
13 Order Proteocephalidea Mola, 1928

A.A. REGO

*Departamento de Helminologia, Instituto Oswaldo Cruz, Av. Brasil 4365,
C.P. 926, 21045-900 Rio de Janeiro, Brazil.*

Introduction

The proteocephalids originated in primitive fishes in Gondwana, probably in South American rivers. Most existing species are actually found in Gondwana (South America, Africa, India, Australia). Some species, however, have dispersed to temperate areas and into hosts other than fishes (e.g. into Europe, Asia, North America) as has occurred with the cosmopolitan genus *Proteocephalus* (family Proteocephalidae), whose species are found in freshwater fishes, amphibians and reptiles. In contrast, representatives of the family Monticelliidae are restricted to tropical areas of South America and their hosts are freshwater fishes, in particular siluriforms. Groups other than the siluroids have recently been found to harbour both monticelliids and proteocephalids, i.e. non-siluriform fishes and other vertebrates. Species of *Nomimoscolex* (Monticelliidae: Zygobothriinae) were recently found in Amphibia and Reptilia (de Chambrier, 1987; de Chambrier & Vaucher, 1992). This may be evidence of the monticelliids commencing a colonization of hosts other than siluriforms. Proteocephalids of fishes are found only in hosts living in freshwater environments, none in marine waters. The subfamily Prosobothriinae Yamaguti, 1959, from marine elasmobranchs, listed by some authors in the order Proteocephalidea, is in my opinion more closely related to the Tetracanthocephalidae. However, Wardle & McLeod (1952) referred these species to the order Lecanicephalidea. [See also Euzet, this volume.]

Some important contributions to the knowledge of the order Proteocephalidea are the works of La Rue (1914), Woodland (1925, 1933a, b, 1934a, b, c), Freze (1965), Brooks (1978), Brooks & Rasmussen (1984) and Rego (1987). The classification of the order is mostly based on the work of Woodland who supported his studies with abundant material collected in South America (the Amazon region) and Africa. The taxonomy at the family level has its foundations in the relationship of the reproductive organs to the longitudinal muscle bundles, as seen in cross-section. The relationship of vitelline follicles to the longitudinal

muscles is fundamental in the subdivision into families. The Proteocephalidae has medullary vitelline follicles and the Monticelliidae has cortical vitelline follicles.

Woodland's scheme of classification has been useful for decades but is now becoming inadequate due to the discovery of forms with intermediate characters. For example, in the recently described subfamily Nupeliinae (see Pavanelli & Rego, 1991) the reproductive organs and vitelline follicles are placed partly in the medulla and partly in the cortex.

It is possible that, in future, modification to the scheme of classification will emphasize the characters of the scolex and suckers more than the present system. Our knowledge of the group so far is incomplete and any tentative attempt to change the current taxonomy will not succeed. For these reasons I shall adopt here a conservative scheme of classification similar to that utilized in reference books and papers such as those of Wardle & McLeod (1952), Yamaguti (1959), Brooks (1978), Brooks & Rasmussen (1984), Schmidt (1986) and principally the excellent treatise on proteocephalids by Freze (1965). Some minor modifications and corrections of some errors of previous authors have been included. For example, *Choanoscolex* La Rue, 1911 was originally placed in Corallobothriinae of the Proteocephalidae but after Brooks & Rasmussen (1984) and Rego (1990) noted the cortical position of the vitelline follicles and reproductive organs, the genus was transferred to Monticellinae of the Monticelliidae. I also accept three genera in Peltidocotylinae (= Othinoscolecinae): *Peltidocotyle*, *Othinoscolex* and *Woodlandiella*, differing from Schmidt (1986) who included only one genus, *Peltidocotyle*. Conservative authors accepted only one or two genera in Monticellinae while I am of the opinion that it is advantageous to split *Monticellia* into several genera, as suggested by Brooks & Rasmussen (1984) and Freze (1965). Consequently, I accept *Spatulifer*, *Gozeella*, *Monticellia* and *Spasskyellina*, and the recently proposed genus *Paramonticellia* Pavanelli & Rego, 1991. *Jauella*, a genus previously placed in Jauelliinae Rego & Pavanelli, 1985, is now moved to Peltidocotyliidae, resulting in the abolition of the subfamily.

For this key, only two families are accepted. The Proteocephalidae is primarily characterized by medullary vitelline follicles, i.e. internal to the longitudinal muscle bundles (when these muscles are weakly developed or absent it is difficult, or not possible, to define the disposition of vitelline follicles and gonads). The Monticelliidae contains genera with mainly cortical vitelline follicles, i.e. external to the longitudinal muscle bundles.

In the Proteocephalidae, the gonads are usually medullary, but in the Monticelliidae they are cortical and medullary, in varied combinations, permitting division into subfamilies.

The relative importance of vitelline follicles and reproductive organs remains to be ascertained. If the position of the vitellarium is fundamental, *Marsypocephalus* (Marsypocephalinae) must remain in the Proteocephalidae, due to the medullary position of the vitellarium in this family but, in contrast to the other Proteocephalidae, the Marsypocephalinae have their testes in the dorsal cortex. This is apparently a monticelliid character. Nevertheless, I prefer to treat the Marsypocephalinae as a member of the Proteocephalidae pending the elucidation of this problem.

The newly established Nupeliinae (Pavanelli & Rego, 1991) was defined as

having its vitellarium and reproductive organs partly medullary and partly cortical. This group is clearly intermediate between the Proteocephalidae and Monticelliidae. The Nupeliinae is provisionally placed here in Monticelliidae.

The identification of proteocephalid and monticelliid species is a difficult task. A major problem is the inadequacy of the descriptions of some species; for instance, in *Endorchis* Woodland, 1934 and *Myzophorus* Woodland, 1934, both of the subfamily Endorchiinae, the position of the uterus, whether cortical or medullary, was not clearly stated which led some workers to doubt the validity of these genera. Rego (1991) invalidated the genus and species of *Endorchis* (synonymizing it with *Nomimoscolex*) and also the subfamily Endorchiinae and provisionally transferred *Myzophorus* to Zygobothriinae. However, I now think that *Myzophorus* is a controversial genus that needs to be re-evaluated.

The subfamilies of the Proteocephalidae are separated generally by the characteristics of the scolex, i.e. presence or absence of a metascolex, armed rostellum, piercing organ and spines on the scolex.

The monticelliid subfamilies are differentiated solely by the position of the reproductive organs in the cortex and/or in the medulla. In the subfamily Monticelliinae, the testes, ovary and uterus are situated in the cortex. In the Zygobothriinae, gonads are entirely medullary but the vitelline follicles are cortical. The other subfamilies exhibit intermediate forms of these characters.

The examination of more specimens is crucial to a precise definition of taxa and phylogenetic affinities. Of particular interest would be phylogeny and affinities of South American proteocephalids and those described from Africa and other continents.

ORDER PROTEOCEPHALIDEA MOLA, 1928

Diagnosis: Strobila small to medium in size. Scolex variable; with four simple acetabula, or suckers may be biloculate, triloculate or tetraloculate; apical sucker or armed rostellum occasionally present. Metascolex present or absent. Segmentation usually distinct. Strobila usually anapolytic. Mature proglottids wider than long or square. Gravid proglottids usually longer than wide. Parenchyma divided into cortical and medullary regions, generally separated by internal longitudinal musculature; longitudinal musculature may be reduced or inconspicuous, especially in Monticelliidae. Reproductive organs medullary or, in various combinations, in medulla and cortex. Vitellarium follicular, generally in lateral fields. Genital pores lateral. Uterus generally with diverticula and with longitudinal apertures in gravid proglottids. Adults in freshwater fish, amphibians and reptiles.

Key to families

- 1a. Vitelline follicles cortical Monticelliidae La Rue, 1911.
Diagnosis: Scolex of varied forms. Testes, ovary and uterus, in various combinations, situated in cortex or medulla. Internal longitudinal musculature sometimes

weakly developed or inconspicuous. In freshwater fishes, rarely amphibians and reptiles. Tropical and subtropical areas of South America. Type-genus *Monticellia* La Rue, 1911.

1b. Vitelline follicles medullary Proteocephalidae La Rue, 1911.

Diagnosis: Scolex of varied forms. Ovary and uterus medullary. Testes medullary except in *Marsypocephalus*. Parenchyma usually divided into cortical and medullary regions by distinct layer of longitudinal muscle fibres. Parasites of fishes, amphibians and reptiles. North and South America, Africa, Europe, Asia, Australia. Type-genus *Proteocephalus* Weinland, 1858.

Family Proteocephalidae La Rue, 1911

Key to subfamilies

1a. Scolex without metascolex 2.

1b. Scolex with metascolex Corallobothriinae Freze, 1965.

Diagnosis: Suckers covered by folds of metascolex tissue, with or without sphincter. Vitellarium and genitalia medullary. In siluriforms. South America, North America, Africa, Russia. Type-genus *Corallobothrium* Fritsch, 1866.

2a. Testes medullary 3.

2b. Testes cortical Marsypocephalinae Woodland, 1933.

Diagnosis: Ovary, vitellarium and uterus medullary. Scolex round, with four lobes, each lobe bearing large sucker with muscular sphincter. Longitudinal musculature conspicuous. In siluriform fishes from Africa. Type and only genus *Marsypocephalus* Wedl, 1861.

3a. Vitellarium follicular, lateral 4.

3b. Vitellarium not follicular, in form of two massive bodies, posterior to ovary Sandonellinae Khalil, 1960.

Diagnosis: Scolex without metascolex, but with highly modified apical organ formed of two lappets. Genitalia medullary. Uterus saccular. Vitellarium near posterior margin of segment. Uterus forms round sac that invades cortex. Strobila craspedote. In African osteoglossid fishes. Type and only genus *Sandonella* Khalil, 1960.

4a. Scolex lacking rostellum or spines. Vitellarium and reproductive organs medullary. Scolex globular. Suckers of various forms

..... Proteocephalinae Mola, 1929.

Diagnosis: Rostellum and metascolex absent. Suckers acetabular uniloculate, biloculate or tetraloculate. Fifth or apical sucker may be present. Vitellarium lateral, medullary. Reproductive organs also medullary (Fig. 13.1). In fishes, amphibians and reptiles. Cosmopolitan. Type-genus *Proteocephalus* Weinland, 1858.

4b. Scolex with armed rostellum or 'piercing organ' 5.

- 5a. Scolex with armed rostellum *Gangesiinae* Mola, 1929.
Diagnosis: Rostellum armed, non-retractile. One, two or several circles of hooks present. Scolex, suckers and neck spined or not. Vitellarium lateral. Ovary bilobed. In siluroid fishes. Africa, Europe, Asia. Type-genus *Gangesia* Woodland, 1924.
- 5b. Scolex with specialized rostellum (piercing organ) of muscular-glandular structure *Acanthotaeniinae* Freze, 1963.
Diagnosis: Scolex and anterior part of strobila covered with dense network of spines. Rostellum terminal. Reproductive organs medullary. Mehlis's gland highly developed. Longitudinal musculature weakly developed. In reptiles of genus *Varanus*. Asia, Australia. Type-genus *Acanthotaenia* Linstow, 1903.

Subfamily Proteocephalinae Mola, 1929

Key to genera

- 1a. Suckers of normal acetabular type 2.
 1b. Suckers modified in various ways 4.
- 2a. Vitellarium apparently absent *TravassIELLA* Rego & Pavanelli, 1987.
Diagnosis: Small worms, filiform. Suckers salient, directed laterally. Vitellarium not observed (Fig. 13.2). Gonads and uterus medullary. Longitudinal musculature inconspicuous, distinction between medulla and cortex difficult to discern (Fig. 13.3). In South American siluroid fishes. Type-species *T. avitellina* Rego & Pavanelli, 1987.
- 2b. Vitellarium present 3.

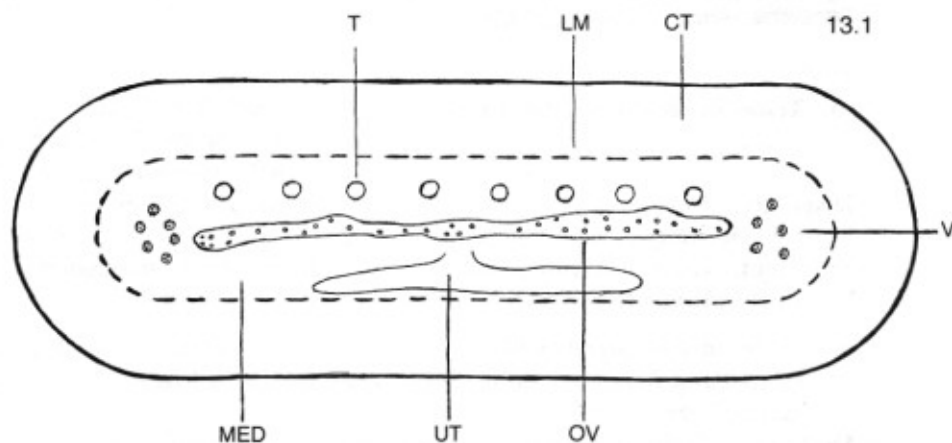
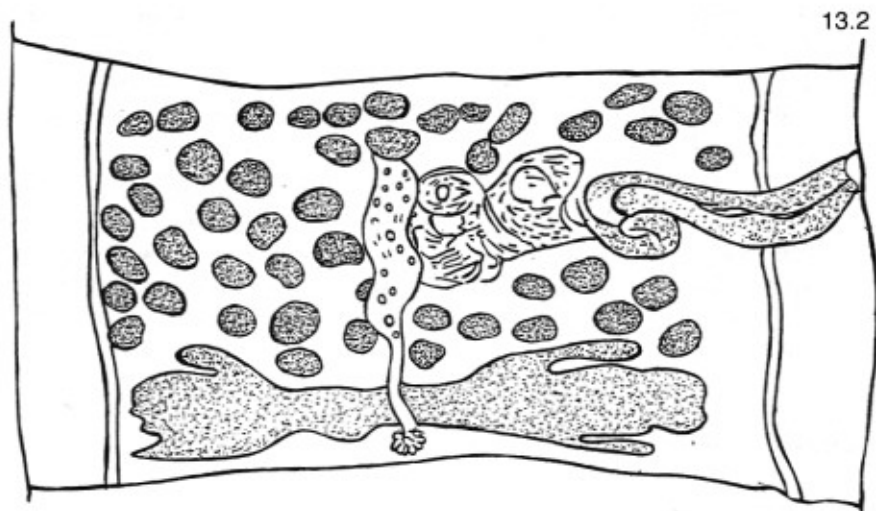
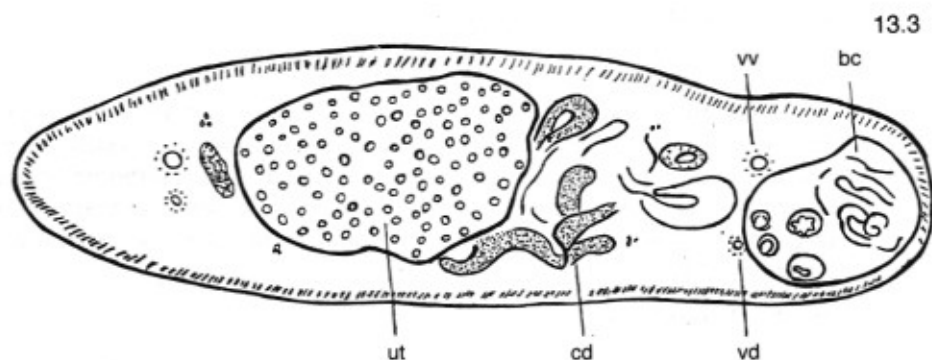


Fig. 13.1 Proteocephalinae, schematic section. T = testes, LM = longitudinal muscle bundles, CT = cortex, V = vitellaria, MED = medulla, UT = uterus, OV = ovary. (Original.)



