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Order Lecanicephalidea Wardle & McLeod, 1952

L. EUZET

*Laboratoire de Parasitologie comparée, Université Montpellier II,
Station Méditerranéenne de l'Environnement Littoral, 1 Quai de
la Daurade, 34200 Sète, France.*

Introduction

Butler (1987a) gave an excellent historical review of the cestodes of selachians placed in the families Lecanicephalidae Braun, 1900 and Cephalobothriidae Pinner, 1928. The question of their systematic position remains outstanding. Some authors, such as Wardle & McLeod (1952), Yamaguti (1959) and Schmidt (1986) grouped them in a special order; others such as Southwell (1930a) and Euzet (1959) kept them in the Tetraphyllidea but in a separate superfamily. Butler (1987a), on the other hand, was inclined to classify them as a single family within the Tetraphyllidea.

When one lists the unique characters of these selachian parasites, one finds only the following features. The scolex is bipartite, the posterior part (*pars basalis*) bearing four circular suckers of the acetabular type and the anterior part (*pars apicalis*) very variable: a muscular sucker, a massive metoporphynchus or a crown of tentacles. Furthermore, there is the anatomy of the proglottid, in which the vagina opens posterior (sometimes to the side of) the cirrus-sac and does not cross the male duct.

Apart from the nature of the host, there are as many differences between these cestodes and the Tetraphyllidea as between the Proteocephalidea and the Tetraphyllidea. Therefore I have followed the scheme of Wardle & McLeod, accepted by Yamaguti (1959) and Schmidt (1986), and classified these cestodes in the order Lecanicephalidea Wardle & McLeod, 1952. However, the systematics within this order remain very confused. The old descriptions and some recent ones are too imprecise to be used. Many poorly characterized and poorly illustrated genera must be rejected. Some others can be retained but as *genera incertae sedis*.

In agreement with Campbell & Williams (1984) and Butler (1987a), I think that the majority of these parasites should be collected again from the type host, in the type locality (if possible) and redescribed to determine their morphology and anatomy.

To attempt a systematic scheme of the Lecanicephalidea, one can use only a few works. Apart from Butler (1987a), one may cite Baer (1948) for *Lecanicephalum* Linton, 1890 and *Parataenia* Linton, 1889; Subhadrappa (1957) for *Polyocephalus* Braun, 1878; Euzet & Combes (1965) for *Tetragonocephalum* Shipley & Hornell, 1905; Campbell & Williams (1984) for *Tylocephalum* Linton, 1890; and Butler (1987a) for *Polyocephalus* Braun, 1878.

The question of the Balanobothriidae Pintner, 1928, often placed close to the Lecanicephalidae, has already been discussed (see Chapter 8 on the Tetraphyllidea). These cestodes are typical onchobothriid tetraphyllideans with a pair of double-pointed hooks per bothridium but the anterior region of the scolex, embedded in the intestinal wall, assumes a globular shape which has masked the presence of four bothridia. While recognizing the difficulties, I propose to subdivide the Lecanicephalidea, according to the morphology of the pars apicalis of the scolex, into four families.

ORDER LECANICEPHALIDEA WARDLE & McLEOD, 1952

(Syn. Lecanicephala Wardle & McLeod, 1952)

Diagnosis: Scolex bipartite; posterior part (pars basalis) with four acetabulate suckers; anterior part (pars apicalis) variable, with muscular sucker, massive metoporphynchus or crown of tentacles. Strobila craspedote or acraspedote, apolytic. Genital pores lateral, irregularly alternating. Testes few or numerous. Vagina opens posteriorly, sometimes laterally, to cirrus-sac, does not cross male duct. Ovary posterior, lobed or bilobed in cross-section. Vitelline follicles in lateral fields or encircling proglottid. Adults in spiral valve of elasmobranchs.

Key to families

- 1a. Pars apicalis divided into numerous unarmed tentacles
..... Polyocephalidae Meggitt, 1924.
- 1b. Pars apicalis undivided 2.
- 2a. Pars apicalis a pedunculated disc, pars basalis with four large acetabula
..... Anteroporidae n. fam.
- 2b. Pars apicalis non-pedunculated 3.
- 3a. Pars apicalis a muscular fungiform metoporphynchus
..... Tetragonocephalidae Yamaguti, 1959.
- 3b. Pars apicalis a large muscular evaginable sucker
..... Lecanicephalidae Braun, 1900.

