TAPEWORMS OF ELASMOBRANCHS, PART I

A Monograph on the Lecanicephalidea

(Platyhelminthes: Cestoda)

KIRSTEN JENSEN

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Cover: Tapeworms and red vase. A fanciful representation of some tapeworms of sharks and rays. Painting by William C. Campbell (acrylic on canvas, 2004).

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A Monograph on the Lecanicephalidea
(Platyhelminthes, Cestoda)

by

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Abstract. This represents the first monographic and phylogenetic treatment of the order Lecanicephalidea. The main objective was to treat the Lecanicephalidea at the generic level, while providing information on morphology, taxonomic history, phylogenetic relationships, geographic distribution, and host associations of the group. Following an introduction to the morphology of the Lecanicephalidea, the phylogenetic placement of the group is addressed. This is followed by a review of the taxonomic history of the group and relationships within, including summaries of 29 previously used classification schemes. Despite the generic focus of this study, the taxonomic status of 137 previously recognized lecanicephalidean species was evaluated, resulting in 65 species considered to be valid, 52 species considered to be *species inquirendae*, 14 considered to be *nomina nuda*, four considered to be non-lecanicephalidean *species inquirendae,* and two species considered to not be belong to the Lecanicephalidea. Two type species, *Lecanicephalum peltatum* and *Polypocephalus radiatus*, and *Anteropora japonica* are redescribed. Seven new species are described. These are: *Anteropora leelongi* Jensen, **n. sp.**, *Eniochobothrium euaxos* Jensen, **n. sp.**, *Hornellobothrium extensivu*m Jensen, **n. sp.**, *Lecanicephalum coangustatum* Jensen, **n. sp.**, *Polypocephalus helmuti* **n. sp.**, *Tetragonocephalum passeyi* Jensen, **n. sp.**, and *Tylocephalum koenneckeorum* Jensen, **n. sp.** Five new combinations were created for lecanicephalidean species (*Polypocephalus caribbensis* **n. comb.**, *P. elongatus* **n. comb.**, *Tetragonocephalum madhualtae* **n. comb.**, *Tetragonocephalum madrassensis* **n. comb.**, and *Tylocephalum rhinobatii* **n. comb.**), and one new combination for a tetraphyllidean

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species previously recognized as a lecanicephalidean (*Pseudanthobothrium aegyptiacus* **n. comb.**). Museums around the world were visited to locate type material. A list of type material is presented for 33 species. In addition, a preliminary list of voucher material of lecanicephalideans is given. The taxonomic status of 43 genera that had been associated with the Lecanicephalidea was evaluated. As a result, 16 genera are considered to belong to other cestode orders, two are considered *genera inquirenda et incertae sedis* (*Calycobothrium* and *Trygonicephalum*), one is determined to be a *nomen nudum* (*Aphanobothrium*), two are considered to be junior synonyms of other lecanicephalidean genera (*Parataenia* and *Spinocephalum*), nine are considered to be lecanicephalidean *genera inquirenda* (*Anthemobothrium*, *Cephalobothrium*, *Flapocephalus*, *Hexacanalis*, *Kystocephalus*, *Sephenicephalum*, *Staurobothrium*, and *Thysanobothrium*), one is considered to be an invalid replacement name for a valid lecanicephalidean genus (*Monoporophyllaeus*), and 12 are recognized to be valid members in the order (*Aberrapex*, *Anteropora*, *Corrugatocephalum*, *Eniochobothrium*, *Healyum*, *Hornellobothrium*, *Lecanicephalum*, *Paraberrapex*, *Polypocephalus*, *Quadcuspibothrium*, *Tetragonocephalum*, and *Tylocephalum*). A key to the valid genera is given. Treatment of the valid genera, in each case, includes comments on the type species and on at least one additional species (mostly the new species). New collections of lecanicephalideans from around the world formed the basis for this taxonomic work. As a result, a total of 22 lecanicephalidean species are treated. Studies mentioning or addressing the species treated here were summarized in a chronology section for each species. Each species is illustrated with a map indicating its geographic distribution, line drawings of, at a minimum, the whole worm, scolex, and proglottid. If material was available, a complete characterization of the microthrix pattern of a species, as observed with scanning electron microscopy, is presented. As part of a character analysis, identification of homologous components of apical structures in lecanicephalideans was attempted. The character analysis resulted in 64 morphological characters that were included in a series of phylogenetic analyses performed to investigate relationships among lecanicephalidean genera. These analyses included 18 lecanicephalidean species, representing the 12 valid genera, and two tetraphyllidean and proteocephalidean species each, used as outgroups. Effects of different amounts of missing data, coding strategies for inapplicable characters and the effect of outgroup selection on tree topology were investigated. None of the trees resulting from these analyses were well supported. In general, these trees suggested a monophyletic Lecanicephalidea relative to the outgroups, a basal position for lecanicephalideans lacking an apical structure, and a clade containing species possessing an apical structure, with a trend towards an increase in apical organ size within this clade. Familial boundaries remain poorly understood and unstable. Consequently, no familial classification scheme for the Lecanicephalidea is proposed at this time. As a result of the new collections, geographic distribution and host associations of the Lecanicephalidea were expanded. For example, major locality records for lecanicephalideans now included the Gulf of Mexico, the Mozambique Channel and the eastern Indian Ocean off Madagascar, the Gulf of Thailand, and the Timor and Arafura Seas off northern Australia. Lecanicephalidean host associations were expanded to include 19 new host species records, one new host genus record (the sawfish genus *Pristis*) and one new host family record (the bamboo shark family Hemiscylliidae). In addition, the literature on larvae identified as lecanicephalideans was summarized. Overall, an underestimated generic diversity and morphological disparity was demonstrated.

INTRODUCTION

> *In a rich bath of pre-digested soup,*
> *Warm in the pulsing bowel, safely shut*
> *From the bright ambient horror of sun and air,*
> *His slender segments ripening loop by loop,*
> *Broods the voluptuous monarch of the gut,*
> *The tapeworm, the prodigious Solitaire.*
>
> — A. D. Hope, *The Kings*
> Hamish Hamilton, London 1960

Lecanicephalidean (*lecano*-, Gr. *lekane*, dish, pot, pan [see *lekos*, Gr., plate]; *kephale*, Gr., head) tapeworms are endoparasites, belonging to the class Cestoda (phylum Platyhelminthes). With almost 650 described genera (Caira and Littlewood 2001), the class Cestoda is the second most diverse group of Platyhelminthes (flatworms) after the Digenea (flukes). In addition to the Lecanicephalidea, 13 orders are currently recognized in the class. As adults, members of these 14 orders parasitize all major groups of vertebrates:

Order	Host group
Amphilinidea	Actinopterygii (ray-finned fishes) and Testudines (turtles)
Gyrocotylidea	Holocephali (chimaeras)
Spathebothriidea	Actinopterygii (ray-finned fishes)
Caryophyllidea	Actinopterygii (ray-finned fishes)
Pseudophyllidea	Actinopterygii (ray-finned fishes), Mammalia (mammals)
Haplobothriidea	Actinopterygii (ray-finned fishes)
Diphyllidea	Elasmobranchii (sharks and rays)
Trypanorhyncha	Elasmobranchii (sharks and rays), Holocephali (ratfish)
Tetraphyllidea	Elasmobranchii (sharks and rays), Holocephali (ratfish)
Lecanicephalidea	Elasmobranchii (sharks and rays)
Proteocephalidea	Actinopterygii (ray-finned fishes), “amphibians,” “reptiles”
Tetrabothriidea	marine homeotherms
Nippotaeniidea	Actinopterygii (ray-finned fishes)
Cyclophyllidea	“amphibians,” “reptiles,” Aves (birds), Mammalia (mammals)

Four of these 14 orders, the Tetraphyllidea, Diphyllidea, Trypanorhyncha, and Lecanicephalidea, are restricted to the Elasmobranchii, or the slightly more inclusive Chondrichthyes (*i.e.*, Elasmobranchii [sharks and rays] and Holocephali [ratfish]).

The order Lecanicephalidea is particularly intriguing because of both the diversity in scolex morphology and the interesting host associations exhibited by its members. These tapeworms live in the spiral intestine of their elasmobranch hosts, with their anterior attachment structure (scolex) embedded in the host’s intestinal mucosa. The lecanicephalideans are among the most poorly known groups of tapeworms. They are also notable for their small body size. Most species of lecanicephalideans range in total length from 2 mm to 5 cm, but the smallest worms measure less than 500 µm.

Morphology and Terminology

The lecanicephalidean body consists of three parts: (1) the scolex, which serves as the anterior attachment structure, (2) the germinative zone, which is the region of proglottid production, and (3) the strobila, which consists of a chain of proglottids. Historically, the terms “proglottid” and “segment,” have both been used to refer to a single compartment of a tapeworm, containing at least one set of reproductive organs. However, it has effectively been argued (Mehlhorn *et al.* 1981) that, in the case of tapeworms, the term proglottid (proglottis in Mehlhorn *et al.* [1981]) should be preferred over segment until consensus is reached on the question of homology of the “repetitive units of the tapeworm body” (p. 255) and the segments of truly metameric invertebrates, such as, for example, annelids or arthropods. Proglottid will be used throughout this work.

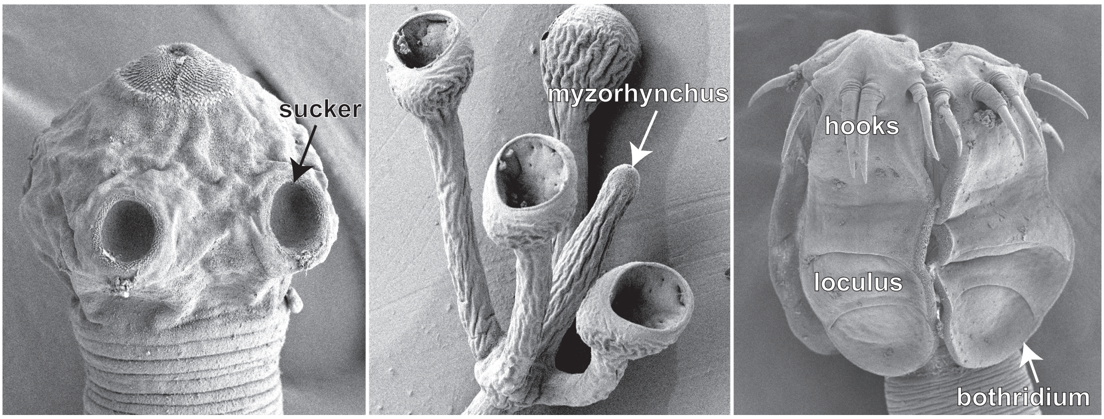


Fig. 1. Scolex terminology.

The morphology of the scolex varies widely among cestode groups and is particularly diverse within the Lecanicephalidea. There are two distinct, general conditions of the scolex in tapeworms. Some possess a central core of tissue (scolex proper), attached to which are two (in some cases four) bothria, consisting of sucking surfaces lacking conspicuously bounded musculature. This scolex type is seen in difossate groups such as the Pseudophyllidea, Diphyllidea, and Trypanorhyncha. The alternate scolex form consists of the scolex proper attached to which are four muscular, membrane-bound organs of attachment (referred to as suckers, bothridia, or acetabula). This scolex type is seen in tetrafossate groups such as the Proteocephalidea, Tetraphyllidea, Cyclophyllidea, and Lecanicephalidea. The term used for the attachment structures in tetrafossate groups depends on the group of tapeworms and/or the preference of the author. Caira *et al.* (1999) demonstrated the homology between the suckers and acetabula of lecanicephalideans, proteocephalideans, and cyclophyllideans, and the bothridia of tetraphyllideans. They argued for the use of the older name, acetabulum, for attachment organs in all of these groups. The term acetabulum has been adopted here. Acetabular shape is a useful diagnostic feature. Therefore, following Caira *et al.* (1999), acetabula are categorized as being either in the form of suckers (round, sessile organs of attachment, lacking obvious proximal surfaces) or in the form of bothridia (variably shaped, non-sessile organs of attachment, possessing clearly identifiable proximal surfaces) (see Fig. 1). In a number of cestode groups, but best exemplified by the Tetraphyllidea, acetabula can be modified in a number of ways; they can be subdivided by septa into loculi, and/or possess several combinations of the following: accessory suckers, pads, hooks, etc. (Fig. 1). The majority of the Lecanicephalidea is considered to possess acetabula in the form of simple, unmodified suckers attached to the scolex proper, equidistantly spaced from one another in a horizontal plain. A few lecanicephalideans, however, possess acetabula that are bothridiate; the bothridia in these taxa are also completely unmodified.

In addition to acetabula, lecanicephalideans, in general, and some members of the cestode orders Tetraphyllidea, Proteocephalidea, and Cyclophyllidea, possess a structure on the apex of the scolex that aids in attachment. Different terminology has been applied to apical structures in different groups (*e.g.*, metoporhynchus in the Lecanicephalidea, myzorhynchus in the Tetraphyllidea [Fig. 1], and rostellum in the Cyclophyllidea). In an attempt to identify homologous features associated with the apical structures across cestode orders, Caira *et al.* (1999) introduced terminology for different parts of apical structures (*e.g.*, apical modification of the scolex proper and apical organ) (Fig. 2). This terminology has been adopted here. Lecani-

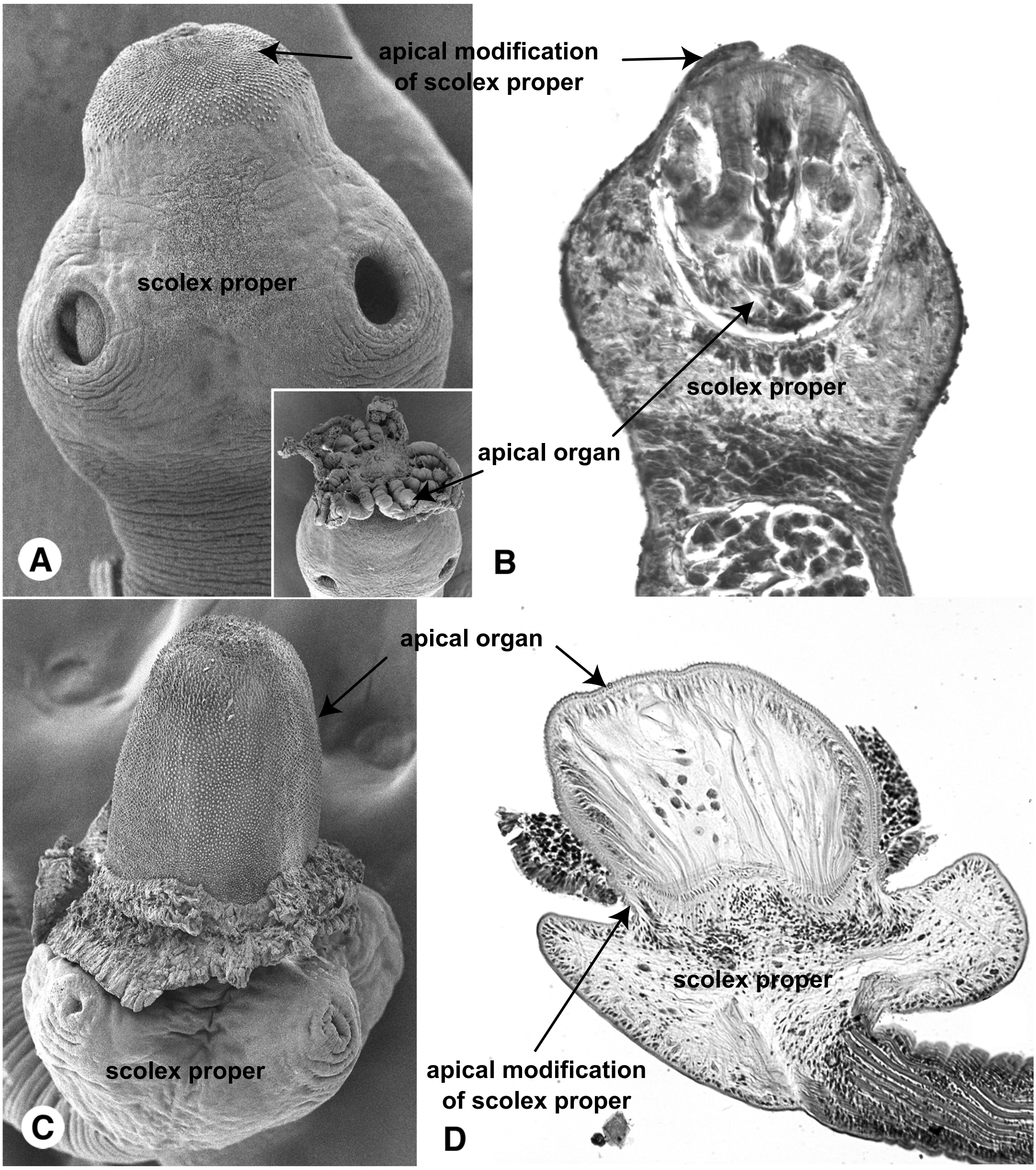


Fig. 2. Apical structure terminology. A-B. *Polypocephalus helmuti* Jensen, **n. sp.** A. Scanning electron micrograph of scolex; note inset of scolex with apical organ tentacles everted. B. Frontal section through scolex. C-D. *Tetragonocephalum passeyi* Jensen, n. sp. C. Scanning electron micrograph of scolex. D. Frontal section through scolex.

cephalideans are the champions of morphological diversity in apical structures. For example, species that possess apical structures that are fungiform, bulbous, small cone-like, or divided into tentacles are known. In 1890 (p. 863), Linton wrote about a small new lecanicephalidean cestode he discovered: “One is tempted, when doing systematic work on any group, to pronounce each new form that meets his eyes the most remarkable of all.” Indeed, given the diversity of lecanicephalidean apical structures, this was a temptation throughout the duration of the present study. That is not to say that all lecanicephalideans possess apical elaborations. Jensen (2001) recently described two unusual new lecanicephalidean genera, both of which lack an apical structure altogether.

All lecanicephalideans are hermaphroditic. Terminology for the proglottid anatomy is illustrated in Figure 3. The female reproductive system consists of the following major organs and their associated ducts: vagina, ovary, vitelline follicles, and uterus. The vagina opens into the genital atrium and extends posteriorly towards the ootype (region between the lobes of the ovary, posterior to the ovarian bridge). The ovary produces ova that get passed, through the muscular oocapt, into the oviduct. Along the length of the oviduct, the vagina enters first, supplying sperm to the for fertilization. Second, the vitelline duct enters, supplying the embryo with vitelline cells that are produced in the vitelline follicles. The embryos are then passed through the Mehlis' gland, which contributes material to produce the eggshell. Leaving the Mehlis' gland, the eggs are carried in the uterine duct into the uterus.

In the male system, the testes produce sperm that pass into ducts called vas efferens, presumably one duct per testis. These vas efferens join to form a single collecting duct, the vas deferens. The vas deferens connects to the cirrus sac, which contains the intromittent organ, the cirrus. The cirrus and the vagina open into a common genital atrium that opens through the genital pore to the outside of the proglottid. This pore is situated laterally or sublaterally in the proglottid. In the Lecanicephalidea the vagina generally opens posterior to the cirrus sac into the genital atrium. This condition is also seen in all, or the majority of taxa in, for example, the Diphyllidea, Cyclophyllidea, and Tetrabothriidea, in addition to a number of taxa in the Proteocephalidea, Cyclophyllidea, Trypanorhyncha, and Pseudophyllidea. Genera and species in the Lecanicephalidea vary in a number of features associated with these reproductive systems (*e.g.*, ovary shape, testes distribution and number, vitelline follicle distribution, etc.).

Diagnostic features for the Lecanicephalidea as a group are few. Historically, the two main characters used to define the Lecanicephalidea have been the presence of an apical structure on the scolex (*i.e.*, a bipartite scolex divided into an anterior apical region, referred to as "pars apicalis," and a posterior scolex proper region, referred to as "pars basalis") with four sucker-like acetabula, and a vagina that opens into the genital atrium posterior to the cirrus sac (Euzet 1994b). This latter character seems to have been used mainly to distinguish lecanicephalideans from their

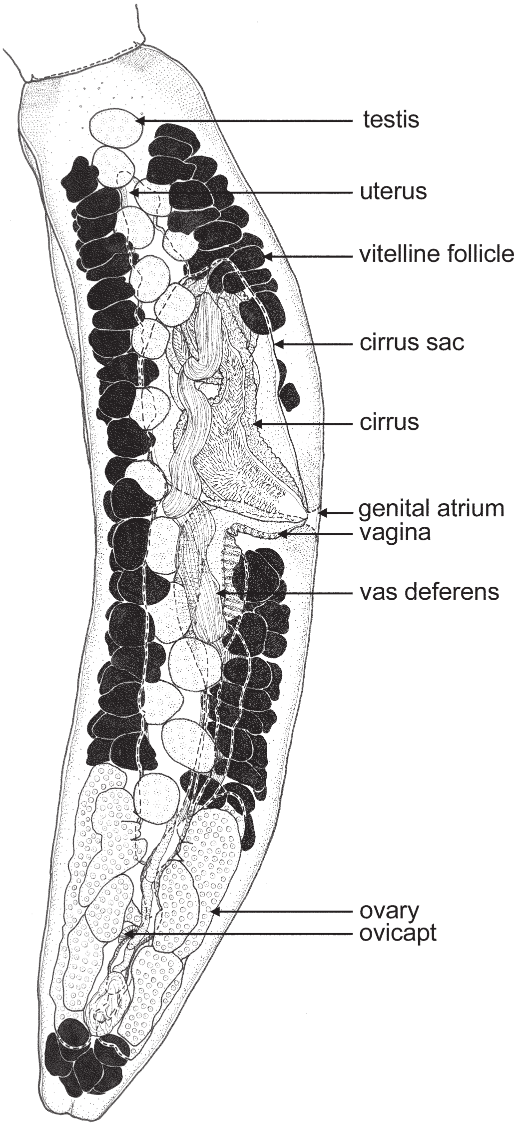


Fig. 3. Proglottid terminology.

close relatives the tetraphyllideans; tetraphyllideans are unusual in that all taxa (not just a subset like, *e.g.*, in the Pseudophyllidea, Proteocephalidea, and Cyclophyllidea) possess a vagina that opens anterior to the cirrus sac into the genital atrium. Unfortunately, the diagnostic features for the Lecanicephalidea are merely a unique combination of non-unique characters; a global synapomorphy for lecanicephalideans has yet to be identified.

Phylogenetic Position within the Class Cestoda

The classification of lecanicephalidean taxa as their own order (*e.g.*, Schmidt 1986; Euzet 1994b), or within any of five different orders, including the Tetraphyllidea (*e.g.*, Butler 1987b), the Tetracestoda (see Perrier 1897), the Diphyllidea (*e.g.*, see Mola 1921), the Cyclophyllidea (see Southwell 1925), and the Taeniidea (see Poche 1926) is an indication that the relationships of the Lecanicephalidea to other cestode orders have been poorly understood. Admittedly, if ordinal status was not granted, the most common placement of lecanicephalidean taxa over time has been within the Tetraphyllidea (*e.g.*, Meggitt 1924; Fuhrmann 1931; Joyeux and Baer 1961). However, despite the extensive literature dealing with cestode classification, only a few of the studies that have included explicit hypotheses of interrelationships have included lecanicephalidean representation. Lecanicephalideans do not appear on the tree provided by Baer (1950), however, the lecanicephalidean family Cephalobothriidae Pintner, 1928 is compared to the Disculicepitidae Joyeux and Baer, 1936 in the text. Baer suggested that the Disculicepitidae gave rise to the Tetraphyllidea, the Proteocephalidea (considered by Baer to be Tetraphyllidea in freshwater fishes), and the Cyclophyllidea. Euzet (1959) provided a tree of the relationships among cestode orders, in which the superfamily Lecanicephaloidea is presented as a basal group within in the Tetraphyllidea. In this scheme the Tetraphyllidea also includes the superfamilies Phyllobothrioidea and Prosobothrioidea. Euzet suggested that this latter lineage, composed of the Phyllobothrioidea and the Prosobothrioidea, gave rise to the order Tetrabothridea [sic]. Freeman (1973) presented a branching diagram illustrating the "pattern of evolution" (p. 543) for the cestodes from their free-living ancestors. In that scenario, a "primitive tetraphyllidean-proteocephalidean" gave rise to the Diphyllidea, Lecanicephalidea, Tetraphyllidea, and primitive Proteocephalidea. In the phylogenetic hypothesis for cestode interrelationships provided by Dubinina (1980), the Lecanicephalidea, Tetraphyllidea, and Proteocephalidea (which subsequently gave rise to the Nippotaeniidea, Tetrabothriata, Cyclophyllidea, and Aporidea) collectively constitute one of two major cestode lineages. Stunkard (1983) adopted Euzet's (1959) tree and classification of the cestodes. Brooks *et al.* (1991) presented a phylogenetic tree of eucestode interrelationships. In their tree, the Lecanicephalidea constitute a monophyletic group with the Tetraphyllidea (including trypanorhynchs and tetrabothriids) and the Proteocephalidea (including the cyclophyllideans). The phylogenetic tree of the orders of eucestodes presented by Brooks and McLennan (1993) was essentially that of Brooks *et al.* (1991). In this scheme, the Lecanicephaliformes form a monophyletic group with two other orders, the Tetraphylliformes and the Proteocephaliformes. Brooks and McLennan's unusually broad concepts of the Tetraphylliformes and Proteocephaliformes complicate comparisons between this and other phylogenetic hypotheses. In their scheme, both orders include subordinal groups for which significant consensus exists considering them to be valid independent orders (*e.g.*, Trypanorhyncha and Cyclophyllidea) (*e.g.*, Schmidt 1986; Khalil *et al*. 1994). It is important to note however, that the phylogenetic trees presented by Brooks *et al.* (1991) and Brooks and McLennan (1993) are not the result of formal phylogenetic analyses, rather they are evolutionary hypotheses. The recent major taxonomic treatments of the Lecanicephalidea (Schmidt 1986; Butler 1987a; Euzet 1994b) did not address the systematic position of the group in a larger framework.

Since 1997, the investigation of cestode interrelationships, including lecanicephalideans, using formal phylogenetic analyses has gained considerable attention.

Modern methods of phylogenetic analysis have been used to analyze both morphological and molecular data. A so-called, “top-down” phylogenetic analysis, employing higher taxonomic categories as terminal taxa, was conducted by Hoberg *et al.* (1997). In that study, the “Lecanicephalidea” appeared as the sister to a group including the Nippotaeniidea, Tetrabothriidea, and the Cyclophyllidea. However, the specific taxa considered lecanicephalideans and/or those that were coded were not specified by Hoberg *et al.* (1997). In 1999, Olson and Caira presented the first phylogenetic hypothesis of cestode interrelationships based on molecular data that included lecanicephalidean representation. The two lecanicephalidean species included in that analysis collectively grouped as the sister to a group consisting of Tetraphyllidea, Proteocephalidea, Tetrabothriidea, Cyclophyllidea, and Nippotaeniidea. But a second placement, that is, as the sister taxon to a group containing the latter three orders only, was suggested as a result of a subset of the analyses. By far the greatest representation of lecanicephalideans up to that time was included in the morphological phylogenetic analysis of Caira *et al.* (1999). In that study, the majority of lecanicephalidean taxa grouped with the tetraphyllidean genera *Pseudanthobothrium* Baer, 1956 and *Echeneibothrium* Van Beneden, 1850, and the proteocephalidean genus *Monticellia* La Rue, 1911, in a clade within the Tetraphyllidea. However, that analysis included representatives of only four cestode orders. In the molecular analysis of Olson *et al.* (1999), the two included lecanicephalidean taxa grouped within the Tetraphyllidea. Hoberg *et al.* (2001) recently presented a phylogeny for the eucestodes based on a combination of morphological and molecular data. In that study, the Lecanicephalidea, represented by the genus *Eniochobothrium* Shipley and Hornell, 1906, was the sister group to a clade containing the Tetraphyllidea, Diphyllidea, Proteocephalidea, Nippotaeniidea, Tetrabothriidea, Mesocestoidata, and Cyclophyllidea. In an expanded version of their 1999 study, which included additional taxa and characters, Caira *et al.* (2001) found the majority of the lecanicephalidean taxa grouped with proteocephalideans, tetrabothriids, and a single cyclophyllidean. This clade was part of a large polytomy including all tetraphyllidean species (and other lecanicephalidean taxa). In the most recent phylogenetic analysis of ordinal relationships (Olson *et al.* 2001), morphology placed the lecanicephalideans in a monophyletic group with tetraphyllideans, proteocephalideans, nippotaeniids, tetrabothriids and cyclophyllideans, while molecular data occasionally grouped the lecanicephalideans with the litobothriids, usually basal to a clade containing the group of taxa indicated above.

From the studies summarized above, it is obvious that the systematic placement of the Lecanicephalidea is unstable and far from resolved. No two phylogenetic analyses have resulted in the same placement of the Lecanicephalidea. In general, these phylogenetic studies suggest that among the tetrafossate cestodes (*i.e.*, those with four acetabula in the form of suckers or bothridia), lecanicephalideans are generally basal. Collectively, these studies indicate that the phylogenetic positions of lecanicephalidean taxa are intimately tied to those of the tetraphyllideans and proteocephalideans.

Taxonomic History of the Lecanicephalidea

The taxonomic history of lecanicephalideans is not only lengthy, but is also confused. At least 25 different authors have addressed the supergeneric classification of lecanicephalidean taxa. No two authors have agreed on the same scheme. The problem is magnified by the fact that the higher classification of cestodes in general, especially at the ordinal level, has been highly unstable. As a result, lecanicephalideans have been recognized at a variety of levels of classification. They have been considered an order (*e.g.*, Hyman 1951; Wardle and McLeod 1952; Yamaguti 1959; Schmidt 1986; Euzet 1994b) or a superfamily (*e.g.*, Southwell 1930; Riser

1955; Euzet 1959; Joyeux and Baer 1961). They have been considered to belong to one or more families within the order Tetraphyllidea (also parasitizing elasmobranchs as their definitive host) (*e.g.*, Braun 1894-1900; Meggitt 1924; Woodland 1927; Fuhrmann 1931; Riser 1955; Euzet 1959; Spasski 1958; Butler 1987a) or within other orders, for example, in the Tetracestoda (see Perrier 1897), the Diphyllidea (see Mola 1921, 1929), the Cyclophyllidea (see Southwell 1925), or the Taeniidea (see Poche 1926). Ignoring the ordinal placement or status, lecanicephalidean genera have been placed into a single family (*e.g.*, Braun 1894-1900; Mola 1921), or have been divided into two families (*e.g.*, Pintner 1928; Wardle and McLeod 1952; Euzet 1959; Joyeux and Baer 1961; Brooks and McLennan 1993), three families (*e.g.*, Meggitt 1924; Poche 1926), or four families (*e.g.*, Yamaguti 1959; Euzet 1994b). Because of this instability, generalizations about the classification of lecanicephalideans, beyond those stated above are difficult. The diversity of classification schemes proposed for, or including lecanicephalideans, is best illustrated in list form. The major classification schemes including lecanicephalideans are summarized in Appendix 1. In this appendix, studies dealing with taxa that, at one point in time, have been considered lecanicephalideans, but actually belong to other cestode orders (*e.g.*, *Discobothrium* Van Beneden, 1871 and *Balanobothrium* Hornell, 1912) are given only cursory attention. Although Lühe's (1910) classification of the cestodes is often cited, it is omitted from discussion here because only freshwater cestodes were treated. The taxonomic histories of individual lecanicephalidean genera are presented in detail in the chronology for each genus.

Relationships within the Lecanicephalidea

The order Lecanicephalidea has never itself been the subject of a comprehensive phylogenetic analysis, although individual lecanicephalidean species have been included in higher level phylogenetic analyses addressing the interrelationships among cestode orders. Limited information on interrelationships within the Lecanicephalidea can be obtained from those studies. Under the name "*Eniochobothrium gracile*" Shipley and Hornell, 1906, the new species of *Eniochobothrium* described in this study was the only lecanicephalidean species included in the analysis performed by Hoberg *et al.* (2001) (see remarks of new species for discussion). Olson and Caira (1999), Olson *et al.* (1999), Kodedová *et al.* (2000), and Olson *et al.* (2001) included two lecanicephalideans (*Cephalobothrium* cf. *aetobatidis* and "*E. gracile*") and Littlewood and Olson (2001) included three lecanicephalideans (*C.* cf. *aetobatidis*, "*E. gracile*," and *Tylocephalum* sp.) in their analyses. The gene loci for which these molecular sequence data were obtained are the complete sequences for the SSU rDNA and 1400 base pairs (D1-D3 region) LSU rDNA for all three taxa, and 825 base pairs of Elongation factor 1-α (Ef-1α) for *C.* cf. *aetobatidis* and "*E. gracile*" only (Olson *et al.* 2001). In the studies including more than one lecanicephalidean species, these taxa were found to be each other's closest relatives. Brooks and McLennan (1993) presented a hypothesis of the relationships among 12 lecanicephalidean genera. Their tree does not appear, however, to have resulted from a phylogenetic analysis. Rather, diagnostic characters were mapped onto an evolutionary tree to lend support to the topology presented. Unfortunately, few characters were identified and those that were identified often are not representative of even a subset of the constituent taxa they are reported to support (*e.g.*, character [3], p. 332, pedunculated suckers in *Tetragonocephalum* Shipley and Hornell, 1905).

Two recent studies have included adequate lecanicephalidean representation to allow for preliminary speculations about relationships within the Lecanicephalidea. Caira *et al.* (1999) included eight lecanicephalidean species from eight genera in their phylogenetic analysis based on morphological data. The complete analysis included a total of 63 cestode taxa. This data set was subsequently expanded (Caira *et al.* 2001) to include 21 lecanicephalidean species in 15 genera (among a total of 127 taxa). Those phylogenetic analyses with greater lecanicephalidean representation were based on 120 and 157 morphological characters, respectively. Unfortunately, the phylogenetic trees resulting from these analyses were largely unresolved and only very weakly supported. However, the primary goal of these studies was not the investigation of the relationships among the taxa included, but rather, the generation of thorough character analyses, resulting in a detailed and explicit articulation of characters that present a starting point for future morphological analyses. In addition, these studies aimed to compare morphological features among disparate taxa, to determine possible homologies among morphologically very diverse structures (*e.g.*, apical structures). The result was the articulation of a number of assumptions about the homologies among different structures, particularly features of the scolex, which are now open for scrutiny by other cestodologists.

Objectives

The taxonomic history and classification of the Lecanicephalidea have been turbulent. The constituency of genera in the Lecanicephalidea has varied dramatically. At the inception of this study, no less than 43 genera had been considered as lecanicephalideans over time. No two authors have agreed on the generic membership of the order. Butler (1987a) gave a very comprehensive and detailed summary of the taxonomic history of the group. In that work she considered the lecanicephalideans to be a family of tetraphyllideans and referred to the group as “a collection of little-known genera” (p. 105). Even though Butler’s study did much to illuminate taxonomic problems within the lecanicephalideans, the controversy about its membership remained. Not surprisingly, the two most recent revisionary treatments of the Lecanicephalidea by Schmidt (1986) and Euzet (1994b) differed considerably in the number of lecanicephalidean genera they recognized. Whereas Schmidt (1986) recognized 11 valid genera, Euzet (1994b) recognized only five.

Over an eight year period, collections of tapeworms from elasmobranch species never before examined for tapeworms have revealed a number of new and interesting forms of lecanicephalideans. New collections also resulted in material that appeared to be consistent with lecanicephalidean forms not seen for almost a century. Most importantly, this new material suggested that lecanicephalidean morphological diversity has heretofore been underestimated. Description of these new forms and verification of the identity of re-collected taxa necessitated the generation of a solid framework for comparisons to existing, valid genera. This was the initial motivation for this study. The primary goal was to prepare a monograph on the Lecanicephalidea at the generic level, with the following six objectives in mind:

(1) To determine the identity of all genera that have been associated with the Lecanicephalidea.
(2) To revise and modernize the concept of the valid lecanicephalidean genera.
(3) To generate a list of valid lecanicephalidean species.
(4) To generate a list of lecanicephalidean type specimens available at museums.
(5) To perform a phylogenetic analysis assessing lecanicephalidean generic interrelationships.
(6) To expand knowledge on lecanicephalidean morphology, geographic distributions, and host associations.

MATERIALS AND METHODS

Specimen Preparation

In general, elasmobranchs were obtained from local fishermen. The elasmobranchs were mainly caught in gill nets. They were opened with a longitudinal incision along the ventral surface of the body from anus to the pericardial cavity. The spiral intestine was then disconnected anteriorly from the stomach and posteriorly from the rectum and opened by longitudinal incision through the center of the chambers from anterior to posterior. Some spiral intestines were examined in the field. In such cases, the internal surfaces of the spiral intestine were examined by eye or under a dissecting microscope. Tapeworms seen were carefully removed from the gut surface with a 1.8 mm micro-dissecting curette or fine forceps and placed in a petri dish in seawater. Subsequently, the spiral intestine was rinsed with seawater using a squirt bottle and the rinse collected. The rinse was then examined and all tapeworms recovered placed in seawater. The tapeworms were then pipetted into a vial with 10% seawater buffered formalin solution for fixation and the vial vigorously shaken to prevent contraction of the worms and facilitate straightening of the strobilae as suggested by L. Euzet (pers. comm.). The spiral intestine was then either discarded or fixed in 10% seawater buffered formalin solution for more thorough investigation in the laboratory. Spiral intestines of animals not examined in the field were placed in a bag or jar with 10% seawater buffered formalin solution and the receptacle immediately vigorously shaken to prevent the tapeworms that were still attached to the gut wall from contracting. Eventually, all tapeworms and spiral intestines fixed in 10% seawater buffered formalin solution were transferred to 70% ethanol for storage.

Light microscopy: Specimens for light microscopy were prepared as whole mounts and for histological sections. Specimens prepared for whole mounts were transferred to distilled water, stained in Delafield's hematoxylin, differentiated in tap water, and then partially dehydrated in 70% ethanol, destained in 70% acid ethanol, washed in 70% alkaline ethanol, and further dehydrated in a graded ethanol series (70% ethanol - 95% ethanol - 100% ethanol [twice]), cleared in methyl salicylate, and mounted on glass slides in Canada balsam. Serial sections were prepared as follows: whole worms, scolices, or proglottids were dehydrated in a conventional graded ethanol series, cleared in xylene, placed in a 1:1 mixture of xylene and paraffin (or Paraplast®) overnight in an oven, transferred to paraffin (or Paraplast®) for several hours, and embedded using tissue embedding rings and metal embedding molds. Serial sections were cut at 10 µm intervals using an American Optics rotary microtome or at 5-8 µm intervals using an Olympus CUT4060 retracting rotary microtome. Sections were floated on 3% sodium silicate on slides on a slide warmer to expand and subsequently allowed to air dry on a slide warmer. Sections were placed in xylene (twice) to remove the paraffin (or Paraplast®), hydrated in a graded ethanol series, stained with Gill's or Delafield's hematoxylin, differentiated in Scott's solution, partially dehydrated in 70% ethanol, counterstained with eosin, further dehydrated in a graded ethanol series, cleared in xylene, and mounted on glass slides in Canada balsam. When gravid proglottids of a species were available, semi-permanent mounts of eggs were prepared as follows: gravid proglottids were placed in a 1:1 mixture of 70% ethanol and lactophenol and left overnight in an open container in a fume hood to allow the ethanol to evaporate. Proglottids were subsequently broken open with insect pins, the eggs isolated and mounted in lactophenol on a glass slide under a cover slip, and twice sealed with nail polish.

Scanning electron microscopy (SEM): The scanning electron microscopical work was conducted at the Biology Electron Microscopy Laboratory, University of Connecticut, Storrs, Connecticut, U.S.A. If available, at least two specimens of each species for which new material was collected were prepared for SEM as follows: Buffered formalin fixed specimens (stored in 70% ethanol) were hydrated in a graded ethanol series, postfixed in 1% osmium tetroxide overnight, dehydrated in a graded ethanol series, and transferred to hexamethyldisilizane (HMDS, Ted Pella Inc., Redding, CA) for 15 min. The excess HMDS was then removed, specimens were air-dried in a fume hood, and mounted on aluminum stubs on double-sided adhesive carbon tape. Specimens were sputter coated with approximately 100Å of gold/palladium and examined with a LEO/Zeiss DSM982 Gemini field emission scanning electron microscope.

Measurements

Measurements were taken using a computer aided electronic measuring system. Images were acquired through a Hitachi HV-C20 3-CCD color camera mounted on a Zeiss Axioscope and measurements were taken using the image analysis software ImagePro® Express. Measurements were directly entered into a spreadsheet program for further analysis. All measurements are given in micrometers (µm) unless otherwise specified. All measurements of reproductive organs were taken from mature proglottids unless otherwise specified. Measurements in the descriptions are given as the range followed in parentheses by the mean, standard deviation, the number of worms examined (n), and the total number of observations (*n*) when more than one measurement was taken per worm.

Preparation of Figures

Line drawings were prepared with the aid of a drawing tube on a Zeiss Axioskop. Scanning electron micrographs were captured as digital images directly from the LEO/Zeiss DSM982 Gemini field emission scanning electron microscope. Plates were prepared using Adobe Photoshop (v. 5.5 and 6.0) and Adobe Illustrator (v. 9.0 and 10.0). Images of histological sections were taken with a Kodak DCS 410 digital system attached to a Nikon N90s camera body mounted on a Zeiss Axioskop and also assembled in Adobe Photoshop or Illustrator. Distribution maps were obtained using Online Map Creation (version 4.1) (http://www.aquarius.geomar.de/omc/omc_intro.html) generating maps using GMT (The Generic Mapping Tools) (Wessel and Smith 1998).

Nomenclature

The lecanicephalidean taxonomic literature is filled with terms referring to the taxonomic or nomenclatural status of any particular taxon reflecting the opinion of the author. Terms such as "*incertae sedis*," "*species inquirenda*" or statements suggesting "suppression" of a taxonomic name are common. It appears, however, that these terms have meant different things to different authors, and in some cases have been used incorrectly. This situation is not unique to the literature of this group. For consistency and clarification, the terms used herein are defined below. Most of these definitions are based on terminology defined by the ICZN (1999) and Schenk and McMasters (1956):

Incertae sedis. This term is used in connection with a genus or species name. It refers to the uncertain systematic position of the taxon within the genus or family. The validity of the taxon is not in question.

Species inquirenda (pl. *species inquirendae*) or *genus inquirendum* (pl. *genera inquirenda*). This term is used in connection with a species or genus. The term refers to the doubtful status of the taxon. Additional investigations are required to determine the validity of the species or genus. The systematic position of this taxon is not in question.

Nomen dubium. This term is used in connection with a genus or species name. The term refers to a taxon that is unidentifiable from its original description and/or type material.

Nomen nudum. This term is used in connection with a genus or species name. The name was invalidly published (without designation, *i.e.*, indication, definition, or description) and, as a consequence, is not available (see ICZN Art. 12 and 13 [1999]).

Suppression. Suppression of a name is a nomenclatural act requiring ruling by the Commission of Zoological Nomenclature. The suggestion by an author in a taxonomic treatment that a genus or species be "suppressed" without the necessary official appeal to the Commission is therefore effectively inconsequential.

Description. A treatment of a new species or any treatment of an existing species for which new information is added either based on new observations of the type specimens or additional, new specimens. The specimens used for the (re-) description should be explicitly stated, as should the source (citation) of the original data.

Lecanicephalidean Species

Despite its generic focus, this work includes descriptions of seven new species. These descriptions require that new species be distinguished from existing congeners. This work essentially necessitated generation of lists of valid species for each lecanicephalidean genus. Prior to this study, a total of 137 species had been described in the Lecanicephalidea. The status of these species as they are understood based on results of this study is presented in Appendix 2. The results provided in that appendix constitute the framework for the taxonomic treatment of the individual species provided below. For the purposes of generation of this comprehensive list, in several cases, the validity of a species was assessed by examination of type material. Most often, however, these taxonomic decisions were made based on the original description, mainly because type material does not appear to exist.

Including the new species described in this monograph, 72 lecanicephalidean species are now considered valid. Three of these are represented by species that were described in existing genera, but are likely to represent two new genera (see Appendix 2). Fifty-two species are considered *species inquirendae*. Among those 52 species are the type species of the nine genera considered to be lecanicephalidean *genera inquirenda*. Most of these nine type species appear to be distinct lecanicephalidean entities. However, their questionable taxonomic status identifies them as lecanicephalidean *species inquirendae*. Fourteen species are considered *nomina nuda*; four species are considered non-lecanicephalidean *species inquirendae*; two species were each considered synonyms of a tetraphyllidean and a trypnorhynchan species.

It should be noted that for five species (*Cephalobothrium gangeticus* Gairola, Malhotra and Sukul, 1989, *Hexacanalis thapari* Shinde, Jadhav and Jadhav, 1992, *Polypocephalus bombayensis* Shinde, Dhule and Jadhav, 1992, *Tetragonocephalum yamagutii* Muralidhar, 1990, and *Tylocephalum aurangabadensis* Jadhav and Shinde, 1988) the actual publication date differs from the date of the volume in which the species was described. Consequently, in each case, the actual publication date was used for the author citation of the species, while the date of the volume was used in the literature cited to facilitate obtaining the paper in the future. This might also be the case for other species. However, since actual publication dates are often unavailable, the date of the volume in which the species was described was used as a default.

In an effort to make the taxonomic literature on lecanicephalideans more broadly accessible, information on species in this group from the primary literature is now electronically available. All lecanicephalideans names were added to a searchable database. The taxomonic information from the original description (i.e., authority, type host, type locality, etc.) for each species addressed in this monograph was entered, including information on synonyms. In addition, the original descriptions, including figures, were scanned and are available as PDFs for download. The database can be accessed via a link on the following website: http://www.tapeworms.org.

Museum Material

The location of type material for many lecanicephalideans was unknown at the inception of this study. Information is distributed among obscure and dispersed sources, often restricted to information provided in the original description. In addition, even if the deposition of type material was cited in a source, the material may no longer exist. To generate the list of lecanicephalidean type material, inquiries about lecanicephalidean holdings were made of museums globally. The museums or institutions targeted were the major museums known to hold cestode collections, as well as those places identified as specimen repositories in the original descriptions of the taxa. Museums reporting significant lecanicephalidean holdings were visited, specimen lists generated and specimen data recorded. Museum abbreviations used are as follows:

BMNH, The Natural History Museum, London, England
CIH, Commonwealth Institute for Helminthology, St. Albans, Herts, England
CNHE, Colección Nacional de Helmintos del Instituto de Biologia, Universidad Nacional Autónoma de México, Mexico City, Mexico
HCUQ, Helminth Collection, Department of Zoology, University of Qatar, Qatar
HWML, Harold W. Manter Laboratory, University of Nebraska State Museum, Lincoln, Nebraska, U.S.A.
KUNHM, University of Kansas Natural History Museum, Division of Invertebrate Zoology, University of Kansas, Lawrence, Kansas, U.S.A.
LRP, Lawrence R. Penner Parasitology Collection, Department of Ecology and Evolutionary Biology, University of Connecticut, Storrs, Connecticut, U.S.A.
MHNG, Muséum d'Histoire Naturelles, Genève, Geneva, Switzerland
MPM, Meguro Parasitological Museum, Tokyo, Japan
NMW, Naturhistorisches Museum Wien, Vienna, Austria
NSMT, National Science Museum, Tokyo, Japan
QM, Queensland Museum, Brisbane, Queensland, Australia
SAMA, Helminthological Collection, South Australian Museum, Adelaide, South Australia, Australia
USNPC, U. S. National Parasite Collection, Beltsville, Maryland, U.S.A.
ZMB, Zoologisches Museum Berlin, Berlin, Germany

Based on information in the original descriptions of the 117 heretofore described lecanicephalidean species (valid species and *species inquirendae*; see Appendix 2), data on type specimen deposition is available for 48 species. Specimens for 20 of the 48 species were said to have been deposited at universities in India. The place of type specimen deposition was not given for the remaining 69 species, several of which represent the types of their genera.

The availability of lecanicephalidean type specimens in museums worldwide was determined, to a large extent, through personal visits aimed at cataloguing the lecanicephalidean holdings in each museum. The museums visited over the course of this study were: the Naturkunde Museum in Berlin, Germany (ZMB) in 1997; the Naturhistorisches Museum in Vienna, Austria (NMW) in 1997; the Muséum d'Histoire Naturelle de Genève in Geneva, Switzerland (MHNG) in 1997; the Natural History Museum in London, England (BMNH) in 1997 and 1999; and the Harold W. Manter Laboratory in Lincoln, Nebraska, USA (HWML) in 1998. Janine N. Caira visited the Meguro Parasitological Museum, Tokyo, Japan (MPM) in 1999 and generated a list of lecanicephalidean specimens in their possession. In addition, lecanicephalidean holdings of the U.S. National Parasite Collection in Beltsville, USA (USNPC) were obtained from lists through individual searches available on-line (http://www.lpsi.barc.usda.gov/bnpcu/parasrch.htm). The curators at the Queensland Museum, Brisbane, Queensland, Australia (QM) and at the Helminthological Collection of the South Australian Museum, Adelaide, South Australia, Australia (SAMA) provided lists of their respective lecanicephalidean holdings. Moreover, as a result of a trip to the Laboratoire de Parasitologie Comparée, Station Méditerranéene de l'Environment Littoral, Université Montpellier II in Sète, France, lecanicephalideans in the personal collection of Prof. Louis Euzet and lecanicephalideans in part of Southwell's collection were catalogued. Over the course of this study, several collections with minor lecanicephalidean representation were also examined (Coll. N. Riser, C. G. Alexander, M. Dailey, and R. Goldstein). Letters written to the curator of the Cestode Laboratory at Marathwada University, India, the designated repository for the majority of Indian lecanicephalidean species, inquiring about the type specimens deposited there remained unanswered. Inquiries about lecanicephalidean specimens at the Department of Zoology at Andhra University, India were enthusiastically answered. However, because of time limitation, specimens of the two lecanicephalidean species deposited there (*Cephalobothrium neoaetobatidis* Sarada, Vijaya Lakshmi and Hanumantha Rao, 1992 and *Cephalobothrium stegostomi* Sarada, Vijaya Lakshmi and Hanumantha Rao, 1993) were not borrowed.

As a result of the museum work described above, type material of five species, for which no indication of type specimens was given in the original description, was located. These species were: *Anteropora japonica* (Yamaguti, 1934) Euzet, 1994 at the MPM, *Polypocephalus radiatus* Braun, 1878 at the ZMB, the lecanicephalidean species described as *Taenia acanthobothria* MacCallum, 1921 and *Tenia* [sic] *narinari* MacCallum, 1917 at the USNPC, and *Tylocephalum kuhli* Shipley and Hornell, 1906 deposited under the name "*Tetragonocephalum kuhlii*" Shipley and Hornell, 1906 at the NMW. The type material of two species, *Tylocephalum yorkei* Southwell, 1925 and *Cephalobothrium variabile* Southwell, 1911, said to have been deposited in the collection of the Liverpool School of Tropical Medicine, U.K. and the Colombo Museum, Colombo, Sri Lanka, respectively, were found in Southwell's collection at the Station Méditerranéene de l'Environment Littoral, Université Montpellier II in Sète, France. *Polypocephalus saoudi* Hassan, 1982 and *Discobothrium aegyptiacus* Hassan, 1982, said to have been deposited in the CIH, were found at the BMNH. The type of *Tylocephalum squatinae* Yamaguti, 1934 (a single mature specimen) was said to have been deposited in the personal collection of S. Yamaguti. A slide labled *Tylocephalum squatinae* was found at the MPM, possibly representing the type specimen. Examination of this specimen is required for confirmation.

The list of lecanicephalidean type material that was assembled as a result of the museum work described above is presented in Appendix 3. This appendix includes information on type material for 33 lecanicephalidean species, including the seven species described in this work. The majority of this material was clearly identified as type material. The list of lecanicephalidean voucher material resulting from the museum work is presented in Appendix 4. These appendices, while reasonably complete, should not be considered to be exhaustive. It is possible that, in the future, additional type material or type material for other species will be found in other collections, or among the voucher specimens of the collections cited above, and that additional voucher material will be located.

New Collections

Because of the lack of available type material, especially for type species of genera, new lecanicephalidean collections from type hosts from as close to the type localities as possible were attempted. Given that the vast majority of lecanicephalidean species have been described from waters around India and Sri Lanka (Fig. 67) and that this type material is the least available, collections representative of these taxa/localities were given highest priority. However, collections from these localities were hampered by the numerous political difficulties associated with obtaining permission to collect in combination with the logistical difficulties associated with working in India and Sri Lanka. As a consequence, collections were conducted instead in the waters off and to the north of the Northern Territory, Australia, in the hope that the fauna in these regions was similar to the Indian fauna. This strategy held promise, since the majority of elasmobranch species reported to host lecanicephalideans in India and Sri Lanka, were reported by Last and Stevens (1994) to occur in the waters of northern Australia. Preliminary data from collections in northern Australia conducted early in the study justified the pursuit of this strategy. Other collections, mainly from the Western Atlantic, were also conducted to re-collect lecanicephalidean species from type localities and type hosts in that region. In order to expand the host and geographic ranges of the group, collections of elasmobranchs from new geographic localities not presently sampled for lecanicephalideans, as well as collections of elasmobranch species not yet reported to host lecanicephalideans, were also conducted.

Abbreviations

AO, apical organ; C, cirrus; CM, circular muscle bundle; CS, cirrus sac; ED, excretory duct; ESV, external seminal vesicle; GA, genital atrium; GP, genital pore; LM, longitudinal muscle; MG, Mehlis' gland; OC, ovicapt; OD, oviduct; ORC, osmoregulatory canal; SR, seminal receptacle; SV, seminal vesicle; T, testis; U, uterus; UD, uterine duct.; UP, uterine pore; VA, vagina; VD, vas deferens; VE, vas efferens; VID, vitelline duct; VTD, vitelline duct; VT, vitellaria.

TAXONOMIC TREATMENT OF GENERA

The generic focus of this monograph required that, before revisionary work on lecanicephalidean genera could be tackled, the actual number and identity of valid genera had to be determined. In addition, over the last 10 years, the generic diagnoses and species descriptions for cestodes have become somewhat more comprehensive. For example, scanning electron microscopy (SEM) is used almost routinely in some groups to determine the often unique microthrix pattern on the body surfaces. Therefore, the generic concept of each genus determined to be valid was revised and modernized to include, for example, data available with SEM.

The concept of a genus rests on the identity of its type species. One of the goals of this study was to thoroughly treat the type species of each genus. Examination of type material is imperative for revisionary work at any level. Unfortunately, type specimens of the type species were not available for many lecanicephalidean genera. In these cases, voucher specimens collected from the type locality and/or type host were examined first, whenever possible, for neotype designation. If no specimens of the type species could be located, the treatment of the type species was restricted to literature accounts. To facilitate progress in our understanding of the lecanicephalidean genera, at least one species, in addition to the type species, was chosen and treated comprehensively. The selection of these additional species was based on availability of new material for study with light microscopy (in whole mounts and histological sections), as well as with SEM. Consequently, the additional species described here are, in several cases, new to science. It was, unfortunately, beyond the scope of this study to provide comprehensive treatments of all 100+ described lecanicephalidean species.

It was, however, possible to treat, at least at some level, all generic names ever associated with the Lecanicephalidea. These will be addressed in six categories, with the genera organized in alphabetical order within each category. Treated first are the non-lecanicephalidean genera with historic ties to the Lecanicephalidea. For each genus, a short history of its association with the Lecanicephalidea is presented. A remarks section addressing the identity of the genus and its taxonomic status follows this short history. Treated next, in order, are genera belonging to the following three categories: (1) *genera inquirenda et incertae sedis*, (2) *nomina nuda*, and (3) junior synonyms of valid lecanicephalidean genera. Again, in each case, an historical account of the genus is presented, followed by a remarks section containing justification for the taxonomic status assigned to that genus. Treated next are lecanicephalidean genera considered to be *genera inquirenda*. A complete taxonomic summary for the genus and type species is given for each of these genera. The historical account combines literature treating either the genus or the type species. Additional information regarding the possible taxonomic status of the genus is presented in the remarks section. The bulk of the monograph is dedicated to comprehensive treatments of valid lecanicephalidean genera. A taxonomic summary for each genus is provided followed by the generic diagnosis, an historical account of the literature that has addressed the taxonomy or systematics of the genus and a remarks section. For each genus this section is followed by the taxonomic treatment of the type species, which consists of the taxonomic summary, chronology, description (if available) and remarks, and similar sections for at least one additional species.

The etymologies provided for the generic and specific names were either taken from the original description, or, if an etymology was not provided in the original description, were generated following translations given in Brown (1956). The historical accounts and chronologies represent a compilation of literature sources in which the taxonomy, systematics, or biology of the taxon is addressed. Each account is in the form of a brief summary as it relates to the taxon treated. Terminology used and opinions presented are those of the respective authors, unless surrounded by brackets, in which case the personal opinion of the present author was added. Ordinal, familial, generic, and specific names of parasites and hosts are presented as they appear in the article cited, regardless of modern concepts of the validity, usage, or spelling of those names. Author citations for families, genera, or species, while seemingly somewhat redundant and inconsistently applied overall, are presented as they were by the respective authors. True misspellings are identified with "*sic*" in brackets, indicating exact transcriptions from the literature. In the taxonomic summary of each genus/species treated, the name of the host species is given as it appeared in the original description; the taxonomically correct name of that host species follows in parentheses. A "?" after the currently valid host species name indicates that there remains some question as to whether the valid host name is the correct identity of the host species given by the author in the original description. "Unverified records" in the taxonomic summary identifies reports of that species from other hosts or localities. Unless this additional material was deposited and could be compared to the original description, these accounts are treated with caution and require confirmation.

Among the 43 genera (or generic names) that had been associated with the Lecanicephalidea, 16 are considered to belong to groups other than the Lecanicephalidea. Detailed generic treatments are provided for the remaining 27 genera. Of these 27 genera, two genera are designated as *genera inquirenda et incertae sedis* (possibly also non-lecanicephalidean genera), one genus is considered a *nomen nudum*, one was determined to be an invalid replacement name for a valid lecanicephalidean genus (treated as part of *Anteropora* Subhapradha, 1955), nine are designated as *genera inquirenda* within in the Lecanicephalidea, three are considered junior synonyms of valid lecanicephalidean genera, and 12 are considered valid.

In addition to the generic treatments, 31 species (22 species in valid genera, nine in *genera inquirenda*) are treated in detail. As indicated above, seven of the 22 descriptions are of species new to science.

A. NON-LECANICEPHALIDEAN GENERA WITH HISTORIC TIES TO THE ORDER

Balanobothrium Hornell, 1912

Type species: *Balanobothrium tenax* Hornell, 1912.

Type host: *Stegostoma tigrinum* (Gmelin, 1789) (= *Stegostoma fasciatum* [Hermann, 1783] ?), Zebra shark (Stegostomatidae, Orectolobiformes).

History of association with the Lecanicephalidea

Hornell (1912): erects the new genus *Balanobothrium* with *B. tenax* as the type species.

Southwell (1925): recognizes *Balanobothrium* Hornell, 1912 in the family Lecanicephalidae, suborder Multivitellata, order Cyclophyllidea.

Poche (1926): includes *Balanobothrium* (along with *Discocephalum*, *Lecanicephalum*, *Cephalobothrium*, *Tylocephalum*, and *Adelobothrium*) in the family Lecanicephalidae Braun (Gamobothriidae Linton, 1889; Gamobothridae Ariola, 1899; Benham, 1901), suborder Phyllobothriinea *nom. nov.*, order Taeniidea *nom. nov.*

Woodland (1927): considers *Balanobothrium* (specifically *B. tenax* and *B. parvum*) a "lecanicephalid" taxon; places *Balanobothrium* in the family Phyllobothriidae, order Tetraphyllidea.

Pintner (1928): does not support the placement of *Balanobothrium* in the family Gamobothriidae; places the genus in the family Balanobothriidae.

Southwell (1930): recognizes *Balanobothrium* Hornell, 1912 in the family Lecanicephalidae, superfamily Lecanicephaloidea, order Eucestoda.

Riser (1955): classifies lecanicephalidean taxa in five families (Lecanicephalidae, Cephalobothriidae, Balanobothriidae [presumably with *Balanobothrium* Hornell, 1912 as type genus of the family], Disculicepitidae, and Echinobothriidae) in the superfamily Lecanicephaloidea, order Tetraphyllidea, superorder

Trixenidea.

Yamaguti (1959): recognizes *Balanobothrium* Hornell, 1912 in the family Lecanicephalidae, order Lecanicephalidea.

Schmidt (1970): presents key to the genera of tapeworms; provides diagnosis for each genus and identifies the type species; includes the family Balanobothriidae (type genus *Balanobothrium*) in the order Lecanicephalidea Baylis, 1920.

Wardle *et al.* (1974): recognize the family Balanobothriidae [and consequently *Balanobothrium*] in the order Lecanicephalidea Baylis, 1920; do not mention any genera they consider to belong in the family; present a key to families in the order Lecanicephalidea.

Jadhav and Shinde (1979): describe a new species of *Balanobothrium* (*B. veravalensis*) in the family Lecanicephalidae.

Shinde *et al.* (1983): describe a new species of *Balanobothrium* (*B. aurangabadensis*) in the family Lecanicephalidae.

Schmidt (1986): recognizes *Balanobothrium* Hornell, 1912 in the family Balanobothriidae Pintner, 1928, order Lecanicephalidea Baylis, 1920.

Butler (1987a): considers lecanicephalideans a family in the order Tetraphyllidea; suggests that *Balanobothrium* Hornell should remain in the family Onchobothriidae Braun [rather than the family Lecanicephalidea] as suggested by Meggitt (1924).

Jadhav *et al.* (1989): describe a new species of *Balanobothrium* (*B. fotedari*) in the family Lecanicephalidae.

Remarks

Hornell (1912) described *Balanobothrium tenax*, the type species, from cestodes recovered on two occasions in the spiral intestine of *Stegostoma fasciatum* (as *Stegostoma tigrinum*), without comment on its placement in higher taxonomic categories, and without comparing it to other taxa. Since the description of this species in 1912, the genus has been placed among tetraphyllideans (*e.g.*, Fuhrmann 1931; Wardle and McLeod 1952; Caira and Pritchard 1986; Butler 1987b) and lecanicephalideans (see chronology). In the most recent taxonomic treatment of the elasmobranch cestode orders Tetraphyllidea and Lecanicephalidea, Euzet (1994a, b) considered *Balanobothrium* to be a tetraphyllidean, in the family Onchobothriidae Braun, 1900. Specimens of a new species of *Balanobothrium* examined as part of two recent phylogenetic analyses based on morphological data (Caira *et al.* 1999, 2001) confirmed the presence of tetraphyllidean proglottid and scolex features in this genus. *Balanobothrium* should be considered to be a member of the order Tetraphyllidea, family Onchobothriidae.

Biporophyllaeus Subramaniam, 1939

Type species: *Biporophyllaeus madrassensis* Subramaniam, 1939.

Type host: *Chiloscyllium griseum* Müller and Henle, 1838, Grey bambooshark (Hemiscylliidae, Orectolobiformes).

History of association with the Lecanicephalidea

Subramaniam (1939): erects the genus *Biporophyllaeus* with *B. madrassensis* as the type species from *Chiloscyllium griseum* from Madras, India; erects the new order Biporophyllaeidea for this species.

Wardle and McLeod (1952): accept the order Biporophyllidea.

Subhapradha (1955): erects the genus *Anteropora* with *A. indica* as the type species from *Narcine timlei* from Madras, India; creates a new order, Anteroporidea (for Biporophyllidea Subramaniam, 1939), and a new family, Monoporophyllaeidae, to house this taxon; recognizes *Anteropora indica* and *Biporophyllaeus madrassensis* as distinct in the same order in two different families, Monoporophyllaeidae and Biporophyllaeidae, respectively; suggests not retaining the ordinal name Biporophyllidea after inclusion of *A. indica*, because this species lacks a uterine pore; proposes the name Lateroporidea to replace Biporophyllidea [note: Subramaniam's name was Biporophyllaeidea, and Subhapradha actually used Anteroporidea instead of Lateroporidea]; ordinal, familial, generic and specific diagnoses are provided.

Yamaguti (1959): suggests suppression of Monoporophyllaeidae Subhapradha, 1959, because no generic name corresponds to the family name; like *Biporophyllaeus*, *Anteropora indica* seems to be described from a detached proglottid of a hyperapolytic tetraphyllidean or trypanorhynchan cestode; suggests that this species should be redescribed from a strobila.

Williams (1962): gives history of Biporophyllaeidea and Anteroporidea; several species of tetraphyllideans possess a functional anterior sucker on detached proglottids; suggests that, based on the fact that *Acanthobothrium pearsoni* and *B. madrassensis* are in related host groups and similar in overall proglottid morphology, *B. madrassensis* is possibly an *Acanthobothrium* proglottid or, at least, a tetraphyllidean.

Shinde and Chincholikar (1977): propose the new generic name *Monoporophyllaeus* for *Anteropora*; propose accepting Lateroporidea (including two families: Biporophyllidae and Monoporophyllaeidae) as suggested by Subhapradha, and designate *Anteropora* as a synonym of the new genus *Monoporophyllaeus*; erect the genus *Mastacembellophyllaeus* with *M. nandedensis* as the type species and place it in the family Monoporophyllaeidae (with *Monoporophyllaeus*) and distinguish it from *Anteropora* [in 1978, Shinde and Jadhav (1978) describe a second species in the genus *Mastacembellophyllaeus* from a freshwater fish].

Schmidt (1986): considers *Biporophyllaeus madrassensis* Subramaniam, 1939 to be a detached proglottid of a tetraphyllidean, trypanorhynchan, or lecanicephalidean cestode.

Euzet (1994a): states that *Biporophyllaeus* should be abandoned and treated as a *genus inquirendum*; the family Biporophyllaeidae Subramaniam, 1939 and the order Biporophyllidea [sic] Wardle and McLeod, 1952 should be ignored.

Remarks

A detailed history of *Biporophyllaeus* as it relates to lecanicephalidean taxa, especially the genus *Anteropora*, is provided in the taxonomic history section of the latter genus. The illustrations in the original description of *B. madrassensis* indicate that Subramaniam's material consisted of detached proglottids that were mistaken to be the whole body of a monozooic (unproglottized, consisting of only a single set of reproductive organs) cestodarian. The opening of the vagina anterior to the cirrus sac and the position of the origin of the vas deferens anterior to the cirrus sac indicate that this is not a lecanicephalidean proglottid, but rather tetraphyllidean-like, as has been suggested by Euzet (1994a). This genus should not be considered to belong to the Lecanicephalidea.

Cathetocephalus Dailey and Overstreet, 1973

Type species: *Cathetocephalus thatcheri* Dailey and Overstreet, 1973.

Type host: *Carcharhinus leucas* (Müller and Henle, 1839), Bull shark (Carcharhinidae, Carcharhiniformes).

History of association with the Lecanicephalidea

Brooks and McLennan (1993): present a tree for the order Lecanicephaliformes Baylis, 1920; based on that tree they recognize *Cathetocephalus* Dailey and Overstreet, 1973 (along with *Staurobothrium* Shipley and Hornell, 1905, *Tetragonocephalum* Shipley and Hornell, 1905, *Disculiceps* Joyeux and Baer, 1935, *Adelobothrium* Shipley, 1900, and *Prosobothrium* Cohn, 1902) in the subfamily Disculicipinae Joyeux and Baer, 1935, family Lecanicephalidae Braun, 1900, order Lecanicephaliformes Baylis, 1920.

Remarks

Dailey and Overstreet (1973) created a new genus and new species for this unusual worm, and placed it in the new family, Cathetocephalidae Dailey and Overstreet, 1973, within the order Tetraphyllidea. The scolex of this taxon is described as greatly laterally expanded, possessing a band of finger-like extensions, and lacking acetabula (Dailey and Overstreet 1973; see also Caira *et al*. 1999). Despite this unusual scolex morphology, the morphology of the proglottids is clearly tetraphyllidean. Brooks and McLennan (1993) gave the presence of a greatly enlarged apical sucker in the form of a myzorhynchus as a synapomorphy for the order Lecanicephaliformes, the order, in which they placed *Cathetocephalus*. Caira *et al.* (1999) presented evidence that the unusual scolex morphology is due to a modification of the scolex proper, and that a so-called "myzorhynchus" (or apical organ according to Caira *et al.* [1999]) is absent. Moreover, in *Cathetocephalus* the vagina clearly opens anterior to the cirrus sac into the genital atrium, which, according to Brooks and McLennan (1993, character 24, p. 326), is a synapomorphy for the Tetraphylliformes rather than the Lecanicephaliformes. There is no evidence supporting a placement of this genus in the Lecanicephalidea. *Cathetocephalus* should be considered a tetraphyllidean genus, a placement supported by essentially all other authors working with this group (*e.g.*, Schmidt 1986; Euzet 1994a).

Diagonobothrium Shipley and Hornell, 1906

Type species: *Diagonobothrium asymmetrum* Shipley and Hornell, 1906.

Type host: "*Myliobatis maculata*" (= *Aetomylaeus maculatus* [Gray, 1834] ?), Mottled eagle ray (Myliobatidae, Myliobatiformes).

History of association with the Lecanicephalidea

Shipley and Hornell (1906): erect the genus *Diagonobothrium* with *D. asymmetrum* as the type species for a single specimen collected from *Myliobatis maculata* from Dutch Bay, Ceylon; provide a cursory description of the worm; internal proglottid anatomy is not described; fail to compare or distinguish the taxon from any other genera or species of cestodes.

Southwell (1925): recognizes *Diagonobothrium* in the order Heterophyllidea [most lecanicephalideans classified in the order Cyclophyllidea] with *Echinobothrium*, *Peltidocotyle*, *Amphoteromorphus*, and *Discocephalum*.

Wardle and McLeod (1952): treat *Diagonobothrium* Shipley and Hornell, 1906 as a *genus inquirendum*, with affinities to Lecanicephala (or Tetraphyllidea or Disculicipitidae); type species is *D. asymmetrum* Shipley and Hornell, 1906 in *Myliobatis maculata* from Ceylon; internal anatomy unknown.

Yamaguti (1959): considers *Diagonobothrium* Shipley and Hornell, 1906 to be a *genus incertae sedis* within the Lecanicephalidea; type species is *D. asymmetricum* [sic] in *Myliobatis maculata* from Ceylon.

Euzet (1994b): addresses status of genus within the Lecanicephalidea; notes species is described from single specimen; probably diphyllidean scolex missing rostellar and cephalic peduncle spines.

Remarks

Shipley and Hornell (1906) described this genus based on a single scolex. It was described as possessing a very large and conspicuous terminal sucker and two bothridia. The few details presented in the original description, as well as the figure accompanying that description, suggest that this specimen represents the scolex of a diphyllidean cestode. Consequently, it must be assumed that the two "bothridia" actually are bothria. The "terminal sucker" is the highly muscular rostellum found in members of the diphyllidean genera *Echinobothrium* Van Beneden, 1849 and *Macrobothridium* Khalil and Abdul-Salam, 1989, and that the rostellar hooks, present in species of these two genera, have been lost. This interpretation has also been suggested by Euzet (1994b). Most recently, Tyler (2001) considered the genus to be a *nomen dubium* within the Diphyllidea.

Diplobothrium Van Beneden, 1889

Type species: *Diplobothrium simile* Van Beneden, 1889.

Type host: *Lamna cornubica* (Gmelin, 1789) (= *Lamna nasus* [Bonnaterre, 1788] ?), Porbeagle (Lamnidae, Lamniformes).

History of association with the Lecanicephalidea

Southwell (1925): recognizes *Diplobothrium* Van Beneden, 1889 in his suborder A, order Cyclophyllidea [along with the genus *Eniochobothrium*].

Wardle and McLeod (1952): treat *Diplobothrium* Beneden, 1889 (= *Tetrabothrium* Olsson, 1867 = *Oriana* Leiper and Atkinson, 1915) as a *genus inquirendum*, with affinities to Lecanicephala (or Tetraphyllidea or Disculicipitidae); type species is *D. simile* in *Lamna cornubica* from Europe based on immature material with no information on internal anatomy; indicate that Lönnberg (1891) considers it a subgenus of *Tetrabothrium*.

Yamaguti (1959): considers *Diplobothrium* Beneden, 1889, (= *Tetrabothrium* Olsson, 1867, *Oriana* Leiper and Atkinson, 1915) to be a *genus incertae sedis* in Lecanicephalidea.

Remarks

In the most recent treatment of this genus (Euzet 1994a), *Diplobothrium* is considered to be a junior synonym of the genus *Dinobothrium*. The proglottid and scolex morphology of species in the genus *Dinobothrium* are clearly tetraphyllidean (Caira *et al*. 1999, 2001). *Dinobothrium* (syn. *Diplobothrium*) is a member of the order Tetraphyllidea, family Phyllobothriidae.

Discobothrium Van Beneden, 1871

Type species: *Discobothrium fallax* Van Beneden, 1871.

Type host: *Raja clavata* Linnaeus, 1758 (as *Raia* [sic] *clavata*), Thornback ray (Rajidae, Rajiformes).

History of association with the Lecanicephalidea

Van Beneden (1871): erects the genus *Discobothrium* with *D. fallax* as the type species; lists this species as parasitizing "*Raia clavata*;" no "new species" or "new genus" designation or diagnosis of the genus or description of the species are given and only the scolex is illustrated; however, this seems to be the first use of this name.

Örley (1885): notes Van Beneden (1871) reporting *Discobothrium fallax* from *Raja clavata* [and *Phyllobothrium fallax* from *Raja rubus*, same taxon?]; transfers *D. fallax* to the genus *Tetrabothrium*; the genus *Discobothrium* is again mentioned (p. 133).

Lönnberg (1889): treats *Discobothrium* and *Echineibothrium* [sic] as distinct genera within the family Phyllobothridae, order Tetraphyllidea; also considers *Discobothrium fallax* and *Echineibothrium* [sic] *variabile* as distinct species.

Monticelli (1891): states that he disagrees with Lönnberg (1889) about *Discobothrium fallax* and comments on *Discobothrium* in general.

Olsson (1893): [considers *Discobothrium fallax* and *Echeneibothrium variabile* identical; see, *e.g.*, Young, 1956].

Braun (1894-1900): lists *Discobothrium*, with *D. fallax* as the only species; comments that Lönnberg (1889, 1890) considered *Discobothrium* to be a valid genus, while Monticelli (1890) and Olsson (1893) considered it to be a junior synonym of *Echeneibothrium*.

de Beauchamp (1905): recognizes *Discobothrium* as a distinct genus from *Echeneibothrium* in the tribe Echeneibothrines, family Phyllobothrides, order Tetraphylles; describes *D. fallax* in detail, including scolex longitudinal sections and proglottid sections, from new material collected at Banyuls from *R. clavata*, *R. macrorhynchus*, and *R. punctata*.

Shipley and Hornell (1905): compare *Discobothrium* (and *Lecanicephalum*) to their new genus *Tetragonocephalum*.

Stiles and Hassall (1912): *Discobothrium* Van Beneden, 1871: de Beauchamp (1905), Braun (1895), Oerley (1885), and Shipley and Hornell (1905); *D. fallax* Van Beneden, 1871: de Beauchamp (1905) (syn. *Echeneibothrium variabile* Monticelli, 1890, Olsson, 1893) (in *Raja clavata*, *R. punctata* and *R.* sp.), Braun (1900), Lönnberg (1889) (in *R. clavata*, Kristineberg), and Oerley (1885) (to *Tetrab*.).

Southwell (1925): recognizes *Discobothrium* Van Beneden, 1870 (syn. *Hornellobothrium* Shipley and Hornell, 1906); considers it an intermediate, interesting link between the order Cyclophyllidea and the order Tetraphyllidea; synonymizes *Discobothrium* and *Hornellobothrium* based on similarity of figures of the scolices of *D. fallax* and *H. cobraformis*, but considers them distinct species; type species is *D. fallax* Van Beneden, 1870 from *Raja clavata*; quotes de Beauchamp's (1905) description of this species; provides justification, based on literature accounts, as to why *Discobothrium* and *Echeneibothrium* are distinct genera.

Woodland (1927): agrees with Braun (1900), based on his comparison of *Discobothrium fallax* and *Echeneibothrium variabile* that these two genera are congeneric, in which case he suggests that *Discobothrium* disappear; states that the lack of loculi, the only objection to placing this species in *Echeneibothrium*, is not valid because distinct loculi are often found.

Southwell (1930): treats *Discobothrium* Van Beneden, 1870 (syn. *Hornellobothrium* Shipley and Hornell, 1906) in the family Lecanicephalidae, superfamily Lecanicephaloidea, order Eucestoda; genus of uncertain taxonomic position, most likely in the family Lecanicephalidae not intermediate between Cyclophyllidea and Tetraphyllidea.

Dollfus (1931): reports and describes larvae from two *Eupagurus* spp.; gives these larvae the temporary name *Echeneibothrium moucheti nom. provis*; states that it is only in the *Echeneibothrium-Discobothrium* group that adults with a scolex like those of the larvae are found.

Fuhrmann (1931): classifies *Discobothrium* in the family Cephalobothriidae (Pintner), along with *Cephalobothrium* and *Tylocephalum* (*ex parte*); within the order Tetraphyllidea, Cephalobothriidae is one of two families (of a total of seven families in the order) containing lecanicephalidean taxa.

Perrenoud (1931): [according to Dollfus (1964): describes a larva found in *Raja* to be either *Discobothrium fallax* or *Cephalobothrium aetobatidis*].

Yamaguti (1934): describes a new species in the genus *Discobothrium*, *D. japonicum,* while also recognizing the genus *Echeneibothrium*.

Sprehn (1934): states that *Discobothrium phallax* [sic] from *Raja clavata* is the only species of lecanicephalidean (Tetraphyllidea, Cephalobothriidae Pintner, 1928) reported from the North Sea/Baltic Sea.

Joyeux and Baer (1936): *Discobothrium fallax* is the only lecanicephalidean taxon treated; place *Discobothrium* Van Beneden, 1871 in the family Cephalobothriidae, order Tetraphyllidea; scolex and proglottid of *Discobothrium fallax* are redescribed and illustrated.

Baer (1948): briefly reviews history of *Discobothrium*; concludes, based on specimen observations that *Discobothrium* is morphologically very close to *Cephalobothrium sensu* Pintner; provisionally considers *Discobothrium* as valid in the family Cephalobothriidae.

Hyman (1951): recognizes *Discobothrium* (along with *Cephalobothrium* and *Tylocephalum*) in the family Cephalobothriidae, order Lecanicephaloidea; presents few diagnostic characters for the family.

Wardle and McLeod (1952): consider *Discobothrium* Beneden, 1870 (= *Hornellobothrium* Shipley and Hornell, 1906) to be a *genus inquirendum* with affinities to the Lecanicephala (or Tetraphyllidea or Disculicipitidae); type species of the genus is *D. fallax* Beneden, 1870.

Khambata and Bal (1953): use the names *Discobothrium quadrisurculi* n. sp. and *Discobothrium redacta* n. sp. for specimens collected from *Trygon sephen*, *Rhychobatus* [sic] *djeddensis* [sic] and *Aetomylaeus maculatus* from Bombay in this abstract.

Riser (1955): considers *Discobothrium fallax* van Beneden, 1871 a species of uncertain taxonomic position that cannot be adequately placed; reports *D. fallax* (three specimens) from *Raja rhina* and *R. inornata* from Monterey Bay; describes species as possessing eversible glandular pad and well developed internal longitudinal muscle bundles; illustrates eggs; agrees with Baer (1948) that Woodland's (1927) figures of *D. fallax* and *E. variabile* were reversed.

Young (1956): briefly summarizes the taxonomic history for *Discobothrium fallax (*and in part *Discobothrium)* as it relates to the genus *Echeneibothrium*; concludes that because of conflicting opinions, *D. fallax* should be considered a *genus* and *species inquirendae*.

Williams (1958): considers *Discobothrium fallax* to be a member of the genus *Echeneibothrium*; recognizes both *Echeneibothrium variabile* and *E. fallax*, but does not seem to consider *Discobothrium* to be a junior synonym of *Echeneibothrium*; comments that worms identified as *Echeneibothrium/Discobothrium fallax* could be either, *E. fallax* or *E. variabile*; notes variation in scolex shape and size of *E. fallax* greater than in any other species in the genus; based on new material from *Raja montagui* from off Cardigan Bay (Wales), investigates tentacles on some scolices of *E. fallax* revealing similar morphology to species of *Polypocephalus* and *Parataenia medusia* as redescribed by Baer (1948).

Yamaguti (1959): considers *Discobothrium* Beneden, 1871 (= *Hornellobothrium* Shipley and Hornell, 1906) to be a *genus incertae sedis*; confirms type species is *D. fallax* Beneden, 1871 in *Raja clavata* from Belgium; recognizes four additional species in this genus (*D. cobraeformis* [sic] Shipley and Hornell, 1906 [= *Hornellobothrium cobraeformis* [sic] Shipley and Hornell] from *Aetiobatis* [sic] *narinari* from Ceylon; *D. japonicum* Yamaguti, 1934 from *Narke japonica* in Japan; *D. quadrisurculi* Khambata and Bal, 1953 from *Trygon sephen*, *Rhynchobatus djeddensis* [sic] and *Aetomylaeus maculatus* in Bombay; *D. redactum* Khambata and Bal, 1953 from *Trygon sephen*, *Rhynchobatus djeddensis* [sic] and *Aetomylaeus maculatus* in Bombay).

Euzet (1959): describes and illustrates *Echeneibothrium fallax* (Van Beneden, 1870) from *Raja clavata* from five localities in Atlantic and Mediterranean; synonymizes *Discobothrium* with *Echeneibothrium*, in the subfamily Echeneibothriinae, family Phyllobothriidae, superfamily Phyllobothrioidea, order Tetraphyllidea; reports *Echeneibothrium fallax* from *Raja asterias*.

Joyeux and Baer (1961): illustrate scolex of *Discobothrium fallax* from *Raja clavata* (after Euzet).

Dollfus (1964): reports Fuhrmann finding a larva from a brachyuran decapod that Perrenoud (1931) described; notes it resembles *Discobothrium fallax*.

Williams (1966): says there is no alternative but to agree with Lönnberg (1889) and de Beauchamp (1905) to recognize *Echeneibothrium* and *Discobothrium* as distinct genera; the species should be regarded as *D. fallax* pending further research; notes that *Tritaphros* and *Pseudanthobothrium* show more similarity with *Echeneibothrium* than does *Discobothrium*; supports Yamaguti's idea that other species may exist; indicates MacCallum's *Taenia acanthobothria* (1921) should be included in future considerations of *Discobothrium*; describes morphology of *D. fallax* briefly; considers it a species wrongly allocated to *Echeneibothrium* by Woodland (1927) and Wardle and McLeod (1952).

Dailey and Mudry (1968): describe *Discobothrium myliobatidis*, consider *Discobothrium* to be a valid genus and *Discobothrium quadrisurculi* and *D. redactum* to be *nomina nuda*; recognize four species of *Discobothrium* (*D. fallax*, *D. cobraeformis* [sic], *D. japonicum*, and *D. myliobatidis*).

Katkansky and Warner (1969): report plerocercoid larvae from rough-sided littleneck clams, *Protothaca laciniata*, from Morro Bay, California; larvae possess a rostellum resembling that described by Wardle and McLeod (1952) in *Echeneibothrium fallax*, but have too many loculi to be that species.

Wardle *et al.* (1974): list *Discobothrium myliobatidis* Dailey and Mudry (1968) in their chapter on the order Tetraphyllidea; assign "it" [presumably the genus *Discobothrium*] to the order Lecanicephalidea as a *genus inquirendum*; do not address any other species of *Discobothrium*, except *D. cobraeformis* [sic] (= *Hornellobothrium cobraeformis* [sic]).

Brooks *et al.* (1981a): describe *Discobothrium arrhynchum*, a species different from all other species in the genus because of its lack of a myzorhynchus; compare the new species in detail to *D. myliobatidis* and *D. japonicum*; neither justification for placement in *Discobothrium*, nor consideration of *Discobothrium* as a lecanicephalidean, is provided.

Brooks *et al.* (1981b): list *Discobothrium* sp. as a parasite of *Urolophus jamaicensis*, presumably referring to *D. caribbensis* Gardner and Schmidt, 1984; consider this species to be endemic to South America; also list *Discobothrium arhynchus* [sic] from *Myliobatis goodei* as a species endemic to South America.

Hassan (1982a): describes *Discobothrium aegyptiacus*; reviews history of genus but offers no opinion as to its validity.

Gardner and Schmidt (1984): describe *Discobothrium caribbensis*; reiterate that Dailey and Mudry (1968) recognized four valid species of *Discobothrium* (*D. fallax*, *D. cobraeformis* [sic], *D. japonicum*, and *D. myliobatidis*); add *D. arrhynchum*; consider *Discobothrium aegyptiacus* a species of *Lecanicephalum* because of its large size.

Schmidt (1986): treats *Discobothrium* Beneden, 1871 (syn. *Hornellobothrium* Shipley and Hornell, 1906), in the family Lecanicephalidae, order Lecanicephalidea; six species, in addition to the type species *D. fallax* Van Beneden, 1871, are recognized: *D. caribbensis*, *D. cobraeformis* [sic], *D. japonicum*, *D. myliobatidis*, *D. quadrisurculi*, and *D. redactum*.

Butler (1987a): considers *Discobothrium* van Beneden as distinct from *Echeneibothrium* van Beneden.

Butler (1987b): notes that *Hornellobothrium* Shipley and Hornell and *Eniochobothrium* Shipley and Hornell are very likely not junior synonyms of *Discobothrium* Van Beneden.

Brooks and McLennan (1993): present a tree for the order Lecanicephaliformes Baylis, 1920; based on that tree they recognize *Discobothrium* van Beneden 1871 (along with *Calycobothrium* Southwell 1911, *Echeneibothrium* van Beneden, 1850, *Lecanicephalum* Linton, 1890, *Hexacanalis* Perrenoud, 1931 *sedis mutabilis*, *incertae sedis*, and *Polypocephalus* Braun, 1878) in the subfamily Lecanicephalinae Braun, 1900 *incertae sedis*, family Lecanicephalidae Braun, 1900, order Lecanicephaliformes Baylis, 1920.

Euzet (1994a): considers *Discobothrium* to be a junior synonym of the tetraphyllidean genus *Echeneibothrium*.

Remarks

The history of the association of *Discobothrium* with the Lecanicephalidea is complex. The early history of its type species, *Discobothrium fallax*, has been thoroughly and comprehensively reviewed and summarized by a number of authors, and thus, does not need to be repeated here beyond the chronology presented above (*e.g.*, Southwell 1925; Woodland 1927; Wardle and McLeod 1952; Young 1956; Williams 1966). Much of the discussion revolves around the identity of *D. fallax*, in particular, whether *D. fallax* is actually a member of the tetraphyllidean genus *Echeneibothrium*, possibly even a junior synonym of *Echeneibothrium variabile* Van Beneden, 1850. In both cases, *Discobothrium* would become a junior synonym of *Echeneibothrium*. Others have treated the two genera as distinct.

Southwell (1925) was the first to link *Discobothrium* to lecanicephalidean taxa by considering *Hornellobothrium* Shipley and Hornell, 1906 to be a junior synonym of *Discobothrium*. This synonymy was also accepted by Southwell (1930), Wardle and McLeod (1952), Yamaguti (1959), and Schmidt (1986). Subsequent to Southwell's work, Woodland (1927) considered *D. fallax* to be a junior synonym of *E. variabile*. He did not comment on the status of *Hornellobothrium*. Over the next 20 years, *Discobothrium* was consistently allied with lecanicephalidean taxa, for example, in the family Cephalobothriidae (see Fuhrmann 1931; Sprehn 1934; Joyeux and Baer 1936; Hyman 1951), as a *genus inquirendum* with affinities to the Lecanicephala (see Wardle and McLeod 1952), or in order Lecanicephalidea (see Schmidt 1986).

The resolution of the true identity of *Discobothrium fallax*, as it relates to this monograph, rests on the question of whether there is evidence to consider this species a lecanicephalidean. This species has been reported by a number of authors from a number of different hosts and localities (see de Beauchamp 1905; Riser 1955; Williams 1958; Euzet 1959). Evidently, *D. fallax* possesses one of the most morphologically plastic scolices known among elasmobranch cestodes. Although controversy remains as to whether the bothridia of *D. fallax* are loculated or simple, there is general agreement about its proglottid anatomy. This morphology is clearly tetraphyllidean rather than lecanicephalidean, given that the vagina opens into the genital atrium anterior to the cirrus sac, and that the vas deferens originates anterior to the cirrus sac (see de Beauchamp 1905; Euzet 1959). Based on proglottid anatomy alone, it seems clear that *D. fallax* is not a lecanicephalidean, but rather a tetraphyllidean (also see Euzet 1994a). *Hornellobothrium* is clearly distinct from *Discobothrium*; these two genera should not be considered synonyms (also see Butler 1987a). Whether *Discobothrium* is, in fact, a synonym of either the tetraphyllidean genus *Echeneibothrium* or *Pseudanthobothrium* remains to be determined. However, given that *Discobothrium* does not appear to be a lecanicephalidean taxon, this issue is not pertinent to this monograph.

None of the eight additional species that have been placed in the genus *Discobothrium* are valid members of the genus. *Discobothrium cobraformis* (Shipley and Hornell, 1906) Schmidt, 1986 is a synonym of *Hornellobothrium cobraformis* Shipley and Hornell, 1906 for the reasons articulated above. *Discobothrium japonicum* Yamaguti, 1934 was transferred to *Anteropora* by Euzet (1994b) and is valid as *Anteropora japonica*. The names *Discobothrium quadrisurculi* Khambata and Bal, 1953 and *Discobothrium redacta* Khambata and Bal, 1953 appeared in an abstract (Khambata and Bal 1953); no morphological features were mentioned, nor was a differential diganosis presented. Thus, these names, as was first suggest by Mudry and Dailey (1968), are considered to be *nomina nuda*. Examination of type material (paratype, USNPC No. 71215) and voucher specimens of *Discobothrium myliobatidis* Dailey and Mudry, 1969 from the Bat eagle ray, *Myliobatis californica* Gill, 1865, from California, from the personal collection of C. G. Alexander, suggested that this taxon is indeed a lecanicephalidean, as suggested by Wardle *et al.* (1974). The proglottid morphology is similar to that of species in the genus *Aberrapex* Jensen, 2001. However, in stark contrast to the two known species of *Aberrapex*, *D. myliobatidis* possesses a prominent muscular apical organ. It seems likely that this taxon represents a distinct lecanicephalidean genus. However, additional material and study are required before this action can be taken. *Discobothrium arrhynchum* Brooks, Mayes and Thorson, 1981 was transferred to the genus *Aberrapex* by Jensen (2001). Examination of type specimens of *Discobothrium aegyptiacus* (holotype and two paratypes, BMNH No. 1998.10.19.78-81) reveals this taxon to be a member of the tetraphyllidean genus *Pseudanthobothrium*. The new combination, *Pseudanthobothrium aegyptiacus* n. comb. is made here. Lastly, close examination of type specimens of *Discobothrium caribbensis* Gardner and Schmidt, 1984 (two paratypes, USNPC No. 77925) revealed the presence of an apical organ in the form of tentacles, invaginated into the scolex proper, as is characteristic of members of the genus *Polypocephalus*. The proglottid anatomy is also consistent with the generic diagnosis of *Polypocephalus* Braun, 1878. The new combination, *Polypocephalus caribbensis* n. comb. is created here for this species.

Disculiceps Joyeux and Baer, 1936

Synonyms: *Discocephalum* Linton, 1890.

Type species: *Disculiceps pileatum* (Linton, 1890) Joyeux and Baer, 1936 (as *Discocephalum pileatum* Linton, 1890).

Type host: "*Carcharias obscurus*" (= *Carcharhinus obscurus* [Lesueur, 1818] ?), Dusky shark (Carcharhinidae, Carcharhiniformes).

History of association with the Lecanicephalidea

Linton (1890): places this genus in the family Tetrabothriidae (in subfamily I, the Phyllobothriinae), but proposes the new family Gamobothriidae to house *Discobothrium*, along with *Lecanicephalum* and *Tylocephalum*.

Braun (1894-1900): recognizes *Discocephalum* Linton, with the type species is *D. pileatum* Linton, in the family Lecanicephalidae (*fam. inq.* = Gamobothriidae), order Tetraphyllidea.

Perrier (1897): recognizes *Discocephalum*, along with three other genera (*Lecanicephalum*, *Tylocephalum*, and *Sciadocephalus*) in the family Gamobothriidae, order Tetracestoda.

Meggitt (1924): provides an abbreviated diagnosis of the genus *Discocephalum* with the type species *D. pileatum* Linton, 1891; includes *Discocephalum* in the family Lecanicephalidae (along with *Discocephalum*, *Lecanicephalum*, *Cephalobothrium*, *Tylocephalum*, and *Adelobothrium*), in the order Tetraphyllidea.

Poche (1926): recognizes *Discocephalum* (along with *Lecanicephalum*, *Cephalobothrium*, *Tylocephalum*, and *Adelobothrium*) in the family Lecanicephalidae Braun (Gamobothriidae Linton, 1889; Gamobothridae Ariola, 1899; Benham, 1901), suborder Phyllobothriinea *nom. nov.*, order Taeniidea *nom. nov.*, as did Meggitt (1924); additionally includes *Balanobothrium*.

Woodland (1927): considers *Discocephalum pileatum* a "lecanicephalid" taxon within the order Tetraphyllidea; *D. pileatum* is not placed in a family.

Southwell (1925): includes *Discocephalum* (along with *Echinobothrium*, *Peltidocotyle*, *Amphoteromorphus*, and *Diagonobothrium*) in the order Heterophyllidea [most lecanicephalideans in Order Cyclophyllidea].

Pintner (1928): erects the families Discocephalidae and Balanobothriidae for *Discocephalum* and *Balanobothrium*, respectively.

Hyman (1951): recognizes *Discocephalum* in the family Discocephalidae, order Lecanicephaloidea; presents few diagnostic characters for the family.

Riser (1955): recognizes the family Disculicepitidae in the superfamily Lecanicephaloidea, order Tetraphyllidea, superorder Trixenidea [*Disculiceps* is implied as type genus of the family].

Yamaguti (1959): treats *Disculiceps* Joyeux and Baer, 1935 (syn. *Discocephalum* Linton, 1890) as a member of the lecanicephalidean family Disculicepitidae.

Schmidt (1970): considers *Disculiceps* as a valid genus in the family Disculicepitidae, order Lecanicephalidea Baylis, 1920, as part of a key to the genera of tapeworms; provides a brief diagnosis for the genus.

Wardle *et al.* (1974): recognize the family Disculicepitidae [and consequently *Disculiceps*] in the order Lecanicephalidea Baylis, 1920; do not list any genera they consider to belong in the family; present a key to families in the order Lecanicephalidea.

Schmidt (1986): considers *Disculiceps* Joyeux and Baer, 1935 (syn. *Discocephalum* Linton, 1890), as a member of the family Disculicepitidae (syn. Discocephalidae Pintner, 1928), order Lecanicephalidea Baylis, 1920.

Nock and Caira (1988): describe the new species, *Disculiceps galapagoensis* and consider it to belong to the family Disculicepitidae, order Lecanicephalidea; a brief history of the genus and a diagnosis of the family provided.

Caira (1990): lists the Lecanicephalidea as one of four cestode orders parasitizing elasmobranchs; illustrates the scolex of *Disculiceps galapagoensis* as an example of a lecanicephalidean taxon.

Brooks and McLennan (1993): present a tree for the order Lecanicephaliformes Baylis, 1920; based on that tree they recognize *Disculiceps* Joyeux and Baer, 1935 (along with *Staurobothrium* Shipley and Hornell, 1905, *Tetragonocephalum* Shipley and Hornell, 1905, *Adelobothrium* Shipley, 1900, *Prosobothrium* Cohn, 1902, and *Cathetocephalus* Dailey and Overstreet, 1973) in the subfamily Disculicipinae Joyeux and Baer, 1935, family Lecanicephalidae Braun, 1900, order Lecanicephaliformes Baylis, 1920.

Remarks

Disculiceps pileatum was originally described under the name *Discocephalum pileatum* as the type species of the genus *Discocephalum*. A complete account of the nomenclatural history of this species (and genus) is given in Nock and Caira (1988). Linton (1890) suggested the creation of the family Gamobothriidae Linton, 1890 for three new genera he described (*i.e.*, *Parataenia* Linton, 1890, *Lecanicephalum* Linton, 1890 and *Discocephalum*), stating as the uniting feature "bothria are united into a globe or disc" (Linton 1890, p. 720). He described the scolex of *D. pileatum* as consisting of a terminal disc and a posterior cervical mass, lacking acetabula altogether. In the description of the anatomy of the proglottids, the vagina was described as opening anterior to the cirrus sac into the genital atrium. The morphology of the scolex and the proglottids do not support placement within the Lecanicephalidea, but rather within or close to the Tetraphyllidea as suggested by Euzet (1994a) in the most recent treatment of the order Tetraphyllidea. Euzet (1994a) treated *Disculiceps* in the tetraphyllidean family Disculicipitidae.

Echeneibothrium Van Beneden, 1850

Type species: *Echeneibothrium minimum* Van Beneden, 1850.

Type host: *Trygon pastinaca* (Linnaeus, 1758) (= *Dasyatis pastinaca* [Linnaeus, 1758] ?), Common stingray (Dasyatidae, Myliobatiformes).

History of association with the Lecanicephalidea

Brooks and McLennan (1993): present a tree for the order Lecanicephaliformes Baylis, 1920; based on that tree they recognize *Echeneibothrium* van Beneden, 1850 (along with *Discobothrium* van Beneden 1871, *Calycobothrium* Southwell 1911, *Lecanicephalum* Linton, 1890, *Hexacanalis* Perrenoud, 1931 *sedis mutabilis*, *incertae sedis*, and *Polypocephalus* Braun, 1878) in the subfamily Lecanicephalinae Braun, 1900 *incertae sedis*, family Lecanicephalidae Braun, 1900, order Lecanicephaliformes Baylis, 1920.

Remarks

Van Beneden first mentioned the genus *Echeneibothrium* in 1849, at which time he listed the names of two species, *E. minimum* and *Echeneibothrium variabile* Van Beneden, 1850. However, this account is too incomplete to constitute a valid diagnosis of the genus. In 1850, Van Beneden provided a more complete generic diagnosis, as well as descriptions accompanied by a number of illustrations of *E. minimum* and *E. variabile*. Van Beneden did not designate a type for his new genus in either paper (Van Beneden 1849, 1850). Braun (1894-1900) reviewed *Echeneibothrium* and established *E. variabile* as the type species, while *Echeneibothrium minimum* is now considered a synonym of *Scalithrium minimum* (Van Beneden, 1850) Ball, Neifar and Euzet, 2003 (Ball *et al.* 2003). The current concept of the genus *Echeneibothrium* (characterized by a scolex possessing an apical structure) has been influenced by, for example, Young (1956), Williams (1966), and Euzet (1994a). The anatomy of the proglottids of *E. variabile* is clearly tetraphyllidean. The position of *Echeneibothrium* within the order Tetraphyllidea has been supported by many authors (*e.g.*, Fuhrmann 1931; Euzet 1959; Yamaguti 1959; Williams 1966; Schmidt 1986; Euzet 1994a). Only Brooks and McLennan (1993) have formally considered *Echeneibothrium* to be a lecanicephalidean. The recent analyses of Caira *et al*. (1999, 2001) support close relationships of members of the genus *Echeneibothrium* and members of a second tetraphyllidean genus, *Pseudanthobothrium*, to lecanicephalidean taxa. Indeed, in their analyses, *Echeneibothrium* grouped with lecanicephalideans, but, as noted by Caira *et al*. (1999, 2001), the grouping resulting from these analyses is very weakly supported.

Echinobothrium Van Beneden, 1849

Type species: *Echinobothrium typus* Van Beneden, 1849.
Type host: "*raie bouclee*."

History of association with the Lecanicephalidea

Wardle and McLeod (1952): consider *Echinobothrium* Beneden, 1849 as a *genus inquirendum*, with affinities to Lecanicephala (or Tetraphyllidea or Disculicipitidae).

Riser (1955): classifies lecanicephalideans into five families (Lecanicephalidae, Cephalobothriidae, Balanobothriidae, Disculicepitidae, and Echinobothriidae) in the superfamily Lecanicephaloidea, order Tetraphyllidea, superorder Trixenidea; [presumably considers *Echinobothrium* Van Beneden, 1849, as the type genus of the family Echinobothriidae].

Remarks

Van Beneden (1849) described *Echinobothrium typus* and placed the species in the family Bothrioides, section Acanthocephales. A year later, Van Beneden (1850) placed the genus in the section Diphyllides. In stark contrast to lecanicephalideans, members of genus *Echinobothrium* are characterized by a unique scolex morphology, possessing two bothria, an apical muscular rostellum with associated rostellar armature and a cephalic peduncle armed with spines with triradiate bases. For the past almost 50 years, the group has been recognized by cestode taxonomists as an order (*e.g.*, Yamaguti 1959; Joyeux and Baer 1961; Schmidt 1986; Tyler 2001).

Guptaia Malhotra, 1985

Type species: *Guptaia garhwalensis* Malhotra, 1985.

Type host: *Schizothorax richardsonii* (Gray, 1832), Snow trout (Cyprinidae, Cypriniformes).

History of association with the Lecanicephalidea

Malhotra (1985): describes the new genus *Guptaia* with *Guptaia garhwalensis* as the type species from the "hill-stream" teleost, *Schizothorax richardsonii*; comments on resemblance to *Tetragonocephalum*; places *Guptaia* in Tetragonocephalidae.

Euzet (1994b): suggests that the species probably belongs to an order other than the Lecanicephalidea; treats *Guptaia* as a *genus incertae sedis* in the Lecanicephalidea.

Remarks

This genus was described by Malhotra (1985) based on five specimens collected from a cyprinid in India. Based on its resemblance to the lecanicephalidean genus *Tetragonocephalum*, Malhotra (1985) placed this genus, along with *Tetragonocephalum*, in the family Tetragonocephalidae Yamaguti, 1959. The type material of *Guptaia garhwalensis* could not be examined for this study. The description of *G. garhwalensis* includes morphological and anatomical features that are generally consistent with those found in lecanicephalideans. However, the illustrations show proglottids that are wider than long, and a cirrus pouch that occupies only a small proportion of the width of the proglottid, features that are very reminiscent of proteocephalidean, rather than lecanicephalidean, anatomy and morphology. *Guptaia* should not be considered to be a lecanicephalidean genus; the correct taxonomic position of this genus, however, remains to be determined.

Litobothrium Dailey, 1969

Type species: *Litobothrium alopias* Dailey, 1969.

Type host: *Alopias superciliosus* (Lowe, 1841), Bigeye thresher (Alopiidae, Lamniformes).

History of association with the Lecanicephalidea

Wardle *et al.* (1974): comment that the lateral expansions of [the lecanicephalidean species] *D. cobraefomis* [sic] and *Eniochobothrium gracile*, approximate the anterior strobilar condition found in species in the order Litobothridea.

Al Kawari *et al.* (1994): describe the new species *Eniochobothrium qatarense*; note similarities to the tetraphyllidean genus *Litobothrium*; review the history of *Litobothrium* (including *L. alopias*, *L. coniforme* [first to use this spelling], *L. gracile*, and *L. daileyi*); consider *Litobothrium*, *Renyxa*, and *Eniochobothrium* to be closely related, all three genera placed in the family Litobothridae; emend diagnosis of the family; consider Dailey's (1969) designation of litobothrideans as an order inconclusive and place Litobothridae in the Lecanicephalidea.

Euzet (1994a and b): recognizes the family Litobothriidae within the order Tetraphyllidea; elaborates on the similarities between the strobilae of *Litobothrium* and *Eniochobothrium*, the latter being treated as *incertae sedis* in the Lecanicephalidea.

Olson and Caira (2001): restate Euzet's (1994) and Al Kawari *et al.*'s (1994) opinion on the affinities between *Litobothrium* and *Eniochobothrium*, but present arguments against this affinity.

Remarks

Dailey (1969) described *Litobothrium alopias* as possessing a single apical sucker followed by "four segments modified into accessory holdfast structures which are cruciform in cross section" (p. 220). To date, eight species of *Litobothrium* have been recognized (Olson and Caira 2001), all exhibiting this general morphology of an apical sucker followed by a number of cruciform "pseudosegments," the number of pseudosegments being species specific. The only justification ever given for placing *Litobothrium* within the Lecanicephalidea is the resemblance of the anterior regions of the strobila to that seen in *Eniochobothrium* (*e.g.*, Wardle *et al.* 1974; Al Kawari *et al.* 1994; Euzet 1994b). But, it seems clear that this resemblance is only superficial. Whereas *Eniochobothrium* possesses a typical tetrafossate scolex (with an apical structure and four acetabula in the form of suckers), *Litobothrium* lacks all resemblance of a tetrafossate scolex. In addition, the details of the modified trough-like anterior region of the strobila are completely different from the cruciform pseudosegments found in *Litobothrium*. Moreover, the proglottids of *Litobothrium* are typically tetraphyllidean with a vagina opening into the genital atrium anterior to the cirrus sac. The question of whether the litobothriideans should be placed in their own order (*e.g.*, Dailey 1969; Schmidt 1986; Olson and Caira 2001) or family within the Tetraphyllidea (Euzet 1994a), remains to be answered. Regardless, this genus does not warrant treatment here.

Phanobothrium Mola, 1907

Type species: *Phanobothrium monticellii* Mola, 1907.

Type host and site of infection: "in der Spiralklappe eines großen Fisches" (Mola, 1907, p. 256) [= in the spiral chambers of a big fish].

History of association with the Lecanicephalidea

Mola (1907): describes and illustrates a new genus and species, *Phanobothrium monticellii*; notes that overall morphology is similar to proteocephalideans: vitellarium is described as "unpaare sackförmige Masse...in der Höhe des Ovariums" (p. 259), vagina is anterior to cirrus sac; does not compare the species to any other cestodes; does not provide information on the taxonomic placement.

Stiles and Hassall (1912): list *Phanobothrium* Mola 1907.

Southwell (1925): treats *Phanobothrium* Mola, 1907 in the suborder Univitellata, order Cyclophyllidea (most lecanicephalideans in Suborder Multivitellata).

Woodland (1927): considers *Phanobothrium monticellii* to be a "lecanicephalid" taxon within the order Tetraphyllidea; does not place *Phanobothrium monticellii* in a family.

Fuhrmann (1931): places lecanicephalideans in two of seven families, the family Lecanicephalidae Braun (syn. Gamobothriidae Linton) and the family Cephalobothriidae (Pintner), order Tetraphyllidea; considers *Phanobothrium* (along with *Staurobothrium*, *Hornellobothrium*, *Eniochobothrium*, and *Calycobothrium* [syn. *Cyclobothrium*], among others), to be "uncertain" and not sufficiently known, but very interesting tetraphyllideans.

Wardle and McLeod (1952): consider *Phanobothrium* Mola, 1907 a *genus inquirendum*, with affinities to Lecanicephala (or Tetraphyllidea or Disculicipitidae); note that the type and only species *P. monticellii* Mola, 1907 is found in selachiens.

Yamaguti (1959): considers *Phanobothrium* Mola, 1907 as a *genus incertae sedis* in the Lecanicephalidea.

Euzet (1994a): notes tetraphyllidean anatomy of *Phanobothrium*; considers it a *genus inquirendum* within the Tetraphyllidea.

Remarks

Mola (1907) erected this genus for a few specimens and fragments he found in the spiral intestine of a big fish ("in der Spiralklappe eines großen Fisches," p. 256) taken from the Indian Ocean. He described the scolex as possessing four elliptical suckers and an apex expanded with a small terminal sucker. He described the terminal sucker as being surrounded by small sickle-shaped hooklets, presumably microtriches. The vagina was described as opening into the genital atrium anterior to the cirrus sac. Furthermore, he noted that this species possesses a vitellarium in the form of an unpaired sack-shaped mass and testes that are cortical in position. While the presence of an apical organ may be evidence for affinities with the lecanicephalideans, cyclophyllideans, or proteocephalideans, the overall scolex morphology and the presence of a long neck is reminiscent of proteocephalidean taxa (tapeworms parasitizing bony fishes). In addition, the presence of a gravid uterus that is several times wider than long, the position of the vagina and the testes in the proglottids as described and illustrated are similar to conditions found in tetraphyllideans or proteocephalideans. Because of its position and morphology (fig. 4 and 5), it appears that the organ described as the vitellarium may actually be the Mehlis' gland. Euzet (1994a) commented on the genus and considered it a *genus inquirendum* in the order Tetraphyllidea. The identity of the host remains uncertain. While the correct taxonomic placement of this taxon cannot be determined at this time, membership in the Lecanicephalidea is not supported.

Pillersium Southwell, 1927

Type species: *Pillersium owenium* Southwell, 1927.

Type host: *Urogymnus asperrimus* (Bloch and Schneider, 1801), Porcupine ray (Dasyatidae, Myliobatiformes).

Material examined: BMNH No. 1977.11.9.83 (type).

History of association with the Lecanicephalidea

Southwell (1927): erects the new genus *Pillersium* with *P. owenium* as the type species in the Order Heterophyllidea; notes that no strobilae were present.

Fuhrmann (1931): considers *Pillersium* in the order Tetraphyllidea (in addition to 13 other lecanicephalidean, tetraphyllidean, and cyclophyllidean genera) as of uncertain systematic status and insufficiently known; recognizes affinities of *Pillersium* to the Lecanicephala (or Tetraphyllidea or Disculicipitidae).

Yamaguti (1959): treats *Pillerisium* [sic] Southwell, 1927 as a *genus incertae sedis*.

Thatcher (1961): reports *Pillersium owenium* Southwell, 1927 (order Lecanicephalidea) from *Carcharhinus limbatus* from the Gulf of Mexico; comments on the incomplete description of this species provided by Southwell (1927); provisionally assigns this name to the two immature and seven larger mature specimens he collected; describes and illustrates these new specimens.

Euzet (1994a): considers *Pillersium* affiliated with the family Phyllobothriidae in the order Tetraphyllidea; the genus is considered as a *genus incertae sedis*.

Remarks

Southwell (1927) described *Pillersium owenium* based on material consisting solely of several scolices. Although he did not explicitly distinguish the species from any other species, he stated that it is easily identifiable based on its possession of a scolex consisting of two bothridia, and lacking accessory suckers. *Pillersium owenium* was placed in the order Heterophyllidea, along with the diphyllidean *Echinobothrium*, the proteocephalideans *Peltidocotyle* Diesing, 1850 and *Amphoteromorphus* Diesing, 1850, the tetraphyllidean *Discocephalum*, and the questionable *Diagonobothrium* by Southwell (1925). Thatcher (1961) considered *P. owenium* to belong to the order Lecanicephalidea. However, the specimens he provisionally assigned to this species, and which formed the basis of his opinion, were later shown to be members of the odd tetraphyllidean genus *Cathetocephalus* (see Dailey and Overstreet 1973). A visit to the British Museum in London revealed two slides of type specimens of *P. owenium*, one slide bearing only a scolex, the other bearing four strobilae, but with no information on the internal anatomy. Unfortunately, no additional information could be obtained from examination of this material, and the identity of this species remains uncertain. However, the limited data available for the morphology of the scolex does not support an association with the lecanicephalideans, consistent with the suggestion by Euzet (1994a). Specimen-based observations support an association with non-hooked tetraphyllideans.

Prosobothrium Cohn, 1902

Type species: *Prosobothrium armigerum* Cohn, 1902.

Type host: *Squalus acanthias* Linnaeus, 1758, Piked dogfish (Squalidae, Squaliformes).

History of association with the Lecanicephalidea

Cohn (1902a): erects the genus *Prosobothrium* with *P. armigerum* as the type species; considers it to be a tetrabothriid.

Southwell (1925): recognizes four genera (*Zygobothrium* Diesing, 1850, *Staurobothrium* Shipley and Hornell, 1906, *Discobothrium* Van

Beneden, 1870 (= *Hornellobothrium* Shipley and Hornell, 1906), and *Prosobothrium* Cohn, 1902) as intermediate between Cyclophyllidea and Tetraphyllidea, not placed in a particular group.

Woodland (1927): [unjustifiably] creates the generic name *Lintoniella adhaerens* [sic] (new generic name for *Prosobothrium* = *Ichthyotaenia* according to Linton); considers the species to be a "lecanicephalid" taxon; within the order Tetraphyllidea; *Lintoniella* (*Prosobothrium*) *adhaerens* is placed in the family Proteocephalidae.

Fuhrmann (1931): recognizes *Prosobothrium* (in addition to 13 other lecanicephalidean, tetraphyllidean, and cyclophyllidean? genera) as of uncertain status and insufficiently known in the order Tetraphyllidea.

Wardle and McLeod (1952): consider *Prosobothrium* Cohn, 1902 to be a *genus inquirendum*, with affinities to Lecanicephala (or Tetraphyllidea or Disculicipitidae).

