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Phyllobothriidae), and a Revised Host-Parasite Checklist for  
Helminths Inhabiting Neotropical Freshwater Stingrays**

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# CESTODE PARASITES IN *POTAMOTRYGON MOTORO* (NATTERER) (CHONDRICHTHYES: POTAMOTRYGONIDAE) FROM SOUTHWESTERN BRAZIL, INCLUDING *RHINEBOTHROIDES MCLENNANAE* N. SP. (TETRAPHYLLIDEA: PHYLLOBOTHRIIDAE), AND A REVISED HOST-PARASITE CHECKLIST FOR HELMINTHS INHABITING NEOTROPICAL FRESHWATER STINGRAYS

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**ABSTRACT:** Specimens of 5 species of cestodes were collected in 6 specimens of the freshwater stingray species *Potamotrygon motoro* (Natterer), collected in the vicinity of Corumba, Mato Grosso do Sul, Brazil. *Acanthobothrium regoi*, *Potamotrygonocestus orinocoensis*, *Rhinebothroides venezuelensis*, and *Rhinebothrium paratrygoni* are reported from *P. motoro* and from southwestern Brazil for the first time. *Rhinebothroides mclennanae* n. sp. appears to be the sister species of *Rhinebothroides glandularis*, the only other member of the genus exhibiting darkly staining glandular cells lying free in the parenchyma surrounding the terminal genitalia. The new species resembles *Rhinebothroides glandularis*, *Rhinebothroides freitasi*, and *Rhinebothroides scorzai* by having poral ovarian arms that extend anteriorly beyond the posterior margin of the cirrus sac, coiled vaginae, and vitelline follicles not interrupted on the poral side in the vicinity of the genital pore. It differs from all 6 previously described members of the genus by possessing an average of 31 testes per proglottid, compared with an average of 45 for *R. glandularis*, 55 for *R. freitasi* and *R. venezuelensis*, 77 for *Rhinebothroides circularisi* and *Rhinebothroides molararai*, and 80 for *R. scorzai*. An updated phylogenetic tree for *Rhinebothroides* is presented.

Stingrays of the family Potamotrygonidae, permanently restricted to neotropical freshwater habitats, host a rich helminth fauna that strongly reflects their Pacific marine ancestry (Brooks, Thorson, and Mayes, 1981; Brooks and Dear-dorff, 1988; Brooks and McLennan, 1991). On 29 May 1988, 6 specimens of *Potamotrygon motoro* (Natterer), collected in the vicinity of Corumba, Mato Grosso do Sul, Brazil, were examined for helminth parasites. Specimens of 5 species of cestodes were collected, 4 of which are reported from *P. motoro* and from the Pantanal region of Brazil for the first time and 1 of which is described herein as a new species.

## MATERIALS AND METHODS

Stingrays were collected with hand-held spears. Cestodes were relaxed in tap water until moribund, then fixed in alcohol-formalin-acetic acid and stored in 70% ethanol. Whole mounts were stained with Mayer's hematoxylin and mounted in Canada balsam. Serial cross sections of proglottids were cut 5  $\mu$ m thick, stained with hematoxylin-eosin, and mounted in Canada bal-

sam. All measurements are in micrometers. Measurements are based on 25 observations unless noted by "n," indicating a higher number of observations as stated in each case.

## DESCRIPTION

### *Rhinebothroides mclennanae* n. sp.

(Figs. 1–4)

*Description (based on examination of 70 specimens):* Strobila craspedote, apolytic, up to 25 mm long, composed of 16–25 proglottids. Scolex with 4 pedicellated, bilobed, elongate bothridia; apical complex lacking. Pedicels contractile, 188–312 long. Bothridia 625–875 long by 281–418 wide; hingelike constriction between lobes; divided into marginal and medial portions by indistinct marginal septum; divided horizontally by 24–29 septa; medial loculi 49–59 in number; marginal loculi 49–59 in number. Immature proglottids squared to longer than wide. Mature proglottids 938–1,950 long by 294–438 wide. Testes in 2 broad fields in anterior  $\frac{2}{3}$  of proglottid, 19–43 in number ( $n = 293$ ;  $\bar{x} = 31$ ); 25–47 in diameter. Cirrus sac in posterior 20–25% of proglottid, 218–344 long by 50–70 wide, containing spined eversible cirrus and internal seminal vesicle, poral end surrounded by darkly staining cells lying free in the parenchyma. External seminal vesicle extending length of cirrus sac, with extensive coiling immediately anterior to cirrus sac, joining cirrus sac near poral end and vas deferens near posterior end of proglottid. Genital atrium shallow; genital pores alternating irregularly 22–33% ( $\bar{x} = 27\%$ ) of total proglottid length from posterior end. Vagina anterior to cirrus sac, coiled; vaginal

