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Daniel R. Brooks

University of Toronto, dnlbrooks@gmail.com

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ORIGINS, DIVERSIFICATION, AND HISTORICAL STRUCTURE OF THE HELMINTH FAUNA INHABITING NEOTROPICAL FRESHWATER STINGRAYS (POTAMOTRYGONIDAE)*

Daniel R. Brooks

Department of Zoology, University of Toronto, Toronto, Ontario, Canada M5S 1A1

ABSTRACT: Members of the freshwater stingray family Potamotrygonidae occur throughout the major river systems of eastern South America that empty into the Atlantic Ocean. Ichthyologists have tended to assume that the ancestor of the potamotrygonids was an Atlantic marine or euryhaline stingray that dispersed into freshwater, presumably during the last marine ingressions 3–5 million years ago. The helminth parasites that inhabit potamotrygonids suggest an alternative perspective on their origin. Phylogenetic and biogeographic analysis of the helminths inhabiting potamotrygonids suggest that the hosts are derived from an ancestral Pacific urolophid stingray that was trapped in freshwater by the uplifting of the Andes beginning perhaps as early as the early Cretaceous period and ending by the mid-Miocene epoch, changing the course of the Amazon River, which previously had flowed into the Pacific Ocean.

Elasmobranchs are an old and diverse group of vertebrates inhabiting areas ranging from marine to fresh water. Marine elasmobranchs retain urea and other organic substances in their blood and tissue fluids, creating an internal osmotic environment comparable to the surrounding sea water. The rectal gland supplements kidney function, secreting salt in a fluid that has twice the concentration of body fluids. Euryhaline elasmobranchs function like marine species under conditions of high salinity; however, in less saline waters their urea concentration drops to 20–50% of marine levels, and rectal gland function either is reduced or stopped (see references in Thorson et al., 1983). Some of these animals, such as the bull sharks and sawfish of Lake Nicaragua, may spend extended periods in fully freshwater habitats.

Members of the stingray family Potamotrygonidae, the only elasmobranchs permanently adapted to freshwater habitats, occur throughout the major river systems of eastern South America. They cannot concentrate urea, although they produce some of the necessary enzymes, and their rectal glands are small and apparently nonfunctional. Not even physiological conditioning can induce these rays to concentrate urea or excrete salt (Thorson et al., 1983). The highly evolved nature of stingrays, relative to sharks and skates, and the absence of totally freshwater species in

any other elasmobranch group, led biologists to assume that potamotrygonids are derived from marine ancestors. The presence of a rectal gland and some of the enzymes for concentrating urea has been accepted as evidence that potamotrygonids are not a particularly old group. Furthermore, ichthyologists have tended to assume that the ancestor of the potamotrygonids was an Atlantic marine or euryhaline stingray that dispersed into fresh water because potamotrygonids are restricted to rivers that empty into the Atlantic Ocean.

Brooks et al. (1981) proposed an alternative perspective of the origins of the potamotrygonids, based on a series of studies using the helminth parasites that inhabit them. They began by establishing a sequence of questions to be answered: (1) Are potamotrygonids inhabited by helminth parasites that are related to helminths inhabiting other elasmobranchs? If not, then parasite evidence could not be used to determine anything about the evolutionary origins of potamotrygonids. If the helminths inhabiting potamotrygonids were related to those found in other elasmobranchs, however, they, their phylogenetic relationships, and their host and geographic affinities might provide evidence bearing on the origins of potamotrygonids. (2) Do the helminths inhabiting potamotrygonids form monophyletic groups? If so, then the most parsimonious hypothesis is that the potamotrygonids themselves are monophyletic and that their common ancestor brought the ancestors of the various helminth groups into fresh water with it. If not, then the most parsimonious explanation is that potamotrygonids are derived from more than 1 marine ancestor. (3) What is (are) the source(s) of

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TABLE I. Geographic distribution of 23 species of parasitic worms inhabiting South American freshwater stingrays. Locality 1, upper Parana, including the lower Mato Grosso; 2, mid-Amazon, near Manaus; 3, upper Amazon, near Leticia; 4, delta of the Orinoco; 5, Lake Maracaibo tributaries; 6, mid- to lower Magdalena. Species are numbered for phylogenetic and biogeographic analysis. +, present at locality; 0, absent at locality.