Riser (1955): describes two species of *Prosobothrium* as lecanicephaloids in the family Disculicepitidae, in the superfamily Lecanicephaloidea, order Tetraphyllidea, superorder Trixenidea.

Brooks and McLennan (1993): present a tree for the order Lecanicephaliformes Baylis, 1920; based on that tree they recognize *Prosobothrium* Cohn (along with *Staurobothrium* Shipley and Hornell, 1905, *Tetragonocephalum* Shipley and Hornell, 1905, *Disculiceps* Joyeux and Baer, 1935, *Adelobothrium* Shipley, 1900, and *Cathetocephalus* Dailey and Overstreet, 1973) in the subfamily Disculicipinae Joyeux and Baer, 1935, family Lecanicephalidae Braun, 1900, order Lecanicephaliformes Baylis, 1920.

Remarks

Cohn (1902a) presented a preliminary description of a cestode he found among Creplin's material in the Greifswalder Collection in Germany. He also provided a brief characterization of this species noting that it would be described in more detail at a later time. The original description was based on material consisting of an unspecified number of worms, and several strobilar fragments, each consisting of 2-3 proglottids, all of which were collected from the stomach (?) of *Squalus acanthias* from the Atlantic Ocean. Cohn (1902a) considered the anterior region of the species to correspond closely to figure 267 of Wagener (1854) illustrating the scolex of a species of *Tetrabothrium* Diesing, 1854 from "*Carcharias Rondoletii*" (Wagener 1854), except that Wagener figured both the scolex and anterior part of the neck as being 'spined.' Later that year, Cohn (1902b) provided a more detailed description and figures of the type species *P. armigerum*. The morphology of the scolex and the internal anatomy of the proglottids suggest that this worm belongs to the order Tetraphyllidea. This placement was previously suggested by other authors, such as Joyeux and Baer (1936), Baer and Euzet (1955), and, most recently, Euzet (1994a). However the familial placement of this non-hooked taxon within the Tetraphyllidea remains controversial. As was suggested by Baer and Euzet (1955) and Euzet (1955), recent molecular work based on ribosomal sequence data (Olson *et al.* 1999, 2001) has supported a close association of *Prosobothrium* with hooked tetraphyllideans (Onchobothriidae).

Sciadocephalus Diesing, 1850

Type species: *Sciadocephalus megalodiscus* Diesing, 1850.

Type host: *Cichla monoculus* Spix and Agassiz, 1831 (Cichlidae, Perciformes).

History of association with the Lecanicephalidea

Perrier (1897): recognizes *Sciadocephalus* (including *S. megalodiscus* from *Cichla monoculus*), along with *Lecanicephalum* (including *L. peltatum* from *Trygon centrura*), *Tylocephalum* (including *T. pingue* from *Rhinoptera quadriloba*) and *Discocephalum* (including *D. pileatum* from *Carcharias obscurus*) in the family Gamobothriidae, order Tetracestoda.

Remarks

Diesing (1850) described the new genus and new species (*Sciadocephalus megalodiscus*) from the freshwater cichlid, *Cichla monoculus*. The species was only very briefly and superficially described; no illustrations were presented. A very brief diagnosis of the genus accompanied the species description. He placed the genus in the tribe Taenioidea, suborder Aprocta, order Cephalocotylea. Woodland (1933) redescribed the species based on limited new material. Although he considered his account to be incomplete, he considered this species to be a proteocephalidean taxon and supported recognition of the genus. In the most recent treatment of the order Proteocephalidea (see Rego 1994), *Sciadocephalus* was treated as a *genus inquirendum*. No evidence currently exists to support placement of this genus in an order other than the Proteocephalidea. Perrier's (1897) initial inclusion of this genus in Linton's family Gamobothriidae was consistent with the vague original diagnosis of the family.

Yogeshwaria Chincholikar and Shinde, 1976

Type species: *Yogeshwaria nagabushani* Chincholikar and Shinde, 1976.

Type host: "*Trygon*" sp., [stingray].

History of association with the Lecanicephalidea

Chincholikar and Shinde (1976): erect the genus *Yogeshwaria* with *Y. nagabushani* as the type species; consider it to most closely resemble *Diagonobothrium asymmetrum* Shipley and Hornell, 1906.

Schmidt (1986): considers *Yogeshwaria* Chincholikar and Shinde, 1976 to be a synonym of *Yogeshwaria* Shinde, 1966 [sic] [*Yogeshwaria* Chincholikar and Shinde, 1976 is actually a junior homonym of *Yogeshwaria* Shinde]; notes material consists of a single specimen, possibly having lost the scolex, no internal anatomy; considers *Y. nagabushani* Chincholikar and Shinde, 1976 from *Trygon* sp. India to be unidentifiable.

Butler (1987a): considers *Yogeshwaria* Chincholikar and Shinde to be unrecognizable.

Euzet (1994b): considers *Y. nagabushani* to be unrecognizable and unrecoverable given that the host species is unknown; suggests that since Chincholikar and Shinde (1976) compared it to *Diagonobothrium asymmetricum* [sic], it might be a diphyllidean; recommends that *Yogeshwaria* should be suppressed; treats it as a *genus inquirendum*.

Remarks

In 1968, Shinde erected the genus *Yogeshwaria* for a dilepidid cestode from a bird, the Yellow wattled lapwing. Eight years later, Chincholikar and Shinde (1976) erected the genus *Yogeshwaria* for a single immature specimen collected from a stingray, *Trygon* sp., from Ratnagiri, India. Given that these taxa are clearly distinct, the latter name must be considered a junior homonym of the former. However, not only is this taxon burdened with a homonym, but also the identity of the taxon cannot be clearly determined. The scolex is described as consisting of two bothria. Little additional information on the genus or the species can be gathered from the description. That the scolex consists of two bothria, instead of four acetabula, suggests that *Yogeshwaria* is not a lecanicephalidean taxon. In fact, Tyler (2001), in his comprehensive treatment of the Diphyllidea, suggests that *Y. nagabushani* be transferred to the genus *Echinobothrium*, alleviating both the problem with homonymy and the need to further treat the genus here.

B. GENERA CONSIDERED TO BE *GENERA INQUIRENDA ET INCERTAE SEDIS*

Calycobothrium Stiles and Hassall, 1912

(Fig. 4)

Taxonomic status: *Genus inquirendum et incertae sedis*.

Synonyms: *Cyclobothrium* Southwell, 1911.

Type and only species: *Calycobothrium typicum* (Southwell, 1911) Stiles and Hassall, 1912 (syn. *Cyclobothrium typicum* Southwell, 1911).

Type host: *Aetobatus narinari* (Euphrasen, 1790) (as *Aetobatis* [sic] *narinari*), Spotted eagle ray (Myliobatidae, Myliobatiformes).

Site of infection: Spiral intestine.

Type locality: Portugal Bay, Ceylon (now Sri Lanka).

Number of specimens on which the original description was based: One.

Type specimens (unverified): Colombo Museum, Colombo, Sri Lanka.

Voucher specimens: BMNH No. 1977.11.9.82.

Material examined: BMNH No. 1977.11.9.82 (voucher).

Etymology: *Kalyx*, *kalykos*, Gr., cup or covering of a flower (*kyklos*, Gr., circle, ring); *bothrion*, Gr., diminutive of *bothros*, trench, pit, trough.

Chronology

Southwell (1911): erects the genus *Cyclobothrium* with *C. typicum* as the type species; distinguishes it from *Thysanobothrium* in that it lacks a cup-like shield bearing suckers, possesses a pair of suckers that corresponds to the central "knob" of Shipley and Hornell and other minor differences (number of tentacles, course of the "penis" and vas deferens); describes the type species *C. typicum*; does not describe proglottid anatomy, notes only that they are acraspedote; examined 20 newly collected specimens of *Thysanobothrium uarnakense* from *Trygon walga* (presumably to compare to *C. typicum*) but does not discuss differences.

Stiles and Hassall (1912): *Cyclobothrium* Southwell, 1911 (not Cerfontaine, 1895, trematode); suggest *Calycobothrium* as replacement name for *Cyclobothrium*, which is preoccupied, same type; *C. typicum* Southwell, 1911 (in *Aetobatis* [sic] *narinari*, Portugal Bay).

Meggitt (1924): treats *Calycobothrium* Southwell, 1911 in the family Polypocephalidae (including *Anthemobothrium*, *Calycobothrium*, and *Polypocephalus*), order Tetraphyllidea; provides an abbreviated diagnosis of the genus.

Southwell (1925): treats *Calycobothrium* (syn. *Cyclobothrium* Southwell, 1911) in the family Lecanicephalidae, suborder Multivitellata, order Cyclophyllidea; cites Southwell's (1911) characters of the genus; considers *Calycobothrium* to be closely related to *Polypocephalus*; recognizes only one species; distinguishes it from *Polypocephalus*; emends the generic diagnosis; reports a single newly collected specimen obtained from *Aetobatis* [sic] *narinari* from Portugal Bay, Ceylon; provides a detailed description of the specimen and illustrates a proglottid [vagina is anterior to cirrus sac!]; reports seeing only two suckers on the damaged "head;" notes that if four suckers are actually present this species belongs in the Cyclophyllidea, if not, it should be moved to the Heterophyllidea.

Poche (1926): includes *Calycobothrium* as one of three genera in the family Polypocephalidae, in the new suborder Phyllobothriinea, order Taeniidea *nom. nov*.

Woodland (1927): considers *Calycobothrium* to be a "lecanicephalid" genus in the family Phyllobothriidae, order Tetraphyllidea.

Southwell (1929): notes *Calycobothrium* because of its position in the family Phyllobothriidae in Woodland's (1927) classification scheme, which he criticizes.

Southwell (1930): treats *Calycobothrium* (syn. *Cyclobothrium* Southwell, 1911) in the family Lecanicephalidae, superfamily Lecanicephaloidea, order Eucestoda; text identical to that of Southwell (1925).

Fuhrmann (1931): places lecanicephalideans in two of seven families, the family Lecanicephalidae Braun (syn. Gamobothriidae Linton) and the family Cephalobothriidae (Pintner), order Tetraphyllidea; considers *Calycobothrium* (syn. *Cyclobothrium*) (along with *Staurobothrium*, *Hornellobothrium*, *Eniochobothrium*, and *Phanobothrium*, among others), to be "uncertain" and not sufficiently known, but very interesting tetraphyllideans.

Wardle and McLeod (1952): treat *Calycobothrium* Stiles, 1912 [sic] (= *Cyclobothrium* Southwell, 1911, preoccupied) as a *genus inquirendum*, with affinities to Lecanicephala (or Tetraphyllidea or Disculicipitidae); say Southwell (1911) believes it to be cyclophyllidean or heterophyllidean, but should be a cephalobothriid.

Yamaguti (1959): treats *Calycobothrium* Southwell, 1911 [sic] (syn. *Cyclobothrium* Southwell, 1911, preoccupied) in the family Lecanicephalidae, order Lecanicephalidea.

Joyeux and Baer (1961): treat *Anthemobothrium*, *Calycobothrium*, *Lecanocephalum* [sic], and *Polypocephalus* in the family Lecanicephalidae.

Schmidt (1970): includes *Calycobothrium* in a key to the genera of tapeworms; gives diagnosis for each genus and names the type species; treats *Calycobothrium* in the family Lecanicephalidae, order Lecanicephalidea Baylis, 1920.

Zaidi and Khan (1976): report *Calycobothrium typicum* from the intestine of *Brachirus orientalis* [= *Euryglossa orientalis*, Oriental sole] from Fish Harbour, Karachi, Arabian Sea; material consists of two specimens with immature proglottids only; present a description for the specimens; identify the specimens as *C. typicum*, but smaller; new host record and first record of this species from Pakistan.

Schmidt (1986): treat *Calycobothrium* Southwell, 1911 [sic] (syn. *Cyclobothrium* Southwell, 1911) in the family Lecanicephalidae, order Lecanicephalidea.

Brooks and McLennan (1993): present a tree for the order Lecanicephaliformes Baylis, 1920; based on that tree they recognize *Calycobothrium* Southwell 1911 (along with *Discobothrium* van Beneden 1871, *Echeneibothrium* van Beneden, 1850, *Lecanicephalum* Linton, 1890, *Hexacanalis* Perrenoud, 1931 *sedis mutabilis*, *incertae sedis*, and *Polypocephalus* Braun, 1878) in the subfamily Lecanicephalinae Braun, 1900 *incertae sedis*, family Lecanicephalidae Braun, 1900, order Lecanicephaliformes Baylis, 1920.

Euzet (1994b): treats *Calycobothrium* Southwell, 1911 (syn. *Cyclobothrium* of Southwell, 1911) as a *genus incertae sedis*; notes that tentacles of *C. typicum* are similar to those of *Polypocephalus* sp. reported by Butler (1987) and that it has a tetraphyllidean proglottid anatomy; indicates it should be redescribed from type host.

Bilqees (1995): cites name as *Calycobothrium typicum* (Southwell, 1911) Zaidi and Khan, 1970; says that *C. typicum* has been reported from *Brachirus orientalis* from Pakistan; [citation probably indicates the authors that reported the species from Pakistan].

Remarks

Southwell (1911) erected the genus, *Cyclobothrium*, for a single specimen of his new species, *Cyclobothrium typicum*, collected from *Aetobatus narinari* from Portugal Bay, Ceylon (now Sri Lanka). The generic diagnosis is brief, as is the description of the new species. The description included only a few very general measurements (*e.g.*, total length, dimensions of the posterior proglottids) and was accompanied by a drawing of the whole worm, a detail of the scolex and a very schematic drawing of the proglottid. Southwell (1911) considered this genus to closely resemble *Thysanobothrium* Shipley and Hornell, 1906. But he noted that the two taxa differed in overall morphology of the scolex. He listed additional minor differences in number and form of the tentacles and the form of the vas deferens and the cirrus. Southwell (1911) did not address the taxonomic position of the new genus within the cestodes. One year later, Stiles and Hassall (1912) reported that the generic name *Cyclobothrium* was preoccupied since it had been used for a trematode described by Cerfontaine in 1895. They suggested the replacement name *Calycobothrium*, although the new combination, *Calycobothrium typicum*, for the type species was not formally indicated. The author citation for this genus and species has been subsequently erroneously cited by different authors (see chronology, *e.g.*, Yamaguti 1959; Schmidt 1986). The nomenclatural act by Stiles and Hassall (1912) resulted in the following names with author citations: *Calycobothrium* Stiles and Hassall, 1912, *nomen novum* for *Cyclobothrium* Southwell, 1911 (primary homonym of *Cyclobothrium* Cerfontaine, 1895); type species *Calycobothrium typicum* (Southwell, 1911) Stiles and Hassall, 1912 (syn. *Cyclobothrium typicum* Southwell, 1911).

The description and figures of the scolex of *Calycobothrium typicum* presented in the original description are difficult to interpret. Southwell (1911) described the scolex as "like a daisy, with a central myzorhynchus bearing a pair of suckers, and surrounded externally by a frill of about 14 long hollow unbranched digitate sucker-like tentacles, arising from the base of the myzorhynchus" (p. 224). The position and form of the sucker-bearing myzorhynchus, while confusing, indicates a scolex morphology unusual among elasmobranch cestodes. Similarities between this and *Polypocephalus*, the other lecanicephalidean genus possessing tentacles, are obvious. Southwell's treatment of this taxon in 1925 is somewhat more extensive. He considered *Calycobothrium* to be closely related to *Polypocephalus*. For reasons that he did not articulate, Southwell (1925) emended the diagnosis of the genus. Although the majority of wording is identical to his treatment of the taxon in 1911, the number of suckers on the myzorhynchus is changed from "a pair" (1911, p. 224) to "four (?)" (1925, p. 319). In addition, several features included in his 1911 diagnosis of the genus are omitted (*e.g.*, acraspedote nature of the proglottids, irregularly alternating pores); also, the description of *C. typicum* is expanded.

A specimen of *Calycobothrium typicum* at the BMNH in London, apparently from Southwell's collection, enhanced understanding of the proglottid anatomy of this species, but did little to contribute to an understanding of the morphology of the scolex. Southwell (1925) cited the host as *Aetobatus narinari* from Portugal Bay, Ceylon, with a collection date of "18.2.09" (p. 319). All the measurements presented in the beginning of Southwell's (1925) description were taken from Southwell (1911). In addition, reproductive organs were described in detail, and measurements of some structures and a new illustration of a proglottid of this species were provided. It appears that the description in 1925 was a composite, based on information from the specimen on which the original description was based and an additional specimen. The one specimen of *C. typicum* located in the BMNH (No. 1977.11.82.9) bears a Liverpool School of Tropical Medicine label that reads: "Calicob. typicum T.S 1910 (Cyclob. typicum) from Aetobatus narinari Portugal Bay 18.12.09 Drawn." The specimen is in several pieces and lacks a scolex. Several of the mature proglottids of this specimen are consistent with, and almost identical to, Southwell's (1925) illustration of the proglottid of *C. typicum* (p. 320, fig. 219). The indication "Drawn" on the museum slide at the BMNH, in addition to very similar measurement data, makes it almost certain that this is the specimen Southwell (1925) had in hand. In the absence of a scolex it cannot be determined whether this specimen is conspecific (or even congeneric) with the one described as *C. typicum* by Southwell 14 years earlier.

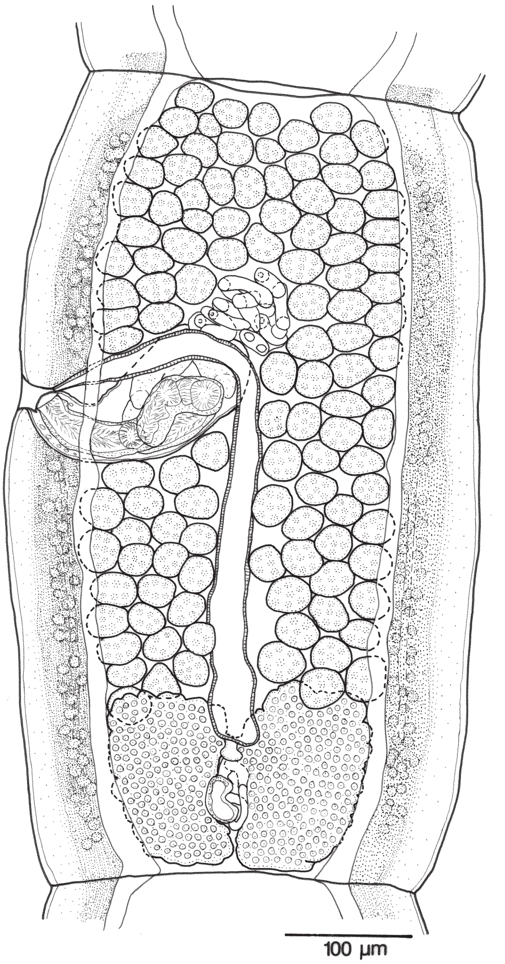


Fig. 4. Line drawing of *Calycobothrium typicum* (Southwell, 1911) Stiles and Hassall, 1912. Mature proglottid (voucher, BMNH No. 1977.11.9.82).

If this museum specimen proves to be a specimen of *C. typicum*, the proglottid is clearly not lecanicephalidean in morphology, but rather of the tetraphyllidean type, possessing a vagina opening into the genital atrium anterior to the cirrus sac, a simple H-shaped ovary and a vas deferens forming small coils anterior to the cirrus sac at its distal end (Fig. 4). To facilitate identification in the future, a brief description of this incomplete specimen is provided below. Measurement data from Southwell (1911, 1925) have not been incorporated.

Worm greater than 3.9 cm long; more than

208 proglottids total. Proglottids acraspedote. Immature proglottids 196 in number, very gradually increasing in size and length to width ratio with maturity. Mature proglottids at least 12, longer than wide; three most posterior mature proglottids 630-643 long by 356-377 wide. Testes 104-118 in total number, 22-37 long by 24-48 wide, in field anterior to ovary, 6-8 columns in dorso-ventral view, one row deep, 17-25 post-vaginal testes, postovarian testes absent. Vas deferens minimal, coiling anterior to cirrus sac, entering cirrus sac at distal end. External seminal vesicle absent. Internal seminal vesicle absent. Cirrus sac pyriform, 170-180 long by 101-125 wide, containing coiled cirrus. Cirrus armed with spinitriches. Ovary H-shaped in dorsoventral view, 134-149 long by 183-211 wide; ovarian lobes superficially lobulated. Vagina opening into genital atrium anterior to cirrus sac, extending along midline of proglottid; vaginal sphincter absent; seminal receptacle not observed. Genital pores lateral, irregularly alternating, 57-59% of proglottid length from posterior end. Uterus not observed. Vitelline condition in form of lateral bands of follicles, each band possibly consisting of several small vitelline follicles. One dorsal and one ventral pair of excretory ducts present.

The only report of *C. typicum* since its original description is that of Zaidi and Khan (1976) who reported collecting two immature specimens of this species from the teleost *Brachirus orientalis* (Bloch and Schneider, 1801), the Oriental sole, in the Arabian Sea. These authors considered this report to be a new host record and the first record of this species from Pakistan. There is some question as to the accuracy of this record. The specimens were immature and considerably smaller in all respects than previously described specimens. Therefore, only the possession of tentacles on the scolex, a feature also present, for example, in *Polypocephalus*, linked Zaidi and Khan's specimens to *Calycobothrium*. Thus, this record should be considered suspect until new material of mature specimens can be collected.

Since its original description, *Calycobothrium typicum* has been placed in a variety of different cestode orders, for example Meggitt (1924) placed the species in the Tetraphyllidea, Southwell (1925) in the Cyclophyllidea, and Poche (1926) in the Taeniidea. Wardle and McLeod (1952) and Euzet (1994b) were less confident in the understanding of this enigmatic taxon and considered it a *genus inquirendum* and a *genus incertae sedis*, respectively. Based on the evidence presented above, it seems apparent that the genus *Calycobothrium* should be considered a *genus inquirendum* with uncertain systematic position (*incertae sedis*), and decisions about its identity and validity are best left until additional information on the morphology of *C. typicum* becomes available.

Trygonicephalum Shinde and Jadhav, 1984

Taxonomic status: *Genus inquirendum et incertae sedis*.

Type and only species: *Trygonicephalum ratnagiriensis* Shinde and Jadhav, 1984.

Type host: *Trygon sephen* (Forsskål, 1775) (= *Pastinachus sephen* [Forsskål, 1775] ?), Cowtail stingray (Dasyatidae: Myliobatiformes).

Site of infection: Spiral intestine.

Type locality: Ratnagiri, India.

Number of specimens on which the original description was based: Three.

Type specimens (unverified): Holotype and paratype deposited in the Zoology Department Marathwada University, Aurangabad, India.

Material examined: None.

Etymology: *Trygoni-*, presumably referring to the genus of host (i.e., *Trygon*) from which these worms were collected; *kephale*, Gr., head.

Chronology

Shinde and Jadhav (1984): erect the genus *Trygonicephalum* with *T. ratnagiriensis* as the type species; describe scolex as consisting of two regions, an anterior large oval disc and two posterior bothria.

Euzet (1994b): treats *Trygonicephalum* as a *genus inquirendum*; notes tetraphyllidean proglottid anatomy and that description does not correspond to any known genus; suggests suppression of *Trygonicephalum* because it cannot be classified among lecanicephalideans or tetraphyllideans.

Remarks

Shinde and Jadhav (1984) erected the genus *Trygonicephalum* for cestodes collected from the Cowtail stingray *Pastinachus sephen* (as *Trygon sephen*) from Ratnagiri, India. Their description is brief. The scolex is described as possessing an anterior "large, oval disc and a posterior region with two oval bothria" (p. 403). The vagina is described as opening into the genital atrium anterior to the cirrus sac. The illustration of the gravid proglottids could be interpreted to suggest the presence of an extensive external seminal vesicle extending to near the posterior of the proglottid. Together, these morphological features, in combination or individually, support different placements of this genus. The scolex morphology is most similar to that of diphyllideans, although rostellar hooks are lacking. The position of the vagina suggests tetraphyllidean affinities. If an extensive external seminal vesicle is indeed present, lecanicephalidean affinities are likely. The holotype and paratype were said to have been deposited in the Zoology Department of Marathwada University, Aurangabad in India. It was not possible to obtain these specimens. Inquiries about the presence of the types in the Zoology Department at Marathwada University remain unanswered. Based solely on the description presented by Shinde and Jadhav (1984), *Trygonicephalum ratnagiriensis* is currently unidentifiable and thus, is treated here as a *genus inquirendum* with uncertain systematic position (*incertae sedis*).

C. GENERA CONSIDERED TO BE *NOMINA NUDA*

Aphanobothrium Seurat cited in Herdmann and Hornell (1906)

Taxonomic status: *Nomen nudum*.

Chronology

Seurat cited in Herdmann and Hornell (1906): use the name "*Aphanobothrium* n.gen." attributing it in a quote from a letter from Seurat in which he suggests that a cestode he found in a pearl oyster be named *Aphanobothrium margaritiferae*.

Seurat (1906a and b): publishes his new species from the pearl oyster in the genus *Tylocephalum* (*T. margaritiferae*).

Stiles and Hassall (1912): list *Aphanobothrium* Seurat in Herdmann and Hornell, 1906 (preceded by *Aphanobothrium* Linstow, 1906); *A. margaritiferae* Seurat, 1906 in Herdmann and Hornell, 1906 (to *Tylocephalum*) (in *Margaritifera margaritifera cumingi*, Gambier Archipelago; adult in "raie-aigle").

Meggitt (1924): recognizes *Tylocephalum* Linton, 1890 in the family Lecanicephalidae, order Tetraphyllidea; considers *Aphanobothrium* Seurat to be a junior synonym of *Tylocephalum*.

Southwell (1925): considers *Aphanobothrium* to be a junior synonym of *Tylocephalum*.

Southwell (1930): considers *Aphanobothrium* to be a junior synonym of *Tylocephalum*.

Yamaguti (1959): considers *Aphanobothrium* Seurat, 1906 to be a junior synonym of *Tylocephalum* Linton, 1890.

Schmidt (1986): considers *Aphanobothrium* Seurat, 1906 to be a junior synonym of *Lecanicephalum* Linton, 1890.

Euzet (1994b): considers *Aphanobothrium*, erected for larvae encapsulated in flesh of *Pintada margaritifera* in French Polynesia and attributed to adults in *Aetobatis narinari* [sic] to be a *genus inquirendum*; no description of the larva is available.

Remarks

The name *Aphanobothrium* is cited extensively throughout the lecanicephalidean literature. It is most often considered to be a junior synonym of *Tylocephalum* Linton, 1890 (see chronology). Most authors attribute the name to Seurat (1906a, b) (*e.g.*, Yamaguti 1959; Schmidt 1986; Euzet 1994b). In 1906, Herdmann and Hornell published a paper on pearl production in the Gulf of Manaar. In that paper, in a discussion on encysted parasites serving as nuclei to induce the formation of pearls in Ceylon pearl oysters, they commented on the parasites Seurat found encysted in pearl oysters in the Gambier Islands. Herdmann and Hornell quoted from a letter from Seurat in which he suggested that the adult of the cestode producing pearls in pearl oysters in Managreva lives in the eagle ray. In that same letter he proposed to call this parasite "*Aphanobothrium*, n.g., *margaritiferae*" (Herdmann and Hornell 1906, p. 17). As it turns out, Seurat actually never used this name in print. In 1906, he described a new species of cestode from pearl oysters from the Gambier Islands in French Polynesia, but placed the species in the genus *Tylocephalum* (*Tylocephalum margaritiferae* Seurat, 1906) (Seurat 1906b). Therefore, the name *Aphanobothrium* is invalid and unavailable and should be considered a *nomen nudum*. Had he carried through with his idea, Seurat would have created a homonym because the name had already been used for a cyclophyllidean tapeworm.

D. LECANICEPHALIDEAN GENERIC SYNONYMS

Parataenia Linton, 1890

Taxonomic status: Junior synonym of *Polypocephalus* Braun, 1878.

Type and only species: *Parataenia medusia* Linton, 1890 (valid as *Polypocephalus medusia* [Linton, 1890] Southwell, 1925).

Type host: "*Trygon centrura* [sic]" (= *Dasyatis centroura* [Mitchill, 1815] ?), Roughtail stingray (Dasyatidae, Myliobatiformes).

Site of infection: Spiral intestine.

Type locality: Woods Hole, Massachusetts, U.S.A.

Number of specimens on which the original description was based: Not indicated in original description.

Type specimens: Not indicated in original description.

Voucher specimens (unverified): (see Appendix 4).

Material examined: USNPC No. 4799 (voucher); MHNG No. 88/11-29 (vouchers); HWML No. 20916 (voucher); 2 slides from Southwell's collection at the Station Méditerranéene de l'Environment Littoral, Université Montpellier II in Sète, France.

Etymology: *Para*, Gr., near; *-taenia*, referring to a similarity to the cyclophyllidean genus *Taenia* ("tentacular proboscides are probably homologues of the proboscis of avian Taeniaedae," Linton [1890], p. 862).

Chronology

Linton (1889): comments on the discovery of the remarkable cestode *Parataenia medusia*, possessing 16 flexible tentacular proboscides, resembling an actinian [anemone], but does not formally describe it.

Linton (1890): erects the new genus *Parataenia* with *Parataenia medusia* as the type species; suggests relationship to *Taenia*, and that tentacular proboscides are probably homologous to proboscis of avian Taeniidae; places it in the family Taeniidae; presents brief diagnosis of the genus; describes the species in some detail including a few measurements.

Braun (1894-1900): recognizes *Parataenia* Linton with the sole species *Parataenia medusia* Linton; considers the genus to be "doubtful" in terms of its position within the classification; lists the genus as a junior synonym of *Polypocephalus*.

Linton (1897): reports collecting two specimens (USNPC No. 4799) from *Dasyatis centrura* [sic] that agree perfectly with original description of species.

Perrier (1897): places *Parataenia* in the tribe Tetrabothriinae, family Tetrabothriidae, order Tetracestoda.

Linton (1900): reports *Parataenia medusia* from two *Dasyatis centrura* [sic] specimens collected in July and August of 1898.

Linton (1901): summarizes three previous instances of *Parataenia medusia* being collected in the Woods Hole region; reports collecting numerous specimens of *P. medusia* from *D. centrura* [sic] collected July 19, 1899; indicates the latter specimens are much smaller than those collected in previous years, and are easily distinguishable from others; provides measurements for the latter specimens.

Linton (1905): reports collecting numerous and few

Parataenia medusia from *Dasyatis say* specimens on July 6 and 24, 1901, respectively, and five and few specimens from *D. say* on August 16 and 18, 1902, respectively, from Beaufort, North Carolina.

Stiles and Hassall (1912): list *Parataenia* Linton, 1889: Linton (1890) [nec *Parataenia* Kerremans, apparently 1892, insect] Taeniaedae, or Tetrabothriidae, near *Echeneibothrium*, Linton (1901), Braun (1895 and 1900) (syn. of *Polypocephalus*); *P. medusia* Linton, 1889: Linton (1890) (in *Trygon centrura* [sic], Woods Hole), Linton (1900), Linton (1901) (in *Dasyatis centrura* [sic]), Linton (1905) (in *D. say*; Beaufort) and Braun (1900); *P. elongatus* Southwell, 1912 (in *Trygon kuhli*).

Maplestone and Southwell (1922): erect the genus *Nematoparataenia* with *N. paradoxa* as the type species from a black swan in Australia; describe anterior of head [scolex] as possessing a cup-shaped cavity and 12 flattened tentacular processes with minute spines; note tentacles are similar to those in species of *Parataenia*, but suggest worm resembles *Parataenia medusia* only in possession of tentacles.

Meggitt (1924): considers *Parataenia* Linton, 1889 (and *Thysanobothrium* Shipley and Hornell, 1906) to be a junior synonym of *Polypocephalus* Braun, 1878.

Linton (1924): reports *Parataenia medusia* from several specimens of *Dasyatis centrura* [sic] collected between 1903 and 1923 (USNPC No.7692); provides measurements for one worm.

Southwell (1925): considers *Parataenia* to be a junior synonym of *Polypocephalus*; recognizes *Polypocephalus medusia* (syn. *Parataenia medusia*, Linton, 1889); restates Linton's description of this species; describes and illustrates the anatomy of a few specimens of this species from *Dasyatis centrura* [sic] he received from Professor Linton [the figure of the proglottid (fig. 215) is not a *Polypocephalus* proglottid!]; considers *P. medusia* to be distinct from *P. radiatus* because of size and number of proglottids.

Poche (1926): recognizes *Parataenia* as a valid genus, rather than as a synonym of *Polypocephalus*, in the family Polypocephalidae Meggitt, suborder Phyllobothriinea *nom. nov.*, order Taeniidea *nom. nov.*; considers family also to include *Anthemobothrium*, *Calycobothrium*, and *Polypocephalus*.

Pintner (1928): *Polypocephalus* = *Parataenia*; recognizes, among others, "even *Parataenia medusia*, *Polypocephalus medusia*, separate from *Polypocephalus radiatus*" in the family Lecanicephalidae (his group A); characterizes family by non-glandular scolex, bilobed uterus, acraspedote.

Mola (1929): considers *Parataenia* to be a junior synonym of *Polypocephalus* Braun, 1878.

Southwell (1930): considers *Parataenia* to be a junior synonym of *Polypocephalus* Braun, 1878.

Woodland (1930): [*Parataenia*, *Thysanobothrium*, and possibly *Anthemobothrium* are considered to be synonyms of *Polypocephalus*]; redescribes in detail (with figures) *Polypocephalus* (*Parataenia*) *medusia* based on four specimens he received of Linton's material from Southwell, collected from *Trygon centrura* [sic] from Woods Hole.

Fuhrmann (1931): considers *Parataenia* to be a junior synonym of *Polypocephalus*, in the family Lecanicephalidae Braun (syn. Gamobothriidae Linton).

Linton (1938): illustrates scolex and tentacles of *Parataenia medusia*.

Baer (1948): describes material of *Parataenia medusia* from *Dasyatis centroura* and compares it to the description of this species given by Southwell (1925); examines museum specimens of *Parataenia elongata* from Ceylon; rejects the synonymy of *Thysanobothrium uarnakense* and *Parataenia elongata* with *Polypocephalus radiatus* because of the lack of information about the internal anatomy of *T. uarnakense* and *P. radiatus*; rejects synonymy of *Parataenia* with *Polypocephalus* until a more detailed study of the latter genus can be conducted; presents a generic diagnosis of *Parataenia*; recognizes two species, *P. medusia* (type species) and *P. elongata* in the genus.

Hyman (1951): considers *Parataenia* to be a junior synonym of *Polypocephalus*, in the family Lecanicephalidea, order Lecanicephaloidea.

Wardle and McLeod (1952): recognize *Parataenia* Linton, 1890, in the family Lecanicephalidae, order Lecanicephala, with the type and only species *P. medusiae* [sic] from *Pastinachus centrourus* [sic] from Massachusetts.

Yamaguti (1959): considers *Parataenia* to be a junior synonym of *Polypocephalus* Braun, 1878; lists among the species in the genus *P. medusia* (Linton, 1889), syn. *Parataenia medusia* Linton in *Trygon centrura* [sic] from Woods Hole, also in *Dasyatis sayi* from Beaufort and *Rhynchobatus granulatus, R. schlegeli*, *R. djeddensis* [sic] from Madras.

Hutton (1964): treats *Parataenia* to be a junior synonym of *Polypocephalus*; reports *Polypocephalus* sp. (= *Parataenia* sp.) from ten species of shrimp from Florida.

Schmidt (1986): considers *Parataenia* to be a junior synonym of *Polypocephalus* Braun 1878; lists *Polypocephalus medusia* (Linton, 1889) Yamaguti, 1959 (syn. *Parataenia medusia* Linton, 1889) in *Trygon centrura* [sic], *Dasyatis say*, *D. americana* and *Rhynchobatus* sp., India, U.S.A. and Colombia, among the species of *Polypocephalus* recognized.

Butler (1987a): notes that *Parataenia* Linton is preoccupied (Stiles and Hassall, 1912).

Euzet (1994b): considers *Parataenia* to be a junior synonym of *Polypocephalus* Braun, 1878.

Remarks

Linton originally used the name *Parataenia* in an abstract in 1889. In 1890, he formally erected the genus for the new species, *Parataenia medusia*, collected from the Roughtail stingray, *Dasyatis centroura* (as *Trygon centrura* [sic]) from Woods Hole, Massachusetts, U.S.A. Linton was struck by the presence of an apical structure in the form of 16 tentacles that could be completely withdrawn into the main body of the scolex (*i.e.*, the scolex proper). Linton was apparently unaware of Braun's (1878) description of *Polypocephalus radiatus* Braun, 1878, a cestode with the same 16 eversible tentacles on the apex of its scolex.

Braun (1894-1900) was the first to place *Parataenia* into synonymy with *Polypocephalus*. This synonymy was accepted by most authors (*e.g.*, Meggitt 1924; Southwell 1930; Fuhrmann 1931; Yamaguti 1959; Schmidt 1986). However, it was rejected by others. For example, Linton continued to use the name *Parataenia medusia* until 1938 (*e.g.*, Linton 1905, 1924, 1938). Poche (1926) considered *Parataenia* a valid genus based on differences in description of the scolex morphology and tentacle position between *Parataenia medusia* and *Polypocephalus radiatus*. Baer (1948) considered *Parataenia* to be valid because he was of the opinion that there was not enough known about the proglottid anatomy of *Polypocephalus radiatus* to accept or reject the synonymy of these two genera. Butler (1987a) stated that, according to Stiles and Hassall (1912), the generic name *Parataenia* was preoccupied. This, however, seems to have been a mistake because *Parataenia* Kerremans, apparently 1892, an insect, was described two years after *Polypocephalus* (Linton 1890).

To evaluate the proposed synonymy of *Polypocephalus* and *Parataenia*, specimens of the type species of both genera were examined. The type specimens of *Polypocephalus radiatus* were borrowed from the Zoologisches Museum Berlin (syntypes, ZMB No. 3182) and, since types were not found, compared to voucher specimens of *Parataenia medusia* (see material examined). Examination of this material suggests that the two species indeed are congeners. As a consequence, *Parataenia* should be considered to be a junior synonym of *Polypocephalus*. The two species described in *Parataenia* therefore are treated as members of *Polypocephalus*.

*Spinocephalum*Deshmukh, 1980

Taxonomic status: Junior synonym of *Tylocephalum* Linton, 1890.

Type and only species: *Spinocephalum rhinobatii* Deshmukh, 1980 (valid as *Tylocephalum rhinobatii* [Deshmukh, 1980] n. comb.).

Type host: *Rhinobatos granulatus* Cuvier, 1829 (as *Rhinobatus* [sic] *granulatus*), Sharpnose guitarfish (Rhinobatidae, Rhinobatiformes).

Site of infection: Spiral intestine.

Type locality: Veraval, west coast of India, India.

Number of specimens on which the original description was based: Four.

Type specimens (unverified): Laboratory of Cestodology, Department of Zoology, Marathwada University, Aurangabad, India.

Voucher specimens: None.

Material examined: None.

Etymology: *Spino*-, "due to presence of spines on scolex" (Deshmukh, 1980, p. 31); *kephale*, Gr., head.

Chronology

Deshmukh (1980): erects the genus *Spinocephalum* with *S. rhinobatii* as the type species; distinguishes it from *Lecanicephalum*, *Tylocephalum*, and *Flapocephalus*.

Campbell and Williams (1984): essentially consider *Spinocephalum* to be a junior synonym of *Tylocephalum*, since spination in the genus is variably developed.

Schmidt (1986): considers *Spinocephalum* to be a junior synonym of *Lecanicephalum* Linton, 1890; lists *Lecanicephalum rhinobatii* (Deshmukh, 1980) (syn. *Spinocephalum rhinobatii* Deshmukh, 1980) from *Rhinobatus* [sic] *granulatus*, India; creates the new combination and consequently lists it as a species of *Lecanicephalum*.

Euzet (1994b): considers *Spinocephalum* Deshmukh, 1980 to be a junior synonym of *Tetragonocephalum* Shipley and Hornell, 1905, because of lateral vitelline follicles; consequently, considers *S. rhinobatii* Deshmukh, 1980 to belong to *Tetragonocephalum*; distinguishing character for species (small spines on metoporhynchus) also found on *Tetragonocephalum uarnak* (Euzet and Combes, 1965).

Remarks

Deshmukh (1980) erected the genus *Spinocephalum* based on four specimens he collected from the Sharpnose guitarfish, *Rhinobatos granulatus* from Veraval, India. A generic diagnosis was presented and the species was described in some detail. Deshmukh distinguished *Spinocephalum* from *Tylocephalum*, *Lecanicephalum*, and *Flapocephalus* Deshmukh, 1979 based on scolex and proglottid features. Type specimens are said to have been deposited in the Laboratory of Cestodology, Department of Zoology, Marathwada University, Aurangabad, India. However, it was not possible to borrow and examine these specimens, because no response to letters of inquiry were received from this institution.

The taxonomic position of this genus has been somewhat controversial. Campbell and Williams (1984) considered *Spinocephalum* to be a synonym of *Tylocephalum*, while Schmidt (1986) considered both genera to be synonyms of *Lecanicephalum*. In the most recent treatment of the group, Euzet (1994b) considered *Spinocephalum* to be a synonym of *Tetragonocephalum* based on vitelline condition and the presence of spines on the apical structure.

The characteristics of *Spinocephalum* can be summarized in short as follows: Scolex bipartite; apical structure muscular, globular, retractable, surface covered with minute spines; scolex proper bearing four suckers; proglottids craspedote; spined cirrus; ovary H-shaped; vagina posterior to cirrus sac; seminal receptacle present; vitelline follicles lateral, vitelline follicles posterior to ovary present. The proglottid anatomy is inconsistent with the diagnoses of *Lecanicephalum* and *Tetragonocephalum* presented in this study. *Spinocephalum* does not exhibit the scolex morphology of species of *Lecanicephalum* (completely retractable apical organ in form of muscular pad covering the entire apical surface of the scolex), nor the characteristic proglottid anatomy of *Tetragonocephalum* (*e.g.*, enlarged genital atrium, restricted field of testes anterior to pore, uterine constriction at level of pore). The characteristics of *Spinocephalum* are consistent with the diagnosis of *Tylocephalum* (see treatment of *Tylocephalum*) presented in this study. The only discrepancy is the description and illustration of a large seminal receptacle in *Spinocephalum*, which is not seen in species of *Tylocephalum*. It likely that Deshmukh (1980) misinterpreted this structure, which actually is the vas deferens forming an external seminal vesicle. Confusion can arise from the fact that in lecanicephalideans the position of the external seminal vesicle is unusual in that it is found in the same position as one would expect to find the seminal receptacle (see *e.g.*, Fig. 15C). *Spinocephalum* is, thus, considered a synonym of *Tylocephalum*. The type species is transferred to *Tylocephalum*, thereby creating the new combination *Tylocephalum rhinobatii* (Deshmukh, 1980) n. comb.

E. LECANICEPHALIDEAN *GENERA INQUIRENDA*

ADELOBOTHRIUM Shipley, 1900

Taxonomic status: *Genus inquirendum.*

Synonyms: None.

Type and only species: *Adelobothrium aetiobatidis* Shipley, 1900.

Etymology: *Adelos*, Gr., unseen, unknown, obscure; *bothrion*, Gr., diminutive of *bothros*, trench, pit, trough.

Adelobothrium aetiobatidis Shipley, 1900
TYPE SPECIES

Taxonomic status: *Species inquirendum.*

Synonyms: None.

Type host: *Aetobatus narinari* (Euphrasen, 1790) (as *Aetiobatis* [sic] *narinari*), Spotted eagle ray (Myliobatidae, Myliobatiformes).

Additional hosts: None.

Site of infection: Spiral intestine.

Type locality: Lifu, Loyalty Islands, New Caledonia.

Additional localities: None.

Number of specimens on which the original description was based: [several].

Type specimens: Not indicated in original description.

Voucher specimens: None.

Material examined: Five putative specimens of *Adelobothrium* sp. (in the author's personal collection).

Etymology: *Aetiobatidis*, referring to the type host of the species, *Aetobatus narinari*.

Unverified records: *Rhynchobatus djeddensis* [sic] (Forsskål, 1775) from Pearl Banks, Ceylon (see Southwell 1912, 1925).

Chronology

Shipley (1900): erects the genus *Adelobothrium* with *A. aetiobatidis* as the type species for several specimens from *Aetiobatis* [sic] *narinari* from Lifu, Loyalty Islands; provides a general, superficial description including some details of the proglottid anatomy; provides schematic illustration of proglottid anatomy; notes the presence of four excretory canals; does not compare or distinguish the taxon from any other genera or species of cestodes; indicates that the species is not consistent with the descriptions of any other cestodes given by Van Beneden, Örley, Zschokke, or Linton.

Stiles and Hassall (1912): *Adelobothrium* Shipley, 1900; *A. aetiobatidis* Shipley, 1900 (in *Aetiobatis* [sic] *narinari*, Lifu, Loyalty Islands).

Southwell (1912): reports collecting new material of *A. aetiobatidis* from *Rhynchobatus djeddensis* [sic] from Ceylon.

Meggitt (1924): recognizes *Adelobothrium* Shipley, 1900 (along with *Discocephalum*, *Lecanicephalum*, *Cephalobothrium,* and *Tylocephalum*) in the family Lecanicephalidae, order Tetraphyllidea; provides an abbreviated diagnosis of the genus; considers *Kystocephalus* Shipley and Hornell, 1906 to be a junior synonym of *Adelobothrium*.

Southwell (1925): considers *Adelobothrium* in the family Lecanicephalidae, suborder Multivitellata, order Cyclophyllidea; quotes Shipley's description of the genus and concludes that *Adelobothrium* is closely related to *Tylocephalum*, differing from it primarily in head [scolex] morphology; considers *Tylocephalum marsupium* to be a junior synonym of *Adelobothrium aetiobatidis*; summarizes Shipley's description of the species; redescribes the species based on a large number of new specimens collected from *Rhynchobatus djeddensis* [sic] from Ceylon; illustrates the "head," cross sections of an immature proglottid, mature proglottid, longitudinal section through a "ripe" proglottid, "ripe" proglottids with cirri everted, gravid proglottid, and eggs; quotes Linton's description of *Tylocephalum marsupium*; concludes that there is little doubt that *T. marsupium* is identical with *A. aetiobatidis*, and that Linton was apparently unaware of the works of Shipley (1900), Shipley and Hornell (1906), and Jameson (1912).

Poche (1926): recognizes *Adelobothrium* in the family Lecanicephalidae Braun (Gamobothriidae Linton, 1889; Gamobothridae Ariola, 1899; Benham, 1901), suborder Phyllobothriinea *nom. nov.*, order Taeniidea *nom. nov.*

Woodland (1927): considers *Adelobothrium* to be a "lecanicephalid" genus provisionally proposed to be included in the family Tetrarhynchidae, order Tetraphyllidea (based on concentrically arranged vitellaria among longitudinal muscle bundles); considers *Tylocephalum marsupium* and *T. dierama* to potentially be junior synonyms of *Adelobothrium aetiobatidis*; comments on the fact that internal organs are intermingled with the longitudinal muscles.

Pintner (1928): considers *Adelobothrium* to belong in the family Cephalobothriidae (group B), characterized by a glandular scolex and craspedote proglottids.

Southwell (1929): addresses *Adelobothrium* concerning the position of the internal organs in relation to the longitudinal muscles, and because of its inclusion in Woodland's classification scheme, which he criticizes.

Southwell (1930): treats *Adelobothrium* Shipley, 1900 in the family Lecanicephalidae, superfamily Lecanicephaloidea, order Eucestoda; repeats much of Southwell's (1925) text, but omits discussion of Linton's (1916) description of *Tylocephalum marsupium* being identical with *A. aetiobatidis* (also as *A. aetobatidis* [sic]); considers *Tylocephalum marsupium* to be a junior synonym of *Adelobothrium aetiobatidis*.

Fuhrmann (1931): recognizes *Adelobothrium* in the family Lecanicephalidae Braun, order Tetraphyllidea; provides new, original illustrations for, among others, *A. aetiobatidis* Shipley and Hornell from *Rhynchobatus djeddensis* [sic] (scolex).

Perrenoud (1931): [according to Wardle and McLeod (1952): recognizes *Adelobothrium* as distinct from *Tylocephalum*].

Hyman (1951): recognizes *Adelobothrium* (along with *Lecanicephalum*, *Polypocephalus* [= *Parataenia*, *Thysanobothrium*], and *Anthemobothrium*) in the family Lecanicephalidae, order Lecanicephaloidea; presents only few characters for the family.

Wardle and McLeod (1952): treat *Adelobothrium* Shipley, 1900 in the family Cephalobothriidae, order Lecanicephala; summarize much of the history of the group.

Yamaguti (1959): treats *Adelobothrium* Shipley, 1900 in the family Adelobothriidae, order Lecanicephalidea; considers *Tylocephalum marsupium* Linton, 1916 as a possible junior synonym of the type species, *A. aetiobatidis* Shipley, 1900.

Joyeux and Baer (1961): treat *Adelobothrium*, with *Cephalobothrium*, *Hexacanalis*, and *Tetragonocephalum*, in the family Cephalobothriidae, superfamily Lecanicephaloidea, order Tetraphyllidea.

Schmidt (1970): presents a key to the genera of tapeworms; includes *Adelobothrium* in the family Adelobothriidae; provides brief diagnoses for each genus and lists the type species.

Wardle *et al.* (1974): recognize the family Adelobothriidae [and consequently *Adelobothrium*] in the order Lecanicephalidea Baylis, 1920; do not mention any genera they consider to belong in the family; present a key to families in the order Lecanicephalidea; list features of the family as part of the key, such as circumcortical vitelline follicles and filamented eggs.

Zaidi and Khan (1976): transfer the species belonging to group B of *Tylocephalum* in Pintner (1928) to the genus *Cephalobothrium*, including *Adelobothrium*.

Campbell and Williams (1984): reject *Tylocephalum marsupium* Linton, 1916 as a junior synonym of *Adelobothrium aetiobatidis* Shipley, 1900 because of morphological differences (proglottid size and testes number).

Schmidt (1986): treats *Adelobothrium* Shipley, 1900 in the family Adelobothriidae, order Lecanicephalidea; includes key to genera in the order.

Brooks and McLennan (1993): present a tree for the order Lecanicephaliformes Baylis, 1920; based on that tree they recognize *Adelobothrium* Shipley, 1900 (along with *Cathetocephalus* Dailey and Overstreet, 1973, *Staurobothrium* Shipley and Hornell, 1905, *Tetragonocephalum* Shipley and Hornell, 1905, *Disculiceps* Joyeux and Baer, 1935, and *Prosobothrium* Cohn, 1902) in the subfamily Disculicipinae Joyeux and Baer, 1935, family Lecanicephalidae Braun, 1900, order Lecanicephaliformes Baylis, 1920.

Euzet (1994b): considers the presence of a metoporhynchus and the possible possession of circumcortical vitellaria to support synonymy of *Adelobothrium* Shipley, 1900 with *Tylocephalum*; suggests that *Adelobothrium aetiobatidis*, reported from *Rhynchobatus djeddensis* [sic] by Southwell (1925), may present a distinct species in the genus *Tylocephalum*.

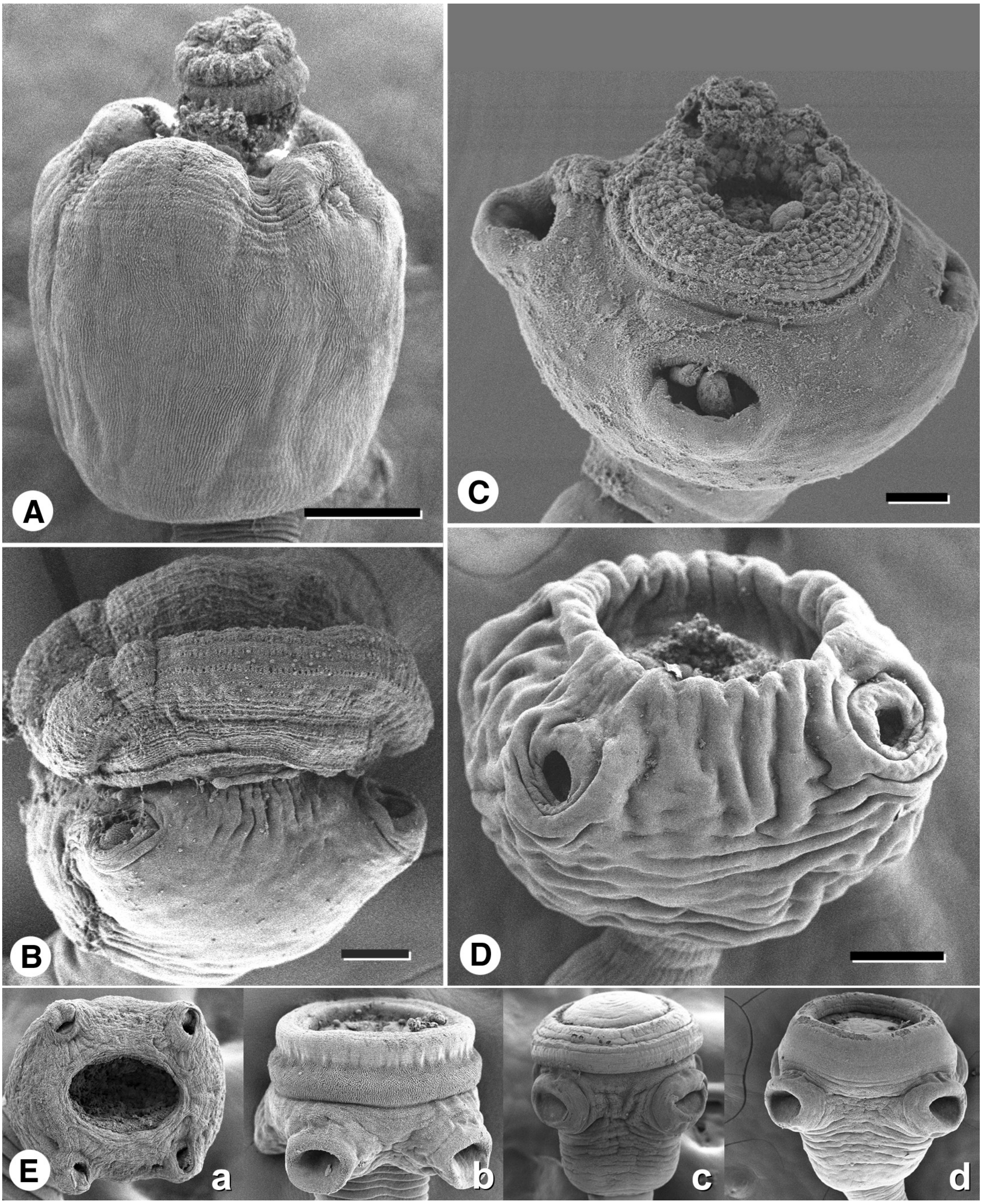


Fig. 5. A-E. Scanning electron micrographs of putative specimens of lecanicephalidean *genera inquirenda*. A. Scolex of putative specimen of *Adelobothrium*. B. Scolex of putative specimen of *Flapocephalus*. C. Scolex of putative specimen of *Kystocephalus*. D. Scolex of putative specimen of *Thysanobothrium*. E. Scolices of putative specimens of "*Cephalobothrium*" and "*Hexacanalis*." Scale bars: A and D, 100 μm; B, 25 μm; C, 10 μm.

Caira *et al.* (2001): include new material of *Adelobothrium* sp. from *Aetobatus narinari* from the Northern Territories, Australia in a phylogenetic analysis based on morphological data; this species groups with the majority of lecanicephalidean taxa included.

Remarks

Shipley (1900) erected the genus *Adelobothrium*, with the type *Adelobothrium aetiobatidis*, for material he collected from the Spotted eagle ray, *Aetobatus narinari*, in New Caledonia. The original description is detailed, and a number of characteristic features are indicated. The scolex is described as consisting of "a rostellum and a very swollen and enlarged collar" (Shipley 1900, p. 546). The arrangement of the suckers is unusual in that they are located at the base of the apical structure, recessed into the scolex proper, and they are directed anteriorly. This species is described as possessing an external seminal vesicle, an unarmed cirrus, vitellaria that encroach on the midline of the proglottid, and a vagina that opens in the genital atrium posterior to the cirrus sac. Although Shipley seems to have had several specimens of this species in his possession, he makes no mention of deposition of type specimens. In 1912, Southwell reported *A. aetiobatidis* from the Giant guitarfish, *Rhynchobatus djiddensis* from Ceylon (now Sri Lanka). This material was described and illustrated in more detail 13 years later (Southwell 1925). In that paper, Southwell commented on the similarities between *Adelobothrium* and *Tylocephalum*. This position is emphasized by the fact that he placed a species of *Tylocephalum* (*i.e.*, *Tylocephalum marsupium* Linton, 1916) in synonymy with *A. aetiobatidis*. *Adelobothrium* has not been reported since Southwell (1925).

Despite the limited available material, *Adelobothrium* has received a considerable amount of mention in the literature. It has been considered a valid genus by most authors that have included it in their taxonomic considerations of larger groups. Yamaguti (1959) recognized the uniqueness of this taxon by placing it in its own family, Adelobothriidae Yamaguti, 1959, in the order Lecanicephalidea. Euzet (1994b), in the most recent treatment of the Lecanicephalidea, was first to suggest that *Adelobothrium* may be a junior synonym of *Tylocephalum*. Nonetheless, given the limited available material, Euzet (1994b) treated it as a *genus inquirendum*.

Examination of specimens seems critical if this issue is to be resolved. Type specimens, if any were deposited, could not be located. No material of this species from the type host (types or vouchers) was found in any of the museum or personal collections examined. However, several specimens, consistent with the description of *Adelobothrium*, were collected from the type host (*Aetobatus narinari*) as a result of new collections in Fog Bay, Northern Territory, Australia (Fig. 5A). These specimens clarified that, although the morphology of the proglottids is similar to that of members in the genus *Tylocephalum*, the morphology of the scolex is quite different. While this material is insufficient to allow redescription of *Adelobothrium*, it is sufficient to suggest that this genus represents a distinct taxon. Determination of its status warrants further study. As a consequence, *Adelobothrium* is considered as a *genus inquirendum* here.

ANTHEMOBOTHRIUM Shipley and Hornell, 1906

Taxonomic status: *Genus inquirendum.*
Synonyms: None.
Type and only species: *Anthemobothrium pulchrum* Shipley and Hornell, 1906.
Etymology: *Anthemon*, Gr., flower; *bothrion*, Gr., diminutive of *bothros*, trench, pit, trough.

Anthemobothrium pulchrum Shipley and Hornell, 1906
TYPE SPECIES

Taxonomic status: *Species inquirendum.*
Synonyms: None.
Type host: *Trygon sephen* (Forsskål, 1775) (= *Pastinachus sephen* [Forsskål, 1775] ?), Cowtail stingray (Dasyatidae, Myliobatiformes).

Additional hosts: None.
Site of infection: Spiral intestine.
Type locality: Dutch Bay, Gulf of Manaar, Ceylon (now Sri Lanka).
Number of specimens on which the original description was based: One.
Type specimens: Not indicated in original description.
Voucher specimens: None.
Material examined: None.
Etymology: *Pulcher*, L., beautiful, pretty, fine.

Chronology

Shipley and Hornell (1906): erect the genus *Anthemobothrium* with *A. pulchrum* as the type species from a single specimen from *Trygon sephen* in Dutch Bay, Ceylon; provide a superficial description of the worm, the scolex is described in a little more detail; no details of proglottid anatomy are given, except for the mention of the uterus full of eggs; the species is not distinguished from any other genus or species of cestodes.

Stiles and Hassall (1912): *Anthemobothrium* Shipley and Hornell, 1906; *A. pulchrum* Shipley and Hornell, 1906.

Meggitt (1924): treats *Anthemobothrium* Shipley and Hornell, 1906 in the family Polypocephalidae (along with *Calycobothrium* and *Polypocephalus*), order Tetraphyllidea; provides an abbreviated diagnosis of the genus.

Southwell (1925): considers *Anthemobothrium* to be junior synonym of *Polypocephalus*; uses the new combination *Polypocephalus pulcher* (syn. *Anthemobothrium pulchrum* Shipley and Hornell, 1906), but does not indicate it as a new combination; quotes characters of the genus from Shipley and Hornell (1906) and considers its only distinguishing feature (*i.e.*, feather-like tentacles in *Anthemobothrium* vs. tubular tentacles in *Polypocephalus*) to be a specific rather than a generic character.

Poche (1926): recognizes *Anthemobothrium* (along with *Calycobothrium* and *Polypocephalus*) in the family Polypocephalidae Meggitt, suborder Phyllobothriinea *nom. nov.*, order Taeniidea *nom. nov.*

Southwell (1930): considers *Anthemobothrium* to be junior synonym of *Polypocephalus* Braun, 1878; recognizes *Polypocephalus pulcher* (syn. *Anthemobothrium pulchrum* Shipley and Hornell, 1906) as a distinct species.

Woodland (1930): addresses *Polypocephalus pulcher* (= *Anthemobothrium pulchrum*), but states that, besides its unusual tentacle morphology, nothing is known about this species.

Fuhrmann (1931): classifies *Anthemobothrium* (along with *Polypocephalus*, *Lecanicephalum* [syn. *Tylocephalum ex parte*, *Tetragonocephalum* and *Cephalobohrium ex parte*], and *Adelobothrium*) in the family Lecanicephalidae Braun (syn. Gamobothriidae Linton), order Tetraphyllidea.

Hyman (1951): recognizes *Anthemobothrium* in the family Lecanicephalidea, order Lecanicephaloidea.

Wardle and McLeod (1952): treat *Anthemobothrium* Shipley and Hornell, 1906 in the family Cephalobothriidae, order Lecanicephala.

Yamaguti (1959): considers *Anthemobothrium* Shipley and Hornell, 1906 to be junior synonym of *Polypocephalus* Braun, 1878; recognizes *P. pulcher* (Shipley and Hornell 1906), syn. *Anthemobothrium pulcher* Shipley and Hornell as distinct among eight species of *Polypocephalus*.

Joyeux and Baer (1961): classify *Anthemobothrium* (along with *Calycobothrium*, *Lecanocephalum* [sic], and *Polypocephalus*) in the family Lecanicephalidae, superfamily Lecanicephaloidea, order Tetraphyllidea.

Schmidt (1986): considers *Anthemobothrium* to be junior synonym of *Polypocephalus* Braun 1878; recognizes 14 species of *Polypocephalus*, among them *P. pulcher*.

Euzet (1994b): considers *Anthemobothrium* as a genus *incertae sedis* within the order Lecanicephalidea, close to *Polypocephalus*; notes that *A. pulchrum* is characterized by tentacles with plumed appearance, but anatomy is unknown; notes that it has not been seen since original description.

Remarks

Since its creation (Shipley and Hornell 1906), some authors have considered the genus *Anthemobothrium* valid (Meggitt 1924; Poche 1926; Joyeux and Baer 1961), while others have not. Southwell (1925) was the first to consider *Anthemobothrium* a junior synonym of *Polypocephalus*, an opinion also adopted, for example, by Fuhrmann (1931) and Schmidt (1986). In the most recent treatment of the order, however, Euzet (1994b) considered *Anthemobothrium* as a genus *incertae sedis* because of the unusual tentacle morphology and the lack of information of the internal anatomy.

Shipley and Hornell (1906) erected the genus *Anthemobothrium*, with the type species *Anthemobothrium pulchrum*, based on a single specimen taken from *Pastinachus sephen* (as *Trygon sephen*) collected from Dutch Bay, Ceylon (now Sri Lanka). Only general features of the worm were included in the description which was accompanied by illustrations of the whole worm, scolex and proglottids. There is no mention of type specimens in any of the literature referring to this species. Thus far, it has not been reported since its original description. Both the diagnosis of the genus and the illustrations of the type species *A. pulchrum* (Shipley and Hornell 1906) are generally consistent with the concept of the genus *Polypocephalus* (see treatment of *Polypocephalus* below). The basic morphology of the scolex is the same, except for its possession of what seem to be more elaborate tentacles, described as "feathered bothridia," like "neatly arranged ostrich feathers or frilled petals of a flower" (Shipley and Hornell [1906], p. 73). The superficial details of the internal anatomy of the proglottids of *A. pulchrum* (Shipley and Hornell 1906; fig. 78a and b) are similar to those found in *Polypocephalus*. Both groups possess few testes arranged in a single column and with what could be interpreted as post-ovarian vitelline follicles. As is true in at least a few species of *Polypocephalus* (*e.g.*, new species described in this study [Fig. 29] and *Polypocephalus rhinobatidis* Subhapradha, 1951 [see Subhapradha 1951]), the gravid uterus of *A. pulchrum* laterally displaces the few testes present.

As a result of new collections conducted as part of this study, a few specimens consistent with the diagnosis of *Anthemobothrium* were collected from the Cowtail stingray, *Pastinachus sephen*, from off the Wessel Islands, Northern Territory, Australia. This material suggests that the unusual morphology of the tentacles (Fig. 6) described by Shipley and Hornell (1906) is real and is quite different from that found in species of *Polypocephalus*. However, additional material is required to allow redescription of this taxon. In particular, the nature of the tentacles should be studied in more detail through histological sections and scanning electron microscopy. This material raises questions about the synonymy of *Anthemobothrium* and *Polypocephalus*. Thus, *Anthemobothrium* is considered as a *genus inquirendum* here.

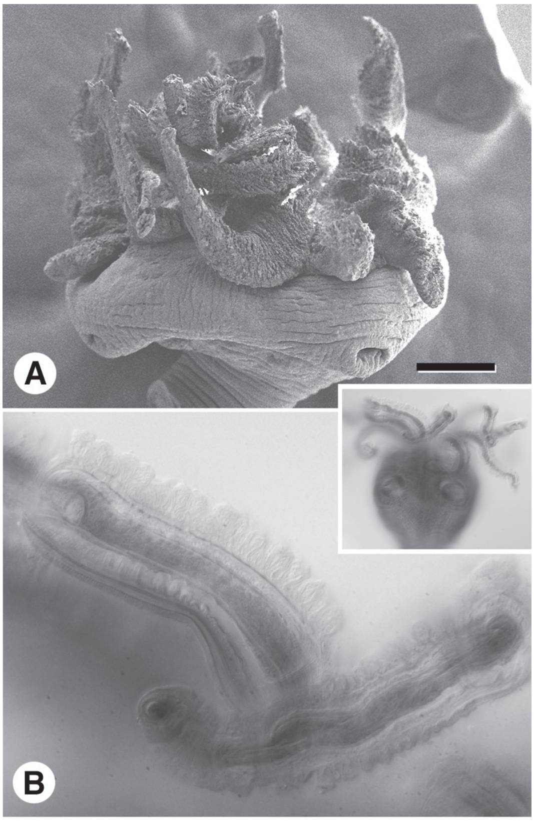


Fig. 6. A-B. Scanning electron micrograph and light microscopical images of putative specimens of *Anthemobothrium* Shipley and Hornell, 1906. A. Scanning electron micrograph of scolex. B. Light microscopical image of tentacles; scolex is shown in inset. Scale bar: A, 100 μm.

CEPHALOBOTHRIUM Shipley and Hornell, 1906

Taxonomic status: *Genus inquirendum*.
Synonyms: None.

Type species: *Cephalobothrium aetobatidis* Shipley and Hornell, 1906.

Species inquirendae: *Cephalobothrium alii* Jadhav and Jadhav, 1993; *C. gymnurai* Zaidi and Khan, 1976; *C. longisegmentum* Wang, 1984; *C. neoaetobatidis* Sarada, Vijaya Lakshmi and Hanumantha Rao, 1992; *C. pteroplateai* Zaidi and Khan, 1976; *C. rhinobatidis* Subhapradha, 1955; *C. singhi* Jadhav and Jadhav, 1993; *C. stegostomi* Sarada, Vijaya Lakshmi and Hanumantha Rao, 1993; *C. subhapradhi* Chincholikar and Shinde, 1977; *C. taeniurai* Ramadan, 1986; *C. trygoni* Shinde and Solunke, 1986; *C. variabile* Southwell, 1911.

Species inquirendae (non-lecanicephalidean): *Cephalobothrium gangeticus* Gairola, Malhotra and Sukul, 1989; *C. ghardagense* Ramadan, 1986.

Etymology: *Kephale*, Gr., head; *bothrion*, Gr., diminutive of *bothros*, trench, pit, trough.

Cephalobothrium aetobatidis Shipley and Hornell, 1906

TYPE SPECIES

Taxonomic status: *Species inquirendum*.

Synonyms: None.

Type host: *Aetobatus narinari* (Euphrasen, 1790) (as *Aetobatis* [sic] *narinari*), Spotted eagle ray (Myliobatidae: Myliobatiformes).

Additional hosts: None.

Site of infection: Spiral intestine.

Type locality: Dutch Bay, Ceylon (now Sri Lanka).

Additional localities: None.

Number of specimens on which the original description was based: One.

Type specimens: Not indicated in original description.

Voucher specimens (unverified): (see Appendix 4).

Material examined: A few putative specimens of *Cephalobothrium* (or *Hexacanalis*) sp. (in the author's personal collection)..

Etymology: *Aetobatidis*, referring to the type host of the species, *Aetobatus narinari*.

Unverified records: *Pristis cuspidatus* Latham, 1794 and *Aetobatis* [sic] *narinari* from Ceylon (see Southwell 1912); *Pteroplatea micrura* (Bloch and Scheoder, 1801) from Ceylon and *Trygon kuhlii* Müller and Henle, 1841 from West Cheval, Pearl Banks, Ceylon (see Southwell 1927); *Aetobatis* [sic] *narinari* from Hawaii (see Yamaguti 1968).

Chronology

Shipley and Hornell (1906): erect the genus *Cephalobothrium* with *C. aetobatidis* as the type species for a single specimen from *Aetobatis* [sic] *narinari* from Dutch Bay, Ceylon; provide a cursory description of this worm; proglottid anatomy is not described; the new taxon is not compared or distinguished from any other genera or species of cestodes.

Stiles and Hassall (1912): *Cephalobothrium* Shipley and Hornell, 1906; *C. abruptum* Southwell, 1911 (in *Pteroplatea micrura*, Portugal Bay); *C. aetobatidis* Shipley and Hornell, 1906 (in *Aetobatis* [sic] *narinari*, Dutch Bay, Ceylon); *C. actobatidis* [sic] Shipley and Hornell, 1906; *C. variabile* Southwell, 1911 (in *Pristis cuspidatus*, Portugal Bay).

Southwell (1912): reports collecting new material of *Cephalobothrium aetobatidis* from *Pristis cuspidatus* and *Aetobatis* [sic] *narinari* from Ceylon.

Jameson (1912): comments that one is likely to find adult stages of *Tylocephalum ludificans* and *T. minus*, described from larval stages, among members of *Tylocephalum*, or allied types described as new genera, occurring in oyster-eating elasmobranchs, such as, for example, *Cephalobothrium aetobatidis*.

Meggitt (1924): treats *Cephalobothrium* Shipley and Hornell, 1906 in the family Lecanicephalidae (along with *Discocephalum*, *Lecanicephalum*, *Tylocephalum*, and *Adelobothrium*), order Tetraphyllidea; provides an abbreviated diagnosis of the genus.

Southwell (1925): treats *Cephalobothrium* in the family Lecanicephalidae, suborder Multivitellata, order Cyclophyllidea; closely allies this genus with *Tylocephalum*; notes that, although in *Tylocephalum* the myzorhynchus is permanently protruded, that of *Cephalobothrium* is usually withdrawn and resembles a deep cup-like sucker; recognizes three species in *Cephalobothrium*; quotes Shipley and Hornell's (1906) description of *C. aetobatidis*; presents no new material; states that this species can be distinguished from *C. abruptum* and *C. variabile* based on size; cautions that the specimen of *C. aetobatidis* might have been a young specimen ('posterior proglottids seemed ripe'); notes that the type specimen is unavailable.

Poche (1926): recognizes *Cephalobothrium* in the family Lecanicephalidae Braun (Gamobothriidae Linton, 1889; Gamobothridae Ariola, 1899; Benham, 1901), suborder Phyllobothriinea *nom. nov.*, order Taeniidea *nom. nov.*

Woodland (1927): treats *Cephalobothrium* as a "lecanicephalid" genus proposed to be included in the family Phyllobothriidae, order Tetraphyllidea, based on disposition of longitudinal muscle bundles and marginal vitellaria.

Southwell (1927): reports collecting new material of *Cephalobothrium aetobatidis* from new hosts, *Pteroplatea micrura* from Ceylon (very large number of specimens) and *Trygon kuhli* from West Cheval, Pearl Banks, Ceylon (a few specimens); follows classification of Southwell (1925).

Pintner (1928): creates two groups, family Lecanicephalidae (group A) and family Cephalobothriidae (group B); the latter group includes *Cephalobothrium*, *Tylocephalum dierama*, *T. kuhli*, *T. ludificans*, *T. yorkei*, *T. translucens*, *T. aetiobatidis*, *Adelobothrium*, and *Tylocephalum pingue*, with glandular scolex and craspedote proglottids.

Mola (1929): reclassifies cestodes and places *Cephalobothrium* in the family Tetraphyllabothridae, order Tetraphyllidea.

Southwell (1929): comments on *Cephalobothrium* concerning the position of the internal organs in relation to the longitudinal muscles; comments on the position of *Cephalobothrium* in the family Phyllobothriidae.

Southwell (1930): treats *Cephalobothrium* Shipley and Hornell, 1906 in the family Lecanicephalidae, superfamily Lecanicephaloidea, order Eucestoda; recognizes three species; repeats text of Southwell (1925).

Fuhrmann (1931): divides *Cephalobothrium* and recognizes "*Cephalobohrium ex parte*" [no details as to the specific taxa included] in the family Lecanicephalidae Braun (syn. Gamobothriidae Linton) and "*Cephalobothrium*" in the family Cephalobothriidae (Pintner), both in the order Tetraphyllidea; provides new illustrations for *Cephalobothrium* sp. from *Trygon walga* (longitudinal sections of the scolex, after Pintner).

Perrenoud (1931): [according to Campbell and Williams, 1984: places *Hexacanalis* in the Cephalobothriidae, along side *Cephalobothrium*].

Hyman (1951): recognizes *Cephalobothrium* (along with *Discobothrium* and *Tylocephalum*) in the family Cephalobothriidae, order Lecanicephaloidea; presents few diagnostic characters for the family.

Wardle and McLeod (1952): treat *Cephalobothrium* Shipley and Hornell, 1906 in the family Cephalobothriidae, order Lecanicephala.

Riser (1955): recognizes the family Cephalobothriidae in the superfamily Lecanicephaloidea, order Tetraphyllidea, superorder Trixenidea [*Cephalobothrium* is implied as the type genus of family].

Yamaguti (1959): treats *Cephalobothrium* Shipley and Hornell, 1906 in the family Lecanicephalidae, order Lecanicephalidea; states that because, according to Pintner (1928), the internal anatomy is of the tetraphyllidean form, the genus is only provisionally retained; suggests that further study of *Cephalobothrium* might reveal that *Hexacanalis* is synonymous with *Cephalobothrium*.

Euzet (1959): lists *Cephalobothrium* as the type genus of the family Cephalobothriidae in the superfamily Lecanicephaloidea, order Tetraphyllidea.

Joyeux and Baer (1961): treat *Cephalobothrium* in the family Cephalobothriidae, superfamily Lecanicephaloidea, order Tetraphyllidea.

Dollfus (1964): reports a larva found in *Raja* that was described by Perrenoud (1931) to be either *Discobothrium fallax* or *Cephalobothrium aetobatidis*.

Yamaguti (1968): reports *Cephalobothrium aetobatidis* from five immature and one mature specimen from *Aetobatis* [sic] *narinari* from Hawaii; includes description and illustrations; considers his new specimens and those from Ceylon to be identical based on agreement of external morphology; notes presence of a large, elliptical seminal receptacle [= external seminal vesicle?] as one of the most important characters; determines that because of an inadequate original description, comparison between his new specimens and those from Ceylon is not possible; considers figures of Shipley and Hornell (1906) misleading as far as scolex is concerned.

Zaidi and Khan (1976): suppress *Hexacanalis* in favor of *Cephalobothrium*; transfer the species belonging to Pintner's (1928) *Tylocephalum* group "B" to *Cephalobothrium*.

Campbell and Williams (1984): note that *Cephalobothrium* Shipley and Hornell, 1906 was never sufficiently described; review history of the genus and the family Cephalobothriidae as created by Pintner (1928); present history of the genus again as it relates to the erection of *Hexacanalis* by Perrenoud (1931): *Hexacanalis* was created by Perrenoud (1931) after examining sections of *C. abruptum* Southwell, 1911; no whole mounts were examined; internal anatomy of *Cephalobothrium* was unknown at the time, and he did not examine Shipley and Hornell's type species, *C. aetobatidis*; created *Hexacanalis* and made *C. abruptum* type species because of difference in host associations, degree of proglottid overlap, scolex shape and histology, and unique osmoregulatory system; consider non-glandularity of the scolex and six osmoregulatory ducts to not warrant creation of a new genus, especially if internal anatomy of *Cephalobothrium* is not known; suggest that *Hexacanalis* should be considered to be a junior synonym of the enigmatic *Cephalobothrium*; note that *Cephalobothrium* itself is only based on the invagination of the metoporhynchus into a large terminal sucker; comment that there is no reason to retain *Cephalobothrium* or *Hexacanalis*, except it is "of practical value and less disruptive" to retain the former genus for species similar to *Tylocephalum* but with lateral rather than circumcortical vitellaria; comment that *Tylocephalum* Linton and *Cephalobothrium* Shipley and Hornell have never been completely described and that their true taxonomic status remains unclarified.

Butler (1987a): following Campbell and Williams's (1984) taxonomic decision, considers *Hexacanalis* Perrenoud a junior synonym of *Cephalobothrium* Shipley and Hornell.

Euzet (1994b): considers *Cephalobothrium* as a *genus inqirendum*; remarks that anatomy of *Cephalobothrium aetobatidis* Shipley and Hornell, 1906 is virtually unknown.

Rego (1985): reports *Cephalobothrium* sp. from *Raja clavata* off the Portuguese coast; notes that this is the first report of *Cephalobothrium* from *Raja* from the Atlantic; notes that compressed quadrangular scolex resembles that of *Hexacanalis*, which Yamaguti (1959) considers to be identical with *Cephalobothrium*; does not identify specimens to species because only limited observations were possible of the reproductive system.

Olson and Caira (1999): include *Cephalobothrium* cf. *aetobatidis* in a phylogenetic analysis based on 18S rDNA (GenBank No. AF124466) and Ef-1α (GenBank No. AF124808) sequence data; lecanicephalideans group in clade with Tetraphyllidea and Proteocephalidea, occasionally basal to group consisting of Cyclophyllidea, Nippotaniidea and Tetrabothriidea; tree supports placement close to, but outside of the Tetraphyllidea.

Olson *et al*. (1999): include *Cephalobothrium* cf. *aetobatidis* in phylogenetic analysis based on 18S ssrDNA sequence data; trees resulting from parsimony analyses place the species outside of the Tetraphyllidea, trees resulting from maximum likelihood place it within the Tetraphyllidea.

Kodedová *et al*. (2000): include *Cephalobothrium aetobatidis* (sequence data from Olson and Caira [1999] from GenBank) in a phylogenetic analysis of Caryophyllidea, Pseudophyllidea and Proteocephalidea based on complete 18S rRNA; *C. aetobatidis* placed basal to a group consisting of Cyclophyllidea, Nippotaniidea, Tetrabothriidea, Proteocephalidea and Tetraphyllidea.

Olson *et al.* (2001): include *Cephalobothrium* cf. *aetobatidis* in a phylogenetic analysis based on complete sequences of the SSU rDNA and partial sequence of the LSU rDNA (GenBank No. AF286927); *C.* cf. *aetobatidis* is usually placed, along with *Eniochobothrium gracile*, basal to group consisting of Cyclophyllidea, Nippotaniidea, Tetrabothriidea, Proteocephalidea and Tetraphyllidea; both lecanicephalidean taxa grouped with the Litobothriidea in some analyses.

Littlewood and Olson (2001): use GenBank sequences of the SSU rDNA for *Cephalobothrium* cf. *aetobatidis* and *Eniochobothrium gracile* (Lecanicephalidae) and *Tylocephalum* sp. (Tetragonocephalidae) for a phylogenetic analysis investigating relationships among major clades of platyhelminths; do not indicate individual placement of taxa, but investigate tree topology on a higher taxonomic level.

Caira *et al.* (2001): include *Cephalobothrium* n. sp. 1 and *Cephalobothrium* n. sp. 2 from *Aetobatus narinari* from Thailand in a phylogenetic analysis based on morphological data; the species group with the majority of lecanicephalidean taxa included; based on the taxa included, monophyly of the genus is not shown.

Remarks

Shipley and Hornell (1906) erected *Cephalobothrium* with *Cephalobothrium aetobatidis* as the type species for a single specimen from the Spotted eagle ray, *Aetobatus narinari*, taken from Dutch Bay, Ceylon (now Sri Lanka). According to Shipley and Hornell (1906), the distinguishing feature of this worm is its possession of a "large, median, circular sucker [that] takes up most of the head," (p. 44) controlled by longitudinal muscles. The only other features described relate to the overall habitus of the worm and its proglottids. The anatomy of *Cephalobothrium* is basically unknown. Shipley and Hornell (1906) did not state the place of deposition for this single specimen. It is therefore almost certain that type material of the type species of *Cephalobothrium* does not exist. *Cephalobothrium aetobatidis* has subsequently been reported, but not redescribed, from the type host *A. narinari* (Southwell 1912; Yamaguti 1968) and from other host species (from *Pristis cuspidatus* by Southwell [1912]; from *Pteroplatea micrura* and *Trygon kuhlii* by Southwell [1927]). However, these records are suspect, considering the lack of information on the anatomy of this cestode species.

The taxonomic history of *Cephalobothrium* is rather complex, closely tied to that of *Hexacanalis* Perrenoud, 1931 and *Tylocephalum*, and unnecessarily complicated by Pintner's (1928) work on this complex of taxa, which, while providing valuable information and details, is difficult to fully comprehend. A simplified overview of the taxonomic history of *Cephalobothrium* is presented here. Although the anatomy of the type species is unknown and therefore the concept of the genus inadequately defined, a relatively large number of species have been described in this genus (see Appendix 2). In addition, many authors have addressed the identity and systematic position of this genus over the last century. In 1928, Pintner created the family Cephalobothriidae for *Cephalobothrium*, *Adelobothrium,* and several species of *Tylocephalum*. Initially, *Cephalobothrium* was considered to be a valid genus in the family Lecanicephalidae Braun, 1900 (*e.g.*, Meggitt 1924; Southwell 1925; Poche 1926), and after 1928, a valid genus in the family Cephalobothriidae (*e.g.*, Fuhrmann 1931; Hyman 1951; Euzet 1959; Joyeux and Baer 1961). Yamaguti (1959), influenced by Pintner's (1928) comments on *Cephalobothrium*, suggested the genus be provisionally retained, pending further investigation. More recently, Campbell and Williams (1984) commented that *Cephalobothrium* should probably not be considered to be valid; according to Campbell and Williams (1984), the only feature distinguishing *Cephalobothrium* from *Tylocephalum* are lateral, rather than circumcortical vitelline follicles. Euzet (1994b) considered *Cephalobothrium* to be a *genus inquirendum*, again, because of the lack of our knowledge about the internal anatomy.

A thorough description of *Cephalobothrium aetobatidis* based on new material collected from the type host, ideally from the type locality, is imperative to conclusively determine the identity of the genus. New collections conducted over the course of this study included tapeworms from the Spotted eagle ray, *Aetobatus narinari*, from the Gulf of Thailand and from Fog Bay in the Northern Territory of Australia. Among the cestodes removed from this host were a few specimens that, when examined with SEM, were more or less reminiscent of the illustrations provided by Shipley and Hornell (1906), accompanying the original description of *C. aetobatidis*, and could be considered to be putative specimens of *Cephalobothrium* (Fig. 5E a and b). Until additional material is available for detailed study, *Cephalobothrium* is considered here to be a *genus inquirendum*.

FLAPOCEPHALUS Deshmukh, 1979

Taxonomic status: *Genus inquirendum*.
Synonyms: None.
Type species: *Flapocephalus trygonis* Deshmukh, 1979.
Species inquirendae: *Flapocephalus saurashtri* Shinde and Deshmukh, 1979.
Etymology: *Flapo-*, "due to the presence of two distinct flaps representing the anterior region of the scolex" (Deshmukh, 1979, p. 264); *kephale*, Gr., head.

Flapocephalus trygonis Deshmukh, 1979
TYPE SPECIES

Taxonomic status: *Species inquirendum*.
Synonyms: None.
Type host: *Trygon sephen* (Forsskål, 1775) (= *Pastinachus sephen* [Forsskål, 1775] ?), Cowtail stingray (Dasyatidae, Myliobatiformes).
Additional hosts: None.
Site of infection: Spiral intestine.
Type locality: Ratnagiri, India.
Number of specimens on which the original description was based: 11.
Type specimens: Deshmukh (1979) indicated that specimens were deposited in the Laboratory of Cestodology, Department of Zoology, Marathwada University, Aurangabad, (M.S.), India.
Voucher specimens: None.
Material examined: Four putative specimens of *Flapocephalus* sp. (in the author's personal collection).
Etymology: *Trygonis*, referring to the type host of the species, *Trygon sephen*.

Chronology

Deshmukh (1979): erects the genus *Flapocephalus* with *F. trygonis* as the type species; distinguishes the new genus from all other lecanicephalidean genera based on scolex morphology, and from *Tylocephalum* and *Lecanicephalum* also based on proglottid morphology.

Campbell and Williams (1984): suspect that *Flapocephalus saurashtrii* [sic] Shinde and Deshmukh, 1979 is actually a member of the genus *Lecanicephalum* since differences between the two genera are not evident; consider status of type species, *F. trygonis* Deshmukh, 1979, as questionable since type material is not available to show that compression of the scolex created the "flaps" [wording according to Deshmukh (1979)].

Schmidt (1986): treats *Flapocephalus* Deshmukh, 1979 in the family Lecanicephalidae, order Lecanicephalidea; recognizes two valid species, *F. trygonis* and *F. saurashtri*.

Euzet (1994b): states that *Flapocephalus* should be suppressed; treats the genus as a *genus inquirendum*; notes the lecanicephalidean scolex (possibly *Lecanicephalum*-type) but tetraphyllidean proglottid anatomy.

Remarks

Flapocephalus is one of the more recently described genera of lecanicephalideans. The type specimens of *Flapocephalus trygonis*, the type of the genus, were collected from a Cowtail stingray, *Pastinachus sephen* (as *Trygon sephen*), at Ratnagiri, India (Deshmukh 1979). The most conspicuous character of the genus as it was described by Deshmukh, is that the anterior region of the scolex is in the form of two "semicircular flaps, placed one above the other, *i.e.*, one is ventral and another is dorsal in position" (Deshmukh 1979; pp. 261-262). The proglottid anatomy of this taxon is reported to be not typically lecanicephalidean; the vagina opens into the genital atrium anterior to the cirrus sac, and a conspicuous, posteriorly originating vas deferens is lacking. Deshmukh (1979) stated that the type specimens were deposited in the Laboratory of Cestodology, Department of Zoology, Marathwada University, Aurangabad, (M.S.), India, from which material has been unavailable. Since its original description, only three authors have addressed the taxonomic position of *Flapocephalus*. These authors differed in their opinions: Campbell and Williams (1984) considered *Flapocephalus* to be indistinguishable from *Lecanicephalum*, Schmidt (1986) considered it to be valid, and Euzet (1994b) treated it as a *genus inquirendum*.

New collections conducted over the course of this study included a specimen of the type host of *F. trygonis*, the Cowtail stingray (*Pastinachus sephen*), collected from Fog Bay in the Northern Territory of Australia. Among the cestodes removed from this host were a few specimens with a scolex conspicuously reminiscent of those described by Deshmukh (1979) (Fig. 5B) when examined with light microscopy. Scanning electron microscopy suggests that these are not two separate flaps, but rather a folded circular disc. The proglottid morphology of these specimens is clearly lecanicephalidean (vagina opens into the genital atrium posterior to the cirrus sac, a vas deferens extending from the level of the ovary anteriorly, the vitelline follicles are large and present posterior to the ovary), unlike the morphology reported for *F. trygonis*. Curiously, the second species placed in the genus *Flapocephalus*, *F. saurashtri*, was described by Shinde and Deshmukh (1979a) as possessing a vagina that opens posterior to the cirrus sac in the genital atrium, the usual lecanicephalidean condition.

If the new material is indeed representative of *Flapocephalus*, several observations can be made. Among lecanicephalidean genera, *Flapocephalus* most closely resembles the genus *Lecanicephalum*, especially in proglottid anatomy. However, the genera seem to differ in their scolex anatomy. The putative specimens of *Flapocephalus* appear to lack the conspicuous circular muscle bundles of the apical modification of the scolex proper and the apical organ characteristic for *Lecanicephalum*. In addition, it remains to be determined whether the apical organ of *Flapocephalus* can be fully retracted into the scolex proper, as is the case in *Lecanicephalum*. Although the genus *Lecanicephalum* was described over 100 years ago and is the type of the order, it contained only two species prior to this study; the range of morphological variation in *Lecanicephalum* is therefore far from fully understood. Given the new data, *Flapocephalus* should be retained as a genus independent of *Lecanicephalum*, but considered as a *genus inquirendum*, at least until additional material can be studied in detail.

HEXACANALIS **Perrenoud, 1931**

Taxonomic status: *Genus inquirendum*.

Synonyms: None.

Type species: *Hexacanalis abruptus* (Southwell, 1911) Perrenoud, 1931.

Species inquriendae: *Hexacanalis indirajii* Murlidhar, 1986; *H. sasoonensis* Srivastava and Capoor, 1980; *H. smythii* Murlidhar, Shinde and Jadhav, 1986; *H. thapari* Shinde, Jadhav and Jadhav, 1992; *H. yamagutii* Shinde and Deshmukh, 1979; *H. zugeis* Shinde and Deshmukh, 1979.

Nomina nuda: *Hexacanalis sephanensis* in Mohekar *et al.* (2002).

Etymology: *Hex*, Gr., six; *canalis*, L., channel, water-pipe.

Hexacanalis abruptus **(Southwell, 1911) Perrenoud, 1931**

TYPE SPECIES

Taxonomic status: *Species inquirendum*.

Synonyms: *Cephalobothrium abruptum* Southwell, 1911; *Lecanicephalum abruptum* (Southwell, 1911) Fuhrmann, 1931?.

Type host: *Pteroplatea micrura* (Bloch and Schneider, 1801) (= *Gymnura micrura* [Bloch and Schneider, 1801] ?), Smooth butterfly ray (Gymnuridae, Myliobatiformes).

Additional hosts: None.

Site of infection: Spiral intestine.

Type locality: Portugal Bay, Ceylon (now Sri Lanka).

Additional localities: None.

Number of specimens on which the original description was based: 87.

Type specimens: Colombo Museum, Colombo, Sri Lanka (now at the Station Méditerranéene de l'Environment Littoral, Université Montpellier II in Sète, France).

Voucher specimens (unverified): (see Appendix 4).

Material examined: A few putative specimens of *Hexacanalis* (or *Cephalobothrium*) sp. (in the author's personal collection).

Etymology: *Abruptus*, L., broken off, separated.

Unverified records: *Trygon kuhli* [sic] and *Pteroplatea micrura* from Ceylon (see Southwell 1912); *Pteroplatea micrura* from Ceylon (see Southwell 1925); *Trygon kuhli* [sic] from Pearl Banks, Ceylon (see Southwell 1927).

Chronology

Southwell (1911): describes the new species *Cephalobothrium abruptum*; reiterates Shipley and Hornell's diagnosis of the genus; distinguishes the species from *C. aetobatidis* based on overall size and shape of head [scolex] and from *C. variabile* based on the presence of only two suckers in the latter species.

Jameson (1912): notes that one is likely that adult stages of *Tylocephalum ludificans* and *T. minus*, described from larval stages, will be found among members of *Tylocephalum*, or allied types described as new genera, occurring in oyster-eating elasmobranchs, such as those described by Southwell (*Cephalobothrium abruptum and C. variabile*).

Southwell (1912): reports collecting material of *Cephalobothrium abruptum* from *Trygon kuhli* and *Pteroplatea micrura* from Ceylon.

Stiles and Hassall (1912): *Cephalobothrium* Shipley and Hornell, 1906; *C. abruptum* Southwell, 1911 (in *Pteroplatea micrura*, Portugal Bay); *C. aetobatidis* Shipley and Hornell, 1906 (in *Aetobatis* [sic] *narinari*, Dutch Bay, Ceylon); *C. aetobatidis* Shipley and Hornell, 1906 (apparently misprint, see *aetobatidis*); *C. variabile* Southwell, 1911 (in *Pristis cuspidatus*, Portugal Bay).

Southwell (1925): reports collecting several new specimens of *Cephalobothrium abruptum* from *Pteroplatea micrura* from Ceylon; redescribes the species and illustrates proglottid cross-section, longitudinal sections of mature proglottids and 'ripe' proglottids.

Southwell (1927): reports newly collected material from *Trygon kuhli* from Pearl Banks, Ceylon (very large number of specimens); classification follows Southwell (1925).

Woodland (1927): proposes that the "lecanicephalid" genus *Cephalobothrium* (including the species *Cephalobothrium abruptum* and *C. variabile*) be included in the family Phyllobothriidae, order Tetraphyllidea, based on the disposition of longitudinal muscle bundles and marginal vitellaria; comments that in *Tylocephalum* (and *Balanobothrium* and *Cephalobothrium*) the internal organs lie internal to the longitudinal muscles of the strobila.

Southwell (1930): lists *Cephalobothrium abruptum* from *Pteroplatea micrura* and *Dasybatus* [sic] *kuhlii*, after Southwell (1911 and 1927); only change from Southwell (1925) is that he notes that eggs are unknown.

Fuhrmann (1931): considers *Cephalobohrium ex parte* to be a junior synonym of *Lecanicephalum* (along with *Tylocephalum ex parte* and *Tetragonocephalum*) in the family Lecanicephalidae Braun (syn. Gamobothriidae Linton), order Tetraphyllidea, while *Cephalobothrium* (along with *Tylocephalum* [*ex parte*] and *Discobothrium*) is considered to be a valid genus in the family Cephalobothriidae (Pintner); considers *Cephalobothrium abruptum* to be a species of *Lecanicephalum* and creates the new combination *Lecanicephalum abruptum*; uses this combination, *L. abruptum* (Southwell), when illustrating the scolex (p. 185 and 213); refers to specimens of sections as cotypes; provides new illustrations of the scolex, of cross sections of the proglottids, and of longitudinal sections of the scolex for *L. abruptum*.

Perrenoud (1931): redescribes *Cephalobothrium abruptum* based on sectioned material only, given to him by Fuhrmann; creates a new genus for this species, *Hexacanalis*, and transfers the species, creating *Hexacanalis abruptus*; places *Hexacanalis* in the family Cephalobothriidae, along side *Cephalobothrium*; according to Campbell and Williams, Perrenoud creates *Hexacanalis* and designates *C. abruptum* as the type species; distinguishes *C. abruptum* from *C. aetobatidis* because it parasitizes a different species of host, possesses less craspedote proglottids, possesses a non-glandular and quadrangular scolex in cross-section, and, with six excretory vessels visible in cross-section, possesses a unique osmoregulatory system.

Wardle and McLeod (1952): recognize *Hexacanalis*

Perrenoud, 1931 in the family Cephalobothriidae, order Lecanicephala, with *H. abruptus* Southwell, 1911 as the type species; comment that *H. abruptus* was reported by Southwell (1911) (as *C. abruptum*, *C. variabile*) in *Pteroplatea micrura*.

Yamaguti (1959): considers *Hexacanalis* Perrenoud, 1931 to be a valid genus with *H. abruptus* (Southwell, 1911) (syn. *Cephalobothrium abruptus* Southwell) as the type species in *Pteroplatea micrura* from Ceylon and the Trivandrum Coast; recognizes one additional species (*H. variabilis* [Southwell, 1911]); comments that *Hexacanalis* might be identical with *Cephalobothrium*, once the latter is studied in more detail.

Joyeux and Baer (1961): classify *Cephalobothrium* (along with *Adelobothrium*, *Hexacanalis*, and *Tetragonocephalum*) in the family Cephalobothriidae, superfamily Lecanicephaloidea, order Tetraphyllidea; illustrate cross-section through *Cephalobothrium abruptum* from *Pteroplatea micrura* (after Fuhrmann).

Schmidt (1970): presents key to the genera of tapeworms; recognizes *Hexacanalis* (along with *Polypocephalus*, *Calycobothrium*, *Staurobothrium*, *Tetragonicephalum* [sic], and *Lecanicephalum*) in the family Lecanicephalidae, order Lecanicephalidea Baylis, 1920; provides diagnosis for each genus and names the type species.

Zaidi and Khan (1976): suppress the genus *Hexacanalis* in favor of *Cephalobothrium*; transfer the species belonging to *Tylocephalum* group "B" in Pintner (1928) to the genus *Cephalobothrium* (*i.e.*, *Cephalobothrium*, *Tylocephalum dierama*, *T. kuhli*, *T. ludificans*, *T. yorkei*, *T. translucens*, *T. aetiobatidis*, *Adelobothrium*, *Tylocephalum pingue* ?).

Campbell and Williams (1984): present the history of *Cephalobothrium* as it relates to the erection of *Hexacanalis* by Perrenoud (1931); note that *Hexacanalis* was created by Perrenoud (1931) after examination of sections of *C. abruptum* Southwell, 1911 (no whole mounts were examined); state that Perrenoud (1931) created *Hexacanalis* and designated *C. abruptum* as the type species, distinguishing it from *C. aetobatidis* because of difference in host association, in proglottid overlap, in scolex shape and histology, and a unique osmoregulatory system; comment that nonglandularity of the scolex and six osmoregulatory ducts does not warrant creation of a new genus, especially since the internal anatomy of *Cephalobothrium* was not known; suggest that *Hexacanalis* should be considered a synonym of the enigmatic *Cephalobothrium*; note, in addition, that there is no reason to retain *Cephalobothrium* or *Hexacanalis* except it is "of practical value and less disruptive" for species similar to *Tylocephalum* but with lateral, rather than circumcortical vitellaria.

Rego (1985): notes that compressed quadrangular scolex of specimens of *Cephalobothrium* sp. he collected, resembles that of *Hexacanalis*, which Yamaguti (1959) considers to be identical with *Cephalobothrium*.

Schmidt (1986): considers *Hexacanalis* Perrenoud, 1931 to be a valid genus in the family Lecanicephalidae, order Lecanicephalidea with *H. abruptus* (Southwell, 1911) Perrenoud, 1931 as the type species; recognizes one species additional (*H. variabilis*).

Butler (1987a): following Campbell and Williams's (1984) taxonomic decision; notes that *Hexacanalis* Perrenoud should be considered a junior synonym of *Cephalobothrium* Shipley and Hornell.

Brooks and McLennan (1993): present a tree for the order Lecanicephaliformes Baylis, 1920; based on that tree they recognize *Hexacanalis* Perrenoud, 1931 *sedis mutabilis*, *incertae sedis* (along with *Calycobothrium* Southwell 1911, *Discobothrium* van Beneden 1871, *Echeneibothrium* van Beneden, 1850, *Lecanicephalum* Linton, 1890, and *Polypocephalus* Braun, 1878) in the subfamily Lecanicephalinae Braun, 1900 *incertae sedis*, family Lecanicephalidae Braun, 1900, order Lecanicephaliformes Baylis, 1920.

Euzet (1994b): assigns *Cephalobothrium abruptum* Southwell, 1911 to the genus *Lecanicephalum* because of its scolex morphology and proglottid anatomy that is consistent with *Lecanicephalum*; concludes that since *C. abruptum* is the type species of *Hexacanalis*, considers *Hexacanalis* to be a junior synonym of *Lecanicephalum*.

Remarks

Hexacanalis was created by Perrenoud (1931) after examination of sectioned material of *Cephalobothrium abruptum*. He considered this species so significantly different from the type species of *Cephalobothrium*, *C. aetobatidis*, to warrant independent generic status. *Cephalobothrium abruptum* was described 20 years earlier by Southwell (1911), based on a large number of specimens. Southwell (1911) said to have deposited type material for this species at the Colombo Museum, Colombo, Sri Lanka. Currently, the type material of *C. abruptum* appears to exist in Southwell's collection at the Station Méditerranéene de l'Environment Littoral, Université Montpellier II in Sète, France. Because the identity of the type species of *Cephalobothrium*, *C. aetobatidis*, is basically unknown, the erection of *Hexacanalis* is highly suspect. Once a stable concept of *Cephalobothrium* has been established, evaluation of this type material will reveal whether it is distinct from *Cephalobothrium*.

Fuhrmann (1931) and Euzet (1994b) considered *C. abruptum* to be a member of the genus *Lecanicephalum*. Consequently, Euzet (1994b) considered *Hexacanalis* to be a junior synonym of *Lecanicephalum*. The morphology of the scolex (a large protrusible sucker rather than a circular muscular sheet) (see Fig. 5E) and the proglottids (obviously craspedote and barely longer than wide rather than weakly craspedote and clearly longer than wide) of *C. abruptum* as described by Southwell (1911) does not agree with the concept of *Lecanicephalum* and should not be considered a species of *Lecanicephalum*. *Hexacanalis* is treated here as a *genus inquirendum*.

One species name, *Hexacanalis sephanensis*, is considered to be a *nomen nudum*. This name was used only in a list of cestode parasites collected from the west coast of Maharashtra, India by Mohekar *et al.* (2002); no authority or literature citation is given. It appears that this species was never described. Therefore, the name *Hexacanalis sephanensis* is not available.

KYSTOCEPHALUS
Shipley and Hornell, 1906

Taxonomic status: *Genus inquirendum*.

Synonyms: None.

Type and only species: *Kystocephalus translucens* Shipley and Hornell, 1906.

Etymology: *Kystis*, -eos, Gr., bladder, sac, cell; *kephale*, Gr., head.

Kystocephalus translucens
Shipley and Hornell, 1906
TYPE SPECIES

Taxonomic status: *Species inquirendum*.

Synonyms: *Tylocephalum translucens* (Shipley and Hornell, 1906) Southwell, 1925; *Lecanicephalum translucens* (Shipley and Hornell, 1906) Schmidt, 1986.

Type host: *Aetobatus narinari* (Euphrasen, 1790) (as *Aetobatis* [sic] *narinari*), Spotted eagle ray (Myliobatidae, Myliobatiformes).

Additional hosts: None.

Site of infection: Spiral intestine.

Type locality: Gulf of Manaar, Ceylon (now Sri Lanka).

Additional localities: None.

Number of specimens on which the original description was based: Two.

Type specimens: Not indicated in original description.

Voucher specimens: None.

Material examined: Two putative specimens of *Kystocephalus* sp. (in the author's personal collection).

Etymology: *Translucens*, presumably referring to the transparent nature of the apical organ.

Chronology

Shipley and Hornell (1906): erect the genus *Kystocephalus* with *K. translucens* as the type species for two specimens from *Aetobatis* [sic] *narinari* from Ceylon; provide a superficial description of the species; do not describe proglottid anatomy; note that this genus is similar to *Tylocephalum* and *Cephalobothrium* in form, but possesses quite unique features [do not state these features].

Stiles and Hassall (1912): *Kystocephalus* Shipley and Hornell, 1906; *K. translucens* Shipley and Hornell, 1906 (in *Aetiobatis* [sic] *narinari*, Coast of Ceylon)

Jameson (1912): notes that one is likely that adult stages of *Tylocephalum ludificans* and *T. minus*, described from larval stages, will be found among members of *Tylocephalum*, or allied types described as new genera, occurring in oyster-eating elasmobranchs, such as, *Kystocephalus translucens*.

Southwell (1925): considers *Kystocephalus* to be a junior synonym of *Tylocephalum*; recognizes *Tylocephalum translucens* (syn. *Kystocephalus translucens*); quotes Shipley and Hornell's description of the species; *T. translucens* appears distinct in the genus *Tylocephalum* and is formally distinguished from *T. dierama* and *T. uarnak*; states that anatomy of *T. translucens* is not known.

Meggitt (1924): considers *Kystocephalus* Shipley and Hornell, 1906 to be a junior synonym of *Adelobothrium* Shipley, 1900 in the family Lecanicephalidae, order Tetraphyllidea.

Southwell (1930): considers *Kystocephalus* to be a junior synonym of *Tylocephalum*; reiterates text of Southwell (1925).

Yamaguti (1959): considers *Kystocephalus* Shipley and Hornell, 1906 to be a junior synonym of *Tylocephalum* Linton, 1890; eight species are recognized in *Tylocephalum*, among them *T. translucens* (Shipley and Hornell, 1906), syn. *Kystocephalus translu*cens Shipley and Hornell.

Schmidt (1986): considers *Kystocephalus* Shipley and Hornell, 1906 to be a junior synonym of *Lecanicephalum* Linton, 1890; recognizes 19 species of *Lecanicephalum*, including the new combination *Lecanicephalum translucens* (Shipley and Hornell, 1906) (syn. *Kystocephalus translucens* Shipley and Hornell, 1906 and *Tylocephalum translucens* [Shipley and Hornell, 1906] Yamaguti, 1959).

Euzet (1994b): considers *Kystocephalus* to be a *genus inquirendum*; notes that *K. translucens* was described as having a myzorhynchus covered by a membrane; this could be either *Tetragonocephalum* with gut epithelium still attached or *Lecanicephalum* with "sucker everted."

Remarks

Kystocephalus was erected by Shipley and Hornell (1906) for two specimens collected from the Spotted eagle ray, *Aetobatus narinari*, from Ceylon (now Sri Lanka). Their description of this new taxon is brief and only general body features are presented. Identifiable characteristic features are the form of the myzorhynchus (*i.e.*, "surrounded and half enclosed in a circular membrane", p. 46), lip-like projections on the genital pore and the conspicuously craspedote nature of the proglottids. Several authors have formally addressed the status of this genus or its type species *K. translucens*. *Kystocephalus* has, at one time or another, been considered a synonym of three different genera. Southwell (1925, 1930) and Yamaguti (1959) considered it to be a junior synonym of *Tylocephalum*, Meggitt (1924) a junior synonym of *Adelobothrium*, and Schmidt (1986) a junior synonym of *Lecanicephalum*. Moreover, Euzet (1994b) suggested that, depending on one's interpretation of the morphology of the myzorhynchus, *Kystocephalus* could be identical with either *Tetragonocephalum* or *Lecanicephalum*. There has been no indication of type specimens in any of the literature referring to the genus or species. Thus, much of this confusion is likely the result of the total absence of study material. Because this taxon has not been recollected since its original description, most of the taxonomic decisions given above were based only on the brief description and illustrations originally provided by Shipley and Hornell (1906).

New collections conducted as part of this study led to the discovery of a mere two specimens of a cestode remarkably consistent with the original illustrations and brief description of *Kystocephalus* (Fig. 5C), from the type host *Aetobatus narinari* off Darwin, Northern Territory, Australia. These specimens suggest that the morphology of *Kystocephalus* may be distinct. Additional material is needed to confirm the true identity of the genus. However, this discovery, 95 years after the original description, speaks of the unique nature of this cestode. *Kystocephalus* should not be considered a synonym of any other lecanicephalidean genus at this time, and is considered as a *genus inquirendum* here.

SEPHENICEPHALUM Shinde, Sarwade and Jadhav, 1980 or 1982 [?]

Taxonomic status: *Genus inquirendum*.

Synonyms: None.

Type species: *Sephenicephalum maharashtrii* Shinde, Sarwade and Jadhav, 1980 or 1982 [?].

Species inquirendae: *Sephenicephalum bombayensis* Hiware, Jadhav and Bhosale, 1994; *S. dnyandevi* Bhagwan and Shinde, 2002.

Nomina nuda: *Sephenicephalum marathwadensis* Pawar, 1983.

Etymology: *Sepheni-*, presumably referring to the type host of *S. maharashtrii*, *Trygon sephen*; *kephale*, Gr., head.

Sephenicephalum maharashtrii Shinde, Sarwade and Jadhav, 1980 or 1982 [?]

TYPE SPECIES

Taxonomic status: *Species inquirendum*.

Synonyms: ?

Type host: [*Trygon sephen*].

Additional hosts: ?

Site of infection: [Spiral intestine].

Type locality: [Ratnagiri, India].

Number of specimens on which the original description was based: ?

Type specimens: ?

Voucher specimens: ?

Material examined: None.

Etymology: *Maharashtrii*, presumably referring to the state or region in India from which the type host was collected.

Chronology

Shinde, Sarwade & Jadhav (1980 or 1982 [?]): [Hiware *et al.* (1993) and Bhagwan & Shinde (2002) state that *Sephenicephalum* was erected by Shinde *et al.* from *Trygon sephen* from Ratnagiri, India; Bhagwan & Shinde (2002) give *S. maharashtrii* as the type species.]

Hiware *et al.* (1993): describe the new species *Sephenicephallum* [sic] *bombayensis*; distinguish *S. bombayensis* from *S. maharashtrii*.

Bhagwan & Shinde (2002): describe the new species *Sephenicephalum dnyandevi*; mention *S. marathwadensis* as a species described by Pawar in 1983; distinguish *S. dnyandevi* from *S. maharahtrii* [sic].

Remarks

Determination of the status of *Sephenicephalum* is difficult. According to Hiware *et al.* (1993), "*Sephenicphallum* [sic] is erected by Shinde *et al.* (1980) from a marine fish, *Trygon sephen* Muller and Henley [sic] (collected at Ratnagiri, West coast of India)" (pg. 174). In the paragraph that follows they state that *S. bombayensis* "comes closer to *S. maharashtrii* Shine *et al.* 1982" (Hiware *et al.* 1993, pg. 174) which presumably is the type species. The only paper cited in Hiware *et al.* (1993) is "Shinde *et al.* (1980)" which is the description of the new genus and species in the Marathwada University Journal of Sciences. No volume, issue, or page numbers are given. Bhagwan and Shinde (2002) stated in their discussion that the "genus *Sephenicephalum* is erected by Shinde *et al.* in 1982 as type species of *Sephenicephalum maharashtrii* from ... *Trygon sephen* ... collected at Ratnagiri (India)" (pg. 199). They also stated that "Pawar (1983) added few more species namely, *S. marathwadensis* from *Narcine brunnea*' (Bhagwan and Shinde 2002, pg. 199). Neither "Shinde *et al.* (1982)" nor "Pawar (1983)" is cited. Reference to *S. maharashtrii* or *S. marathwadensis* could not be found in any other publication or database. Neither Shinde *et al.* (1980 or 1982), nor Pawar (1983), was obtainable. Based on the limited information available, the genus *Sephenicephalum* and *S. maharashtrii* are considered to be a *genus inquirendum* and a *species inquirendum*, respectively. *Sephenicephalum marathwadensis* is considered to be a *nomen nudum*, since it appears that this species were never actually described. Based on the scolex and proglottid morphology illustrated in the original descriptions, *Sephenicephalum bombayensis* and *S. dnyandevi* might be more appropriately placed in a genus other than *Sephenicephalum*. They are both described as possessing tentacles on their scolex, superficially similar to tentacles in species of *Polypocephalus*, however the proglottid morphology is not consistent with species in that genus. To determine the correct placement of these species, additional information, ideally from newly collected material, is imperative. Consequently, *S. bombanyensis* and *S. dnyandevi* are considered to be *species inquirendae*.

STAUROBOTHRIUM
Shipley and Hornell, 1905

Taxonomic status: *Genus inquirendum*.
Synonyms: None.
Type and only species: *Staurobothrium aetobatidis* Shipley and Hornell, 1905.
Etymology: *Stauros*, Gr., cross; *bothrion*, Gr., diminutive of *bothros*, trench, pit, trough.

Staurobothrium aetobatidis
Shipley and Hornell, 1905
TYPE SPECIES
(Fig. 7A and B)

Taxonomic status: *Species inquirendum*.
Synonyms: None.
Type host: *Aetobatus narinari* (Euphrasen, 1790) (as *Aetobatis* [sic] *narinari*), Spotted eagle ray (Myliobatidae, Myliobatiformes).
Additional hosts: None.
Site of infection: Spiral intestine.
Type locality: Marichchukaddi, Ceylon (now Sri Lanka).
Number of specimens on which the original description was based: “a considerable number” (Shipley and Hornell, 1905, p. 49).
Type specimens: Not indicated in original description.
Voucher specimens: Two slides from Southwell’s collection at the Station Méditerranéene de l’Environment Littoral, Université Montpellier II in Sète, France.
Material examined: Two slides from Southwell’s collection at the Station Méditerranéene de l’Environment Littoral, Université Montpellier II in Sète, France.
Etymology: *Aetobatidis*, referring to the type host of the species, *Aetobatus narinari*.
Unverified records: *Aetobatis* [sic] *narinari* from Ceylon Pearl Banks (see Southwell 1925).

