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# 10 Order Pseudophyllidea Carus, 1863

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## Introduction

During this revision of the Order Pseudophyllidea Carus, 1863, characters regarded as significant at the family and generic levels have been re-evaluated, supported by re-examination of type material whenever possible. For reasons given in more detail in the text, the use of such characters as eggs operculate or not, or embryonated or not when laid, is not considered to be useful at the family level. A number of synonymies at the family level have therefore been made.

## ORDER PSEUDOPHYLLIDEA CARUS, 1863

**Diagnosis:** Scolex usually present; with two bothria, one dorsal, one ventral; armed or unarmed. Scolex rarely absent or replaced by pseudoscolex or scolex deformatus. Bothria rarely absent. External segmentation usually present, complete or incomplete; rarely absent. Internal segmentation complete or not. Proglottids craspedote or acraspedote, usually wider than long, anapolytic. Reproductive organs usually single, rarely double or multiple. Genital pores single or double, dorsal, ventral or marginal. Testes numerous, medullary. Cirrus-sac usually present, rarely absent. Ovary medullary, posterior. Vitellarium follicular, rarely compact; follicles usually cortical, sometimes in medulla, sometimes intruding between longitudinal muscle bundles. Uterus variable in shape; uterine sac present or absent; uterine pore present, ventral. First larval stage in crustaceans, second usually in fish but rarely in other vertebrate groups. Adults predominantly in fish, also in other vertebrate groups.

## Key to families:

- 1a. Genital pore and uterine pore both on ventral surface ..... 5.  
 1b. Genital pore mediodorsal to marginal, uterine pore ventral ..... 2.
- 2a. Genital pore dorsal, median ..... Bothriocephalidae Blanchard, 1849.  
 (Syns Ptychobothriidae Lühe, 1902; Acompscephalidae Rees, 1969.)  
 2b. Genital pore marginal or submarginal ..... 3.
- 3a. Genital pore submarginal ..... Echinophallidae Schumacher, 1914.  
 (Syn. Parabothriocephalidae Yamaguti, 1959.)  
 3b. Genital pore marginal ..... 4.
- 4a. Vitellarium compact ..... Philobythiidae Campbell, 1977.  
 4b. Vitellarium follicular ..... Triaenophoridae Lönnberg, 1889.  
 (Syn. Amphicotylidae Ariola, 1899.)
- 5a. Cirrus-sac present ..... Diphylobothriidae Lühe, 1910.  
 (Syn. Dibothriocephalidae Lühe, 1902.)  
 5b. Cirrus-sac absent ..... Cephalochlamydidae Yamaguti, 1959.

## Family Bothriocephalidae Blanchard, 1849

(Syns Ptychobothriidae Lühe, 1902; Acompscephalidae Rees, 1969)

The families Bothriocephalidae and Ptychobothriidae have been distinguished traditionally by the presence of operculated, unembryonated eggs in the first family and of unoperculated, embryonated eggs in the second. Both characters are difficult to apply accurately and consistently. The presence or absence of an operculum is frequently difficult to establish and the information is often missing from descriptions and diagnoses. The degree of embryonation *in utero* is readily established in some cases but not in others and is known to vary in some pseudophyllideans according to temperature, e.g. in species of *Triaenophorus* (see Kuperman, 1973, transl. 1981). While the family and generic diagnoses of the Bothriocephalidae and Ptychobothriidae given by Yamaguti (1959) and Schmidt (1986) are consistent within each author's system in respect of the operculate or non-operculate condition of the eggs, there are inconsistencies with regard to embryonation. Schmidt's diagnosis of the Ptychobothriidae states that they have embryonated eggs but in his diagnoses of *Senga* Dollfus, 1934 and *Polyonchobothrium* Diesing, 1854 the eggs are described as not embryonated. The information is not given for the eight other genera in the family. Yamaguti's (1959) treatment of *Senga* is similar to that of Schmidt. Personal observations on *Polyonchobothrium polypteri* have shown that some embryos are developed to the point of having oncospherical hooks, although the majority in the terminal part of the uterus are not developed to this stage. These inconsistencies highlight the absence of reliable information on these points. The use of operculum and of

embryonation as family characters is considered unreliable and consequently the Ptychobothriidae has been synonymized with the Bothriocephalidae. The status of individual genera allocated to both families and to the Acompscephalidae Rees, 1969 is discussed below.

*Acompscephalum* Rees, 1969 is synonymous with *Anantrum* Overstreet, 1968, which has priority. Rees (1969) erected the family Acompscephalidae because her genus lacked external segmentation and had no scolex or specialized attachment organs. *Anantrum* is the only pseudophyllidean genus completely devoid of external segmentation although in many genera it is incomplete. Overstreet (1968) placed his genus in the Bothriocephalidae. Jensen & Heckmann (1977), also placed *Anantrum* in the Bothriocephalidae because of the variation in scolex shape and in external segmentation found in this family. Overstreet (1968) and Jensen & Heckmann (1977) did not specify their view of the composition of the family. As treated by Yamaguti (1959), it contained three genera all with normal scoleces. In the Bothriocephalidae of Schmidt (1986), *Anantrum* is the only genus to lack attachment organs. Its eggs, according to Jensen & Heckmann (1977) and Overstreet (1968), but not Rees (1969), are operculate. We consider it a member of the Bothriocephalidae.

*Penetrocephalus* Rao, 1960 was erected for *Bothriocephalus ganapatii*, a name first used by Rao (1954) without a description and used again in 1960. The same cestode was described by Subhadrachari (1955) as *B. penetratus*. Rao (1960) distinguished it by its initially dibothriate scolex, lacking an apical disc, which penetrated the gut wall of the host to enter the liver, subsequently becoming encapsulated and degenerate. Also, the posterolateral margins of the proglottids were markedly craspedote. Protasova (1977) declared *B. ganapatii* Rao, 1954 a *nomen nudum* and retained *B. penetratus* in *Bothriocephalus*. *Penetrocephalus* is treated here as a synonym of *Bothriocephalus* since, following Protasova (1977), the location of the scolex and the craspedote proglottids are not considered sufficient to justify the genus.

*Alloptychobothrium* Yamaguti, 1968 is provisionally retained. Erected for *A. spilonopteri* from flying fish, *Cypselurus spilonopterus* from Hawaii by Yamaguti (1968), it closely resembles *Plicatobothrium* Cable & Michaelis, 1967 from *C. bahiensis* from Curaçao. The major difference is that *Plicatobothrium* has a conspicuous Y-shaped uterine sac (Cable & Michaelis, 1967); a uterine sac is said to be lacking in *Alloptychobothrium* and the eggs are said to be embryonated (Yamaguti, 1968).

*Circumoncobothrium* Shinde, 1968 was distinguished by an uninterrupted circle of hooks on the apical disc. The type and subsequent species are all based on single specimens (Shinde, 1968a, 1977; Shinde & Chincholikar, 1977; Shinde & Jadhav, 1976; Chincholikar & Shinde, 1977) and the continuity of the hook circle is probably a fixation artefact resulting from pressure. It is synonymous with *Senga* Dollfus, 1934, species of which occur in the same hosts.

*Oncobothriocephalus* Yamaguti, 1959 was established by Yamaguti (1959) for *Ptychobothrium armatum* Fuhrmann, 1902 from *Turdus parochus* in Egypt. The species had been listed as a species of *Polyonchobothrium* Diesing, 1854 by Meggitt (1930). According to Tadros (1968), it is morphologically consistent with *P. polypteri* (Levdig, 1853) and may have been a fish parasite ingested by a bird,

or the collection data attributing it to a bird host may have been in error. Following Tadros (1968), Protasova (1977) and Schmidt (1986), it is regarded as a synonym of *Polyonchobothrium*.

*Ptychobothrioides* Yamaguti, 1959 was erected for *Bothriocephalus spiraliiceps* Volz, 1900 from *Falco concolor* in Abyssinia. As pointed out by Tadros (1966), its characters resemble those of *Ptychobothrium* Lönnerberg, 1889, with which he synonymized it. It is regarded as a *genus inquirendum*, following Protasova (1977).

## Family diagnosis

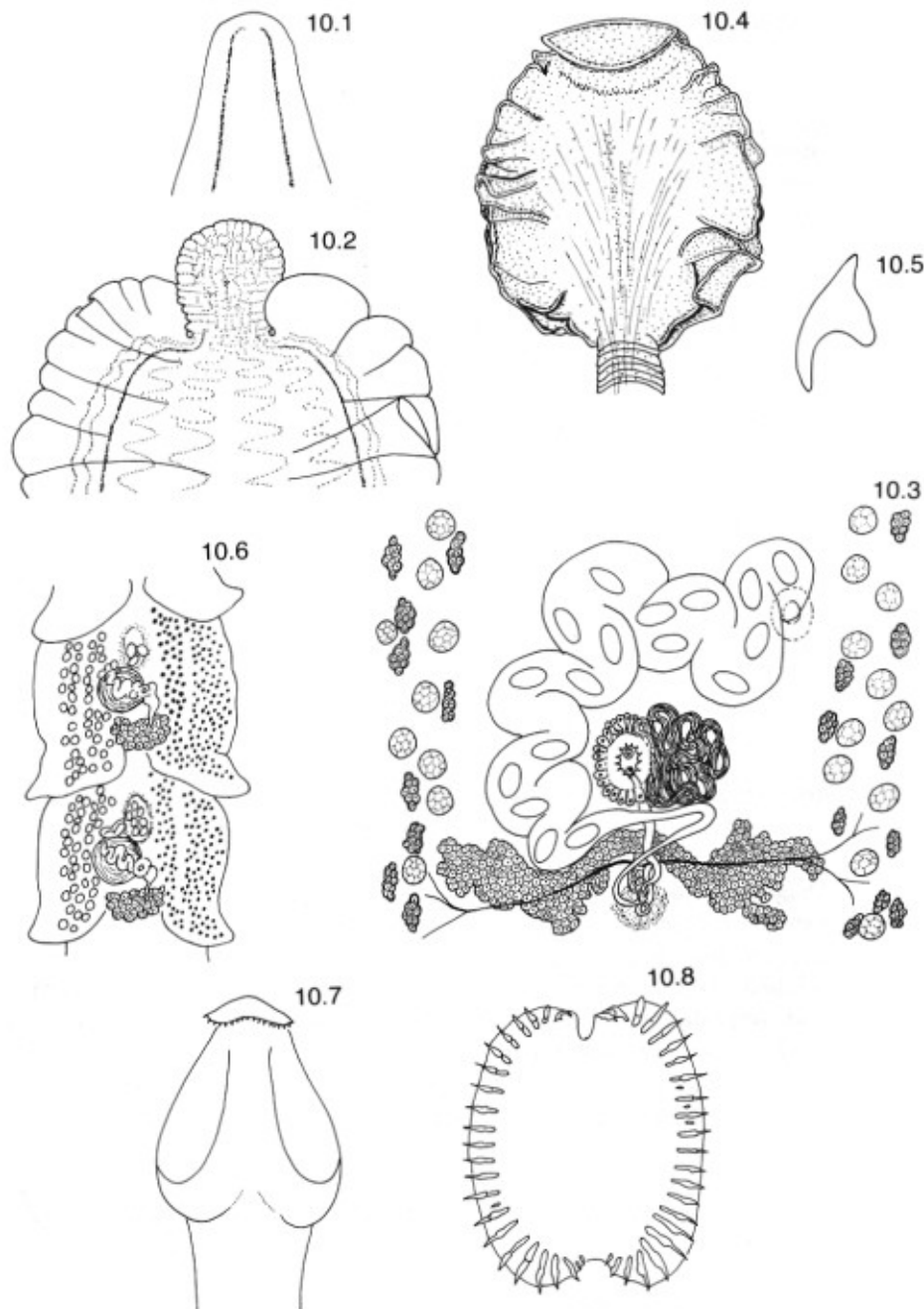
Scolex variable in shape, usually with two bothria; rarely lacking attachment organs. Apical disc present or absent; if present, armed or unarmed. Bothria weakly to strongly developed; margins inrolled or crenulated or not. External segmentation present or absent, complete or not. Strobila rarely spirally twisted. Proglottids craspedote or not, usually wider than long. Genital pores dorsal, median or submedian. Testes in dorsal medulla. Ovary posterior. Vitelline follicles usually cortical, may be intermingled with longitudinal muscle fibres. Uterus opens ventrally through median or submedian uterine pore. Eggs operculate or not, embryonated or not. In teleosts. Type-genus *Bothriocephalus* Rudolphi, 1808.

## Key to genera

- 1a. External segmentation completely absent. Scolex unarmed. Bothria and apical disc absent .....  
 ..... *Anantrum* Overstreet, 1968. (Figs 10.1–10.3)  
 (Syn. *Acompscephalum* Rees, 1969.)

**Diagnosis:** Scolex variable in shape (conical to papilliform; mushroom-shaped). Strobila spirally twisted or not. Genital pores dorsomedian. Testes medullary in two lateral bands. Ovary bilobed, posterior, median. Vitelline follicles cortical, mainly in two lateral fields dorsally and ventrally. Uterus with uterine sac; uterine pore ventral, slightly submedian, irregularly alternating. Eggs operculate, unembryonated. In marine teleosts (*Synodus* spp.). Western Atlantic, eastern Pacific. Type-species *A. tortum* (Linton, 1905).

- 1b. External segmentation present. Bothria present; apical disc present or absent ..... 2.
- 2a. Scolex armed ..... 3.
- 2b. Scolex unarmed ..... 5.
- 3a. Scolex strongly compressed laterally; apical disc armed marginally with numerous tiny hooks. In marine teleosts .....  
 ..... *Oncodiscus* Yamaguti, 1934. (Figs 10.4–10.6)



**Figs 10.1-10.3** *Anantrum tortum* (Linton, 1905). 10.1. Scolex, relaxed. 10.2. Scolex, contracted. 10.3. Reproductive organs. After Rees (1969).

**Figs 10.4-10.6** *Oncodiscus sauridae* Yamaguti, 1934. 10.4. Scolex. 10.5. Hook. 10.6. Gravid proglottids, testes shown on left, vitelline follicles on right. After Yamaguti (1934).

**Figs 10.7, 10.8** *Senga besnardi* Dollfus, 1934. 10.7. Scolex. 10.8. Apical disc. After Dollfus (1934a).

**Diagnosis:** Bothria well-developed with strongly crenulated margins. Apical disc bilobed. Neck absent. External segmentation complete. Proglottids craspedote with a median posterior notch. Genital pore dorsomedian, slightly post-equatorial. Cirrus-sac large, thin-walled. Cirrus protrusible, unarmed. Ovary transversely elongate, lobed, posterior. Vagina distended and muscular distally, opens anteriorly to cirrus-sac. Vitelline follicles circumcortical. Uterine duct coils forward to large uterine sac; uterine pore ventral, median, equatorial. Eggs operculate, unembryonated. In marine teleosts. Japan, India. Type-species *O. sauridae* Yamaguti, 1934.

3b. Scolex rectangular; apical disc armed with hooks arranged in two semicircles or four quadrants. In freshwater teleosts ..... 4.

4a. Hooks on scolex arranged in two semicircles .....  
 ..... *Senga Dollfus*, 1934. (Figs 10.7, 10.8)  
 (Syn. *Circumoncobothrium* Shinde, 1968.)

**Diagnosis:** Bothria shallow with well-developed margins. Apical disc indented dorsally and ventrally. Neck absent. External metamerism present but incomplete. Proglottids acraspedote, wider than long except when gravid. Genital pores dorsal, virtually median. Testes medullary, in two lateral fields. Ovary compact, median, posterior. Vitelline follicles cortical, continuous around margins of proglottid. Uterus loops forward, uterine sac opens ventrally by median pore near anterior margin of proglottid. Eggs anoperculate, unembryonated. In freshwater teleosts. India, Pakistan, China. Type-species *S. besnardi* Dollfus, 1934.

4b. Hooks arranged in four quadrants .....  
 ..... *Polyonchobothrium* Diesing, 1854. (Figs 10.9–10.11)  
 (Syns *Tetracampos* Wedl, 1861; *Oncobothriocephalus* Yamaguti, 1959.)

