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A NEW SPECIES OF *ACANTHOBOTHRIMUM* VAN BENEDEN, 1849 (EUCESTODA: TETRAPHYLLIDEA: ONCHOBOTHRIIDAE) IN *DASYATIS LONGUS* GARMAN (CHONDRICHTHYES: MYLIOBATIFORMES: DASYATIDIDAE) FROM CHAMELA BAY, JALISCO, MEXICO

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ABSTRACT: A new species of *Acanthobothrium* in *Dasyatis longus* from Chamela Bay, Jalisco, Mexico, is a member of a presumed clade of species diagnosed by being anapolytic or nearly so, having more than 100 testes per proglottis, with immature and mature proglottides wider than long to square, aspinose scolex, muscular bothridia fused to the scolex at their posterior ends, H- to V-shaped ovaries, relatively short symmetrical to asymmetrical ovarian arms that extend anteriorly to, or nearly to, the cirrus sac, and vitellaria arranged in fields rather than a single row of follicles. The new species most closely resembles *Acanthobothrium terezae* from the freshwater stingray *Potamotrygon motoro* in the following characters: bothridial hooks longer than 200 μm with inner hooks having bent asymmetrical prongs, an average of 130–140 testes per proglottis, and shallow genital atria located posterior to midline of proglottis. The new species differs from *A. terezae* by having outer hooks approximately the same size and shape as the inner hooks, inner hooks averaging 230 μm rather than 313 μm in total length, and cirrus sacs averaging 255 μm rather than 450 μm in length. The new species is unique among all described species of *Acanthobothrium* by having a cleft in the posterior margin of each apical bothridial pad. The apparent close relationship of the new species to one inhabiting a Neotropical freshwater stingray provides support for the hypothesized Pacific marine ancestry of Neotropical freshwater stingrays and raises the possibility that the Neotropical freshwater stingrays may not be monophyletic.

One of the most species-rich genera of tetraphyllidean eucestodes is *Acanthobothrium* van Beneden, 1849. During the course of an inventory of the parasite fauna of fish from Chamela Bay, Jalisco State, Mexico, we collected numerous specimens of a new species of *Acanthobothrium* inhabiting *Dasyatis longus* Garman. The new species adds to our understanding of the evolution of Neotropical freshwater stingrays (family Potamotrygonidae).

MATERIALS AND METHODS

Commercial fishermen captured specimens of *Dasyatis longus* with long lines 1–2 km from the shore of Chamela Bay, Jalisco State, Mexico (19°31'N, 105°04'E). Cestodes were removed from the spiral valve of the host, killed with hot tap water, transferred immediately to AFA for 24–48 hr, then stored in 70% ethanol. Specimens were stained either with Mayer's carmalum or Ehrlich's hematoxylin and mounted in Canada balsam for examination as whole mounts. Serial sections of proglottides were cut 7–10 μm thick, stained with Masson's trichrome, and mounted in Canada balsam for examination. Specimens were prepared for scanning electron microscopy by postfixation in 1% osmium tetroxide, and processed in Peldri II (Pelco International, Riverdale, California) prior to sputter coating with gold. Specimens were examined using a Hitachi S-2500 scanning electron microscope. Figures were drawn with the aid of a drawing tube. Measurements are in micrometers unless otherwise stated; for some traits, ranges are given, followed by, in parentheses, mean values \pm 1 standard deviation (\bar{x} = mean; n = sample size). Hook measurements follow Euzet (1956) modified as follows: for each parameter, mean value \pm 1 standard deviation is given followed by, in parentheses, its range. CHIBUNAM refers to the Colección Helmintológica del Instituto de Biología, Universidad Nacional Autónoma de México, Mexico City, Mexico; UNSMHWML refers to the University of Nebraska State Museum, Harold W Manter Laboratory, Division of Parasitology, Lincoln, Nebraska, U.S.A.; MNHG INV refers

to the Museum of Natural History, Geneva, Switzerland, Division of Invertebrates; FIOCRUZ Helm Col refers to the Coleção Helmintológica, FIOCRUZ, Instituto Oswaldo Cruz, Rio de Janeiro, Brasil.

DESCRIPTION

Acanthobothrium cleofanus n. sp.