13.2



13.3

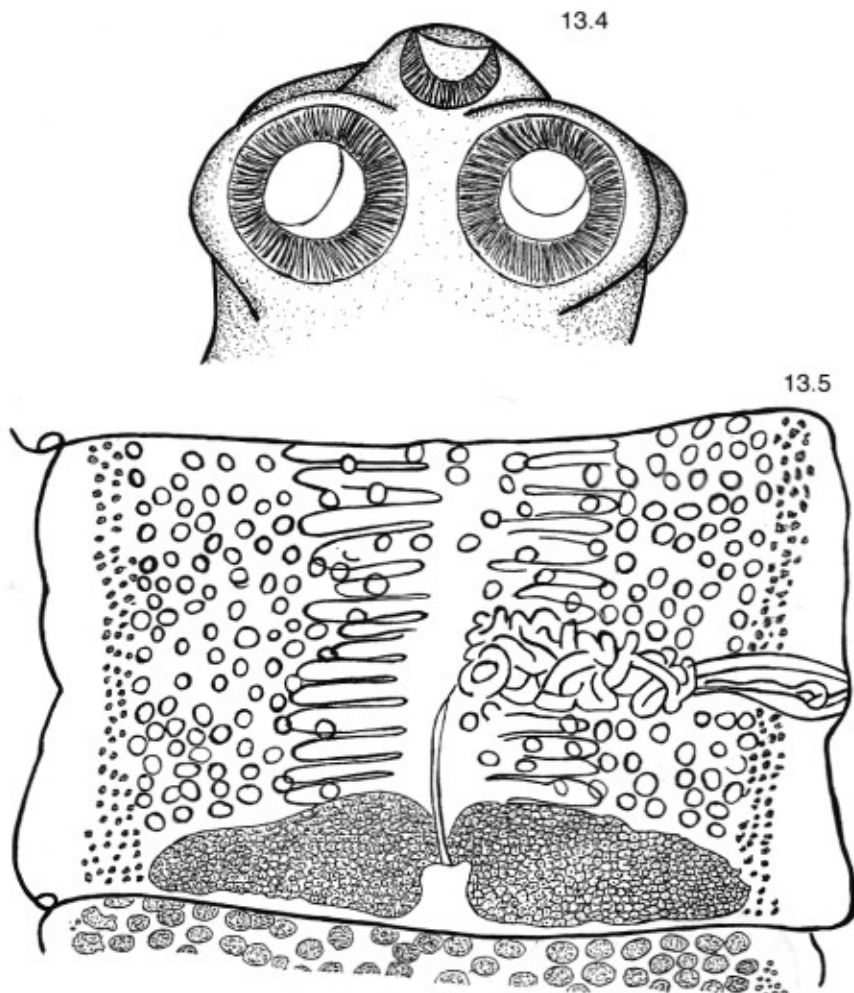
Figs 13.2, 13.3 *Travassiaella avitellina* Rego & Pavanelli, 1987. 13.2. Mature proglottid. 13.3. Transverse section of gravid proglottid. (After Rego & Pavanelli, 1987.)

- 3a. Testes in continuous field throughout proglottids (Fig. 13.5)
 *Proteocephalus* Weinland, 1858.
 (Syn. *Ichthyotaenia* Lönnberg, 1894.)

Diagnosis: Scolex with four suckers of normal type, fifth or apical sucker may be present (Fig. 13.4). Reproductive organs and vitellarium medullary. Vitellarium lateral. In fishes, amphibians and reptiles. Cosmopolitan. Type-species *P. filicollis* (Rudolphi, 1802).

- 3b. Testes in two lateral fields *Ophiotaenia* La Rue, 1911.
 (Syns *Batrachotaenia* Rudin, 1917; *Solenotaenia* Beddard, 1913; *Testudo-*
taenia Freze, 1965.)

Diagnosis: Scolex and internal features as in *Proteocephalus*, except for testes distributed in two lateral fields (Fig. 13.6). In fishes, amphibians and reptiles. Cosmopolitan. Type-species *O. perspicua* La Rue, 1911.



Figs 13.4, 13.5 *Proteocephalus osculatus* (Goeze, 1782). 13.4. Scolex. 13.5. Mature proglottid. (After Nybelin, 1942.)

- 4a. Suckers not highly modified, large, posterior margin notched, sucker heart-shaped (Fig. 13.7) *Crepidobothrium* Monticelli, 1900.
(Syn. *Ophidotaenia* Beddard, 1913.)

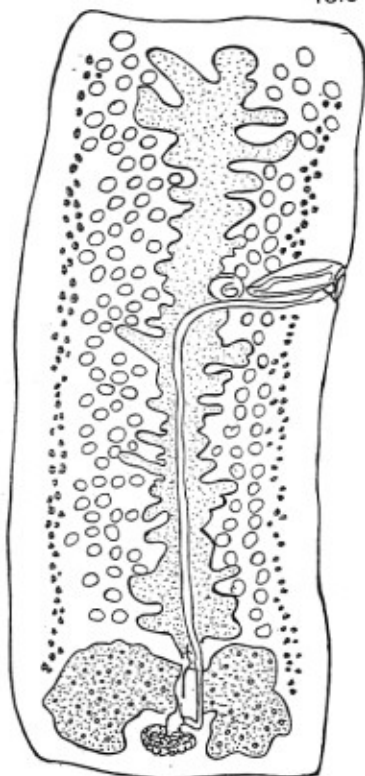
Diagnosis: Scolex large. Testes in two lateral fields. Ovary bilobed, near posterior margin of proglottid. Uterus median, with lateral branches. In South American snakes. Type-species *C. gerrardi* (Baird, 1860).

- 4b. Suckers highly modified 5.

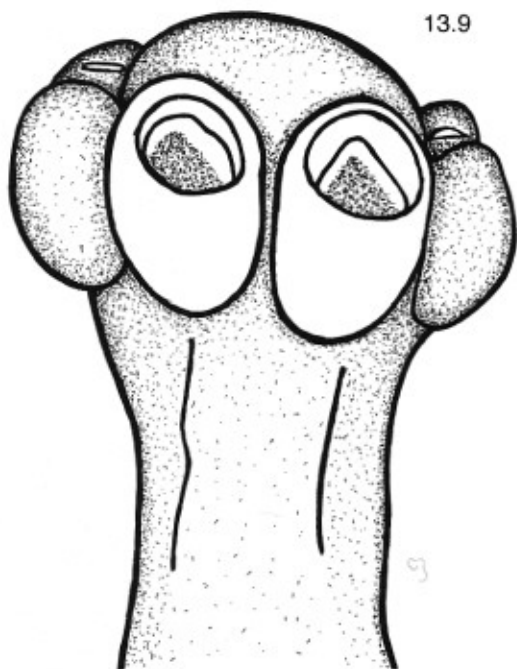
- 5a. Suckers pedunculate, located in protruding part of scolex (Fig. 13.8)
..... *Macrobothriotaenia* Freze, 1965.

Diagnosis: Scolex wider than neck. Genital pore slightly postequatorial. Proglot-

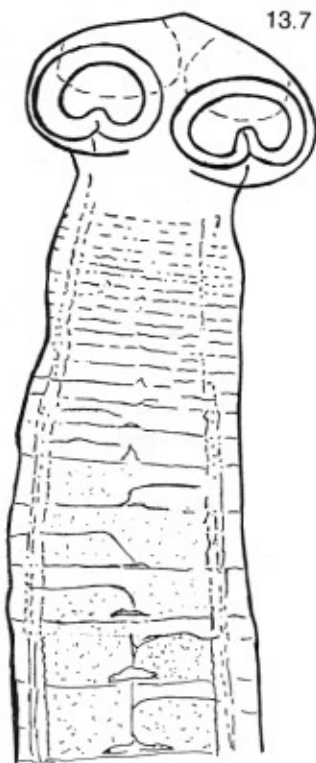
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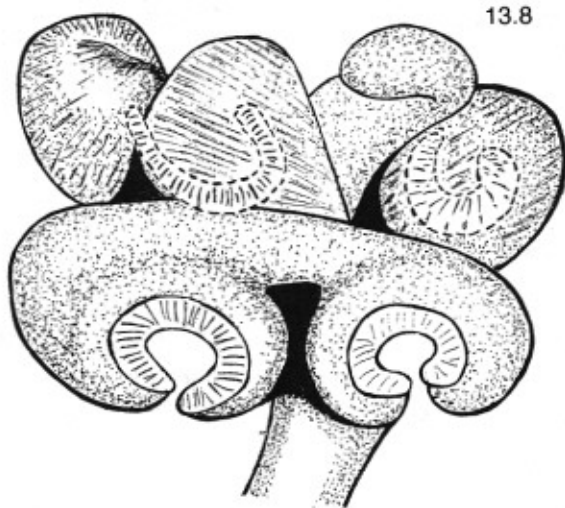
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13.8



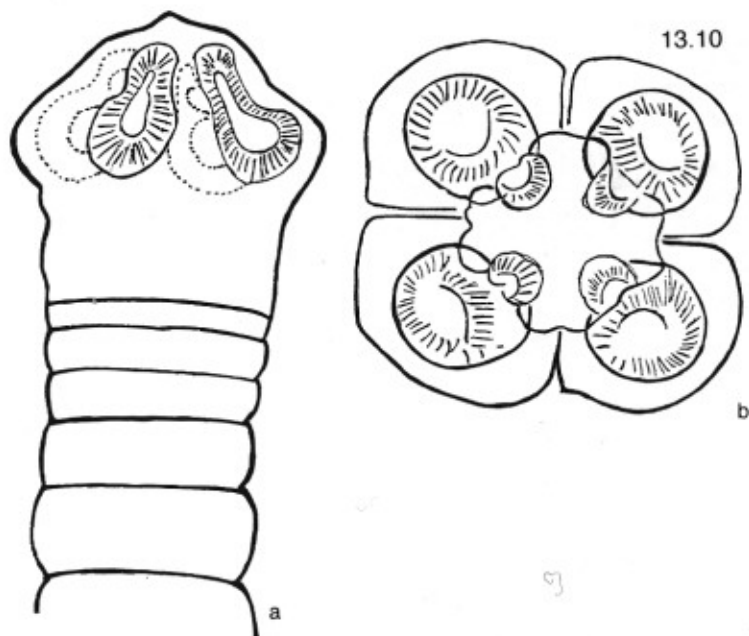


Fig. 13.6 *Ophiotaenia cohospes* (Cordero, 1946). Mature proglottid. (After Cordero, 1946.)

Fig. 13.7 *Crepidobothrium gerrardi* (Baird, 1860). Scolex and immature proglottids. (After Dollfus, 1932.)

Fig. 13.8 *Macrobothriotaenia ficta* (Meggitt, 1927). Scolex. (After Meggitt, 1927d.)

Fig. 13.9 *Brayela karuatayi* (Woodland, 1934). Scolex. (After Woodland, 1934a.)

Fig. 13.10 *Tejidotaenia appendiculata* (Baylis, 1947). a. Anterior region. b. Scolex, apical view. (After Baylis, 1947.)

tids longer than wide. Testes in two fields. Cirrus-sac large. Ovary transversely elongated. In Indian snakes. Type-species *M. ficta* (Meggitt, 1927).

5b. Suckers not pedunculate 6.

6a. Each sucker divided into two equal compartments (biloculate), apparently eight suckers, but only four have apertures (Fig. 13.9)

..... *Brayela Rego*, 1984.

Diagnosis: Scolex dome-shaped. Testes in two lateral fields. Uterus longitudinal tube without diverticula. In South American siluroid fish. Type-species *B. karuatayi* (Woodland, 1934).

6b. Suckers with two unequal cavities, or four cavities 7.

7a. Suckers divided into two unequal cavities (Fig. 13.10)

..... *Tejidotaenia Freze*, 1965.

Diagnosis: Small worms. Strobila consists of few proglottids. Testes in two lateral fields. Ovary large, alate. Vitellarium lateral. Uterus with diverticula. In Surinam monitors of South America. Type-species *T. appendiculata* (Baylis, 1947).

