped. In intestine of birds (Caprimulgiformes) and mammals (Primates); Asia. Type-species *P. macrotestis* (Belopol'skaya, 1954) Yamaguti, 1958.

**10b. Vitellarium does not extend into hindbody ..... 11.**

**11a. Genital pore extracaecal, anterior to one caecum at level of pharynx; cirrus-sac crosses caecum ..... *Pseudocephalotrema* Combes & Jourdane, 1969. (Fig. 57.10)**

**Diagnosis**: Body < 1 mm long, oval to pyriform. Tegument spinous. Oral sucker well developed, subterminal. Ventral sucker well developed, equatorial. Prepharynx short. Pharynx small. Oesophagus shorter than caeca. Caeca short, widely divergent, terminate anterior to ventral sucker and testes. Testes symmetrical, entire, at level of ventral sucker. Cirrus-sac well developed, arcuate to sinuous, in forebody, passes from anterior to ventral sucker, across left caecum to open mid-laterally at level of pharynx. Cirrus-sac contains tubular seminal vesicle, pars prostatica and ejaculatory duct. Genital pore opens mid-laterally at level of pharynx. Ovary entire, anterior to middle of testes and ventral sucker. Seminal receptacle present. Uterus fills most of hindbody, posterior to testes. Eggs numerous. Vitellarium in two lateral fields near ends of caeca. Excretory vesicle V- to Y-shaped. In intestine of mammals (Insectivora) and experimentally in birds (Columbiformes); Europe. Type-species *P. pyrenicum* Combes & Jourdane, 1969 (emend.).

**11b. Genital pore not at caecal level, cirrus-sac does not usually cross caecum, but, if it does, then genital pore not at level of pharynx ..... 12.**

**12a. Cirrus-sac not much longer than diameter of ventral sucker; genital pore dorsal ..... ..... *Aototrema* Bean-Knudsen, Uhazy & Wagner, 1987. (Fig. 57.11)**

**Diagnosis**: Body *c.* 1 mm long, oval to pyriform, occasionally wider than long. Tegument spinous. Oral sucker well developed, subterminal. Ventral sucker well developed, larger than oral sucker, equatorial. Prepharynx present. Pharynx present. Oesophagus absent. Caeca short, widely divergent, terminate anterior to ventral sucker and testes. Testes symmetrical, entire, at level of ventral sucker, extend anterior to ventral sucker. Cirrus-sac well developed, transverse, straight, in forebody, postcaecal, intertesticular, about as long as diameter of ventral sucker, contains tubular seminal vesicle, pars prostatica and ejaculatory duct. Genital pore opens dorsally and submedially between caeca and ventral sucker. Ovary entire, posterior to middle of testes, at level of ventral sucker. Seminal receptacle well developed, between ovary and testes. Uterus in hindbody, with descending transverse and ascending limbs, surrounding ventral sucker. Eggs rather large, numerous. Vitellarium in two lateral fields anterior to caeca, at level of pharynx and oral sucker. Excretory vesicle Y-shaped. In intestine of mammals (Primates); South America. Type-species *A. dorsogenitalis* Bean-Knudsen, Uhazy & Wagner, 1987.

**12b. Cirrus-sac at least twice as long as diameter of ventral sucker; genital pore ventral ..... 13.**

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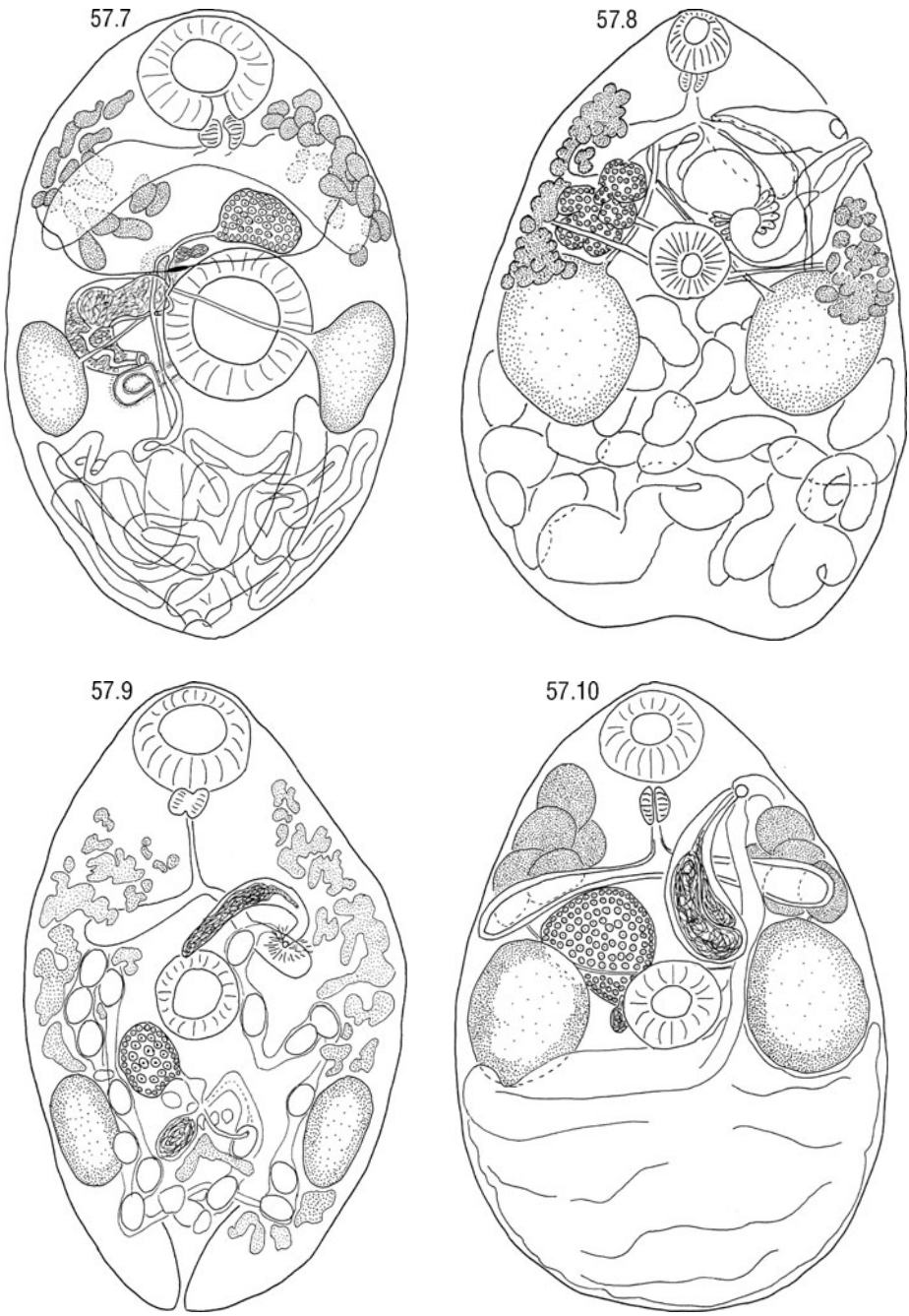



**Fig. 57.7.** *Limatulum oklahomense* Macy, 1931. After Yamaguti (1971).
**Fig. 57.8.** *Pithecotrema kelloggi* Tang & Tang, 1982. After Tang & Tang (1982).
**Fig. 57.9.** *Pseudocryptotropa nycticebi* (Rohde, 1962). After Rohde (1962).
**Fig. 57.10.** *Pseudocephalotrema baeri* Jourdane, 1976. After Jourdane (1976).

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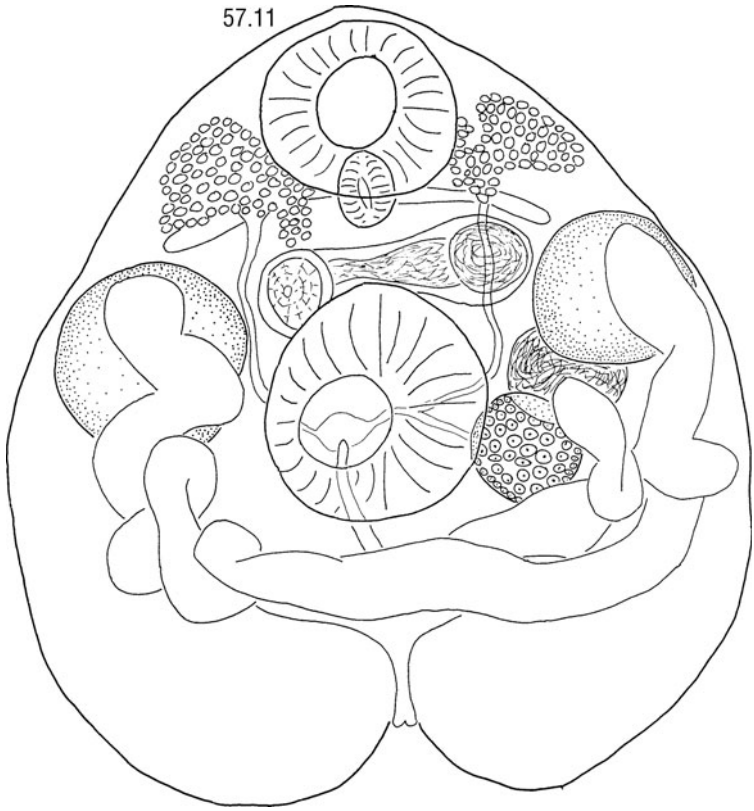



**Fig. 57.11.** *Aototrema dorsogenitalis* Bean-Knudsen, Uhazy & Wagner, 1987. After Bean-Knudsen *et al.* (1987).

**13a. Genital atrium prominent, muscular or armed ..... 14.**
**13b. Genital atrium not prominent, neither muscular nor armed ..... 15.**

**14a. Genital atrium muscular, sucker-like ..... *Oryzomytrema* Thatcher, 1982. (Fig. 57.12)**
**Diagnosis**: Body < 1 mm long, oval to round. Tegument spinous. Oral sucker well developed, subterminal. Ventral sucker well developed, equatorial. Prepharynx absent. Pharynx well developed. Oesophagus short or absent. Caeca short, widely divergent, in forebody, pretesticular. Testes symmetrical, entire to irregular, at level of ventral sucker, extending posterior to ventral sucker. Cirrus-sac well developed, long, postcaecal, oriented transversely, recurved, passes from posterior to ventral sucker, around ventral sucker across body to genital opening. Cirrus-sac contains elongate seminal vesicle, pars prostatica and ejaculatory duct; ejaculatory duct long, surrounded by gland-cells. Genital pore opens mid-laterally, posterior to caeca, at level of ventral sucker, surrounded by muscular, sucker-like, genital atrium. Ovary entire to irregular, extends anterior to testes, at level of ventral sucker. Uterus extensive, mostly in hindbody; uterine loops extend anterior to caeca. Eggs numerous. Vitellarium in two lateral fields anterior to caeca, at level of pharynx and oral sucker. Excretory vesicle Y-shaped. In intestine of mammals (Rodentia); South America. Type-species *O. tristoma* Thatcher, 1982.

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**14b. Genital atrium armed ..... ..... *Caluromytrema* Lamothe-Argumedo & Pineda-Lopez, 1989. (Fig. 57.13)**

**Diagnosis:** Body < 1 mm long, oval. Tegument spinous. Oral sucker subterminal. Ventral sucker pre-equatorial. Prepharynx absent. Pharynx present. Oesophagus absent. Caeca short, widely divergent, end at level of ventral sucker. Testes symmetrical, entire to irregular, post-acetabular, in hindbody, embedded among uterine loops. Cirrus-sac large, slightly arcuate, oriented transversely, mostly in hindbody, contains sinuous seminal vesicle, pars prostatica and ejaculatory duct. Genital atrium expanded, armed with spines. Genital pore posterior to ventral sucker, between ventral sucker and lateral margin of body. Ovary entire, median, in hindbody. Seminal receptacle absent. Uterus extensive, mostly posterior to cirrus-sac, with uterine loops extending close to caeca. Eggs numerous. Vitellarium in two lateral fields from caeca to pharynx. Excretory vesicle Y-shaped. In intestine of mammals (Marsupialia); Mexico. Type-species *C. martindelcampoi* Lamothe-Argumedo & Pineda-Lopez, 1989.

**15a. Vitellarium not anterior to caeca, restricted to zone between caecal ends and testes ..... ..... *Procyonophilus* Thatcher, 1982. (Fig. 57.14)**

**Diagnosis**: Body < 1 mm long, pyriform. Tegument spinous. Oral sucker well developed, subterminal. Ventral sucker pre-equatorial. Prepharynx short. Pharynx present. Oesophagus short. Caeca short, pretesticular, at level of ventral sucker or more posterior. Testes symmetrical, entire, postequatorial. Cirrus-sac very large, transverse, straight, mostly pre-acetabular and postcaecal bifurcation. Cirrus-sac contains sinuous seminal vesicle, pars prostatica and ejaculatory duct. Ovary entire to irregular, median, extends anterior to testes, at level of ventral sucker. Uterus

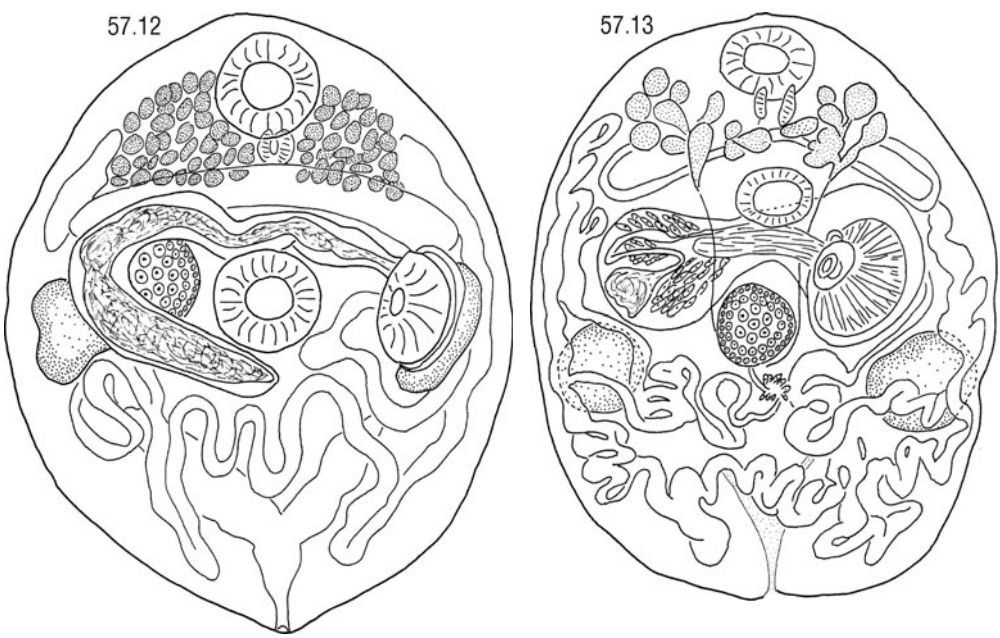



**Fig. 57.12.** *Oryzomytrema tristoma* Thatcher, 1982. After Thatcher (1982).
**Fig. 57.13.** *Caluromytrema martindelcampoi* Lamothe-Argumedo & Pineda-Lopez, 1989. After Lamothe-Argumedo & Pineda-Lopez (1989).

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extensive, with uterine loops extending from anterior to caeca to near posterior end of body. Genital pore opens submedially at lateral margin of ventral sucker. Eggs numerous. Vitellarium comprises a few large follicles in two fields lateral to ventral sucker and ovary, postcaecal and pretesticular. Excretory vesicle Y-shaped. In intestine of mammals (Carnivora); South America. Type-species *P. panamensis* Thatcher, 1982.

**15b. Vitellarium anterior to caeca, not restricted to zone between caecal ends and testes .... 16.**

**16a. Vitellarium extends posterior to testes ..... *Matovius* Jančev, 1970. (Fig. 57.15)**
**Diagnosis:** Body < 1 mm long, oval. Tegument spinous. Oral sucker well developed, subterminal. Prepharynx short. Pharynx present. Oesophagus shorter than caeca. Caeca short, pretesticular. Ventral sucker equatorial. Testes symmetrical, entire, in hindbody. Cirrus-sac very large, oriented anteriorly, arcuate, mostly posterior to intestinal bifurcation, passes anteriorly from between testes and around ventral sucker to overlap one caecum. Cirrus-sac contains large seminal vesicle, pars prostatica and ejaculatory duct. Cirrus present, very long when everted. Genital pore opens midlaterally, anterior to ventral sucker, posterior to pharynx, at level of intestinal bifurcation, ventral to one caecum. Ovary entire to irregular, submedian, at level of ventral sucker. Seminal receptacle large, often larger than ventral sucker, posterior to ovary and intertesticular. Uterus in hindbody, fills intertesticular and post-testicular regions. Eggs small, operculate. Vitellarium extensive, extends from near pharynx to near posterior extremity. Excretory vesicle Y-shaped. In intestine of mammals (Chiroptera, Insectivora); Europe. Type-species: *M. rhinolophi* Jančev, 1970.

**16b. Vitellarium does not extend posterior to testes ..... 17.**

**17a. Metraterm expanded, pigmented; uterine loop extends anterior to caeca across oesophagus; in mammals ..... *Proechimytrema* Thatcher, 1982. (Fig. 57.16)**
**Diagnosis:** Body *c.* 1 mm long, oval. Tegument spinous. Oral sucker terminal to subterminal. Ventral sucker equatorial. Prepharynx short. Pharynx well developed. Oesophagus shorter than caeca. Caeca short, pretesticular. Testes symmetrical, entire, at level of ventral sucker or more posterior. Cirrus-sac elongate, oriented transversely, arcuate, partly intercaecal and partly postcaecal and passes from posterolateral to ventral sucker around ventral sucker to near caecal end, contains large seminal vesicle, pars prostatica and ejaculatory duct. Genital pore opens ventrally, midway between ventral sucker and body margin, posterior to caecum, at level of ventral sucker, surrounded by gland-cells. Ovary entire to irregular, submedian, at level of ventral sucker. Uterus mostly in hindbody, but uterine loop extends precaecally. Metraterm expanded, pigmented. Eggs numerous. Vitellarium comprises few large follicles, precaecal near pharynx. Excretory vesicle Y-shaped. In intestine of mammals (Rodentia); South America. Type-species *P. phanerotermina* Thatcher, 1982.

**17b. Metraterm not expanded, not pigmented; uterine loop does not extend anterior to caeca across oesophagus; in birds ..... *Mosesia* Travassos, 1928. (Fig. 57.17)**
(Syns *Pleuropsolus* Mehra, 1935; *Mosesiella* Oshmarin, 1963)
**Diagnosis:** Body *c.* 1 mm long, oval to pyriform. Tegument spinous. Oral sucker terminal to subterminal. Ventral sucker in middle third of body. Prepharynx short to absent. Pharynx present. Oesophagus shorter than caeca. Caeca moderately long, end anterior to middle of testes, at level of ventral sucker to more posterior. Testes symmetrical to oblique, entire to irregular, in hindbody. Cirrus-sac oriented anteriorly to transversely, arcuate, mostly posterior to intestinal bifurcation, curves around ventral sucker and opens at genital pore. Cirrus-sac contains large seminal vesicle, pars prostatica and ejaculatory duct. Genital pore submedian to mid-lateral, at level of or slightly

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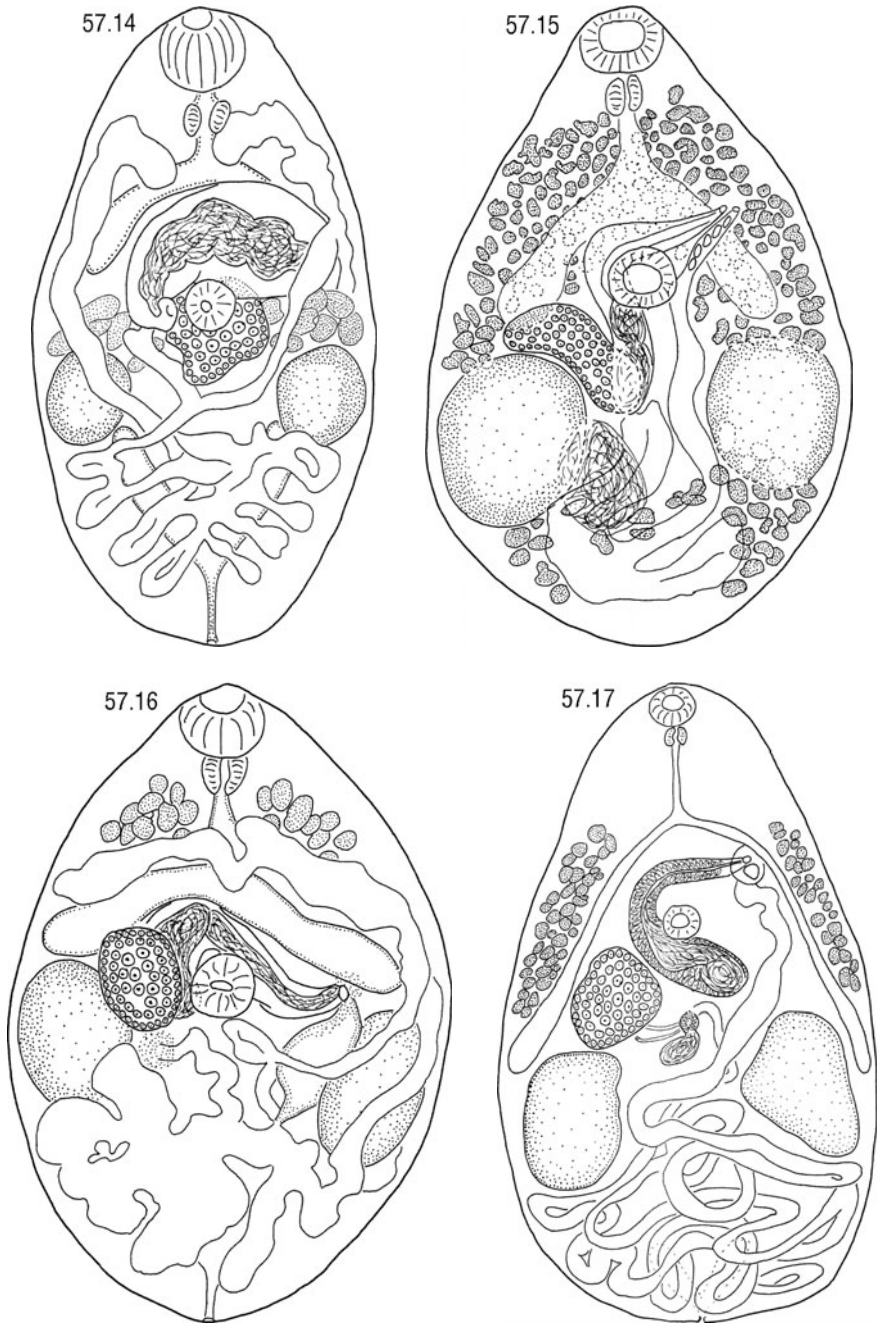



**Fig. 57.14.** *Procyonophilus panamensis* Thatcher, 1982. After Thatcher (1982).
**Fig. 57.15.** *Matovius rhinolophi* Jančev, 1970. After Jančev (1970).
**Fig. 57.16.** *Proechimytrema phanerotermina* Thatcher, 1982. After Thatcher (1982).
**Fig. 57.17.** *Mosesia chordeilesia* McMullen, 1935. After Yamaguti (1971).

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anterior to ventral sucker. Ovary entire to irregular, submedian, at level of ventral sucker, mostly pretesticular. Uterus fills most of body posterior to testes. Metraterm present but not expanded. Eggs numerous. Vitellarium mostly extracaecal in forebody. Excretory vesicle V-shaped. In intestine of birds (Caprimulgiformes, Cuculiformes, Charadriiformes, Passeriformes); North and South America, Asia. Type-species *M. mosesi* Travassos, 1921.

**18a. Cirrus-sac oriented posteriorly, genital pore posterior to proximal part of cirrus-sac, submedial to lateral ..... 19.**

**18b. Cirrus-sac not oriented posteriorly, genital pore at level of or anterior to proximal part of cirrus-sac ..... 20.**

**19a. Caeca do not extend to posterior end of body, ovary entire to irregular, parasites of mammals ..... *Postorchigenes* Tubangui, 1928. (Fig. 57.18)**
(Syns *Czosnowia* Zdzitowiecki, 1967; *Chiropterotarbus* Bay-Smith, 1972; *Zygodendrium* Salem, 1976)

**Diagnosis**: Body 0.5–4 mm long, oval to pyriform or elongate. Tegument spinous. Oral sucker terminal to subterminal. Ventral sucker pre-equatorial. Prepharynx short to absent. Pharynx present. Oesophagus short to moderately long. Caeca long, end posterior to middle of testes, often extend posterior to testes. Testes symmetrical to oblique, entire to irregular, in hindbody. Cirrus-sac oriented posteriorly to nearly transversely, arcuate, posterior to intestinal bifurcation, near ventral sucker. Cirrus-sac contains seminal vesicle, pars prostatica and ejaculatory duct. Genital pore submedian to lateral, at level of or slightly posterior to ventral sucker, at level of or slightly anterior to testes. Ovary entire to irregular, submedian at level of ventral sucker, pretesticular. Uterus fills most of body posterior to testes; uterine loops may extend anterior to ventral sucker. Metraterm present. Eggs numerous. Vitellarium in forebody, mostly surrounds caeca posterior to oesophagus, occasionally reaches level of pharynx. Excretory vesicle V-shaped. In intestine of mammals (Chiroptera) and reptiles (Squamata); South America, Asia. Type-species *P. ovatus* Tubangui, 1928.

**19b. Caeca extend to posterior end of body, ovary distinctly lobed to irregular, parasites of birds ..... *Lecithodollfusia* Odening, 1964. (Fig. 57.19)**

**Diagnosis**: Body < 1 mm long, oval to pyriform. Tegument spinous. Oral sucker terminal to subterminal. Prepharynx short to absent. Pharynx well developed. Oesophagus elongate. Caeca long, extend well past testes to near posterior end of body, terminate alongside stem of excretory bladder. Ventral sucker equatorial to pre-equatorial. Testes paired, symmetrical, entire, partly to fully in hindbody. Cirrus-sac oriented posteriorly to nearly transversely, arcuate, posterior to the intestinal bifurcation, proximal portion of cirrus-sac near ventral sucker. Cirrus-sac contains seminal vesicle, pars prostatica and ejaculatory duct. Ovary distinctly lobed to irregular, submedian at level of ventral sucker and extending anteriorly, pretesticular. Uterus fills most of hindbody, uterine loops may extend anterior to ventral sucker. Metraterm well developed. Genital pore lateral, at level of or slightly posterior to ventral sucker, at level of or slightly anterior to testes. Eggs numerous. Vitellarium in forebody, extends from pharynx to surround caeca. Excretory vesicle V-shaped. Intestinal parasites of birds; Eurasia. Type-species *L. arenula* (Creplin, 1825) Odening, 1964.

**20a. Genital pore close to oral sucker ..... *Cephalotrema* Baer, 1944. (Fig. 57.20)**

**Diagnosis:** Body < 0.5 mm long, oval to elliptical. Tegument spinous. Oral sucker large, subterminal. Ventral sucker large, pre-equatorial. Prepharynx absent. Pharynx present. Oesophagus

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short. Caeca long, extend posterior to testes. Testes symmetrical, entire, at level of ventral sucker or in hindbody. Cirrus-sac oriented anteriorly, sinuous, courses from dorsal to ventral sucker, across caecum to near oral sucker, contains bipartite seminal vesicle, pars prostatica and ejaculatory duct, surrounded by prostatic cells. Genital pore opens near lateral margin of oral sucker. Ovary entire to irregular, at level of ventral sucker, testicular to pretesticular. Seminal receptacle and Laurer's canal present. Uterus convoluted in hindbody, mostly posterior to testes, uterine loops overlap testes. Eggs small. Vitellarium in two lateral clusters from acetabular zone to pharynx. Excretory vesicle V-shaped. Intestinal parasites of mammals (Insectivora); Europe. Type-species *C. minutum* Baer, 1944 (syn. of *C. elasticum* (Bregenzer, 1916) Brendow, 1970).

**20b. Genital pore distant from oral sucker ..... 21.**

**21a. Vitellarium extends posterior to testes ..... ..... *Combesia* Mas-Coma, Roset & Mantoliu, 1985. (Fig. 57.21)**

**Diagnosis:** Body about 1 mm long, oval to elongate. Tegument reported as aspinous. Oral sucker subterminal. Ventral sucker large, in middle third of body. Prepharynx absent. Pharynx present. Oesophagus absent. Caeca long, extend posterior to testes to near posterior end of body. Testes symmetrical, entire, in hindbody. Cirrus-sac very large, oriented anteriorly, arcuate, mostly posterior to intestinal bifurcation, courses anteriorly from between testes posterior to ventral sucker, curves and passes dorsally to ventral sucker, contains large seminal vesicle, pars prostatica and ejaculatory duct. Cirrus present, very long when everted. Genital pore submedian to midlateral in forebody, well posterior to intestinal bifurcation, intercaecal. Ovary entire to irregular, at level of ventral sucker, pretesticular. Seminal receptacle well developed, posterior to testes. Uterus in hindbody, mostly intertesticular and posterior to testes. Eggs numerous. Vitellarium confluent across body in forebody, does not extend anterior to intestinal bifurcation, mostly post-testicular in hindbody, disposed in two lateral groups of follicles tracking caeca. In intestine of mammals (Insectivora); Eurasia. Type-species *C. macrobursata* (Chertkova & Rodonaja, 1965) Mas-Coma, Roset & Mantoliu, 1985.

**21b. Vitellarium does not extend posterior to testes ..... 22.**

**22a. Cirrus oriented transversely, genital pore at level of proximal part of cirrus ..... ..... *Maxbraunium* Caballero & Cerecero, 1942. (Fig. 57.22)**

**Diagnosis**: Body 1–2 mm long, oval. Tegument spinous. Oral sucker large, subterminal. Ventral sucker large, in middle third of body. Prepharynx absent. Pharynx present. Oesophagus absent. Caeca long, extend posterior to middle of testes. Testes symmetrical, entire, at level of ventral sucker or more posterior. Cirrus-sac large, oriented transversely, mostly anterior to ventral sucker, overlaps caecum, contains large bipartite or recurved seminal vesicle, pars prostatica and ejaculatory duct. Cirrus present, spinous or not. Genital pore submedian to sublateral, anterior to level of ventral sucker, near one caecum. Ovary entire to irregular, at level of ventral sucker, mostly pretesticular. Seminal receptacle present. Uterus in hindbody, posterior to testes. Eggs numerous. Vitellarium in two lateral groups that track caeca and extend from level of cirrus-sac to anterior margin of testes. Excretory vesicle V-shaped. In intestine of mammals (Chiroptera); Asia, Africa and the Americas. Type-species *M. tubiporum* (Braun, 1900) Caballero & Cerecero, 1942.

**22b. Cirrus sac oriented anteriorly, genital pore anterior to proximal part of cirrus ..... 23.**

**23a. Genital pore median, at anterior margin of ventral sucker ..... ..... *Ornithodendrium* Oshmarin & Dotsenko, 1950. (Fig. 57.23)**

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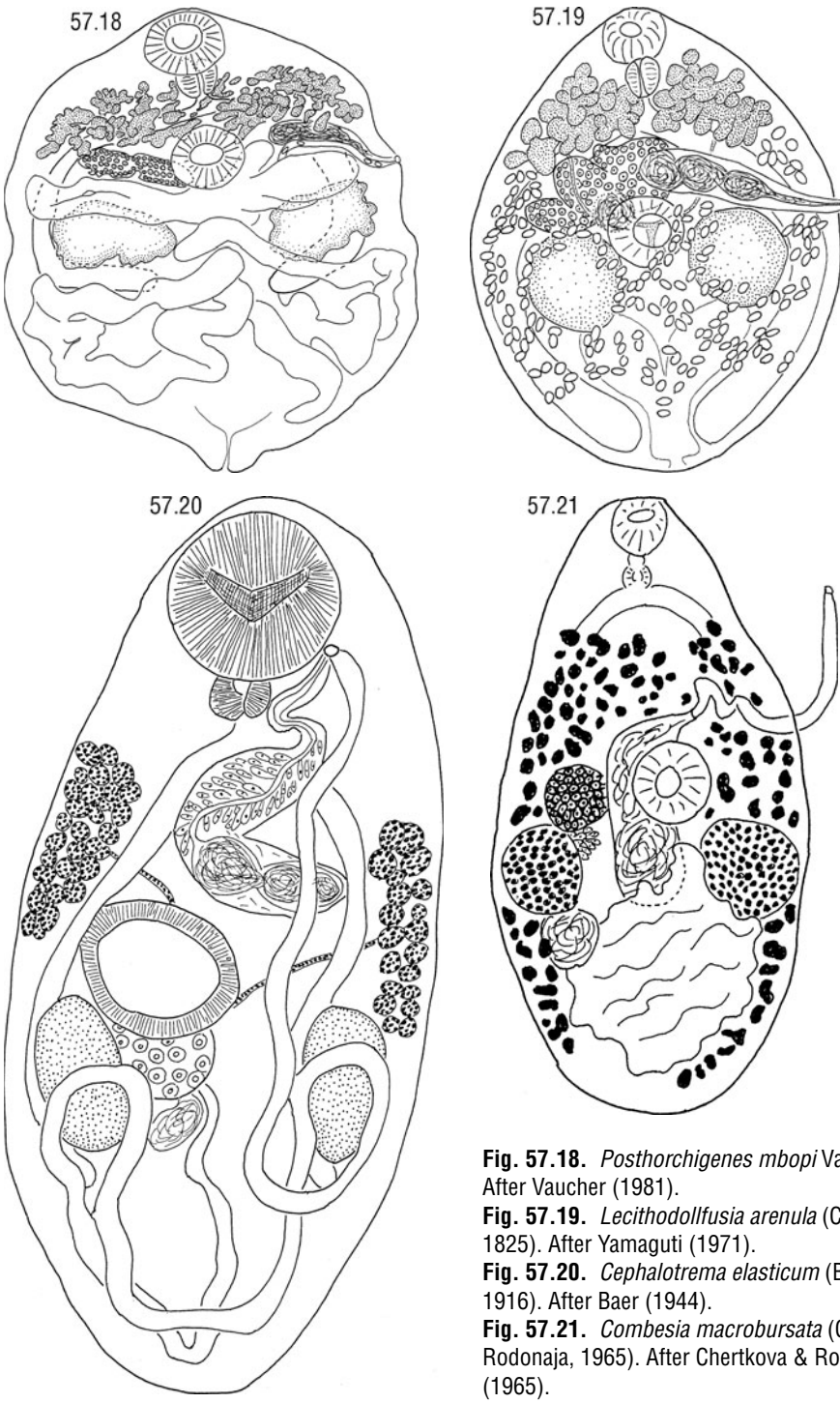



**Fig. 57.18.** *Posthorchigenes mbopi* Vaucher, 1981. After Vaucher (1981).
**Fig. 57.19.** *Lecithodollfusia arenula* (Creplin, 1825). After Yamaguti (1971).
**Fig. 57.20.** *Cephalotrema elasticum* (Bregenzer, 1916). After Baer (1944).
**Fig. 57.21.** *Combesia macrobursata* (Chertkova & Rodonaja, 1965). After Chertkova & Rodonaja (1965).

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**Diagnosis:** Body *c.* 2 mm long, fusiform. Oral sucker well developed, terminal. Ventral sucker well developed, in middle third of body. Prepharynx absent. Pharynx well developed. Oesophagus present. Caeca long, extend posterior to centre of testes to near posterior end of body. Testes symmetrical, entire, posterolateral to ventral sucker. Cirrus-sac claviform, mostly overlapping ventral sucker. Genital pore median, immediately anterior to ventral sucker. Ovary entire, at level of ventral sucker, overlaps testes. Seminal receptacle well developed. Uterus mostly in hindbody; loops may extend anterior to ventral sucker. Eggs numerous. Vitellarium in forebody, surrounds anterior portion of caeca. In birds (Galliformes, Passeriformes); Eurasia. Type-species *O. imanense* Oshmarin & Dotsenko, 1950.

**23b. Genital pore submedian to lateral, not median and at anterior margin of ventral sucker .... 24.**

**24a. Genital pore submedial posterior to anterior margin of ventral sucker ..... ..... *Parabascus* Looss, 1907. (Fig. 57.24)**

(Syns *Parabascoides* Stunkard, 1938; *Palitrema* Gogate, 1939; *Limatuloides* Dubois, 1964)

**Diagnosis:** Body from 0.5 to 3 mm long, oval. Tegument spinous. Oral sucker subterminal. Ventral sucker pre-equatorial. Prepharynx short to absent. Pharynx present. Oesophagus short to moderately long. Caeca long, extend posterior to testes. Testes symmetrical to oblique, entire, in hindbody. Cirrus-sac oriented anteriorly or transversely, mostly posterior to ventral sucker, intercaecal, contains seminal vesicle, pars prostatica and ejaculatory duct. Genital pore submedian to mid-lateral at level of or posterior to ventral sucker; male and female genital pores may open separately or side by side. Ovary entire to irregular, at level of ventral sucker, pretesticular. Seminal receptacle present. Uterus in hindbody, loops posterior to testes, overlapping or surrounding them. Eggs numerous. Vitellarium in region of ventral sucker or more anterior, typically extends to intestinal bifurcation, may extend to level of pharynx. Excretory vesicle V-shaped. In intestine of mammals (Chiroptera); Europe, Asia and the Americas. Type-species *P. lepidotus* Looss, 1907.

**24b. Genital pore submedian to lateral or anterolateral, near one caecum, anterior to ventral sucker ..... 25.**

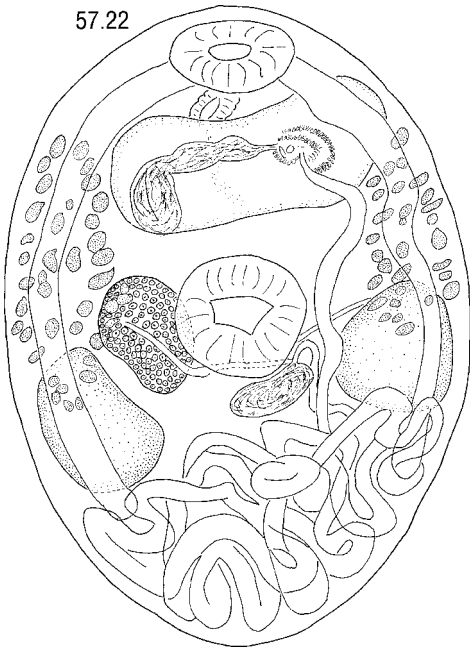
**25a. Genital pore submedian to mid-lateral near one caecum, cirrus-sac does not cross caecum ..... *Philandrophilus* Thatcher, 1970. (Fig. 57.25)**

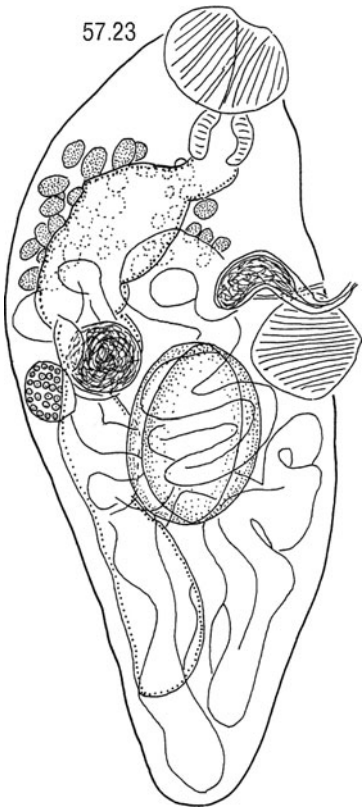
**Diagnosis:** Body 3–4 mm long, flattened, pyriform. Tegument spinous. Oral sucker terminal. Ventral sucker pre-equatorial. Prepharynx short to absent. Pharynx well developed. Oesophagus short. Caeca long, extend posterior to testes. Testes symmetrical, irregularly lobed, in hindbody. Cirrus-sac large, arcuate, courses from dorsal to ventral sucker, ends mid-laterally near caecum, contains seminal vesicle, pars prostatica and ejaculatory duct. Cirrus well developed. Genital pore submedian to mid-lateral, anterior to ventral sucker, intercaecal near one of caeca. Ovary irregular, at level of ventral sucker, pretesticular. Seminal receptacle present. Uterus in hindbody, overlaps caeca and testes. Metraterm well developed. Eggs numerous. Vitellarium follicular, in two lateral clusters at level of ventral sucker, pretesticular. Excretory vesicle Y-shaped, stem with muscular sphincter. In intestine of mammals (Marsupialia); Central America. Type-species *P. magnacirrus* Thatcher, 1970.

**25b. Genital pore anterolateral, cirrus-sac crosses caecum ..... ..... *Niviventertrema* Dronen, Homesley & Cleveland, 1995. (Fig. 57.26)**

**Diagnosis**: Body 1–2 mm long, elongate. Tegument spinous. Oral sucker subterminal. Ventral sucker pre-equatorial. Prepharynx short. Pharynx well developed. Oesophagus short. Caeca long, extend posterior to testes. Testes symmetrical, irregularly lobed, in hindbody. Cirrus-sac arcuate,

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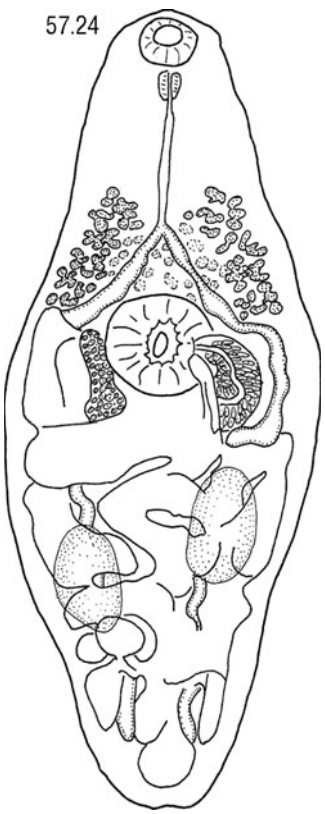
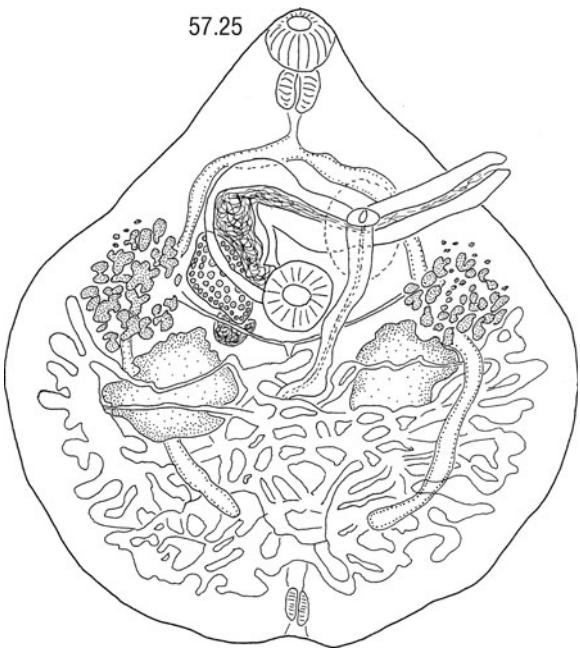




**Fig. 57.22.** *Maxbraunium tubiporum* (Braun, 1900). After Caballero & Cerecero (1942).
**Fig. 57.23.** *Ornithodendrium imanense* Oshmarin & Dotsenko, 1951. After Yamaguti (1971).
**Fig. 57.24.** *Parabascus lepidotus* Looss, 1907. After Yamaguti (1971).

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in forebody, passes from anterior to ventral sucker across caecum to anterolateral margin close to level of pharynx, contains seminal vesicle, pars prostatica and ejaculatory duct. Genital pore on anterolateral margin of body at level of pharynx. Ovary irregular to lobed, at level of ventral sucker, pretesticular. Seminal receptacle present. Uterus in hindbody, mostly post-testicular. Eggs operculate. Vitellarium follicular, in two lateral clusters at level of ventral sucker, pretesticular. Excretory vesicle Y-shaped, with fairly long stem. In intestine of mammals (Rodentia); China. Type-species *N. yunnanense* Dronen, Homesley & Cleveland, 1995 (emend.).



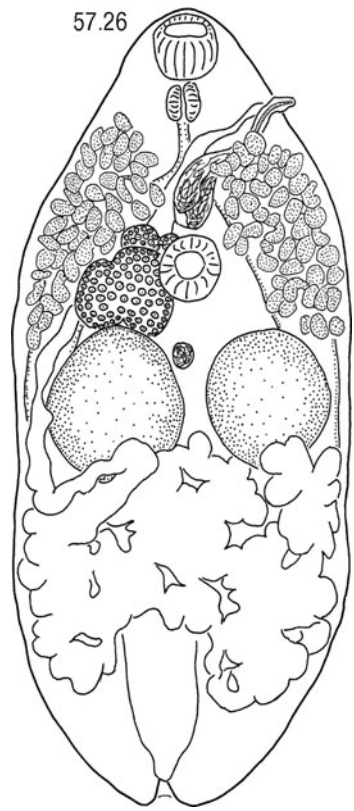




**Fig. 57.25.** *Philandrophilus magnacirrus* Thatcher, 1970. After Thatcher (1970).
**Fig. 57.26.** *Niviventertrema yunnanense* Dronen, Homesley & Cleveland, 1995. After Dronen *et al.* (1995).

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# 58 Family Pleurogenidae Looss, 1899

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## Introduction

Looss (1899) erected the subfamily Pleurogenetinae [*sic*] Looss, 1899 for *Pleurogenes* Looss, 1896 and *Prosotocus* Looss, 1899. Odhner (1910) elevated the subfamily Lecithodendriinae Lühe, 1901 to family rank and allocated the 'brachycoelid' digeneans, i.e. those with short caeca, between two subfamilies, the Lecithodendriinae for parasites of mammals with a median or submedian genital pore, comprising *Lecithodendrium* Looss, 1896, *Phaneropsolus* Looss, 1899 and *Pycnoporus* Looss, 1899, and the subfamily Pleurogeninae Looss, 1899 for parasites of amphibians with a lateral or sublateral genital pore, comprising *Pleurogenes* and *Prosotocus*. Odening (1959b) recognized the importance of the presence or absence of the cirrus and cirrus-sac for distinguishing the pleurogenids from the lecithodendriids and elevated the Pleurogeninae to family rank.

Khotenovskii (1970b) accepted the Pleurogenidae Looss, 1899 and divided it into two subfamilies, the Pleurogeninae for amphibian parasites possessing a well-developed cirrus-sac with the genital pore opening laterally or sublaterally and the Parabascinae Yamaguti, 1958 (although the correct name is Phaneropsolinae Mehra, 1935) for mammalian parasites possessing a cirrus-sac and a genital pore opening medially or submedially. We accept the Pleurogenidae at family rank, but also recognize the family Phaneropsolidae Mehra, 1935 (Lotz & Font, Chapter 57, this volume).

The life-cycle of *Cephalouterina dicamptodoni* Senger & Macy, 1953 was reported by Anderson *et al*. (1966) as having a non-virgulate xiphidiocercarial stage. This suggests that *C. dicamptodoni* may not belong in the Pleurogenidae. If related genera, such as *Cryptotropa* Strand, 1928 and perhaps *Magniuterina* Shimazu, 2004, also lack virgulate xiphidiocercariae, then the subfamily Cryptotropinae Yamaguti, 1958 may need to be removed from the Pleurogenidae.

Odening (1964c) assigned *Aliptrema* Ruiz & Leão, 1955 to the Ochetosomatidae Leão, 1944. *Aliptrema* and *Prosthopycoides* Martin, 1966 are quite similar anatomically and differ from typical pleurogenids. Their relationship to each other and to the virgulate digeneans must await elucidation of life-history and molecular characters.

Fotedar (1970) erected *Pleurochis* Fotedar, 1970 for *P. nenei* Fotedar, 1970, from the anuran *Bufo viridis* collected in Kashmir, but did not compare it with *Nenimandijea kashmirensis* Kaw, 1950 described by Kaw (1950) from the same host species, also from Kashmir. The description of

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*P. nenei* matches that of *N. kashmirensis*. Therefore, we consider *Pleurochis* to be a synonym of *Nenimandijea* Kaw, 1950. Members of *Nenimandijea* are very similar anatomically to species in the genus *Prosotocus*. Future work may reveal that the two genera are not distinct.

Mañé-Garzón & Gil (1963) erected *Iquitos* Mañé-Garzón & Gil, 1963 for *I. ceii* Mañé-Garzón & Gil, 1963, which they described from the anuran *Rana palmipes* from Peru. They placed *I. ceii* in the Brachycoelidae Looss, 1899 and therefore did not attempt to differentiate *Iquitos* from *Langeronia* Caballero & Bravo-Hollis, 1949. As the diagnosis by Mañé-Garzón & Gil (1963) matches that of Caballero & Bravo-Hollis (1949) for *Langeronia*, we consider *Iquitos* to be a synonym of *Langeronia*.

Caballero & Caballero (1969) erected *Brenesia* Caballero & Caballero, 1969 for *B. chabaudi* Caballero & Caballero, 1969, which they described from the anuran *Rana pipiens* collected in Costa Rica. Sullivan (1971), without mentioning the paper by Caballero & Caballero (1969), described *Pseudosonsinotrema echinophallus* Sullivan, 1971 from the same host species, also in Costa Rica. The descriptions of the two species match and therefore we consider *P. echinophallus* to be a junior synonym of *B. chabaudi*. However, we concur with Sullivan (1971) that the species belongs in *Pseudosonsinotrema* Dollfus, 1951. Therefore we consider *Brenesia* to be a synonym of *Pseudosonsinotrema*.

## Family Pleurogenidae Looss, 1899

**Diagnosis:** Body small to medium, robust, pyriform, ovoid to elongate. Tegument covered with well-developed spines. Oral sucker round, terminal to subterminal. Ventral sucker round, median, pre-equatorial or equatorial, occasionally postequatorial. Prepharynx short or absent. Pharynx small. Oesophagus short to elongate. Caeca paired, short, medium or long. Testes two, symmetrical to oblique, entire or rarely lobed, in fore-, mid- or hindbody. Cirrus-sac present, prominent and well developed, contains seminal vesicle, well-developed pars prostatica and ejaculatory duct. Cirrus small to large. Genital pore marginal, lateral or sublateral, typically extracaecal or caecal, rarely intercaecal, usually in forebody or at level of ventral sucker, occasionally in hindbody. Ovary submedian, in mid-body. Seminal receptacle and Laurer's canal present. Uterus coiled, typically filling posterior half of body, but extent is variable. Metraterm present, variable in prominence but often well developed. Eggs operculate, small. Vitellarium follicular, variable in extent. Excretory vesicle V- to Y-shaped; flame-cell formula 2[(2 + 2 + 2) + (2 + 2 + 2)] or 2[(3 + 3 + 3) + (3 + 3 + 3)], occasionally reported otherwise; pore terminal or nearly so. Cercaria virgulate. In amphibians and less frequently, reptiles, occasionally reported in fish and mammals but probably only accidental infections; cosmopolitan. Type-genus *Pleurogenes* Looss, 1896.

## Key to genera

**1a. Vitellarium extends from level of pharynx into hindbody and reaches level of testes; testes are in posterior third of body ..... 2.**

**1b. Vitellarium usually does not extend posterior to ventral sucker but, if it does, it does not extend to level of pharynx anteriorly ..... 3.**

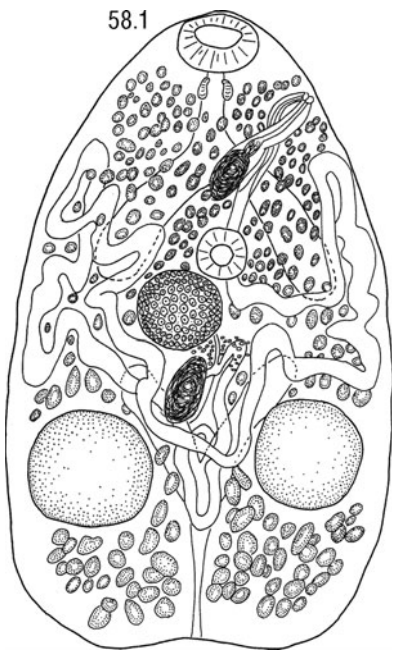
**2a. Vitellarium extends to near posterior end of body .....**
**..... *Cryptotropa* Strand, 1928. (Fig. 58.1)**
(Syn. *Cryptotrema* Ozaki, 1926, pre-occupied)

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**Diagnosis:** Body small, oval to elongate. Oral sucker small, subterminal. Ventral sucker equatorial to pre-equatorial, just posterior to intestinal bifurcation. Prepharynx short. Pharynx small. Oesophagus short. Intestinal bifurcation in forebody. Caeca short, end at level of ventral sucker. Testes symmetrical, entire, in posterior third of body. Cirrus-sac claviform, disposed anteriorly from near intestinal bifurcation to open into genital atrium, may be entirely extracaecal, contains seminal vesicle, pars prostatica and ejaculatory duct. Cirrus present. Genital atrium small. Genital pore opens on anterolateral margin of body at level of pharynx or oral sucker. Ovary anterior to testes near ventral sucker (anterior or posterior), entire. Uterus in hindbody extends from testes to caecal ends (may overlap testes posteriorly). Eggs small, operculate. Vitellarium in fore- and hindbody, extends from near oral sucker to near posterior end of body. Excretory vesicle Y- to V-shaped. In intestine of amphibians and reptiles; Madagascar, India, Asia. Type-species *C. kuretanii* (Ozaki, 1926) Strand, 1928.

**2b. Vitellarium does not extend to near posterior end of body .....**
**..... *Cephalouterina* Senger & Macy, 1953. (Fig. 58.2)**

**Diagnosis:** Body small, ellipsoidal. Oral sucker subterminal. Ventral sucker equatorial to pre-equatorial, just posterior to intestinal bifurcation. Prepharynx short. Pharynx present. Oesophagus short. Caeca short, end at level of ventral sucker. Testes symmetrical, entire, in posterior third of body. Cirrus-sac claviform, extending anteriorly from near intestinal bifurcation, contains seminal vesicle, weakly developed pars prostatica and ejaculatory duct. Genital atrium small. Genital pore opens dorsally close to anterolateral margin of body at level of oral sucker. Ovary anterior to testes,



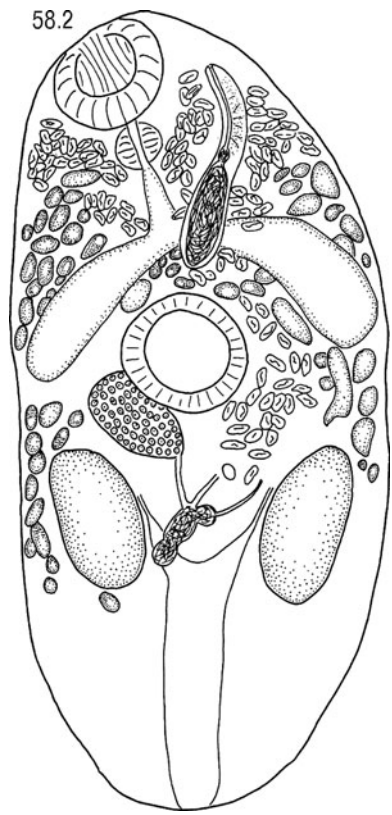




**Fig. 58.1.** *Cryptotropa kuretanii* (Ozaki, 1926) Strand, 1928. After Prudhoe & Bray (1982).
**Fig. 58.2.** *Cephalouterina dicamptodoni* Senger & Macy, 1953. After Senger & Macy (1953).

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near ventral sucker, entire. Uterus passes anteriorly from ovary to anterior to caeca, most prominent anterior to caeca. Eggs small, operculate, not numerous, with short abopercular spine. Vitellarium in fore- and hindbody, extends from near oral sucker to level of testes, does not extend to near posterior end of body. Excretory vesicle Y-shaped. In intestine of amphibians; North America, Africa, Asia. Type-species *C. dicamptodoni* Senger & Macy, 1953.

**3a. Testes in anterior third of body, extracaecal and anterior to caeca; ovary posterior to testes ..... 4.**

**3b. Testes in middle or posterior third of body, not extracaecal and not anterior to caeca; ovary anterior to or at level of testes ..... 5.**

**4a. Caeca long, terminate near posterior end of body ..... ..... *Mehraorchis* Srivastava, 1934. (Fig. 58.3)**

**Diagnosis:** Large virgulate digeneans. Body 2–5 mm long, oval to elongate. Oral sucker terminal to subterminal. Ventral sucker equatorial to pre-equatorial. Prepharynx short. Pharynx well developed. Oesophagus elongate. Intestinal bifurcation in forebody. Caeca long, extend to near posterior end of body. Testes symmetrical, entire, in anterior third of body, precaecal. Cirrus-sac muscular, extending anteriorly from near intestinal bifurcation, contains well-developed seminal vesicle, pars prostatica and ejaculatory duct. Genital atrium small. Genital pore opens on anterolateral margin of body at level of oral sucker. Ovary posterior to testes near ventral sucker, entire. Uterus fills most of hindbody. Metraterm present. Eggs small, operculate, numerous. Vitellarium pre-equatorial, surrounds testes, may extend somewhat posterior to ovary. Excretory vesicle V-shaped. Encysted in hepatic system or free in intestine of amphibians and reptiles; India. Type-species *M. ranarum* Srivastava, 1934.

**4b. Caeca short, terminate in anterior or middle third of body ..... ..... *Prosotocus* Looss, 1899. (Fig. 58.4)**

**Diagnosis:** Body small, oval, pyriform to round. Oral sucker terminal to subterminal. Ventral sucker pre- to postequatorial. Prepharynx short to absent. Pharynx small. Oesophagus short to elongate. Intestinal bifurcation in forebody. Caeca short, usually terminate anterior to ventral sucker in anterior or middle third of body. Testes symmetrical, entire, in anterior third of body, precaecal. Cirrus-sac large, muscular, extending anteriorly from ventral sucker zone, contains coiled seminal vesicle, well-developed pars prostatica and eversible cirrus. Genital atrium narrow, short. Genital pore opens on lateral to anterolateral margin of body from level of caeca to near level of pharynx. Ovary posterior to testes, anterior to ventral sucker or in ventral sucker zone, entire or irregular. Uterus fills most of hindbody, may extend into forebody with occasional uterine loop extending anterior to testes. Metraterm present, not strongly developed. Eggs small, operculate, numerous. Vitellarium in anterior third of body, precaecal, mostly pretesticular. Excretory vesicle V-shaped. In intestine of amphibians; Europe, western and southern Asia. Type-species *P. confusus* (Looss, 1896) Looss, 1899.

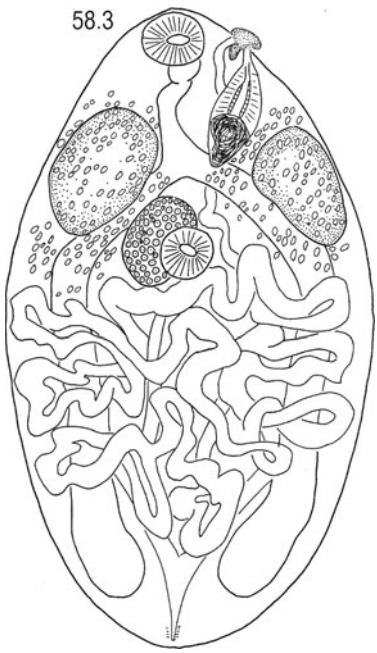
**5a. Genital pore median, in forebody, opens inside longitudinal ventral sucker zone ..... 6.**

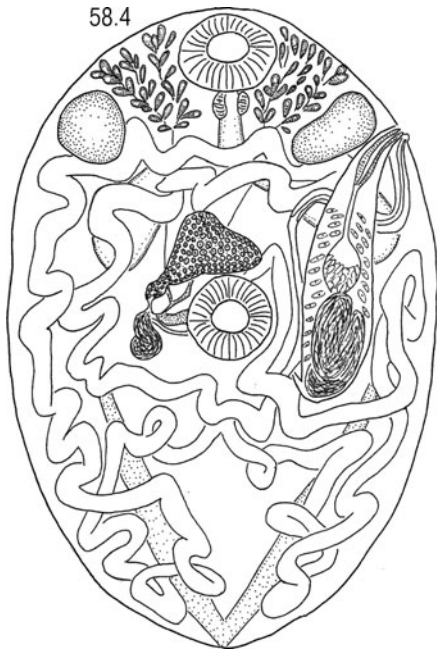
**5b. Genital pore lateral or sublateral, opens outside longitudinal ventral sucker zone ..... 8.**

**6a. Genital pore opens closer to pharynx than to ventral sucker, cirrus-sac wholly anterior to ventral sucker ..... *Loxogenoides* Kaw, 1943. (Fig. 58.5)**

(Syns *Krullitrema* Ogata, 1954; *Larelmintha* Lautenschlager & Cheng, 1958)

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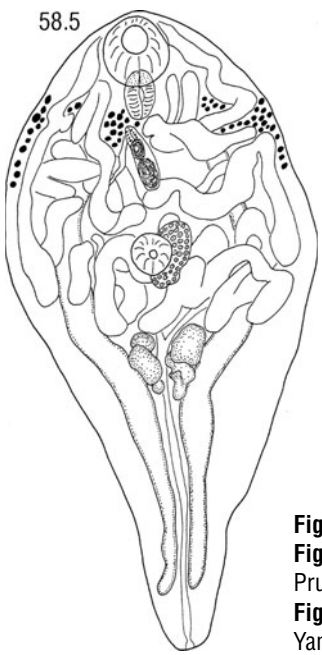




**Fig. 58.3.** *Mehraorchis ranarum* Srivastava, 1934. After Yamaguti (1971).
**Fig. 58.4.** *Prosotocus confusus* (Looss, 1984) Looss, 1899. After Prudhoe & Bray (1982).
**Fig. 58.5.** *Loxogenoides polyorchis* (Lautenschlager & Cheng, 1958) Yamaguti, 1971. After Yamaguti (1971).

**Diagnosis:** Large virgulate digeneans. Body 2–6 mm long, elongate, pyriform to oval. Oral sucker subterminal. Ventral sucker pre-equatorial. Prepharynx absent. Pharynx well developed. Oesophagus short. Intestinal bifurcation in forebody. Caeca long, extend to near posterior end of body. Testes symmetrical, lobed, in posterior half of body. Cirrus-sac elongate, extending anteriorly

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from anterior margin of or anterior to ventral sucker, contains bipartite seminal vesicle, small pars prostatica and coiled ejaculatory duct surrounded by prostatic cells. Genital atrium small. Genital pore opens submedially at level of pharynx or intestinal bifurcation. Ovary anterior to testes in ventral sucker zone, irregular. Uterus pre-equatorial, extensive or not. Metraterm present. Eggs operculate, small. Vitellarium in anterior third of body, mainly precaecal. Excretory vesicle T- or Y-shaped. In intestine of amphibians; North America. Type-species *L. bicolor* (Krull, 1933) Kaw, 1943.

**6b. Genital pore opens close to ventral sucker; cirrus-sac overlaps ventral sucker ..... 7.**

**7a. Caeca long, extend posterior to testes; vitellarium extends back to level of anterior margin of testes but not to level of pharynx ..... *Aliptrema* Ruiz & Leão, 1955. (Fig. 58.6)**

**Diagnosis:** Body small, elongate to oval. Oral sucker large, subterminal. Ventral sucker equatorial. Prepharynx present. Pharynx well developed. Oesophagus short. Intestinal bifurcation in mid-forebody. Caeca long, extend posteriorly beyond testes. Testes symmetrical, entire, in posterior half of body, in hindbody, intercaecal. Cirrus-sac small, recurved, in ventral sucker zone, posterior to intestinal bifurcation and intercaecal, about size of ventral sucker, contains seminal vesicle (pars prostatica not reported) and ejaculatory duct. Genital pore opens submedially immediately anterior to ventral sucker. Ovary anterior to testes in ventral sucker zone, entire. Uterus convoluted in post-testicular zone, extends to near oral sucker. Metraterm not well developed. Eggs operculate, small. Vitellarium in middle third of body between testes and intestinal bifurcation. Excretory vesicle Y-shaped. In oral cavity and oesophagus of reptiles; South America. Type-species *A. ribeiroi* Ruiz & Leão, 1955.

**7b. Caeca short, not reaching level of testes; vitellarium precaecal, not reaching level of testes ..... *Prosthopycoides* Martin, 1966. (Fig. 58.7)**

**Diagnosis:** Body small, oval. Oral sucker large, subterminal. Ventral sucker postequatorial. Prepharynx short. Pharynx small. Oesophagus short. Intestinal bifurcation in mid-forebody. Caeca short, widely divergent, terminate in forebody, not reaching level of testes. Testes symmetrical, entire, in forebody. Cirrus-sac thin-walled, small, recurved in ventral sucker zone, posterior to intestinal bifurcation, about size of ventral sucker, contains coiled seminal vesicle, prostatic cells and eversible cirrus. Genital pore opens medially immediately anterior to ventral sucker. Ovary in testicular zone, in forebody, entire. Uterus convoluted in post-testicular zone, extends anteriorly to level of caeca. Metraterm not well developed. Eggs operculate, small. Vitellarium in two lateral pretesticular groups, posterolateral to oral sucker, anterior to caeca. Excretory vesicle V-shaped. In intestine of amphibians; North America. Type-species *P. lynchi* (Ingles, 1936) Martin, 1966.

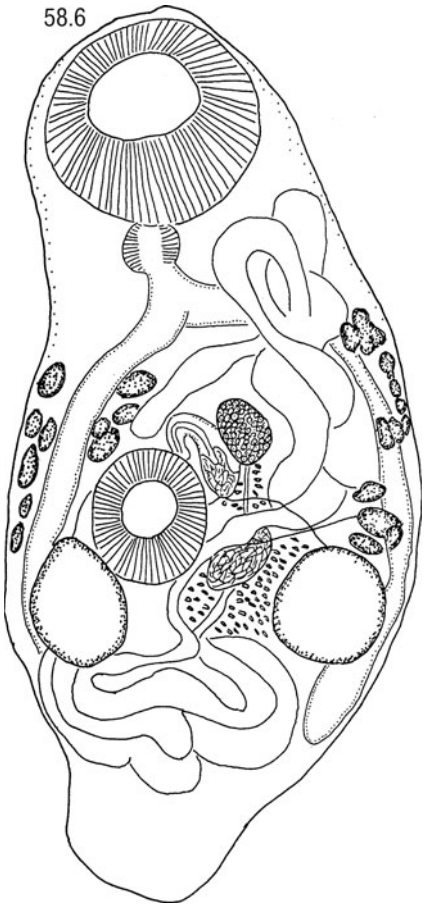
**8a. Genital pore sublateral, opens between longitudinal ventral sucker zone and lateral margin ..... 9.**
**8b. Genital pore marginal ..... 12.**

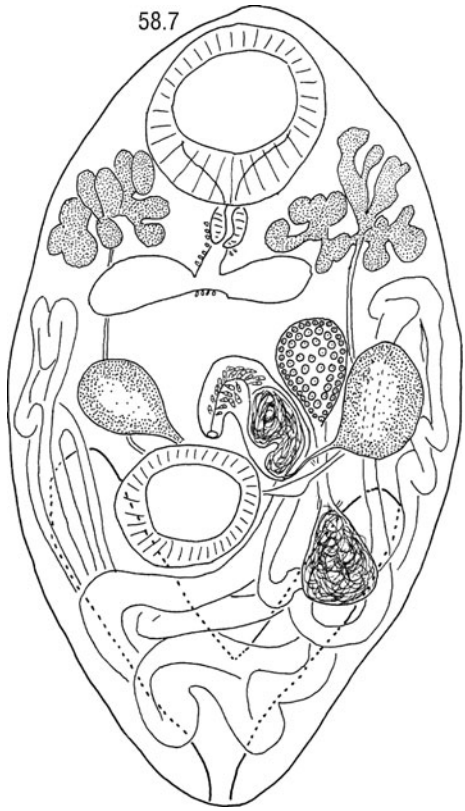
**9a. Uterine loops extend into forebody; testes embedded among uterine loops ..... 10.**
**9b. Uterine loops do not extend into forebody; testes anterior to uterine loops ..... 11.**

**10a. Genital pore opens on dorsal surface anterior to caeca; vitellarium confluent ventral to caeca ..... *Loxogenes* Stafford, 1905. (Fig. 58.8)**

**Diagnosis:** Body small, oval to subglobular. Oral sucker subterminal. Ventral sucker equatorial to postequatorial. Prepharynx short or absent. Pharynx well developed. Oesophagus short. Intestinal

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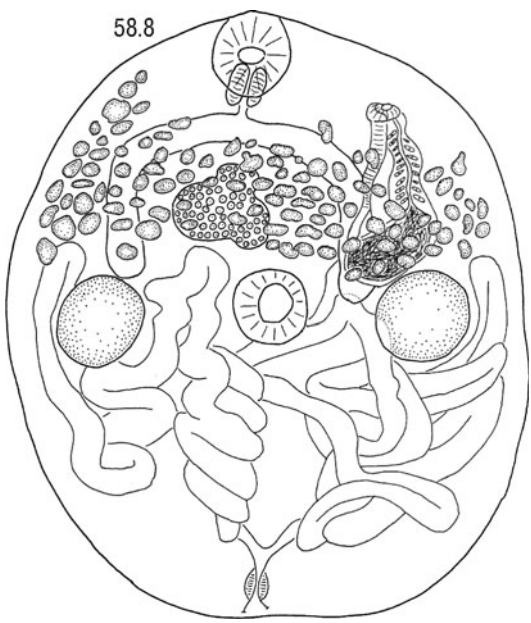




**Fig. 58.6.** *Aliptrema ribeiroi* Ruiz & Leão, 1955. After Yamaguti (1971).
**Fig. 58.7.** *Prosthopycoides lynchi* (Ingles, 1936) Martin, 1966. After Prudhoe & Bray (1982).
**Fig. 58.8.** *Loxogenes arcanum* (Nickerson, 1900) Stafford, 1905. After Prudhoe & Bray (1982).

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bifurcation in mid-forebody. Caeca short, terminate anterior to or at anterior margin of testes. Testes symmetrical, entire to irregular, equatorial in ventral sucker zone. Cirrus-sac well developed, muscular, sinuous, extending anteriorly from mid-body, contains seminal vesicle, well-developed pars prostatica and muscular ejaculatory duct/cirrus. Genital pore opens dorsally, sublateral at level of pharynx, anterior to caeca. Ovary intercaecal, anterior to testes and ventral sucker, irregular to lobed. Uterine coils occupy most of hindbody, extend into forebody. Metraterm well developed, muscular. Eggs operculate, small. Vitellarium confluent across body, ventral to caeca, between pharynx and ventral sucker. Excretory vesicle V-shaped. Encysted in hepatic system and alimentary tract of amphibians; North America. Type-species *L. arcanum* (Nickerson, 1900) Stafford, 1905.

**10b. Genital pore opens on ventral surface posterior to caeca; vitellarium in two groups lateral and anterior to caeca ..... *Nenimandijea* Kaw, 1950. (Fig. 58.9)**
(Syn. *Pleurorchis* Fotedar, 1971)

**Diagnosis:** Body small, oval to round. Oral sucker subterminal. Ventral sucker equatorial. Prepharynx short or absent. Pharynx present. Oesophagus short or absent. Intestinal bifurcation in mid-forebody. Caeca short, terminate anterior to testes. Testes symmetrical to oblique, entire, equatorial, in ventral sucker zone. Cirrus-sac well developed, S-shaped, extending anteriorly from posterior to ventral sucker and testes, contains seminal vesicle, well-developed pars prostatica and muscular ejaculatory duct/cirrus. Genital pore opens ventrally, sublateral at level of testes, posterior to caeca. Ovary anterior to ventral sucker, median to submedian, entire. Uterine coils occupy most of hindbody; loops may extend into forebody to level of pharynx. Metraterm poorly developed. Eggs small, numerous. Vitellarium anterior to ventral sucker and anterior to caeca. Excretory vesicle V-shaped. In intestine of amphibians; India and Japan. Type-species *N. kashmirensis* Kaw, 1950.

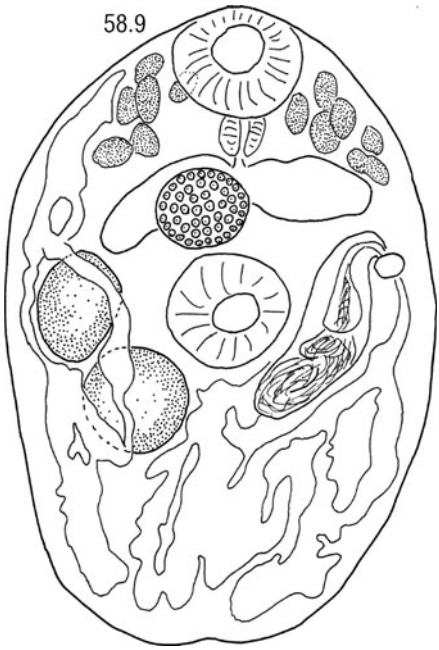
**11a. Genital pore opens posterior to level of intestinal bifurcation; uterus posterior to testes; testes not embedded among uterine loops; caeca reach testes ..... ..... *Langeronia* Caballero & Bravo-Hollis, 1949. (Fig. 58.10)**
(Syn. *Iquitos* Mañé-Garzón & Gil, 1963)

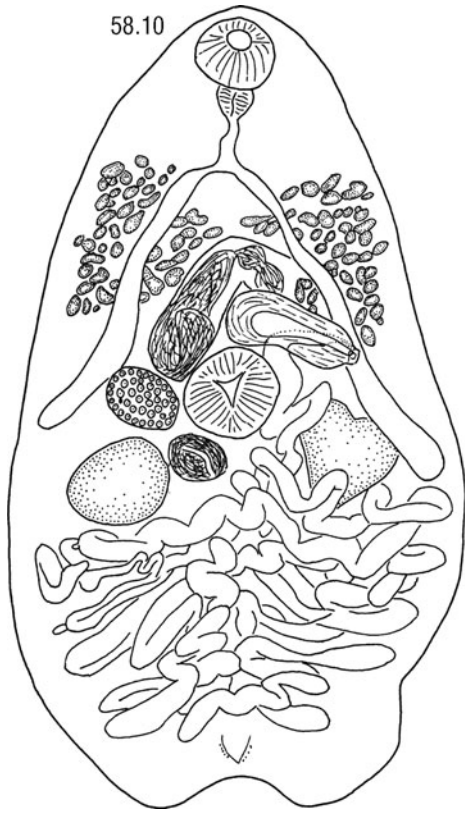
**Diagnosis:** Body small, pyriform. Oral sucker terminal to subterminal. Ventral sucker equatorial. Prepharynx short or absent. Pharynx present. Oesophagus long. Intestinal bifurcation in mid-forebody. Caeca long, extend to testes or beyond. Testes symmetrical, entire to irregular, posterior to ventral sucker. Cirrus-sac well developed, sinuous, between intestinal bifurcation and ventral sucker, extending transversely from close to ovary to opposite caecum, contains coiled seminal vesicle, well-developed pars prostatica and ejaculatory duct/cirrus. Genital pore opens sublaterally, ventrally to caecum, between ventral sucker and intestinal bifurcation. Ovary anterior to testes in ventral sucker zone, entire to irregular. Uterine coils occupy most of post-testicular hindbody. Metraterm poorly developed. Eggs small, operculate, numerous. Vitellarium in forebody between level of pharynx and ventral sucker. Excretory vesicle V-shaped. In intestine of amphibians; North and South America. Type-species *L. macrocirra* Caballero & Bravo-Hollis, 1949.

**11b. Genital pore opens at level of intestinal bifurcation; uterus extends anterior to testes; testes embedded among uterine loops; caeca do not reach testes ..... ..... *Magniuterina* Shimazu, 2004. (Fig. 58.11)**

**Diagnosis:** Body small to medium, oval to elliptical. Oral sucker subterminal. Ventral sucker preequatorial. Prepharynx short. Pharynx present. Oesophagus short. Intestinal bifurcation in mid-forebody. Caeca short, terminate in ventral sucker zone. Testes symmetrical, entire, posterior to

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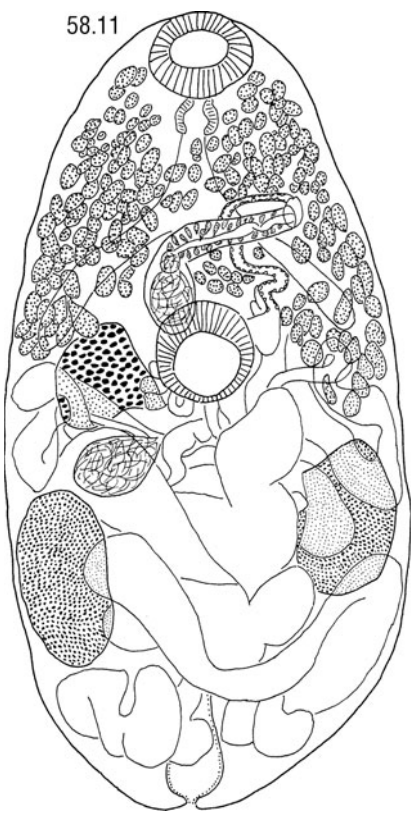




**Fig. 58.9.** *Nenimandijea kashmirensis* Kaw, 1950. (Drawing is of *Pleurorchis nenei* Fotedar, 1970). After Fotedar (1970).
**Fig. 58.10.** *Langeronia macrocirra* Caballero y C. & Bravo-Hollis, 1949. After Caballero y C. & Bravo-Hollis (1949).
**Fig. 58.11.** *Magniuterina leoi* (Uchida, Uchida & Kamei, 1986) Shimazu, 2004. After Shimazu (2004).

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ventral sucker, in posterior third of body, embedded among uterine loops. Cirrus-sac claviform and curved, extending anteriorly from ventral sucker ventrally across caecum, contains bipartite seminal vesicle, small pars prostatica surrounded by prostatic cells and protrusible cirrus. Genital pore opens sublaterally on ventral surface anterior to caecum at level of intestinal bifurcation. Ovary at level of ventral sucker or slightly posterior, anterior to testes, entire. Uterine coils occupy most of hindbody. Metraterm long, surrounded by gland-cells. Eggs small, operculate, numerous, with short abopercular spine. Vitellarium in forebody between level of pharynx and ovary. Excretory vesicle Y-shaped. In intestine of amphibians; Japan. Type-species *M. leoi* (Uchida, Uchida & Kamei, 1986) Shimazu, 2004.

**12a. Caeca long, extend well posterior to ventral sucker; testes in hindbody; if testes not at posterior end of body, caeca extend past testes ..... 13.**

**12b. Caeca short to mid-length; testes do not extend posterior to ventral sucker or barely so; caeca do not extend past testes ..... 14.**

**13a. Gonads deeply lobed; testes anterior to uterine coils; stem of excretory vesicle without folds ..... *Pleurolobatus* Kaw, 1943. (Fig. 58.12)**

**Diagnosis:** Body large (2–5 mm long), ovate. Oral sucker terminal to subterminal. Ventral sucker pre-equatorial. Prepharynx short or absent. Pharynx small. Oesophagus short. Intestinal bifurcation in mid-forebody. Caeca long, terminate posterior to testes in posterior third of body. Testes symmetrical, deeply lobed, in hindbody, in middle third of body. Cirrus-sac claviform, anterior to ventral sucker, extending obliquely from ovary across caecum, contains coiled seminal vesicle, pars prostatica surrounded by prostatic cells and long ejaculatory duct. Genital pore opens on lateral margin of body anterior to ventral sucker and posterior to intestinal bifurcation. Ovary deeply lobed, at level of ventral sucker to slightly anterior, pretesticular. Uterine loops occupy most of post-testicular hindbody. Metraterm well developed, muscular. Eggs small, operculate, numerous. Vitellarium in forebody between level of pharynx and testes, ventral to caeca. Excretory vesicle V-shaped; stem lacks folds. In hepatic system of amphibians; Japan. Type-species *P. lobatus* (Ozaki, 1926) Kaw, 1943.

**13b. Gonads entire; testes embedded among uterine folds; stem of excretory vesicle with folds ..... *Pleurogenes* Looss, 1896. (Fig. 58.13)**
(Syn. *Candidotrema* Dollfus, 1951)

**Diagnosis:** Body small to medium-sized, elongate to spherical. Oral sucker terminal to subterminal. Ventral sucker pre-equatorial. Prepharynx short or absent. Pharynx small. Oesophagus short. Intestinal bifurcation in mid-forebody. Caeca long, terminate in posterior third of body. Testes symmetrical to oblique, entire, posterior to ventral sucker, in posterior third of body, embedded among uterine loops. Cirrus-sac large, claviform, extending anteriorly from near ventral sucker across caecum, contains coiled seminal vesicle, large pars prostatica surrounded by prostatic cells and ejaculatory duct. Genital pore opens on lateral margin of body anterior to ventral sucker and posterior to intestinal bifurcation. Ovary at level of ventral sucker, anterior to testes, entire. Uterine coils occupy most of hindbody. Metraterm long, muscular, S-shaped, passes dorsal to cirrus-sac and enters genital atrium anterior to male system. Eggs small, operculate, numerous. Vitellarium primarily in anterior half of body between level of pharynx and ovary or slightly more posterior. Excretory vesicle Y-shaped; stem with distinct longitudinal folds. In intestine and hepatic system of amphibians; cosmopolitan. Type-species *P. claviger* (Rudolphi, 1819) Looss, 1896.

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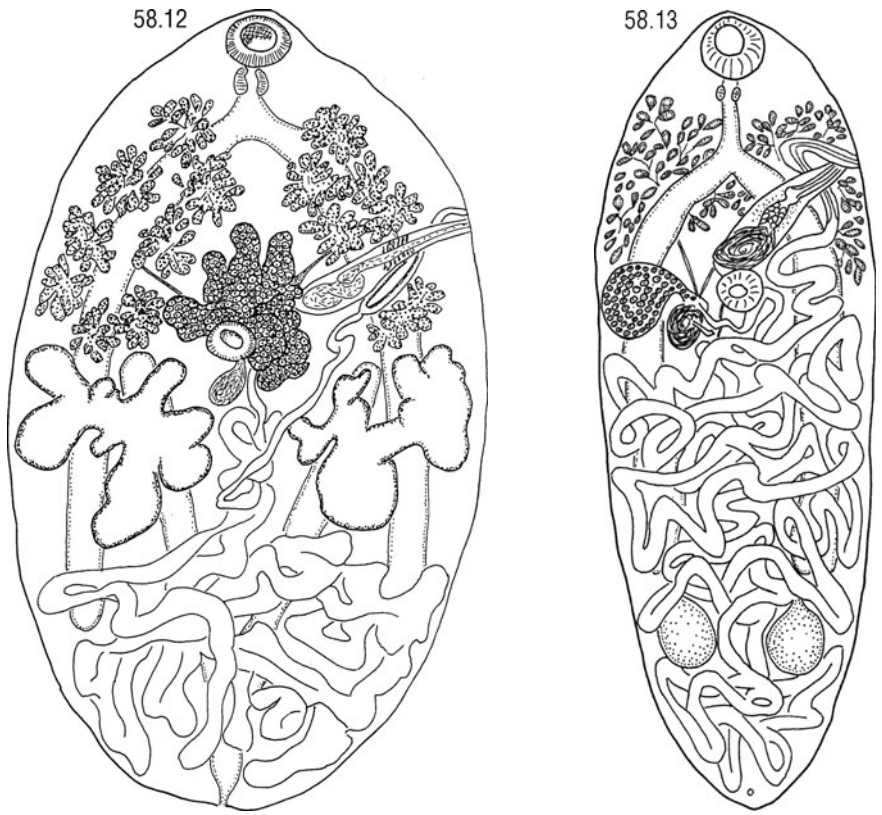


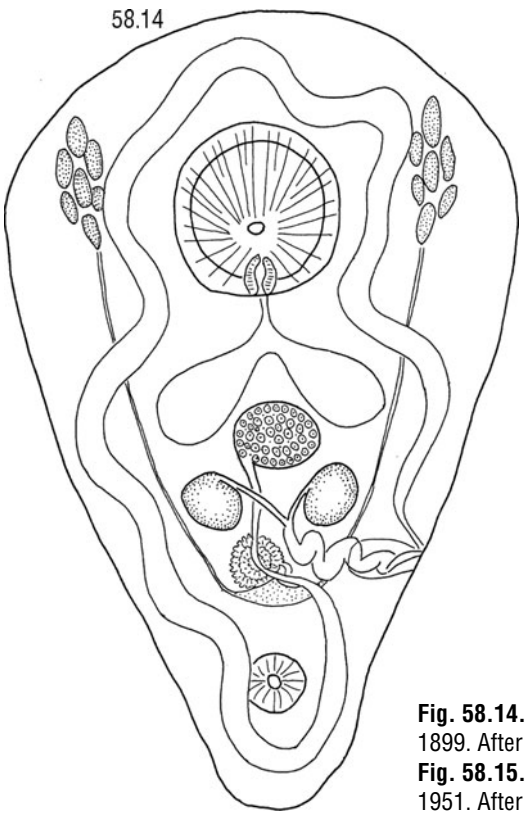

**Fig. 58.12.** *Pleurolobatus lobatus* (Ozaki, 1926). After Yamaguti (1971).
**Fig. 58.13.** *Pleurogenes claviger* (Rudolphi, 1819) Looss, 1899. After Yamaguti (1971).

**14a. Ventral sucker in posterior third of body; genital pore posterior to caeca; ovary irregular to lobed ..... *Brandesia* Stossich, 1899. (Fig. 58.14)**

**Diagnosis:** Body small, pyriform to oval. Oral sucker large subterminal. Ventral sucker in posterior third of body. Prepharynx short or absent. Pharynx well developed. Oesophagus short to absent. Intestinal bifurcation in anterior forebody. Caeca short, terminate in mid-forebody. Testes large, symmetrical, entire to irregular, anterior to ventral sucker, in middle third of body. Cirrus-sac large, claviform, extending mainly transversely from near ventral sucker or anterior to it, contains coiled seminal vesicle, large pars prostatica surrounded by prostatic cells and ejaculatory duct. Genital pore opens on lateral margin of body, in posterior half of body, at or about level of ventral sucker, posterior to caeca. Ovary in middle third of body, anterior to ventral sucker, at level of testes, irregular to lobed. Uterine coils occupy most of body. Metraterm short, surrounded by gland-cells. Eggs small, operculate. Vitellarium composed of few large follicles on each side at level of oral sucker. Excretory vesicle Y-shaped. In intestinal crypts of amphibians; Europe and Africa. Type-species *B. turgida* (Brandes, 1888) Stossich, 1899.

**14b. Ventral sucker in middle third of body; genital pore anterior to caeca; ovary entire or irregular ..... 15.**

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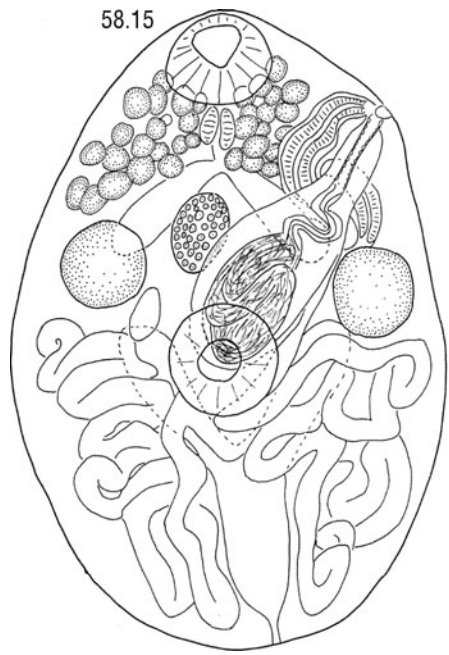




**Fig. 58.14.** *Brandesia turgida* (Brandes, 1888) Stossich, 1899. After Yamaguti (1971).
**Fig. 58.15.** *Pseudosonsinotrema chamaeleonis* Dollfus, 1951. After Prudhoe & Bray (1982).