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sphincter and seminal receptacle present. Ovary bilobed in frontal view, X-shaped in cross section; aporal lobe 468–812 long, extending anteriorly to level of posterior extent of testicular field; poral lobe 218–375 long, extending anteriorly to level of cells surrounding pos-

terior of genital pore; 125–188 wide at isthmus. Vitelline follicles lateral, extending from anterior extent of testicular fields to near posterior end of proglottid, not interrupted near genital pore; 9–25 in diameter. Terminal gravid attached proglottids 1,625–2,218 long by 362–456 wide, tapered posteriorly with spinose quadrilobed posterior ends; lacking ovaries and with degenerating testes. Genital pore 25–31% ( $\bar{x}$  = 27%) of proglottid length from posterior end. Uterus saccate with 44–64 ( $\bar{x}$  = 55) lateral diverticula. Eggs 15–18 in diameter, oncospheres 14–17 in diameter, not embryonated in utero.

#### Taxonomic summary

*Type host:* *Potamotrygon motoro* (Natterer) (Chondrichthyes: Myliobatiformes: Potamotrygonidae).

*Type locality:* Vicinity of Corumba, Mato Grosso do Sul, Brazil.

*Site of infection:* Middle third of spiral valve.

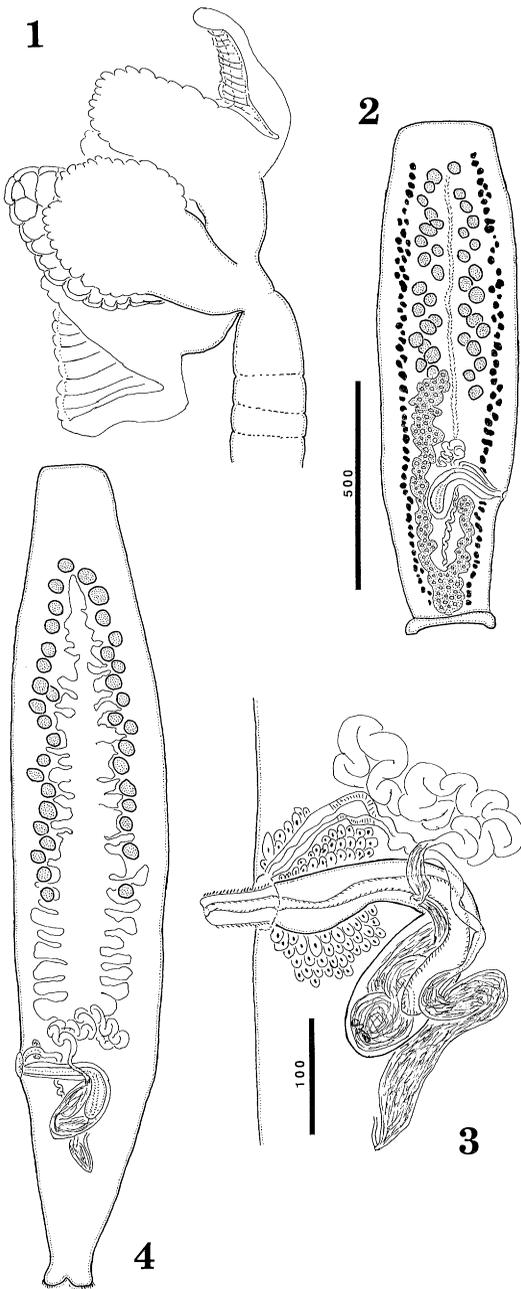
*Specimens deposited:* Holotype: Instituto Oswaldo Cruz no. 32.814a. Paratypes: Instituto Oswaldo Cruz no. 32.814b–f (75 specimens); Harold W. Manter Laboratory, Division of Parasitology, University of Nebraska State Museum no. 34091 (2 specimens).

*Etymology:* The species is named for Deborah A. McLennan.