Chronology

Shipley and Hornell (1905): erect the genus *Staurobothrium* with *S. aetiobatidis* as the type species for a “considerable number” of specimens taken from *Aetobatis* [sic] *narinari* from Marichchukaddi, Ceylon; a general description of the worm is given, but proglottid anatomy is not described; indicate only that no existing figures or descriptions were found corresponding to this species, but this taxon is not formally compared to or distinguished from any other genera or species of cestodes; comment that *Staurobothrium* superficially resembles *Cylindrophorus* (but without hooks), *Calyptrobothrium* (but without terminal sucker), but place it within the Phyllobothriidae, close to *Phyllobothrium*.

Stiles and Hassall (1912): *Staurobothrium* Shipley and Hornell, 1905 (Phyllobothriidae); *S. aetiobatidis* Shipley and Hornell, 1905 (in *Aetiobatis* [sic] *narinari*; Marichchukaddi, Ceylon).

Southwell (1925): presents a detailed description of *S. aetiobatidis* and illustrates the proglottids; considers *Staurobothrium* to be intermediate between the order Cyclophyllidea and the order Tetraphyllidea; quotes Shipley and Hornell’s diagnosis of *Staurobothrium* and description of *S. aetiobatidis*; notes that two new specimens had been collected from *Aetobatis* [sic] *narinari* from the Ceylon Pearl Banks and, “through the kindness of Sir Arthur Shipley”, are compared to the type species.

Poche (1926): considers *Staurobothrium* in the family Phyllobothriidae, suborder Phyllobothriinea *nom. nov.*, order Taeniidea *nom. nov.*, along with *Hornellobothrium* and 22 tetraphyllidean genera.

Southwell (1930): treats *Staurobothrium* Shipley and Hornell, 1905 in the family Lecanicephalidae, superfamily Lecanicephaloidea, order Eucestoda; does not consider *Staurobothrium* to be intermediate between Cyclophyllidea and Tetraphyllidea; reiterates text of Southwell (1925).

Fuhrmann (1931): classifies lecanicephalideans in two of seven families in the order Tetraphyllidea, the family Lecanicephalidae Braun (syn. Gamobothriidae Linton) and the family Cephalobothriidae (Pintner); considers *Staurobothrium* not to belong to either of these lecanicephalidean families, but to be uncertain and not sufficiently known, but a very interesting genus in the Tetraphyllidea.

Wardle and McLeod (1952): treat *Staurobothrium* Shipley and Hornell, 1905 in the family Cephalobothriidae, order Lecanicephala.

Yamaguti (1959): treats *Staurobothrium* Shipley and Hornell, 1905 as a *genus incertae sedis* in the order Lecanicephalidea.

Joyeux and Baer (1961): consider *Staurobothrium* to be a genus in the subfamily Phyllobothriinae, family Phyllobothriidae, superfamily Phyllobothrioidea, order Tetraphyllidea (all other lecanicephalidean genera are in the superfamily Lecanicephaloidea).

Schmidt (1970): treats *Staurobothrium* in the family Lecanicephalidae, order Lecanicephalidea.

Schmidt (1986): treats *Staurobothrium* Shipley and Hornell, 1905 in the family Lecanicephalidae, order Lecanicephalidea; includes key to genera in the order.

Brooks and McLennan (1993): present a tree for the order Lecanicephaliformes Baylis, 1920; based on that tree they recognize *Staurobothrium* Shipley and Hornell, 1905 (along with *Adelobothrium* Shipley, *Cathetocephalus* Dailey and Overstreet, 1973, *Tetragonocephalum* Shipley and Hornell, 1905, *Disculiceps* Joyeux and Baer, 1935, and *Prosobothrium* Cohn, 1902) in the subfamily Disculicipinae Joyeux and Baer, 1935, family Lecanicephalidae Braun, 1900, order Lecanicephaliformes Baylis, 1920.

Euzet (1994b): treats *Staurobothrium* as a *genus incertae sedis* in the order Lecanicephalidea; notes lecanicephalidean proglottid anatomy, but with four pedunculated, round bothridia and an apical papilla (that was apparently not seen by Southwell [1925]); notes that scolex morphology might justify establishment of a new family.

Remarks

In 1905, Shipley and Hornell erected the new genus *Staurobothrium* for several worms collected from *Aetobatus narinari* in Ceylon (now Sri Lanka). They named the type species *Staurobothrium aetiobatidis*. The most characteristic feature of these worms is the relatively large scolex, which is remarkably cruciform in shape and which possesses an apical structure in form of a "slight papilla with rings around it" (p. 50). In addition, *S. aetiobatidis* was described as possessing craspedote proglottids and a follicular uterus. Southwell (1925) reported collecting two specimens of this species from the type host from the Pearl Banks of Ceylon, which he was able to compare with the type species. He described the scolex and proglottids of *S. aetiobatidis* in some detail and provided the first illustrations of two proglottids. He did, however, not observe the "terminal papilla" on the scolex (Southwell 1925, p. 333). Although the accuracy of the description of the vagina as being "anterior to that of the vas deferens" and "dialating into a very large muscular receptaculum seminis" (Southwell 1925, p. 334) are doubtful, the anatomy of the proglottid does suggest a lecanicephalidean affiliation. This genus has not been reported since Southwell's account.

Most authors considered *Staurobothrium* a valid lecanicephalidean genus (see chronology). Yamaguti (1959) and Euzet (1994b) considered it a *genus incertae sedis*, while Joyeux and Baer (1961) placed it among tetraphyllidean taxa.

Examination of part of Southwell's collection at the Station Méditerranéene de l'Environment Littoral, Université Montpellier II in Sète, France, revealed the presence of two slides of *S. aetiobatidis*, one with four scolices, the other with the four corresponding strobilae. A strobila and a scolex each are illustrated in Figure 7A and B, respectively. The morphology of these scolices agrees perfectly with the description of *S. aetiobatidis* provided by Shipley and Hornell (1905), and the presence an apical structure in the form of a small, inconspicuous papilla on the apex is confirmed. Three of the four strobilae are immature and provide no information of the reproductive anatomy. Mature proglottids are present on the fourth strobila (Fig. 7A). However, owing to the poor condition of this specimen, only the following general comments can be made concerning the proglottid anatomy: The testes are distributed

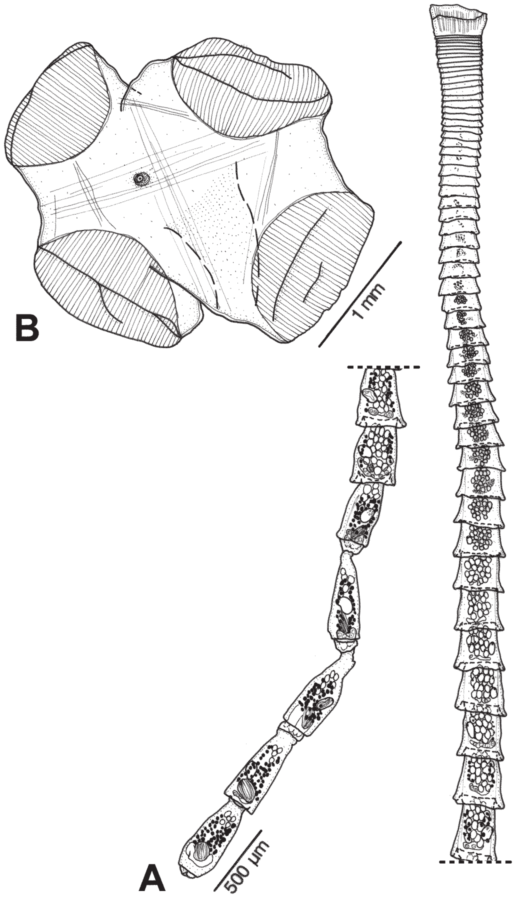


Fig. 7. A-B. Line drawings of *Staurobothrium aetobatidis* Shipley and Hornell, 1905 (vouchers, see Appendix IV). A. Strobila. B. Scolex.

in a single field anterior to the ovary. The vitelline follicles are lateral, but encroach on the midline of the proglottid. The vas deferens originates at the level of the ovary and forms an extensive external seminal vesicle. The position of the vagina in relation to the cirrus sac could not be determined. In combination, the presence of an apical structure on the scolex and the preliminary available information on the anatomy of the proglottids support the lecanicephalidean identity of *Staurobothrium*. Unfortunately, new material is required to provide a comprehensive diagnosis of this genus. *Staurobothrium* is considered as a *genus inquirendum* here.

THYSANOBOTHRIUM Shipley and Hornell, 1906

Taxonomic status: *Genus inquirendum.*
Synonyms: None.
Type and only species: *Thysanobothrium uarnakense* Shipley and Hornell, 1906.
Etymology: *Thysanos*, Gr., fringe, tassel; *bothrion*, Gr., diminutive of *bothros*, trench, pit, trough.

Thysanobothrium uarnakense Shipley and Hornell, 1906
TYPE SPECIES

Taxonomic status: *Species inquirendum.*
Synonyms: None.
Type host: *Trygon uarnak* (Forsskål, 1775) (= *Himantura uarnak* [Forsskål, 1775] ?), Honeycomb stingray (Dasyatidae, Myliobatiformes).
Additional hosts: None.
Site of infection: Spiral intestine.
Type locality: Ceylon (now Sri Lanka).
Additional localities: None.
Number of specimens on which the original description was based: Not indicated in original description.
Type specimens: Not indicated in original description.
Voucher specimens: None.
Material examined: Three putative specimens of *Thysanobothrium* sp. (in the author's personal collection).
Etymology: *Uarnakense*, referring to the type host of the species, *Trygon uarnak*.
Unverified records: *Trygon walga* Müller and Henle, 1841 from Ceylon (see Southwell 1911).

Chronology

Shipley and Hornell (1906): erect the genus *Thysanobothrium* with *T. uarnakense* as the type species for more than one specimen from *Trygon uarnak* from Ceylon; provide a superficial description of the worms making note of the exceptional size (7 cm); proglottid anatomy is not described, except for the mention of the uterus full of eggs; *T. uarnakense* is not compared or distinguished from any other genera or species of cestodes.

Southwell (1911): examined 20 newly collected specimens of *Thysanobothrium uarnakense* from *Trygon walga*; notes that the original description agrees perfectly with these specimens; distinguishes his new genus *Cyclobothrium* from *Thysanobothrium* noting that *Cyclobothrium* lacks a cup-like shield bearing suckers, possesses a pair of suckers that corresponds to the central "knob" described by Shipley and Hornell and possesses a number of other minor differences (*e.g.*, number of tentacles, course of the penis and vas deferens).

Stiles and Hassall (1912): *Thysanobothrium* Shipley and Hornell, 1906; *T. uarnakense* Shipley and Hornell, 1906 (in *Trygon uarnak*; Dutch Bay)

Meggitt (1924): treats *Thysanobothrium* Shipley and Hornell, 1906 as a junior synonym of *Polypocephalus* Braun, 1878 in the family Polypocephalidae, order Tetraphyllidea.

Southwell (1925): considers *Thysanobothrium* to be a junior synonym of *Polypocephalus*; considers *Thysanobothrium uarnakense* to be a junior synonym of *Polypocephalus radiatus* and restates Shipley and Hornell's (1906) original description of *Thysanobothrium uarnakense* concluding that *T. uarnakense* is inseparable from *Polypocephalus radiatus* Braun, 1878.

Southwell (1930): considers *Thysanobothrium* to be a junior synonym of *Polypocephalus* Braun, 1878; reiterates text of Southwell (1925); considers *Thysanobothrium uarnakense* to be a junior synonym of *Polypocephalus radiatus*; omits reference to earlier classification scheme.

Woodland (1930): questions, but follows Southwell's (1925) decision and considers *T. uarnakense* to be a junior synonym of *P. radiatus*.

Fuhrmann (1931): considers *Thysanobothrium* to be a junior synonym of *Polypocephalus* in the family Lecanicephalidae Braun (syn. Gamobothriidae Linton), order Tetraphyllidea.

Baer (1948): does not accept synonymy of *Thysanobothrium uarnakense* and *Parataenia elongata* with *Polypocephalus radiatus*, because of the lack of information about the internal anatomy of *T. uarnakense* and *P. radiatus*; does not further comment on the validity or identity of *Thysanobothrium*.

Hyman (1951): considers *Thysanobothrium* to be a junior synonym of *Polypocephalus* in the family Lecanicephalidea, order Lecanicephaloidea.

Wardle and McLeod (1952): states that *Thysanobothrium uarnakense* Shipley and Hornell, 1906 is probably a junior synonym of *P. radiatus* Braun, 1878; does not address the status of *Thysanobothrium*.

Yamaguti (1959): considers *Thysanobothrium* Shipley and Hornell, 1906 to be a junior synonym of *Polypocephalus* Braun, 1878 and *Thysanobothrium uarnakense* Shipley and Hornell, 1906 to be a junior synonym *P. radiatus* Braun, 1878.

Schmidt (1986): considers *Thysanobothrium* Shipley and Hornell, 1906 to be a junior synonym of *Polypocephalus* Braun 1878 and *Thysanobothrium uarnakense* to be a junior synonym of *Polypocephalus radiatus* Braun, 1878.

Euzet (1994b): treats *Thysanobothrium* as a junior synonym of *Polypocephalus* Braun, 1878.

Remarks

The new genus *Thysanobothrium* was erected by Shipley and Hornell (1906) for specimens of the new species, *Thysanobothrium uarnakense*, collected from the Honeycomb stingray, *Himantura uarnak* (as *Trygon uarnak*) in Ceylon (now Sri Lanka). The scolex of this species was described as a "cup-like external bowl, which surrounds a central portion, and between this cup-like shield and the central portion a number of simple tentacles protrude" (Shipley and Hornell 1905, p. 78). These authors comment on the uniqueness of the tentacles, seeming unaware of the genera with tentacles *Polypocephalus* and *Parataenia*, described at least 15 years earlier. Shipley and Hornell (1906) did not describe the anatomy of the proglottids in detail; they noted only the gravid nature of the posterior proglottids. Southwell (1911) reported having collected 20 specimens of this species from the Dwarf whipray, *Himantura walga* (Müller and Henle, 1841) (as *Trygon walga*), presumably from Ceylon (now Sri Lanka), but did not provide any additional information. There is no indication of type specimens in the original description or any of the later literature referring to this species. *Thysanobothrium* has not been reported since Southwell (1911).

The description of *T. uarnakense* as possessing tentacles has led all authors addressing the taxonomic position of the genus to place *Thysanobothrium* in synonymy with *Polypocephalus* (see chronology). Some authors (Southwell 1930; Woodland 1930; Wardle and McLeod 1952) even placed *T. uarnakense* in synonymy with the type species of *Polypocephalus*, *P. radiatus*.

As part of the present study, cestodes were collected from the type host, *Himantura uarnak*, from Fog Bay, Northern Territory, Australia. This material included a few cestodes, superficially very consistent with the description of *T. uarnakense*. These specimens are large and the overall gestalt of the strobila and the proglottids is very similar to that described for *Thysanobothrium*. The morphology of the scolex, however, differs somewhat from that originally described for this taxon. Although, the specimens possess a cup-shaped scolex (Fig. 5D), similar to that described in *Thysanobothrium*, tentacles protruding from the opening were not observed. Rather, the entire margin on the anterior of the scolex is weakly corrugated.

Although this configuration could possibly be interpreted as invaginated tentacles, this is clearly not the case. In addition, the fact that the scolex is described as cup-like by Shipley and Hornell (1906) would be very unusual for a species of *Polypocephalus*. In *Polypocephalus*, even when the tentacles are everted, the aperture through which the tentacles evert remains slightly constricted. Additional specimens of this taxon, ideally from the type locality and type host, are needed to unequivocally determine the identity of *Thysanobothrium*. Until then, the evidence at hand does not support the synonymy of *Thysanobothrium* with *Polypocephalus*. Moreover, the additional data provided on the type specimens of *P. radiatus* (see treatment of *Polypocephalus*) does not support the synonymy of *P. radiatus* with *T. uarnakense*. *Thysanobothrium* is considered as a *genus inquirendum* here.

F. VALID LECANICEPHALIDEAN GENERA

ABERRAPEX
Jensen, 2001

Taxonomic status: Valid.

Synonyms: None.

Type species: *Aberrapex senticosus* Jensen, 2001.

Other species: *Aberrapex arrhynchum* (Brooks, Mayes and Thorson, 1981) Jensen, 2001.

Etymology: *Aberro*, L., to go astray; *apex*, L., summit, top; is named for the fact that the scolex of this taxon deviates from the more usual scolex form of lecanicephalideans in lacking an apical structure.

Diagnosis (Modified from Jensen [2001].)

Worms euapolytic. Scolex with four acetabula; acetabula bothridiate in form, simple, facially unmodified; distal and proximal surfaces covered with blade-like spinitriches. Apical modification of scolex proper and apical organ absent. Proglottids craspedote, laciniate. Testes numerous, in several columns, anterior to ovary. Vas deferens extending from ootype to cirrus sac. External seminal vesicle present or absent. Cirrus sac pyriform. Cirrus unarmed. Ovary H-shaped in dorso-ventral view, tetralobed in cross-section. Vagina lateral, extending from ootype to cirrus sac, then laterally to genital pore, opening posterior to cirrus sac into genital atrium. Genital pores lateral, irregularly alternating. Uterus median, saccate. Vitellaria follicular, lateral, extending entire length of proglottid, interrupted by ovary. Eggs unknown. Parasites of eagle rays in the genus *Myliobatis* Cuvier (ex Duméril), 1816 (Myliobatidae). Gulf of California (Mexico) and southern Atlantic Ocean (Uruguay).

Chronology

Caira *et al.* (1999): include a species of *Aberrapex* (*A. senticosus* under the name "'*Discobothrium*' n. sp.") in a phylogenetic analysis based on morphological data; the species grouped outside of the majority of the other lecanicephalidean taxa included in the analysis.

Caira *et al.* (2001): include the species of *Aberrapex* (*A. senticosus* under the name "'*Discobothrium*' n. sp.") from Caira *et al.* (1999) in a more comprehensive phylogenetic analysis based on morphological data; the species grouped outside of the majority of the other lecanicephalidean taxa included in the analysis, with two other lecanicephalidean taxa: *Paraberrapex manifestus* as "new genus 2 n. sp." and *Healyum pulvis* as "new genus 3 n. sp."

Jensen (2001): erects the genus *Aberrapex* with *A. senticosus* as the type species; considers it to be a lecanicephalidean despite its lack of an apical structure.

Remarks (Modified from Jensen [2001]. Copyright 2001, The Journal of Parasitology. Used with permission.)

Specimens of this new genus and species were collected from the Bat eagle ray (*Myliobatis californica*) from the Gulf of California. This genus was erected by Jensen in 2001, and, like *Paraberrapex*, is unusual among lecanicephalideans in that it lacks a modification of the apex of the scolex. Similar to the majority of lecanicephalidean taxa, *Aberrapex* possesses acetabula that are simple and facially unmodified. Unlike the majority of lecanicephalidean taxa, however, these acetabula are bothridiate, not sucker-like, in form. Several features of the proglottids are unmistakably lecanicephalidean. For example, the vagina opens into the genital atrium posterior to the cirrus sac and the vas deferens is expanded to form an external seminal vesicle that extends from near the ootype to the cirrus sac. As a consequence, Jensen (2001) emended the diagnosis of the order Lecanicephalidea to include lecanicephalidean taxa lacking an apical structure.

Aberrapex senticosus Jensen, 2001

TYPE SPECIES

(Figs. 8, 9, and 12A-E)

Synonyms: None.

Type host: *Myliobatis californica* Gill, 1865, Bat eagle ray (Myliobatidae, Myliobatiformes).

Additional hosts: None.

Site of infection: Spiral intestine.

Type locality: Santa Rosalia (27°19'N, 112°17'W), Baja California, Mexico (Fig. 8).

Additional localities: None.

Number of specimens on which the original description was based: 14.

Type specimens: Holotype (CNHE No. 4188) and two paratypes (CNHE No. 4189); three paratypes (USNPC No. 91208); two paratypes (HWML No. 16374); seven paratypes (six whole worms and cross-sections) (LRP Nos. 2152-2158).

Voucher specimens: None.

Material examined: CNHE No. 4188 (holotype); CNHE No. 4189, USNPC No. 91208, HWML No. 16374, and LRP Nos. 2152-2158 (paratypes).

Etymology: The specific epithet *senticosus* (L., full of briers or thorns) refers to the entire scolex being covered with large spinitriches giving it a prickly appearance.

Chronology

Caira *et al.* (1999): include this species under the name "*Discobothrium*" n. sp. in a phylogenetic analysis based on morphological data; the

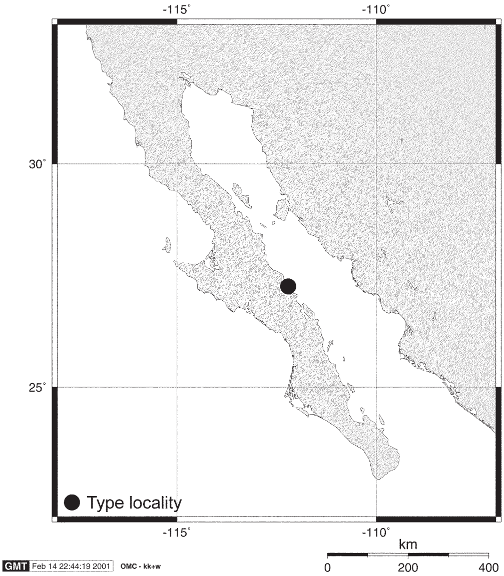


Fig. 8. Geographic distribution of *Aberrapex senticosus* Jensen, 2001.

species grouped outside of the majority of the other lecanicephalidean taxa included in the analysis.

Caira *et al.* (2001): include this species as "*Discobothrium*" n. sp. from Caira *et al.* (1999) in a more comprehensive phylogenetic analysis based on morphological data; again, the species grouped outside of the majority of the other lecanicephalidean taxa included in the analysis, along with two other lecanicephalidean taxa (*Paraberrapex manifestus* as "new genus 2 n. sp." and *Healyum pulvis* as "new genus 3 n. sp.").

Jensen (2001): describes *Aberrapex senticosus* as the type species of the new genus *Aberrapex*.

Description (Modified from Jensen [2001]. Copyright 2001, The Journal of Parasitology. Used with permission.) (Based on 14 whole worms.)

Worms 1,485-6,333 (3,650 ± 1,606; 14) long; maximum width at terminal proglottid; 31-38 (35 ± 2; 14) proglottids, euapolytic. Scolex 100-130 (113 ± 8.5; 14) long by 125-170 (152 ± 14.5; 14) wide, consisting of four acetabula. Acetabula bothridiate in form, cup-shaped, 80-112 (94 ± 8.7; 14; 28) long by 45-85 (73 ± 9.2; 13; 24) wide. Apical modification of scolex proper and apical organ absent.

Distal and proximal surfaces of acetabula and scolex proper between acetabula densely covered with large blade-like spinitriches and long filitriches (Fig. 12B and C, respectively), giving scolex "spined" appearance. Scolex proper at apex of scolex covered with long filitriches (Fig. 12D). Strobila covered with long filitriches; filitriches becoming wider towards posterior margins of proglottids (Fig. 12E).

Cephalic peduncle absent. Proglottids craspedote, laciniate. Immature proglottids 29-36 (34 ± 1.8; 14) in number, initially wider than long, becoming longer than wide with maturity; two most posterior immature proglottids 151-690 (417 ± 159.5; 14; 28) long by 111-364 (214 ± 59.9; 14; 28) wide. Mature proglottids 1-2 in number; mature proglottids in which testes are not degenerated 808-1,323 (1,052 ± 167.9; 11) long by 151-333 (244 ± 58.6; 11) wide; fully mature proglottids in which most testes are degenerated 1,283-1,973 (1,701 ± 253.3; 6) long by 202-323 (276 ± 41.9; 6) wide. Testes 20-40 (28 ± 5.6; 14; 37) in number, 35-90 (59 ± 16.1; 14; 42) long by 50-115 (69 ± 15.2; 14; 42) wide, in single field extending from anterior margin of proglottid to ovary, slightly overlapping anterior margins of ovary, 2-4 irregular columns in dorso-ventral view, essentially one row deep in cross-section (Fig. 9E), postvaginal testicular field absent. Vas deferens in maturing proglottids in form of thin tube, extending along lateral margin of proglottid from level of ovarian bridge to cirrus sac, entering cirrus sac at distal end; vas deferens in proglottids in which testes are degenerated enlarged to form conspicuous external seminal vesicle. External seminal vesicle extensive, saccate, extending more or less along midline of proglottid from ootype to cirrus sac. Internal seminal vesicle absent. Cirrus sac pyriform, angled anteriorly, 55-110 (75 ± 20.1; 14) long by 32-80 (57 ± 15.6; 14) wide in mature proglottids with testes, 127-182 (163 ± 24.9; 6) long by 130-150 (138 ± 9.5; 6) wide in mature proglottids in which testes are degenerated, containing coiled cirrus. Cirrus unarmed. Ovary H-shaped in dorso-ventral view, tetralobed in cross-section (Fig. 9F), 50-215 (113 ± 53.4; 12) long by 77-232 (136 ± 47.4; 12) wide in mature proglottids with testes, 335-444 (379 ± 57.4; 4) long by 120-192 (165 ± 39.0; 4) wide in mature proglottids in which testes are degenerated, lobulated, symmetrical; ovarian bridge at center of ovary. Mehlis' gland at posterior margin of ovary. Vagina extending along lateral margin of proglottid from ootype to genital pore, opening into genital atrium posterior to cirrus sac; vaginal sphincter absent. Genital pores lateral, irregularly alternating, 52-72% (60 ± 5.0; 14; 20) of proglottid length from posterior end. Uterus saccate, extending anteriorly along median line of proglottid to anterior of cirrus sac, stopping short of anterior margin of proglottid; uterine duct entering uterus slightly posterior to level of genital pore; uterine pore absent. Vitellaria follicular, medullary, in lateral columns, 2-3 vitelline follicles on each side of proglottid in cross-section (Fig. 9E), extending entire length of proglottid, interrupted by ovary, slightly overlapping anterior and posterior margins of ovary; vitelline fol-

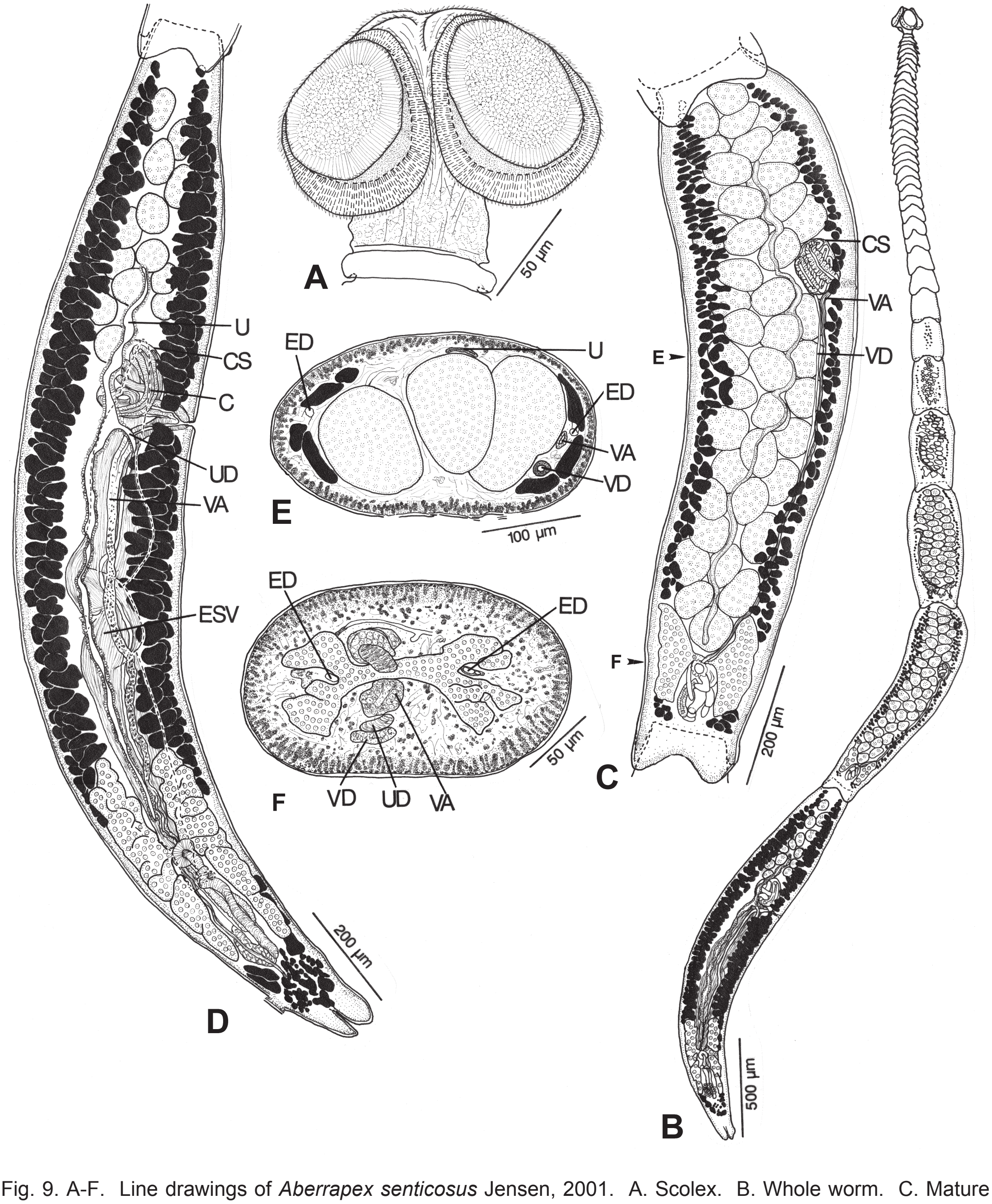


Fig. 9. A-F. Line drawings of *Aberrapex senticosus* Jensen, 2001. A. Scolex. B. Whole worm. C. Mature proglottid; numbered arrows indicate location of sections shown in Figures E and F. D. Terminal mature proglottid. E. Cross-section through mature proglottid at level of testes. F. Cross-section through mature proglottid at level of ovary. (Taken from Jensen [2001]. Copyright 2001, The Journal of Parasitology. Used with permission.)

licles 9-42 (17 ± 6.9; 14; 39) long by 7-60 (24 ± 13.4; 14; 39) wide in mature proglottids with testes, 25-57 (38 ± 9.3; 6; 15) long by 37-90 (60 ± 13.8; 6; 15) in mature proglottids with degenerated testes. Single pair of excretory ducts (Fig. 9E and F). Eggs not observed.

Remarks (Modified from Jensen [2001]. Copyright 2001, The Journal of Parasitology. Used with permission.)

Proglottids of this species were considered mature when the organs of the male and female reproductive system were fully formed and functional. Upon reaching maturity, proglottids of this species continue to change markedly in their overall appearance and size (and the size of the organs they contain) while maturing further. The most conspicuous change is the degeneration of most of the testes in older mature proglottids. Consequently, measurements are provided for some features both in proglottids in which testes are present and in proglottids in which testes are degenerated.

The taxon, *Aberrapex senticosus*, has been included under the name "'*Discobothrium*' n. sp." in two phylogenetic analyses addressing the interrelationships among tetraphyllidean, lecanicephalidean, and diphyllidean cestodes (Caira *et al.* 1999; Caira *et al.* 2001). The genus *Aberrapex* was created by Jensen (2001) to house this taxon now that its position among lecanicephalideans is more fully understood. The type material of *A. senticosus* includes some of the specimens used by Caira *et al.* (1999) and Caira *et al.* (2001) to code for this species.

Aberrapex senticosus was recovered from five of the 32 specimens of *Myliobatis californica* examined (prevalence: 15.6%).

Aberrapex arrhynchum (Brooks, Mayes and Thorson, 1981) Jensen, 2001

(Figs. 10, 11, and 12F-K)

Synonyms: *Discobothrium arrhynchum* Brooks, Mayes and Thorson, 1981.

Type host: *Myliobatis goodei* Garman, 1885, Southern eagle ray (Myliobatidae, Myliobatiformes).

Additional hosts: None.

Site of infection: Spiral intestine.

Type locality: Rîo de la Plata estuary, near Montevideo, Uruguay (Fig. 10).

Additional localities: None.

Number of specimens on which the original description was based: 30.

Type specimens: USNPC No. 75722 (holotype); USNPC No. 75723 and HWML No. 21003 (paratypes).

Voucher specimens: None.

Material examined: USNPC No. 75723 (paratypes); HWML No. 21003 (paratypes).

Etymology: The specific epithet *arrhynchum* (*a*-, Gr., without) refers to the lack of a myzorhynchus in this species.

Chronology

Brooks *et al.* (1981a): describe the new species *Discobothrium arrhynchum* as a species unique among all other species in the genus in its lack of a myzorhynchus; justification for the placement in *Discobothrium* or the taxonomic placement of the genus itself are not given.

Brooks *et al.* (1981b): list *Discobothrium arhyn-*

Fig. 10. Geographic distribution of *Aberrapex arrynchum* (Brooks, Mayes and Thorson, 1981) Jensen, 2001.

chus [sic] as a parasite of *Myliobatis goodei*; consider it endemic to South America.

Jensen (2001): transfers the species to the genus *Aberrapex* creating the new combination *Aberrapex arrhynchum*; emends the description of *A. arrhynchum* and presents SEM data.

Description (Emended from Brooks *et al.* [1981a]. Modified from Jensen [2001]. Copyright 2001, The Journal of Parasitology. Used with permission.) (Based on one paratype [USNPC No. 75723]; 21 paratypes [HWML No. 21003]; one scolex prepared for SEM and strobila cross-section series [HWML No. 21003].)

Distal surfaces of acetabula covered with large blade-like spinitriches and long filitriches (Fig. 12G), large blade-like spinitriches absent from posterior third of distal surfaces (Fig. 12I); proximal surfaces of acetabula and scolex proper between acetabula densely covered with large blade-like spinitriches and long filitriches (Fig. 12H). Scolex proper at apex of scolex and strobila covered with dense long filitriches only (Fig. 12J and K, respectively). Proglottids craspedote, weakly laciniate. Vagina opening into genital atrium posterior to cirrus sac. Vas deferens in mature proglottids in form of thin tube, extending along lateral margin of proglottid from ootype to cirrus sac, entering cirrus sac at anterior-distal end. Ovary H-shaped in dorso-ventral view, tetralobed in cross-section. Uterine duct extending along lateral margin of proglottid from ootype to level of genital pore, entering uterus at extreme anterior margin of uterus. Uterus extending, parallel to uterine duct, along midline of proglottid from level of anterior margin of ovary to posterior margin of cirrus sac. Vitelline follicles extending entire length of proglottid, interrupted by ovary, slightly overlapping anterior and posterior margins of ovary.

Remarks (Modified from Jensen [2001]. Copyright 2001, The Journal of Parasitology. Used with permission.)

The description of *Discobothrium arrhynchum*, under the new name *Aberrapex arrhynchum*, was emended by Jensen (2001) to include additional information and new observations based on the 22 type specimens indicated above and one unmounted paratype prepared for SEM. Examination of this material suggested a slightly different interpretation of some of the characters described by Brooks *et al.* (1981a). The existence of modest lateral projections on the posterior margins of the proglottids of *A. arrhynchum* suggest that this species should be considered to be laciniate, rather than only craspedote. This fact is, however, often obscured in worms not mounted in a perfect dorso-ventral plane. In addition, Jensen (2001) commented that the vagina, which is rather narrow and difficult to distinguish from the vas deferens, enters the genital atrium posterior, rather

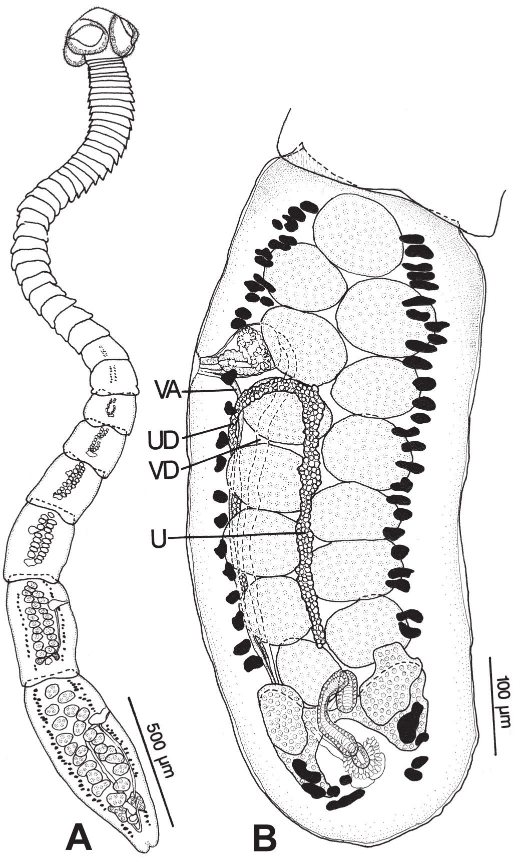


Fig. 11. A-B. Line drawings of *Aberrapex arrhynchum* (Brooks, Mayes and Thorson, 1981) Jensen, 2001. A. Whole worm (paratype, HWML No. 21003). B. Mature proglottid of paratype (HWML No. 21003). (Taken from Jensen [2001]. Copyright 2001, The Journal of Parasitology. Used with permission.)

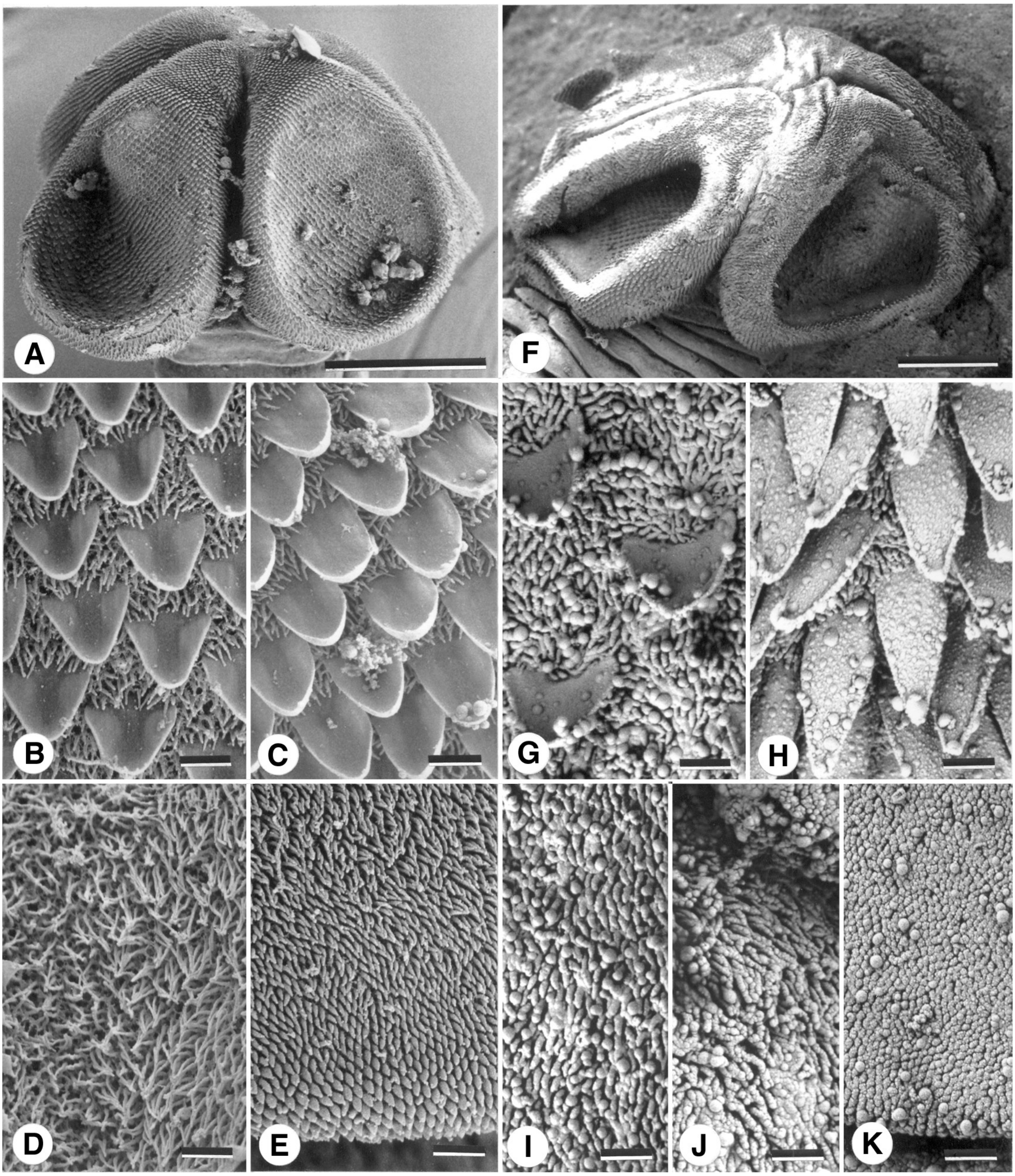


Fig. 12. A-K. Scanning electron micrographs of *Aberrapex senticosus* Jensen, 2001 and *Aberrapex arrhynchum* (Brooks, Mayes and Thorson, 1981) Jensen, 2001. A-E. *Aberrapex senticosus*. A. Scolex. B. Microtriches on distal acetabular surface. C. Microtriches on proximal acetabular surface. D. Microtriches on surface of scolex proper at apex of scolex. E. Microtriches on surface of strobila; note enlarged microtriches at posterior margin of proglottid. F-K. *Aberrapex arrhynchum* (paratype, HWML No. 21003). F. Scolex. G. Microtriches on distal acetabular surface. H. Microtriches on proximal acetabular surface. I. Microtriches on posterior third of distal acetabular surface; note absence of blade-like spinitriches from this region. J. Microtriches on surface of scolex proper at apex of scolex. K. Microtriches on surface of strobila. Scale bar: A and F, 50 µm; B-E and G-K, 1 µm. (Taken from Jensen [2001]. Copyright 2001, The Journal of Parasitology. Used with permission.)

than anterior, to the cirrus sac. Brooks *et al.* (1981a) described the ovary as being bialate, probably referring to the shape of the ovary in dorso-ventral view. Examination of paratypes revealed that the ovary is tetralobed in cross-section. Whereas Brooks *et al.* (1981a, p. 1240) described the vitellaria as consisting of "follicles extending nearly entire length of proglottid," and figured follicles that stop short of the posterior margins of the ovary (Brooks *et al.*, 1981a, fig. 2), examination of the type specimens suggests that postovarian vitelline follicles are also present. In addition to these character reinterpretations, data on microthrix form and distribution, and observations on the uterus and uterine duct and the extent of the vas deferens were included by Jensen (2001) for the first time. These observations on the morphology and anatomy of the type specimens, specifically the lack of a modified apex of the scolex, along with the presence of acetabula that are bothridiate in form, large blade-like spinitriches on all scolex surfaces except the apex of the scolex proper, a cirrus lacking microtriches, and a lateral vagina that opens posterior to the cirrus sac in the genital atrium, clearly identified *A. arrhynchum* as belonging to the genus *Aberrapex*.

The taxonomic status of *Discobothrium* is discussed among the "non-lecanicephalidean" genera. As described there in detail, *Discobothrium* includes a wide diversity of taxa, none of which are morphologically consistent with the type species *Discobothrium fallax*. *Aberrapex arrhynchum* also differs substantially from the latter species. For example, whereas *D. fallax* was illustrated by Van Beneden (1871) as having a large muscular fungiform apical structure, *A. arrhynchum* lacks an apical structure altogether. In their redescriptions of *D. fallax* based on newly collected material, both Euzet (1959) and Williams (1966) suggested that it possesses a vagina that is median in position in the proglottid, opening anterior to the cirrus sac into the genital atrium, whereas *A. arrhynchum* possesses a vagina that is lateral in position in the proglottid and that opens posterior to the cirrus sac into the genital atrium.

ANTEROPORA
Subhapradha, 1955

Taxonomic status: Valid.

Invalid replacement name: *Monoporophyllaeus* Shinde and Chincholikar, 1977.

Type species: *Anteropora indica* Subhapradha, 1955.

Other species: *Anteropora japonica* (Yamaguti, 1934) Euzet, 1994; *A. leelongi* Jensen, n. sp.

Etymology: *Anteropora* likely refers to the position of the genital pore in the anterior third of the proglottid (*ante*, anterior, L., before; *porus*, L., hole).

Diagnosis (Modified from Euzet [1994b].)

Worms hyperapolytic. Scolex with four acetabula; acetabula bothridiate in form, simple, facially unmodified; apical modification of scolex proper slightly enlarged and expanded, aperture at apex present or absent; rim of apical modification of scolex proper covered with blade-like spinitriches; apical organ muscular and/or glandular, non-invaginable, possibly retractable. Proglottids weakly craspedote. Testes few, in single column anterior to ovary. Vas deferens minimal in size, extending from ootype to cirrus sac. External seminal vesicle absent. Internal seminal vesicle present or absent. Cirrus sac elongated oval or pyriform. Cirrus armed. Ovary H-shaped in dorso-ventral view; each lateral lobe consisting of a few large lobules, essentially tetralobed in cross-section. Vagina extending along median line in proglottid, opening into genital atrium at same level or posterior to cirrus sac. Genital pores sublateral, irregularly alternating. Uterus saccate, extending along median line in proglottid. Vitellaria follicular, in lateral columns, extending from posterior to genital pore to posterior margin of proglottid, interrupted by ovary. One dorsal and one ventral pair of excretory ducts present. Eggs single, with bipolar filaments. Parasites of Sleeper rays (Narkidae), Numbfishes (Narcinidae), and the Epaulette shark, *Hemiscyllium ocellatum* (Bonnaterre, 1788) (Hemiscylliidae). Northern India Ocean (India) and western Pacific Ocean (Japan and Australia).

Chronology

Subhapradha (1955): erects *Anteropora* with the type species *A. indica* based on a number of worms [detached proglottids] from *Narcine timlei* in Madras, India; creates a new order, Anteroporidea (for Biporophyllidea Subramaniam, 1939), and a new family, Monoporophyllaeidae, to house this taxon; recognizes *A. indica* and *Biporophyllaeus madrassensis* as distinct species in two different families, Monoporophyllaeidae and Biporophyllaeidae, respectively, in the same order; notes that the ordinal name Biporophyllidea cannot be retained after inclusion of *A. indica*, because this species lacks a uterine pore; proposes the name Lateroporidea to replace Biporophyllidea [note: Subramaniam's name was Biporophyllaeidea, and Subhapradha actually used Anteroporidea instead of Lateroporidea]; provides ordinal, familial, generic and specific diagnoses.

Shinde and Chincholikar (1977): propose the new generic name *Monoporophyllaeus* for *Anteropora*, so that the family name Monoporophyllaeidae, not originally based on a generic name, can be retained; propose to accept Lateroporidea (including two families, Biporophyllidae and Monoporophyllaeidae) as suggested by Subhapradha (1955) and designate *Anteropora* as a synonym of the new genus *Monoporophyllaeus*; *Anteropora* is distinguished from Shinde and Chincholikar's newly described taxon *Mastacembellophyllaeus nandedensis*.

Schmidt (1986): suggests that neither *Monoporophyllaeus* nor *Anteropora* should be recognized as valid until the entire worm is known.

Euzet (1994b): considers *Anteropora* (syn. *Monoporophyllaeus* Shinde and Chincholikar, 1977) a valid genus in the family Anteroporidae, order Lecanicephalidea.

Remarks

It appears that only Subhapradha (1955) and Euzet (1994b) provided a generic diagnosis for *Anteropora*. Euzet's (1994b) diagnosis was consistent with the diagnosis provided by Subhapradha (1955). In an attempt to standardize generic diagnoses among the lecanicephalidean genera, the most recent diagnosis of *Anteropora* by Euzet (1994b) was modified, incorporating apical structure terminology suggested by Caira *et al.* (1999, 2001) and expanded to include morphological and anatomical features not included in previous generic diagnoses of the genus. The emendations suggested here are based on specimen observations resulting in a reinterpretation of the following features: *Anteropora* is considered to be hyperapolytic rather than apolytic, following the terminology as articulated by Caira *et al.* (1999); the proglottids are considered to be weakly craspedote rather than acraspedote, and the pores appear to be sublateral in position rather than lateral. While Subhapradha's (1955) description noted the absence of longitudinal excretory ducts in his familial diagnosis of the Monoporophyllaeidae Subhapradha, 1955, a new family created to house *Anteropora*, in both species of *Anteropora* examined in this study (*A. japonica* and the new species described herein) a dorsal and a ventral pair of excretory ducts are visible.

Closely related to the taxonomic history of *Anteropora* is that of the genera *Biporophyllaeus*, *Monoporophyllaeus,* and, tangentially, *Mastacembellophyllaeus* Shinde and Chincholikar, 1977. Williams (1962) provided a summary of the history of each of these. A more detailed and updated account of the history of these taxa is presented below in chronological order.

Prior to the erection of *Anteropora*, Subramaniam (1939) described a new genus and species of cestodarian, *Biporophyllaeus madrassensis*, from the spiral intestine of *Chiloscyllium griseum* from Madras, India. Unfortunately, Subramaniam (1939) created some confusion when assigning his new genus to higher taxonomic categories. He listed Biporophyllaedea [sic] as one of four orders in the subclass Cestodaria and then proceeded to provide a definition of a new order he referred to as "Caryophyllaeidea." However, the order Caryophyllaeidea, as well as the family Caryophyllaeidae Leuckart, 1878, had been created more than 60 years earlier (see Mackiewicz 1994). It appears that Subramaniam mistakenly used the ordinal name Caryophyllaeidea and actually meant to use the name of the order Biporophyllaedea [sic], which is defined for the first time in his paper. Wardle and McLeod (1952) accepted the order Biporophyllidea.

In 1955, Subhapradha erected a new genus, *Anteropora*, which she considered to belong in the same order as *Biporophyllaeus*. The description of the type species of *Anteropora*, *A. indica*, was based on specimens collected from an electric ray, *Narcine timlei* (Bloch and Schneider, 1801), off the coast of Madras, India. Similar to Subramaniam (1939) placing *Biporophyllaeus* in the subclass Cestodaria, Subhapradha (1955) considered *Anteropora* to be a monozooic (*i.e.*, unproglottized and containing only a single set of reproductive organs) cestodarian. *Anteropora* was placed in a new family, Monoporophyllaeidae, in the "new" order Anteroporidea (ordinal name suggested first was Lateroporidea, p. 46). Subhapradha (1955) suggested this new ordinal name as a replacement name for Biporophyllidea of Subramaniam (1939), because, according to Subhapradha (1955), *A. indica* belonged in the same order as *Biporophyllaeus madrassensis* that is, in the order Biporophyllidea. As a consequence of inclusion of *A. indica* in the group, this ordinal name could not be retained, because this taxon lacked a uterine pore. Within Subhapradha's (1955) Anteroporidea, *A. indica* and *B. madrassensis* are recognized in two different families, Monoporophyllaeidae and Biporophyllaeidae Subhapradha, 1955, respectively.

Yamaguti (1959) suggested that the family name Monoporophyllaeidae should be "suppressed," because there was no generic name corresponding to the family name. Yamaguti (1959) was the first author to note that *A. indica* and *B. madrassensis* appear to have been described from detached proglottids of hyperapolytic tetraphyllidean or trypanorhynchan cestodes. As a consequence, Yamaguti (1959) did not classify *Anteropora* or *Biporophyllaeus* in any particular order among the fish cestodes, but rather suggested both should be redescribed from a specimen with a strobila. Williams (1962) noted that several species of tetraphyllideans (*e.g.*, *Acanthobothrium pearsoni* Williams, 1962) possess a functional anterior sucker on detached proglottids. Based on the fact that *A. pearsoni* and *B. madrassensis* are found in related host groups and are similar in overall proglottid morphology, Williams (1962) suggested that *B. madrassensis* is possibly the proglottid of a species of *Acanthobothrium* Van Beneden, 1850 or at least a tetraphyllidean. Williams commented on the similarities between *A. indica* and *B. madrassensis*, but not on the taxonomic status of the former species. In 1977, Shinde and Chincholikar resurrected the family name Monoporophyllaeidae, which had been rejected by Yamaguti (1959). Ignoring the fact that one of Yamaguti's motivations in suppressing the family was that he considered *A. indica* and *B. madrassensis* to be detached proglottids of cestodes in existing orders and not cestodarians, Shinde and Chincholikar (1977) proposed the new generic name *Monoporophyllaeus* to replace *Anteropora*. This made *Anteropora* a synonym of the former genus. In addition, Shinde and Chincholikar (1977) suggested the ordinal name, Lateroporidea, to include two families (Biporophyllidae and Monoporophyllaeidae) as suggested by Subhapradha (1955), be accepted. They did acknowledge that Subhapradha (1955) had actually used the name Anteroporidea for the order, but provided no justification for their choice of Lateroporidea over Anteroporidea. Additionally, Shinde and Chincholikar (1977) erected the new genus and species *Mastacembellophyllaeus nandedensis* Shinde and Chincholikar, 1977 in the family Monoporophyllaeidae (with *Monoporophyllaeus*).

Schmidt (1986) concluded, as had Yamaguti (1959), that the order Biporophyllidea erected by Subramaniam (1939) based on *Biporophyllaeus madrassensis* was dubious because *Biporophyllaeus* likely represented a detached proglottid of a tetraphyllidean, trypanorhynchan, or lecanicephalidean cestode. He reiterated that two ordinal names, Anteroporidea and Lateroporidea, had been proposed by Subhapradha (1955) to replace Biporophyllidea. He agreed with Yamaguti (1959) that Monoporophyllaeidae should be suppressed because this name was not based on a generic name, but was created by Subhapradha (1955) to house *Anteropora*. As had Yamaguti (1959), in addition to *B. madrassensis*, Schmidt (1986) considered *A. indica* to be based on detached proglottids of tetraphyllidean, trypanorhynchan, or lecanicephalidean cestodes. Lastly, he suggested that *Monoporophyllaeus*, as well as *Anteropora*, be considered valid until the entire worms are known. Euzet (1994b) agreed with Yamaguti (1959) and Schmidt (1986) reiterating that *Anteropora indica* was described from a detached proglottid. He proposed that *Anteropora* be retained and that the family Monoporophylleidae and the genus *Monoporophyllaeus* be suppressed. As a consequence, as had been suggested by Euzet (1994b), *Monoporophyllaeus* is considered a synonym of *Anteropora* here.

Monoporophyllaeus Shinde and Chincholikar, 1977 (invalid replacement name for *Anteropora*)

Shinde and Chincholikar (1977): propose the replacement name *Monoporophyllaeus* for *Anteropora*; propose accepting Subhapradha's Lateroporidea (including two families: Biporophyllidae and Monoporophyllaeidae) and designate *Anteropora* as a synonym of the new genus *Monoporophyllaeus*; erect the genus *Mastacembellophyllaeus* with the type species *M. nandedensis* within the family Monoporophyllaeidae (along with *Monoporophyllaeus*).

Schmidt (1986): mentions that *Monoporophyllaeus* Shinde and Chincholikar, 1977 was proposed to replace *Anteropora* Subhapradha, 1957 [is actually 1955] and comments that neither should be recognized as valid until the entire worm is known.

Euzet (1994b): proposes to retain *Anteropora* Subhapradha, 1957 [is actually 1955] (ICZN Article 23f) as valid; says that this would lead to the suppression of Monoporophylleidae Subhapradha, 1957 [is actually 1955] and *Monoporophyllaeus* Shinde and Chincholikar, 1977, the latter having been created to replace *Anteropora*; considers *Monoporophyllaeus* to be a junior synonym of *Anteropora* Subhapradha, 1957 [is actually 1955].

Remarks on *Monoporophyllaeus*

In 1955, Subhapradha erected a new family, Monoporophyllaeidae, to house *Anteropora indica*. Yamaguti (1959) suggested this family name be suppressed because it was not based on a generic name, and thus, violated Article 13.2 of the International Code of Zoological Nomenclature (ICZN 2000). Shinde and Chincholikar (1977), apparently fond of the family name Monoporophyllaeidae, ignored Yamaguti's arguments for suppression of this name and proposed that *Anteropora* be replaced by the new name *Monoporophyllaeus*, in order to validate Monoporophyllaeidae. There is, however, no justification for the use of this replacement name; *Monoporophyllaeus* must be considered an objective synonym.

Anteropora indica Subhapradha, 1955

TYPE SPECIES

(Fig. 13)

Synonyms: None.

Type host: *Narcine timlei* (Bloch and Schneider, 1801), Spotted numbfish (Narcinidae, Rhinobatiformes).

Additional hosts: None.

Site of infection: Spiral intestine.

Type locality: Madras, India (Fig. 13)

Additional localities: None.

Number of specimens on which the original description was based: "60 examined" (Subhapradha, 1955, p. 44).

Type specimens: Not indicated in original description.

Voucher specimens: None.

Material examined: None.

Etymology: It is likely that the specific epithet refers the type locality for this species.

Chronology

Subhapradha (1955): erects the genus *Anteropora* with *A. indica* as the type species for specimens collected from *Narcine timlei* in Madras, India; establishes the order, Anteroporidea to replace Biporophyllidea Subramaniam, 1939; erects the family Monoporophyllaeidae to house this new genus and species; considers *Anteropora indica* and *Biporophyllaeus madrassensis* as distinct taxa representing two families, Monoporophyllaeidae and Biporophyllaeidae, respectively, in the same order; states that the ordinal name Biporophyllidea

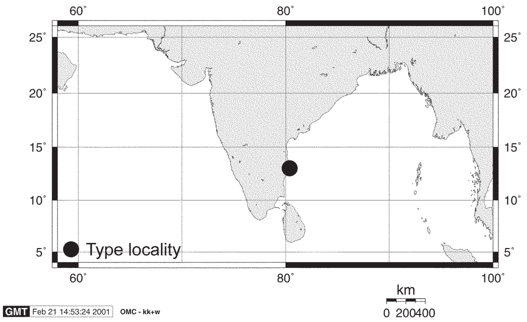


Fig. 13. Geographic distribution of *Anteropora indica* Subhapradha, 1955.

cannot be retained after inclusion of *A. indica*, because it possesses only one pore; the name Lateroporidea is proposed to replace Biporophyllidea [note: actually, Subramaniam's name for the order was Biporophyllaedae, and Subhapradha used Anteroporidea, not Lateroporidea]; provides ordinal, familial, generic and specific diagnoses.

Yamaguti (1959): does not place *Anteropora indica* within his classification of fish cestodes; comments that *A. indica* appears to have been described from a detached proglottid of a hyperapolytic tetraphyllidean or trypanorhynchan cestode, just as *Biporophyllaeus*; recommends this species be redescribed from specimens possessing strobilae.

Williams (1962): notes that several species of tetraphyllideans possess a functional anterior sucker on detached proglottids; suggests that *B. madrassensis* is possibly an *Acanthobothrium* proglottid or at least a tetraphyllidean, because both *Acanthobothrium pearsoni* and *B. madrassensis* parasitize related host groups and are similar in overall proglottid morphology; considers *Anteropora indica* to be problematic, but does not comment on its status.

Schmidt (1986): considers *Anteropora indica* Subhapradha, 1957 [is actually 1955] as a doubtful species and of uncertain status in the order Tetraphyllidea; suggests that *A. indica* is a detached proglottid of a tetraphyllidean, trypanorhynchan, or lecanicephalidean cestode.

Euzet (1994b): comments that *Anteropora indica* was described from a detached proglottid; notes that its anatomy is similar to that of *Discobothrium japonicum*; proposes that *Anteropora* Subhapradha, 1957 [is actually 1955] (ICZN Article 23f) be retained as a valid genus; proposes that Monoporophylleidae Subhapradha, 1957 [is actually 1955] and *Monoporophyllaeus* Shinde and Chincholikar, 1977 be suppressed.

Remarks

Most modern authors (*e.g.*, Yamaguti 1959; Schmidt 1986; Euzet 1994b) agree that the original description of *Anteropora indica* was based on detached proglottids rather than whole worms. Verification of this suspicion with specimens would be useful. Unfortunately, no specimens of this species were available for study. Deposition of type specimens was not indicated in the original description and no type material has been located since. In addition, this species has not been reported since its original description in 1955. Fortunately, Subhapradha's description of the detached proglottids of *A. indica* is accompanied by illustrations that are sufficiently detailed as to allow recognition of the unique morphology of the proglottids of this genus and species. Collection of new material from the type host and type locality is strongly recommended to facilitate a reasoned analysis of its taxonomic status, and, if warranted, a description the genus *Anteropora* beyond proglottid anatomy.

Anteropora japonica (Yamaguti, 1934) Euzet, 1994

(Figs. 14-15)

Synonyms: *Discobothrium japonicum* Yamaguti, 1934.

Type host: *Narke japonica* (Temminck and Schlegel, 1850), Japanese sleeper ray (Narkidae: Rhinobatiformes).

Additional hosts: None.

Site of infection: Spiral intestine.

Type locality: Kuki, Pacific Coast of Japan (Fig. 14).

Additional localities: Maisaka and Koki (Kochi), Pacific Coast of Japan.

Number of specimens on which the original description was based: Not indicated in original description.

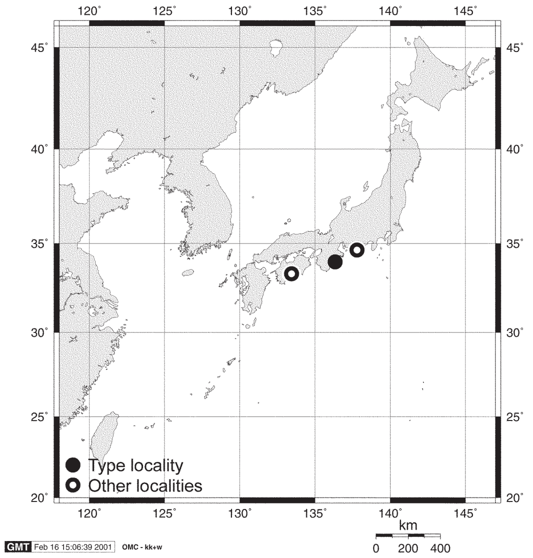


Fig. 14. Geographic distribution of *Anteropora japonica* (Yamaguti, 1934) Euzet, 1994.

Type specimens: MPM No. 22795 (= SY31-13 to SY31-16).

Voucher specimens: MPM No. 22892 (= SY72-75 and SY72-76) (from Yamaguti, 1952).

Material examined: MPM No. 22795 (= SY31-13 to SY31-16) (types); MPM No. 22892 (= SY72-75 and SY72-76) (vouchers).

Etymology: It is likely that the specific epithet refers to either the type locality or the type host of this species.

Chronology

Yamaguti (1934): describes *Discobothrium japonicum*; distinguishes it from *D. fallax* and *D. cobraeformis* [sic]; considers it to be an aberrant taxon in the Tetraphyllidea.

Iwata (1939): compiles list of "cestoids" from Japan using the classification of Fuhrmann (1931); includes *Discobothrium japonicum* from *Narke japonica*.

Yamaguti (1952): reports *D. japonicum* from two additional localities in Japan, Maisaka and Koki [= Kochi?]; redescribes the species and illustrates the genital complex.

Yamaguti (1959): recognizes *Discobothrium japonicum* Yamaguti, 1934 in *Narke japonica* in Japan as a valid species in the genus *Discobothrium*; says it is a synonym of the type species [*D. fallax* ?] according to Riser (1955).

Kamegai and Ichihara (1972): summarize helminth parasites reported by Yamaguti from Japan; include *Discobothrium japonicum* from *Narke japonica*, reported in Yamaguti (1934) and Yamaguti (1952), from Kuki, Kochi, and Maisaka.

Schmidt (1986): considers *Discobothrium japonicum* Yamaguti, 1934, from *Narke japonica*, Japan as one of seven valid species of *Discobothrium*.

Euzet (1994b): recognizes anatomical similarities between *Discobothrium japonicum* and *Anteropora indica*; transfers *D. japonicum* to *Anteropora* creating the new combination *Anteropora japonica* (Yamaguti, 1934) Euzet, 1994.

Description (Modified from Yamaguti [1934, 1952].) (Based on examination of MPM No. 22795 [= SY31-13 to SY31-16], types [consisting of four incomplete worms with scolices, six strobilar fragments of immature proglottids and five gravid detached proglottids], and MPM No. 22892 [= SY72-75 and SY72-76], vouchers [consisting of two incomplete worms with scolices, one strobilar fragment of immature proglottids and numerous mature and gravid detached proglottids].)

Worms with scolices at least 16 mm long; maximum width at level of scolex; maximum width of strobila up to 264, consisting of up to 178 proglottids. Scolex 317-676 long by 411-862 wide, bearing four acetabula. Acetabula bothridiate in form, cup-shaped, 169-309 (254 ± 49.6; 6; 14) long by 146-328 (250 ± 56.0; 6; 12) wide. Apex of scolex proper "pedunculated," bearing apical organ. Apical organ in form of muscular pad (Fig. 15A and B), 140-191 wide. Rim of apical modification of scolex proper with conspicuous spinitriches, visible with light microscopy.

Cephalic peduncle absent. Immature proglottids at least 178 in number, initially wider than long. Terminal proglottids on immature strobila longer than wide, 500-850 long by 187-280 wide. Detached gravid proglottids 1,394-4,245 (2,959 ± 671.4; 38) long by 212-807 (495 ± 122.5; 38) wide; constriction present, in anterior fourth to sixth of length of proglottid, region anterior to constriction possibly forming functional sucker. Testes six in number, 110-214 (150 ± 24.9; 15; 35) long by 107-237 (165 ± 34.7; 15; 35) wide in detached proglottids, anterior to ovary, in single column in dorso-ventral view, one row deep in cross-section. Two vas efferens merging with one another medially at posterior margin of ovary to form vas deferens. Vas deferens minimal, extending along median line of proglottid from posterior margin of ovary to cirrus sac. External seminal vesicle and internal seminal vesicle absent. Cirrus sac in form of elongated oval, 186-309 (235 ± 40.2; 13) long by 38-64 wide in detached proglottids, containing coiled cirrus. Cirrus armed. Ovary H-shaped in dorso-ventral view, 166-319 (232 ± 44.4; 13) long by 179-316 (261 ± 43.9; 13) wide in detached proglottids; each ovarian lobe consisting of two to three large lobules; each lobule 72-150 (108 ± 20.4; 10; 24) long, with smooth margins. Vagina thin-walled, extending along median line of proglottid, opening into genital atrium at same level as cirrus sac; vaginal sphincter absent; seminal receptacle not observed. Genital pores lateral, irregularly alternating, 58-76% (66 ± 5.1; 35) of proglottid length from posterior end in detached proglottids. Uterus extending along median line of proglottid from ovary to anterior constriction of proglottid; uterine duct not observed; uterine pore absent. Vitellaria follicular, in lateral columns, 1-2 vitelline follicles on each side of proglottid in cross-section, extending from slightly anterior to ovary to near posterior margin of proglottid, interrupted by, but overlapping with ovary slightly; vitelline follicles 32-81 (53 ± 13.4; 15; 35) long by 33-107 (53 ± 15.5; 15; 35) wide. One dorsal and one ventral pair of excretory ducts present. Eggs single, with bipolar filaments, 11-18 (15 ± 1.6; 11; 26) long by 11-17 (15 ± 1.4; 11; 26) wide; filaments 30-100 long.

Remarks

Yamaguti (1934) did not indicate deposition of type specimens in the original description of *Anteropora japonica* (as *Discobothrium japonicum*). However, the majority of Yamaguti's collection is currently housed at the Meguro Parasitological Museum (MPM) in Tokyo, Japan. Visits to the MPM revealed a total of six slides of specimens of *A. japonica* (all labeled *D. japonicum*). The first lot (MPM No. 22795 [= SY31-13 to SY31-16], types) consists of whole mounts of incomplete worms with scolices, pieces of strobila, and detached proglottids. Comparison with Yamaguti's (1934) description of *A. japonica* suggested that these specimens were among those illustrated in the original description. The second lot of specimens of *A. japonica* deposited at the MPM (MPM No. 22892 [= SY72-72 and SY72-75], vouchers) consists of specimens from the type host, but also includes specimens from additional localities. These were the specimens Yamaguti used in his redescription of *A. japonica* in 1952, from which detailed drawings of the terminal genitalia and ootype were produced. Because of the overwhelming resemblance of the proglottids of *A. japonica* to those of *A. indica*, Euzet (1994b) transferred the species to the genus *Anteropora*. The overall size of detached proglottids of *A. japonica* and *A. indica* are similar (1,394-4,000 long by 212-807 wide vs. 1,120 long by 420 wide, respectively), as is the description of the shape of the ovary, the number of testes (6 vs. 3-6, respectively) and the morphology and size of the eggs (11-18 vs. 15, respectively). Not surprisingly, these two species have never formally been distinguished from one another. Two conspicuous differences exist between the proglottids of the two. Whereas in *A. japonica* the posterior extent of the uterus is the anterior margin of the ovary, in *A. indica* the posterior extent of the uterus is posterior to the ovary. In addition, whereas the vitelline follicles in *A. japonica* extend from only slightly anterior to the anterior margin of the ovary to the posterior margin of the proglottid, in *A. indica* the vitelline follicles extend from the posterior margin of the cirrus sac to only the posterior margin of the ovary. No doubt additional differences between *A. japonica* and *A. indica* will be found when the morphology of the whole worm of *A. indica* becomes known.

Anteropora japonica is redescribed here from the type specimens and from voucher

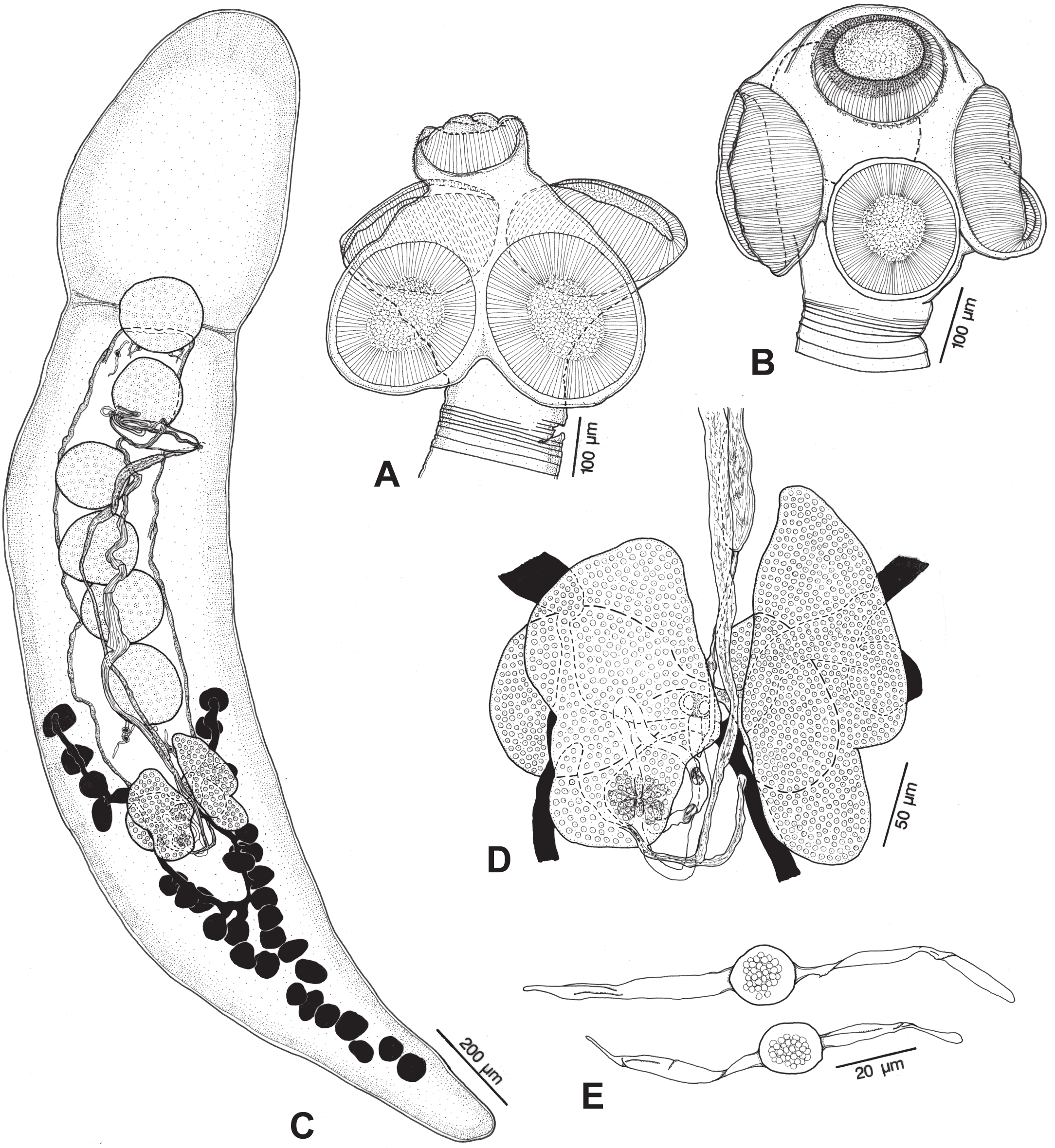


Fig. 15. A-E. Line drawings of *Anteropora japonica* (Yamaguti, 1934) Euzet, 1994. A. Scolex (holotype, MPM No. 22795 [SY31-13]). B. Scolex (paratype, MPM No. 22795 [SY31-16]). C. Detached proglottid (paratype, MPM No. 22795 [SY31-14]). D. Detail of ootype (paratype, MPM No. 22795 [SY31-14]). E. Eggs (paratype, MPM No. 22795 [SY31-16]).

specimens. A number of measurements are provided for features not included in the original description (*e.g.*, cirrus sac, ovary, and overall size of the scolex). In addition, measurements from the original description (Yamaguti, 1934) and the subsequent description by Yamaguti (1952) have been modified based on new observations and measurements taken of the type and voucher specimens as part of this study. For example, the cirrus sac length was expanded from 180-280 to 166-319. Yamaguti (1934) described the "terminal sucker of the myzorhynchus" (p. 78) as being 160 in diameter. According to the revised terminology (Caira *et al.*, 1999) that structure should now be considered to be an apical organ which is in the form of a muscular pad. The width of this structure is given here as 140-191. The apical organ was described by Yamaguti (1934, p. 78) as possessing a "free border with exceedingly minute spines." It seems clear that these spines should now be considered microtriches. Yamaguti described *A. japonica* as possessing a neck, 120 long (1934) and 150-200 wide (1952). Examination of the type and voucher specimens suggests that the region immediately posterior to the scolex is a short extension of the scolex proper (rather than a true cephalic peduncle as defined by Caira *et al.* [1999]), followed by a region in which proglottization is faintly visible. *Anteropora japonica* is therefore here considered to lack a cephalic peduncle.

Anteropora leelongi Jensen, n. sp.

(Figs. 16-18)

Type host: *Hemiscyllium ocellatum* (Bonnaterre, 1788), Epaulette shark (Hemiscylliidae, Orectolobiformes).

Additional hosts: None.

Site of infection: Spiral intestine.

Type locality: Yorkeys Knob (16°49'S, 145°43'E), Cairns, Queensland, Australia (Fig. 16).

Additional localities: None.

Number of specimens on which the original description was based: 13 (two incomplete specimens with scolices, nine detached proglottids, one proglottid cross-section series and one specimen prepared for SEM).

Type specimens: Holotype (whole mount of incomplete specimen with scolex) (QM No. G 222890), three paratypes (whole mounts of detached proglottids) (QM Nos. G 222891-222893); four paratypes (whole mounts of one incomplete specimen with scolex and three detached proglottids) (USNPC No. 94574); four paratypes (three whole mounts of detached proglottids and one proglottid cross-section series) (LRP Nos. 3262-3265); one paratype specimen prepared for SEM (LRP).

Etymology: This species is named in honor of Warren Leelong who, in 1991, assisted with the collection of Epaulette sharks from which these worms were obtained.

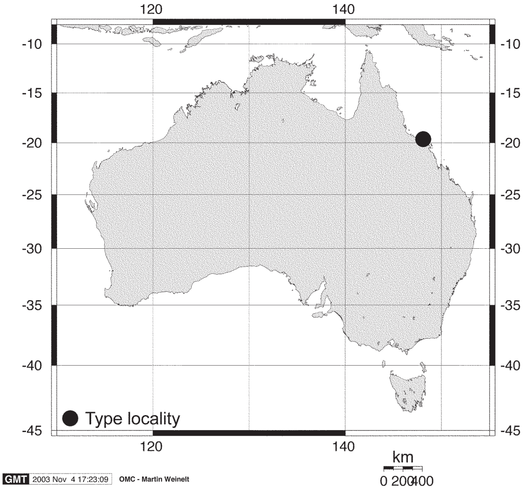


Fig. 16. Geographic distribution of *Anteropora leelongi* Jensen, n. sp.

Chronology

Caira *et al.* (1999): include this species as "*Anteropora* n. sp." in a phylogenetic analysis based on morphological data; the species groups with the majority of lecanicephalidean taxa included.

Description (Based on two incomplete specimens with scolices, nine detached proglottids, one proglottid cross-section series, and one specimen prepared for SEM.)

Worms at least 3,928-5,150 long; maximum width at level of scolex; 87-99 proglottids, hyperapolytic. Scolex 321-378 long by 511-568 wide, bearing four acetabula. Acetabula bothridiate in form, approximately round, 198-221 (207 ± 10.4; 2; 4) long by 207-233 (224 ± 11.7; 2; 4) wide. Apical modification of scolex proper slightly expanded, with aperture at apex, housing apical organ. Apical organ in form of muscular, glandular, conical pad (Fig. 17B), non-eversible, non-protrusible, 130-141 long by 134-145 wide; glandular cells distributed throughout mus-

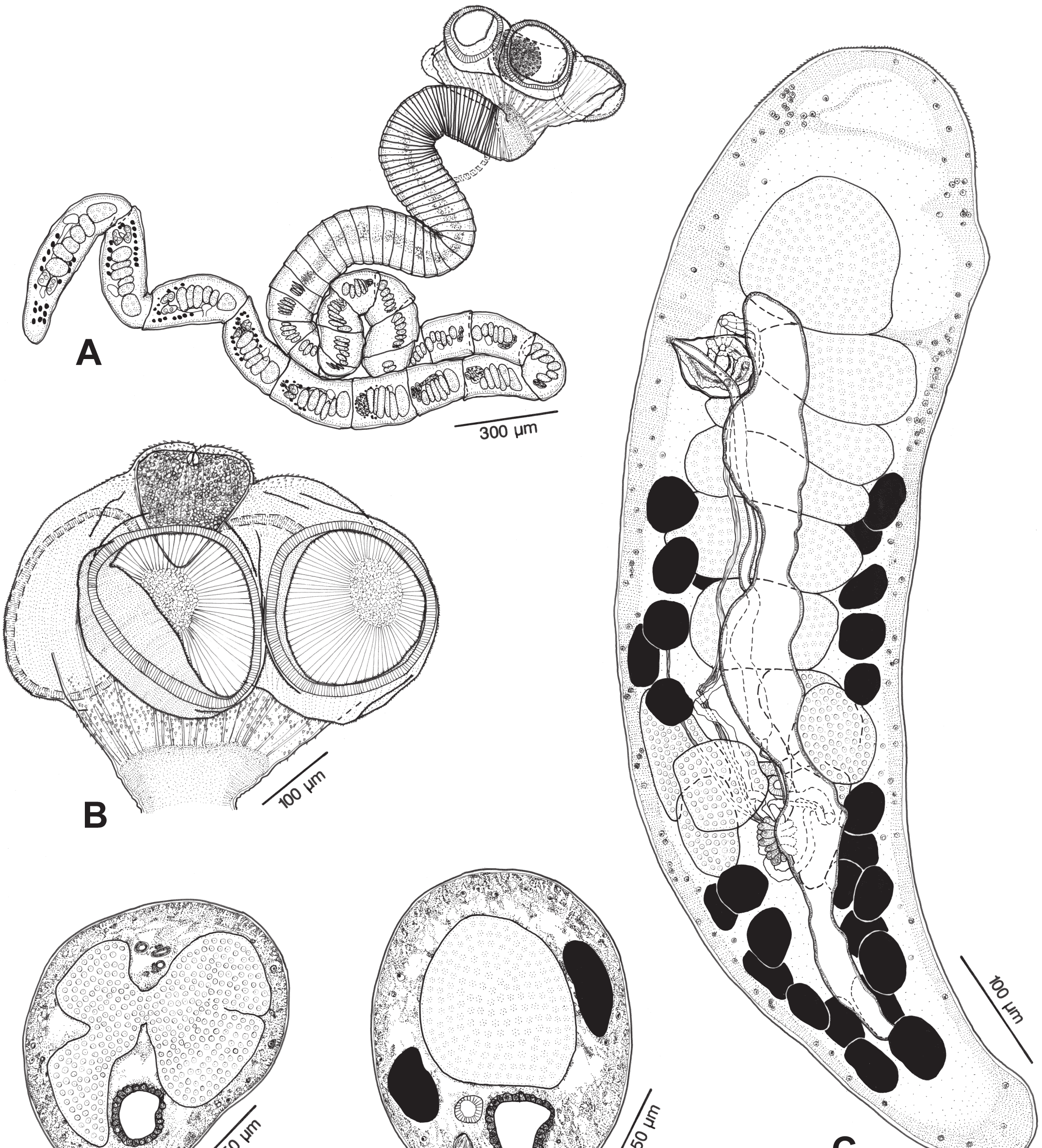


Fig. 17. A-E. Line drawings of *Anteropora leelongi* Jensen, n. sp. A. Whole worm (holotype, QM No. G 222890). B. Scolex (USNPC No. 94574). C. Detached proglottid (QM G 222892). D. Cross-section through mature proglottid at level of ovarian bridge (LRP No. 3265). E. Cross-section through mature proglottid between ovary and cirrus sac (LRP No. 3265).

culature of pad.

Scolex proper anterior to acetabula covered with blade-like spiniform and long filitriches (Fig. 18E); scolex proper posterior to bothridiate acetabula covered with large broad spinitriches and long filitriches (Fig. 18F). Proximal and distal acetabular surfaces covered with blade-like spiniform and long filitriches; blade-like microtriches larger on proximal than distal acetabular surface (Fig. 18C and B, respectively). Apical modification of scolex proper covered with short, broad blade-like spinitriches and long filitriches (Fig. 18D).

Cephalic peduncle absent. Proglottids craspedote, non-laciniate. Posterior-most immature proglottids longer than wide, 277-532 long by 126-137 wide. Detached proglottids mature or gravid, 996-1,632 (1,303 ± 204.7; 8) long by 231-489 (359 ± 91.5; 9) wide. Testes six in number, 59-163 (99 ± 25.9; 9; 36) long by 116-222 (159 ± 24.9; 9; 36) wide in detached proglottids, arranged in single column anterior to ovary, one row deep in cross-section. Two vas efferens merging with one another medially at posterior margin of ovary to form vas deferens. Vas deferens extending along median line of proglottid from posterior margin of ovary to level of cirrus sac. External seminal vesicle absent. Internal seminal vesicle present. Cirrus sac pyriform, horizontal, 87-149 (112 ± 26.1; 9) long by 54-94 (68 ± 14.4; 9) wide in detached proglottids, containing coiled cirrus. Cirrus armed. Ovary irregularly H-shaped in dorso-ventral view, 154-276 (203 ± 39.3; 8) long by 171-329 (247 ± 56.4; 8) wide in detached proglottids, essentially tetralobed in cross-section (Fig. 17D); each ovarian lobe consisting of three lobules; each lobule 76-152 (105 ± 24.0; 8; 18) long; lobule margins smooth. Vagina thin-walled, opening into genital atrium at same level as cirrus sac, extending along median line of proglottid from ootype to genital pore; vaginal sphincter absent; seminal receptacle not observed. Genital pores sublateral, irregularly alternating, 64-76% (69 ± 4.2; 8) of proglottid length from posterior end in detached proglottids. Uterus extending along median line entire length of proglottid; uterine duct not observed; uterine pore absent. Vitellaria follicular, in lateral columns, 1-2 vitelline follicles on each side of proglottid in cross-section (Fig. 17E), extending from posterior margin of cirrus sac to near posterior margin of proglottid, interrupted by, but slightly overlapping ovary; vitelline follicles 31-93 (59 ± 16.7; 9; 27) long by 37-101 (61 ± 19.6; 9; 26) wide. One dorsal and one ventral pair

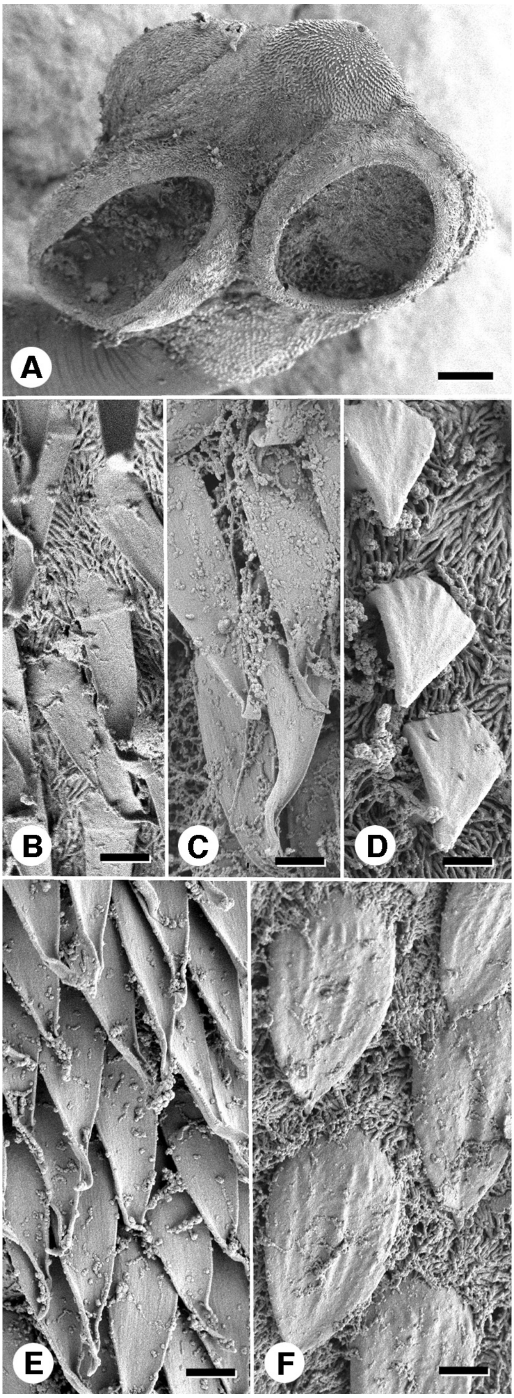


Fig. 18. A-F. Scanning electron micrographs of *Anteropora leelongi* Jensen, n. sp. A. Scolex. B. Microtriches on distal acetabular surface. C. Microtriches on proximal acetabular surface. D. Microtriches on surface of apical modification of scolex proper. E. Microtriches on surface of scolex proper. F. Microtriches on scolex proper posterior to acetabula. Scale bars: A, 50 µm; B-F, 1 µm.

of excretory ducts present. Eggs present in detached proglottids, 13-17 (14 ± 1.2; 6; 47) in diameter, with bipolar filaments.

Remarks

The overall similarity of proglottid features is striking among *Anteropora indica*, *A. japonica*, and *A. leelongi*. *Anteropora leelongi* can be distinguished from *A. japonica* based on the form of the apical organ and the cirrus sac. The apical organ in *A. leelongi* is in the form of a muscular, internally highly glandular cone, completely surrounded by the apical modification of the scolex proper, and the cirrus sac is pyriform. In contrast, the apical organ of *A. japonica* is in the form of a flat muscular pad, the anterior surface of which appears free of the apical modification of the scolex proper, and the cirrus sac is in the form of an elongated oval. In addition, in *A. leelongi* the anterior extent of the vitelline follicles is only slightly posterior to the genital pore and the uterus extends far beyond the posterior margin of the ovary, whereas in *A. japonica* the anterior extent of the vitelline follicles is close to the anterior margin of the ovary and the uterus does not extend posterior to the ovary. *Anteropora leelongi* is more difficult to distinguish from *A. indica*, especially since information on the scolex morphology is not available for the latter species. *Anteropora leelongi* possesses six testes, whereas *A. indica* is described as possessing 3-6 testes. *Anteropora leelongi* can be further distinguished from *A. indica* based on the extent of the vitelline follicles (from posterior to the genital pore to posterior margin of proglottid vs. from genital pore, stopping short of posterior margin of proglottid, respectively).

CORRUGATOCEPHALUM
Caira, Jensen and Yamane, 1997

Taxonomic status: Valid.

Synonyms: None.

Type and only species: *Corrugatocephalum ouei* Caira, Jensen and Yamane, 1997.

Etymology: *Corrugatocephalum* (*corrugatus*, L., wrinkled, ridged; *kephale*, Gr., head) refers to the ridged or corrugated nature of the apical organ of this tapeworm.

Diagnosis (Modified from Caira *et al.* [1997].)

Worms apolytic. Scolex with four acetabula; acetabula in form of suckers; apical modification of scolex proper surrounding apical organ; apical organ cylindrical, partially retractable, with vertical corrugations throughout internal surface. Proglottids acraspedote. Testes few, in single column, anterior to ovary. Vas deferens expanded to form conspicuous external seminal vesicle. External seminal vesicle saccate, extensive, extending from ootype to anterior margin of proglottid. Internal seminal vesicle absent. Cirrus sac pear-shaped. Cirrus unarmed. Ovary irregular in form in dorso-ventral view, consisting of three lobes, irregular in cross-section. Vagina median in position in proglottid, opening into genital atrium posterior to cirrus sac. Genital pores sublateral, irregularly alternating. Uterus unknown. Vitellaria follicular, in lateral columns, extending from cirrus sac to posterior margin of proglottid, interrupted by ovary, but slightly overlapping ovary. Excretory ducts unknown. Eggs unknown. Parasites of lamniform sharks in the genus *Megachasma* Taylor, Compagno and Struhsaker, 1983 (Megachasmidae). Western Atlantic Ocean (Japan).

Chronology

Caira *et al.* (1997): erect the genus *Corrugatocephalum* with *C. ouei* as the type species in Lecanicephalidae; emend the familial diagnosis of Euzet (1994b) to include this species.

Remarks

This genus was created for specimens obtained from a stranded Megamouth shark in Japan. The generic diagnosis is modified here for two main reasons. First, since the erection of *Corrugatocephalum* (Caira *et al.*, 1997), progress has been made determining homologies in apical structures among different cestode orders (Caira *et al.*, 1999 and 2001). The unified terminology regarding these scolex structures suggested by Caira *et al.* (1999 and 2001) has been incorporated into the diagnosis of this genus. In addition, reexamination of type specimens has led to a modified interpretation of two proglottid features. The shape of the ovary in cross-section is now considered to be irregular (as also characterizes species of *Healyum* Jensen, 2001 and *Quadcuspibothrium* Jensen, 2001), rather than bilobed. The position of the genital pore should be considered to be sublateral; Caira *et al.* (1997) mistakenly described the genital pore as lateral.

Corrugatocephalum ouei Caira, Jensen and Yamane, 1997

TYPE SPECIES

(Figs. 19-21)

Synonyms: None.

Type Host: *Megachasma pelagios* Taylor, Compagno and Struhsaker, 1983, Megamouth shark (Megachasmidae, Lamniformes).

Additional hosts: None.

Site of infection: Spiral intestine.

Type locality: Hakata Bay (40˚50'N, 130˚50'E), Fukuoka, northern Kyushu, Japan (Fig. 19).

Additional localities: None.

Number of specimens on which the original description was based: 11 complete worms and two incomplete worms with scolices.

Type specimens: Holotype (NSMT- Pl No. 4698); paratypes (NSMT- Pl No. 4698, USNPC No. 86985 and HWML No. 39285) (whole mounts and cross-sections); SEM stubs retained in the personal collection of J. N. Caira at the University of Connecticut, Storrs, Connecticut, U.S.A.

Voucher specimens (unverified): [possibly spirit material at the BMNH].

Material examined: USNPC No. 86985 (paratypes).

Etymology: The specific epithet, *ouei*, honors Kazuhisa Oue who, while pursuing his passion for birds, found the stranded Megamouth shark from which this worm was described.

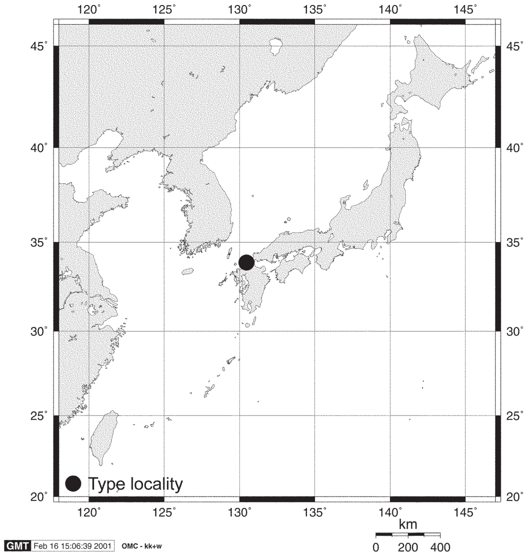


Fig. 19. Geographic distribution of *Corrugatocephalum ouei* Caira, Jensen and Yamane, 1997.

Chronology

Caira *et al.* (1997): erect the genus *Corrugatocephalum* with *C. ouei* as the type species in the family Lecanicephalidae; emend the familial diagnosis of Euzet (1994b) to include this species.

Caira *et al.* (1999): include *Corrugatocephalum ouei* in a phylogenetic analysis based on morphological data; the species groups with the majority of lecanicephalidean taxa included.

Caira *et al.* (2001): include *Corrugatocephalum ouei* from Caira *et al.* (1999) in a more comprehensive phylogenetic analysis based on morphological data; the species groups with the majority of lecanicephalidean taxa included.

Description (Modified from Caira *et al.* [1997].) (Based on 11 complete worms and two incomplete worms with scolices.)

Worms 1.9-5.5 mm (3.3 ± 0.12; 11) long, euapolytic; greatest width at level of scolex. Strobila with 21-35 (29 ± 5; 10) proglottids, greatest strobilar width 116-227 (169 ± 32; 9) slightly posterior to scolex at proglottid number 4-18 (10 ± 5; 8) (Fig. 20B). Scolex 243-540 (370 ± 100; 12) long by 251-494 (349 ± 83; 13) wide. Scolex proper 142-332 (235 ± 69; 13) long by 251-494 (349 ± 83; 13) wide, bearing four acetabula. Acetabula in form of suckers, round, 82-146 (117 ± 20; 12; 24) in diameter. Apical modification of scolex proper bearing

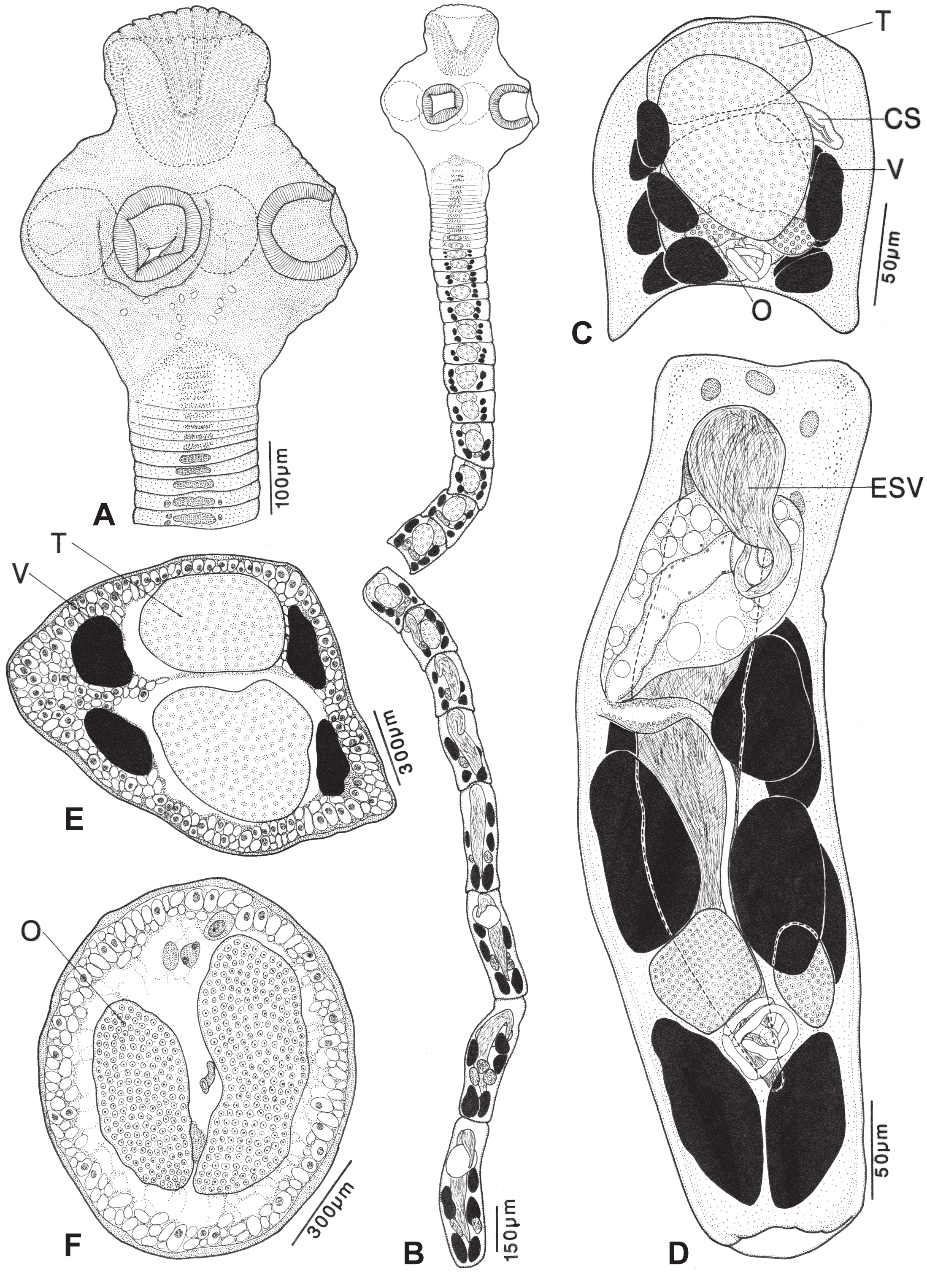


Fig. 20. A-F. Line drawings of *Corrugatocephalum ouei* Caira, Jensen and Yamane, 1997. A. Scolex. B. Whole worm. C. Mature proglottid. D. Terminal mature proglottid. E. Cross-section through mature proglottid at level of testes. F. Cross-section through terminal proglottid at level of ovary. (Slightly modified from Caira *et al.*, [1997].)

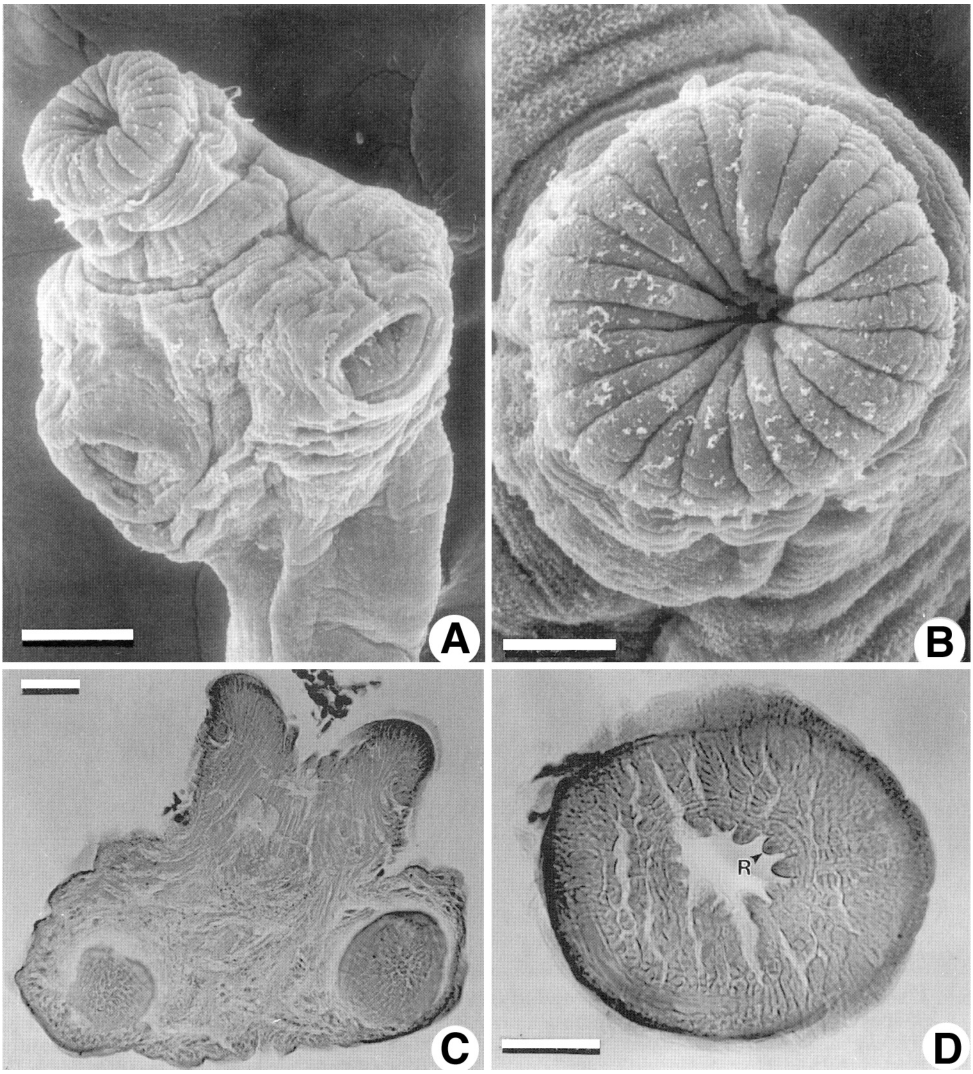


Fig 21. A-D. Scanning electron micrographs and histological sections of *Corrugatocephalum ouei* Caira, Jensen and Yamane, 1997. A-B. Scanning electron micrographs. A. Scolex. B. Apical view of apical organ. C-D. Histological sections. C. Frontal section through scolex of paratype (NSMT-Pl No. 4698). D. Cross-section through apical organ of paratype (NSMT-Pl No. 4698). Arrow indicates ridge on internal surface of apical organ. Scale bars: A, 40 μm; B, 20 μm; C, 50 μm; D, 40 μm. (Slightly modified from Caira *et al.* [1997])

apical organ (Fig. 20A). Apical organ cylindrical, sucker-like, with corrugated internal surface (Fig. 21B and D), 128-498 (196 ± 98; 12) long by 120-243 (177 ± 43; 12) wide, at least partially retractable. Microtriches not observed.

Cephalic peduncle absent. Immature proglottids 9-17 (13 ± 2; 11) in number, wider than long. Mature proglottids in anterior half of strobila 6-16 (11± 3; 11) in number, initially wider than long, then longer than wide; last of which 60-216 (162 ± 50; 11) long by 78-176 (129 ± 25; 11) wide. Mature proglottids in posterior half of strobila 5-9 (6 ± 1; 11) in number, longer than wide; terminal proglottid 308-583 (440 ± 96; 10) long by 80-140 (118 ± 19; 10) wide. Testes three (3 ± 0; 13; 39) in number, 33-110 (70 ± 19; 11; 55) long by 26-100 (67 ± 19; 11; 55) wide, aligned along median axis of proglottid, arranged dorso-ventrally, one testis in anterior of proglottid, two testes superimposed in posterior half of proglottid (Fig. 20C), present only in proglottids in anterior half of strobila, degenerated in mature proglottids in posterior half of strobila (Fig. 20B). Vas deferens forming prominent external seminal vesicle, extending almost entire length of proglottid, 274-519 (361 ± 63; 11; 29) long by 30-66 (51 ± 10; 11; 29) wide (Fig. 20B and D). Internal seminal vesicle absent. Cirrus sac pyriform, 69-184 (122 ± 30; 9; 14) long by 51-86 (72 ± 12; 9; 15) wide, in anterior half of proglottid, containing armed cirrus surrounded by numerous spherical vesicles (Fig. 20D). Ovary asymmetrical in dorso-ventral view (Fig. 20D), irregular in cross-section (Fig. 20F), 38-120 (83 ± 31; 8) long by 76-112 (91 ± 12; 8) wide, consisting of three lobes. Vagina thin walled, extending along median line of proglottid from ootype to genital pore. Genital pores sublateral, pre-equatorial, 56-74% (63 5; 10; 16) of proglottid length from posterior end, alternating irregularly. Uterus not seen. Vitelline follicles large, in lateral columns, arranged in five pairs of dorso-ventral follicles, three pairs on aporal side, two pairs on poral side of proglottid, posterior-most pair on poral and aporal side post-ovarian; individual vitelline follicles 44-121 (89 ± 19; 10; 30) long by 30-64 (45 ± 11; 10; 30) wide. Excretory ducts not observed. Eggs unknown.

Remarks

Caira *et al.* (1997) described this unusual lecanicephalidean from 13 complete and incomplete specimens collected from one Megamouth shark (*Megachasma pelagios*). A complete description was presented, accompanied by illustrations. Although scolices were prepared for SEM, no microthrix data could be obtained for the species. The species has not been reported since.

ENIOCHOBOTHRIUM Shipley and Hornell, 1906

Taxonomic status: Valid.

Synonyms: None.

Type species: *Eniochobothrium gracile* Shipley and Hornell, 1906.

Other species: *Eniochobothrium euaxos* Jensen, n. sp.; *E. qatarense* Al Kawari, Saoud and Wanas, 1994.

Species inquirendae: *Eniochobothrium trygonis* Chincholikar and Shinde, 1978.

Etymology: *Eniocho-*, named "in view of the Cestode's many-caped-coachman-like appearance" (Shipley and Hornell, 1906, p. 65); *bothrion*, Gr., diminutive of *bothros*, trench, pit, trough.

Diagnosis (Modified from Al Kawari *et al.* [1994].)

Worms apolytic. Scolex with four acetabula; acetabula in form of suckers; distal and proximal surfaces of acetabula covered with blade-like spinitriches; apical modification of scolex proper cone-shaped with small terminal aperture, housing apical organ; rim of apical modification of scolex proper covered with spinitriches; apical organ small, glandular, non-eversible, non-protrusible. Proglottids craspedote, non-laciniate. Strobila divided into anterior region consisting of laterally expanded, non-reproductive proglottids, forming a trough, and the reproductive region consisting of proglottids with internal reproductive anatomy. Testes numerous, in field anterior to ovary. Vas deferens extending from ootype to distal end of cirrus sac, in form of expanded duct in gravid proglottids. External seminal vesicle absent. Internal seminal vesicle present. Cirrus sac U-shaped, thick walled. Cirrus armed, opening into genital atrium through recessed papillae. Ovary H-shaped in dorso-ventral view, bilobed in cross-section. Vagina absent (possibly present in *E. qatarense*). Genital pores lateral, irregularly alternating. Uterus saccate, extending along median line of proglottid, stopping short of level of genital pore. Vitellaria follicular, in lateral fields, multiple follicles on each side of proglottid in cross-section, restricted in distribution between anterior margin of ovary and genital pore. One dorsal and one ventral pair of excretory ducts present. Eggs arranged in cocoons. Parasites of rays in the genus *Rhinoptera* Cuvier, 1829 (Rhinopteridae). Indian Ocean (Sri Lanka), Arabian Gulf, and Timor Sea (Australia).

Chronology

Shipley and Hornell (1906): erect the genus *Eniochobothrium* with *E. gracile* as the type species for a few specimens from *Rhinoptera javanica* from Dutch Bay, Ceylon; provide a detailed description of overall appearance of the worm, including the distinctive anterior expansion of the strobila; internal proglottid anatomy is not described; comment that the form of this genus is so distinctive that it may deserve erection of a new family.

Stiles and Hassall (1912): *Eniochobothrium* Shipley and Hornell, 1906; *E. gracile* Shipley and Hornell, 1906 (in *Rhinoptera javanica*, Dutch Bay).

Meggitt (1924): treats *Eniochobothrium* Shipley and Hornell, 1906 in the family Phyllobothriidae, order Tetraphyllidea; provides an abbreviated diagnosis of the genus.

Southwell (1925): treats *Eniochobothrium* in the suborder A, order Cyclophyllidea; repeats Shipley and Hornell's (1906) original diagnosis of the genus.

Poche (1926): treats *Eniochobothrium* Shipley and Hornell, 1906 as a genus "*Phyllobothriineorum sedis incertae*" (p. 376); comments on the possible necessity of creating a new family for this genus in the future.

Southwell (1930): classifies lecanicephalideans in two of seven families in the order Tetraphyllidea, the family Lecanicephalidae Braun (syn. Gamobothriidae Linton) and the family Cephalobothriidae (Pintner); considers *Eniochobothrium* Shipley and Hornell, 1906 not to belong to either of these lecanicephalidean families, but to be of uncertain systematic status, most likely in the family Lecanicephalidae; same text as that of Southwell (1925).

Fuhrmann (1931): considers *Eniochobothrium* to be a very interesting genus of uncertain status and insufficiently known in the Tetraphyllidea.

Wardle and McLeod (1952): treat *Eniochobothrium* Shipley and Hornell, 1906 as a *genus inquirendum*, with affinities to Lecanicephala (or Tetraphyllidea or Disculicipitidae).

Yamaguti (1959): treats *Eniochobothrium* Shipley and Hornell, 1906 as a *genus incertae sedis*.

Joyeux and Baer (1961): consider *Eniochobothrium*, along with *Hornellobothrium*, as a genus that is insufficiently described, in the order Tetraphyllidea.

Chincholikar and Shinde (1978a): describe a second species in the genus (*Eniochobothrium trygonis*).

Schmidt (1986): treats *Eniochobothrium* Shipley and Hornell, 1906 in the family Lecanicephalidae, order Lecanicephalidea.

Butler (1987a): notes that *Eniochobothrium* Shipley and Hornell is very likely not a junior synonym of *Discobothrium* Van Beneden.

Euzet (1994b): treats *Eniochobothrium* as *incertae sedis* in the Lecanicephalidea; notes that it is easily recognizable and has not been found again (in the type host) since its original description; suggests three hypotheses to explain the similarities of *Eniochobothrium* to *Litobothrium*: similarity as a result of convergence, *Eniochobothrium* and *Litobothrium* are identical and *Rhinoptera* (host of *Eniochobothrium*) is an "accidental" host in which development of the parasite is not completed or the worm retains its "true" scolex, or *Eniochobothrium* and *Litobothrium* are identical and *Rhinoptera* is a host error.

Al Kawari *et al*. (1994): lists diagnostic features of genus *Eniochobothrium*; describes a third species in the genus (*Eniochobothrium qatarense*) and suggests that *Litobothrium*, *Renyxa*, and *Eniochobothrium* are closely related and belong to the family Litobothridae; emend the diagnosis of this family accordingly; consider Dailey's (1969) designation of litobothrideans as an order inconclusive and places the Litobothridae in the Lecanicephalidea.

Olson and Caira (2001): restate Euzet's (1994) and Al Kawari *et al*.'s (1994) opinion on a connection between *Litobothrium* and *Eniochobothrium*, but present arguments against this association.

Remarks

Shipley and Hornell (1906) erected this genus for *Eniochobothrium gracile* from a few specimens collected from *Rhinoptera javanica* Müller and Henle, 1841 from Dutch Bay, Ceylon (now Sri Lanka). Although lacking in specific detail, the description and its accompanying illustrations clearly outlined the highly unusual and unique overall morphology of this taxon. Given this distinctive morphology, it is surprising that this genus would go unreported from its original description until 1994, when Al Kawari *et al.* (1994) described a second species of *Eniochobothrium*, *E. qatarense*. Their detailed description of *E. qatarense*, accompanied by illustrations and scanning electron micrographs, did much to further our understanding of this obscure taxon. Earlier, Chincholikar and Shinde (1978a) had described a new species they called *Eniochobothrium trygonis* Chincholikar and Shinde, 1978. The placement in the genus was most likely because of its (slightly) laterally expanded anterior region (more reminiscent of species in the genus *Hornellobothrium*). However, as has also been stated by Al Kawari *et al.* (1994), the scolex morphology and proglottid anatomy *E. trygonis* is not consistent with the concept of *Eniochobothrium* of Shipley and Hornell (1906) and Al Kawari *et al.* (1994).