**15a. Metraterm prominent, thick-walled** ..... ***Pseudosonsinotrema*** **Dollfus, 1951. (Fig. 58.15)**
(Syn. *Brenesia* Caballero & Caballero, 1969)

**Diagnosis:** Body small, oval. Oral sucker terminal to subterminal. Ventral sucker equatorial to pre-equatorial. Prepharynx short or absent. Pharynx present. Oesophagus short. Intestinal bifurcation in mid-forebody. Caeca short, terminate in forebody. Testes symmetrical, entire or irregular, in anterior half of body, near caecal ends. Cirrus-sac large, claviform, extending obliquely from ventral sucker zone, contains coiled seminal vesicle, large pars prostatica surrounded by prostatic cells and ejaculatory duct. Genital pore opens on lateral margin of body in anterior half of body at level of intestinal bifurcation to pharynx. Ovary anterior to ventral sucker, postbifurcal, entire to irregular. Uterine coils occupy most of hindbody, may extend anterior to testes. Metraterm long, very thick-walled, muscular, S-shaped, dorsal to cirrus-sac, enters genital atrium anterior to male system. Eggs small, operculate. Vitellarium composed of few large follicles extending from oral sucker to caeca. Excretory vesicle V- to Y-shaped. In intestine of amphibians and reptiles; North America, Central America, Africa. Type-species *P. chamaeleonis* Dollfus, 1951.

**15b. Metraterm inconspicuous, not thick-walled** ..... ***Pleurogenoides*** **Travassos, 1921. (Fig. 58.16)**
(Syns *Sonsinotrema* Balozet & Callot, 1938; *Indopleurogenes* Yamaguti, 1971; *Paraindopleurogenes* Kalyankar & Palladwar, 1977; *Ompoktrema* Varma & Singh, 1982)

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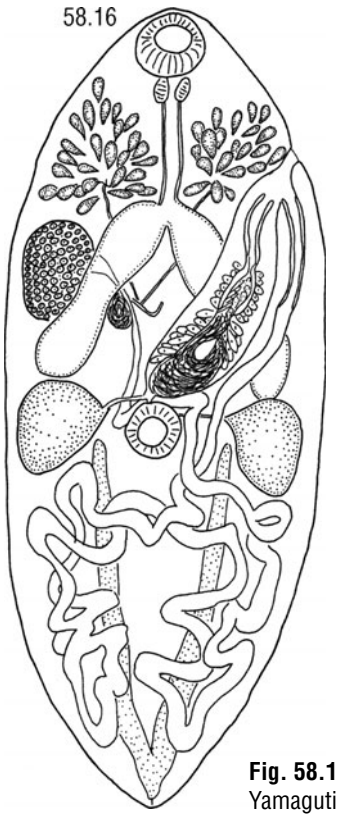



**Fig. 58.16.** *Pleurogenoides medians* (Olsson, 1876) Travassos, 1921. After Yamaguti (1971).

**Diagnosis:** Body small, oval to elongate. Oral sucker terminal to subterminal. Ventral sucker in middle third of body. Prepharynx short or absent. Pharynx well developed. Oesophagus short. Intestinal bifurcation in mid-forebody. Caeca short to moderately long, terminate near anterior margin of testes, never extend past testes. Testes symmetrical, entire to irregular, caecal or postcaecal, never precaecal, in ventral sucker zone or anterior to ventral sucker. Cirrus-sac well developed, claviform, straight to recurved, extending mainly anteriorly or obliquely from near ventral sucker or anterior to it across the caecum, contains coiled seminal vesicle, pars prostatica surrounded by prostatic cells and ejaculatory duct. Genital pore opens on anterolateral margin of body between level of intestinal bifurcation and level of pharynx. Ovary in middle third of body in forebody, pretesticular, entire to irregular. Uterine coils occupy most of body posterior to testes. Metraterm not well developed. Eggs small, operculate. Vitellarium composed of few follicles extending from pharynx to caeca, may be arranged in two lateral groups or confluent across body. Excretory vesicle V-shaped. In intestine of amphibians and reptiles, occasionally reported from fish; Europe, Africa. Type-species *P. tener* (Looss, 1898) Travassos, 1921.

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# 59 Family Prosthogonimidae Lühe, 1909

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## Introduction

The family Prosthogonimidae Lühe, 1909 contains small to medium-sized digeneans which occupy unusual sites in birds and mammals. They occur in birds most often under the nictitating membrane or in the oviduct, bursa Fabricii or cloaca, and in mammals in the body-cavity, intestine or liver. The family-group name was first used by Lühe (1909) for the subfamily Prosthogoniminae Lühe, 1909 (for *Prosthogonimus* Looss, 1899); Lahille (1922) was apparently the first to use the name at family rank.

The family has been, historically, closely connected within the plagiorchioids with the Cephalogonimidae Looss, 1899 because, among other morphological characters, both families have the genital pore close to the anterior extremity of the body. Here, they are treated separately because, despite their morphological similarities, large and small subunit ribosomal RNA gene sequences analysed by Olson *et al.* (2003) suggest that the Cephalogonimidae and Prosthogonimidae are not that closely related. They appear in separate clades, the former as a sister group of the Telorchiidae Dollfus, 1925 and the latter as a sister group of the Pleurogenidae Travassos, 1921.

Nicoll (1914) placed *Prosthogonimus* in the Cephalogonimidae, but Odhner (1910), Poche (1926) and Travassos (1928b) all placed it in the Lepodermatidae Looss, 1899 (now a synonym of the Plagiorchiidae Lühe, 1901[1]), from which Baer (1924) excluded it. Poche (1926) treated the Lepodermatidae and Prosthogonimidae as synonyms of the Plagiorchiidae.

Mehra (1931) placed the Prosthogoniminae in the Lepodermatidae, containing *Prosthogonimus* (syn. *Prymnoprion* Looss, 1899) and *Schistogonimus* Lühe, 1909, noting that the subfamily had a Y-shaped excretory vesicle, which he regarded as consistent with the Lepodermatidae. He disagreed with Nicoll's (1914) inclusion of it in the Cephalogonimidae, but Sinha (1932) followed Nicoll (1914). Mehra (1937) continued to treat the Prosthogoniminae as a lepodermatid subfamily.

[1] Although the name Lepodermatidae is the older of the two, the name Plagiorchiidae has been retained under ICZN Art. 40.2 in the interests of stability because it is the name in prevailing usage.

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Sudarikov & Nguyen (1968) proposed the subfamily Praeuterogoniminae Sudarikov & Nguyen Thi Le, 1968 for a new genus and species, *Praeuterogonimus skrjabini* Sudarikov & Nguyen Thi Le, 1968, from the small intestine of *Rattus* sp. in Vietnam. The subfamily was based on the extensive development of the vitellarium, distinctive in the family in extending between pharyngeal level and the posterior extremity, the pretesticular position of the uterus and the position of the genital pore, which is very slightly submedian at the level of the oral sucker (but see below). The distribution of the vitelline follicles and of the uterus is distinctive and both extend the scope of the family characters, but, in this relatively small family, there seems to be little value in erecting another monotypic taxon and the subfamily has not been adopted here.

## Genera and subgenera

The two major reviewers of the family, Skrjabin (1962) and Yamaguti (1971), both recognized *Prosthogonimus, Cephalotrema* Baer, 1944 (but see below), *Mediogonimus, Ophthalmogonimus* Oshmarin in Skrjabin, 1962 and *Schistogonimus*. Several other genera have been added more recently.

The type-genus, *Prosthogonimus*, contains many nominal species. Twenty-three species had been placed in the genus *sensu lato* by 1936; these Witenberg & Eckman (1939) reduced to seven, but Yamaguti (1971) listed almost 50. Over about 36 years, Skrjabin and co-workers (Skrjabin & Baskakov, 1925; Skrjabin & Massino, 1925; Skrjabin, 1962) erected the subgenera *Prosthogonimus, Prosthogenotrema, Macrogenotrema, Mediogenotrema, Politogenotrema, Primagenotrema* and *Ultragenotrema*. The literature on the dates and authorities of some subgenera is confused, see, *inter alii*, Skrjabin (1962) and the USDA *Index-Catalogue* (1966–68), and Yamaguti (1971). Skrjabin (1962) himself attributed the same names to different authorities, citing the nominal subgenus as *Prosthogonimus* Skrjabin & Baskakov, 1925, but also dating it as 1941 (it should be Lühe, 1899 according to the Principle of Coordination). He (Skrjabin, 1962) attributed *Macrogenotrema* and *Politogenotrema* to Skrjabin & Baskakov (1925) but gave the date as 1941 elsewhere in his text, whereas the *Index-Catalogue* credits *Macrogenotrema* and *Ultragenotrema* to Skrjabin & Massino, 1925 (it has no entry for *Politogenotrema*). Skrjabin gave 'Skrjabin & Baskakov, 1941' as the authority for *Primagenotrema* (but cited no reference, and attempts to trace it have failed). Both Skrjabin (1962) and the *Index-Catalogue* gave 'Skrjabin & Gnedina, 1941' as the authority for *Prosthogenotrema* but without a citation and attempts to trace it have failed; therefore, neither reference appears in the bibliography. Skrjabin & Baskakov (1925) presented survey results but nothing on the subgenera and their diagnoses, while Skrjabin & Massino (1925) listed *Ultragenotrema* and *Macrogenotrema*, attributing them to Skrjabin & Baskakov (1925); neither paper has a bibliography, so references cannot be traced, and neither fulfils the criteria required for the names to be available. They may have planned further publications. Yamaguti (1971) credited all subgenera except *Prosthogonimus* to Skrjabin & Bashkirova (a consistent error for Baskakov) in 1925 (*Prosthogenotrema, Macrogenotrema, Politogenotrema*) or 1941 (*Mediogenotrema, Primagenotrema*), although for *Prosthogenotrema* and *Politogenotrema* he dated the type-species as 1941. The authority adopted in these keys is Skrjabin (1941), which appears to be the best supported.

Panin (1957) recognized the subgenera *Prosthogonimus, Macrogenotrema* and *Mediogenotrema* (attributing them to 'Skrjabin & Baskakov, 1941' without citing a reference) but not *Primagenotrema, Prosthogenotrema* or *Politogenotrema*. He considered the type-species of *Primagenotrema* to be synonymous with a species of *Mediogenotrema*, which made the former a synonym of the latter, and

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the types of *Prosthogenotrema* and *Politogenotrema* to be inadequately described. Boddeke (1960) listed the type-species of the subgenera *Macrogenotrema, Mediogenotrema* and *Primagenotrema* as synonyms of *Prosthogonimus ovatus* (Rudolphi, 1803), so all three would fall as synonyms of the nominal genus (and subgenus, if recognized). Furthermore, Yamaguti (1971) pointed out that *P. fuelleborni* Skrjabin & Massino, 1925, allocated to *Politogenotrema* by Skrjabin & Massino (1925), was regarded as a host-induced variant of *Prosthogonimus ovatus* by Boddeke but had been treated as synonymous with *P. putschkowskii* Skrjabin, 1912 by Witenberg & Eckman (1939). Also, Krasnolobova (1969) had treated *P. anatinus* Markov, 1903, listed under *Primagenotrema* by Skrjabin (1962), as a synonym of *Prosthogonimus pellucidus* (Linstow, 1873), which Skrjabin (1962) allocated to *Politogenotrema*, but which Boddeke (1960) synonymized with *Prosthogonimus ovatus*. Witenberg & Eckman (1939) regarded *P. anatinus* Markov, 1902, later the type of *Mediogenotrema*, as a poorly described species *inquirenda*. Skrjabin (1962) continued to recognize the subgenera *Prosthogonimus, Macrogenotrema, Politogenotrema, Prosthogenotrema* and *Primagenotrema* (including about 37 species in *Prosthogonimus* (*sensu lato*)), but did not include *Mediogenotrema* or *Ultragenotrema*.

Further indicating the difficulty of distinguishing between species, Boddeke (1960) regarded *P. ovatus* and *P. cuneatus* not as distinct, but as age- and host-induced morphological variations. Annotations in Yamaguti's (1971) list of nominal species clearly indicate the problems he and others had in establishing the limits of species and higher groups. He (Yamaguti, 1971) suppressed all the above subgenera except *Prosthogonimus*, but erected a new subgenus, *Prosthogonimoides* Yamaguti, 1971, for *Prosthogonimus sudarikovi* Oshmarin, 1946 and *P. macroskrjabini* Mosgovoi & Mishenina, 1959, in which the vitellarium was restricted to the zone of the ventral sucker and ovary. He suppressed *Ultragenotrema* (presumably already abandoned by Skrjabin (1962), who had not included it) on the grounds either that no type had been cited or that it was *P. ovatus*, already the type of the subgenus *Prosthogonimus*.

As indicated by Yamaguti's (1971) list of nominal species and confirmed here, the literature is so deeply divided about the validity and position of species of *Prosthogonimus* that it is not useful to recognize subgenera at present. The situation is unlikely to be resolved without good redescriptions, preferably supported by experimental infections to investigate the extent of age- and host-induced variations in morphology, or without DNA sequences to establish the validity of significant species. Currently, continuing to utilize subgenera raises more problems than it resolves.

*Cephalotrema* Baer, 1944, based on *C. minutum* Baer, 1944 from European rodents, was originally assigned to the Lecithodendriidae Lühe, 1901 and Pleurogenetinae Looss, 1899 by Baer (1944). Although treated as a prosthogonimid by Yamaguti (1958b, 1971) and Skrjabin (1962), it was restored to its original family and subfamily by Combes & Jourdane (1969). Cribb & Spratt (1990) concurred. In these keys, it is regarded as a phaneropsolid (see Lotz & Font, Chapter 57, this volume).

Angel (1973) described two new genera from birds in South Australia, *Cylindrotrema* Angel, 1973 from the caecum of the black swan *Cygnus atratus* (Latham) and *Mawsonotrema* Angel, 1973 from the liver ducts of the fairy penguin *Eudyptula minor* (Forster). Prosthogonimid characteristics are generally considered to include an armed body-surface but, according to Angel, the surface of *Cylindrotrema*, although in good condition, had no spines. *Mawsonotrema* is discussed below.

*Coelomotrema aegyptiacum* Jones & El-Azazy, 1986 was based on three specimens from *Rattus norvegicus* in Egypt (Jones & El-Azazy, 1986). The species name is emended here to conform with the neuter generic name. The specimens were believed to be from the body-cavity, a conclusion supported by the feeble development of the suckers. This species was originally placed in

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*Coelomotrema* Angel, 1970, based on *C. antechinomes* Angel, 1970 from the body-cavity of two species of Australian dasyurid marsupials (Angel, 1970) and later found in a third dasyurid by Cribb & Spratt (1990). Although close to *Coelomotrema*, the African species is considered here to represent a distinct genus, based on: the vestigial oral sucker; the poorly developed ventral sucker; a median genital pore at the anterior extremity rather than submedian and lateral to the oral sucker; a pyriform rather than oval ovary; and the larger, more elongate body. It also has relatively smaller testes, slightly larger eggs and is parasitic in an African rodent rather than in Australian marsupials. The genus is named *Tahratrema* n.g., after the locality of collection in Tahra village, Sharkia Province, and the species is transferred as *T. aegyptiacum* (Jones & El-Azazy, 1986) n. comb. It resembles *Coryphogonimus* Cribb & Spratt, 1990, based on *C. aglaos* Cribb & Spratt, 1990, from *Rattus fuscipes* in Australia, but differs in: the poor development of the suckers; the shorter caeca, which terminate anteriorly to the testes; the unlobed ovary and testes; the more restricted vitelline fields; and the position of the genital pore at the anterior extremity rather than dorsal to the oral sucker. Although Cribb & Spratt's (1990) abstract states that the caeca end 'in front of testes', this is clearly unintentional, as elsewhere they are illustrated and described as 'terminating blindly in hindbody posterior to testes'. *Coryphogonimus*, distinguished primarily by the position of the genital pore directly dorsal to the oral sucker, is a rodent parasite, occupying the gall-bladder, bile-ducts and capsules on the surface of the liver. *Coelomotrema* and *Tahratrema* have been retained in the prosthogonimids, although Zamparo *et al*. (2003a) considered the former to be a lecithodendriid, without elaborating reasons. As defined by Lotz & Font (Chapter 54, this volume), the lecithodendriids comprise taxa with lobed and entire ovaries, occasionally in the same genus.

*Mediogonimus* Woodhead & Malewitz, 1936, from the liver of rodents in Michigan, USA, was originally placed in the 'Plagiorchiidae, subfamily Prosthogoniminae as defined by Travassos, 1928, since it possesses every family [*sic*] characteristic' (Woodhead & Malewitz, 1936). Travassos (1928b), however, did not give diagnoses of the family or subfamily. Woodhead & Malewitz characterized it by a median genital pore posterior to the oral sucker at pharyngeal level, but without further discussion of its position. It is retained here within the Prosthogonimidae, pragmatically and without total conviction, because the position of the genital pore is not dissimilar to that of some others in the family.

*Praeuterogonimus skrjabini* Sudarikov & Nguyen Thi Le, 1968 was placed in the Prosthogonimidae by Sudarikov & Nguyen (1968) on the basis of its symmetrical postovarian testes, its lobed ovary and the anterior position of the genital pore, which is said to be at the level of the posterior margin of the oral sucker in the holotype but at various levels along the length of the oral sucker in other specimens. The authors did not specify whether the genital pore was dorsal or ventral, but it appears to be illustrated as ventral in their figure 2b, although the figure legend does not specify the view. If ventral, its position resembles that in *Mediogonimus* and, if dorsal, that in *Coryphogonimus*. It is described in the text as submedian but is illustrated as virtually median.

Krasnolobova (1969) demonstrated experimentally that *Schistogonimus rarus* (Braun, 1901) was an atypical form of *Prosthogonimus acutus* (Rudolphi, 1803) and synonymized *Schistogonimus* with *Prosthogonimus*; Mehra (1937) had distinguished them by the proximity of the male and female pores and the extent of the uterine coils beyond the caeca in *Prosthogonimus*, as opposed to separate pores and intercaecal coils in *Schistogonimus*. This suggests that these characters should be used cautiously at generic level. A close relationship between them was demonstrated by Olson *et al*. (2003), who showed that, according to large and small subunit ribosomal RNA gene sequences, *P. ovatus* and *S. rarus* were, although distinct species, very close and could be congeneric. *Schistogonimus* is treated here as a synonym of *Prosthogonimus*, pending new evidence to the contrary.

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The genus most recently assigned to the family is *Whallwachsia* Zamparo, Brooks & Causey, 2003, described for the new species *W. illuminata* Zamparo, Brooks & Causey, 2003, from the intestine of *Amazilia saucerrottei* and bile-duct of *Tolmomyias sulphurescens* in Costa Rica (Zamparo *et al.*, 2003a).

## Genera *incertae sedis*

The morphological characters by which the family has traditionally been recognized are: the spined tegument; caeca ending short of the posterior extremity; testes symmetrical or subsymmetrical, usually entire; cirrus-sac present, contains seminal vesicle and prostatic cells; genital pore at or very close to the anterior extremity; ovary pretesticular, more or less deeply lobed; a largely post-testicular uterus that usually occupies most of the hindbody; eggs small, numerous; vitelline fields restricted, with follicles frequently in bunches; excretory vesicle Y-shaped; and the unusual sites occupied in the hosts. The assignment of various genera has widened the concept of the family, with the result that some characters previously regarded as definitive are no longer treated as such. Consequently, the allocation of some genera is not straightforward.

The genital pore is not at the anterior extremity in *Mediogonimus* (medioventral, immediately posterior to the oral sucker), *Whallwachsia* (described and illustrated as submedian and submarginal ('lateral or ventral to sinistral cecum'; Zamparo *et al.*, 2003a), *Mawsonotrema* (median, ventral, at anterior margin of ventral sucker), *Coryphogonimus* (median, on the dorsal surface dorsal to the oral sucker) or *Praeuterogonimus* (more or less median, at the level of the posterior margin of the oral sucker or more anterior). *Cylindrotrema* was described as having an unarmed tegument (Angel, 1973). *Whallwachsia* has diagonal rather than symmetrical or subsymmetrical testes (Zamparo *et al.*, 2003a). The vitelline fields of *Praeuterogonimus* are very extensive and atypical of the family. The ovary is not lobed in *Coelomotrema, Tahratrema* or *Mawsonotrema* and is slightly to deeply lobed in *Coryphogonimus*.

*Mawsonotrema* was described as lacking a cirrus-sac. Angel (1973) placed it in the Prosthogonimidae despite the position of the genital pore immediately anterior to the ventral sucker. She considered it to conform to Yamaguti's (1971) diagnosis of the family in: the armed tegument; caeca terminating short of the posterior extremity; symmetrical testes in the hindbody; a pretesticular ovary; the presence of Laurer's canal; numerous small eggs; vitelline follicles in bunches; and a Y-shaped excretory vesicle. It differed, however, in: the position of the genital pore; absence of a cirrus-sac and seminal receptacle; presence of a well-developed pars prostatica; and distribution of the uterine coils, which did not fill the hindbody. Because the Prosthogonimidae is primarily characterized by the position of the genital pore at or close to the anterior extremity, *Mawsonotrema* is regarded here as a genus *incertae sedis* within the Plagiorchioidea. It has some characters in common with the Renicolidae Dollfus, 1939 (e.g. body-shape and spination, absence of a prepharynx and absence of a cirrus-sac), but differs in the shape and position of the ovary, the presence of Laurer's canal (not reported in the renicolids) and the site in the host.

## *Mawsonotrema* Angel, 1973 (Fig. 59.1)

**Diagnosis:** Body small, plump, with maximum width anterior to equator, densely spined. Suckers well developed; ventral sucker with deep cavity, usually larger than oral sucker, in anterior third or half of body. Prepharynx said to be absent. Pharynx well developed. Oesophagus short. Intestinal

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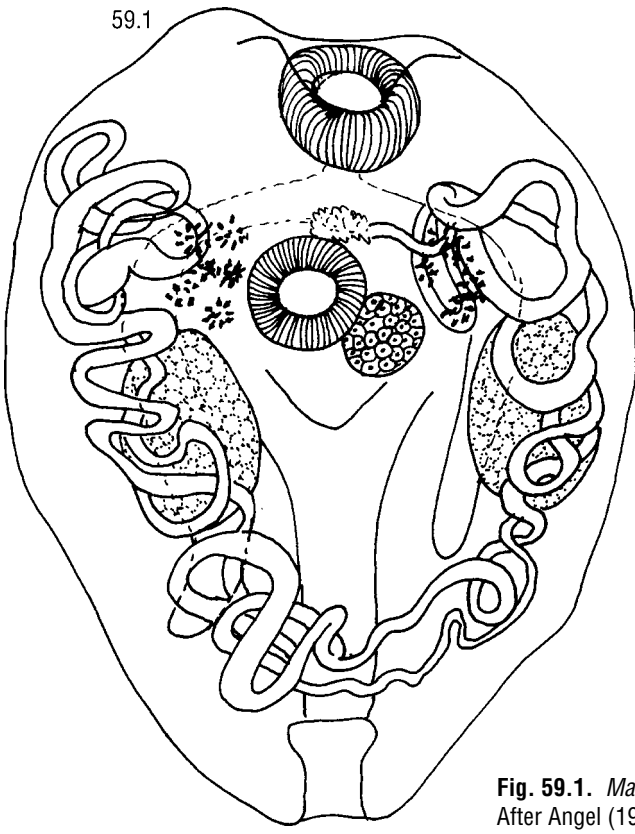



**Fig. 59.1.** *Mawsonotrema eudyptulae* Angel, 1973. After Angel (1973).

bifurcation anterior to ventral sucker. Caeca vary in width, terminate posterior to testes, well short of posterior extremity. Testes entire, oval, more or less symmetrical, dorsal to caeca in about middle of body. Vasa efferentia unite close to Mehlis' gland. Seminal vesicle said to run dorsally to ventral sucker, then narrows to form thick-walled tube surrounded by prominent prostatic cells. Cirrus-sac said to be absent. Genital pore median, ventral, at anterior margin of ventral sucker. Ovary round, entire, usually submedian, at or just anterior to level of anterior margin of testes. Mehlis' gland and Laurer's canal present. Seminal receptacle absent. Uterus forms coils on each side of hindbody posterior to level of testes, but not between them, and on either side in forebody; metraterm present. Eggs almost round. Vitelline follicles in lateral fields anterodorsal to ventral sucker, form five to eight bunches of follicles on each side, contiguous or not, medial to or overlap caeca. Excretory vesicle Y-shaped, bifurcates posterior to ventral sucker; pore terminal. In liver ducts of birds (fairy penguin, *Eudyptula minor*); Australia. Type- and only species *M. eudyptulae* Angel, 1973.

In describing *Whallwachsia*, Zamparo *et al*. (2003a) listed the genera included by Angel (1973) in the Prosthogonimidae, i.e. *Prosthogonimus* (syn. *Schistogonimus), Cephalotrema, Praeuterogonimus, Coelomotrema, Mediogonimus, Mawsonotrema* and *Cylindrotrema*, and considered *Cephalotrema* and *Coelomotrema* to be lecithodendriids. Their discussion centres on the relationships of the taxon as indicated by DNA sequencing and cladistic analysis. Of the two autapomorphies suggested for the Prosthogonimidae by Brooks *et al.* (1985, 1989), the genital

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pore at the anterior extremity and a deeply lobed ovary, they relinquished the first in the process of accommodating the genus in the family, placing *Whallwachsia* in the Prosthogonimidae because of its lobed ovary, which they considered to be the defining morphological character of the family. They distinguished it from all other genera by the non-terminal position of the genital pore (amending the family diagnosis to accommodate it), the oblique testes and the elongate rather than pyriform body. This combination of characters is distinctive, but the genus is not the only one assigned to the family in which the genital pore is not at the anterior extremity (see the diagnoses of *Mediogonimus, Praeuterogonimus, Coryphogonimus* and *Mawsonotrema*). Zamparo *et al*. (2003a) did not discuss the morphology of their specimens in relation to that of these genera. They amended the family diagnosis to include 'marginal genital pores', but that of *Whallwachsia* is 'lateral or ventral to the sinistral cecum', rather than marginal. Given that the purpose of these keys is identification of taxa by means of adult morphological characters, *Whallwachsia* is treated here as a genus *incertae sedis* within the Plagiorchioidea. This is a pragmatic position and the systematic allocation of this genus, and of others included here, will be subject to change in the light of further studies incorporating a variety of approaches.

## Genus *Whallwachsia* Zamparo, Brooks & Causey, 2003 (Fig. 59.2)

**Diagnosis:** Body elongate, tapers at anterior and posterior extremities, armed. Oral sucker subterminal, almost round. Ventral sucker in anterior half of body, similar in size to oral sucker. Prepharynx short. Pharynx present. Oesophagus short. Intestinal bifurcation well anterior to ventral sucker. Caeca long, slender, end in post-testicular region far anterior to posterior extremity. Testes entire, intercaecal, in midbody, oblique, non-contiguous, separated by uterus. Cirrus-sac dorsal to ventral sucker, contains internal seminal vesicle, prostatic cells and cirrus. External seminal vesicle absent. Genital pore anterolateral to ventral sucker, lateral or ventral to left caecum. Ovary multilobular, dextral between ventral sucker and anterior testis. Mehlis' gland postovarian, dorsal to seminal receptacle. Laurer's canal said to be absent. Uterus forms transverse loops in posterior region of hindbody, crossing posterior parts of caeca; ascending coils almost entirely intercaecal, pass between testes. Metraterm present. Vitelline follicles in lateral fields between about level of anterior margin of ventral sucker and posterior margin of anterior testis, few follicles encroach slightly on outer margins of caeca; right field longer than left field. Excretory vesicle I-shaped; pore subterminal, ventral. In intestine and bile-duct of birds (*Amazilia saucerrottei, Tolmomyias sulphurescens*); Costa Rica. Type- and only species *W. illuminata* Zamparo, Brooks & Causey, 2003.

## Family Prosthogonimidae Lühe, 1909

(Syns Prosthogoniminae Lühe, 1909; Praeuterogoniminae Sudarikov & Nguyen Thi Le, 1968)

**Diagnosis:** Body small to medium-sized, tapered anteriorly, rounded posteriorly, typically spinous (*Cylindrotrema* said to be unarmed). Oral sucker present, well or poorly developed. Ventral sucker in anterior half of body. Prepharynx usually present, rarely said to be absent. Pharynx present. Oesophagus present. Intestinal bifurcation in anterior third of body, or more anterior. Caeca simple, usually do not reach posterior extremity. Testes in hindbody, symmetrical or subsymmetrical. Cirrus-sac elongate. Male and female ducts open separately or together at genital pore(s) at or close to anterior extremity of body, median or submedian, dorsal or ventral. Ovary between ventral

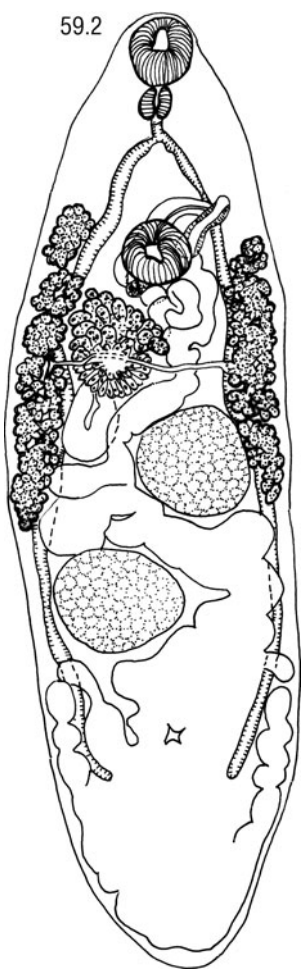
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sucker and testes or dorsal to ventral sucker. Seminal receptacle and Laurer's canal usually present. Uterus usually occupies most of hindbody. Eggs small, numerous. Vitelline follicles often form bunches in lateral fields but, rarely, may be more extensive. Excretory vesicle usually Y-shaped; pore terminal. In bursa Fabricii, oviduct, cloaca or under nictitating membrane of birds, and intestine, liver or body-cavity of mammals; cosmopolitan. Type-genus *Prosthogonimus* Lühe, 1899.

## Key to genera

**1a. Vitelline follicles in extensive fields between about pharyngeal level and posterior extremity, more or less confluent in post-testicular region ..... ..... *Praeuterogonimus* Sudarikov & Nguyen Thi Le, 1968. (Fig. 59.3)**

**Diagnosis:** Body medium-sized, elongate-oval, armed with needle-shaped spines. Oral sucker well-developed; opening appears terminal. Ventral sucker in anterior quarter of body-length, well developed, subequal to oral sucker. Prepharynx said to be absent. Pharynx well developed, similar in size to oral and ventral suckers. Oesophagus short. Intestinal bifurcation in anterior quarter of



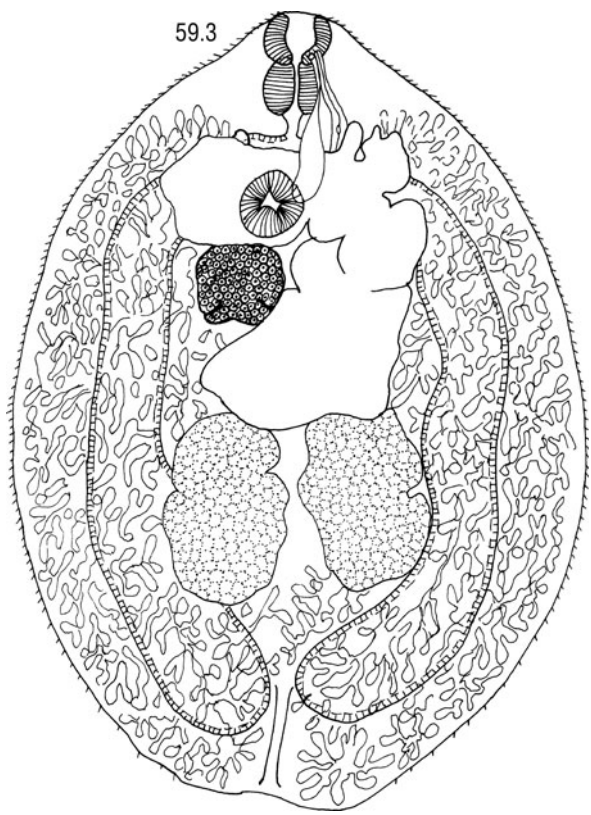




**Fig. 59.2.** *Whallwachsia illuminata* Zamparo, Brooks & Causey, 2003. After Zamparo *et al.* (2003a).
**Fig. 59.3.** *Praeuterogonimus skrjabini* Sudarikov & Nguyen Thi Le, 1968. After Sudarikov & Nguyen (1968).

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body. Caeca dilate, extend close to posterior extremity but do not reach it. Testes symmetrical, indented, close together just inside posterior half of body. Cirrus-sac elongate, tubular, reaches mid-level of ventral sucker, contains elongate internal seminal vesicle (no other contents described). Genital pore more or less median, at level of posterior margin of oral sucker in holotype but more anterior in other specimens; position (whether dorsal or ventral) not stated. Ovary just posterior to ventral sucker, submedian, lobed. Mehlis' gland posterior to ovary. Laurer's canal not mentioned. Uterine coils pretesticular, lateral to ovary, posterior, lateral and anterior to ventral sucker, said not to cross caeca but illustrated as encroaching beyond them at bifurcal level. Metraterm present. Eggs operculate. Vitelline follicles occupy all available space from posterior extremity to about level of pharynx, more or less confluent in post-testicular region. Excretory vesicle tubular; pore opens within indentation on posterior extremity. In small intestine of rodents (*Rattus* sp.); Asia (Vietnam). Type- and only species *P. skrjabini* Sudarikov & Nguyen Thi Le, 1968.

**1b. Vitelline follicles in more restricted lateral fields, most commonly between levels of intestinal bifurcation and testes ..... 2.**

**2a. Genital pore median, on dorsal or ventral surface or at anterior extremity ..... 3.**
**2b. Genital pore submedian to marginal ..... 5.**

**3a. Genital pore median, on dorsal surface dorsal to oral sucker ..... ..... *Coryphogonimus* Cribb & Spratt, 1990. (Fig. 59.4)**

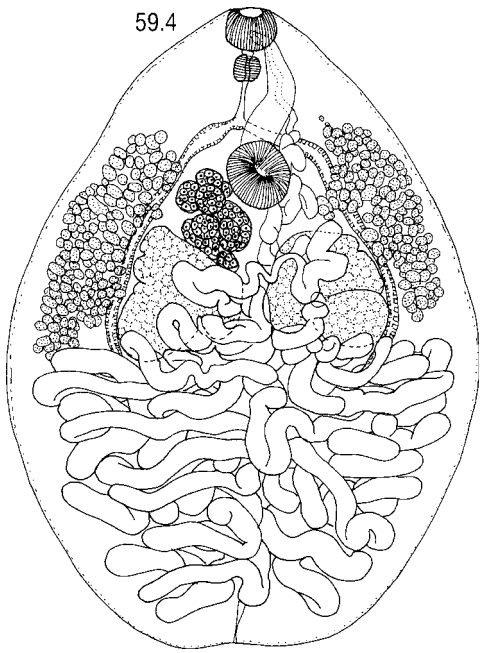
**Diagnosis:** Body oval, small, strongly flattened, spinous. Oral sucker terminal, opens ventroterminally, smaller than ventral sucker. Ventral sucker in anterior half of body. Prepharynx short. Pharynx well developed. Oesophagus distinct, well developed. Intestinal bifurcation closely anterior to ventral sucker. Caeca somewhat arcuate, terminate posteriorly beyond level of testes but do not reach posterior extremity. Testes symmetrical in mid-region of body, posterior to ventral sucker, almost entire to deeply lobed. Cirrus-sac elongate, on right or left of mid-line, reaches or just overlaps anterior margin of ventral sucker, contains large tubulovesicular seminal vesicle, prostatic cells and ejaculatory duct. Genital pore median, directly dorsal to oral sucker. Ovary submedian, posterodorsal to ventral sucker, opposite cirrus-sac, slightly to deeply lobed. Laurer's canal opens dorsally at intertesticular level. Seminal receptacle canalicular, very small, usually visible only in sections. Uterus forms extensive coils in post-testicular space; some coils at level of and between testes. Eggs operculate. Vitelline follicles in two lateral groups between about level of anterior margin of ventral sucker and posterior margins of testes; fields may encroach slightly into forebody. Excretory vesicle Y-shaped, extends to mid-testicular level; pore terminal. In bile-ducts, gall-bladder and encapsulated on liver of rodents (*Rattus fuscipes*); Australia. Type-species *C. aglaos* Cribb & Spratt, 1990.

**3b. Genital pore median, on ventral surface or at anterior extremity ..... 4.**

**4a. Genital pore at anterior extremity; oral sucker vestigial; ventral sucker very poorly developed; ovary pyriform, entire ..... *Tahratrema* n.g. (Fig. 59.5)**

**Diagnosis:** Body large, soft, tapered anteriorly, rounded posteriorly, armed with spines, which are densely packed anteriorly but sparse in posterior region of body. Oral sucker vestigial, represented only by aggregation of cells with densely staining cytoplasm. Ventral sucker larger but small in relation to body-size, poorly developed, with weakly developed muscle fibres, lacks lumen, at about 9–13% of body-length. Oral opening subterminal. Pharynx well developed, protrudes slightly into oral cavity. Oesophagus short, very slender, surrounded by densely staining cells. Intestinal bifurcation at *c.* 7–8% of body-length. Caeca dilate anteriorly, narrower posteriorly, approach or may

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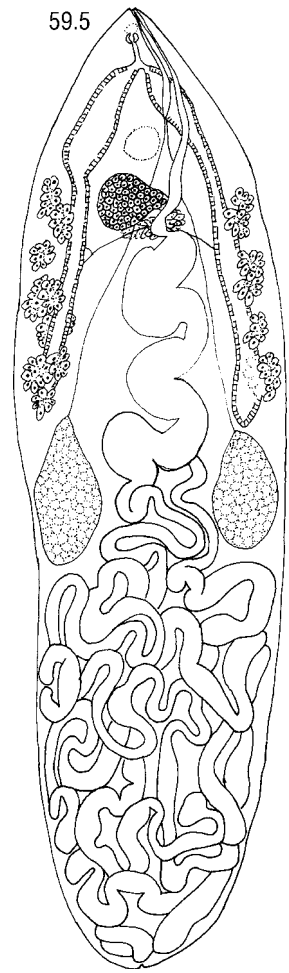




**Fig. 59.4.** *Coryphogonimus aglaos* Cribb & Spratt, 1990. After Cribb & Spratt (1990).
**Fig. 59.5.** *Tahratrema aegyptiacum* (Jones & El-Azazy, 1986) n. comb. After Jones & El-Azazy (1986).

slightly overlap level of testes but terminate at less than half of body-length. Testes symmetrical, usually just posterior to caecal ends in mid-region of body, entire, irregular oval, attenuate anteriorly. Vasa efferentia from anterior extremity of each testis pass forward to converge at proximal end of cirrus-sac, apparently not uniting. Cirrus-sac elongate, slender, on right or left side of body, contains bipartite internal seminal vesicle; prostatic cells present distally. Genital pore at anterior extremity of body. Male and female ducts open very close together. Ovary pyriform, entire, posterior to ventral sucker and far anterior to testes. Laurer's canal (visible in sections) broad, opens dorsally posterior to level of ovary. Canalicular seminal receptacle present, small, postovarian, visible only in sections. Mehlis' gland diffuse, posterior to ovary. Uterus with descending and ascending limbs, which pass between testes; coils occupy all available space in hindbody posterior to testes; ascending limb becomes dilate as it passes forward. Metraterm present, muscular. Eggs small, numerous, operculate, embryonated. Vitelline follicles in two restricted lateral fields between level of ovary or ventral sucker and about level of caecal ends; follicles form distinct bunches, nine on one side and seven on other. Excretory vesicle visible only in sectioned material as wide tube reach-

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ing level of ovary; pore terminal. In abdominal cavity of rodents (*Rattus norvegicus*); Africa (Egypt). Type- and only species *T. aegyptiacum* (Jones & El-Azazy, 1986) n. comb.

**4b. Genital pore ventral, immediately posterior to oral sucker; suckers well developed; ovary deeply lobed ..... *Mediogonimus* Woodhead & Malewitz, 1936. (Fig. 59.6)**

**Diagnosis:** Body small, spinous, pyriform, oval when fixed; deep red when alive. Oral and ventral suckers about equal in size, well developed. Ventral sucker in anterior two-fifths of body. Prepharynx not mentioned but apparently present. Pharynx well developed, muscular. Oesophagus short. Intestinal bifurcation approximately midway between suckers. Caeca extend posteriorly beyond testes but do not reach posterior extremity. Testes symmetrical in mid-body, overlie caeca, indented. Cirrus-sac oval, straight or slightly convoluted, extends from pharyngeal level almost to ventral sucker, contains seminal vesicle and cirrus; prostatic cells? Genital pore median, ventral, immediately posterior to oral sucker. Ovary submedian, at level of ventral sucker, may partly overlap it, deeply lobed, more or less pretesticular. Mehlis' gland large, medial to ovary. Seminal receptacle medial to ovary, posterior to ventral sucker. Laurer's canal present. Uterus forms coils at testicular level; coils fill post-testicular space but do not extend into forebody. Eggs operculate, with or without posterior spine (?).Vitelline follicles in two lateral fields between levels of intestinal bifurcation and testes, not extending posteriorly beyond testes; follicles slightly overlap lateral margins of caeca. Excretory vesicle Y-shaped; pore in indentation at posterior extremity. In liver of microtid and murid rodents; USA, Europe. Type-species *M. ovilacus* Woodhead & Malewitz, 1936.

**5a. Ovary entire, oval; vitelline follicles in pretesticular lateral fields; in body-cavity of Australian dasyurids ..... *Coelomotrema* Angel, 1970. (Fig. 59.7)**

**Diagnosis:** Body plump, medium in size, tapered anteriorly, rounded posteriorly, armed with slender spines. Suckers small; ventral sucker larger than oral sucker, within anterior sixth of body. Prepharynx short. Pharynx small but well developed. Oesophagus short. Intestinal bifurcation clearly anterior to ventral sucker. Caeca quite short, with ends reaching anterior margins of testes. Testes in mid-body, symmetrical, entire, irregular oval. Cirrus-sac elongate, extends to level of ventral sucker, contains seminal vesicle, prostatic cells distally and ejaculatory duct. Genital pore submedian, marginal, at level of oral sucker. Male and female ducts open close together. Ovary entire, rounded, slightly submedian, closer to ventral sucker than to testes. Mehlis' gland and seminal receptacle close to ovary. Laurer's canal opens just posterior to level of ovary. Uterus forms narrow descending and wider ascending limbs; coils fill most of body posterior to testes. Metraterm well developed. Vitelline follicles in bunches, seven on left and nine on right, in pretesticular lateral fields. Excretory vesicle described as large, prominent and tube-like posteriorly, widening anteriorly, reaching level of ovary; pore terminal. In body-cavity of dasyurid marsupials (*Antechinomys, Antechinus*); Australia. Type- and only species *C. antechinomes* Angel, 1970.

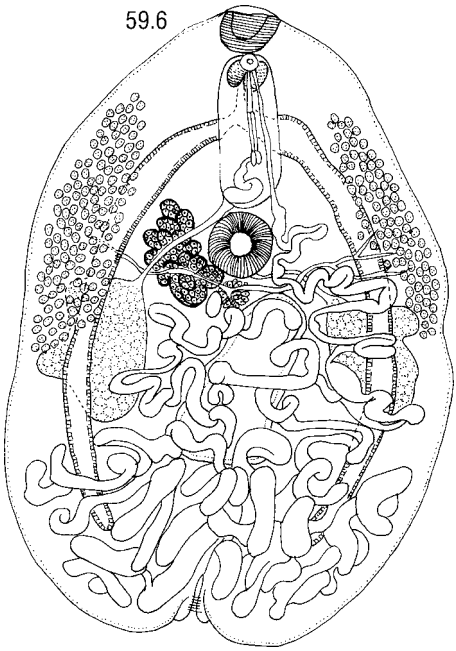
**5b. Ovary lobed; vitelline follicles not confined to pretesticular fields; in birds ..... 6.**

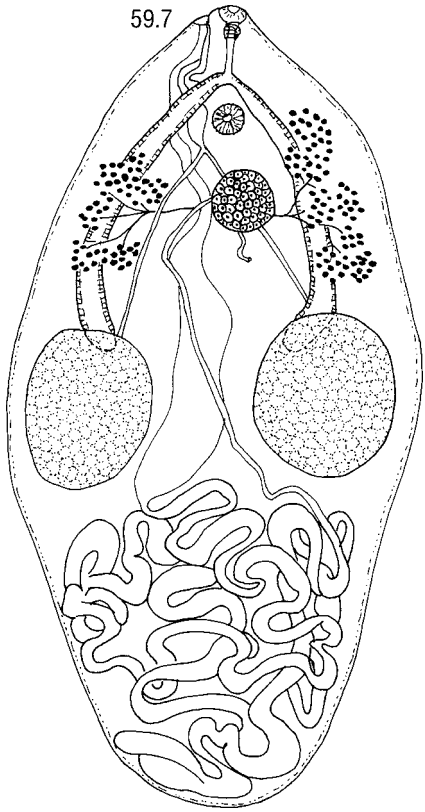
**6a. Ventral sucker over-reaches caeca laterally; in caecum or under nictitating membrane .. 7.**

**6b. Ventral sucker intercaecal; in caecum, cloaca, bursa Fabricii or oviduct ..... ..... *Prosthogonimus* Lühe, 1899. (Fig. 59.8)**

(Syns subgenus *Prosthogonimus* Lühe, 1899; *Macrogenotrema* Skrjabin, 1941; *Mediogenotrema* Skrjabin, 1941; *Politogenotrema* Skrjabin, 1941; *Primagenotrema* Skrjabin, 1941; *Prosthogenotrema* Skrjabin, 1941; *Prosthogonimoides* Yamaguti, 1971; *Prymnoprion* Looss, 1899; *Schistogonimus* Lühe, 1909; *Ultragenotrema* Skrjabin, 1941)

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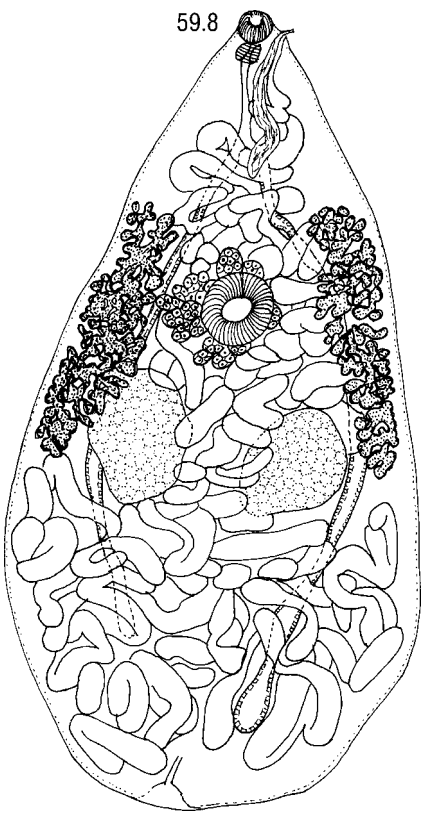




**Fig. 59.6.** *Mediogonimus ovilacus* Woodhead & Malewitz, 1936. After Woodhead & Malewitz (1936).
**Fig. 59.7.** *Coelomotrema antechinomes* Angel, 1970. After Angel (1970).
**Fig. 59.8.** *Prosthogonimus ovatus* (Rudolphi, 1803) Lühe, 1899. After Skrjabin (1962).

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**Diagnosis:** Body flattened, oval, elliptical or pyriform, with greatest diameter posterior to equator. Oral sucker and pharynx comparatively small. Ventral sucker larger than oral sucker, at or near junction of anterior and middle third of body. Prepharynx present. Oesophagus short. Intestinal bifurcation usually in anterior quarter of body. Caeca usually end short of posterior extremity. Testes in hindbody, usually symmetrical, usually medial to caecum. Cirrus-sac slender, elongate, usually reaches further than caecum, contains tubular internal seminal vesicle. Male and female genital pores open close together, submedian, marginal, at level of oral sucker. Ovary deeply multilobed, median or submedian, posterolateral, posterior to or partly dorsal to ventral sucker, between and just anterior to testes. Seminal receptacle and Mehlis' gland often postovarian, may be displaced medially or laterally. Laurer's canal present. Uterus may cross caeca in post-testicular field, tends to fill post-testicular space, forms descending and ascending coils. Vitelline follicles in mainly extracaecal fields, which may encroach across caeca, in mid-region of body or more anterior. Excretory vesicle Y-shaped; pore terminal. In oviduct, bursa Fabricii or cloaca of birds; cosmopolitan. Type-species *P. ovatus* (Rudolphi, 1803) Lühe, 1899.

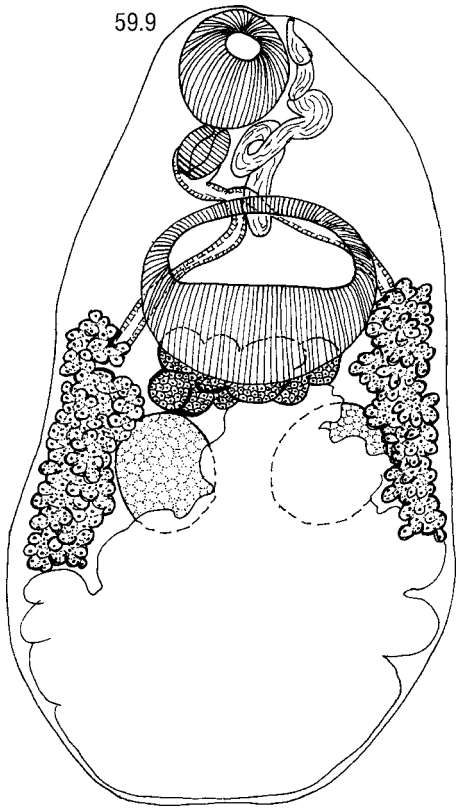
**7a. Tegument armed; under nictitating membrane of birds; in former USSR ..... ..... *Ophthalmogonimus* Oshmarin in Skrjabin, 1962. (Fig. 59.9)**

**Diagnosis:** Body small, elongate-oval, armed with spines. Oral sucker and pharynx well developed. Ventral sucker much larger than oral sucker, in anterior half of body, transversely elongate, overlaps caeca laterally. Oesophagus short. Intestinal bifurcation in anterior quarter of body. Caeca short, terminate in region of gonads. Testes symmetrical, in about middle third of body, oval, entire. Cirrus-sac elongate, winding, extends into bifurcal region. Genital pore submedian, lateral to oral sucker; male and female ducts open close together. Ovary transversely elongate, deeply lobed, posterodorsal to ventral sucker. Mehlis' gland? Laurer's canal? Uterus fills all post-testicular space. Vitelline follicles in two lateral fields from about mid-level of ventral sucker to just posterior to testes. Excretory vesicle and pore? Under nictitating membrane of birds; former USSR. Type-species *O. sudarikovi* Oshmarin in Skrjabin, 1962.

**7b. Tegument said to be unarmed; in caecum of swan; Australia ..... ..... *Cylindrotrema* Angel, 1973. (Fig. 59.10)**

**Diagnosis:** Body medium in size, cylindrical, narrowing anteriorly, said to be unarmed (spines possibly lost, although specimen said to be in good condition). Suckers well developed; ventral sucker larger than oral sucker, in anterior third of body. Prepharynx short. Pharynx well developed. Oesophagus short. Intestinal bifurcation about level with anterior rim of ventral sucker. Caeca narrow, fairly straight, terminate just short of posterior extremity. Testes oval, symmetrical, not contiguous, just posterior to mid-level of hindbody. Vasa efferentia join near posterior rim of ventral sucker. Cirrus-sac elongate, contains internal seminal vesicle and prostatic cells, extends posteriorly beyond ventral sucker. Genital pore submedian on left at level of oral sucker. Ovary median, anterior to and separated from testes, highly lobed. Mehlis' gland, Laurer's canal and seminal receptacle not observed. Uterus forms descending limb ventral to testes, then coils which fill posterior region of body; ascending coils overlap posterior parts of caeca, but are mainly intercaecal anteriorly. Vitelline follicles in hindbody, form distinct bunches, which overlap caeca laterally and medially; fields extend anteriorly and posteriorly somewhat beyond ovariotesticular zone. Excretory vesicle and pore not described. In caecum of birds (*Cygnus atratus*); Australia. Type- and only species *C. cygni* Angel, 1973.

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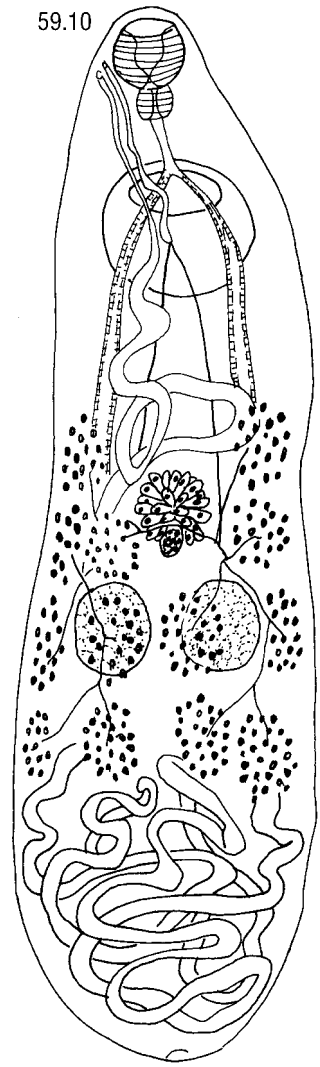




**Fig. 59.9.** *Ophthalmogonimus sudarikovi* Oshmarin in Skrjabin, 1962. Uterus in outline only. After Skrjabin (1962).
**Fig. 59.10.** *Cylindrotaenia cygni* Angel, 1973. Dorsal view. After Angel (1973).

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# 60 Family Renicolidae Dollfus, 1939

D.I. Gibson

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## Introduction

Renicolids are parasites of the kidneys and ureters of birds that feed on bivalves and/or fishes. Like many digenean tissue parasites, their morphology tends to be somewhat atypical for the group as a whole, i.e. they have an enlarged uterus and reduced sucker(s). *Renicola* Cohn, 1904 was erected by Cohn (1904) for *Monostoma pingue* Mehlis in Creplin, 1846, originally described from the kidneys of *Podiceps cristatus* in Germany. *Renicola* was included in his new family Troglotrematidae Odhner, 1914 by Odhner (1914), but Dollfus (1939) considered this family artificial and erected the Renicolidae Dollfus, 1939 for this genus, on which he commented, 'qui me semble parallèle aux Gymnophallidae'. La Rue (1957) proposed the superfamily Renicoloidea Dollfus, 1939, and even the suborder Renicolata La Rue, 1957 and the order Renicolida La Rue, 1957, on the basis of the epithelial excretory vesicle of the cercaria. Odening (1971) accepted the superfamily but placed it in the suborder Plagiorchiata La Rue, 1957. Yamaguti (1971) considered that La Rue had gone too far, judging from general adult morphology and the fact that 'nothing' was known of the life-history. Yamaguti (1958b) recognized this group only at the subfamily level within the Troglotrematidae, but later (Yamaguti 1971) accepted the family within the superfamily Troglotrematoidea Odhner, 1914. Cable (1965) thought that the renicolids belonged to the Plagiorchioidea Lühe, 1901, and he (Cable 1974) indicated a close relationship with the Plagiorchiidae Lühe, 1901. La Rue's suborder Renicolata was accepted by Smogorzhevskaya (1976), and Sudarikov *et al.* (1986) recognized the group at full ordinal level as the Renicolida La Rue, 1957. Nevertheless, Schell (1985) recognized it only at superfamily level, as the Renicoloidea. The most recent review of the family is that of Sudarikov & Sten'ko (1984). In a molecular study (partial lsrD NA), which lacked renicolid material, Tkach *et al.* (2000a) implied a link with the Microphalloidea Ward, 1901. More recently, Tkach *et al.* (2001b), in a molecular phylogeny of the suborder Plagiorchiata based on large subunit rDNA sequences, indicated that the renicolids come within that group and close to the Eucotylidae Cohn, 1904, a family whose members are also found in the kidneys of birds. Based on morphology, classical taxonomists have included the eucotylids within the Cyclocoeloidea Stossich, 1902 (see Kanev *et al.*, 2002a). In the most recent molecular phylogeny of the Digenea, based on ssrDNA and lsrDNA, placed the Renicolidae within the Microphalloidea close to the Eucotylidae Cohn, 1904 (Olson *et al.,* 2003). Consequently, in this work, the renicolids are treated as microphalloids.

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There are more than 50 nominal species of *Renicola* (see Sudarikov & Sten'ko, 1984, who provided a key to 52 renicolid species, all but five in *Renicola*), so attempts have been made to split the genus. *Stamparia* Nezlobinsky, 1926 was erected by Nezlobinsky (1926) for material from pelicans in Macedonia and compared with *Renicola*. It was provisionally accepted by Dollfus (1946a), but he considered the diagnostic characters (testes symmetrical and entire versus asymmetrical and more or less irregular in shape) to be feeble. Sudarikov (1951) included it as a subgenus of *Renicola*, but it was considered a synonym of *Renicola* by Yamaguti (1958b), and this has been accepted by subsequent workers.

Wright (1957) subdivided *Renicola* into three groups: (i) the 'pelecani-group' – one species with a spindle-shaped body and a long oesophagus; (ii) the 'mediovitellata-group' – one species with dorsal vitelline follicles in a linear series between the caeca; and (iii) the 'pinguis-group' – the majority of the remaining species (? without distinctive features). In addition, he listed one species with no apparent affinities and in need of reanalysis. *Renicola* was examined in detail by Odening (1962a), who made the major attempt to split up the genus. He erected two new genera for existing species: *Pseudorenicola* Odening, 1962, based on the position of the ovary anterolateral rather than posterolateral to the ventral sucker; and *Neorenicola* Odening, 1962, based on the apparent presence of only one testis (probably the fusion of two). Both genera at that time contained only single species, so there was little logistical benefit. *Pseudorenicola* was accepted by Smogorzhevskaya (1976) but not by Yamaguti (1971) or Sudarikov *et al*. (1986). Both of Odening's genera were accepted by Shigin (1983). Yamaguti accepted *Neorenicola* as a subgenus of *Renicola*, but Groschaft (1982) showed that it is a synonym of *Nephromonorcha* Leonov, 1958, a genus omitted by Yamaguti (1971) but recognized by Groschaft (1982). The latter was erected as *incertae sedis* by Leonov (1958) for *N. skrjabini* Leonov, 1958 from gulls and terns on the Black Sea coast of the Ukraine. Groschaft, who erroneously considered *N. monorchis* (Dollfus & Capron, 1958) as the type-species, gave an amended diagnosis and key to the species of *Nephromonorcha*. Although this genus was listed as a synonym of *Renicola* by Alekseev *et al*. (1969), it has been accepted by some authors (e.g. Sudarikov & Sten'ko, 1984; Sudarikov *et al*., 1986; Bartoli, 1989).

Odening (1962a) went a step further and split *Renicola* into three subgenera: *Renicola* with the vitellarium extracaecal and testes tending to overlap the gut-caeca ventrally or dorsally, parasitic in a range of bird orders; *Anatirenicola* Odening, 1962 with the vitellarium mainly intercaecal or dorsal almost in two rows, parasitic in anseriforms; and *Wrightrenicola* Odening, 1962 with the vitellarium ventral to the caeca, often rather wide in the intercaecal region, parasitic in ardeiforms. These subgenera were not accepted by Yamaguti (1971), who considered such variations in vitelline distribution as specific differences.

Riley & Wynne Owen (1972) divided the family into four groups based on the form of the excretory vesicle, although this feature was known for only 12 species, only eight of them named. These are: (i) a Y-shaped excretory vesicle, bifurcating just posterior to the ventral sucker, and arms reaching close to the level of the pharynx; (ii) a Y-shaped excretory vesicle, bifurcating well posterior to the ventral sucker, and with a commissure between the arms just posterior to the ventral sucker and arms reaching close to the level of the pharynx; (iii) a Y-shaped excretory vesicle, bifurcating well posterior to the ventral sucker, and arms terminating in the mid-body region; and (iv) a V-shaped excretory vesicle with a short stem and long arms reaching the level of the pharynx. This division is impractical, as the excretory vesicle is very difficult to see in whole-mount preparations; no subsequent workers appear to have commented on this proposal.

In this work, only *Renicola* and *Nephromonorcha* are recognized as valid. This is on the grounds that a single testis is generally considered a good generic criterion for non-teratological specimens. However, as the testes are commonly contiguous and often difficult to discern in their

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entirety in species of *Renicola, Nephromonorcha* is recognized with some degree of hesitance, especially as two vasa efferentia are retained. Furthermore, this still leaves *Renicola* as a large, unwieldy genus with 90% of the species of the family (see Sudarikov & Sten'ko, 1984).

When one examines the species of the genus, one could group them in other ways. For example, in some species the pharynx is deeply embedded in the wall of the oral sucker. The differences that have been used in the past are of questionable phylogenetic significance in taxa where the material is often in poor condition and where the features are distorted or obscured by the uterus. In this work, none of the aforementioned divisions of *Renicola* are considered satisfactory. The group is in dire need of a detailed study using molecular techniques, after which morphological variations can be reassessed.

## Family Renicolidae Dollfus, 1939

**Diagnosis:** Body stout, medium to small, rounded to oval, subpyriform or claviform, often attenuated posteriorly. Tegument armed with small spines. Oral sucker present, sometimes large and wide. Ventral sucker small, in middle third of body. Prepharynx absent. Pharynx small, may be deeply embedded anteriorly in wall of oral sucker. Oesophagus short to apparently absent. Intestinal bifurcation in anterior half of body. Caeca two, reach middle of body or close to posterior extremity, blind. Testes usually two, close together or contiguous, occasionally fused into single mass with two vasa efferentia, often irregularly lobate, symmetrical to oblique, close to ventral sucker, in or close to middle third of body. Cirrus-sac absent. Seminal vesicle saccular, in forebody. Pars prostatica and ejaculatory duct short, indistinct. Genital atrium small. Genital pore median, in anterior half of body, anterior to ventral sucker. Ovary irregularly lobate, submedian, anterior to one of two testes or anterolateral to single testis, usually anterolateral to ventral sucker but occasionally posterolateral. Laurer's canal not reported. Seminal receptacle (?blind) present, small, globular to oval. Uterus winding, usually fills most of body anterior to testes, not present at extremities (especially posteriorly), may form large uterine sac ventromedially. Eggs small, numerous, operculate, often attenuated towards opercular pole, embryonated in distal uterus. Vitellarium follicular; follicles in lateral clusters in middle or, less often, posterior third of body, sometimes more extensive. Excretory vesicle Y-shaped (V-shaped also reported); arms simple, but lateral diverticula and/or commissure in anterior hindbody present in some species, usually reach well into anterior region of body; pore terminal. Life-cycle and cercarial type variable; usually use marine prosobranchs as first and bivalve molluscs or fishes as second intermediate hosts. Adults in kidneys and ureters of aquatic birds; especially in Palaearctic Region. Type-genus *Renicola* Cohn, 1904.

## Key to genera

**1a. Two testes (often contiguous, may overlap) ..... *Renicola* Cohn, 1904. (Fig. 60.1)**
(Syns *Stamparia* Nezlobinski, 1926; *Anatirenicola* Odening, 1962 (subgenus); *Pseudorenicola* Odening, 1962; *Wrightrenicola* Odening, 1962 (subgenus))

**Diagnosis:** Body rounded to oval, subpyriform or claviform, often more attenuated posteriorly and rounded anteriorly. Testes two, symmetrical to tandem, close together, often contiguous and/or overlapping. Ovary lobed or not. Vitellarium comprises few to many follicles; lateral field often restricted to middle third of body, sometimes more extensive. Type-species *R. pinguis* (Mehlis in Creplin, 1846) Cohn, 1904.

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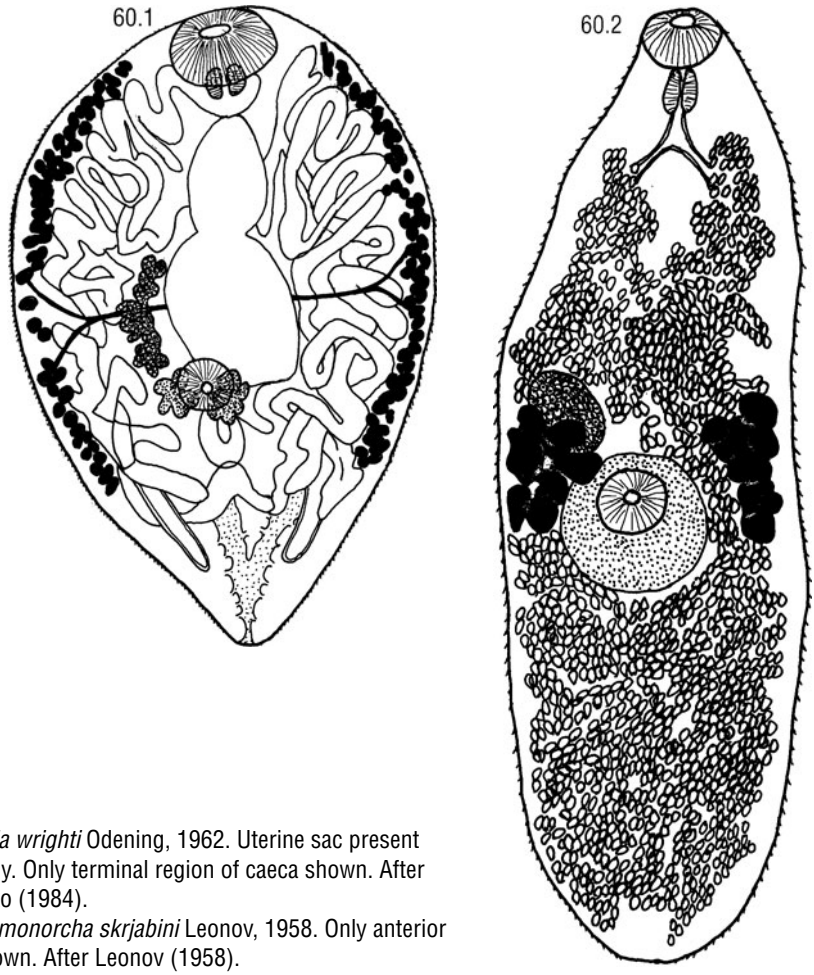



**Fig. 60.1.** *Renicola wrighti* Odening, 1962. Uterine sac present ventrally in forebody. Only terminal region of caeca shown. After Sudarikov & Sten'ko (1984).
**Fig. 60.2.** *Nephromonorcha skrjabini* Leonov, 1958. Only anterior region of caeca shown. After Leonov (1958).

**1b. Testes fused to form single mass ..... *Nephromonorcha* Leonov, 1958. (Fig. 60.2)**
(Syn. *Neorenicola* Odening, 1962)

**Diagnosis:** Body oval, slightly more tapered anteriorly, rounded posteriorly. Testes fused to form single mass, median, dorsal or posterodorsal to ventral sucker. Ovary often lobed. Vitellarium composed of relatively few follicles; lateral vitelline fields not extensive, tend to be concentrated in middle third of body. Type-species *N. skrjabini* Leonov, 1958.

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# 61 Family Renschetrematidae Yamaguti, 1971

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## Introduction

Rohde (1964) described some intestinal trematodes from bats of Malaysia, which he placed in the new genus *Renschetrema* Rohde, 1964. This genus was attributed to the family Microphallidae Ward, 1901 and subfamily Maritrematinae Nicoll, 1907. Because of their morphological distinctness, Yamaguti (1971) created the new subfamily Renschetrematinae Yamaguti, 1971 for them, which is here raised to full family rank as the Renschetrematidae Yamaguti, 1971.

Examination of the type-series from the collections of the Natural History Museum, London, and several of Rohde's personal specimens[1] has allowed a complete definition of the genus. It is essentially defined by two well-separated dorsal genital pores, the absence of a genital atrium, cirrus, phallus (see definition in Deblock, Chapter 47, this volume) and metraterm, the presence of a voluminous and fibrillar accessory sac of a unique type (resembling the dart-sac in the reproductive system of gastropods) associated with the male genital pore, and a vitellarium composed of numerous, densely packed follicles, either distributed all over the body or more scattered anteriorly. These characteristics preclude the inclusion of *Renschetrema* in the Microphallidae. Also, the two species initially described seem to belong to two different genera. The type-species (*R. malayi* Rohde, 1964) has a microphallid-like general habitus, with a rather thin, linguiform body, two genital pores at the level of the ventral sucker, an obvious digestive tract and a vitellarium that is more postcaecal than precaecal. *Renschetrema* sp. of Rohde (1964) may be related and is said to agree with *R. rohdei* Matskási, 1973 by Matskási (1973). The second named species, *R. sandoshami* Rohde, 1964, is notably different, with a bulky, thick and round or oval body, the genital pores are more anterior, situated laterally in the forebody, the vitellarium is profuse, very dense and uniformly distributed almost throughout the body and the digestive tract is not visible. In my opinion, these discrepancies justify the erection of *Rohdetrema* n.g.

One specimen from the intestine of *Rhinolophus luctus* captured on 7 September 1963 at Uly Champevoh, Janda Baik Pahang, Malaysia, and named *Renschetrema malayi* Rohde, 1964

[1] Rohde's collection of renschetrematids has now been registered in the collection of the Natural History Museum, Department of Zoology, Parasitic Worms Division, accession numbers 2003.9.5.1–11.

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appears morphologically different from *R. malayi*. It is defined by a relatively large body (485 µm × 290 µm, well flattened), a habitus like *Rohdetrema sandoshami* n. comb. with abundant vitelline follicles, with two equatorial genital pores like *Renschetrema malayi* but anatomically well differentiated by its tegument and the stouter canal of the male accessory sac. It should be considered as another species of *Renschetrema*, different from that described by Matskási (1973b) as *R. rohdei* in Vietnam and by Kifune (1984) as *R. indicum* Kifune, 1984 in India.

## Family Renschetrematidae Yamaguti, 1971

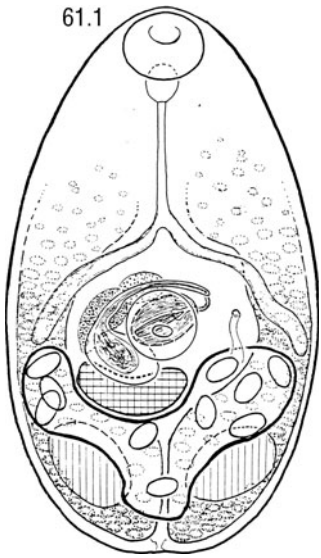
**Diagnosis:** Body very small (≤ 500 µm), either pyriform and flattened dorsoventrally, or transversely ovoid and thick. Tegument with small spines; spination decreasing from anterior extremity to mid-body. Suckers of medium size, subequal, well separated. Oral sucker subterminal. Ventral sucker equatorial, embedded in parenchyma. Digestive tract present or not distinguishable. Testes two, ovoid, lateral, symmetrical and postovarian, more or less well separated by uterine coils. Male terminal genitalia free in parenchyma; in intercaecal space, seminal vesicle and ejaculatory canal are more or less retort-shaped, curving around ventral sucker. Copulatory organ absent (no cirrus or phallus). Prostatic gland and prostatic chamber free in dorsal parenchyma. One accessory sac present, ovoid, voluminous, slightly fibrous, evoking gastropod dart-sac, with fibrous and fusiform bullet-like formation in long axis of sac; wide canal joins distal part of sac to male genital pore. Genital atrium absent. Genital pores two, well separated, both dorsal and sinistral, either equatorial and postcaecal at level of ovary, or far anterior close to sinistrolateral margin of body; female pore slightly posterior to male pore. Ovary ovoid, dextrolateral at ventral sucker level (on opposite side of body to genital pores). Oötype, Laurer's canal and Mehlis' gland not observed. Seminal receptacle posterior to ovary, presumably canalicular. Female accessory sac absent. Uterine coils in hindbody, not very numerous, form relatively short, thick branches (with V- or Y-like appearance). Female terminal genitalia joining female genital pore with very short, annular, specialized formation of tegument, but no metraterm. According to position of genital pores, terminal genital tracts are situated either in intercaecal spaces or between suckers. Eggs numerous, relatively large (25–36 µm), unembryonated *in utero*, regularly ovoid, with operculum very rarely obvious; mucron absent. Vitellarium comprises numerous rounded follicles of variable size (larger than the eggs or not), serried and distributed dorsally and ventrally all over body, either equally between posterior extremity and oral sucker, or unequally between posterior extremity and ventral sucker with anterior extensions progressively more scarce and diffuse. Vitelloducts long, medial, transverse, rather indistinct. Flame-cell formula not known. Excretory vesicle short, I-shaped, in intertesticular region; pore terminal, median. Biology unknown. In intestine of bats; southern Asia (Malaysia, India, Vietnam). Type-genus *Renschetrema* Rohde, 1964.

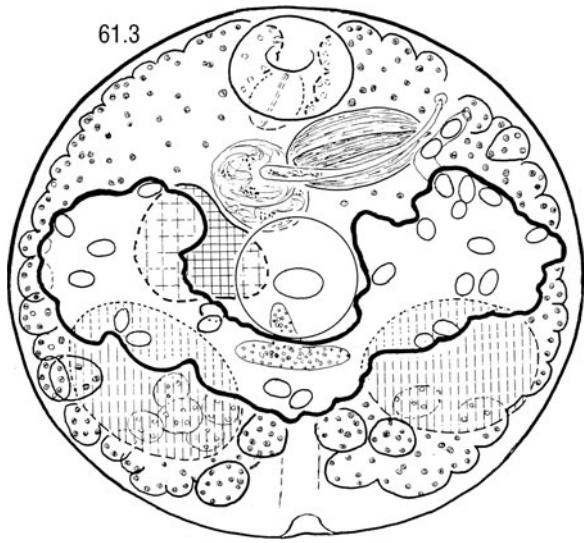
## Key to genera

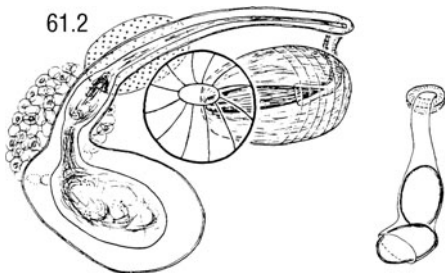
**1. Body linguiform, rather thin; both genital pores at level of ventral sucker; digestive tract obvious; vitellarium more postcaecal than precaecal ..... ..... *Renschetrema* Rohde, 1964. (Figs 61.1, 61.2)**

**Diagnosis:** Body linguiform, slender and relatively transparent. Digestive tract distinct. Prepharynx short. Pharynx globular. Oesophagus rectilinear. Intestinal bifurcation in posterior forebody.

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**Figs 61.1, 61.2.** *Renschetrema malayi* Rohde, 1964. 61.1. Syntype, ventral view. Original. 61.2. Terminal genitalia, semi-schematic ventral view. Original.
**Fig. 61.3.** *Rohdetrema sandoshami* (Rohde, 1964) n. comb. Type, semi-schematic ventral view. Original.

Caeca widely divergent, anterior to ventral sucker, ending at level of ovary. Genital pores dorsosinistral, in ventral sucker region. Both terminal genital tracts postcaecal, well separated. Male genital tract large, retort-shaped, curving around ventral sucker, or not; male accessory sac varying in position, anterior or posterior to distal male genital tract. Uterine loops not very numerous, mainly in hindbody, disposed in Y-shape with three short, thick branches. Vitelline follicles very dense in postcaecal region, more diffuse in precaecal region and just reaching pharyngeal level. Type-species *R. malayi* Rohde, 1964.

**2. Body stout, thick and round or oval; both genital pores dorsal anteriorly situated, lateral in forebody; digestive tract not visible; vitellarium profuse, dense and uniformly distributed almost throughout body ..... *Rohdetrema* n.g. (Fig. 61.3)**

**Diagnosis:** Body stout, thick and oval. Digestive tract indistinct. Dorsal genital pores far from equatorial region, close to anterior and sinistrolateral margin of body. Terminal genital tracts in forebody. Male accessory sac in forebody between suckers. Uterine loops disposed in shape of thick, wide V-shape or semicircular arch posterolateral to ventral sucker. Vitelline follicles symmetrical, very dense ventrally and dorsally, covering all organs of body except for ventral sucker region and oral sucker. Type-species *R. sandoshami* (Rohde, 1964) n. comb.

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# 62 Family Stomylotrematidae Poche, 1926

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## Introduction

Stomylotrematids are parasites of the digestive tract, especially the caecum, bursa Fabricii or cloaca of birds, characterized by a marginal genital pore and symmetrical testes in the forebody or anterior hindbody. Poche (1926) erected the family for *Stomylotrema* Looss, 1900. Skrjabin (1947a) detailed the convoluted history of the type-species, namely *S. perpastum* Braun, 1902. Later, McIntosh (1936a) added *Laterotrema* Semenov, 1928. Odening (1964c) erected the subgenus *Lecithodollfusia* Dollfus, 1964 for *Laterotrema arenula* (Creplin, 1825). We agree with Khotenovskii's (1970) action in raising *Lecithodollfusia* to generic rank, but he placed it in the Pleurogenidae Looss, 1899, whereas we (Lotz & Font, Chapter 57, this volume) place it in the Phaneropsolidae Mehra, 1935. The genus S*rivastavatrema* Singh, 1962 was aligned with *Laterotrema* in the family Laterotrematidae Yamaguti, 1958 by Yamaguti (1971).

## Family Stomylotrematidae Poche, 1926

(Syn. Laterotrematidae Yamaguti, 1958)

**Diagnosis:** Body 1–3 mm long, broadly oval. Tegument thick, spinous or smooth. Oral sucker, large, round, terminal to subterminal. Ventral sucker well developed, round, median, pre-equatorial to postequatorial. Prepharynx short to absent. Pharynx well developed. Oesophagus short to long, occasionally absent. Intestinal bifurcation in mid-forebody. Caeca paired, extend to near posterior end of body. Testes paired, entire, symmetrical, in middle third of body. Cirrus-sac present, oriented anteriorly to transversely, in forebody. Genital pore marginal, at level of ventral sucker or in forebody, typically at level of pharynx. Ovary submedian to sublateral, equatorial to pre-equatorial, entire. Seminal receptacle and Laurer's canal present. Uterus well developed with descending and ascending sections. Eggs operculate, small, numerous. Vitellarium follicular, in forebody or in fore- and hindbody. Excretory vesicle V- to Y-shaped with long stem; pore terminal. In digestive tract, especially caecum, bursa Fabricii or cloaca of birds (Caprimulgiformes, Charadriiformes, Ciconiiformes, Gruiformes, Passeriformes, Strigiformes): cosmopolitan. Type-genus *Stomylotrema* Looss, 1900.

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## Key to genera

**1a. Vitellarium comprises two lateral groups each composed of single vertical row of follicles that extends into posterior half of body; ventral sucker in posterior half of body; ovary near pharynx ..... *Stomylotrema* Looss, 1900. (Fig. 62.1)**
(Syn. *Khalilloosia* Hilmy, 1948)

**Diagnosis:** Body 1–3 mm long, oval. Tegument muscular, without spines. Oral sucker large, subterminal. Ventral sucker large, with diameter > 50% of body-width, postequatorial. Prepharynx short. Oesophagus short to absent. Caeca long, extend to near posterior end of body. Testes anterior to ventral sucker. Cirrus-sac anterior to ventral sucker, oblique, directed anteriorly. Cirrus-sac contains seminal vesicle, pars prostatica and ejaculatory duct. Genital pore opens at anterolateral margin of body, at level of pharynx or oral sucker. Ovary pretesticular, in forebody, nearly at level of pharynx. Uterus postovarian, appears to surround ventral sucker. Eggs thick-shelled, small, operculate, numerous. Vitellarium in two lateral groups composed of single rows of follicles. Excretory vesicle V- to Y-shaped; paired arms with irregular outpocketings. In posterior alimentary tract, especially caecum, rectum, bursa Fabricii or cloaca of birds (Caprimulgiformes, Charadriiformes, Ciconiiformes, Gruiformes, Passeriformes, Strigiformes); Americas, Africa, Eurasia. Type-species *S. perpastum* Braun, 1902.

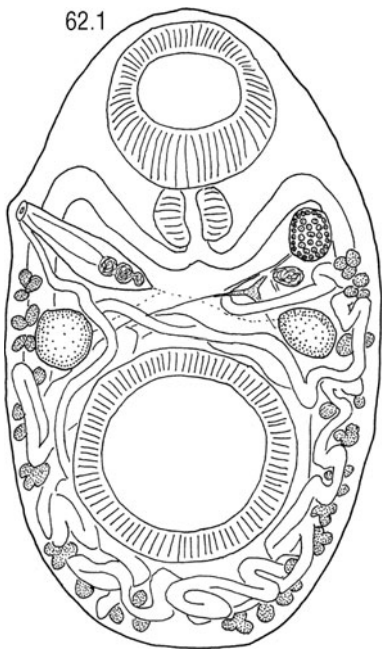
**1b. Vitellarium comprises two lateral grape-like clusters of follicles that do not extend into posterior half of body; ventral sucker not in posterior half of body; ovary well posterior to pharynx ..... 2.**

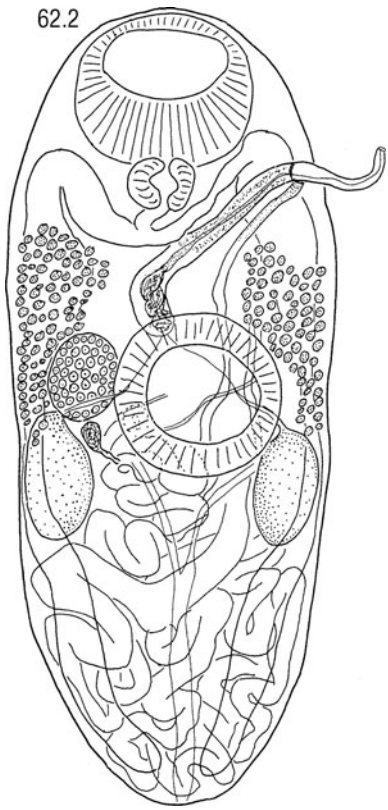
**2a. Testes wholly or partly posterior to ovary ..... *Laterotrema* Semenov, 1928. (Fig. 62.2)**
(Syn. *Pseudolaterotrema* Yamaguti, 1939)

**Diagnosis:** Body 1–3 mm long, oval, elongate. Tegument spinous. Oral sucker well developed, subterminal. Ventral sucker equatorial to pre-equatorial. Prepharynx short to absent. Oesophagus short to absent. Caeca long, extend posterior to testes to near posterior end of body. Testes equatorial, symmetrical to slightly oblique. Cirrus-sac mostly anterior to ventral sucker, directed transversely or anteriorly, contains seminal vesicle, pars prostatica and ejaculatory duct. Genital pore opens anterolaterally on margin of body, at level of pharynx or oral sucker. Ovary submedian, pretesticular, distant from pharynx. Uterus fills most of hindbody, occasionally extends into forebody. Eggs small, operculate, numerous. Vitellarium two grape-like clusters, mostly pre-equatorial, extending from near pharynx to mid-level of ventral sucker, occasionally to level of testes. Excretory vesicle Y-shaped with long stem. In intestinal tract, cloaca or bursa Fabricii of birds (Passeriformes); North America, Eurasia. Type-species *L. vexans* (Braun, 1901) Semenov, 1928.

**2b. Testes wholly or partly anterior to ovary ..... *Srivastavatrema* Singh, 1962. (Fig. 62.3)**
**Diagnosis:** Body 1–3 mm long, elongate. Tegument spinous or apparently smooth. Oral sucker well developed, subterminal. Ventral sucker equatorial to pre-equatorial. Prepharynx short to absent. Oesophagus short to elongate. Intestinal bifurcation in anterior forebody. Caeca long, extend posterior to ventral sucker to near posterior end of body. Testes in forebody or mostly in forebody, symmetrical. Cirrus-sac mostly anterior to ventral sucker, directed anteriorly, contains bipartite seminal vesicle, pars prostatica and ejaculatory duct. Genital pore opens anterolaterally on margin of body, at level of intestinal bifurcation or pharynx. Ovary submedian, post-testicular, distant from pharynx. Laurer's canal not reported. Uterus fills most of hindbody. Eggs small, operculate, numerous. Vitellarium forms grape-like clusters, in forebody, well posterior to intestinal bifurcation. Excretory vesicle Y-shaped. In intestinal tract of birds (Passeriformes); southern Asia. Type-species *S. indicum* Singh, 1962.

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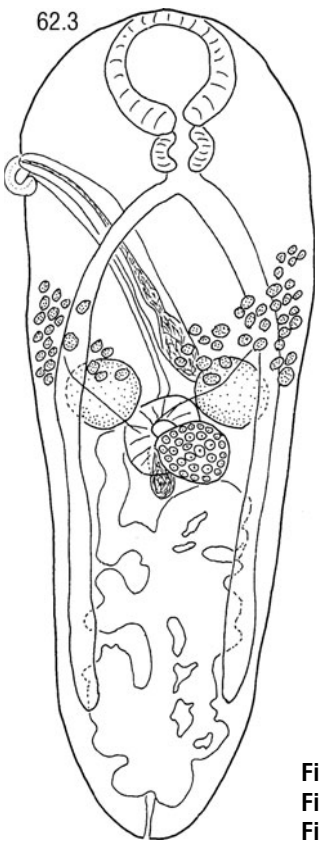




**Fig. 62.1.** *Stomylotrema perpastum* Braun, 1902. After Yamaguti (1971).
**Fig. 62.2.** *Laterotrema cincli* Yamaguti, 1939. After Yamaguti (1971).
**Fig. 62.3.** *Srivastavatrema indicum* Singh, 1962. After Yamaguti (1971).

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# 63 Family Taiwantrematidae Fischthal & Kuntz, 1981

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## Introduction

Known only from the original record of *Taiwantrema arborophilae* Fischthal & Kuntz, 1981 from the Taiwan hill-partridge *Arborophila crudigularis* (Galliformes: Phasianidae) in Taiwan (Fischthal & Kuntz, 1981b), this family includes a small, somewhat microphallid-like worm with a single testis and a large, muscular cirrus-sac. It was originally compared with the heterophyid genus *Procerovum* Onji & Nishio, 1916, but its distinct muscular cirrus-sac and lack of ventrogenital sac or gonotyl preclude its placement in the Heterophyidae Leiper, 1909. Numerous type-specimens have been examined (USNPC 76256–7) and most of the original authors' observations confirmed. The material is not in ideal condition, but most features can be detected, apart from the posterior extent of the caeca, which are obscured by vitelline follicles; Fischthal & Kuntz (1981b) stated that the caeca reached just past the testis. The family is retained here as valid, but needs further investigation using new material.

## Family Taiwantrematidae Fischthal & Kuntz, 1981

**Diagnosis:** Body small, pyriform. Tegument spinous. Eye-spot pigment not seen. Oral sucker oval, subterminal. Ventral sucker just in posterior half of body, small. Prepharynx short. Pharynx oval, small. Oesophagus long. Intestinal bifurcation in posterior forebody. Caeca reach at least to level of uterus, but exact point of termination not seen (obscured by vitelline follicles). Testis single, oval, in mid-hindbody. Cirrus-sac with strongly marked circular muscle fibres in wall, lies more or less transversely across posterior hindbody. Seminal vesicle large, oval, fills much of cirrus-sac. Pars prostatica in distal part of cirrus-sac. Cirrus formed, nearly always seen extruded, narrows distally. Genital atrium small. Genital pore just anterodextral or sinistral to ventral sucker. Ovary oval, pretesticular, lateral, on opposite side of body to genital pore. Seminal receptacle mediodorsal to ovary. Laurer's canal not detected. Uterus short, between testis and ventral sucker. Eggs large, usually relatively few (fewer than six), sometimes more (*c.* 50), tanned, operculate. Metraterm short, narrow, surrounded by scattered gland-cells, enters posterior part of genital atrium.