#### Remarks

*Rhinebothroides mclennanae* is the seventh species named to this genus of cestodes, all of which are restricted to potamotrygonid stingrays. The new species appears to be the sister species of *Rhinebothroides glandularis* Brooks, Mayes, and Thorson, 1981, the only other member of the genus exhibiting darkly staining glandular cells lying free in the parenchyma surrounding the terminal genitalia. We are not aware that this feature is found in any other tetraphyllideans and consider it a synapomorphy for *R. glandularis* plus *R. mclennanae*. The new species further resembles *R. glandularis*, *Rhinebothroides freitasi* (Rego, 1979) Brooks, Mayes, and Thorson, 1981, and *Rhinebothroides scorzai* (Lopez-Neyra and Diaz-Ungria, 1958) Mayes, Brooks, and Thorson, 1981, and differs from *Rhinebothroides moralarai* (Brooks and Thorson, 1976) Mayes, Brooks, and Thorson, 1981, *Rhinebothroides venezuelensis* Brooks, Mayes, and Thorson, 1981, and *Rhinebothroides circularisi* Mayes, Brooks, and Thorson, 1981, by having poral ovarian arms that extend anteriorly beyond the posterior margin of the cirrus sac, coiled vaginae, and vitelline follicles not interrupted on the poral side in the vicinity of the genital pore. *Rhinebothroides mclennanae* differs from all 6 previously described members of the genus by possessing substantially fewer testes per proglottid (an average of 31, with a range of 19–43). *Rhinebothroides glandularis* averages 45 testes per proglottid, with a range of 41–51, *R. freitasi* averages 55 with a range of 48–64, *R. venezuelensis* averages 53 with a range of 45–64, *R. circularisi* and *R. moralarai* average 77 with a range of 66–88, and *R. scorzai* averages 80 with a range of 60–99.

Figure 5 depicts a phylogenetic tree for *Rhinebothroides* species, based on the characters used by Brooks, Mayes, and Thorson (1981) for the same taxa. The new tree differs only in the inclusion of *R. mclennanae*, which is corroborated as the sister species of *R. glan-*



FIGURES 1–4. *Rhinebothroides mclennanae* n. sp. 1. Scolex. 2. Mature attached proglottid. 3. Terminal genitalia. 4. Gravid attached proglottid. Scale bar indicating 500  $\mu$ m is for Figures 1, 2, 4; scale bar indicating 100  $\mu$ m is for Figure 3.