Comments

Polyocephalidae Meggitt, 1924. Subhadrappa (1951) described two species of *Polycephalus* (*P. coronatus* from *Rhynchobatus djeddensis* Forsskal, 1871 and *P.*

affinis from *Rhinobatos granulatus* Cuvier, 1824) with a scolex in which the tentacles are united in pairs but bifid at their extremity. This special character could represent a criterion for a new genus, but the apical division of the tentacles is very difficult to observe while they are retracted into the interior of the pars basalis.

Genera incertae sedis

Two doubtful genera are close to *Polycephalus*.

Anthemobothrium Shipley & Hornell, 1906. The type-species is *A. pulchrum* Shipley & Hornell, 1906, a small cestode parasitic in *Trygon sephen* = *Hypolophus sephen*. The difference is in the tentacles which according to Shipley & Hornell (1906) have a plumed appearance. The anatomy is unknown. This parasite does not seem to have been reported since the original description.

Calycobothrium Southwell, 1911 (syn. *Cyclobothrium* of Southwell, 1911) is based on a single individual collected from *Aetobatis narinari*. The scolex does not appear to have a pars basalis with four acetabula. The short, bulky tentacles are arranged in a circle around a disc in the centre of which a pore opens. This arrangement of the tentacles is close to that illustrated by Butler (1987b) in *Polycephalus* sp. from *Himantura* sp. However, in this cestode, the scolex has a pars basalis with four acetabula. As described by Southwell (1911), the anatomy of *Calycobothrium typicum* is of the tetraphyllidean type. This parasite should be redescribed from the type host.

Anteroporidae n. fam.

The genus *Anteropora* was created with a single species, *A. indica* Subhadrappa, 1957. This parasite from the spiral valve of *Narcine timlei* represents, from the evidence, a detached proglottid. Schmidt (1986) considered the genus to be doubtful. When examining the anatomy of this proglottid, one observes a marked similarity to the anatomy of *Discobothrium japonicum* found by Yamaguti (1934) in the spiral valve of *Narke japonica*. In both cestodes, the vagina opens behind the cirrus-sac, there is a small number of testes in a single median row, and the lateral vitelline follicles do not extend in front of the genital pore. These two cestodes of Torpediniformes belong to the same genus, which I place in the Lecanicephalidea, as did Wardle & McLeod (1952). I have discussed, in connection with *Discobothrium fallax* van Beneden, 1870, the validity of *Discobothrium* van Beneden, 1870 and concluded that it was a synonym of *Echeneibothrium* van Beneden, 1870 (see Chapter 8). The species placed in *Discobothrium* (such as *D. japonicum*) should be renamed at the generic level. In accordance with Article 23 (f) of the *International Code of Zoological Nomenclature*, I propose to retain *Anteropora* Subhadrappa, 1957 and to place the parasite found by Yamaguti in *Narke japonica* in this genus. We therefore have *Anteropora japonica* (Yamaguti, 1934) n. comb. (syn. *Discobothrium japonicum* Yamaguti, 1934). This new concept of *Anteropora* entails the suppression of the Monoporophylleidae

Subhapradha, 1957, since the family name is to be rejected as it does not correspond to that of a genus included in the family. This leads to the suppression of *Monoporophylleus* Shinde & Chincholikar, 1977, created to replace *Anteropora* in order to put the generic name into agreement with that of the family. It becomes a synonym of *Anteropora*.

Tetragonocephalidae Yamaguti, 1959

The description by Euzet & Combes (1965) of a lecanicephalidean from *Dasyatis violacea* in the Mediterranean, attributed to *Tetragonocephalum uarnak* Shipley & Hornell, 1905, poses the problem of the type of host specificity exhibited by the Lecanicephalidea. Given the confusion in the group, no conclusion can be reached at present.

Given the inadequacy of old descriptions, several questions remain to be answered.

Adelobothrium Shipley, 1900. Shipley's (1900) description of *A. aetobatidis*, parasite of *Aetobatis narinari*, shows that the scolex has a structure of the metoporthynchus type. The description of the anatomy suggest that the vitelline follicles are circumcortical. If this is so, *Adelobothrium* will be synonymous with *Tylocephalum*. The species described by Southwell (1925) as *Adelobothrium aetobatidis* Shipley, 1900 but from *Rhynchobatus djeddensis* is perhaps a different species but should be also placed in *Tylocephalum* because the vitelline follicles are circum-medullary.