Parasite species	Locality					
	1	2	3	4	5	6
1. <i>Acanthobothrium quinonesi</i>	0	0	0	0	+	+
2. <i>Acanthobothrium regoi</i>	0	0	0	+	0	0
3. <i>Acanthobothrium amazonensis</i>	0	0	+	0	0	0
4. <i>Acanthobothrium terezae</i>	+	0	0	0	0	0
8. <i>Potamotrygonocestus magdalenensis</i>	0	0	0	0	0	+
9. <i>Potamotrygonocestus orinocoensis</i>	0	0	0	+	0	0
10. <i>Potamotrygonocestus amazonensis</i>	0	0	+	+	+	0
13. <i>Rhinebothroides moralarai</i>	0	0	0	0	0	+
14. <i>Rhinebothroides venezuelensis</i>	0	0	0	+	+	0
15. <i>Rhinebothroides circularisi</i>	0	0	+	0	0	0
16. <i>Rhinebothroides scorzai</i>	+	0	0	+	0	0
17. <i>Rhinebothroides freitasi</i>	0	+	0	0	0	0
18. <i>Rhinebothroides glandularis</i>	0	0	0	+	0	0
19. <i>Rhinebothroides mclennanae</i>	+	0	0	0	0	0
26. <i>Eutetrarhynchus araya</i>	+	+	0	+	0	0
27. <i>Rhinebothrium paratrygoni</i>	+	+	0	+	0	0
28. <i>Paraheteronchocotyle tsalickisi</i>	0	0	+	0	0	0
29. <i>Potamotrygonocotyle amazonensis</i>	0	0	+	0	0	0
30. <i>Echinocephalus daileyi</i>	0	0	+	+	0	0
31. <i>Paravitellotrema overstreeti</i>	0	0	0	0	0	+
32. <i>Terranova edcaballeroi</i>	0	0	0	+	0	0
33. <i>Megapriapus ungriai</i>	0	0	0	+	0	0
34. <i>Leiperia gracile</i>	+	0	0	0	0	0
35. <i>Brevimulticaecum</i> sp.	+	0	0	0	0	0

the helminths? The geographic distribution of their marine sister groups would provide an estimate of the general geographic area from which the ancestral potamotrygonid and its helminth fauna came. (4) What has been the pattern of diversification for the helminth fauna in potamotrygonids? For example, if they arrived relatively recently in freshwater and had speciated as a result of independent dispersal, potamotrygonids and their parasites should not show correlated patterns of speciation with organisms that evolved in the freshwater habitats. (5) And finally, how long ago did potamotrygonids arrive in freshwater habitats? Correlated biogeographic and phylogenetic patterns often can provide a robust estimate of age of groups, even in the absence of a fossil record; in fact, as I will show later, this study provides just such an example. In addition, the degree of complexity of a geographic distribution pattern for a group of species often is correlated with the length of time the group has been in an area.

Twenty-four species of parasitic worms have been found inhabiting potamotrygonids thus far. Four of the 24 parasite species listed in Table I inhabit either teleosts (*Paravitellotrema overstreeti*, *Terranova edcaballeroi*) or crocodilians

(*Leiperia gracile*, *Brevimulticaecum* sp.), and local potamotrygonids appear to have picked them up, at least on occasion (in my experience, they are not commonly found in potamotrygonids). Nineteen of the remaining 20 species of parasites are restricted to potamotrygonids (the exception being *Megapriapus ungriai*, the only acanthocephalan known to inhabit elasmobranchs and whose relationships to other acanthocephalans is uncertain). The closest relatives to those species inhabit marine stingrays, so it seems likely that most of the parasite groups inhabiting potamotrygonids were brought into neotropical freshwater habitats with the ancestor of the stingrays themselves.