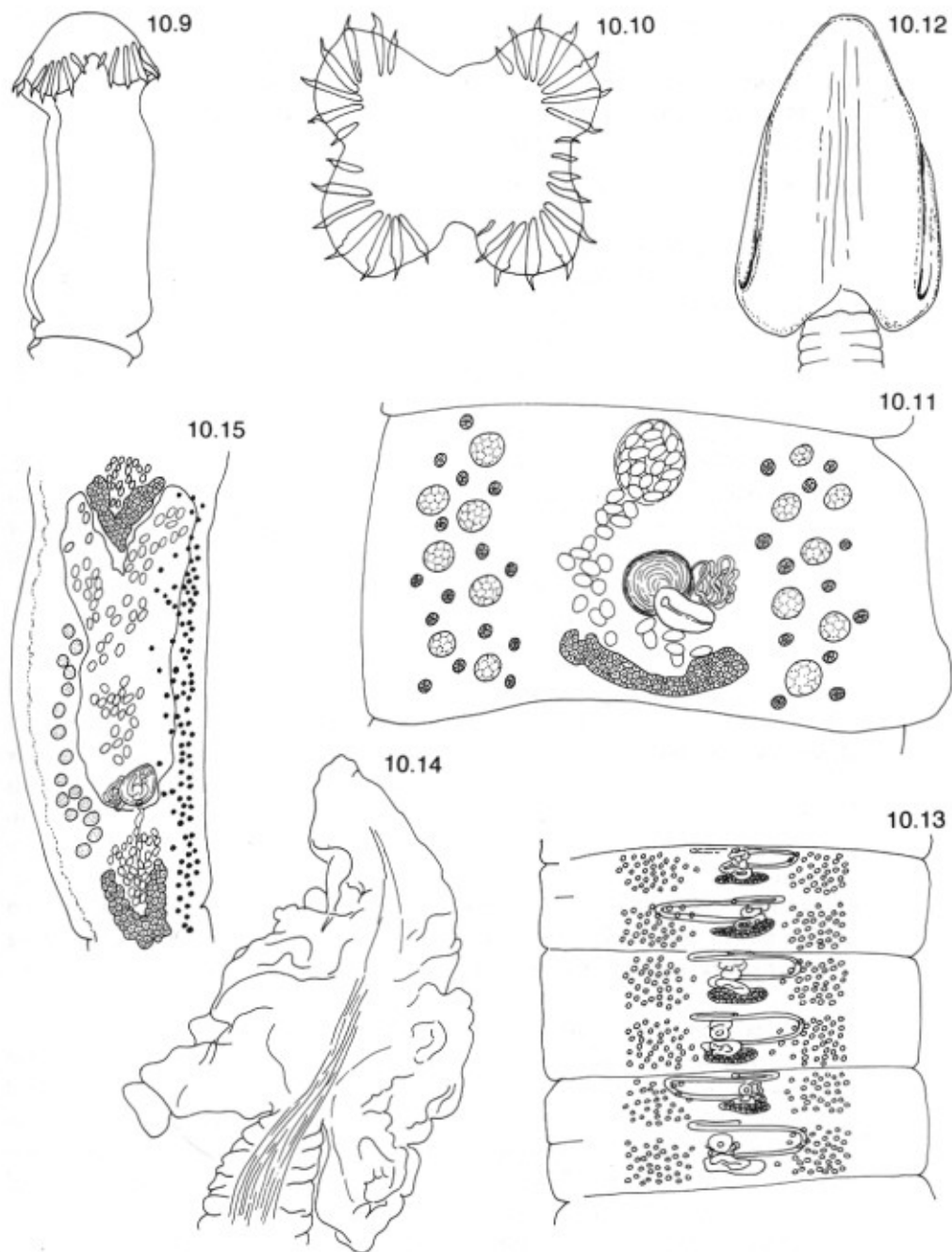
**Diagnosis:** Scolex rectangular. Bothria shallow; apical disc present, armed. External segmentation present but feebly demarcated. Genital pore median, dorsal, pre-equatorial. Testes medullary, in two lateral fields. Ovary posterior, bilobed, transversely elongated. Vitelline follicles cortical, in lateral bands dorsally and ventrally, occasionally continuous around lateral margins of proglottid. Uterus loops forward, forms small uterine sac which opens midventrally near anterior margin of proglottid. Eggs anoperculate, not fully embryonated when laid. In freshwater teleosts. Africa, Asia, India, Australia, Russia. Type-species *P. polypteri* (Leydig, 1853).

5a. Scolex fan-shaped or sagittate; bothrial margins crenulated ..... 6.

5b. Scolex otherwise ..... 8.

6a. Uterine pore distinctly submedian .....  
 ..... *Ptychobothrium* Lönnberg, 1889. (Figs 10.12, 10.13)

**Diagnosis:** Scolex unarmed, laterally compressed, heart- or arrowhead-shaped in lateral view. Bothria well-developed with smooth or slightly crenulated margins. Apical disc absent. Neck absent. External segmentation incomplete. Proglottids acraspedote. Genital pore dorsal, median, pre-equatorial. Cirrus-sac thin-walled. Testes in dorsal medulla, in two lateral fields. Ovary compact, posterior. Vagina



**Figs 10.9-10.11** *Polyonchobothrium polypteri* (Leydig, 1853). 10.9. Scolex. 10.10. Apical disc. Both after Jones (1980). 10.11. Mature proglottid.

**Figs 10.12, 10.13** *Ptychobothrium belones* (Dujardin, 1845). 10.12. Scolex. 10.13. Maturing proglottids. After Yamaguti (1934).

**Figs 10.14, 10.15** *Plicatobothrium cypseluri* Cable & Michaelis, 1967. 10.14. Scolex. 10.15. Gravid proglottid. Original.

recurved, opens anterior to cirrus-sac. Vitelline follicles intermingled with the longitudinal muscle bundles. Uterus sigmoid, alternating irregularly. Uterine sac present; uterine pore ventral, opening near anterior margin of proglottid. Eggs thin-shelled, anoperculate, embryonated. In marine teleosts (Belonidae). Pacific, Atlantic. Type-species *P. belones* (Dujardin, 1845).

6b. Uterine pore midventral ..... 7.

7a. Uterine sac Y-shaped .....

..... *Plicatobothrium* Cable & Michaelis, 1967. (Figs 10.14, 10.15)

**Diagnosis:** Scolex triangular to fan-shaped, unarmed, no apical disc. Bothria deep with crenulated margins, not connected by apical groove. Neck absent. Strobila acraspedote, external segmentation incomplete. Genital pore dorsomedian, post-equatorial. Testes medullary, lateral, extend from level of ovary to behind arms of uterine sac. Ovary posterior, median, enclosed by arms of uterine sac of succeeding proglottid. Vitelline follicles in lateral fields, intermingled with longitudinal muscle fibres, which are not grouped into bundles. Uterine sac with short anterior arms extending into the preceding proglottid; opens ventrally by median pore at posterior end of sac. Eggs anoperculate, not developed to point of having oncospherical hooks when laid. In marine teleosts (flying fish, *Cypselurus*). Caribbean, Indian Ocean. Type-species *P. cypseluri* Cable & Michaelis, 1967.

7b. Uterine sac inconspicuous or absent .....

..... *Alloptychobothrium* Yamaguti, 1968. (Figs 10.16, 10.17)

**Diagnosis:** Scolex arrowhead-shaped in lateral view; bothrial margins strongly crenulated. Neck absent. External segmentation complete or not. Proglottids wider than long, craspedote or not. Genital pore mid-dorsal. Testes in one or two layers in submedian medulla. Ovary posterior, median, arcuate and transversely elongated. Vagina well-developed. Vitelline follicles lateral, continuous in midline and between proglottids. Uterus in median field, opening midventrally; no uterine sac. Eggs not operculated, contain oncospheres. In marine teleosts (flying fish, *Cypselurus*). Pacific Ocean. Type-species *A. spilonopteri* Yamaguti, 1968.

8a. Scolex elongated; strong, with powerful plicated apical disc .....

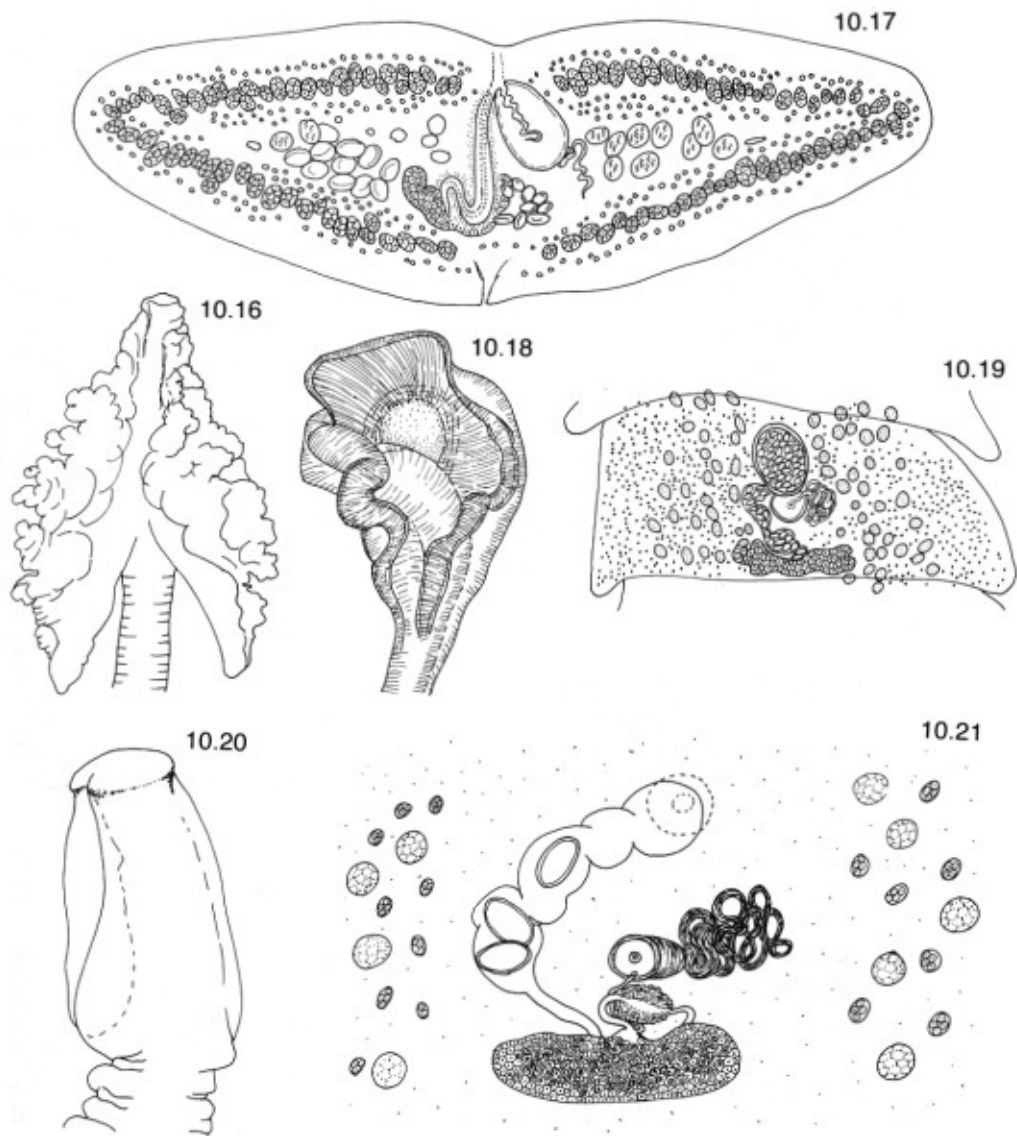
*Tetrapapillocephalus* Protasova & Mordvinova, 1986. (Figs 10.18, 10.19)

**Diagnosis:** Scolex strongly developed with powerful, unarmed, four-lobed apical disc with plicated edges; bothria poorly developed. External segmentation present, with secondary divisions anteriorly. Genital pore dorsal, more or less median. Vagina opens anteriorly to cirrus-sac. Testes medullary, in two lateral fields. Ovary posterior, lobed, bialate. Vitelline follicles cortical, continuous between proglottids. Uterine sac median, opens midventrally? Eggs anoperculate, partly embryonated. In marine teleosts (*Saurida undosquamis*, *Beryx splendens*). Indian Ocean. Type-species *T. magnus* Protasova & Mordvinova, 1986.

8b. Scolex elongated or not; apical disc present or absent, not strongly developed or plicated ..... 9.

9a. Eggs operculate when laid ..... 10.

9b. Eggs not operculate ..... 11.



**Figs 10.16, 10.17** *Alloptychobothrium spilonotopteri* Yamaguti, 1968. 10.16. Scolex, original. 10.17. Mature proglottid in transverse section, after Yamaguti (1968).

**Figs 10.18, 10.19** *Tetrapapillocephalus magnus* Protasova & Mordvinova, 1986. 10.18. Scolex. 10.19. Gravid proglottid. After Protasova & Mordvinova (1986).

**Figs 10.20, 10.21** *Bothriocephalus scorpii* (Müller, 1776). 10.20. Scolex. 10.21. Reproductive organs.

10a. Vitelline follicles cortical. Eggs unembryonated when laid .....  
 ..... *Bothriocephalus* Rudolphi, 1808. (Figs 10.20, 10.21)  
 (Syns *Dibothrium* Diesing, 1850; *Penetrocephalus* Rao, 1960; *Schyzocotyle*  
 Akhmerov, 1960.)

**Diagnosis:** Scolex usually elongated, occasionally pyriform or rounded; unarmed; apical disc present; bothria shallow or deep, with non-crenulated

margins, may be connected by apical groove. External segmentation present. Proglottids wider than long. Genital pores dorsomedian. Testes medullary in two lateral fields. Cirrus unarmed. Ovary median, posterior, transversely elongated, bialate or not. Uterine sac present. Uterine pore ventral, median or slightly submedian, anterior to genital pore. Eggs operculate. In marine and freshwater teleosts. Cosmopolitan. Type-species *B. scorpii* (Müller, 1776).

**10b. Vitelline follicles medullary, intermingled with testes. Eggs embryonated when laid** ..... *Taphrobothrium* Lühe, 1899. (Figs 10.22, 10.23)

**Diagnosis:** Scolex elongate, apical disc present but unarmed, bothria surficial. External segmentation present but incomplete. Proglottids wider than long. Genital pores dorsal, median. Cirrus-sac muscular. Ovary posterior, transversely elongated. Uterus sigmoid. Uterine sac present; uterine pore ventral submedian. Eggs thin-shelled, operculate. In marine teleosts. Japan. Type-species *T. japonense* Lühe, 1899.

**11a. Bothrial margins fused except for anterior aperture surrounded by powerful sphincter. In marine teleosts** ..... *Clestobothrium* Lühe, 1899. (Fig. 10.24)

**Diagnosis:** Scolex broadly oval, robust with deep bothria connected by apical groove. Neck absent. Strobila muscular. External segmentation distinct. Genital pores mid-dorsal. Testes in two lateral fields. Ovary median, transversely elongated. Vitelline follicles cortical, continuous around lateral margins of proglottid. Uterine coils median, terminating in large uterine sac; uterine pore midventral. Eggs anoperculate, unembryonated. In marine fish. Mediterranean, Atlantic. Type-species *C. crassiceps* (Rudolphi, 1819).

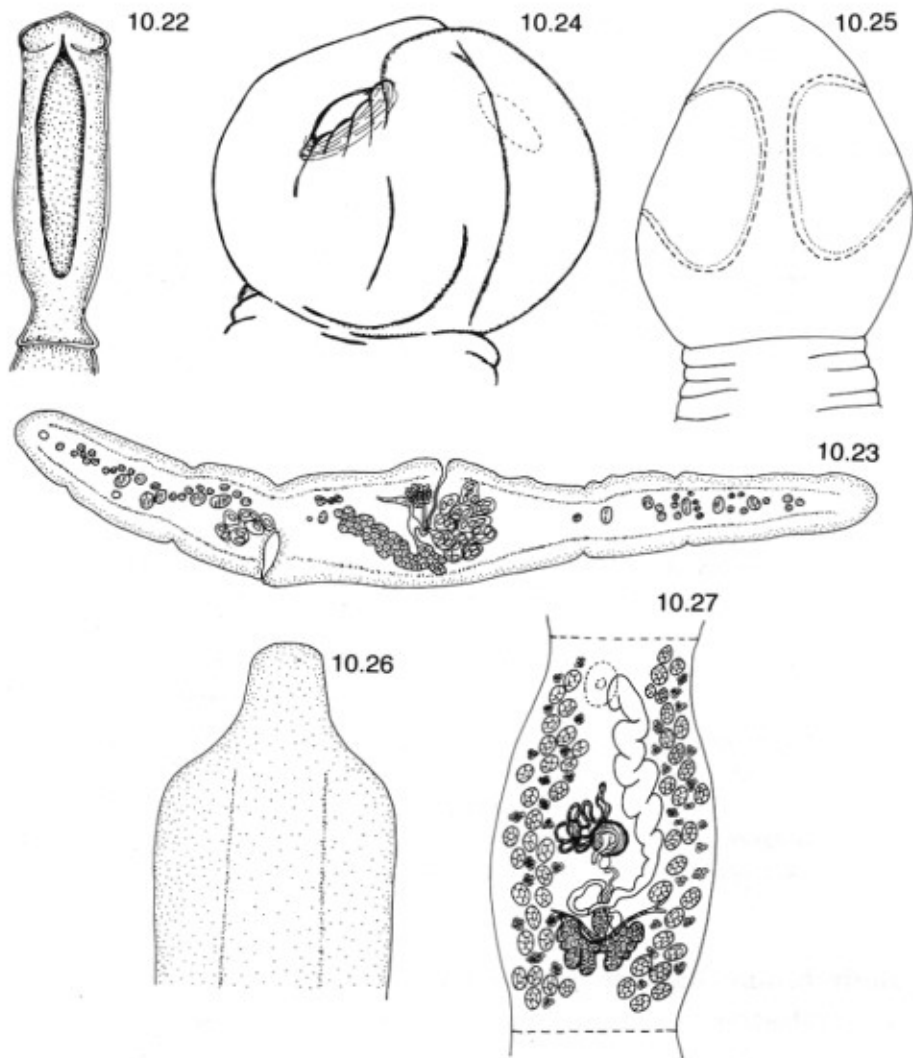
**11b. Bothrial margins not fused; sphincter absent. In freshwater teleosts** .... 12.

**12a. Scolex subpyriform; bothrial cavities deep. In freshwater teleosts of the Middle East** ..... *Coelobothrium* Dollfus, 1970. (Fig. 10.25)

**Diagnosis:** Scolex subpyriform, unarmed, apex rounded, no apical disc or apical groove. Bothrial cavities large, very deep with narrow apertures. Neck absent. External segmentation incomplete. Genital pore dorsal, almost median. Testes medullary, in two lateral fields. Ovary posterior, transversely elongated. Seminal receptacle well-developed. Vitelline follicles present throughout cortex. Uterine sac large, occupying all the proglottid; uterine pore ventral, slightly submedian. Eggs anoperculate. In freshwater fish (*Varicorbinus damascinus umbla*). Iran. Type-species *C. monodi* Dollfus, 1970.

**12b. Scolex thimble-shaped; bothrial cavities shallow. In African freshwater teleosts** ..... *Ichthybothrium* Khalil, 1971. (Figs 10.26, 10.27)

**Diagnosis:** Scolex slightly dorsoventrally flattened, unarmed. Bothria shallow, margins not inrolled. Strobila weakly muscled; external segmentation incomplete; proglottids acraspedote. Genital pore dorsal, median. Testes medullary in lateral fields. Cirrus-sac thick-walled; cirrus unarmed. Vagina opens behind cirrus-sac. Ovary posterior, bialate. Uterine duct sinuous, uterine sac opens at ventral submedian uterine pore. Vitelline follicles cortical, in two lateral fields dorsally and



**Figs 10.22, 10.23** *Taphrobothrium japonense* Lühe, 1899. 10.22. Scolex. 10.23. Gravid proglottid, transverse section. After Yamaguti (1934).