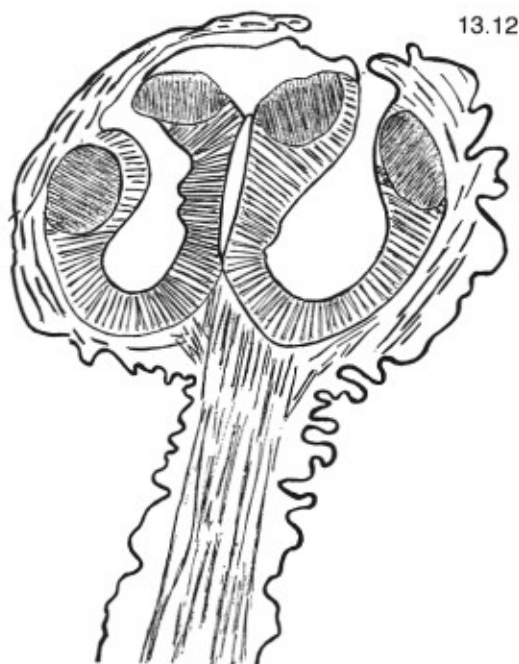
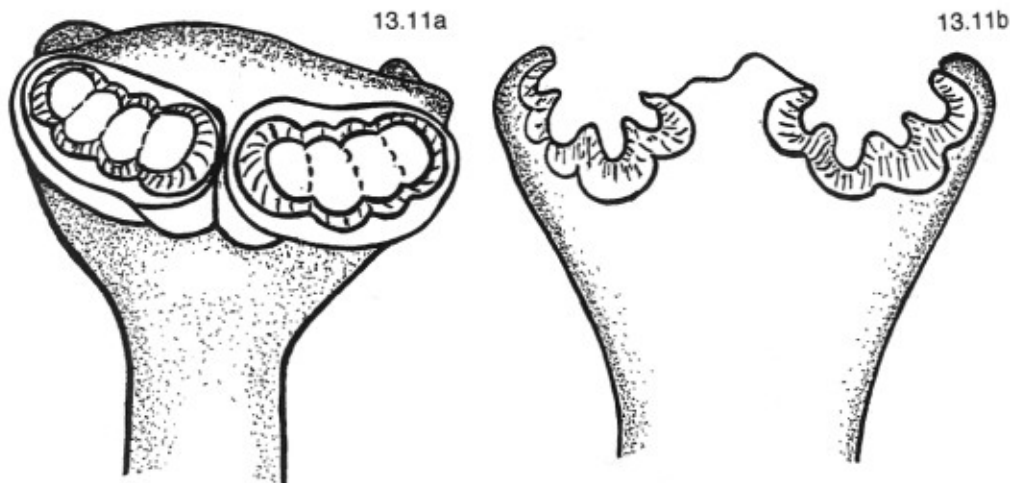


Fig. 13.11 *Deblocktaenia ventosaloculata* (Deblock, Rosé & Broussart, 1962). a. Scolex. b. Section of scolex. (After Deblock *et al.*, 1962.)

Fig. 13.12 *Megathylacus jandia* Woodland, 1934. Section of scolex. (After Woodland, 1934a.)

7b. Cavity of each sucker divided into four muscular chambers by septa (Fig. 13.11) *Deblocktaenia* Odening, 1963.

Diagnosis: Suckers transverse, apertures directed anteriorly. Scolex much wider than neck. Proglottids very elongated. Genital pores pre-equatorial. Testes in two lateral fields. Vagina with sphincter. Uterus with diverticula. In colubrid snakes from Madagascar. Type-species *D. ventosaloculata* (Deblock, Rosé & Broussart, 1962).

Subfamily Coralbothriinae Freze, 1965

Key to genera

- 1a. Suckers with sphincter 2.
 1b. Suckers without sphincter 3.

2a. Suckers large, saccular, hidden under folds of tissue; each sucker has strong muscular sphincter that completely encircles aperture of sucker (Fig. 13.12) *Megathylacus* Woodland, 1934.

Diagnosis: Scolex large, quadrilobate. Metascolex developed. Suckers with sphincter (Fig. 13.12). Longitudinal musculature well developed. Genital pore near middle of proglottid margin. Reproductive organs medullary. Vitellarium lateral. In South American siluriform fishes. Type-species *M. jandia* Woodland, 1934.

2b. Scolex as in *Megathylacus* but differs in having sphincter muscles concentrated at only one side of sucker orifice *Megathylacoides* Jones, Kerly & Sneed, 1956.

Diagnosis: Suckers with incomplete sphincter (Fig. 13.13). Mature proglottids

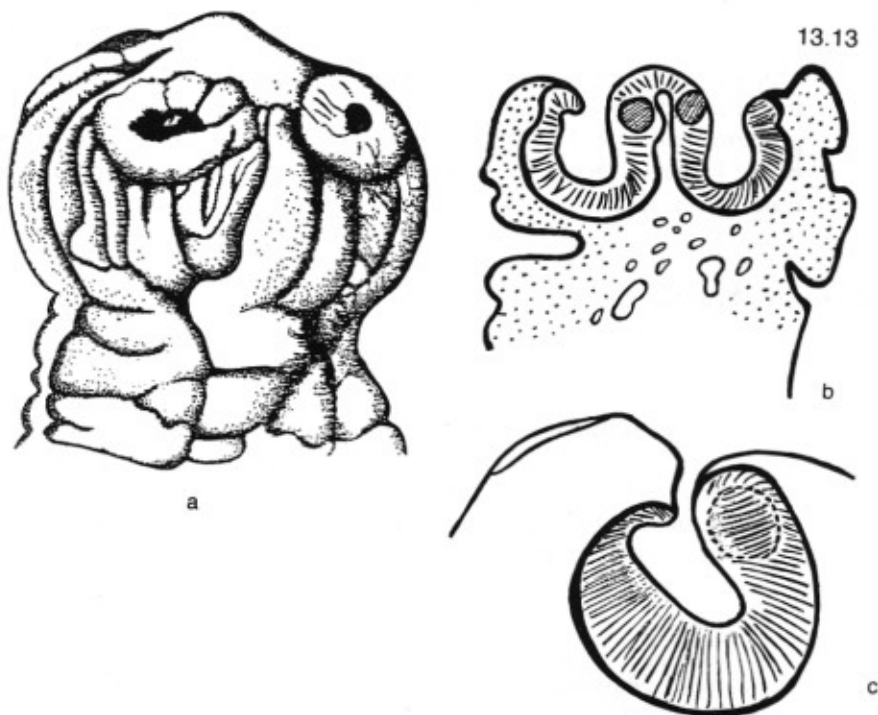


Fig. 13.13 *Megathylacoides giganteum* (Essex, 1928). a. Scolex. b. Section of scolex. c. Detail of sucker. (After Essex, 1928.)

longer than wide. Testes in single layer. Ovary bilobed, posterior. Vitelline follicles lateral. Uterus with anterior pore. In siluroid fishes of North America. Type-species *M. giganteum* (Essex, 1928).

3a. Metascolex well developed 4.

3b. Metascolex relatively weakly developed
..... *Corallotaenia* Freze, 1965.

Diagnosis: Small worms. Suckers of common type, surrounded by some folds of tissue (Fig. 13.14). Vitelline follicles lateral. Mature proglottids longer than broad. Testes in one layer. In fishes from North and South America. Type-species *C. parva* (Larsch, 1941).

4a. Scolex with corolla-like metascolex. Suckers hidden by folds of metascolex (Figs 13.15, 13.16). Uterine diverticula mainly lateral
..... *Corallobothrium* Fritsch, 1886.

Diagnosis: Large worms. Proglottids numerous, broader than long. Genital pore in anterior half of proglottid margin. Longitudinal musculature massive, forming bundles. Uterus with lateral diverticula. Vitellarium lateral, converging at posterior margin. Testes in several layers. In siluroid fishes from Africa and North America. Type-species *C. solidum* Fritsch, 1886.

4b. Scolex with folded metascolex, four typical suckers and small apical sucker (Fig. 13.17). Uterus transverse, with anterior and posterior diverticula ...
..... *Paraproteocephalus* Chen, 1962.

Diagnosis: Proglottids wider than long. Longitudinal musculature consisting of powerful bundles of fibres. Vitellarium lateral, converging towards ovary at posterior end (Fig. 13.18). Testes in one field. Uterine stem divided into two lateral branches each with diverticula anteriorly and posteriorly. In siluroid fishes from Russia (Far-East). Type-species *P. parasiluri* (Zmeev, 1936).

Subfamily Acanthotaeniinae Freze, 1963

Key to genera

1a. Eggs not contained in capsules *Acanthotaenia* von Linstow, 1903.
(Syn. *Rostellotaenia* Freze, 1963.)

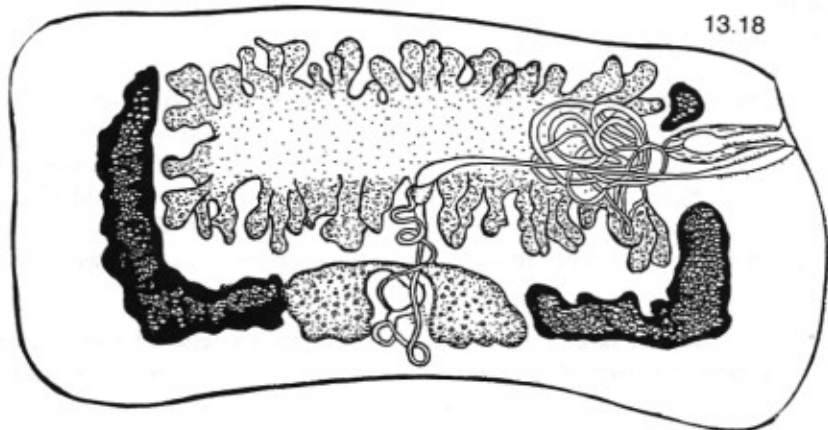
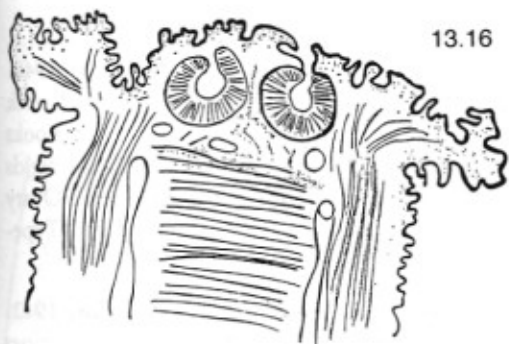
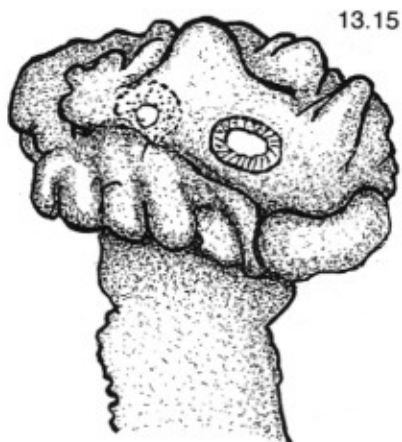
Diagnosis: Scolex and anterior part of strobila covered with spines (Fig. 13.19). Apical muscular organ (piercing organ) present. External segmentation sometimes indistinct. Longitudinal musculature weakly developed. Testes in two fields.

Fig. 13.14 *Corallotaenia parva* (Larsch, 1941). Scolex. (After Larsch, 1941.)

Fig. 13.15 *Corallobothrium fimbriatum* (Essex, 1928). Scolex. (After Essex, 1928.)

Fig. 13.16 *C. solidum* Fritsch, 1886. Longitudinal section of scolex. (After Fritsch, 1886.)

Figs 13.17, 13.18 *Paraproteocephalus parasiluri* (Zmeev, 1936). 13.17. Scolex. (After Zmeev, 1936.) 13.18. Gravid proglottid. (After Freze, 1965.)



Uterus with numerous, irregular diverticula (Fig. 13.20). In varanid reptiles from Africa, Australia, India, Malaysia. Type-species *A. shipleyi* von Linstow, 1903.

1b. Eggs contained in membranous capsules (Fig. 13.23)
 *Kapsulotaenia* Freze, 1963.
 (Syn. *Capsulotaenia* Freze, 1963.)

Diagnosis: Scolex and anterior part of strobila covered with spines. Apical region of scolex developed as 'piercing organ' (Fig. 13.21). Proglottids usually longer than wide (Fig. 13.22). Uterus with developed diverticula. Mehlis's gland strongly developed. Musculature weakly developed. In monitors (Reptilia) in Indonesia, Australia. Type-species *K. sandgroundi* (Carter, 1943).

Subfamily Gangesiinae Mola, 1929

Key to genera

1a. Rostellum armed with one or two circles of hooks 3.
 1b. Rostellum armed with several circles of minute hooks 2.

2a. Testes lacking in anterior median region of proglottids
 *Electrotaenia* Nybelin, 1942.

Diagnosis: Scolex quadrilobulate, each lobe bearing sucker. Scolex and neck covered with small spines. Rostellum with several circles of minute hooks (Fig. 13.24). Genital atrium deep, muscular. Cirrus-sac small. Testes in two fields (Fig. 13.25). Vitellarium lateral, fields curved in posterior part of segment. Ovary bilobed, at posterior margin of proglottid. In siluroid fishes from Africa. Type-species *E. malopteruri* (Fritsch, 1886).

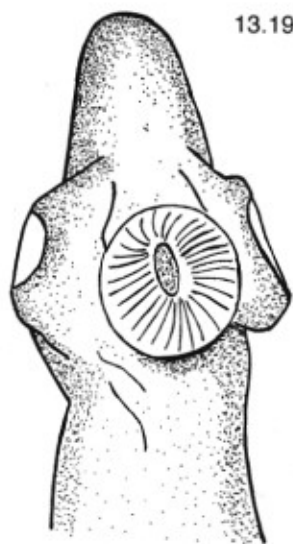
2b. Testes fill entire field anterior to ovary *Silurotaenia* Nybelin, 1942.