Lecanicephalidae Braun, 1900

The type-species was redescribed by Baer (1948). It is probable that several cestodes placed in the genera *Cephalobothrium* Shipley & Hornell, 1906, *Hexacanal* Perrenoud, 1931 or *Tylocephalum* belong to this family.

Cephalobothrium Shipley & Hornell, 1906. The three species described in this genus do not provide adequate information for a definition of the genus. The anatomy of *C. aetobatidis* Shipley & Hornell, 1906, the type-species, is virtually unknown. The scolex and anatomy of *C. abruptum* Southwell, 1911 from *Pteroplatea micrura* are consistent with the genus *Lecanicephalum*, to which it is assigned here. *C. variabile* Southwell, 1911 from *Pristis cuspidatus* and *Trygon (Dasyatis) kuhli* has a scolex like that of *Tylocephalum* but the vagina is anterior to the cirrus-sac and the anatomy is, therefore, of the tetraphyllidean type. *Cephalobothrium* is treated here as a *genus inquirendum*.

Hexacanal Perrenoud, 1931. This genus is based mainly on the osmoregulatory system of *Cephalobothrium abruptum*. As this is the type-species, which has now been transferred to *Lecanicephalum*, *Hexacanal* becomes a synonym of this genus.

Staubothrium Shipley & Hornell, 1905. *S. aetobatidis* Shipley & Hornell, 1905 from *Aetobatis narinari* has an anatomy of the lecanicephalidean type with the vagina posterior to the cirrus-sac. The scolex was described as having four large round pedunculated bothridia and a tiny apical papilla but Southwell (1925), who examined specimens from *A. narinari*, did not see an apical papilla. Because of the anatomy of the proglottid, I place *Staubothrium* Shipley & Hornell, 1905 in the Lecanicephalidea but as a *genus incertae sedis* because the peculiar morphology of the scolex may justify a new family.

Comments on problematic genera

Spinocephalum Deshmukh, 1980. The type-species *S. rhinobatii* Deshmukh, 1980 was collected from *Rhinobatus granulatus* = *Rhinobatos granulatus* at Veraval (west coast of India). This species belongs to *Tetragonocephalum*, having lateral vitelline follicles. The only character given to distinguish the genus was the presence of small spines on the metoporphynchus (Deshmukh, 1980). However, as already remarked by Campbell & Williams (1984), these small spines had been noted by Euzet & Combes (1965) on the scolex of *T. uarnak* Shipley & Hornell, 1906. *Spinocephalum* is a synonym of *Tetragonocephalum*.

A certain number of genera classified as Lecanicephalidea do not belong to this order and are so badly defined that they cannot be classified. They are, in chronological order:

Aphanobothrium Seurat, 1906. Southwell (1925) gave this genus as a synonym of *Tylocephalum* Linton, 1890. *Aphanobothrium* was created by Seurat (1906) for larvae encapsulated in the flesh of *Pintada margaritifera* in the Gambier Islands (French Polynesia). The larvae were attributed to adult cestodes parasitic in *Aetobatis narinari* but without a description. As *A. narinari* has been cited as host of about ten lecanicephalideans, apparently belonging to several of the families defined above, one cannot decide on the synonymy of *Aphanobothrium*. It should be considered a *genus inquirendum*.

Kystocephalus Shipley & Hornell, 1906. The scolex of the type-species from *Aetobatis narinari* is described as having a myzorhynchus covered by a membrane. This could correspond to a scolex of *Tetragonocephalum* detached from the intestinal wall with a fragment of epithelium or a *Lecanicephalum* with the apical sucker more or less everted. Since its anatomy is poorly known, the precise synonymy of *Kystocephalus* cannot be decided and it should be considered a *genus inquirendum*.