The uncertainty about the identity of *Eniochobothrium* has led to the questionable taxonomic position of the genus. For example, Meggitt (1924) considered *Eniochobothrium* valid in the family Phyllobothriidae, Southwell (1925) placed *Eniochobothrium* in an unspecified suborder (suborder A) apart from the remaining lecanicephalidean genera; Schmidt (1986) considered the genus valid in the order Lecanicephalidea; and Al Kawari *et al.* (1994) placed it in the family Litobothriidae, in the order Lecanicephalidea. More commonly, however, *Eniochobothrium* has been considered a genus of uncertain taxonomic position and not sufficiently known to be placed (*e.g.*, Poche 1926; Southwell 1930; Fuhrmann 1931; Wardle and McLeod 1952; Joyeux and Baer 1961; Euzet 1994b).

The lateral expansion of the anterior proglottids forming a trough-like region in *Eniochobothrium* has been the cause of speculation about the affinities between this genus and two other genera, *Litobothrium* (including *Renyxa* Kurochkin and Slankis, 1973) and *Hornellobothrium*, each of which also exhibits an anterior modified region of the strobila. Wardle *et al.* (1974) appear to have been the first to comment on this similarity. The possible affinities between *Eniochobothrium* and *Litobothrium* were subsequently addressed in more detail by Euzet (1994b), Al Kawari *et al.* (1994), and Olson and Caira (2001). While Euzet (1994b) proposed three hypotheses to explain the similarities (see chronology), Al Kawari *et al.* (1994) actually emend the diagnosis of the family Litobothriidae Dailey, 1969 to include *Eniochobothrium*. Olson and Caira (2001), however, presented convincing morphological arguments against the close affinities of these genera.

A peculiarity of species of *Eniochobothrium* is the fact that specimens seem to readily “lose their heads” (paraphrased from Shipley and Hornell 1906, p. 64). Specimens without scolices seem to be encountered more commonly in this taxon than in other cestode genera. Shipley and Hornell (1906) commented that their limited preserved material of *E. gracile* lacked scolices; Al Kawari *et al.* (1994) commented that the scolex of *E. qatarense* “was easily detached from the rest of the strobila” (p. 98); and, on average only one of approximately 25 specimens of the new species described below were found with their scolices attached. This speaks to the apparent fragile connection between the scolex and the anterior trough region of the strobila. Whether this lack of a scolex is an artifact of removal from the wall of the spiral intestine, or whether the trough serves as the primary attachment structure instead of the scolex, which might consequently be already detached in specimens *in situ*, remains to be investigated. Preliminary data suggests that the latter might be the case. Histological sections of at least five specimens of the new species of *Eniochobothrium* described in this study *in situ*, cut both horizontally and vertically to the surface of the spiral intestine, were prepared. Scolices could not be observed in any of the histological sections examined.

Most of the generic diagnoses presented for *Eniochobothrium* have paraphrased or repeated the original diagnosis of Shipley and Hornell (1906) (*e.g.*, Meggitt 1924; Southwell 1930; Schmidt 1986). Information on the internal anatomy of the proglottids in these diagnoses is limited to cirrus and cirrus sac features, and the position of the genital pore. Based on their work with *E. qatarense*, Al Kawari *et al.* (1994) provided a more complete diagnosis of *Eniochobothrium*. This diagnosis has been further modified here. Species specific characteristics, such as the number of testes or the number of eggs per cocoon were omitted. Scolex and proglottid terminology was standardized. For clarification, the strobila is considered to consist of the anterior trough region (consisting of laterally expanded, non-reproductive proglottids) and the posterior reproductive region (consisting of reproductive proglottids). The only potentially controversial emendation to Al Kawari *et al.*'s (1994) diagnosis made here concerns the vagina. In the description of *E. qatarense*, the vagina is described as "hardly traced in whole-mounted specimens," appearing as a "short tube which lies in front of the cirrus pouch and opens on the genital atrium immediately anterior to the male opening" in sectioned material (Al Kawari *et al.* 1994, p. 101). The vagina of *E. qatarense* was consequently not figured by Al Kawari *et al.* (1994). Over 100 specimens of the new species of *Eniochobothrium* described as part of this study were prepared and examined as whole mounts. A vagina was not observed. In addition, proglottids of four different worms, at varying stages of maturity, were serially cross-sectioned and one proglottid was sectioned longitudinally (all at 5 µm intervals). Again, a duct identifiable as the vagina was not observed in any of these preparations. The vagina was the only part of the female reproductive system that was lacking from this new species of *Eniochobothrium*. A more detailed morphological investigation into this issue, possibly using transmission electron microscopy, is imperative. Until further evidence is presented, the generic diagnosis of *Eniochobothrium* was emended to read: "Vagina absent (possibly present in *E. qatarense*)."

Eniochobothrium gracile Shipley and Hornell, 1906

TYPE SPECIES

(Fig. 22)

Synonyms: None.

Type host: *Rhinoptera javanica* Müller and Henle, 1841, Javanese cownose ray (Rhinopteridae, Myliobatiformes).

Additional hosts: None.

Site of infection: Spiral intestine.

Type locality: Dutch Bay, Ceylon (now Sri Lanka) (Fig. 22).

Additional localities: None.

Number of specimens on which the original description was based: Two or three.

Type specimens: Not indicated in original description.

Voucher specimens: None.

Material examined: None.

Etymology: *Gracilis*, L., slender, thin.

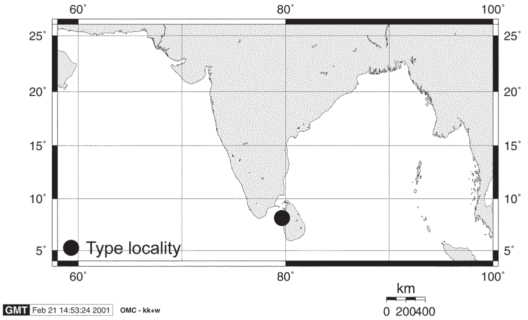


Fig. 22. Geographic distribution of *Eniochobothrium gracile* Shipley and Hornell, 1906.

Chronology

Shipley and Hornell (1906): erect the genus *Eniochobothrium* with *E. gracile* as the type species for a few specimens from *Rhinoptera javanica* from Dutch Bay, Ceylon; provide a detailed description of the overall appearance of the worm, but the proglottid anatomy is not described; suggest that the form of this genus is so distinct that it deserves generic recognition and possibly even the establishment of a new family.

Stiles and Hassall (1912): *Eniochobothrium* Shipley and Hornell, 1906; *E. gracile* Shipley and Hornell, 1906 (in *Rhinoptera javanica*, Dutch Bay).

Jameson (1912): says that one is likely to find adult stages of *Tylocephalum ludificans* and *T. minus* among members of *Tylocephalum*, occurring in oyster-eating elasmobranchs, such as those described by Shipley and Hornell (*e.g.*, *Eniochobothrium gracile*).

Southwell (1925): reiterates some details of the original description of *Eniochobothrium gracile* from Shipley and Hornell (1906); notes that the possession of four suckers warrants placement in the order Cyclophyllidea, but is unable to classify it further; notes that even if shape of strobila is an abnormal condition, the scolex is distinct from other genera.

Southwell (1930): lists *Eniochobothrium gracile* as type species of *Eniochobothrium*, which is of uncertain systematic position, most likely in the family Lecanicephalidae; same text as that of Southwell (1925).

Wardle and McLeod (1952): list *E. gracile* Shipley and Hornell, 1906 as the type and only species of *Eniochobothrium*; consider *Eniochobothrium* as a *genus inquirendum* with affinities to Lecanicephala (or Tetraphyllidea or Disculicipitidae).

Yamaguti (1959): recognizes *E. gracile* Shipley and Hornell, 1906 as the type species of *Eniochobothrium* Shipley and Hornell, 1906, which is considered as a *genus incertae sedis*.

Wardle *et al.* (1974): comment that the lateral expansions of *D. cobraefomis* [sic] and *Eniochobothrium gracile*, approximate the anterior strobilar condition found in species in the order Litobothridea.

Schmidt (1986): recognizes *Eniochobothrium gracile* Shipley and Hornell, 1906 as the type species of *Eniochobothrium*; one additional species of *Eniochobothrium*, *E. trygonis*, is recognized.

Al Kawari *et al.* (1994): distinguish their new species *Eniochobothrium qatarense* from *E. gracile* and *E. trygonis*.

Euzet (1994b): recognizes *Eniochobothrium gracile* as type and only species in the genus *Eniochobothrium*, which is considered to be *incertae sedis*.

Olson and Caira (1999): [see chronology of *Eniochobothrium euaxos* Jensen, n. sp.].

Olson *et al.* (1999): [see chronology of *Eniochobothrium euaxos* Jensen, n. sp.].

Kodedová *et al.* (2000): [see chronology of *Eniochobothrium euaxos* Jensen, n. sp.].

Olson *et al.* (2001): [see chronology of *Eniochobothrium euaxos* Jensen, n. sp.].

Littlewood and Olson (2001): [see chronology of *Eniochobothrium euaxos* Jensen, n. sp.]

Hoberg *et al.* (2001): include morphological data (for "Lecanicephalidea") and sequence data of specimen(s) identified as *Eniochobothrium gracile* as a representative taxon for the Lecanicephalidea in a phylogenetic analysis among orders of Eucestoda using a total evidence approach.

Remarks

Shipley and Hornell (1906) erected the genus for only a few specimens of these "small but very remarkable Cestodes" (p. 64), they named *Eniochobothrium gracile*. The specimens of this species were unusual because of the presence of a laterally expanded region of the strobila, forming a trough-like structure. Shipley and Hornell (1906) recognized the unique strobilar morphology of these worms and concentrated on describing the different parts of the strobila at length. Interestingly, although Shipley and Hornell (1906) had only limited material available to them for their original description, they did note that the preserved specimens "had all lost their heads" (p. 64). The only features of the internal anatomy indicated in the original description were those associated with the cirrus and the cirrus sac.

Assuming that the two to three specimens on which the original description was based constitute the type material, Shipley and Hornell (1906) did not state whether these specimens were deposited. There has been no mention of the type material of *E. gracile* since its description. Moreover, *E. gracile* has not been reported since 1906. While it appears at this time that the concept of the genus is, more or less, understood, and it is possible to identify cestodes as belonging to the genus *Eniochobothrium*, our knowledge of the type species *E. gracile* is still limited. Collections of new material from the type host and, ideally, the type locality are suggested to redescribe this species.

Eniochobothrium euaxos Jensen, n. sp.

(Figs. 23-25)

Type host: *Rhinoptera* sp., Cownose ray (Rhinopteridae, Myliobatiformes).

Additional hosts: None.

Site of infection: Spiral intestine.

Type locality: Dundee Beach (12°50'S, 130°12'E), Fog Bay, Northern Territory, Australia (Fig. 23).

Additional localities: None.

Number of specimens on which the original description was based: 36 (25 whole mounts [four with scolices, 21 lacking scolices], four specimen cross-section series, one specimen longitudinal section series, four lactophenol preparations of eggs, and two specimens prepared for SEM).

Type specimens: Holotype (QM No. G 222894), seven paratypes (five whole mounts, one specimen cross-section series, and one lactophenol preparation of eggs) (QM Nos. G 222895-222901); eight paratypes (six whole mounts, one proglottid cross-section series, and one lactophenol preparation of eggs) (USNPC Nos. 94575-94576); five paratypes (four whole mounts and one lactophenol preparation of eggs) (KUNHM Nos. 002102-002106); 13 paratypes (nine whole mounts, two proglottid cross-section series, one specimen longitudinal section series, and one lactophenol preparation of eggs (LRP Nos. 3266-3278); two paratype specimens prepared for SEM (LRP).

Sequence data: Ef-1α, partial (Olson and Caira, 1999); 18S rDNA, complete (Olson and Caira, 1999); 28s rDNA, partial (GenBank No. AF286928) (Olson *et al.*, 2001).

Etymology: The specific epithet *euaxos* (Gr., easily broken) was chosen to refer to the fact that the connection between the scolex and the strobila is very fragile and, thus, the scolex in this species is readily detached.

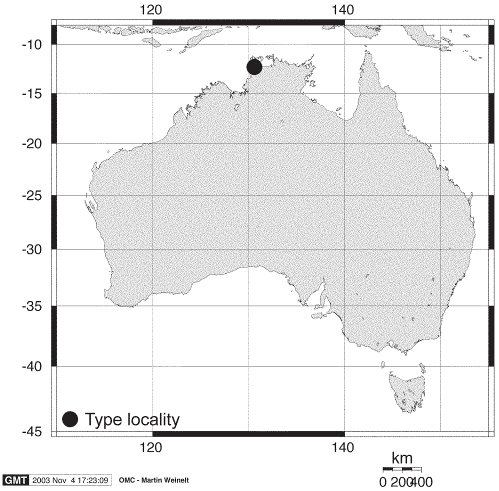


Fig. 23. Geographic distribution of *Eniochobothrium euaxos* Jensen, n. sp.

Chronology

Caira *et al.* (1999): include *Eniochobothrium euaxos* under the name *Eniochobothrium* sp. in a phylogenetic analysis based on morphological data; the species groups with the majority of the other lecanicephalidean taxa included in the analysis.

Olson and Caira (1999): include *Eniochobothrium euaxos* under the name *Eniochobothrium gracile* in molecular phylogenetic analysis based on 18S rDNA (GenBank No. AF124465) and Ef-1α (GenBank No. AF124809); results confirm taxonomic position of *E. euaxos* within Lecanicephalidea.

Olson *et al.* (1999): include *Eniochobothrium euaxos* under the name *Eniochobothrium gracile* (along with *Cephalobothrium* cf. *aetobatidis*) in molecular phylogenetic analysis based on 18S ssrDNA (GenBank No. AF124465); results from parsimony analyses place *E. euaxos* (and *C.* cf. *aetobatidis*) outside of the Tetraphyllidea, while results from maximum likelihood analyses place *E. euaxos* (and *C.* cf. *aetobatidis*) among the tetraphyllideans.

Kodedová *et al.* (2000): include *Eniochobothrium euaxos* under the name *Eniochobothrium gracile* in a molecular phylogenetic analysis of the Caryophyllidea, Pseudophyllidea, and Proteocephalidea based on complete 18S rRNA sequence (sequence data of Olson and Caira [1999] obtained from GenBank); resulting tree suggests *E. euaxos* is basal to a group consisting of Cyclophyllidea, Nippotaniidea, Tetrabothriidea, Proteocephalidea, and Tetraphyllidea; litobothriideans appear to be basal to these two groups combined.

Caira *et al.* (2001): include *Eniochobothrium euaxos* under the name *Eniochobothrium* sp. from Caira *et al.* (1999) in a more comprehensive phylogenetic analysis based on morphological data; the species groups with the majority of lecanicephalidean taxa included.

Olson *et al.* (2001): include *Eniochobothrium euaxos* under the name *Eniochobothrium gracile* in a molecular phylogenetic analysis based on complete sequences of the SSU rDNA (GenBank No. 124465) and partial sequence of the LSU rDNA (GenBank No. 286928); *E. euaxos* (along with *Cephalobothrium* cf. *aetobatidis* and *Tylocephalum* sp.) is usually placed basal to a group consisting of Cyclophyllidea, Nippotaniidea, Tetrabothriidea, Proteocephalidea, and Tetraphyllidea; *E. euaxos* (along with *Cephalobothrium* cf. *aetobatidis* and *Tylocephalum* sp.) grouped with the Litobothriidea in some analyses.

Littlewood and Olson (2001): use GenBank sequences of the SSU rDNA for *Cephalobothrium* cf. *aetobatidis* (Lecanicephalidae), *Eniochobothrium euaxos* under the name *Eniochobothrium gracile* (Lecanicephalidae) (GenBank No. 124465), and *Tylocephalum* sp. (Tetragonocephalidae) in a phylogenetic analysis investigating relationships among major clades of platyhelminths.

Hoberg *et al.* (2001): include morphological data (for "Lecanicephalidea") and sequence data of *Eniochobothrium euaxos* under the name *Eniochobothrium gracile* (GenBank No. 124465) as a representative taxon for the Lecanicephalidea in a phylogenetic analysis among orders of Eucestoda using a total evidence approach.

Description (Based on 25 whole mounts [four with scolices, 21 lacking scolices], four specimen cross-section series, one specimen longitudinal section series, four lactophenol preparations of eggs, and two specimens prepared for SEM.)

Worms 1,724-2,406 (2,112 ± 350.8; 3) long; worms lacking scolex 1,524-3,247 (2,232 ± 509.6; 25) long; maximum width at level of trough; 29-39 (33 ± 2.0; 24) proglottids total, euapolytic. Strobila divided into two regions, anterior trough region and posterior reproductive region. Trough region of strobila consisting of non-reproductive proglottids, expanded laterally, U-shaped in cross-section (Fig. 25B). Reproductive region of strobila consisting of reproductive proglottids which mature and develop reproductive organs.

Scolex 88-101 (94 ± 5.9; 4) long by 76-80 (78 ± 1.5; 4) wide, bearing four acetabula. Acetabula in form of suckers, sessile, 34-40 (37 ± 2.3; 4; 8) long by 25-29 (28 ± 1.5; 4; 8) wide. Apical modification of scolex proper in form of conical extension with small apical aperture (Fig. 25A and C), housing apical organ. Apical organ glandular, non-eversible, non-protrusible, 36-42 (39 ± 3.0; 4) long by 21-25 (23 ± 1.5; 4) wide.

Distal surfaces of acetabula, rims of acetabula and scolex proper posterior to acetabula covered with large blade-like spinitriches and small triangular microtriches (Fig. 25E-G). Scolex proper at level of and anterior to acetabula covered with small triangular microtriches (Fig. 25D and E). Apical modification of scolex covered with small tubercles (glands?) and small triangular microtriches (Fig. 25C). Proglottids of trough covered with short scale-like triangular microtriches, increasing in size towards posterior margin of proglottid (Fig. 25H). Reproductive proglottids of strobila covered with long pointed filitriches (Fig. 25J); filitriches becoming shorter and triangular at posterior margin of proglottid.

Cephalic peduncle absent. Non-reproductive and reproductive proglottids craspedote, non-laciniate. Trough 523-777 (659 ± 65.9; 25) long by 218-353 (274 ± 32.7; 24) wide, consisting of 18-25 (22 ± 1.8; 24) non-reproductive proglottids. Reproductive region of strobila 970-2,573 (1,572 ± 490.1; 25) long by 523-777 (659 ± 65.9; 25) wide, consisting of 8-12 (10 ± 1.2; 25) reproductive proglottids; immature proglottids 6-11 (9 ± 1.5; 25) in number, initially wider than long, becoming longer than wide; posterior most immature proglottid 77-320 (170 ± 67.7; 25) long by 124-214 (171 ± 21.0; 25) wide; mature proglottids 0 or 1 in number, longer than wide, 312-1,070 (744 ±

197.5; 22) long by 189-290 (230 ± 24.3; 22) wide; gravid proglottids 0-1 in number, 899-1,550 (1,202 ± 196.0; 11) long by 233-344 (301 ± 38.9; 11) wide. Testes 35-48 in number, 10-37 (24 ± 6.6; 23; 69) long by 10-34 (23 ± 5.6; 23; 69) wide in mature proglottids, anterior to ovary, in multiple irregular columns in dorso-ventral view, 1-2 rows deep in cross-section. Vas deferens with glandular wall proximally, in form of expanded duct in older mature and gravid proglottids, extending along lateral margin of proglottid from ootype to level of cirrus sac, then along median line of proglottid anteriorly, stopping short of anterior margin of proglottid, then extending posteriorly, entering cirrus sac at distal end, extensive in gravid proglottids. External seminal vesicle absent. Internal seminal vesicle present, most conspicuous in gravid proglottids. Cirrus sac U-shaped, thick walled, 242-467 (371 ± 59.4; 22) long by 42-73 (62 ± 7.3; 22) wide in mature proglottids, containing long uncoiled cirrus base, restricted to distal end of cirrus sac, and coiled cirrus. Cirrus armed. Ovary H-shaped in dorso-ventral view, bilobed in cross-section (Fig. 24D), 90-396 (240 ± 78.2; 22) long by 89-176 (128 ± 24.6; 23) wide, lobulated. Vagina not observed. Genital pores lateral, irregularly alternating, 70-84% (76 ± 3.7; 22) of proglottid length from posterior end. Uterus median, extending from posterior margin of ovary to approximately posterior margin of cirrus sac; uterine duct not observed; uterine pore absent. Vitellaria follicular, medullary, in two lateral fields, multiple vitelline follicles on each side of proglottid in cross-section, extending from middle of cirrus sac to level of ovarian bridge; vitelline follicles 8-37 (19 ± 6.4; 23; 69) long by 11-44 (28 ± 8.1; 23; 69) wide. One dorsal and one ventral pair of excretory ducts present. Eggs grouped in cocoons (Fig. 24F). Each cocoon containing 40-51 (45 ± 4.0; 4; 8) eggs, free cocoons 104-123 (115 ± 6.9; 4; 8) long by 80-92 (86 ± 4.2; 4; 8) wide. Eggs subspherical, thin-walled. Oncospheres, 8-15 (11 ± 1.7; 8; 24) long by 11-21 (14 ± 2.8; 8; 24) wide.

Remarks

A large number of specimens of this species were recovered from an as-of-yet unidentified species of cownose ray (genus *Rhinoptera*). *Eniochobothrium euaxos* can be easily distinguished from *E. qatarense* in that it possesses testes on the poral side of the proglottid anterior to the genital pore; this field of testes is absent in *E. qatarense*. In addition, *E. euaxos* has slightly fewer proglottids than *E. qatarense* (29-36 vs. 39-43) and a shorter cirrus sac (242-476 vs. 630-1,170). In *E. euaxos* each cocoon contains 40-51 eggs, whereas *E. qatarense* is described as possessing cocoons ("egg balls" [Al Kawari *et al.* 1994, p. 102]) containing ten eggs. *Eniochobothrium euaxos* is difficult to distinguish from *E. gracile* because the description provided by Shipley and Hornell (1906) is lacking in detail. Nonetheless, *E. euaxos* can be distinguished from *E. gracile* in that the former species possesses fewer total number of proglottids than does the latter (29-36 vs. 42-44, respectively). Moreover, Shipley and Hornell (1906) described the region of the strobila immediately posterior to the trough as "another isthmus, consisting again of about eighteen segments," followed by "some six or eight segments which very rapidly increase in size" (p. 64). In contrast, the entire reproductive strobila in *E. euaxos* consists of only 8-12 proglottids. In addition, *E. gracile* has been described (and has been illustrated) to possess a "short neck of three segments (p. 64). This region is lacking in specimens of *E. euaxos*. While Shipley and Hornell (1906) described the apex of the scolex of *E. gracile* as "pointing forward" and representing the "rostrum," which is unarmed (p. 64), the presence of an apical structure/organ is not noted. The apical organ of *E. euaxos* is quite conspicuous, similar in overall dimensions to the acetabula.

Eniochobothrium euaxos is the taxon referred to as "*Eniochobothrium* sp." in the phylogenetic analyses based on morphology of Caira *et al.* (1999, 2001). Although the source of the type material of this species and the source of the material used to code this species in Caira *et al.* (1999, 2001) is identical, the Caira *et al.* specimens were not included in the type series. *Eniochobothrium euaxos* has also been included in several phylogenetic analyses based on molecular data. So

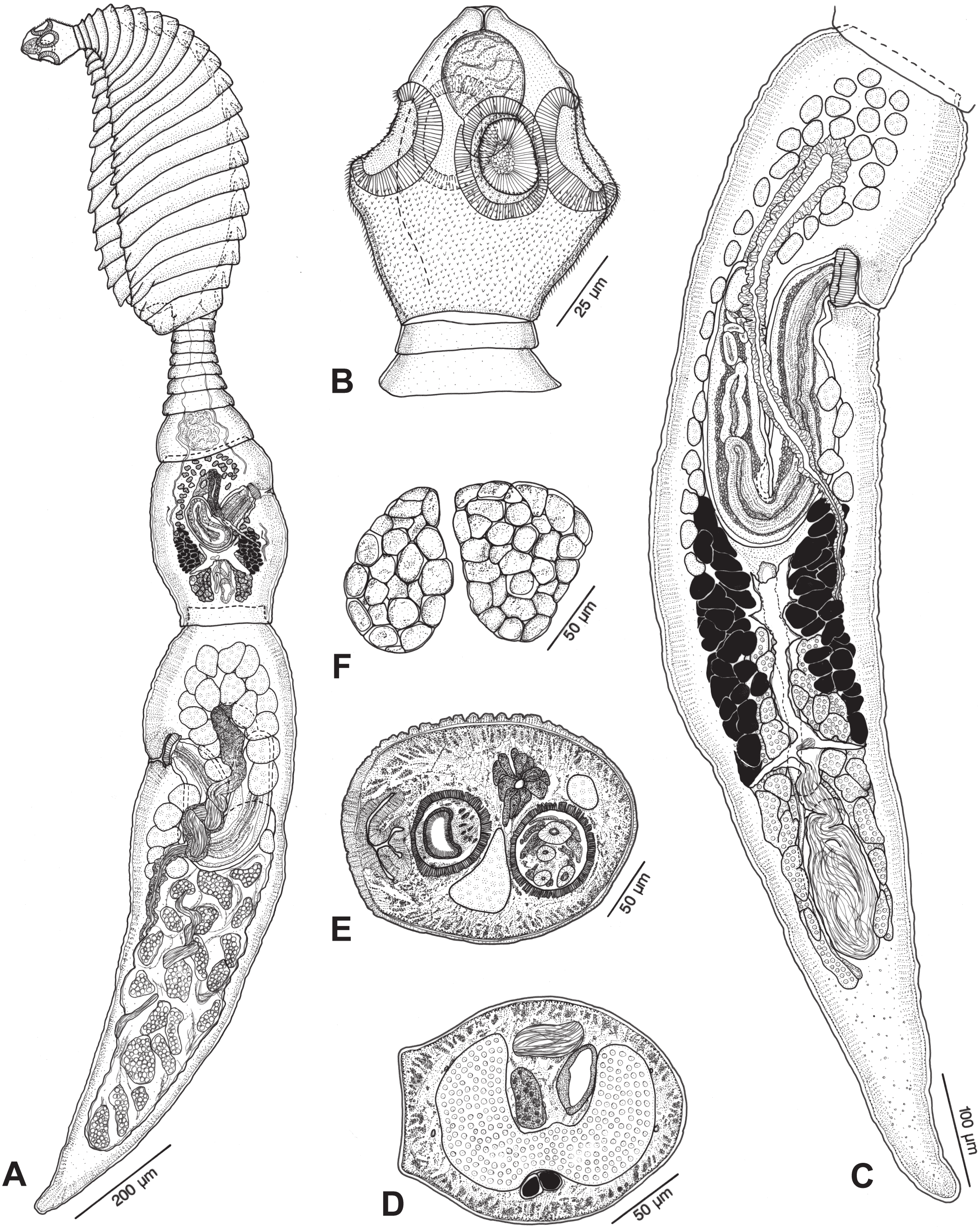


Fig. 24. A-F. Line drawings of *Eniochobothrium euaxos* Jensen, n. sp. A. Whole worm (holotype, QM No. G 22894). B. Scolex (holotype, QM No. G 22894). C. Mature terminal proglottid (QM No. G 22898). D. Cross-section through mature proglottid at level of ovarian bridge (USNPC No. 94575). E. Cross-section through mature proglottid at level of genital pore (USNPC No. 94575). F. Cocoons, note numerous eggs (QM No. G222900).

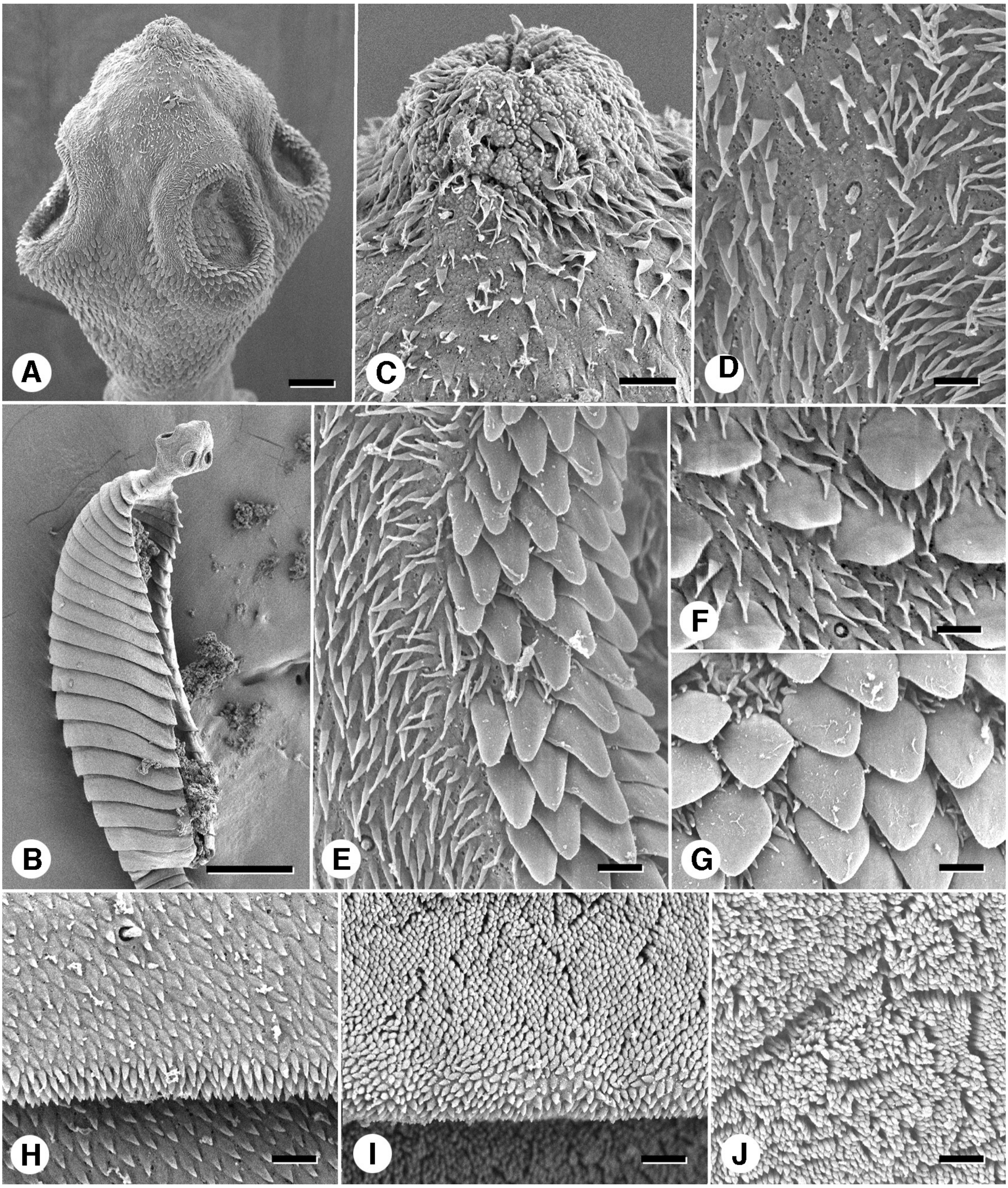


Fig. 25. A-J. Scanning electron micrographs of *Eniochobothrium euaxos* Jensen, n. sp. A. Scolex. B. Anterior strobila of non-reproductive proglottids forming trough. C. Apical modification of scolex proper. D. Microtriches on scolex proper. E. Microtriches on boundary of scolex proper and proximal acetabular surface. F. Microtriches on distal acetabular surface. G. Microtriches on scolex proper posterior to acetabula. H. Microtriches on surface of non-reproductive proglottids of trough. I. Microtriches on posterior margin of reproductive proglottids. J. Microtriches on surface of reproductive proglottids. Scale bars: A, 10 μm; B, 100 μm; C, 2.5 μm; D-J, 1 μm.

far, the complete sequence of the SSU rDNA, and partial sequences of the Ef-1α and 28S rDNA gene of *E. euaxos* were submitted to GenBank, however, under the incorrect name *Eniochobothrium gracile*. This name was first used in the analysis of Olson and Caira (1999). The specimens of *E. euaxos* that were sequenced were taken from at least one of the same host individuals as the type material of *E. euaxos*. Subsequently, sequence data of *E. euaxos* under the incorrect name have been used in several different studies (Olson *et al*. 1999; Kodedová *et al*. 2000; Olson *et al.* 2001; Littlewood and Olson 2001; Hoberg *et al*. 2001).

HEALYUM Jensen, 2001

Taxonomic status: Valid.

Synonyms: None.

Type species: *Healyum harenamica* Jensen, 2001.

Other species: *Healyum pulvis* Jensen, 2001.

Etymology: This genus was named in honor of Claire J. Healy without whose off-site assistance the collections in the Gulf of California would not have been possible.

Diagnosis (Modified from Jensen [2001]. Copyright 2001, The Journal of Parasitology. Used with permission.)

Worms euapolytic. Scolex with four acetabula; acetabula in form of suckers; rims of acetabula with blade-like spinitriches; apical modification of scolex proper in form of shallow dome with small aperture at apex, housing apical organ; apical organ small, possibly glandular. Proglottids craspedote, nonlaciniate. Testes few, anterior to ovary. Vas deferens in form of expanded duct, extending from ootype to anterior margin of proglottid. External and internal seminal vesicle absent. Cirrus sac pyriform. Cirrus unarmed. Ovary irregular in form in dorso-ventral view, irregular in cross-section, consisting of three lobes. Vagina opening into genital atrium posterior to cirrus sac. Genital pores sublateral, irregularly alternating. Uterus along median line in proglottid, saccate. Vitellaria follicular, in lateral columns, extending almost entire length of proglottid, interrupted by ovary. Eggs unknown. Parasites of manta rays in the genus *Mobula* Rafinesque, 1810 (Mobulidae). Gulf of California (Mexico).

Chronology

Caira *et al.* (2001): include a species of *Healyum* (*H. pulvis* under the name "n. gen. 3 n. sp.") in a comprehensive phylogenetic analysis based on morphological data; the species of *Healyum* groups outside of the majority of lecanicephalidean taxa included.

Jensen (2001): erects the genus *Healyum* with *H. harenamica* as the type species; describes a second species of *Healyum*, *H. pulvis*.

Remarks (Modified from Jensen [2001]. Copyright 2001, The Journal of Parasitology. Used with permission.)

The presence of an apical organ on the scolex, acetabula in the form of simple suckers, a vagina that opens into the genital atrium posterior to the cirrus sac and an external seminal vesicle that extends from posterior of the ootype to the cirrus sac led Jensen (2001) to place this genus in the order Lecanicephalidea.

Jensen (2001) distinguished *Healyum* from the lecanicephalidean genera *Aberrapex, Anteropora*, *Eniochobothrium*, *Hornellobothrium*, *Lecanicephalum*, *Paraberrapex* Jensen, 2001, *Polypocephalus,* and *Tylocephalum*, based on its possession of an ovary that is irregular in form (consisting of three lobes) in dorso-ventral view, rather than H-shaped. In addition, she noted that *Healyum* differs from *Anteropora* in its possession of sucker-like acetabula rather than acetabula that are bothridiate in form. It differs from *Tetragonocephalum* in that it lacks a greatly enlarged genital atrium as is present in the latter genus. Unlike *Lecanicephalum*, *Healyum* possesses a trilobed, rather than bilobed ovary in cross-section. Unlike *Polypocephalus*, the apical organ of *Healyum* is not subdivided into tentacles. *Healyum* lacks a large fungiform apical organ such as that seen in *Tetragonocephalum* and *Tylocephalum*. Its lack of laterally expanded immature proglottids in the anterior region of the strobila, before the proglottids narrow again and develop internal anatomy, further distinguishes it from *Eniochobothrium* and *Hornellobothrium*. *Healyum* further differs from *Aberrapex* and *Paraberrapex* in its possession of an apical organ. The proglottid anatomy of *Healyum* is most similar to that of *Corrugatocephalum* and *Quadcuspibothrium*. All three taxa have few testes (to date, the only species known in these genera consistently have three testes) that are arranged in one to two columns in dorso-ventral view, are two layers deep in cross-section, are only visible in barely mature proglottids, and are degenerated in fully mature proglottids. In addition, these taxa possess an extensive external seminal vesicle that extends almost the entire length of proglottid, and few, relatively large vitellaria. While the ovary in dorso-ventral view appears similarly trilobed in these genera, cross-sections through the ovary of *C. ouei* revealed an asymmetrically bilobed ovary; the ovary of *Healyum* and *Quadcuspibothrim* however consists of three distinct lobes. Nonetheless, *Healyum* and *Quadcuspibothrium* are easily distinguished from *Corrugatocephalum* based on their possession of a dome-shaped apical modification of the scolex proper that bears an aperture at its center and that houses a small apical organ internally; *Corrugatocephalum* lacks a dome-shaped apical modification of the scolex proper but possesses a unique apical structure, *i.e.* a large apical organ in the form of a cylinder that is sucker-like and bears vertical corrugations throughout its internal surface. *Healyum* and *Quadcuspibothrium* can be easily distinguished based on acetabular shape; acetabula in *Healyum* are in the form of suckers, while in *Quadcuspibothrium* each acetabulum bears four points on its margin. *Healyum* can be further distinguished from *Quadcuspibothrium* based on its possession of vitelline follicles arranged in two irregular lateral columns, rather than distinctly paired vitelline follicles.

Healyum harenamica Jensen, 2001

TYPE SPECIES

(Figs. 26, 28A-D and 29A-E)

Synonyms: None.

Type host: *Mobula japanica* (Müller and Henle, 1941), Spinetail mobula (Mobulidae, Myliobatiformes).

Additional hosts: None.

Site of infection: Spiral intestine.

Type locality: Punta Arena (24°04'N, 109°50'W), Baja California Sur, Mexico (Fig. 26).

Additional localities: None.

Number of specimens on which the original description was based: 16.

Type specimens: Holotype (CNHE No. 4186); paratypes (CNHE No. 4187, USNPC No. 9121, HWML No. 16376, and LRP Nos. 2180-2184).

Voucher specimens: None.

Material examined: CNHE No. 4186 (holotype); CNHE No. 4187, USNPC No. 9121, HWML No. 16376, and LRP Nos. 2180-2184 (paratypes).

Etymology: The specific epithet *harenamica* (*harena*, L., sand; *mica*, L., grain) was chosen to describe the unusually small size of individuals of this species.

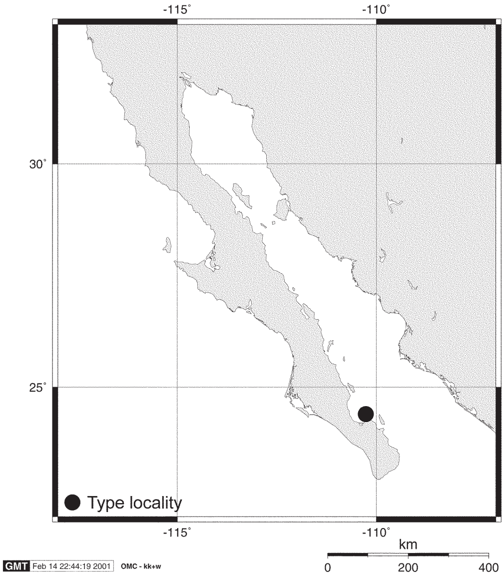


Fig. 26. Geographic distribution of *Healyum harenamica* Jensen, 2001.

Chronology

Jensen (2001): describes *Healyum harenamica* as the type species of the new genus *Healyum*.

Description (Modified from Jensen [2001]. Copyright 2001, The Journal of Parasitology. Used with permission.) (Based on 16 whole worms.)

Worms 495-860 (700 ± 128.4; 16) long; maximum width usually at level of scolex; 10-17 (14 ± 2.4; 16) proglottids, euapolytic. Scolex 150-250 (183 ± 33.9; 16) long by 190-290 (234 ± 29.2; 15) wide, consisting of four acetabula. Acetabula in form of suckers, sessile, 51-75 (62 ± 6.8; 16; 32) in diameter. Apical modification of scolex proper slightly expanded with small aperture at center (Fig. 29B), housing apical organ. Apical organ 21-36 (27 ± 3.9; 16) wide, glandular, and possibly eversible and/or protrusible. Rims of acetabula covered with blade-like spinitriches and pointed filitriches (Fig. 29E). Scolex proper covered with short filitriches (Fig. 29C).

Cephalic peduncle very short. Strobila covered with short filitriches (Fig. 29D). Proglottids craspedote, non-laciniate. Immature proglottids 8-15 (12 ± 2.2; 16) in number, wider than long; two most posterior immature proglottids 32-76 (53 ± 14.3; 16; 32) long by 115-237 (164 ± 30.9; 15; 30) wide. Mature proglottids one or two in number, longer than wide; non-terminal mature proglottids 62-105 (82 ± 13.5; 14) long by 115-175 (145± 20.4; 13) wide; terminal mature proglottids 145-290 (186 ± 45.8; 16) long by 95-147 (113 ± 17.2; 15) wide. Testes three in number, 20-55 (33 ± 8.3; 16; 32) long by 29-62 (43 ± 8.3; 15; 30) wide, distributed anterior to ovary, slightly overlapping anterior margins of ovary, two columns in dorso-ventral view, two rows deep in cross-section, degenerated in terminal proglottid. Vas deferens expanded to form extensive external seminal vesicle. External seminal vesicle, saccate, extending from ootype to anterior margin of proglottid, then posteriorly to distal region of cirrus sac. Internal seminal vesicle absent. Cirrus sac pyriform, slightly angled anteriorly, 39-58 (49 ± 5.9; 14) long by 31-42 (35 ± 3.4; 15) wide, containing coiled cirrus. Cirrus unarmed. Ovary consisting of three lobes, irregular in shape in dorso-ventral view, trilobed in cross-section, 44-85 (64 ± 12.1; 16) long by 54-77 (63 ± 9.7; 15) wide; ovarian lobes smooth, almost round, 24-44 (34 ± 5.7; 16; 32) long by 29-45 (35 ± 4.1; 115; 30) wide. Mehlis' gland posterior to ovary. Vagina thick-walled, opening into genital atrium posterior to cirrus sac; vaginal sphincter absent; seminal receptacle not observed. Genital pores sublateral, irregularly alternating, 69-81% (70 ± 5; 16) of proglottid length from posterior end. Uterus inconspicuous in mature proglottids, extending from ovarian bridge to level of genital pore; uterine duct not observed; uterine pore absent. Vitellaria follicular, medullary, one dorsal and one ventral column of vitelline follicles on each lateral margin of proglottid, extending entire length of proglottid, interrupted by ovary; vitelline follicles 21-55 (33 ± 8.1; 16; 48) long by 24-51 (32 ± 6.5; 15; 45) wide. Excretory ducts not observed. Eggs not observed.

Remarks (Modified from Jensen [2001]. Copyright 2001, The Journal of Parasitology. Used with permission.)

Individuals of this species are so small that they were recovered only from a spiral intestine that was fixed in the field and subsequently examined using a dissecting microscope upon return to the laboratory. *Healyum harenamica* was recovered from only one of nine specimens of *Mobula japanica* for which the spiral intestine was examined (prevalence: 11.1%).

Healyum pulvis Jensen, 2001

(Figs. 27, 28E-G and 29F-J)

Synonyms: None.

Type host: *Mobula japanica* (Müller and Henle, 1941), Spinetail mobula (Mobulidae, Myliobatiformes).

Additional hosts: None.

Site of infection: Spiral intestine.

Type locality: Punta Arena (24˚04'N, 109˚50'W), Baja California Sur, Mexico (Fig. 27).

Additional localities: None.

Number of specimens on which the origi-

nal description was based: 11.

Type specimens: Holotype (CNHE No. 4184); paratypes (CNHE No. 4185; USNPC No. 91213; HWML No. 16377, and LRP Nos. 2185-2188).

Voucher specimens: None.

Material examined: CNHE No. 4184 (holotype); CNHE No. 4185, USNPC No. 91213, HWML No. 16377, and LRP Nos. 2185-2188 (paratypes).

Etymology: The specific epithet *pulvis* (L., dust, powder) was chosen to emphasize the minute size of the individuals of this species.

Chronology

Caira *et al.* (2001): include *Healyum pulvis* under the name "n. gen. 3 n. sp." in a comprehensive phylogenetic analysis based on morphological data; the species groups, along with two other lecanicephalidean taxa (*Aberrapex senticosus* and *Paraberrapex manifestus*) lacking an apical structure outside of the majority of lecanicephalidean taxa included.

Jensen (2001): erects the new genus *Healyum* with *H. harenamica* as the type species; describes a second species of *Healyum*, *H. pulvis*.

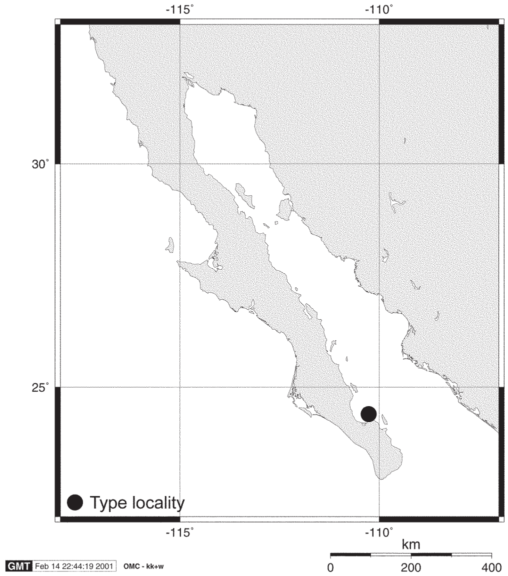


Fig. 27. Geographic distribution of *Healyum pulvis* Jensen, 2001.

Description (Modified from Jensen [2001]. Copyright 2001, The Journal of Parasitology. Used with permission.) (Based on 11 whole worms.)

Worms 375-650 (471 ± 70.5; 11) long; maximum width at level of scolex or at anterior third of strobila; 7-11 (9 ± 1.1; 11) proglottids, euapolytic. Scolex 65-135 (95 ± 18; 11) long by 100-160 (122 ± 19.8; 11) wide, consisting of four acetabula. Acetabula sucker-like in form, sessile, 27-37 (31 ± 2.8; 10; 20) in diameter. Apical modification of scolex proper slightly expanded with small aperture at center (Fig. 29G), housing apical organ. Apical organ inconspicuous, possibly glandular.

Rims of acetabula covered with tongue depressor-like spinitriches and pointed filitriches (Fig. 29J). Scolex proper covered with short filitriches (Fig. 29H). Strobila covered with short filitriches (Fig. 29I).

Cephalic peduncle short. Proglottids craspedote, non-laciniate. Immature proglottids 6-10 (7 ± 1.1; 11) in number, wider than long; two posterior-most immature proglottids 34-88 (54 ± 15.6; 11; 22) long by 70-130 (97 ± 18.4; 11; 22) wide. Mature proglottids one or two in number, longer than wide; non-terminal mature proglottids 82-105 (93 ± 16.3; 2) long by 95-110 (102 ± 10.6; 2) wide; terminal mature proglottids 125-220 (171 ± 27.3; 11) long by 55-100 (78 ± 15.8; 11) wide. Testes three in number, 10-27 (17 ± 4.2; 11; 22) long by 19-38 (28 ± 5.5; 11; 22) wide, anterior to ovary, overlapping anterior margins of ovary, arranged in one column in dorso-ventral view, one row deep in cross-section, degenerated in terminal proglottid. Vas deferens expanded to form conspicuous external seminal vesicle. External seminal vesicle saccate, extending from ootype to anterior margin of proglottid, then posteriorly to enter cirrus sac at distal end. Internal seminal vesicle absent. Cirrus sac pyriform, slightly angled anteriorly, 34-50 (41 ± 5.6; 11) long by 20-31 (26 ± 3.2; 11) wide, containing coiled cirrus. Cirrus unarmed. Ovary consisting of three lobes, irregular in shape in dorso-ventral view, trilobed in cross-section, 38-61 (47 ± 7.4; 11) long by 40-71 (55 ± 9.7; 11) wide; ovarian lobes smooth, almost round, 19-35 (26 ± 4; 11; 22) long by 20-35 (28 ± 4.4; 11; 22) wide. Mehlis' gland not

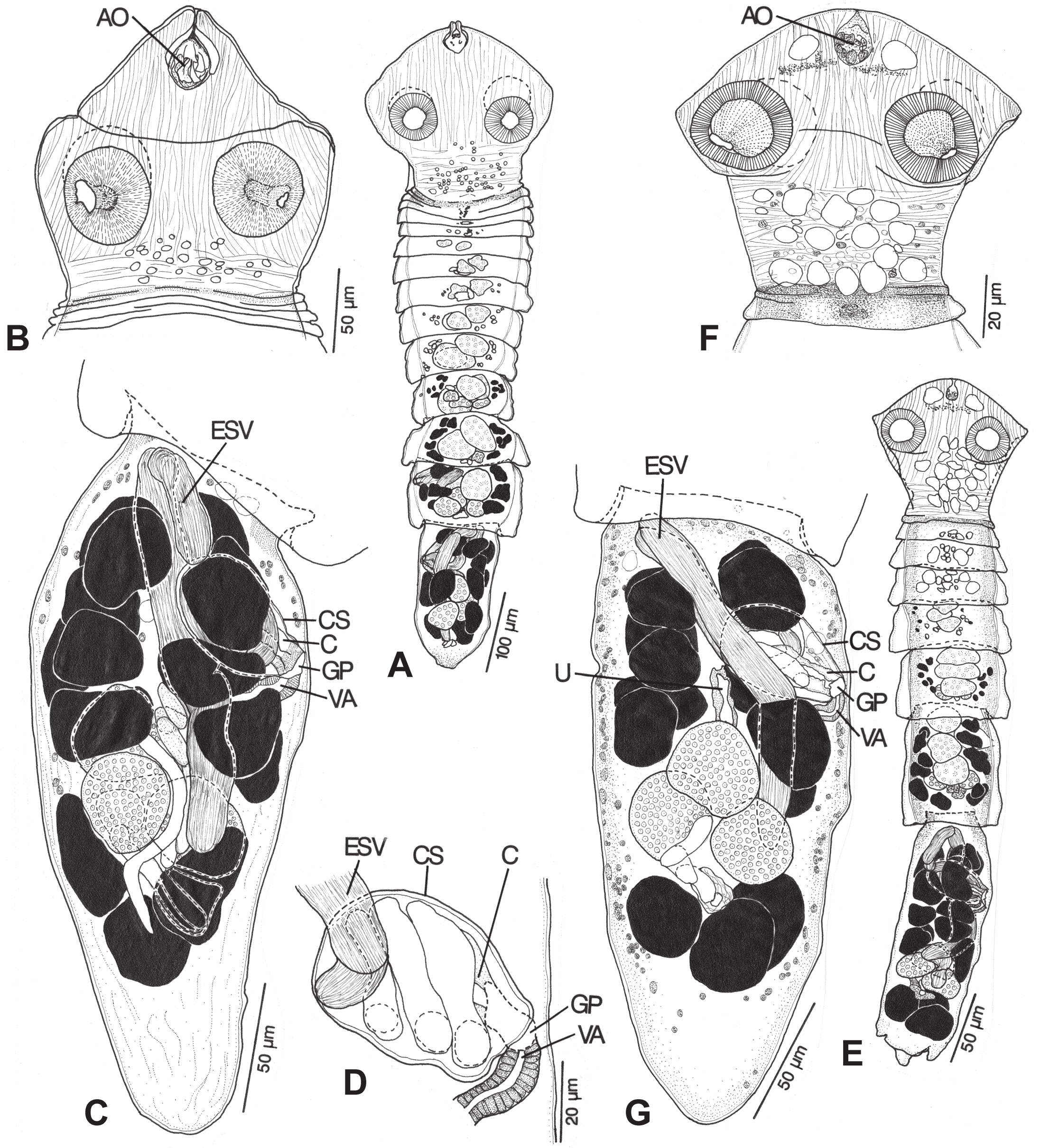


Fig. 28. A-G. Line drawings of *Healyum harenamica* Jensen, 2001 and *Healyum pulvis* Jensen, 2001. A-D. *Healyum harenamica*. A. Whole worm. B. Scolex. C. Mature terminal proglottid. D. Detail of terminal genitalia. E-G. *Healyum pulvis*. E. Whole worm. F. Scolex. G. Mature terminal proglottid. (Taken from Jensen [2001]. Copyright 2001, The Journal of Parasitology. Used with permission.)

observed. Vagina thick-walled, opening into genital atrium posterior to cirrus sac; vaginal sphincter absent; seminal receptacle not observed. Genital pores sublateral, irregularly alternating, 64-81% (70 ± 4.7; 11) of proglottid length from posterior end. Uterus, uterine duct and uterine pore not observed. Vitellaria follicular, medullary, one dorsal and one ventral column of vitelline follicles on each lateral margin of proglottid, extending entire length of proglottid, interrupted by ovary in terminal proglottid; vitelline follicles 13-35

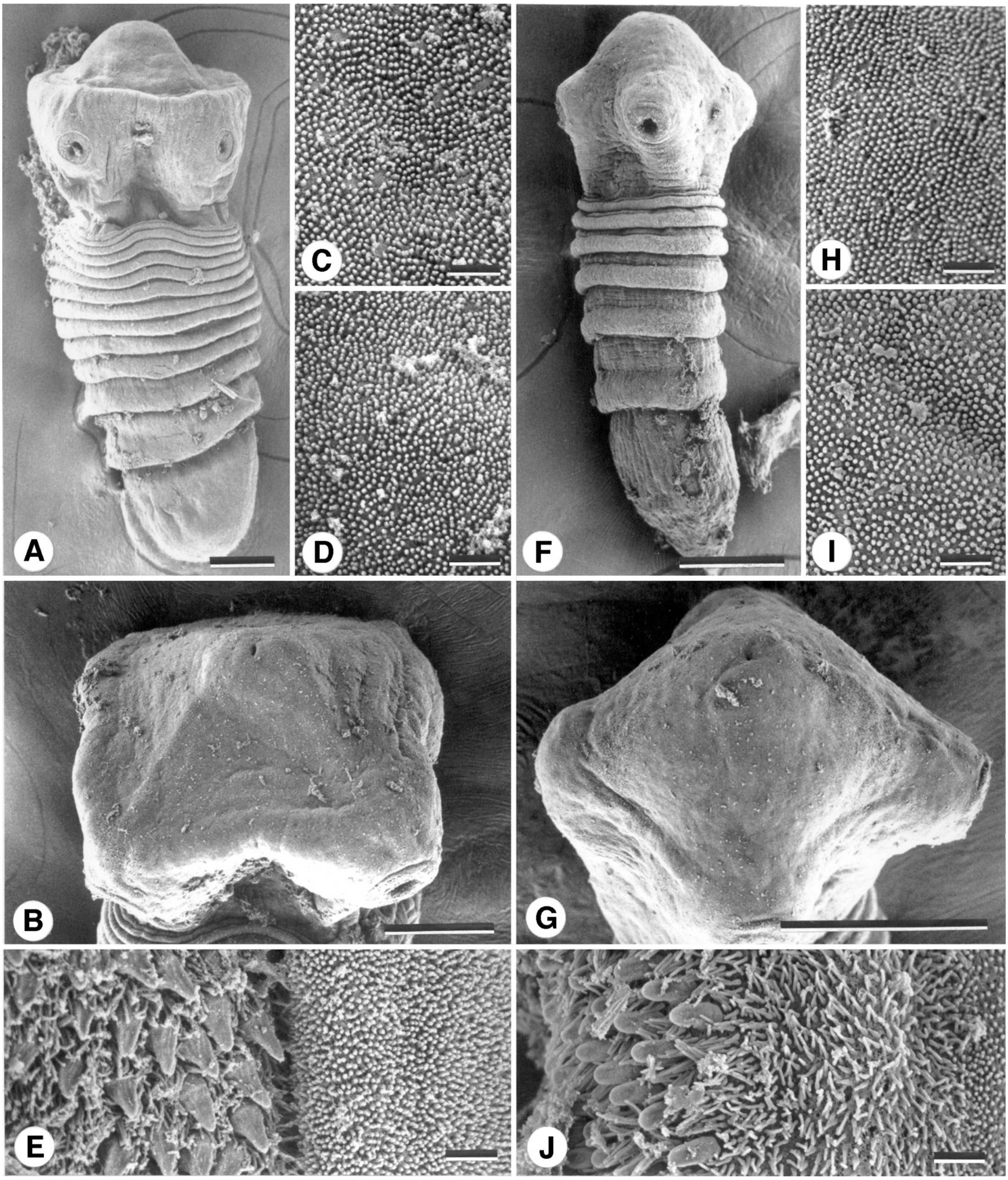


Fig. 29. A-J. Scanning electron micrographs of *Healyum harenamica* Jensen, 2001 and *Healyum pulvis* Jensen, 2001. A-E. *Healyum harenamica*. A. Whole worm. B. Apical view of scolex; note aperture at apex of apical modification of scolex proper. C. Microtriches on surface of scolex proper. D. Microtriches on proglottid. E. Microtriches on acetabular rim. F-J. *Healyum pulvis*. F. Whole worm. G. Apical view of scolex; note aperture at apex of apical modification of scolex proper. H. Microtriches on surface of scolex proper. I. Microtriches on proglottid. J. Microtriches on acetabular rim. Scale bars: A, B, F and G, 50 µm; C-D and H-J, 1 µm. (Taken from Jensen [2001]. Copyright 2001, The Journal of Parasitology. Used with permission.)

(23 ± 5.4; 10; 30) long by 16-36 (23 ± 4.2; 10; 30) wide. Excretory ducts not observed. Eggs not observed.

Remarks (Modified from Jensen [2001]. Copyright 2001, The Journal of Parasitology. Used with permission.)

Jensen (2001) distinguished *Healyum pulvis* from *H. harenamica*, the only other species in the genus, in that it has a smaller scolex than *H. harenamica* (65-135 long by 100-160 wide vs. 150-250 long by 190-290 wide) and the suckers of *H. pulvis* are smaller in diameter than those of *H. harenamica* (27-37 vs. 51-75). Whereas the apical organ of *H. pulvis* is very inconspicuous and gland-like, the apical organ of *H. harenamica* is obvious and possibly protrusible. *Healyum pulvis* can further be distinguished from *H. harenamica* based on the shape of the spinitriches on the acetabular rims; whereas *H. pulvis* possesses spinitriches that are tongue depressor-like in form, the spinitriches on the acetabular rims of *H. harenamica* are blade-like in form. In addition, the maximum width of the strobila in *H. pulvis* is smaller than the maximum width of the strobila of *H. harenamica* (90-150 vs. 170-320) and *H. pulvis* has relatively fewer proglottids than does *H. harenamica* (7-11 vs. 10-17, respectively).

Healyum pulvis was the taxon referred to as "new genus 3 n. sp." in the phylogenetic analysis presented by Caira *et al.* (2001). The type material of *H. pulvis* includes some of the specimens used to code this species by Caira *et al.* (2001).

As for *H. harenamica*, individuals of *H. pulvis* were recovered only from spiral intestines that had been fixed in the field and subsequently examined using a dissecting microscope in the laboratory. Jensen (2001) recovered *H. pulvis* from all nine specimens of *Mobula japanica* for which the spiral intestine was examined (prevalence: 100%).

HORNELLOBOTHRIUM
Shipley and Hornell, 1906

Taxonomic status: Valid.

Synonyms: None.

Type species: *Hornellobothrium cobraformis* Shipley and Hornell, 1906.

Other species: *Hornellobothrium extensivum* Jensen, n. sp.

Putative species: "*H. cobraformis*" specimen A of Butler (1987b); "*H. cobraformis*" specimen B of Butler (1987b).

Etymology: *Hornell-*, presumably named after a family member of J. Hornell; *bothrion,* Gr., diminutive of *bothros*, trench, pit, trough.

Diagnosis (Based on Shipley and Hornell [1906].)

Worms euapolytic. Scolex with four acetabula; acetabula bothridiate in form, simple, facially unmodified; distal and proximal surfaces of acetabula and scolex proper at level of and posterior to acetabula covered with blade-like spinitriches and pointed filitriches. Apical modification of scolex proper in form of small conical extension with aperture at apex or in form of "a constricted stalk" (Shipley and Hornell, 1906, p. 45), housing/bearing apical organ. Apical organ small, non-eversible, non-protrusible, glandular and/or muscular or in form of "knob-like rostellum" (Shipley and Hornell, 1906, p. 45). Proglottids craspedote, non-laciniate. Immature proglottids at anterior of strobila conspicuously expanded laterally (length to width ratio of immature proglottids usually exceeding 1:4), more posterior proglottids often bearing reproductive organs, not conspicuously expanded laterally. Testes numerous, anterior to ovary. Vas deferens expanded to form external seminal vesicle. External seminal vesicle saccate, extending from ootype to cirrus sac. Internal seminal vesicle absent. Cirrus sac pyriform. Cirrus unarmed. Ovary in form of lobes radiating in all directions in dorso-ventral view, radiating dorso-ventrally in cross-section (essentially bilobed). Vagina opening into genital atrium anterior to cirrus sac, extending along median line of proglottid. Genital pores lateral, irregularly alternating. Uterus saccate, median. Vitellaria follicular, in lateral columns, anterior to ovary. One dorsal and one ventral pair of excretory ducts present. Eggs unknown. Parasites of the Spotted eagle ray, *Aetobatus narinari* (Myliobatidae). Northern Indian Ocean (Sri Lanka) and Timor Sea (Australia).

Chronology

Shipley and Hornell (1906): erect the genus *Hornellobothrium* with *H. cobraformis* as the type species for "great numbers of this curious and very minute species" from *Aetobatis* [sic] *narinari* from Ceylon; provide a superficial diagnosis of the genus; the anterior widening of the strobila is described; internal proglottid anatomy is not; a differential diagnosis from any other genus or species of cestode is not provided.

Meggitt (1924): treats *Hornellobothrium* Shipley and Hornell, 1906 in the family Phyllobothriidae, order Tetraphyllidea, along with *Eniochobothrium* and 24 tetraphyllidean and proteocephalidean genera; provides an abbreviated diagnosis of the genus.

Southwell (1925): considers *Hornellobothrium* Shipley and Hornell, 1906 to be a junior synonym of *Discobothrium* Van Beneden, 1870 based on similarity between figures of the scolices of *D. fallax* and *H. cobraformis*, but considers these to be distinct species; considers *Discobothrium* intermediate between Cyclophyllidea and Tetraphyllidea.

Poche (1926): modifies the list of 26 lecanicephalidean, tetraphyllidean, and proteocephalidean genera Meggitt (1924) considers to be valid in the family Phyllobothriidae; consequently, considers *Hornellobothrium* Shipley and Hornell, 1906 a valid genus in the family Phyllobothriidae, suborder Phyllobothriinea *nom. nov.*, order Taeniidea *nom. nov.*, along with 22 tetraphyllidean genera and *Staurobothrium*.

Southwell (1930): considers *Hornellobothrium* to be a junior synonym of *Discobothrium* Van Beneden, 1870; considers *Discobothrium* as a genus of uncertain taxonomic position, most likely in the family Lecanicephalidae, not intermediate between Cyclophyllidea and Tetraphyllidea.

Fuhrmann (1931): classifies lecanicephalideans in two of seven families in the order Tetraphyllidea, the family Lecanicephalidae Braun (syn. Gamobothriidae Linton) and the family Cephalobothriidae (Pintner); considers *Hornellobothrium* not to belong to either of these lecanicephalidean families, but to be of uncertain systematic status and not sufficiently known, but a very interesting genus in the Tetraphyllidea.

Wardle and McLeod (1952): consider *Hornellobothrium* Shipley and Hornell, 1906 to be a junior synonym of *Discobothrium* Beneden, 1870, and *Discobothrium* as a *genus inquirendum*, with affinities to Lecanicephala (or Tetraphyllidea or Disculicipitidae).

Yamaguti (1959): considers *Hornellobothrium* Shipley and Hornell, 1906 to be a junior synonym of *Discobothrium* Beneden, 1871, and *Discobothrium* as a *genus incertae sedis*.

Schmidt (1986): considers *Hornellobothrium* Shipley and Hornell, 1906 to be a junior synonym of *Discobothrium* Beneden, 1871.

Butler (1987a): considers *Hornellobothrium* Shipley and Hornell and *Eniochobothrium* Shipley and Hornell as unlikely junior synonyms of *Discobothrium* Van Beneden.

Butler (1987b): redescribes *Hornellobothrium cobraformis* Shipley and Hornell, 1906 based on 15 newly collected specimens; treats *Hornellobothrium* as a valid genus in the family Lecanicephalidae Braun, 1900, order Tetraphyllidea Carus, 1863, with affinities to *Discobothrium myliobatidis* Mudry and Dailey, 1968, but not *Discobothrium fallax*.

Euzet (1994b): provisionally classifies *Hornellobothrium* in the order Lecanicephalidea, but treats it as a *genus incertae sedis*.

Caira *et al*. (1999): include an unidentified species of *Hornellobothrium* (as *Hornellobothrium* sp.) in a phylogenetic analysis based on morphological data; the species groups with the majority of lecanicephalidean taxa included.

Caira *et al.* (2001): include three unidentified species of *Hornellobothrium* in a more comprehensive phylogenetic analysis than that of Caira *et al.* (1999) based on morphological data; the species included are *Hornellobothrium* sp. from Caira *et al.* (1999) as *Hornellobothrium* n. sp. 1 and two additional species of *Hornellobothrium* (*Hornellobothrium* n. sp. 2 and *Hornellobothrium* n. sp. 3); the species group with the majority of lecanicephalidean taxa included; based on the taxa included in the analysis the genus appears monophyletic.

Remarks

As is the case for many other lecanicephalidean genera, the identity of *Hornellobothrium* is difficult to determine. The genus *Hornellobothrium* was erected by Shipley and Hornell (1906) to house a new species of tapeworm found in great numbers in the spiral intestine of *Aetobatus narinari* from Ceylon (now Sri Lanka). Since 1906, no additional species in this genus have been formally described. *Hornellobothrium cobraformis*, the name given to the type species by Shipley and Hornell (1906), referred to the laterally expanded anterior region of the strobila in this species, which, according to these authors, resembled the "hood of a cobra" (p. 45). This is the most characteristic feature of the genus *Hornellobothrium*. While possessing distinct proglottid morphology, the only other lecanicephalidean genus in which immature proglottids are expanded laterally to this extent is in *Eniochobothrium*. However, the morphology of laterally expanded anterior regions in *Hornellobothrium* and *Eniochobothrium* is somewhat different. In *Hornellobothrium*, the increase and subsequent decrease in proglottid width in the anterior of the strobila is gradual in both directions and the region of expanded proglottids is flat. It seems reasonable to assume that the proglottids of this anterior, laterally expanded region will go on to become reproductive proglottids. However, in *Eniochobothrium*, although the increase in width of the proglottids in the anterior trough region of the strobila is gradual from anterior to posterior, the transition from the non-reproductive to the reproductive region of the strobila is abrupt. In addition, in *Eniochobothrium* the lateral margins are bent towards one another, resulting in the trough-like appearance. It seems unlikely that the non-reproductive proglottids of the trough go on to become reproductive proglottids. This would suggest a very interesting mode of proglottid production and differentiation, which should be investigated in the future.

The limited information provided by Shipley and Hornell (1906) in the generic diagnosis of *Hornellobothrium* and the description of the type species *H. cobraformis*, complicates recognition and identification of this taxon. As a result, the majority of authors that have addressed the status of *Hornellobothrium* over the last century have either considered it to be a synonym of the "lecanicephalidean" genus *Discobothrium* (*e.g.*, Southwell 1925; Yamaguti 1959; Schmidt 1986) or have considered it to be of uncertain status (Fuhrmann 1931; Euzet 1994b). Only three authors, besides Shipley and Hornell (1906), have stood fast in the recognition of *Hornellobothrium* as a valid genus. Meggitt (1924) and Poche (1926), who basically followed Meggitt's (1924) classification, placed this genus in the family Phyllobothriidae, within the orders Tetraphyllidea and Taeniidea, respectively. In 1987, Butler (1987a) stated that she did not believe *Hornellobothrium* (and *Eniochobothrium*) to be junior synonyms of *Discobothrium*, in part, based on different host associations (*Hornellobothrium* and *Eniochobothrium* in rays of the family Myliobatidae, and *Discobothrium* [*i.e.*, *D. fallax*] in the skate family Rajidae). That same year, Butler (1987b) collected the first new material of what she identified as specimens of *H. cobraformis* reported in 71 years. She redescribed the type species based on those voucher specimens (Butler 1987b) and consequently recognized *Hornellobothrium* as a valid genus, placing it in the family Lecanicephalidae, order Tetraphyllidea.

The generic diagnosis of *Hornellobothrium* given by Shipley and Hornell (1906) was very general and brief, and entirely lacking in information on the proglottid anatomy. Meggitt (1924) presented an even more abbreviated diagnosis of the genus. Butler (1987b) did not provide a diagnosis of the genus. The generic diagnosis presented here is the first comprehensive diagnosis for *Hornellobothrium*. The morphology of the apical structure of *H. cobraformis* as described by Shipley and Hornell (1906) ("knob-like rostellum, on a constricted stalk" [p. 45]) differs from the morphology of the apical structure/organ in either Butler's voucher material of what she identified as *H. cobraformis* (Fig. 31B and E), and from the morphology of this structure seen in specimens of the new species of *Hornellobothrium* described as part of the present study (Fig. 33B). The diagnosis of *Hornellobothrium* presented here accommodates all of these possible apical structure morphologies.

Hornellobothrium cobraformis Shipley and Hornell, 1906

TYPE SPECIES

(Fig. 30)

Synonyms: *Discobothrium cobraformis* (Shipley and Hornell, 1906) Southwell, 1925.

Type host: *Aetobatus narinari* (Euphrasen, 1790) (as *Aetobatis* [sic] *narinari*), Spotted eagle ray (Myliobatidae, Myliobatiformes).

Additional hosts: None.

Site of infection: Spiral intestine.

Type locality: Ceylon (now Sri Lanka) (Fig. 30).

Additional localities: None.

Number of specimens on which the original description was based: "great numbers" (Shipley and Hornell, 1906, p. 45).

Type specimens: Not indicated in the original description; indicate that "5 sent to England" (Shipley and Hornell, 1906, p. 45).

Voucher specimens: None.

Material examined: None.

Etymology: *Cobra-*, referring to the hooded snake, the anterior region of which this tapeworm species resembles; *forma*, L., shape, figure.

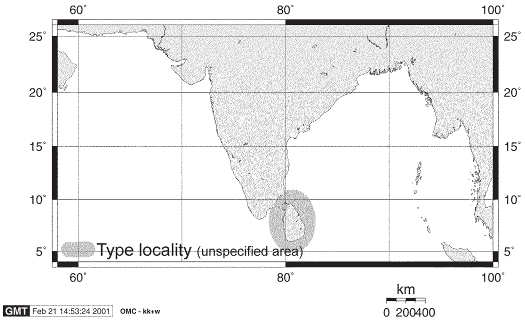


Fig. 30. Geographic distribution of *Hornellobothrium cobraformis* Shipley and Hornell, 1906.

Chronology

Shipley and Hornell (1906): describe *Hornellobothrium cobraformis* as the type species of the genus *Hornellobothrium* from "great numbers of this curious and very minute species" from *Aetobatis* [sic] *narinari* in Ceylon; provide a general description of the worm; the anterior expansion of the strobila is noted; internal proglottid anatomy is not described; a differential diagnosis is not provided.

Southwell (1925): considers *Hornellobothrium cobraformis* Shipley and Hornell, 1906 to be a junior synonym of *Discobothrium cobraformis* (Shipley and Hornell, 1906); quotes Shipley and Hornell's description of *H. cobraformis*.

Southwell (1930): considers *Hornellobothrium cobraformis* Shipley and Hornell, 1906 from *Stoasodon narinari*, Pearl Banks, Ceylon to be a junior synonym of *Discobothrium cobraformis* (Shipley and Hornell, 1906); same text as that of Southwell (1925).

Yamaguti (1959): considers *Hornellobothrium cobraformis* Shipley and Hornell, 1906 to be a junior synonym of *Discobothrium cobraeformis* [sic] Shipley and Hornell, 1906; *D. cobraformis* is one of five species placed in the genus *Discobothrium*.

Dailey and Mudry (1968): recognize *D. cobraeformis* [sic] as one of four species in the genus *Discobothrium*.

Wardle *et al.* (1974): list *Discobothrium myliobatidis* Dailey and Mudry (1968) in their chapter on the order Tetraphyllidea; assign "it" [presumably the genus *Discobothrium*] to the order Lecanicephalidea as a *genus inquirendum*; do not mention any other species of *Discobothrium*, except *D. cobraefomis* [sic] (= *Hornellobothrium cobraeformis* [sic]); comment that the lateral expansions of *D. cobraformis* and *Eniochobothrium gracile*, approximate the anterior strobilar condition found in species in the order Litobothridea.

Schmidt (1986): considers *Hornellobothrium cobraeformis* [sic] Shipley and Hornell, 1906 to be a junior synonym of *Discobothrium cobraformis* Shipley and Hornell, 1906; *D. cobraformis* is one of seven species of *Discobothrium* recognized.

Butler (1987b): redescribes *Hornellobothrium cobraformis* Shipley and Hornell, 1906 based on 15 newly collected specimens from *Aetobatis*

[sic] *narinari* from Moreton Bay, Queensland, Australia; comments on *H. cobraformis*'s affinities to *Discobothrium myliobatidis* Mudry and Dailey, 1968, but not to *Discobothrium fallax*.

Euzet (1994b): comments on the poorly known anatomy of *Hornellobothrium cobraformis* and notes that the species was recently recovered by Butler (1987b).

Remarks

Shipley and Hornell (1906) described *Hornellobothrium cobraformis* as the type species of their new genus *Hornellobothrium*, from a large number of specimens from the Spotted eagle ray, *Aetobatus narinari*, from Sri Lanka. Shipley and Hornell (1906) did not comment on the designation of type material of this species, but stated that five specimens of the type series of *H. cobraformis* were sent to England. These specimens have not been seen since that time. If type material was designated, the location of the type material is unknown.

Subsequent to the original description, no reports of *H. cobraformis* existed until 1987. At that time, Butler (1987b) collected specimens of what she identified as *H. cobraformis* from the type host, *Aetobatus narinari*, from Moreton Bay, Queensland, Australia. She redescribed *H. cobraformis* based on 15 specimens, including SEM data. Butler (1987b) reported her material to consist of only immature specimens. Therefore, data on the anatomy were not presented. Of those 15 voucher specimens on which the redescription was based, Butler deposited two vouchers at the Queensland Museum in Brisbane, Australia (QM GL4641 and GL4642). Examination of these two voucher specimens revealed that Butler's (1987b) "*H. cobraformis*" appears to not be conspecific with Shipley and Hornell's (1906) *H. cobraformis*. In addition, these two vouchers of "*H. cobraformis*" do not appear to be conspecific with respect to one another. Before providing evidence supporting these statements, descriptions of the two voucher specimens of "*H. cobraformis*" are presented.

Description of "*Hornellobothrium cobraformis*" specimen A (mature) (QM No. GL4642) (Fig. 31A-C)

Worm 3,245 long; maximum width 362 at level of at mature proglottids; proglottids 43 in number, 16 proglottids with evidence of internal anatomy, euapolytic. Scolex 86 long by 150 wide, bearing four acetabula. Acetabula bothridiate in form, 72-79 long by 65-69 wide, facially unmodified. Apical modification of scolex proper in form of small, conical extension with small aperture, housing apical organ. Apical organ 27 wide, appearing glandular. Spinitriches covering scolex proper at level of, and posterior to, acetabula.

Cephalic peduncle absent. Proglottids craspedote, non-laciniate; overlap of adjacent proglottids 10-15% of proglottid length. Immature proglottids 41 in number, forming laterally expanded anterior region of strobila (Fig. 31A), before narrowing again; two most posterior immature proglottids 203-251 long by 246-287 wide. Mature proglottids two in number, slightly wider than long, 310-327 long by 326-356 wide. Testes 11-12 in number, 46-59 (55 ± 5.2; 1; 5) long by 68-75 (71 ± 3.0; 1; 5) wide, anterior to and overlapping ovary, two columns in dorso-ventral view, two rows deep in cross-section. Vas deferens extending from ootype to level of cirrus sac. Internal seminal vesicle not observed. Cirrus sac pyriform. Cirrus unarmed. Ovary consisting of multiple lobes radiating from ootype in dorso-ventral view; ovarian lobes smooth. Mehlis' gland not observed. Vagina thin-walled, opening into genital atrium anterior to cirrus sac; vaginal sphincter and seminal receptacle not observed. Genital pores lateral, irregularly alternating, 48-63% of proglottid length from posterior end. Uterus extending from level of ovary to anterior of genital pore, not reaching anterior margin of proglottid; uterine duct entering uterus at anterior end; uterine pore not observed. Vitellaria follicular, medullary, lateral, multiple vitelline follicles in each lateral margin, extending from anterior margin of proglottid to anterior margin with ovary, overlapping anterior margin of ovary; vitelline follicles 9-25 (18 ± 6.4; 1; 5) long by 23-42 (33 ± 8.1; 1; 5) wide. One dorsal and one ventral pair of excretory ducts present. Eggs not observed.

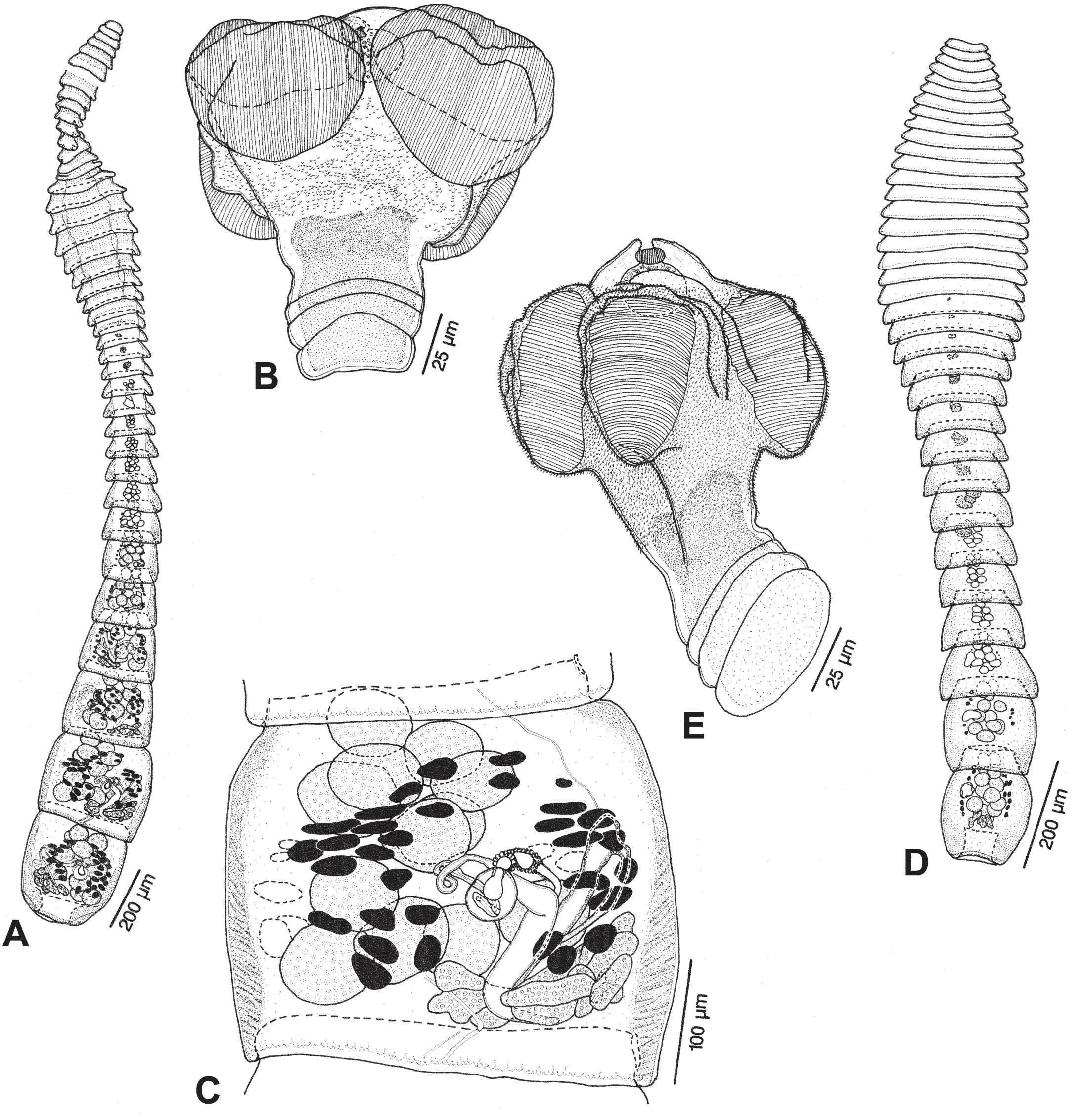


Fig. 31. A-E. Line drawings of Butler's (1987b) "*Hornellobothrium cobraformis*" specimen A and B. A-C. Specimen A (QM No. GL4642, voucher). A. Whole worm. B. Scolex. C. Mature proglottid. D-E. Specimen B (QM No. GL4641, voucher). D. Whole worm. E. Scolex.

Description of "*Hornellobothrium cobraformis*" specimen B (immature) (QM No. GL4641) (Fig. 31D and E)

Worm 1,788 long; maximum width 274 at approximately proglottid 20; 38 proglottids total, 13 proglottids with evidence of internal anatomy. Scolex 101 long by 110 wide, bearing four acetabula. Acetabula bothridiate in form, 64-70 long by 46 wide, facially unmodified. Apical modification of scolex proper in form of small, conical extension with small aperture, housing apical organ. Apical organ 22 wide, appearing glandular and muscular. Spinitriches covering distal and proximal acetabular surfaces and scolex proper at level of, and posterior to acetabula.

Cephalic peduncle absent. Proglottids craspedote, non-laciniate; overlap of adjacent proglottids 26-27% of proglottid length. Immature proglottids forming laterally expanded anterior region of strobila (Fig. 31D), greater than seven times wider than long at maximal width, before narrowing again; three most posterior immature proglottids 174-212 long by 155-172 wide, terminal immature proglottid longer than wide. Testes 11-12 in number, anterior to ovary, slightly overlapping anterior margin of ovary, 2-3 columns in dorso-ventral view, two rows deep. Genital pores lateral, irregularly alternating, located slightly anterior to middle of proglottid. Additional details of internal anatomy not observed.

Several morphological differences suggest that Butler's (1987b) "*H. cobraformis*" is not conspecific with *H. cobraformis sensu* Shipley and Hornell. Shipley and Hornell (1906) implied that *H. cobraformis* consisted of approximately 31 proglottids. Butler's material consisted of one mature and one immature specimen; the mature specimen possesses 43 proglottids. In addition, Shipley and Hornell (1906) stated that the widest proglottid is the 10th or 11th proglottid and the 24th is square, whereas in the two voucher specimens deposited by Butler (QM No. GL4641 and GL4642) the widest proglottids are the 19th and 21st proglottids, respectively, and the 36th and 39th proglottids, respectively, are square. *Hornellobothrium cobraformis sensu* Shipley and Hornell (1906) and "*H. cobraformis*" *sensu* Butler (1987b) also differ in the morphology of structures at the apex of their scolices. While the apical structure of *H. cobraformis* was described as "a knob-like rostellum, on a constricted stalk" (Shipley and Hornell 1906, p. 45), in "*H. cobraformis*" the apical modification of the scolex proper is in the form of a small, conical extension with an aperture at the center, housing a small, glandular and/or muscular apical organ. Again, collections of new material of the type species *H. cobraformis* are necessary to confirm the unusual morphology of the apical structure, as well as to describe the proglottid anatomy.

Finally, as mentioned above, there is some evidence to suggest that the two voucher specimens of "*Hornellobothrium cobraformis*" deposited by Butler (1987b) may not be conspecific with one another. While both specimens exhibit about equal numbers of proglottids, specimen A (QM No. GL4642) possesses two mature proglottids and is almost twice as long as the specimen B (QM No. GL4641). In addition, the proglottids of specimen B are much more craspedote than those of specimen A, and the immature proglottids are narrower in the former than in the latter specimen (155-172 vs. 245-287, respectively). This suggests that in Spotted eagle rays (*Aetobatus narinari*) from Moreton Bay, Queensland, at least two new species of *Hornellobothrium* await description.

Hornellobothrium extensivum Jensen, n. sp.

(Figs. 32-34)

Type host: *Aetobatus narinari* (Euphrasen, 1790), Spotted eagle ray (Myliobatidae, Myliobatiformes).

Additional hosts: None.

Site of infection: Spiral intestine.

Type locality: Lee Point (12°20'S 130°54'E), Darwin, Northern Territory, Australia (Fig. 32).

Additional localities: None.

Number of specimens on which the original description was based: 28 (20 whole mounts, two specimen cross-section series, two specimen longitudinal section series, and four specimens prepared for SEM).

Type specimens: Holotype (QM No. G 222902), five paratypes (four whole mounts and one specimen cross-section series) (QM Nos. G 222903-222907); five paratypes (USNPC No. 94577); three paratypes (KUNHM Nos. 002107-002109); 10 paratypes (seven whole mounts, one specimen cross-section series, and two specimen longitudinal section series) (LRP Nos. 3279-3288); four paratype specimens prepared for SEM (LRP).

Etymology: The specific epithet *extensivum* (*extensivus*, L., spread or stretched out, wide, large) refers to the broad anterior region of the strobila in this species.

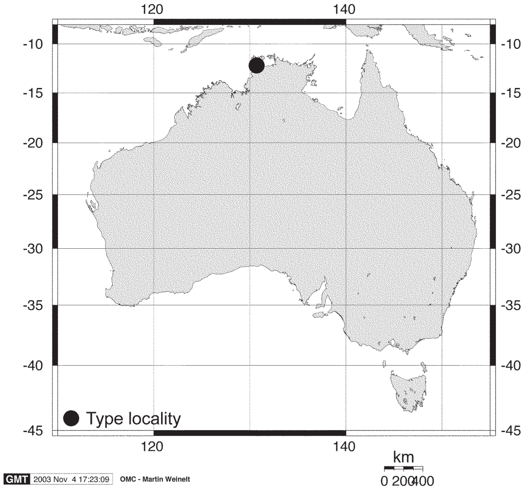


Fig. 32. Geographic distribution of *Hornellobothrium extensivum* Jensen, n. sp.

Chronology

Caira *et al.* (2001): include *Hornellobothrium extensivum* as "*Hornellobothrium* n. sp. 2" in a comprehensive phylogenetic analysis based on morphological data; include two additional species of *Hornellobothrium* (*Hornellobothrium* n. sp. 1 and *Hornellobothrium* n. sp. 3); the species grouped with the majority of lecanicephalidean taxa included; based on the taxa limited included in the analysis the genus appears monophyletic.

Description (Based on 20 whole mounts, two specimen cross-section series, two specimen longitudinal section series, and four specimens prepared for SEM.)

Worms 1,337-2,847 (1,831 ± 367.2; 20) long; maximum width 212-339 (272 ± 31.6; 20) at anterior third of strobila; 24-39 (32 ± 4.0; 20) proglottids total, 7-21 (13 ± 2.9; 20) proglottids with evidence of internal anatomy, euapolytic. Scolex 108-158 (129 ± 13.3; 20) long by 145-173 (159 ± 8.5; 20) wide, consisting of four acetabula. Acetabula bothridiate in form, 83-103 (93 ± 5.4; 20; 39) long by 60-83 (68 ± 5.3; 20; 39) wide, facially unmodified. Apical modification of scolex proper in form of small, conical extension with small aperture at center (Fig. 34A), housing apical organ. Apical organ 19-27 (22 ± 2.2; 20) wide, appearing glandular.

Distal and proximal surfaces of acetabula and scolex proper at level of and posterior to acetabula covered with blade-like spinitriches and pointed filitriches (Fig. 34D-F). Scolex proper anterior to acetabula and apical modification of scolex proper covered with pointed filitriches (Fig. 34C). Surface of laterally expanded proglottids covered with pointed filitriches, filitriches becoming larger and broader at posterior margin of proglottid (Fig. 34G). Surface of reproductive proglottids covered with long filitriches (Fig. 34H).

Cephalic peduncle absent. Proglottids strongly craspedote, non-laciniate; overlap of adjacent proglottids 11-38% (24 ± 5.5; 20; 63) of proglottid length. Immature proglottids 23-38 (31 ± 3.9; 20) in number, conspicuously expanded laterally (Fig. 34B), greater than 12 times wider than long at maximal width, before narrowing again; two most posterior immature proglottids 125-322 (218 ± 44.0; 20; 40) long by 121-289 (172 ± 38.9; 20; 40) wide. Mature proglottids 1-3 in number, longer than wide; two most posterior mature proglottids 247-546 (367 ± 82.4; 20; 35) long by 133-237 (179 ± 22.5; 20; 35) wide. Testes 10-13 (11 ± 0.9; 20; 40) in number, often degenerated in terminal proglottid, 32-75 (45 ± 8.4; 20; 76) long by 30-85 (49 ± 9.4; 20; 76) wide, anterior to and overlapping ovary, 1-2 columns in dorso-ventral view, two rows deep in cross-section (Fig. 33E). Vas deferens expanded to form conspicuous external seminal vesicle in more mature proglottids. External seminal vesicle saccate, extending from posterior to ootype to slightly anterior to cirrus sac, then extending posteriorly, entering cirrus sac at distal end. Internal seminal vesicle absent. Cirrus sac pyriform, tilted posteriorly, 35-82 (59 ± 11.6; 19; 34) long by 22-51 (38 ± 6.7; 19; 34) wide, containing coiled cirrus. Cirrus unarmed. Ovary consisting of multiple longitudinal lobes radiating from ootype in anteroposterior and dorso-ventral plane, 33-180 (89 ± 43.9; 20; 35) long by 77-162 (109 ± 21.2; 19; 34) wide, essentilly bilobed in cross-section (Fig. 33D); ovarian lobes smooth. Vagina thin-walled, extending obliquely from ootype to genital pore, opening into genital atrium anterior to cirrus sac; seminal receptacle not observed. Genital pores lateral, irregularly

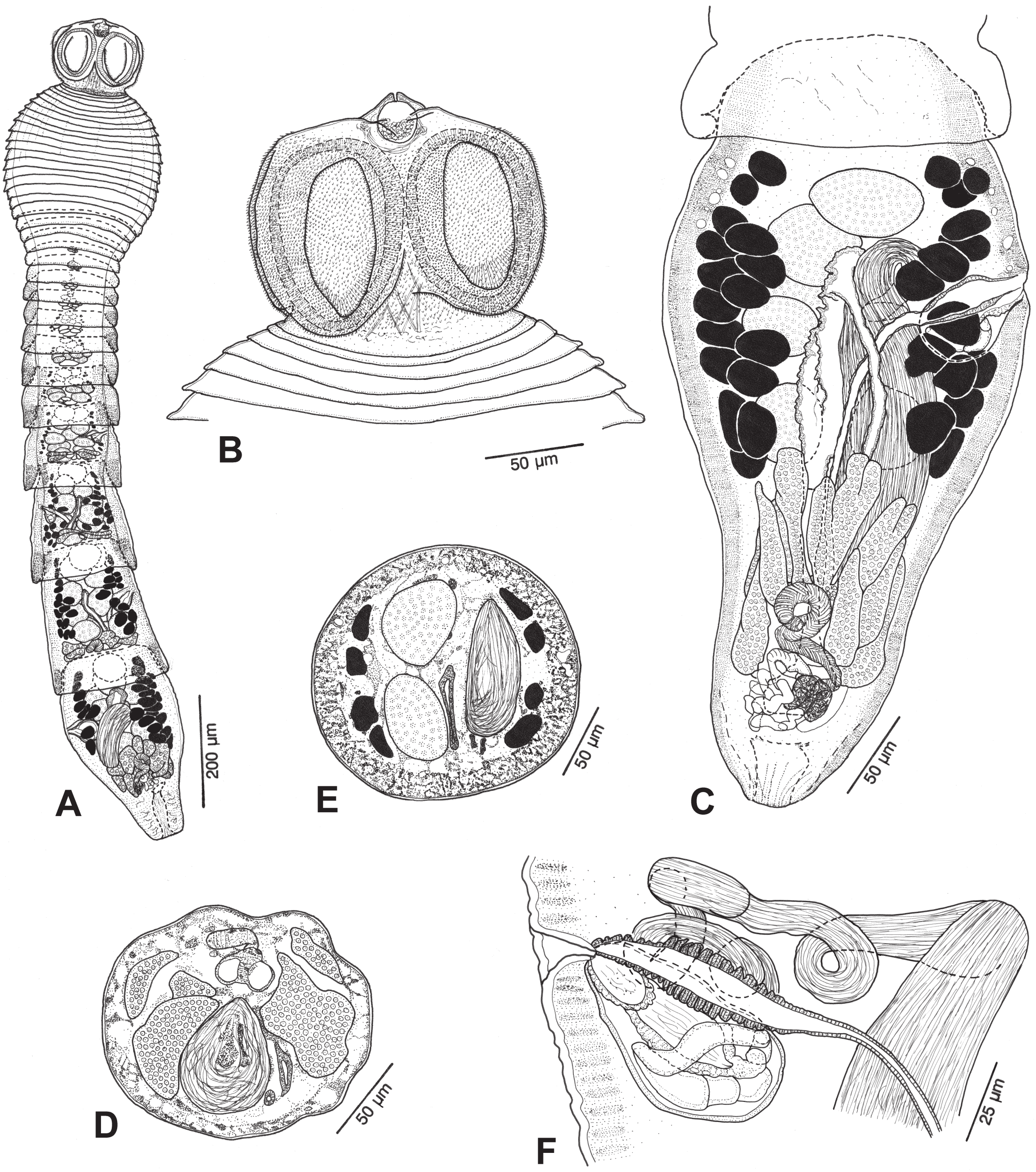


Fig. 33. A-F. Line drawings of *Hornellobothrium extensivum* Jensen, n. sp. A. Whole worm (holotype, QM No. G 222902). B. Scolex (USNPC No. 94577). C. Mature terminal proglottid (QM No. G 222906). D. Cross-section through mature proglottid at level of ovarian bridge (QM No. G 222907). E. Cross-section through mature proglottid between ovary and cirrus sac (QM No. G 222907). F. Terminal genitalia (USNPC No. 94577).

alternating, 42-79% (65 ± 7.2; 20; 35) of proglottid length from posterior end. Uterus extending from posterior of ovary to level anterior of genital pore, not reaching anterior margin of proglottid; uterine duct entering uterus at anterior end; uterine pore not observed. Vitellaria follicular, medullary, in lateral columns, multiple vitelline follicles on each lateral margin in cross-section, extending from anterior margin of proglottid to an-

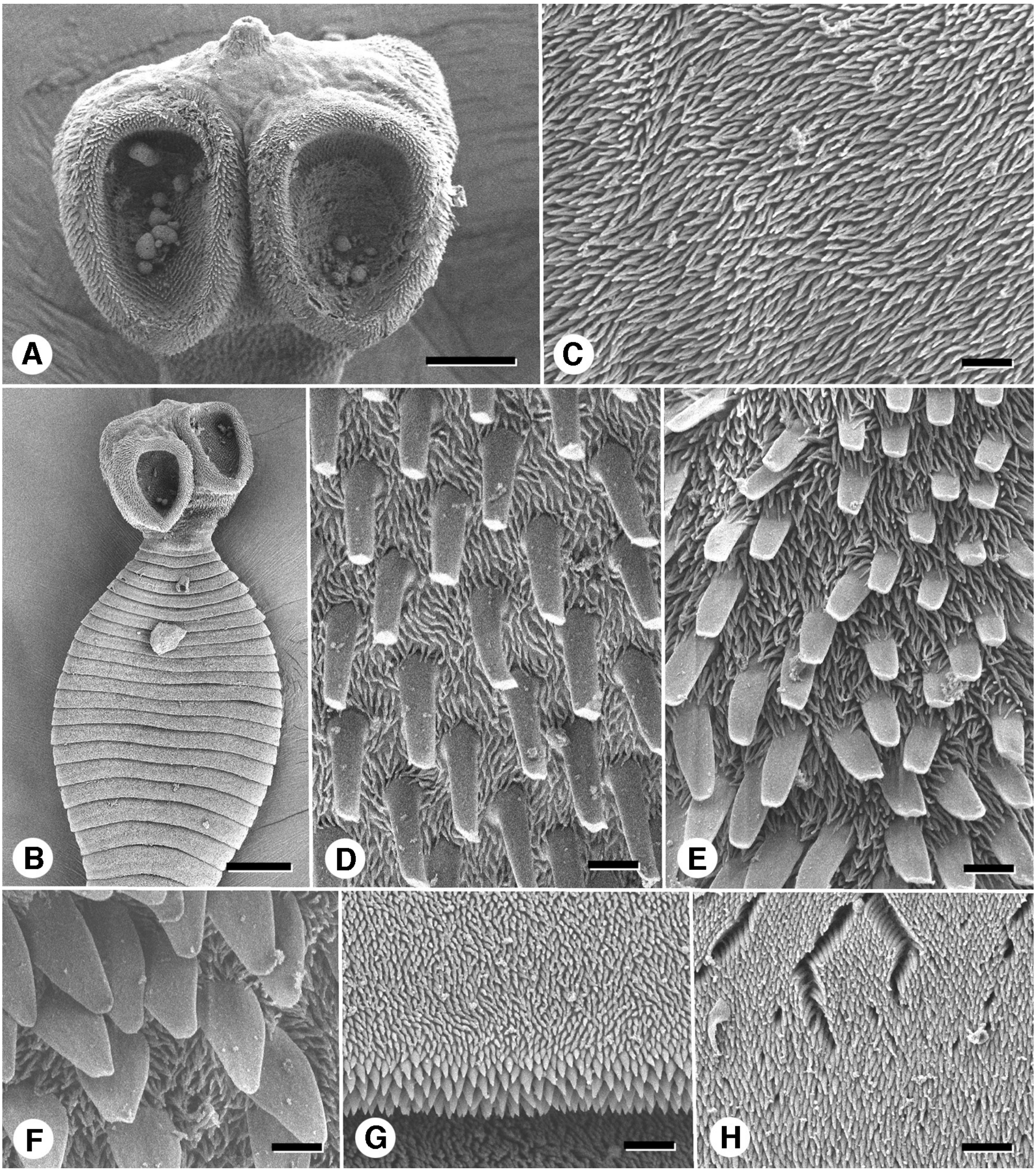


Fig. 34. A-H. Scanning electron micrographs of *Hornellobothrium extensivum* Jensen, n. sp. A. Scolex. B. Anterior strobila of laterally expanded, non-reproductive proglottids. C. Microtriches on surface of scolex proper. D. Microtriches on distal acetabular surface. E. Microtriches on proximal acetabular surface. F. Microtriches on scolex proper posterior to acetabula. G. Microtriches on laterally expanded, non-reproductive proglottids; note larger microtriches on posterior margin. H. Microtriches on reproductive proglottids. Scale bars: A, 25 μm; B, 50 μm; C-H, 1 μm.

terior margin of ovary, slightly overlapping anterior margin of ovary; vitelline follicles 11-42 (23 ± 7.2; 20; 85) long by 11-42 (24 ± 6.4; 20; 85) wide. One dorsal and one ventral pair of excretory ducts present. Eggs not observed.

Remarks

Although the genus *Hornellobothrium* was erected almost a century ago, *H. extensivum* is only the second species described. *Hornellobothrium extensivum* and *H. cobraformis* can be distinguished from one another based on the different morphologies of the structures at the apex of the scolex. The apical modification of the scolex proper in *H. extensivum* is in the form of a small, conical extension with an aperture at the apex, housing a small, glandular apical organ. In contrast, the apical structure of *H. cobraformis* is described as "a knob-like rostellum, on a constricted stalk" (Shipley and Hornell, 1906, p. 45). In addition, in *H. extensivum* the proglottids are strongly craspedote and the genital pores are positioned in the anterior half of the proglottids, whereas in *H. cobraformis*, the proglottids are less craspedote and the genital pores appear to be positioned in the posterior half of the proglottids (see Shipley and Hornell, 1906, plate I, fig. 9).

The comparison of *H. extensivum* to Butler's two museum specimens (QM GL 4641 and 4642) is difficult since her available material consists of only one specimen each. A rigorous comparison is therefore not possible. Superficial comparisons of these two specimens with *H. extensivum* suggests that neither is conspecific with *H. extensivum*. The proglottids of *H. extensivum* are more craspedote than those of Butler's specimen A and the mature proglottids are narrower (133-237 vs. 326-356). Compared to Butler's specimen B, *H. extensivum* possesses an overall larger scolex and lacks a muscular component of the apical organ. Furthermore, mature worms of *H. extensivum* possess approximately the same number of proglottids as does the immature specimen B, suggesting that specimens of this later species will obtain a greater number of proglottids overall.

Hornellobothrium extensivum is the taxon referred to as "*Hornellobothrium* n. sp. 2" in the phylogenetic analysis of Caira *et al.* (2001). One of the paratypes of *H. extensivum* (*i.e.*, the series of longitudinal sections) was among the specimens used to code this species in Caira *et al.* (2001).

LECANICEPHALUM Linton, 1890

Taxonomic status: Valid.

Synonyms: None

Type species: *Lecanicephalum peltatum* Linton, 1890.

Other species: *Lecanicephalum coangustatum* Jensen, n. sp.

Species inquirendae: *Lecanicephalum maharashtrae* Chincholikar and Shinde, 1978; *L. ratnagiriensis* Hiware and Jadhav, 1999.

Nomina nuda: *Lecanicephalum schmidti* in Al Kawari (1992); *Lecanicephalum* (as *Lacaenicephalum*) *trygoni* in Mohekar *et al.* (2002).

Etymology: *lecano-*, from Gr. *lekane*, dish, pot, pan (see *lekos*, Gr., plate); *kephale*, Gr., head.

Diagnosis (Modified from Yamaguti [1959].)

Worms euapolytic. Scolex with four acetabula; acetabula in form of suckers; apical modification of scolex proper with aperture at apex, fully expandable, conspicuous circular muscle bundles responsible for change in diameter of aperture, bearing apical organ; apical organ in form of circular, muscular and glandular sheet, completely retractable into apical modification of scolex proper; retraction facilitated by circular muscle bundle in apical organ. Proglottids weakly craspedote, nonlaciniate. Testes numerous, in 1-2 columns, anterior to ovary. Vas deferens extensive, in form of expanded duct, extending from ootype to cirrus sac, or slightly anterior to cirrus sac. External and internal seminal vesicles absent. Cirrus sac J-shaped, tilted anteriorly, positioned almost parallel to lateral margin of proglottid. Cirrus conspicuously armed. Ovary H-shaped in dorso-ventral view, bilobed in cross-section. Vagina medial or sublateral in position in proglottid, conspicuously expanded distally, opening into genital atrium posterior to cirrus sac. Genital pores lateral, irregularly alternating. Uterus saccate, median. Vitellaria follicular, in lateral columns, extending entire length of proglottid, interrupted by ovary. One dorsal and one ventral pair of excretory ducts present. Eggs small (according to Yamaguti, 1959). Parasites of stingrays in the genus *Dasyatis* Rafinesque, 1810 (Dasyatidae). Western Atlantic Ocean (U.S.A.).

Chronology

Braun (1878): erects the new genus *Polypocephalus*, and comments on and illustrates a second lecanicephalidean from *Rhinobatus* [sic] *granulatus* [possibly a species of *Lecanicephalum*].

Linton (1890): erects the genus *Lecanicephalum* with *L. peltatum* as the type species; provides a brief diagnosis of the genus and describes *L. peltatum* in some detail including measurements; believes this species, which he found on three different occasions in *Trygon centrura* [sic], is closely related to Van Beneden's *Discobothrium fallax* and might even be generically identical; places *Lecanicephalum* (and *Tylocephalum*) among the Tetrabothriidae (in subfamily I, the Phyllobothriinae), although bothrial morphology is inconsistent with that of the family; suggests, however, upon further investigation, to include these taxa, along with *Discocephalum*, in a new group, for which he suggests the name Gamobothriidae, "or some equivalent term" (p. 720).

Braun (1894-1900): recognizes *Lecanicephalum* Linton in the family Lecanicephalidae (*fam. inq*. = Gamobothriidae), order Tetraphyllidea, with the type species *L. peltatum* Linton.

Perrier (1897): recognizes *Lecanicephalum* (along with *Tylocephalum*, *Discocephalum* and *Sciadocephalus*) in the family Gamobothriidae, order Tetracestoda.

Shipley and Hornell (1905): initially consider their new genus *Tetragonocephalum* to be very similar, if not identical to *Lecanicephalum*; describe *Tetragonocephalum* and distinguish it from *Lecanicephalum*.

Stiles and Hassall (1912): *Lecanicephalum* Linton, 1890: Linton (1891), Braun (1895 and 1900) and Shipley and Hornell (1905) (*Lecanicephalus* for *Lecanicephalum*).

Mola (1921): reclassifies all cestodes and places *Lecanicephalum* in the subfamily Lecanicephalinae, family Dibothriophyllidae, order Diphyllidea.

Meggitt (1924): considers *Lecanicephalum* Linton, 1891 as a valid genus in the family Lecanicephalidae (including *Discocephalum*, *Lecanicephalum*, *Cephalobothrium*, *Tylocephalum*, and *Adelobothrium*), order Tetraphyllidea; provides an abbreviated diagnosis of the genus.

Southwell (1925): considers *Lecanicephalum* (nec *Lecanocephalus* Diesing, 1839 [= *Goezia*, Zeder, 1800]) in the family Lecanicephalidae, suborder Multivitellata, order Cyclophyllidea, based on its possession of four suckers; repeats Linton's definition of the genus; places *Lecanicephalum* in the order Cyclophyllidea, suborder Multivitellata; [figure 215 labeled "*Polypocephalus medusia* = *Parataenia medusia*. Ripe segment, mounted entire." (p. 316) in Southwell (1925) looks to be a proglottid of *Lecanicephalum*].

Poche (1926): recognizes *Lecanicephalum* (along with *Discocephalum*, *Cephalobothrium*, *Tylocephalum*, *Adelobothrium*, and *Balanobothrium*) in the family Lecanicephalidae Braun (Gamobothriidae Linton, 1889; Gamobothridae Ariola, 1899; Benham, 1901), suborder Phyllobothriinea *nom. nov.*, order Taeniidea *nom. nov.*

Woodland (1927): considers *Lecanicephalum* a "lecanicephalid" genus in the family Phyllobothriidae (Tetraphyllidea) (based on disposition of longitudinal muscle bundles and marginal vitellaria), along with *Cephalobothrium*, *Polypocephalus*, and *Calycobothrium*.

Mola (1929): classifies cestodes in general and places *Lecanicephalum* in the subfamily Lecanicephalinae, family Dibothriophyllidae, order Diphyllidea.

Southwell (1929): comments on the classification schemes proposed by Poche (1926), Woodland (1927), and Pintner (1928) and on the position of *Lecanicephalum* (along with *Cephalobothrium*, *Polypocephalus*, and *Calycobothrium*) in Woodland's scheme in the family Phyllobothriidae.

Southwell (1930): considers *Lecanicephalum* (nec *Lecanocephalus* Diesing, 1839 [= *Goezia*, Zeder, 1800]) as a valid genus in the family Lecanicephalidae, superfamily Lecanicephaloidea, order Eucestoda; basically same text as that of Southwell (1925).

Fuhrmann (1931): classifies *Lecanicephalum* (syn. *Tylocephalum ex parte*, *Tetragonocephalum* and *Cephalobohrium ex parte*) in the family Lecanicephalidae Braun (syn. Gamobothriidae Linton), along with *Polypocephalus* (syn. *Parataenia* and *Thysanobothrium*), *Anthemobothrium*, and *Adelobothrium*.

Baer (1948): provides diagnosis of the genus *Lecanicephalum*; studies new material of *Lecanicephalum peltatum* from *Dasyatis centroura* from Woods Hole; describes in detail the scolex and segment morphology based on whole mounts and histological sections; considers the material Southwell (1925) described as *L. peltatum* to not be conspecific and suggests leaving it as *species inquirenda*.

Hyman (1951): recognizes *Lecanicephalum* (along with *Polypocephalus* [= *Parataenia*, *Thysanobothrium*], *Anthemobothrium*, and *Adelobothrium*) in the family Lecanicephalidae, order Lecanicephaloidea; few characters for the family are presented.

Wardle and McLeod (1952): consider *Lecanicephalum* Linton, 1890 a valid genus in the family Lecanicephalidae, order Lecanicephala, with type and only species, *L. peltatum* Linton, 1890.

Riser (1955): classifies lecanicephalideans in five families (Lecanicephalidae, Cephalobothriidae, Balanobothriidae, Disculicepitidae and Echinobothriidae) in superfamily Lecanicephaloidea, order Tetraphyllidea, superorder Trixenidea [with *Lecanicephalum* as type genus of the family].

Euzet (1959): considers *Lecanicephalum* as type genus of the family Lecanicephalidae, superfamily Lecanicephaloidea, order Tetraphyllidea.

Yamaguti (1959): treats *Lecanicephalum* Linton, 1890 (nec *Lecanocephalus* Diesing, 1851) in the family Lecanicephalidae, order Lecanicephalidea.

Joyeux and Baer (1961): recognize *Lecanocephalum* [sic] (along with *Anthemobothrium*, *Calycobothrium*, and *Polypocephalus*) in the family Lecanicephalidae, superfamily Lecanicephaloidea, order Tetraphyllidea.

Schmidt (1970): considers *Lecanicephalum* (along with *Polypocephalus*, *Calycobothrium*, *Staurobothrium*, *Hexacanalis*, and *Tetragonicephalum* [sic]) as a valid genus in the family Lecanicephalidae, order Lecanicephalidea Baylis, 1920, as part of a key to the genera of tapeworms; provides a brief diagnosis for the genus.

Wardle *et al.* (1974): recognize the family Lecanicephalidae [and consequently *Lecanicephalum*] in the order Lecanicephalidea Baylis, 1920; do not mention any genera they consider to belong in the family; present a key to families in the order Lecanicephalidea; mention features of the family as part of the key, such as lateral vitelline follicles and non-filamented eggs.

Schmidt (1986): considers *Lecanicephalum* Linton, 1890 (with the synonyms *Aphanobothrium* Seurat, 1906, *Kystocephalus* Shipley and Hornell, 1906, *Spinocephalum* Deshmukh, 1980, *Tylocephalum* Linton, 1890) a valid genus in the family Lecanicephalidae, order Lecanicephalidea; 14 species are recognized in the genus: *L. peltatum*, *L. aegyptiacus*, *L. aetiobatidis*, *L. dierama*, *L. madhukarii*, *L. maharashtrae*, *L. marsupium*, *L. pinguis* [sic], *L. rhinobatii*, *L. simile*, *L. singhii*, *L. squatinae*, *L. translucens*, and *L. yorkei*; five additional species are listed as belonging to the genus but are considered as unidentifiable from their original descriptions: *L. ludificans*, *L. maragritiferae*, *L. minus*, *L. minutum*, and *L. unionifactor*.

Brooks and McLennan (1993): present a tree for the order Lecanicephaliformes Baylis, 1920; based on that tree they recognize *Lecanicephalum* Linton, 1890 (along with *Calycobothrium* Southwell 1911, *Discobothrium* van Beneden 1871, *Echeneibothrium* van Beneden, 1850, *Hexacanalis* Perrenoud, 1931 *sedis mutabilis*, *incertae sedis*, and *Polypocephalus* Braun, 1878) in the subfamily Lecanicephalinae Braun, 1900 *incertae sedis*, family Lecanicephalidae Braun, 1900, order Lecanicephaliformes Baylis, 1920.

Euzet (1994b): recognizes *Lecanicephalum* Linton, 1890 (syn. *Hexacanalis* Perrenoud, 1931) as the only valid genus in the family Lecanicephalidae Braun, 1900, order Lecanicephalidea Wardle and McLeod, 1952.

Caira *et al.* (1999): include a species in the genus *Lecanicephalum*, *L. peltatum*, from *Dasyatis centrura* [sic] from Woods Hole (Baer's [1948] material) in a phylogenetic analysis based on morphological data; this species groups with the majority of the other lecanicephalidean taxa included in the analysis.

Caira *et al.* (2001): include two species in the genus *Lecanicephalum* (*L. peltatum* from Caira *et al.*

[1999] and an unidentified species, *Lecanicephalum* sp.) in a more comprehensive phylogenetic analysis based on morphological data; the two species group with the majority of the other lecanicephalidean taxa included in the analysis; the two species of *Lecanicephalum* group as sister taxa in the analysis.