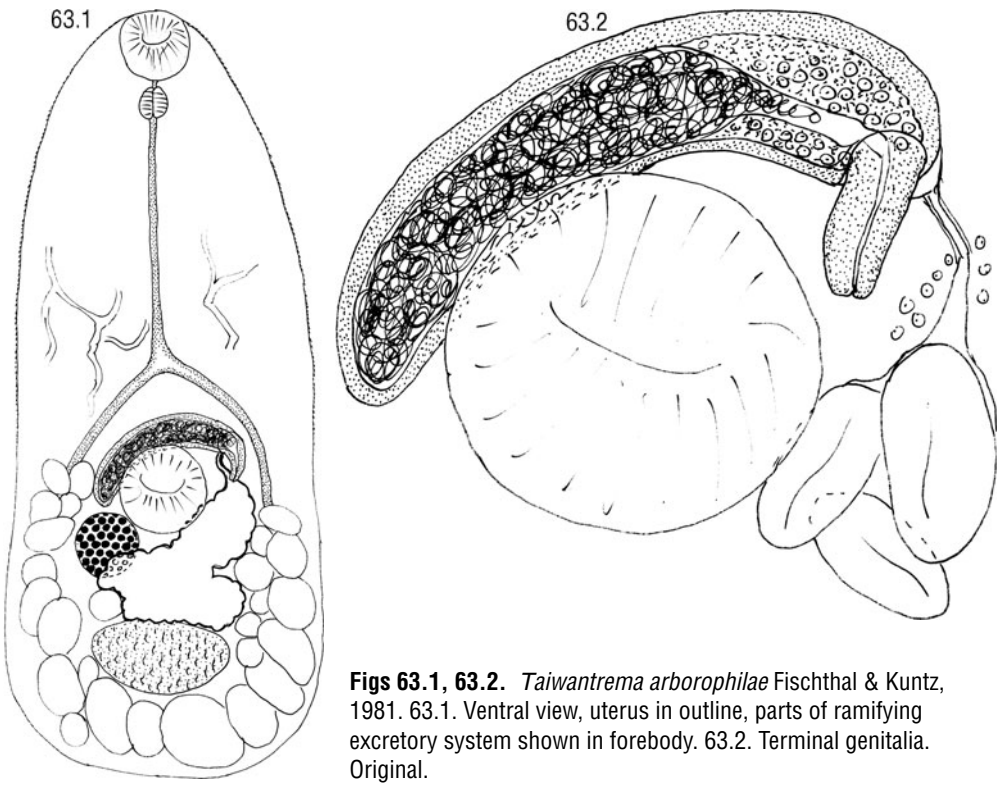
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Vitellarium follicular; field U-shaped, from level of ventral sucker to posterior extremity. Excretory vesicle Y-shaped, dividing immediately posterior to testes; arms reach into forebody where they ramify and reach oral sucker; pore ventrally subterminal. In galliform bird; Taiwan. Type-genus *Taiwantrema* Fischthal & Kuntz, 1981.

## *Taiwantrema* Fischthal & Kuntz, 1981 (Figs 63.1, 63.2)

**Diagnosis:** With characters of family. Type-species *T. arborophilae* Fischthal & Kuntz, 1981.




**Figs 63.1, 63.2.** *Taiwantrema arborophilae* Fischthal & Kuntz, 1981. 63.1. Ventral view, uterus in outline, parts of ramifying excretory system shown in forebody. 63.2. Terminal genitalia. Original.

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# 64 Family Zoogonidae Odhner, 1902

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## Introduction

Zoogonids are common and widespread gastro-intestinal parasites, mainly of marine fishes. They are characterized by a spinous tegument, a lateral genital pore, a restricted field of vitelline follicles and a canalicular seminal receptacle. There are two types of female genital system, one with one or a few median vitelline follicles and untanned eggs (Zoogoninae Odhner, 1902) and the other with paired fields of vitelline follicles and tanned eggs (Lepidophyllinae Stossich, 1903). The early taxonomic history of the Zoogonidae Odhner, 1902 was discussed by Bray (1987a, b). Dollfus (1952) considered the two groups to have family status as the Zoogonidae and Steganodermatidae Yamaguti, 1934, and Skrjabin (1957) recognized the superfamily Zoogonoidea Odhner, 1902 to include these two families. The molecular studies of Hall *et al*. (1999), Cribb *et al*. (2001b) and Olson *et al*. (2003) have indicated that the Zoogonidae may be paraphyletic, but it would be premature to base systematic changes on these results.

Three cladistic studies on the family have been published. The work of Bray (1987a, b) was reanalysed by Brooks (1990). He came to several conclusions as to the status of genera that contradicted those of Bray, but refrained 'from making formal designations', awaiting a revision of the Zoogonidae with 'a larger database'. Nevertheless, Brooks & McLennan (1993) republished the same trees and, without explanation, found the data set sufficient to warrant a rash of renaming and synonymies. On the whole, I think that Brooks' (1990) view is valid, i.e. it is probably too early to sink all the genera he did, but in some instances it appears that the case is well made. He found the Lepidophyllinae (*sensu* Bray) to be paraphyletic and divided it into three subfamilies, one including the single genus *Lecithostaphylus* Odhner, 1911 and another *incertae sedis* with three genera radiating from a polytomy. These subfamilies are not recognized here.

Brooks & McLennan (1993) reduced the number of genera in the Zoogoninae to three, *Zoogonoides* Odhner, 1902, *Diphterostomum* Stossich, 1903 and *Zoogonus* Odhner, 1902. *Neozoogonus* Arai, 1954 and *Pseudozoogonoides* Zhukov, 1957 were sunk into *Zoogonoides; Glaucivermis* Overstreet, 1971, *Parvipyrum* Pritchard, 1963 and *Brevicreadium* Manter, 1954 were sunk into *Diphterostomum*; and *Proparvipyrum* Fischthal, 1980 was sunk into *Zoogonus*. This is in contrast to Bray (1987a), who recognized nine genera. The character relating to the division

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of the vitelline mass was shown not to be a generic character in Brooks & McLennan's analysis, whereas the atrial sac, short saccate caeca and the position of the genital pore appear to be important diagnostic features. The atrial sac is not reported as present in all *Zoogonoides* species (Bray, 1987a), but this is not reflected in Brooks & McLennan's analysis, unless the character 'genital atrium lacking' (one of the autamorphies of *Z. laevis* Linton, 1940) actually refers to the lack of an atrial sac. As this analysis has, therefore, highlighted such a high level of homoplasy and so much of the resolution is based on single characters, and as no matrix was published allowing additions and reanalyses of the work, I agree with Brooks (1990) that altering designations on the basis of this analysis is premature and believe that it would reflect badly on the usefulness of the keys as an aid to identifying worms.

Bilqees *et al*. (2003b) erected *Neodiptherostomum* [*sic*] Bilqees, Shaukat & Haseeb, 2003 based on two specimens from *Pseudosciaena diacanthus* (Sciaenidae) in the Arabian Sea. It appears to be very similar to *Diphterostomum*, including the lamellar muscular lips, but differs in having numerous vitelline follicles in the hindbody. It seems likely that these authors have interpreted stained parts of embryonating eggs, in inconspicuous membranous capsules, as vitelline follicles. This genus is, therefore, considered a synonym of *Diphterostomum* pending the finding of more specimens and the confirmation, or otherwise, of these findings.

Yamaguti (1934) stated that his new genus *Cephaloporus* Yamaguti, 1934 represented a new subfamily, the Cephaloporinae Yamaguti, 1934, in the family Paramphistomidae Fischoeder, 1901. Travassos (1934) used the taxon at the family level, including *Cephaloporus* and *Plectognathotrema* Layman, 1930. This family has long been recognized as close to the Zoogonidae. *Cephaloporus* was considered an aberrant zoogonid by Price (1937), and the family was considered synonymous with the Zoogonidae by Brooks *et al*. (1985). Price (1937), on the other hand, thought that *Plectognathotrema* was an aberrant fellodistomid and this designation has been followed in Volume 1 of this series (Bray, 2002b). Despite the inclusion by Brooks *et al*. (1985) of the Cephaloporidae in the Zoogonidae, neither Brooks (1990) nor Brooks & McLennan (1993) included cephaloporid genera in their phylogeny of the Zoogonidae. The excretory system is poorly known in 'cephaloporid' genera. Its only description in the genera included here in the Zoogonidae is by Bray (1985), verified on a sectioned specimen, who described the excretory pore as dorsal and the vesicle as I-shaped and directed posteriorly in *Cephaloporus bakeri* Bray, 1985. The type-genus of the family, *Cephaloporus*, is indeed amphistomatous, the posterior displacement of the ventral sucker presumably causing the dorsal aspect of the excretory pore. The only other 'cephaloporid' genus with zoogonid affinities, *Yamagutiplectognathotrema* Parukhin, 1977, is not truly amphistomatous and the excretory system is not known.

*Anarhichotrema* Shimazu, 1973 and *Neolissorchis* Machida, 1985 were both originally placed in the Lissorchiidae Magath, 1917. This family, as defined by Bray (Chapter 8, this volume), contains only freshwater species. They have several features indicating their best situation to be in the Zoogonidae, e.g. spiny tegument, lateral genital pore and canalicular seminal vesicle. The filamented eggs are, however, unusual for the family. Both genera are known only from the type-species, *A. ochotense* Shimazu, 1973 from *Anarhichas orientalis* (Anarhichadidae), Okhotsk Sea (Shimazu, 1973) and *N. genge* Machida, 1985 from *Petroschmidtia toyamensis* (Zoarcidae) and *Enophrys diceraus* (Cottidae) off Japan (Machida, 1985; Machida & Araki, 1994). They are considered synonymous, as their descriptions completely agree, and they come from deep-water teleosts from adjacent areas.

*Koiea* Bray & Campbell, 1995 is unusual in that it has a Y-shaped excretory vesicle and testes at the posterior extremity (Bray & Campbell, 1995). The type-species, *K. notacanthi* Bray & Campbell, 1995, was reported from the deep-water eel *Notacanthus chemnitzi. Steganodermatoides notocanthi*

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Korotaeva, 1994 from *N. macrorhynchus* from the southern Pacific Ocean (Korotaeva, 1994) is clearly congeneric and should be transferred as *Koiea notocanthi* (Korotaeva, 1994) n. comb.

*Lecithostaphylus* Odhner, 1911 was considered a subgenus of *Steganoderma* Stafford, 1904 by Bray (1987b) but as the only genus in the subfamily Lecithostaphylinae Odhner, 1911 by Brooks (1990). It differs from *Steganoderma* in having a pedunculate ventral sucker (Brooks & McLennan's (1993) diagnostic character) and longer caeca. Its generic status is recognized here, based on its distinctive position in Brooks' phylogeny. Brooks (1990) pointed out that members of this taxon often inhabit fishes of the beloniform families Exocoetidae and Belonidae, but recent findings indicate that they may also be common in damselfishes (Pomacentridae) (Cribb *et al*., 1992; Toman, 1992). *L. fugus* Zhang, Qiu & Li, 1986 from the tetraodontid *Takifugu* is probably a fellodistomid, possibly *Lintonium* Stunkard & Nigrelli, 1930. With the recognition of the generic status of *Lecithostaphylus, Steganoderma* has lost most of its species and is now based mainly on the type-species, with the only other likely members being *S. atherinae* Price, 1934 (which Brooks & McLennan, 1993, placed in *Lepidophyllum*) and *S. rhiphidium* Wang, 1986.

Bray & Justine (2008) re-examined the holotype, and only specimen, of *Dupliciporia haeckeli* Reimer, 1985, the type-species of the genus. They concluded that it had a longitudinal division of the ventral sucker and a lobed, infundibuliform oral sucker, making it the oldest available name for a small group of genera with these characteristics. They considered *Parasteganoderma* Machida & Araki, 1990 and *Liliaoralis* Korotaeva, 1994 as junior synonyms of *Dupliciporia* (see Machida & Araki, 1990; Korotaeva, 1994). In addition to these two diagnostic characteristics, the circular bands on the eggshell are another characteristic of most species now included in the genus, although they were not detected in the poorly fixed type-specimen of *D. haeckeli*. Korotaeva (1994) did not describe the longitudinal division of the ventral sucker of *Liliaoralis*, but the lobed, infundibuliform oral sucker and the banded eggshells strongly indicate that it belongs in *Dupliciporia*. Three of the four known species, *D. haeckeli, D. cataluphi* (Korotaeva, 1994) and *D. lanterna* Bray & Justine, 2008 are parasites of fishes of the family Priacanthidae.

Brooks & McLennan (1993) sank *Neosteganoderma* Byrd, 1964 and *Steganodermatoides* Parukhin & Lyadov, 1979 into *Proctophantastes* Odhner, 1911. In their tree (their figure 43), *Steganodermatoides* is monophyletic, but both *Neosteganoderma* and *Proctophantastes* are undefined as clades and are jointly paraphyletic. These three genera are certainly close. *Steganodermatoides* has been recognized here, as it is monophyletic and has the autapomorphy of a row of large papillae across the internal equator of the ventral sucker. The implication is that the internal muscular ridge and dorsal cleft of the ventral sucker (as in *Proctophantastes* and *Neosteganoderma*) is plesiomorphic relative to the condition in *Steganodermatoides*. On the other hand, this condition could be considered an autapomorphy of *Proctophantastes* + *Neosteganoderma*, which are here considered synonymous. Previously, they had been distinguished by minor characters of the genital atrium and periatrial gland. Machida *et al*. (2006) described two new species, *Neosteganoderma physiculi* Machida, Kamegai & Kuramochi, 2006 and *Proctophantastes nettastomatis* Machida, Kamegai & Kuramochi, 2006, along with a redescription of the type-species of *Neosteganoderma. P. nettastomatis* fits clearly into the current concept of *Proctophantastes*, whereas *N. physiculi* differs materially in lacking the equatorial division of the ventral sucker. It shares with members of the genus *Dupliciporia* a lobed oral sucker and raised bands on the eggs, but differs in the long caeca opening to the outside through separate ani and the lack of a longitudinal division of the ventral sucker.

*Panopula* Overstreet & Pritchard, 1977 forms a monophyletic group within the large clade designated *Deretrema* Linton, 1910 by Brooks & McLennan (1993). It is retained as valid in this key.

The monotypic freshwater genera *Limnoderetrema* Bray, 1987 and *Pseudochetosoma* Dollfus, 1951 are retained, despite having been subsumed in *Deretrema* by Brooks & McLennan (1993).

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The autapomorphy of Brooks & McLennan's *Deretrema* is 'elongate, coiled seminal vesicle'. In *Limnoderetrema*, the seminal vesicle is saccular. Torres & Neira (1991) expanded *Limnoderetrema* to include *Steganoderma macrophallus* Szidat & Nani, 1951 and *L. tolosai* Torres & Neira, 1991, both from freshwater atherinids in Argentina, but Viozzi *et al.* (2000) considered that the Argentinian forms should, at least for the present, be retained in *Steganoderma. Limnoderetrema* as presented here is based on the type-species only and the status of the Argentinian forms must await further study. *Pseudochetosoma* is, indeed, very similar to *Deretrema*, particularly in its site in the gall-bladder and the lack of tegumental spines, but it is restricted to freshwater fishes of south-east Europe, the Middle East and North Africa, and differs from *Deretrema* in its short, saccular excretory vesicle.

The type-, and so far only, species of *Parazoogonus* Wang, 1986 is reported from *Acipenser* in the 'middle reaches' of the Yangtze River, China (Wang W., 1986). It appears close to *Proparvipyrum* Fischthal, 1980 in *Mullus* from the Israeli coast of the Mediterranean Sea (Fischthal, 1980). Apart from the host and the type of water body, the only difference that might sustain a generic distinction is the long excretory vesicle, which reaches the level of the testes in *Parazoogonus*. The latter genus is retained as distinct based on these observations.

*Pseudopalaeorchis* Kamegai, 1970 was erected as a monorchiid genus by Kamegai (1970) from the beryciform fish *Monocentris japonicus* in the Sea of Japan. A second species was erected from the same host-species from Mozambique by Reimer (1985). Although the cirrus-sac and metraterm are described as being lined with 'fine hair-like' spines, the illustrations show the terminal genitalia to be very similar to those of such lepidophyllines as *Neosteganoderma, Proctophantastes* and *Steganodermatoides*. Bray & Gibson (1986) described the ejaculatory duct of *Neosteganoderma glandulosum* Byrd, 1964 as having 'at about its middle, a radial layer of hyaline spine-like structures'. They were not sure whether these were 'spines or fragments of longitudinal muscle'. The terminal genitalia, the sinistromarginal genital pore and the female proximal system strongly indicate that this genus is a lepidophylline zoogonid. As stated above, the terminal genitalia indicate affinities with *Neosteganoderma, Proctophantastes* and *Steganodermatoides*, but the tiny undivided ventral sucker distinguishes it from these genera.

Brooks & McLennan (1993) sank *Urinatrema* Yamaguti, 1934 and a group of three poorly known *Steganoderma* species into *Lepidophyllum*. As their figure 42 indicated that these three groups of species each formed a clade, *Urinatrema* is recognized as valid, based on the distinctive characters given in the key. The status of the three *Steganoderma* species must await a restudy of these forms.

## Genera *inquirenda*

*Pseudocypseluritrema* Parukhin, 1974 has a median genital pore and an unarmed tegument and is reported from the stomach of its host (Parukhin, 1974). It is not a zoogonid and might be a hemiuroid. It is reported in a flying fish, a common host of lepidophylline zoogonids.

As far as one can tell from the perfunctory description and figure, *Plectognathotrematoides* Parukhin, 1971 *nec* Yamaguti, 1971, is not a 'cephaloporid'-like zoogonid, despite its recovery from a balistid (Parukhin, 1971). The extensive vitelline fields, the non-lateral genital pore and the apparent lack of tegumental spines are not zoogonid features, and the more or less mid-ventral ventral sucker, the testes in the hindbody and the long undulating tubular seminal vesicle are not 'cephaloporid' features.

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## Family Zoogonidae Odhner, 1902

(Syns Cephaloporidae Yamaguti, 1934; Steganodermatidae Yamaguti, 1934; Dupliciporiidae Reimer, 1985)

**Diagnosis:** Body small to large, elongate cylindrical to flattened spatulate. Body-surface usually spinous; spines occasionally absent or lost. Oral sucker subterminal to terminal, globular to infundibuliform. Ventral sucker small to large, simple or ornamented or divided transversely, may bear muscular lips, usually in about mid-region of body. Prepharynx long to short or practically absent. Pharynx globular to oval, small to large. Oesophagus long to absent. Intestinal bifurcation in forebody or anterior hindbody. Caeca two, occasionally single, saccular, short saccular to long, terminating in forebody to reaching close to posterior extremity. Testes two, oval to globular, lobed or entire, symmetrical, oblique or tandem, in hindbody or posterior forebody. Cirrus-sac well developed, short saccular to elongate cylindrical, straight to sharply recurved. Seminal vesicle internal; shape saccular, narrow sinuous tubular or bipartite. Pars prostatica usually prominent, narrow to vesicular. Ejaculatory duct muscular, may form protuberant cirrus bearing spine-like structures or bosses. Genital atrium either small, simple or large, pocketed and muscular, surrounded by gland-cells. Genital pore ventrally or occasionally dorsally submarginal or more usually marginal, usually sinistral, usually in forebody, occasionally lateral to ventral sucker or in anterior hindbody. Ovary entire to multilobate, in hindbody or posterior forebody, usually pretesticular. Canalicular seminal receptacle present. Laurer's canal present. Mehlis' gland usually present. Uterus normally reaches posteriorly beyond gonads, up to posterior extremity, contains numerous eggs. Eggs may lack tanned capsules (i.e. possess membranous capsule) or have thin to thick tanned capsule, occasionally filamented. Vitellarium small, a single mass or pair of masses, or divided into follicles in one median or usually in two lateral fields, in fore- or hindbody. Excretory vesicle short, saccular to long tubular, I-shaped (occasionally reported Y-shaped); pore posteriorly terminal to subterminal. In alimentary tract, gall-bladder, bile-ducts or urinary-bladder of teleosts and occasionally elasmobranchs; cosmopolitan. Type-genus *Zoogonus* Looss, 1901.

### Key to subfamilies

**1a. Vitellarium forms one or two compact masses, or several follicles, in undivided median field; egg capsules weakly tanned or membranous ..... Zoogoninae Odhner, 1902.**

**1b. Vitellarium forms paired fields of follicles; egg capsule strongly tanned, forming operculate shell ..... Lepidophyllinae Stossich, 1903.**

## Subfamily Zoogoninae Odhner, 1902

(Syns Diphterostominae Stossich, 1903; Parvipyrinae Yamaguti, 1970)

**Diagnosis:** Body small, oval. Body-surface usually spinous. Ventral sucker small to large, simple or bearing muscular lips. Testes entire, symmetrical to oblique, in hindbody or lateral to ventral sucker. Seminal vesicle bipartite, occasionally tubular. Genital atrium small, may possess atrial sac. Periatrial gland absent. Genital pore marginal, in forebody or beside ventral sucker, or in anterior hindbody, usually sinistral. Ovary entire, in hindbody or dorsal to ventral sucker, pre- or post-testicular. Mehlis' gland weakly developed. Uterus mainly postgonadal. Egg capsules membranous or weakly

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tanned. Vitellarium small single mass, two small masses or small field of follicles, in median region of hindbody. Excretory vesicle short, saccular; pore terminal or ventrally subterminal. Cercariaeum with stylet. Two sporocyst generations in gastropods. In alimentary tract of marine teleosts and elasmobranchs; cosmopolitan. Type-genus *Zoogonus* Looss, 1901.

## Key to genera

**1a. Caecum single ..... *Parvipyrum* Pritchard, 1963. (Fig. 64.1)**
**Diagnosis:** Body small, pyriform. Body-surface spinous anteriorly (spines often lost). Oral sucker globular, subterminal. Ventral sucker large, in mid- to posterior body region, with distinct thickened lips. Prepharynx distinct, short. Pharynx small, oval. Oesophagus distinct, slightly longer than pharynx. Single caecum reaches about mid-level of ventral sucker. Testes oval, in anterior hindbody, symmetrical to oblique. Cirrus-sac claviform, arcuate. Seminal vesicle bipartite. Pars prostatica vesicular. Ejaculatory duct short; cirrus often formed. Genital atrium distinct. Genital pore marginal, sinistral, at level of mid- to posterior level of ventral sucker. Ovary oval, large, pretesticular; median to submedian, at level of cirrus-sac. Uterus confined to short hindbody. Miracidium enclosed in membranous capsule. Vitellarium single, compact, intertesticular. Excretory vesicle a globular sac; pore terminal. In intestine of marine teleosts (*Acanthurus* spp.); off Hawaii, New Caledonia. Type-species *P. acanthuri* Pritchard, 1963.

**1b. Two caeca ..... 2.**

**2a. Genital pore at level of mid- to posterior forebody ..... 6.**
**2b. Genital pore at level of ventral sucker or anterior hindbody ..... 3.**

**3a. Intestinal bifurcation in posterior forebody ..... 4.**
**3b. Intestinal bifurcation in hindbody or dorsal to ventral sucker ..... 5.**

**4a. Excretory vesicle short, saccular; in marine teleosts .....**
**..... *Proparvipyrum* Fischthal, 1980. (Fig. 64.2)**
**Diagnosis:** Body small, elongate-oval. Body-surface spinous. Body constricted immediately posterior to oral sucker (forming a 'neck'). Oral sucker subglobular, subterminal. Ventral sucker small, more or less equatorial. Prepharynx long. Pharynx small. Oesophagus long. Intestinal bifurcation in posterior forebody. Caeca very short, saccular, terminate in forebody or at level of ventral sucker. Testes symmetrical to sub-symmetrical in anterior hindbody. Cirrus-sac large, recurved. Seminal vesicle bipartite. Pars prostatica vesicular. Ejaculatory duct muscular. Genital atrium small, distinct. Genital pore sinistral, marginal, level with posterior part of ventral sucker or in anterior hindbody. Ovary large, elongate oval, at level of ventral sucker, pretesticular. Uterus fills most of hindbody. Metraterm muscular. Miracidium large, surrounded by membranous capsule. Vitellarium single, at level of posterior part of ovary. Excretory vesicle small, saccular; pore terminal. In intestine of marine teleosts (*Mullus*); eastern Mediterranean. Type-species *P. israelense* Fischthal, 1980.

**4b. Excretory vesicle long, I-shaped, reaches testes; in freshwater sturgeon .....**
**..... *Parazoogonus* Wang, 1986. (Fig. 64.3)**
**Diagnosis:** Body small, fusiform. Tegument spinous. Oral sucker subglobular, subterminal. Ventral sucker small, just pre-equatorial. Prepharynx short. Pharynx small. Oesophagus long. Intestinal

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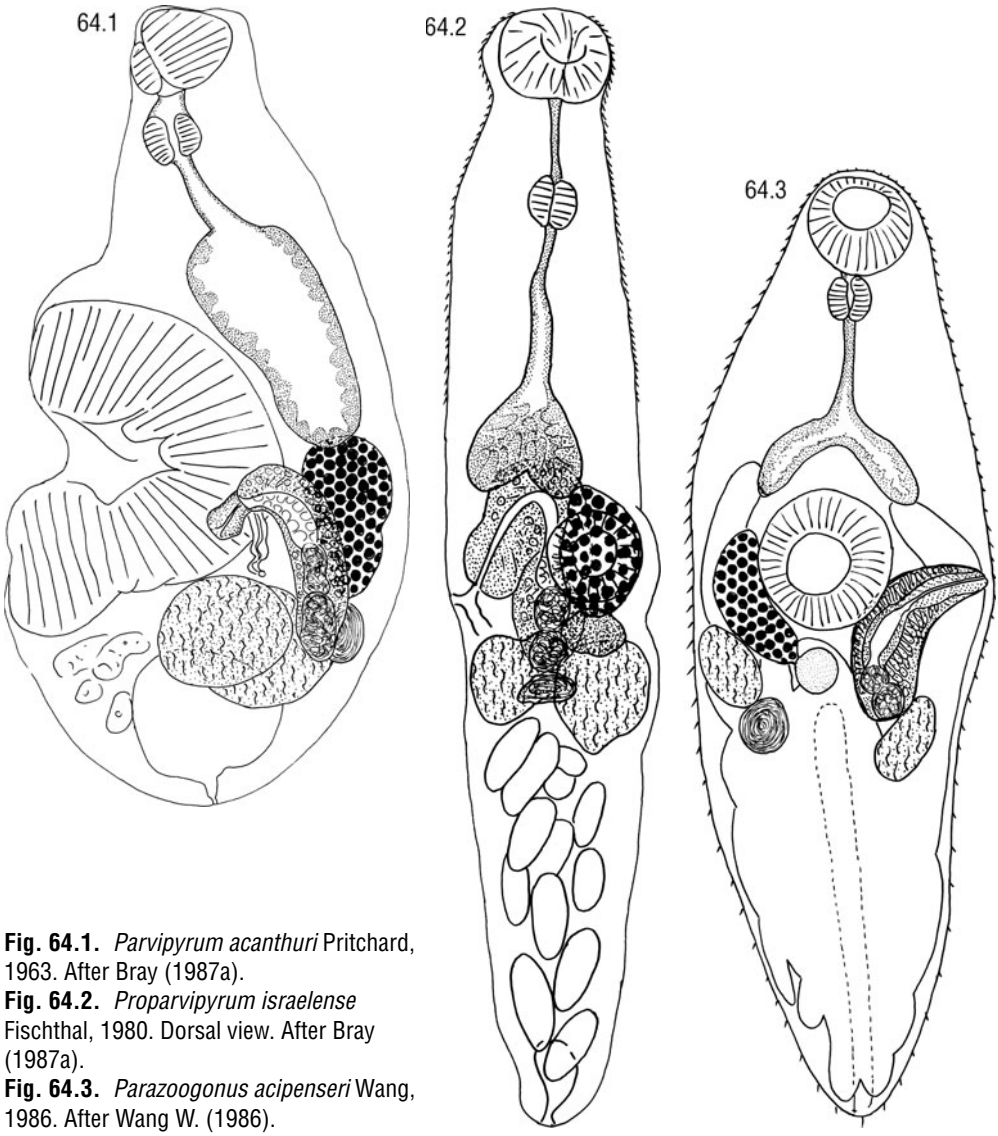



**Fig. 64.1.** *Parvipyrum acanthuri* Pritchard, 1963. After Bray (1987a).
**Fig. 64.2.** *Proparvipyrum israelense* Fischthal, 1980. Dorsal view. After Bray (1987a).
**Fig. 64.3.** *Parazoogonus acipenseri* Wang, 1986. After Wang W. (1986).

bifurcation in posterior forebody. Caeca short, saccular, end in forebody. Testes oblique, in anterior hindbody. Cirrus-sac claviform. Seminal vesicle bipartite. Pars prostatica vesicular. Ejaculatory duct muscular. Genital pore sinistromarginal, at level of posterior part of ventral sucker. Ovary large, elongate-oval, at level of ventral sucker, pretesticular. Uterus fills most of hindbody. Metraterm muscular. Miracidium large, surrounded by membranous capsule. Vitellarium forms single mass, at level of posterior part of ovary. Excretory vesicle I-shaped, reaches testes; pore terminal. In intestine of freshwater *Acipenser*; China. Type-species *P. acipenseri* Wang, 1986.

**5a. Caeca short, saccular, divergent ..... *Zoogonus* Looss, 1901. (Fig. 64.4)**

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**Diagnosis:** Body small, pyriform to elongate-oval. Tegument spinous. Oral sucker globular, subterminal, similar in size to ventral sucker. Ventral sucker in anterior half of body. Prepharynx distinct, short to long. Pharynx oval. Oesophagus long, reaches posterior margin of ventral sucker or into hindbody. Intestinal bifurcation dorsal to ventral sucker or in anterior hindbody. Caeca short, saccular, divergent, reaching to about mid-hindbody. Testes large, symmetrical, in anterior hindbody. Cirrus-sac elongate, reaches into hindbody. Seminal vesicle bipartite. Pars prostatica vesicular. Ejaculatory duct narrow. Genital atrium small. Genital pore marginal, sinistral or dextral, at or about level of ventral sucker. Ovary globular to oval, median, between caeca, post-testicular. Uterus fills hindbody posterior to gonads. Miracidium surrounded by membranous sac (? or very thin shell). Vitellarium forms single compact mass or occasionally bilobed mass. Excretory vesicle a short sac; pore terminal. Tailless xiphidiocercaria. First intermediate hosts are gastropods. Metacercariae in echinoderms, polychaetes and gastropods. Adults in lower intestine and rectum of marine teleosts; cosmopolitan. Type-species *Z. mirus* Looss, 1901 (syn. of *Z. rubellus* (Olsson, 1868)).

**5b. Caeca long, pass into posterior half of hindbody ..... *Neozoogonus* Arai, 1954. (Fig. 64.5)**
**Diagnosis:** Body small, oval to elongate oval. Tegument spinous anteriorly. Oral sucker infundibuliform and terminal or globular and subterminal, larger than to similar in size to ventral sucker. Ventral sucker circular, small, just pre-equatorial. Prepharynx distinct, short to long. Pharynx globular. Oesophagus long, narrow. Intestinal bifurcation in anterior hindbody or dorsal to ventral sucker. Caeca long, reach well past testes, almost to posterior extremity. Testes oval, symmetrical to oblique, in anterior half of hindbody. Cirrus-sac claviform, curved. Seminal vesicle bipartite, saccular or tubular (?). Pars prostatica vesicular. Ejaculatory duct long. Genital atrium distinct, with atrial sac. Genital pore dextral or sinistral, at level of ventral sucker or in anterior hindbody. Ovary globular to oval, post-testicular. Uterus fills much of post-testicular hindbody. Metraterm muscular. Miracidium surrounded by membranous capsule. Vitellarium a single irregular mass, adjacent to ovary or often just postovarian. Excretory vesicle short, saccular; pore terminal. In intestine of marine teleosts; north-eastern Pacific Ocean, Caribbean Sea. Type-species *N. californicus* Arai, 1954.

**6a. Vitelline mass single or double ..... 7.**
**6b. Vitellarium a single, small median field of follicles ..... ..... *Brevicreadium* Manter, 1954. (Fig. 64.6)**
**Diagnosis:** Body small, pyriform. No spines seen on tegument. Oral sucker globular, subterminal. Ventral sucker large, prominent, with prominent transverse muscular lips. Prepharynx short. Pharynx globular. Oesophagus short, distinct. Intestinal bifurcation in forebody. Caeca short, saccular, just overlapping ventral sucker. Testes oval, sub-symmetrical to symmetrical in anterior hindbody. Cirrus-sac elongate oval. Seminal vesicle bipartite; proximal part larger. Pars prostatica vesicular. Ejaculatory duct muscular. Genital atrium distinct. Genital pore marginal, sinistral, in mid-forebody. Ovary oval, anterior to right testis. Uterus mainly dorsal to ventral sucker, not reaching posteriorly beyond testes. Metraterm partly in form of prominent globular sphincter. Eggs numerous with thin, but distinctly tanned, shells. Vitellarium forms undivided small group of about 18 follicles lying along posterior margin of ventral sucker. Excretory vesicle short, narrow, reaches right testis; pore ventrally subterminal. In intestine of marine teleost (*Conger*); off New Zealand. Type-species *B. congeri* Manter, 1954.

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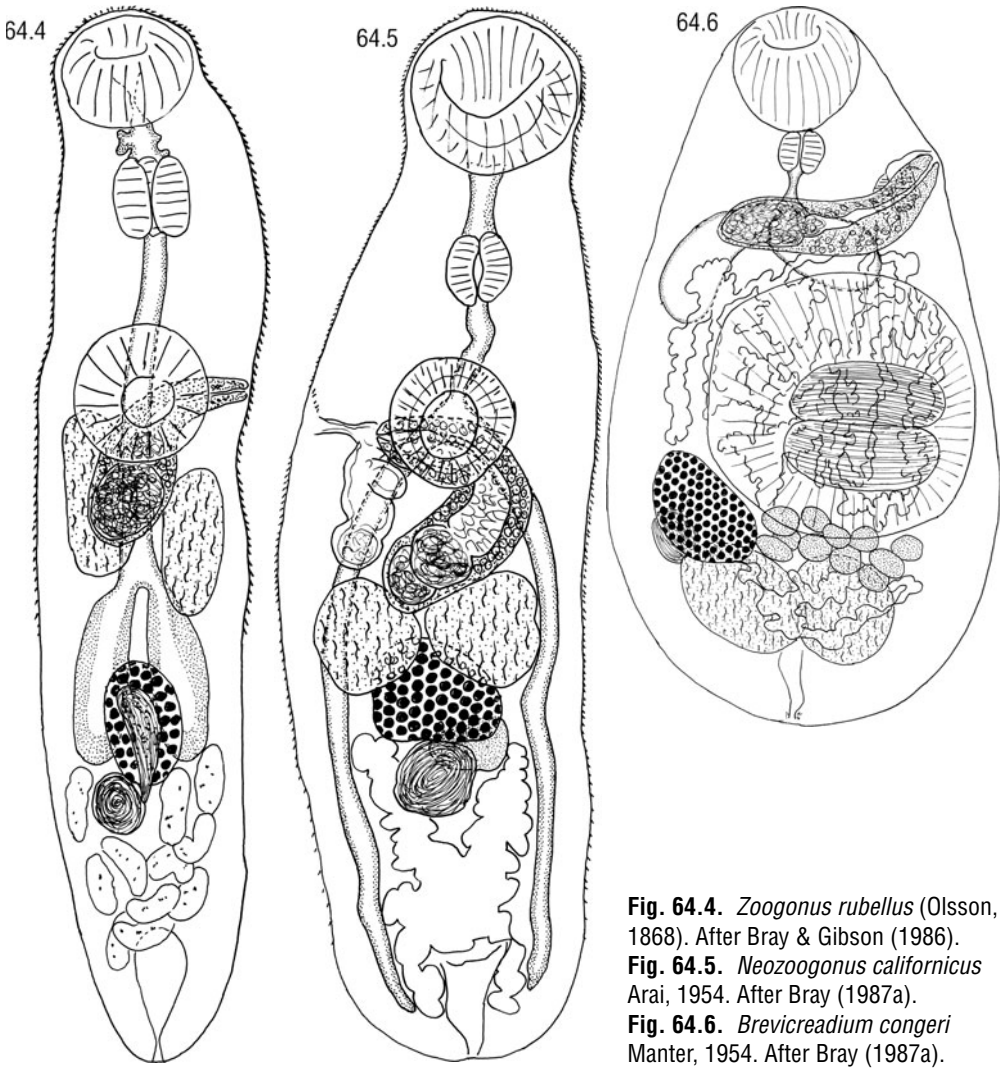



**Fig. 64.4.** *Zoogonus rubellus* (Olsson, 1868). After Bray & Gibson (1986).
**Fig. 64.5.** *Neozoogonus californicus* Arai, 1954. After Bray (1987a).
**Fig. 64.6.** *Brevicreadium congeri* Manter, 1954. After Bray (1987a).

**7a. Vitelline mass single ..... *Zoogonoides* Odhner, 1902.** (**Fig. 64.7**)
**Diagnosis:** Body small, pyriform to elongate-oval. Tegument spinous; spines usually restricted to forebody, occasionally also in hindbody. Oral sucker globular, subterminal, smaller than to about equal to ventral sucker. Ventral sucker in anterior half or middle of body. Prepharynx short. Pharynx globular. Oesophagus distinct. Intestinal bifurcation in posterior forebody. Caeca reach close to level of testes or just beyond. Testes oval, symmetrical to slightly oblique, just posterior to or at level of ventral sucker. Cirrus-sac claviform, short to long, straight or curved. Seminal vesicle bipartite. Pars prostatica oval, vesicular. Ejaculatory duct short to long, with annular wrinkles (? spined). Genital atrium distinct. Atrial sac usually evident. Genital pore usually sinistral, lateral in mid- to posterior forebody. Ovary oval, between or slightly posterior to testes. Uterus fills much of hindbody. Metraterm muscular. Miracidium in membranous capsule (or very thin shell). Vitellarium a single subglobular to oval mass, normally between ovary and seminal receptacle.

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Excretory vesicle small, oval; pore terminal. Tailless xiphidiocercaria in gastropods. Metacercariae in echinoderms, polychaetes, lamellibranchs and gastropods. Adults in posterior intestine and rectum of marine teleosts; northern hemisphere. Type-species *Z. viviparus* (Olsson, 1868).

**7b. Vitelline masses two ..... 8.**

**8a. Caeca long, parallel ..... 9.**
**8b. Caeca short, saccular, divergent ..... *Diphterostomum* Stossich, 1903. (Fig. 64.8)**
(Syns *Diphtherostomum* Stafford, 1905; *Zoonogenus* Nicoll, 1912; *Neodiptherostomum* Bilqees, Shaukat & Haseeb, 2003)

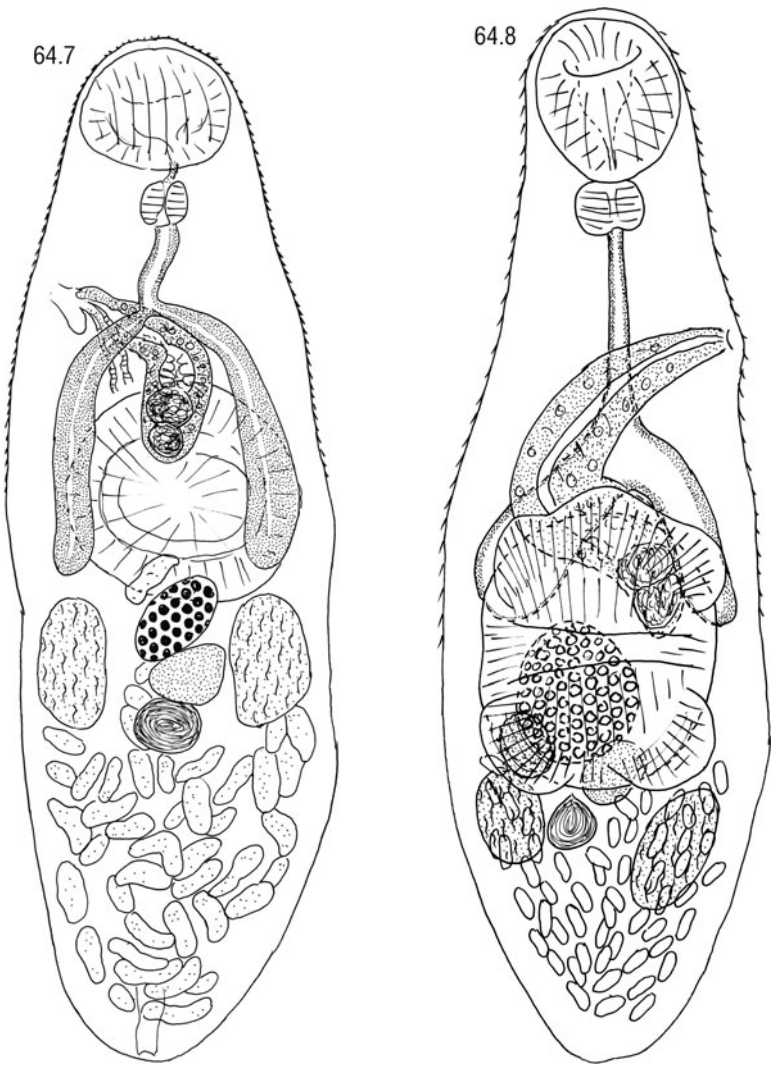



**Fig. 64.7.** *Zoogonoides viviparus* (Olsson, 1868). After Bray & Gibson (1986).
**Fig. 64.8.** *Diphterostomum brusinae* (Stossich, 1888). After Bray & Gibson (1986).

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**Diagnosis:** Body small, pyriform to elongate-oval. Tegument spinous, to limited extent or covering body-surface. Oral sucker globular, subterminal. Ventral sucker in middle or posterior half of body, often large, muscular, or sometimes smaller, more weakly developed, in some species bearing lamellar muscular lips. Prepharynx short. Pharynx oval. Oesophagus normally distinct, long, occasionally short or apparently absent. Intestinal bifurcation in forebody. Caeca very short, saccular, divergent, terminate in posterior forebody or just overlap ventral sucker. Testes oblique to symmetrical, posterior, lateral or anterolateral to ventral sucker. Cirrus-sac variable, elongate, reflexed or not, reaches past anterior margin of ventral sucker or not. Seminal vesicle bipartite. Pars prostatica vesicular. Ejaculatory duct usually long. Genital atrium small. Genital pore marginal or submarginal, in forebody, usually sinistral, occasionally dextral. Ovary globular to oval, submedian, just anterior to or between testes. Uterus fills much of hindbody. Miracidium surrounded by membranous sac or very thin shell. Vitellarium forms two subequal masses. Excretory vesicle small, saccular; pore terminal. Sporocysts in gastropods. Tailless xiphidiocercariae. Metacercariae encyst in invertebrates, or on plants or sedentary animals. Adults in intestine, pyloric caeca and rectum of marine teleosts or spiral valve of elasmobranchs; cosmopolitan. Type-species *D. brusinae* (Stossich, 1888) Stossich, 1903.

**9a. Tegumental spines in forebody thorn-like; testes tandem to diagonal ..... ..... *Glaucivermis* Overstreet, 1971. (Fig. 64.9)**

**Diagnosis:** Body small, fusiform. Tegument spinous throughout; forebody spines large, thorn-like; hindbody spines small, fine. Oral sucker infundibuliform, terminal. Ventral sucker in mid-body, lacks muscular lips. Prepharynx short. Pharynx oval. Oesophagus long. Intestinal bifurcation in posterior forebody. Caeca reach mid-level of ventral sucker. Testes tandem to oblique. Cirrus-sac arcuate. Seminal vesicle bipartite. Pars prostatica vesicular. Ejaculatory duct muscular. Cirrus with small papillae. Genital atrium muscular. Genital pore marginal, sinistral, in posterior forebody. Ovary oval, anterior to or between testes. Uterus fills most of hindbody. Eggs with thin, but distinct, operculate shell. Metraterm muscular. Vitellarium forms two masses at posterior edge of ovary. Excretory vesicle small, saccular; pore terminal. In intestine and pyloric caeca of marine teleosts (*Menticirrhus*); Gulf of Mexico. Type-species *G. spinosus* Overstreet, 1971.

**9b. Tegumental spines small, acuminate; testes symmetrical to oblique ..... ..... *Pseudozoogonoides* Zhukov, 1957. (Fig. 64.10)**

**Diagnosis:** Body small, pyriform. Tegument spinous; spines in regular transverse rows. Oral sucker globular, subterminal. Ventral sucker rounded, in middle of body or posterior part of body, usually subequal to slightly or distinctly larger than oral sucker. Prepharynx short. Pharynx globular. Oesophagus distinct. Intestinal bifurcation in forebody. Caeca narrow, reach just into hindbody. Testes symmetrical, at level of ventral sucker. Cirrus-sac claviform, straight or curved. Seminal vesicle bipartite. Pars prostatica vesicular. Ejaculatory duct distinct. Genital atrium with atrial sac. Genital pore marginal, sinistral, in mid-forebody. Ovary oval, submedian, post-testicular. Uterus fills much of hindbody. Miracidium surrounded by membranous or very weakly tanned egg capsule. Vitellarium forms two subequal masses. Excretory vesicle slightly elongate sac; pore terminal. Metacercariae encyst in teleosts. Adults in intestine and rectum of teleosts (occasionally in spiral valve of elasmobranchs); Arctic, northern Atlantic and northern Pacific Oceans. Type-species *P. microacetabulum* (Shulman-Albova, 1952) Zhukov, 1957 (syn. of *P. subaequiporus* (Odhner, 1911)).

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## Subfamily Lepidophyllinae Stossich, 1903

(Syns Lecithostaphylinae Odhner, 1911; Cephaloporinae Yamaguti, 1934; Steganodermatinae Yamaguti, 1934; Pseudopalaeorchiinae Yamaguti, 1971; Hudsoniinae Campbell, 1975)

**Diagnosis:** Body small to large, cylindrical to flattened, oval to spatulate. Tegument usually spinous. Prepharynx usually short to absent. Spines occasionally present in lining of alimentary system. Intestinal bifurcation in forebody. Caeca two. Genital pore in forebody. Mehlis' gland well developed. Eggs with tanned, operculate shells. Vitellarium forms two symmetrical fields of distinct globular to subglobular follicles. Excretory system usually I-shaped, occasionally Y-shaped; pore terminal or subterminal. In alimentary tract, gall-bladder, bile-duct or urinary-bladder of marine and freshwater teleosts; cosmopolitan. Type-genus *Lepidophyllum* Odhner, 1902.

## Key to genera

**1a. Body flattened spatulate; testes deeply lobed; in urinary bladder of marine teleosts .... 2.**

**1b. Body more or less oval or rounded in cross-section, oval to pyriform or fusiform in ventral view; testes more or less entire; not usually found in urinary-bladder ..... 3.**

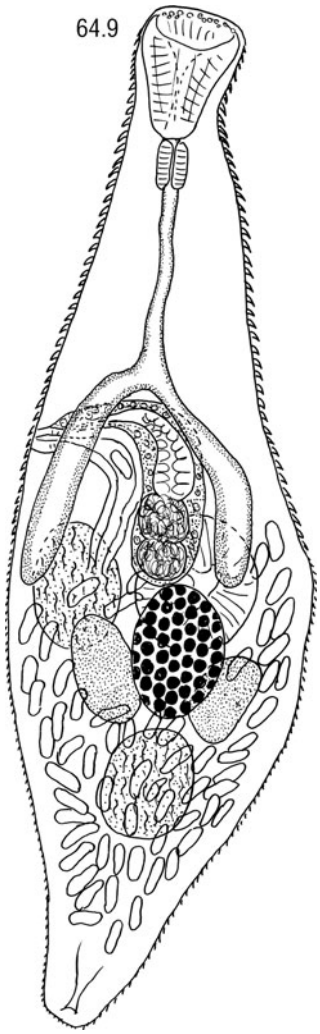
**2a. Caeca narrow, reach level of testes; ovary subglobular to slightly lobed; vitellarium entirely in hindbody ..... *Lepidophyllum* Odhner, 1902. (Fig. 64.11)**
(Syn. *Paralepidophyllum* Yamaguti, 1934)

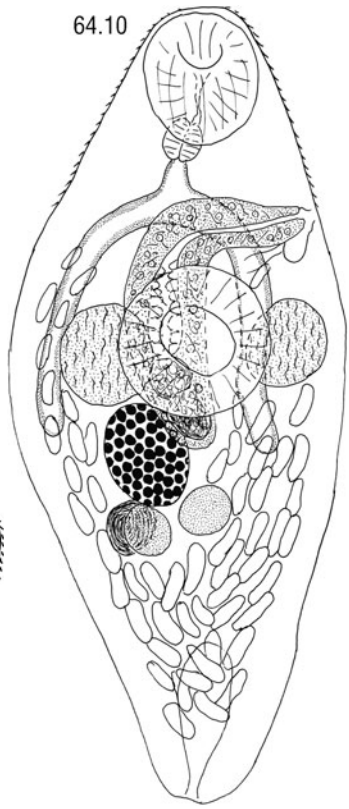
**Diagnosis:** Body broadly pyriform to ampullaceous, strongly flattened dorsoventrally. Tegument spinous. Oral sucker small, globular. Ventral sucker small, rounded, in anterior half of body. Prepharynx short. Pharynx globular. Oesophagus distinct. Intestinal bifurcation in forebody. Caeca reach into hindbody usually to level of vitellarium or testes. Testes lobed to deeply lobed, postovarian, symmetrical, in mid- to anterior hindbody. Cirrus-sac narrow, elongate. Seminal vesicle bipartite. Pars prostatica long. Ejaculatory duct short; junction with pars prostatica indistinct. Genital pore sinistral, dorsally submarginal or marginal, in mid- to anterior forebody. Ovary oval to slightly lobate, in anterior hindbody, submedian. Seminal receptacle distinct, may be large, postovarian. Mehlis' gland distinct. Uterus mainly post-testicular, may occupy bulk of region or be surrounded by broad band of parenchyma. Metraterm muscular. Eggs operculate, tanned; filaments of eggshell material in uterus. Vitellarium forms two groups of about nine to 13 distinct globular follicles, anterior to anteromedial to testes, in hindbody. Excretory vesicle elongate in posterior hindbody; pore dorsally subterminal. In urinary bladder of marine teleosts; Arctic, northern Atlantic and northern Pacific Oceans. Type-species *L. steenstrupi* Odhner, 1902.

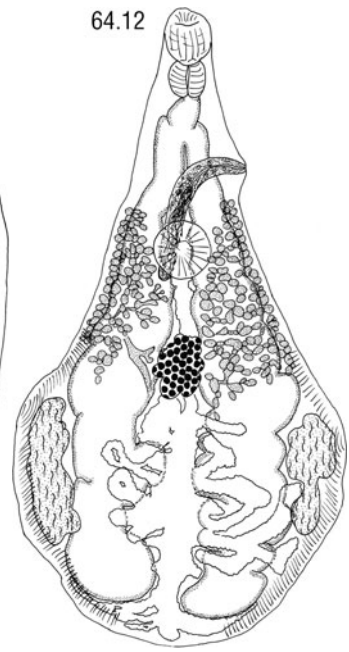
**2b. Caeca dilate or diverticulate, almost reach posterior extremity; ovary deeply lobed; vitellarium in posterior forebody, lateral to ventral sucker and in hindbody; in *Hexagrammos* spp. ... ..... *Urinatrema* Yamaguti, 1934. (Fig. 64.12)**

**Diagnosis:** Body spatulate, with crinkled lateral edge; strong radial musculature in hindbody. Tegument spinous. Oral sucker oval, subterminal. Ventral sucker slightly larger than oral sucker, rounded. Prepharynx short. Pharynx oval. Oesophagus short, distinct. Intestinal bifurcation in forebody. Caeca dilate or diverticulate, almost reach posterior extremity. Testes longitudinally elongate, lobate, symmetrical, extracaecal, in mid-hindbody. Cirrus-sac long, narrow or claviform, reaches ventral sucker. Seminal vesicle bipartite; proximal portion elongate sinuous; distal portion

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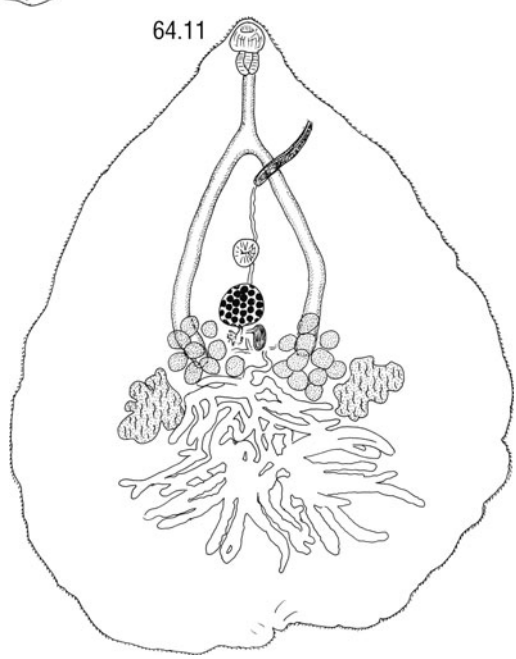




**Fig. 64.9.** *Glaucivermis spinosus* Overstreet, 1971. Dorsal view. After Bray (1987a).
**Fig. 64.10.** *Pseudozoogonoides subaequiporus* (Odhner, 1911). After Bray & Gibson (1986).
**Fig. 64.11.** *Lepidophyllum steenstrupi* Odhner, 1902. After Bray & Gibson (1986).
**Fig. 64.12.** *Urinatrema hispidum* Yamaguti, 1934. After Bray (1987b).

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smaller, saccate. Pars prostatica well developed. Ejaculatory duct present. Genital pore sinistromarginal, in posterior forebody. Ovary deeply lobate, median in anterior hindbody, pretesticular. Uterus mainly ventral to caeca, mainly postovarian. Metraterm muscular. Eggs with thin, tanned shells. Vitellarium forms two lateral groups of many small follicles, pretesticular; fields reach ventral sucker or into forebody. Excretory vesicle said to be Y-shaped; pore dorsally subterminal. In urinary bladder of marine teleosts (*Hexagrammos*); northern Pacific Ocean. Type-species *U. hispidum* Yamaguti, 1934.

**3a. Caeca short, saccular, divergent or, if narrow, not reaching into hindbody ..... 4.**
**3b. Caeca narrow, reach well into hindbody or to testes or beyond ..... 7.**

**4a. Genital pore at level of oral sucker or pharynx; in freshwater teleosts ..... ..... *Limnoderetrema* Bray, 1987. (Fig. 64.13)**

**Diagnosis:** Body small, oval. Tegument spinous, at least anteriorly. Oral sucker subglobular, subterminal. Ventral sucker subequal with oral sucker. Prepharynx short. Pharynx oval. Oesophagus distinct. Intestinal bifurcation dorsal to ventral sucker. Caeca short, saccular, divergent, reach to about posterior edge of ventral sucker or to level of testes. Testes oval, symmetrical, level with ventral sucker or in anterior hindbody. Cirrus-sac claviform, reach to or close to ventral sucker. Seminal vesicle saccular. Pars prostatica vesicular. Ejaculatory duct narrow. Genital atrium small. Genital pore at level of oral sucker or pharynx, sinistral, marginal. Ovary rounded, intertesticular. Uterus post-testicular. Metraterm narrow. Eggs tanned. Vitelline follicles few (ten to 14), in lateral fields reaching from testes to level between oesophagus and oral sucker. Excretory vesicle almost reaches ovary; pore terminal. In intestine and gall-bladder of freshwater teleosts; New Zealand. Type species *L. minutum* (Manter, 1954) Bray, 1987.

**4b. Genital pore usually in mid- to posterior forebody; in marine teleosts ..... 5.**

**5a. Excretory vesicle Y-shaped; testes close to posterior extremity ..... ..... *Koiea* Bray & Campbell, 1995. (Fig. 64.14)**

**Diagnosis:** Body fusiform. Tegument spinous. Oral sucker subterminal. Ventral sucker rounded, small, in mid-body. Prepharynx wide, short. Pharynx large. Oesophagus long. Intestinal bifurcation in posterior forebody. Caeca short, narrow, parallel, terminate blindly close to mid-hindbody. Testes two, oblique, close to posterior extremity. Cirrus-sac elongate-oval, lies across forebody. Seminal vesicle coiled, tubular. Pars prostatica vesicular. Ejaculatory duct muscular. Genital atrium distinct. Genital pore close to ventrosinistral margin in mid-forebody. Ovary median, pretesticular, separated from testes by uterus, just posterior to level of caecal ends. Uterus extensive, from level of middle of posterior testis to level of cirrus-sac; field narrower between caeca. Metraterm short, muscular, with distinct sphincter distally. Eggs numerous, tanned. Vitellarium forms two small lateral fields of follicles along inner margin of caeca. Excretory vesicle Y-shaped; arms reach into forebody; pore dorsally subterminal. In deep-sea eels (*Notacanthus*); northern Atlantic and southern Pacific Oceans. Type-species *K. notacanthi* Bray & Campbell, 1995.

**5b. Excretory vesicle I-shaped; testes well separated from posterior extremity ..... 6.**

**6a. Ovary pretesticular (occasionally intertesticular) ..... ..... *Brachyenteron* Manter, 1934. (Fig. 64.15)**
(Syns *Cypseluritrematoides* Yamaguti, 1970; *Prolateroporus* Yamaguti, 1971)

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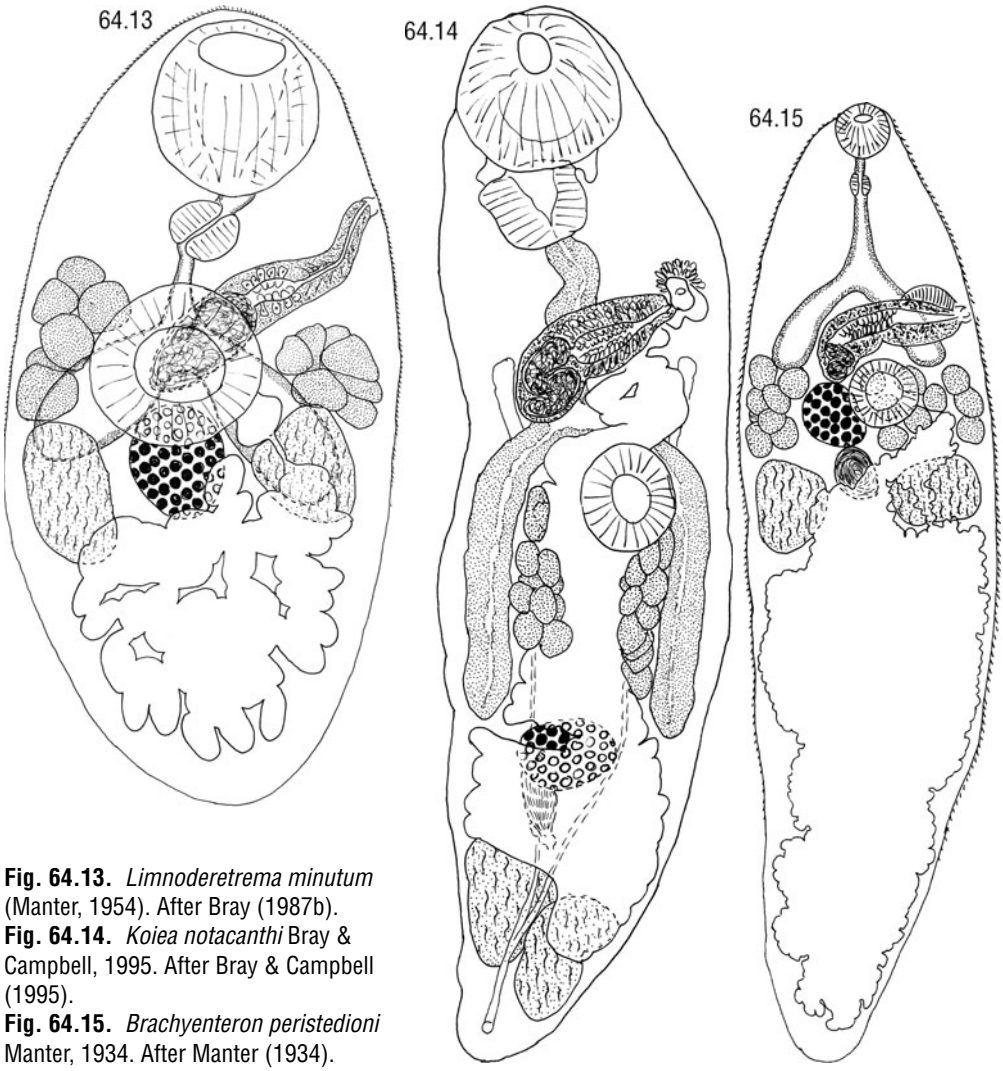



**Fig. 64.13.** *Limnoderetrema minutum* (Manter, 1954). After Bray (1987b).
**Fig. 64.14.** *Koiea notacanthi* Bray & Campbell, 1995. After Bray & Campbell (1995).
**Fig. 64.15.** *Brachyenteron peristedioni* Manter, 1934. After Manter (1934).

**Diagnosis:** Body fusiform to pyriform. Tegument spinous to varying degrees or apparently smooth. Oral sucker globular or infundibuliform. Ventral sucker in about mid-region of body, may have tegumental pit on posterior lip. Prepharynx distinct. Pharynx globular. Oesophagus usually distinct, may be long. Intestinal bifurcation in forebody. Caeca short, divergent, saccular, end in forebody or at level of ventral sucker. Testes subglobular, smooth, symmetrical or subsymmetrical, close to or overlapping ventral sucker. Cirrus-sac claviform to elongate claviform, reach ventral sucker or not. Seminal vesicle bipartite or elongate and coiled. Pars prostatica vesicular, oval to elongate. Ejaculatory duct long, may be extruded as cirrus. Genital pore sinistral, marginal or submarginal at or near level of intestinal bifurcation or pharynx. Ovary globular, overlaps ventral sucker or in forebody, pretesticular (often dextral) or intertesticular. Uterus fills most of hindbody. Metraterm thick-walled, muscular. Eggs numerous, tanned, operculate. Vitellarium forms two lateral fields of follicles in forebody or at and around level of ventral sucker, entirely posterior to cirrus-sac on poral

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side. Excretory vesicle elongate saccular; pore terminal or dorsally subterminal. In intestine and gall-bladder of marine teleosts; cosmopolitan. Type-species *B. peristedioni* Manter, 1934.

**6b. Ovary post-testicular ..... *Panopula* Overstreet & Pritchard, 1977. (Fig. 64.16)**
**Diagnosis:** Body fusiform. Tegument spinous over entire body-surface. Oral sucker large, globular to infundibuliform, subterminal to terminal. Ventral sucker subequal to or larger than oral sucker, may have tegumental pit on posterior lip. Prepharynx short. Pharynx oval to globular. Oesophagus distinct. Intestinal bifurcation in forebody. Caeca short, saccular, reach testes or just overlap ventral sucker. Testes symmetrical, level with mid- to anterior part of ventral sucker or in posterior forebody. Cirrus-sac large, claviform. Seminal vesicle bipartite or coiled. Pars prostatica wide, vesicular. Ejaculatory duct long, muscular. Genital atrium simple, distinct. Genital pore in mid-forebody, sinistrolateral or sublateral. Ovary globular to oval, smooth to irregular, posterodorsal to ventral sucker, post-testicular. Seminal receptacle large. Mehlis' gland large, prominent. Uterus occupies much of hindbody, may extend dorsally to ventral sucker. Metraterm thick-walled, muscular. Eggs inconspicuously operculate, tanned. Vitellarium forms two lateral fields of follicles in mid- to posterior forebody; poral field may be divided by cirrus-sac. Excretory vesicle saccular; pore terminal. In intestine of deep-sea teleosts; northern Atlantic Ocean, Gulf of Panama. Type-species *P. cavernossa* Overstreet & Pritchard, 1977.

**7a. Ventral sucker divided equatorially or longitudinally by ridge or row of papillae ..... 17.**
**7b. Ventral sucker not divided ..... 8.**

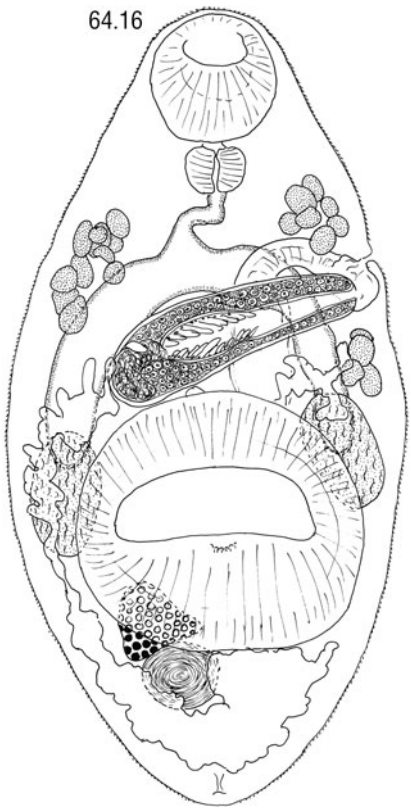
**8a. Vitellarium in hindbody ..... 9.**
**8b. Vitellarium extends into or is confined to forebody ..... 14.**

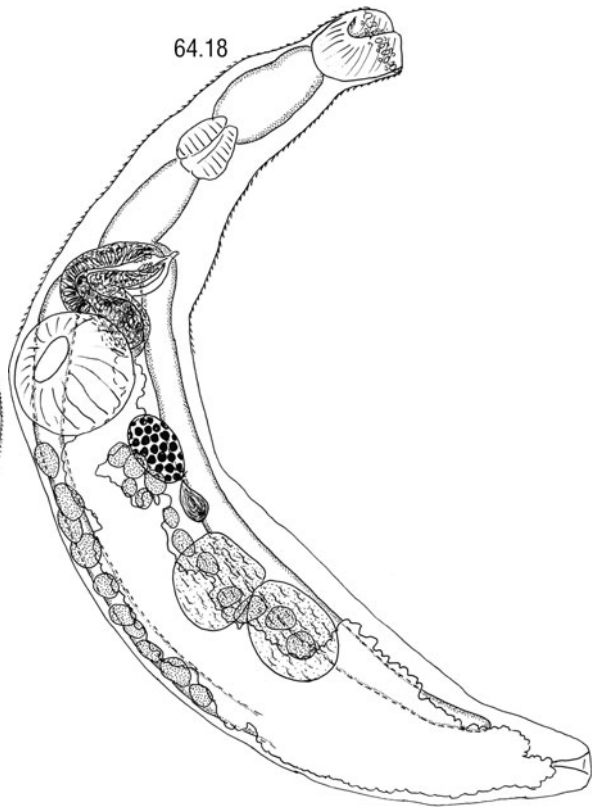
**9a. Eggs filamented; ovary multilobate ..... *Anarhichotrema* Shimazu, 1973. (Fig. 64.17)**
(Syn. *Neolissorchis* Machida, 1985)
**Diagnosis:** Body squat, fusiform. Tegument spinous. Oral sucker subglobular, subterminal. Ventral sucker oval, in anterior third of body. Prepharynx short. Pharynx oval. Oesophagus long. Intestinal bifurcation dorsal to ventral sucker or in anterior hindbody. Caeca reach close to posterior extremity, to testes or just beyond. Testes oval, entire, tandem, contiguous or adjacent. Cirrus-sac claviform, reaches into anterior hindbody. Internal seminal vesicle broadly tubular, undulating, large. Pars prostatica short. Ejaculatory duct short. Genital pore left or right, lateral, level with middle of ventral sucker. Ovary immediately pretesticular, multilobate, transversely elongate. Canalicular seminal receptacle present, empty. Uterus mainly pretesticular, fills most of space between gonads and ventral sucker. Eggs tanned, operculate, with long unipolar filament. Metraterm thin-walled. Vitellarium follicular; lateral fields reach from about level of ovary to posterior extremity, where they are confluent. Excretory vesicle I-shaped, reaches testes; pore terminal. In deep-water teleosts; north-western Pacific Ocean. Type-species *A. ochotense* Shimazu, 1973.

**9b. Eggs not filamented; ovary entire or irregular ..... 10.**

**10a. Two to six rows of enlarged circumoral spines present ..... ..... *Overstreetia* Bray, 1985. (Fig. 64.18)**
**Diagnosis:** Body elongate, fusiform. Tegument spinous in forebody. Two to six rows of enlarged circumoral spines. Oral sucker subterminal. Ventral sucker circular, in anterior half of body, of similar size to or larger than oral sucker. Prepharynx long. Pharynx pyriform. Oesophagus distinct. Intestinal bifurcation in posterior forebody. Caeca reach fairly close to posterior extremity. Testes two, oval, tandem, in mid-hindbody. Cirrus-sac recurved, in forebody. Seminal vesicle

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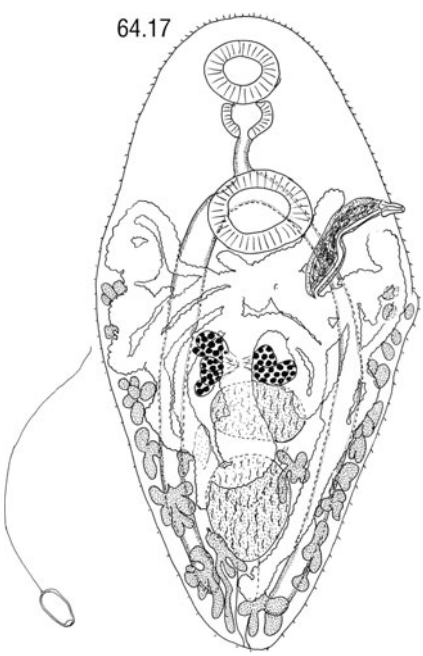




**Fig. 64.16.** *Panopula cavernossa* Overstreet & Pritchard, 1977. After Overstreet & Pritchard (1977).
**Fig. 64.17.** *Anarhichotrema ochotense* Shimazu, 1973. After Shimazu (1973).
**Fig. 64.18.** *Overstreetia sodwanaensis* Bray, 1985. After Bray (1985).

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saccular becoming tubular, undivided, with thick muscular wall distally. Pars prostatica vesicular. Ejaculatory duct short. Genital atrium small. Genital pore submarginal or marginal, sinistral, in posterior forebody. Ovary oval, pretesticular. Canalicular seminal receptacle immediately post-ovarian. Uterus fills most of hindbody. Eggs numerous, operculate, tanned. Vitellarium forms two lateral fields of few (nine to 12) follicles between ventral sucker and posterior testis. Excretory vesicle short; pore terminal. In intestine of marine teleosts (*Atherinomorus*); south-western Indian Ocean and off eastern Australia. Type-species *O. sodwanaensis* Bray, 1985.

**10b. No enlarged circumoral spines present ..... 11.**

**11a. Body squat to oval; caeca reach at least to testes; cirrus-sac claviform; unpocketed ejaculatory duct and metraterm ..... 12.**

**11b. Body elongate, narrow; caeca not reaching testes; cirrus-sac elongate, undulating; pockets in ejaculatory duct and metraterm ..... *Pseudopalaeorchis* Kamegai, 1970. (Fig. 64.19)**

**Diagnosis:** Body elongate, tapers anteriorly. Tegument spinous. Oral sucker small, terminal, cup-shaped. Ventral sucker small, rounded, undivided, in mid-body. Prepharynx short, distinct. Pharynx small, oval. Oesophagus very long. Intestinal bifurcation in posterior forebody. Caeca reach only to level of ovary. Testes tandem to almost tandem, in mid-hindbody, oval, entire. Cirrus-sac elongate, sinuous, almost reaches ovary. Internal seminal vesicle bipartite, occasionally unipartite. Pars prostatica long, wide, vesicular. Ejaculatory duct long, deeply pocketed. Genital pore sinistrolateral, about half way between intestinal bifurcation and ventral sucker. Ovary oval, pretesticular. Canalicular seminal receptacle present. Uterus mainly post-testicular, with some coils intercaecal, pre-ovarian. Metraterm deeply pocketed, surrounded by gland-cells. Eggs reniform, embryonated. Vitellarium in two asymmetrical lateral fields of few follicles; one field pre-ovarian and sinistral; other postovarian and dextral. Excretory vesicle unknown; pore subterminal. In marine teleosts (*Monocentris*); Sea of Japan, off Mozambique. Type-species *P. elongatus* Kamegai, 1970.

**12a. Ventral sucker rounded, with mid-ventral aperture; seminal vesicle saccular to elongate ..... 13.**[1]

**12b. Ventral sucker shaped like inflated balloon, with narrow, anterior aperture surrounded by strong sphincter; seminal vesicle bipartite ..... ..... *Sacculoacetabulum* Machida & Kuramochi, 1999. (Fig. 64.20)**

**Diagnosis:** Body squat, pyriform. Tegument spinous. Oral sucker subglobular, subterminal. Ventral sucker large, balloon-like, with small anterior aperture surrounded by strong muscular sphincter. Prepharynx absent. Pharynx oval. Oesophagus distinct. Intestinal bifurcation in posterior forebody. Caeca reach testes. Testes large, oval, symmetrical, in anterior part of hindbody. Cirrus-sac claviform, not reaching into hindbody. Seminal vesicle bipartite. Pars prostatica short, oval to tubular. Ejaculatory duct long. Genital atrium deep. Genital pore dextrolateral, bifurcal. Ovary oval, pretesticular, median, dorsal to ventral sucker. Canalicular seminal receptacle present. Uterus mainly post-testicular. Metraterm distinct, surrounded by gland-cells. Eggs small. Vitellarium in two symmetrical fields of about eight to 13 regular follicles, between mid-level of ventral sucker and mid-testis. Excretory vesicle unknown; pore terminal. In marine teleosts (*Triodon*); off Japan. Type-species *S. ohjibah* Machida & Kuramochi, 1999.

**13a. Ventral sucker sessile; caeca reach testes ..... *Steganoderma* Stafford, 1904. (Fig. 64.21)**
(Syn. *Nordosstrema* Issaitschikow, 1928)

[1] See Addendum.

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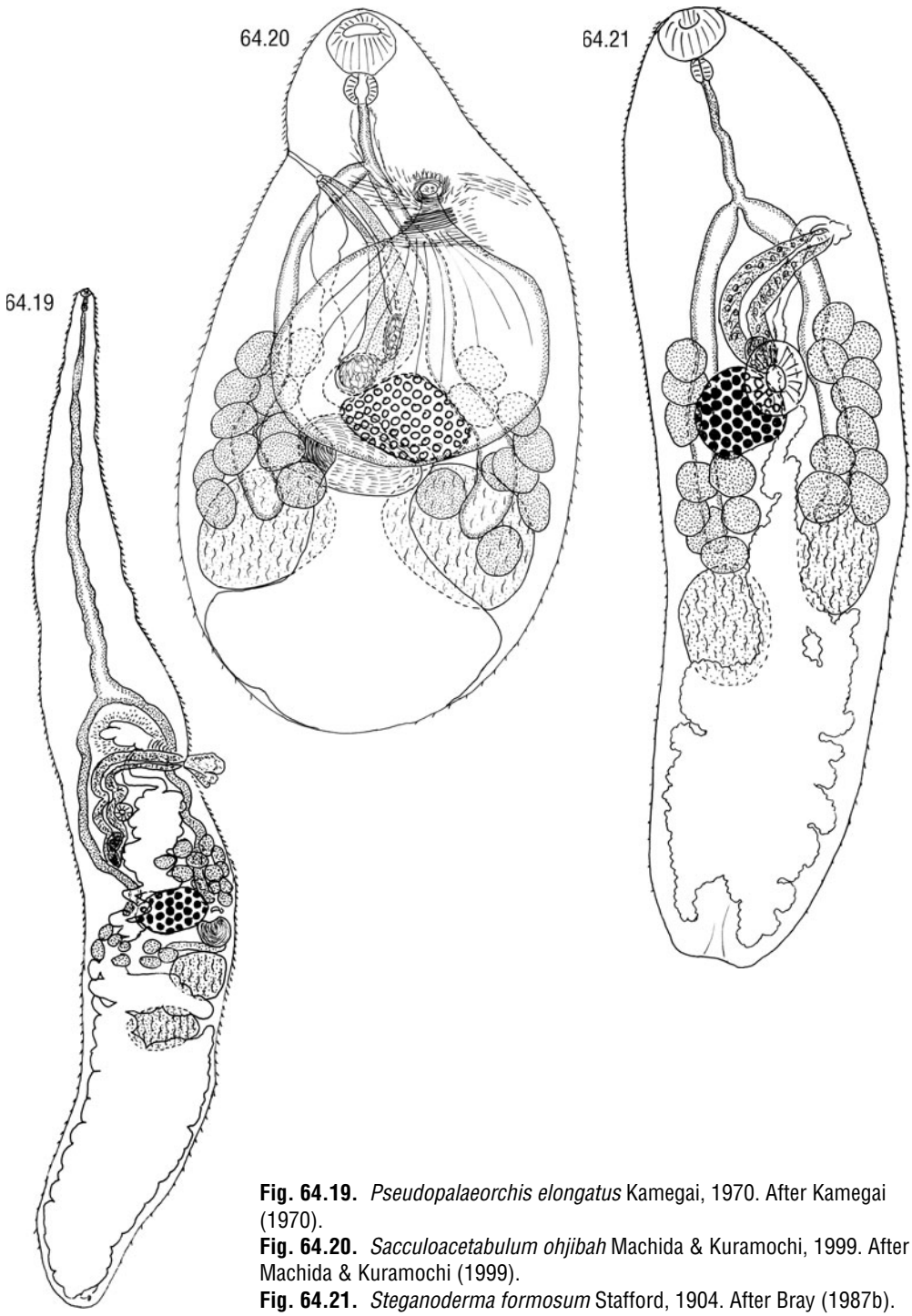



**Fig. 64.19.** *Pseudopalaeorchis elongatus* Kamegai, 1970. After Kamegai (1970).
**Fig. 64.20.** *Sacculoacetabulum ohjibah* Machida & Kuramochi, 1999. After Machida & Kuramochi (1999).
**Fig. 64.21.** *Steganoderma formosum* Stafford, 1904. After Bray (1987b).

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**Diagnosis:** Body elongate-oval or pyriform, flattened. Tegument spinous. Oral sucker small to large, subglobular. Ventral sucker rounded, about equal to oral sucker or smaller, sessile. Prepharynx short. Pharynx small to large. Oesophagus absent to long. Intestinal bifurcation in mid-forebody. Caeca reach testes. Testes oval, symmetrical or oblique, in anterior or mid-hindbody. Cirrus-sac claviform, straight or curved. Seminal vesicle saccular. Pars prostatica long, vesicular. Ejaculatory duct short. Genital atrium small. Genital pore sinistral, in mid- to anterior forebody, sublateral. Ovary globular to irregularly oval, pretesticular, submedian to median, close to or overlapping ventral sucker. Uterus in hindbody, mainly post-testicular, but may have significant pretesticular portion. Metraterm muscular. Eggs numerous, operculate, tanned. Vitellarium in symmetrical fields of about eight to ten regular follicles, mainly in lateral regions of anterior part of hindbody. Excretory vesicle saccular, short; pore terminal. In intestine of marine teleosts (cosmopolitan) and freshwater teleosts (South America). Type-species *S. formosum* Stafford, 1904.

**13b. Ventral sucker pedunculate; caeca extend beyond testes ..... ..... *Lecithostaphylus* Odhner, 1911. (Fig. 64.22)**
(Syns *Manteroderma* Skrjabin, 1957; *Cypseluritrema* Yamaguti, 1970; *Steganoderma* (*Opisthoarchiotrema*) Gupta & Sharma, 1974)

**Diagnosis:** Body oval to elongate-oval. Tegument spinous. Oral sucker small, globular. Ventral sucker rounded, about equal to oral sucker or larger, pedunculate, but may be withdrawn. Prepharynx short, distinct. Pharynx small to large. Oesophagus absent to long. Intestinal bifurcation in mid- to posterior forebody. Caeca reach past testes or close to posterior extremity. Testes oval, symmetrical or oblique, in anterior or mid-hindbody. Cirrus-sac claviform, straight or curved. Seminal vesicle saccular to elongate, straight or coiled. Pars prostatica short, vesicular. Ejaculatory duct short. Genital atrium small. Genital pore sinistral, in mid- to anterior forebody, lateral to sublateral. Ovary globular to irregularly oval, pretesticular, median or submedian, in anterior part of hindbody or overlaps ventral sucker. Uterus in hindbody, mainly post-testicular, but may have significant pretesticular portion. Metraterm muscular. Eggs numerous, operculate, tanned. Vitelline fields symmetrical, about eight to 16 regular follicles, mainly in lateral regions of anterior hindbody. Excretory vesicle saccular, short; pore terminal. In intestine of marine teleosts; cosmopolitan. Type-species *L. retroflexus* (Molin, 1859).

**14a. Genital pore lateral to oral sucker or pharynx; ventral sucker at or close to posterior extremity ..... 15.**
**14b. Genital pore lateral in mid-forebody; ventral sucker in mid- or anterior part of body .... ..... 16.**

**15a. Body fusiform; testes in forebody; caeca terminate in forebody ..... ..... *Cephaloporus* Yamaguti, 1934. (Fig. 64.23)**

**Diagnosis:** Body fusiform. Tegument spinous. Oral sucker subglobular, subterminal. Ventral sucker oval, at posterior extremity. Prepharynx absent. Pharynx oval. Oesophagus long. Intestinal bifurcation in anterior third of body. Caeca diverge, reach posterior margin of testes. Testes symmetrical, lateral, just postequatorial. Cirrus-sac claviform. Internal seminal vesicle saccular or bipartite. Pars prostatica wide, long, with numerous gland-cells. Ejaculatory duct long. Genital pore lateral at level of oral sucker or pharynx. Ovary lobed, pretesticular. Canalicular seminal receptacle present. Uterus mainly postequatorial, anterior to ventral sucker, passes between testes. Metraterm narrow, of similar length to cirrus-sac. Eggs numerous. Vitellarium follicular; follicles oval or lobate; lateral fields reach between bifurcal level and anterior margin of testes. Excretory

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vesicle short, claviform, narrow distally, directed posteriorly; pore dorsal to uterus. In Monacanthidae; off Japan and South Africa. Type-species *C. monacanthi* Yamaguti, 1934.

**15b. Body pyriform; testes lateral to ventral sucker; caeca reach posterior part of ventral sucker ..... *Yamagutiplectognathotrema* Parukhin, 1977. (Fig. 64.24)**
(Syn. *Plectognathotrematoides* Yamaguti, 1971 *nec* Parukhin, 1971)

**Diagnosis:** Body pyriform. Tegument spinous. Oral sucker terminal, oval. Ventral sucker rounded, postequatorial. Prepharynx absent. Pharynx oval, small. Oesophagus long. Intestinal bifurcation in mid-forebody. Caeca reach posterior edge of ventral sucker. Testes two, irregularly lobed, symmetrical, at level of ventral sucker. Cirrus-sac claviform, short, not reaching ventral sucker. Internal seminal vesicle saccular. Pars prostatica vesicular, short. Ejaculatory duct long, rectilinear, eversible. Genital pore dorso-sublateral at level of pharynx or anterior part of oesophagus. Ovary

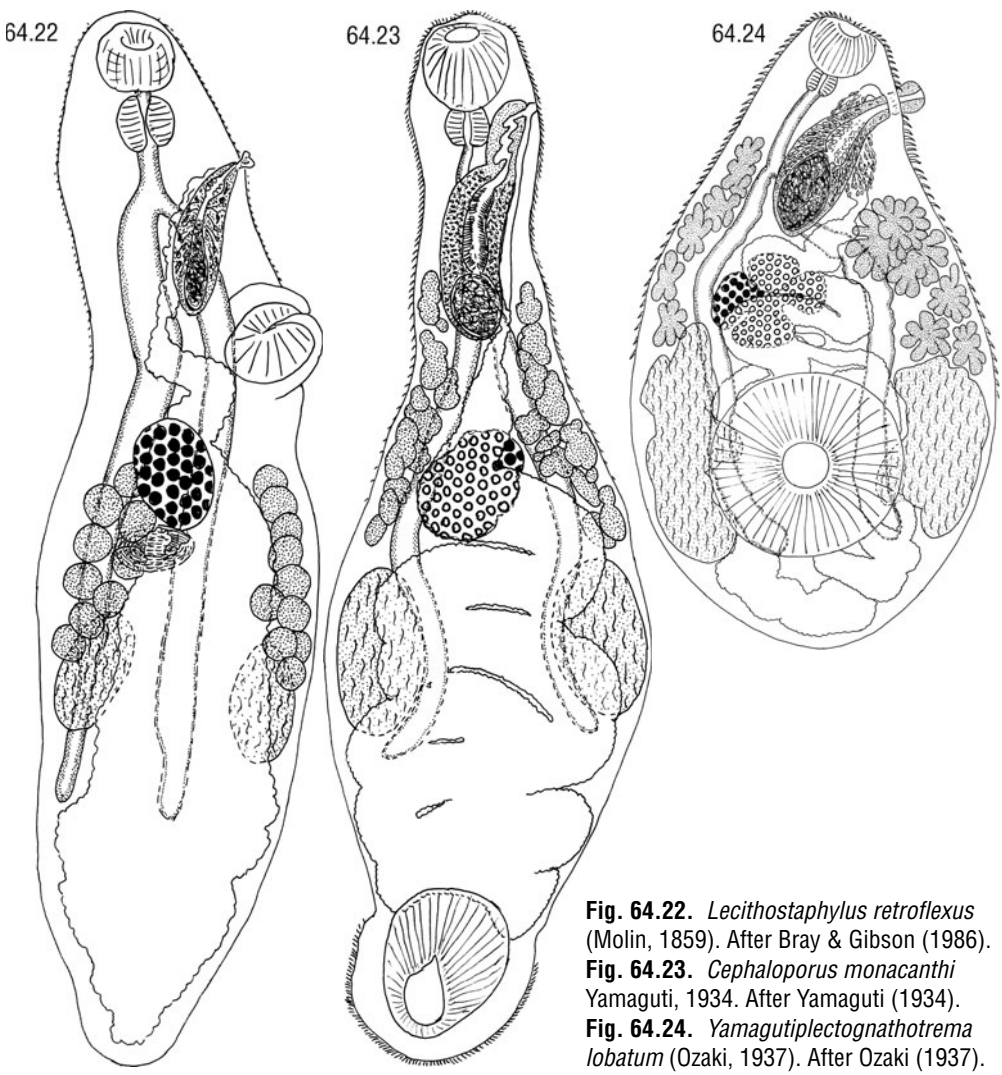



**Fig. 64.22.** *Lecithostaphylus retroflexus* (Molin, 1859). After Bray & Gibson (1986).
**Fig. 64.23.** *Cephaloporus monacanthi* Yamaguti, 1934. After Yamaguti (1934).
**Fig. 64.24.** *Yamagutiplectognathotrema lobatum* (Ozaki, 1937). After Ozaki (1937).

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four-lobed, submedian, pretesticular. Seminal receptacle present, probably canalicular. Uterus reaches posterior extremity. Metraterm well differentiated. Eggs small. Vitelline follicles lobed, grouped in rosettes, form lateral fields in forebody. Excretory vesicle and pore? In *Monacanthus*; off Japan. Type-species *Y. lobatum* (Ozaki, 1937) Parukhin, 1977 (emend.).

**16a. Excretory vesicle long, saccular; in marine teleosts ..... ..... *Deretrema* Linton, 1910. (Fig. 64.25)**

**Diagnosis:** Body oval to pyriform. Tegument with spines or not. Oral sucker globular, subterminal. Ventral sucker usually distinctly larger than oral, sessile. Prepharynx short. Pharynx oval. Oesophagus long (occasionally short). Intestinal bifurcation in forebody. Pharynx and/or oesophagus often spinous internally. Caeca reach testes or beyond. Testes oval, symmetrical to sub-symmetrical, in anterior hindbody (occasionally at anterior edge of ventral sucker). Cirrus-sac small, claviform. Seminal vesicle tubular, coiled, saccular or bipartite. Pars prostatica weakly to well developed. Ejaculatory duct may form cirrus. Genital pore marginal (occasionally ventral), in mid- or occasionally posterior forebody. Ovary entire, oval to globular, pre- or occasionally posttesticular. Uterus mostly postgonadal to substantially pregonadal. Metraterm weakly developed. Eggs numerous, tanned, operculate. Vitellarium in posterior half of forebody, sometimes overlaps ventral sucker, with relatively few follicles (six to ten). Excretory vesicle elongate saccular; pore terminal. In gall-bladder and intestine of marine teleosts; cosmopolitan. Type-species *D. fusillus* Linton, 1910.