Yogeshwaria Chincholikar & Shinde, 1976. The type-species of the genus, *Y. nagabushani* Chincholikar & Shinde, 1976, was collected from a *Trygon* sp. at Ratnagiri (west coast of India). This species, based on a single immature specimen, was characterized by a scolex with two bothria (*sic*). This species is not recognizable and, the host species being unknown, cannot be recovered again. *Yogeshwaria* should be suppressed. It is treated here as a *genus inquirendum*. Chincholikar & Shinde (1976) compared their species with *Diagonobothrium asymmetricum* Shipley & Hornell, 1906 from *Myliobatis maculata* = *Aetomyelus*

maculatus which, described from a single specimen, probably represents a diphyllidean scolex which has lost the rostellar spines and those of the cephalic peduncle.

Flapocephalus Deshmukh, 1979. The type-species is *F. trygonis* Deshmukh, 1977 from *Trygon sephen* = *Hypolophus sephen* collected at Ratnagiri (west coast of India). From the morphology of the scolex, this cestode belongs to the Lecanicephalidea. Its very compressed scolex appears to be of the *Lecanicephalum* type but its anatomy, with the vagina opening anterior to the cirrus-sac, is of the tetraphyllidean type. The morphological and anatomical features given by Deshmukh (1979) to characterize *Flapocephalus* are not found in *F. saurashtri* Shinde & Deshmukh, 1979. In this species, based on a single individual from *A. sephen* = *Hypolophus sephen*, one cannot distinguish the two lobes of the pars apicalis given as the principal character of the genus. However, the anatomy with the vagina posterior to the cirrus-sac is of the Lecanicephalid type. *Flapocephalus* is not recognizable and should be suppressed. It is treated here as a *genus inquirendum*.

Trygonicephalum Shinde & Jadhav, 1984. The type-species *T. ratnagiriensis* Shinde & Jadhav, 1984, was collected from *Trygon sephen* = *Hypolophus sephen* at Ratnagiri on the west coast of India. According to Shinde & Jadhav (1984), the scolex has a large oval apical disc and two bothridia. The anatomy is of the tetraphyllidean type with the vagina anterior to the cirrus-sac. This description does not correspond to any known genus. *Trygonicephalum* cannot be classified among the tetraphyllideans or the Lecanicephalideans and should be suppressed. It is treated here as a *genus inquirendum*.

Guptaia Malhotra, 1985. The type-species, placed in the Lecanicephalidae, is *G. garhwalensis* Malhotra, 1985. It was collected in fresh water in a cyprinid teleost, *Schizothorax richardsoni*. This cestode probably belongs to another order and should be excluded from the Lecanicephalidea. It is to be treated as a *genus incertae sedis*.

Lecanicephalidea incertae sedis

Eniochobothrium Shipley & Hornell, 1906 has only one species, *E. gracile* Shipley & Hornell, 1906, collected once in Sri Lanka from *Rhinoptera javanica*. Since Southwell (1930a), it has been considered to belong to the Lecanicephalidae or as *incertae sedis* in this family (Yamaguti, 1959) or as *genus inquirendum* among the Lecanicephalida (Wardle & McLeod, 1952). From the general description, the scolex has 'four suckers and a conspicuous rostellum'. The morphology of the strobila is unique. There are three regions: an anterior with very enlarged proglottids and a posterior region of four to five broad sexually mature proglottids, separated by a mid-region of about ten narrow proglottids. The genital pores alternate irregularly and there is a large cirrus-sac containing an evaginable cirrus. The vitelline follicles are lateral. The remainder of the anatomy is unknown. Despite a strobila which renders this cestode easily recognizable, this parasite has not been found again in the type-host (*R. javanica*) since the original description,

although this stingray had been examined several times by Southwell and by Indian researchers.

When studying cestodes of elasmobranchs, one is struck by the strange resemblance between the strobila of *Eniochobothrium* and that of *Litobothrium* Dailey, 1969 (syn. *Renyxa* Kurochin & Slankis, 1973). However, in *Litobothrium* the scolex is represented by a simple apical sucker. The anatomy is of the tetraphyllidean type and it is parasitic in Lamniformes (Alopiidae and Odontaspidae).

Several hypotheses could be advanced to explain these similarities and dissimilarities: *Eniochobothrium* and *Litobothrium* are different cestodes and the morphological resemblance of the strobila is the result of convergence; or *Eniochobothrium* is identical with *Litobothrium* and *Rhinoptera javanica* is an accidental host in which the parasite does not develop fully and has retained the true scolex; or the host has been confused and its presence in *Rhinoptera* is an error. Only further research will permit a decision between these different hypotheses.

