2011

TAPEWORMS OF ELASMOBRANCHS (Part III) A Monograph on the Phyllobothriidae (Platyhelminthes, Cestoda)

Timothy R. Ruhnke

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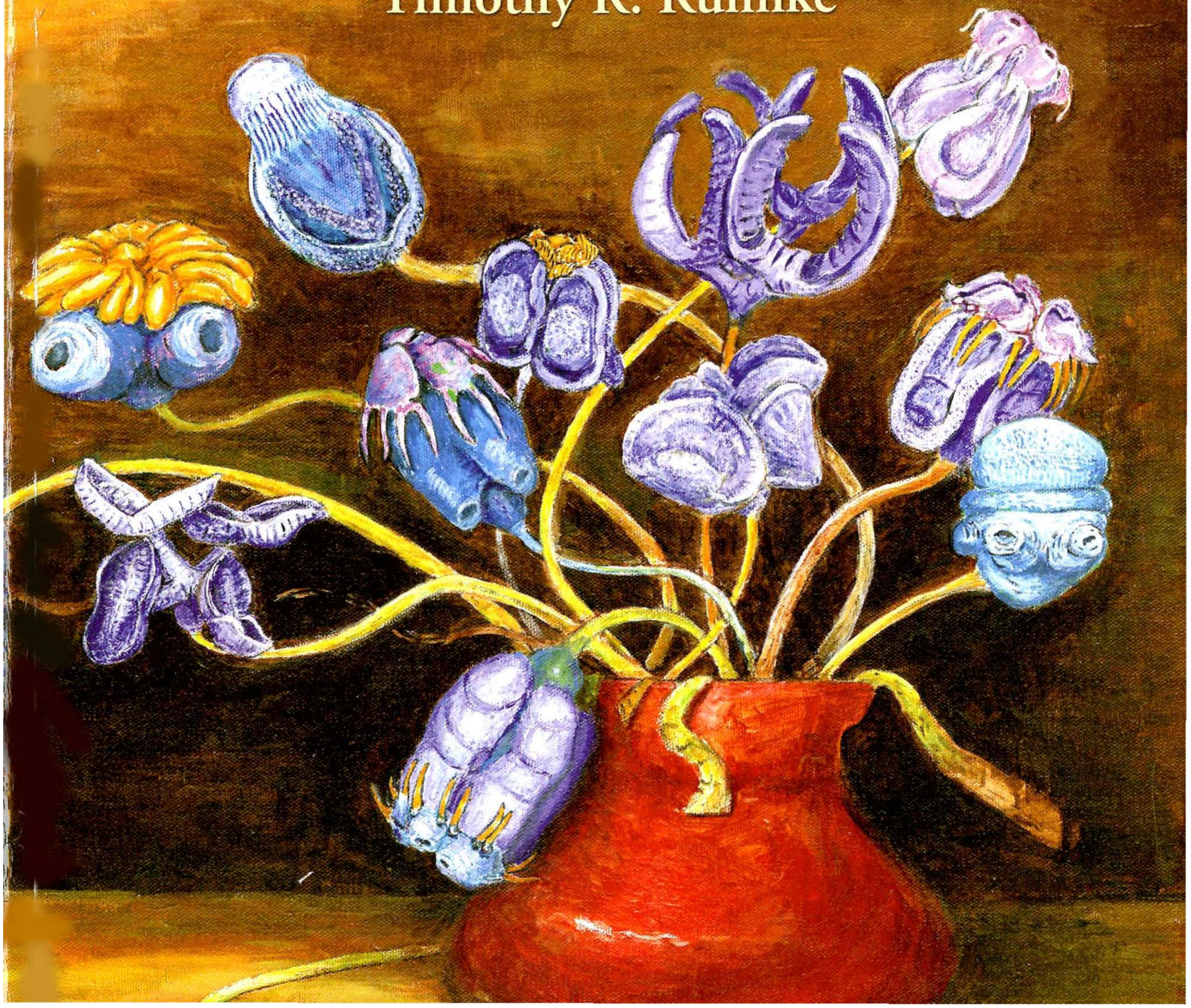

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TAPEWORMS OF ELASMOBRANCHS (Part III)
A Monograph on the Phyllobothriidae
(Platyhelminthes, Cestoda)

by

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Abstract. This monograph aims to provide information on the taxonomic status of all genera associated with the tetraphyllidean family Phyllobothriidae. Full treatments of the three valid species of the type genus, *Phyllobothrium,* in addition to the 47 valid species of *Clistobothrium, Crossobothrium, Marsupiobothrium, Monorygma, Nandocestus, Orectolobicestus, Orygmatobothrium, Paraorygmatobothrium, Ruhnkecestus,* and *Scyphophyllidium* are provided, as is a taxonomic history of the family. Of the valid genera historically associated with the family, only *Phyllobothrium* is considered to be an unambiguous member of the family. The genera *Bibursibothrium, Calyptrobothrium, Cardiobothrium, Clistobothrium, Crossobothrium, Doliobothrium, Flexibothrium, Marsupiobothrium, Monorygma, Nandocestus, Orectolobicestus, Orygmatobothrium, Paraorygmatobothrium, Ruhnkecestus, Scyphophyllidium,* and *Thysanocephalum* are valid, but are considered provisional members of the family. The taxonomic status of the remaining genera was also addressed. *Aocobothrium, Dittocephalus, Hoaleshwaria, Phanobothrium,* and *Shindeobothrium* are considered *nomina dubia. Phyllobothrideum* has been determined to be a *nomen ad interim. Bilocularia, Biporophyllaeus, Cyatocotyle, Kowsalyabothrium, Maccallumiella, Mastacembellophyllaeus, Pillersium, Pithophorus,* and *Polipobothrium* are considered *genera inquirendae. Anindobothrium, Anthobothrium, Carpobothrium, Caulobothrium, Caulopatera, Ceratobothrium, Dinobothrium, Gastrolecithus, Guidus, Mixophyllobothrium, Myzocephalus, Myzophyllobothrium, Pelichnibothrium, Rhoptrobothrium, Trilocularia,* and *Zyxibothrium* are considered valid, but *incertae sedis* with respect to their familial placements. *Anthocephalum, Echeneibothrium, Rhabdotobothrium, Rhinebothrium, Rhinebothroides, Rhodobothrium, Scalithrium,* and *Spongiobothrium* are valid members

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of the Rhinebothriidea. *Clydonobothrium, Escherbothrium, Notomegarhynchus, Pararhinebothroides, Pentaloculum, Phormobothrium, Pseudanthobothrium,* and *Tritaphros* are considered provisional members of the Rhinebothriidea, and *Shindeiobothrium* is considered *genus inquirendum* within that order. *Duplicibothrium* and *Glyphobothrium* are members of the Serendipidae, and *Myliobatibothrium* is considered a *genus inquirendum* within that family. At the specific level, in addition to the type species, *Phyllobothrium lactuca, P. riseri* and *P. serratum* are considered valid species of *Phyllobothrium.* Of the remaining species that have been associated with *Phyllobothrium*, 26 are species that are valid members of other rhinebothriidean or tetraphyllidean genera. Nine species names of *Phyllobothrium* were designated for larval forms. Thirty-five additional species are considered valid, but *incertae sedis* members of *Phyllobothrium* or other genera, six are considered *species inquirendae* within *Phyllobothrium* or other genera, four species are considered *nomina dubia* within *Phyllobothrium* or other genera, and two species of *Phyllobothrium* are considered to be *nomina nuda*. The valid species of *Clistobothrium* are the type species, *C. carcharodoni,* in addition to *C. montaukensis* and *C. tumidum*. The valid species of *Crossobothrium* include the type species, *C. laciniatum,* in addition to *C. antonioi, C. campanulatum, C. dohrni,* and *C. pequeae.* Of the six other species associated with *Crossobothrium,* four are valid members of *Paraorygmatobothrium*, one is *incertae sedis*, and one is *incertae sedis* within *Phyllobothrium*. *Marsupiobothrium alopias* is the sole valid member of its genus. Of the seven other species names associated with *Marsupiobothrium,* four species are *incertae sedis*, one is *incertae sedis* within *Orygmatobothrium,* and two are valid species of *Guidus.* Valid species of *Monorygma* include the type species, *M. perfectum*, in addition to *M. macquariae,* and *M. magnum*. Of the eight other species names associated with *Monorygma*, two were originally designated for larval forms and both are *species inquirendae*. In addition, one species is a synonym, one is *nomen nudum,* one is *nomen dubium*, one is *species inquirenda,* and two are *incertae sedis. Nandocestus* is represented by the monotypic *Nandocestus guariticus*. *Orectolobicestus* is represented by the type species, *O. tyleri,* in addition to *O. chiloscylii, O. kelleyae, O. lorettae, O. mukahensis,* and *O. randyi*. *Orygmatobothrium* is represented by the type species, *Orygmatobothrium musteli* in addition to *O. juani* and *O. schmitti*. Of the 12 other species names associated with *Orygmatobothrium*, one is a synonym, two are *incertae sedis*, three are valid species within other genera, one was originally designated for a larval form and is considered a *nomen dubium* within *Anthobothrium*, three others are *nomina dubia*, one is a *species inquirenda*, and one is a *species inquirenda* within *Pithophorus*. In addition to the type species *Paraorygmatobothrium prionacis, P. angustum, P. arnoldi, P. bai, P. barberi, P. exiguum, P. filiforme, P. floraformis* **n. comb.**, *P. janineae, P. kirstenae, P. leuci* **n. comb**, *P. mobedii, P. musteli* **n. comb.**, *P. nicaraugensis* n.comb., *P. orectolobi* **n. comb.**, *P. paulum* **n. comb.**, *P. roberti, P. rodmani, P. sinuspersicense, P. taylori, P. triacis,* and *P. typicum* **n. comb.** are valid members of the genus. A key to the species of *Paraorygmatobothrium* is provided. *Ruhnkecestus* is represented by the monotypic *R. latipi.* The type of *Scyphophyllidium* is *S. giganteum*, and *S. uruguayense* is an additional species. Of the three additional species that have been associated with *Scyphophyllidium*, one is a valid member of *Paraorygmatobothrium,* one was designated for a larval form and is *incertae sedis*, and one is a *nomen dubium. Chimaerocestos* is currently placed within its own family, the Chimaerocestidae, but should be considered a phyllobothriid the status of which is *incertae sedis*. Phylogenetic information clearly indicates the family to be either paraphyletic or polyphyletic. A number of genera are either members or likely members of the Rhinebothriidea. No evidence exists for the monophyly of the remaining genera from sharks, although putative monophyletic subsets exist within the shark phyllobothriids.

INTRODUCTION

Phyllobothriids
their taxonomy broken
catch-all cestode group

— T. R. Ruhnke (2010)

The family Phyllobothriidae Braun, 1900 (*phyll* Gr. leaf; *bothrios* Gr. *pit*) is one of several families of tapeworms parasitizing elasmobranchs, that belongs to the order Tetraphyllidea in the class Cestoda (Phylum Platyhelminthes). In the most recent complete treatment of the Tetraphyllidea, Euzet (1994) recognized eight families. Since then, several of these, either in entirety (*e.g.*, see Caira et al. 2005) or in part (*e.g.*, Healy et al. 2009) have been transferred to other cestode orders. Five of the families recognized by Euzet (1994) remain. These are the Prosobothriidae Baer and Euzet, 1955, Dioecotaeniidae Schmidt, 1969, Chimaerocestidae Williams and Bray, 1984, Onchobothriidae Braun, 1900, and Phyllobothriidae. However, all five of these families would benefit greatly from closer scrutiny as the monophyly of most, at least relative to other major tetraphyllidean taxa, seems unlikely.

This monograph focuses on what is arguably one of the most problematic of these families, the Phyllobothriidae. This family is of particular interest because of its apparent polyphyletic nature. Based on the current concept of the family, no feature, or set of morphological features, is sufficient to diagnose the family relative to others in the Tetraphyllidea. Little is known of the biology of many of these species. Indeed, many species are known only from the morphology of few adult specimens (see Williams 1968a). Given its size, and somewhat complicated history, this family was determined to be an ideal subject for a full monographic treatment.

History of the Phyllobothriidae

The concept of the Phyllobothriidae can be traced back to Van Beneden (1850), who recognized the tribe Phyllobothriens. Within this taxon he housed the genera *Anthobothrium* Van Beneden, 1850, *Echeneibothrium* Van Beneden, 1849, and *Phyllobothrium* Van Beneden, 1850. Carus (1863) recognized the phyllobothriids as a sub-family, the Phyllobothridea, housing the same three genera. Ariola (1899) recognized the Phyllobothriidae within the tribe Pleuoporina. Braun (1900), in defining the Tetraphyllidea, recognized the family Phyllobothriidae Braun, 1900, in addition to the Ichthyotaeniidae Ariola, 1899, Onchobothriidae Braun, 1900, and Lecanicephalidae Braun, 1900. He defined the Phyllobothriidae as the cestodes having an unarmed scolex, with four sessile or pedunculed bothridia. The bothridia may be simple, divided into loculi, or possess accessory suckers. The neck could be present or absent. The genital pores are marginal and alternate regularly or irregularly, with proglottids often separating away from the strobila before maturity.

In perhaps the first report of the difficulty in applying this taxonomic scheme, de Beauchamp (1905) noted that confusion was present in reference to the variable bothridial morphologies exhibited by species in the family. As a consequence, workers could interpret characters of the genera differently and thus fit disparate species into them. Linton (1924) recognized six genera within the family but also noted the difficulties in classifying species within the phyllobothriid genera.

In what should be considered the first comprehensive treatment of the family, Southwell (1925, p. 144) provided the following diagnosis, taken from that of Braun: "Head unarmed, with four pedunculated or sessile bothridia, which are simple, complicated, or divided up into areolae, or furnished with accessory suckers. Neck present or absent. Genital pores marginal, unilateral, or regularly or irregularly alternating; eggs often spindle-shaped; segments frequently separate from the chain before maturity".

Southwell (1925) listed 28 genera in his monograph after the diagnosis, but stated "The investigations of the author have shown that many of the twenty-eight genera recorded above are merely synonyms, and it has been found possible to sub-divide into the following eight genera" (Southwell 1925, p. 145). Thus, Southwell distilled the list of 28 genera through synonymization into the following eight genera: *Anthobothrium* Van Beneden, 1850, *Carpobothrium* Shipley and Hornell, 1906, *Echeneibothrium* Van Beneden, 1849, *Myzophyllobothrium* Shipley and Hornell, 1906, *Orygmatobothrium* Diesing, 1863, *Phyllobothrium* Van Beneden, 1850, and *Pithophorus* Southwell, 1925. Later, Southwell (1930) further reduced the number of phyllobothriid genera he recognized to five, while proposing the superfamily Phyllobothroidea. However, most if not all of the genera synonymized by Southwell (1925, 1930) were in fact clearly diagnosable taxa. Therefore, the actions of Southwell retarded understanding of phyllobothriid taxonomic diversity.

In their treatment of all cestode orders, Wardle and McLeod (1952) listed the genera added since Van Beneden's establishment of the Phyllobothriens, and noted Southwell's (1925, 1930) merging of genera. They recognized 11 phyllobothriid genera. Euzet (1959) utilized Southwell's superfamily Phyllobothroidea to house both the Phyllobothriidae and Onchobothriidae Braun, 1900. Within the Phyllobothriidae, he recognized the subfamily Phyllobothriinae Beauchamp, 1905 with ten genera; Echeneibothriinae Beauchamp, 1905 with three genera; Rhinebothriinae Euzet, 1953 with three genera; and Thysanocephalinae Euzet, 1953 for one genus. Yamaguti (1959) recognized 18 genera within the Phyllobothriidae. He also erected the Trilocularidae Yamaguti, 1959 for *Trilocularia* Olsson, 1867. In his key to the cestode genera, Schmidt (1986) recognized and provided species lists for 27 phyllobothriid genera. In the most recent consideration of the family, Euzet (1994) followed his earlier of scheme of recognizing subfamilies within the Phyllobothriidae. However, he added the Trilocullariinae Yamaguti, 1959 to accommodate three genera, and expanded the generic holdings of the Phyllobothriinae to include 15 genera, Echeneibothriinae to include five genera, the Thysanocephalinae to include three genera, and the Rhinebothriinae for six genera.

Brooks and Barriga (1995) erected the Serendipidae for the type genus *Serendip* Brooks and Barriga, 1995, in addition to the genera *Duplicibothrium* Williams and Campbell, 1978 and *Glyphobothrium* Williams and Campbell, 1977. Species in these three genera are parasitic in stingrays of the genus *Rhinoptera* Cuvier, 1829. Most recently, Healy et al. (2009) proposed the erection of the Rhinebothriidea as a separate order of cestodes for a suite of phyllobothriid species from batoid fishes. Healy et al. (2009) included the phyllobothriid genera *Anthocephalum* Linton, 1890, *Echeneibothrium* Van Beneden, 1849, *Rhabdotobothrium* Euzet, 1953, *Rhinebothrium* Linton, 1890, *Rhinebothroides* Mayes, Brooks and Thorson, 1981, *Rhodobothrium* Linton, 1889, *Scalithrium* Ball, Neifar, and Euzet, 2003, and *Spongiobothrium* Linton, 1889 in this new order. An analysis of complete 18S rDNA and partial (D1–D3) 28S rDNA revealed this group of taxa to be phylogenetically distinct from other cestode lineages. In addition, the presence of bothridial stalks differentiates the rhinebothriideans from species in other cestode orders. The Rhinebothriidea is recognized here as valid, and thus its genera despite previous inclusion in the Phyllobothriidae, are not treated in this monograph.

The taxonomic history of the Phyllobothriidae has been plagued by poorly defined genera and species. Since the inception of the family, various authors have provided different conceptions of the generic and species level taxonomy of the phyllobothriid cestodes. Essentially, the family has historically been defined within the Tetraphyllidea by what species within it lack, bothridial hooks. Diagnosis of taxa based on the absence of features is a hallmark of paraphyletic or polyphyletic groups. The presence of bothridial hooks has historically been considered a defining feature for the tetraphyllidean family Onchobothriidae, although Olson et al. (2001) provided phylogenetic evidence that the onchobothriids were also a paraphyletic group. Similarly, although a number of genera have been housed in the Phyllobothriidae, and many species are located within these genera, there is no morphological evidence to suggest that the family is phylogenetically cohesive. Most of the species are poorly known, and many of the genera are polyphyletic entities. For example, Wardle and McLeod (1953, p. 247) referred to *Phyllobothrium* Van Beneden, 1850 as "a lumber room of forms". Ruhnke (1993 a, b; 1994 a, b; 1996 a, b) analyzed the morphological variation of species that had been allocated to *Phyllobothrium*, thus beginning the taxonomic renovation of this problematic genus. As currently constituted, *Anthobothrium* is also a polyphyletic taxon (see Neifar et al. 2002; Ruhnke and Caira 2009). Clearly, a species level assessment for genera in the family is needed in advance of a phylogenetic analysis for a broad sample of members in [illegible]s family.

Objectives

This monograph has three primary goals. First, to morphologically evaluate membership in the Phyllobothriidae with the goal of circumscribing a suite of tetraphyllidean genera that, upon more formal phylogenetic analysis, are likely to comprise a monophyletic assemblage of taxa. Second, to formally assess all nominal genera ever assigned to the Phyllobothriidae in order to make recommendations regarding their most appropriate taxonomic placements. Finally, to provide full taxonomic treatments of all species belonging to the suite of genera determined to sufficiently morphologically cohesive as to belong to the Phyllobothriidae. Thus, this monograph was prepared with the following seven specific objectives in mind:

(1) To assess the taxonomic status of all genera historically associated with the Phyllobothriidae, and to provide information on the systematic position for those genera.
(2) To provide a listing of all type species and type hosts of phyllobothriid genera.
(3) To provide a generic diagnosis of *Phyllobothrium* and a species account of the type species, *Phyllobothrium lactuca* Van Beneden, 1850.
(4) To determine other valid species of *Phyllobothrium,* provide accounts for them, and to provide accounts of problematic species that have been associated with the genus.
(5) To assess the valid and problematic species for species of *Clistobothrium* Daily and Vogelbein, 1990, *Crossobothrium* Linton, 1889, *Marsupiobothrium* Yamaguti, 1952, *Monorygma* Diesing, 1863, *Nandocestus* Reyda, 2008, *Orectolobicestus* Ruhnke, Caira and Carpenter, 2006, *Orygmatobothrium* Diesing, 1863, *Paraorygmatobothrium* Ruhnke, 1994, *Ruhnkecestus* Caira and Durkin, 2006, and *Scyphophyllidium* Woodland, 1927, and to provide accounts for these species.
(6) To provide a listing of species names for the species in all of the genera treated in the monograph.
(7) To provide information on host associations for the valid species of *Phyllobothrium* and the valid species of *Clistobothrium, Crossobothrium, Marsupiobothrium, Monorygma, Nandocestus, Orectolobicestus, Orygmatobothrium, Paraorygmatobothrium, Ruhnkecestus,* and *Scyphophyllidium.*

Choice of phyllobothriid genera to monograph

Information is provided for all 79 nominal genera that have ever been assigned to the Phyllobothriidae at one time or another. Of these, only the type genus, *Phyllobothrium,* is unambiguously a valid member of the family. However, in this monograph, 16 other genera are considered as provisionally valid members of the family pending phylogenetic assessment. A summary of the taxonomic status as a result of study for this monograph, including type species and type hosts, is given for each of these in Appendix 1. It should be noted that these genera fall into two categories. Ten of these 16 genera are essentially fully consistent with the concept of the family as circumscribed below, and thus full taxonomic treatments are provided. The remaining six genera, are somewhat less consistent with the familial concept and thus are treated in less detail. The 10 genera for which descriptions, geographic distributions, and illustrations are provided for the valid species are: *Phyllobothrium, Clistobothrium, Crossobothrium, Marsupiobothrium, Monorygma, Nandocestus, Orectolobicestus, Orygmatobothrium, Paraorygmatobothrium, Ruhnkecestus,* and *Scyphophyllidium*. Full treatment of these genera was facilitated by the availability of high quality descriptions for many of their species. The morphology of bothridial spinitriches indicates that four of these eleven genera may form a clade.

The six additional genera that, while considered provisional members of the family, are not fully treated are: *Bibursibothrium* McKenzie and Caira, 1998, *Calyptrobothrium* Monticellli, 1893, *Cardiobothrium* McKenzie and Caira, 1998, *Doliobothrium* Malek, Caira and Ruhnke, 2010, *Flexibothrium* McKenzie and Caira, 1998, and *Thysanocephalum* Linton, 1889.

With respect to the remaining 62 genera, five are considered *nomina dubia*, one is considered a *nomen ad interim*, nine are considered *genera inquirenda*, and 17 are considered *incertae sedis* within the Phyllobothriidae. Nine genera are considered confirmed members of the Rhinebothriidea, eight should be considered provisional members of the Rhinebothriidea, and one is considered a *genus inquirendum* within the new order. Two genera are members of the Serendipidae, and two others should be considered *genera inquirendae* within the Serendipidae. Finally, eight genera are considered synonyms of other tetraphyllidean or rhinebothriidean genera.

Admittedly, this monograph is conspicuous in its lack of a formal treatment of the phylogenetic relationships of phyllobothriid taxa. In addition, there is no clear distinction between those genera considered provisional members of the family and some of the genera considered *incertae sedis*. However, given the complex history and likely polyphyly of the family, this endeavor was determined to be well beyond the scope of this work. Instead, what is presented here is a formal hypothesis of membership in the Phyllobothriidae which is now ready for rigorous testing in a phylogenetic context. As the phylogenetic relationships of the phyllobothriid genera become more well known relative to the other tetraphyllideans, it is hoped that other genera may be similarly treated in conjunction with a revised classification of genera in the family and of the family in general.

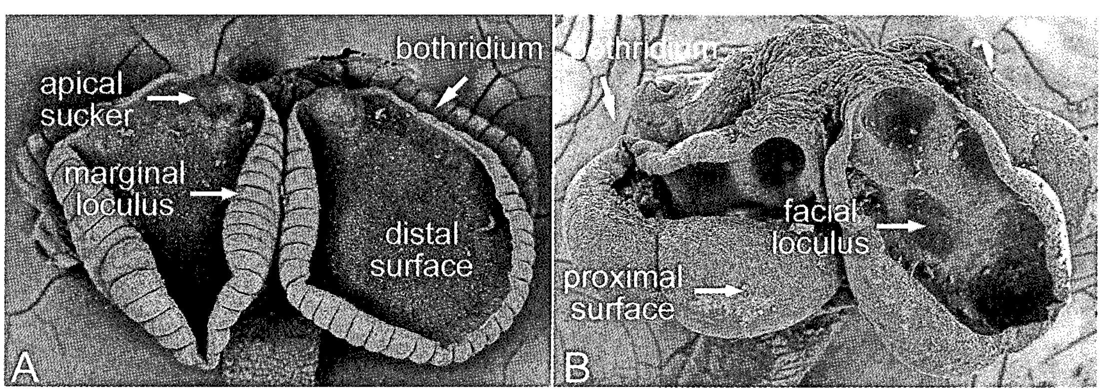

Fig. 1. Scolex terminology.

Morphology and Terminology

Like many tapeworms, the body of phyllobothriids consists of three parts: the scolex, a germinative zone, and the strobila. The scolex is anterior, and serves as the organ of attachment. The germinative zone is the area of proglottid production, and the strobila is comprised of a chain of proglottids. In the literature, the terms "proglottid" and "segment" have both been used to refer to serially repeated reproductive structures of cestodes, each harboring at least one set of reproductive organs. Mehlhorn et al. (1981) argued that the term proglottid should be used until the issue 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, has been resolved. The serially repeated units of cestodes will be referred to as proglottids in this monograph.

The morphology of the scolex is quite diverse among phyllobothriid cestodes, perhaps reflecting their various phylogenetic origins. However, the scolices of all phyllobothriids consist of four muscular, membrane-bound organs of attachment, referred to in the orders Proteocephalidea, Tetraphyllidea, Cyclophyllidea, and Lecanicephalidea as acetabula by Caira et al. (1999). Within the phyllobothriid cestodes, these specialized acetabula are referred to as bothridia. In phyllobothriids, the bothridia are variably shaped, non-sessile organs of attachment and exhibit identifiable proximal and distal surfaces (see Fig. 1). The bothridia of phyllobothriid species can be modified in a variety of ways. For example, most species possess an apical sucker (Figs. 1–2). The periphery of the bothridia in some phyllobothriid species bears marginal loculi (Fig. 1). In other phyllobothriids, the bothridia may be facially loculated (Fig. 1) or quite foliose (Fig. 3). In others, muscle bundles may be present on the periphery or face of the bothridia (Fig. 2).

All phyllobothriids are hermaphroditic. Terminology for selected elements of proglottid anatomy is illustrated in Figure 4. The relationships for the organs of the female reproductive system are as follows. In phyllobothriids, the vagina opens into the genital atrium, generally is curved and passes anteriorly to the cirrus-sac or vas deferens, then in a medial position extends posteriorly towards the ootype (region between the lobes of the ovary, posterior to the ovarian bridge). The ovary produces ova that pass through the muscular oocapt into the oviduct. As the oviduct extends posteriorly into the ootype, the vagina enters, supplying sperm for fertilization of ova. The vitelline duct enters the ootype, supplying the embryo with vitelline cells that are produced in the vitelline follicles. The developing embryos then pass through the Mehlis' gland, which contributes material to produce the eggshell. Leaving the Mehlis' gland, the eggs are carried in a uterine duct into the uterus. In many of the phyllobothriid species observed, the uterine

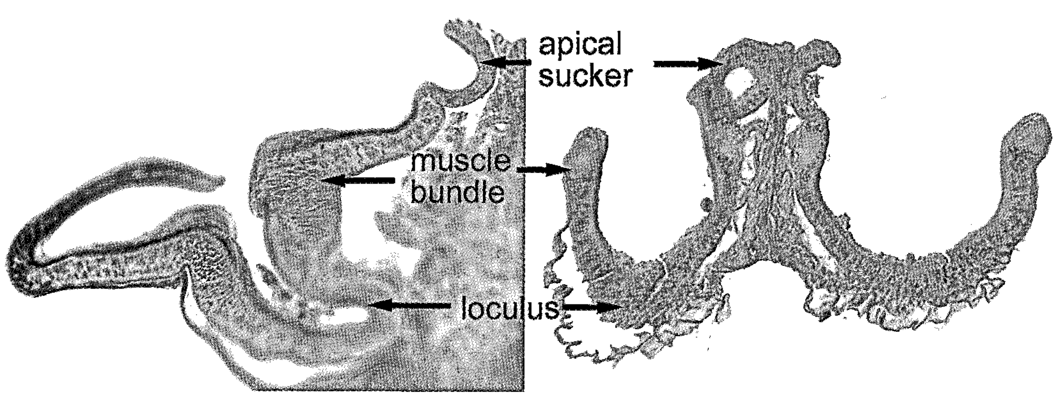

Fig. 2. Apical sucker and bothridial muscle morphology, sagittal section.

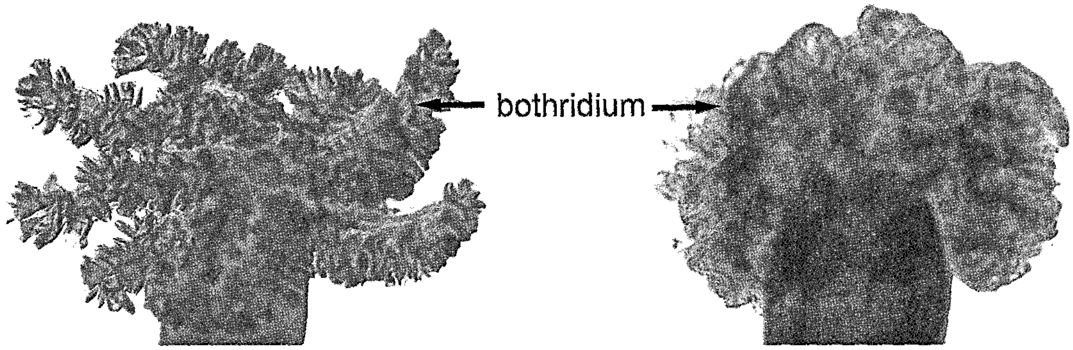

Fig. 3. Foliose bothridial morphology.

duct extends anteriorly and enters the uterus just posterior to the level of the cirrus-sac. The eggs of phyllobothriids can be round, but many are spindle shaped; all appear to be inoperculate.

The relationship of the male organs is as follows. Testes produce sperm that pass into vas efferens. In phyllobothriid species, proglottids typically have at least a few dozen testes. Vas efferens from individual testes join to form a single vas deferens. The vas deferens enters into the cirrus-sac. Inside the cirrus-sac, a sperm duct is typically associated with the copulatory organ, the cirrus. The cirrus is invaginated inside the cirrus-sac; it is usually armed with spinitriches. Both the cirrus and the vagina open into a common genital atrium which is associated with the genital pore. The genital pore is the reproductive opening to the outside of the proglottid. In phyllobothriids, this pore is situated laterally. In some phyllobothriid species, the genital pores are unilateral, but in most species, the pores alternate irregularly along the length of the strobila.

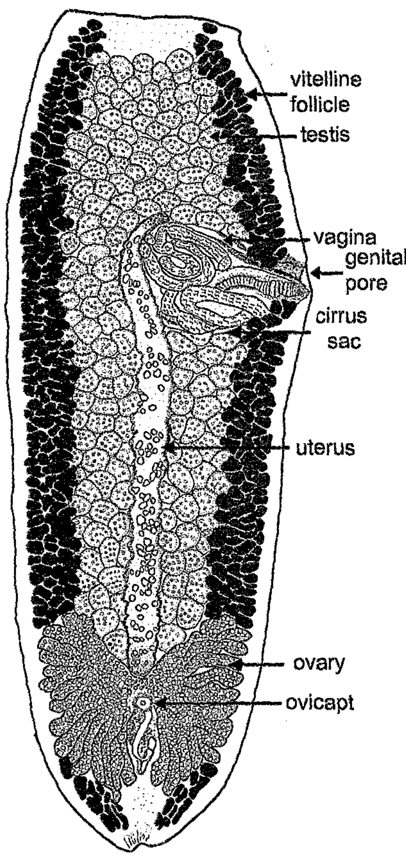

Fig. 4. Proglottid terminology.

Genera and species in the Phyllobothriidae vary in many of the features associated with these reproductive systems (*e.g.*, ovary shape, testes distribution and number, vitelline follicle distribution, etc.).

A key to *Phyllobothrium* and 16 other provisional genera of the Phyllobothriidae is provided below. Illustrations and micrographs for 12 of the genera are included in this monograph. Descriptions and illustrations for all genera can be found at the Global Cestode Database (http://tapewormdb.uconn.edu).

Key to *Phyllobothrium* and 16 genera provisionally assigned to Phyllobothriidae Braun, 1900

1(a) Bothridia facially loculated 2
1(b) Bothridia lacking facial loculi 3

2(a) Bothridia with apical sucker and marginal loculi. ***Cardiobothrium*** (pg. 23)
2(b) Bothridia lacking apical sucker and marginal loculi ...... ***Ruhnkecestus*** (pg. 169)

3(a) Vitelline follicles circum-medullary 4
3(b) Vitelline follicles lateral 5

4(a) Bothridia with marginal loculi; specialized anterior region of bothridia in form of sucker .... ***Nandocestus*** (pg. 84)
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MATERIALS AND METHODS

Specimen Preparation

For a number of the study species, host sharks, skates and rays were obtained from local fishermen. Froese and Pauly (2009) was followed for common names and taxonomy of host elasmobranchs. Hosts were opened via a ventral longitudinal incision. The spiral intestine was removed and also opened using a longitudinal incision. Spiral intestines or, in some cases, a seawater rinse of their contents were examined in the field either by eye or under a dissecting microscope. Specimens were removed from the intestinal surface with either a 1.8 mm micro-dissecting curette or fine forceps and placed in a petri dish in seawater. Specimens were either placed into vials or bags with 10% seawater-buffered formalin (9:1) solution for fixation. For more recent collections, the vial or bag was relatively vigorously shaken to prevent contraction of the worms and facilitate straightening of the specimens as suggested by L. Euzet (pers. com.). In some instances, the spiral intestine was fixed in 10% seawater buffered formalin solution for more thorough investigation in the laboratory. Eventually, all formalin fixed tapeworms and spiral intestines were transferred to 70% ethanol for storage.

Light microscopy: Specimens were prepared as both whole mounts and as histological sections. Specimens prepared as whole mounts were transferred to distilled water, stained in either Gill's or Delafield's hematoxylin, washed and differentiated in tap water, destained, dehydrated in a graded ethanol series, cleared in either xylene or methyl salicylate, and mounted on glass slides in Canada balsam. Some specimens were counterstained in Fast green. Serial sections were prepared as follows: whole worms, scolices, or proglottids were dehydrated in an ethanol series, cleared in xylene or Hemo-De®, placed in a 1:1 mixture of clearant and Paraplast® overnight in an oven, then transferred to Paraplast® for several hours, and embedded using tissue embedding rings and metal embedding molds. Ten micrometer (µm) sections were cut using an American Optics rotary microtome. Sections were floated on a solution of albumin or 3% sodium silicate on slides, placed on a slide warmer to expand, then allowed to air dry on a slide warmer. These slides were placed in xylene, or Hemo-De® (twice) to remove the Paraplast®, hydrated in a graded ethanol series, stained with Gill's or Delafield's hematoxylin, differentiated in Scott's solution, dehydrated in an ethanol series, counterstained with eosin, further dehydrated, cleared in xylene or Hemo-De®, and mounted on glass slides in Canada balsam. Eggs from gravid proglottids from some species were studied by breaking the proglottids open, and examining the contents in water or 70% ethanol.

Scanning electron microscopy (SEM): In most cases, 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 and specimens were air-dried in a fume hood. Some specimens were dried to the critical point using liquid carbon dioxide. Specimens were then mounted on aluminum stubs using carbon paint, or double-sided adhesive carbon tape, sputter coated with approximately 100Å of gold/palladium, and examined with a LEO/Zeiss DSM982 Gemini field emission scanning electron microscope, or a Coates and Welter field emission scanning electron microscope. SEM investigations were conducted at the Biology Electron Microscopy Laboratory, University of Connecticut, Storrs, Connecticut, U.S.A. Microthrix terminology follows Chervy (2009).

Measurements

Measurements were taken directly by optical reticle, logged onto data sheets, then entered into Microsoft Excel spreadsheets for analysis. All measurements are given in micrometers unless otherwise indicated. Measurements of reproductive organs were taken from mature or terminal proglottids unless otherwise specified. The progression of measurements for descriptions in the text are as follows: the range, followed in parentheses by the mean, the standard deviation, the number of worms examined (n), and the total number of observations *(n)* when more than one measurement was taken per worm. In some cases, only the range is given, or the range, followed in parentheses by the mean, or the number of observations.

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, or scanned from polaroids using a Canoscan 3200f flatbed scanner. Plates were prepared using Adobe Photoshop (v. 6.0). Images of whole mounted specimens, histological sections and eggs were taken with a Leica DFC 480 digital camera attached to a Zeiss Axioskop, a Spot camera attached to a Zeiss Axioskop, or a Leica EZ4D digital camera/stereoscope system. Most images were processed using Leica LAS or EZ software. Distribution maps were obtained using Online Map Creation (version 4.4) (http://www.aquarius.geomar.de/omcl omc intro.html) generating maps using GMT (The Generic Mapping Tools) (Wessel and Smith 1998).

Nomenclature

Nomenclatural terms used in the text are defined below. These terms apply to the rank of family and below. Most of these definitions follow the International Code of Zoological Nomenclature (ICZN 1999) and Schenk and McMasters (1956). A set of criteria as to knowledge of host identification, designation of type specimens, and quality of the description were applied in determing the status of phyllobothriid genera, and species within the genera.

Incertae sedis (pl. *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. In this monograph, *incertae sedis* was applied where the host species was known, the description of the taxon allowed for identification, but the familial or generic placement was unclear.

Species inquirenda (pl. *species inquirendae*) or *genus inquirendum* (pl. *genera inquirenda*). The term refers to the doubtful status of the taxon. Further investigtion is required in order to determine its identity. In this monograph, *species inquirenda* or *genus inquirendum* was applied where the host species was either known, of questionable identity or unknown, the description of the taxon was insufficient to allow for identification, and the type specimens were unknown or in poor condition.

Nomen dubium (pl. *nomina dubia*). The term refers to a name of unknown or doubtful application. The term may be used for a taxon that is unidentifiable from its original description and/or type material. This term can be used in connection with a genus or species name. In this monograph, *nomen dubium* was applied where the host species was unknown or unknowable, the description of the taxon was insufficient to allow for identification, and the type specimens were unknown, or in poor condition.

Nomen ad interim. The term refers to a name used temporarily ("for the meantime").

Nomen nudum (pl. *nomina nuda*). 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]). In this monograph, *nomen nudum* was applied where a species name was published in the absence of a description.

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 voucher specimens.

Museum Material

The museums or institutions targeted for their phyllobothriid material were the major museums known to hold cestode collections, as well as places identified as specimen repositories in the original descriptions of the taxa. Museum abbreviations used are given below:

B.B.C.C., Bipin Bihari (Post Graduate) College, affiliated to Bundelkhand University, Jhansi, India.

BMNH, The Natural History Museum, London, England.

CHIOC, Helminthological Collection of the Oswaldo Cruz Institute, Rio de Janeiro, Brazil.

HWML, Harold W. Manter Laboratory, University of Nebraska State Museum, Lincoln, Nebraska, U.S.A.

IPMB, Borneo Marine Research Institute, Universiti Malaysia Sabah, Kota Kinabalu, Sabah, Malaysia.

LRP, Lawrence R. Penner Parasitology Collection, Department of Ecology and Evolutionary Biology, University of Connecticut, Storrs, Connecticut, U.S.A.

MACN-Pa, Parasitology Collection, Argentine Museum of Natural Sciences, Buenos Aires, Argentina.

MHNLS, La Salle Natural History Museum, Caracas, Venezuela.

MHNP, Museum of Natural History, Lima, Peru.

MNHN, Museum of Natural History, Paris, France.

MPM, Meguro Parasitological Museum, Tokyo, Japan.

MZUM (P), Muzium Zoologi, Universiti Malaya, Kuala Lumpur, Malaysia.

MZUSP, Museum of Zoology, University of São Paulo, São Paulo, Brazil.

QM, Queensland Museum, Brisbane, Queensland, Australia.

USNPC, U.S. National Parasite Collection, Beltsville, Maryland, U.S.A.

Information on museum specimen whereabouts was gleaned from original and subsequent descriptions of species. Lists of specimens available at the Meguro Parasitological Museum and the British Museum of Natural History were provided by Janine Caira. Online databases of type and voucher specimens were made available by staff at the U.S. National Parasite Collection and the Harold W. Manter Laboratory. Phyllobothriid study specimens were also made available by Prof. L. Euzet, Universite Montpellier II in Sète, France, from his personal collection, and those held by him of J. Baer and T. Southwell. Un-accessioned Euzet and Baer material examined for the purposes of this study have been deposited at the Museum of Natural History, Paris, France, and un-accessioned Southwell specimens at the Natural History Museum, London, England.

Abbreviations

AO, apical organ; DE, dorsal excretory duct; ED, excretory duct; MB, muscle bundle; NC, nerve chord; O, ovary; OC, ovicapt; T, testis; U, uterus; UD, uterine duct; V, vitellaria; VA, vagina; VE, ventral excretory duct.

TAXONOMIC TREATMENTS

Taxonomic status of genera historically associated with the Phyllobothriidae

For the genera allocated to the Phyllobothriidae, a summary of their taxonomic status as a result of study for this monograph, including their type species and type hosts, is given in Appendix 1. Of the 79 phyllobothriid genera erected, only the type genus, *Phyllobothrium,* is an unambiguous member of the family. In this monograph, 16 other valid genera are considered provisional members of the Phyllobothriidae, five are considered *nomina dubia*, one is considered *nomen ad interim*, nine are considered *genera inquirenda,* and 17 other valid genera are now considered of uncertain familial status (*incertae sedis*) with respect to the Phyllobothriidae. Nine genera are members of the Rhinebothriidea, eight should be considered provisional members of the Rhinebothriidea, and one genus should be considered a *genus inquirendum* within that order. Two genera are members of the Serendipidae, and two others should be considered *genera inquirenda* within the Serendipidae. Eight genera are considered synonyms of other tetraphyllidean or rhinebothriidean genera.

Problematic Phyllobothriid Genera

Anindobothrium Marques, Brooks and Lasso, 2001 *incertae sedis*

This genus was erected by Marques et al. (2001) for *Anindobothrium anacolum* (Brooks, 1977) Marques, Brooks and Lasso, 2001. The type species was originally described as *Caulobothrium anacolum* Brooks, 1977 by Brooks (1977). *Anindobothrium anacolum* was taken from the Chupare stingray, *Himantura schmardae* (Werner, 1904), collected 15 km west of La Cienaga, Magdalena, Colombia. The bothridia of the type species were described as bearing weakly developed apical suckers, lacking longitudinal septa, but possessing transverse septa. No marginal loculi were described, but these were reported in the two other species Marques et al. (2001) added to the genus. The scolex morphology of the type species, *A. anacolum*, does conform to that for other rhinebothriidean species. Verification of the bothridial condition in *A. anacolum* with scanning electron microscopy would be valuable. *Anindobothrium guariticus* Marques, Brooks and Lasso, 2001 was designated the type species of *Nandocestus* by Reyda (2008). *Anindobothrium* should be considered valid, but *incertae sedis* with respect to the Phyllobothriidae.

Anthobothrium Van Beneden, 1850 *incertae sedis*

This genus was erected by Van Beneden (1850) for *Anthobothrium cornucopia* Van Beneden, 1850 as its type. *Anthobothrium cornucopia* was collected from a shark identified as *Galeus canis* (= *Galeorhinus galeus* [L., 1758], the Tope shark) off the coast of Belgium. The genus is characterized by an absence of apical suckers on the bothridia, and a presence of one or two muscular bands on the central face of each bothridium. In addition, the proglottids of *Anthobothrium* are laciniate. The taxonomic history of *Anthobothrium* is complicated (see Williams et al. 2004; Ruhnke and Caira 2009). Ruhnke and Caira (2009) considered the genus to house eight valid species. At present, *Anthobothrium* should be considered valid, but *incertae sedis* with respect to the Phyllobothriidae.

Aocobothrium Mola, 1907 *nomen dubium*

The genus was erected by Mola (1907) for *Aocobothrium carrucci* Mola, 1907 collected from an unknown freshwater teleost. Type specimens of *A. carrucci* are unknown. These cestodes are quite possibly proteocephalideans. Given that no type specimens are known, and the host species is unknown, *Aocobothrium* should be considered a *nomen dubium.*

Bilocularia* Obersteiner, 1914 *genus inquirendum

The genus was erected for the type species *Bilocularia hyperapolytica* Obersteiner, 1914, taken from the Gulper shark, *Centrophorus granulosus* (Bloch and Schneider, 1801), collected near Naples, Italy. The original description contains only illustrations of proglottids. Until new collections allow for a better understanding of other aspects of its morphology, *Bilocularia* should be considered a *genus inquirendum.*

Biporophyllaeus* Subramaniam, 1939 *genus inquirendum

The genus was erected by Subramaniam (1939) for *Biporophyllaeus madrassensis* Subramaniam, 1939, taken from the Gray bambooshark, *Chiloscyllium griseum* Müller and Henle, 1838, near Madras, India. The presence of a proboscis on the scolex is mentioned, but only proglottids were illustrated. The order Biporophyllidea (see Wardle and McLeod 1952) and Biporophyllidae Subramaniam, 1939 were also erected to house the genus. These taxa have not been used in subsequent classifications (*e.g.*, Schmidt 1986; Euzet, 1994). *Biporophyllaeus* should be considered a *genus inquirendum.*

Carpobothrium* Shipley and Hornell, 1906 *incertae sedis

This genus was erected for *Carpobothrium chiloscyllii* Shipley and Hornell, 1906. The type species was collected from the Slender bambooshark, *Chiloscyllium indicum* (Gmelin, 1789). The illustrations of Shipley and Hornell (1906) are difficult to interpret. The bothridia are described as stalked, and do not appear to possess apical suckers. Two flaps emerge from the base of the bothridia, one anterior and one posterior. The anterior flap appears to be slightly heartshaped, and the posterior one rounded. The proglottid anatomy was not described. Three other species of *Carpobothrium* have subsequently been described: *Carpobothrium megaphallum* Subhapradha, 1955, *Carpobothrium rhinei* Sarada, Vijaya Lakshmi and Hanumantha Rao, 1995, and *Carpobothrium shindei* Hiware, Jadhav, Shinde and Kadam, 1999. However, their descriptions do not readily allow for comparison to *C. chiloscyllii*. *Carpobothrium* is a valid genus, but should be considered *incertae sedis* with respect to the Phyllobothriidae.

Caulobothrium* Baer, 1948 *incertae sedis

The genus was erected by Baer (1948) for *Caulobothrium longicolle* (Linton, 1890) Baer, 1948. The type species was originally described by Linton (1890) from the Bullnose eagle ray *Myliobatis freminvillii* Lesueur, 1824, collected from Woods Hole, Massachusetts, U.S.A. *Caulobothrium* is a relatively well known tetraphyllidean genus that possesses paired facial loculi and bothridial stalks, as seen in *Rhinebothrium.* Euzet (1994) placed *Caulobothrium* in the Rhinebothriinae. Despite these similarities, Healy et al. (2009) found no molecular evidence to support such affinities. Indeed, six species of *Caulobothrium* fell outside of the Rhinebothriidea clade, and nested in a group containing shark phyllobothriids. *Caulobothrium* is a valid genus, but should be considered *incertae sedis* with respect to the Phyllobothriidae.

Caulopatera* Cutmore, Bennett and Cribb, 2010 *incertae sedis

Cutmore et al. (2010) erected *Caulopatera* Cutmore, Bennett and Cribb, 2010 for for *Caulopatera pagei* Cutmore, Bennett and Cribb, 2010. The type species was described from the grey carpetshark *Chiloscyllium punctatum* Müller and Henle. *Caulopatera* was described as possessing stalked, circular, uniloculate bothridia, which lack an apical sucker. Cutmore et al. (2010) stated that *Caulopatera* most closely resembled *Carpobothrium* in that both genera possess uniloculate, stalked bothridia, and testes that are completely anterior to the cirrus-sac (see Shipley and Hornell 1906; Subhadpradha 1955; Cutmore et al.,2010). Like *Carpobothrium*, *Caulopatera* should be considered *incertae sedis* with respect to the Phyllobothriidae.

Ceratobothrium* Monticelli, 1892 *incertae sedis

The genus was erected by Monticelli (1892) for *Ceratobothrium xanthocephalum*

Monticelli, 1892. This species was collected from *Lamna cornubica* (= *Lamna nasus* [Bonnaterre, 1788]), the Porbeagle. Specimens identified as *C. xanthocephalum* have since been reported from the Shortfin mako shark, *Isurus oxyrinchus* Rafinesque, 1810 (see Euzet 1959; Olson et al. 1999). *Ceratobothrium xanthocephalum* possesses biloculate bothridia, and the anterior loculus (coded as such by Caira et al. 2001) is smaller than the posterior loculus, which comprises the bulk of the bothridium. A pair of muscular horns is located on the lateral edges at the junction between the two loculi. This bothridial morphology is similar to that of *Dinobothrium* Van Beneden, 1889 and *Gastrolecithus* Yamaguti, 1952. The proglottid morphology is somewhat peculiar, in that the vas deferens projects medially into the anterior fifth of the proglottid. The vagina also curves anteriorly, then recurves posteriorly at the anterior margin of the vas deferens (see Euzet 1959). This vaginal morphology is also present in *Dinobothrium.* Based on scolex and proglottid morphology, *Ceratobothrium* may be closely related to *Dinobothrium* and *Gastrolecithus. Ceratobothrium* is considered valid, but should be considered *incertae sedis* with respect to the Phyllobothriidae.

Cyatocotyle Mola, 1908 *genus inquirendum*

This genus was erected for *Cyatocotyle marchesettii* Mola, 1908, taken from *Carcharias lamia* (= *Carcharodon carcharias* [L., 1758]), the Great white shark from the Indian archipelago. Euzet (1994) considered *Cyatocotyle* a *genus inquirendum,* and stated that the genus was created for *"Tetrabothrius aus charchrias rondeletti* Wagener, 1854 which is said to be a composite species" (Euzet 1994, p. 156). This taxon is considered to be a *genus inquirendum.*

Dinobothrium Van Beneden, 1889 *incertae sedis*

The genus was erected by Van Beneden (1889) for *Dinobothrium septaria* Van Beneden, 1889. This species was collected from *Lamna cornubica* (= *L. nasus*), the Porbeagle, taken from Ostende, Belgium. *Dinobothrium septaria* possesses biloculate bothridia, and the anterior loculus (coded as such by Caira et al. 2001) is smaller than the posterior loculus, which comprises the bulk of the bothridium. A pair of bifid muscular horns is located on the lateral edges at the junction between the two loculi. The bothridial morphology of *Dinobothrium* is similar to that of *Ceratobothrium* and *Gastrolecithus.* The proglottid morphology is similar to that of *Ceratobothrium,* as the vagina extends anteriorly into the anterior extremety of the proglottid (see Euzet 1959), then recurves posteriorly. Euzet (1959) also illustrated a muscular spinchter near the lateral end of the vagina. Based on scolex and proglottid morphology, *Dinobothrium* may be closely related to *Ceratobothrium and Gastrolecithus. Dinobothrium* is considered valid but should be considered *incertae sedis* with respect to the Phyllobothriidae.

Diplobothrium Van Beneden, 1889 (synonym of *Dinobothrium*)

Diplobothrium was erected by Van Beneden (1889) for *Diplobothrium simile* Van Beneden, 1889, collected from *Lamna cornubica* near Ostende, Belgium. *Diplobothrium* was listed as a synonym of *Dinobothrium* Van Beneden, 1889 by Euzet (1994). In this monograph, *Diplobothrium* is considered a junior synonym of *Dinobothrium.*

Dittocephalus Parona, 1887 *nomen dubium*

Euzet (1994) noted that there was a paucity of information on the genus, but that the anatomy of the type is indicative of a pseudophyllidean. Its collection from an elasmobranch is in doubt. Euzet (1994) considered this taxon a *genus inquirendum.* Given that no type specimens are known to exist, in addition to the doubtful nature of its host, *Dittocephalus* should be considered a *nomen dubium.*

Gastrolecithus Yamaguti, 1952 *incertae sedis*

This genus was erected by Yamaguti (1952) for *Gastrolecithus planus* (Linton, 1922) Yamaguti 1952. *Gastrolecithus planus* was reported by Linton (1922a) as *Dinobothrium planum* Linton, 1922, from the Basking shark, *Cetorhinus maximus* (Gunnerus, 1765), taken from Menamsha Bite, Martha's Vineyard, Massachusetts, U.S.A. *Gastrolecithus planus* is a very large cestode. Linton (1922a) reported his largest specimen as being 54.5 cm in length, with a scolex width of 10 mm. *Gastrolecithus planus* possesses biloculate bothridia, and the anterior loculus (coded as such by Caira et al. 2001) is smaller than the posterior loculus. A pair of bifid muscular horns is located on the lateral edges at the junction between the two loculi. This bothridial morphology is similar to that of *Ceratobothrium* and *Dinobothrium*. The dimensions of the proglottid remain much wider than long throughout the strobila. The scolex morphology of *Gastrolecithus* is similar to that for *Ceratobothrium* and *Dinobothrium*, and these three genera may be phylogenetically related. *Gastrolecithus* is considered valid, but should be considered *incertae sedis* with respect to the Phyllobothriidae.

Guidus Ivanov, 2006 *incertae sedis*

This genus was erected for *Guidus argentinense* Ivanov, 2006 and the additional species *G. antarcticus* (Wojciechowska, 1991) Ivanov, 2006 of Wojciechowsk (1991) and *G. awii* (Rocka and Zdzitowiecki, 1998) Ivanov, 2006. *Guidus argentinense* was described by Ivanov (2006) from the Broadnose skate, *Bathyraja brachyurops* (Fowler, 1910), taken from coastal waters off Buenos Aires Province, Argentina. *Guidus argentinense* and *G. antarcticus* possess goblet shaped bothridia. The bothridial rim of these species is associated with a band of muscles that can serve to draw the periphery of the bothridium into an anterior position. The bothridia also each bear a small apical sucker. Ivanov (2006) provided morphological arguments that served to distinguish *Guidus* from *Marsupiobothrium*. *Guidus* is a valid genus, but should be considered *incertae sedis* with respect to the Phyllobothriidae.

Hoaleshwaria Shinde and Chincholikar, 1975 *nomen dubium*

This genus was erected for *Hoaleshwaria marathwadensis* Shinde and Chincholikar, 1975. *Hoaleshwaria marathwadensis* was collected from *Trygon* sp. [sic] near Ratnagiri, India. The species was described from a single worm. Little detail is available from the descriptions or illustrations of Shinde and Chincholikar (1975b). It would be difficult to recognize the species upon re-collection, given the poor quality of the description, and the fact that the host species is essentially unknown. Given the lack of this information, *Hoaleshwaria* should be considered a *nomen dubium*.

Inermiphyllidium Riser, 1955 (synonym of *Rhodobothrium*)

Inermiphyllidium was erected by Riser (1955) for *Inermiphyllidium brachyascum* Riser, 1955, collected from *Aetobatus californicus* (= *Myliobatis californica* Gill, 1865, the Bat eagle ray), taken from Monterey Bay, California, U.S.A. Campbell and Carvajal (1979) declared *Inermiphyllidium* a synonym of *Rhodobothrium*. In this monograph, *Inermiphyllidium* is considered a junior synonym of *Rhodobothrium*.

Kowsalyabothrium Muralidhar, Shinde and Jadhav, 1987 *genus inquirendum*

This genus was erected for its type species, *Kowsalyabothrium indirapriyadarshinii* Muralidhar, Shinde and Jadhav, 1987. The type host for the species was identified as *Trygon centrura* [sic]. *Trygon centrura* could be an archaic reference to *Dasyatis centroura* (Mitchell, 1815). If so, Muralidhar et al. (1987) must have collected *K. indirapriyadarshinii* from some other host species, as *D. centroura* does not occur in the coastal waters of east India. The figures provided in the description of *K. indirapriyadarshinii* are consistent with species of *Paraorygmatobothrium*. Given the lack of host identification and type specimens, *Kowsalyabothrium* should be considered a *genus inquirendum*.

Maccallumiella Yamaguti, 1959 *genus inquirendum*

Yamaguti (1959) erected this genus for *Maccallumiella patina* (MacCallum, 1921) Yamaguti, 1959. This species was originally described by MacCallum (1921) as *Taenia patina* MacCallum, 1921. This species was collected from a siluriform teleost at Bandjermassin, Borneo. The host species was identified in the original description of MacCallum (1921) as "Ikan patin". "Ikan patin" was listed as *Pangasius* sp. by Wong (2003). Euzet (1994) stated that the morphology of the species was suggestive of a proteocephalidean and considered this taxon a *genus inquirendum*. *Maccallumiella* is considered here a *genus inquirendum*.

Mastacembellophyllaeus Shinde and Chincholikar, 1977 _genus inquirendum_

This genus was erected for *Mastacembellophyllaeus nandedensis* Shinde and Chincholikar, 1977, taken from the Zig-zag eel, *Mastacembellus armatus* (Lacepède, 1800). Euzet (1994) noted that Shinde and Chincholikar (1977a) erected the genus based on a tetraphyllidean proglottid. Given the host taxon, it is likely that the proglottid was that of a proteocephalidean. Euzet (1994) considered this taxon a *genus inquirendum*. *Mastacembellophyllaeus* is considered here a *genus inquirendum*.

Mixophyllobothrium Shinde and Chincholikar, 1980 _incertae sedis_

This genus was erected by Shinde and Chincholikar (1980) for *Mixophyllobothrium okamuri* Shinde and Chincholikar, 1980 as its type. Two specimens of the species were collected from the cowtail stingray, *Pastinachus sephen* (Forsskål, 1775) at Ratnagiri, India. The type slides are listed as having been deposited in the cestodology laboratory, Department of Zoology, Marathwada University, Aurangabad, India. The scolex illustration of *M. okamuri* is rudimentrary, but the scolex is described as large in comparison to the strobila of the worms, and the bothridia have paired apical suckers. The bothridia are described as foliate and petal-like. The proglottids possess 280–290 testes. Euzet (1994), in his account of this genus, misspelled it as *Myxophyllobothrium*. *Mixophyllobothrium* is a valid genus, but should be considered *incertae sedis* with respect to the Phyllobothriidae.

Myzocephalus Shipley and Hornell, 1906 _incertae sedis_

This genus was erected by Shipley and Hornell (1906) for *Myzocephalus narinari* Shipley and Hornell, 1906. The species was taken from the Spotted eagle ray, *Aetobatis narinari* (Euphrasen, 1790) from Dutch Bay, Sri Lanka. Based on its possession of a metascolex, Euzet (1994) placed *Myzocephalus* in the phyllobothriid subfamily Thysanocephalinae. Jensen and Caira (2006) suggested that the metascolex structures of *Myzocephalus*, along with those of *Rhoptrobothrium* Shipley and Hornell, 1906 and *Myzophyllobothrium* Shipley and Hornell, 1906 were cephalic peduncle extensions they termed remi. Thus, they considered these morphological extensions to be non-homologous to those of *Thysanocephalum* because Caira et al. (1999) determined the "metascolex" of *Thysanocephalum* to consist of highly folded continuations of the bothridia. *Myzocephalus* is a valid genus, but should be considered *incertae sedis* with respect to the Phyllobothriidae.

Myzophyllobothrium Shipley and Hornell, 1906 _incertae sedis_

This genus was erected by Shipley and Hornell (1906) for *Myzophyllobothrium rubrum* Shipley and Hornell, 1906, taken from *Aetobatus narinari* in Puttalam Lake, Ceylon. As is the case with *Myzocephalus*, the placement of *Myzophyllobothrium* in the subfamily Thysanocephalinae by Euzet (1994) based on the presence of a "metascolex" is doubtful, based on reasoning provided by Jensen and Caira (2006). *Myzophyllobothrium* is a valid genus, but should be considered *incertae sedis* with respect to the Phyllobothriidae.

Pelichnibothrium Monticelli, 1889 _incertae sedis_

This genus was erected for *Pelichnibothrium speciosum* Monticelli, 1889. *Pelichnibothrium speciosum* was collected from the Longnose lancetfish, *Alepisaurus ferox* Lowe, 1833 at Madeira, Portugal. The original description of the type species was of a larval form from a teleost. Adults of this species were subsequently reported from the Blue shark, *Prionace glauca* (L., 1758) (see Yamaguti 1934). However, Scholz et al. (1998) provided evidence of proglottid development in *P. speciosum* taken from the intestines of *A. ferox*. They hypothesized that *A. ferox* may represent a second intermediate host or paratenic host for *P. speciosum*. In addition, Scholz et al. (1998) determined that *Prionacestus bipartitus* Mete and Euzet, 1996 was a junior synonym of *Pelichnibothrium*. This genus is valid, but should be considered *incertae sedis* with respect to the Phyllobothriidae.

Phanobothrium* Mola, 1907 *nomen dubium

The genus was erected by Mola (1907) for *Phanobothrium monticellii* Mola, 1907. Specimens were taken from the spiral intestine of a "big fish". The bothridia of *P. monticellii* appear to be uniloculate, and the proglottids are associated with lateral musculature. Given that no type specimens exist and the identity of the host taxon is unknown, *Phanobothrium* should be considered a *nomen dubium*.

Phyllobothrideum* Olsson, 1867 *nomen ad interim

Phyllobothrideum was a name used by Olsson (1867) as "*Phyllobothrideum Acanthiae vulgaris* n. sp. inquir." for specimens collected from *Acanthias vulgaris* (= *Squalus acanthias* L., 1758, the Piked dogfish). Scudder (1884) referenced this genus as *Phyllobothridium* [sic], and considered the name to be a *nomen ad interim* (*i.e.*, a provisional name). Euzet (1952) suggested that Olsson (1867) used *Phyllobothrideum* as a temporary name. This conclusion is supported by the fact that Olsson (1867) initially used "n. sp. inquir." (= new *species inquirenda*) in his first reference to "*Phyllobothrideum Acanthiae vulgaris.*" Olsson (1867) also indicated that he contemplated applying the generic name *Trilocularia* to this taxon. Olsson (1870) later formally erected *Trilocularia* to house the species he had originally (Olsson 1867) referred to as "*Phyllobothrideum Acanthiae vulgaris* n. sp. inquir". Thus, *Phyllobothrideum* should be considered a *nomen ad interim* (*i.e.*, a provisional name).

Pillersium* Southwell, 1927 *genus inquirendum

The genus was erected for *Pillersium owenium* Southwell, 1927. *Pillersium owenium* was collected from the Porcupine ray, *Urogymnus asperrimus* (Bloch and Schneider, 1801), collected from the Pearl Banks, Ceylon (= Sri Lanka). The genus is known only from scolices. Southwell (1927) described the scolex as bearing only a pair of bothridia, but examination of his scolex illustration indicates that the bothridia may be paired and fused dorsoventrally. In addition, the bothidia appear to be stalked, as in species of the Rhinebothriidea (see Healy et al. 2009). At present, *Pillersium* must be considered a *genus inquirendum*.

Pithophorus* Southwell, 1925 *genus inquirendum

Pithophorus was proposed by Southwell (1925) to house the species *Orygmatobothrium tetraglobum* Southwell, 1912 as *Pithophorus tetraglobus* (Southwell, 1912) Southwell, 1925. This species was collected from *Rhynchobatus djeddensis* [sic] (Forsskål, 1775), the Giant guitarfish, taken from the Pearl Banks, Ceylon (= Sri Lanka). A key feature of the diagnosis of the genus is the description of the bothridia of *P. tetraglobus* as "globular (rarely cylindrical), hollow, and open both anteriorly and posteriorly" Southwell (1925, p. 244). An examination of scolices of Southwell's voucher specimens of *P. tetraglobus* (BMNH 2010.3.3.1–4) does not allow for the resolution of the interpretation of this bothridial feature. The posterior portion of the bothridium could be interpreted to be open, however, examination at higher magnification revealed that this could also be an artifact of bothridial folding. It is unclear if the posterior portion of the bothridia are truly open, or merely appear to be open as an artifact of bothridial folding. The scolices of the type specimens are in poor condition. This genus should be considered a *genus inquirendum* until new material of the species can be collected and the bothridial form confirmed.

Polipobothrium* Mola, 1908 *genus inquirendum

The genus was erected for its type species, *Polipobothrium vaccarii* Mola, 1908. Mola (1908) collected the species from the Basking shark *Selache maxima* (= *Cetorhinus maximus* [Gunnerus, 1765]). The bothridial faces of *P. vaccarii* were described as bearing a vertical row of nine suckers or loculi. Euzet (1994) noted that since its description, no phyllobothriid resembling *P. vaccarii* has been collected from *C. maximus.* Euzet (1994) considered the genus and species doubtful. At present, *Polipobothrium* should be considered a *genus inquirendum.*

***Prionacestus* Mete and Euzet, 1996 (synonym of *Pelichnibothrium*)**

Prionacestus was erected by Mete and Euzet (1996) for the type *Prionacestus bipartitus* Mete and Euzet, 1996. This species was collected from *Prionace glauca*. Scholz et al. (1998) provided evidence that *Prionacestus bipartitus* Mete and Euzet, 1996 was conspecific with *Pelichnibothrium speciosum* Monticelli, 1889. Thus, *Prionacestus* is a junior synonym of *Pelichnibothrium.*

***Proboscidosaccus* Gallien, 1949 (synonym of *Rhodobothrium*)**

Proboscidosaccus was erected by Gallien (1949) for *Proboscidosaccus enigmaticus* Gallien, 1949 for larvae from *Mactra solida* L. Campbell and Carvajal (1979) declared *Proboscidosaccus* a synonym of *Rhodobothrium* Linton, 1889. In this monograph, *Proboscidosaccus* is considered a junior synonym of *Rhodobothrium.*

***Reesium* Euzet, 1955 (synonym of *Dinobothrium*)**

Reesium was erected by Euzet (1955) for *Reesium paciferum* (Sproston, 1948) Euzet, 1955, collected from *Cetorhinus maximus* (Gunnerus, 1765), the Basking shark. *Reesium* was listed by Euzet (1994) as a synonym of *Dinobothrium* Van Beneden (1889). In this monograph, *Reesium* is considered a junior synonym of *Dinobothrium.*

Rhoptrobothrium* Shipley and Hornell, 1906 *incertae sedis

This genus was erected by Shipley and Hornell (1906) for *Rhoptrobothrium myliobatidis* Shipley and Hornell, 1906, taken from *Myliobatis maculata* (= *Aetomylaeus maculatus* [Gray, 1834]), the Mottled eagle ray, collected off the coast of Ceylon (= Sri Lanka). As in the cases of *Myzocephalus* and *Myzophyllobothrium*, the placement of *Rhoptrobothrium* in the Thysanocephalinae by Euzet (1994) based on the the presence of a "metascolex" is doubtful based on reasoning provided in Jensen and Caira (2006). *Rhoptrobothrium* is a valid genus, but should be considered *incertae sedis* with respect to the Phyllobothriidae.

Shindeobothrium* Shinde and Chincholikar, 1975 *nomen dubium

Euzet (1994) noted that although Shinde and Chincholikar (1975a) compared this genus to *Mixophyllobothrium* Shinde and Chincholikar, 1980, their description was incomplete and the illustrations were of insufficient quality to allow recognition of the species. According to Euzet, the type species, *Shindeobothrium indica* Shinde and Chincholikar, 1975, was based on a single specimen from *Trygon* sp. [sic], and has yet to be recollected. Reference to description from a single specimen was mentioned by Shinde and Chincholikar (1975b) in their erection of *Hoaleshwaria*, so it is conceivable that Euzet (1994) mistakenly referred to that account for *Shindeobothrium*. The original reference of the genus was not retrievable for study, so this problem cannot be resolved at present. However, Shinde et al. (1983) referred to *S. indica* in their description of *Shindeobothrium carchariasi* Shinde, Sarwade and Pawar 1983. Owing to the confusion with its morphology and host identity, *Shindeobothrium* should be considered a *nomen dubium*.

***Sphaerobothrium* Euzet, 1959 (synonym of *Rhodobothrium*)**

Sphaerobothrium was erected by Euzet (1959) for *Sphaerobothrium lubeti* Euzet, 1959, collected from *Myliobatis aquila* (L., 1758), the Common eagle ray, taken near Arcachon, France. *Sphaerobothrium* was declared a synonym of *Rhodobothrium* by Campbell and Carvajal (1979), and was listed as a synonym of that genus by Euzet (1994). In this monograph, *Sphaerobothrium* is considered a junior synonym of *Rhodobothrium*.

Trilocularia* Olsson, 1870 *incertae sedis

Trilocularia has a somewhat complicated taxonomic history, which was summarized in some detail by Euzet (1952). The type species of the genus was first referred to by Olsson (1867; pg. 42) as "*Phyllobothrideum Acanthiae vulgaris* n. sp. inquir." However, Olsson indicated his intention to use the name *Trilocularia* for the species in that original account. Subsequent authors (*e.g.*, Scudder 1884; Odhner 1904; Euzet 1952) recognized *Phyllobothrideum* as a provisional name. The genus *Trilocularia* was formally erected by Olsson (1870), with *Trilocularia gracilis* Olsson, 1870 as its type. Although, essentially synonymous with "*Phyllobothrideum Acanthiae vulgaris*," given that the latter was proposed as a provisional name only, *Trilocularia gracilis* should be considered the valid name of this species. The family Trilocularidae Yamaguti, 1959 was erected by Yamaguti (1959), with *Trilocularia* as its type. Euzet (1994) recognized the latter taxon as a subfamily (*i.e.*, Triloculariinae), housed within the Phyllobothriidae. *Trilocularia* is characterized by the presence of bothridia each bearing three facial loculi. *Trilocularia gracilis* is hyperapolytic, and free proglottids bear large spinitriches on their anterior surfaces. At present, *Trilocularia* is a valid genus, but should be considered *incertae sedis* with respect to the Phyllobothriidae.

***Urogonoporus* Lühe, 1902 (synonym of *Trilocularia*)**

Urogonoporus was erected by Lühe (1902) for *Urogonoporus armatus* Lühe, 1902, taken from *Squalus acanthias* L., 1758, the Piked dogfish L., 1758. The genus was erected based on morphology from free proglottids. Euzet (1959) listed *Urogonoporus* as a synonym of *Trilocularia*. In this monograph, *Urogonoporus* is considered a junior synonym of *Trilocularia*.

Zyxibothrium* Hayden and Campbell, 1981 *incertae sedis

The genus was erected for *Zyxibothrium kamienae* Hayden and Campbell, 1981. *Zyxibothrium kamienae* was reported by Hayden and Campbell (1981) as being collected from the Smooth skate, *Malacoraja senta* (Garman, 1885). This genus was included in the Triloculariidae by Schmidt (1986), but future studies should also compare *Z. kamienae* to species of *Echeneibothrium*. *Zyxibothrium* is a valid genus, but should be considered *incertae sedis* with respect to the Phyllobothriidae.

Phyllobothriid genera allocated or provisionally allocated to the Rhinebothriidea Healy, Caira, Jensen, Webster, and Littlewood, 2009

Healy et al. (2009) erected the order Rhinebothriidea, and transferred a number of genera that had been previously assigned to the Phyllobothriidae (see Euzet 1994) to the new order. The following genera should no longer be considered members of the Phyllobothriidae: *Anthocephalum* Linton, 1890; *Echeneibothrium* Van Beneden, 1849; *Rhabdotobothrium* Euzet, 1953; *Rhinebothrium* Linton, 1890; *Rhinebothroides* Mayes, Brooks and Thorson, 1981; *Rhodobothrium* Linton, 1889; *Scalithrium* Ball, Neifar and Euzet, 2003, and *Spongiobothrium* Linton, 1889. Furthermore, Healy et al. (2009) considered the genera *Clydonobothrium* Euzet, 1959, *Escherbothrium* Berman and Brooks, 1994, *Phormobothrium* Alexander, 1963, *Pseudanthobothrium* Baer, 1956, and *Tritaphros* Lönnberg, 1889 likely candidates for inclusion in the new order. These five genera are considered provisional members of the Rhinebothriidea, in addition to the genera *Notomegarhynchus* Ivanov and Campbell, 2002, *Pararhinebothroides* Zamparo, Brooks and Barriga, 1999, and *Pentaloculum* Alexander, 1963. Most recently, Tan et al. (2009) erected *Biotobothrium* Tan, Zhou and Yang, 2009 for *Biotobothrium platyrhina* Tan, Zhou and Yang, 2009, taken from *Platyrhina sinensis* Bloch and

Schneider, 1801. This genus should also be considered a provisional member of the Rhinebothriidea. *Shindeiobothrium* Jadhav, Shinde and Deshmukh, 1981 is a valid genus, but should be considered *incertae sedis* with respect to the Rhinebothriidea.

Phyllobothriid genera that should be considered members of the Serendipidae Brooks and Barriga, 1995

Duplicibothrium Williams and Campbell, 1978

This genus erected by Williams and Campbell (1978) for *Duplicibothrium minutum* Williams and Campbell 1978, collected from the Cownose ray, *Rhinoptera bonasus* (Mitchill, 1815), taken from Chesapeake Bay, Virginia. *Duplicibothrium* was transferred to the Serendipidae Brooks and Barriga, 1995 by Ruhnke et al. (2000). Species of *Duplicibothrium* possess the features of the Serendipidae, such as testes that are distributed into the ovarian field, a digitiform ovary radiating from a central isthmus and vitelline fields that converge dorsally, except dorsal to the cirrus-sac and ovary.

Glyphobothrium Williams and Campbell, 1977

This genus was erected by Williams and Campbell (1977) for *Glyphobothrium zwerneri* Williams and Campbell 1977, collected from the Cownose ray, *Rhinoptera bonasus* (Mitchill, 1815), taken from Chesapeake Bay, Virginia. *Glyphobothrium* was transferred to the Serendipidae by Brooks and Barriga (1995). *Glyphobothrium zwerneri* possesses the features of the Serendipidae, such as bothridial fusion, testes that are distributed into the ovarian field, a digitiform ovary radiating from a central isthmus and vitelline fields that converge dorsally, except dorsal to the cirrus-sac and ovary.

Myliobatibothrium Shinde and Mohekar, 1983 ***genus inquirendum***

This genus was erected for *Myliobatibothrium alii* Shinde and Mohekar, 1983, taken from *Myliobatis nieuhofii* [sic] (= *Aetomylaeus nichofii* [Bloch and Schneider, 1801]), the Banded eagle ray, collected from the Arabian Sea (= Persian Gulf), near Ratnagiri, India. The specimens of the type species are described by Shinde and Mohekar (1983) as short, thin, and delicate. The bothridia are stalked, broad posteriorly and narrow anteriorly. Shinde and Mohekar (1983) describe eight small oval loculi at the posterior margins of the bothridia. The bothridial architecture of this genus compares to that of the serendip genus *Duplicibothrium*. At present, this taxon is considered a *genus inquirendum* within the Serendipidae.

Tiarabothrium Shipley and Hornell, 1906 ***genus inquirendum***

This genus was erected by Shipley and Hornell (1906) for *Tiarabothrium javanicum* Shipley and Hornell, 1906. The species was collected from *Rhinoptera javanica* Müller and Henle, 1841 of the coast of Ceylon (= Sri Lanka). Ruhnke et al. (2000) noted the similarities between *Tiarabothrium* and *Glyphobothrium*. They listed *Tiarabothrium* as a covert member of the Serendipidae. Euzet (1994) considered the taxon *genus inquirendum*. *Tiarabothrium* should be considered *genus inquirendum* within the Serendipidae.

Chimaerocestidae Williams and Bray, 1984

Chimaerocestos Williams and Bray, 1984 ***incertae sedis***

Chimaerocestos was erected as the type genus of Chimaerocestidae by Williams and Bray (1984). The type and only species is *Chimaerocestos prudhoei* Williams and Bray, 1984, taken from the Spearnose chimaera, *Rhinochimaera atlantica* Holt and Byrne, 1909. Specimens of *C. prudhoei* are laciniate and can attain large size, as Williams and Bray (1984) reported a length of 330 mm for a specimen. The ovary appears lobate, but was described as annular (forming a ring). The vitelline follicles are found in two fields only at the level of the ovary. The remaining features of the species are comparable to other phyllobothriids, and *Chimaerocestos*, while valid, could be thought of as *incertae sedis* within the Phyllobothriidae.

PHYLLOBOTHRIIDAE Braun, 1900

Diagnosis (modified from Euzet [1994]).

Scolex with four bothridia, simple or loculate, with or without anterior accessory sucker; metascolex sometimes present. Strobila acraspedote or craspedote, anapolytic, apolytic, euapolytic, or hyperapolytic. Genital pores lateral, irregularly alternating. Testes numerous; postvaginal testes generally present. Ovary posterior, bilobed or tetralobed in cross section. Vagina anterior to cirrus-sac. Vitelline follicles circummedullary or in two lateral fields, each field consisting of dorsal and ventral columns of follicles. Uterus medioventral, uterine duct present or absent. Adults in spiral intestine of elasmobranchs.

Type genus: *Phyllobothrium* Van Beneden, 1850.

Remarks

Within the Phyllobothriidae, only the type genus *Phyllobothrium* is an unambiguous member of the Phyllobothriidae. That is, no other genera are morphologically comparable to the three species of *Phyllobothrium*. In this monograph, a conservative approach has been taken and 15 other valid genera have been provisionally included within the Phyllobothriidae. Ten of these genera are treated in this monograph. Future study may find some or most to be related to *Phyllobothrium*, and thus unambiguous members of the family.

Genera provisionally allocated to the Phyllobothriidae that are treated in this monograph

Clistobothrium Dailey and Vogelbeing, 1990; *Crossobothrium*, Linton, 1889; *Marsupiobothrium*, 1952; *Monorygma* Diesing, 1863; *Nandocestus*, Reyda 2008; *Orectolobicestus* Ruhnke, Caira and Carpenter, 2006 *Orygmatobothrium* Diesing, 1863; *Paraorygmatobothrium* Ruhnke, 1994; *Ruhnkecestus* Caira and Durkin, 2006; *Scyphophyllidium*, Woodland,1927.

Genera provisionally allocated to the Phyllobothriidae that are not treated in this monograph

As stated above, only the type genus *Phyllobothrium* is unambiguously valid. As with the ten genera listed above, the taxonomically valid genera described below are considered provisionally valid members of the Phyllobothriidae.

***Bibursibothrium* McKenzie and Caira, 1998**

This genus was erected for *Bibursibothrium gouldeni* McKenzie and Caira, 1998. *Bibursibothrium gouldeni* was collected from the Longnose sawshark, *Pristiophorus cirratus* (Latham, 1794) in the Bass Strait off of San Remo, Victoria, Australia. The scolex morphology of *Bibursibothrium* is peculiar in that the bothridia are modified to form bisaccate pouches. An apical sucker is present on each bothridium. At present, *Bibursibothrium* is known only from its type species (see McKenzie and Caira 1998). *Bibursibothrium* is considered valid and a provisional member of the Phyllobothriidae.

***Calyptrobothrium* Monticelli, 1893**

This genus was erected by Monticelli (1893) for *Calyptrobothrium riggii* Monticelli, 1893, and was collected from the Spotted torpedo, *Torpedo marmorata* Risso, 1810. *Calyptrobothrium* was considered a synonym of *Phyllobothrium* by Southwell (1925), but Euzet (1994) recognized it as a separate genus. *Calyptrobothrium* possesses unmodified, uniloculate bothridia, with a relatively large apical sucker. Euzet (1959) provided an excellent account of *C. riggi*. *Calyptrobothrium* is considered valid, as well as a provisional member of the Phyllobothriidae.

***Cardiobothrium* McKenzie and Caira, 1998**

This genus was erected by McKenzie and Caira (1998) for *Cardiobothrium beveridgei* McKenzie and Caira, 1998. *Cardiobothrium beveridgei* was collected from the Longnose sawshark, *Pristiophorus cirratus,* in the Bass Strait off of San Remo, Victoria, Australia. The scolex morphology of *Cardiobothrium* is characterized by four open bothridia, each bearing an apical sucker and four facial loculi, arranged in two tandem pairs. Marginal loculi are also present on the bothridia. The proglottid morphology is characteristic of other phyllobothriids. At present, *Cardiobothrium* is known only from its type species (see McKenzie and Caira 1998). *Cardiobothrium* is considered valid and a provisional member of the Phyllobothriidae.

***Doliobothrium* Malek, Caira and Ruhnke, 2010**

Malek et al. (2010) erected *Doliobothrium* Malek, Caira and Ruhnke, 2010 for *Doliobothrium haselii* Malek, Caira and Ruhnke, 2010 and *Doliobothrium musculosum* (Subhapradha, 1955) Malek, Caira and Ruhnke, 2010. *Doliobothrium* differs from all other phyllobothriid genera in the possession of bothridia that both lack apical suckers and are tubular in form, bearing proximal and distal apertures (see Malek et al. 2010). The proglottids of *Doliobothrium* are similar to those seen in *Orectolobicestus*, *Paraorygmatobothrium,* and *Ruhnkecestus*, all of which also parasitize sharks. These four genera also share the presence of serrate gladiate spinitriches on their proximal bothridial surfaces. *Doliobothrium* should be considered a provisional member of the Phyllobothriidae, and is very likely a member of the clade containing *Orectolobicestus*, *Paraorygmatobothrium*, *Ruhnkecestus,* and *Thysanocephalum*.

Doliobothrium haselii was collected from *Carcharhinus* cf. *dussumieri* in the Persian Gulf off Iran and *D. musculosum* was collected from the carcharhiniform shark *Rhizoprionodon acutus* (Rüppell, 1837) in the Timor Sea. The two species differ from one another in total length, testis number, and total number of proglottids.

***Flexibothrium* McKenzie and Caira, 1998**

This genus was erected for *Flexibothrium ruhnkei* McKenzie and Caira, 1998. *Flexibothrium ruhnkei* was collected from the Longnose sawshark, *Pristiophorus cirratus,* in the Bass Strait off of San Remo, Victoria, Australia. *Flexibothrium* is only known from its type species (see McKenzie and Caira 1998). The bothridia of *F. ruhnkei* possess an apical sucker and numerous weakly developed marginal loculi. The posterior margin of each bothridium is recurved anteriorly toward apical sucker and fused to distal surface of bothridium. The result of this fusion is the formation of two lateral, open grooves on either side of the upturned flap of each bothridium. The proglottid morphology is similar to other phyllobothriids, although the vagina curves strongly anteriorly from the genital atrium. *Flexibothrium* is considered valid, as well as a provisional member of the Phyllobothriidae.

***Thysanocephalum* Linton, 1890** (Fig. 5)

This genus was erected by Linton (1890) for a species he referred to as *Thysanocephalum crispum* Linton, 1890. It is clear from Linton's text that he was renaming *Phyllobothrium thysanocephalum* Linton, 1889. This was an incorrect nomenclatural action, and *Thysanocephalum crispum* should be considered a *nomen nudum*. Braun (1900) used the correct name for the species, *Thysanocephalum thysanocephalum* (Linton, 1889) Braun, 1900. *Thysanocephalum thysanocephalum* is a parasite of the Tiger shark, *Galeocerdo cuvier* (Péron and Lesueur, 1822). At present, the most complete account of the species is that of Euzet (1959). Specimens of this species can attain an impressive size. Linton (1889) reported lengths of up to one meter for *T. thysanocephalum.* The scolex of *T. thysanocephalum* is biloculate, with lateral muscular prongs present between the loculi (see Fig. 5B). *Thysanocephalum* has been described as possessing a metascolex. Caira et al. (1999) determined that the "metascolex" of *Thysanocephalum* is actually a folded continuation of the acetabular loculus rather than an elaboration of the cephalic peduncle. These bothridial folds continue to enlarge relative to the size of the scolex proper as the

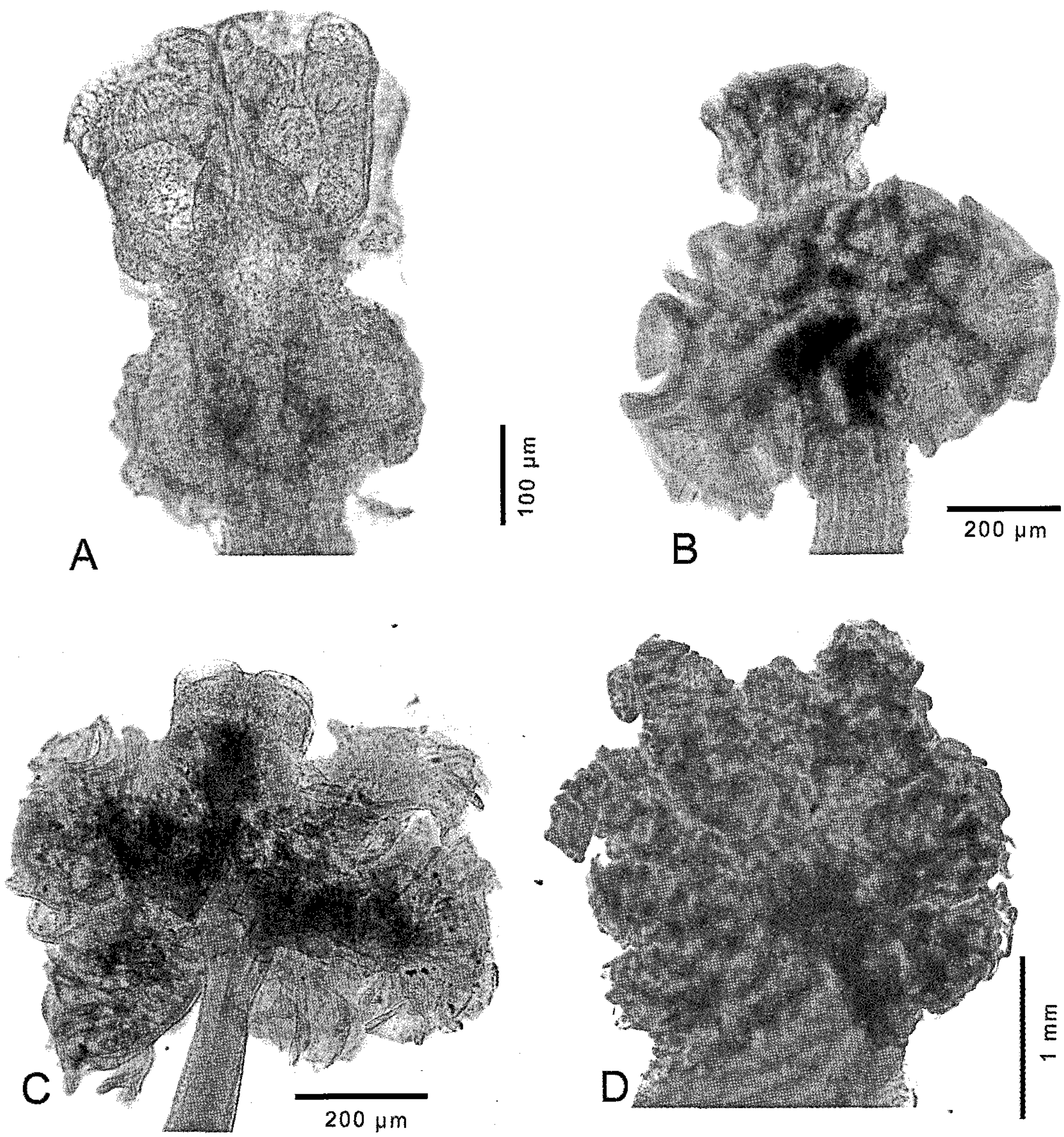

Fig. 5. Scolex development of *Thysanocephalum thysanocephalum* (Linton, 1890) Braun, 1900. A. Scolex of immature specimen (LRP 7400). B. Scolex of immature specimen (LRP 7399). C. Scolex of immature specimen (USNPC 7691). Scolex of mature specimen (USNPC 17273).

worm increases in size (see Fig. 5 A–D), until the "scolex proper" becomes obscured (see Fig. 5D, in addition to Euzet 1959).

Greenwood (2007) demonstrated a phylogenetic association between *T. thysanocephalum* and species of *Paraorygmatobothrium* based on regions of the 28S rDNA. Caira et al. (2001) coded *T. thysanocephalum* as having serrated spinitriches on its proximal bothridial surfaces. This character state is also present in species of *Paraorygmatobothrium, Orectolobicestus* and *Ruhnkecestus* (see Caira and Durkin 2006; Ruhnke et al. 2006b; Ruhnke and Carpenter 2008, respectively). A more comprehensive account of *Thysanocephalum* is needed. At present, *Thysanocephalum* should be considered valid, and a provisional member of the Phyllobothriidae.

Taxonomic Treatment of Phyllobothriid Genera

Taxonomic treatments of species allocated to *Phyllobothrium* and 10 other phyllobothriid genera are provided below. An attempt was made to provide either a full treatment or at least an account for all species allocated to these genera. A listing of species names housed within these 11 genera, their taxonomic status, and the reference associated with the name is given in Appendix 2. For each genus, the valid species are fully treated, and accounts are provided for other species that have been placed within them. In order to prevent multiple accounts of species within the text, species names that are synonyms are listed in the account or treatment of the valid species name.

PHYLLOBOTHRIUM Van Beneden, 1850

Taxonomic status: Valid.
Synonyms: None.
Type species: *Phyllobothrium lactuca* Van Beneden, 1850
Other species: *Phyllobothrium riseri* Ruhnke, 1996; *P. serratum* Yamaguti, 1952.

Diagnosis (modified from Ruhnke 1996a)

Worms anapolytic, robust, craspedote, without distinct neck. Scolex with four muscular bothridia and glandular apical organ. Bothridia extremely foliose, distinctly bifid posteriorly. Immature proglottids much wider than long. Mature proglottids slightly wider than long, gravid; dehisced proglottids longer than wide. Proglottids multitesticulate; testes pre- and post-poral in frontal view, distributed in multiple dorso-ventral rows in cross section. Cirrus-sac oval. Cirrus bearing spinitriches. Genital pores lateral, irregularly alternating, in middle third of proglottid; genital atrium well developed. Vaginal sphincter present; vagina opening into genital atrium anterior to cirrus-sac. Ovary posterior, H-shaped in frontal view, tetralobed in cross section. Uterus ventral, reaching posterior margin of cirrus-sac in mature proglottids, reaching anterior margin of cirrus-sac in gravid proglottids. Vitellarium follicular, follices arranged in two lateral fields, each consisting of multiple columns of follicles, partially or completely interrupted by cirrus-sac. Parasites of triakid sharks.

Remarks

Species of *Phyllobothrium* differ from those in all other phyllobothriid genera except *Thysanocephalum*, in their possession of highly folded, posteriorly bifid bothridia. *Phyllobothrium* differs from *Thysanocephalum* in possession of uniloculate rather than biloculate bothridia. Species of *Phyllobothrium* also exhibit a glandular organ on the apex of the scolex not found in other genera. The generic diagnosis provided here is consistent with the original diagnosis provided by Van Beneden (1850).

The taxonomy of *Phyllobothrium* has been perhaps the most problematic of all tetraphyllidean genera. Southwell (1925), in what should be considered the first treatment of the genus, made a number of ill-advised taxonomic decisions. He considered 12 other genera, fully or in part, as synonyms of *Phyllobothrium.* Southwell's (1925) taxonomic decisions provided the framework for subsequent allocation of species to the genus. The ultimate result of this taxonomic regime was a genus comprised of a suite of unrelated species. This condition was reflected in Wardle and McLeod's (1952, p. 247) commentary on *Phyllobothrium*: "It seems almost impossible to find characteristics which are peculiar to this genus alone, and which occur in every species of it. In the present state of our knowledge, it must be regarded as a lumber room of forms which cannot be fitted into other phyllobothriid genera". Wardle and McLeod (1952) provided a key to the 23 known species allocated to *Phyllobothrium* to aid in their identification.

Yamaguti (1959) considered the genera *Crossobothrium, Anthocephalum, Calyptrobothrium,* and *Bilocularia* as synonyms, and recognized 32 species within the genus. Euzet (1959) provided descriptions and a key for seven species of *Phyllobothrium*, but considered *Crossobothrium* and *Calyptrobothrium* to be valid independent genera. Williams

(1968a) provided a comprehensive taxonomic history of *Phyllobothrium* and suggested that the rampant generic synonymization applied to *Phyllobothrium* might have been a mistaken taxonomic approach. He considered seven species allocated to *Phyllobothrium* as members of *Crossobothrium*. Williams (1968a) treated 22 species as valid member of *Phyllobothrium,* but did not provide a diagnosis of the genus. He noted that little was known of these species, except for "scant knowledge of the morphology of a few adult worms" (Williams 1968a, p. 235), and that of the many species allocated to *Phyllobothrium*, only three, *Phyllobothrium lactuca* Van Beneden, 1850, *P. dagnallium* Southwell, 1927 and *P. serratum* Yamaguti, 1952 had characters consistent with Van Beneden's (1850) original diagnosis of the genus. Williams (1968a) acknowledged the problematic status of the genus, but did not suggest any formal changes in the classification with respect to *Phyllobothrium*. Williams' (1968a) monograph on *Phyllobothrium* remains the most thorough treatment of the taxonomic history and literature for the genus.

Schmidt (1986) listed 42 valid species of *Phyllobothrium*. He considered the genera *Anthocephalum*, *Bilocularia*, *Calyptrobothrium* and *Crossobothrium* as synonyms of *Phyllobothrium*. Schmidt's (1986) diagnosis of *Phyllobothrium* did not include any features unique to species of the genus relative to other tetraphyllideans. Euzet (1994) provided a more restrictive diagnosis of *Phyllobothrium,* and considered *Anthocephalum* as a synonym of *Phyllobothrium.* He noted that the former name could be resurrected to house species whose bothridia bear an accessory sucker and marginal loculi.

Ruhnke (1993a, b; 1994a, b; 1996a, b) addressed the confusing taxonomic nature of *Phyllobothrium. Clistobothrium* was considered valid (Ruhnke 1993a); *Paraorygmatobothrium* was erected for species with serrated spinitriches on their proximal bothridial surfaces (Ruhnke 1994a); *Anthocephalum* was resurrected (Ruhnke 1994b) for species whose bothridia possess marginal loculi; and *Crossobothrium* was considered valid (Ruhnke 1996a). Ruhnke (1996b) provided a restricted diagnosis of *Phyllobothrium*, consistent with that of Van Beneden (1850). He recognized only three valid species: the type, *P. lactuca,* in addition to *P. riseri,* and *P. serratum.* Ruhnke (1993b) treated 36 species that had been allocated to *Phyllobothrium* at one time or another. The taxonomic status for most of these species remains problematic.

Subsequent studies involving the taxonomic entity *Phyllobothrium* continue to be plagued by the broad systematic vision of the genus advanced by Southwell (1925). For example Sanmartín et al. (2000) reported *Phyllobothrium lactuca* from the Undulate ray, *Raja undulata* Lacepede, 1802. The identification of this cestode is almost certainly mistaken as species of *Phyllobothrium sensu stricto* have only been reported from triakid sharks (see Ruhnke 1996b). However, the species they collected could be similar to *Phyllobothrium radioductum* Kay, 1942, which also shares a foliose bothridia similar to *P. lactuca.*

The phylogenetic affinities of *Phyllobothrium* relative to other tetraphyllidean genera are not fully understood. Evidence appears to be mounting for a relationship to some other phyllobothriid genera from sharks. Phylogenetic analyses of Caira et al. (1999) based on morphological data indicated a relationship between *Phyllobothrium lactuca* and such other phyllobothriid genera from sharks as *Thysanocephalum, Orygmatobothrium,* and *Monorygma.* Their expanded morphological phylogenetic study of elasmobranch cestodes (Caira et al. 2001) indicated a phylogenetic linkage between *Phyllobothrium lactuca, P. riseri,* and *Thysanocephalum thysanocephalum.* A molecular phylogenetic study of cestodes by Olson et al. (2001) of small and large ribosomal DNA sequence data revealed a phylogenetic relationship between *Phyllobothrium* cf. *lactuca, "Marsupiobothrium* sp.", *Thysanocephalum thysanocephalum, "Crossobothrium longicolle",* and *Clistobothrium montaukensis* Ruhnke, 1993.

In terms of host/parasite evolutionary affinities, there does appear to be evidence for a historical relationship between species of *Phyllobothrium* and hosts species of the family Triakidae, at least based on existing host records. (see Yamaguti 1952; Euzet 1959; Ruhnke 1996b) Certainly, other triakid species should be sampled for additional species of this genus.

Phyllobothrium lactuca Van Beneden, 1850
TYPE SPECIES
(Figs. 6–9)

Synonyms: None.
Taxonomic status: Valid.
Type host: *Mustelus vulgaris* Cloquet, 1821 [sic] (= *Mustelus mustelus* [L., 1758]) the Smoothhound (Carcharhiniformes: Triakidae).
Additional host: *Mustelus canis* (Mitchell, 1815) [sic] = *Mustelus* sp.
Site of infection: Spiral intestine.
Type locality: Coast of Belgium (Fig. 6).
Additional localities: Corcarneau, France; Sète, France (Fig. 6).
Type material: Not listed.
Voucher specimens: MNHN Paris HEL 120–126 (Fig. 7).
Material examined: MNHN Paris HEL 120–126.
Etymology: Not given, but presumably, the species is named for the resemblance of its scolex to a head of lettuce (genus *Lactuca*).

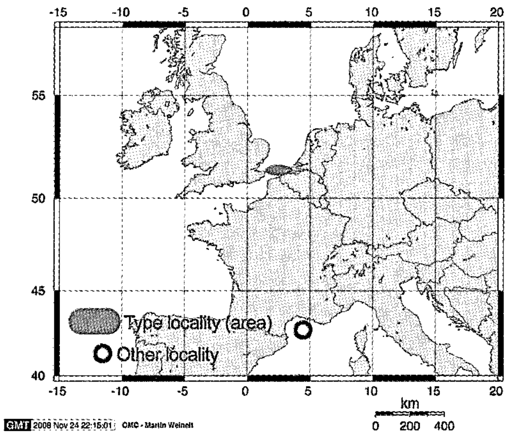

Fig. 6. Geographic distribution of *Phyllobothrium lactuca* Van Beneden, 1850.

Description (modified from Euzet [1959] and Ruhnke [1996b]).

Worms slightly craspedote, anapolytic, 100–150 mm long. Scolex with four bothridia, 2–4.9 mm wide, 4.9 mm wide when bothridia are relaxed, 2–2.1 mm wide when contracted, with glandular apical organ. Apical organ covered with small, round structures, no filitriches observed on surface. Bothridia 2.4–2.6 mm (n=1, n=2) long when relaxed, foliose, posteriorly bifid; each with apical sucker 100–138 (120 ± 16; n=2; n=7) long x 128 –155 wide (144 ± 11; n=2; n=7). All bothridial surfaces covered with filitriches. Anterior region of strobila 0.57–1.4 mm (0.86 ± 0.47; n=3) wide; dorsal and ventral surfaces scutellate; surface of scutes comprised of acicular filitriches.

Immature proglottids much wider than long. Mature proglottids initially somewhat wider than long, becoming longer than wide with maturity; dehisced proglottids longer than wide, 0.97–1.8 mm (1.3 ± 0.3; n=2; n=12) long x 1.2–1.6 mm wide (1.4 ± 0.1; n=2; n=12); proglottid length to width ratio 0.65–1.4:1 (0.97 ± 0.25; n=2; n=12). Testes numerous, pre-ovarian, inter-vitellarian interrupted by uterus and cirrus-sac, 41–80 (59 ± 10; n=2; n=13) in diameter, medullary, 2–3 rows deep in cross-section, 21–26 (23 ± 2; n=1; n=4) in number in cross-section anterior to cirrus-sac. Cirrus-sac oval, curved anteriorly, 462–707 (548 ± 68; n=2; n=12) long x 232–413 wide (311 ± 60; n=2; n=12)

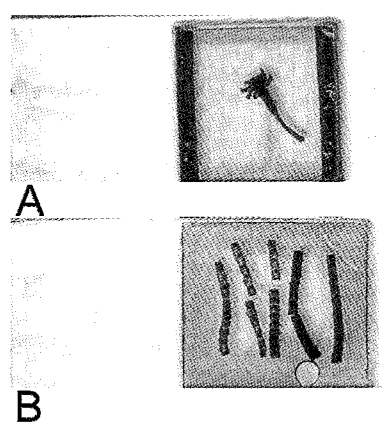

Fig. 7. Voucher specimens of *Phyllobothrium lactuca* Van Beneden, 1850. A. MNHN HEL 120). B. MNHN HEL 121.