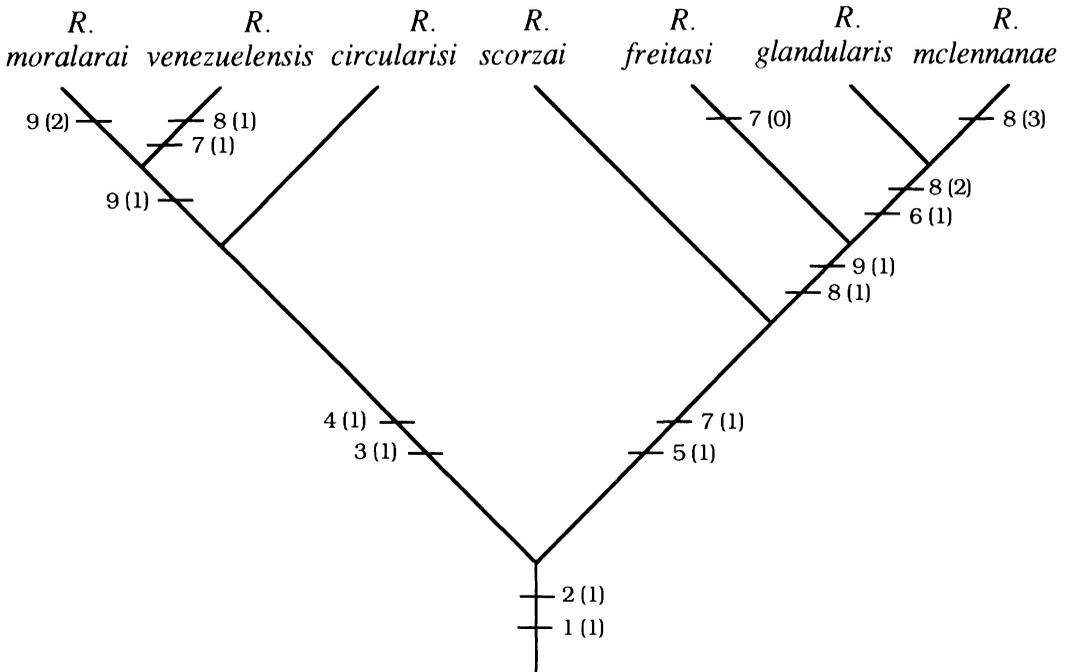


FIGURE 5. Phylogenetic tree for 7 species of *Rhinebothroides*. Numbers accompanying slash marks on tree refer to putative synapomorphies as follows: 1-1, external seminal vesicle joining cirrus sac near poral end; 2-1, aporal ovarian lobes elongate; 3-1, vitellaria interrupted near genital pore on pore side; 4-1, poral ovarian lobe extending anteriorly only to posterior end of cirrus sac; 5-1, vagina coiled; 6-1, darkly staining glandular cells lying free in the parenchyma surrounding the terminal genitalia; 7-0, proglottids acraspedote; 7-1, proglottids craspedote; 8-1, averages of 53–55 testes per proglottid; 8-2, an average of 45 testes per proglottid; 8-3, an average of 31 testes per proglottid; 9-1, 49–59 loculi per bothridium; 9-2, 41–45 loculi per bothridium.

*dularis*. Outgroup comparisons relied on several levels of outgroups including phyllobothriids having medial and marginal loculi and genitalia located near the ovary (see also Brooks, Mayes, and Thorson, 1981), and general tetraphyllidean and general eucestode traits as suggested by a phylogenetic analysis of the higher level relationships among major eucestode groups (Brooks et al., 1991). Six characters could be polarized unambiguously in this manner as the apomorphic states in binary transformation series: external seminal vesicle joining cirrus sac near poral end (1-1 in Table I and Fig. 5); elongate aporal ovarian lobes (2-1 in Table I and Fig. 5); vitellaria interrupted near genital pore on pore side (3-1 in Table I and Fig. 5); poral ovarian lobe extending anteriorly only to posterior end of cirrus sac (4-1 in Table I and Fig. 5); vagina coiled (5-1 in Table I and Fig. 5); and darkly staining glandular cells lying free in the parenchyma surrounding the terminal genitalia (6-1 in Table I and Fig. 5). Three additional transformation series provided ambiguous information, for which outgroup comparisons were augmented by functional outgroup analysis and phylogenetic optimization (Brooks and McLennan, 1991; Wiley et al., 1991).

First, functional outgroup analysis and optimization of testes number per proglottid (character 8 in Table I and Fig. 5) are consistent with the hypothesis that the plesiomorphic condition in *Rhinebothroides* is a range

of 60–99 testes per proglottid, with averages of 77–80 (*R. scorzai* has 60–99 testes per proglottid reported for it, whereas *R. circularisi* and *R. molararai* have 66–88 reported). Four species have derived conditions: *R. venezuelensis* has an average of 53; *R. freitasi* has an average of 55; *R. glandularis* has an average of 45; and *R. mclennanae* has an average of 31. Based on character optimization, we consider the conditions exhibited by *R. venezuelensis* and *R. freitasi* to be convergent traits (8-1 in Table I and Fig. 5), the condition exhibited by *R. glandularis* to be derived from that found in *R. freitasi* (8-2 in Table I and Fig. 5), and that found in *R. mclennanae* to be derived from that found in *R. glandularis* (8-3 in Table I and Fig. 5).

Second, the number of medial loculi per bothridium (which is the same as the number of marginal loculi per bothridium in *Rhinebothroides*) (character 9 in Table I and Fig. 5) also varies greatly among these species, and the structure of the bothridia themselves makes it more difficult to assess loculi number consistently. However, the number of bothridial loculi has been used as an important taxonomic character for other tetraphyllidean groups, such as *Rhinebothrium* and its relatives, and *Echeneibothrium* and its relatives. Current reports list *R. molararai* as having 45–49 medial loculi per bothridium, *R. venezuelensis* as having 51–53 loculi, *R. circularisi* as having 69–79, *R. scorzai* as having 69–79, *R. freitasi* as having approximately 59, *R. glandularis*

TABLE I. Data matrix summarizing character argumentation for 9 transformation series for 7 species of *Rhinebothroides*.\*