Remarks

Linton (1890) erected this new genus for specimens he collected on three different occasions from the Roughtail stingray, *Dasyatis centroura* (as *Trygon centrura* [sic]), at Woods Hole, Massachusetts, U.S.A. He named the type species *Lecanicephalum peltatum*. Linton (1890) did not indicate whether type material was designated or where the specimens on which the original description was based were deposited. Although the description of *L. peltatum* (see Linton, 1890) contained a fair amount of detail, the morphology of the scolex was only superficially described and the generic diagnosis was brief. Subsequently, the most comprehensive treatment of the genus was provided by Baer (1948). Baer had collected new material of the type species, *L. peltatum*, from the type host (*Dasyatis centroura*) and type locality (Woods Hole, Massachusetts, U.S.A.). For the first time, the unusual and complex morphology of the scolex was described in detail. In addition, based on his observations, Baer (1948) presented a more complete generic diagnosis of *Lecanicephalum* than that of Linton (1890). However, the most comprehensive diagnosis of *Lecanicephalum* was provided by Yamaguti (1959). While most generic diagnoses presented in this study were modified from the diagnosis presented in the most recent treatment of the group (*i.e.*, Euzet 1994b), the diagnosis presented here for *Lecanicephalum* was modified from Yamaguti (1959), because it is most consistent with the concept of *Lecanicephalum* resulting from this study. This diagnosis is, however, essentially consistent with the other diagnoses of *Lecanicephalum* in existence, and, specifically, differs only slightly from that presented by Euzet (1994b). Yamaguti's (1959) diagnosis of *Lecanicephalum* was modified to reflect the terminology used throughout this study, especially terminology associated with features of the scolex. In addition, the morphology of the scolex and the vas deferens were described in more detail. Members of *Lecanicephalum* are considered to be euapolytic rather than apolytic; proglottids are considered to be weakly craspedote rather than acraspedote; external and internal seminal vesicles are considered to be absent rather than present ("external seminal vesicle" was interpreted as vas deferens in the form of an expanded duct, not a distinct structure).

Linton (1890) suggested a new family name, Gamobothriidae, to house *Lecanicephalum* (along with *Tylocephalum* and *Discocephalum*). However, Gamobothriidae is not a valid family name, because it was not based on a generic name. In 1900, the family name Lecanicephalidae was suggested by Braun (1894-1900).

Most authors have recognized *Lecanicephalum* as a genus in the Lecanicephalidae, however, the family itself was placed in several orders. The family Lecanicephalidae was recognized in the order Tetraphyllidea (*e.g.*, Braun, 1894-1900; Euzet, 1959; Joyeux and Baer, 1961), Cyclophyllidea (see Southwell 1925), Taeniidea (see Poche 1926), and, finally, in the Lecanicephaloidea (see Hyman 1951) (or Lecanicephala according to Wardle and McLeod 1952; Lecanicephalidea according to Yamaguti 1959).

Two species names, *Lecanicephalum schmidti* and *L. trygoni*, are considered to be *nomina nuda*. Al Kawari (1992) described *Lecanicephalum schmidti* in her Ph.D. thesis. Al Kawari (1992) is not a published thesis and, consequently, does not meet ICZN Art. 8.1.3 (1999). The name *L. trygoni* (as *Laceanicephalum* [sic] *trygoni*) was used only in a list of cestode parasites collected from the west coast of Maharashtra, India by Mohekar *et al.* (2002); no authority or literature citation is given. It appears that this species was never described. Therefore, both names, *L. schmidti* and *L. trygoni*, are not available.

Lecanicephalum peltatum Linton, 1890

TYPE SPECIES

(Figs. 35-37)

Synonyms: None.

Type host: "*Trygon centrura* [sic]" (= *Dasyatis centroura* [Mitchill, 1815] ?), Roughtail stingray (Dasyatidae, Myliobatiformes).

Additional hosts: None.

Site of infection: Spiral intestine.

Type locality: Woods Hole, Massachusetts, U.S.A. (Fig. 35).

Additional localities: None.

Number of specimens on which the original description was based: At least nine.

Type specimens: Neotype (USNPC No. 7677 [specimen 3]) (see Fig. 36) (type specimens not indicated in original description).

Voucher specimens: USNPC No. 7677 (specimens 4 and 5) (see Fig. 36).

Voucher specimens (unverified): (see Appendix 4).

Material examined: MHNG No. 87/7-29; HWML No. 20937.

Etymology: *peltatus*, L., shield-shaped, armed with a shield.

Unverified records: *Dasyatis sayi* (Lesueur, 1817) (as *D. say* [sic]) from Beaufort, North Carolina, U.S.A. (see Linton, 1905); *Pristis cuspidatus*, *Trygon kuhlii* [sic], and *Pteroplatea micrura* from Ceylon (see Southwell, 1925); *Dasyatis americana* Schroeder, 1928 from Cartagena, Colombia (see Brooks and Mayes, 1980).

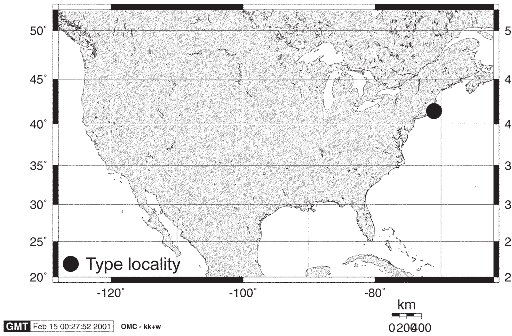


Fig. 35. Geographic distribution of *Lecanicephalum peltatum* Linton, 1890.

Chronology

Linton (1890): describes *Lecanicephalum peltatum* as the type species of the new genus *Lecanicephalum*; reports finding specimens of this species on three different occasions from *Trygon centrura* [sic]; believes that *L. peltatum* is closely related to Van Beneden's *Discobothrium fallax* and might even be generically identical; describes the species in some detail, including measurements.

Perrier (1897): recognizes *Lecanicephalum peltatum* from *Trygon centrura* [sic] as the only species in the genus *Lecanicephalum*.

Linton (1900): reports *Lecanicephalum peltatum* from a single specimen of *Dasyatis centrura* [sic] collected at Woods Hole in July of 1898.

Braun (1894-1900): recognizes *Lecanicephalum peltatum* Linton as the type species of *Lecanicephalum* Linton in the family Lecanicephalidae (*fam. inq.* = Gamobothriidae), order Tetraphyllidea.

Linton (1901): summarizes two previous instances of *Lecanicephalum peltatum* collected in the Woods Hole region; reports four additional specimens from *D. centrura* [sic] collected at Woods Hole on July 19, 1899.

Linton (1905): reports one to several specimens of *Lecanicephalum peltatum* from *Dasyatis say* collected on July 9 and 29, 1901, and three specimens from *D. say* collected August 18, 1902, all from Beaufort, North Carolina.

Stiles and Hassall (1912): *Lecanicephalum* Linton, 1890: Linton (1891), Braun (1895 and 1900) and Shipley and Hornell (1905) (*Lecanicephalus*); *L. peltatum* Linton, 1890 (in *Trygon centrura* [sic]; Woods Hole): Linton (1900), Linton (1901) (in *Dasyatis centrura* [sic]), Linton (1905) (in *D. say*) and Braun (1900); *Lecanicephalus* Shipley and Hornell, 1905 (for *Lecanicephalum*).

Southwell (1911): [Brooks and Mayes (1980) cite Southwell (1911) as reporting *Lecanicephalum peltatum* from *Trygon kuhli* [sic], *Pteroplatea micrura*, and *Pristis cuspidatus* from Ceylon; however, Southwell (1911) only described *Cephalobothrium abruptum* from *Pteroplatea micrura* and *Cephalobothrium variabile* from *Pristis cuspidatus*].

Linton (1924): reports *Lecanicephalum peltatum* from several specimens of *Dasybatis* [sic] *centrura* [sic] collected between 1903 and 1922 (USNPC No. 7677), and in 1923 at Woods Hole.

Southwell (1925): reports collecting ten new specimens of *Lecanicephalum peltatum* from *Pristis cuspidatus*, *Trygon kuhlii*, and *Pteroplatea micrura* from Ceylon; provides scolex measurements and describes the proglottid anatomy in detail; comments that Linton's specimens of *L. peltatum* from *Dasyatis centrura* [sic], of which he seems to have material, differ from these specimens in a number of aspects; illustrates a proglottid.

Woodland (1927): recognizes *Lecanicephalum peltatum* as a species of the "lecanicephalid" genus *Lecanicephalum*.

Pintner (1928): recognizes *Lecanicephalum peltatum* as a possible member of the "lecanicephalidean" family Lecanicephalidae (group A), along with *Tylocephalum uarnaki* (= *trygonis*?), possibly *Tylocephalum minutum*, even *Parataenia medusia*, *Polypocephalus medusia*, separate from *Polypocephalus radiatus*), possessing a non-glandular scolex, bilobed uterus and acraspedote proglottids.

Southwell (1929): comments on the classification schemes proposed by Poche (1926), Woodland (1927) and Pintner (1928); claims that Pintner stated that *Lecanicephalum peltatum* = *Discocephalum fallax*.

Southwell (1930): repeats description of *Lecanicephalum peltatum* he provided in 1925; indicates that specimens were not fully mature; omits remarks section; reproduces illustration of proglottid presented in 1925.

Fuhrmann (1931): recognizes *Lecanicephalum* in the family Lecanicephalidae Braun (syn. Gamobothriidae Linton), order Tetraphyllidea; provides new illustrations of cross-sections of the proglottid of *Lecanicephalum peltatum* (Southwell).

Linton (1938): illustrates scolex of *Lecanicephalum peltatum*; finds mode of attachment similar to that of *Discocephalum pileatum*.

Baer (1948): studies new material of *Lecanicephalum peltatum* from *Dasyatis centroura* from Woods Hole, Massachusetts, U.S.A.; describes in detail the scolex and segment morphology based on whole mounts and histological sections; considers the material Southwell (1925) described as *L. peltatum* from other host species to not be conspecific and suggests to consider it as *species inquirenda*.

Wardle and McLeod (1952): recognize *L. peltatum* Linton, 1890 as type and only species in the genus *Lecanicephalum* Linton, 1890.

Euzet (1954): notes that mode of attachment of *Lecanicephalum peltatum* resembles that of *Echeneibothrium variabile*.

Yamaguti (1959): recognizes *Lecanicephalum peltatum* as the type species of *Lecanicephalum* Linton, 1890 (nec *Lecanocephalus* Diesing, 1851), collected from *Dasyatis centrura* [sic] at Woods Hole and *Pristis cuspidatus*, *Trygon kuhlii*, and *Pteroplatea micrura* in Ceylon.

Brooks and Mayes (1980): report *Lecanicephalum peltatum* Linton, 1890 from *Dasyatis americana* from Cartagena, Colombia; this presents both, a new host and new locality record for this species; deposit voucher (HWML No. 20937).

Brooks *et al.* (1981): list *Lecanicephalum peltatum* as a parasite of *Dasyatis americana* from South America.

Schmidt (1986): recognizes *Lecanicephalum peltatum* Linton, 1890 as the type species of *Lecanicephalum*.

Euzet (1994b): recognizes *Lecanicephalum peltatum* Linton, 1890 as the type species of the genus *Lecanicephalum*.

Caira *et al.* (1999): include "*Lecanicephalum peltatum*" from *Dasyatis centrura* [sic] from Woods Hole (Baer's [1948] material; MHNG No. 87 [conspecificity with *L. peltatum* as described in this study is suspect]) in a phylogenetic analysis based on morphological data; this species groups with the majority of the other lecanicephalidean taxa included in the analysis.

Caira *et al.* (2001): include "*Lecanicephalum peltatum*" [conspecificity with *L. peltatum* as described in this study is suspect] from Caira *et al.* (1999) and one additional species of *Lecanicephalum* in a more comprehensive phylogenetic analysis based on morphological data; the species group with the majority of the other lecanicephalidean taxa included in the analysis.

Description (Modified from Linton [1890].) (Based on one neotype and two voucher specimens [see below, *i.e.*, specimens 3-5] [USNPC No. 7677].) Note: Measurements taken from Linton (1890) are in bold. Mean, standard deviation and number of specimens are not given in cases in which the ranges were expanded by using measurements provided by Linton (1890).

Worms 8.036-14 mm long; maximum width at scolex; 49-61 (55 ± 6.0; 3) proglottids, apolytic. Scolex 447 long by 601-661 (637 ± 31.5; 3) wide (**680-900 in diameter**), bearing four acetabula. Acetabula sucker-like in form, 86-100 wide. Apical modification of scolex proper fully expandable, conspicuous circular muscle bundles present, bearing apical organ; apical organ in form of circular, muscular and glandular sheet.

Cephalic peduncle absent. Proglottids slightly craspedote, non-laciniate. Immature proglottids 43-53 (46 ± 5.8; 3) in number, initially wider than long, becoming longer than wide; two most posterior immature proglottids 348-515 (415 ± 67.3; 3; 6) long by 299-447 (359 ± 68.8; 3; 6) wide. Mature proglottids 6-9 (8 ± 1.5; 3) in number, 748-1,500 long by 260-510 wide. Testes 19-24 (21 ± 2.3; 3; 9) in number, 49-82 (62 ± 8.9; 3; 15) long by 61-112 (78 ± 12.9; 3; 15) wide, extending from anterior margin of proglottid to ovary, slightly overlapping anterior margins of ovary, 2-3 columns in dorso-ventral view (Fig. 36), one row deep in cross-section. Vas deferens extensive, in form of expanded duct, extending more or less along median line of proglottid from ootype to anterior to cirrus sac, then extending posteriorly, entering cirrus at distal end. External and internal seminal vesicles absent. Cirrus sac pyriform, tilted anteriorly, positioned almost parallel to lateral margin of proglottid, 190-379 long by 110-247 wide, containing coiled cirrus. Cirrus armed (microtriches **6 long**). Ovary H-shaped in dorso-ventral view, 144-253 (206 ± 39.4; 3; 6) long by 238-290 (264 ± 24.4; 3; 6) wide, lobulated, symmetrical; ovarian bridge at center of ovary. Vagina medial or sublateral in position in proglottid, extending from ootype to genital pore, widening to 2-3 times original width before opening into genital atrium posterior to

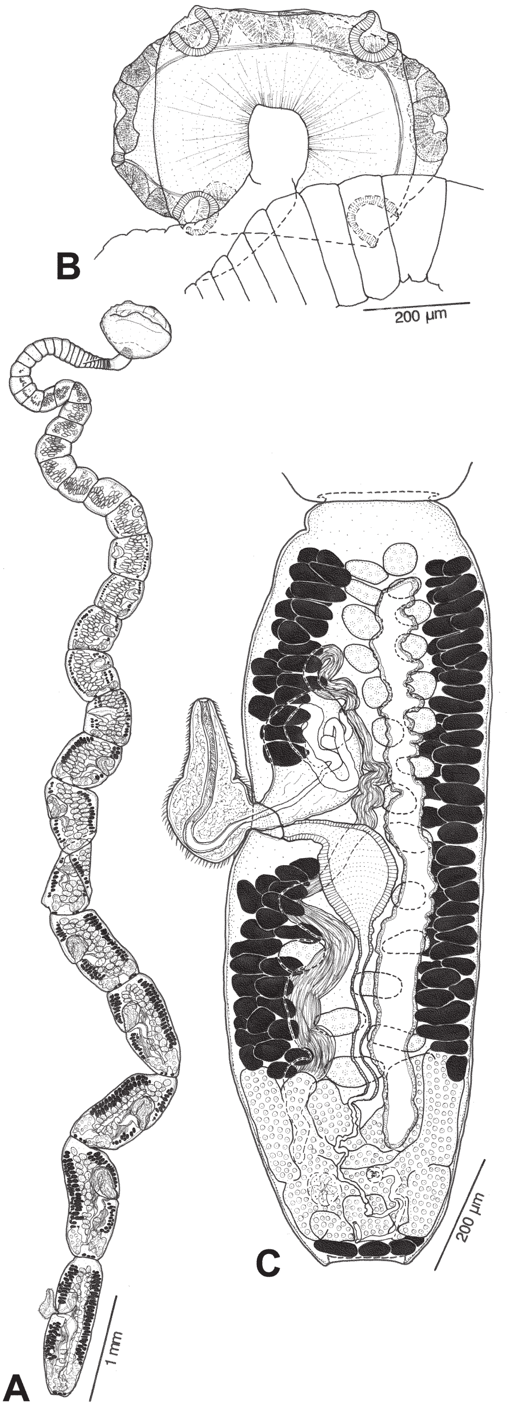


Fig. 36. A-C. Line drawings of *Lecanicephalum peltatum* Linton, 1890. A. Whole worm (neotype, USNPC No. 7677). B. Scolex (voucher, USNPC No. 7677). C. Mature proglottid (neotype, USNPC No. 7677).

Table 1. Reports of *Lecanicephalum peltatum*.

CITATION	HOST*	COLL. DATE	LOCALITY	NO. OF SPECIMENS	COMMENTS
Linton (1890)	*Trygon centrura*	July 29, 1886	Woods Hole, Massachusetts	1	
		July 10, 1887		4-5	
		August 1, 1887		4-5	
Linton (1900)	*Dasyatis centrura*	July 29, 1898	Woods Hole	9	
Linton (1901)	*Dasyatis centrura* (*Trygon centrura*)	July 19, 1899	Woods Hole region	4	
Linton (1905)	*Dasyatis say*	July 09, 1901	Beaufort, North Carolina	1	
		July 24, 1901		several	
		August 18, 1902		3	
Linton (1924)	*Dasybatis centrura*	June 02, 1903-1922	Woods Hole region	few fragments	
		July (1) 2, 1903-1922		a fragment	
		August, 1903-1922		many	collected by MacCallum
		September, 1903-1922		few, 22, 1, 3	USNPC No. 7677
		July & August, 1923		2 to many	
Southwell (1925)	*Dasyatis centrura*			few	"presented by Professor Edwin Linton" (Southwell, 1925 p. 253)
Baer (1948)	*Dasyatis centrura*	[November, 1947]	Woods Hole	[large number]	MHNG No. 87/7-29
Brooks & Mayes (1980)	*Dasyatis americana*	1975-1976	Cartagena, Colombia		HWML No. 20937

* as given in publication

cirrus sac; vaginal sphincter absent. Genital pores lateral, irregularly alternating, 50-59% (54 ± 3.6; 3; 6) of proglottid length from posterior end. Uterus saccate, extending along median line of proglottid from near ootype to anterior margin of proglottid; uterine duct not observed; uterine pore absent. Vitellaria follicular, medullary, in lateral columns, 2-3 vitelline follicles on each side of proglottid in cross-section, extending entire length of proglottid, interrupted by ovary, slightly overlapping anterior margins of ovary; vitelline follicles 22-44 (34 ± 6.5; 3; 15) long by 51-89 (67 ± 14.3; 3; 15) wide. Single pair of excretory ducts present. Eggs not observed.

Remarks

Lecanicephalum peltatum has been reported several times since its original description. Reports of "*L. peltatum*" are summarized in Table 1.

Linton (1890) appeared not to have designated type specimens. Moreover, Linton's specimens used in his 1890 description of *L. peltatum* could not be located at any of the museums visited or in any of the personal collections examined as part of this study. It therefore seemed reasonable to assume that the type material of Linton (1890) was lost. Because *Lecanicephalum* is the type genus of the type family of the order, designation of a neotype seemed justified. Linton (1924), Baer (1948), and Brooks and Mayes (1980) all deposited voucher material of specimens identified as *L. peltatum* in various museums (see Tab. 1). The selection of a neotype from a metatype (specimen collected by Linton himself, from the type host and the type locality) seemed most appropriate.

The metatype deposited by Linton (1924) (USNPC No. 7677) consisted of one slide with five specimens (specimens 1-5) (Fig. 37). Closer examination of this material revealed that, of the five specimens, two were

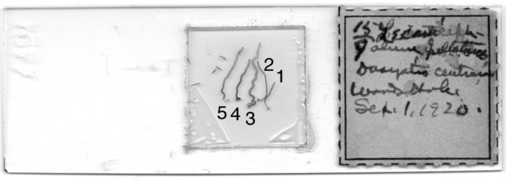


Fig. 37. USNPC No. 7677. Neotype (specimen 3) and 2 vouchers (specimens 4 and 5) of *Lecanicephalum peltatum*.

immature (specimens 1 and 2), not allowing for detailed comparison with Linton’s (1890) original description of *L. peltatum*. The remaining three specimens (specimens 3-5) were consistent with the original description of *L. peltatum* (Linton 1890). One of these three specimens (specimen 3) was chosen as the neotype because, in possessing 61 proglottids, it was most similar to Linton’s (1890) description of *L. peltatum* as possessing 60 proglottids. Measurements of the other two specimens (specimens 4 and 5) were included in the description of *L. peltatum* presented here, but these specimens remain voucher specimens.

Voucher specimens of *L. peltatum* deposited by Baer (1948) (MHNG No. 87/7-29) and Brooks and Mayes (1980) (HWML No. 20937) were also examined. The conspecificity of this material with *L. peltatum* is suspect. More thorough examination of this material is required to conclusively determine the identity of these specimens.

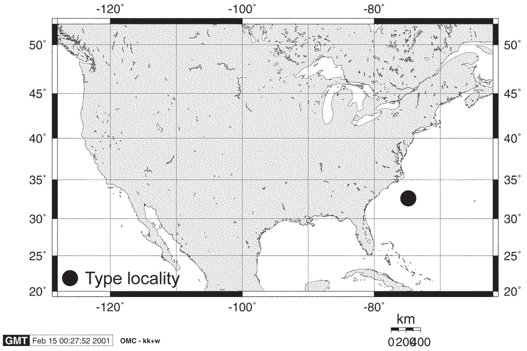


Fig. 38. Geographic distribution of *Lecanicephalum coangustatum* Jensen, n. sp.

Lecanicephalum coangustatum Jensen, n. sp.

(Figs. 38-40)

Type host: *Dasyatis centroura* (Mitchill, 1815), Roughtail stingray (Dasyatidae, Myliobatiformes).

Additional hosts: None.

Site of infection: Spiral intestine.

Type locality: Western Atlantic Ocean off South Carolina (77°32.08’N, 33°13.53’W), U.S.A. (Fig. 38).

Additional localities: None.

Number of specimens on which the original description was based: 31 (25 whole mounts, two specimen cross-section series, two scolex longitudinal section series, and two specimens prepared for SEM).

Type specimens: Holotype (USNPC No. 94578), 10 paratypes (eight whole mounts, one specimen cross-section series, and one scolex longitudinal-section series) (USNPC No. 94579); seven paratypes (KUNHM Nos. 002110-002116); 11 paratypes (nine whole mounts, one specimen cross-section series, and one scolex longitudinal section series) (LRP Nos. 3289-3299); two paratype specimens prepared for SEM (LRP).

Etymology: *Coangusto*, *-atus*, L., confine, compress, enclose.

Chronology

Caira *et al.* (2001): include *Lecanicephalum coangustatum* under the name “*Lecanicephalum* sp.” in a phylogenetic analysis based on morphological data; the species grouped with the majority of the other lecanicephalidean taxa included in the analysis.

Description (Based on 25 whole mounts, two specimen cross-section series, two scolex longitudinal section series, and two specimens prepared for SEM.)

Worms 2,000-7,156 (3,120 ± 1,126.4; 25) long; maximum width at scolex; 12-34 (17 ± 5.4; 25) proglottids, euapolytic. Scolex 207-463 (286 ± 54.4; 23) long by 279-444 (339 ± 43.9; 25) wide, bearing four acetabula. Acetabula sucker-like in form, 61-96 (72 ± 9.0; 25; 47) long by 54-89 (70 ± 7.1; 22; 43) wide. Apical modification of scolex proper with aperture at apex (Fig. 40B), fully expandable (Fig. 40A and C), with conspicuous circular muscle bundles responsible for change in diameter of aperture (Fig. 40D), bearing apical organ; apical organ in form of circular, muscular and glandular sheet (Fig. 40C), completely retractable into apical modification of scolex proper (Fig. 40B and D); retraction

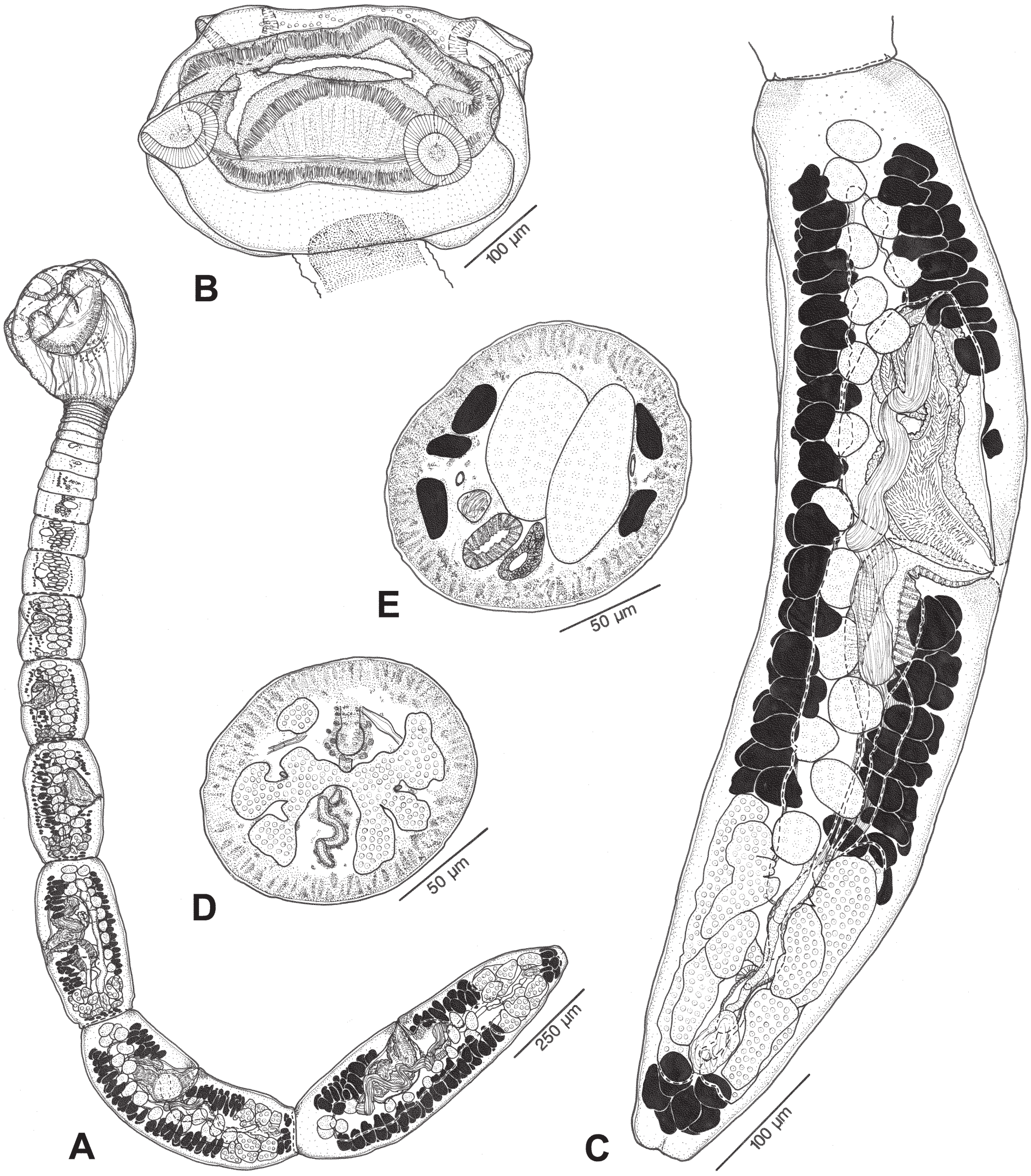


Fig. 39. A-E. Line drawings of *Lecanicephalum coangustatum* Jensen, n. sp. A. Whole worm (holotype, USNPC No. 94578). B. Scolex (USNPC No. 94579). C. Mature terminal proglottid (USNPC No. 94579). D. Cross-section through mature proglottid at level of ovarian bridge (LRP No. 3298). E. Cross-section through mature proglottid between ovary and cirrus sac (LRP No. 3298).

facilitated by circular muscle bundle in apical organ (Fig. 40C and D).

Rims of acetabula covered with pointed filitriches (Fig. 40E). Scolex proper covered with pointed filitriches (Fig. 40F). Apical modification of scolex proper covered with pointed filitriches (Fig. 40G). Surface of apical organ covered with small tubercles, suggesting glandular surface (Fig. 40I). Strobila covered with long filitriches (Fig. 40H).

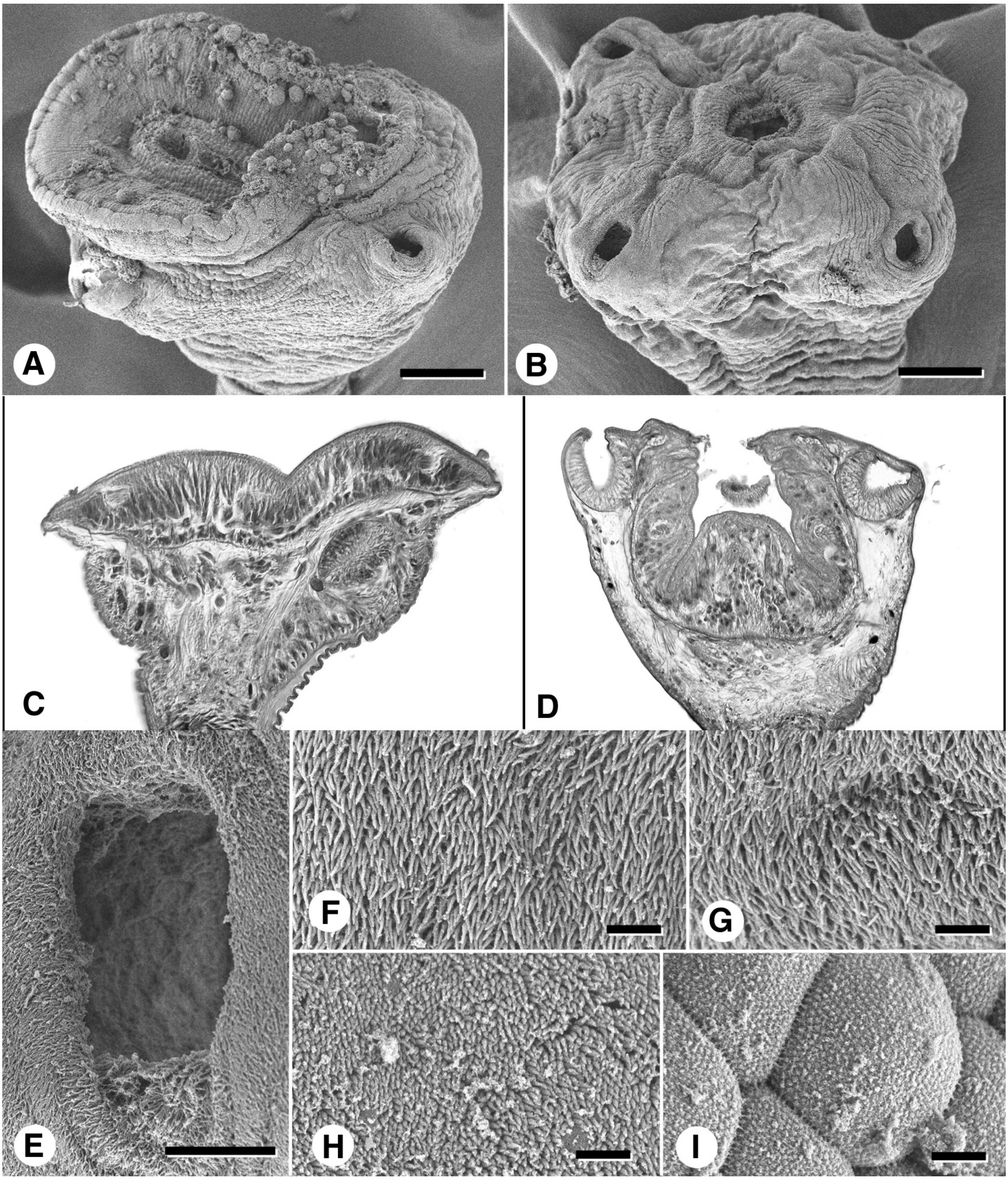


Fig. 40. A-I. Scanning electron micrographs and histological sections of *Lecanicephalum coangustatum* Jensen, n. sp. A. Scolex with apical organ protruded. B. Scolex with apical organ retracted. C. Longitudinal section through scolex with apical organ protruded (LRP No. 3299). D. Longitudinal section through scolex with apical organ retracted (USNPC No. 94579). E. Acetabulum. F. Microtriches on surface of scolex proper. G. Microtriches on rim of acetabulum. H. Microtriches on surface of strobila. I. Surface of apical organ. Scale bars: A and B, 50 µm; C, 10 µm; D-G, 1 µm.

Cephalic peduncle absent. Proglottids weakly craspedote, non-laciniate. Immature proglottids 10-30 (15 ± 4.9; 25) in number, initially wider than long, becoming longer than wide with maturity; two most posterior immature proglottids 126-450 (271 ± 73.0;

25; 50) long by 114-225 (171 ± 28.5; 25; 50) wide. Mature proglottids 2-4 (3 ± 0.7; 25) in number, 327-1,028 (614 ± 182.8; 25; 61) long by 138-268 (207 ± 29.0; 25; 61) wide. Testes 13-19 (15 ± 1.5; 24; 49) in number, 22-60 (38 ± 6.6; 24; 118) long by 32-64 (47 ± 7.1; 24; 118) wide, anterior to ovary, extending from anterior margin of proglottid to ovary, slightly overlapping anterior margins of ovary, 1-2 irregular columns in dorso-ventral view, one row deep in cross-section (Fig. 39E). Vas deferens extensive, in form of expanded duct, extending more or less along median line of proglottid from ootype to cirrus sac, entering cirrus at distal end. External and internal seminal vesicle absent. Cirrus sac J-shaped, tilted anteriorly, positioned almost parallel to lateral margin of proglottid, 111-271 (185 ± 39.5; 25; 60) long by 60-154 (110 ± 18.7; 25; 60) wide, containing coiled cirrus. Cirrus armed, with conspicuous microtriches at base. Ovary H-shaped in dorso-ventral view, essentially bilobed in cross-section (Fig. 39D), 67-252 (142 ± 54.8; 25; 60) long by 76-181 (139 ± 25.1; 25; 59) wide, lobulated, symmetrical. Vagina extending more or less along median line of proglottid from ootype to genital pore, widening to 2-3 times original width before opening into genital atrium posterior to cirrus sac; vaginal sphincter absent. Genital pores lateral, irregularly alternating, 41-65% (54 ± 4.9; 25; 61) of proglottid length from posterior end. Uterus saccate, extending along median line of proglottid from near ootype to anterior margin of proglottid; uterine duct entering uterus slightly posterior to level of genital pore; uterine pore absent. Vitellaria follicular, medullary, in two columns on each lateral margin of proglottid, essentially two vitelline follicles on each side of proglottid in cross-section (Fig. 39E), columns extending entire length of proglottid, interrupted by ovary, slightly overlapping anterior margins of ovary; vitelline follicles 11-36 (21 ± 6.0; 25; 124) long by 11-65 (36 ± 10.4; 25; 124) wide. Single pair of excretory ducts present (Fig. 39D and E). Eggs not observed.

Remarks

Lecanicephalum coangustatum was collected from the Roughtail stingray, *Dasyatis centroura*, the type host of *L. peltatum*. The type locality of *L. coangustatum* are the waters off South Carolina, U.S.A., while Linton (1890) reported *L. peltatum* from the waters off Massachusetts and North Carolina, with Woods Hole, Massachusetts, U.S.A. as the type locality. It was not immediately apparent that this second species of *Lecanicephalum* existed in *Dasyatis centroura*. Conspecificity of these two species was initially assumed, because *L. coangustatum* and *L. peltatum* parasitize the same host species and were collected in relatively close proximity to one another (South Carolina vs. Massachusetts and North Carolina). However, several features distinguishing the two suites of specimens could be identified. *Lecanicephalum coangustatum* is generally smaller than *L. peltatum* (2,000-7,156 vs. 8,036-14,000) and consists of fewer proglottids (12-34 vs. 49-61). The mature proglottids of *L. coangustatum* are more elongate (length to width ratio of 3:1) than those of *L. peltatum* (length to width ratio of 2.5:1), and the ovary is narrower in the former than in the latter species (76-181 vs. 238-290). In addition, *L. coangustatum* has a relatively larger scolex than *L. peltatum*; the scolex contributes 9.2% and 4.2%, respectively, to the total length of each worm.

Lecanicephalum coangustatum is the taxon referred to as "*Lecanicephalum* sp." in the phylogenetic analysis of Caira *et al.* (2001). The type material of *L. coangustatum* includes some of the specimens used to code this species by Caira *et al.* (2001).

PARABERRAPEX
Jensen, 2001

Taxonomic status: Valid.

Synonyms: None.

Type and only species: *Paraberrapex manifestus* Jensen, 2001.

Etymology: The generic name *Paraberrapex* (*par*, L., equal) indicates the close resemblance of the scolex of this taxon to that of *Aberrapex*.

Diagnosis (Modified from Jensen [2001].)

Worms euapolytic. Scolex with four acetabula; acetabula bothridiate in form, simple, facially unmodified; distal and proximal surfaces of acetabula covered with blade-like spinitriches; apical modification of scolex proper and apical organ absent. Proglottids craspedote, non-laciniate. Testes numerous, arranged in two irregular columns, anterior to ovary, post-vaginal testes absent. Vas deferens extending from near posterior margin of proglottid to anterior margin of cirrus sac. External seminal vesicle absent. Cirrus sac pyriform. Cirrus unarmed. Ovary H-shaped in dorso-ventral view, bilobed in cross-section. Vagina extending along median line of proglottid from ootype to cirrus sac, opening into genital atrium posterior to cirrus sac. Genital pores lateral, irregularly alternating. Uterus median, saccate. Vitellaria follicular, lateral, extending entire length of proglottid. Eggs grouped in cocoons. Parasites of sharks of the family Squatinidae. Gulf of California (Mexico).

Chronology

Caira *et al.* (2001): include a species of *Paraberrapex* (*P. manifestus* under the name "n. gen. 2 n. sp.") in a comprehensive phylogenetic analysis based on morphological data; this species grouped outside of the majority of the other lecanicephalidean taxa included in the analysis, along with two other lecanicephalidean taxa (*Aberrapex senticosus* as "'*Discobothrium*' n. sp." and *Healyum pulvis* as "new genus 3 n. sp.").

Jensen (2001): erects the new genus *Paraberrapex* with *P. manifestus* as the type species; considers it to be a lecanicephalidean despite its lack of an apical structure; in Caira *et al.* (2001) *P. manifestus* (as n. gen. 2 n. sp.) groups outside of the majority of lecanicephalidean taxa.

Remarks (Modified from Jensen [2001]. Copyright 2001, The Journal of Parasitology. Used with permission.)

Jensen (2001) noted that *Paraberrapex* clearly exhibits the lecanicephalidean proglottid condition in that the vagina opens into the genital atrium posterior to the cirrus sac. Although, unlike many lecanicephalideans, the vas deferens is not extensive or expanded to form an external seminal vesicle, the extent of the vas deferens is consistent with the condition seen in most lecanicephalidean genera in that it extends from near the posterior margin of the proglottid to the cirrus sac. These proglottid characters, despite the absence of an apical modification of the scolex proper and an apical organ on the scolex, warranted inclusion of this genus in the Lecanicephalidea.

Paraberrapex can be distinguished from ten of the 11 other valid lecanicephalidean genera recognized, in its lack of any kind of modification of the apex of the scolex. In addition, *Paraberrapex* differs from *Anteropora*, *Corrugatocephalum*, *Healyum*, *Polypocephalus*, and *Quadcuspibothrium* in its possession of testes arranged in 2-3 irregular columns rather than essentially in a single column. It differs from *Lecanicephalum* in its possession of acetabula that are bothridiate rather than sucker-like in form. Whereas *Paraberrapex* possesses an ovary that is bilobed in cross-section and vitelline follicles arranged in two lateral columns on each side of the proglottid, *Tetragonocephalum* possesses an ovary that is circular in cross-section and *Tylocephalum* possesses circum-medullary vitelline follicles or vitelline follicles that are arranged in multiple lateral columns on each side of the proglottid. In addition, it differs from *Eniochobothrium* and *Hornellobothrium* in its lack of laterally expanded proglottids in the anterior region of the strobila. *Paraberrapex* most closely resembles *Aberrapex.* Both taxa lack an apical structure on the scolex. However, *Paraberrapex* can be distinguished from the latter genus on the basis of a vagina that is medial in position medial rather than lateral throughout its length in the proglottid, an ovary that is bilobed rather than tetralobed in cross-section, and acetabular surfaces covered with slender blade-like spinitriches rather than large blade-like spinitriches. Thus, the scolex of *Paraberrapex* does not possess the "spined" appearance of that of *Aberrapex*.

Paraberrapex manifestus Jensen, 2001
TYPE SPECIES
(Figs. 41-43)

Synonyms: None.

Type host: *Squatina californica* Ayres, 1859, Pacific angelshark (Squatinidae, Squatiniformes).

Additional hosts: None.

Site of infection: Spiral intestine.

Type locality: Santa Rosalia (27°19'N, 112°17'W), Baja California, Mexico (Fig. 41).

Additional localities: None.

Number of specimens on which the original description was based: 42 (26 whole worms, 11 detached proglottids, cross-section series of one specimen, and four lactophenol preparations of eggs).

Type specimens: Holotype (CNHE No. 4179); paratypes (CNHE Nos. 4180 and 4181; USNPC Nos. 91209-91211; HWML No. 16375; LRP Nos. 2159-2179).

Voucher specimens: None.

Material examined: CNHE No. 4179 (holotype); CNHE Nos. 4180 and 4181, USNPC Nos. 91209-91211, HWML No. 16375, and LRP Nos. 2159-2179 (paratypes).

Etymology: The specific epithet *manifestus* (L., clear, evident, apparent) was chosen to emphasize the unusual clarity of the mounted, detached proglottids in which all reproductive organs and their associated duct work are readily apparent.

Chronology

Caira *et al.* (2001): include *Paraberrapex manifestus* under the name "n. gen. 2 n. sp." in a comprehensive phylogenetic analysis based on morphological data; the species grouped with two other lecanicephalidean taxa (*Aberrapex senticosus* as "'*Discobothrium*' n. sp." and *Healyum pulvis* as "new genus 3 n. sp.") outside of the majority of the other lecanicephalidean taxa included in the analysis.

Jensen (2001): describes *Paraberrapex manifestus* as the type species of *Paraberrapex*.

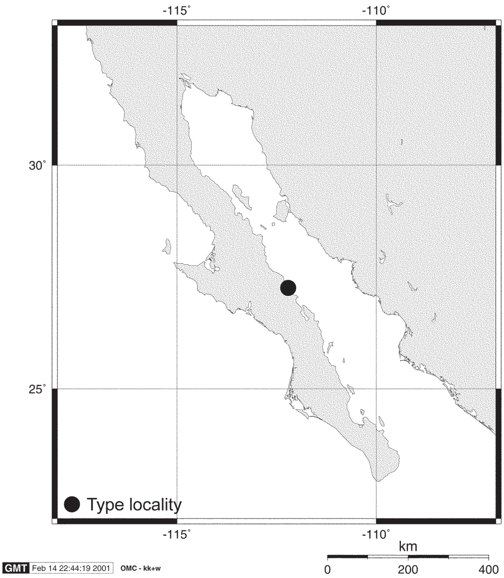


Fig. 41. Geographic distribution of *Paraberrapex manifestus* Jensen, 2001.

Description (Modified from Jensen [2001]. Copyright 2001, The Journal of Parasitology. Used with permission.) (Based on 26 whole worms, 11 detached proglottids, cross-section series of one specimen and four lactophenol preparations of eggs.)

Worms 1,050-2,378 (1,692 ± 337.2; 26) long; maximum width at level of scolex; 11-17 (13 ± 1.7; 26) proglottids, euapolytic. Scolex 165-278 (213 ± 28; 26) long by 192-343 (261 ± 33; 26) wide, consisting of four acetabula. Acetabula bothridiate in form, facially unmodified, 128-218 (162 ± 17.7; 26; 45) long by 95-197 (138 ± 22.1; 26; 46) wide. Apical modification of scolex proper and apical organ absent. Distal and proximal surfaces of acetabula and region of scolex proper anterior to acetabula densely covered with blade-like spinitriches and pointed filitriches (Fig. 43B, C and E, respectively). Scolex proper at apex of scolex covered with long filitriches only (Fig. 43D).

Cephalic peduncle absent. Strobila covered with long filitriches; filitriches becoming wider towards posterior margins of proglottids (Fig. 43F). Proglottids slightly craspedote, non-laciniate. Immature proglottids 10-15 (12 ± 1.6; 26) in number, initially wider than

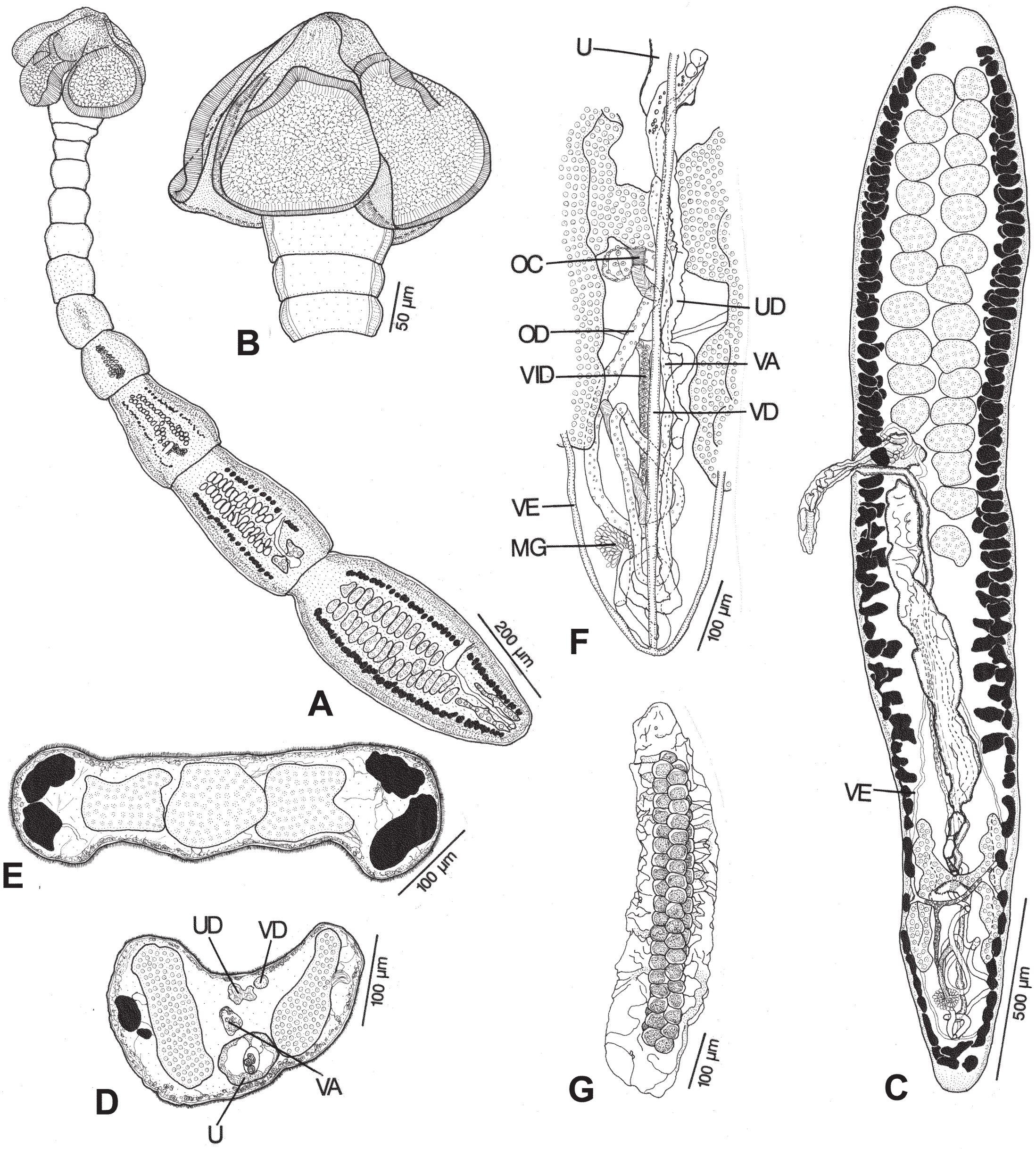


Fig. 42. A-G. Line drawings of *Paraberrapex manifestus* Jensen, 2001. A. Whole worm. B. Scolex. C. Detached mature proglottid. D. Cross-section through mature proglottid at level of ovarian bridge. E. Cross-section through mature proglottid anterior to genital pore. F. Detail of ootype of detached proglottid. G. Cocoon, note numerous eggs. (Taken from Jensen [2001]. Copyright 2001, The Journal of Parasitology. Used with permission.)

long, becoming longer than wide with maturity, two most posterior immature proglottids 56-525 (230 ± 104.3; 26; 53) long by 90-232 (146 ± 39.9; 26; 53) wide. Mature proglottids rarely more than one in number, longer than wide; mature terminal proglottids 424-929 (648 ± 128.7; 25) long by 162-252 (192 ± 24.7; 25) wide; mature and gravid detached proglottids 2,074-3,087 (2,647 ± 351.1; 11) long by 293-616 (489 ± 100.9; 11) wide. Testes in mature attached and detached proglottids 20-38 (28 ± 4.9; 37; 53) in number, 17-107 (44

± 28.2; 36; 108) long by 30-160 (65 ± 34.6; 108; 36) wide, extending from anterior margin of proglottid to slightly posterior to genital pore, stopping short of ovary, 2-3 columns in dorso-ventral view, one row deep in cross-section (Fig. 42E), postvaginal and postovarian testes absent. Vas efferens visible in detached proglottids only, branching into two ducts at posterior limit of testes extending posteriorly along left and right margins of proglottid to anterior margin of postovarian field of vitelline follicles, then merging with one another medially to form vas deferens. Vas deferens extending along median line of proglottid from posterior to ovary to level of cirrus sac, 12-20 (14 ± 2.3; 11) wide in detached proglottids at level of ovary, coiling anterior to cirrus sac, entering cirrus sac at distal end. External and internal seminal vesicles absent. Cirrus sac pyriform, slightly angled anteriorly, 35-80 (56 ± 10.8; 24) long by 22-42 (32 ± 5.9; 23) wide in attached mature proglottids, 97-155 (131 ± 18.7; 9) long by 45-100 (72 ± 21; 9) wide in detached proglottids, containing coiled cirrus. Cirrus unarmed, 37-52 (45 ± 6.6; 7) wide at base in detached proglottids, in one specimen at least 1,900 long, very narrow. Ovary H-shaped in dorso-ventral view, bilobed in cross-section (Fig. 42D), 57-135 (86 ± 20.3; 24) long by 47-102 (70 ± 15.9; 24) wide in mature attached proglottids, 313-586 (415 ± 81.2; 10) long by 162-364 (248 ± 57.3; 10) wide in detached proglottids, lobulated, symmetrical; ovarian bridge 22-72 (43 ± 19.5; 8) wide in detached proglottids, center of bridge 56-72% (63 ± 5.7; 10) from posterior end of ovary; ovicapt 30-52 (41 ± 8.4; 10) long by 65-97 (85 ± 12.4; 10) wide in detached proglottids, with large lumen. Mehlis' gland posterior to ovary, 47-97 (70 ± 14.1; 11) in diameter in detached proglottids. Vagina slender, extending from ootype along median line of proglottid to cirrus sac, opening into genital atrium posterior to cirrus sac; vaginal sphincter absent. Genital pores lateral, irregularly alternating, 34-57% (44 ± 6.3; 26) of proglottid length from posterior end in mature attached proglottids, 49-64% (57 ± 4.7; 11) of proglottid length from posterior end in detached proglottids. Uterus saccate, extending along median line of proglottid from slightly anterior to ovarian

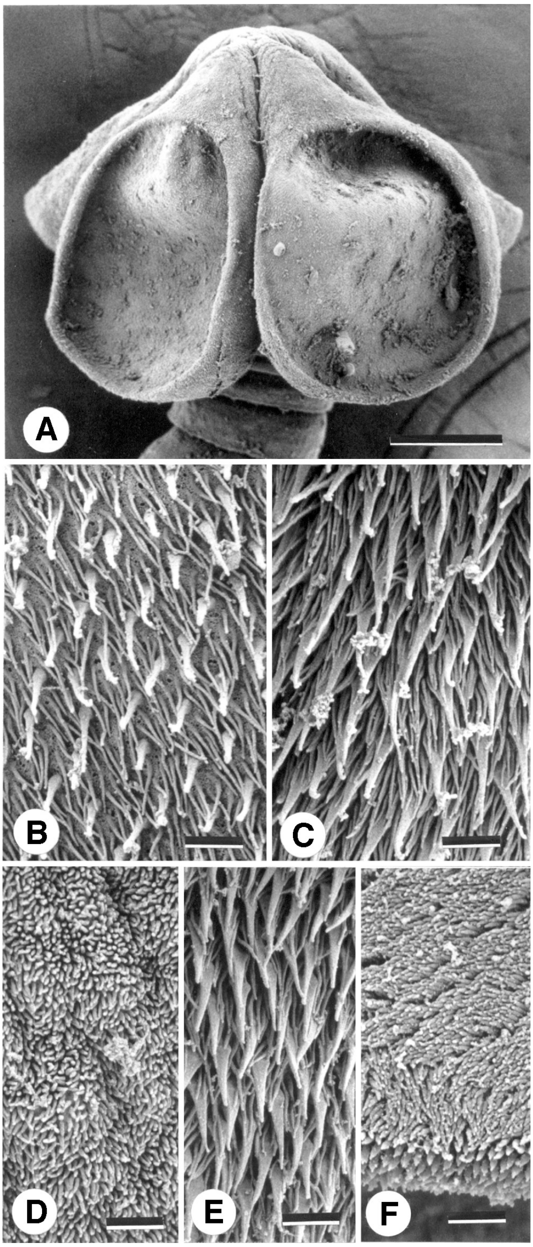


Fig. 43. A-F. Scanning electron micrographs of *Paraberrapex manifestus* Jensen, 2001. A. Scolex. B. Microtriches on distal acetabular surface. C. Microtriches on proximal acetabular surface. D. Microtriches on surface of scolex proper at apex of scolex. E. Microtriches on surface of scolex proper anterior to acetabula. F. Microtriches on proglottids and posterior margin of proglottids; note widening of long filitriches at posterior margin of proglottid. Scale bars: A, 50 µm; B-F, 1 µm. (Taken from Jensen [2001]. Copyright 2001, The Journal of Parasitology. Used with permission.)

bridge to about level of genital pore; uterine duct visible in detached proglottids, entering uterus at 37-78% (53 ± 15; 10) of uterus length from posterior end; uterine dehiscence seen in one detached proglottid 25% of uterus length from posterior end. Vitellaria follicular, medullary, in lateral columns, two vitelline follicles on each lateral margin of proglottid in cross-section (Fig. 42E), extending throughout entire length of proglottid, uninterrupted by ovary; vitelline follicles 7-20 (11 ± 3.4; 15; 39) long by 7-25 (14 ± 4.4; 15; 39) wide in mature attached proglottids, 22-60 (41 ± 10.2; 11; 33) long by 25-95 (58 ± 20.2; 11; 33) wide in detached proglottids. Excretory ducts not observed. Eggs, 20-39 (30 ± 5.5; 4; 96) in diameter, grouped in cocoons (Fig. 42G). Each cocoon containing 69-111 (84 ± 13.5; 4; 16) eggs, elongate, thin-walled; free cocoons 505-727 (637 ± 63.1; 4; 16) long by 91-182 (134 ± 26; 4; 16) wide.

Remarks (Modified from Jensen [2001]. Copyright 2001, The Journal of Parasitology. Used with permission.)

Paraberrapex manifestus is the taxon referred to as "new genus 2 n. sp." in the phylogenetic analysis of Caira *et al.* (2001). The type material of *P. manifestus* includes some of the specimens used to code this species in Caira *et al.* (2001).

Paraberrapex manifestus was recovered from eight of the 12 specimens of *Squatina californica* examined (prevalence: 66.7%).

POLYPOCEPHALUS Braun, 1878

Taxonomic status: Valid.

Synonyms: *Parataenia* Linton, 1890.

Type species: *Polypocephalus radiatus* Braun, 1878.

Other species: *Polypocephalus affinis* Subhapradha, 1951; *P. alii* Shinde and Jadhav, 1981; *P. bombayensis* Shinde, Dhule and Jadhav, 1992; *P. caribbensis* (Gardner and Schmidt, 1984) n. comb.; *P. coronatus* Subhapradha, 1951; *P. digholensis* Deshmukh, Jadhav and Shinde, 1982; *P. djeddensis* Jadhav and Shinde, 1989; *P. elongatus* (Southwell, 1912) n. comb.; *P. helmuti* Jensen, n. sp.; *P. indicus* Deshmukh, Jadhav and Shinde, 1982; *P. karbharii* Deshmukh, Jadhav and Shinde, 1982; *P. katpurensis* Shinde and Jadhav, 1981; *P. lintoni* Subhapradha, 1951; *P. maharashtra* Deshmukh, Jadhav and Shinde, 1982; *P. medusia* (Linton, 1890) Southwell, 1925; *P. moretonensis* Butler, 1987; *P. prathibhai* Deshmukh, Jadhav and Shinde, 1982; *P. ratnagiriensis* Jadhav, Shinde and Sarwade, 1986; *P. rhinobatidis* Subhapradha, 1951; *P. rhynchobatidis* Subhapradha, 1951; *P. saoudi* Hassan, 1982; *P. singhii* Shinde and Jadhav, 1981; *P. thapari* Shinde and Jadhav, 1981; *P. vesicularis* Yamaguti, 1960; *P. vitellaris* Subhapradha, 1951.

Species inquirendae: *Polypocephalus trygoni* Jadhav & Threlfall, 1986.

Nomina nuda: *Polypocephalus braunii* Shinde, 1981 in Jadhav and Shinde (1989) and Shinde *et al.* (1981); *P. testicularis* in Jadhav and Shinde (1989).

Etymology: *Polypus*, L., the many-footed, the coral animal; *kephale*, Gr., head.

Diagnosis (Modified from Euzet [1994b].)

Worms euapolytic or apolytic. Scolex with four acetabula; acetabula in form of suckers; apical modification of scolex proper with terminal expandable aperture at apex, housing apical organ in tentacular pouch; apical organ divided into tentacles; tentacles completely invaginable into tentacular pouch, glandular tissue in and at base of tentacular pouch. Proglottids craspedote (non-laciniate) or acraspedote. Testes few (4, 6, or 12), in single column, anterior to ovary. Vas deferens extensive, in form of expanded duct, or forming external seminal vesicle, extending from ootype to cirrus sac. Internal seminal vesicle present or absent. Cirrus sac pyriform. Cirrus armed. Ovary H-shaped in dorso-ventral view, tetralobed in cross-section. Vagina extending along median or lateral line of proglottid, opening into genital atrium posterior to cirrus sac or at same level. Genital pores lateral or sublateral, irregularly alternating. Uterus saccate, along median line of proglottid. Vitellaria follicular, in lateral columns, anterior to ovary; vitelline follicles lateral to ovary or posterior to ovary present or absent. One dorsal and one ventral pair of excretory ducts present. Eggs with two filaments. Parasites of rays in the orders Rhinobatiformes and Myliobatiformes, and the Spadenose shark, *Scoliodon laticaudus* Müller and Henle, 1838 (Carcharhinidae). Eastern and northern Indian Ocean, western Atlantic Ocean (U.S.A. and Jamaica), Timor Sea (Australia), Red Sea (Egypt), and the western Pacific Ocean (Japan and Australia).

Chronology

Braun (1878): erects the new genus *Polypocephalus* with *P. radiatus* as the type species from *Rhinobatus* [sic] *granulatus*; describes, among other features, glands at base of tentacles.

Scudder (1884a and b): lists *Polypocephalus* Braun, 1878 in a compilation of generic names of recent and fossil animals from the earliest time to the end of 1879.

von Linstow (1889): [according to Stiles and Hassall (1912): as *Polycephalus* [sic]].

Braun (1894-1900): lists *Polypocephalus* Braun, with its only species *Polypocephalus radiatus* Braun, as valid, but doubtful in terms of its position within the classification; lists *Parataenia* as a synonym; comments on skin glands found associated with the apical structure of *P. radiatus*.

Shipley and Hornell (1904): report finding a single specimen of *Polypocephalus* in *Taeniura melanospilos* from Ceylon.

de Beauchamp (1905): addresses elasmobranch cestode classification first, followed by treatments of individual taxa; lists *Polypocephalus* Braun (*Parataenia* Linton) in the classification (first) part as the only genus found in elasmobranchs in the order Tetracotyles; does not list the order (or *Polypocephalus*) in the second part dealing with individual genera and species.

Stiles and Hassall (1912): *Polypocephalus* Braun, 1878: Braun (1895 and 1900), de Beauchamp (1905) (*Parat*. Lint.) and Scudder (1884); 1889: *Polycephalus* [sic] Linstow, 1889 (for *Polypocephalus*).

Meggitt (1924): considers *Polypocephalus* Braun, 1878 as a valid genus in his new family Polypocephalidae (along with *Anthemobothrium* and *Calycobothrium*), order Tetraphyllidea; considers *Parataenia* Linton, 1889 and *Thysanobothrium* Shipley and Hornell, 1906 junior synonyms of *Polypocephalus*; provides an abbreviated diagnosis of the genus; includes "*P. tortus* (Linstow, 1904) (*Anthobothrium tortum*), *Phoca barbata* – Linstow, 1904, 682 " (p. 143) beneath *Polypocephalus* entry [relevance unclear].

Southwell (1925): considers *Polypocephalus* as a valid genus in the family Lecanicephalidae, suborder Multivitellata, order Cyclophyllidea; lists *Parataenia*, *Thysanobothrium*, and *Anthemobothrium* as synonyms of *Polypocephalus*; recognizes three species; emends the generic diagnosis; notes that Linton was probably unaware of Braun's description when describing *Parataenia* and likening the tentacles to the proboscides of avian taeniids.

Poche (1926): recognizes *Polypocephalus* (along with *Anthemobothrium*, *Calycobothrium*, and *Parataenia*) in the family Polypocephalidae Meggitt, suborder Phyllobothriinea *nom. nov.*, order Taeniidea *nom. nov.*

Woodland (1927): considers *Polypocephalus* a "lecanicephalid" genus; proposes it be included in the family Phyllobothriidae, order Tetraphyllidea, based on disposition of longitudinal muscle bundles and marginal vitellaria.

Pintner (1928): "*Polypocephalus* = *Parataenia*."

Mola (1929): reclassifies cestodes and places *Polypocephalus* (syn. *Parataenia* Linton, 1889) in the subfamily Polypocephaliinae, family Ichthyotaeniidae, order Tetraphyllidea.

Southwell (1929): comments on the classification schemes proposed by Poche (1926), Woodland (1927), and Pintner (1928); comments on the position of *Polypocephalus* (along with *Cephalobothrium*, *Lecanicephalum*, and *Calycobothrium*) in the family Phyllobothriidae in Woodland's scheme.

Southwell (1930): considers *Polypocephalus* Braun, 1878 (syn. *Parataenia*, *Thysanobothrium*, and *Anthemobothrium*) as a valid genus in the family Lecanicephalidae, superfamily Lecanicephaloidea, order Eucestoda; same text as that of Southwell (1925); recognizes two instead of three species.

Woodland (1930): provides a history of the genus; redescribes in detail (with figures) *Polypocephalus* (*Parataenia*) *medusia* based on four specimens of Linton's material collected from *Trygon centrura* [sic] from Woods Hole that he received from Southwell; redescribes in detail (with figures) *Polypocephalus radiatus* (syn. *Parataenia elongatus*) based on four slides he received of Southwell's material collected from *Trygon kuhli* [sic] and *T. sephen*; presents a diagnosis of the genus based on these two species; addresses the systematic placement of the genus; regards *Polypocephalus* as a primitive and probably isolated tetraphyllid form, with no close affinities to the Tetragonocephalidae; establishes the new family Polypocephalidae, for the genus *Polypocephalus* [not the first use of this name, see Meggitt, 1924].

Fuhrmann (1931): classifies *Polypocephalus* (syn. *Parataenia* and *Thysanobothrium*) in the family Lecanicephalidae (syn. Gamobothriidae Linton), order Tetraphyllidea, one of two families (out of a total of seven in the order) containing lecanicephalidean genera.

Baer (1948): rejects synonymy of *Thysanobothrium uarnakense* and *Parataenia elongata* with *Polypocephalus radiatus*, because of the lack of information about the internal anatomy of *T. uarnakense* and *P. radiatus*; rejects *Parataenia* as synonym of *Polypocephalus* until a more detailed study of this latter genus can be conducted.

Hyman (1951): considers *Polypocephalus* (= *Parataenia*, *Thysanobothrium*) (along with *Lecanicephalum, Anthemobothrium*, and *Adelobothrium*) as a valid genus in the family Lecanicephalidae, order Lecanicephaloidea; few characters for the family are presented.

Subhapradha (1951): summarizes history of the genus; has collected new material of *P. radiatus* and *P. medusia* and describes six new species of *Polypocephalus*; divides *Polypocephalus* species in two groups: *medusia*-group (large tentacular cavity, poor developed longitudinal muscles, bent uterus, elongated ovary), including *P. medusia*, *P. vitellaris*, and *P. rhynchobatidis*; *rhinobatidis*-group (inner muscle bundles in tentacles, narrow tentacular cavity, well developed longitudinal muscles, straight uterus, massive ovary), including *P. rhinobatidis*, *P. radiatus*, *P. lintoni*, *P. coronatus*, and *P. affinis*; based on tentacular cavity development, the *medusia*-group is primitive (with *P. medusia* most primitive), considers *P. lintoni* to be the second evolutionary stage and *P. rhinobatidis* next; lists all features common to *Polypocephalus* and redefines the genus.

Wardle and McLeod (1952): treat *Polypocephalus* Braun, 1878 in the family Cephalobothriidae, order Lecanicephala, with *P. radiatus* Braun, 1878 as the type species; separately recognize *Parataenia* Linton, 1890 in the family Lecanicephalidae, order Lecanicephala.

Yamaguti (1959): considers *Polypocephalus* Braun, 1878 (syn. *Parataenia* Linton, 1889, *Thysanobothrium* Shipley and Hornell, 1906 and *Anthemobothrium* Shipley and Hornell, 1906) as a valid genus in the family Lecanicephalidae, order Lecanicephalidea, with *P. radiatus* Braun, 1878 (syn. *Thysanobothrium uarnakense* Shipley and Hornell, 1906, [?] *Parataenia elongata* Southwell, 1912) as the type species; recognizes eight additional species (*P. affinis* Subhapradha, 1951, *P. coronatus* Subhapradha, 1951, *P. lintoni* Subhapradha, 1951, *P. medusia* (Linton, 1889) (syn. *Parataenia medusia* Linton), *P. pulcher* (Shipley and Hornell 1906) (syn. *Anthemobothrium pulcher* Shipley and Hornell), *P. rhynchobatidis* Subhapradha, 1951, *P. rhinobatidis* Subhapradha, 1951, and *P. vitellaris* Subhapradha, 1951).

Joyeux and Baer (1961): classify *Polypocephalus* as a valid genus in the family Lecanicephalidae, superfamily Lecanicephaloidea, order Tetraphyllidea.

Wardle *et al.* (1974): notes that Subhapradha (1951) described six species of *Polypocephalus*; do not mention in which of the five families of lecanicephalideans they place *Polypocephalus*.

Schmidt (1986): treats *Polypocephalus* Braun 1878 (syn. *Parataenia* Linton, 1889, *Thysanobothrium* Shipley and Hornell, 1906, *Anthemobothrium* Shipley and Hornell, 1906) as a valid genus in the family Lecanicephalidae, order Lecanicephalidea; recognizes a total of 14 species: *P. radiatus*, *P. affinis*, *P. alii*, *P. coronatus*, *P. kapurensis*, *P. lintoni*, *P. medusia*, *P. pulcher*, *P. rhinobatidis*, *P. rhynchobatidis*, *P. singhii*, *P. thapari*, *P. vesicularis*, and *P. vitellaris*.

Brooks and McLennan (1993): present a tree for the order Lecanicephaliformes Baylis, 1920; based on that tree they recognize *Polypocephalus* Braun, 1878 (along with *Calycobothrium* Southwell 1911, *Discobothrium* van Beneden

1871, *Echeneibothrium* van Beneden, 1850, *Lecanicephalum* Linton, 1890, and *Hexacanalis* Perrenoud, 1931 *sedis mutabilis*, *incertae sedis*) in the subfamily Lecanicephalinae Braun, 1900 *incertae sedis*, family Lecanicephalidae Braun, 1900, order Lecanicephaliformes Baylis, 1920.

Euzet (1994b): treats *Polypocephalus* Braun, 1878 (syn. *Parataenia* Linton, 1889 and *Thysanobothrium* Shipley and Hornell, 1906) as a valid genus in the family Polypocephalidae, order Lecanicephalidea.

Caira *et al*. (1999): include a species of *Polypocephalus* (*Polypocephalus* n. sp. from *Dasyatis americana*) as the single exemplar taxon for this genus in a phylogenetic analysis based on morphological data; the species grouped with the majority of the other lecanicephalidean taxa included in the analysis.

Caira *et al*. (2001): include three species of *Polypocephalus* (*Polypocephalus* n. sp. from Caira *et al*. (1999) as *Polypocephalus* n. sp. 1, *Polypocephalus* n. sp. 2 from *Rhinoptera* sp., and *Polypocephalus* n. sp. 3 from *Dasyatis centrura* [sic]) in a more comprehensive phylogenetic analysis based on morphological data; the species grouped with the majority of the other lecanicephalidean taxa included in the analysis; based on the limited taxa included the genus is monophyletic.

Remarks

Polypocephalus was the first lecanicephalidean genus described. Braun (1878) erected *Polypocephalus* for specimens he recovered from the spiral intestine of the ray *Rhinobatus granulatus*, naming the type species *P. radiatus*. Braun (1878) commented that based on his knowledge, no tapeworm was known up to that time to possess a large number of tentacles protruding from the scolex. The designation of type material or the location of its deposition was not addressed by Braun (1878). The unusual morphology of the scolex (*i.e.*, the presence of tentacles) made *Polypocephalus* easily recognizable, despite the apparent lack of type material.

In the original description, Braun (1878) commented that the position of *Polypocephalus* in the cestode classification was uncertain. Relatively soon thereafter, Meggitt (1924) created the family Polypocephalidae to house *Polypocephalus*, along with *Anthemobothrium* and *Calycobothrium*. However, since then, most authors have not recognized the family and the majority have placed *Polypocephalus* in the family Lecanicephalidae (*e.g.*, Southwell 1925; Fuhrmann 1931; Hyman 1951; Joyeux and Baer 1961; Schmidt 1986). The exception was Woodland (1930), who established a new family, Polypocephalidae, apparently unaware of Meggitt's (1924) earlier work. In the most recent key to the Lecanicephalidea by Euzet (1994b), *Polypocephalus* was, again, recognized in its own family, the Polypocephalidae.

Two of the most comprehensive diagnoses presented for *Polypocephalus* were those by Yamaguti (1959) and Euzet (1994b). The diagnosis presented here was modified from that of Euzet (1994b) to include additional features that had also been included by Yamaguti (1959). This diagnosis also includes the standard terminology used throughout this study. The diagnosis presented here is consistent with both of these previous diagnoses.

While at this time only one of the described species of *Polypocephalus* is formally considered to be a *species inquirenda*, it should be noted that a large number of the species are inadequately described; 15 of the 26 valid species of *Polypocephalus* in existence (including the new species) have been described from less than five specimens. Moreover, for 21 of the 26 species the place of deposition of types specimens was either not mentioned or type specimens were said to have been deposited at the Zoology Department, Marathwada University, Aurangabad, India, and are thus effectively unavailable for study. The understanding of the genus would benefit greatly from comprehensive redescriptions of these existing species, including neotype designation where appropriate and/or deposition of voucher material.

Two species names, *Polypocephalus braunii* and *Polypocephalus testicularis*, are considered to be *nomina nuda*. The name *P. testicularis* was used only in Jadhav and Shinde's (1989) discussion of *Polypocephalus djeddensis*; no authority or literature citations is given. It appears that this species was never described. *Polypocephalus braunii* Shinde 1981 has been referred to in the literature only twice (Jadhav and Shinde 1989; Shinde *et al.* 1991). In both cases, no author citation was given, but Shinde (1981) is given as literature citation. Reference to this species name could not be found in any other publication or database, and Shinde (1981) was not obtainable. Consequently, it is assumed that a description of this species is unlikely to exist for taxonomic study. Therefore, both names, *P. testicularis* and *P. braunii*, should be considered as not available.

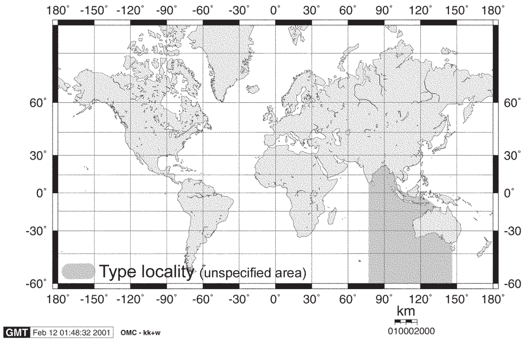


Fig. 44. Geographic distribution of *Polypocephalus radiatus* Braun, 1878.

Polypocephalus radiatus Braun, 1878

TYPE SPECIES

(Figs. 44-45)

Synonyms: None

Type host: *Rhinobatos granulatus* Cuvier, 1828 (as *Rhinobatus* [sic] *granulatus*), Sharpnose guitarfish (Rhinobatidae, Rhinobatiformes).

Additional hosts: None.

Site of infection: Spiral intestine.

Type locality: [East-Indian Ocean] (Fig. 44).

Additional localities: None.

Number of specimens on which the original description was based: "Very numerous."

Type specimens: Syntypes (ZMB No. 3182-1, 3182-2 and 3182-4) (type specimens not indicated in original description).

Voucher specimens (unverified): (see Appendix 4).

Material examined: ZMB No. 3182-1, 2 and 4 (syntypes); ZMB No. 3182-3 (Lecanicephalum sp.).

Etymology: *radiatus*, L., rayed, beaming, shining.

Unverified records: *Trygon sephen* from Chilka Lake, Orissa (see Southwell, 1925); *Rhynchobatus djeddensis* [sic] from Adyar, India (see Subhapradha, 1951).

Chronology

Braun (1878): describes *Polypocephalus radiatus* as type species of the new genus *Polypocephalus*, describes glands at base of tentacles.

Braun (1894-1900): considers *Polypocephalus radiatus* Braun the only species in the genus *Polypocephalus* Braun; in a section on skin glands comments on those [glands] found associated with the apical structure of *P. radiatus*.

Stiles and Hassall (1912): *P. radiatus* Braun, 1878 (in *Rhinobatus* [sic] *granulosus*): Braun (1895 and 1900) and Linstow (1889) (for *Polypocephalus*); *P.* sp. Shipley and Hornell (1904) (in *Taeniura melanospilos*; Trincomalee off Ceylon).

Southwell (1925): considers *Polypocephalus radiatus* (syn. *Thysanobothrium uarnakense* and *Parataenia elongatus*) as a valid species in the genus *Polypocephalus*; summarizes Braun's description; notes that Linton was probably unaware of Braun's description when describing *Parataenia* and liking the tentacles to the proboscides of avian taeniids; notes that *P. radiatus* possesses four suckers and therefore belongs to the order Cyclophyllidea; considers *Thysanobothrium uarnakense* to be inseparable from *Polypocephalus radiatus* Braun, 1878; *Parataenia elongatus* was believed [by others] to differ from *P. radiatus* in that it was ten times longer, but he believes that they are identical; restates dimensions given by Southwell (1912); describes new material of *P. radiatus* (scolex and a fragment) obtained from *Trygon sephen* from Chilka Lake, Orissa;

comments that these specimens differs from *P. medusia*, which remains distinct in length; concludes that *P. radiatus*, *T. uarnakense* and *Parataenia elongatus* are identical, with the name *Polypocephalus radiatus* having priority.

Woodland (1927): proposes that the "lecanicephalid" *Polypocephalus radiatus* be included in the family Phyllobothriidae, order Tetraphyllidea, along with *Lecanicephalum peltatum*, *Cephalobothrium abruptum*, *C. variabile*, *Tylocephalum yorkei*, *P. medusia*, and *Calycobothrium typicum*, based on disposition of longitudinal muscle bundles and marginal vitellaria.

Pintner (1928): creates two groups, family Lecanicephalidae (A): (including *Tylocephalum uarnaki* (= *trygonis*?), possibly *Tylocephalum minutum*, possibly *Lecanicephalum peltatum*, even *Parataenia medusia* Linton, 1889, and *Polypocephalus medusia* Southwell, 1925, which should be considered separate from *Polypocephalus radiatus* Braun, 1878), with non-glandular scolex, bilobed uterus, and acraspedote proglottids and family Cephalobothriidae (B), with glandular scolex and craspedote proglottids.

Woodland (1930): redescribes in detail (with figures) *Polypocephalus radiatus* (syn. *Parataenia elongatus*) based on four slides he received of Southwell's material collected from *Trygon kuhli* and *T. sephen*.

Southwell (1930): reports *Polypocephalus radiatus* (syn. *Thysanobothrium uarnakense* and *Parataenia elongatus*) from *Dasybatus* [sic] *uarnak* and *D. kuhli*, Pearl Banks, Ceylon (Southwell) and *D. sephen* from Chilka Lake, Orissa, India (Southwell); basically same text as that of Southwell (1925).

Baer (1948): rejects synonymy of *Thysanobothrium uarnakense* and *Parataenia elongata* with *Polypocephalus radiatus*, because of the lack of information about the internal anatomy of *T. uarnakense* and *P. radiatus*.

Subhapradha (1951): reports *P. radiatus* from ten newly collected specimens from *Rhynchobatus djeddensis* [sic] in Adyar, India; redescribes and illustrates the species in detail; divides *Polypocephalus* species in two groups and places *P. radiatus* in the *rhinobatidis*-group (inner muscle bundles in tentacles, narrow tentacular cavity, well developed longitudinal muscles, straight uterus, massive ovary).

Wardle and McLeod (1952): note that *Polypocephalus radiatus* Braun, 1878 is probably synonymous with *Parataenia elongatus* Southwell, 1912 and *Thysanobothrium uarnakense* Shipley and Hornell, 1906.

Yamaguti (1959): recognizes *Polypocephalus radiatus* Braun, 1878 as the type species of *Polypocephalus*; considers *Thysanobothrium uarnakense* Shipley and Hornell, 1906, [?] *Parataenia elongata* Southwell, 1912 synonyms of *P. radiatus*.

Reimer (1975): reports one occurrence of a larva of *Polypocephalus* sp. from *Bullia melanoides* from Madras, India; describes larvae as having 14 tentacles with circular musculature giving them a ridged appearance; considers it close in morphology to *P. lintoni*, could also be *P. radiatus*, *P. rhynchobatidis*, *P. rhinobatidis*, or *P. vitellaris*.

Schmidt (1986): recognizes *Polypocephalus radiatus* Braun, 1878 as the type species of *Polypocephalus*; considers *Thysanobothrium uarnakense* and *Parataenia elongata* to be synonyms of *P. radiatus*.

Hartwich and Kilias (1992): list syntypes of *Polypocephalus radiatus* Braun from *Rhinobatus* [sic] *granulatus*, locality not given, in the collection of the Zoologisches Museum Berlin, Berlin, Germany (ZMB Verm. Entoz. 3182).

Description (Modified from Braun [1878].) (Based the three syntypes: ZMB 3182-1, 3182-2, and 3182-4; all three are incomplete specimens with scolices; only those features are described that were visible in these immature specimens.) Note: Mean, standard deviation and number of specimens are not given in cases in which the ranges were expanded by using measurements provided by Braun (1878).

Worms at least 9,728-14,353 (11,766 ± 2,361.0; 3) long; maximum width at level of scolex; consisting of at least 127 proglottids. Scolex (omitting length of tentacles) 276-356 long by 277-372 (331 ± 48.8; 3) wide, bearing four acetabula. Acetabula sucker-like in form, sessile, 56-90 (69 ± 10.8; 3; 8) long by 56-111 (71 ± 22.6; 2; 5) wide, protrusible. Apical modification of scolex proper with expandable aperture at apex. Apical organ divided into 16 tentacles (Fig. 45C). Tentacles 339-491 long by 40-71 (55 ± 10.3; 3; 9) wide. Tentacular pouch 211-238 (225 ± 13.8; 3) long from rim of apical modification of scolex proper to its base.

Cephalic peduncle absent. Proglottids slightly craspedote, non-laciniate, overlap of adjacent proglottids 8-10% (11 ± 5.7; 3; 8) of proglottid length. Immature proglottids generally wider than long, posterior most three proglottids 221-509 long by 200-339 wide. Mature or gravid proglottids not observed. Testes six in total number, 33-77 (56 ± 17.2; 2; 6) long by 95-151 (119 ± 22.6; 2; 6) wide in immature proglottids, anterior to ovary, in single column in dorso-ventral view. Presence and/or form of vas deferens, external and internal seminal vesicle not observed. Cirrus sac pyriform, containing coiled cirrus. Cirrus armed. Ovary barely visible. Vagina not seen. Genital pores lateral, irregularly alternating, 51-55% (53 ± 1.9; 2; 4) of proglottid length from posterior end. Uterus and vitellaria not observed. Excretory ducts not observed. Eggs not observed.

Remarks

Braun (1878) erected the genus *Polypocephalus*, with *P. radiatus* as the type species, for specimens collected from the ray *Rhinobatos granulatus*. According to Braun (1878), the ray had been preserved whole for study of its excretory system, without particular attention to proper fixation of the spiral intestine. He presented this explanation for the limited information provided in the description that followed. Interestingly, Braun (1878) did not explicitly state the locality from which this ray was collected, but stated "*Rhinobatus* [sic] *granulatus* Cuv., a species of ray living in east-Indian oceans…" [translated]. Moreover, Braun (1878) did not state whether type material was designated. Type material of this species was not noted in the literature until in 1992, Hartwich and Kilias published a list of types of Cercomeromorphae (Platyhelminthes) in the collection of the Zoologisches Museum Berlin, in Berlin, Germany (ZMB) and listed syntypes of *Polypocephalus radiatus* Braun from *Rhinobatos granulatus*. This type material consists of four slides, bearing one specimen each. Examination of these four syntypes revealed that one (ZMB No. 3182-3) was actually a specimen in the genus *Lecanicephalum*. The redescription of *P. radiatus* presented here was based on measurements taken from the remaining three specimens.

Since its original description (Braun 1878), *Polypocephalus radiatus* has been reported from host species other than *Rhinobatos granulatus* (*e.g.*, see Southwell 1925, Woodland 1930 and Subhapradha 1951). While *P. radiatus* has been considered to be a valid species since its original description, other species, *Parataenia elongata* Southwell, 1912 (see Southwell 1925, 1930; Woodland 1930; Wardle and McLeod 1952; Yamaguti 1959; Schmidt 1986) and *Thysanobothrium uarnakense* (see Southwell 1925, 1930; Wardle and McLeod 1952; Yamaguti 1959; Schmidt 1986), have been placed in synonymy with *P. radiatus*. In the present study, *Parataenia* is considered to be a junior synonym of *Polypocephalus* (see treatment of *Parataenia*). Although, *Parataenia elongata* has been intimately tied to *Polypocephalus* (routinely considered to be a junior synonym of *Polypocephalus radiatus*) since 1925 (Southwell 1925), the combination *Polypocephalus elongatus* n. comb. appears not to have been formally created. It is used here for the first time. However, *Polypocephalus elongatus* should not be considered to be a synonym of *Polypocephalus radiatus*. Southwell (1912) described *Polypocephalus elongatus* (as *Parataenia elongatus*) as obtaining a total length of 39-50 mm, and possessing proglottids that are wider than long, whereas *P. radiatus* obtains a total length of approximately only 10-14 mm, and bears immature proglottids that are longer than wide. Similarly, *T. uarnakense* can be distinguished from *P. radiatus* based on its larger size overall. It should not be considered a synonym of *P. radiatus*. Shipley and Hornell (1906) described *T. uarnakense* as obtaining a total length of 7 cm and possessing a scolex that is at least 500 wide, whereas *P. radiatus* obtains a total length of approximately 10-14 mm and possesses a scolex that is 277-372 wide.

Voucher specimens tentatively identi-

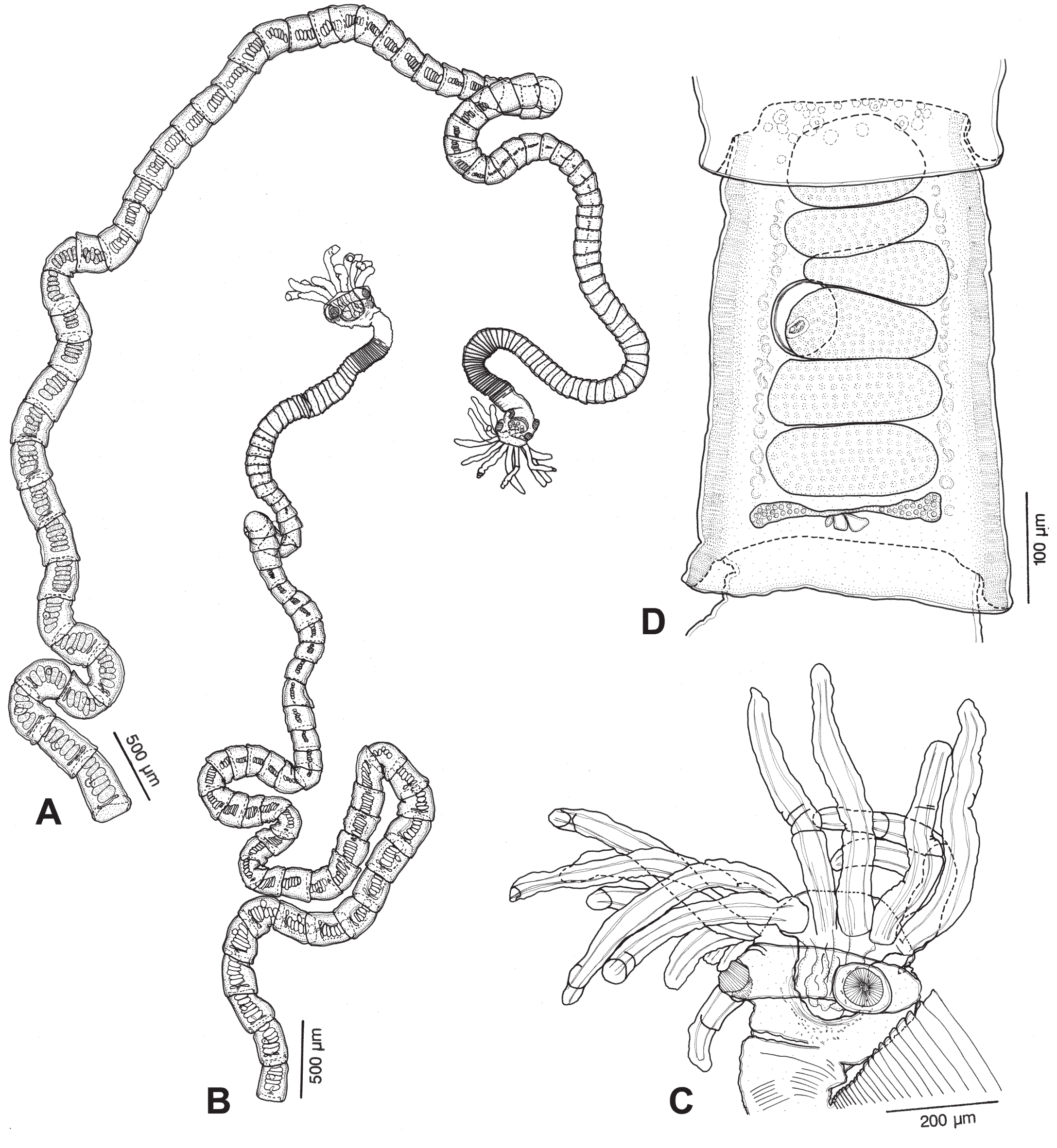


Fig. 45. A-E. Line drawings of *Polypocephalus radiatus* Braun, 1878. A. Whole worm (syntype, ZMB No. 3182-1). B. Whole worm (syntype, ZMB No. 3182-1). C. Scolex (syntype, ZMB No. 3182-1). D. Immature proglottid (syntype, ZMB No. 3182-1).

fied as *Polypocephalus radiatus* from an unknown source, collected from *Trygon kuhlii* have been deposited at the British Museum of Natural History in London (BMNH No. 1950.12.6.104-110) and specimens identified as *Polypocephalus* cf. *radiatus* from a stingaree have been deposited by J. W. Fielding at the Queensland Museum in Australia (QM No. GL11017).

Polypocephalus helmuti Jensen, n. sp.

(Figs. 46-48)

Type host: *Rhinoptera* sp., Cownose ray (Rhinopteridae, Myliobatiformes).

Additional hosts: None.

Site of infection: Spiral intestine.

Type locality: Dundee Beach, Fog Bay (12°50'S 130°12'E), Northern Territory, Australia (Fig. 46).

Additional localities: None.

Number of specimens on which the original description was based: 41 (20 whole mounts, three specimen cross-section series, three specimen longitudinal section series, eight lactophenol preparations of eggs, and seven specimens prepared for SEM).

Type specimens: Holotype (QM No. G 222908), seven paratypes (four whole mounts, one specimen cross-section series, one specimen longitudinal section series, and one lactophenol preparation of eggs) (QM Nos. G 222909-222915); eight paratypes (four whole mounts, one specimen cross-section series, one specimen longitudinal section series, and two lactophenol preparations of eggs) (USNPC No. 94580); four paratypes (three whole mounts and one lactophenol preparation of eggs) (KUNHM Nos. 002117-002120); 14 paratypes (eight whole mounts, one specimen cross-section series, one specimen longitudinal section series, and four lactophenol preparations of eggs) (LRP Nos. 3300-3313); seven paratype specimens prepared for SEM (LRP).

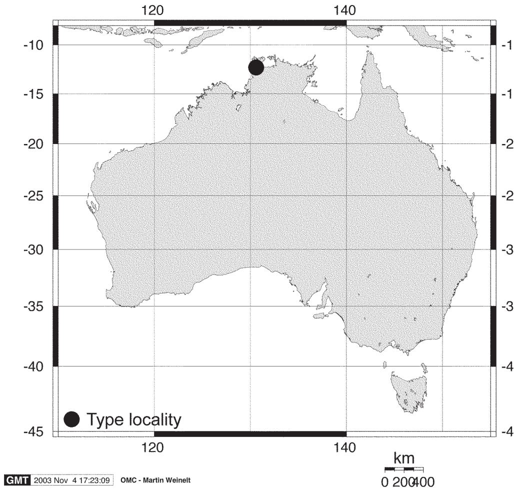


Fig 46. Geographic distribution of *Polypocephalus helmuti* Jensen, n. sp.

Etymology: The species was named in honor of the authors' father, Helmut Jensen, who provided valuable culinary and parasitological field assistance during the 1997 field trip to Australia, over the course of which this species was collected.

Chronology

Caira *et al.* (2001): include *Polypocephalus helmuti* a "*Polypocephalus* n. sp. 2" and two additional species of *Polypocephalus* in a phylogenetic analysis based on morphological data; the species grouped with the majority of the other lecanicephalidean taxa included in the analysis; based on the limited taxa included the genus is monophyletic

Description (Based on 20 whole mounts, three specimen cross-section series, three specimen longitudinal section series, eight lactophenol preparations of eggs, and seven specimens prepared for SEM.)

Worms 585-1,659 (1,094 ± 279.8; 20) long; maximum width at level of scolex (Fig. 48A); 2-5 proglottids, euapolytic. Scolex 170-245 (208 ± 19.4; 20) long by 179-261 (216 ± 20.1; 15) wide, bearing four acetabula. Acetabula sucker-like in form (Fig. 48B), sessile, 54-82 (68 ± 7.9; 19; 38) long by 45-71 (59 ± 5.5; 19; 38) wide. Apical modification of scolex proper with expandable aperture at apex, housing apical organ. Apical organ divided into 16 tentacles (Fig. 48C). Tentacles 187-415 (251 ± 70.6; 3; 8) long by 14-16 (15 ± 0.5; 3; 8) wide, completely invaginable, with glandular surface. Tentacular pouch 119-175 (141 ± 15.0; 20) long by 111-159 (136 ± 13.8; 20) wide. Scolex proper covered with pointed filitriches (Fig. 48G), more dense in region between acetabula (Fig. 48H). Rims and distal acetabular surface covered with blade-like spinitriches and pointed filitriches (Fig. 48F). Apical modification of scolex proper covered with ivy leaf-shaped spinitriches and pointed filitriches (Fig. 48E). Tips of tentacles covered with tubercles suggesting a glandular surface (Fig. 48D).

Cephalic peduncle absent. Strobila covered with long filitriches (Fig. 48I). Proglottids acraspedote. Immature proglottids 0-2 in number, wider than long, 22-144 (56 ± 36.0; 18; 19) long by 91-152 (124 ± 16.2; 18; 19) wide. Mature proglottids 0-1 in number, square to longer than wide, 167-632 (277 ± 145.9; 11) long by 111-163 (143 ± 13.9; 11) wide. Gravid proglottids 0-3 in number, 239-790 (542 ± 141.6; 18; 24) long by 70-245 (163 ± 38.5; 18; 24) wide. Posterior third of terminal proglottid (mature or gravid) reflexed towards genital pore (Fig. 48A). Testes six in number, 14-36 (22 ± 6.0; 11; 33) long by 42-76 (58 ± 9.3; 11; 33) wide in mature proglottids, anterior to genital pore, in single column in dorso-ventral view, one row deep in cross-section, displaced to lateral margin of proglottid by uterus, or degenerated in gravid proglottids. Vas deferens extensive, extending from ootype to cirrus sac, looping at level of and anterior to cirrus sac, entering cirrus sac at distal end. External seminal vesicle absent. Internal seminal vesicle present, visible in gravid proglottids. Cirrus sac pyriform, angled anteriorly, 67-152 (111 ± 25.2; 20; 30) long by 35-80 (58 ± 13.1; 20; 30) wide in mature and gravid proglottids, containing coiled cirrus. Cirrus armed. Ovary consisting of four unequal lobes, H-shaped in dorso-ventral view, tetralobed in cross-section (Fig. 47F), 65-213 (113 ± 43.2; 11) long by 51-107 (76 ± 16.1; 11) wide, degenerated in older gravid proglottids; ovarian margins smooth. Vagina thin-walled, opening into genital atrium at same level as cirrus sac; vaginal sphincter absent; seminal receptacle not observed. Genital pores lateral, irregularly alternating, 24-47% (33 ± 5.7; 20; 32) of proglottid length from posterior end in mature and gravid proglottids. Uterus somewhat lateral in mature proglottids, extending entire length of proglottid in gravid proglottids; uterine duct not observed; uterine pore absent. Vitellaria follicular, medullary, one dorsal and one ventral column of vitelline follicles on each lateral margin of proglottid (Fig. 47G), extending from near anterior margin to posterior margin of proglottid, interrupted by, but overlapping ovary; vitelline follicles 9-29 (17 ± 4.3; 10; 30) long by 8-29 (20 ± 3.9; 10; 30) wide. Single pair of excretory ducts present. Eggs in younger gravid proglottids single, with bipolar filaments, oncospheres 12-17 (14 ± 1.3; 5; 25) in maximal length (Fig. 47H); eggs in older gravid proglottids contained in fibrous-appearing matrix, oncospheres 21-21 (24 ± 1.9; 5; 25) in maximal length (Fig. 47I).

Remarks

Of the 25 species of *Polypocephalus* recognized in this monograph (see Appendix 2), *P. helmuti* can be distinguished from *P. coronatus*, *P. indicus*, *P. lintoni*, *P. moretonensis*, *P. rhynchobatidis*, *P. saoudi*, *P. vesicularis*, and *P. vitellaris* based on the presence of six rather than four testes, and from *P. maharashtra* based on the presence of six rather than 12 testes. In addition, all nine of these species of *Polypocephalus* have from ten (*P. saoudi* with 10-16 proglottids) to 120 proglottids (*P. moretonensis*), whereas *P. helmuti* has a maximum of five proglottids. The total length of gravid worms of *P. helmuti* is less than 2 mm, while *P. digholensis*, *P. elongatus*, *P. karbharii*, *P. katpurensis*, *P. prathibhai*, *P. pulcher*, *P. radiatus*, *P. ratnagiriensis*, *P. rhinobatidis*, and *P. singhii* are all greater than 5 mm in total length. *Polypocephalus helmuti* possesses a smaller scolex than *P. alii* and *P. djeddensis* (170-245 x 179-261 vs. 410 x 430 and 1,635 x 1,435, respectively). Distinguishing *P. helmuti* from *P. affinis* and *P. thapari* is somewhat more difficult owing to the limited nature of the original descriptions of the latter two species. *Polypocephalus affinis* is described as having tentacles that occur in pairs, whereas *P. helmuti* possesses unpaired tentacles. In addition, *P. affinis* appears to be larger and possess a greater number of proglottids than *P. helmuti* (3,640 total length and an illustration of an incomplete worm with 21 proglottids [see Subhapradha 1951] vs. 585-1,659 total length and a maximum of five proglottids). While the position of the genital pore is not described in *P. thapari*, the original figure indicates a genital pore that is located at the level of the second testis (counting from poste-

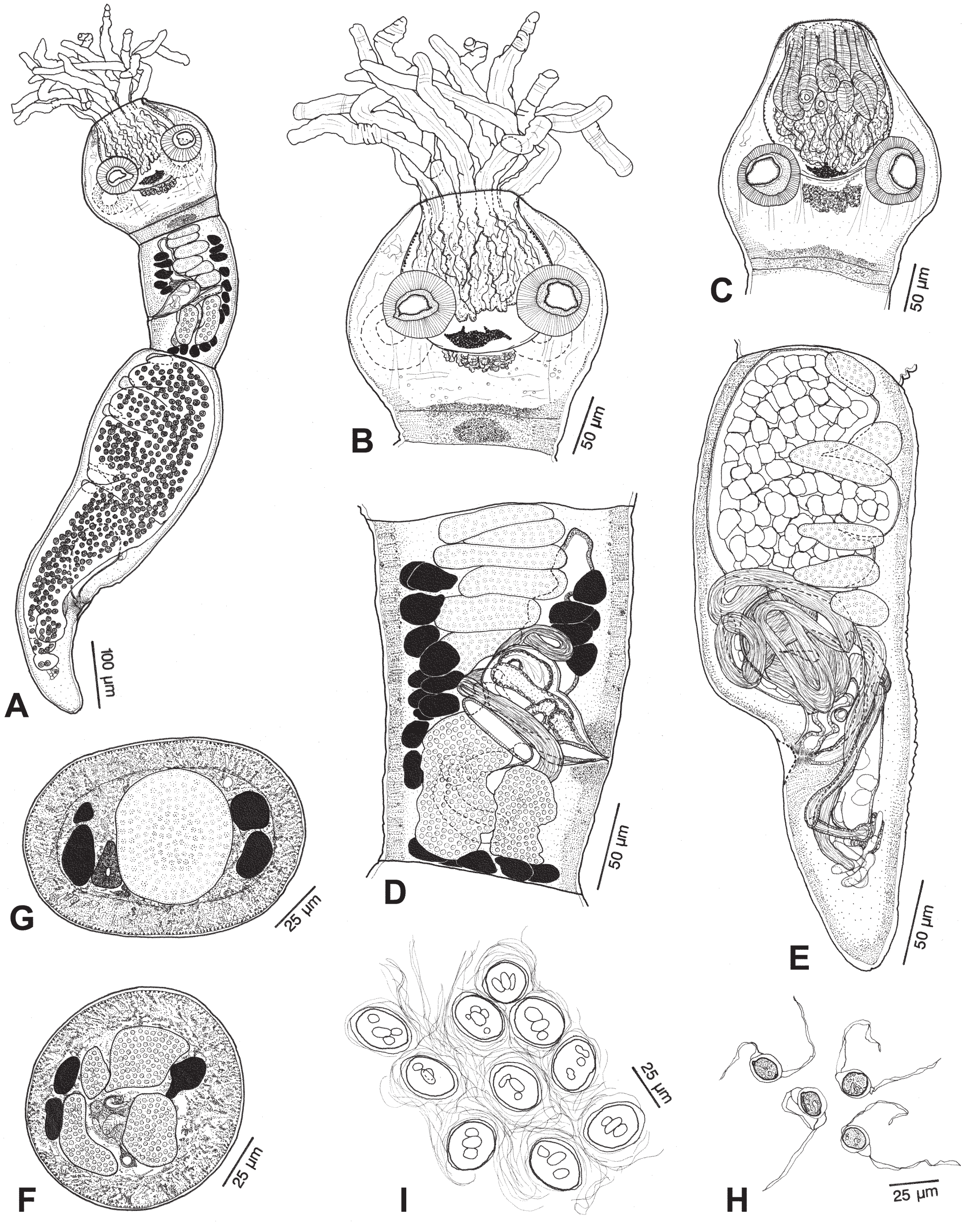


Fig. 47. A-I. Line drawings of *Polypocephalus helmut*i Jensen, n. sp. A. Whole worm (holotype, QM No. G 222908). B. Scolex with tentacles everted (holotype, QM No. G 222908). C. Scolex with tentacles invaginated (USNPC No. 94580). D. Mature proglottid (USNPC No. 94580). E. Gravid terminal proglottid (LRP No. 3306). F. Cross-section through mature proglottid at level of ovarian bridge (QM No. G 222913). G. Cross-section through mature proglottid anterior to genital pore (QM No. G 222913). H. Eggs in early gravid proglottid (QM No. G 222915). I. Eggs in older gravid proglottid (QM No. G 222915).

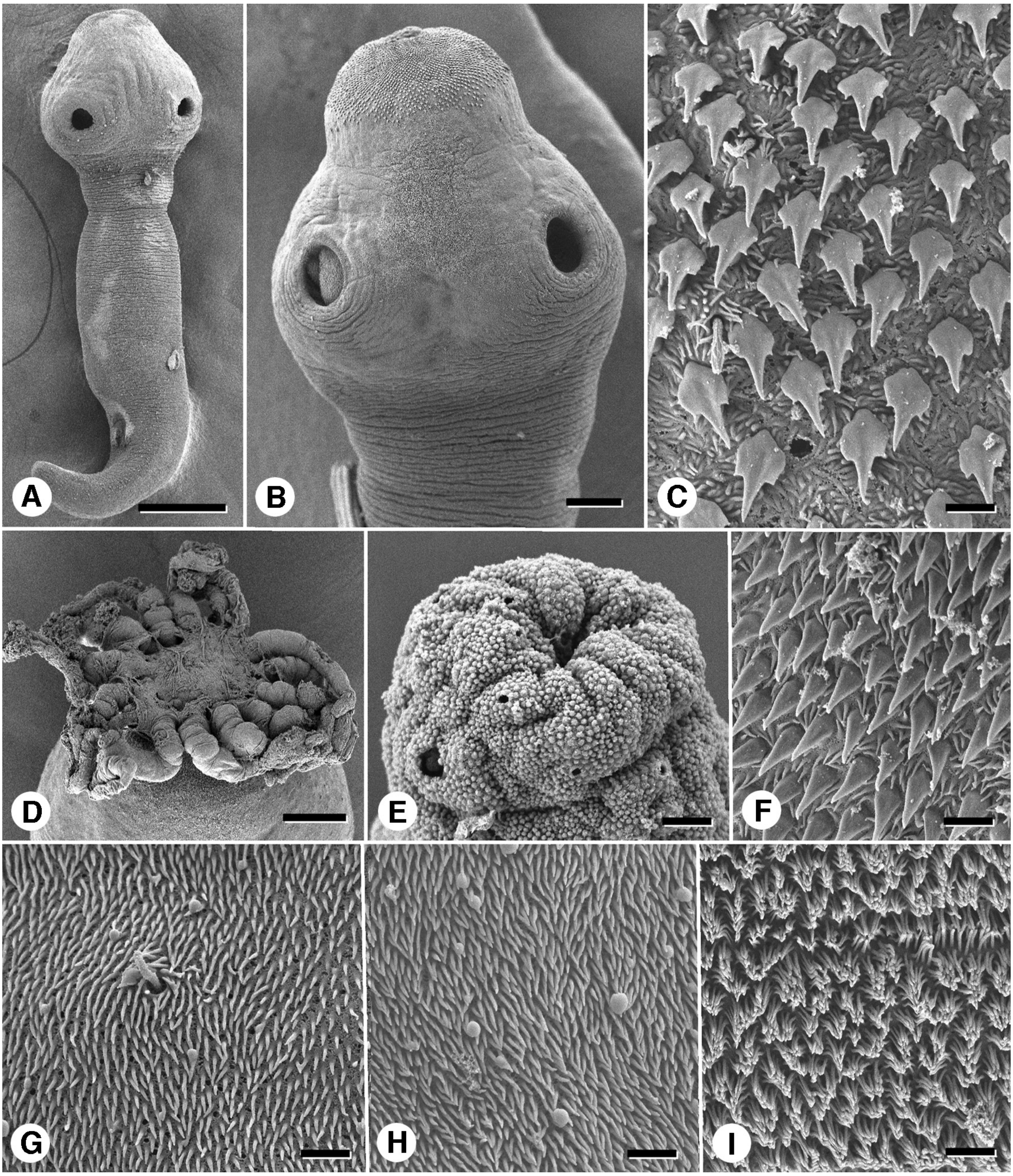


Fig. 48. A-I. Scanning electron micrographs of *Polypocephalus helmuti* Jensen, n. sp. A. Whole worm. B. Scolex with tentacles invaginated. C. Everted tentacles. D. Surface of tentacles. E. Microtriches on surface of apical modification of scolex proper. F. Microtriches on distal acetabular surface. G. Microtriches on surface of scolex proper anterior to acetabula. H. Microtriches on surface of scolex proper between acetabula. I. Microtriches on surface of strobila. Scale bars: A, 100 μm; B, 25 μm; C, 25 μm; E-I, 1 μm.

rior to anterior). In contrast, the genital pore of *P. helmuti* is positioned posterior to all of the testes. Based on overall size, *P. helmuti* is most similar to *P. bombayensis* and *P. medusia*. The cirrus sac of *P. bombayensis* is horizontal in orientation in the proglottid and the species is depicted as possessing a genital pore positioned in the anterior third of the proglottid (Shinde *et al.* 1991), in contrast, the cirrus sac in *P. helmuti* is clearly tilted anteriorly and the genital pore is located in the posterior third of the proglottid. *Polypocephalus helmuti* has fewer proglottids than *P. medusia* (a maximum of five proglottids vs. 10-15 based on illustrations of three worms of the latter species from the original figures of Linton [1890]). In addition, the largest specimen of *P. helmuti* measures 1,659, whereas specimens of *P. medusia* are said to reach a total length of 6,000; the terminal proglottid of the largest specimen alone measuring 1,800 (Linton 1890).

QUADCUSPIBOTHRIUM
Jensen, 2001

Taxonomic status: Valid.

Synonyms: None.

Type and only species: *Quadcuspibothrium francisi* Jensen, 2001.

Etymology: The name *Quadcuspibothrium* (*quad-*, L. prefix, four; *cuspis*, L., a point) refers to the unique form of the bothridiate acetabula, each of which terminate in four points.

Diagnosis (Modified from Jensen [2001]. Copyright 2001, The Journal of Parasitology. Used with permission.)

Worms euapolytic. Scolex with four acetabula; acetabula weakly stalked, bothridiate in form, diamond-shaped; rims of acetabula covered with large blade-like spinitriches; apical modification of scolex proper in form of conical extension with pore-like aperture at center, housing apical organ; apical organ small, glandular, non-eversible, non-protrusible. Proglottids craspedote, non-laciniate. Testes few, anterior to ovary. Vas deferens forming expanded duct, extending from ootype to anterior margin of proglottid. Cirrus sac pyriform. Cirrus unarmed. Ovary irregular in form in dorso-ventral view, consisting of three lobes, trilobed in cross-section. Vagina extending from ootype region to cirrus sac, opening into genital atrium posterior to cirrus sac. Genital pores sublateral, irregularly alternating. Uterus median, saccate. Vitellaria follicular, lateral, in field anterior and posterior to ovary. Eggs unknown. Parasites of rays in the genus *Mobula* (Mobulidae). Gulf of California (Mexico).

Chronology

Caira *et al.* (2001): include a species of *Quadcuspibothrium* (*Q. francisi* as "n. gen. 4 n. sp.") in a phylogenetic analysis based on morphological data; the species grouped with the majority of the other lecanicephalidean taxa included in the analysis, as a sister taxon to *Corrugatocephalum ouei*.

Jensen (2001): erects the genus *Quadcuspibothrium* with *Q. francisi* as the type species.

Remarks (Modified from Jensen [2001]. Copyright 2001, The Journal of Parasitology. Used with permission.)

Jensen (2001) argued that the presence of an apical organ, facially unmodified acetabula, a vagina opening posterior to the cirrus sac into the genital atrium and an external seminal vesicle extending from posterior to the ootype to the cirrus sac places this genus most appropriately in the Lecanicephalidea.

Quadcuspibothrium can easily be distinguished from the other 11 valid lecanicephalidean genera based on the unique shape of its acetabula. In *Quadcuspibothrium*, each acetabulum bears four points at its margin: one anteriorly, one posteriorly and two laterally (subequatorial in position), giving the acetabulum a diamond-shaped appearance. The margins of the acetabula of the other 11 valid lecanicephalidean genera are either round, oval or ovoid, but never pointed. *Quadcuspibothrium* differs further from *Anteropora*, *Lecanicephalum*, *Polypocephalus*, *Tylocephalum*, *Eniochobothrium*, *Hornellobothrium*, *Aberrapex*, and *Paraberrapex*, in its possession of an ovary that is irregular in form (consisting of three lobes) in dorso-ventral view, rather than H-shaped. *Quadcuspibothrium* lacks the greatly enlarged genital atrium of *Tetragonocephalum*. It is most similar, in both strobilar and proglottid anatomy, to *Corrugatocephalum* and *Healyum*. The proglottids exhibited by taxa in these three genera bear only three testes arranged in one to two columns in dorso-ventral view and, two layers deep in cross-section. In addition, the testes in these taxa are degenerated in fully mature proglottids. An extensive vas deferens or external seminal vesicle extending almost the entire length of proglottid is present in all three genera, and few, relatively large vitellaria are the most prominent features of the terminal proglottids. Apart from acetabular morphology, *Quadcuspibothrium* can be further distinguished from *Corrugatocephalum* in that it possesses an ovary that is trilobed rather than asymmetrically bilobed in cross-section, and an apical organ that is small and glandular rather than in the form of a large, corrugated cylinder. *Quadcuspibothrium* can be further distinguished from *Healyum* based on its possession of distinctly paired vitelline follicles, rather than vitelline follicles arranged in two irregular lateral columns.

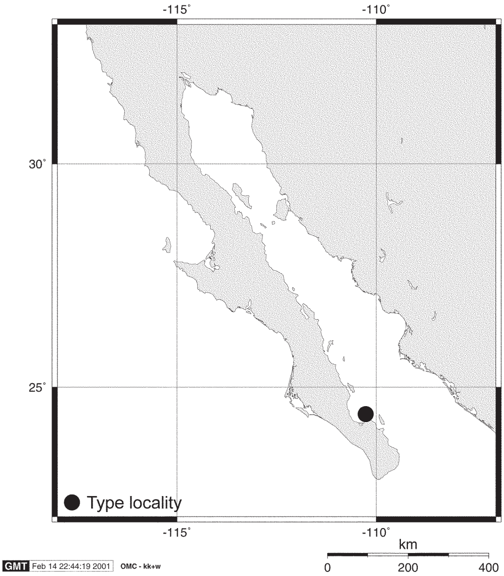


Fig. 49. Geographic distribution of *Quadcuspibothrium francisi* Jensen, 2001.

Quadcuspibothrium francisi Jensen, 2001

TYPE SPECIES
(Figs. 49-51)

Synonyms: None.

Type host: *Mobula japanica* (Müller and Henle, 1941), Spinetail mobula (Mobulidae, Myliobatiformes).

Additional hosts: None.

Site of infection: Spiral intestine.

Type locality: Punta Arena (24°04'N 109°50'W), Baja California Sur, Mexico (Fig. 49).

Additional localities: None.

Number of specimens on which the original description was based: 20.

Type specimens: Holotype (CNHE No. 4182) and four paratypes (CNHE No. 4183); five paratypes (USNPC No. 91214); two paratypes (HWML No. 16378); 11 paratypes (eight whole worms, cross and longitudinal section series, and SEM material) (LRP Nos. 2189-2198).

Voucher specimens: None.

Material examined: CNHE No. 4182 (holotype); CNHE No. 4183, USNPC No. 91214, HWML No. 16378, and LRP Nos. 2189-2198 (paratypes).

Etymology: This species is named after Francis, our faithful camp companion at Punta Arena, Mexico, the type locality of this species.