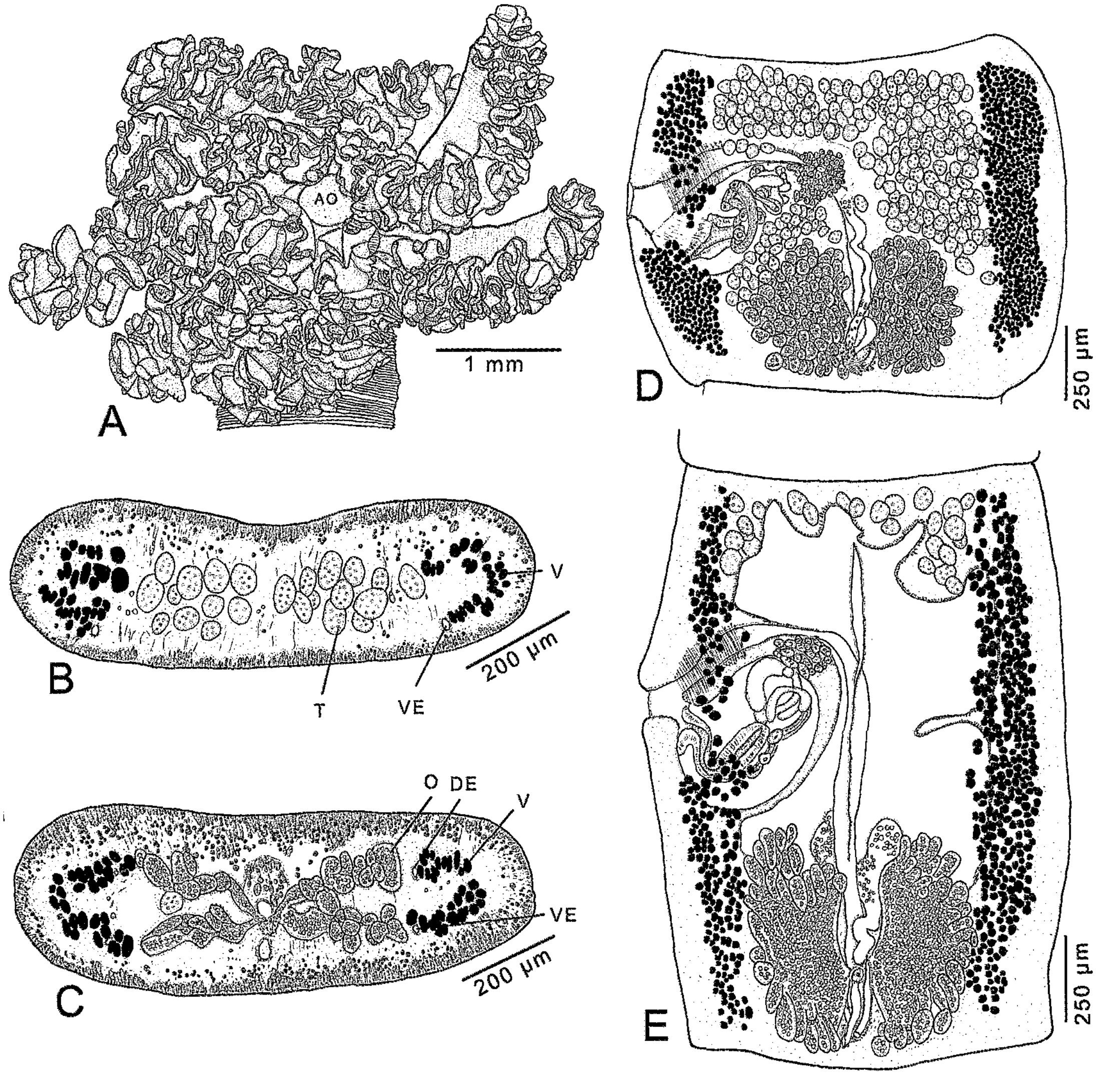

Fig. 8. Line drawings of *Phyllobothrium lactuca* Van Beneden, 1850. A. Scolex of voucher (MNHN Paris HEL 120). B. Cross-section of proglottid posterior to cirrus-sac and anterior to ovary of voucher (MNHN Paris HEL 124). C. Cross-section of proglottid through ovary of voucher (MNHN Paris HEL 124). D. Mature proglottid of voucher (MNHN Paris HEL 121). E. Dehisced proglottid of voucher (MNHN Paris HEL0121). (Taken from Ruhnke [1996b], copyright 2006. Used with permission.)

in mature proglottids; length to width ratio 1.4–2.5:1 (1.8 ± 0.3; n=2; *n*=12), length to proglottid width ratio 0.3–0.56:1 (0.4 ± 0.1; n=2; *n*=12). Cirrus-sac containing coiled cirrus armed with spinitriches. Vas deferens coiled, anterior and medial to cirrus-sac. Genital pores lateral, 54–65% (58 ± 3; n=2; *n*=10) of proglottid length from posterior end, irregularly alternating. Genital atrium present. Vagina median, extending anteriorly from ovary to mid-level of proglottid, then laterally along anterior margin of cirrus-sac to genital atrium. Vaginal sphincter present. Ovary near posterior end of proglottid, H-shaped in frontal view, 460–720 (540 ± 85; n=2; *n*=12) long x 580–800 (693 ± 70; n=2; *n*=12) wide, tetralobed in cross-section. Ovicapt posterior to ovarian bridge, 48–55 (51 ± 2; n=2; *n*=6) in diameter in mature proglottids. Uterus median ventral to vagina, extending from an-

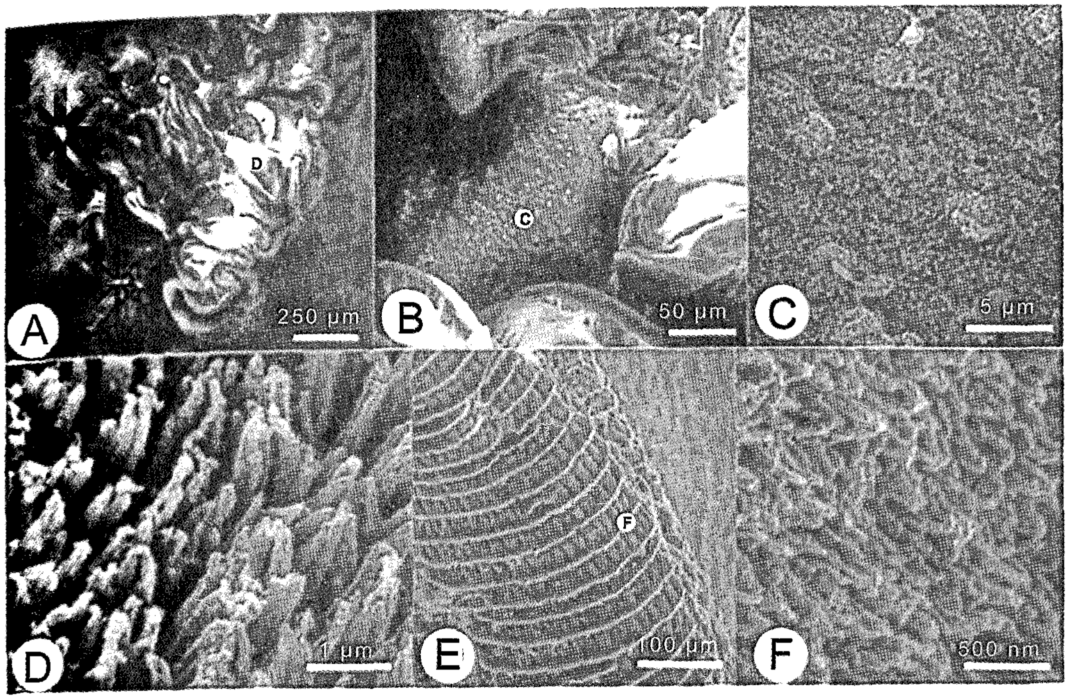

Fig. 9. Scanning electron micrographs of *Phyllobothrium lactuca* Van Beneden, 1850. A. Scolex (letter indicate regions of scolex in enlarged photo D). B. Scolex apex (letter indicate regions of scolex in enlarged photo C). C. Apical surface of scolex. D. Bothridial surface. E. Anterior surface of strobila. F. Surface of anterior strobila. (Taken from Ruhnke [1996b], copyright 2006. Used with permission.)

terior margin of ovary to level of cirrus-sac in mature proglottids, to anterior margin of proglottid in dehisced proglottids. Uterine duct present. Vitellarium follicular; follicles 23–47 (35±6; n=2; *n*=29) in diameter, in two lateral bands; each band with 13–18 dorsal and 7–18 ventral follicles in cross-section, follicles partially interrupted by the cirrus-sac.

Remarks

The name *Phyllobothrium lactuca* was used by Van Beneden (1849), but was not described until a year later (Van Beneden 1850). The whereabouts of the type material for *P. lactuca* is unknown. Woodland (1927) provided an account of the species from specimens taken from *M. mustelus*. Euzet (1959) provided the first comprehensive revision of the species, and his specimens (MNHN Paris HEL 120–126) are considered here representative of the species. Williams (1968a) provided a lengthy account of the taxonomic history of this species, including the fact that worms consistent with *P. lactuca* were originally figured by Leuckart (1820) for *Bothriocephalus flos* Leukart, 1820 and *Bothriocephalus echeneis* Leukart, 1820, and that these descriptions were most likely composite accounts of several species. Van Beneden's (1850) plate was also a composite, as the free proglottid figured (plate IV, fig. 7) is likely a species of *Paraorygmatobothrium*. Williams (1968a) summarized the records of *P. lactuca* and concluded that the majority of these records are likely of other phyllobothriid species. With respect to *P. lactuca*, Williams (1968a) ended his account with the statement, "The adults are restricted to the anterior region of the spiral intestine of species of *Mustelus* in european waters" (pg. 239).

Phyllobothrium lactuca differs from *P. riseri* in length (100–250 vs. 65–105 mm), and cirrus-sac width (232–413 vs. 112–197 and 251–422). *Phyllobothrium lactuca* differs from *P. riseri* in ovicapt diameter (48–55 vs. 38–40). *Phyllobothrium lactuca* differs from *P. serratum* in apical sucker diameter (100–138 x 128–155 vs. 150–180), mature proglottid width (1.2–1.6 vs.1.6–2.9), and testis number in cross-section (21–26 vs. 37–60).

The present treatment was based on the specimens of Euzet (1959). The host Euzet (1959) reported for these specimens is *Mustelus canis* (Mitchill, 1815), a host species not found in European waters. The specimens may actually have been taken from *M. mustelus* (Euzet pers. comm.). However, they are here considered to be from *Mustelus* sp. In addition, a number of records of specimens that might best be referred to as *Phyllobothrium* cf. *lactuca* exist. For example, specimens similar in morphology to *P. lactuca* have been collected from species of *Mustelus* from the Sea of Japan (Yamaguti 1952), and New Zealand (Robinson 1959; Alexander 1963). Genbank records of 18S rDNA and 28S rDNA sequences (accession numbers AF286999 and AF286960) were deposited by Olson et al. (2001) from specimens identified by them as *P. lactuca* collected from *Mustelus asterias* Cloquet, 1821 in Scottish waters. The Genbank sequences of Olson et al. (2001) should be considered as being of *P.* cf. *lactuca*. Specimens identified as *P.* cf. *lactuca* (Ruhnke pers. obs.; Greenwood 2007) have been collected from *Mustelus antarcticus* Günther, 1870 and *M. mento* Cope, 1877. So it is clear that cestodes comparable to *P. lactuca* occur routinely in sharks of the genus *Mustelus*. Future study will determine whether these samples constitute a complex of species, or perhaps a single, widespread species.

Phyllobothrium riseri Ruhnke, 1996
(Figs. 10–13)

Synonyms: None.
Taxonomic status: Valid.
Type host: *Triakis semifasciata* Girard, 1854, the Leopard shark (Carcharhiniformes: Triakidae).
Site of infection: Spiral intestine.
Type locality: Monterrey Bay, CA. U.S.A. (Fig. 10).
Additional localities: Elkhorn Slough, Castroville, CA, U.S.A.; Hermosa Beach Pier, Hermosa Beach, CA, U.S.A.; San Luis Obisbo Bay, CA, U.S.A.; Santa Cruz, CA, U.S.A., El Barril, Baja California, Mexico (Fig. 10).
Type material: Holotype USNPC 85428; Paratypes USNPC 85429, HWML 38553 (Fig. 11A).
Voucher specimens: LRP 7401; HWML 31659.
Material examined: Holotype, USNPC 85428; paratypes USNPC 85429, HWML 38553 (Fig. 11A); LRP 7401; HWML 31659.
Etymology: This species was named for Dr. Nathan W. Riser, who provided study material of the species, and who was also generous in conservations and communications with the author (T. Ruhnke) about tetraphyllidean tapeworms.

Description (modified from Ruhnke [1996a]).
Worms craspedote, apoltyic, 65–105 mm (81 ± 15; n=5) long; maximum width 1.8–2.3 mm (1.97 ± 0.25; n=5) at scolex. Strobila with more than 100 proglottids. Scolex 1.8–2.3 mm (1.97 ± 0.25; n=5) wide, with four bothridia and glandular apical organ. Apical organ covered with small round structures; no microtriches observed on apical surface. Bothridia foliose, posteriorly bifid, each with apical

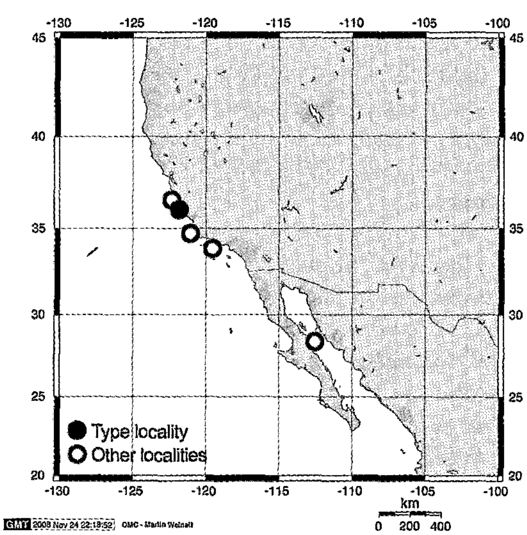

Fig. 10. Geographic distribution of *Phyllobothrium riseri* Ruhnke, 1996.

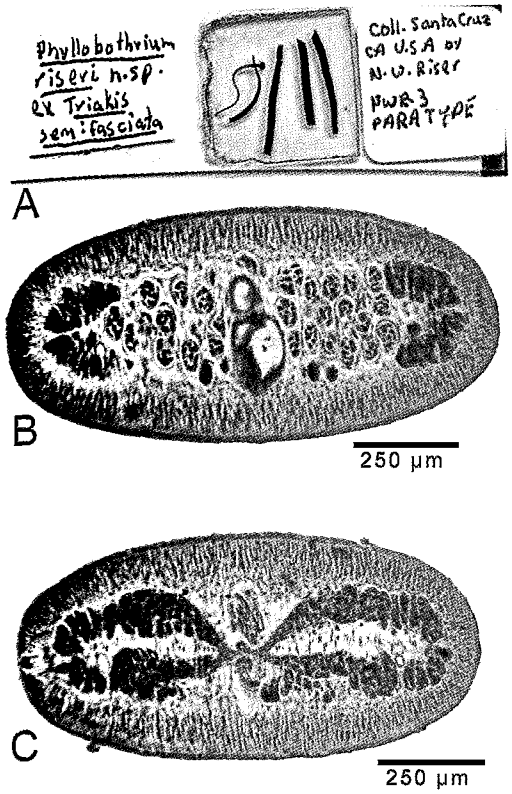

Fig. 11. Photomicrographs of *Phyllobothrium riseri* Ruhnke, 1996. A. Paratype (HWML 38554). B. Cross-section of proglottid posterior to cirrus-sac and anterior to ovary of paratype (HWML 38553). C. Cross-section of proglottid through ovary of paratype (HWML 38553).

sucker 110–160 (138 ± 18; n=3; *n*=7) in diameter. All bothridial surfaces covered with aristate gladiate spinitriches and acicular filitriches. No distinct neck observed.

Immature proglottids much wider than long. Mature proglottids initially wider than long, becoming longer than wide with maturity, fully-gravid proglottids generally twice as long as wide. Mature and gravid proglottids 0.8–2.2 mm (1.4 ± 0.5; n=6; *n*=15) long x 0.9–1.7 mm (1.26 ± 0.3; n=6; *n*=15) wide; length to width ratio 0.43–1.8:1 (1.2 ± 0.4; n=6; *n*=15), with dorsal and ventral pair of excretory ducts. Testes numerous, pre-ovarian, intervitellarian, interrupted by uterus and cirrus-sac, generally round, medullary, numbering 22–42 (27 ± 6; n=2; *n*=9) in cross-section anterior to cirrus-sac, 3–4 rows deep in cross-section, 36–70 (51 ± 9; n=6; *n*=18) in diameter in mature proglottids. Cirrus-sac oval; angled anteriorly in gravid proglottids, 331–587 (437 ± 66; n=6; *n*=14) long x 112–197 (167 ± 29; n=6; *n*=14) wide, containing coiled cirrus armed with spinitriches. Vas deferens coiled, slightly anterior and medial to cirrus-sac. Genital pores lateral, 52–65% (59 ± 4; n=6; *n*=16) of proglottid length from posterior end, irregularly alternating. Genital atrium present. Vagina median, extending anteriorly from ovary to middle of proglottid, then laterally along anterior margin of cirrus-sac to genital atrium. Vaginal sphincter present. Ovary near posterior end of proglottid. H-shaped in frontal view, 163–660 (364 ± 147; n=6; *n*=16) long x 450–1075 (754 ± 211; n=6; *n*=16) wide, tetralobed in cross-section. Ovicapt ventral, at posterior margin of ovarian bridge 38–40 (39 ± 1; n=3; *n*=5) in diameter in mature proglottids. Mehlis' gland posterior to ovicapt. Uterus median, ventral to vagina, extending from anterior margin of ovary to posterior margin of cirrus-sac in mature proglottids, extending to anterior margin of cirrus-sac in gravid proglottids. Uterine duct not observed. Vitellarium follicular; follicles in two lateral bands; each band with 6–15 dorsal and 6–19 ventral follicles in cross-section interrupted by cirrus-sac. Eggs round, 20–25 (23 ± 2; n=3; *n*=9) in diameter.

Remarks

Phyllobothrium riseri was first reported in the literature by Riser (1955) as *P. lactuca*, collected from *Triakis semifasciata* from localities of the central coast of California (see Fig. 10). This species has also been collected from the Gulf of California (see Fig. 10). *Phyllobothrium riseri* differs from *P. lactuca* and *P. serratum* in length (65–105 mm vs. 100–250 and 134–220 mm, respectively), and cirrus-sac width (112–197 vs. 232–413 and 251–422, respectively). *Phyllobothrium riseri* differs from *P. lactuca* in ovicapt diameter (38–40 vs. 48–55) and further differs from *P. serratum* in maximum worm width (1.8–2.25 mm vs. 2.5–3 mm).

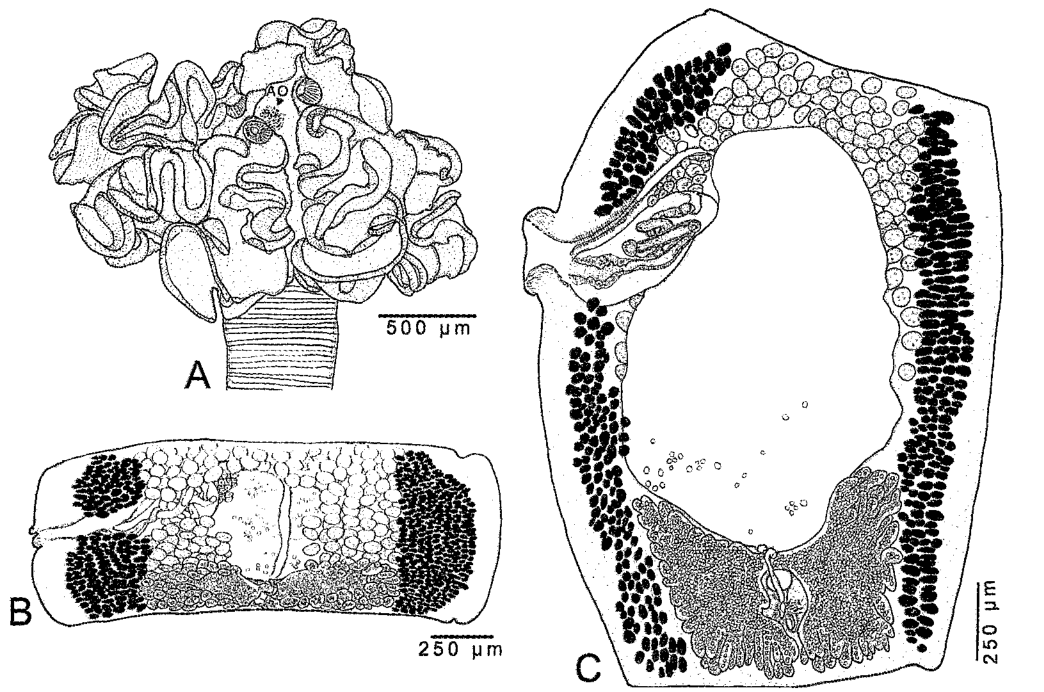

Fig. 12. Line drawings of *Phyllobothrium riseri* Ruhnke, 1996. A. Scolex of holotype (USNPC 85428). B. Partially gravid proglottid of paratype (USNPC 85429). C. Fully gravid proglottid of holotype (USNPC 85428).

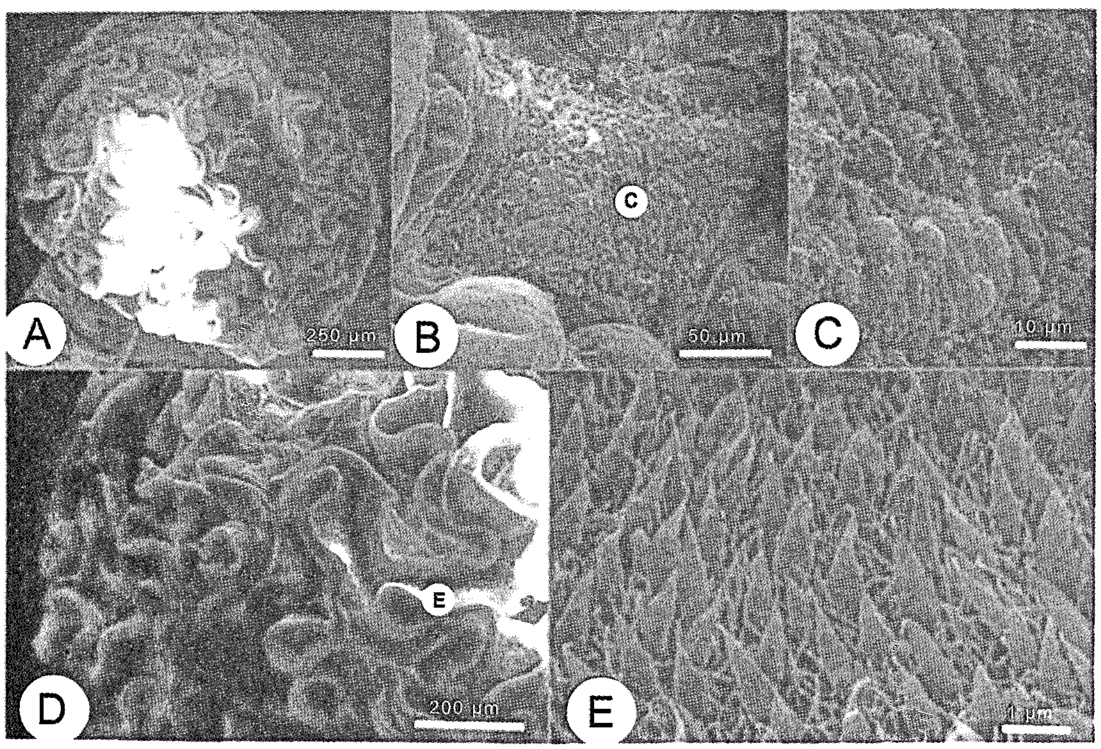

Fig. 13. Scanning electron micrographs of *Phyllobothrium riseri* Ruhnke, 1996. A. Scolex. B. Scolex apex (letter indicate regions of scolex in enlarged photo C). C. Apical surface of scolex. D. Enlarge view of bothridium (letter indicate regions of scolex in enlarged photo E). E. Bothridial surface. (Taken from Ruhnke [1996b], copyright 2006. Used with permission.)

Phyllobothrium serratum Yamaguti, 1952
(Figs. 14–16)

Synonyms: None.
Taxonomic status: Valid.
Type host: Triakis scyllium Müller and Henle, 1839, the Banded houndshark.
Site of infection: Spiral intestine.
Type locality: Hamazima, Japan (Fig. 14).
Additional localities: Tsingtao, China (identified as *P. tumidum*, from Williams [1968a]) (Fig. 14).
Type material: Syntypes, MPM 22715 (Fig. 15).
Material examined: Syntypes, MPM 22715 (Fig. 15).
Etymology: "The name refers to the fine serrations of the cuticle" (Yamaguti 1952).

Description (modified from Ruhnke [1996b]).

Worms craspedote, apolytic, 134–220 mm long; maximum width 2.5–3 mm at scolex when bothridia contracted. Scolex with four bothridia and glandular apical organ. Bothridia foliose, posteriorly bifid; each with apical sucker 125–180 in diameter.

Immature proglottids much wider than long. Mature proglottids initially wider than long, becoming longer than wide; gravid proglottids much longer than wide with maturity. Mature and gravid proglottids 0.85–4.1 mm (2.3 ± 1.4; n=3; *n*=18) long x 1.6–2.9 mm (2.1 ± 0.5; n=2; *n*=3) wide; proglottid length to width ratio 0.27–2.29:1 (1.2 ± 0.9; n=3; *n*=18), with dorsal and ventral pair of excretory ducts and lateral pair of nerve-cords. Testes numerous, pre-ovarian, medullary, intervitelline, 50–83 (62 ± 13; n=3; *n*=17) long x 55–100 (77 ± 11; n=3; *n*=17) wide in mature proglottids, 3–4 rows deep in cross-section, interrupted by uterus and cirrus-sac, numbering 37–60 (47 ± 10; n=2; *n*=4) in cross-section anterior to cirrus-sac. Cirrus-sac oval; angled anteriorly in gravid proglottids; 641–1072 (838 ± 113; n=3; *n*=16) long x 251–422 (334 ± 66; n=3; *n*=16) wide, length to width ratio 1.8–3.4:1 (2.6 ± 1.5; n=3; *n*=16); length to proglottid width ratio 0.26–0.63: (0.44 ± 0.11 n=3; *n*=16), containing coiled cirrus armed with spinitriches. Vas deferens coiled, median and anterior to cirrus-sac. Genital pores lateral, 48–56% (52 ± 3; n=3; *n*=18) of proglottid length from posterior end, irregularly alternating. Genital atrium present. Vagina median, extending anteriorly from ovary to middle of proglottid, then laterally along anterior margin of cirrus-sac to genital atrium. Vaginal sphincter present. Ovary near posterior end of proglottid, follicular, H-shaped in frontal view, 200–1075 (589 ± 288; n=3; *n*=21) long x 600–2,087 (1,152 ± 311; n=3; *n*=21) wide, tetralobed in cross-section. Ovicapt at posterior margin of ovarian bridge, 28–38 (32 ± 3; n=3; *n*=9) in diameter in mature proglottids. Mehlis' gland dorsal, posterior to ovicapt. Uterus median, ventral to vagina, extending from anterior margin of ovary to near anterior margin of proglottid in full mature and gravid proglottids. Some posterior proglottids with medial ventral dehiscence. Uterine duct not observed. Vitellarium follicular; follicles in two lateral bands, each band with 9–17 dorsal and 8–16 ventral follicles in cross-section follicles 18–75 (38 ± 18; n=3; *n*=14) long x 28–62 (45 ± 11; n=3; *n*=14) wide in mature and gravid proglottids, follicles interrupted by cirrus-sac. Eggs 27–32 (29 ± 2; n=2; *n*=5) in diameter.

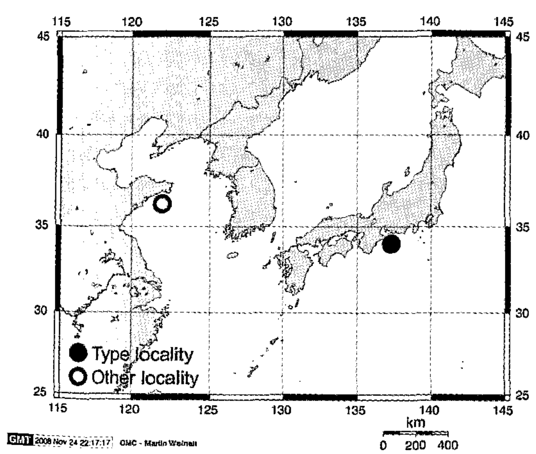

Fig. 14. Geographic distribution of *Phyllobothrium serratum* Yamaguti, 1952.

Remarks

Specimens of *Phyllobothrium serratum* are known from the single collection of Yamaguti (1952). *Phyllobothrium serratum* differs from *P. riseri* in length (134–220 mm vs.

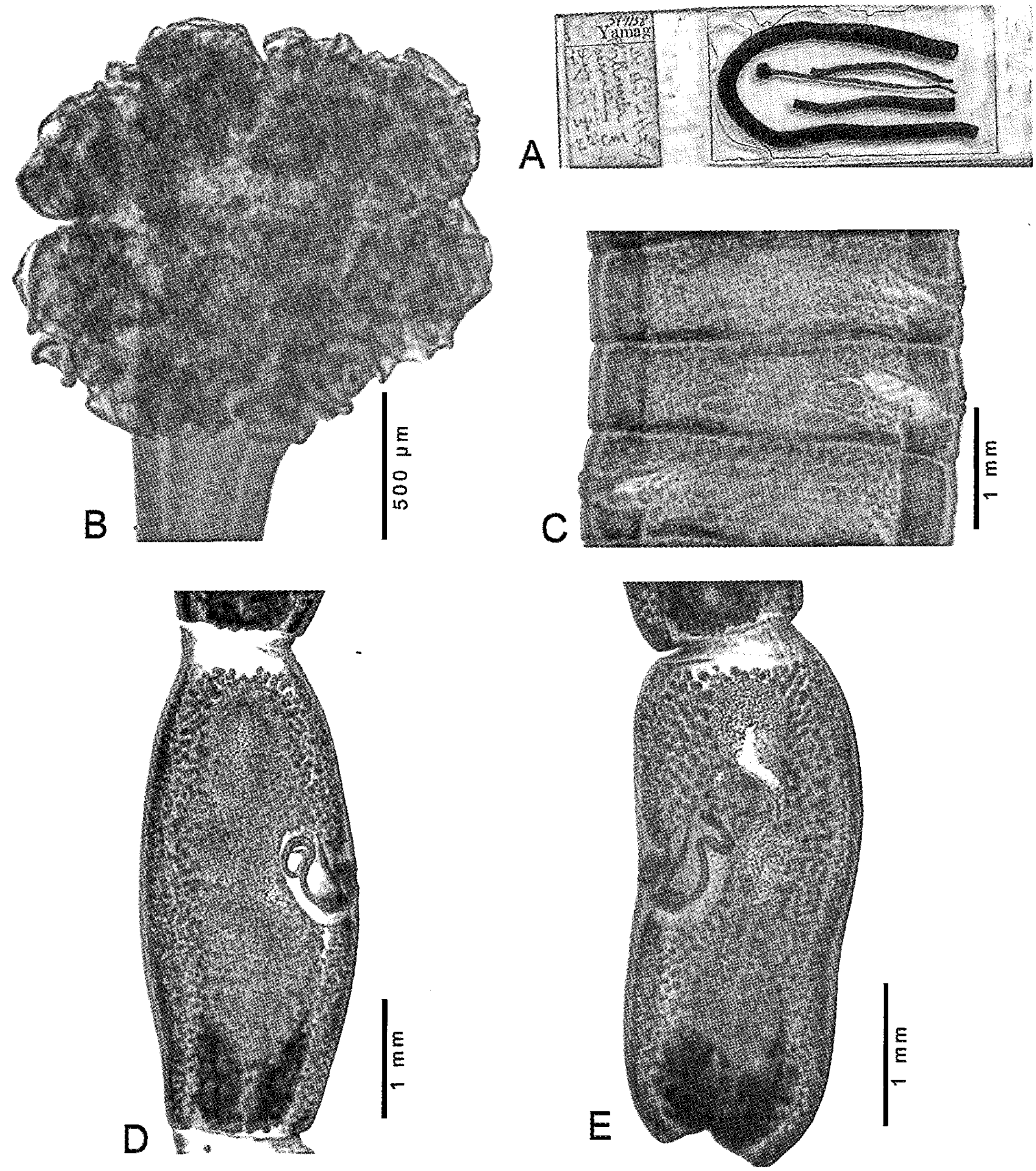

Fig. 15. Photomicrographs of *Phyllobothrium serratum* Yamaguti, 1952. A. Syntype (MPM 22715). B. Scolex of syntype (MPM 22715). C. Partially gravid proglottid of syntype (MPM 22715). D. Gravid proglottid of syntype (MPM 22715). Gravid terminal proglottid of syntype (MPM 22715).

65–105 mm), and cirrus-sac width (251–422 vs. 112–197). *Phyllobothrium serratum* differs from *P. riseri* in maximum worm width (2.5–3 mm vs. 1.8–2.25 mm). *Phyllobothrium serratum* differs from *P. lactuca* in proglottid development (apolytic vs. anapolytic), mature proglottid width (1.6–2.9 vs. 1.2–1.6), and testis number in cross-section (37–60 vs. 21–26).

Tseng (1933) and Hsü (1935) reported specimens of *Phyllobothrium tumidum* Linton, 1922 from *T. scyllium*. It seems apparent that their specimens were *P. serratum*, however that species did not yet exist in the literature. In addition, *P. tumidum* possesses

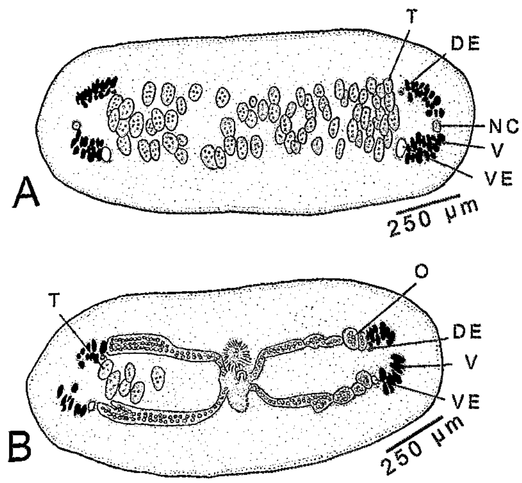

Fig. 16. Line drawings of *Phyllobothrium serratum* Yamaguti, 1952. A. Cross-section of proglottid anterior to cirrus-sac of syntype (MPM 22715). B. Cross-section of proglottid through ovary of syntype (MPM 22715). (Taken from Ruhnke [1996b], copyright 2006. Used with permission.)

a foliose bothridial morphology that is similar to *P. serratum,* especially when the bothridia are contracted. Therefore, both of these accounts were probably of *P. serratum,* and this is reflected in Fig. 14.

Other species of *Phyllobothrium*

A number of species have historically been placed in *Phyllobothrium* as a result of a variety of proposed generic synonyms, and 85 species names have been in some way historically associated with the genus (see Appendix 2). Of these, only three are considered here to be valid members of *Phyllobothrium*: *P. lactuca, P. riseri,* and *P. serratum.* Of the remaining 82 species names, 18 are synonyms of species treated in this monograph and three are problematic members of genera treated in this monograph. The status of the 61 remaining species names is summarized below. Two of these names are synonyms of two of the remaining 59 problematic species. The status of these species is summarized in Appendix 2.

Phyllobothrium arctowskii* Wojciechowska, 1991 *incertae sedis

Wojciechowska (1991a) described *Phyllobothrium arctowskii* from *"Bathyraja* sp. 2" in the area of the South Shetlands-Admiralty Bay, Antarctica. This species has uniloculate bothridia with round apical suckers. Wojciechowska (1991a) described the bothridia as being leaf like, with strongly folded margins. The vitelline follicles are figured as approaching the midline of the proglottid, and are not interrupted by the ovary. This species was transferred to *Anthocephalum* by Rocka and Zdzitowiecki (1998), but *P. arctowskii* lacks well-defined marginal loculi, its vagina is not sinuous, and it does not have vitelline follicles interrupted by the ovary, as in species of *Anthocephalum* (see Ruhnke and Seaman 2009). The morphological features of *P. arctowskii* are not consistent with the generic diagnosis of *Phyllobothrium* (see Ruhnke 1996a) in that the bothridial are not foliose and posteriorly bifid. A new genus of tetraphyllidean will likely need to be erected to house *P. arctowskii*. Thus, *P. arctowskii* should be considered *incertae sedis*. Type material: Holotype No. 926, and paratypes No. 926a, b are at the Institute of Parasitology, Polish Academy of Sciences; BMNH 1992.1.6.30. Material examined: BMNH 1992.1.6.30.

Phyllobothrium auricula* Van Beneden, 1858 *incertae sedis (Fig. 17)

Phyllobothrium auricula was collected from *Trygon pastinaca* (= *Dasyatis pastinaca* [L., 1758]), the common stingray. The host was presumably collected on the Belgium coast. The original description of Van Beneden (1858) was quite brief, but a more detailed account was provided by Euzet (1959). Euzet (1959) reported on specimens he identified as *P. auricula* from Concarneau, Arcachon, and Séte, France. *Phyllobothrium auricula* was declared by Euzet (1959) to be the senior synonym of *Phyllobothrium foliatum* Linton 1890. For example, examination of Linton's (1890) description of *P. foliatum* revealed these two species to be quite similar. The bothridia of *P. auricula* exhibit partial dorsal/ventral fusion, and are marginally loc-

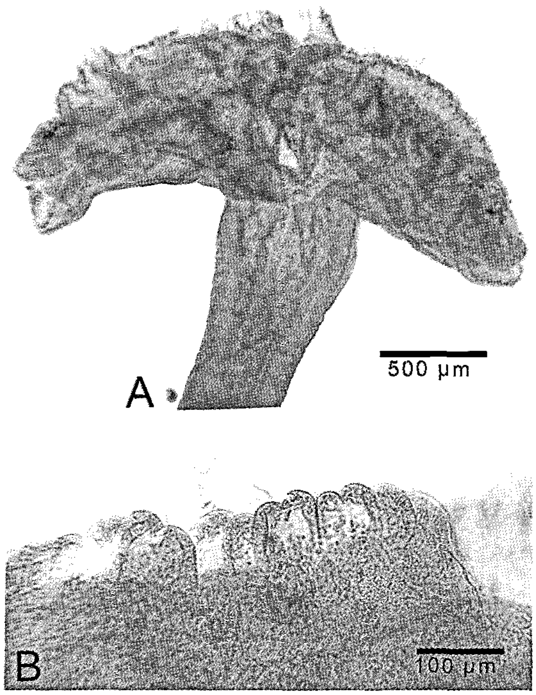

Fig. 17. Photomicrographs of *Phyllobothrium auricula* Van Beneden, 1858. A. Scolex of voucher (MNHN Paris HEL 127). B. Bothridial loculi of voucher (MNHN Paris HEL 127).

ulate. The posteriorly recurved cirrus-sac (in some proglottids), and sinuous vagina of *P. auricula* are similar to species of *Anthocephalum*. *Phyllobothrium auricula* resembles *P. discopygi, P. foliatum,* and *P. loculatum* is its possession of bothridial marginal loculi and dorsal ventral fusion of the bothridia. *Phyllobothrium auricula* is thus likely a member of the Rhinebothriidea (see Healy et al. 2009). This species is valid, but should be considered *incertae sedis*. Type material: not specified. Material examined: MNHN Paris HEL 127-129.

Phyllobothrium biacetabulatum* Yamaguti, 1960 *incertae sedis (Fig.18)

This species was described by Yamaguti (1960) for specimens collected from *Rhinobatus schlegeli* Müller and Henle, 1841, the Yellow guitarfish, in the Inland Sea, Japan. The similarities between *P. biacetabulum* and species of *Anthocephalum* are many. For example, the bothridia of *P. biacetabulum* possess marginal loculi, the cirrus-sac is posteriorly recurved, and the vitelline follicles are interrupted by the genital pore and ovary. However, unlike species of *Anthocephalum, P. biacetabulum* bears two or three anterior loculi on each bothridium. Thus, this species is valid, but should be considered *incertae sedis* until such time as its morphology can be studied in more detail and compared to other rhinebothriideans, the order of which it is most likely a member. Type material: MPM 22785. Material examined: MPM 22785.

Phyllobothrium blakei* Shipley and Hornell, 1906 *incertae sedis

Phyllobothrium blakei was described by Shipley and Hornell (1906) from *Trygon kuhli* (= *Neotrygon kuhlii* [Müller and Henle, 1841]), the Bluespotted stingray, collected from the Gulf of Manaar, Ceylon (= Sri Lanka). Specimens of *P. blakei* were described as a delicate and measuring about 10 mm in length (see Shipley and Hornell 1906). Shipley and Hornell (1906) also described the

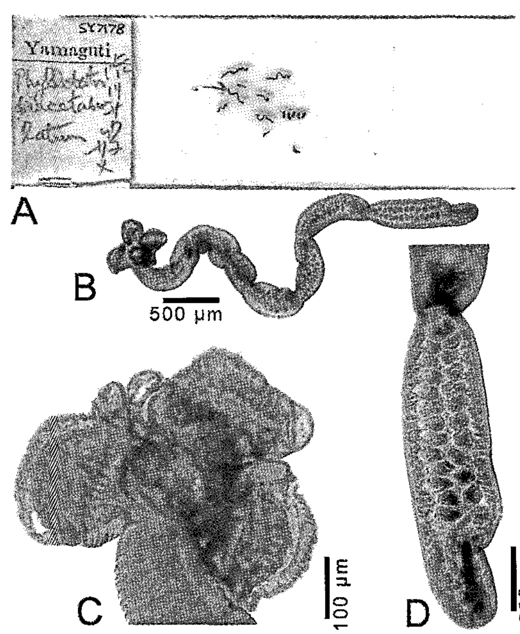

Fig. 18. Photomicrographs of *Phyllobothrium biacetabulatum* Yamaguti, 1960. A. Type slide (MPM 22785). B. Entire specimen of type (MPM 22785). Scolex of type (MPM 2278). Terminal proglottid of type (MPM 22785).

scolex of *P. blakei* as having crumpled edges, twisted, and showing "numerous little bays and rounded recesses which at first sight might easily be taken for small circular suckers". While the figure of this species is somewhat schematic, this description is consistent with the bothridial marginal loculi of *Anthocephalum*. In addition, the host for *P. blakei* is *Neotrygon kuhlii*, and diamond rays are hosts for six of the existing species of *Anthocephalum* (see Ruhnke 1994b; Ruhnke and Seaman 2009). Thus, *P. blakei* is likely a member of the order Rhinebothriidea (see Healy et al. 2009). At present, the species should be considered *incertae sedis*. Type material: not specified. Material examined: none.

Phyllobothrium blochii Srivastav and Srivastava, 1988 *incertae sedis*

This species was described by Srivastav and Srivastava (1988) from *Zygaena blochii* (= *Eusphyra blochii* [Cuvier, 1816]), the Wingheaded shark, collected at Puri, Orissa, India. Examination of the original figures and description of *P. blochii* (see Srivastav and Srivastava 1988) reveals that it is likely a species of *Paraorygmatobothrium*. The bothridia of *P. blochii* are uniloculate, with an apical sucker and are not foliose or posteriorly bifid. The illustrated proglottid is much longer than wide, and the genital pore is in the anterior fifth of the proglottid. Examination of the type specimens, if available, would do much to resolve the identity of this species. At present, *P. blochii* should be considered *incertae sedis*. Type material: Holotype B.B.C.C./1205, paratypes B.B.C.C./1206–1208. Material examined: none.

Phyllobothrium bombayensis Srivastava and Capoor, 1979 *incertae sedis*

This species was described by Srivastava and Capoor (1979) from *Scoliodon laticaudus* Müller and Henle, 1839, Spadenose shark, collected from Sasoon Dock, Bombay, India. Srivastava and Capoor (1979) compared *Phyllobothrium bombayensis* to *P. lactuca*, *Phyllobothrium magnum* Hart, 1936, and *Phyllobothrium radioductum* Kay, 1942. Based on its possession of bothridial marginal loculi, a more likely candidate genus for placement of this species is *Orectolobicestus* (see Ruhnke et al. 2006b). Examination of the type specimens, if available, would do much to resolve the identity of this species. In addition, given that serrated spinitriches on the bothridial surfaces are key to the identity of *Orectolobicestus*, examination of this species with SEM is critical. At present, *P. bombayensis* should be considered *incertae sedis*. Type material: holotype is listed as being at the Department of Zoology, University of Allahabad, India. Material examined: none.

Phyllobothrium brassica Van Beneden, 1871 *nomen nudum*

This name first used by Van Beneden (1871) for cestodes from "*Spinax acanthias*" (= *Squalus acanthias* L., 1758), the Spiny dogfish, but was not accompanied by a description or illustrations. As noted by Southwell (1925), *P. brassica* should thus be considered a *nomen nudum*.

Phyllobothrium britannicum Williams, 1968 *incertae sedis*

This species was described from *Raja montagui* Fowler, 1910, the Spotted ray taken from near Plymouth, U.K. Williams (1968a) described *P. britannicum* as a relatively large, apolytic worm, measuring up to 17 cm in fixed specimens, with a scolex ranging up to 8 mm wide. The posterior mature proglottids measured approximately 2.5 mm wide, and range from being slightly wider than long to being slightly longer than wide. The free proglottids are 3.5–4 mm x 2 mm. In comparing the species to *P. lactuca*, Williams (1968a) noted that the bothridia of *P. britannicum* were slightly bifid, but the bothridial margins were not folded. In addition, *P. britannicum* appears to be apolytic (see Williams 1968a, fig. 13), although Williams (1968a) described the species as euapolytic. In terms of the position of *P. brittanicum* in *Phyllobothrium*, Williams (1968a, p. 245) commented, "The species may eventually be considered far removed from *P. lactuca* but at present there appears to be no alternative but to place it somewhere near this form." *Phyllobothrium britannicum* is morphologically similar to other uniloculate phyllobothriids from *Raja* such as *P. piriei* Williams, 1968; *P. radioductum* Kay, 1942; and *P. williamsi* Schmidt, 1986. At present, *P. britannicum* should be considered a valid species, but *incertae sedis* with respect to *Phyllobothrium*. Type material: not specified. Material examined: none.

Phyllobothrium caudatum* (Zschokke and Heitz, 1914) Southwell, 1925 *species inquirenda

Phyllobothrium caudatum was originally described as *Pelichnibothrium caudatum* Zschokke and Heitz, 1914 by Zschokke and Heitz (1914) from the Chum salmon, *Oncorhynchus keta* (Walbaum, 1792). In addition to *Oncorhynchus*, species of *Coregonus* and *Parasilurus* have been reported as hosts for *P. caudatum* (see Williams 1968a). Although its inclusion in *Pelichnibothrium* is of an uncertain nature, transfer of this larval species to *Phyllobothrium* by Southwell (1925) was not warranted, as it lacks bifid, foliose bothridia, and no glandular apical organ is present on the scolex. *Phyllobothrium ketae* was described by Canavan (1928) from *O. ketae*. Williams (1968a) did not accept *P. ketae* as a valid species, as he believed the plerocercoid on the type slide (USNPC 49817) identical in morphology to *P. caudatum*, and thus it should be considered a junior synonym of *P. caudatum*. *Pelichnibothrium caudatum* should be considered a *species inquirenda*. Type material: not specified. Material examined: none.

***Phyllobothrium centrurum* Southwell, 1925 (synonyn of *Anthocephalum gracile* Linton, 1890)**

Phyllobothrium centrurum was proposed by Southwell (1925) as a replacement name for the species *Anthocephalum gracile* Linton 1890, in order to remove the homonomy established when Southwell (1925) transferred the species to *Phyllobothrium*. This homonym was precipitated because *Phyllobothrium gracile* Wedl, 1855 was already a member of that genus. Ruhnke (1994b) considered *Anthocephalum* to be valid and mistakenly used the name *Anthocephalum centrurum* (Southwell, 1925) Ruhnke, 1994 rather than *Anthocephalum gracile* Linton 1890 for the type species when he resurrected the genus. Ruhnke (1994b) also transferred *Phyllobothrium gracile* Wedl, 1855 to *Anthocephalum*, creating a new homonym *Anthocephalum gracile* (Wedl, 1855) Ruhnke, 1994. This homonym is resolved below (see pg. 40). The name *Anthocephalum gracile* should apply to the species described by Linton (1890) as the type species of *Anthocephalum*. *Phyllobothrium centrurum* Southwell, 1925 and *Anthocephalum centrurum* (Southwell, 1925) Ruhnke, 1994 are synonyms of *Anthocephalum gracile* Linton 1890. *Anthocephalum* was included as a member of the Rhinebothriidea by Healy et al. (2009). Type material: not specified. Material examined: none.

Phyllobothrium chamissonii* (Linton, 1905) Southwell and Walker, 1936 *species inquirenda

This species was originally described as *Taenia chamissonii* Linton, 1905 by Linton (1905). The species was collected from the Atlantic White-sided dolphin, *Lagenorhynchus acutus* (Gray, 1828). The species was transferred to *Monorygma* by Meggitt (1924) as *Monorygma chamissonii* (Linton, 1905) Meggitt, 1924. Based on its morphological condition as "a true bladder worm" and not a plerocercus, Linton (1905) postulated that the adult form of *P. chamissonii* would not be an elasmobranch, and would likely be a marine mammal, perhaps the Killer Whale, *Orcinus orca* (L., 1758). It seems possible that Linton (1905) must have based the original generic assignment of *Taenia*, species of which are parasites of terrestrial mammalian carnivores, on the "bladder worm" morphological condition. Consequently, the true taxonomic home of this larval species is questionable. At present, the original species name, *T. chamissonii,* should be retained, and the species should be considered *species inquirenda*. Type material: not specified. Material examined: none.

Phyllobothrium compactum* Southwell and Prashad, 1920 *incertae sedis

This species was described by Southwell and Prashad (1920) from *Trygon kuhli* (= *Neo-*

trygon kuhlii [Müller and Henle, 1841]), the Bluespotted stingray, taken from Anaivilundum Paar, Sri Lanka. *Phyllobothrium compactum* is a robust cestode, with the longest specimens measuring 51 mm. The maximum width of the species was 4 mm, occurring at the middle part of the specimens. The scolex illustrated by Southwell and Prashad (1920, Figs. 6 and 7) appears to be contracted. The morphology of this species resembles that of *Rhodobothrium*. The host for this species, *N. kuhli,* is consistent with *P. compactum* being a covert member of *Rhodobothrium.* However, material should be studied in order to see if *P. compactum* has the features of *Rhodobothrium. Phyllobothrium compactum* is considered possibly to be a member of the order Rhinebothriidea (see Healy et al. 2009). At present, the species should be considered valid, but *incertae sedis* with respect to *Phyllobothrium.* Type material: Zoological Survey of India, ZEV 7255/7. Material examined: none.

Phyllobothrium crispum (Molin, 1858) Southwell, 1925 *nomen dubium*

Phyllobothrium crispum was originally described by Molin (1858) as *Tetrabothrium (Anthobothrium) crispum* Molin, 1858, collected from *Mustelus plebejus* (= *Mustelus asterias* Cloquet, 1821), the Starry smoothhound near Patovii, Italy. The original description was quite brief, and no figures were provided. For now, the species should be referred to by its originial name, *Tetrabothrium (Anthobothrium) crispum.* Given that there is also no mention of type material, the species to which this name was applied is essentially unknown, and there for should be considered a *nomen dubium.* Type material: not specified. Material examined: none.

Phyllobothrium dagnallium Southwell, 1927 *incertae sedis*

Phyllobothrium dagnallium was described from *Rhynchobatis ancylostumus* (= *Rhina ancylostoma* Bloch and Schneider, 1801), the Brownmouth guitarfish and has also been reported from *Chiloscyllium indicum* (Gmelin, 1789), the Slender bambooshark by Southwell (1927). The type locality is the Pearl Banks, Ceylon (= Sri Lanka). Southwell (1927) described this as a large anapolytic species, up to 18 cm long, with a maximum width 2.1 mm, and strobila with several hundred proglottids. The testes are numerous, but testes are absent from the post-vaginal field.

Williams (1968a, p. 241) lists several other host species for *P. dagnallium,* but these most likely refer to other cestode species. For example, the report by Myers (1959) of *P. dagnallium* in *Lamna nasus* almost certainly is of a species of *Clistobothrium*. Examination of Southwells' specimens (BMNH 2010.2.14.1–3, 2010.2.14.4, and 2010.2.14.5–8) verified *C. indicum* as an additional host, but not *Galeocerdo cuvier*, the Tiger shark. This latter shark species was given as a host for *P. dagnallium* by Southwell (1927). The fact that *P. dagnallium* lacks foliose bothridia, an apical organ, and a vaginal spinchter preclude it from being placed in *Phyllobothrium.* The morphology of *P. dagnallium* is not consistent with a currently known genus, and the species should be considered *incertae sedis.* Type material: BMNH 2010.2.14.1–3. Material examined: types BMNH 2010.2.14.1–3; vouchers BMNH 2010.2.14.4, 2010.2.14.5–8.

Phyllobothrium dasybati Yamaguti, 1934 *incertae sedis*

The species was described from *Dasybatus akajei* (= *Dasyatis akajei* [Müller and Henle, 1841]), the Red stingray, collected from the Pacific coast, Japan. In overall morphology, this species most closely resembles *Paraorygmatobothrium*. Given that the single type specimen of *P. dasybati* was of poor quality, new material is needed to resolve its generic placement. At present, the species should be considered *incertae sedis.* Type material: MPM 22695. Material examined: MPM 22695.

Phyllobothrium delphini (Bosc, 1802) Van Beneden, 1868 *species inquirenda*

Phyllobothrium delphini was originally described by Bosc (1802) as *Hydatis delphinii* Bosc, 1802. *Phyllobothrium delphini* is a name that has been applied to larval cestodes from a variety of marine mammals. Williams

(1968a) provided an excellent summary of the confusing history of this species. Aznar et al. (2007) sequenced nuclear ribosomal DNA of larvae they identified as *P. delphini* from three species of Mediterranean cetaceans. The *P. delphini* sequence was phylogenetically grouped with two other larval types, and larvae identified as *Monorygma grimaldi* from cetaceans (see Aznar et al. 2007). These in turn grouped with homologous sequences of *Clistobothrium montaukensis* Ruhnke, 1993 and a plerocercoid taken from *Loligo gahi* D'Orbigny, 1835. It is highly likely that *P. delphini* and the other larval types are life history stages of a species of *Clistobothrium carcharodoni* Dailey and Vogelbein, 1990 or *Clistobothrium tumidum,* both of which are parasitic in Great white sharks. This species should be considered a *species inquirenda* until its conspecificity with respect to adult forms can be formally assessed. Type material: not specified. Material examined: none.

Phyllobothrium dipsadomorphi* Shipley, 1900 *nomen dubium

This species was described by Shipley (1900) for specimens from *Dipsadomorphus irregularis* (= *Boiga irregularis* Merrem, 1802), the Brown tree snake, collected from Blanche Bay, New Britain, Bismarck Archipelago. Southwell (1925) transferred this species into *Anthobothrium* without explanation. *Phyllobothrium dipsadomorphi* was described as a relatively large cestode, measuring up to 70 mm in length. The scolex was described as bearing four bothridia, but bothridial apical suckers were not observed. The presence of a species belonging to a genus normally parasitic in marine elasmobranchs in a arboreal snake seems highly improbable. It is likely that this species may actually represent a proteocephalidean taxon, as species of that cestode lineage do occur in snakes (see de Chambrier and Paulino 1997).

Unfortunately, the whereabouts of the type material is not known, and the description does not allow the identity to be established at this time. Therefore, *P. dipsadomorphi* should be considered a *nomen dubium.* Type material: not specified. Material examined: none.

Phyllobothrium discopygi* Campbell and Carvajal, 1987 *incertae sedis

This species was described by Campbell and Carvajal (1987) from *Discopyge tschudi* Heckel, 1846, the Apron ray, collected from the Pacific Ocean off Coquimbo, Chile. This is a long cestode, being up to 60 mm in length, with approximately 350 proglottids. The bothridia of *P. discopyge* are fused dorsoventrally and bear marginal loculi, and in these respects, it is inconsistent with *Phyllobothrium.* These morphological features are also present in *P. auricula, P. foliatum,* and *P. loculatum.* This species is likely a member of the Rhinebothriidea. At present, the species should be considered *incertae sedis.* Type material: holotype USNPC 79660; paratypes USNPC 79661. Material examined: USNPC 79661.

Phyllobothrium fallax* Van Beneden, 1871 *nomen nudum

The name *Phyllobothrium fallax* is known from a list of species reported by Van Beneden (1871) from *Raja rubus* (= *Raja clavata* L., 1758), the Thornback ray, collected off the Belgian coast. The name was not accompanied by a description or illustrations. As noted by Southwell (1925), *P. fallax* is a *nomen nudum.*

Phyllobothrium foliatum* Linton, 1890 *incertae sedis (Fig. 19)

This species was described by Linton (1890) from *Dasyatis centroura* (Mitchill, 1815), the Roughtail stingray, collected from Woods Hole, Massachusetts. Type material is unknown, but a voucher specimen, USNPC 7674, was studied. The bothridia of *P. foliatum* are marginally loculate, and appear to exhibit dorso-ventral fusion. The bothridial condition of *P. foliatum* is similar to that of *P. auricula, P. discopygi,* and *P. loculatum.* This species is a likely member of the Rhinebothriidea. At present, the species should be considered *incertae sedis.* Type material: not specified. Material examined: voucher (deposited by Linton) USNPC 7674.

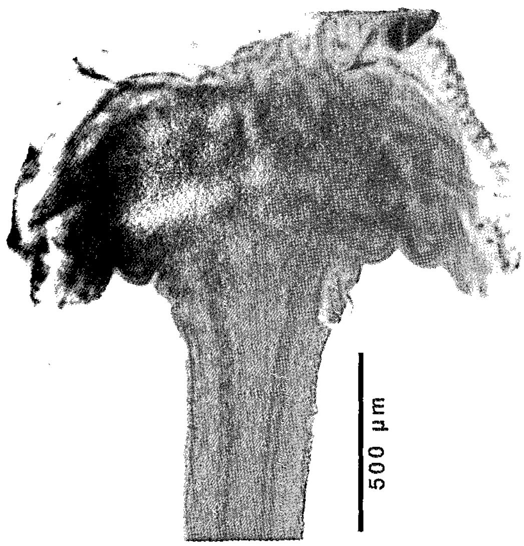

Fig. 19. Photomicrograph of *Phyllobothrium foliatum* Linton, 1890. Scolex of voucher (USNPC 7674).

Phyllobothrium georgiense* Wojciechowska, 1991 *incertae sedis

This species was described by Wojciechowska (1991a) from *Raja georgiana* (= *Amblyraja georgiana* [Norman, 1938]), the Antarctic starry skate, collected from South Georgia, Antarctica. It was reported to be euapolytic, 60–170 mm long, and 1.8 mm in maximum width. *Phyllobothrium georgiense* is similar to *P. arctowskii* Wojciechowska, 1991, *P. rakusai* Wojciechowska, 1991, and *P. siedleckii* Wojciechowska, 1991. *Phyllobothrium georgiense* is illustrated with more developed marginal loculi, and the former three species possess uniloculate bothridia having weakly-developed marginal loculi that could even be described as slightly crenulate (see Wojciechowska 1991a, figs. 2a, 2c and 3a). In these four species, the vitelline follices are not interrupted by the ovary, and approach the midline of the proglottid. Rocka (2003) transferred *P. georgiense* to *Anthocephalum*. Given that *P. georgiense* lacks a posteriorly recurved cirrus-sac, lacks a sinuous vagina, and does not have vitelline follicles interrupted by the ovary, it should not be placed in that genus (see Ruhnke and Seaman 2009). Ruhnke and Seaman (2009) mistakenly gave Rocka and Zdzitowiecki (1998) as the citation for the taxonomic action of Rocka (2003). Clearly, *P. georgiense*, *P. arctowskii* and *P. siedleckii* and *P. rakusai* could eventually constitute a new generic entity of tetraphyllideans from antarctic skates. At present, the species should be considered *incertae sedis*. Type material: holotype (No. 1244), paratypes (Nos. 1221b, c, d, 1223a and 1243) in the author's collection in the Institute of Parasitology, Polish Academy of Sciences; paratype BMNH 1992.1.6.27. Material examined: BMNH 1992.1.6.27.

***Phyllobothrium gracile* Wedl, 1855 (valid as *Anthocephalum wedli* nom. nov.)**

Phyllobothrium gracile was described by Wedl (1855) from cestodes taken from the Spotted torpedo, *Torpedo marmorata* Risso, 1810. The species was transferred to *Anthocephalum* by Ruhnke (1994b), thereby establishing the name *Anthocephalum gracile* (Wedl, 1855) Ruhnke, 1994. However, it is now clear that this action created a homonym of *Anthocephalum gracile* Linton, 1890. To resolve this nomenclatural problem, the replacement name *Anthocephalum wedli* nom. nov. is hereby proposed. *Phyllobothrium gracile* Wedl, 1855 and *Anthocephalum gracile* (Wedl, 1855) Ruhnke, 1994 are synonyms of *Anthocephalum wedli* nom. nov.

Phyllobothrium hallericola* Church and Schmidt, 1990 *incertae sedis (Fig. 20)

This species was described by Church and Schmidt (1990) from *Urobatis halleri* Cooper, 1863, the Round stingray, collected from Puerto Peñasco, Mexico. These worms have a maximum length of approximately 20 mm in length, and the strobila consists of 80–100 proglottids. Church and Schmidt (1990) described the bothridia as being uniloculate, with an indistinct apical sucker. While not originally described, examination of paratypes revealed the presence of marginal loculi on the bothridia (see Fig. 20C), although the condition of the paratype scolices made observation of them difficult. The genital pore is posteriorly recurved (see Fig. 20D) as in *Anthocephalum*. In addition, the host for *P. hallericola*, *U. halleri*, is the same as that for *Anthocephalum duszynskii* Ruhnke, 1994,

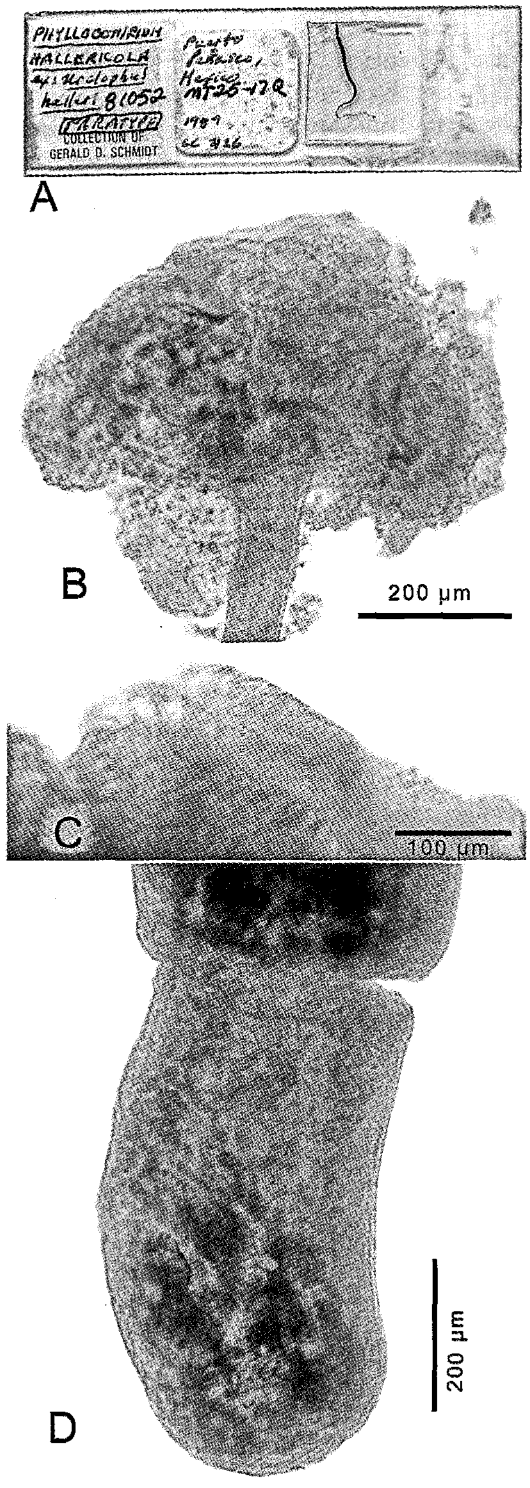

Fig. 20. Photomicrographs of *Phyllobothrium hallericola* Church and Schmidt, 1990. A. Paratype (USNPC 81052). B. Scolex of paratype (USNPC 81052). C. Bothridial loculi of paratype (USNPC 81052). C. Terminal proglottid of paratype (USNPC 81052).

and the two species share the same type locality, Puerto Peñasco, Mexico. This species is a likely member of the Rhinebothriidea. Given the condition of the type specimens, collection of additional material is required before generic placement of this species can be made. At present, the species should be considered *incertae sedis*. Type material: holotype, USNPC 81051; paratypes, USNPC 81052 (Fig. 20A). Material examined: USNPC 81052 (Fig. 20A).

Phyllobothrium hyperapolytica **(Obersteiner, 1914) Williams, 1958** ***species inquirenda***

This species was originally described by Obersteiner (1914) as *Bilocularia hyperapolytica* Obersteiner, 1914, collected from *Centrophorus granulosus* (Bloch and Schneider, 1801) the Gulper shark, near the Zoological Station, Naples, Italy. Williams (1958) transferred the species to *Phyllobothrium,* and Alexander (1963) transferred it to *Monorygma* as *Monorygma hyperapolytica* (Obersteiner, 1914) Alexander, 1963. Williams (1958) redescribed this species from specimens taken from *Scymnus licha* (= *Dalatias licha* Bonnaterre, 1788; the kitefin shark) from western British Isles. Williams (1968a) noted that Alexander's host specimens for *P. hyperapolytica* were from *Dalatias licha*, and he was reluctant to accept the taxonomic conclusions of Alexander (1963). In any event, the original description of Obersteiner (1914) provides only figures of free proglottids, and no types are known for the species. Indeed, the species may not even be that of a tetraphyllidean. Until such time that types are recovered or similar material is collected from the type host, *Phyllobothrium hyperapolytica* is a junior synonym of *B. hyperapolytica*, and in turn, this species should be considered a *species inquirenda*. Type material: not specified. Material examined: None.

Phyllobothrium inchoatum **Leidy, 1891** ***nomen dubium***

Phyllobothrium inchoatum is a larval form collected from the blubber of *Mesoplodon sowerbiensis* (Blainville), Sowerby's whale, collected off the Falkland Islands. The precise collection locality is not known. Leidy (1891) described the scolex of *P. inchoatum* as retracted, globose, with four bothridia. Given the brief nature of its description, and that it is known from a single report, the species should be considered a *nomen dubium*.

Phyllobothrium kingae Schmidt, 1978 (syn. of *Anthocephalum kingae* [Schmidt, 1978] Ruhnke and Seaman, 2009)

Phyllobothrium kingae, a species described by Schmidt (1978) from the Yellow stingray *Urobatis jamaicensis* (Cuvier, 1816), collected from Discovery Bay, Jamaica. *Phyllobothrium kingae* was transferred to *Anthocephalum* by Ruhnke and Seaman (2009). This species should be considered a member of the Rhinebothriidea.

Phyllobothrium lintoni (Southwell, 1912) Southwell, 1930 *incertae sedis*

This species was originally described by Southwell (1912) as *Spongiobothrium lintoni* Southwell, 1912, collected from *Rhynchobatus djeddensis* (Forsskål, 1775), the Giant guitarfish near Ceylon (= Sri Lanka). The worms were described as being up to 20 mm long, with 12 proglottids. The bothridial margins are loculate. In these respects, the species is inconsistent with *Phyllobothrium.* Of particular interest is the presence of musculature that creates a pouch in the middle of the bothridium and divides the bothridium into anterior and posterior halves. Southwell (1912) noted that this caused the bothridia to move like parts of a hinge. This bothridial morphology is inconsistent with that of all other phyllobothriid genera, and likely represents a genus new to science. At present, the species should be retained in its original genus, and considered *incertae sedis.* Type material: Not designated. Material examined: None.

Phyllobothrium loculatum Yamaguti, 1952 *incertae sedis*

This species was described by Yamaguti (1952) from *Heterodontus zebra* (Gray, 1831), the Zebra bullhead shark, collected in the East China Sea, Japan. Yamaguti (1952) described specimens ranging in size from 20 to 40 mm. The bothridia appear to exhibit dorsal-ventral fusion, possess an apical sucker, and exhibit over 50 marginal loculi. The posterior proglottids of this species are still much wider than long. The cirrus-sac is very narrow, and the genital pore is positioned in the posterior half of the proglottid. In these respects, the species is inconsistent with *Phyllobothrium.* The bothridial condition of *P. loculatum* is similar to *P. auricula* and *P. foliatum.* At present, the species should be considered *incertae sedis.* Type material: Syntypes, MPM 22784. Material examined: Syntypes, MPM 22784.

Phyllobothrium loliginis (Leidy, 1887) Linton, 1897 *species inquirenda* (Fig. 21)

Phyllobothrium loliginis was originally described by Leidy (1887) as *Taenia loliginus* Leidy, 1887 from the squid *Ommastrephes sagittatus* (Lamarck, 1798) (= *Todarodes sagittatus* [Lamarck, 1798]), collected from Mount Desert, Maine, U.S.A. Williams (1968a) considered this species to potentially be a synonym of *P. tumidum*, presenting it as: "[? Larva of *P. tumidum* Linton, 1922]" (Williams, 1968a, p. 272). The whereabouts of the type material for *P. loliginus* is unknown, but Linton (1897) considered the species to be valid, and deposited specimens he identified as *P. loliginus* from the Northern squid, *Ommastrephes illecebrosus* Verrill, 1880. Large nuclear ribosomal DNA sequence data of cestode larvae from the Patagonian squid, *Loligo gahi* Smith, 1881, were nearly 100% identical with a LSU sequence of *Clistobothrium montaukensis* (see Brickle et al. 2001). Voucher specimens (USNPC 35734) deposited by MacCallum and identified as *P. loliginus* do share the somewhat foliose bothridial morphology of *C. montaukensis*, and the dorsal longitudinal muscle bundle characteristic of species of *Clistobothrium*. Even though its placement in *Taenia* is certainly incorrect, this species should be referred to as *T. loliginus,* and considered a *species inquirenda*. Type material: unknown. Material examined: USNPC 35734.

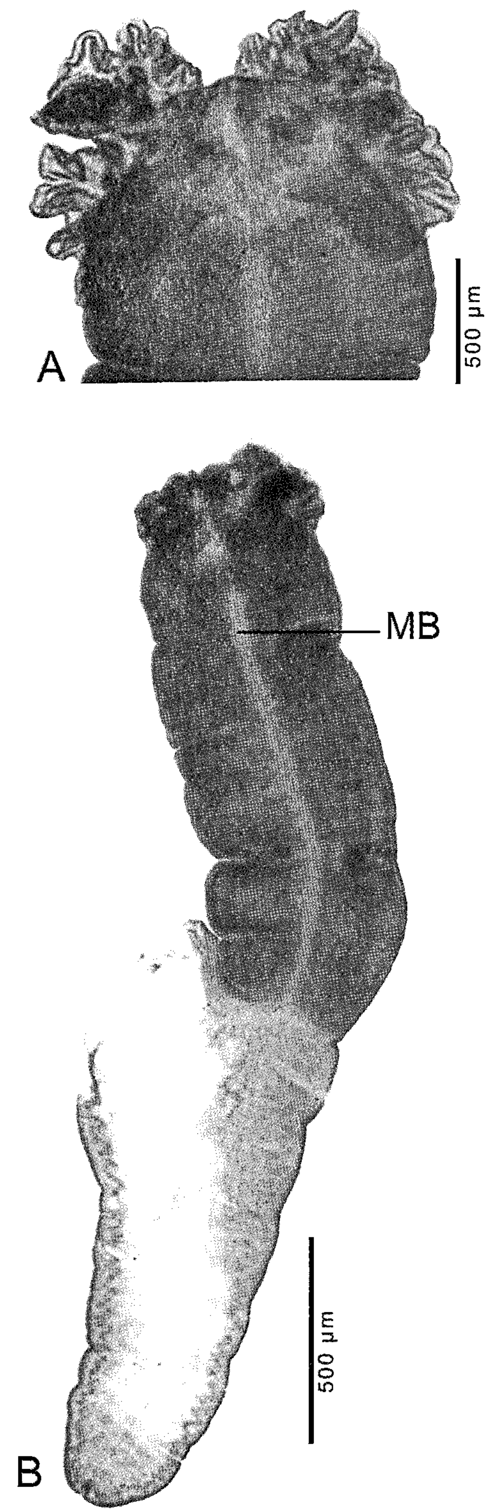

Fig. 21. Photomicrographs of *Phyllobothrium loliginis* (Leidy, 1887) Linton, 1897. A. Scolex of voucher (USNPC 35734). B. Voucher (USNPC 35734).

Phyllobothrium marginatum Yamaguti, 1934 _incertae sedis_

This species was described by Yamaguti (1934) from *Squatina japonica* Bleeker, 1858, the Japanese angelshark, collected from Toyama Bay, Japan. The type specimen of *P. marginatum* was in poor condition, as the mounting medium is cloudy, making study of it difficult. However, the scolex bears uniloculate bothridia, with apical suckers and the proglottid morphology is similar to species of *Paraorygmatobothrium,* as the vitelline fields are interrupted by the ovary. Further action on this species will require fresh specimens. At present, the species should be considered *incertae sedis.* Type material: MPM 22694. Material examined: MPM 22694.

Phyllobothrium microsomum Southwell and Hilmy, 1929 _incertae sedis_

This species was described by Southwell and Hilmy (1929) from *Ginglymostoma concolor* (= *Nebrius ferrugineus* [Lesson, 1831]), the Tawny nurse shark, collected from the Pearl Banks, Ceylon (= Sri Lanka). The specimens of *P. microsomum* were quite small, measuring 2.2–2.4 mm in total length. The bothridia of the species were illustrated as having marginal loculi (see Southwell and Hilmy 1929, fig. 1); but the species was described as lacking apical suckers on the bothridia. The genital pore is in the posterior half of the terminal proglottid. The morphology of *P. microsomum* is similar to species *Anthocephalum.* Future studies should include both morphological and molecular comparison in order to test for such a relationship. Southwell and Hilmy's description of *P. microsomum* as lacking apical suckers also requires confirmation. This species should be considered *incertae sedis*. Type material: not specified. Material examined: none.

Phyllobothrium minimum Subhapradha, 1955 _incertae sedis_

This species was described by Subhapradha (1955) from *Rhynchobatus djiddensis* (Forsskål, 1775), the Giant guitar fish, collected from the coastal waters of Madras, India. Subhapradha (1955) described this as a small species, with the largest of specimens measuring only 2 mm in length. Her figures included a bothridium, a terminal proglottid and a free proglottid. Distinct marginal loculi are present on the bothridium. The description of *P. minimum* as possessing marginal loculi compares it to species of *Anthocephalum* and *Orectolobicestus*. Given the anterior position of the genital pore, affinity with the latter genus seems more likely. However, species of *Orectolobicestus* have been reported from bamboo sharks (genus *Orectolobus* Bonaparte, 1834). Ideally, new material from the Giant guitarfish should be collected in order to make more critical comparisons to species of *Anthocephalum* and *Orectolobicestus*. This species should be considered *incertae sedis*. Type material: not specified. Material examined: none.

Phyllobothrium minutum Shipley and Hornell, 1906 *incertae sedis*

This species was described by Shipley and Hornell (1906) for specimens taken from *Carcharias melanopterus* (= *Carcharhinus melanopterus* [Quoy and Gaimard, 1824]), the Blacktip reef shark, collected from Ceylon (= Sri Lanka). This is a small worm, measuring up to 8 mm in length, possessing 80–100 proglottids, with a small whiplike neck. Shipley and Hornell (1906) described *P. minutum* as possessing an accessory sucker or areola at the center, rather than the apex of the bothridia. Given their illustration of the scolex (fig. 32), and the fact that the species possesses laciniations, it seems likely that this is a species of *Anthobothrium*. However, at present, *P. minutum* should be considered *incertae sedis*. Type material: not specified. Material examined: none.

Phyllobothrium myliobatidis Brooks, Mayes and Thorson, 1981 *incertae sedis* (Fig. 22)

Phyllobothrium myliobatidis was described by Brooks et al. (1981) for specimens taken from *Myliobatis goodei* Garman, 1885, the Southern eagle ray, collected from Rio de la Plata estuary, Uruguay. According to Brooks, Mayes and Thorson (1981) this species is thin, up to 30 mm long, with 50–75 proglottids. The scolex is up to 2.5 mm wide. The bothridia are stalked and marginally loculate. A cephalic peduncle is present. Immature proglottids are wider than long, the mature proglottid are much longer than wide (Fig. 22B), with dimensions of 465–2418 x 251–474. There are 122–150 testes per proglottid. The cirrus-sac is posteriorly recurved, and the genital pore is 73–85% of length from posterior end of proglottid. The ovary is H-shaped in frontal view, with lobes expanding posteriorly as proglottids mature. The presence of bothridial stalks, bothridial marginal loculi and a posteriorly recurved cirrus-sac indicate a potential relationship between *P. myliobatidis* and species of *Anthocephalum* (see Ruhnke 1994b; Ruhnke and Seaman 2009). *Phyllobothrium myliobatidis* differs from species of *Anthocephalum* in that it apparently lacks apical suckers on the bothridia, as well as genital pore position (anterior third of proglottid vs. posterior third of proglottid). Future studies should include verification of apical sucker absence of *P. myliobatidis*. *Phyllobothrium myliobatidis* is likely a member of the order Rhinebothriidea. At present, the species should be considered *incertae sedis*. Type material: holotype USNPC 75728; paratype USNPC 75729. Material examined: USNPC 75729.

Phyllobothrium pammicrum Shipley and Hornell, 1906 *species inquirenda*

Phyllobothrium pammicrum was described by Shipley and Hornell (1906) for specimens taken from *Carcharias melanopterus* (= *Carcharhinus melanopterus* [Quoy and Gaimard, 1824]), the Blacktip reef shark, taken from Gulf of Manaar, coast of Ceylon (= Sri Lanka). Shipley and Hornell (1906) reported a length of 11–13 mm, with a maximum width of 500 µm. The scolex bears four bothridia, but the authors explicitly mentioned that no areolas (suckers) were present on the bothridia. According to Shipley and Hornell (1906), the species possesses a number of unusual strobilar features. The genital pores are unilateral. They reported no evidence of immature proglottids that were wider than long, or even as long as wide. At first evidence of proglottid formation, the proglottids were of roughly the same dimensions

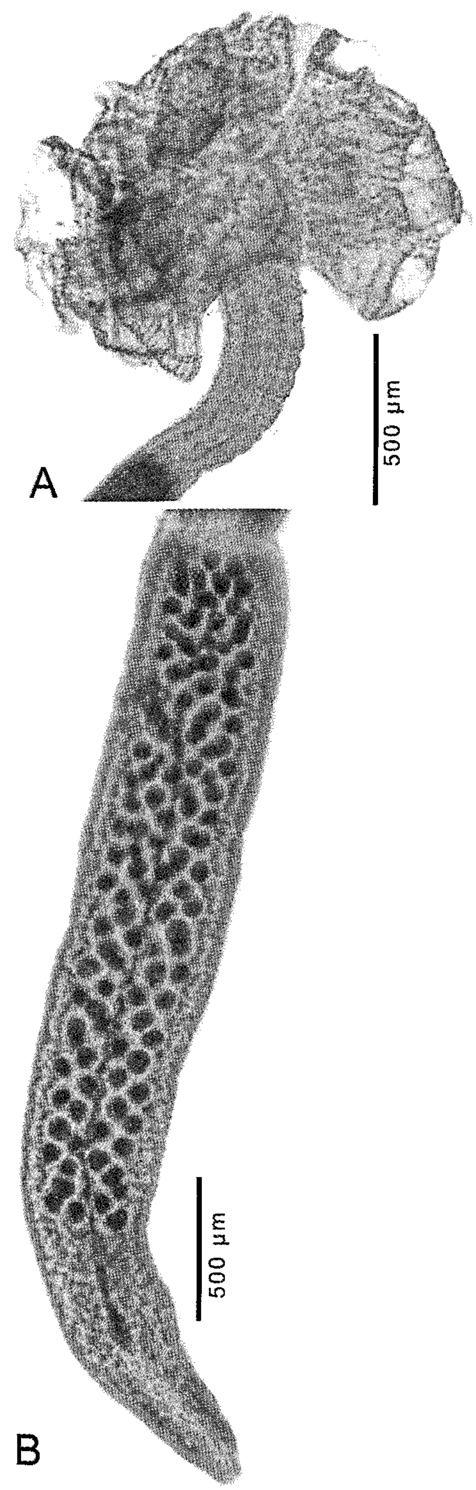

Fig. 22. Photomicrographs of *Phyllobothrium myliobatidis* Brooks, Mayes and Thorson, 1981. A. Scolex of paratype (USNPC 75729). B. Terminal proglottid of paratype (USNPC 75729).

as the posterior proglottids.

Given that the description and illustration are somewhat superficial, collection of new material of *P. pammicrum* from *C. melanopterus* at or near the type locality would be needed to verify the unusual morphology of this species. No judgment can be made as to in which genus *P. pammicrum* should be placed, and it should be considered a *species inquirenda*. Type material: not specified. Material examined: none.

Phyllobothrium panjadi (Shipley, 1909) Southwell, 1930 *incertae sedis*

This species was described by Shipley and Hornell (1906) as *Anthobothrium crispum* Shipley and Hornell, 1906 for specimens taken from *Myliobatis maculata* (= *Aetomylaeus maculatus* [Gray, 1834]), the Mottled eagle ray taken from Gulf of Manaar, coast of Ceylon (= Sri Lanka). Subsequently, Shipley (1909) provided the replacement name *Anthobothrium panjadi* Shipley, 1909, as the original name was a homonym of *Anthobothrium crispum* Molin, 1858. Southwell (1930) transferred the species into *Phyllobothrium*. However, neither of these two genera appears to be appropriate repositoiries for this species. For example, the bothridia of *P. panjadi* are not posteriorly bifid as in *Phyllobothrium*, and the strobila does not possess laciniations, as in *Anthobothrium*. The size, scolex morphology and host species are consistent with species of the genus *Rhodobothrium*. It should be noted that the chain of proglottids originally illustrated by Shipley and Hornell (1906) is positioned upside down. At present, this species should be retained in its original genus, *Anthobothrium*, and considered *incertae sedis*. Type material: not specified. Material examined: none.

Phyllobothrium pastinacae Mokhtar-Maamouri and Zamali, 1981 *incertae sedis*

Phyllobothrium pastinacae was originally described by Mokhtar-Maamouri and Zamali (1981) from *Dasyatis pastinaca* (L., 1758), the Common stingray, taken from the Gulf of Tunis, Tunisia. According to Mokhtar-Maamouri and Zamali (1981), the species is

65–200 mm in length. The bothridia were quite long, but were contracted in fixed specimens. The bothidia possess apical suckers and marginal loculi. The cephalic peduncle measured 3–5 mm in length. There were 250–330 proglottids per worm. The mature proglottids were initially as wide as long, but became longer than wide. The genital pore was located in the posterior third of the proglottid. The eggs were filamented.

The figures of *P. pastinacae* presented by Mokhtar-Maamouri and Zamali (1981) bear a resemblance to *Anthocephalum* (see Ruhnke 1994b; Ruhnke and Seaman 2009), and the species is most likely a covert member of that genus. As such, *P. pastinaeae* is likely a member of the Rhinebothriidea. This species should be considered *incertae sedis*. Type material: holotype, MNHN 90HB148cVII; paratypes, MNHN 90HB149cVII, MNHN 90HB15ocVII. Material examined: none.

Phyllobothrium physeteris* (Diesing, 1863) Meggitt, 1924 *nomen dubium

Phyllobothrium physeteris was originally described as *Cysticercus physeteri* Diesing, 1863, for a larval form from the Bowhead whale, *Balaena mysticetus* L., 1758. Williams (1968a) noted that previous authors, while accepting the species as valid, thought *P. physeteris* perhaps was identical to *P. delphini*. The species should be referred to by its original name, *C. physeteri* and is considered here a *nomen dubium*. Type material: not specified. Material examined: none.

Phyllobothrium piriei* Williams, 1968 *incertae sedis

Phyllobothrium piriei was described by Williams (1968a) for specimens taken from *Raja naevus* (= *Leucoraja naevus* [Müller and Henle, 1841]), the Cuckoo ray, collected off Aberdeen, North Sea, United Kingdom. Williams (1968b) provided a comprehensive decription of this species. The worms are euapolytic and approximatley 50 mm long. The scolex is characterized by four bifid bothridia. The bothridia exhibited faint marginal loculi. The bothridal apical suckers are 90 µm in diameter. The posteriormost proglottids are about 2 mm long. The genital pore is lateral and near the middle of the proglottid. Free proglottids attain a size of 3.5 mm long x 1.2 mm wide. Proglottids possess an average of 150 testes. However, *P. piriei* does not exhibit the foliose bothridial morphology of *Phyllobothrium*, nor does it exhibit the vaginal sphincter exhibited by species in that genus. As with *P. britannicum*, *P. piriei* should be compared to other uniloculate phyllobothriids from *Raja*, in addition to *P. radioductum* Kay, 1942; and *P. williamsi* (Williams, 1968) Schmidt, 1986. A new generic entity may be erected to house these species. New collections of these species would be ideal in order to study bothridial morphology with SEM, and compare DNA sequence of these species to other tetraphyllideans. At present, this species should be considered *incertae sedis*. Type material: not specified. Material examined: none.

Phyllobothrium pristis* Watson and Thorson, 1976 *incertae sedis (Fig. 23)

Phyllobothrium pristis was described by Watson and Thorson (1976) for specimens from *Pristis perotteti* Müller and Henle, 1841, the Large-tooth sawfish, taken from Rio San Juan, San Carlos, Nicaragua; Rio Tipitapa, Los Cocos, Nicaragua; and Rio Colorado, Barra del Colorado, Costa Rica. Watson and Thorson (1976) described worms that were 145–265 mm long. The scolex measured 375–555 x 525–810. The scolex illustrated by Watson and Thorson (1976, fig. 30) is uniloculate with an apical sucker, but the bothridia are not foliose. However, the bothridia of the holotype are uniloculate and foliose, and bear an apical sucker (see Fig. 23A). Therefore, the scolex illustrated by Watson and Thorson (1976) may not be that of *P. pristis*. The mature proglottids are slightly long than wide, measuring 960–1,430 x 980–1,170. There are 230–334 testes per proglottid. The genital pore of *P. pristis* is approximately 67% from posterior end of the proglottid.

Phyllobothrium pristis cannot be placed in *Phyllobothrium*, as its bothridia are not distinctly bifid, and its vagina lacks a muscular sphincter. At present, its generic placement is unclear. Collection of additional material is needed in order to clarify the both-

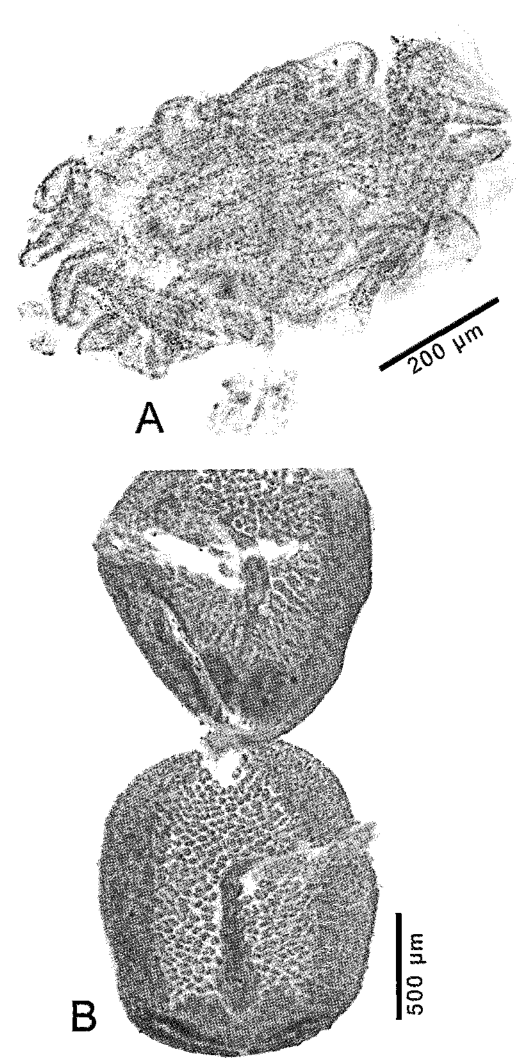

Fig. 23. Photomicrographs of *Phyllobothrium pristis* Watson and Thorson, 1976. A. Scolex of holotype (USNPC 61337). B. Posterior proglottids of holotype (USNPC 61337).

ridial morphology of the species, and to fully resolve its identity. Type material: holotype, USNPC 61337. Material examined: holotype, USNPC 61337.

Phyllobothrium ptychocephalum* Wang, 1984 *incertae sedis

Phyllobothrium ptychocephalum was described by Wang (1984) for specimens taken from *Dasyatis kuhlii* (= *Neotrygon kuhlii*), the Bluespotted stingray, collected from Fujian Province, China. Wang (1984) stated that *P. ptychocephalum* resembled *P. pastinacae*, but differed from that species in that the bothridia of *P. ptychocephalum* lacked accessory suckers. This species should not be placed in *Phyllobothrium*, as it lacks foliose, postiorly bifid bothridia, and an apical organ on the scolex. The bothridial and proglottid morphology of *P. ptychocephalum* is similar to *Spongiobothrium variabile*. The proglottids of both species lack post poral testes and the genital pores of both are in the posterior half of the proglottid, and the cirrus-sacs are posteriorly recurved. The bothridia of *S. variabile* exhibit medial loculi. This may also be case for *P. ptychocephalum*, but the scolex illustration does not allow for a decision concerning this morphology. Examinations of specimens of *P. ptychocephalum* would be needed to determine whether the species should be transferred to *Spongiobothrium*. If *P. ptychocephalum* indeed belongs to *Spongiobothrium*, then this species would be a member of the order Rhinebothriidea. At present, this species should be considered *incertae sedis*. Type material: not specified. Material examined: none.

Phyllobothrium radioductum* Kay, 1942 *incertae sedis (Fig. 24)

This species was described by Kay (1942) for specimens taken from *Raja binoculata* Girard, 1855, the Big skate, collected from Friday Harbor, Washington, U.S.A. This species ranges in size from 26 to 58 mm and the strobila is comprised of 144–290 proglottids. The strobilar surface is scaly. The scolex is roughly of equal length and width (1.8–2 mm), and the bothridia of *P. radioductum* are uniloculate, folded, and possess an apical sucker. The anterior proglottids were wider than long and posterior proglottids ranged from as wide as long to being slightly longer than wide. The genital pore was approximately 50% from the posterior end of the proglottid. Kay (1942) compared *P. radioductum* to *P. lactuca* and *P. vagans* Haswell, 1902. However, *P. radioductum* does not possess the distinct bifid bothridia of *P. lactuca*, and exhibits euapolytic proglottid development, compared to the anapolytic condition in *P. lactuca*. The bothridial morphology of *P. radioductum* and *P. vagans* also differs (*i.e.*, foliose vs. marginally loculate). Unfortunately, this species is only known from the holotype specimen. At this time it should be considered *incertae sedis*. Type material: holotype, USNPC 36801 (Fig. 24A). Material examined: holotype, USNPC 36801 (Fig. 24A).

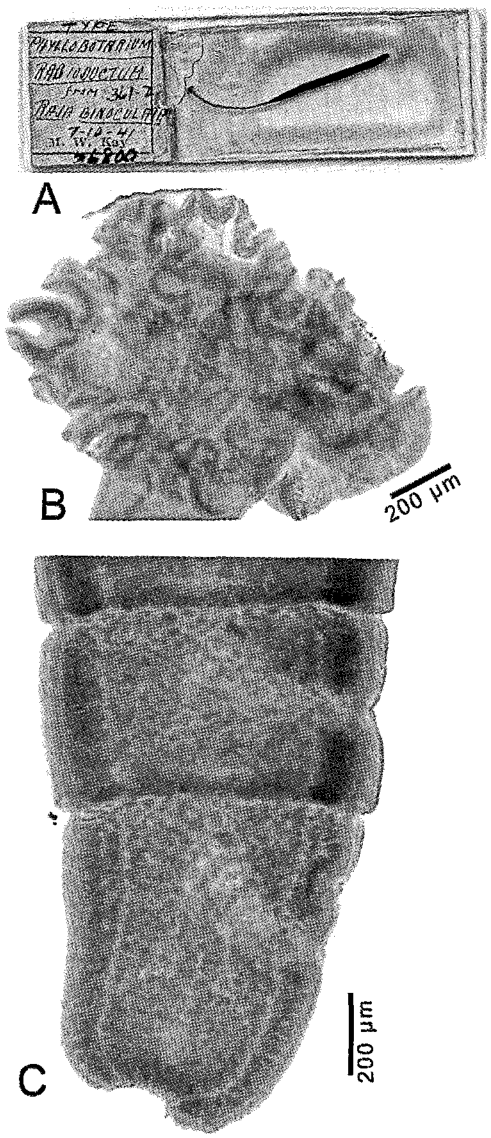

Fig. 24. Photomicrographs of *Phyllobothrium radioductum* Kay, 1942. A. Holotype slide (USNPC 36801). B. Scolex of holotype (USNPC 36801). C. Terminal proglottid of holotype (USNPC 36801).

Phyllobothrium rakusai Wojciechowska, 1991 *incertae sedis*

Phyllobothrium rakusai was described by Wojciechowska (1991a) for specimens taken from *Bathyraja maccaini* Springer, 1971, McCain's skate. The species was collected from Bransfield's Strait, shelf around Joinville and Elephant Islands, Antarctica. The species was described as euapolytic, 50–140 mm long and 1.4 mm in maximum width. The strobila of *P. rakusai* is composed of 130–193 proglottids. The scolex measures 0.9–1.6 long x 1.4–1.8 wide. The bothridia are folded, possess weak marginal loculi, and have an apical sucker measuring 250–310 in diameter. Immature proglottids are wider than long, mature proglottids measure 2.4–2.9 x 1.1–1.3. There are 120–165 testes per proglottid. The genital pore is approximately 50% from the posterior end of the proglottid. Of particular morphological interest, the vitelline follicles approach the midline of the proglottid, and are not interrupted by the ovary.

The genus *Phyllobothrium* is not an appropriate taxon to house *P. rakusai,* as this species lacks foliose, posteriorly bifid bothridia, and is euapolytic, as opposed to apolytic. *Phyllobothrium rakusai* resembles *Phyllobothrium arctowskii* and *Phyllobothrium siedleckii* in that these three species possees weakly-developed marginal loculi on their bothridia that could even be described as slightly crenulate (see Wojciechowska 1991a, figs. 2a, 2c and 3a). In these three species, as well as *P. georgiense*, the vitelline follices are not interrupted by the ovary, and approach the midline of the proglottid. Rocka (2003) transferred *P. rakusai* to *Anthocephalum* as *Anthocephalum rakusai* (Wojciechowska, 1991) Rocka, 2003. However, *P. rakusai* lacks complete marginal loculi, and does not have vitelline follicles interrupted at the level of the ovary. Thus it should not be placed in *Anthocephalum.* Ruhnke and Seaman (2009) mistakenly gave Rocka and Zdzitowiecki (1998) as the citation for this synonomy. It is possible that *P. rakusai*, *P. arctowskii*, *P. siedleckii* and possibly *P. georgiense* could eventually constitute a new generic entity of tetraphyllideans from antarctic skates. However, a detailed study of all type material, in addition to new collection of material for SEM and DNA sequencing, would be recommended before taking such an action. At present, this species should be considered *incertae sedis*. Type material: holotype, No. 904; paratypes, Nos. 904a, b, c in the collection of Wojciechowska at the Institute of Parasitology, Polish Academy of Sciences; paratype, BMNH 1992.1.6.28. Material examined: paratype, BMNH 1992.1.6.28.

Phyllobothrium rhinoptera Vijayalakshmi and Sarada, 1996 _species inquirenda_

Vijayalakshmi and Sarada (1996) described this species from 10 specimens taken from *Rhinoptera javanica* Müller and Henle, 1841, the Javanese cownose ray, Waltair, Andrha Pradesh, India. The scolex is described as being foliated, but the illustration is very poor. Vijayalakshmi and Sarada (1996) compared *P. rhinoptera* to a small subset of nominal *Phyllobothrium* species, but examination of the type specimens will be critical in determining the eventual taxonomic placement of this species. At present, *P. rhinoptera* should be considered *species inquirenda*. Type material: holotype and paratype apparently deposited in the Department of Zoology, Andra University, Waltair, India. Material examined: none.

Phyllobothrium riggii (Monticelli, 1893) Southwell, 1925 (synonym of _Calyptrobothrium riggii_)

Phyllobothrium riggii was originally described by Monticelli (1893) as *Calyptrobothrium riggi* Monticelli, 1893, and is the type of that genus. This species was described from specimens in the collection of the Museum of Zoology at the University of Palermo. These specimens were collected the from the Spotted torpedo, *Torpedo marmorata* Risso, 1810, presumably from Gulf of Trieste. The synonomy of this genus with *Phyllobothrium* by Southwell (1925) was ill-advised, as *C. riggi* does not share the identifying features of *Phyllobothrium* (see Ruhnke 1996b). *Phyllobothrium riggii* should be considered a junior synonym of *Calyptrobothrium riggi*. Type material: not specified. Material examined: none.

Phyllobothrium rudicornis (Drummond, 1839) Ronald, 1959 (synonym of _Anthocephalus rudicornis species inquirenda_)

Phyllobothrium rudicornis was originally described by Drummond (1839) as *Anthocephalus rudicornis* Drummond, 1839, for larval cestodes taken from *Hippoglossus vulgaris* (= *Hippoglossus hippoglossus* L, 1758), the Atlantic halibut. Williams (1968a, pg. 273) stated that "Ronald (1959, p. 70) refers to *Phyllobothrium rudicornis* as a larval cestode in *Hippoglossus hippoglossus* as having been first described by Drummond (1838). No evidence exists at present for rejecting this name." *Anthocephalus* Rudophi, 1819 is a genus within the Trypanorhyncha. The illustrations and description of Drummond (1839) are suggestive of a trypanorhynch. *Phyllobothrium rudicornis* should be considered a synonym of *A. rudicornis*, and this species should be considered a *species inquirenda*. Type material: not specified. Material examined: none.

Phyllobothrium salmonis Fujita, 1922 _species inquirenda_

Phyllobothrium salmonis was proposed by Fujita (1922) for larvae from the Chum salmon, *Onchorhynchus keta* (Walbaum, 1792) and the Cherry salmon, *Onchorhynchus masou* (Brevoort, 1856) from the coast of Japan. Williams (1968a) summarized the history of this larval species, and accepted the name as valid, but also noted that it might be a synonym of *P. caudatum*. This species should be considered a *species inquirenda*. Type material: not specified. Material examined: none.

Phyllobothrium septaria (Van Beneden, 1889) Southwell, 1925 (synonym of _Dinobothrium septaria_)

The name *Phyllobothrium septaria* was created when Southwell (1925) synonymized *Dinobothrium* and *Phyllobothrium* thereby transferring all species of the former to the latter genus. Van Beneden (1889) described this species from specimens taken from the Porbeagle, *Lamna cornubica* (= *Lamna na-*

sus [Bonnaterre, 1788]), collected near Ostende, Belgium. The species was established as the type species of *Dinobothrium* by Van Beneden (1889) as *Dinobothrium septaria* Van Beneden, 1889. Southwell's (1925) synonymization of these genera was ill-advised, as *D. septaria* does not share the identifying features of *Phyllobothrium* (see Ruhnke 1996b). *Phyllobothrium septaria* should be considered a junior synonym of *Dinobothrium septaria*. Type material: not specified. Material examined: none.

Phyllobothrium siedleckii Wojciechowska, 1991 *incertae sedis*

Phyllobothrium siedlickii was described by Wojciechowska (1991a) for specimens taken from *Bathyraja eatonii* (Günther, 1876), Eaton's skate. The species was collected from Bransfield's Strait, shelf around Joinville and Elephant Island, Antarctica. *Phyllobothrium siedleckii* was described as euapolytic. Specimens were 36–62 mm long, and 1.6 mm in maximum width. The strobila of *P. siedleckii* is composed of 85–146 proglottids. The scolex measures 0.8–1 mm long x 1.1–1.2 mm wide. The bothridia are folded, possess weak marginal loculi, and have an apical sucker measuring 185–220 µm in diameter. Immature proglottids are wider than long, mature proglottids measure 0.6–1.9 mm x 0.7–1.5 mm. There are 85–105 testes per proglottid. The genital pore is approximately 50% from the posterior end of the proglottid. The vitelline follicles approach the midline of the proglottid, and are not interrupted by the ovary. The genus *Phyllobothrium* is not an appropriate taxon to house *P. siedleckii*, as this species lacks foliose, posteriorly bifid bothridia, and is euapolytic, as opposed to apolytic. Rocka and Zdzitowiecki (1998) transferred *P. siedleckii* into *Anthocephalum* as *Anthocephalum siedleckii* (Wojciechowska, 1991) Rocka and Zdzitowiecki, 1998, but *P. siedlickii* lacks complete marginal loculi, and does not have vitelline follicles interrupted at the level of the ovary. Thus it should not be placed in *Anthocephalum*. As noted previously for *P. rakusai*, *P siedleckii* is similar to *P. arctowskii*, *P. georgiense* and *P. rakusai*, and these four species could eventually constitute a new generic entity of tetraphyllideans from antarctic skates. However, a detailed study of all type material, in addition to new collection of material for SEM and DNA sequencing, would be recommended before taking such an action. At present, this species should be considered *incertae sedis*. Type material: holotype, No. 911; paratypes Nos. 908 a and b, in the collection of Wojciechowska at the Institute of Parasitology, Polish Academy of Sciences; paratype, BMNH 1992.1.6.28. Material examined: paratype, BMNH 1992.1.6.28.

Phyllobothrium sinuosiceps Williams, 1959 *incertae sedis* (Fig. 25)

This species was described for specimens from *Hexanchus griseus* (Bonnaterre, 1788), the Bluntnose sixgill shark. Host specimens were collected from the Celtic Sea, 54°0'N, 11°15'W. Williams (1959) described *P. sinuosiceps* as a sizable tapeworm, attaining an average length of 200 mm, with a scolex width of 3.2–6 mm. The bothridia are uniloculate, foliose, and possess an apical sucker. The free proglottids are approximately three time as long as wide. This species is euapolytic, and lacks posteriorly bifid bothridia and a vaginal sphincter. In these respects, it is inconsistent with *Phyllobothrium*. This species resembles *Crossobothrium* in some respects, but lack the laciniate proglottids found in species of that genus. At present, the generic position of this species is questionable, and *P. sinuosiceps* should be considered *incertae sedis*. Type material: BMNH 1959.10.14.1/2 (Fig. 25A). Material examined: BMNH 1959.10.14.1/2 (Fig. 25A).

Phyllobothrium speciosum (Monticelli, 1889) Southwell, 1925 (synonym of *Pelichnibothrium speciosum* Monticelli, 1889)

This species was originally established as the type species of *Pelichnibothrium* by Monticelli (1889) for larval specimens collected from the Longnose lancetfish, *Alepisaurus ferox* Lowe, 1833. The new combination *Phyllobothrium speciosum* (Monticelli, 1889) Southwell, 1925 was established when Southwell (1925) synonymized *Pelichnibothrium*

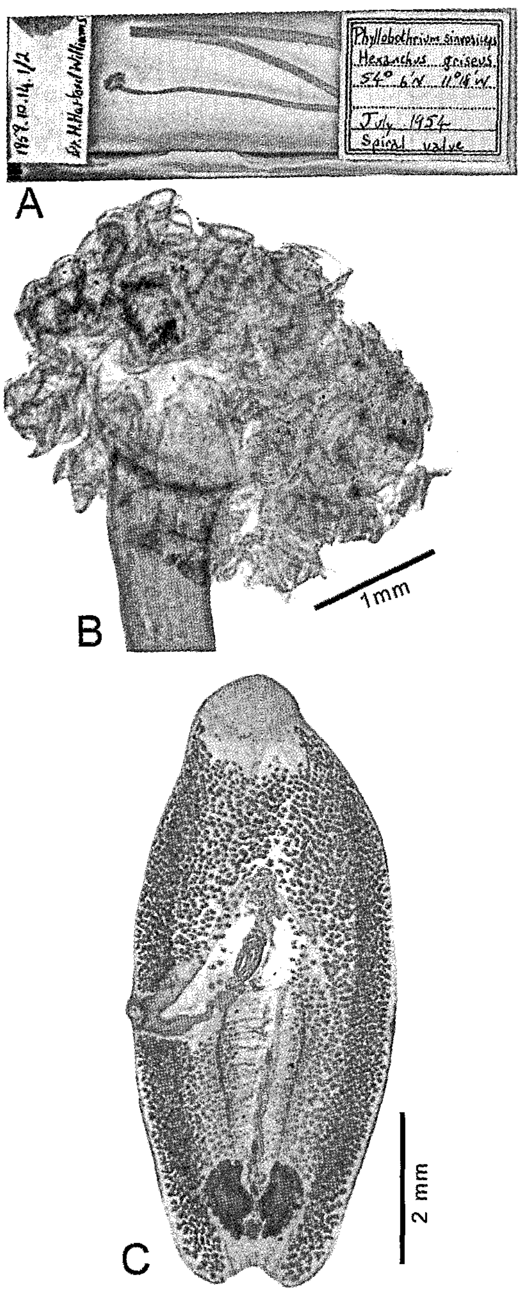

Fig. 25. Photomicrographs of *Phyllobothrium sinuosiceps* Williams, 1959. A. Type slide (BNHM 1959.10.14.1/2). B. Scolex of type (BNHM 1959.10.14.1/2). C. Free proglottid of type (BNHM 1959.10.14.1/2).

and *Phyllobothrium*. The taxonomic history of this species is somewhat complicated, but the Southwell's (1925) synonymy of *Pelichnibothrium* and *Phyllobothrium* was ill-advised, as *Pelichnibothrium* does not share the identifying features of *Phyllobothrium* (see Ruhnke 1996b). *Phyllobothrium speciosum* should be considered a junior synonym of *Pelichnibothrium speciosum* Monticelli, 1889. Type material: not specified. Material examined: none.

