14 Order Tetrabothriidea Baer, 1954

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Introduction

The family Tetrabothriidae Linton, 1891 is a monophyletic assemblage of six genera that occur as parasites of marine homoeotherms (Hoberg, 1989). Although cestodes of this family are a predominant component of the parasite faunas of seabirds, pinnipeds and cetaceans, aspects of their higher taxonomy and biology have remained enigmatic. Historically, tetrabothriids have been classified among the Pseudophyllidea (Nybelin, 1922), Cyclophyllidea (Fuhrmann, 1932; Wardle & McLeod, 1952; Yamaguti, 1959; Schmidt, 1986), as the suborder Tetrabothriata of the Tetraphyllidea (Spasskii, 1958, 1992; Temirova & Skryabin, 1978; Ryzhikov *et al.*, 1985), or in the separate order Tetrabothriidea (Baer, 1954a; Galkin, 1987a). Divergent opinions concerning the ordinal classification of this taxon have centred upon interpretations of the structural homology of the scolex (Baylis, 1926; Rees, 1956; Andersen & Lysfjord, 1982) and the significance of a typically compact and anteroventral vitelline gland that defines the family (Wardle & McLeod, 1952; Hoberg, 1989). Unambiguous support of a tetraphyllidean ancestry for the Tetrabothriidae resides in recognition of an homologous pattern of morphogenesis for the holdfast in metacestodes representing these taxa (Hoberg, 1987a; Brooks *et al.*, 1991). Whether considered to represent a separate order with tetraphyllidean affinities (as presented herein) or a suborder of the Tetraphyllidea, it is clear that the placement of the Tetrabothriidae as a family of the Cyclophyllidea (as presented in most traditional classifications) cannot be supported based on morphological, phylogenetic and biological criteria (Hoberg, 1989).

Cycles for tetrabothriids have yet to be elucidated but are considered to involve crustaceans, cephalopods, and (or) teleosts as intermediate and paratenic hosts, and homoeotherms as definitive hosts (Baer, 1954a; Temirova & Skryabin, 1978; Jones, 1988). Although patterns of transmission are unknown, the infective larval stage has been identified as a uniacetabulate plerocercoid (Hoberg, 1987a).

A unique heterochronic sequence in postlarval ontogeny of the adult scolex, initiated within the definitive host, has been defined and postulated as a uniform pattern of development within the family (Hoberg, 1989; Hoberg *et al.*, 1991). The apparent morphological similarities of undifferentiated larval tetrabothriids and other tetraphyllideans will complicate recognition of the former in the intermediate host (Hoberg, 1987a).

Identification at the generic level relies primarily on the structure of the scolex, bothridia and auricular appendages, and the configuration of the genital atrium. The genus *Chaetophallus* Nybelin, 1916, recognized here, is considered a synonym of *Tetrabothrius* Rudolphi, 1819 by some authorities (Baer, 1954a; Temirova & Skryabin, 1978). The validity of other genera is not currently disputed. However, differentiation among congeners, particularly in the genera *Tetrabothrius, Anophryocephalus* Baylis, 1922 and *Trigonocotyle* Baer, 1932 may be problematic due to interspecific homogeneity and broad intraspecific variation of some otherwise diagnostic attributes (Hoberg, 1987b, 1990; Hoberg *et al.*, 1991). Incomplete descriptions in previous taxonomic treatments have also hindered the separation of some species. Re-evaluation of many species of *Tetrabothrius* appears to be necessary due to an inadequate documentation of intraspecific variation and a lack of consistency for some morphological traits (Hoberg, 1989). Particularly significant is the progressive increase in dimensions (with increasing maturity and changes in physiological condition) of the genital atrium (and associated male and female ducts), cirrus-sac and vitelline gland (Murav'eva & Popov, 1976; Hoberg, 1987b). To allow for accurate comparisons among taxa, intraspecific variation must be documented and measurements must be presented with reference to the degree of development of the proglottids and strobila. Thus, to characterize the full extent of intraspecific variation for specific characters, it is necessary to define the stage of ontogeny of the strobila where maximum dimensions are observed. The following terminology is recommended (see Hoberg, 1987a): immature (genital anlagen visible to presence of undifferentiated male and female organs); mature (male and female systems completely functional, tubular uterus narrow); postmature (male and female systems well defined; tubular uterus expanded but not containing developing oncospheres); pregravid (expanded uterus contains undifferentiated oncospheres); gravid (oncospheres fully developed; uterine pore patent).