**16b. Excretory vesicle short, saccular; in freshwater teleosts ..... ..... *Pseudochetosoma* Dollfus, 1951. (Fig. 64.26)**

(Syn. *Ochetosoma* (*Pseudochetosoma*) Dollfus, 1951)

**Diagnosis:** Body pyriform. No spines on tegument. Oral sucker subglobular, subterminal. Ventral sucker larger than oral. Prepharynx short. Pharynx small. Oesophagus long. Intestinal bifurcation in posterior forebody. Caeca reach into hindbody, occasionally to testes. Testes oval to irregularly oval, symmetrical to sub-symmetrical, in mid-hindbody. Cirrus-sac claviform, mainly in forebody. Seminal vesicle coiled, tubular. Pars prostatica weakly developed. Genital pore submarginal, sinistral, in mid-forebody. Ovary pyriform, anterior to right testis. Uterus fills hindbody; significant portion anterior to testes. Metraterm weakly developed. Eggs numerous; shell thin, tanned. Vitelline follicles irregular and numerous, lateral in area between posterior margin of ventral sucker and oesophagus; fields may be confluent in forebody. Excretory vesicle short, saccular; pore terminal. In gall-bladder or intestine of freshwater teleosts; Palaearctic region. Type-species *P. salmonicola* Dollfus, 1951.

**17a. Ventral sucker divided longitudinally; oral sucker infundibuliform with several anterior lobes; eggshell with two raised bands ..... *Dupliciporia* Reimer, 1985. (Fig. 64.27)**

(Syns *Parasteganoderma* Machida & Araki, 1990; *Liliaoralis* Korotaeva, 1994)

**Diagnosis:** Body fusiform, widest in hindbody or elongate, narrow. Tegument spinous. Oral sucker infundibuliform, with four to eight anteriorly directed lobes. Small pore may occur on body-surface dorsally to oral sucker, opens into gap dorsal to dorsal lobe of oral sucker. Ventral sucker transversely elongate, divided longitudinally by internal muscular ridge, in anterior half or middle of body. Prepharynx short, absent or long. Pharynx subglobular. Oesophagus long. Intestinal bifurcation in posterior forebody. Caeca reach testes. Testes oval, oblique, symmetrical or tandem in anterior or mid-hindbody. Cirrus-sac claviform, large, transverse, often curved. Internal seminal vesicle broad tubular, undulating. Pars prostatica vesicular. Ejaculatory duct long or short, straight. Genital pore sinistromarginal, just postbifurcal or bifurcal. Ovary oval,

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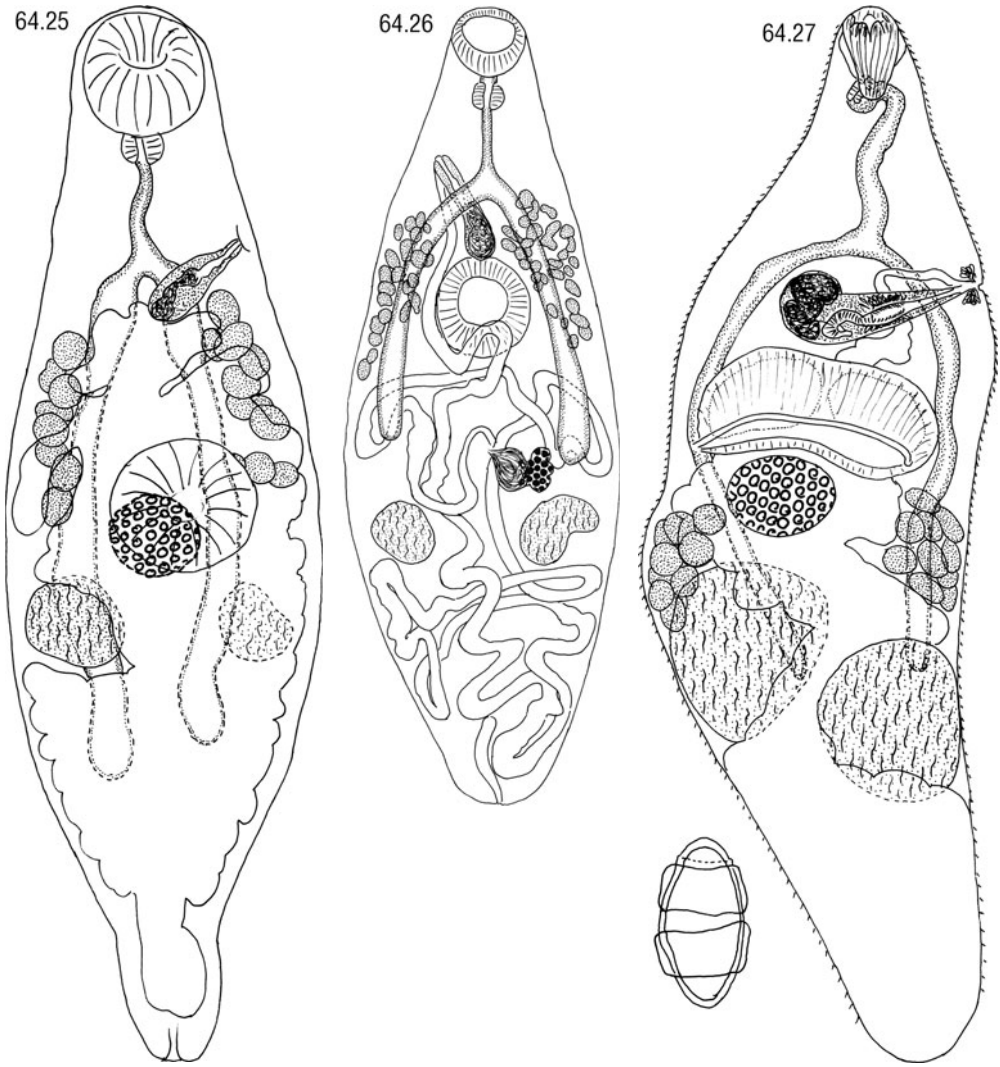



**Fig. 64.25.** *Deretrema nahaense* Yamaguti, 1942. After Cribb *et al.* (1999b).
**Fig. 64.26.** *Pseudochetosoma salmonicola* Dollfus, 1951. Dorsal view. After Dollfus (1952).
**Fig. 64.27.** *Dupliciporia cephaloporum* (Machida & Araki, 1990). After Machida & Araki (1990).

pretesticular, close to ventral sucker. Uterus fills much of hindbody, mainly post-testicular. Eggs elliptical; shell usually with two raised bands. Metraterm ensheathed by gland-cells. Vitellarium two small lateral fields of nine or ten follicles, pretesticular, in hindbody. Excretory vesicle not reaching testes; pore terminal. In marine teleosts (usually Priacanthidae); Indo-West Pacific region. Type-species *D. haeckeli* Reimer, 1985.

**17b. Ventral sucker divided equatorially; oral sucker subglobular to infundibuliform, unlobed; egg-shell smooth ..... 18.**

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**18a. Ventral sucker divided equatorially by internal ridge and external cleft ..... ..... *Proctophantastes* Odhner, 1911. (Fig. 64.28)**
(Syn. *Neosteganoderma* Byrd, 1964)

**Diagnosis:** Body pyriform, widest at level of ventral sucker. Tegument spinous. Oral sucker large, globular or infundibuliform. Ventral sucker large, transversely elongate, divided equatorially by dorsal cleft and ventral ridge. Prepharynx short. Pharynx oval. Oesophagus distinct, short to long. Intestinal bifurcation in mid- to posterior forebody. Caeca reach vitello-testicular zone. Testes symmetrical to oblique in anterior hindbody. Cirrus-sac large, muscular, straight, curved or recurved. Seminal vesicle coiled, tubular. Pars prostatica long, wide, vesicular. Ejaculatory duct long, muscular, with spine-like tegumentary extensions. Genital atrium small, simple to large, irregularly pocketed; periatrial gland ensheaths distal parts of metraterm and cirrus-sac; in addition to genital atrium, there may be several small, isolated, claviform, membrane-bound sacs. Genital pore sinistral, submarginal to marginal, in mid- to posterior forebody. Ovary subglobular, submedian, in anterior hindbody, inter- or pretesticular. Uterus mainly post-testicular. Metraterm muscular. Eggs numerous, tanned, operculate. Vitellarium forms two symmetrical, lateral fields of few follicles, pretesticular, in anterior hindbody. Excretory vesicle elongate, saccular; pore terminal or dorsally subterminal. In intestine of deep-sea marine teleosts; cosmopolitan. Type-species *P. abyssorum* Odhner, 1911.

**18b. Ventral sucker divided equatorially by internal row of large papillae ..... ..... *Steganodermatoides* Parukhin & Lyadov, 1979. (Fig. 64.29)**
(Syns *Hudsonia* Campbell, 1975 *nec* Edwards, 1923 or Leroux, 1940; *Allosteganoderma* Campbell, 1983)

**Diagnosis:** Body fusiform to elongate-fusiform. Tegument bears large, prominent spines. Oral sucker globular to transversely elongate, subterminal to terminal. Ventral sucker large, in about middle of body; internal equator bears five to seven large papillae. Prepharynx distinct. Pharynx oval. Oesophagus long. Intestinal bifurcation in posterior forebody. Caeca reach testes. Testes symmetrical to diagonal in mid- or posterior hindbody. Cirrus-sac large, curved. Seminal vesicle bipartite, coiled-tubular or (?) saccular. Pars prostatica long, convoluted. Ejaculatory duct muscular. Genital atrium large, muscular, surrounded by gland-cells (periatrial gland). Genital pore on left margin of mid- to posterior forebody. Ovary oval, pretesticular, submedian. Uterus in hindbody, mainly in pretesticular zone. Metraterm strongly muscular with glandular sheath. Eggs tanned, operculate, numerous. Vitellarium forms two symmetrical lateral fields of follicles at posterior edge of ventral sucker. Excretory vesicle saccular, reaches testes or not; pore terminal. In alimentary system (particularly posterior intestine and rectum) of deep-sea teleosts; cosmopolitan. Type-species *S. kergeleni* Parukhin & Lyadov, 1979.

## Addendum

*Prosteganoderma* Hassanine, 2007, based on *P. brayi* Hassanine, 2007 from *Scarus ghobban*, in the Red Sea off Egypt, differs from *Steganoderma* and *Lecithostaphylus* in possessing a prominent fleshy fold around the ventral sucker and in having a pretesticular uterus (Hassanine, 2007).

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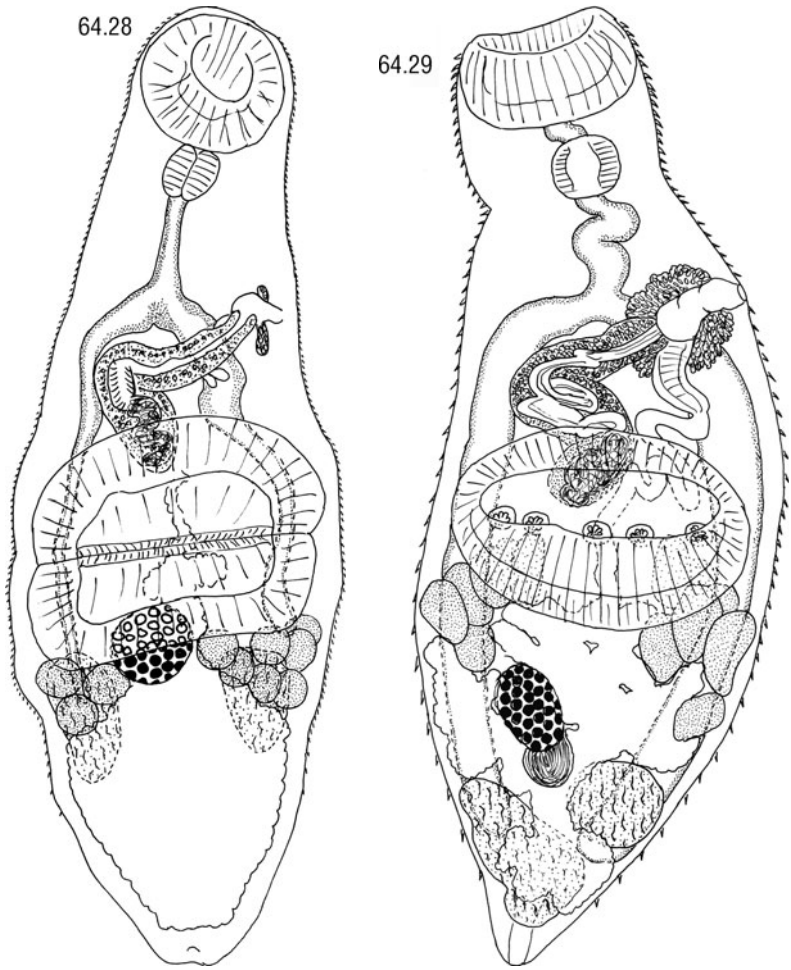



**Fig. 64.28.** *Proctophantastes abyssorum* Odhner, 1911. After Bray & Gibson (1986).
**Fig. 64.29.** *Steganodermatoides agassizi* (Campbell, 1975). After Campbell (1975).

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# 65 Family Didymozoidae Monticelli, 1888*

S.E. Pozdnyakov[1] & D.I. Gibson[2]

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## Introduction

Adult didymozoids are tissue parasites of marine fishes and are especially common in oceanic pelagic fishes, such as scombroids. In addition to occupying an atypical site, they may also be encapsulated, sometimes in pairs that may exhibit varying degrees of sexual dimorphism. In fact, they can be so unusual in form as to be hardly recognizable as digeneans and, even until recently (e.g. Kearn, 1998), have been treated as a subclass in their own right and, by several Russian authors, e.g. Pozdnyakov (1993, 1996), as a suborder within the Digenea. However, Gibson & Bray (1979) agreed with very early work on the group and treated the group as arising from hemiuroid stock, a position supported more recently by molecular work (e.g. Barker *et al*., 1993). For the purpose of these keys, the group is treated as a family within the Hemiuroidea Looss, 1899.

## Morphology

The morphological characters of taxonomic importance are the shape of the body, the structure of the male and female reproductive systems and, to a lesser degree, the structure of the alimentary and excretory systems. The use of the presence or absence of a ventral sucker and a number of other morphological characters for systematic purposes is considered controversial (Pozdnyakov, 1996).

* This chapter, based on Pozdnyakov (1996), was given to the editors in Russian. The text was translated by Dr A.K. Kostadinova and then adapted and updated by David Gibson, who edited the classification to reflect both recent studies and the arrangement followed in the present volumes and added data on hosts, distribution, etc. The translation was funded with help from the Zoology Research Fund, NHM.

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## Morphology of adult worms

**Body-size** varies from 3 mm to 12 m. The smallest species of the genera *Skrjabinozoum* Nikolaeva & Parukhin, 1969, *Philopinna* Yamaguti, 1936 and *Paraphilopinna* Zhukov, 1971 are 3–8 mm in length, whereas 'giants', such as *Epithelionematobothrium makairi* (Nikolaeva, 1978) and *Unitubulotestis istiophorusi* Nikolaeva & Dubina, 1985, reach 3 and 1 m, respectively. *Nematobibothrioides histoidii* Noble, 1974, at 12 m, is the longest of all trematodes.

Body-size is associated with a somewhat formal approach to species description, especially when new taxa are described solely on the basis of metrical data, ignoring the identical topography of internal organs. It should be remembered that, before reaching a length of 1 m or more, the worm must first have attained a length of a few centimetres.

**Body-shape** in didymozoids is extremely diverse (Fig. 65.1). Two main structural types can be distinguished:

- 'Nematobothriid' type, characterized by the body being more or less elongate. Its length is significantly greater than its width. The shape of the body is filiform, rarely tape-like or spindle- or lancet-shaped. The anterior and posterior extremities are strongly tapered. The following variations occur within this type:
  - (a) 'Philopinnoid' – body spindle- or lancet-shaped.
  - (b) 'Atalostrophinoid' – body strongly elongate, tape-like. Anterior extremity tapered; posterior extremity tapered or rounded.
  - (c) 'Nematobothrioid' – body filiform, round in cross-section. Anterior and posterior extremities tapered; posterior extremity sometimes broadly oval.
- 'Didymozoid' type, characterized by the body being differentiated into two regions: anterior region, smooth, elongate and usually round in cross-section, rarely, with first third dorsoventrally flattened; and posterior region, always wider than anterior. Its shape is extremely diverse, with the following modifications:
  - (a) 'Didymozoic' – anterior region elongate, round in cross-section or flattened anteriorly, attached terminally or subterminally to posterior region. Posterior region round in cross-section, elongate, with round anterior and posterior extremities.
  - (b) 'Didymocylindric' – anterior region thin, round in cross-section, somewhat widened anteriorly, attached to middle of posterior region or nearly so. Posterior region elongate, round in cross-section.
  - (c) 'Lampridídymozoic' – anterior region thin, long, round in cross-section, attached to posterior region subterminally. Posterior region ventrally flattened or slightly concave; lateral and dorsal margins rounded.
  - (d) 'Didymocystic' – anterior region elongate, slender, either conical or widened and slightly flattened in its first third, attached at flattened edge of posterior region. Posterior region spherical, hemispherical or globular; ventral surface flattened, sometimes slightly concave.
  - (e) 'Melanocystic' – anterior region thin, elongate and slightly widened anteriorly, attached to middle of concave surface of posterior region. Posterior region disc-like, ventrally concave.
  - (f) 'Didymosulcic' – anterior region thin, not long, with conical or broadly rounded anterior extremity, attached to posterior region subterminally, between lateral lobes. Posterior

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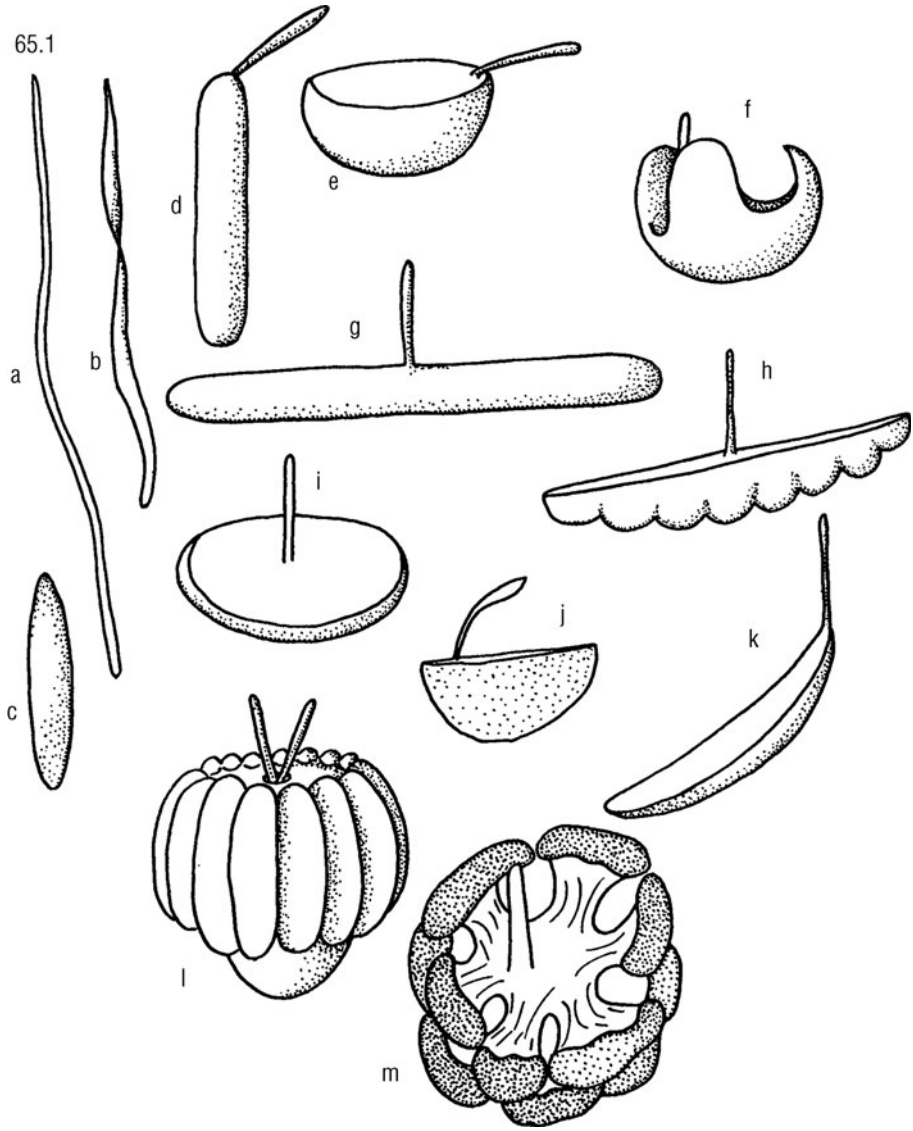



**Fig. 65.1.** Body-form in the Didymozoidae: a–c. Variants of the 'nematobothriid' type; d–m. Variants of the 'didymozoid' type. See text.

region with complex shape; its anterior region more or less divided by deep furrow (which goes from ventral to dorsal surface). As a result, anterior part of posterior region is divided into two lobes. Posterior extremity of posterior region is conical and curved ventrally.

(g) 'Platocystic' – anterior region thin, elongate, with widened or flattened anterior third, attached at the margin of right side of posterior region. Posterior region strongly flattened laterally, with semi-lunar shape.

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(h) 'Lobatozoic' – anterior region thin, elongate, round in cross-section, tapered anteriorly or widened in anterior third, attached to side of posterior region devoid of lobes. Posterior region with variable shape, with numerous regularly or irregularly located protrusions, invaginations and lobes.
(i) 'Neodidymozoic' – anterior region thin and conical or thick and cylindrical, attached at the stem of posterior region. Posterior region with 'stem' giving rise to numerous, complex interwoven diverticula.
(j) 'Colocyntotrematic' – posterior regions of paired worms (two individuals) fused. Anterior region elongate, round in cross-section. Fused posterior regions usually spherical or shaped like Greek amphora, gourd or bunch of bananas.

Body-shape in didymozoids is a stable character with an important adaptive value. In this chapter, the structural types and their modifications are considered useful taxonomic criteria at the subfamily level.

**Body-colour.** The colour of live worms is determined by their internal content. Usually, it is yellow or yellow-brown due to the eggs filling the strongly developed uterus. Frequently, the ovary and vitellarium are seen as white or grey 'strings'. The actual colour of the body is greyish-white or milky-white.

**Attachment organs.** The organs of attachment in didymozoids are suckers only; they can be distome, with an oral and ventral sucker, or monostome, with only an oral sucker. The oral sucker can be terminal or subterminal. Since the worms parasitize host tissues and are usually in capsules, the functional requirement for suckers is significantly reduced. The oral sucker in most species is small and the ventral sucker is partly or completely reduced. However, significant variations also occur. The oral sucker is usually well developed in nemathobothriines, whereas in didymozoines it is typically small. The ventral sucker is reduced in the overwhelming majority of didymozoids. Ginetsinskaya (1968) assumed that the reduction of the ventral sucker in trematodes should be viewed as secondary. The opinions of experts on the taxonomic importance of this character (i.e. presence/absence of a ventral sucker) have diverged. Sometimes, the number of suckers in digeneans has been given great significance (Skrjabin, 1951), e.g. at the familial level in the Sanguinicolidae von Graff, 1907 and Schistosomatidae Stiles & Hassall, 1898. In other cases (Witenberg, 1923; Bykhovskaya-Pavlovskaya, 1983), the absence of a ventral sucker is considered of little importance. Mayr (1971) suggested that the taxonomic weight of regressive characters is low, but did not reject the use in classification of characters subjected to parallelism and reduction. The presence/absence of a ventral sucker is considered as useful at generic level in this group.

**Alimentary system.** Didymozoids have the same gut-structure as other trematodes. It consists of a pharynx, oesophagus and intestine (caecum or caeca); as with other hemiuroids, a prepharynx is absent. Within the family, some variations are observed. A generalized scheme for the anterior extremity of didymozoids is given in Fig. 65.2.

The mouth is located at the base of the subterminal or terminal oral sucker and leads directly to the pharynx.

The pharynx has a diverse form; most frequently, its length is greater than its width. In species of some genera (*Maccallumtrema* Yamaguti, 1970, *Neodidymozooides* Yamaguti, 1970) its length considerably exceeds the width and it looks like a long, muscular tube. In members of the genera *Allonematobothrium* Yamaguti, 1965, *Allonematobothrioides* Yamaguti, 1970, *Atalostrophion* MacCallum, 1915 and *Neonematobothrioides* Yamaguti, 1970, it is completely lost and the mouth opens into the oesophagus.

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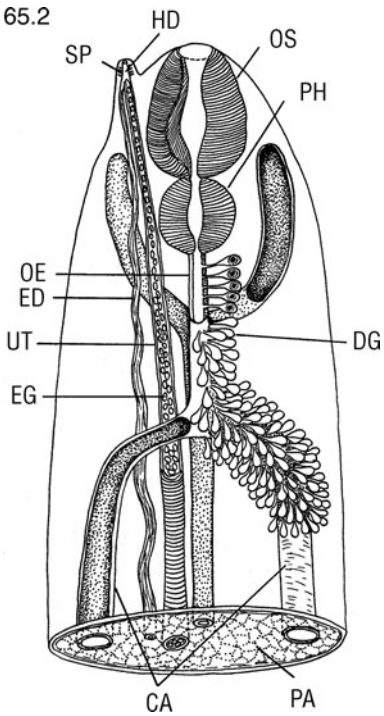



**Fig. 65.2.** Structure of the anterior extremity of didymozoids (diagrammatic). *Abbreviations*: OS, oral sucker; PH, pharynx; OE, oesophagus; DG, digestive glands; CA, caeca; ED, ejaculatory duct; UT, uterus; EG, eggs; HD, hermaphroditic duct; SP, sphincter of the hermaphroditic duct; PA, parenchyma.

In the great majority of species, the oesophagus is a long tube. Sometimes (*Neometanematobothrioides, Opisthorchinematobothrium* Yamaguti, 1970, *Epithelionematobothrium* Yamaguti, 1970), it is connected distally, at the intestinal bifurcation, to specialized 'stomach' regions, the 'Drüsenmagen' (Gibson & Bray, 1979), on each side, which appear to be a modification of the distal region of the intestinal caeca. The 'Drüsenmagen', also called 'precaecal sacs', may be a simple widening (*Neometanematobothrioides* Yamaguti, 1970, *Opisthorchinematobothrium*) or possess well-developed muscular walls (*Epithelionematobothrium*). In species of *Neometadidymozoon* Yamaguti, 1971, the oesophagus is a thick tube with strongly developed muscular walls. In species of *Epithelionematobothrium*, it forms numerous regular diverticula surrounded by numerous gland-cells. Gland-cells surround the alimentary system of many didymozoid species. They may cover only the oesophagus (*Didymosulcus orbitalis* Yamaguti, 1970), the entire oesophagus and distal part of the caeca (*Opisthorchinematobothrium parathunni* Yamaguti, 1970), the oesophagus, distal part of the caeca and the pharynx (*Allonematobothrium epinepheli* Yamaguti, 1965), the posterior part of the oesophagus and distal part of the caeca (*Nematobothrioides kalikali* Yamaguti, 1965) or only the distal part of the caeca (*Metanematobothrioides opakapaka* Yamaguti, 1965). A schematic illustration of the structure of the anterior region of the alimentary system is shown in Fig. 65.3.

The intestine in didymozoids is usually bifurcate and simple. The two blind cylindrical caeca usually reach the posterior extremity. Sometimes, their posterior ends unite to form a cyclocoel (*Philopinna*). This union may be located in the mid-body; if so, the intestine continues posteriorly as a single caecum (*Paraphilopinna*). Species of *Angionematobothrium* Yamaguti, 1970 possess a single caecum. In some species with the body divided into regions (*Koellikeria* Cobbold, 1860), the caeca are short and terminate in the posterior part of the anterior region or just in the anterior

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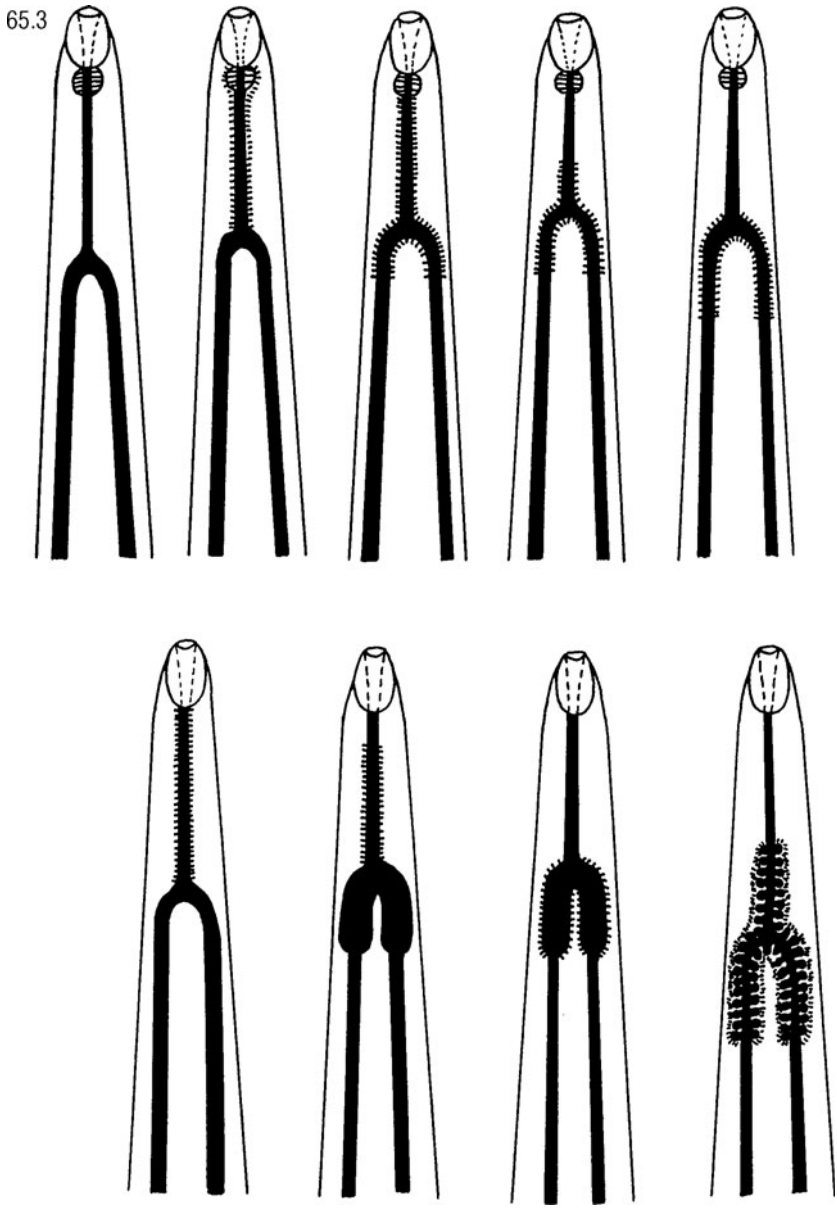



**Fig. 65.3.** Structure of the anterior parts of the alimentary system (diagrammatic).

part of the posterior region of the body. In *Halvorsenius* Gibson, MacKenzie & Cottle, 1981, the caeca are atrophied and presumably non-functional.

Some details of the alimentary system structure, namely the presence or absence of a pharynx and presence of a cyclocoel or a single caecum, are here considered of generic importance, whereas the presence of differences in the gland-cells surrounding particular parts of the gut are criteria considered useful at the species level.

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**Reproductive system.** Among didymozoids, both hermaphroditic and gonochoristic forms exist. This character was given a high taxonomic value, at family level, by Pozdnyakov (1996) and is used in the present work as an important key feature separating groups of subfamilies.

The **male reproductive system** consists of testes, vasa efferentia and an ejaculatory duct. There are usually two testes, rarely one. A single testis is observed in taxa belonging to both hermaphroditic (*Unitubulotestis* Yamaguti, 1953, *Procerozoum* Kamegai, 1971, *Epithelionematobothrium* Yamaguti, 1970, *Brasicystis* Thatcher, 1979) and gonochoristic genera (*Koellikerioides* Yamaguti, 1970, *Coeliotrema* Yamaguti, 1938). The testes are usually very elongate, with rounded extremities, and oval in cross-section. In forms with fused hindbodies, they have no constant shape (*Colocyntotrema* Yamaguti, 1951, *Annulocystis* Yamaguti, 1970). There are also variations in testicular location. In 'nematobothriid' forms, they are in the first third of the body and may extend to more than two-thirds of the body-length or reach the posterior extremity. The testes may be parallel, oblique or tandem (Fig. 65.4). In 'didymozoid' forms, they are usually in the first third of the posterior region of the body, in its lateral margins; their extent in the posterior region of the body is highly variable and, in some cases, their anterior extremities are in the anterior region of the body (*Lepidodidymocystis* Yamaguti & Kamegai, 1969, *Metadidymocystis* Yamaguti, 1970, *Neolampridídymozoon* Wierzbicka, 1980, *Neometadidymozoon* Yamaguti, 1971). In didymozoids with fused posterior regions, the location of the testes is not always constant.

The vasa efferentia are usually thin-walled tubes (rarely, they possess thick, muscular walls). They can be short or very long and spirally coiled. In nematobothriines with the testes in tandem, one of the vasa efferentia is short and the other is long. This is less expressed in forms with oblique testes. Their distal ends unite to form the ejaculatory duct (this could also be interpreted as the vas deferens), which is usually long and frequently spirally coiled or forms numerous irregular coils. When this duct is replete with sperm, 'temporary' seminal vesicles are formed, the presence or absence of which should not be used as a diagnostic character.

The number of testes and their location in the body are used as diagnostic characters at the level of tribes and genera, while their relative position is useful at the species level.

The **female reproductive system** consists of an ovary, oviduct, vitellarium, vitelline ducts, seminal receptacle, Juel's organ, Mehlis' gland, 'uterine' oötype, uterine seminal receptacle, uterus and metraterm (Fig. 65.5).

The ovary is long and thread-like; it may form secondary, tertiary or rarely quaternary branches. In most 'nematobothriid' forms, it is unbranched, except for species of *Metanematobothrium* Yamaguti, 1938, *Maccallozoum* Ishii, 1935 and *Opisthorchinematobothrium*, which have a bifid ovary, with one part directed to the anterior extremity and the other to the posterior extremity. In forms with the 'didymozoid' body-type, species with a branched ovary predominate. 'Nematobothriid' didymozoids have, with rare exceptions, the ovary in the anterior half of the body. In most cases, it forms coils in the sagittal or frontal planes and the coils are not symmetrical with respect to the main body axis. In 'didymozoid' forms, the ovary is peripheral, either along the dorsal surface or along the lateral margins of the posterior region of the body.

The oviduct is a short, rarely long, tube connecting the ovary with the ovovitelline duct, which is formed by the union of the distal parts of the oviduct and the common vitelline duct. The ovovitelline duct in many didymozoids is poorly developed and leads immediately into the oötype.

The shape of the vitellarium is analogous to that of the ovary. In 'nematobothriid' forms it is in the posterior half of the body, while in 'didymozoid' forms it is branched (in rare cases simple, but, if so, very long and strongly coiled). It leads to a short common vitelline duct that joins the distal part of the oviduct to form the ovovitelline duct.

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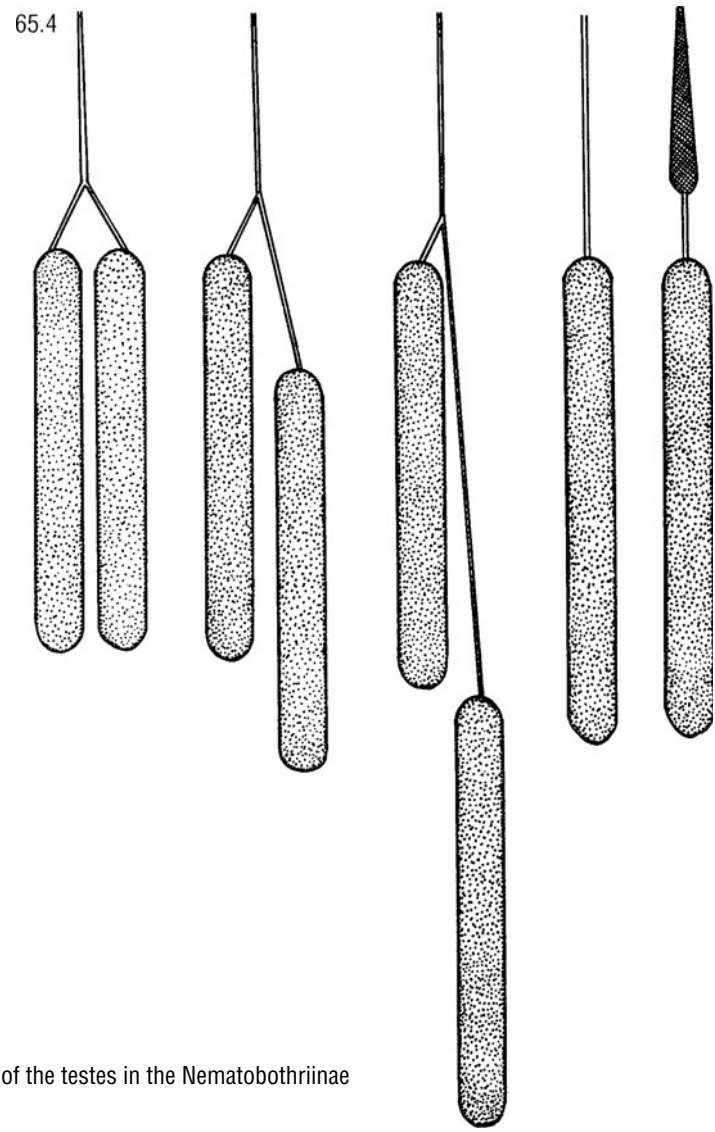



**Fig. 65.4.** Relative position of the testes in the Nematobothriinae (diagrammatic).

The oötype is of the hemiuroid type and represents the proximal part of the uterus surrounded by Mehlis' gland. An oötype of this type is referred to as a 'uterine oötype' (Gibson & Bray, 1979). Its length is very variable.

Mehlis' gland, which surrounds the 'uterine oötype' with gland-cells of differing degrees of density, is strongly developed in most didymozoids. In some species (*Angionematobothrium jugulare* Yamaguti, 1970, *Neodidymozooides microstoma* Yamaguti, 1970), it consists of morphologically different cells. Large cells surround the proximal part of the 'uterine oötype' (further in some cases), often with some interruption, followed by small cells that surround most of the oötype.

The form of the seminal receptacle is variable and it is often reduced; in many cases, a uterine seminal receptacle occurs. In some, a more or less muscular, vesicular, blind seminal receptacle

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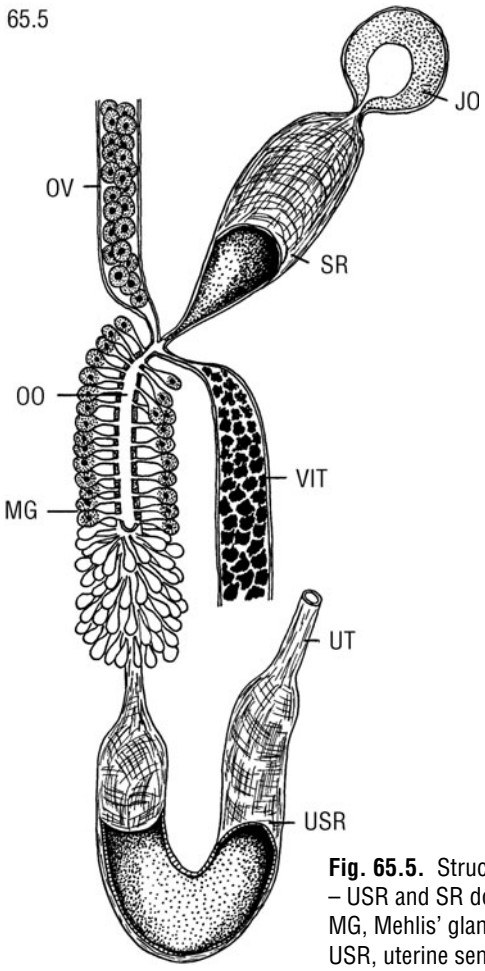



**Fig. 65.5.** Structure of the genital junction (generalized diagrammatic – USR and SR do not occur together). *Abbreviations*: JO, Juel's organ; MG, Mehlis' gland; OO, oötype; OV, ovary; SR, seminal receptacle; USR, uterine seminal receptacle; UT, uterus; VIT, vitellarium.

may be present, which opens via a duct into the ovovitelline duct or into the oviduct proximally to its junction with the vitelline duct. The shape of the seminal receptacle may also vary, depending on the degree to which it is filled with spermatozoa. In some, the seminal receptacle, oviduct and vitelline duct appear to unite as they lead into the 'uterine oötype'. In others, Laurer's canal may be present, the seminal receptacle may be reduced to a rudimentary form and Juel's organ (either rudimentary or fully developed) may be present (Gibson & Bray, 1979; Gibson, 1996). Juel's organ is present in relatively few members of *Unitubulotestis, Neounitubulotestis* Yamaguti, 1971, *Allonematobothrioides* and *Halvorsenius*. Gibson & Bray (1979) assumed that Juel's organ serves as a disposal unit for excess ova, spermatozoa and vitelline cells. Variations in the structure of the central part of the female reproductive system are shown in Fig. 65.6.

The uterus is a differentiated long tube with the proximal part transformed into an oötype ('uterine oötype') and the distal part into a metraterm with a well-developed musculature. The proximal region may also form a uterine seminal receptacle.

The terminal part of the reproductive system in didymozoids is most frequently a hermaphroditic duct into which open the distal ends of the ejaculatory duct and metraterm. The distal part

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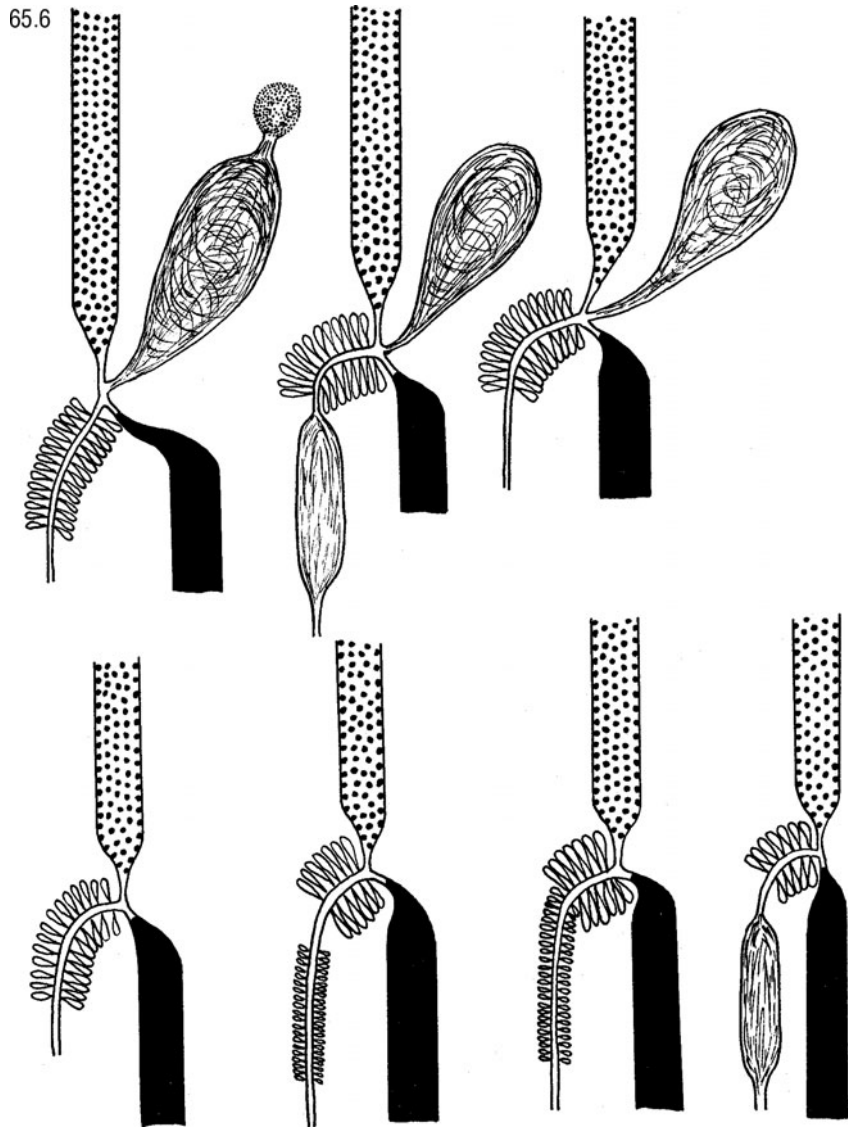



**Fig. 65.6.** Structural variations of the genital junction (diagrammatic).

of the hermaphroditic duct opens via a genital pore, which is medial and just posterior to the oral sucker, often in a small depression. In many species, the hermaphroditic duct passes through a small genital sucker (? or genital papilla) with a well-developed musculature. In some species (e.g. *Nematobothrium scombri* (Taschenberg, 1879)), the terminal part of the hermaphroditic duct can be everted, forming a 'temporary' sinus-organ. Some publications (Self *et al.,* 1963; Noble, 1974; Thulin, 1980) indicate that, in *Ovarionematobothrium texomense* (McIntosh & Self, 1955) and *Nematobibothrioides histoidii* Noble, 1974, the distal parts of the ejaculatory duct and metraterm are not united but open separately at the tip of the small genital sucker.

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The structural type of the reproductive system is useful at the subfamilial level. Various modifications of parts of the reproductive system are used to distinguish tribes and genera.

**Excretory system.** The excretory vesicle in didymozoids with the 'nematobothriid' body-type is usually Y-shaped and the excretory pore is posteriorly terminal or subterminal. The main stem of the vesicle runs towards the anterior extremity, where it divides into two short arms ending just posteriorly to the level of the pharynx. In *Nematobibothrioides histoidii*, these short arms possess numerous diverticula.

Forms with a 'didymozoid' body-type exhibit more diverse shapes of the excretory vesicle. It is Y-shaped in *Metadidymocystis* Yamaguti, 1970 and *Didymocodium* Yamaguti, 1970. Most genera (e.g. *Neometadidymozoon* and *Lepidodidymocystis*) possess a saccular excretory vesicle entirely located in the posterior part of the body. The excretory pore is terminal. In didymozoids with fused posterior regions, the excretory vesicles of the two worms can be fused and apparently lack a common excretory pore (*Neodiplotrema* Yamaguti, 1938, *Colocyntotrema*), or are saccular (*Didymosphaera* Mamaev, 1968). The shape of the excretory vesicle in this work is useful at the generic level.

**Nervous system.** This is represented by pharyngeal ganglia close to the level of the pharynx and united by stout commissures. One pair of nerve-cords is lateral and extends anteriorly, forming branches at the level of the oral sucker. Lateral (the most well developed) and ventral nerve cords pass towards the posterior end of the body; they are connected by commissures. The uniform structure of the nervous system does not allow its use as a diagnostic criterion.

## Life-cycle

The complete life-cycle of a didymozoid is not known. However, it is expected to be similar to that of some other hemiuroids. There are several illustrations of miracidia (e.g. Baylis, 1938; Self *et al.*, 1963; Dollfus, 1966). The parthenitae have not been reported but are assumed to occur in molluscs. The cercariae are assumed to be cystophorous, like other hemiuroid cercariae (e.g. La Rue, 1957; Nikolaeva, 1965; Shul'ts & Gvozdev, 1972; Cable, 1974; Kurochkin & Nikolaeva, 1978; Køie & Lester, 1985; Lester & Newman, 1986), but many of the records may represent other hemiuroid groups. What stage should be considered the metacercariae is open to question, but Nikolaeva (1965) indicated that some occur in cirripedes and Madhavi (1968) that some occur in copepods, and it does seem likely that they occur in invertebrates. Others (e.g Pozdnyakov, 1996) use this term for the larvae in the intestine of teleosts and squid, but it seems more likely that these are a subsequent stage, i.e. juveniles in a paratenic host or third intermediate host. These juveniles may be quite large and differ in morphology. Early on, some were referred to as *Distoma* (or *Cercaria*) *fenestratum* Linton, 1907, but in recent years a larval-group nomenclature has been developed for them: this is outlined in detail below after the keys to the adult forms.

## Classification

Although the first didymozoids were described by Rudolphi (1819) early in the 19th century, their nomenclatural recognition was first made by Monticelli (1888) 69 years later. Monticelli coined the family name Didymozoonidae Monticelli, 1888; this was corrected to Didymozoidae by Poche (1907), who has been indicated as the authority for the family in subsequent works

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(MacCallum, 1917; Poche, 1926; Dawes, 1946; Yamaguti, 1958b, 1971[1]). However, following the ICZN (Article 50.4), it is clear that the authority for this family-group name is Monticelli.

Braun (1893) made one of the first attempts to evaluate the position of didymozoids among the trematodes. He recognized two families, the Distomidae Cobbold, 1860 (including *Koellikeria*) and the Didymozoonidae (with *Didymozoon* Taschenberg, 1878 and *Nematobothrium* van Beneden, 1858). MacCallum (1917) presented a system in which he recognized three genera in the Didymozoidae, namely *Koellikeria, Nematobothrium* and *Atalostrophion*. Dollfus (1926) proposed his system, which represents a classification of the didymozoid structural types, with an indication of the genera belonging to gonochoristic or hermaphroditic forms. Generally, his system consisted of four groups:

- The first group included elongate worms with a cylindrical body, undifferentiated into regions (but not forms with tape-like bodies). These were divided into: (a) hermaphroditic and (b) gonochoristic forms.
- The second group included worms with the body divided into two regions. This group was further divided into: (a) hermaphroditic forms with both specimens of a pair within the capsule identical in structure; and (b) gonochoristic forms with worms of the pair within the capsule with a different structure.
- The third group included extremely long, filiform (but not tape-like) forms with a body that was not differentiated into regions. This group was further divided into: (a) hermaphroditic worms showing a trend towards gonochorism; and (b) full hermaphrodites.
- The fourth group included forms with a tape-like body.

Dollfus understood the obvious artificiality of his system and stated that it was only a step in the study of these trematodes. There are a number of fundamental features of this system that should be noted: the clear distinction between gonochoristic and hermaphroditic forms and the use of body-shape for systematics.

Dawes (1946) included in the Didymozoidae the genera *Nematobothrium, Wedlia* Cobbold, 1860, *Koellikeria, Didymocystis* Ariola, 1902 and *Didymozoon*.

The system was substantially developed in a major work on the world fauna of didymozoids by Ishii (1935). This study is important because, in addition to using data from the literature, Ishii worked with original material. As a result, he described a number of new species, erected new genera and subfamilies and reanalysed the infrastructure of the family in the light of the new data. Ishii recognized four subfamilies and nine genera within the Didymozoidae.

Skrjabin (1955) accepted the system of Ishii in his extensive work on the group, while making further additions and reassessing some details. The elevation of the Didymozoidae to the subordinal rank is the most significant change (although it had earlier been elevated to ordinal rank by Skrjabin & Shul'ts (1937)), as well as the erection of the new subfamily Philopinninae Skrjabin & Shul'ts, 1937.

The classification of the 'Didymozoata Skrjabin & Shul'ts, 1937' has not been subjected to significant rearrangements, but its subsequent development has been mainly due to Yamaguti (1958b, 1965, 1970, 1971), who extended it by describing new forms. Thus, Yamaguti (1958b), in accepting the system of Ishii, recognized ten subfamilies and 22 genera. Following his study of the trematode fauna of Hawaiian fishes, he (Yamaguti, 1965, 1970) erected 42 new genera in

[1] Yet Yamaguti (1971) accepted Monticelli as the authority for the superfamily Didymozooidea.

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11 new subfamilies, most of which consisted of a monotypic genus. Yamaguti (1971) considerably expanded the system of the Didymozoidae, recognizing it at the superfamily rank, with a single family, 23 subfamilies and 75 genera.

Following the works of Yamaguti, which significantly contributed to our knowledge of the group, the classification has not changed much, apart from some small rearrangements within subfamilies and some generic revisions (Nikolaeva, 1978; Pozdnyakov, 1987, 1989b, 1990). Nikolaeva (1975, 1981, 1985) considered the group to represent a suborder with a single family, the Didymozoidae. She (Nikolaeva, 1975) rightly stressed that many subfamilies and genera recognized by Yamaguti (1970, 1971) are not significantly different and the discrimination of new taxa above species level is based on the site in the host. She (Nikolaeva, 1975, 1981, 1985) agreed with the group concept of Yamaguti, recognized 23 subfamilies with 81 genera, and revised the infrastructure of the Koellikeriinae by resurrecting *Wedlia* and synonymizing *Tricharrhen* Poche, 1926 with *Koellikeria*. Mamaev (1968a) analysed the relationships between didymozoids with fused posterior body-regions (*Didymosphaera, Colocyntotrema, Phacelotrema* Yamaguti, 1951, *Opepherotrema* Yamaguti, 1951) and suggested that they represent a monophyletic lineage; he assumed that they could be accommodated in a separate subfamily.

Data gathered in recent decades in many cases conflict with the system of Yamaguti (1971); this is mainly associated with difficulties in accommodating newly described forms into existing genera or subfamilies. Many of the monotypic genera and subfamilies are distinguished by very insignificant characters, and this has led to an extreme expansion of the system and difficulties in discriminating genera and their subfamilial groupings. The difficulties in understanding the system of Yamaguti are also due to an almost total lack of explanation and evidence. Yamaguti's view on the taxonomic significance of the characters used for differentiation is unclear. His eclectic approach led to arbitrary interpretations of the weighting of the characters used in forming the hierarchy of the system. As a result, taxa of the same rank are erected on the basis of characters of differing taxonomic value. Subfamilies are partly erected on the basis of complete or incomplete hermaphroditism, or on the basis of the degree of sexual dimorphism, or on the body being divided into sections or not, or on the basis of the degree of fusion of the posterior body-regions, or on the presence/absence of lobes and indentations in the posterior region of the body. In addition, Yamaguti used, as distinguishing characters at generic level, the site in the host (*Dermatodidymocystis* Yamaguti, 1970, *Coeliodidymocystis* Yamaguti, 1970) and the branching of the ovary and vitellarium. At the subfamilial level, he also used the shape of the body and the degree of lobation (*Lobatozoum* Ishii, 1936, *Lagenocystis* Yamaguti, 1970, *Kamegaia* Yamaguti, 1970, etc.). Along with using the degree of branching of the reproductive organs as a generic character, he (e.g. Yamaguti, 1970) widely applied it for distinguishing species, and especially those of *Didymocystis* (*sensu lato*). Thus, in addition to the excessive partitioning characteristic of Yamaguti's system, its main failure is the unnecessary formalization of the criteria on which it is based, which has led to the application of characters of different taxonomic weight for distinguishing taxa of the same rank. This clearly explains the large number of monotypic genera and subfamilies in Yamaguti's system.

Gibson & Bray (1979), when revising the Hemiuroidea Looss, 1899, treated the didymozoids as a superfamily arising from hemiuroid stock close to the Dictysarcidae Skrjabin & Guschanskaja, 1955. Following standard phylogenetic protocols, Gibson (1996) included the group as a family within the Hemiuroidea, a situation, as indicated above, confirmed by molecular studies (e.g. Barker *et al*., 1993) and reflecting the relationships attributed to the group by workers earlier in the 20th century. Nevertheless, Pozdnyakov (1996) considered that didymozoids cannot be accommodated in a single family. He recognized them at subordinal level and

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divided them into two families, one for hermaphroditic and one for gonochoristic forms. Hermaphroditic forms in turn fall into three large natural groups: elongate forms with simple, undifferentiated bodies and a linear arrangement of the internal organs (Nematobothriinae Ishii, 1935); forms with bodies divided into two regions and with a different arrangement of the internal organs (Didymozoinae Monticelli, 1888); and forms with more or less fused posterior body-regions (Neodiplotrematinae Yamaguti, 1958). The Didymodiclinidae Pozdnyakov, 1993 included three subfamilies: the filiform Didymodiclininae Pozdnyakov, 1993; the Koellikeriinae Ishii, 1935, with bodies divided into regions; and the Nephrodidymotrematinae Yamaguti, 1970, with fused posterior body-regions. Thus, architectonic characters, which have higher taxonomic value than structural, were used as a basis for the subfamilies. Of the subfamilies that he recognized, only the Nephrodidymotrematinae is monotypic. Groups of genera that he considered to be related were placed in tribes within the subfamilies. Pozdnyakov's (1996) system is essentially followed in this work, except that the group is treated as a single family within the Hemiuroidea, as in Gibson (1996).

There are a few new changes. *Syncorpozoum* Ku & Shen, 1965, *Indodidymozoon* Madhavi, 1982, *Platocystoides* Madhavi, 1982, *Oculonematobothrium* Murugesh, Krishna Sai Ram & Madhavi, 1992 and *Helicodidymozoon* Anderson & Cribb, 1994 are recognized. *Renodidymocystis* Madhavi, 1982 is considered a synonym of *Lobatozoum* Ishii, 1935 and *Reniforma* Yamaguti, 1970 a synonym of *Gonapodasmius* Ishii, 1935. *Rhopalotrema* Anderson, 1998 is treated here as a synonym of *Neometadidymozoon* Yamaguti, 1971, as the two genera appear morphologically very similar (see Anderson, 1998), although Anderson & Barker (1998) presented molecular evidence in support of this taxon. *Pseudocoeliodidymocystis* Shen, 1990 is considered a genus *inquirendum*.

The Didymozoidae is one of the most difficult, possibly the most difficult, group of digeneans to deal with. Interpretation and, hence, keying is problematic – hence users need to take into consideration diagnoses and host group, as well as the 'key' features. Due to the complexity of these worms, the illustrations presented here tend to be diagrammatic. See Yamaguti (1970, 1971) and the original descriptions for more natural representations of the genera. Similarly, due to difficulties in identification and the lack of investigations on certain host groups and in certain regions, users may need to be wary of some of the host and distribution data presented below.

## Genera *inquirenda*

## Genus *Brasicystis* Thatcher, 1979

**Diagnosis:** Didymozoinae. Hermaphroditic, encapsulated in pairs. Capsule oval or irregular in shape, on gill lamellae. Body divided into two regions. Anterior region flat, narrow, attached to edge of anterior part of posterior region. Posterior region laterally flattened, may have ventral concavity anteriorly. Oral sucker, pharynx and oesophagus present. Ventral sucker absent. Caeca reach close to posterior extremity. Testis single, tubular, elongate, winding, between region of concavity in posterior region and posterior extremity. Seminal receptacle present. Genital pore at level of oral sucker. Ovary single, tubular, shorter than testis. Uterine coils in posterior region. Eggs small, numerous. Vitellarium single, tubular, long, winding, reaches to posterior extremity. Excretory system? In subcutaneoous tissues of branchial and buccal region of freshwater (sciaenid) fishes; Neotropical. Type-species *B. bennetti* Thatcher, 1979.

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## Genus *Lepidodidymocystis* Yamaguti & Kamegai, 1969

**Diagnosis:** Didymozoinae. Capsule spherical. Anterior region small, flattened, tapered anteriorly. Posterior region wide, almost hemispherical dorsally, truncated anteriorly and conical at posterior extremity. Median furrow present on concave ventral margin of posterior region, dividing it into two lobes, between which anterior region is attached to posterior. Oral sucker and pharynx present. Oesophagus long, surrounded by gland-cells. Caeca strongly curved, extending close to posterior extremity. Ventral sucker in posterior region, close to its junction with anterior region. Testes along concave side of posterior region. Vasa efferentia and ejaculatory duct long. Genital pore ventral to oral sucker. Genital junction in anterior part of posterior region, close to its junction with anterior region. Ovary unbranched, curved, along axis of posterior region. Seminal receptacle present. Mehlis' gland not large. Vitellarium long, unbranched, curved along convex margin of posterior region. Excretory vesicle not determined. Under scales and in lateral line of sciaenid fishes; eastern Pacific. Type-species *L. irwini* Yamaguti & Kamegai, 1969.

## Genus *Pseudocoeliodidymocystis* Shen, 1990

**Diagnosis:** Didymozoinae. Cyst subspherical, contains single worm; complete hermaphrodite. Anterior region slender (specimen damaged); posterior region 'bowl-shaped' (i.e. appears deeply concave in illustration). Sucker near posterior extremity of posterior region (?). Testes two, elongate, in anterior part of posterior region. Ovary tubular, unbranched. Genital junction near middle of posterior region. Seminal receptacle present near sucker. Uterine coils fill much of posterior region. Eggs small, thin-shelled. Vitellarium similar to ovary, extends to marginal areas of posterior region. Excretory system not known. In tissues (stomach wall) of scombrids (*Auxis*); off China. Type-species *P. xishaensis* Shen, 1990.

## Genus *Sicuotrema* Yamaguti, 1970

**Diagnosis:** Gonapodasmiinae. Capsule elliptical. Anterior regions elongate but not long, widened in anterior third. Posterior regions fused, elliptical. Pharynx present. Ventral sucker absent. Oesophagus short. Caeca reach posterior region. Two elongate, curved testes in each individual. Vasa efferentia short. Ejaculatory ducts long. Ovary and vitellarium branched. Genital junctions of two individuals symmetrical in periphery of posterior region. Seminal receptacle present. Genital pore ventral to oral sucker. Excretory system not known. On fins of scombrid fishes (*Auxis*); Pacific Ocean. Type-species *S. auxis* Yamaguti, 1970.

## Genus *Neogonapodasmius* Radhakrishnan & Nair, 1981

**Diagnosis:** Didymodiclinidae: Koellikeriinae. Encapsulated. Sexual dimorphism strongly expressed. Ventral sucker absent. Pharynx absent. Oesophagus simple, long. Caeca reach close to posterior extremity. *Male*: Smaller than female. Body not differentiated into regions, round in cross-section. Testes two, parallel, reach close to posterior extremity. Vasa efferentia? Ejaculatory duct long. Primordia of female genital system present. *Female*: Body divided into filiform anterior

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region and widened posterior region. Genital junction approximately in middle of posterior region. Ovary branched, curved, in anterior half of posterior region. Mehlis' gland large. Seminal receptacle? Vitellarium analogous to ovary in form, postovarian. Excretory system not studied. In fins of hemirhamphid fishes (*Hemirhamphus*); Indian Ocean. Type-species *N. hemirhamphi* Radhakrishnan & Nair, 1981.

## Genus *Glomeritrema* Yamaguti, 1942

**Diagnosis:** Didymozoidae: Nematobothriinae. Individuals in capsules. Capsule with capillary net. Body elongate, filiform. Pharynx present. Caeca not reaching close to posterior extremity. Testis long, curved. Vas efferens similar in form to testis. Ovary elongate, unbranched. Seminal receptacle? Uterus with single loop. Genital pore at level of oral sucker. Vitellarium? Excretory system not known. In subcutaneous tissues of istiophorid fishes; Pacific Ocean. Type-species *G. subcuticola* Yamaguti, 1942.

## Genus *Paralichthytrema* Szidat, 1960

**Diagnosis:** Didymozoidae: Nematobothriinae. Body filiform; surface with 'cuticular scales'; anterior extremity with cap-like widening. Oral sucker, pharynx and ventral sucker absent. Oesophagus short. Testis probably single? Genital pore apical. Terminal parts of caeca, ovary, vitellarium, seminal receptacle and excretory vesicle not known. In gills of pleuronectiform fishes; south-westen Atlantic. Type-species *P. patagonicum* Szidat, 1960.

## Family Didymozoidae Monticelli, 1888

(Syns Didymozoidae Poche, 1907; Didymozooidae Ishii, 1935; Koellikeriadae MacCallum & MacCallum, 1915; Koellikereiidae Ishii, 1935; Didymodiclinidae Pozdnyakov, 1993)

**Diagnosis:** Hermaphroditic or gonochoristic digeneans. Found free in host tissues or paired in capsules. Body extremely diverse in form and size, divided into two regions or not, unarmed. Oral sucker present. Ventral sucker present or absent, usually well forward in body. Alimentary system of typical pattern, with elements of reduction. Prepharynx absent. Pharynx present or absent. Caeca two, simple, may occasionally form cyclocoel; 'Drüsenmagen' present or absent. Gland-cells present or absent around pharynx, oesophagus and anterior region of caeca. Testes usually two, rarely one, of variable shape and location. Terminal genitalia usually much reduced. Male and female ducts may fuse to form short hermaphroditic duct before opening via genital pore. Sinus-sac or cirrus-sac absent. Genital pore midventral in anterior body, between suckers when latter are present. Ovary and vitellarium thread-like, branched or not. Uterine seminal receptacle or blind seminal receptacle present; Juel's organ present or absent. Laurer's canal absent. Uterus very long. Metraterm often well developed. Eggs small, operculate. Excretory vesicle Y-shaped, rarely saccular; pore terminal or subterminal. Mainly in tissues of marine teleosts (mainly perciforms, especially scombroids); in warmer oceanic waters; rarely in such fishes in fresh water (South America). Miracidium spined anteriorly, with one to three rows of spines. Juveniles spindle-shaped; oral sucker present; ventral sucker present or absent; alimentary system formed; gland-cells surrounding anterior part of alimentary system present or absent; 'Drüsenmagen' present or

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absent; excretory vesicle spherical, rarely Y-shaped. In tissues of marine teleosts (especially scombroids); warmer parts of major oceans and associated seas, rarely in fresh water. Type-genus *Didymozoon* Taschenberg, 1879.

## Key to subfamilies

**1a. Hermaphroditic forms; single and free or encysted in pairs ..... 2.**
**1b. Gonochoristic forms; usually encysted in pairs ..... 4.**

**2a. Body long, thin, not divided into regions; usually not encysted in pairs ..... ..... Nematobothriinae Ishii, 1935.**
**2b. Body divided into two regions, with wider posterior region; usually encysted in pairs ... 3.**

**3a. Posterior body-regions of partners separate ..... Didymozoinae Monticelli, 1888.**
**3b. Posterior body-regions of partners more or less fused ..... Gonapodasmiinae Ishii, 1935.**

**4a. Posterior regions of partners not fused ..... 5.**
**4b. Posterior regions of partners fused ..... Nephrodidymotrematinae Yamaguti, 1958.**

**5a. Body filiform or moderately elongate, not divided into regions; sexual dimorphism not strongly expressed ..... Didymodiclininae Pozdnyakov, 1993.**
**5b. Body divided into regions, with elongate anterior region and wide posterior region; sexual dimorphism strongly expressed ..... Koellikeriinae Ishii, 1935.**

## Subfamily Didymozoinae Monticelli, 1888

(Syns Didymozooinae Ishii, 1935; Didymozoinae Yamaguti, 1958; Adenodidymocystiinae Yamaguti, 1970; Neodidymozoinae Yamaguti, 1970)

**Diagnosis:** Worms adjacent to one another in capsule. Body divided into two distinct regions. Anterior region elongate, narrow, usually round in cross-section; anterior third may be dorsoventrally flattened. Posterior region greatly enlarged, cylindrical, spindle-shaped, disc-like, spherical or hemispherical, occasionally with dorsal furrow. Hindbody surface smooth, rarely lobed or with numerous protrusions and indentations. Pharynx present or absent. Oesophagus long or short. Caeca extend to posterior region of body. Gland-cells around oesophagus and anterior part of caeca present or absent. Testes two, entirely in posterior region, rarely extending into anterior region, occasionally branched. Uterus very long, strongly coiled. Excretory vesicle usually saccular, rarely Y-shaped. Type-genus *Didymozoon* Taschenberg, 1879.

## Key to tribes

**1a. Ventral sucker present; testes in both regions of body ..... ..... Metadidymocystini Pozdnyakov, 1993.**

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**1b. Ventral sucker absent or occasionally present; testes in posterior region of body ..... 2.**

**2a. Posterior region entire ..... Didymozoini Monticelli, 1888.**
**2b. Posterior region with 'trunk' section possessing secondary branches with protrusions and indentations ..... Neodidymozoini Yamaguti, 1970.**

## Tribe Didymozoini Monticelli, 1888

**Diagnosis:** Posterior region entire, not divided into trunk and secondary branches with indents. Ventral sucker absent (except *Indodidymozoon*). Testes in posterior region of body. Type-genus *Didymozoon* Taschenberg, 1879.

## Key to genera

**1a. Mucous glands in posterior region present; posterior region massive, with collar-like ridges surrounding its flattened surface ..... *Adenodidymocystis* Yamaguti, 1970. (Fig. 65.7)**
**Diagnosis:** Capsule spherical. Anterior region elongate, round in cross-section, conical anteriorly and widened at middle. Posterior region massive, hemispherical. Anterior region attached to about middle of flattened surface of posterior region. Flattened surface of posterior region surrounded by two well-developed collar-like ridges, one with well-developed muscular tubercle. Numerous 'mucous' glands along convex surface of posterior region; secretions collected into wide duct opening via wide mid-dorsal pore. Pharynx present. Caeca distinctly widened in posterior region. Genital pore ventral, at level of pharynx. Ovary and vitellarium branched. Seminal receptacle present. Excretory system not studied. In intestinal wall of scombrids (*Katsuwonus*); Pacific Ocean. Type-species *A. intestinalis* Yamaguti, 1970.

**1b. Mucous glands in posterior region absent; posterior region not as above ..... 2.**

**2a. Posterior region of body flattened on one or both sides ..... 3.**
**2b. Posterior region of body widened but not flattened ..... 4.**

**3a. Posterior region of body flattened on one side, semicircular; vitellarium with one or two coiled branches, along convex surface of posterior region ..... ..... *Platocystis* Yamaguti, 1938. (Fig. 65.8)**
(Syn. *Dermatodidymocystis* Yamaguti, 1970)
**Diagnosis:** Encysted in pairs; capsule disc-shaped. Anterior region thin, but slightly or noticeably widened in its anterior third. Posterior region flat on one side, with semicircular shape. Anterior region attached to right side of posterior region, close to edge. Pharynx present. Oesophagus short. Testes in posterior region, close to junction between anterior and posterior regions. Genital pore at level of oral sucker. Genital junction in anterior third of posterior region or somewhat closer to its middle. Ovary branched or not, in anterior and middle part of posterior region. Seminal receptacle present. Simple or two-branched vitellarium along convex border of posterior region; branches coiled. Excretory system not known. Under skin/scales of scombrids (*Thunnus*); Atlantic, Pacific and Indian Oceans. Type-species *P. alalongae* Yamaguti, 1938.

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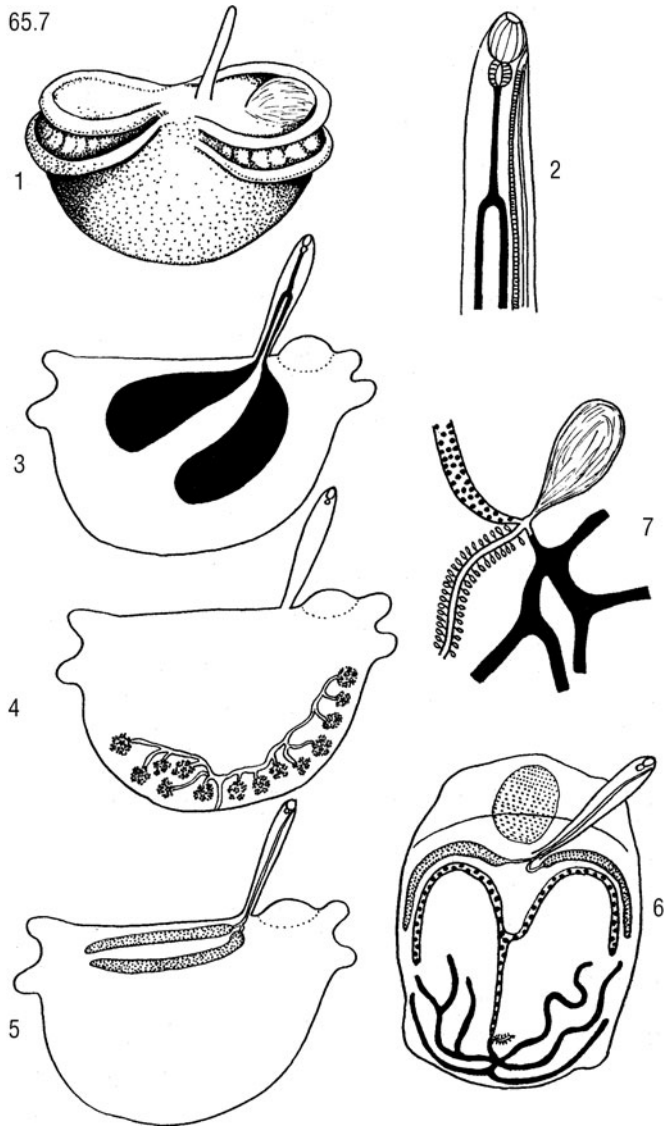



**Fig. 65.7.** *Adenodidymocystis* (diagrammatic). 1, Entire worm; 2, anterior extremity; 3, alimentary system; 4, location of the mucous glands; 5, male reproductive system; 6, location of the gonads (ventral view); 7, genital junction.

**3b. Posterior region of body dorsoventrally flattened; vitellarium not coiled but radially branched ..... *Platocystoides* Madhavi, 1982. (Fig. 65.9)**

**Diagnosis:** Encysted in pairs. Anterior region long, slender, attached to centre of posterior region. Posterior region flattened, disc-like, with distinct furrows on ventral surface that divide it into number of digitiform lobes radiating from centre. Oral sucker and pharynx present. Caeca narrow in anterior region, not traceable in posterior region. Testes two, elongate, close to one another on

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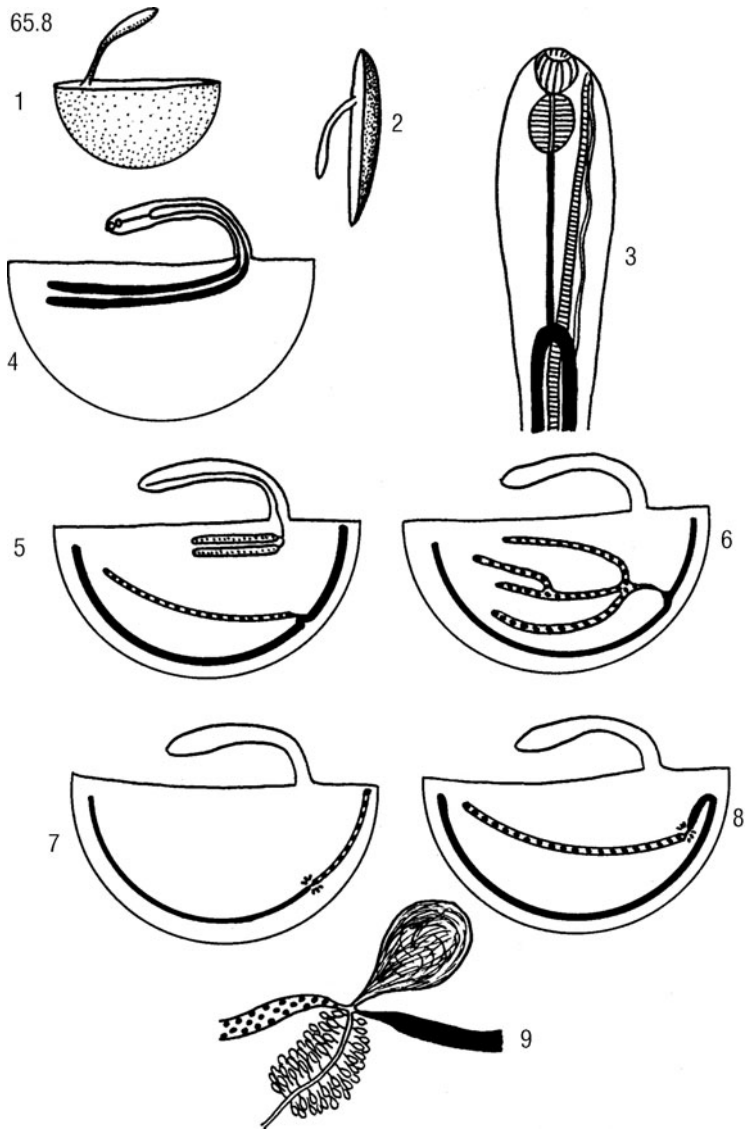



**Fig. 65.8.** *Platocystis* (diagrammatic). 1, Entire worm, lateral view; 2, entire worm, ventral view; 3, anterior extremity; 4, location of the alimentary system; 5, relative position of the testes, ovary and vitellarium; 6–8, location of the ovary and vitellarium; 9, genital junction.

dextral side of posterior region. Ovary consists of several branches, radiating from genital junction to margins of posterior region. Uterine coils fill entire posterior region; uterine reservoir small. Eggs small, numerous. Vitellarium divided into several branches all radiating from genital complex; branches in two groups of three and four. Excretory system not known. Under scales of sphyraenids; Indian Ocean. Type-species *P. polyaster* (Job, 1962) Madhavi, 1982.

**4a. Posterior body-region divided anteriorly into two lateral lobes by median furrow ..... ..... *Didymosulcus* Pozdnyakov, 1990. (Fig. 65.10)**

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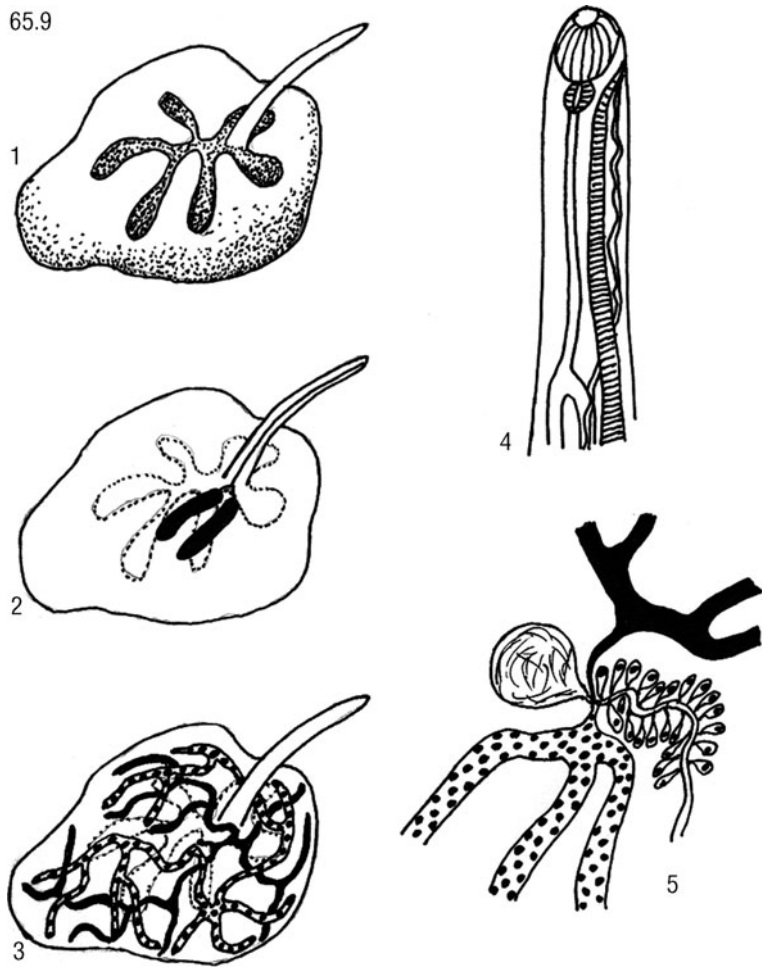



**Fig. 65.9.** *Platocystoides* (diagrammatic). 1, Entire worm; 2, location of testes; 3, location of the ovary and vitellarium; 4, anterior extremity; 5, region of genital junction.

**Diagnosis:** Capsule shape spherical or globular; pair closely opposed to each other ventrally, rarely unencysted. Anterior region thin, elongate, of relatively equal width or conical. Anterior part of posterior region enlarged and divided anteriorly by median furrow into two symmetrical lateral lobes; posterior part conical and curved ventrally. Anterior region of body attached to posterior region close to its divided anterior part. Pharynx present, sometimes reduced. Oesophagus relatively long. Gland-cells around oesophagus and anterior parts of caeca present or absent. Testes two, one in each lateral lobe of posterior region. Genital pore opens at level of pharynx or oral sucker, on tip of what appears to be small genital sucker. Ovary and vitellarium elongate, long, branched or not. Seminal receptacle present or absent. Excretory vesicle elongate, occupies central part of posterior region. In tissues of scombrid fishes (especially *Thunnus*), occasionally in istiophorids; Pacific and Indian Oceans.Type-species *D. katsuwonicola* (Okada, 1926) Pozdnyakov, 1990.

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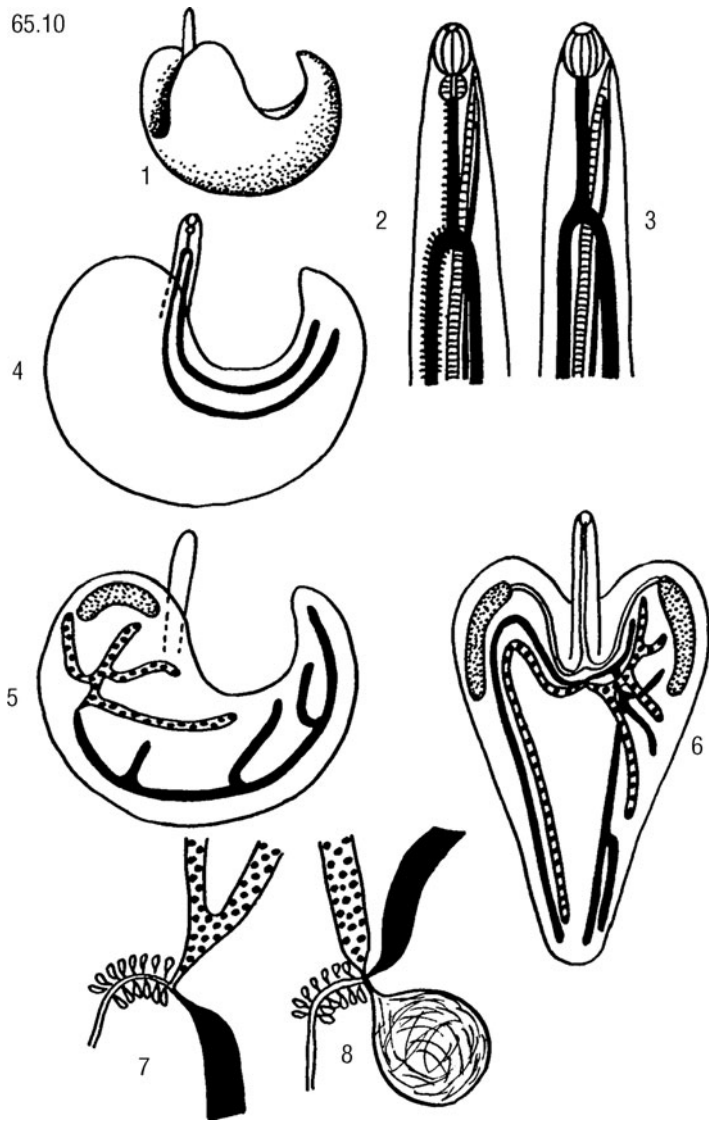



**Fig. 65.10.** *Didymosulcus* (diagrammatic). 1, Entire worm; 2–3, structural variations of the anterior extremity; 4, location of the alimentary system; 5, location of the gonads, lateral view; 6, same, ventral view; 7–8, structural variations of the genital junction.

**4b. Posterior region of body without median furrow ..... 5.**

**5a. Posterior region of body with regularly or irregularly alternating lobes .....**
**..... *Lobatozoum* Ishii, 1935. (Fig. 65.11)**
(Syns *Lobatocystis* Yamaguti, 1965; *Kamegaia* Yamaguti, 1970; *Yamaguticystis* Nikolaeva & Dubina, 1968; *Renodidymocystis* Madhavi, 1982; *Lepidodidymozoon* Shen, 1984)
**Diagnosis:** Capsule more or less moniliform. Anterior region elongate, thin, round in cross-section, tapered at anterior extremity or widened in anterior third. Posterior region much widened,

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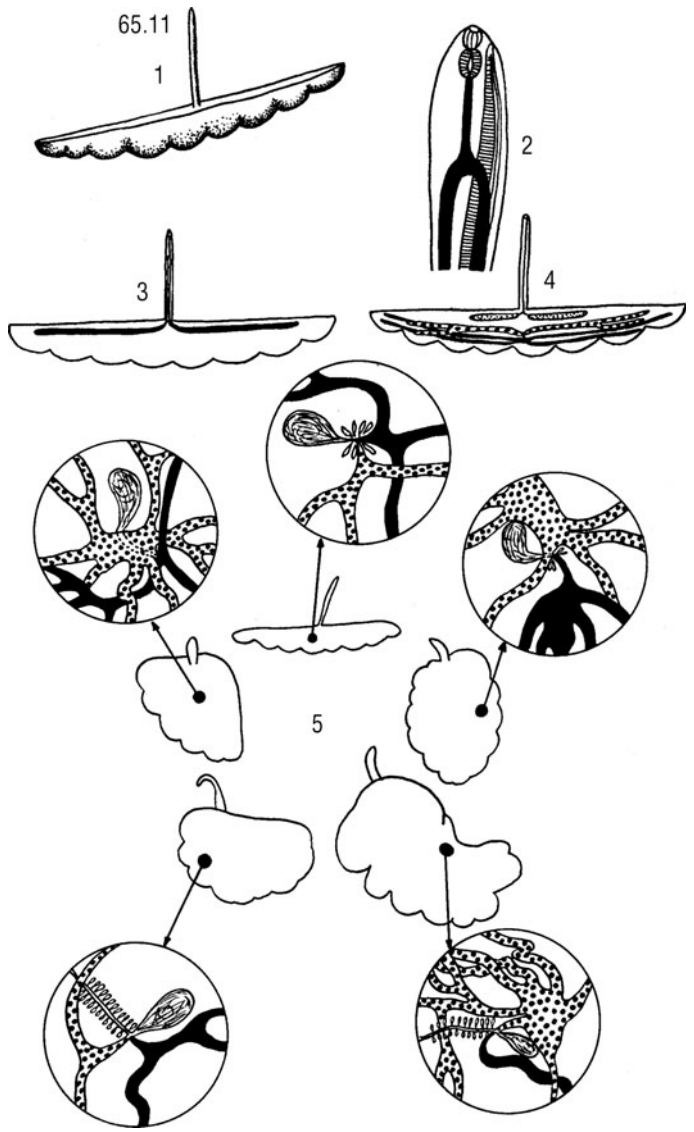



**Fig. 65.11.** *Lobatozoum* (diagrammatic). 1, Entire worm; 2, anterior extremity; 3, location of the alimentary system; 4, location of the testes, ovary and vitellarium; 5, structural variations and location of the genital junction.

diverse in shape, with numerous regularly or irregularly alternating protrusions, indentations or lobes. Anterior region attached to region devoid of lobes. Pharynx present. Oesophagus relatively long, may be surrounded by gland-cells. Testes elongate, long, rarely branched. Genital pore at level of oral sucker or pharynx. Ovary with short 'trunk', from which three to seven branches, with or without secondary branches, arise. Mehlis' gland and seminal receptacle present. Vitellarium branched. Excretory system not known. In tissues of scombrid fishes, occasionally in sphyraenids and serranids; Pacific, Indian and Atlantic Oceans. Type-species *L. multisacculatum* Ishii, 1935.