Phyllobothrium squali* Yamaguti, 1952 *incertae sedis (Fig. 26)

Phyllobothrium squali was originally described by Yamaguti (1952) for specimens taken from *Squalus sucklii* (= *Squalus acanthias* L., 1758), the Spiny dogfish. These specimens were collected from Onahama, Hukusima Prefecture, Japan. This species has also been reported from Krapec, Bulgaria in the Black Sea (Vasileva et al. 2002), Concarneau, France in the Mediterranean Sea (Euzet 1959), and the Irish Sea (McCullough and Fairweather 1983). Several other authors have reported *P. squali* since its original designation. Euzet (1959) provided an account of *P. squali* under the name *Crossobothrium squali* from both the Velvet belly lantern shark *Etmopterus spinax* (L., 1758) and *S. acanthias,* collected from Concarneau, France. Vasileva et al. (2002) concluded that Euzet's specimens from *E. spinax* were not conspecific to specimens of *P. squali* collected from *S. acanthias* from the Black Sea and the Japanese coast. They also noted that *Crossobothrium* could not be applied as a genus to these species, as Ruhnke (1996a) had provided a restricted generic concept of that genus. McCullough and Fairweather (1983) provided scanning electron micrographs of a specimen they identified as *P. squali* from the Irish Sea. The presence of maiziform (= gongylate) spinitriches on the distal bothridial surfaces reported by McCullough and Fairweather (1983) is interesting, as these structures are similar to those seen in *Orygmatobothrium* species (see Ivanov 2008), and also in *Paraorygmatobothrium barberi* Ruhnke, 1994, *Paraorygmatobothrium bai* Ruhnke and Carpenter, 2008, and *Paraorygmatobothrium rodmani* Ruhnke and Carpenter, 2008 (see Ruhnke 1994a; Ruhnke and Carpenter 2008). Although Vasileva et al. (2002) chose to retain inclusion of *P. squali* in *Phyllobothrium,* the species does not share the derived

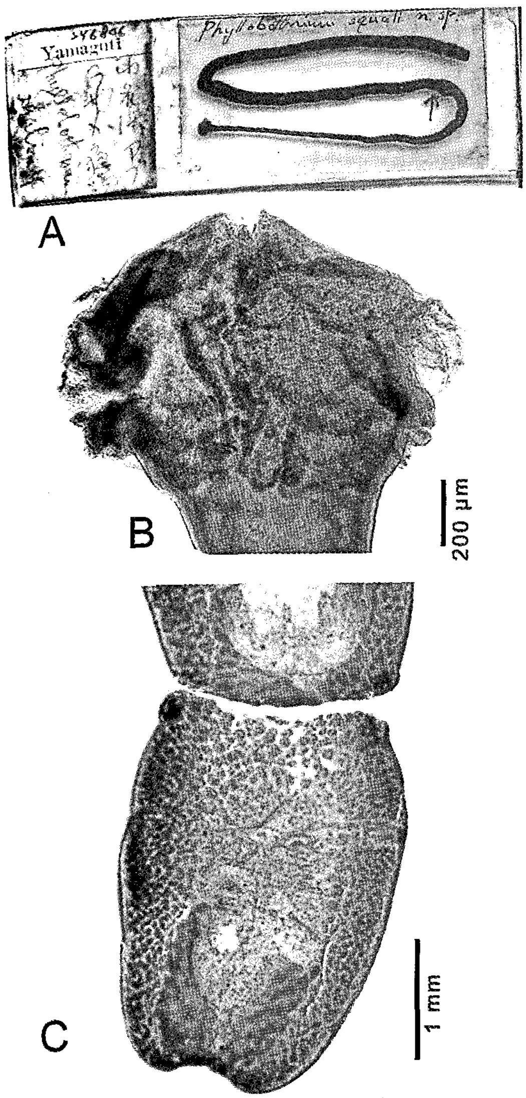

Fig. 26. Photomicrographs of *Phyllobothrium squali* Yamaguti, 1952. A. Holotype slide (MPM 22778). B. Scolex of holotype (MPM 22778). C. Terminal proglottid of holotype MPM (22778).

features of that genus as circumscribed here. For example the bothridia of *P. squali* are not bifid, an apical organ and vaginal sphincter are lacking, and the species bears gongylate, rather that gladiate spinitriches on its distal bothridial surfaces. In the future, a new generic entity will need to be erected in order to house *P. squali,* the specimens from *E. spinax,* and perhaps other new species from squalid sharks. At present, this species should be considered *incertae sedis.* Type material: MPM 22778. Material examined: MPM 22778.

Phyllobothrium thridax **Van Beneden, 1850 *incertae sedis*** (Fig. 27)

This species was described by Van Beneden (1850) for specimens taken from *Squatina angelus* (= *Squatina squatina* [L., 1758]), the Angelshark, collected from the coast of Belgium. Euzet (1959) collected specimens of *P. thridax* from Concarneau, Arcachon, Banyuls and Séte, France. *Phyllobothrium thridax* is a very long, threadlike cestode. Euzet (1959) described specimens 40–50 cm in length. The bothridia are foliose, but not posteriorly bifid, and are weakly marginally loculate. *Phyllobothrium thridax* is similar in morphology to *P. pristis,* but its scolex is not similar to that illustrated by Watson and Thorson (1976) for *P. pristis. Phyllobothrium unilaterale* Southwell, 1925 was described by Southwell (1925) for specimens with unilateral genital pores that Zschokke (1888) identified as *P. thridax. Phyllobothrium unilaterale* was considered a synonym of *P. thridax* by Euzet, and is considered a synonym of *P. thridax* here. At present, *P. thridax* should be

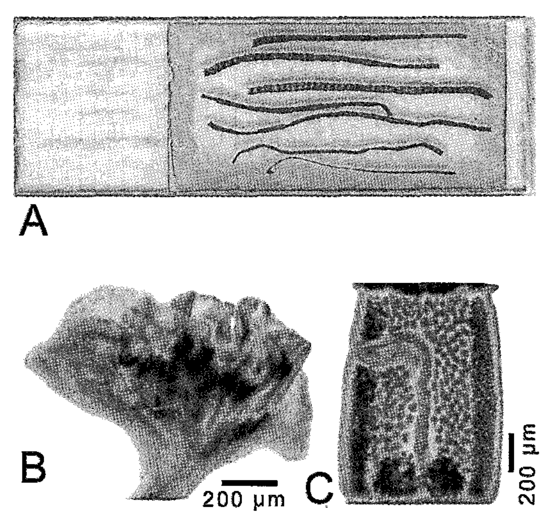

Fig. 27. Photomicrographs of *Phyllobothrium thridax* Van Beneden, 1850. A. Voucher slide (MNHN Paris HEL 130). B. Scolex of voucher (MNHN Paris HEL 130). Mature proglottid of voucher (MNHN Paris HEL 130).

considered *incertae sedis*. Type material: not specified. Material examined: MNHN HEL 130–131 (Fig. 27A).

***Phyllobothrium thysanocephalum* Linton, 1889 (synonym of *Thysanocephalum thysanocephalum*)**

Phyllobothrium thysanocephalum was originally described by Linton (1889) for large worms from the Tiger shark, *Galeocerdo cuvier*, collected from Woods Hole, Massachusetts. In 1890, Linton erected the genus *Thysanocephalum*, with *Phyllobothrium thysanocephalum* as its type, but inexplicably used the name *Thysanocephalum crispum*. Braun (1900) was the first to note that the valid name for this species is *Thysanocephalum thysanocephalum* (Linton, 1889) Linton, 1890. *Phyllobothrium thysanocephalum* should be considered a synonym of *Thysanocephalum thysanocephalum. Thysanocephalum* should be recognized as a valid genus within the Phyllobothriidae (see Euzet 1994). Phylogenetic evidence from microthrix structures (Caira et al. 2001) and nuclear ribosomal DNA (Greenwood 2007) allies *T. thysanocephalum* with species of *Paraorygmatobothrium*. Type material: not specified. Material examined: LRP 7399–4700, USNPC 7691, USNPC 17273.

Phyllobothrium trygoni* Jadhav, 1985 *species inquirenda

Phyllobothrium trygoni was described by Jadhav (1985) for specimens collected from *Trygon sephen* (= *Pastinachus sephen* [Forsskål, 1775]), the Cowtail stingray, near Bombay (= Mumbai), India. This species is very poorly described, and very poorly illustrated. Until type or newly collected material can be examined, *P. tygoni* should be considered a *species inquirenda*. Type material: not specified. Material examined: none.

Phyllobothrium vagans* Haswell, 1902 *incertae sedis

Haswell (1902) described *P. vagans* from the Port Jackson shark, *Heterodontus portjacksoni* (Meyer, 1793), but used the term "Cestracion" for the host of *Phyllobothrium vagans* and he provided no type locality. Williams (1968a) indicated Haswell's material was collected in New Zealand. Examination of voucher specimens of *P. vagans* collected from *H. portusjacksoni*, taken from Tasmania, revealed that the *P. vagans* has uniloculate bothridia with marginal loculi. These were described by Haswell as finely crenulate. *Phyllobothrium vagans* cannot be considered a species of *Phyllobothrium*, as it lacks foliose, bifid bothridia, an apical organ, and a vaginal sphincter. At present, no judgement can be made about its possible generic assignment, and the species should be considered *incertae sedis*. Type material: not specified. Material examined: BMNH 1975.1.8.18–28.

***Phyllobothrium variabile* (Linton, 1889) Southwell, 1930 (synonym of *Spongiobothrium variabile*)**

This species was originally established as the type species of *Spongiobothrium. Spongiobothrium variabile* was described for specimens from the Rough tail stingray, *Trygon centroura* (= *Dasyatis centroura* [Mitchill, 1815]), collected from Woods Hole, Massachusetts. The name *Phyllobothrium variabile* (Linton, 1889) Southwell, 1930 was proposed by Southwell (1930) when he synonymized *Spongiobothrium* and *Phyllobothrium*. Southwell's (1930) synonymy of these two genera was ill-advised, as *S. variabile* shares features in common with stingray cestodes such as *Rhinebothrium*, as opposed to *Phyllobothrium* (see Ruhnke 1996b). In her review of the rhinebothriines, Healy (2006) recognized *Spongiobothrium* as a valid genus. Thus, as the type species of *Spongiobothrium, S. variablile*, is a valid species of the Rhinebothriidea. *Phyllobothrium variabile* is considered a synonym of *Spongiobothrium variabile*. Type material: not specified. Material examined: none

Phyllobothrium williamsi* Schmidt, 1986 *incertae sedis

Williams (1968a) described *Phyllobothrium minutum* Williams, 1968 from *Raja fullonica* (= *Leucoraja fullonica* [L., 1758]), the Shageen ray, from the west coast of Scotland. Schmidt (1986) noted the homonymy between this species and *Phyllobothrium minutum*

Shipley and Hornell, 1906, and gave the replacement name *Phyllobothrium williamsi* Schmidt, 1986 for this species. It is interesting that Williams used the specific epithet *minutum* (L. minute) for a species that achieves a size of 9 cm. A cestode that can easily be seen with the naked eye is hardly minute. The illustrations of Williams (1968a) indicate the presence of marginal loculi on the bothridium of *P. williamsi.* This species lacks the bifid bothridia, apical organ, and vaginal sphincter of *Phyllobothrium,* and should not be considered a member of that genus. However, *P. minutum* is similar to other species described from skates, such as *P. britannicum*, *P. piriei* and *P. radioductum.* The generic placement of *P. williamsi* and these species is currently unclear. Detailed comparison of these species, including SEM and DNA sequencing, may result in the erection of a new genus to house them. At present, *P. williamsi* should be considered *incertae sedis.* Type material: not specified. Material examined: none.

CLISTOBOTHRIUM Dailey and Vogelbein, 1990

Taxonomic status: Valid.

Type species: *Clistobothrium carcharodoni* Dailey and Vogelbein, 1990

Other species: *Clistobothrium tumidum* (Linton, 1922) Ruhnke, 1993; *C. montaukensis* Ruhnke, 1993.

Etymology: *Clisto* (Gr.) = closed; *bothrios* (Gr.) = pit.

Diagnosis (modified from Ruhnke [1993a]).

Phyllobothriidae. Worms apolytic. Scolex with two dorsal and two ventral stalked bothridia and dome-shaped or cruciform apical region. Myzorhynchus absent. Each bothridium with single apical, round sucker and posterior loculus. Posterior loculus foliose or in form of folding flap of tissue. Neck short; immature proglottids wider than long; mature proglottids at least twice as long as wide. Strobila with distinct longitudinal dorsomedian band of muscles. Testes numerous, intervascular, in two irregular fields; post-vaginal testes present. Cirrus-sac extending medially with proximal portion directed anteriorly (L-shaped). Cirrus armed with spinitriches. Genital atrium present. Vagina ventral to, and opening anterior to, cirrus-sac. Ovary posterior, bilobed in cross section. Uterus ventral, reaching only to posterior margin of cirrus-sac in mature proglottids; reaching anterior margin of cirrus-sac in gravid proglottids. Egg surface mammilated or spinose. Parasites of Lamniformes.

Remarks

Dailey and Vogelbein (1990) considered *Clistobothrium* to be different from all phyllobothriid genera based primarily on its unique scolex structure. In addition, *Clistobothrium* differs from all other phyllobothriid genera in its possession of a longitudinal band of dorsomedian muscles extending throughout the strobila. The L-shaped cirrus-sac of these species is also apparently unique among the phyllobothriids.

Clistobothrium is known only from lamnid sharks. Given that three species remained to be examined for *Clistobothrium,* it seems likely that additional diversity in the genus remains to be discovered.

Clistobothrium carcharodoni Dailey and Vogelbein, 1990
TYPE SPECIES
(Figs. 28–29)

Synonyms: None.

Taxonomic status: Valid.

Type Host: *Carcharodon carcharias* (L., 1758), Great white shark.

Site of Infection: Spiral intestine.

Type locality: Off Pt. Dume (33°55'N, 118°48'W), Los Angeles County, California, U.S.A. (Fig. 28).

Type material: Holotype USNPC 80985; paratypes USNPC 80896 (Fig. 29A) and HWML 31397.

Specimens examined: Paratypes USNPC 80896 and HWML 31397.

Etymology: The species is named its host genus, *Carcharodon* Smith, 1833.

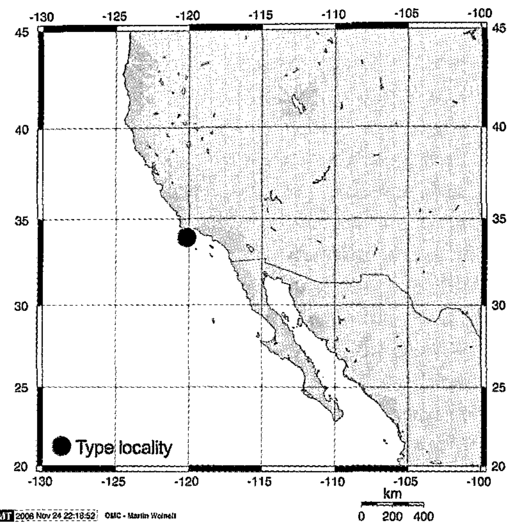

Fig. 28. Geographic distribution of *Clistobothrium carcharodoni* Dailey and Vogelbein, 1990..

Description (modified from Dailey and Vogelbein [1990] and Ruhnke [1993a]).

Worms slightly craspedote, apolytic 24–40 mm (33) in length, maximum width 1,500–1,950 (1,733) at scolex. Scolex with four bothridia, 736–1,260 (819) long x 605–901 (667) wide; bothridia with suckers ringed by folded lappet or hood on retractable stalks separated by a cruciform-shaped apex. Sucker diameter 417–461 (438) long x 333–398 (371) wide. Neck 374–494 (436) long.

Strobila with 73–85 (79) proglottids and distinct band of dorsomedian longitudinal muscles band; muscle band 70–85 (76) wide in anterior and 50–73 (63) wide in posterior proglottids. Anterior proglottids wider 681–915 (797) than long 348–390 (369). Mature proglottids longer than wide, 563–1,504 (982) long x 640–873 (737) wide. In gravid worms, terminal proglottids approximately 2.5 times longer than wide, 1,426–2,765 (1,851) long x 679 – 912 (790) wide. Testes spherical to oblong, 91–123 (107) in number; antiporal, 43–69 (59) in number, with approximately equal numbers occurring pre-porally 15–24 (20) and postporally 24–30 (26); testes 32–67 (53) long x 24–59 (33) wide. Vas deferens forming small mass of coils at anteromedial margin of cirrus-sac in mature proglottids. Cirrus-sac L-shaped, 408–670 (564 ± 91; n=4; n=13) long x 145–229 (198 ± 37; n=4; n=13) wide, containing cirrus. Cirrus coiled, expanded proximally, and armed with spinitriches. Genital pores lateral, irregularly alternating, positioned 60–68% (65 ± 3; n=5; n=13) from posterior margin of mature proglottids; genital atrium present. Vagina median, extending from ovary anteriorly and crossing ventrally the proximal portion of cirrus-sac, extending laterally to genital trium, 30–135 (72 ± 34; n=5; n=10) wide above cirrus-sac in mature proglottids. Ovary posterior to testes, H-shaped in frontal view, 210–420 (295 ± 68; n=5; n=11) long x 320–500 (425 ± 63; n=5; n=11) wide. Vitelline follicles 12–30 (21 ± 6; n=4; n=8) long x 40–80 (59 ± 15; n=4; n=8) wide. Eggs round, mammilated, 21–24 (23 ± 1; n=4; n=9) in diameter, found in terminal and free proglottids.

Remarks

In the original description of *C. carcharodoni,* Dailey and Vogelbein (1990) were mistaken in their estimation of the size of the egg and the width of the scolex, and Ruhnke (1993a) provided emended measurements for these features. Ruhnke (1993a) was first to observe the dorsomedian band of longitudinal muscles that extends throughout the length of the strobila. Dailey and Vogelbein (1990) described *C. carcharodoni* as anapolytic. However, given that the type series included a (free) proglottid, and the posterior proglottids of some of the specimens, although containing eggs, were not completely gravid. The species should be considered apolytic.

Clistobothrium carcharodoni differs from *C. tumidum* and *C. montaukensis* in possessing bothridia with suckers ringed by a folded lappet, rather than bothridia with foliose loculi that are posterior and lack the lappet. Among other characters, *Clistobothrium carcharodoni* further differs from *C. tumidum* in cirrus-sac length (408–670 vs. 316–411), and further differs from *C. montaukensis* in testes number (91–123 vs. 198–263).

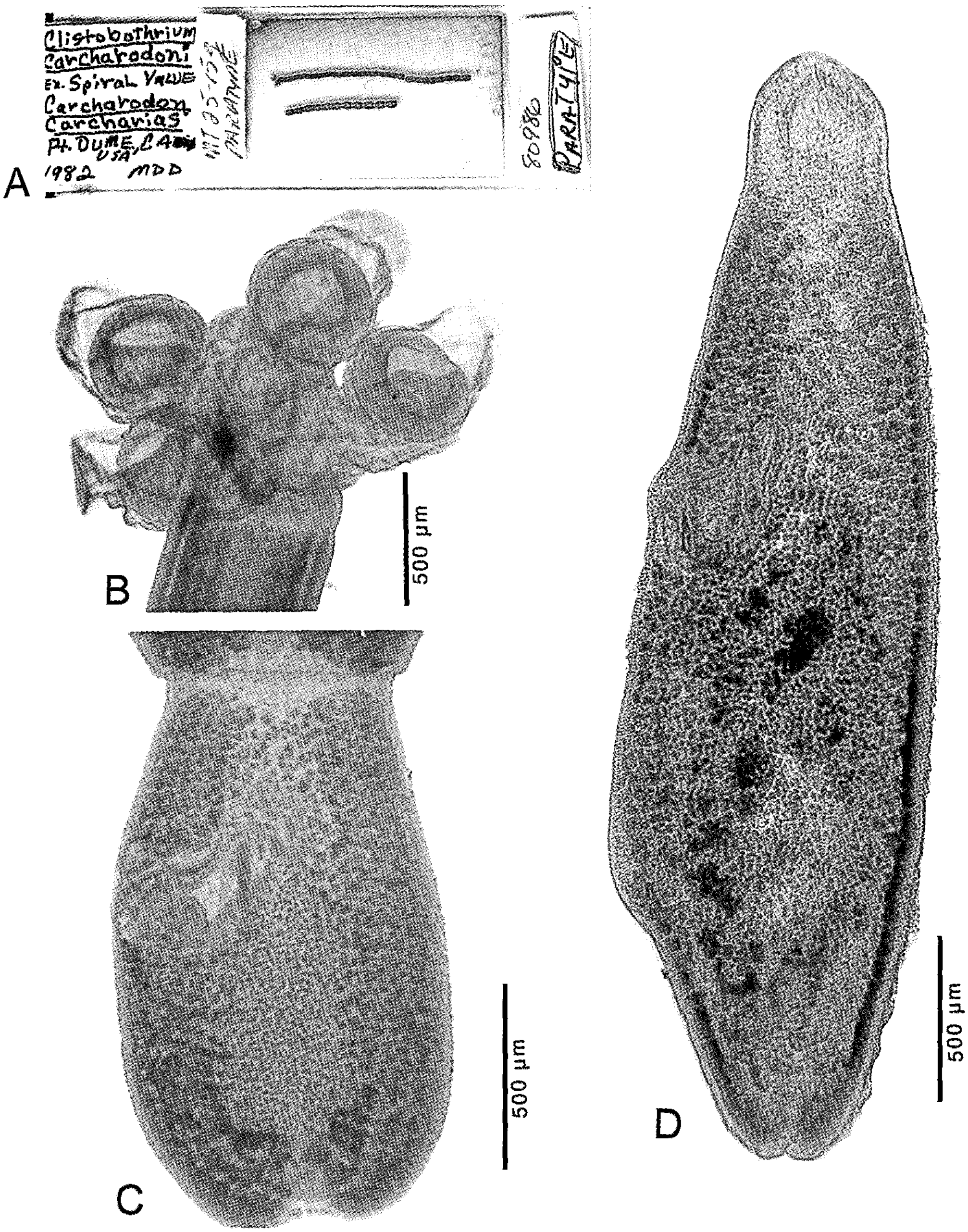

Fig. 29. Photomicrographs of *Clistobothrium carcharodoni* Dailey and Vogelbein, 1990. A. Slide of paratype (USNPC 80986). B. Scolex of paratype (USNPC 80986). C. Terminal proglottid of paratype (USNPC 80986). D. Free proglottid of paratype (HWML 31397).

Clistobothrium montaukensis Ruhnke, 1993
(Figs. 30–33)

Synonyms: None.
Taxonomic status: Valid.
Type Host: *Isurus oxyrinchus* Rafinesque, 1810, the Shortfin mako shark.
Site of Infection: Spiral intestine.
Type locality: Montauk, Long Island, U.S.A. (Fig. 30).
Additional localities: Yarmouth, Massachusetts, U.S.A.; El Barril, Baja, Mexico; Sète, France (Fig. 30).
Type material: Holotype, USNPC 82489; paratypes USNPC 82490 (Fig. 31A), HWML 35289, LRP 7402–7404.
Additional material: Vouchers, MNHN Paris HEL 132–134.
Material examined: Holotype, all paratypes, and voucher MNHN HEL 132–134.
Etymology: The species is named for its type locality.

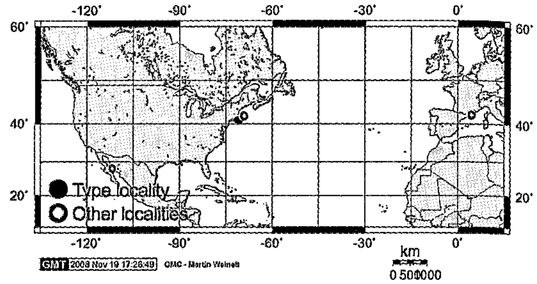

Fig. 30. Geographic distribution of *Clistobothrium montaukensis* Ruhnke, 1993.

Description (modified from Ruhnke [1993a]).

Worms apolytic, slightly craspedote; 38.5–119.5 mm (73.5 ± 34.3; n=4) long, maximum width 2,475–3,750 (3,000 ± 522; n=7) at scolex, apolytic, slightly craspedote. Scolex with large, domeshaped apical region, apical region covered with long filitriches. Scolex 2,100–3,650 (3,000 ± 544; n=7) long x 2,475–3,750 (3,000 ± 522; n=7) wide, with two ventral and two dorsal large, foliose bothridia, each with one round, muscular, anterior accessory sucker 310–500 (372 ± 52; n=9; *n*=18) in diameter. Bothridia 1,750–2,125 (1,970 ± 159; n=5) long x 1,350–1,500 (1,465 ± 89; n=5) wide. Proximal surface of bothridia covered with gladiate spinitriches; distal bothridial surface not observed. Neck short, 950–3,700 (2,110 ± 1,125; n=5) long, covered with long filitriches.

Strobila with more than 100 proglottids, with distinct dorsomedian muscle band; muscle band 63–160 (91 ± 33; n=8) wide in anterior proglottids, 30–58 (45 ± 8; n=9) wide in posterior proglottids. Anterior proglottids much wider than long, immature proglottids at midworm 525–800 (669 ± 86; n=4; *n*=8) long x 1,050–1,300 (1,191 ± 92; n=4; *n*= 8) wide, terminal and subterminal proglottids 1,400–3,200 (2,122 ± 569; n=6; *n*=13) long x 865–1,212 (1,035 ± 127; n=6; *n*=13) wide, generally twice as long as wide, with dorsal and ventral pair of lateral excretory ducts and a pair of lateral nerve cords in cross section. Free proglottids 6–7 mm (6.7±0.6; n=5) long by 2–3 mm (2.5±0.4; n=5) wide. Testes round, 33–72 (56 ± 12; n=5; *n*=17) in diameter, numbering 198–263 (242 ± 28; n=6; *n*=8) in dorsal

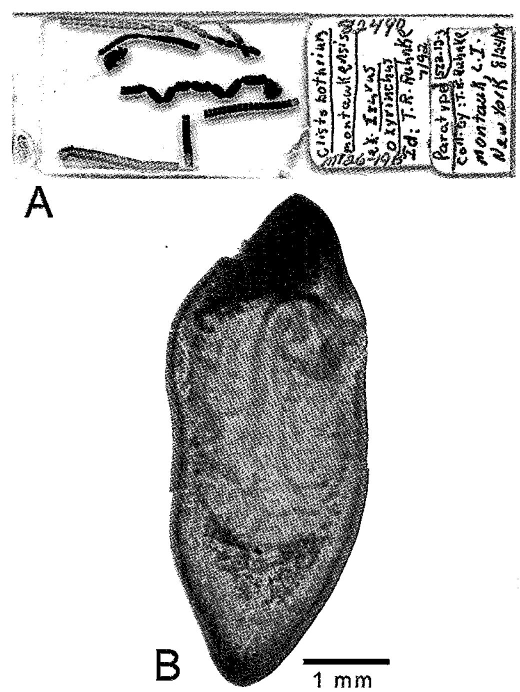

Fig. 31. Photomicrographs of *Clistobothrium montaukensis* Ruhnke, 1993. A. Paratype slide (USNPC 82490). B. Free proglottid paratype (HWML 35289).

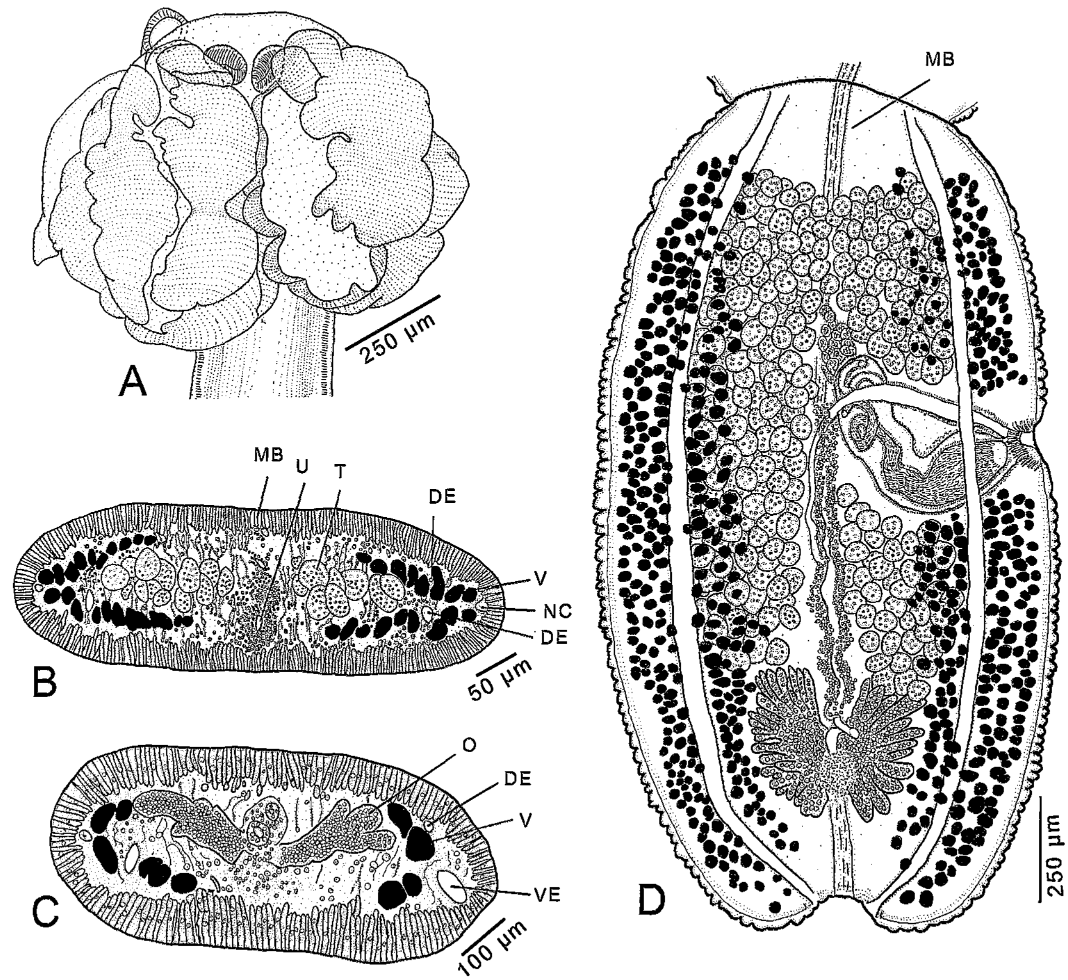

Fig. 32. Line drawings of *Clistobothrium montaukensis* Ruhnke, 1993. A. Scolex of holotype (USNPC 82490). B. Cross-section of proglottid posterior to cirrus-sac and anterior to ovary of paratype (HWML 35289). C. Cross-section of proglottid through ovary of paratype (HWML 35289). D. Mature proglottid of paratype (USNPC 82490). (Taken from Ruhnke [1993a], copyright 1993. Used with permission.)

or ventral view, distributed in two irregular fields between ventral excretory ducts in cross section. Vas deferens coiled, medial, in anterior third of proglottid. Cirrus-sac dorsal, L-shaped, proximal portion of cirrus-sac immediately posterior to vas deferens, 519–737 (638 ± 66; n=4; n=10) long x 123–251 (173 ± 39; n= 4; n=10) wide, opening into a genital atrium. Cirrus long, coiled inside cirrus-sac, expanded proximally, armed with slender spinitriches. Genital pores lateral, irregularly alternating, positioned in 57–64% (61 ± 3; n=8; n=14) from posterior end of mature proglottids. Vagina median, extending from ovary anteriorly and crossing proximal portion of cirrus-sac ventrally and extending laterally to genital atrium, 28–170 (78 ± 45; n=6; n=12) wide anterior to cirrus-sac. Ovary posterior, H-shaped in frontal view, with conspicuous lateral lobes, positioned between ventral excretory ducts, 330–550 (409 ± 83; n=3; n=5) long x 375–500 (429 ± 48; n=3; n= 5) wide; bilobed and dorsal in cross section. Mehlis' gland posterior to ovary. Uterus ventral, beginning anterior to ovary and extending to posterior margin of cirrus-sac in mature

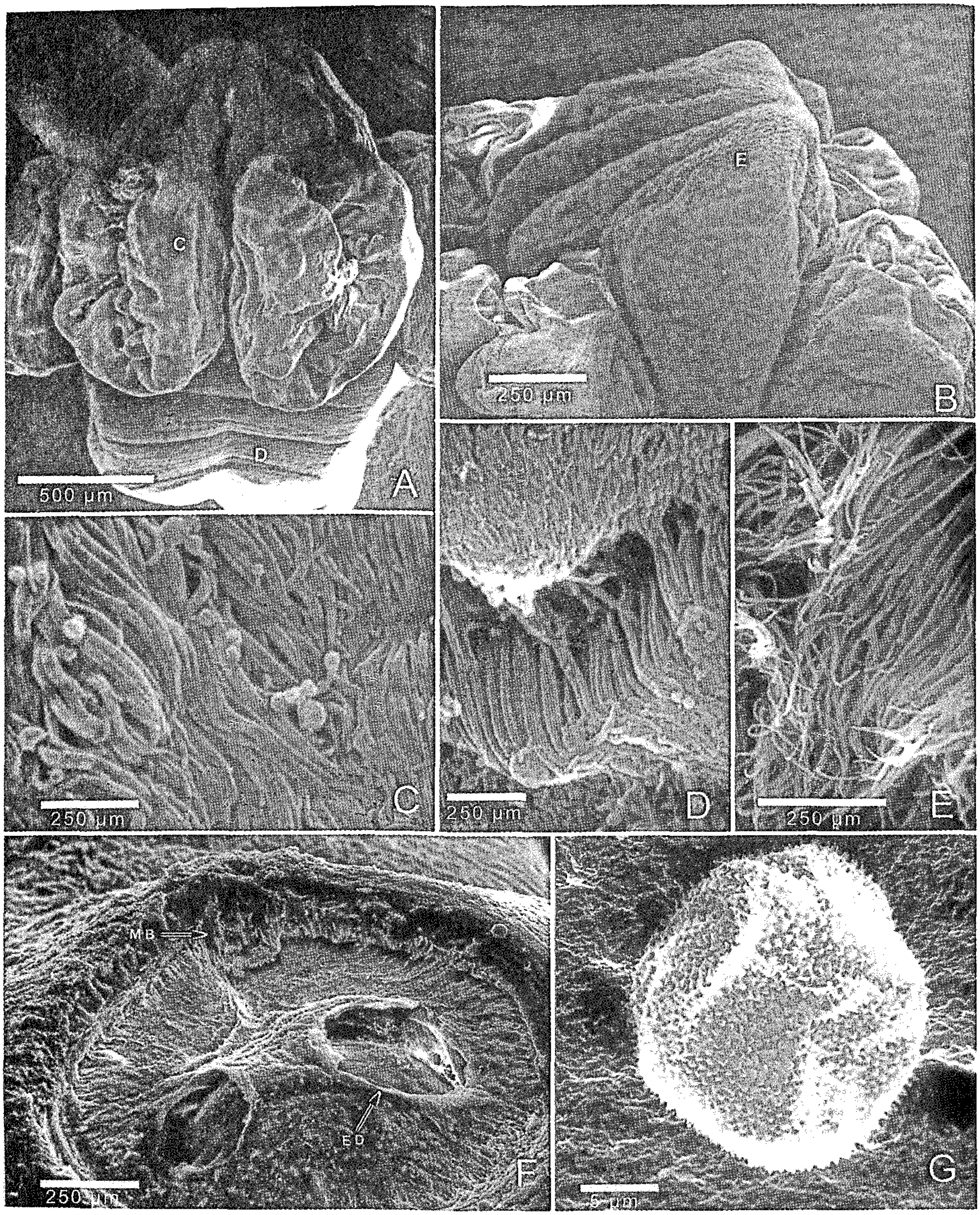

Fig. 33. Scanning electron micrographs of *Clistobothrium montaukensis* Ruhnke, 1993. A. Scolex (letters indicate regions of scolex in enlarged photos C and D). B. Scolex apex (letter indicates region of scolex in enlarged photo E). C. Proximal surface of bothridium. D. Anterior surface of neck. E. Surface of scolex apex. F. Cross-section of strobila (MB=longitudinal muscle bundle.). G. Egg. (Taken from Ruhnke [1993a], copyright 1993. Used with permission.)

proglottids; no uterine duct observed. Uterus extending to anterior margin of cirrus-sac in free proglottids. Vitellaria follicular, distributed dorsally and ventrally, extending to median third of proglottid in cross section; follicles 20–30 (26 ± 3; n=4; *n*=11) long by 22–42 (31 ± 5; n=4; *n*= 11) wide, reduced at level of ovary, interrupted by the cirrus-sac. Eggs round 21–28 (26 ± 1.4; n=6; *n*=35) in diameter, surface covered with small spinose projections, found only in free proglottids.

Remarks

Clistobothrium montaukensis differs from *C. carcharodoni* in the shape of the posterior loculus (foliose vs. lappet-like) and number of testes per proglottid (198–263 vs. 91–123). *Clistobothrium montaukensis* differs from *C. tumidum* in cirrus-sac length (519–737 vs. 316–411). Whereas in *C. montaukensis,* the proximal portion of the cirrus-sac crosses and lies dorsal to the anterior portion of the vagina (see Fig. 32D), but the cirrus-sac does not cross the vagina in *C. tumidum* (Fig. 35E). Specimens collected from *I. oxyrinchus* at Séte, France were identified as *Phyllobothrium tumidum* by Euzet (1959). These specimens (MNHN HEL 132-134) were examined and they are consistent in morphology with *C. montaukensis*. Similarly, the species is also now known from the Gulf of California, Mexico, based on the specimens reported here from El Barril, Baja Mexico.

Clistobothrium tumidum (Linton, 1922) Ruhnke, 1993

(Figs. 34–35)

Synonym: *Phyllobothrium tumidum* Linton, 1922.

Taxonomic status: Valid.

Type Host: *Carcharodon carcharias* (L., 1758), the Great white shark.

Site of Infection: Spiral intestine.

Type locality: Woods Hole, Massachusetts, U.S.A. (Fig. 34).

Additional locality: Montauk, Long Island, NY, U.S.A. (Fig. 34).

Type material: Lectotype USNPC 7631 (Fig. 35B); paralectotypes USNPC 7630, 7631.

Voucher specimens: UNSPC 35802, 082491; HWML 35290 (Fig. 35A), LRP 7405.

Specimens examined: USNPC 7630–7632, HWML 35290, LRP 7405.

Etymology: An etymology was not given by Linton (1922). However, the word *tumidum* translates from Latin as swollen. Specimens of *Clistobothrium* could be perceived to look swollen when viewed fresh in an open spiral intestine (Ruhnke pers. obs.).

Description (modified from Ruhnke [1993a]).

Worms slightly craspedote, euapolytic. Maximum width 3 mm at scolex. Scolex with dome-shaped apical region and dorsal and ventral pairs of bothridia. Each bothridium with apical sucker and single foliose posterior loculus; apical sucker 280–360 (307 ± 35; n=4; *n*=12) in diameter.

Strobila with more than 100 proglottids. Strobila with distinct dorsomedian muscle band, muscle band 75–120 (98 ± 32; n=2) wide in anterior proglottids, 33–62 (49 ± 12; n=4) wide in posterior proglottids. Mature proglottids 1,625–1,925 long (1,761 ± 106; n=4; *n*=7) long x 1,025–1,800 (1,457 ± 231; n=4; *n*=7) wide. Free proglottids (Fig. 35G) 3.5–6.5 (4.9 ± 1; n=7) long x 2–2.5 (2.1 ± 0.2; n=7) wide. Testes 234–307 (282 ± 33; n=4) in number in mature proglottids in dorsal or ventral view, distributed in two irregular fields. Mature proglottids with thin-walled, L-shaped, dorsal cirrus-sac, 316–411 (376 ± 41; n=4) long x 105–168 (126 ± 30; n=4) wide, opening into genital atrium. Cirrus armed, coiled inside cirrus-sac, expanded proximally.

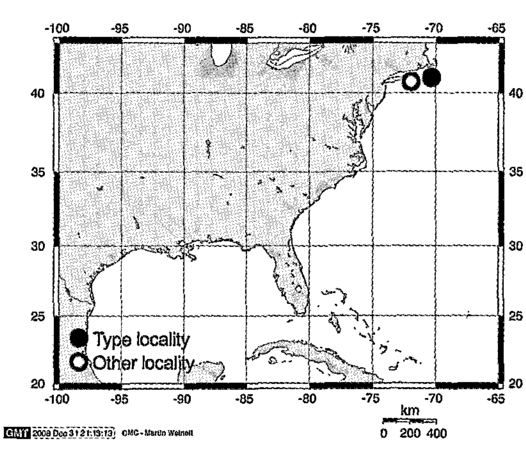

Fig. 34. Geographic distribution of *Clistobothrium tumidum* (Linton, 1922) Ruhnke, 1993.

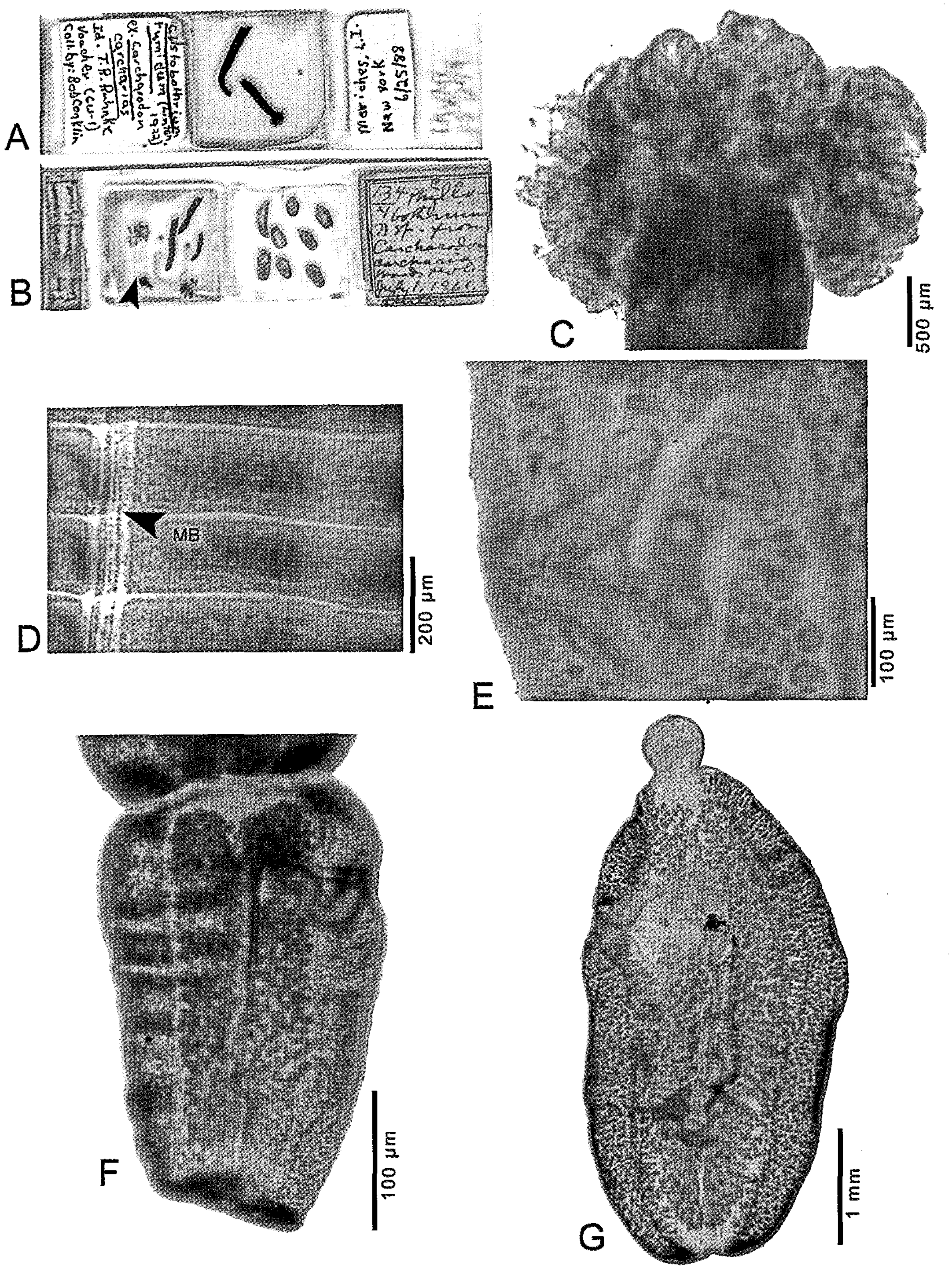

Fig. 35. Photomicrographs of *Clistobothrium tumidum* (Linton, 1922) Ruhnke, 1993. A. Voucher (HWML 35290). B. Lectotype and paralectotypes (USNPC 7631), arrow indicates lectotype. C. Scolex of voucher (HWML 35290). D. Immature proglottids of voucher (HWML 35290). E. Cirrus-sac of paralectotype (USNPC 7631). F. Terminal proglottid of lectotype (USNPC 7631). G. Free proglottid of paralectotype (USNPC 7631).

Genital pores lateral, irregularly alternating, positioned 61–76% (67 ± 4; n=5; *n*=9) from posterior end of mature proglottids. Vagina median, extending anteriorly, then laterally and anteriorly over proximal portion of cirrus-sac to genital atrium. Ovary posterior, H-shaped in frontal view, 420–520 (477 ± 37; n=3; *n*=6) long x 470–600 (538 ± 47; n=3; *n*=6) wide in mature proglottids, bilobed in cross section. Uterus ventral, extending to posterior margin of cirrus-sac in mature proglottids, extending to anterior margin of cirrus-sac in gravid free proglottids. Vitellaria follicular, in two lateral bands, with 5–7 dorsal and 5–7 ventral irregular columns of follicles per band, vitellaria interrupted by cirrus-sac. Some free proglottids with a midventral pore-like dehiscence. Eggs round, 20–27 (24 ± 2; n=3; *n*=8) in diameter in free proglottids, surface mammilated.

Remarks

Linton (1922b) described this species as *Phyllobothrium tumidum* from the Great white shark. However, he included a specimen from the Shortfin mako shark in the type series (USNPC 7632). Unfortunately, this specimen is immature and its conspecificity with *C. tumidum* cannot be determined. Given that a holotype was not designated by Linton (1922b) for this species, Ruhnke (1993a) designated a lectotype from one of the partial worms on the "type" slide catalogued USNM 7631. This strobila was drawn by Linton and most clearly depicts the proglottid structure of the specimens in the type series. The remaining specimens of USNPC 7630 and 7631 are paralectotypes.

Clistobothrium tumidum differs from *C. carcharodoni* in the shape of the posterior loculus (foliose vs. lappet-like), diameter of the apical sucker (280–360 vs. 417–461), and number of testes in mature proglottids (234–307 vs. 91–123). *Clistobothrium tumidum* differs from *C. montaukensis* in cirrus-sac length (316–411 vs. 519–737). In addition, whereas in *C. tumidum*, the cirrus-sac does not cross the vagina. In *C. montaukensis* and *C. carcharodoni* the proximal portion of the cirrus-sac crosses and lies dorsal to the anterior portion of the vagina.

CROSSOBOTHRIUM Linton, 1889

Taxonomic Status: Valid.
Type species: *Crossobothrium laciniatum* Linton, 1889.
Other species: *Crossobothrium antonioi* Ivanov, 2009*; *Crossobothrium campanulatum* Klaptocz, 1906; *C. dohrni* (Oerley, 1885) Ruhnke, 1996; *Crossobothrium pequeae* Ivanov, 2009*.
* recently described species
Etymology: No etymology was given by Linton (1889), but *Crosso* (Gr.) = fringed or tasseled, and *bothrios* (Gr.) = pit.

Diagnosis (modified from Ruhnke [1996a]).

Phyllobothriidae. Worms apolytic, craspedote lacinate. Scolex with two dorsal and two ventral stalked bothridia. Myzorhynchus absent. Each bothridium with single apical sucker and single posterior loculus. Neck absent; immature proglottids wider than long; mature proglottids as long as wide. Free proglottids up to twice as long as wide. Strobila with field of longitudinal muscle fibers at the boundary of the cortex and medulla. Testes numerous, intervascular, in 2–4 irregular fields, post-vaginal testes present. Cirrus-sac oval; cirrus armed with spinitriches. Genital atrium present. Vagina ventral to, opening anterior to cirrus-sac. Ovary posterior, lobate, tetralobed in cross-section. Vitellarium follicular, in two lateral bands, follicles per band increasing at level of ovary; number of follicles per band reduced at level of cirrus-sac. Uterus ventral, reaching anterior margin of cirrus-sac in gravid proglottids. Parasites of Hexanchiformes and Odontaspidae.

Remarks

Species in *Crossobothrium* differ from species in all other phyllobothriid genera in their possession of a field of longitudinal muscle fibers that are situated at the boundary of the cortex and the medulla. A greater number of vitelline follicles per band at the level of, and posterior to, the ovary, relative to the rest of the vitelline field also appear to differentiate species in this genus from species in other phyllobothriid genera. Species of *Crossobothrium* further differ from species in the genera *Paraorygmatobothrium* (see Ruhnke 1994a), *Anthocephalum* (see Ruhnke 1994b), and *Phyllobothrium* (see Ruhnke 1996a) in bearing apical suckers whose distal surfaces are covered with papillar projections, with the papillar projections bearing short filitriches and a single central cilium.

Crossobothrium has had a confusing taxonomic history. The genus was originally described for *Crossobothrium laciniatum* Linton, 1889, but was synonymized with *Phyllobothrium* by Southwell (1925). Euzet (1959) considered *Crossobothrium* to be valid and recognized four species. He transferred *C. longicolle* (Molin, 1858) Euzet, 1959, *C. squali* (Yamaguti, 1952) Euzet, 1959, and *C. triacis* (Yamaguti, 1952) Euzet, 1959, and also recognized *C. angustum* (Linton, 1889) Linton 1890. However, he considered *C. laciniatum* to be synonymous with *Phyllobothrium dohrni* (Oerley, 1885) Zschokke, 1888. In a fit of lumping, Euzet (1959) considered *C. filiforme* (Yamaguti, 1952) Euzet, 1959 and *Crossobothrium prionacis* (Yamaguti, 1934) Euzet, 1959 to be synonyms of *C. angustum*. Williams' (1968a) taxonomic scheme of *Crossobothrium* included the four species recognized by Euzet (1959), in addition to *P. filiforme* Yamaguti, 1952 and *Phyllobothrium prionacis* Yamaguti, 1934, which he believed represented valid species. However, *Crossobothrium*, as envisioned by Euzet (1959) and Williams (1968a), appears to be an unnatural grouping of species. *Crossobothrium laciniatum* is the type species by monotypy (see Linton 1889). Linton (1901) also transferred *Orygmatobothrium angustum* to *Crossobothrium*. Euzet (1959) mistakenly considered *C. laciniatum* a synonym of *P. dohrni*. In addition, it appears that the morphology of *C. angustum* became the "*Crossobothrium* type" to students of the Tetraphyllidea (see Euzet 1959; Williams 1968a). Linton's (1901) synonymy involving *O. angustum* and Southwell's (1925) synonymy of *Crossobothrium* with *Phyllobothrium* apparently led to the decades old case of "mistaken identity" regarding the genus. In addition, Southwell (1925) considered *O. angustum* as a synonym of *P. musteli*. *Crossobothrium angustum* should not be considered synonymous with *P. musteli*, and both of these species are transferred to *Paraorygmatobothrium* in this monograph. Euzet (1994) was in error when he listed *C. angustum* as the type of *Crossobothrium*.

Presently, the valid species of *Crossobothrium* are known from species in the shark families Hexanchidae and Odontotaspidae. *Crossobothrium laciniatum* was described from the odontotaspid shark *Carcharias taurus* Rafinesque, 1810 the Sand tiger shark, *C. campanulatum* was described from the hexanchid shark *Hexanchus griseus* (Bonnaterre, 1788), the Bluntnose sixgill shark, and *C. dohrni* was described from the hexanchid shark *Heptranchias perlo* (Bonnaterre, 1788), the Sharpnose sevengill shark. No species of *Crossobothrium* have been described from the three other odontaspid sharks: *Carcharias tricuspidatus* Day, 1878, the Indian sand tiger, *Odontaspis ferox* (Risso, 1810), the Smalltooth sand tiger, and *Odontaspis noronhai* (Maul, 1955), the Bigeye sand tiger. In addition, undescribed species of *Crossobothrium* may also exist in two other hexanchid sharks, *Hexanchus nakamurai* (Teng, 1962), the Bigeyed sixgill shark, and *Notorynchus cepedianus* (Péron, 1807) the Broadnose sevengill shark.

Crossobothrium laciniatum Linton, 1889

TYPE SPECIES

(Figs. 36–39)

Synonym: *Phyllobothrium laciniatum* (Linton, 1889) Yamaguti, 1959.

Taxonomic status: Valid.

Type Host: *Carcharias taurus* Rafinesque, 1810 the Sand tiger shark.

Site of Infection: Spiral intestine.

Type locality: Woods Hole, Massachusetts, U.S.A. (Fig. 36).

Additional localities: Vineyard Sound, Massachusetts, U.S.A.; northwestern Atlantic Ocean (36°26'N 75°41'W and 34°50'N 76°5'W) (Fig. 36).

Type material: Unknown.

Voucher specimens: BNHM 1996.8.8.5–6, 1996.8.8.7–8; HWML 39126, 39127; LRP 7406–7409; USNPC 4718–4723, 4738, 4781, 7667–7668, 24625, 34800, 34887, 34945, 34993, 35002, 35020, 35717, 35836, 35838, 35959, 36017, 49602, 49603, 86806, 86807.

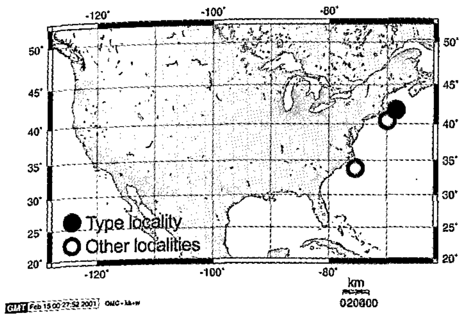

Fig. 36. Geographic distribution of *Crossobothrium laciniatum* Linton, 1889.

Specimens examined: BNHM 1996.8.8.5–6, 1996.8.8.7–8; HWML 39126, 39127; LRP 7406–7409; USNPC 86806, 86807.

Etymology: The species was named for its laciniate proglottid morphology.

Description (modified from Ruhnke [1996b]).

Worms apolytic, slightly craspedote, 56–136 mm (105 ± 29; n=9) long, maximum width 2,175–3,050 (2,583 ± 266; n=10), generally at scolex. Proglottids with dorsal and ventral pair of laciniations, 72–450 in number. Scolex 2,175–3,050 (2,583 ± 266; n=10) wide; with four bothridia, apical surface covered with filitriches. Bothridia slightly

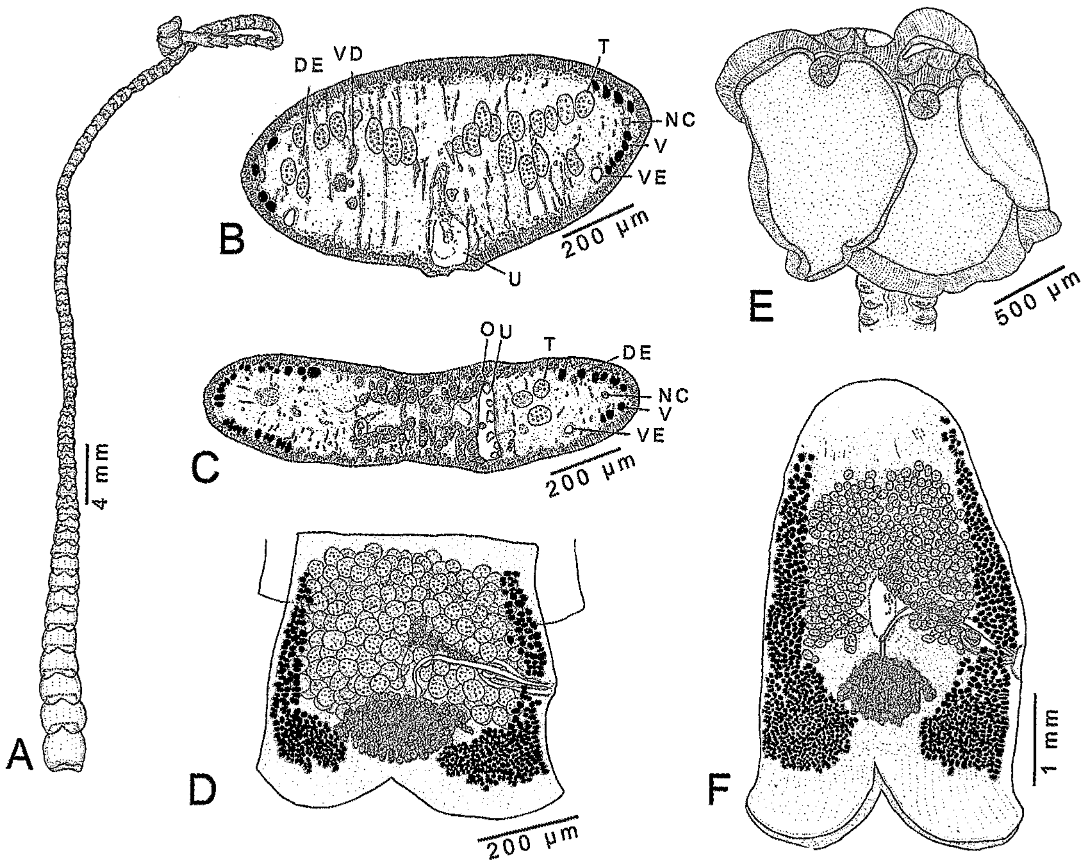

Fig. 37. Line drawings of *Crossobothrium laciniatum* Linton, 1889. A. Scolex of voucher (USNPC 86806). B. Cross section of free proglottid at level of testes of voucher (HWML 39126). C. Cross section of free segment at ovary of voucher (HWML 39126). D. Mature proglottid of voucher (USNPC 86807). E. Scolex of voucher (USNPC 86807). F. Mature free proglottid of voucher (HWML 39127). (Taken from Ruhnke [1996a], copyright 1996. Used with permission.)

stalked, each with single loculus and round apical sucker; apical sucker 155–230 (196 ± 18; n=12; *n*=30) in diameter. Proximal surfaces of bothridia covered with aristate gladiate spinitriches. Distal locular surfaces covered with filitriches and lingulate spinitriches. Surfaces inside apical suckers covered with filitriches and papillar projections; papillar projections covered with filitriches, with single central cilium. Neck absent. Surface of anterior strobila covered with filitriches.

Proglottids with dorsal and ventral pair of laciniations, and dorsal and ventral pair of excretory ducts and lateral pair of nerve chords. Mature proglottids 1.2–2.7 mm (1.9 ± 0.5; n=7; *n*=13) long x 1.5–2.6 mm (2 ± 1.4; n=7; *n*=13) wide, length to width ratio 0.8–1.2:1 (0.9 ± 0.1; n=7; *n*=13) longitudinal muscle fibers situated and the boundary of the cortex and medulla. Free proglottids 1.9–6 mm (3.7 ± 1.4; n=14) long x 1.3–3.5 mm (2.2 ± 0.8; n=14) wide, length to width ratio 1.4–1.8:1 (1.6 ± 0.1; n=14). Mature attached and free proglottids with 126–282 (186 ± 46; n=16; *n*=20) testes when viewed dorsally or ventrally in whole mount, generally preovarian, intervitelline, interrupted by cirrus-sac, 49–175 (103 ± 46; n=16; *n*=60) long x 58–170 (102 ± 31; n=20; *n*=60) wide, medullary, 2–3 irregular rows deep in cross section. Cirrus-sac in mature attached proglottids oval, 358–534 (451 ± 67; n=7; *n*=11) long x 16–197 (149 ± 67; n=7; *n*=11) wide, length to width ratio 0.2–0.28:1 (0.23 ± 0.03; n=6; *n*=10); cirrus-sac in mature free proglottids 385–774 (632 ± 130; n=8) long x 122–267 (212 ± 51; n=8) wide, length to width ratio 0.2–0.3:1 (0.26 ± 0.04; n=8), containing coiled cirrus, cirrus armed with spinitriches. Internal seminal vesicle present. Vas deferens coiled, bordering proximal portion of cirrus-sac, extending at angle anteriorly to middle of proglottid in mature proglottids. Genital pores lateral, 36–54% (45 ± 5; n=8; *n*=14) of proglottid length from posterior end of proglottid in mature attached proglottids, 29–40% (33 ± 3.5; n=14) of proglottid length from posterior end of proglottid in free proglottids; genital pores irregularly alternating. Genital atrium shallow. Vagina median, extending anteriorly from ovary to midlevel of proglottid, then laterally along anterior margin of cirrus-sac, or at level of cirrus-sac, to genital atrium. Ovary near posterior end of proglottid, in single median mass, digitiform, 260–780 (513 ± 169; n=20; *n*=21) long x 510–1,250 (782 ± 251; n=21; *n*=21) wide, tetralobed in cross section. Ovicapt 55–77 (66 ± 7; n=12) in diameter in mature proglottids, entirely obscured by ovarian field. Oviduct ventral to ovicapt, looping anterior to seminal receptacle, forming fertilization duct. Vitellarium follicular; follicles generally round, 25–112 (55 ± 26; n=19; *n*=58) in diameter, in two lateral bands; each band with 2–4 dorsal follicles and 2–5 ventral follicles anterior to ovary, vitelline field extended toward midline at level of ovary, slightly reduced at cirrus-sac. Uterus ventral to vagina, extending from ootype region to proximal extremity of vas deferens in mature and free proglottids. Uterine duct not observed. Eggs round, 20–37 (27 ± 5; n=9; *n*=23) in diameter, found in attached and free proglottids.

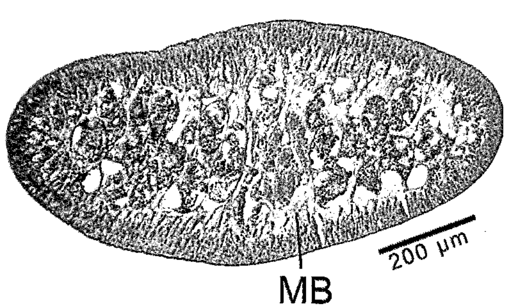

Fig. 38. Photomicrograph of *Crossobothrium laciniatum* Linton, 1889. Cross section of proglottid at level of testes above cirrus-sac (LRP 7408).

Remarks

Ruhnke (1996b) emended Linton's (1889) original description of this species, and a modified version of Ruhnke's emended description is provided above. Linton (1889) made no mention of the type specimens of *C. laciniatum*, and the location of these specimens is unknown. The worms described here are fully consistent with the original description and drawings of this species by Linton (1889), although his description dealt with

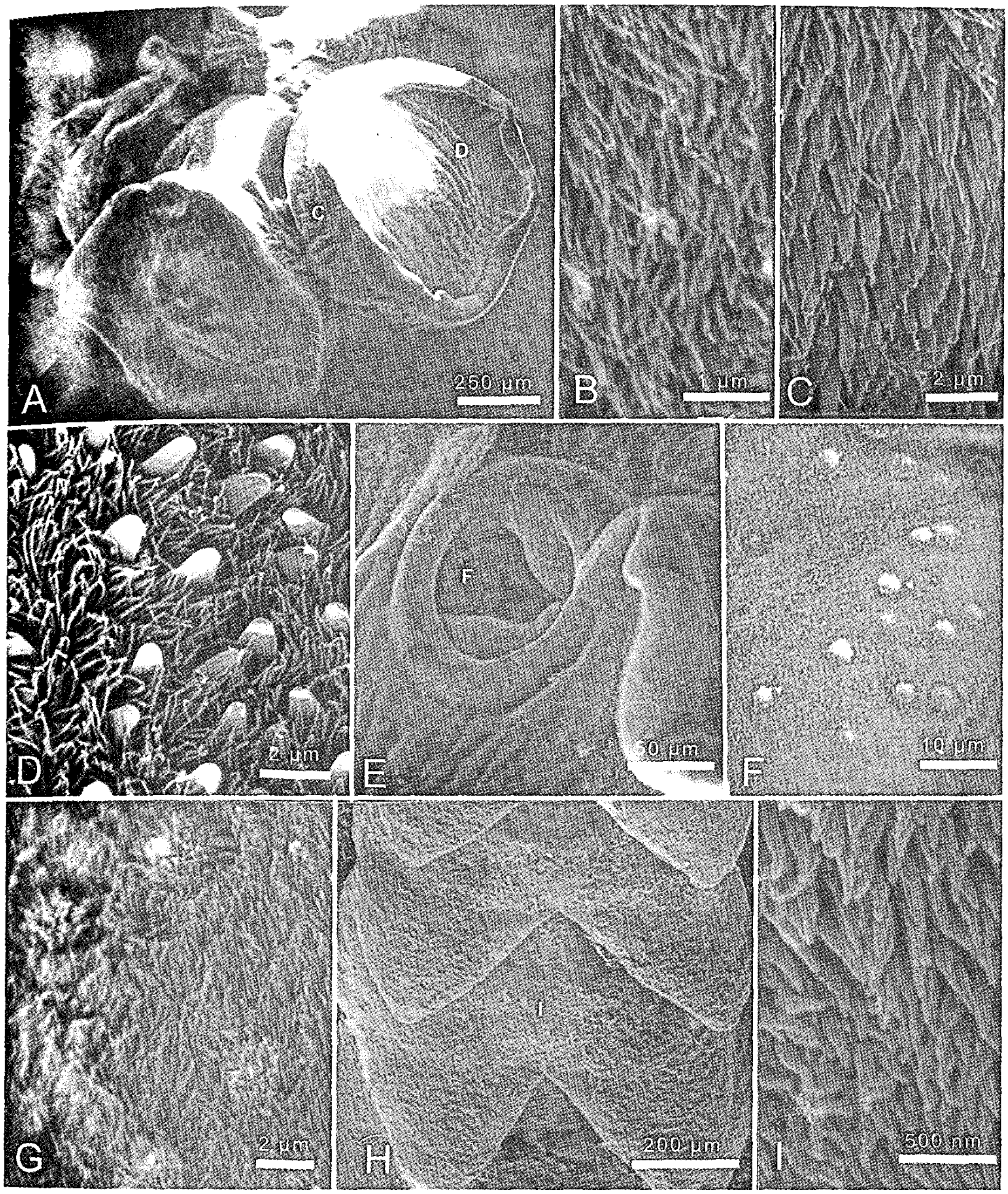

Fig. 39. Scanning electron micrographs of *Crossobothrium laciniatum* Linton, 1889. A. Scolex (letter indicate regions of scolex in enlarged photos B-D). B. Scolex apex. C. Proximal surface of bothridium. D. Distal surface of bothridium. E. Apical sucker (letter indicates region enlarged in photo F). F. Surface of apical suker. G. Enlarged view of apical sucker surface. H. Anterior region of strobila (letter indicates region enlarged in photo I). I. Surface of anterior strobila. (Taken from Ruhnke [1996a], copyright 1996. Used with permission.).

more general aspects of morphology. The specimens studied here were collected from the same host species from a locality that is relatively near the type locality (northwestern Atlantic Ocean; Woods Hole, Massachusetts vs. North Carolina coast).

Southwell (1925) considered the species synonymous with *Phyllobothrium dohrni* and transferred *C. laciniatum* to *Phyllobothrium*. This taxonomic decision was followed by Yamaguti (1952), questioned by Williams (1968a), but accepted by Schmidt (1986). Most recently, Euzet (1994) in a key to cestodes, listed *Crossobothrium* as a valid genus, but gave *C. angustum* (Linton, 1889) (= *Orygmatobothrium angustum* Linton, 1889) as the type species. This was simply a nomenclatural error, and *C. angustum* is transferred to *Paraorygmatobothrium* Ruhnke, 1994 in this monograph.

Crossobothrium laciniatum differs from *C. campanulatum* in that the margins of its bothridia lack loculi rather than bear marginal loculi, and also in testes shape (round vs. oblong), and genital pore position from posterior end of proglottid in free proglottids (29–40% vs. 40–57%).

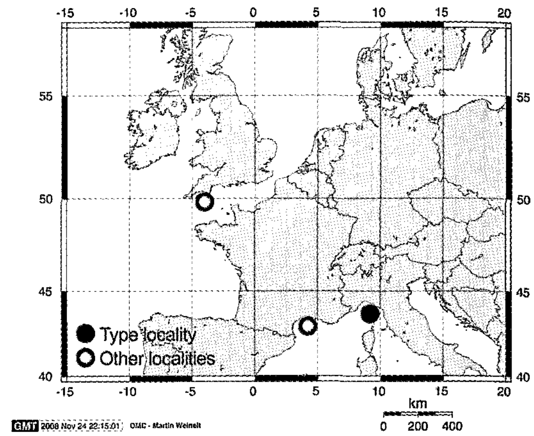

Fig. 40. Geographic distribution of *Crossobothrium campanulatum* Klaptocz, 1906.

Crossobothrium campanulatum Klaptocz, 1906

(Figs. 40–41)

Taxonomic status: Valid.

Type Host: *Notidanus griseus* (= *Hexanchus griseus* [Bonnaterre, 1788]), the Bluntnose sixgill shark.

Site of Infection: Spiral intestine.

Type locality: Barcola, Gulf of Triest, Italy (Fig. 40).

Additional localities: Corcarneau, Sète, France; Porcupine Bay, U.K. (Fig. 40).

Type material: Not specified.

Voucher specimens: MNHN HEL 135–137; BNHM 1976.4.12.92–93.

Specimens examined: MNHN HEL 135–137; BNHM 1976.4.12.92–93.

Etymology: Not given.

Description (modified from Euzet [1959] and Ruhnke [1996]).

Worms acraspedote, apolytic, 150–200 mm long, maximum width 3-5 mm. Proglottids 350–400 in number; proglottids with dorsal and ventral pair of laciniations. Scolex tetratothridiate; bothridia slightly stalked. Margins of bothridia with incomplete loculi and an apical sucker; apical sucker 130–150 in diameter.

Mature proglottids 2–2.8 mm long x 3.5–4.3 mm wide. Free proglottids 3.9–4.4 mm (4 ± 0.2; n=7) long x 2.9–3.5 (3.3 ± 0.2; n=7) wide. Testes 180–230 in number; testes oblong, 83–140 (112 ± 15; n=6; *n*=24) long x 58–170 (81 ± 10; n=7; *n*=24) wide. Cirrus-sac elongate oval, 500–1000 long x 150–300 wide. Enlarged sperm duct present inside cirrus-sac. Genital pores lateral, 40–57% (48 ± 0.1; n=7) of proglottid length from posterior end of proglottid. Ovary near posterior end of proglottid, H-shaped in frontal view, 525–725 (618 ± 62; n=7) long x 1,200–1,500 (1,400 ± 110; n=7) wide. Ovicapt 75–85 (80 ± 4; n=5) in diameter in free proglottids. Vitellarium follicular; vitelline follicles in two lateral fields, follicles 70–105 (86 ± 10; n=7; *n*=34) long x 38–70 (50 ± 8; n=7; *n*=34) wide, vitelline field expanded medially at level at and posterior to ovary, vitelline field reduced at cirrus-sac.

Remarks

Crossobothrium campanulatum was originally described by Klaptocz (1906) for specimens collected from *H. griseus*. Southwell (1925) considered this species to be a synonym of *P. dohrni* and also considered *C. laciniatum* and *Orygmatobothrium velamentum* Yoshida, 1917 to be synonyms of *P. dohrni*. *Phyllobothrium dohrni* was described as *Orygmatobothrium dohrni,* and originally collected from *Heptanchus cinereus* (= *Heptranchias perlo* [Bonnaterre, 1788]). The tax-

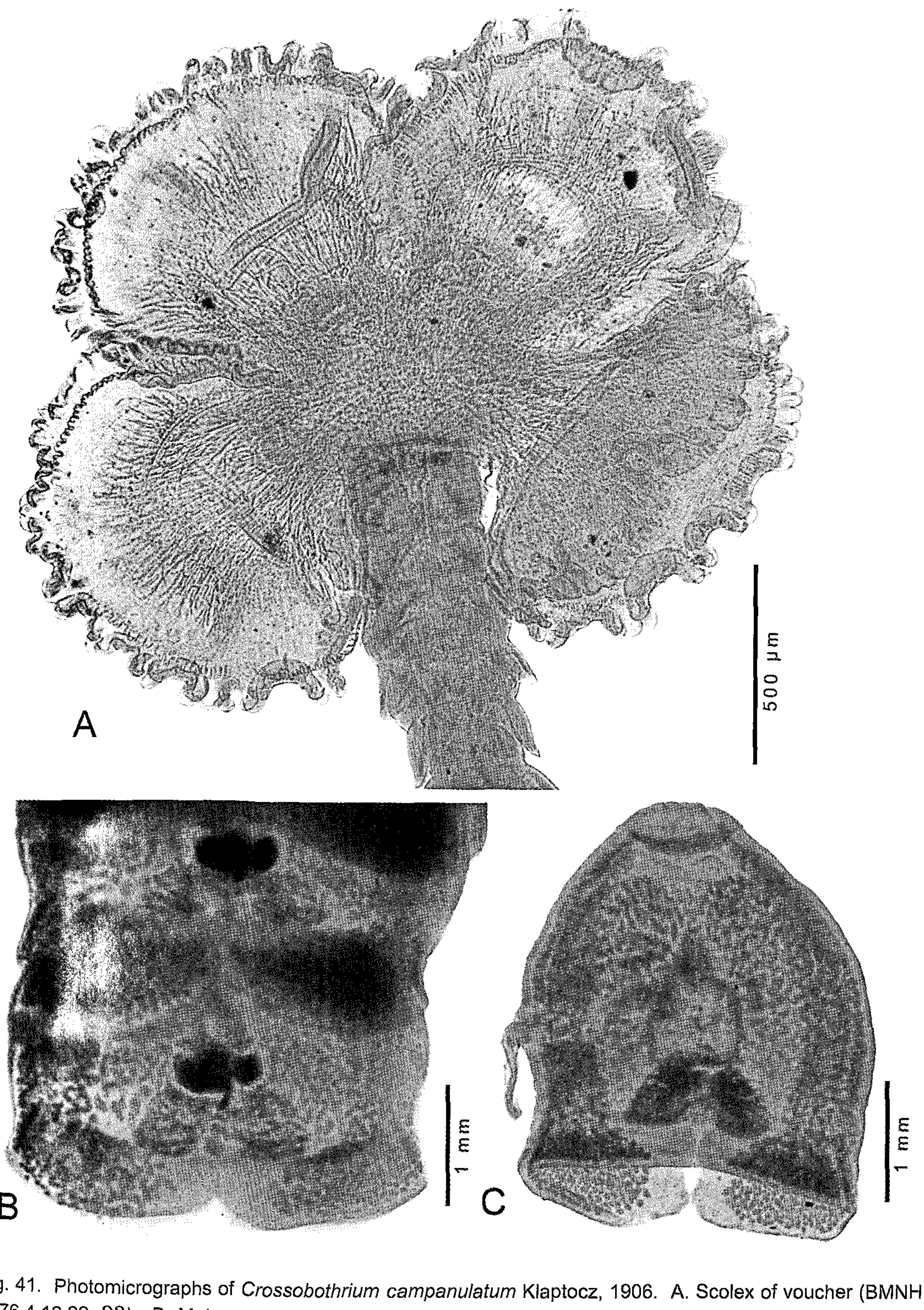

Fig. 41. Photomicrographs of *Crossobothrium campanulatum* Klaptocz, 1906. A. Scolex of voucher (BMNH 1976.4.12.92–93). B. Mature proglottid of voucher (MNHN Paris HEL 136). C. Free proglottid of voucher (MNHN Paris HEL 135).

onomic scheme of Southwell (1925) was followed by both Rees (1946) and Euzet (1959); Williams (1968a) accepted these synonyms as "probable". In his treatment of *Crossobothrium,* Ruhnke (1996b) mistakenly overlooked *C. campanulatum,* basing his description of *Crossobothrium dohrni* on observations from light and electron microscopy of specimens from *Hexanchus griseus* and also material taken from *Hexanchus* sp.

The primary argument for recognizing *C. campanulatum* as a species distinct from *C. dohrni* at this time is that neither species is well known, and their type hosts differ. Thus far, critical morphological comparisons do not exist for worms from these two hexanchid species and until such comparisons can be made, both species should be considered valid.

Crossobothrium campanulatum differs from *C. laciniatum* its possession of incomplete marginal loculi rather than lacking marginal loculi, testes shape (oblong vs. round), and in possession of genital pores in free proglottids that are more anterior in position from the posterior margin of the proglottid (40–57% vs. 29–40%). A comprehensive description of this species, including quantitative morphological information from a larger number of specimens, is still needed.

Crossobothrium dohrni (Oerley, 1885) Ruhnke, 1996
(Figs. 42–43)

Synonyms: *Orygmatobothrium dohrni* Oerley, 1885; *Phyllobothrium dohrni* (Oerley, 1885) Zschokke, 1888.
Taxonomic status: Valid.
Type host: *Heptanchus cinereus* (= *Heptranchias perlo* [Bonnaterre, 1788]), the Sharpnose sevengill shark.
Site of infection: Spiral intestine.
Type locality: Zoological Station of Naples, Italy (Fig. 42).
Type material: Not specified.
Etymology: The species was named for Professor A. Dohrn, Director of the Zoological Station of Naples at the time the species was collected.

Remarks

Crossobothrium dohrni was described briefly by Oerley (1885). Even though the original description suffers from its brevity, the figures and text indicate the species possesses the key characteristics of *Crossobothrium.* The proglottids are laciniate. The illustration of the scolex seems to indicate the presence of apical suckers. The species was redescribed in detail by Zschokke (1888) when he transferred it to *Phyllobothrium,* but he listed hosts as *Heptanchus griseus* (= *Hexanchus griseus*), *Scymnus licha* (= *Dalatias licha*) and *Mustelus vulgaris* (= *Mustelus mustelus*). Joyeux and Baer (1936) provided a description of what they identified as *P. dohrni.* They described the specimens as being 80–100 mm in length, having a scolex 0.8–1 mm long, and proglottids with 150–200 testes. In addition to *Heptranchias perlo,* they listed *Hexanchus griseus, Mustelus hinnulus* (= *Mustelus asterias*) and *Scymnus lichia* (= *Dalatias licha*) as hosts. A more useful description of *C. dohrni* will require acquisition of specimens from the type host, *H. perlo.*

As noted in the remarks addressing *Crossobothrium campanulatum,* the taxonomic scheme initated by Southwell (1925), synonymizing three species with *P. dohrni,* broad-

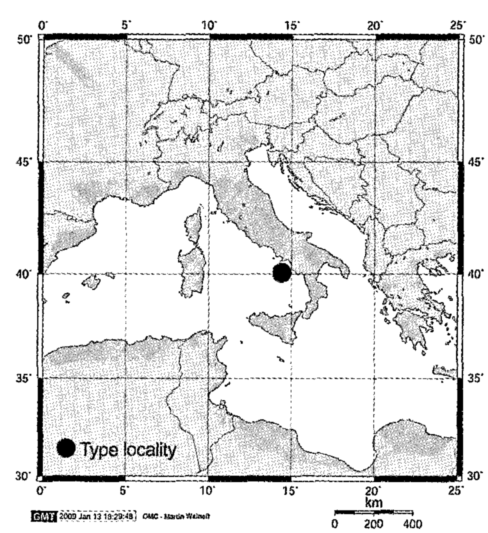

Fig. 42. Geographic distribution of *Crossobothrium dohrni* (Oerley, 1885) Ruhnke, 1996.

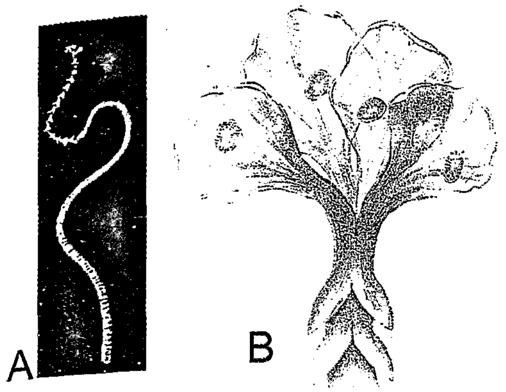

Fig. 43. Photomicrograph and line drawing of *Crossobothrium dohrni* (Oerley, 1885) Ruhnke, 1996. A. Entire specimen. B. Scolex. No scale bars available. (Taken from Oerley [1885].)

ened the application of the name "*P. dohrni*" to include specimens from *Notaidanus griseus* (= *H. griseus*) and *Heptanchus cinereus* (= *Heptranchias perlo*). Subsequent authors (*e.g.*, Rees 1946; Euzet 1959; Williams 1968a; Ruhnke 1996b) referred cestodes taken from *Hexanchus griseus* to either *P. dohrni* or *C. dohrni*, depending on opinion as to the generic placement of the species. Until the conspecificity of cestodes from *Heptranchias perlo* and *Hexanchus griseus,* and perhaps other hexanchid sharks can be assessed, *C. campanulatum* and *C. dohrni* should be considered valid.

Recently described species of *Crossobothrium*

Crossobothrium antonioi **Ivanov, 2009**

Crossobothrium antonioi was decribed by Ivanov (2009) for specimens taken from the Broadnose sevengill shark, *Notorynchus cepedianus* (Péron, 1807), collected from Puerto Quequén, Buenos Aires Province, Argentina. *Crossobothrium antonioi* exhibits more than 700 testes per proglottid, whereas *C. laciniatum* and *C. campanulatum* have been described as having up to 282 and 230 testes per proglottid, respectively. *Crossobothrium antonioi* also differs from the other species is various aspects of size (see Ivanov 2009).

Crossobothrium pequeae **Ivanov, 2009**

Crossobothrium pequeae was decribed by Ivanov (2009) for specimens taken from the Broadnose sevengill shark, *Notorynchus cepedianus,* also collected from Puerto Quequén, Buenos Aires Province, Argentina. *Crossobothrium pequeae* is shorter than *C. campanulatum* (63–138 mm vs. 150–200 mm). *Crossobothrium pequeae* differs from *C. laciniatum* in scolex width (1,150–1,750 vs. 2,175–3,050), and in spinithrix morphology on the proximal bothridial surfaces (conical vs. aristate) and distal bothridial surfaces (slender conical vs. wide large blade-like).

Other species placed in *Crossobothrium*

Six species have been placed in *Crossobothrium* in addition to the three valid species treated in the above section. Four of these species have already been transferred to *Paraorygmatobothrium* or are transferred to *Paraorygmatobothrium* in this monograph. One species is considered *incertae sedis* within *Phyllobothrium*. The remaining species are discussed below.

Crossobothrium longicolle **(Molin, 1858) Euzet, 1959 (synonym of *Tetrabothrium [Eutetrabothrium] longicolle*)** (Fig. 44)

This species was originally described by Molin (1858) as *Tetrabothrium* (*Eutetrabothrium*) *longicolle* Molin, 1858, from specimens collected from *Scyllium stellare* (Bonaparte) (= *Scyliorhinus stellaris* [L., 1758]), the Nursehound. The description is very brief. Molin (1858) gave the type locality as "Longit. 0.015–0.175; Lat. 0.001–0.003". No figures accompanied Molin's description. Southwell (1925) transferred this species to *Phyllobothrium.* Euzet (1959) provided a redescription of *C. longicolle* from specimens taken from *S. stellaris,* collected from Sète, France. These specimens have now been deposited in the MNHN (HEL 138). According to Euzet (1959), his specimens were 150–300 mm in length. The bothridia are uniloculate, and each possess a round apical sucker. Initial mature proglottids are as wide as long, and terminal

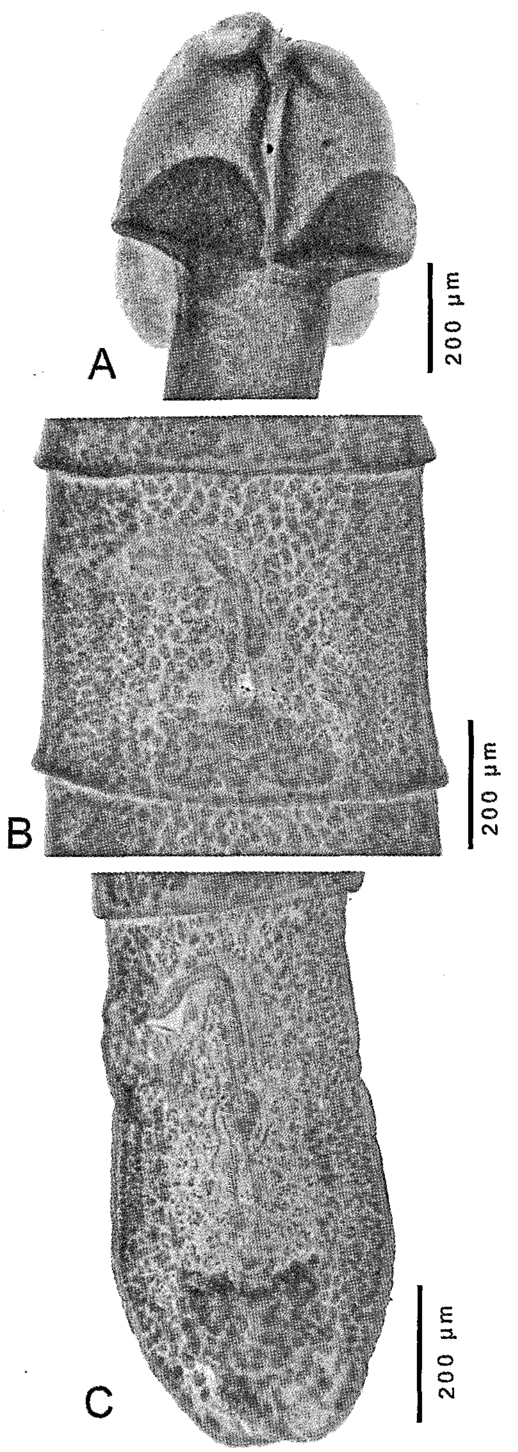

Fig. 44. Photomicrographs of *Crossobothrium longicolle* (Molin, 1858) Euzet, 1959 incertae sedis. A. Scolex of voucher (MNHN Paris HEL 138). B. Mature proglottid of voucher (MNHN Paris HEL 138. C. Terminal proglottid of voucher (MNHN Paris HEL 138).

proglottids at least twice as long as wide. Examination of the specimens of Euzet (1959) reveals them to lack proglottid laciniations of *Crossobothrium*. Furthermore, this species lacks the foliose, posteriorly bifid bothridia of *Phyllobothrium*. In a number of respects, this species resembles *P. squali*, however, appropriate generic placement must await the collection and study of additional material. Scanning electron microscopy of this species would be particularly rewarding. Euzet's (1959) listing of *Monorygma perfectum* (Van Beneden, 1853) Zschokke, 1888 and *M. elegans* Monticelli, 1890 as synonyms of *C. longicolle* is not followed here. *Monorygma perfectum* is accepted as the valid type species of *Monorygma*.

Olson et al. (2001) sequenced complete 18S rDNA and partial (D1–D3) 28S rDNA (Genbank records AF286997 and AF286958, respectively) of what they identified as *C. longicolle*, taken from hosts identified as *Scyliorhinus canicula* (L., 1758), the Small-spotted catshark. It is curious that sequences of their specimens of *C. longicolle* are identical to those for a specimen identified as *Phyllobothrium squali* collected from *S. acanthias* (Ruhnke unpubl.). This indicates a potential host and/or cestode identification problem with respect to the work of Olson et al. (2001). Until comparable sequence of *C. longicolle* is available from specimens taken from individuals verified as the type host, the records AF286997 and AF286958 should not be considered as belonging to *C. longicolle*. *Crossobothrium longicolle* should be considered a synonym of *Tetrabothrium* (*Eutetrabothrium*) *longicolle*, and *T. longicolle* is at present *incertae sedis*. Type material: unknown. Material examined: MNHM Paris HEL 138.

MARSUPIOBOTHRIUM Yamaguti, 1952

Taxonomic status: Valid.

Type species: *Marsupiobothrium alopias* Yamaguti, 1952.

Other species: None.

Etymology: No etymology was given by Yamaguti (1952), but presumably, *Marsupio* (Gr.) = pouch; *bothrios* (Gr.) = pit.

Diagnosis (modified from Ivanov [2006]).

Phyllobothriidae. Worms euapolytic. Scolex with four sessile saclike bothridia, myzorhynchus absent. Each bothridium with conspicuously muscular periphery, muscular perimeter, anterior and posterior muscular pad, and apical sucker. Bothridial aperture oblique to longitudinal axis of scolex; muscular sphincter consists of two muscular pads, one anterior and one posterior; accessory sucker-like structure on distal bothridial surface. Strobila scutellate. Testes numerous, evenly distributed in preovarian field in mature proglottids; postvaginal testes present. Cirrus-sac oval, curved slightly anteriorly; cirrus armed with spinitriches. Genital pores lateral, in anterior third of proglottid. Ovary lobulated, H-shaped in frontal view. Vagina opening anterior to cirrus-sac, vaginal sphincter present. Vitellarium follicular, follicles lateral, extending full length of proglottid, interrupted by cirrus-sac and vagina. Uterus ventral, extending anteriorly to level of cirrus-sac. Parasites of Alopiidae.

Remarks

Yamaguti (1952) originally erected *Marsupiobothrium* for *M. alopias,* specimens of which were collected from *Alopias vulpinus* (Bonnaterre, 1788). In his remarks on the species, Yamaguti (1952) transferred *Orygmatobothrium forte* Linton, 1924 to the genus. Ivanov (2006), in what must be considered the most comprehensive account of the genus to date, redescribed its type species, *M. alopias,* and emended the generic diagnosis. Interestingly, she discovered what appears to be an accessory sucker-like structure (referred to by her as a sucker) on the distal surface of each bothridium. The presence of this accessory structure was verified in this treatment. The combination of the distinct bothridial muscle morphology in combination with the presence of the secondary accessory stucture distinguish *Marsupiobothrium* from other phyllobothriid genera.

Marsupiobothrium alopias Yamaguti, 1952

TYPE SPECIES

(Figs. 45–47)

Taxonomic status: Valid.
Type host: *Alopias vulpinus* (Bonnaterre, 1788), Thin-tail thresher shark.
Site of infection: Spiral intestine.
Type locality: Pacific Ocean, Japan (Fig. 45).
Type material: MPM 22698 (Fig. 46A).
Material examined: MPM 22698 (Fig. 46A).
Etymology: This species was named for the genus of its type host.

Description (modified from Ivanov [2006]).

Worms craspedote, euapolytic, 25.4–26.2 mm long; greatest width at level of mature proglottids; 73–91 per worm. Scolex composed of four bothridia, lacking apical organ (Fig. 47A), 375 x 550–660. Bothridia pyriform, saclike, conspicuously muscular, 305–345 (326 ± 22) long x 225–265 (245 ± 17) wide, attached to scolex proper, with muscular sphincter. Bothridia with anterior accessory sucker and sucker-like structure on distal bothridial surfaces. Bothridial aperture oblique to scolex axis. Sphincter encircling bothridial aperture formed by anterior and

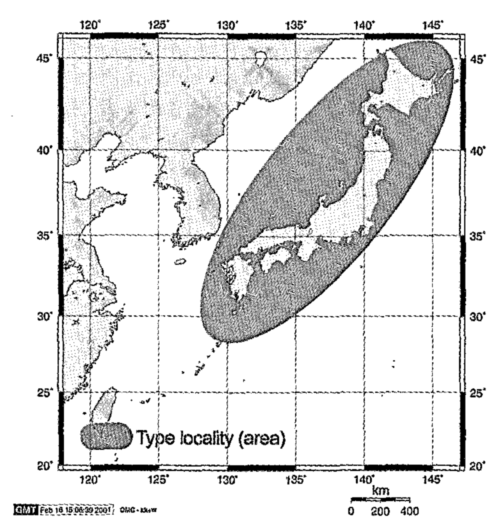

Fig. 45. Geographic distribution of *Marsupiobothrium alopias* Yamaguti, 1952.

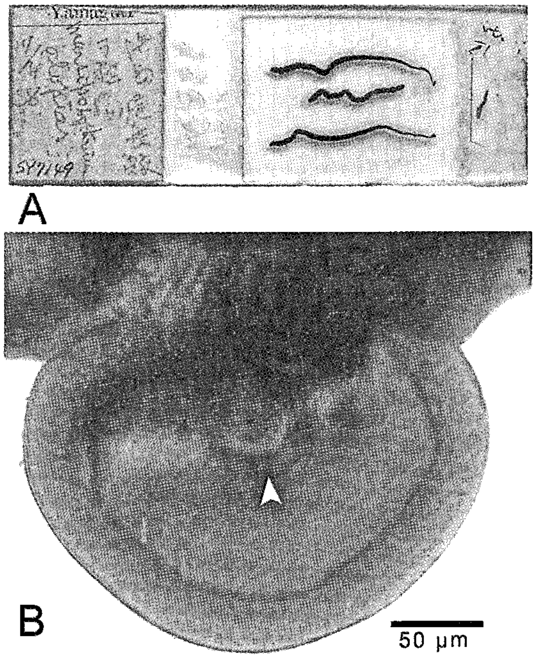

Fig. 46. Photomicrographs of *Marsupiobothrium alopias* Yamaguti, 1952. A. Syntype slide (MPM 22698). B. Bothridium of syntype (MPM 22698), arrow indicates accessory sucker inside bothridia.

posterior bands of musculature, a few muscular fibers form continuous sphincter externally to muscular pads; muscular pads 40–50 thick. Accessory suckers on bothridial distal surface (inside pouch); anterior sucker underneath anterior muscular pad, 50–67 (59 ± 5) in diameter; sucker-like structure at level of mid-bothridium, 50–68 (62 ± 5) in diameter (Fig. 46B). Bothridial musculature 25–32 (30 ± 3) thick. Neck 6.7–7.8 mm long. Surface of neck and entire strobila scutellate.

Immature proglottids wider than long. Mature proglottids as wide as long. Terminal proglottids longer than wide, 470–880 (666 ± 173) long x 810–1,060 (924 ± 103) wide, length-to-width ratio 0.56–0.86:1 (0.71:1); terminal proglottids 1,000–1,300 x 600–750, length-to-width ratio 1.66–1.73:1; 4–6 mature proglottids per strobila. Testes oval, 43–75 (60 ± 11) long x 32–65 (49 ± 9) wide; one row deep; 155–187 (172 ± 13) in number in mature proglottids, 34–47 (41) postvaginal testes, extending anteriorly from anterior margin of ovary to anterior margin of proglottid. Cirrus-sac oval, slightly curved anteriorly in mature proglottids, 250–375 (335 ± 39) long x 75–150 (107± 24) wide, occupying 39–79% (58) of proglottid width; containing cirrus covered with short spinitriches; surrounded by numerous gland cells inside cirrus-sac. Vas deferens coiled, extending anteriorly from anterior margin of cirrus-sac. Genital atrium present; genital pores marginal, unilateral, 59–73% (65 ± 4) from posterior margin of proglottid. Vagina thick-walled, anterior to cirrus-sac, with muscular sphincter, running anteriorly to bulk of vas deferens, descending posteriorly, reaching ootype region posterior to ovarian isthmus. Ovary lobulated, H-shaped in frontal view, 125–250 (178 ± 56) long x 237–675 (487 ± 159) wide at ovarian isthmus. Mehlis gland conspicuous, posterior to ovarian isthmus. Vitellarium follicular, vitelline follicles in two lateral fields, each field consists of 2–3 dorsal and 2–3 ventral columns of follicles, 18–30 (25 ± 4) long x 13– 20 (16 ± 2) wide, extending entire length of proglottid, interrupted at level of cirrus-sac and vagina. Uterus extending anteriorly along median line of proglottid from ovarian isthmus to anterior margin of cirrus-sac.

Remarks

Marsupiobothrium alopias was orginally described by Yamaguti (1952) from *A. vulpinus.* An excellent redescription of *M. alopias* was provided by Ivanov (2006), which has been modified somewhat in this account. At present, *M. alopias* is considered to be the only valid species. The status of other species that have been referred to the genus over time is detailed below.

Other species of *Marsupiobothrium*

Seven species have been identified as having been allocated to *Marsupiobothrium,* in addition to *M. alopias* (see Appendix 2). One of these species is considered *incertae sedis* within *Orygmatobothrium.* None of the remaining six can be considered valid species of the genus. Information on these species and their present status is provided.

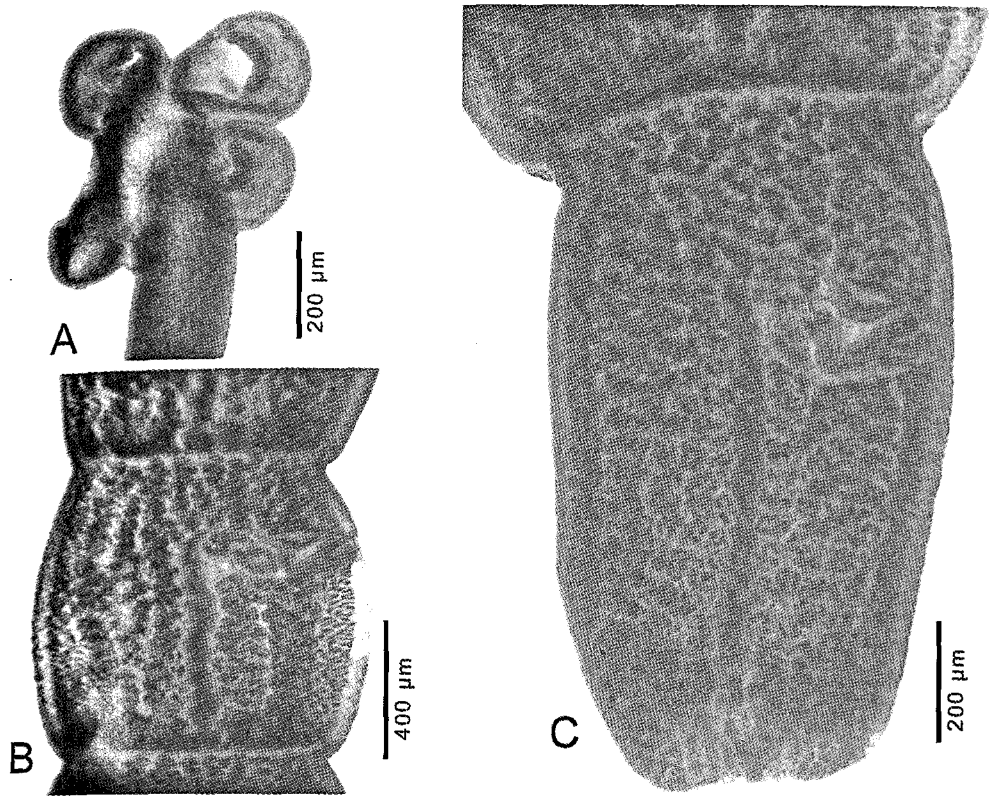

Fig. 47. Photomicrographs of *Marsupiobothrium alopias* Yamaguti, 1952. A. Scolex of syntype (MPM 22698). B. Proglottid of syntype (MPM 22698). C. Terminal proglottid of syntype (MPM 22698).

Marsupiobothrium antarcticum Wojciechowska, 1991 (synonym of _Guidus antarcticus_ [Wojciechowska, 1991] Ivanov, 2006)

Marsupiobothrium antarcticum was described by Wojciechowska (1991b) for worms from McCain's skate, *Bathyraja maccaini* Springer, 1971, collected near Joinville Island, Antarctica. Ivanov (2006) transferred this species to *Guidus* Ivanov, 2006, making the combination *Guidus antarcticus* (Wojciechowska, 1991) Ivanov, 2006. Type material: Holotype, No. 904, paratypes, Nos. 905 a and b at the Institute of Parasitology, Polish Academy of Sciences; paratypes, BMNH 1992.1.6.31. Material examine: none.

Marsupiobothrium awii Rocka and Zdzitowiecki, 1998 (synonym of _Guidus awii_ [Rocka and Zdzitowiecki, 1998] Ivanov, 2006)

Marsupiobothrium awii was described by Rocka and Zdzitowiecki (1998) for specimens from McCain's skate, *Bathyraja maccaini* Springer, 1971, collected from the Weddell Sea. Ivanov (2006) transferred the species to *Guidus,* making the combination *Guidus awii* (Rocka and Zdzitowiecki, 1998) Ivanov, 2006. Type material: Holotype, MZPW 1818; paratype BMNH 1997.11.3.1. Material examine: none.

Marsupiobothrium gobelinus Caira and Runkle, 1993 _incertae sedis_

Marsupiobothrium gobelinus was described for specimens from *Mitsukurina owstoni* Jordan, 1898, the Goblin shark, collected east southeast of Ulladulla, New South Wales, Australia. Caira and Runkle (1993), in their description of *M. gobelinus,* noted that placing the species into a genus was problematic, and correctly pointed out the fact that many phyllobothriid genera were characterized by absence of features, as opposed to exhibition of unique features. They placed *M. gobelinus* in *Marsupiobothrium* because such placement would require no change to the generic diagnosis. Indeed, they commented, "We are not tremendously confident in this placement of the species, but at present this would appear to be the most sensible course of action" (Caira and Runkle 1993, p. 86). The species is valid, but should be considered *incertae sedis*. Type material: holotype, QM GL18272, paratypes QM GL18273–18286, USNPC 82574 and HWML 35514. Material examined: none.

Marsupiobothrium karbharii **Deshmukh and Shinde, 1975 *incertae sedis***

Deshmukh and Shinde (1975) described *Marsupiobothrium karbharii* for worms from *Rhynchobatus djeddensis* (Forsskål, 1775), the Giant guitarfish, collected near Veraval, on the west coast of India. They described the bothridia of the species as oval, with slit-like openings, possessing apical suckers. The genital pores are approximately 50% from the posterior end of the proglottid. The descriptions and illustrations of *M. karbharii, M. rhinobati,* and *M. rhynchobati* indicate similarity in the morphology of the bothridia and proglottids. These three species may be synonymous or closely related. However, the quality of the description and illustrations of this species does not allow for such a conclusion to be drawn at this time. The species is valid, but until type specimens or new material can be studied, *M. karbharii* should be considered *incertae sedis*. Type material: not specified. Material examined: none.

Marsupiobothrium rhinobati **Shinde and Deshmukh, 1980 *incertae sedis***

Shinde and Deshmukh (1980) described *Marsupiobothrium rhinobati* for worms from *Rhinobatus granulatus* (= *Glaucostegus granulatus* [Cuvier, 1829]), the Sharpnose guitarfish, collected near Veraval, on the west coast of India. As with *M. karbharii,* they described the bothridia of the species as oval, with slit-like openings, and possessing apical suckers. As with *M. karbharii,* and *M. rhynchobati,* the description and illustration of the scolex are not sufficient to understand this bothridial morphology. The genital pores are approximately 50% from the posterior end of the proglottid. The descriptions and illustrations of *M. rhinobati, M. karbharii,* and *M. rhynchobati* indicate similarity in the morphology of the bothridia and proglottids. These three species may be synonymous or closely related. However, the quality of the illustrations does not allow for such a conclusion to be drawn at this time. The species is valid, but until type specimens or new material can be studied, *M. rhinobati* should be considered *incertae sedis*. Type material: not specified. Material examined: none.

Marsupiobothrium rhynchobati **Shinde and Deshmukh, 1980 *incertae sedis***

This species was described for specimens taken from *Rhynchobatus djeddensis* (Forsskål, 1775), the Giant guitarfish, collected near Veraval, west coast of India. Shinde and Deshmukh (1980) described the bothridia of the species as oval, with slit-like openings, and possessing apical suckers. The description and illustration of the scolex are not sufficient to understand this bothridal morphology. The genital pores are approximately 50% from the posterior end of the proglottid. The descriptions and illustrations of *M. rhynchobati, M. karbharii,* and *M. rhinobati* indicate similarity in the morphology of the bothridia and proglottids. These three species may be synonymous or closely related. The species is valid, but until type specimens or new material can be studied, *M. rhynchobati* should be considered *incertae sedis*. Type material: not specified. Material examined: none.

MONORYGMA Diesing, 1863

Taxonomic status: Valid.

Type species: *Monorygma perfectum* (Van Beneden, 1853) Diesing, 1863.

Other species: *Monorygma macquariae* Johnston, 1937; *M. magnum* (Hart, 1936) Williams, 1968.

Etymology: An etymology was not given, but presumably, *Mono* (Gr.) = one, *orygma* (Gr.) = pit.

Diagnosis (modified from Euzet [1994]).

Phyllobothriidae. Worms large, anapolytic worms, slightly acraspedote. Scolex with four bothridia and glandular apical organ, myzorhynchus absent. Bothridia biloculate, posterior loculus larger than anterior loculus. Anterior loculus with posterior lateral projections. Proglottids numerous, initially much wider than long, mature and gravid proglottids as long as wide to over twice as long as wide. Testes numerous, round, in two irregular dorso-ventral columns in cross-section, post-vaginal testes present. Cirrus-sac oval, much longer than wide. Cirrus armed with spinitriches. Vas deferens medial to cirrus-sac, extending to mid-line. Genital atrium present. Vagina opening anterior to cirrus-sac. Ovary posterior, lobate, tetralobed in cross-section. Vitellarium follicular, circum-medullary, field reduced dorsal and ventral to ovary and uterus. Uterus ventral, saccate, extending to posterior margin of cirrus-sac. Multiple proglottids gravid on strobila. Eggs fusiform. Parasites of Squaliformes.

Remarks

Monogrygma was erected by Diesing (1863) to house *Monorygma perfectum* (Van Beneden, 1853) Diesing, 1863, a species originally described as *Anthobothrium perfectum* Van Beneden, 1853. *Monorygma* differs from other phyllobothriid taxa treated in this monograph in that the bothridia of species can best be described as being biloculate, as opposed to uniloculate with an apical sucker. This interpretation comes from the fact the posterior margin of the anterior region of each bothridium is essentially straight, rather than curved. As a consequence, this region is not in the form of a round sucker, like those seen in many other genera.