Taxonomic characters at the species level have included unique features of the scolex (when apparent), composition of the longitudinal musculature, structure of the genital atrium (incorporating length of male canal and aspects of the atrial vagina) and cirrus-sac, and number of testes. Apparent overlap in some diagnostic characters in species of *Tetrabothrius, Anophryocephalus* and *Trigonocotyle* is extensive and mensural attributes may be dramatically influenced by individual variation and physiological condition (age) of the proglottid (Murav'eva & Popov, 1976; Hoberg, 1987b; Hoberg *et al.*, 1991). Consequently, qualitative characters, particularly the form of the genital atrium and genital papillae, relative positions of the apertures of the male canal and vagina, presence and location of genital sphincters and occasionally the structure of the bothridia and auricles (especially in *Anophryocephalus* and *Trigonocotyle*) are of critical importance. The most significant characters, those of the genital atrium, cannot be completely

evaluated from whole-mounted specimens. The longitudinal musculature and genital atrium with associated ducts must be viewed either in histological or hand-cut thick sections (transverse), thus augmenting the difficulty of accurate identification of genera and species.

The speciose genus *Tetrabothrius* with 42 nominal species in avian and eight species in cetacean hosts has been partitioned into four subgenera (Baer, 1954a; Murav'eva, 1975; Temirova & Skryabin, 1978; Odening, 1982). Recognition of *Tetrabothrius* (*Tetrabothrius*) spp., *T. (Neotetrabothrius)* spp., *T. (Oriana)* spp. and *T. (Culmenamniculus)* spp. was based on apparent structural differences in the genital atrium, presence or absence of genital papillae within the atrium, and the relationships of the male canal and atrial region of the vagina. A phylogenetic basis for these subgenera has not yet been established and inadequate descriptions of the genital atrium for many species continue to obscure their accurate placement. Thus designation at the subgeneric level necessitates careful consideration of the variation inherent in some diagnostic characters and may be limited by the quality of material available for study.

Phylogenetic analyses currently support monophyly for the Tetrabothriidae and provide foundation for the six genera (*Tetrabothrius, Chaetophallus, Trigonocotyle, Anophryocephalus, Strobilocephalus* Baer, 1932 and *Priapocephalus* Nybelin, 1922) presented in the key (Hoberg, 1989). Preliminary comments on taxonomic problems within the genus *Trigonocotyle* have been presented (Hoberg, 1990). The genus *Anophryocephalus* has been revised (Hoberg *et al.*, 1991) and results of phylogenetic reconstruction, historical biogeography and host-parasite co-evolution summarized (Hoberg & Adams, 1992; Hoberg, 1992).

ORDER TETRABOTHRIIDEA BAER, 1954

Diagnosis: Eucestoda. Scolex usually with four muscular bothridia. Vitelline gland compact, anteroventral to ovary. Uterus a transverse tube dorsal to ovary; with single or multiple pores. Parasites of marine homoeotherms. Type-family Tetrabothriidae Linton, 1891.

Family Tetrabothriidae Linton, 1891

Diagnosis: Strobila diminutive to large, proglottids numerous, usually craspedote, wider than long. Scolex lacking rostellum. Bothridia rectangular to round, flat or sucker-like, possessing auriculate muscular appendages; or bothridia and appendages lacking (*Priapocephalus* Nybelin, 1922). Neck present. Genital atrium unilateral, muscular, complex. Cirrus-sac ovoid or elongate. Testes few to numerous. Ovary highly lobate, transversely elongate. Vitelline gland compact, anteroventral to ovary. Uterus a transverse tube; dorsal pore(s) present. Strobilar stage in seabirds and marine mammals. Type-genus *Tetrabothrius* Rudolphi, 1819.

Key to genera

1a. **Scolex with four auriculate bothridia. Genital atrium muscular, well developed, with distinct male atrial canal. Vitelline gland compact, anteroventral to ovary. Genital ducts usually between osmoregulatory canals. Uterine pore single, dorsal, median** ..... 2a.

