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Miocene marine incursions and marine/freshwater transitions: Evidence from Neotropical fishes

Nathan R. Lovejoy [a,*], James S. Albert [b], William G.R. Crampton [a]

[a] *Department of Life Sciences, University of Toronto at Scarborough, 1265 Military Trail, Toronto, Ont. MIC 1A4, Canada*
[b] *Department of Biology, University of Louisiana at Lafayette, P.O. Box 42451, Lafayette, LA 70504, USA*

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Abstract

Amazonian rivers contain a remarkable fauna of endemic species derived from taxa that generally occur in oceans and seas. Several hypotheses have been proposed to explain the origin of marine-derived lineages, including opportunistic invasions via estuaries, vicariance related to uplift of the Andes, and vicariance related to Miocene marine incursions and connections. Here, we examine available data for marine-derived lineages of four groups: stingrays (Myliobatiformes), drums (Sciaenidae), anchovies (Engraulididae), and needlefish (Belonidae). Geographic distributions, age estimates (determined using fossils, biogeography, and molecular data sets), and phylogenies for these taxa are most compatible with origination during the Miocene from marine sister groups distributed along the northern coast of South America. We speculate that unique ecological and biogeographic aspects of the Miocene upper Amazonian wetland system, most notably long-term connections with marine systems, facilitated the evolutionary transition from marine to freshwater habitats.

Keywords: Amazon; Biogeography; Fishes; Freshwater; Marine; Pebas/Solimões; Systematics

1. Introduction

Neogene paleogeographic and paleoenvironmental changes, such as the emergence of the Andes, incursions of marine waters into formerly freshwater systems, and the reorientation of major river drainages, have exerted profound effects on the evolution of the South American aquatic biota. Here, we consider the possible influence of Miocene marine incursions and connections on the evolution of the Amazonian fish fauna. In particular, we examine the possibility that Miocene marine incursions may have prompted the evolutionary transition from marine to freshwater habitats. This hypothesis makes several phylogenetic and biogeographic predictions, which we test using fish clades for which appropriate data are available.

The Neotropical ichthyofauna is dominated by fishes that have a relatively ancient association with freshwater habitats, such as the Characiformes and Siluriformes. The geographic distribution of these taxa in freshwater of both South America and Africa (and other continents, in the case of Siluriformes) suggests that their initial diversification occurred prior to the Cretaceous breakup of Gondwana. However, the Amazon Basin is also home to a diverse assemblage of freshwater representatives of predominantly marine fish lineages, such as stingrays, needlefishes, and anchovies (Roberts, 1972; Goulding, 1980). These freshwater species or groups, based on available biogeographic, phylogenetic, and/or taxonomic data, appear to have entered South America more recently (since the isolation of the continent by the Cretaceous opening of the Atlantic). Such taxa display a diversity of biogeographic and phylogenetic patterns, categorized here as four types (Fig. 1): (1) species whose ranges currently span freshwater, estuarine, and marine habitats, such as the bull shark *Carcharhinus leucas* (de Carvalho and McEachran, 2003a) and the sawfish *Pristis pristis* (de Carvalho and McEachran, 2003b); (2) species whose ranges include the lower reaches of rivers and their estuaries and are probably tolerant of brackish water, such as the herrings *Rhinosardinia amazonica* and *Rhinosardinia bahiensis* (Whitehead, 1985); (3) species that are unique and endemic freshwater representatives of marine clades and whose distributions are sometimes distant from marine waters, such as the anchovy *Jurengraulis juruensis* (Whitehead et al., 1988); and (4) species that appear to be members of endemic Neotropical freshwater radiations with distributions that encompass multiple river basins, such as stingrays of the

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* Corresponding author.
E-mail address: lovejoy@utsc.utoronto.ca (N.R. Lovejoy).