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**5b. Posterior region of body without lobes ..... 6.**

**6a. Posterior region of body subglobular ..... 7.**
**6b. Posterior region of body cylindrical ..... 8.**

**7a. Posterior region of body hemispherical; anterior region attached close to or at anterior margin of flattened surface of posterior region; pharynx present .....**
**..... *Didymocystis* Ariola, 1902. (Fig. 65.12)**
(Syns *Coeliodidymocystis* Yamaguti, 1970; *Didymocystoides* Yamaguti, 1970; *Lagenocystis* Yamaguti, 1970; *Univitellodidymocystis* Yamaguti, 1970)

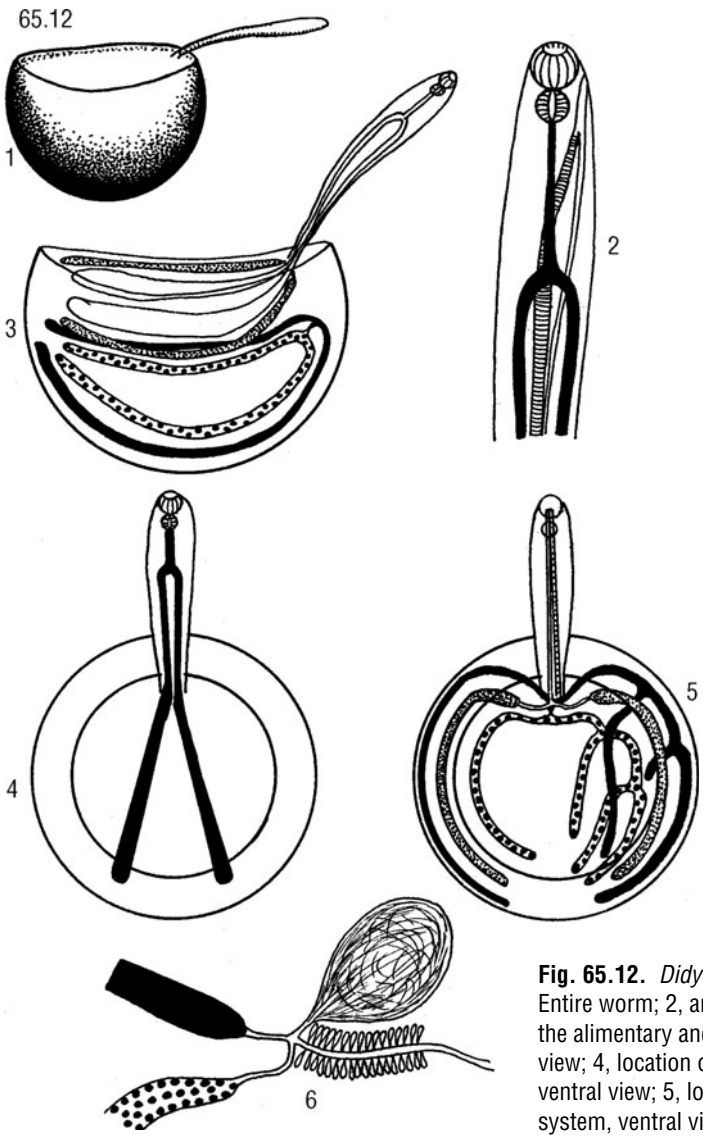



**Fig. 65.12.** *Didymocystis* (diagrammatic). 1, Entire worm; 2, anterior extremity; 3, location of the alimentary and reproductive system, lateral view; 4, location of the alimentary system, ventral view; 5, location of the reproductive system, ventral view; 6, genital junction.

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**Diagnosis:** Capsule spherical or globular. Anterior region thin, elongate, sometimes with its anterior third widened. Posterior region hemispherical, with cup-like concavity of variable size on its flattened surface. Anterior region attached relatively close to anterior margin of flattened surface of posterior region. Pharynx present. Testes unbranched. Ovary and vitellarium branched or not. Seminal receptacle present. Excretory vesicle saccular. In tissues of scombrids (especially *Thunnus*), also in many other groups, such as carangids, priacanthids, sphyraenids and istiophorids; Pacific, Indian and Atlantic Oceans. Type-species *D. reniformis* Ariola, 1902.

7b. **Posterior region of body disc-like, one side slightly concave, other slightly convex; anterior region attached to middle of concave surface of posterior region; pharynx present ..... ..... *Melanocystis* Yamaguti, 1970. (Fig. 65.13)**

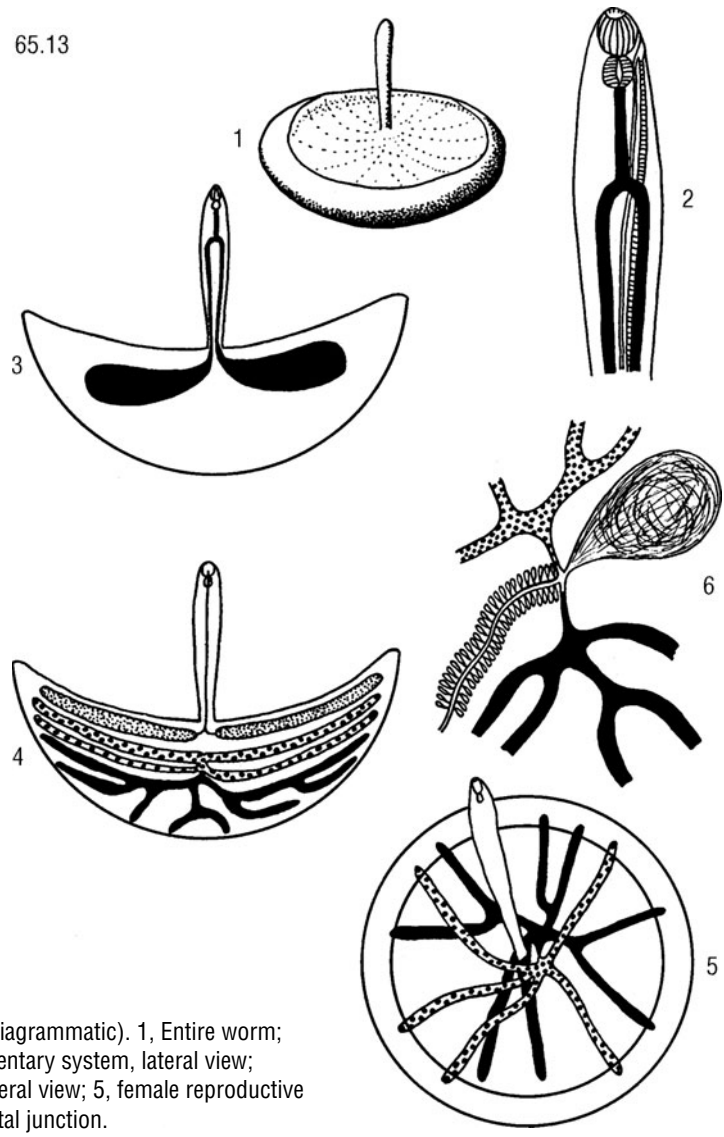



**Fig. 65.13.** *Melanocystis* (diagrammatic). 1, Entire worm; 2, anterior extremity; 3, alimentary system, lateral view; 4, location of the gonads, lateral view; 5, female reproductive system, ventral view; 6, genital junction.

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**Diagnosis:** Capsule disc-like. Anterior region elongate, round in cross-section, relatively wide, somewhat tapered anteriorly. Posterior region disc-like, widened; width greater than length. Ventral surface flat and somewhat concave; dorsal surface convex. Anterior region attached at middle of concave surface of posterior region. Pharynx present. Oesophagus long, thin. Caeca wide, opposed, oriented laterally, in posterior region; contents black. Testes elongate, symmetrical, in posterior region, close to junction with anterior region. Genital pore at level of oral sucker. Genital junction closer to posterior extremity of posterior region. Ovary branched; branches radial. Seminal receptacle and well-developed Mehlis' gland present. Vitellarium with similar structure to ovary but with twice number of branches. Excretory system not known. In tissues (especially gut-wall and gill muscles) of scombrid fishes; Indian and Pacific Oceans. Type-species *M. kawakawa* Yamaguti, 1970.

7c. **Posterior region of body bell-shaped; anterior region attached to middle of flattened surface of posterior region; pharynx present .. *Oesophagocystis* Yamaguti, 1970. (Fig. 65.14)**
**Diagnosis:** Capsule globular. Anterior region elongate, relatively small, attached to flattened surface of posterior regions. Posterior region bell-shaped, round in cross-section. Pharynx present.

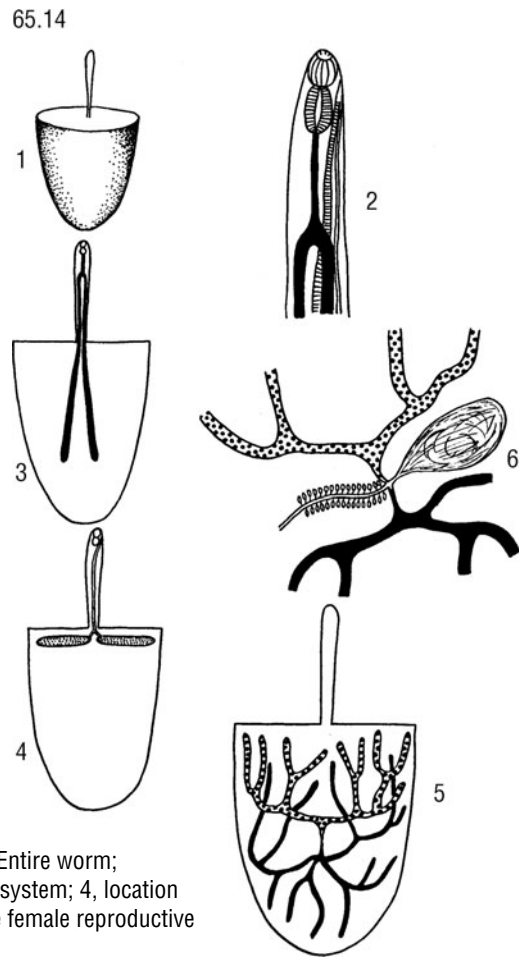



**Fig. 65.14.** *Oesophagocystis* (diagrammatic). 1, Entire worm; 2, anterior extremity; 3, location of the alimentary system; 4, location of the male reproductive system; 5, location of the female reproductive system; 6, genital junction.

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Oesophagus short. Testes elongate, symmetrical, close to junction of anterior and posterior regions. Genital pore lateral at level of pharynx. Genital junction in middle of posterior region. Ovary branched; branches in anterior half of posterior region. Mehlis' gland and seminal receptacle present. Vitellarium branched; branches in posterior region. In tissues (especially gut-wall) of scombrid fishes; Pacific and Atlantic Oceans. Type-species *O. dissimilis* (Yamaguti, 1938) Yamaguti, 1970.

**7d. Posterior region of body reniform; anterior region elongate, slightly widened anteriorly; pharynx absent ..... *Didymophaselus* Pozdnyakov & Gordeev, 1993. (Fig. 65.15)**

**Diagnosis:** Capsule globular. Anterior region elongate, slightly widened in its anterior third, attached subterminally to anterior part of posterior region. Posterior region reniform. Pharynx absent. Oesophagus thin, short, with gland-cells surrounding anterior part. Testes elongate, parallel, in anterior half of posterior region. Genital pore ventral to oral sucker. Genital junction in anterior part of posterior region and displaced towards base of its convex extremity. Mehlis' gland

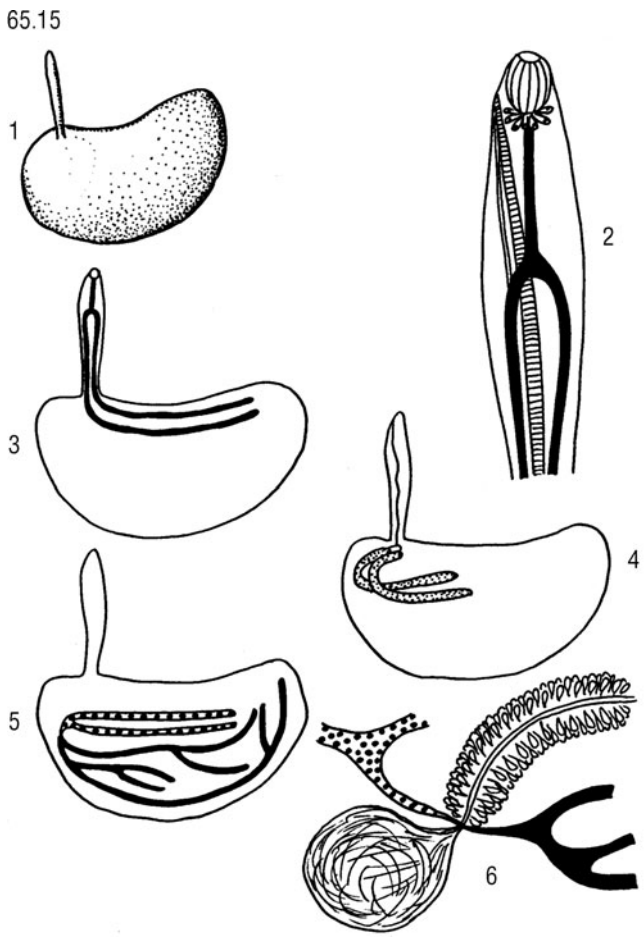



**Fig. 65.15.** *Didymophaselus* (diagrammatic). 1, Entire worm; 2, anterior extremity; 3, location of the alimentary system; 4, location of the male reproductive system; 5, location of the female reproductive system; 6, genital junction.

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well developed. Seminal receptacle present. In musculature of scombrids (*Allothunnus*); Pacific Ocean. Type-species *D. allothunni* Pozdnyakov & Gordeev, 1993.

**8a. Anterior region of body attached terminally or subterminally to posterior region ..... ..... *Didymozoon* Taschenberg, 1879. (Fig. 65.16)**
(Syn. *Didymozoum* Ishii, 1935)

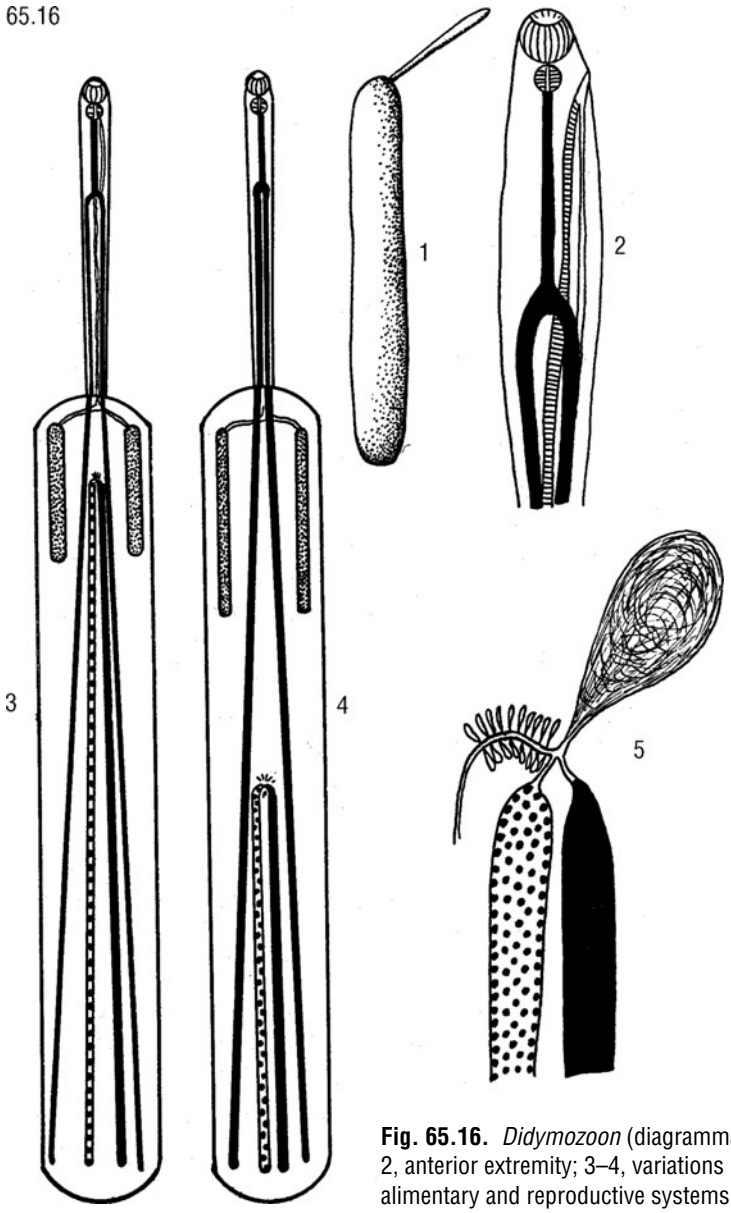



**Fig. 65.16.** *Didymozoon* (diagrammatic). 1, Entire worm; 2, anterior extremity; 3–4, variations in the location of the alimentary and reproductive systems; 5, genital junction.

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**Diagnosis:** Capsule cylindrical or spherical. Anterior region long, attached terminally or subterminally to posterior region; its proximal extremity may be flattened. Posterior region widened, cylindrical, with rounded anterior and posterior extremities, sometimes spiral or with indentations of secondary origin. Pharynx present. Testes, elongate, parallel or slightly interwoven in anterior third of posterior region. Genital pore ventral to oral sucker. Genital junction in first or second third of posterior region. Seminal receptacle present. Ovary and vitellarium elongate, usually unbranched, rarely with two branches, in posterior region of body. Excretory system not known. In tissues of scombrid fishes (especially) and in sphyraenids, platycephalids, priacanthids, serranids, xiphiids and istiophorids; Indian, Pacific and Atlantic Oceans (and associated seas). Type-species *D. sphyraenae* Taschenberg, 1879.

**8b. Anterior region attached in middle or close to middle of posterior region ..... 9.**

**9a. Ventral sucker absent ..... *Didymocylindrus* Ishii, 1935. (Fig. 65.17)**
(Syns *Allodidymozoon* Yamaguti, 1959; *Didymoproblema* Ishii, 1935)
**Diagnosis:** Capsule cylindrical. Anterior region elongate, cylindrical, sometimes with anterior third widened, perpendicular to posterior region, attached in about its middle. Posterior region elongate, round in cross-section. Ventral sucker absent. Pharynx present. Oesophagus long. Caeca in both regions of body; in posterior region, they are directed either opposite or parallel on one side. Position of testes similar to that of caeca. Genital pore ventral or subventral at level of pharynx. Genital junction in middle of posterior region. Ovary and vitellarium normally branched, rarely unbranched. Seminal receptacle present. Excretory system not known. In tissues of scombrid, sphyraenid and occasionally platycephalid fishes; Indian and Pacific Oceans. Type-species *D. filiformis* Ishii, 1935.

**9b. Ventral sucker present ..... *Indodidymozoon* Madhavi, 1982. (Fig. 65.18)**
**Diagnosis:** Encysted in pairs, completely or incompletely hermaphroditic. Narrow anterior region attaches ventrally to wider, elongate, usually longer posterior region. Oral sucker terminal. Ventral sucker small, near junction of anterior and posterior regions. Pharynx present. Oesophagus long, constricted proximally. Caeca simple, terminate near posterior extremity of posterior region. Testes cylindrical, lateral, extend throughout hind part of posterior region; length variable. Genital pore at level of oral sucker. Ovary single, filamentous, extends from near posterior extremity of posterior region to genital junction. Laurer's canal short, terminates in Juel's organ. Uterus passes towards posterior extremity, forms variable number of loops by alternately descending and ascending before entering anterior region. Eggs small. Vitellarium single, filamentous, longer than ovary, extends on opposite side to ovary, but may cross and reverse sides several times. Excretory duct extends medially through posterior region, usually forms small vesicle at posterior extremity; pore terminal. In tissues of platycephalid fishes; Indo-Pacific Ocean. Type-species *I. madhaviae* Anderson & Cribb, 1994 (syn. *I. platycephali* Madhavi, 1982).[2]

## Tribe Metadidymocystini Pozdnyakov, 1993 (emend.)

**Diagnosis:** Posterior region not divided into trunk and secondary branches with indentations. Ventral sucker present. Testes two, in both regions of body. Type-genus *Metadidymocystis* Yamaguti, 1970.

[2] See Anderson & Cribb (1994) for a key to and discussion of this genus.

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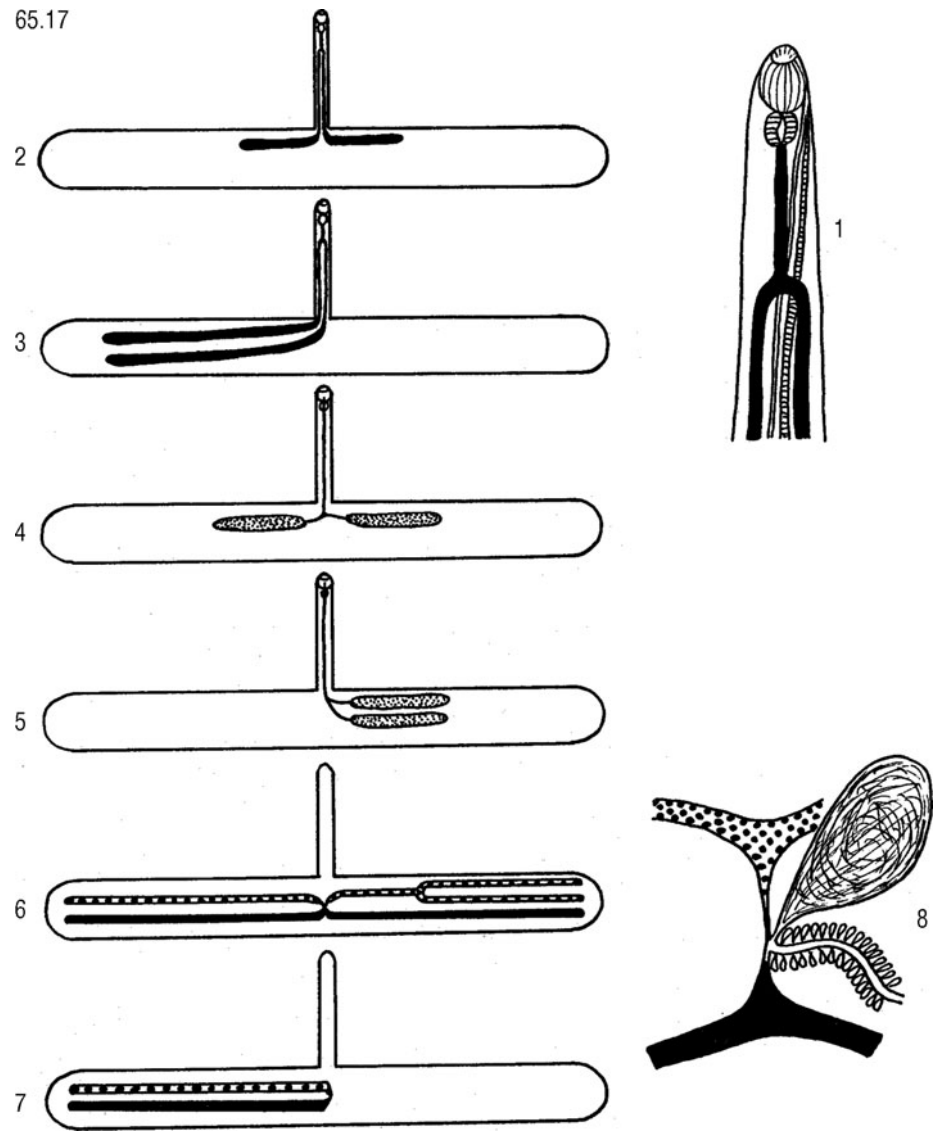



**Fig. 65.17.** *Didymocylindrus* (diagrammatic). 1, Anterior extremity; 2–3, variations in the location of the alimentary system; 4–5, variations in the location of the male reproductive system; 6–7, variations in the location of the female reproductive system; 8, genital junction.

## Key to genera

**1a. Posterior region of body widened and flattened; pharynx present ..... ..... *Metadidymocystis* Yamaguti, 1970. (Fig. 65.19)**
(Syn. *Lampridiydymozoon* Yamaguti, 1971)

**Diagnosis:** Worms encapsulated or not. Capsules fusiform. Anterior region thin, elongate, conical anteriorly, round in cross-section, attached subterminally to posterior region. Posterior region

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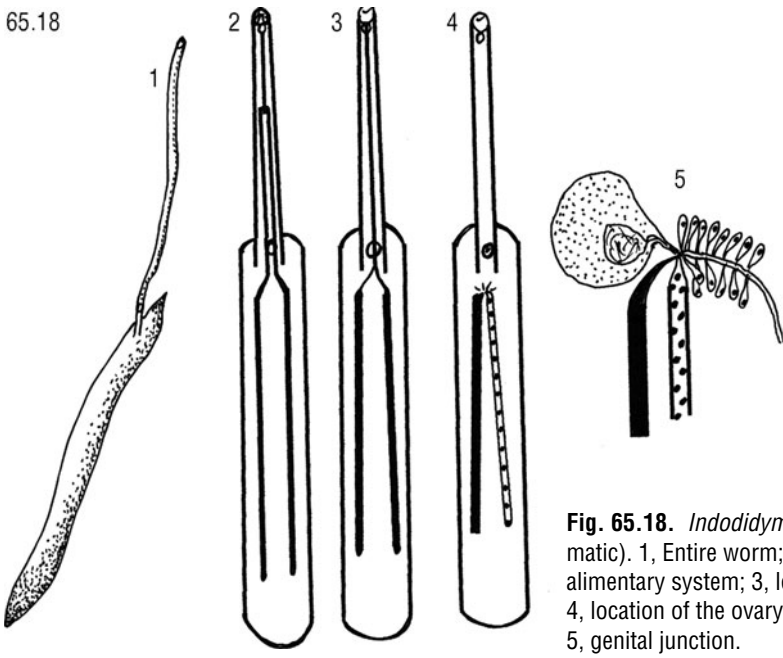



**Fig. 65.18.** *Indodidymozoon* (diagrammatic). 1, Entire worm; 2, location of the alimentary system; 3, location of the testes; 4, location of the ovary and vitellarium; 5, genital junction.

widened and flattened; ventral surface slightly concave; dorsal surface convex. Pharynx present. Oesophagus long, surrounded by gland-cells. Caeca start in anterior half of anterior region and extend to posterior extremity. Ventral sucker present. Testes long, lateral, extend from intestinal bifurcation to close to posterior extremity. Vasa efferentia short. Vas deferens long. Genital junction submedian, at about middle of posterior region. Genital pore at level of oral sucker. Ovary long, unbranched, forms numerous coils in anterior half of posterior region. Mehlis' gland large. Vitellarium unbranched, forms coils in posterior part of posterior region, Excretory system Y-shaped. In tissues (especially muscles) of lamprids (*Lampris*); Pacific and Atlantic Oceans. Type-species *M. cymbiformis* Yamaguti, 1970.

**1b. Posterior region of body not as above; pharynx absent ..... 2.**

**2a. Posterior region of body widened, round in cross-section, sickle-shaped ..... ..... *Neolamprididdymozoon* Wierzbicka, 1980. (Fig. 65.20)**

**Diagnosis:** Capsule spindle-shaped. Anterior region thin, elongate, somewhat widened posteriorly to ventral sucker, shorter than posterior region and attached to it subterminally. Posterior region widened, round in cross-section, elongate, sickle-shaped. Pharynx absent. Oesophagus short, without surrounding gland-cells. Caeca reach close to posterior extremity of posterior region. Ventral sucker present. Testes long, in both regions of body. Genital pore at level of oral sucker. Genital junction at one-third of length of posterior region. Ovary long, thin, unbranched, forms transverse coils in first third of posterior region. Seminal receptacle present. Vitellarium with similar structure to ovary, but in posterior two-thirds of posterior region. Excretory vesicle elongate, bifurcated proximally. In tissues (especially muscles) of lamprids (*Lampris*); Atlantic and Pacific Oceans. Type-species *N. tenuicolle* (Rudolphi, 1819) Wierzbicka, 1980.

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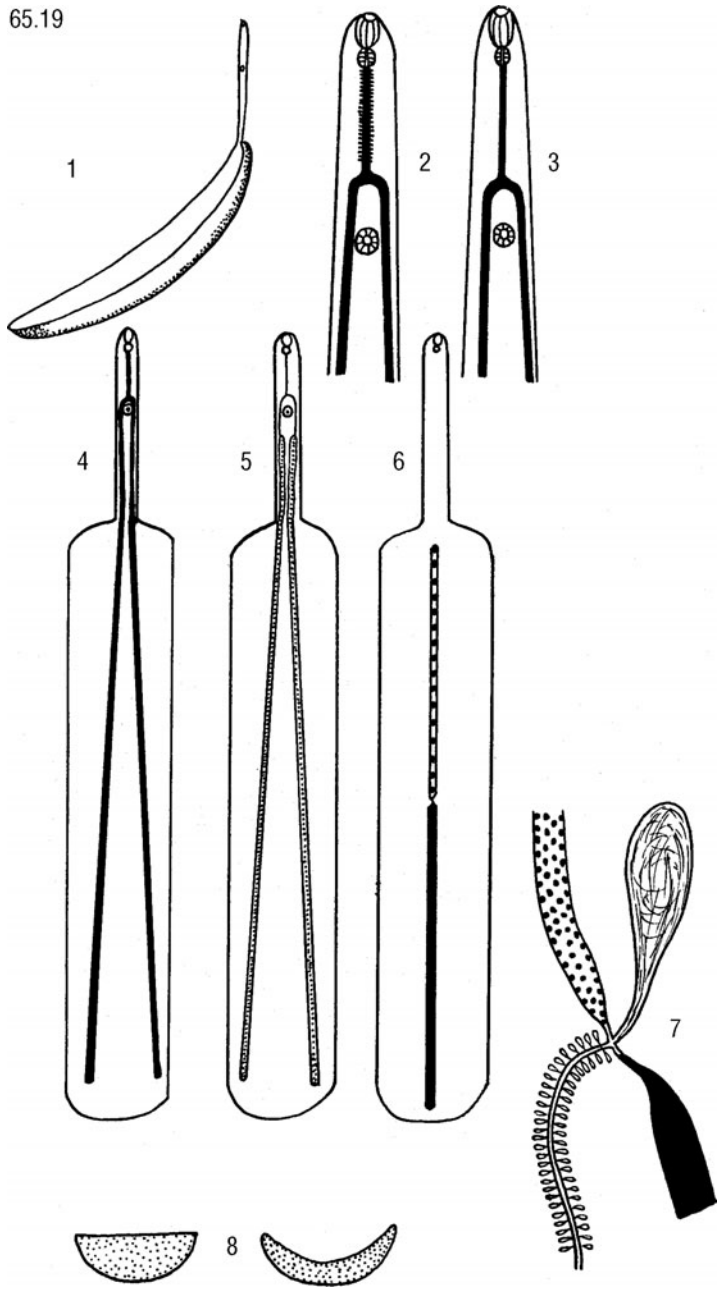



**Fig. 65.19.** *Metadidymocystis* (diagrammatic). 1, Entire worm; 2–3, variations of anterior parts of the alimentary system; 4, location of the alimentary system; 5, location of the testes; 6, location of the ovary and vitellarium; 7, genital junction; 8, cross-section of posterior region.

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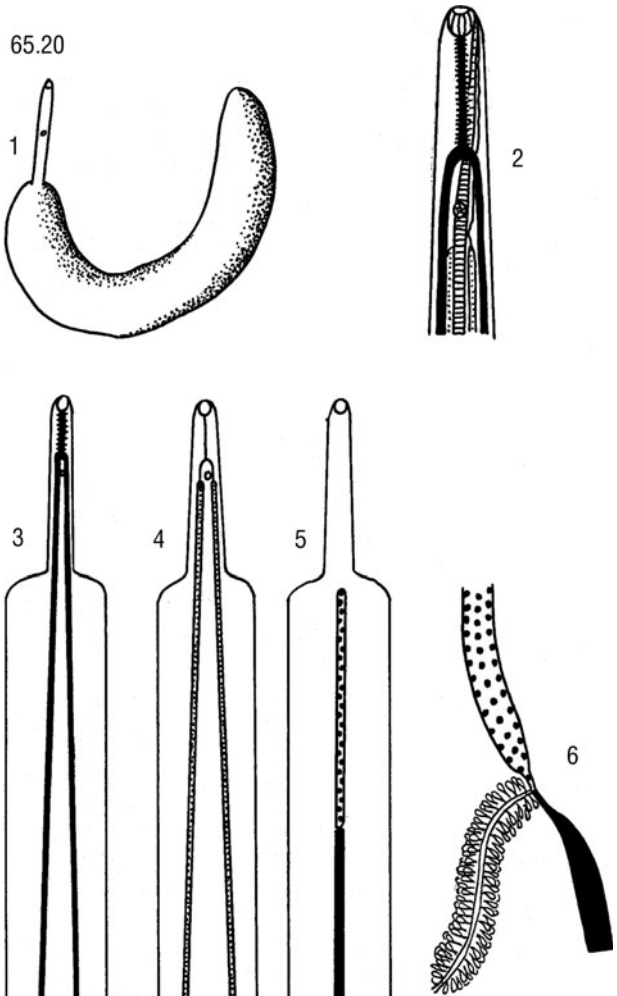



**Fig. 65.20.** *Neolampridídymozoon* (diagrammatic). 1, Entire worm; 2, anterior extremity; 3, location of the alimentary system; 4, location of the testes; 5, location of the ovary and vitellarium; 6, genital junction.

**2b. Posterior region of body with variable shape: cylindrical, flattened laterally or tapered posteriorly, often with numerous tubercles** ..... ..... *Neometadídymozoon* **Yamaguti, 1971. (Fig. 65.21).**
(Syn. *Rhopalotrema* Anderson, 1998)

**Diagnosis:** Capsule cylindrical, globular or spherical. Anterior region elongate, thin, round in cross-section, attached subterminally to posterior region. Posterior region cylindrical, flattened laterally or tapered towards posterior extremity; in mature worms, posterior region may be tubercular due to formation of secondary protrusions and indentations. Pharynx present. Oesophagus long, surrounded by gland-cells. Caeca reach close to posterior extremity. Ventral sucker present. Testes in both regions of body. Genital pore ventral

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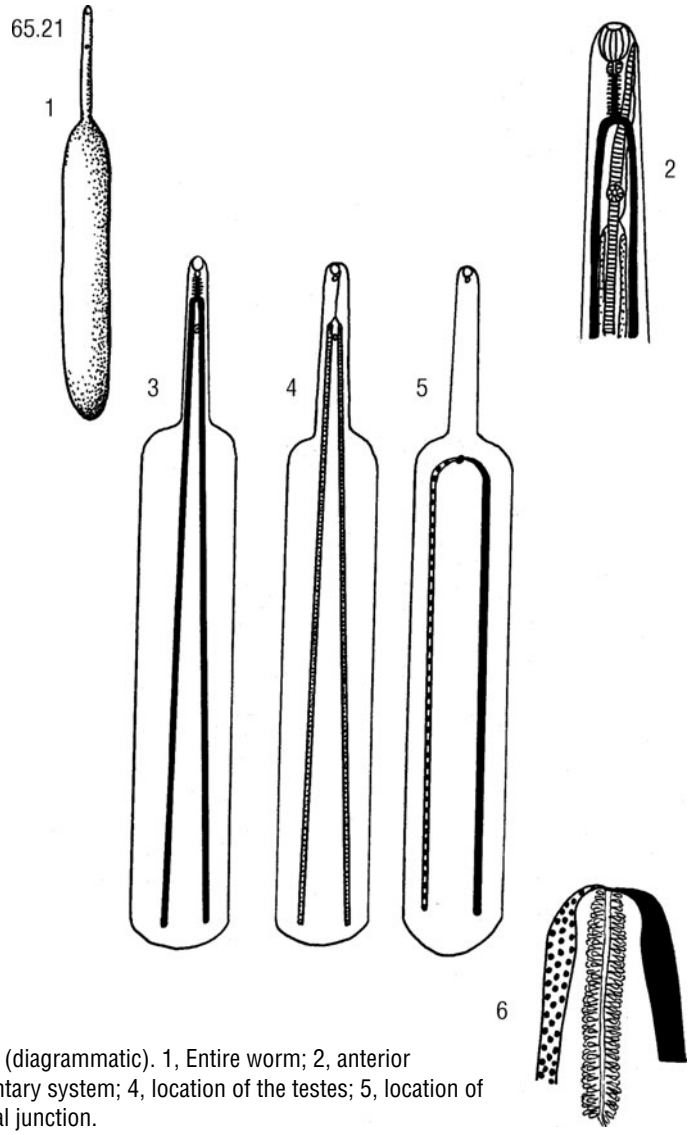



**Fig. 65.21.** *Neometadidymozoon* (diagrammatic). 1, Entire worm; 2, anterior extremity; 3, location of the alimentary system; 4, location of the testes; 5, location of the ovary and vitellarium; 6, genital junction.

to pharynx. Ovary and vitellarium unbranched. Seminal receptacle absent. Mehlis' gland large. Excretory vesicle long, saccular in mature worms. In tissues of priacanthid fishes (*Priacanthus*); Indo-Pacific Ocean. Type-species *N. polymorphis* (Oshmarin & Mamaev, 1963) Yamaguti, 1971.

## Tribe Neodidymozoini Yamaguti, 1970

**Diagnosis:** Posterior region fimbriate, i.e. consisting of central trunk from which arise numerous digitiform protrusions (often branched) and depressions. Ventral sucker usually absent, occasionally present. Testes restricted to posterior region. Type-genus *Neodidymozoon* Yamaguti, 1970.

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## Key to genera

**1a. Trunk of posterior region covered with numerous digitiform protrusions; distinct broad lobes attached to trunk absent ..... *Metadidymozoon* Yamaguti, 1970. (Fig. 65.22)**

**Diagnosis:** Capsule globular; walls with capillary system. Anterior region conical. Posterior region with wide trunk possessing secondary lobes, which end in numerous terminal digitiform protrusions. Oral sucker and pharynx present. Oesophagus short. Caeca narrow. Ventral sucker absent. Testes two, in trunk of posterior region. Genital pore ventral to oral sucker. Ovary unbranched. Ovary and vitellarium mainly in secondary lobes and terminal protrusions. Genital junction at middle of trunk of posterior region. Seminal receptacle absent. Hermaphroditic duct short. Vitellarium branched. Excretory system not known. In gill-arches of istiophorid fishes; Indian and Pacific Oceans. Type-species *M. branchiale* Yamaguti, 1970.

**1b. Trunk of posterior region with broad terminal lobes ..... 2.**

**2a. Anterior region elongate, stout, truncate; ventral sucker present ..... ..... *Neodidymozoon* Yamaguti, 1970. (Fig. 65.23)**

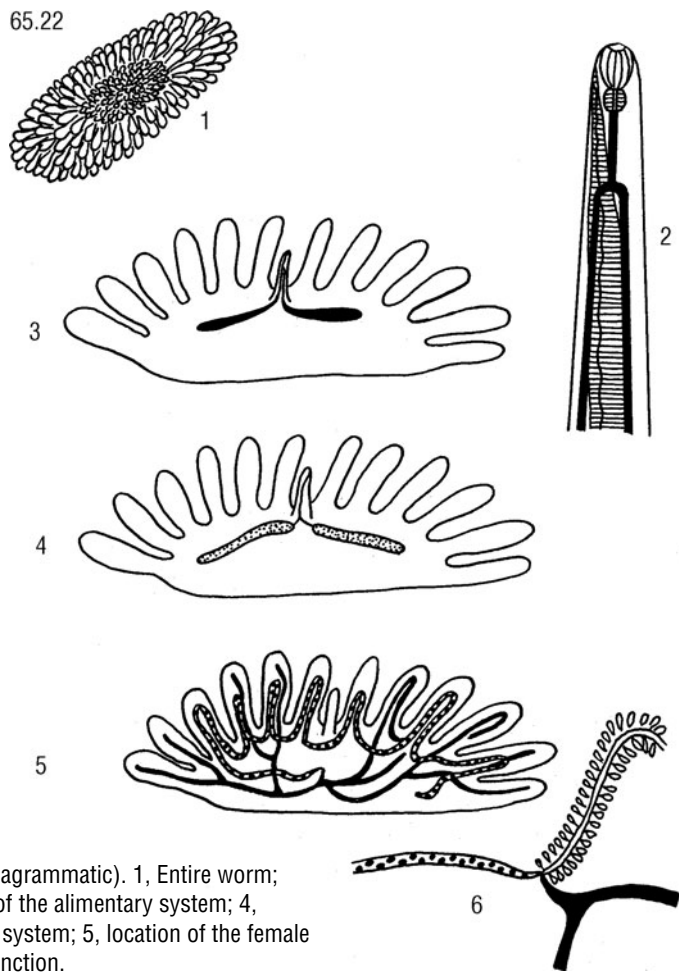



**Fig. 65.22.** *Metadidymozoon* (diagrammatic). 1, Entire worm; 2, anterior extremity; 3, location of the alimentary system; 4, location of the male reproductive system; 5, location of the female reproductive system; 6, genital junction.

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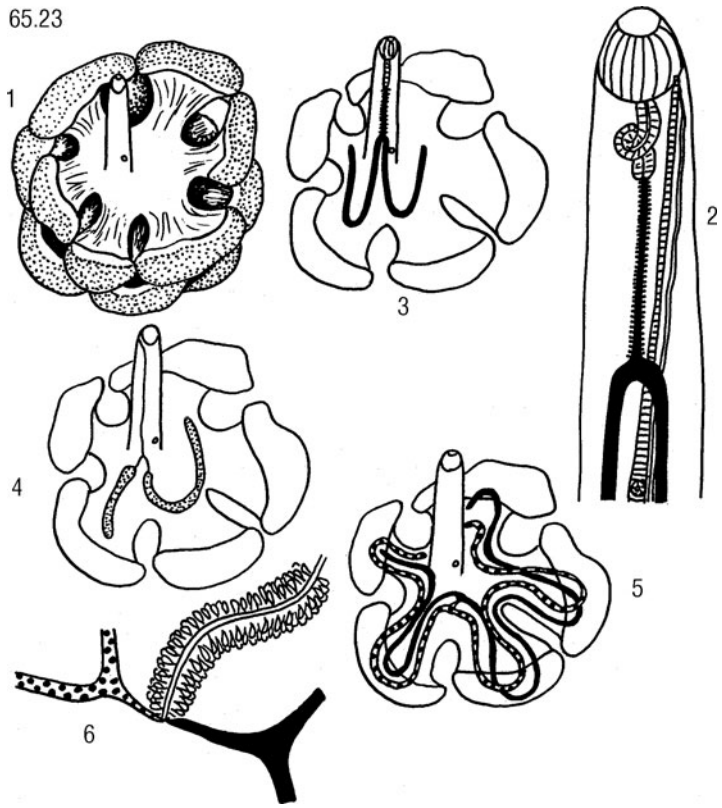



**Fig. 65.23.** *Neodidymozoon* (diagrammatic). 1, Entire worm; 2, anterior extremity; 3, location of the alimentary system; 4, location of the male reproductive system; 5, location of the female reproductive system; 6, genital junction.

**Diagnosis:** Capsule spherical. Anterior region elongate, stout, cylindrical, truncate, attached to middle of trunk of posterior region. Posterior region with trunk bearing number of terminal lobes. Pharynx present. Oesophagus long, reaches posterior region, surrounded by gland-cells. Caeca in trunk of posterior region. Ventral sucker present, on trunk close to junction between two regions of body. Testes long, in trunk part of posterior region. Vasa efferentia short, fusing at junction of two regions. Ejaculatory duct long, passes along entire length of anterior region. Genital pore ventral to oral sucker. Genital junction at centre of trunk of posterior region. Ovary with two branches but without secondary branches; main part forms coils in terminal protrusions. Seminal receptacle present. Mehlis' gland large. Vitellarium with similar structure to ovary. Excretory system not known. In tissues of istiophorid teleosts; Pacific and Indian Oceans. Type-species *N. macrostoma* Yamaguti, 1970.

**2b. Anterior region narrow, conical; ventral sucker absent .....**
**..... *Maccallumtrema* Yamaguti, 1970. (Fig. 65.24)**
(Syns *Makairatrema* Yamaguti, 1970; *Neodidymozooides* Yamaguti, 1970)

**Diagnosis:** Capsule spherical. Anterior region narrow, conical, attached to middle of trunk of posterior region. Trunk of posterior region with numerous lobes which may be subdivided

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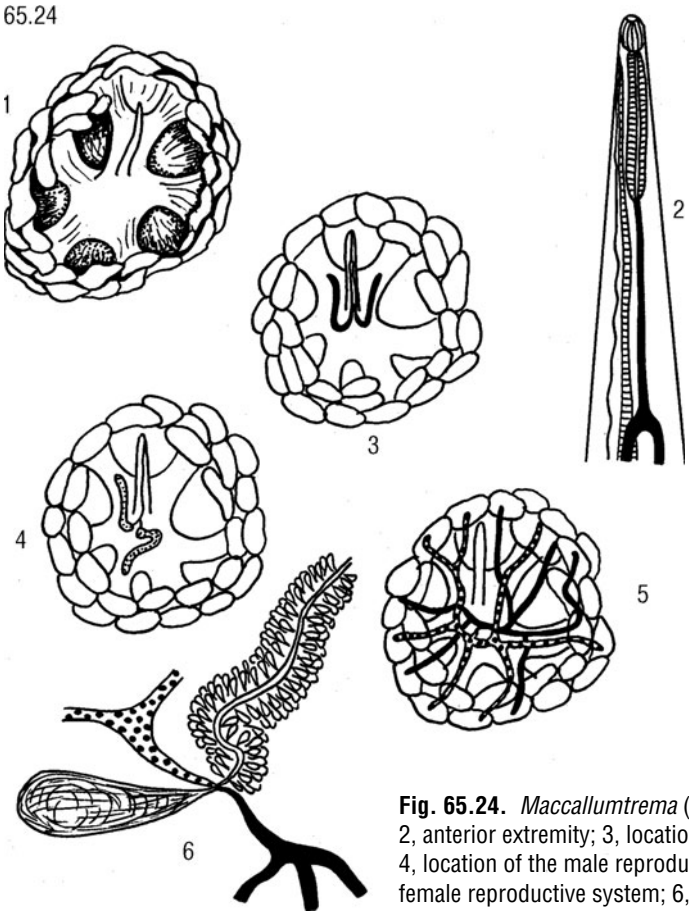



**Fig. 65.24.** *Maccallumtrema* (diagrammatic). 1, Entire worm; 2, anterior extremity; 3, location of the alimentary system; 4, location of the male reproductive system; 5, location of the female reproductive system; 6, genital junction.

terminally. Pharynx substantially larger than oral sucker. Ventral sucker absent. Oesophagus long, devoid of gland-cells. Caeca extend into posterior region. Testes long, elongate, in trunk of posterior region. Genital pore at mid-level of oral sucker. Genital junction at centre of trunk of posterior region. Ovary branched or not; branches mainly in terminal lobes of posterior region. Seminal receptacle present or not. Mehlis' gland large. Vitellarium with similar structure to ovary. Excretory system not known. In tissues of istiophorid and xiphiid teleosts; Pacific and Atlantic Oceans. Type-species *M. xiphiados* (MacCallum & MacCallum, 1916) Yamaguti, 1970.

## Subfamily Didymodiclininae Pozdnyakov, 1993

**Diagnosis:** Sexual dimorphism weakly expressed. Body of both sexes elongate, filiform, round in cross-section. Oral sucker present. Ventral sucker present or absent. Pharynx present. Oesophagus simple, usually long, rarely short. Caeca simple, blind, reach close to posterior extremity. Gland-cells around oesophagus and anterior parts of caeca present or absent. Excretory vesicle Y-shaped. *Male*: Testes two, long, parallel, reach close to posterior extremity. Vasa efferentia short. Ejaculatory duct long. Rudiments of female genital system usually absent, rarely present. *Female*: Genital

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junction at about mid-body. Ovary and vitellarium usually unbranched, rarely branched; ovary in anterior half and vitellarium in posterior half of body. Seminal receptacle present or absent. Uterus long, forms numerous loops. Metraterm well developed. Eggs small, numerous. Type-genus *Didymodiclinus* Pozdnyakov, 1993.

## Key to genera

**1a. Ventral sucker present** ..... ***Didymodiclinus*** **Pozdnyakov, 1993. (Fig. 65.25)**
**Diagnosis:** Encapsulated or not. Body filiform, long. Ventral sucker present. Oesophagus simple, long or short. Caeca reach close to posterior extremity. Gland-cells around oesophagus and anterior parts of caeca present or absent. *Male*: Smaller than female. Testes two, parallel, reach close to posterior extremity. Rudiments of female genital system absent. *Female*: Larger than male. Genital junction approximately at mid-body. Ovary long, narrow, curved, in anterior half of body. Seminal receptacle present or absent. Vitellarium similar to ovary in form, in posterior half of body. In tissues of wide range of perciform and occasionally beloniform fishes (e.g. serranids, exoecetids); Indian, Atlantic and Pacific Oceans. Type-species *D. pacificus* (Yamaguti, 1938) Pozdnyakov, 1993.

**1b. Ventral sucker absent** ..... ***Paragonapodasmius*** **Yamaguti, 1938. (Fig. 65.26)**
**Diagnosis:** Not encapsulated. Body elongate, filiform. Ventral sucker absent. Pharynx present. Oesophagus long, narrow, rarely short. Caeca reach close to posterior extremity. Gland-cells around anterior parts of caeca present or absent. *Male*: Smaller than female. Testes curved, long, reach close to posterior extremity or not. Rudiments of female genital system present or absent. *Female*: Ovary long, unbranched, in anterior half of body. Seminal receptacle present. Vitellarium similar in form to ovary, in posterior half of body. In wide range of perciform and occasionally scorpaeniform fishes; Pacific Ocean. Type-species *P. managatuwo* Yamaguti, 1938.

## Subfamily Gonapodasmiinae Ishii, 1935[3]

(Syns Annulocystiinae Yamaguti, 1970; Colocyntotrematinae Yamaguti, 1958; Didymocodiinae Yamaguti, 1970; Neodiplotrematinae Yamaguti, 1958; Opepherocystiinae Yamaguti, 1970; Opepherotrematinae Yamaguti, 1958; Osteodidymocodiinae Yamaguti, 1970; Phacelotrematinae Yamaguti, 1971; Pseudocolocyntotrematinae Yamaguti, 1970; Reniforminae Yamaguti, 1970)

**Diagnosis:** Worms in capsule fused, but with anterior regions free; degree of fusion of posterior regions varies from fusion at one end only to full union of two or more individuals. Ventral sucker absent. Pharynx present. Oesophagus long. Caeca extend into posterior region. Gland-cells around oesophagus present or absent. Testes elongate or compact, unbranched or, rarely, branched, one or two in each individual. Ovary and vitellarium branched or not. Seminal receptacle present or absent. Mehlis' gland well developed. Excretory vesicle tubular, rarely saccular. Type-genus *Gonapodasmius* Ishii, 1935.

[3] His reinterpretation of some of the main features of *Gonapodasmius* enabled Pozdnyakov (1996) to transfer this genus to this subfamily, which he called the Neodiplotrematinae; however, the family-group name based on *Gonapodasmius* itself has priority. Note that the concept of this subfamily used here is quite different from that of Yamaguti (1971).

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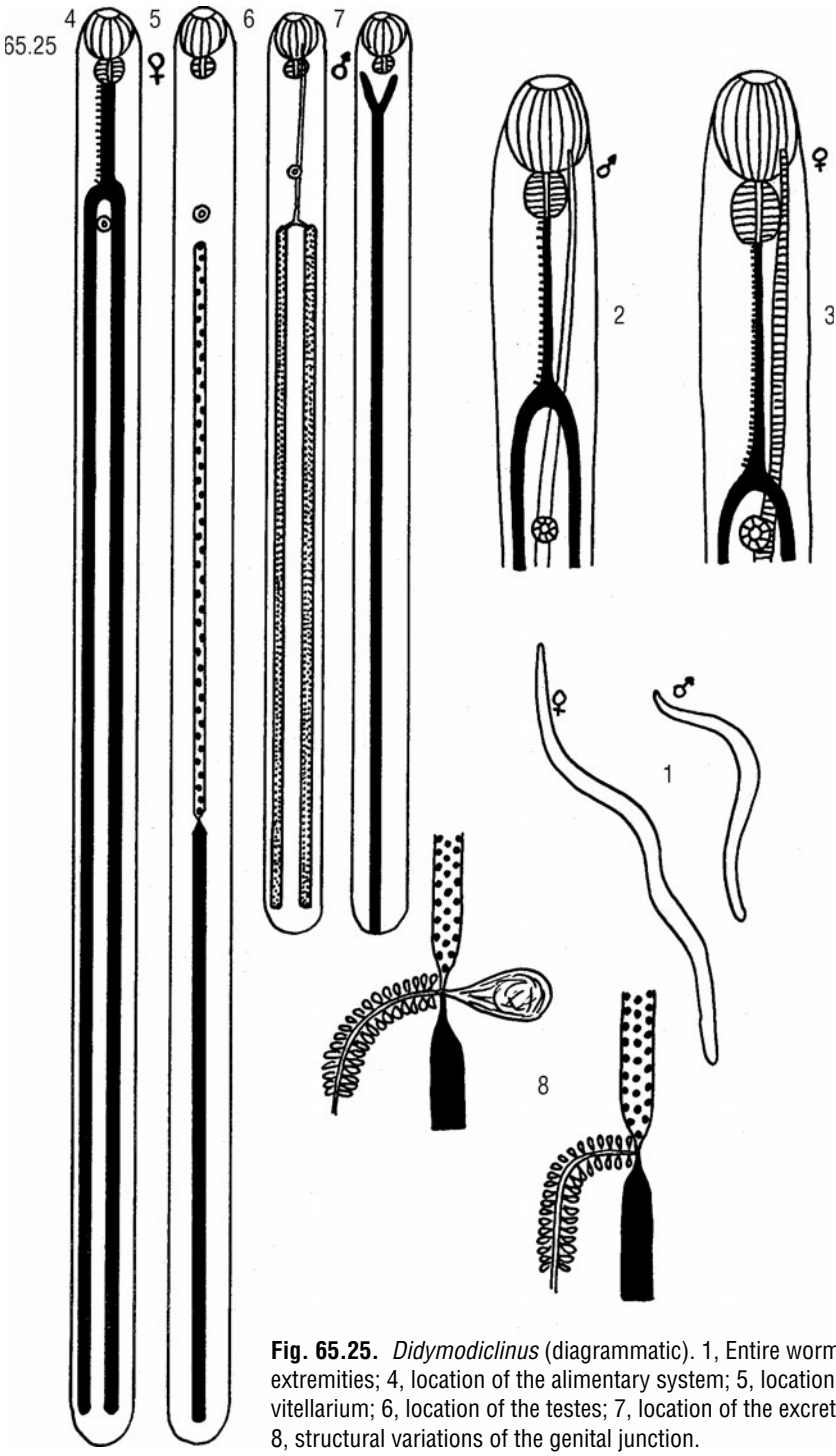



**Fig. 65.25.** *Didymodiclinus* (diagrammatic). 1, Entire worms; 2–3, anterior extremities; 4, location of the alimentary system; 5, location of the ovary and vitellarium; 6, location of the testes; 7, location of the excretory vesicle; 8, structural variations of the genital junction.

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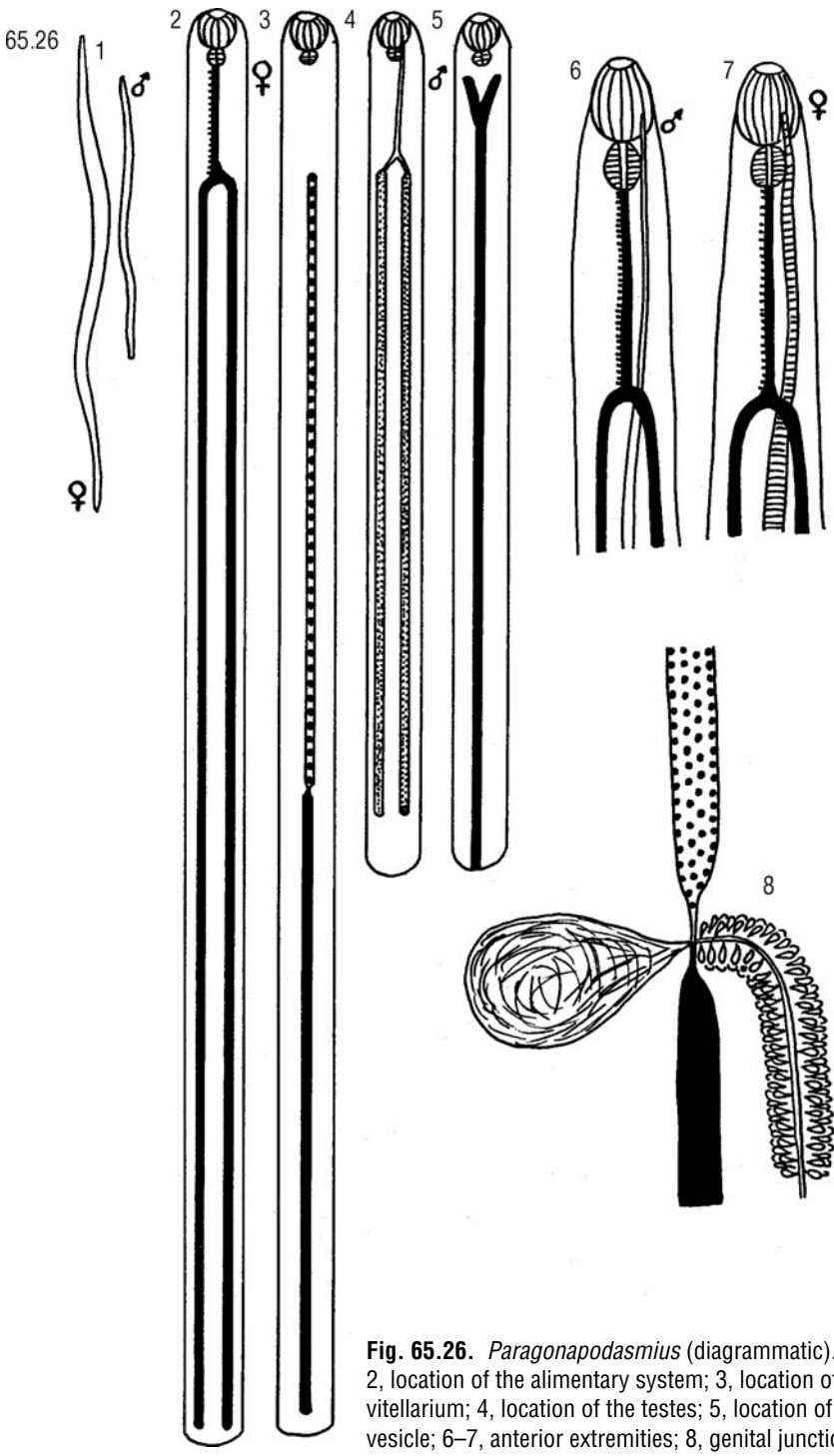



**Fig. 65.26.** *Paragonapodasmius* (diagrammatic). 1, Entire worms; 2, location of the alimentary system; 3, location of the ovary and vitellarium; 4, location of the testes; 5, location of the excretory vesicle; 6–7, anterior extremities; 8, genital junction.

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## Key to tribes

**1a. Individuals not entirely fused; anterior regions free, attached to non-fused parts of posterior region, which is often lobed ..... Gonapodasmiini Ishii, 1935.**
**1b. Individuals completely fused; anterior regions in special cavity and emerge from common opening on fused posterior region, which is usually globular ..... ..... Colocyntotrematini Yamaguti, 1958.**

## Tribe Gonapodasmiini Ishii, 1935[4]

(Syn. Neodiplotrematini Yamaguti, 1970 *sensu* Pozdnyakov (1996))

**Diagnosis:** Posterior regions of body not entirely fused, often lobed. Anterior regions not attached to posterior region through common atrium in fused posterior regions. Type-genus *Gonapodasmius* Ishii, 1935.

## Key to genera

**1a. Each of fused individuals possesses two testes ..... 2.**
**1b. Each of fused individuals possesses one testis ..... 5.**

**2a. Posterior region not divided into numerous tubular protrusions ..... 3.**
**2a. Posterior region divided into numerous tubular protrusions ..... ..... *Gonapodasmius* Ishii, 1935.[5] (Fig. 65.27)**
(Syn. *Reniforma* Yamaguti, 1970)

**Diagnosis:** Capsule spherical. Capillary net in capsule tissue present. Anterior regions elongate, round in cross-section, tapering anteriorly, slightly separated from each other. Posterior regions consist of numerous long spiral tubular protrusions, which end blindly; latter fuse in centre, forming short, well-developed trunk region; fibrous material arising from capsule may fill some spaces between tubular prostrusions. Oesophagus short. Caeca reach posterior region. Gland-cells around oesophagus present or absent. Two testes in each fused individual, in small tubular protrusions close to trunk part of posterior region. Genital pore ventral to pharynx. Both genital junctions in trunk part. Ovary and vitellarium branched. Mehlis' gland large. Seminal receptacle absent. Excretory system Y-shaped, bifurcates close to intestinal bifurcation. In gill tissues of wide range of teleosts (e.g. haemulids, polyprionids, serranids, priacanthids); Atlantic and Pacific Oceans. Type-species *G. haemuli* (MacCallum & MacCallum, 1916) Ishii, 1935.

**3a. Posterior regions fused at one end ..... 4.**

[4] His reinterpretation of some of the main features of *Gonapodasmius* enabled Pozdnyakov (1996) to transfer this genus to this tribe, which he called the Neodiplotrematini; however, the family-group name based on *Gonapodasmius* itself has priority.

[5] The interpretation of some of the main features of this genus is quite different from that of Yamaguti (1971) and is based on a redescription of the type-species by Pozdnyakov (1996).

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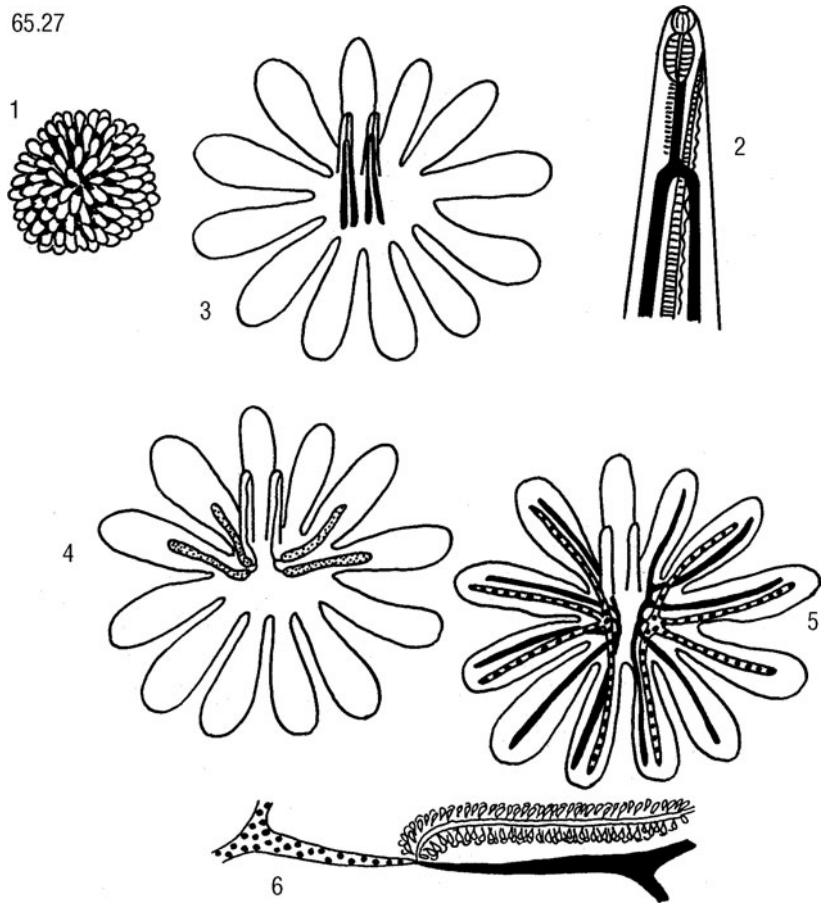



**Fig. 65.27.** *Gonapodasmius* (diagrammatic). 1, Entire worms; 2, anterior extremity; 3, location of the alimentary system; 4, location of the testes; 5, location of the ovaries and vitellaria; 6, genital junction.

**3b. Posterior regions fused only at their anterior and posterior ends, forming ring ..... ..... *Annulocystis* Yamaguti, 1970. (Fig. 65.28)**
(Syn. *Univitellannulocystis* Yamaguti, 1970)

**Diagnosis:** Capsule elongate, moniliform, containing two or three fused individuals, rarely single individual with fused anterior and posterior parts of posterior region, forming ring. Anterior region narrow, elongate, with slightly widened anterior third. Fused posterior regions form ring with regularly alternating diverticula on its outer margin; outer margin in young individuals without diverticula. Oesophagus short. Caeca reach posterior region. Testes two, in posterior region, parallel, at junction of anterior and posterior regions. Vasa efferentia short. Ejaculatory duct long. Genital pore ventral to oral sucker. Genital junction usually in centre of posterior region. Ovary with two branches. Mehlis' gland large. Seminal receptacle present or absent. Vitellarium simple or with two branches. Excretory system not known. In tissues of scombrid fishes (*Auxis* and *Katsuwonus*); Pacific and Atlantic Oceans. Type-species *A. auxis* Yamaguti, 1970.

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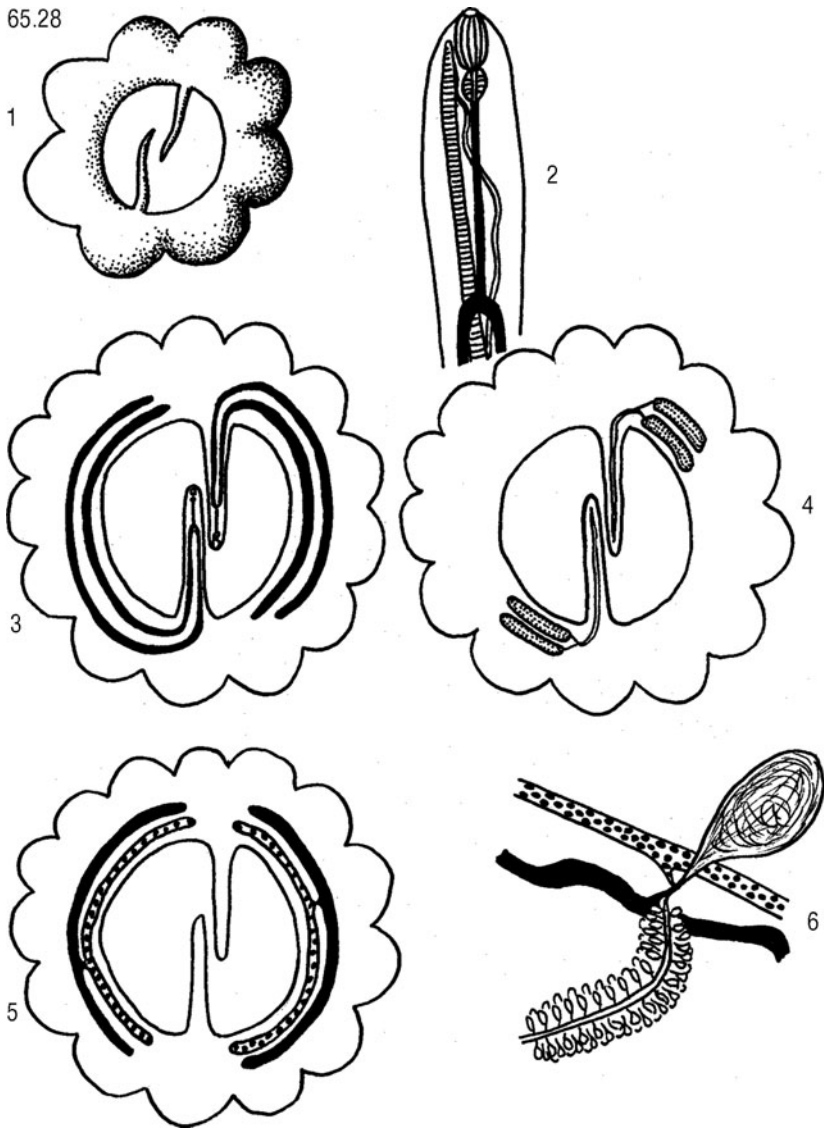



**Fig. 65.28.** *Annulocystis* (diagrammatic). 1, Entire worms; 2, anterior extremity; 3, location of the alimentary system; 4, location of the testes; 5, location of the ovaries and vitellaria; 6, genital junction.

**4a. Posterior region without protruding terminal lobes** ..... ..... ***Neodiplotrema*** **Yamaguti, 1938. (Fig. 65.29)**
(Syn. *Diplotrema* Yamaguti, 1938 *nec* Spenser, 1900)

**Diagnosis:** Capsule spindle-shaped. Anterior region long, thin, attached to middle of flattened side of posterior region. Posterior region elongate, hemispherical in cross-section, with one flat side. Posterior regions fused at one end only; body at fusion round in cross-section. Oesophagus short. Caeca directed towards non-fused ends of posterior region. Testes two, in

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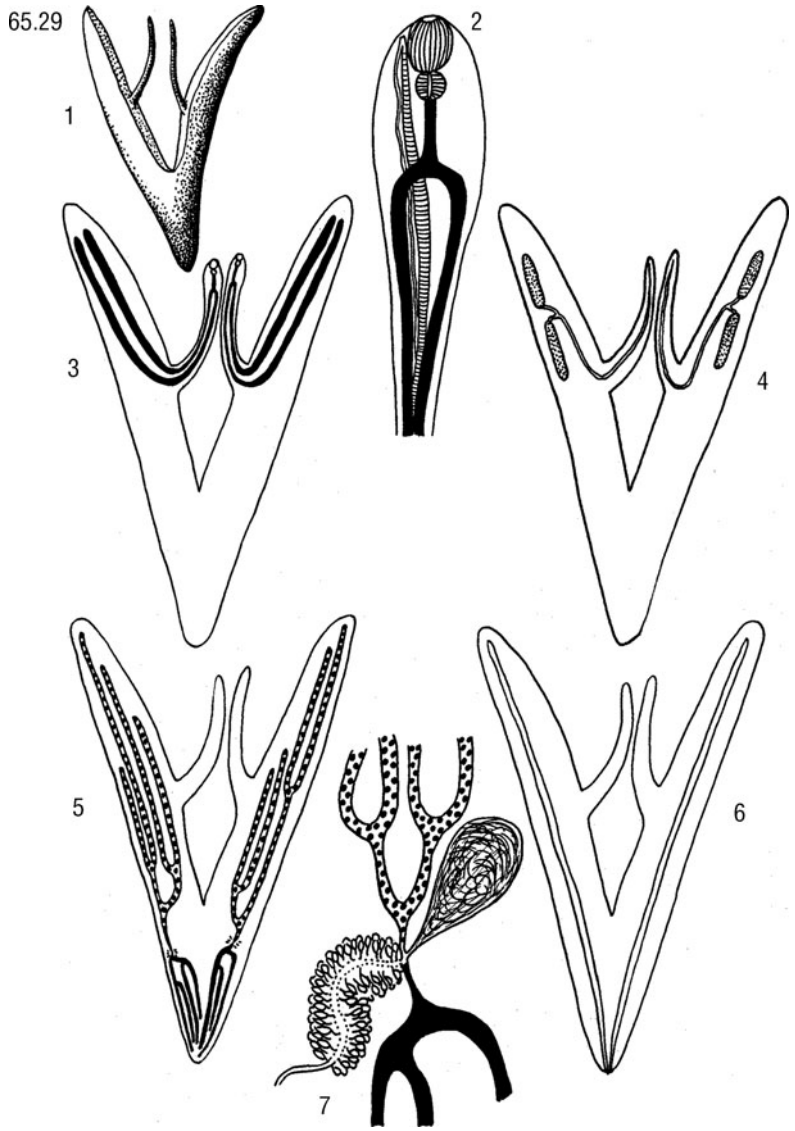



**Fig. 65.29.** *Neodiplotrema* (diagrammatic). 1, Entire worms; 2, anterior extremity; 3, location of the alimentary system; 4, location of the testes; 5, location of the ovary and vitellarium; 6, location of the excretory vesicles; 7, genital junction.

posterior region, shifted towards non-fused ends. Vasa efferentia short. Vas deferens long. Genital pore at level of oral sucker. Ovary branched, lies along entire length of posterior region. Seminal receptacle present. Vitellarium branched, confined to fused part of body. Excretory vesicle elongate, long; terminal parts of excretory vesicles of paired individuals fused. In gill tissues of scombrids (*Katsuwonus*); Pacific Ocean. Type-species *N. pelamidis* (Yamaguti, 1938) Yamaguti, 1970.

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**4b. Posterior region with protruding terminal lobes .....**
**..... *Syncorpozoum* Ku & Shen, 1965. (Fig. 65.30)**

**Diagnosis:** Capsule lobate. Anterior regions elongate, narrow; posterior regions broad, elongate, with posterior halves fused; margins of posterior body folded, forming numerous small lobes. Ventral sucker absent. Pharynx present. Oesophagus relatively long. Caeca said to be wider in anterior part of body. Testes two, tubular, short, in anterior region of posterior part of body close to base of anterior body. Genital pore ventral to oral sucker. Ovary and vitellarium tubular, unbranched, coiled, extend throughout length of fused and separate regions of posterior part of body. Seminal receptacle present. Excretory system not known. In branchial chambers of priacanthids (*Priacanthus*); South China Sea. Type-species *S. hainanense* Ku & Shen, 1965.

**5a. Posterior region without protruding terminal lobes; 'vestibular cavity' present .....**
**..... *Opepherocystis* Yamaguti, 1970. (Fig. 65.31)**

**Diagnosis:** Capsule globular. Anterior regions elongate, at some distance from each other. Posterior region spherical, contains 'vestibular cavity', which opens mid-ventrally via 'vestibular canal'. Oesophagus short. Caeca reach posterior region, where they are greatly enlarged. Testes elongate, long, one in each fused individual. Genital pore ventral to oral sucker. Ovary and vitellarium

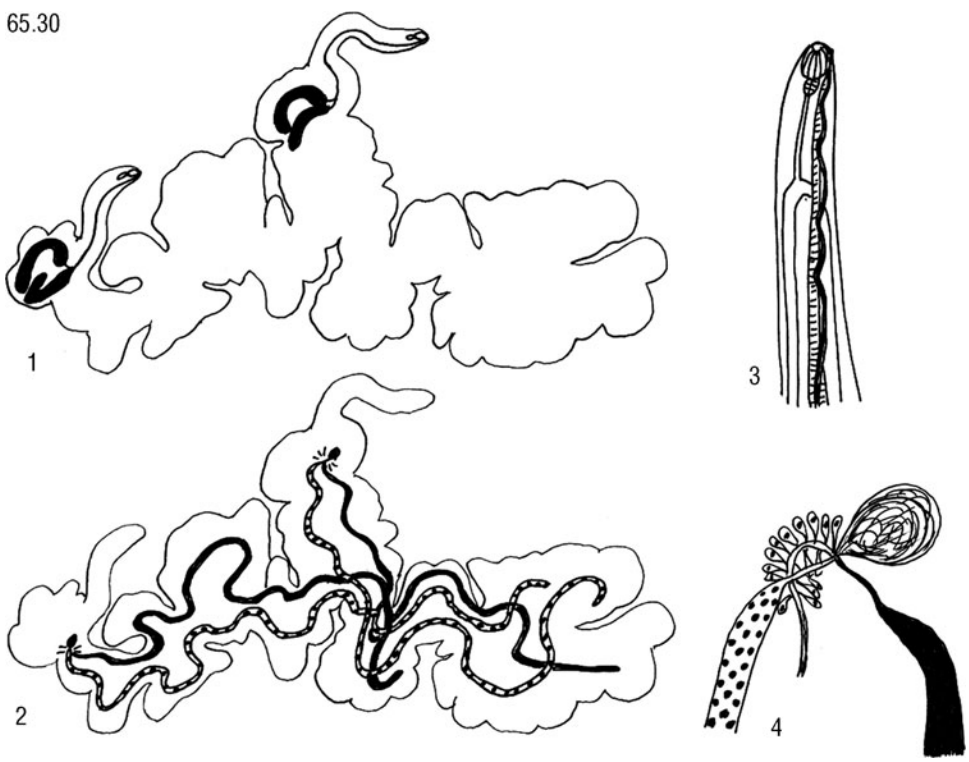



**Fig. 65.30.** *Syncorpozoum* (diagrammatic). 1, Location of the testes; 2, location of the ovaries and vitellaria; 3, anterior extremity; 4, genital junction.

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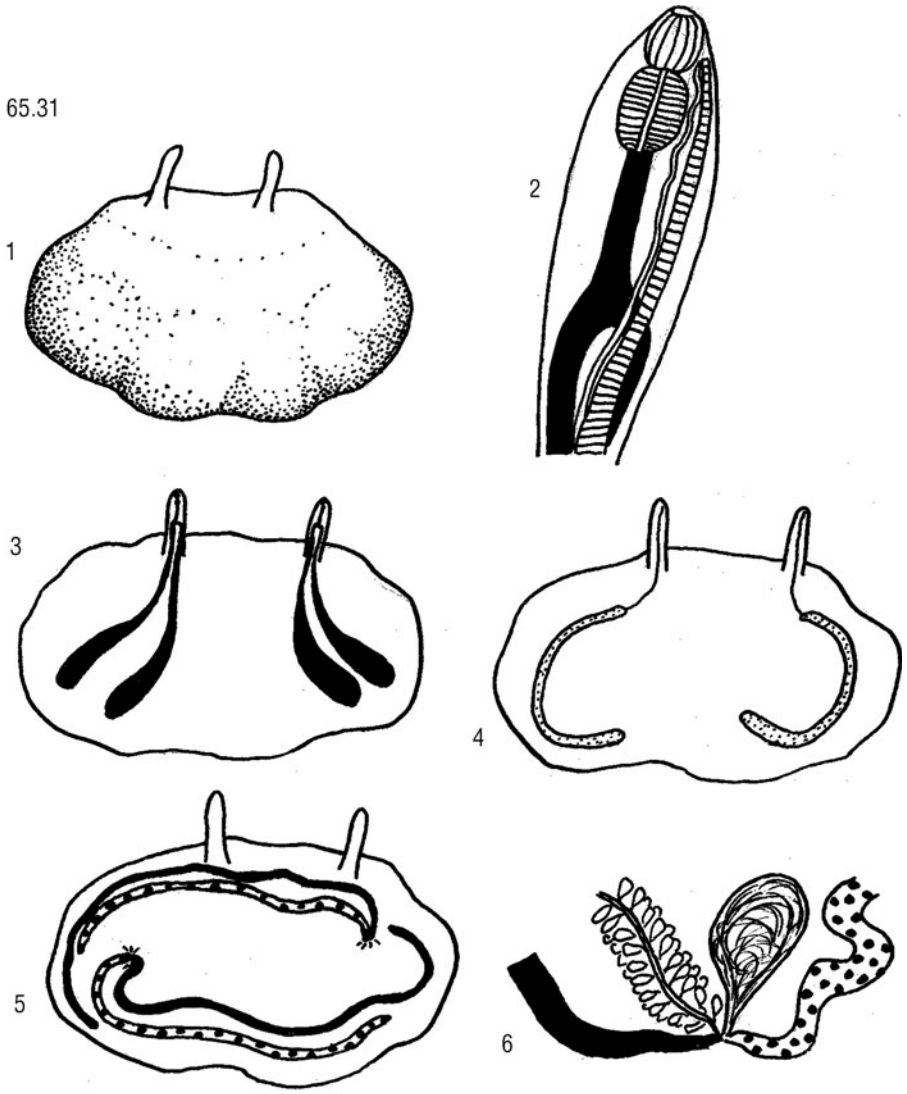



**Fig. 65.31.** *Opepherocystis* (diagrammatic). 1, Entire worms; 2, anterior extremity; 3, location of the alimentary system; 4, location of the testes; 5, location of the ovaries and vitellaria; 6, genital junction.

unbranched. Seminal receptacle present. Excretory system not known. In wall of pyloric caeca of scombrids (*Euthynnus*); Pacific Ocean. Type-species *O. kawakawa* Yamaguti, 1970.[6]

**5b. Posterior region with protruding terminal lobes; 'vestibular cavity' absent ..... ..... *Allodidymocodium* Yamaguti, 1970. (Fig. 65.32)**
(Syn. *Osteodidymocodium* Yamaguti, 1970)

[6] Pozdnyakov (1996, p. 100) also lists this taxon as a species of *Allodidymocodium*.

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**Diagnosis:** Capsule flattened. Capillary network present in capsule tissue. Anterior regions elongate, well separated from each other. Posterior regions consist of central part and irregularly located terminal lobes; 'vestibular cavity' absent. Oesophagus long. Caeca reach posterior region. One long testis in each fused individual, present in central part of posterior region and extending into terminal lobes. Genital pore ventral to oral sucker. Ovary and vitellarium unbranched. Seminal receptacle absent. Excretory system not known. In gut-wall and head of scombrids (*Euthynnus*); Pacific Ocean. Type-species *A. unitubulare* Yamaguti, 1970.

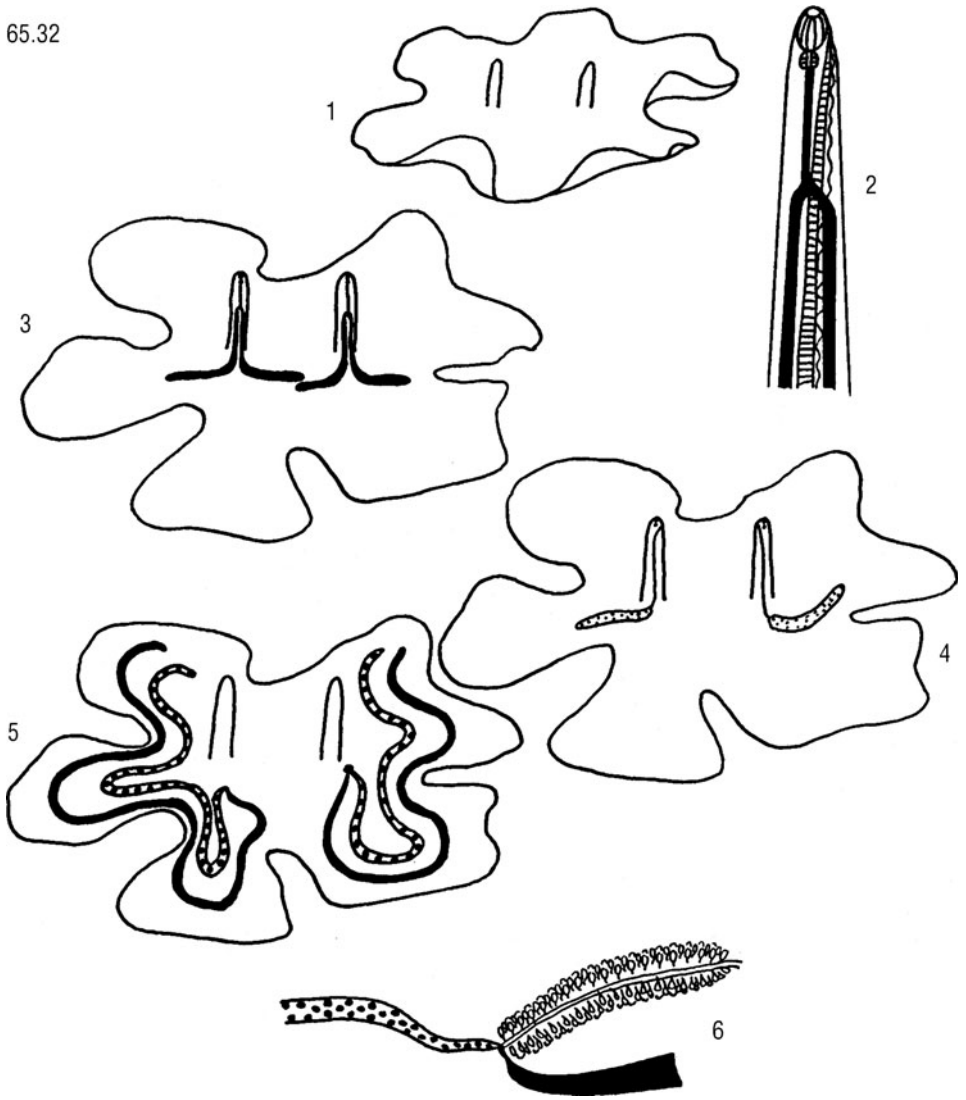



**Fig. 65.32.** *Allodidymocodium* (diagrammatic). 1, Entire worms; 2, anterior extremity; 3, location of the alimentary system; 4, location of the testes; 5, location of the ovaries and vitellaria; 6, genital junction.

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## Tribe Colocyntotrematini Yamaguti, 1958

**Diagnosis:** Posterior regions completely fused. Anterior regions emerge from common atrium in fused posterior regions of body. Type-genus *Colocyntotrema* Yamaguti, 1951.

## Key to genera

**1a. One testis in each fused individual; posterior region disc-like ..... ..... *Opepherotrema* Yamaguti, 1951. (Fig. 65.33)**

**Diagnosis:** Capsule disc-like. Anterior regions elongate, round in cross-section. Posterior region disc-like, with opening in its centre, leading to cavity where junction of anterior and posterior regions is located. Oesophagus thin, short. Caeca reach posterior region. One testis in each individual, in posterior region, close to junction with anterior region. Genital pore ventral to oral sucker. Ovary and vitellarium unbranched. Seminal receptacle absent. Excretory system not known. In gut-wall (pyloric caeca) of scombrids (*Auxis*); Pacific Ocean. Type-species *O. planum* Yamaguti, 1951.

**1b. Two testes in each fused individual; posterior region not disc-like ..... 2.**

**2a. Posterior region branched; testes branched ..... ..... *Didymocodium* Yamaguti, 1970. (Fig. 65.34)**

**Diagnosis:** Capsule round. Capillary network present in capsule. Anterior regions elongate, long, slightly widened anteriorly. Fused posterior regions branched; their terminal lobes are flattened and divided into secondary and tertiary lobes. Oesophagus long. Caeca extend into posterior region. Each fused individual with pair of branched testes; testes form two sub-symmetrical groups of four or five lobes in centre of posterior region. Vasa efferentia short; ejaculatory duct long. Genital pore at level of pharynx. Genital junctions opposite, in centre of posterior region. Ovary and vitellarium branched. Seminal receptacle present. Mehlis' gland large. Excretory vesicles Y-shaped, reach close to anterior extremity. Gut-wall (pyloric caeca) of scombrids (*Euthynnus, Auxis*); Pacific and Indian Oceans. Type-species *D. euthynni* Yamaguti, 1970.

**2b. Posterior region unbranched; testes unbranched ..... 3.**

**3a. Posterior region with dome-shaped protrusion on its terminal part or with terminal disc ..... 4.**

**3b. Posterior region globular, without dome-shaped protrusion terminally ..... ..... *Didymosphaera* Mamaev, 1968. (Fig. 65.35)**

(Syns *Opepherotrematoides* Yamaguti, 1970; *Triplocystoides* Yamaguti, 1970)

**Diagnosis:** Capsule spherical. Two or three individuals fused in capsule. Anterior regions free, long, round in cross-section or flattened, widened in anterior third, in cylindrical canal representing invaginated anterior part of body. Posterior regions fused, globular. Internal organs in periphery of posterior region. Oesophagus short. Caeca extend into posterior region. Two testes in each fused individual. Vasa efferentia short; ejaculatory duct long. Genital pore at level of oral sucker. Ovary and vitellarium branched. Mehlis' gland more or less well developed. Seminal receptacle present. Saccular excretory vesicles occupy central area of fused posterior region. In body-cavity (especially among pyloric caeca) of scombrids (*Auxis*, *Euthynnus*); Pacific and Indian Oceans. Type-species *D. mirabilis* Mamaev, 1968.