1b. **Scolex massive, globular to conical with collar at base, without bothridia or appendages. Genital ducts ventral to osmoregulatory canals. Cirrus-sac elongate, pyriform. Genital atrium without muscular modification. Testes primarily lateral to female organs. Vitelline gland with tendency to be follicular. Uterine pores dorsal, multiple** .... ***Priapocephalus*** **Nybelin, 1922. (Figs 14.1–14.3)**

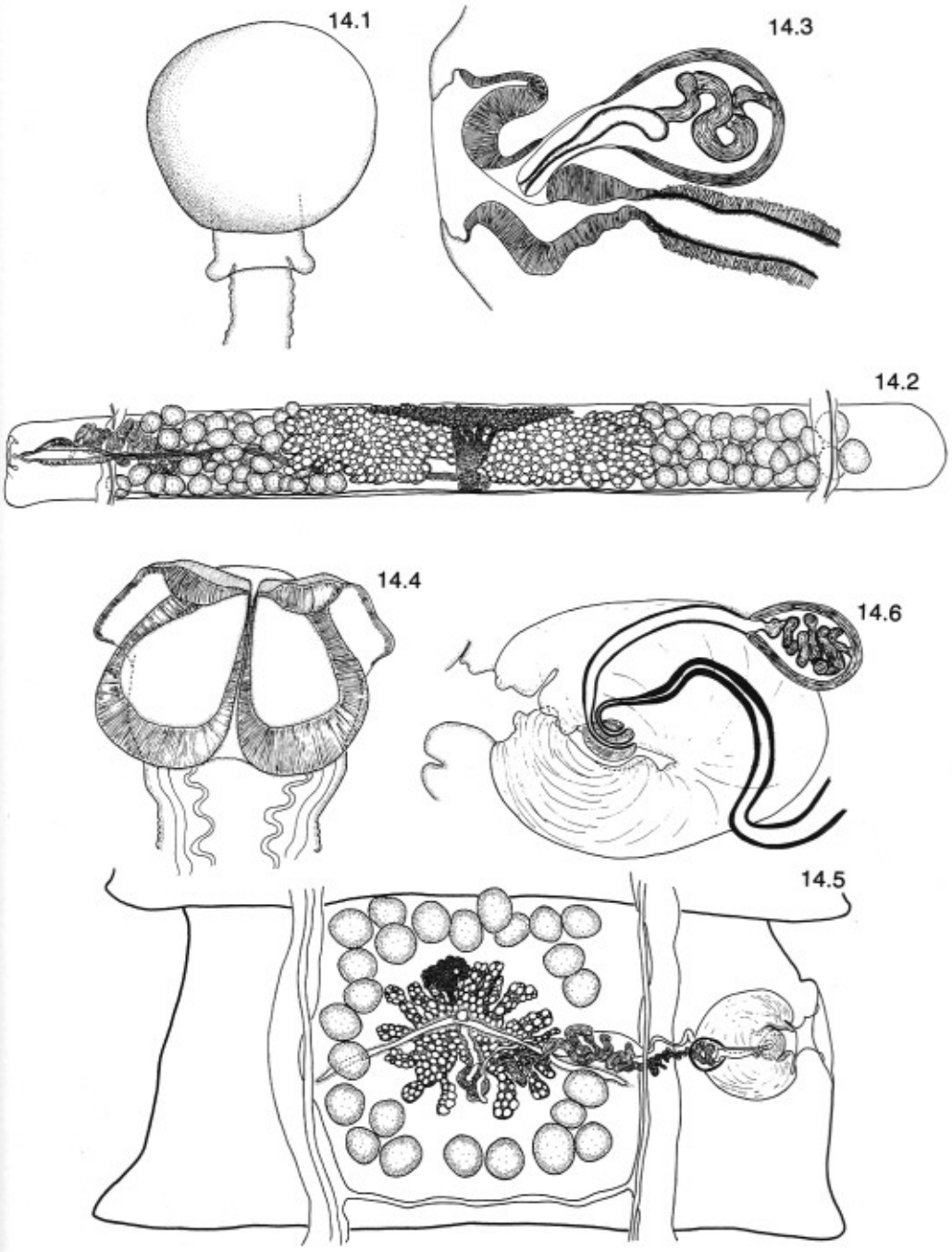
Diagnosis: Scolex conical to globular, massive, with collar-like basal region; bothridia and auricles absent. Genital pores ventrolateral. Male atrial canal absent. Cirrus-sac elongate to pyriform; cirrus spinose. Testes numerous (> 200) situated laterally. Vas deferens voluminous. Vagina armed with hair-like spines, aperture ventral to cirrus. Vaginal and inner seminal receptacles present. Ovary slightly poral, highly lobate. Vitelline gland branched, anteroventral to ovary. Uterus saccate. In Cetacea. Cosmopolitan. Type-species *P. grandis* Nybelin, 1922.