(Fig. 1A, B, D, E)

Description (based on 40 specimens): Strobila acraspedote, anapolytic, 3.7–6.7 (5.0 \pm 1.0, n = 10) cm long; composed of 97–150 (120 \pm 15, n = 10) proglottides. Scolex 731–1,030 (919 \pm 75; n = 39) wide, composed of 4 sessile trilobulate bothridia; each bothridium with apical sucker and pad, armed with pair of bifid hooks. Bothridia with thick muscular walls; 477–719 (636 \pm 51; n = 40) long by 286–477 (417 \pm 38, n = 40) wide. Locular wall dividing anterior and middle loculi relatively thick and muscular, between middle and posterior loculi relatively thin. Anterior loculus 127–235 (172 \pm 26, n = 40) long, middle loculus 70–140 (113 \pm 17, n = 40) long, posterior loculus 25–76 (54 \pm 15, n = 40) long. Ratio of loculi lengths 1:0.6:0.3. Apical sucker 108–159 (136 \pm 11, n = 40) in diameter; pads muscular, 232–331 (289 \pm 22, n = 40) wide. Posterior edge of apical muscular pads extending posteriorly over handles of hooks, divided in middle to form 2 curved extensions, 1 over each hook. Outer prongs of bothridial hooks shorter than inner prongs; inner prong of hooks twisted. Hook formula for external hooks (n = 40):

$$\frac{106 \pm 5 (95-117) \quad 145 \pm 10 (117-170) \quad 57 \pm 6 (47-69)}{227 \pm 13 (198-258)}$$

Hook formula for internal hooks (n = 40):

$$\frac{105 \pm 7 (88-117) \quad 146 \pm 9 (121-164) \quad 58 \pm 9 (38-72)}{232 \pm 14 (192-263)}$$

Cephalic peduncle unspined, 1,150–3,530 (1,770 \pm 510, n = 39) long. Immature proglottides wider than long; terminal proglottides 1,050–2,230 (1,700 \pm 310, n = 31) long by 331–750 (539 \pm 115, n = 29) wide. Testes 114–172 (140 \pm 12, n = 38) in number, 32–64 (44 \pm 8, n = 37) in diameter; 43–64 (14 \pm 2, n = 39) preporally, 6–11 (8 \pm 1, n = 39) postporally, 19–33 (26 \pm 3, n = 39) antiporally. Testis size and number greatly reduced or lacking in terminal proglottides. Cirrus sac slightly posterior to midproglottis, containing spined eversible cirrus; extending medially to mid-proglottis, curved posteriorly in terminal proglottides. Cirrus sac 134–337 (255 \pm 49, n = 36) long, 127–235 (170 \pm 26, n = 36) wide. Cirrus 1,197 μm long when extended, slightly