Diagnosis: Large worms. Scolex, suckers and neck covered with small spines (Fig. 13.26). Rostellum armed with several circles of minute hooks. Genital atrium shallow, not muscular. Cirrus-sac small, round. Testes in single field (Fig. 13.27). Ovary bilobed, large, at posterior margin of proglottid. Vitelline follicles lateral to osmoregulatory canals. In siluroid fishes from Europe. Type-species *S. siluri* (Batsch, 1786).

3a. One or two circles of small hooks (Fig. 13.28). Vitelline bands extend throughout lateral edge of proglottid *Gangesia* Woodland, 1924.

Diagnosis: Suctorial surface of sucker covered with spines. Mature proglottid square. Vitellarium lateral, extending entire length of proglottid (Fig. 13.29), medullary, partly cortical (?). Testes in continuous field. Cirrus-sac variable. In siluroid fishes of Europe, India, Japan. Type-species *G. bengalensis* (Southwell, 1913).

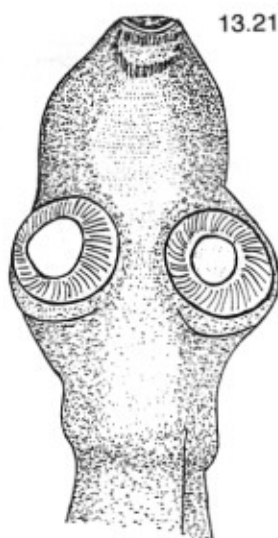
3b. One circle of large hooks (Fig. 13.30). Lateral vitelline bands concentrated in posterior part of proglottid *Vermaia* Nybelin, 1942.



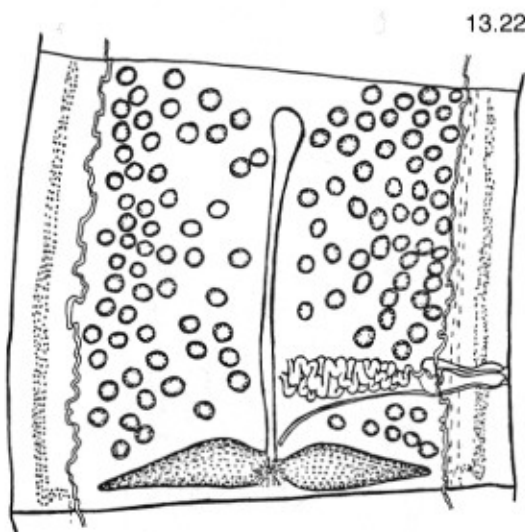
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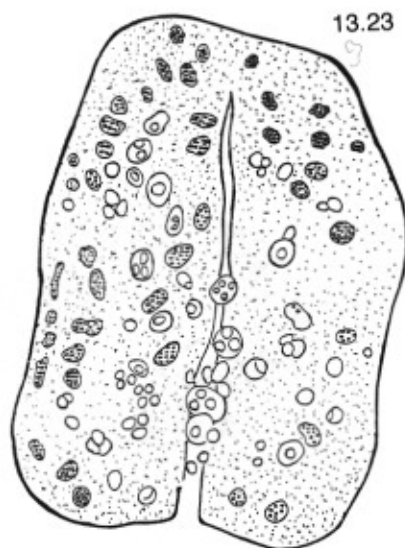
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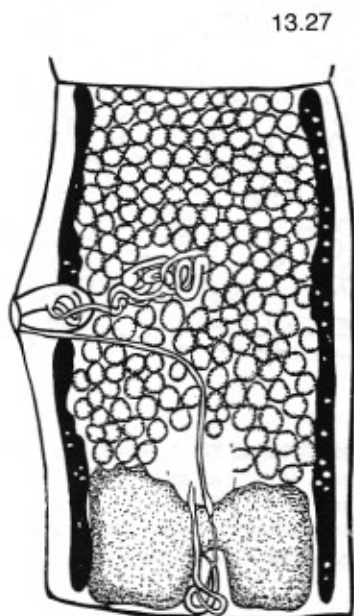
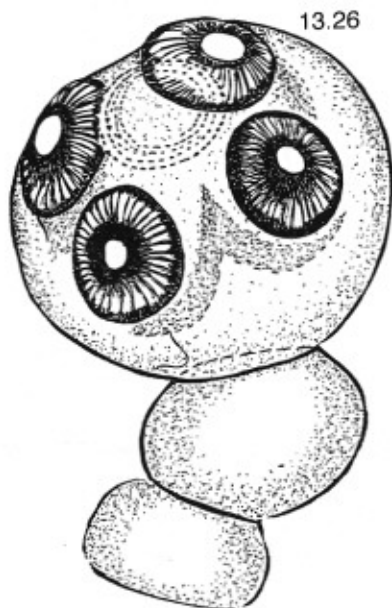
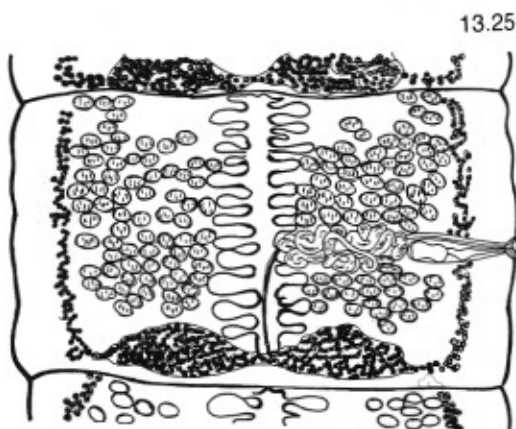
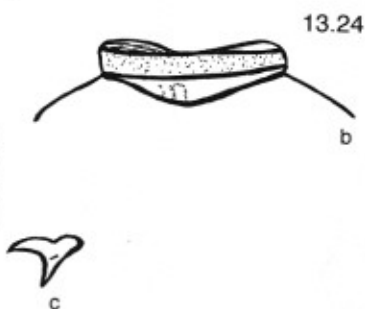
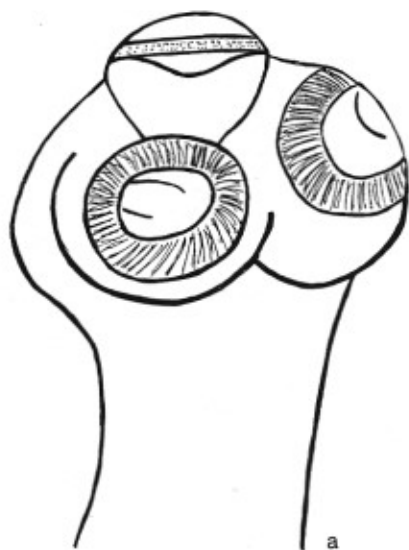


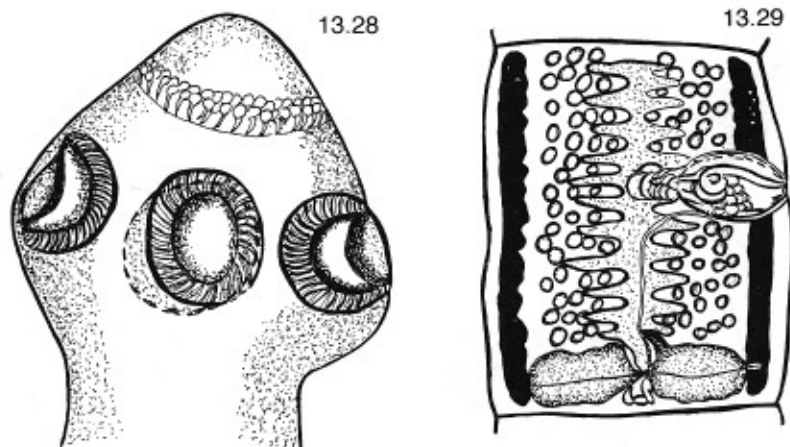
13.23

Figs 13.19, 13.20 *Acanthotaenia shipleyi* von Linstow, 1903. 13.19. Scolex. 13.20. Mature proglottid. (After Yamaguti, 1954b.)

Figs 13.21, 13.22 *Kapsulotaenia sandgroundi* (Carter, 1943). 13.21. Scolex. (After Freze, 1965.) 13.22. Mature proglottid. (After Carter, 1943.)

Fig. 13.23 *K. varia* (Beddard, 1913). Gravid proglottid. (After Beddard, 1913.)





Figs 13.24, 13.25 *Electrotaenia malopteruri* (Fritsch, 1886); 13.24. a. Scolex; b. Detail of rostellum; c. Hook. (After Nybelin, 1942.) 13.25. Gravid proglottid. (After Janicki, 1928.)
Figs 13.26, 13.27 *Silurotaenia siluri* (Batsch, 1786). 13.26. Scolex. 13.27. Gravid proglottid. (After Freze, 1965.)
Figs 13.28, 13.29 *Gangesia parasiluri* Yamaguti, 1934. 13.28. Scolex. 13.29. Mature proglottid. (After Yamaguti, 1934.)

Diagnosis: Scolex, neck and proglottids covered with spines. Posterior proglottids longer than wide. Longitudinal musculature weakly developed. Vitellarium in short lateral fields (Fig. 13.31), but completely developed only in posterior proglottids. Genital pore in anterior half of lateral margin. Cirrus-sac small. Testes in two fields, anterior to ovary. Uterus with numerous diverticula. Eggs embryonated in uterus. In Indian siluroid fishes. Type-species *V. pseudotropii* (Verma, 1928).

Subfamily Marsypocephalinae Woodland, 1933

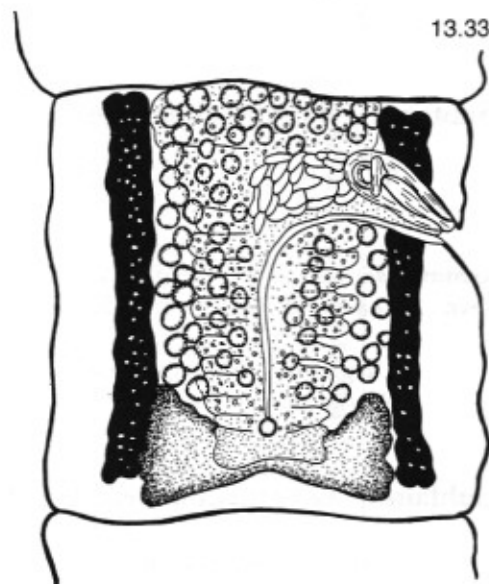
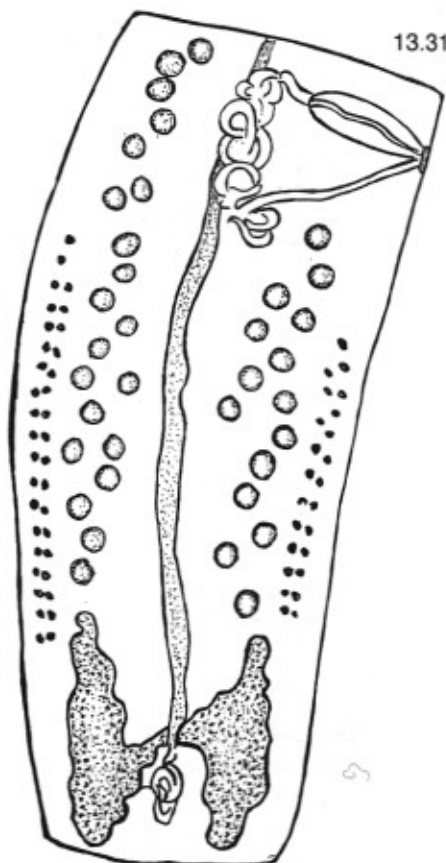
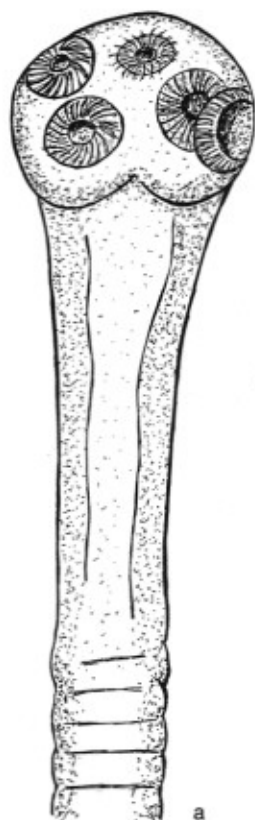
The subfamily contains one genus only.

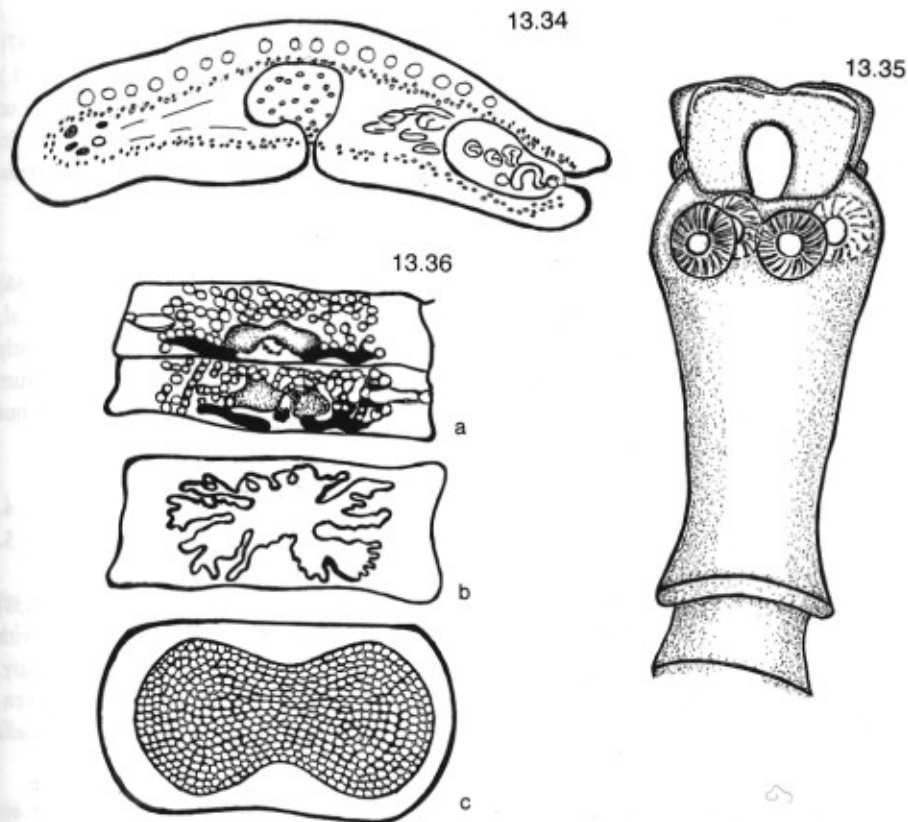
Genus *Marsypocephalus* Wedl, 1861 (Figs 13.32–13.34)
 (Syn. *Loennbergia* Fuhrmann & Baer, 1925)

Diagnosis: With the characters of the subfamily. Type-species *M. rectangulus* Wedl, 1861.