Chronology

Caira *et al.* (2001): include *Quadcuspibothrium francisi* as "n. gen. 4 n. sp." in a phylogenetic analysis based on morphological data; the species grouped with the majority of the other lecanicephalidean taxa included in the analysis, as sister taxon *to Corrugatocephalum ouei*.

Jensen (2001): describes *Quadcuspibothrium francisi* as type species of the new genus *Quadcuspibothrium*.

Description (Modified from Jensen [2001]. Copyright 2001, The Journal of Parasitology. Used with permission.) (Based on 20 whole worms.)

Worms 420-768 (538 ± 89.4; 15) long; maximum width at level of scolex; 5-8 (7 ± 0.8; 20) proglottids, euapolytic. Scolex 140-202 (169.5 ± 19.4; 11) long by 180-303 (232 ± 33.5; 14) wide, consisting of four acetabula. Acetabula weakly stalked, bothridiate in form, diamond-shaped, 82-137 (107 ± 13.2; 12; 20) long by 78-165 (125 ± 22.8; 19; 36) wide. Apical modification of scolex proper in form of small, conical extension with pore-like aperture at apex (Fig. 51A and B), housing apical organ. Apical organ glandular and possibly eversible and/or protrusible.

Rims of acetabula covered with large blade-like spinitriches and pointed filitriches (Fig. 51D). Surfaces of scolex proper, stalks and distal and proximal surfaces of acetabula covered with pointed filitriches only (Fig. 51B, C, E and F, respectively). Strobila covered with elongate, pointed filitriches (Fig. 51G).

Cephalic peduncle short. Proglottids craspedote, non-laciniate. Immature proglottids 4-6 (5 ± 0.7; 20) in number, wider than long; two most posterior immature proglottids 17-102 (53 ± 19.6; 20; 40) long by 45-95 (68 ± 13.4; 20; 40) wide. Mature proglottids one or two in number, longer than wide; non-terminal mature proglottids 65-137 (104 ± 20.9; 10) long by 62-85 (73 ± 7.4; 10) wide; terminal mature proglottids 137-283 (194 ± 33.6; 20) long by 47-90 (68 ± 12.1; 20) wide. Testes three in number, 13-30 (21 ± 4.7; 15; 32) long by 15-42 (27 ± 6.4; 15; 23) wide, anterior to ovary, arranged in one column in dorso-ventral view, two rows deep in cross-section, generally degenerated in terminal proglottid, postvaginal and postovarian testes absent. Vas deferens in form of expanded duct, extending from ootype to anterior margin of proglottid, then posteriorly to distal region of cirrus sac, entering cirrus sac at distal end. External and internal seminal vesicle absent. Cirrus sac pyriform, slightly angled anteriorly, 38-57 (45 ± 7.1; 6) long by 14-19 (16 ± 2; 6) wide, containing coiled cirrus. Cirrus unarmed. Ovary consisting of three lobes, irregular in shape in dorso-ventral view, trilobed in cross-section, 30-67 (42 ± 9.6; 18) long by 27-65 (44 ± 10.8; 18) wide; ovarian lobes smooth, almost round, 20-45 (28 ± 5.8; 19; 38) long by 12-37 (24 ± 6; 19; 38) wide. Mehlis' gland at posterior margin of ovary. Vagina thin-walled, extending along median line of proglottid from ootype to cirrus sac, opening into genital atrium posterior to cirrus sac; vaginal sphincter absent; seminal receptacle not observed. Genital pores sublateral, irregularly alternating, 73-86% (80 ± 4; 18) of proglottid length from posterior end. Uterus saccate, extending along median line of proglottid to level of genital pore; uterine duct not observed; uterine pore absent. Vitellaria follicular, conspicuous, medullary, lateral, extending almost entire length of proglottid, somewhat interrupted by ovary

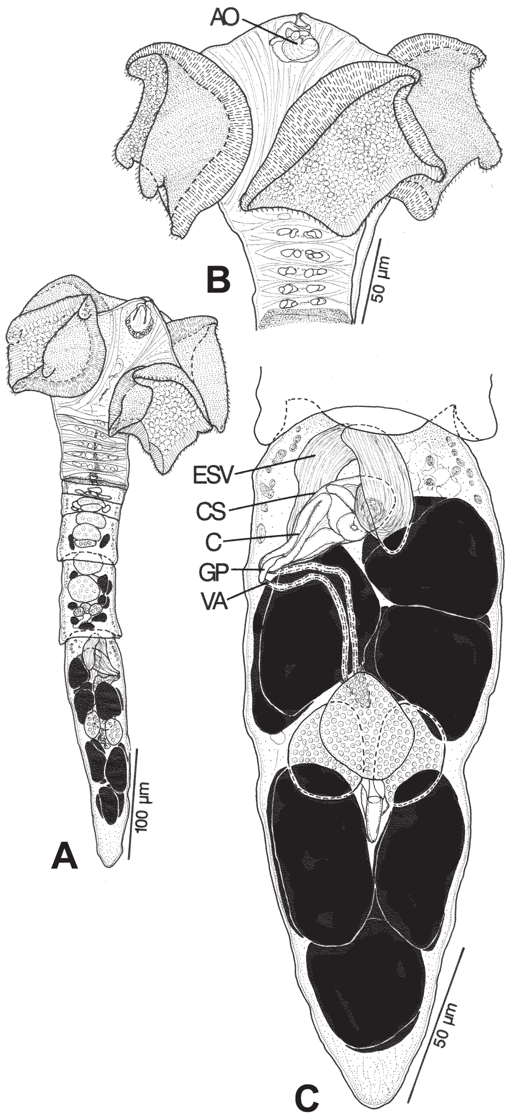


Fig. 50. A-E. Line drawings of *Quadcuspibothrium francisi* Jensen, 2001. A. Whole worm. B. Scolex. C. Mature terminal proglottid. (Taken from Jensen [2001]. Copyright 2001, The Journal of Parasitology. Used with permission.)

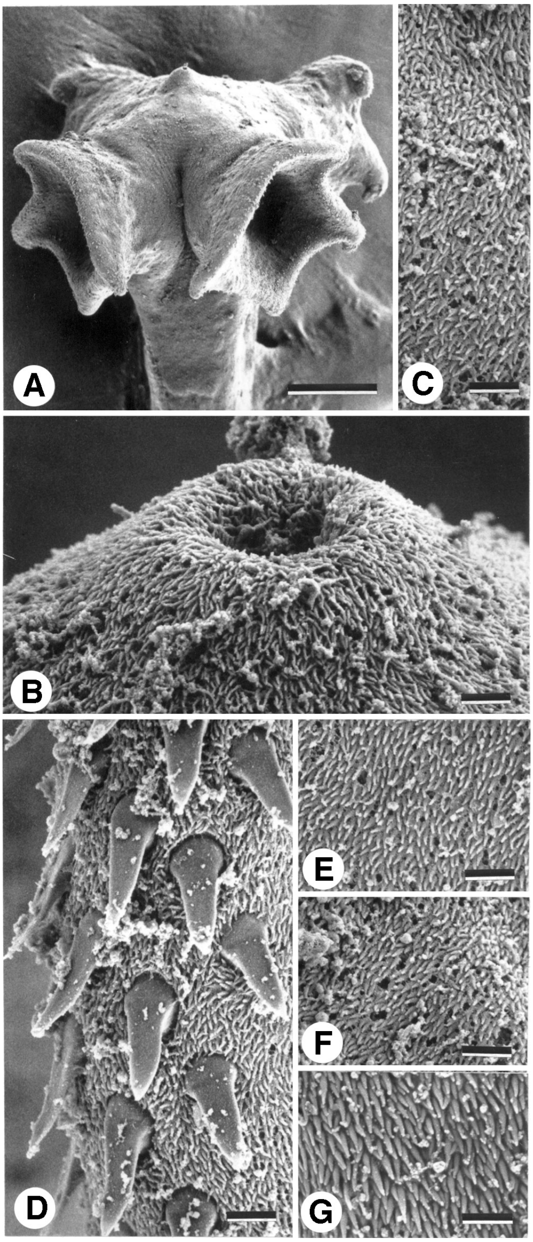


Fig. 51. A-G. Scanning electron micrographs of *Quadcuspibothrium francisi* Jensen, 2001. A. Scolex. B. Enlarged view of apical modification of scolex proper with aperture at apex and microtriches on scolex proper. C. Microtriches on acetabular stalks. D. Microtriches on acetabular rims. E. Microtriches on distal acetabular surface. F. Microtriches on proximal acetabular surface. G. Microtriches on proglottid. Scale bars: A, 50 µm; B-G, 1 µm. (Taken from Jensen [2001]. Copyright 2001, The Journal of Parasitology. Used with permission.)

in terminal proglottid; vitelline follicles 12 in number, 21-67 (35 ± 10.1; 19; 38) long by 14-44 (28± 7.3; 19; 38) wide; one dorsal and one ventral column of vitelline follicles on each lateral margin of proglottid. Excretory ducts not observed. Eggs not observed.

Remarks

Quadcuspibothrium francisi is the taxon referred to as “new genus 4 n. sp.” in the phylogenetic analysis by Caira *et al*. (2001).

Again, as was the case with *Healyum harenamica* and *H. pulvis*, individuals of *Q. francisi* are so tiny that they were recovered only from a spiral intestine that was fixed in the field and subsequently examined using a dissecting microscope upon return to the laboratory. *Quadcuspibothrium francisi* was recovered from only one of nine specimens of *Mobula japanica* from which the spiral intestine was examined (prevalence: 11.1%).

TETRAGONOCEPHALUM Shipley and Hornell, 1905

Taxonomic status: Valid.

Synonyms: None.

Type species: *Tetragonocephalum trygonis* Shipley and Hornell, 1905.

Other species: *Tetragonocephalum alii* Deshmukh and Shinde, 1979; *T. aurangabadensis* Shine and Jadhav, 1990; *T. bhagawatii* Shinde, Mohekar and Jadhav, 1985; *T. madhualtae* (Andhare and Shinde, 1994) n. comb.; *T. madrasensis* (Andhare and Shinde, 1994) n. comb.; *T. passeyi* Jensen, n. sp.; *T. raoi* Deshmukh and Shinde, 1979; *T. ratnagiriensis* Shinde and Jadhav, 1990; *T. sephensis* Deshmukh and Shinde, 1979; *T. shipleyi* Shinde, Mohekar and Jadhav, 1985; *T. simile* (Pintner, 1928) Ivanov and Campbell, 2000; *T. uarnak* (Shipley and Hornell, 1906) Pinter, 1928; *T. yamagutii* Muralidhar, 1990.

Species inquirendae: *Tetragonocephalum aetiobatidis* Shipley and Hornell, 1905; *T. akajeiensis* Yang, Lui and Lin, 1995; *T. janardane* Wankhede, 1990.

Nomina nuda: *Tetragonocephalum meen-*

ae in Mohekar *et al*. (2002); *T. shindei* Shipley and Hornell, 1906 in Mohekar *et al*. (2002); *T*. (as *Tetragonicephalum*) *karachiensis* Bilqees and Fatima, 1982 in Bilqees (1995); *T*. (as *Tetragonicephalum*) *stegostomai* Bilqees and Fatima, 1982 in Bilqees (1995); *T*. (as *Tetragonicephalum*) *varium* Bilqees and Fatima, 1982 in Bilqees (1995).

Etymology: *Tetragono*-, "from the square cushion which forms the larger part of the head" (Shipley and Hornell, 1905, p. 52); *kephale*, Gr., head.

Diagnosis (Modified from Yamaguti [1959].)

Worms apolytic or anapolytic (spent proglottids seen occasionally); conspicuous longitudinal muscle bundles in outer perimeter of proglottids, extending entire length of strobila. Scolex with four acetabula; acetabula in form of suckers; apical modification of scolex proper cylindrical, bearing apical organ; apical organ large, globular, muscular, with glandular surface, non-invaginable, non-retractable. Proglottids acraspedote. Testes numerous, essentially in two dorsal and two ventral columns, anterior to cirrus sac. Vas deferens extending from ovary to cirrus sac. External seminal vesicle absent. Internal seminal vesicle present. Cirrus sac pyriform. Cirrus armed. Ovary oval in form in dorsoventral view, ring-shaped in cross-section. Vagina opening into genital atrium posterior to cirrus sac, extending along median line in proglottid. Genital pores lateral, irregularly alternating; genital atrium large. Uterus saccate, extending along median line entire length of proglottid, conspicuously narrowing at level of cirrus sac. Vitellaria follicular, in lateral columns, distributed throughout length of proglottid, interrupted by cirrus sac and ovary. One dorsal and one ventral pair of excretory ducts present. Eggs single, lacking polar filaments. Parasites of stingrays (Dasyatidae). Northern Indian Ocean (India and Sri Lanka) and Arafura Sea (Australia).

Chronology

Shipley and Hornell (1905): erect the genus *Tetragonocephalum* with *T. trygonis* as the type species for a number of specimens taken from *Trygon walga* in Ceylon; provide a general description of the worm (proglottids are acraspedote); proglottid anatomy is not described, except for the mention of large atria and a uterus that is dumb-bell-shaped; briefly distinguish it from *Lecanicephalum* and *Discobothrium*; following Braun's classification, place *Tetragonocephalum* in the family Lecanicephalidae, not far from *Lecanicephalum*.

Shipley and Hornell (1906): state that, since their description of *Tetragonocephalum* in 1905, they have determined this taxon to be identical to Linton's genus *Tylocephalum*; transfer *Tetragonocephalum trygonis* described in 1905 to *Tylocephalum* to create the new combination, *Tylocephalum trygonis* (Shipley and Hornell, 1905).

Stiles and Hassall (1912): *Tetragonocephalum* Shipley and Hornell, 1905 (tod. [usually "m"] trygonis) (Lecanicephalidae): Shipley and Hornell (1906) (syn. of *Tylocephalum* Lint.); *T. aetiobatidis* Shipley and Hornell, 1905 (in *Aetiobatis* [sic] *narinari*; Ceylon): Shipley and Hornell (1906) (*aetobatidis*); *T. aetobatidis* Shipley and Hornell (1906) (for *aetiobatidis*) (in *Aetiobatis* [sic] *narinari*; Ceylon); *T. trygonis* Shipley and Hornell, 1905 (in *Trygon walga*; Ceylon): Shipley and Hornell (1906) (to *Tylocephalum*); *T. atiobatis* Shipley and Hornell, 1905 (misprint for *aetiobatides* [misprint?]).

Southwell (1925): treats *Tetragonocephalum* as a junior synonym of *Tylocephalum* (other synonyms are *Kystocephalus* and *Aphanobothrium*); emends Linton's generic diagnosis of *Tylocephalum*; suggests that since Linton based the genus *Tylocephalum* on a single immature specimen he called *T. pingue*, which is unrecognizable, the second species described, *T. trygonis*, should become the type species of *Tylocephalum*.

Poche (1926): comments on Southwell's (1925) classification scheme; elaborates on description of three species of *Tylocephalum* (*T. uarnak*, *T. trygonis*, and *T. minutum*); comments that *T. pingue* cannot be replaced by *T. trygonis* as new type species as suggested by Southwell (1925); if Southwell's observation of the vitelline condition in these three species is correct, they should be considered species of the genus *Tetragonocephalum*; considers it likely that

Southwell misinterpreted the morphology of *T. trygonis*; is undecided about *T. uarnak* and *T. minutum*; retains *Tetragonocephalum* as a synonym of *Tylocephalum* in the family Lecanicephalidae, suborder Phyllobothriinea *nom. nov.*, order Taeniidea *nom. nov.*

Pintner (1928): creates two groups; family Lecanicephalidae (A), with *Tylocephalum uarnaki* = *Tylocephalum trygonis* as the "most well known representative," characterized by nonglandular scolex, bilobed uterus, acraspedote proglottids; and family Cephalobothriidae (B), containing, among others, *Tylocephalum pingue*, characterized by a glandular scolex, craspedote proglottids; comments that the member of group A are distinct from those of group B; considers the type species of *Tylocephalum* (*i.e.*, *T. pingue*) to be a member of group B; reasons that since *T. trygonis*, type species of *Tetragonocephalum*, is a member of group A, that *Tetragonocephalum* should be preserved.

Southwell (1930): treats *Tetragonocephalum* as a junior synonym of *Tylocephalum* (other synonyms are *Kystocephalus* and *Aphanobothrium*); same text as that of Southwell (1925); names *Tylocephalum trygonis* Shipley and Hornell, 1906 as type species of *Tylocephalum*.

Fuhrmann (1931): *Tetragonocephalum* is considered a junior synonym of *Lecanicephalum* (as are *Tylocephalum ex parte* and *Cephalobohrium ex parte*) in the family Lecanicephalidae Braun (syn. Gamobothriidae Linton), order Tetraphyllidea.

Perrenoud (1931): suggests that *Tetragonocephalum* Shipley and Hornell, 1905, which had fallen into synonymy with *Tylocephalum*, be resurrected for Pinter's (1928) "*Tylocephalum* group A," with *T. trygonis* as the type species; Pintner's (1928) "*Tylocephalum* group B" should retain *Tylocephalum* as its current name.

Baer (1948): gives history of the genus *Tylocephalum* and addresses its relationship to *Tetragonocephalum*; notes that eventhough Southwell (1925) suggested *T. trygonis* as the type species of *Tylocephalum* to replace *T. pingue*, *Tetragonocephalum* must be resurrected [with *Tetragonocephalum trygonis* as the type species]; reiterates taxonomic decisions made by Pintner (1928).

Wardle and McLeod (1952): treat *Tetragonocephalum* Shipley and Hornell, 1905 as a valid genus in the family Lecanicephalidae, order Lecanicephala, with *T. trygonis* Shipley and Hornell, 1905 (= *Tylocephalum trygonis* Southwell, 1925 = *Tetragonocephalum uarnaki* [sic] Shipley and Hornell, 1906) as the type species.

Yamaguti (1959): considers *Tetragonocephalum* Shipley and Hornell, 1905 a valid genus in the new family Tetragonocephalidae, order Lecanicephalidea, with *T. trygonis* Shipley and Hornell, 1905 (syn. *Tylocephalum trygonis* [Shipley and Hornell, 1905] Shipley and Hornell, 1906) as the type species.

Euzet (1959): recognizes *Tetragonocephalum* in the family Lecanicephalidae, superfamily Lecanicephaloidea, order Tetraphyllidea.

Joyeux and Baer (1961): classify *Tetragonocephalum* (along with *Adelobothrium*, *Cephalobothrium*, and *Hexacanalis*) in the family Cephalobothriidae, superfamily Lecanicephaloidea, order Tetraphyllidea.

Euzet and Combes (1965): review the histories of *Tetragonocephalum* and *Tylocephalum*; emphasize that since "*T. trygonis*" [genus was not specified] had been indicated previously as the type of the genus *Tetragonocephalum* it cannot be made the type species of *Tylocephalum* as suggested by some authors; conclude that *Tetragonocephalum* must be resurrected; consider *Tetragonocephalum* to be valid and place it in the family Lecanicephalidae.

Schmidt (1970): considers *Tetragonicephalum* [sic] (along with *Polypocephalus*, *Calycobothrium*, *Staurobothrium*, *Hexacanalis*, and *Lecanicephalum*) as valid in the family Lecanicephalidae, order Lecanicephalidea Baylis, 1920; presents key to the genera of tapeworms; gives diagnosis for each genus and designates the type species.

Wardle *et al.* (1974): recognize the family Tetragonocephalidae [and consequently *Tetragonocephalum*] in the order Lecanicephalidea Baylis, 1920; do not list any genera they consider to belong in the family; present a key to families in the order Lecanicephalidea; note features of the family as part of the key, such as "posterior holdfast region without suckers" (p. 118), a postovarian bilobed vitellarium and testes distributed in the anterior region of the proglottid.

Freeman (1982): comments on the presence and/or morphology of oncospheres and coracidia in the genus *Tetragonocephalum* (= *Tylocephalum*); adopts the opinion of Baer (1948) and Euzet and Combes (1965) that *Tylocephalum* should be suppressed and *Tetragonocephalum* considered valid.

Freeman (1983): summarizes the literature on larval lecanicephalideans (order Lecanicephalidea); most have been referred to as belonging to the genera *Tetragonocephalum* or *Tylocephalum*, but never confirmed; adopts the opinion of Baer (1948), Euzet and Combes (1965), and Schmidt (1970) that *Tylocephalum* should be suppressed and *Tetragonocephalum* considered valid.

Campbell and Williams (1984): reject *Tetragonocephalum* as a junior synonym of *Tylocephalum* because of clear morphological differences between *Tetragonocephalum uarnak*, as described by Euzet and Combes (1965), and *Tylocephalum*; state there is no evidence to justify inclusion of *Tetragonocephalum* in any other family than Lecanicephalidae; suggest that *Tetragonocephalum uarnak* should be used as a reference for the genus *Tetragonocephalum* until observations on the type species, *T. trygonis*, from the type locality confirm that this genus is not synonymous with *Tylocephalum*.

Schmidt (1986): treats *Tetragonicephalum* [sic] Shipley and Hornell, 1905 as valid in the family Lecanicephalidae, order Lecanicephalidea.

Brooks and McLennan (1993): present a tree for the order Lecanicephaliformes Baylis, 1920; based on that tree they recognize *Tetragonocephalum* Shipley and Hornell, 1905 (along with *Staurobothrium* Shipley and Hornell, 1905, *Disculiceps* Joyeux and Baer, 1935, *Adelobothrium* Shipley, 1900, *Prosobothrium* Cohn, 1902, and *Cathetocephalus* Dailey and Overstreet, 1973) in the subfamily Disculicipinae Joyeux and Baer, 1935, family Lecanicephalidae Braun, 1900, order Lecanicephaliformes Baylis, 1920.

Euzet (1994b): considers *Tetragonocephalum* Shipley and Hornell, 1905 as valid in the family Tetragonocephalidae, order Lecanicephalidea, with *Spinocephalum* Deshmukh, 1980 as a synonym.

Ivanov and Campbell (2000): present arguments as to the validity of *Tetragonocephalum* and *Tylocephalum* as distinct genera; list several characteristics that distinguish the two genera: "*Tetragonocephalum*"-type, with acraspedote proglottids, proglottids very much longer than wide, testes anterior to cirrus sac, vitelline follicles lateral, and an enlarged genital pore and enormous genital atrium (including *T. trygonis*, *T. uarnak*, *T. minutum*, *T. simile*, *T. yamagutii*, *T. raoi*, *T. alii*, and *T. sephensis*); "*Tylocephalum*"-type, with craspedote quadrangular proglottids, testes in field anterior to ovary and a shallow genital atrium (including *T. pingue*, *T. marsupium*, *T. bonasum*, *T. yorkei*, *T. squatinae*, *T. campanulatum*, *T. elongatum*, *T. minimum*, and *T. brooksi*).

Caira *et al.* (2001): include a species of *Tetragonocephalum* (*Tetragonocephalum* sp. from *Himantura* sp.) in a phylogenetic analysis based on morphological data; the species groups with the majority of the other lecanicephalidean taxa included in the analysis.

Remarks

The taxonomic history of *Tetragonocephalum* is confusing, mainly because of the issue of its potential synonymy with *Tylocephalum*. *Tetragonocephalum* was erected by Shipley and Hornell (1905) for two new species, *T. trygonis* and *T. aetiobatidis*, collected in Ceylon (now Sri Lanka). *Tetragonocephalum trygonis* was designated as the type species. While the generic diagnosis was very brief and only superficially addressed the scolex morphology, which is similar in these two species, the species descriptions contained some detail on the proglottid morphology and anatomy. The most conspicuous feature of *T. trygonis* described by Shipley and Hornell (1905) was the form of the uterus. The uterus was described as "dumb-bell-shaped" (p. 52), because it is divided into an anterior and posterior "chamber" by a constriction across the large genital atrium. This feature, which appears to be unique to *Tetragonocephalum*, continues today to be the most useful feature for identifying members of *Tetragonocephalum*. This distinctive feature was not described by Shipley and Hornell (1905) for the second species, *T. aetiobatidis*, and, in fact, one year later, Shipley and Hornell (1906) declared that *Tetragonocephalum* was identical with Linton's genus *Tylocephalum*, described in 1890. They transferred the two species of *Tetragonocephalum* already in existence to *Tylocephalum*. In that same publication Shipley and Hornell (1906) described, among others, what they considered to be another species of *Tylocephalum*, *Tylocephalum uarnak*. *Tetragonocephalum* remained a junior synonym of *Tylocephalum* for approximately the next 20 years (see Southwell 1925; Poche 1926). The taxonomy was complicated during that time by the fact that Southwell (1925) considered the type species of *Tylocephalum*, *Tylocephalum pingue* Linton, 1890, to be unrecognizable and suggested *Tylocephalum trygonis* replace it as type species. Under the rules of zoological nomenclature, this was not a valid action, as was recognized by, for example, Poche (1926). *Tylocephalum pingue* must remain the type by original monotypy. In 1928, Pintner subdivided lecanicephalidean taxa into two families, the Lecanicephalidae and the Cephalobothriidae. While also addressing the placement of, for example, *Polypocephalus* and *Lecanicephalum*, his work concentrated on the classification of species of *Tylocephalum* and *Cephalobothrium*. Pintner (1928) suggested that species recognized as *Tylocephalum* or *Cephalobothrium* be divided into two groups, those that were acraspedote with unusually long proglottids (group A, such as "*T. uarnaki*" [sic]), and those that were strongly craspedote with proglottids of "normal" length (group B, such as *C. aetobatidis* and *Tylocephalum pingue*). Pinter (1928) concluded that since the type species of *Tylocephalum* (*i.e.*, *T. pingue*) was a member of group B, and *T. trygonis*, the type species of *Tetragonocephalum*, was a member of group A, *Tetragonocephalum* should be considered valid. Pinter's taxonomic decision to recognize *Tetragonocephalum* as distinct from *Tylocephalum* was subsequently accepted by Perrenoud (1931) and Baer (1948), and *Tetragonocephalum* has been considered to be a valid genus since. In 1959, Yamaguti created the new family Tetragonocephalidae to house *Tetragonocephalum* and presented a very comprehensive diagnosis of the genus. Euzet and Combes (1965) redescribed *Tetragonocephalum uarnak* in great detail further clarifying the concept of *Tetragonocephalum*.

In the most recent treatment addressing the taxonomic status of species in the genera *Tetragonocephalum* and *Tylocephalum*, Ivanov and Campbell (2000) sorted out the generic identities of the species that had been placed in the "*Tetragonocephalum*/*Tylocephalum*" complex, doing much to facilitate work in these groups. Given that the proglottids of *Tetragonocephalum* are very distinctive and easily distinguished from those of *Tylocephalum* (see generic diagnoses of both), it is unfortunate that the similarity in scolex morphology has caused such taxonomic confusion.

Five species names, *Tetragonocephalum meenae*, *T. shindei* Shipley and Hornell, 1906, *T. karachiensis* Bilqees and Fatima, 1982, *T. stegostomai* Bilqees and Fatima, 1982, and *T. varium* Bilqees and Fatima, 1982, the latter three names listed as *Tetragonicephalum* [sic], are considered to be *nomina nuda*. *Tetragonocephalum meenae* and *T. shindei* were used only in a list of cestode parasites collected from the west coast of Maharashtra, India by Mohekar *et al.* (2002); no literature citations were given. Shipley and Hornell did not use the name and did not describe *T. shindei*. In fact, it appears that neither species was ever actually described. *Tetragonocephalum karachiensis*, *T. stegostomai* , and *T. varium* were used only in a list of cestode parasites from marine fishes from Pakistan by Bilqees (1995). Bilqees and Fatima (1982) was given as the authority of all four species, however, the citation listed in the reference section is incomplete, and appears as Bilqees and Fatima (1980). Reference to these species names could not be found in any other publication or database, and Bilqees and Fatima (1980) was not obtainable. Consequently, it is assumed that the description of these species does not actually exist for taxonomic study. Therefore, the five names mentioned above-should be considered to be not available.

The generic diagnosis presented here has been modified from Yamaguti (1959) because it was the most comprehensive diagnosis and best reflects the current concept of the genus. In general, the diagnosis presented here is consistent with both, the diagnosis of Yamaguti (1959) and that of Euzet (1994b). The following re-interpretations of features were incorporated in the diagnosis: the cirrus is considered to be armed and the ovary oval in dorso-ventral view, whereas Yamaguti (1959) considered the cirrus to be unarmed and the ovary somewhat bilobed. Similar to Yamaguti (1959), the external seminal vesicles is considered to be absent and an internal seminal vesicle is present, whereas Euzet (1994b) considered both to be present.

Tetragonocephalum trygonis Shipley and Hornell, 1905

TYPE SPECIES

(Fig. 52)

Synonyms: *Tylocephalum trygonis* (Shipley and Hornell, 1905) Shipley and Hornell, 1906.

Type host: *Trygon walga* Müller and Henle, 1841 (= *Himantura walga* [Müller and Henle, 1841] ?), Dwarf whipray (Dasyatidae, Myliobatiformes).

Additional hosts: None.

Site of infection: Spiral intestine.

Type locality: Ceylon (now Sri Lanka) (Fig. 52).

Additional localities: None.

Number of specimens on which the original description was based: "A number."

Type specimens: Not indicated in original description.

Voucher specimens (unverified): (see Appendix 4).

Material examined: NMW Nos. 2147 and 2164 (vouchers); BMNH No. 1978.9.1.12-13 (vouchers).

Etymology: *Trygonis*, referring to the type host of the species, *Trygon walga*.

Unverified records: *Aetobatis* [sic] *narinari* and *Trygon walga* from Ceylon (see Shipley and Hornell 1906); *Trygon* sp. (kuhlii?) from Orissa, India (see Southwell 1925); *Dasyatis violacea* (Bonaparte, 1832) from the Mediterranean Sea (see Euzet 1952, 1954, 1959).

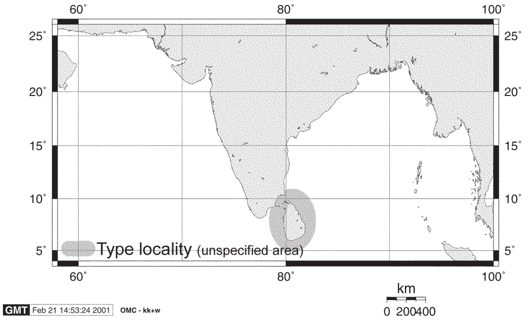


Fig. 52. Geographic distribution of *Tetragonocephalum trygonis* Shipley and Hornell, 1905.

Chronology

Shipley and Hornell (1905): erect the genus *Tetragonocephalum* with *T. trygonis* as the type species for a number of specimens from *Trygon walga* from Ceylon; provide a general description of the species, noting its acraspedote proglottids; do not describe proglottid anatomy, except for the mention of large atria and a dumb-bell-shaped uterus.

Shipley and Hornell (1906): transfer *Tetragonocephalum trygonis* to *Tylocephalum* to create the new combination, *Tylocephalum trygonis* (Shipley and Hornell, 1905) Shipley and Hornell, 1906; report *Tylocephalum trygonis* from *Aetobatis* [sic] *narinari*; collect new material from *Trygon walga*; augment original description of species including information on arrangement of pores and protruding genital pore.

Jameson (1912): notes that one is likely to find adult stages of *Tylocephalum ludificans* and *T. minus,* described from larval stages, among members of *Tylocephalum*, or allied types described as new genera, occurring in oyster-eating elasmobranchs, such as, for example, *Tylocephalum* (*Tetragonocephalum*) *trygonis*.

Stiles and Hassall (1912): *Tetragonocephalum* Shipley and Hornell, 1905 (tod. [usually "m"] *trygonis*) (Lecanicephalidae): Shipley and Hornell (1906) (syn. of *Tylocephalum* Lint.); *T. aetiobatidis* Shipley and Hornell, 1905 (in *Aetiobatis* [sic] *narinari*; Ceylon): Shipley and Hornell (1906) (*aetobatidis*); *T. aetobatidis*

Shipley and Hornell (1906) (for *aetiobatidis*) (in *Aetiobatis* [sic] *narinari*; Ceylon); *T. trygonis* Shipley and Hornell, 1905 (in *Trygon walga*; Ceylon): Shipley and Hornell (1906) (to *Tylocephalum*); *T. atiobatis* Shipley and Hornell, 1905 (misprint for *aetiobatides* [misprint?]).

Southwell (1925): recognizes *Tylocephalum trygonis*; redescribes the species from 15 new specimens collected from *Trygon* sp. (*kuhli*?) from Orissa, India; illustrates scolex longitudinal sections, immature, ripe and gravid proglottids; designates it as type species of the genus *Tylocephalum* because *T. pingue* is impossible to identify.

Pintner (1928): creates two groups, family Cephalobothriidae (group B) and family Lecanicephalidae (group A), which includes *Tylocephalum uarnaki* (= *trygonis*?), possibly *Tylocephalum minutum*, possibly *Lecanicephalum peltatum*, even *Parataenia medusia*, *Polypocephalus medusia*, separate from *Polypocephalus radiatus*, with non-glandular scolex, bilobed uterus and acraspedote proglottids; considers *Tylocephalum uarnaki* a synonym of *Tylocephalum trygonis*.

Southwell (1929): comments on the classification schemes proposed by Poche (1926), Woodland (1927), and Pintner (1928); mentions *Tylocephalum*, mainly in regard to the controversy about the disposition of the vitellarium as single mass or arranged in multiple follicles in the species *T. uarnak*, *T. minutum* (also as *T. minutus*) and *T. trygonis*.

Southwell (1930): recognizes *Tylocephalum trygonis*; basically same text as that of Southwell (1925); again, justifies, why *T. trygonis* should be type species over *T. pingue*.

Perrenoud (1931): suggests *Tetragonocephalum* Shipley and Hornell, 1905, which had fallen into synonymy with *Tylocephalum*, should be resurrected for Pinter's (1928) "*Tylocephalum* group A," with *T. trygonis* as the type species.

Baer (1948): gives history of the genus *Tylocephalum* including comments on how it relates to *Tetragonocephalum*; counts *T. trygonis* as one of 11 [12 were counted] species in *Tylocephalum*; notes that, even though Southwell (1925) suggested *T. trygonis* as the type species of *Tylocephalum* to replace *T. pingue*, *Tetragonocephalum* must be resurrected.

Euzet (1952): reports *Tetragonocephalum trygonis* Shipley and Hornell, 1905 from *Trygon violacea* from Mediterranean Sea.

Wardle and McLeod (1952): recognizes *Tetragonocephalum trygonis* Shipley and Hornell, 1905 (= *Tylocephalum trygonis* Southwell, 1925 = *Tetragonocephalum uarnaki* Shipley and Hornell, 1906) as the type species of *Tetragonocephalum* Shipley and Hornell, 1905; comments that two additional species were recognized by Pintner (1928) in the genus, *T. minutum* and *T. simile* [these were actually described as *Tylocephalum*].

Euzet (1954): describes and illustrates attachment of *Tetragonocephalum trygonis* in *Dasyatis violacea*.

Yamaguti (1959): recognizes *Tetragonocephalum trygonis* Shipley and Hornell, 1905 (syn. *Tylocephalum trygonis* [Shipley and Hornell, 1905] Shipley and Hornell, 1906) as type species of *Tetragonocephalum* Shipley and Hornell, 1905.

Euzet (1959): reports, redescribes, and illustrates *Tetragonocephalum trygonis* (in superfamily Lecanicephaloidea Southwell, 1930, family Lecanicephalidae Pintner, 1929) from *Dasyatis violacea* from Sète; notes strong resemblance to *Tylocephalum uarnak* (Shipley and Hornell) as described by Southwell (1925); reuses his earlier drawing of the attachment of this worm (Euzet, 1954).

Euzet and Combes (1965): review the history of *Tetragonocephalum* and *Tylocephalum*; emphasize that since "*T. trygonis*" [genus is unclear] had been indicated previously as the type of the genus *Tetragonocephalum* it cannot be made the type species of *Tylocephalum* as suggested by some authors; conclude that *Tetragonocephalum* must be resurrected; consider *Tetragonocephalum* to be valid and place it in the family Lecanicephalidae.

Campbell and Williams (1984): do not consider *Tetragonocephalum* a junior synonym of *Tylocephalum* because of clear morphological differences between *Tetragonocephalum uarnak* as described by Euzet and Combes (1963) and *Tylocephalum*; suggest that *Tetragonocephalum uarnak* should be used as a reference for the genus *Tetragonocephalum* until observations on the type species, *T. trygonis*, from the type locality confirm that this genus is not synonymous with *Tylocephalum*.

Schmidt (1986): recognizes *Tetragonicephalum* [sic] *trygonis* Shipley and Hornell, 1905 (syn. *Tylocephalum trygonis* [Shipley and Hornell, 1905], Shipley and Hornell, 1906) as type and only species in the genus.

Ivanov and Campbell (2000): recognize *Tetragonocephalum trygonis* as type species of *Tetragonocephalum*; consider the species to be of the "*Tetragonocephalum*"-type, that is, with acraspedote strobila, testes anterior to cirrus sac, lateral vitelline follicles, large genital atrium and bisaccate uterus, distinct from the "*Tylocephalum*" type.

Remarks

Tetragonocephalum trygonis was described by Shipley and Hornell (1905) as the type species of their new genus *Tetragonocephalum*, based on a number of specimens from the ray *Himantura walga* (as *Trygon walga*) from Ceylon (now Sri Lanka). They do not appear to have designated type material.

Tetragonocephalum trygonis has been reported from a number of different hosts since its original description (see *e.g.*, Shipley and Hornell 1906; Southwell 1925; Euzet 1952). Shipley and Hornell's (1905) description of *T. trygonis* as possessing a "dumb-bell-shaped" uterus (p. 52), a large genital atrium and acraspedote proglottids, allows the genus to be easily distinguished from other genera. Unfortunately, the description of *T. trygonis* does not contain enough detail to unambiguously recognize it and evaluate synonymies with other species.

Characterized by the features mentioned above, *Tetragonocephalum trygonis* is not a member of *Tylocephalum* as was suggested first by Shipley and Hornell (1906). In addition, Southwell's (1925) suggestion that "*T. trygonis*" replace *Tylocephalum pingue* as the type species, was a nomenclatural error and will not be addressed further.

No reference to the possible existence of type material of *Tetragonocephalum trygonis* could be found. Examination of the lecanicephalidean holdings at the Naturhistorisches Museum Wien in Vienna, Austria (NMW) revealed the presence of two specimens (NMW No. 2147 and 2164) identified as "*Tetragonocephalum trygonis*" from A. Shipley's collection, from *Aetobatus narinari* and an unknown host, respectively. The identity of the host species provides reason to believe that this material was collected subsequent to the description of *T. trygonis* and does not represent the material on which the original description was based. Examination of the specimens revealed that, while the specimen from the unknown host (NMW No. 2164) could be identified as, at least, belonging to the genus *Tetragonocephalum*, the specimen from *Aetobatus narinari* (NMW No. 2147) proved to be inconsistent with the diagnosis of *Tetragonocephalum*, tentatively identified here as belonging to the genus *Tylocephalum*. In addition, two specimens identified as "*T. trygonis*" were found deposited at the British Museum of Natural History in London (BMNH). Both voucher specimens (BMNH No. 1978.9.1.12-13) are craspedote and consistent with the generic diagnosis of *Tylocephalum*, rather than *Tetragonocephalum*.

Tetragonocephalum passeyi Jensen, n. sp.

(Figs. 53-55)

Type host: *Himantura undulata* (Bleeker, 1852), Leopard whipray (Dasyatidae, Myliobatiformes).

Additional hosts: None.

Site of infection: Spiral intestine.

Type locality: east of Wessel Islands (10°40'S 137°07'E), Arafura Sea, Australia (Fig. 53).

Additional localities: None.

Number of specimens on which the original description was based: 29 (20 whole mounts, two proglottid cross-section series, one scolex longitudinal section series, three lactophenol preparations of eggs, and three specimens prepared for SEM).

Type specimens: Holotype (QM No. G 222916), seven paratypes (five whole mounts, one proglottid cross-section series, and one lactophenol preparation of eggs) (QM Nos. G 222917-222923); six

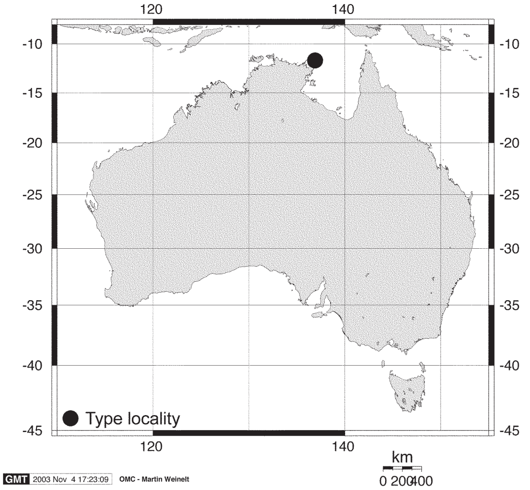


Fig. 53. Geographic distribution of *Tetragonocephalum passeyi* Jensen, n. sp.

paratypes (five whole mounts and one lactophenol preparation of eggs) (USNPC No. 94581); five paratypes (four whole mounts and one lactophenol preparation of eggs) (KUNHM Nos. 002121-002125); 7 paratypes (five whole mounts, one proglottid cross-section series, and one scolex longitudinal section series) (LRP Nos. 3314-3320); three paratype specimens prepared for SEM (LRP).

Etymology: This species is named in honor of Raymond Passey, captain of the F. V. Ocean Harvest, intending to express my gratitude for his permitting J. N. Caira and the author to collect tapeworms aboard the Ocean Harvest for two very productive weeks in 1999.

Chronology

Caira *et al.* (2001): include *Tetragonocephalum passeyi* as "*Tetragonocephalum* sp." in a phylogenetic analysis based on morphological data; the species grouped with the majority of the other lecanicephalidean taxa included in the analysis.

Description (Based on 20 whole mounts, two proglottid cross-section series, one scolex longitudinal section series, three lactophenol preparations of eggs, and three specimens prepared for SEM.)

Worms 11,657-28,718 (18,983 ± 3,759; 20) long; maximum width at scolex; 18-33 (28 ± 3.8; 22) proglottids, apolytic. Scolex 437-720 (558 ± 69.1; 17) long by 379-672 (565 ± 72.0; 20) wide, consisting of scolex proper and apical organ. Scolex proper 250-443 (306 ± 58.7; 14) long by 366-672 (565 ± 71.4) wide, bearing four acetabula. Acetabula sucker-like in form, 88-123 (105 ± 6.6; 20; 40) long by 94-133 (111 ± 8.6; 20; 40) wide. Apical modification of scolex proper cylindrical, bearing apical organ. Apical organ large, globular, muscular, with glandular surface, 224-353 (313 ± 42.2; 15) long by 299-460 (371 ± 39.9; 20) wide, non-invaginable, non-retractable.

Rims of acetabula and scolex proper covered with pointed filitriches (Fig. 55B and C). Surface of apical organ covered with tubercles suggesting a glandular surface (Fig. 55D and E). Strobila covered with long filitriches (Fig. 55F).

Cephalic peduncle absent. Proglottids acraspedote. Immature proglottids 12-25 (20 ± 3.4; 20) in number, initially wider than long, becoming longer than wide (3-10 [6 ±1.9; 20] immature proglottids longer than wide); two posterior-most immature proglottids 400-1,256 (702 ± 200.8; 19; 38) long by 210-401 (287 ± 40.5; 19; 38) wide. Mature proglottids 2-3 (3 ± 0.5; 20) in number, two posterior-most mature proglottids 692-1,751 (1,133 ± 263.4; 20; 40) long by 229-446 (2328 ± 44.1; 20; 40) wide. Gravid proglottids 3-6 (5 ± 0.8; 20) in number, 1,424-3,588 (2,662 ± 481.8; 20; 40) long by 399-658 (533 ± 68.0; 20; 40) wide; strobila of two of 20 specimens bearing single spent proglottid. Testes 54-73 (62 ± 5.9; 12; 18) in number, 19-39 (28 ± 4.4; 20; 60) long by 44-82 (55 ± 8.2; 20; 60) wide, extending from anterior margin of proglottid to anterior margin of cirrus sac, two irregular columns in dorso-ventral view, two rows deep in cross-section (Fig. 54E). Vas deferens extending from level of ovary to cirrus sac, entering cirrus sac at distal end. External seminal vesicle absent. Internal seminal vesicle present. Cirrus sac pyriform, oriented anteriorly, 97-268 (142 ± 35.2; 20; 39) long by 93-191 (144 ± 22.1; 20; 39) wide, 173-429 (272 ± 52.8; 20; 40) long by 140-314 (203 ±

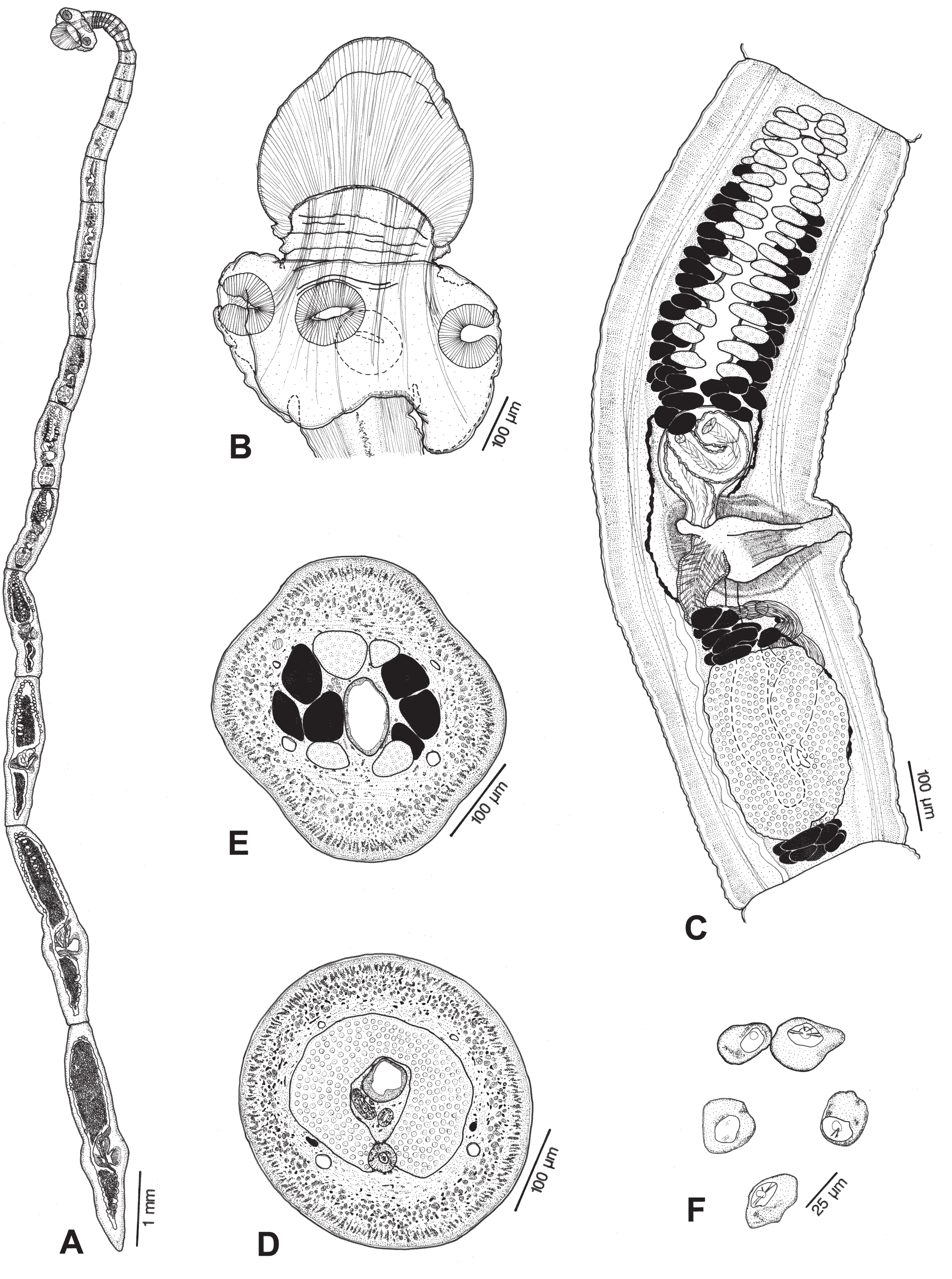


Fig. 54. A-F. Line drawings of *Tetragonocephalum passeyi* Jensen, n. sp. A. Whole worm (holotype, QM No. G 222916). B. Scolex (QM No. G. 222919). C. Mature proglottid (USNPC No. 94581). D. Cross-section through mature proglottid at level of ovarian bridge (QM No. G 222922). E. Cross-section through mature proglottid anterior to genital pore (QM No. G 222922). F. Eggs (QM No. G 222923).

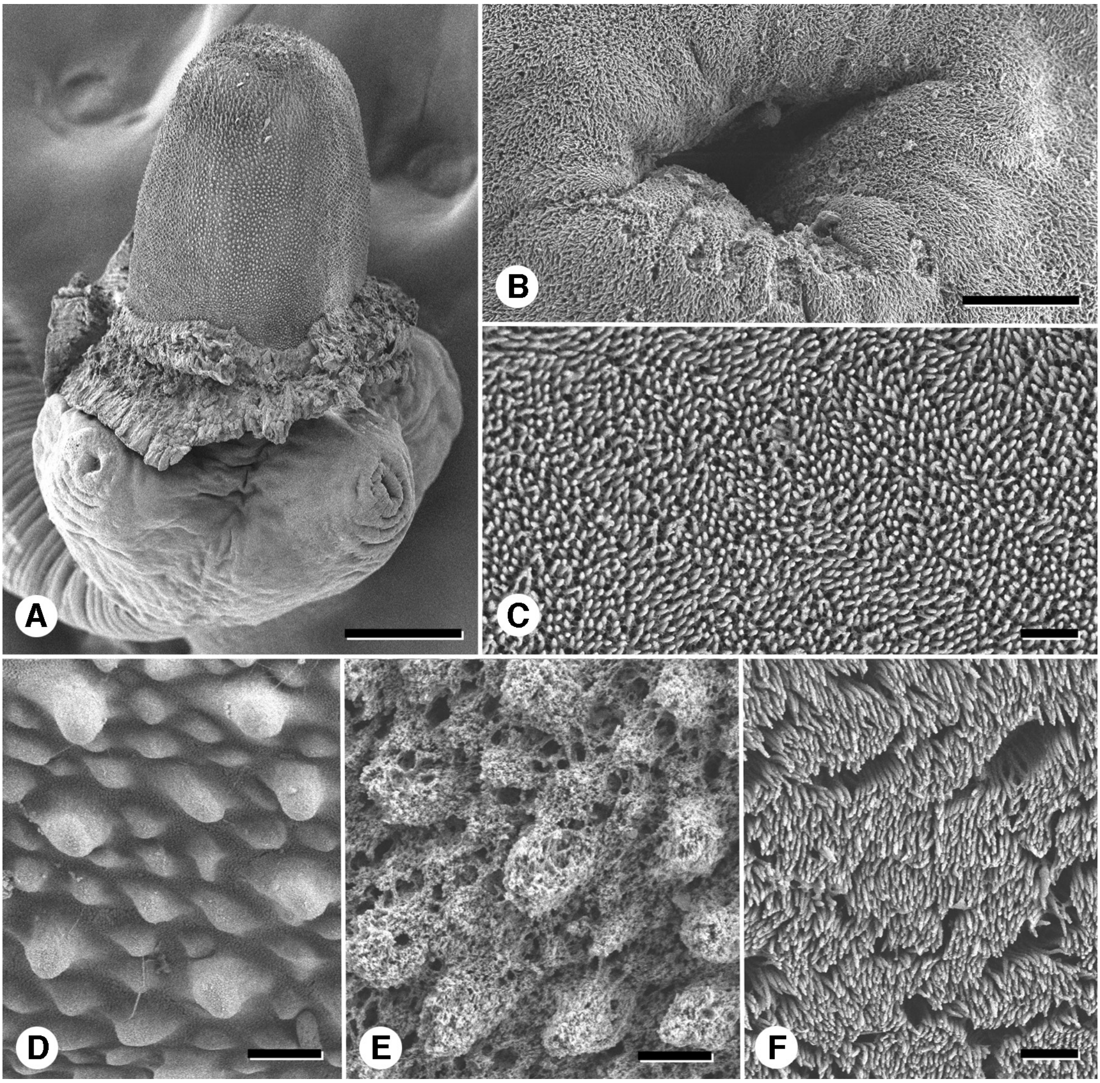


Fig. 55. A-F. Scanning electron micrographs of *Tetragonocephalum passeyi* Jensen, n. sp. A. Scolex. B. Sucker. C. Microtriches on surface of scolex proper. D. Surface of apical organ, prior to attachment. E. Surface of apical organ, post attachment. F. Microtriches on surface of strobila. Scale bars: A, 100 µm; B, 10 µm; C and F, 1 µm; D-E, 2.5 µm.

30.7; 20; 40) wide in posterior most gravid proglottids, containing coiled cirrus. Cirrus armed. Ovary oval in dorso-ventral view, ring-shaped in cross-section (Fig. 54D), 135-370 (254 ± 51.2; 20; 39) long by 97-246 (189 ± 31.2; 20; 40) wide, symmetrical; ovarian bridge at center of ovary. Mehlis' gland posterior to ovarian bridge. Vagina extending along median line from ootype to genital pore, opening into large genital atrium posterior to cirrus sac; vaginal sphincter absent. Genital pores lateral, irregularly alternating, 34-49% (40 ± 3.1; 20; 40) of proglottid length from posterior end. Genital atrium expanded, conspicuous. Uterus bisaccate, extending along median line of proglottid from posterior margin of ovary to anterior margin of proglottid, constricted at level of genital atrium; uterine duct not observed; uterine pore absent. Vitellaria follicular, medullary, in lateral columns, 2-3 vitelline follicles on each side of proglottid in cross-section (Fig. 54E), extending entire length of proglottid, stopping short of anterior margin of proglottid, interrupted by cirrus sac, genital atrium and ovary; vitelline follicles 20-41 (27 ± 4.7; 20; 59) long by 37-78 (53 ± 7.8; 20; 59) wide. One dorsal and one ventral pair of excretory ducts present (Fig. 54D and E). Eggs single, lacking polar filaments (Fig. 54F), 19-36 (27 ± 5.4; 3; 19) long by 24-39 (31 ± 5.0; 3; 19) wide, adhering to one another in uterus; hexacanths in eggs of older gravid proglottids. Hexacanth 10-13 (11 ± 0.8; 3; 19) long by 15-19 (17 ± 1.3; 3; 19) wide.

Remarks

In this study, 13 species of *Tetragonocephalum* are recognized as valid (see Appendix 2); *Tetragonocephalum passeyi* is distinguished from each below. *Tetragonocephalum passeyi* is longer than *T. yamagutii* (11-28 mm vs. 6.05-7 mm) and conspicuously shorter than *T. shipleyi* (11-28 mm vs. 40 mm). *Tetragonocephalum passeyi* possesses fewer proglottids than does *T. alii*, *T. trygonis*, and *T. simile* (11-38 vs. 55-60, greater than 60 [according to Shipley and Hornell 1905, fig. 3], and about 60 [according to Pintner, 1928, fig. 37], respectively). The diameter of the acetabula of *T. passeyi* (88-123 x 94-133) is larger than those of *T. yamagutii* (30-40 x 40-50), *T. shipleyi* (50 in diameter), *T. bhagawatii* (56 in diameter), and *T. aurangabadensis* (67 in diameter). *Tetragonocephalum passeyi* differs in testes number from *T. ratnagiriensis*, *T. madhualtae*, *T. aurangabadensis*, and *T. madrasensis* (54-73 vs. 40-44, 45, 105-110, and 125-130, respectively). The gravid proglottids of *T. passeyi* obtain a maximum length of 3,588, whereas the gravid proglottids of *T. uarnak* obtain a length of 5,000. *Tetragonocephalum passeyi* can be distinguished from *T. ratnagiriensis* and *T. sephensis* based on the length of the ovary (135-370 vs. 455 and 540, respectively). *Tetragonocephalum passeyi* is most similar to *T. raoi*. However, *T. passeyi* lacks small papillae protruding from the acetabula, which are present in *T. raoi*. The two species can be further distinguished in that the gravid proglottids of *T. passeyi* are less elongate (length to width ratio of 6:1) than those of *T. raoi* (length to width ratio of 8:1).

TYLOCEPHALUM Linton, 1890

Taxonomic status: Valid.

Synonyms: *Spinocephalum* Deshmukh, 1980.

Type species: *Tylocephalum pingue* Linton, 1890.

Other species: *Tylocephalum bonasum* Campbell and Williams, 1984; *T. brooksi* Ivanov and Campbell, 2000; *T. campanulatum* Butler, 1987; *T. elongatum* Subhapradha, 1955; *T. marsupium* Linton, 1916; *T. koenneckeorum* Jensen, n. sp.; *T. pandurangi* Shinde and Mahajan, 1994; *T. rhinobatii* (Deshmukh, 1980) n. comb.; *T. singhii* Jadhav and Shinde, 1981; *T. squatinae* Yamaguti, 1934; *T. yorkei* Southwell, 1925.

Species inquirendae: *Tylocephalum alii* Andhare and Shinde, 1994; *T. aurangabadensis* Jadhav and Shinde, 1988; *T. bombayensis* Jadhav, 1983; *T. chiralensis* Vijayalakshmi and Sarada, 1995; *T. dierama* Shipley and Hornell, 1906; *T. hanmantraoi* Shinde and Jadhav, 1990; *T. kuhli* Shipley and Hornell, 1906; *T. ludificans* Jameson, 1912; *T. madhukarii* Chincholikar and Shinde, 1980; *T. margaritiferae* Seurat, 1906; *T. minimum* Subhapradha, 1955; *T. minus* Jameson, 1912; *T. minutum* Southwell, 1925.

Nomina nuda: *Tylocephalum mehdii* in Mohekar *et al.* (2002);

Non-lecanicephalidean species: *Tylocephalum unionifactor* (Shipley and Hornell, 1904) Herdmann in Southwell 1924 subjective junior synonym of *Tetrarhynchobothrium unionifactor* (Shipley and Hornell, 1904) Beveridge and Campbell, 1988 (Trypanorhyncha).

Etymology: *Tylo-*, Gr., *tyle*, *tylos*, knot, knob, callus, lump, bolt; *kephale*, Gr., head.

Diagnosis (Modified from Williams and Campbell [1984].)

Worms euapolytic or apolytic; conspicuous longitudinal muscle bundles in outer perimeter of proglottids, extending entire length of strobila. Scolex with four acetabula; acetabula in form of suckers; apical modification of scolex proper cylindrical, bearing apical organ; apical organ large, globular, muscular, with glandular surface, non-invaginable, non-retractable. Proglottids craspedote, non-laciniate. Testes numerous, anterior to, but overlapping with ovary at anterior margin. Vas deferens expanded to form external seminal vesicle. External seminal vesicle conspicuous, extending from ovary to cirrus sac. Internal seminal vesicle present or absent. Cirrus sac pyriform. Cirrus unarmed or armed. Ovary H-shaped in dorso-ventral view, each side consisting of lobes radiating from ovarian bridge, bilobed in cross-section. Vagina opening into genital atrium posterior to cirrus sac or at same level, extending along median line in proglottid. Genital pores lateral, irregularly alternating. Uterus saccate, extending along median line entire length of proglottid. Vitellaria follicular, circumcortical or in numerous lateral columns encroaching on median line of proglottid, extending length of proglottid, interrupted by ovary or not. Two or more pairs of excretory ducts present. Eggs single. Parasites of rays in the families Dasyatidae, Myliobatidae, Rhinidae, Rhinobatidae and Rhinopteridae, and sharks in the family Squatinidae. Western Atlantic Ocean (U.S.A. and Venezuela) Northern Indian Ocean (India and Sri Lanka), Western Pacific Ocean (Japan and Queensland, Australia) and Arafura Sea (Australia).

Chronology

Linton (1890): erects the genus *Tylocephalum* with *T. pingue* as the type species for a single small cestode specimen, based on a lack of costae and presence of a supplementary disc; a brief diagnosis of the genus is presented and the species (based on the one immature specimen) is described in some detail including some measurements on the living and fixed specimen; suggests a possible close relationship to *Discocephalum*; notes that if the acetabular disc of *Tylocephalum* were to divide in the adult, it would resemble *Discobothrium*; exact systematic position doubtful; places *Tylocephalum* in the subfamily I, the Phyllobothriinae, family Tetrabothriidae, although "bothrial" morphology does not match that of the family; suggests, upon further investigation, to include *Tylocephalum* (along with *Discocephalum* and *Lecanicephalum*), for example in the Gamobothriidae "or some equivalent term."

Braun (1894-1900): considers *Tylocephalum* Linton as valid in the family Lecanicephalidae (*fam. inq.* = Gamobothriidae), order Tetraphyllidea.

Perrier (1897): recognizes *Tylocephalum* (including *T. pingue* from *Rhinoptera quadriloba*) as one of four genera in the family Gamobothriidae, order Tetracestoda (along with *Lecanicephalum*, *Discocephalum*, and *Sciadocephalus*).

Shipley and Hornell (1906): determine Linton's *Tylocephalum* to be valid and *Tetragonocephalum*, a genus they described in 1905, to be a junior synonym of *Tylocephalum*.

Stiles and Hassall (1912): *Tylocephalum* Linton, 1890 (Tetrabothriidae, Phyllbothriinae): Linton (1901) and Braun (1895 and 1900); *T. margaritiferae* Seurat, 1906 (larva in *Margaritifera margaritifera cumingi*; adult in *Aetiobatis narinari*; Lagon des Gambier, Pacific Ocean): Seurat (1908) and Seurat in Herdmann and Hornell (1906) (in *M.c.*; adult in *A.n.*); *T. pingue* Linton, 1890 (in *Rhinoptera quadriloba*; Woods Hole): Linton (1901) (in *R. bonasus*) and Braun (1900); *T. trygonis* (Shipley and Hornell, 1905) Shipley and Hornell (1906) (in *Trygon walga*; Ceylon); *T. ludificans* Jameson, 1912 (in *Margaritifera vulg.*; Gulf of Manaar); *T. minus* (Linton, 1907) Jameson, 1912 (in *Margaritifera vulg.*; Gulf of Manaar).

Mola (1921): reclassifies cestodes and places *Tylocephalum* "and etc." [?] in the subfamily Lecanicephalinae, family Dibothriophyllidae, order Diphyllidea.

Hornell (1922): writes about pearl formation in the Indian pearl oyster; believes that the spherical cestode larvae in the tissues of the pearl oyster and the nuclei in cyst pearls are not tetrarhynchid larvae, but possibly larvae of *Tylocephalum* or a related genus.

Meggitt (1924): treats *Tylocephalum* Linton, 1890 (syn. *Aphanobothrium* Seurat) as a valid genus in the family Lecanicephalidae (along with *Discocephalum*, *Lecanicephalum*, *Cephalobothrium*, and *Adelobothrium*), order Tetraphyllidea; provides an abbreviated diagnosis of the genus.

Southwell (1925): considers *Tylocephalum* (syn. *Tetragonocephalum*, *Kystocephalus*, and *Aphanobothrium*) a valid genus in the family Lecanicephalidae, suborder Multivitellata, order Cyclophyllidea; emends Linton's generic diagnosis; states that, since Linton based the description of *Tylocephalum* on a single immature specimen he called *T. pingue*, which is unrecognizable, the next species described, *Tylocephalum trygonis* [originally described as *Tetragonocephalum trygonis*], should be considered as the type species; includes six species in the genus *Tylocephalum* (not *T. pingue*) and three doubtful species; notes that *T. uarnak*, *T. trygonis*, and *T. minutum* have a single small vitelline gland posterior to the ovary, which actually places the genus *Tylocephalum* as intermediate between the two cyclophyllidean suborders Univitellata and Multivitellata.

Poche (1926): recognizes *Tylocephalum* (along with *Discocephalum*, *Lecanicephalum*, *Cephalobothrium*, *Adelobothrium*, and *Balanobothrium*) in the family Lecanicephalidae Braun (Gamobothriidae Linton, 1889; Gamobothridae Ariola, 1899; Benham, 1901), suborder Phyllobothriinea *nom. nov.*, order Taeniidea *nom. nov.*; retains *Tetragonocephalum* as a synonym of *Tylocephalum*; elaborates on three species of *Tylocephalum* (*T. uarnak*, *T. trygonis*, and *T. minutum*), which are said to possess a single vitellarium posterior to the ovary and should therefore not be considered to belong to the genus *Tylocephalum*, as defined by its type species, *T. pingue*; notes that if Southwell's observation of the vitelline condition in these three species is correct, they should be considered species of the genus *Tetragonocephalum*; notes that *T. pingue* cannot be replaced by *T. trygonis* as the new type species as suggested by Southwell (1925); it is likely that the type specimens of *T. pingue* may still exist or the species could be recollected.

Woodland (1927): does not include *Tylocephalum* as a "lecanicephalid" genus in the family Phyllobothriidae, order Tetraphyllidea, because not enough is known about the type species, whether *T. pingue* or *T. trygonis*; comments on the odd anatomy of *Tylocephalum trygonis* and *T. uarnak* with small bilobed vitelline glands posterior to ovary [??]; comments that in *Tylocephalum* (and *Balanobothrium* and *Cephalobothrium*) the internal organs lie internal to the longitudinal muscles of the strobila.

Pintner (1928): creates two groups, family Lecanicephalidae (A), with *Tylocephalum uarnaki* [sic] = *Tylocephalum trygonis* as the "most well known representative," characterized by nonglandular scolex, bilobed uterus, acraspedote proglottids; and family Cephalobothriidae (B), containing, among others, *Tylocephalum pingue*, characterized by a glandular scolex, craspedote proglottids; comments that the member of group A are distinct from those of group B; considers the type species of *Tylocephalum* (*i.e.*, *T. pingue*) to be a member of group B.

Mola (1929): reclassifies cestodes and places *Tylocephalum* and "etc." [?] in the subfamily Lecanicephalinae, family Dibothriophyllidae, order Diphyllidea.

Southwell (1929): comments on the classification schemes proposed by Poche (1926), Woodland (1927) and Pintner (1928); discusses *Tylocephalum*, mainly in regard to the controversy about the disposition of the vitellarium as single or in follicles in the species *T. uarnak*, *T. minutum* (also as *T. minutus*), and *T. trygonis*; comments on *Tylocephalum* (along with *Cephalobothrium* and *Adelobothrium*) concerning the position of the internal organs in relation to the longitudinal muscles; addresses the position of *Tylocephalum* and *Adelobothrium* in Woodland's (1927) scheme in the family Tetrarhynchidae.

Southwell (1930): treats *Tylocephalum* (syn. *Tetragonocephalum*, *Kystocephalus*, and *Aphanobothrium*) as a valid genus in the family Lecanicephalidae, superfamily Lecanicephaloidea, order Eucestoda; same text as that of Southwell (1925); considers *Tylocephalum trygonis* Shipley and Hornell, 1906 as type species; includes six species (not *T. pingue*) and two doubtful species (*species inquirendae*).

Fuhrmann (1931): classifies members of the genus *Tylocephalum* in two of seven families within the order Tetraphyllidea: family Lecanicephalidae Braun (syn. Gamobothriidae Linton) including *Lecanicephalum* (syn. *Tylocephalum ex parte*, *Tetragonocephalum*, and *Cephalobothrium ex parte*), *Polypocephalus* (syn. *Parataenia* and *Thysanobothrium*), *Anthemobothrium*, and *Adelobothrium*, and family Cephalobothriidae (Pintner) including *Cephalobothrium*, *Tylocephalum* (*ex parte*), and *Discobothrium*.

Perrenoud (1931): suggests that the name *Tylocephalum* should be applied to Pintner's (1928) "*Tylocephalum*" group B; [according to Wardle and McLeod (1952): places six species in this genus all from India and Ceylon (possibly some synonyms), including *T.* (= *Tetragonocephalum*) *aetiobatidis*, *T. dierama*, *T. kuhli*, *T. ludificans*, *T. yorkei*, and *T. translucens*].

Subramaniam (1940): comments that the number of testicular vesicles can be used as a character to distinguish between species of *Tylocephalum*.

Subramaniam (1941): elaborates on the taxonomic status of *Tylocephalum* as possessing a cyclophyllidean head [scolex] and tetraphyllidean proglottids.

Baer (1948): gives history of the genus *Tylocephalum* as it relates to *Tetragonocephalum*; says that *Tylocephalum* currently contains 11 species [12 could actually be counted in his paper], and possibly *Kystocephalus translucens*; concludes that *T. ludificans*, *T. minus*, and *T. margaritifera* [sic] are species known from larvae only and should be considered *nomina nuda*; suggests "to remove the type species of the genus *Tylocephalum*, *T. pingue*, from the nomenclature because it is impossible to recognize and has not been seen since its original description" [loosely translated], resulting in a "disappearance" of the genus; notes that, even though Southwell (1925) suggested "*T. trygonis*" replace *T. pingue* as the type species of *Tylocephalum*, *Tetragonocephalum* must be resurrected.

Hyman (1951): recognizes *Tylocephalum* in the family Cephalobothriidae (along with *Cephalobothrium* and *Discobothrium*), order Lecanicephaloidea; few characters for the family are presented; comments on the fact that little is known about life cycle, except for accounts of what is believed to be *Tylocephalum* larvae in pearl oysters.

Wardle and McLeod (1952): recognizes *Tylocephalum* Linton, 1890 as a valid genus in the family Cephalobothriidae, order Lecanicephala, with *T. pingue* Linton, 1890 as the type species.

Yamaguti (1959): treats *Tylocephalum* Linton, 1890 (syn. *Kystocephalus* Shipley and Hornell, 1906, *Aphanobothrium* Seurat, 1906) as a valid genus in the family Lecanicephalidae, order Lecanicephalidea, with *T. pingue* Linton, 1890 as the type species; recognizes seven additional species: *T. aetiobatidis* (Shipley and Hornell, 1905) Shipley and Hornell, 1906, syn. *Tetragonocephalum aetiobatidis* Shipley and Hornell, 1905; *T. dierama* Shipley and Hornell, 1906, syn. *T. kuhli* Shipley and Hornell, 1906; *T. marsupium* Linton, 1916, syn. *Adelobothrium aetobatidis* Shipley [acc. to Southwell (1930]); *T. simile* Pintner, 1928; *T. squatinae* Yamaguti, 1934; *T. translucens* (Shipley and Hornell, 1906), syn. *Kystocephalus translucens* Shipley and Hornell; *T. yorkei* Southwell, 1925; five additional species are considered unidentifiable from their original descriptions (*T. ludificans* Jameson, 1912, synonym of *T. dierama* acc. to Southwell [1930]; *T. margaritiferae* Seurat, 1906; *T. minus* Jameson, 1912, identical to *T. ludificans* Jameson, 1912 acc. to Southwell; *T. minutum* Southwell, 1925; *T. unionifactor* Herdmann and Hornell, 1903).

Euzet and Combes (1965): review the history of *Tylocephalum* and address the species included in the genus; reject *Tylocephalum* in favor of *Tetragonocephalum* because it has priority; emphasize that since "*T. trygonis*" [genus is unclear] had been indicated previously as the type of the genus *Tetragonocephalum* it cannot be made the type species of *Tylocephalum* as suggested by some authors.

Freeman (1982): comments on the presence and/or morphology of oncospheres and coracidia in the genus *Tetragonocephalum* (= *Tylocephalum*); adopts the opinion of Baer (1948) and Euzet and Combes (1965) that *Tylocephalum* should be suppressed and *Tetragonocephalum* considered valid.

Freeman (1983): summarizes the literature on larval lecanicephalideans (order Lecanicephalidea); most have been referred to as belonging to the genera *Tetragonocephalum* or *Tylocephalum*, but never confirmed; adopts the opinion of Baer (1948), Euzet and Combes (1965), and Schmidt (1970) that *Tylocephalum* should be suppressed and *Tetragonocephalum* considered valid.

Campbell and Williams (1984): note that *Tylocephalum* Linton and *Cephalobothrium* Shipley and Hornell have never been completely described and the true taxonomic status of neither is clear; reject *Tetragonocephalum* as a junior synonym of *Tylocephalum* because of clear morphological differences between *Tetragonocephalum uarnak* as described by Euzet and Combes (1965) and *Tylocephalum*; designate a neotype for *T. pingue* and justify this action (consistent with the original description of Linton and other authors' perceptions of the genus); emend diagnosis of *Tylocephalum* Linton, 1890, listing *Rhinoptera bonasus* as the type host and Woods Hole as the type locality, and Sakonnet Point, Rhode Island and Chesapeake Bay as additional localities.

Schmidt (1986): considers *Tylocephalum* Linton, 1890 (along with *Aphanobothrium* Seurat, 1906, *Kystocephalus* Shipley and Hornell, 1906, and *Spinocephalum* Deshmukh, 1980) to be a junior synonym of *Lecanicephalum* Linton, 1890.

Euzet (1994b): recognizes *Tylocephalum* as a valid genus in the family Tetragonocephalidae, order Lecanicephalidea.

Caira *et al*. (1999): include a species of *Tylocephalum* as "*Tylocephalum* sp." from *Rhinoptera steindachneri* as an exemplar species for the genus in a phylogenetic analysis based on morphological data; the species groups with the majority of the other lecanicephalidean taxa included in the analysis.

Ivanov and Campbell (2000): present arguments as to the validity of *Tylocephalum* and *Tetragonocephalum* as distinct genera; list several characteristics that distinguish the two genera: "*Tylocephalum*"-type, with craspedote quadrangular proglottids, testes in field anterior to ovary and a shallow genital atrium (include *T. pingue*, *T. marsupium*, *T. bonasum*, *T. yorkei*, *T. squatinae*, *T. campanulatum*, *T. elongatum*, *T. minimum*, and *T. brooksi*); "*Tetragonocephalum*"-type, with acraspedote proglottids, proglottids very much longer than wide, testes anterior to cirrus sac, vitelline follicles lateral and an enlarged genital pore and enormous genital atrium (include *T. trygonis*, *T. uarnak*, *T. minutum*, *T. simile*, *T. yamagutii*, *T. raoi*, *T. alii*, and *T. sephensis*); emend the generic diagnosis of *Tylocephalum* of Euzet (1994b); consider *Tylocephalum ludificans*, *T. minus*, and *T. margaritiferae species inquirendae* (ICZN1999, pp. 111 and 116), not *nomina nuda* as had Baer (1948); note that the internal anatomy of *Tylocephalum dierama*, *T. translucens*, *T. aetiobatidis*, and *T. kuhli* has never been described; consider the following species as *species inquirendae*: *Tylocephalum madhukarii*, *T. singhii*, *T. aurangabadensis*, *T. bombayensis*, *T. chiralensis*, *T. hanmantraoi*, *T. madrasensis*, *T. madhulatae*, and *T. alii*.

Caira *et al.* (2001): include a species of *Tylocephalum* as "*Tylocephalum* sp." from Caira *et al.* (1999) in a more comprehensive phylogenetic analysis based on morphological data; the species grouped with the majority of the other lecanicephalidean taxa included in the analysis.

Olson *et al.* (2001): include specimens identified as *Tylocephalum* sp. in a molecular phylogenetic analysis based on complete sequences of the SSU rDNA (GenBank No. AJ287586) and partial sequence of the LSU rDNA (GenBank No. AF286926); specimens identified as *Tylocephalum sp.* (along with *Cephalobothrium* cf. *aetobatidis* and *Eniochobothrium gracile*) are usually placed basal to group consisting of Cyclophyllidea, Nippotaniidea, Tetrabothriidea, Proteocephalidea and Tetraphyllidea; specimens identified as *Tylocephalum* sp. (along with *Cephalobothrium* cf. *aetobatidis* and *E. gracile*) grouped with the Litobothriidea in some analyses.

Littlewood and Olson (2001): use GenBank sequence of the SSU rDNA of *Tylocephalum* sp. (Tetragonocephalidae) (GenBank No. AJ287586) in a phylogenetic analysis investigating relationships among major clades of platyhelminths.

Remarks

The taxonomic history of *Tylocephalum* is intertwined with that of *Tetragonocephalum*. *Tylocephalum* was erected by Linton (1890) for a new species, *T. pingue*, collected from the Cownose ray, *Rhinoptera bonasus* (Mitchill, 1815) (as *Rhinoptera quadriloba*) in Woods Hole, Massachusetts, U.S.A. The description is based on a single, immature specimen. The generic diagnosis is very brief and addresses only the form of the scolex in any detail. Whether this specimen was deposited, was not stated by Linton (1890).

Consequently, the proglottid anatomy of the type species of *Tylocephalum* is unknown and essentially no type material exists.

In 1906, Shipley and Hornell synonymized the genus *Tetragonocephalum*, which they had described in 1905, with Linton's *Tylocephalum*. As was the case for *Tetragonocephalum*, the taxonomy of *Tylocephalum* became more complicated when Southwell (1925) considered the type species of *Tylocephalum*, *T. pingue*, to be unrecognizable. As a consequence, he suggested "*Tylocephalum*" *trygonis* (type species of *Tetragonocephalum*, which was considered a junior synonym of *Tylocephalum* at that time) replace *Tylocephalum pingue* as type species. Again, as mentioned above in the remarks on *Tetragonocephalum* and *Tetragonocephalum trygonis*, this constituted a nomenclatural error on the part of Southwell (1925). *Tylocephalum pingue* must remain the type of the genus by original monotypy. Pintner (1928) recognized that *Tylocephalum* and *Tetragonocephalum* were distinct genera and elucidated morphological features associated with *Tylocephalum* (in the broader sense) (*i.e.*, strongly craspedote with proglottids of "normal" length, and a non-glandular scolex). Baer (1948) presented a detailed history of the genus and its relationship to *Tetragonocephalum*. Because the type species of *Tylocephalum*, *T. pingue*, remained poorly known, Baer suggested it would be appropriate "to remove the type species of the genus *Tylocephalum*, *T. pingue*, from the nomenclature" [loosely translated, p. 73] because this species is impossible to recognize by its scolex alone and has not been seen since its original description. However, this action would orphan the other species in the genus as it would leave them without a generic name. This too, was a nomenclatural unsound suggestion. Euzet and Combes (1965) came to a similar conclusion about the uncertain identity of *Tylocephalum* as had Baer (1948). However, several authors considered *Tylocephalum* to be a valid genus (*e.g.*, Hyman 1951; Wardle and McLeod 1952; Yamaguti 1959). Campbell and Williams (1984) brought the necessary clarity to the "identity crisis" of *Tylocephalum*. They argued that the type of *Tylocephalum* was indeed lost and designated a neotype for *Tylocephalum pingue*, based on new material they collected from the type host close to the type locality. In addition, Campbell and Williams (1984) redescribed *T. pingue* based on this new material and presented an emended generic diagnosis for *Tylocephalum*, for the first time including information on proglottid anatomy. Euzet (1994b) recognized *Tylocephalum* and *Tetragonocephalum* as distinct and placed both in the family Tetragonocephalidae. Most recently, Ivanov and Campbell (2000) listed the species that should be recognized in *Tylocephalum* and emended the generic diagnosis to include their new species, *Tylocephalum brooksi*. Admittedly, the account of *Tylocephalum* presented above is abbreviated. The potential affinities of *Tylocephalum* to *Cephalobothrium* have been ignored here. More detailed information on the relationship between these two genera was presented by Pintner (1928), Perrenoud (1931), Baer (1948), and, most recently, by Campbell and Williams (1984).

Several comprehensive diagnoses of *Tylocephalum* exist in the literature (*e.g.*, Yamaguti 1959; Campbell and Williams 1984; Euzet 1994b; Ivanov and Campbell 2000). These diagnoses are generally consistent with one another and with the diagnosis presented here. The generic diagnosis presented above has been modified from Campbell and Williams (1984) because it is most comprehensive and best reflects the current concept of the genus. To accommodate the new species of *Tylocephalum* described below, the only emendation incorporated was that *Tylocephalum* is now considered to possess either an unarmed or armed cirrus.

One species name, *Tylocephalum mehdii*, is considered to be a *nomen nudum*. This name was used only in a list of cestode parasites collected from the west coast of Maharashtra, India by Mohekar *et al.* (2002); no authority or literature citation was given. It appears that this species was never formally described. Therefore, the name, *Tylocephalum mehdii*, should be considered to be not available.

Tylocephalum pingue Linton, 1890
TYPE SPECIES
(Figs. 56-57)

Synonyms: None.

Type host: "*Rhinoptera quadriloba*" (= *Rhinoptera bonasus* [Mitchill, 1815] ?), Cownose ray (Rhinopteridae, Myliobatiformes).

Additional hosts: None.

Site of infection: Spiral intestine.

Type locality: Woods Hole, Massachusetts, U.S.A. (Fig. 56).

Additional localities: Sakonnet Point, Rhode Island and Chesapeake Bay, Virginia, U.S.A.

Number of specimens on which the original description was based: One (immature).

Type specimens: Neotype (USNPC No. 77631) and paraneotypes (USNPC No. 77632, BMNH No. 1984.6.11.1-2, and at HWML) deposited by Campbell and Williams (1984); (type specimens not indicated in original description).

Voucher specimens: None.

Material examined: USNPC No. 77631 (neotype); USNPC No. 77632 (paraneotype); USNPC No. 36053 (voucher, "T. pingue"); USNPC No. 35865 (voucher, "T. pingue").

Etymology: *pinguis*, L., fat.

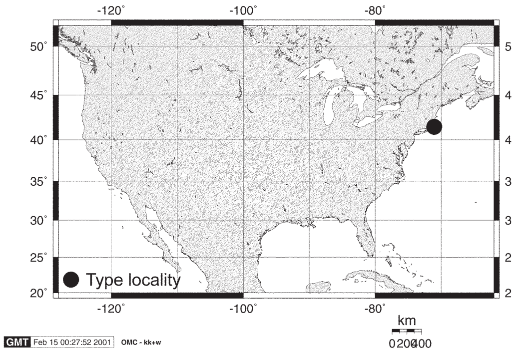


Fig. 56. Geographic distribution of *Tylocephalum pingue* Linton, 1890.

Chronology

Linton (1890): describes *Tylocephalum pingue* as type species of the new genus *Tylocephalum* based on one small cestode specimen that lacks costae and possesses a supplementary disc; proposes close relationship to *Discocephalum*; a brief diagnosis of the genus is presented and the species (based on one immature specimen) is described in some detail including some measurements on the living and fixed specimen.

Braun (1894-1900): recognizes *Tylocephalum pingue* Linton as the type species of the genus *Tylocephalum* Linton in the family Lecanicephalidae (*fam. inq.* = Gamobothriidae), order Tetraphyllidea.

Perrier (1897): recognizes *Tylocephalum* (including *T. pingue* from *Rhinoptera quadriloba*) as one of four genera in the family Gamobothriidae, order Tetracestoda (along with *Lecanicephalum*, *Discocephalum*, and *Sciadocephalus*).

Linton (1901): indicates one previous instance of *Tylocephalum pingue* being collected in the Woods Hole region from *Rhinoptera bonasus*.

Stiles and Hassall (1912): *Tylocephalum* Linton, 1890 (Tetrabothriidae, Phyllobothriidae): Linton (1901) and Braun (1895 and 1900); among others, *T. pingue* Linton, 1890 (in *Rhinoptera quadriloba*, Woods Hole): Linton (1901) (in *R. bonasus*) and Braun (1900).

MacCallum (1921): reports *Tylocephalum pingue* from *Aetobatus narinari* from Singapore; includes description and illustrations [deposited specimens at USNPC].

Southwell (1925): states that, since Linton based the genus on a single immature specimen he called *T. pingue*, which is unrecognizable and may be identical to any of the species of *Tylocephalum*, the next species described (*T. trygonis* from *Trygon walga*) should become the type species; includes six species (not *T. pingue*) and three doubtful species.

Poche (1926): comments that *Tylocephalum pingue* cannot be replaced by *T. trygonis* as new type species as suggested by Southwell (1925); considers it likely that the type of *T. pingue* may still exist or that the species is recollected; retains *Tetragonocephalum* as a synonym of *Tylocephalum*.

Woodland (1927): does not include *Tylocephalum* as a "lecanicephalid" genus in the family Phyllobothriidae, order Tetraphyllidea, because not enough is known about the type species, whether it be *T. pingue* or *T. trygonis*.

Pintner (1928): creates two groups of lecanicephalideans, family Lecanicephalidae (A) including *Tylocephalum uarnaki* [sic] (= *trygonis*?), possibly *Tylocephalum minutum*, possibly *Lecanicephalum peltatum*, even *Parataenia medusia*, *Polypocephalus medusia*, separate from *Polypocephalus radiatus*, with non-glandular scolex, bilobed uterus, acraspedote proglottids, and the family Cephalobothriidae (B) including *Cephalobothrium*, *Tylocephalum dierama*, *T. kuhli*, *T. ludificans*, *T. yorkei*, *T. translucens*, *T. aetiobatidis*, *Adelobothrium*, *Tylocephalum pingue*, with glandular scolex, craspedote proglottids.

Southwell (1930): justifies why *Tylocephalum trygonis* [originally described as *Tetragonocephalum trygonis*] should be considered the type species of the genus over *Tylocephalum pingue*.

Linton (1938): illustrates scolex of *Tylocephalum pingue*.

Baer (1948): gives history of the genus *Tylocephalum* as it relates to *Tetragonocephalum*; says that *Tylocephalum* currently contains 11 species [actually 12 in his paper], and possibly *Kystocephalus translucens*; concludes that *T. ludificans*, *T. minus*, and *T. margaritifera* [sic] are species known form larvae only and should be considered *nomina nuda*; suggests "to remove the type species of the genus *Tylocephalum*, *T. pingue*, from the nomenclature because it is impossible to recognize and has not been seen since its original description" [loosely translated], resulting in a "disappearance" of the genus; notes that even though Southwell (1925) suggested *T. trygonis* as the type species of *Tylocephalum* to replace *T. pingue*, *Tetragonocephalum* must be resurrected.

Wardle and McLeod (1952): recognize *T. pingue* Linton, 1890 as the type species of *Tylocephalum* Linton, 1890.

Yamaguti (1959): recognizes *Tylocephalum pingue* Linton, 1890 as type species of *Tylocephalum* Linton, 1890 (syn. *Kystocephalus* Shipley and Hornell, 1906, *Aphanobothrium* Seurat, 1906).

Euzet and Combes (1965): review the history of *Tylocephalum*, and address the species included in the genus; reject *Tylocephalum* in favor of *Tetragonocephalum* because the latter has priority; emphasize that since "*T. trygonis*" [genus is unclear] had been indicated previously as the type of the genus *Tetragonocephalum* it cannot be made the type species of *Tylocephalum* as suggested by some authors; agree with Baer's (1948) decision about "removing" *T. pingue* from the nomenclature.

Shinde (1976): redescribes *Tylocephalum pingue* from one specimen collected from *Trygon* sp. from Ratnagiri, India; notes three differences between his material and the species described by Linton (1890): neck present, neck same width as scolex, ovary bilobed (vs. transverse band); notes that this is the first report of this species from India.

Zaidi and Khan (1976): transfer the species belonging to the *Tylocephalum* group "B" in Pintner (1928) to the genus *Cephalobothrium* (*i.e.*, *Cephalobothrium*, *Tylocephalum dierama*, *T. kuhli*, *T. ludificans*, *T. yorkei*, *T. translucens*, *T. aetiobatidis*, *Adelobothrium*, *Tylocephalum pingue*?).

Campbell and Williams (1984): review history of *Tylocephalum pingue* Linton, 1890; recognize *T. pingue* as the type species described based on scolex morphology only; note that no type specimens seem to exist; redescribe the species based on 24 specimens of newly collected material; designate a neotype for *T. pingue* and justify this action (consistent with the original description of Linton and other authors' perception of the genus); describe the proglottid anatomy in great detail; emend the diagnosis of *Tylocephalum* Linton, 1890, listing *Rhinoptera bonasus* as the type host and Woods Hole as the type locality, and Sakonnet Point, RI and Chesapeake Bay as additional localities; note that MacCallum deposited several specimens of *T. pingue* (USNPC 35865, USNPC 56053 [= 36053?] and material from a cownose ray at the New England Aquarium dated 1914), all not consistent with the description of *T. pingue*.

Schmidt (1986): transfers *Tylocephalum pinguis* [sic] Linton, 1890 to *Lecanicephalum* creating the new combination *Lecanicephalum pinguis* [sic] (Linton, 1890); *L. pinguis* [sic] is one of 19 species of *Lecanicephalum* recognized.

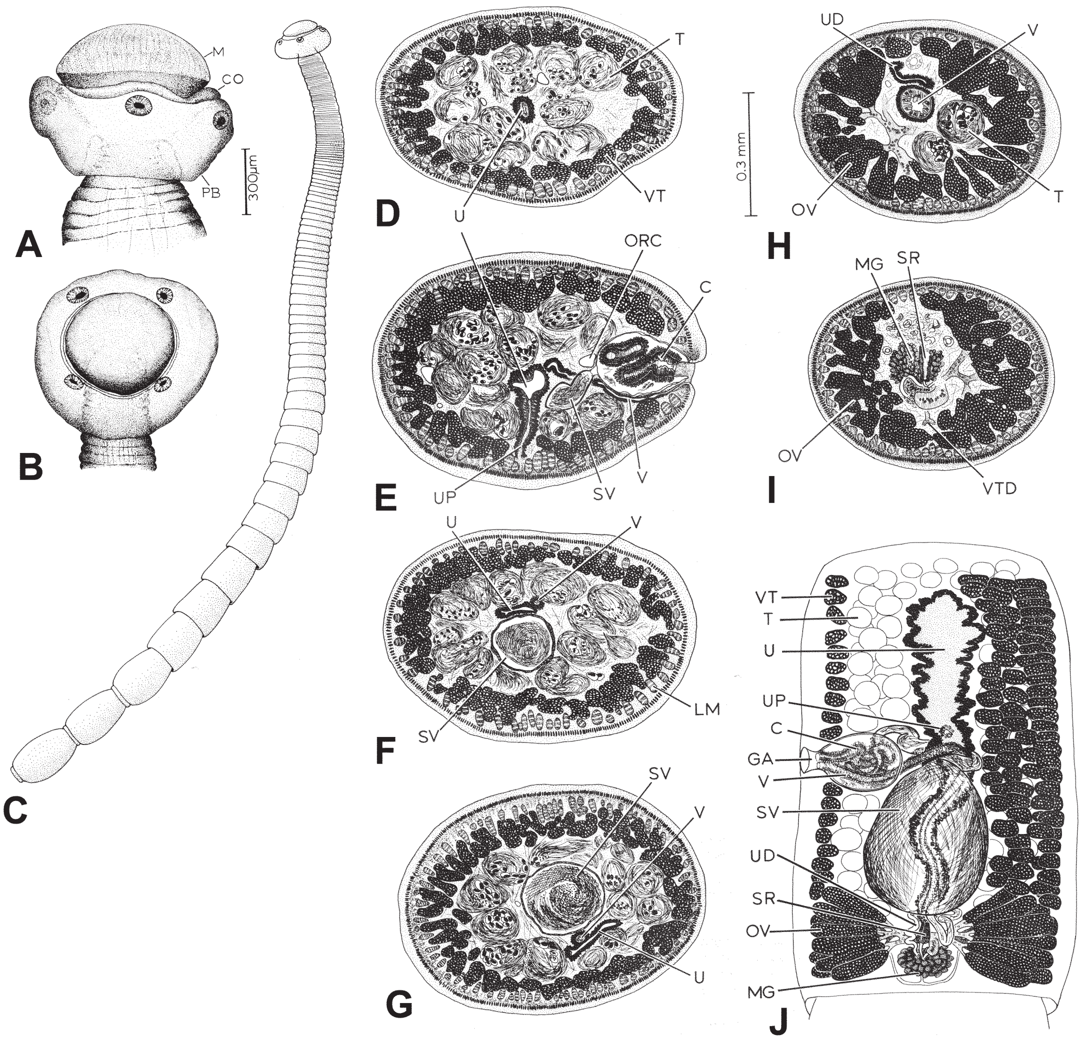


Fig. 57. A-J. Line drawings of *Tylocephalum pingue* Linton, 1890. A. Scolex, dorsoventral view. B. Scolex, apical view. C. Entire worm. D. Transverse section anterior to cirrus sac. E. Transverse section at level of genital atrium. F. Transverse section just posterior to cirrus sac. G. Transverse section just anterior to ovary. H. Transverse section just anterior to ovarian isthmus. I. Transverse section through ootype complex. J. Schematic diagram of reproductive system (dorsal view) reconstructed from frontal and transverse serial sections. (Taken from Campbell and Williams [1984], with slight modification. Copyright 1984, The Helminthological Society of Washington. Used with permission.)

Ivanov and Campbell (2000): recognize *Tylocephalum pingue* as type species of *Tylocephalum*; consider the species to be of the "*Tylocephalum*"-type, that is, with craspedote strobila, testes anterior to ovary, shallow genital atrium and saccate uterus, distinct from the "*Tetragonocephalum*" type.

Remarks

Because the taxonomic history of the genus *Tylocephalum* was so intimately tied to the identity of its type species *Tylocephalum pingue*, the reader is referred to the remarks section of the genus presented above. In summary, because its description was based on a single immature specimen, type material was lacking and the species had not been reported for almost a century, *T. pingue* was redescribed from newly collected material from the type host and close to the type locality by Campbell and Williams (1984). This redescription was based on neotype material they deposited.

Specimens identified as *T. pingue* had been deposited by MacCallum in the U.S. Parasite Collection in Beltsville Maryland, U.S.A. (USNPC Nos. 36053 and 35865). However, as was articulated in detail by Campbell and Williams (1984), these specimens are not conspecific (in one case not even congeneric) with *T. pingue*.

Tylocephalum koenneckeorum Jensen, n. sp.

(Figs. 58-60)

Synonyms: None.

Type host: *Rhynchobatus australiae* Whitley, 1939, Whitespotted wedgefish (Rhinidae, Rhinobatiformes).

Additional hosts: None.

Site of infection: Spiral intestine.

Type locality: east of Wessel Islands (10°30'S 136°43'E), Arafura Sea, Australia (Fig. 58).

Additional localities: None.

Number of specimens on which the original description was based: 22 (20 whole mounts, one proglottid cross-section series, and one specimen prepared for SEM).

Type specimens: Holotype (QM No. G 222924), six paratypes (five whole mounts and one proglottid cross-section series) (QM Nos. G 222925-222930); five paratypes (USNPC No. 94582); three paratypes (KUNHM Nos. 002126-002128); six paratypes (six whole mounts) (LRP Nos. 3331-3336); one paratype specimen prepared for SEM (LRP).

Voucher specimens: None.

Etymology: This species is named in honor of Barbara and Brian Koennecke, who assisted J. N. Caira and the author with collections of elasmobranchs for part of our 1999 expedition to Nhulunbuy-Gove, Australia, during which this species was collected.

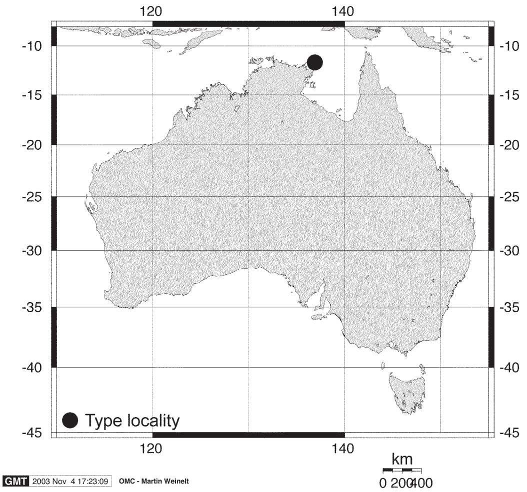


Fig. 58. Geographic distribution of *Tylocephalum koenneckeorum* Jensen, n. sp.

Description (Based on 20 whole mounts, one proglottid cross-section series, and one specimen prepared for SEM.) Note: Measurements of cirrus sac, ovary, genital pore positon and vitelline follicles are taken from two posterior-most mature proglottids only.

Worms 4,443-14,116 (8,014 ± 2,487; 20) long; maximum width at scolex; 27-80 (47 ± 12.0; 20) proglottids, euapolytic. Scolex 102-143 (123 ± 10.6; 17) long by 178-262 (215 ± 22.8; 19) wide, bearing four acetabula and apical organ. Acetabula sucker-like in form, 25-38 (31 ± 4.0; 19; 36) long by 27-46 (36 ± 4.9; 20; 40) wide. Apical modification of scolex proper essentially absent. Apical organ large, globular, conspicuously muscular, non-invaginable, non-retractable, with glandular surface.

Scolex proper covered with pointed filitriches (Fig. 60C). Surface of apical organ covered with tubercles, suggesting glandular surface (Fig. 60B). Strobila covered with long filitriches (Fig. 60D).

Cephalic peduncle absent. Proglottids craspedote, non-laciniate, overlap of adjacent proglottids 3-13% (6 ± 2.5; 20; 58) of proglottid length. Immature proglottids 24-69 (41 ± 10.4; 20) in number, initially wider than long, 22-37% (29 ± 4.1; 20) of total number of proglottids longer than wide; two most posterior immature proglottids 213-498 (368 ± 71.0; 20; 40) long by 110-200 (158 ± 23.1; 20; 40) wide. Mature proglottids 3-11 (6 ± 2.0; 20) in number, two most posterior mature proglottids 615-1,646 (1,206 ± 252.1; 20; 40) long by 116-228 (174 ± 26.7; 20; 40) wide. Gravid proglottids not observed. Testes 31-43 (37 ± 3.0; 20; 35) in number, 26-53 (42 ± 5.2; 20; 98) long by 22-61 (43 ± 8.2; 20; 98) wide, extending from anterior margin of proglottid to ovary, slightly overlapping anterior margins of ovary, 2-3 columns in dorso-ventral view, two rows deep in cross-section (Fig. 59F). Vas deferens extending along median line of proglottid (sublaterally in less mature proglottids) from ootype to cirrus sac, entering cirrus sac at distal end; vas deferens in fully mature proglottids extensive, forming external seminal vesicle at its posterior extent. Internal seminal vesicle absent. Cirrus sac pyriform, bent and oriented anteriorly, 88-186 (142 ± 23.1; 20; 36) long by 63-128 (91 ± 14.7; 20; 36) wide, containing coiled cirrus. Cirrus armed. Ovary H-shaped in dorso-ventral view, each side consisting of lobes radiating from ovarian bridge, bilobed in cross-section (Fig. 59G), 110-333 (218 ± 56.7; 20; 38) long by 86-165 (117 ± 20.5; 20; 38) wide. Vagina extending along median line of proglottid (somewhat sublaterally) from ootype to genital pore, opening into genital atrium posterior to cirrus sac; vaginal sphincter absent. Genital pores lateral, irregularly alternating, 59-73% (64 ± 2.7; 20; 40) of proglottid length from posterior end. Uterus saccate, extending along median line of proglottid from near ootype to anterior margin of proglottid; uterine duct not observed; uterine pore absent. Vitellaria follicular, medullary, in lateral columns, 2-4 vitelline follicles on each side of proglottid in cross-section (Fig. 59F), extending entire length of proglottid, interrupted by ovary, slightly overlapping anterior margins of ovary, vitelline follicles 19-59 (32 ± 8.1; 20; 100) long by 28-77 (47 ± 10.0; 20; 100) wide. Greater than two pairs of excretory ducts. Eggs not observed.

Remarks Note: Dimensions are given as length by ("x") width.

In this study, 11 species of *Tylocephalum* are recognized (see Appendix 2); *Tylocephalum koenneckeorum* is distinguished from each species below. It differs from *T. campanulatum*, *T. elongatum*, and *T. yorkei* based on its shorter total length (4-14 mm vs. 29-62 mm, up to 95 mm, and 8 cm, respectively). In addition, *Tylocephalum koenneckeorum* possesses fewer proglottids than *T. campanulatum* and *T. elongatum* (27-80 vs. 150-594 and greater than 400, respectively). It can further be distinguished from *T. yorkei* in its possession of a genital pore in the anterior half of the proglottid, rather than in the posterior half. The scolex of *Tylocephalum koenneckeorum* (102-143 x 178-262) is significantly smaller than that of *T. brooksi* (715-986 x 486-650), *T. pingue sensu* Linton (1890) (1160 long), or *T. rhinobatii* (400-420 x 260-410). In addition, *T. koenneckeorum* differs from *T. pingue sensu* Campbell and Williams (1984), *T. bonasum*, and *T. pandurangi* in possessing fewer testes (31-43 vs. 68-93, 53-62, and 110-120, respectively). *Tylocephalum koenneckeorum* can be further distinguished from *T. pandurangi* in possessing a smaller ovary (110-333 x 86-165 vs. 530 x 190). No gravid proglottids were observed and testes are in 2-3 columns in *Tylocephalum koenneckeorum*, whereas gravid proglottids are present in *T. singhii*, and testes are in 4-6 columns. *Tylocephalum koenneckeorum* can be distinguished from *T. marsupium* (measurements *sensu* Campbell and Williams 1984) based on the fact that the former species possesses almost half as many testes (31-43 vs. 60-74) and its proglottids do not overlap the following ones 75% of their length (1-13% in *T. koenneckeorum*). *Tylocephalum koenneckeorum* is most similar to *T. squatinae*. However, in *T. koenneckeorum*, the vitelline follicles are in lateral columns that do not encroach on the median line of the proglottid, and are interrupted by the ovary, whereas in *T. squatinae* the vitelline follicles encroach on the median line of the proglottid and extend the entire length of the proglottid without interruption by the ovary. *Tylocephalum koenneckeorum* can be further distinguished from *T. squatinae* in its posses-

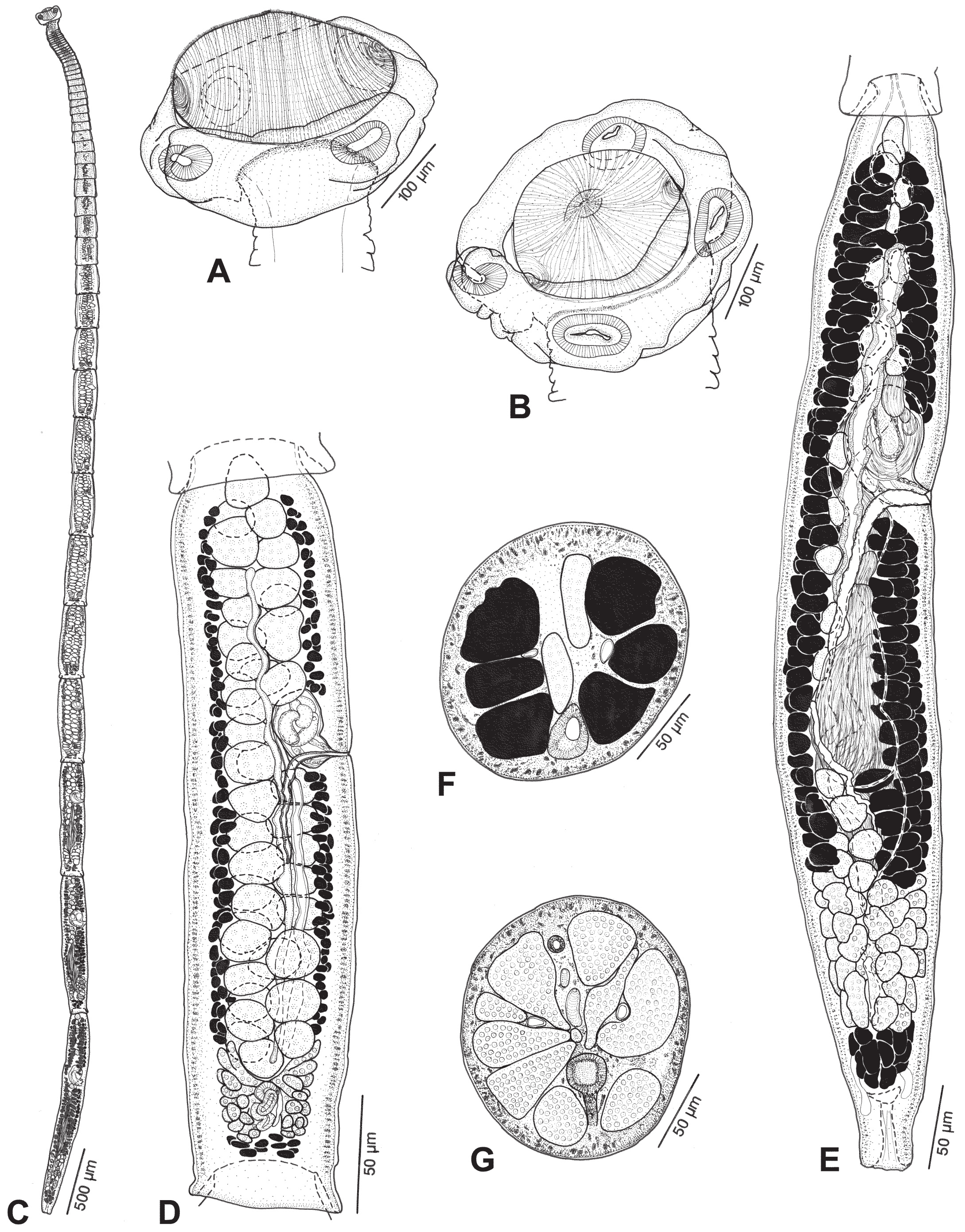


Fig. 59. A-G. Line drawings of *Tylocephalum koenneckeorum* Jensen, n. sp. A. Scolex, lateral view (QM No. G 222925). B. Scolex, apical view (LRP No. 3335). C. Whole worm (holotype, QM No. G 222924). D. Early mature proglottid (QM No. G 222926). E. Mature terminal proglottid (USNPC No. 94582). F. Cross-section through mature proglottid anterior to genital pore (QM No. G 222930). G. Cross-section through mature proglottid at level of ovary (QM No. G 222930).

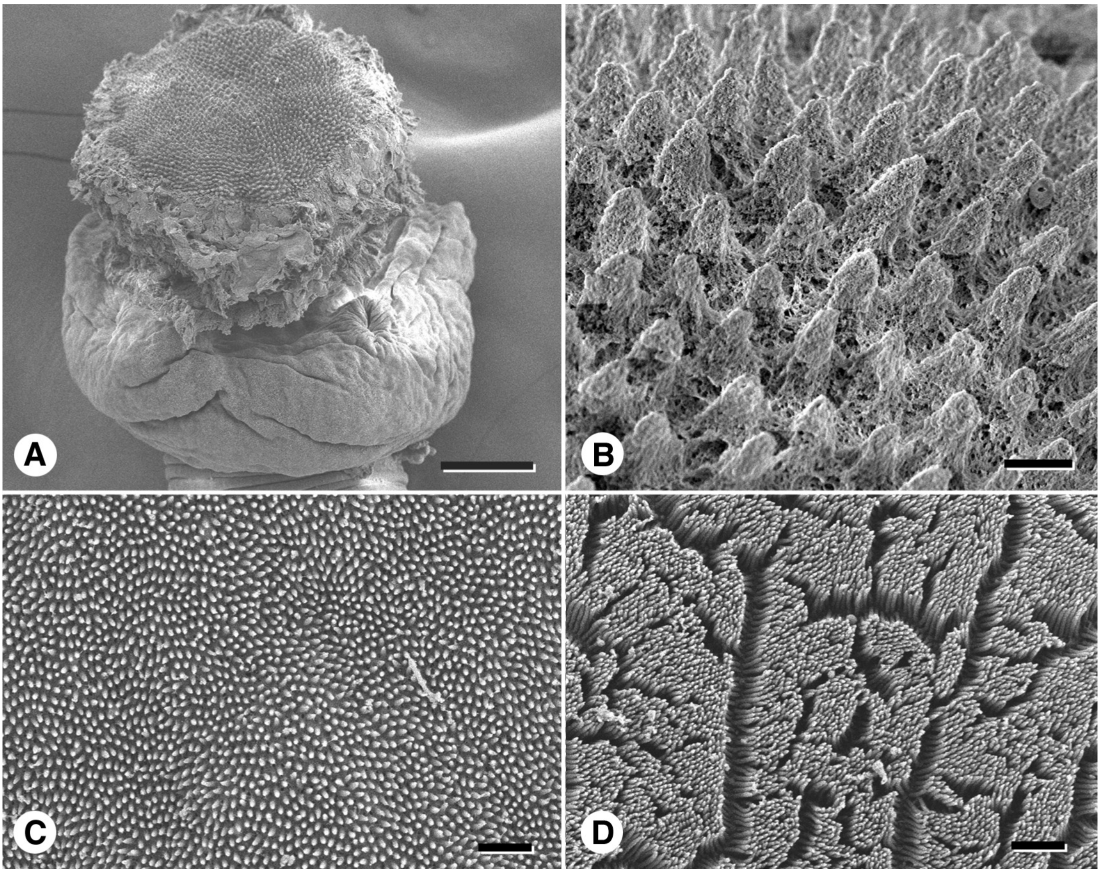


Fig. 60. A-D. Scanning electron micrographs of *Tylocephalum koenneckeorum* Jensen, n. sp. A. Scolex. B. Surface of apical organ. C. Microtriches on surface of scolex proper. D. Microtriches on surface of strobila. Scale bars: A, 50 µm; B, 2.5 µm; C and D, 1 µm.

sion of more elongate proglottids and a cirrus sac that extends across half the width of the proglottid, rather than squarish proglottids and a cirrus sac that extends across a third the width of the proglottid.

General discussion

This study revealed remarkable generic diversity within the Lecanicephalidea. As a result of collections of specimens representing new genera and collections of specimens representing existing genera that were poorly known and that had not been seen in almost a century, the number of valid lecanicephalidean genera has increased from five (Euzet 1994b) to 12. This number is expected to rise to as high as 21 if the nine genera categorized here as *genera inquirenda* are determined to be valid. Additionally, three known species (*Discobothrium myliobatidis*, *Lecanicephalum xiamenensis* Yang, Lui and Lin, 1995, and *Tenia* [sic] *narinari*) appear to belong to two, as of yet undescribed genera (see Appendix 2); and among the newly collected material, examples of at least two additional new genera have been found.

The new collections made as part of this study resulted in material representing a large number of species new to science, only a small subset of which has been described here. The genus *Polypocephalus* is by far the most specious lecanicephalidean genus, with 26 valid species. This genus is followed by *Tetragonocephalum* and *Tylocephalum* with

14 and 12 species, respectively. The number of species in the remaining nine valid genera collectively total 20 (see Appendix 2).

An interesting phenomenon, which has already been documented for a number of other elasmobranch tapeworm genera in the Diphyllidea (*e.g.*, Tyler and Caira 1999) and the Tetraphyllidea (Caira 1992; Nasin *et al.* 1997; Ghoshroy and Caira 2001; Olson and Caira 2001; Caira and Tracy 2002), is the occurrence of multiple congeners in the same host species. This phenomenon was encountered here, quite routinely, in the Lecanicephalidea. Two or more species in six of the nine non-monotypic genera of lecanicephalideans (*i.e.*, *Healyum*, *Hornellobothrium*, *Lecanicephalum*, *Polypocephalus*, *Tetragonocephalum*, and *Tylocephalum*) have been found co-occurring in a single host species. A comprehensive species-level analysis is necessary to determine wether these co-occurring congeners are actually sister taxa.

Apart from the unexpected diversity of lecanicephalideans, new collections further revealed considerable morphological disparity. Histology and SEM suggest that, in particular, the "apical organ" of the scolex, characteristic of almost all lecanicephalideans, is an amazingly complex attachment structure. It can exhibit a combination of muscles, glands and surface features, such as microtriches, and is worthy of significant attention. However, evidence is beginning to accumulate that suggests that not all lecanicephalidean taxa possess such an apical structure. This evidence therefore calls into question a feature that has previously been considered by many authors (*e.g.*, Yamaguti 1959; Schmidt 1986; Euzet 1994b) to be diagnostic for lecanicephalideans. Detailed studies are needed of this and other "diagnostic" features (*e.g.*, four acetabula, a vagina that opens into the genital atrium posterior to the opening of the cirrus sac) of the elasmobranch cestodes known as lecanicephalideans.