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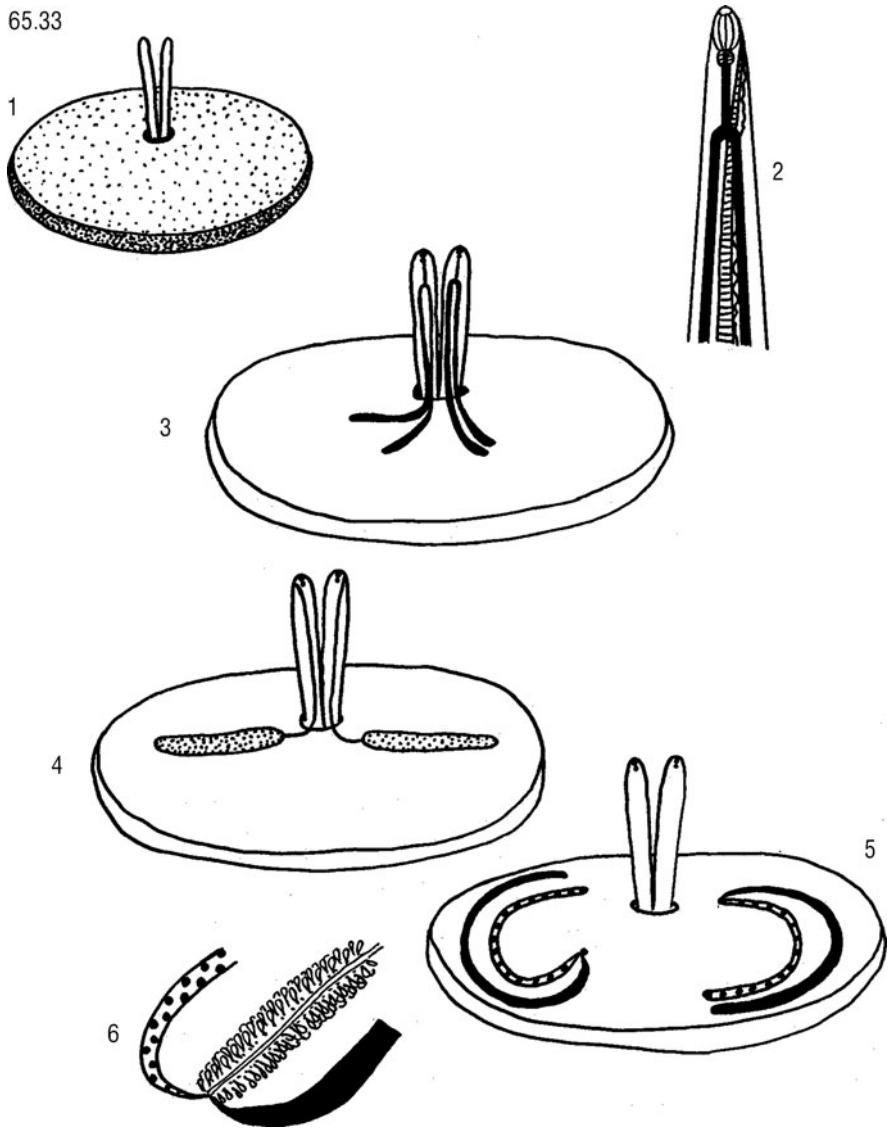



**Fig. 65.33.** *Opepherotrema* (diagrammatic). 1, Entire worms; 2, anterior extremity; 3, location of the alimentary system; 4, location of the testes; 5, location of the ovaries and vitellaria; 6, genital junction.

**4a. Posterior region of body spherical** ..... **5.**
**4b. Posterior region of body not spherical** ..... **6.**

**5a. Posterior region of body with longitudinal furrows** .....
..... *Colocyntotrema* **Yamaguti, 1951. (Fig. 65.36)**

**Diagnosis:** Capsule spherical, with transverse furrows. Anterior regions elongate and widened at anterior extremity, attached to aperture in posterior region. Posterior region spherical,

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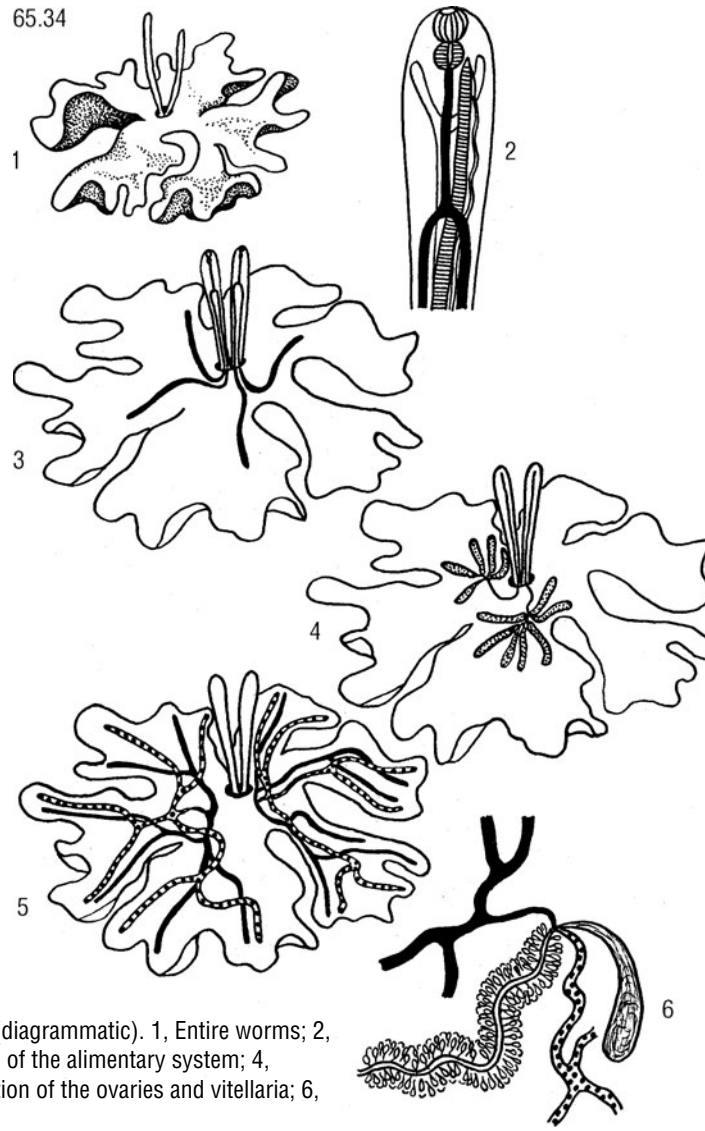



**Fig. 65.34.** *Didymocodium* (diagrammatic). 1, Entire worms; 2, anterior extremity; 3, location of the alimentary system; 4, location of the testes; 5, location of the ovaries and vitellaria; 6, genital junction.

with longitudinal furrows giving impression that it is lobed; each lobe divided anteriorly by additional furrow at about one-quarter of its length, thus forming secondary lobes; posterior part of posterior region possesses more or less developed dome-like protrusion. Oesophagus short. Caeca extend into posterior region. Testes two in each fused individual; shape very diverse, varying from shapeless mass to spherical. Genital pore ventral to oral sucker. Ovary and vitellarium branched, peripheral in posterior region. Seminal receptacle present. Excretory vesicles within dome-like protrusion. In gut-wall (especially pyloric caeca) of scombrids (*Auxis*) and istiophorids; Pacific, Indian and Atlantic Oceans. Type-species *C. auxis* Yamaguti, 1951.

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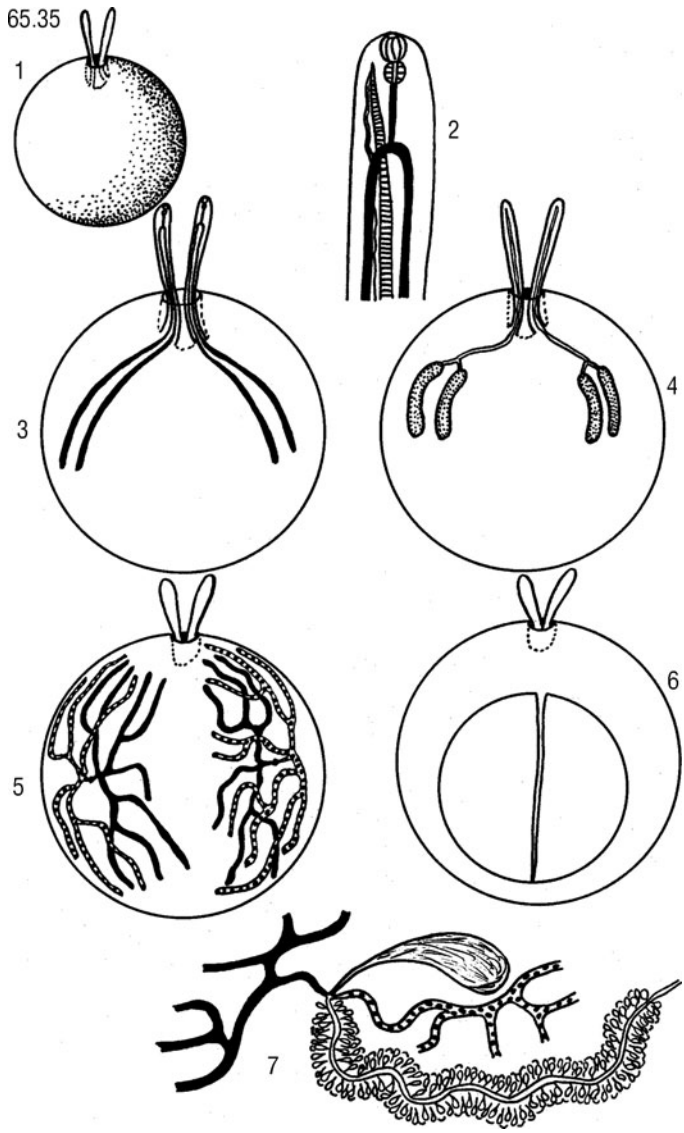



**Fig. 65.35.** *Didymosphaera* (diagrammatic). 1, Entire worms; 2, anterior extremity; 3, location of the alimentary system; 4, location of the testes; 5, location of the ovaries and vitellaria; 6, location of the excretory vesicles; 7, genital junction.

**5b. Posterior region of body without longitudinal furrows** ..... ..... ***Pseudocolocyntotrema*** **Yamaguti, 1970. (Fig. 65.37)**

**Diagnosis:** Capsule spherical. Anterior regions narrow, elongate, slightly widened anteriorly, round in cross-section, attached to cavity in posterior region, where they can invaginate. Fused posterior regions spherical. Oesophagus long. Caeca reach posterior region. Two testes in each fused individual. Vasa efferentia short; ejaculatory duct long. Genital pore at level of pharynx.

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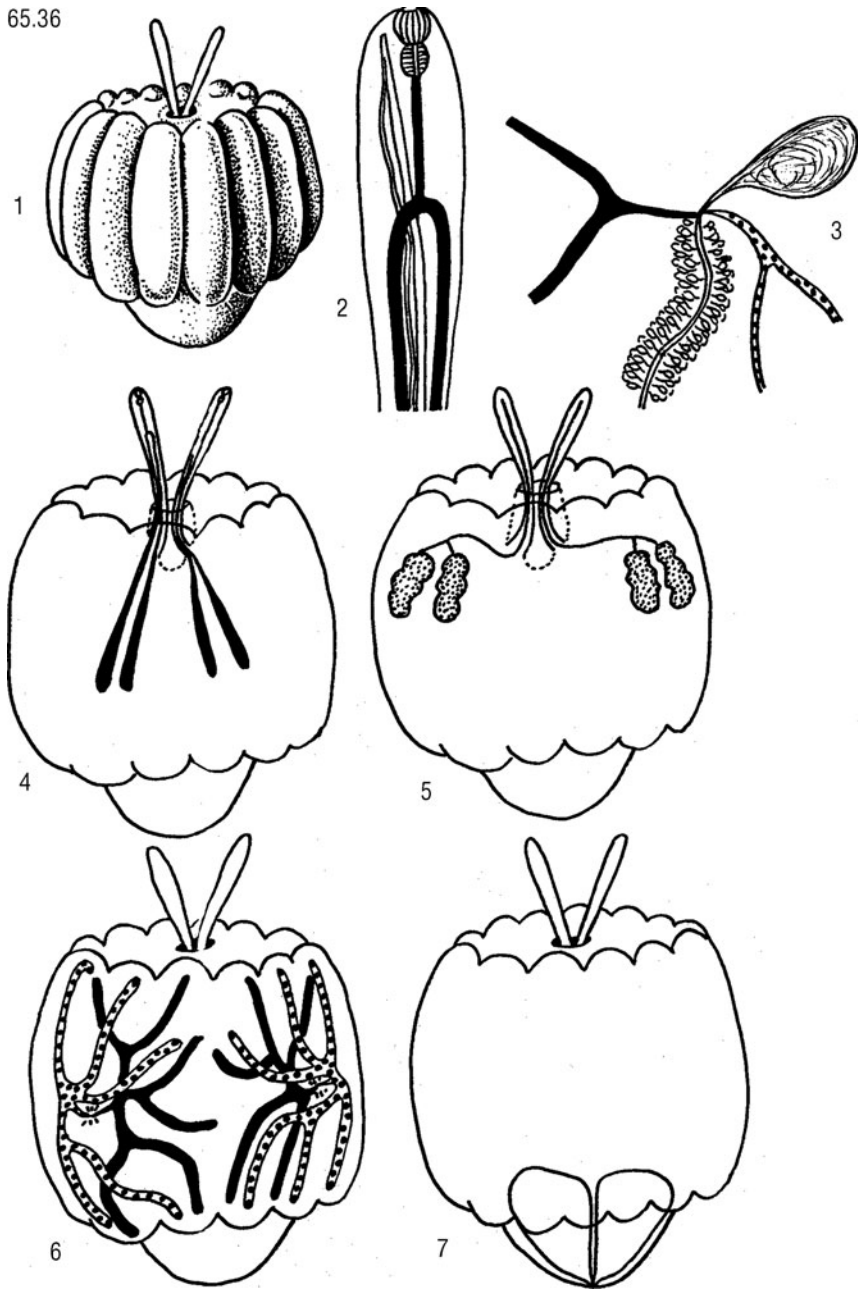



**Fig. 65.36.** *Colocyntotrema* (diagrammatic). 1, Entire worms; 2, anterior extremity; 3, genital junction; 4, location of the alimentary system; 5, location of the testes; 6, location of the ovaries and vitellaria; 7, location of the excretory vesicles.

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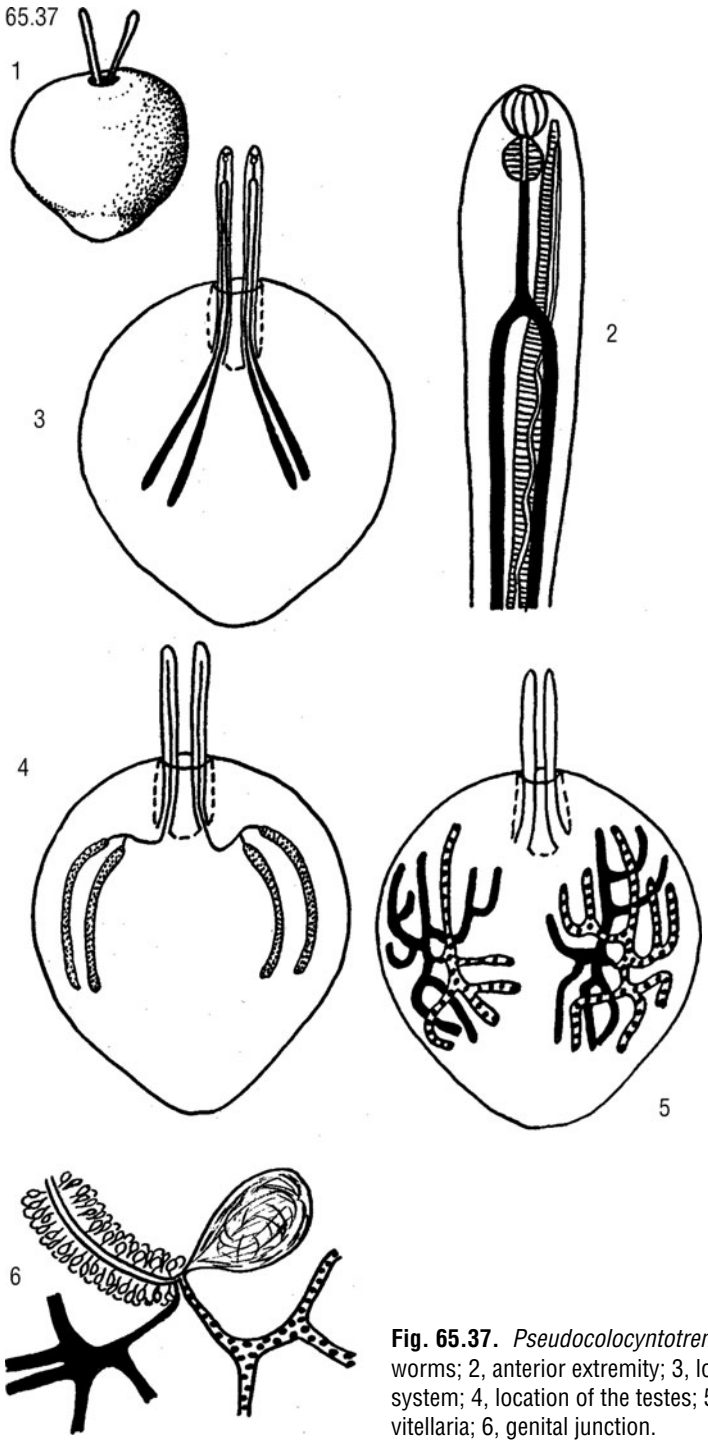



**Fig. 65.37.** *Pseudocolocyntotrema* (diagrammatic). 1, Entire worms; 2, anterior extremity; 3, location of the alimentary system; 4, location of the testes; 5, location of the ovaries and vitellaria; 6, genital junction.

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Genital junction of individuals symmetrical. Ovary and vitellarium branched. Seminal receptacle present. Excretory vesicles saccular, in posterior part of posterior region. In gut-wall (especially pyloric caeca) of scombrids (*Euthynnus, Auxis*); Pacific, Indian and Atlantic Oceans. Type-species *P. yaito* Yamaguti, 1970.

**6a. Posterior region of body elongate, with longitudinal furrows ..... ..... *Phacelotrema* Yamaguti, 1951. (Fig. 65.38)**

**Diagnosis:** Capsule cucumber-shaped, thin-walled, transparent. Anterior region narrow, elongate, round in cross-section. Posterior region skittle-shaped, with three or four deep longitudinal furrows; terminal part disc-like and distinctly separated from main part. Oesophagus simple, narrow, not long. Caeca reach terminal disc in posterior region. Two elongate, wide testes in each individual, in first third of posterior region. Genital pore ventral to oral sucker. Genital junction in terminal disc of posterior region. Ovary and vitellarium branched. Seminal receptacle present. Excretory vesicles saccular, enclosed in terminal disc. In gut-wall (especially pyloric caeca) of scombrids (*Auxis*, *?Katsuwonus*); Pacific, Indian and Atlantic Oceans. Type-species *P. claviforme* Yamaguti, 1951.

**6b. Posterior region of body skittle-shaped, without longitudinal furrows ..... ..... *Allopseudocolocyntotrema* Yamaguti, 1970. (Fig. 65.39)**

**Diagnosis:** Capsule skittle-shaped, with poorly developed capillary system. Anterior regions elongate, long, widened anteriorly. Posterior region skittle-shaped, with anterior aperture leading to cavity within which anterior regions are attached, possesses dome-like structure terminally. Oesophagus short, simple, thin. Caeca reach posterior region. Two oval to globular testes in each individual, in anterior half of posterior region. Genital pore ventral to oral sucker. Genital junction in anterior half of posterior region. Ovary and vitellarium branched. Seminal receptacle present. Mehlis' gland not large. Excretory system not known. In gut-wall of scombrids (*Euthynnus*); Pacific, Atlantic and Indian Oceans. Type-species *A. claviforme* Yamaguti, 1970.

## Subfamily Koellikeriinae Ishii, 1935

**Diagnosis:** Sexual dimorphism strongly expressed. Male and female with differing size and body-shape. Male substantially smaller than female. Body usually divided into two regions. Anterior region in both sexes elongate, may be more or less widened and flattened in its anterior third. Posterior region spherical, reniform, flattened or cylindrical with bluntly rounded extremities; sometimes, posterior extremity of posterior region lobed. Oral sucker present. Ventral sucker absent, sometimes present. Pharynx occasionally absent. Oesophagus simple, long or short. Caeca simple, reach close to posterior extremity or end close to junction of anterior and posterior regions of body. Gland-cells around oesophagus and anterior parts of caeca present or absent. Excretory vesicle Y-shaped or saccular. *Male*: Body filiform, undivided or divided into two regions. Testes two or one, extend either along whole body-length or located in posterior region. Vasa efferentia short or long. Ejaculatory duct long. *Female*: Body always divided into two regions. Special cavity where male is located present or absent. Genital junction with variable location in posterior region. Ovary branched or not. Seminal receptacle present, rarely absent. Uterus forms numerous loops. Metraterm well developed. Type-genus *Koellikeria* Cobbold, 1860.

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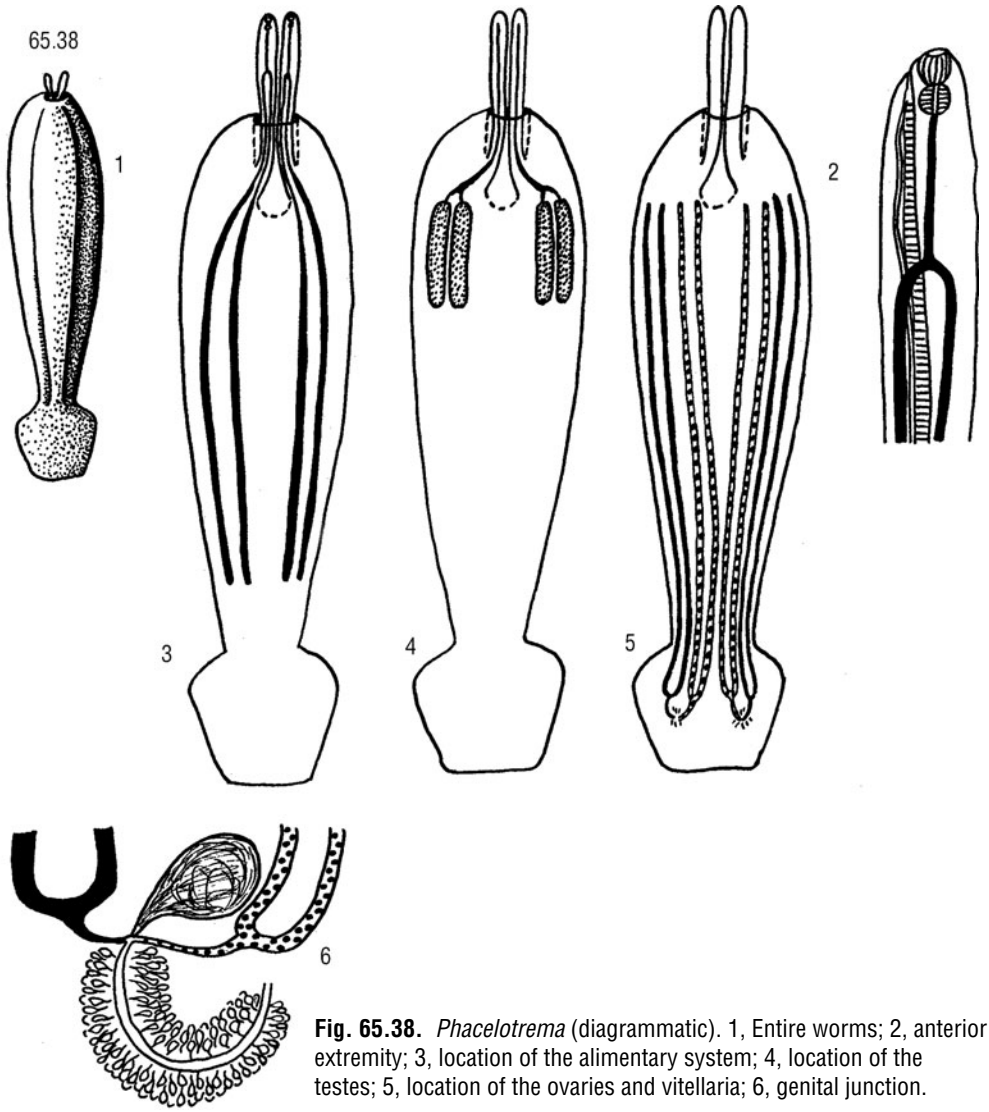



**Fig. 65.38.** *Phacelotrema* (diagrammatic). 1, Entire worms; 2, anterior extremity; 3, location of the alimentary system; 4, location of the testes; 5, location of the ovaries and vitellaria; 6, genital junction.

## Key to tribes

**1a. Posterior body-region of female tape-like, spherical, cylindrical or reniform; male with two testes; ventral sucker present or absent ..... 2.**

**1b. Posterior body-region of female with shape of tetragonal plate, spherical or reniform; male with single testis; ventral sucker absent ..... Coeliotrematini Pozdnyakov, 1993.**

**2a. Ventral sucker present; pharynx present; female with special cavity for location of male .. ..... Koellikeriini Ishii, 1935.**

**2b. Ventral sucker absent; pharynx present or absent; female with or without special cavity for location of male ..... Wedliini Pozdnyakov, 1993.**

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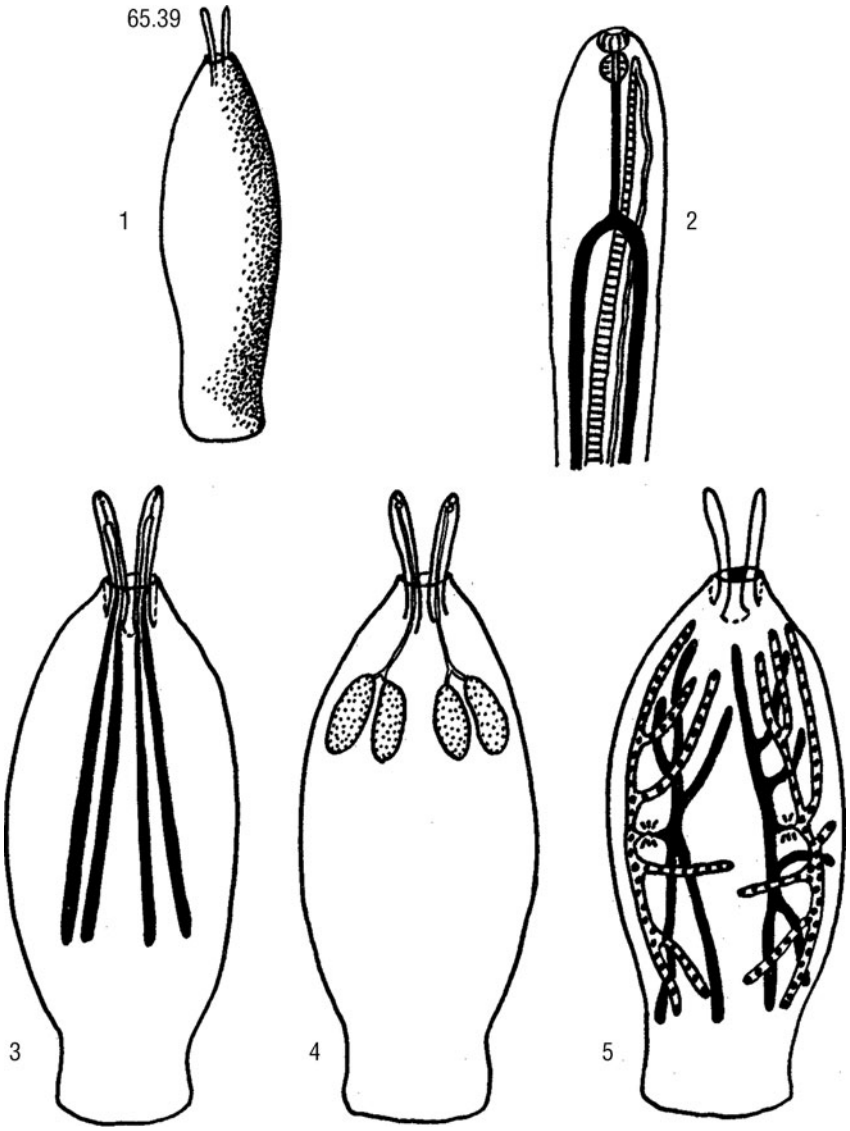



**Fig. 65.39.** *Allopseudocolocyntotrema* (diagrammatic). 1, Entire worms; 2, anterior extremity; 3, location of the alimentary system; 4, location of the testes; 5, location of the ovaries and vitellaria.

## Tribe Koellikeriini Ishii, 1935

**Diagnosis:** Ventral sucker present. Posterior region of female with a special cavity for male. Male with two testes. Pharynx present. Type-genus *Koellikeria* Cobbold, 1860.

## Key to genera

**1a. Posterior body-region of female tape-like, cylindrical or reniform; Koelliker's organ absent; male body not divided into regions ..... 2.**

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**1b. Posterior body-region of female reniform with dorsal groove; Koelliker's organ present on concave ventral surface; male body divided into regions ..... ..... *Patellokoellikeria* Yamaguti, 1970. (Fig. 65.40)**

**Diagnosis:** Encapsulated. Sexual dimorphism strongly expressed. Ventral sucker present. Oesophagus short. Gland-cells around oesophagus present. Caeca simple, reach into posterior region. Excretory vesicle long. *Male*: Anterior region elongate, round in cross-section. Posterior region disc-like. Testes long, curved, in posterior region of body. Vasa efferentia short, stout. Ejaculatory duct long. Rudiments of female genital system present. Genital pore ventral, at level of oral sucker. *Female*: Anterior region elongate, round in cross-section. Posterior region widened, concave ventrally and dorsally. Ventral surface with depression (Koelliker's organ) with muscular canal. Ovary and vitellarium unbranched. Seminal receptacle present. Mehlis' gland large. Genital pore ventral to oral sucker. Excretory system not known. In subcutaneous tissues of carangids (*Seriola*); Pacific Ocean. Type-species *P. seriolae* Yamaguti, 1970.

**2a. Posterior body-region of female tape-like, with vestigial male genital system present; male flattened, with vestigial female genital system ..... ..... *Multtubovarium* Mamaev, 1970. (Fig. 65.41)**

**Diagnosis:** Encapsulated. Body elongate, flattened or not. Body-regions poorly distinguished. Anterior region widened at anterior extremity and tapered towards junction with posterior region. Posterior region with equal width along its length. Pharynx present. Ventral sucker present. Excretory vesicle Y-shaped. Male with rudiments of female, and female with rudiments of male genital system, or rudiments absent. Male smaller than female. *Male*: Testes long, curved, extend from anterior part of posterior region towards posterior extremity. Vasa efferentia and ejaculatory duct short. *Female*: Genital junction at mid-body. Ovary and vitellarium branched or not, in posterior region. Seminal receptacle present or absent. Mehlis' gland poorly developed. In tissues (head, gills, orbits, fins) of ephippid and beloniform (hemirhamphid and exocoetocid) fishes; Pacific Ocean. Type-species *M. amphibolum* Mamaev, 1970.

**2b. Posterior body-region of female cylindrical or reniform, without elements of male genital system; male filiform, round in cross-section, without elements of female genital system ..... *Koellikeria* Cobbold, 1860. (Fig. 65.42)**

(Syns *Didymostoma* Ariola, 1902; *Tricharrhen* Poche, 1926; *Koellikerizoum* Ishii, 1935)

**Diagnosis:** Encapsulated or not. Filiform male located on surface of female body. Ventral sucker present. Gland-cells around oesophagus present or absent. Oesophagus short. Excretory vesicle Y-shaped. *Male*: Body elongate, filiform, slightly widened at anterior extremity. Caeca reach close to posterior extremity. Testes two, long, parallel. Genital pore medioventral to oral sucker. *Female*: Body divided into two regions. Anterior region elongate, thin, round in cross-section, slightly widened anteriorly. Caeca reach anterior part of posterior region. Posterior region widened, round in cross-section, more or less horseshoe-shaped. Genital junction close to junction of anterior and posterior region. Ovary long, curved, branched or not. Seminal receptacle present. Vitellarium long, unbranched, curved, extends along entire length of posterior region. In tissues (especially gills) of range of oceanic fishes (bramids, molids, exocoetids); Atlantic, Pacific and Indian Oceans. Type-species *K. filicollis* (Rudolphi, 1819) Cobbold, 1860.

## Tribe Coeliotrematini Pozdnyakov, 1993

**Diagnosis:** Ventral sucker absent. Posterior region of female with special cavity for male. Pharynx present. Male with single testis. Type-genus *Coeliotrema* Yamaguti, 1938.

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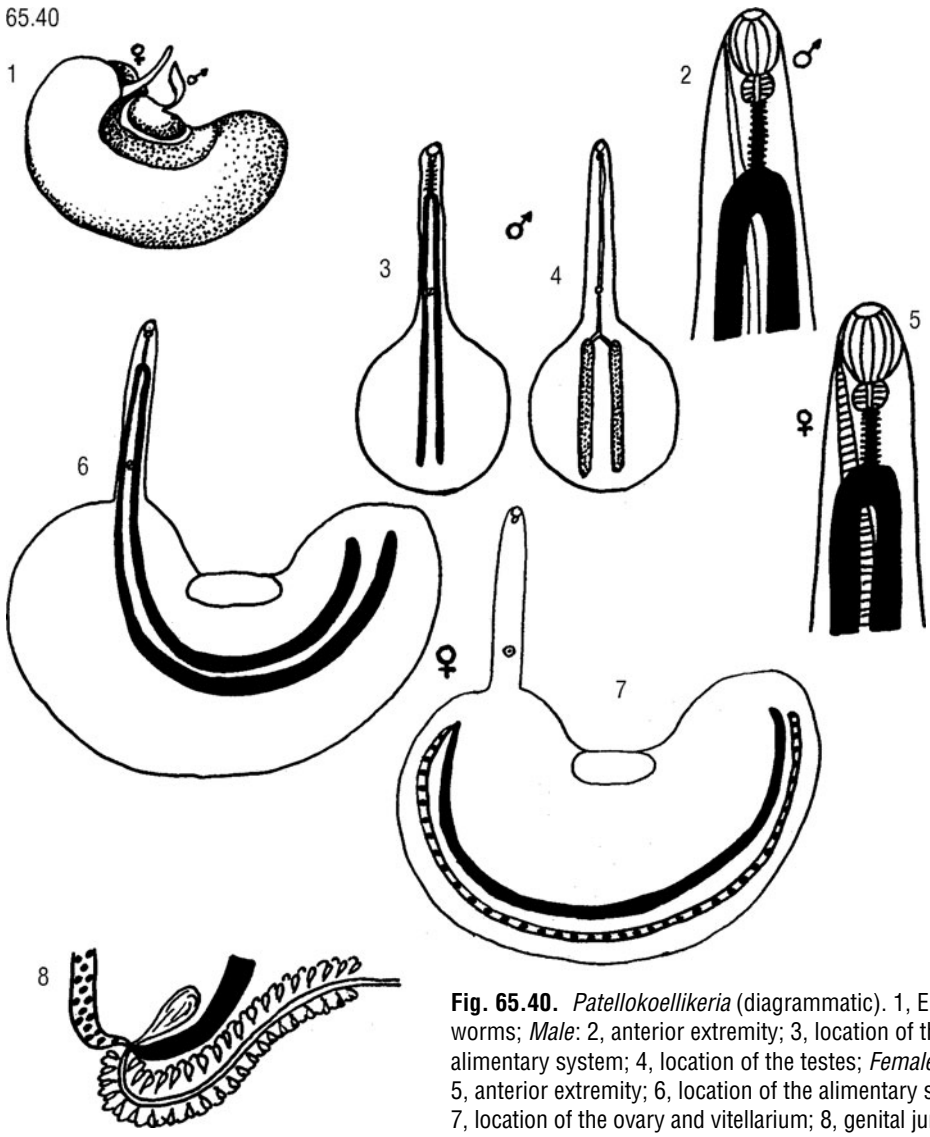



**Fig. 65.40.** *Patellokoellikeria* (diagrammatic). 1, Entire worms; *Male*: 2, anterior extremity; 3, location of the alimentary system; 4, location of the testes; *Female*: 5, anterior extremity; 6, location of the alimentary system; 7, location of the ovary and vitellarium; 8, genital junction.

## Key to genera

**1a. Posterior body-region of female with shape of tetragonal plate; posterior region of male reniform ..... *Coeliotrema* Yamaguti, 1938. (Fig. 65.43)**

**Diagnosis:** Encapsulated. Male with rudimentary female genital system. Body of female with special cavity for male. Body divided into two regions in both sexes. Anterior region in both sexes with widened and flattened anterior third. Posterior two-thirds of anterior region thin, round in cross-section. Posterior region of male and female with different form. Oesophagus short, without gland-cells. Caeca extend into posterior region. Excretory system not known. *Male*: Posterior

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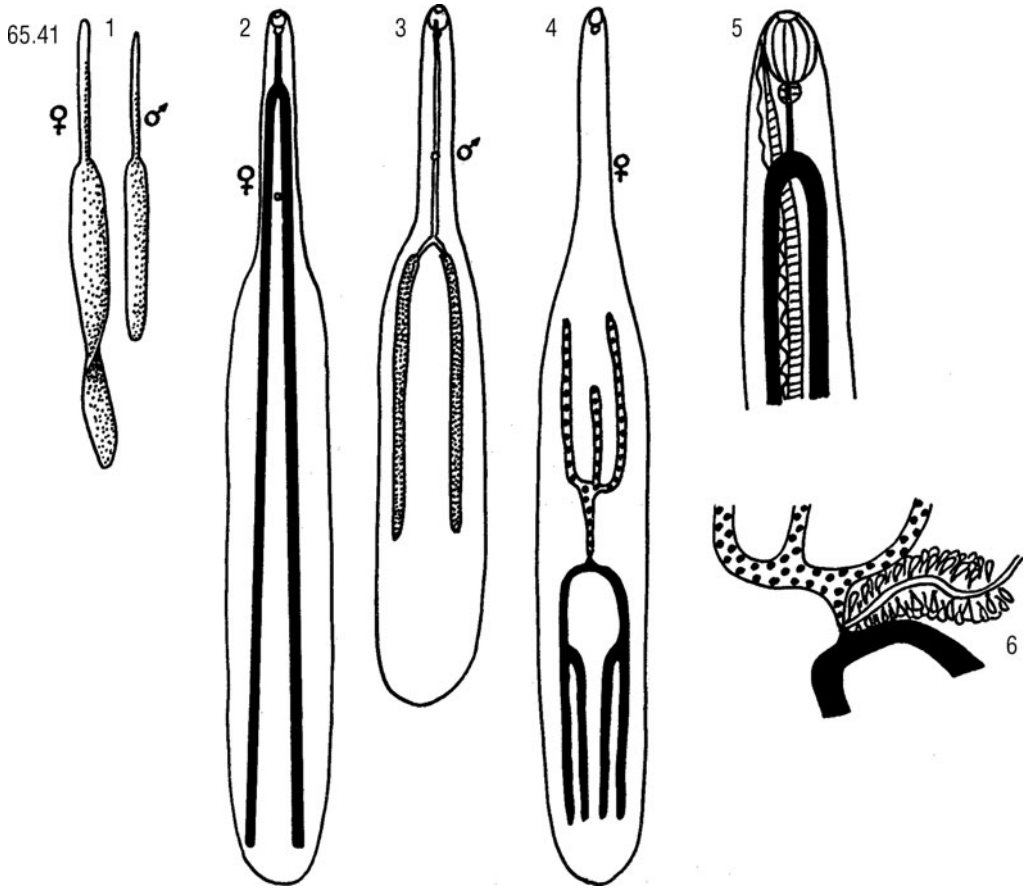



**Fig. 65.41.** *Multtubovarium* (diagrammatic). 1, Entire worms; 2, location of the alimentary system; 3, location of the testes; 4, location of the ovary and vitellarium; 5, anterior extremity; 6, genital junction.

region widened, hemispherical. Testis single. Ejaculatory duct long. Genital pore ventral to oral sucker. *Female*: Posterior region flattened, symmetrical. Cavity for male in mid-body at junction of anterior and posterior regions. Genital junction at posterior margin of posterior region. Ovary long, with two branches, curved, close to centre of posterior region. Seminal receptacle present. Vitellarium similar to ovary in form, closer to periphery of posterior region. In and around gut-wall of scombrid fishes (*Thunnus*); Pacific Ocean. Type-species *C. thynni* Yamaguti, 1938.

**1b. Posterior region of male and female spherical or globular ..... ..... *Koellikerioides* Yamaguti, 1970. (Fig. 65.44)**

**Diagnosis:** Encapsulated. Male in special cavity in body of female. Body divided into two regions in both sexes. Anterior regions of both sexes widened in anterior third, gradually tapered posteriorly. Posterior regions not so similar. Oesophagus short. Caeca extend into posterior region. Excretory system not known. *Male*: Posterior region spherical or reniform. Testis single. Ejaculatory duct long. Genital pore ventral to oral sucker. *Female*: Posterior region globular or spherical.

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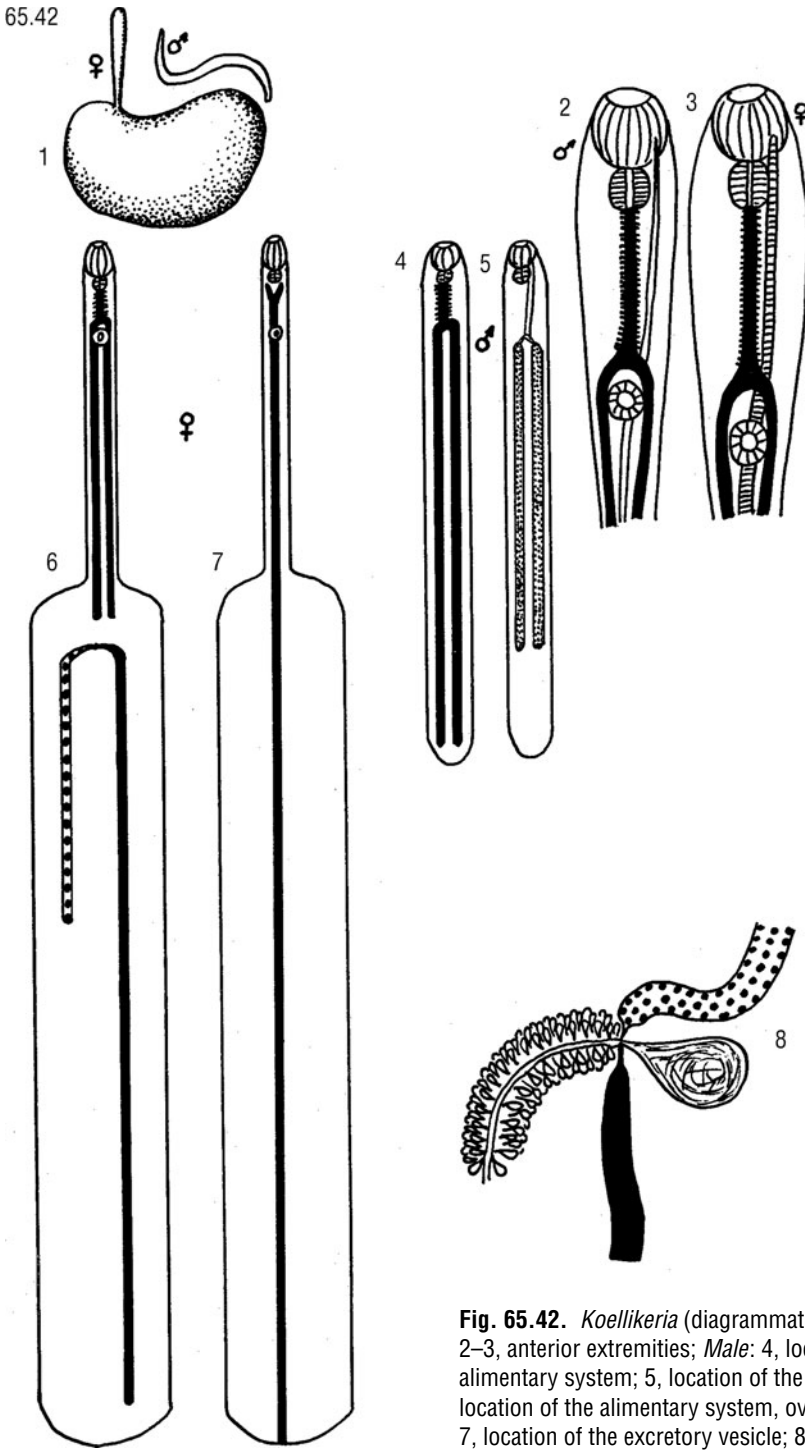



**Fig. 65.42.** *Koellikeria* (diagrammatic). 1, Entire worms; 2–3, anterior extremities; *Male*: 4, location of the alimentary system; 5, location of the testes; *Female*: 6, location of the alimentary system, ovary and vitellarium; 7, location of the excretory vesicle; 8, genital junction.

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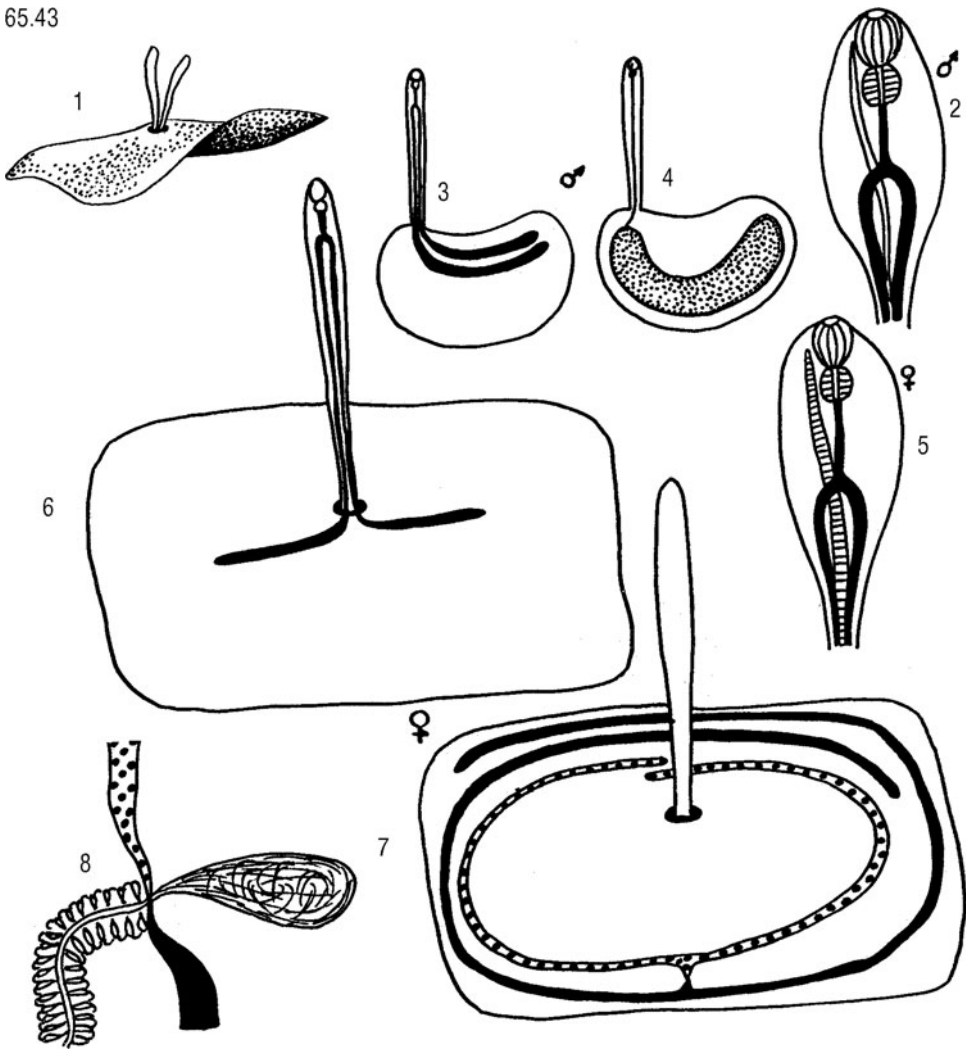


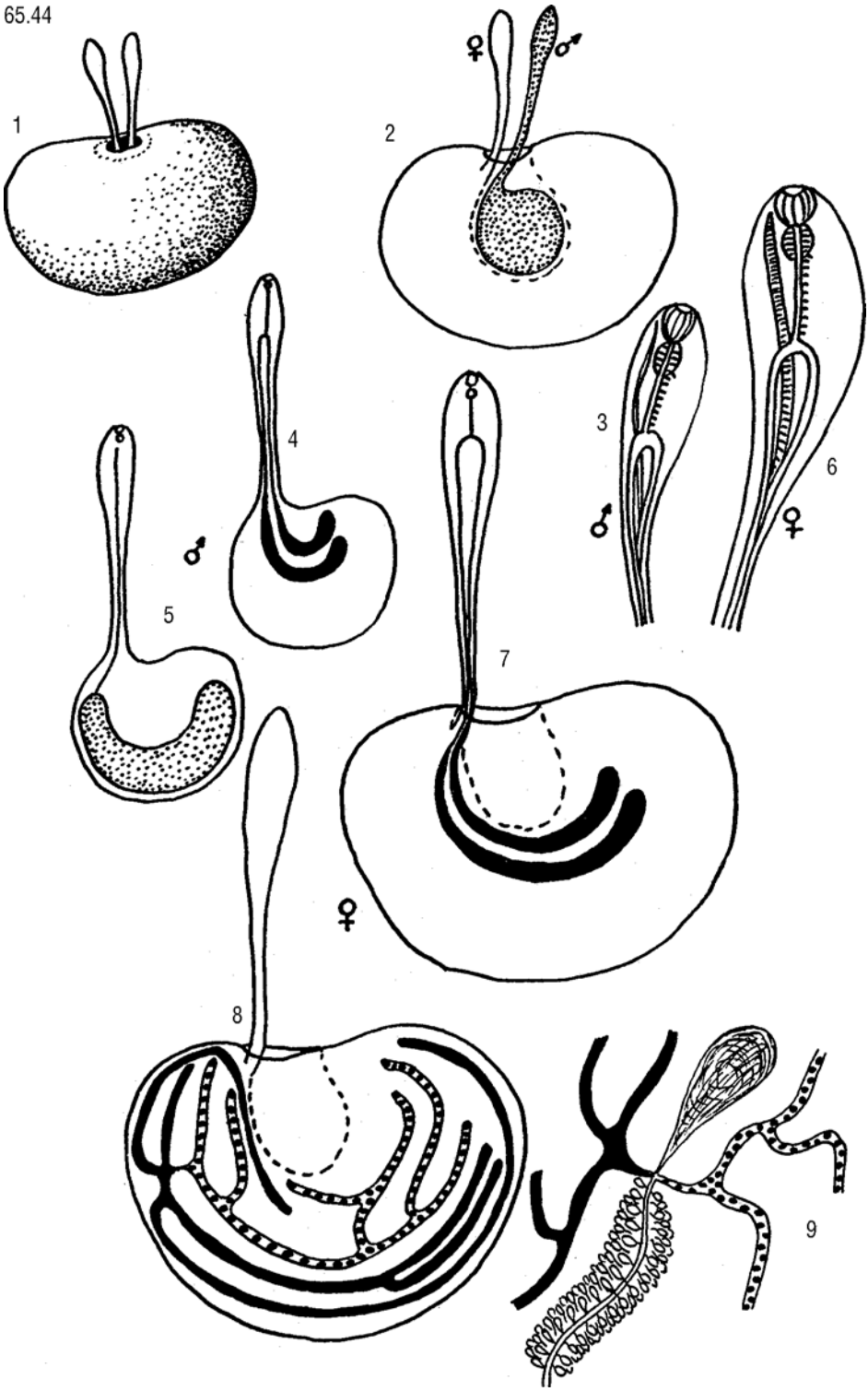

**Fig. 65.43.** *Coeliotrema* (diagrammatic). 1, Entire worms; *Male*: 2, anterior extremity; 3, location of the alimentary system; 4, location of the testis; *Female*: 5, anterior extremity; 6, location of the alimentary system; 7, location of the ovary and vitellarium; 8, genital junction.

Ovary long, branched. Seminal receptacle present. Vitellarium similar to ovary in form. In tissues of gut-wall and gills of scombrid fishes (mainly *Thunnus*, occasionally *Katsuwonus*); Pacific, Atlantic and Indian Oceans. Type-species *K. internogastricus* Yamaguti, 1970.

## Tribe Wedliini Pozdnyakov, 1993

**Diagnosis:** Ventral sucker absent. Posterior body region of female with or without special cavity for male. Pharynx present or absent. Male with two testes. Type-genus *Wedlia* Cobbold, 1860.

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## Key to genera

**1a. Female body cylindrical, round in cross-section; special cavity for male in female body absent; posterior region of male with small lobes ..... ..... *Didymonaja* Pozdnyakov, 1987. (Fig. 65.45)**

**Diagnosis:** Encapsulated. Male and female without rudimentary primordia of female and male genital system, respectively. Special cavity for male in female body absent. Body divided into two regions in both sexes. Anterior region spoon-shaped, similar in male and female. Posterior region of male oval and slightly lobed; posterior region of female elongate and round in cross-section. Pharynx absent. Oesophagus long, thin. Caeca extend to posterior region. Excretory system? Gland-cells around oesophagus and anterior parts of caeca absent. *Male*: Two reniform testes in posterior region. Vasa efferentia long; ejaculatory duct long. Genital pore ventrolateral to oral sucker. *Female*: Body cylindrical. Ovary long, unbranched, in anterior part of posterior region. Seminal receptacle present. Uterus forms tight loops, occupying almost entire posterior region. Genital pore ventrolateral to oral sucker. Vitellarium long, with two branches, extends along entire length of posterior region. In gill-tissues of scombrids (*Thunnus*); Pacific Ocean. Type-species *D. branchialis* Pozdnyakov, 1987.

**1b. Female body spherical; cavity for male present in female body; posterior region of male entire ..... *Wedlia* Cobbold, 1860. (Fig. 65.46)**

**Diagnosis:** Encapsulated or not. Male in special cavity in female body. Body divided into regions in both sexes. Anterior region narrow, frequently widened anteriorly. Posterior region widened. Pharynx present (sometimes absent?). Oesophagus may be surrounded by gland-cells. Caeca extend into posterior region. Excretory vesicle saccular; pore? *Male*: Posterior region entire. Testes two, curved or not, rarely branched, entirely in posterior region. Vasa efferentia usually short; ejaculatory duct long. Genital pore ventral to oral sucker. *Female*: Body spherical. Genital junction close to one of margins of posterior region. Ovary long, branched, curved, in posterior region. Seminal receptacle present. Genital pore ventral to oral sucker. Vitellarium similar to ovary in structure, in posterior region. In tissues (gills, buccal cavity, body-cavity, gut-wall, pyloric caeca) of scombrids (*Thunnus*); Atlantic, Indian and Pacific Oceans. Type-species *W. bipartita* (Wedl, 1855) Cobbold, 1860.

## Subfamily Nematobothriinae Ishii, 1935

(Syns Atalostrophiinae Yamaguti, 1958; Philopinninae Skrjabin, 1955; Skrjabinozoinae Yamaguti, 1971)

**Diagnosis:** Hermaphroditic, free in host tissues, rarely in capsules. Body not divided into regions, fusiform, tape-like or filiform, round in cross-section, rarely flattened. Oral sucker present. Ventral sucker present or absent. Pharynx present or absent. Gland-cells around oesophagus and anterior part of caeca present or absent. Oesophagus and caeca simple, rarely

**Fig. 65.44.** (*Opposite*) *Koellikerioides* (diagrammatic). 1, Entire worms; 2, relative location of male and female; *Male*: 3, anterior extremity; 4, location of the alimentary system; 5, location of the testis; *Female*: 6, anterior extremity; 7, location of the alimentary system; 8, location of the ovary and vitellarium; 9, genital junction.

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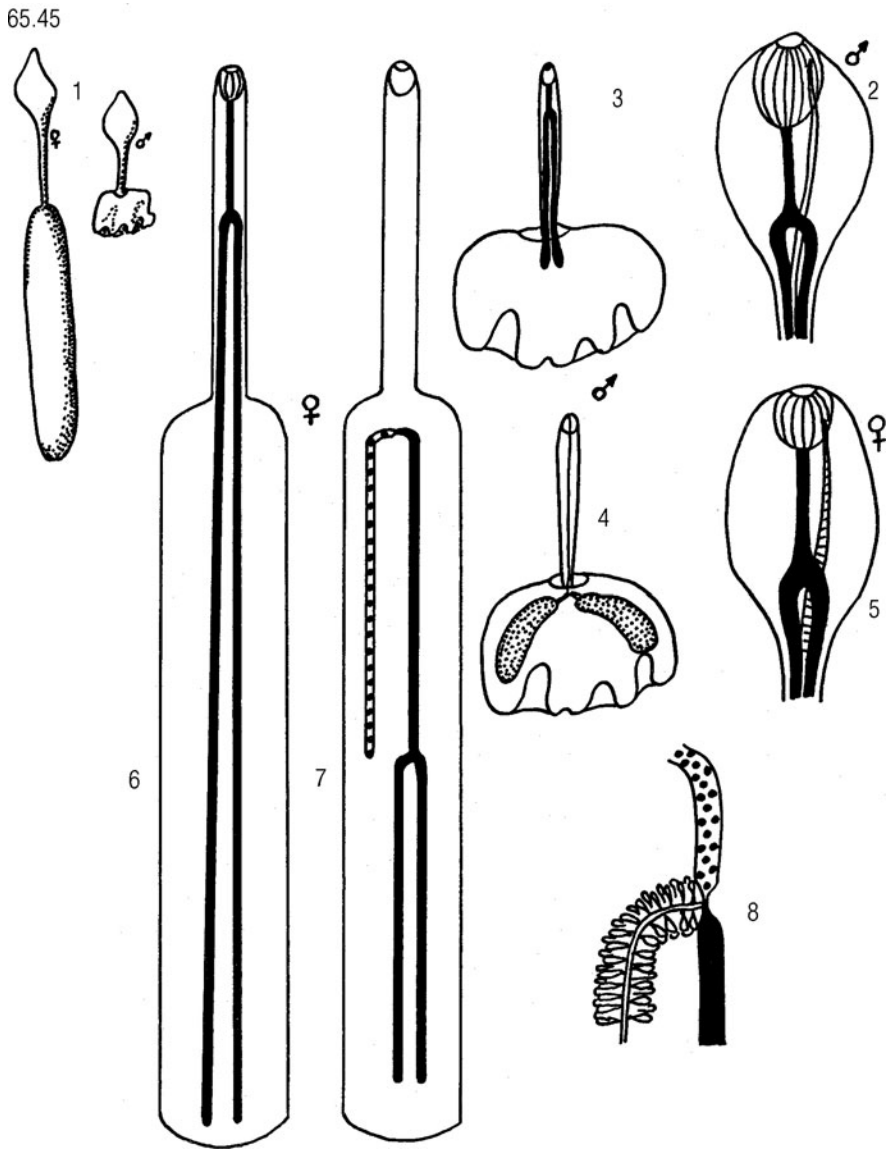



**Fig. 65.45.** *Didymonaja* (diagrammatic). 1, Entire worms; *Male*: 2, anterior extremity; 3, location of the alimentary system; 4, location of the testes; *Female*: 5, anterior extremity; 6, location of the alimentary system; 7, location of the ovary and vitellarium; 8, genital junction.

with diverticula. Caeca blind, in some cases with fused distal ends; rarely, single caecum present. Testes elongate, usually two, rarely one, parallel, oblique or in tandem. Genital pore ventral to pharynx or oral sucker. Ovary and vitellarium very elongate, usually unbranched, rarely branched. Ovary in anterior half of body. Mehlis' gland well developed or not. Seminal receptacle and Juel's organ present or absent. Uterus long, with one, two or three loops, rarely more. Metraterm well developed. Hermaphroditic duct present, sometimes absent. Eggs small, numerous. Vitellarium in posterior half of body. Excretory vesicle Y-shaped; stem normally long,

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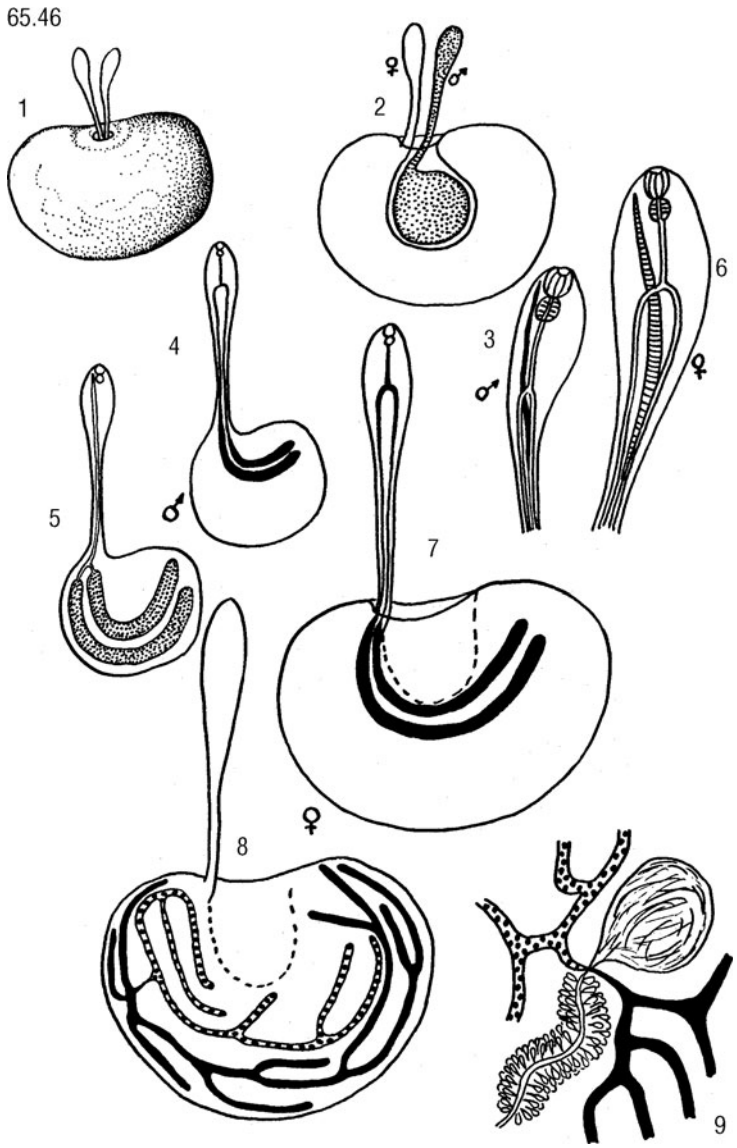



**Fig. 65.46.** *Wedlia* (diagrammatic). 1, Entire worms; 2, relative location of male and female; *Male*: 3, anterior extremity; 4, location of the alimentary system; 5, location of the testes; *Female*: 6, anterior extremity; 7, location of the alimentary system; 8, location of the ovary and vitellarium; 9, genital junction.

narrow; bifurcation usually at level of intestinal bifurcation; arms may have diverticula. Type-genus *Nematobothrium* van Beneden, 1858.

## Key to tribes

**1a. Ventral sucker present** ..... **2.**
**1b. Ventral sucker absent** ..... **3.**

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**2a. Caeca form cyclocoel ..... Philopinnini Skrjabin, 1955.**
**2b. Caeca blind ..... Allonematobothriini Pozdnyakov, 1993.**

**3a. Testes two ..... Nematobothriini Ishii, 1935.**
**3b. Testis one ..... Unitubulotestini Pozdnyakov, 1993.**

## Tribe Nematobothriini Ishii, 1935

**Diagnosis:** Ventral sucker absent. Two testes. Type-genus *Nematobothrium* van Beneden, 1858.

## Key to genera

**1a. Body long, filiform or flattened ..... 2.**
**1b. Body short, fusiform ..... *Skrjabinozoum* Nikolaeva & Parukhin, 1969. (Fig. 65.47)**
**Diagnosis:** Not encapsulated. Body elongate-oval, short, fusiform, round in cross-section. Pharynx present. Oesophagus short. Caeca reach close to posterior extremity. Gland-cells around pharynx and anterior part of oesophagus present or absent. Testes elongate, parallel or interwoven in anterior third of body. Vasa efferentia short. Ejaculatory duct long. Genital pore ventrolateral to oral sucker, on papilla. Genital junction at about middle of body. Ovary and vitellarium long, unbranched, in anterior and posterior half of body, respectively. Mehlis' gland large. Seminal receptacle present or absent. Excretory vesicle Y-shaped; pore? In tissues (gut-wall, pyloric caeca, throat, operculum) of beloniform (exocoetid, hemirhamphid) and perciform (nomeid, centrolophid) fishes; Pacific, Atlantic and Indian Oceans. Type-species *S. exocoetidi* Nikolaeva & Parukhin, 1969.

**2a. Body dorsoventrally flattened ..... 3.**
**2b. Body filiform, round in cross-section ..... 7.**

**3a. Pharynx present; testes parallel ..... 4.**
**3b. Pharynx absent; testes not parallel ..... 5.**

**4a. Testes reach close to posterior extremity; oesophagus with diverticula and surrounded by gland-cells ..... *Neonematobothrium* Yamaguti, 1965. (Fig. 65.48)**
**Diagnosis:** Not encapsulated. Body long, thin, dorsoventrally flattened. Pharynx present. Oesophagus very long; anterior part simple; posterior part with numerous diverticula, surrounded by gland-cells. Caeca curved, reach close to posterior extremity. Testes parallel, long, curved, reach close to posterior extremity. Genital pore ventral, posterior to pharynx. Genital junction at about mid-body. Ovary and vitellarium single, long, narrow, unbranched, in anterior and posterior half of body, respectively. Seminal receptacle present. Uterus with three loops. Excretory system? In subcutaneous tissues (operculum and fins) of scombrid fishes (*Euthynnus*); Pacific and Indian Oceans. Type-species *N. kawakawa* Yamaguti, 1965.

**4b. Testes not reaching posterior extremity; oesophagus without diverticula; gland-cells present around anterior part of alimentary system ..... ..... *Neounitubulotestis* Yamaguti, 1971. (Fig. 65.49)**
**Diagnosis:** Not encapsulated. Body long, curved, dorsoventrally flattened. Pharynx present. Oesophagus long, thin, lacks diverticula. Gland-cells present around oesophagus and anterior part

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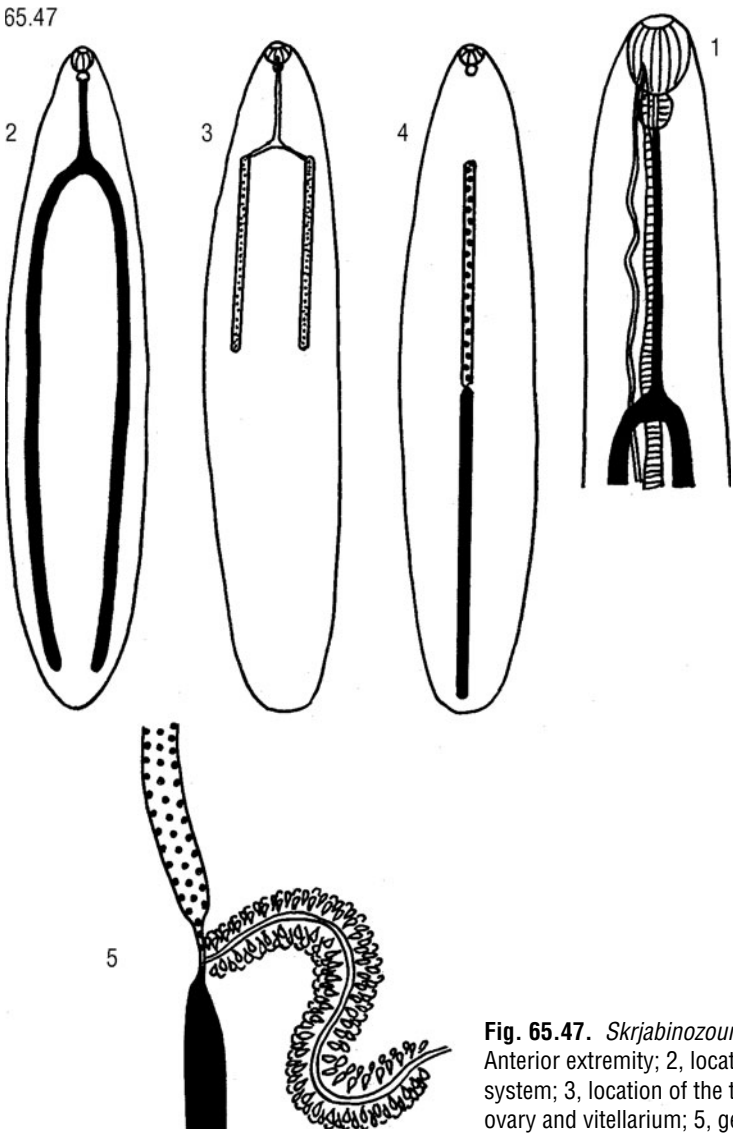



**Fig. 65.47.** *Skrjabinozoum* (diagrammatic). 1, Anterior extremity; 2, location of the alimentary system; 3, location of the testes; 4, location of the ovary and vitellarium; 5, genital junction.

of caeca. Caeca reach close to posterior extremity. Testes narrow, long, parallel, not reaching posterior extremity. Vasa efferentia short. Ejaculatory duct long. Genital pore ventral at tip of small genital sucker or papilla, posterior to pharynx. Ovary single, long, unbranched, in anterior half of body. Genital junction at about mid-caecal length. Seminal receptacle and Juel's organ present. Uterus forms three loops. Vitellarium with similar shape to ovary, in posterior half of body. Excretory system? In tissues (orbit, body musculature) of gempylid fishes; Atlantic and Pacific Oceans. Type-species *N. orbitarium* (Dollfus, 1956) Yamaguti, 1971.

**5a. Caecum single; testes diagonal in anterior half of body .....**
**..... *Angionematobothrium* Yamaguti, 1970. (Fig. 65.50)**

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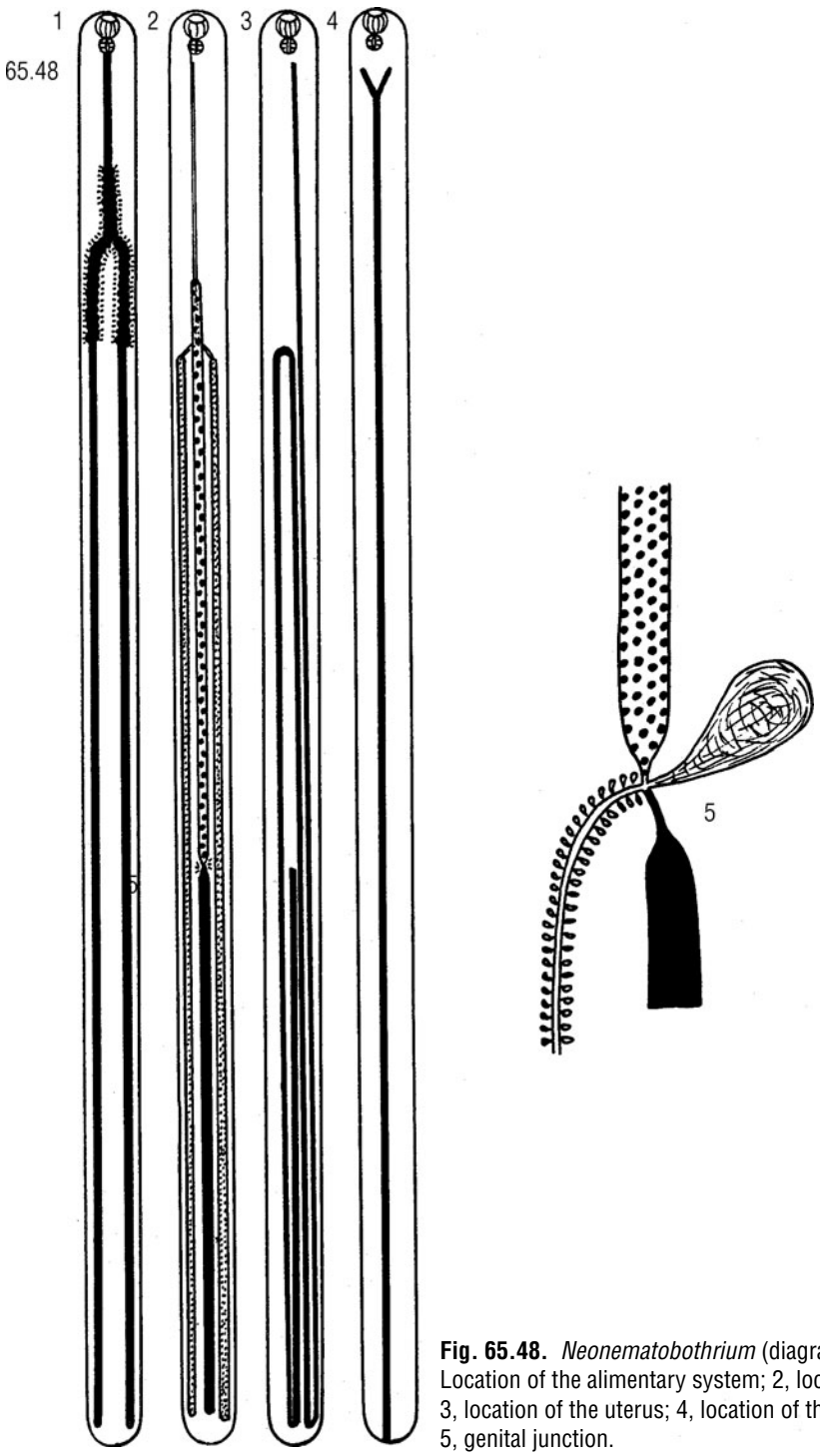



**Fig. 65.48.** *Neonematobothrium* (diagrammatic). 1, Location of the alimentary system; 2, location of the gonads; 3, location of the uterus; 4, location of the excretory vesicle; 5, genital junction.

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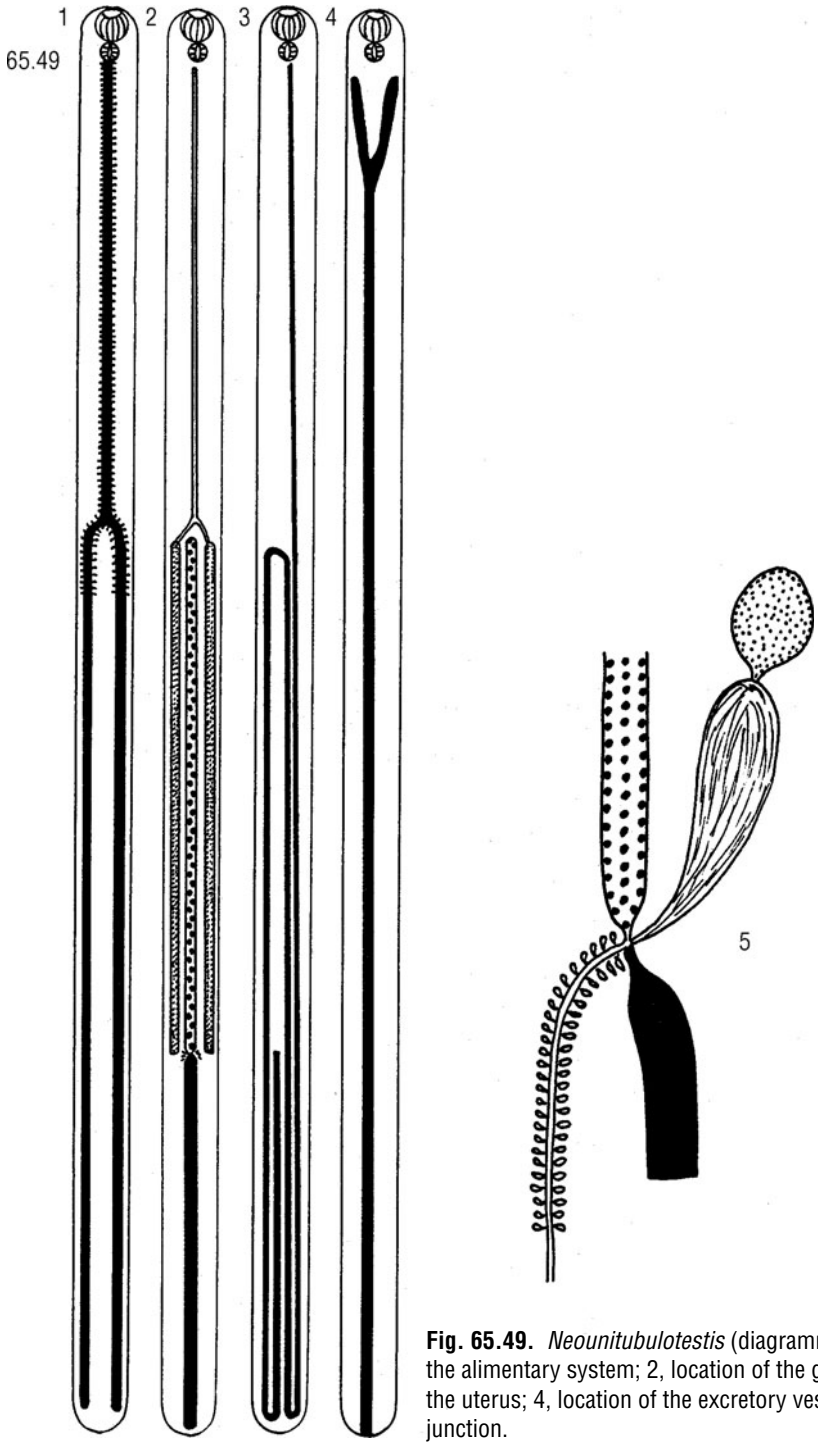



**Fig. 65.49.** *Neounitubulotestis* (diagrammatic). 1, Location of the alimentary system; 2, location of the gonads; 3, location of the uterus; 4, location of the excretory vesicle; 5, genital junction.

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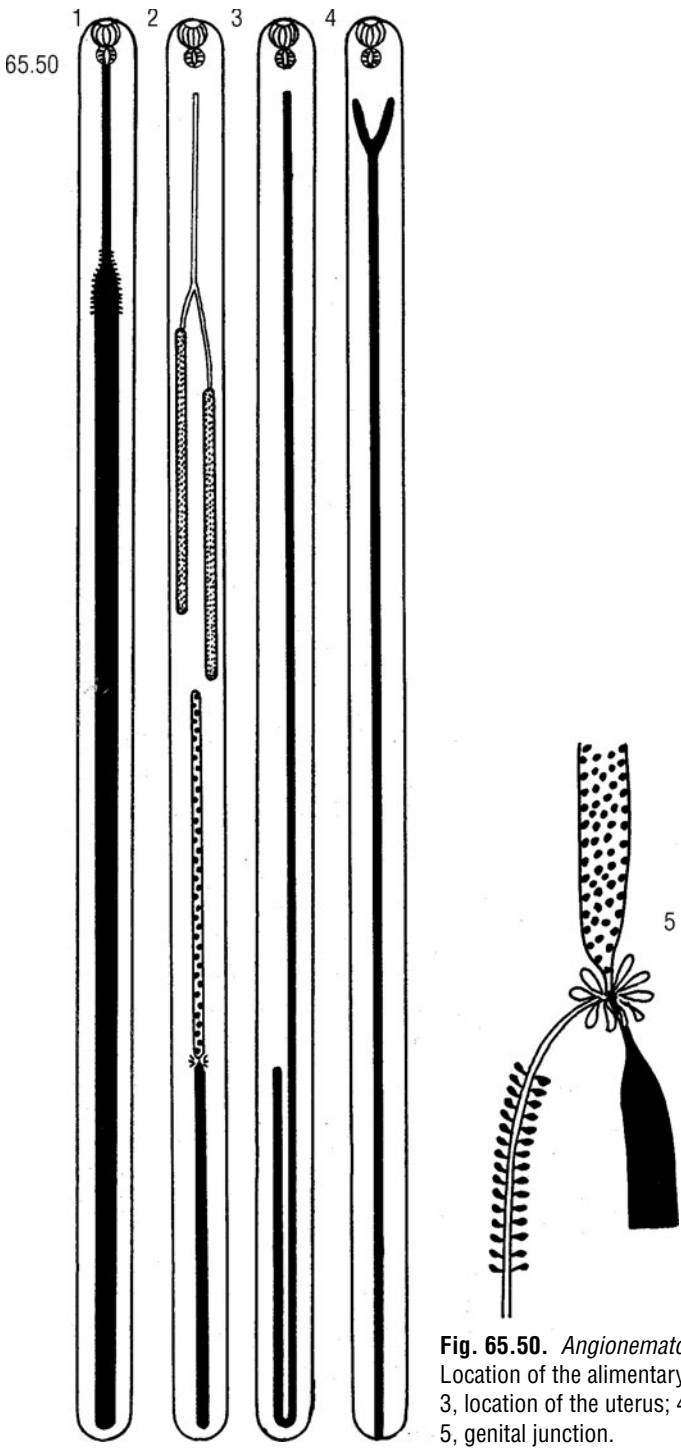



**Fig. 65.50.** *Angionematobothrium* (diagrammatic). 1, Location of the alimentary system; 2, location of the gonads; 3, location of the uterus; 4, location of the excretory vesicle; 5, genital junction.

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**Diagnosis:** Not encapsulated. Body elongate, dorsoventrally flattened. Pharynx present. Oesophagus long, thin. Caecum single, reaching close to posterior extremity. Gland-cells present around caecum. Testes long, diagonal, at different levels in anterior part of body. Ejaculatory duct stout, long. Genital pore ventral, posterior to pharynx. Ovary long, curved, unbranched, about middle of body, between ends of testes and genital junction. Seminal receptacle absent. Mehlis' gland large. Proximal part of uterus covered with gland-cells. Uterus with single loop. Vitellarium similar to ovary in form, in posterior half of body. Excretory arms unite anteriorly; pore? In tissues (veins, under tongue) of istiophorid and scombrid (*Thunnus*) fishes; Pacific and Indian Oceans. Type-species *A. jugulare* Yamaguti, 1970.

**5b. Two caeca; testes diagonal to tandem ..... 6.**

**6a. Testes diagonal, one reaching into posterior half of body; gland-cells around anterior part of alimentary system absent ..... *Atalostrophion* MacCallum, 1915. (Fig. 65.51)**
(Syn. *Atalosparganum* Ishii, 1935)

**Diagnosis:** Not encapsulated. Body long, dorsoventrally flattened. Pharynx absent. Oesophagus long, thin. Gland-cells absent. Caeca two, narrow, reach close to posterior extremity. Testes two, diagonal. Posterior testis partly in posterior half of body or reaching close to posterior extremity. Genital pore ventral to oral sucker. Genital junction at about mid-body. Ovary long, unbranched, in anterior half of body. Seminal receptacle present. Uterus with three loops. Vitellarium similar in form to ovary but in posterior half of body. Excretory system? In tissues (branchial cavity, gills, muscles) of scombrid (*Sarda*, *Thunnus*, *Scomber*) and serranid (*Epinephelus*) fishes; Atlantic Ocean. Type-species *A. sardae* MacCallum, 1915.

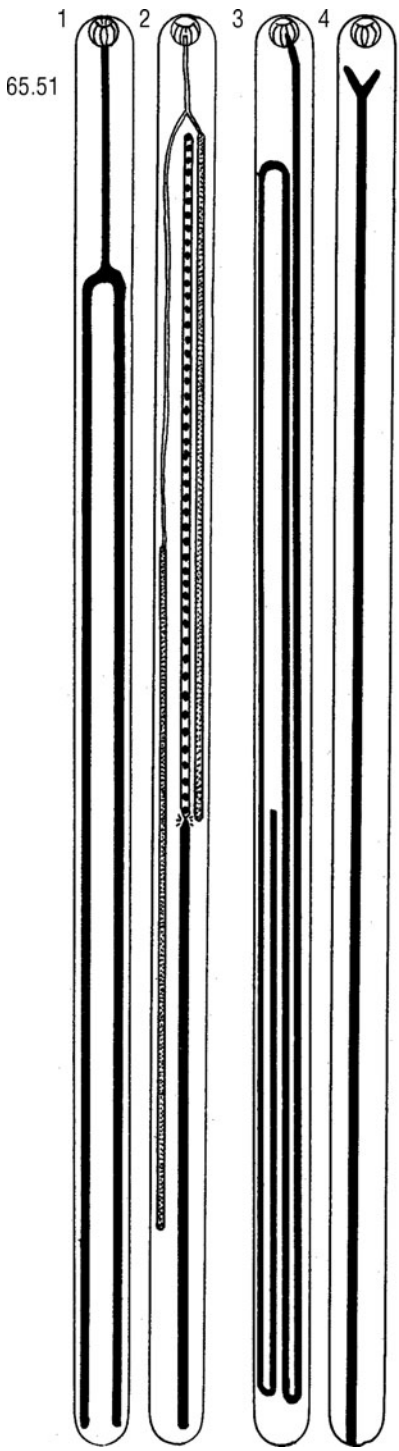
**6b. Testes obliquely tandem, one reaches close to posterior extremity; no gland-cells around anterior part of alimentary system ..... ..... *Halvorsenius* Gibson, MacKenzie & Cottle, 1981. (Fig. 65.52)**

**Diagnosis:** Not encapsulated. Body long, dorsoventrally flattened. Oral sucker, alimentary system and terminal genitalia atrophied. Oesophagus long, thin. Gland-cells absent. Caeca two, narrow, vestigial, lacking lumen, reach close to posterior extremity. Testes, long, obliquely tandem; posterior testis reaches close to posterior extremity. Vasa efferentia differing in length, short from anterior testis, long from posterior testis. Genital pore ventral, posterior to pharynx. Genital junction at two-thirds of body-length. Ovary long, unbranched, in anterior half of body. Juel's organ and uterine seminal receptacle present. Uterus forms three loops. Vitellarium similar in form to ovary, in posterior half of body. Excretory vesicle Y-shaped; pore? In connective tissues (pericardium, peritoneum, muscles, orbit, etc.) of scombrid fishes (*Scomber*); North Atlantic Ocean. Type-species *H. exilis* Gibson, MacKenzie & Cottle, 1981.

**7a. Pharynx absent ..... *Allonematobothrioides* Yamaguti, 1970. (Fig. 65.53)**

**Diagnosis:** Two individuals in capsule. Body elongate, round in cross-section, widened at anterior extremity. Pharynx absent. Oesophagus short. Caeca reach close to posterior extremity. Gland-cells around oesophagus and anterior parts of caeca present or absent. Testes parallel, in anterior third of body. Vasa efferentia short, ejaculatory duct long. Genital pore ventral to oral sucker. Genital junction at about mid-body. Ovary long, thin, unbranched, in anterior half of body. Seminal receptacle present. Juel's organ present or absent. Uterus forms three loops. Vitellarium with similar structure to ovary, in posterior half of body. Excretory system Y-shaped; bifurcation near intestinal bifurcation; pore subterminal. In tissues (branchio-oesophageal region) of scombrids (*Scomber*); Pacific and Indian Oceans. Type-species *A. scombri* Yamaguti, 1970.

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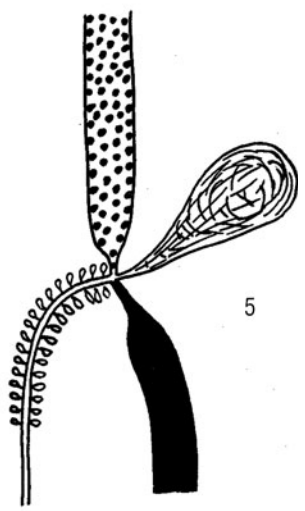




**Fig. 65.51.** *Atalostrophion* (diagrammatic). 1, Location of the alimentary system; 2, location of the gonads; 3, location of the uterus; 4, location of the excretory vesicle; 5, genital junction.