2a. **Bothridia each with single, laterally directed auricular appendage. Auricles fused anteriorly to form apical complex or organ** ..... 3.

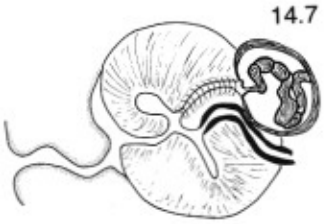
2b. **Auricles independent, not fused to form apical organ. Genital atrium muscular or reduced** ..... 4.

3a. **Bothridia rectangular. Cirrus-sac ovoid. Testes surround female organs** ..... ***Tetrabothrius*** **Rudolphi, 1819. (Figs 14.4–14.9)** (Syns *Tetrabothrium (Eutetrabothrium)* Diesing, 1854; *Amphoterocotyle* Diesing, 1863; *Diplobothrium* Lönnberg, 1891 *nec* van Beneden, 1889; *Prosthecocotyle* Monticelli, 1892; *Bothridiotaenia* Lönnberg, 1896; *Oriana* Leiper & Atkinson, 1914; *Porotaenia* Szpotanska, 1917; *Neotetrabothrius* Nybelin, 1929; *Trigonocotyle* Guiart, 1935 *nec* Baer, 1932; *Paratetrabothrius* Yamaguti, 1940).

Diagnosis: Scolex rectangular with four flat or cup-shaped rectangular bothridia, each with a laterally directed muscular auricular appendage. Auricles fused to form apical organ. Genital pores unilateral; ducts between poral osmoregulatory canals, rarely ventral. Genital atrium deep, muscular. Cirrus-sac not extending beyond osmoregulatory canals. Cirrus enters genital atrium through well defined male atrial canal, dorsal to vaginal aperture. Vaginal and inner seminal receptacles present. Ovary multilobate, extending to osmoregulatory canals. Vitelline gland compact, preovarian, ventral. Uterus saccate, slightly lobate, situated dorsally and extending beyond osmoregulatory canals when gravid. Median dorsal uterine pore present. In marine birds (Podicipediformes, Gaviiformes, Sphenisciformes, Procellariiformes, Pelecaniformes and Charadriiformes; rarely Anseriformes) and mammals (Odontoceti and Mysticeti). Cosmopolitan. Type-species *T. macrocephalus* (Rudolphi, 1810).



Figs 14.1-14.3 *Priapocephalus eschrichtii* Murav'eva & Treshchev, 1970. 14.1. Scolex. 14.2. Mature proglottid, ventral view. 14.3. Genital atrium, transverse section, view from anterior. **Figs 14.4-14.6** *Tetrabothrius (Culmenamniculus) laccocephalus* Spätlich, 1909. 14.4. Scolex. 14.5. Mature proglottid, dorsal view. 14.6. Genital atrium, transverse section, view from anterior.



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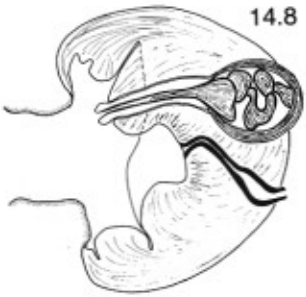

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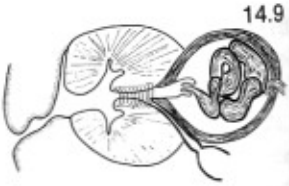

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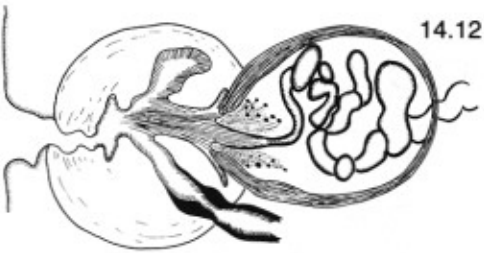