**Fig. 10.24** *Clestobothrium crassiceps* (Rudolphi, 1819). Scolex.

**Fig. 10.25** *Coelobothrium monodi* Dollfus, 1970. Scolex. After Dollfus (1970).

**Figs 10.26, 10.27** *Ichthyobothrium ichthybori* Khalil, 1971. 10.26. Scolex. 10.27. Mature proglottid. After Khalil (1971).

ventrally. Eggs anoperculate, embryonated. In African freshwater teleosts (*Ichthyborus*). Type-species *I. ichthybori* Khalil, 1971.

### Family Philobothiidae Campbell, 1977

Our knowledge of the morphology of members of this small family is based on the descriptions of the two known species by Campbell (1977, 1979). The family

is unusual in that its members have a single, transversely elongate, lobed vitellarium.

### Family diagnosis

Scolex with bothria; apical disc weakly developed or absent. Strobila distinctly segmented, craspedote. One set of genitalia per proglottid. Testes medullary, median. Cirrus-sac with unarmed cirrus. Genital pores marginal; irregularly alternating. Vagina enters genital atrium anterior to cirrus-sac. Ovary in posterior medulla. Vitellarium single, lobed, transversely elongate, medullary, postovarian. Uterus diverticulate. Uterine pore ventromedian. In deep-sea teleosts. Type-genus *Philobythos* Campbell, 1977.

### Key to genera

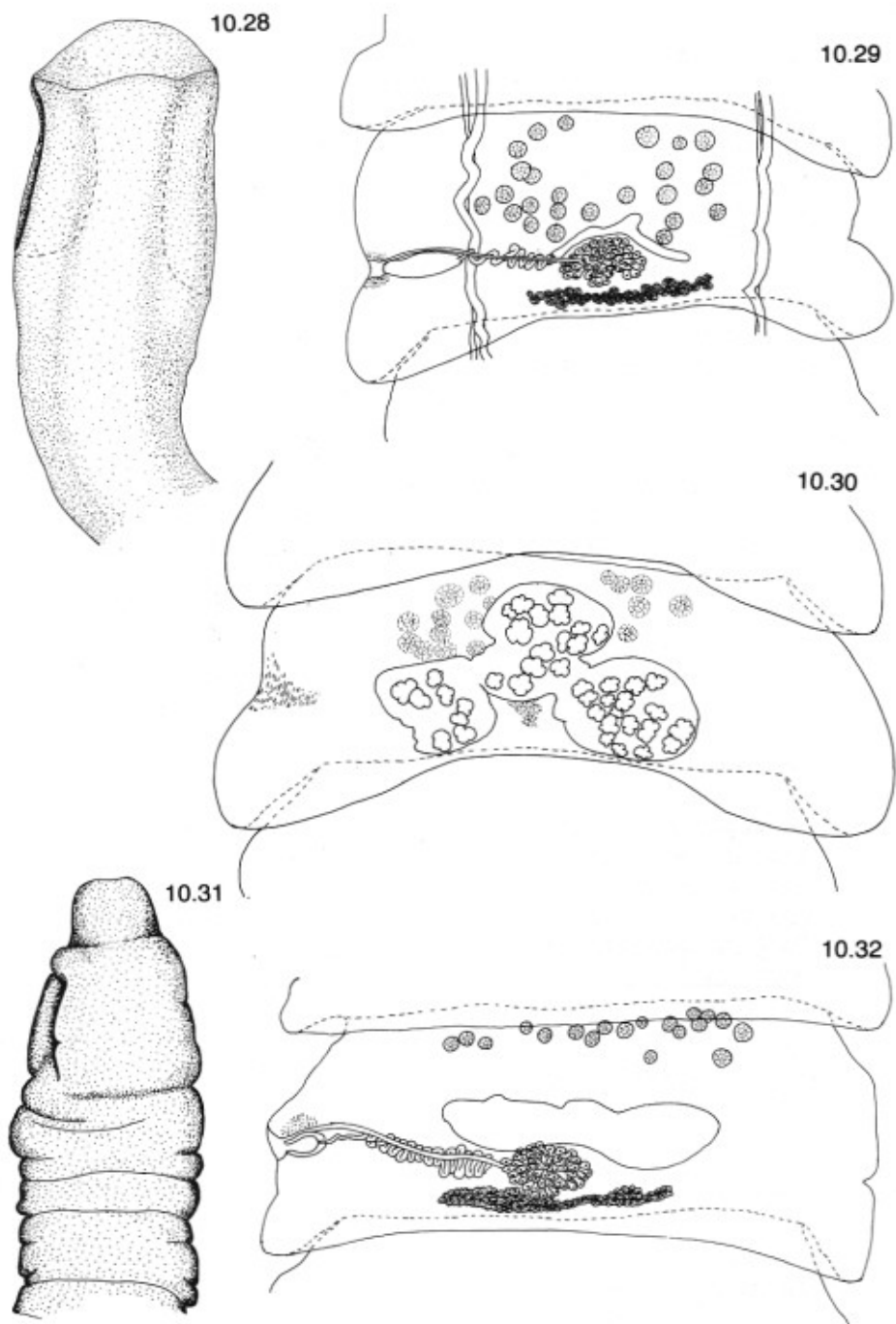
- 1a. Scolex with apical disc. Testes in field surrounding female system. Oncospheres in clusters of three to five within membranous capsule .....  
 ..... *Philobythos* Campbell, 1977. (Figs 10.28–10.30)  
 Diagnosis: With characters of family. In Stephanoberycidae and Macrouridae. North Atlantic Ocean. Type-species *P. atlanticus* Campbell, 1977.
- 1b. Scolex without apical disc. Testes restricted to anterior extremity of proglottid. Oncospheres single within membranous capsule .....  
 ..... *Philobythoides* Campbell, 1979. (Figs 10.31, 10.32)  
 Diagnosis: With characters of family. In Alepocephalidae. Northern Atlantic. Type-species *P. stunkardi* Campbell, 1979.

### Family Echinophallidae Schumacher, 1914

(Syn. Parabothriocephalidae Yamaguti, 1959)

The Parabothriocephalidae cannot be distinguished from the Echinophallidae, which has priority. The differences of double genitalia and a spiny cirrus are not valid at family level and, in addition, *Bothriocotyle* and *Paratelemerus* with single sets of genitalia and conspicuously armed cirri represent intermediate forms.

The type-species of *Parabothriocephaloides*, *P. segmentatus* Yamaguti, 1934, and that of *Parabothriocephalus*, *P. gracilis* Yamaguti, 1934, occur together, in the same host species and individuals of *Psenopsis anomala*, the type host of both species. Yamaguti (1934) distinguished *Parabothriocephaloides* by its pseudoscolex, prominent posterolateral proglottid margins in the anterior part of the strobila, vaginal sphincter and cortical vitelline follicles. He stated, however, that the scolex of *Parabothriocephalus gracilis* was easily detached. Possibly, detachment and replacement of the scolex by a pseudoscolex may occur in *Parabothriocephaloides segmentatus*. This occurs in the triaenophorid *Fistulicola plicatus* (Rudolphi, 1819) Lühe, 1899, indicating that the presence of a pseudoscolex is



**Figs 10.28-10.30** *Philobythos atlanticus* Campbell, 1977. 10.28. Scolex. 10.29. Mature proglottid. 10.30. Gravid proglottid.

**Figs 10.31, 10.32** *Philobythoides stunkardi* Campbell, 1979. 10.31. Scolex, modified after Campbell (1979). 10.32. Early gravid proglottid.

not necessarily a generic feature but that both states may co-exist. Furthermore, Campbell, Correia & Haedrich (1982) have shown that a vaginal sphincter may be present or absent in the genus *Parabothriocephalus* and that in this genus the distribution of the vitelline follicles is variable. It is medullary in the type-species, circumcortical with intrusions into the medulla in *P. macruri* Campbell *et al.*, 1982 and circumcortical in *P. sagitticeps* (Sleggs, 1927) (see Yamaguti, 1934; Campbell *et al.*, 1982; Jensen, 1976). The posterolateral expansion of the anterior proglottids is not a generic character. *Parabothriocephaloides*, therefore, falls within the range of variation now known to occur in *Parabothriocephalus*, with which it is synonymized.

*Atelemerus* and *Paratelemerus* have in the past been differentiated from closely related forms by the presence of a field of spines on the posterior border of each proglottid. Our observations on worms identified as *Echinophallus* indicate that this is not a good generic criterion, as it is easily lost at fixation. This feature apart, the type-species of *Atelemerus* and *Echinophallus* are indistinguishable (and from the same host) and we consider them synonymous.

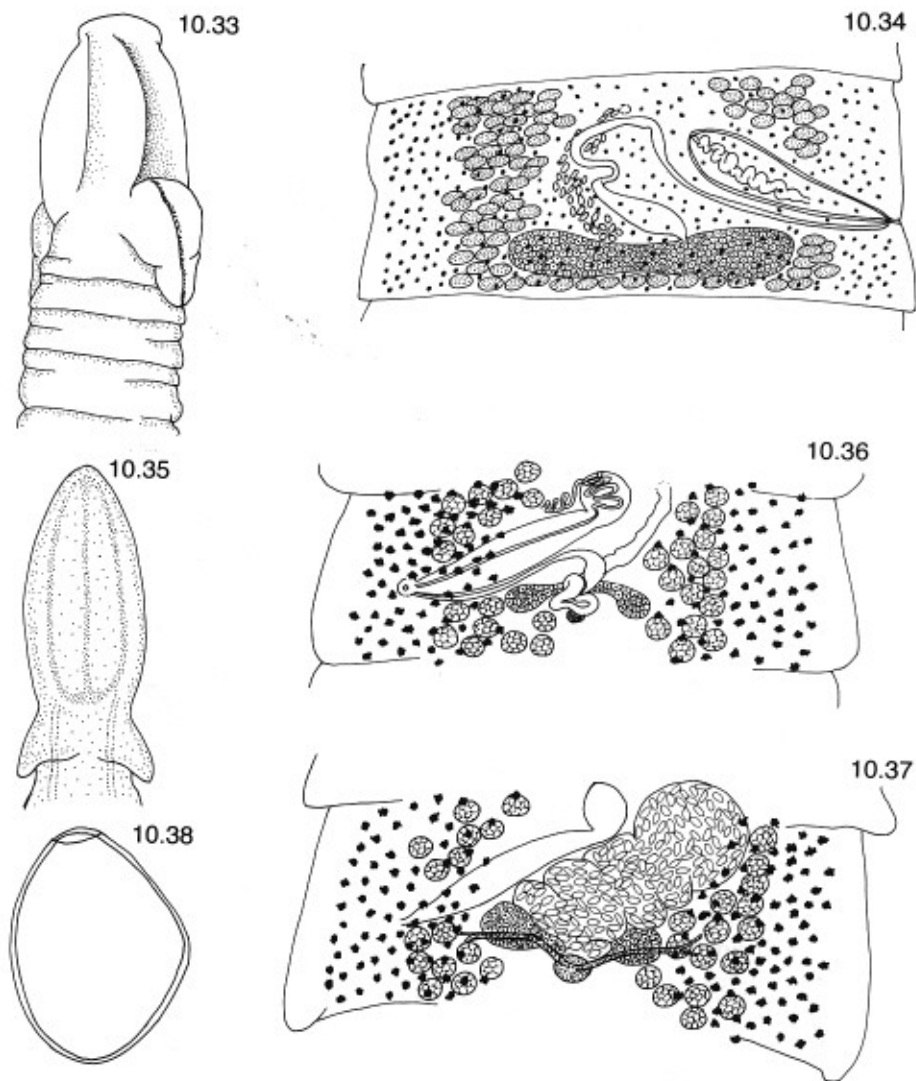
We have retained *Paratelemerus* as distinct, but without much conviction. We believe that careful critical study of new material of a number of genera from centrolophid fishes, i.e. *Paratelemerus*, *Bothriocotyle*, *Parabothriocephalus*, *Neobothriocephalus* and *Glossobothrium*, will lead to a reduction in the number of recognized valid genera. *Metabothriocephalus* Yamaguti, 1968 has also been provisionally retained pending the availability of new material.

### Family diagnosis

Scolex persistent or replaced by pseudoscolex. Apical disc present or absent; if present, may be inconspicuous; unarmed. Bothria usually shallow, weak; rarely with posterior appendages. Strobila usually flattened, rectilinear, rarely spiral and concave ventrally. Segmentation complete or not. Proglottids usually wider than long. One or two sets of genitalia per proglottid. Genital pores single or double, dorsosubmarginal. Cirrus-sac small to large, may cross midline. Cirrus armed or not. Testes medullary. Ovary posterior. Vitelline follicles either cortical with or without intrusions into medulla, or medullary. Uterine pore ventral, median or submedian. Eggs operculate or not, unembryonated. In marine teleosts. Type-genus *Echinophallus* Schumacher, 1914.

### Key to genera

- |   |    |
|---|----|
| 1a. Genitalia single .....                                      | 2. |
| 1b. Genitalia double .....                                      | 7. |
| 2a. Bothria with prominent posterior appendages .....           |    |
| ..... <i>Glossobothrium</i> Yamaguti, 1952. (Figs 10.33, 10.34) |    |
- Diagnosis:** Scolex elongated with unarmed apical disc; each bothrium with a linguiform fluted appendage projecting from its base. Neck absent. External



**Figs 10.33, 10.34** *Glossobothrium nipponicum* Yamaguti, 1952. 10.33. Scolex. 10.34. Gravid proglottid, after Yamaguti (1952).

**Figs 10.35-10.38** *Neobothriocephalus aspinosus* Mateo & Bullock, 1966. 10.35. Scolex. 10.36. Mature proglottid. 10.37. Gravid proglottid. 10.38. Egg. After Mateo & Bullock (1966).

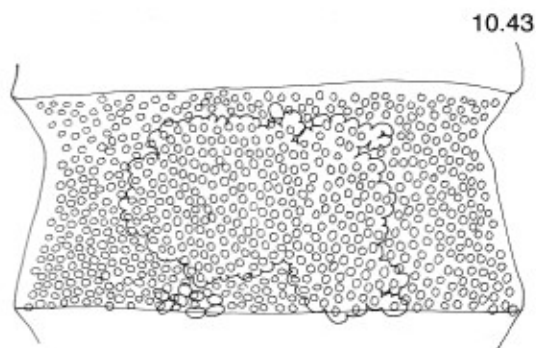
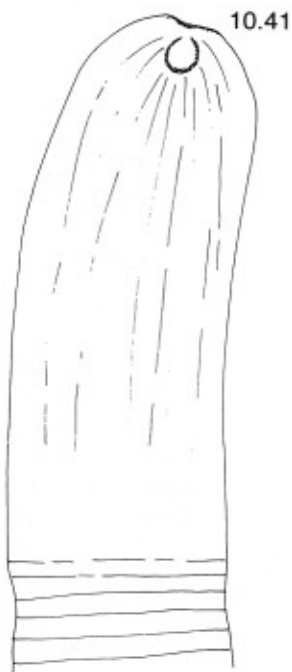
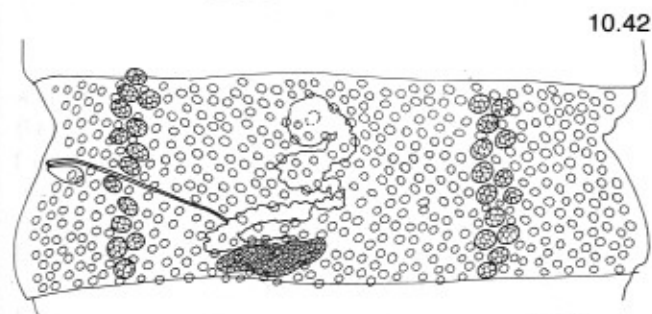
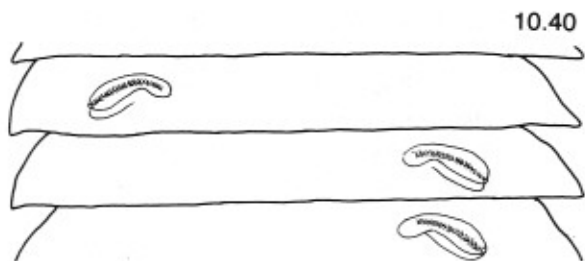
metamerism present. Proglottids short, imbricated anteriorly, with salient posterior margins. Genital pore marginal, postequatorial. Cirrus-sac claviform, invested with gland cells. Cirrus armed with tiny spines. Ovary bialate, posterior, slightly poral. Vagina with proximal muscular dilation, opens behind cirrus-sac. Vitelline follicles cortical, diffuse. Uterine duct sigmoid; uterine sac opens midventrally near anterior margin of proglottid. Eggs operculate, unembryonated. In marine teleosts. Japan. Type-species *G. nipponicum* Yamaguti, 1952.

- 2b. Bothria lacking posterior appendages ..... 3.
- 3a. Eggs with lateral swelling .....  
 ..... *Neobothriocephalus* Mateo & Bullock, 1966. (Figs 10.35–10.38)  
**Diagnosis:** Scolex ovoid, unarmed; bothria shallow. External segmentation almost complete. Proglottids cuneate, wider than long except at posterior end. Genital pore dorsosubmarginal. Cirrus-sac oblique, large. Cirrus unarmed. Testes medullary in two lateral bands. Vaginal sphincter present; vagina aspinose, without distal dilation. Ovary posterior, slightly poral, bialate. Vitelline follicles mainly cortical in dorsal and ventral fields, not continuous around margin of proglottid; few medullary. Uterus sigmoid or sinuous; uterine sac opens ventromedially. Eggs operculate, unembryonated. In marine fish. Peru, Chile. Type-species *N. aspinosus* Mateo & Bullock, 1966.
- 3b. Eggs without lateral swelling ..... 4.
- 4a. Strobila spiral, concave ventrally .....  
 ..... *Bothriocotyle* Ariola, 1900. (Figs 10.39, 10.40)  
**Diagnosis:** Scolex conical, with shallow bothria and distinct small sucker at posterior margin; apical disc absent. External segmentation distinct, craspedote. Genital pore dorsal; closer to margin than median line; irregularly alternating. Cirrus-sac large. Cirrus armed with large spines. Testes numerous; in single medullary layer. Ovary bilobed, medullary, near cirrus-sac. Vitelline follicles medullary, ventral. Uterus with long narrow duct and small sac. Uterine pore ventral; median. Eggs anoperculate. Parasite of marine teleosts (*Centrolophus*). Mediterranean. Type-species *B. solinosomum* Ariola, 1900.
- 4b. Strobila more or less flattened ..... 5.
- 5a. Vagina often expanded distally or proximally, spinose or not; genital pore distinctly dorsosubmarginal ..... 6.
- 5b. Vagina straight, narrow, unarmed; genital pore almost marginal .....  
 ..... *Metabothriocephalus* Yamaguti, 1968. (Figs 10.41–10.43)  
**Diagnosis:** Scolex not clearly demarcated from neck; apical disc indistinct; small, oval, subapical bothrium, surrounded by condensed tissue, on each flat surface. Strobila muscular, fleshy; proglottids wider than long with salient posterior margins. Genital pore pre-equatorial. Cirrus-sac small. Testes medullary, in two lateral fields, relatively few. Ovary slightly poral, transversely elongated. Vagina opens anterior to cirrus-sac. Vitelline follicles entirely cortical. Uterine sac median, opens midventrally. Eggs thick-shelled, operculate, unembryonated. In marine teleosts (*Myripristis* spp.). Hawaii. Type-species *M. menpachi* Yamaguti, 1968.