Subfamily Sandonellinae Khalil, 1960

The subfamily contains one genus only.





Figs 13.30, 13.31 *Vermaia pseudotropii* (Verma, 1928); 13.30. a. Scolex; b. Rostellum and hooks. 13.31. Mature proglottid. (After Verma, 1928.)

Figs 13.32-13.34 *Marsypocephalus* Wedl, 1861. *M. rectangulus* Wedl, 1861. 13.32. Scoleces. 13.33. Mature proglottid. (After Janicki, 1928.) 13.34. *M. heterobranchus* Woodland, 1925. Transverse section of proglottid.

Figs 13.35, 13.36 *Sandonella sandoni* (Lynsdale, 1960). 13.35. Scolex. 13.36. a. Gravid proglottids; b. Uterus (without eggs); c. Uterus (with eggs). (After Khalil, 1960.)

Genus *Sandonella* Khalil, 1960 (Figs 13.35, 13.36)

Diagnosis: With the characters of the subfamily. Type-species *S. sandoni* (Lynsdale, 1960).

Family Monticelliidae La Rue, 1911

Key to subfamilies

- | | |
|----------------------------|----|
| 1a. Testes medullary | 2. |
| 1b. Testes cortical | 3. |

- 2a. Ovary and uterus entirely medullary
 *Zygobothriinae* Woodland, 1933. (Fig. 13.37)
 (Syn. *Postgangesiinae* Akhmerov, 1969.)
Diagnosis: Scolex varied, with metascolex present or not. Suckers uniloculate or biloculate. Gonads medullary. Vitellarium cortical, lateral or dorsoventral. In freshwater fishes from South America and Russia. Type-genus *Zygobothrium* Diesing, 1850.
- 2b. Ovary and uterus partly cortical, partly medullary
 *Nupeliinae* Pavanelli & Rego, 1991. (Fig. 13.38)
Diagnosis: Scolex simple. Suckers of normal type. Vitellarium mostly cortical, some follicles in medulla. Uterus and ovary partly medullary. Testes mostly medullary, some between longitudinal muscle fibres. Longitudinal musculature scattered, irregular. In South American siluroid fishes. Type and only genus *Nupelia* Pavanelli & Rego, 1991.
- 3a. Ovary cortical or partly cortical 4.
 3b. Ovary medullary 5.
- 4a. Ovary partly cortical *Rudolphiellinae* Woodland, 1935. (Fig. 13.39)
Diagnosis: Scolex truncate. Massive wrinkled metascolex present, with longitudinal furrows. Suckers in central protuberance of scolex. Uterus medullary. Ovary partly medullary, partly cortical. Testes in dorsal cortex. Vitellarium in ventral cortex. In South American siluroid fishes. Type and only genus *Rudolphiella* Fuhrmann, 1916.
- 4b. Ovary entirely cortical *Monticelliinae* Mola, 1929. (Fig. 13.40)
Diagnosis: Scolex bears four suckers, uniloculate or biloculate. Metascolex present or absent. Uterus and gonads cortical. Vitelline fields lateral, ventral or crescent-shaped. Uterus with lateral diverticula. Longitudinal musculature variable. In South American freshwater fishes. Type-genus *Monticellia* La Rue, 1911.
- 5a. Uterus medullary *Ephedrocephalinae* Mola, 1929. (Fig. 13.41)
Diagnosis: Scolex with folded metascolex, collar-like, behind suckers. Four stalked suckers of common type. Strobila with median furrows. Uterus and ovary entirely medullary. Testes in dorsal cortex. Vitellarium in ventral cortex. Longitudinal musculature very strong. In South American siluroid fishes. Type and only genus *Ephedrocephalus* Diesing, 1850.
- 5b. Uterus cortical *Peltidocotylinae* Woodland, 1934. (Fig. 13.42)
 (Syn. *Othinoscotecinae* Woodland, 1933.)
Diagnosis: Scolex with four suckers or no suckers. Suckers of normal type (uniloculate) or biloculate, forming two separate cavities. Metascolex present. Ovary medullary. Uterus cortical. Testes in dorsal cortex. Vitelline follicles cortical, in two bands, dorsal and ventral. In South American siluroid fishes. Type-genus *Peltidocotyle* Diesing, 1850.

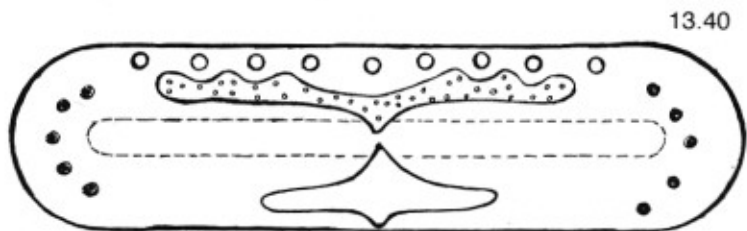
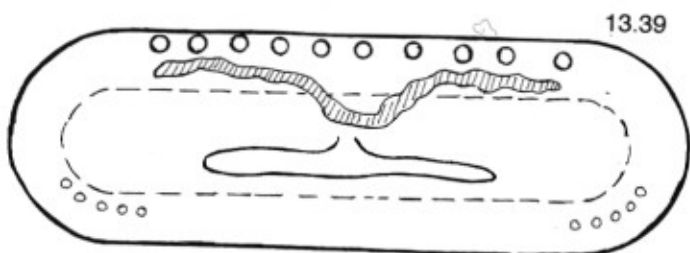
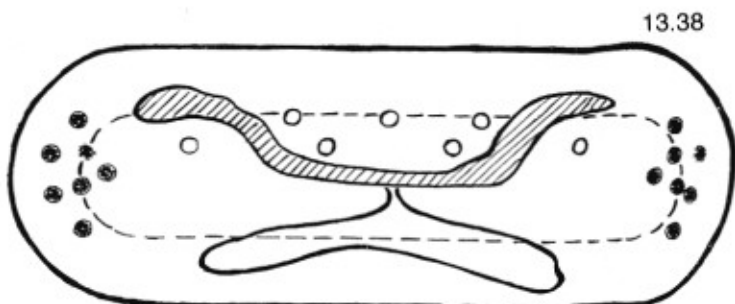
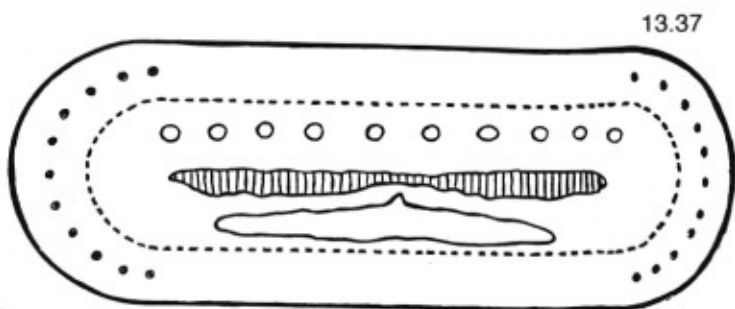


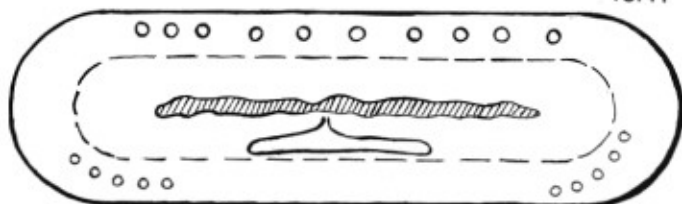
Fig. 13.37 Zygobothriinae. Schematic section. Vitelline follicles cortical, genitalia medullary. (Original.)

Fig. 13.38 Nupeliinae Pavanelli & Rego, 1990. Transverse section of proglottid. Schematic. (Original.)

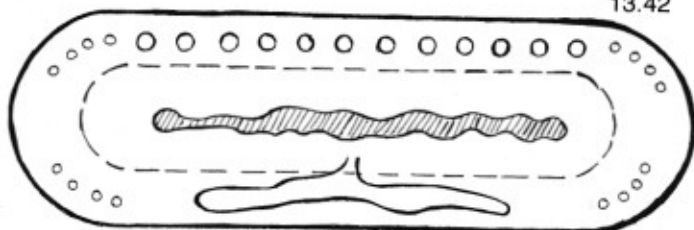
Fig. 13.39 Rudolphiellinae. Schematic section. Vitelline follicles and testes cortical; uterus medullary; ovary partially medullary, partially cortical. (Original.)

Fig. 13.40 Monticelliinae. Schematic section. Vitelline follicles and gonads in the cortex. (Original.)

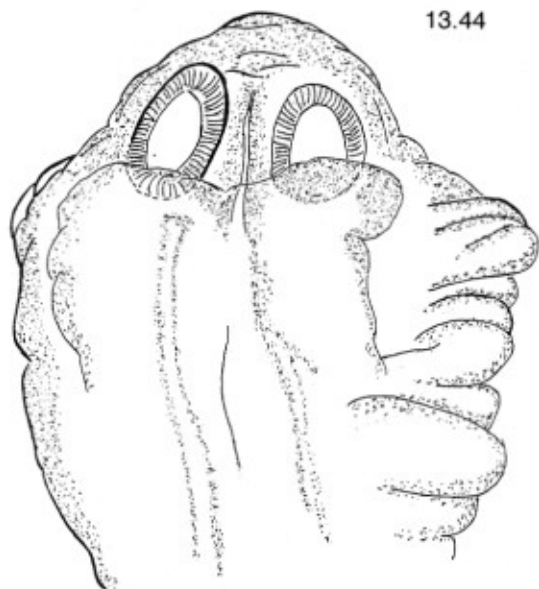
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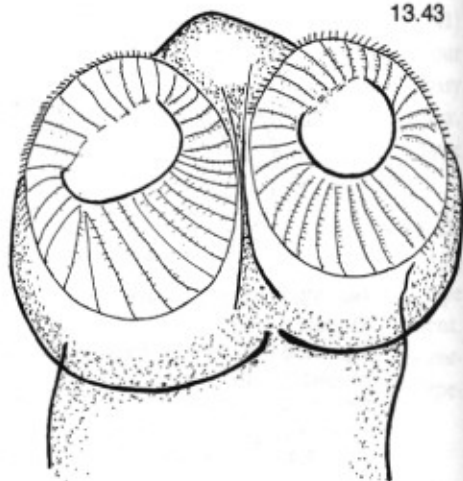


Fig. 13.41 Ephedrocephalinae. Vitelline follicles cortical; testes cortical; ovary and uterus medullary. (Original.)

Fig. 13.42 Peltidocotylineae. Schematic section. Ovary medullary; vitelline follicles, testes and uterus cortical. (Original.)

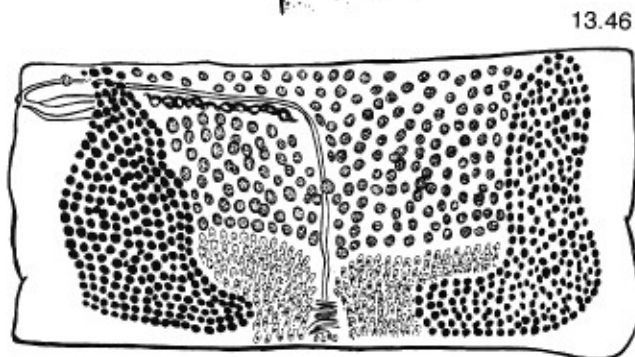
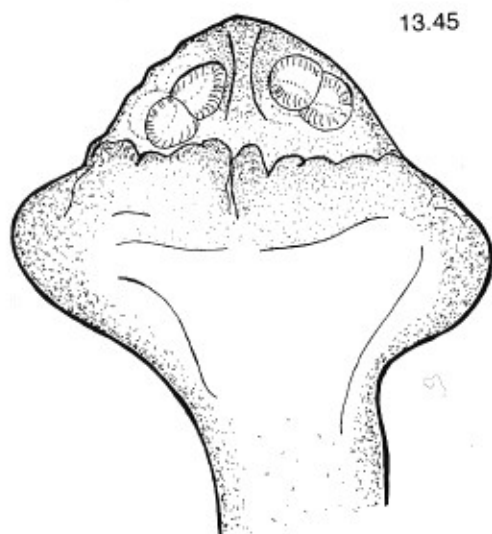
Fig. 13.43 *Spasskyellina spinulifera* (Woodland, 1934). Scolex. (After Rego, 1990.)

Fig. 13.44 *Spatulifer rugosa* (Woodland, 1935). Scolex. (After Rego, 1989.)

Subfamily Monticelliinae Mola, 1929

Key to genera

- 1a. Suckers armed with several rows of minute spines. Uterine diverticula weakly developed *Spasskyellina* Freze, 1965.
Diagnosis: Scolex globose (Fig. 13.43). No metascolex. Small worms. Ovary, testes and uterus entirely cortical. Uterine slit formed early. Uterine diverticula narrow. Longitudinal musculature weakly developed. In South American siluroid fishes. Type-species *S. lenba* (Woodland, 1933).
- 1b. Suckers without spines. Uterus with well developed diverticula 2.
- 2a. Scolex with well developed metascolex. Suckers hidden by folds of tissue 3.
- 2b. Scolex with weakly developed metascolex or without metascolex 4.