Fourteen of the 19 species belonging to groups inhabiting elasmobranchs are members of 3 clades (Fig. 1), whereas the remaining species each represent a different clade. On the basis of this information, it would appear that the helminth fauna of potamotrygonids is an assemblage of monophyletic groups and single species, supporting the hypothesis that potamotrygonids arose from a single invasion of freshwater habitats in South America.

Phylogenetic hypotheses postulating the sister groups for some, but not all, of the helminths

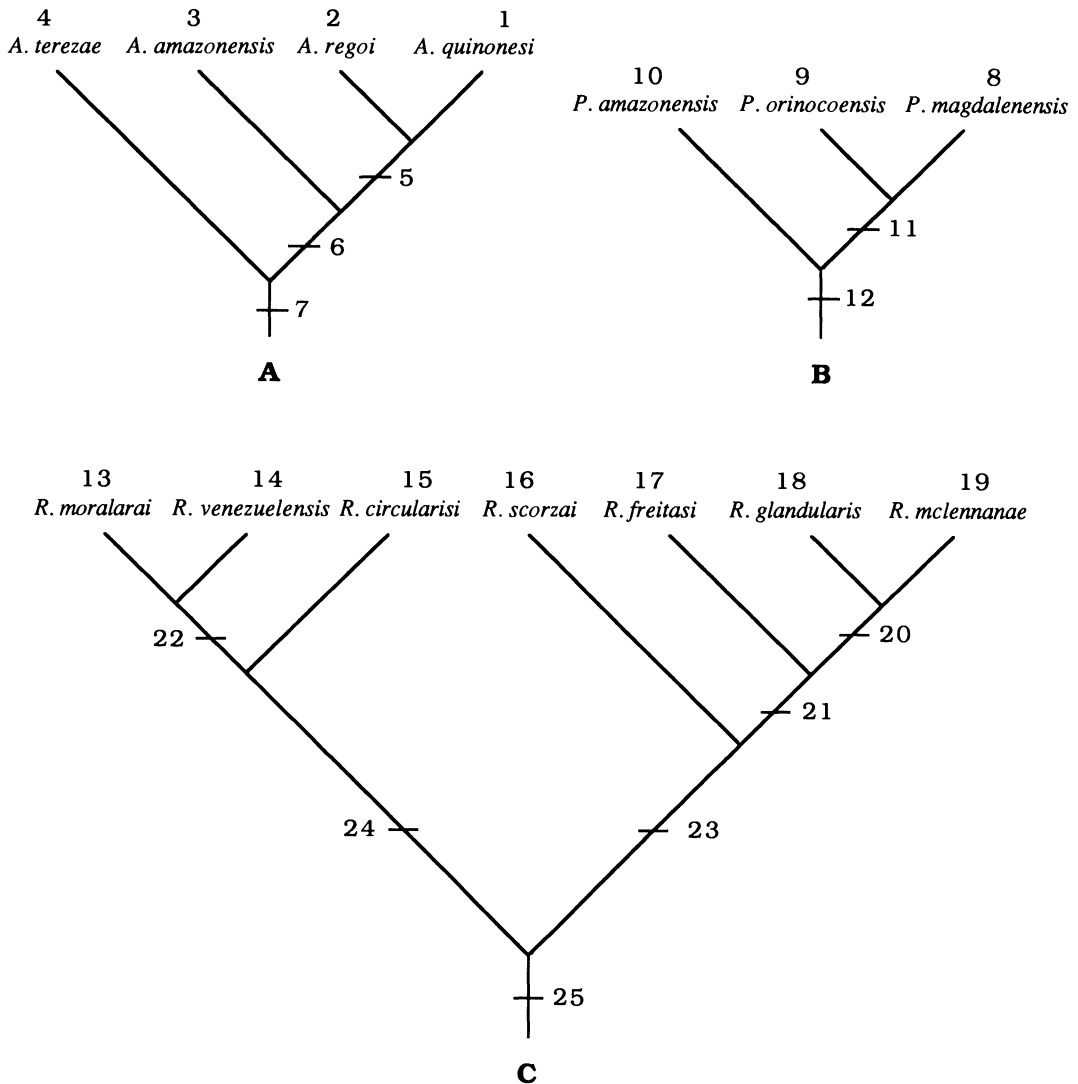


FIGURE 1. Phylogenetic trees for *Potamotrygonocestus*, the species-group of *Acanthobothrium* inhabiting potamotrygonid stingrays, and *Rhinebothroides*, coded for Brooks parsimony analysis (numbers above species names represent extant species; numbers above nodes indicate the phylogenetic relationships among extant species; see Brooks and McLennan [1991] for discussion of the method). A. Species group within *Acanthobothrium*. B. Species within *Potamotrygonocestus*. C. Species within *Rhinebothroides*.

inhabiting potamotrygonids indicate that the helminth fauna of potamotrygonids arose in the Pacific Ocean, and that many of the closest relatives of the helminth fauna of potamotrygonids inhabit urolophid stingrays. This suggests that the ancestor of the potamotrygonids was a marine urolophid living in the Pacific Ocean. This observation, by itself, is troublesome, because no potamotrygonid is known from river systems that empty into the Pacific Ocean. Consideration of the pattern of diversification for the helminth

species inhabiting potamotrygonids provides additional relevant information.

The geographic distribution patterns for the parasites of potamotrygonids are complex; some of the parasite species appear to be restricted to single river systems whereas others are more widespread (Table I). Table II is a data matrix for 6 localities based on the phylogenetic relationships and distributions of the stingray helminths. Phylogenetic analysis of the data matrix derived using parasites and their phylogenetic