**Figs 10.39, 10.40** *Bothriocotyle solinosomum* Ariola, 1900. 10.39. Two views of scolex. 10.40. Three proglottids showing positions of terminal genitalia. Modified after Ariola (1902).

**Figs 10.41–10.43** *Metabothriocephalus menpachi* Yamaguti, 1968. 10.41. Scolex. 10.42. Mature proglottid. 10.43. Gravid proglottid.

**Figs 10.44, 10.45** *Paratelemerus seriotelella* Gulyaev, Korotaeva & Kurochkin, 1989. 10.44. Pseudoscolex. 10.45. Mature proglottid. Modified after Gulyaev *et al.* (1989).



- 6a. Cirrus-sac large, reaching into aporal part of proglottid and to anterior edge of proglottid .....

*Paratelemerus* Gulyaev, Korotaeva & Kurochkin, 1989. (Figs 10.44, 10.45)

**Diagnosis:** Scolex replaced by pseudoscolex. External segmentation distinct. 18–21 proglottids, only the last one to three have fully-formed genital apparatus. Posterolateral margins of proglottid spined. Genital pore dorsosubmarginal, postequatorial. Testes lateral, confluent behind ovary. Cirrus conspicuously armed with large spines. Ovary posterior, median or slightly poral, bialate. Vagina strongly recurved, muscular, dilated proximally. Vaginal sphincter present or absent. Uterine duct winding on aporal side of cirrus-sac. Uterine sac small, median, opens ventromedially? Eggs? In marine fish (Centrolophidae, Stromateidae). Off north-western Australia. Type-species *P. seriolella* Gulyaev, Korotaeva & Kurochkin, 1989.

- 6b. Cirrus-sac smaller, not reaching midline, not reaching anterior edge of proglottid .....

*Parabothriocephalus* Yamaguti, 1934. (Figs 10.46, 10.47)

(Syn. *Parabothriocephaloides* Yamaguti, 1934.)

**Diagnosis:** Scolex with two surficial bothria but no apical disc; easily detached. Neck absent. External segmentation almost complete. Proglottids wedge-shaped, longer than wide. Genital pore dorsosubmarginal. Testes medullary in two lateral fields, or confluent in mid-line. Cirrus-sac muscular. Cirrus spinose. Vagina narrow proximally, often expanded and sometimes muscular distally; vaginal armature and/or sphincter present or absent. Ovary poral, lobed, bialate. Vitelline follicles may be circumcortical, perhaps intruding into medulla, or medullary. Uterine duct sigmoid or not; uterine sac invades preceding proglottid. Uterine pore midventral or slightly antiporal. Eggs operculate, unembryonated; anopercular boss present or absent. In marine teleosts. Japan, Atlantic and Pacific Oceans. Type-species *P. gracilis* Yamaguti, 1934.

- 7a. Genital pores dorsosubmarginal, very close to lateral margin .....

*Paraechinophallus* Protasova, 1975. (Fig. 10.48)

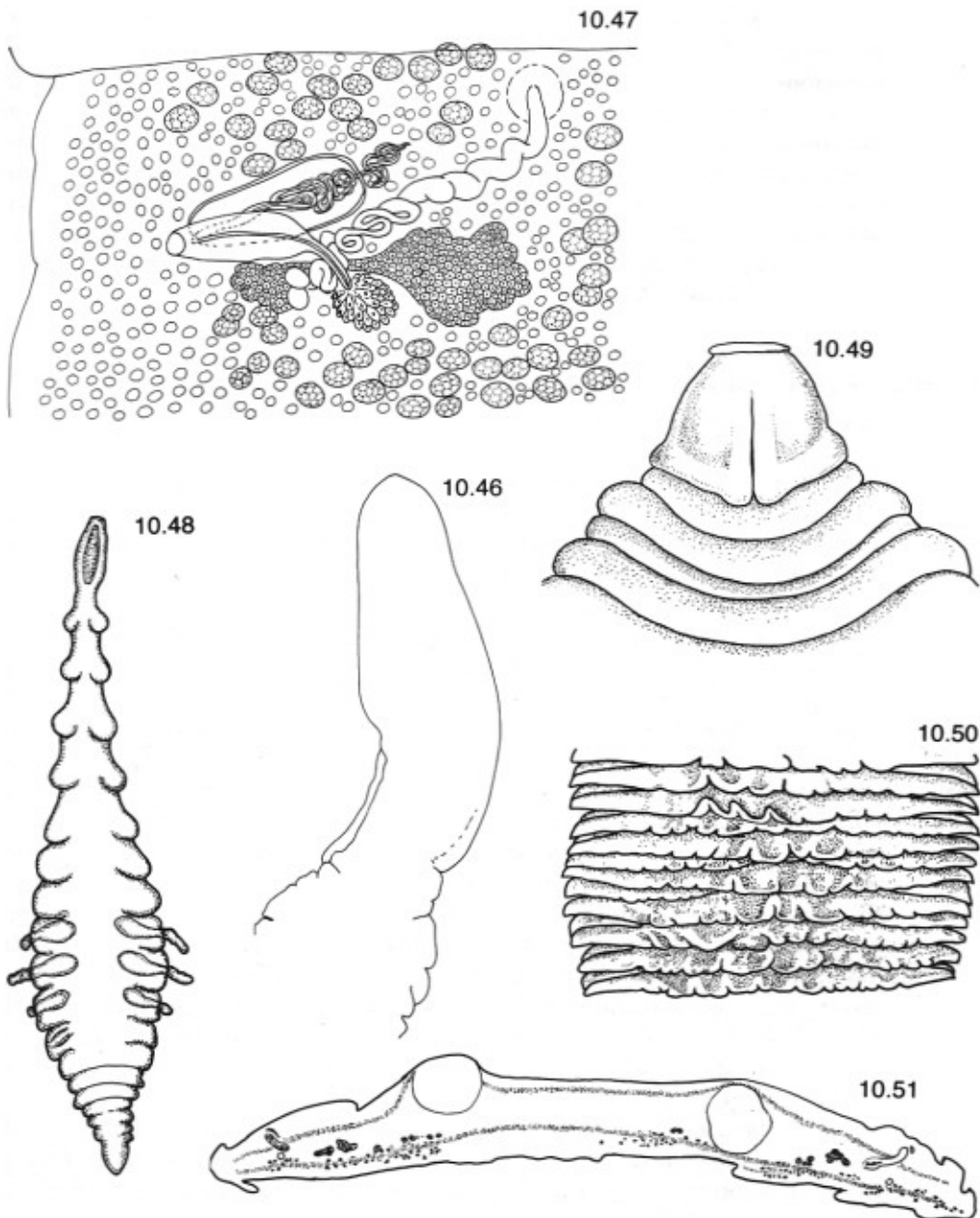
**Diagnosis:** Scolex with two shallow bothria and inconspicuous apical disc, lost in older worms. Pseudoscolex trapezoidal. External segmentation distinct; posterior border of proglottid lobed, overlapping following proglottid. Genitalia double. Cirrus-sac large, muscular. Cirrus with large spines at base. Testes medullary, median to ovaries, but with gap in median region. Ovary lobed, posteromedian to cirrus-sac. Uterus forms sac just closer to median line than to proglottid margin; pore ventral, anterior. Eggs operculate, unembryonated. Vitelline follicles fill cortical parenchyma, intrude into medulla in lateral parts of proglottid. In marine teleosts (Centrolophidae). Pacific (Japan, Hawaii). Type-species *P. japonica* (Yamaguti, 1934).

- 7b. Genital pores dorsal, well away from margin of proglottid up to halfway to median line .....

*Echinophallus* Schumacher, 1914. (Figs 10.49–10.51)

(Syns *Amphitretus* Blanchard, 1894 preoccupied; *Acanthophallus* Lühe, 1910 preoccupied; *Atelemerus* Guiart, 1935.)

**Diagnosis:** Scolex with two shallow bothria and inconspicuous apical disc; in young worms only. Pseudoscolex trapezoidal. Proglottids weakly to strongly



**Fig. 10.46.** *Parabothriocephalus johnstoni* Prudhoe, 1969. Scolex, original. **Fig. 10.47.** *P. macruri* Campbell, Correia & Haedrich, 1982, mature proglottid, adapted from Campbell *et al.* (1982).

**Fig. 10.48** *Paraechinophallus japonicus* (Yamaguti, 1934.) Whole worm. Modified after Yamaguti (1934).

**Figs 10.49-10.51** *Echinophallus wagneri* (Monticelli, 1890). 10.49. Scolex. 10.50. Surface view of proglottids. 10.49 and 10.50 modified after Ariola (1902). 10.51. Transverse section of gravid proglottid, modified after Schumacher (1914).

craspedote with armed or unarmed thickened posterior borders. Genitalia double per proglottid. Cirrus-sac large, muscular. Cirrus with long spines. Testes numerous, medullary, in two fields median to genital pores, either side of and a few posterior to ovary, continuous between proglottids. Ovary lobate, posterior to cirrus-sac. Vitelline follicles mostly cortical, abundant laterally, continuous between proglottids. Uterus tubular, convoluted; later forming globular sac, median to genital pore. Uterine pore submedian, near anterior margin of proglottid. Eggs operculate, unembryonated. In marine teleosts (Centrolophidae and Sparidae). Mediterranean, North Atlantic, Great Australian Bight, Pacific (Japan). Type-species *E. wagneri* (Monticelli, 1890).

## Family Triaenophoridae Lönnberg, 1889

(Syn. Amphicotylidae Ariola, 1899)

The families Triaenophoridae and Amphicotylidae have been distinguished by the presence of operculated eggs in the former but not the latter. Amphicotylid eggs are embryonated when laid but triaenophorid eggs may be embryonated or not. As discussed above for the Bothriocephalidae and Ptychobothriidae, these characters are not suitable for use at family level. The Amphicotylidae is, therefore, synonymized with the Triaenophoridae.

*Fistulicola* Lühe, 1899 and *Pseudeubothrium* Yamaguti, 1958, both with type-species which parasitize *Xiphias gladius*, ostensibly differ in the (occasional) presence of a pseudoscolex, a slightly poral ovary in *Fistulicola* and in the presence of a neck and a median ovary in *Pseudeubothrium*. It is not known whether a pseudoscolex may occur in *Pseudeubothrium* but it may be present or absent in *Fistulicola*, which precludes its use for separating the genera. The two type-species, *F. plicatus* (Rudolphi, 1819) and *P. xiphiados* Yamaguti, 1968, have similarly-shaped scoleces, very wide proglottids with markedly expanded margins, circumcortical vitelline follicles, a large cirrus-sac which may just extend into the medulla in *Pseudeubothrium*, and thick-shelled embryonated eggs. *Fistulicola* has operculate eggs but the presence or absence of an operculum in *Pseudeubothrium* eggs was not mentioned by Yamaguti (1968). The type specimens (USNM Helm. Coll. No. 63871) do not include gravid proglottids and the internal organs cannot be clearly distinguished. The differences between the two genera are not sufficient to separate them and they are regarded as synonymous.

*Pseudeubothrioides* Yamaguti, 1968 was synonymized by Schmidt (1986) with *Pseudeubothrium*, here treated as synonymous with *Fistulicola*. Following an examination of the type specimens, however, (USNM Helm. Coll. No. 63872), *Pseudeubothrioides* is provisionally recognized as valid.

*Pachybothrium* Pozdniakov, 1983 is preoccupied, but is treated here as a synonym of *Amphigonoporus*. *A. carvalhoi* is reported from *Mola mola* off Brazil (Mendes, 1944) and *P. dogieli* from *M. ramsayi* in the Tasman Sea (Pozdniakov, 1983). The only feature which may be significantly different is the quoted distribution of the vitelline follicles. In *A. carvalhoi* the follicles are essentially cortical with a few in the muscular region and the medulla, the follicles are only in the 'ventral' plane (dorsal in figure). In *P. dogieli* the follicles are said to be

mainly medullary and partly cortical, and to surround the testes. These distinctions may be of value at the specific level, or may be interpretational differences. In either case, we do not consider them enough to distinguish the genera, or to warrant the erection of a new name.

*Probothriocephalus* Campbell, 1979 is transferred to the Triaenophoridae because it has a marginal genital pore and we can find no feature of generic value distinguishing *Probothriocephalus*, *Flexiphallus* Protasova & Parukhin, 1986, *Heterovitellus* Protasova & Parukhin, 1986 and *Partitiotestis* Protasova & Parukhin, 1986. In erecting their three genera, Protasova & Parukhin (1986) did not refer to *Probothriocephalus*. *Partitiotestis* is said to be distinguished by the testes being discontinuous between proglottids but Protasova & Parukhin's (1986) figure 2b shows the testicular fields of adjacent proglottids coming very close to each other. Protasova & Parukhin (1986) distinguished *Flexiphallus* from *Heterovitellus* by the cirrus-sac of the former lying at an angle to the longitudinal axis of the proglottid, rather than perpendicular, and by the vitellarium being cortical rather than cortical and intermuscular. We do not consider these features adequate to distinguish genera and, therefore, consider *Flexiphallus*, *Heterovitellus* and *Partitiotestis* synonyms of *Probothriocephalus*.

*Blanchardella* Moniez, 1895 (new name for *Leuckartia* Moniez, 1880 *nec* Agassiz, 1862 (cocenterate) or Claus, 1862 (crustacean)) may be a synonym of *Eubothrium* as suggested by Schmidt (1986), but if so it takes precedence. It seems unwise, however, to do away with the well-known genus *Eubothrium* and, therefore, we consider *Blanchardella* a genus *inquirendum*.

*Pseudobothrium* Guiart, 1935 is not recognizable from Guiart's description. Dollfus (1940) was unable to pronounce on its validity. It is regarded here as a genus *inquirendum*.

## Family diagnosis

Scolex usually present but may be replaced by pseudoscolex or scolex deformatus. Apical disc present or absent; if present, armed or unarmed. Bothria present or absent; weak or shallow to well-developed, occasionally with projecting posterior margins. Segmentation present or absent. Proglottids usually wider than long. Reproductive organs single or double. Genital pores marginal. Testes medullary. Cirrus-sac small to large. Cirrus armed or not. Ovary posterior. Vitelline follicles cortical and/or medullary; may intrude between longitudinal muscles. Uterine pore ventral, usually median; rarely double. Eggs operculate or not, embryonated or not. In freshwater and marine teleosts. Type-genus *Triaenophorus* Rudolphi, 1793.

## Key to genera

- |                          |    |
|--------------------------|----|
| 1a. Scolex armed .....   | 2. |
| 1b. Scolex unarmed ..... | 3. |

- 2a. Scolex armed with two dorsal and two ventral trident-shaped hooks .....  
 ..... *Triænocephalus* Rudolphi, 1793. (Figs 10.52, 10.53)  
 (Syns *Rhytelminthus* Zeder, 1800; *Rhytis* Zeder, 1800; *Tricuspidaria*  
 Rudolphi, 1793.)

**Diagnosis:** Scolex with apical disc bearing hooks. Bothria shallow. Neck absent. Strobila transversely folded but external metamerism absent. Genital pore marginal. Testes medullary, numerous. Cirrus-sac transverse; cirrus unarmed. Ovary posterior, slightly poral, multilobed, bialate. Vitelline follicles cortical, diffuse. Uterus weakly coiled; uterine sac present; uterine pore opens ventrally, slightly submedian on poral side. Eggs operculate, unembryonated or wholly or partly embryonated, depending on temperature. In carnivorous freshwater teleosts (mainly *Esox*). Circumboreal. Type-species *T. nodulosus* (Pallas, 1781) (type by monotypy).

- 2b. Scolex armed with several alternating rows of small hooks on margin of apical disc .....  
 ..... *Ancistrocephalus* Monticelli, 1890. (Figs 10.54–10.56)  
 (Syn. *Ancistrocephalus* Lühe, 1899.)