Taxa	Characters								
	1	2	3	4	5	6	7	8	9
OG	0	0	0	0	0	0	0	0	0
MO	1	1	1	1	0	0	0	0	2
VE	1	1	1	1	0	0	1	1	1
CI	1	1	1	1	0	0	0	0	0
SC	1	1	0	0	1	0	1	0	0
FR	1	1	0	0	1	0	0	1	1
GL	1	1	0	0	1	1	1	2	1
MC	1	1	0	0	1	1	1	3	1

\* OG, outgroup; MO, *R. moralarai*; VE, *R. venezuelensis*; CI, *R. circularis*; SC, *R. scorzai*; FR, *R. freitasi*; GL, *R. glandularis*; MC, *R. mclennanae*. 1-0, no external seminal vesicle joining cirrus sac near poral end; 1-1, external seminal vesicle joining cirrus sac near poral end; 2-0, aporal ovarian lobes not elongate; 2-1, aporal ovarian lobes elongate; 3-0, vitellaria not interrupted near genital pore on pore side; 3-1, vitellaria interrupted near genital pore on pore side; 4-0, poral ovarian lobe extending anterior to posterior end of cirrus sac; 4-1, poral ovarian lobe extending anteriorly only to posterior end of cirrus sac; 5-0, vagina not coiled; 5-1, vagina coiled; 6-0, no darkly staining glandular cells lying free in the parenchyma surrounding the terminal genitalia; 6-1, darkly staining glandular cells lying free in the parenchyma surrounding the terminal genitalia; 7-0, proglottids acraspedote; 7-1, proglottids craspedote; 8-0, averages of 77-80 testes per proglottid; 8-1, averages of 53-55 testes per proglottid; 8-2, an average of 45 testes per proglottid; 8-3, an average of 31 testes per proglottid; 9-0, 69-79 loculi per bothridium; 9-1, 49-59 loculi per bothridium; 9-2, 41-45 loculi per bothridium.

*dularis* as having 51-59, and *R. mclennanae* as having 49-59. If we begin conservatively by recognizing 2 categories of loculi number, 69-79 and 45-59, functional outgroup analysis is consistent with the hypothesis that the plesiomorphic condition is 69-79 medial loculi, because *R. scorzai* and *R. circularis* are basal members of their respective subclades within *Rhinebothroides*. Character optimization supports either the hypothesis that 45-59 loculi is the plesiomorphic condition or that 69-79 is the plesiomorphic condition, because each hypothesis requires convergent evolution of the derived state. We have adopted the hypothesis that 69-79 loculi is the plesiomorphic condition, because two criteria (character optimization and functional outgroup analysis) are consistent with it. Using the plesiomorphic condition as a reference point, 2 groups of species exhibit derived conditions for numbers of bothridial loculi. First, the reported values of *R. freitasi*, *R. glandularis*, and *R. mclennanae* fall within 49-59 loculi, and we consider them to have the same state (9-1 in Table I and Fig. 5). Second, there appear to be 2 ways of interpreting the observations that *R. venezuelensis* has 51-53 loculi and *R. moralarai* has 45-49 loculi. On one hand, the total range of 45-53 loculi exhibited by the 2 species is not broader, and does not differ substantially from, that exhibited by the *R. freitasi-R. glandularis-R. mclennanae* group; therefore, these 2 species could be considered to exhibit a common trait that is convergent with the condition found in the *R. freitasi-R. glandularis-R. mclennanae* group. Alternatively, it could be recognized that although the value for *R. venezuelensis* falls within the values re-

ported for the *R. freitasi-R. glandularis-R. mclennanae* group, the values for *R. moralarai* fall below them. The only difference between the alternatives is the recognition of an autapomorphic trait for *R. moralarai*, so the phylogenetic tree topology is not affected. We have chosen the latter interpretation, which results in the hypothesis that the condition found in *R. venezuelensis* (9-1) is convergent with that found in the *R. freitasi-R. glandularis-R. mclennanae* group (9-1) and is plesiomorphic to the condition found in *R. moralarai* (9-2 in Table I and Fig. 5).

Third, proglottids of *Rhinebothroides* species may be craspedote or acraspedote (character 7 in Table I and Fig. 5). The general plesiomorphic condition among all eucestodes is acraspedote, but the derived condition, craspedote proglottids, appears to be a relatively common and convergent trait. Treating the craspedote condition as apomorphic for *Rhinebothroides* leads to the postulate that craspedote proglottids have appeared 2 times independently (7-1 in Fig. 5) and have been secondarily lost once (7-0 in Fig. 5).

