
8 Order Tetrphyllidea Carus, 1863

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Introduction

A historical account of the systematics of the cestodes of selachians would be too long to give here. It may be found in the monograph by Southwell (1925) or in the text by Wardle & McLeod (1952). I remark simply that the individuality of these parasites was recognized as early as 1850 by van Beneden. At this date, this author grouped together under the name 'Tetrphyllides' the 'phyllobothriens' and 'phylacanthis' (currently in the Tetrphyllidea) and the 'phyllobothriens' (currently Trypanorhyncha). The last were separated by Diesing (1863) into a distinct order.

The initial subdivision by van Beneden into the 'phyllobothriens' (now the Phyllobothriidae) and the 'phylacanthis' (now the Onchobothriidae) is to be found in almost all the subsequent works on the systematics of the order Tetrphyllidea.

A third family, the Lecaniccephalidae Braun, 1900 (Gamobothriidae Linton, 1901) was added to the first two. It is roughly this subdivision of the order into three families which is found in the work of Southwell (1925), although the Lecaniccephalidae (in which the scolex has four round suckers) was placed in the Cyclophyllidea. Since 1930, new families and orders have been proposed to define the systematics of the Tetrphyllidea.

The family Disculicipitidae Joyeux & Baer, 1936 was erected to replace the Discocephalidae Pintner, 1928, preoccupied. Joyeux & Baer (1936a) proposed the generic name *Disculiceps* in place of *Discocephalum* with, as type-species, *Disculiceps pileatum* (Linton, 1890), synonym *Discocephalum pileatum* Linton, 1890. This amendment appears to be in conformity with Article 55(b) of the *International Code of Zoological Nomenclature*, but has apparently not been submitted for a decision by the appropriate Commission. Pending this, we will conserve *Disculiceps* and the family Disculicipitidae Joyeux & Baer, 1936.

In 1952, Wardle & McLeod elevated some families to ordinal rank. The

classification of the Tetrphyllidea at that time was as follows:

Tetrphyllidea Carus, 1863: Phyllobothriidae Braun, 1900; Onchobothriidae Braun, 1900.

Disculicipitidea Wardle & McLeod, 1952: Disculicipitidae Joyeux & Baer, 1936.

Lecanicephala Wardle & McLeod, 1952: Lecanicephalidae Braun, 1900; Cephalobothriidae Pintner, 1928.

In 1959, Euzet completed a classification of the Tetrphyllidea proposed as a draft in 1953. Subsequent work has shown that the criteria utilized did not have the significance previously attributed to them. In particular, assembling in the superfamily Prosobothrioidea the families Prosobothriidae, Platybothriinae, Phoreiobothriidae, Reesiinae and Gastroleicithidae is artificial. This classification should be abandoned.

Yamaguti (1959) erected the family Triloculariidae with *Trilocularia* Olsson, 1867 as type-genus. This parasite of *Squalus acanthias* (L., 1758) does in fact present a very singular arrangement of the genital system. In my opinion, this anatomy is a direct consequence of the fact that *Trilocularia acanthiaevulgaris* (Olsson, 1867) is a hyperapolytic species. This anatomy, which is close to that found in the proglottid of *Potamotrygonocestus magdalenensis* Brooks & Thorson, 1976, is not fundamentally different from that of the phyllobothriid tetrphyllideans.

Schmidt (1986) added to the Triloculariidae the genera *Pentaloculum* Alexander, 1963, a parasite of *Typhlonarke aysoni* (Hamilton, 1902) (Torpedinidae) and *Zyxibothrium* Hayden & Campbell, 1981, a parasite of *Raja senta* Garman, 1885 (Rajidae). These three genera do not appear to have much in common except the scolex, in which the four bothridia have a surface divided by muscular septa and a small number of loculi. Although in my opinion these three genera do not constitute a natural group, I have retained them together but in the subfamily Triloculariinae Yamaguti, 1959, which I place in the Phyllobothriidae.

After 1960, some new genera have been classified in new families of the Tetrphyllidea, or the same taxa have been placed in distinct orders. These are, in chronological order: *Litobothrium* Dailey, 1969, family Litobothriidae Dailey, 1969, order Litobothriidae Schmidt, 1986; *Dioecotaenia* Schmidt, 1969, family Dioecotaeniidae Schmidt, 1969, order Dioecotaeniidea Schmidt, 1986; *Cathetocephalus* Dailey & Overstreet, 1973, family Cathetocephalidae Dailey & Overstreet, 1973; and *Chimaerocestos* Williams & Bray, 1984, family Chimaerocestidae Williams & Bray, 1984.

In all these cestodes, one finds the characters of the Tetrphyllidea, whether in morphology of the scolex or in the anatomy of the genital system. I propose to maintain them within the Tetrphyllidea but, in recognition of their uniqueness, to distinguish them at family level.

Comments on controversial genera are given below.

Family Onchobothriidae Braun, 1900

The systematic position of the genera *Ceratobothrium* Monticelli, 1892 and *Thysanocephalum* Linton, 1890 which many authors have placed in the

Onchobothriidae will be discussed below. I have placed them in the Phyllobothriidae.

Balanobothrium Hornell, 1912. Fuhrmann (1931) gave an excellent illustration of the scolex of *B. parvum*, which he placed in the Onchobothriidae. The anterior part of the scolex, sunken into the intestinal wall of the host, forms a globular mass within which one can, however, distinguish four bothridia each marked by an anterior sucker and a pair of minute forked hooks. The posterior part of the scolex forms a sort of collar representing the free part of the four bothridia. After Fuhrmann (1931), authors were divided in their opinions on the systematic position of *Balanobothrium*. Yamaguti (1959) and Schmidt (1986) maintained it in the Lecanicephalidae; Perrenoud (1931), Wardle & McLeod (1952) and Joyeux & Baer (1961) placed it in the Onchobothriidae. Baer & Euzet (1962), having examined Southwell's material, were of the second opinion.

Cylindrophorus Diesing, 1863. Euzet (1952) discussed the validity of this genus erected by Diesing (1863) from the illustration given by Wagener (1854) of *Tetrabothrium aus Charcharias rondeletii*. It has been recognized (Cohn, 1902a; Mola, 1903) that these diagrams represent two different tetrabhyllideans. One, *Prosobothrium* Cohn, 1902 has an unarmed scolex; the other, *Platybothrium* Linton, 1890 has a scolex with bothridia armed with characteristic hooks. The genus *Cylindrophorus*, not having a type-species, represents a *nomen nudum* and should disappear from the nomenclature.

Phyllobothroides Southwell, 1911. This generic name was used by Southwell (1911) for *P. kerkhami*, a parasite of *Chiloscyllium indicum*. Southwell (1925) synonymized this species with *Pedibothrium longispine* Linton, 1909. *Phyllobothroides* Southwell, 1911 falls into synonymy with *Pedibothrium* Linton, 1909.

Pinguicollum Riser, 1955. Riser (1955) created this genus for *Onchobothrium pinguicollum* Sleggs, 1927. The host is a *Raja* sp. caught on the Pacific coast of California. Hart (1936) described under the name *Pedibothrium pinguicollum* an onchobothriid collected from *Raja binoculata* Girard, 1854 in Puget Sound (Pacific coast of the USA). He assigned this parasite to the species described by Sleggs but placed it in the genus *Pedibothrium* Linton, 1909. This generic attribution was seriously doubted by Wardle & McLeod (1952). Riser (1955) found, on the Pacific coast of the USA in several species of *Raja* (including *R. binoculata*), a common onchobothriid which he compared with the species described by Sleggs and recovered by Hart. Riser made this species the type of the new genus *Pinguicollum*. It differs from *Acanthobothrium* in having 'the hooks fused in a common matrix, immobile phyllidia and a pseudoscolex'. The definition of this pseudoscolex has not been determined and the presence of a special structure at the level of the scolex is not evident in the illustration of *Pinguicollum pinguicollum* by Riser. The special morphology of the scolex of this cestode probably results from its being embedded in the wall of the spiral intestine. The fact

that the bothridial hooks are united into one structure (matrix) does not seem to be a genuine character. In species of *Acanthobothrium*, the base of the hooks is always close and sometimes united (for example, in *A. confusum* Baer & Euzet, 1962). It does not seem useful to create a genus for this single character. I consider *Pinguicollum* Riser, 1955 synonymous with *Acanthobothrium* van Beneden, 1849.

Spiniloculus Southwell, 1925. The scolex of the type-species, *S. mavensis* Southwell, 1925, a parasite of *Mustelus* sp., was described as being formed by four bothridia. Each bothridium, divided into two by a transverse septum, is separated from a broad flat muscular anterior region by a cushion bearing a C-shaped hook on its lateral extremities. In an addendum, Southwell (1930a) amended the description of *S. mavensis* from material collected from *Chiloscyllium indicum*. He emphasized that the bothridia are not divided by a transverse septum and that this morphology was found in the bothridia of the type-specimens of *S. mavensis* from *Mustelus* species. Southwell then gave a new diagnosis of the genus. As a result of this, the onchobothriid tetraphyllidean in *Ginglymostoma cirratum* Muller & Henle (Ginglymostomatidae) found at Ratnagiri (India) and named *Spinibiloculus* by Deshmukh & Shinde (1980) comes within the genus *Spiniloculus*. *Spinibiloculus* was differentiated from *Spiniloculus* by having four simple bothridia without a transverse septum. On the other hand, the hooks, situated at the same site in the bothridium, have a similar morphology. The anatomy is very close but the position of the vagina of *Spinibiloculus ratnagiriensis*, given as posterior to the cirrus-sac, should be re-examined. It should be added that Subhadrappa (1957) described *Spiniloculus mavensis*, from *Chiloscyllium griseum* (Muller & Henle, 1841), with bothridia not subdivided by a transverse septum. Williams (1964) and Caira (1987) have already noted the difference between the description by Subhadrappa and that by Southwell. Caira (1990) returned to the problem of the scolex morphology of *Spiniloculus*. She gave a diagnosis detailing it as 'each bothridium divided into 3 loculi with 2 transverse costae, anterior costa conspicuous, posterior costa inconspicuous externally. Each bothridium with a pair of simple, hollow, U-shaped hooks; bases of hooks widely separated; 1 hook on each posterolateral corner of anteriormost loculus'. This diagnosis has not been followed here. The anterior loculus should be regarded as part of the muscular plateau found in front of the hooks in the bothridium of the majority of the Onchobothriidae. The second fold, which is very inconsistent in *Spiniloculus*, corresponds without doubt to the shape of the bothridium when the scolex is attached to the intestinal wall. Its presence is perhaps linked to the area of insertion of the longitudinal musculature on the internal face of the bothridium.

There remains the question of the systematic position of the hosts. *Spiniloculus mavensis* was described from a *Mustelus* sp. from the eastern coast of Australia. It seems that this cestode has not since been seen in a host of this genus. In contrast, *S. mavensis* was reported from *Chiloscyllium indicum* by Southwell (1925), from *C. griseum* by Subhadrappa (1957) and from *Hemisicyllium punctatum* (= *C. punctatum*) by Williams (1964) and Caira (1990).

S. ratnagiriensis (Deshmukh & Shinde, 1980) is an intestinal parasite of *Ginglymostoma concolor* (= *Nebrius ferrugineus*). *Chiloscyllium* and *Ginglymostoma* are classified in the Orectolobiformes. Given this, the presence of *Spiniloculus* in *Mustelus* (Carchariniformes, Triakidae) is doubtful.

I should add that the genera *Chiloscyllium* and *Nebrius* are parasitized by another onchobothriid genus, *Yorkeria* Southwell, 1927, which is an argument in favour of the individuality of the tetracystids of Orectolobiformes.

Acrobothrium Baer, 1948 (*nec* Olsson, 1872). The genus has been synonymized with *Acanthobothrium* van Beneden, 1849 by Yamaguti (1959) and Euzet (1959). The only character separating the two genera, the morphology of the hooks, is not sufficient, this being quite variable in *Acanthobothrium*. Williams (1966b) further specified that the name *Acrobothrium* should not have been used because it had already been used by Olsson, 1872 for another cestode, *Acrobothrium typicum*, a parasite of the teleost *Lota vulgaris* in fresh water. [See Chapter 4.]

Circulobothrium Shinde & Chincholikar, 1975. The type-species, *C. singhi*, was described from a single individual collected from a *Trygon* sp. at Ratnagiri (India). The material appears to be in bad condition. The illustration of the scolex shows only a single hook of peculiar morphology although the authors state in their description 'one pair of hooks per bothridium'. The anatomy of the proglottids appears to be of the tetracystid type although the ovary is not shown. This cestode is not recognizable and cannot be found again because the host species is unknown. A type-specimen does not seem to have been deposited. *Circulobothrium* is regarded as a *genus inquirendum*.

Family Phyllobothriidae Braun, 1900

Subfamily *Thysanocephalinae* Euzet, 1953

Thysanocephalum Linton, 1890. Many authors have placed *Thysanocephalum* in the Onchobothriidae but, in *T. thysanocephalum*, the bothridia have, on the flat anterior region, two small lateral projections. These muscular structures are very different from the sclerified hooks which characterize the Onchobothriidae. For this reason, I retain *Thysanocephalum* in the Phyllobothriidae. The description and illustration of the anterior region of young stages of *T. thysanocephalum* by Subhadrachar (1957) show that the metascolex is, in the beginning, composed of four small simple lobes which form, by folding, the metascolex of the adult. Including all tetracystids with a well-developed metascolex in the subfamily *Thysanocephalinae* is practical but probably artificial. *Thysanocephalum* is a parasite of large sharks of the family Carcharinidae while *Myzocephalus* and *Myzophyllobothrium* are parasites of stingrays (Myliobatidae and Dasyatidae). Of these genera, *Thysanocephalum* is the best known.

Three other genera of tetracystids parasitic in Myliobatiformes have been described as having a metascolex.

Rhoptrbothrium Shipley & Hornell, 1906. This genus has not been retained because it is based on a single immature individual, the anatomy of which is unknown. As Southwell (1925) noted, this parasite of Myliobatidae is close to *Myzocephalus* Shipley & Hornell, 1906, as the bothridia have an anterior sucker. It is treated as a *genus inquirendum*.

Myxophyllobothrium Shinde & Chincholikar, 1981. The genus is characterized by a scolex with four bothridia, each with an anterior sucker and a metascolex with four distinct lobes, highly folded. Apart from the nature of the host, *Trygon sephen* = *Hypolophus sephen* (Forsskal, 1775) which is a dasyatid, nothing separates this genus from *Myzocephalus*, of which I consider it a synonym.

Shindeobothrium Shinde & Chincholikar, 1975. The description of the type-species, *S. indica*, is based on a single individual found in the spiral valve of *Trygon* sp. at Ratnagiri on the west coast of India. This parasite appears to have a small scolex and a metascolex. The resemblance to *Myxophyllobothrium* was noted by Shinde & Chincholikar (1975). However, the description is incomplete and the illustration too poor to allow recognition of this cestode, which has not been found again, the host species being unknown. *Shindeobothrium* should be suppressed and is treated here as a *genus inquirendum*.

Subfamily Echeneibothriinae de Beauchamp, 1905

Discobothrium van Beneden, 1870. The validity of this genus is controversial. For some authorities, *Discobothrium*, type-species *D. fallax* van Beneden, 1870, characterized by a scolex with a large apical myzorhynchus and four round suckers of the acetabulate type, should be placed in the Lecanicephalidae. However, the anatomy (Euzet, 1959; Williams, 1966a), with the vagina anterior to the cirrus-sac and crossing the vas deferens, is of the phyllobothriid type. According to Euzet (1959), who studied live specimens of *D. fallax*, the scolex has a voluminous apical myzorhynchus and the four small bothridia have a loculate surface. The bothridia can be withdrawn into the scolex leaving, on the surface, a round depression which could be taken for an acetabulum. With loculate bothridia and proglottids lacking postvaginal testes, this parasite belongs to *Echeneibothrium* and should be designated *E. fallax* (van Beneden, 1870). This proposal will be retained here. *Discobothrium* is a synonym of *Echeneibothrium*. The remaining species placed in *Discobothrium* should be renamed and their systematic position determined.

Subfamily Phyllobothriinae de Beauchamp, 1905

Many phyllobothriids have been grouped together in this subfamily. If their anatomy is of the tetraphyllidean type, the scolex is extremely varied. It is, moreover, on the morphology of the scolex that the genera are distinguished. It follows that, in certain cases, the state of contraction of this organ is what impedes the generic attribution of a parasite. Among the genera classified in this family, a certain number should no longer be recognized either because they are synonyms of an older genus or because they are inadequately described. Amongst these, the following should be mentioned.

Anthocephalum Linton, 1890. The type-species, *A. gracile* Linton, 1890, a parasite of *Dasyatis centroura* (Mitchill, 1815) has been renamed by Linton (1890) as *Anthobothrium gracile* (Linton, 1890). The scolex consists of four bothridia, each with an anterior accessory sucker and a border marked by a regular row of loculi. It should be placed in *Phyllobothrium*. However, in *Phyllobothrium*, the species name *P. gracile* Wedl, 1855 has been used for a parasite of *Torpedo marmorata*. Southwell (1925) renamed the parasite of *Dasyatis centroura* as *P. centrurum* Southwell, 1925. *Anthocephalum* could be resurrected by grouping together the species currently placed in *Phyllobothrium* which have bothridia with an accessory sucker and a loculated margin, and an anatomy without postvaginal testes on the poral side.

Aocobothrium Mola, 1907. The genus contains one species parasitic in an unknown teleost living in fresh water. Based on the anatomy, particularly the route of the vagina anterior to the cirrus-sac, this cestode would be placed in the Tetracophyllidea. The scolex with four sacciform bothridia opening anteriorly is similar to that of *Scyphophyllidium* Woodland, 1927. I propose to suppress this genus, since the host is not a selachian but an unknown freshwater teleost; it is treated here as a *genus inquirendum*.