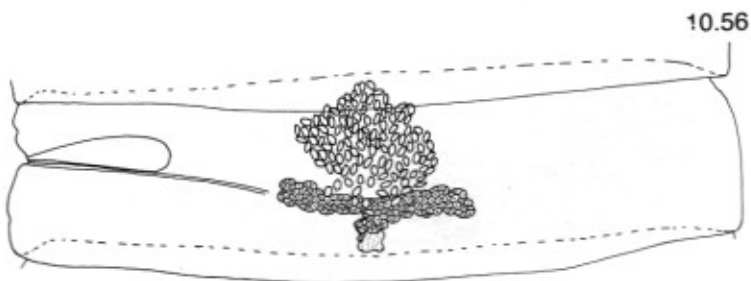
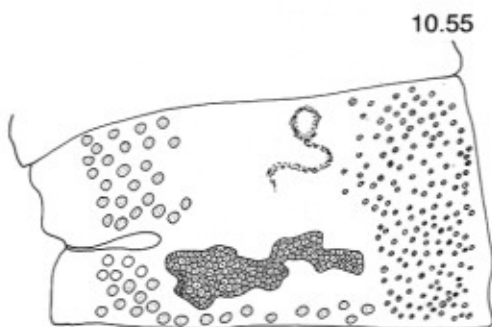
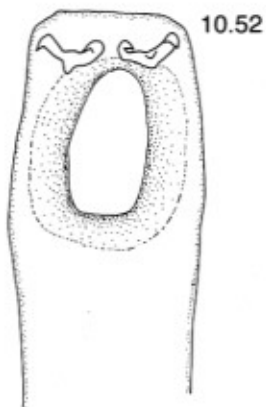
**Diagnosis:** Apical disc hooks most numerous adjacent to the bothrial surfaces. Neck absent. External metamerism distinct; proglottids wider than long; longitudinal musculature well-developed. Testes medullary in two lateral fields, confluent at posterior end of proglottid. Cirrus protrusible. Genital pore marginal. Ovary posterior, lobed. Vitelline follicles mainly medullary but with cortical layer just external to longitudinal muscles. Uterus alternating irregularly without reference to genital pores. Eggs thick-shelled, operculate, unembryonated. In marine teleosts (sunfish). Mediterranean Sea, Atlantic and Pacific Oceans. Type-species *A. microcephalus* (Rudolphi, 1819).

- 3a. Reproductive organs double per proglottid .....  
 ..... *Amphigonoporus* Mendes, 1944. (Figs 10.57–10.59)  
 (Syn. *Pachybothrium* Pozdniakov, 1983 *nec* Baer & Euzet, 1962.)

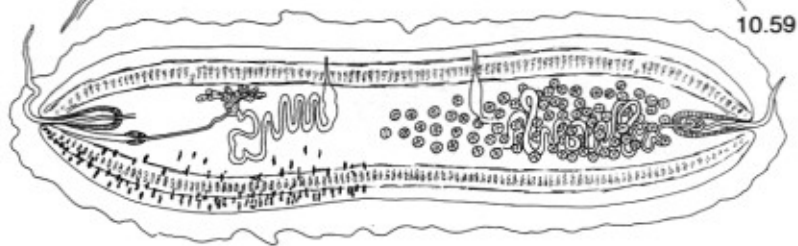
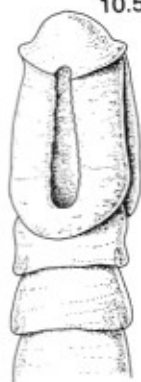
**Diagnosis:** Scolex with distinct apical disc and deep bothria, scolex deformatum occasionally present. External segmentation clearly visible. Genital pores lateral. Cirrus-sac thick-walled. Cirrus protrusible, unarmed. Testes numerous; fields continuous across medulla; median to cirrus-sacs. Ovary small, lobate; just median to ventral osmoregulatory canals. Uterus double, sacciform. Uterine pores double. Vitelline follicles mainly cortical, but some reach into medulla, in dorsal field only or surrounding testicular region. Osmoregulatory canals not known. In *Mola* spp. Type-species *A. carvalhoi* Mendes, 1944.

- 3b. Reproductive organs single per proglottid ..... 4.

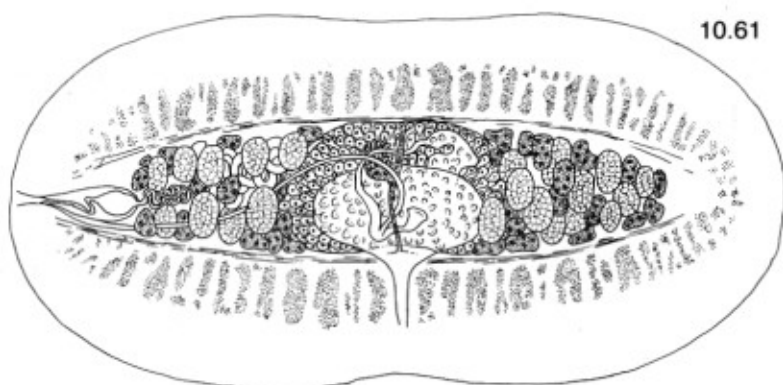
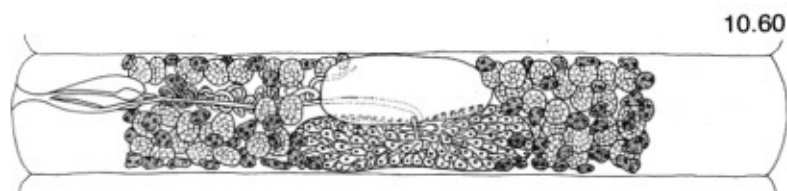
**Figs 10.52, 10.53** *Triænocephalus nodulosus* (Pallas, 1781). 10.52. Scolex. 10.53. Hooks.  
**Figs 10.54–10.56** *Ancistrocephalus microcephalus* (Rudolphi, 1819). 10.54. Scolex. 10.55. Mature proglottid. 10.56. Gravid proglottid.  
**Figs 10.57–10.59** *Amphigonoporus carvalhoi* Mendes, 1944. 10.57. Scolex. 10.58. Mature proglottid. 10.59. Transverse section of mature proglottid. In 10.58 and 10.59, testes omitted on left, vitelline follicles omitted on right. All modified after Mendes (1944).

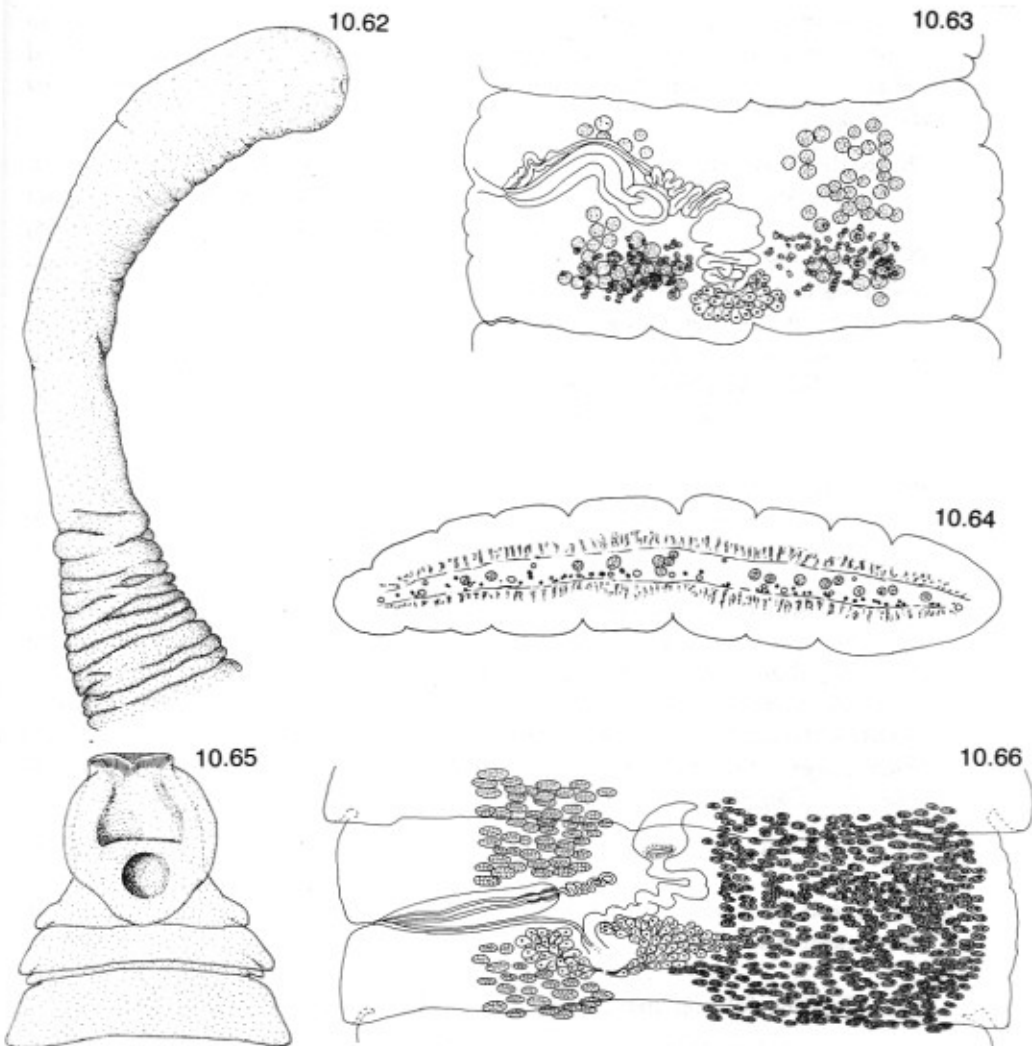


10.57



- 4a. Scolex replaced by scolex deformatus ..... 5.  
 4b. Scolex [or pseudoscolex?] usually present ..... 6.
- 5a. Vitelline follicles intermingled with testes, continuous throughout length of proglottid ..... *Abothrium* van Beneden, 1871. (Figs 10.60, 10.61)  
**Diagnosis:** Scolex deformatus present, unarmed, apical disc and bothria absent. Strobila robust. External segmentation distinct. Genital pores lateral, alternating irregularly. Cirrus-sac small. Cirrus unarmed. Testes numerous, in lateral fields. Ovary symmetrical, median. Uterus with median coils. Uterine pore median. Vitelline follicles medullary, in two lateral fields. Osmoregulatory canals 10–25. In teleosts, mainly Gadiformes. Type-species *A. gadi* van Beneden, 1871.
- 5b. Vitelline follicles partly cortical and partly medullary, not intermingled with testes ..... *Parabothrium* Nybelin, 1920. (Figs 10.62–10.64)  
**Diagnosis:** Scolex deformatus present, unarmed, apical disc and bothria absent. Strobila robust. External segmentation distinct. Genital pores lateral, alternating irregularly. Cirrus-sac large. Testes numerous, in lateral fields, confluent in anterior part of proglottid. Ovary lobate, median. Uterus saccular, becoming lobulate to stellate. Uterine pore median. Vitelline follicles in two ventrolateral fields; in posterior part of proglottid only. Osmoregulatory canals 18–50. In gadid teleosts. Type-species *P. bulbiferum* Nybelin, 1920 [now considered a synonym of *P. gadipollachii* (Rudolphi, 1810)].
- 6a. Bothria divided ..... 7.  
 6b. Bothria undivided ..... 8.





**Figs 10.60, 10.61** *Abothrium gadi* van Beneden, 1871. 10.60. Mature proglottid. 10.61. Mature proglottid in transverse section. Both modified after Nybelin (1922).

**Figs 10.62-10.64** *Parabothrium bulbiferum* Nybelin, 1920. 10.62. Scolex deformatus. 10.63. Mature proglottid. 10.64. Transverse section of mature proglottid.

**Figs 10.65, 10.66** *Amphicotyle heteropleura* (Diesing, 1850). 10.65. Scolex. 10.66. Mature proglottid; vitelline follicles omitted porally, testes omitted aporally.

7a. Bothria each with one division forming posterior sucker. Vitelline follicles cortical, in lateral fields. Osmoregulatory canals four .....  
 ..... *Amphicotyle* Diesing, 1863. (Figs 10.65, 10.66)

**Diagnosis:** Scolex trapezoid, with apical disc. Strobila robust. External segmentation distinct anteriorly, obscured by secondary wrinkles posteriorly. Genital pores lateral, alternating irregularly. Cirrus-sac large. Cirrus protrusible, armed.

Testes numerous in lateral fields or single field. Ovary symmetrical, median to poral. Uterus with median coils. Vitelline follicles in two lateral dorsal and ventral fields, continuous longitudinally. In teleosts. Type-species *A. heteropleura* (Diesing, 1850).

7b. Bothria divided into several loculi. Vitelline follicles medullary and cortical, surrounding proglottid. Osmoregulatory canal system reticulate, about 10–14 ..... *Pseudamphicotyla Yamaguti*, 1959. (Figs 10.67, 10.68)

**Diagnosis:** Scolex slightly elongate, with apical disc. Bothria two. External segmentation distinct, with or without secondary wrinkles. Genital pores, irregularly alternating. Cirrus-sac present. Cirrus spined. Testes numerous, in one continuous layer. Ovary slightly poral. Uterus saccular, globular to oval. Uterine pore median. Vitelline follicles continuous longitudinally. In teleosts (Pentaceroptidae). Type-species *P. quinquarii* (Yamaguti, 1952).

8a. Ovary dendritic. In abyssal fish ..... *Pistana Campbell & Gartner*, 1982. (Figs 10.69–10.71)

**Diagnosis:** Scolex unarmed, arrowhead-shaped; bothria deep with freely-projecting posterior margins; apical disc absent. Neck absent. External metamerism distinct. Genital pore marginal, postequatorial. Cirrus-sac elongated, extending into medulla. Cirrus unarmed. Testes in two lateral fields. Ovary posterior, slightly poral, bialate. Vagina expanded distally, opens posterior to cirrus-sac. Vitelline follicles circumcortical. Uterus median. Uterine sac pyriform, opens midventrally. Eggs operculate, embryonated. In abyssal marine teleosts (*Eurypharynx pelecanoioides*). Western North Atlantic. Type-species *P. eurypharyngis* Campbell & Gartner, 1982.

8b. Ovary not dendritic ..... 9.

9a. Apical disc present ..... 10.

9b. Apical disc absent ..... 13.

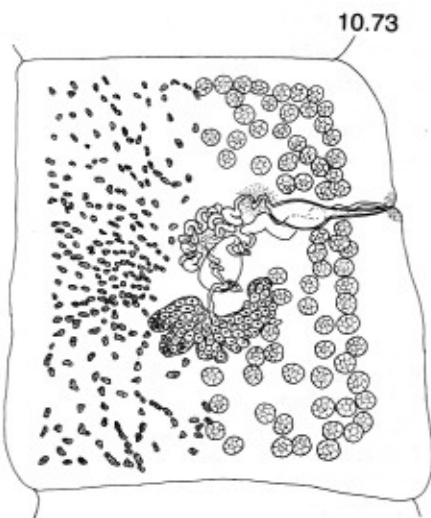
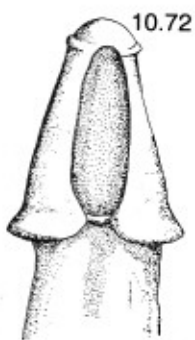
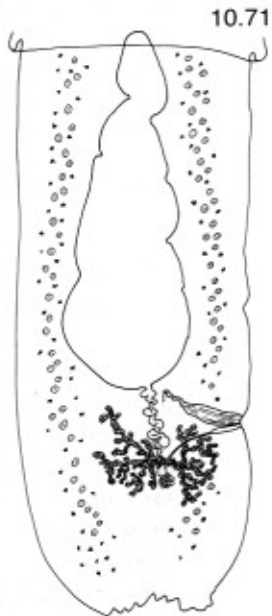
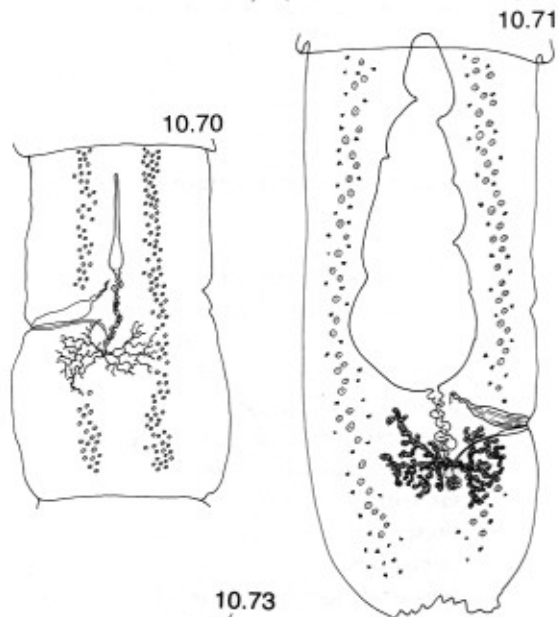
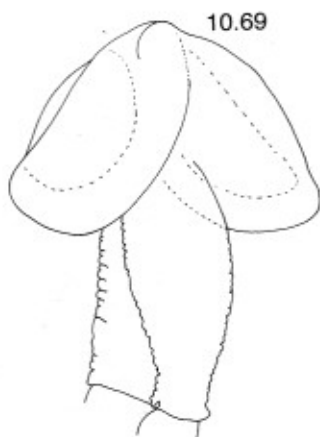
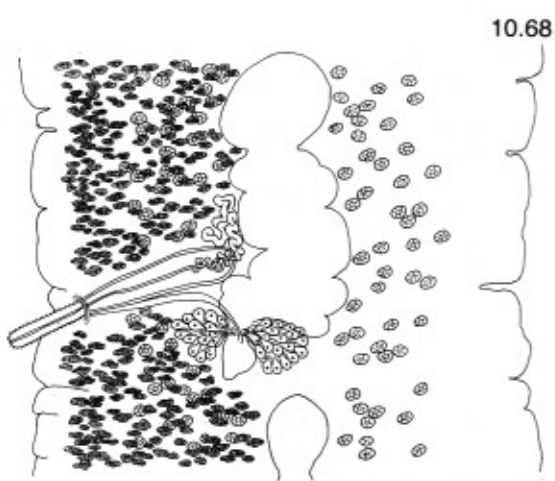
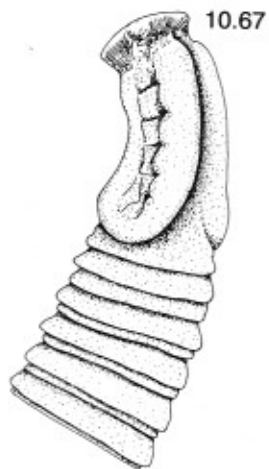
10a. Vitelline follicles mainly medullary. Uterus with long lateral pouches ..... *Marsipometra Cooper*, 1917. (Figs 10.72–10.74)

**Diagnosis:** Scolex pyramidal or sagittate. Bothria oval, deep or shallow. External segmentation present. Genital pores lateral, alternating irregularly. Cirrus-sac large. Cirrus protrusible. Testes numerous, lateral fields confluent anterior to uterus, and usually posterior to ovary. Ovary reniform, with lobulate wings, median. Uterus saccate, forms long lateral pouches. Uterine pore median.