Unless a global synapomorphy can be identified, the monophyly of the Lecanicephalidea will be in question. As mentioned earlier, the traditional diagnostic features (presence of an apical structure on the scolex with four sucker-like acetabula, and a vagina that opens into the genital atrium posterior to the cirrus sac) present merely a unique combination of non-unique characters, and, as has been shown in this study, are not present in all species. While a number of highly unusual (and possibly unique) characters were found in different subsets of lecanicephalidean species (*e.g.*, relatively few, large vitelline follicles, a ring-shaped or trilobed ovary in cross-section, relatively few testes in a single column), characters unique to the lecanicephalideans are not immediately apparent. In this study much effort was deticated to attempting to identify one or more synapomorphies for the Lecanicephalidea. Data collected from the disparate suite of taxa examined here using light microscopy (of whole mounts and histological sections) represent a number of useful, potentially synapomorphic, diagnostic characters for the lecanicephalideans. These include basic features of the male reproductive system (*e.g.*, the presence of the vas deferens or external seminal vesicle originating at the level of the ootype region and extending the length of the proglottid to the cirrus sac), as well as several features of the scolex, such as acetabula sucker-like or bothridiate in form, always facially unmodified (*i.e.*, lacking accessory suckers, facial loculi, marginal loculi, etc.). However, most intriguing was a character discovered using SEM. The majority of the lecanicephalidean taxa examined here exhibited a form of microthrix that was not observed in any of the over 80 species of tetraphyllideans and other outgroup taxa examined using SEM by Caira *et al.* (1999, 2001). This microthrix form is illustrated in Caira *et al.* (1999, fig. 83) and described as the "long, pointed filiform" microthrix type (p. 127). Caira *et al.* (1999), however, coded this feature for their phylogenetic analysis as a 'regular' long filiform microthrix. This was despite the fact that the length to width ratio of this microthrix form was not nearly as great as that seen in the truly long filitriches on the strobilar surface of most tetraphyllidean and lecanicephalidean species (*e.g.*, see Figs. 25J and 60D). In addition, this microthrix form tapers gradually in width along its entire length, as opposed to being constant in width long its length but with an acuminate apex. Because of these obvious differences, this microthrix form was coded in the analyses in the present study as a unique character state (*e.g.*, see characters 22, 24, 26, 28). Perhaps most interesting is the fact that all lecanicephalidean species included in the analysis for which SEM data were available, whether or not they possessed an apical structure, exhibited this form of microthrix somewhere on the external surfaces of the body. It would be most informative to conduct a detailed comparison of these two microthrix forms, that is the shorter, pointed microthrix form and the longer, 'regular' form, using transmission electron microscopy.

Key to lecanicephalidean genera

1(a) Anterior region of strobila laterally expanded **2**
1(b) Anterior region of strobila unmodified **3**

2(a) Anterior region of strobila forming trough; vagina absent.. ***Eniochobothrium***
2(b) Anterior region of strobila wide; vagina present............***Hornellobothrium***

3(a) Apical structure on scolex absent **4**
3(b) Apical structure on scolex present **5**

4(a) Entire scolex conspicuously covered with large spiniform microtriches; ovary tetralobed in cross-section ....***Aberrapex***
4(b) Scolex not conspicuously covered with large spiniform microtriches; ovary bilobed in cross-section.. .***Paraberrapex***

5(a) Apical organ divided into tentacles.....................................***Polypocephalus***
5(b) Apical organ undivided **6**

6(a) Ovary consisting of three lobes (in dorso-ventral view); with fewer than six pairs of vitelline follicles on each side of proglottid **7**
6(b) Ovary H-shaped or oval (in dorsoventral view) (not refering to shape of individual lobes, but rather shape of entire ovary); with six or more vitelline follicles on each side of proglottid **9**

7(a) Acetabula bothridiate in form, diamond-shaped.........***Quadcuspibothrium***
7(b) Acetabula in form of simple suckers **8**

8(a) Apical organ internal, small, inconspicuous; worms less than 1 mm in total length.. .**Healyum**
8(b) Apical organ large, in form of prominent corrugated sucker; worms greater than 1.9 mm in total length ....***Corrugatocephalum***

9(a) Vitelline follicles lacking anterior to cirrus sac...........................***Anteropora***
9(b) Vitelline follicles present anterior to cirrus sac **10**

10(a) Expanded genital atrium present; postporal testes absent ....***Tetragonocephalum***
10(b) Expanded genital atrium absent; postporal testes present.......................... **11**

11(a) Apical organ in form of muscular and glandular sheet, completely retractable into scolex proper, with cnspicuous circular muscle bundle; vagina conspicuously expanded and muscular ....***Lecanicephalum***
11(b) Apical organ in form of conspicuous muscular cushion; vagina not conspicously expanded or muscular ....***Tylocephalum***

PHYLOGENETIC RELATIONSHIPS

Selection of Taxa

The phylogenetic analyses were conducted using species as terminal taxa. A total of 18 lecanicephalidean species was included in the analyses. The primary goal was to include at least one representative of each of the 12 valid lecanicephalidean genera. All known species were included for six of the 12 genera, *i.e.*, the monotypic genera *Corrugatocephalum*, *Paraberrapex*, and *Quadcuspibothrium*, and the ditypic genera *Aberrapex*, *Healyum*, and *Lecanicephalum*. Only a single species was included for the genera *Eniochobothrium*, *Hornellobothrium*, and *Tetragonocephalum*. Two species each were included for the remaining three genera (*i.e.*, *Anteropora*, *Polypocephalus*, and *Tylocephalum*). In summary, of the 18 species included, seven are type species and 11 are additional species. Because of the completeness of the available material, and consequently of the data, inclusion of new species was given priority over inclusion of existing non-type species. Species included in the analyses were restricted to those treated in detail in the taxonomic section of this study.

To ensure the accuracy of the data, coding was done from actual specimens, rather than from accounts in the literature. In all cases, the specimens used for coding consisted of type material for the species in question. In a few cases, in which only one or two specimens were available (*e.g.*, *Polypocephalus saoudi* and *Tylocephalum pingue*), information given in the original description was used as a source of supplemental information.

Selection of Characters

The character list generated by Caira *et al.* (1999), as slightly modified and expanded two years later (Caira *et al.* 2001), served as the framework for the character list used in the phylogenetic analyses conducted in the present study. Because of the more restricted taxonomic focus of this study, a subset of characters of the Caira *et al.* (2001) list was selected. These characters were reassessed and modified to apply to the taxa included here. The characters consisted of features observed from examination of whole mounts, histological sections, and with SEM. A total of 64 characters was assembled (Table 2). Of these 64 characters, 19 involve features associated with the scolex (characters 1-19) and 33 features associated with the strobila (characters 20 and 33-64), all observed with light microscopy. The remaining 12 characters (characters 21-32) describe the microthrix patterns seen on a variety of surfaces of the scolex and strobila; these can be observed only with the aid of scanning electron microscopy.

Character States and Character Coding

An attempt was made to articulate binary characters. However, in cases in which this was not possible, multistate characters were generated and the multiple states of the character were treated as unordered in all analyses. Of the 64 characters generated, 20 were binary, 25 characters had three states, and 19 characters had four states. In the cases of a few of the 4-state characters, especially the microthrix characters, not all four states were used in coding for the taxa included (see, *e.g.*, Character 22). However, the unused states appear in the character list for consistency, so that microtriches of the same form were given the same coding regardless of the surface on which they were found. The numbering of the character states does not imply polarity. A clear distinction was made between polymorphic, unknown, and inapplicable character codings. A polymorphic coding was used only in cases in which two character states of the same character were observed to be present in the same taxon. An unknown character coding ("?") was used if the character could not be coded because of physical or optical limitations. For example, specimens were unavailable for examination with SEM for *Anteropora japonica*, *Lecani-*

Table 2. Character list.

NO.	CHARACTER
1	Configuration of scolex: 0=undivided; 1=4 stalks.
2	Apical modification of scolex proper (in adult): 0=absent; 1=present.
3	Aperture on apical modification of scolex proper: 0=absent; 1=present; 9=N/A.
4	Opening of aperture on apical modification of scolex proper: 0=not changeable in diameter; 1=changeable in diameter; 9=N/A.
5	Apical organ on scolex: 0=absent; 1=present.
6	Association of apical organ with scolex proper: 0=embedded; 1=partially connected; 9=N/A.
7	Internal glandularity of apical organ: 0=nonglandular; 1=glandular throughout; 2=glandular at base; 9=N/A.
8	Glandular papillae on surface of apical organ: 0=absent; 1=present; 9=N/A.
9	Muscularity of apical organ: 0=nonmuscular; 1=individual muscule strands; 2=conspicuous muscular organ; 9=N/A.
10	Aperture on apical organ: 0=absent; 1=present; 9=N/A.
11	Retraction of apical organ into scolex proper: 0=non-retractable; 1=retractable into scolex proper; 9=N/A.
12	Invagination of apical organ into scolex proper: 0=non-invaginable; 1=invaginable; 9=N/A.
13	Rings of circular muscles in apical organ: 0=absent; 1=present; 9=N/A.
14	Apical organ tentacles: 0=absent; 1=present; 9=N/A.
15	Acetabular form: 0=sucker-like; 1=bothridiate.
16	Acetabular attachment: 0=completely sessile; 1=free posteriorly only; 2=free both anteriorly and posteriorly.
17	Facial acetabular modifications: 0=absent; 1=present.
18	Pointed extensions on margins of acetabulum: 0=absent; 1=present.
19	Cephalic peduncle: 0=absent; 1=with inconspicuous posterior boundary; 2=with conspicuous posterior boundary.
20	Modification of anterior segments: 0=absent; 1=laterally expanded; 2=forming a suctorial trough.
21	Spinitriches on scolex proper: 0=absent; 1=pointed blade-like; 2=round blade-like; 3=tridentate.
22	Filitriches on scolex proper: 0=absent; 1=short; 2=long; 3=medium and tapering along length (pointed).
23	Spinitriches on modified apex of scolex proper: 0=absent; 1=pointed blade-like; 2=round blade-like; 3=tridentate; 9=N/A.
24	Filitriches on modified apex of scolex proper: 0=absent; 1=short; 2=long; 3=medium and tapering along length (pointed); 9=N/A.
25	Spinitriches on distal acetabular surface: 0=absent; 1=pointed blade-like; 2=round blade-like; 3=tridentate; 9=N/A.
26	Filitriches on distal acetabular surface: 0=absent; 1=short; 2=long; 3=medium and tapering along length (pointed); 9=N/A.
27	Spinitriches on proximal acetabular surface: 0=absent; 1=pointed blade-like; 2=round blade-like; 3=tridentate; 9=N/A.
28	Filitriches on proximal acetabular surface: 0=absent; 1=short; 2=long; 3=medium and tapering along length (pointed); 9=N/A.
29	Spinitriches on stalks: 0=absent; 1=pointed blade-like; 2=round blade-like; 3=tridentate; 9=N/A.
30	Filitriches on stalks: 0=absent; 1=short; 2=long; 3=medium and tapering along its length (pointed); 9=N/A.
31	Spinitriches on strobila: 0=absent; 1=pointed blade-like; 2=round blade-like; 3=tridentate; 9=N/A.
32	Filitriches on strobila: 0=absent; 1=short; 2=long; 3=medium and tapering along length (pointed); 9=N/A.
33	Discrete longitudinal muscle bundles in proglottid cross-section: 0=absent; 1=present.
34	Proglottid margins 0=acraspedote; 1=craspedote only; 2=laciniate.
35	Proglottid apolysis: 0=anapolytic; 1=apolytic; 2=euapolytic; 3=hyperapolytic.
36	Posterior extent of primary field of testes: 0=not reaching ovary; 1=extending to, or overlapping with ovary.
37	Number of columns of testes anterior to cirrus sac in dorso-ventral view: 0=1; 1=2; 2=greater than 2.
38	Number of layers of testes in cross-section anterior to cirrus sac: 0=1; 1=greater than 1.
39	Position of vas deferens in relation to its exit from cirrus sac: 0=lateral and anterior; 1=posterior; 2=anterior, lateral and posterior; 3=lateral and posterior.
40	Vas deferens size: 0=minimal; 1=expanded duct; 2=expanded sac (*i.e.*, ESV).
41	Position of junction of proximal end of vas deferens : 0=near cirrus sac; 1= near ovarian bridge.
42	Internal seminal vesicle: 0=absent; 1=present.
43	Cirrus sac shape: 0=pyriform; 1=U-shaped; 2=cigar-shaped.
44	Cirrus sac orientation: 0=straight; 1=tilted anteriorly; 2=tilted posterioly.
45	Spinitriches on cirrus: 0=absent; 1=present.
46	Genital atrium: 0=minimal; 1=expanded to form large cavity; 2=recessed, with muscular pad.
47	Position of genital pore: 0=lateral; 1=sublateral.
48	Vagina: 0=absent; 1=present.
49	Position of opening of vagina relative to cirrus: 0=anterior to cirrus; 1=posterior to cirrus; 2=at same level; 9=N/A.
50	Position of vagina in proglottid: 0=medial; 1=lateral; 9=N/A.
51	Course of vagina: 0=straight; 1=sinuous; 9=N/A.
52	Seminal receptacle: 0=absent; 1=present.
53	Ovary shape in dorso-ventral view: 0=H; 1=trilobed; 2=oval.
54	Ovary shape in cross-section: 0=bilobed; 1=tetralobed; 2=trilobed; 3=ring.
55	Form of ovarian margins: 0=smooth; 1=lobulated.
56	Ovary left/right symmetry: 0=symmetrical; 1=asymmetrical.
57	Distribution of vitelline element(s): 0=lateral; 1=circumsegmental.
58	Number of lateral vitelline elements in cross-section: 0=2; 1=4; 2=greater than 4.
59	Anterior extent of vitelline elements in proglottid: 0=to anterior margin; 1=not reaching anterior margin; 2=not reaching gential pore.
60	Posterior extent of vitelline elements: 0=stopping at anterior margin of ovary; 1=extending to posterior margin of proglottid.
61	Lateral interruption of vitelline elements by ovary: 0=not interrupted; 1=interrupted; 9=N/A.
62	Anterior extent of uterus in mature proglottid: 0=extending approximately to anterior margin; 1=extending anterior to genital pore but not reaching anterior margin; 2=not extending anterior to genital pore.
63	Uterus shape: 0=vertically elongate sac; 1=anterio-posteriorly bissaccate.
64	Number of excretory ducts in cross-section: 0=2; 1=4; 2=greater than 4.

cephalum peltatum, *Polypocephalus saoudi*, and *Tylocephalum pingue*. These taxa, thus, received the bulk of the unknown ("?") codings and, as a consequence, their placement (in particular, because of higher percentage of unknown ["?"] character codings for microthrix characters) should be treated with caution. Despite elimination of characters that did not apply to lecanicephalideans, in general, several characters remained that were inapplicable to a subset of taxa included in these analyses (*e.g.*, apical organ characters in species lacking an apical organ). Species for which a character did not apply were coded with a distinct character state ("9") for this character.

Phylogenetic Analyses

Outgroup taxa were selected from among orders that have routinely been shown to be closely associated with the Lecanicephalidea, specifically, the orders Tetraphyllidea and Proteocephalidea (Caira *et al.* 1999, 2001; Olson and Caira 1999; Olson *et al*. 1999). A diverse assortment of species from these two orders was selected, primarily based on availability of specimens for study. Outgroup taxa chosen included two tetraphyllideans, one from each of the two major families, the Phyllobothriidae Braun, 1900 (unarmed, *i.e.*, lacking hooks) and the Onchobothriidae (armed, *i.e.*, possessing hooks). The phyllobothriid taxon was *Rhinebothrium corymbum* Campbell, 1975, coded from specimens collected from the Southern stingray, *Dasyatis americana* from the Gulf of Mexico off Florida, U.S.A. The onchobothriid taxon was *Acanthobothrium parviuncinatum* Young, 1956, coded from specimens collected from Haller's round ray, *Urobatis halleri* (Garman, 1863) from Puertecitos, Baja California, Mexico. In addition, two proteocephalidean species were used as outgroups. *Proteocephalus perplexus* La Rue, 1911 was coded from specimens collected from the Bowfin, *Amia calva* Linnaeus, 1766 from Hay Bay, Lake Ontario, Canada. Specimens were not examined for the second proteocephalidean outgroup species, *Euzetiella tetraphylliformis* de Chambrier, Rego and Vaucher, 1999. This species was coded from its original description (de Chambrier *et al*. 1999).

The full data matrix is shown in Table 3. All analyses were run using the phylogenetic analysis programs PAUP* 4.0b8 (Swofford 2002) on a 500MHz Macintosh PowerPC G3. In all analyses, all characters were given equal weight, multistate characters were treated as unordered, and the character state optimization setting Acctran was in effect. In all analyses, multiple states occurring in a single taxon (in all cases present in a single individual) were interpreted as "polymorphic." Because of the relatively low number of taxa, it was possible to perform all analyses detailed below under the Branch and Bound search routine. In each case, a strict consensus tree was generated for analyses resulting in more than one most parsimonious tree (MPT).

A. Effect of character exclusions

Five primary analyses were conducted including a total of 22 taxa (18 ingroup taxa and the four outgroup taxa) but varying the percentage of unknown ("?") character codings in the matrix by employing different character exclusion rule scenarios. Details of the five primary analyses are as follows:

1- **Inclusive Analysis:** In this analysis, all 64 characters were included for the 18 ingroup and four outgroup taxa. The complete data matrix consisted of 1,408 taxon/character combinations, 94 (*i.e.*, 6.7%) of which were unknown ("?").

2- **40% Exclusion Rule Analysis:** In this analysis, characters for which 40% or more of the 22 taxa were coded as unknown were excluded, *i.e.*, characters for which nine or more taxa were coded with a "?." In this analysis, two characters (character 25 and 26) were excluded. The resulting data matrix consisted of 1,364 taxon/character combinations, 74 (*i.e.*, 5.4%) of which were unknown ("?").

3- **30% Exclusion Rule Analysis:** In this analysis, characters for which 30% or more of the 22 taxa were coded as unknown were excluded, *i.e.*, characters for which seven or more taxa were

Character 1: Rhyncheal apparatus (RA): 0=absent; 1=present. (1)*
Character 2: Construction of the tentacle hooks of the RA: 0=hollow; 1=solid; 9=N/A (not applicable in taxa lacking bothria and in taxa lacking an RA).
Character 3: Metabasal armature of the tentacles of the RA: 0=heteroacanthous; 1=homeoacanthous; 9=N/A (not applicable in taxa lacking bothria and in taxa lacking an RA).
Character 4: Chainettes on tentacles of the RA: 0=absent; 1=throughout length of tentacle; 2=restricted to base of tentacle; 9=N/A (not applicable in taxa lacking bothria and in taxa lacking an RA).
Character 5: Point of attachment of retractor muscles of tentacles to the tenacle bulbs of the RA: 0=anterior; 1=posterior; 2=middle; 9=N/A (not applicable in taxa lacking bothria and in taxa lacking an RA).
Character 6: Course of tentacle sheaths of the RA: 0=straight; 1=sinuous; 2=coiled; 9=N/A (not applicable in taxa lacking bothria and in taxa lacking an RA).
Character 7: Posterior extent of bothria relative to tentacle bulbs of the RA: 0=not reaching anterior margin of bulbs; 1=extending beyond posterior margin of bulbs; 9=N/A (not applicable in taxa lacking bothria and in taxa lacking an RA).
Character 8: Extension of scolex in lateral plane: 0=absent; 1=present. (2)
Character 9: Configuration of scolex: 0=undivided; 1=2 pedicels; 2=4 stalks. (3)
Character 10: Apical modification of scolex proper (in adult): 0=absent; 1=present. (4)
Character 11: Invagination of apical modification of scolex proper: 0=noninvaginable; 1=invaginable; 9=N/A. (5)
Character 12: Aperture on apical modification of scolex proper: 0=absent; 1=present; 9=N/A. (6)
Character 13: Opening of aperture on apical modification of scolex proper: 0=not changeable in diameter; 1=changeable in diameter; 9=N/A. (7)
Character 14: Field of multiple papillae surrounding posterior margin of apical modification of scolex proper: 0=absent; 1=present; 9=N/A. (10)
Character 15: Apical organ on scolex: 0=absent; 1=present. (11)
Character 16: Hooks on apical organ: 0=absent; 1=present; 9=N/A (not applicable in taxa lacking an apical organ).
Character 17: Apical organ hook arrangement: 0=1 or more continuous rings; 1=distinct dorso-ventral groups; 9=N/A (not applicable in taxa lacking an apical organ and in taxa lacking apical organ hooks).
Character 18: Apical organ hook shape: 0=similar in shape; 1=dissimilar in shape; 9=N/A (not applicable

coded with a "?." In this analysis, five characters (character 25-28 and 64) were excluded. The resulting data matrix consisted of 1,298 taxon/character combinations, 51 (*i.e.*, 3.9%) of which were unknown ("?").

4- **20% Exclusion Rule Analysis:** In this analysis, characters for which 20% or more of the 22 taxa were coded as unknown were excluded, *i.e.*, characters for which four or more taxa were coded with a "?." In this analysis, 12 characters (character 8, 21-28, 31, 32, and 64) were excluded. The resulting data matrix consisted of 1,144 taxon/character combinations, 13 (*i.e.*, 1.1%) of which were unknown ("?").

5- **10% Exclusion Rule Analysis:** In this analysis, characters for which 10% or more of the 22 taxa were coded as unknown were excluded, *i.e.*, characters for which two or more taxa were coded with a "?." In this analysis, 16 characters (character 8, 21-28, 31, 32, 50, 51, and 62-64) were excluded. The resulting data matrix consisted of 1,056 taxon/character combinations, three (*i.e.*, 0.3%) of which were unknown ("?").

Trees for the figures were generated using MacClade 4.0 (Maddison and Maddison 2000). For the primary phylogenetic hypothesis that was chosen for presentation in this study, decay values were calculated and mapped on the tree to assess the robustness of the topology using MacClade 4.0. In addition, characters, the mappings of which were unambiguous, were mapped directly onto that tree. Character state trees were generated and are shown separately for for each the ambiguous characters, that is, those characters for which several equally parsimonious character reconstructions were possible.

B. Effect of outgroup selection

Four analyses were performed to examine the effect of outgroup selection on the results of the analysis. All four analyses included all 18 ingroup taxa and employed the 20% Exclusion Rule (excluding 12 characters). These analyses differed with respect to the outgroups utilized: analyses using two of the four outgroup taxa (always one tetraphyllidean taxon and one proteocephalidean taxon) in all four possible combinations were run. The results of these analyses were compared to the 20% Exclusion Rule Analysis using all four outgroup taxa detailed above.

C. Effect of inapplicable character coding

Finally, because of the implications of the inapplicable coding strategy on the analysis, the effect of substituting the unknown coding "?" for the inapplicable coding "9" was explored, albeit cursory, including all 18 ingroup and all four outgroup taxa. To facilitate direct comparison with the 20% Exclusion Rule Analysis detailed above, the same 12 characters excluded above were excluded for this analysis, resulting in a matrix of the same size, with "?'s" instead of "9's." The resulting data matrix consisted of 1,144 taxon/character combinations, 155 (*i.e.*, 13.5%) of which were unknown ("?").

Results

A. Interrelationships of lecanicephalidean genera and the effect of character exclusions

1- Inclusive Analysis: The Branch and Bound analysis of the data matrix with 22 taxa and all 64 characters resulted in two equally parsimonious trees, each 219 steps in length, with a consistency index (CI) of 0.548, a retention index (RI) of 0.679, and a homoplasy index (HI) of 0.479. Fifty-four of the 64 characters included were parsimony informative. The strict consensus tree of the two trees resulting from this analysis is shown in Figure 61A.

2- 40% Exclusion Rule Analysis: The Branch and Bound analysis of the data matrix with 22 taxa and 62 characters (*i.e.*, two characters excluded) resulted in two equally parsimonious trees, each 203 steps in length, with a CI of 0.542, an RI of 0.683, and an HI of 0.481. Fifty-two of the 62 characters included were parsimony informative. The strict consensus tree of the two trees resulting from this analysis is shown in Figure 61A (same as tree resulting from Inclusive Analysis).

3- 30% Exclusion Rule Analysis: The Branch and Bound analysis of the data matrix with 22 taxa and 59 characters (*i.e.*, five characters excluded) resulted in two equally parsimonious trees, each 212 steps in length, with a CI of 0.547, an RI of 0.681, and an HI of 0.488. Forty-nine of the 59 characters included were parsimony informative. The strict consensus tree of the two trees resulting from this analysis is shown in Figure 61A (same as tree resulting from Inclusive and 40% Exclusion Rule Analysis).

4- 20% Exclusion Rule Analysis: The Branch and Bound analysis of the data matrix with 22 taxa and 52 characters (*i.e.*, 12 characters excluded) resulted in three equally parsimonious trees, each 181 steps in length, with a CI of 0.497, an RI of 0.664, and an HI of 0.503. Forty-three of the 52 characters included were parsimony informative. The strict consensus tree of the three trees resulting from this analysis is shown in Figure 62. Decay values for each node, generated by executing a decay index command file that was created in MacClade 4.0 in PAUP* 4.0b8, are given on the branch leading to the node. The states of 40 of the 52 characters could be mapped onto the tree; these are shown in Figure 63. The character state mappings for seven of these 40 characters was initially considered ambiguous. The ambiguity in those cases was associated with the state leading up to the single polytomy in the ingroup - in all seven characters, the four branches connected to the node exhibited the same state. The possible coding options for these seven characters was either as four independent origins in the four lineages or as a synapomorphy on the branch leading up to the polytomy. Applying the parsimony criterion, the latter coding option was chosen for the seven characters. The remaining 12 characters were ambiguous, that is, several equally parsimonious character mapping options exist. As a consequence, these characters were not mapped on the consensus tree. Rather, individual character state trees are presented for these 12 characters (Figs. 64-66).

5- **10% Exclusion Rule Analysis:** The Branch and Bound analysis of the data matrix with 22 taxa and 48 characters (*i.e.*, 16 characters excluded) resulted in two equally parsimonious trees, each 164 steps in length, with a CI of 0.506, an RI of 0.681, and an HI of 0.494. Forty of the 48 characters included were parsimony informative. The strict consensus tree of the two trees resulting from this analysis is shown in Figure 61B.

B. Effect of outgroup selection

The results of the four Branch and Bound analyses using two of the four target outgroup taxa in all four possible combinations and excluding the same 12 characters as in the 20% Exclusion Rule Analysis (*i.e.*, characters 8, 21-28, 31, 32, and 64) are as follows:

(1) *Proteocephalus perplexus* and *Acanthobothrium parviuncinatum* as outgroups: Nine equally parsimonious trees of 166 steps with a CI of 0.524, an RI of 0.658, and an HI of 0.476 resulted. The strict consensus tree of the nine trees is shown in Figure 61C.

(2) *Proteocephalus perplexus* and *Rhinebothrium corymbum* as outgroups: Eight equally parsimonious trees of 170 steps with a CI of 0.518, an RI of 0.650, and an HI of 0.482 resulted. The strict consensus tree of the eight trees is shown in Figure 61D.

(3) *Euzetiella tetraphylliformis* and *Acanthobothrium parviuncinatum* as outgroups: Four equally parsimonious trees of 166 steps with a CI of 0.524, an RI of 0.658, and an HI of 0.476 resulted. The strict consensus tree of the four trees is shown in Figure 61D (same as tree resulting from outgroup analysis 2).

(4) *Euzetiella tetraphylliformis* and *Rhinebothrium corymbum* as outgroups: Four equally parsimonious trees of 171 steps with a CI of 0.515, an RI of 0.645, and an HI of 0.485 resulted. The strict consensus tree of the four trees is shown in Figure 61E.

C. Effect of inapplicable character coding

The Branch and Bound analysis of the data matrix with all four outgroups, excluding the same 12 characters as in the 20% Exclusion Rule Analysis (*i.e.*, character 8, 21-28, 31, 32, and 64), but in which all inapplicable character codings (“9”) were replaced with unknown character codings (“?”) resulted in seven equally parsimonious trees, each 155 steps in length, with a CI of 0.477, an RI of 0.612, and an HI of 0.523. The strict consensus tree of the two trees resulting from this analysis is shown in Figure 61F.

Discussion

The topologies of the consensus trees resulting from the Inclusive Analysis, and the analyses in which the 40% Exclusion Rule and the 30% Exclusion Rule were enforced, were identical (for topology see Fig. 61A). The topology of the consensus tree in which the 20% Exclusion Rule was enforced (Fig. 61) was congruent with the above trees; it differed only in that *Eniochobothrium euaxos* and *Hornellobothrium extensivum* were independently part of the polytomy with two other clades of lecanicephalideans, rather than part of the polytomy as each other’s closest relative. The strict consensus tree from this latter analysis was chosen as the principal tree for discussion because it was the result of the analysis in which the most strict of the exclusion rules was employed, and, thus, was likely to provide the most conservative hypothesis of relationships. Decay values (see Fig. 62), however, indicate that

Fig. 61. A-F. Strict consensus trees of the Inclusive, 40%, 30%, and 10% Exclusion Rule Analyses, effect of outgroup selection Analyses 1-4, and the effect of inapplicable character coding Analysis. A. Inclusive Analysis, 40% and 30% Exclusion Rule Analyses. B. 10% Exclusion Rule Analysis. C. Effect of outgroup selection Analysis 1. D. Effect of outgroup selection Analyses 2 and 3. E. Effect of outgroup selection Analysis 4. F. Effect of inapplicable character coding Analysis.

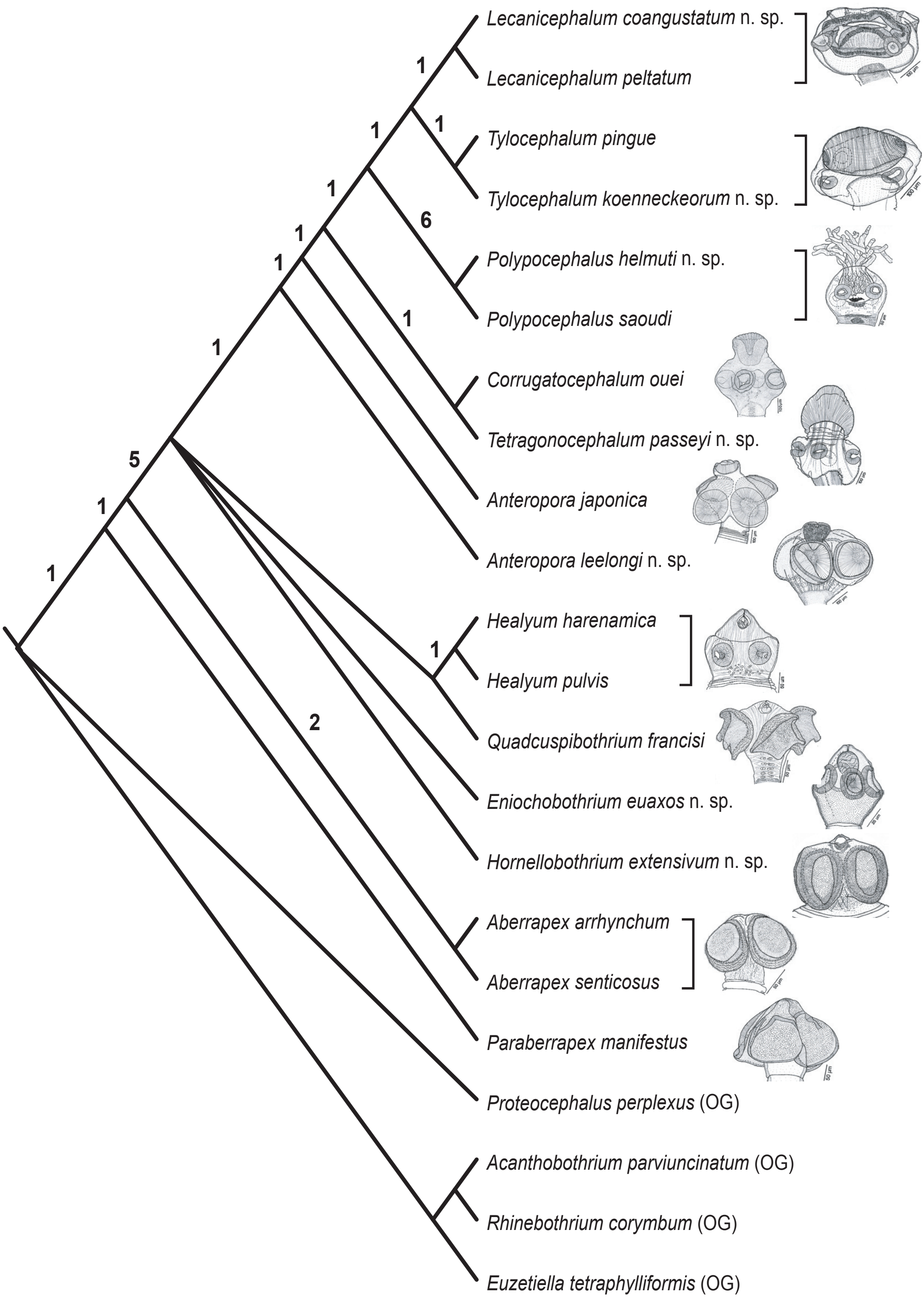
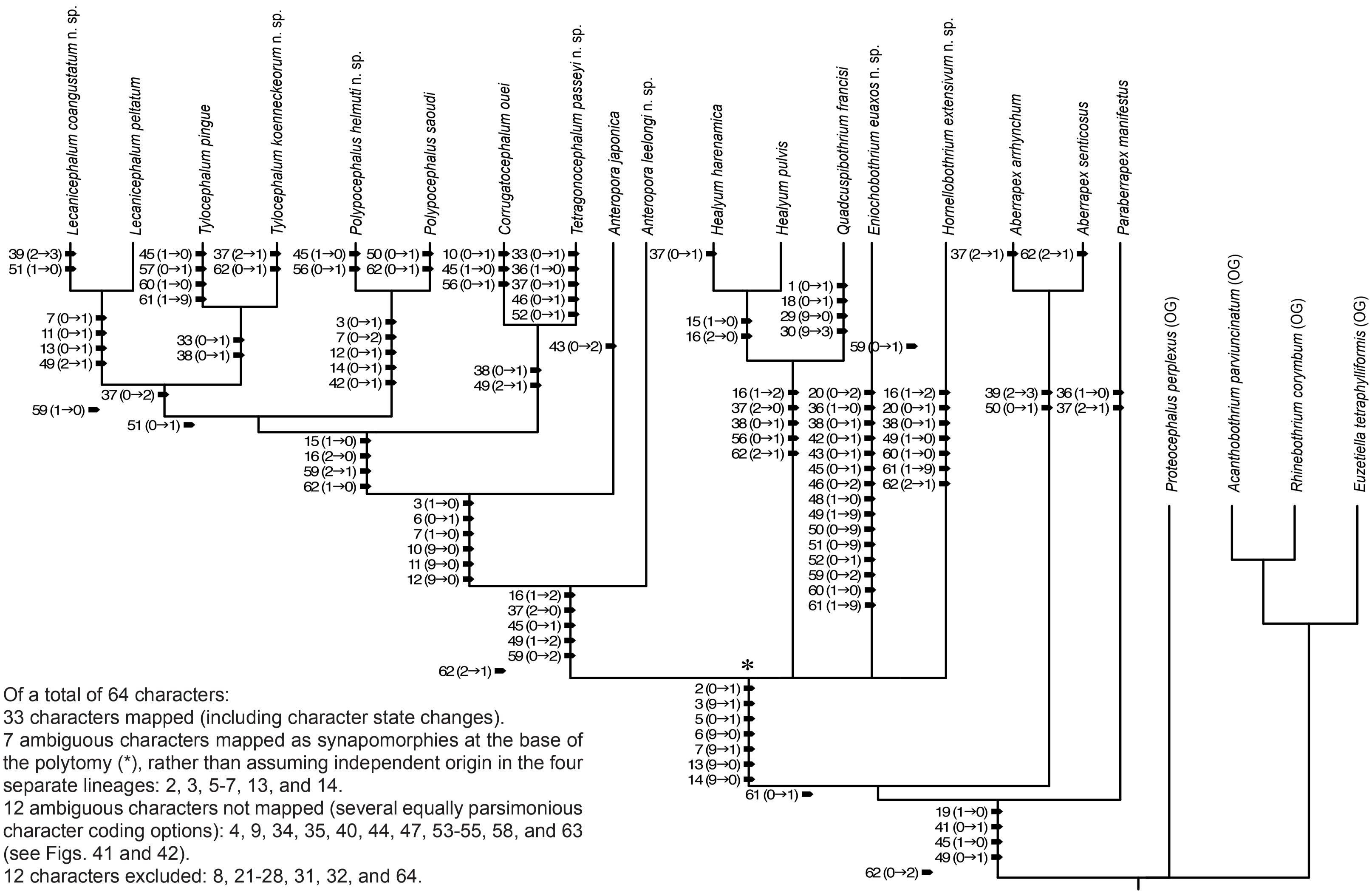


Fig. 62. Strict consensus of three most parsimonious trees of the 20% Exclusion Rule Analysis. Branch and Bound Search: Length: 181; CI: 0.497; RI: 0.664, HI: 0.503. Note: Decay index values for each clade are shown.



Of a total of 64 characters:
33 characters mapped (including character state changes).
7 ambiguous characters mapped as synapomorphies at the base of the polytomy (*), rather than assuming independent origin in the four separate lineages: 2, 3, 5-7, 13, and 14.
12 ambiguous characters not mapped (several equally parsimonious character coding options): 4, 9, 34, 35, 40, 44, 47, 53-55, 58, and 63 (see Figs. 41 and 42).
12 characters excluded: 8, 21-28, 31, 32, and 64.

Fig. 63. Character mapping onto the strict consensus tree of the 20% Exclusion Rule Analysis.

there is little support for most branches on this tree. The consensus tree resulting from the 10% Exclusion Rule Analysis (Fig. 61B), in which a quarter of the total 64 characters were excluded, differed significantly from the trees resulting from the first four analyses. Although the tree resulting from the 10% Exclusion Rule Analysis also supported the monophyly of the Lecanicephalidea, a clade consisting of lecanicephalideans possessing an apical structure, and the basal placement of *Paraberrapex manifestus* together with the two species of *Aberrapex*, the relationships among the more derived lecanicephalideans was incongruent with the hypothesis of the relationships of these taxa represented by the principal tree (Fig. 62). Specifically, the consensus tree resulting from the 10% Exclusion Rule Analysis (Fig. 61B) supported the following topology: (*Anteropora*, *Polypocephalus*, (*Corrugatocephalum*, (*Healyum*, *Quadcuspibothrium*))). Because this was the only analysis resulting in a tree with a different topology (again, with weak support) this hypothesis will not be discussed further, but should be taken as indication of the preliminary nature of these phylogenetic analyses.

The character mappings (Fig. 63) are illuminating in a number of respects. Despite the low decay value of "1" for the branch leading to the clade consisting of all lecanicephalideans, five characters support the monophyly of this group. Specifically, these characters code for (1) the condition of the cephalic peduncle (character 19), (2) the position of the junction of the proximal end of the vas deferens (character 41), (3) the presence/absence of spinitriches on the cirrus (character 45), (4) the position of the opening of the vagina relative to the cirrus (character 49), and (5) the anterior extent of the uterus in mature proglottids (character 62). Nonetheless, support for this clade is low, since two of the five characters exhibit a CI below 0.5 (characters 49 and 62), while the remaining three characters exhibit a CI of 0.5 or greater (characters 19, 41, and 45). Three clades had decay values greater than one. These included the clade consisting of *Aberrapex arrhynchum* and *A. senticosus*, which had a decay value of "2" and was supported by two unambiguous characters (39 and 50). Both of these characters code for proglottid features; each appears at least two more times on the tree. The clade consisting of lecanicephalideans possessing an apical structure had a decay value of "5" and was supported by seven characters. Not surprisingly, all seven of these characters code for features associated with the apical modification of the scolex proper or the apical organ. The clade consisting of the two species of *Polypocephalus* had the highest decay value "6" but was supported by surprisingly few characters (*i.e.*, five). All five of these characters had a CI of 0.5 or greater. Four of these five characters involved features of either the apical modification of the scolex proper or the apical organ (3, 7, 12, and 14); the fifth character was a proglottid character. Worthy of note is the fact that 15 unambiguous characters are autapomorphic in *Eniochobothrium euaxos*; most of these are associated with proglottid features. This speaks to the unusual proglottid anatomy of this taxon.

While the analyses supported the monophyly of almost all the lecanicephalidean genera (except for a paraphyletic *Anteropora*), not too much emphasis should be placed on this result because of low support values on most branches and inadequate taxon sampling in several of the genera. The clade of species of *Polypocephalus* and that of species of *Aberrapex* were supported by decay values of six and two, respectively; the clades of species of *Healyum*, *Lecanicephalum*, and *Tylocephalum* were supported by decay values of one. All species of *Aberrapex*, *Healyum,* and *Lecanicephalum* (*i.e.*, two of two, each) were included in the analyses. However, the taxon sampling was less comprehensive for the remaining six genera; two of three species of *Anteropora*, one of three species of *Eniochobothrium*, one of two species of *Hornellobothrium*, and only two of 26 species of *Polypocephalus*, two of 11 species of *Tylocephalum*, and one of 12 species of *Tetragonocephalum* were included. Therefore, one should refrain from assuming monophyly especially of these latter three genera until more species can be included.

The identity and number of outgroups had a definite effect on tree topology. Three

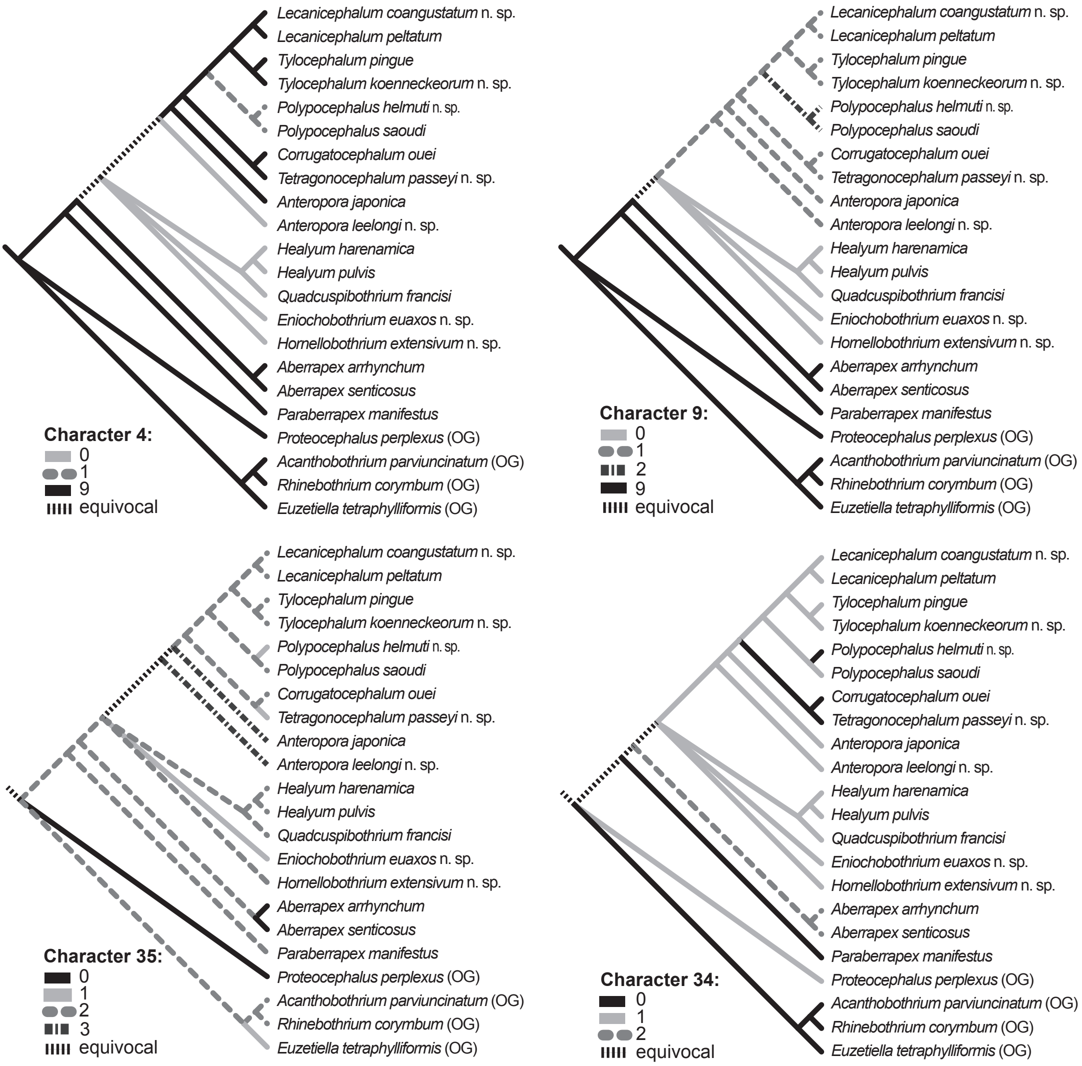


Fig. 64. Character state trees for the ambiguous characters 4, 9, 34, and 35.

of the four analyses (*i.e.*, Analyses 1-3) in which only two of the four outgroup taxa were utilized (in each case always one tetraphyllidean and one proteocephalidean) resulted in congruent trees, but, all of which were significantly less resolved (Fig. 61C and D) than the tree resulting from the 20% Exclusion Rule Analysis (Fig. 62) using all four outgroup taxa. The trees resulting from all three of these analyses supported both the basal position of the lecanicephalidean taxa lacking an apical structure and a monophyletic subgroup of lecanicephalideans (*i.e.*, those taxa bearing an apical structure). However, the relationships among the basal taxa (*Aberrapex* and *Paraberrapex*) were unresolved with respect to the outgroups and therefore did not necessarily support a monophyletic Lecanicephalidea. The tree resulting from the fourth analysis (Fig. 61E) (with the proteocephalidean *Euzetiella tetraphylliformis* and the tetraphyllidean *Rhinebothrium corymbum* as outgroups) was similar in resolution to the tree resulting from the 20% Exclusion Rule

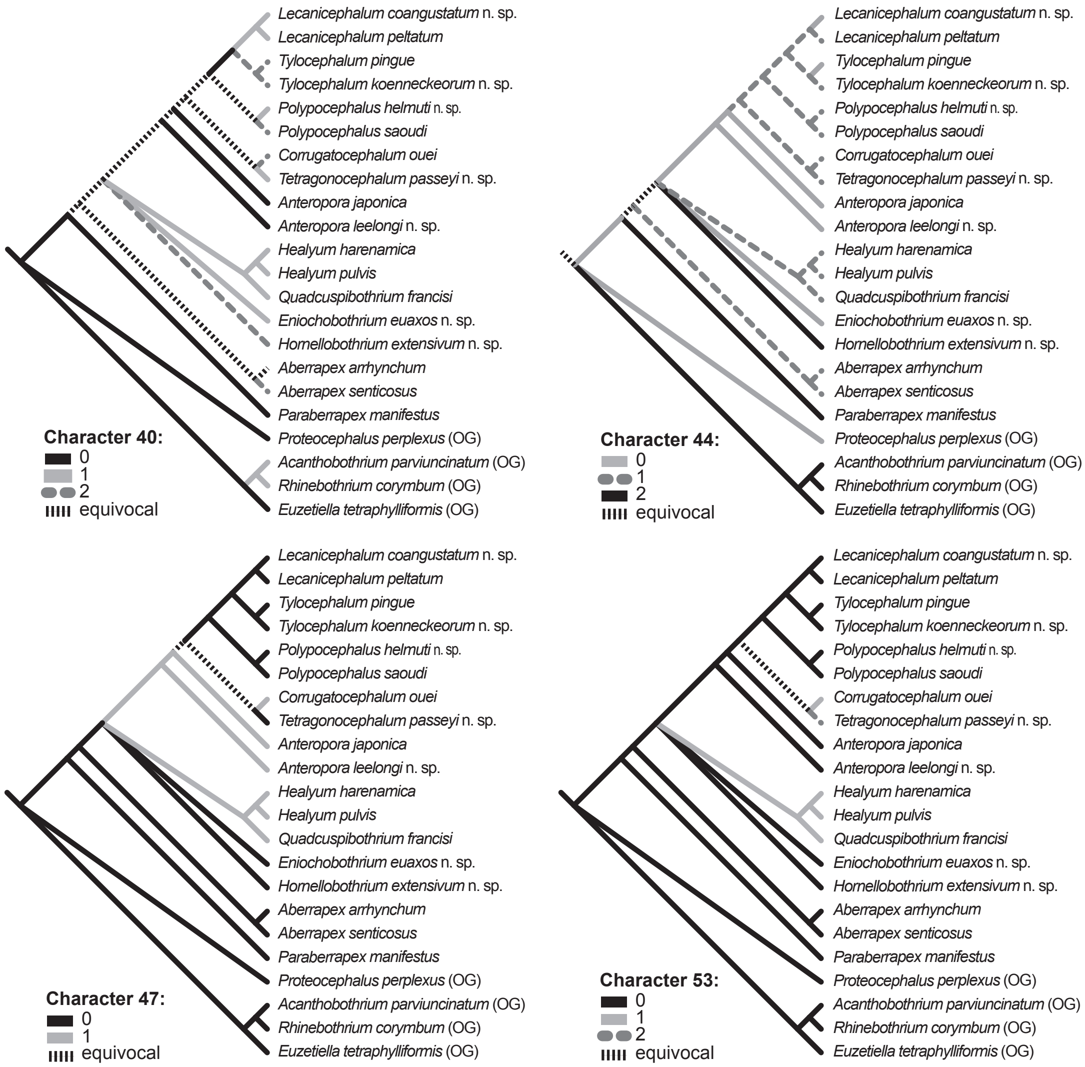


Fig. 65. Character state trees for the ambiguous characters 40, 44, 47, and 53.

Analysis (Fig. 62), however it supported a different topology. In the tree resulting from this fourth analysis, the Lecanicephalidea were not monophyletic (*Euzetiella tetraphylliformes* was the basal member of a clade containing it and the lecanicephalideans bearing an apical structure, with the lecanicephalidean taxa lacking an apical structure in a polytomy basal to that clade) and the hypothesized relationships among lecanicephalideans bearing an apical structure were unlike those supported by any other topology resulting from this study.

The results of previous phylogenetic analyses focusing on elasmobranch tapeworm interrelationships (Caira *et al.* 1999, 2001) suggested affinities between the lecanicephalidean taxa included in those analyses and members of the tetraphyllidean genera *Pseudanthobothrium* and *Echeneibothrium*. As indicated in the introduction, members of these two genera are very unusual among tetraphyllideans in their possession of apical structures. Unlike the apical structure

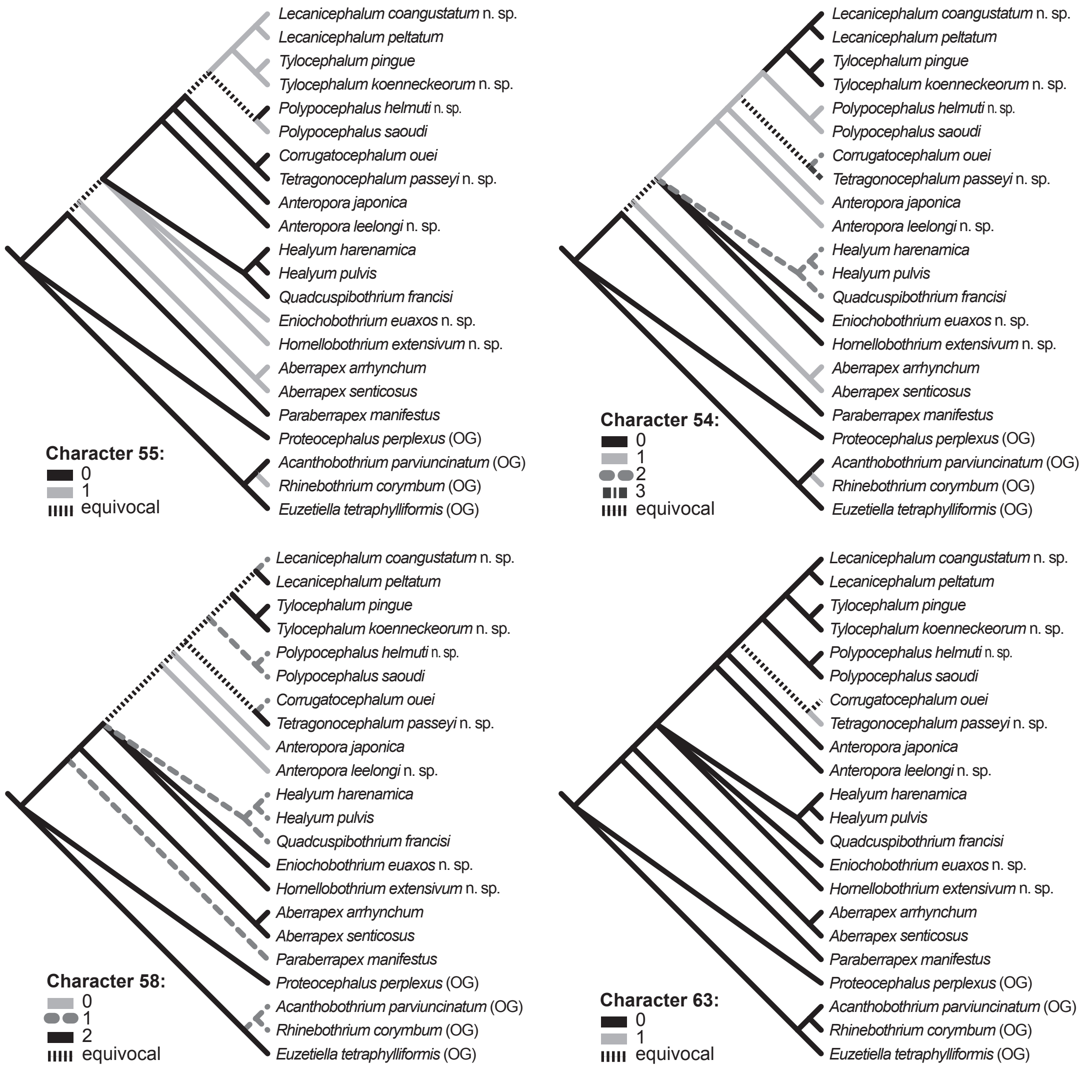


Fig. 66. Character state trees for the ambiguous characters 54, 55, 58, and 63.

in lecanicephalideans, however, the apical modification of the scolex proper in these tetraphyllideans can be completely or partially invaginated into the scolex proper. The morphology of the apical structure of *Echeneibothrium* and *Pseudanthobothrium* is very complex and is poorly understood. The apical structures are not known in enough detail to definitively code for individual features associated with these structures. A number of preliminary observations suggest that the homology between the apical structure of lecanicephalideans and that of tetraphyllideans may be suspect.

A pronounced effect associated with strategies for coding inapplicable characters was apparent. The substitution of the unknown character coding ("?") for a unique character state designated to represent coding of inapplicable characters ("9") resulted in greater than 10-fold increase in the amount of missing data in the data matrix. Analysis of this matrix using the 20% Exclusion Rule parameters resulted in trees that were 26 steps shorter and much less resolved than those resulting from the former coding. However, the monophyly of the Lecanicephalidea and a monophyletic group consisting of lecanicephalideans bearing apical structures was supported (Fig. 61F). Despite less resolution among lecanicephalidean genera in general in the consensus tree resulting from the runs based on the "?" matrix, a clade consisting of *Anteropora*, *Polypocephalus*, *Corrugatocephalum*, *Healyum*, and *Quadcuspibothrium* was observed, as was seen in the tree resulting from the 10% Exclusion Rule Analysis.

The Lecanicephalidea have not figured prominently in cestode phylogenetic analyses to date. The only phylogenetic trees with adequate lecanicephalidean representation to allow for any meaningful comparison with the results found here are those by Brooks and McLennan (1993) and Caira *et al.* (1999, 2001). Even in these cases, the number of genera represented was small, and thus, comparisons are limited. Unfortunately, nine of the 12 "lecanicephalidean" genera included in Brooks and McLennan's (1993) phylogenetic hypothesis, were not included in the present analysis. This is because either they are not lecanicephalideans (*Cathetocephalus*, *Prosobothrium*, *Disculiceps*, *Discobothrium*, and *Echeneibothrium*), or are considered *genera inquirenda* here (*Adelobothrium*, *Calycobothrium*, *Staurobothrium*, and *Hexacanalis*). The remaining three genera (*Tetragonocephalum*, *Polypocephalus*, and *Lecanicephalum*) form a polytomy after the exclusion of the nine taxa listed above. The topology of the consensus tree resulting from the 20% Exclusion Rule Analysis that was chosen to be presented in this study is not consistent with any of the groupings resulting from the Caira *et al.* (1999) study. Although, the interrelationships among the genera in Caira *et al.* (2001) was largely unresolved, there are some similarities between the tree generated here and that resulting from Caira *et al.* (2001). For example, the lecanicephalidean genera in the Caira *et al.* (2001) tree, except for *Cephalobothrium*, appear to be monophyletic. However, the few groupings within the lecanicephalidean clade that do exist in the tree presented by Caira *et al.* (2001) are not consistent with the results from this study.

As it stands, the main supraspecific taxonomic category of current utility in the Lecanicephalidea is genus; familial boundaries are unstable and controversial. While the number of lecanicephalidean families created over the history of the group has been somewhat conservative (of the six lecanicephalidean families that have been used at some point in time, four are recognized in the most recent treatment of the group by Euzet [1994b]), the generic membership in these families has varied widely. For example, Wardle and McLeod (1952) recognized three genera (*Lecanicephalum*, *Parataenia*, and *Tetragonocephalum*) in the family Lecanicephalidae, Yamaguti (1959) six (*Lecanicephalum*, *Calycobothrium*, *Cephalobothrium*, *Hexacanalis*, *Polypocephalus*, and *Tylocephalum*), Schmidt (1986) nine (*Lecanicephalum*, *Calycobothrium*, *Hexacanalis*, *Staurobothrium*, *Flapocephalus*, *Eniochobothrium*, *Tetragonicephalum* [sic], *Discobothrium*, and *Polypocephalus*), while Euzet (1994b) recognized only *Lecanicephalum* in Lecanicephalidae. No attempt has been made previously to address this issue using phylogenetic analyses. Even the results of the preliminary phylogenetic analyses at hand, it is not clear that this task can be completed now. The trees are only weakly supported and significant effects of outgroup selection and inapplicable character coding were seen. As a consequence, no familial classification scheme will be proposed at this time. A more expanded analysis with more intensive sampling of lecanicephalideans and additional characters is needed to obtain a stable hypothesis of the relationships among lecanicephalideans before a family level organization should be attempted.

GEOGRAPHIC DISTRIBUTION

Geographic records of lecanicephalideans at the inception of this study (prior to 1997) suggested an extensive circumtropical/subtropical distribution, between 45°N and 35°S latitude (Fig. 67), with the majority of lecanicephalideans (40 of the 58 known species) having been described from the waters surrounding India and Sri Lanka. Remaining locality records include Japan, eastern Australia, the Arabian Gulf, Egypt, Uruguay, Jamaica, South China, and the Dry Tortuga Islands, most for individual species. The regions most conspicuously lacking in lecanicephalidean records were much of the waters surrounding Australia and South America, all of Africa, and the entire eastern Pacific Ocean (except for the single record from California [Dailey and Mudry 1968]).

The new collections and specimens examined over the course of this study have significantly expanded the known geographic distributions of lecanicephalideans. New geographic localities are illustrated in Figure 68.

Significant new locality records for lecanicephalideans include the Gulf of Mexico, the coast of Tanzania, the Mozambique Channel and the eastern Indian Ocean off Madagascar, the Gulf of Thailand, the South China Sea off Singapore, the Timor and Arafura Seas off northern Australia, the eastern Indian Ocean off Western Australia, as well as the waters around New Caledonia and Tahiti (Fig. 68).

Gaps in the geographic distributions of lecanicephalideans continue to be filled each time collections are conducted in a new locality. For example, no record of lecanicephalideans existed for the Gulf of California prior to this study, and only a single lecanicephalidean species had been reported from the eastern Pacific Ocean in general (see Dailey and Mudry 1968). Collections from the Gulf of California conducted as part of this study revealed the first records of lecanicephalidean cestodes from this body of water (Jensen 2001). Jensen (2001) suggested that the lack of previous records of lecanicephalideans from the Gulf of California was the result of a lack of sampling from this particular geographic region. Furthermore, she pointed out that it was surprising that this relatively small body of water yielded four new genera and five new species of Lecanicephalidea. Prior to her study, lecanicephalidean cestodes had been reported from only two of the 79 species of elasmobranchs reported from the Gulf of California from other localities around the world. Jensen's (2001) study increased the total number of lecanicephalidean species described from elasmobranchs of the eastern Pacific Ocean from one to six. This example suggests that lecanicephalideans may actually be distributed in tropical and subtropical waters in most major bodies of waters.

It is, however, safe to say that lecanicephalideans are not polar species. So far, no records of lecanicephalideans exist north of 45°N or south of 35°S. The waters around India and Sri Lanka remain the region from which the greatest number of species of lecanicephalideans have been described. However, this heterogeneous distribution is likely to become more homogeneous over time as data from other tropical and subtropical locations are accumulated. For example, a number of new species of lecanicephalideans from northern Australia, that were not included in this study, are awaiting description. In addition, new collections from waters around Borneo are planned in the near future and new locality records for lecanicephalideans are expected. New locality records are also expected from western Africa and western Middle and South America.

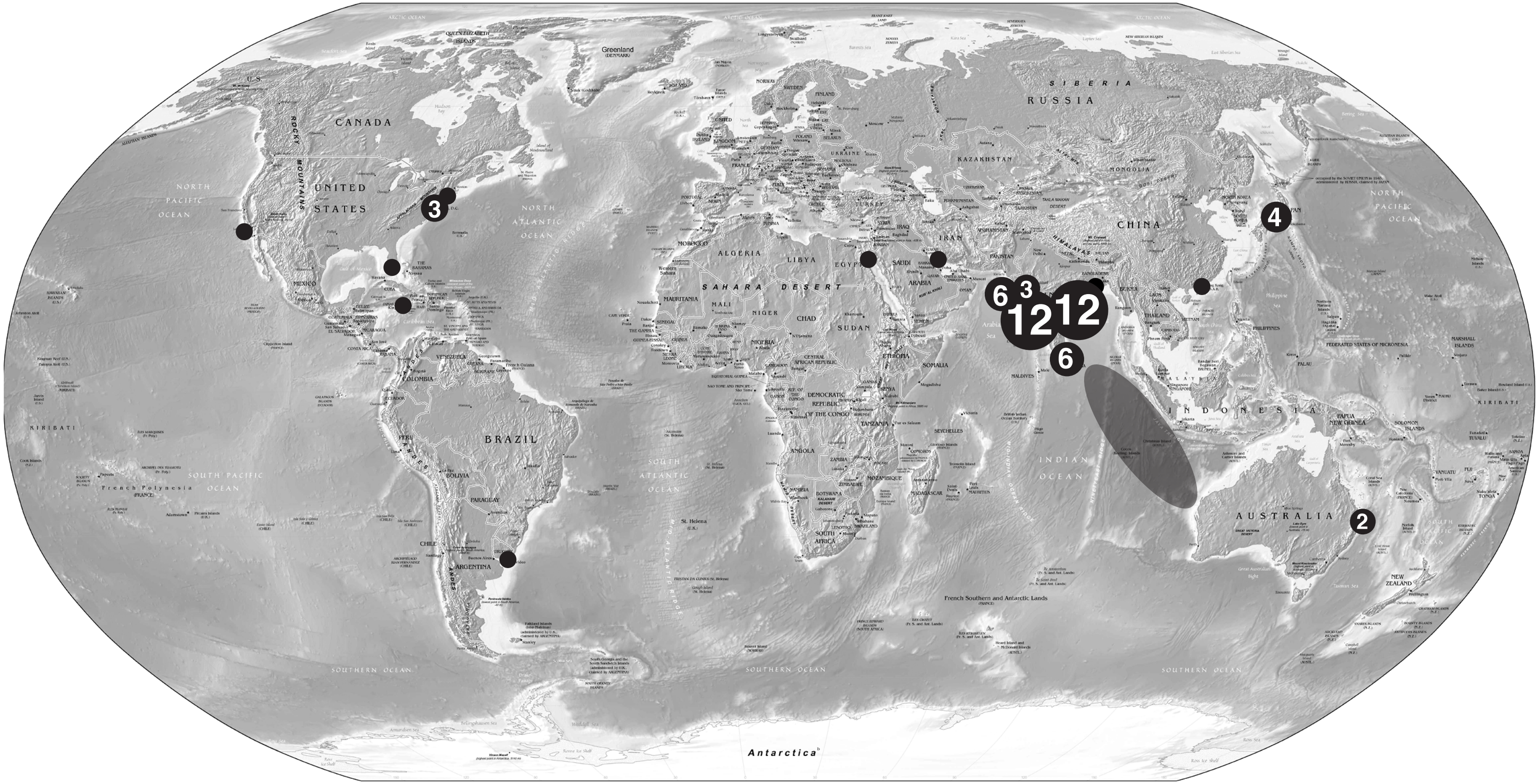


Fig. 67. Known geographic distribution of lecanicephalideans at inception of the project.
● Type locality of valid lecanicephalidean species at inception of project (⬬ indicated unspecified type locality).

Note: The solid dots represent single species; dots with numbers represent multiple species from that locality.

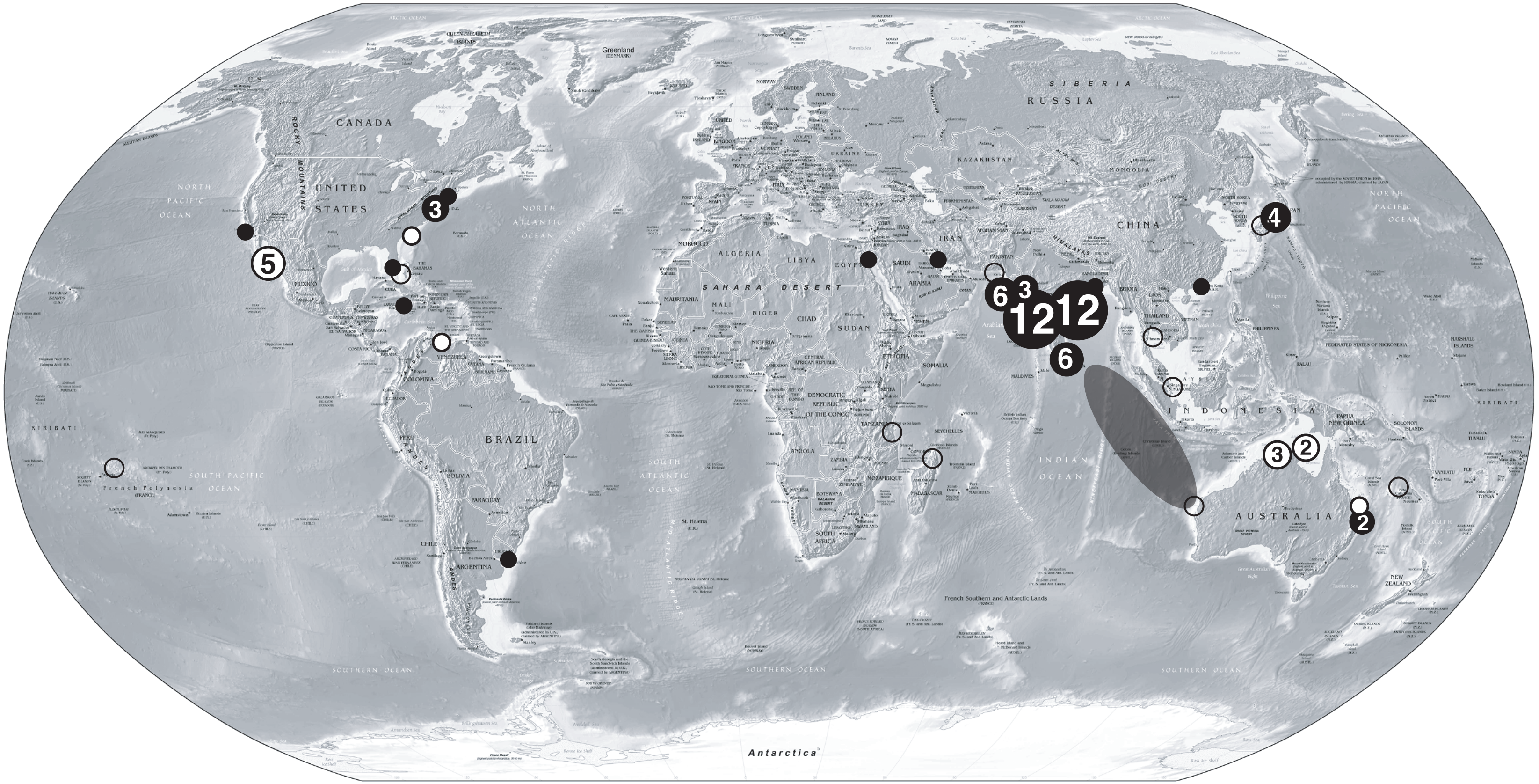


Fig. 68. Known geographic distribution of lecanicephalideans at conclusion of project.

- ● Type localities of valid lecanicephalidean species at inception of project (⬬ indicates unspecified type locality).
- ○ Type localities of lecanicephalidean described after 1996, including species described as part of this study.
- ◎ Other lecanicephalidean records, mainly of undescribed species.

Note: The solid dots represent single species; dots with numbers represent multiple species from that locality; open dots represent an as of yet undetermined number of species.

HOST ASSOCIATIONS AND LIFE CYCLES

Several, conflicting hypotheses about the interrelationships of extant elasmobranchs have been suggested (*e.g.*, Compagno 1973, 1977; Maisey 1984; Shirai 1992; de Carvalho 1996; Shirai 1996). The trees presented in the two most recent studies (de Carvalho 1996; Shirai 1996), in general, show two major clades of Elasmobranchii: the Squalea, including the sevengill sharks or the spiny dogfishes, angel sharks and sawsharks, and all the batoids (skates and rays), and the Galea, including sharks in the orders Lamniformes (*e.g.*, mako and thresher sharks), Carcharhiniformes (*e.g.*, whaler sharks and catsharks), Orectolobiformes (*e.g.*, wobbegongs and nurse sharks), and Heterodoniformes (horn sharks). The conflicting, more traditional view (*e.g.*, Compagno 1977; Maisey 1984) is that the Elasmobranchii consists of a clade including all modern shark groups and a clade including all the batoids (skates and rays). Discussions of host associations of lecanicephalideans in this study are based on this latter, more traditional view. The classification schemes utilized for elasmobranchs follow Compagno (1984a, b) for sharks and Carpenter and Niem (1999) for batoids. Thirty families of sharks (Compagno 1986) and 20 families of batoids (Carpenter and Niem 1999) are currently recognized.

Lecanicephalidean species have been reported from 34 species of elasmobranchs (Tab. 4). Adult lecanicephalideans are primarily parasites of rays; however, a few records from sharks do exist. Lecanicephalideans have been reported from 30 species in 19 genera in nine of 20 families of batoids and from four species in four genera in four of 30 families of sharks. The ray families Dasyatidae and Myliobatidae include the greatest number of host species; all five genera of dasyatids and three of the four genera of myliobatids have been found to host lecanicephalideans.

The original list of elasmobranchs known to host lecanicephalideans at the inception of this project is expanded to include the results from new collections of elasmobranch species not previously reported to host lecanicephalideans conducted over the course of this study in Table 5. For the sake of completeness, Table 5 includes a number of records of lecanicephalideans that resulted from this study but have not yet been described in detail (here or elsewhere). It should be noted that a species was considered to host lecanicephalideans if lecanicephalideans were recovered from one or more individuals of an elasmobranch species, even if, in rare cases, only a single individual of that species was sampled. Nineteen new lecanicephalidean host records are presented, bringing the total number of elasmobranch species known to host lecanicephalideans to 53. Lecanicephalideans are now known to parasitize 47 species of batoids in 20 genera, in 12 of 20 families. Most of the new host records are species of rays in the families Dasyatidae. As a result of these new collections, for example, the number of dasyatid species now known to host lecanicephalideans has almost doubled. In addition, members of both genera of sawfishes are now known to host lecanicephalidean cestodes. Also, lecanicephalideans are now known to parasitize six species of sharks in five genera, in four of 30 families. Specifically, the list of sharks known to host lecanicephalideans could be expanded to include the family Hemiscylliidae (bamboo sharks), as well as a second species of *Squatina* (angel sharks)

The diversity of elasmobranch groups parasitized by lecanicephalideans was much more extensive than anticipated based on existing records at the inception of the project. As mentioned above, lecanicephalideans have been reported from 12 of those 20 families. The number of species and genera in each batoid family that host lecanicephalideans is presented in Table 6. Also presented in Table 6 are the number of batoid species examined for lecanicephalideans in this study and how many of those were not found to host lecanicephalideans. Unfortunately, no published reports of negative data were found to augment these data. Twenty-one species of batoids examined in this study did not host lecanicephalideans. Overall, of the ap-

Table 4. Known host associations of adult lecanicephalideans at inception of project.

	FAMILY	GENUS	SPECIES
BATOIDS	Dasyatidae (Stingrays)	*Dasyatis* Rafinesque, 1810	*D. akajei* (Müller & Henle, 1841)*
			D. centroura (Mitchill, 1815)
			D. fluviorum Ogilby, 1908
			D. kuhlii (Müller & Henle, 1841)
			D. zugei (Müller & Henle, 1841)
		Himantura Müller & Henle, 1837	*H. marginata* (Blyth, 1860)*
			H. uarnak (Forsskål, 1775)
			H. walga (Müller & Henle, 1841)
		Pastinachus Rüppel, 1829	*P. sephen* (Forsskål, 1775)
		Taeniura Müller & Henle, 1837	*T. lymma* (Forsskål, 1775)
		Urogymnus Müller & Henle, 1837	*Urogymnus* sp.*
	Gymnuridae (Butterfly rays)	*Gymnura* Müller & Henle, 1837	*G. micrura* (Bloch & Schneider, 1801)*
	Myliobatidae (Eagle rays)	*Aetobatus* Blainville, 1816	*A. flagellum* (Bloch & Schneider, 1801)
			A. narinari (Euphrasen, 1790)
		Aetomylaeus Garman, 1908	*A. maculatus* (Gray, 1834)*
		Myliobatis Cuvier (ex Duméril), 1816	*M. californica* Gill, 1865*
			M. goodie Garman, 1885
	Mobulidae (Devil rays)	*Mobula* Rafinesque, 1810	*M. eregoodootenkee* Garman, 1913
	Rhinopteridae (Cownose rays)	*Rhinoptera* Cuvier, 1829	*R. adspersa* Müller & Henle, 1841
			R. bonasus (Mitchill, 1815)
			R. javanica Müller & Henle, 1841
	Narcinidae (Numbfishes)	*Narcine* Henle, 1834	*N. timlei* (Bloch & Schneider, 1801)
	Narkidae (Sleeper rays)	*Narke* Kaup, 1826	*N. japonica* (Temminck & Schlegel, 1850)
	Pristidae (Sawfishes)	*Anoxypristis* White & Moy-Thomas, 1941	*A. cuspidatus* (Latham, 1794)*
	Rajidae (Skates)	*Okamejei* Ishiyama, 1958	*O. hollandi* (Jordan & Richardson, 1909)*
	Rhinobatidae (Guitarfishes)	*Rhinobatos* Linck, 1790	*R. granulatus* Cuvier, 1929
			R. schlegelii Müller & Henle, 1841
	Rhinidae (Wedgefishes)	*Rhina* Bloch & Schneider, 1801	*R. ancylostoma* (Bloch & Schneider, 1801)
		Rhynchobatus Müller & Henle, 1837	*R. djiddensis* (Forsskål, 1775)
	Urolophidae (Stingarees)	*Urolophus* Müller & Henle, 1837	*U. jamaicensis* (Cuvier, 1816)
SHARKS	Carcharhinidae (Requiem sharks)	*Scoliodon* Müller & Henle, 1837	*S. laticaudus* Müller & Henle, 1838
	Megachasmidae (Megamouth shark)	*Megachasma* Taylor, Compagno & Struhsaker, 1983	*M. pelagios* Taylor, Compagno & Struhsaker, 1983
	Squatinidae (Angel sharks)	*Squatina* Duméril, 1806	*S. japonica* Bleeker, 1858
	Stegostomatidae (Zebra sharks)	*Stegostoma* Müller & Henle, 1837	*S. fasciatum* Hermann, 1783*

* Hosts of species in undescribed genera or *species inquirendae*.

proximately 530 species of batoids (FishBase 2000), conservatively, less than 15% have been examined for lecanicephalideans. From these data it is possible to predict whether a species sampled from a given family is a likely candidate to host lecanicephalideans. For example, with five of five genera and 19 of 43 species in the batoid family Dasyatidae known to host lecanicephalideans, it would seem wise to examine additional members of this family. The same is true for the Myliobatidae. Similarly, existing host records suggest that lecanicephalideans are also likely to be found to parasitize additional species of cownose rays (Rhinopteridae), wedgefishes (Rhinidae), sawfishes (Pristidae), devil rays (Mobulidae), and guitarfishes (Rhinobatidae). These groups should be targeted if the goal of further expanding the known range of host associations of the Lecanicephalidea is to be met.

Families of batoids that have not been reported to host lecanicephalideans are the Arhynchobatidae (softnose skates), Anacanthobatidae (legskates), Hexatrygonidae (sixgill stingrays), Hypnidae (coffin rays), Platy-

Table 5. Known host associations of adult lecanicephalideans at conclusion of project.

	FAMILY	GENUS	SPECIES
BATOIDS	Dasyatidae (Stingrays)	*Dasyatis* Rafinesque, 1810	*D. akajei* (Müller & Henle, 1841)*‡
			D. americana Hildebrand & Schroeder, 1928‡
			D. centroura (Mitchill, 1815)
			D. fluviorum Ogilby, 1908
			D. kuhlii (Müller & Henle, 1841)
			D. leylandi Last, 1987‡
			D. microps (Annandale, 1908)‡
			D. zugei (Müller & Henle, 1841)
		Himantura Müller & Henle, 1837	**_H. draco_ (Compagno & Heemstra, 1984)‡**
			H. granulata (Macleay, 1883)‡
			H. jenkinsii (Annandale, 1909)‡
			H. marginata (Blyth, 1860)*
			H. micropthalma (Chen, 1948)‡
			H. uarnak (Forsskål, 1775)
			H. undulata (Bleeker, 1852)
			H. walga (Müller & Henle, 1841)
		Pastinachus Rüppel, 1829	*P. sephen* (Forsskål, 1775)
		Taeniura Müller & Henle, 1837	*T. lymma* (Forsskål, 1775)
			T. meyeni Müller & Henle, 1841‡
		Urogymnus Müller & Henle, 1837	*Urogymnus* sp.
	Gymnuridae (Butterfly rays)	*Gymnura* Müller & Henle, 1837	*G. micrura* (Bloch & Schneider, 1801)*
	Myliobatidae (Eagle rays)	*Aetobatus* Blainville, 1816	*A. flagellum* (Bloch & Schneider, 1801)
			A. narinari (Euphrasen, 1790)
		Aetomylaeus Garman, 1908	*A. maculatus* (Gray, 1834)*
			A. vespertilio (Bleeker, 1852)‡
		Myliobatis Cuvier (ex Duméril), 1816	**_M. australis_ Macleay, 1881‡**
			M. californica Gill, 1865*
			M. goodie Garman, 1885
			M. longirostris Applegate & Fitch, 1964‡
	Mobulidae (Devil rays)	*Mobula* Rafinesque, 1810	*M. eregoodootenkee* Garman, 1913
			M. japanica (Müller & Henle, 1841)
	Rhinopteridae (Cownose rays)	*Rhinoptera* Cuvier, 1829	*R. adspersa* Müller & Henle, 1841
			R. bonasus (Mitchill, 1815)
			R. javanica Müller & Henle, 1841
			R. steindachneri Evermann & Jenkins, 1891‡
	Narcinidae (Numbfishes)	*Narcine* Henle, 1834	*N. timlei* (Bloch & Schneider, 1801)
	Narkidae (Sleeper rays)	*Narke* Kaup, 1826	*N. japonica* (Temminck & Schlegel, 1850)
	Pristidae (Sawfishes)	*Anoxypristis* White & Moy-Thomas, 1941	*A. cuspidatus* (Latham, 1794)*‡
		Pristis Linck, 1790	**_P. clavata_ Garman, 1906‡**
	Rajidae (Skates)	*Okamejei* Ishiyama, 1958	*O. hollandi* (Jordan & Richardson, 1909)*
	Rhinobatidae (Guitarfishes)	*Rhinobatos* Linck, 1790	*R. granulatus* Cuvier, 1929
			R. schlegelii Müller & Henle, 1841
			R. typus Bennett, 1830‡
	Rhinidae (Wedgefishes)	*Rhina* Bloch & Schneider, 1801	*R. ancylostoma* (Bloch & Schneider, 1801)
		Rhynchobatus Müller & Henle, 1837	*R. djiddensis* (Forsskål, 1775)
			R. australiae Whitley, 1939
	Urolophidae (Stingarees)	*Urolophus* Müller & Henle, 1837	*U. jamaicensis* (Cuvier, 1816)
SHARKS	Carcharhinidae (Requiem sharks)	*Scoliodon* Müller & Henle, 1837	*S. laticaudus* Müller & Henle, 1838
	Hemiscylliidae (Bamboo sharks)	**_Hemiscyllium_ Müller & Henle, 1837**	**_H. ocellatum_ (Bonnaterre, 1788)**
	Megachamidae (Megamouth shark)	*Megachasma* Taylor, Compagno & Struhsaker, 1983	*M. pelagios* Taylor, Compagno & Struhsaker, 1983
	Squatinidae (Angel sharks)	*Squatina* Duméril, 1806	**_S. californica_ Ayres, 1859**
			S. japonica Bleeker, 1858
	Stegostomatidae (Zebra sharks)	*Stegostoma* Müller & Henle, 1837	*S. fasciatum* Hermann, 1783*

Note: New lecanicephalidean host records resulting from this study are indicated in bold.
* Hosts of species in undescribed genera or *species inquirendae*.
‡ New (unpublished) lecanicephalidean host records.

Table 6. Families of batoids hosting lecanicephalideans.

FAMILY	No. of genera hosting lecanicephalideans	No. of species hosting lecanicephalideans	No. of species examined during this study not hosting lecanicephalideans
Rhinidae (wedgefishes)	2 of 2 genera (100%)	3 of 5 species (60%)	0 of 3 species
Rhinopteridae (cownose rays)	1 of 1 genus (100%)	4 of 8 species (50%)	0 of 3 species
Dasyatidae (stingrays)	5 of 5 genera (100%)	19 of 43 species (44%)	2 of 16 species
Pristidae (sawfishes)	2 of 2 genera (100%)	2 of 7 species (29%)	1 of 3 species
Myliobatidae (eagle rays)	3 of 4 genera (75%)	8 of 20 species (21%)	0 of 5 species
Mobulidae (devil rays)	1 of 2 genera (50%)	2 of 15 species (13%)	2 of 3 species
Rhinobatidae (guitarfishes)	3 of 8 genera (30%)	3 of 47 species (11%)	4 of 5 species
Narkidae (sleeper rays)	1 of 4 genera (25%)	1 of 10 species (10%)	N/A
Gymnuridae (butterfly rays)	1 of 1 genus (100%)	1 of 12 species (8%)	0 of 5 species
Narcinidae (numbfishes)	1 of 5 genera (20%)	1 of 23 species (4%)	2 of 2 species
Urolophidae (stingarees)	1 of 4 genera (25%)	1 of 37 species (3%)	5 of 6 species
Rajidae (skates)	1 of 22 genera (4%)	1 of 215 species (0.5%)	5 of 5 species

N/A = not applicable.

rhinidae (thornback rays), Plesiobatidae (giant stingarees), Potamotrygonidae (freshwater stingrays), and Torpedinidae (torpedos).

A number of lecanicephalideans are normally associated with sharks. The monotypic lecanicephalidean genus *Corrugatocephalum* is found only in the Megamouth shark, *Megachasma pelagios*. This shark is itself classified in a monotypic genus in the monotypic family Megachasmidae. The host associations of *Anteropora* are even more puzzling. Two of the three known species (*A. indica* and *A. japonica*) parasitize electric rays in the families Narcinidae and Narkidae. But the third species (*A. leelongi*) parasitizes the Epaulette shark, *Hemiscyllium ocellatum* in the shark family Hemiscylliidae. The well documented lecanicephalidean preference for rays as definitive hosts, might suggest electric rays as the more basal host group for *Anteropora*, in which case the occurrence of *Anteropora leelongi* in *H. ocellatum* may represent a host switching event. This hypothesis should be tested with collections from additional species of electric rays and bamboo sharks. An alternative explanation is that *A. leelongi* actually belongs to a distinct genus, which would then be restricted to the Epaulette shark. However, the compelling similarity of the unique morphology of the proglottid of *A. leelongi* to that of *A. indica* and *A. japonica* does not justify a separate generic placement at this time. The isolated reports of a species of *Polypocephalus* from the Spadenose shark (*Scoliodon laticaudus*) (Deshmukh *et al*. 1982) and a species of *Cephalobothrium* from the Zebra shark (*Stegostoma fasciatum*) (Sarada *et al*. 1993), the latter considered as a *species inquirendum* here, require confirmation.

None of the lecanicephalidean species examined in this study were found to parasitize more than one host species. This suggests that lecanicephalideans might exhibit strict host specificity (oioxenous specificity *sensu* Euzet and Combes [1980], see Caira *et al.* [2003]). Reports of a few lecanicephalidean species from more than one host species do appear in the literature (*e.g.*, see the Unverified records section for *Lecanicephalum peltatum*, *Polypocephalus radiatus*, and *Tetragonocephalum trygonis*). These records should be considered suspect for a number of reasons, and need to be confirmed. For example, in addition to its type host (*i.e.*, *Rhinobatos granulatus*), *Polypocephalus radiatus* has been reported from *Pastinachus sephen* (see Southwell, 1925), *Rhynchobatus djiddensis* (see Subhapradha 1951), and *Dasyatis kuhlii* (see BMNH No. 1950.12.6.104-110). The fact that the specimens of *Polypocephalus* examined by Southwell (1925) and Subhapradha (1951) are described as possessing four testes, while the type specimens exhibit six testes, casts doubt on the accuracy of these identifications. New collections of *Polypocephalus* from these two host species, made over the course of the present study, indicate that each species is parasitized by at least two species of *Polypocephalus*, neither of which appears to be *P. radiatus*. Although it is possible that individual lecanicephalidean species parasitize more than one host species, existing data are likely too limited for this pattern to be detected. To date, work on the Lecanicephalidea has been restricted to individual collections resulting in the description of new lecanicephalidean taxa. Future, more comprehensive lecanicephalidean faunal studies involving a wide diversity of elasmobranch species in a given geographic region will be necessary if a complete picture of lecanicephalidean host specificity is to be generated.

The Lecanicephalidea and their elasmobranch hosts are likely to be an ideal system for the investigation of co-speciation. Caira and Jensen (2001) articulated five criteria of considerable importance in co-evolutionary studies. They suggested that four of the five criteria influence the accuracy of the co-evolutionary estimate (*i.e.*, monophyly, correct identifications, availability of reasonably accurate phylogenies, and comprehensive sampling of parasite and host groups). They argued that the fifth criterion, a high degree of host specificity, is desirable if co-speciation in the system is to be recovered. Application of these criteria to the lecanicephalideans leads to the following observations. The monophyly of batoids is not in question (*e.g.*, de Carvalho 1996; Shirai 1996); monophyly of the lecanicephalideans (or at least a subgroup within that taxon) has been demonstrated (Caira *et al.* 1999, 2001). The identifications of these cestodes and their hosts have become much more reliable in recent years, and collection efforts targeting these groups have intensified. Studies addressing the phylogenetic relationships among batoids are increasing in taxon sampling and the trees resulting from these efforts are becoming more stable. The majority of elements of the phylogenies proposed by Nishida (1990), Shirai (1996), and McEachran *et al.* (1996) are shared. The major factor limiting a formal investigation of co-speciation in this system at this time is the lack of a more inclusive, rigorously obtained hypothesis of the phylogenetic relationships among the Lecanicephalidea.

Until a species level phylogenetic hypothesis for the lecanicephalideans is available, it remains to be investigated if patterns of specificity at the generic level hold true. At present, of the 12 recognized genera of lecanicephalideans, six genera (*Corrugatocephalum*, *Healyum*, *Hornellobothrium*, *Lecanicephalum*, *Paraberrapex*, and *Quadcuspibothrium*) are restricted to a single species of host. Two genera are restricted to a single batoid genus (*Aberrapex* in the *Myliobatis*, and *Eniochobothrium* in *Rhinoptera*), and one genus is restricted to a single batoid family (*Tetragonocephalum* in the Dasyatidae). The broadest host range is found in *Anteropora*, *Tylocephalum*, and *Polypocephalus*, each of which parasitizes elasmobranchs in three, six, and seven families, respectively.

No complete life cycle is currently known for any lecanicephalidean species. However, the literature is rich with reports of organisms identified as larval lecanicephalideans. These larvae have been reported from a diversity of invertebrate groups, mainly molluscs and crustaceans, and a few teleosts (*e.g.*, see Jameson 1912; Dollfus 1923; Southwell 1924; Hutton 1964; Cheng and Rifkin 1968; Sakaguchi 1973; Reimer 1975; Wolf 1976; Cake 1977; Butler 1984; Owens 1985; Brockerhoff and Jones 1995; Moravec *et al.* 1997). Early in the last century, a particularly active area of investigation was the possible involvement of larvae of the lecanicephalidean genus *Tylocephalum* in pearl production in pearl oysters from Sri Lanka (*e.g.*, see Seurat 1906a, b; Herdmann and Hornell 1906; Jameson 1912; Southwell 1924). Jameson (1912) was the first to propose a life cycle for a lecanicephalidean, in this case, *Tylocephalum minus* Jameson, 1912. He suggested that an egg, or a free-swimming larva that hatched from an egg, was ingested by the pearl oyster and developed into a globular cyst. When this oyster was eaten by an “oyster-eating” elasmobranch, the larva developed into the adult form. According to Butler (1984), a similar life cycle was outlined by Cheng (1976). Butler herself (1984) hypothesized about the life cycles of both *Tylocephalum* and *Polypocephalus*, noting that for both genera the first intermediate host is unknown.

A few different early larval stages of lecanicephalideans have been reported. For example, Euzet and Combes (1965) reported hexacanths (six-hooked embryos) in the eggs of the lecanicephalidean species *Tetragonocephalum uarnak* (Shipley and Hornell, 1906) Pintner, 1928. Cheng (1966) reported *Tylocephalum* as possessing a coracidium (a free swimming hexacanth surrounded by a ciliated membrane, that hatches from the egg). This report was, however, disputed by Cake and Menzel (1980). In general, most studies reporting lecanicephalidean larvae refer to the stages encountered simply as "metacestode larvae" (*i.e.*, larvae beyond the hexacanth stage). Feeding experiments in which molluscs or crustaceans infected with larvae suspected to be lecanicephalideans were fed to several different species of elasmobranchs (Southwell 1924), gobies (Hutton *et al.* 1959), a horn shark (Sakaguchi 1973), and a stingray (Butler, 1984), were all unsuccessful.

Much of the life cycle work conducted to date has focused on the occurrence of lecanicephalidean metacestode larvae in macroinvertebrate hosts. Butler (1984) noted that metacestodes of *Tylocephalum* have been found in bivalves, crustaceans, teleosts, and molluscivorous gastropods, while metacestodes of *Polypocephalus* have been found in molluscs, crustaceans, and teleosts. Cake (1979) reported plerocercoids of *Polypocephalus* from bay scallops in the Gulf of Mexico. He suggested that bay scallops became infected either by ingesting eggs or by ingesting procercoid larvae in an "unknown intermediate crustacean host" (p. 168). Cake and Menzel (1980) suggested that eggs of *Tylocephalum* are ingested directly by filter-feeding gastropods. Cake and Menzel (1980) found the same to be true for oysters, since it is unlikely, given size-selected feeding that an oyster would ingest an infected copepod. They also suggested that predaceous gastropods (*e.g.*, the lightning whelk or the Southern oyster drill) might become infected with metacestodes of *Tylocephalum* by ingesting infected oysters. This hypothesis that oysters might become infected by ingesting eggs directly was also promoted by Butler (1984).

Unfortunately, identification of lecanicephalidean larvae to species is currently not possible using morphological data. The use of molecular data to help with larval identification is promising (see, *e.g.*, Brickle *et al.* 2001), but has not been exploited in lecanicephalideans. Even identification of larvae to genus is sometimes uncertain because the morphological transitions from larva to adult are extensive. Despite this fact, two species of lecanicephalideans (*Tylocephalum margaritiferae* and *T. minus*) have been described based only on larval forms taken from molluscan from molluscan intermediate hosts. In both cases, oysters of the genus *Margaritifera* Schumacher, 1817 (Seurat, 1906a, b; Jameson 1912) served as the intermediate host.

Although no work on life cycles of lecanicephalideans was done as part of this study, the interesting nature of this topic lends itself to comments on possible life cycle scenarios in the Lecanicephalidea. It should be emphasized, however, that the identification of lecanicephalidean larvae, even to genus is problematic. The only exception may be larvae of *Polypocephalus*. Members of this genus appear to develop their distinctive tentacular apical organ as larval stages making identification of larvae belonging to this genus very straightforward. That having been said, examination of the literature suggests an interesting trend in the intermediate host associations of the lecanicephalideans groups summarized in Table 7. The literature suggests that larvae of *Polypocephalus* prefer invertebrates and are more commonly found associated with macrocrustaceans than with molluscs; only one record exists for a larva of *Polypocephalus* from a teleost (Butler 1984). Larvae of genera other than *Polypocephalus* (*e.g.*, those identified as *Tylocephalum*), however, are most commonly found associated with molluscan intermediate hosts. Larvae of this genus have only occasionally been found in teleosts and only rarely in crustaceans.

While no complete life cycles are known for any lecanicephalidean species, data based on adult and larval host associations suggest a few interesting scenarios. Species of *Polypocephalus* have been reported as adults in stingrays (Dasyatidae) and guitarfishes

Table 7. Selected reports of lecanicephalidean larvae.

PARASITE TYPE (and reference)	INTERMEDIATE HOST		LOCALITY
***Tylocephalum* larva**			
Butler (1984)	Crustacea:	3 species of slipper lobsters	Moreton Bay, QLD, Australia
Dollfus (1923)	Mollusca:	*Meleagina occa* & *M. irradians*	Nossi-Be, Madagascar
Sparks (1963)	Mollusca:	*Crassostrea virginica*	West Loch, Pearl Harbor, HI, U.S.A.
Sindermann & Rosenfield (1967)	Mollusca:	oysters	Japan and Taiwan
Cheng & Rifkin (1968)	Mollusca:	*Tapes semidecussata* (clam)	Kaneohe Bay, Oahu, HI, U.S.A.
Katkansky & Warner (1969)	Mollusca:	*Protothaca laciniata* (rough-sided littleneck clams)	Morro Bay, CA, U.S.A.
Sakaguchi (1973)	Mollusca:	marine molluscan shellfishes (10 species from 3 localities)	Japan
Cheng (1975)	Mollusca:	*Crassostrea gigas* (Japanese oyster)	coasts of Hong Kong & China
Reimer (1975)	Mollusca:	*Thais rudolphi* (oyster drill)	Madras, India
Wolf (1976)	Mollusca:	*Crassostrea commercialis* (Sydney rock oyster)	New South Wales & southern Queensland, Australia
Cake (1976)	Mollusca:	16 species of gastropods & 32 species of pelecypods	Northern Gulf of Mexico, U.S.A.
Cake (1977)	Mollusca:	13 species of gastropods & 28 species of pelecypods	Eastern Gulf of Mexico, U.S.A.
Stephen (1978)	Mollusca:	*Crassostrea madrasensis* (India backwater oyster)	estuary at Mulki, Karnataka, India
Cake & Menzel (1980)	Mollusca:	*Crassostrea virginica* (oyster), *Busycon contrarium*, *Murex pomum* & *Thais haemastoma canaliculata* (molluscivorous gastropods)	Eastern Gulf of Mexico, U.S.A.
Butler (1984)	Mollusca:	14 species	Moreton Bay, QLD, Australia
Liu *et al.* (1985)	Mollusca:	*Crassostrea gigas* (oyster)	Taiwan
Deleón Rodriguez *et al.* (1987)	Mollusca:	*Crassostrea virginica* (oyster)	Mecoacán, Tabasco, Mexico
Chandra (1981) (in Chandra [1983])	teleost:	[4 species of teleosts]	
Butler (1984)	teleost:	*Sillago ciliata* (Sand silago)	Moreton Bay, QLD, Australia
Murugesh (1995)	teleost:	*Scomberomorus guttatus* (Indi-Pacific king mackerel)	Visakhapatnam coast, Bay of Bengal, India
Moravec *et al.* (1997)	teleost:	*Epinephelus morio* (red grouper)	Yucatan, Mexico
***Polypocephalus* larva**			
Anantaraman (1959)	Crustacea:	*Squilla holochista* (stomatopod)	coast of Madras, India
Hutton (1964)	Crustacea:	10 species of shrimp	Florida, U.S.A.
Reimer (1984)	Crustacea:	*Penaeus japonicus* & *Metapenaeus monocerus*(shrimp)	coast of P.R. Mozambique
Butler (1984)	Crustacea:	stomatopods, portunids, penaeids & alpheids	Moreton Bay, QLD, Australia
Owens (1985)	Crustacea:	*Penaeus merguiensis* (banana prawn)	Gulf of Carpentaria, Australia
Brockerhoff & Jones (1995)	Crustacea:	*Portunus pelagicus* (blue-swimmer crab)	Hervey Bay, QLD, Australia
Reimer (1975)	Mollusca:	*Bullia melanoides* (bullia shell, gastropod)	Madras, India
Cake (1976)	Mollusca:	*Argopecten irradians concentricus* (bay scallop) (pelecypod)	Northern Gulf of Mexico
Butler (1984)	Mollusca:	6 species	Moreton Bay, QLD, Australia
Butler (1984)	teleost:	*Spheroides hamiltoni* [sic] (puffer)	Moreton Bay, QLD, Australia
***Cephalobothrium* larva**			
Chandra & Hanumantha Rao (1981)	Crustacea:	*Charybdis* (*Charybdis*) *cruciata* (crab)	Waltair, India

(Rhinobatidae), and in a species each of devils rays (Mobulidae), wedgefishes (Rhinidae), eagle rays (Myliobatidae), cownose rays (Rhinopteridae), stingarees (Urolophidae), and requiem sharks (Carcharhinidae). As a consequence, it does not seem unreasonable to speculate that, in general, these elasmobranchs become infected by feeding on macrocrustaceans infected with larval lecanicephalideans. Naturally, feeding strategies and stomach content data of the elasmobranch hosts should be taken into account when speculating about the life cycles that rely on trophic associations for completion. Whether macrocrustaceans ingest eggs directly or ingest infected smaller invertebrates, such as copepods that have consumed the eggs and are infected with first larval stages, remains to be determined.

Data on host associations of adults and larvae of *Tylocephalum*, however, suggest a slightly different life cycle scenario. Species of *Tylocephalum* have been reported as adults from cownose rays (Rhinopteridae) and wedgefishes (Rhinidae), and from a species each of stingrays (Dasyatidae), eagle rays (Myliobatidae), guitarfishes (Rhinobatidae), and angel sharks (Squatinidae). Again, in general, it is possible that these elasmobranchs become infected by ingesting molluscs infected with larval stages of *Tylocephalum*. As noted in the introduction, studies have suggested that oysters (and other filter feeding molluscs) may become directly infected by ingesting eggs (see Cake and Menzel 1980; Butler 1984) and predaceous gastropods may become infected by feeding on molluscs infected with first stage larvae (see Cake and Menzel 1980). Life cycle work in these groups is critically needed.

CONCLUSIONS

The primary goal of this monograph of the Lecanicephalidea was to establish a solid framework, especially at the generic level, on which future revisionary work on this group can build. In addition to supplying information in the form of taxonomic, systematic and biological data on the Lecanicephalidea, an attempt was made to identify key areas of research in this taxon that have been neglected (*e.g.*, sperm ultrastructure, life cycles). It is hoped that this monograph will serve as a resource to all future workers in the field of elasmobranch tapeworm systematics, especially those working on lecanicephalideans. The hypothesis of the interrelationships of lecanicephalideans, though not well supported, may allow the evolutionary implications of host associations and other broad evolutionary questions, such as the possible role of coevolution to be addressed in this system in the future.

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LITERATURE CITED

Note: Literature citations in square brackets were found as citions but were unobtainable.

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Appendix 1. Classification schemes relevant to the Lecanicephalidea.

Note: Lecanicephalidean genera (*genera inquirenda et incertae sedis*, *nomina nuda*, junior synonyms, *genera inquirenda* and valid genera) are indicated in bold.

Lönnberg (1889)

- Order Taeniada
  - Family Taeniidae
    - *Taenia*
- Order Tetraphyllida
  - Family Phyllobothridae
    - *Tetrabothrium*, *Anthobothrium*, *Phyllobothrium*, *Discobothrium*, *Echineibothrium* [sic], *Tritaphros*, *Trilocularia*
  - Family Phyllacanthidae
    - *Acanthobothrium*, *Onchobothrium*
  - Family Phyllorhynchidae
    - *Tetrarhynchus*
- Order Diphyllida
    - *Echinobothrium*
- Order Pseudophyllida
  - Family Bothriocephalidae
    - *Bothriocephalus*, *Ptychobothrium*, *Abothrium*
  - Family Ligulidae
    - *Schistocephalus*
  - Family Triaenophoridae
    - *Triaenophorus*
- Order Monobothrida
    - *Cyathocephalus*

Linton (1890)

Note: Only the genera in the subfamilies Phyllobothriinae and Phyllacanthinae are listed. Genera other than *Parataenia* are omitted from from the Taeniidae.

- Order Cestoidea
  - Family Pseudophyllidae Van Beneden
  - Family Tetrabothriidae Diesing (Tetraphyllidae [in part] Van Beneden)
    - Subfamily Phyllobothriinae Van Beneden
      - *Anthobothrium*, *Echeneibothrium*, *Rhinebothrium*, *Spongiobothrium*, *Discocephalum*, *Phyllobothrium*, *Anthocephalum*, *Orygmatobothrium*, *Crossobothrium*, ***Lecanicephalum***, ***Tylocephalum***
    - Subfamily Phyllacanthinae Van Beneden
      - *Calliobothrium*, *Acanthobothrium*, *Phoreiobothrium*, *Platybothrium*, *Thysanocephalum*
  - Family IV Tetrarhynchidae
    - Subfamily Dibothriorhynchinae
    - Subfamily Tetrabothriorhynchinae
  - Family V Taeniidae
      - ***Parataenia***

Braun (1894-1900)

Note: Only the genera in the families Onchobothriidae, Phyllobothriidae and Lecanicephalidae, and those *incertae sedis* are listed.

- Class Cestodes s. str. (excl. Cestodaria Mont.)
  - Order Pseudophyllidea Carus, 1863
    - Family Bothriocephalidae Cobb.
      - Subfamily Ligulinae Mont. and Crety.
      - Subfamily Dibothriocephalinae Lühe.
      - Subfamily Ptychobothriinae Lühe.
      - Subfamily Trianophorinae Lühe.
      - Subfamily Cyathocephalinae Lühe.
  - Order Tetraphyllidea Carus
    - Family Onchobothriidae (= Phyllacanthiens v. Ben.)
      - *Onchobothrius*, *Calliobothrium*, *Acanthobothrium*, *Prosthecobothriunm*, *Thysanocephalum*, *Platybothrium*, *Phoreiobothrium*, *Ceratobothrium*, *Cylindrophorus*
    - Family Phyllobothriidae (= Phyllobothriens v. Ben.)
      - *Anthobothrium*, *Monorygma*, *Trilocularia*, *Orygmatobothrium*, *Phyllobothrium*, *Dinobothrium*, *Calyptrobothrium*, *Crossobothrium*, *Diplobothrium*, *Tritaphros*, *Echeneibothrium* (*Discobothrium*, *Rhinebothrium*), *Spongiobothrium* (*Pelichnibothrium*, *Octobothrium*)
    - Family Lecanicephalidae = Gamobothriidae Lint. (*Fam. inq.*)
      - *Discocephalum*, ***Lecanicephalum*, *Tylocephalum***
    - Family Ichthyotaeniidae Ariola.
  - Order Cyclophyllidea v. Ben.
    - Family Taeniidae Ludw.
      - Subfamily Mesocestoidinae Stiles.
      - Subfamily Tetrabothriinae
      - Subfamily Anoplocephalinae R. Blanch.
      - Subfamily Dipylidiinae Raill.
      - Subfamily Davaineinae (= Echinocotylinae Perr. p. p.)
      - Subfamily Taeniinae Perr.
  - Order Diphyllidea Carus
    - Family Echinobothriidae Pintn.
  - Order Trypanorhyncha Dies.
- Genera *incertae sedis*: *Amphoteromorphus*, *Ephedrocephalus*, *Marsypoephalus*, ***Parataenia***, *Peltidocotyle*, ***Polypocephalus***, *Sciadocephalus*, *Tetracampos*, *Zygobothrium*

Perrier (1897)

Note: Only the genera in the families Tetrabothriidae and Gamobothriidae are listed (authorities are omitted).

- Class Cestoides
  - Order Cestodaria
    - Family Caryophyllaeidae
    - Family Archigetidae
  - Order Dicestoda
    - Family Bothriocephalidae
      - Tribe Bothridiinae
      - Tribe Bothriocephalinae
      - Tribe Bothrimoninae
      - Tribe Ligulinae
    - Family Bothriotaeniidae
    - Family Leuckartiidae
    - Family Triaenophoridae
  - Order Trypanorhyncha
    - Family Echinobothriidae
    - Family Rhynchobothriidae
    - Family Tetrarhynchidae
  - Order Tetracestoda
    - Family Tetracamipdae
    - Family Mesocestoidae
    - Family Tetrabothriidae
      - Tribe Calliobothriinae
        - *Calliobothrium*, *Acanthobothrium*, *Onchobothrium*, *Phoreiobothrium*, *Cylindrophorus*, *Prosthecobothriunm*, *Platybothrium*, *Polyonchobothrium*
      - Tribe Phyllobothriinae
        - *Echeneibothrium*, *Rhinebothrium*, *Spongiobothrium*, *Phyllobothrium*, *Anthobothrium*, *Crossobothrium*, *Anthocephalum*
      - Tribe Tetrabothriinae

Appendix 1. Continued.

- *Dinobothrium*, *Diplobothrium*, *Tetrabothrium*, *Ceratobothrium*, *Phyllobothrium*, *Monorygma*, *Calyptrobothrium*, *Pelichnibothrium*, *Zygobothrium*, *Orygmatobothrium*, *Marsypocephalus*, *Prosthecocotyle*, *Octobothrium*, ***Parataenia***, *Amphoterocotyle*, *Amphoteromorphus*, *Peltidocotyle*, *Ephedocephalus*
- Family Gamobothriidae
    - ***Lecanicephalum***, ***Tylocephalum***, *Discocephalum*, *Sciadocephalus*
- Family Taeniidae
    - Tribe Tetracotylinae
    - Tribe Echinocotylinae
    - Tribe Hymenolepinae
    - Tribe Taeniinae
    - Tribe Anoplocephalinae

Ariola (1899)

- Subclass Cestoda
    - Order Dibothria
        - Tribe Atomiosoma
            - Family Ligulidae
            - Family Tricuspidaridae
            - Family Bothriomonidae
            - Family Cyathobothridae
        - Tribe Tomiosoma
            - Family Leuckartidae
            - Family Dibothriorhynchidae
            - Family Dibothriotetrarhynchidae
            - Family Dibothridae
    - Order Tribothria
        - Family Scyphocephalidae
    - Order Tetrabothria
        - Suborder Tetrabothriina
            - Tribe Mesoporina
                - Family Tetracampidae
                - Family Amphilocotylidae
            - Tribe Pleuroporina
                - Family Tetrabothridae
                - Family Phyllobothridae
                - Family Calliobothridae
                - Family Tetrabothriorhynchidae
                - Family Gamobothridae
        - Suborder Tetracotylina
            - Tribe Mesoporina
                - Family Mesocestoidae
            - Tribe Pleuroporina
                - Family Ichthyotaeniidae
                - Family Anoplotaeniidae
                - Family Hymenolepidae
                - Family Taeniidae
                - Family Echinocotylidae
    - Order Octobothria
        - Family Octobothridae

de Beauchamp (1905)

Note: *Polypocephalus*, among other genera, is placed in this order; the order is not given in the second part of the publication where individual genera and species are treated.

- Order Pseudophylles Van Beneden or Bothriocephalides *sensu latiori*
- Order Tetraphylles Van Beneden
    - Family Phyllacanthides
        - *Acanthobothrium*, *Onchobothrium*
    - Family Phyllobothrides
        - Tribe Phyllobothrines
            - *Phyllobothrium*, *Monorygma*
        - Tribe Echeneibothrines
            - *Discobothrium*, *Echeneibothrium*
    - Family Gamobothrides
- Order Diphylles Van Beneden
    - Family Echinobothides
        - *Echinobothrium*
- Order Trypanorhynques Diesing
    - Family Rhynchobothrides
        - *Rhynchobothrius*
- Order Tetracotyles Diesing or Teniades *sensu latiori*
    - [***Polypocephalus*** (***Parataenia***)]

Mola (1921)

Note: Subfamilies are listed only in the family Bothriocephalidae; genera are listed only in the subfamily Lecanicephalinae.

- Cestodes
    - Order Pseudophyllidea
        - Family Ligulidae
        - Family Bothriocephalidae
    - Order Monophyllidea
    - Order Diphyllidea
        - Family Dibothriophyllidae
            - Subfamily Amphicotylinae
            - Subfamily Solenophorinae
            - Subfamily Lecanicephalinae
                - ***Lecanicephalum***, ***Tylocephalum*, etc.**
            - Subfamily Bothrimoninae
            - Subfamily Dittocephalinae
        - Family Dibothriacanthidae
    - Order Tetraphyllidea
        - Family Tetraphyllacanthidae
        - Family Tetraphyllabothridae
        - Family Proteocephalidae
    - Order Cyclophyllidea
        - Family Tetrabothriidae
        - Family Mesocestoididae
        - Family Anoplocephalidae
        - Family Davaineidae
        - Family Dilepididae
        - Family Hymenolepididae
        - Family Taeniidae
        - Family Acoleidae
        - Family Ambiliidae
        - Family Fimbriariidae
    - Order Rhynchophyllidea
        - Family Dibothriorhynchidae
        - Family Tetrabothriorhynchidae

Meggitt (1924)

Note: Families are listed only for the order Tetraphyllidea. Genera are listed only in the families Lecanicephalidae, Onchobothriidae, Phyllobothriidae and Polypocephalidae.

- Class Cestoda
    - Subclass Cestodaria Monticelli, 1892
    - Subclass Rhynchostomida Plehn, 1905
    - Subclass Cestoda s. str.
        - Order Cyclophyllidea Carus
        - Order Pseudophyllidea Carus, 1863

Appendix 1. Continued.

Order Tetraphyllidea
Family Ichthyotaeniidae Ariola, 1899
Family Lecanicephalidae Braun, 1900
Adelobothrium, ***Cephalobothrium***, *Discocephalum*, ***Lecanicephalum***, ***Tylocephalum***
Family Onchobothriidae Braun, 1900
Acanthobothrium, *Balanobothrium*, *Calliobothrium*, *Ceratobothrium*, *Cylindrophorus*, *Onchobothrium*, *Pedibothrium*, *Phyllobothroides Platybothrium*, *Prosthecobothrium*, *Thysanocephalum*
Family Phyllobothriidae Braun, 1900
Anthobothrium, *Aocobothrium*, *Bilocularia*, *Calyptobothrium*, *Carpobothrium*, *Dinobothrium*, *Diplobothrium*, *Echeneibothrium*, ***Eniochobothrium***, ***Hornellobothrium***, *Monorygma*, *Myzocephalus*, *Myzophyllobothrium*, *Oriana*, *Orygmatobothrium*, *Pelichnibothrium*, *Peltidocotyle*, *Phyllobothrium*, *Prosobothrium*, *Rhinebothrium*, *Rhoptrobothrium*, *Spongiobothrium*, *Tiarabothrium*, *Trilocularia*, *Tritaphros*, *Zygobothrium*
Family Polypocephalidae *nov. fam.*
Anthemobothrium, ***Calycobothrium***, ***Polypocephalus***
Order Trypanorhyncha Diesing, 1863

Southwell (1925)

Order Pseudophyllidea Carus, 1863
Order Cyclophyllidea Braun, 1900
Suborder Univitellata (all species & genera from Cyclophyllidea Braun, 1900 [= superfamily Taenioidea Stiles, 1906], incl. *Phanobothrium*)
Suborder Multivitellata
Family Proteocephalidae La Rue, 1914
Family Lecanicephalidae Braun, 1900 (syn. Gamobothriidae Linton, 1889, Polypocephalidae Meggitt, 1924) (not Lecanocephalidae Diesing, 1861, nematode family)
Balanobothrium, ***Calycobothrium***, ***Polypocephalus***, ***Cephalobothrium***, ***Tylocephalum***, ***Lecanicephalum***, ***Adelobothrium***
Suborder A (not defined)
Diplobothrium (= *Oriana*), ***Eniochobothrium***
Order Tetraphyllidea Braun, 1900
Order Trypanorhyncha Diesing, 1863
Order Heterophyllidea, new
Echinobothrium, *Peltidocotyle*, *Amphoteromorphus*, *Discocephalum*, *Diagonobothrium*
Genera intermediate between Cyclophyllidea & Tetraphyllidea:
Zygobothrium, ***Staurobothrium***, *Discobothrium* (= ***Hornellobothrium***), *Prosobothrium*

Poche (1926)

Note: Only genera in the families Phyllobothriidae, Lecanicephalidae, Polypocephalidae and in genera *Phyllobothriineorum sedis incertae* are listed.