Bilocularia Obersteiner, 1913. *B. hyperapolytica* Obersteiner, 1913, the only species of the genus, was considered synonymous with *Calyptrobthrium rigii* Monticelli, 1893 by Euzet (1959). In these two hyperapolytic tetracophyllideans, the morphology of the scolex with a large globular accessory sucker and an anatomy in which the postvaginal testicular field is absent are similar. However, taking into account the generally oioxenous specificity of the Tetracophyllidea, this synonymy is doubtful. *Bilocularia* is said to be a parasite of *Centrophorus granulosus* (Schneider, 1801), while *Calyptrobthrium* has been recovered from *Torpedo nobiliana* Bonaparte, 1835 on both sides of the North Atlantic. Since its discovery, *B. hyperapolytica* has not been found again in the type-host. The genus is considered a *genus inquirendum*.

Biporophyllaeus Subramanian, 1939. The genus was erected with the type *B. madrasensis* Subramanian, 1939, a parasite of *Chiloscyllium indicum* (Gmelin, 1789). Obviously, it is a case of a detached proglottid from a tetracophyllidean parasite, which cannot be linked with a known species in this selachian. The genus *Biporophyllaeus* should be abandoned; it is treated here as a *genus inquirendum*. The family Biporophyllaeidae Subramanian, 1939 and the order Biporophyllidea [sic] Wardle & McLeod, 1952 should also disappear.

Carpobothrium Shipley & Hornell, 1906. The very brief diagnosis given by Shipley & Hornell (1906) deals only with the morphology of the scolex. My proposed diagnosis is based on the description of *C. megaphallum* Subhadrappa, 1957, a parasite of *Chiloscyllium griseum* Muller & Henle, 1838. *C. indicum* (Gmelin, 1789), the host of *Carpobothrium chiloscylli* Shipley & Hornell, 1906, is closely related to *Chiloscyllium griseum*. It transpires that the parasites of *Rhyn-*

chobatus djeddensis (Forsskal, 1775) (Rhynchobatidae) and of *Urogymnus asperimus* Bloch & Schneider, 1801 (Dasyatidae), described by Southwell (1925) under the name of *Carpobothrium chiloscyllyi*, do not belong to *Carpobothrium* as defined here. These species, which should be collected again from the type-hosts, correspond to a taxonomic unit which has yet to be defined.

Cyatocotyle Mola, 1908. Mola (1908) created this genus for *Tetrabothrius auscharcharias rondeletti* Wagener, 1854 which is said to be a composite species. Wagener (1854) did not describe the anatomy. That given by Mola for *C. marchesetti* is notable for a vagina opening in front of the cirrus-sac. The scolex is reminiscent of that of *Prosobothrium* Cohn, 1902 and partly of *Platybothrium auriculatum* Yamaguti, 1952. *Cyatocotyle* should be suppressed; it is treated here as a *genus inquirendum*.

Hoaleshwaria Shinde & Chincholikar, 1975. This genus with the type-species *H. marathwadensis* Shinde & Chincholikar (1975) was described from a single individual collected from *Trygon* sp. The species cannot be recognized either from its description or illustration. The host species being unknown, it cannot be obtained again. *Hoaleshwaria* should be suppressed; it is treated here as a *genus inquirendum*.

Pithophorus Southwell, 1925. Southwell (1925) described this cestode with four tubular bothridia open at each end from *Rhynchobatus djeddensis* (Forsskal, 1775) (Rajiformes, Rhynchobatidae). *P. tetraglobus* does not seem to have been recovered since its original description. The other species placed in *Pithophorus* are parasites of sharks (Orectolobiformes, Lamniformes, Carcharhiniformes). Their systematic position should be reviewed, particularly their relationship with the genera *Scyphobhyllidium* Woodland, 1927 and *Marsupiobothrium* Yamaguti, 1952, also reported from sharks.

Polipobothrium Mola, 1908. The scolex of the type-species *P. vaccarii* Mola, 1908, has four bothridia each with a regular row of nine small suckers on the margin. From the illustration, the scolex is borne on a long cephalic peduncle. The anatomy conforms to the tetraphyllidean type. The type-host is a large shark, *Selache maxima* = *Cetorhinus maximus* (Günner, 1765). Since the work of Mola, no phyllobothriid corresponding to *Polipobothrium* has been found in *C. maximus*. The genus and species should be considered doubtful; it is treated as a *genus inquirendum*.

Reesium Euzet, 1955. Euzet erected the genus for *Dinobothrium paciferum* Sproston, 1948 from *Cetorhinus maximus* (Günner, 1765). The characters on which this separation was based (presence of strong spines on the strobila, structure of the ovary) are not of major significance at generic level. *Reesium* is considered to be a synonym of *Dinobothrium* van Beneden, 1889.

Spongiobothrium Linton, 1889. The scolex of the type-species, *S. variabile* Linton, 1889 from *Dasyatis centroura*, has four highly folded bothridia with a surface

divided by septa into loculi but without an accessory sucker. The last character led Southwell (1925) to synonymize the genus with *Anthobothrium* but the synonymy is doubtful. *S. variabile* should be obtained again from the type-host to verify whether the genus is valid. The discovery in *D. pastinaca* of *Phyllobothrium pastinacae* Mokhtar-Maamouri & Zamali, 1981 with highly folded loculated bothridia, but with an accessory sucker, calls into question the exact structure of the bothridia of *Spongiobothrium*. It is treated here as a *genus inquirendum*.

Myliobatibothrium Shinde & Mohekar, 1983. The type-species, *M. alii* Shinde & Mohekar, 1983 was found in *Myliobatis nieuhofii* (Muller & Henle) at Ratnagiri on the west coast of India. The illustration given of the scolex makes this species very difficult to place. From the description, the bothridia are simple except for a row of eight loculi on the posterior border, but the diagram shows, in the centre of each bothridium, a pouch-like structure broadly open anteriorly. The anatomy is of the phyllobothriid type although the vagina has not been noted as anterior to the cirrus-sac. Shinde & Mohekar [*sic*] (1983) placed this genus close to *Duplicibothrium* Williams & Campbell, 1978. The description and illustration being inadequate, *Myliobatibothrium* is considered a *genus incertae sedis* pending the recovery and redescription of this parasite from material from the type-host. On the subject of this tetraphyllidean, there is a question of what is represented by the host name *Myliobatis nieuhofii* (Muller & Henle) quoted by Shinde & Mohekar (1983). Researches of the date of the description by Muller & Henle have failed to reveal any trace of this fish in the ichthyological literature, but *Aetomyleus nichofii* Schneider, 1801 has been found. What is the relationship between these two species?

Pelichnibothrium Monticelli, 1889. The three individuals described in this genus (Monticelli, 1889; Yamaguti, 1952; Euzet, 1959) correspond to a postlarval stage of the phyllobothriid tetraphyllideans. The scolex has four bothridia with a simple border and an accessory sucker, and an apical sucker as in all the plerocercoids of the *Scolex pleuronectis* type. Behind the scolex, a strobilate region is followed by a long appendix corresponding to the posterior vesicle of the plerocercoid. This posterior part is comparable with that which characterizes the large plerocercoids found in the intestine of cephalopods. The anatomy of proglottids of the strobilate region is characteristic of the Tetraphyllidea. It is not possible to say to which adult this postlarva corresponds.

Pillersium Southwell, 1927. The genus is known only from a single species, *P. oweni* Southwell, 1927, parasite of *Urogymnus asperrimus* (Bloch & Schneider, 1901). According to Southwell (1927), the scolex has only two bothridia with highly folded margins. The anatomy is not known. The systematic position of this strange cestode is difficult to determine. I believe it to be affiliated to the Phyllobothriidae because, from Southwell's illustration, it is possible that the Y-shaped scolex is composed of four bothridia fused into dorsoventral pairs.

Subfamily Triloculariinae Yamaguti, 1959

Kowsalyabothrium Muralidhar, Shinde & Jadhav, 1989. I place this genus, with some doubt, close to the Triloculariinae but it should be treated as a *genus inquirendum*. In this parasite of *Trygon centrura*, the bothridia with a distinct (?) accessory sucker resemble those of species of *Crossobothrium*. The same applies to the anatomy of the proglottids. The presence of a longitudinal septum dividing the bothridium into two, the main character of the genus, is to be confirmed. This will be difficult because the host cited is doubtful. Is *Trygon centrura* from India a synonym of *Dasyatis centroura* (Mitchill, 1815)? *D. centroura* is a species whose geographical distribution is limited to the North Atlantic. This stingray has never been reported from the Indian Ocean.

Subfamily Rhinebothriinae Euzet, 1953

Rhinebothrium Linton, 1890 currently contains about forty species (see Butler, 1987b) which do not correspond in all things, particularly in the structure of the bothridium, to the type-species. In *R. flexile* Linton, 1890, the surface of the bothridium is divided by muscular septa into two symmetrical rows of loculi plus an unpaired loculus at the extremity. From the structure of the bothridia, divisions will be proposed in the genus but only when the Rhinebothriinae described by Shipley & Hornell and by Southwell from Myliobatiformes in the Indian Ocean have been reviewed.

It would probably be necessary to include in the Rhinebothriinae the parasites of selachians initially described as *Echeneibothrium* although lacking a myzorhynchus. Several species currently placed in the genus *Anthobothrium*, which have a scolex with four bothridia with a surface partly or entirely divided by muscular septa, should be placed in the Rhinebothriinae. Examples are *A. taeniurae* Saoud, 1963 and *A. sexorchidum* Williams, 1964, both parasites of *Taeniura lymna* (Forsskal, 1875) (Dasyatidae) and *A. amuletum* Butler, 1987, a parasite of *Rhinobatus armatus* (Rhinobatidae).

Shindeiobothrium Jadhav, Shinde & Deshmukh, 1981. The scolex of this cestode has four bothridia said to be sessile, which is difficult to verify given the apparent state of compression of the scolex. These bothridia may correspond to the *Rhinebothrium* type but the presence of a large central space renders this doubtful. Regarding the distribution of the testes in the proglottid, there is a contradiction between the description (preovarian testes) and the illustration in which the testes descend on each side of the ovary almost as far as the posterior extremity of the proglottid. Pending a redescription of the type-species, *S. karbharae*, a parasite of *Trygon sephen* = *Hypolophus sephen* (Forsskal, 1775), *Shindeiobothrium* is considered a *genus inquirendum*. The type-species is close to *Echeneibothrium ceylonicum* Shipley & Hornell, 1906, a parasite of *T. kublii* (= *Dasyatis kublii*) (Muller & Henle, 1841).

Two species of tetrphyllideans described under *Echeneibothrium* may in fact represent distinct genera.

Echeneibothrium smitii Shinde, Deshmukh & Jadhav, 1981. This parasite from the spiral valve of *Trygon sephen* = *Hypolophus sephen* (Forsskal, 1775) on the

west coast of India, should be recovered again for a more detailed study. The original description, based on two individuals, states that the centre of the scolex has a myzorhynchus, the presence of which is not evident in the illustration (Shinde *et al.*, 1981). If this observation is accurate, this parasite would represent the first *Echeneibothrium* found in Myliobatiformes. In *E. smitii*, the bothridia, which have a single row of seven loculi, are carried at the extremity of a very long pedicel (four times the length of the bothridium) which forms an enlargement at the base of the bothridium. The anatomy is of the *Rhinebothrium* or *Echeneibothrium* type without postvaginal testes on the poral side. If this species is found again, the unique morphology of the scolex would characterize a new genus. This parasite, which is a phyllobothriid, was erroneously classified by its authors in the Onchobothriidae.

Echeneibothrium javanicum Shipley & Hornell, 1906. This species, parasite of *Rhinoptera javanica*, considered by Southwell as a synonym of *Rhinebothrium cancellatum* Linton, 1890, was placed in the genus *Echeneibothrium* although the scolex has no myzorhynchus. The synonymy being incorrect, *E. javanicum* appears to be a species which should be placed in the Rhinebothriinae, since the bothridia are subdivided into numerous loculi by muscular septa. However, the distribution of the loculi is unique. From the description and illustration, two regions can be distinguished in the bothridia: the anterior region divided into three longitudinal rows of loculi and the posterior into one transverse row of seven loculi. Unfortunately, the anatomy is poorly known. This cestode appears close to *Duplicibothrium* Williams & Campbell, 1978. In this parasite of *Rhinoptera bonasus*, the bothridium is also divided into two parts but the anterior region has only a single longitudinal row of loculi (Figs 8.1, 8.2). The anatomy of *Duplicibothrium* is unusual, with testes throughout the length of the proglottid (anterior and posterior to the ovary) and circum-medullary vitelline follicles. I retain *Echeneibothrium javanicum* as a *species incertae sedis* pending its recovery from the type-host, *Rhinoptera javanica* Muller & Henle, 1841, in the type locality.

Tiarabothrium Shipley & Hornell, 1906. The type-species, *T. javanicum* Shipley & Hornell, 1906, is a parasite of *Rhinoptera javanica*. The scolex has four sessile bothridia divided into twelve loculi by transverse septa. The bothridia are on the surface of a voluminous central mass of dense connective tissue. From the illustration by Shipley & Hornell (1906), this mass does not have the structure of a myzorhynchus. Southwell (1925) synonymized *Tiarabothrium* with *Echeneibothrium* but, given the systematic position of the host (Dasysatidae), I think it should be placed with Rhinebothriinae. Known only from two individuals, this parasite should be obtained again from the type-host and revised to determine its exact status and position. It is treated here as a *genus inquirendum*.

Maccallumiella Yamaguti, 1959. Yamaguti (1959) created for *Taenia patini* MacCallum, 1921, from *Arius* sp. (Teleostei, Siluriformes), the genus *Maccallumiella* and the family Maccallumiellidae which he tentatively appended to the Tetraphyllidea. The nature of the host and the route of the vagina posterior to the cirrus-sac suggest that this may be a proteocephalidean. It is treated here as a *genus incertae sedis*.

Mastacembellophyllaeus Shinde & Chincholikar, 1977 should be suppressed because it is based on an isolated tetraphyllidean proglottid. It is treated here as a *genus inquirendum*.

Platybothrium Hornell, 1923 is represented by a larva. It cannot be assimilated to *Platybothrium* Linton, 1890 (Onchobothriidae) and the characters of the larva are not sufficiently distinctive for the creation of a new genus. It is considered to be a *genus inquirendum*.

Dittocephalus Parona, 1887. This cestode has an extraordinary scolex with two suckers (bothria, bothridia?) each borne on a trisegmented peduncle. What little is known of the anatomy indicates that it is of the pseudophyllidean type because the genital pore is mid-ventral. The operculated egg also resembles that of the Pseudophyllidea. The selachian host is doubtful. The genotype is unknown and the taxon is not a tetraphyllidean. It is regarded as a *genus inquirendum*.

Phanobothrium Mola, 1907. The host is unknown but was presumed to be a selachian. The anatomy is tetraphyllidean with the vagina anterior to the cirrus-sac. The spinous scolex has four oblong suckers and a single large apical organ like that of some proteocephalideans. The single vitelline gland described by Mola (1907) could be Mehlis's gland. The genus is treated here as a *genus inquirendum*.

Neolitobothrium Bilqees, 1983 is represented by an individual from the spiral valve of *Myrmillo manazo* (Mustelidae). The route of the vagina was not described but the anatomy indicates that this is a tetraphyllidean. *N. hexalaciniatum* Bilqees, 1983 may be only a fragment of a *Calliobothrium* sp. which has lost its scolex and the anterior region of the strobila. This has been observed in many individuals of *C. verticillatum* collected *post mortem* from *Mustelus mustelus*. *Neolitobothrium* should be considered a *genus inquirendum*.

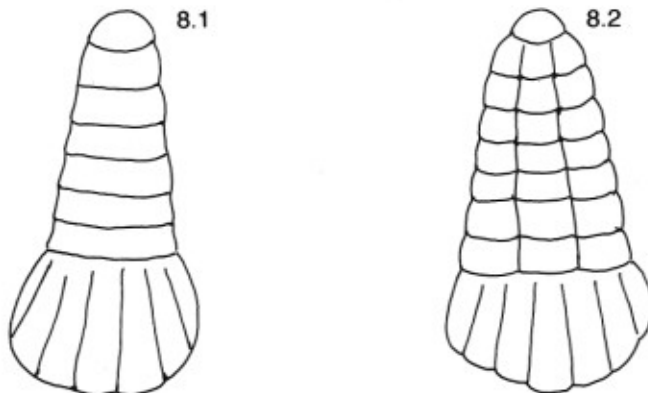


Fig. 8.1 Septa and loculi in bothridium of *Duplicibothrium*. (After Williams & Campbell, 1978.)
 Fig. 8.2 Septa and loculi in bothridium of *Echeneibothrium javanicum*. (After Shipley & Hornell, 1906.)

ORDER TETRAPHYLLEIDA CARUS, 1863

Diagnosis: Scolex with four sessile or pedunculated bothridia of various shapes; hooks present or absent. Rarely, scolex lacks bothridia, suckers and armature; or has four sessile glandular discs; or may be cushion-like with a complex velum; or consists of a single apical sucker. Metascolex sometimes present. Strobila usually hermaphroditic, sexes rarely separate; usually single, rarely multiple; craspedote or not; anapolytic, euapolytic or rarely hyperapolytic. Genital pores lateral or sublateral, irregularly alternating. Testes numerous; postvaginal testes present or not on poral side. Ovary posterior, bilobed or tetralobed in cross-section. Vagina anterior to cirrus-sac crossing the vas deferens. Vitelline follicles medullary, usually lateral, sometimes encircling proglottid, rarely condensed around the ovary. Uterus medioventral; uterine pores sometimes present, median. Eggs may be grouped in cocoons. Adults in spiral valve of elasmobranchs and holocephalids.