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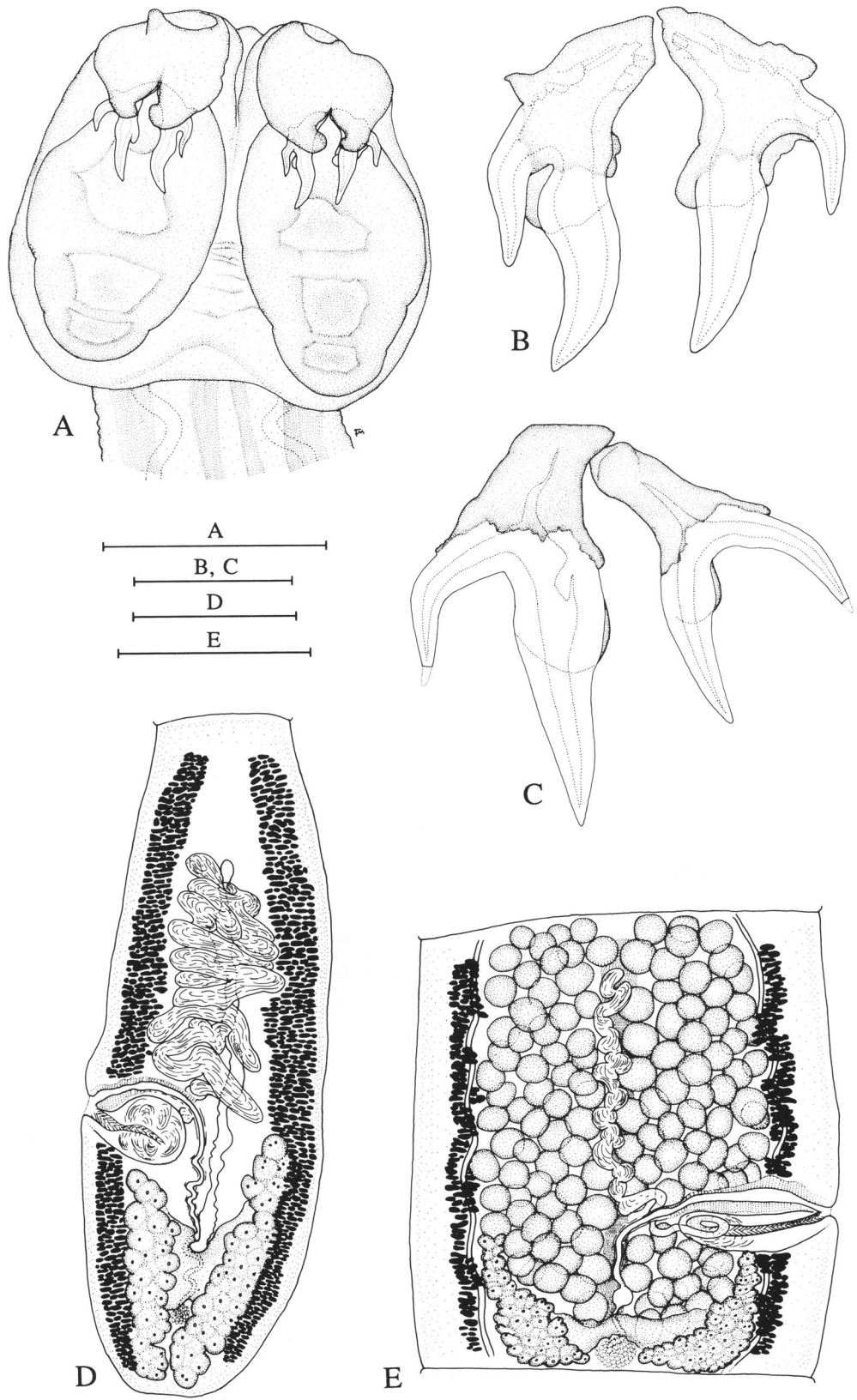


FIGURE 1. *Acanthobothrium cleofanus* n. sp. A. Scolex (scale bar = 500 μ m). B. Enlargement of pair of bothridial hooks (scale bar = 100 μ m). C. *Acanthobothrium terezae*, enlargement of pair of bothridial hooks (scale bar = 100 μ m). *Acanthobothrium cleofanus* n. sp. D. Terminal attached proglottis (scale bar = 500 μ m). E. Mature nonterminal attached proglottis (scale bar = 300 μ m). In B and C, inner hooks are on the left, outer hooks on the right.

swollen at base; spines thin, averaging 13 long basally, 3 long at tip. Vas deferens coiled, extending anteriorly from cirrus sac to near anterior end of proglottis, filled with sperm in terminal proglottides. Genital atrium shallow. Genital pore located 54–65% ($60 \pm 3\%$, $n = 36$) of total length of proglottis from anterior end, irregularly alternating. Vagina anterior to cirrus sac, vaginal wall glandular, vaginal sphincter present as a muscular thickening of the distal portion of the vagina. Vagina looping posteriorly on aporal side of midline, slightly coiled in terminal proglottides. Ovary near posterior end of proglottis, X-shaped in cross section, with foliose lobes; shape in frontal view changing as proglottides mature: nearly U-shaped in immature proglottides, H-shaped in mature proglottides (Fig. 1E), and inverted A- or V-shaped in terminal proglottides (Fig. 1D). Ovary 26–51 (44 ± 7 , $n = 9$) wide at isthmus; arms unequal in length. Aporal arm 445–840 (616 ± 99 , $n = 32$) long, extending to anterior margin of cirrus sac; poral arm 299–738 (501 ± 103 , $n = 32$) long, extending to level of posterior margin of cirrus sac. Mehlis' gland immediately posterior to ovarian isthmus; seminal receptacle at level of or slightly anterior to isthmus. Vitelline follicles elongate oval in shape, 13–32 (19 ± 6 , $n = 34$) wide, 35–69 (51 ± 10 , $n = 34$) long, extending as narrow bands on each side of proglottis. Uterus saccate, narrowly elongate in terminal attached proglottides, expanded laterally filling available preovarian space in detached proglottides. Eggs not observed.