Hornellobothrium Shipley & Hornell, 1906. Type-species *H. cobraeformis* Shipley & Hornell, 1906. This minute species (2 mm) from *Aetobatis narinari* was recently recovered by Butler (1987b) who described its morphology precisely. The scolex is composed of four sessile masses (bothridia?) covered with spines and an apical organ which appears to be erectile. The species seems to be euapolytic. The anatomy is very poorly known. We have provisionally classified this genus in the Lecanicephalidea.

Family Polypocephalidae Meggitt, 1924

Diagnosis: Scolex with pars apicalis divided into evaginable tentacles (sometimes paired) able to project suddenly to the exterior; pars basalis cushion-like, bearing four acetabula. Strobila craspedote or acraspedote, apolytic. Genital pores lateral, irregularly alternating. Testes few (four or six), large, aligned along median axis of proglottid. External and internal seminal vesicles present. Ovary bilobed, posterior. Vagina posterior to cirrus-sac. Vitelline follicles lateral. Type and only genus *Polypocephalus* Braun, 1878.

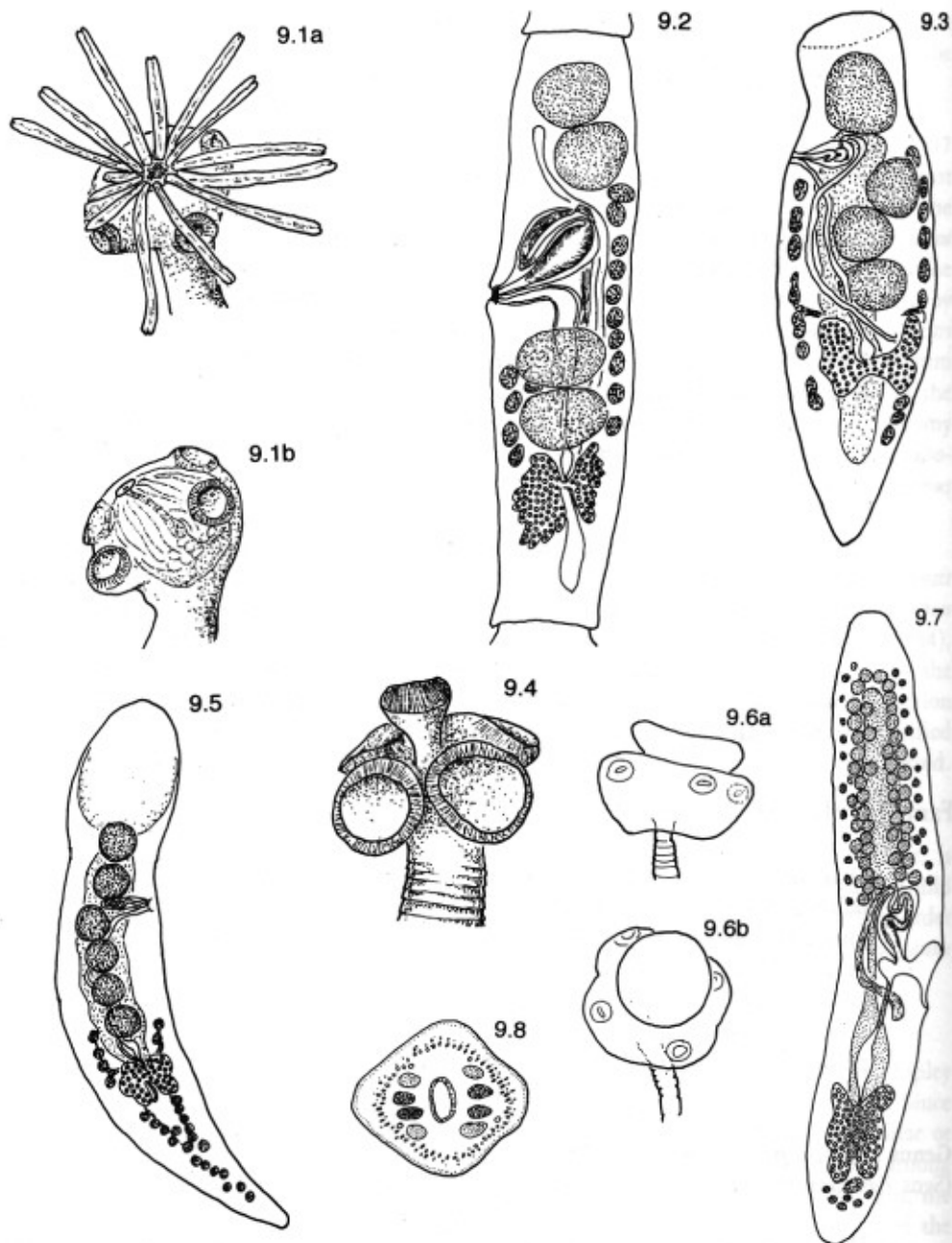
Genus *Polypocephalus* Braun, 1878 (Figs 9.1, 9.2)