Monorygma perfectum (Van Beneden, 1853) Diesing, 1863
TYPE SPECIES
(Figs. 48–51)

Synonyms: *Anthobothrium perfectum* Van Beneden, 1853; *Phyllobothrium perfectum* (Van Beneden, 1853) Southwell, 1925.
Taxonomic status: Valid.
Type host: *Somniosus microcephalus* (Bloch and Schneider, 1801), the Greenland shark.
Site of infection: Spiral intestine.
Type locality: Not specified.
Additional localities: Godhavn, Greenland; Umivik, Greenland, Storfjorden, Greenland (Fig. 48).
Type material: Unknown.
Additional material: Vouchers, BMNH 1979.1.15.39–43 (Fig. 49A); MNHN HEL 39–146.
Specimens examined: Vouchers, BMNH 1979.1.15.39–43 (Fig. 49A); MNHN HEL 139–146.
Etymology: Not specified.

Description

Worm anapolytic, slightly craspedote, 30 cm (n=1) in length, maximum width 5 mm (n=1) at gravid proglottids. Strobila with 403 proglottids (n=1). Scolex 0.9–5 mm (n=5) long by 1–5 mm (n=5) wide, with four bothridia. Bothridia biloculate; anterior loculus with lateral projections, 470–660 (n=2) long by 470–660 (n=2) wide, posterior loculus 1.2–1.5 mm (n=2) long by 1.2 mm (n=2) wide. Bothridial surfaces with aciculate spinitriches. Anterior strobila covered with aciculate spinitriches.

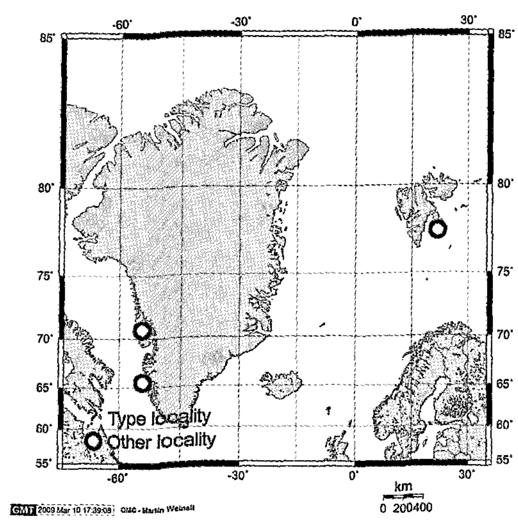

Fig. 48. Geographic distribution of *Monorygma perfectum* (Van Beneden, 1853) Diesing, 1863.

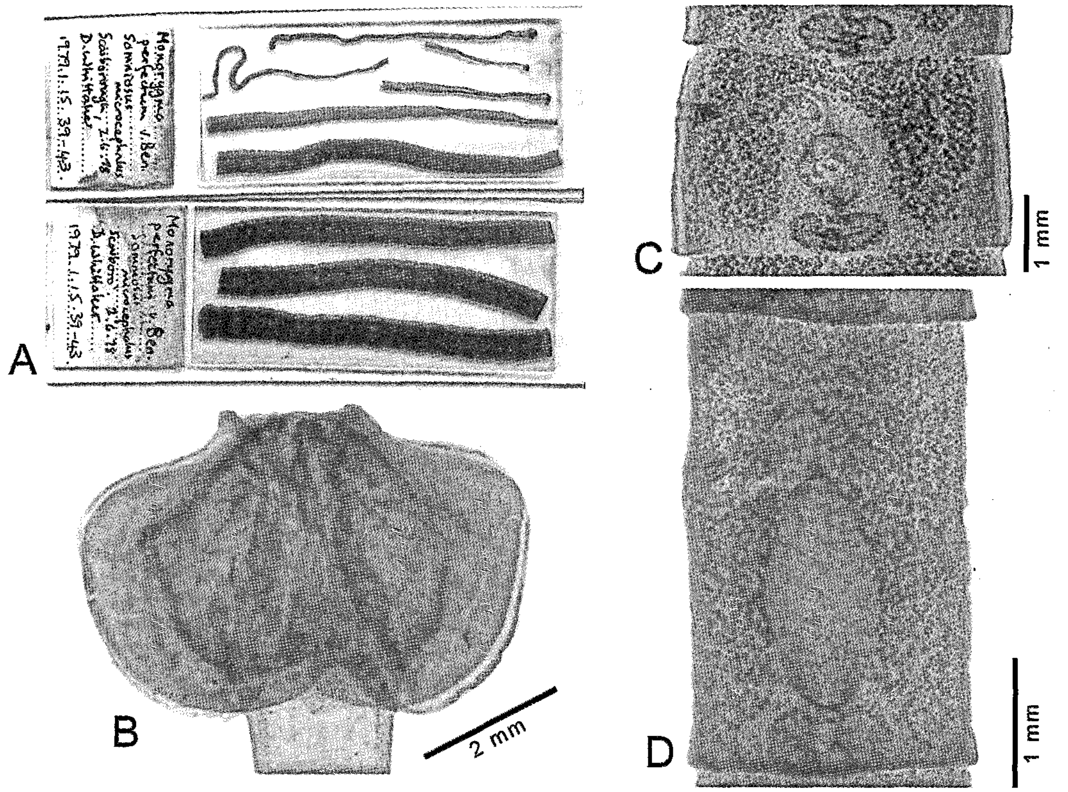

Fig. 49. Photomicrographs of *Monorygma perfectum* (Van Beneden, 1853) Diesing, 1863. A. Voucher slides (BMNH 1979.1.15.39-43). B. Scolex of voucher (MNHN Paris HEL 143). C. Mature proglottid of voucher (BMNH 1979.1.15.39-43). D. Gravid proglottid of voucher (MNHN Paris HEL 139).

Immature proglottids much wider than long. Mature proglottids (Fig. 49C) 0.8–2.8 mm (n=2; n=4) long x 1–5 mm wide (n=2; n=4). Gravid proglottids 2.5–4.4 mm (n=2; n=5) long x 2.5–5 mm wide (n=2; n=5), with dorsal and ventral pair of excretory ducts. Proglottids with 610–665 (n=2; n=4) testes. Testes oblong, 14–45 (27 ± 9; n=8; n=15) long x 40–88 (64 ± 13; n=8, n=15) wide. Cirrus-sac elongate oval, 841–1290 (n=2; n=8) long x 200–325 (n=2; n=8) wide in mature and gravid proglottids, angled anteriorly, containing armed, coiled cirrus. Vas deferens coiled, median, bordering proximal portion of cirrus-sac. Genital pores lateral, 60–65% (n=3; n=8) of proglottid length from posterior end, irregularly alternating. Vagina median, extending anteriorly from ovary to midlevel of proglottid, then laterally along anterior margin of vas deferens and cirrus-sac to genital pore. Genital atrium present. Ovary near posterior

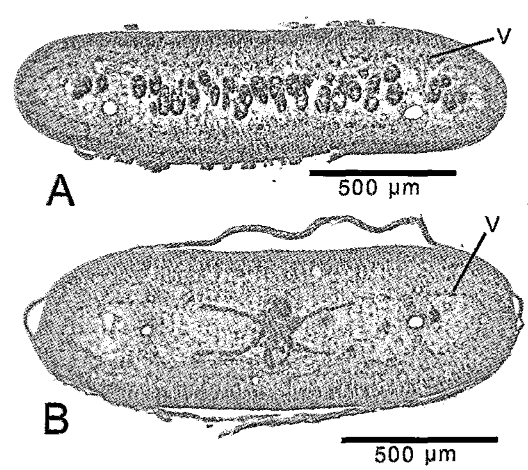

Fig. 50. Photomicrographs of *Monorygma perfectum* (Van Beneden, 1853) Diesing, 1863. A. Cross section of proglottid at level of testes anterior to cirrus-sac of voucher (MNHN Paris HEL 141). B. Cross section of proglottid at ovary of voucher (MNHN Paris HEL 142).

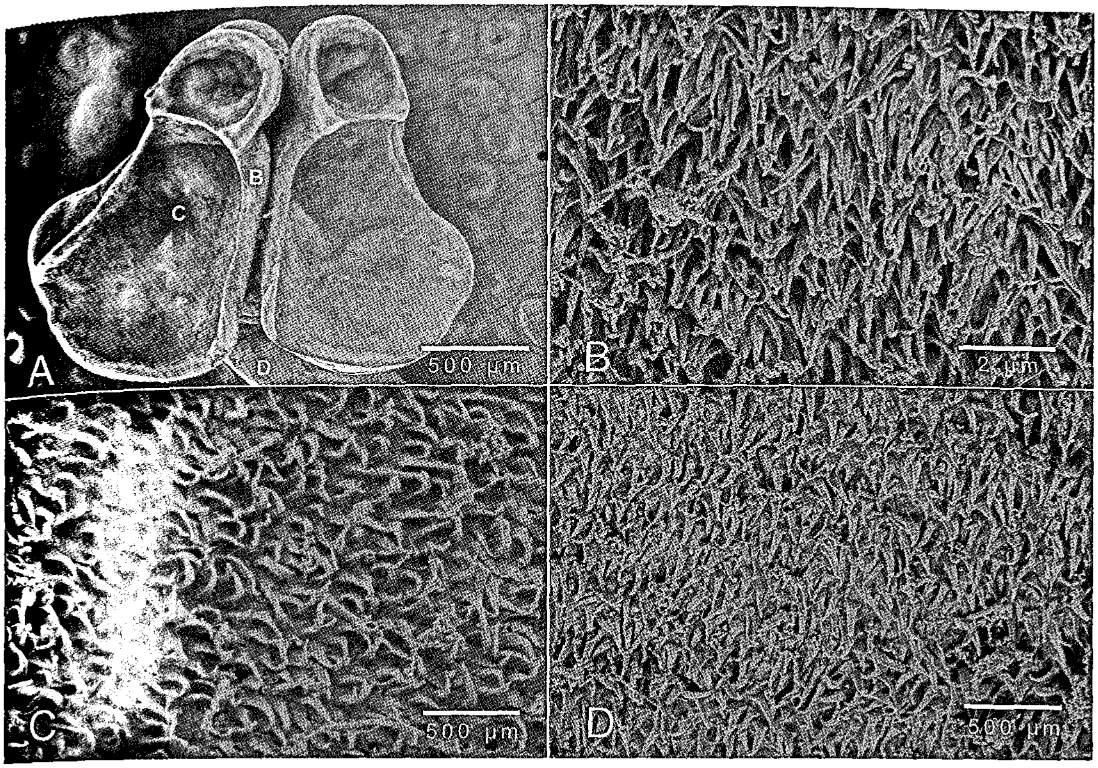

Fig. 51. Scanning electron micrographs of *Monorygma perfectum* (Van Beneden, 1853) Diesing, 1863. A. Scolex (letter indicate regions of scolex in enlarged photos B–D). B. Proximal surface of bothridium. C. Distal surface of bothridium. D. Surface of strobila near scolex.

end of proglottid, lobate, 500–700 (n=2; *n*=6) long x 1,050–1,300 (n=2; *n*=6) wide. Ovicapt 110–130 (n=2; *n*=6) in diameter. Mehlis' gland posterior to ovicapt. Uterus saccate ventral to vagina, extending from anterior margin of ovary to level of cirrus-sac in gravid proglottids. Uterine duct present, median, parallel and dorsal to uterus, extending anteriorly, entering uterus posterior to cirrus-sac. Vitellarium follicular, round, follicles round, circum-medullary, field reduced dorsal and ventral to ovary and uterus.

Remarks

This species was originally described by Van Beneden (1853) as *Anthobothrium perfectum*. The type locality was not specified by Van Beneden. Diesing (1863) erected *Monorygma* for *M. perfectum*. Southwell (1925) considered the species a member of *Phyllobothrium*. However, this species does not exhibit the foliose, posteriorly bifid bothridial morphology of *Phyllobothrium*, nor does it exhibit the laciniate proglottid morphology of *Anthobothrium*. This species has since been reported by Euzet (1959), and is likely to have a comparable distribution to that for its type host, *S. microcephalus*. *Monorygma perfectum* differs from *M. macquariae* in size (30 cm vs. over 50 cm), anterior loculus size (470–660 vs. 900), and genital pore position from posterior end of proglottid (50% vs. 60–65%). *Monorygma perfectum* differs from *M. magnum* in size (30 cm vs. 48 cm), anterior loculus diameter (470–660 vs. 1 mm) and testes shape (oblong vs. round).

Monorygma macquariae Johnston, 1937

(Figs. 52–53)

Taxonomic status: Valid.
Type host: *Somniosus* sp.

Site of infection: Spiral intestine.
Type locality: Macquariae Island, Australia (Fig. 52).
Type material: Not specified.
Etymology: The species is named for its type locality.

Description (modified from Johnston [1937]).

Worms large, anapolytic, slightly craspedote. Partial specimen measuring over 50 cm. Largest proglottids measuring 7 mm long by 3 mm wide. Scolex 3.1 mm long by 4.5 mm wide; anterior loculus 900 in diameter, anterior loculus with posterior lateral projections. Neck short, 2 mm wide. Testes numerous, 100 in diameter, in two irregular rows in cross section, post-vaginal testes present. Cirrus-sac 1,800–2,000 long x 400–500 wide. Genital pores irregularly alternating, approximately 50% from posterior end of proglottid. Ovary posterior, tetralobed in cross-section. Eggs elliptical, 100 long by 38 wide.

Remarks

Johnston (1937) described this species from specimens taken from an individual of *Somniosus* sp. that washed up on a beach at Macquarie Island, Australia. Although brief, the description provided by Johnston (1937) is consistent with the generic diagnosis of *Monorygma*. *Monorygma macquariae* differs from *M. perfectum* in length (over 50 cm vs. 30 cm), anterior loculus diameter (900 vs. 470–660), and genital pore position (60–65% vs. 50%).

Future studies of *M. macquariae* should include comparison with specimens of *M. magnum* collected from *Somniosus pacificus* Bigelow and Schroeder, 1944, taken from Northern Pacific localities in order to assess the possible conspecificity of these species. In addition, the identity of *Somniosus* from the waters near Macquariae Island, Australia needs to be resolved.

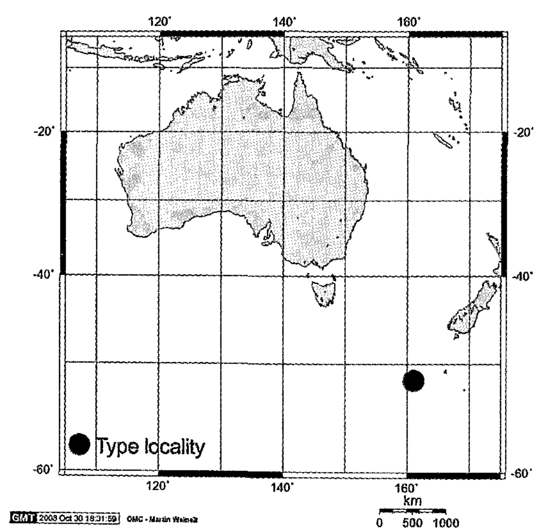

Fig. 52. Geographic distribution of *Monorygma macquariae* Johnston, 1937.

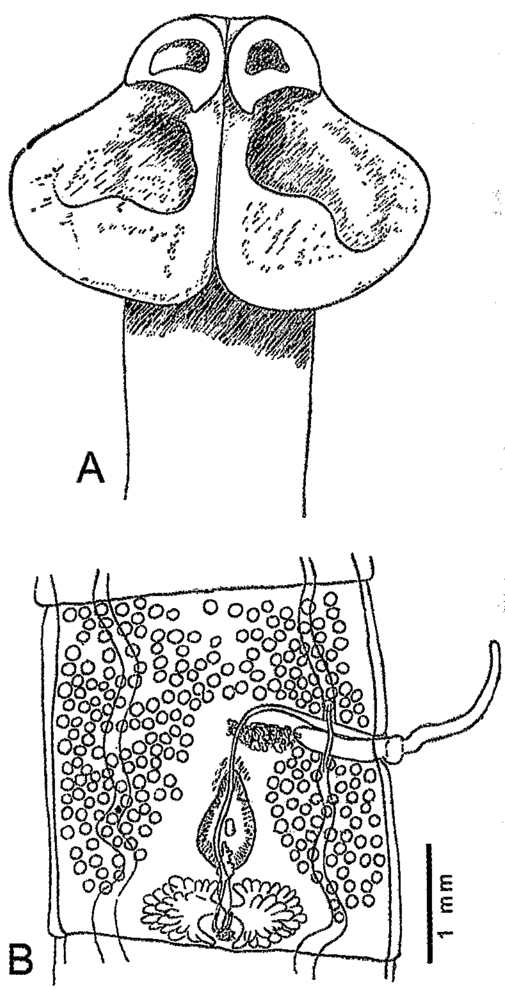

Fig. 53. Line drawings of *Monorygma macquariae* Johnston, 1937. A. Scolex (no scale available). B. Proglottid. (Taken from Johnston [1937].)

Monorygma magnum (Hart, 1936) Williams, 1968

(Figs. 54–55)

Synonym: *Phyllobothrium magnum* Hart, 1936.

Taxonomic status: Valid.

Type host: *Somniosus microcephalus* (actual identification likely *Somniosus pacificus* Bigelow and Schroeder, 1944, the Pacific sleeper shark, as *S. microcephalus* does not occur in Pacific waters).

Site of infection: Spiral intestine.

Type locality: Puget Sound, Washington, U.S.A (Fig. 54).

Additional locality: Moser Bay, Alaska, U.S.A. (Fig. 53).

Type material: Unknown.

Additional material: Voucher, USNPC 7669 (Fig. 55A).

Specimen examined: Voucher, USNPC 7669 (Fig. 55A).

Etymology: Not given, but presumably named for the large size of the specimens.

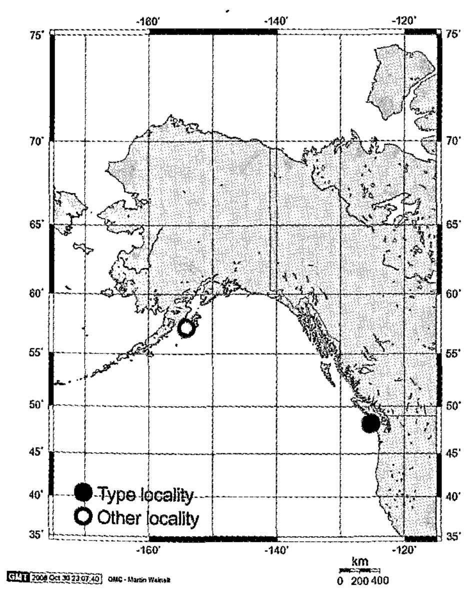

Fig. 54. Geographic distribution of *Monorygma magnum* (Hart, 1936) Williams, 1968.

Description (modified from Hart 1936).

Worms up to 48 cm long, maximum width 5 mm. Strobila with over 250 proglottids. Scolex 2.5 mm long by 4.2 mm wide, with four bothridia. Bothridia biloculate, anterior loculus 1 mm in diameter, anterior loculus with lateral projections. Proglottids with ventral pair of excretory ducts. Terminal proglottids slightly longer than wide. Testes round, 100 in diameter. Cirrus-sac an elongate oval, 1100 long by 400 wide, angled slightly anteriorly. Vas deferens medial to proximal portion of cirrus-sac. Genital pores lateral, irregularly alternating. Vagina medial, extending anteriorly from ovary to midlevel of proglot-

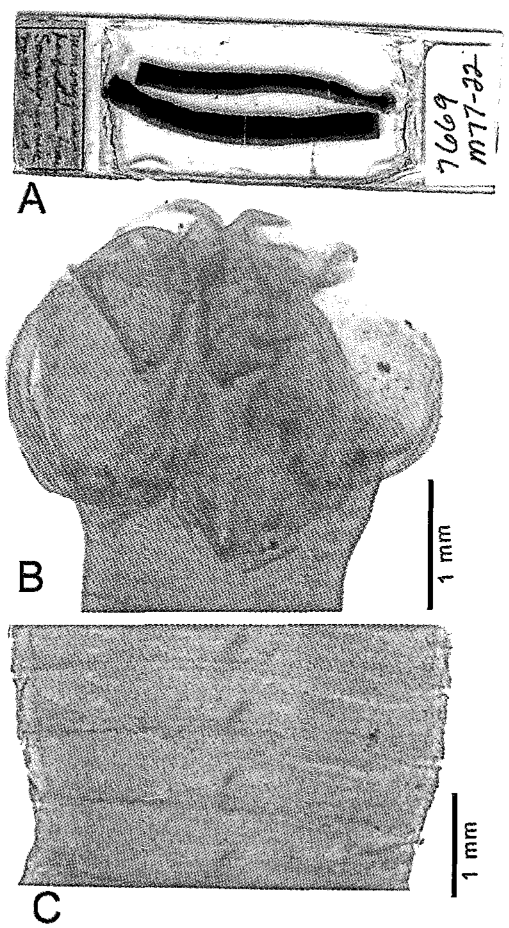

Fig. 55. Photomicrographs *Monorygma magnum* (Hart, 1936) Williams, 1968. A. Voucher slide (USNPC 7669). B. Scolex of voucher (USNPC 7669). No scale available. C. Proglottids of partial worm of voucher (USNPC 7669).

tid, then laterally along anterior margin of vas deferens and cirrus-sac to genital pore. Ovary lobate, posterior. Eggs spindle shaped, 80 long x 40 wide.

Remarks

Monorygma magnum differs from *M. perfectum* in total length (up to 48 cm vs. 30 cm), anterior loculus diameter (1,000 vs. 470–660) and testes shape (round vs. oblong). Although evidence for comparison is scant, *M. magnum* may differ from *M. macquariae* in size (total length of partial specimen over 50 cm vs. up to 48 cm). Future studies of *M. magnum* should include a comparison of it to specimens of *M. macquariae* in order to assess the possible conspecificity of these species. As available material for both of these species is meager, new material will be needed in order to address this issue.

Other species of *Monorygma*

In addition to the three valid species of *Monorygma*, eight other species have been associated with the genus (see Appendix 2). One of these speices is a synonym. Information on the other seven species and their present status is provided.

Monorygma chamissonii (Linton, 1905) Meggitt, 1924 *species inquirenda*

Monorygma chamissonii (Linton, 1905) Meggitt 1924 was originally described as *Taenia chamissonii* Linton, 1905 by Linton (1905). The larval species was collected from the Atlantic White-sided dolphin, *Lagenorhynchus acutus* (Gray, 1828). The species was transferred to *Phyllobothrium* by Southwell and Walker (1936). Based in its morphological condition as "a true bladder worm" and not a plerocercus, Linton (1905) postulated that the host of the adult form of *M. chamissonii* would not be an elasmobranch, but would likely be a marine mammal, perhaps the Killer Whale, *Orcinus orca*. Linton's (1905) original generic assignment of this species presumably was based, at least in part, on the resemblance between this larval stage and the bladder-bearing cysticerci of cestodes of terrestrial mammalian carnivores. Until the true taxonomic home of this species is determined, *M. chamissonii* should be referred to as *T. chamissonii* and considered a *species inquirenda*. Type specimens: not specified. Material examined: none.

Monorygma chlamydoselachi Lönnberg, 1898 *incertae sedis*

Monorygma chlamydoselachi was described by Lönnberg (1898) for specimens from the hexanchiform shark, *Chlamydoselachus anguineus* Garman, 1884 (the Frilled shark). The type locality is not known. Southwell (1925) considered the species a member of *Phyllobothrium*, and included a translation of Lönnberg's (1898) description in his account. The species does not share the characteristics of *Phyllobothrium* (see Ruhnke 1996b). Examination of specimens of this species revealed that they are not consistent in morphology with the type species of *Monorygma, M. perfectum* but are consistent with the description of Lönnberg (1889), and are from the same host species, *C. anguineus*. Williams (1968a) noted that Baer (1956) and Euzet (1959) thought *M. chlamydoselachi* to be synonymous with *M. perfectum*. Williams rejected this synonomy after viewing the same specimens of *M. chlamydoselachi* examined in this study. This species should be considered *incertae sedis*. Type specimens: not specified. Material examined: BNHM 1935.4.16.180–189.

Monorygma dentatum Linstow, 1907 *nomen dubium*

The description of Linstow (1907) is of an immature worm, collected south of the Cape Verde Islands (9°23'N 25°31'W). The host species was not identified in the original description. Schmidt (1986) transferred *M. dentatum* to *Phyllobothrium*. Given this, *M. dentatum* should be considered *nomen dubium*, as it is clearly of doubtful application. Type specimens: not specified. Material examined: none.

Monorygma elegans Monticelli, 1890 _nomen nudum_

The name *Monorygma elegans* appeared in a footnote in Monticelli (1890), in reference to specimens collected from *Scyllium catulus* (= *Scyliorhinus canicula*) and *S. stellare* (= *Scyliorhinus stellaris*). No description or figures accompany the use of the name. Thus, the species should be considered a *nomen nudum*. Type specimens: not specified. Material examined: none.

Monorygma grimaldi (Moniez, 1889) Baylis, 1919 _species inquirenda_

Monorygma grimaldi was described by Moniez (1889) as *Taenia grimaldi* Moniez, 1889 for larval cestodes taken from a cetacean. Baylis (1919) transferred the species to *Monorygma*. *Monorygma grimaldi* is one of two larval types historically reported from cetaceans and pinnipeds, the other being *Phyllobothrium delphini* (see Agusti et al. 2005; Aznar et al., 2007). *Phyllobothrium delphini* is usually found in the subcutaneous blubber of the abdominal region. *Monorygma grimaldi* is normally found in the peritoneum of the abdominal cavity (see Agusti et al. 2005). Agusti et al. (2005) provided a morphological and a molecular comparison between these two forms. *Monorygma grimaldi* is small, has a scolex that is invaginated, and is connected to the bladder through a very long and thin filament (see Southwell and Walker 1936). Agusti et al. (2005) found tight genetic identity of partial (D1–D3) lsrDNA between *P. delphini* and *M. grimaldi*. These two in turn were closely allied with *Clistobothrium montaukensis* and a cestode larval form taken from a squid. It is possible that the larval species *M. grimaldi* corresponds to one of the two species of *Clistobothrium* known from Great white sharks, *C. carcharodoni* and *C. tumidum*. At present, *M. grimaldi* should be referred to as *T. grimaldi*, and considered a *species inquirenda*. Type specimens: not specified. Material examined: none.

Monorygma megacotyla Yamaguti, 1952 _incertae sedis_ (Fig. 56)

This species was described for worms taken from *Cephaloscyllium umbratile* Jordan and Fowler, 1903, the Blotchy swell shark collected from Nagasaki, Japan. Yamaguti (1952) described this species as attaining a length greater than 80 mm and a maximum width of 2 mm. The proglottids numbered over 600. The scolex bears a disc shaped apical structure. The bothridia appear to be biloculate. The immature proglottids are much wider than long, and the posterior-most proglottids observed were 1.3 mm wide.

Monorygma megacotyla does appear to share the biloculate bothridial morphology with *M. perfectum*, *M. macquariae*, and *M. magnum*. However, the species is substantially smaller in size relative to the other species. The posterior-most proglottids of *M. megacotyla* available for study do not appear to be mature, and are thus difficult to compare to *M. perfectum*. Additional material will be needed to solve this taxonomic issue, and at present, *M. megacotyla* should be considered *incertae sedis*. Type specimens: MPM 23166. Material examined: MPM 23166.

Monorygma rotundum Klaptocz, 1906 _species inquirenda_

Monorygma rotundum was described for specimens taken from *Notidanus griseus* (= *Hexanchus griseus* [Bonnaterre, 1788]), the Bluntnose sixgill shark. The species was collected from the Gulf of Triest, Barcola, Italy. Southwell (1925) transferred this species to *Phyllobothrium*, but it does not share the features peculiar to that genus, such as foliose, posteriorly bifid bothridia. However, it also lacks the diagnostic features of *Monorygma*. For example, *M. rotundum* is uniloculate, and species of *Monorygma* are biloculate. Klaptocz's (1906) illustration of the posterior strobila of *M. rotundum* appears to be from an immature worm. Based on the limited information provided in the description and figures, this species should be considered *species inquirenda*. Type specimens: not specified. Material examined: none.

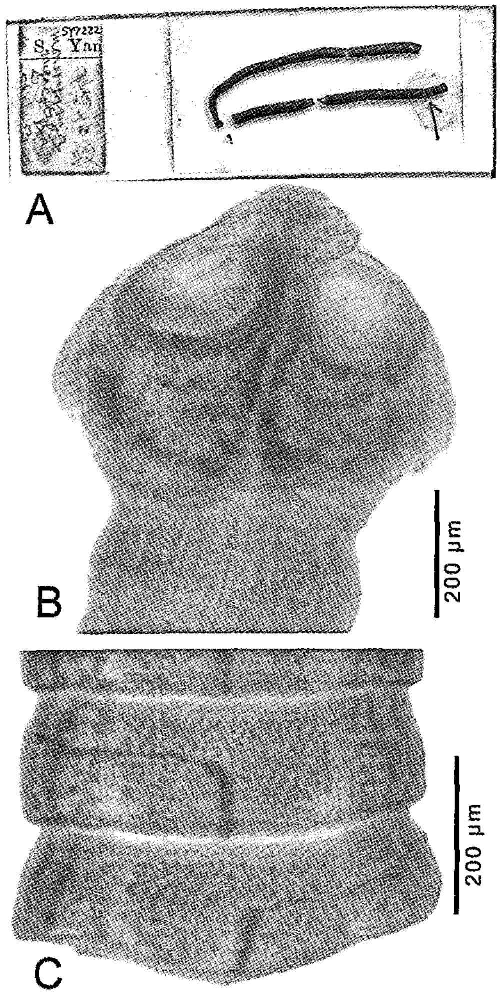

Fig. 56. Photomicrographs *Monorygma megacotyla* Yamaguti, 1952. A. Syntype slide (MPM 23166). Scolex of syntype (MPM 23166). B. Proglottids of syntype (MPM 23166).

NANDOCESTUS Reyda, 2008

Taxonomic status: Valid.

Type species: *Nandocestus guariticus* (Marques, Brooks and Lasso, 2001) Reyda, 2008.

Other species: None.

Etymology: The genus was named for Prof. Fernando Marques.

Diagnosis (modified from Reyda [2008])

Worms craspedote, euapolytic. Scolex with four sessile bothridia; myzorhynchus absent. Each bothridium with rim, single apical sucker, and single posterior loculus with numerous marginal loculi, lacking facial septa. Proximal surfaces of marginal loculi covered with moderately capilliform filitriches and cyrillionate spinitriches; distal surfaces of bothridia, apical suckers, and marginal loculi covered with capilliform filitriches and serrate gladiate spinitriches. Neck and strobila scutellate; scutes irregularly overlapping, comprised of densely packed, capilliform filitriches. Terminal proglottid longer than wide. Testes medullary, anterior to ovary, one to two rows deep in cross section, post-vaginal testes present. Genital pores sub-marginal. Cirrus-sac elongate oval, containing cirrus armed with filitriches and spinitriches. Vaginal opening anterior to cirrus-sac into genital atrium; seminal receptacle present. Ovary posterior, lobulated, H-shaped in frontal view, tetralobed in cross section. Uterus ventral, extending from ootype to level of genital atrium. Vitellarium follicular, follicles circum-medullary, partially interrupted by uterus, ovary, and cirrus-sac. Eggs spherical or semispherical, with punctate shell. Parasites of Potamotrygonidae.

Remarks

Reyda (2008) considered *Nandocestus* to most closely resemble the phyllobothriid genera *Cardiobothrium*, *Anthocephalum*, and *Orectolobicestus* on the basis of their possession of a single apical sucker and marginal bothridial loculi. *Nandocestus* differs from these genera in exhibiting circum-medullary, rather than lateral, vitelline follicles. *Nandocestus* is also similar to species of *Paraorygmatobothrium* and *Ruhnkecestus* in its possession of serrated spinitriches on the bothridium. However, it conspicuously differs from these latter two genera in the possession of circum-medullary vitelline follicles.

Nandocestus guariticus (Marques, Brooks and Lasso, 2001) Reyda, 2008
TYPE SPECIES
(Figs. 57–59)

Synonym: *Anindobothrium guariticus* Marques, Brooks and Lasso, 2001.
Taxonomic status: Valid.
Type Host: *Paratrygon aiereba* Müller and Henle, 1841, the Discus ray.
Additional host: *Potamotrygon* cf. *castexi*.
Site of Infection: Spiral intestine.
Type locality: Caño Guaritico, Hato El Frío, Orinoco Basin, Venezuela, 07°52'N, 69°20'W (Fig. 57).
Additional localities: Madre de Dios River at Boca Manu, Madre de Dios Department, Peru, 12°17.47'S, 70°53.86'W (Fig. 57).
Type material: Holotype, MHNLS 6215; paratype, MHNLS 6216.
Voucher specimens: USNPC 99940–99942; LRP 4071–4081 (including whole mounts, cross sections and SEM specimens); MZUSP 6391a–6391d; MHNP 2691–2693.
Etymology: This species is named for its type locality.

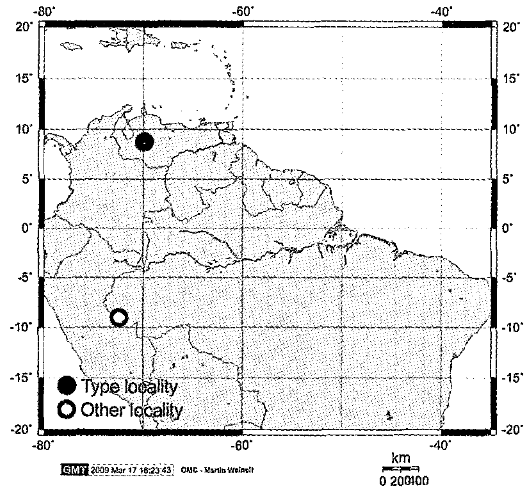

Fig. 57. Geographic distribution of *Nandocestus guariticus* (Marques, Brooks and Lasso, 2001) Reyda, 2008.

Description (modified from Reyda [2008]).

Worms craspedote, euapolytic, 13–28 (21 ± 5; n=7) mm long, greatest width at level of scolex or near terminal proglottid; 89–132 (105 ± 17; n=8) proglottids per worm. Scolex 2,300–4,850 (3,218 ± 827; n=7) long, consisting of scolex proper and extensive cephalic peduncle with inconspicuous posterior boundary. Scolex proper 580–900 (721 ± 103; n= 8) wide, maximum width at midlevel, bearing four sessile bothridia; each bothridium with rim, 400–600 (470 ± 69; n=7; *n*=9) long x 290–420 (363 ± 46; n=6) wide, with single apical sucker and 35–43 (38 ± 3; n=6; *n*=7) marginal loculi. Apical sucker 70–90 (78 ± 6; n=6; *n*=12) in diameter; marginal loculi 45–80 (53±15; n=5) wide. Proximal surfaces of bothridia covered with capilliform filitriches. Proximal surfaces of marginal loculi covered with capilliform filitriches and cyrillionate spinitriches. Edges of bothridial rims covered with capilliform filitriches. Distal surfaces of bothridia, apical suckers, and marginal loculi covered with capilliform filitriches and serrate gladiate spinitriches. Cilia distributed throughout bothridial rim and distal bothridial surfaces. Neck 2,000–4,500 (2,882 ± 817; n=7) long, slightly expanded at junction with scolex proper, scutellate; scutes irregularly overlapping, comprised of densely packed capilliform filitriches with triangular tip.

Terminal mature proglottids 830–1,400 (1,024 ± 177; n=7) long x 330–870 (573 ± 223; n=7) wide, length to width ratio 1.1–2.8 (2 ± 0.6; n=7). Genital pores submarginal, irregularly alternating, 60–80% (71±7; n=7) of proglottid length from posterior end. Testes irregularly oval, 40–110 (64 ± 15; n=11; *n*=26) long x 30–75 (45 ± 12; n=11; *n*=26) wide, 1–2 layers deep, 141–190 (169 ± 18; n=8) in number. Cirrus-sac 270–440 (373 ± 64; n=8) long x 160–210 (181 ± 17; n=8) wide. Cirrus covered with filitriches and stellate (star-shaped) spinitriches on base; base 68–100 (84 ± 23; n= 2) wide; distal portion of cirrus covered with filitriches only. Vagina sinuous or coiled, 102–150 (122 ± 25; n= 3) wide near genital atrium in free mature proglottids, 40–70 (56 ± 13; n=4) wide near genital atrium in free gravid proglottids. Seminal receptacle 63–105 (85 ± 20; n= 5) in diameter. Ovary 180–370 (251 ± 79; n=6) long x 360–440 (406 ± 34; n=5) wide. Vitellarium follicular, follicles circum-medullary, partially interrupted by

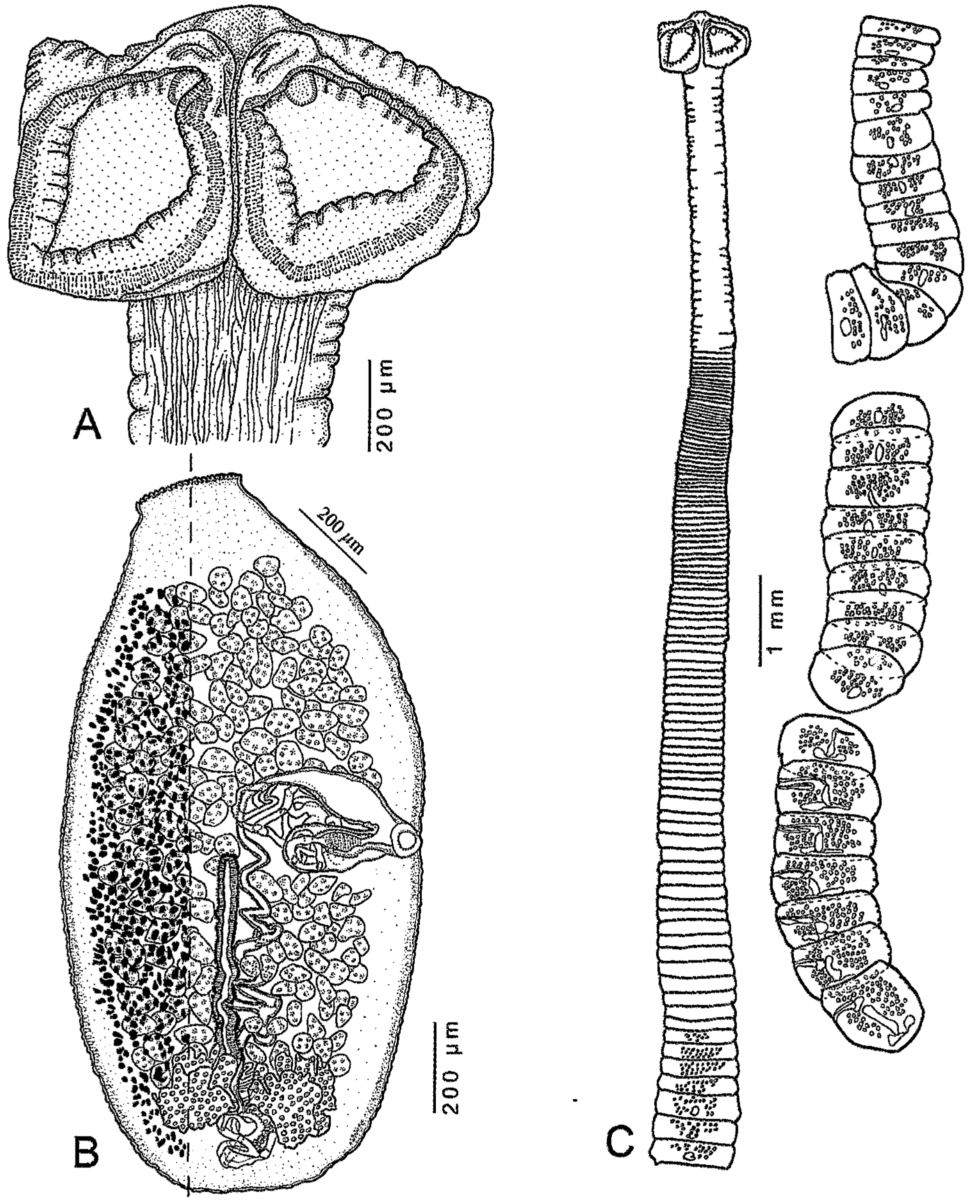

Fig. 58. Photomicrographs of *Nandocestus guariticus* (Marques, Brooks and Lasso, 2001) Reyda, 2008. A. Scolex. B. Terminal proglottid. C. Entire specimen. (Taken from Reyda [2008], copyright 2008. Used with permission.)

uterus, ovary, and cirrus-sac. Eggs spherical or semispherical 30–35 (33.6 ± 1.9; n=13) in diameter, with papillate shell. Embryonated eggs not observed.

Free proglottids larger and with conspicuously more developed cirrus-sac, vagina, and ovary than terminal proglottids of the strobila, 1,475–3,450 (2,375 ± 705; n=7) long x 770–1,075 (920 ± 96; n=7) wide, length to width ratio 1.9–3.5 (2.6 ± 0.6; n=7). Genital pores 46–64% (57 ± 5; n= 7) of proglottid length from posterior end. Cirrus-sac 270–440 (373 ± 64; n=8) long x 160–210 (181 ± 17; n=8) wide. Cirrus covered with filitriches

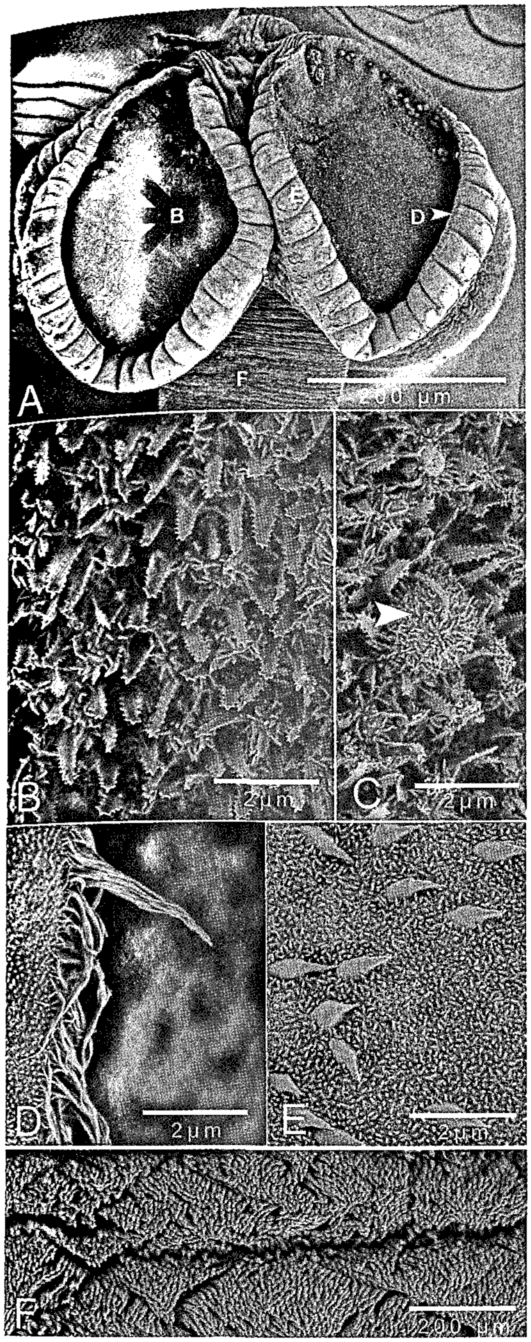

Fig. 59. Scanning electron micrographs of *Nandocestus guariticus* (Marques, Brooks and Lasso, 2001) Reyda, 2008. A. Scolex (letter indicate regions of scolex in enlarged photos B, D–F). B. Enlarged view of distal bothridial surface. C. Enlarged view of cilium on distal bothridial surface. D. Enlarged view of rim of bothridium. E. Enlarged view of proximal bothridial surface near bothridial rim. F. Enlarged view of neck. (Taken from Reyda [2008], copyright 2008. Used with permission.)

and stellate spinitriches at base; base 68–100 (84 ± 22; n=2) wide; distal portion of cirrus covered with filitriches only. Vagina sinuous or coiled, 102–150 (122.3 ± 24.8; 3) wide near genital atrium in free mature proglottids, 40–70 (56.3 ± 13.8; n=4) wide near genital atrium in free gravid proglottids. Seminal receptacle 63–105 (85 ± 20; n=5) in diameter. Ovary 180–370 (252 ± 79; n=6) long x 360–440 (406 ± 34; n=5) wide.

Remarks

Nandocestus guariticus was originally described by Marques et al. (2001) as *Anindobothrium guariticus* Marques, Brooks and Lasso, 2001. At present, the species is the sole member of *Nandocestus,* and has been found in two species of freshwater stingray, *Paratrygon aiereba* and *Potamotrygon* cf. *castexi.* Evidence from spinithrix morphology indicates a potential close relationship between this species and species of *Orectolobicestus, Paraorygmatobothrium,* and *Ruhnkecestus.* The presence of *N. guariticus* in freshwater stingrays represents both a host capture of a species from a shark cestode lineage, and an evolutionary incursion of an oceanic cestode clade into freshwater.

Reyda (2008) interpreted the anterior region of the strobila of *N. guariticus* as a "cephalic peduncle with an inconspicuous posterior boundary" (Reyda 2008, pg. 685). This region has been considered a neck in this account. The surface of this region in *N. guariticus* is comprised of densely packed long filitriches with triangular tip, the same morphological condition found for species of *Orectolobicestus,* and *Paraorygmatobothrium.* A typical cephalic peduncle would not have a weakly demarcated posterior boundary.

ORECTOLOBICESTUS Ruhnke, Caira and Carpenter, 2006

Taxonomic status: Valid.

Type species: *Orectolobicestus tyleri* Ruhnke, Caira and Carpenter, 2006.

Other species: *Orectolobicestus chiloscyllii* (Subhapradha, 1955) Ruhnke, Caira and Carpenter, 2006; *O. kelleyae* Ruhnke, Caira and Carpenter, 2006; *O. lorettae* Ruhnke, Caira and Carpenter, 2006; *O. mukahensis* Ruhnke, Caira and Carpenter; *O. randyi* Ruhnke, Caira and Carpenter, 2006.

Etymology: The genus was named in recognition of the fact that its species parasitize sharks of the order Orectolobiformes (carpet sharks).

Diagnosis (taken from Ruhnke et al. 2006b).

Phyllobothriidae. Worms slightly craspedote, euapolytic. Scolex with four bothridia; each bothridium with single apical sucker and posterior loculus; posteior loculus with marginal loculi, lacking facial septa. Proximal surfaces of bothridia covered with serrate or trifid spinitriches and capilliform filitriches; distal surfaces covered with gongylate spinitriches and capilliform filitriches. Neck scutellate; scutes comprised of densely packed, capilliform filitriches. Terminal proglottids at least twice as long as wide. Testes medullary, one row deep in cross-section post-vaginal testes present. Genital pore lateral, in anterior third of mature proglottids; shallow genital atrium present. Vagina opens anterior to cirrus-sac. Ovary posterior, H-shaped in frontal view. Uterus ventral, extending anteriorly to level of cirrus-sac in mature proglottids. Uterine duct present, joining uterus medially, posterior to cirrus-sac. Vitellarium follicular, follicles lateral distributed in dorsal and ventral columns, interrupted by ovary and cirrus-sac. Parasites of orectolobiform sharks.

Remarks

This genus differs from all phyllobothriid genera except *Cardiobothrium, Crossobothrium,* and *Nandocestus* in its possession of loculi on the margins of its bothridia. It differs from *Cardiobothrium* in that it possesses serrate gladiate rather than coniform spinitriches on its proximal bothridial surfaces and gongylate columnar rather than coniform spinitriches on its distal bothridial surfaces. In addition, it lacks facial loculi. It differs from *Crossobothrium* in lacking laciniate proglottids. *Orectolobicestus* differs from *Nandocestus* in that the vitelline follicles are lateral and interrupted by the ovary, rather than circum-medullary. The five species of *Orectolobicestus* for which SEM data are available possess an unusual form of spinithrix on their distal bothridial surfaces. This spinithrix form most closely resembles the gongylate type seen in *Orygmatobothrium, Phyllobothrium squali* and some species of *Paraorygmatobothrium* (see Whittaker and Carvajal 1980; McCullough and Fairweather 1983; Ruhnke 1994a). However, the projections of the spinitriches seen in *Orectolobicestus* species are restricted to the distal tips of the spinithrix, rather than extending throughout the length of the structure, as in the former three taxa.

The six species of *Orectolobicestus* have been described from three species of *Chiloscyllium.* Given that there are eight valid species of *Chiloscyllium,* perhaps ten or more species of the genus remain to be discovered.

Orectolobicestus tyleri Ruhnke, Caira and Carpenter, 2006

TYPE SPECIES

(Figs. 60–63)

Synonyms: None.

Taxonomic status: Valid.

Type host: *Chiloscyllium punctatum* Müller and Henle, 1838, the Brownbanded bamboo shark.

Site of infection: Spiral intestine.

Type locality: South China Sea off Mukah (02°54'N, 112°06'E), Sarawak, Malaysia (Fig. 60).

Type material: Holotype and paratype, MZUM(P) 160 (h) (Fig. 61); paratypes MZUM(P) 160 (h) 161 (p), LRP 3874–3877, USNPC 9749, IMPB 77.32.02. Remaining paratypes retained in the collection of T. R. Ruhnke.

Material examined: All type specimens were examined.

Etymology: This species was named for Dr. Gaines Tyler.

Description (taken from Ruhnke et al. [2006b]).

Worms slightly craspedote, euapolytic, 4.3–6.9 (5.6 ± 1; n=12) mm long; maximum width 576–864 (718 ± 91; n=12) at scolex. Proglottids 7–17 (12 ± 4; n=13) in number. Scolex 442–643 (517 ± 68; n=12) long, with four bothridia. Bothridia with 34–38 (36 ± 2; n=2, *n*=4) marginal loculi and one round apical sucker; apical sucker 73–103 (89 ± 10; n=4, *n*=7) in diameter. Proximal surfaces of all but rims of bothridia covered with capilliform filitriches (Fig.63B). Proximal surfaces of marginal loculi covered with capilliform filitriches and serrate gladiate spinitriches in which marginal protrusions are distributed throughout their length. Distal surfaces of apical suckers, marginal loculi and bothridia covered with capilliform filitriches and modified gongylate columnar spinitriches in which protrusions are restricted to distal-most tips of spinitriches, many with bristle-like termini. Neck 422–816 (618 ± 126; n=13) long, scutellate. Scutes irregularly overlapping; each comprised of densely packed, capilliform filitriches.

Terminal proglottids 1,290–2,860 (1,852 ± 452; n=13) long x 220–360 (291 ± 41; n=13) wide; terminal proglottid length/width ratio 3.6–8.9:1 (6.5 ± 1.8; n=13). Posterior proglottids with 62–95 (79 ± 10; n=13, *n*=15) testes. Testes slightly oblong, 25–59 (40 ± 8; n=13,

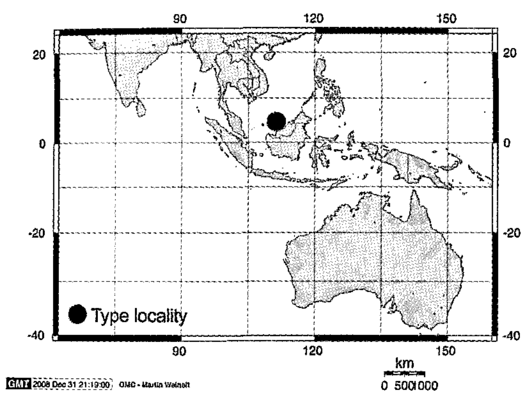

Fig. 60. Geographic distribution of *Orectolobicestus tyleri* Ruhnke, Caira and Carpenter, 2006; *O. mukahensis* Ruhnke, Caira and Carpenter, 2006; *O. kelleyae* Ruhnke, Caira and Carpenter, 2006; and *O. randyi* Ruhnke, Caira and Carpenter, 2006.

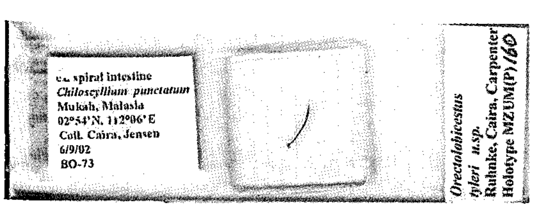

Fig. 61. *Orectolobicestus tyleri* Ruhnke, Caira and Carpenter, 2006. Holotype slide (MZUM[P] 160[h].)

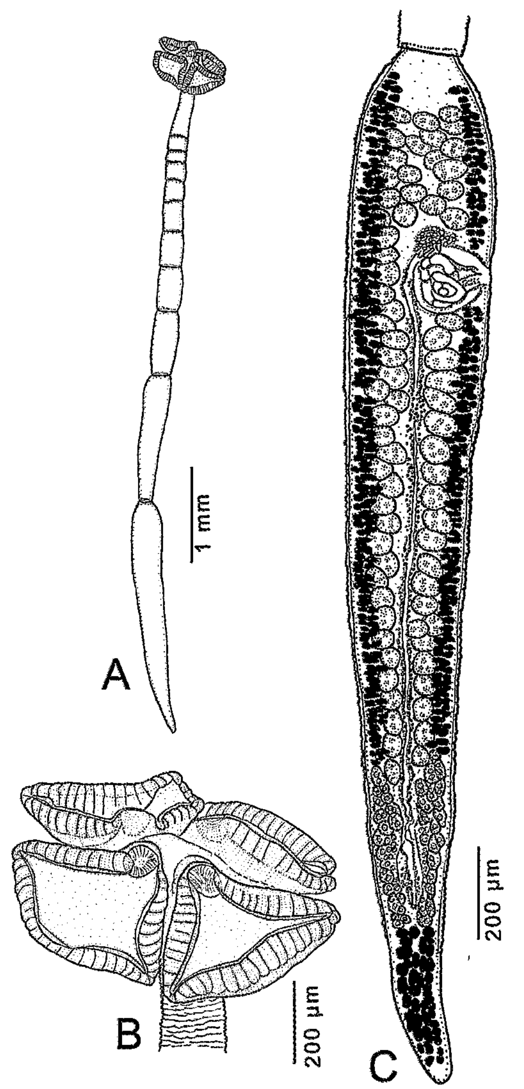

Fig. 62. Line drawings of *Orectolobicestus tyleri* Ruhnke, Caira and Carpenter, 2006. A. Holotype (MZUM[P] 160 [h]). B. Scolex of holotype (MZUM[P] 160 [h]). C. Terminal proglottid of holotype (MZUM[P] 160 [h]). (Taken from Ruhnke, Caira and Carpenter [2006], copyright 2006. Used with permission.)

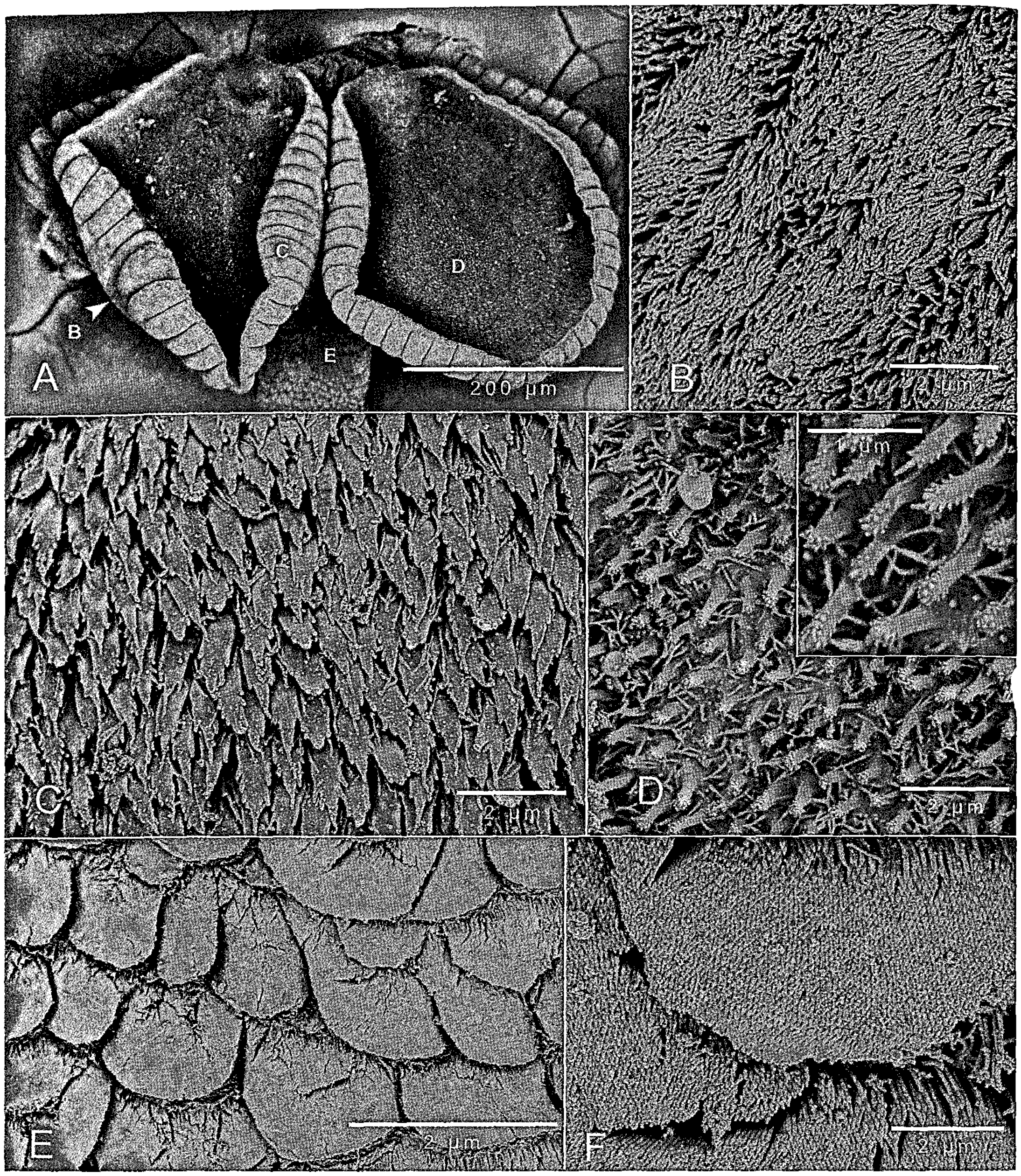

Fig. 63. Scanning electron micrographs of *Orectolobicestus tyleri* Ruhnke, Caira and Carpenter, 2006. A. Scolex. White numbers indicate locations at which Fig. 63B–D were taken. B. Proximal surface of bothridium, not on surface of marginal loculus. C. Proximal surface of bothridium at marginal loculus. D. Distal surface of bothridium; inset provides enlarged view of distal surface microtriches. E. Scutes on anterior regions of strobila. F. Enlarged view of scutes; note scutes composed of elongate filitriches. (Taken from Ruhnke, Caira and Carpenter [2006], copyright 2006. Used with permission.)

n=39) long x 29–63 (48 ± 8; n=13, *n*=39) wide, with testis length/width ratio 0.5–1.5:1 (0.8 ± 0.2; n=13, *n*=39), one row deep in cross-section. Cirrus-sac pyriform, 113–178 (156 ± 18; n=10) long x 63–143 (91 ± 24; n=10) wide, contains coiled cirrus. Cirrus armed with spinitriches. Vas deferens coiled, median, anterior to cirrus-sac bordering its proximal region, enters cirrus-sac on antero-medial margin. Genital pores lateral, 72–84% (78 ± 3; n=9, *n*=11) of proglottid length from posterior end, irregularly alternating. Vagina median, extending anteriorly from ovary to anterior third of proglottid, then laterally, ventral to vas deferens and along anterior margin of cirrus-sac to genital atrium. Vagina opens anterior to cirrus and vagina into common genital atrium. Ovary near posterior end of proglottid, H-shaped in frontal view, 245–451 (316 ± 71; n=9) long x 125–235 (159 ± 33; n=9) wide, tetralobed in cross-section. Ovicapt 25–38 (29 ± 4; n=9, *n*=10) at posterior margin of ovarian bridge. Mehlis' gland posterior to ovicapt. Uterus ventral to vagina, extending from anterior margin of ovary to posterior margin of cirrus-sac in mature proglottids. Uterine duct present, median, parallel and dorsal to uterus, extending to posterior margin of cirrus-sac, enters uterus at level of posterior margin of cirrus-sac. Vitellarium follicular; follicles oblong, 10–50 (22 ± 7; n=9, *n*=45) long x 25–55 (40 ± 7; n=9, *n*=45) wide, in two lateral bands each with two dorsal and two ventral row of follicles, interrupted by ovary and cirrus-sac.

Remarks

Among other features, *Orectolobicestus tyleri* differs from *O. randyi* and *O. kelleyae* in its possession of spinitriches on its proximal bothridial surfaces that are fully serrated, rather than trifid. *Orectolobicestus tyleri* differs from, *O. lorettae* and *O. mukahensis* in proglottid number (7–17 vs. 13–23 and 19–29, respectively), and also differs from *O. lorettae* in the morphology of spinitriches on the distal surfaces of the apical suckers and bothridia (projections restricted to the distal tip vs. projections distributed from distal third to tip). *Orectolobicestus tyleri* differs from *O. chiloscyllii* in maximum length (6.9 mm vs. 12 mm).

Orectolobicestus chiloscyllii (Subhapradha, 1955) Ruhnke, Caira and Carpenter, 2006

(Figs. 64–65)

Synonym: *Phyllobothrium chiloscyllii* Subhapradha, 1955.
Taxonomic status: Valid.
Type host: *Chiloscyllium griseum* Müller and Henle, 1838, the Slender bambooshark.
Site of infection: Spiral intestine.
Type locality: Madras Coast, India (Fig. 64).
Type material: Not specified.
Specimens examined: None.
Etymology: This species is named for genus of the host, *Chiloscyllium* Müller and Henle, 1837.

Description (modified from Ruhnke et al. [2006b]).

Worms up to 12 mm long. Proglottids 6–18 in number. Scolex with four bothridia. Bothridia 750 in diameter, with marginal loculi and single round apical sucker; apical sucker 75 in diameter. Neck 1–2 mm long. Posterior proglottids 2,300 long x 250 wide. Proglottids with 55–80 testes.

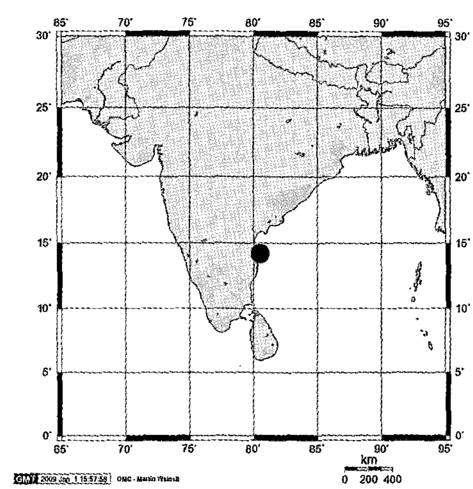

Fig. 64. Geographic distribution of *Orectolobicestus chiloscylii* (Subhapradha, 1955) Ruhnke, Caira and Carpenter, 2006.

Remarks

The information and illustrations provided by Subhapradha (1955) support the transfer of this species from *Phyllobothrium* to *Orectolobicestus* by Ruhnke et al. (2006b). Ruhnke (1993b) questioned the placement of this species in *Phyllobothrium* when he treated the taxonomy and systematics of that genus. Based on Subhapradha's illustrations, unlike *Phyllobothrium*, *O. chiloscylii* exhibits marginal bothridial loculi, vitelline follicles that are interrupted by the ovary; and intact, rather than posteriorly bifid, bothridia that are flat rather than ruffled. The species is consistent with features of *Orectolobicestus* (see Ruhnke et al. 2006b).

In addition to *C. griseum*, Subhapradha (1955) also listed the batoid species *Rhynchobatus dijeddensis* Forsskäl, *Rhinobatus granulatus* Cuvier, and *R. schlegelii* Müller and Henle in her list of hosts of *P. chiloscyllii*. However, Ruhnke et al. (2006b) considered *Chiloscyllium griseum* to be the type host. This assumption is supported by the fact that the five other species of *Orectolobicestus* are also found in bamboo sharks. The presence of worms from this host provides further support for the affinities between this and other *Orectolobicestus* species, all of which are known only from sharks of the genus *Chiloscyllium*.

Orectolobicestus chiloscyllii differs from *O. tyleri, O. lorettae, O. mukahensis, O. kelleyae,* and *O. randyi* in maximum length (12 vs. 6.9, 5.8, 5.3, 8.3, and 9.8 mm, respectively). It differs from *O. lorettae* and *O. randyi* in apical sucker diameter (75 vs. 78–115 and 81–149, respectively), and from *O. kelleyae* and *O mukahensis* in terminal proglottid length (2,300 vs. 595–843 and 326–930, respectively) and number of proglottids (6–18 vs. 27–38 and 19–29, respectively).

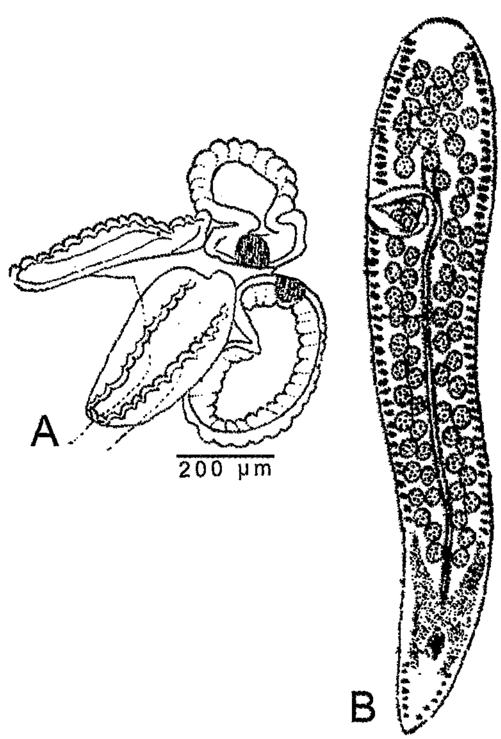

Fig. 65. Line drawings of of *Orectolobicestus chiloscylii* (Subhapradha, 1955) Ruhnke, Caira and Carpenter, 2006. A. Scolex. B. Terminal proglottid (no scale provided). (Taken from Subhapradha [1955]).

Orectolobicestus kelleyae Ruhnke, Caira and Carpenter, 2006

(Figs. 60, 66–68)

Taxonomic status: Valid.
Type host: *Chiloscyllium griseum* (Gmelin, 1789), the Slender bamboo shark.
Type locality: South China Sea off Mukah (02°54'N, 112°06'E), Sarawak, Malaysia (Fig. 60).
Site of infection: Spiral intestine.
Type material: Holotype, MZUM(P) 164(h) (Fig. 66); paratypes MZUM(P) 165(p); LRP 3886–3888; USNPC 97496; IMPB 77.32.04. Remaining paratypes retained in T.R. Ruhnke's collection.
Material examined: All types were examined.
Etymology: This species is named for Kelley Carpenter, mother of S.D. Carpenter.

Description (taken from Ruhnke et al. [2006b]).

Worms euapolytic, slightly craspedote, 4.8–8.3 (6.7 ± 1.3; n=5) mm long; maximum width 732–868 (806 ± 69; n=3) at level of scolex. Proglottids 27–38 (31 ± 4; n=5) in

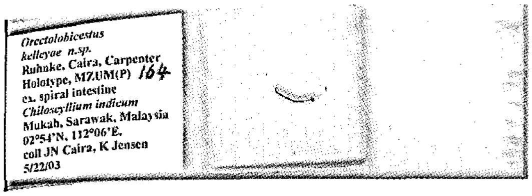

Fig. 66. *Orectolobicestus kelleyae* Ruhnke, Caira and Carpenter, 2006. Holotype slide (MZUM[P] 164[h]).

number. Scolex 471–508 (490 ± 26; n=2) long, with four bothridia. Bothridia 446–657 (542 ± 101; n=3, *n*=5) long x 322–595 (450 ± 99; n=4, *n*=5) wide, each with 32–34 (33 ± 1; n=2, *n*=4) marginal loculi and single round apical sucker; apical sucker 81–99 (93 ± 6; n=5, *n*=11) in diameter. Proximal surfaces of all but rims of bothridia covered with capilliform filitriches. Proximal surfaces of marginal loculi covered with capilliform filitriches and serrate gladiate spinitriches with two to three marginal protrusions restricted to distal-most tip of spinithrix; median protrusion usually longest. Distal surfaces of apical suckers, marginal loculi and bothridia covered with capilliform filitriches and modified gongylate columnar spinitriches in which protrusions are restricted to distal-most tips of spinitriches. Neck 992–1,748 (1,374 ± 323; n=5) long, scutellate. Scutes spathate, irregularly overlapping; each comprised of densely packed, capilliform filitriches.

Terminal proglottids 595–843 (686 ± 100; n=7) long x 223–298 (248 ± 25; n=6) wide; length/width ratio 2.2–3.7:1 (3 ± 0.6; n=7). Posterior proglottids with 75–85 (79 ± 6; n=3) testes. Testes oblong, 12–36 (22 ± 6; n=6, *n*=18) long x 33–53 (40 ± 7; n=6, *n*=18) wide; length/width ratio 0.3–0.9:1 (0.5 ± 0.2; n=6, *n*=18). Cirrus-sac oval, 84–119 (101 ± 1; n=5) long x 23–33 (29 ± 4; n=5) wide, contains coiled cirrus armed with spinitriches. Vas deferens coiled, median, overlaps proximal portion of cirrus-sac, anterior to cirrus-sac. Genital pores lateral, 73–83% (76 ± 4; n=5) of proglottid length from posterior end, irregularly alternating. Vagina median, extending anteriorly from ovary to anterior third of proglottid, then laterally, ventral to vas deferens, along anterior margin of cirrus-sac,

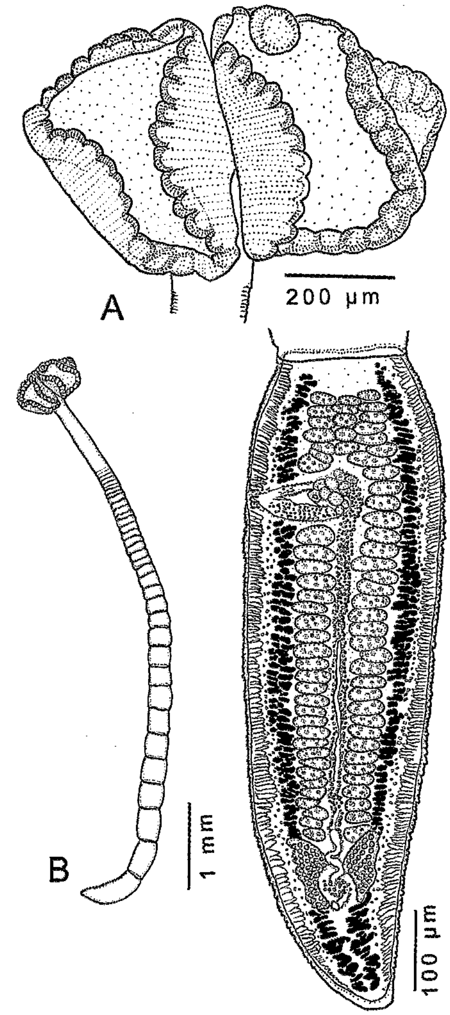

Fig. 67. Line drawings of *Orectolobicestus kelleyae* Ruhnke, Caira and Carpenter, 2006. A. Scolex of holotype (MZUM[P] 164[h]). B. Holotype (MZUM[P] 164[h]). C. Terminal proglottid of paratype (LRP 3886). (Taken from Ruhnke, Caira and Carpenter [2006], copyright 2006. Used with permission.)

opening in genital atrium anterior to cirrus. Cirrus and vagina open into common genital atrium. Ovary near posterior end of proglottid, H-shaped in frontal view, 125–180 (153 ± 39; n=2) long x 109–149 (126 ± 21; n=3) wide, tetralobed in cross-section. Ovicapt 17–19 (n=2) in diameter, at posterior margin of ovarian bridge. Mehlis' gland posterior to ovicapt. Uterus ventral to vagina, extending from anterior margin of ovary to posterior margin of cirrus-sac in mature proglottids.

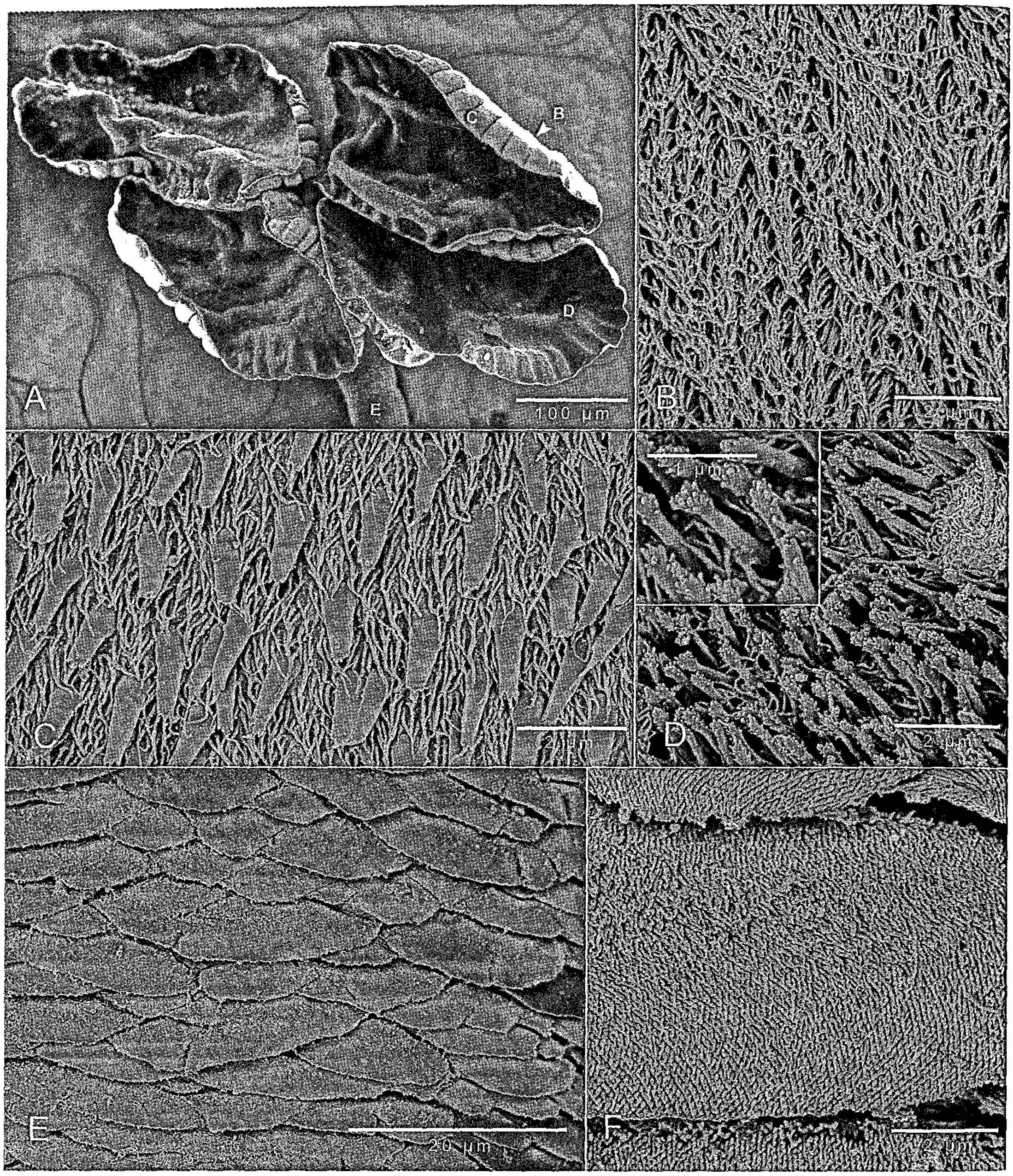

Fig. 68. Scanning electron micrographs of *Orectolobicestus kelleyae* Ruhnke, Caira and Carpenter, 2006. A. Scolex. White numbers indicate locations at which Fig. 68B–F were taken. B. Proximal surface of bothridium, not on surface of marginal loculus. C. Proximal surface of bothridium at marginal loculus. D. Distal surface of bothridum; inset shows enlarged view of microtriches. E. Scutes on anterior regions of strobila. F. Enlarged view of scutes; note scutes composed of elongate filitriches. (Taken from Ruhnke, Caira and Carpenter [2006], copyright 2006. Used with permission.)

Uterine duct present, median, parallel and dorsal to uterus, extending to posterior margin of cirrus-sac in mature proglottids, then entering uterus at level of posterior margin of cirrus-sac. Vitellarium follicular; follicles in two lateral bands, 4–20 (8 ± 3; n=6, n=18) long x 6–23 (16 ± 4; n=6, n=18) wide, interrupted by ovary and cirrus-sac.

Remarks

Orectolobicestus kelleyae can be clearly differentiated from *O. tyleri, O. lorettae,* and *O. mukahensis* by its possession of spinitriches on its proximal bothridial surfaces that are trifid rather than serrated throughout their length. *Orectolobicestus kelleyae* differs from *O. tyleri, O. lorettae, O. randyi,* and *O. chiloscyllii* in proglottid number (27–38 vs. 7–17, 13–23, 11–22 and 6–18, respectively). In addition, the species possesses a cirrus-sac that is narrower than that of *O. tyleri* and *O. lorettae* (23–33 vs. 63–143 and 58–143, respectively).

Orectolobicestus lorettae Ruhnke, Caira and Carpenter, 2006
(Figs. 69–72)

Taxonomic status: Valid.
Type host: *Chiloscyllium* cf. *punctatum,* the Bamboo shark.
Site of infection: Spiral intestine.
Type locality: Coral Sea off Cairns (16°55'S, 145°41'E), Northern Territories, Australia (Fig. 69).
Type material: Holotype, QM G 225674 (Fig. 70); paratypes, QM G225675–225767, LRP 3878–3881, USNPC 97494. Remaining paratypes retained in the collection of T.R. Ruhnke.

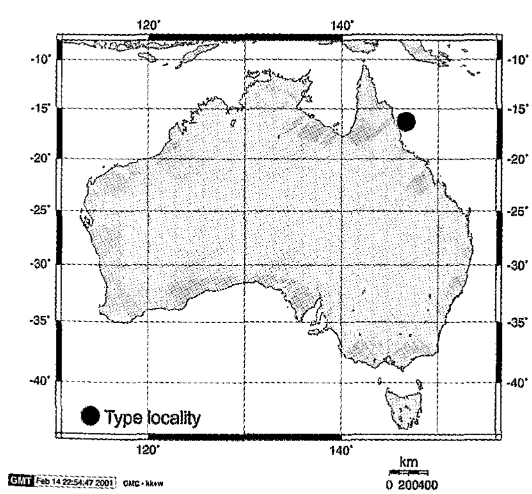

Fig. 69. Geographic distribution of *Orectolobicestus lorettae* Ruhnke, Caira and Carpenter, 2006.

Material examined: All type material was examined.
Etymology: This species was named for T.R. Ruhnke's mother, Loretta Ruhnke.

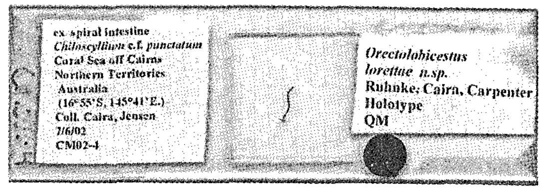

Fig. 70. *Orectolobicestus lorettae* Ruhnke, Caira and Carpenter, 2006. Holotype slide (QM G 225674).

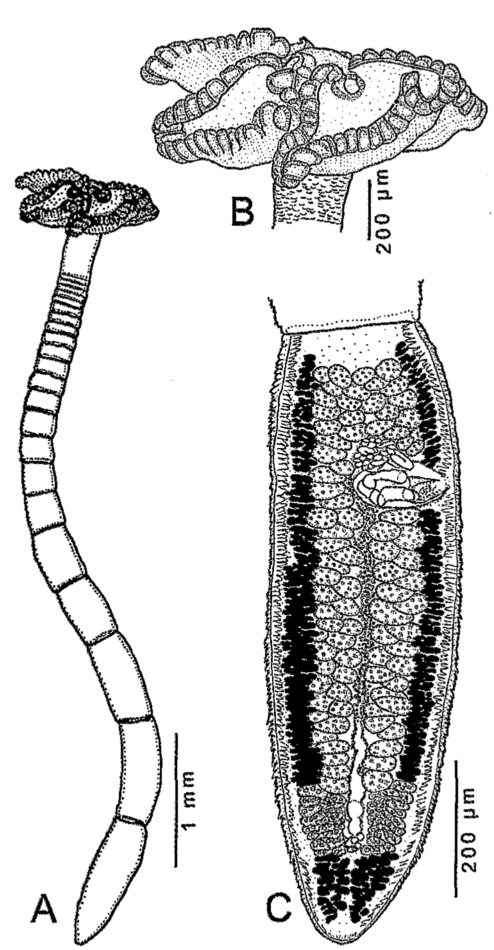

Fig. 71. Line drawings of *Orectolobicestus lorettae* Ruhnke, Caira and Carpenter, 2006. A. Holotype (QM G 225674). B. Scolex of holotype (QM G 225674). C. Terminal proglottid of holotype (QM G 225674). (Taken from Ruhnke, Caira and Carpenter [2006], copyright 2006. Used with permission.)

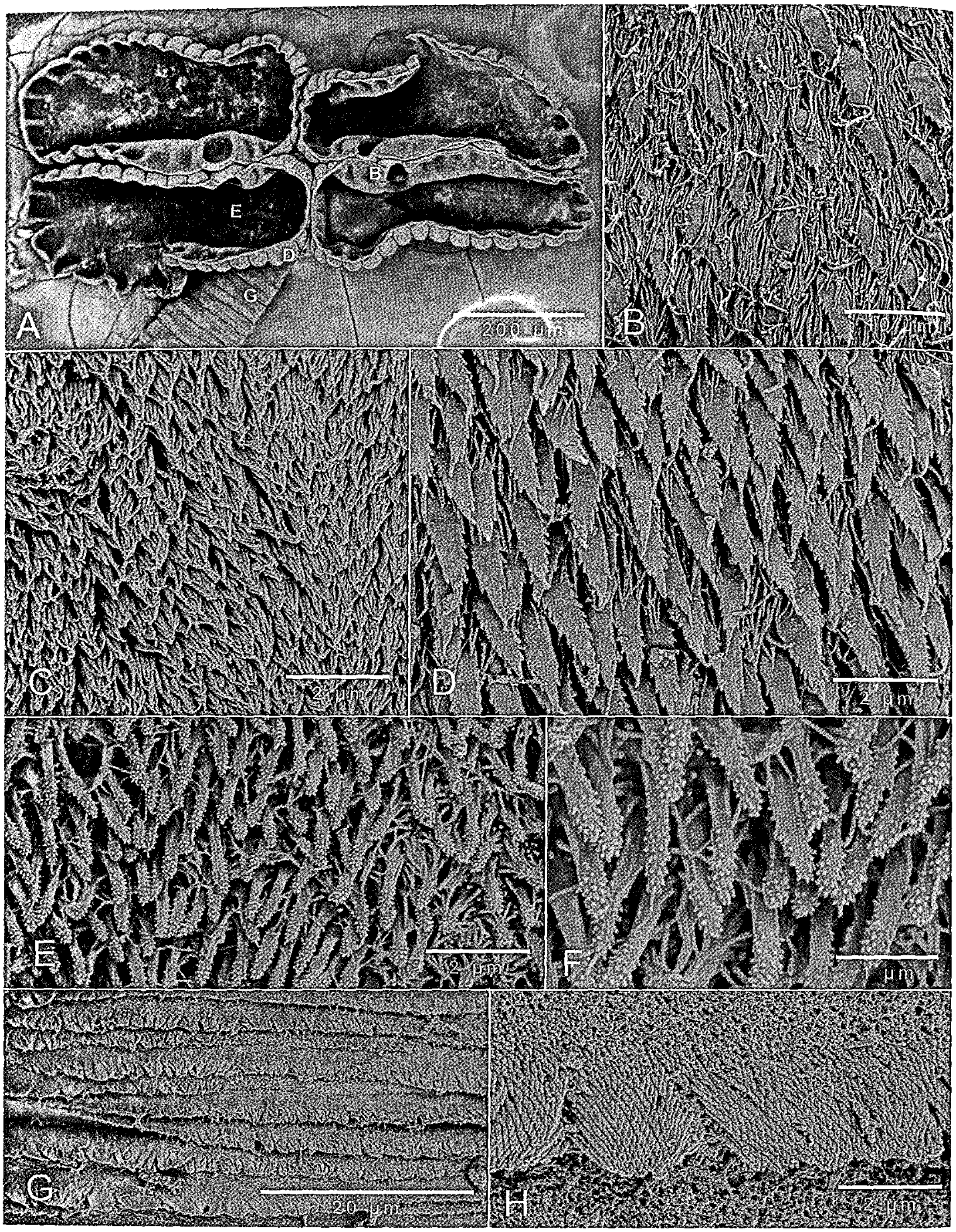

Fig. 72. Scanning electron micrographs of *Orectolobicestus lorettae* Ruhnke, Caira and Carpenter, 2006. A. Scolex. White numbers indicate location at which Fig. 72B–F were taken. B. Detail of lateral portion of apical sucker; note microthrix differences between distal surface of sucker, margin of sucker and proximal surface of bothridium. C. Proximal surface of bothridium, not on surface of marginal loculus. D. Proximal surface of bothridium at marginal loculus. E. Distal surface of bothridium. F. Enlarged view of distal surface of bothridium. G. Scutes on anterior regions of strobila. H. Enlarged view of scutes; note scutes composed of elongate filitriches. (Taken from Ruhnke, Caira and Carpenter [2006], copyright 2006. Used with permission.)

Description (taken from Ruhnke et al. [2006b]).

Worms euapolytic, slightly craspedote, 3.3–5.8 (4.6 ± 0.8; n=17) mm long; maximum width 732–1,488 (944 ± 209; n=17) at scolex. Proglottids 13–23 (18 ± 3; n=17) in number. Scolex with four bothridia; bothridia 303–744 (503 ± 112; n=13, *n*=26) long x 310–744 (535 ± 112; n=13, *n*=26) wide, each with 30–42 (34 ± 3; n=11, *n*=24) marginal loculi and a single, round apical sucker; apical sucker 78–115 (95 ± 8; n=17, *n*=62) in diameter. Proximal surfaces and all but rims of bothridia covered with capilliform filitriches. Proximal surfaces of marginal loculi covered with capilliform filitriches and serrate gladiate spinitriches in which marginal protrusions are distributed throughout their length. Distal surfaces of apical suckers, marginal loculi, and bothridia covered with capilliform filitriches and modified gongylate columnar spinitriches with protrusions restricted to several longitudinal rows on middle third, many with bristle-like terminus (aristate) (differing from typical gongylate spinitriches where protrusions are distributed throughout circumference of their distal third). Neck 288–816 (585 ± 148; n=11) long, scutellate. Scutes conspicuously elongate; each scute comprised of densely packed, capilliform filitriches.

Terminal proglottids 806–1376 (1057 ± 143; n=17) long x 161–310 (248 ± 38; n=17) wide; length/width ratio 3.1–7.1:1 (4.4 ± 1.1; n=17). Posterior proglottids with 81–112 (94 ± 9; n=15) testes. Testes oblong, 14–37 (24 ± 5; n=15, *n*=43) long x 25–58 (42 ± 7; n=15, *n*=43) wide; testes length/width ratio 0.6–0.9:1 (0.6 ± 0.1; n=15, *n*=43). Cirrus-sac oval, 94–186 (127 ± 25; n=14) long x 44–87 (61 ± 14; n=14) wide, containing coiled cirrus. Cirrus armed with spinitriches. Vas deferens coiled anterior to cirrus-sac, median, bordering proximal portion of cirrus-sac. Genital pores lateral, 72–79% (76 ± 2; n=17) of proglottid length from posterior end, irregularly alternating. Vagina median, extending anteriorly from ovary to anterior third of proglottid, then laterally, ventral to vas deferens, along anterior margin of cirrus-sac, opening in genital atrium anterior to cirrus. Ovary near posterior end of proglottid, H-shaped in frontal view, 179–306 (233 ± 40; n=15) long x 105–186 (148 ± 24 n=15) wide, tetralobed in cross-section. Ovicapt 25–34 (30 ± 4; n=16) in diameter at posterior margin of ovarian bridge. Mehlis' gland posterior to ovicapt. Uterus ventral to vagina, extending from anterior margin of ovary to posterior margin of cirrus-sac in mature proglottids. Uterine duct present, median, parallel and dorsal to uterus, extending to posterior margin of cirrus-sac in mature proglottids, then enters uterus at level of posterior margin of cirrus-sac. Vitellarium follicular; follicles 5–19 (10 ± 3; n=15, *n*=45) long x 16–45 (27 ± 7; n=15, *n*=45) wide, in two lateral bands each with two to three dorsal and two to three ventral rows of follicles, interrupted by ovary and cirrus-sac.

Remarks

Among other features, *Orectolobicestus lorettae* clearly differs from *O. tyleri* and *O. mukahensis* in its possession of neck scutes that are elongate rather than spathate. *Orectolobicestus lorettae* differs from *O. kelleyae* and *O. randyi* in possession of spinitriches on its proximal bothridial that are serrate throughout their length rather than trifid. *Orectolobicestus lorettae* differs from *O. chiloscyllii* in proglottid length (806–1,376 vs. 2300). *Orectolobicestus lorettae* further differs from *O. kelleyae* in testes number (81–112 vs. 55–80).

Orectolobicestus mukahensis Ruhnke, Caira and Carpenter, 2006

(Figs. 60, 73–75)

Taxonomic status: Valid.

Type host: *Chiloscyllium indicum* (Gmelin, 1789), the Slender bamboo shark.

Type locality: South China Sea off Mukah (02°54'N, 112°06'E), Sarawak, Malaysia (Fig. 60).

Site of infection: Spiral intestine.

Type material: Holotype MZUM(P) 162(h) (Fig. 73); paratypes MZUM(P) 163(p), LRP 3882–3885, USNPC 97495, IMPB 77.32.03. Remaining paratypes retained in T.R. Ruhnke's collection.

Material examined: All types were examined.
Etymology: This species is named for its type locality.

Description (taken from Ruhnke et al. [2006b]).

Worms euapolytic, slightly craspedote, 1.8–5.3 (3.9 ± 1.2; n=8) mm long; maximum width 521–781 (622 ± 81; n=8) at level of scolex. Proglottids 19–29 (24 ± 3; n=6) in number. Scolex 304–606 (437 ± 94; n=9) long, with four bothridia. Bothridia 223–459 (319 ± 64; n=9, *n*=23) long x 143–397 (259 ± 71; n=9, *n*=18) wide, each with 25–35 (30 ± 3; n=9, *n*=18) marginal loculi and a single round apical sucker; apical sucker 62–99 (78 ± 12; n=9, *n*=24) in diameter. Proximal surfaces and all but rims of bothridia covered with capilliform filitriches. Proximal surfaces of marginal loculi covered with capilliform filitriches and serrate gladiate spinitriches in which marginal protrusions are generally restricted to distal half of length. Distal surfaces of apical suckers, marginal loculi and bothridia covered with capilliform filitriches and modified gongylate columnar spinitriches in which protrusions are generally restricted to dorsal and ventral margins of distal half of spinithrix. Neck 508–1,054 (791 ± 252; n=5) long, scutellate. Scutes spathate, irregularly overlapping; each comprised of densely packed,

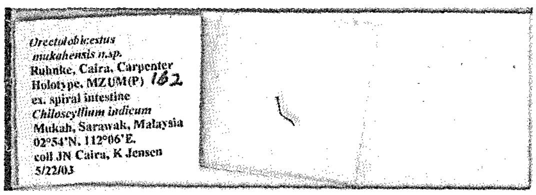

Fig. 73. *Orectolobicestus mukahensis* Ruhnke, Caira and Carpenter, 2006. Holotype slide (MZUM[P] 162 [h]).

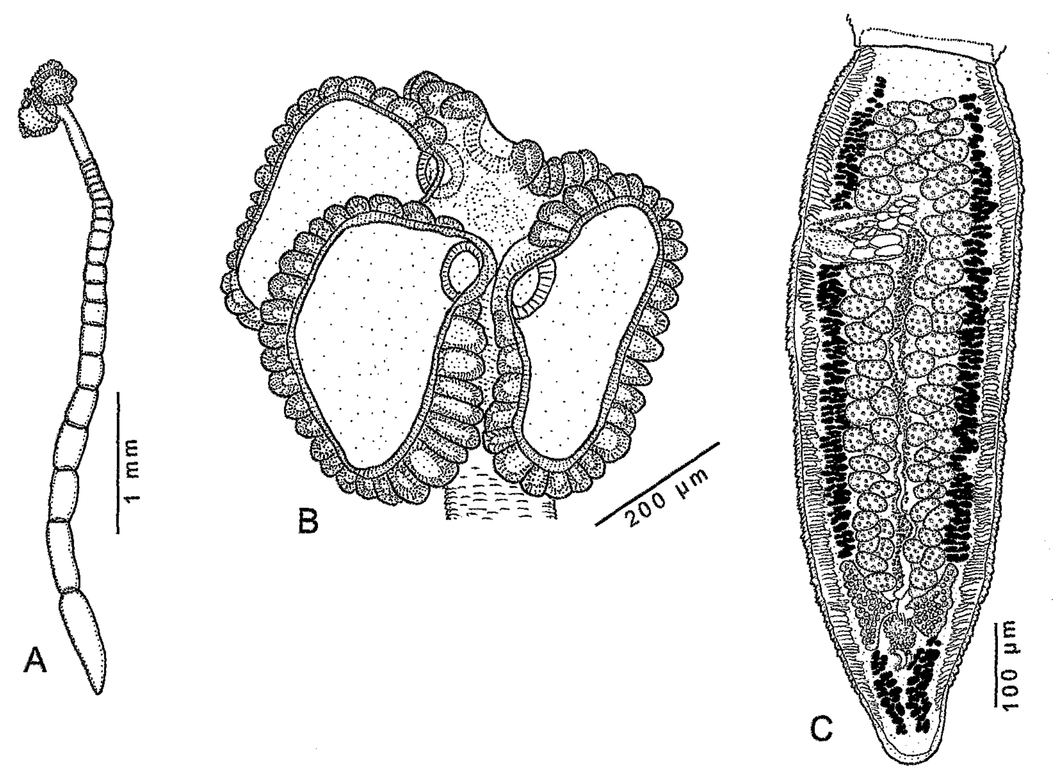

Fig. 74. Line drawings of *Orectolobicestus mukahensis* Ruhnke, Caira and Carpenter, 2006. A. Holotype (MZUM[P] 162 [h]). B. Scolex of holotype (MZUM[P] 162 [h]). C. Terminal proglottid of holotype (MZUM[P] 162 [h]). (Taken from Ruhnke, Caira and Carpenter [2006], copyright 2006. Used with permission.)

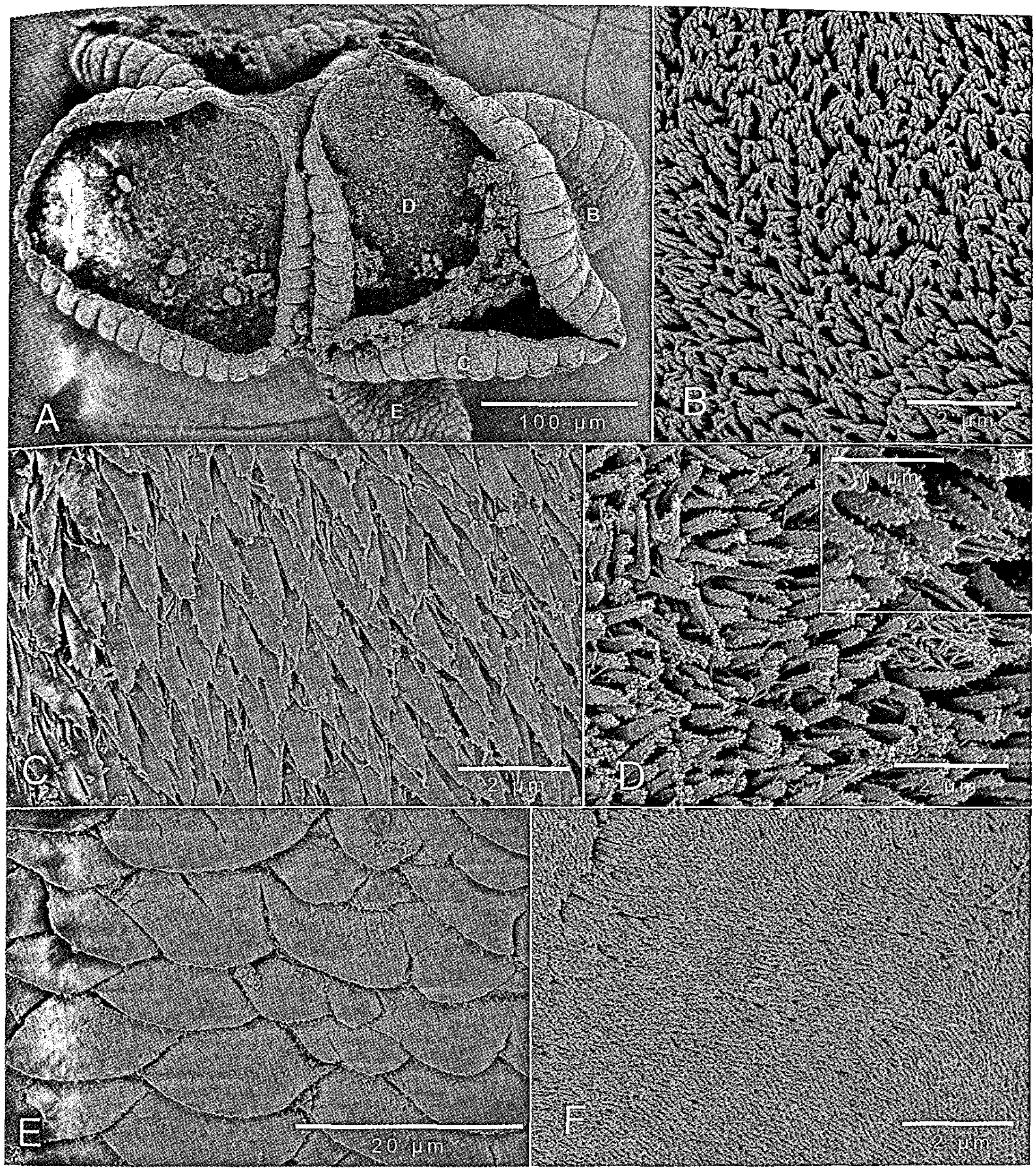

Fig. 75. Scanning electron micrographs of *Orectolobicestus mukahensis* Ruhnke, Caira and Carpenter, 2006. A. Scolex. White numbers indicate locations at which Fig. 75B–F were taken. B. Proximal surface of bothridium, not on surface of marginal loculus. C. Proximal surface of bothridium at marginal loculus. D. Distal surface of bothridium; inset shows enlarged view of microtriches. E. Scutes on anterior regions of strobila. F. Enlarged view of scutes; note scutes composed of elongate filitriches. (Taken from Ruhnke, Caira and Carpenter [2006], copyright 2006. Used with permission.)

capilliform filitriches.

Terminal proglottids 326–930 (675 ± 221; n=8) long x 173–358 (233 ± 58; n=8) wide, with length/width ratio 1.7–4.3:1 (3 ± 1; n=8); posterior proglottids with 72–91 (80 ± 10; n=3) testes. Testes oblong, 5–30 (17 ± 8; n=7, *n*=20) long x 16–53 (41 ± 10; n=7, *n*=20) wide. Cirrus-sac oval, 85–97 (94 ± 6; n=4) long x 30–71 (41 ± 17; n=5) wide, contains coiled cirrus. Cirrus armed with spinitriches. Vas deferens coiled, median, bordering proximal anterior portion of cirrus-sac, anterior to cirrus-sac. Genital pores lateral, 76–79% (78 ± 1; n=7) of proglottid length from posterior end, irregularly alternating. Vagina median, extending anteriorly from ovary to anterior third of proglottid, then laterally, ventral to vas deferens, along anterior margin of cirrus-sac, opening into genital atrium anterior to cirrus. Ovary near posterior end of proglottid, H-shaped in frontal view, 105–109 (107 ± 3; n=2) long x 112–118 (115 ± 4; n=2) wide, tetralobed in cross-section. Ovicapt 20 (n=2) in diameter at posterior margin of ovarian bridge. Mehlis' gland posterior to ovicapt. Uterus ventral to vagina, extending from anterior margin of ovary to posterior margin of cirrus-sac in mature proglottids. Uterine duct present, median, parallel and dorsal to uterus, extending to posterior margin of cirrus-sac in mature proglottids, then enters uterus at level of posterior margin of cirrus-sac. Vitellarium follicular; follicles 3–9 (7 ± 2; n=5, *n*=15) long x 9–28 (18 ± 6; n=5, *n*=15) wide, in two lateral bands each with two to three dorsal and two to three ventral row of follicles, interrupted by ovary and cirrus-sac.

Remarks

Orectolobicestus mukahensis is distinguished from *O. chiloscyllii* and *O. randyi* in total length (1.8–5.3 vs. 12 and 5.7–9.8, respectively), and differs from *O. chiloscylii, O. kelleyae,* and *O. tyleri* in proglottid number (19–29 vs. 6–18, 27–38, and 7–17, respectively). The species further differs from *O. chiloscylii, O. randyi,* and *O. tyleri* in proglottid length (326–930 vs. 2,300, 1,290–2,860, and 955–1,364, respectively). *Orectolobicestus mukahensis* differs conspicuously from *O. lorettae* in its possession of neck scutes that are spathate rather than elongate. *Orectolobicestus mukahensis* differs from *O. tyleri, O. lorettae,* and *O. kelleyae* possession of spinitriches on its proximal bothridial surfaces that are serrated rather than having two to three marginal protrusions restricted to the distal most tip.

Orectolobicestus randyi Ruhnke, Caira and Carpenter, 2006

(Figs. 60, 76–78)

Taxonomic status: Valid.
Type host: *Chiloscyllium hasselti* Bleeker, 1852, the Indonesian bamboo shark.
Type locality: South China Sea off Mukah (02°54'N, 112°06'E), Sarawak, Malaysia (Fig. 60).
Site of infection: Spiral intestine.
Type material: Holotype, MZUM(P) 166(h) (Fig. 76); paratype, MZUM(P) 167(p), LRP 3889–3891, USNPC 97497, IMPB 77.32.05. Remaining paratypes retained in T.R. Ruhnke's collection.
Material examined: All types were examined.
Etymology: This species is named for Randy Carpenter, father of S.D. Carpenter.

Description (taken from Ruhnke et al. [2006b]).

Worms euapolytic, slightly craspedote, 5.7–9.8 (7.3 ± 1.6; n=6) mm long; maximum width 921–1,495 (1,166 ± 198; n=11) at level of scolex. Proglottids 11–22 (17 ± 3; n=8) in number. Scolex (Figs. 77B, 78A) 502–893 (724 ± 88; n=11) long, with four bothridia. Bothridia 502–856 (684 ± 76; n=11, *n*=21) long x 422–856 (611 ± 126; n=11, *n*=18) wide, each with 30–41 (37 ± 4; n=6; *n*=12) marginal loculi and single round apical sucker; apical sucker 81–149 (112 ± 17; n=10, *n*=26) in diameter. Proximal surfaces of all but rims of bothridia covered with capilliform filitriches (Fig. 78B). Proximal surfaces of marginal loculi covered with capilliform filitriches and serrate gladiate spinitriches with three marginal protrusions restricted to distal-most tip of spinitriches; median protrusion

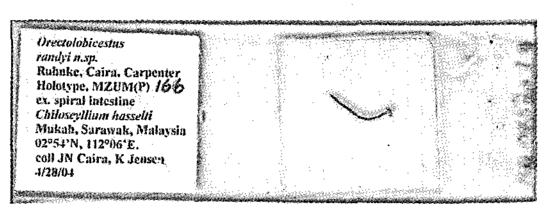

Fig. 76. *Orectolobicestus randyi* Ruhnke, Caira and Carpenter, 2006. Holotype slide (MZUM[P] 166[h]).

longest. Distal surfaces of apical suckers, marginal loculi and bothridia covered with capilliform filitriches and modified gongylate gladiate spinitriches in which protrusions are restricted to distal half of spinitriches; protrusions arranged along lateral margins and throughout circumference of distal-most tip of spinitriches. Neck 614–1,364 (831 ± 222; n=11) long, scutellate. Scutes elongate, irregularly overlapping, consisting of densely packed, capilliform filitriches.