Taxonomic summary

Host: *Dasyatis longus* Garman (Chondrichthyes: Myliobatiformes: Dasyatidae).

Site of infection: Spiral valve.

Locality: Chamela Bay, Jalisco, México (19°31'N, 105°04'E); June 1994.

Holotype: CHIBUNAM no. 2670.

Paratypes: CHIBUNAM no. 2671 (25 specimens); MNHG INV 38576 (5 specimens); MNHG INV 38576 (5 specimens); UNSMHWML 38576 (5 specimens).

Etymology: The specific epithet, meaning "cleft," refers to the distinct structure of the apical pad, which is diagnostic for this species.

Remarks

Acanthobothrium van Beneden, 1849 currently contains more than 80 nominal species. Within that collection, there is a group characterized by the following features: (1) strobilae anapolytic or nearly so; (2) more than 100 proglottides per strobila; (3) bothridia fused to the scolex at their posterior ends; (4) bothridial hooks usually large, more than 150 μm long, with prongs short relative to the handle, giving them a stumpy appearance or with asymmetrical prongs, the outer prong being much shorter than the inner one; (5) more than 100 testes per proglottis, usually averaging 150 or more; (6) all except terminal proglottides wider than long or square; (7) foliose ovarian arms, usually flat or low H- to V-shaped, extending anteriorly to the level of the cirrus sac, sometimes with asymmetrical arms; (8) genital pores indistinct and located at or posterior to midline of proglottis; and (9) vitellaria in fields rather than single rows of follicles, especially in the oldest proglottides. These traits are lacking or relatively rare in other tetraphyllideans, so we consider them synapomorphies, diagnosing those species as a clade within the genus.

Within the above clade are 13 species that exhibit bothridial hooks with asymmetrical prongs. This trait is highly unusual among members of *Acanthobothrium* and is restricted to the species within the clade diagnosed in the preceding paragraph. Therefore, we consider this trait a synapomorphy diagnosing a clade containing *A. cleofanus*, *Acanthobothrium coronatum* (Rudolphi, 1819) van Beneden, 1849 (inhabiting *Scyliorhinus stellaris* (Linnaeus, 1758) from the Mediterranean Sea), *Acanthobothrium crassicolle* Wedl, 1855 (inhabiting *Dasyatis pastinaca* (Linnaeus, 1758) from the northeast Atlantic Ocean and Mediterranean Sea), *Acanthobothrium herdmanni* Southwell, 1912 (inhabiting *Dasyatis kuhli* (Müller and Henle, 1841) from Ceylon, *Acanthobothrium ijimae* Yoshida, 1917 (inhabiting *Dasyatis akajei* Lindberg and Legeza, 1959 from the western Pacific Ocean, Ceylon, and the northern Atlantic Ocean), *Acanthobothrium grandiceps* Yamaguti, 1952 (inhabiting *D. akajei* and *Dasyatis zugei* (Müller and Henle, 1841) from the East China Sea), *Acanthobothrium latum* Yamaguti, 1952 (inhabiting *D. akajei* from the Sea of Ariake, Japan), *Acanthobothrium micracanthum* Yamaguti, 1952

(inhabiting *D. akajei*, *D. zugei*, and *Pteroplatea micrura* (Müller and Henle, 1841) from the East China Sea), *Acanthobothrium rhynchobatidis* Subhadrappa, 1955 (inhabiting *Rhynchobatus djiddensis* (Forsskal, 1775) from India), *Acanthobothrium robustum* Alexander, 1953 (inhabiting *Rhinobatos productus* Girard, 1855 from California), *Acanthobothrium septentrionale* Baer and Euzet, 1962 (inhabiting *Raja* sp. from the North Sea), *Acanthobothrium terezae* Rêgo and Dias, 1974 (inhabiting *Paratrygon aerieba* (Müller and Henle, 1841) from Brazil), and possibly *Acanthobothrium intermedium* Perrenoud, 1931 (inhabiting *D. pastinaca* from New Zealand) (see Euzet, 1956; Goldstein, 1967; Williams, 1969; Schmidt, 1986).