**Figs 10.67, 10.68** *Pseudamphicotyla quinquarii* (Yamaguti, 1952). 10.67. Scolex. 10.68. Mature proglottid, vitelline follicles omitted aporally. Both modified after Yamaguti (1952).

**Figs 10.69–10.71** *Pistana eurypharyngis* Campbell & Gartner, 1982. 10.69. Scolex. 10.70. Early mature proglottid. 10.71. Gravid proglottid.

**Figs 10.72–10.74** *Marsipometra hastata* (Linton, 1898). 10.72. Scolex. 10.73. Mature proglottid. Vitelline follicles omitted porally, testes omitted aporally. 10.74. Gravid proglottid. All modified after Beaver & Simer (1940).



Vitelline follicles medullary or in muscle zone, in right and left ventral fields, continuous longitudinally. Osmoregulatory canals 4-6 or 4 convoluted and branched. In *Polyodon* (Acipenseriformes). Type-species *M. bastata* (Linton, 1898).

10b. Vitelline follicles entirely or mainly cortical ..... 11.

11a. Scolex sagittate. Proglottids much wider than long, strongly craspedote with extended posterolateral margins .....

..... *Fistulicola* Lühe, 1899. (Figs 10.75, 10.76)  
(Syn. *Pseudeubothrium* Yamaguti, 1968.)

**Diagnosis:** Apical disc present but unarmed; bothrial margins smooth. Scolex may be replaced by pseudoscolex. Neck absent. External metamerism complete. Genital pores marginal. Cirrus-sac large. Cirrus protrusible. Testes medullary, in single field. Ovary slightly poral, bialate. Vitelline follicles circumcortical. Uterus strongly coiled, muscular distally. Uterine pore anterior beneath velum of preceding proglottid, ventrally submedian on poral side. Eggs operculate, embryonated. In marine teleosts (*Xiphias gladius*, *Zeus faber*). Atlantic, Pacific, Mediterranean. Type-species *F. plicatus* (Rudolphi, 1819).

11b. Scolex not sagittate. Proglottids lack extended posterolateral margins ...  
..... 12.

12a. Scolex elongate. Uterus strongly coiled, forms half-loop; uterine pore submedian, poral .....

..... *Pseudeubothrioides* Yamaguti, 1968. (Figs 10.77-10.79)

**Diagnosis:** Scolex with simple bothria with smooth margins. Apical disc present, unarmed. Neck present. External metamerism present. Proglottids wider than long except when fully gravid; not strongly craspedote, with salient posterior margins and almost parallel sides. Genital pores marginal, pre-equatorial. Cirrus-sac cortical, oblique, muscular. Testes medullary, confluent posteriorly but few present in preovarian region. Ovary median, transversely elongate, bialate. Vagina opens behind cirrus-sac. Vitelline follicles cortical. Uterine sac muscular. Uterine pore at or just behind level of genital pore. Eggs thick-shelled, not embryonated. In marine teleosts (*Lepidocybium flavobrunneum*). Hawaii. Type-species *P. lepidocybii* Yamaguti, 1968.

12b. Scolex subglobular to elongate, may be deformed. Uterus saccate, oval; uterine pore median .....

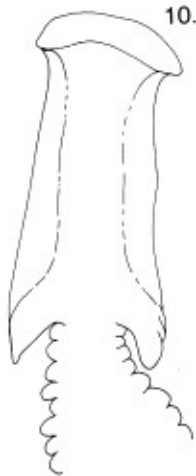
..... *Eubothrium* Nybelin, 1920. (Figs 10.80-10.82)

**Diagnosis:** Scolex with apical disc, distinct or poorly developed; scolex deformatum may occur. External segmentation distinct. Genital pores lateral, irregularly

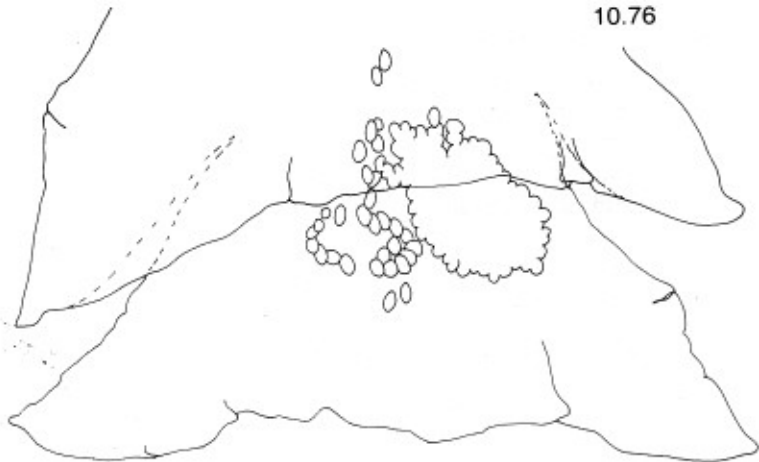
**Figs 10.75, 10.76** *Fistulicola plicatus* (Rudolphi, 1819). 10.75. Scolex. 10.76. Gravid proglottid.  
**Figs 10.77-10.79** *Pseudeubothrioides lepidocybii* Yamaguti, 1968. 10.77. Scolex. 10.78. Mature proglottid. 10.79. Gravid proglottid. 10.77 after Yamaguti (1968).

**Figs 10.80-10.82** *Eubothrium* Nybelin, 1920. 10.80. *E. crassum* (Bloch, 1779), scolex. 10.81. *E. salvelini* (Schränk, 1790), mature proglottid. 10.82. *E. rugosum* (Batsch, 1786), transverse section of mature proglottid, after Nybelin (1922).

10.75



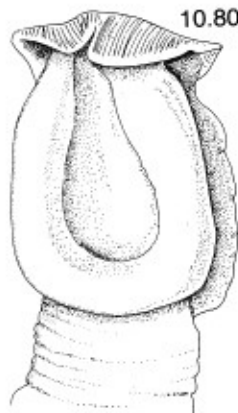
10.76



10.82



10.80



10.77



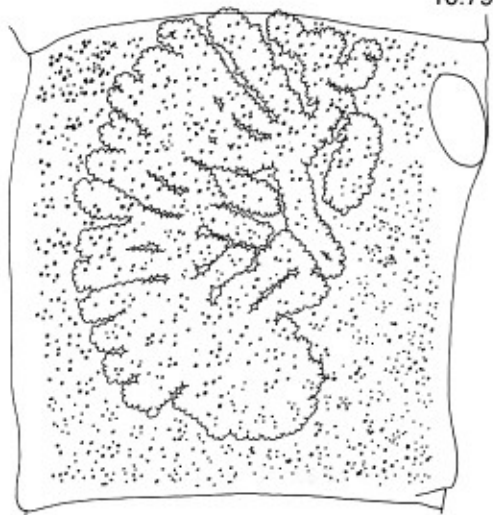
10.81



10.78



10.79



alternating. Cirrus-sac small. Cirrus unarmed. Testes numerous, in two lateral fields which may be almost confluent. Ovary reniform, median. Vitelline follicles cortical, or among longitudinal muscles or occasionally in medulla; in lateral fields, not confluent ventrally or dorsally, not continuous longitudinally. In freshwater and marine teleosts. Type-species *E. rugosum* (Batsch, 1786).

13a. Vitelline follicles medullary ..... 14.

13b. Vitelline follicles cortical ..... 16.

14a. Scolex sagittate with freely projecting posterior margins .....  
*Anonchocephalus* Lühe, 1902. (Figs 10.83, 10.84)

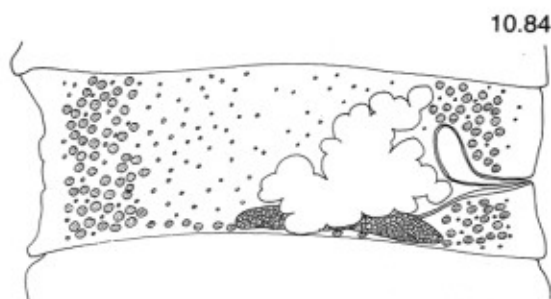
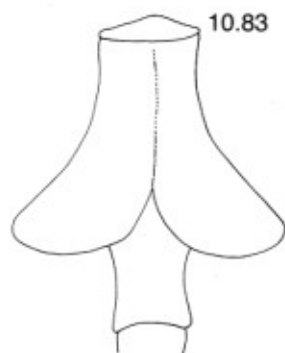
**Diagnosis:** Scolex unarmed. Apical disc absent. Neck absent. External segmentation present. Proglottids wider than long. Genital pore marginal, post-equatorial. Cirrus-sac elongated, muscular. Cirrus armed with spines. Testes medullary, in two lateral fields united at the posterior margin of the proglottid. Ovary posterior, poral, compact. Vagina opens posterior to cirrus-sac. Vitelline follicles ventral to testes. Uterus coiled, narrow, with large, muscular uterine sac opening midventrally. Eggs thin-shelled, operculate, embryonated. In marine teleosts. Chile. Type-species *A. chilensis* (Riggenbach, 1896).

14b. Scolex otherwise ..... 15.

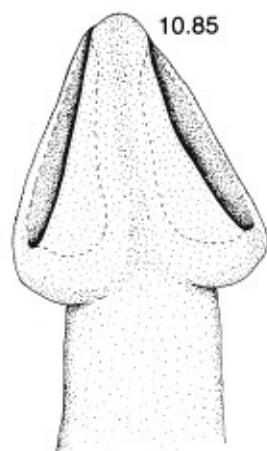
15a. Vitelline follicles in lateral bands .....  
*Bathybotrium* Lühe, 1902. (Figs 10.85–10.87)

**Diagnosis:** Scolex oval to heart-shaped, no apical disc. External segmentation distinct. Reproductive organs single. Genital pores lateral, alternating irregularly. Testes numerous, lateral fields unite anterior to ovary. Cirrus-sac large. Cirrus unarmed. Ovary irregular, median. Uterus lobulate, median, pre-ovarian. Uterine pore median or slightly poral. Vitelline follicles few, in medulla. Osmoregulatory canals? In cyprinids. Type-species *B. rectangulum* (Bloch, 1782).

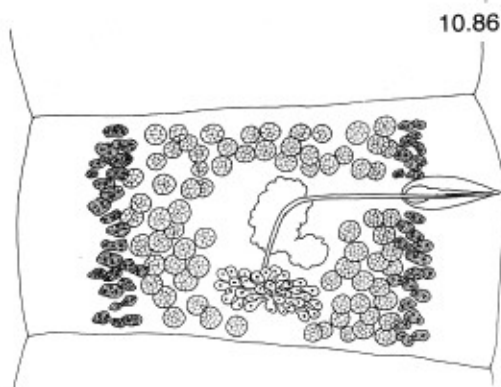
15b. Vitelline follicles surrounding proglottid .....  
*Fissurobotrium* Roitman, 1965. (Figs 10.88–10.90)



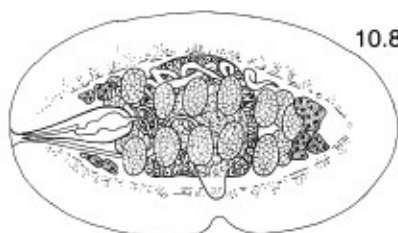
**Figs 10.83, 10.84** *Anonchocephalus chilensis* (Riggenbach, 1896). 10.83. Scolex (after Riggenbach, 1895). 10.84. Mature proglottid.



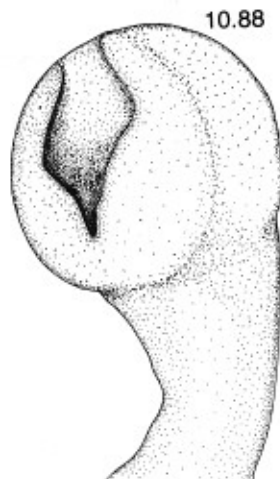
10.85



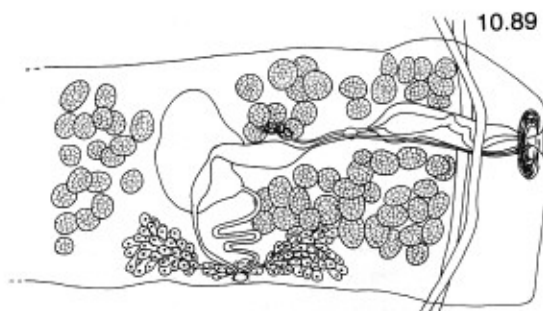
10.86



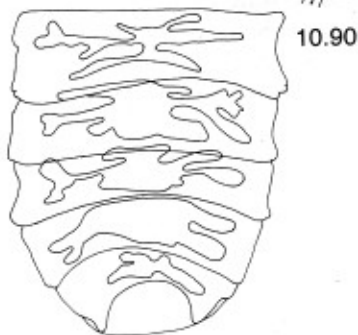
10.87



10.88



10.89



10.90

**Figs 10.85-10.87** *Bathybothrium rectangulum* (Bloch, 1782). 10.85. Scolex. 10.86. Mature proglottid. 10.87. Transverse section of mature proglottid, modified after Nybelin (1922).

**Figs 10.88-10.90** *Fissurobothrium unicum* Roitman, 1965. 10.88. Scolex. 10.89. Mature proglottid, aporal extremity and vitelline follicles omitted. 10.90. Terminal proglottids, showing uterine configuration. All modified after Roitman (1965).

**Diagnosis:** Scolex rounded, no apical disc. Bothria deep, sucker-like. External segmentation present. Genital pores lateral, [alternating?]. Cirrus-sac present. Cirrus unarmed. Testes numerous, in two lateral fields. Ovary symmetrical, lobed, median. Uterus with large lateral branches. Uterine pore slit-like. Vitelline follicles medullary. Osmoregulatory canals four. In cyprinids. Type-species *F. unicum* Roitman, 1965.

**16a. Scolex sagittate. Vitelline follicles confined to posterior half of proglottid** ..... *Eubothrioides* Yamaguti, 1952. (Figs 10.91, 10.92)

**Diagnosis:** Scolex unarmed. Bothria elongated; margins may be slightly crenulated. Neck absent. External metamerism distinct. Strobila fleshy. Proglottids imbricated, trapezoidal, much wider than long. Genital pore marginal, slightly postequatorial. Cirrus-sac small, not extending into medulla. Cirrus unarmed. Testes in two narrow lateral fields medial to nerve cords. Ovary posterior, slightly poral, transversely elongated, not distinctly bialate. Vagina dorsal or ventral to cirrus-sac. Vitelline follicles cortical, diffuse. Uterus in mid-field; uterine sac small, opens midventrally near anterior margin of proglottid. Eggs operculate, elongated pyriform with attenuated end inclined to one side; partly embryonated. In marine teleosts (*Zenopsis nebulosa*). Japan. Type-species *E. lamellatus* Yamaguti, 1952.

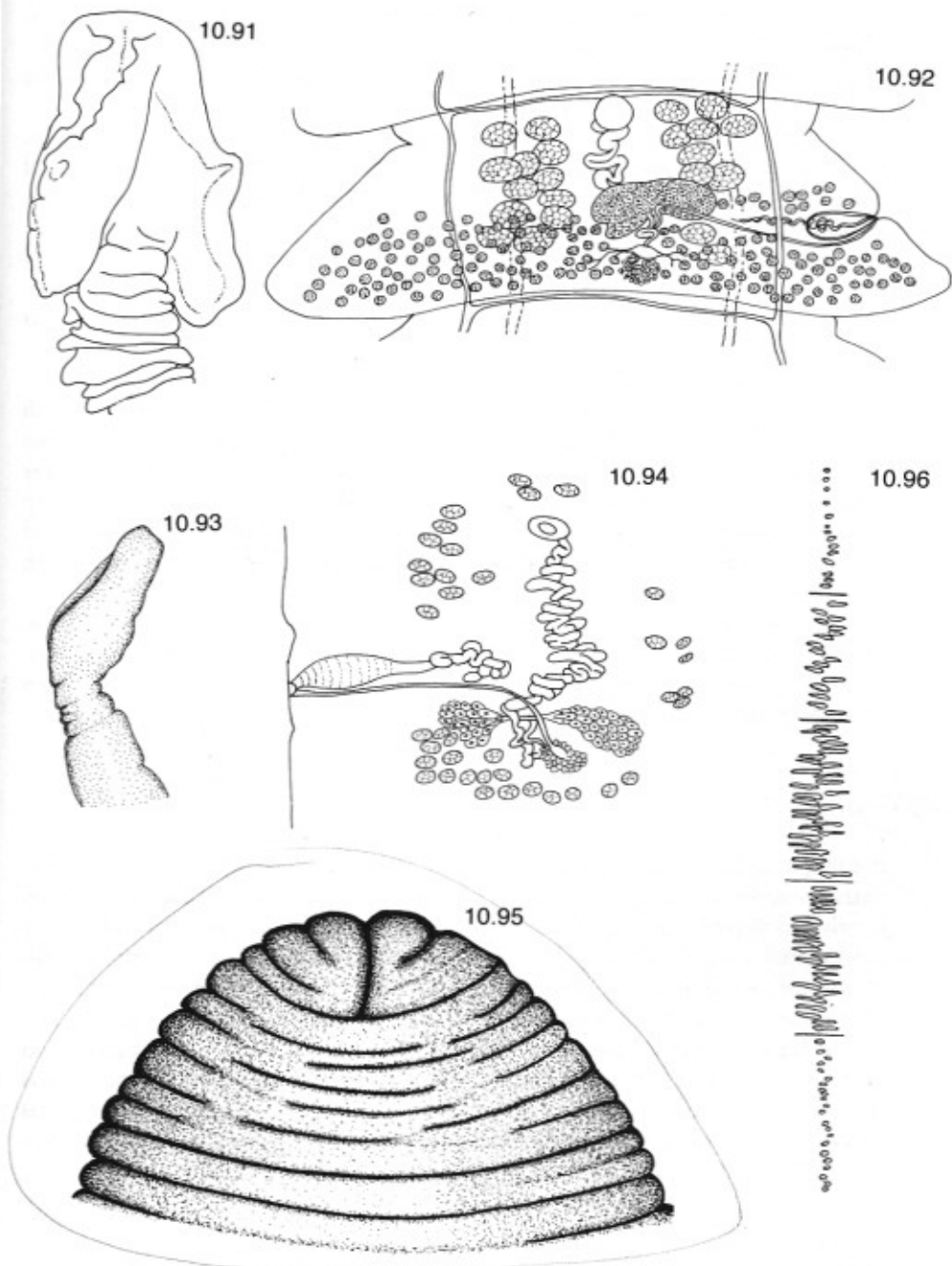
**16b. Scolex not sagittate. Vitelline follicles continuous longitudinally** .....  
..... *Probothriocephalus* Campbell, 1979. (Figs 10.93, 10.94)  
(Syns *Heterovitellus* Protasova & Parukhin, 1986; *Partitiotestis* Protasova & Parukhin, 1986; *Flexiphallus* Protasova & Parukhin, 1986.)