Terminal proglottids 955–1,732 (1,271 ± 284; n=11) long x 211–374 (291 ± 60; n=11) wide; length/width ratio 3.2–7.8:1 (4.5 ± 1.2; n=11). Posterior proglottids with 75–112 (96 ± 14; n=5) testes. Testes oblong, 19–50 (30 ± 10; n=9, *n*=27) long x 33–65 (49 ± 11; n=9, *n*=27) wide. Cirrus-sac oblong, 69–167 (130 ± 32; n=8) long x 36–87 (59 ± 17; n=7) wide, contains coiled cirrus. Cirrus armed with spinitriches. Vas deferens coiled, median, overlaps proximal portion of cirrus-sac, anterior to cirrus-sac. Genital pores lateral, 66–77% (73 ± 4; n=8) of proglottid length from posterior end, irregularly alternating. Vagina median, extending anteriorly from ovary to anterior third of proglottid, then laterally, ventral to vas deferens, along anterior margin of cirrus-sac, to genital atrium, opening anterior to cirrus in common genital atrium. Ovary near posterior end of proglottid, H-shaped in frontal view, 106–240 (159 ± 49; n=7) long x 108–221 (156 ± 46; n=6) wide, tetralobed in cross-section. Ovicapt 16–28 (23 ± 6; n=3) in diameter at posterior margin of ovarian bridge. Mehlis' gland posterior to ovicapt. Uterus ventral to vagina, extending from anterior margin of ovary to posterior margin of cirrus-sac in mature proglottids. Uterine duct present, median, parallel and dorsal to uterus, extending to posterior margin of cirrus-sac in mature proglottids, then enters uterus at level of posterior margin of cirrus-sac. Vitellarium follicular; follicles oblong, 6–19 (11 ± 4; n=10, *n*=29) long x 10–33 (20 ± 6; n=10, *n*=29) wide, in two lateral bands, each with two to three dorsal and two to three ventral row of follicles, interrupted by ovary and cirrus-sac.

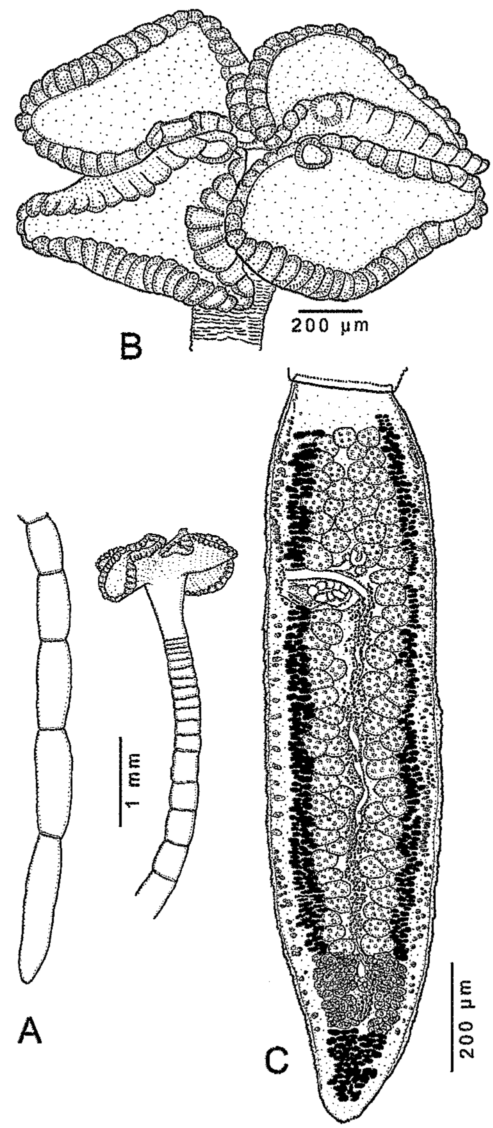

Fig. 77. Line drawings of *Orectolobicestus randyi* Ruhnke, Caira and Carpenter, 2006. A. Holotype (MZUM[P] 166[h]). B. Scolex of paratype (LRP 3889). C. Terminal proglottid of paratype (LRP 3891). (Taken from Ruhnke, Caira and Carpenter [2006], copyright 2006. Used with permission.)

Remarks

Orectolobicestus randyi differs from *O. tyleri, O. lorettae,* and *O. mukahensis* in the possession of spinitriches on its proximal bothridial surfaces that are trifid, rather serrate throughout their length. *Orectolobicestus randyi* differs from *O. mukahensis, O. kel-*

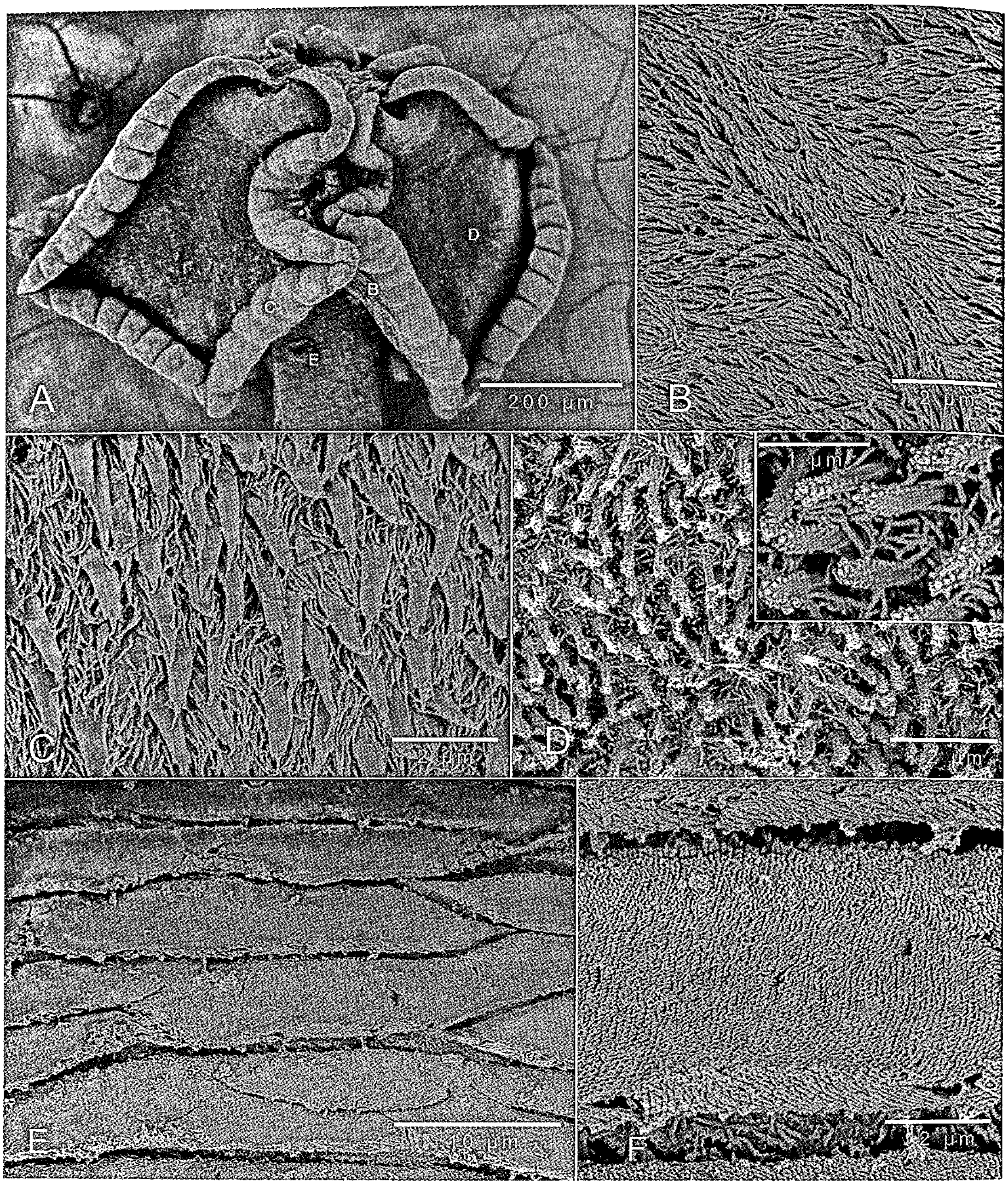

Fig. 78. Scanning electron micrographs of *Orectolobicestus randyi* Ruhnke, Caira and Carpenter, 2006. A. Scolex. Letters indicate locations at which Figs. 78B–F were taken. B. Proximal surface of bothridium, not on surface of marginal loculus. C. Proximal surface of bothridium at marginal loculus. D. Distal surface of bothridum; inset shows enlarged view of microtriches. E. Scutes on anterior regions of strobila. F. Enlarged view of scutes; note scutes composed of elongate filitriches. (Taken from Ruhnke, Caira and Carpenter [2006], copyright 2006. Used with permission.)

leyae, and *O. chiloscyllii* in proglottid length (955–1,364 vs. 326–930, 595–843, and 2,300). *Orectolobicestus randyi* differs from *O. lorettae* in total length (5.7–9.8 vs. 3.3–5.5 mm).

ORYGMATOBOTHRIUM Diesing, 1863

Taxonomic Status: Valid.

Type species: *Orygmatobothrium musteli* (Van Beneden, 1850) Diesing, 1863.

Other species: *Orygmatobothrium juani* Ivanov, 2008; *O. schmittii* Suriano and Labriola, 2001.

Etymology: An etymology was not given by Diesing, 1863, but presumably, *Orygma* (Gr.) = pit; *bothrios* (Gr.) = pit.

Diagnosis

Phyllobothriidae. Worms craspedote, euapolytic. Scolex with four bothridia. Bothridia uniloculate, with anterior apical sucker and central circular, accessory organ. Proximal bothridial surfaces with trifid spinitriches with long medial projection, and filitriches. Distal bothridial surfaces covered with gongylate columnar spinitriches and filitriches. Cephalic peduncle present. Neck present, scutellate. Immature proglottids wider than long. Mature proglottids at least twice as long as wide. Surface of proglottids comprised of capilliform filitriches. Testes numerous, distributed in one or more rows in cross section, round; post-vaginal testes present. Cirrus-sac elongate oval, curved strongly anteriorly (J-shaped), containing armed cirrus. Vas deferens coiled, anterior to cirrus-sac. Shallow genital atrium present. Vagina median, extending anteriorly from Mehlis' gland to mid-level of proglottid, then laterally along anterior margin of vas deferens, opening anterior to cirrus into common genital atrium. Genital pores in anterior half of proglottid. Ovary H-shaped in frontal view, tetralobed in cross section. Uterus ventral, saccate in free gravid proglottids, extending anterior from ovary to level of cirrus-sac. Vitellarium follicular; follicles distibuted in two lateral fields, extending entire length of proglottid, interrupted by cirrus-sac. Parasites of Triakidae.

Remarks

Orygmatobothrium was erected by Diesing (1863) for *Anthobothrium musteli* Van Beneden, 1850 (*pro parte*). The genus differs from all other tetraphyllidean genera in possessing a central accessory organ on its bothridial surfaces. Ivanov (2008) referred to this structure as a glandulomuscular organ, but the structural nature of this organ is yet to be determined. *Orygmatobothrium* resembles some species of *Paraorygmatobothrium, Orectolobicestus*, and *Phyllobothrium squali* in possessing gongylate columnar spinitriches on its distal bothridial surfaces.

At present, reports of *Orygmatobothrium* species are restricted to species of the houndshark genus *Mustelus*. Given that there are 27 valid species of *Mustelus* (see Agbayani 2006), it is certain that many species of *Orygmatobothrium* remain to be discovered.

Orygmatobothrium musteli (Van Beneden, 1850) Diesing, 1863 redes.

TYPE SPECIES

(Figs. 79–81)

Synonyms: *Anthobothrium musteli* Van Beneden, 1850 (*pro parte*); *Orygmatobothrium versatile* (Diesing, 1854) Diesing, 1863; *Tetrabothrium versatile* Diesing, 1854.

Taxonomic status: Valid.

Type host: *Mustelus mustelus* (L., 1758), the Smooth-hound.

Site of infection: Spiral intestine.

Type locality: Coast of Belgium (Fig. 79).

Additional locality: Plymouth, United Kingdom (Fig. 79).

Type specimens: Not specified.

Voucher specimens: BNHM 1965.2.23.172–182 (Fig. 80A).

Specimens examined: BNHM 1965.2.23.172–182 (Fig. 80A).

Etymology: The species was named for its host species.

Description

Worms craspedote, euapolytic, 23–40 mm (31.6 ± 6; n=9) long; maximum width 668–1,240 (1,037 ± 198; n=7) at scolex. Proglottids 65–90 (77 ± 10; n=5) in number. Scolex with four bothridia. Bothridia uniloculate, each with a single apical sucker and central

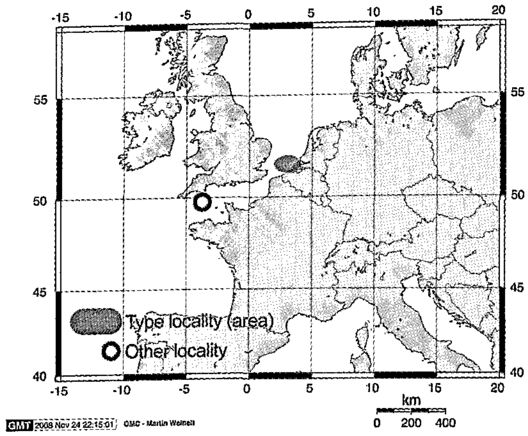

Fig. 79. Geographic distribution of *Orygmatobothrium musteli* (Van Beneden, 1850) Diesing, 1863.

accessory organ. Apical sucker 75–100 (83 ± 9; n =5; *n*=10) in diameter; accessory organ 95–140 (117 ± 15; n=7; *n*=13), accessory organ:apical sucker diameter ratio 1.1–1.9:1 (1.4 ± 0.2; n=4; *n*=8). Neck scutellate.

Immature proglottids at mid-strobila much wider than long, 127–223 (177 ± 33; n=7) long x 668–1,177 (972 ± 180; n= 7) wide. Terminal proglottids 1,160–1,840 (1,650 ± 328; n=5) long x 660–920 (830 ± 118; n=5) wide, terminal proglottid length to width ratio 1.4–2.7:1 (2 ±0.5; n=5). Free proglottids 2.9–4.1 mm (3.5 ± 0.5; n=5) long x 1–1.2 mm (1.1 ± 0.1; n=5) wide; free proglottid length to width ratio 2.5–4.1 (3.2 ± 0.6; n=5). Testes 312–350 (n=4) in number; testes round, 50–75 (57 ± 8; n=4; *n*=10) in diameter in terminal proglottids. Cirrus-sac elongate oval, curved anteriorly, 300–440 (382 ± 52; n=6) long x 100–130 (112 ± 12; n=6) wide in terminal proglottids; 541–684 (595 ± 58; n=5) long x 143–175 (162 ±1 3; n=5) wide in free proglottids. Cirrus coiled, armed with spinitriches. Vas deferens coiled, median, bordering proximal portion of cirrus-sac, anterior to cirrus-sac. Genital pores lateral, 61–70% (66 ± 4; n=6) of proglottid length from posterior end of terminal proglottids, irregularly alternating. Genital pores 66–82% (72 ± 7; n=5) of proglottid length from posterior end of free proglottids. Vagina median, extending anteriorly from ovary to mid-level of proglottid, then laterally along anterior margin of vas deferens to genital pore, opening anterior to cirrus into common genital atrium. Ovary near posterior end of proglottid, H-shaped in frontal view, 300–520 (n=4) long x 335–440 (n=4) wide in terminal proglottids, 684–875 (n=5) long x 477–541 (n=5) wide in free proglottids. Ovicapt at posterior margin of ovarian bridge. Mehlis' gland posterior to ovicapt. Uterus ventral to vagina, extending from anterior margin of ovary to level of cirrus-sac in free proglottids. Uterine duct present, median, parallel and dorsal to uterus, extending to posterior margin of cirrus-sac, then entering uterus at level of posterior margin of cirrus-sac. Vitellarium follicular; vitelline follicles oblong, in two lateral fields, each field consisting of 3–4 dorsal and 3–4 ventral columns of follicles, interrupted by cirrus-sac. Eggs not observed.

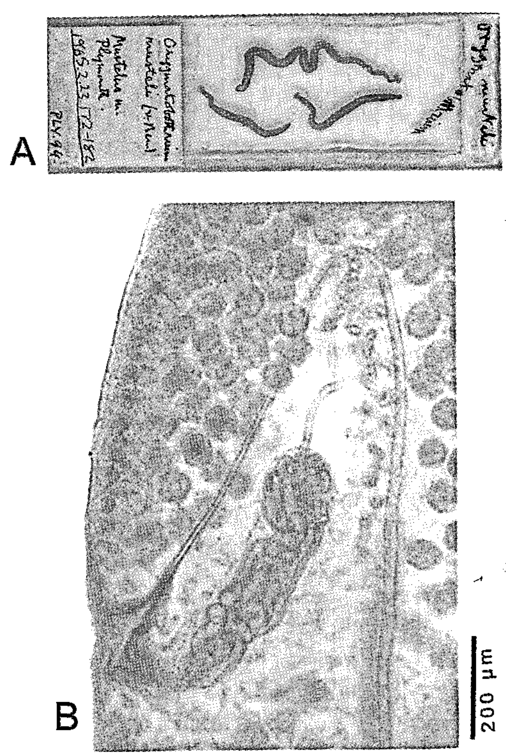

Fig. 80. Photomicrographs of *Orygmatobothrium musteli* (Van Beneden, 1850) Diesing, 1863. A. Voucher slide (BNHM 1965.2.23.172-182). B. Terminal genitalia of voucher (BNHM 1965.2.23.172-182).

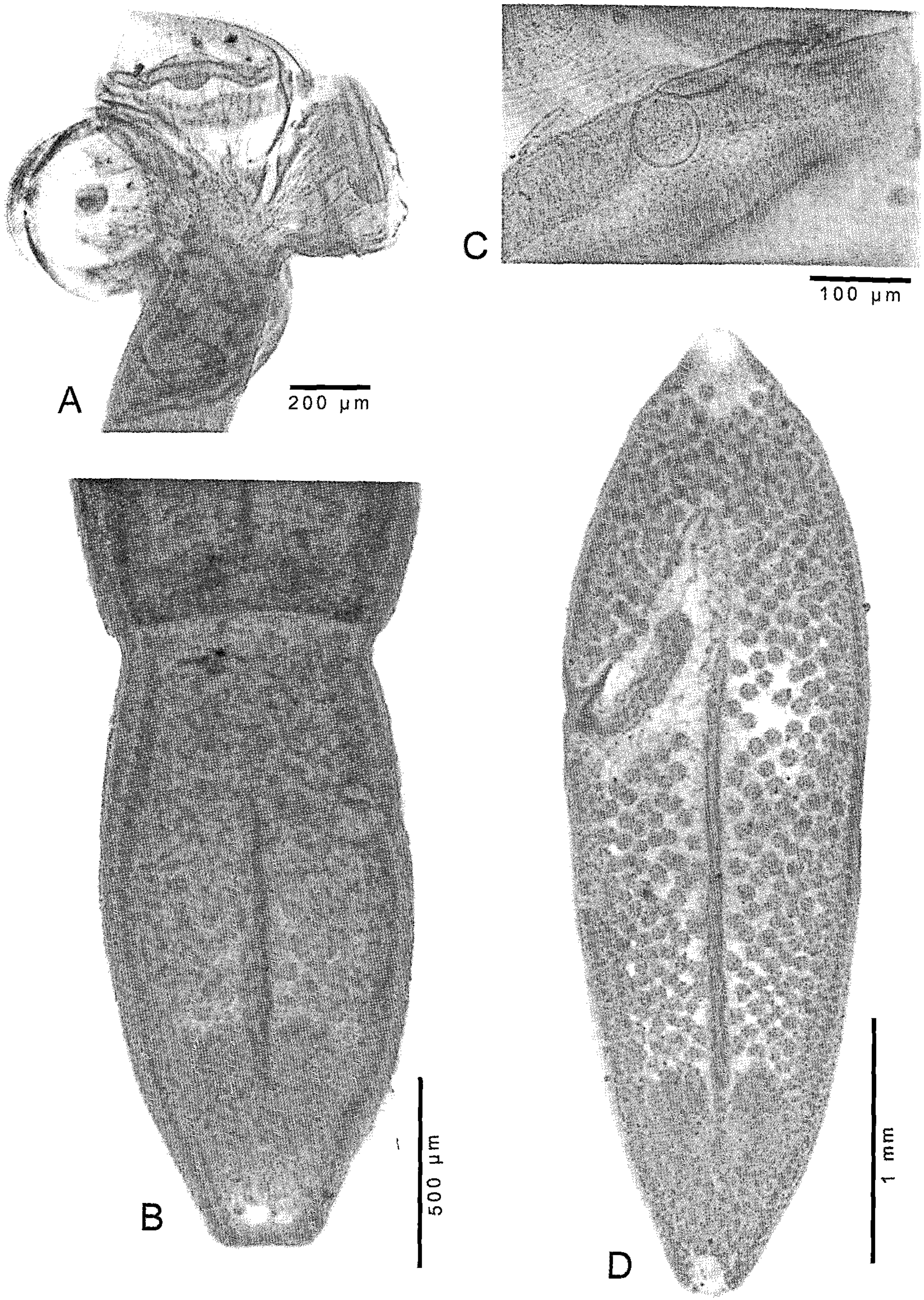

Fig. 81. Photomicrographs of *Orygmatobothrium musteli* (Van Beneden, 1850) Diesing, 1863. A. Scolex of voucher (BNHM 1965.2.23.172-182). B. Terminal proglottid of voucher (BNHM 1965.2.23.172-182). C. Apical sucker of voucher (BNHM 1965.2.23.172-182). D. Free proglottid of voucher (BNHM 1965.2.23.172-182).

Remarks

Orygmatobothrium musteli was originally described as *Anthobothrium musteli* by Van Beneden (1850) for specimens taken from hosts he reported as *Mustelus vulgaris, Galeus canis,* and *Scyllium canicula.* Diesing (1863) listed *Anthobothrium musteli* as a synonym of *Orygmatobothrium versatile* when he erected the genus *Orygmatobothrium.* This created the name *Orygmatobothrium musteli* (Van Beneden, 1850) Diesing, 1863, but also, despite Diesing actions, established *O. musteli* as the name of the type species of the genus, as it is the older of the two names. Southwell (1925) correctly noted that Van Beneden's original description was a composite of two species. Southwell (1925) recognized one of these as *Phyllobothrium musteli* (Van Beneden, 1850) Southwell, 1925. However, that species is transferred to *Paraorygmatobothrium* in this monograph (see pg. 146). Southwell (1925) concluded that the other species was consistent with Diesing's (1863) concept of *Orygmatobothrium,* as it possessed "two accessory suckers" (Southwell 1925, p. 203). Woodland (1927) provided an account of *O. musteli* from a host he reported as *Mustelus vulgaris* (= *M. mustelus*) from Plymouth, United Kingdom. Euzet (1959) considered *O. versatile* to be a synonym of *O. musteli.*

Given the lack of type material, the description of *O. musteli* provided in this monograph was based entirely on material collected from Plymouth, U.K. This locality is located 500–600 km across the English Channel from the Belgian coast, the type locality area for *O. musteli.* Differences between these and the specimens of Euzet (1959) precluded inclusion of Euzet's specimens in the description. Euzet's (1959) account of *O. musteli* was based on specimens of *Orygmatobothrium* from *Mustelus mustelus* and *"M. canis"* collected from Sète and Concarneau, France. The specimens from Plymouth, U.K. (BMNH 1965.2.23.172–182) differ from those described by Euzet (1959) in several respects. For example, the specimens differ in maximum width (668–1,240 vs. 1,500–2,000, respectively), accessory sucker diameter (75–110 vs. 50–60), proglottid number (65–90 vs. 160–200), and testes number (312–350 in free proglottids vs. 380–440). In addition, the free proglottid illustrated by Euzet (1959) is approximately 7 mm long x 2 mm wide. The free proglottids of the Plymouth, U.K. specimens are 2.9–4.1 long x 1–1.2 mm wide. The size differences between these two lots of specimens could be attributed to development or fixation procedure, however, the differences in proglottid number and testes number indicate that the species found in the Mediterranean and perhaps also Concarneau, and may constitute a different species.

Orygmatobothrium musteli differs from *O. schmittii* in proglottid number (65–90 vs. 43–63), testes number (312–350 in free proglottids vs. 198–287 in mature proglottids) and genital pore position from the posterior end of the proglottid (61–70% vs. 44–56%). *Orygmatobothrium musteli* differs from *O. juani* in total length (23–40 mm vs. 39–62.9 mm), free proglottid dimensions (mean of 3.5 x 1.1 mm vs. mean of 8.9 x 2.2 mm), and genital pore position from posterior end of posterior proglottids (61–70% vs. 48–54%).

Orygmatobothrium juani Ivanov, 2008

(Figs. 82–84)

Taxonomic status: Valid.

Type host: *Mustelus fasciatus* (Garman, 1913), the Striped smooth-hound shark.

Site of infection: Spiral intestine.

Type locality: Puerto Quequén (38°32'S, 58°42'W), Buenos Aires Province, Argentina (Fig. 82).

Type specimens: Holotype and five paratypes MACN-Pa 445 1–6 (Fig. 83A).

Specimens examined: MACN-Pa445 1.

Etymology: *Orygmatobothrium juani* was named for the V. Ivanov's son, Juan Pastorino.

Description (modified from Ivanov [2008]).

Worms craspedote, euapolytic 39.0–62.9 (51.6 ± 9.7, n=12) mm long; maximum width 1,100–1,600 (1,341 ± 203, n=12) at level of scolex; 59–83 proglottids (71 ± 9, n=12) per worm. Scolex lacking apical organ, composed of four bothridia and short cephalic peduncle, 780–1,220 (1,000 ± 174, n=12) long

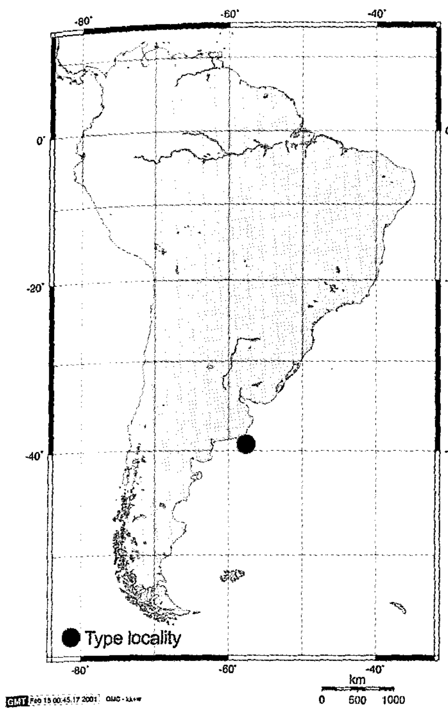

Fig. 82. Geographic distribution of *Orygmatobothrium juani* Ivanov, 2008.

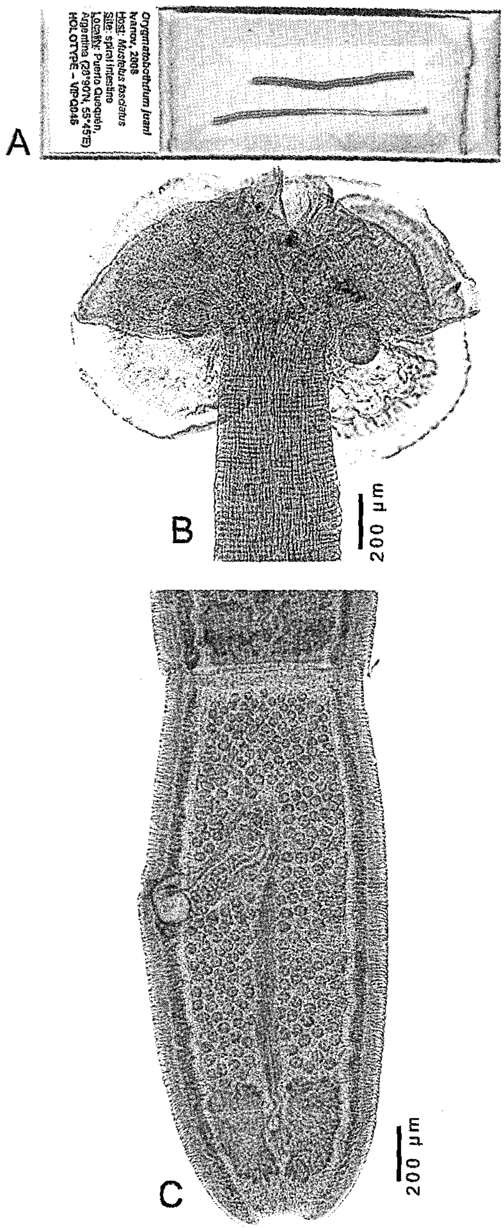

Fig. 83. Photomicrographs of *Orygmatobothrium juani* Ivanov, 2008. A. Holotype slide (MACN-Pa 445 1). B. Scolex. C. Terminal proglottid of holotype (MACN-Pa 445 1).

x 1,100–1,600 (1,341 ± 203, n=12) wide. Bothridia stalked, 700–890 (803 ± 68, n=12, *n*=16) long x 700–910 (816 ± 76, n=12, *n*=16) wide, with apical sucker and central accessory organ, bothridial margin cleft at level of apical sucker forming two lobes that do not overlap, ring of marginal muscles formed by four to five muscular fibers. Apical suckers 75–110 (90 ± 11, n=12, *n*=17) long x 75–120 (96 ± 11, n=12, *n*=17) wide; accessory organ 88–200 (158 ± 26, n=12, *n*=17) in diameter; accessory organ:accessory sucker ratio 1–2:1 (1.6 ± 0.3, n=12, *n*=16). Bothridial stalks 162–250 (204 ± 43, n=12, *n*=17) long. Center and margins of bothridial apical sucker covered with papilliform filitriches, 0.10–0.13 (0.12 ± 0.01, n=7) long in center surface, 0.28–0.46 (0.35 ± 0.06, n= 5) long in marginal surface. Distal bothridial surfaces covered with gongylate columnar spinithriches with protrusions covering distal two-thirds of microthrix length; gongylate columnar spinitriches 1.1–3.1 (1.9 ± 0.5, n= 33) long x 0.4–1 (0.6 ± 0.2, n= 33) wide at base; interspersed with papilliform filitriches, 0.3–0.6 (0.4± 0.1, n= 15) long x 0.1 wide (n= 15). Proximal bothridial surfaces covered with trifid spinitriches with median projection conspicuously larger than lateral basal projections; trifid spinitriches 2.6–3.2 (2.8 ±

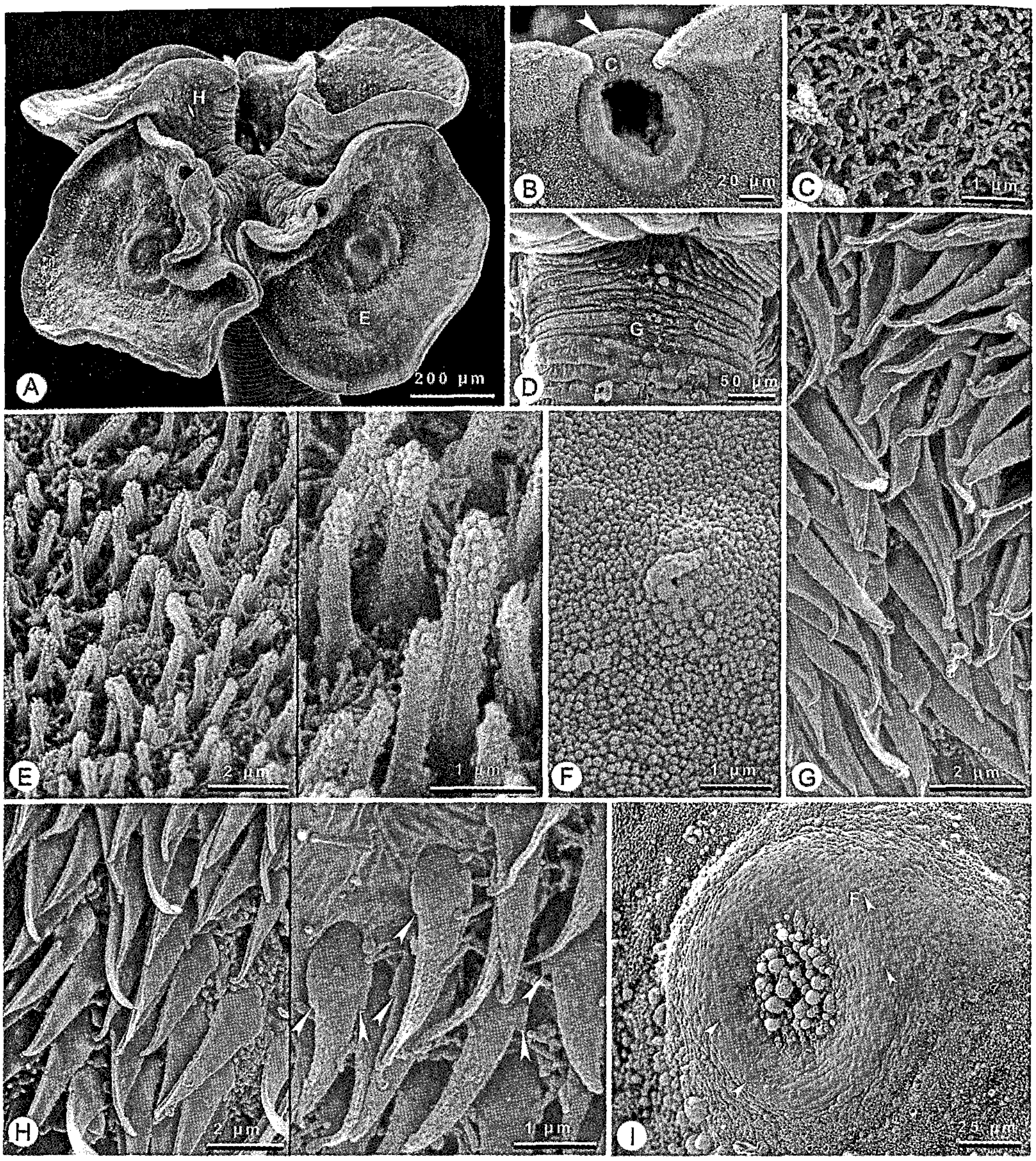

Fig. 84. Scanning electron micrographs of *Orygmatobothrium juani* Ivanov, 2008. A. Scolex (letters indicate regions in photos E and H). B. Accessory sucker (letter indicate region in photo C, arrow indicates cleft without overlapped margins). C. Surface of accessory sucker. D. Region of cephalic peduncle and germinative zone (letter indicate regions in photo G). E. Distal bothridial surface. F. Outer surface of central glandulomuscular organ. G. Surface of cephalic peduncle. H. Proximal bothridial surface, arrows indicate position of projections in trifid microtriches. I. Glandulomuscular organ (letter indicate regions in photo F, arrows indicate rounded projections with cilia). (Taken from Ivanov [2008], copyright 2008. Used with permission.)

0.2, n= 21) long interspersed with filitriches with pointed tip, 0.35–0.60 (0.44 ± 0.07, n= 20) long x 0.07–0.12 (0.10 ± 0.01, n= 20) wide at base. Central and marginal surfaces of accessory organ covered with papilliform filitriches with rounded tip, 0.11–0.15 (0.13 ± 0.02, n= 12) in diameter; marginal surface covered with numerous rounded projections with cilia. Cephalic peduncle 110–250 (177 ± 57, n=12) long x 235–375 (291 ± 63, n=12) wide; neck 13.2–29.4 mm long. Cephalic peduncle surface covered with gladiate spinitriches, 2.95–3.91 (3.28 ± 0.33, n= 15) long x 0.81–0.96 (0.89 ± 0.06, n= 8) wide at base. Surface of neck and entire strobila scutellate, surface of scutes comprised of densely packed capilliform filitriches; two ventral and two dorsal scutes on neck, becoming irregular in shape and number in mature proglottids.

Immature proglottids wider than long, 56–79 (66 ± 12, n=12) in number. Mature proglottids longer than wide, 1,000–2,220 (1,485 ± 381, n=12, *n*=25) long x 660–980 (820 ± 94, n=12, *n*=25) wide; length to width ratio 1.11–3.36:1 (1.98 ± 0.6; n=12, *n*=25), 3–4 (4 ± 0.5, n=12) per strobila. Detached gravid proglottids longer than wide, 5.9–11.5 mm (8.9 ± 1.8, n=15) long x 1.6–2.8 mm (2.2 ± 0.4, n= 15) wide; length to width ratio 3.05–5.42:1 (4.10 ± 0.70). Testes spherical, 28–50 (39 ± 5, n=12, *n*=60) in diameter, one row deep in cross-section; 262–469 (344 ± 72, n=12, *n*=25) in number in mature proglottids, extending anteriorly from anterior margin of ovary to anterior margin of proglottid, degenerating in detached gravid proglottids; 47–110 (74 ± 20, n=12, *n*=25) postvaginal testes. Cirrus-sac oval, slightly curved anteriorly, 310–500 (401 ± 64, n=12, *n*=30) long x ure proglottids, occupying 48–54% (51 ± 2) of proglottid width; containing cirrus with basal swelling and slender distal portion, covered with both short filitriches and thorn-like spinitriches, larger at basal swelling. Vas deferens extensive, highly coiled, extending anteriorly to vaginal bend. Vagina thick-walled, anterior to cirrus-sac, running anteriorly to bulk of vas deferens, descending posteriorly, forming a seminal receptacle at level of ootype region. Vagina entering common genital atrium anterior to cirrus; genital atriium 62–100 (75 ± 22 n=12, *n*=50) deep; marginal genital pores alternate irregularly, 46–60% (53 ± 4, n=12, *n*=50) from posterior margin of proglottid; genital pore region covered with numerous papillae. Ovary lobulated, H-shaped in frontal view, tetralobed in cross section, aporal lobe 150–385 (260 ± 76, n=12, *n*=30) long, poral lobe 155–400 (265 ± 81, n=12, *n*=30) long; 250–510 (393 ± 83, n=12, *n*=30) wide at ovarian isthmus in mature proglottids. Mehlis' gland 52–130 (78 ± 24) long x 57–150 (87 ± 32) wide. Vitellarium follicular; vitelline follicles in two lateral fields, each field consisting of one to two dorsal and one to two ventral columns of follicles, not overlapping testicular field or excretory ducts, 20–30 (25 ± 4, n=12, *n*=50) long x 13–20 (15 ± 2, n=12, *n*=50) wide, interrupted dorsal and ventrally at level of cirrus-sac and vagina, extending throughout the entire proglottid length. Uterus saccate running anteriorly to level of genital pore, formed in mature proglottids. Eggs oval, with ornamented shell, 30–32 (31 ± 1, n=15) long x 22–25 (24 ± 1.7, n=15) wide; onchospheres 15–17 (17 ± 1, n=15) in diameter.

Remarks

Orygmatobothrium juani differs from *O. musteli* in free proglottid dimensions (mean of 8.9 x 2.2 vs. mean of 3.5 x 1.1 mm), and genital pore position from posterior end of posterior proglottids (48–54% vs. 61–70%). Among other features, *O. juani* differs from *O. schmittii* in testes size (30–40 vs. 60–105). In addition, the testes are distributed in one layer (one testis deep in cross sections) and extend anteriorly from anterior margin of ovarian lobes in *O. juani*; whereas in *O. schmittii*, the testes are in three to four layers deep and extend anteriorly from the ovarian bridge.

Orygmatobothrium schmittii Suriano and Labriola, 2001

(Figs. 85–87)

Taxonomic Status: Valid.

***Type host*:** *Mustelus schmitti* Springer, 1939, the Narrownose smooth-hound shark.

***Site of infection*:** Spiral intestine.

***Type locality*:** Mar del Plata (38°00'S, 57°33'W), Buenos Aires Province, Argentina (Fig. 85).

Additional locality: Puerto Quequén (38°32'S, 58°42'W), Buenos Aires Province, Argentina (Fig. 85).

***Type specimens*:** Holotype and paratype, MACN-PA 382/1–2.

Specimens examined: MACN-Pa 444/1–5 (Fig. 86A).

Description (modified from Ivanov [2008]).

Worms craspedote, euapolytic, 32.6–50.6 (38.6 ± 7, n=15) mm long; maximum width 1,170–1,800 (1,500 ± 253, n=15) at level of scolex; proglottids 43–63 (54 ± 7, n=15) in number. Scolex lacking an apical organ, composed of four stalked bothridia, 750–1,300 (1,058 ± 214, n=15) long x 1,170–1,800 (1,500 ± 253, n=15) wide Bothridia 600–950 (777 ± 120, n=15, *n*=20) long x 730–1,080 (827 ± 136; n=15, *n*=20) wide, with apical sucker and central accessory organ, bothridial margin cleft at level of apical sucker forming two overlapping lobes. Submarginal ring of musculature on perimeter of bothridium comprised of 4–5 muscle fibers. Apical sucker 60–160 (98 ± 35, n=15, *n*=20) long x 75–185 (108 ± 37, n=15, *n*=20) wide, accessory organ 85–190 (125 ± 35, n=15, *n*=20) in diameter; accessory organ:apical sucker ratio 0.8–1.4:1 (1.1 ± 0.15, n=15, *n*=20). Central and marginal surfaces of apical sucker covered with papilliform filitriches with rounded tips, 0.1–0.2 (n=12) long x 0.04–0.06 (n= 12) wide. Distal bothridial surfaces covered with gongylate columnar spinitriches with protrusions covering distal two-thirds of microthrix length, gongylate columnar spinitriches 2.2–3.6 (3 ± 0.3, n= 24) long x 0.8–1 (0.9 ± 0.1, n= 19) wide at base; interspersed with papilliform filitriches 0.2–0.5 (0.4 ± 0.1, n= 14) long x 0.05–0.08 (n= 10) wide. Proximal bothridial surfaces covered with trifid spinitriches with median projection conspicuously larger than lateral basal projections, trifid spinitriches 3.5–4.4 (4 ± 0.3, n= 11) long x 1.2–1.5 (1.3 ± 0.1, n= 8) wide at base; interspersed with filitriches with pointed tips, 1–1.6 (1.2 ± 0.3, n= 4) long x 0.07–0.12 (n= 6) wide at base. Central and marginal surfaces of accessory organ covered with papilliform filitriches with rounded tips, 0.2–0.3 (n= 24) long x 0.06–0.09 wide (n= 24); marginal surfaces covered with numerous rounded projections with cilia. Scolex proper covered with gladiate spinitriches, 3.2–3.6 (3.4 ± 0.2, n= 15) long x 1.47–1.51 (n= 8) wide at base. Cephalic peduncle 110–250 (177 ± 57, n=12) long x 235–375 (291 ± 63, n=12) wide. Neck 207–350 (264 ± 52, n=15) long x 225–325 (282 ± 43, n=15) wide. Cephalic peduncle covered with gladiate microtriches, 2–2.9 (n= 15) long x 0.9–1 (n= 8) wide at base. Surface of germinative zone and entire strobila covered with scutes; surface of scutes formed by densely packed capilliform filitriches (round pointed), 2 long; two ventral and two dorsal elongate scutes on germinative zone becoming irregular in shape and number in mature proglottids.

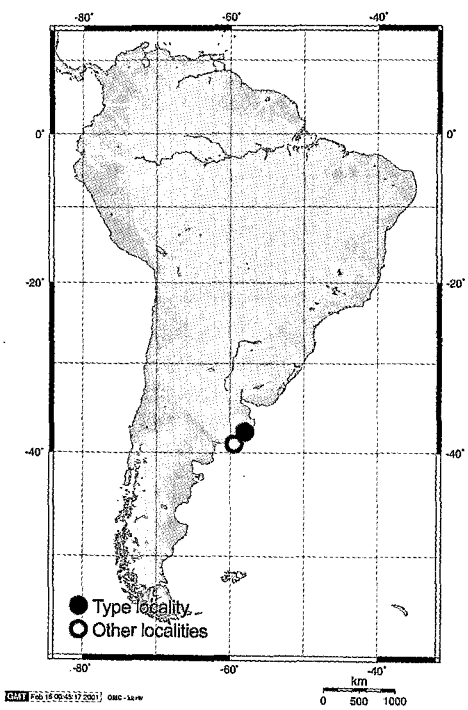

Fig. 85. Geographic distribution of *Orygmatobothrium schmittii* Suriano and Labriola, 2001.

Immature proglottids wider than long; 40–60 (49 ± 8, n=15) in number. Mature proglottids longer than wide, 940–2,580 (1591 ± 451, n=15, *n*=34) long x 700–1,160 (964 ± 169, n=15, *n*=34) wide; length to width ratio 1.02–2.89:1 (1.68 ± 0.5) 2–6 (4 ± 2, n=15) mature proglottids per strobila. Detached mature proglottids 3.3–3.8 mm (3.5 ± 0.35, n= 10) long x 1,140–1,400 (1,270 ± 184, n= 10) wide; length to width ratio 2.68–2.85:1 (2.77 ± 0.12, n= 10). Detached gravid proglottids 4.1–13.4 (8.1 ± 2.8, n=15) long x 1.4–3 (2.1 ± 0.5, n= 15) wide; length to width ratio 2.8–5.8:1 (3.7 ± 0.9, n= 15). Testes oval, 60–105 (82 ± 14, n=15, *n*=75) long x 55–95 (78 ± 10, n=15, *n*=75) wide, three rows deep

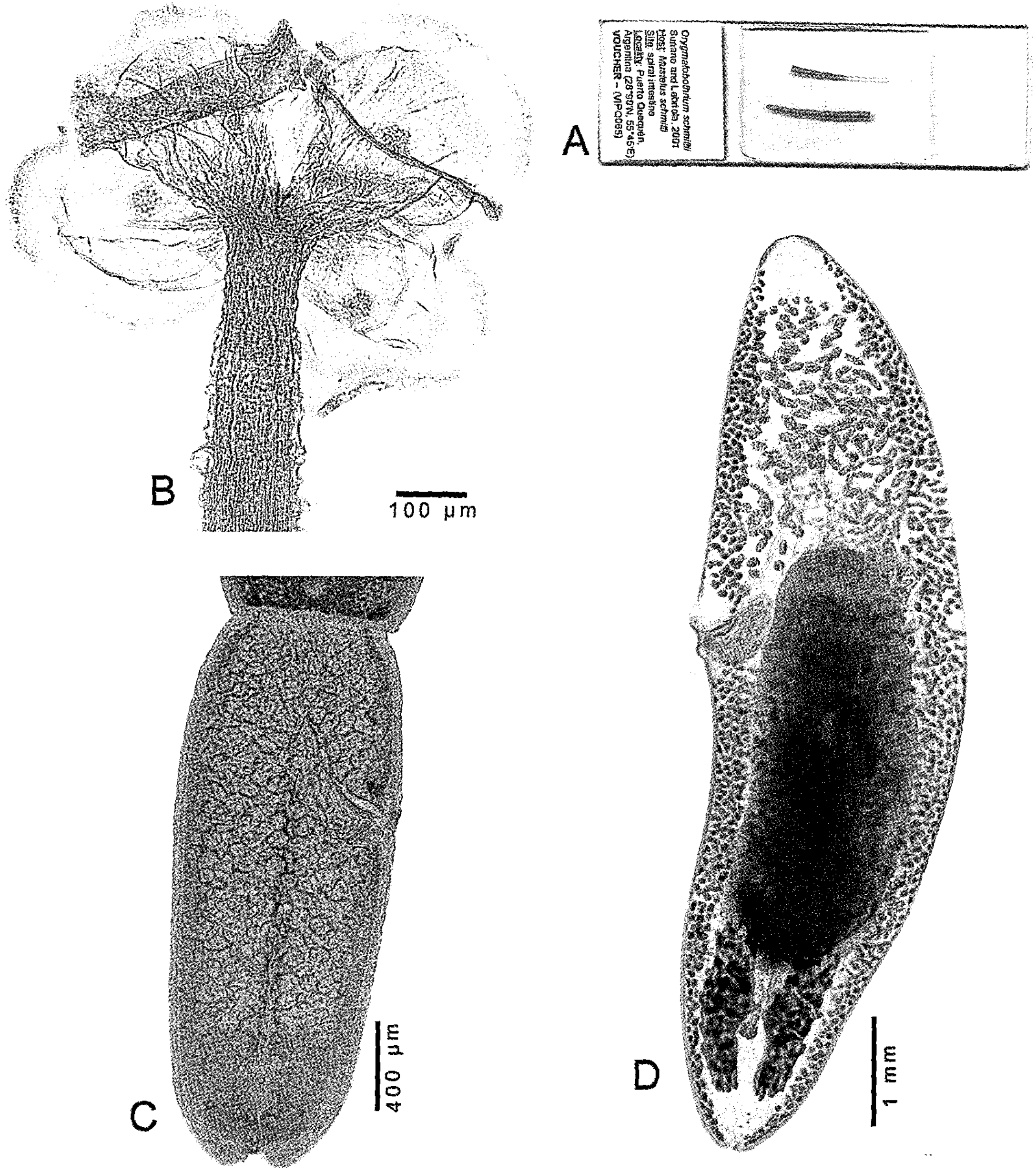

Fig. 86. Photomicrographs of *Orygmatobothrium schmittii* Suriano and Labriola, 2001. A. Voucher slide. B. Scolex of voucher. C. Terminal proglottid of voucher. D. Free proglottid of voucher.

in cross-section, 198–287 (236 ± 28, n=15, *n*=25) in number in mature proglottids, extending anteriorly from ovarian isthmus to anterior margin of proglottid, degenerating in detached gravid proglottids, 47–74 (58 ± 9, n=15, *n*=25) postvaginal testes. Cirrus-sac oval, slightly curved anteriorly, 350–610 (471 ± 76, n=15, *n*=30) long x 110–230 (169 ± 32, n=15, *n*=30) wide in mature proglottids, occupying 44–56% (51 ± 4) of proglottid width, containing cirrus with basal swelling and slender distal portion, both covered with papilliform filitriches and coniform spinitriches, larger at basal swelling. Vas deferens extensive, highly coiled, extending anteriorly to vaginal bend. Vagina thick-walled, opening

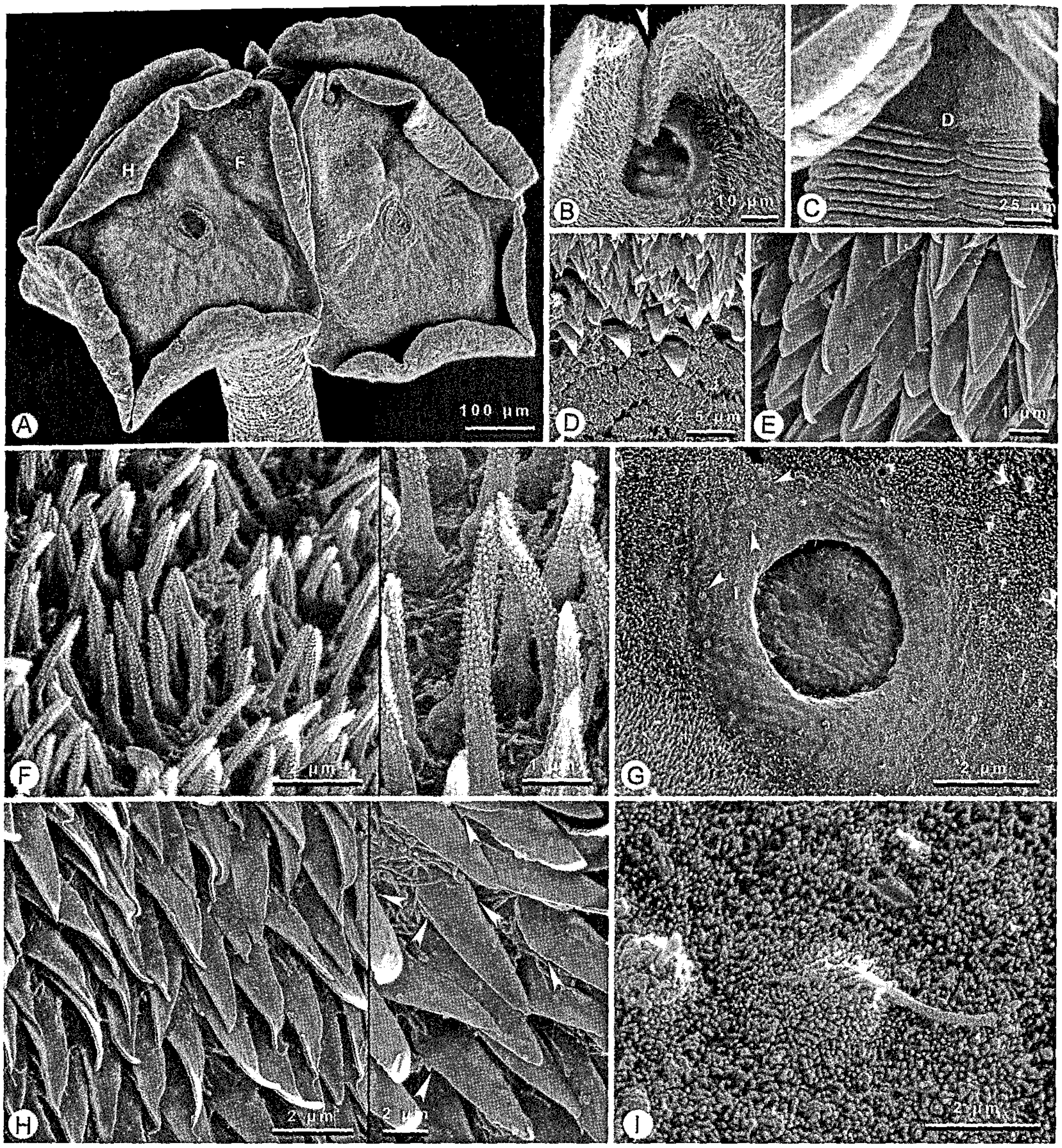

Fig. 87. Scanning electron micrographs of *Orygmatobothrium schmittii* Suriano and Labriola, 2001. A. Scolex (letters indicate regions in photos F and H). B. Accessory sucker (arrow indicates cleft with overlapped margins). C. Cephalic peduncle (letters indicate regions in photo D). D. Surface of cephalic peduncle. E. Surface of scolex proper. F. Distal bothridial surface (inset shows enlarged view of microtriches). G. Glandulomuscular organ (letter indicate region in photo I, arrows indicate rounded projections with cilia). H. Proximal bothridial surface (arrows indicate position of projections in trifid microtriches). I. Surface of Glandulomuscular organ. (Taken from Ivanov [2008], copyright 2008. Used with permission.)

anterior to cirrus in common genital atrium, running anteriorly to bulk of vas deferens, descending posteriorly, forming a seminal receptacle at level of ootype region, Mehlis' gland 90–125 (108 ± 17) long x 57–100 (89 ± 9) wide. Vagina and cirrus-sac join into genital atrium; genital atrium 75–140 (100 ± 20, n=15, *n*=50) deep; genital pores marginal, alternating irregularly, 59–72% (64 ± 4, n=15, *n*=50) from posterior margin of proglottid; genital pore region covered with numerous papillae. Ovary lobulated, H-shaped in frontal view, tetralobed in cross section at level of isthmus, 375–660 (527 ± 93, n=15, *n*=30) wide at ovarian isthmus in mature proglottids. Aporal ovarian lobe slightly longer than poral lobe; aporal ovarian lobe 310–770 (453 ± 128, n=15, *n*=30) long, poral ovarian lobe 275–700 (439 ± 120, n=15, *n*=30) long. Vitellarium follicular, vitelline follicles in two lateral fields, each field consisting of three to four dorsal and three to four ventral columns of follicles, follicles overlapping testicular field, 25–60 (40 ± 14, n=15, *n*=50) long x 15–35 (25 ± 6, n=15, *n*=50) wide, extending throughout the entire proglottid length, interrupted dorsally and ventrally at level of cirrus-sac and vagina. Uterus saccate, running anteriorly up to genital pore level, formed in mature proglottids. Eggs oval, shells ornamented, 30–35 (32 ± 1.8, n=15) long x 25–26 (25 ± 0.5, n=15) wide; onchospheres 15–17 (16.6 ± 0.8, n=15) in diameter.

Remarks

Suriano and Labriola (2001) described *Orygmatobothrium schmittii* from ten specimens collected from *Mustelus schmitti* off Mar del Plata, Argentina. Ivanov (2008) provided an excellent redescription of this species, and a slightly modified version of that work is presented here. Ivanov (2008) commented on the poor condition of the type specimens of *O. schmitti* and her redescription is based entirely on newly collected specimens.

Orygmatobothrium schmitti differs from *O. musteli* in proglottid number (43–63 vs. 65–90), testes number (198–287 in mature proglottids vs. 312–350 in free proglottids) and genital pore position from the posterior end of the proglottid (44–56% vs. 61–70%). Among other features, *Orygmatobothrium schmittii* differs from *O. juani* can be distinguished by testes size (60–105 vs. 30–40). In *O. schmitti,* the testes are 3–4 layers deep in section and extend anteriorly from the ovarian bridge, and in *O. juani,* the testes are distributed in one layer (one testis deep in cross sections) and extend anteriorly from anterior margin of ovarian lobes.

Ivanov (2008) noted that Ostrowski de Núñez (1973) reported the presence of *O. velamentum* from *M. schmitti* captured in coastal waters off Mar del Plata, but that the morphology of these specimens are consistent with her redescription of *O. schmittii.*

Other species of *Orygmatobothrium*

Only the above three nominal species of *Orygmatobothrium* are accepted as valid in this monograph. With respect to the other species, two are transferred to *Paraorygmatobothrium* in this monograph and one species is considered a member of *Crossobothrium* (see Appendix 2). The taxonomic status of each of the eight other nominal species is given below.

Orygmatobothrium crenulatum* Linton, 1897 *species inquirenda

Orygmatobothrium crenulatum was described by Linton (1897) for several specimens taken from *Dasyatis centroura* (Mitchill, 1815), the Roughtail stingray, collected from Woods Hole, Massachusetts, U.S.A. The type slides (USNPC 5506) are of material sectioned throught the bothridium. The illustrations of the scolex and bothridial sections are similar to the morphology of *Orygmatobothrium paulum* Linton, 1897, a species transferred to *Paraorygmatobothrium* below. It is possible that *O. crenulatum* is a synonym of *O. paulum.* Both species can be described as having bothridia that have a locular periphery ringed with a distinct band of muscles. This muscular condition has the effect of drawing the posterior portion of the loculus toward the apical plane. Linton (1897) stated that his specimens were young, with the proglottids not well developed. Perhaps their presence in *D. centroura* represents an accidental infection, as *O. paulum* is normally a cestode of the Tiger shark, *Galeocero cuvier.* At present, this species should be considered a *species inquirenda.* Type material: USNPC 5506. Material examined: none.

Orygmatobothrium forte* Linton, 1924 *incertae sedis (Fig. 88)

This species was originally described by Linton (1924) for specimens taken from

Cestracion zygaena (= *Sphyrna zygaena* [L., 1758]), the Smooth hammerhead shark, collected from Woods Hole, Massachusetts, U.S.A. Yamaguti (1952) transferred *O. forte* to *Marsupiobothrium*. However, the species lacks the accessory sucker-like structure found on the distal bothridial surface of *M. alopias*. *Orygmatobothrium forte* does not exhibit the diagnostic feature of *Orygmatobothrium*, the accessory organ on the center of the bothridium. However, *O. forte* does possess a band of musculature on the periphery of each bothridium. This bothridial condition is similar to that in *Marsupiobothrium* and *Scyphophyllidium uruguayense* Brooks, Marques, Perroni and Sidagis, 1999. At present, *O. forte* must be considered *incertae sedis* until additional material is available for study. Type material: USNPC 7671 (Fig. 88A). Material examined: USNPC 7671 (Fig. 88A).

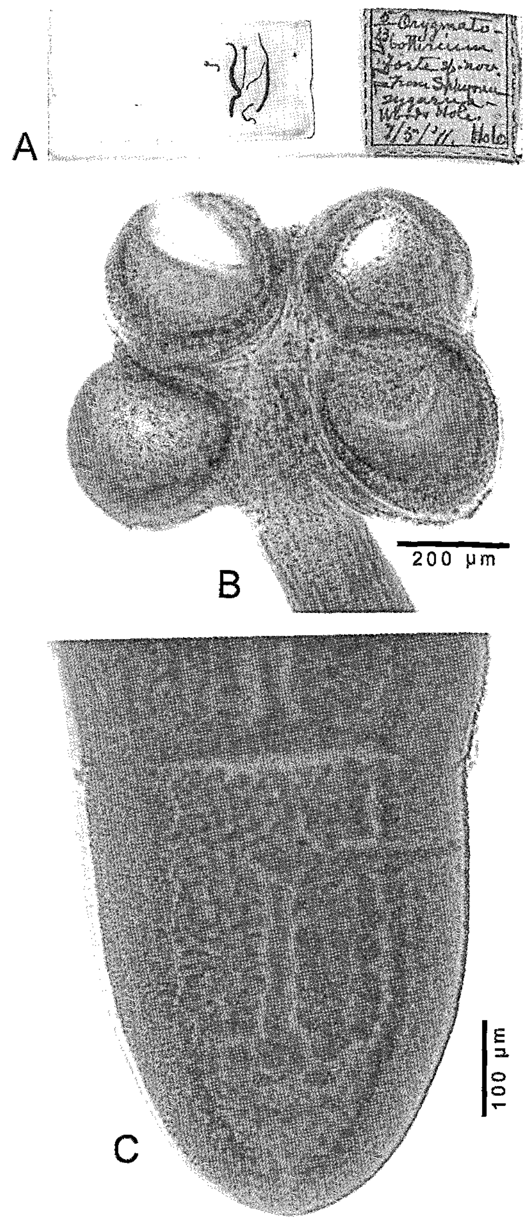

Fig. 88. Photomicrographs of *Orygmatobothrium forte* Linton, 1924. A. Type slide (USNPC 7671). B. Scolex of type (USNPC 7671). C. Terminal proglottid of type (USNPC 7671).

Orygmatobothrium longicolle* Zschokke, 1889 *nomen dubium

Zschokke (1889) described *Orygmatobothrium longicolle* from *Mustelus laevis* (= *Mustelus mustelus* [L., 1758]), the Smooth-hound, collected near Naples, Italy. Zschokke's description and illustration of the scolex (Zschokke 1889, fig. 148) are consistent with the diagnosis of *Orygmatobothrium*. However, as noted by Zschokke (1889), his material was insufficient for a complete description. As a consequence *O. longicolle* cannot be differentiated from the other species of the genus. At least one of these, *O. musteli*, has also been reported from *M. mustelus*. In addition, no type specimens apparently exist for this species. *Orygmatobothrium longicolle* should be considered a *nomen dubium*. Type material: not specified. Material examined: none.

Orygmatobothrium plicatum* Yamaguti, 1934 *nomen dubium

Yamaguti (1934) provided a description and figures for this species, collected from a "skate" taken from Toyama Bay, Japan. However, Caira (pers. comm.) found that the MPM notation lists *Cirrhitichthys*, a genus of hawkfish, as the host for *O. plicatum*. Given that species of *Orygmatobothrium* parasitize sharks of the family Triakidae, this host data are somewhat problematic. The only type slide was found to consist of sectioned material and thus was of little use in comparison to other species of *Orygmatobothrium*. Given this information, combined with the lack of host identification, *O. plicatum,* should be considered a *nomen dubium*. Type material: MPM 22780. Material examined: MPM 22780.

Orygmatobothrium tetraglobum* Southwell, 1912 *species inquirenda

Orygmatobothrium tetraglobum was transferred to, and designated the type species of *Pithophorus* by Southwell (1925). The species is housed under the name *Pithophorus tetraglobus*. This species should be considered a *species inquirenda*. Material examined: BMNH 2010.3.3.1–4.

Orygmatobothrium velamentum* Yoshida, 1917 *species inquirenda

Yoshida (1917) described *Orygmatobothrium velamentum* from specimens taken from *Cynias manazo* (= *Mustelus manazo* Bleeker, 1854), the Star spotted smooth hound, collected near Hiroshima, Japan. Yoshida described his specimens as being 30–40 mm long, with bothridia bearing two small accessory suckers, one anterior, with the second central. He noted that contraction of the bothridium could make the central sucker difficult to see, and that such a condition was common. In fact, the central accessory organ is not immediately apparent in Yoshida's (1917) illustration. Examination of new material from *M. manazo,* or discovery of the type specimens for *O. velamentum,* will be critical in solving the taxonomic status of this species. At present, this species should be considered *species inquirenda*. Type material: not specified. Material examined: none.

Orygmatobothrium wyatti* (Leiper and Atkinson, 1914) Southwell, 1925 *nomen dubium

Orygmatobothrium wyatti was originally described as *Anthobothrium wyatti* Leiper and Atkinson, 1914 by Leiper and Atkinson (1914) for larval cestodes taken from *Trematomus bernacchii* Boulenger, 1902, the Emerald rockcod, taken from Antarctic waters. Southwell transferred *A. wyatti* to *Orygmatobothrium,* presumably because the larvae were described with two tandem suckers on the bothridia. Given that the description is very brief, and no types are known to exist for this species, *A. wyatti* should be considered a *nomen dubium*. Type material: not specified. Material examined: none.

Orygmatobothrium zschokkei* Woodland, 1927 *nomen dubium

Orygmatobothrium zschokkei was proposed as a replacement name by Woodland (1927) for *Anthobothrium* (*Orygmatobothrium*) *musteli* of Zschokke (1889). Zschokke collected his specimens from species of *Mustelus*. Woodland (1927) detailed differences between *O. zschokkei* and *O. musteli*. However, he considered *O. velamentum* to be synonymous with *O. musteli*. The whereabouts of Zchokke's specimens are unknown. At present, *Orygmatobothrium zschokkei* should be considered a *nomen dubium*. Type material: not specified. Material examined: none.

PARAORYGMATOBOTHRIUM Ruhnke, 1994

Taxonomic status: Valid.

Type species: *Paraorygmatobothrium prionacis* (Yamaguti, 1934) Ruhnke, 1994.

Other species: *Paraorygmatobothrium angustum* (Linton, 1889) n. comb.; *P. arnoldi* Ruhnke and Thompson, 2006; *P. bai* Ruhnke and Carpenter, 2008; *P. barberi* Ruhnke, 1994; *P. exiguum* (Yamaguti, 1935) Ruhnke, 1994; *P. filiforme* (Yamaguti, 1952) Ruhnke, 1996; *P. floraformis* (Southwell, 1912) n. comb.; *P. janineae* Ruhnke, Healy and Shapero, 2006; *P. kirstenae* Ruhnke, Healy and Shapero, 2006; *P. leuci* (Watson and Thorson, 1976) n. comb; *P. mobedii* Malek, Caira and Haseli, 2010*; *P. musteli* (Van Beneden, 1850) n. comb.; *P. nicaraguensis* (Watson and Thorson, 1976) n. comb.; *P. orectolobi* (Butler, 1987) n. comb.; *P. paulum* (Linton, 1897) n. comb.; *P. roberti* Ruhnke and Thompson, 2006; *P. rodmani* Ruhnke and Carpenter, 2008; *P. sinuspersicense* Malek, Caira and Haseli, 2010*; *P. taylori* Cutmore, Bennett and Cribb, 2009*; *P. triacis* (Yamaguti, 1952) Ruhnke, 1996; *P. typicum* (Subhapradha, 1955) n. comb.

* recently described species

Etymology: This genus was named for the fact that Ruhnke (1994) postulated that the species of the genus *Paraorygmatobothrium* was related to *Orygmatobothrium* (*para* [Gr.] = near).

Diagnosis (modified from Ruhnke et al. [2006a]).

Phyllobothriidae. Worms craspedote, apolytic or euapolytic. Scolex with four bothridia, each bothridium with single apical sucker and oval posterior loculus. Proximal bothridial surface covered with serrate gladiate spinitriches and filitriches, distal locular surfaces covered with filitriches and either serrate gladiate spinitriches or gongylate columnar spinitriches. Cephalic penduncle present or absent. Neck present, scutellate, scutes comprised of capilliform filitriches with triangular tip. Strobila scutellate. Immature proglottids wider than long. Mature proglottids at least twice as long as wide. Testes numerous, medullary, one row deep in cross section, post-vaginal testes present. Shallow genital atrium present, genital pore lateral. Cirrus-sac pyriform or oval, containing cirrus armed with spinitriches. Vagina median, opening anterior to cirrus in common genital atrium. Ovary posterior, H-shaped in frontal view, tetralobed in cross section. Uterus ventral, saccate, reaching posterior margin or anterior margin of cirrus-sac in mature proglottids . Uterine duct present, joining uterus medially posterior to cirrus-sac. Vitellarium follicular, lateral, follicles distributed two lateral bands, may extend to midline of proglottid in dorsal and ventral fields, interrupted by cirrus-sac, reduced or interrupted by ovary. Eggs spindle shaped or round. Parasites of Galeomorpha.

Remarks

Species of *Paraorygmatobothrium* are most similar to *Ruhnkecestus latipi,* and species of *Orectolobicestus* in possessing serrated spinitriches on their proximal bothridial surfaces, and in exhibiting an interruption of the columns of vitelline follicles at the level of the ovary. Some species of *Paraorygmatobothrium* are similar to *Nandocestus guariticus* in also possessing serrate gladiate spinitriches on their distal bothridial surfaces. However, the species of *Paraorygmatobothrium* differ from *N. guariticus* in possessing serrate gladiate spinitriches on their proximal bothridial surfaces, as opposed to cyrillionate (jug-shaped) spinitriches. Species of *Paraorygmatobothrium* differ from *Ruhnkecestus* in lacking facial loculi on the bothridium, and species of *Orectolobicestus* in lacking regular marginal loculi on the bothridium. Species in *Paraorygmatobothrium, Ruhnkecestus, Nandocestus,* and *Orectolobicestus* may share a phylogenetic kinship with *Thysanocephalum thysanocephalum,* as this species too possesses serrate gladiate spinitriches on its bothridial surfaces (see Caira et al. 2001).

Ruhnke (1994a) erected *Paraorygmatobothrium* for three cestode species collected from sharks. He subsequently transferred two species to the genus (Ruhnke 1996b). Ruhnke et al. (2006a) described two additional new species to the genus collected from hemigaleid sharks. Ruhnke and Thompson (2006) described two new species of *Paraorygmatobothrium* collected from two species of lemon sharks (*Negaprion* Whitley, 1940). Most recently, Ruhnke and Carpenter (2008) described two new species of *Paraorygmatobothrium* collected from two species of hound sharks (genus *Mustelus*). Seven phyllobothriid species are herein transferred to *Paraorygmatobothrium,* bringing the total number of species to 18. However, the present members of *Paraorygmatobothrium* may only represent a fraction of the eventual biodiversity of this genus. In fact, worms that are morphologically consistent with the diagnosis of *Paraorygmatobothrium* have been observed from a number of other carcharhinid and sphyrnid shark species (Ruhnke pers. obs.). For example, within *Carcharhinus* Blainville, 1816, specimens of *Paraorygmatobothrium* species have been observed from *Carcharhinus acronotus* (Poey, 1860), *C. amblyrhynchoides* (Whitley, 1934), *C. amboinensis* (Müller and Henle, 1839), *C. falciformis* (Müller and Henle, 1839), *C. melanopterus* (Quoy and Gaimard, 1824), and *C. plumbeus* (Nardo, 1827). Within *Sphyrna* Rafinesque 1810, cestodes that potentially belong to this genus have been collected from *S. lewini*

(Griffith and Smith, 1834) and *S. mokarran* (Rüppell, 1837). With this apparent diversity among carcharhiniform sharks, species of *Paraorygmatobothrium* should become an ideal system for the study of host-parasite co-phylogeny.

The strategy that will be employed here for morphological comparisons among the 18 species of *Paraorygmatobothrium* is as follows: each of the 11 currently valid species will be differentiated from one another. The seven species that are herein transferred to *Paraorygmatobothrium* will each be differentiated from existing species upon their individual treatments. Thus, of the transferred species, the only species compared to all other species is the last one transferred. A summary of the similarities and differences among the species of *Paraorygmatobothrium* is provided in Table 1.

Paraorygmatobothrium prionacis (Yamaguti, 1934) Ruhnke, 1994

TYPE SPECIES

(Figs. 89–92)

Synonyms: *Phyllobothrium prionacis* Yamaguti, 1934; *Crossobothrium prionacis* (Yamaguti, 1934) Williams, 1968; *Anthobothrium minutum* Guiart, 1935.

Taxonomic status: Valid.

Type host: *Prionace glauca* (L., 1758), Blue shark.

Site of infection: Spiral Intestine.

Type locality: Pacific coast, Japan (Fig. 89).

Additional localities: Sète, France, Concarneau; France; Roscoff, France; Montauk, Long Island, U.S.A.; South Yarmouth, Massachusetts, U.S.A.; Woods Hole, Massachusetts, U.S.A.; La Paz, Baja California Sur, Mexico (Fig. 89).

Type material: Unknown.

Voucher specimens: USNPC 82938, USNPC 82939, HWML 36770–36773 (Fig. 90A), HWML 37548, LRP 7415–7417, MPM 19580–19581.

Material examined: USNPC 82938, USNPC 82939, HWML 36770–36773 (Fig. 90A), HWML 37548, LRP 7415–7417, MPM 19580–19581.

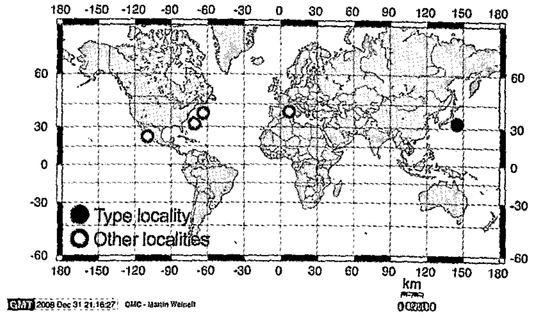

Fig. 89. Geographic distribution of *Paraorygmatobothrium prionacis* (Yamaguti, 1934) Ruhnke, 1994.

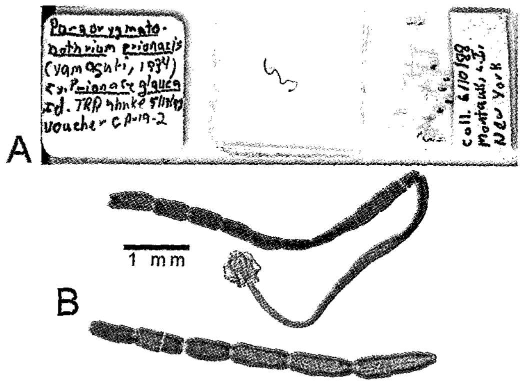

Fig. 90. Photomicrographs of *Paraorygmatobothrium prionacis* (Yamaguti, 1934) Ruhnke, 1994. A. Slide of voucher (HWML 36771). B. Entire specimen of voucher (LRP 7415).

Etymology: This species was named for the genus of its host shark species.

Description (modified from Ruhnke [1994a]).

Worms craspedote, euapolytic, 7.2–19.3 mm (11.7 ± 3.2; n=19) long; maximum width 400–750 (548 ± 101; n=16) at scolex. Proglottids 11–29 (21 ± 6; n=11) in number. Scolex 430–620 (553 ± 77; n=7) long, apical surface covered with capilliform filitriches, with four bothridia. Bothridia 420–620 (531 ± 55; n=14; *n*=28) long x 270–440 (308 ± 61; n=7; *n*=8) wide, each with single loculus and round, anterior apical sucker; apical sucker 80–118 (98 ± 9; n =17; *n*=35) in diameter. Proximal surfaces of bothridia covered with serrate gladiate spinitriches and papilliform filitriches. Distal locular surface and distal

Table 1. Morphological comparison of species of *Paraorygmatobothrium* Ruhnke, 1994.

Character	*P. prionacis*	*P. angustum* n.comb.	*P. arnoldi*	*P. bai*	*P. barberi*	*P. exiguum*	*P. filiforme*	*P. floraformis* n.comb.
Worm length (mm)	7.2–19.3	6.4–11.4	6.2–8.4	15.6–41.2	20–36	5.2–8.2	11.8–23.7	2–4.5
Maximum width	400–750	269–500	211–388	307–998	530–880	410–580	430–530	150–434
Proglottid number	11–29	18–29	14–31	14–27	47–67	12–20	31–50	10–19
Bothridial length	420–620			300–450	380–730	300–420		
Bothridial width	270–440	201–225	87–192	179–370	213–480	170–300	250–330	86–112
Apical sucker diameter	80–118	42–55	40–54	65–77	55–80	50–85	50–60	20–37
Mature proglottid length	860–1,475	822–1,479	384–1,067	1,080–4,096	1,200–2,550	925–1,475	950–1,800	469–1,160
Mature proglottid width	190–350	201–480	116–340	205–563	400–940	250–430	250–450	144–288
Testes number	34–62	67–83	68–134	100–145	135–215	33–59	72–123	43–81
Testes length (or diameter)	26–70	14–45	10–36	31–78	38–68	30–72	30–50	10–40
Testes width	30–80	40–88	10–50		55–90	45–80	43–70	27–59
Cirrus-sac length	108–214	102–201	59–156	196–369	250–450	135–187	170–200	78–139
Cirrus-sac width	60–127	30–91	24–58	83–225	113–238	87–142	68–135	31–59
Genital pore psn	48–59	71–74	60–70	68–75	64–78	74–83	67–75	77–87
Ovary length	103–250	197–387	50–127	320–700	410–630	175–310	250	86–285
Ovary width	155–228	119–300	53–155	158–440	410–730	143–260	250	44–149

Character	*P. janineae*	*P. kirstenae*	*P. leuci* n.comb.	*P. mobedii**	*P. musteli* n.comb.	*P. nicaraguensis* n. comb.	*P. orectolobi* n. comb.
Worm length (mm)	10–28.9	8.7–25	10.1–42	5.7–14.4	7.3–14	9.5–22	13–65
Maximum width	561–1021	372–489	420–825	188–238	485–952	374–630	490–840
Proglottid number	59–104	33–64	30–68	13–24	12–27	24–25	90
Bothridial length			225–615	110–250	233–534	225–435	400–710
Bothridial width			195–405	109–264	136–512	203–330	330–550
Apical sucker diameter	66–139	43–61	68–82	31–59	50–62	43–68	78–122
Mature proglottid length	409–1,560	605–1,637	1,130–5,270	727–1,495	1,164–2,172	600–2,370	2,300–4000
Mature proglottid width	198–627	248–395	185–750	158–264	320–683	270–465	460–820
Testes number	122–219	104–164	83–151	49–85	128–153	70–132	124–193
Testes length (or diameter)	7–53	26–50	43–104	13–48	22–62	21–54	49
Testes width	26–53	40–78		25–56	28–62	36–75	
Cirrus-sac length	165–343	169–250	157–750	85–127	275–300	180–340	
Cirrus-sac width	40–218	94–137	75–180	37–85	180–300	71–136	
Genital pore psn	65–79	66–77	58–61	71–86	65–80	64–65	52–56
Ovary length	119–290	116–279	164–810	154–309	291–687	144–390	
Ovary width	73–350	165–266	185–525	76-148	184–398	179–330	

Character	*P. paulum* n. comb.	*P. roberti*	*P. rodmani*	*P. sinuspersicense**	*P. taylori**	*P. triacis*	*P. typicum* n. comb.
Worm length (mm)	5–13	6.6–17.1	13–29	6.3–13.2	25.9–32.9	35–46	3.3–4.1
Maximum width	340–640	365–683	631–1,248	229–425	480–983	800–920	175–320
Proglottid number	20–37	16–36	14–27	13–24	41–43	47–68	10–15
Bothridial length		192–432	301–776	106–268	324–488		115–163
Bothridial width	185–408	149–384	240–776	87–260	215–332		95–153
Apical sucker diameter	43–68	43–68	48–78	31–53	60–76	75–88	30–38
Mature proglottid length	672–1,375	614–1,880	1,203–3,900	531–995	1,137–2,608	1,450–2,125	475–770
Mature proglottid width	143–300	197–439	416–840	170–308	381–983	790–1,005	128–210
Testes number	37–68	82–141	108–280	51–79	139–197	176–238	46–63
Testes length (or diameter)	17–50	15–56	19–86	15–34	34–76	38–78	18–27
Testes width	23–80	27–74	38–115	22–58	44–97	45–80	27–45
Cirrus-sac length	100–162	90–221	204–527	87–154	202–444		63–80
Cirrus-sac width	60–121	37–90	174–355	31–67	99–198		25–38
Genital pore psn	46–68	61–76	67–80	70–94	57–84	69–75	73–82
Ovary length	84–168	146–257	320–877	98–247	193–370	450	90–138
Ovary width	107–250	123–207	390–598	78-197	241-525	661	100–130

* recently described species.

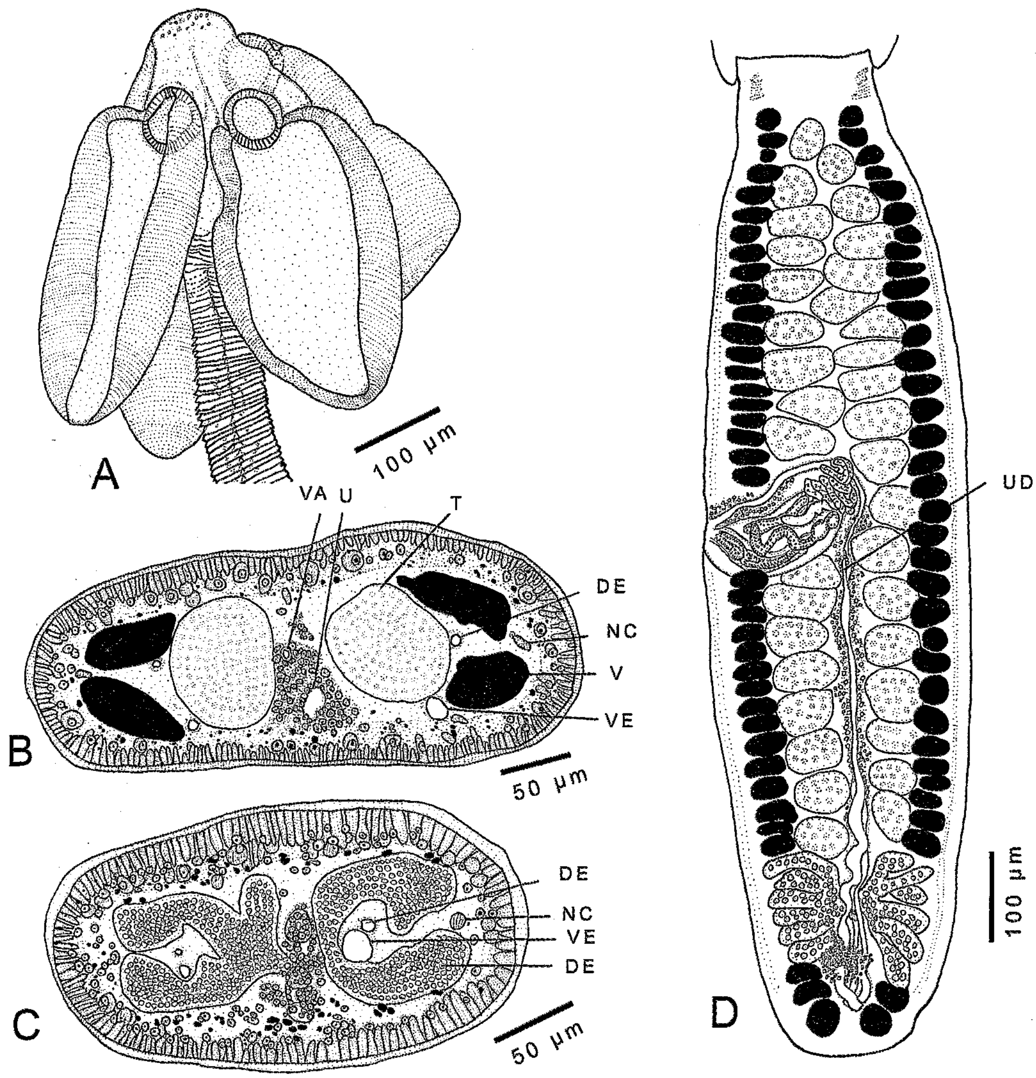

Fig. 91. Line drawings of *Paraorygmatobothrium prionacis* (Yamaguti, 1934) Ruhnke, 1994. A. Scolex of voucher (USNPC 82939). B. Cross-section of proglottid posterior to cirrus-sac and anterior to ovary of voucher (HWML 36773). C. Cross-section of proglottid through ovary of voucher (HWML 36772). D. Mature proglottid of voucher (USNPC 82938). (Taken from Ruhnke [1994a], copyright 1994. Used with permission.)

surface of apical sucker covered with slender serrate gladiate spinitriches and capilliform filitriches. Cephalic peduncle absent. Neck 1.8–4.6 mm (2.8 ± 0.8; n=13) long; dorsal and ventral surfaces scutellate; scutes comprised of densely packed capilliform filitriches with triangular tips.

Immature proglottids 150–375 (271 ± 69; n=6; *n*=12) long x 150–275 (220 ± 42; n= 6; *n*=12) wide. Mature proglottids 860–1,475 (1,132 ± 133; n=13; *n*=25) long x 190–350 (282 ± 43; n=13; *n*=25) wide, generally three times as long as wide, with dorsal and ventral pair of excretory ducts and lateral pair of nerve chords. Free proglottids 1,250–1,575 (1,370 ± 156; n=5) long x 275–475 (365 ± 80; n=5) wide. Mature proglottids with 34–62 (49 ± 8; n=12; *n*=22) testes. Testes medullary, slightly oblong, 26–70 (40 ± 8; n=13; *n*=47) long x 30–80 (56 ± 12; n=13; *n*=47) wide; arranged in 2–4 (2.7 ± 0.6; n=12; *n*=22) irregular columns pre-porally; in 2–3 (2.2 ± 0.4; n=12; *n*=22) ir-

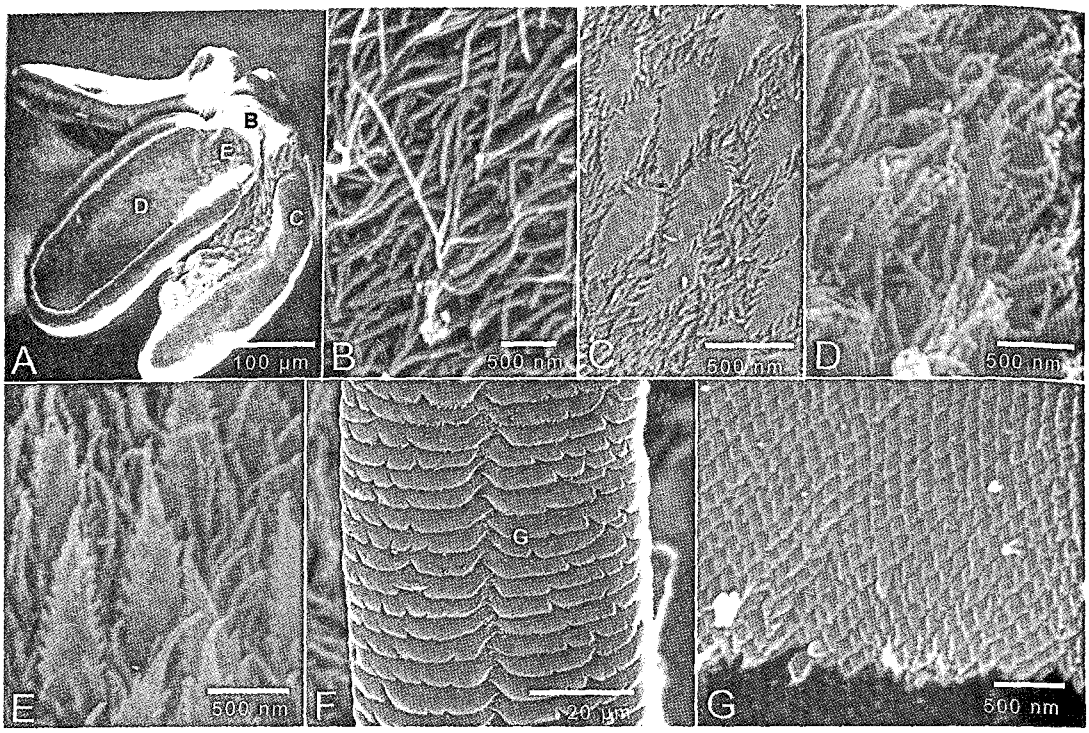

Fig. 92. Scanning electron micrographs of *Paraorygmatobothrium prionacis* (Yamaguti, 1934) Ruhnke, 1994. A. Scolex (letter indicate regions of scolex in enlarged photos B–E). B. Apical surface of scolex. C. Proximal surface of bothridium. D. Distal surface of bothridrium. E. Distal surface of apical sucker. F. Anterior region of neck (letter indicates region of neck in enlarged photo G). G. Neck surface. (Taken from Ruhnke [1994a], copyright 1994. Used with permission.)

regular columns post-porally, one row deep in cross-section. Cirrus-sac pyriform, 108–214 (153 ± 26; n=13; *n*=21) long x 60–127 (85 ± 25; n=13; *n*=21) wide, containing armed, coiled cirrus. Vas deferens coiled, median, bordering proximal portion of cirrus-sac, anterior to cirrus-sac. Genital pores lateral, 48–59% (53 ± 3; n=15; *n*=24) of proglottid length from posterior end, irregularly alternating, unilateral in five of 20 specimens. Vagina median, extending anteriorly from ovary to mid-level of proglottid, then laterally along anterior margin of cirrus-sac to genital pore. Shallow genital atrium present. Ovary near posterior end of proglottid, H-shaped in frontal view, 103–250 (165 ± 43; n=12; *n*=16) long x 155–228 (184 ± 20; n=12; *n*=16) wide, tetralobed in cross section. Ovicapt at posterior margin of ovarian bridge, 23–35 (29 ± 3; n=10; *n*=14) in diameter, weakly developed in mature proglottids. Mehlis' gland posterior to ovicapt. Uterus ventral to vagina, extending from anterior margin of ovary to posterior margin of cirrus-sac in mature proglottids, to anterior margin of cirrus-sac in free proglottids. Uterine duct present, median, parallel and dorsal to uterus, extending to posterior margin of cirrus-sac in mature and free proglottids, entering uterus at level of posterior margin of cirrus-sac. Vitellarium follicular; follicles 12–33 (21 ± 5; n=12; *n*=42) long x 19–50 (34 ± 11; n= 12; *n*=42) wide, in two lateral fields, each field consisting of 1–2 dorsal and 1–2 ventral columns of follicles, interrupted by ovary and cirrus-sac. Eggs spindle-shaped, 52–70 (62 ± 5; n=4; *n*=16) long x 16–22 (20 ± 2; n=4; *n*=16) wide, viewed only in free proglottids.

Remarks

Ruhnke (1994a), in erecting the genus *Paraorygmatobothrium,* transferred *Phyllobothrium prionacis* to *Paraorygmatobothri-*

um and designated it the type species. Inquiries of the Meguro Parasitological Museum revealed that, although much of Yamaguti's collection is located there, the type-specimens of *P. prionacis* are not there, and their whereabouts are unknown. Euzet (1959) reported *P. prionacis* from the blue shark, collected from the coast of France, but considered it synonymous with *Crossobothrium angustum* (Linton, 1889) (= *Paraorygmatobothrium angustum* [Linton, 1889] n. comb, see pg. 119). The synonymy of these two species was not accepted by Williams (1968a) or Schmidt (1986). This synonymy is not supported by the morphological evidence, as these two species can be differentiated by several features (see pg. 116, Table 1). *Anthobothrium minutum* Guiart, 1935 was reported by Guiart (1935) from *Galeus glaucus* (= *Prionace glauca*). This species is hereby considered a junior synonym of *P. prionacis*. *Paraorygmatobothrium prionacis* has now been reported from both eastern and western Atlantic waters, as well as Pacific waters. It seems likely that this species has a world-wide distribution, as does its host, *Prionace glauca*.

Paraorygmatobothrium prionacis differs from all other species of *Paraorygmatobothrium* except *P. exiguum*, *P. janineae*, and *P. triacis* in apical sucker diameter (see Table 1). Among other features, *P. prionacis* differs from *P. triacis* in total length (7.2–19.3 mm vs. 35–46 mm), differs from *P. janineae* in proglottid number (11–29 vs. 59–104) and differs from *P. exiguum* in genital pore position (48–59 vs. 74–83).

Curran and Caira (1995) discussed the site specificity of *P. prionacis* from *P. glauca* in a site specificity study of tetraphyllidean tapeworms.

Paraorygmatobothrium angustum (Linton, 1889) n. comb.

(Figs. 93–96)

Synonyms: *Orygmatobothrium angustum* Linton, 1889; *Crossobothrium angustum* (Linton, 1889) Linton, 1901; *Phyllobothrium angustum* (Linton, 1889) Euzet, 1952.

Taxonomic status: Valid.

Type host: *Carcharhinus obscurus*, (Lesueur, 1818), the Dusky shark.

Type locality: Woods Hole, Massachusetts, U.S.A. (Fig. 93).

Additional locality: Northwestern Atlantic Ocean, off North Carolina (Fig. 93).

Site of infection: Spiral intestine.

Type material: Neotype USNPC 7666 (Fig. 94A).

Material deposited: Vouchers, USNPC 102713, LRP 7410–7414.

Material examined: Neotype USNPC 7666; vouchers, USNPC 102713, LRP 7410–7414.

Etymology: Not given, but presumably, *angustum* (l.) = "narrow", in reference to the narrow strobilar morphology of this species.

Redescription (based on nine specimens).

Worms slightly craspedote, euapolytic, 6.4–11.4 (9.3 ± 1.6; n=8) mm long; maximum width 269–500 (382 ± 64; n=8) at scolex. Proglottids 18–29 (22 ± 3; n=8) in number. Scolex 217–391 (289 ± 61; n=8) long, with four bothridia. Bothridia 201–225 (210 ± 9; n=7) wide; each with a single loculus and round apical sucker; apical sucker 42–55 (50 ± 5; n=6) in diameter. Proximal surfaces of bothridia covered with serrate gladiate spinitriches and

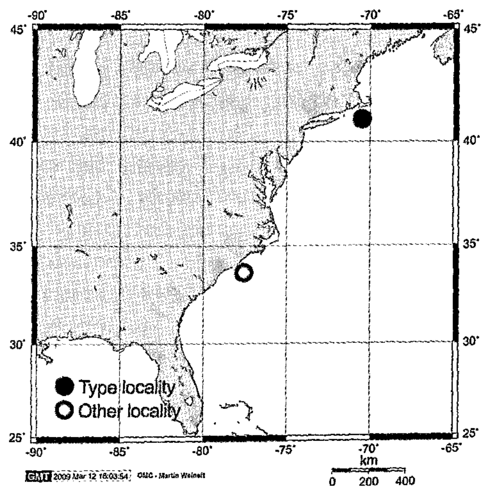

Fig. 93. Geographic distribution of *Paraorygmatobothrium angustum* (Linton, 1889) n. comb.

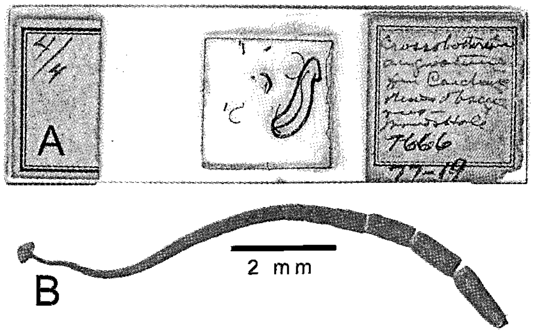

Fig. 94. Photomicrographs of *Paraorygmatobothrium angustum* (Linton, 1889) n. comb. A. Slide of neotype (USNPC 7666). B. Entire neotype (USNPC 7666).

papilliform filitriches. Distal locular surfaces and distal surface of apical sucker covered with serrate gladiate spinitriches and papilliform filitriches. Cephalic peduncle absent. Neck 1.3–1.6 (1.4 ± 0.2; n=3) mm long; dorsal and ventral surfaces scutellate; scutes comprised of densely packed capilliform filitriches with triangular tips.

Immature proglottids 178–328 (226 ± 50; n=7) long x 190–280 (226 ± 34; n=7) wide, initially wider than long. Terminal proglottids 822–1,479 (1,267 ± 196; n=9) long x201–480 (316 ± 84; n=9) wide, length:width ratio 2.9–5.1 (4.2 ± 0.8; n=9. Testes 67–83 (75 ± 7; n=9) in number; oblong, 14–45 (27 ± 9; n=8; *n*=15) long x40–88 (64 ± 13; n=8, *n*=15) wide. Cirrus-sac oval, 102–201 (151 ± 32; n=7) long x 30–91 (65 ± 21; n=7) wide, containing coiled cirrus; cirrus armed with spinitriches. Vas deferens coiled, median, bordering proximal portion of cirrus-sac, anterior to cirrus-sac, posterior to vagina. Genital pores lateral, 71–74% (73 ± 1; n=8) of proglottid length from posterior end, irregularly alternating. Vagina median, extending anteriorly from ovary to midlevel of proglottid, then laterally along anterior margin of vas deferens and cirrus-sac to genital pore. Shallow genital atrium present. Ovary near posterior end of proglottid, H-shaped in frontal view, 197–387 (264 ± 62; n=7) long x 119–300 (199 ± 62; n=7) wide. Ovicapt, at posterior margin of ovarian bridge, weakly developed in mature proglottids. Mehlis' gland posterior to ovicapt. Uterus ventral to vagina, extending from anterior

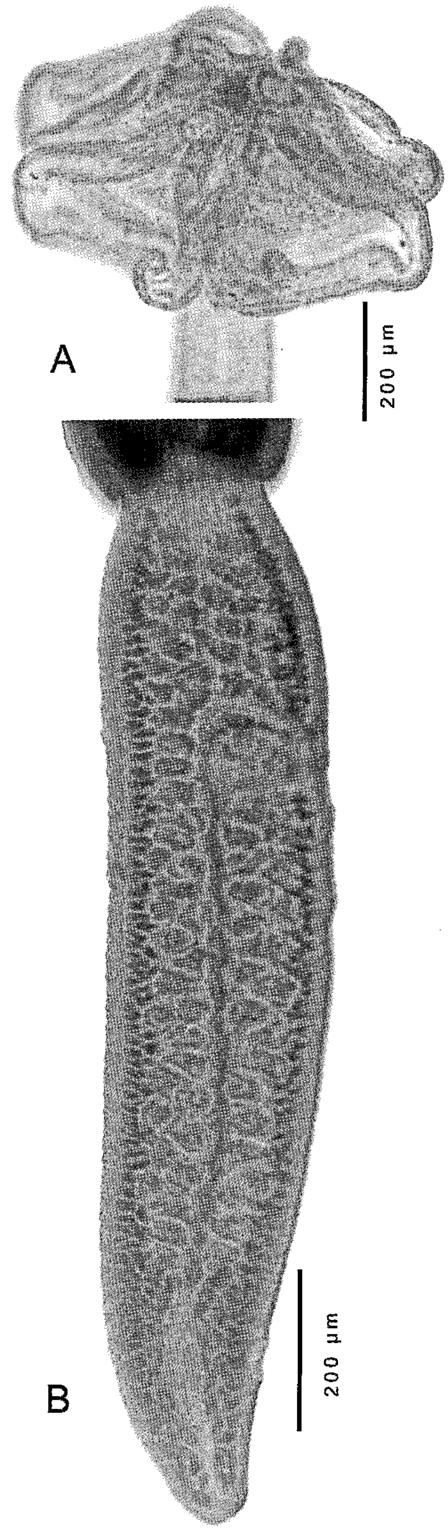

Fig. 95. Photomicrographs of *Paraorygmatoboth rium angustum* (Linton, 1889) n. comb. A. Scolex o voucher (LRP 7410). B. Mature proglottid of vouche (LRP 7411).

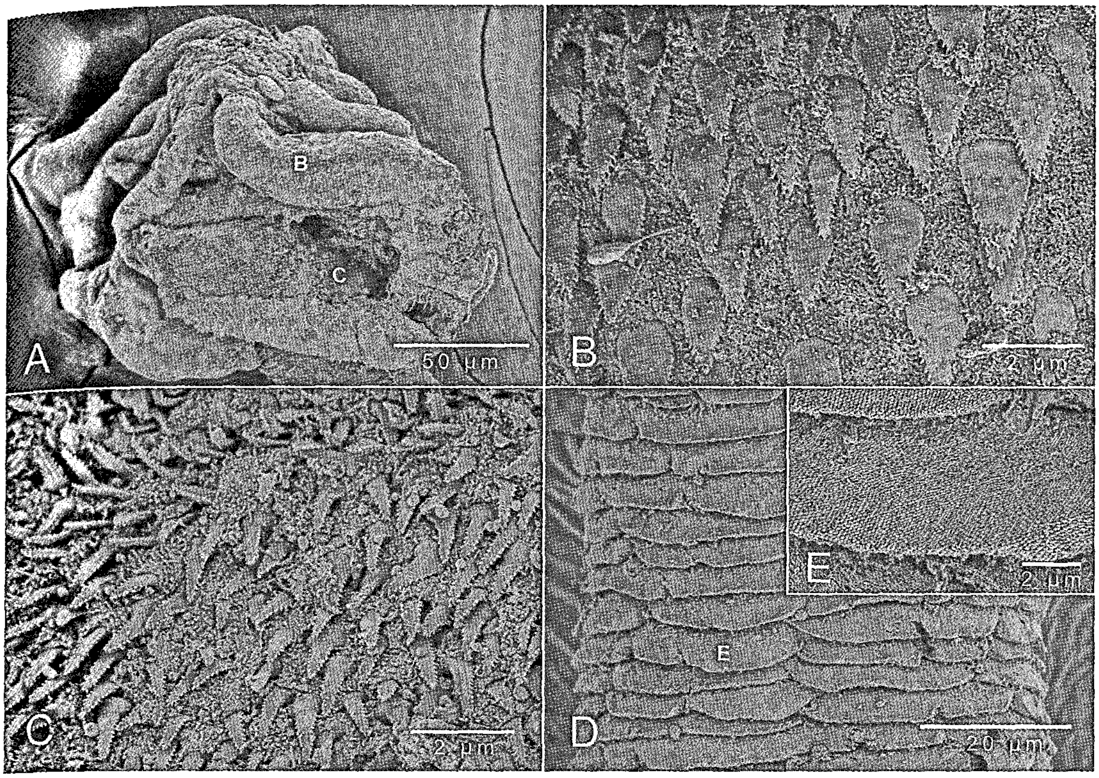

Fig. 96. Scanning electron micrographs of *Paraorygmatobothrium angustum* (Linton, 1889) n. comb. A. Scolex (letter indicate regions of scolex in enlarged photos B–C). B. Proximal surface of bothridium. C. Distal surface of bothridrium. E. Anterior region of neck (letter indicate region of neck in enlarged photos E). E. Neck surface.

margin of ovary to posterior margin of cirrus-sac in mature proglottids. Uterine duct present, median, parallel and dorsal to uterus, extending anteriorly, entering uterus posterior to cirrus-sac. Vitellarium follicular, vitelline follicles oblong, in two lateral fields, each with 2–3 dorsal and 2–3 ventral columns of follicles, interrupted by ovary and cirrus-sac.

Remarks

Paraorygmatobothrium angustum n. comb. was originally described by Linton (1889) for worms from the Dusky shark. No type slides were present at the U.S. National Parasite Collection. Given the confusion that has surrounded the identity of this species, a voucher (USNPC 7666), collected by V. N. Edwards and identified as "*Crossbothrium angustum*" by Linton, is designated as a neotype for this species (see Fig. 94A).

Paraorygmatobothrium angustum n. comb. differs from the existing species of *Paraorygmatobothrium* except *P. arnoldi, P. filiforme,* and *P. roberti* in testes number (see Table 1). Among other features, it differs from *P. arnoldi* in genital pore position (71–74 vs. 60–70), differs from *P. filiforme* in total length (6.4–11.4 mm vs. 11.8–23.7 mm), and differs from *P. roberti* in proglottid number (67–82 vs. 82–141).

Paraorygmatobothrium arnoldi Ruhnke and Thompson, 2006
(Figs. 97–100)

Taxonomic status: Valid.

Type host: *Negaprion acutidens* (Rüppell, 1837), the Sicklefin lemon shark.

Type locality: Dundee Beach, Timor Sea, Northern Territories, Australia (Fig. 98).

Additional locality: Darwin, Timor Sea, Northern Territories, Australia (Fig. 98).

Site of infection: Spiral intestine.

Type material: Holotype, QM G 225519 (Fig. 97); paratypes QM G 22550–225522, USNPC 97301, LRP 3781–3786. Remaining paratypes are in the collection of T.R. Ruhnke.

Material examined: All types were examined.