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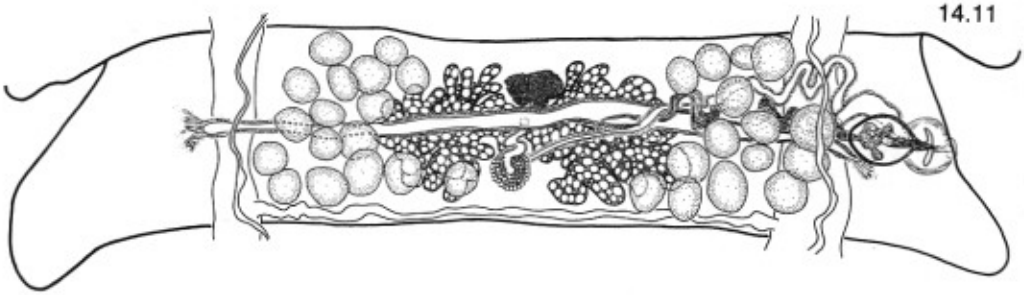

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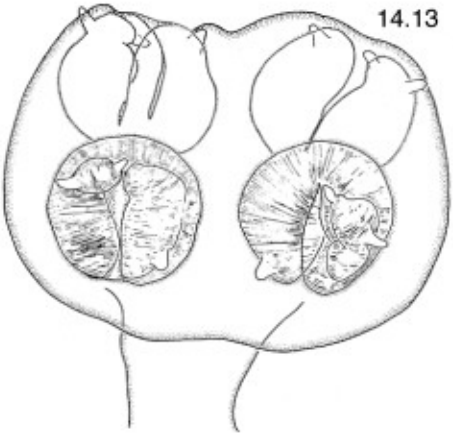

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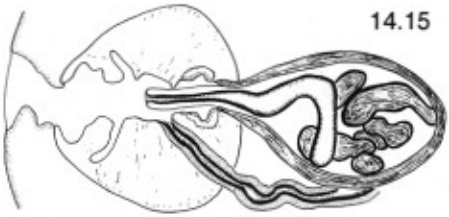

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Figs 14.7–14.9 Genital atria among subgenera of *Tetrabothrius* spp. shown in transverse section, viewed from the anterior. 14.7. *Tetrabothrius (Tetrabothrius) macrocephalus* Rudolphi, 1819. Modified from Baer (1954a). 14.8. *Tetrabothrius (Oriana) erostris* Lönnberg, 1896. 14.9. *Tetrabothrius (Neotetrabothrius) eudyptidis* (Lönnberg, 1896). Modified from Baer (1954a).
Figs 14.10–14.12 *Chaetophallus umbrella* (Fuhrmann, 1899). 14.10. Scolex. Modified from Fuhrmann (1921). 14.11. Mature proglottid, dorsal view. 14.12. Genital atrium, transverse section, view from anterior.
Figs 14.13–14.15 *Trigonocotyle sexitesticulae* Hoberg, 1990. 14.13. Scolex. 14.14. Mature proglottid, dorsal view. 14.15. Genital atrium, transverse section, view from anterior. All modified from Hoberg (1990).

Key to subgenera

Ia. **Genital atrium lacking distinct genital papilla** ..... **II**

Ib. **Genital atrium with prominent genital papilla** ..... **III**

IIa. **Male canal and atrial region of vagina independent, apertures separate near centre of atrium, vagina ventral** .... ***Tetrabothrius (Tetrabothrius)* Rudolphi, 1819. (Fig. 14.7)**

IIb. **Male canal and atrial vagina fused distally to form common duct with single aperture opening into genital atrium** .... ***Tetrabothrius (Neotetrabothrius)* Nybelin, 1929. (Fig. 14.9)** (Syn. *Tetrabothrius (Uniamniculus)* Murav'eva, 1975.)

IIIa. **Apertures of male canal and vagina located on apex of ventrally decurved papilla** .... ***Tetrabothrius (Culmenamniculus)* Murav'eva, 1975. (Fig. 14.6)**

IIIb. **Aperture of male canal on apex of papilla, vaginal aperture separate, ventral at base of papilla** .... ***Tetrabothrius (Oriana)* Leiper & Atkinson, 1914. (Fig. 14.8)** (Syn. *Tetrabothrius (Biamniculus)* Murav'eva, 1975.)