(Syns *Parataenia* Linton, 1889; *Thysanobothrium* Shipley & Hornell, 1906)

Diagnosis: With the characters of the family. In Rajiformes and Myliobatiformes. Cosmopolitan. Type-species *P. radiatus* Braun, 1878.

Family Anteroporidae n. fam.

Diagnosis: Scolex with pars apicalis a pedunculated muscular disc, pars basalis with four large bothridia-like acetabula. Strobila acraspedote, apolytic. Genital



Figs 9.1, 9.2 *Polypocephalus* Braun, 1978. 9.1a, b. Scolex showing two different shapes. 9.2. Mature proglottid, dorsal view. (After Baer, 1948.)

Figs 9.3-9.5 *Anteropora* Subhapradha, 1957. 9.3. Mature proglottid, dorsal view. (After Subhapradha, 1957.) 9.4, 9.5. *A. japonica* (Yamaguti, 1934). 9.4. Scolex. 9.5. Mature proglottid, dorsal view. (After Yamaguti, 1934.)

Figs 9.6-9.8 *Tetragonocephalum* Shipley & Hornell, 1905. 9.6a, b. Scolex, showing two shapes. 9.7. Mature proglottid, dorsal view. 9.8. Transverse section showing lateral vitelline follicles. (After Euzet & Combes, 1965.)

pores lateral, irregularly alternating. Testes few (four or six) aligned along median axis of proglottid. Ovary lobate, posterior. Vagina posterior to cirrus-sac. Vitelline follicles lateral, posterior to genital pore. Type and only genus *Anteropora* Subhadrada, 1957.

Genus *Anteropora* Subhadrada, 1957 (Figs 9.3–9.5)
(Syn. *Monoporophylleus* Shinde & Chincholikar, 1977)

Diagnosis: With the characters of the family. In Torpedinidae. Japan, India.
Type-species *A. indica* Subhadrada, 1957.

Family Tetragonocephalidae Yamaguti, 1959

Diagnosis: Scolex with pars apicalis a fungiform metoporphynchus, not invaginable. Type-genus *Tetragonocephalum* Shipley & Hornell, 1905.

Key to genera

1a. Vitelline follicles lateral
..... *Tetragonocephalum* Shipley & Hornell, 1905. (Figs 9.6–9.8)
(Syn. *Spinocephalum* Deshmukh, 1980.)