Key to families

- 1a. Scolex with one attachment organ 2.
- 1b. Scolex with four attachment organs 3.
- 2a. Scolex a large organ lacking bothridia. One to 24 strobilae per scolex
..... Cathetocephalidae Dailey & Overstreet, 1973.
- 2b. Scolex a single sucker, followed by pseudoscolex modified from anterior
proglottids Litobothriidae Dailey, 1969.
- 3a. Scolex with four organs forming a crumpled collar and one globular apical
organ embedded in gut wall of host
..... Disculicipitidae Joyeux & Baer, 1936.
- 3b. Scolex with only four organs 4.
- 4a. Scolex with four cup-shaped glandular organs
..... Prosobothriidae Baer & Euzet, 1955.
- 4b. Scolex with four muscular organs (bothridia) 5.
- 5a. Strobila with sexes completely separate
..... Diocotaeniidae Schmidt, 1969.
- 5b. Strobila with hermaphroditic proglottids 6.
- 6a. Bothridia with hooks Onchobothriidae Braun, 1900.
- 6b. Bothridia unarmed 7.
- 7a. Strobila with vitelline follicles in two lateral fields throughout proglottid
..... Phyllobothriidae Braun, 1900.
- 7b. Strobila with vitelline follicles confined to two lateral fields in posterior part
of proglottid Chimacrocestidae Williams & Bray, 1984.

Family Cathetocephalidae Dailey & Overstreet, 1973

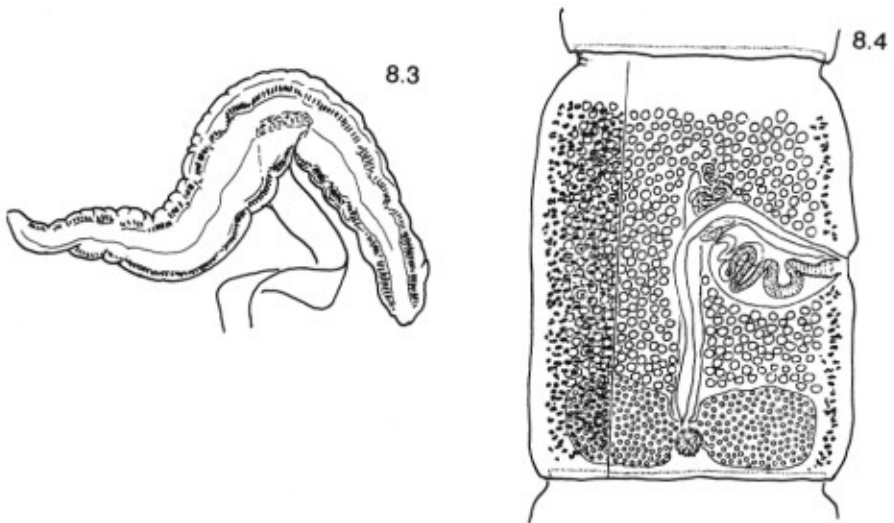
Diagnosis: Scolex a single transverse fleshy organ lacking bothridia, suckers or armature. Apical surface highly rugose with fleshy papilliform projections on leading and trailing edges. Posterior surface of scolex smooth with central transverse fold extending entire width. One to 24 strobila per scolex. Strobila slightly craspedote, apolytic. Genital pores lateral, irregularly alternating. Testes numerous. Large ovary, median, posterior, bilobed in cross-section. Vagina anterior to cirrus-sac. Vitelline follicles circum-medullary. Type and only genus *Cathetocephalus* Dailey & Overstreet, 1973.

Genus *Cathetocephalus* Dailey & Overstreet, 1973 (Figs 8.3, 8.4)

Diagnosis: With the characters of the family. In Carcharinidae. Cosmopolitan. Type-species *C. thatcheri* Dailey & Overstreet, 1973.

Family Litobothriidae Dailey, 1969

Diagnosis: Scolex (pseudoscolex?) a single apical sucker followed by anterior modified proglottids. Neck present or absent. Strobila craspedote and lacinated. Euapolytic. Genital pores lateral, irregularly alternating. Testes numerous; postvaginal testes present on poral side. Ovary median, posterior, bilobed or tetralobed in cross-section. Vagina anterior to cirrus-sac. Vitelline follicles circum-



Figs 8.3, 8.4 *Cathetocephalus* Dailey & Overstreet, 1973. 8.3. Scolex. 8.4. Mature proglottid, dorsal view. Vitelline follicles, circum-medullary, drawn only on the left. (After Dailey & Overstreet, 1973.)

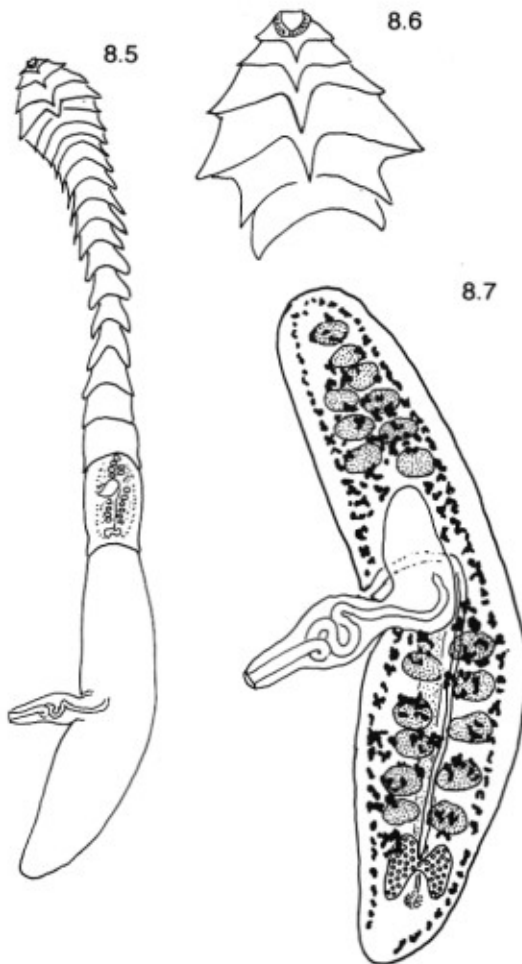
medullary, extending throughout length of proglottid including posterior to ovary. Uterus medioventral, from ovary to level of cirrus-sac. Type and only genus *Litobothrium* Dailey, 1969.

Genus *Litobothrium* Dailey, 1969 (Figs 8.5-8.7)

(Syn. *Renyxa* Kurochkin & Slankis, 1973)

Diagnosis: With the characters of the family. In Lamniformes (Alopiidae, Odontaspidae, Mitsukurinidae). Pacific Ocean. Type-species *L. alopias* Dailey, 1959.

Renyxa Kurochkin & Slankis, 1973 is synonymized with *Litobothrium*. Although the number and morphology of the proglottids following the apical sucker may be good criteria for separating species, they are insufficient to distinguish two genera among these tetracystid parasites of *Alopias*. I note



Figs 8.5-8.7 *Litobothrium* Dailey, 1969. 8.5. Strobila *in toto*. 8.6. Anterior part of strobila showing apical sucker and modified proglottid. 8.7. Mature proglottid, dorsal view. (After Dailey, 1969.)

the resemblance of the strobila to that of *Eniochobothrium* Shipley & Hornell, 1906 (see Chapter 9).

Family Disculicipitidae Joyeux & Baer, 1936

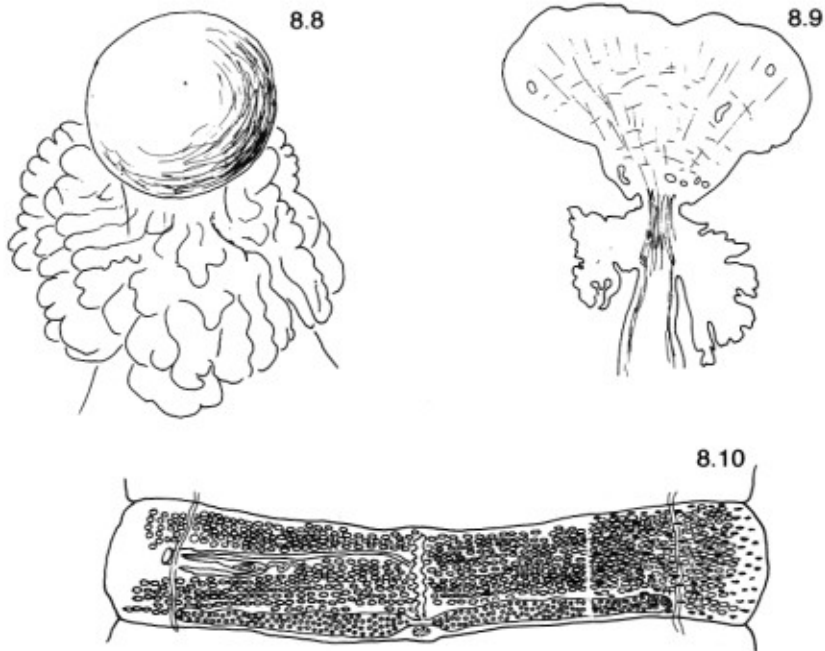
(Syn. Discocephalidae Pintner, 1928)

Diagnosis: Scolex divided into large cushion-like region variable in size, embedded within intestinal wall and followed by complex, frilled velum, probably in four parts (bothridia?). Strobila acraspedote, anapolytic. Genital pores sublateral ventral, irregularly alternating. Testes very numerous; postvaginal testes present on poral side. Ovary medioposterior, bilobed in cross-section. Vagina anterior to cirrus-sac. Vitelline follicles circum-medullary. Uterus median with lateral outgrowths. Type and only genus *Disculiceps* Joyeux & Baer, 1936.

Genus *Disculiceps* Joyeux & Baer, 1936 (Figs 8.8–8.10)

(Syn. *Discocephalum* Linton, 1890, preoccupied)

Diagnosis: With the characters of the family. In Carcharinidae. Cosmopolitan. Type-species *D. pileatum* (Linton, 1890).



Figs 8.8–8.10 *Disculiceps* Joyeux & Baer, 1936. 8.8. Scolex (original). 8.9. Longitudinal section of the scolex. 8.10. Anatomy, ventral view. Vitelline follicles circum-medullary, drawn only on the right. (After Nock & Caira, 1988.)

Family Prosobothriidae Baer & Euzet, 1955

Diagnosis: Scolex with four sessile glandular discs. Neck densely spinose. Strobila acraspedote, euapolytic. Genital pores lateral, irregularly alternating. Testes numerous; postvaginal testes present on poral side. Ovary posterior, bilobed in cross-section. Vagina anterior to cirrus-sac. Vaginal sphincter present. Vitelline follicles circum-medullary (some postovarian). Eggs (24) clustered in cocoon. Type and only genus *Prosobothrium* Cohn, 1902.

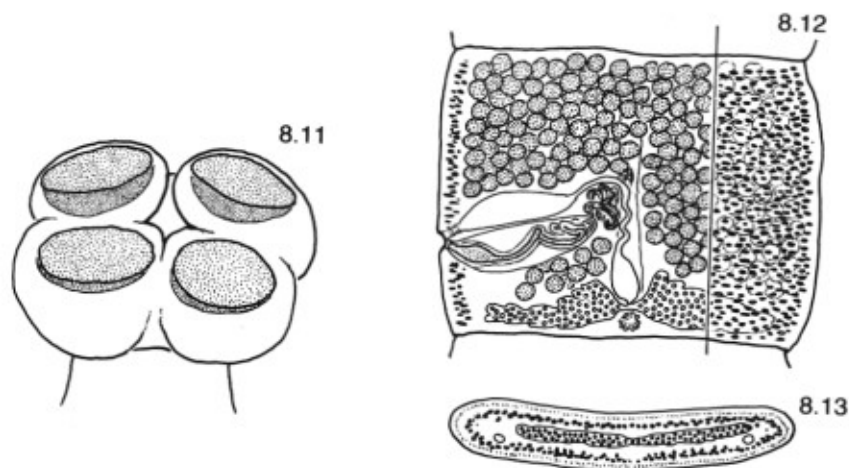
Genus *Prosobothrium* Cohn, 1902 (Figs 8.11–8.13)

(Syn. *Lintoniella* Woodland, 1927)

Diagnosis: With the characters of the family. In Carcharinidae. Cosmopolitan. Type-species *P. armigerum* Cohn, 1902.

Family Dioecotaeniidae Schmidt, 1969

Diagnosis: Sexes separated. Strobilae dimorphic in size and shape. Scolex with four bothridia, each subdivided into loculi by transverse and longitudinal septa. Myzorhynchus absent. **Male strobila.** Proglottids with genital pores lateral irregularly alternating. Testes in circle in two layers on both sides of cirrus-sac. External seminal vesicle absent, internal seminal vesicle present. Cirrus long, spinose. **Female strobila.** Proglottid with posterior bilobed ovary. Vaginal pore absent. Vagina median, convoluted. Seminal receptacle present in lobe of ovary, irregularly alternating. Two vitelline glands surrounding lobes of ovary laterally.



Figs 8.11–8.13 *Prosobothrium* Cohn, 1902. 8.11. Scolex. 8.12. Mature proglottid, dorsal view, vitelline follicles circum-medullary, drawn only on the right. 8.13. Transverse section through the ovarian region. (After Euzet, 1959.)

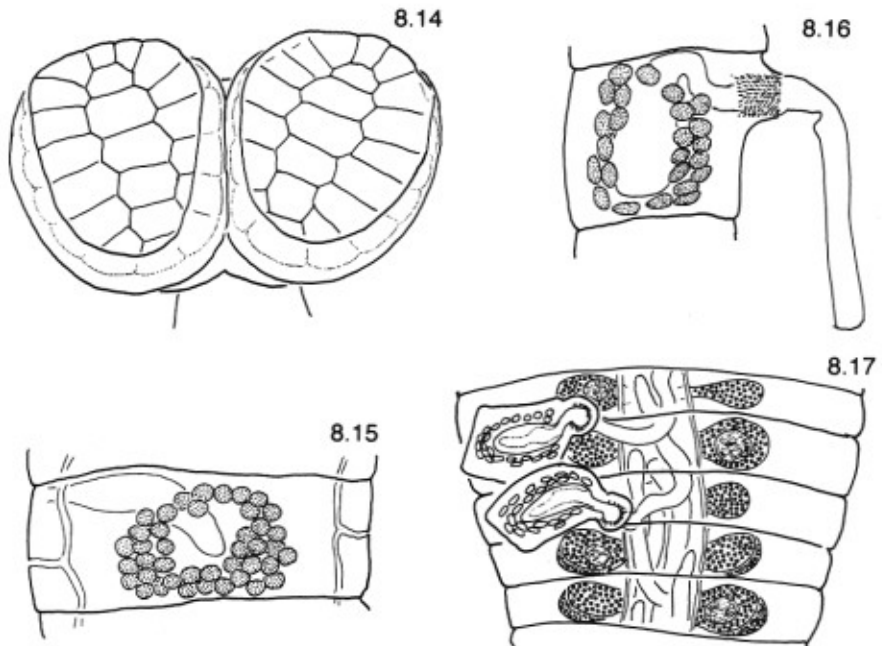
Uterus a bilobed transverse sac anterior to ovary. Sperm transfer by hypodermic impregnation. Type and only genus *Dioecotaenia* Schmidt, 1969.

Genus *Dioecotaenia* Schmidt, 1969. (Figs 8.14–8.17)

Diagnosis: With the characters of the family. In Rhinopteridae. American North Atlantic. Type-species *D. cancellata* (Linton, 1890).

Family Onchobothriidae Braun, 1900

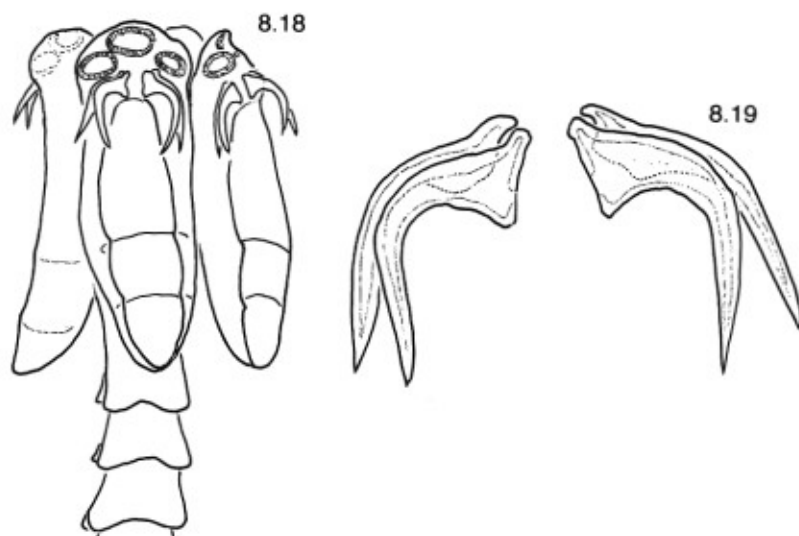
Diagnosis: Scolex with four sessile muscular bothridia each armed with simple or forked hooks; bothridial surface simple or divided by transverse septa, anterior muscular pad with or without sucker. Strobila acraspedote or craspedote; apolytic or euapolytic. Genital pores lateral, irregularly alternating. Testes numerous; postvaginal testes present or absent on poral side. Ovary posterior, bilobed or tetralobed in cross-section. Uterus medioventral; uterine pores sometimes present, median. Eggs may be grouped in cocoons. Adults in spiral valve of elasmobranchs. Type-genus *Onchobothrium* De Blainville, 1828.



Figs 8.14–8.17 *Dioecotaenia* Schmidt, 1969. 8.14. Scolex. 8.15. Male proglottid. 8.16. Male proglottid with cirrus evaginated and seminal vesicle filled. 8.17. Female proglottid with two male proglottids attached by hypodermic impregnation. (After Schmidt, 1969.)