Among described species of *Acanthobothrium*, *A. cleofanus* is distinctive by virtue of possessing a distinct medial cleft in each apical pad (Figs. 1A, 2A, B). *Acanthobothrium robustum*, *A. ijimae*, and *A. septentrionale* were described as having 2, 2, and 3 apical suckers, respectively, whereas *A. cleofanus* has a single sucker only. *Acanthobothrium cleofanus* also differs from these 3 species by having bothridial hooks averaging 230 μm rather than approximately 150 μm in total length, smaller bothridia than *A. ijimae* and *A. septentrionale*, and larger bothridia than *A. robustum*. It also has an average of 140 rather than 100–115 testes per proglottis, cirrus sacs reaching to proglottis rather than only to the middle of the poral testicular field, and genital pores more posterior to mid-proglottis. The new species is similar to *A. coronatum* in average strobilar length, possession of bothridial hooks with relatively short inner prongs averaging 220–230 μm in total length, vaginal sphincter, shallow genital atrium, and lack of velum, but differs in other respects. The bothridia of *A. coronatum* tend to be larger than those of *A. cleofanus*, although the range of bothridial length in the 2 species overlaps slightly, being 477–719 for *A. cleofanus* and 700–900 for *A. coronatum*. *Acanthobothrium cleofanus* has larger apical accessory suckers than *A. coronatum* (108–159 vs. 80–90 μm), fewer proglottides (97–150 vs. 200–350), and a higher average number of testes (140 vs. 106). The new species has generally smaller cirrus sacs than *A. coronatum* (255 μm long by 170 μm wide vs. 480 μm long by 280 μm wide), which curve slightly to the posterior and extend medially to the midline of the proglottis. By contrast, the cirrus sacs of *A. coronatum* are straight and do not reach the midline of the proglottis. The unequal ovarian arms of *A. cleofanus* extend to the level of the cirrus sac, whereas the equal arms of *A. coronatum* extend only about halfway to the cirrus sac. The bothridia of the new species are completely fused to the scolex (Fig. 1A), whereas those of *A. coronatum* are only slightly attached at the posterior margins (Euzet, 1956). *Acanthobothrium cleofanus* is similar to *A. crassicolle*, *A. herdmanni*, *A. intermedium*, *A. latum*, *A. micracanthum*, and *A. rhynchobatidis* by having 100–172 testes per proglottis, mid- to postmarginal genital pores, unequal ovarian arms, and poral ovarian arms extending anteriorly to the posterior margin of the cirrus sac. The new species differs from these 6 latter species by having shorter strobilae (averaging 50 mm vs. 70–169 mm in the other 6 species), fewer proglottides per strobila (averaging 120 vs. 400 or more in other 6 species), and having cirrus sacs curving posteriorly in terminal proglottides rather than extending medially only. The cirrus sacs of *A. crassicolle*, *A. herdmanni*, *A. intermedium*, *A. latum*, and *A. micracanthum* do not extend medially to the midline of the proglottis, whereas, in *A. cleofanus*, they do. *Acanthobothrium intermedium* was originally described as having a spined peduncle (Perrenoud, 1931; Euzet, 1956), which differs from those of *A. cleofanus* and all other species discussed above. The original specimens of *A. intermedium* have been lost (Williams, 1969) and synonymy with *A. crassicolle* is generally accepted (Williams, 1969; Schmidt, 1986), so it is possible that the report of spinose peduncles for the specimens described as *A. intermedium* was in error.

Acanthobothrium cleofanus appears most similar to *A. terezae*. We obtained 2 paratypes of *A. terezae* (FIOCRUZ Helm Col nos. 31.215a–b) for detailed comparison with our material. Specimens of both *A. cleofanus* and *A. terezae* are anapolytic, acraspedote, and exhibit thick-walled, muscular bothridia attached at the base to a thick peduncle. They both have robust bothridial hooks, foliose U- to V-shaped ovaries, and vitellaria distributed as a narrow band of follicles extending the length of the proglottis. Both species exhibit a similar average number of testes, 140 for *A. cleofanus* and 130 for *A. terezae*; furthermore, in both species approximately 50% of the testes occur in the aporal field. In the other species discussed above, the aporal field contains an average of 57% of the testes in a given proglottis. The ratio of locular lengths