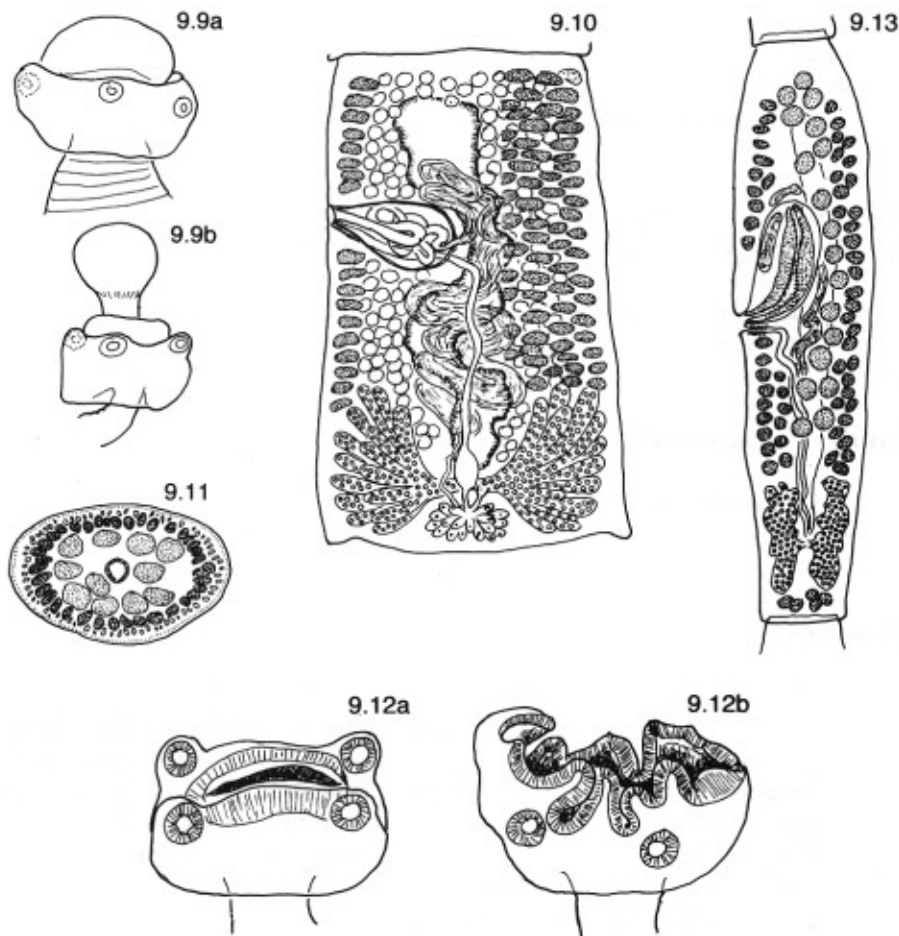
Diagnosis: Scolex with pars apicalis a fungiform metoporphynchus covered with minute spines; pars basalis cushion-like bearing four acetabula. Strobila acraspedote, apolytic. Proterogynous. Genital pores lateral, enlarged, irregularly alternating. Testes anterior, numerous, no postvaginal testes on poral side. External and internal seminal vesicles present. Ovary posterior, bilobed, circular in cross-section. Vagina posterior to cirrus-sac. Vitelline follicles anterior and posterior to ovary. Uterus bisacculate. In Myliobatiformes. Cosmopolitan. Type-species *T. trygonis* Shipley & Hornell, 1905.

1b. Vitelline follicles circum-medullary
..... *Tylocephalum* Linton, 1890. (Figs 9.9–9.11)

Diagnosis: Scolex with pars apicalis a fungiform metoporphynchus, not invaginable; pars basalis cushion-like, bearing four acetabula. Strobila craspedote. Genital pores lateral, irregularly alternating. Testes numerous, anterior. Postvaginal testes present on poral side. External seminal vesicle only. Ovary posterior, bilobed in cross-section. Uterus medioventral. In Rhinopteridae. North Atlantic. Type-species *T. pingue* Linton, 1890.

Family Lecanicephalidae Braun, 1900

Diagnosis: Scolex with pars apicalis a large circular sucker, highly polymorphic, invaginable or evaginating entirely to resemble a metoporphynchus; pars basalis cushion-like, bearing four acetabula. Strobila acraspedote, apolytic. Genital pores



Figs 9.9-9.11 *Tylocephalum* Linton, 1890. 9.9a, b. Scolex showing two shapes. 9.10. Mature proglottid, dorsal view. 9.11. Transverse section showing circum-medullary vitelline follicles. (After Campbell & Williams, 1984.)

Figs 9.12, 9.13 *Lecanicephalum* Linton, 1890. 9.12a, b. Scolex showing two shapes. 9.13. Mature proglottid, dorsal view. (After Baer, 1948.)

lateral, irregularly alternating. Testes numerous; postvaginal testes present on poral side. External and internal seminal vesicles present. Ovary posterior, bilobed in cross-section. Vitelline follicles lateral, anterior and posterior to ovary. Type and only genus *Lecanicephalum* Linton, 1890.

Genus *Lecanicephalum* Linton, 1890 (Figs 9.12, 9.13)
(Syn. *Hexacanalus* Perrenoud, 1931)

Diagnosis: With the characters of the family. In Myliobatiformes. Cosmopolitan. Type-species *L. peltatum* Linton, 1890.