Key to genera

- 1a. Bothridia divided by one or two transverse septa 2.
 1b. Bothridia undivided 10.
- 2a. Bothridia divided by two transverse septa 3.
 2b. Bothridia divided by one transverse septum 8.
- 3a. Bothridia with two pairs of hooks
 *Calliobothrium* van Beneden, 1850. (Figs 8.18, 8.19)
Diagnosis: Scolex with four bothridia each divided into three loculi by two transverse septa. In front of the bothridium a pad with one or three suckers and two pairs of simple articulated hooks. Strobila craspedote, laciniated or not, euapolytic. Genital pore lateral, irregularly alternating. Testes numerous, in two lateral fields; postvaginal testes present on poral side. Ovary posterior. Vagina anterior to cirrus-sac. Vitelline follicles lateral. Uterus sac-shaped, medioventral. Uterine pores medioventral. Eggs grouped in cocoon. In Mustelidae. Cosmopolitan. Type-species *C. verticillatum* (Rudolphi, 1819).
- 3b. Bothridia with one pair of hooks 4.
- 4a. Paired hooks similar 5.
 4b. Paired hooks dissimilar 6.
- 5a. Hooks with one prong, base joined
 *Onchobothrium* De Blainville, 1828. (Figs 8.20, 8.21)



Figs 8.18, 8.19 *Calliobothrium* van Beneden, 1850. 8.18. Scolex. 8.19. Hooks. (After Euzet, 1959.)

Diagnosis: Scolex with four bothridia, each divided into three loculi by two transverse septa. In front of each bothridium a muscular pad with one accessory sucker and two thorn-shaped hooks. Pair of hooks joined at their base by a horseshoe-like plate. Bases with tubercles or hair-like process. Strobila acraspedote, apolytic. Genital pore lateral, irregularly alternating. Testes numerous in two lateral fields; postvaginal testes present on poral side. Vagina anterior to cirrus-sac. Ovary posterior, tetralobed in cross-section. Vitelline follicles lateral. Uterus medioventral. Eggs spherical. In Rajidae. Cosmopolitan. Type-species *O. uncinatum* (Rudolphi, 1819).

5b. Hooks forked with two prongs *Acanthobothrium* van Beneden, 1849. (Figs 8.22–8.24)
(Syns *Acrobothrium* Baer, 1948; *Euonchobothrium* Diesing, 1854; *Petalcephalus* Jeude, 1829; *Petalostoma* Jeude, 1829; *Prosthecobothrium* Diesing, 1863.)

Diagnosis: Scolex with four bothridia, each divided into three loculi by two transverse septa; in front of each bothridium a muscular pad with accessory sucker and pair of symmetrically forked hooks. Cephalic peduncle sometimes present. Strobila acraspedote, euapolytic. Genital pore lateral, irregularly alternating. Testes numerous; postvaginal testes present on poral side. Cirrus spinose. Ovary posterior, tetralobed in cross-section. Vagina anterior to cirrus-sac. Vitelline follicles lateral. Uterus sac-shaped, medioventral. Eggs spherical. In elasmobranchs. Cosmopolitan. Type-species *A. coronatum* (Rudolphi, 1819).

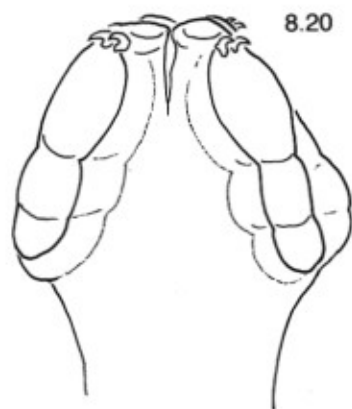
6a. Hooks dissimilar, lateral hook with one prong, median hook forked with two prongs *Acanthobothroides* Brooks, 1977. (Figs 8.25–8.27)

Diagnosis: Scolex with four sessile bothridia, each divided into three loculi by two transverse septa. In front of each bothridium, a muscular pad with accessory sucker and pair of dissimilar hooks. Medial hook with base and single prong, lateral hook with handle and two prongs. Strobila slightly craspedote, euapolytic. Genital pores lateral, irregularly alternating. Testes numerous; postvaginal testes present on poral side. Cirrus spinose. Ovary posterior bilobed in cross-section. Vagina anterior to cirrus-sac. Vitelline follicles lateral. In freshwater Dasysatidae. South America. Type-species *A. thorsoni* Brooks, 1977.

6b. Hooks forked with two prongs but dissimilar handles 7.

7a. One sclerotized plate between handle of hooks *Platybothrium* Linton, 1890. (Figs 8.28, 8.29)

Diagnosis: Scolex spinose with four sessile bothridia each divided into three loculi by two transverse septa. Anterior loculus with one lateral lobule. In front of each bothridium a muscular pad with accessory sucker and two dissimilar hooks. Hooks with two prongs and unequal base. Neck and strobila with large spines. Strobila acraspedote, euapolytic. Genital pores lateral, irregularly alternating. Testes numerous in two lateral fields; postvaginal testes present or not on poral side. Cirrus spinose. Ovary posterior, bilobed in cross-section. Vagina anterior to cirrus-sac. Vitelline follicles circum-medullary. Uterus



8.20



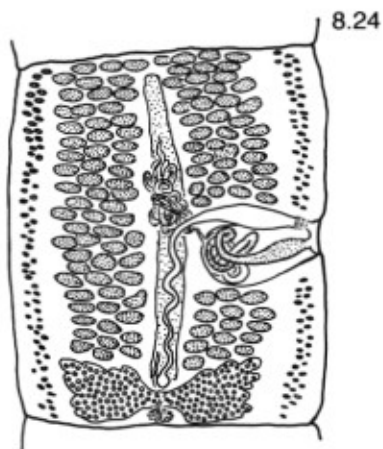
8.21



Figs 8.20, 8.21 *Onchobothrium* De Blainville, 1828. 8.20. Scolex. 8.21. Hooks, ventral and lateral view. (After Euzet, 1959.)



8.22



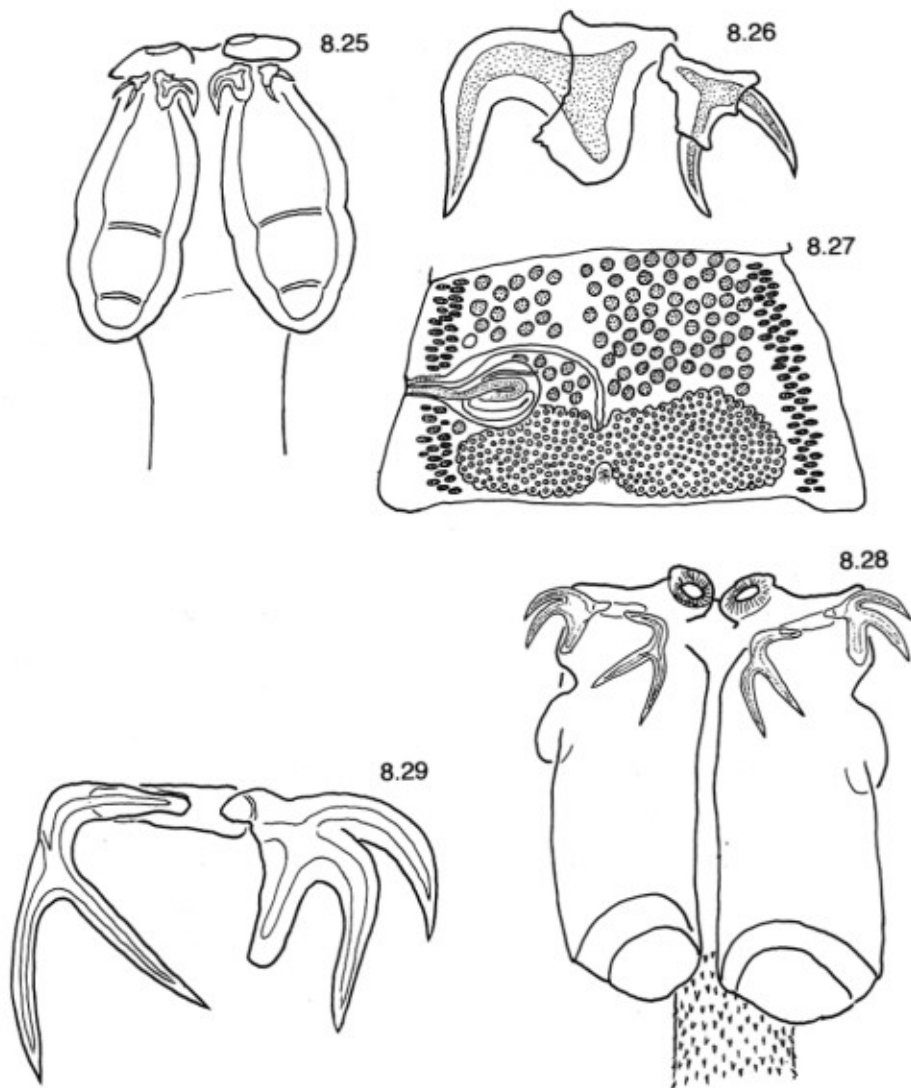
8.24



8.23



Figs 8.22-8.24 *Acanthobothrium* van Beneden, 1849. 8.22. Scolex. 8.23. Hooks, morphology. 8.24. Mature proglottid. (After Euzet, 1959.)



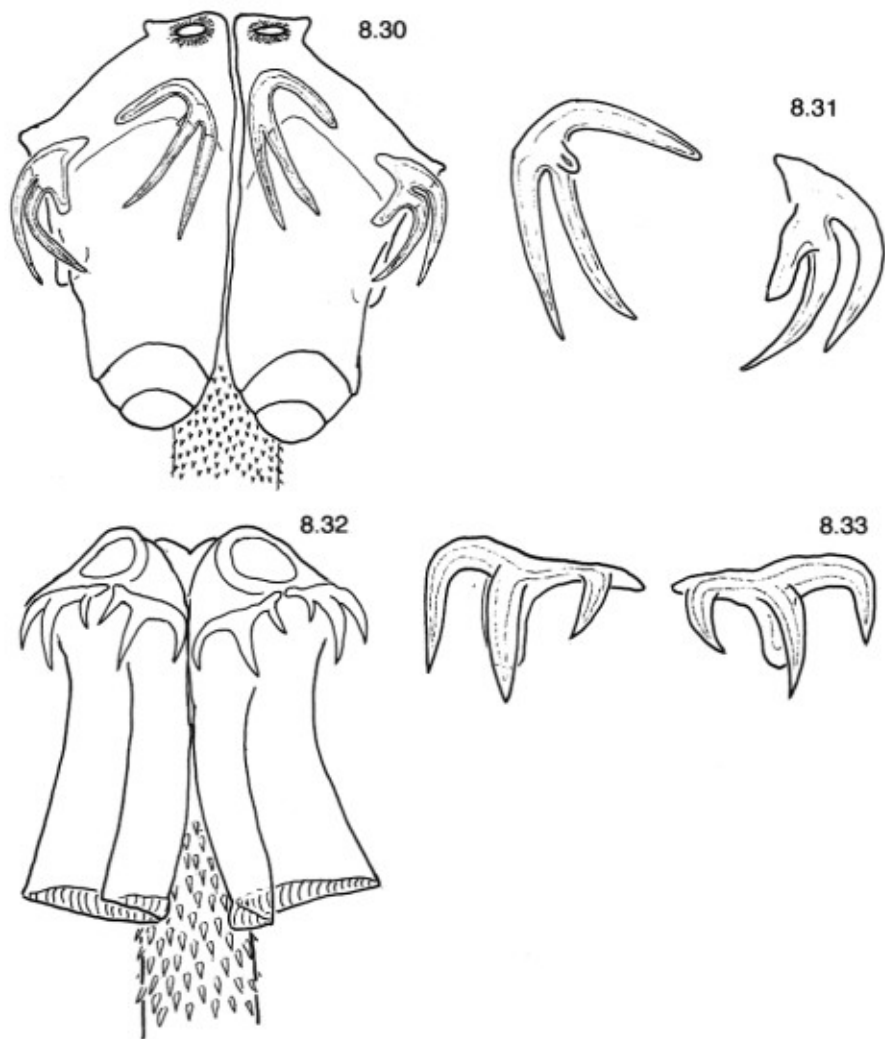
Figs 8.25-8.27 *Acanthobothroides* Brooks, 1977. 8.25. Scolex. 8.26. Hooks. 8.27. Mature proglottid. (After Brooks, 1977.)

Figs 8.28, 8.29 *Platybothrium* Linton, 1890. 8.28. Scolex. 8.29. Hooks. (After Euzet, 1959.)

medioventral. Eggs subspherical. In Carcharinidae. Cosmopolitan. Type-species *P. cervinum* Linton, 1890.

7b. No plate between handle of hooks
 *Dicranobothrium* Euzet, 1953. (Figs 8.30, 8.31)

Diagnosis: Scolex with four sessile bothridia, each divided into three loculi by two transverse septa. Anterior loculus with lateral minute lobe. In front of each bothridium, a muscular pad with accessory sucker and two dissimilar hooks with



Figs 8.30, 8.31 *Dicranobothrium* Euzet, 1953. 8.30. Scolex. 8.31. Hooks (no plate between hooks). (After Euzet, 1959.)

Figs 8.32, 8.33 *Phoreiobothrium* Linton, 1889. 8.32. Scolex. 8.33. Hooks. (After Euzet, 1959.)

two prongs. Neck and strobila spinose. Strobila acraspedote, euapolytic. Genital pore lateral, irregularly alternating. Testes numerous, in two lateral fields; postvaginal testes present on poral side. Ovary posterior, bilobed in cross-section. Vagina anterior to cirrus-sac. Vitelline follicles circum-medullary. Uterus medio-ventral. In Carcharinidae. Cosmopolitan. Type-species *D. spinulifera* (Southwell, 1912).

8a. Bothridia with loculated posterior compartment
 *Phoreiobothrium* Linton, 1889. (Figs 8.32, 8.33)

Diagnosis: Scolex with four bothridia. In front of each a muscular pad with accessory sucker and one pair of hooks with three (or two) unequal prongs. Bothridia simple with posterior margin divided into single row of loculi. Neck present, with large spines. Strobila acraspedote, euapolytic. Genital pore lateral, irregularly alternating. Testes numerous, in two lateral fields; postvaginal testes present on poral side. Ovary posterior, bilobed in cross-section. Vagina muscular, anterior to cirrus-sac. Vitelline follicles lateral. Uterus sac-shaped, medioventral. In Carchariniformes. Cosmopolitan. Type-species *P. lasium* Linton, 1889.

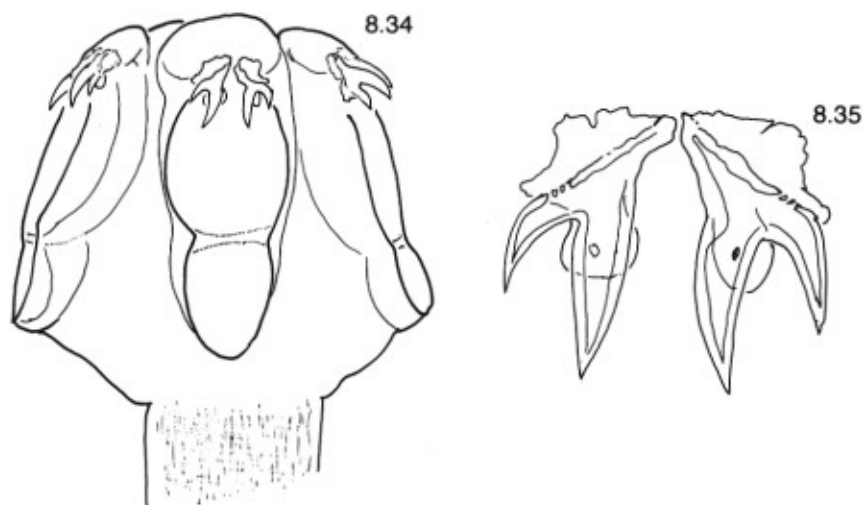
8b. Bothridia with one posterior compartment, not loculated 9.

9a. Bothridium with two forked hooks each with small handle
 *Uncibilocularis* Southwell, 1925. (Figs 8.34, 8.35)

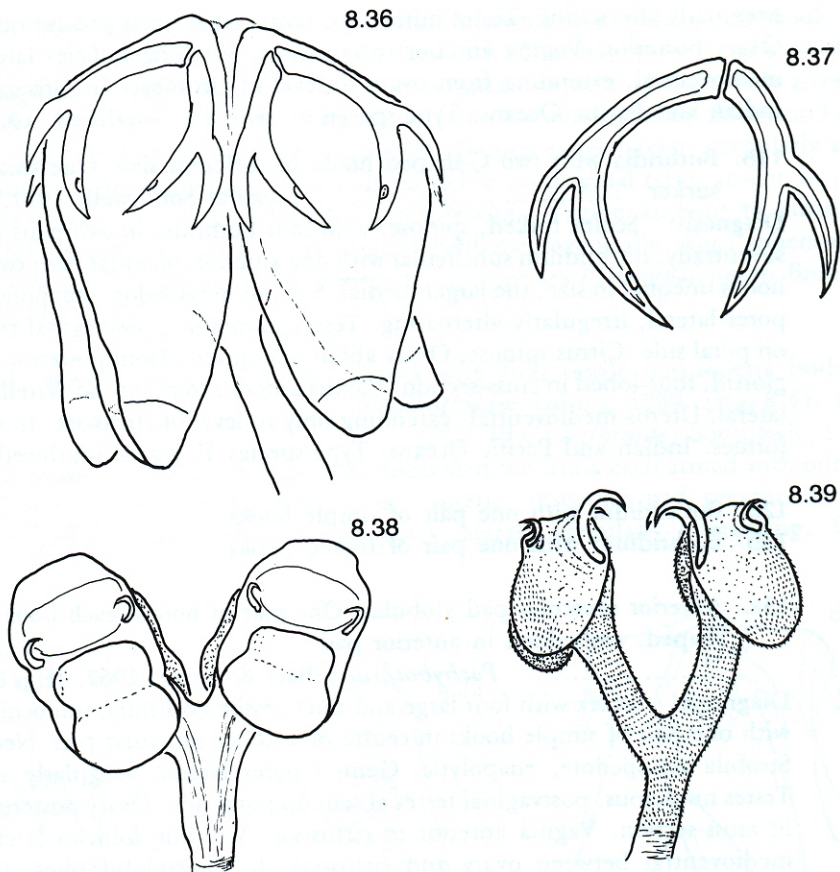
Diagnosis: Scolex with four sessile bothridia each divided into two loculi by one transverse septum. In front of each bothridium one small muscular pad (accessory sucker?) and one pair of symmetrical forked hooks with unequal prongs. Strobila acraspedote, apolytic. Genital pores lateral, irregularly alternating. Testes few, in two lateral fields; postvaginal testes present on poral side. Cirrus spinose. Ovary posterior. Vagina anterior to cirrus-sac. Vitelline follicles lateral. Uterus ventral with lateral projections. Eggs spherical. In Myliobatiformes. Indian and Pacific Oceans. Type-species *U. trygonis* Shipley & Hornell, 1927.