Table I presents a data matrix summarizing the above character argumentation in a format suitable for computer-assisted analysis. Phylogenetic analysis of this matrix using the PAUP 3.0 computer program (all characters ordered, rooted with an all-zero outgroup function, Acctran or Deltran optimization, Branch and Bound option) produces the tree shown in Figure 5, with a consistency index of 75%.

## DISCUSSION

We collected specimens of 4 other species of cestodes in the *P. motoro* from near Corumba. These included *Potamotrygonocetus orinocoensis* Brooks, Mayes, and Thorson, 1981, *Acanthobothrium regoi* Brooks, Mayes, and Thorson, 1981, and *R. venezuelensis* Brooks, Mayes, and Thorson, 1981, which were known previously only from the delta of the Orinoco River in Venezuela (Brooks, Mayes, and Thorson, 1981) and which had never been collected in *P. motoro*. In addition, we collected specimens of *Rhinebothrium paratrygoni* Rego and Dias, 1976, known previously from the delta of the Orinoco River, the Rio Salobra, Mato Grosso, Brazil, and near Hohenau, Paraguay, but never previously collected in *P. motoro*. Thus, this report constitutes new host and locality records for all 4 species. Voucher specimens of them have been deposited in the collection of the Instituto Oswaldo Cruz (nos. 32.816a-f [*P. orinocoensis*, 15 specimens], 32.817a-f [*A. regoi*, 20 specimens], 32.818a-f [*R. venezuelensis*, 78 specimens], and 32.819a-f [*R. paratrygoni*, 7 specimens]) and the Harold W. Manter Laboratory, University of Nebraska State Museum (nos. 34094 [*P. orinocoensis*, 2 specimens], 34093 [*A. regoi*, 2 specimens], 34092 [*R. venezuelensis*, 3 specimens], and 34095 [*R. paratrygoni*, 1 specimen]).

TABLE II. Host-parasite list for helminths inhabiting neotropical freshwater stingrays, revised according to the taxonomy and nomenclature of Rosa (1985).\*