**Diagnosis:** Scolex conical to elongate, no apical disc. Bothria shallow, weak with wide apertures. External segmentation distinct or indistinct, secondary wrinkles may occur. Genital pores postequatorial, alternating irregularly. Testes numerous, in two widely-separated medullary fields, confluent medially posterior to ovary. Cirrus-sac small to large, not reaching mid-line. Ovary bilobed, poral. Vagina thin-walled. Uterus coiled tubular proximally, saccular distally, may intrude into preceding proglottid when gravid. Uterine pore median. Eggs operculate or not, unembryonated, may have tubercle at poles. Vitelline follicles circumcortical, occasionally also between muscle bundles, continuous longitudinally. In deep-water teleosts. Type-species *P. muelleri* Campbell, 1979.

## Family Diphylobothriidae Lühe, 1910

(Syn. Dibothriocephalidae Lühe, 1902)

The family name Diphylobothriidae was established by Lühe (1910) as a substitute for his family Dibothriocephalidae erected in 1902. The family was originally meant to contain a number of forms similar to the long-known broad tapeworm of man – first described as *Taenia lata* by Linnaeus (1758) which was also the type-species of the family. However, due to priority rules when changing the family name in 1910, the relatively unknown and unsatisfactorily described *Diphylobothrium stemmacephalum* Cobbold, 1858 from porpoise became the type-species of the family.



**Figs 10.91, 10.92** *Eubothrioides lamellatus* Yamaguti, 1952. 10.91. Scolex. 10.92. Mature proglottid. After Yamaguti (1952).

**Figs 10.93, 10.94** *Probothrioccephalus muelleri* Campbell, 1979. 10.93. Scolex. 10.94. Mature proglottid. Both after Campbell (1979).

**Figs 10.95, 10.96** *Ligula intestinalis* (Linnaeus, 1758). 10.95. Anterior end of plerocercoid, after Cooper (1918). 10.96. Schematic representation of genital primordia, after Dubinina (1966).

The descriptions of *Tetragonoporus* Skryabin, 1961 and *Polygonoporus* Skryabin, 1967 show many characters similar to *Diplogonoporus* Lönnberg, 1872. They are synonymized with *Diplogonoporus* until better descriptions may prove otherwise. They are all parasites of cetaceans.

*Adenocephalus* Nybelin, 1931, *Cordicephalus* Wardle, McLeod & Stewart, 1947 and *Flexobothrium* Yurakhno, 1988 are all regarded as synonyms of *Diphyllobothrium*. Presently, no characters can be found which justify generic separation between them.

*Capooria* Malhotra, 1985 superficially resembles members of the family Bothriocephalidae. The characters employed to allocate it to the Diphyllobothriidae require confirmation. Pending a redescription, it is treated here as a *genus inquirendum*.

*Pyramicocephalus* Monticelli, 1890 is also synonymized with *Diphyllobothrium*. Monticelli founded the genus on small wrinkled plerocercoids with scoleces with deep marginal bothrial grooves, found in some marine fish species but the adult worm, so far, lacks a distinct description. A few *Diphyllobothrium* species exist (e.g. *D. hians* from the same host) which possess scoleces with deep marginal bothrial grooves and crenulated bothrial edges. Due to the lack of a good description of the adult worm, *Pyramicocephalus* is synonymized with *Diphyllobothrium*.

*Spirometra* Faust, Campbell & Kellogg, 1929 is recognized as a valid genus, although some, e.g. Schmidt (1986), synonymized it with *Diphyllobothrium*. There are, however, enough morphological and life-cycle differences between them to justify separation at generic level.

### Family diagnosis

Pseudophyllidea. Strobila medium to large, usually acraspedote, anapolytic. External segmentation complete or not. Scolex of various shapes, occasionally poorly developed. Bothria usually well developed, of various shapes; occasionally represented only by shallow slits; rarely hypertrophied. Osmoregulatory canals cortical or medullary, numerous or not. Reproductive organs usually single, may be double or occasionally multiple. Testes numerous, medullary. Cirrus-sac present. Ovary posterior. Male and female ducts open together or separately on midventral surface. Vitelline follicles cortical, may intrude between longitudinal muscle bundles. Uterus of various shapes, opens ventrally, posteriorly to genital pore(s). Larval stages in fish, reptiles and occasionally other groups. Adults in reptiles, birds and mammals. Type-genus *Diphyllobothrium* Cobbold, 1858.

### Key to genera

- 1a. External segmentation confined to anterior portion of strobila ..... 2.
- 1b. External segmentation complete throughout strobila ..... 3.

- 2a. One set of reproductive organs per proglottid .....  
 ..... *Ligula* Bloch, 1782. (Figs 10.95, 10.96)  
 (Syn. *Braunia* Leon, 1908.)

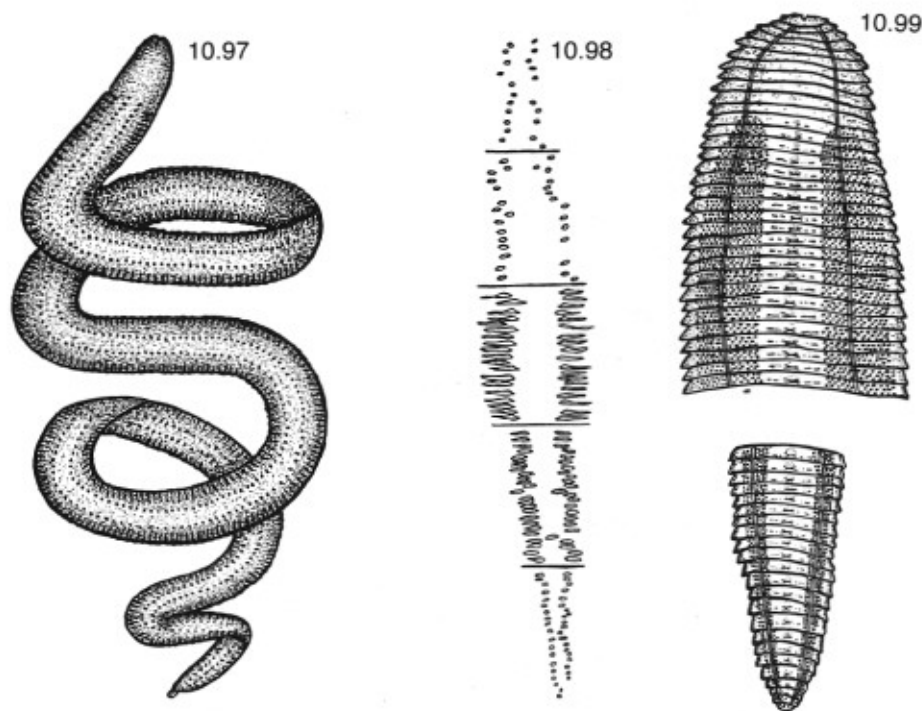
**Diagnosis:** Fleishy worms up to 400 mm long by 7–8 mm wide. Anterior portion of strobila segmented, rest unsegmented but transversely wrinkled. Anterior end of strobila bluntly pointed with poorly developed scolex; bothria represented only by two shallow tiny slits. One set of reproductive organs per proglottid. Adults in fish-eating birds. Large fleshy plerocercoids in body-cavity of cyprinids. Circumboreal. Type-species *L. intestinalis* (L., 1758).

- 2b. Two sets of reproductive organs per proglottid .....  
 ..... *Digramma* Cholodkowsky, 1915. (Figs 10.97, 10.98)

**Diagnosis:** As *Ligula* except two sets of genitalia per proglottid. Type-species *D. alternans* (Rudolphi, 1810).

- 3a. Scolex poorly developed, bothria represented only by two tiny slits in anterior-most part of strobila ..... *Schistocephalus* Creplin, 1829. (Fig. 10.99)  
 (Syn. *Schistorhynchus* Zschokke, 1896.)

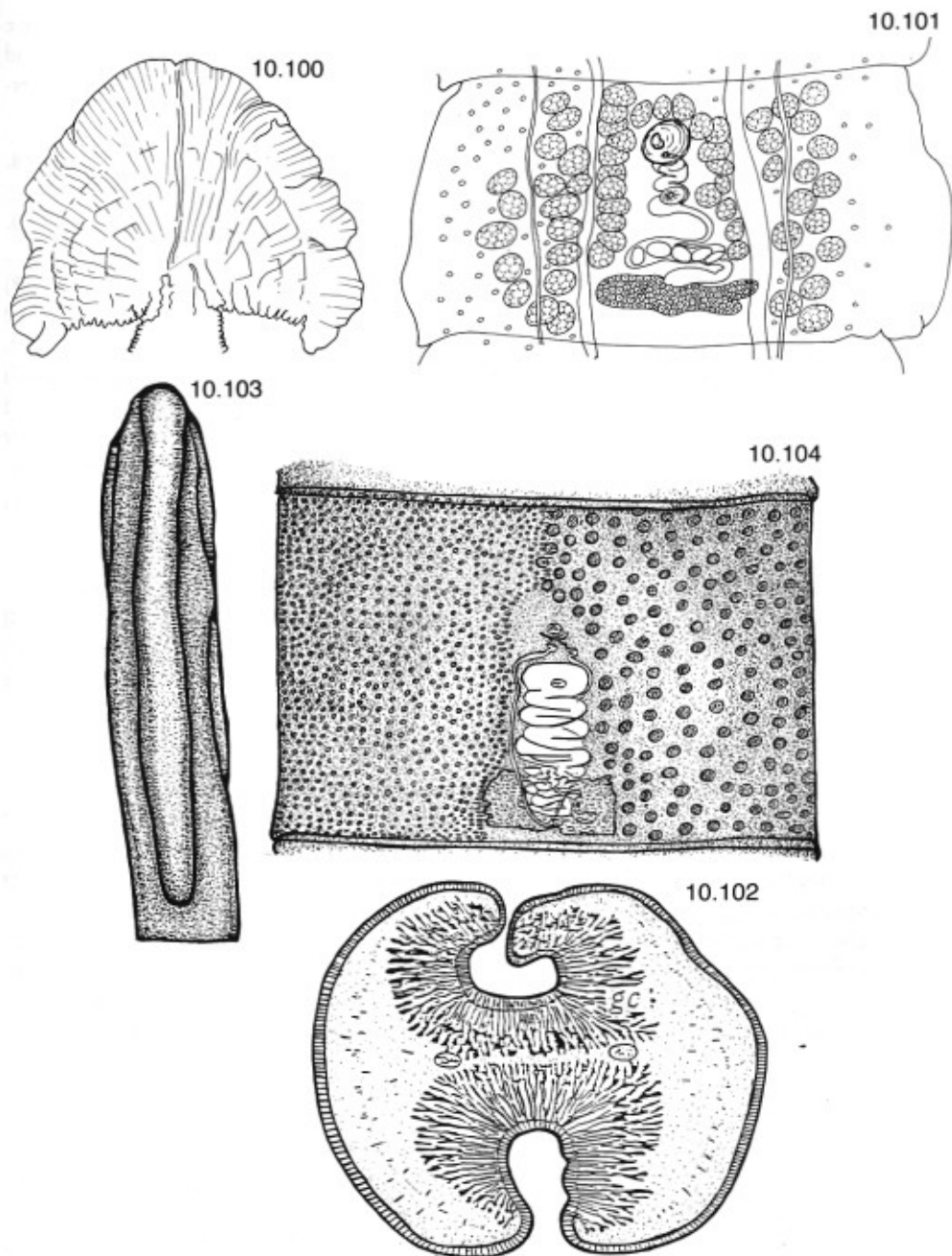
**Diagnosis:** Fairly small and lanceolate worms, maximum length around 200 mm. Proglottids wider than long and distinctly craspedote. Well-developed



**Figs 10.97, 10.98** *Digramma interrupta* (Rudolphi, 1810). 10.97. Plerocercoid, after Chen (1973). 10.98. Schematic representation of genital primordia, after Dubinina (1966).  
**Fig. 10.99** *Schistocephalus solidus* (Müller, 1776). After Dubinina (1966).

parenchymal longitudinal muscles. Adults in fish-eating birds. Large segmented plerocercoids in body-cavity of sticklebacks and other small freshwater fish. Type-species *S. solidus* (Müller, 1776).

- 3b. Scolex distinct and well developed ..... 4.
- 4a. Scolex broad and fan-like, bothrial margins frilled or crenulated .....  
 ..... *Duthiersia* Perrier, 1873. (Figs 10.100, 10.101)  
**Diagnosis:** Small worms not exceeding 200 mm in length. Posterior bothrial apertures present in Asiatic forms, absent in African forms. Vaginal sphincter present; vagina opens behind cirrus-sac. Uterus tubular, laterally looped and rosette-like. In varanid lizards in south eastern Asia and Africa. Type-species *D. expansa* Perrier, 1873.
- 4b. Scolex more or less spoon-shaped with two distinct bothria, bothrial edges usually plain, no inrolling of bothrial edges ..... 5.
- 4c. Scolex modified ..... 10.
- 5a. Proglottids very craspedote. Vitelline follicles cortical as single layer in wing-like expansions ..... *Glandicephalus* Fuhrmann, 1921. (Fig. 10.102)  
**Diagnosis:** Fairly small worms around 200 mm long. Strobila thick, external metamerism well marked, proglottids with wing-like expansions. Testes in single layer. Uterus strongly serpentine. In Antarctic seals. Type-species *G. antarcticus* (Blair, 1853).
- 5b. Normal segmentation ..... 6.
- 6a. Cirrus-sac composite, dorsal portion representing external seminal vesicle of other genera .....  
 ..... *Spirometra* Faust, Campbell & Kellogg, 1929. (Figs 10.103, 10.104)  
**Diagnosis:** Scolex spoon- or finger-like in marginal outline with bothria fading indefinitely into mid-dorsal and mid-ventral furrows of strobila. Usually medium sized worms, weakly muscular, distinct neck. Uterus simple spiral of closely appressed coils, widening into sac before uterine pore. Eggs pointed at both ends. Adults mainly in cat-like carnivores, occasionally in canids and humans. Plerocercoids (spargana) in all vertebrate groups except fish. Circumtropical and subtropical but also in USA and southern Europe. Type-species *S. erinaceieuropaei* (Rudolphi, 1819).
- 6b. Cirrus-sac and seminal vesicle separate ..... 7.
- 7a. Usually only one set of reproductive organs per proglottid .....  
 ..... *Diphyllbothrium* Cobbold, 1858. (Figs 10.105–10.107)  
 (Syns *Adenocephalus* Nybelin, 1931; *Cordicephalus* Wardle, McLeod & Stewart, 1947; *Diancyrobothrium* Bacigalupo, 1945; *Dibothriocephalus* Lühe, 1899; *Flexobothrium* Yurakhno, 1988; *Gatesius* Stiles, 1908; *Lueheella* Baer, 1924; *Pyramicocephalus* Monticelli, 1890.)  
**Diagnosis:** Worms of various sizes. Scolex with two distinct bothria. Vitelline follicles numerous in single layer continuous across proglottids. Uterus with



**Figs 10.100, 10.101** *Duthiersia fimbriata* (Diesing, 1850). 10.100. Scolex. 10.101. Mature proglottid.

**Fig. 10.102** *Glandicephalus antarcticus* (Blair, 1853). Scolex in transverse section, showing glands. After Fuhrmann (1920b).

**Figs 10.103, 10.104** *Spirometra erinaceieuropaei* (Rudolphi, 1819). 10.103. Scolex. After Meggitt (1924b). 10.104. Mature proglottid. After Faust, Campbell & Kellogg (1929).

several loops which may be parallel or rosette-shaped. Testes usually in single layer. Parenchymal muscles fairly well developed. Adults in fish-eating birds and mammals (terrestrial and marine). Plerocercoids in fish. Type-species *D. stem-macephalum* Cobbold, 1858.

7b. Two or more sets of reproductive organs per proglottid ..... 8.

8a. Not more than two sets of reproductive organs per proglottid ..... 9.

8b. More than two sets of reproductive organs per proglottid .....

..... *Hexagonoporus* Gubanov in Delyamure, 1955. (Fig. 10.108)

(Syns *Polygonoporus* Skryabin, 1967; *Tetragonoporus* Skryabin, 1961.)

**Diagnosis:** Strobila up to 30 m long. Apical disc fleshy; unlobed. Bothria short, fleshy. Strobila expands rapidly behind scolex, then narrows. Proglottids much wider than long. Four to 14 pairs of reproductive organs per proglottid, arranged side by side. External seminal vesicle present. Ovary bilobed, transversely elongated. Vitelline follicles cortical. Uterus with five to seven loops on each side. In cetaceans. Antarctica. Type-species *H. physeteris* Gubanov in Delyamure, 1955.

9a. Osmoregulatory canals cortical, not numerous .....

..... *Diplogonoporus* Lönnberg, 1892. (Figs 10.109, 10.110)

(Syn. *Krabbea* Blanchard, 1894.)

**Diagnosis:** Very large worms with weak musculature. Proglottids short and very wide. Large seminal vesicle. Uterine coils parallel or rosette-shaped. In cetaceans. Type-species *D. balaenopterae* Lönnberg, 1899.

9b. Osmoregulatory canals medullary, numerous (35 to 70) .....