TABLE II. Matrix listing 6 river systems in eastern South America and the binary codes representing the phylogenetic relationships for members of the helminth parasite groups inhabiting freshwater stingrays residing in those areas. Presence of a species in an area is indicated by 1 for the number associated with the species in Table I, plus 1 for each number indicating the relative phylogenetic relationships among members of *Acanthobothrium*, *Potamotrygonocestus*, and *Rhinebothroides* in Figure 1.

Area	Binary code
Leticia, upper Amazon	00100110010100100000000110011100000
Manaus, middle Amazon	00000000000000001000101011100000000
Upper Parana River	0101111010110101001111111101000111
Orinoco Delta	01001110111101010100111111100101100
Lake Maracaibo	10001110010101000000010110000000000
Magdalena River	10001111001110000000010110000010000

relationships as characters (a method proposed by Brooks [1981] and named Brooks parsimony analysis or BPA by Wiley [1988]; see Brooks and McLennan [1991] for discussion of the method) produces the area cladogram shown in Figure 2.

This area cladogram has a consistency index of 81%, supporting a qualitative assessment that approximately 80% of the species occur in these areas as a result of common phylogenetic history.

On the basis of this initial analysis, the upper Parana, Orinoco, and Maracaibo localities appear to be composite areas. Recoding the data matrix, separating the upper Parana, the Orinoco, and Lake Maracaibo into multiple areas (Table III), and performing a phylogenetic analysis of this matrix, produces a new area cladogram (Fig. 3) with a consistency index of 91%. This new area cladogram highlights 5 evolutionary components that have contributed to this helminth fauna. The first component is the historical geological, or vicariant, backbone linking the upper Amazon, upper Parana, Orinoco, and Magdalena areas. These areas all contain species whose phylogenetic relationships correspond to a common set of biogeographic relationships. The remaining components of the parasite distribution patterns involve 4 sequences of dispersal from these areas along the following routes: from the upper Amazon into the Orinoco and Maracaibo areas; from the upper Parana to the mid-