Class Cestoidea Rud.
Subclass Amphilinoidei *nom. nov.*
Order Amphilinidea Poche
Family Amphilinidae Claus
Order Gyrocotylidea *nom. nov.*
Family Gyrocotylidae Benham
Subclass Taenioinei *nom. nov.*
Order Bothriocephalidea Dies.
Tribe Caryophyllaeoidae *nom. nov.*
Family Cyathocephalidae Nybelin
Family Caryophyllaeidae Claus
Tribe Diphyllobothridoidae *nom. nov.*
Family Diphyllobothriidae Lühe
Family Lüheellidae Baer
Tribe Bothriocephaloidae *nom. nov.*
Family Bothriocephalidae E. Blanchard
Tribe Triaenophoroidae *t. nov.*
Family Triaenophoridae E. Blanchard
Family Amphicotylidae Ariola
Family Echinophallidae Schumacher
Tribe Tetrabothrioidae *t. nov.*
Family Tetrabothriidae Fuhrmann
Order Echinobothriidea *nom. nov.*
Family Echnobothriidae Perrier
Order Tetrarhynchidea *nom. nov.*
Suborder Haplobothriinea *so. nov.*
Family Haplobothriidae Meggitt
Suborder Tetrarhynchinea *nom. nov.*
Subtribe Tetrarhynchoinae *nom. nov.*
Family Tentaculariidae *nom. nov.*
Subtribe Aporhynchoinae *st. nov.*
Family Aporhynchidae *f. nov.*
Order Taeniidea *nom. nov*.
Suborder Phyllobothriinea *nom. nov.*
Family Onchobothriidae Braun
Family Phyllobothriidae Braun
Anthobothrium, *Aocobothrium*, *Bilocularia*, *Calyptobothrium*, *Carpobothrium*, *Dinobothrium*, *Diplobothrium*, *Echeneibothrium*, ***Hornellobothrium***, *Monorygma*, *Myzocephalus*, *Myzophyllobothrium*, *Oriana*, *Orygmatobothrium*, *Pelichnibothrium*, *Phyllobothrium*, *Prosobothrium*, *Rhinebothrium*, *Rhoptrobothrium*, *Spongiobothrium*, *Tiarabothrium*, *Trilocularia*, *Tritaphros*, ***Staurobothrium***
Family Lecanicephalidae Braun
Adelobothrium, ***Cephalobothrium***, *Discocephalum*, ***Lecanicephalum***, ***Tylocephalum***, *Balanobothrium*
Family Proteocephalidae La Rue
Family Monticelliidae Fuhrmann & Baer
Family Polypocephalidae Meggitt
Anthemobothrium, ***Calycobothrium***, ***Polypocephalus***, ***Parataenia***
Genera *Phyllobothriineorum sedis incertae*:
Eniochobothrium, *Merocestus*, *Amphoteromorphus*, *Peltidocotyle*, *Marsypocephalus*
Suborder Taeniinea *nom. nov.*
Family Phanobothriidae *f. nov.*
Family Mesocestoididae Benham
Family Anoplocephalidae Kholodkovsky
Family Davaineidae Fuhrmann
Family Nemtotaeniidae Lühe
Family Dilepididae Railliet & Henry
Family Hymenolepididae Railliet & Henry
Family Taeniidae Haldeman
Family Diplopsthidae *f. nov.*
Family Acoleidae Ransom
Family Amabiliidae Fuhrmann
Fam. *Cestoideorum* ? *sedis incertae* Nematoparataeniidae *f. nov.*

Appendix 1. Continued.

Woodland (1927)

Note: Genera and species mentioned are only those considered "lecanicephalids."

- Order Pseudophyllidea
- Order Cyclophyllidea
- Order Tetraphyllidea
  - Family Phyllobothriidae *sens. nov.*
    - ***Lecanicephalum*** (*L. peltatum*), ***Cephalobothrium*** (*C. abruptum*, *C. variabile*), *Balanobothrium* (*B. tenax*, *B. parvum*), ***Polypocephalus*** (*P. radiatus*, *P. medusia*), ***Calycobothrium*** (*C. typicum*), ***Tylocephalum*** *yorkei*
  - Family Tetrarhynchidae Cobbold (Trypanorhyncha Diesing)
    - ***Adelobothrium*** (*A. aetiobatidis*)
  - Family Proteocephalidae
    - *Lintoniella adhaerens* (= *Prosobothrium adherens*)
- not placed: ***Tylocephalum*** (*T. trygonis*, *T. uarnak*), *Phanobothrium monticelli*, *Discocephalum pileatum*)

Pintner (1928)

- Order Amphilinidea
  - Family Amphilinidae
  - Family Gyrocotylidae
- Order Cestodes s. str.
  - Family Bothriocephalidae
  - Family Echinobothriidae
  - Family Tetrarhynchidae
  - Family Tetraphyllidae
  - Family Proteocephalidae
  - Family Taeniidae
  - Family Discocephalidae
  - Family Tetragonocephalidae
  - Family Cephalobothriidae
  - Family Balanobothriidae

Mola (1929)

Note: Subfamilies are listed only in the families Dibothriophyllidae and Ichthyotaeniidae. Genera are listed only in the subfamilies Lecanicephalinae and Polypocephaliinae and in the family Tetraphyllabothridae.

- Class Cestodaria Monticellli, 1892 (= Amphilinoinei Poche, 1925)
  - Order Amphilinidea Poche, 1922
    - Family Amphilinidae Claus, 1879
  - Order Gyrocotylidea Poche, 1925
    - Family Gyrocotylidae Benham, 1901
  - Order Caryophyllidea Mola, 1929
    - Family Caryophyllaeidae Claus, 1879
- Class Cestoda Monticelli, 1892
  - Order Pseudophyllidea Mola, 1921
    - Family Ligulidae Claus, 1861
    - Family Bothriocephalidae E. Blanchard, 1849
  - Order Monophyllidea Mola, 1921
    - Family Cyathocephalidae Nybelin, 1922
    - Family Discocephalidae Mola, 1929
  - Order Diphyllidea Mola, 1921
    - Family Dibothriophyllidae Mola, 1921
      - Subfamily Amphicotylinae Mola, 1921
      - Subfamily Solenophorinae Mont. & Crety, 1891
      - Subfamily Lecanicephalinae Mola, 1921
        - ***Lecanicephalum***, ***Tylocephalum***
      - Subfamily Bothrimoninae Mola, 1921
      - Subfamily Dittocephalinae Mola, 1921
    - Family Dibothriacanthidae Mola, 1921
  - Order Tetraphyllidea Carus, 1863
    - Family Tetraphyllacanthidae Mola, 1921
    - Family Tetraphyllabothridae Mola, 1921
      - *Anthobothrium*, *Phyllobothrium*, *Orygmatobothrium*, *Calyptrobothrium*, *Crossobothrium*, *Diplobothrium*, *Tritaphros*, *Echeneibothrium*, *Rhinebothrium*, *Prosobothrium*, *Dinobothrium*, *Cyatocotyle*, *Polipobothrium*, *Aocobothrium*, *Spongiobothrium*, *Monorygma*, *Trilocularia*, ***Cephalobothrium***
    - Family Ichthyotaeniidae Ariola, 1899
      - Subfamily Monticelliinae Mola, 1929
      - Subfamily Ephedrocephalinae Mola, 1929
      - Subfamily Proteocephalinae Mola, 1929
      - Subfamily Polypocephaliinae Mola, 1929
        - ***Polypocephalus*** (= ***Parataenia***)
  - Order Cyclophyllidea Van Beneden, 1850
    - Suborder Cyclophyllanacanthidae Mola, 1929
      - Tribe Tetrabothrioidae Mola, 1929
        - Family Tetrabothriidae Fuhr., 1907
        - Family Mesocestoididae Fuhr., 1907
      - Tribe Anoplocephalioidae Mola, 1929
        - Family Anoplocephalidae Mola, 1929
        - Family Linstowidae Mola, 1929
        - Family Thysanosomidae Mola, 1929
        - Family Nematotaeniidae Lühe, 1910
    - Suborder Cyclophyllacantha Mola, 1929
      - Tribe Viscoioidae Mola, 1929
        - Family Viscoidae Mola, 1929
      - Tribe Davaineioidae Mola, 1929
        - Family Davaineidae Mola, 1929
        - Family Ophryocotylidae Mola, 1929
        - Family Idiogenidae Mola, 1929
      - Tribe Dilepinioidae Mola, 1929
        - Family Dilepinidae Mola, 1929
        - Family Dipylidiidae Mola, 1929
        - Family Paruteriidae Mola, 1929
      - Tribe Phanobothrioidae Mola, 1929
        - Family Phanobothridae Poche, 1925
      - Tribe Taenioidae Mola, 1929
        - Family Taeniidae Perrier, 1897
      - Tribe Hymenolepidioidae Mola, 1929
        - Family Hymenolepididae Fuhrm. 1907
        - Family Diploposthidae Poche, 1925
      - Tribe Acoleinidae Mola, 1929
        - Family Acoleinidae Fuhr., 1907
      - Tribe Amabilinioidae Mola, 1929
        - Family Ambilinidae Fuhr., 1907
      - Tribe Fimbriarioidae Mola, 1929
        - Family Fimbriariidae Wolffhügel, 1900
      - Tribe Echinorhynchotioidae Mola, 1929
        - Family Echinorhynchotiidae Mola, 1929
  - Order Rhynchophyllidea Mola, 1921
    - Family Dibothriorhynchidae Mola, 1921
    - Family Tetrabothriorhynchidae Mola, 1921

Southwell (1930)

Note: Only the genera in the family Lecanicephalidae and those of uncertain systematic position are listed.

- Order Eucestoda *nov.*
  - Superfamily Dibothriocephaloidea Stiles, 1906
    - Family Dibothriocephalidae Lühe, 1902
    - Family Triaenophoridae Nybelin, 19020

Appendix 1. Continued.

- Family Ptychobothriidae Lühe, 1902
- Family Amphicolylidae Nybelin, 1920
- Family Echinophallidae Schumacher, 1914

Superfamily Tetrarhynchoidea, *nov.* (syn. Trypanorhyncha Diesing, 1863)

- Family Tetrarhynchidae Cobbold, 1864
- Family Coenomorphidae Lühe, 1910
- Family Haplobothriidae Meggitt, 1924

Superfamily Phyllobothrioidea, *nov.* (syn Tetraphyllidea Carus, 1863)

- Family Phyllobothriidae Braun, 1900
- Family Onchobothriidae Braun, 1900

Superfamily Lecanicephaloidea, *nov.*

- Family Lecanicephalidae Braun, 1900
  - ***Lecanicephalum***, ***Cephalobothrium***, ***Tylocephalum***, ***Adelobothrium***, ***Balanobothrium***, ***Polypocephalus***, ***Calycobothrium***, ***Staurobothrium***; of uncertain systematic position, probably in this family: ***Eniochobothrium***, *Discobothrium*

Superfamily Proteocephaloidea, *nov.*

- Family Proteocephalidae La Rue, 1911

Superfamily Taenioidea Zwicke, 1841 (syn. Cyclophyllidea Braun, 1900)

- Family Taeniidae Ludwig, 1886
- Family Anoplocephalidae Cholodkowsky, 1902
- Family Davaineidae Fuhrmann, 1907
- Family Hymneolepididae Railliet & Henry, 1909
- Family Dilepididae Railliet & Henry, 1909
- Family Mesocetoididae Fuhrmann, 1907
- Family Nematotaeniidae Lühe, 1910
- Family Ambiliidae Fuhrmann, 1908
- Family Acoleidae Ransom, 1909
- Family Tetrabothriidae Linton, 1891
- Family Dioicocestidae *nov.*

Genera of uncertain systematic position: *Echinobothrium*, *Discocephalum*, *Diagonobothrium*, *Pillersia* [sic]

Fuhrmann (1931)

Note: Only the genera in the families Phyllobothriidae, Onchobothriidae, Lecanicephalidae, Cephalobothriidae, Discocephalidae and those insufficiently known in the Tetraphyllidea are listed.

- Class Cestoidea
  - Subclass Cestodaria Monticelli
    - Order Amphilinidea Poche
    - Order Gyrocotylidea
  - Subclass Cestoda
    - Order Tetraphyllidea
      - Family Phyllobothriidae Van Beneden
        - *Phyllobothrium* (syn. *Monorygma*, *Crossobothrium* and *Anthocephalum*), *Anthobothrium* (syn. *Spongiobothrium*), *Orygmatobothrium*, *Dinobothrium*, *Scyphophyllidium*, *Carpobothrium*, *Trilocularia*, *Bilocularia*, *Calyptrobothrium*, *Tritaphros*, *Ceratobothrium*, *Myzophyllobothrium* (syn. *Rhoptrobothrium*), *Echeneibothrium* (syn. *Tiarabothrium* and *Rhinebothrium*)
      - Family Onchobothriidae Braun
        - *Onchobothrium*, *Acanthobothrium*, *Calliobothrium*, *Uncibilocularis*, *Platybothrium*, *Pedibothrium*, *Spiniloculus*, *Balanobothrium*, *Yorkeria*, *Cylindrophorus* (syn. *Phoreiobothrium*), *Thysanocephalum* (syn. *Myzocephalus*?) [sic]
      - Family Lecanicephalidae Braun (syn. Gamobothriidae Linton)
        - ***Lecanicephalum*** (syn. ***Tylocephalum*** ex parte, ***Tetragonocephalum*** and ***Cephalobohrium*** ex parte), ***Polypocephalus*** (syn. ***Parataenia***, ***Thysanobothrium***), ***Anthemobothrium***, ***Adelobothrium***
      - Family Cephalobothriidae (Pintner)
        - ***Cephalobothrium***, ***Tylocephalum*** (ex parte), *Discobothrium*
      - Family Proteocephalidae La Rue
      - Family Monticelliidae La Rue
      - Family Discocephalidae Pintner
        - *Discocephalum*
    - Uncertain and not sufficiently known, but very interesting genera: *Diplobothrium*, ***Staurobothrium***, ***Hornellobothrium***, ***Eniochobothrium***, *Pelichnibothrium*, *Pithophorus*, ***Calycobothrium*** (syn. ***Cyclobothrium***), *Pillersium*, *Polipobothrium*, *Aocobothrium*, *Cyatocotyle*, *Prosobothrium*, *Phanobothrium*, *Merocestus*
    - Order Diphyllidea
    - Order Tetrarhynchidea
    - Order Pseudophyllidea
    - Order Cyclophyllidea

Joyeux and Baer (1936)

- Class Cestoidea
  - Subclass Cestodaria Monticelli, 1892
    - Order Gyrocotylidea Fuhrmann, 1931
    - Order Amphilinidea Poche, 1926
  - Subclass Cestoda Carus, 1885
    - Order Tetrarhynchidea Olsson, 1893
    - Order Diphyllidea Carus, 1863
    - Order Tetraphyllidea Carus, 1863
      - Family Cephalobothriidae Pintner, 1928
      - Family Disculicipitidae Joyeux & Baer, 1936
      - Family Ichthyotaeniidae Ariola, 1899 (syn. Proteocephalidae La Rue, 1911)
      - Family Phyllobothriidae Braun, 1900
      - Family Onchobothiidae Braun, 1900
    - Order Pseudophyllidea Carus, 1863
    - Order Cyclophyllidea Braun, 1900

Hyman (1951)

Note: Classification below order is presented omly for the order Lecanicephaloidea.

- Class Cestoda
  - Subclass Cestodaria
    - Order Amphilinidea
    - Order Gyrocotylidea
    - Order Tetraphyllidea
    - Order Lecanicephaloidea
      - Family Lecanicephalidae
        - ***Lecanicephalum***, ***Polypocephalus*** (= ***Parataenia***, ***Thysanobothrium***), ***Anthemobothrium***, ***Adelobothrium***
      - Family Cephalobothriidae
        - ***Cephalobothrium***, ***Discobothrium***, ***Tylocephalum***
      - Family Discocephalidae
        - *Discocephalum*
    - Order Proteocephaloidea
    - Order Diphyllidea
    - Order Typanorhyncha or Tetrarhynchoidea

Appendix 1. Continued.

- Order Pseudophyllidea
- Order Nippotaeniidea
- Order Taenioidea or Cyclophyllidea
- Order Aporidea

Wardle and McLeod (1952)

Note: Classification below order is presented only for the order Lecanicephala.

- Class Cestodaria
  - Order Amphilinidea Poche, 1922
  - Order Gyrocotylidea new order [sic]
  - Order Biporophyllidea Subramanian [sic], 1939
- Class Cestoda
  - Order Proteocephala new order
  - Order Tetraphyllidea Braun, 1900
  - Order Disculicepitidea new order
  - Order Lecanicephala new order
    - Family Lecanicephalidae Braun, 1900, emended Pintner, 1928
      - ***Lecanicephalum***, ***Tetragonocephalum***, ***Parataenia***
    - Family Cephalobothriidae Pintner, 1928
      - ***Cephalobothrium***, ***Hexacanalis***, ***Tylocephalum***, ***Polypocephalus***, ***Adelobothrium***, ***Anthemobothrium***, ***Staurobothrium***
  - *Genus Inquirendum* (Lecanicephala, tetraphyllidea or Disculicepitidea): ***Calycobothrium*** (= ***Cyclobothrium***, preoccupied), *Diplobothrium* (= *Tetrabothrium*, = *Oriana*), ***Eniochobothrium***, *Phanobothrium*, *Discobothrium* (= ***Hornellobothrium***), *Prosobothrium*, *Echinobothrium*, *Pillersium*, *Diagonobothrium*
  - Order Trypanorhyncha Diesing, 1863
  - Order Cyclophyllidea Braun, 1900
  - Order Aporidea Fuhrmann, 1933
  - Order Nippotaeniidea Yamaguti, 1939
  - Order Caryophyllidea new order
  - Order Spathebothridea new order
  - Order Pseudophyllidea Carus, 1863

Riser (1955)

- Superorder Trixenidea *nov.*
  - Order Tetraphyllidea (= Tetraphyllidea Carus, 1863, *sensu* Fuhrmann, 1930, plus Diphyllidea Carus, 1863, and Tetrabothridea Baer, 1954)
    - Superfamily Phyllobothrioidea Southwell, 1930
      - Family Phyllobothriidae Braun, 1900
      - Family Onchobothriidae Braun, 1900
      - Family Echeneibothriidae *nov.*
    - Superfamily Lecanicephaloidea Southwell, 1930
      - Family Lecanicephalidae Braun, 1900, *sensu* Baer, 1948
      - Family Cephalobothriidae Pintner, 1928
      - Family Balanobothriidae Pintner, 1928
      - Family Disculicipitidae Joyeux et Baer, 1935
      - Family Echinobothriidae Fuhrmann, 1930
    - Superfamily Proteocephaloidea Southwell, 1930
    - Superfamily Tetrabothrioidea *nov.* (= Tetrabothridea Baer, 1948)
  - Order Pseudophyllidea Carus, 1863
  - Order Trypanorhyncha Diesing, 1863, *sensu* Dollfus, 1942
- Superorder Dixenidea *nov.* (= Order Cyclophyllidea Braun, 1900)

Euzet (1956)

- Order Tetraphyllidea Carus, 1863
  - Superfamily Phyllobothriides *nov.*
    - Family Phyllobothriidae Braun
      - Subfamily Phyllobothriinae
      - Subfamily Echeneibothriinae *nov.*
      - Subfamily Rhinebothriinae *nov.*
      - Subfamily Thysanocephalinae *nov.*
    - Family Onchobothriidae Braun
  - Superfamily Lecanicephalides *nov.*
    - Family Lecanicephalidae Braun
    - Family Cephalobothriidae Pintner
  - Superfamily Prosobothriides *nov.*
    - Family Prosobothriidae Baer & Euzet
    - Family Phoreiobothriidae Baer & Euzet
- not placed: Family Disculicepitidae Joyeux & Baer

Spasski (1958)

- Order Tetraphyllidea (Beneden, 1849) Carus, 1863
  - Suborder Phyllobothriata Spassky *n. nov.* = Tetraphyllata Spassky, 1957
    - Superfamily Lecanicephaloidea Southwell, 1930
      - Family Tetraphyllidae (syn. Lecanicephalidae Braun, 1900)
      - Family Cephalobothriidae Pintner, 1928
    - Superfamily Phyllobothrioidea Southwell, 1930
      - Family Phyllobothriidae (Ariola, 1899) Braun, 1900
      - Family Onchobothriidae Braun, 1900
  - Suborder Proteocephalata Spassky, 1957
  - Suborder Tetrabothriata (Ariola, 1899) Skrjabin, 1940
  - Suborder Nippotaeniata, n. subordo
- Order Trypanorhyncha Diesing, 1863
- Order Cyclophyllidea Braun, 1900 = Taeniidea (Carus, 1863)
  - Suborder Anoplocephalata Skrjabin, 1933 = Cyclophyllacantha Mola, 1929
  - Suborder Taeniata Skrjabin & Schulz, 1937
  - Suborder Mesocestoidata Skrjabin, 1940
- Order Pseudophyllidea (Beneden, 1949) Carus, 1863

Euzet (1959)

- Order Tetraphyllidea Carus, 1863
  - Superfamily Phyllobothrioidea Southwell, 1930
    - Family Phyllobothriidae Braun, 1900
      - Subfamily Phyllobothriinae de Beauchamp, 1905
      - Subfamily Echeneibothriinae de Beauchamp, 1905
      - Subfamily Rhinebothriinae Euzet, 1953
      - Subfamily Thysanocephalinae Euzet, 1953
    - Family Onchobothriidae Braun, 1900
  - Superfamily Prosobothrioidea *nov.*
    - Family Prosobothriidae Baer & Euzet, 1955
      - Subfamily Prosobothriinae *nov.*
      - Subfamily Platybothriinae *nov.*
    - Family Phoreiobothriidae
      - Subfamily Phoreiobothriinae *nov.*
      - Subfamily Reesiinae *nov.*
    - Family Gastrolecithidae Euzet, 1955
  - Superfamily Lecanicephaloidea Southwell, 1930
    - Family Lecanicephalidae Braun, 1900, *sensu* Baer, 1948
    - Family Cephalobothriidae Pintner, 1928
- Systematic position not established: Family Disculicepitidae Joyeux & Baer, 1936

Appendix 1. Continued.

Yamaguti (1959)

Note: Classification below order is presented only for the Lecanicephalidea.

Subclass Cestodaria Monticelli, 1892
Order Amphilinidea Poche, 1922
Order Gyrocotylidea Poche, 1926
Order Caryophyllidea Ben. in Olsson, 1893
Subclass Eucestoda Southwell, 1930
Order Spathebothriidea Wardle & McLeod, 1952
Order Pseudophyllidea Carus, 1863
Order Diphyllidea Ben. in Carus, 1863
Order Tetraphyllidea Carus, 1863
Order Lecanicephalidea Baylis, 1920
Family Lecanicephalidae Braun, 1900
Lecanicephalum (nec *Lecanocephalus* Diesing, 1851), ***Calycobothrium*** (syn. ***Cyclobothrium***, preoccupied), ***Cephalobothium***, ***Hexacanalis***, ***Polypocephalus*** (syn. ***Parataenia***, ***Thysanobothrium***, ***Anthemobothrium***), ***Tylocephalum*** (syn. ***Kystocephalus***, ***Aphanobothrium***)
Family Adelobothriidae n. fam.
Adelobothrium
Family Balanobothriidae Pintner, 1928
Balanobothrium
Family Disculicepitidae Joyeux & Baer, 1935 (syn. Discocephalidae Pintner, 1928)(nec Fieber, 1861 [Hemiptera])
Disculiceps (syn. *Discocephalum*, nec *Discocephala* Laporte-Castelnau, 1832; Macquart, 1838; *Discocephalus* Ehrenberg, 1829; Kirschbaum, 1858; Leger, 1892; Gemminger & Harold, 1868)
Family Tetragonocephalidae n. fam.
Tetragonocephalum
Genera Incertae Sedis in Lecanicephalidea: *Diagonobothrium*, *Diplobothrium*, *Discobothrium* (syn. ***Hornellobothrium***), ***Eniochobothrium***, *Phanobothrium*, *Pillerisium* [sic], ***Staurobothrium***
Order Nippotaeniidea Yamaguti, 1939
Order Trypanorhyncha Diesing, 1863
Order Proteocephalidea Mola, 1928

Joyeux and Baer (1961)

Note: Classification below order is presented only for the Tetraphyllidea.

Class Cestoda Carus
Order Haplobothrioidea Baer
Order Pseudophyllidea Carus
Order Tetrarhynchidea Claus
Order Diphyllidea Van Beneden
Order Tetraphyllidea Carus
Superfamily Phyllobothrioidea Southwell
Family Phyllobothriidae Braun
Subfamily Phyllobothiinae Carus
Anthobothrium Calyptrobothrium, *Carpobothrium*, *Ceratobothrium*, *Crossobothrium*, *Dinobothrium*, *Inermiphyllidium*, *Marsupiobothrium*, *Monorygma*, *Orygmatobothrium*, *Phyllobothrium*, *Pillersium*, *Pithophorus*, *Polypobothrium*, *Scyphophyllidium*, *Sphaerobothrium*, ***Staurobothrium***
Subfamily Echeneibothriinae de Beauchamp
Clydonobothrium, *Echeneibothrium*, *Pseudanthobothrium*, *Tritaphros*
Subfamily Rhinebothriinae Euzet
Caulobothrium, *Rhabdotobothrium*, *Rhinebothrium*, *Tiarabothrium*
Subfamily Thysanocephalinae Baer & Euzet
Myzocephalus, *Myzophyllobothrium*, *Rhoptrobothrium*, *Thysanocephalum*
Family Onchobothriidae Braun
Acanthobothrium, *Balanobothrium*, *Calliobothrium*, *Onchobothrium Pediobothrium* [sic], *Pinguicollum*, *Spiniloculus*, *Uncibilocularis*, *Yorkeria*
Superfamily Lecanicephaloidea Southwell
Family Lecanicephalidae Braun
Anthemobothrium, *Calycobothrium*, ***Lecanocephalum*** [sic], ***Polypocephalus*** (= ***Parataenia***)
Family Cephalobothriidae Pintner
Adelobothrium, ***Cephalobothrium***, ***Hexacanalis***, ***Tetragonocephalum***
Superfamily Prosobothrioidea Euzet
Family Prosobothiidae Baer & Euzet
Subfamily Platybothriinae Euzet
Dicranobothrium, *Platybothrium*
Family Phoreiobothriidae Baer & Euzet
Subfamily Phoreiobothiinae Euzet
Phoreiobothrium
Subfamily Reesiinae Euzet
Reesium, *Trilocularia*
Family Gastrolecithidae Euzet
Gastrolecithus
Family Disculicepitidae Joyeux & Baer
Disculiceps
Genera insufficiently described: ***Eniochobothrium***, ***Hornellobothrium***
Order Nippotaeniidea Yamaguti
Order Ichthytaeniidea *nov. nom. pro* Proteocephala Wardle & McLeod nec Blainville
Order Tetrabothridea Baer
Order Cyclophyllidea Van Beneden
Order Aporidea Fuhrmann

Schmidt (1970)

Note: Classification below order is presented only for the Lecanicephalidea only.

Subclass Cestodaria Monticelli, 1891
Subclass Eucestoda Southwell, 1930
Order Carylophyllidea Beneden in Olsson, 1893
Order Spathebothridea Wardle & McLeod, 1953
Order Trypanorhyncha Diesing, 1863
Order Pseudophyllidea Carus, 1863
Order Lecanicephalidea Baylis, 1920
Family Balanobothriidae Pintner, 1928
Balanobothrium
Family Disculicepitidae Joyeux & Baer, 1935
Disculiceps
Family Adelobothriidae Yamaguti, 1959
Adelobothrium
Family Lecanicephalidae Braun, 1900
Polypocephalus, ***Calycobothrium***, ***Staurobothrium***, ***Hexacanalis***, ***Tetragonicephalum*** [sic], ***Lecanicephalum***
Order Aporidea Fuhrmann, 1934
Order Tetraphyllidea Carus, 1863
Order Diphyllidea Beneden in Carus, 1863
Order Litobothridea Dailey, 1969
Order Nippotaeniidea Yamaguti, 1939
Order Proteocephalidea Mola, 1928
Order Cyclophyllidea Beneden in Braun, 1900

Appendix 1. Continued.

Wardle, McLeod and Radinovsky (1974)

Order Gyrocotylidea Poche, 1926
Order Amphilinidea Poche, 1922
Order Caryophyllidea Benden (in Olsson, 1893)
Order Spathebothridea Wardle and McLeod, 1952
(Spathebothrididea Ronald, 1958; Spathebothriidea Yamaguti, 1959)
Order Pseudophyllidea Carus, 1863
Order Diphyllidea, new order
Order Proteocephalidea Mola, 1928
Order Tetraphyllidea Carus, 1863
Order Litobothridea Dailey, 1969
Order Lecanicephalidea Baylis, 1920
Order Trypanorhyncha Diesing, 1863
Order Mesocestoididea,new order
Order Tetrabothriidea Baer, 1954 (as Tetrabothridea)
Order Nematotaeniidea, new order
Order Taeniidea, new order
Order Davaineidea, new order
Order Anoplocephalidea, new order
Order Hymenolepididea, new order
Order Dilepididea, new order
Order Cyclophyllidea Braun, 1900
Order Aporia, new order

Schmidt (1986)

Note: Familial classification is presented only for the Lecanicephalidea and Tetraphyllidea. Only the genera in the families of Lecanicephalidea and taxa in the Tetraphyllidea of doubtful or uncertain status are listed.

Subclass Cestodaria Monticelli, 1891
Subclass Eucestoda Southwell, 1930
Order Carylophyllidea Beneden in Carus, 1863
Order Spathebothridea Wardle & McLeod, 1952
Order Trypanorhyncha Diesing, 1863
Order Pseudophyllidea Carus, 1863 (syn. Diphyllidea Wardle, McLeod & Radinowski, 1974)
Order Lecanicephalidea Baylis, 1920
Family Balanobothriidae Pintner, 1928
Balanobothrium Hornell, 1912
Family Disculicepitidae Joyeux & Baer, 1935 (syn. *Discocephalidae* Pintner, 1928)
Disculiceps Joyeux et Baer, 1935 (syn. *Discocephalum* Linton, 1890)
Family Lecanicephalidae Braun, 1900
Polypocephalus (syn. ***Parataenia***, ***Thysanobothrium***, ***Anthemobothrium***), ***Calycobothrium*** (syn. ***Cyclobothrium***), ***Staurobothrium***, ***Hexacanalis***, ***Flapocephalus***, ***Eniochobothrium***, ***Tetragonicephalum*** [sic], *Discobothrium* (syn. ***Hornellobothrium***), ***Lecanicephalum*** (syn. ***Aphanobothrium***, ***Kystocephalus***, ***Spinocephalum***, ***Tylocephalum***)
Family Adelobothriidae Yamaguti, 1959
Adelobothrium
Order Aporidea Fuhrmann, 1934
Order Tetraphyllidea Carus, 1863
Family Onchobothriidae Braun, 1900
Family Cathetocephalidae Dailey & Overstreet, 1973
Family Triloculariidae Yamaguti, 1959 (syn. Urogonoporidae Odhner, 1904)
Family Phyllobothriidae Braun, 1900
Tetraphyllidea of doubtful or uncertain status: Order Biporophyllidea Subramaniam, 1939, Order Anteroporidea and Lateroporidea, both Subhapardha, 1957, Monoporophyllaeidae Subhapradha, 1957, ***Anteropora indica***, ***Monoporophyllaeus***, *Mastembellophyllaeus*, *Pleurocercus tandani*, *Pleurocercus puriensis*, *Tritaphros retzii*, *Spinibiloculus*, *Yogeshwaria*
Order Diphyllidea Beneden in Carus, 1963
Order Litobothridea Dailey, 1969
Order Nippotaeniidea Yamaguti, 1939
Order Proteocephalidea Mola, 1928
Order Dioecotaeniidea ord. n.
Order Cyclophyllidea Beneden in Braun, 1900

Brooks and McLennan (1993)

Note: Classification below order is presented only for the Lecanicephaliformes.

Subcohort Eucestoda Southwell, 1930
Order Pseudophylliformes Carus, 1863
Order Nippotaeniiformes Yamaguti 1939
Order Tetraphylliformes Carus, 1863
Order Proteocephaliformes Mola, 1928
Order Lecanicephaliformes Baylis 1920
Family Lecanicephalidae Braun, 1900
Subfamily Lecanicephalinae Braun, 1900 *incertae sedis* *Discobothrium*, ***Calycobothrium***, *Echeneibothrium*, ***Lecanicephalum***, ***Hexacanalis*** (*sedis mutabilis*, *incertae sedis*), ***Polypocephalus***
Subfamily Disculicipinae Joyeux & Baer, 1935
Staurobothrium, ***Tetragonocephalum***, *Disculiceps*, ***Adelobothrium***, *Prosobothrium*, *Cathetocephalus*

Euzet (1994b)

Order Lecanicephalidea Wardle & McLeod, 1952
Family Polypocephalidae Meggitt, 1924
Polypocephalus (syn. ***Parataenia***, ***Thysanobothrium***)
Family Anteroporidae n. fam.
Anteropora (syn. ***Monoporophylleus***)
Family Tetragonocephalidae Yamaguti, 1959
Tetragonocephalum (syn. ***Spinocephalum***), ***Tylocephalum***
Family Lecanicephalidae Braun, 1900
Lecanicephalum (syn. ***Hexacanalis***)

Appendix 2. List of species of lecanicephalideans.

(Note: Type species are indicated in bold.)

SPECIES	TYPE HOST[*]	TYPE LOCALITY	TYPE MATERIAL	# OF SPECIMENS	SOURCE
VALID SPECIES					
Aberrapex senticosus Jensen, 2001	*Myliobatis californicus*	Santa Rosalia, Baja California, Mexico	see Appendix III	14	Jensen (2001)
Aberrapex arrhynchum (Brooks, Mayes & Thorson, 1981) Jensen, 2001 (syn. *Discobothrium arrhynchum* Brooks, Mayes & Thorson, 1981)	*Myliobatis goodei*	Río de la Plata estuary, near Montevideo, Uruguay	see Appendix III	30	Brooks *et al.* (1981a)
Anteropora indica Subhapradha, 1955	*Narcine timlei*	Madras, India	not given	not given	Subhapradha (1955)
Anteropora japonica (Yamaguti, 1934) Euzet, 1994 (syn. *Discobothrium japonicum* Yamaguti, 1934)	*Narke japonica*	Kuki, Pacific coast, Japan	not given (see Appendix III)	not given	Yamaguti (1934)
Anteropora leelongi Jensen, **n. sp.**	*Hemiscyllium ocellatum*	Yorkey's Knob, Cairns, QLD, Australia	see Appendix III	13	this study
Corrugatocephalum ouei Caira, Jensen & Yamane, 1997	*Megachasma pelagios*	Hakata Bay, Fukuoka, northern Kyushu, Japan	see Appendix III	14	Caira *et al.* (1997)
Eniochobothrium gracile Shipley & Hornell, 1906	*Rhinoptera javanica*	Dutch Bay, Ceylon	not given	2 or 3	Shipley & Hornell (1906)
Eniochobothrium euaxos Jensen, **n. sp.**	*Rhinoptera* sp.	Dundee Beach, Fog Bay, NT, Australia	see Appendix III	36	this study
Eniochobothrium qatarense Al Kawari, Saoud & Wanas, 1994	*Rhinoptera adspersa*	Qatari waters, Arabian Gulf	see Appendix III	10	Al Kawari *et al.* (1994)
Healyum harenamica Jensen, 2001	*Mobula japanica*	Punta Arena, Baja California Sur, Mexico	see Appendix III	16	Jensen (2001)
Healyum pulvis Jensen, 2001	*Mobula japanica*	Punta Arena, Baja California Sur, Mexico	see Appendix III	11	Jensen (2001)
Hornellobothrium cobraformis Shipley & Hornell, 1906 (syn. *Discobothrium cobraformis* [Shipley & Hornell, 1906] Southwell, 1925)	*Aetobatis narinari*	Ceylon	not given	great numbers	Shipley & Hornell (1906)
Hornellobothrium extensivum Jensen, **n. sp.**	*Aetobatus narinari*	Lee Point, Darwin, NT, Australia	see Appendix III	28	this study
Lecanicephalum peltatum Linton, 1890	*Trygon centrura*	Woods Hole, MA, U.S.A.	not given	at least 9	Linton (1890)
Lecanicephalum coangustatum Jensen, **n. sp.**	*Dasyatis centroura*	Western Atlantic Ocean off South Carolina, U.S.A.	see Appendix III	31	this study
Paraberrapex manifestus Jensen, 2001	*Squatina californica*	Santa Rosalia, Baja California, Mexico	see Appendix III	42	Jensen (2001)
Polypocephalus radiatus Braun, 1878	*Rhinobatus granulatus*	[East-Indian Ocean]	not given (ZMB Verm. Entoz. 3182, 4 syntypes)	very numerous	Braun (1878)
Polypocephalus affinis Subhapradha, 1951	*Rhinobatus granulatus*	Madras, India	not given	1	Subhapradha (1951)

Appendix 2. Continued.

SPECIES	TYPE HOST[*]	TYPE LOCALITY	TYPE MATERIAL	# OF SPECIMENS	SOURCE
Polypocephalus alii Shinde & Jadhav, 1981	*Rhynchobatus djeddensis*	Ratnagiri, west coast of India, India	holotype and paratypes deposited in the Zoology Department, Marathwada University, Aurangabad, India	3	Shinde & Jadhav (1981)
Polypocephalus bombayensis Shinde, Dhule & Jadhav, 1992	*Aetobatus flagellum*	Kakinada, A.P., India	not given	not given	Shinde *et al.* (1991)
Polypocephalus caribbensis (Gardner & Schmidt, 1984) **n. comb.** (syn. *Discobothrium caribbensis* Gardner & Schmidt, 1984)	*Urolophus jamaicensis*	Discovery Bay, Jamaica	see Appendix III	5	Gardner & Schmidt (1984)
Polypocephalus coronatus Subhapradha, 1951	*Rhynchobatus djeddensis*	Madras and Adyar, India	not given	>400	Subhapradha (1951)
Polypocephalus digholensis Deshmukh, Jadhav & Shinde, 1982	*Dicerobatis eregoodoo*	Veraval, west coast of India	holotype deposited in the Zoology Department, Marathwada University, Aurangabad, India	2	Deshmukh *et al.* (1982)
Polypocephalus djeddensis Jadhav & Shinde, 1989	*Rhynchobatus djeddensis*	Ratnagiri, M.S., west coast of India	not given	not given	Jadhav & Shinde (1989)
Polypocephalus elongatus (Southwell, 1912) **n. comb.** (syn. *Parataenia elongatus* Southwell, 1912)	*Trygon kuhli*	Ceylon	not given	44	Southwell (1912)
Polypocephalus helmuti Jensen, **n. sp.**	*Rhinoptera* sp.	Dundee Beach, Fog Bay, NT, Australia	see Appendix III	41	this study
Polypocephalus indicus Deshmukh, Jadhav & Shinde, 1982	*Cercharias laticaudus*	Bombay, west coast of India	holotype deposited in the Zoology Department, Marathwada University, Aurangabad, India	4	Deshmukh *et al.* (1982)
Polypocephalus karbharii Deshmukh, Jadhav & Shinde, 1982	*Dicerobatis eregoodoo*	Veraval, west coast of India	holotype deposited in the Zoology Department, Marathwada University, Aurangabad, India	4	Deshmukh *et al.* (1982)
Polypocephalus katpurensis Shinde & Jadhav, 1981	*Rhynchobatus djeddensis*	Ratnagiri, west coast of India	holotype and paratypes deposited in the Zoology Department, Marathwada University, Aurangabad, India	3	Shinde & Jadhav (1981)
Polypocephalus lintoni Subhapradha, 1951	*Rhynchobatus djeddensis*	Madras and Adyar, India	not given	58	Subhapradha (1951)
Polypocephalus maharashtra Deshmukh, Jadhav & Shinde, 1982	*Trygon sephen*	Ratnagiri, west coast of India	holotype deposited in the Zoology Department, Marathwada University, Aurangabad, India	2	Deshmukh *et al.* (1982)
Polypocephalus medusia (Linton, 1890) Southwell, 1925 (syn. ***Parataenia medusia*** Linton, 1890)	*Trygon centrura*	Woods Hole, MA, U.S.A.	not given	not given	Linton (1890)

Appendix 2. Continued.

SPECIES	TYPE HOST*	TYPE LOCALITY	TYPE MATERIAL	# OF SPECIMENS	SOURCE
Polypocephalus moretonensis Butler, 1987	*Dasyatis fluviorum*	Moreton Bay, QLD, Australia	see Appendix III	1	Butler (1987b)
Polypocephalus prathibhai Deshmukh, Jadhav & Shinde, 1982	*Trygon sephen*	Ratnagiri, west coast of India	holotype deposited in the Zoology Department, Marathwada University, Aurangabad, India	2	Deshmukh *et al.* (1982)
Polypocephalus ratnagiriensis Jadhav, Shinde & Sarwade, 1986	*Trygon zugei*	Ratnagiri, Arabian Sea, India	not given	20	Jadhav *et al.* (1986)
Polypocephalus rhinobatidis Subhapradha, 1951	*Rhinobatus granulatus*	Madras, west coast of India	not given	>100	Subhapradha (1951)
Polypocephalus rhynchobatidis Subhapradha, 1951	*Rhynchobatus djeddensis*	Madras, west coast of India	not given	2	Subhapradha (1951)
Polypocephalus saoudi Hassan, 1982	*Taeniura lymma*	El-Ghardaga, Red Sea, Egypt	see Appendix III	33	Hassan (1982b)
Polypocephalus singhii Shinde & Jadhav, 1981	*Rhynchobatus diddensis*	Veraval, west coast of India	not given	2	Shinde & Jadhav (1981)
Polypocephalus thapari Shinde & Jadhav, 1981	*Trygon sephen*	Veraval, west coast of India	not given	4	Shinde & Jadhav (1981)
Polypocephalus vesicularis Yamaguti, 1960	*Rhinobatus schlegeli*	Inland Sea, Japan	not given	1 immature specimen & 8 fragments	Yamaguti (1960)
Polypocephalus vitellaris Subhapradha, 1951	*Rhynchobatus djeddensis*	Madras, India	not given	1	Subhapradha (1951)
Quadcuspibothrium francisi Jensen, 2001	*Mobula japanica*	Punta Arena, Baja California Sur, Mexico	see Appendix III	20	Jensen (2001)
Tetragonocephalum trygonis Shipley & Hornell, 1905 (syn. *Tylocephalum trygonis* [Shipley & Hornell, 1905] Shipley & Hornell, 1906)	*Trygon walga*	Ceylon	not given	a number	Shipley & Hornell (1905)
Tetragonocephalum alii Deshmukh & Shinde, 1979	*Trygon sephen*	Ratnagiri, west coast of India	not given	3	Deshmukh & Shinde (1979)
Tetragonocephalum aurangabadensis Shinde & Jadhav, 1990	*Trygon zugei*	Ratnagiri, M. S., west coast of India	not given	10	Shinde & Jadhav (1990)
Tetragonocephalum bhagawatii Shinde, Mohekar & Jadhav, 1985	*Trygon sephen*	Ratnagiri, India	not given	2	Shinde *et al.* (1985)
Tetragonocephalum madhualtae (Andhare & Shinde, 1994) **n. comb.** (syn. *Tylocephalum madhualtae* Andhare & Shinde, 1994)	*Trygon zugei*	Waltair, A.P., India	not given	not given	Andhare & Shinde (1994)
Tetragonocephalum madrasensis (Andhare & Shinde, 1994) **n. comb.** (syn. *Tylocephalum madrasensis* Andhare & Shinde, 1994)	*Trygon zugei*	Madras, A.P., India	not given	not given	Andhare & Shinde (1994)
Tetragonocephalum passeyi Jensen, **n. sp.**	*Himantura undulata*	east of Wessle Islands, Arafura Sea, Australia	see Appendix III	29	this study
Tetragonocephalum raoi Deshmukh & Shinde, 1979	*Trygon zugei*	Veraval, west coast of India	not given	5	Deshmukh & Shinde (1979)
Tetragonocephalum ratnagiriensis Shinde & Jadhav, 1990	*Trygon zugei*	Ratnagiri, M. S., west coast of India	not given	7	Shinde & Jadhav (1990)

Appendix 2. Continued.

SPECIES	TYPE HOST[*]	TYPE LOCALITY	TYPE MATERIAL	# OF SPECIMENS	SOURCE
Tetragonocephalum sephensis Deshmukh & Shinde, 1979	*Trygon sephen*	Ratnagiri, west coast of India	not given	3	Deshmukh & Shinde (1979)
Tetragonocephalum shipleyi Shinde, Mohekar & Jadhav, 1985	*Trygon sephen*	Ratnagiri, India	not given	5	Shinde *et al.* (1985)
Tetragonocephalum simile (Pintner, 1928) Ivanov & Campbell, 2001 (syn. *Tylocephalum simile* Pintner, 1928; *Lecanicephalum simile* [Pintner, 1928] Schmidt, 1986)	*Trygon walga*	Gulf of Manaar, Ceylon	not given	not given	Pintner (1928)
Tetragonocephalum uarnak (Shipley & Hornell, 1906) Pintner, 1928 (syn. *Tylocephalum uarnak* Shipley & Hornell, 1906)	*Trygon uarnak*	Gulf of Manaar, Ceylon	not given	few	Shipley & Hornell (1906)
Tetragonocephalum yamagutii Muralidhar, 1990	*Trygon walga*	Madras, Tamil Nadu, east coast of India	holotype and paratype, deposited in the Cestodology laboratory, Zoology Department, Marathwada University, Aurangabad, India	7	Muralidhar (1988)
Tylocephalum pingue Linton, 1890 (syn. *Lecanicephalum pingue* [Linton, 1890] Schmidt, 1986)	*Rhinoptera quadriloba*	Woods Hole, MA, U.S.A.	not given	1	Linton (1890)
Tylocephalum bonasum Campbell & Williams, 1984	*Rhinoptera bonasus*	Sakonnet Point, RI, U.S.A.	see Appendix III	7	Campbell & Williams (1984)
Tylocephalum brooksi Ivanov & Campbell, 2000	*Rhinoptera bonasus*	Gulf of Venezuela, Caimáre Chico, Venezuela	see Appendix III	9	Ivanov & Campbell (2000)
Tylocephalum campanulatum Butler, 1987	*Rhina ancylostomus*	Moreton Bay, QLD, Australia	see Appendix III	25	Butler (1987b)
Tylocephalum elongatum Subhapradha, 1955	*Rhynchobatus djeddensis*	Madras coast, Ceylon	not given	[several]	Subhapradha (1955)
Tylocephalum koenneckeorum Jensen, **n. sp.**	*Rhynchobatus djeddensis*	east of Wessle Islands, Arafura Sea, Australia	see Appendix III	22	this study
Tylocephalum marsupium Linton, 1916 (syn. *Lecanicephalum marsupium* [Linton, 1916] Fuhrmann, 1931; *Hexacanalis* [?] *marsupium* [Linton, 1916] Dollfus, 1948 in Chandler [1954])	*Aetobatus narinari*	Dry Tortuga Islands, FL, U.S.A.	not given	2	Linton (1916)
Tylocephalum pandurangi Shinde & Mahajan, 1994	*Trygon sephen*	Bombay, M.S., west coast of India	not given	13	Shinde & Mahajan (1993/1994)
Tylocephalum rhinobatii (Deshmukh, 1980) **n. comb.** (syn. ***Spinocephalum rhinobatii*** Deshmukh, 1980; *Lecanicephalum rhinobatii* [Deshmukh, 1980] Schmidt, 1986)	*Rhinobatus granulatus*	Veraval, west coast of India	specimens deposited in the Laboratory of Cestodology, Department of Zoology, Marathwada University, Aurangabad, India	4	Deshmukh (1980)
Tylocephalum singhii Jadhav & Shinde, 1981 (syn. *Lecanicephalum singhii* [Jadhav & Shinde, 1981] Schmidt, 1986)	*Trygon zugei*	Bombay, India	types deposited in the Zoology Department, Marathwada University, Aurangabad, India	3	Jadhav & Shinde (1981)
Tylocephalum squatinae Yamaguti, 1934 (syn. *Lecanicephalum squatinae* [Yamaguti, 1934] Schmidt, 1986)	*Squatina japonica*	Toyama Bay, Japan	type in Yamaguti's personal collection (see Appendix III)	single mature specimen	Yamaguti (1934)

Appendix 2. Continued.

SPECIES	TYPE HOST[*]	TYPE LOCALITY	TYPE MATERIAL	# OF SPECIMENS	SOURCE
Tylocephalum yorkei Southwell, 1925 (syn. *Cephalobothrium yorkei* [Southwell, 1925] Zaidi & Khan. 1976; *Lecanicephalum yorkei* [Southwell, 1925] Schmidt, 1986)	*Aetobatis narinari*	Puri, Orissa, India	type specimens are in the collections of the Liverpool School of Tropical Medicine (see Appendix III)	numerous specimens	Southwell (1925)
new genus 1: *Discobothrium myliobatidis* Dailey & Mudry, 1968	*Myliobatis californicus*	Long Beach Harbor, CA, U.S.A.	see Appendix III	5	Dailey & Mudry (1968)
new genus 2: *Lecanicephalum xiamenensis* Yang, Lui & Lin, 1995	*Raja holandi*	Xiamen, South Fujian, China	not given ?	?	Yang *et al.* (1995)
new genus 2: *Tenia* [sic] *narinari* MacCallum, 1917	*Aetobatis narinari*	?	not given	[1]	MacCallum (1917)
SPECIES INQUIRENDAE					
Adelobothrium aetiobatidis Shipley, 1900	*Aetiobatis narinari*	Lifu, Loyalty Islands, New Caledonia	not given	1	Shipley (1900)
"*Anoplocephala globocephala*" MacCallum, 1921	"a small ray"	Singapore	not given	not given	MacCallum (1921)
Anthemobothrium pulchrum Shipley & Hornell, 1906 (syn. *Polypocephalus pulcher* [Shipley & Hornell, 1906] Southwell, 1925)	*Trygon sephen*	Dutch Bay, Gulf of Manaar, Ceylon	not given	1	Shipley & Hornell (1906)
Cephalobothrium aetobatidis Shipley & Hornell, 1906	*Aetobatis narinari*	Dutch Bay, Ceylon	not given	1	Shipley & Hornell (1906)
Cephalobothrium alii Jadhav & Jadhav, 1993	*Trygon sephen*	Ratnagiri, M.S., west coast of India	not given	not given	Jadhav & Jadhav (1993)
Cephalobothrium gymnurai Zaidi & Khan, 1976	*Gymnura* sp.	Fish Harbour Karachi, Pakistan	not given	2	Zaidi & Khan (1976)
Cephalobothrium longisegmentum Wang, 1984	*Dasyatis kuhlii*	Fujian Province, China	not given ?	?	Wang (1984)
Cephalobothrium neoaetobatidis Sarada, Vijaya Lakshmi & Hanumantha Rao, 1992	*Rhina ancylostomus*	Waltair Coast, India	not given	7	Sarada *et al.* (1992)
Cephalobothrium pteroplateai Zaidi & Khan, 1976	*Pteroplatea micrura*	Fish Harbour Karachi, Pakistan	not given	17	Zaidi & Khan (1976)
Cephalobothrium rhinobatidis Subhapradha, 1955	*Rhinobatus granulatus*	Madras Coast, India	not given	not given	Subhapradha (1955)
Cephalobothrium singhi Jadhav & Jadhav, 1993	*Trygon sephen*	Ratnagiri, M.S., west coast of India	not given	not given	Jadhav & Jadhav (1993)
Cephalobothrium stegostomi Sarada, Vijaya Lakshmi & Hanumantha Rao, 1993	*Stegostoma fasciatum*	Waltair Coast, India	not given	8	Sarada *et al.* (1993)
Cephalobothrium subhapradhi Chincholikar & Shinde, 1977	not given	Ratnagiri, Maharashtra, India	not given	not given	Chincholikar & Shinde (1977)
Cephalobothrium taeniurai Ramadan, 1986	*Taeniura lymma*	Al-Ghardaga, Red Sea, Egypt	holotype (No. 342) & paratype (No. 343) deposited in the Helminthological Collection, Zoology Department, Faculty of Science, Ain Shams University, Cairo, Egypt	2	Ramadan (1986)

Appendix 2. Continued.

SPECIES	TYPE HOST[*]	TYPE LOCALITY	TYPE MATERIAL	# OF SPECIMENS	SOURCE
Cephalobothrium trygoni Shinde & Solunke, 1986	*Trygon sephen*	Waltair, A.P., India	holotype deposited in Department of Zoology, Marathwada University, Aurangabad, India	4 [6 specimens collected]	Shinde & Solunke (1986)
Cephalobothrium variabile Southwell, 1911 (syn. *Hexacanalis variabile* [Southwell, 1911] Perrenoud, 1931)	*Pristis cuspidatus*	Portugal Bay, Pearl Banks, Ceylon	Colombo Museum, Colombo, Ceylon (now Sri Lanka)	47	Southwell (1911)
Eniochobothrium trygonis Chincholikar & Shinde, 1978	*Trygon sephen*	Ratnagiri, Maharashtra, India	not given	4	Chincholikar & Shinde (1978a)
Flapocephalus trygonis Deshmukh, 1979	*Trygon sephen*	Ratnagiri, India	specimens deposited in the Laboratory of Cestodology, Department of Zoology, Marathwada University, Aurangabad, (M.S.), India	11	Deshmukh (1979)
Flapocephalus saurashtri Shinde & Deshmukh, 1979	*Trygon sephen*	Veraval, Gujrat, India	not given	1	Shinde & Deshmukh (1979a)
Hexacanalis abruptus (Southwell, 1911) Perrenoud, 1931 (syn. *Cephalobothrium abruptum* Southwell, 1911; *Lecanicephalum abruptum* [Southwell, 1911] Fuhrmann, 1931?)	*Pteroplatea micrura*	Portugal Bay, Ceylon	Colombo Museum, Colombo, Ceylon (now Sri Lanka)	87	Southwell (1911)
Hexacanalis indirajii Murlidhar, 1986	*Trygon sephen*	Kakinada, Andhra Pradesh, India	not given	5	Murlidhar (1986)
Hexacanalis sasoonensis Srivastava & Capoor, 1980	*Trygon marginatus*	Sasoon Dock (Bombay), India	holotype at Department of Zoology, University of Allahabad, Allahabad, India	1	Srivastava & Capoor (1980)
Hexacanalis smythii Murlidhar, Shinde & Jadhav, 1986	*Trygon centrura*	Kakinada, India	not given	7	Murlidhar *et al.* (1986)
Hexacanalis thapari Shinde, Jadhav & Jadhav, 1992	*Trygon zugei*	Ratnagiri, M.S., India	not given	not given	Shinde *et al.* (1991)
Hexacanalis yamagutii Shinde & Deshmukh, 1979	*Dicerobatis eregoodoo*	Veraval, west coast of India	specimens deposited in Zoology Department, Marathwada University, Aurangabad, India	4	Shinde & Deshmukh (1979b)
Hexacanalis zugeis Shinde & Deshmukh, 1979	*Trygon zugei*	Ratnagiri, west coast of India	specimens deposited in Zoology Department, Marathwada University, Aurangabad, India	20	Shinde & Deshmukh (1979b)
Kystocephalus translucens Shipley & Hornell, 1906 (syn. *Tylocephalum translucens* [Shipley & Hornell, 1906] Southwell, 1925; *Lecanicephalum translucens* [Shipley & Hornell, 1906] Schmidt, 1986)	*Aetobatis narinari*	Gulf of Manaar, Ceylon	not given	2	Shipley & Hornell (1906)
Lecanicephalum maharashtrae Chincholikar & Shinde, 1978	*Trygon sephen*	Ratnagiri, Maharashtra, India	type specimen deposited in the Cestodology Laboratory, Department of Zoology, Marathwada University, Aurangabad, India	1	Chincholikar & Shinde (1978b)

Appendix 2. Continued.

SPECIES	TYPE HOST[*]	TYPE LOCALITY	TYPE MATERIAL	# OF SPECIMENS	SOURCE
Lecanicephalum ratnagiriensis Hiware & Jadhav, 1999	*Trygon sephen*	Ratnagiri, Maharashtra, India	holotypes and paratypes deposited in Helminthological lab, Dept. of Zoology, Dr. B.A.M. Marathwada University, Aurangabad, India	5	Hiware & Jadhav (1999)
Polypocephalus trygoni Jadhav & Threlfall, 1986	?	[India]	?	?	[Jadhav & Threlfall (1986)]; see Shinde *et al.* (1991)
Sephenicephalum maharashtrii Shinde, Sarwade & Jadhav, 1980 or 1982 [?]	[*Trygon sephen*]	[Ratnagiri, India]	?	?	see Hiware *et al.* (1993); Bhagwan & Shinde (2002
Sephenicephalum bombayensis Hiware, Jadhav & Bhosale, 1993)	*Trygon zugai*	Bomaby, M.S., India	not given	[several ?]	Hiware *et al.* (1993)
Sephenicephalum dnyandevi Bhagwan & Shinde, 2002	*Trygon sephen*	Bombay, India	not given	13	Bhagwan & Shinde (2002)
Staurobothrium aetobatidis Shipley & Hornell, 1905	*Aetiobatis narinari*	Marichchukaddi, Ceylon	not given	a considerable number	Shipley & Hornell (1905)
"*Taenia acanthobothria*" MacCallum, 1921	*Aetiobatis narinari*	Batavia, Java, Indonesia	not given (see Appendix III)	several	MacCallum (1921)
Tetragonocephalum aetiobatidis Shipley & Hornell, 1905 (syn. *Tylocephalum aetiobatidis* [Shipley & Hornell, 1905] Shipley & Hornell, 1906; *Lecanicephalum aetiobatidis* [Shipley & Hornell, 1905] Schmidt, 1986)	*Aetiobatis narinari*	Marichchukaddi, Ceylon	not given	1	Shipley & Hornell (1905)
Tetragonocephalum akajeiensis Yang, Lui & Lin, 1995	*Dasyatis akajei*	Xiamen, South Fujian, China	not given ?	?	Yang *et al.* (1995)
Tetragonocephalum janardane Wankhede, 1990	*Trygon zugei*	Ratnagiri, India, Arabian Sea	not given	not given	Wankhede (1990)
Thysanobothrium uarnakense Shipley & Hornell, 1906 (syn. *Polypocephalus uarnakense* [Shipley & Hornell, 1906] Butler, 1987 ?)	*Trygon uarnak*	Ceylon	not given	not given	Shipley & Hornell (1906)
Tylocephalum alii Andhare & Shinde, 1994	*Trygon zugei*	Waltair, A.P.,India	not given	not given	Andhare & Shinde (1994)
Tylocephalum aurangabadensis Jadhav & Shinde, 1988	*Aetobatis narinari*	Malwan, Arabian Sea, India	holotype and paratypes, Cestodes/220-235/, deposited in Cestodology Lab. Departments of Zoology, Marathwada University, Aurangabad, 431004, India	15	Jadhav & Shinde (1987)
Tylocephalum bombayensis Jadhav, 1983	*Trygon sephen*	Arabian Sea	not given	4	Jadhav (1983)
Tylocephalum chiralensis Vijayalakshmi & Sarada, 1995	*Dasyatis* (*Himantura*) *uarnak*	Chirala, Andhra Pradeh, India	holotype and paratype specimens will be deposited in the Department of Zoology, Andhra University, Waltair, India	6	Vijayalakshmi & Sarada (1995)

Appendix 2. Continued.

SPECIES	TYPE HOST[*]	TYPE LOCALITY	TYPE MATERIAL	# OF SPECIMENS	SOURCE
Tylocephalum dierama Shipley & Hornell, 1906 (syn. *Cephalobothrium dierama* [Shipley & Hornell, 1906] Zaidi & Khan, 1976; *Lecanicephalum dierama* [Shipley & Hornell, 1906] Schmidt, 1986)	*Myliobatis maculata*	Gulf of Manaar, Ceylon	not given	a specimen or 2	Shipley & Hornell (1906)
Tylocephalum hanmantraoi Shinde & Jadhav, 1990	*Rhynchobatus djeddensis*	Bombay, M.S., west coast of India	not given	not given	Shinde & Jadhav (1990)
Tylocephalum kuhli Shipley & Hornell, 1906[†]	*Trygon kuhli*	Dutch Bay Spit, Ceylon	not given	1	Shipley & Hornell (1906)
Tylocephalum ludificans Jameson, 1912 (syn. *Lecanicephalum ludificans* [Jameson, 1912] Schmidt 1986)	*Margaritifera vulgaris* [larval host]; *Aetobatis narinari* [possible host of adult]	Gulf of Manaar, Ceylon	type in Prof. Herdmann's Collection	not given	Jameson (1912)
Tylocephalum madhukarii Chincholikar & Shinde, 1980 (syn. *Lecanicephalum madhukarii* [Chincholikar & Shinde, 1980] Schmidt, 1986)	*Trygon sephen*	Ratnagiri, Maharashtra, India	deposited in the Cestodology Laboratory, Marathwada University, Aurangabad, India	1	Chincholikar & Shinde (1980)
Tylocephalum margaritiferae Seurat, 1906 (syn. *Lecanicephalum margaritiferae* [Seurat, 1906] Schmidt, 1986)	*Margaritifera margaritifera* [larval host]; *Aetobatis narinari* [possible host of adult]	Gambier Islands, South Pacific Ocean, French Polynesia	not given	not given	Seurat (1906a)
Tylocephalum minimum Subhapradha, 1955	*Rhynchobatum djeddensis*	Madras coast, Ceylon	not given	not given	Subhapradha (1955)
Tylocephalum minus Jameson, 1912 (syn. *Lecanicephalum minus* [Jameson, 1912] Schmidt, 1986)	*Margaritifera vulgaris* [larval host]	Gulf of Manaar, Ceylon	not given	not given	Jameson (1912)
Tylocephalum minutum Southwell, 1925 (syn. *Lecanicephalum minutum* [Southwell, 1925] Schmidt, 1986; *Tetragonocephalum minutum* [Southwell, 1925] Ivanov & Campbell, 2000)	*Urogymnus* sp. (*asperrimus* ?)	Ceylon Pearl Banks, Ceylon	not given	20	Southwell (1925)
NOMINA NUDA					
Discobothrium quadrisurculi Khambata & Bal, 1953	*Trygon sephen*, *Rhychobatus* [sic] *djeddensis* & *Aetomylaeus maaculatus*	Bombay, India	not given	not given	Khambata & Bal (1953)
Discobothrium redacta Khambata & Bal, 1953	*Trygon sephen*, *Rhychobatus* [sic] *djeddensis* & *Aetomylaeus maculatus*	Bombay, India	not given	not given	Khambata & Bal (1953)
Hexacanalis sephanensis	?	?	?	?	see Mohekar *et al.* (2002)
Lecanicephalum schmidti Al Kawari, 1992	*Rhynchobatus djiddensis*	Qatari waters, Arabian Gulf	paratypes deposited in the Helminthological Collection, Department of Zoology, University of Qatar, Qatar	13	Al Kawari (1992)
Lecanicephalum (as *Laceanicephalum*) *trygoni*	?	?	?	?	see Mohekar *et al.* (2002)

Appendix 2. Continued.

SPECIES	TYPE HOST[*]	TYPE LOCALITY	TYPE MATERIAL	# OF SPECIMENS	SOURCE
Polypocephalus braunii Shinde, 1981	?	?	?	?	see Jadhav & Shinde (1989); Shinde *et al.* (1991)
Polypocephalus testicularis	?	?	?	?	see Jadhav & Shinde (1989)
Sephenicephalum marathwadensis Pawar, 1983	[*Narcina brunnea*]	?	?	?	see Bhagwan & Shinde (2002)
Tetragonocephalum (as *Tetragonicephalum*) *karachiensis* Bilqees & Fatima, 1980 or 1982 [?]	?	?	?	?	see Bilqees (1995)
Tetragonocephalum meenae	?	?	?	?	see Mohekar *et al.* (2002)
Tetragonocephalum shindei Shipley & Hornell, 1906	?	?	?	?	see Mohekar *et al.* (2002)
Tetragonocephalum (as *Tetragonicephalum*) *stegostomai* Bilqees & Fatima, 1980 or 1982 [?]	?	?	?	?	see Bilqees (1995)
Tetragonocephalum (as *Tetragonicephalum*) *varium* Bilqees & Fatima, 1980 or 1982 [?]	?	?	?	?	see Bilqees (1995)
Tylocephalum mehdii	?	?	?	?	see Mohekar *et al.* (2002)
***SPECIES INQUIRENDAE* (NON-LECANICEPHALIDEAN)**					
Calycobothrium typicum (Southwell, 1911) Stiles & Hassall, 1912 (syn. ***Cyclobothrium typicum*** Southwell, 1911)	*Aetobatis narinari*	Portugal Bay	Colombo Museum, Colombo, Ceylon (now Sri Lanka)	1	Southwell (1911)
Cephalobothrium gangeticus Gairola, Malhotra & Sukul, 1989	*Mystus vittatus*	River Ganges, Allahabad, India	holotype (No. PCLS/110/86) deposited in the Parasitological Collections, Department of Zoology, University Allahabad, Allahabad, U.P., India	10	Gairola *et al.* (1987)
Cephalobothrium ghardagense Ramadan, 1986	*Scarus bicolar*	Al-Ghardaga, Red Sea, Egypt	holotype (No. 341) deposited in the Helminthological Collection, Zoology Department, Faculty of Science, Ain Shams University, Cairo, Egypt	1	Ramadan (1986)
Trygonicephalum ratnagiriensis Shinde & Jadhav, 1984	*Trygon sephen*	Ratnagiri, India	holotype and paratype deposited in the Zoology Department, Marathwada University, Aurangabad, India	3	Shinde & Jadhav (1984)

Appendix 2. Continued.

SPECIES	TYPE HOST*	TYPE LOCALITY	TYPE MATERIAL	# OF SPECIMENS	SOURCE
NON-LECANICEPHALIDEAN SPECIES					
Pseudanthobothrium aegyptiacus (Hassan, 1982) **n. comb.** (syn. *Discobothrium aegyptiacus* Hassan, 1982; *Lecanicephalum aegyptiacus* [Hassan, 1982] Schmidt, 1986)	*Raja circularis*	Alexandria, Mediterranean Sea, AR. Egypt	BMNH Nos. 1998.10.19.78-81 (originally CIH No. S1053/A [holotype]; CIH No. S1053/B [paratypes])	13	Hassan (1982a)
Tetrarhynchobothrium unionifactor (Shipley & Hornell, 1904) Beveride & Campbell, 1988 (syn. *Tetrarhynchus unionifactor* Shipley & Hornell, 1904; *Tentacularia unionifactor* (Shiopley & Hornell, 1904) Southwell, 1929; *Tylocephalum unionifactor* (Shipley & Hornell, 1904) Herdmann in Southwell, 1924; *Lecanicephalum unionifactor* [Shipley & Hornell, 1904] Schmidt, 1986)	*Margaritifera vulgaris* (larval host); *Rhinoptera javanica* (adult host)	Gulf of Manaar, Ceylon	NMW (= VNHM) No. 60 (metacestode); NMW Nos.3328 and 3330 (adults)	?	see Herdmann in Southwell (1924); Beveridge & Campbell (1998)

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[*] Type host is reported as given in the orginal description.

[†] Deposited under the name *Tetragonocephalum kuhlii*.

Abbreviations: BMNH, The Natural History Museum, London, U.K.; CIH, Commonwealth Institute of Helminthology, St. Albans, Herts, U.K.; NMW, Naturhistorishce Museum Wien Vienna, Austria; VNHM, Vienna Naturhistorisches Museum, Vienna, Austria; ZMB, Zoologisches Museum Berlin, Berlin, Germany.

Appendix 3. Location of lecanicephalidean type material.

SPECIES	MUSEUM NO.	STATUS	HOST[*]	LOCALITY	COLLECTOR
Aberrapex arrhynchum	USNPC No. 75722	Holotype	*Myliobatis goodei*	Rio de la Plata estuary, Uruguay	Brooks *et al.*
(as *Discobothrium arrhynchum*)	USNPC No. 75723	Paratype			
	HWML No. 21003	Paratype			
Aberrapex senticosus	CNHE No. 4188	Holotype	*Myliobatis califonicus*	Santa Rosalia, Baja, Mexico	Caira & Jensen
	CNHE No. 4189	Paratypes			
	USNPC No. 91208	Paratypes			
	HWML No. 16374	Paratypes			
	LRP No. 2152-2158	Paratypes			
Anteropora japonica	MPM No. 22795 [SY31-13]	Holotype	*Narke japonica*	Kuki, Pacific Coast, Japan	Yamaguti
(as *Discobothrium japonicum*)	MPM No. 22795 [SY31-14]	Paratypes			
	MPM No. 22795 [SY31-15]	Paratypes			
	MPM No. 22795 [SY31-16]	Paratypes			
Anteropora leelongi Jensen, n. sp.	QM No. G 222890	Holotype	*Hemiscyllium ocellatum*	Yorkeys Knob, Cairns, QLD, Australia	Caira
	QM Nos. G 222891-222893	Paratypes			
	USNPC No. 94574	Paratypes			
	LRP Nos. 3262-3265	Paratypes			
Cephalobothrium variabile	Coll. Southwell[†]	Type	*Pristis cuspidatus*	not given	Southwell?
Corrugatocephalum ouei	NSMT-Pl No. 4698	Holotype/Paratypes	*Megachasma pelagios*	Hakata Bay, Fukuoka, Japan	Caira & Jensen
	HWML No. 39285	Paratypes			
	USNPC No. 86985	Paratypes			
"*Discobothrium myliobatidis*"	USNPC No. 71215	Holotype/Paratype	*Myliobatis californicus*	California, U.S.A.	M.D. Dailey
Eniochobothrium euaxos Jensen, n. sp.	QM No. G 222894	Holotype	*Rhinoptera* sp.	Dundee Beach, Fog Bay, NT, Australia	Caira *et al.*
	QM Nos. G 222895-222901	Paratypes			
	USNPC Nos. 94575-94576	Paratypes			
	KUNHM Nos. 002102-002106	Paratypes			
	LRP Nos. 3266-3278	Paratypes			
Eniochobothrium qatarense	HCUQ No. 6111.87	Holotype	*Rhinoptera adspersa*	Arabian Gulf	
	HCUQ No. 6112.87	Paratype			
Healyum harenamica	CNHE No. 4186	Holotype	*Mobula japanica*	Punta Arena, Baja, Mexico	Caira & Jensen
	CNHE No. 4187	Paratypes			
	USNPC No. 91212	Paratypes			
	HWML No. 16374	Paratypes			
	LRP Nos. 2180-2184	Paratypes			
Healyum pulvis	CNHE No. 4184	Holotype	*Mobula japanica*	Punta Arena, Baja, Mexico	Caira & Jensen
	CNHE No. 4185	Paratypes			
	USNPC No. 91213	Paratypes			
	HWML No. 16377	Paratypes			
	LRP Nos. 2185-2188	Paratypes			

Appendix 3. Continued.

SPECIES	MUSEUM NO.	STATUS	HOST*	LOCALITY	COLLECTOR
Hornellobothrium extensivum Jensen, n. sp.	QM No. G 222902	Holotype	*Aetobatus narinari*	Lee Point, Darwin, NT, Australia	Caira *et al.*
	QM Nos. G 222903-222907	Paratypes			
	USNPC No. 94577	Paratypes			
	KUNHM Nos. 002107-002109	Paratypes			
	LRP Nos. 3279-3288	Paratypes			
Lecanicephalum peltatum	USNPC No. 7677	[Neotype]	*Dasyatis centroura*	Wood's Hole, MA, U.S.A.	E. Linton
Lecanicephalum coangustatum Jensen, n. sp.	USNPC No. 94578	Holotype	*Dasyatis centroura*	Western Atlantic Ocean off South Carolina, U.S.A.	Tyler & Healy
	USNPC No. 94579	Paratypes			
	KUNHM Nos. 002110-002116	Paratypes			
	LRP Nos. 3289-3299	Paratypes			
Paraberrapex manifestus	CNHE No. 4179	Holotype	*Squatina californica*	Santa Rosalia, Baja, Mexico	Caira & Jensen
	CNHE Nos. 4180 & 4181	Paratypes			
	USNPC Nos. 91209-91211	Paratypes			
	HWML No. 16375	Paratypes			
	LRP Nos. 2159-2179	Paratypes			
Polypcephalus caribbensis	USNPC No. 77924	Holotype	*Urolophus jamaicensis*	Jamaica	G.D. Schmidt
(as *Discobothrium caribbensis*)	USNPC No. 77925	Paratype			
Polypocephalus helmuti Jensen, n. sp.	QM No. G 222908	Holotype	*Rhinotera* sp.	Dundee Beach, Fog Bay, NT, Australia	Caira *et al.*
	QM Nos. G 222909-222915	Paratypes			
	USNPC No. 94580	Paratypes			
	KUNHM Nos. 002117-002120	Paratypes			
	LRP Nos. 3300-3313	Paratypes			
Polypocephalus moretonensis	QM No. GL4637	Holotype	*Dasyatis fluviorum*	Moreton Bay, QLD, Australia	S. Butler
Polypocephalus radiatus	ZMB No. 3182	syntypes	*Rhinobatus granulatus*	not given	Braun
Polypocephalus saoudi	BMNH No. 1998.11.2.1-4 (originally CIH No. S1052/A [holotype] & CIH No. S1052/B [paratypes])	Holotype/Paratypes	*Taeniura lymma*	Egypt	S.H. Hassan
Quadcuspibothrium francisi	CNHE No. 4182	Holotype	*Mobula japanica*	Punta Arena, Baja, Mexico	Caira & Jensen
	CNHE No. 4183	Paratypes			
	USNPC No. 91214	Paratypes			
	HWML No. 16378	Paratypes			
	LRP Nos. 2189-2198	Paratypes			
Taenia acanthobothria	USNPC No. 36019	Type	*Aetobatis narinari*	Batavia, Java, Indonesia	G. A. MacCallum
Tenia [sic] *narinari*	USNPC No. 35813	Type	*Aetobatis narinari*	[New York Aquarium ?, NY, U.S.A.]	G. A. MacCallum
Tetragonocephalum passeyi Jensen, n. sp.	QM No. G 222916	Holotype	*Himantura undulata*	east of Wessle Islands, Arafura Sea, Australia	Caira & Jensen
	QM Nos. G 222917-222923	Paratypes			
	USNPC No. 94581	Paratypes			
	KUNHM Nos. 002121-002125	Paratypes			
	LRP Nos. 3314-3320	Paratypes			

Appendix 3. Continued.

SPECIES	MUSEUM NO.	**STATUS**	**HOST**[*]	**LOCALITY**	**COLLECTOR**
Tetragonocephalum kuhlii	NMW No. 2149	Typus	*Trygon kuhlii*	?	Shipley
Tylocephalum bonasum	USNPC No. 77633	Holotype	*Rhinoptera bonasus*	Rhode Island, U.S.A.	Campbell & Williams
	USNPC No. 77634	Paratypes			
Tylocephalum brooksi	USNPC No. 90262	Holotype	*Rhinoptera bonasus*	Venezuela	Ivanov & Campbell
	USNPC No. 90263	Paratype			
	HWML Nos. 59996-59999	Paratypes			
Tylocephalum campanulatum	QM No. GL4638	Holotype	*Rhina ancylostoma*	Moreton Bay, QLD, Australia	S. Butler
	QM No. GL4639	Paratype			
	QM No. GL4640	Paratype			
Tylocephalum koenneckeorum Jensen, n. sp.	QM No. G 222924	Holotype	*Rhynchobatus australiae*	east of Wessle Islands, Arafura Sea, Australia	Caira & Jensen
	QM Nos. G 222925-222930	Paratypes			
	USNPC No. 94582	Paratypes			
	KUNHM Nos. 002126-002128	Paratypes			
	LRP Nos. 3331-3336	Paratypes			
Tylocephalum marsupium	USNPC No. 8990	Type	*Aetobatus narinari*	Dry Tortuga Islands, FL, U.S.A.	E. Linton
Tylocephalum pingue	USNPC No. 77631	Neotype	*Rhinoptera bonasus*	Rhode Island, U.S.A.	Campbell & Williams
	USNPC No. 77632	Paraneotypes			
	BMNH No. 1984.6.11.1-2	Paraneotypes			R.A. Campbell
Tylocephalum squatinae	MPM No. SY31-06	Type? (specimen was not borrowed; status speculative)			Coll. S. Yamaguti ?
Tylocephalum yorkei	Coll. Southwell[†]	Cotype	*Aetobatus narinari*	?	Southwell?
	BMNH No. 1932.11.21.160-162	Cotype			

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[*] Type host is reported as given in the orginal description.

[†] At the Station Méditerranéene de l'Environment Littoral, Université Montpellier II in Sète, France.

Appendix 4. Location of lecanicephalidean vouchers (preliminary).

Note: This is only a list of museum holdings; the species identification of most of these specimens was not verfied.

SPECIES[*]	MUSEUM NO.	**STATUS**	**HOST[†]**	**LOCALITY**	**DATE**	**COLLECTOR**
Adelobothrium sp.	L. No. 17133	voucher	*Himantura uarnak*	Nickol Bay, WA, Australia	11 Nov. 1986	B. Robertson (Aust. Elas. Survey)
Adelobothrium sp.	SAMA No. 17245	voucher	*Rhina ancylostomus*	Fog Bay, NT, Australia	29 Sept. 1986	B. Robertson (Aust. Elas. Survey)
Adelobothrium sp.	SAMA No. 17132	voucher	*Rhina ancylostomus*	Fog Bay, NT, Australia	29 Sept. 1986	B. Robertson (Aust. Elas. Survey)
"*Anoplocephala globocephala*"	USNPC No. 35728	voucher	"ray cromis"	Singapore		G. A. MacCallum
Anteropora japonica (as *Discobothrium japonicum*)	MPM No. 22892 [SY72-75]	voucher				Coll. S. Yamaguti
Anteropora japonica (as *Discobothrium japonicum*)	MPM No. 22892 [SY72-76]	voucher				Coll. S. Yamaguti
Anthemobothrium pulchrum	Coll. Southwell[‡]	voucher ?	*Pristis cuspidatus*		19 Feb. 1911	
Cephalobothrium abruptum	Coll. Southwell[‡]	voucher ?	*Trygon kuhli*		30 Mar. 1914	P. B. ?
Cephalobothrium abruptum	Coll. Southwell[‡]	voucher ?				
Cephalobothrium abruptum	MHNG No. 87/84-92	voucher	*Pteroplatea* sp.	Ceylon		
Cephalobothrium aetobatidis	Coll. Southwell[‡]	voucher ?	*Pleroplatea micrura*		6 Nov. 1908	
Cephalobothrium aetobatidis	Coll. Southwell[‡]	voucher ?	*Trygon kuhli*	West Cheval, Ceylon ?	24 Nov. 1924	T. Southwell ?
Cephalobothrium aetobatidis	Coll. Southwell[‡]	voucher ?	*Pristis cuspidatus*			
Cephalobothrium aetobatidis	MPM No. 15389 [B, Hawaii, 3601-3700, 6]	voucher ?				Coll. S. Yamaguti
Cephalobothrium aetobatidis	MPM No. 15390 [B, Hawaii, 3601-3700, 7]	voucher ?				Coll. S. Yamaguti
Cephalobothrium variabile	BMNH No. 1965.2.23.201-206	voucher	*Dasybatus kuhli*	Ceylon		
Cephalobothrium variabile	BMNH No. 1979.12.18.134-153	voucher	*Dasybatis* (*Trygon*) *kuhli*	Ceylon		
Cephalobothrium variabile	MHNG No. 87/74-78	voucher	*Trygon kuhlii*	Ceylon		
Cephalobothrium variabile	Coll. Southwell[‡]	voucher ?	*Pristis cuspidatus*		Jul. 1922	T. Southwell ?
Cephalobothrium sp.	BMNH No. 1988.3.4.3-12	voucher	*Dasyatis uarnak*	Tanzania		L. Savioli
Cephalobothrium sp.	Coll. Southwell[‡]	voucher ?				
Cephalobothrium sp.	Coll. Southwell[‡]	voucher ?	*Ginglymostoma concolor*	Pearl Banks, Ceylon	9 Mar. 1921	
Cephalobothrium sp.	Coll. Southwell[‡]	voucher ?				
Discobothrium fallax	BMNH No. 1976.4.12.105	voucher	Raja clavata	?		G. Rees
Discobothrium fallax	BMNH No. 1989.1.6.28	voucher	*Raja clavata*	Plymouth, U.K.		
Hornellobothrium cobraformis	Coll. Southwell[‡]	voucher ?				
Hornellobothrium sp.	QM No. GL4641	voucher	*Aetobatus narinari*	Moreton Bay, QLD, Australia	1981	S. Butler
Hornellobothrium sp.	QM No. GL4642	voucher	*Aetobatus narinari*	Moreton Bay, QLD, Australia		S. Butler
Lecanicephalum peltatum	Coll. Southwell[‡]	voucher ?				
Lecanicephalum peltatum	Coll. Southwell[‡]	voucher ?	*Dasyatis centroura*			E. Linton ?
Lecanicephalum peltatum	Coll. Southwell[‡]	voucher ?	*Zygaena malleus*			
Lecanicephalum peltatum	Coll. Southwell[‡]	voucher ?	*Pristis cuspidatus*, *Trygon kuhli* and *Pteroplatea micrura*			

Appendix 4. Continued.

SPECIES[*]	MUSEUM NO.	STATUS	HOST[†]	LOCALITY	DATE	COLLECTOR
Lecanicephalum peltatum	Coll. Southwell[‡]	voucher ?	*Pristis cuspidatus*			
Lecanicephalum peltatum	Coll. Southwell[‡]	voucher ?	*Pteroplatea micrura*			
Lecanicephalum peltatum	Coll. Southwell[‡]	voucher ?	*Pristis cuspidatus*			
Lecanicephalum peltatum	HWML No. 20937	voucher	*Dasyatis americana*	Colombia, South America		D. R. Brooks and M. A. Mayes
Lecanicephalum peltatum	MHNG No. 87/7-29	voucher	*Dasyatis centrura*	Woods-Hole, MA, U.S.A.		
Lecanicephalum peltatum	USNPC No. 7677	voucher	*Dasyatis centroura*	Woods-Hole, MA, U.S.A.		E. Linton
Lecanicephalum peltatum	USNPC No. 34953	voucher	*Dasyatis centroura*	Woods-Hole, MA, U.S.A.		G. A. MacCallum
Lecanicephalum pingue [as *pinguis*]	HWML No. 34675	voucher	*Rhinoptera bonasus*	Maryland, U.S.A.		
Lecanicephalum sp.	BMNH No. 1988.6.20.90-93	voucher	unidentified ray	Shark Bay, WA, Australia		R. A. Bray
Lecanicephalum sp.	SAMA No. 17012	voucher	*Dasyatis leylandi*	Fog Bay, NT, Australia	26 Sept. 1986	B. Robertson (Aust. Elas. Survey)
Lecanicephalum sp.	SAMA No. 17013	voucher	*Dasyatis leylandi*	Fog Bay, NT, Australia	27 Sept. 1986	B. Robertson (Aust. Elas. Survey)
Lecanicephalum sp.	SAMA No. 17070	voucher	*Himantura uarnak*	Broome, WA, Australia	11 May 1986	B. Robertson (Aust. Elas. Survey)
Lecanicephalum sp.	SAMA No. 17071	voucher	*Aptychotrema bouganvillii*	Broome, WA, Australia	11 May 1987	B. Robertson (Aust. Elas. Survey)
Lecanicephalum sp.	SAMA No. 17122	voucher	*Dasyatis leylandi*	Bunbury, WA, Australia	12 Nov. 1986	B. Robertson (Aust. Elas. Survey)
Lecanicephalum sp.	SAMA No. 17011	voucher	*Rhynchobatus djiddensis*	Flat Top Island, QLD, Australia	25 Oct. 1985	B. Robertson (Aust. Elas. Survey)
Lecanicephalum sp.	BMNH No. 1978.8.31.74-78	voucher	*Dasyatis zugei*	Penang, Malaysia		C. Betterton
Parataenia medusia	Coll. Southwell[‡]	voucher ?	*Rhynchobatus columnae*?	Puri, Orissa, India	22 Mar. 1913	
Parataenia medusia	Coll. Southwell[‡]	voucher ?	*Dasyatis centroura*			E. Linton ?
Parataenia medusia	MHNG No. 88/11-29	voucher	*Dasyatis centrura*	Woods-Hole, MA, U.S.A.		
Parataenia medusia	USNPC No. 4799	voucher	*Dasyatis centroura*	Woods-Hole, MA, U.S.A.		E. Linton
Parataenia medusia	USNPC No. 7692	voucher	*Dasyatis centroura*	Woods-Hole, MA, U.S.A.		V. N. Edwards
Polypocephalus medusia	Coll. Southwell[‡]	voucher ?				
Polypocephalus medusia	Coll. Southwell[‡]	voucher ?	*Dasybatus* sp.	Pearl Banks, Ceylon	24 Sept. 1928	
Polypocephalus medusia	Coll. Southwell[‡]	voucher ?	*Ginglymostoma concolor*	Pearl Banks, Ceylon	9 Mar. 1921	
Polypocephalus medusia	Coll. Southwell[‡]	voucher ?				
Polypocephalus medusia	HWML No. 20916	voucher	*Dasyatis americana*	Colombia, South America		D. R. Brooks and M. A. Mayes
Polypocephalus moretonensis	QM No. GL13003	voucher	*Charybdis callianassa*	Moreton Bay, QLD, Australia	Feb. 1989	J. D. Shields
Polypocephalus pulcher	Coll. Southwell[‡]	voucher ?	*Ginglymostoma concolor*	Pearl Banks, Ceylon	9 Mar. 1921	
Polypocephalus radiatus	Coll. Southwell[‡]	voucher ?				
Polypocephalus radiatus?	BMNH No. 1950.12.6.104-110	voucher	*Trygon kuhlii*?	Queensland, Australia		
Polypocephalus cf. *radiatus*	QM No. GL11017	voucher	stingaree	?		J. W. Fielding
"*Polypocephalus rhinobati*" (undescribed species)	MPM No. [SY74-10]	type?				Coll. S. Yamaguti
Polypocephalus striatus =*Parataenia elongatus*	Coll. Southwell[‡]	voucher	ray			
Polypocephalus sp.	BMNH No. 1978.9.1.11	voucher	*Dasyatis zugei*	?		
Polypocephalus sp.	Coll. Southwell[‡]	voucher ?	*Galeocerdo tigrinum*	West Cheval, Ceylon ?	10 Feb. 1925	
Polypocephalus sp.	QM No. GL18305	voucher	*Scylla serrata*	Moreton Bay, QLD, Australia	Jan. 1992	D. A. Hudson

Appendix 4. Continued.

SPECIES[*]	MUSEUM NO.	**STATUS**	**HOST[†]**	**LOCALITY**	**DATE**	**COLLECTOR**
Polypocephalus sp.	QM No. GL211365	voucher	*Portunus pelagicus*	Hervey Bay, QLD, Australia	1 Aug. 1992	A. Brockerhoff
Polypocephalus sp.	QM No. GL211366	voucher	*Portunus pelagicus*	Hervey Bay, QLD, Australia	1 Aug. 1992	A. Brockerhoff
Polypocephalus sp.	SAMA No. 17067	voucher	*Aptychotrema bouganvillii*	Sanpan Mouth, May River, NT, Australia	11 Sept. 1986	B. Robertson (Aust. Elas. Survey)
Polypocephalus sp.	SAMA No. 17068	voucher	*Aptychotrema bouganvillii*	Broome, WA, Australia	5 Nov. 1986	B. Robertson (Aust. Elas. Survey)
Polypocephalus sp.	SAMA No. S17538(1)	voucher	*Dasytis brevicaudata*	Eastern Shoal, SA, Australia	25 Jun. 1985	B. Robertson (Aust. Elas. Survey)
Polypocephalus sp.	SAMA No. 17063	voucher	*Dasyatis sephen*	Nickol Bay, WA, Australia	11 Nov. 1986	B. Robertson (Aust. Elas. Survey)
Polypocephalus sp.	SAMA No. 17064	voucher	Dasyatis sephen	Nickol Bay, WA, Australia	11 Nov. 1987	B. Robertson (Aust. Elas. Survey)
Polypocephalus sp.	SAMA No. 17065	voucher	*Dasyatis sephen*	Nickol Bay, WA, Australia	11 Nov. 1986	B. Robertson (Aust. Elas. Survey)
Polypocephalus sp.	SAMA No. 17608	voucher	*Dasyatis leylandi*	Cape Van Diemen, NT, Australia	26 Sept. 1986	B. Robertson (Aust. Elas. Survey)
Polypocephalus sp.	SAMA No. 17069	voucher	*Himantura uarnak*	Cape Van Diemen, NT, Australia	25 Sept. 1986	B. Robertson (Aust. Elas. Survey)
Polypocephalus sp.	SAMA No. S17573	voucher	*Pristis zijsron*	Balgal, QLD, Australia	13 Sept. 1985	R. Speare
Polypocephalus sp.	SAMA No. 17066	voucher	*Rhynchobatus djiddensis*	Fog Bay, NT, Australia	27 Sept. 1986	B. Robertson (Aust. Elas. Survey)
Staurobothrium aetobatidis	Coll. Southwell[‡]	voucher	*Aetobatis narinari*			Coll. T. Southwell ?
Tetragonocephalum aetiobatidis	NMW No. 2151	voucher	*Aetiobatis narinari*	?		Coll. A. E. Shipley
Tetragonocephalum aetiobatidis	NMW No. 2152	voucher	*Aetiobatis narinari*	?		Coll. A. E. Shipley
Tetragonocephalum trygonis	BMNH No. 1978.9.1.12-13	voucher	*Dasyatis zugei*	?		
Tetragonocephalum trygonis	NMW No. 2147	voucher	*Aetiobatis narinari*	?		Coll. A. E. Shipley
Tetragonocephalum trygonis	NMW No. 2164	voucher	?	?		Coll. A. E. Shipley
Tetragonocephalum uarnaki	NMW No. 2137	voucher	*Trygon uarnak*	?		Coll. A. E. Shipley
Tetragonocephalum uarnaki	NMW No. 2138	voucher	*Trygon uarnak*	?		Coll. A. E. Shipley
Tetragonocephalum uarnaki	NMW No. 2139	voucher	*Trygon uarnak*	?		Coll. A. E. Shipley
Tetragonocephalum uarnaki	NMW No. 2140	voucher	*Trygon uarnak*	?		Coll. A. E. Shipley
Tetragonocephalum uarnaki	NMW No. 2141	voucher	*Trygon uarnak*	?		Coll. A. E. Shipley
Tetragonocephalum uarnaki	NMW No. 2143	voucher	*Trygon uarnak*	?		Coll. A. E. Shipley
Tetragonocephalum uarnaki	NMW No. 2146	voucher	*Trygon uarnak*	?		Coll. A. E. Shipley
Tetragonocephalum uarnaki	NMW No. 2160	voucher	*Trygon uarnak*	?		Coll. A. E. Shipley
Tetragonocephalum uarnaki	NMW No. 2161	voucher	*Trygon uarnak*	?		Coll. A. E. Shipley
Tetragonocephalum uarnaki	NMW No. 2162	voucher	*Trygon uarnak*	?		Coll. A. E. Shipley
Tetragonocephalum uarnaki	NMW No. 2163	voucher	*Trygon uarnak*	?		Coll. A. E. Shipley
Tetragonocephalum sp.	NMW No. 2144	voucher	*Trygon walga*	?		Coll. A. E. Shipley
Tetragonocephalum sp.	NMW No. 2145	voucher	*Trygon uarnak*	?		Coll. A. E. Shipley
Tetragonocephalum sp.	NMW No. 2148	voucher	*Trygon walga*	?		Coll. A. E. Shipley
Tetragonocephalum sp.	NMW No. 2167	voucher	Trygon walga	?		Coll. A. E. Shipley
Tetragonocephalum sp.	NMW No. 2168	voucher	*Trygon walga*	?		Coll. A. E. Shipley
Tetragonocephalum sp. ?	NMW No. 2155	voucher	?	?		Coll. A. E. Shipley
Tetragonocephalum sp. ?	NMW No. 2166	voucher	*Trygon uarnak*	?		Coll. A. E. Shipley
Tylocephalum aetiobatidis	Coll. Southwell[‡]	voucher	*Rhynchobatis djiddensis*		9 Aug. 1923	

Appendix 4. Continued.

SPECIES[*]	MUSEUM NO.	STATUS	HOST[†]	LOCALITY	DATE	COLLECTOR
Tylocephalum aetiobatidis = *Adelobothrium aetiobatidis*	Coll. Southwell[‡]	voucher	*Rhynchobatis djeddensis*			
Tylocephalum dierama	Coll. Southwell[‡]	voucher	Trygon kuhli			
Tylocephalum dierama and *Parataenia* sp.	Coll. Southwell[‡]	voucher	*Trygon kuhli*	Portugal Bay, Ceylon	7 Nov. 1910	
Tylocephalum dieram and *Polypocephalus elongatus*	Coll. Southwell[‡]	voucher	*Trygon kuhli*			
Tylocephalum dierami	Coll. Southwell[‡]	voucher	*Rhychobatis djeddensis*	Ceylon	28 Apr. 1909	
Tylocephalum dierami	Coll. Southwell[‡]	voucher	ray	Ceylon		
Tylocephalum dierami	Coll. Southwell[‡]	voucher	*Trygon kuhli*			
Tylocephalum dierami, Tylocephalum trygonis and *Tylocephalum uarnak*	Coll. Southwell[‡]	voucher	ray	Ceylon		
Tylocephalum dierami?	Coll. Southwell[‡]	voucher	*Rhynchobatis djeddensis*	Ceylon	28 Apr. 1909	
Tylocephalum pingue [as *pinguis*]	USNPC No. 36053	voucher	*Aetobatus narinari*	Singapore		G. A. MacCallum
Tylocephalum squatinae	MPM No. [SY31-6]	?				Coll. S. Yamaguti
Tylocephalum trygonis	Coll. Southwell[‡]	voucher ?		Chilka, India		
Tylocephalum trygonis	Coll. Southwell[‡]	voucher ?	*Trygon walga*			
Tylocephalum trygonis and *Tylocephalum dierama*	Coll. Southwell[‡]	voucher ?	*Trygon kuhli*			
Tylocephalum uarnak	Coll. Southwell[‡]	voucher ?	*Trygon kukli* and *Trygon walga*		27 Nov. 1910	
Tylocephalum uarnak	Coll. Southwell[‡]	voucher ?	*Aetobatus narinari*			
Tylocephalum uarnak	Coll. Southwell[‡]	voucher ?	*Trygon kuhli*	Ceylon		
Tylocephalum uarnak	Coll. Southwell[‡]	voucher ?	*Urogymnus* sp.	Ceylon		J. Hornell ?
Tylocephalum uarnak	Coll. Southwell[‡]	voucher ?	*Urogymnus* sp.	Ceylon		J. Hornell ?
Tylocephalum uarnak	Coll. Southwell[‡]	voucher ?	*Trygon* sp.	Tamblegam, Ceylon ?	6 Sept. 1911	
Tylocephalum uarnak	Coll. Southwell[‡]	voucher ?				
Tylocephalum uarnak	Coll. Southwell[‡]	voucher ?	*Trygon walga*			
Tylocephalum uarnak	MHNG No. 87/79-83	voucher	*Trygon uarnak*	Ceylon		
Tylocephalum uarnak and *Parataenia* sp.	Coll. Southwell[‡]	voucher ?	*Trygon kuhli*	Portugal Bay, Ceylon	7 Nov. 1910	
Tylocephalum uarnak and *Tylocephalum dierami*	Coll. Southwell[‡]	voucher ?	*Trygon kuhli*			
Tylocephalum uarnak and *Tylocephalum trygonis*	Coll. Southwell[‡]	voucher ?	*Trygon walga*			
Tylocephalum yorkei	Coll. Southwell[‡]	voucher ?	*Aetobatus narinari*	Puri, Orissa, India	3 Feb. 1912	
Tylocephalum yorkei	Coll. Southwell[‡]	voucher ?	*Aetobatus narinari*	Puri, Orissa, India	3 Feb. 1912	
Tylocephalum sp.	BMNH No. 1920.11.20.1-5	voucher	*Rhynchobatus ancylostomus*	India		H. A. B. ?

Appendix 4. Continued.

SPECIES[*]	MUSEUM NO.	**STATUS**	**HOST[†]**	**LOCALITY**	**DATE**	**COLLECTOR**
Tylocephalum sp.	BMNH No. uncatalogued	voucher	*Rhynchobatus ancylostomus*	?		R. H. Whitehouse
Tylocephalum sp.	Coll. Southwell[‡]	voucher ?				
Tylocephalum sp.	Coll. Southwell[‡]	voucher ?				
Tylocephalum sp.	Coll. Southwell[‡]	voucher ?	*Zygaena malleus*			
Tylocephalum sp.	Coll. Southwell[‡]	voucher ?	*Dasybatus* sp.	Pearl Banks, Ceylon	24 Sept. 1928	
Tylocephalum sp.	SAMA No. 19079	voucher	*Dasyatis brevicaudata*	Stoney Point, VIC, Australia	2 Feb. 1990	I. Beveridge
Tylocephalum sp.	SAMA No. S17539(4)	voucher	*Dasyatis brevicaudata*	Eastern Shoal, SA, Australia	25 Jun. 1985	B. Robertson (Aust. Elas. Survey)
Tetragonocephalidae	BMNH No. 1978.9.1.8-10	voucher	*Dasyatis zugei*	Penang, Malaysia		
Tetragonocephalidae	NMW No. 2150	voucher	*Trygon walga*	?		Coll. A. E. Shipley
Tetragonocephalidae	NMW No. 2153	voucher	*Trygon walga*	?		Coll. A. E. Shipley
Tetragonocephalidae	NMW No. 2154	voucher	*Trygon walga*	?		Coll. A. E. Shipley
Lecanicephalidea	SAMA No. 17126	voucher	*Aptychotrema bouganvillii*	Sanpan Mouth, May River, NT, Australia	11 Sept. 1986	B. Robertson (Aust. Elas. Survey)
Lecanicephalidea	SAMA No. 17127	voucher	*Aptychotrema bouganvillii*	Shark Bay, WA, Australia	21 Nov. 1986	B. Robertson (Aust. Elas. Survey)
Lecanicephalidea	SAMA No. 17124	voucher	*Aetobatus narinari*	Fog Bay, NT, Australia	4 Oct. 1986	B. Robertson (Aust. Elas. Survey)
Lecanicephalidea	SAMA No. 17123	voucher	*Aetomylaeus nichofii*	Nickol Bay, WA, Australia	11 Nov. 1986	B. Robertson (Aust. Elas. Survey)
Lecanicephalidea	SAMA No. 17606	voucher	*Carcharhinus brachyurus*	Geraldton, WA, Australia	27 Nov. 1986	B. Robertson (Aust. Elas. Survey)
Lecanicephalidea	SAMA No. 17113	voucher	*Carcharhinus limbatus*	Darwin Harbour, NT, Australia	28 Aug. 1986	B. Robertson (Aust. Elas. Survey)
Lecanicephalidea	SAMA No. 17114	voucher	*Carcharhinus limbatus*	Fog Bay, NT, Australia	4 Oct. 1986	B. Robertson (Aust. Elas. Survey)
Lecanicephalidea	SAMA No. 17116	voucher	*Carcharhinus limbatus*	Nickol Bay, WA, Australia	11 Nov. 1986	B. Robertson (Aust. Elas. Survey)
Lecanicephalidea	SAMA No. 17117	voucher	*Carcharhinus limbatus*	Nickol Bay, WA, Australia	11 Nov. 1986	B. Robertson (Aust. Elas. Survey)
Lecanicephalidea	SAMA No. 17115	voucher	*Carcharhinus limbatus*	Geraldton, WA, Australia	27 Nov. 1986	B. Robertson (Aust. Elas. Survey)
Lecanicephalidea	SAMA No. 17131	voucher	*Dasyatis fluviorum*	Fog Bay, NT, Australia	28 Sept. 1986	B. Robertson (Aust. Elas. Survey)
Lecanicephalidea	SAMA No. 17080	voucher	*Dasyatis sephen*	Fog Bay, NT, Australia	29 Sept. 1986	B. Robertson (Aust. Elas. Survey)
Lecanicephalidea	SAMA No. 17081	voucher	Dasyatis sephen	Nickol Bay, WA, Australia	11 Nov. 1986	B. Robertson (Aust. Elas. Survey)
Lecanicephalidea	SAMA No. 17082	voucher	*Dasyatis sephen*	Nickol Bay, WA, Australia	11 Nov. 1986	B. Robertson (Aust. Elas. Survey)
Lecanicephalidea	SAMA No. 17083	voucher	*Dasyatis sephen*	Nickol Bay, WA, Australia	11 Nov. 1986	B. Robertson (Aust. Elas. Survey)
Lecanicephalidea	SAMA No. 17084	voucher	*Dasyatis sephen*	Nickol Bay, WA, Australia	11 Nov. 1986	B. Robertson (Aust. Elas. Survey)
Lecanicephalidea	SAMA No. 17085	voucher	*Dasyatis sephen*	Nickol Bay, WA, Australia	11 Nov. 1986	B. Robertson (Aust. Elas. Survey)
Lecanicephalidea	SAMA No. 17248	voucher	*Dasyatis sephen*	Nickol Bay, WA, Australia	11 Nov. 1986	B. Robertson (Aust. Elas. Survey)
Lecanicephalidea	SAMA No. 17086	voucher	*Dasyatis sephen*	Nickol Bay, WA, Australia	11 Nov. 1986	B. Robertson (Aust. Elas. Survey)
Lecanicephalidea	SAMA No. 17087	voucher	*Dasyatis sephen*	Nickol Bay, WA, Australia	11 Nov. 1986	B. Robertson (Aust. Elas. Survey)
Lecanicephalidea	SAMA No. 17088	voucher	*Dasyatis sephen*	Nickol Bay, WA, Australia	11 Nov. 1986	B. Robertson (Aust. Elas. Survey)
Lecanicephalidea	SAMA No. 17089	voucher	*Dasyatis sephen*	Nickol Bay, WA, Australia	11 Nov. 1986	B. Robertson (Aust. Elas. Survey)
Lecanicephalidea	SAMA No. 17090	voucher	*Dasyatis sephen*	Nickol Bay, WA, Australia	11 Nov. 1986	B. Robertson (Aust. Elas. Survey)
Lecanicephalidea	SAMA No. 17091	voucher	*Dasyatis sephen*	Nickol Bay, WA, Australia	11 Nov. 1986	B. Robertson (Aust. Elas. Survey)
Lecanicephalidea	SAMA No. 17092	voucher	*Dasyatis sephen*	Shark Bay, WA, Australia	22 Nov. 1986	B. Robertson (Aust. Elas. Survey)
Lecanicephalidea	SAMA No. 17121	voucher	*Dasyatis leylandi*	Bunbury, WA, Australia	12 Nov. 1986	B. Robertson (Aust. Elas. Survey)

Appendix 4. Continued.

SPECIES[*]	MUSEUM NO.	STATUS	HOST[†]	LOCALITY	DATE	COLLECTOR
Lecanicephalidea	SAMA No. 17607	voucher	*Dasyatis leylandi*	Cape Van Diemen, NT, Australia	3 Oct. 1986	B. Robertson (Aust. Elas. Survey)
Lecanicephalidea	SAMA No. 17118	voucher	*Gymnura australis*	Snapper Island, QLD, Australia	12 Oct. 1985	B. Robertson (Aust. Elas. Survey)
Lecanicephalidea	SAMA No. 17250	voucher	*Gymnura australis*	Nickol Bay, WA, Australia	11 Nov. 1986	B. Robertson (Aust. Elas. Survey)
Lecanicephalidea	SAMA No. 17119	voucher	*Gymnura australis*	Nickol Bay, WA, Australia	11 Nov. 1986	B. Robertson (Aust. Elas. Survey)
Lecanicephalidea	SAMA No. 17120	voucher	*Gymnura australis*	Nickol Bay, WA, Australia	11 Nov. 1986	B. Robertson (Aust. Elas. Survey)
Lecanicephalidea	SAMA No. 17249	voucher	*Gymnura australis*	Nickol Bay, WA, Australia	11 Nov. 1986	B. Robertson (Aust. Elas. Survey)
Lecanicephalidea	SAMA No. 17129	voucher	Himantura toshi	Nickol Bay, WA, Australia	11 Nov. 1986	B. Robertson (Aust. Elas. Survey)
Lecanicephalidea	SAMA No. 17130	voucher	*Himantura toshi*	Nickol Bay, WA, Australia	11 Nov. 1986	B. Robertson (Aust. Elas. Survey)
Lecanicephalidea	SAMA No. 17093	voucher	*Himantura uarnak*	Snapper Island, QLD, Australia	11 Sept. 1986	B. Robertson (Aust. Elas. Survey)
Lecanicephalidea	SAMA No. 17094	voucher	*Himantura uarnak*	Fog Bay, NT, Australia	26 Sept. 1986	B. Robertson (Aust. Elas. Survey)
Lecanicephalidea	SAMA No. 17095	voucher	*Himantura uarnak*	Fog Bay, NT, Australia	27 Sept. 1986	B. Robertson (Aust. Elas. Survey)
Lecanicephalidea	SAMA No. 17096	voucher	*Himantura uarnak*	Cape Van Diemen, NT, Australia	25 Sept. 1986	B. Robertson (Aust. Elas. Survey)
Lecanicephalidea	SAMA No. 17097	voucher	*Himantura uarnak*	Cape Van Diemen, NT, Australia	25 Sept. 1986	B. Robertson (Aust. Elas. Survey)
Lecanicephalidea	SAMA No. 17098	voucher	*Himantura uarnak*	Cape Van Diemen, NT, Australia	25 Sept. 1986	B. Robertson (Aust. Elas. Survey)
Lecanicephalidea	SAMA No. 17099	voucher	*Himantura uarnak*	Cape Van Diemen, NT, Australia	25 Sept. 1986	B. Robertson (Aust. Elas. Survey)
Lecanicephalidea	SAMA No. 17100	voucher	*Himantura uarnak*	Cape Van Diemen, NT, Australia	28 Sept. 1986	B. Robertson (Aust. Elas. Survey)
Lecanicephalidea	SAMA No. 17109	voucher	*Himantura uarnak*	Cape Van Diemen, NT, Australia	25 Sept. 1986	B. Robertson (Aust. Elas. Survey)
Lecanicephalidea	SAMA No. 17110	voucher	*Himantura uarnak*	Fog Bay, NT, Australia	26 Sept. 1986	B. Robertson (Aust. Elas. Survey)
Lecanicephalidea	SAMA No. 17111	voucher	*Himantura uarnak*	Nickol Bay, WA, Australia	11 Nov. 1986	B. Robertson (Aust. Elas. Survey)
Lecanicephalidea	SAMA No. 17112	voucher	*Himantura uarnak*	Broome, WA, Australia	5 Nov. 1986	B. Robertson (Aust. Elas. Survey)
Lecanicephalidea	SAMA No. 17125	voucher	*Myliobatis australis*	Esperance, WA, Australia	20 Dec. 1986	B. Robertson (Aust. Elas. Survey)
Lecanicephalidea	SAMA No. 17108	voucher	*Pristis cuspidatus*	Tommy Cut Creek, NT, Australia	13 Sept. 1986	B. Robertson (Aust. Elas. Survey)
Lecanicephalidea	SAMA No. 17128	voucher	*Rhina ancylostomus*	Nickol Bay, WA, Australia	5 Nov. 1986	B. Robertson (Aust. Elas. Survey)
Lecanicephalidea	SAMA No. 17102	voucher	*Rhynchobatus djiddensis*	Broome, WA, Australia	5 Nov. 1986	B. Robertson (Aust. Elas. Survey)
Lecanicephalidea	SAMA No. 17101	voucher	*Rhynchobatus djiddensis*	MacKay, QLD, Australia	11 Oct. 1985	B. Robertson (Aust. Elas. Survey)
Lecanicephalidea	SAMA No. 17103	voucher	*Rhynchobatus djiddensis*	Fog Bay, NT, Australia	1 Oct. 1986	B. Robertson (Aust. Elas. Survey)
Lecanicephalidea	SAMA No. 17104	voucher	Rhynchobatus djiddensis	Cape Van Diemen, NT, Australia	25 Sept. 1986	B. Robertson (Aust. Elas. Survey)
Lecanicephalidea	SAMA No. 17105	voucher	*Rhynchobatus djiddensis*	Fog Bay, NT, Australia	27 Sept. 1986	B. Robertson (Aust. Elas. Survey)
Lecanicephalidea	SAMA No. 17106	voucher	*Rhynchobatus djiddensis*	Fog Bay, NT, Australia	27 Sept. 1986	B. Robertson (Aust. Elas. Survey)
Lecanicephalidea	SAMA No. 28296	voucher	*Aetobatis narinari*	Fog Bay, NT, Australia	1986	B. Robertson (Aust. Elas. Survey)
Lecanicephalidea	SAMA No. 28297	voucher	*Rhynchobatus djeddensis*	Fog Bay, NT, Australia	1987	B. Robertson (Aust. Elas. Survey)
Lecanicephalidea	SAMA No. 28298	voucher	*Dasyatis sephen*	Nickol Bay, WA, Australia	1988	B. Robertson (Aust. Elas. Survey)
Lecanicephalidea	SAMA No. 28299	voucher	*Dasyatis sephen*	Nickol Bay, WA, Australia	1989	B. Robertson (Aust. Elas. Survey)
Lecanicephalidea	SAMA No. 17107	voucher	*Rhynchobatus djeddensis*	Fog Bay, NT, Australia	28 Sept. 1986	B. Robertson (Aust. Elas. Survey)

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[*] Species given as written on slide or as entered in museum database.

[†] Type host is reported as given in the orginal description.

[‡] At the Station Méditerranéene de l'Environment Littoral, Université Montpellier II in Sète, France.

TAXONOMIC INDEX

Note: The Abstract, Chronology sections, Figure captions, and Appendix 1 are not indexed.

ABOUT THE AUTHOR

This monograph is the main product of Kirsten's Ph.D. research, funded by a National Science Foundation (NSF) PEET (Partnership for Enhancing Expertise in Taxonomy) grant awarded to J. Caira and C. Henry in 1995.

Kirsten Jensen received her M.S. (1996) and Ph.D. (2001) in Parasitology in the Department of Ecology and Evolutionary Biology at the University of Connecticut with Dr. Janine N. Caira. While having received little introduction to parasitology during her two years of Vordiplom at the Universität Potsdam, Germany, Kirsten became intrigued with tapeworms of sharks and rays soon after starting her Masters work on elasmobranch tapeworms in Janine Caira's lab. Kirsten's Masters work was funded by an NSF Biotic Surveys and Inventory (BS&I) project to survey the metazoan parasites of sharks and rays in the Gulf of California awarded to J. N. Caira and G. W. Benz in 1993. Her Masters work involved the faunal study of species of the tetraphyllidean genus *Acanthobothrium* in three sympatric species of round stingrays of the genus *Urobatis* from the Gulf of California. In general, her main interests lie in parasitology, especially the taxonomy, morphology, and systematics of elasmobranch tapeworms. During her graduate career, Kirsten was involved in projects investigating the phylogenetic relationships among elasmobranch tapeworms, and studies of co-evolution and host-specificity. In 2001, Kirsten was awarded a two-year Lerner Grey Postdoctoral Fellowship to work at the American Museum of Natural History in New York. She was Co-PI on an NSF BS&I grant to survey the sharks and rays and their metazoan parasites in Malaysian Borneo. During her post-doc, Kirsten studied the lecanicephalideans from sharks and rays from Malaysian Borneo, a study that is ongoing. Over the last seven years her research has allowed her to travel to countries such as Mexico, Australia, Madagascar, Japan, Malaysia, and Senegal in pursuit of these worms. As of January 2004, Kirsten is an Assistant Professor in the Department of Ecology and Evolutionary Biology and an Assistant Research Scientist in the Natural History Museum and Biodiversity Research Center at the University of Kansas. Her research will continue to focus on taxonomy and systematics, and biodiversity of marine cestodes, but will also involve questions relating to the assessment of homologies of morphological features in tapeworms, host specificity, and coevolution.

Kirsten Jensen examining a specimen of *Himantura gerrardi* for parasites on a trawler out of Sematan, Sarawak, Malaysian Borneo, May 2003. Photo by G.P.J. Naylor.

Scanning electron micrograph of *Polypocephalus* sp.

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