9b. Bothridia with one pair of hooks, each hook with two prongs and large handle *Megalonchos* Baer & Euzet, 1962. (Figs 8.36, 8.37)

Diagnosis: Scolex with four bothridia, each divided into two unequal loculi by transverse septum. In front of each bothridium, one pair of forked hooks dissimilar in size with very long handle. Strobila acraspedote, apolytic. Genital pores lateral, irregularly alternating. Testes numerous; postvaginal testes absent



Figs 8.34, 8.35 *Uncibilocularis* Southwell, 1925. 8.34. Scolex. 8.35. Hooks. (Original.)



Figs 8.36, 8.37 *Megalonchos* Baer & Euzet, 1962. 8.36. Scolex. 8.37. Hooks. (After Southwell, 1930a.)

Fig. 8.38 *Spiniloculus* Southwell, 1925. Scolex. (After Williams, 1964.)

Fig. 8.39 *Yorckeria* Southwell, 1930. Scolex. (After Williams, 1964.)

on poral side. Ovary posterior. Vagina anterior to cirrus-sac. Vitelline follicles? In *Hemigaleus balfouri* (Carchariniformes). Sri Lanka. Type-species *M. mandleyi* (Southwell, 1927).

- 10a. Scolex forked, bothridia paired, united dorsoventrally 11.
- 10b. Scolex not forked, with anterior muscular pad 12.

11a. Bothridia with two C-shaped hooks of equal size. One large accessory sucker *Spiniloculus* Southwell, 1925. (Fig. 8.38)
(Syn. *Spinibiloculus* Deshmukh & Shinde, 1980)

Diagnosis: Scolex forked, spinose, with four simple bothridia each with one very large accessory sucker. One pair of C-shaped hooks situated at the posterolateral corner of accessory sucker. Strobila acraspedote, euapolytic. Genital pores lateral,

irregularly alternating. Testes numerous; postvaginal testes present on poral side. Ovary posterior. Vagina anterior to cirrus-sac. Vitelline follicles lateral. Uterus medioventral, extending from ovary to level of cirrus-sac. In Orectolobiformes. Indian and Pacific Oceans. Type-species *S. mavensis* Southwell, 1925.

11b. Bothridia with two C-shaped hooks of different size. One small accessory sucker *Yorkeria* Southwell, 1927. (Fig. 8.39)

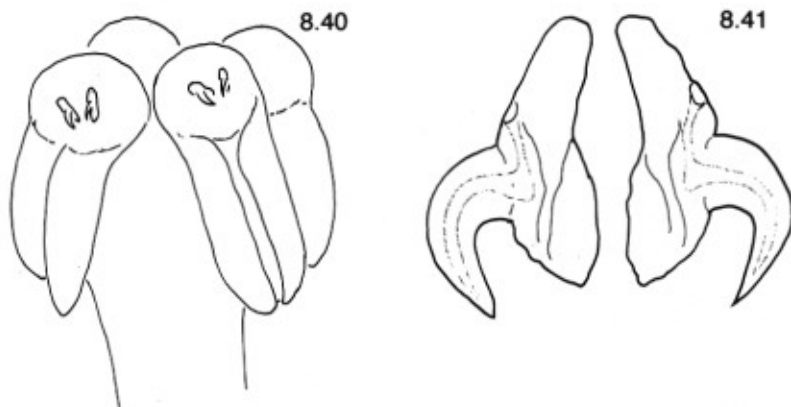
Diagnosis: Scolex forked, spinose, with four bothridia in two pairs united dorsoventrally. Bothridium subcircular with one anterior muscular pad; two C-shaped hooks unequal in size, the larger medial. Strobila acraspedote, euapolytic. Genital pores lateral, irregularly alternating. Testes numerous, postvaginal testes absent on poral side. Cirrus spinose. Ovary about one-quarter from posterior end of proglottid, four-lobed in cross-section. Vagina anterior to cirrus-sac. Vitelline follicles lateral. Uterus medioventral, extending only to level of cirrus-sac. In Orectolobiformes. Indian and Pacific Oceans. Type-species *Y. parva* Southwell, 1927.

12a. Bothridium with one pair of simple hooks 13.

12b. Bothridium with one pair of forked hooks 14.

13a. Anterior muscular pad globular. One pair of hooks, each hook rosethorn-shaped, embedded in anterior pad
..... *Pachybothrium* Baer & Euzet, 1962. (Figs 8.40, 8.41)

Diagnosis: Scolex with four large and thick sessile bothridia, uniloculate, armed with one pair of simple hooks in centre of anterior muscular pad. Neck present. Strobila acraspedote, euapolytic. Genital pores lateral, irregularly alternating. Testes numerous, postvaginal testes absent on poral side. Ovary posterior, bilobed in cross-section. Vagina anterior to cirrus-sac. Vitelline follicles lateral. Uterus medioventral between ovary and cirrus-sac. In Orectolobiformes. Indian and Pacific Oceans. Type-species *P. butsoni* (Southwell, 1911).



Figs 8.40, 8.41 *Pachybothrium* Baer & Euzet, 1962. 8.40. Scolex. 8.41. Hooks. (After Baer & Euzet, 1962.)

13b. Anterior accessory sucker. Bothridium with one pair of simple hooks

..... *Potamotrygonocestus* Brooks & Thorson, 1976. (Figs 8.42–8.44)

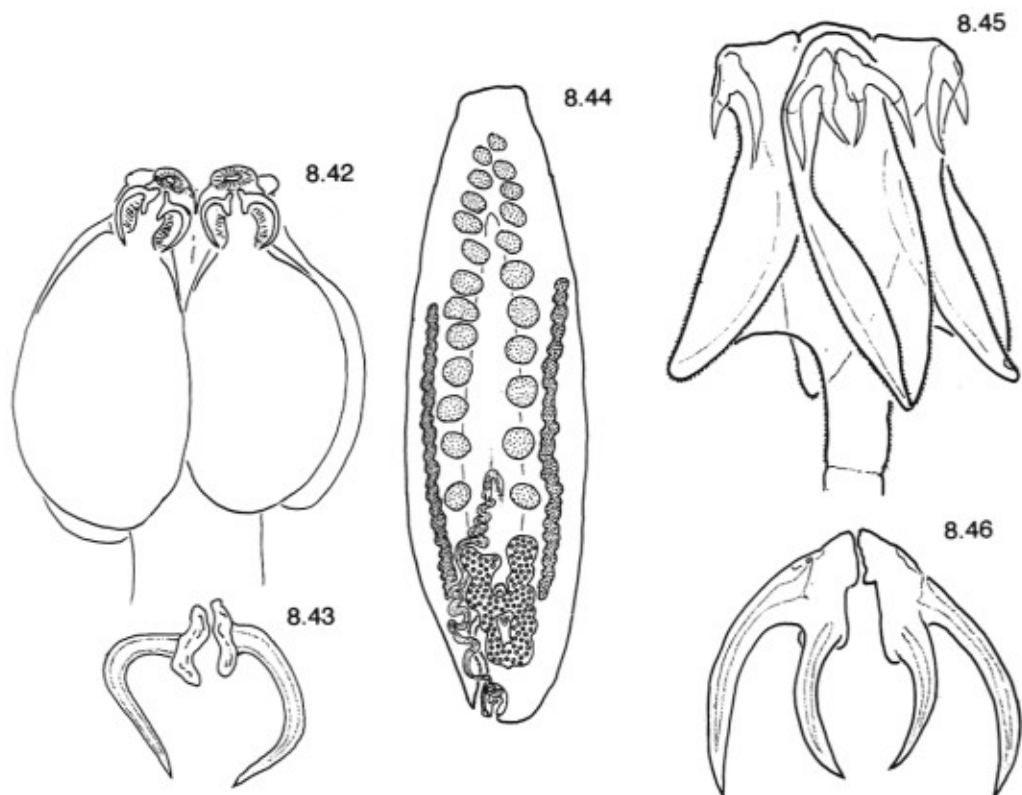
Diagnosis: Scolex with four sessile non-septate bothridia. Each with accessory sucker and pair of symmetrical hooks, each hook with one prong. Scolex and neck spinose. Strobila acraspedote, euapolytic. Genital pores lateral, irregularly alternating. Testes numerous, in two lateral fields; postvaginal testes absent on poral side. Ovary posterior, bilobed in cross-section. Vagina anterior to cirrus-sac. Vitelline follicles lateral. Uterus sac-shaped medioventrally. Eggs spherical. In freshwater Dasyatidae. South America. Type-species *P. magdalenensis* Brooks & Thorson, 1976.

14a. Postvaginal testes absent. Scolex with four sessile non-septate bothridia

..... *Pedibothrium* Linton, 1909. (Figs 8.45, 8.46)

(Syn. *Phyllobothroides* Southwell, 1911.)

Diagnosis: Scolex with four large undivided bothridia each armed with one pair of asymmetrical two-pronged hooks; anterior muscular pad present. Strobila acraspedote, euapolytic. Genital pores lateral, irregularly alternating. Testes



Figs 8.42–8.44 *Potamotrygonocestus* Brooks & Thorson, 1976. 8.42. Scolex. 8.43. Hooks. 8.44. Mature proglottid, dorsal view. (After Brooks & Thorson, 1976.)

Figs 8.45, 8.46 *Pedibothrium* Linton, 1909. 8.45. Scolex. 8.46. Hooks. (After Caira, 1992.)

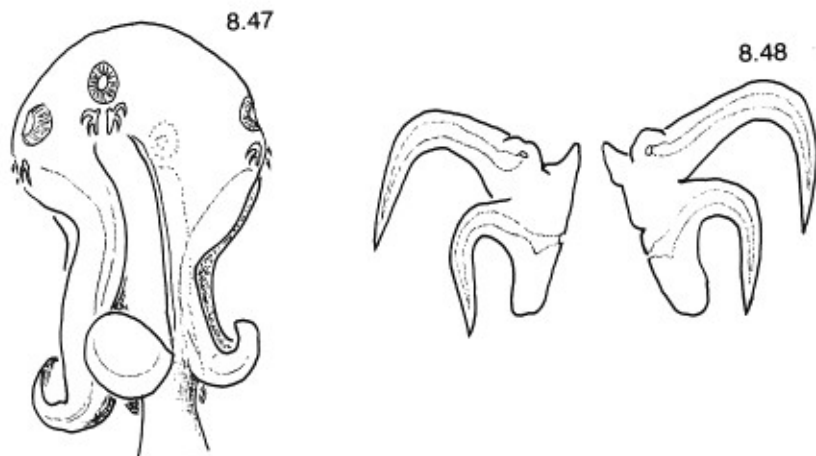
numerous; postvaginal testes absent on poral side. Ovary posterior. Vagina anterior to cirrus-sac. Vitelline follicles lateral (some postovarian). Uterus medioventral between ovary and cirrus-sac. In Orectolobiformes. Cosmopolitan. Type-species *P. globicephalum* Linton, 1909.

14b. Postvaginal testes present. Scolex bulbous, embedded in gut wall
 *Balanobothrium* Hornell, 1911. (Figs 8.47, 8.48)

Diagnosis: Scolex with four flattened sessile undivided bothridia, each with apical accessory sucker and pair of minute hooks, each hook with two prongs. Strobila acraspedote, apolytic. Genital pores lateral, irregularly alternating. Testes numerous; postvaginal testes present on poral side. Cirrus spinose. Ovary posterior, bilobed in cross-section. Vagina anterior to cirrus-sac. Vitelline follicles lateral. Uterus ventral with lateral diverticulum. Entire scolex enlarged, bulbous, embedded in gut wall of host. In elasmobranchs. Pacific and Indian Oceans. Type-species *B. tenax* Hornell, 1912.

Family Phyllobothriidae Braun, 1900

Diagnosis: Scolex with four sessile or pedunculated muscular bothridia, simple or divided by septa, with or without anterior accessory sucker; apical myzorhynchus may be present; metascolex sometimes present. Strobila acraspedote or craspedote; anapolytic, apolytic, euapolytic or hyperapolytic. Genital pores lateral, irregularly alternating. Testes numerous; postvaginal testes present or not on poral side. Ovary posterior, bilobed or tetralobed in cross-section. Vagina anterior to cirrus-sac, crossing the vas deferens. Vitelline follicles lateral, sometimes well developed dorsally and ventrally. Uterus medioventral, uterine pore may be present. Eggs sometimes grouped in cocoons. Adults in spiral valve of elasmobranchs. Type-genus *Phyllobothrium* van Beneden, 1850.



Figs 8.47, 8.48 *Balanobothrium* Hornell, 1911. 8.47. Scolex. (After Fuhrmann, 1931). 8.48. Hooks. (Original.)

Key to subfamilies

- 1a. Scolex with four small bothridia followed by strong metascolex
 *Thysanocephalinae* Euzet, 1953.
- 1b. Scolex with four bothridia without metascolex 2.
- 2a. Scolex with apical glandulomuscular myzorhynchus
 *Echeneibothriinae* de Beauchamp, 1905.
- 2b. Scolex without myzorhynchus 3.
- 3a. Scolex with four undivided bothridia with simple, crumpled or loculated
 margin *Phyllobothriinae* de Beauchamp, 1905.
- 3b. Scolex with four bothridia totally divided into loculi by muscular septa
 4.
- 4a. Number of loculi reduced *Triloculariinae* Yamaguti, 1959.
- 4b. Loculi numerous *Rhinebothriinae* Euzet, 1953.

Subfamily *Thysanocephalinae* Euzet, 1953

Diagnosis: *Phyllobothriidae*. Scolex with four minute bothridia with or without anterior muscular pad or sucker and one large metascolex crumpled or tetralobed. Postvaginal testes present. Vitelline follicles lateral.

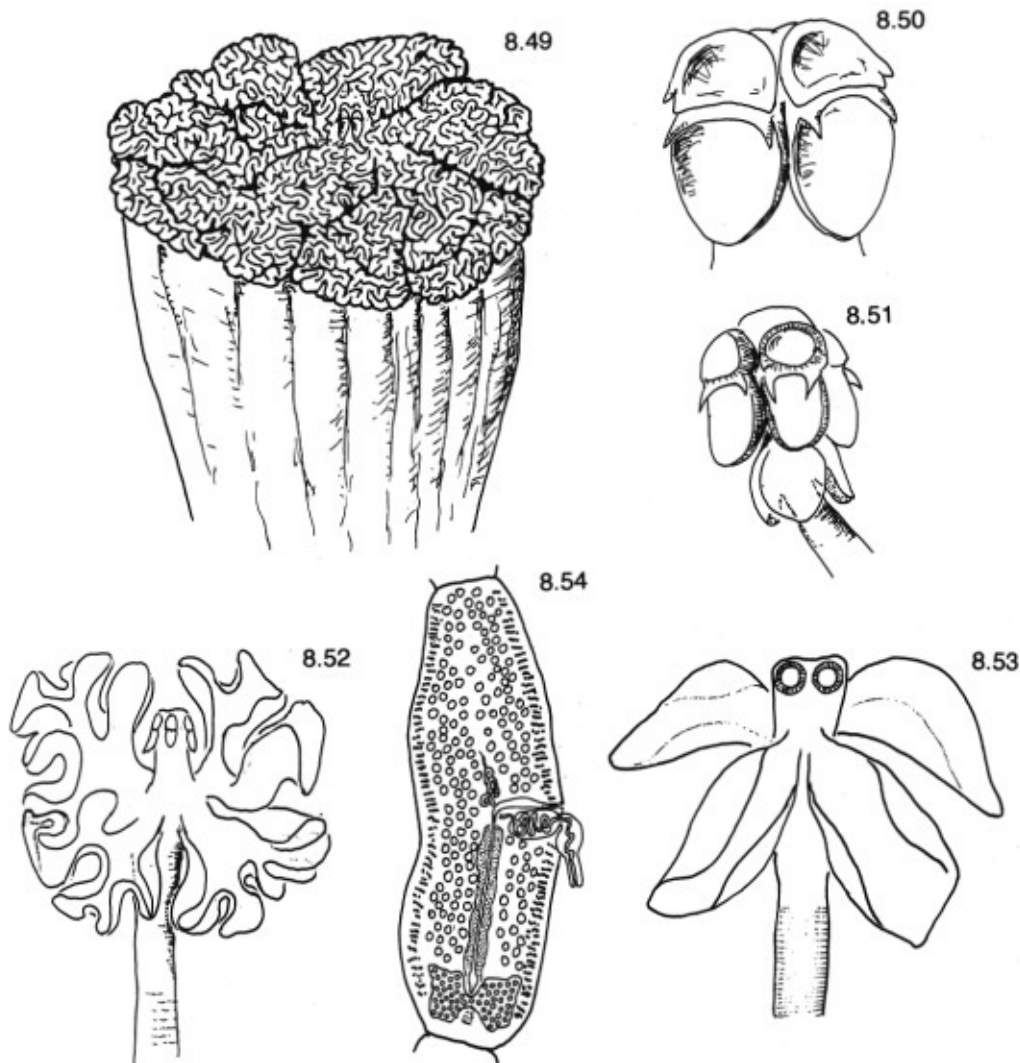
Key to genera

- 1a. Metascolex with four indistinct parts, very frilled and crumpled. Scolex with
 four minute bothridia each with anterior muscular pad
 *Thysanocephalum* Linton, 1889. (Figs 8.49–8.51)

Diagnosis: Scolex very small with four sessile bothridia each with two minute muscular prongs and one anterior muscular pad forming lateral auriculum. Strobila acraspedote, apolytic. Genital pores irregularly alternating. Testes numerous, postvaginal testes present on poral side. Ovary posterior. Vagina anterior to cirrus-sac. Vitelline follicles forming marginal strips along entire length of proglottid. In *Carcharinidae*. Cosmopolitan. Type-species *T. thysanocephalum* (Linton, 1889).