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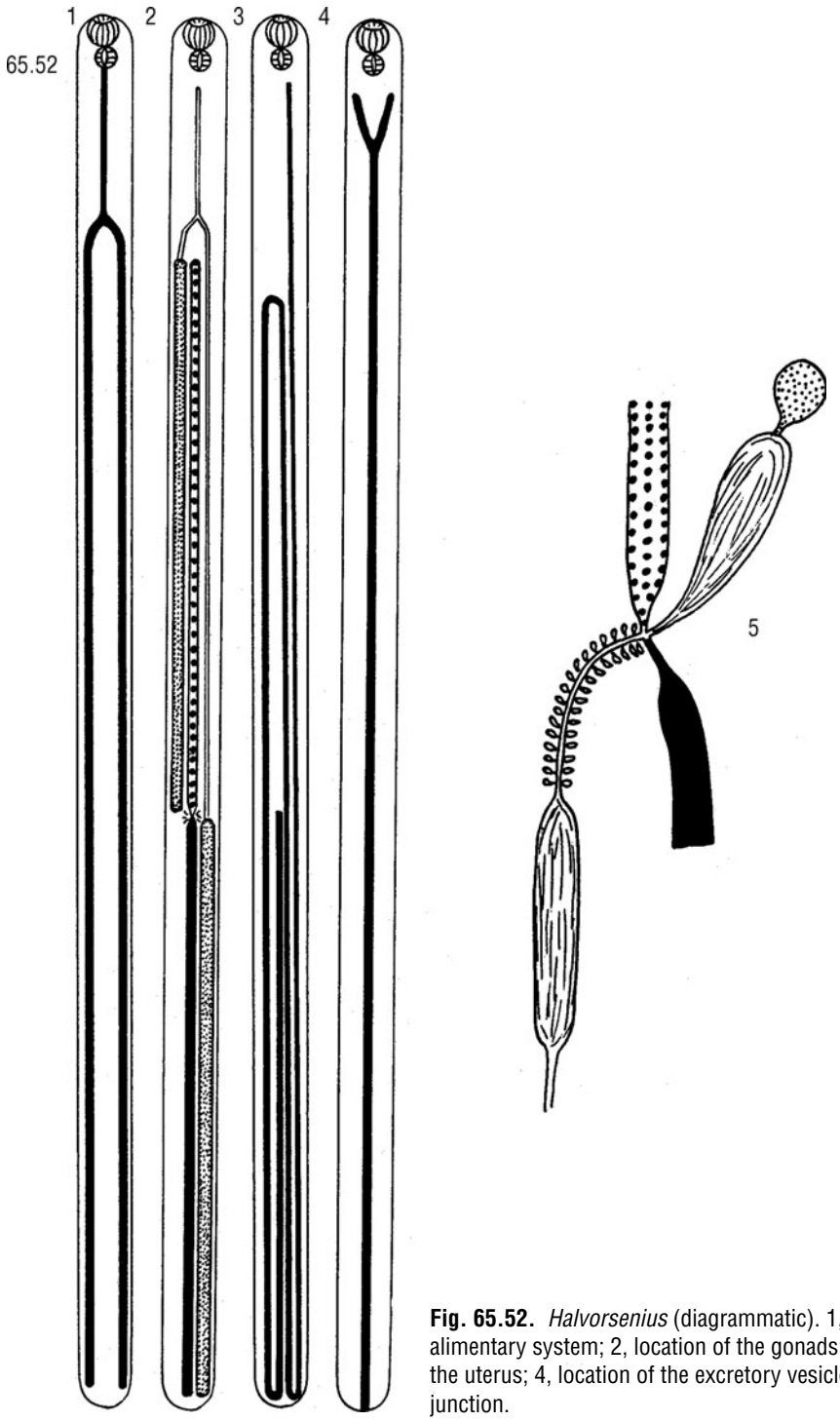



**Fig. 65.52.** *Halvorsenius* (diagrammatic). 1, Location of the alimentary system; 2, location of the gonads; 3, location of the uterus; 4, location of the excretory vesicle; 5, genital junction.

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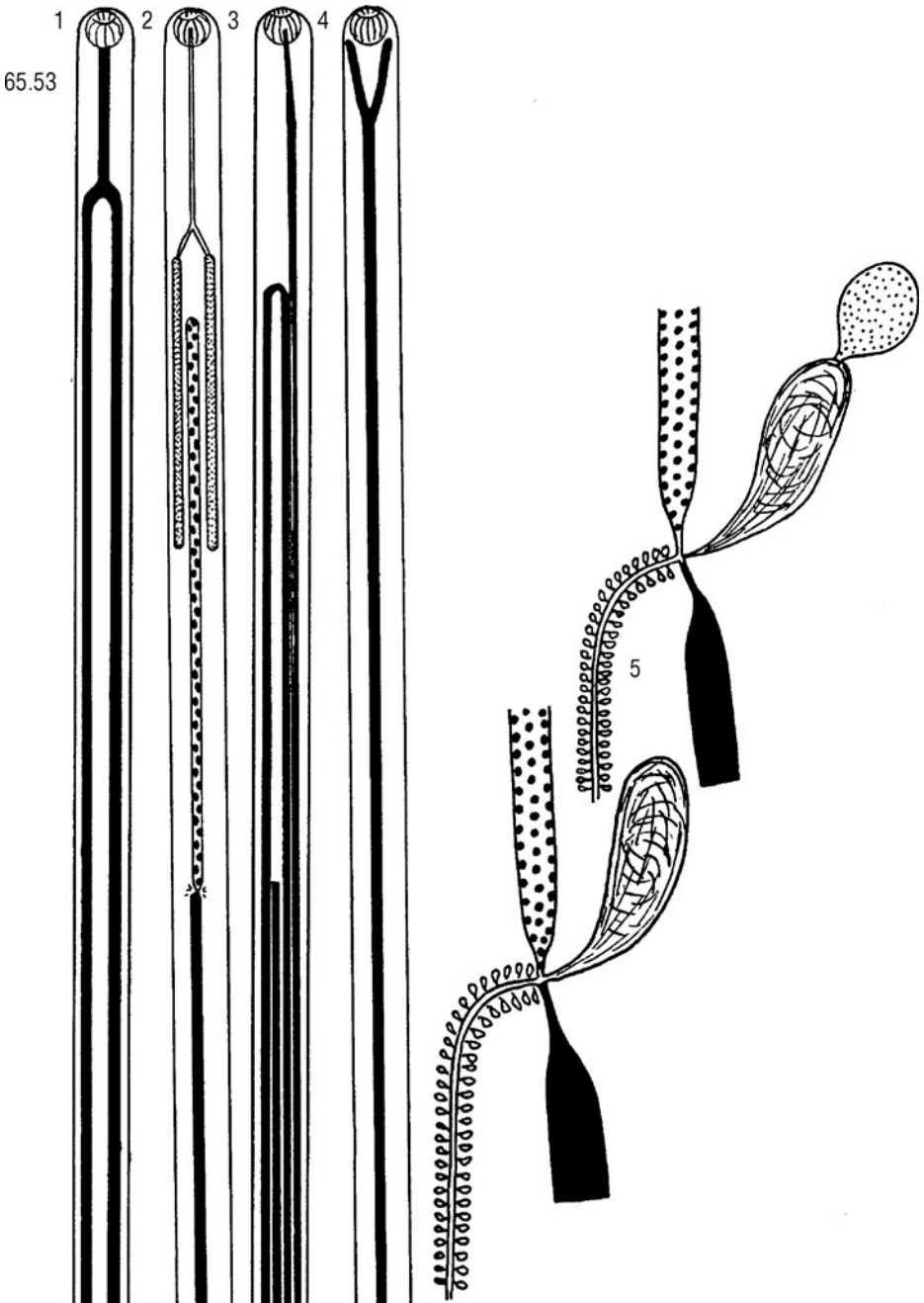



**Fig. 65.53.** *Allonematobothrioides* (diagrammatic). 1, Location of the alimentary system; 2, location of the gonads; 3, location of the uterus; 4, location of the excretory vesicle; 5, structural variations of the genital junction.

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**7b. Pharynx present ..... 8.**

**8a. Testes parallel ..... 9.**
**8b. Testes not parallel ..... 12.**

**9a. Testes in anterior half of body ..... 10.**
**9b. Testes reach into posterior half of body or close to posterior extremity ..... 11.**

**10a. Prominent gland-cells around some anterior parts of alimentary system ..... ..... *Nematobothrioides* Yamaguti, 1965. (Fig. 65.54)**

**Diagnosis:** Not encapsulated. Body long, thin. Pharynx present. Caeca reach close to posterior extremity. Gland-cells cover proximal or distal end of oesophagus as well as anterior parts of caeca. Testes parallel but not long. Vasa efferentia short. Ejaculatory duct long. Genital pore ventral at level of pharynx or oral sucker. Genital junction at about mid-body. Ovary long, unbranched, curved, in anterior half of body. Seminal receptacle present or absent. Uterus with single loop. Vitellarium with similar form to ovary, in posterior half of body. Excretory system not known. In tissues (branchial region, orbit, gut-wall, pyloric caeca, kidneys) of scombrid (*Scomber*), lutjanid and exocoetid fishes; Pacific, Indian and Atlantic Oceans. Type-species *N. kalikali* Yamaguti, 1965.

**10b. Gland-cells around anterior parts of alimentary system absent or indistinct ..... ..... *Nematobothrium* van Beneden, 1858. (Fig. 65.55)**

(Syns *Benedenozoum* Ishii, 1935; *Maclarenozoum* Ishii, 1935)

**Diagnosis:** Two individuals in capsule. Body filiform, long. Pharynx present. Oesophagus simple. Caeca reach close to posterior extremity, rarely slightly anterior. Gland-cells around anterior parts of alimentary system absent or indistinct. Testes parallel, elongate but not long. Vasa efferentia short. Ejaculatory duct long. Genital pore at tip of small genital sucker, ventral to oral sucker or pharynx. Genital junction at about mid-body. Ovary long, unbranched, in anterior half of body. Seminal receptacle present, rarely absent. Uterus with three loops. Vitellarium with similar form to ovary, in posterior half of body. Excretory vesicle Y-shaped; bifurcation near intestinal bifurcation. In various tissues of range of teleosts (sciaenids, molids, scombrids, sparids); Atlantic, Indian and Pacific Oceans. Type-species *N. filarina* van Beneden, 1858.

**11a. Testes reach close to posterior extremity; 'Drüsenmagen' present ..... ..... *Opisthorchinematobothrium* Yamaguti, 1970. (Fig. 65.56)**

**Diagnosis:** Not encapsulated. Body long, narrow, round in cross-section; anterior end widened. Pharynx present. Oesophagus long; 'Drüsenmagen' present at intestinal bifurcation. Gland-cells present around oesophagus and 'Drüsenmagen'. Caeca wide, reaching various levels close to posterior extremity. Testes long, narrow, reach close to posterior extremity. Genital pore ventral to oral sucker. Genital junction at one-third of body-length. Ovary narrow, long, branched; two branches originate from short 'trunk' region, one in anterior half of body and other in posterior half. Seminal receptacle present. Uterus with three loops. Vitellarium narrow, long, unbranched, in posterior half of body. Excretory vesicle 'tubular'; pore terminal. In connective tissues of muscles, kidneys, urinary ducts, etc. of scombrid fishes (*Thunnus*); Pacific and Indian Oceans. Type-species *O. parathunni* Yamaguti, 1970.

**11b. Testes not reaching into posterior third of body; 'Drüsenmagen' absent ..... ..... *Paranematobothrium* Nikolaeva & Tkachuk, 1979. (Fig. 65.57)**

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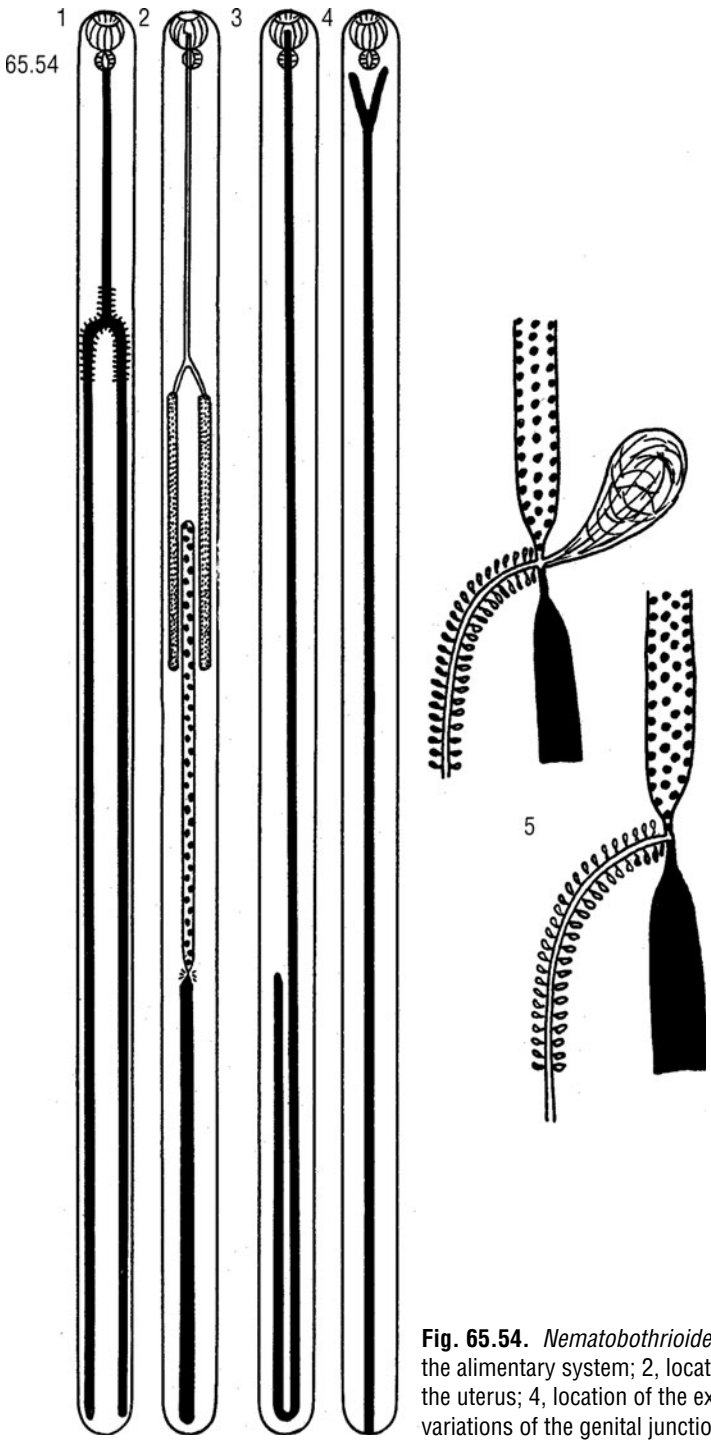



**Fig. 65.54.** *Nematobothrioides* (diagrammatic). 1, Location of the alimentary system; 2, location of the gonads; 3, location of the uterus; 4, location of the excretory vesicle; 5, structural variations of the genital junction.

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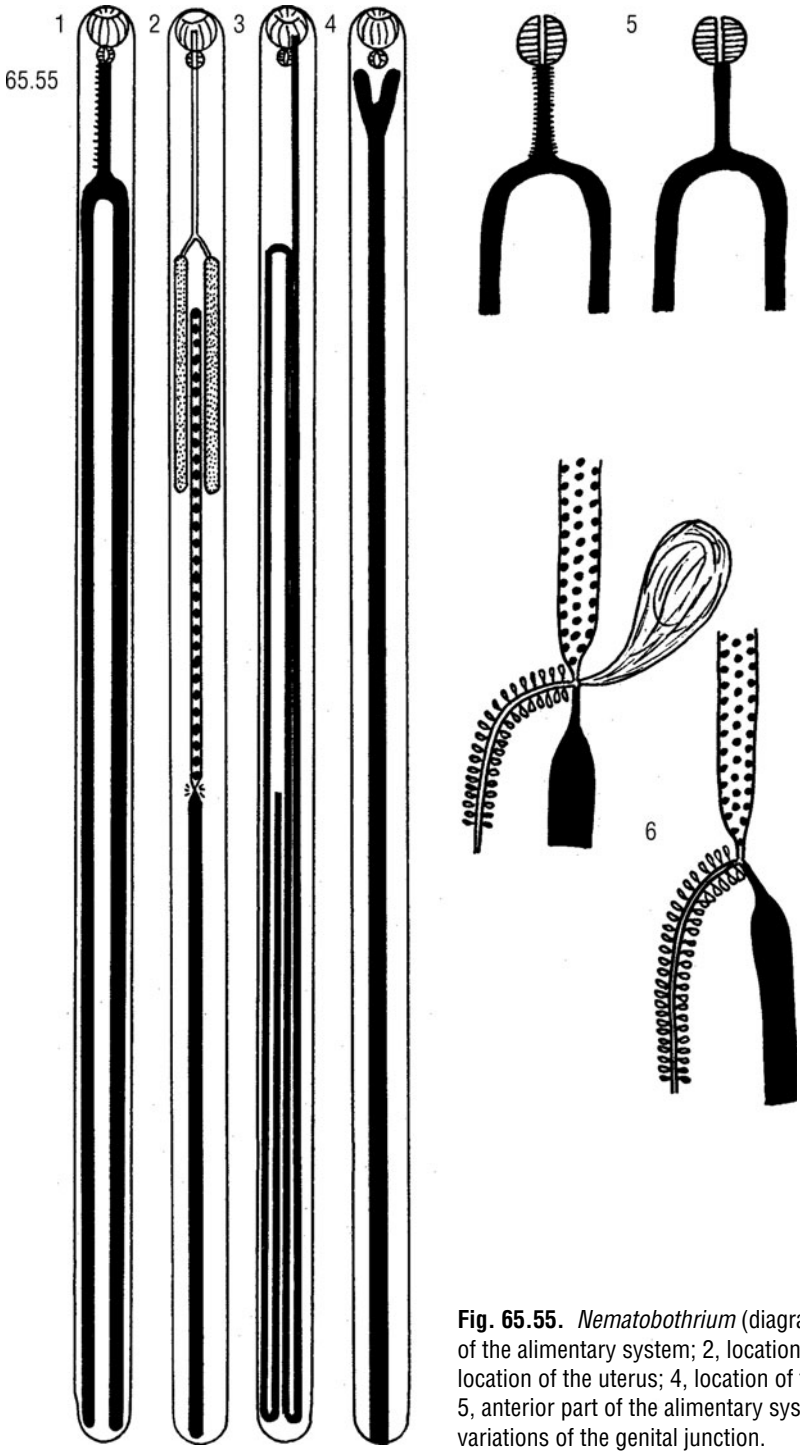



**Fig. 65.55.** *Nematobothrium* (diagrammatic). 1, Location of the alimentary system; 2, location of the gonads; 3, location of the uterus; 4, location of the excretory vesicle; 5, anterior part of the alimentary system; 6, structural variations of the genital junction.

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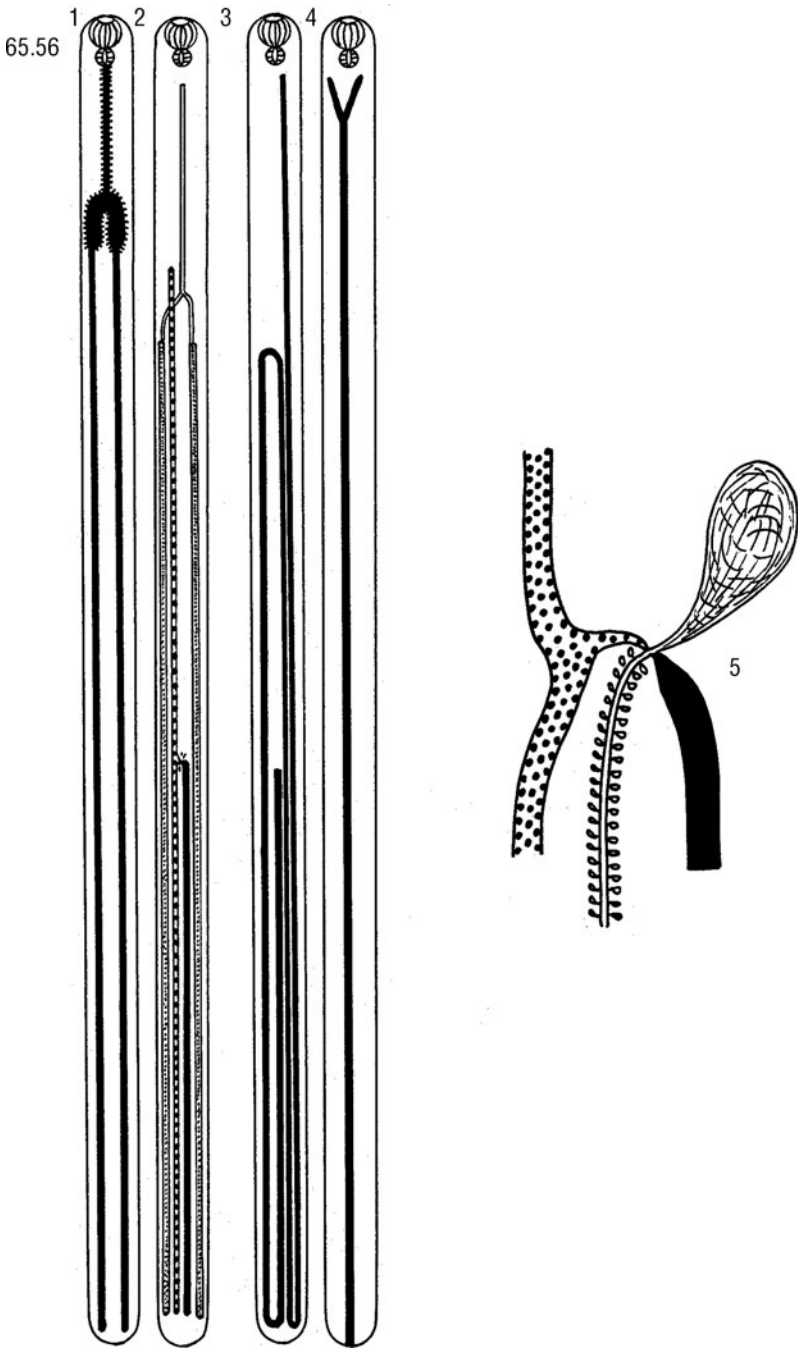



**Fig. 65.56.** *Opisthorchinematobothrium* (diagrammatic). 1, Location of the alimentary system; 2, location of the gonads; 3, location of the uterus; 4, location of the excretory vesicle; 5, genital junction.

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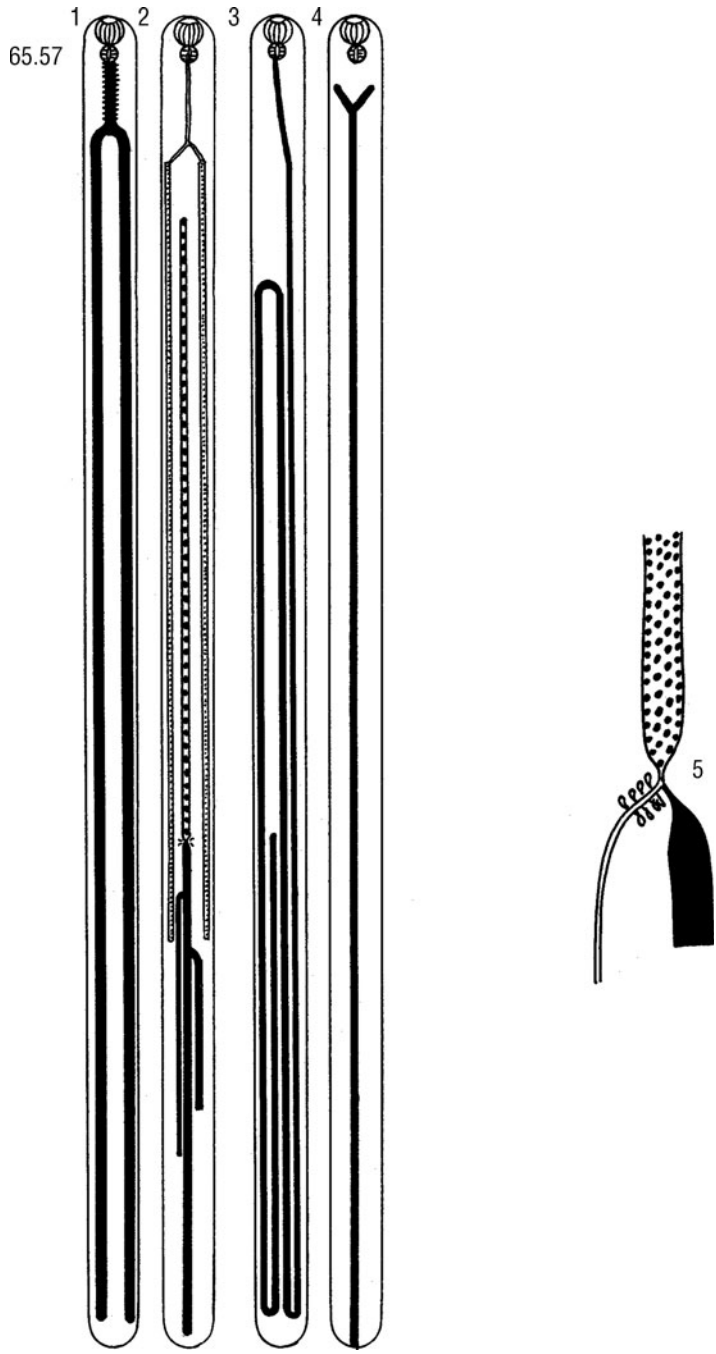



**Fig. 65.57.** *Paranematobothrium* (diagrammatic). 1, Location of the alimentary system; 2, location of the gonads; 3, location of the uterus; 4, location of the excretory vesicle; 5, genital junction.

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**Diagnosis:** Not encapsulated. Body long, widened anteriorly. Pharynx present. Oesophagus short. 'Drüsenmagen' absent. Caeca reach close to posterior extremity. Gland-cells present around oesophagus. Testes long, parallel, only reach into posterior half of body. Genital pore ventral to oral sucker. Genital junction anterior to mid-body. Ovary long, thin, unbranched, curved, in anterior half of body. Seminal receptacle absent. Uterus with three loops. Vitellarium long, thin, branched, in posterior half of body; secondary branches of vitellarium present. Excretory vesicle Y-shaped, long, bifurcates close to intestinal bifurcation. In body-cavity of scombrids (*Scomber*); Indian and Atlantic Oceans. Type-species *P. triplovitellatum* Nikolaeva & Tkachuk, 1979.

**12a. Testes oblique, posterior one reaching close to posterior extremity; gland-cells surround anterior part of alimentary system ..... ..... *Allometanematobothrioides* Yamaguti, 1965. (Fig. 65.58)**

**Diagnosis:** Not encapsulated. Body narrow, long. Pharynx present. Oesophagus very long, narrow. Gland-cells surround anterior part of alimentary system (not shown in figure). Caeca curved, reach close to posterior extremity. Testes long, curved, oblique; posterior testis reaches close to posterior extremity. Ejaculatory duct very long. Genital pore ventral, posterior to pharynx. Ovary single, long, unbranched, mainly in middle of body. Seminal receptacle present. Mehlis' gland long. Uterus with three loops. Vitellarium with similar form to ovary, in posterior third of body. Excretory vesicle Y-shaped, bifurcates at level of intestinal bifurcation; pore almost terminal. In oesophago-branchial tissues of scombrids (*Scomber*); Pacific and Indian Oceans. Type-species *A. lepidocybii* Yamaguti, 1965.

**12b. Testes in tandem in anterior half of body; no gland-cells around anterior parts of alimentary system ..... *Orbitonematobothrium* Yamaguti, 1970. (Fig. 65.59)**

**Diagnosis:** Not encapsulated. Body long, narrow. Pharynx present. Oesophagus long, narrow. No glands around anterior part of alimentary system. Caeca not reaching posterior extremity. Testes two, elongate, tandem, in anterior half of body. Genital pore ventral, posterior to pharynx. Genital junction at about mid-body. Ovary single, long, unbranched, mainly in anterior half of body. Seminal receptacle present. Uterus with three loops. Vitellarium with similar form to ovary, in posterior half of body. Excretory vesicle Y-shaped, bifurcates at about level of intestinal bifurcation; pore terminal. In orbit of scombrid fishes (*Thunnus*); Pacific Ocean. Type-species *O. periocular* Yamaguti, 1970.

## Tribe Allonematobothriini Pozdnyakov, 1993

**Diagnosis:** Ventral sucker present. Testes two. Type-species *Allonematobothrium* Yamaguti, 1965.

## Key to genera

**1a. Body elongate to filiform, dorsoventrally flattened ..... 2.**
**1b. Body filiform, round in cross-section ..... 6.**

**2a. Pharynx present; ovary and vitellarium unbranched ..... 3.**

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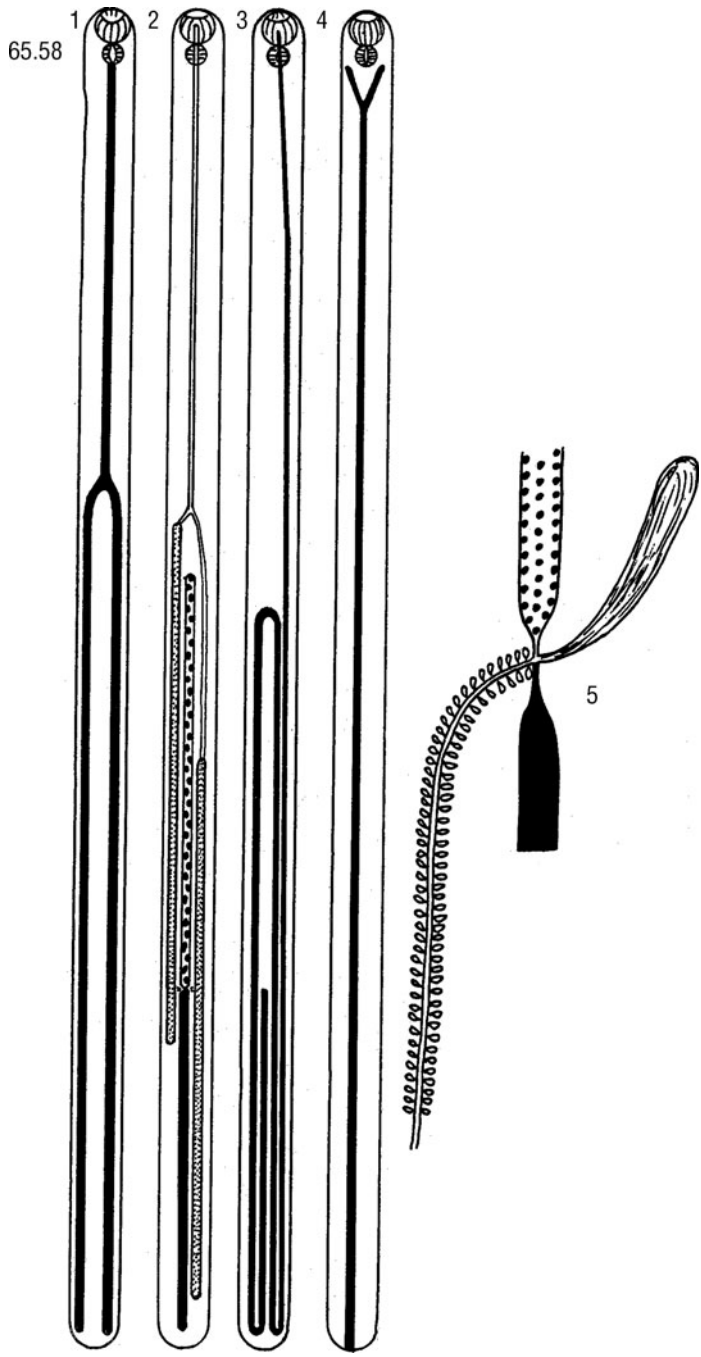



**Fig. 65.58.** *Allometanematobothrioides* (diagrammatic). 1, Location of the alimentary system; 2, location of the gonads; 3, location of the uterus; 4, location of the excretory vesicle; 5, genital junction.

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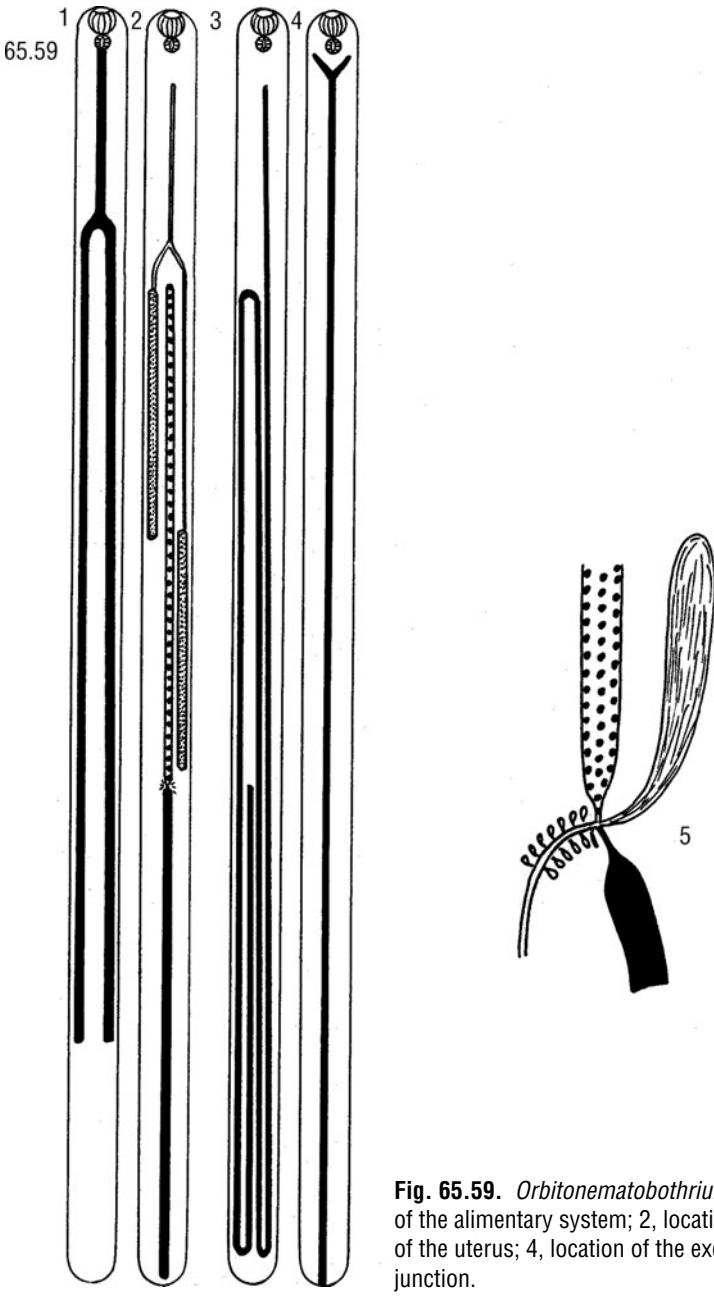



**Fig. 65.59.** *Orbitonematobothrium* (diagrammatic). 1, Location of the alimentary system; 2, location of the gonads; 3, location of the uterus; 4, location of the excretory vesicle; 5, genital junction.

**2b. Pharynx absent; ovary branched; vitellarium unbranched** ..... ..... ***Maccallozoum*** **Ishii, 1935. (Fig. 65.60)**

**Diagnosis:** Not encapsulated. Body long, tape-like, flattened. Pharynx absent. Oesophagus long. Caeca reach close to posterior extremity. Testes long, parallel, occupy third of body-length. Genital junction in mid-hindbody. Ovary filiform, with two branches; short branch directed anteriorly;

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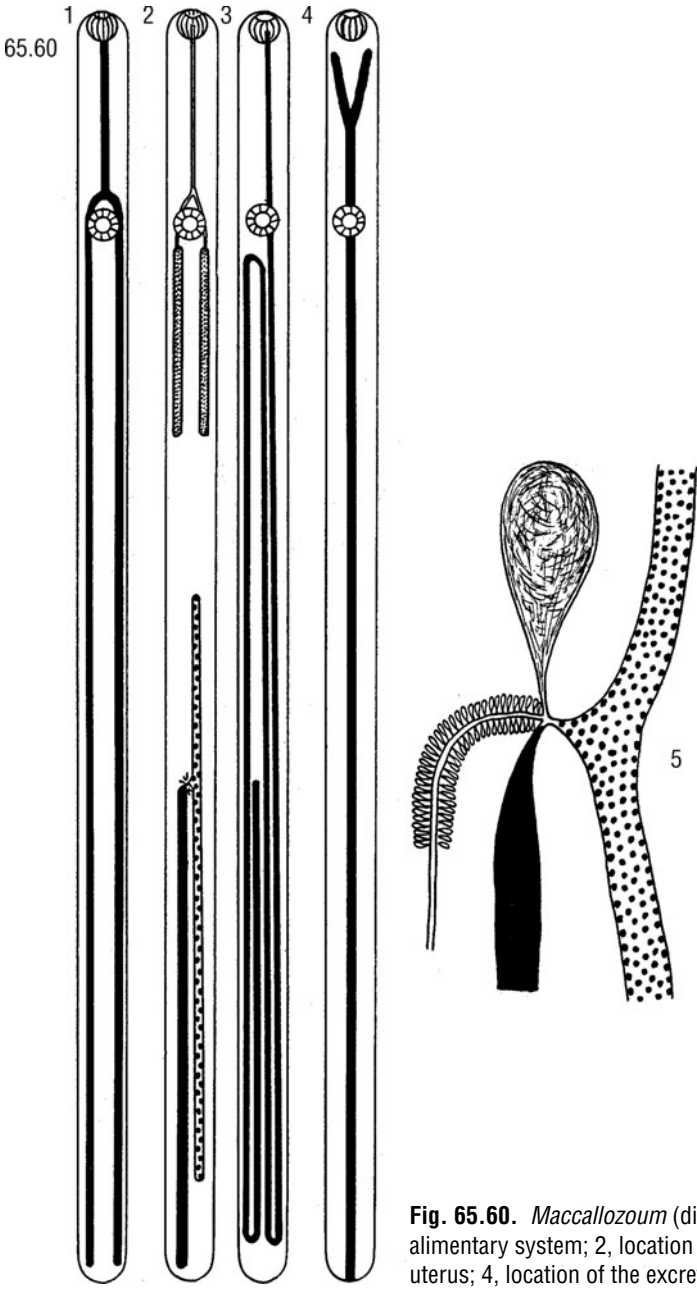



**Fig. 65.60.** *Maccallozoum* (diagrammatic). 1, Location of the alimentary system; 2, location of the gonads; 3, location of the uterus; 4, location of the excretory vesicle; 5, genital junction.

long branch directed posteriorly. Seminal receptacle present. Uterus with three loops. Vitellarium long, unbranched, in posterior half of body. Excretory system Y-shaped, bifurcates close to intestinal bifurcation; pore? In tissues of branchial and buccal cavities of serranids (*Epinephelus*); Atlantic Ocean. Type-species *M. epinepheli* (MacCallum, 1917) Ishii, 1935.

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**3a. Testes parallel** ..... **4.**
**3b. Testes obliquely tandem** ..... ***Neonematobothrioides* Yamaguti, 1970. (Fig. 65.61)**
**Diagnosis:** Not encapsulated. Body elongate, dorsoventrally flattened. Pharynx present. Oesophagus long. Caeca long but not reaching close to posterior extremity. Gland-cells surround posterior part of oesophagus and significant part of caeca (not shown in figure). Testes tubular, obliquely tandem. Vasa efferentia stout, long. Ejaculatory duct long. Genital pore ventral to oral sucker. Genital junction slightly posterior to mid-body. Ovary filiform, unbranched, arises at level of posterior testis, in second or third quarter of body. Both seminal receptacle and uterine seminal receptacle claimed to be present. Excretory vesicle long; anterior regions not known; pore terminal. Vitellarium similar in form to ovary, in posterior half of body. In subcutaneous connective tissue of scombrid (*Thunnus*) and ovaries of myctophid fishes; Pacific and Atlantic Oceans. Type-species *N. poonui* Yamaguti, 1970.

**4a. Posterior regions of paired worms helically intertwined** ..... ***Helicodidymozoon* Anderson & Cribb, 1994. (Fig. 65.62)**
**Diagnosis:** Occur as helically intertwined pairs, completely hermaphroditic. Anterior region attached subterminally to longer, wider, spirally twisted posterior region. Oral sucker terminal. Ventral sucker present or apparently absent, in anterior region. Oesophagus simple. Caeca simple, terminate near posterior extremity. Gland-cells around anterior part of alimentary system absent. Testes cylindrical, paired, extend marginally in anterior half or sometimes almost full length of posterior region. Genital pore at level of oral sucker. Genital junction near anterior extremity of posterior region. Ovary unbranched, filamentous, extends from genital junction to near posterior extremity. Uterus runs towards posterior extremity, forms five loops (two anterior and three posterior) by alternately descending and ascending before entering anterior region of body. Eggs small. Vitellarium unbranched, filamentous, longer than ovary. Excretory system? In tissues of platycephalid teleosts, Western Pacific. Type-species *H. tortor* Anderson & Cribb, 1994.

**4b. Posterior regions of paired worms not helically intertwined** ..... **5.**

**5a. Gland-cells surround anterior part of alimentary system; excretory vesicle without diverticula** ..... ***Metanematobothrioides* Yamaguti, 1965. (Fig. 65.63)**
(Syn. *Indoglomeritrema* Madhavi & Rao, 1983)
**Diagnosis:** Not encapsulated. Body thin, long, dorsoventrally flattened. Pharynx present. Oesophagus short. Caeca reach close to posterior extremity. Gland-cells cover anterior part of caeca. Testes parallel, long, reach close to posterior extremity (one may be somewhat longer than other). Vasa efferentia short, wide. Ejaculatory duct wide, long, almost straight. Genital pore ventral to pharynx. Ovary long, thin, unbranched, in anterior half of body. Seminal receptacle absent. Uterus with single loop. Vitellarium single, unbranched, between posterior extremity and genital junction, which is at about mid-hindbody. Excretory vesicle Y-shaped, without diverticula; stem branches close to intestinal bifurcation; pore terminal. In branchial tissues of lutjanid and serranid (*Epinephelus*) fishes; Indian and Pacific Oceans. Type-species *M. opakapaka* Yamaguti, 1965.

**5b. Gland-cells around anterior part of alimentary system absent; excretory vesicle with diverticula** ..... ***Nematobibothrioides* Noble, 1974. (Fig. 65.64)**
**Diagnosis:** Not encapsulated. Body extremely long, dorsoventrally flattened except for region anterior to ventral sucker, which is oval in cross-section. Pharynx present. Oesophagus long, thin. No gland-cells around anterior part of alimentary system. Caeca reach close to posterior extremity.

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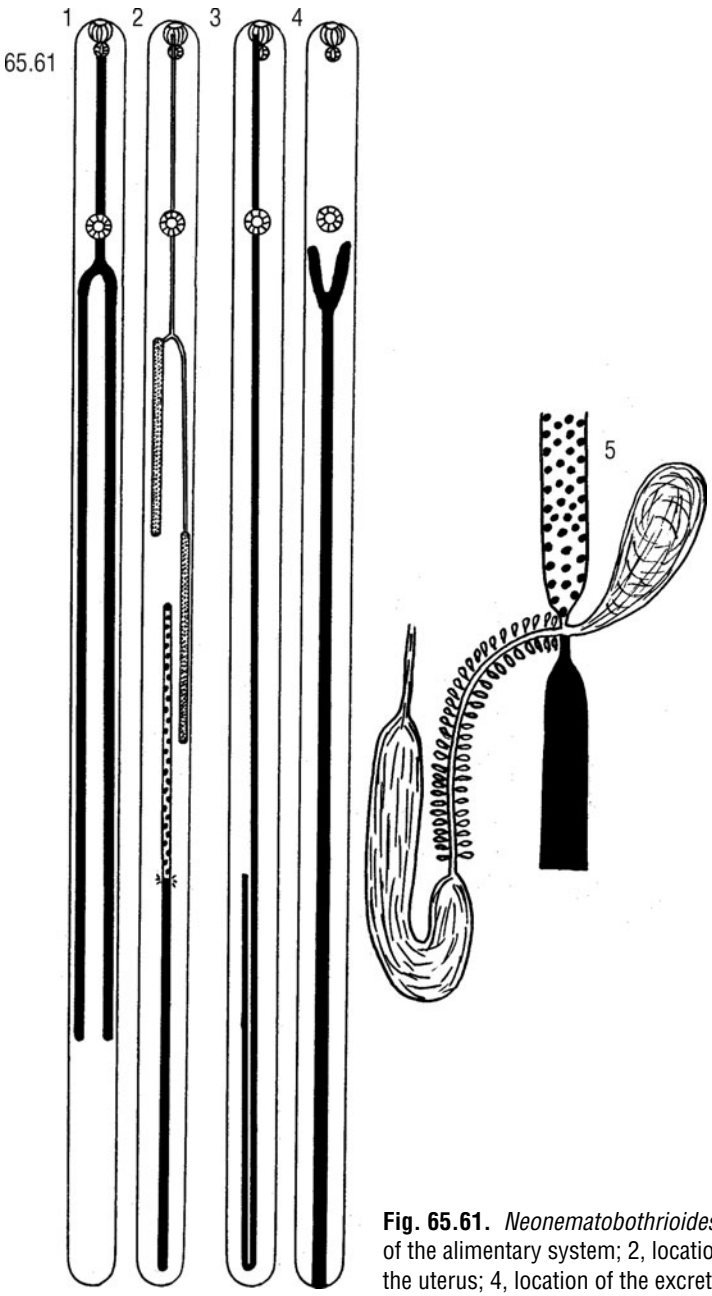



**Fig. 65.61.** *Neonematobothrioides* (diagrammatic). 1, Location of the alimentary system; 2, location of the gonads; 3, location of the uterus; 4, location of the excretory vesicle; 5, genital junction.

Testes parallel, extend along entire length of body, lateral to caeca. Ejaculatory duct long, with well-developed muscular wall. Male and female genital pores separate, at tip of small genital sucker ventral to pharynx. Ovary filiform, in anterior half of body. Seminal receptacle absent. Mehlis' gland large. Uterine seminal receptacle present. Uterus with single loop. Vitellarium similar in form to ovary, but sometimes with small branches, in posterior half of body. Excretory

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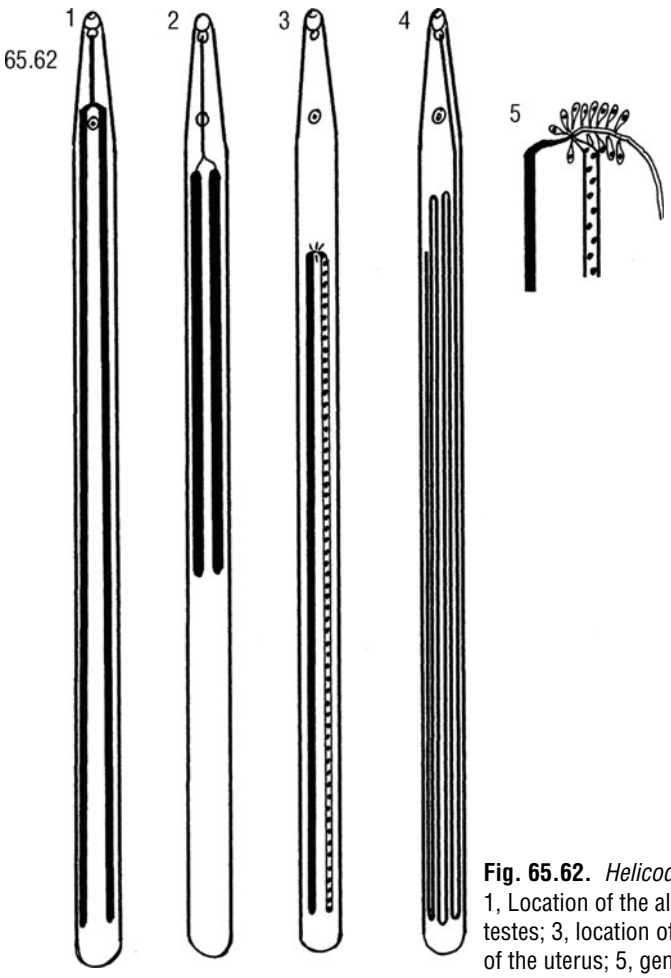



**Fig. 65.62.** *Helicodidymozoon* (diagrammatic). 1, Location of the alimentary system; 2, location of the testes; 3, location of the ovary and vitellarium; 4, location of the uterus; 5, genital junction.

vesicle Y-shaped; arms with numerous diverticula; pore terminal. In connective tissues of molid fishes; Atlantic Ocean. Type-species *N. histoidii* Noble, 1974.

**6a. Pharynx present; ovary with two branches or unbranched; vitellarium with two branches (one anterior and one posterior to genital junction) ..... 7.**
**6b. Pharynx present or absent; ovary and vitellarium unbranched ..... 8.**

**7a. Testes reach close to posterior extremity; ovary with two branches; gland-cells may surround anterior part of alimentary system; in marine teleosts ..... ..... *Metanematobothrium* Yamaguti, 1938. (Fig. 65.65)**

**Diagnosis:** Not encapsulated. Body thin, long. Pharynx present. Caeca reach close to posterior extremity. Gland-cells around oesophagus present or absent. Testes long, parallel, extend along almost entire body-length. Vasa efferentia and ejaculatory duct long. Genital pore ventral to pharynx. Genital junction at about mid-hindbody. Ovary filiform, thin, with two branches; one

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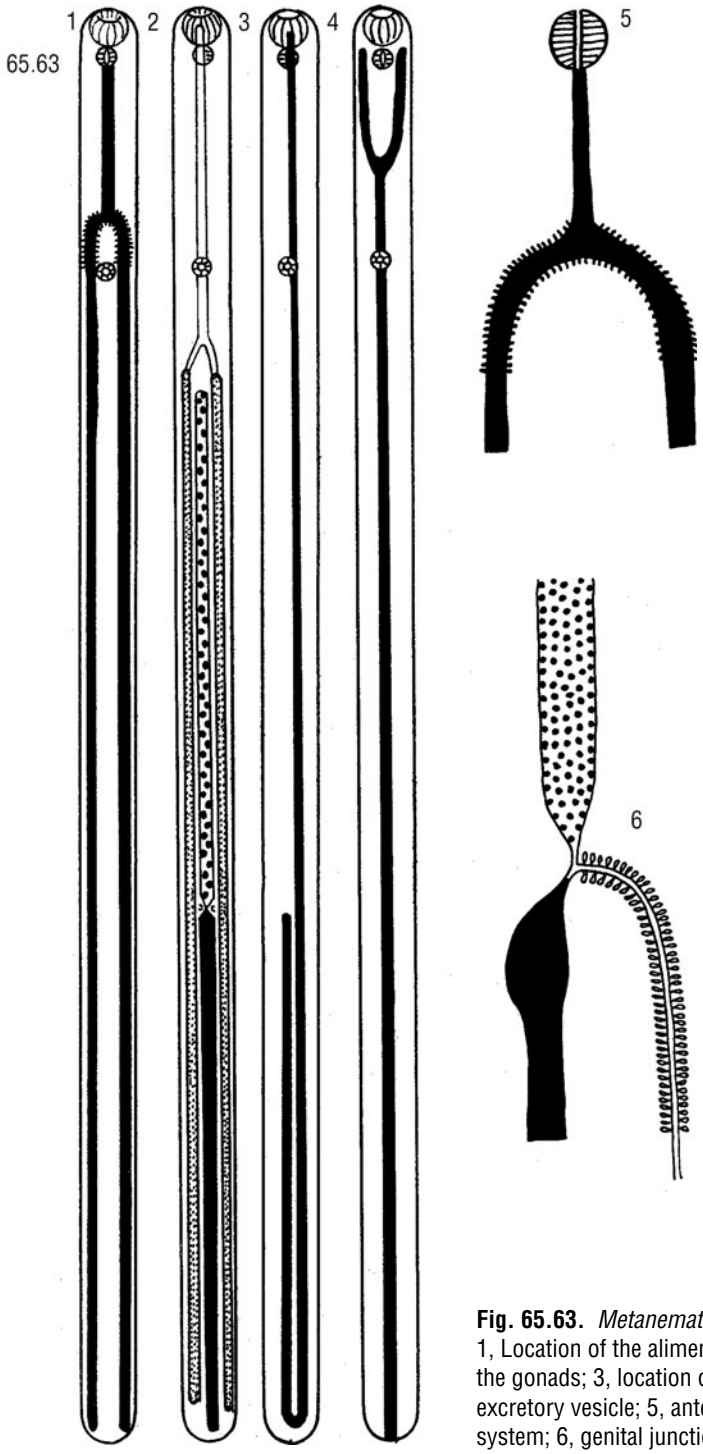



**Fig. 65.63.** *Metanematobothrioides* (diagrammatic). 1, Location of the alimentary system; 2, location of the gonads; 3, location of the uterus; 4, location of the excretory vesicle; 5, anterior part of the alimentary system; 6, genital junction.

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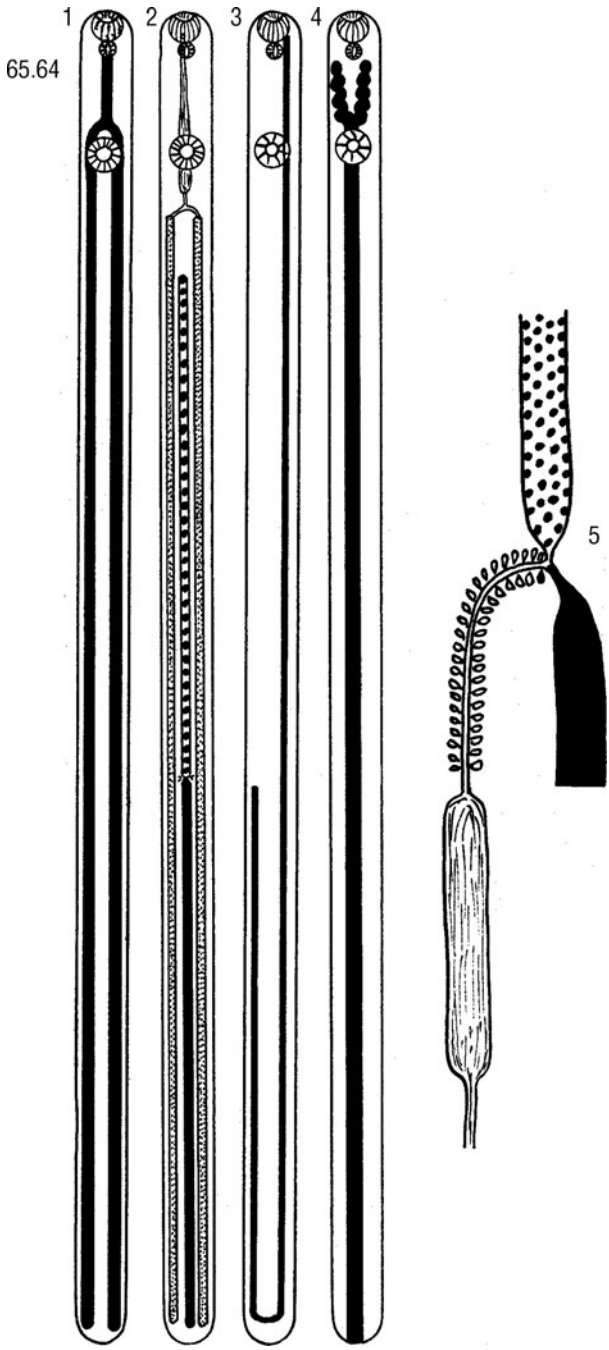



**Fig. 65.64.** *Nematobibothrioides* (diagrammatic). 1, Location of the alimentary system; 2, location of the gonads; 3, location of the uterus; 4, location of the excretory vesicle; 5, genital junction.

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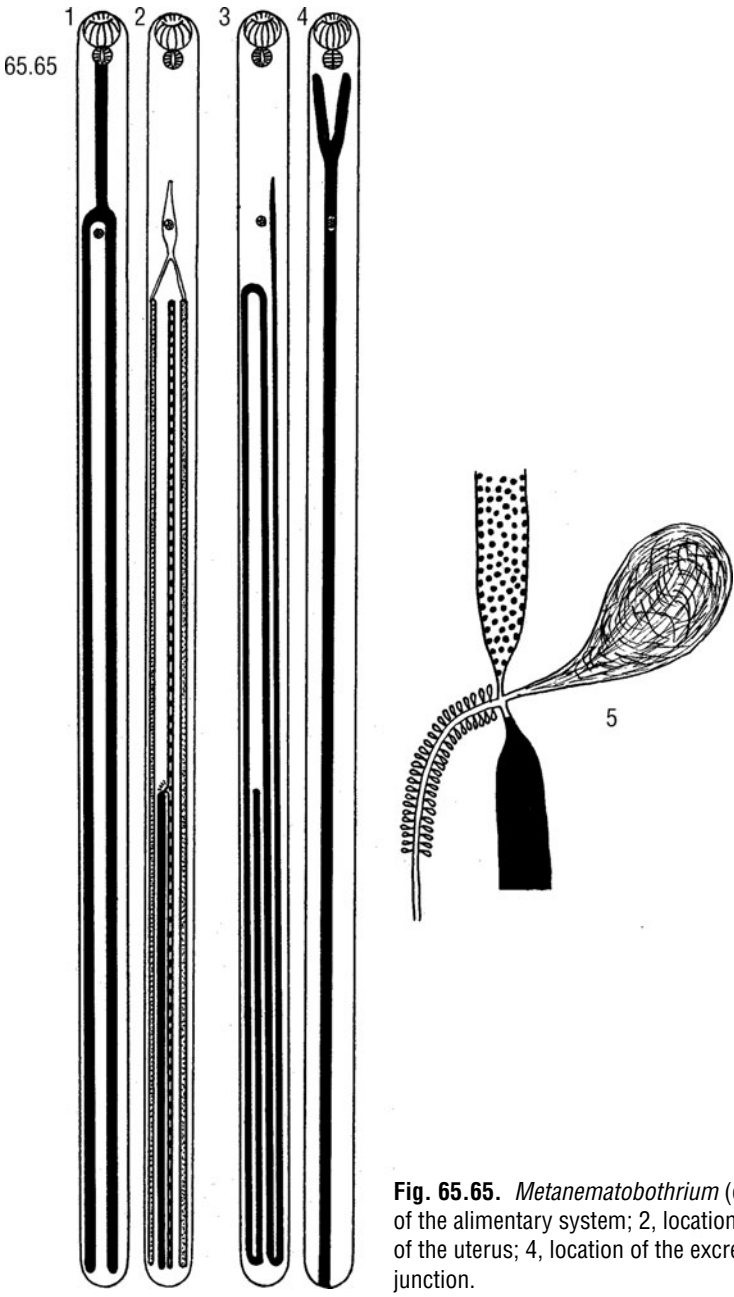



**Fig. 65.65.** *Metanematobothrium* (diagrammatic). 1, Location of the alimentary system; 2, location of the gonads; 3, location of the uterus; 4, location of the excretory vesicle; 5, genital junction.

branch directed anteriorly, other posteriorly. Seminal receptacle present. Uterus forms three loops with numerous coils. Vitellarium filiform, thin, usually with two branches. Excretory vesicle Y-shaped, branches just posteriorly to intestinal bifurcation; pore terminal. In muscles, pericardium, body-cavity and gills, etc. of scombrids and exocoetids; Pacific, Indian and Atlantic Oceans. Type-species *M. guernei* (Moniez, 1891) Yamaguti, 1938.

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**7b. Testes in anterior half of body; ovary unbranched; gland-cells surround anterior part of alimentary system; in freshwater fishes ..... ..... *Ovarionematobothrium* Yamaguti, 1971. (Fig. 65.66)**

**Diagnosis:** Not encapsulated. Body very long, filiform. Pharynx present. Oesophagus short, narrow. Gland-cells around oesophagus present. Caeca reach close to posterior extremity, atrophied posteriorly. Testes elongate, thin, parallel, in anterior half of body; one somewhat longer than other. Male and female genital pores open separately at tip of small genital sucker, ventral to oral sucker. Ovary filiform, unbranched, in anterior half of body. Seminal receptacle present. Uterus with three loops. Vitellarium with two branches, long; one branch directed anteriorly; other posteriorly. Excretory vesicle Y-shaped, branches just posteriorly to intestinal bifurcation; pore? In ovary of freshwater (catostomid) fishes; North America. Type-species *O. texomense* (McIntosh & Self, 1955) Yamaguti, 1971.

**8a. Testes parallel, in anterior half of body; pharynx present; 'Drüsenmagen' absent ..... ..... *Allonematobothrium* Yamaguti, 1965. (Fig. 65.67)**

**Diagnosis:** Encapsulated; capsule spherical or globular. Body filiform, long. Pharynx present. Oesophagus thin, long. 'Drüsenmagen' absent. Caeca simple, reach close to posterior extremity. Gland-cells around oesophagus and anterior part of caeca present. Testes long, parallel, reach almost to mid-body. Genital pore ventral at level of oral sucker. Genital junction close to mid-body. Ovary and vitellarium long, unbranched. Seminal receptacle absent. Uterus with single loop. Excretory vesicle Y-shaped, bifurcates close to intestinal bifurcation; pore? In fins or branchial and buccal cavities of serranid, lutjanid and carangid fishes; Pacific and Atlantic Oceans. Type-species *A. epinepheli* Yamaguti, 1965.

**8b. Testes oblique; pharynx absent; 'Drüsenmagen' present ..... ..... *Neometanematobothrioides* Yamaguti, 1970. (Fig. 65.68)**

**Diagnosis:** Not encapsulated. Body very long. Pharynx absent. Oesophagus long, surrounded by gland-cells (not shown in figure). 'Drüsenmagen' present. Testes oblique. Vasa efferentia of differing lengths. Ejaculatory duct long. Genital pore medioventral to oral sucker. Ovary and vitellarium filiform, unbranched. Seminal receptacle present. Uterus with single loop. Excretory system not studied. In tissues of orbit or branchial and buccal cavities of rachycentrid and carangid (*Seriola*) fishes; Pacific and Atlantic Oceans. Type-species *N. periorbitalis* Yamaguti, 1970.

## Tribe Philopinnini Skrjabin, 1955

**Diagnosis:** Ventral sucker present. Caeca fused at posterior end of body or in posterior third. Type-genus *Philopinna* Yamaguti, 1936.

## Key to genera

**1a. Caeca fused distally to form cyclocoel; ovary and vitellarium parallel, in posterior half of body ..... *Philopinna* Yamaguti, 1936. (Fig. 65.69)**

**Diagnosis:** Body elongate-fusiform, flattened dorsoventrally. Pharynx present. Oesophagus short, thin. Caeca simple, form cyclocoel. Gland-cells around oesophagus present or absent. Testes symmetrical, elongate, slightly curved. Vasa efferentia short. Ejaculatory duct long. Genital pore

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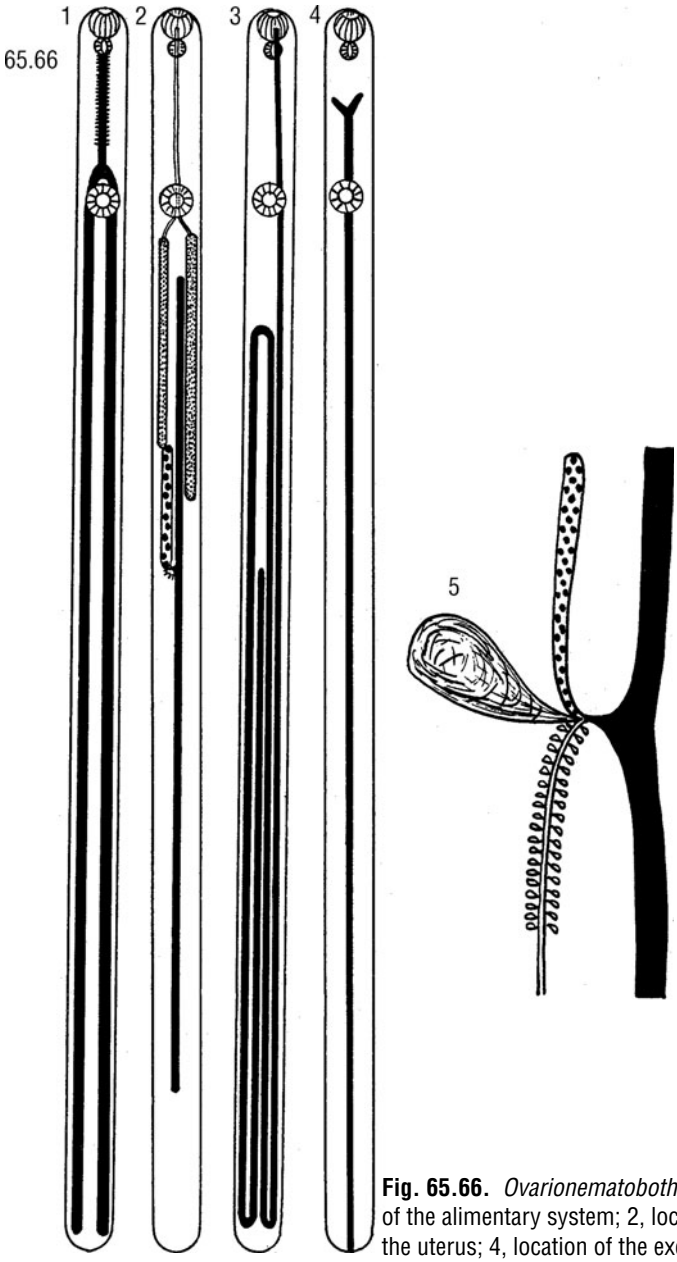



**Fig. 65.66.** *Ovarionematobothrium* (diagrammatic). 1, Location of the alimentary system; 2, location of the gonads; 3, location of the uterus; 4, location of the excretory vesicle; 5, genital junction.

ventral to oral sucker. Genital junction at one-third of body-length. Ovary long, unbranched, curved, in posterior half of body, lateral. Seminal receptacle present. Mehlis' gland well developed. Vitellarium single, unbranched, parallel to ovary, lateral on opposite side to ovary, in posterior half of body. Excretory vesicle Y-shaped, reaches intestinal bifurcation; pore terminal. In tissues (fins, orbit, intestine) of freshwater fishes (cyprinids); Japan and Egypt. Type-species *P. higai* Yamaguti, 1936.

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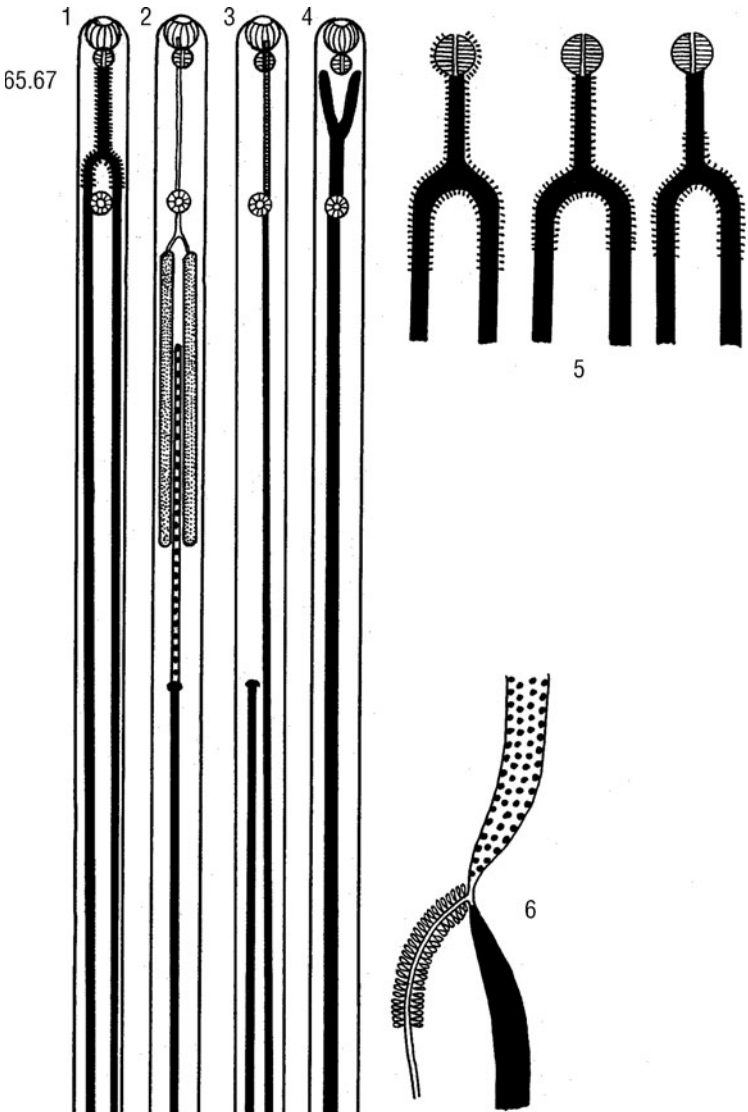



**Fig. 65.67.** *Allonematobothrium* (diagrammatic). 1, Location of the alimentary system; 2, location of the gonads; 3, location of the uterus; 4, location of the excretory vesicle; 5, anterior part of the alimentary system; 6, genital junction.

**1b. Caeca fused at one-third of body-length, forming single 'trunk'; vitellarium postovarian** ..... ***Paraphilopinna*** **Zhukov, 1971. (Fig. 65.70)**

**Diagnosis:** Not encapsulated. Body moderately elongate. Pharynx present. Oesophagus short. Caeca fused to form common 'trunk' at one-third of body-length. Testes parallel, in anterior half

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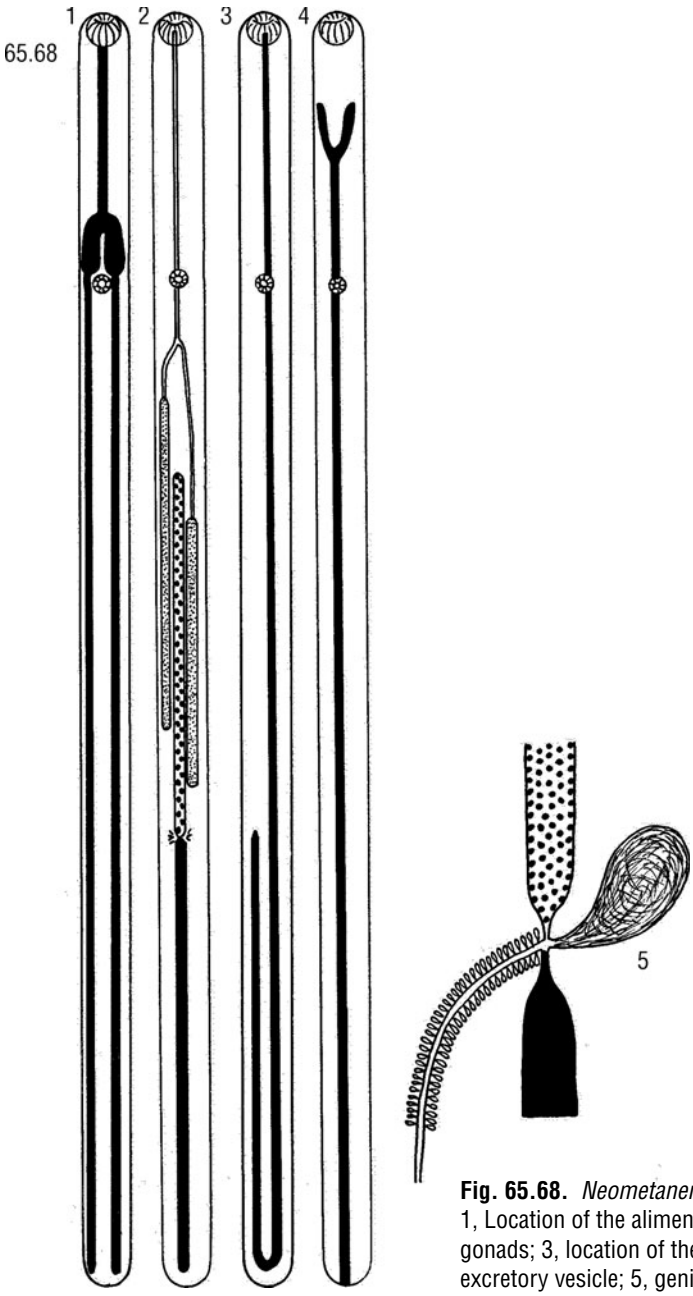



**Fig. 65.68.** *Neometanematobothrioides* (diagrammatic). 1, Location of the alimentary system; 2, location of the gonads; 3, location of the uterus; 4, location of the excretory vesicle; 5, genital junction.

of body. Genital pore ventral to oral sucker. Genital junction close to posterior third of body. Ovary elongate, unbranched, mainly posterior to testes. Seminal receptacle present. Vitellarium similar in form to ovary, postovarian, in posterior third of body. Excretory system not known. In tissues (gonads, urinary system, liver) of cobitid and lateolabracid fishes; Yellow Sea. Type-species *P. fluvialis* Zhukov, 1971.

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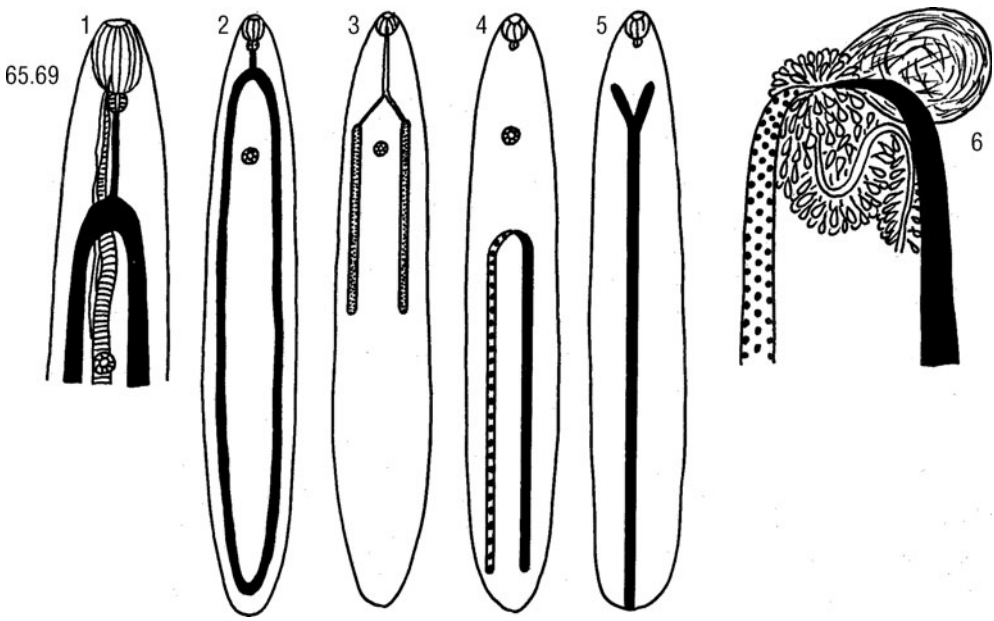



**Fig. 65.69.** *Philopinna* (diagrammatic). 1, Anterior extremity; 2, location of the alimentary system; 3, location of the testes; 4, location of the ovary and vitellarium; 5, location of the excretory vesicle; 6, genital junction.

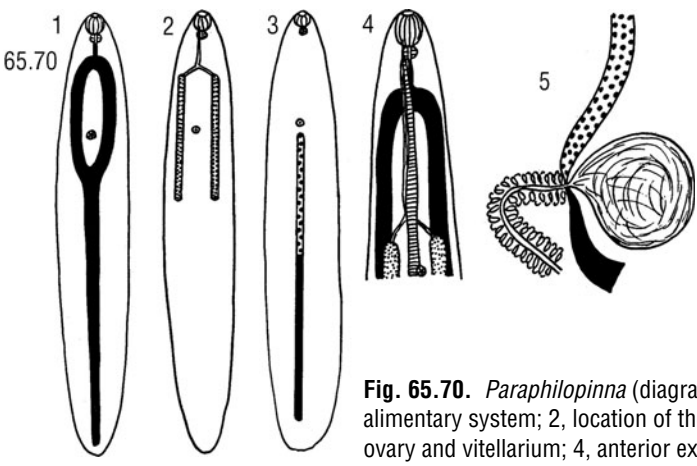



**Fig. 65.70.** *Paraphilopinna* (diagrammatic). 1, Location of the alimentary system; 2, location of the testes; 3, location of the ovary and vitellarium; 4, anterior extremity; 5, genital junction.

## Tribe Unitubulotestini Pozdnyakov, 1993 (emend.)

**Diagnosis:** Ventral sucker absent. Testis single. Type-genus *Unitubulotestis* Yamaguti, 1953.

## Key to genera

**1a. Body dorsoventrally flattened ..... 2.**
**1b. Body filiform, round in cross-section ..... 3.**

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**2a. Testis extends into posterior region of body; 'Drüsenmagen' absent ..... ..... *Procerozoum* Kamegai, 1971. (Fig. 65.71)**

**Diagnosis:** Not encapsulated. Body long, dorsoventrally flattened. Pharynx present. Oesophagus long, thin. 'Drüsenmagen' absent. Caeca reach close to posterior extremity. Ventral sucker absent. Testis long, thin, curved, in posterior half of body. Vas efferens narrow, long. Ejaculatory duct muscular, long. Genital pore ventral, posterior to pharynx. Genital junction at mid-body. Ovary filiform, thin, curved, bifurcate terminally, in anterior half of body. Seminal receptacle absent. Uterus with three loops, with numerous transverse coils. Vitellarium similar in form to ovary, in posterior region of body. Excretory vesicle Y-shaped, branches anterior to intestinal bifurcation; pore? In body-cavity and operculum of exocoeticid and scombrid fishes; Pacific Ocean. Type-species *P. abei* Kamegai, 1971.

**2b. Testis in anterior half of body; 'Drüsenmagen' present ..... ..... *Oculonematobothrium* Murugesh, Krishna Sai Ram & Madhavi, 1992. (Fig. 65.72)**

**Diagnosis:** Not encapsulated. Body long, slender, ribbon-like. Oral sucker small. Pharynx rudimentary. Oesophagus long, narrow. 'Drüsenmagen' present (distal region of caeca enlarged and surrounded by gland-cells); remainder of caeca sinuous, narrow, terminate near posterior extremity. Ventral sucker absent. Testis single, tubular, in anterior third of body, does not reach back to genital junction. Vas deferens forms narrow, sinuous seminal vesicle that runs beside metraterm. Genital pore posteroventral to oral sucker. Genital junction anterior to mid-body. Seminal receptacle indistinct. Ovary long, tubular, winds in anterior third of body anterior to genital junction. Uterus with three loops. Metraterm well developed, long. Eggs elliptical, filamented. Vitellarium tubular, unbranched, in posterior half of body, extending between genital junction and variable distance from posterior extremity. Excretory system not known. In orbital cavity of stromateids (*Pampus*); Indian Ocean. Type-species *O. orbitum* Murugesh, Krishna Sai Ram & Madhavi, 1992.

**3a. 'Drüsenmagen' present; no gland-cells surround anterior parts of alimentary system ..... ..... *Epithelionematobothrium* Yamaguti, 1970. (Fig. 65.73)**

**Diagnosis:** Not encapsulated. Body long, thin. Pharynx present. Oesophagus short. Thick-walled 'Drüsenmagen' present. Gland-cells surrounding anterior parts of alimentary system absent. Caeca reach close to posterior extremity; 'epithelial' lining distinct. Testis long, curved, preovarian. Vas efferens thin, long. Ejaculatory duct muscular, long. Genital pore ventral, posterior to pharynx. Genital junction in posterior region of body. Ovary filiform, unbranched, posttesticular, in anterior region of hindbody. Seminal receptacle present. Uterus with single loop. Vitellarium similar in form to ovary, in posterior region of body. Excretory system not known. In connective tissue of stomach wall and body-cavity of mullid and istiophorid fishes; Pacific and Indian Oceans. Type-species *E. mulloidichthydis* Yamaguti, 1970.

**3b. Caeca simple, without 'Drüsenmagen'; gland-cells may surround anterior parts of alimentary system ..... *Unitubulotestis* Yamaguti, 1953. (Fig. 65.74)**

**Diagnosis:** Encapsulated. Body elongate. Pharynx present. Oesophagus thin, simple. 'Drüsenmagen' absent. Gland-cells around oesophagus present or absent. Caeca reach close to posterior extremity. Testis more or less elongate, curved or not. Genital pore at level of pharynx. Genital junction close to anterior or posterior third of body. Ovary long, unbranched, curved or not, in anterior half of body. Juel's organ present or absent. Uterus with single loop, forms numerous transverse coils. Vitellarium with analogous form to ovary, in posterior half of body. Excretory system Y-shaped; branches anterior to intestinal bifurcation; pore? In buccal and branchial tissues, body-cavity and mesenteries of carangid, istiophorid, scombrid, mullid and exocoetid fishes; Pacific, Indian and Atlantic Oceans. Type-species *U. carangis* Yamaguti, 1953.

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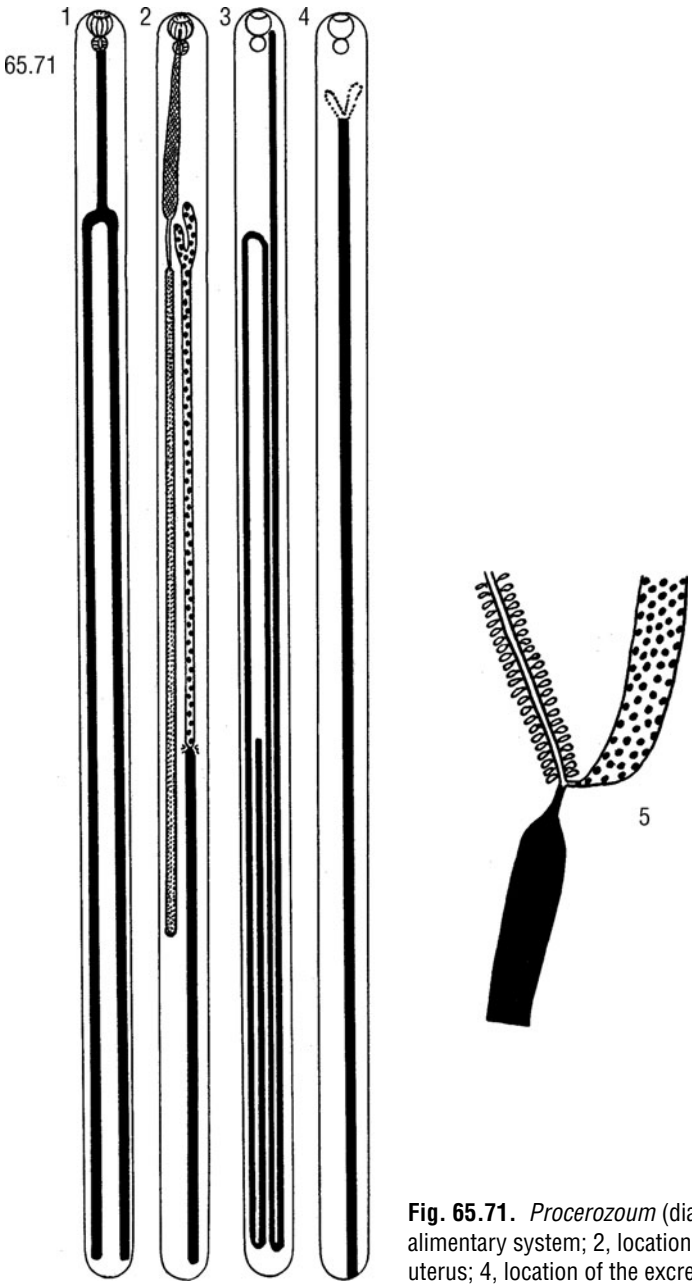



**Fig. 65.71.** *Procerozoum* (diagrammatic). 1, Location of the alimentary system; 2, location of the gonads; 3, location of the uterus; 4, location of the excretory vesicle; 5, genital junction.

## Subfamily Nephrodidymotrematinae Yamaguti, 1970

**Diagnosis:** Posterior regions of individuals in fused capsule. Sexual dimorphism strongly expressed. Body divided into two regions. Anterior regions elongate, widened in anterior third. Posterior regions fused on one side, such that males and females cannot be separated. Male substantially smaller than female. Ventral

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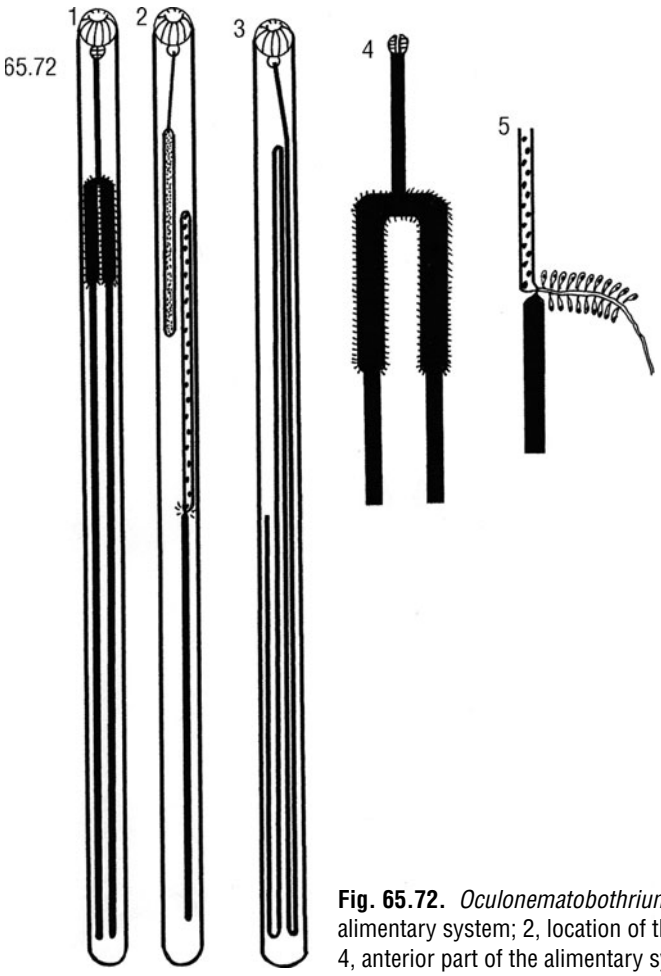



**Fig. 65.72.** *Oculonematobothrium* (diagrammatic). 1, Location of the alimentary system; 2, location of the gonads; 3, location of the uterus; 4, anterior part of the alimentary system; 5, genital junction.

sucker absent. Pharynx present. Oesophagus short, surrounded by gland-cells. Caeca extend into posterior region. *Male*: Testis single, recurved, occupies most of posterior region. Ejaculatory duct long. Genital pore ventral to oral sucker. Rudiments of female genital system present. *Female*: Ovary and vitellarium branched, long. Seminal receptacle present. Genital pore ventral to oral sucker. Excretory system not known. In kidneys of scombrid (*Thunnus*) fishes; Pacific Ocean. Type-genus *Nephrodidymotrema* Yamaguti, 1970.

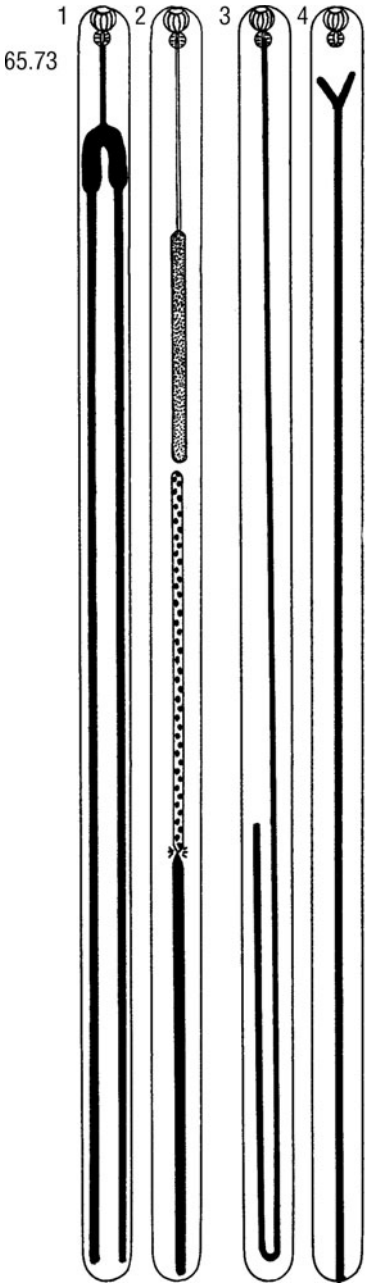
## Genus *Nephrodidymotrema* Yamaguti, 1970 (Fig. 65.75)

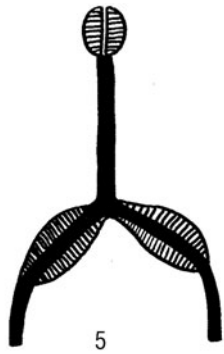
**Diagnosis:** With characters of subfamily. Type-species *N. ahi* Yamaguti, 1970.

## Classification of juvenile didymozoids

Juvenile specimens of the Didymozoidae, which are occasionally encountered in the intestines of a range of fish and squid third intermediate or paratenic hosts, possess a rather uniform structure.