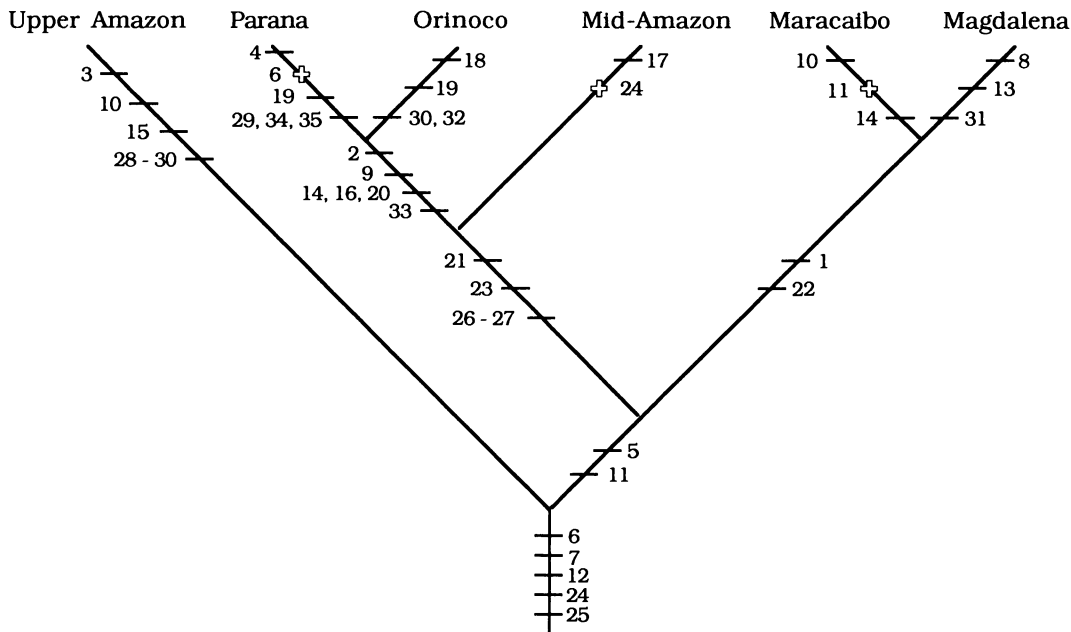


FIGURE 2. Area cladogram depicting relationships among the upper Amazon, upper Parana, middle Amazon, Orinoco, Maracaibo, and Magdalena areas based on the phylogenetic relationships of the helminths known to inhabit freshwater stingrays in those areas. Numbers represent codes for species of *Potamotrygonocestus*, the species group of *Acanthobothrium* inhabiting potamotrygonid stingrays, and *Rhinebothroides* and their phylogenetic relationships (1–25), plus taxa represented by single species (26–35) (see Fig. 1 and Table I). +, putative secondary absence of the taxa represented by the number(s) accompanying the +.

TABLE III. Matrix listing 6 river systems in eastern South America and the binary codes representing the phylogenetic relationships for members of the helminth parasite groups inhabiting freshwater stingrays residing in those areas, based on duplicating the upper Parana River, Orinoco River delta, and Lake Maracaibo areas 3 times following the method described by Brooks and McLennan (1991). Presence of a species in an area is indicated by 1 for the number associated with the species in Table I, plus 1 for each number indicating the relative phylogenetic relationships among members of *Acanthobothrium*, *Potamotrygonocestus*, and *Rhinebothroides* in Figure 1. ?, taxon not known from the area.

Area	Binary code
Leticia, upper Amazon (MA)	00100110010100100000000110011100000
Upper Parana River (P1)	00010011????0001000000101000100111
Upper Parana River (P2)	0100111010110100000001011000000000
Upper Parana River (P3)	????????00000011101011100000000
Manaus, mid-Amazon (UA)	????????00001000101011100000000
Orinoco Delta (O ₁)	010011101011????????0000001100
Orinoco Delta (O ₂)	?????00101????????1100000000
Orinoco Delta (O ₃)	????????00000101101010000100000
Orinoco Delta (O ₄)	????????01000000010110000000000
Lake Maracaibo (Mar ₁)	1000111????????????00000000000
Lake Maracaibo (Mar ₂)	?????00101????????00000000000
Lake Maracaibo (Mar ₃)	????????01000000010110000000000
Magdalena River (Mag)	1000111001110000000010110000010000

Amazon to the Orinoco; from the upper Parana to the Orinoco; and from the Orinoco to the upper Parana. Such complex distribution patterns also support the conclusion that potamotrygonids have been in the neotropics for a long time.