- 1b. Metascolex with four distinct folded lobes 2.
- 2a. Scolex with four bothridia each with anterior sucker
 *Myzocephalus* Shipley & Hornell, 1906. (Fig. 8.52)
 (Syn. *Myxophyllobothrium* Shinde & Chincholikar, 1981.)

Diagnosis: Scolex small with metascolex in four crumpled folds. Genital pores irregularly alternating. Strobila anatomy unknown. In *Myliobatidae*. Indian Ocean. Type-species *M. narinari* Shipley & Hornell, 1906.



Figs 8.49–8.51 *Thysanocephalum* Linton, 1889. 8.49. Adult scolex and metasclex. 8.50. Scolex. (After Euzet, 1959.) 8.51. Young scolex and metasclex. (After Subhadrappa, 1957.)
Fig. 8.52 *Myzocephalus* Shipley & Hornell, 1906. Scolex. (After Shipley & Hornell, 1906.)
Figs 8.53, 8.54 *Myzophyllobothrium* Shipley & Hornell, 1906. 8.53. Scolex and metasclex. 8.54. Mature proglottid. (After Shipley & Hornell, 1906.)

2b. Scolex with four bothridia without anterior suckers
 *Myzophyllobothrium* Shipley & Hornell, 1906. (Figs 8.53, 8.54)

Diagnosis: Scolex small with four large circular bothridia. Metasclex divided into four distinct parts with smooth edges. Red pigment at base of metasclex. Strobila acraspedote, apolytic. Genital pores lateral, irregularly alternating. Testes numerous; postvaginal testes present on poral side. Ovary posterior. Vagina anterior to cirrus-sac. Vitelline follicles lateral. Uterus median, ventral, extending

from ovary to level of cirrus-sac. In Myliobatiformes. Indian Ocean. Type-species *M. rubrum* Shipley & Hornell, 1906.

Subfamily Echeneibothriinae de Beauchamp, 1905

Diagnosis: Phyllobothriidae. Scolex with apical myzorhynchus. Four bothridia, smooth or divided by septa. Postvaginal testes absent. Parasites of Rajidae.

Key to genera

1a. Scolex with four smooth bothridia each with simple or loculated margin 2.

1b. Scolex with four bothridia partially or totally divided by septa 3.

2a. Bothridia cup-shaped with simple margin
Pseudoanthobothrium Baer, 1956. (Fig. 8.55)

Diagnosis: Scolex with four pedunculated bothridia. Myzorhynchus present. Strobila acraspedote, euapolytic. Genital pores irregularly alternating. Testes few, anterior; postvaginal testes absent on poral side. Ovary posterior, X-shaped in cross-section. Vagina anterior to cirrus-sac. Vitelline follicles lateral. In Rajidae. North Atlantic. Type-species *P. hanseni* Baer, 1956.

2b. Bothridia with one marginal row of loculi
Clydonobothrium Euzet, 1959. (Fig. 8.56)

Diagnosis: Scolex with small apical myzorhynchus and four large bothridia with crumpled and loculated margin. Accessory sucker absent. Strobila acraspedote, anapolytic. Genital pores lateral, irregularly alternating. Testes anterior to cirrus-sac; postvaginal testes absent on poral side. Ovary posterior. Vagina anterior to cirrus-sac. Vitelline follicles lateral. In Rajidae. North Atlantic. Type-species *C. elegantissimum* (Lönnerberg, 1889).

3a. Bothridia with incomplete septa
Phormobothrium Alexander, 1963. (Fig. 8.57)

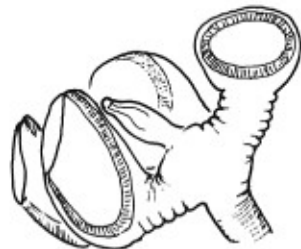
Diagnosis: Scolex apical with myzorhynchus and four pedunculate bothridia. Each bothridium with few incomplete longitudinal ridges. Strobila acraspedote, euapolytic (?) Genital pores lateral, irregularly alternating. Testes few; postvaginal testes absent on poral side. Ovary posterior. Vagina anterior to cirrus-sac. Vitelline follicles lateral. In Rajidae. New Zealand. Type-species *P. affine* (Olsson, 1867).

3b. Bothridia totally septate 4.

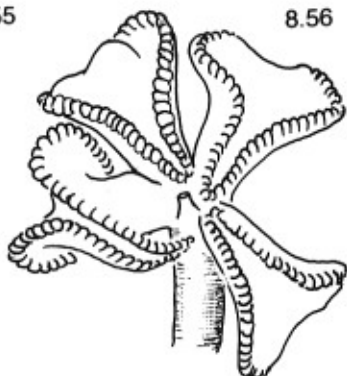
4a. Bothridia divided into three loculi
Tritaphros Lönnerberg, 1889. (Fig. 8.58)

Diagnosis: Scolex with small myzorhynchus and four sessile bothridia. Each bothridium divided into three large loculi by two longitudinal septa. Strobila slightly craspedote, anapolytic. Genital pores lateral, irregularly alternating.

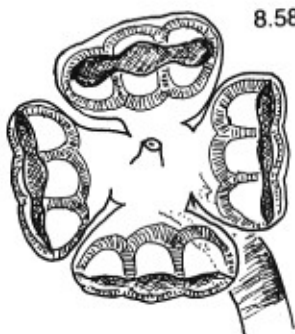
8.55



8.56



8.58



8.57

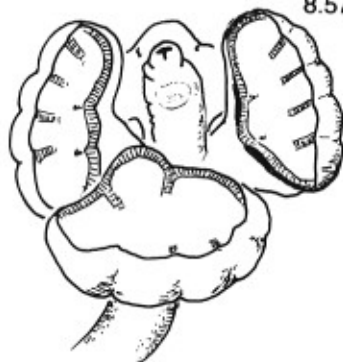


Fig. 8.55 *Pseudanthobothrium* Baer, 1956. Scolex. (After Baer, 1956.)

Fig. 8.56 *Clydonobothrium* Euzet, 1959. Scolex. (After Euzet, 1959.)

Fig. 8.57 *Phormobothrium* Alexander, 1963. Scolex. (After Alexander, 1963.)

Fig. 8.58 *Tritaphros* Lönnberg, 1889. Scolex. (After Euzet, 1959.)

Testes anterior; postvaginal testes absent on poral side. Ovary posterior, X-shaped in cross-section. Vagina anterior to cirrus-sac. Vitelline follicles in lateral fields. In Rajidae. North Atlantic, western Mediterranean. Type-species *T. retzii* Lönnberg, 1889.

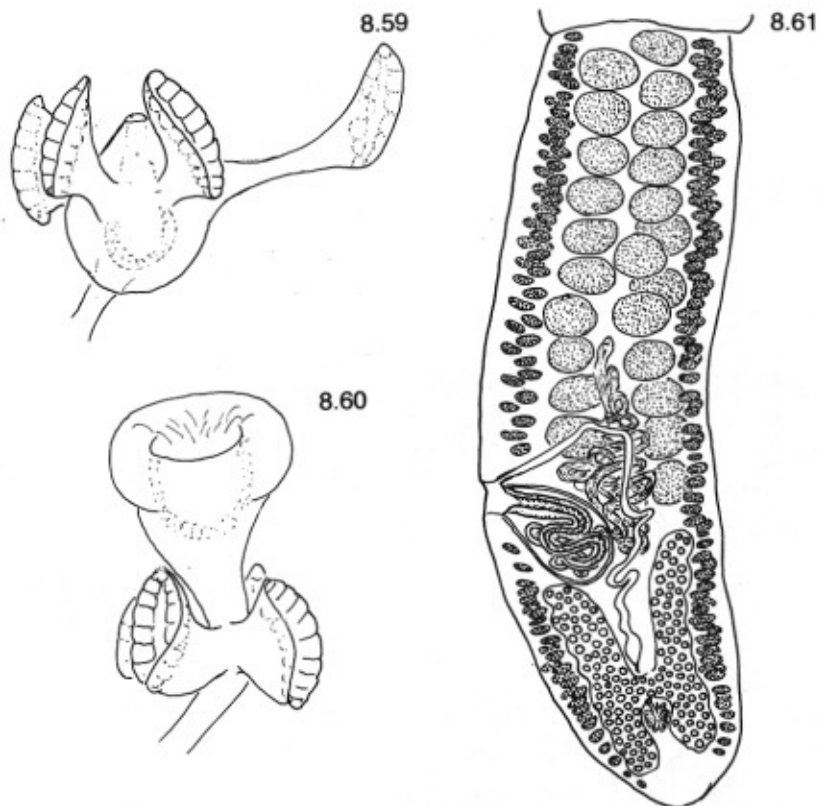
4b. Bothridia divided into numerous loculi

..... *Echeneibothrium* van Beneden, 1850. (Figs 8.59–8.61)
(Syn. *Discobothrium* van Beneden, 1870.)

Diagnosis: Scolex with apical retractile myzorhynchus of variable size and four pedunculated or sessile bothridia each divided by transverse and longitudinal septa. Strobila acraspedote or slightly craspedote, euapolytic. Genital pores lateral, irregularly alternating. Testes few; postvaginal testes absent on poral side. Ovary posterior, X-shaped in cross-section. Vagina anterior to cirrus-sac. Vitelline follicles lateral. Uterus median tubular. In Rajidae. Cosmopolitan. Type-species *E. variabile* van Beneden, 1850.

Subfamily Phyllobothriinae de Beauchamp, 1905

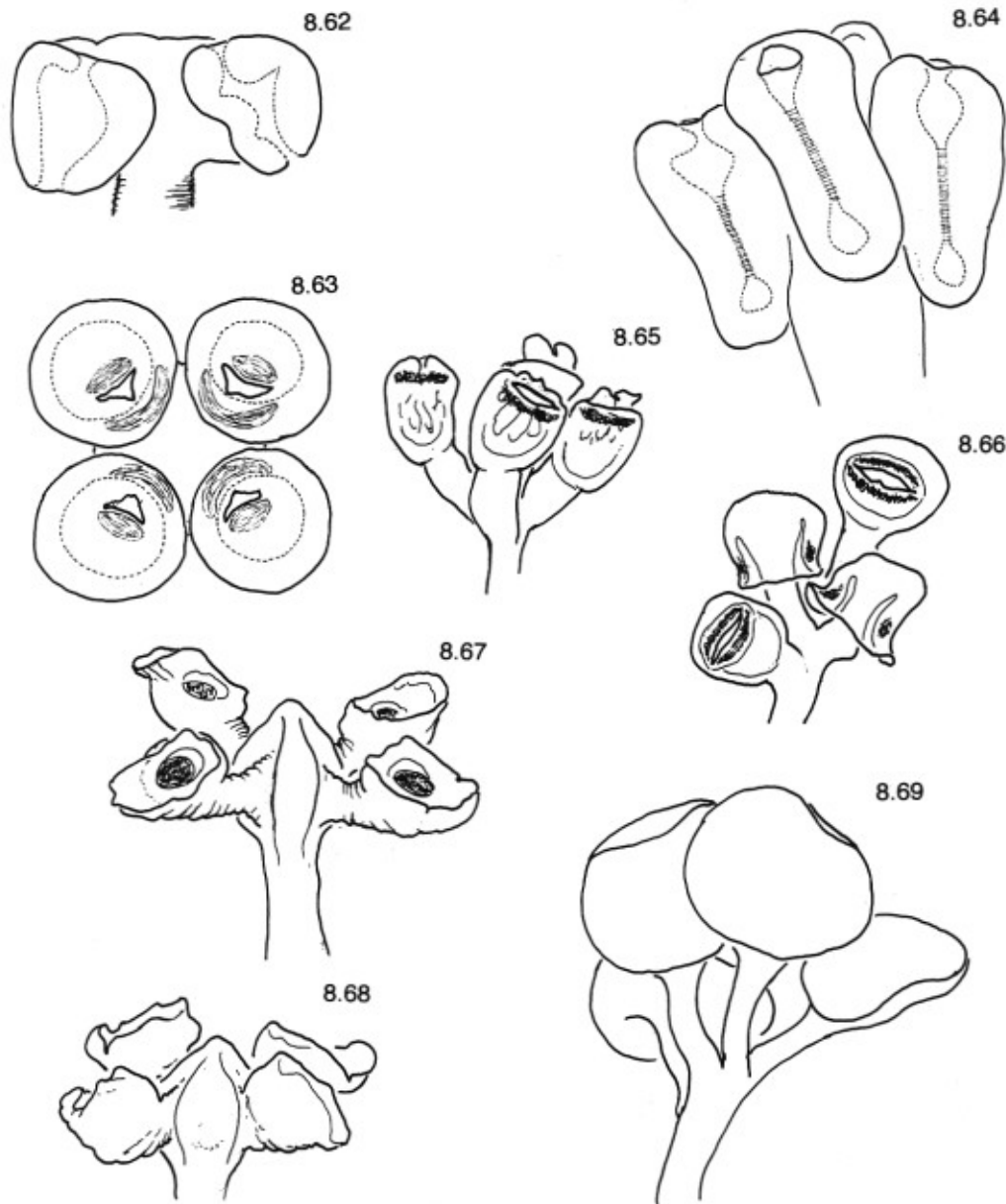
Diagnosis: Phyllobothriidae. Scolex unarmed, with four bothridia without loculi, with simple, crumpled or loculated margin. No myzorhynchus.



Figs 8.59-8.61 *Echeneibothrium* van Beneden, 1850. 8.59. Scolex with invaginated myzorhynchus. 8.60. Scolex with everted myzorhynchus. 8.61. Mature proglottid. (After Euzet, 1959.)

Key to genera

- 1a. Bothridia without accessory sucker 2.
 1b. Bothridia with accessory sucker 7.
- 2a. Bothridia sessile, tubular, with anterior and posterior opening
 *Pitbophorus* Southwell, 1925. (Figs 8.62, 8.63)
Diagnosis: Scolex with four globular or cylindrical hollow bothridia, each open at both anterior and posterior ends. Strobila acraspedote. Genital pores lateral, irregularly alternating. Testes numerous; postvaginal testes present on poral side. Ovary bilobed in cross-section. Vagina anterior to cirrus-sac. Vitelline follicles lateral. In elasmobranchs. Pacific Ocean, Indian Ocean, Sea of Japan. Type-species *P. tetraglobus* (Southwell, 1911).
- 2b. Bothridia non-tubular 3.
- 3a. Bothridia globular, pouch-shaped 4.
 3b. Bothridia non-globular with simple or crimped margin 5.



Figs 8.62, 8.63 *Pithophorus* Southwell, 1925. 8.62. Scolex, lateral view. 8.63. Scolex, apical view. (After Subhadrappa, 1957.)

Fig. 8.64 *Scyphophyllidium* Woodland, 1927. Scolex. (After Euzet, 1959.)

Figs 8.65, 8.66 *Carpobothrium* Shipley & Hornell, 1906. 8.65. Scolex contracted. 8.66. Scolex with everted bothridia. (After Subhadrappa, 1957.)

Figs 8.67, 8.68 *Clistobothrium* Dailey & Vogelbein, 1990. 8.67. Scolex, with bothridia extended. 8.68. Scolex contracted. (After Dailey & Vogelbein, 1990.)

Fig. 8.69 *Anthobothrium* van Beneden, 1850. Scolex. (After Euzet, 1959.)