Figs 13.45, 13.46 *Goezeella siluri* Fuhrmann, 1916. 13.45. Scolex. 13.46. Mature proglottid. (After Brooks & Rasmussen, 1984.)

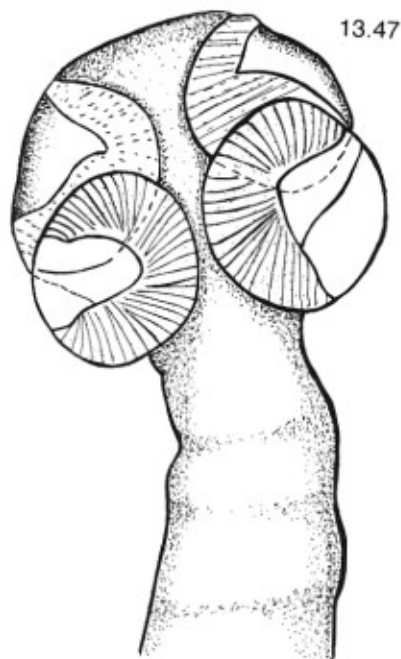
- 3a. Uniloculate suckers, in apical part of scolex
 *Spatulifer* Woodland, 1934.
Diagnosis: Developed metascolex (Fig. 13.44). Vitelline fields in semi-crescent pattern. Longitudinal musculature generally weakly developed. In South American siluroid fishes. Type-species *S. surubim* Woodland, 1934.
- 3b. Biloculate suckers (Fig. 13.45), hidden by folds of tissue
 *Goetzeella* Fuhrmann, 1916.
Diagnosis: Metascolex developed, collar-like. Ovary mostly cortical, but central parts of ovary remain in medulla. Vitelline follicles distributed in several rows in ventral cortex, curved towards ovary (Fig. 13.46). Uterus with developed diverticula. Secondary transverse folds in strobila. In South American siluroid fishes. Type-species *G. siluri* Fuhrmann, 1916.
- 4a. Metascolex weakly developed, represented by some folds of tissue in base of suckers 5.
- 4b. No metascolex, no wrinkles, no folds of tissue in base of suckers
 *Monticellia* La Rue, 1911.
Diagnosis: Scolex round. Suckers of normal type (Fig. 13.47). Vitellarium and reproductive organs cortical. Vitellarium lateral or semi-crescentic in cross-section. Longitudinal musculature sometimes weakly developed. In South American freshwater fishes. Type-species *M. coryphicephala* (Monticelli, 1892).
- 5a. Metascolex, represented by some folds of tissue in base of sucker (Fig. 13.48), suckers elongate
 *Choanoscolex* La Rue, 1911.
Diagnosis: Longitudinal musculature weakly developed. Uterus with many lateral outgrowths. Vitellarium lateral or crescent-shaped in section. In freshwater fishes. South America. Type-species *C. abscisus* (Riggenbach, 1895).
- 5b. Metascolex weakly developed, represented by some wrinkles in tissue of scolex; suckers of normal type, covered by layers of tissue (Fig. 13.49)
 *Paramonticellia* Pavanelli & Rego, 1991.
Diagnosis: Ovary mainly cortical but partly medullary (Fig. 13.50). Uterus cortical. Vitellarium crescent-shaped in cross-section. Genital pore anterior. Longitudinal musculature well developed. In siluroid fishes of South America. Type-species *P. itaipuensis* Pavanelli & Rego, 1991.

Subfamily Zygothriinae Woodland, 1933

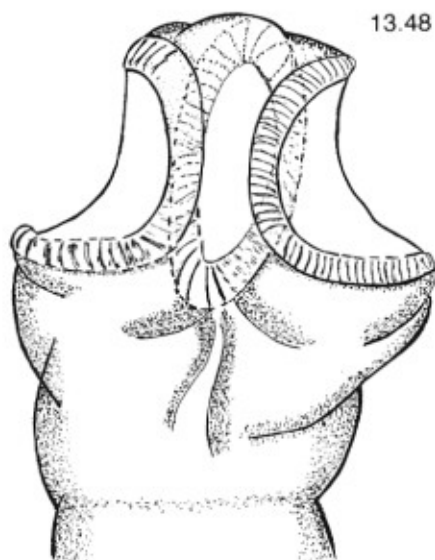
(Syn. Postgangesiinae Akhmerov, 1969)

Key to genera

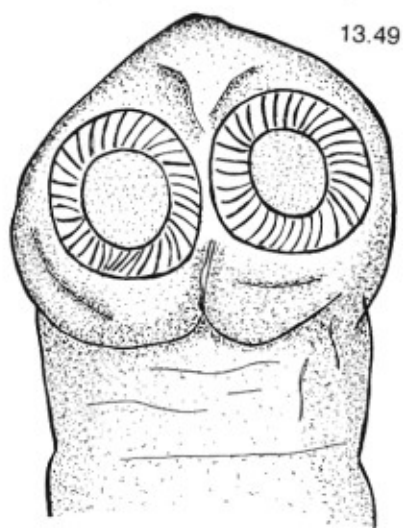
- 1a. Scolex without metascolex 2.
- 1b. Scolex with massive folded metascolex, consisting of circular wrinkled wall enclosing cavity at base of which lie four bilobate uniloculate suckers (Figs 13.51, 13.52) *Amphoteromorphus* Diesing, 1850.



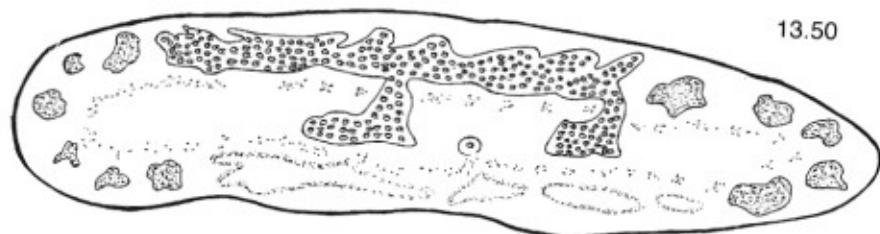
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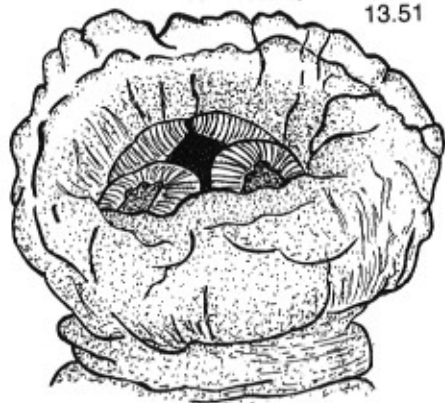
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Fig. 13.47 *Monticellia coryphicephala* (Monticelli, 1891). Scolex. (After Rego & Pavanelli, 1990.)

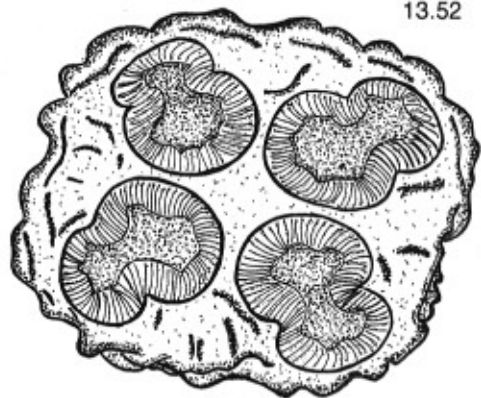
Fig. 13.48 *Choanoscolex abscisus* (Riggenbach, 1895). Scolex. (After Rego, 1990.)

Figs 13.49, 13.50 *Paramonticellia itaipuensis* Pavanelli & Rego, 1991. 13.49. Scolex. 13.50. Section of gravid proglottid. (After Pavanelli & Rego, 1991.)

13.51



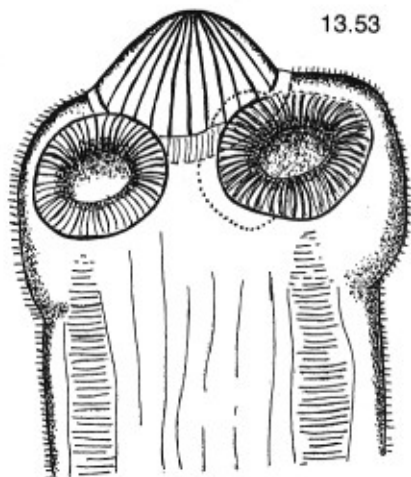
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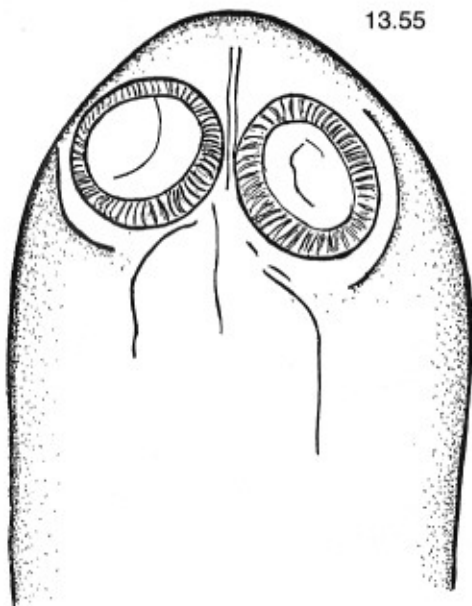
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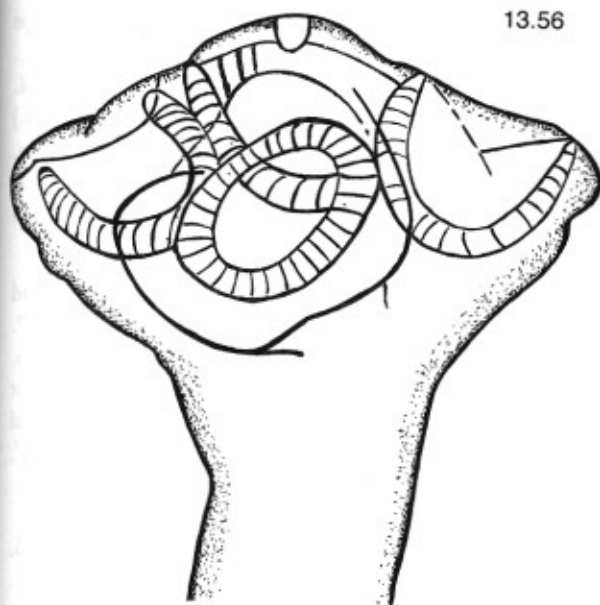


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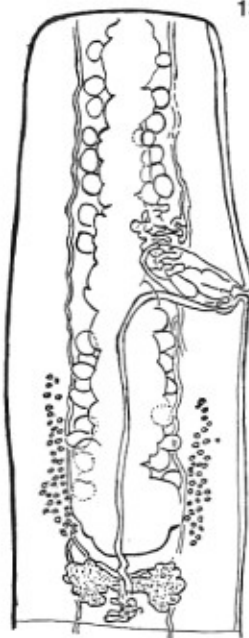


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Figs 13.51, 13.52 *Amphoteromorphus peniculus* Diesing, 1850. 13.51. Scolex. 13.52. Scolex, section. (After Woodland, 1933.)

Figs 13.53, 13.54 *Postgangesia orientale* Akhmerov, 1969. 13.53. Scolex. 13.54. Proglottid. (After Akhmerov, 1969.)

Fig. 13.55 *Nomimoscolex lopesi* Rego, 1990. Scolex. (After Rego, 1990.)

Figs 13.56, 13.57 *Vaucheriella bicheti* de Chambrier, 1987. 13.56. Scolex. 13.57. Proglottid. (After de Chambrier, 1987.)

Diagnosis: Strobila with numerous proglottids, broader than long. Thin layer of longitudinal muscle fibres. Genital pores usually unilateral. Vitellarium distributed in more or less triangular pattern, in dorsal and ventral cortex. Gonads and uterus medullary. In South American siluroid fishes. Type-species *A. peniculus* Diesing, 1850.

2a. Apical organ present. Scolex and neck with spines. (Fig. 13.53)
 *Postgangesia* Akhmerov, 1969.

Diagnosis: Ovary bilobed, massive. Uterus with lateral diverticula, outgrowths begin anteriorly (Fig. 13.54). Vitellarium lateral, in cortex. Testes, ovary and uterus medullary. Genital pore median. In siluroid fishes from Russia. Type-species *P. orientale* Akhmerov, 1969.

2b. No apical organ, no spines in scolex 3.

3a. Suckers modified, bothridia-like, with two openings, or with projections 6.

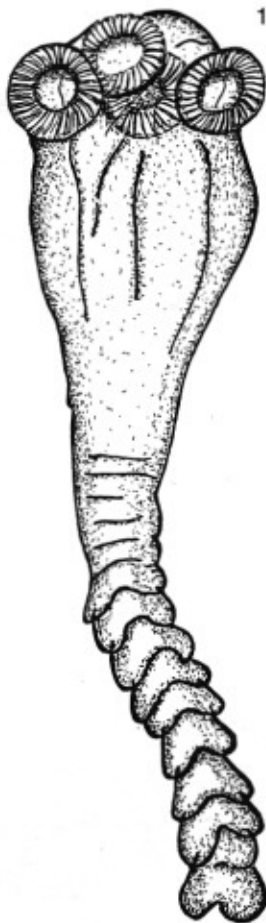
3b. Suckers not modified 4.