Etymology: This species is named for Tim Ruhnke's grandfather, the late Arnold Ruhnke.

Description (modified from Ruhnke and Thompson [2006]).

Worms slightly craspedote, euapolytic, 6.2–8.4 (6.3 ± 0.8; n=19) mm long; maximum width 211–388 (317 ± 57.4; n=21) at scolex.

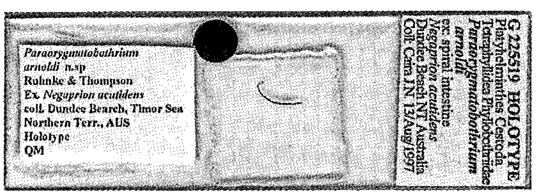

Fig. 97. Holotype slide of *Paraorygmatobothrium arnoldi* Ruhnke and Thompson, 2006 (QM G 225519).

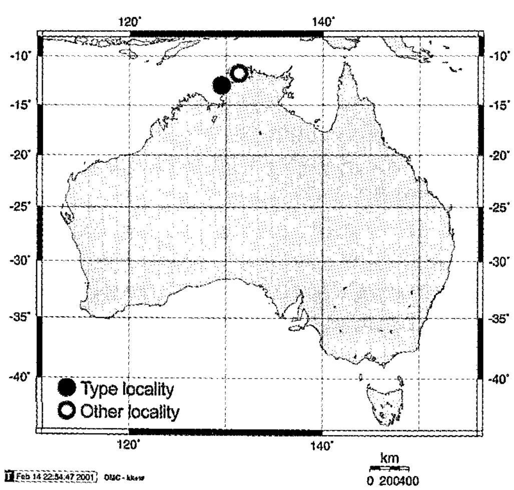

Fig. 98. Geographic distribution of *Paraorygmatobothrium arnoldi* Ruhnke and Thompson, 2006.

Proglottids 14–31 (20 ± 4.8; n=19) in number. Scolex (154–399 (250 ± 66; n=21) long, with four bothridia. Bothridia 87–192 (130 ± 32; n=18; *n*=19) wide, each with single loculus and round apical sucker, periphery of bothridia ringed with bundle of longitudinal muscles. Apical sucker 40–54 (46 ± 5; n=12; *n*=16) in diameter. Apical surface of scolex proper covered with filitriches. Distal locular surface and distal surface of apical sucker covered with serrate gladiate spinitriches and capilliform filitriches. Cilia present on distal bothridial surface. Proximal surfaces of bothridia covered with serrate gladiate spinitriches and capilliform filitriches. Rim of bothridium covered with capilliform filitriches. Cephalic peduncle absent. Neck 0.5–3.3 (1.6 ± 0.7; n=26) mm long; dorsal and ventral surfaces scutellate, scutes comprised of densely packed capilliform filitriches with triangular tips.

Immature proglottids Initially wider than long, becoming longer than wide. Terminal proglottids 384–1,067 (639 ± 190; n=20) long x 116–340 (192 ± 54; n=20) wide, length to width ratio 2.1–5:1 (3.4 ± 0.8; n=20), with dorsal and ventral pair of excretory ducts and lateral pair of nerve chords. Testes 68–134 (92 ± 19; n=13) in number, oblong, 10–36 (17 ± 6; n=18 *n*=31) long x 10–50 (29 ± 11; n=18, *n*=31) wide, length to width ratio 0.3–1.1:1 (0.6 ± 0.2; n=18; *n*=31). Cirrus-sac pyriform, 59–156 (101 ± 32; n=16) long x 24–58 (41 ± 10; n=16) wide, cirrus-sac length to width ratio 1.2–3.3:1 (2.5 ± 0.5; n=16); containing coiled cirrus. Cirrus armed with spinitriches. Vas deferens coiled, median, bordering proximal portion of cirrus-sac, anterior to cirrus-sac, posterior to vagina. Genital pores lateral, 60–70% (63 ± 4; n=9) of proglottid length from posterior end, irregularly alternating. Vagina median, extending anteriorly from ovary to midlevel of proglottid, then laterally along anterior margin of vas deferens and cirrus-sac to genital pore. Shallow genital atrium present. Ovary near posterior end of proglottid, H-shaped in frontal view, 50–127 (83 ± 28; n= 6) long x 53–155 (102 ± 36; n=6) wide, tetralobed in cross section. Ovicapt 27–49 (36 ± 9; n=5) in diameter, at posterior margin

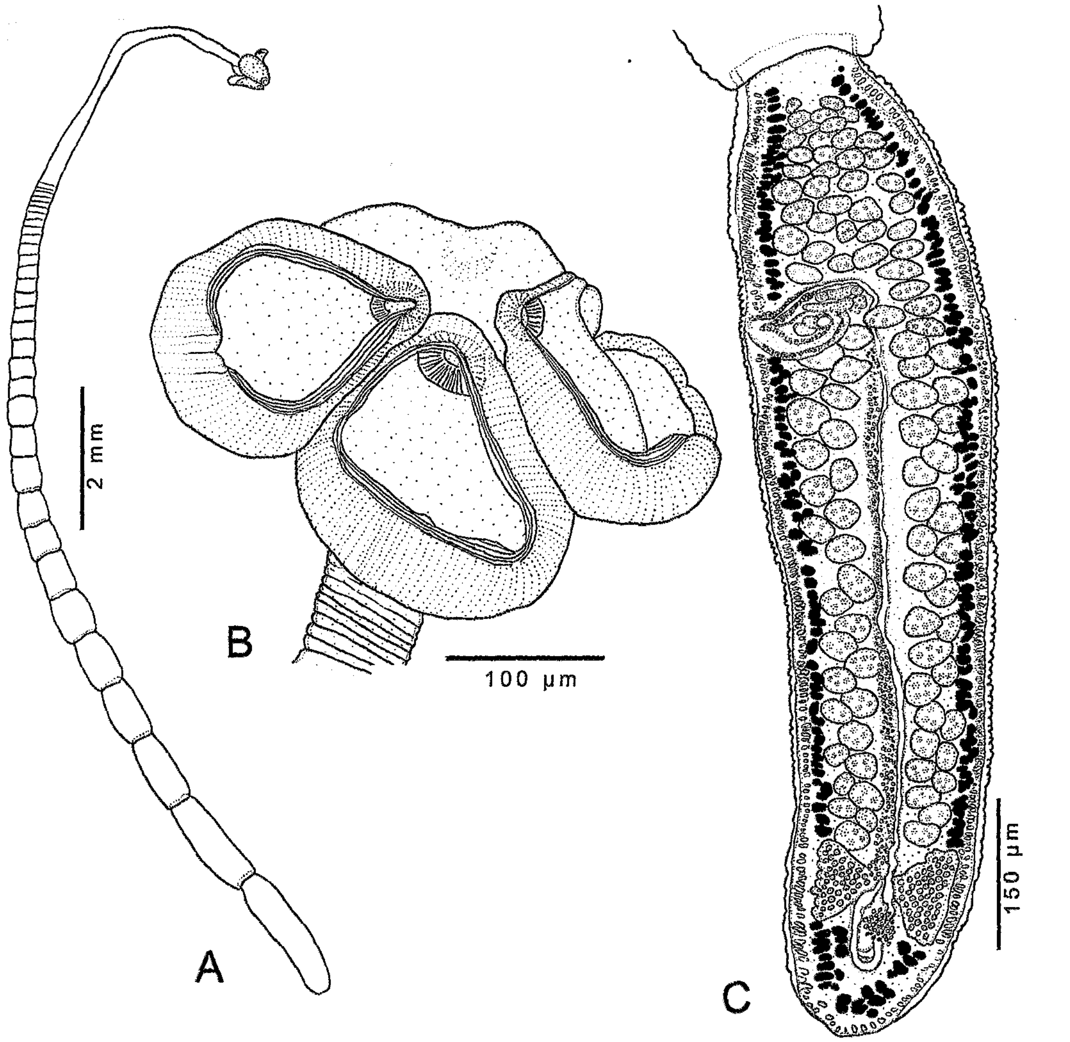

Fig. 99. Line drawings of *Paraorygmatobothrium arnoldi* Ruhnke and Thompson, 2006. A. Holotype (QM G 225519). B. Scolex of paratype (QM G 225521). C. Terminal proglottid of holotype (QM G 225519). (Taken from Ruhnke and Thompson ([2006], copyright 2006. Used with permission.)

of ovarian bridge, weakly developed in mature proglottids. Mehlis' gland posterior to ovicapt. Uterus ventral to vagina, extending from anterior margin of ovary to posterior margin of cirrus-sac in mature proglottids. Uterine duct present, median, parallel and dorsal to uterus, extending anteriorly, entering uterus posterior to cirrus-sac. Vitellarium follicular, vitelline follices oblong, 4–10 (7 ± 2; n=13; *n*=17) long x 7–24 (14 ± 5; n=13; *n*=17) wide, in two lateral fields, each with two dorsal and two ventral columns of follicles, interrupted by ovary and cirrus-sac.

Remarks

Paraorygmatobothrium arnoldi differs from all other species of *Paraorygmatobothrium* except *P. prionacis, P. angustum, P. exiguum,* and *P. roberti* in total length (see Table 1). Among other features, *P. arnoldi* differs from *P. prionacis* and *P. angustum* in bothridial width (87–192 vs. 270–440 and 201–225, respectively), and from *P. prionacis* in apical sucker diameter (40–54 vs. 80–118), and differs from *P. prionacis, P. angustum,* and *P. exiguum* in genital pore position

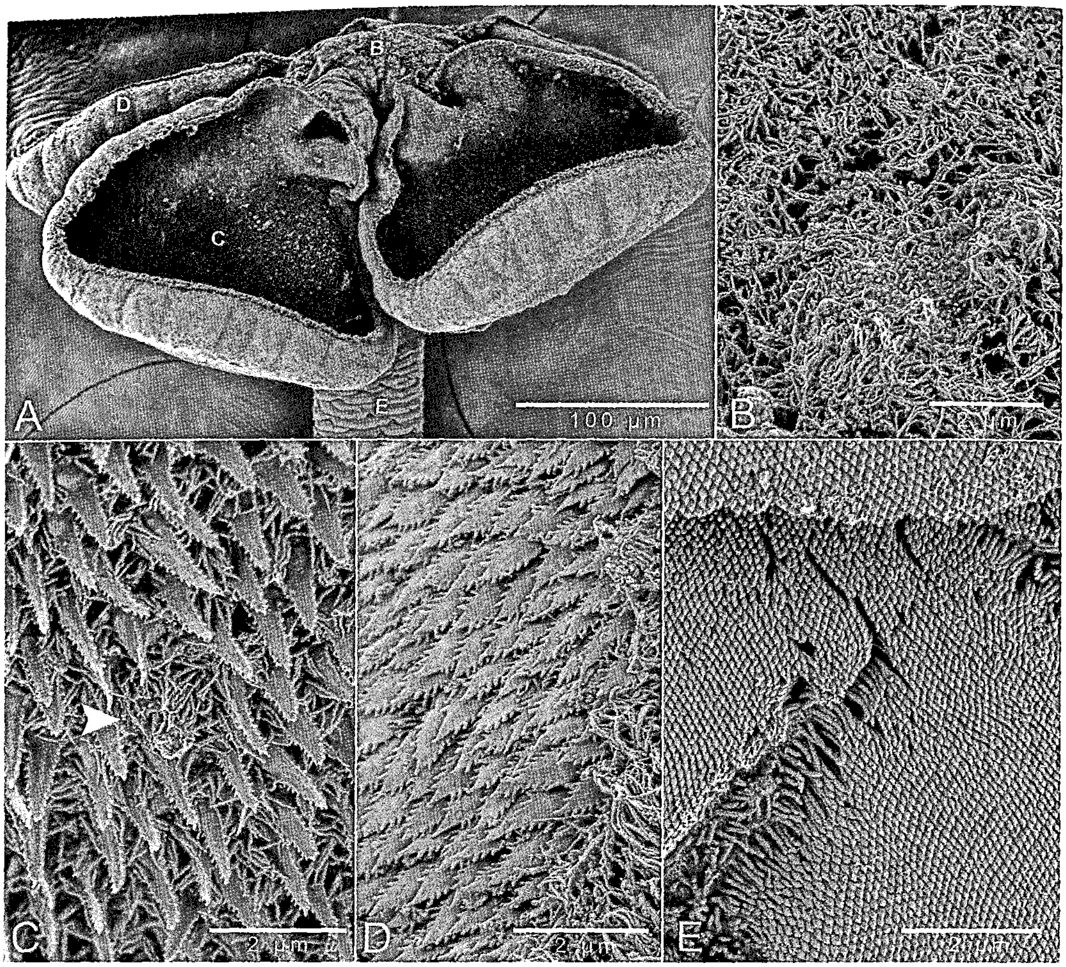

Fig. 100. Scanning electron micrographs of *Paraorygmatobothrium arnoldi* Ruhnke and Thompson, 2006. A. Scolex (letter indicate regions of scolex in enlarged photos B–E). B. Apical surface of scolex. C. Distal surface of bothridrium (arrow indicates cilium). D. Proximal surface of bothridrium. E. Surface of anterior region of neck. (Taken from Ruhnke and Thompson [2006], copyright 2006. Used with permission.)

(60–70 vs. 48–59, 71–74, and 74–83, respectively). The species differs from *P.roberti* in ovary length (50–127 vs. 146–257).

Paraorygmatobothrium bai Ruhnke and Carpenter, 2008

(Figs. 101–104)

Taxonomic status: Valid.

Type host: *Mustelus mustelus* (L., 1758) the Smooth-hound.

Site of infection: Spiral intestine.

Type locality: Off Soumbédioune (14°40'42"N, 17°27'42"W), near Dakar, Senegal, western Atlantic Ocean (Fig. 101).

Additional locality: Off Ouakam (14°42'54"N, 17°29'28"W), near Dakar, Senegal, Atlantic Ocean (Fig. 101)

Type material: Holotype, MNHN HEL 52 (Fig. 102A); paratypes MNHN Paris HEL 53, LRP 4181-4184, USNPC 100855–100856, additional paratype deposited in the Département de Biologie Animale, Université Cheikh Anta Diop de Dakar, Dakar, Senegal. Remaining paratypes retained in T.R. Ruhnke's collection.

Material examined: All types examined.

Etymology: This species is named for Dr. Cheikh Ba, of the Département de Biologie Animale, Faculté des Sciences et Techniques, Université Cheikh Anta Diop de Dakar, Dakar, Senegal.

Description (taken from Ruhnke and Carpenter [2008]).

Worms slightly craspedote, apolytic, 15.6–41.2 (30.6 ± 7.3; n=12) mm long; maximum width 307–998 (617 ± 180; n=19) at level of scolex. Proglottids 14–27 (19 ± 4; n=14) in number. Scolex 370–768 (568 ± 116; n=15) long, with four bothridia. Bothridia with short stalks, 300–450 (345 ± 56; n=13) long x 179–370 (263 ± 48; n=13) wide, each with single loculus and round apical sucker; apical sucker 65–77 (70 ± 5; n=7; *n*=11) in diameter. Bothridial stalks covered with papilliform filitriches. Proximal surface of bothridia covered with serrate gladiate spinitriches and acicular filitriches. Distal locular surface and distal surface of apical sucker covered with slender gongylate columnar spinitriches and papilliform filitriches. Cephalic peduncle absent. Neck scutellate; surface of scutes comprised of densely packed capilliform filitriches with triangular tips.

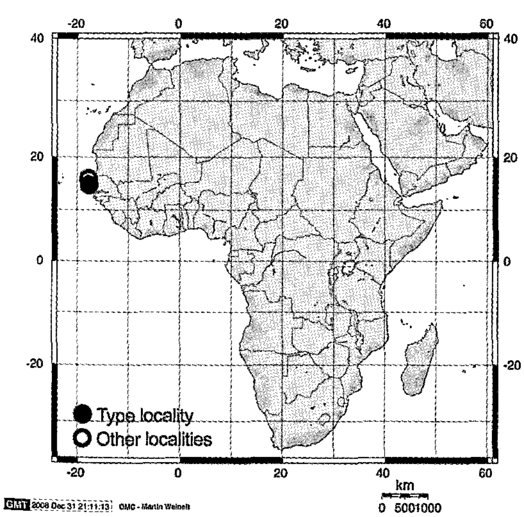

Fig. 101. Geographic distribution of *Paraorygmatobothrium bai* Ruhnke and Carpenter, 2008.

Immature proglottids initially wider than long, becoming longer than wide. Terminal and subterminal proglottids 1,080–

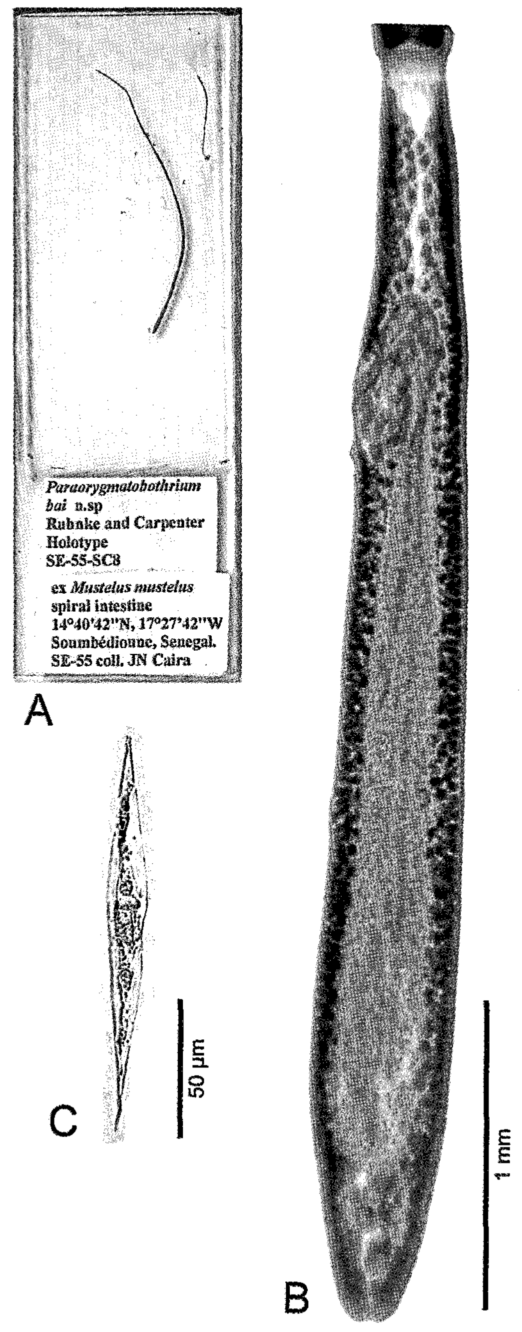

Fig. 102. Photomicrographs of *Paraorygmatobothrium bai* Ruhnke and Carpenter, 2008. A. Slide of holotype (MNHN HEL 52). B. Terminal proglottid of holotype (MNHN HEL 52). C. Egg.

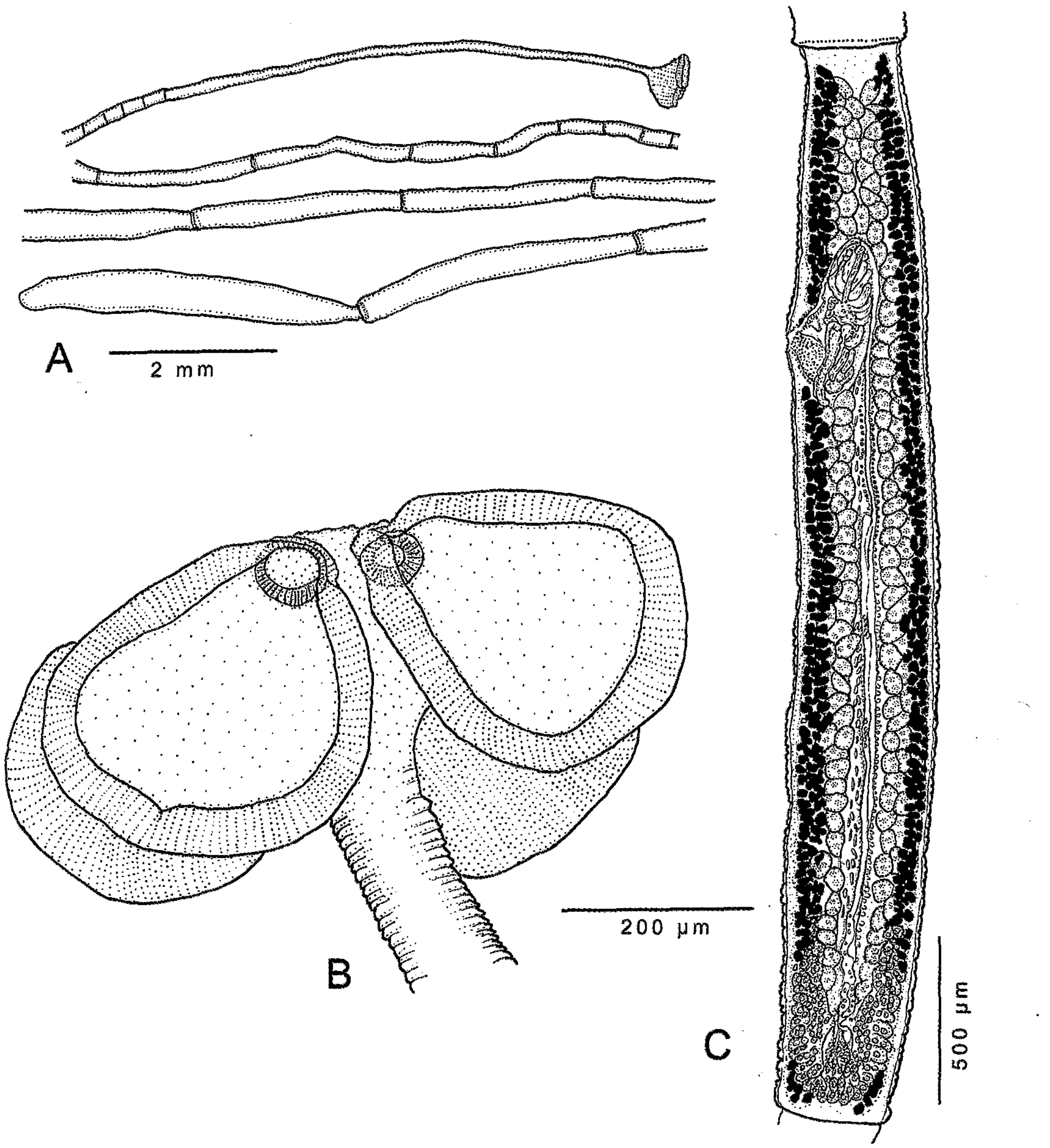

Fig. 103. Line drawings of *Paraorygmatobothrium bai* Ruhnke and Carpenter, 2008. A. Paratype (LRP 4183). B. Scolex of paratype (LRP 4181). C. Mature proglottid of holotype (MNHN HEL 52). (Taken from Ruhnke and Carpenter [2008], copyright 2008. Used with permission.)

4,096 (2,521 ± 710; n=17, *n*=48) long x 205–563 (357 ± 92; n=17, *n*=48) wide, length to width ratio 4–11:1 (7.3 ± 1.8; n=17, *n*=48). Terminal proglottids typically gravid. Testes 100–145 (124 ± 14; n=17) in number; testes round, 31–78 (49 ± 10; n=17, *n*=50) in diameter in terminal and subterminal proglottids. Cirrus-sac J-shaped, 196–369 (291 ± 58; n=18) long x 83–225 (152 ± 37; n=18) wide, containing coiled cirrus. Cirrus armed with spinitriches. Vas deferens coiled, median, overlapping proximal portion of cirrus-sac, anterior to cirrus-sac. Genital pores lateral, 68–75% (71 ± 2; n=18) of proglottid length

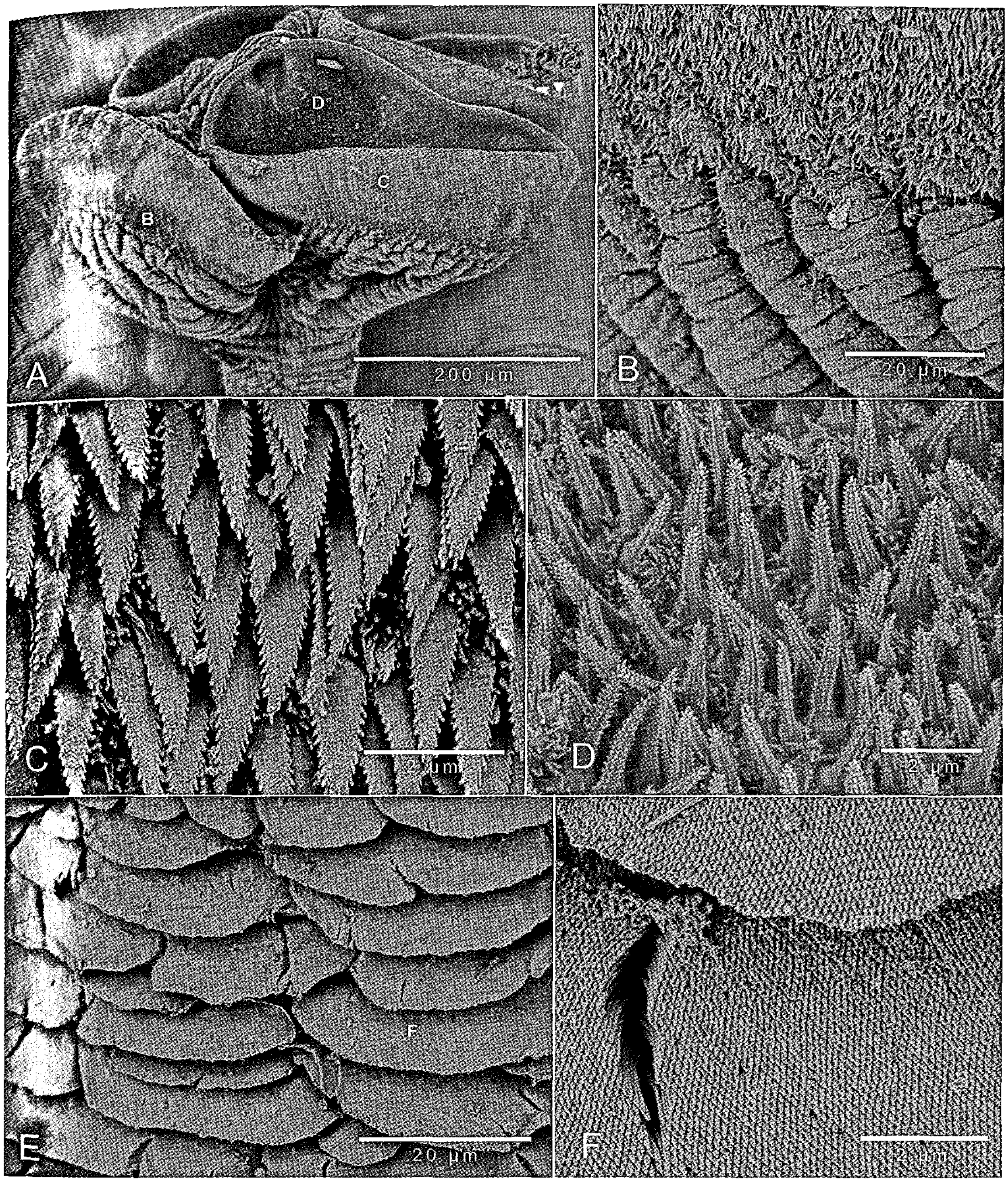

Fig. 104. Scanning electron micrographs of *Paraorygmatobothrium bai* Ruhnke and Carpenter, 2008. A. Scolex (letter indicate regions of scolex in enlarged photos B–D). B. Border between bothridial disc and bothridial stalk. C. Proximal surface of bothridium. D. Distal surface of bothridium. E. Anterior region of neck (letter indicate region of neck in enlarged photos F). F. Neck surface. (Taken from Ruhnke and Carpenter [2008], copyright 2008. Used with permission.)

from posterior end. Vagina median, extending anteriorly from Mehlis' gland to mid-level of proglottid, then laterally along anterior margin of vas deferens, then to shallow genital atrium. Ovary near posterior end of proglottis, H-shaped in frontal view, 320–700 (476 ± 110; n=17) long x 158–440 (284+ 110; n=16) wide, tetralobed in cross-section.

Ovicapt 31–50 (42 ± 6.5; n=17) in diameter in terminal proglottids, at posterior margin of ovarian bridge. Mehlis' gland posterior to ovicapt. Uterus ventral to vagina, extending from anterior margin of ovary to level of cirrus-sac. Uterine duct present, median, parallel and dorsal to uterus, enters uterus posterior to cirrus-sac in posterior proglottids. Vitellarium follicular; follicles 10–73 (31 ± 14; n=17, *n*=50) x 13–78 (33 ± 15; n=17, *n*=50), in two lateral fields each with 3–4 dorsal and 3–4 ventral columns of follicles, extending entire length of proglottid, interrupted by ovary and cirrus-sac. One dorsal and one ventral pair of excretory ducts. Eggs spindle-shaped, 135–155 (143 ± 5; n=2: *n*=10) long x 12–15 (14 ± 1; n=2: *n*=10) wide.

Remarks

Paraorygmatobothrium bai can be distinguished from all existing species of *Paraorygmatobothrium* except *P. rodmani* in that specimens retain proglottids that become fully gravid while attached to the strobila. That is, *P. bai* and *P. rodmani* are essentially apolytic, whereas all other of their congeners are euapolytic or hyperapolytic. *Paraorygmatobothrium bai* differs from *P. rodmani* in testes shape (round vs. oblong). In all other features, the ranges of these two species overlap. However, Ruhnke and Carpenter (2008) conducted t-test comparisons of character means, and revealed statistically significant differences (p<0.0001) between these two species in the cases of a number of features. For example, *P. bai* is significantly longer than *P. rodmani* (mean 30.6 vs. 19.7), and has significantly narrower terminal and subterminal proglottids than *P. rodmani* (mean length:width ratio 7.3:1 vs. 3.9:1). In addition, *P. bai* has significantly fewer testes than *P. rodmani* (mean 124 vs. 162).

Paraorygmatobothrium barberi Ruhnke, 1994
(Figs. 105–108)

Taxonomic status: Valid.

Type host: *Triakis semifasciata* Girard 1854, the Leopard shark.

Site of infection: Spiral intestine.

Type locality: Hermosa Beach Pier (33°51.6'N, 188°23.8'W), Hermosa Beach, California U.S.A. (Fig. 105).

Additional localities: El Barril, Mexico; San Fransiquito, Mexico; Monterrey Bay, California, U.S.A. (Fig. 105).

Type material: Holotype USNPC 82936; paratypes USNPC 82937, HWML 36769 (Fig. 106A), LRP 7418, 7420–7423.

Voucher specimens: LRP 7419, 7424–7425.

Material examined: All type and voucher specimens were examined.

Etymology: This species is named for Kenneth Barber, who was responsible for recovering the leopard shark spiral intestine containing the type specimens of this species.

Description (modified from Ruhnke [1994a]).

Worms slightly craspedote, apolytic, 20–36 mm (28 ± 5; n=13) long; maximum width 530–880 (740 ± 95; n=13), generally at level of mature proglottids. Proglottids 47–67 (56 ± 7; n=11) in number. Scolex 450–780 (596 ± 117; n=11) long x 450–880 (670 ± 130; n=14) wide, with four bothridia; apical surface of scolex covered with long filitriches. Bothridia 380–730 (556 ± 112; n=8; *n*=17) long x 213–480 (299 ± 77; n=11; *n*=14) wide,

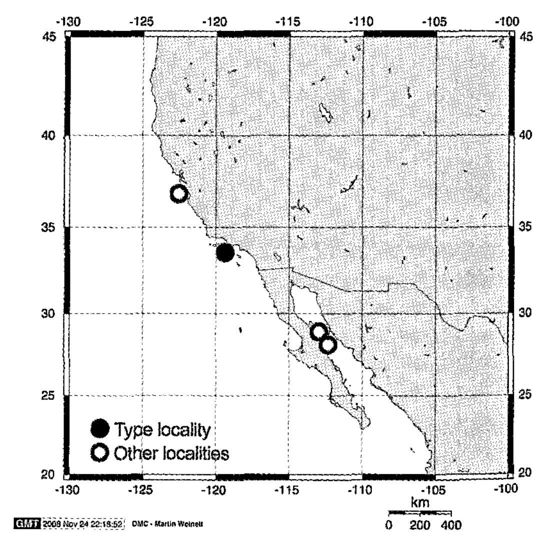

Fig. 105. Geographic distribution of *Paraorygmatobothrium barberi* Ruhnke, 1994.

each with single loculus and round, apical sucker, 55–80 (68 ± 6; n=18; *n*=38) in diameter. Bothridial loculus with circular band of muscles in the central portion of the bothridia. Proximal surfaces of bothridia covered with serrate gladiate spinitriches and acicular filitriches. Distal locular surfaces of bothridia covered with papilliform filitriches and gongylate columnar spinitriches; distal surfaces of bothridia inside apical sucker covered with papilliform filitriches and serrate gladiate spinitriches. Cephalic peduncle absent. Neck 4.6–11 (7 ± 2; n=13) long; dorsal and ventral surfaces scutellate; surface of scutes comprised of capilliform filitriches with a triangular tip.

Immature proglottids wider than long, 280–510 (376 ± 80; n=9; *n*=18) long x 360–760 (613 ± 115; n=9; *n*=18) wide. Mature proglottids generally twice as long as wide, 1,200–2,550 (1,808 ± 371; n=15; *n*=27) long x 400–940 (777 ± 132; n=15; *n*=27) wide, with dorsal and ventral pair of excretory ducts lateral pair of nerve chords. Free proglottids 4.7–6.8 mm (5.7 ± 1; n=5) long x 1–1.5 mm (1.4 ± 0.2; n=5) wide. Mature proglottids with 135–215 (176 ± 23; n=17) testes. Testes oblong, 38–68 (51 ± 8; n=17; *n*=34) long x 55–90 (74 ± 9; n=17; *n*=34) wide, generally arranged in 6–8 irregular columns, in 6–10 (7 ± 2; n=16; *n*=17) irregular columns preporally; in 5–7 (6 ± 1; n=16; *n*=17) Irregular columns post–porally; one row deep in cross-section. Cirrus-sac oval, 250–450 (350 ± 52; n=17; *n*=24) long x 113–238 (201 ± 35; n=17; *n*=24) wide, containing coiled cirrus. Cirrus armed with spinitriches. Vas deferens coiled, median, bordering proximal portion

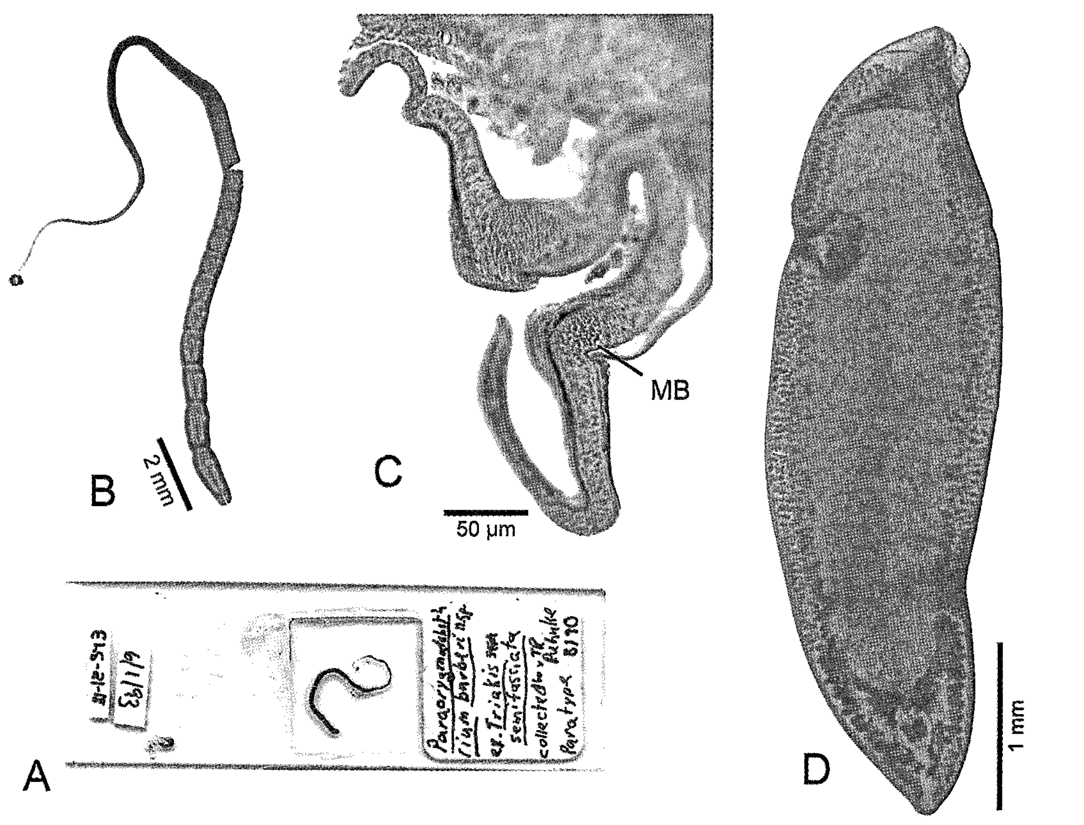

Fig. 106. Photomicrographs of *Paraorygmatobothrium barberi* Ruhnke, 1994. A. Slide of paratype (HWML 36769). B. Entire specimen of paratype (LRP 7418). C. Frontal section of scolex of paratype (HWML 36769). D. Free proglottid of voucher (LRP 7419).

of cirrus-sac, anterior to cirrus-sac, enlarged with sperm and overlapping anterior portion of cirrus-sac in terminal proglottids. Genital pores marginal, 64–78% (73 ± 4; n=16) of proglottid length from posterior end of proglottid, generally irregularly alternating, unilateral in eight of 20 specimens. Vagina median, extending anteriorly from ovary to mid-level of proglottid, then laterally along anterior margin of cirrus-sac to shallow genital atrium. Ovary near posterior end of proglottid. H-shaped in frontal view, 410–630 (505 ± 89; n=14; *n*=15) long x 410–730 (565 ± 89; n=14; *n*=15) wide, composed of many lateral finger-like follicles, tetralobed in cross-section. Ovicapt at posterior margin of ovarian bridge, 45–65 (55 ± 5; n=15; *n*=20) in diameter in mature proglottids. Mehlis' gland posterior to ovicapt. Uterus ventral to vagina, extending from anterior margin of ovary to anterior-proximal extremity of vas deferens in mature proglottids and free proglottids. Uterine duct parallel to uterus, extending to posterior margin of cirrus-sac in mature and free proglottids, then entering uterus at level of posterior margin of cirrus-sac. Vitellarium follicular; follicles 18–50 (27 ± 7; n=16; *n*=33) long x 43–75 (58 ± 10; n=16; *n*=33) wide, in two lateral bands each with 3–5 dorsal and 3–5 ventral columns of follicles, completely interrupted by ovary and cirrus-sac. Eggs round, 24–28 (26 ± 1; n=3; *n*=24) in diameter, seen in mature and free proglottids.

Remarks

Paraorygmatobothrium barberi differs from other species of the genus in possessing a circular band of muscles in the central portion of the bothridia. Furthermore, *P. barberi* differs from all species of *Paraorygmatobothrium* except *P filiforme, P. janineae, P. kirstenae,* and *P. triacis* in number of proglottids (see Table 1). Among other features, *P. barberi* differs from *P. filiforme* in testes number (135–215 vs. 72–123), differs from *P. filiforme, P. janineae,* and *P. kirstenae* in ovary length (410–630 vs. 250, 119–290 and 116–279), and differs from *P. triacis* in total length (20–36 vs. 35–46 mm).

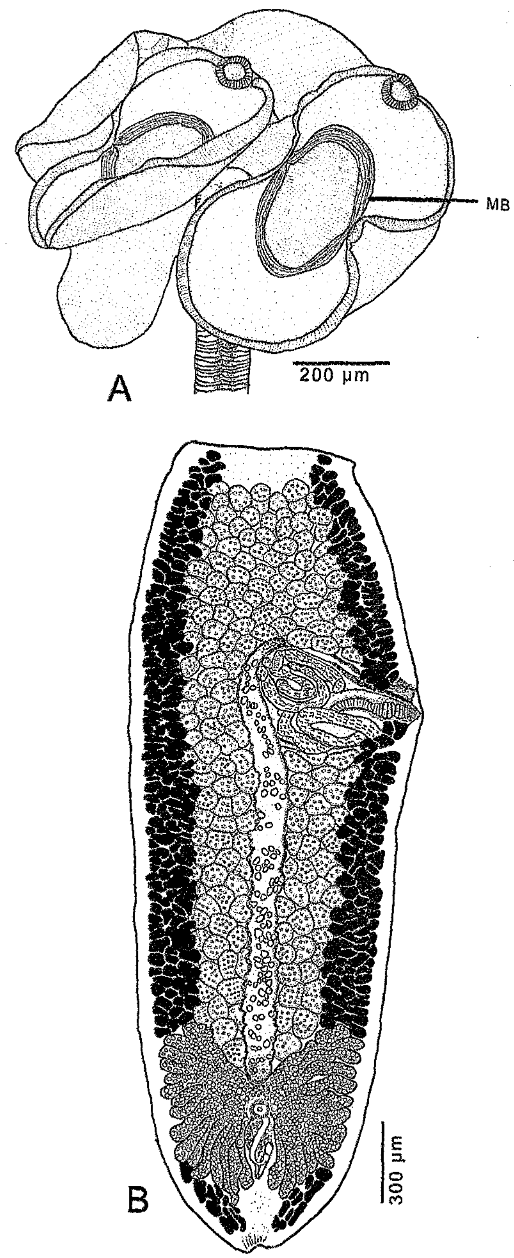

Fig. 107. Line drawings of *Paraorygmatobothrium barberi* Ruhnke, 1994. A. Scolex of paratype (USNPC 82937). B. Terminal proglottid of holotype (USNPC 82936). (Taken from Ruhnke [1994a], copyright 1994. Used with permission.)

Riser (1955) was the first to examine and publish on material of this species, although at the time he considered his specimens to be conspecific with *Orygmatobothrium musteli.*

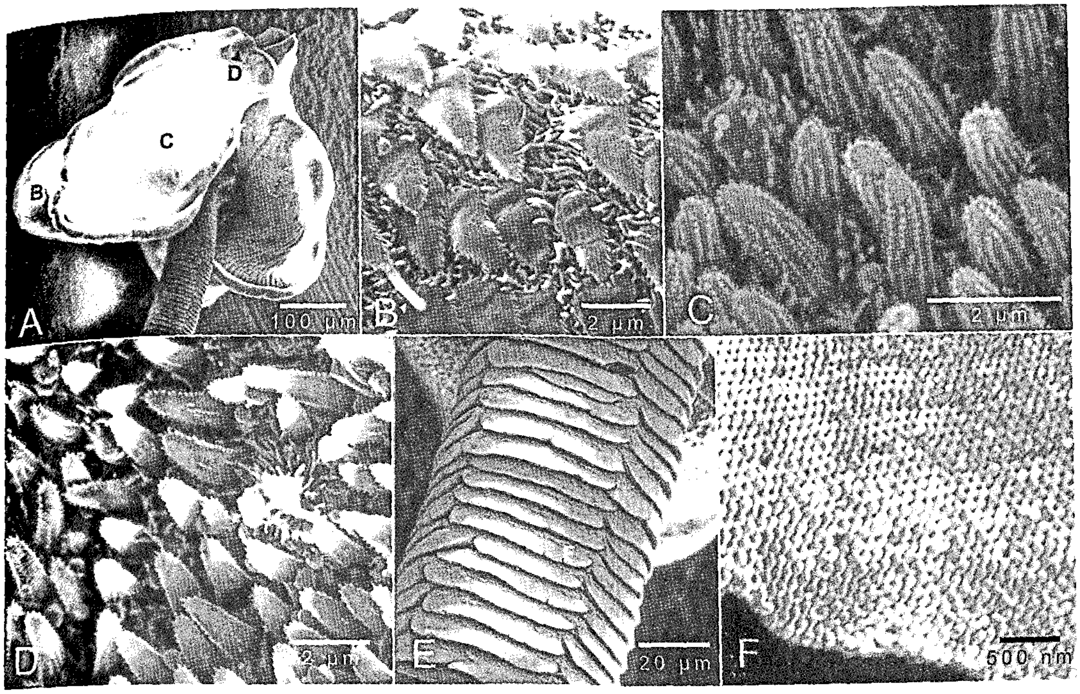

Fig. 108. Scanning electron micrographs of *Paraorygmatobothrium barberi* Ruhnke, 1994. A. Scolex (letter indicate regions of scolex in enlarged photos B–D). B. Proximal surface of bothridium. C. Distal surface of bothridium. D. Distal surface of bothridium on apical sucker. E. Anterior region of neck (letter indicate region of neck in enlarged photos F). F. Neck surface. (Taken from Ruhnke [1994a], copyright 1994. Used with permission.).

Riser (1955) also reported specimens consistent with *P. barberi* from the sharks *Mustelus henlei* and *Galeorhinus galeus*. Critical comparisons have not been made of specimens from these sharks, but Riser's (1955) findings indicate that *P. barberi* may be distributed more widely among eastern Pacific triakid sharks than is currently envisioned.

Additional localities: Northwestern Atlantic Ocean, near Montauk, Long Island, New York, U.S.A.; Concarneau, France (Fig. 109).

Type material: Holotype and paratypes, MPM 22775 (Fig. 110A).

***Paraorygmatobothrium exiguum* (Yamaguti, 1935) Ruhnke, 1994**

(Figs. 109–112)

Synonyms: *Anthobothrium parvum* Yamaguti, 1934; *Anthobothrium exiguum* Yamaguti, 1935.

Taxonomic status: Valid.

Type host: *Alopias vulpinus* Bonnaterre, 1788, the Thin-tail thresher shark.

Site of infection: Spiral intestine.

Type locality: Kuki, Mie Prefecture, Japan (Fig. 109).

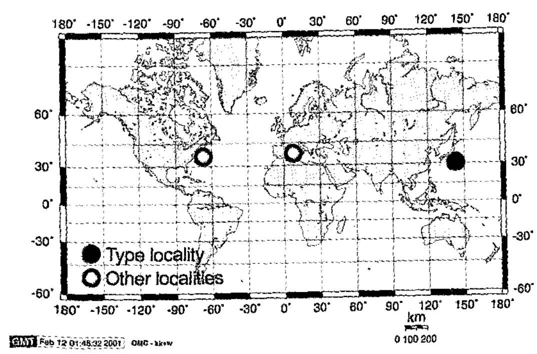

Fig. 109. Geographic distribution of *Paraorygmatobothrium exiguum* (Yamaguti, 1935) Ruhnke, 1994.

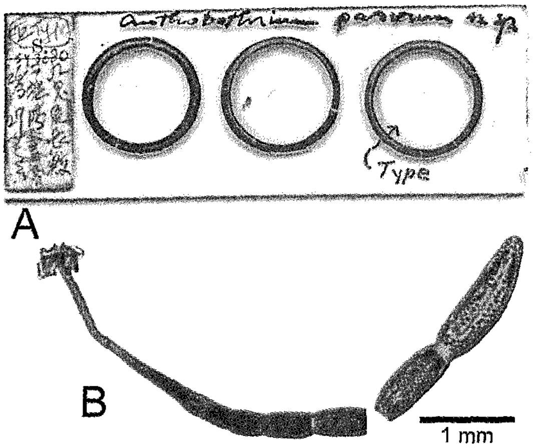

Fig. 110. Photomicrographs of *Paraorygmatobothrium exiguum* (Yamaguti, 1935) Ruhnke, 1994. A. Slide of type (MPM 22775). B. Entire specimen of voucher (HWML 36774).

Voucher specimens: USNPC 82490, HWML 36774, MPM 19852, LRP 7426.

Material examined: Holotype and paratype (MPM 22775), voucher specimens USNPC 82490, HWML 36774, MPM 19852, LRP 7426.

Etymology: Not given, but presumably, from L. *exiguus* (=small), in reference to the small, slight morphology of the species.

Description (modified from Ruhnke [1994a]).

Worms craspedote, euapoltyic, 5.2–8.2 mm (6.6 ± 0.9; n=16) long (Fig. 110B); maximum width 410–580 (466 ± 74; n=11) at scolex. Proglottids 12–20 (15 ± 4; n=14) in number. Scolex 380–490 (412 ± 45; n=5) long, with four bothridia. Bothridia 300–420 (350 ± 38; n=9) long x 170–300 (249 ± 49; n=9) wide, each with single loculus and round apical sucker;

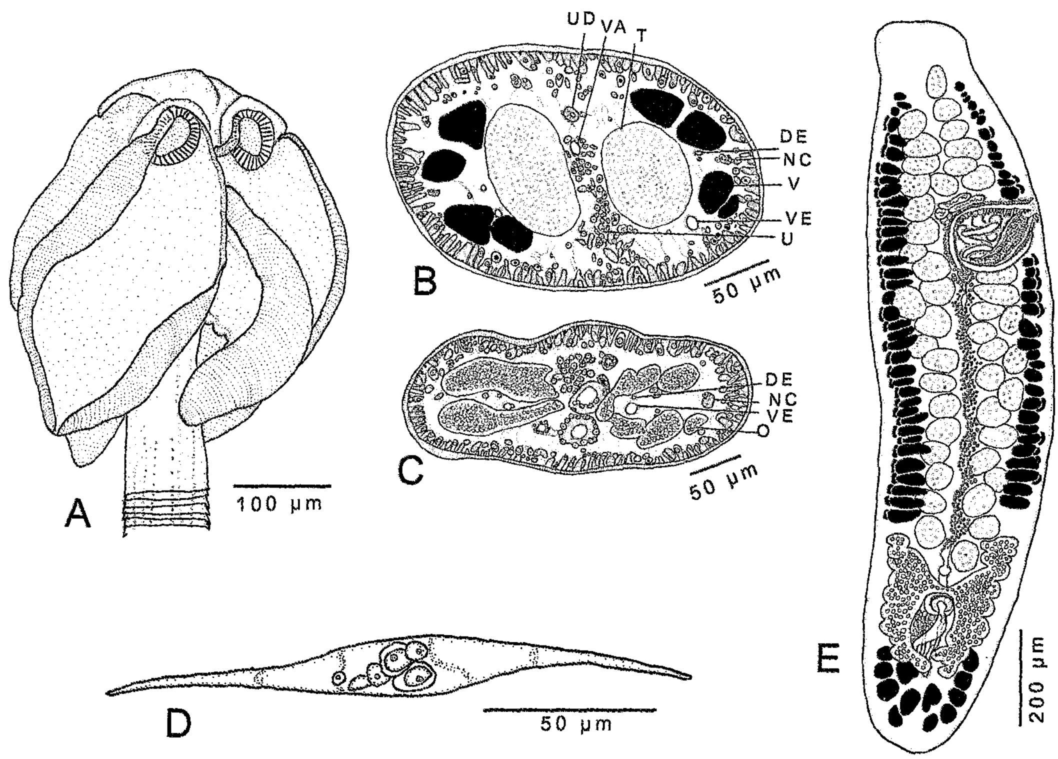

Fig. 111. Line drawings of *Paraorygmatobothrium exiguum* (Yamaguti, 1935) Ruhnke, 1994. A. Scolex of voucher (USNPC 82490). B. Cross-section of proglottid posterior to cirrus-sac and anterior to ovary of voucher (HWML 36774). C. Cross-section of proglottid through ovary of voucher (HWML 36774). D. Egg of voucher. E. Mature proglottid of voucher (USNPC 82490). (Taken from Ruhnke [1994a], copyright 1994. Used with permission.)

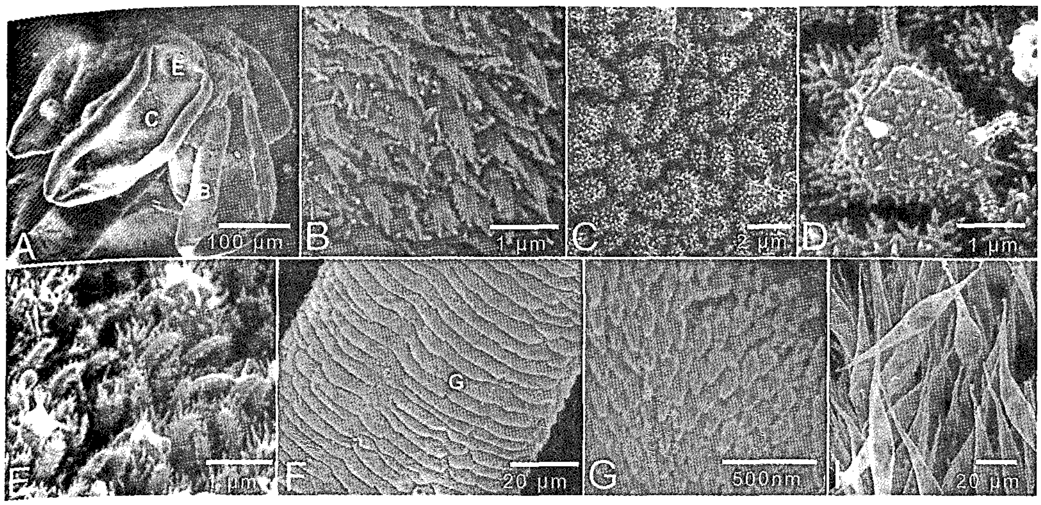

Fig. 112. Scanning electron micrographs of *Paraorygmatobothrium exiguum* (Yamaguti, 1935) Ruhnke, 1994. A. Scolex (letter indicate regions of scolex in enlarged photos B–E). B. Proximal surface of bothridium. C. Distal surface of bothridium. D. Enlarge view of distal surface of bothridium. E. Distal surface of bothridium on apical sucker. F. Anterior region of neck (letter indicate region of neck in enlarged photos G). G. Neck surface. H. Eggs. (Taken from Ruhnke [1994a], copyright 1994. Used with permission.)

apical sucker 50–85 (66 ± 7; n=15; *n*=28) in diameter. Apical surface covered with filitriches. Proximal surfaces of bothridia covered with serrate gladiate spinitriches and acicular filitriches (Fig. 112B). Distal locular surfaces of bothridia "bumpy"; surface of bumps covered with papilliform filitriches and gongylate columnar spinitriches. Distal surfaces of bothridia inside apical suckers covered with filitriches and dorso-ventrally thickened serrate gladiate spinitriches. Cephalic peduncle absent. Neck 1–2 mm (1.4 ± 0.6; n=9) long, dorsal and ventral surfaces scutellate; scutes comprised of densely packed capilliform filitriches with a triangular tip.

Immature proglottids 125–190 (153 ± 25; n=6; *n*=10) long x 130–205 (182 ± 26; *n*=6; n=10) wide. Mature proglottids 925–1475 (1204 ± 182; n=13; *n*=14) long x 250–430 (341 ± 54; n=13; *n*=14) wide, generally three times as long as wide, with dorsal and ventral pair of excretory ducts and lateral pair of nerve chords. Free proglottids 2,480–3,100 (2,836 ± 223; n=5) long x wide 40–750 (648 ± 98; n=5). Testes 33–59 (49 ± 7; n=16) in number; testes oblong, 30–72 (47 ± 15; n=14; *n*=45) long x 45–80 (61 ± 9; n=14; *n*=45) wide, arranged in 2–4 (2.9 ± 0.7; n=16) irregular columns pre-porally; in 2–4 (2.6 ± 0.7; n=16) irregular columns post-porally, medullary, one row deep in cross-section. Cirrus-sac oval, 135–187 (159 ± 14; n=14; *n*=15) long x 87–142 (99 ± 15; n=14; *n*=15) wide, containing armed, coiled cirrus. Vas deferens coiled, median, bordering proximal portion of cirrus-sac, anterior to cirrus-sac. Genital pores marginal, 74–83% (78 ± 2.8; n=15; n=16) of proglottid length from posterior end, generally irregularly alternating, unilateral in nine of 16 specimens. Vagina median, extending anteriorly from ovary to midlevel of proglottid, then laterally along anterior margin to cirrus-sac to genital pore. Ovary near posterior end of proglottid, H-shaped in frontal view, 175–310 (246 ± 46; n=11; *n*=12) long x 143–260 (214 ± 36; n=11; *n*=12) wide,lobed in cross section. Ovicapt at posterior margin of ovarian bridge, 26–37 (32 ± 3; n=13; *n*=15) in diameter in mature proglottids. Mehlis' gland posterior to ovicapt. Uterus ventral to vagina, extending from anterior margin of ovary to posterior margin of cirrus-sac in mature proglottids, to anterior margin of cirrus-sac in free proglottids. Uterine duct present in mature and free proglottids, median, parallel to uterus, dorsal to vagina, extending to posterior margin of cirrus-sac in mature and free proglottids, entering uterus at level of posterior margin of cirrus-sac. Vitellarium follicular; follicles 12–35 (22 ± 7; n=13; *n*=42) long x 25–70 (42 ± 10; n=13; *n*=42) wide in two lateral bands each consisting of two dorsal and two ventral columns of follicles in cross section, interrupted by ovary and cirrus-sac. Egg-shells spindle-shaped 145–170 (156 ± 10; n=16) long x 15–20 (17 ± 1; n=16) wide, seen only in free proglottids.

Remarks

This species was originally described by Yamaguti (1934) as *Anthobothrium parvum* Yamaguti, 1934. However, this name was pre-occupied by *Anthobothrium parvum* Stossich, 1895, so Yamaguti (1935) renamed the species *Anthobothrium exiguum* Yamaguti, 1935. *Paraorygmatobothrium exiguum* differs from all species of *Paraorygmatobothrium* except *P. prionacis* in testes number (see Table 1). It differs from *P. prionacis* in bothridial length (300–420 vs. 420–620) and genital pore position (74–83% vs. 48–59%). Ruhnke (1994) listed the coastal waters of Japan and Long Island as localities for *P. exiguum*. Euzet (1959) reported specimens of *"Crossobothrium angustum"* from *A. vulpinus* taken from Concarneau, France. Examination of these specimens indicates that they are indeed consistent with the description of *P. exiguum*. These data suggest that this species may have a worldwide distribution as does its host, *A. vulpinus*.

Paraorygmatobothrium filiforme (Yamaguti, 1952) Ruhnke, 1996

(Figs. 113–114)

Synonyms: *Phyllobothrium filiforme* Yamaguti, 1952; *Crossobothrium filiforme* (Yamaguti, 1952) Williams, 1968.

Taxonomic status: Valid.

Type host: *Alopias vulpinus* Bonnaterre, 1788, the Thin-tail thresher shark.

Site of infection: Spiral intestine.

Type locality: Japanese coastal waters (Fig. 113).

Type material: Syntypes, MPM 22697 (Fig. 112A).

Material examined: Syntypes, MPM 22697 (Fig. 112A).

Etymology: Not given, but presumably, L. *filiforme* (= thread-like, filamentous).

Description (modified from Ruhnke [1996a]).

Worms slightly craspedote, euapolytic, 11.8–23.7 mm (17 ± 5; n=5) long; maximum width 430–530 (487 ± 39; n=6) at scolex. Proglottids 31–50 (38 ± 9; n=4) in number. Scolex with four bothridia. Bothridia 250–330 (282 ± 27; n=4; *n*=8) wide, each with a single loculus and round apical sucker. Apical sucker 50–60 (54±3; n=4; *n*=8) in diameter. Cephalic peduncle absent. Neck 2.4–4 mm (3.6 ± 1; n=5) long, dorsal and ventral surfaces scutellate.

Mature proglottids 950–1,800 (1,247 ± 291; n=5; *n*=9) long x 250–450 (356 ± 56; n=5; *n*=9) wide. Testes 72–123 (102 ± 16; n=6; n=13) in number; testes oblong, 30–50 (39 ± 6; n=5; *n*=25) long x 43–70 (57 ± 7; n=5; *n*=25) wide, arranged in 4–6 irregular longitudinal columns, one row deep in cross-section. Cirrus-sac 170–200 (185 ± 11; n=5; *n*=8) long x 68–135 (88 ± 38; n=5; *n*=8) wide. Genital pores marginal, 67–75% (72 ± 4; n=5; *n*=10) of proglottid length from posterior end, generally irregularly alternating, unilateral in one of five specimens. Ovary H-shaped in frontal view, 250 long x 250 wide. Ovicapt at poste-

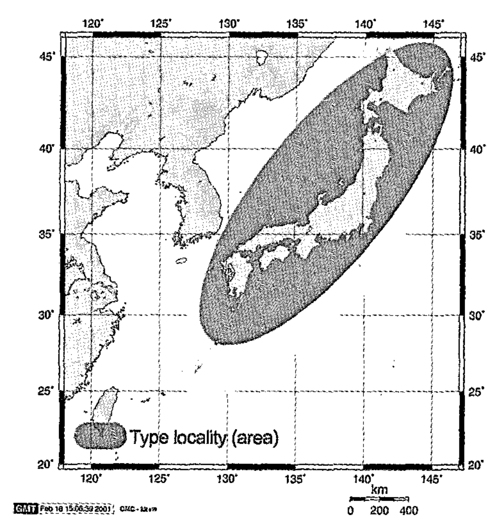

Fig. 113. Geographic distribution of *Paraorygmatobothrium filiforme* (Yamaguti, 1952) Ruhnke, 1996.

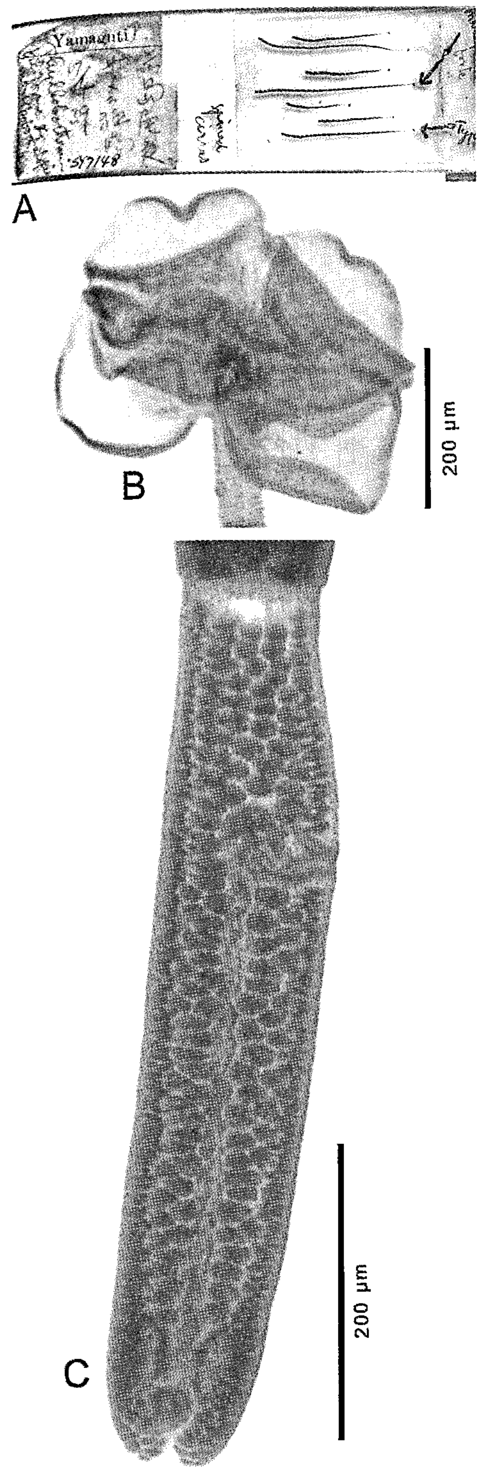

Fig. 114. Photomicrographs of *Paraorygmatobothrium filiforme* (Yamaguti, 1952) Ruhnke, 1996. A. Slide of type (MPM 22697). B. Scolex of type (MPM 22697). C. Terminal proglottid of type (MPM 22697).

rior margin of ovarian bridge, 35–42 (38 ± 3; n=4; n=6) in diameter in mature proglottids. Uterus ventral, median, extending from anterior margin of ovary to posterior margin of cirrus-sac in mature proglottids. Vitellarium follicular; follicles oblong, 10–28 (18 ± 4; n=5; *n*=21) long x 28–55 (43 ± 8; n=5; *n*=21) wide, in two lateral fields, each consisting of 2–3 dorsal and 2–3 ventral columns of follicles; completely interrupted by ovary and cirrus-sac.

Remarks

Paraorygmatobothrium filiforme Yamaguti, 1952 was originally described by Yamaguti (1952) as *Phyllobothrium filiforme.* However, Euzet (1959) considered this species a junior synonym of *Crossobothrium angustum* (= *Paraorygmatobothrium angustum*). Williams (1968a) considered Euzet's (1959) synonymy ill-advised, but transferred *P. filiforme* to *Crossobothrium.* Ruhnke (1996b) transferred the species to *Paraorygmatobothrium* when he resolved the taxonomic status of *Crossobothrium,* and this species is consistent with the generic diagnosis of *Paraorygmatobothrium.*

Paraorygmatobothrium filiforme differs from all species of *Paraorygmatobothrium* except *P barberi, P. kirstenae, P. roberti,* and *P. triacis* in proglottid number (see Table 1). This species differs from *P. barberi,* and *P. triacis* in maxiumum width (430–530 vs. 530–880 and 800–920), differs from *P. barberi, P. kirstenae* and *P. triacis* in testes number (72–102 vs. 135–215, 104–164, and 176–238, respectively). *P. filiforme* differs from *P. roberti* in ovary width (250 vs. 123–207).

Paraorygmatobothrium floraformis (Southwell, 1912) n. comb.

(Figs. 115–117)

Synonyms: *Anthobothrium floraformis* Southwell, 1912; *Phyllobothrium floraforme* (Southwell, 1912) Southwell, 1930.

Taxonomic status: Valid.

Type host: *Carcharias bleekeri* (= *Carcharhinus sorrah* [Müller and Henle, 1839]) the Spottail shark).

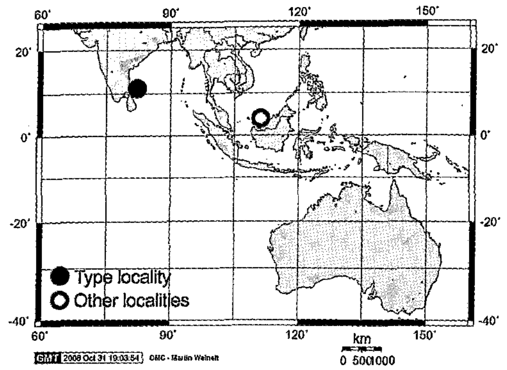

Fig. 115. Geographic distribution of *Paraorygmatobothrium floraformis* (Southwell, 1912) n. comb.

Site of infection: Spiral intestine.

Type locality: Periya Paar Karai, Ceylon (= Sri Lanka) (Fig. 115).

Additional localities: Sarawak, Malaysian Borneo (Fig. 115).

Type material: Not specified.

Voucher specimens: LRP 7427–7430 (Fig 116A).

Material examined: LRP 7427–7430.

Etymology: Not specified, but Southwell (1912) noted the resemblance of the scolex to that of a four-petalled flower.

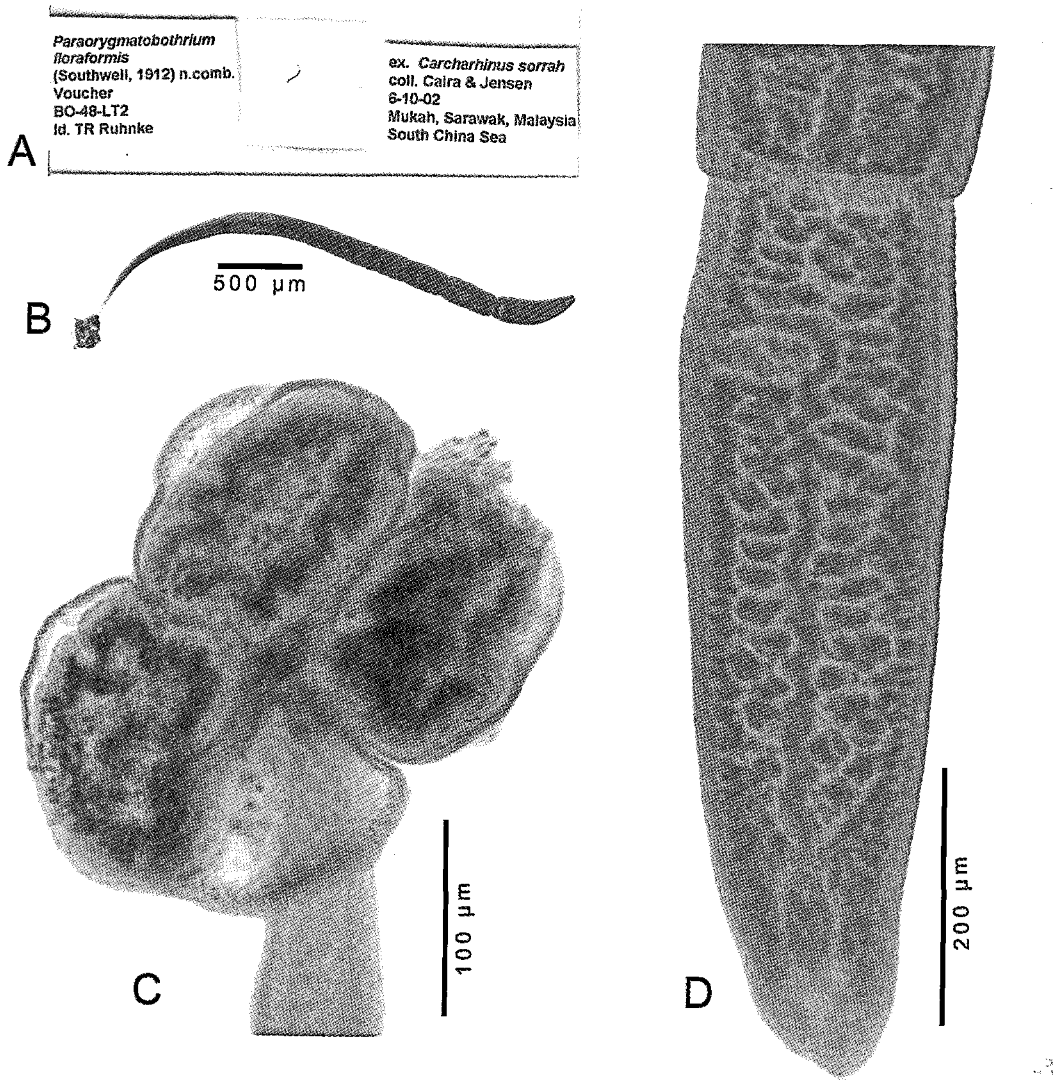

Fig. 116. Photomicrographs of *Paraorygmatobothrium floraformis* (Southwell, 1912) n. comb. A. Slide of voucher (LRP 7427). B. Entire voucher (LRP 7427). C. Scolex of voucher (LRP 7428). D. Terminal proglottid of voucher (LRP 7428).

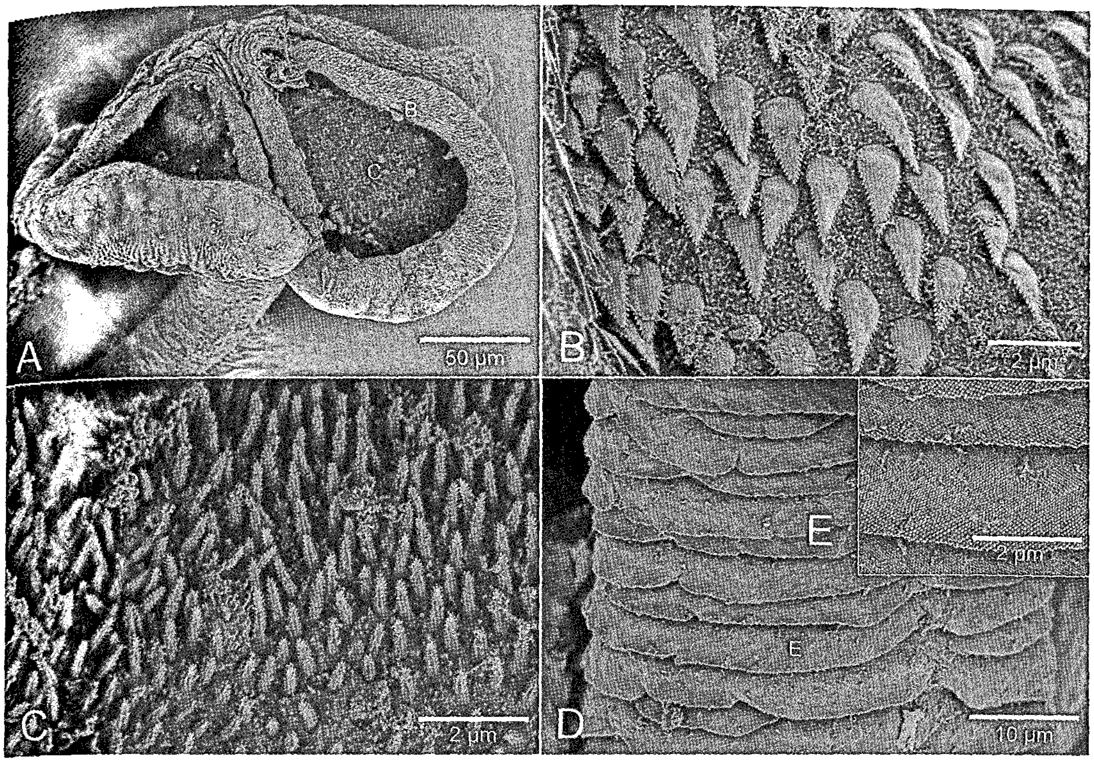

Fig. 117. Scanning electron micrographs of *Paraorygmatobothrium floraformis* (Southwell, 1912) n. comb. A. Scolex (letter indicate regions of scolex in enlarged photos B–C). B. Proximal surface of bothridium. C. Distal surface of bothridium. D. Anterior region of neck (letter indicate region of neck in enlarged photos E). E. Neck surface.

Redescription (based on 12 whole mounted specimens, and two scolices prepared for SEM).

Worms craspedote, euapoltyic, 2–4.5 (3.3 ± 0.7; n=12) mm long, maximum width 150–434 (264 ± 93; n=12) at scolex, strobila consisting of 10–19 (15 ± 3; n=12) proglottids. Scolex with four bothridia, 161–167 long x 150–434 wide. Bothridia uniloculate, 86–112 wide; apical sucker 20–37 (30 ± 6; n=6; *n*=8) in diameter. Proximal surfaces of bothridia covered with serrate gladiate spinitriches and papilliform filitriches. Distal locular surface and distal surface of apical sucker covered with gongylate columnar spinitriches and papilliform filitriches. Cephalic peduncle absent. Neck 0.5–1.6 (1 ± 0.4; n=10) mm long, dorsal and ventral surfaces scutellate, scutes comprised of densely packed capilliform filitriches.

Immature proglottids initially wider than long. Terminal proglottids 469–1,160 (687 ± 213; n=10) long x 144–288 (219 ± 50; n=8) wide, terminal proglottid length to width ratio 1.6–4.2:1 (3.1 ± 0.9; n=8). Testes 43–81 (57 ± 13; n=7) in number; testes oblong, 10–40 (19 ± 7; n=8; *n*=22) long x 27–59 (38 ± 8; n=8; *n*=22) wide, one row deep in cross-section. Cirrus-sac oval 78–139 (105 ± 22; n=6) long x 31–59 (41 ± 11; n=6) wide, proximal side of cirrus-sac extends past midline of proglottid. Vas deferens coiled, anterior to cirrus-sac, posterior to vagina. Genital pores lateral, 77–87% (81 ± 3; n=6) from posterior end of proglottid. Vagina median, extending anteriorly from Mehlis' gland to midlevel of proglottid, then laterally along anterior margin of vas deferens, then to shallow genital atrium. Ovary near posterior end of proglottis, H-shaped in frontal view, 86–285 (145 ± 67; n=8) long x 44–149 (104 ± 41; n=8) wide. Ovicapt 19–43 (28 ± 9; n=5) in diameter in terminal proglottids, at posterior margin of ovarian bridge. Uterus ventral to vagina, extending from anterior margin of ovary to level of cirrus-sac. Vitellarium follicular; follicles 7–24 (13 ± 6; n=7, *n*=21) long x 5–32 (15 ± 8; n=7, *n*=21) wide, in two lateral fields, each with 2–3 dorsal and 2–3 ventral follicles, extending entire length of proglottid, interrupted by ovary and cirrus-sac.

Remarks

Southwell (1912) described this species as *Anthobothrium floraformis* and subsequently transferred the species to *Phyllobothrium* (see Southwell 1930). While the species lacks the diagnostic features of *Phyllobothrium,* such as foliose, posteriorly bifid bothridia, its morphology is completely consistent with the diagnosis of *Paraorygmatobothrium. Paraorygmatobothrium floraformis* n. comb. differs from existing species of the genus in total length and apical sucker diameter (see Table 1).

Paraorygmatobothrium janineae Ruhnke, Healy and Shapero, 2006

(Figs. 118–121)

Taxonomic status: Valid.

Type host: *Hemipristis elongata* Klunzinger, 1871, the Snaggletooth shark.

Site of infection: Spiral intestine.

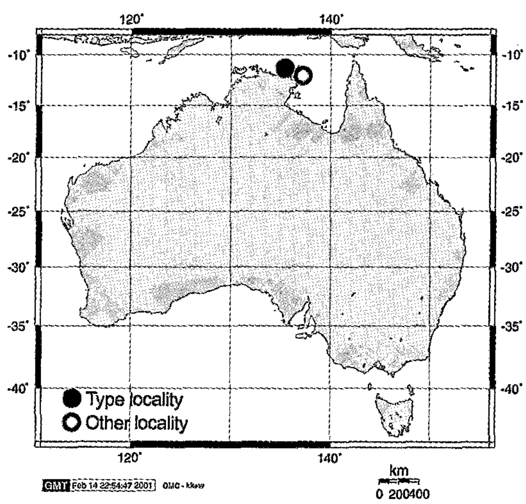

Fig. 118. Geographic distribution of *Paraorygmatobothrium janineae* Ruhnke, Healy and Shapero, 2006.

Type locality: Northern Territory (136.51°S, 10.34°E), Australia, Arafura Sea, Pacific Ocean (Fig. 118).

Additional localities: Northern Territory (136.27°S, 10.36°E, 136.59°S, 10.32°E, and 137.06°S, 10.56°E), Australia, Arafura Sea, Pacific Ocean (Fig. 118).

Type material: Holotype, QM G 225285 (see Fig. 119A); paratypes, LRP 3376–3379, 3780A–C, QM G 225286–225287; USNPC 96657–96659.

Material examined: All type specimens were examined.

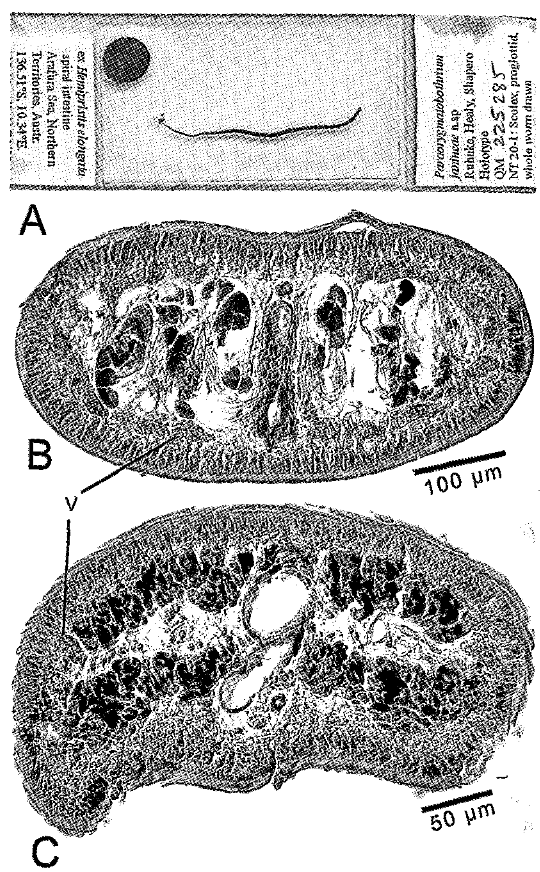

Fig. 119. Photomicrographs of *Paraorygmatobothrium janineae* Ruhnke, Healy and Shapero, 2006. A. Slide of holotype (QM GL 255285). B. Cross-section of proglottid posterior to cirrus-sac and anterior to ovary of voucher (LRP 3780). C. Cross-section of proglottid through ovary of voucher (LRP 3780). (Cross sections taken from Ruhnke et al. [2006], copyright 2006. Used with permission.)

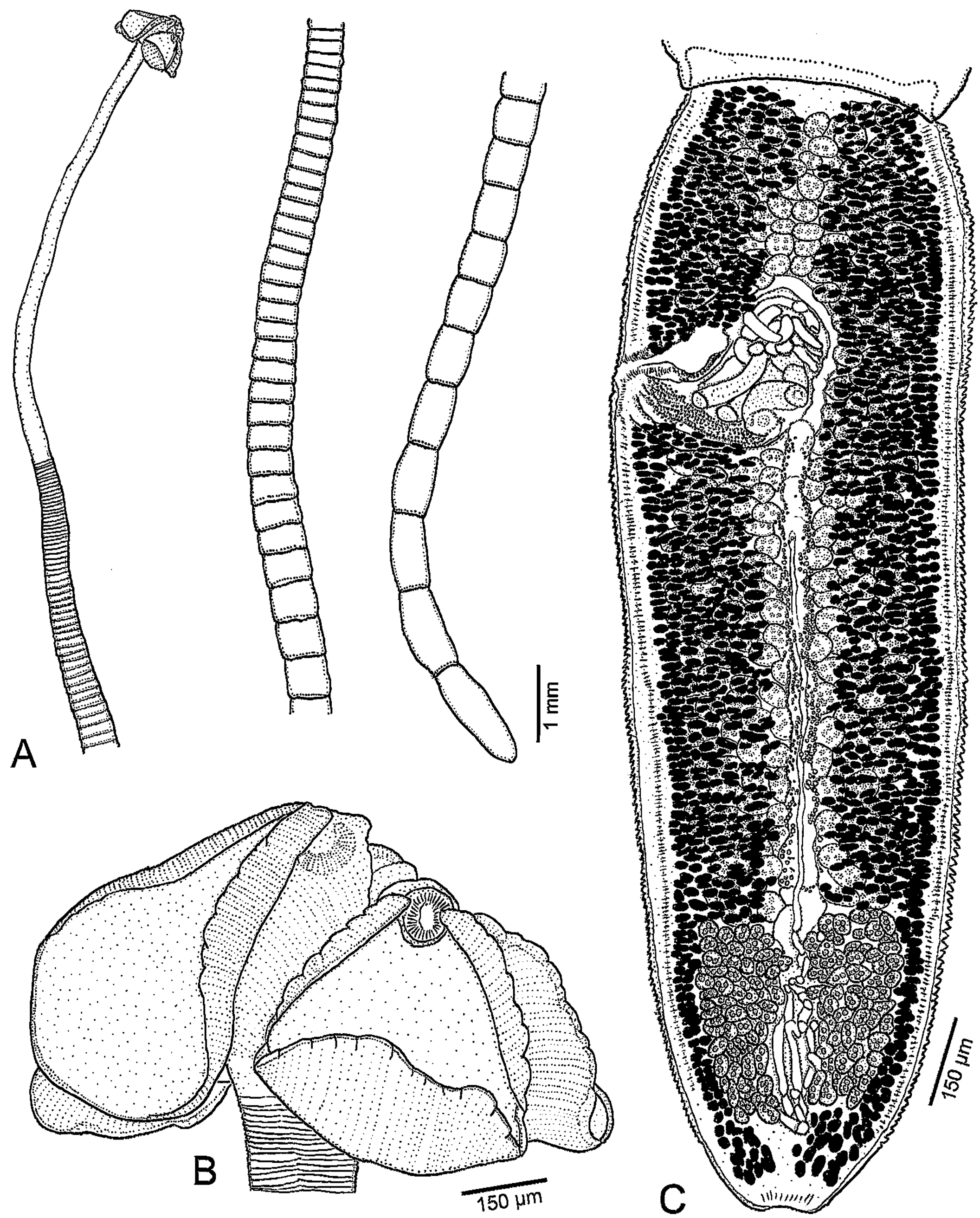

Fig. 120. Line drawings of *Paraorygmatobothrium janineae* Ruhnke, Healy and Shapero, 2006. A. Entire holotype (QM GL 255285). B. Scolex of holotype (QM GL 255285). C. Terminal proglottid of holotype (QM GL 255285). (Taken from Ruhnke, Healy and Shapero [2006], copyright 2006. Used with permission.)

Etymology: This species is named for Dr. Janine Caira.

Description (modified from Ruhnke et al. [2006a]).

Worms euapolytic, craspedote, 10–28.9 mm (17.2 ± 6; n=13) long; maximum width

561–1,021 (716 ± 151; n=16) at scolex. Proglottids 59–104 (81 ± 14; n=13) in number. Scolex 211–429 (316 ± 75; n=17) long, with four bothridia. Bothridia with single loculus and round apical sucker; apical sucker 66–139 (91 ± 15; n=18; *n*=32) in diameter, weak marginal loculi present. Distal bothridial surface covered with gongylate columnar spinitriches and capilliform filitriches. Proximal surfaces of bothridia covered with serrate gladiate spinitriches and capilliform filitriches. Cephalic peduncle present, covered with serrate gladiate spinitriches. Neck 2.5–4.9 mm (3.6 ± 0.9; n=15) long, surface of neck and proglottids covered with scutes, surface of scutes comprised of densely packed, capilliform filitriches with triangular tips.

Immature proglottids in middle third of strobila 46–330 (144 ± 70; n=14; *n*=39) long x 198–627 (392 ± 101; n=14; *n*=39) wide, length:width ratio 0.12–1.24:1 (0.39 ± 0.23; n=14, *n*=39). Terminal proglottids 409–1,560 (866 ± 344; n=16) long x 198–627 (392 ± 101; n=16) wide, length to width ratio 2.1–4.4:1 (2.8 ± 0.6; n=16). Testes (162 ± 35; n=8) in number; testes oblong, 7–53 (22 ± 11; n=9; *n*=27) long x 26–53 (39 ± 8; n=9; *n*=27) wide, one row deep in cross section. Cirrus-sac pyriform, 165–343 (226 ± 58; n=8) long x 40–218 (102 ± 61; n=8) wide in terminal proglottids, containing coiled cirrus. Cirrus armed with spinitriches. Vas deferens coiled, median, overlapping proximal portion of cirrus-sac, anterior to cirrus-sac. Genital pores lateral, 65–79% (74 ± 4; n=9) of proglottid length from posterior end, irregularly alternating. Vagina median, extending anteriorly from ovary, then laterally along anterior margin of vas deferens to genital pore. Shallow genital atrium present. Ovary near posterior end of proglottid, H-shaped in frontal view, 119–290 (217 ± 79; n=5; *n*=6) long x 73–350 (177 ± 117; n=5; *n*=6) wide, tetralobed in cross section. Ovicapt at posterior margin of ovarian bridge. Uterus ventral to vagina, extending from anterior margin of ovary to posterior margin of cirrus-sac in mature proglottids. Uterine duct present, dorsal to uterus, entering uterus near posterior margin of cirrus-sac. Vitellarium follicular, follicles in two lateral fields, 3–20 (11 ± 6; n=8; *n*=24) long x 12–44

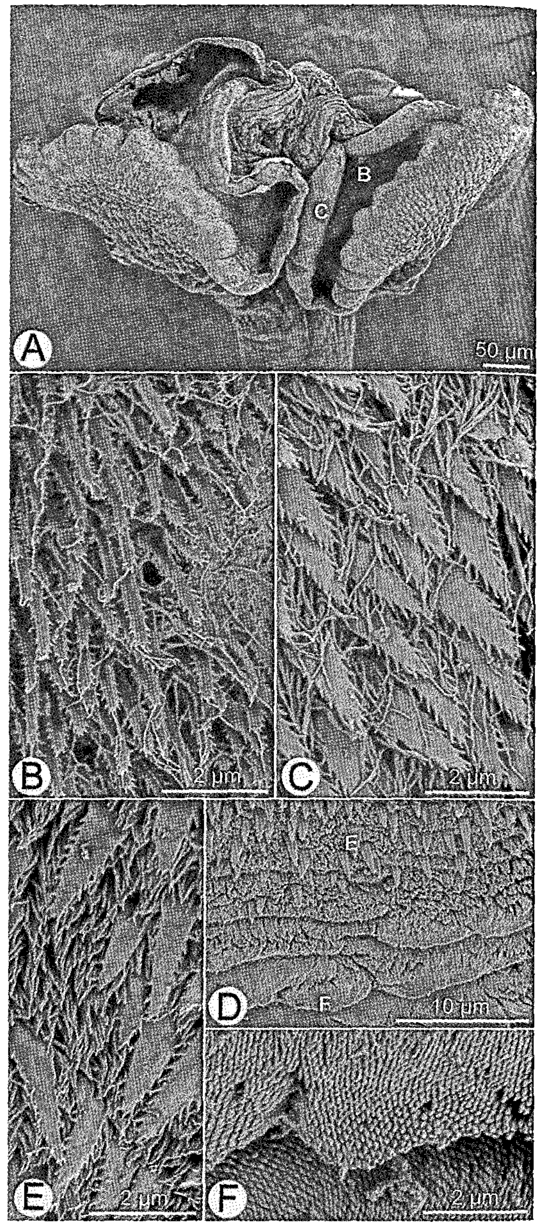

Fig. 121. Scanning electron micrographs of *Paraorygmatobothrium janineae* Ruhnke, Healy and Shapero, 2006. A. Scolex (letter indicate regions of scolex in enlarged photos B–C). B. Distal surface of bothridium. C. Proximal surface of bothridium. D. Border of cephalic peduncle and neck (letter indicate regions of scolex in enlarged photos E–F). E. Surface of cephalic peduncle. F. Neck surface. (Taken from Ruhnke, Healy and Shapero [2006], copyright 2006. Used with permission.)

(23 ± 9; n=8; *n*=24) wide, extending dorsally and ventrally almost to midline of proglottid,

fields reduced at level of ovary, interrupted by cirrus-sac.

Remarks

Paraorygmatobothrium janineae can be distinguished all other species of *Paraorygmatobothrium* except *P. kirstenae* in its possession of a cephalic peduncle. In addition, in *P. janineae* and *P kirstenae* are further differentiated in that both species, the vitelline field extends toward the dorsal and ventral midline of the proglottid, with the field interrupted at the level of the cirrus-sac, and reduced at the level of the ovary. In all other species of *Paraorygmatobothrium,* the vitelline follicles are restricted to the lateral margins of the proglottid, and are completely interrupted at the level of the cirrus-sac and ovary. *Paraorygmatobothrium janineae* differs from *P. kirstenae* in maximum width (561–1,021 vs. 372–489) and apical sucker diameter (66–139 vs. 43–61).

Paraorygmatobothrium kirstenae Ruhnke, Healy and Shapero, 2006
(Figs. 122–125)

Taxonomic status: Valid.
Type host: *Hemigaleus microstoma* Bleeker, 1852, the Sicklefin weasel shark.
Type locality: off Mukah (02°54'00"N, 112°06'00"E), Sarawak, Malaysia, South China Sea (Fig. 123).
Additional locality: Northern Territory (136°43'S, 10°30'E), Australia, Arafura Sea, Pacific Ocean (Fig. 123).
Site of infection: Spiral intestine.
Type material: Holotype, MZUM(P) 157 (Fig. 122); paratypes IPMB 77.32.01, LRP 3373–3375, USNPC 96655–96656. Remaining paratypes retained in T.R. Ruhnke's collection.
Material examined: All types were examined.
Etymology: This species is named for Dr. Kirsten Jensen.

Description (taken from Ruhnke et al. [2006a]).

Worms euapolytic, craspedote, 8.7–25 mm (14.3 ± 6.5; n=6) long; maximum width 372–489 (415 ± 48; n=7) at scolex. Proglottids 33–64 (46 ± 13; n=7) in number. Scolex 130–240 (185 ± 78; n=3) long, with four bothridia. Bothridia with single loculus and round apical sucker; apical sucker 43–61 (51 ± 8; n=4; *n*=5) in diameter. Distal bothridial surface covered with gongylate columnar spinitriches, capilliform filitriches, and cilia. Proximal surfaces of bothridia covered with serrate gladiate spinitriches and capilliform filitriches. Cephalic peduncle present, covered with gladiate spinitriches. Neck present, surface of neck and proglottids covered with scutes, surface of scutes comprised of densely packed, capilliform filitriches with triangular tips.

Immature proglottids in middle third of strobila wider than long, 56–316 (176 ± 108;

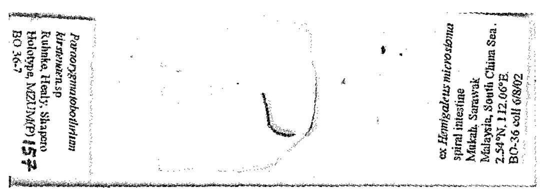

Fig. 122. Holotype of *Paraorygmatobothrium kirstenae* Ruhnke, Healy and Shapero, 2006 (MZUM[P] 157).

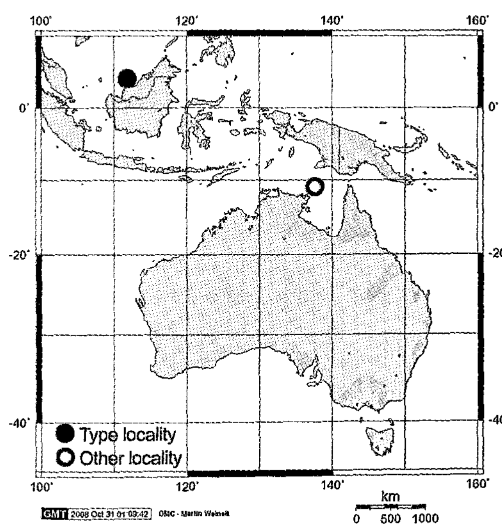

Fig. 123. Geographic distribution of *Paraorygmatobothrium kirstenae* Ruhnke, Healy and Shapero, 2006.

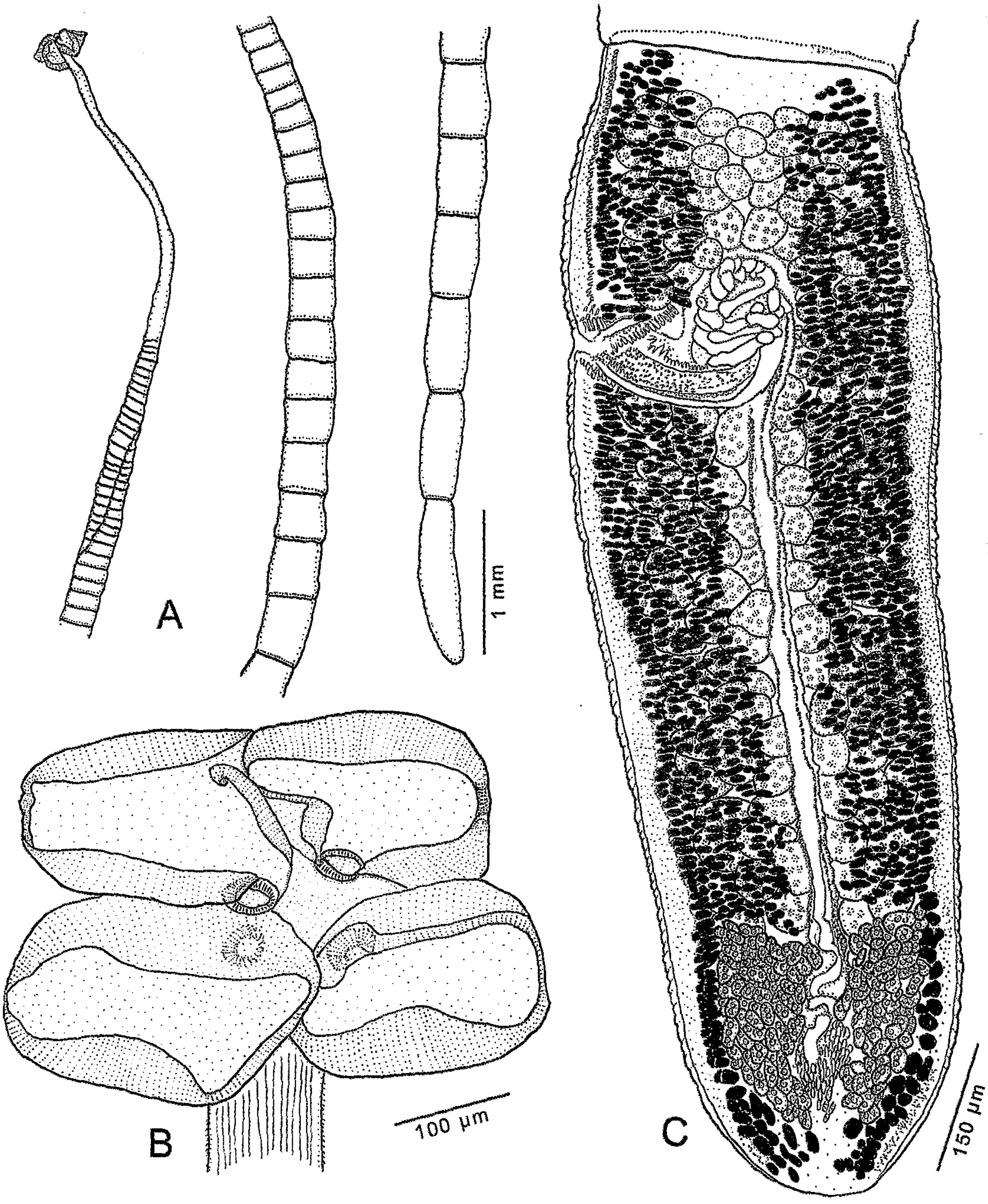

Fig. 124. Line drawings of *Paraorygmatobothrium kirstenae* Ruhnke, Healy and Shapero, 2006. A. Entire worm. B. Scolex. C. Terminal proglottid. (Taken from Ruhnke, Healy and Shapero [2006], copyright 2006. Used with permission.)

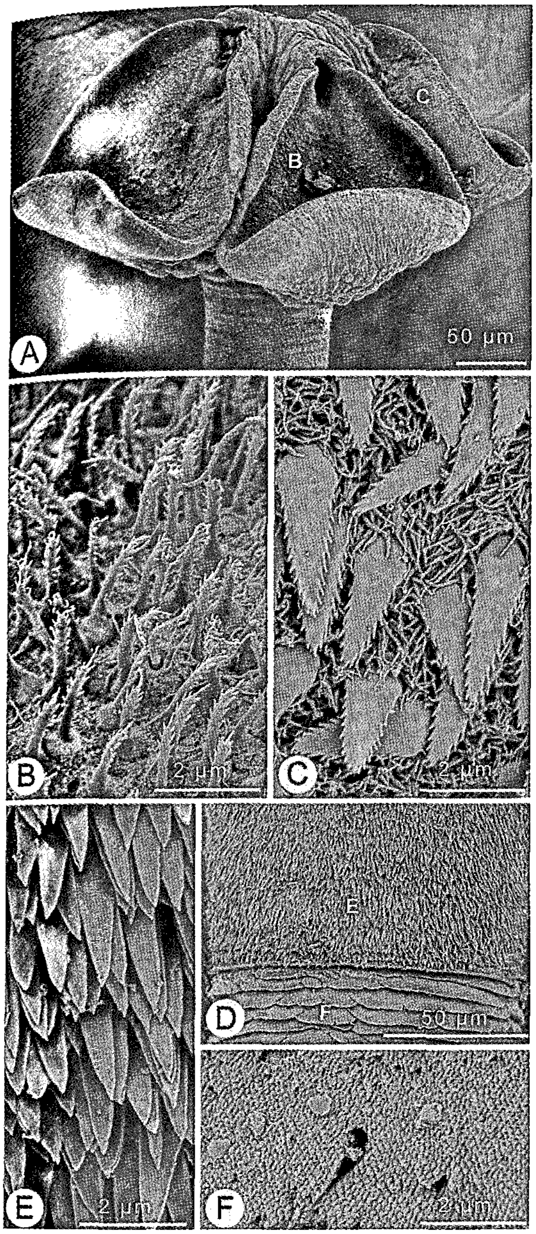

Fig. 125. Scanning electron micrographs of *Paraorygmatobothrium kirstenae* Ruhnke, Healy and Shapero, 2006. A. Scolex (letter indicate regions of scolex in enlarged photos B–C). B. Distal surface of bothridium. C. Proximal surface of bothridium. D. Border of cephalic peduncle and neck (letter indicate regions of scolex in enlarged photos E–F). E. Surface of cephalic peduncle. F. Neck surface. (Taken from Ruhnke, Healy and Shapero [2006], copyright 2006. Used with permission.)

n=7; *n*=12) long x 124–434 (312 ± 112; n=7; *n*=12) wide, length to width ratio 0.29–0.8:1 (0.53 ± 0.19; n=7; *n*=12). Terminal proglottids 605–1,637 (1,256 ± 382; n=10) long x 248–395 (335 ± 52; n=10) wide, length to width ratio 1.54–5.1:1 (3.8 ± 1.1; n=10). Testes 104–164 (139 ± 24; n=10; *n*=11) in number; testes oblong, 26–50 (37 ± 8; n=9; *n*=19) long x 40–78 (53 ± 11; n=9; *n*=19) wide. Cirrus-sac pyriform, 169–250 (218 ± 36; n=6) long x 94–137 (113 ± 21; n=6) wide, containing coiled cirrus. Cirrus armed with spinitriches. Vas deferens coiled, median, overlapping proximal portion of cirrus-sac, anterior to cirrus-sac. Genital pores lateral, 66–77% (70 ± 3.3; n=10) of proglottid length from posterior end, irregularly alternating. Vagina medial, extending anteriorly from ovary, then laterally along anterior margin of vas deferens to genital pore. Shallow genital atrium present. Ovary near posterior end of proglottid, H-shaped in frontal view, 116–279 (205 ± 57; n=9) long x 165–266 (220 ± 36; n=9) wide. Ovicapt 31–47 (40 ± 8; n=9) in diameter, at posterior margin of ovarian bridge. Uterus ventral to vagina, extending from anterior margin of ovary to posterior margin of cirrus-sac in mature proglottids. Uterine duct not observed. Vitellarium follicular follicles in two lateral fields; follicles 7–19 (13 ± 4; n=6; *n*=15) long x 16–37 (25 ± 6; n=6; *n*=15) wide; extending dorsally and ventrally almost to midline of proglottid, field reduced at level of ovary and interrupted by cirrus-sac.

Remarks

Of all existing species of *Paraorygmatobothrium, P. kirstenae* is most similar in morphology to *P. janineae*. Like *P. janineae, P. kirstenae* differs from all other *Paraorygmatobothrium* species in its possession of a cephalic peduncle and lateral fields of vitelline follicles that are extended dorsally and ventrally toward the midline of the proglottid. However, these two species differ in a number of size aspects. For example, *P. kirstenae* is smaller than *P. janineae* in total length (average 14.3 mm vs. 17.2 mm), maximum width (372–489 vs. 561–1,021), scolex length (130–240 vs. 211–429), and apical sucker diameter (43–61 vs. 66–139). The two species also differ most conspicuously in number of proglottids per strobila (33–64 vs. 59–104 in *P. janineae*) and number of testes per progolottid (average 139 vs. 162 in *P. janineae*). *Paraorygmatobothrium kirstenae* also differs from *P. janineae* in the spinithrix morphology of the cephalic peduncle, with *P. kirstenae* bearing gladiate spinitriches and *P. janineae* bearing serrate gladiate spinitriches in that region.

Paraorygmatobothrium leuci (Watson and Thorson, 1976) n. comb.

(Figs. 126–128)

Synonym: *Phyllobothrium leuci* Watson and Thorson, 1976.
Taxonomic status: Valid
Type host: *Carcharhinus leucas* (Müller and Henle, 1839), the Bull shark.
Site of infection: Spiral intestine.
Type locality: Rio San Juan, San Juan del Norte, Nicaragua (Fig. 126).
Type material: Holotype, USNPC 61339 (Fig. 127).
Material examined: Holotype, USNPC 61339 (Fig. 127).
Etymology: Not given, but presumably named for its type host.