The question of how long ago the ancestor of the potamotrygonids arrived in neotropical freshwater habitats can be approached from several perspectives. Assumptions about the evolutionary sequence of osmoregulatory modifications and observations of current geographic distribution led many ichthyologists to think that potamotrygonids were the recently derived descendants of marine stingrays. The most common evolutionary scenario postulated that the potamotrygonid ancestor moved from the Atlantic Ocean into the Amazon basin during the marine ingression of the Pliocene epoch 3–5 million years ago. Subsequent to this invasion, a population was isolated from the ancestor, progressively adapting to fresh water and spreading

throughout South America by stream capture. The area cladogram (Fig. 3), however, is consistent with the geographic distribution patterns of endemic members of the fish fauna, many of whose members have fossil representatives reaching back into the Mesozoic era. It is congruent also with hypothesized geological history of the region, which links the origins of the major South American river systems with the uplifting of the Andes beginning early in the Cretaceous period, especially the reversal of flow of the Amazon in the mid-Miocene epoch (see Brooks et al. [1981] and Windley [1986] for discussion and references to the geological evidence supporting this interpretation; see Fig. 4 for a pictorial representation of the biogeographic history suggested by the area cladogram). It appears, then, that potamotrygonids are not relatively recent invaders of the neotropics.

The geography of South America prior to the mid-Miocene epoch differed in three significant ways from what we see today: Africa and South America were joined (i.e., there was no Atlantic Ocean at the mouth of the Amazon), the Andes began sweeping upward from the south beginning in the early Cretaceous period and moving northward, and the Amazon River flowed into the Pacific Ocean until the mid-Miocene epoch, when it was blocked by Andean orogeny, becoming an inland sea and eventually opening to the Atlantic Ocean. Thus, if potamotrygonids are a relatively old component of neotropical freshwater diversity east of the Andes, they must have come from the Pacific Ocean, which is today west of the Andes. If this is the case, the parasites inhabiting potamotrygonids, or their closest relatives, should inhabit marine stingrays whose geographic distribution is consistent with a hypothesis that the group originated as a result of marine invasion of South America no later than the mid-Miocene epoch.

Enlarging the spatial scale of this study to include the geographic distribution of the marine relatives of the parasites inhabiting potamotrygonids provides additional support for the hypothesis that these stingrays and their parasites originated from marine ancestors that were isolated in South America from the Pacific Ocean by the Andean orogeny. The closest relatives of the parasites inhabiting potamotrygonids occur in Pacific marine (primarily urolophid) stingrays, and those members of 2 groups for which phylogenetic hypotheses exist appear to exhibit circum-Pacific rather than trans-Pacific distribu-