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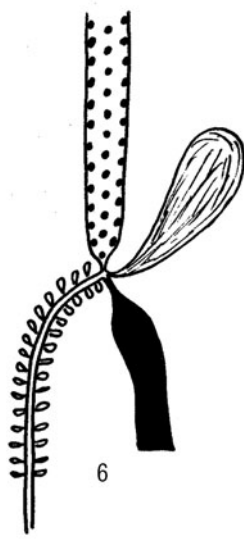




**Fig. 65.73.** *Epithelionematobothrium* (diagrammatic). 1, Location of the alimentary system; 2, location of the gonads; 3, location of the uterus; 4, location of the excretory vesicle; 5, anterior part of the alimentary system; 6, genital junction.

Their rapid morphogenesis and formation of the adult stage start only after reaching the final sites within the definitive host, usually pelagic, piscivorous teleosts and especially scombroids. It has been suggested that scientific names be given to these juveniles, often referred to as metacercariae,[7]

[7] True metacercariae are expected to occur in invertebrates, as indicated above, especially crustaceans, as in the case of many other hemiuroid groups.

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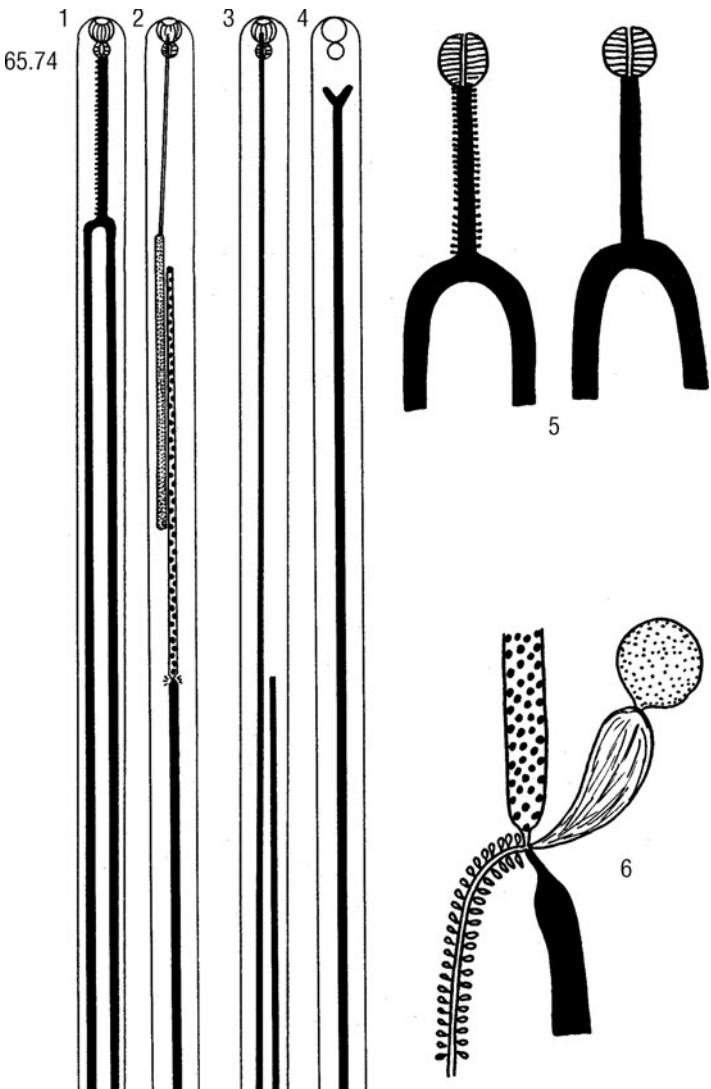



**Fig. 65.74.** *Unitubulotestis* (diagrammatic). 1, Location of the alimentary system; 2, location of the gonads; 3, location of the uterus; 4, location of the excretory vesicle; 5, anterior part of the alimentary system; 6, genital junction.

for identification purposes (Yamaguti, 1942a; Fischthal & Kuntz, 1964b; Nikolaeva, 1964, 1965, 1970; Kurochkin & Nikolaeva, 1978; Parukhin, 1989). In the past, these 'larvae' have been known under names such as *Distoma fenestratum* Linton, 1907. In other cases, juveniles with different structures have been given numerical (Nikolaeva, 1964, 1965, 1970; Gaevskaya & Nigmatullin, 1976; Kurochkin & Nikolaeva, 1978; Køie & Lester, 1985) or alphabetical (Fischthal & Kuntz, 1964b; Gaevskaya, 1977) labels. Such juveniles have been assigned to particular structural 'types' (Monilicaecum, Torticaecum, Postmonilicaecum, Posttorticaecum, Premonilicaecum, Pretorticaecum), not to be confused with generic names, as proposed by Yamaguti (1942a, 1970,

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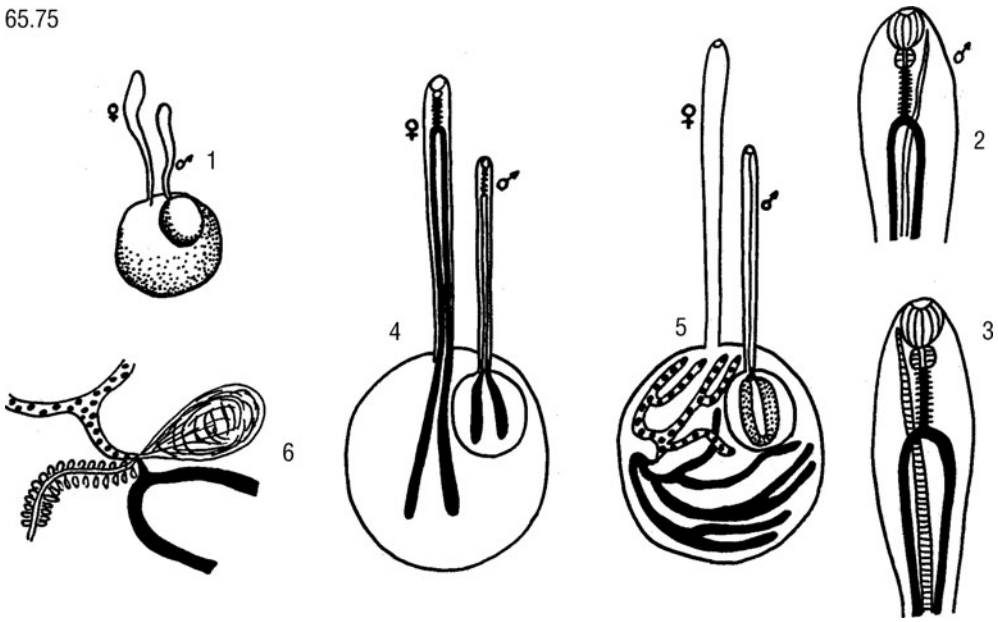



**Fig. 65.75.** *Nephrodidymotrema* (diagrammatic). 1, Entire worms; 2, anterior extremity of male; 3, anterior extremity of female; 4, location of the alimentary system; 5, location of the gonads; 6, genital junction.

1971, 1975), Overstreet & Hochberg (1975), Shimazu (1978), Nagasawa & Marumo (1979), Naidenova *et al.* (1985), Parukhin (1989) and Pozdnyakov (1989a).

Kurochkin & Nikolaeva (1978) suggested a provisional nomenclatural system for the didymozoid juveniles, differentiating 11 genera based on the presence or absence of a ventral sucker, pharynx, 'Drüsenmagen' and gland-cells around the oesophagus and/or anterior parts of the caeca. Køie & Lester (1985) criticized some aspects of this system. They agree with Yamaguti (1970, 1975), who suggested that new generic and species names should not be given to juvenile didymozoids. Køie & Lester (1985) considered that the degree of development of certain characters of these juveniles change with age, which makes it impossible to classify them to either generic or specific level. They suggested a numerical and alphabetical arrangement of juveniles, which Pozdnyakov (1996) believed would lead to some confusion. At the same time, he agreed that the morphological characters of such didymozoid juveniles do change to a degree with age. This mainly depends on the stage recovered from the second intermediate, third intermediate (?paratenic) or definitive host. The examination of ample and diverse material of didymozoid juveniles, from fish and squid in the Pacific Ocean, has shown that all morphological changes characteristic of the larvae at this stage take place within the range of their particular structural 'types'. On the other hand, it is impossible to confidently identify whether or not we are dealing with the members of a given subfamily, tribe or genus. It may be that, as a result of a more detailed and intensive study of the developmental cycles of didymozoids and their morphogenesis, it will be possible to link the structural 'type' of juvenile with a given taxonomic group of adult. Given the conditional nature of the juvenile classification, Pozdnyakov (1996) considered that the view of Yamaguti (1970, 1975), in relation to the necessity of using structural 'types' for identification

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purposes, should be followed. Both Yamaguti and Køie & Lester (1985) rightly considered that the description of new, or even provisional, genera for juvenile didymozoids should be discouraged, since, eventually, when their affiliation with known genera becomes established, a large number of synonyms will be formed. The provisional system suggested by Kurochkin & Nikolaeva (1978) is nothing more than the structural 'types' of juvenile in the sense of Yamaguti (1942a, 1970, 1975).

It should be agreed that structural 'types' of juvenile didymozoids are not considered as genera and, moreover, there should be no assignation of type-species. In view of the above comments, the system and key for structural 'types' of didymozoid juveniles are proposed as follows (Fig. 65.76).

Juveniles of the Anesophagus type described by Kurochkin & Nikolaeva (1978) represent an early stage of the development of the Pseudotorticaecum type. The observation on the absence of the oesophagus in these larvae is evidently erroneous, since study of abundant material has shown the presence of an oesophagus surrounded by numerous glands in juveniles with a similar structure. It should be stressed that the presence of a well-developed alimentary system possessing all the elements observed in adult forms is a characteristic feature for didymozoid juveniles, and there are no adult didymozoids lacking an oesophagus. It should also be noted that the 'larval' types Posttorticaecum and Pseudomonilicaecum proposed by Yamaguti (1970, 1975) are of little use. These developmental stages are found in the definitive host, being an intermediate stage between the juvenile from the third intermediate (paratenic) host and the young adult.

## Keys to forms of didymozoid juveniles

**1a. Ventral sucker absent** ..... **2.**
**1b. Ventral sucker present** ..... **3.**

**2a. No gland-cells surround oesophagus and anterior parts of caeca** ..... **type Anacetabulum of Kurochkin & Nikolaeva (1978). (Fig. 65.76.3)**
Body elongate, considerably tapered anteriorly and rounded posteriorly. Oral sucker terminal. Ventral sucker absent. Pharynx small. Oesophagus long, narrow. Caeca curved, with poorly developed chambers of caecal lumina. No gland-cells surround oesophagus and anterior parts of caeca. Excretory vesicle spherical, posterior to caeca.

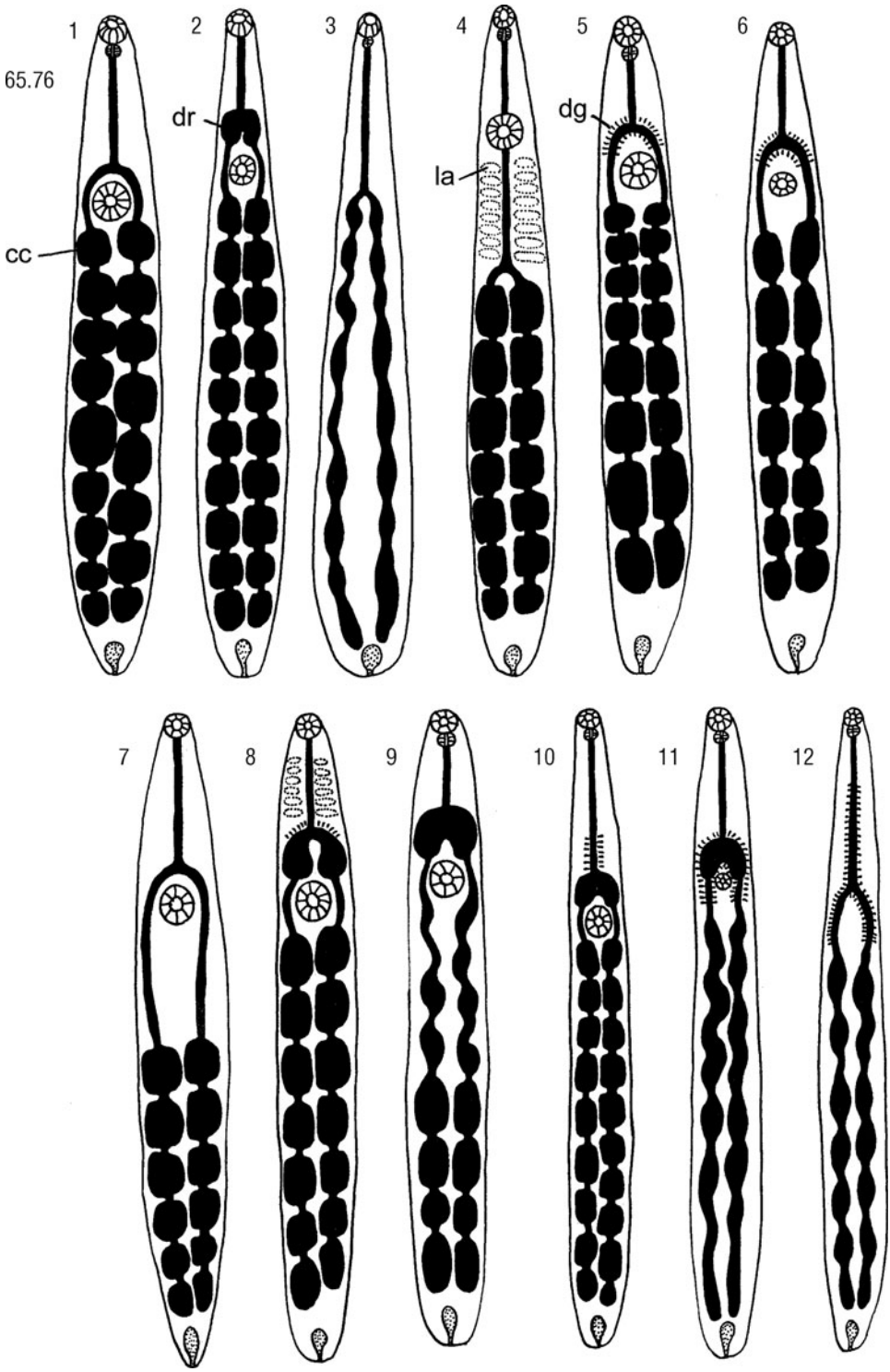
**2b. Gland-cells surround oesophagus and anterior parts of caeca** ..... **type Pseudoanacetabulum of Pozdnyakov (1996). (Fig. 65.76.12)**
Body moderately long, tapered anteriorly and bluntly rounded posteriorly. Oral sucker terminal. Ventral sucker absent. Pharynx small. Oesophagus long, thin. 'Drüsenmagen' absent. Caeca curved, with poorly developed chambers. Oesophagus and anterior parts of caeca surrounded by gland-cells. Excretory vesicle saccular, posterior to caeca.

**3a. Pharynx present** ..... **4.**
**3b. Pharynx absent** ..... **9.**

**4a. 'Drüsenmagen' absent** ..... **5.**
**4b. 'Drüsenmagen' present** ..... **7.**

**5a. Intestinal bifurcation anterior to ventral sucker** ..... **6.**

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**5b. Intestinal bifurcation posterior to ventral sucker ..... type Postacetabulicaecum of Kurochkin & Nikolaeva (1978). (Fig. 65.76.4)**
Body elongate, rather long, with conical, tapered anterior extremity. Oral sucker terminal. Ventral sucker large, shifted towards anterior extremity. Pharynx present. Oesophagus long, extends into hindbody. 'Drüsenmagen' absent. Intestinal bifurcation posterior to mid-body. Chambers of caecal lumina well developed. Excretory vesicle saccular, posterior to caeca. Regularly alternating chambers and lacunae present in parenchyma between ventral sucker and intestinal bifurcation.

**6a. No gland-cells surround oesophagus and anterior parts of caeca ..... type Torticaecum of Yamaguti (1942a). (Fig. 65.76.1)**
Body moderately elongate, fusiform. Oral sucker terminal. Ventral sucker larger than oral, sunk in parenchyma. Pharynx well developed, rarely poorly developed. Oesophagus long, narrow. 'Drüsenmagen' absent. Intestinal bifurcation anterior to ventral sucker. Chambers of caecal lumina well developed, occupy two-thirds of posterior part of body. Gland-cells around oesophagus and anterior parts of caeca absent. Parenchymal glands in subtegumental layer well developed. Excretory vesicle saccular, posterior to caeca.

**6b. Gland-cells surround oesophagus and anterior parts of caeca ..... type Neotorticaecum of Kurochkin & Nikolaeva (1978). (Fig. 65.76.5)**
Body elongate. Anterior region somewhat tapered; posterior region bluntly rounded. Oral sucker subterminal. Ventral sucker larger than oral, in anterior quarter of body. Pharynx present. Oesophagus short, thin. 'Drüsenmagen' absent. Intestinal bifurcation surrounded by gland-cells, anterior to ventral sucker. Caeca form chambers posterior to ventral sucker; chambers increase in size towards posterior extremity. Excretory vesicle saccular, in posterior end posterior to caeca, or long, reaches ventral sucker.

**7a. Gland-cells surround anterior parts of alimentary system ..... 8.**
**7b. No gland-cells surround anterior parts of alimentary system ..... type Paramonilicaecum of Kurochkin & Nikolaeva (1978). (Fig. 65.76.9)**
Body elongate, slightly tapering towards anterior extremity, with bluntly rounded extremities. Oral sucker large, terminal. Ventral sucker larger than oral. Pharynx small. Oesophagus short, thin. 'Drüsenmagen' present, anterior to ventral sucker. Caeca form well-developed chambers only in posterior third of body. No gland-cells surround anterior parts of alimentary system. Excretory vesicle saccular, with well-developed walls, posterior to caeca.

**8a. Gland-cells around distal part of oesophagus anterior to 'Drüsenmagen' ..... type Neomonilicaecum of Kurochkin & Nikolaeva (1978). (Fig. 65.7.10)**
Body elongate, long. Oral sucker large, terminal. Ventral sucker larger than oral. Pharynx small. Oesophagus long, narrow, with distal region surrounded by gland-cells. 'Drüsenmagen' distinct. Caeca form chambers, which are particularly well developed in posterior third of body. Gland-

**Fig. 65.76.** (*Opposite*) 'Types' of didymozoid metacercariae. 1, Torticaecum; 2, Monilicaecum; 3, Anacetabulum; 4, Postacetabulicaecum; 5, Neotorticaecum; 6, Pseudotorticaecum; 7, Paratorticaecum; 8, Pseudomonilicaecum; 9, Paramonilicaecum; 10, Neomonilicaecum; 11, Allomonilicaecum; 12, Pseudoanacetabulum. *Abbreviations*: cc, caecal chambers; Dr, 'Drüsenmagen'; la, lacunae; dg, digestive glands.

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cells around distal part of oesophagus anterior to 'Drüsenmagen'. Excretory vesicle tear-shaped, posterior to caeca. Regularly alternating lacunae distinguishable in parenchyma.

**8b. Gland-cells surround 'Drüsenmagen' and anterior parts of caeca ..... ..... type Allomonilicaecum of Pozdnyakov (1996). (Fig. 65.76.11)**
Body elongate, filiform, tapered at both extremities. Oral sucker terminal. Ventral sucker smaller than oral. Pharynx small. Oesophagus long, thin. 'Drüsenmagen' present. Caeca curved, with poorly developed chambers. Gland-cells surround 'Drüsenmagen' and anterior part of caeca. Excretory vesicle saccular, posterior to caeca.

**9a. 'Drüsenmagen' absent ..... 10.**
**9b. 'Drüsenmagen' present ..... 11.**

**10a. No gland-cells around oesophagus and anterior parts of caeca ..... ..... type Paratorticaecum of Kurochkin & Nikolaeva (1978). (Fig. 65.76.7)**
Body elongate, tapered at extremities. Oral sucker spherical, terminal. Ventral sucker large. Pharynx absent. Intestinal bifurcation anterior to ventral sucker. 'Drüsenmagen' absent. Caeca form chambers from about mid-body to posterior extremity. No gland-cells around oesophagus and anterior parts of caeca. Well-developed parenchymal gland-cells present in subtegumental layer. Excretory vesicle saccular, with well-developed walls, posterior to caeca.

**10b. Gland-cells surround oesophagus and anterior parts of caeca ..... ..... type Pseudotorticaecum of Kurochkin & Nikolaeva (1978). (Fig. 65.76.6)**
Body elongate, tapered anteriorly. Oral sucker terminal. Ventral sucker present. Pharynx absent. Oesophagus short, thin, surrounded by gland-cells. Intestinal bifurcation surrounded by gland-cells, anterior to ventral sucker. 'Drüsenmagen' absent. Caecal chambers developed posterior to ventral sucker. Excretory vesicle saccular, posterior to caeca.

**11a. No gland-cells around distal part of oesophagus anterior to 'Drüsenmagen' ..... ..... type Monilicaecum of Yamaguti (1942a). (Fig. 65.76.2)**
Body moderately elongate, considerably tapered anteriorly. Oral sucker terminal. Ventral sucker larger than oral, sunk in parenchyma. Pharynx absent. Oesophagus narrow, short or long. Gland-cells around oesophagus absent. 'Drüsenmagen' well developed, anterior to ventral sucker. Caeca curved, form alternating chambers. Excretory vesicle saccular, posterior to caeca.

**11b. Gland-cells surround distal part of oesophagus and/or anterior 'Drüsenmagen' ..... ..... type Pseudomonilicaecum of Kurochkin & Nikolaeva (1978). (Fig. 65.76.8)**
Body elongate, more or less tapered anteriorly. Oral sucker terminal. Ventral sucker smaller or larger than oral. Pharynx absent. Oesophagus long, thin. 'Drüsenmagen' very distinct, anterior to ventral sucker. Gland-cells surround distal part of oesophagus and/or anterior 'Drüsenmagen'. Caeca form well-developed chambers posterior to ventral sucker. Excretory vesicle saccular, thick-walled, posterior to caeca. Regularly alternating lacunae present in anterior half of body.

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# 66 Genera *incertae sedis*, genera *inquirenda*, *nomina nuda*, larval or collective names and recently erected genera

*Including contributions from*
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This chapter includes diagnoses of genera *incertae sedis* and lists of other digenean names not used elsewhere in these volumes of keys.

## Genera *incertae sedis* in the superfamily Plagiorchioidea (*sensu lato*)

*T. Pojmańska*

### Genus *Allocorrigia* Turner & Corkum, 1977

*Allocorrigia* was established by Turner & Corkum (1977) for a progenetic metacercaria found in crayfish, and affiliated to the family Dicrocoeliidae Looss, 1899. Indeed the morphology of the only species of this genus, *A. filiformis* Turner & Corkum, 1977, resembles that of other dicrocoeliids, especially those of the genera *Corrigia* Shtrom, 1940 and *Skrjabinosomum* Evranova, 1944. Nevertheless, it differs from all the dicrocoeliids by an enormously long body with separated gonads, the large, deeply lobed, 'finger-like' follicles of the vitellarium and the lack of a seminal receptacle. The main differences concern, however, some biological characters, such as the involvement of aquatic animals as its hosts and the tendency to progenesis in the second intermediate host. For this reason, *Allocorrigia* has been excluded from the family Dicrocoeliidae and left as a genus *incertae sedis* in the superfamily Plagiorchioidea. The determination of its affinities and proper position within this superfamily needs some further, perhaps genetic, studies.

### Genus *Allocorrigia* Turner & Corkum, 1977 (Fig. 66.1)

**Diagnosis:** Body very long, narrow; hindbody very long. Tegument armed with spines. Suckers small. Oral sucker terminal. Ventral sucker smaller than oral, near anterior extremity. Prepharynx short. Pharynx muscular. Oesophagus very short or absent. Intestinal bifurcation in anterior fore-

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body. Caeca asymmetrical, not reaching close to posterior extremity. Testes longitudinally elongate, tandem, in anterior quarter of body, distant from ventral sucker and from one another. Cirrus-sac large, elongate, between intestinal bifurcation and ventral sucker. Seminal receptacle absent. Genital pore bifurcal. Ovary round, distant from posterior testis. Uterus with non-coiled descending and ascending limbs, intercaecal. Vitellarium posterior to ovary, composed of large, deeply lobed (digitiform) follicles, loosely arranged in two long bands overlapping caeca. Excretory vesicle I-shaped, reaches level of vitelline zone. Progenetic metacercariae in antennal and green glands of crayfish; first intermediate and final host (if any exist) not known; USA. Type-species *A. filiformis* Turner & Corkum, 1977.

## Genus *Neodicrocoelium* Agrawal & Sharma, 1990

*Neodicrocoelium* was established by Agrawal & Sharma (1990a) for a digenean found in the intestine of the fish *Channa marulius* in India. As its morphology did not fit any of the subfamilies in the family Dicrocoeliidae Looss, 1899, the authors erected the subfamily Neodicrocoeliinae Agrawal & Sharma, 1990.

Although such features as the position of the ovary posterior to the testes and the long, tubular excretory vesicle relate *Neodicrocoelium* to the dicrocoeliids, it differs from all other genera by the extraordinary structure of the vitellarium, which is dispersed throughout the whole body, by the non-operculate eggs and by its aquatic final host. For this reason *Neodicrocoelium* is transferred from the Dicrocoeliidae to the genera *incertae sedis* in the superfamily Plagiorchioidea, until its proper position within this superfamily is determined.

It seems very probable that *Paradictinogryptus*, previously established in the family Dicrocoeliidae by Agrawal & Sharma (1989) (and treated in the family Dicrocoeliidae as a *nomen nudum* because of its very poor description) is the senior synonym of *Neodicrocoelium* Agrawal & Sharma, 1990 (the same fish host and the same locality of collection), but Agrawal & Sharma (1990a) did not consider such a possibility.

## Genus *Neodicrocoelium* Agrawal & Sharma, 1990 (Fig. 66.2)

**Diagnosis:** Body longitudinally oval. Tegument unspined. Oral sucker larger than ventral. Ventral sucker at about middle of body length. Pharynx muscular, relatively large. Oesophagus short. Intestinal bifurcation in mid-forebody. Caeca narrow, reach to posterior extremity. Testes just posterior to ventral sucker, symmetrical. Cirrus-sac saccular, between intestinal bifurcation and ventral sucker. Genital pore posterior to intestinal bifurcation. Ovary median, just posterior to testes, larger than testes. Uterus occupies whole body. Eggs non-operculate. Vitelline follicles small, extremely numerous, dispersed throughout entire body. Excretory vesicle tubular, reaching to ovary. In intestine of fish (*Channa*); India. Type-species *N. gayaparsadai* Agrawal & Sharma, 1990.

## Genera *incertae sedis* in the superfamily Plagiorchioidea (*sensu lato*) and other superfamilies

*V.V. Tkach*

It is not yet clear in which families the following genera should be placed.

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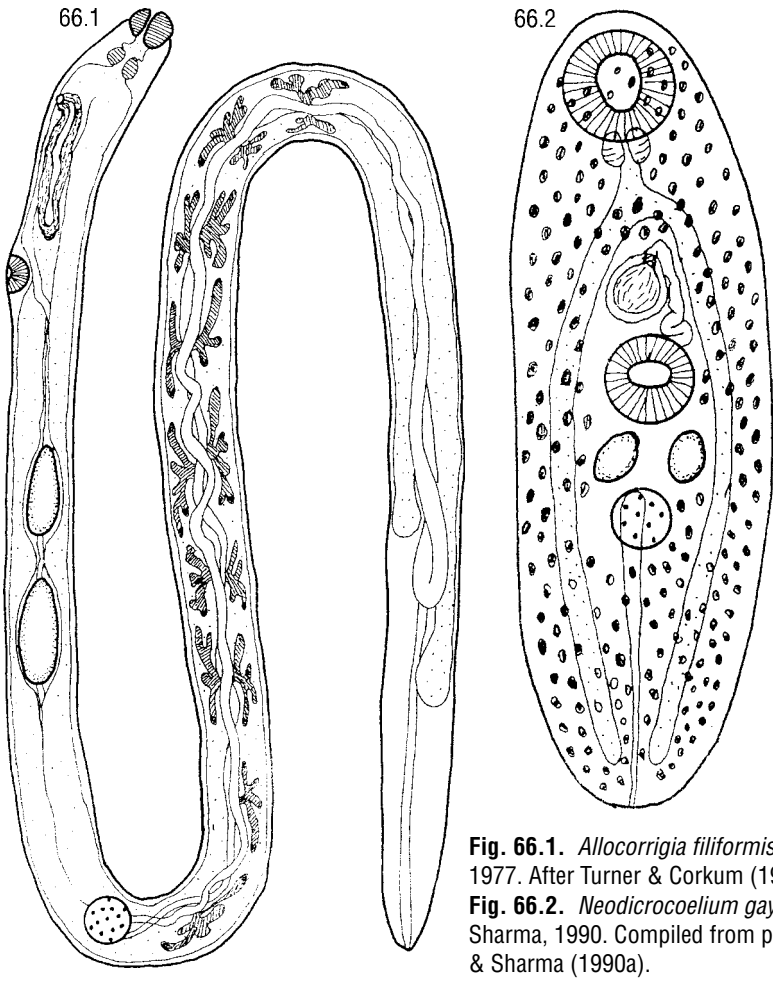



**Fig. 66.1.** *Allocorrigia filiformis* Turner & Corkum, 1977. After Turner & Corkum (1977).
**Fig. 66.2.** *Neodicrocoelium gayaparsadai* Agrawal & Sharma, 1990. Compiled from photographs in Agrawal & Sharma (1990a).

## Genus *Deurithitrema* Blair, 1985 (Fig. 66.3)

**Diagnosis:** Body elongate, with dorsoventrally compressed forebody and cylindrical or subcylindrical hindbody. Tegument spinous. Oral sucker ventrally subterminal. Ventral sucker preequatorial, slightly larger than oral sucker. Prepharynx very short. Pharynx present. Oesophagus absent. Intestinal bifurcation in anterior forebody. Caeca reach posterior end of body. Testes ovoid, tandem, contiguous or almost so in middle third of body. Cirrus-sac extends well into hindbody, contains bipartite (usually) seminal vesicle, pars prostatica and ejaculatory duct with spines around opening into genital atrium. Genital atrium muscular. Genital pore median or almost so, immediately anterior to ventral sucker. Ovary ovoid, median or submedian, between ventral sucker and anterior testis. Seminal receptacle between ovary and anterior testis. Laurer's canal present. Uterus coiled, intercaecal, reaches posterior end of body. Metraterm short. Vitellarium follicular, in lateral fields from ventral sucker to slightly into post-testicular region. Excretory vesicle small,

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appears to receive single ventrolateral duct from each side posterior to uterine coils; pore terminal. In kidneys of crocodiles; Australia. Type-species *D. gingae* Blair, 1985.

## Genera *Heterorchis* Baylis 1915 and *Kalipharynx* Boeger & Thatcher, 1983

The systematic position of *Heterorchis* Baylis 1915 and *Kalipharynx* Boeger & Thatcher, 1983, described from African and Amazonian lungfishes, has never been clear. Baylis (1915) allocated *Heterorchis* to the Plagiorchiidae Lühe, 1901, while subsequent authors (e.g. Vassiliadès & Richard, 1970b; Yamaguti, 1971) considered it a member of the Fellodistomidae Nicoll, 1909. Prudhoe & Bray (1982) suggested, however, that this genus did not belong to the Fellodistomidae, and thus its affinities remain unclear. The highly unusual organization of the excretory vesicle in the type-species, *H. crumenifer* Baylis, 1915, does not allow for a confident familial allocation of this genus. *Kalipharynx* is very similar to *Heterorchis* in general morphology and many anatomical details. It is also parasitic in lungfish, although on a different continent. The two genera differ mainly in the structure of the internal seminal vesicle, which is bipartite in *Heterorchis*, but undivided saccular in *Kalipharynx*. Information on the structure of the excretory vesicle in *Kalipharynx* is not available. Boeger & Thatcher (1983) placed this genus in the Fellodistomidae and emphasized the similarity of their new genus to *Heterorchis*. At the time of publication these authors were most probably unaware of the opinion of Prudhoe & Bray (1982). Thus, both genera are considered here as *incertae sedis*.

## Genus *Heterorchis* Baylis 1915 (Fig. 66.4)

**Diagnosis:** Body elliptical. Tegument armed with spines; spination almost reaches posterior end of body. Oral sucker subterminal. Ventral sucker larger than oral sucker, in anterior third of body. Prepharynx very short with characteristic lateral diverticula immediately anterior to pharynx. Pharynx present. Oesophagus very short. Intestinal bifurcation near anterior margin of ventral sucker. Caeca reach almost to posterior end of body. Testes two, oval, longitudinally elongate, entire, in hindbody, oblique, intercaecal or somewhat overlapping caeca. Cirrus-sac long, claviform, extends into hindbody, contains bipartite seminal vesicle. Genital pore extracaecal, submarginal, sinistral, at level of pharynx. Ovary slightly lobate, dextral, immediately anterior to right testis, near posterodextral margin of ventral sucker. Seminal receptacle elongate. Laurer's canal not observed. Uterus occupies intertesticular space and most of space posterior to testes, reaching close to posterior extremity and extracaecally. Eggs numerous. Vitellarium consists of numerous follicles of irregular shape arranged in two lateral extracaecal fields extending from level of posterior margin of ventral sucker to level of posterior end of posterior testis. Excretory vesicle voluminous, with very inflated oval stem reaching posterior end of cirrus-sac and ovary and two short branches; pore dorsal, unusually large. In intestine of lungfish; Africa. Type-species *H. crumenifer* Baylis 1915.

## Genus *Kalipharynx* Boeger & Thatcher, 1983 (Fig. 66.5)

**Diagnosis:** Body elongate, rounded at anterior end and tapered posteriorly, widest at level of ventral sucker. Tegument spined, with spination reaching at least to level of ventral sucker. Oral

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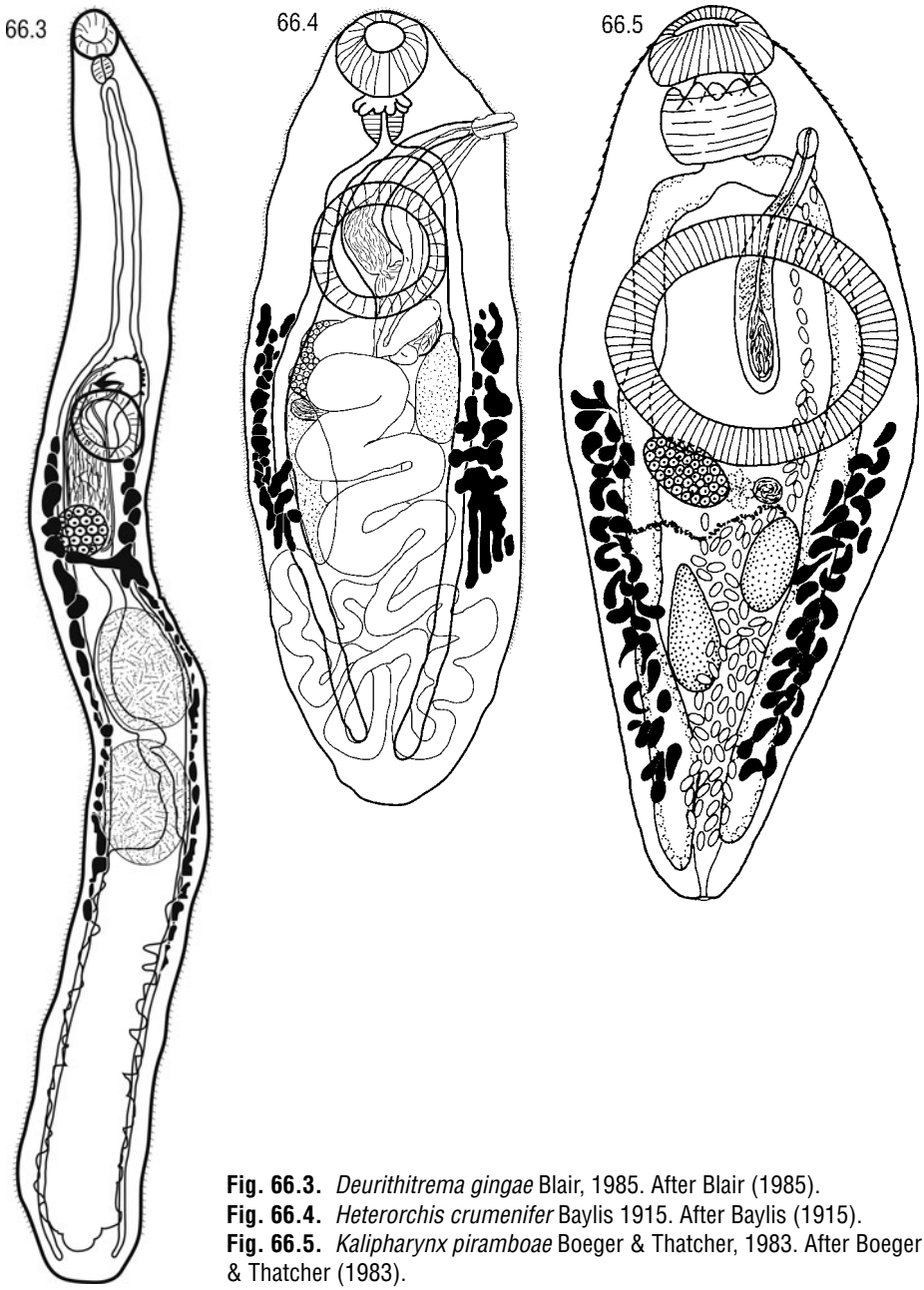



**Fig. 66.3.** *Deurithitrema gingae* Blair, 1985. After Blair (1985).
**Fig. 66.4.** *Heterorchis crumenifer* Baylis 1915. After Baylis (1915).
**Fig. 66.5.** *Kalipharynx piramboae* Boeger & Thatcher, 1983. After Boeger & Thatcher (1983).

sucker subterminal. Ventral sucker very large, up to four times larger in diameter than oral sucker. Prepharynx indistinct. Pharynx very large, powerful, similar in size to oral sucker. Oesophagus very short. Intestinal bifurcation near anterior margin of ventral sucker. Caeca almost reach posterior end of body. Testes elongate, entire, in hindbody, postovarian, intercaecal, oblique, in posterior third of body. Cirrus-sac long, oriented along median axis of body, with posterior half

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overlapping ventral sucker, contains undivided saccular seminal vesicle. Genital pore extracaecal, submedian, sinistral, at level of posterior margin of pharynx. Ovary oval, submedian at posterodextral margin of ventral sucker. Seminal receptacle present. Laurer's canal not observed. Uterus passes between testes, occupies most of intertesticular space in hindbody and reaches posterior extremity. Eggs numerous. Vitellarium consists of numerous small follicles arranged in two lateral extracaecal fields extending from level of posterior margin of ventral sucker to level just anterior to ends of caeca. Excretory vesicle unknown; pore terminal. In intestine of Amazonian lungfish. Type-species *K. piramboae* Boeger & Thatcher, 1983.

## Genera *Wallinia* Pearse, 1920, *Glossidium* Looss, 1899, *Macrolecithus* Hasegawa & Ozaki, 1926, *Vietosoma* Van Cleave & Mueller, 1932 and *Pseudomagnivitellinum* Dronen & Underwood, 1980

These five genera have been included at different times and by different authors in the family Macroderoididae McMullen, 1937, and in some cases (*Wallinia* Pearse, 1920, *Macrolecithus* Hasegawa & Ozaki, 1926, *Vietosoma* Van Cleave & Mueller, 1932) in the subfamily Walliniinae Yamaguti, 1958. Yamaguti (1958b) included the Walliniinae in the Allocreadiidae Looss, 1902; however, in his later monograph, Yamaguti (1971) transferred *Macrolecithus* and *Vietosoma* to the Macroderoidinae (Macroderoididae) and considered *Wallinia* the only genus within the Walliniinae (also Macroderoididae).

Recently, Pérez-Ponce de León *et al*. (2007) have demonstrated that *Wallinia*, along with another related genus, *Margotrema* Lamothe-Argumedo, 1970, belongs, in fact, to the Allocreadiidae, being most closely related to the *Crepidostomum* Braun, 1900 and *Bunodera* Railliet, 1896. These authors also commented on the lack of certainty about the phylogenetic affinities and systematic position of *Vietosoma* and some other genera previously considered in the Walliniinae. Thus, *Wallinia* is considered here as an allocreadiid, whereas *Macrolecithus* and *Vietosoma*, as well as two additional genera usually associated with the Macroderoididae but not included in the corresponding chapter in this volume, namely *Pseudomagnivitellinum* Dronen & Underwood, 1980 and *Glossidium* Looss, 1899, are considered as genera *incertae sedis*.

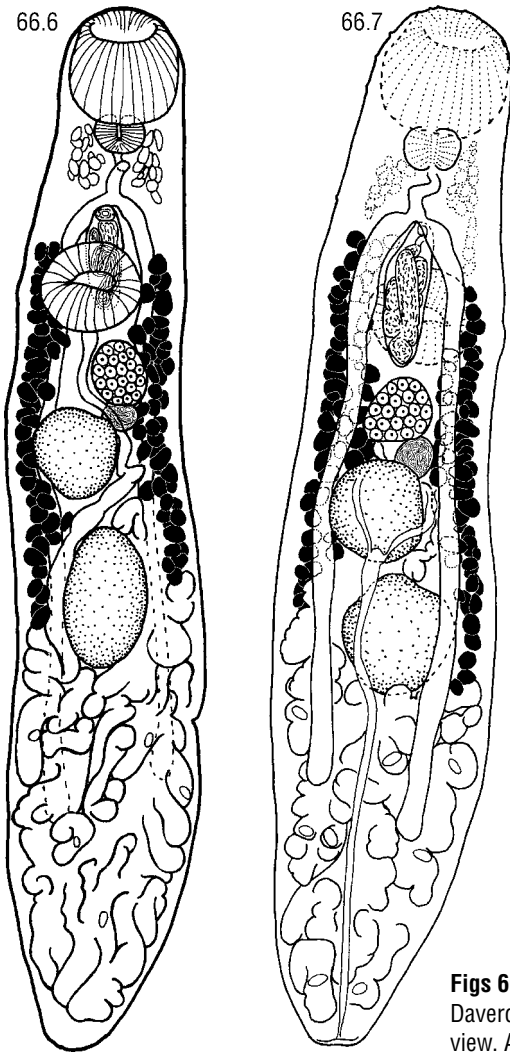
*Afromacroderoides* Khalil, 1972 was considered a synonym of *Glossidium* by Mashego & Saayman (1989). Bray *et al*. (2006) concurred with this opinion, which is also accepted here.

*Paramacrolecithus* Srivastava & Ghosh, 1967 was originally placed in the Walliniinae (Allocreadiidae). Later, Yamaguti (1971) considered it a subgenus of *Macrolecithus*. Due to the lack of substantial morphological differences, I consider these genera to be synonymous.

## Genus *Wallinia* Pearse, 1920 (Figs 66.6, 66.7)

**Diagnosis:** Body elongate. Tegument unspined. Oral sucker comparatively large, subterminal. Ventral sucker somewhat larger than oral sucker, in anterior half of body. Prepharynx absent. Pharynx well developed. Oesophagus present. Intestinal bifurcation in mid-forebody. Caeca terminate in middle of posttesticular region. Testes diagonal or nearly tandem, intercaecal, equatorial to just postequatorial. Cirrus-sac dorsal to ventral sucker, encloses winding, tubular, seminal vesicle, well-differentiated prostatic complex and short cirrus. Genital pore median, in forebody, immediately postbifurcal. Ovary submedian, pretesticular. Seminal receptacle between ovary and anterior testis. Laurer's canal present. Uterus passes between testes, reaching posterior end of body.

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**Figs 66.6, 66.7.** *Wallinia chavarriae* Choudhury, Daverdin & Brooks, 2002. 66.6. Ventral view. 66.7. Dorsal view. After Choudhury *et al.* (2002).

Vitellarium consists of two lateral fields of follicles extending from level of anterior margin of ventral sucker to level of anterior or posterior testis. Excretory vesicle tubular, narrow, reaches anterior testis; pore terminal. In intestinal of fishes; neotropics. Type-species *W. valenciae* Pearse, 1920.

## Genus *Glossidium* Looss, 1899 (Figs 66.8, 66.9)

(Syn. *Afromacroderoides* Khalil, 1972)

**Diagnosis:** Body elongate, tapered toward both extremities. Tegument armed with spines. Oral sucker subterminal. Ventral sucker in anterior half of body. Prepharynx short. Pharynx large. Oesophagus present or indistinct. Intestinal bifurcation in mid-forebody. Caeca wide, not reaching

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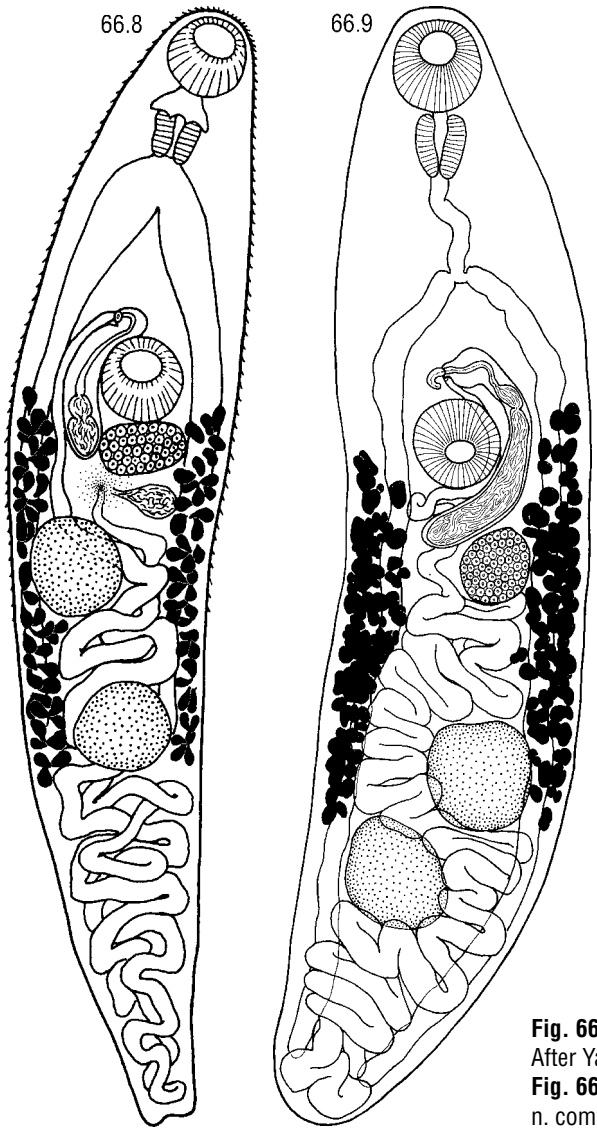



**Fig. 66.8.** *Glossidium pedatum* Looss, 1899. After Yamaguti (1971).
**Fig. 66.9.** *Glossidium lazerae* (Khalil, 1972) n. comb. Original.

to posterior extremity. Testes postovarian, diagonal, separated by uterus, usually in posterior half of body. Cirrus-sac claviform, lateral or anterolateral to ventral sucker, encloses bipartite seminal vesicle, prostatic complex and cirrus. Genital pore median or submedian, immediately anterior to ventral sucker. Ovary oval, entire, median or submedian, immediately posterior to ventral sucker or separated from ventral sucker by proximal part of cirrus-sac. Seminal receptacle immediately posterior to ovary. Laurer's canal present. Uterus passes between testes, reaching posterior body end. Vitellarium in two narrow lateral fields of follicles extending from level of anterior margin of ventral sucker to level of anterior or posterior testis. Excretory system Y-shaped. In intestine of freshwater fishes; Africa. Type-species *G. pedatum* Looss, 1899.

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## Genus *Macrolecithus* Hasegawa & Ozaki, 1926 (Figs 66.10, 66.11)

(Syn. *Paramacrolecithus* Srivastava & Ghosh, 1967)

**Diagnosis:** Body elongate. Tegument unspined. Oral sucker subterminal. Ventral sucker somewhat smaller or slightly larger than oral sucker. Prepharynx absent. Pharynx well developed. Oesophagus short or relatively long. Intestinal bifurcation in forebody. Caeca terminate in middle of post-testicular region or extend to posterior extremity. Testes tandem, in middle of hindbody. Cirrus-sac small, between ventral sucker and intestinal bifurcation, contains bipartite seminal vesicle, prostatic complex and cirrus. Genital pore median or submedian, postbifurcal. Ovary median, at varying distance between ventral sucker and anterior testis. Seminal receptacle present. Uterus may or may not extend posteriorly to testes. Vitellarium consists of numerous follicles extending in lateral fields from level of pharynx or intestinal bifurcation to posterior body end; fields may merge or almost merge in post-testicular region. Excretory vesicle I-shaped, tubular, reaches posterior testis or ovary; pore terminal. In digestive tract of freshwater fishes; Palaearctic and Southeast Asia. Type-species *M. gotoi* Hasegawa & Ozaki, 1924.

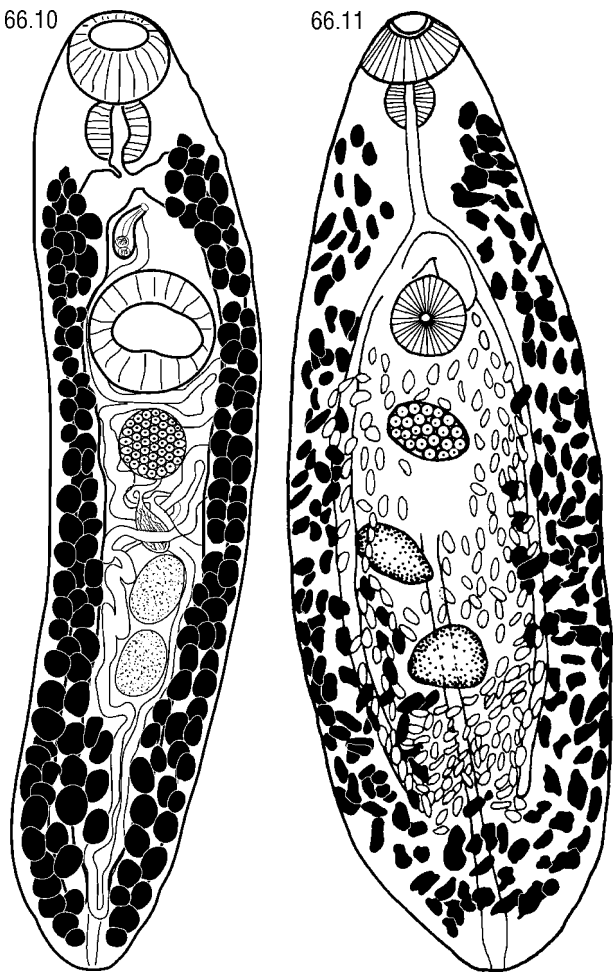



**Fig. 66.10.** *Macrolecithus gotoi* Hasegawa & Ozaki, 1924. After Yamaguti (1971).
**Fig. 66.11.** *Macrolecithus rasborai* (Srivastava & Ghosh, 1967). After Srivastava & Ghosh (1967).

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## Genus *Vietosoma* Van Cleave & Mueller, 1932 (Fig. 66.12)

**Diagnosis:** Body small, pyriform. Tegument armed with spines. Oral sucker subterminal, larger than ventral sucker. Ventral sucker pre-equatorial. Prepharynx distinct. Pharynx moderately developed. Oesophagus very short or almost indistinct. Intestinal bifurcation midway between oral and ventral suckers. Caeca terminate just posterior to testes. Cirrus-sac pyriform, anterodextral to ventral sucker and partly overlapping it, contains bipartite seminal vesicle, prostatic complex and simple ejaculatory duct. Genital pore slightly submedian, immediately anterior to ventral sucker. Ovary median or slightly submedian, strongly lobed, partly overlapping ventral sucker and right testis. Seminal receptacle present. Uterus passing between testes and almost reaches posterior extremity. Metraterm well differentiated. Eggs large, not very numerous. Vitelline follicles large, extend in lateral fields from level of pharynx to, or somewhat beyond, ends of caeca. Excretory vesicle tubular, reaches ovary; pore terminal. In digestive tract of freshwater fishes; North America. Type-species *V. parvum* Van Cleave & Mueller, 1932.

## Genus *Pseudomagnivitellinum* Dronen & Underwood, 1980 (Fig. 66.13)

**Diagnosis:** Body elongate, with rounded extremities. Tegument finely spined anteriorly. Suckers almost equal in size. Oral sucker subterminal. Ventral sucker in anterior third of body. Prepharynx short. Pharynx well developed. Oesophagus short. Intestinal bifurcation immediately anterior to ventral sucker. Caeca terminate near posterior end of body. Testes postovarian, diagonal, in middle third of body. Cirrus-sac claviform, curved around left side of ventral sucker, encloses bipartite seminal vesicle, prostatic complex and cirrus. Genital pore median, immediately anterior to ventral sucker. Ovary submedian, between ventral sucker and anterior testis. Uterus passes between testes and occupies most of space posterior to testes, reaching posterior end of body. Eggs numerous. Vitelline follicles large, in two short fields extending from level of intestinal bifurcation to level of posterior margin of anterior testis. Excretory vesicle I-shaped. In digestive tract of freshwater fishes; North America. Type-species *P. ictalurum* Dronen & Underwood, 1980.

## Genus *Kaurma* Chatterji, 1936 (Figs 66.14–66.16)

Three species of *Kaurma* Chatterji, 1936 have been described from freshwater turtles in different regions of South-east Asia. Initially the genus was allocated by Chatterji (1936) to the Allocreadiidae Stossich, 1904 and later transferred to the Omphalometridae Looss, 1899 (see Yamaguti, 1971). Detailed morphological re-examination of *K. intermedia* Rohde, 1963 and *K. orientalis* Yamaguti, 1937 deposited in the Natural History Museum, London demonstrated that the similarity of representatives of this genus with omphalometrids (all of which are parasites of mammals) is superficial and the organization of the cirrus-sac in this genus is very different from that in members of the Omphalometridae and the Plagiorchiidae. Unfortunately, at this point in time it is impossible to confidently allocate this genus into any known family and it is considered here as a genus *incertae sedis*.

**Diagnosis:** Body flattened, oval, with rounded extremities. Suckers similar in size. Oral sucker subterminal. Ventral sucker in middle of body. Prepharynx absent. Oesophagus short or indistinct. Intestinal bifurcation in forebody. Caeca reach posterior body end. Testes tandem, strongly

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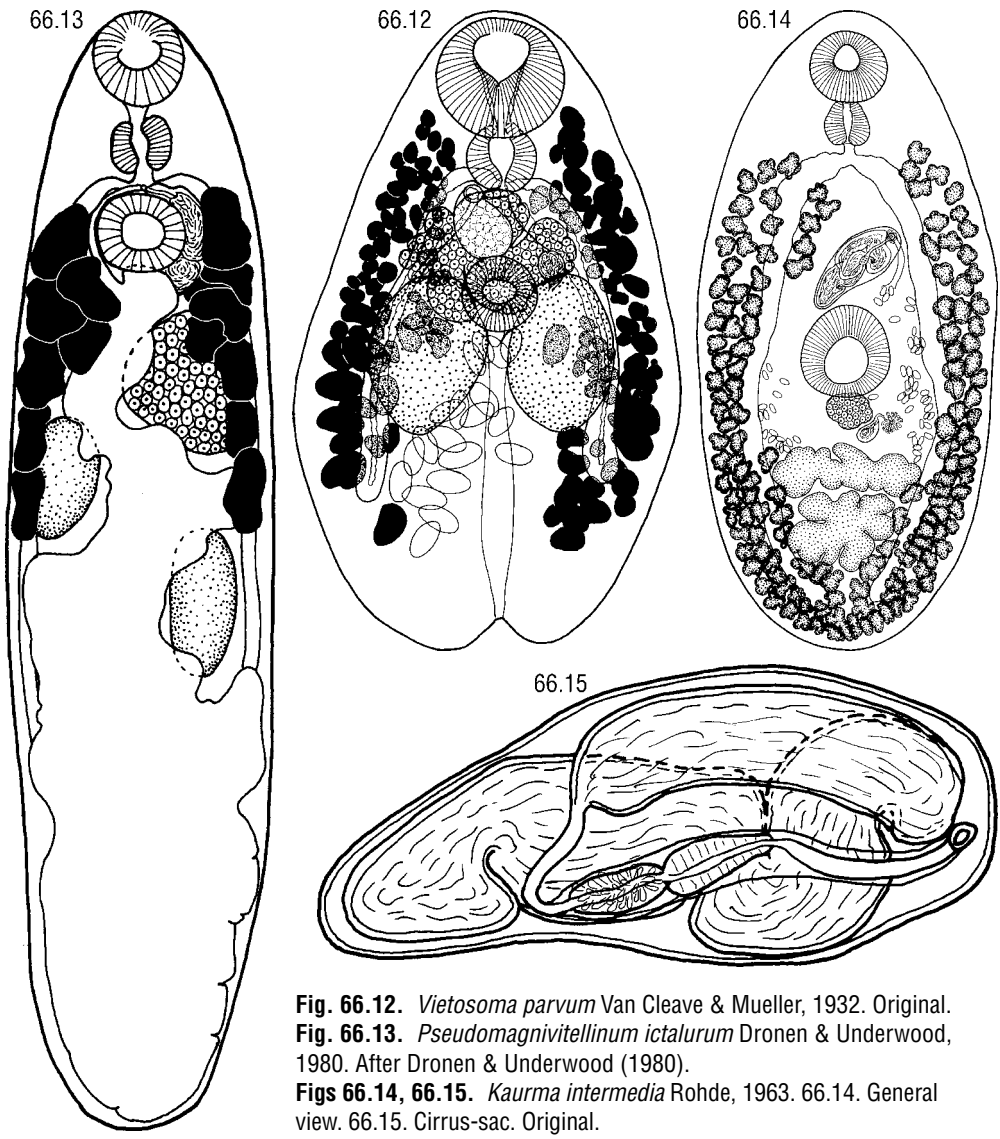



**Fig. 66.12.** *Vietosoma parvum* Van Cleave & Mueller, 1932. Original.
**Fig. 66.13.** *Pseudomagnivitellinum ictalurum* Dronen & Underwood, 1980. After Dronen & Underwood (1980).
**Figs 66.14, 66.15.** *Kaurma intermedia* Rohde, 1963. 66.14. General view. 66.15. Cirrus-sac. Original.

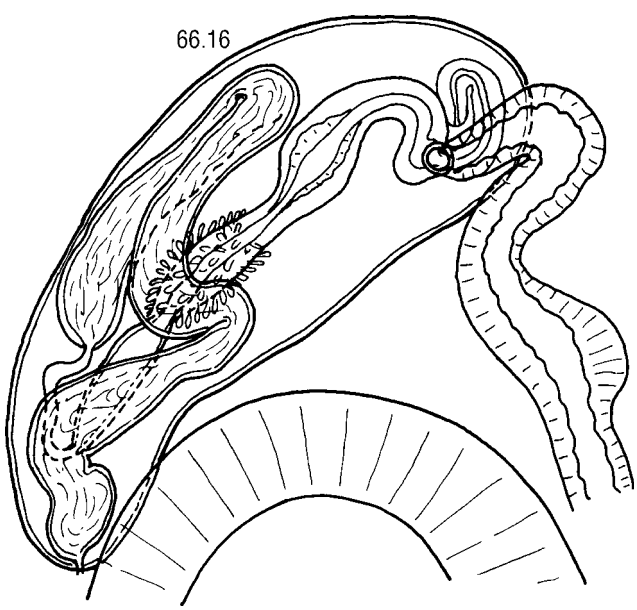
indented or lobed, near posterior end of body. Cirrus-sac well developed, contains winding tubular seminal vesicle, pars prostatica, complex coiled ejaculatory part and protrusible cirrus. Genital pore submedian, sinistral, halfway between intestinal bifurcation and ventral sucker. Ovary median or slightly submedian, immediately posterior to or slightly overlaps ventral sucker. Seminal receptacle and Laurer's canal present. Uterus winds between anterior testis and ventral sucker. Metraterm well differentiated. Eggs few, large. Vitellarium consists of numerous large follicles of irregular shape, forms U-shaped uninterrupted field extending continuously from level of intestinal bifurcation posteriorly, confluent at posterior extremity. Excretory vesicle Y-shaped. Intestinal parasites of freshwater turtles; South-east Asia. Type-species *K. longicirra* Chatterji, 1936.

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## Genus *Astioglossimetra* Bilqees, Khatoon & Khan, 2002 (Fig. 66.17)

This genus was described recently by Bilqees *et al*. (2002) from sea turtles off Pakistan. The description is very superficial, incomplete and contradictory, particularly in details of the organization of the cirrus-sac. Although the type- and only known species, *Astioglossimetra karachiensis* Bilqees, Khatoon & Khan, 2002, bears a resemblance to members of both *Astiotrema* Looss, 1900 and *Neoastiotrema* Tkach, 2008, proposed in this volume for *Astiotrema trituri* Grabda, 1959 (see Tkach, Chapter 23), more data are necessary to appropriately allocate this species in the system. This is especially so because both *Astiotrema* and *Neoastiotrema* are known only from freshwater habitats and hosts. The original authors state that the seminal vesicle is either 'smooth' or bipartite, attributes that are mutually exclusive and may potentially put this species into two different families or even superfamilies. Thus, *Astioglossimetra* remains temporarily a genus *incertae sedis*.

**Diagnosis:** Body small, delicate. Oral sucker larger than ventral sucker. Ventral sucker in anterior third or half of body. Prepharynx apparently absent. Pharynx and oesophagus prominent. Intestinal bifurcation in mid-forebody. Caeca not reaching beyond posterior testis. Testes rounded, oblique or almost tandem, in posterior third of body. Cirrus-sac large, extending well into hindbody, contains prominent 'smooth' or bipartite seminal vesicle. Genital pore postbifurcal, in forebody. Ovary rounded, pretesticular, adjacent to base of cirrus-sac. Seminal receptacle present, between ovary and anterior testis. Uterus reaches posterior end of body. Vitellarium forms lateral fields consisting of small follicles, extends from level of intestinal bifurcation to posterior testis. Excretory



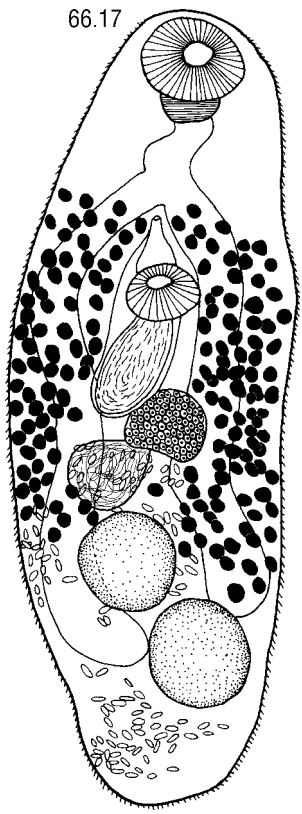




**Fig. 66.16.** *Kaurma orientalis* Yamaguti, 1937. Cirrus-sac. Original.
**Fig. 66.17.** *Astioglossimetra karachiensis* Bilqees, Khatoon & Khan, 2002. After Bilqees *et al*. (2002).

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system 'not prominent'. In intestine of sea turtles; Arabian Sea. Type-species *A. karachiensis* Bilqees, Khatoon & Khan, 2002.

## Genera *Pseudastiotrema* Wang, 1982 and *Ochetosomoides* Wang, 1982

Wang P.-q. (1982a) described two new genera, *Pseudastiotrema* Wang, 1982 and *Ochetosomoides* Wang, 1982, from marine fishes off China. The author considered the first of these genera as closely related to *Parastiotrema* Miller, 1940, a genus based on a single poor specimen from freshwater fish in North America and now synonymized with *Alloglossidium* Simer, 1929 (see Font & Lotz, Chapter 34, this volume). *Pseudastiotrema rhynchobati* Wang, 1982, reported from the elasmobranch *Rhynchobatus djeddensis*, somewhat resembles macroderoidids in the topology of some organs (but not the uterus or vitellarium). However, a poor drawing and superficial description do not permit a confident placement of this species and genus into any of the known families. Depending on details of the structure of the cirrus-sac and excretory vesicle, for instance, it can be placed in either the Macroderoididae or in a very distantly related group such as the Opisthorchioidea Looss, 1899. It seems likely that this is an accidental parasite of elasmobranchs (see Bray & Cribb, 2003). There are similar problems with *Ochetosomoides scomberomori* Wang, 1982, which was originally placed in the Ochetosomatidae Leão, 1945 (= Reniferidae Pratt, 1902; see Tkach, Chapter 41, this volume). It bears only a superficial resemblance to some reniferids in the position of the genital pore, the shape of the cirrus-sac and the relative position of testes and ovary. On the other hand, the presence of an external seminal vesicle, the position of the uterus and the distribution of vitelline follicles in this species are unlike those in reniferids. The external seminal vesicle, spined tegument and marine fish host prompted Bray (2005a) to include this genus in the key to the family Lepocreadiidae Odhner, 1905.

## Genus *Pseudastiotrema* Wang, 1982 (Fig. 66.18)

**Diagnosis:** Body elliptical, with rounded extremities. Tegument spined. Oral sucker larger than ventral sucker. Oral sucker subterminal. Ventral sucker pre-equatorial. Prepharynx absent. Pharynx large. Oesophagus absent. Caeca reach posterior body end. Testes entire, oblique, close to each other in middle third of body. Cirrus-sac arches around left margin of ventral sucker; details of seminal vesicle structure unknown. Genital pore median, between intestinal bifurcation and ventral sucker. Ovary entire, median, between ventral sucker and anterior testis close to ventral sucker. Uterus occupies most of hindbody, but does not extend beyond ends of caeca. Vitellarium consists of numerous follicles forming U-shaped uninterrupted field extending from level of ventral sucker to posterior end of body and confluent posteriorly. In marine fishes; north-western Pacific Ocean. Type-species *P. rhynchobati* Wang, 1982.

## Genus *Plagioglyphe* Krasnolobova, 1973 (Fig. 66.19)

*Plagioglyphe* Krasnolobova, 1973 was established for *Plagiorchis fastuosus* Szidat, 1924, *P. morosovi* Sobolev, 1946, *P. obtusus* Strom, 1940 and *Opisthioglyphe megastomus* Baer, 1943 based on the fact that in all these species the uterus does not extend posteriorly beyond the posterior testis. In the former three species, parasitic in birds, the uterus extends into the space between the testes,

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whereas, in the latter species, parasitic in insectivores, the uterus terminates anteriorly or laterally to the anterior testis. *Plagioglyphe megastomus* (Baer, 1943) is transferred in this volume into a separate genus, *Neoplagioglyphe* Tkach, 2008 (see Tkach, Chapter 38, this volume). Krasnolobova (1987) placed *Plagiorchis obtusus, P. morosovi* and *P. pseudofastuosus* Belopol'skaja, 1975 into synonymy with *Plagioglyphe fastuosus* (Szidat, 1924). At the same time, she transferred an additional species, *Plagiorchis arcuatus* Strom, 1924, to *Plagioglyphe* despite the highly controversial data available on the life-cycle of this species, which suggests an affinity with the Haematoloechidae Freitas & Lent, 1939. Odening (1959a) considered *P. fastuosus* among the opisthioglyphines (included in the Telorchiidae Looss, 1899 in this volume; Font & Lotz, Chapter 43), whereas Krasnolobova (1973, 1987) concluded that it is closer to the plagiorchiids. In any case, almost all available descriptions and drawings of *P. fastuosus* and its synonyms are relatively poor and based on deformed and/or young specimens; therefore, additional studies are necessary to clarify their phylogenetic affinities and systematic position. As a consequence, *Plagioglyphe* is considered as a genus with an uncertain systematic position.

**Diagnosis:** Body small, elliptical, moderately elongate. Oral sucker subterminal, always larger than ventral sucker. Ventral sucker in anterior third of body. Prepharynx indistinct. Pharynx well developed. Oesophagus short or indistinct. Intestinal bifurcation in forebody. Caeca reach posterior extremity. Testes postovarian, diagonal, in posterior half of body. Cirrus-sac well developed, arches along margin of ventral sucker, contains bipartite seminal vesicle. Genital pore median. Ovary rounded, submedian, just posterior to ventral sucker. Uterus between ventral sucker and posterior testis, reaches between testes. Eggs not very numerous. Vitellarium consists of numerous large follicles forming lateral fields extending from oral sucker to posterior extremity, confluent posterior to testes and usually, but not always, anterior to ventral sucker. Excretory vesicle Y-shaped. In intestine of birds; Eurasia. Type-species *P. fastuosus* (Szidat, 1924) Krasnolobova, 1973.

## Genus *Astiotrema* Looss, 1900 (Figs 66.20, 66.21)

(Syn. *Astia* Looss, 1899 *nec* Agassiz, 1849 and Keyserling, 1879)

*Astiotrema* Looss, 1900 has been considered a member of the Plagiorchiidae by the majority of authors, usually as a type-genus of the subfamily Astiotrematinae Baer, 1924. Representatives of this genus have been described from fishes, reptiles (snakes and turtles) and caudate amphibians. Prudhoe & Bray (1982) suggested that it represents a composite group of genera. In the molecular phylogenetic studies of Tkach *et al.* (2001b) and Olson *et al.* (2003) a parasite of snakes, *A. monticelli* Stossich, 1904, was shown to be not closely related to *Plagiorchis* Lühe, 1899 and other plagiorchioid digeneans. Our recent molecular phylogenetic results (V.V. Tkach, R.A. Bray & R.M. Cable, unpublished) using a wider representation of *Astiotrema* species have demonstrated that *A. monticelli* from European snakes, *A. reniferum* (Looss, 1898) from turtles in south-eastern Asia and *A. turneri* Bray, van Oosterhout, Blais & Cable, 2006 from African fishes form a monophyletic clade closest to heterophyids, whereas *A. trituri* Grabda, 1959, a parasite of newts, is very close to *Plagiorchis*. Based on these results and substantial morphological and biological differences, a new genus, *Neoastiotrema* Tkach, 2008, is established for *A. trituri* in this volume (Tkach, Chapter 23). Members of *Astiotrema* from snakes, fishes and turtles possess an undivided, sac-like seminal vesicle and their cercariae, as reported for *A. monticelli*, develop in rediae (Shevchenko & Vergun, 1960), a condition that agrees with the placement of *Astiotrema* among the opisthorchioids in molecular phylogenetic analyses. Thus, *Astiotrema* is removed from the Plagiorchiidae and temporarily considered as *incertae sedis*.

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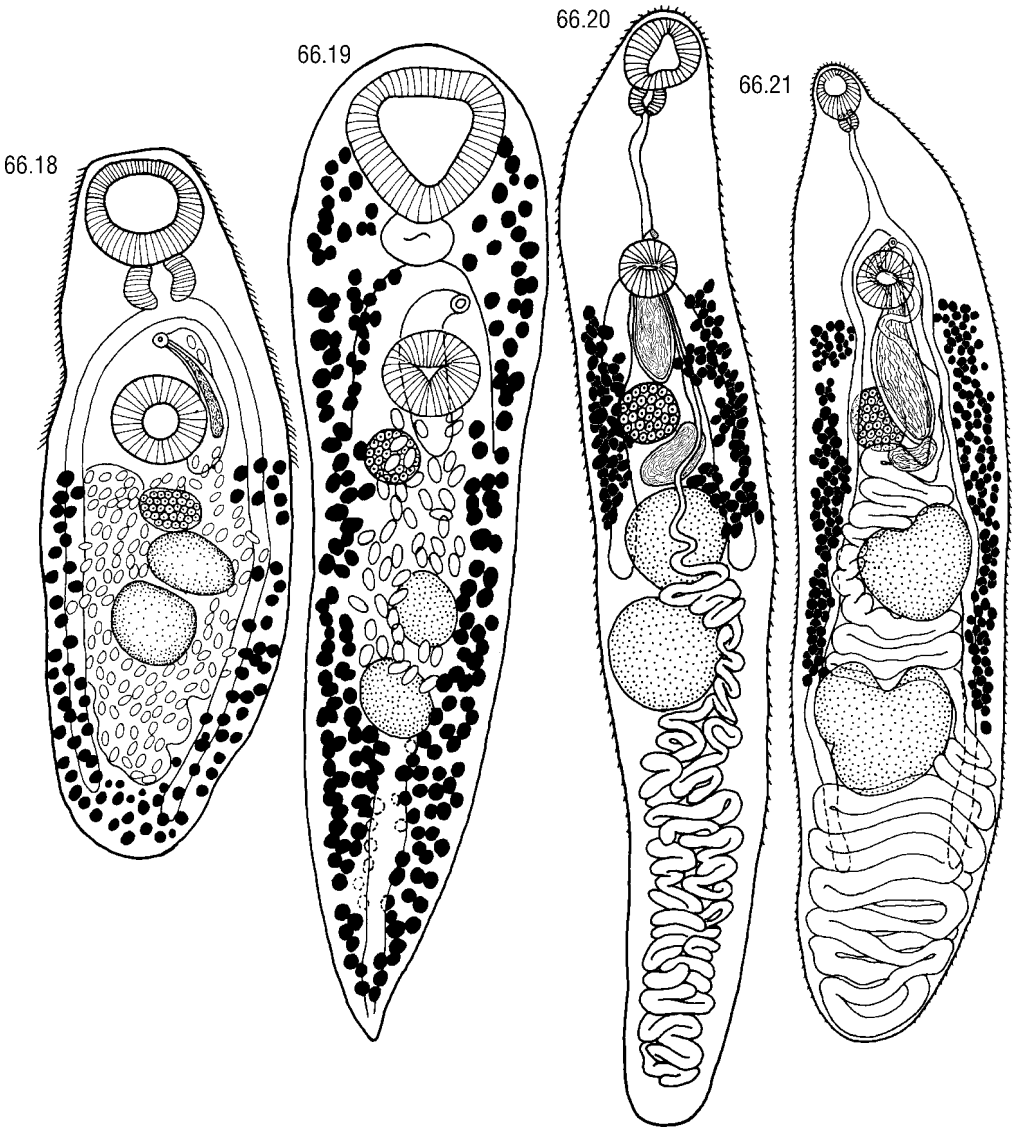



**Fig. 66.18.** *Pseudastiotrema rhynchobati* Wang, 1982, After Wang P.-q. (1982a).
**Fig. 66.19.** *Plagioglyphe fastuosus* (Szidat, 1924). After Skrjabin & Antipin (1958a).
**Fig. 66.20.** *Astiotrema monticelli* Stossich, 1904. After Sharpilo & Iskova (1989).
**Fig. 66.21.** *Astiotrema reniferum* (Looss, 1898). Original.

As listed by Bray *et al.* (2006), three genera have been synonymized with *Astiotrema*. Yeh & Fotedar (1958), Fotedar (1971) and Kumari *et al.* (1973) considered *Gauhatiana* Gupta, 1955, *Tremiorchis* Mehra & Negi, 1925 and *Pseudoparamacroderoides* Gupta & Agarwal, 1968, respectively, synonyms of *Astiotrema*. However, in this volume the above genera are not considered synonyms of *Astiotrema* (see Pojmańska, Chapter 12 and Font & Lotz, Chapter 34). Yeh & Fotedar (1958) radically reduced the number of species in *Astiotrema* by synonymizing 16 species

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and suggesting the transfer of *A. emydis* Ejsmont, 1930 to *Leptophallus* Lühe, 1909. Some of these synonymies seem to be not fully justified and need to be re-examined. It is now certain that *Astiotrema (sensu stricto)* does not belong to the Plagiorchiidae, and its phylogenetic affinities, systematic position and species composition need a detailed revision involving both morphological and molecular data.

**Diagnosis:** Body elongate, usually spatulate. Tegument spined. Oral sucker subterminal. Ventral sucker in anterior third of body or at border between anterior and middle thirds. Sucker ratio variable. Prepharynx usually indistinct. Pharynx well developed. Oesophagus present, of varying length. Intestinal bifurcation in posterior forebody or dorsal to ventral sucker. Caeca terminate close to posterior extremity or some distance short of it, exceptionally in middle third of body, just anterior to posterior testis. Testes oblique, entire or notched; anterior testis equatorial or postequatorial. Cirrus-sac almost entirely filled with thick-walled unipartite seminal vesicle, reaches ovary. Genital pore immediately anterior to ventral sucker, median or slightly submedian. Ovary submedian, pre-equatorial, at base of cirrus-sac or lateral to it. Seminal receptacle sometimes very large, rounded or kidney-shaped, postovarian. Uterus inter- and postcaecal, fills most of hindbody posterior to ovary, reaches posterior body extremity. Vitellarium in extracaecal fields of variable length, extends between intestinal bifurcation and caecal extremities. Excretory vesicle Y-shaped; stem passes between testes and bifurcates into two short arms between ovary and anterior testis. In gastro-intestinal tract of fishes and reptiles; Palaearctic, Indo-Malayan and Ethiopian regions. Type-species *A. reniferum* (Looss, 1898) Looss, 1900.

## Genus *Turquinella* nom. nov. (Fig. 66.22)

(Syn. *Turquinia* Otero, 1989 *nec* Šilhavý, 1979)

*Turquinia* Otero, 1989 was established for *T. cubensis* Otero, 1989 described from the lizard *Anolis argenteolus* from Cuba (Otero, 1989). The author was apparently unaware, however, that this generic name was pre-occupied by *Turquinia* Šilhavý, 1979, an opilionid arthropod. The genus is, therefore, renamed. The overall morphology of this genus is in general similar to members of the Plagiorchiidae. However, some morphological characters, such as the position of the genital pore close to the oral sucker and a very long stem of the excretory vesicle apparently bifurcating just posterior to the ventral sucker, and the inadequate description of some other essential morphological characters (such as the organization of the cirrus-sac) make familial allocation of this genus problematic. It may prove to be close to *Parahaplometroides* Thatcher, 1963, parasitic in lizards in Central and South America, but this may only be confirmed upon re-examination of type or new specimens.

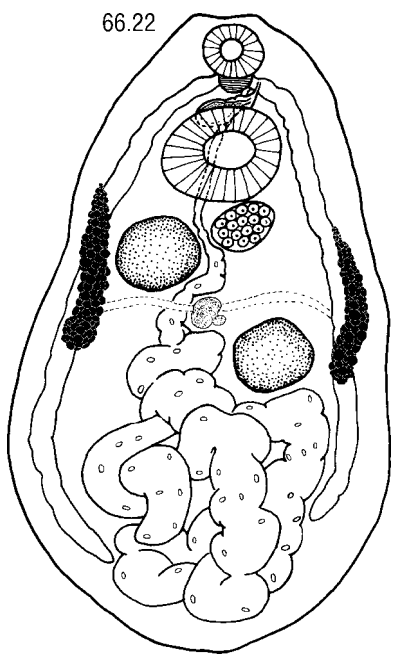
**Diagnosis:** Body plump, with narrower anterior half and wide, rounded posterior half. Tegument spined. Oral sucker subterminal, smaller than ventral sucker. Ventral sucker very close to anterior end of body. Prepharynx and oesophagus absent. Pharynx present. Intestinal bifurcation in midforebody. Caeca almost reach posterior extremity. Testes oblique, in middle third of body, separated by uterine coils. Cirrus-sac at anterior margin of ventral sucker, partly overlapping it; details of structure and seminal vesicle unknown. Genital pore at level of pharynx, very close to oral sucker. Ovary oval, immediately posterolateral to ventral sucker and close to right testis. Mehlis' gland between testes. Laurer's canal not reported. Uterus occupies most of intercaecal space in hindbody. Eggs numerous. Vitellarium in form of two short lateral, extra- and supracaecal fields

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of small follicles extending between ventral sucker and posterior testis. Excretory vesicle Y-shaped, with long stem bifurcating just posteriorly to ventral sucker. In stomach of lizards; Cuba. Type-species *T. cubensis* (Otero, 1989) n. comb.

## Genus *Neoparalepoderma* Chattopadhyaya, 1970 (Fig. 66.23)

This genus was established by Chattopadhyaya (1970b) for *Neoparalepoderma chitinoides* Chattopadhyaya, 1970. This species has not been reported since and the description does not allow its placement into any of the currently recognized families with reasonable confidence. The combination of the excretory vesicle with arms reaching the anterior extremity, the lack of a seminal receptacle and some other morphological features is somewhat puzzling. In addition, the author mentioned (but did not provide a more detailed description or drawing) an 'oval chitinous structure, perhaps associated with the cirrus-sac'. It is difficult to assess some structures shown by Chattopadhyaya (1970b) on the original illustration. What appears to be a seminal receptacle is shown, but the author wrote that it was lacking. Besides, the drawing contradicts the description regarding its orientation. Although the figure legend says that the drawing is ventral, the descrip-



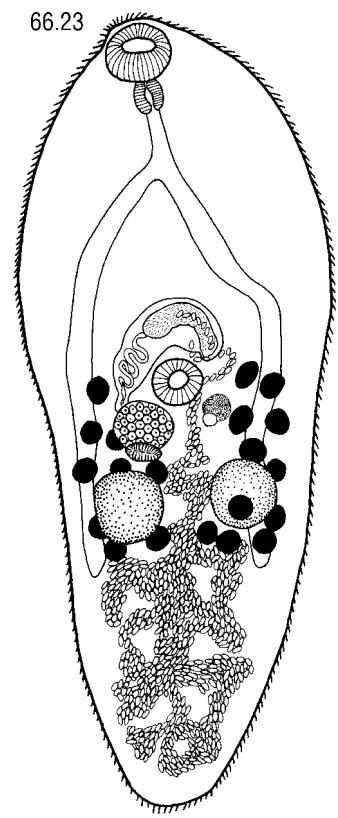




**Fig. 66.22.** *Turquinella cubensis* (Otero, 1989) n. comb. After Otero (1989).
**Fig. 66.23.** *Neoparalepoderma chitinoides* Chattopadhyaya, 1970, probable dorsal view. After Chattopadhyaya (1970b).

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tion suggests that it is dorsal or flipped by the publisher. Thus, it is difficult to properly allocate this genus until more is known about morphology of its type-species.

**Diagnosis:** Body flattened, elongate, forebody wider than hindbody. Tegument armed with spines. Suckers relatively small. Oral sucker subterminal, larger than ventral sucker. Ventral sucker in middle of body. Prepharynx absent. Oesophagus short. Intestinal bifurcation in anterior forebody. Caeca terminate just posterior to testes, at substantial distance from posterior end of body. Testes symmetrical, entire, almost round, at border between middle and posterior thirds of body. Cirrus-sac claviform, arches around left and anterior margins of ventral sucker; contains highly convoluted seminal vesicle, broad pars prostatica and spiny, muscular cirrus. Oval chitinous structure present, perhaps associated with cirrus-sac. Genital pore anterolateral to ventral sucker. Ovary posterosinistral to ventral sucker. Seminal receptacle lacking. Uterus inter- and postcaecal, passes between testes and occupies most of post-testicular space in hindbody. Eggs numerous. Vitellarium consists of two sparse groups of nine or ten large follicles extending from level of ventral sucker to ends of caeca. Excretory vesicle Y-shaped with stem bifurcating posterior to testes and arms reaching anterior extremity; pore terminal;. In intestine of sea turtles; India. Type-species *N. chitinoides* Chattopadhyaya, 1970.

## Genus *Ganeo* Klein, 1905 (*incertae sedis*)

*D.I. Gibson*

Lotz & Font (Chapter 54, this volume), excluded *Ganeo* from the Lecithodendriidae Lühe, 1901 and related families as it is known to have a non-virgulate xiphidocercaria and it parasitizes a pulmonate snail as a first intermediate host. In view of this, it is here considered as *incertae sedis*.

## Genus *Ganeo* Klein, 1905 (Fig. 66.24)

**Diagnosis:** Body oval, elongate-oval or elongate-pyriform. Tegument armed with fine, scale-like spines. Oral sucker small, ventro-subterminal. Ventral sucker small, just in anterior half of body. Prepharynx short. Pharynx small, much smaller than oral sucker. Oesophagus long. Intestinal bifurcation in mid-forebody; caeca long, narrow, end blindly in posterior half of hindbody. Testes two, globular, oblique or occasionally symmetrical, contiguous or close together, intracaecal, one or both in forebody, usually with one testis approximately median and anterior to ventral sucker and other dextral and lateral, anterolateral or posterolateral to ventral sucker. No external seminal vesicle. Cirrus-sac elongate-claviform, thin-walled, extends anterolaterally or anteriorly and then laterally from level dorsal to ventral sucker towards genital pore, contains rather small, looped seminal vesicle, long and very well-developed pars prostatica and short or long ejaculatory duct. Genital atrium indistinct to distinct invagination of body wall. Genital pore sinistromarginal, at level of oesophagus or just posterior. Ovary similar in size to smaller than testes, contiguous with or posterior or posterolateral to one testis, dextral, posterodextral or just posterior to ventral sucker. Seminal receptacle present posterior to ovary. Uterus long, narrow, much coiled, fills intracaecal field posterior to ovary and extends close to posterior extremity; distal region not coiled, extends directly towards genital pore on sinistral side of forebody. Eggs small, oval, numerous. Vitellarium follicular, in two, mainly extracaecal fields, between levels of ventral sucker or ovary to just, occasionally well, anterior to caecal extremities. Excretory

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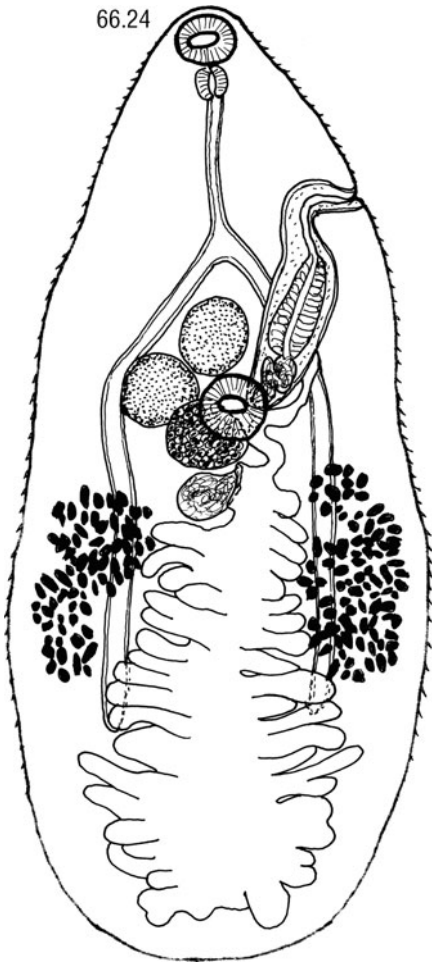



**Fig. 66.24.** *Ganeo tigrinus* Mehra & Negli, 1928. After Moravec & Sey (1989b).

system V-shaped, with terminal pore. In intestine of amphibians (mainly anurans), occasionally in fishes and reptiles; South Asia, especially Indian subcontinent, China, Africa. Type-species *G. glottoides* Klein, 1905.

## Genera *inquirenda*

*Distoma* Retzius, 1782
*Festucaria* Schrank, 1788
*Leptosoma* Stafford, 1904
*Monostoma* Zeder, 1800
*Navigiolum* Onji & Nishio, 1916
*Plectognathotrematoides* Parukhin, 1971
*Pronopharynx* Cohn, 1904

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## Larval names

*Cercaria* Müller, 1773
*Cercariaeum* Diesing, 1855
*Cystagora* Stafford, 1905
*Dicranocercaria* Szidat, 1932
*Echinocercaria* Lutz, 1924
*Furcocercaria* Lamarck, 1815
*Mesocercaria* Bosma, 1934
*Xiphidiocercaria* Diesing, 1855

## *Nomina nuda*

*Neobilharzia* Szidat, 1942
*Omnipharynx* Nicholls & Brooks, 1969

## Genera erected since Volumes 1 and 2

Several new genera have been erected since the earlier volumes of this series. These are listed below under the families of their original assignation.

## Volume 1

Aspidogastridae Poche, 1907: *Neosychnocotyle* Snyder & Tkach, 2007 (Snyder & Tkach, 2007).

Brachylaimidae Joyeux & Foley, 1930: *Tinamutrema* Zamparo, Brooks & Causey, 2003 (Zamparo *et al.*, 2003b).

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