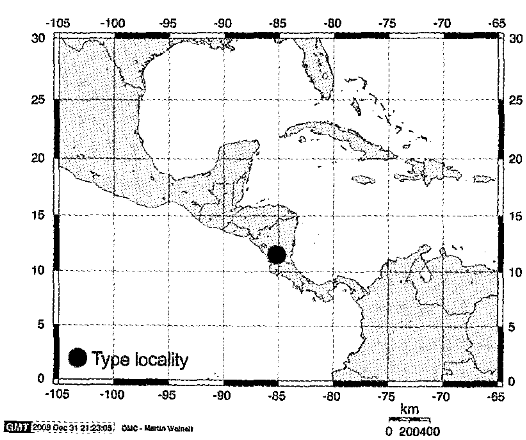

Fig. 126. Geographic distribution of *Paraorygmatobothrium leuci* (Watson and Thorson, 1976) n. comb.

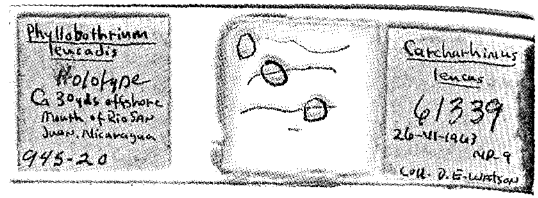

Fig. 127. Holotype of *Paraorygmatobothrium leuci* (Watson and Thorson, 1976) n. comb. (USNPC 61339).

Description (modified from Watson and Thorson [1976]).

Worms slightly craspedote, euapolytic, 10.1–42.0 mm (17.7) long, with 30–68 proglottids. Scolex 300–615 (458) long x 420–825 (584) wide. Bothridia thin, edges thickened, sometimes folded to form boat-shaped structure; 225–615 (436) long x 195–405 (301) wide. Accessory sucker 68–82 (74) in diameter. Cephalic peduncle absent. Neck 4.5– 8.5 mm (6.2) long.

Immature proglottids initially wider than long, proglottids at mid-strobila wider than long, mature proglottids longer than wide. Mature proglottids 1.13–5.27 mm (1.87 mm) long x 185–750 (423) wide. Testes 83–151 (122) in number, number 32–68 (45) anterior to cirrus-sac, 43–104 (85) in diameter. Genital pores unilateral, 58–61% from posterior end of proglottid. Cirrus-sac J-shaped, 157–750 (239) long x 75–180 (97) wide. Cirrus armed with spinitriches. Vas deferens coiled. Vagina with sphincter near poral end, poral end surrounded by gland cells. Uterus reaching level of genital pore. Ovary symmetrical, H-shaped In frontal view, 164–810 (246) x 185–525 (266). Mehlis' gland 43–120 (53) in diameter, posterior to ovary. Vitellarium follicular; vitelline follicles in two lateral bands each with 1–2 dorsal and 1–2 ventral columns of follicles, extending entire length of proglottid, interrupted by ovary and cirrus-sac. Two gravid apolytic proglottids 5 mm long x 710 wide and 7.43 mm long x 840 wide, respectively. Genital pore one-fourth to one-third the distance from anterior end of proglottid. Testes number 120 in small proglottid, 90–150 (130) in diameter, and 103 in larger specimen, 71–96 (86) in diameter. Cirrus-sac in small proglottid 180 long, partially extruded; in larger proglottid 390 long x 225

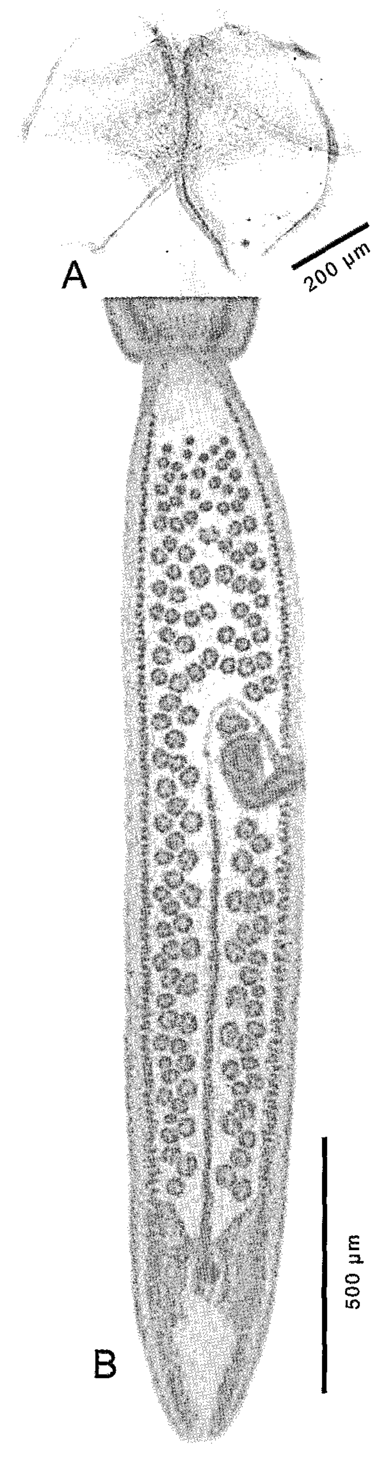

Fig. 128. Photomicrographs of *Paraorygmatobothrium leuci* (Watson and Thorson, 1976) n. comb. A. Scolex of holotype (USNPC 61339). B. Terminal proglottid of holotype (USNPC 61339).

wide. Cirrus covered armed with spinitriches. Vas deferens confined between cirrus-sac and bend in vagina. Ovary 825 long x 450 wide, and 975 long x 480 wide. Mehlis' gland 107 and 144 long. Eggs thin-shelled, with or without a small knob on one or both ends, 25–29 (27) long x 21–27 (24) wide.

Remarks

Paraorygmatobothrium leuci n. comb. differs from all existing species of *Paraorygmatobothrium* except *P. prionacis* and *P. arnoldi* in genital pore position (see Table 1). Among other features, *P. leuci* n. comb. differs from *P. prionacis* in proglottid number (30–68 vs. 11–29) and testes number (83–151 vs. 34–62), and differs from *P. arnoldi* in total length (6.2–8.4 vs. 10.1–42 mm) and maximum width (420–825 vs. 211–388).

Paraorygmatobothrium musteli (Van Beneden, 1850) n. comb.

(Figs. 129–131)

Synonyms: *Anthobothrium musteli* Van Beneden, 1850 (pro part); *Phyllobothrium musteli* (Van Beneden, 1850) Southwell, 1925.

Taxonomic status: Valid.

Type host: *Mustelus vulgaris* Cloquet, 1821 (= *Mustelus mustelus* Linck, 1790).

Additional host: *Mustelus canis* (Mitchell, 1815 [sic] = *Mustelus* sp.

Site of infection: Spiral intestine.

Type locality: Not given, but likely coastal Belgium (Fig. 129).

Additional locality: Séte, France (Fig. 129).

Type material: Not specified.

Material examined: Seventeen voucher specimens, 12 free proglottids, mounted on three slides (MNHN Paris HEL 147–148).

Etymology: Not given, but presumably, the species was named for the genus name of its host.

Redescription (based on 17 whole mounted specimens and 12 free proglottids).

Worms craspedote, euapoltyic, 7.3–14 (9.8 ± 1.4; n=11) mm long, maximum width 485–952 (762 ± 169; n=10) at scolex; strobila consisting of 14–27 (20 ± 5; n=8) proglottids. Scolex with four bothridia, 587–830 long x 485–952 wide. Bothridia uniloculate, 233–534 long x 136–512 wide, apical sucker 50–62 (56 ± 3; n=9; *n*=17) in diameter. Cephalic peduncle absent. Neck scutellate, 1.4–2 mm long.

Immature proglottids initially wider than long 262–999 (645 ± 224; n=5; *n*=8) long x 272–592 (380 ± 117; n=5; *n*=8) wide at mid-strobila, length to width ratio 1–2.7:1 (1.7 ± 0.6; n=5, *n*=8). Terminal proglottids 1,164–2,172 (1,804 ± 326; n=9) long x 320–683 (536 ± 126; n=9) wide, terminal proglottid length to width ratio 2.4–5.2 (3.5 ± 0.8; n=9). Testes 128–153 (138 ± 6; n=5) in number; testes oblong, 22–62 (39 ± 13; n=6; *n*=12) long x 28–62 (48 ± 12; n=6; *n*=12) wide. Cirrus-sac pyriform 275–300 (290 ± 17; n=8) long x 180–300 (219 ± 42; n=8) wide. Vas deferens coiled, anterior to cirrus-sac, dorsal and extending slightly anterior to vagina. Genital pores lateral, 65–80% (72 ± 5; n=9) from posterior end of terminal proglottid. Vagina median, extending anteriorly from Mehlis' gland to mid-level of proglottid, then laterally to shallow genital atrium. Ovary near posterior end of proglottis, H-shaped in frontal view, 291–687 (471 ± 143; n=5) long x by 184–398 (281 ± 106; n=8) wide. Ovicapt at posterior margin of ovarian bridge. Uterus ventral to vagina, extending from anterior margin of ovary to level of cirrus-sac. Vitellarium follicular; follicles in two lateral fields, each with 3–5 dorsal and 3–5 ventral follicles, extending entire length of proglottid, interrupted by ovary and cirrus-sac.

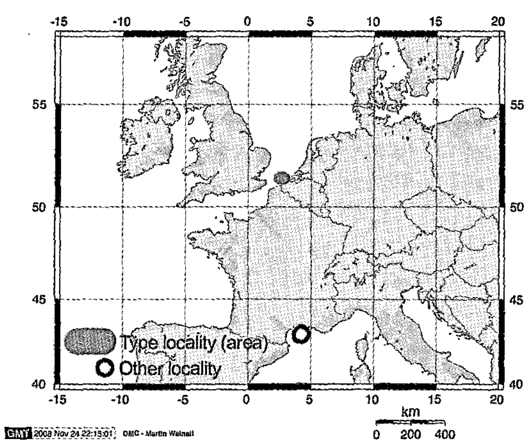

Fig. 129. Geographic distribution of *Paraorygmatobothrium musteli* (Van Beneden, 1850) n. comb.

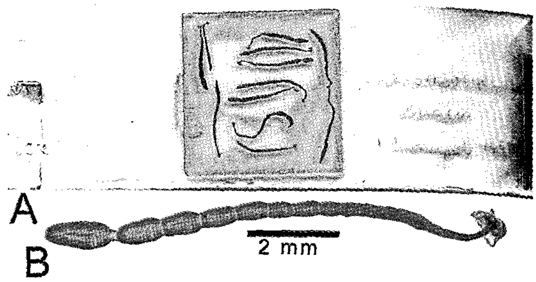

Fig. 130. Photomicrographs of *Paraorygmatobothrium musteli* (Van Beneden, 1850) n. comb. A. Voucher slide (MNHN Paris 147). B. Entire specimen of voucher (MNHN Paris 147).

Remarks

Paraorygmatobothrium musteli n. comb. was originally described as *Anthobothrium musteli* by Van Beneden (1850) for worms from *M. mustelus*. Southwell (1925, p. 173) stated that "it appears certain that Van Beneden, 1850, under the name *A. musteli*, described two different worms, viz.: (1) a larval form which Diesing, under the name *O. versatile*, made the type of the genus *Orygmatobothrium*; Zschokke (1889) described the adult worm under the name *Anthobothrium* (*Orygmatobothrium*) *musteli*, in some detail; and (2) an adult form measuring 75 mm to 100 mm, which in this paper is referred to the genus *Phyllobothrium* and named *P. musteli* (Van Ben., 1850, *pro parte*)." It is this second species that is transferred to *Paraorygmatobothrium*. This species lacks the laciniate proglottid morphology of *Anthobothrium*, and the foliose, posteriorly bifid bothridial morphology of *Phyllobothrium*. However, this species is consistent with the diagnosis of *Paraorygmatobothrium*.

Paraorygmatobothrium musteli n. comb. differs from all existing species of *Paraorygmatobothrium* except *P. arnoldi, P. bai, P. barberi, P. janineae, P. kirstenae, P. leuci, P. roberti,* and *P. rodmani* in testes number (see Table 1). *Paraorygmatobothrium musteli* n. comb. differs from *P. arnoldi* in maximum width (485–952 vs. 211–388) and terminal

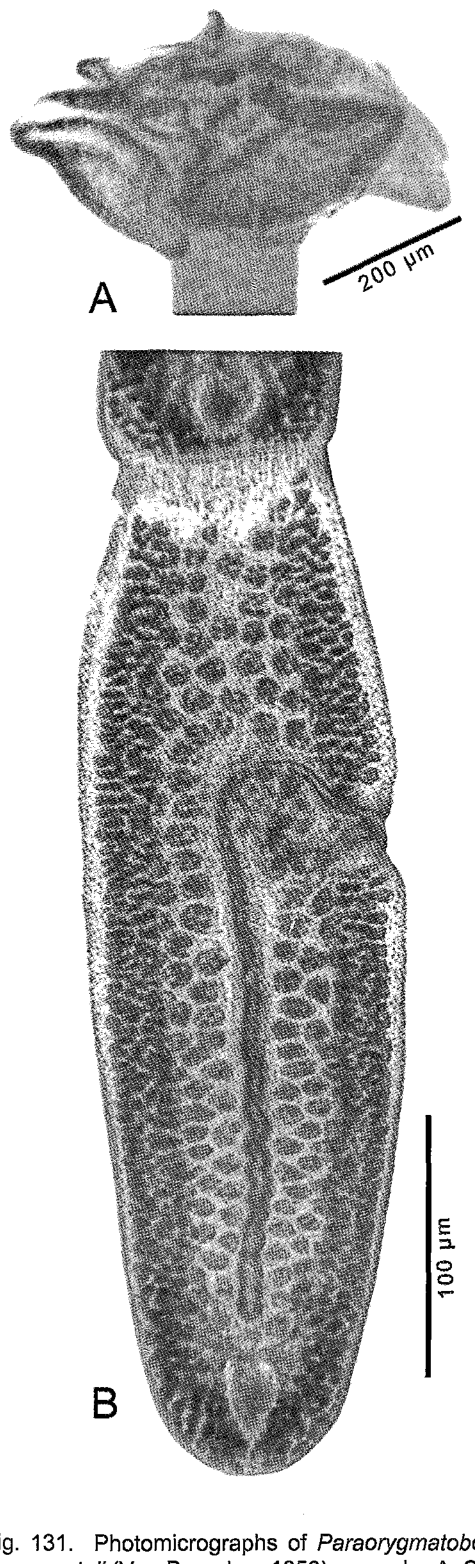

Fig. 131. Photomicrographs of *Paraorygmatobothrium musteli* (Van Beneden, 1850) n. comb. A. Scolex of voucher (MNHN Paris HEL 148). B. Terminal proglottid of voucher (MNHN Paris HEL 148).

proglottid length (1,164–2,172 vs. 384–1,067). *Paraorygmatobothrium musteli* n. comb. differs from *P. bai* and *P. barberi* in total length (7.3–14 mm vs. 15.6–41.2 mm, and 20–36 mm, respectively), and differs from *P. barberi, P. janineae, P. kirstenae,* and *P. leuci* in number of proglottids (14–27 vs. 47–67, 59–104, 33–64, and 30–68, respectively). The species differs from *P. roberti* in cirrus-sac dimensions (275–300 long by 180–300 wide vs. 90–221 long by 37–90 wide), and differs from *P. rodmani* in proglottid development condition (*i.e.*, euapolytic vs. apolytic).

Paraorygmatobothrium musteli n. comb. represents the second species of the genus reported from *M. mustelus*, in addition to *P. bai.* In addition to the features mentioned above, *Paraorygmatobothrium musteli* n. comb. differs from *P. bai* in apical sucker diameter (50–62 vs. 65–77), testis shape (oblong vs. round), and proglottid development condition (*i.e.*, euapolytic vs. apolytic).

***Paraorygmatobothrium nicaraguensis* (Watson and Thorson, 1976) n. comb.**

(Figs. 132–133)

***Synonym*:** *Phyllobothrium nicaraguensis* Watson and Thorson, 1976.
***Taxonomic status*:** Valid.
***Type host*:** *Carcharhinus leucas* (Müller and Henle, 1839), the Bull shark.
***Site of infection*:** Spiral intestine
***Type locality*:** Rio San Juan, San Juan del Norte, Nicaragua (Fig. 132).
***Type material*:** Holotype, USNPC 61340 (Fig. 133A).
Material examined: Holotype (Fig. 133A).
***Etymology*:** This species is named for its type locality.

Description (modified from Watson and Thorson [1976]).

Worms euapolytic, slightly craspedote, 9.5–22 (13.5) mm long; strobila with 24–25 proglottids in larger specimens. Scolex 285–450 (391) long x 374–630 (469) wide. Bothridia uniloculate, with thickened, folded edges, 225–435 (335) long x 203–330 (274) wide.

Bothridial apical suckers 43–68 (54) in diameter. Cephalic peduncle absent. Neck 3.5–5.3 mm (4.9) long x 60–120 (106) wide.

First few proglottids nearly as long as wide, immature proglottids then longer than wide. Mature proglottids 600–2,370 (1410) long x 270–465 (372) wide. Testes 70–132 (107) in number; testes slightly oblong, 21–54 (32) long x 36–75 (46) wide. Genital pore unilateral, 64–65% from posterior end of posterior proglottids. Cirrus-sac oval, 180–340 (220) long x 71–136 (94) wide. Cirrus armed with spinitriches. Vas deferens tightly coiled, anterior to cirrus-sac. Ovary posterior, H-shaped in frontal view, consisting of lobules radiating laterally, 144–390 (212) long x 179–330 (264) wide. Poral portion of vagina surrounded by gland cells. Mehlis' gland between posterior halves of ovary, 51–79 (68) in diameter. Vitellarium follicular, follicles in two lateral bands, extending entire length of proglottid, interrupted by ovary and cirrus- sac.

Gravid free proglottids 3.15–5.21 mm long x 510–750 wide (n=2); testes 85–88 (n=2) in number. Genital pore at junction of first and second fourths of proglottid. Cirrus-sac 270–375 (n=2) long x 128–188 (n=2) wide, pushed forward by packed uterus. Cirrus spinitriches 5 long. Ovary 525–825 (n=2) long x 375–465 (n=2) wide. Mehlis' gland 121–161 (n=2) long. Bulging uterus in larger proglottid 3.23 mm long x 428 at widest point. Eggs somewhat collapsed, spindle-shaped, with long filaments at each end, 141 long x 13 wide (including filaments).

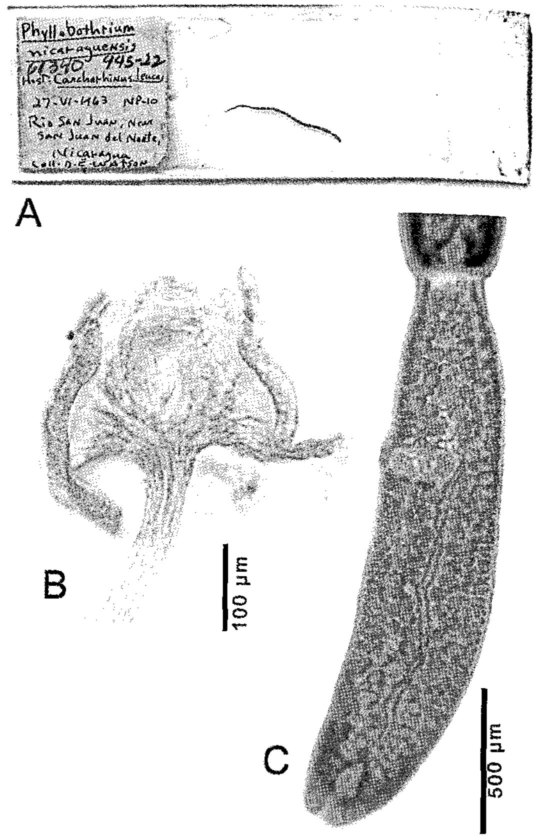

Fig. 133. Photomicrographs of *Paraorygmatobothrium nicaraguensis* (Watson and Thorson, 1976) n. comb. A. Holotype slide (USNPC 61340). B. Scolex of holotype (USNPC 61340). C. Terminal proglottid of holotype (USNPC 61340).

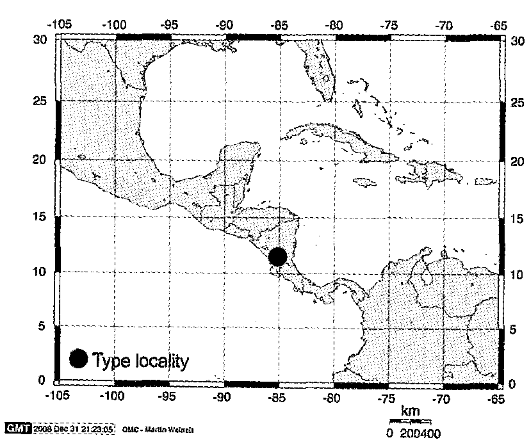

Fig. 132. Geographic distribution of *Paraorygmatobothrium nicaraguensis* (Watson and Thorson, 1976) n. comb.

Remarks

Paraorygmatobothrium nicaraguensis n. comb. differs from all existing species of *Paraorygmatobothrium* except *P. arnoldi*, *P. barberi*, *P. janineae*, and *P. roberti* in genital pore position (see Table 1). *Paraorygmatobothrium nicaraguensis* n. comb. differs from *P. arnoldi* in total length (9.5–22 vs. 6.2–8.4), differs from *P. barberi* and *P. janineae* in number of proglottids (24–25 vs. 47–67 and 59–104). In most features, the ranges of *P. nicaraguensis* n. comb. overlap those of *P.*

roberti (see Table 1). However, in some cases, the mean for *P. nicaraguensis* n. comb. was found to be outside the range of *P. roberti.* For example, the cirrus-sac width of *P. nicaraguensis* n. comb. was larger than *P. roberti* (mean of 94 vs. range of 37–90), and exhibited a greater ovarian width (mean 264 vs. range of 123–207).

Paraorygmatobothrium nicaraguensis n. comb. is the second species of the genus, in addition to *P. leuci,* reported from *C. leucas.* In addition to genital pore position, *Paraorygmatobothrium nicaraguensis* n. comb. differs from *P. leuci* in proglottid number (24–25 vs. 30–68) and testis shape (oblong vs. round).

Paraorygmatobothrium orectolobi (Butler, 1987) n. comb.

(Figs. 134–135)

Synonym: *Phyllobothrium orectolobi* Butler, 1987.
Taxonomic status: Valid.
Type host: *Orectolobus maculatus* (Bonnaterre, 1788), the Spotted wobbegon.
Site of infection: Spiral intestine.
Type locality: Moreton Bay, Queensland, Australia (Fig. 134).
Type material: Holotype (Fig. 135A); paratypes QM GL4618–4620.

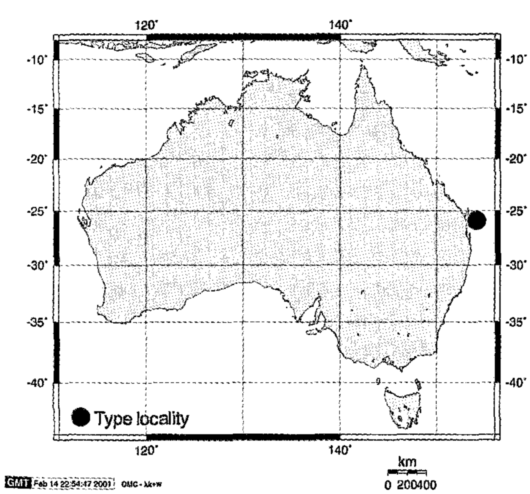

Fig. 134. Geographic distribution of *Paraorygmatobothrium orectolobi* (Butler, 1987) n. comb.

Material examined: Holotype, QM GL4617 (Fig. 135A); paratypes QM GL4618–4620.
Etymology: The species is named for its type host.

Descripton (modified from Butler [1987]).

Worms craspedote, euapolytic, 13–65 long, one strobila with over 90 proglottids. Scolex 400–590 long x 490–840 wide, bearing four stalked bothridia; bothridia uniloculate, 400–710 long by 330–550 wide, margins free and undivided. Apical sucker diameter 78–122. Width of neck immediately posterior to scolex 88–162; neck scutellate.

Immature proglottids almost square, length increasing with maturation. Posterior proglottids 2,300–4,000 long x 460–820 wide, free proglottids 3,800–9,100 long x 650–1,150 wide. Testes 124–193 in number, round, average 49 in diameter, testes pre-ovarian. Genital pore lateral, irregularly alternating, 52–56% from posterior end of proglottid. Cirrus-sac oval, 140–340 long x 60–200 wide; cirrus armed with spinitriches. Vas deferens median, coiled, anterior to cirrus-sac. Vagina opening anterior to cirrus-sac. Ovary H-shaped in frontal view, tetralobed in cross section. Uterus saccular, thin-walled, extending from slightly anterior to ovary to posterior of genital pore. Uterine duct extending anterodorsally from ootype to join uterus a third the way back from its anterior limit. Viteliarium follicular, vitelline follicles in two lateral fields, each field consisting of 3–4 dorsal and 3–4 ventral columns of follicles, extending entire length of proglottid, interrupted by ovary and cirrus-sac. Eggs spindle shaped, 69 long x 22 wide.

Remarks

Paraorygmatobothrium orectolobi n. comb. was originally placed in *Phyllobothrium* by Butler (1987). However, this species lacks the defining features of that genus, such as foliose, posteriorly bifid bothridia. It is consistent with the diagnosis of *Paraorygmatobothrium. Paraorygmatobothrium orectolobi* n. comb. differs from all existing species of *Paraorygmatobothrium* except *P. prionacis* in genital pore position (see Table 1). Among other features, *P. orectolobi* n. comb.

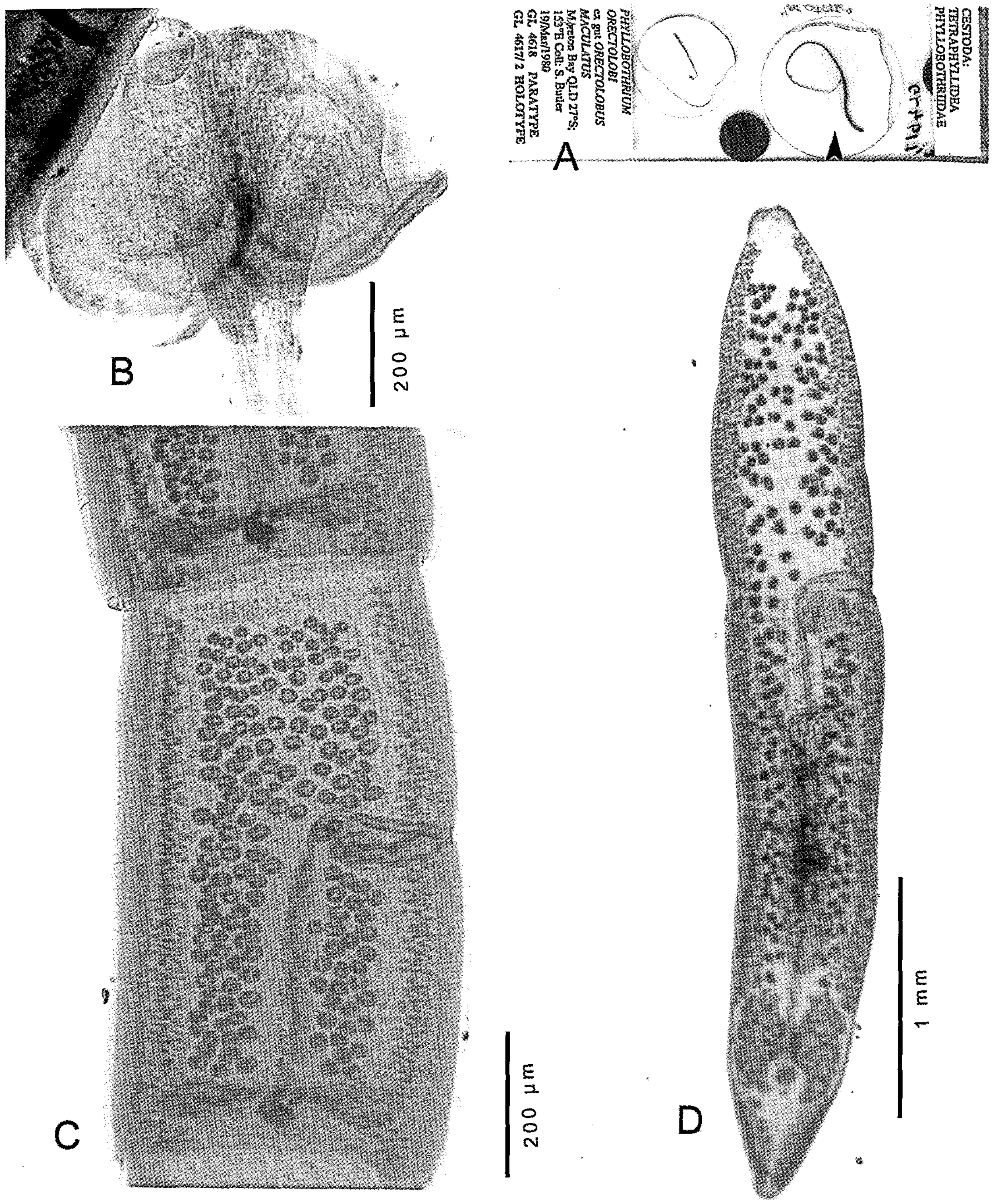

Fig. 135. Photomicrographs of *Paraorygmatobothrium orectolobi (*Butler, 1987) n. comb. A. Holotype and paratype slide (QM GL 4617/2 and 4618), arrow indicates holotype. B. Scolex of holotype (QM GL 4617/2). C. Proglottid of holotype (QM GL 4617/2). D. Free proglottid of paratype (USNPC 61340). E. Free proglottid of paratype (QM GL 4617).

differs from *P. prionacis* in proglottid number (90 vs. 11–29), posterior proglottid dimensions (2,300–4,000 by 460–820 vs. 860–1,475 by 190–350), and testes number (124–193 vs. 34–62).

Paraorygmatobothrium paulum (Linton, 1897) n. comb.

(Figs. 136–140)

Synonyms: *Orygmatobothrium paulum* Linton, 1897; *Phyllobothrium paulum* (Linton, 1897) Southwell,1925; *Monorygma galeocerdonis* MacCallum, 1921.

Taxonomic status: Valid.

Type host: *Galeocerdo cuvier* (Pèron and Lesueur, 1822), the Tiger shark.

Site of infection: Spiral intestine.

Type locality: Woods Hole, Massachusetts, U.S.A. (Fig. 137).

Additional localities: Montauk, New York, U.S.A.; Horn Island Mississippi, U.S.A.; Darwin, Australia (Fig. 137).

Type material: USNPC 4798 (vialed specimen).

Material examined: USNPC 7672 (see Fig. 136A); USNPC 102714; LRP 7431–7437.

Material deposited: USNPC 102714; LRP 7431–7437.

Etymology: Not given, but presumably, L. *paulum* (= small), in reference to the diminutive size of the species.

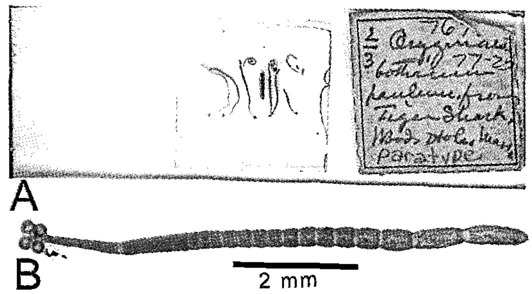

Fig. 136. Photomicrographs of *Paraorygmatobothrium paulum* (Linton, 1897) n. comb. A. Slide of voucher (USNPC 7672). B. Entire specimen of voucher (USNPC 7672).

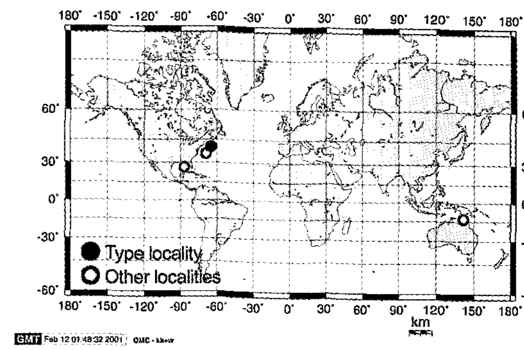

Fig. 137. Geographic distribution of *Paraorygmatobothrium paulum* (Linton, 1897) n. comb.

Redescription (based on 27 whole mounted worms, three cross sectioned worms and two worms prepared for SEM).

Worms euapolytic, slightly craspedote, 5–13 (8.3 ± 2.2; n=16) mm long; maximum width 340–640 (494 ± 103; n=13) at scolex. Proglottids 20–37 (29 ± 5; n=8) in number. Scolex with four bothridia. Bothridia 185–408 (250 ± 64; n=11) wide, each with a single loculus, locular periphery ringed with a band of muscles and round apical sucker; apical sucker 43–68 (54 ± 6; n=28, *n*=47) in diameter. Distal locular surface and distal surfaces of apical sucker covered with serrate gladiate spinitriches and acicular filitriches. Proximal surfaces of bothridia covered with serrate gladiate spinitriches and papilliform filitriches. Rims of bothridia covered with slender capilliform filitriches. Bothridial stalks covered with serrate gladiate spinitriches with few lateral projections. Neck scutellate, 0.5–1.3 (0.8 ± 0.28; n=6) mm long; scutes composed of densely arranged capilliform filitriches.

Terminal and subterminal proglottids 672–1,375 (986 ± 216; n=13; *n*=15) long x 143–300 (225 ± 52; n=13; *n*=15) wide, terminal proglottid length to width ratio 2.7–6.7:1 (4.7 ± 1.4; n=13; *n*=15). Free proglottids (Fig. 138B) 1,560–2,256 (1,989 ± 285; n=7) long x 336–504 (411 ± 53; n=7) wide. Testes 37–68 (58 ± 5; n=14; *n*=17) in number; testes oblong, 17–50 (33 ± 9; n=10 *n*=23) long x 23–80 (50 ± 16; n=23, *n*=80) wide. Cirrus-sac pyriform, 100–162 (143 ± 17; n=11; *n*=14) long x 60–121 (83 ± 18; n=11; *n*=14) wide, containing coiled cirrus. Cirrus armed with spinitriches. Vas deferens coiled, median, bordering proximal portion of cirrus-sac, anterior to cirrus-sac, posterior to vagina. Genital pores lateral, 46–68% (58 ± 3.4; n=14; *n*=17) of proglottid length from posterior end in terminal and subterminal

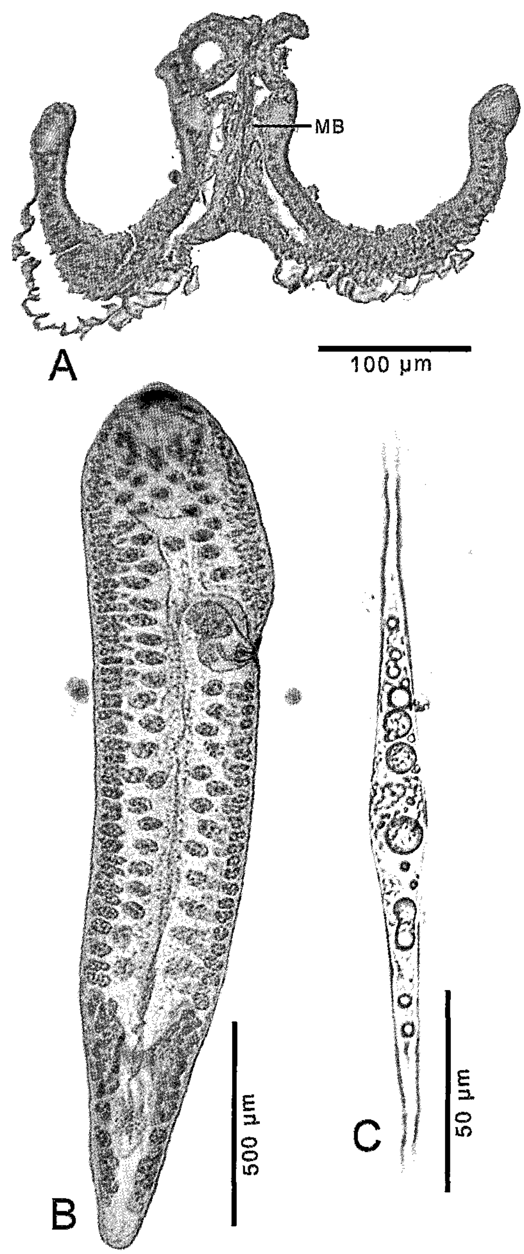

Fig. 138. Photomicrographs of *Paraorygmatobothrium paulum* (Linton, 1897) n. comb. A. Frontal section of voucher (LRP 7431). B. Free proglottid of voucher (LRP 7432). C. Egg.

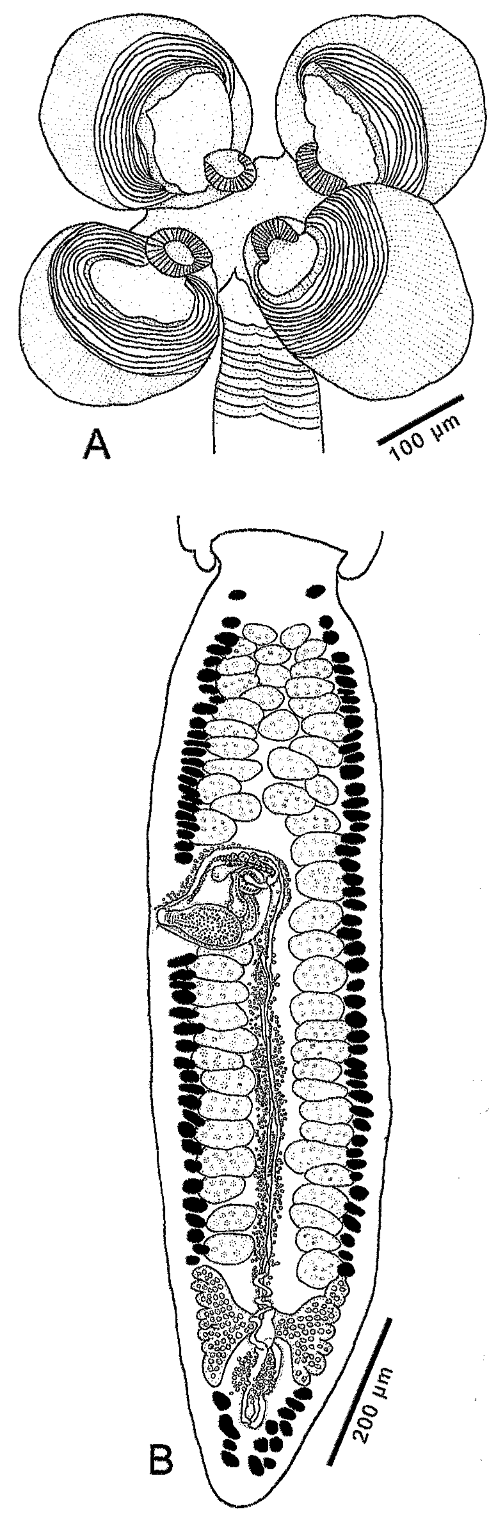

Fig. 139. Line drawings of *Paraorygmatobothrium paulum* (Linton, 1897) n. comb. A. Scolex of voucher (LRP 7433). B. Terminal proglottid of voucher (LRP 7434).

proglottids, irregularly alternating. Vagina median, extending anteriorly from ovary to midlevel of proglottid, then laterally along anterior margin of vas deferens and cirrus-sac to genital pore. Shallow genital atrium

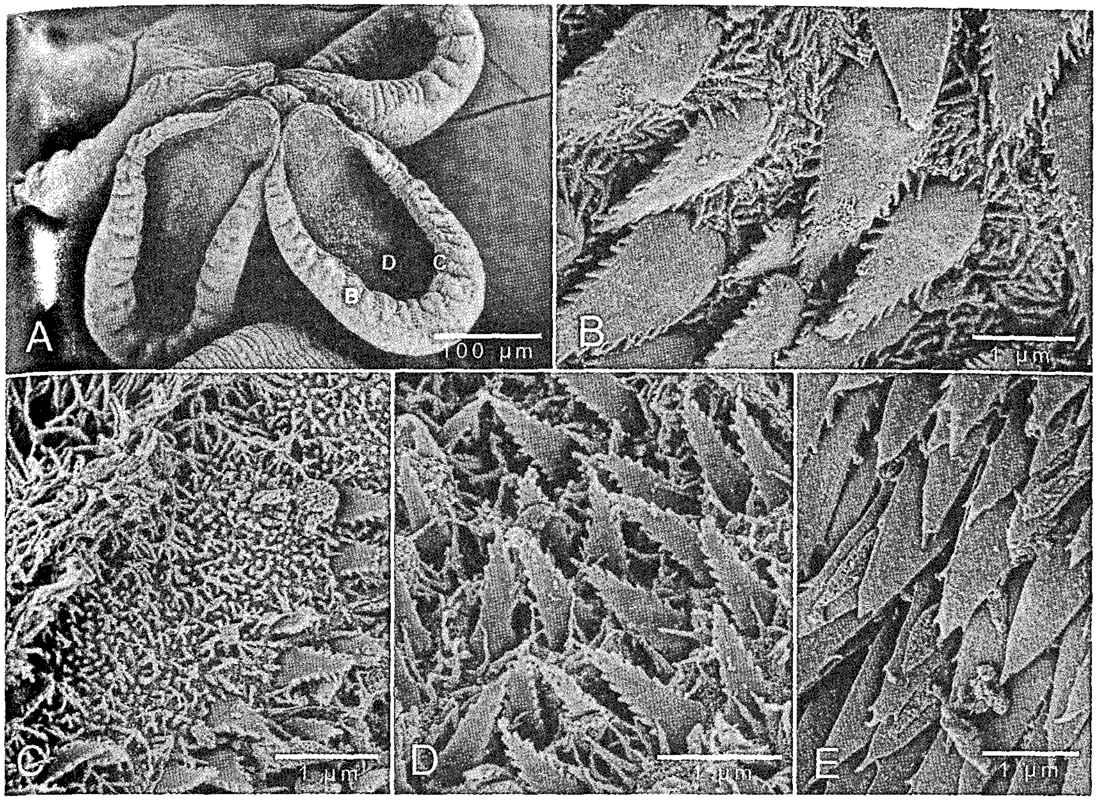

Fig. 140. Scanning electron micrographs of *Paraorygmatobothrium paulum* (Linton, 1897) n. comb. A. Scolex (letter indicate regions of scolex in enlarged photos B–D). B. Proximal surface of bothridium. C. Rim of bothridium. D. Distal surface of bothridium. E. Surface of bothridial stalk.

present. Ovary near posterior end of proglottid, H-shaped in frontal view, 84–168 (128 ± 47; n=9) long x 107–250 (164 ± 47; n=9) wide, tetralobed in cross section. Ovicapt 26–28 (28 ± 1; n=4; *n*=5) in diameter, at posterior margin of ovarian bridge. Mehlis' gland posterior to ovicapt. Uterus ventral to vagina, extending from anterior margin of ovary to posterior margin of cirrus-sac in mature proglottids. Uterine duct present, median, parallel and dorsal to uterus, extending to posterior margin of cirrus-sac in mature and free proglottids, entering uterus at level of posterior margin of cirrus-sac. Vitellarium follicular, vitelline follicles in two lateral fields, oblong, 9–29 (15 ± 6; n=8 *n*=15) long x 10–38 (24 ± 8; n=8, *n*=15) wide, each field consisting of 2–3 dorsal and 2–3 ventral columns of follicles, extending entire length of proglottid, interrupted by ovary and cirrus-sac. Eggs spindle shaped, 160 long x 20 wide.

Remarks

Paraorygmatobothrium paulum n. comb. was originally described by Linton (1897) as a species of *Orygmatobothrium,* and was subsequently transferred to *Phyllobothrium* by Southwell (1925). This species lacks the central circular, glandular organ of *Orygmatobothrium* and the foliose, posteriorly bifid bothridia of *Phyllobothrium*, but is fully consistent with the diagnosis of *Paraorygmatobothrium. Monorygma galeocerdonis* MacCallum, 1921 is a synonym of *P. paulum* n. comb., as MacCallum's (1921) description and figures of *M. galeocerdonis* are fully consistent with those provided in this monograph for *P. paulum* n. comb. It should be noted that USNPC 7672 is listed in the USNPC database as a paratype, and the word paratype had been emended on the slide label (see Fig. 138A). If the date of collection given in the USNPC database is correct (Collector VN

Edwards, collected 7/5/1911), the specimen cannot be a paratype, as *P. paulum* n. comb. was described in 1897.

Paraorygmatobothrium paulum n. comb. differs from all species in the genus in its possession of bothridia that have a locular periphery ringed with a distinct band of muscles. This muscular condition has the effect of drawing the posterior portion of the loculus toward the apical plane (see Fig. 138A). The species differs from all other species of *Paraorygmatobothrium* except for *P. prionacis, P. angustum, P. exiguum,* and *P. floraformis* in testis number (see Table 1). Among other features, *P. paulum* n. comb. differs from *P. prionacis* in apical sucker diameter (43–68 vs. 80–118), and differs from *P. angustum, P. exiguum* and *P. floraformis* in genital pore position (46–68 vs. 71–74, 74–83, and 77–87).

Paraorygmatobothrium roberti Ruhnke and Thompson, 2006

(Figs. 141–144)

Taxonomic status: Valid.

Type host: *Negaprion brevirostris* (Poey, 1868), the Lemon shark.

***Type locality*:** Florida Keys, near Islamorada, U.S.A (Fig. 141).

Site of infection: Spiral intestine.

Type material: Holotype specimen, USNPC 97298; four paratypes, USNPC 97299–972300 (see Fig. 142); six paratypes LRP 3787–3792. Remaining paratypes retained in the collection of T.R. Ruhnke.

Material examined: All type specimens were examined.

***Etymology*:** This species is named for the late Robert Ruhnke, T.R. Ruhnke's father.

Description (modified from Ruhnke and Thompson [2006]).

Worms euapolytic, slightly craspedote, 6.6–17.1 (9.9 ± 2.4; n=26) mm long; maximum width 365–683 (513 ± 91; n=30) at scolex. Proglottids 16–36 (26 ± 6; n=18) in number. Scolex 211–566 (354 ± 78; n=27) long, with four bothridia. Bothridia 192–432 (316 ± 70; n=20, *n*=22) long x 149–384 (226 ± 59; n=20, *n*=22) wide; each with a single loculus and round apical sucker; apical sucker 43–68 (54 ± 6; n=28, *n*=47) in diameter. Apical surface of scolex proper covered with capilliform filitriches. Distal locular surface and distal surface of apical sucker covered with serrate gladiate spinitriches and capilliform filitriches. Proximal surfaces of bothridia covered with serrate gladiate spinitriches and capilliform filitriches. Rims of bothridia covered with capilliform filitriches. Neck 1.2–4.1 (2.5 ± 0.8; n=29) mm long; dorsal and ventral surfaces scutellate, surface of scutes comprised of densely packed capilliform filitriches with triangular tips.

Terminal proglottids 614–1,880 (1,250 ± 331; n=29) long x 197–439 (311 ± 61; n=29) wide, terminal proglottid length to width ratio 1.9–6.2:1 (4.1 ± 0.95; n=29), with dorsal and ventral pair of excretory ducts and lateral pair of nerve chords. Testes 82–141 (114 ± 15; n=24) in number; testes oblong, 15–56 (34 ± 9; n=31 *n*=85) long x 27–74 (51 ± 10; n=31, *n*=85) wide, testes length to width ratio 0.3–1.4: (0.7 ± 0.2; n=31; *n*=80). Cirrus

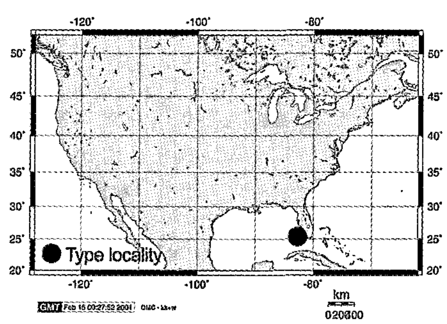

Fig. 141. Geographic distribution of *Paraorygmatobothrium roberti* Ruhnke and Thompson, 2006.

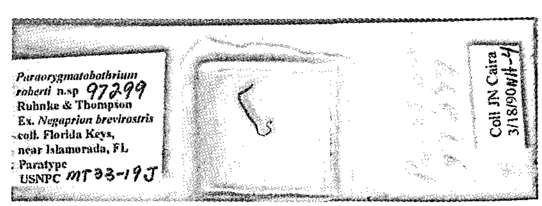

Fig. 142. Paratype slide of *Paraorygmatobothrium roberti* Ruhnke and Thompson, 2006 (USNPC 97299).

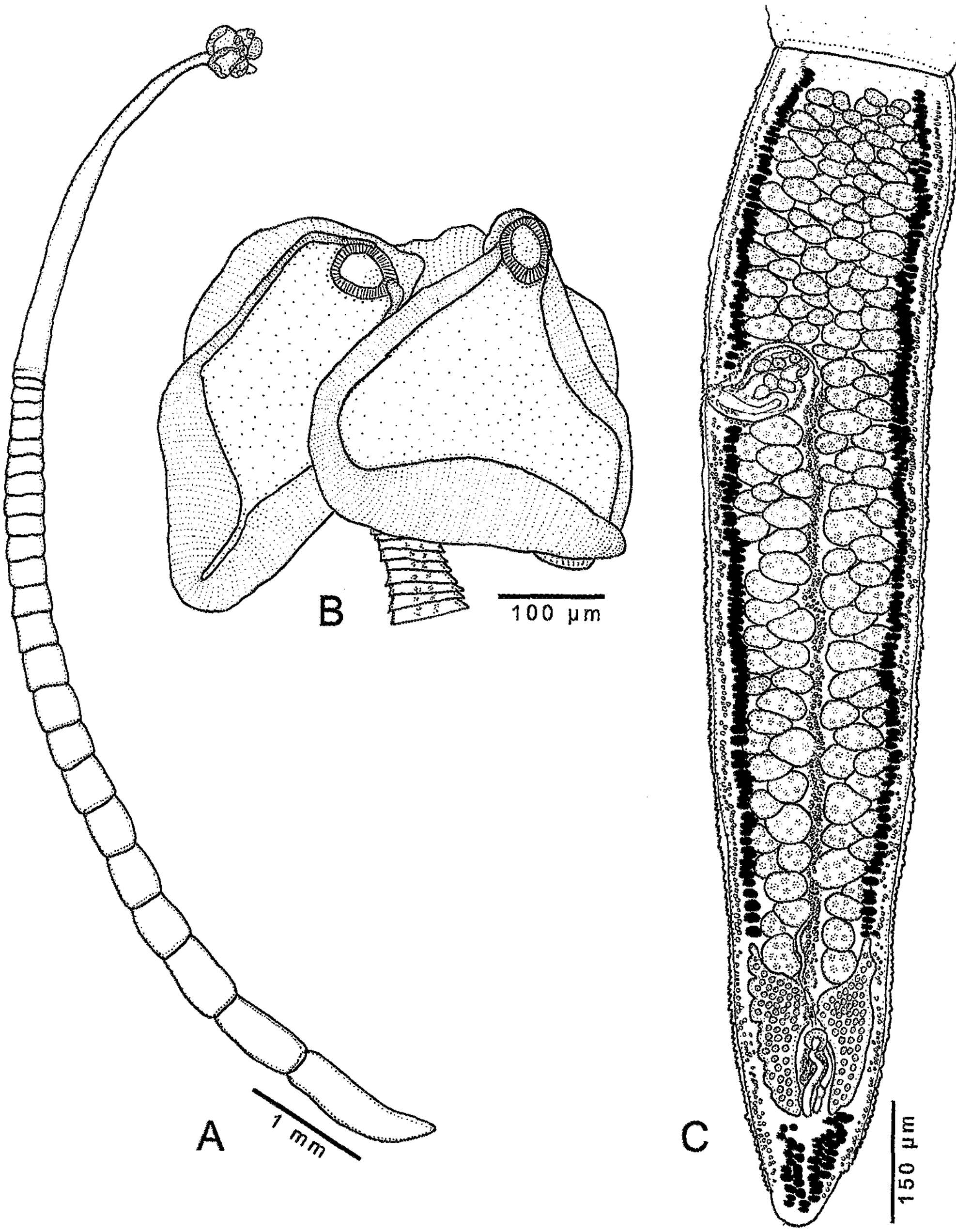

Fig. 143. Line drawings of *Paraorygmatobothrium roberti* Ruhnke and Thompson, 2006. A. Entire specimen of paratype. B. Scolex of paratype. C. Terminal proglottid of holotype (USNPC 97298). (Taken from Ruhnke and Thompson [2006], copyright 2006. Used with permission.)

sac pyriform, 90–221 (140 ± 32; n=29) long x 37–90 (61 ± 13; n=29) wide, cirrus-sac length to width ratio 1.7–3.6:1 (2.3 ± 0.5; n=29), containing coiled cirrus. Vas deferens coiled, median, bordering proximal portion of cirrus-sac, anterior to cirrus-sac, posterior to vagina. Genital pores lateral, 61–76% (70 ± 3.4; n=16) of proglottid length from posterior end in terminal proglottids, irregularly alternating. Vagina median, extending anteriorly from ovary to midlevel of proglottid, then laterally along anterior margin of

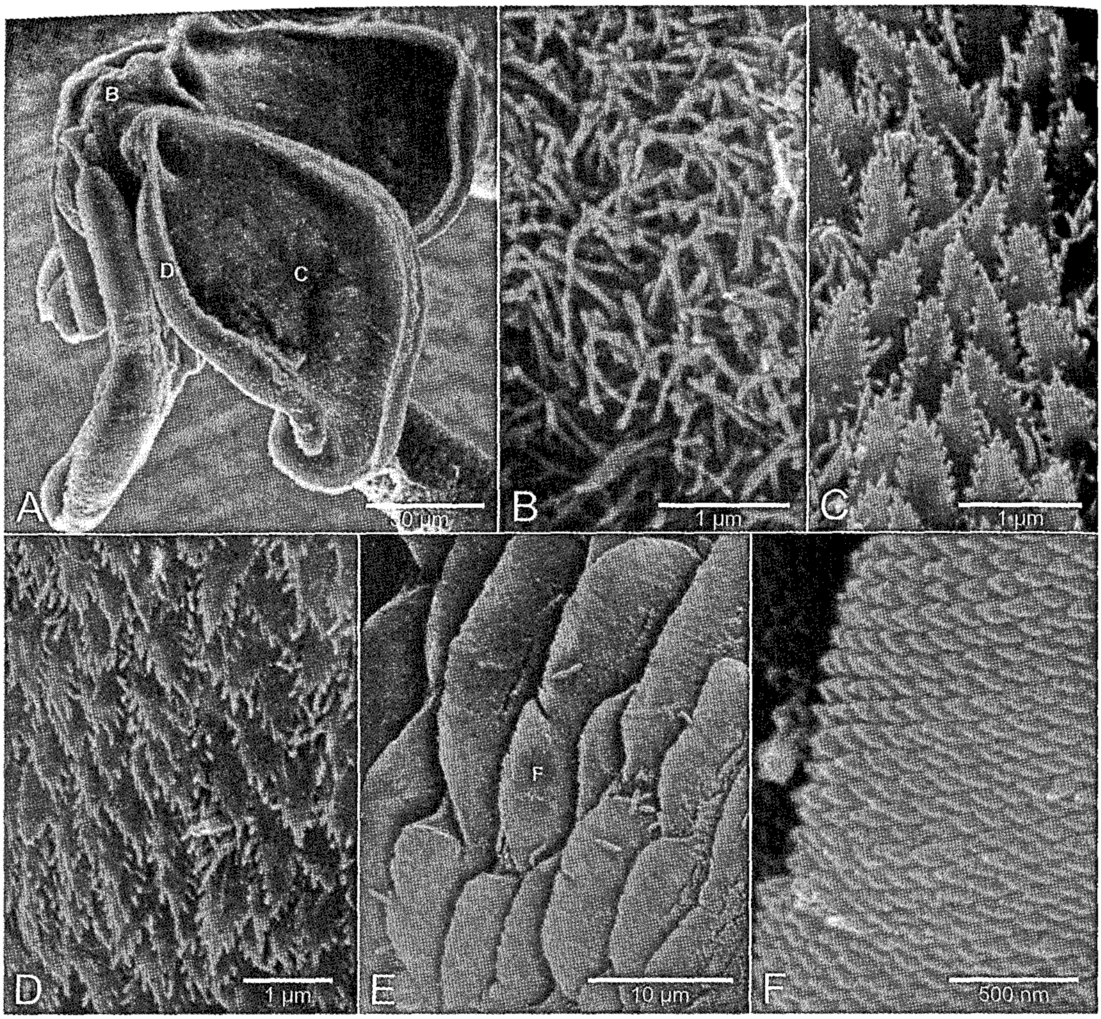

Fig. 144. Scanning electron micrographs of *Paraorygmatobothrium roberti* Ruhnke and Thompson, 2006. A. Scolex (letter indicate regions of scolex in enlarged photos B–D). B. Apical surface of scolex. C. Distal surface of bothridium. D. Proximal surface of bothridium. E. Anterior region of neck (letter indicates region of neck in enlarged photo F). F. Surface of neck. (Taken from Ruhnke and Thompson [2006], copyright 2006. Used with permission.)

vas deferens and cirrus-sac to genital pore. Shallow genital atrium present. Ovary near posterior end of proglottid, H-shaped in frontal view, 146–257 (208 ± 38; n=11) long x 123–207 (168 ± 27; n=11) wide, tetralobed in cross section. Ovicapt 28–33 (29 ± 2; n=8) in diameter, at posterior margin of ovarian bridge, weakly developed in terminal proglottids. Mehlis' gland posterior to ovicapt. Uterus ventral to vagina, extending from anterior margin of ovary to posterior margin of cirrus-sac in mature proglottids . Uterine duct present, median, parallel and dorsal to uterus, extending to posterior margin of cirrus-sac in mature proglottids, entering uterus at level of posterior margin of cirrus-sac. Vitellarium follicular, vitelline follicles in two lateral fields, oblong, 6–24 (11 ± 24; n=26 *n*=75) long x 7–32 (18 ± 5; n=26, *n*=75) wide, vitelline follicle length to width ratio 0.19–0.88:1 (0.53 ± 0.13; n=26; *n*=74), each field with 2–3 dorsal and 2–3 ventral columns of follicles, extending entire length of proglottid, interrupted by ovary and cirrus-sac.

Remarks

Paraorygmatobothrium roberti can be distinguished from existing species of *Paraorygmatobothrium* except for *P. prionacis, P. angustum, P. arnoldi, P. bai, P. exiguum, P. floraformis, P. leuci, P. musteli, P. nicaraguensis, P. paulum,* and *P. rodmani* in proglottid number (see Table 1). It differs from *P. floraformis* in total length (6.6–17.1 mm vs. 2–4.5 mm), differs from *P. prionacis,* and *P. floraformis* in apical sucker diameter (43–68 vs. 80–118, and 20–37, respectively), and differs from *P. prionacis, P. angustum, P. exiguum, P. floraformis,* and *P. paulum* in testes number (82–141 vs. 34–62, 67–83, 33–59, 43–81, and 37–68, respectively). *P. roberti* differs from *P. bai, P. musteli,* and *P. rodmani* in cirrus-sac dimensions (90–221 by 37–90 vs. 196–369 by 83–225, 275–300 by 180–300, and 204–527 by 174–355, respectively). *Paraorygmatobothrium roberti* can be further differentiated from *P. arnoldi* in ovary length (146–257 vs. 50–127), and from *P. leuci* in testis shape (oblong vs. round). In all features, the ranges of *P. nicaraguensis* overlap those of *P. roberti* (see Table 1). However, in some cases, the mean for *P. roberti* was found to be outside the range of *P. nicaraguensis.* For example, the cirrus-sac length of *P. roberti* was shorter than that of *P. nicaraguensis* (mean of 140 vs. range of 180–340).

Paraorygmatobothrium rodmani Ruhnke and Carpenter, 2008

(Figs. 145–148)

Taxonomic status: Valid.

Type host: *Mustelus antarcticus* Günther, 1870, the Gummy shark.

Type locality: Off Port Albert (38°40'S, 146°41'E), Victoria, Australia (Fig. 146).

Site of infection: Spiral intestine.

Type material: Holotype, QM G230361 (Fig. 145A); paratypes, QM G230362, LRP 4185–4188, USNPC 100854; remaining paratypes retained in the collection of T.R. Ruhnke.

Material examined: All type specimens were examined.

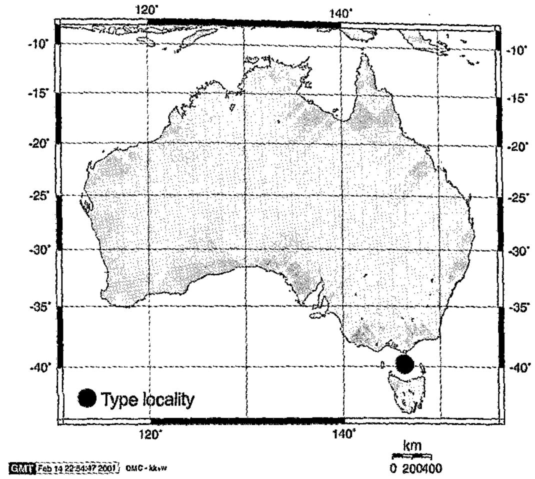

Fig. 145. Geographic distribution of *Paraorygmatobothrium rodmani* Ruhnke and Carpenter, 2008.

Etymology: This species is named for Dr James E. Rodman, former Program Director, Directorate for Biological Sciences, Division of Environmental Biology, National Science Foundation.

Description (taken from Ruhnke and Carpenter [2008]).

Worms slightly craspedote, apolytic, 13–29 (19.7 ± 4.2; n=23) mm long; maximum width 631–1,248 (838 ± 137; n=24) at scolex or terminal proglottid. Proglottids 14–27 (18 ± 3; n=24) in number. Scolex 456–1,440 (725 ± 246; n=26) long x 553–1,248 (822 ± 177; n=26) wide, with four bothridia. Bothridia 301–776 (472 ± 107; n=27) long x 240–776 (394 ± 130; n=14) wide; each bothridium with single loculus and round apical sucker; apical sucker 48–78 (65 ± 8; n=23) in diameter. Proximal surface of bothridia covered with serrate gladiate spinitriches and papilliform filitriches. Distal locular surface and distal surface of apical suckers covered with slender gongylate columnar spinitriches and papilliform filitriches. Cephalic peduncle absent. Neck scutellate, 2.6–7 (3.9 ± 1.4; n= 25) mm long; surface of scutes comprised of densely packed capilliform filitriches with triangular tips.

Proglottids with dorsal and ventral pair of excretory ducts. Immature proglottids at

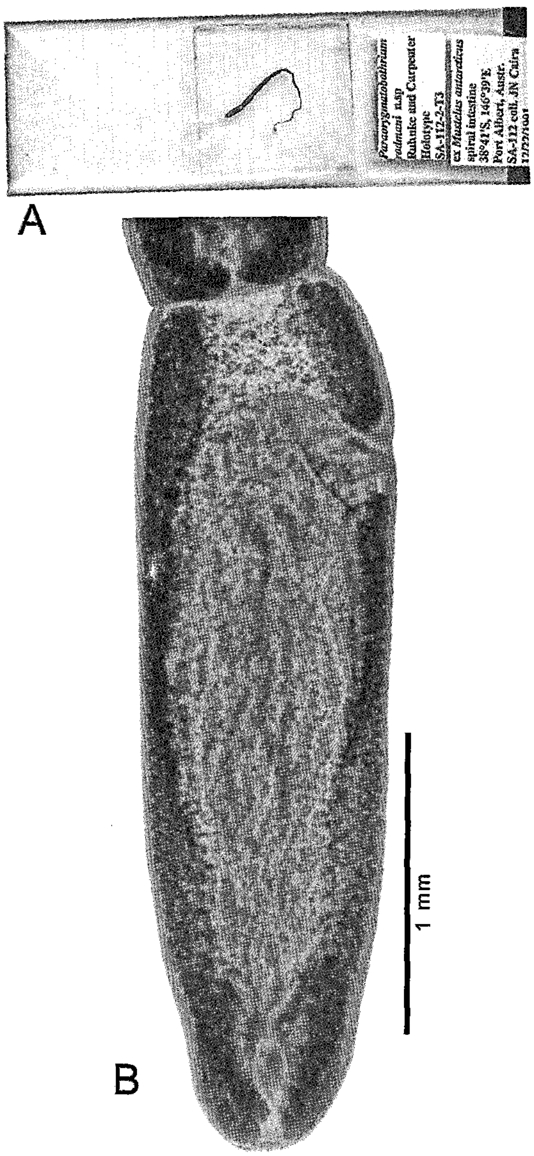

Fig. 146. Photomicrographs of *Paraorygmatobothrium rodmani* Ruhnke and Carpenter, 2008. A. Holotype slide (QM G 230361). B. Terminal proglottid of holotype (QM G 230361). (Terminal proglottid photograph taken from Ruhnke and Carpenter [2008], copyright 2008. Used with permission.)

mid-strobila 286–1,248 (649 ± 215; n=27, *n*=68) long x 156–495 (330 ± 89; n=27, *n*=68) wide. Terminal and subterminal proglottids 1,203–3,900 (2,364 ± 527; n=26, *n*=70) long x 416–840 (614 ± 95; n=26, *n*=70) wide; length to width ratio 2–7:1 (3.9 ± 0.9; n=26, *n*=70). Testes 108–280 (162 ± 33; n=25) in number; testes slightly oblong, 19–86 (50 ± 13; n=24, *n*=70) long x 38–115 (61 ± 15; n=24, *n*=70) wide. Cirrus-sac J-shaped, 204–527 (333 ± 55; n=23) long x 174–355 (266 ± 49; n=23) wide, containing coiled cirrus. Cirrus armed with spinitriches. Vas deferens coiled, median, bordering proximal portion of cirrus-sac, anterior to cirrus-sac. Genital pores lateral, 67–80% (74 ± 4; n=25) of proglottid length from posterior end, irregularly alternating. Vagina median, extends anteriorly from Mehlis' gland to mid-level of proglottis, then laterally and ventrally through field of vas deferens to shallow genital atrium. Ovary near posterior end of proglottis, H-shaped in frontal view, 320–877 (563 ± 145; n=25) long x 390–598 (474 ± 54; n=25) wide, tetralobed in cross-section. Ovicapt 37–65 (52 ± 8; n=23) at posterior margin of ovarian bridge. Mehlis' gland posterior to ovicapt. Uterus ventral to vagina, extending from anterior margin of ovary to level of cirrus-sac in gravid proglottids. Uterine duct, median, parallel and dorsal to uterus, enters uterus slightly posterior to level of cirrus-sac. Vitellarium follicular; follicles oblong, in two lateral fields, 20–61 (36 ± 10; n=24, *n*=72) long x 13–86 (59 ± 15; n=24, *n*=72) wide, each field with 3–5 dorsal and 3–5 ventral rows of follicles, extending entire length of proglottid, interrupted by ovary and cirrus-sac. Eggs spindle-shaped, 122–143 (131 ± 7; n=2; *n*=12) long.

Remarks

Paraorygmatobothrium rodmani can be distinguished from the all of its congeners except *P. bai* in that it retains proglottids that become fully gravid attached to the strobila (see Fig. 145B). That is, *P. rodmani*, like *P. bai* is essentially apolytic (vs. euapolytic) *Paraorygmatobothrium rodmani* differs from *P. bai* in testis shape (oblong vs. round). In all other features, the ranges of these two species overlap. However, Ruhnke and Carpenter (2008) conducted t-test comparisons of character means, and revealed statistically significant differences ($p<0.0001$) between these two species in several cases. For example, *P. rodmani* is statistically significantly shorter than *P. bai* (mean 19.7 vs. 30.6) and has a significantly wider terminal and sub-

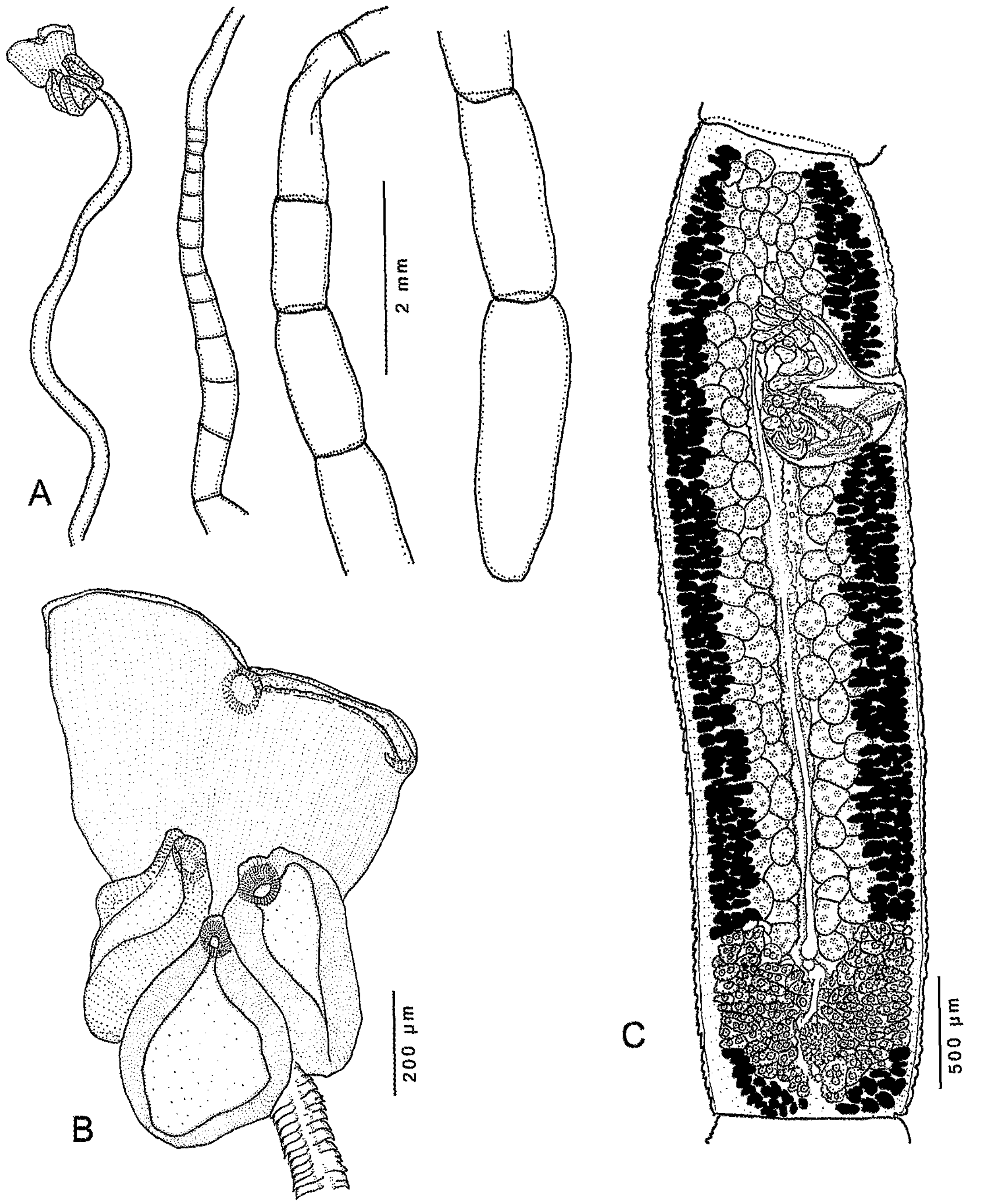

Fig. 147. Line drawings of *Paraorygmatobothrium rodmani* Ruhnke and Carpenter, 2008. A. Holotype (QM G 230361). B. Scolex of holotype (QM G 230361). C. Mature proglottid of paratype (LRP 4185). (Taken from Ruhnke and Carpenter [2008], copyright 2008. Used with permission.)

terminal proglottis morphology than *P. bai* (mean length to width ratio 3.9:1 vs. 7.3:1). In addition, *P. rodmani* has significantly more testes than *P. bai* (mean 162 vs 124).

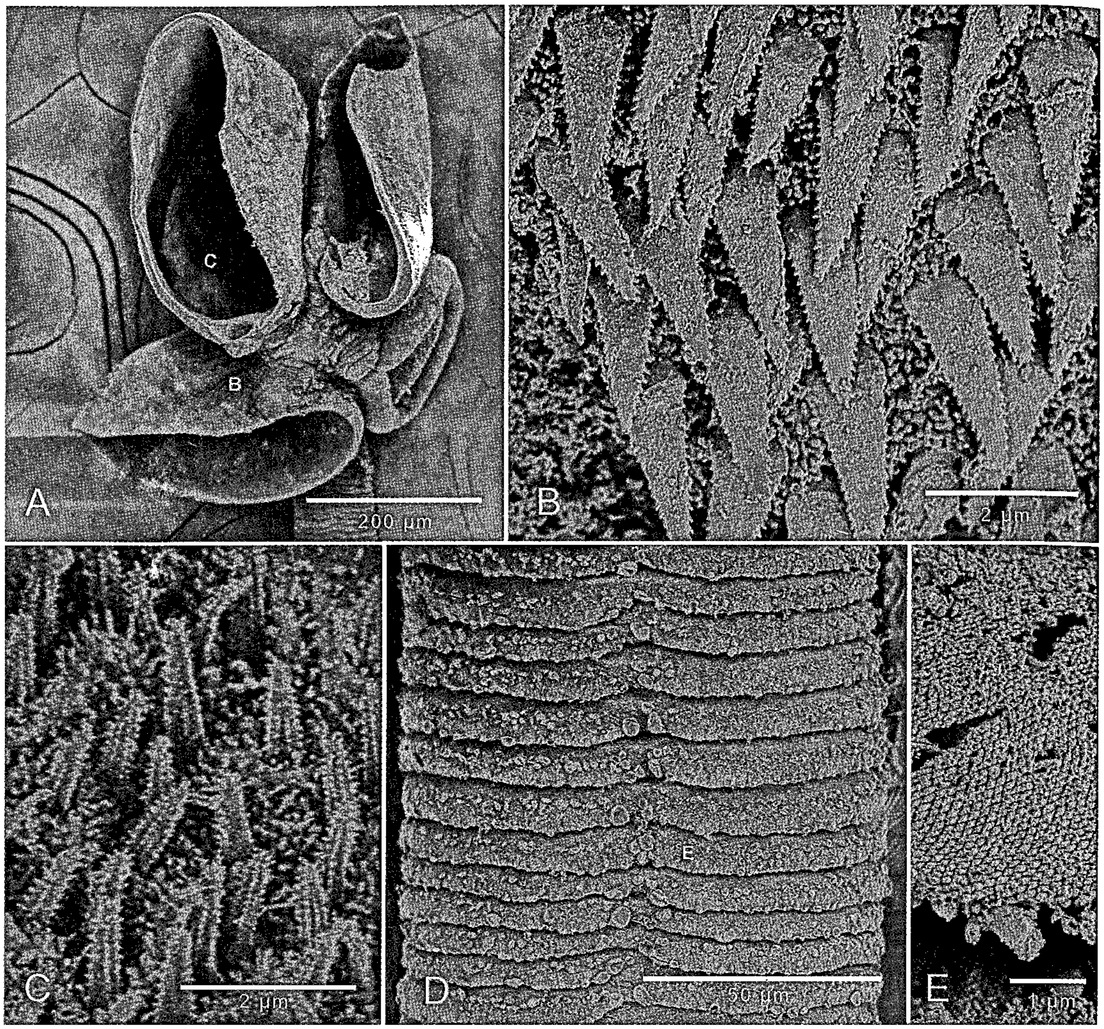

Fig. 148. Scanning electron micrographs of *Paraorygmatobothrium rodmani* Ruhnke and Carpenter, 2008. A. Scolex (letter indicate regions of scolex in enlarged photos B–D). B. Proximal surface of bothridium. C. Distal surface of bothridrium. D. Anterior region of neck (letter indicates region of neck in enlarged photo E). E. Surface of neck. (Taken from Ruhnke and Carpenter [2008], copyright 2008. Used with permission.)

Paraorygmatobothrium triacis (Yamaguti, 1952) Ruhnke, 1996

(Figs. 149–150)

Synonyms: *Phyllobothrium triacis* Yamaguti, 1952; *Crossobothrium triacis* (Yamaguti, 1952) Williams, 1968.

Taxonomic status: Valid.

Type host: *Triakis scyllium* Müller and Henle, 1839, the Banded houndshark.

Site of infection: Spiral intestine.

Type locality: Japanese coastal waters (Fig. 149).

Type material: Syntypes, MPM 22696 (Fig. 150A).

Material examined: Syntypes (Fig. 150A).

Etymology: This species is named for its type host.

Description (modified from Ruhnke [1996a]). Worms craspedote, euapolytic, 35–46 mm long; maximum width 800–920 at scolex. Proglottids 47–68 (n=2) in number. Scolex with

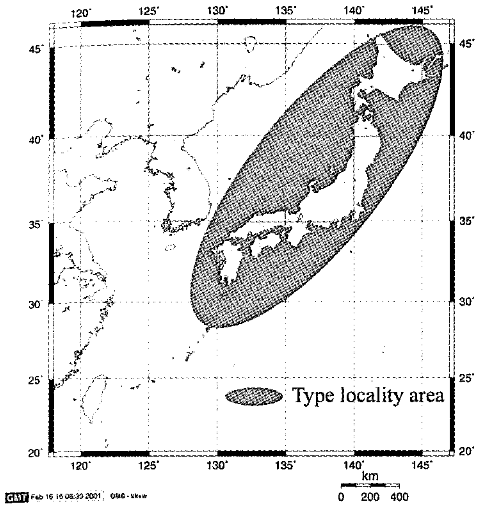

Fig. 149. Geographic distribution of *Paraorygmatobothrium triacis* (Yamaguti, 1952) Ruhnke, 1996.

four bothridia. Bothridia with a single loculus and round apical sucker; apical sucker 75–88 (81 ± 6; n=2; *n*=5) in diameter. Cephalic peduncle absent. Neck 8.4–9.7 mm long, dorsal and ventral surfaces of neck scutellate.

Mature proglottids 1,450–2,125 long by 790–1,005 wide. Testes 176–238 in number; testes oblong, 38–78 (51 ± 15; n=2; *n*=14) long x 45–80 (68 ± 10; n=2; *n*=5) wide, arranged in 6–10 irregular longitudinal columns, one row deep in cross section. Cirrus-sac pyriform, 171 long x 86 wide. Genital pores marginal, 69–75% (71 ± 4; n=2; n=5) of proglottid length from posterior end, irregularly alternating. Ovary posterior, H-shaped in frontal view, 450 long x 661 wide. Ovicapt at posterior margin of ovarian bridge, 47–53 (49 ± 3; n=2; n=4) in diameter in mature proglottids. Uterus ventral, median, extending from anterior margin of ovary to proximal margin of cirrus-sac in mature proglottids. Vitellarium follicular, vitelline follicles oblong, 18–28 (24 ± 3; n=2; n=9) long x 31–75 (46 ± 12; n=2; n=9) wide, in two lateral fields; each field consisting of 4–6 dorsal and 4–6 ventral rows of follicles, extending entire length of proglottid, interrupted by ovary and cirrus-sac.

Remarks

Paraorygmatobothrium triacis is known from only two whole specimens, plus a number of free proglottids. The species was described by Yamaguti (1952) as *Phyllobothrium triacis*, and the species was transferred to *Crossobothrium* by Williams (1968a). However, neither genus is the proper home for this species, and Ruhnke (1996a) transferred it to *Paraorygmatobothrium*.

Euzet (1959) referred to specimens from *Mustelus mustelus* and *M. canis* as *Crossobothrium triacis*. The specimens examined by Euzet (1959) from *M. mustelus* actually represent *Paraorygmatobothrium musteli*, and allocation of these specimens to *C. triacis* by Euzet (1959) was ill-advised.

Paraorygmatobothrium triacis can be distinguished from existing species of the genus except for *P. leuci* and *P. orectolobi* in total length (see Table 1). *Paraorygmatobothrium triacis* differs from *P. leuci* in testes number (176–238 vs. 83–151), and differs from *P. orectolobi* in genital pore position (69–75% vs. 52–56%).

Paraorygmatobothrium typicum (Subhapradha, 1955) n. comb.

(Figs. 151–153)

Synonym: *Phyllobothrium typicum* Subhapradha, 1955.
Taxonomic status: Valid.
Type host: *Rhizoprionodon acutus* (Rüppell, 1837), Milk shark.
Site of Infection: Spiral intestine
Type locality: Madras Coast, India (Fig. 151).
Additional localities: Sarawak, Malaysia; Dundee Beach, Australia (Fig. 152).
Type material: Not specified.
Additional material: LRP 7438–7440 (Fig. 152A).
Specimens examined: LRP 7438–7440.
Etymology: Unknown.

Description (based on eight whole mounted specimens, and two scolices prepared for

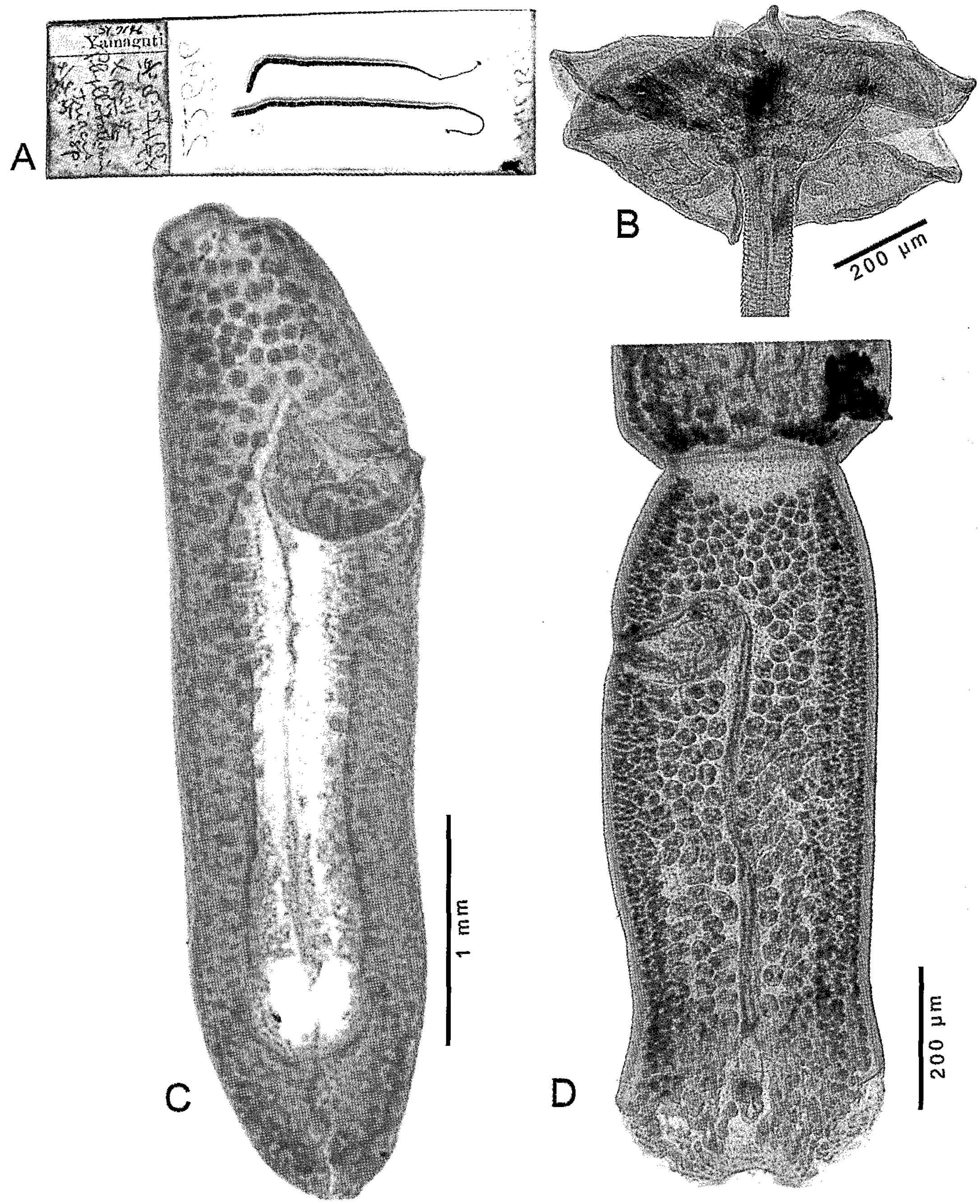

Fig. 150. Photomicrographs of *Paraorygmatobothrium triacis* (Yamaguti, 1952) Ruhnke, 1996. A. Syntype slide (MPM 22696). B. Scolex of syntype (MPM 22696). C. Free proglottid of syntype (MPM 22696). D. Terminal proglottid of syntype (MPM 22696).

SEM).

Worms slightly craspedote, hyperapolytic, 3.3–4.1 (3.8 ± 0.34; n=8) mm long; maximum width 175–320 (250 ± 56; n=6) at scolex. Proglottids 10–15 (13 ± 2; n=8) in number. Scolex with four bothridia; both-

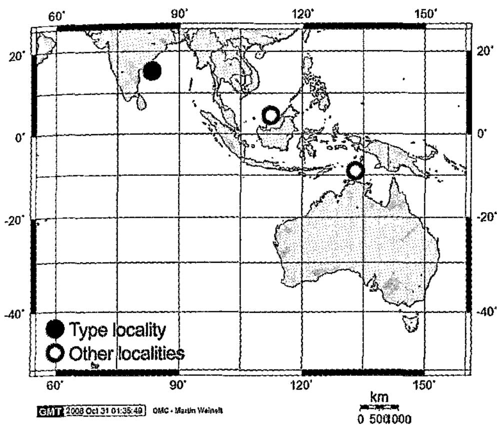

Fig. 151. Geographic distribution of *Paraorygmatobothrium typicum* (Subhapradha, 1955) n. comb.

ridia 115–163 (136 ± 20; n=5) long x 95–153 (122 ± 23; n=5) wide; each bothridium with single loculus and round apical sucker; apical sucker 30–38 (34 ± 3; n=7; *n*=9) in diameter. Proximal surfaces of bothridia covered with serrate gladiate spinitriches and papilliform filitriches. Bothridial rim covered with capilliform filitriches. Distal locular surface and distal surface of apical suckers covered with serrate gladiate spinitriches and papilliform filitriches. Cephalic peduncle absent. Neck scutellate, 0.8–1.3 (1.1 ± 0.2; n= 4) mm long; scutes paired; surface of scutes comprised of densely packed capilliform filitriches with triangular tips.

Immature proglottids at mid-strobila 75–145 (108 ± 36; n=4) long x 100–150 (129 ± 21; n=4) wide. Terminal proglottids 475–770 (605 ± 121; n=5) long x 128–210 (171 ± 36; n=5) wide; length to width ratio 2.7–4.9:1 (3.6 ± 0.9; n=5). Testes 46–63 (56 ± 6; n=4; *n*=5) in number; testes slightly oblong, 18–27 (21 ± 4; n=4, *n*=6) long x 27–45 (35 ± 7; n=4, *n*=6) wide. Cirrus-sac oval, 63–80 (73 ± 9; n=3) long x 25–38 (31 ± 7; n=3) wide, containing coiled cirrus. Vas deferens coiled, median, bordering proximal, anterior to cirrus-sac. Genital pores lateral, 73–82% (78 ± 4; n=5) of proglottid length from posterior end, irregularly alternating. Vagina median, extending anteriorly from Mehlis' gland to mid-level of proglottid, then laterally and ventrally through field of vas deferens to shallow genital atrium. Ovary near posterior end of proglottid, H-shaped in frontal view, 90–138 (108 ± 26; n=3) long x 100–130 (118 ± 16; n=3) wide. Mehlis' gland posterior to ovary. Uterus ventral to vagina, extending from anterior margin of ovary to level of cirrus-sac in gravid proglottids. Vitellarium follicular; in two lateral fields, each field with 1–2 dorsal and 1–2 ventral rows of follicles, extending entire length of proglottid, interrupted by ovary and cirrus-sac. With one dorsal and one ventral pair of excretory ducts.

Remarks

Paraorygmatobothrium typicum n. comb. was described by Subhapradha (1955) as *Phyllobothrium typicum,* but is not consistent in morphology with the diagnosis of that genus, as it lacks foliose, posteriorly bifid bothridia. The species here is consistent with the diagnosis of *Paraorygmatobothrium. Paraorygmatobothrium typicum* n. comb. can be distinguished from existing species of the genus except for *P. floraformis* in total length (see Table 1). *Paraorygmatobothrium typicum* n. comb. differs from *P. floraformis* in cirrus-sac dimensions (63–80 long by 25–38 wide vs. 78–139 long by 31–59 wide) and spinithrix morphology of the distal bothridial surface (serrate gladiate vs. gongylate columnar).

Recently described species of *Paraorygmatobothrium*

***Paraorygmatobothrium mobedii* Malek, Caira and Haseli, 2010**

Malek et al. (2010) described *Paraorygmatobothrium mobedii* from *Carcharhinus* cf. *dussumieri* (Müller and Henle) in the Persian Gulf. Malek et al. (2010) compared *P. mebedii* to ten of its congeners for which SEM data were available. *Paraorygmatobothrium mobedii* species resembles *P. bai, P. barberi, P. exiguum,* and *P. rodmani* and differs from *P. arnoldi, P. janineae, P. kirstenae, P. prionacis, P. roberti,* and *P. taylori* in its possession of distal bothrdial surfaces bearing gongylate columnar spinitriches rather than serrate gladiate spinitriches. Unlike *P. exiguum,* the gongylate columnar spinitriches of *P. mobe-*

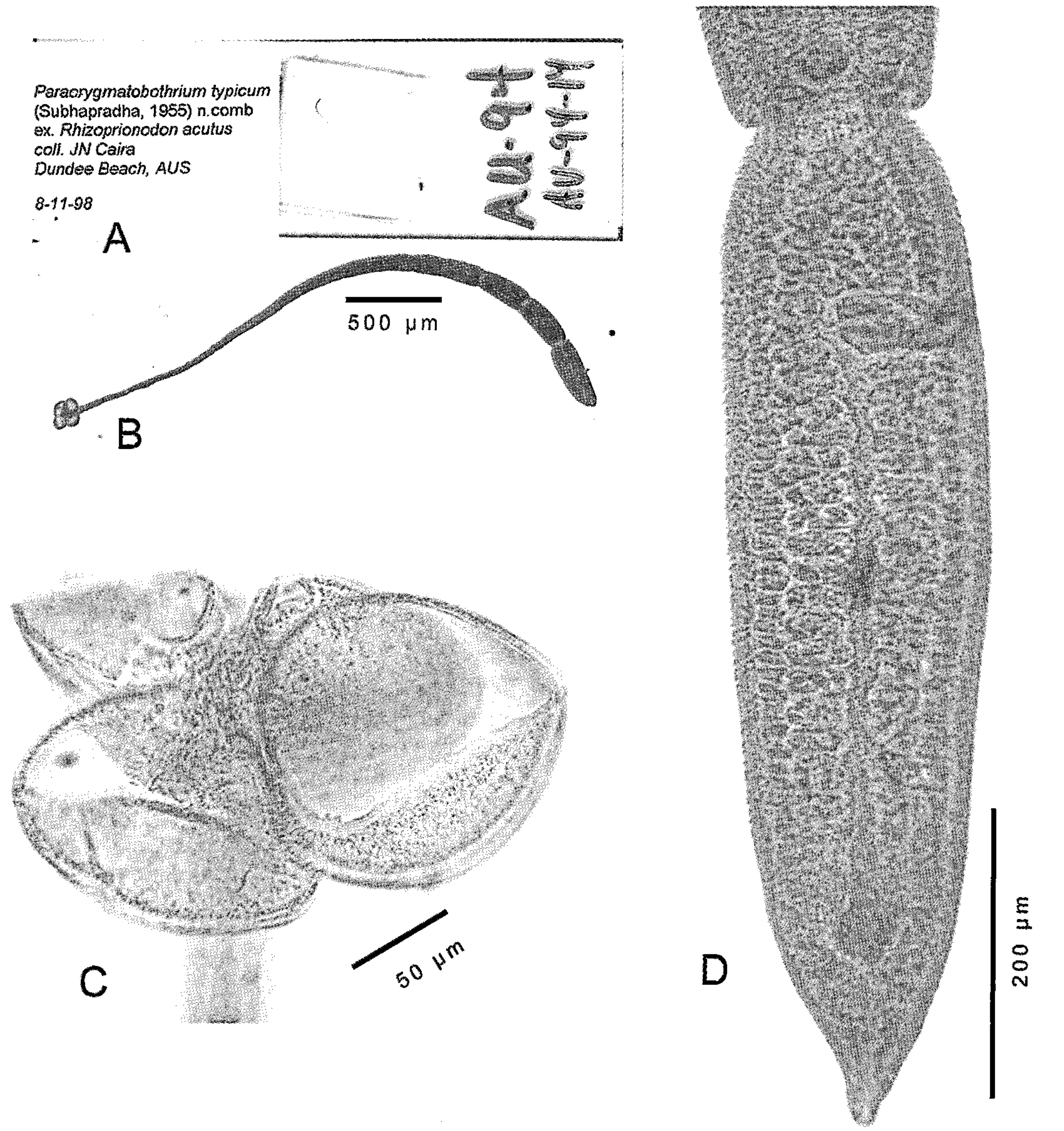

Fig. 152. Photomicrographs of *Paraorygmatobothrium typicum* (Subhapradha, 1955) n. comb. A. Voucher slide (LRP 7438). B. Entire specimen of voucher (LRP 7438). C. Scolex of voucher (LRP 7439). D. Terminal proglottid of voucher (LRP 7440).

dii are not arranged on 'bumps' (see Ruhnke 1994a). *Paraorygmatobothrium mobedii* is generally shorter in total length than *P. bai*, *P. barberi*, and *P. rodmani*.

Paraorygmatobothrium sinuspersicense Malek, Caira and Haseli, 2010

Malek et al. (2010) described *Paraorygmatobothrium sinuspersicense* from *Carcharhinus* cf. *dussumieri* (Müller and Henle) in the Persian Gulf. As with *P. mobedii*, Malek et al. (2010) compared *P. sinuspersicense* to 11 of its congeners for which SEM data were available. *Paraorygmatobothrium sinuspersicense* resembled *P. bai*, *P. barberi*, *P. exiguum*, *P. mobedii*, and *P. rodmani* and differs from *P. arnoldi*, *P. janineae*, *P. kirstenae*, *P. prionacis*, *P. roberti*, and *P. taylori* in its pos-

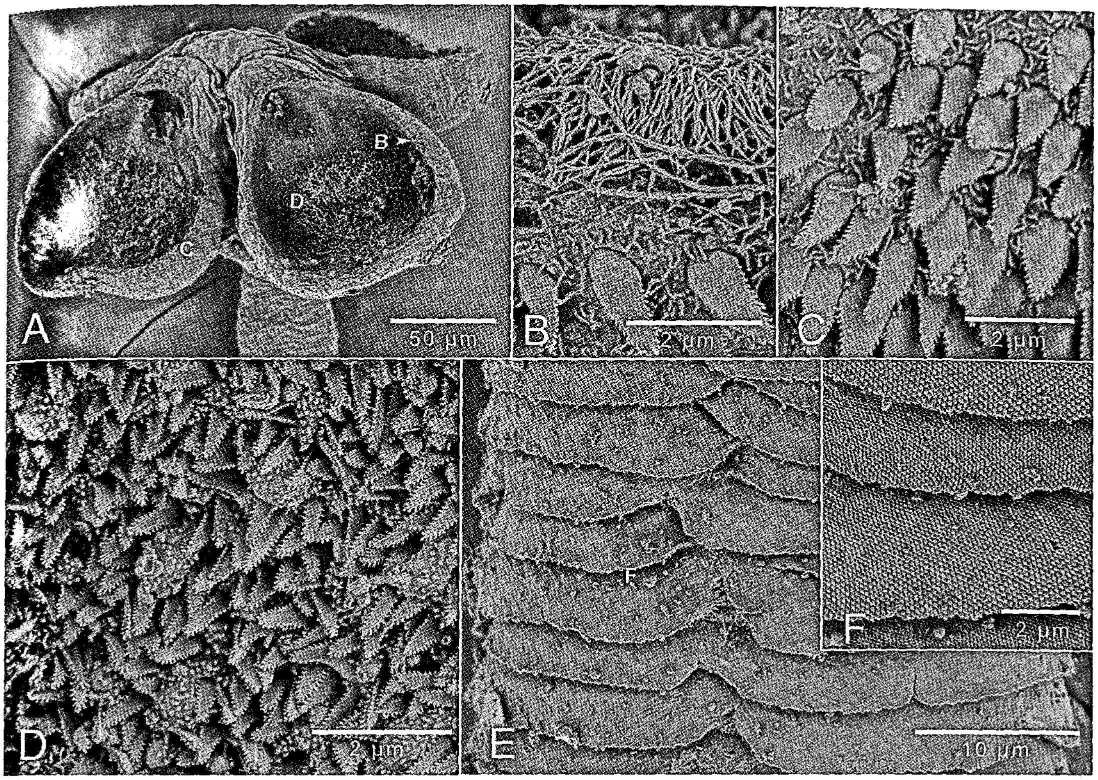

Fig. 153. Scanning electron micrographs of *Paraorygmatobothrium typicum* (Subhapradha, 1955) n. comb. A. Scolex (letter indicate regions of scolex in enlarged photos B–D). B. Bothridial rim. C. Proximal surface of bothridium. D. Distal surface of bothridium. E. Anterior region of neck (letter indicates region of neck in enlarged photo F). F. Surface of neck.

session of distal bothrdial surfaces bearing gongylate columnar spinitriches rather than serrate gladiate spinitriches. *Paraorygmatobothrium sinuspersicense* differed from *P. exiguum* in not having its gongylate columnar spinitriches arranged on 'bumps' (see Ruhnke 1994a). In addition, *P. sinuspersicense* was found to be shorter in total length than *P. bai, P. barberi, P. rodmani,* and *P. taylori. Paraorygmatobothrium sinuspersicense* differs from *P. mobedii* in cirrus-sac shape, testis shape, and testes distribution (see Malek et al. 2010).

Paraorygmatobothrium taylori Cutmore, Bennett and Cribb, 2009

Cutmore et al. (2009) described *Paraorygmatobothrium taylori* from the Australian weasel shark, *Hemigaleus australiensis* White, Last and Compagno, 2005. This species is a valid member of *Paraorygmatobothrium* and is distinguished from all other species except *P. janineae* and *P. kirstenae* in its possession of a cephalic peduncle. In addition, *P. taylori, P. janineae,* and *P. kirstenae* possess vitelline fields that extend toward the dorsal and ventral midline of the proglottid, with the field interrupted at the level of the cirrus-sac, and reduced at the level of the ovary. *Paraorygmatobothrium taylori* can be distinguished from these two species in its possession of prominent, semicircular muscle bands in each bothridium. The latter bothridial morphology is similar to that of *P. barberi* (see Ruhnke 1994a).

Key to Species of *Paraorygmatobothrium*

1(a) Vitelline follicles interrupted by the ovary....................3
1(b) Vitelline follicles not interrupted by the ovary; follicles approaching proglottid midline; cephalic peduncle present....................2

2(a) Circular band of muscles at center portion of bothridia present ... ***P. taylori***
2(b) Circular band of muscles absent....................21

3(a) Circular band of muscles present at center of bothridia ....***P. barberi***
3(b) Bothridia not as above....................4

4(a) Specimens typically apolytic 5
4(b) Specimens typically either euapolytic or hyperapolytic 6

5(a) Testes round....................***P. bai***
5(b) Testes oblong....................***P. rodmani***

6(a) Genital pore position <65% from posterior end of proglottid; proglottid number >30 7
6(b) Specimen morphology not as above 8

7(a) Proglottids ≤70 in number....................***P. leuci*** n. comb.
7(b) Proglottids >70 in number....................***P. orectolobi*** n. comb.

8(a) Bothridial margin ringed with band of muscles; posterior portion of bothridia pulled toward apical plane....................***P. paulum*** n. comb.
8(b) Bothridial morphology not as above 9

9(a) Maximum proglottid number ≤20....................10
9(b) Maximum proglottid number >20....................12

10(a) Apical sucker diameter ≥45 µm....................***P. exiguum***
10(b) Apical sucker diameter <45 µm 11

11(a) Cirrus-sac length typically ≥80 µm; cirrus-sac width typically ≥35 µm .... ***P. floraformis*** n. comb.
11(b) Cirrus-sac length typically <80 µm; cirrus-sac width typically <35 µm.................... ***P. typicum*** n. comb.

12(a) Apical sucker diameter ≥75 µm or greater....................13
12(b) Apical sucker diameter <75 µm 14

13(a) Total length ≥25 mm....................***P. triacis***
13(b) Total length <25 mm ....***P. prionacis***

14(a) Maximum number of testes <90; genital pore position >70% from posterior end of proglottid.................... ***P. angustum*** n. comb.
14(b) Proglottid morphology not as described above....................15

15(a) Proglottids >30 in number .... *P. filiforme*
15(b) Proglottids generally ≤30 in number 16

16(a) Ovary length <130 µm .... *P. arnoldi*
16(b) Ovary width ≥130 µm 17

17(a) Cirrus-sac width ≥170 µm .... *P. musteli*
17(b) Cirrus-sac width <170 µm 18

18(a) Cirrus-sac length typically ≥200 µm; ovary width typically ≥180 µm .... *P. nicaraguensis* n.comb.
18(b) Cirrus-sac length typically <200 µm; ovary width typically <180 µm 19

19(a) Testes number typically >85 .... *P. roberti*
19(b) Testes number typically ≤85 20

20(a) Cirrus-sac elongate oval .... *P. sinuspersicense*
20(b) Cirrus-sac pyriform .... *P. mobedii*

21(a) Apical sucker diameter ≤65 µm .... *P. kirstenae*
21(b) Apical sucker diameter >65 µm .... *P. janineae*

RUHNKECESTUS Caira and Durkin, 2006

Taxonomic status: Valid.
Synonyms: None.
Type and only known species: *Ruhnkecestus latipi* Caira and Durkin, 2006.
Etymology: This genus was named in honor of Dr. Tim Ruhnke.

Diagnosis (taken from Caira and Durkin [2006]).

Phyllobothriidae. Worms weakly craspedote euapolytic. Scolex with four bothridia, each with one apical, three central, and two posterior loculi. Marginal loculi lacking. Proximal and distal bothridial surfaces covered with serrate gladiate spinitriches and capilliform filitriches. Cephalic peduncle absent. Neck present. Neck and strobila scutellate; scutes comprised of densely arranged capilliform filitriches. Immature proglottids wider than long. Mature proglottids longer than wide. Testes numerous in poral and aporal fields, anterior to ovary, one row deep in cross-section. Cirrus-sac elongate oval, containing armed cirrus. Genital pores unilateral or occasionally irregularly alternating. Genital atrium shallow. Vagina median, opening anterior to cirrus-sac. Ovary posterior, H-shaped in frontal view, tetralobed in cross-section. Uterus ventral, reaching cirrus-sac. Uterine duct present. Vitellarium follicular; follicles distributed in two lateral fields; each field consisting of multiple follicles, partially interrupted dorsally and ventrally by cirrus-sac, interrupted at midlevel of ovary.

Remarks

Caira and Durkin (2006) presented a very detailed differentiation of *Ruhnkecestus* from other tetraphyllidean and phyllobothriid taxa. Caira and Durkin (2006) also differentiated the genus from the phyllobothriid subfamilies as they were defined by Euzet (1994), and noted that *Ruhnkecestus* was fully consistent with the subfamilial diagnosis of the Phyllobothriinae of Euzet (1994) as emended by Caira and Durkins (2006). *Ruhnkecestus* most closely resembles *Cardiobothrium*, *Orectolobicestus*, and *Paraorygmatobothrium*. The primary similarity to *Cardiobothrium* is the presence of facial bothridial loculi. However, *Ruhnkecestus* differs from *Cardiobothrium* in lacking bothridial marginal loculi and an apical sucker. In addition, *Cardiobothrium* lacks strobilar scutes and serrated spinitriches from its proximal bothridial surfaces. *Ruhnkecestus* most closely resembles *Orectolobicestus* and *Paraorygmatobothrium*. In all three genera the genital pores are anterior, and the fields of vitelline follicles are interrupted at least to some extent by the ovary. All three taxa also possess a scutellate neck, with the scutes comprised of capilliform filitriches with triangular tips. *Ruhnkecestus* shares the presence of serrate gladiate spinitriches on the proximal bothridial surfaces with species of *Paraorygmatobothrium* and some species of *Orectolobicestus* (see Ruhnke 1994a; Ruhnke and Thompson 2006; Ruhnke et al. 2006a, b; Ruhnke and Carpenter 2008). However, all species of *Orectolobicestus* and *Paraorygmatobothrium* possess an apical sucker, a feature that appears to be lacking from the bothridia of *Ruhnkecestus*.