- 4a. Bothridial opening without muscular pad
 *Scyphobhyllidium* Woodland, 1927. (Fig. 8.64)
Diagnosis: Scolex with four globular, sessile bothridia with irregular anterior opening. Accessory sucker absent. Strobila acraspedote, anapolytic. Genital pores lateral, irregularly alternating. Testes numerous; postvaginal testes present on poral side. Ovary posterior, bilobed in cross-section. Vitelline follicles in wide lateral bands. In Carcharinidae. North Atlantic. Type-species *S. giganteum* (van Beneden, 1858).
- 4b. Bothridial opening with muscular pad
 *Carpobothrium* Shipley & Hornell, 1906. (Figs 8.65, 8.66)
Diagnosis: Scolex with four pedunculated bothridia each with a single flap surrounding a slit-like opening. No marginal loculi on the flap. A pair of muscular pads at the base of the flap. Strobila acraspedote, apolytic. Genital pores lateral, irregularly alternating. Testes numerous; no postvaginal testes on poral side. Cirrus-sac U-shaped. Ovary posterior. Vagina large, anterior to cirrus-sac. Vitelline follicles lateral. Uterus median, extending from ovary to cirrus-sac. In Orcetolobiformes. Indian Ocean. Type-species *C. chiloscyllii* Shipley & Hornell, 1906.
- 5a. Bothridia with one central sucker
 *Clistobothrium* Dailey & Vogelbein, 1990. (Figs 8.67, 8.68)
Diagnosis: Scolex with four pedunculated bothridia separated by a large cruciform apex. Each bothridium with large bowl-shaped sucker and folding lap-pet that projects over sucker opening when extended. Strobila acraspedote, anapolytic. Genital pore lateral, irregularly alternating. Testes numerous; postvaginal testes present on poral side. Ovary posterior. Vagina anterior to cirrus-sac. Vitelline follicles in wide lateral bands. Uterus median, reaching only to posterior margin of cirrus-sac. In Carcharinidae. American coast of Pacific. Type-species *C. carcharodoni* Dailey & Vogelbein, 1990.
- 5b. Bothridia without central sucker 6.
- 6a. Bothridia simple, disc-shaped
 *Anthobothrium* van Beneden, 1850. (Fig. 8.69)
Diagnosis: Scolex with four bothridia, pedunculate with a simple edge. Accessory sucker absent. Sometimes one central muscular sucker. Strobila craspedote, lacinated, euapolytic. Genital pores irregularly alternating. Testes numerous; postvaginal testes present on poral side. Ovary posterior. Vitelline follicles lateral. In Carchariniformes. Cosmopolitan. Type-species *A. cornucopia* van Beneden, 1850.
- 6b. Bothridia crimped, sometimes retractile
 *Rhodobothrium* Linton, 1889. (Figs 8.70, 8.71)
 (Syns *Proboscidosaccus* Gallien, 1949; *Inermiphyllidium* Riser, 1955;
Sphaerobothrium Euzet, 1959.)
Diagnosis: Scolex with four large subspherical bothridia supported by pedicel. Bothridia trumpet-shaped when relaxed with convex adherent surface traversed by numerous convolutions forming an irregular pattern. Accessory sucker absent.

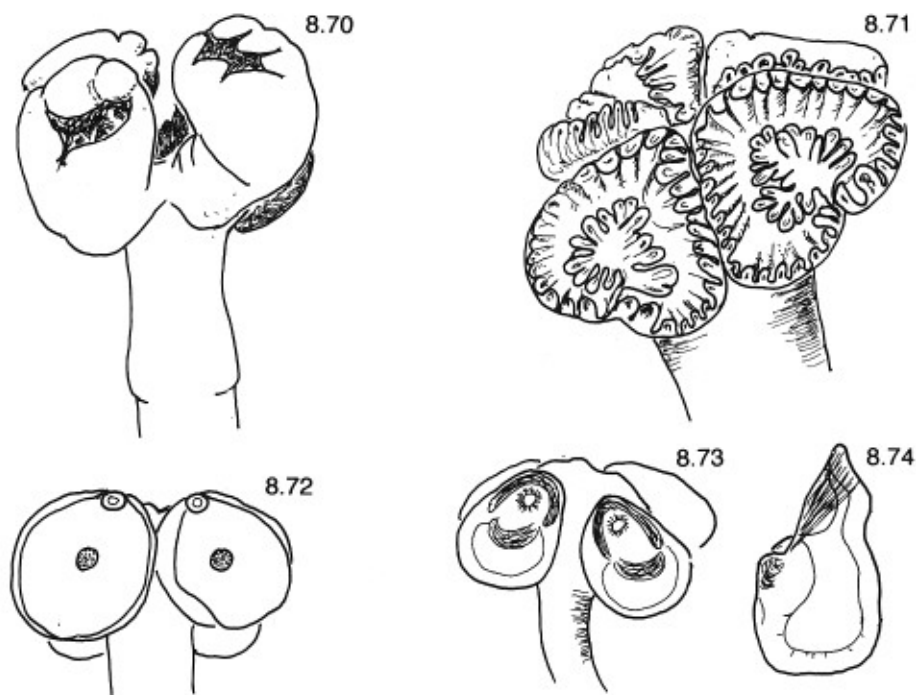
Strobila acraspedote, apolytic, proglottid triangular. Testes numerous; post-vaginal testes present on poral side. Ovary posterior, tetralobed in cross-section. Vagina anterior to cirrus-sac. Vitelline follicles lateral. Uterus median, sac-like with lateral diverticula. In Myliobatiformes. Cosmopolitan. Type-species *R. pulvinatum* Linton, 1889.

7a. Bothridia with central glandular disc
 *Orygmatobothrium* Diesing, 1863. (Fig. 8.72)

Diagnosis: Scolex with four bothridia each with simple or crumpled margin. Accessory sucker present. One glandular circular organ near centre of each bothridium. Strobila acraspedote, euapolytic. Genital pores irregularly alternating. Testes numerous; postvaginal testes present on poral side. Ovary posterior, tetralobed in cross-section. Vitelline follicles lateral. In Mustelidae. Cosmopolitan. Type-species *O. musteli* (van Beneden, 1850).

7b. Bothridia without central glandular disc 8.

8a. Bothridia globular, pouch-shaped
 *Marsupiobothrium* Yamaguti, 1952. (Figs 8.73, 8.74)



Figs 8.70, 8.71 *Rhodobothrium* Linton, 1889. 8.70. Scolex contracted. 8.71. Scolex extended. (After Euzet, 1959.)

Fig. 8.72 *Orygmatobothrium* Diesing, 1863. Scolex. (After Euzet, 1959.)

Figs 8.73, 8.74 *Marsupiobothrium* Yamaguti, 1952. 8.73. Scolex. 8.74. Bothridium. (After Yamaguti, 1952.)

Diagnosis: Scolex with four sessile bothridia each shaped like pyriform sac, opening of which is provided with sphincter-like muscle especially in posterior region. Submarginal accessory sucker present at anterior end of each bothridium. Strobila acraspedote, euapolytic. Genital pores lateral, irregularly alternating. Testes numerous; postvaginal testes present on poral side. Ovary posterior with two long slender wings. Vitelline follicles in two extensive lateral fields. In Alopiidae (Carchariniformes). Pacific. Type-species *M. alopias* Yamaguti, 1952.

8b. Bothridia not pouch-shaped 9.

9a. Bothridia with crumpled or loculated margin
 *Phyllobothrium* van Beneden, 1850. (Figs 8.75–8.79)
 (Syn. *Anthocephalum* Linton, 1890.)

Diagnosis: Scolex with four bothridia each sessile or pedunculated. One accessory sucker present. Margin of bothridia folded, curled, with or without loculi. Apical glandular organ sometimes present. Strobila craspedote or acraspedote, apolytic or anapolytic. Genital pores lateral, irregularly alternating, sometimes unilateral along part of strobila. Testes numerous; postvaginal testes present or not on poral side. Ovary posterior, four-lobed or bilobed in cross-section. Vitelline follicles lateral. In elasmobranchs. Cosmopolitan. Type-species *P. lactuca* van Beneden, 1850.

9b. Bothridia with simple margin 10.

10a. Bothridia with anterolateral bifid lobe 11.

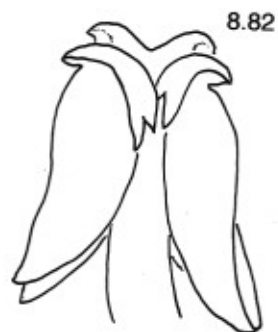
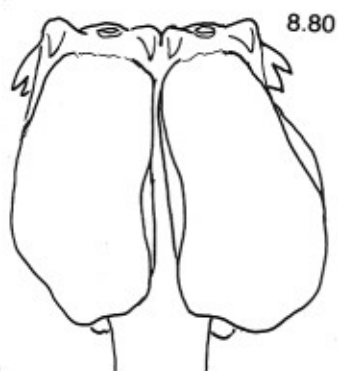
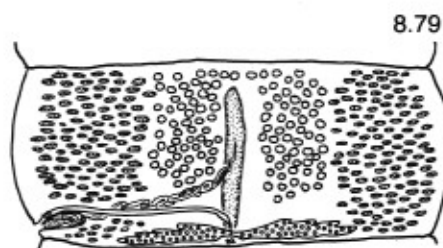
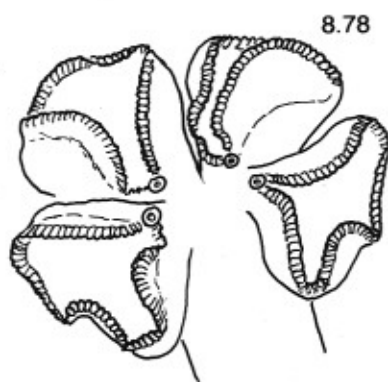
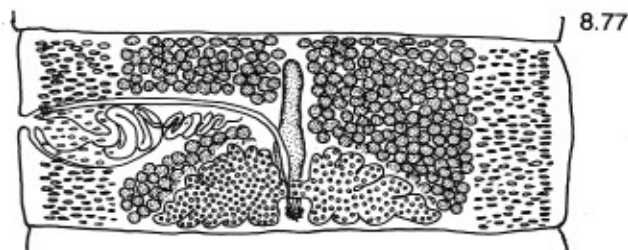
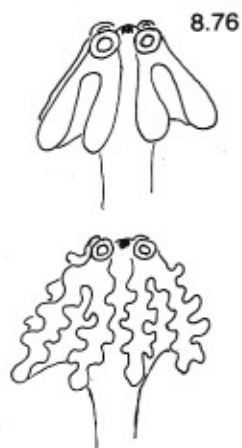
10b. Bothridia without bifid lobe 12.

11a. Proglottid with lateral vitelline follicles
 *Dinobothrium* van Beneden, 1889. (Figs 8.80, 8.81)
 (Syns *Diplobothrium* van Beneden, 1889; *Reesium* Euzet, 1955.)

Diagnosis: Scolex with four sessile bothridia, large, not folded, on margin each surmounted by muscular pad with two little prongs, extremity of muscular pad terminated by bifid lobe. One accessory sucker present on medial surface of muscular pad. Strobila acraspedote, anapolytic. Genital pores lateral, irregularly alternating. Testes numerous; postvaginal testes present on poral side. Ovary posterior, tetralobed in cross-section. Vitelline follicles lateral. In Lamniformes. Cosmopolitan. Type-species *D. septaria* van Beneden, 1889.

11b. Proglottid with ventral vitelline follicles
 *Gastrolecithus* Yamaguti, 1952. (Figs 8.82, 8.83)

Diagnosis: Scolex large with four sessile concave bothridia, paired dorsoventrally. Each bothridium with one anterior muscular pad, one accessory sucker and two little lateral prongs and bifid crest-like appendage at its anterodorsal corner. Strobila craspedote, anapolytic. Genital pores lateral, irregularly alternating. Testes numerous; postvaginal testes present on poral side. Ovary bilobed in cross-section. Vagina anterior to cirrus-sac. Vitelline follicles ventral. In Cetorhinidae. Cosmopolitan. Type-species *G. planus* (Linton, 1922).



- 12a. Accessory sucker circular 13.
 12b. Accessory sucker triangular with two posterolateral muscular prongs
 14.

13a. Accessory sucker cup-shaped. Postvaginal testes present
 *Crossobothrium* Linton, 1889. (Fig. 8.84)

Diagnosis: Scolex with four bothridia, each sessile with accessory sucker and simple edge. Strobila acraspedote, euapolytic. Genital pore lateral, irregularly alternating. Testes numerous; postvaginal testes present on poral side. Ovary posterior, tetralobed in cross-section. Vagina anterior to cirrus-sac. Vitelline follicles lateral. In Pleurotremata. Cosmopolitan. Type-species *C. angustum* (Linton, 1889).

13b. Accessory sucker globular. Postvaginal testes absent
 *Calytrobthrium* Monticelli, 1893. (Fig. 8.85)

Diagnosis: Scolex with four sessile bothridia with simple edge. Accessory sucker large, subspherical. Strobila acraspedote, hyperapolytic. Genital pores lateral, irregularly alternating. Testes numerous; postvaginal testes absent on poral side. Ovary posterior. Vagina anterior to cirrus-sac. Vitelline follicles lateral. In Torpedinidae. North Atlantic and Mediterranean. Type-species *C. riggii* Monticelli, 1893.

14a. Vitelline follicles lateral
 *Ceratobothrium* Monticelli, 1892. (Fig. 8.86)

Diagnosis: Scolex with four sessile bothridia each directly below large muscular pad bearing two projecting horn-like appendages consisting mainly of circular muscle fibres. Yellowish scolex (scolex deformatus) often embedded in gut wall. Strobila acraspedote, apolytic. Genital pores lateral, irregularly alternating. Testes numerous; postvaginal testes present on poral side. Cirrus-sac long, oblique anteriorly. Ovary posterior, X-shaped in cross-section. Vagina anterior to cirrus-sac. In Lamniformes. Cosmopolitan. Type-species *C. xanthocephalum* Monticelli, 1892.

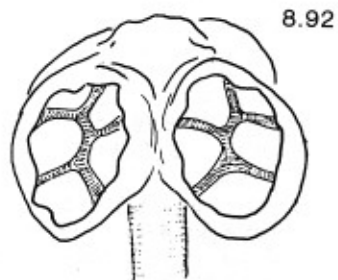
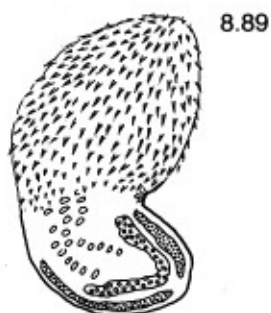
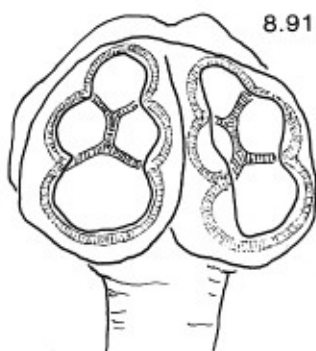
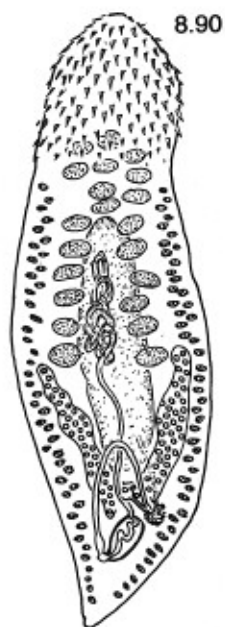
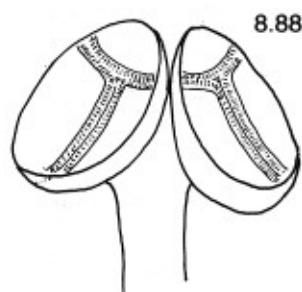
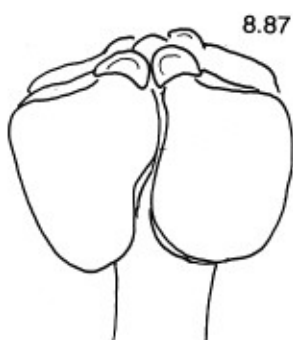
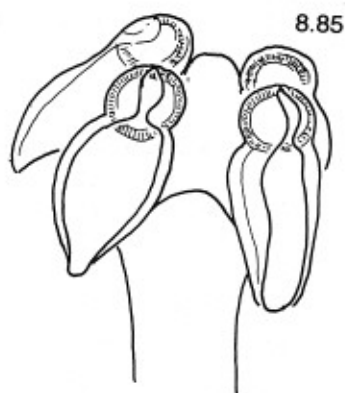
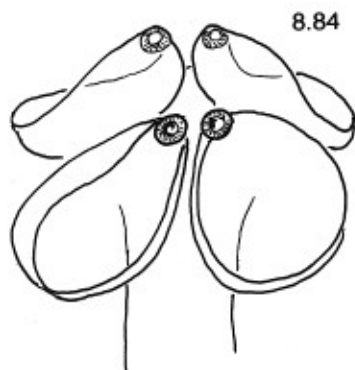
14b. Vitelline follicles circum-medullary
 *Monorygma* Diesing, 1863. (Fig. 8.87)

Diagnosis: Scolex with apical glandular mass and four large sessile bothridia each with anterior muscular pad, horseshoe-shaped, bearing two small lateral appendages. Strobila acraspedote, anapolytic. Genital pores lateral, irregularly alternating. Genital atrium present. Testes numerous; postvaginal testes present on poral side. Ovary posterior. Vagina anterior to cirrus-sac. Uterus saccate, between ovary and cirrus-sac. In Squaliformes. North Atlantic and Mediterranean. Type-species *M. perfectum* (van Beneden, 1853).

Figs 8.75-8.79 *Phyllobothrium* van Beneden, 1850. 8.75. Scolex of *P. lactuca* van Beneden, 1850. 8.76. Bothridial complication in *P. lactuca*. 8.77. Mature proglottid of *P. lactuca* with postvaginal testes. 8.78. Scolex of *P. gracile* Wedl, 1855. 8.79. Mature proglottid of *P. gracile* without postvaginal testes. (After Euzet, 1959.)

Figs 8.80, 8.81 *Dinobothrium* van Beneden, 1889. 8.80. Scolex. 8.81. Cross-section showing lateral vitelline follicles. (After Euzet, 1959.)

Figs 8.82, 8.83 *Gastrolecithus* Yamaguti, 1952. 8.82. Scolex, lateral view. 8.83. Cross-section showing ventral vitelline follicles. (After Euzet, 1959.)



Subfamily Triloculariinae Yamaguti, 1959

Diagnosis: Scolex with four bothridia divided by septa into few loculi. No metascolex or myzorhynchus.

Key to genera

1a. Scolex with four bothridia each divided into three loculi. Hyperapolytic.

Genital pore posterior *Trilocularia* Olsson, 1867. (Figs 8.88–8.90)
(Syns *Phyllobothrideum* Olsson, 1867; *Urogonoporus* Lühe, 1901.)