3b. **Bothridia rounded. Cirrus-sac elongate. Genital atrium spinose. Testes lateral and postovarian** ..... ***Chaetophallus* Nybelin, 1916. (Figs 14.10–14.12)**

Diagnosis: Scolex rounded to rectangular with four rounded bothridia, each with a laterally directed muscular auricle. Genital pores unilateral, slightly ventral; ducts between osmoregulatory canals. Genital atrium deep, muscular, with

short bristle-like spines lining luminal surface; long hair-like spines extend from near base of cirrus-sac for length of male canal. Cirrus-sac not extending beyond osmoregulatory canals. Vagina entering genital atrium ventral to male canal; dilated proximally to form vaginal seminal receptacle; inner seminal receptacle present. Ovary multilobate, not attaining osmoregulatory canals. Vitelline gland compact, preovarian. Uterus saccate; median dorsal uterine pore present. In Procellariiformes. Southern Hemisphere. Type-species *C. robustus* Nybelin, 1916.

4a. Auricular appendages independent, often weakly muscular. Three auricles on each bothridium. Cirrus-sac elongate. Genital atrium muscular, well developed ..... ***Trigonocotyle*** **Baer, 1932. (Figs 14.13–14.15)**

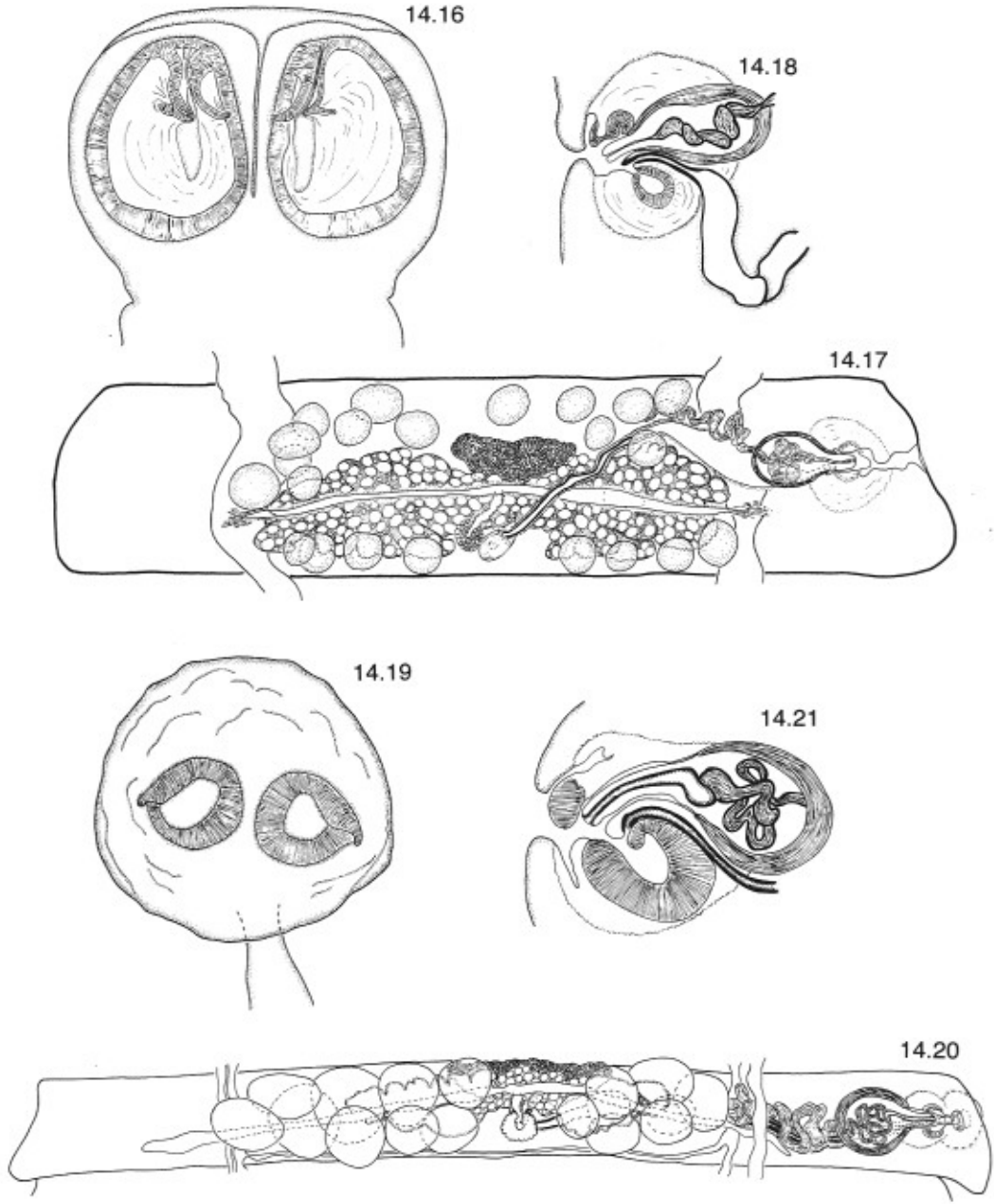
Diagnosis: Scolex rectangular to cuboidal, with four robust and highly muscular bothridia, each with three fleshy to muscular auricular appendages. Auricles independent; apical development slight. Genital pores unilateral; ducts between osmoregulatory canals. Genital atrium deep, genital papillae absent; aperture of atrial vagina ventral and adjacent to orifice of male atrial canal. Cirrus-sac elongate to pyriform; cirrus spinose. Testes relatively few, surrounding female gonads. Vagina with spinose atrial region; inner seminal receptacle present. Ovary strongly bilobed, slightly lobate. Vitelline gland compact, preovarian. Uterus saccate, extending beyond osmoregulatory canals when gravid; median pore present. In Odontoceti. Cosmopolitan. Type-species *T. globicephalae* Baer, 1954.