Ruhnkecestus latipi Caira and Durkin, 2006
TYPE SPECIES
(Figs. 154–156)

Taxonomic status: Valid.

Type host: *Scoliodon laticaudus* Müller and Henle, 1838, the Spadenose shark.

Type locality: Mukah (02°85'49"N, 112°80'69"E), Sarawak, Borneo, Malaysia (Fig. 154).

Site of infection: Spiral intestine.

Type material: Holotype MZUM(P) 137h; paratypes USNPC 96410, SBC C-C-00005, LRP 3748 (SEM specimen and its strobiliar voucher).

Etymology: This species was named for Captain Latip Sait.

Description (modified from Caira and Durkin [2006]).

Worms weakly craspedote, euapolytic, 15–17 mm (16 ± 1.5, n=2) long; maximum width 710–789 (750 ± 56, n=2), generally at level of scolex. Neck 5.8–6.3 mm (6.0 ± 0.3, n=3) long, surface conspicuously scutellate. Proglottids 50–59 (54 ± 5, n= 3) in number. Scolex with four bothridia, 430–475 (453 ± 31.8, n=2) long x 710–789 (750 ± 56, n=2) wide. Bothridia acetabulate in form, 320–450 (382 ± 59.3, n=2, *n*=5) long x 360–410 (377 ± 28, n=2, *n*=6) wide; each bearing a total of six facial loculi: one anterior, three central, and two posterior in position; middle loculus of central triplet slightly posterior to lateral and medial loculi of triplet. Anterior loculus 128–135 (133 ± 4.3, n=2, *n*=3) long x 100–123 (113 ± 11.5, n=2, *n*=3) wide; lateral and medial loculi of triplet symmetrical, 125–145 (138 ± 7.7, n=2, *n*=5) long x 100–105 (104 ± 2.5, n=2, *n*=4) wide; central loculus of triplet 128–163 (145 ± 24.7, n=2) long x 105–110 (108 ± 2.5, n=2, *n*=3) wide; lateral and medial loculi of pair symmetrical, 250–285 (265 ± 13, n=2, *n*=7) long x 195–213 (199 ± 7, n=2, *n*=6) wide. Proximal bothridial surfaces covered with serrate gladiate spinitriches and capilliform filitriches. Distal bothridial surfaces covered with slightly larger serrate gladiate spinitriches and capilliform filitriches throughout. Apex of scolex densely covered with capilliform filitriches and numerous cilia with basal swelling bearing small bumps. Neck and strobila scutellate; scutes irregular, comprised of densely packed, capilliform filitriches.

Immature proglottids 51–58 (52 ± 5, n=3) in number, wider than long. Mature proglottids 1–2 (1.7 ± 0.6, n=3) in number, 680–940 (803 ± 106.6, n=3, *n*=4) long x 360–490 (404

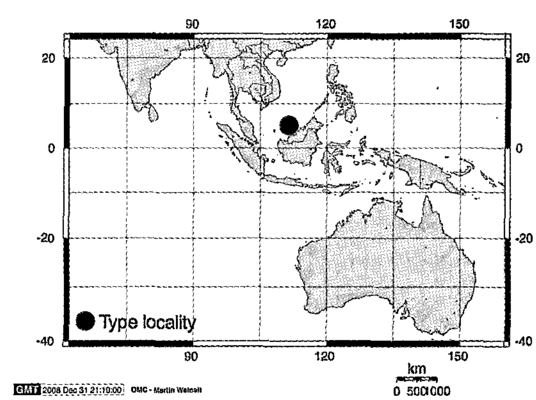

Fig. 154. Geographic distribution of *Ruhnkecestus latipi* Caira and Durkin, 2006.

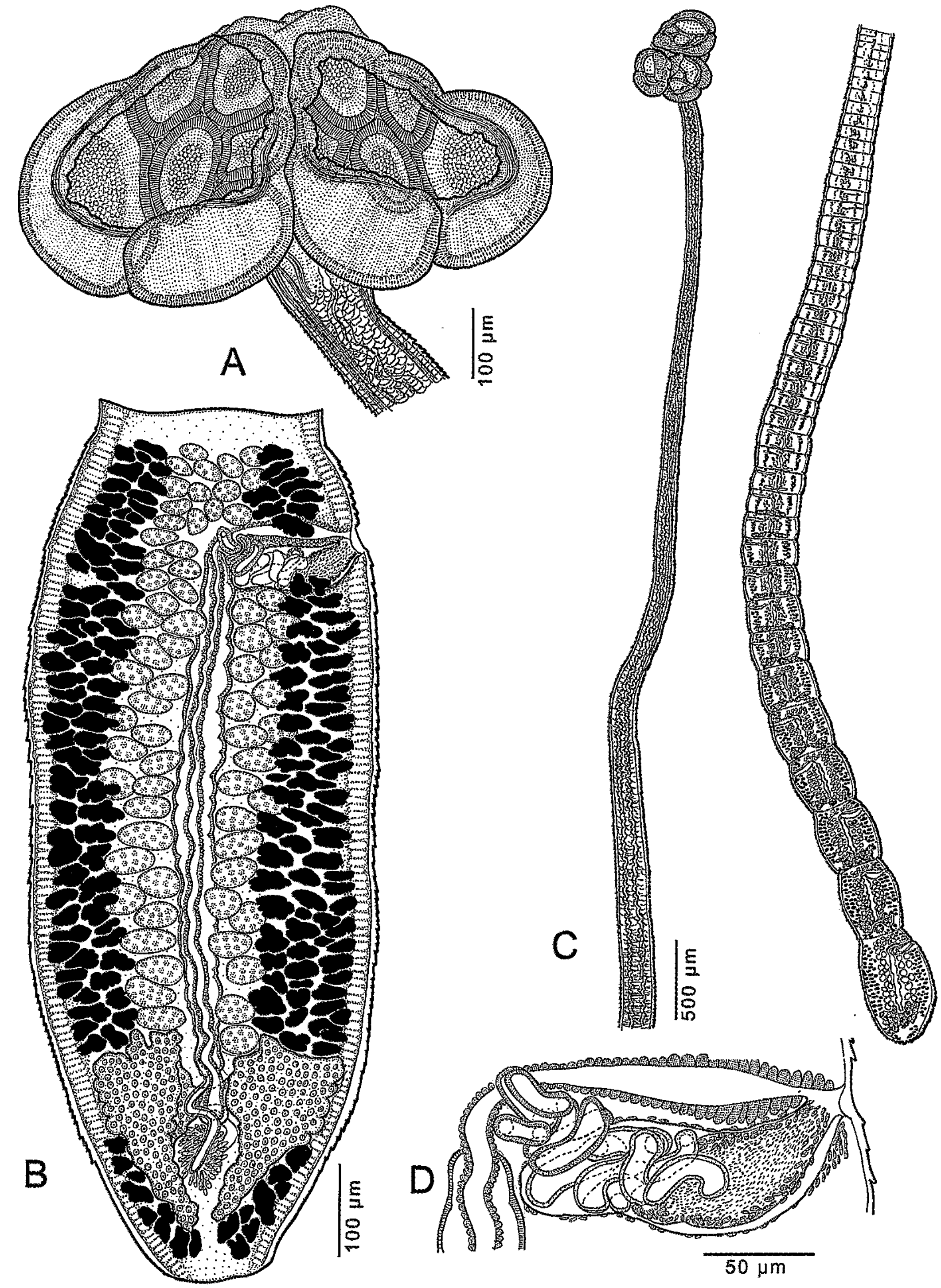

Fig. 155. Line drawings of *Ruhnkecestus latipi* Caira and Durkin, 2006. A. Scolex. B. Terminal proglottid. C. Entire specimen. (Taken from Caira and Durkin [2006]. copyright 2006. Used with permission.)

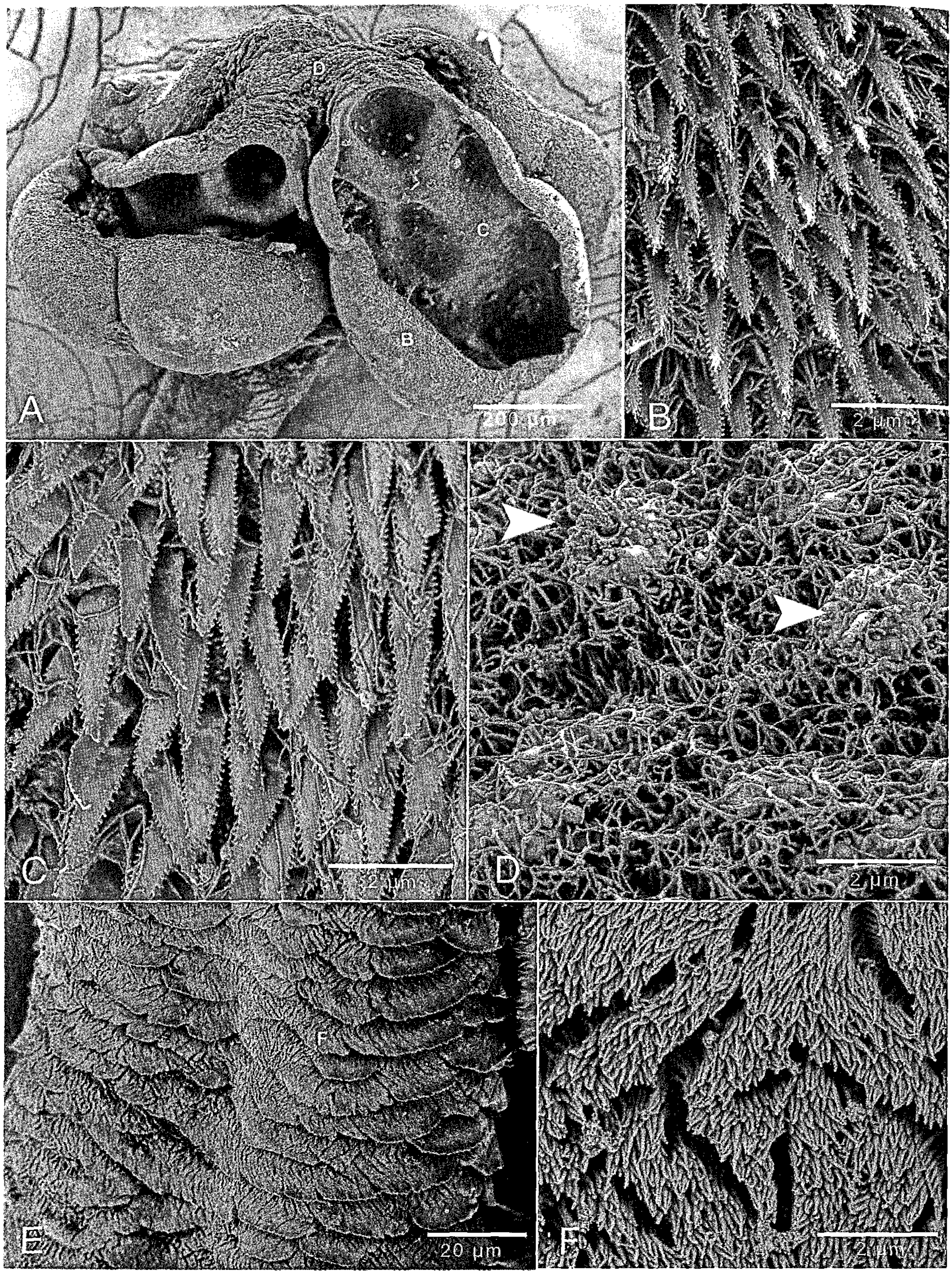

Fig. 156. Scanning electron micrographs of *Ruhnkecestus latipi* Caira and Durkin, 2006. A. Scolex (letters indicate region of scolex in enlarged photos B–D). B. Enlarged view of microtriches on proximal bothridial surface. C. Enlarged view of microtriches on distal bothridial surface. D. Enlarged view of apex of scolex proper. Note cilia at arrows. E. Scutellate arrangement of elongate filitriches on neck (letter indicated region of neck in enlarged photo F). F. Enlarged view of filitriches comprising scutes on neck. (Taken from Caira and Durkin [2006]. copyright 2006. Used with permission.)

± 58.5, n=3, *n*=4) wide; length to width ratio 1.6–2.4:1 (2:1 ± 0.35, n=3, *n*=4). No gravid proglottids seen. Testes slightly oblong; 58–70 (63 ± 5, n=3, *n*=5) in total number; 17–22 (19 ± 2.1, n=3, *n*=5) in postporal field, extending from anterior of proglottid to anterior margin of ovary, generally arranged in one to two irregular columns in aporal region of proglottid and one irregular column in postporal region of proglottid, one row deep in cross-section, 28–48 (35 ± 5.6, n=3, *n* =9) long x 38–55 (47 ± 7.3, n=3, *n*=9) wide in most regions of proglottid; poral, and aporal testes anterior to cirrus-sac slightly smaller than those throughout more posterior regions of proglottid. Cirrus-sac elongate oval, 120–148 (140 ± 13.4, n=3, *n*=4) long x 38–52 (47 ± 6.6, n=3, *n*=4) wide, containing coiled cirrus armed with spinitriches. Vas deferens minimal, coiled, median, bordering proximal portion of anterior margin of cirrus-sac. Genital pores marginal, 86–88% (87 ± 0.5, n=3, *n*=4) of proglottid length from posterior of proglottid, unilateral in two of three mature strobilae examined. Genital atrium shallow. Vagina median, extending from genital atrium, along anterior margin of cirrus-sac to midline of proglottid then posteriorly to ovarian bridge; vaginal wall glandular distally. Ovary near posterior end of proglottid, H-shaped in frontal view, tetralobed in cross-section, 210–233 (224 ± 12, n=3) long x 230–320 (279 ± 46, n=3) wide, lobulated. Ovicapt at posterior margin of ovarian bridge, 26–29 (28 ± 2, n=3) in diameter. Mehlis' gland posterior to ovicapt, 63–90 (79 ± 15, n=3) long x 60–85 (69 ± 14, n=3) wide. Uterus ventral to vagina, extending along midline of proglottid from anterior margin of ovarian bridge to level of genital pore. Uterine duct present, anterior extent not determined. Vitellarium follicular; follicles in two lateral fields each consisting of 5–8 columns of irregularly shaped follicles, extending from near anterior margin of proglottid to posterior margin of proglottid, interrupted at anterior margin of ovary and partially by cirrus-sac. Excretory ducts lateral. Eggs not seen.

Remarks

Caira and Durkin (2006) noted that *R. latipi* was the first cestode species reported from *S. laticaudus*. However, Srivastava and Capoor (1979) described *Phyllobothrium bombayensis* from *Scoliodon sorrakowah* (= *Scoliodon laticaudus*) and Shinde (1978) described *Pithophorus yamaguttii* Shinde, 1978 from *Scoliodon* sp. The latter species is likely from *S. laticaudus*, as it is the only known species in the genus. Both of these species are poorly known, and were poorly illustrated. *Phyllobothrium bombayensis* is considered *incertae sedis* (see pg. 36). The description of *P. yamaguttii* indicates that each bothridium is essentially hollow, opening at both ends. In addition, the vitelline follicles are described as being distributed all along the margins of the proglottid, but no vitelline follices are illustrated in the proglottid shown. The proglottid of *P. yamagutii* is consistent with *Ruhnkecestus* in testis arrangement and genital pore position. As noted above (p. 18), *Pithophorus* is considered a *genus inquirendum* and *P. yamagutii* should be considered a *nomen dubium* until such time as the type material (if it exists) can be located and studied.

SCYPHOPHYLLIDIUM Woodland, 1927

Taxonomic status: Valid.

Synonyms: None.

Type species: *Scyphophyllidium giganteum* (Van Beneden, 1858) Woodland, 1927.

Additional species: *Scyphophyllidium uruguayense* Brooks, Marques, Perroni and Sidagis, 1999.

Etymology: Not given, but presumably, *Scyphos* (Gr.) = cup; *phyllo* (Gr.) = leaf.

Diagnosis

Worms slightly craspedote, anapolytic. Scolex with four bothridia. Bothridia uniloculate, cuplike, with short stalks, with indistinct apical sucker. Neck present. Immature proglottids wider than long. Mature and gravid proglottids generally as long as wide. Proglottids multi-testiculate; testes oblong, distributed throughout proglottid, post-poral testes present. Cirrus-sac elongate oval, containing coiled armed cirrus. Vas deferens coiled, median to proximal portion of cirrus-sac. Genital pores in anterior third of proglottid. Vagina median, opening anterior to cirrus-sac. Genital pores irregularly alternating. Ovary near posterior end of proglottis, H-shaped in frontal view, ovary wider than long. Uterus saccate, extending from anterior margin of ovary to level of cirrus-sac. Uterine duct present. Vitellarium follicular; follicles distributed in two lateral fields, extending entire length of proglottid. Eggs spindle-shaped. Parasites of Triakidae.

Remarks

Woodland (1927) erected *Scyphophyllidium* for specimens he collected from *Galeus vulgaris* (= *Galeorhinus galeus* L., 1758), the Tope shark, from Plymouth, England. *Scyphophyllidium* was characterized for its unique scolex morphology, which is comprised of four cylindrical or globular bothridia. Woodland (1927) did not describe a sucker, but examination of vouchers (MNHN HEL 149–153) reveals that a faint apical sucker is present on the bothridium. Riser (1955) reported *S. giganteum* from *Galeorhinus zyopterus* (= *G. galeus*), collected from the eastern Pacific Ocean off of coastal California. Euzet (1959) examined preserved specimens that he identified as *S. giganteum*, collected from *G. galeus* off Concarneau, France. Although Euzet referred to Riser's (1955) study, he made no mention of Riser's observations concerning *S. giganteum*. Euzet (1959) reported the bothridia to be globular, as did Woodland (1927) and Riser (1955), and that the anterior openings of the bothridia were not accessory bothridial suckers, as did Riser (1955). Other authors (*e.g.*, Yamaguti 1959; Schmidt 1986; Euzet 1994) have characterized the genus as having globular bothridial lacking both apical accessory bothridial suckers and posterior openings.

Scyphophyllidium giganteum (Van Beneden, 1858) Woodland, 1927

TYPE SPECIES

(Figs. 157–158)

Synonyms: *Anthobothrium giganteum* Van Beneden, 1858; *Phyllobothrium giganteum* (Van Beneden, 1858) Southwell, 1930.

Taxonomic status: Valid.

Type host: *Galeus vulgaris* (= *Galeorhinus galeus* [L., 1758]), the Tope shark.

Site of infection: Spiral intestine.

Type locality: Coast of Belgium (Fig. 157).

Additional localities: Plymouth, U.K., Concarneau, France (Fig. 157).

Type material: Not specified.

Voucher specimens: MNHN HEL 149–153; BMNH 1965.2.23.188-190, 1991.7.11.42; LRP 7441.

Material examined: MNHN HEL 149–153; BMNH 1965.2.23.188-190, 1991.7.11.42; LRP 7441.

Etymology: Not specified, but presumably, named for its large size.

Description (modified from Woodland [1927] and Euzet [1959]).

Worms slightly craspedote, anapolytic, 95–120 mm long; maximum width 1.3–1.8 mm, at level of proglottid. Scolex 1 mm long x 1.2–1.8 mm wide, with four bothridia. Bothridia uniloculate, cup-like, 630–650 long x 350–400

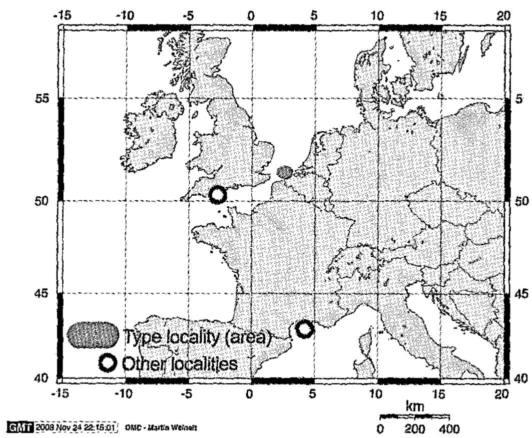

Fig. 157. Geographic distribution of *Scyphophyllidium giganteum* (Van Beneden, 1858) Woodland, 1927.

wide, with short stalks. Bothridial rim lined with thick muscle bands, apical sucker present, indistinct. Neck 25–30 mm long.

Immature proglottids wider than long. Mature proglottids 0.75–1 mm long x 1.3–1.8 mm wide. Gravid proglottids 1.2–2.1 mm long x 1.6–1.8 mm wide. Testes 250–300 in number; testes oblong, 25–30 long x 50–75 wide. Cirrus-sac elongate oval, 350–400 long x 90–150 wide, containing coiled armed cirrus. Vas deferens coiled, medial to proximal portion of cirrus-sac. Genital pores lateral, 69–80% of proglottid length from posterior end of proglottid. Vagina median, extending anteriorly from Mehlis' gland to mid-level of proglottid, then laterally along anterior margin of vas deferens, then to shallow genital atrium. Ovary near posterior end of proglottid, H-shaped in frontal view, 280–410 long x 890–1,000 wide, tetralobed in cross-section. Mehlis' gland posterior to ovicapt. Uterus saccate, extending from ovary to anterior

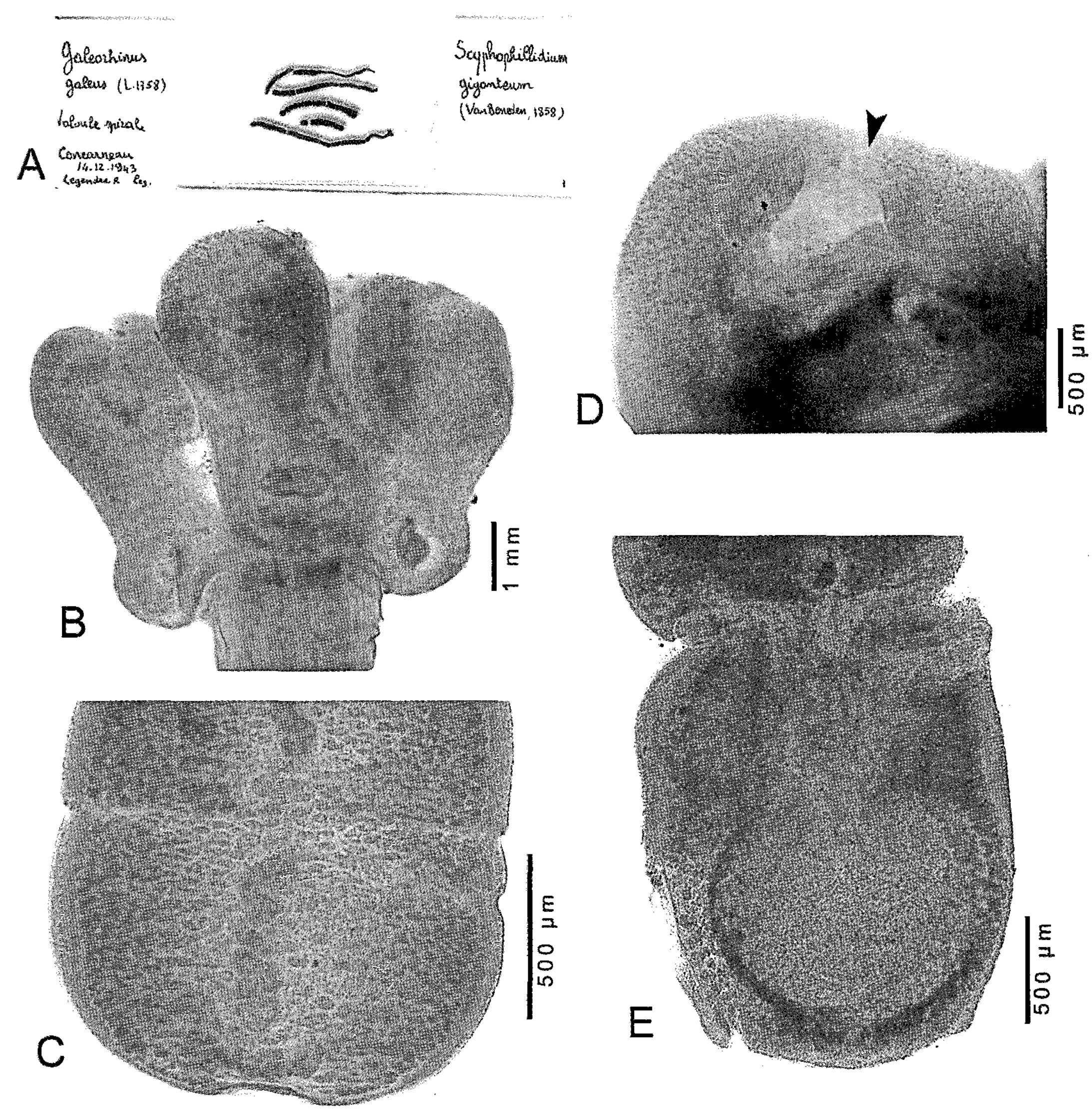

Fig. 158. Photomicrographs of *Scyphophyllidium giganteum* (Van Beneden, 1858) Woodland, 1927. A. Voucher (MNHN HEL 150). B. Scolex of voucher (LRP 7441; specimen prepared for SEM). C. Terminal proglottid of voucher (MNHN HEL 152). D. Bothridium of voucher (LRP 7441) (arrow indicates apical sucker). E. Terminal gravid proglottid of voucher (MNHN HEL 149).

end of proglottid. Uterine duct present. Vitellarium follicular, in two lateral fields, each field with 7–10 dorsal and 7–10 ventral columns of follicles, extending entire length of proglottid, interrupted by cirrus-sac. Eggs spindle-shaped, 156–172 long x 15–17 wide.

Remarks

Scyphophyllidium giganteum was originally described as *Anthobothrium giganteum* by Van Beneden (1858), then designated as the type species of *Scyphophyllidium* by Woodland (1927). Southwell (1930) synonymized *S. giganteum* with *Phyllobothrium giganteum* when he synonymized *Scyphophyllidum* with *Phyllobothrium*, but this synonymy was in general not followed by other authors (see Wardle and McLeod 1952). *Scyphophyllidium giganteum* does not possess the posteriorly bifid, foliose bothridia of *Phyllobothrium*. The description provided above for *S. giganteum* was prepared from information given in Woodland (1927), Euzet (1959) and data from Euzet's study specimens (MNHN Paris HEL 149–153).

Scyphyphyllidium giganteum differs from *S. uruguayense* in total length (95–120 mm vs. 155–258 mm), neck length (25–30 mm vs. 34–41 mm), and mature proglottid architecture (wider than long vs. wider than long to longer than wide).

Scyphophyllidium uruguayense Brooks, Marques, Perroni and Sidagis, 1999
(Figs. 159–160)

Taxonomic status: Valid.

Type Host: *Mustelus mento* (Cope, 1877), the Speckled smooth-hound.

Site of infection: Spiral valve.

Type locality: La Paloma, Uruguay (Fig. 159).

Type material: Holotype MNHG INV 25448; paratypes MNHG INV 25449–50, USNPC 88542 (Fig. 160A).

Materials examined: USNPC 88542 (Fig. 160A).

Etymology: The species is named for the country of Uruguay, its type locality.

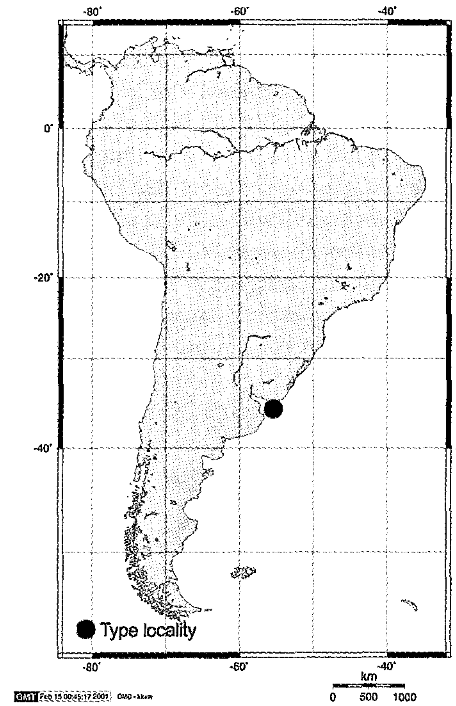

Fig. 159. Geographic distribution of *Scyphophyllidium uruguayense* Brooks, Marques, Perroni and Sidagis, 1999.

Description (modified from Brooks et al. [1999]).

Worms weakly craspedote, anapolytic, 155–258 mm long, comprised of 255–294 proglottids. Scolex 1.21–1.40 mm wide, comprising four globular bothridia and apical glandular mass of cells. Bothridia 572–890 (731, n=10) long x 572–731 (652, n=10) wide, with anterior but no posterior opening. Apical suckers 64–97 wide, positioned medially on anterior rim of each bothridium. Neck 34–41 mm long, scutellate; scutes 32–63 wide. Immature proglottids wider than long.

Mature proglottids 0.64–1.18 mm long x 1.52–2.13 mm wide. Testes 19–41 in diameter, 266–409 (369, n=24) in number; 43–104 (78, n=24) preporally, 80–135 (105, n=24) postporally, 143–236 (186, n=24) aporally. Cirrus-sac elliptical to irregularly shaped, 349–464 (392, n=20) long x 127–254 (163, n=20) wide, extending medially, 19–23% (22, n=20) of proglottid width; containing cirrus;

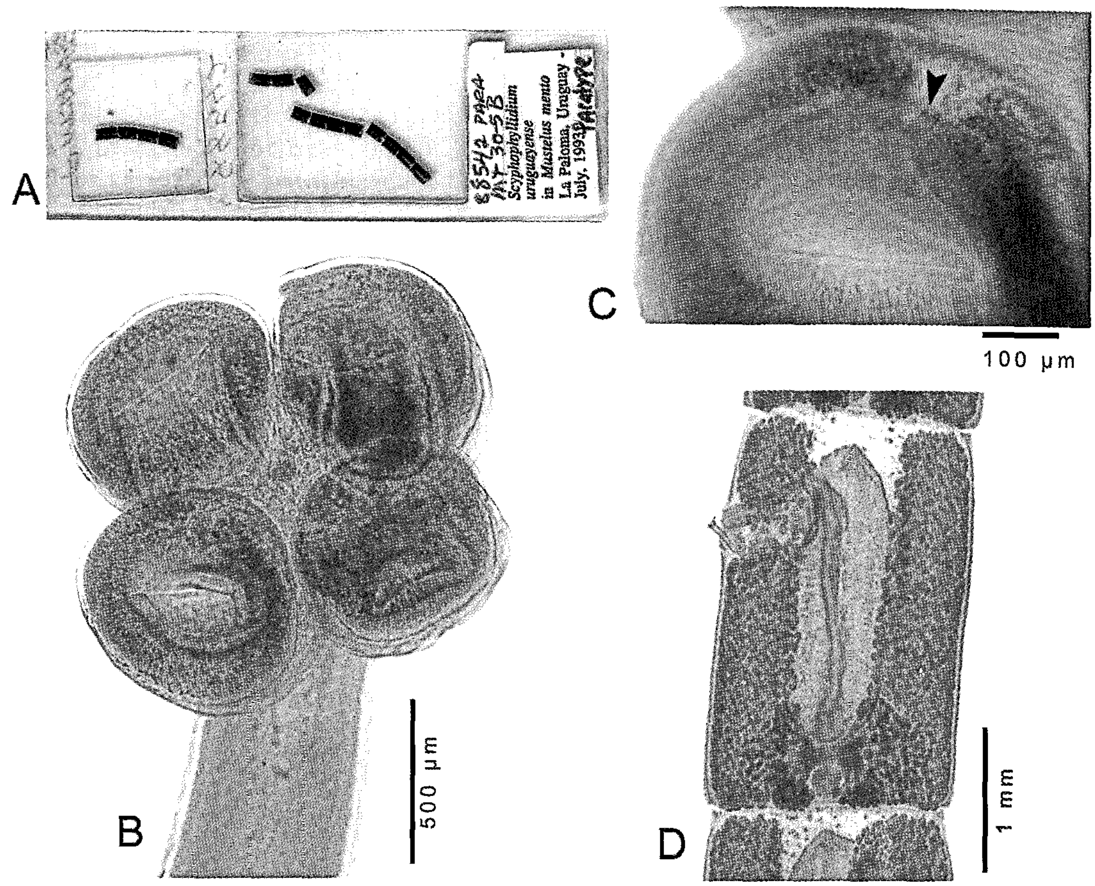

Fig. 160. Photomicrographs of *Scyphophyllidium uruguayense* Brooks, Marques, Perroni and Sidagis, 1999. A. Paratype slide (USNPC 88542). B. Scolex of paratype (USNPC 88542). C. Bothridium of paratype (USNPC 88542) (arrow indicates apical sucker). D. Gravid proglottid (USNPC 88542).

cirrus armed with spinitriches. Vas deferens convoluted; coils mediolateral to cirrus-sac poral to midline of proglottid. Genital atrium indistinct; genital pores irregularly alternating, 67–77% (72, n=20) from posterior end of proglottid; closer to anterior end in younger proglottids. Ovary near posterior end of proglottid, H-shaped in frontal view, tetralobed in cross-section; 1.18– 1.64 mm wide, extending 72–86% (79.5, n=20) of proglottid width. Vagina opening anterior to cirrus-sac, extending medially to midproglottid anterior to vas deferens, then posteriorly, convoluted immediately anterior to ovarian isthmus; terminal portion expanded into distinct seminal receptacle. Vaginal sphincter glandular extending length of cirrus-sac. Seminal receptacle distinct. Mehlis' gland prominent, 127–165 in diameter. Uterine duct extending anteriorly dorsal and poral to vagina, joining uterus near level of genital atrium, highly glandular, becoming expanded prior to appearance of eggs. Vitellarium follicular, vitelline follicles lateral, extending entire length of proglottid, reduced in number at level of cirrus-sac and ovary, occasionally overlapping lateral ovarian digits; 32–64 (48, n=100) in diameter.

Gravid proglottids 0.98–3.3 mm long x 1.36–2.51 mm wide; changing from wider than long to longer than wide. Cirrus-sac elliptical to irregularly shaped, 413–508 (467, n=20) long x 222–273 (249, n=20) wide, extending medially 19–31% (23%, n=20) of proglottid width; cirrus armed with spinitriches. Vas deferens convoluted; coils medial to cirrus-sac, poral to midline of proglottid. Genital atrium indistinct; genital pores irregularly alternating 66–77% (71%, n=20) from posterior end of proglottid, closer to anterior end in younger proglottids. Ovary at posterior end of proglottid, H-shaped in frontal view, tetralobed in cross-section; 1.12–1.91 mm wide, extending 62–84% (77%, n=20) of proglottid width. Uterus ventral, saccate, lacking diverticula but with occasional lateral folds; occupying available pre-ovarian space. Vitellarium follicular, lateral; vitelline follicles extending entire length of proglottid; follicles from each side of proglottid extending medially; reduced in number at level of cirrus-sac and ovary, occasionally overlapping lateral ovarian digits. Vitelline follicles 32–64 in diameter, Excretory ducts in dorsal and ventral pair, ventral ducts medial to dorsal ducts; terminal genitalia passing between osmoregulatory ducts.

Remarks

Brooks et al. (1999) provided a detailed discussion comparing their specimens of *Scyphophyllidium uruguayense* to the morphological data for *S. giganteum* provided by Woodland (1927), Riser (1955), and Euzet (1959). Comparisons made in this monograph have been restricted to specimens of *S. giganteum* taken from European waters. Until more detailed study of Riser's specimens of *Scyphophyllidium* can be made, the assumption that they are conspecific with *S. giganteum* should not be made. Indeed, Brooks et al. (1999) postulated that given the geographic and host differences, the European specimens of *S. giganteum*, Riser's specimens of *S. giganteum*, and the specimens of *S. uruguayense* represented three separate species.

Scyphophyllidium uruguayense and *S. giganteum* are morphologically similar in a number of respects, inluding possession of an anapolytic proglottid development, and possession of large, globular bothridia. S. *uruguayense* differs from *S. giganteum* in total length (155–258 mm vs. 95–120 mm), neck length (34–41 mm vs. 25–30 mm), and mature proglottid architecture (wider than long to longer than wide vs. wider than long).

Problematic species of *Scyphophyllidium*

Three additional species have been associated with the genus *Scyphophyllidium,* in addition to *S. giganteum* and *S. uruguayense*. One of these species is recognized as a valid member of *Paraorygmatobothrium* (see pg. 119). The remaining two are discussed below: one is associated with a larval form, and the other is considered a *nomen dubium.*

Scyphophyllidium arabiansis* Shinde and Chincholikar, 1977 *nomen dubium

Scyphophyllidium arabiansis was superficially described by Shinde and Chincholikar (1977) from small worms collected from a stingray, *Trygon* sp. [sic]. The species was collected from Ratnagiri, Maharashtra, India. The scolex is described as being 240 long by 160 wide. The illustrations of the species are of poor quality. The bothridia appear to be uniloculate, without an apical sucker (described as sucker-like and sessile by Shinde and Chincholikar [1977b]). The terminal proglottids are also small in size, measuring less than 100 mm in length. The placement of *S. arabiansis* in the Tetraphyllidea is questionable, and this species may in fact be allied more closely to the Lecanicephalidea. Given that the specific identification for the type host of *S. arabiansis* is not known, and use of the description to identify specimens to species would be difficult, it should be considered a *nomen dubium.*

Scyphophyllidium pruvoti* (Guiart, 1933) Joyeux and Baer, 1936 *incertae sedis

This species was originally described by Guiart (1933) as *Diplobothrium pruvoti* Guiart, 1933 from cestode larvae taken from the European squid, *Loligo vulgaris* (Lamarck, 1798). This larval species was transferred to *Scyphophyllidium* by Joyeux and Baer (1936). The illustrations provided by Guiart (1933) suggest a worm that is similar in morphology to *P. loliginis*, thus *S. pruvoti* may actually be a larva of *Clistobothrium.* Given that *Diplobothrium* is a synonym of *Dinobothrium,* this larval species should be referred to as *S. pruvoti,* but considered *incertae sedis.*

This monograph is an attempt to provide a comprehensive treatment of the Phyllobothriidae. While only the type genus, *Phyllobothrium*, is considered to be an unambiguously valid member of the family, 16 other genera are considered to represent at least provisional members of the family. Ten of these (*i.e., Clistobothrium, Crossobothrium, Marsupiobothrium, Monorygma, Nandocestus, Orectolobicestus, Orygmatobothrium, Paraorygmatobothrium, Ruhnkecestus,* and *Scyphophyllidium*) are formally treated in this monograph. A total of 48 species were found to be valid within the 11 monographed genera. Additional accounts were provided for all problematic species in these 11 genera. The remaining six genera, *i.e., Bibursibothrium, Calyptrobothrium, Cardiobothrium, Doliobothrium, Flexibothrium,* and *Thysanocephalum* while recognized as provisional members of the family, were not treated in full. The primary reason that these genera are considered to be provisional members of the family is that their monophyly relative to *Phyllobothrium,* and also to one another, remains to be tested. Nonetheless, these genera share a number of features in common. With the exception of *Calyptrobothrium* and *Nandocestus*, they are parasitic in sharks. In all 17 of these genera, the uterus extends to near the level of the cirrus-sac, rather than to near the anterior margin of the proglottid as seen in most other non-hooked tetraphyllidean genera. In addition, in most of the species in these 17 genera, the cirrus-sac is conspicuously anterior in position. However, it should be noted that none of these features is unique among tetraphyllidean taxa and thus the utility of these features in circumscribing a truly monophyletic assemblage of genera, even in combination, is yet to be determined. Clearly, as additional phylogenetic information becomes available, the concept of the family will likely change. But, it is hoped that this monograph will serve as a starting point for the testing of an explicit hypothesis regarding membership in the Phyllobothriidae.

DISCUSSION

Taxonomic and Phylogenetic Considerations

Phylogenetic investigations that have included phyllobothriid genera have been conducted utilizing both morphological and molecular data. Caira et al. (1999) initiated a study of the phylogenetic relationships of the tetraphyllideans, and Caira et al. (2001) expanded that study to include 127 taxa. In the latter paper, a total of 157 morphological characters were coded for analysis. No evidence for the monophyly of the Phyllobothriidae sensu lato was found in these analyses. With respect to the 17 valid and provisionally valid phyllobothriid genera, both of the Caira et al. treatements included representation of all but *Scyphophyllidium*, *Nandocestus*, *Doliobothrium*, *Orectolobicestus*, *Ruhnkecestus*, the latter four of which had not yet been described. In both cases, the genera treated here occurred independently in three different regions on the resulting trees. *Clistobothrium* grouped wtih the taxa that were ultimately assigned to the Rhinebothriidea by Healy et al. (2009), *Paraorygmatobothrium*, *Crossobothrium*, *Monorygma*, *Orygmatobothrium*, *Thysanocephalum*, *Phyllobothrium*, and *Calyptrobothrium* grouped together, but along with the genera *Chimaerocestos*, *Dinobothrium*, and *Gastrolecithus*, which were explicitly here excluded from the Phyllobothriidae. The relationships of the remaining four genera (*i.e.*, *Bibursibothrium*, *Marsupiobothrium*, *Cardiobothrium*, and *Flexibothrium*) were unresolved relative to the tetraphyllidean and lecanicephalidean taxa. The analyses of Caira et al. were among the first to suggest that the rhinebothriidean taxa (then the Rhinebothriidae) might benefit from transfer to their own order.

This action was formally taken by Healy et al. (2009) who erected the order Rhinebothriidea and formally transferred a number of genera previously recognized as phyllobothriids to that order. That work represented a very important step in the taxonomic reorganition of the Phyllobothriidae. The assemblage of genera transferred to the new order included *Anthocephalum*, *Echeneibothrium*, *Rhabdotobothrium*, *Rhinebothrium*, *Rhinebothroides*, *Rhodobothrium*, *Scalithrium*, and *Spongiobothrium*. In addition, the Rhinebothriidea may potentially house the genera *Biotobothrium*, *Clydonobothrium*, *Escherbothrium*, *Notomegarhynchus*, *Pararhinebothroides*, *Pentaloculum*, *Phormobothrium*, *Pseudanthobothrium,* and *Tritaphros* (see Healy et al. 2009, and Appendix 1).

Another potential suite of taxonomic associations exists among some species considered here as *incertae sedis* taxa. Wojciechowska (1991a) described *Phyllobothrium georgiense*, *P. arctowskii*, *P. rakusai*, and *P. siedleckii* from Antarctic skates. These species were transferred to *Anthocephalum* (see Rocka 2003; Rocka and Zdzitowiecki 1998), but Ruhnke and Seaman (2009) provided evidence against that taxonomic action. In these four species, the vitelline follices are not interrupted by the ovary, and approach the midline of the proglottid. It is likely that these species will ultimately be placed in a new generic entity within either the Rhinebothriidea or Tetraphyllidea.

A number of other taxa considered as *incertae sedis* taxa here are also likely species within the Rhinebothriidea. For example, *Phyllobothrium auricula*, *P. biacetabulatum*, *P. discopygi*, *P. foliatum*, *P. loculatum*, *P. microsomum*, and *P. myliobatidis* all possess bothridial marginal loculi, and are likely members of the Rhinebothriidea. Furthermore, *P. auricula*, *P. discopyge*, *P. foliatum*, and *P. loculatum* also exhibit dorsal/ventral fusion of the bothridia. These latter four species should be critically compared, as they too may constitute a new generic entity within the Rhinebothriidea. Two other *incertae sedis* species that are candidates for inclusion in the Rhinebothriidea are *P. ptychocephalum* and *P. pastinacae*.

An interesting aspect of the existing and additional potential members of the Rhinebothriidea is their association with batoid, rather than selachimorph (shark), hosts. In fact, current data are beginning to suggest that an expanded concept of the Phyllobothriidae is likely to include taxa almost exclusively parasitic in sharks. The question, however, is which genera are truly allied with *Phyllobothrium*? It is useful to consider the group of genera that appear to be emerging.

For example, there exists a cluster of genera that is characterized by the presence of serrated spinitriches on their proximal and/or distal bothridial surfaces. This group includes the following genera treated here: *Nandocestus*, *Orectolobicestus*, *Paraorygmatobothrium*, *Ruhnkecestus*, as well as two genera not fully treated here, *Doliobothrium* and *Thysanocephalum*. Preliminary molecular work has been conducted that has included several of these genera. For example, Greenwood (2007) found phylogenetic affinities between species of *Paraorygmatobothrium* and *Thysanocephalum* based on regions of the 28S rDNA.

Although not treated here, morphological evidence suggests a phylogenetic kinship between the lamniform cestode genera *Ceratobothrium*, *Dinobothrium* and *Gastrolecithus*. A pair of muscular horns are located on the lateral edges between the loculi of species in these genera. In addition, in both *Ceratobothrium* and *Dinobothrium*, the vagina extends to the anterior extremity of the proglottid. A suprageneric taxon might be appropriate to erect in order to house these three genera.

Host Associations and Biodiversity

A listing of host species for the 11 formally fully treated genera is provided in Appendix 2. With the exception of *Nandocestus* *guariticus*, the remaining species are parasitic in sharks. In combination, these species parasitize host sharks of five orders and ten families. There are several host-parasite taxonomic correspondences apparent within this list. For example, species of *Clistobothrium* are restricted to sharks of the family Lamnidae, and species of *Monorygma* are restricted to species of the Somniosidae. The three valid species of *Phyllobothrium* are parasitic in triakid sharks. Two of the three species of *Crossobothrium* are parasitic in hexanchiform sharks. Species of *Orygmatobothrium* are presently restricted to triakid sharks of the genus *Mustelus* Linck 1790.

From a biodiversity standpoint, the most interesting host associations are exhibited by the cestode lineage comprised of the genera *Nandocestus*, *Orectolobicestus*, *Paraorygmatobothrium*, and *Ruhnkecestus*. Again, with the exception of *N. guariticus*, these species are exclusively found in sharks (Appendix 2). Species of *Paraorygmatobothrium* have been reported from sharks of five families. Species of this genus have been reported from 76% (16 of 21) of the carcharhiniform host species given in Appendix 2. Given the host diversity in this order, the known number of *Paraorygmatobothrium* species is likely to be a gross underestimation of its overall diversity. For example, 18 species of *Paraorygmatobothrium* have now been reported from 16 carcharhiniform species of the families Carcharhinidae, Hemigaleiidae, and Triakidae. Froese and Pauley (2009) listed 91 species in these three shark families. Furthermore, three species of *Paraorygmatobothrium* have been found in two species of *Mustelus*, and two species from sharks of the genus *Triakis* Müller and Henle 1839. Agbayani (2006b, c) listed 27 valid species of *Mustelus* and five species of *Triakis*. Surely, a number of new species of *Paraorygmatobothrium* await discovery from the 70 candidate host species for which no published data are available. As previously noted, cestodes that are morphologically consistent with the diagnosis of *Paraorygmatobothrium* have been observed from six species of *Carcharhinus* and two species of *Sphyrna* (pers. obs.).

The genera considered members or likely members of the Rhinebothriidea are at present exclusively parasitic in batoid fishes (see Appendix 1). For example, the nine species of *Anthocephalum* (see Ruhnke and Seaman 2009) have thus far been reported from the batoid genera *Dasyatis* (Garman, 1880), *Torpedo* Duméril, 1806, and *Urobatis* Garman, 1913. Ruhnke and Seaman (2009) noted that the present species diversity of *Anthocephalum* was found in a total of seven species in the above genera, representing just 10% of the species diversity in those genera. Ruhnke and Seaman (2009) concluded that if past patterns of the host-specificity of tetraphyllideans were assumed, there could be between 60 to 80 additional species of *Anthocephalum* hosted by species in just these three batoid genera. Healy et al. (2009) included four putatively (unnamed) rhinebothriid genera in their phylogenetic analysis of the new order. Obviously, the diversity of the Rhinebothriidea is also poorly understood.

Conclusions

The primary objective of this monograph was to provide information on the taxonomic status of all genera that have been associated with the Phyllobothriidae. In addition, detailed descriptions were provided for valid species in 11 of these genera, 10 of which are hosted by sharks. Information was provided for the problematic species in these genera in order to facilitate future research on them. Eighteen genera from batoid fishes are either valid, probable or *genera inquirenda* members of the Rhinebothriidea. There is no evidence for the monophyly of the remaining genera from sharks, although morphological evidence indicates that monophyletic subsets exist within this larger group.

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Appendix 1. Generic membership in the Phyllobothriidae.

GENUS	(STATUS)	TYPE SPECIES	TYPE HOST SPECIES
Phyllobothriidae (*sensu stricto*)			
	Phyllobothrium Van Beneden, 1850	*Phyllobothrium lactuca* Van Beneden, 1850	*Mustelus mustelus* (L., 1758)
Phyllobothriidae (provisional, treated)			
	Clistobothrium Dailey and Vogelbein, 1990	*Clistobothrium carcharodoni* Dailey and Vogelbein, 1990	*Carcharodon carcharias* (L., 1758)
	Crossobothrium Linton, 1889	*Crossobothrium laciniatum* Linton, 1889	*Carcharias taurus* (Rafinesque, 1810)
	Marsupiobothrium Yamaguti, 1952	*Marsupiobothrium alopias* Yamaguti, 1952	*Alopias vulpinus* (Bonnaterre, 1788)
	Monorygma Diesing, 1863	*Monorygma perfectum* (Van Beneden, 1853) Diesing, 1863	*Somniosus microcephalus* (Bloch and Schneider, 1801)
	Nandocestus Reyda, 2008	*Nandocestus guariticus* (Marques, Brooks and Lasso, 2001) Reyda, 2008	*Paratrygon aiereba* Müller and Henle, 1841
	Orectolobicestus Ruhnke, Caira and Carpenter, 2006	*Orectolobicestus tyleri* Ruhnke, Caira and Carpenter, 2006	*Chiloscyllium punctatum* Müller and Henle, 1838
	Orygmatobothrium Diesing, 1863	*Orygmatobothrium musteli* (Van Beneden, 1850) Diesing, 1863	*Mustelus mustelus* (L., 1758)
	Paraorygmatobothrium Ruhnke, 1994	*Paraorygmatobothrium prionacis* (Yamaguti, 1934) Ruhnke, 1994	*Prionace glauca* (L., 1758)
	Ruhnkecestus Caira and Durkin, 2006	*Ruhnkecestus latipi* Caira and Durkin, 2006	*Scoliodon laticaudus* Müller and Henle, 1838
	Scyphophyllidium Woodland, 1927	*Scyphophyllidium giganteum* (Van Beneden, 1858) Woodland, 1927	*Galeorhinus galeus* (L., 1758)
Phyllobothriidae (provisional, not treated)			
	Bibursibothrium McKenzie and Caira, 1998	*Bibursibothrium gouldeni* McKenzie and Caira, 1998	*Pristiophorus cirratus* (Latham, 1794)
	Calyptrobothrium Monticelli, 1893	*Calyptrobothrium riggii* Monticelli, 1893	*Torpedo marmorata* Risso, 1810
	Cardiobothrium McKenzie and Caira, 1998	*Cardiobothrium beveridgei* McKenzie and Caira, 1998	*Pristiophorus cirratus* (Latham, 1794)
	Doliobothrium Caira, Malek and Ruhnke, 2010	*Doliobothrium haselii* Caira, Malek and Ruhnke, 2010	*Carcharhinus* cf. *dussumieri* (Müller and Henle, 1839)
	Flexibothrium McKenzie and Caira, 1998	*Flexibothrium ruhnkei* McKenzie and Caira, 1998	*Pristiophorus cirratus* (Latham, 1794)
	Thysanocephalum Linton, 1889	*Thysanocephalum thysanocephalum* (Linton, 1889) Braun, 1900	*Galeocerdo cuvier* (Pèron and Lesueur, 1822)
Phyllobothriidae (*nomina dubia*)			
	Aocobothrium Mola, 1907	*Aocobothrium carrucci* Mola, 1907	unknown teleost
	Dittocephalus Parona, 1887	*Dittocephalus linstowi* Parona, 1887	*Squalus* sp.
	Hoaleshwaria Shinde and Chincholikar, 1975	*Hoaleshwaria marathwadensis* Shinde and Chincholikar, 1975	*Trygon* sp.
	Phanobothrium Mola, 1907	*Phanobothrium monticellii* Mola, 1907	"big fish"
	Shindeobothrium Shinde and Chincholikar, 1975	*Shindeobothrium indica* Shinde and Chincholikar, 1975	*Trygon* sp.
Phyllobothriidae (*nomen ad interim*)			
	Phyllobothrideum Olsson, 1867		
Phyllobothriidae (*genera Inquirenda*)			
	Bilocularia Obersteiner, 1914	*Bilocularia hyperapolytica* Obersteiner, 1914	*Centrophorus granulosus* (Bloch and Schneider, 1801)
	Biporophyllaeus Subramaniam, 1939	*Biporophyllaeus madrassensis* Subramaniam, 1939	*Chiloscyllium griseum* Müller and Henle, 1838
	Cyatocotyle Mola, 1908	*Cyatocotyle marchesettii* Mola, 1908	*Carcharodon carcharias* (L., 1758)
	Kowsalyabothrium Muralidhar, Shinde and Jadhav, 1987	*Kowsalyabothrium indirapriyadarshinii* Muralidhar, Shinde and Jadhav, 1987	*Trygon centrura* [sic]
	Maccallumiella Yamaguti, 1959	*Maccallumiella patina* (MacCallum, 1921) Yamaguti, 1959	"Ikan patin"
	Mastacembellophyllaeus Shinde and Chincholikar, 1977	*Mastacembellophyllaeus nandedensis* Shinde and Chincholikar, 1977	*Masttacembellus armatus* (Lacepède, 1800)

Appendix 1. Continued.

GENUS (STATUS)	TYPE SPECIES	TYPE HOST SPECIES
Phyllobothriidae (*genera inquirenda*) continued.		
Pillersium Southwell, 1927	*Pillersium owenium* Southwell, 1927	*Urogymnus asperrimus* (Bloch and Schneider, 1801)
Pithophorus Southwell, 1925	*Pithophorus tetraglobus* (Southwell, 1912) Southwell, 1925	*Rhynchobatus djiddensis* (Forsskål, 1775)
Polipobothrium Mola, 1908	*Polipobothrium vaccarii* Mola, 1908	*Cetorhinus maximus* (Gunnerus, 1765)
Phyllobothriidae (*incertae sedis*)		
Anindobothrium Marques, Brooks and Lasso, 2001	*Anindobothrium anacolum* (Brooks, 1977) Marques, Brooks and Lasso, 2001	*Himantura schmardae* (Werner, 1904)
Anthobothrium Van Beneden, 1850	*Anthobothrium cornucopia* Van Beneden, 1850	*Galeorhinus galeus* (L., 1758)
Carpobothrium Shipley and Hornell, 1906	*Carpobothrium chiloscyllii* Shipley and Hornell, 1906	*Chiloscyllium indicum* (Gmelin, 1789)
Caulobothrium Baer, 1948	*Caulobothrium longicolle* (Linton, 1890) Baer, 1948	*Myliobatis freminvillii* Lesueur, 1824
Caulopatera Cutmore, Bennett and Cribb, 2010	*Caulopatera pagei* Cutmore, Bennett and Cribb, 2010	*Chiloscyllium punctatum* Müller and Henle, 1838
Ceratobothrium Monticelli, 1892	*Ceratobothrium xanthocephalum* Monticelli, 1892	*Lamna nasus* (Bonnaterre, 1788)
Chimaerocestos Williams and Bray, 1984*	*Chimaerocestos prudhoei* Williams and Bray, 1984	*Rhinochimaera atlantica* Holt and Byrne, 1909
Dinobothrium Van Beneden, 1889	*Dinobothirum septaria* Van Beneden, 1889	*Lamna nasus* (Bonnaterre, 1788)
Gastrolecithus Yamaguti, 1952	*Gastrolecithus planus* (Linton, 1922) Yamaguti 1952	*Cetorhinus maximus* (Gunnerus, 1765)
Guidus Ivanov, 2006	*Guidus argentienense* Ivanov, 2006	*Bathyraja brachyurops* (Fowler, 1910)
Mixophyllobothrium Shinde and Chincholikar, 1980	*Mixophyllobothrium okamuri* Shinde and Chincholikar, 1980	*Pastinachus sephen* (Forsskål, 1775)
Myzocephalus Shipley and Hornell, 1906	*Myzocephalus narinari* Shipley and Hornell, 1906	*Aetobatis narinari* (Euphrasen, 1790)
Myzophyllobothrium Shipley and Hornell, 1906	*Myzophyllobothrium rubrum* Shipley and Hornell, 1906	*Aetobatis narinari* (Euphrasen, 1790)
Pelichnobothrium Monticelli, 1889	*Pelichnibothrium speciosum* Monticelli, 1889	*Alepisaurus ferox* Lowe, 1833
Rhoptrobothrium Shipley and Hornell, 1906	*Rhoptrobothrium myliobatidis* Shipley and Hornell, 1906	*Aetomylaeus maculatus* (Gray, 1834)
Trilocularia Olsson, 1867	*Trilocularia gracilis* Olsson, 1870	*Squalus acanthias* L., 1758
Zyxibothrium Hayden and Campbell, 1981	*Zyxibothrium kamienae* Hayden and Campbell, 1981	*Malacoraja senta* (Garman, 1885)
Rhinebothriidea (confirmed genera)		
Anthocephalum Linton, 1890	*Anthocephalum gracile* Linton, 1890	*Dasyatis centroura* (Mitchill, 1815)
Echeneibothrium Van Beneden, 1850	*Echeneibothrium variabile* Van Beneden, 1850	*Raja clavata* L., 1758
Rhabdotobothrium Euzet, 1953	*Rhabdotobothrium dollfusi* Euzet, 1953	*Dasyatis pastinaca* (L., 1758)
Rhinebothrium Linton, 1890	*Rhinebothrium flexile* Linton, 1890	*Dasyatis centroura* (Mitchill, 1815)
Rhinebothroides Mayes, Brooks and Thorson, 1981	*Rhinebothroides moralarai* (Brooks and Thorson, 1976) Mayes, Brooks and Thorson, 1981	*Potamotrygon magdalenae* (Duméril, 1865)
Rhodobothrium Linton, 1889	*Rhodobothrium pulvinatum* Linton, 1889	*Dasyatis centroura* (Mitchill, 1815)
Scalithrium Ball, Neifar, and Euzet, 2003	*Scalithrium minimum* (Van Beneden, 1850) Ball, Neifar, and Euzet, 2003	*Dasyatis pastinaca* (L., 1758)
Spongiobothrium Linton, 1889	*Spongiobothrium variabile* Linton, 1889	*Dasyatis centroura* (Mitchill, 1815)
Rhinebothriidea (provisional members)		
Biotobothrium Tan, Zhou and Yang, 2009	*Biotobothrium platyrhina* Tan, Zhou and Yang, 2009	*Platyrhina sinensis* Bloch and Schneider, 1801
Clydonobothrium Euzet, 1959	*Clydonobothrium elegantissimum* (Lönnberg, 1889) Euzet, 1959	*Dipturus batis* (L., 1758)
Escherbothrium Berman and Brooks, 1994	*Escherbothrium molinae* Berman and Brooks, 1994	*Urotrygon chilensis* (Günther, 1872)

Appendix 1. Continued.

GENUS (STATUS)	TYPE SPECIES	TYPE HOST SPECIES
Rhinebothriidea (provisional members) continued		
Notomegarhynchus Ivanov and Campbell, 2002	*Notomegarhynchus navonae* Ivanov and Campbell, 2002	*Atlantoraja castelnaui* (Miranda Ribeiro, 1907)
Pararhinebothroides Zamparo, Brooks and Barriga, 1999	*Pararhinebothroides hobergi* Zamparo, Brooks and Barriga, 1999	*Urobatis tumbesensis* (Chirichigno and McEachran, 1979)
Pentaloculum Alexander, 1963	*Pentaloculum macrocephalum* Alexander, 1963	*Typhlonarke aysoni* (Hamilton, 1902)
Phormobothrium Alexander, 1963	*Phormobothrium affine* (Olsson, 1866) Alexander, 1963	*Amblyraja radiata* (Donovan, 1808)
Pseudanthobothrium Baer, 1956	*Pseudanthobothrium hanseni* Baer, 1956	*Amblyraja radiata* (Donovan, 1808)
Tritaphros Lönnberg, 1889	*Tritaphros retzii* Lönnberg, 1889	*Raja clavata* L., 1758
Rhinebothriidea (*incertae sedis*)		
Shindeiobothrium Jadhav, Shinde and Deshmukh, 1981	*Shindeiobothrium karbharae* Jadhav, Shinde and Deshmukh, 1981	*Dasyatis zugei* (Müller and Henle, 1841)
Serendipidae *sensu stricto*		
Duplicibothrium Williams and Campbell, 1978	*Duplicibothrium minutum* Williams and Campbell, 1978	*Rhinoptera bonasus* (Mitchill, 1815)
Glyphobothrium Williams and Campbell, 1977	*Glyphobothrium zwerneri* Williams and Campbell, 1977	*Rhinoptera bonasus* (Mitchill, 1815)
Serendipidae (*genera inquirenda*)		
Myliobatibothrium Shinde and Mohekar, 1983	*Myliobatibothrium alii* Shinde and Mohekar, 1983	*Aetomylaeus nichofii* (Bloch and Schneider, 1801)
Tiarabothrium Shipley and Hornell, 1906	*Tiarabothrium javanicum* Shipley and Hornell, 1906	*Rhinoptera javanica* Müller and Henle, 1841
Phyllobothriid genus *nomen ad interim*		
Phyllobothrideum Olsson, 1866	*Phyllobothrideum acanthiaevulgaris* Olsson, 1866	*Squalus acanthias* L., 1758
Phyllobothriid genera that should be considered synonyms of other tetraphyllidean or rhinebothriidean genera		
Diplobothrium Van Beneden, 1889	*Diplobothrium simile* Van Beneden, 1889	*Lamna nasus* (Bonnaterre, 1788)
Inermiphyllidium Riser, 1955	*Inermiphyllidium pulvinatum* (Linton, 1890) Riser, 1955	*Dasyatis centroura* (Mitchill, 1815)
Prionacestus Mete and Euzet, 1996	*Prionacestus bipartitus* Mete and Euzet, 1996	*Prionace glauca* (L., 1758)
Proboscidosaccus Gallien, 1949	*Proboscidosaccus enigmaticus* Gallien, 1949	*Mactra solida* (L., 1758)
Reesium Euzet, 1955	*Reesium paciferum* (Sproston, 1948) Euzet, 1955	*Cetorhinus maximus* (Gunnerus, 1765)
Sphaerobothrium Euzet, 1959	*Sphaerobothrium lubeti* Euzet, 1959	*Myliobatis aquila* (L., 1758)
Urogonoporus Lühe, 1901	*Urogonoporus armatus* Lühe, 1901	*Squalus acanthias* L., 1758

* classified by Williams and Bray (1984) in the Chimaerocestidae, but included for its similarities to other phyllobothriid taxa

Appendix 2. Status of species names associated with monographed taxa.

SPECIES NAME	STATUS	REFERENCE
Anthocephalus rudicornis Drummond, 1839	larval form; *species inquirenda*	Drummond (1839)
Anindobothrium guariticus Marques, Brooks and Lasso, 2001	synonym of *Nandocestus guariticus* Marques, Brooks and Lasso, 2001	Marques et al. (2001)
Anthobothrium crispum Shipley and Hornell, 1906	homonym of *Tetrabothrium (Anthobothrium) crispum* Molin, 1858	Shipley and Hornell (1906)
Anthobothrium dipsadomorphi (Shipley, 1900) Southwell, 1925	synonym of *Phyllobothrium dipsadomorphi* Shipley, 1900	Southwell (1925)
Anthobothrium exiguum Yamaguti, 1935	replacement name for *Anthobothrium parvum* Yamaguti, 1934; synonym of *Paraorygmatobothrium exiguum* (Yamaguti, 1935) Ruhnke, 1994	Yamaguti (1935)
Anthobothrium floraformis Southwell, 1912	synonym of *Paraorygmatobothrium floraformis* (Southwell, 1912) n. comb.	Southwell (1912)
Anthobothrium giganteum Van Beneden, 1858	synonym of *Scyphophyllidium giganteum* (Van Beneden, 1858) Woodland, 1927	Van Beneden (1858)
Anthobothrium minutum Guiart, 1935	synonym of *Paraorygmatobothrium prionacis* (Yamaguti, 1934) Ruhnke, 1994	Guiart (1935)
Anthobothrium musteli Van Beneden, 1850 (pro parte)	synonym of *Paraorygmatobothrium musteli* (Van Beneden, 1850) n. comb.	Van Beneden (1850)
Anthobothrium musteli Van Beneden, 1850 (pro parte)	synonym of *Orygmatobothrium musteli* Van Beneden, 1850	Van Beneden (1850)
Anthobothrium panjadi Shipley, 1909	replacement name for *Phyllobothrium crispum* Shipley and Hornell, 1906	Shipley (1909)
Anthobothrium parvum Yamaguti, 1934	homonym of *Anthobothrium parvum* Stossich, 1895	Yamaguti (1934)
Anthobothrium perfectum Van Beneden, 1853	synonym of *Monorygma perfectum* (Van Beneden, 1853) Diesing, 1863	Van Beneden (1853)
Anthobothrium wyatti Leiper and Atkinson, 1914	synonym of *Orygmatobothrium wyatti* (Leiper and Atkinson, 1914) Southwell, 1925 *nomen dubium*	Leiper and Atkinson (1914)
Anthocephalum arctowskii (Wojciechowska, 1991) Rocka and Zdzitowiecki, 1998	synonym of *Phyllobothrium arctowskii* Wojciechowska, 1991	Rocka and Zdzitowiecki (1998)
Anthocephalum centrurum (Southwell, 1925) Ruhnke, 1994	synonym of *Anthocephalum gracile* Linton, 1890	Ruhnke (1994)
Anthocephalum gracile (Wedl, 1855) Ruhnke, 1994	homonym of *Anthocephalum gracile* Linton, 1890; *Anthocephalum wedli* nom. nov.	Ruhnke (1994)
Anthocephalum gracile Linton, 1890	valid; type species	Linton (1890)
Anthocephalum kingae (Schmidt, 1979) Ruhnke and Seaman, 2009	valid	Ruhnke and Seaman (2009)
Anthocephalum rakusai (Wojciechowska, 1991) Rocka, 2003	synonym of *Phyllobothrium rakusai* Wojciechowska, 1991	Rocka (2003)
Anthocephalum siedlickii (Wojciechowska, 1991) Rocka and Zdzitowiecki, 1998	synonym of *Phyllobothrium siedlickii* Wojciechowska, 1991 *incertae sedis*	Rocka and Zdzitowiecki (1998)
Anthocephalum wedli nom. nov.	valid; replacement name for *Anthocephalum gracile* (Wedl, 1855) Ruhnke, 1994	see pg. 41
Bilocularia hyperapolytica Obersteiner, 1914	*species inquirenda*	Obersteiner (1914)
Calyptrobothrium riggi Monticelli, 1893	valid; type species	Monticelli (1893)
Caulopatera pagei Cutmore, Bennett and Cribb, 2010	valid	Cutmore et al. (2010)
Clistobothrium carcharodoni Dailey and Vogelbein, 1990	valid; type species	Dailey and Vogelbein (1990)
Clistobothrium montaukensis Ruhnke, 1993	valid	Ruhnke (1993)
Clistobothrium tumidum (Linton, 1922) Ruhnke, 1993	valid	Ruhnke (1993)
Crossobothrium angustum (Linton, 1889) Linton, 1901	synonym of *Paraorygmatobothrium angustum* (Linton, 1889) Ruhnke, 1996	Linton (1901)
Crossobothrium antonioi Ivanov, 2009	valid	Ivanov (2009)
Crossobothrium campanulatum Klaptocz, 1906	valid	Klaptocz (1906)
Crossobothrium dohrni (Oerley, 1885) Ruhnke, 1996	valid	Oerley (1885)
Crossobothrium filiforme (Yamaguti, 1952) Williams, 1968	synonym of *Paraorygmatobothrium filiforme* (Yamaguti, 1952) Ruhnke, 1996	Williams (1968)
Crossobothrium laciniatum Linton, 1889	valid; type species	Linton (1889)
Crossobothrium longicolle (Molin, 1858) Euzet, 1959	synonym of *Tetrabothrium longicolle* Molin, 1858 *incertae sedis*	Euzet (1959)
Crossobothrium pequeae Ivanov, 2009	valid	Ivanov (2009)
Crossobothrium prionacis (Yamaguti, 1934) Williams, 1968	synonym of *Paraorygmatobothrium prionacis* (Yamaguti, 1934) Ruhnke, 1994	Williams (1968)
Crossobothrium squali (Yamaguti, 1952) Williams, 1968	synonym of *Phyllobothrium squali* Yamaguti, 1952 *incertae sedis*	Williams (1968)
Crossobothrium triacis (Yamaguti, 1952) Williams, 1968	synonym of *Paraorygmatobothrium triacis* (Yamaguti, 1952) Ruhnke, 1996	Williams (1968)
Cysticercus physeteri Diesing, 1863	larval form; *nomen dubium*	Diesing (1863)
Dinobothrium septaria Van Beneden, 1889	valid; type species	Van Beneden (1889)
Diplobothrium pruvoti Guiart, 1933	synonym of *Scyphophyllidium pruvoti* (Guiart, 1933) Joyeux and Baer, 1936 *incertae sedis*	Guiart (1935)
Doliobothrium haselii Malek, Caira and Ruhnke, 2010	valid; type species	Malek et al. (2010)
Doliobothrium musculosum (Subhapradha, 1955) Malek, Caira and Ruhnke, 2010	valid	Malek et al. (2010)

Appendix 2. Continued.

SPECIES NAME	STATUS	REFERENCE
Guidus antarcticus (Wojciechowska, 1991) Ivanov, 2006	valid	Ivanov (2006)
Guidus argentinense Ivanov, 2006	valid; type species	Ivanov (2006)
Guidus awii (Rocka and Zdzitowiecki, 1998) Ivanov, 2006	valid	Ivanov (2006)
Hydatis delphinii Bosc, 1802	larval form; *species inquirenda*	Bosc (1802)
Marsupiobothrium alopias Yamaguti, 1952	valid; type species	Yamaguti (1952)
Marsupiobothrium antarcticum Wojciechowska, 1991	synonym of *Guidus antarcticus* (Wojciechowska, 1991) Ivanov, 2006	Wojciechowska (1991)
Marsupiobothrium awii Rocka and Zdzitowiecki, 1998	synonym of *Guidus awii* (Rocka and Zdzitowiecki, 1998) Ivanov, 2006	Rocka and Zdzitowiecki (1998)
Marsupiobothrium forte (Linton, 1924) Yamaguti, 1952	synonym of *Orygmatobothrium forte* Linton, 1924	Yamaguti (1952)
Marsupiobothrium gobelinus Caira and Runkle, 1993	*incertae sedis*	Caira and Runkle (1993)
Marsupiobothrium karbharii Deshmukh and Shinde, 1975	*incertae sedis*	Deshmukh and Shinde (1975)
Marsupiobothrium rhinobati Shinde and Deshmukh, 1980	*incertae sedis*	Shinde and Deshmukh (1980)
Marsupiobothrium rhynchobati Shinde and Deshmukh, 1980	*incertae sedis*	Shinde and Deshmukh (1980)
Monorygma chamissonii (Linton, 1905) Meggitt 1924	synonym of *Taenia chamissonii* Linton, 1905	Meggitt (1924)
Monorygma chlamydoselachi Lönnberg, 1898	*incertae sedis*	Lönnberg (1898)
Monorygma dentatum Linstow, 1907	*nomen dubium*	Linstow (1907)
Monorygma elegans Monticelli, 1890	*nomen nudum*	Monticelli (1890)
Monorygma galeocerdonis MacCallum, 1921	synonym of *Paraorygmatobothrium paulum* (Linton, 1897) n. comb.	MacCallum (1921)
Monorygma grimaldi (Moniez, 1889) Baylis, 1919	synonym of *Taenia grimaldi* Moniez, 1889	Baylis (1919)
Monorygma macquariae Johnston, 1937	valid	Johnston (1937)
Monorygma magnum (Hart, 1936) Williams, 1968	valid	Williams (1968)
Monorygma megacotyla Yamaguti, 1952	*incertae sedis*	Yamaguti (1952)
Monorygma perfectum (Van Beneden, 1853) Diesing, 1863	valid; type species	Diesing (1863)
Monorygma rotundum Klaptocz, 1906	*species inquirenda*	Klaptocz (1906)
Nandocestus guariticus (Marques, Brooks and Lasso, 2001) Reyda, 2008	valid; type species	Reyda (2008)
Orectolobicestus chiloscyllii (Subhapradha, 1955) Ruhnke, Caira and Carpenter, 2006	valid	Subhapradha (1955)
Orectolobicestus kelleyae Ruhnke, Caira and Carpenter, 2006	valid	Ruhnke et al. (2006b)
Orectolobicestus lorettae Ruhnke, Caira and Carpenter, 2006	valid	Ruhnke et al. (2006b)
Orectolobicestus mukahensis Ruhnke, Caira and Carpenter, 2006	valid	Ruhnke et al. (2006b)
Orectolobicestus randyi Ruhnke, Caira and Carpenter, 2006.	valid	Ruhnke et al. (2006b)
Orectolobicestus tyleri Ruhnke, Caira and Carpenter, 2006	valid	Ruhnke et al. (2006b)
Orygmatobothrium angustum Linton, 1889	synonym of *Paraorygmatobothrium angustum* (Linton, 1889) n. comb.	pg. 121
Orygmatobothrium crenulatum Linton, 1897	*species inquirenda*	Linton (1897)
Orygmatobothrium dohrni Oerley, 1885	synonym of *Crossobothrium dohrni* (Oerley, 1885) Ruhnke, 1996	Oerley (1885)
Orygmatobothrium forte Linton, 1924	*incertae sedis*	Linton (1924)
Orygmatobothrium juani Ivanov, 2008	valid	Ivanov (2008)
Orygmatobothrium longicolle Zschokke, 1889	*nomen dubium*	Zschokke (1889)
Orygmatobothrium musteli (Van Beneden, 1850) Diesing, 1863	valid; type species	Van Beneden (1850)
Orygmatobothrium paulum Linton, 1897	synonym of *Paraorygmatobothrium paulum* (Linton, 1897) n. comb.	Linton (1897)
Orygmatobothrium plicatum Yamaguti, 1934	*nomen dubium*	Yamaguti (1934)
Orygmatobothrium schmittii Suriano and Labriola, 2001	valid	Suriano and Labriola (2001)
Orygmatobothrium tetraglobum Southwell, 1912	synonym of *Pithophorus tetraglobus* (Southwell, 1912) Southwell, 1925 *species inquirenda*	Southwell (1912)
Orygmatobothrium velamentum Yoshida, 1917	*species inquirenda*	Yoshida (1917)
Orygmatobothrium versatile (Diesing, 1854) Diesing, 1863	synonym of *Orygmatobothrium musteli* Van Beneden, 1850	Diesing (1863)
Orygmatobothrium wyatti (Leiper and Atkinson, 1914) Southwell, 1925	*nomen dubium*; synonym of *Anthobothrium wyatti* Leiper and Atkinson, 1914	Southwell (1925)
Orygmatobothrium zschokkei Woodland, 1927	*nomen dubium*	Woodland (1927)

Appendix 2. Continued.

SPECIES NAME	STATUS	REFERENCE
Paraorygmatobothrium angustum (Linton, 1889) n. comb.	valid	pg. 121
Paraorygmatobothrium arnoldi Ruhnke and Thompson, 2006	valid	Ruhnke and Thompson (2006)
Paraorygmatobothrium bai Ruhnke and Carpenter, 2008	valid	Ruhnke and Carpenter (2008)
Paraorygmatobothrium barberi Ruhnke, 1994	valid	Ruhnke (1994a)
Paraorygmatobothrium exiguum (Yamaguti, 1935) Ruhnke, 1994	valid	Ruhnke (1994a)
Paraorygmatobothrium filiforme (Yamaguti, 1952) Ruhnke, 1996	valid	Ruhnke (1996a)
Paraorygmatobothrium floraformis (Southwell, 1912) n. comb.	valid	pg. 137
Paraorygmatobothrium janineae Ruhnke, Healy and Shapero, 2006	valid	Ruhnke et al. (2006a)
Paraorygmatobothrium kirstenae Ruhnke, Healy and Shapero, 2006	valid	Ruhnke et al. (2006a)
Paraorygmatobothrium leuci (Watson and Thorson, 1976) n. comb.	valid	pg. 146
Paraorygmatobothrium mobedii Malek, Caira and Haseli, 2010	valid	Malek et al. (2010)
Paraorygmatobothrium musteli (Van Beneden, 1850) n. comb.	valid	pg. 147
Paraorygmatobothrium nicaraguensis (Watson and Thorson, 1976) n. comb.	valid	pg. 149
Paraorygmatobothrium orectolobi (Butler, 1987) n. comb.	valid	pg. 151
Paraorygmatobothrium paulum (Linton, 1897) n. comb.	valid	pg. 153
Paraorygmatobothrium prionacis (Yamaguti, 1934) Ruhnke, 1994	valid; type species	Ruhnke (1994a)
Paraorygmatobothrium roberti Ruhnke and Thompson, 2006	valid	Ruhnke and Thompson (2006)
Paraorygmatobothrium rodmani Ruhnke and Carpenter, 2008	valid	Ruhnke and Carpenter (2008)
Paraorygmatobothrium sinuspersicense Malek, Caira and Haseli, 2010	valid	Malek et al. (2010)
Paraorygmatobothrium taylori Cutmore, Bennett and Cribb, 2009	valid	Cutmore et al. (2009)
Paraorygmatobothrium triacis (Yamaguti, 1952) Ruhnke, 1996	valid	Ruhnke (1996a)
Paraorygmatobothrium typicum (Subhapradha, 1955) n. comb	valid	pg. 163
Pelichnobothrium caudatum Zschokke and Heitz, 1914	larval form; *species inquirenda*	Zschokke and Heitz (1914)
Pelichnobothrium speciosum Monticelli, 1889	valid	Monticelli (1889)
Phyllobothrium angustum (Linton, 1889) Euzet, 1952	synonym of *Paraorygmatobothrium angustum* (Linton, 1889) n. comb.	Euzet (1952)
Phyllobothrium arctowskii Wojciechowska, 1991	*incertae sedis*	Wojciechowska (1991a)
Phyllobothrium auricula Van Beneden, 1858	*incertae sedis*	Van Beneden (1858)
Phyllobothrium biacetabulatum Yamaguti, 1960	*incertae sedis*	Yamaguti (1960)
Phyllobothrium blakei Shipley and Hornell, 1906	*incertae sedis*	Shipley and Hornell (1906)
Phyllobothrium blochii Srivastav and Srivastava, 1988	*incertae sedis*	Srivastav and Srivastava (1988)
Phyllobothrium bombayensis Srivastava and Capoor, 1979	*incertae sedis*	Srivastava and Capoor (1979)
Phyllobothrium brassica Van Beneden, 1871	*nomen nudum*	Van Beneden (1871)
Phyllobothrium brittanicum Williams, 1968	*incertae sedis*	Williams (1968a)
Phyllobothrium caudatum (Zschokke and Heitz, 1914) Southwell, 1925	synonym of *Pelichnobothrium caudatum* Zschokke and Heitz, 1914 *species inquirenda*	Zschokke and Heitz (1914)
Phyllobothrium centrurum Southwell, 1925	synonym of *Anthocephalum gracile* Linton, 1890	Southwell (1925)
Phyllobothrium chamissonii (Linton, 1905) Southwell and Walker, 1936	synonym of *Taenia chamissonii* Linton, 1905 *species inquirenda*	Southwell and Walker (1936)
Phyllobothrium chiloscyllii Subhapradha, 1955	synonym of *Orectolobicestus chiloscyllii* (Subhapradha, 1955) Ruhnke, Caira and Carpenter, 2006	Subhapradha (1955)
Phyllobothrium chlamydoselachi (Lönnberg, 1898) Southwell, 1925	synonym of *Monorygma chlamydoselachi* Lönnberg, 1898 *incertae sedis*	Southwell (1925)
Phyllobothrium compactum Southwell and Prashad, 1920	*incertae sedis*	Southwell and Prashad (1920)
Phyllobothrium crispum (Molin, 1858) Southwell, 1925	*nomen dubium*; synonym of *Tetrabothrium* (*Anthobothrium*) *crispum* Molin, 1858	Southwell (1925)
Phyllobothrium dagnallium Southwell, 1927	*incertae sedis*	Southwell (1927)
Phyllobothrium dasybati Yamaguti, 1934	*incertae sedis*	Yamaguti (1934)
Phyllobothrium delphinii (Bosc, 1802) Van Beneden, 1868	synonym of *Hydatis delphinii* Bosc, 1802 *species inquirenda*	Van Beneden (1868)
Phyllobothrium dentatum (Linstow, 1907) Schmidt, 1986	synonym of *Monorygma dentatum* Linstow, 1907 *nomen dubium*	Schmidt (1986)
Phyllobothrium dipsadomorphi Shipley, 1900	*nomen dubium*	Shipley (1900)

Appendix 2. Continued.

SPECIES NAME	STATUS	REFERENCE
Phyllobothrium discopygi Campbell and Carvajal, 1987	*incertae sedis*	Campbell and Carvajal (1987)
Phyllobothrium dohrni (Oerley, 1885) Zschokke, 1889	synonym of *Crossobothrium dohrni* (Oerley, 1885) Ruhnke, 1996	Zschokke (1889)
Phyllobothrium fallax Van Beneden, 1871	*nomen nudum*	Van Beneden (1871)
Phyllobothrium filiforme Yamaguti, 1952	synonym of *Paraorygmatobothrium filiforme* (Yamaguti, 1952) Ruhnke, 1996	Yamaguti (1952)
Phyllobothrium floraforme (Southwell, 1912) Southwell, 1930	synonym of *Paraorygmatobothrium floraformis* (Southwell, 1925) n. comb.	Southwell (1930)
Phyllobothrium foliatum Linton, 1890	*incertae sedis*	Linton (1890)
Phyllobothrium georgiense Wojciechowska, 1991	*incertae sedis*	Wojciechowska (1991)
Phyllobothrium giganteum (Van Beneden, 1858) Southwell, 1930	synonym of *Scyphophyllidium giganteum* (Van Beneden, 1858) Woodland, 1927	Southwell (1930)
Phyllobothrium gracile Wedl, 1855	synonym of *Anthocephalum wedli* nom. nov.	Wedl (1855)
Phyllobothrium hallericola Church and Schmidt, 1990	*incertae sedis*	Church and Schmidt (1990)
Phyllobothrium hyperapolytica (Obersteiner, 1914) Williams, 1958	synonym of *Bilocularia hyperapolytica* Obersteiner, 1914	Williams (1958)
Phyllobothrium inchoatum Leidy, 1891	larval form, *nomen dubium*	Leidy (1891)
Phyllobothrium ketae Canavan, 1928	synonym of *Pelichnobothrium caudatum* Zschokke and Heitz, 1914	Canavan (1928)
Phyllobothrium kingae Schmidt, 1978	synonym of *Anthocephalum kingae* (Schmidt, 1979) Ruhnke and Seaman, 2009	Schmidt (1978)
Phyllobothrium laciniatum (Linton, 1889) Yamaguti, 1959	synonym of *Crossobothrium laciniatum* Linton, 1889	Linton (1889)
Phyllobothrium lactuca Van Beneden, 1850	valid; type species	Van Beneden (1850)
Phyllobothrium leuci Watson and Thorson, 1976	synonym of *Paraorygmatobothrium leuci* (Watson and Thorson, 1976) n. comb.	pg. 146
Phyllobothrium lintoni (Southwell, 1912) Southwell, 1930	synonym of *Spongiobothrium lintoni* Southwell, 1912	Southwell (1930)
Phyllobothrium loculatum Yamaguti, 1952	*incertae sedis*	Yamaguti (1952)
Phyllobothrium loliginis (Leidy, 1887) Linton, 1897	synonym of *Taenia loliginus* Leidy, 1887 *species inquirenda*	Linton (1897)
Phyllobothrium magnum Hart, 1936	synonym of *Monorygma magnum* (Hart, 1936) Williiams, 1968	Hart (1936)
Phyllobothrium marginatum Yamaguti, 1934	*incertae sedis*	Yamaguti (1934)
Phyllobothrium microsomum Southwell and Hilmy, 1929	*incertae sedis*	Southwell and Hilmy (1929)
Phyllobothrium minimum Subhapradha, 1955	*incertae sedis*	Subhapradha (1955)
Phyllobothrium minutum Shipley and Hornell, 1906	*incertae sedis*	Shipley and Hornell (1906)
Phyllobothrium minutum Williams, 1968	homonym of *Phyllobothrium minutum* Shipley and Hornell, 1906; replaced by *P. williamsi* Schmidt, 1867	Williams (1968a)
Phyllobothrium musteli (Van Beneden, 1850) Southwell, 1925	synonym of *Paraorygmatobothrium musteli* (Van Beneden, 1850) n. comb.	pg. 147
Phyllobothrium myliobatidis Brooks, Mayes and Thorson, 1981	*incertae sedis*	Brooks, Mayes and Thorson (1981)
Phyllobothrium nicaraguensis Watson and Thorson, 1976	synonym of *Paraorygmatobothrium nicaraguensis* (Van Beneden, 1850) n. comb.	pg. 149
Phyllobothrium orectolobi Butler, 1987	synonym of *Paraorygmatobothrium orectolobi* (Butler, 1987) n. comb.	pg. 151
Phyllobothrium pammicrum Shipley and Hornell, 1906	*species inquirenda*	Shipley and Hornell (1906)
Phyllobothrium panjadi (Shipley, 1909) Southwell, 1930	synonym of *Anthobothrium panjadi* Shipley, 1909 *incertae sedis*	Southwell (1930)
Phyllobothrium pastinacae Mokhtar-Maamouri and Zamali, 1981	*incertae sedis*	Mokhtar-Maamouri and Zamali (1981)
Phyllobothrium paulum (Linton, 1897) Southwell, 1925	synonym of *Paraorygmatobothrium paulum* (Linton, 1897) n. comb.	pg. 153
Phyllobothrium perfectum (Van Beneden, 1853) Southwell, 1925	synonym of *Monorygma perfectum* (van Beneden, 1853) Diesing, 1863	Southwell (1925)
Phyllobothrium physeteris (Diesing, 1863) Meggitt, 1924	synonym of *Cysticercus physeteri* Diesing, 1863 *nomen dubium*	Meggitt (1924)
Phyllobothrium piriei Williams, 1968	*incertae sedis*	Williams (1968a)
Phyllobothrium prionacis Yamaguti, 1934	synonym of *Paraorygmatobothrium prionacis* (Yamaguti, 1934) Ruhnke, 1994	Yamaguti (1934)
Phyllobothrium pristis Watson and Thorson, 1976	*incertae sedis*	Watson and Thorson (1976)
Phyllobothrium ptychocephalum Wang, 1984	*incertae sedis*	Wang (1984)
Phyllobothrium radioductum Kay, 1942	*incertae sedis*	Kay (1942)
Phyllobothrium rakusai Wojciechowska, 1991	*incertae sedis*	Wojciechowska (1991)
Phyllobothrium rhinoptera Vijayalakshmi and Sarada, 1996	*species inquirenda*	Vijayalakshmi and Sarada (1996)
Phyllobothrium riggii (Monticelli, 1893) Southwell, 1925	synonym of *Calyptrobothrium riggii* Monticelli, 1893	Southwell (1925)
Phyllobothrium riseri Ruhnke, 1996	valid	Ruhnke (1996)

Appendix 2. Continued.

SPECIES NAME	STATUS	REFERENCE
Phyllobothrium rotundum (Klaptocz, 1906) Southwell, 1925	synonym of *Monorygma rotundum* Klaptocz, 1906 *species inquirenda*	Southwell (1925)
Phyllobothrium rudicornis (Drummond, 1839) Ronald, 1959	synonym of *Anthocephalus rudicornis* Drummond, 1839 *species inquirenda*	Ronald (1959)
Phyllobothrium salmonis Fujita, 1922	*species inquirenda*	Fujita (1922)
Phyllobothrium septaria (Van Beneden, 1889) Southwell, 1925	synonym of *Dinobothrium septaria* Van Beneden, 1889	Southwell (1925)
Phyllobothrium serratum Yamaguti, 1952	valid	Yamaguti (1952)
Phyllobothrium siedleckii Wojciechowska, 1991	*incertae sedis*	Wojciechowska (1991)
Phyllobothrium sinuosiceps Williams, 1959	*incertae sedis*	Williams (1959)
Phyllobothrium speciosum (Monticelli, 1889) Southwell, 1925	synonym of *Pelichnobothrium speciosum* Monticelli, 1889	Monticelli (1889)
Phyllobothrium squali Yamaguti, 1952	*incertae sedis*	Yamaguti (1952)
Phyllobothrium thridax Van Beneden, 1850	*incertae sedis*	Van Beneden (1850)
Phyllobothrium thysanocephalum Linton, 1889	synonym of *Thysanocephalum thysanocephalum* (Linton, 1889) Linton, 1890	Linton (1889)
Phyllobothrium triacis Yamaguti, 1952	synonym of *Paraorygmatobothrium triacis* (Yamaguti, 1952) Ruhnke, 1996	Yamaguti (1952)
Phyllobothrium trygoni Jadhav, 1985	*species inquirenda*	Jadhav (1985)
Phyllobothrium tumidum Linton, 1922	synonym of *Clistobothrium tumidum* (Linton, 1922) Ruhnke, 1993	Linton (1922)
Phyllobothrium typicum Subhapradha, 1955	synonym of *Paraorygmatobothrium typicum* (Subhapradha, 1955) n. comb.	pg. 163
Phyllobothrium unilaterale Southwell, 1925	synonym of *Phyllobothrium thridax* Van Beneden, 1850 *incertae sedis*	Southwell (1925)
Phyllobothrium vagans Haswell, 1902	*incertae sedis*	Haswell (1902)
Phyllobothrium variabile (Linton, 1889) Southwell, 1930	synonym of *Spongiobothrium variabile* Linton, 1889	Southwell (1930)
Phyllobothrium williamsi Schmidt, 1986	*incertae sedis*; replacement name for *Phyllobothrium minutum* Williams, 1968	Schmidt (1986)
Pithophorus tetraglobus (Southwell, 1912) Southwell, 1925	*species inquirenda*	Southwell (1925)
Pithophorus yamaguttii Shinde, 1978	*nomen dubium*	Shinde (1978)
Ruhnkecestus latipi Caira and Durkin, 2006	valid; type species	Caira and Durkin (2006)
Scyphophyllidium arabiansis Shinde and Chincholikar, 1977	*nomen dubium*	Shinde and Chincholikar (1977)
Scyphophyllidium giganteum (Van Beneden, 1858) Woodland, 1927	valid; type species	Woodland (1927)
Scyphophyllidium pruvoti (Guiart, 1933) Joyeux and Baer, 1936	larval form; *incertae sedis*	Joyeux and Baer (1936)
Scyphophyllidium uruguayense Brooks, Marques, Perroni and Sidagis, 1999	valid	Brooks, Marques, Perroni and Sidagis (1999)
Spongiobothrium lintoni Southwell, 1912	*incertae sedis*	Southwell (1912)
Spongiobothrium variabile Linton, 1890	valid; type species	Linton (1890)
Taenia chamissonii Linton, 1905	larval form; *species inquirenda*	Linton (1905)
Taenia grimaldi Moniez, 1889	larval form; *species inquirenda*	Moniez (1889)
Taenia loliginus Leidy, 1887	larval form; *species inquirenda*	Leidy (1887)
Tetrabothrium (*Anthobothrium*) *crispum* Molin, 1858	*nomen dubium*	Molin (1858)
Tetrabothrium (*Eutetrabothrium*) *longicolle* Molin, 1858	*incertae sedis*	Molin (1858)
Tetrabothrium versatile Diesing, 1854.	synonym of *Orygmatobothrium musteli* Van Beneden, 1850	Diesing (1854)

Appendix 3. Host list for valid phyllobothriid species formally treated in this monograph.

ORDER	FAMILY	HOST SPECIES	PARASITE SPECIES
Rajiformes	Potamotrygonidae	*Paratrygon aiereba* Müller and Henle, 1841, Discus ray	*Nandocestus guariticus* (Marques, Brooks and Lasso, 2001) Reyda 2008
Carcharhiniformes	Carcharhinidae	*Carcharhinus* cf. *dussumieri* (Müller and Henle), Whitecheek shark	*Paraorygmatobothrium sinuspersicense* Malek, Caira and Haseli, 2010
	Carcharhinidae	*Carcharhinus* cf. *dussumieri* (Müller and Henle), Whitecheek shark	*Paraorygmatobothrium mobedii* Malek, Caira and Haseli, 2010
	Carcharhinidae	*Carcharhinus leucas* (Müller and Henle, 1839), Bull shark	*Paraorygmatobothrium leuci* (Watson and Thorson, 1976) n. comb
	Carcharhinidae	*Carcharhinus leucas* (Müller and Henle, 1839), Bull shark	*Paraorygmatobothrium nicaraguensis* (Watson and Thorson, 1976) n. comb.
	Carcharhinidae	*Carcharhinus obscurus* (Lesueur, 1818) Dusky shark	*Paraorygmatobothrium angustum* (Linton, 1889) n. comb.
	Carcharhinidae	*Carcharhinus sorrah* (Müller and Henle, 1839), Spottail shark	*Paraorygmatobothrium floraformis* (Southwell, 1912) n. comb.
	Carcharhinidae	*Galeocerdo cuvier* (Pèron and Lesueur, 1822), Tiger shark	*Paraorygmatobothrium paulum* (Linton, 1897) n. comb.
	Carcharhinidae	*Negaprion acutidens* (Rüppell, 1837), Sicklefin lemon shark	*Paraorygmatobothrium arnoldi* Ruhnke and Thompson, 2006
	Carcharhinidae	*Negaprion brevirostris* (Poey, 1868), Lemon shark	*Paraorygmatobothrium roberti* Ruhnke and Thompson, 2006
	Carcharhinidae	*Prionace glauca* (Linnaeus, 1758), Blue shark	*Paraorygmatobothrium prionacis* (Yamaguti, 1934) Ruhnke, 1994
	Carcharhinidae	*Rhizoprionodon acutus* (Rüppell, 1837), Milk shark	*Paraorygmatobothrium typicum* (Subhapradha, 1955) n. comb
	Carcharhinidae	*Scoliodon laticaudus* Müller and Henle, 1838, Spadenose shark	*Ruhnkecestus latipi* Caira and Durkin, 2006
	Hemigaleidae	*Hemigaleus australiensis* White, Last and Compagno, 2005, Australian weasel shark	*Paraorygmatobothrium taylori* Cutmore, Bennett and Cribb, 2009
	Hemigaleidae	*Hemigaleus microstoma* Bleeker, 1852, Sicklefin weasel shark	*Paraorygmatobothrium kirstenae* Ruhnke, Healy and Shapero, 2006
	Hemigaleidae	*Hemipristis elongata* Klunzinger, 1871, Snaggletooth shark	*Paraorygmatobothrium janineae* Ruhnke, Healy and Shapero, 2006
	Triakidae	*Galeorhinus galeus* (Linnaeus, 1758), Tope shark	*Scyphophyllidium giganteum* (Van Beneden, 1858) Woodland, 1927
	Triakidae	*Mustelus antarcticus* Günther, 1870, Gummy shark	*Paraorygmatobothrium rodmani* Ruhnke and Carpenter, 2008
	Triakidae	*Mustelus fasciatus* (Garman, 1913), Striped smooth-hound shark	*Orygmatobothrium juani* Ivanov, 2008
	Triakidae	*Mustelus mento* (Cope, 1877), Speckled smooth-hound	*Scyphophyllidium uruguayense* Brooks, Marques, Perroni and Sidagis, 1999
	Triakidae	*Mustelus mustelus* (Linnaeus, 1758), Smooth-hound	*Orygmatobothrium musteli* (Van Beneden, 1850) Diesing, 1863
	Triakidae	*Mustelus mustelus* (Linnaeus, 1758), Smooth-hound	*Paraorygmatobothrium bai* Ruhnke and Carpenter, 2008
	Triakidae	*Mustelus mustelus* (Linnaeus, 1758), Smooth-hound	*Paraorygmatobothrium musteli* (Van Beneden, 1850) n. comb
	Triakidae	*Mustelus mustelus* (Linnaeus, 1758), Smooth-hound	*Phyllobothrium lactuca* Van Beneden, 1850
	Triakidae	*Mustelus schmitti* Springer, 1939, Narrownose smooth-hound shark	*Orygmatobothrium schmittii* Suriano and Labriola, 2001
	Triakidae	*Triakis scyllium* Müller and Henle, 1839, Banded houndshark	*Paraorygmatobothrium triacis* (Yamaguti, 1952) Ruhnke, 1996
	Triakidae	*Triakis scyllium* Müller and Henle, 1839, Banded houndshark	*Phyllobothrium serratum* Yamaguti, 1952
	Triakidae	*Triakis semifasciata* Girard 1854, Leopard shark	*Phyllobothrium riseri* Ruhnke, 1996
	Triakidae	*Triakis semifasciata* Girard 1854, Leopard shark	*Paraorygmatobothrium barberi* Ruhnke, 1994
Hexanchiformes	Hexanchidae	*Heptranchias perlo* (Bonnaterre, 1788), Sharpnose sevengill shark	*Crossobothrium dohrni* (Oerley, 1885) Ruhnke, 1996
	Hexanchidae	*Hexanchus griseus* (Bonnaterre, 1788), Bluntnose sixgill shark	*Crossobothrium campanulatum* Klaptocz, 1906
	Hexanchidae	*Notorynchus cepedianus* (Péron, 1807), Broadnose sevengill shark	*Crossobothrium antonioi* Ivanov, 2009
	Hexanchidae	*Notorynchus cepedianus* (Péron, 1807), Broadnose sevengill shark	*Crossobothrium pequeae* Ivanov, 2009

Appendix 3. Continued.

ORDER	FAMILY	HOST SPECIES	PARASITE SPECIES
Lamniformes	Alopiidae	*Alopias vulpinus* (Bonnaterre, 1788), Thin-tail thresher shark	*Marsupiobothrium alopias* Yamaguti, 1952
	Alopiidae	*Alopias vulpinus* (Bonnaterre, 1788), Thin-tail thresher shark	*Paraorygmatobothrium exiguum* (Yamaguti, 1935) Ruhnke, 1994
	Alopiidae	*Alopias vulpinus* (Bonnaterre, 1788), Thin-tail thresher shark	*Paraorygmatobothrium filiforme* (Yamaguti, 1952) Ruhnke, 1996
	Lamnidae	*Carcharodon carcharias* (Linnaeus, 1758), Great white shark	*Clistobothrium carcharodoni* Dailey and Vogelbein, 1990
	Lamnidae	*Carcharodon carcharias* (Linnaeus, 1758), Great white shark	*Clistobothrium tumidum* (Linton, 1922) Ruhnke, 1993
	Lamnidae	*Isurus oxyrinchus* Rafinesque, 1810, Shortfin mako shark	*Clistobothrium montaukensis* Ruhnke, 1993
	Odontaspididae	*Carcharias taurus* (Rafinesque, 1810), Sand tiger shark	*Crossobothrium laciniatum* Linton, 1889
Orectolobiformes	Hemiscylliidae	*Chiloscyllium* cf. *punctatum*, Bamboo shark	*Orectolobicestus lorettae* Ruhnke, Caira and Carpenter, 2006
	Hemiscylliidae	*Chiloscyllium hasseltii* Bleeker, 1852, Indonesian bamboo shark	*Orectolobicestus randyi* Ruhnke, Caira and Carpenter, 2006
	Hemiscylliidae	*Chiloscyllium indicum* (Gmelin, 1789), Slender bambooshark	*Orectolobicestus chiloscyllii* (Subhapradha, 1955) Ruhnke, Caira and Carpenter, 2006
	Hemiscylliidae	*Chiloscyllium indicum* (Gmelin, 1789), Slender bambooshark	*Orectolobicestus kelleyae* Ruhnke, Caira and Carpenter, 2006
	Hemiscylliidae	*Chiloscyllium indicum* (Gmelin, 1789), Slender bambooshark	*Orectolobicestus mukahensis* Ruhnke, Caira and Carpenter, 2006
	Hemiscylliidae	*Chiloscyllium punctatum* Müller and Henle, 1838, Brownbanded bamboo shark	*Orectolobicestus tyleri* Ruhnke, Caira and Carpenter, 2006
	Orectolobidae	*Orectolobus maculatus* (Bonnaterre, 1788), Spotted wobbegon	*Paraorygmatobothrium orectolobi* (Butler, 1987) n. comb.
Squaliformes	Somniosidae	*Somniosus microcephalus* (Bloch and Schneider, 1801), Greenland shark	*Monorygma perfectum* (Van Beneden, 1853) Diesing, 1863
	Somniosidae	*Somniosus pacificus* Bigelow and Schroeder, 1944, Pacific sleeper shark	*Monorygma magnum* (Hart, 1936) Williams, 1968
	Somniosidae	*Somniosus* sp.	*Monorygma macquariae* Johnston, 1937

TAXONOMIC INDEX

Note: The Abstract, Figure captions, Table and the Appendices are not indexed.

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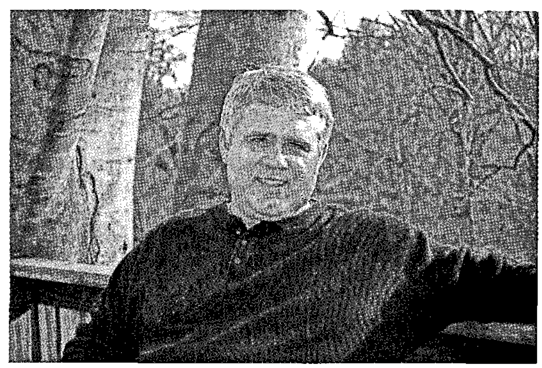
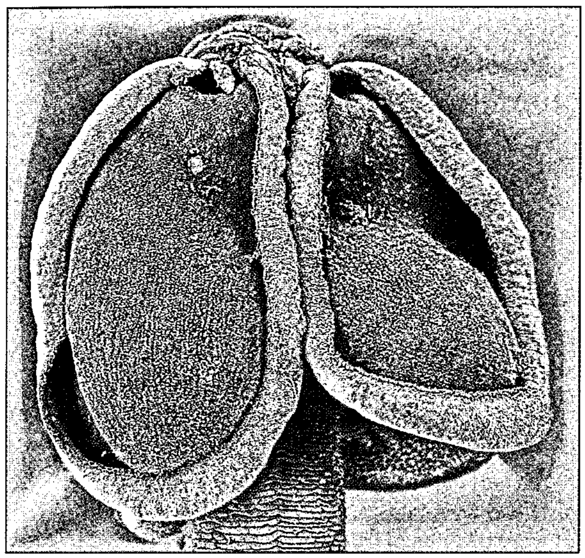
ABOUT THE AUTHOR

Tim Ruhnke grew up on a farm in southeast Nebraska. His early academic interest was in history. Tim enrolled at the University of Nebraska-Lincoln. As a result of courses with John Janovy, Jr., Tim became interested in zoology and parasitology. Further coursework with John Lynch sparked an interested in systematics and evolution. After completion of an M.S. degree in 1988 with John Janovy, Jr. at UN-L, Tim began his Ph.D. studies with Janine Caira at the University of Connecticut. A dissertation project concerning the taxonomic renovation of *Phyllobothrium* followed. After completing his Ph.D. in 1993, Tim remained in Janine Caira's lab for a one year post-doctoral stint working on NSF-BS&I (DEB No. 9300796) – "A systematic survey of the metazoan parasites of elasmobranchs from the Sea of Cortez". Tim has been a faculty member at West Virginia State University since 1995. In addition to participation in the above project, Tim has also collaborated the projects NSF-BS&I (DEB No. 0103640) – "A survey of the sharks and rays of Malaysian Borneo and their metazoan parasites", NSF-BS&I (DEB Nos. 0542846 and 0542941) Collaborative Research – "A survey of the elasmobranchs and their metazoan parasites of Indonesian Borneo (Kalimantan)", and NSF-PEET (DEB No. 9521943) – "Monography of the Diphyllidea, Lecanicephalidea, and Tetraphyllidea – A program to train cestodologists of the future". Tim was the Co-PI on NSF-PEET (DEB No. 0118882) – "Enhancing taxonomy in the Cestoda: Monography of selected tetraphyllidean groups". This project was headed by Janine Caira. This monograph is one of the main products of the project. Tim's research will continue to focus on the phyllobothriid taxa from sharks, in addition to selected rhinebothriidean taxa.

Tim has been married to the lovely Alice Moritz Ruhnke since 1989. Their two sons are Michael, born in 1997, and Luke, born in 2003. The Ruhnkes currently reside in Charleston, West Virginia.





Scanning electron micrograph of *Paraorygmatobothrium* sp.