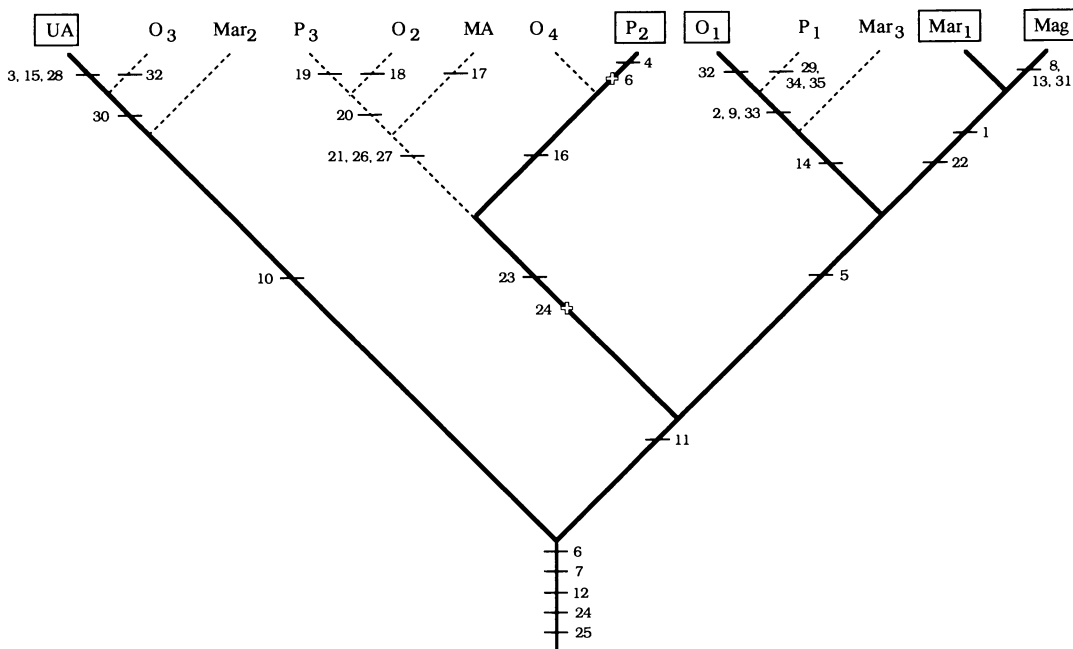


FIGURE 3. Area cladogram depicting relationships among the upper Amazon, upper Parana, middle Amazon, Orinoco, Maracaibo, and Magdalena areas based on the phylogenetic relationships of the helminths known to inhabit freshwater stingrays in those areas, produced by duplicating composite areas according to the Brooks parsimony analysis method described by Brooks and McLennan (1991). UA, upper Amazon; MA, middle Amazon; O, Orinoco; Mar, Maracaibo; Mag, Magdalena; P, Parana. Numbers represent codes for species of *Potamotrygonocestus*, the species group of *Acanthobothrium* inhabiting potamotrygonid stingrays, and *Rhinebothroides* and their phylogenetic relationships (1–25), plus taxa represented by single species (26–35) (see Fig. 1 and Table I). +, Putative secondary absence of the taxa represented by the number(s) accompanying the +. Solid lines, putative vicariant events; dashed lines, putative dispersal events.

tion patterns (Brooks et al., 1981; Brooks and Deardorff, 1988). A similar Pacific origin has been suggested for Amazonian freshwater anchovies (Nelson, 1984) and possibly for neotropical freshwater needlefish (Collette, 1982). In addition, each of the parasite species inhabiting potamotrygonids probably requires a mollusc or arthropod intermediate host, so it seems likely that mollusc and arthropod species derived from marine ancestors also moved into neotropical freshwater habitats along with the ancestor of the potamotrygonids.

As a consequence of this study and the others cited above, we now recognize the possibility that a sizeable component of current neotropical freshwater diversity might be derived from Pacific marine ancestors. Because the uplifting of the Andes has rendered this portion of the neotropical biota nonrenewable, we should be interested in the conservation status of potamotrygonids. This is especially true now that potamotrygonids have become popular in the tropical fish trade.

Finally, I suggested above that correlations of geographic distribution patterns and phylogenetic relationships of helminths could provide a robust estimate of the age of origin for a group, even in the absence of a fossil record. A decade after the first proposal of Pacific origins of the potamotrygonids, potamotrygonid fossils have been collected recently from deposits of the mid-Miocene epoch in the Amazonian portion of Peru (Frailey, 1986) and Colombia (J. Lundberg, pers. comm.). Thus, this study represents a graphic empirical example of the utility of combining parasite phylogeny and historical biogeography to answer questions about evolutionary origins in the manner first envisioned by von Ihering, Kellogg, Harrison, and Johnston, amplified by Metcalf, and kept alive by Manter until the advent of modern methods of phylogenetic systematics (see Klassen, 1992).