for *A. cleofanus* is 1:0.6:0.5, whereas for *A. terezae* it is approximately 1:0.6:0.8 (the excessively flattened condition of the paratypes of *A. terezae* did not permit precise measurements). In the new species, the apical sucker averages 136 μm in diameter; precise measurements of the apical suckers of the paratypes of *A. terezae* could not be obtained, but in the original description, Rêgo and Dias (1976) state a diameter of 87 μm . Strobilae of *A. cleofanus* are shorter than those of *A. terezae* (50 vs. 99 mm), largely because they have fewer proglottides (120 vs. 230).

Acanthobothrium cleofanus further differs from *A. terezae* by having inner and outer bothridial hooks that are virtually identical in shape (Fig. 1B), whereas those of *A. terezae* differ both in size and shape (Fig. 1C). The shape of the outer hooks of *A. terezae* are typical of most species of *Acanthobothrium*, and the shape of the inner hooks is highly similar to both hooks of *A. cleofanus*. The condition exhibited by *A. terezae* may thus be an evolutionary transition from the condition exhibited by most members of the genus to that found in *A. cleofanus*. The hooks on each bothridium of *A. cleofanus* are approximately equal in total length, a condition common to most members of the genus. In *A. terezae*, by contrast, the total length for the inner hooks of *A. terezae* (average 313 μm) is substantially greater than that of the outer hooks (average 226 μm) or the hooks of *A. cleofanus* (average 230 μm). This appears to be an autapomorphic trait for *A. terezae*. Finally, as mentioned above, *A. cleofanus* differs from *A. terezae* and all other reported species of *Acanthobothrium* by having a cleft in the posterior margin muscular apical pads of each bothridium (Figs. 1A, 2A, B). If *A. terezae* is the sister species of *A. cleofanus*, it might exhibit a similar structure, but we could not confirm the details of the structure of the bothridial apical pads of *A. terezae* due to the excessively flattened nature of the scoleces of the paratypes we examined. This character is readily visible using scanning electron microscopy and should be re-evaluated by examination of additional specimens of *A. terezae*.

DISCUSSION

If *A. cleofanus* is the sister species of *A. terezae*, as suggested above, it offers 2 significant pieces of information about the evolution the helminth fauna of Neotropical freshwater stingrays (family Potamotrygonidae). First, *A. cleofanus* provides further corroboration for the hypothesis that potamotrygonids have a Pacific marine ancestry (Brooks et al., 1981; Brooks and Deardorff, 1988; Brooks, 1992, 1995; Brooks and McLennan, 1991, 1993), because it occurs in a marine host inhabiting the eastern Pacific coast. Second, *A. cleofanus* offers at least partial refutation of the hypothesis that potamotrygonids are derived from a urolophid ancestor (Brooks et al., 1981). This study presents the first evidence that *A. terezae*, which inhabits *Potamotrygon motoro* (Natterer, 1841) and *Paratrygon aerieba*, is not the sister species of the clade containing *Acanthobothrium quinonesi* Mayes, Brooks, and Thorson, 1978, *Acanthobothrium regoi* Brooks, 1981, and *Acanthobothrium amazonensis* Mayes, Brooks, and Thorson, 1978, all of which inhabit species of *Potamotrygon*. The latter 3 species are highly similar to species of *Acanthobothrium* inhabiting species of *Urolophus* (including *Urobatis* of some authors), suggesting a relationship between *Urolophus* and *Potamotrygon*. The putative sister species relationship between *A. cleofanus*, which inhabits a member of *Dasyatis*, and *A. terezae* suggests a relationship between *Dasyatis* and the monotypic *Paratrygon*. In fact, none of the species of the putative clade of *Acanthobothrium* species of which *A. ter-*