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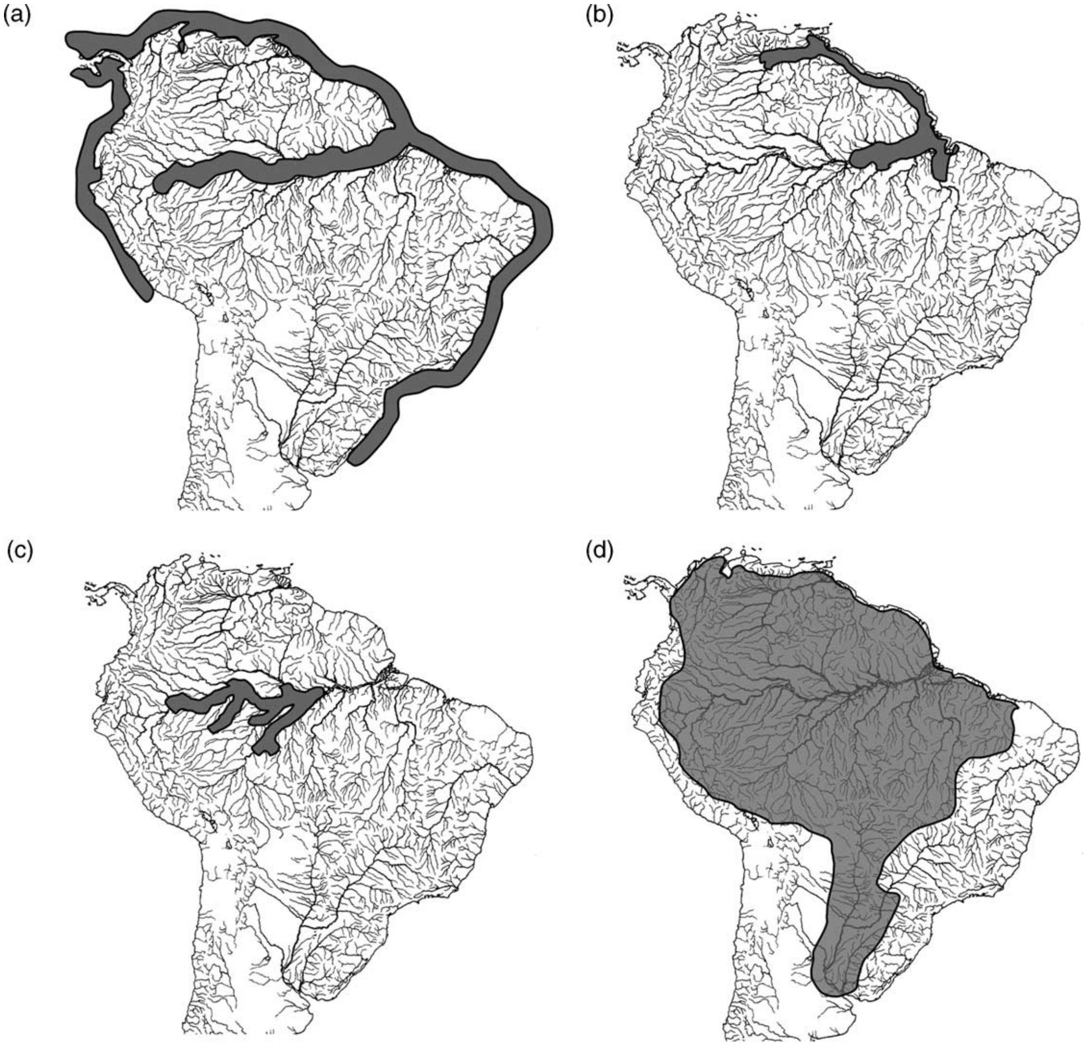

Fig. 1. Examples of four distribution types (in grey) of marine-derived species and lineages in the Amazon: (a) Type 1, the bullshark *Carcharhinus leucas* (Compagno, 1984; de Carvalho and McEachran, 2003a); (b) Type 2, the herring *Rhinosardinia amazonica* (Whitehead, 1985); (c) Type 3, the anchovy *Jurengraulis juruensis* (Whitehead et al., 1988); and (d) Type 4, stingrays of the family Potamotrygonidae (de Carvalho et al., 2003; Rosa, 1985).

family Potamotrygonidae (Lovejoy, 1996; Lovejoy et al., 1998).