Host species Parasite species
<i>Potamotrygon magdalenae</i> (Valenciennes, 1865) <i>Potamotrygonocestus magdalenensis</i> Brooks and Thorson, 1976 <i>Acanthobothrium quinonesi</i> Mayes, Brooks, and Thorson, 1978 <i>Rhinebothroides moralarai</i> (Brooks and Thorson, 1976) Mayes, Brooks, and Thorson, 1981 <i>Paravitellotrema overstreeti</i> Brooks, Mayes, and Thorson, 1979
<i>Potamotrygon yepezi</i> Castex and Castello, 1970 <i>Potamotrygonocestus amazonensis</i> Brooks, Mayes, and Thorson, 1981 <i>Acanthobothrium quinonesi</i> Mayes, Brooks, and Thorson, 1978 <i>Rhinebothroides venezuelensis</i> Brooks, Mayes, and Thorson, 1981
<i>Potamotrygon orbignyi</i> (Castelnau, 1855) <i>Eutetrarhynchus araya</i> (Woodland, 1934) Rego and Dias, 1976 <i>Potamotrygonocestus amazonensis</i> Mayes, Brooks, and Thorson, 1981 <i>Potamotrygonocestus orinocoensis</i> Brooks, Mayes, and Thorson, 1981 <i>Acanthobothrium regoi</i> Brooks, Mayes, and Thorson, 1981 <i>Rhinebothrium paratrygoni</i> Rego and Dias, 1976 <i>Rhinebothroides venezuelensis</i> Brooks, Mayes, and Thorson, 1981 <i>Rhinebothroides glandularis</i> Brooks, Mayes, and Thorson, 1981 <i>Rhinebothroides scorzai</i> (Lopez-Neyra and Diaz-Ungria, 1958) Mayes, Brooks, and Thorson, 1981 <i>Echinocephalus daileyi</i> Deardorff, Brooks, and Thorson, 1981
<i>Potamotrygon constellata</i> (Vaillant, 1880) <i>Potamotrygonocestus amazonensis</i> Mayes, Brooks, and Thorson, 1981 <i>Acanthobothrium amazonensis</i> Mayes, Brooks, and Thorson, 1978 <i>Rhinebothroides circularisi</i> Mayes, Brooks, and Thorson, 1981 <i>Paraheteronchocotyle isalickisi</i> Mayes, Brooks, and Thorson, 1981 <i>Potamotrygonocotyle amazonensis</i> Mayes, Brooks, and Thorson, 1981 <i>Echinocephalus daileyi</i> Deardorff, Brooks, and Thorson, 1981
<i>Potamotrygon motoro</i> (Natterer, 1841) <i>Eutetrarhynchus araya</i> (Woodland, 1934) Rego and Dias, 1976 <i>Potamotrygonocestus orinocoensis</i> Brooks, Mayes, and Thorson, 1981 <i>Acanthobothrium regoi</i> Brooks, Mayes, and Thorson, 1981 <i>Acanthobothrium terezae</i> Rego and Dias, 1976 <i>Rhinebothrium paratrygoni</i> Rego and Dias, 1976 <i>Rhinebothroides scorzai</i> (Lopez-Neyra and Diaz-Ungria, 1958) Mayes, Brooks, and Thorson, 1981 <i>Rhinebothroides venezuelensis</i> Brooks, Mayes, and Thorson, 1981 <i>Leiperia gracile</i> (Diesing, 1835) <i>Brevimulticaecum</i> sp.
<i>Potamotrygon falkneri</i> Castex and Maciel, 1963 <i>Eutetrarhynchus araya</i> (Woodland, 1934) Rego and Dias, 1976 <i>Rhinebothrium paratrygoni</i> Rego and Dias, 1976
<i>Potamotrygon histrix</i> (Muller and Henle, 1844) (these records may not all refer to <i>P. histrix</i> ) <i>Eutetrarhynchus araya</i> (Woodland, 1934) Rego and Dias, 1976 <i>Potamotrygonocestus travassosi</i> Rego, 1979 species inquirenda <i>Rhinebothrium paratrygoni</i> Rego and Dias, 1976 <i>Rhinebothroides freitasi</i> Rego, 1979 <i>Megapiapus ungriai</i> Lopez-Neyra and Diaz-Ungria, 1958
<i>Paratrygon aiereba</i> (Muller and Henle, 1841) <i>Rhinebothroides scorzai</i> (Lopez-Neyra and Diaz-Ungria, 1958) Mayes, Brooks, and Thorson, 1981
<i>Paratrygon</i> sp. (as <i>Elipesurus</i> sp.) <i>Acanthobothrium terezae</i> Rego and Dias, 1976 <i>Rhinebothrium paratrygoni</i> Rego and Dias, 1976 <i>Rhinebothroides scorzai</i> (Lopez-Neyra and Diaz-Ungria, 1958) Mayes, Brooks, and Thorson, 1981

TABLE II. Continued.

Host species Parasite species
<i>Trygon</i> sp. (this could have been a species of <i>Plesiotrygon</i> , <i>Paratrygon</i> , or <i>Potamotrygon</i> ) <i>Eutetrarhynchus araya</i> (Woodland, 1934) Rego and Dias, 1976

\* Parasite records are from Woodland (1934), Lopez-Neyra and Diaz-Ungria (1958), Brooks and Thorson (1976), Rego and Diaz (1976), Mayes, Brooks, and Thorson (1978, 1981a, 1981b), Brooks, Mayes, and Thorson (1979, 1981), Rego (1979), Brooks, Thorson, and Mayes (1981), and Deardorff et al. (1981).

Brooks, Mayes, and Thorson (1981) suggested that identification of host species for helminths inhabiting neotropical freshwater stingrays was tentative in some cases, due to the confused nomenclature of the potamotrygonids. Because of this, they reported that they had deposited representative specimens of their hosts in the U.S. National Museum of Natural History. Subsequently, Rosa (1985) revised the family, including examination of the specimens deposited by Brooks, Mayes, and Thorson, and clarified many of the nomenclatural problems. According to Rosa's study, all previous records for *Potamotrygon histrix* and *Potamotrygon reticulatus* in the delta of the Orinoco River in Venezuela should be assigned to *Potamotrygon orbignyi*, and all records for *Potamotrygon circularis* collected near Leticia, Colombia, should be assigned to *Potamotrygon constellata*. Table II is a new host-parasite checklist for helminths inhabiting potamotrygonids reflecting Rosa's findings.

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