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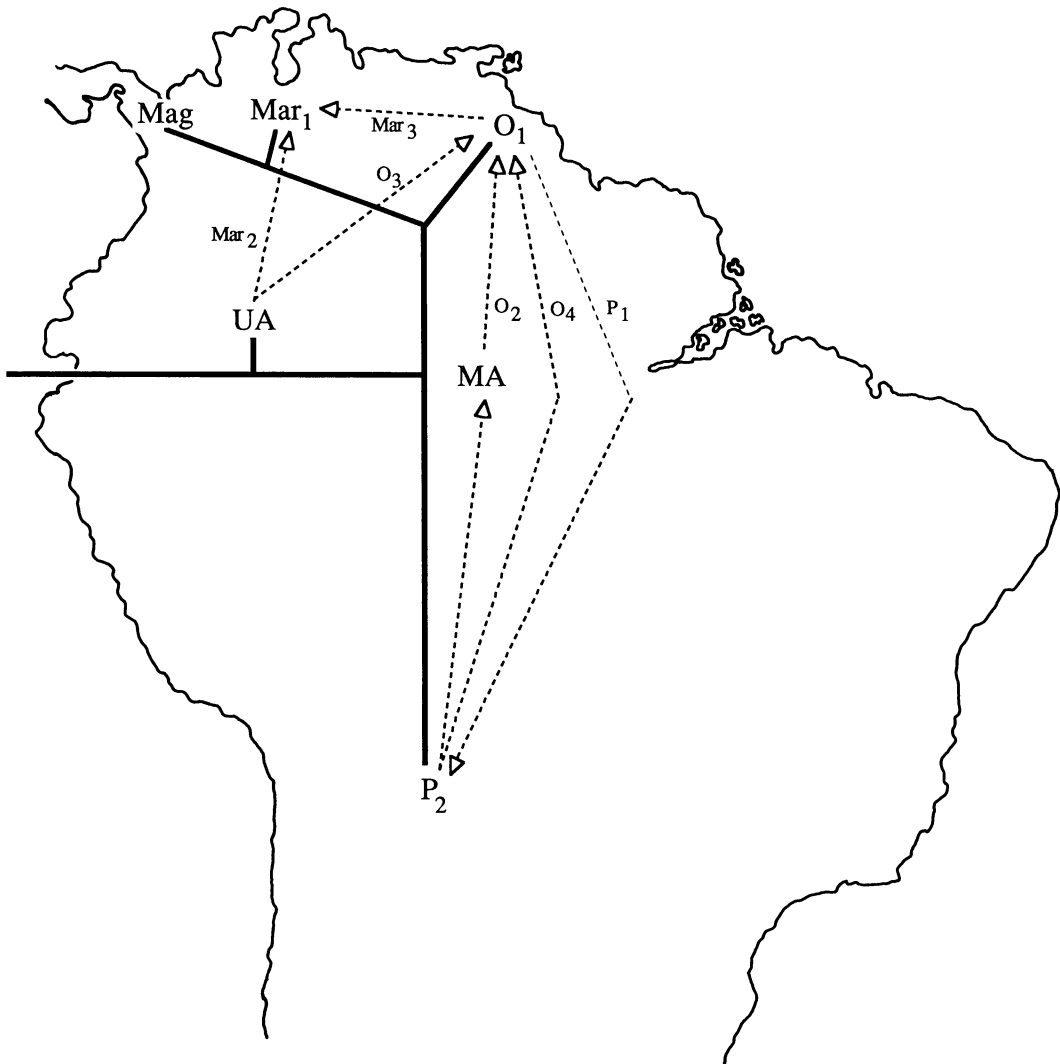


FIGURE 4. Map of South America showing complex patterns of evolutionary diversification for the helminth fauna of potamotrygonid stingrays. Heavy solid lines, putative vicariant elements; dashed lines, putative dispersal elements. UA, upper Amazon; O, Orinoco; MA, middle Amazon; Mar, Maracaibo; Mag, Magdalena; P, Parana.

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