- 4a. Vitellarium occupies entire length of proglottids. Suckers of normal type (Fig. 13.55). No metascolex present
 *Nomimoscolex* Woodland, 1934.
 (Syn. *Endorchis* Woodland, 1934.)
- Diagnosis:** Proglottids usually longer than wide. Gonads and uterus medullary. Vitellarium cortical, lateral. Uterus with developed diverticula. Longitudinal musculature developed or inconspicuous. In freshwater fishes from South America. Type-species *N. piraeeba* Woodland, 1934.
- 4b. Vitellarium lateral but restricted to posterior part of proglottid, behind genital pore *Vaucherella* de Chambrier, 1987.
- Diagnosis:** Suckers of normal type (Fig. 13.56). Genital pore lateral, median. Vagina with sphincter. Vitellarium in ventral cortex, lateral, limited to posterior part of proglottid (Fig. 13.57). Gonads and uterus medullary. Longitudinal musculature weakly developed. In snakes from South America. Type-species *V. bicheti* de Chambrier, 1987.
- 5a. Longitudinal musculature in one layer, conspicuous 6.
- 5b. Longitudinal musculature in two layers, inconspicuous
 *Myzophorus* Woodland, 1934.
- Diagnosis:** Scolex swollen, sometimes with slight folds (Fig. 13.58). Proglottids lacinated or not (Fig. 13.59). Ovary medullary, but some portions intrude into dorsal cortex. Uterus mostly medullary. Testes medullary. Vitellarium lateral, cortical. In siluroid fishes. South America. Type-species *M. admonticellia* Woodland, 1934.
- 6a. Suckers trilobulate, bothridia-like (Fig. 13.60)
 *Gibsoniela* Rego, 1984.
- Diagnosis:** Proglottids wider than long. Longitudinal musculature in regular bundles. Vitellarium cortical, disposed in semi-crescent pattern, some follicles invade medulla close to muscles. Ovary medullary, but some follicles cross longitudinal muscles into cortex (Fig. 13.61). Uterus with few diverticula. In siluroid fishes. South America. Type-species *G. mandube* (Woodland, 1935).
- 6b. Suckers not trilobulate 7.
- 7a. Suckers large, globose, each has two openings (Fig. 13.62)
 *Zygothbrium* Diesing, 1850.
- Diagnosis:** Surface of scolex is very wrinkled. Proglottids craspedote (Fig. 13.63), with median notch on each surface. Proglottids very numerous, broader than long. Vitellarium in dorsal and ventral cortex. In South American siluroid fishes. Type-species *Z. megagephalum* Diesing, 1850.

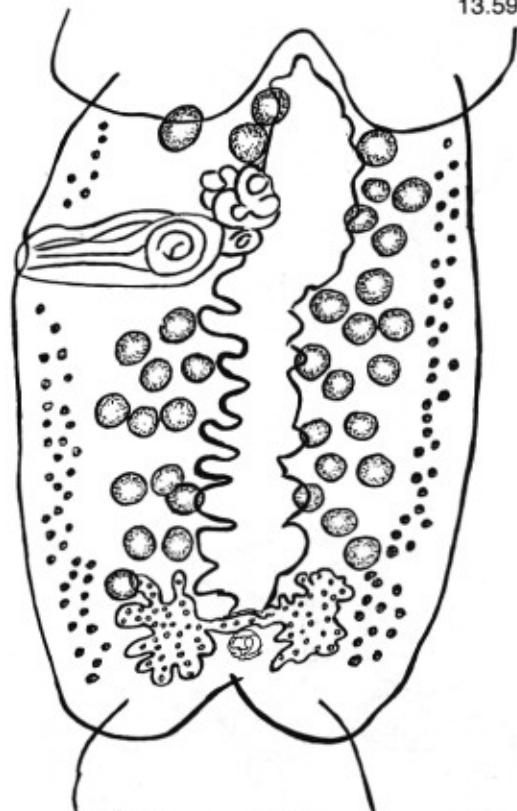
Figs 13.58, 13.59 *Myzophorus piraeeba* Woodland, 1935. 13.58. Scolex and immature proglottids. 13.59. Mature proglottid. (After Rego, 1984a.)

Figs 13.60, 13.61 *Gibsoniela mandube* (Woodland, 1935). 13.60. Scolex. (After Rego, 1984b.) 13.61. Section at level of ovary; vitelline follicles partially cortical. (Original.)

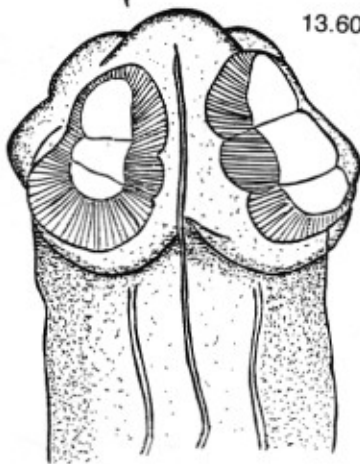
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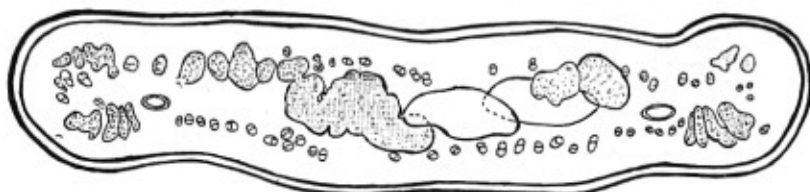
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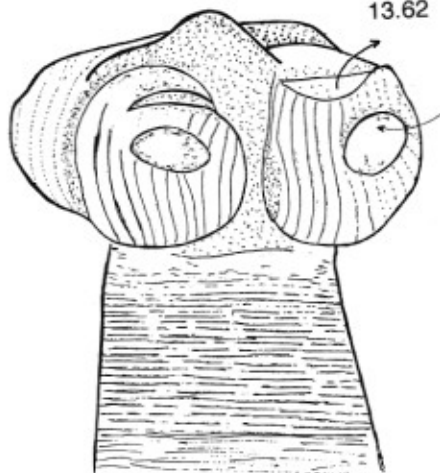
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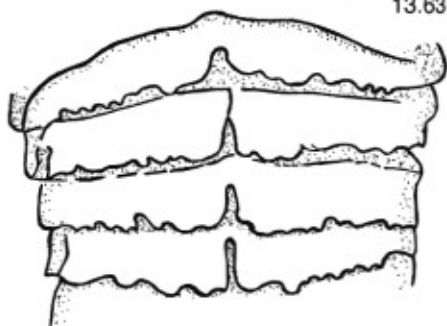
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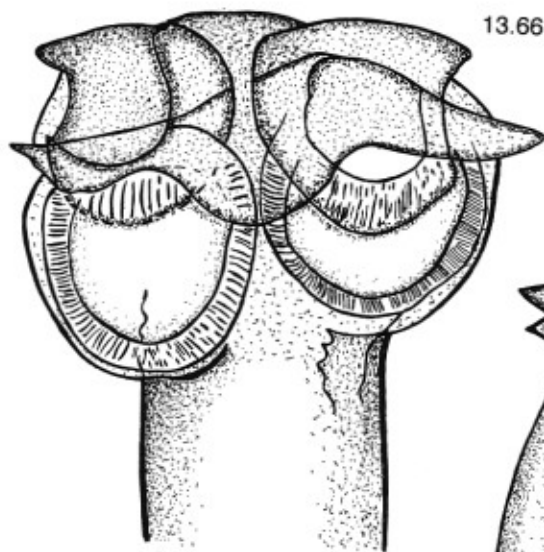
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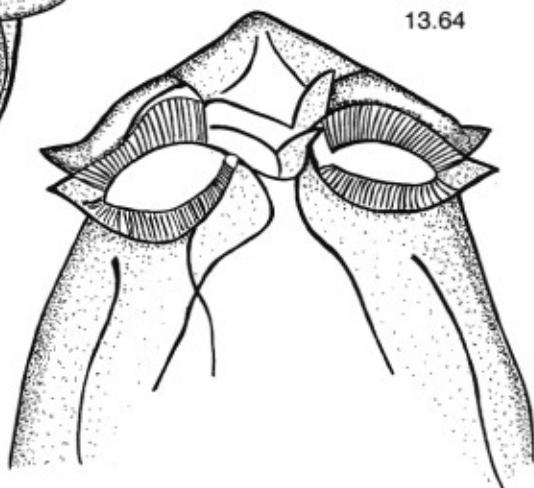
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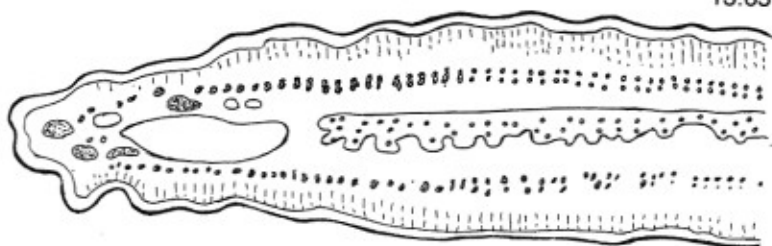
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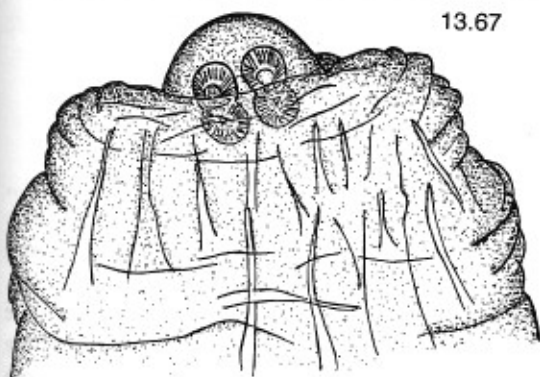


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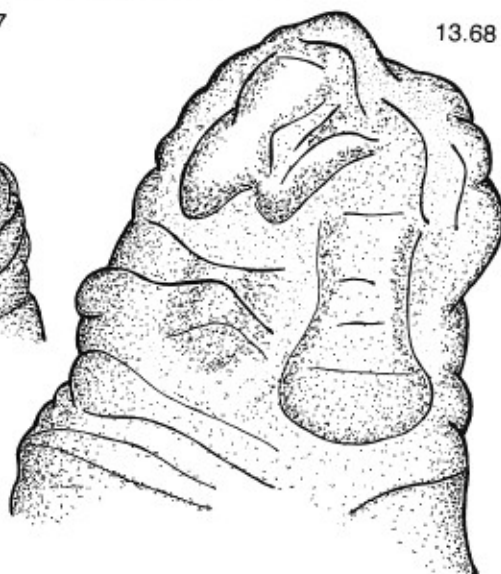


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Figs 13.62, 13.63 *Zygobothrium megacephalum* Diesing, 1850. 13.62. Scolex. 13.63. Proglottids with lappets. (After Woodland, 1933b.)

Figs 13.64, 13.65 *Houssayela sudobim* (Woodland, 1935). 13.64. Scolex. 13.65. Transverse section of proglottid. (After Woodland, 1935a.)

Fig. 13.66 *Harriscolex kaparari* (Woodland, 1935). Scolex. (After Rego, 1990.)

Fig. 13.67 *Peltidocotyle rugosa* Diesing, 1850. Scolex. (After Rego, 1990.)

Fig. 13.68 *Othinoscolex lenha* Woodland, 1933. Scolex. (After Woodland, 1933b.)

7b. Suckers without two openings 8.

8a. Suckers small, each with four horny projections (Fig. 13.64)
Houssayela Rego, 1987.

Diagnosis: Scolex small. Strobila with numerous proglottids. Most proglottids broader than long. Longitudinal musculature well developed. Uterus with numerous diverticula. Vitellarium cortical, in semi-crescent pattern, some follicles invade medulla (Fig. 13.65). In South American siluroid fishes. Type-species *H. sudobim* (Woodland, 1935).

8b. Suckers not small, with two triangular projections (Fig. 13.66)
Harriscolex Rego, 1987.

Diagnosis: Scolex with dome-shaped anterior end. Proglottids broader than long. Vitellarium cortical, in dorsal and ventral bands. Testes in single field. Longitudinal musculature well developed. In siluroid fishes of South America. Type-species *H. kaparari* (Woodland, 1935).