4b. Auricular appendages paired or single. Genital atrium reduced dorsally. Prominent muscular chamber ventral to vaginal aperture. Genital pores ventrolateral ..... **5.**

5a. Scolex rounded to rectangular. Bothridia sucker-like. Auricular appendages paired, muscular, located along anterior margin of each bothridium. Neck relatively long. Dorsal osmoregulatory canals atrophied. Ovary in posterior region of proglottid, surrounded and overlapped by testes .... ***Anophryocephalus*** **Baylis 1922. (Figs 14.16–14.18)**

Diagnosis: Scolex intricate, with four ornate, rounded sucker-like bothridia each with two fused or independent auricular appendages at anterior margin; apertures of bothridia complex, with membranous opercula or enveloped in parenchyma. Dorsal osmoregulatory canals present, atrophied posteriorly. Genital pores unilateral, often ventrolateral; ducts between osmoregulatory canals. Genital atrium with prominent muscular chamber ventral to vaginal aperture and muscular pad slightly dorsal and adjacent to orifice of male canal. Cirrus-sac ovoid to elongate. Testes large, relatively few; dorsal and overlapping ovary. Ovary massive. Vitelline gland compact, ovoid to elongate; anteroventral to ovary. Vaginal and inner seminal receptacles present. Atrial vagina spinose in some species, entering genital atrium ventral to male canal. Uterus a transverse sac, often contained within osmoregulatory canals when gravid; median dorsal pore present. In Phocidae and Otariidae. Holarctic. Type-species *A. anophrys* Baylis, 1922.

5b. Scolex globular, massive (may exceed 5 mm diameter). Bothridia sucker-like, slightly triangular, located at base of hypertrophied apex of scolex. Auricular



Figs 14.16-14.18 *Anophryocephalus anophrys* Baylis, 1922. 14.16. Scolex. 14.17. Mature proglottid, dorsal view. 14.18. Genital atrium, transverse section, view from anterior. All modified from Hoberg *et al.*, 1991.

Figs 14.19-14.21 *Strobilocephalus triangularis* (Diesing, 1850). 14.19. Scolex. 14.20. Mature proglottid, dorsal view. 14.21. Genital atrium, transverse section, view from anterior.

apppendages single, laterally directed. Cirrus-sac massive, ovoid, thick-walled ..... *Strobilocephalus* Baer, 1932. (Figs 14.19–14.21)

Diagnosis: Scolex with hypertrophied apical region and four triangular, muscular, sucker-like, auriculate bothridia located near base. Genital pores ventrolateral; ducts between osmoregulatory canals. Genital atrium with prominent muscular chamber ventral to aperture of vagina; muscular pad situated adjacent to orifice of male canal. Male canal opens into atrium on papilla dorsal to vagina. Cirrus spinose. Testes few, surrounding female gonads. Vagina armed with hair-like spines. Inner seminal receptacle present. Ovary bilobed, transversely elongate, extending to osmoregulatory canals. Vitelline gland compact, anteroventral to ovary. Uterus a transverse sac extending between osmoregulatory canals when gravid; median dorsal pore present. In Odontoceti. Cosmopolitan. Type-species *S. triangularis* (Diesing, 1850).