..... *Multiductus* Clarke, 1962. (Figs 10.111–10.113)

**Diagnosis:** Strobila long (up to 18 m), proglottids numerous, craspedote. Scolex globular, bothria deep. Two layers of longitudinal muscle fibres, inner layer always arranged in bundles, outer layer in bundles in some regions. Osmoregulatory canals connected by anastomoses. Two sets of genitalia, symmetrically placed. Testes medullary, in more than one layer. Vitelline follicles cortical, between longitudinal muscle layers. Uterine sac and uterine duct present. In sperm whale. Antarctica. Type-species *M. physeteris* Clarke, 1962.

10a. Scolex with fused bothrial edges ..... 11.

10b. Scolex otherwise ..... 12.

11a. Bothria forming cups ..... *Baylisia* Markowski, 1952. (Fig. 10.114)

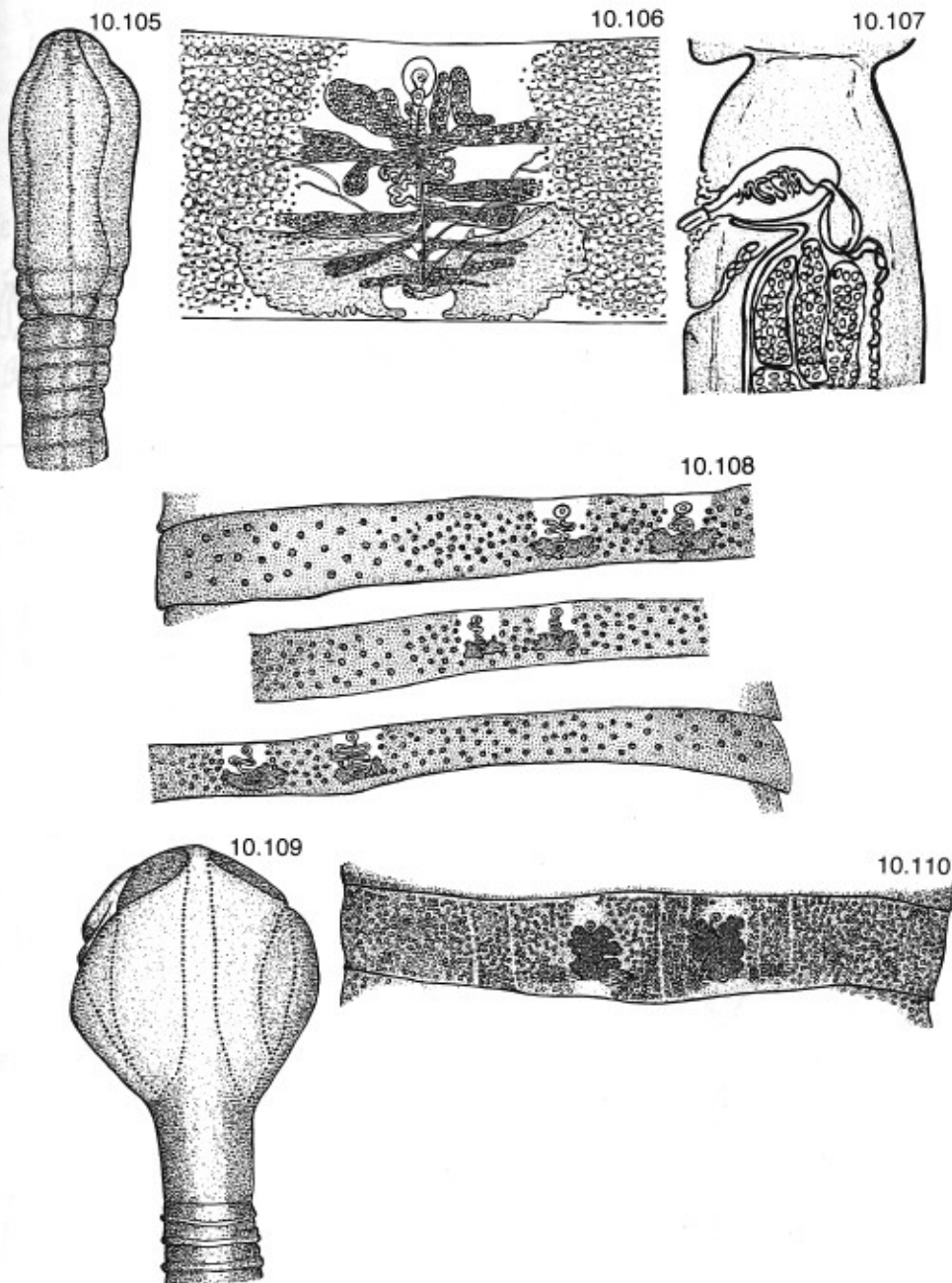
**Diagnosis:** Scolex short with two cup-shaped bothria. Inner longitudinal and transverse muscles strongly developed. Two sets of reproductive organs per proglottid. In crabeater seal. Antarctic. Type-species *B. baylisi* Markowski, 1952.

11b. Bothria forming tubes .....

..... *Botbridium* Blainville, 1824. (Figs 10.115, 10.116)

(Syns *Prodictoelia* Leblond, 1836; *Solenophorus* Creplin, 1839.)

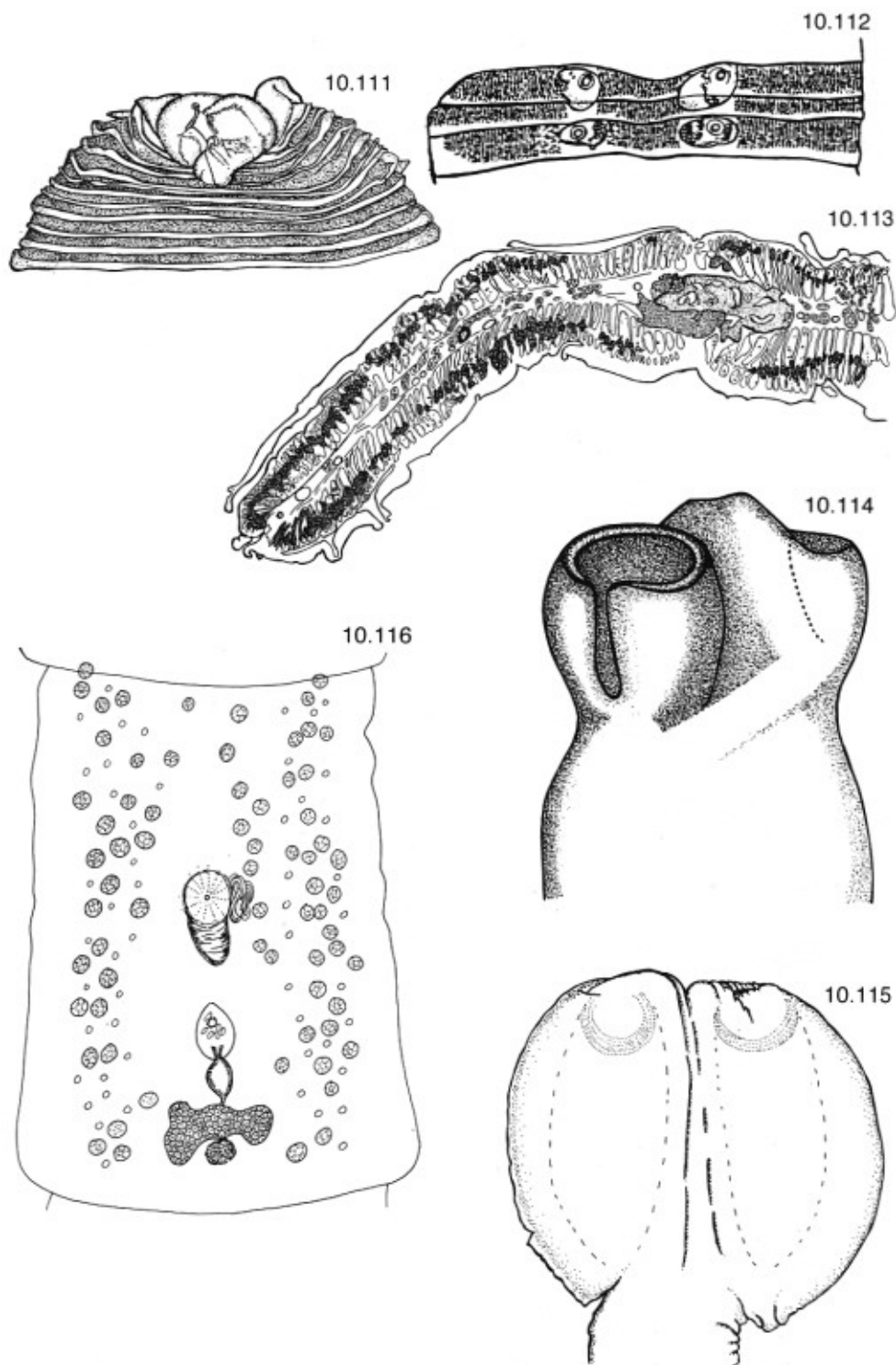
**Diagnosis:** Moderate-sized worms up to 500 mm long by 6 mm wide. Strobila with numerous short proglottids. Uterus with thick duct and dorsal sac. Testes

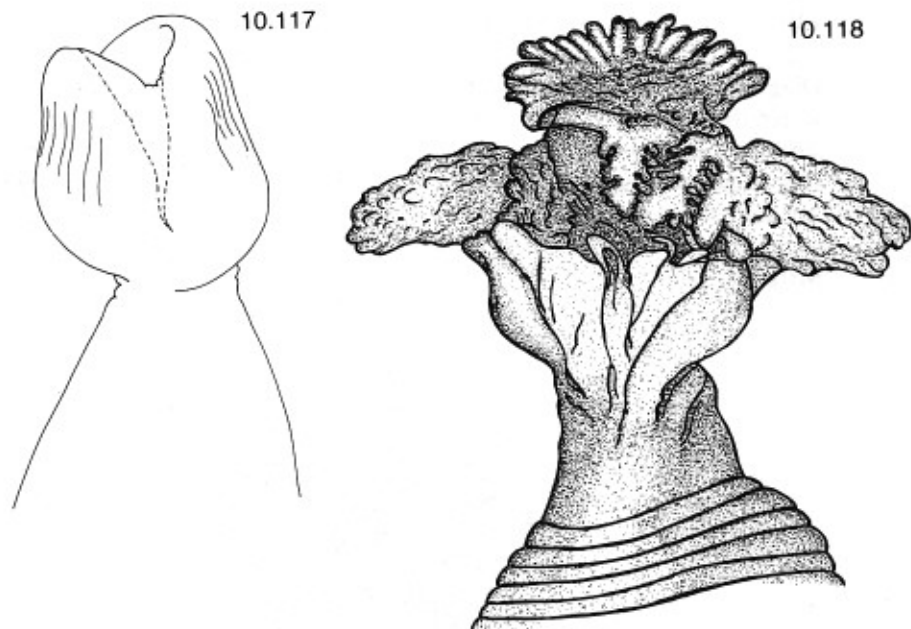


**Figs 10.105-10.107** *Diphyllobothrium latum* (Linnaeus, 1758). 10.105. Scolex. 10.106. Mature proglottid, central region. 10.107. Relationships of terminal genital ducts in sagittal section. After Rausch & Hilliard (1970).

**Fig. 10.108** *Hexagonoporus physeteris* Gubanov in Delyamure, 1955. Mature proglottid. After Gubanov in Delyamure (1955).

**Figs 10.109, 10.110** *Diplogonoporus balaenopterae* (Lönnerberg, 1891). 10.109. Scolex. After Delyamure (1955). 10.110. Mature proglottid. After Yamaguti (1942).





**Figs 10.111-10.113** *Multiductus physeteris* Clarke, 1962. 10.111. Scolex. 10.112. Mature proglottids. 10.113. Transverse section of half of a mature proglottid. After Clarke (1962).  
**Fig. 10.114** *Baylisia baylisi* Markowski, 1952. Scolex. After Markowski (1952).  
**Figs 10.115, 10.116** *Bothridium pithonis* Blainville, 1824. 10.115. Scolex. 10.116. Mature proglottid.  
**Fig. 10.117** *Scyphocephalus secundus* Tubangui, 1938. Scolex. After Tubangui (1938).  
**Fig. 10.118** *Baylisiella tecta* (Linstow, 1892). Scolex. After Markowski (1952).

in two lateral bands. In boid snakes and varanid lizards. Africa, Sri Lanka, India and Philippines. Type-species *B. pithonis* Blainville, 1824.

12a. Bothria hypertrophied to form many complex folds ..... 13.

12b. Anterior end of scolex invaginated to form sucking organ; bothria rudimentary ..... *Scyphocephalus* Riggenbach, 1898. (Fig. 10.117)

**Diagnosis:** Proglottids wider than long. Genital pore median, pre-equatorial. Testes numerous, confluent medially in anterior and posterior regions of proglottid. Cirrus-sac occupies entire depth of medulla. Ovary bilobed, posterior. Seminal receptacle present. Vaginal opening posterior to that of cirrus-sac. Vitelline follicles circumcortical. Uterus with few coils. In varanid lizards. Southeast Asia. Type-species *S. bisulcatus* Riggenbach, 1898.

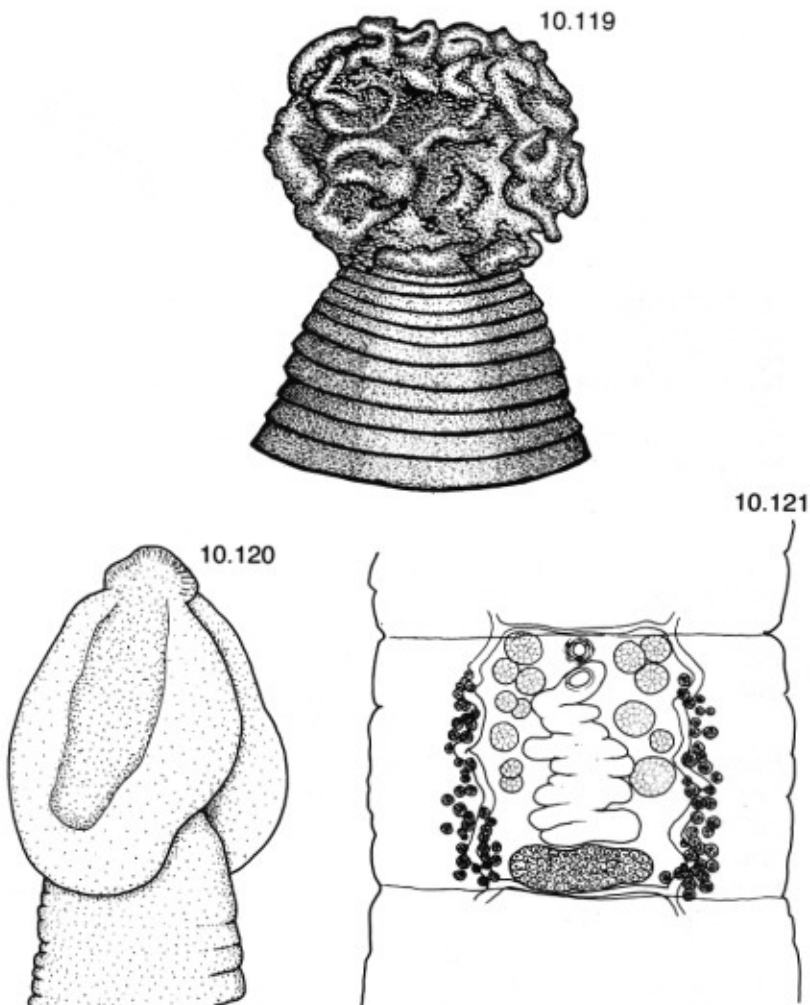
13a. Anterior bothrial margins expanded to form cauliflower-like apical organ ..... *Baylisiella* Markowski, 1952. (Fig. 10.118)

**Diagnosis:** Scolex usually embedded deep in intestinal wall of host. Strobila thick, tapering towards end. Proglottids short and wide. Testes in two or three layers. In elephant seals. Antarctic. Type-species *B. tecta* (Linstow, 1892).

13b. All of bothria hypertrophied to form many complex folds .....

..... *Plicobothrium* Rausch & Margolis, 1969. (Fig. 10.119)

**Diagnosis:** Strobila muscular with many proglottids (more than 6000) all much wider than long. Arrangement of proglottids in sequential groups throughout strobila indicates multiplication by transverse division of primary segment. Two sets of genital organs in tandem position, sometimes present in segments not divided externally. Testes and vitelline follicles in separate lateral fields. Large cirrus-sac. In cetaceans. Atlantic. Type-species *P. globicephalae* Rausch & Margolis, 1969.



**Fig. 10.119** *Plicobothrium globicephalae* Rausch & Margolis, 1969. Scolex. After Rausch & Margolis (1969).

**Figs 10.120-10.121** *Cephalochlamys namaquensis* (Cohn, 1906). 10.120. Scolex. 10.121. Mature proglottid.

**Family Cephalochlamydidae Yamaguti, 1959****Family diagnosis**

Pseudophyllidea. Scolex like an arrowhead, with two (dorsal and ventral) elongated bothria united at apex. Neck distinct. Segmentation apparent after appearance of genitalia. Inner longitudinal musculature well developed. Longitudinal osmoregulatory canals connected by transverse canal in posterior region of each proglottid. Few testes, in medulla, arranged in two submedian groups anterior to ovary. No cirrus-sac. Male aperture joins vagina at base of genital atrium, which opens ventrally in median line near anterior border of proglottid. Ovary bilobed or entire, situated posteriorly in proglottid. Vitelline follicles extend length of proglottid in two lateral fields of cortex, and may converge posteriorly. Uterus in transverse slings between longitudinal osmoregulatory vessels anterior to ovary; ventral uterine pore posterior to genital atrium. Eggs thin-shelled, embryonated, not operculate. Parasites of the intestine of anurans and caudates. Type and only genus *Cephalochlamys* Blanchard, 1908.

**Genus *Cephalochlamys* Blanchard, 1908 (Figs 10.120, 10.121)**

(Syns *Chlamydocephalus* Cohn, 1906, *nec* Diesing, 1850, *nec* Schmarida, 1859; *Pseudocephalochlamys* Yamaguti, 1959)

**Diagnosis:** With characters of family. Type-species *C. namaquensis* (Cohn, 1906).