Diagnosis: Scolex with four sessile bothridia each divided into three loculi (one apical, two posterior) by muscular septa. No myzorhynchus. Strobila filiform, hyperapolytic. Free proglottids with large anterior spines. Genital pore near posterior end of proglottid. Testes few, anterior; postvaginal testes absent on poral side. Ovary posterior, U-shaped. Vitelline follicles lateral. Uterus median with lateral diverticulum. In Squalidae. North Atlantic and Mediterranean. Type-species *T. acanthiaevulgaris* Olsson, 1867.

1b. Scolex with four bothridia each, with more than three loculi. Apolytic.

Genital pore lateral 2.

2a. Bothridia divided into four symmetrical loculi

..... *Zyxibothrium* Hayden & Campbell, 1981. (Fig. 8.91)

Diagnosis: Scolex with four sessile bothridia each divided into four loculi (one anterior, two median, one posterior) by muscular septa. No myzorhynchus. Strobila slightly craspedote, apolytic. Genital pore marginal, irregularly alternating. Testes anterior; postvaginal testes absent on poral side. Ovary posterior, U-shaped, bilobed in cross-section. Vagina anterior to cirrus-sac. Vitelline follicles lateral. Uterus sac-shaped. In *Raja*. North Atlantic. Type-species *Z. kamiense* Hayden & Campbell, 1981.

2b. Bothridia divided into five asymmetrical loculi

..... *Pentaloculum* Alexander, 1963. (Fig. 8.92)

Diagnosis: Scolex with four sessile bothridia each divided by muscular septa into five radial loculi more or less equal in size. No myzorhynchus. Strobila small, slightly craspedote, apolytic. Genital pore lateral, irregularly alternating. Testes numerous; postvaginal testes absent on poral side. Ovary posterior. Vagina anterior to cirrus-sac. Vitelline follicles lateral. In *Torpedo aysoni*. New Zealand. Type-species *P. macrocephalum* Alexander, 1963.

Fig. 8.84 *Crossobothrium* Linton, 1889. Scolex. (After Euzet, 1959.)

Fig. 8.85 *Calyptrobothrium* Monticelli, 1893. Scolex. (After Euzet, 1959.)

Fig. 8.86 *Ceratobothrium* Monticelli, 1892. Scolex. (After Euzet, 1959.)

Fig. 8.87 *Monorygma* Diesing, 1863. Scolex. (After Euzet, 1959.)

Figs 8.88–8.90 *Trilocularia* Olsson, 1867. 8.88. Scolex. 8.89. Young proglottid. 8.90. Mature proglottid. (After Euzet, 1959.)

Fig. 8.91 *Zyxibothrium* Hayden & Campbell, 1981. Scolex. (After Hayden & Campbell, 1981.)

Fig. 8.92 *Pentaloculum* Alexander, 1963. Scolex. (After Alexander, 1963.)

Subfamily Rhinebothriinae Euzet, 1953

Diagnosis: Scolex with four bothridia divided by septa into numerous loculi. No myzorhynchus.

Key to genera

- 1a. Postvaginal testes absent on poral side 2.
 1b. Postvaginal testes present on poral side 3.

- 2a. Ovarian lobes unequal, poral lobes shorter
 *Rhinebothroides* Mayes, Brooks & Thorson, 1981. (Figs 8.93, 8.94)

Diagnosis: Scolex with four pedunculated bothridia, subdivided into loculi by several transverse septa, and one longitudinal, muscular septum. No myzorhynchus. Strobila acraspedote, apolytic. Genital pores lateral, irregularly alternating. Testes numerous, anterior to cirrus-sac; postvaginal testes absent on poral side. Ovary posterior with greatly reduced poral lobe in dorsal view, X-shaped in cross-section. Vagina anterior to cirrus-sac. Vitelline follicles lateral. Only in freshwater Dasyatidae (*Potamotrygon*). South America. Type-species *R. moralarai* (Brooks & Thorson, 1976).

- 2b. Ovarian lobes equal *Rhinebothrium* Linton, 1889. (Figs 8.95, 8.96)

Diagnosis: Scolex with four pedunculated bothridia, subdivided into loculi by several transverse septa and one longitudinal septum. Bothridial margin entire or loculated. No myzorhynchus. Cephalic peduncle short or absent. Strobila acraspedote or slightly craspedote. Euapolytic. Genital pore lateral. Testes few to numerous, anterior to cirrus-sac; postvaginal testes absent on poral side. Ovary posterior, X-shaped in cross-section. Vagina anterior to cirrus-sac. Vitelline follicles lateral. Uterus simple, median. Eggs isolated or in cocoon. In Myliobatiformes, Rajiformes. Cosmopolitan. Type-species *R. flexile* Linton, 1890.

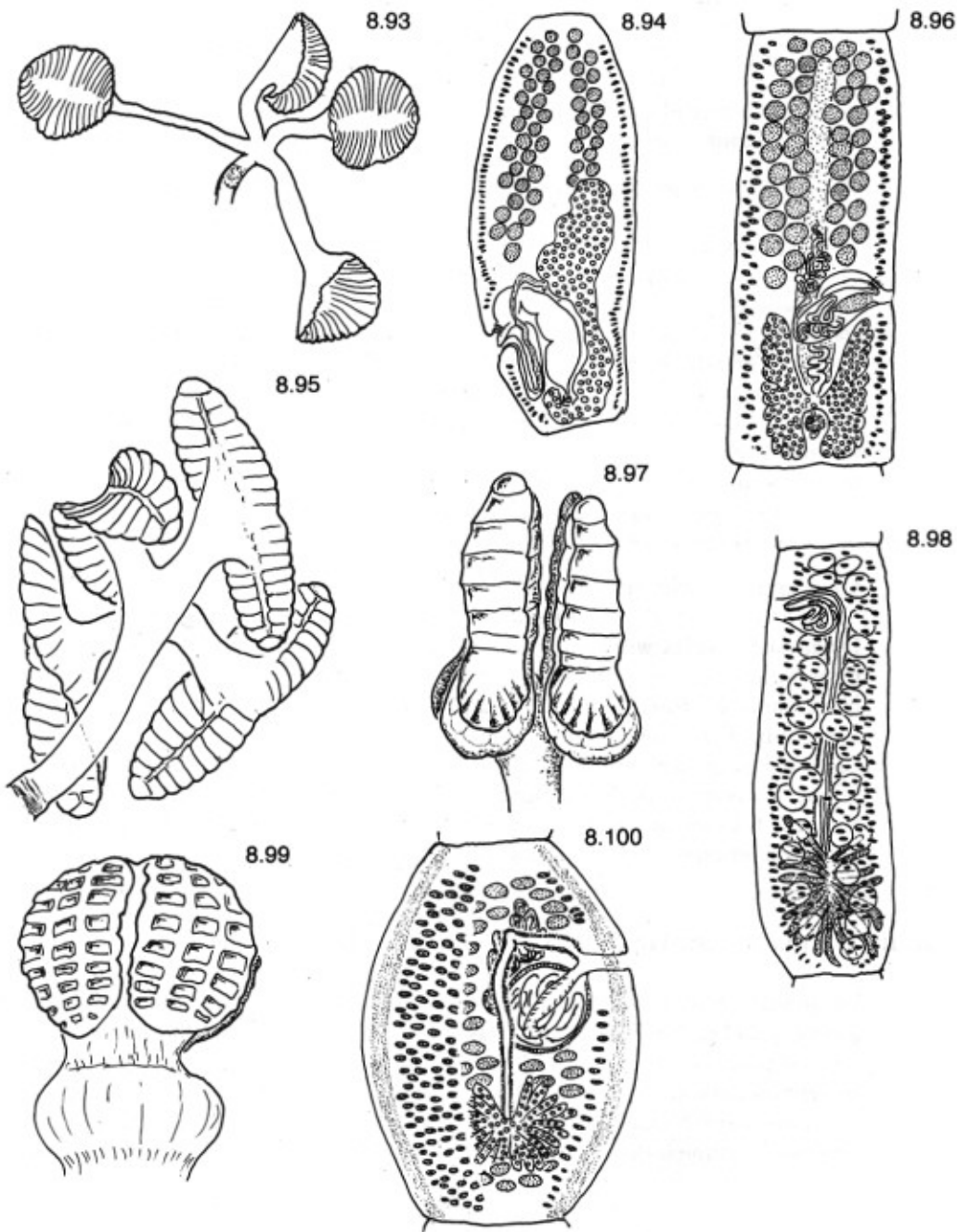
- 3a. Bothridium in two parts, posterior part with longitudinal septa only
 *Duplicibothrium* Williams & Campbell, 1978. (Figs 8.97, 8.98)

Diagnosis: Scolex forked with four sessile bothridia, dorsal and ventral fused into two pairs. Bothridia subdivided into loculi by transverse septa except at base where they form cup with few radial loculi. No myzorhynchus. Cephalic peduncle present. Strobila acraspedote, apolytic. Genital pores submarginal, irregularly alternating. Testes medullary; postvaginal testes present on poral side. Cirrus-sac anterior. Ovary posterior with radiating lobules. Vagina anterior to cirrus-sac. Vitelline follicles circum-medullary. In Rhinobatidae. North Atlantic. Type-species *D. minutum* Williams & Campbell, 1978.

- 3b. Bothridium with transverse and longitudinal septa 4.

- 4a. Bothridium sessile with three longitudinal rows of loculi
 *Glyphobothrium* Williams & Campbell, 1977. (Figs 8.99, 8.100)

Diagnosis: Scolex globular with four sessile bothridia fused to scolex. Each bothridium subdivided into three longitudinal rows of loculi by several transverse and two longitudinal septa. No myzorhynchus. Strobila craspedote, apolytic.



Figs 8.93, 8.94 *Rhinebothroides* Mayes, Brooks & Thorson, 1981. 8.93. Scolex. 8.94. Mature proglottid. (After Mayes *et al.*, 1981.)

Figs 8.95, 8.96 *Rhinebothrium* Linton, 1889. 8.95. Scolex. 8.96. Mature proglottid. (After Euzet, 1959.)

Figs 8.97, 8.98 *Duplicibothrium* Williams & Campbell, 1978. 8.97. Scolex. 8.98. Mature proglottid. (After Williams & Campbell, 1978.)

Figs 8.99, 8.100 *Glyphobothrium* Williams & Campbell, 1977. 8.99. Scolex. 8.100. Mature proglottid, vitelline follicles only on the left side. (After Williams & Campbell, 1978.)

Genital atrium present. Genital pore lateral, irregularly alternating. Testes numerous; postvaginal testes present on poral side. Ovary posterior, X-shaped in cross-section. Vagina glandular, anterior to cirrus-sac. Vitelline follicles circum-medullary, extending full length of proglottid. In Rhinobatidae. American North-Atlantic. Type-species *G. zwernerii* Williams & Campbell, 1974.

4b. Bothridium pedunculated with two longitudinal rows of loculi 5.

5a. Cephalic peduncle very long
 *Caulobothrium* Baer, 1948. (Figs 8.101–8.103)

Diagnosis: Scolex with four sessile bothridia; divided into loculi by several transverse septa, and one longitudinal septum. No myzorhynchus. Cephalic peduncle greatly developed. Strobila craspedote or not, apolytic. Genital pores lateral, irregularly alternating. Testes numerous; postvaginal testes present on poral side. Cirrus-sac large with spinose cirrus. Ovary posterior, X-shaped in cross-section. Vagina anterior to cirrus-sac. Vaginal sphincter present. Vitelline follicles lateral, well-developed dorsally and ventrally. Uterus median with lateral diverticula. In Myliobatidae. North Atlantic and Mediterranean. Type-species *C. longicolle* (Linton, 1890).

5b. Cephalic peduncle short or absent
 *Rhabdotobothrium* Euzet, 1953. (Figs 8.104, 8.105)

Diagnosis: Scolex with four pedunculated bothridia, subdivided into loculi by several transverse septa and one median longitudinal septum. No myzorhynchus. Neck short or absent. Strobila craspedote, euapolytic. Genital pores lateral, irregularly alternating. Testes numerous; postvaginal testes present on poral side. Cirrus-sac large with spinose cirrus. Ovary posterior, X-shaped in cross-section. Vagina anterior to cirrus-sac, forming large loop in anterior half of proglottid. Vitelline follicles lateral. Uterus median, sac-like. In Dasyatidae. North Atlantic and Mediterranean. Type-species *R. dollfusi* Euzet, 1953.

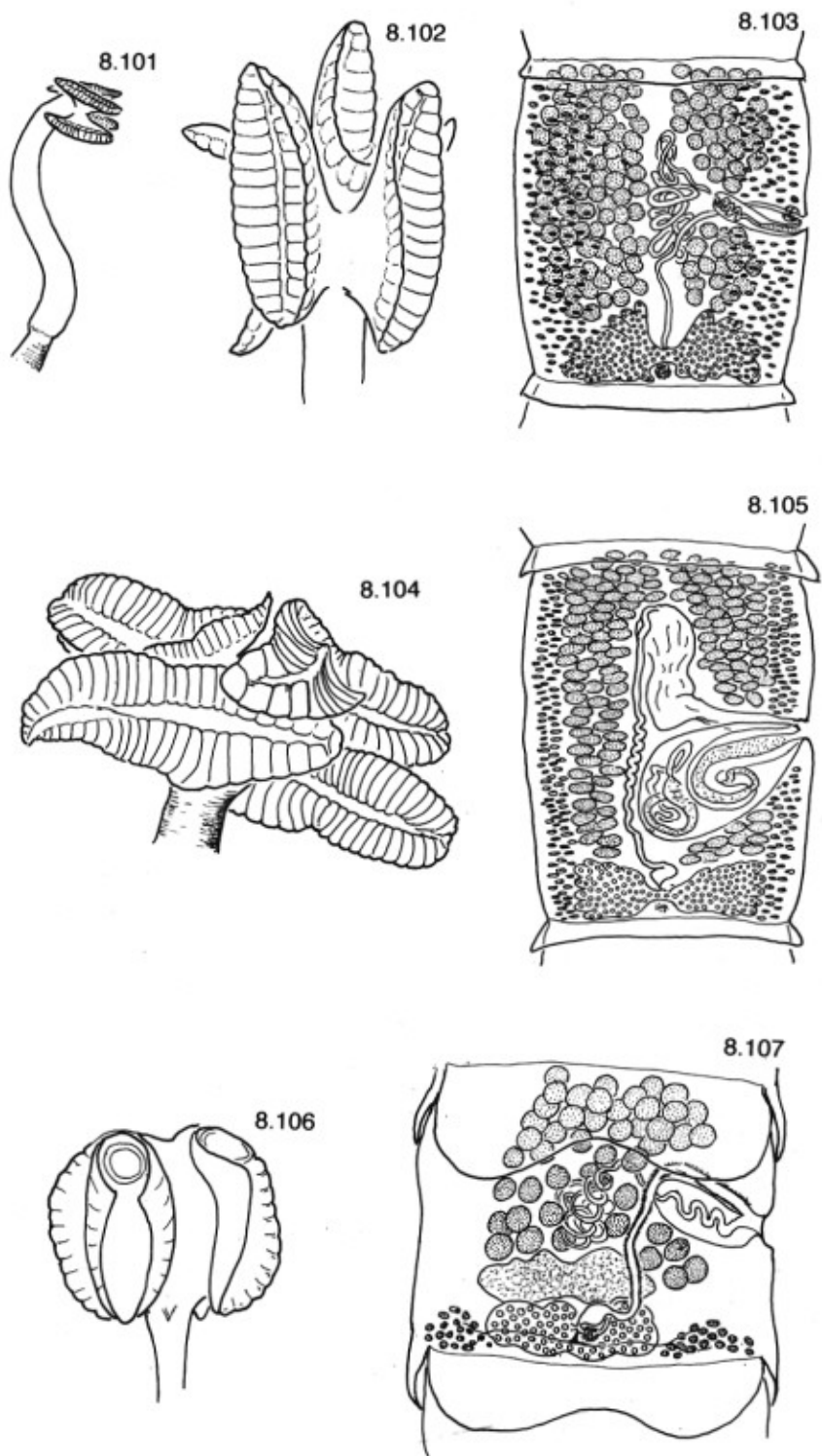
Family Chimaerocestidae Williams & Bray, 1984

Diagnosis: Scolex with four bothridia with loculated margin and large anterior accessory sucker. Strobila strongly craspedote, with four-lobed velum. Anapolytic. Genital pores lateral, irregularly alternating. Testes numerous; postvaginal testes present on poral side. Ovary median, posterior, in form of swollen lobed ring surrounding large Mehlis's gland. Vagina anterior to cirrus-sac. Vaginal sphincter present. Vitelline follicles in two postero-lateral fields, restricted to level of ovary,

Figs 8.101, 8.103 *Caulobothrium* Baer, 1948. 8.101. Scolex with large cephalic peduncle. 8.102. Scolex. 8.103. Mature proglottid. (After Euzet, 1959.)

Figs 8.104, 8.105 *Rhabdotobothrium* Euzet, 1953. 8.104. Scolex. 8.105. Mature proglottid. (After Euzet, 1953.)

Figs 8.106, 8.107 *Chimaerocestos* Williams & Bray, 1984. 8.106. Scolex. 8.107. Mature proglottid. (After Williams & Bray, 1984.)



some follicles in four lobes of velum. Uterus sac-shaped. Eggs (15) clustered in cocoon. In Holocephala. Type and only genus *Chimaerocestos* Williams & Bray, 1984.

Genus *Chimaerocestos* Williams & Bray, 1984 (Figs 8.106, 8.107)

Diagnosis: With the characters of the family. In Holocephala (*Rhinochimaera atlantica*). North Atlantic. Type-species *C. prudhoei* Williams & Bray, 1984.