Subfamily Peltidocotylinae Woodland, 1934

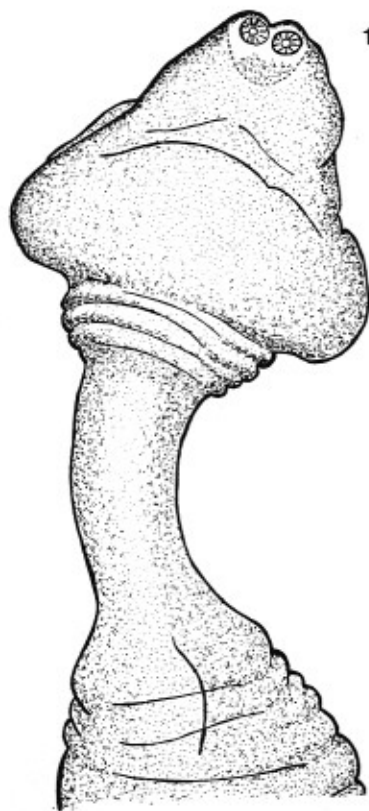
(Syn. Othinoscolecinae Woodland, 1933)

Key to genera

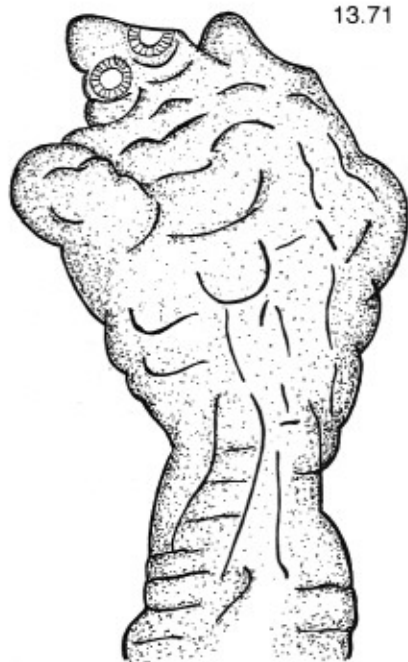
- 1a. Suckers divided into two loculi by transverse septum (Fig. 13.67)
 *Peltidocotyle* Diesing, 1850.
Diagnosis: Scolex large, with well developed metascolex provided with longitudinal furrows. Strobila wide behind scolex, tapering toward posterior end. Secondary transverse grooves present in strobila. Longitudinal musculature strongly developed. Vitellarium cortical in dorsal and ventral bands. Ovary medullary. Uterus mostly cortical. Testes in dorsal cortex. In South American siluroid fishes. Type-species *P. rugosa* Diesing, 1850.
- 1b. Suckers absent or of common type 2.
- 2a. Suckers absent *Othinoscolex* Woodland, 1933.
Diagnosis: Surface of scolex covered by irregular mass of thick folds (Fig. 13.68). No suckers or attachment areas observed. Secondary transverse creases of strobila highly developed. Proglottids many times broader than long. Uterus with small diverticula. Vitellarium cortical, in dorsal and ventral bands. Longitudinal musculature layer thin. In South American siluroid fishes. Type-species *O. lenha* Woodland, 1933.
- 2b. Suckers present, uniloculate 3.
- 3a. Uterus medullary, but with diverticula in cortex (Fig. 13.70)
 *Jauella* Rego & Pavanelli, 1985.
Diagnosis: Scolex small, retractile. Suckers small, apical. Metascolex cone-shaped, with few folds of tissue (Fig. 13.69). Vitellarium in dorsal and ventral bands. Testes in dorsal cortex. In South American siluroid fishes. Type-species *J. glandicephalus* Rego & Pavanelli, 1985.
- 3b. Uterus entirely cortical *Woodlandiella* Freze, 1965.
Diagnosis: Scolex with very wrinkled metascolex. Four suckers on apical part of scolex (Fig. 13.71). Proglottids much broader than long. Secondary folds of strobila highly developed. Longitudinal musculature well marked. Vitellarium in dorsal and ventral bands. In South American siluroid fishes. Type-species *W. myzofera* (Woodland, 1933).

Subfamily Ephedrocephalinae Mola, 1929

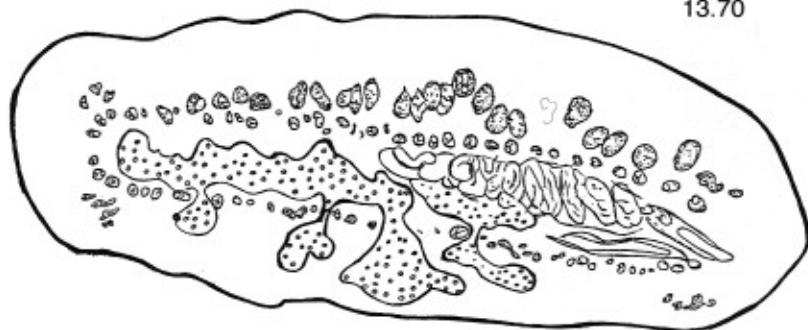
The subfamily contains one genus only.



13.69



13.71



13.70

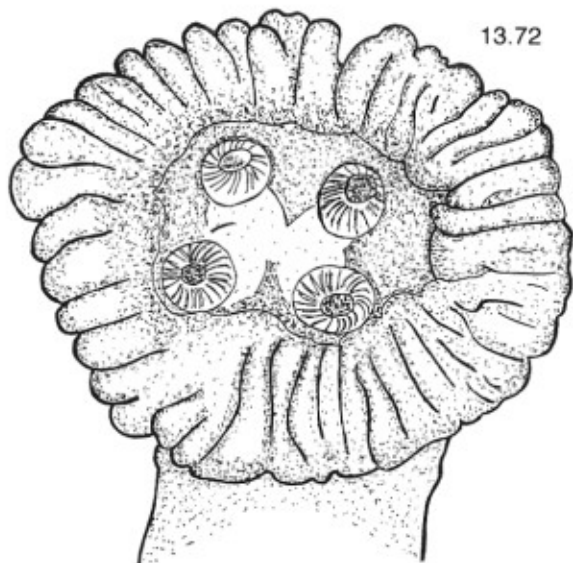
Figs 13.69, 13.70 *Jauella glandicephalus* Rego & Pavanelli, 1985. 13.69. Scolex. 13.70. Section of gravid proglottid; uterus partially cortical. (After Rego & Pavanelli, 1985.)

Fig. 13.71 *Woodlandiella myzofera* (Woodland, 1933). Scolex. (After Woodland, 1933b.)

Genus *Ephedrocephalus* Diesing, 1850 (Fig. 13.72)

Diagnosis: With the characters of the subfamily. Type-species *E. microcephalus* Diesing, 1850.

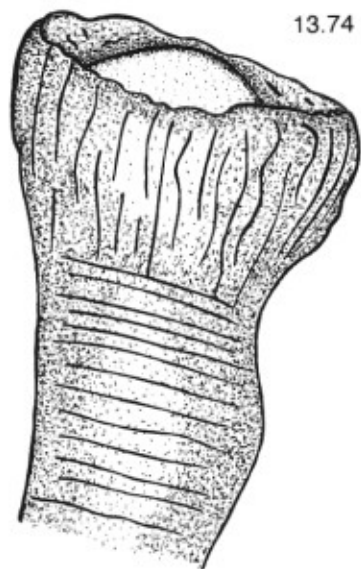
13.72



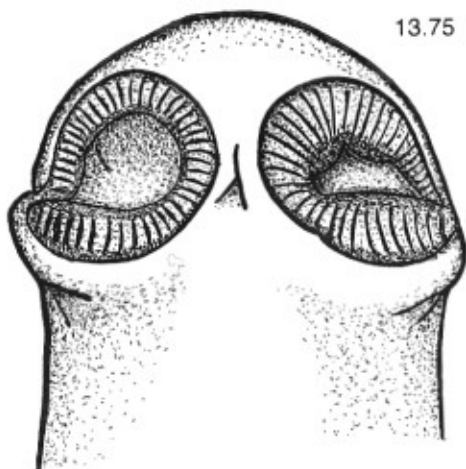
13.73



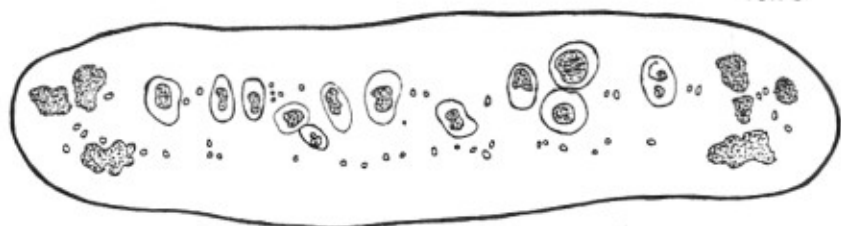
13.74



13.75



13.76



Subfamily Rudolphielliinae Woodland, 1935

(Syn. *Amphilaphorchidiinae* Woodland, 1934)

The subfamily contains one genus only.

Genus *Rudolphiella* Fuhrmann, 1916 (Figs 13.73, 13.74)

(Syn. *Amphilaphorchis* Woodland, 1934)

Diagnosis: With the characters of the subfamily. Type-species *R. lobosa* (Riggenbach, 1896).

Subfamily Nupeliinae Pavanelli & Rego, 1991

The subfamily contains one genus only.

Genus *Nupelia* Pavanelli & Rego, 1991 (Figs 13.75, 13.76)

Diagnosis: With the characters of the subfamily. Type-species *N. portoricensis* Pavanelli & Rego, 1991.

Genera inquirenda**Genus *Sciadocephalus* Diesing, 1850**

Diagnosis: Scolex umbrella-shaped (Fig. 13.77). Four central suckers and small apical sucker. Internal longitudinal muscle layer absent. No differentiation between cortex and medulla. Type-species *S. megalodiscus* Diesing, 1850 *species inquirenda*.

The position of the gonads and vitellarium was not established by Woodland (1933a), who redescribed the species. The scolex is similar to *Corallobothriinae*.

Genus *Manaosia* Woodland, 1935

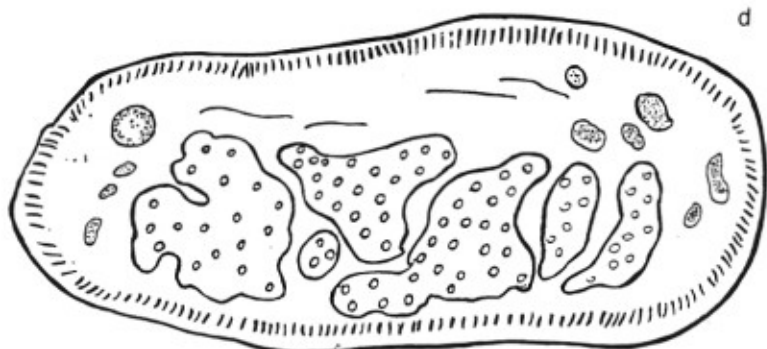
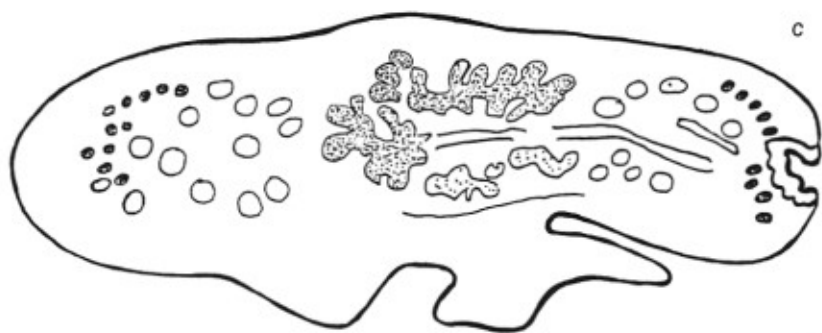
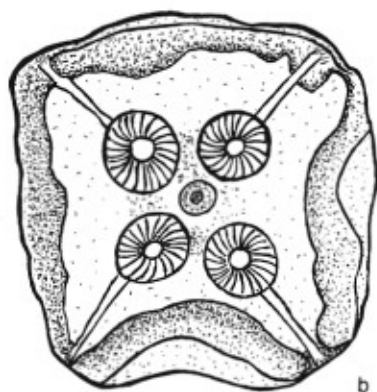
Diagnosis: Scolex large, with large suckers submerged in scolex tissue and opening as small apertures on its surface (Fig. 13.78). Longitudinal muscle bundles well

Fig. 13.72 *Ephedrocephalus microcephalus* Diesing, 1850. Scolex. (After Mola, 1906.)

Fig. 13.73 *Rudolphiella myoides* (Woodland, 1934). 13.73. Scolex. (After Woodland, 1934b.)

Fig. 13.74 *R. piranabu* (Woodland, 1934). Scolex. (After Woodland, 1934b.)

Figs 13.75, 13.76 *Nupelia portoricensis* Pavanelli & Rego, 1991. 13.75. Scolex. 13.76. Section of proglottid. (After Pavanelli & Rego, 1991.)



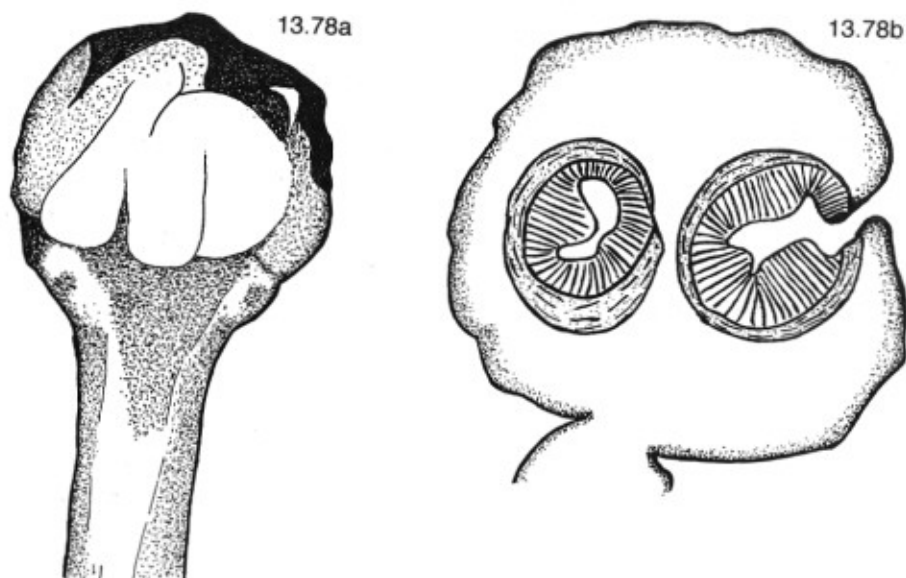


Fig. 13.77 *Sciadocephalus megalodiscus* Diesing, 1850. a. Entire specimen. b. Apical view of scolex. c. Transverse section at level of ovary. d. Transverse section at level of uterus. (After Woodland, 1933b.)

Fig. 13.78 *Manaosia bracademoca* Woodland, 1935. a. Scolex. b. Scolex in section. (After Woodland, 1935b.)

developed. Testes probably cortical. Ovary partly cortical and partly medullary. Type-species *M. bracademoca* Woodland, 1935 *species inquirenda*.

Woodland (1935b) does not refer to the position of the vitellarium and uterus.

The genus *Cangatiella* Pavanelli & Machado dos Santos, 1991 was inadvertently omitted from this key. It belongs in the subfamily Proteocephalinae. For a full discussion, see Pavanelli & Machado dos Santos (1991).

Genus *Cangatiella* Pavanelli & Machado dos Santos, 1991

The important generic characters are: Longitudinal osmoregulatory canals medullary. Vitelline follicles do not extend beyond osmoregulatory canals; follicles intrude into the longitudinal muscle layer. Egg provided with polar filaments. In siluriform fish. Brazil. Type-species *C. arandasi* Pavanelli & Machado dos Santos, 1991.