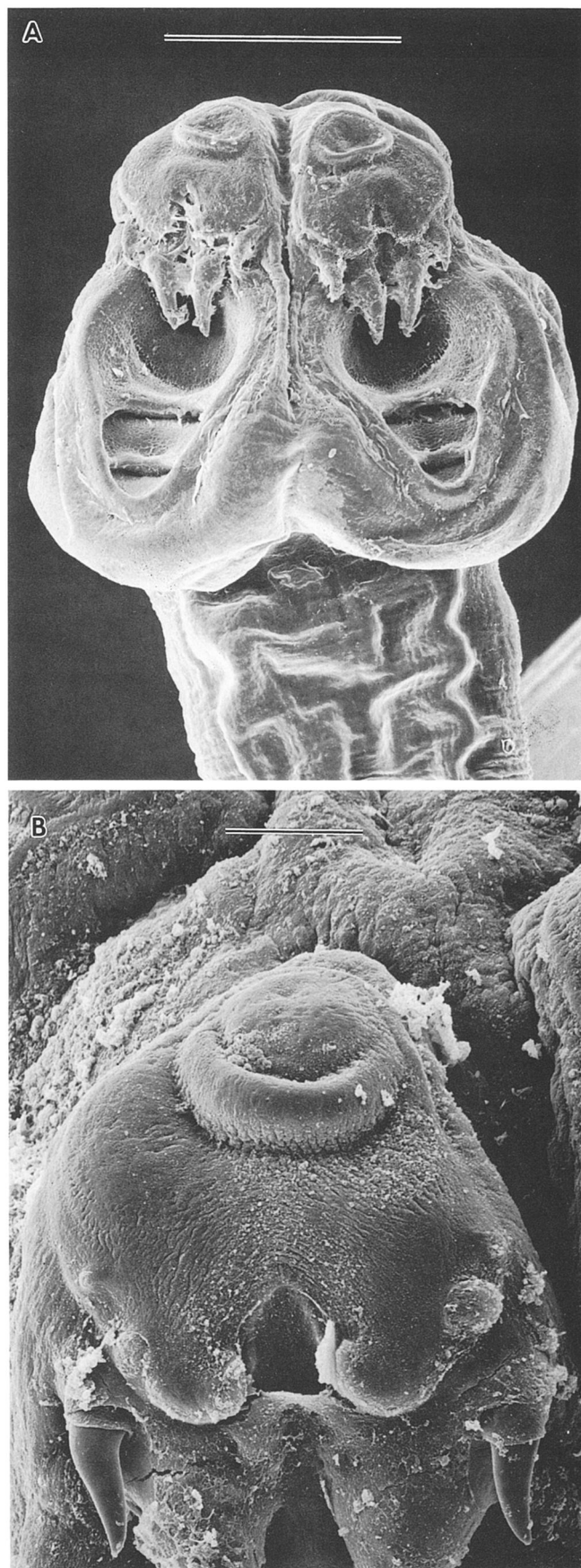


FIGURE 2. *Acanthobothrium cleofanus* n. sp., scanning electron photomicrographs emphasizing structure of bothridial apical pads. A. Scolex (scale bar = 300 μm). B. Enlargement of bothridial apical pad (scale bar = 50 μm).

ezae and *A. cleofanus* are members inhabit urolophid stingrays. This provides a strong indication that the helminth fauna of potamotrygonids is not monophyletic, suggesting 1 of 2 possibilities. First, it is possible that the helminth fauna of potamotrygonids represents a mixture of resident and colonizer clades, involving parasites from urolophid and dasyatidid hosts. In this case, current phylogenetic hypotheses indicating closer relationships between dasyatidids and potamotrygonids than between urolophids and potamotrygonids would suggest that the colonizers are from urolophids. The second possibility is that the helminths of freshwater stingrays represent 2 resident faunas, suggesting that potamotrygonids themselves are not monophyletic, perhaps with *Paratrygon* Duméril, 1865 (and possibly *Plesiotrygon* Rosa, Castello and Thorson, 1987, for which no parasites are as yet reported) being most closely related to dasyatidids, and *Potamotrygon* Garman, 1877 being most closely related to urolophids. In this case, the current high levels of homoplasy depicted in phylogenetic studies of stingray taxa might result from the polyphyletic status of the Potamotrygonidae. In either case, additional studies of helminths inhabiting marine stingrays along the eastern Pacific coast, those inhabiting species of *Potamotrygon*, and especially of those inhabiting the monotypic *Plesiotrygon* and *Paratrygon*, will be necessary to resolve the original source of each of the parasite groups. Furthermore, new phylogenetic analyses of stingray relationships considering the possibility that potamotrygonids are not monophyletic should be investigated.

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