The diversity of biogeographic patterns exhibited by marine-derived species and lineages in Amazonia suggests that an array of processes and events probably is involved in their origin and evolution. Type 1 taxa, such as the bullshark, are physiologically tolerant of varying salinities, and movements between habitat types may occur repetitively and opportunistically at the level of the individual organism. Type 2 taxa may be the products of recent or incipient speciation, possibly as a result of divergence between marine and estuarine populations (Beheregaray and Sunnucks, 2001; Beheregaray et al., 2002; Bilton et al., 2002). Type 3 and 4 marine-derived lineages (MDLs) may be the products of considerably older biogeographic events (e.g. Lovejoy et al., 1998) and are the focus of this article. Table 1 lists marine-derived fishes from the Amazon Basin; our study considers the subset of type 3 and 4 taxa with sufficient phylogenetic data for analysis. Other potential MDLs include iniid dolphins (Grabert, 1984; Cassens et al., 2000; Hamilton et al., 2001); manatees (Domning, 1982, 2001); several invertebrate taxa, including shrimp, crabs, and molluscs (Nuttall, 1990; Wesselingh et al., 2002); and various marine-derived parasite lineages (e.g. Brooks et al., 1981; Marques, 2000; Boeger and Kritsky, 2003). These taxa are not treated here.

Roberts (1972), comparing the fish faunas of the Congo and Amazon basins, noted the higher number of fish MDLs in Amazonian rivers and suggested this difference could be due to the relative accessibility of the two systems to marine invaders. Whereas the Congo is isolated by rapids in its lower reaches, the lower Amazon is not, and its vast estuaries may have served as an arena for the evolution of freshwater tolerance. An alternative vicariance-based hypothesis, presented by Brooks et al. (1981; see also Brooks, 1992), states that stingrays and other marine-derived fish taxa were isolated in a Pacific-derived inland sea by the emergence of the Andes. However, this analysis has been criticized (Lovejoy, 1997), and its paleogeographic underpinning is out of date; for example the idea that ‘the Amazon River flowed into the Pacific Ocean until the mid-Miocene epoch, when it was blocked by Andean

Table 1
Marine-derived Amazonian fish species and lineages

	Marine-derived genera/species	Biogeographic type (see text)	Reference
Carcharhinidae (Requiem sharks)	*Carcharhinus leucas*	Type 1	de Carvalho and McEachran (2003a)
Pristidae (Sawfishes)	*Pristis pectinata*, *pristis pristis*	Type 1	de Carvalho and McEachran (2003b)
Myliobatiformes (Stingrays)	*Potamotrygonidae*: *Potamotrygon*, *Paratrygon, Plesiotrygon* (1 MDL)	Type 4	Lovejoy (1996); Lovejoy et al. (1998); Marques (2000)
Megalopidae (Tarpons)	*Megalops atlanticus* (possible in Amazon)	Type 1	Ferraris (2003a)
Ophichthidae (Snake eels)	*Stictorhinus potamius*	Type 3	Böhlke and McCosker (1975)
Clupeidae (Herrings)	*Rhinosardinia amazonica*, *Rhinosardinia bahiensis*	Type 2	Whitehead (1985)
Engraulididae (Anchovies)	*Amazonsprattus*, *Anchoa? Anchovia*, *Anchoviella*, *Jurengraulis*, *Lycengraulis*, *Pterengraulis* (multiple MDLs)	Probably types 1, 2, 3, and 4	Whitehead et al. (1988)
Pristigasteridae (Pristigasterids)	*Ilisha amazonica*, *Pellona*, *Pristigaster* (multiple MDLs)	Probably types 3 and 4	Whitehead (1985); de Pinna and Di Dario (2003)
Batrachoididae (Toadfishes)	*Potamobatrachus trispinosus*, *Thalassophryne amazonica* (probably 2 MDLs)	Type 3	Collette (2003a)
Belonidae (Needlefishes)	*Belonion*/*Potamorrhaphis*, *Pseudotylosurus* (2 MDLs)	Type 4	Lovejoy and Collette (2001)
Hemiramphidae (Halfbeaks)	*Hyporhamphus brederi*	Type 3	Collette (2003b)
Sygnathidae (Pipefishes)	Three species reported from Atlantic drainages of South America (one or more possible in Amazon)	Type 1	Ferraris (2003b)
Sciaenidae (Drums)	*Plagioscion*, *Pachypops*, *Pachyurus*, *Petilipinnis* (probably 2 MDLs)	Type 4	Casatti (2000; 2003)
Mugilidae (Mullets)	*Agonostomus monticola*	Type 1	Goulding (1980)
Gobiidae (Gobies)	*Awaous*, *Dormitator*, *Eleotris*, *Gobiodes*, *Microphilypnus*	All type 1 or 2, except Microphilypnus (Type 4)	Kullander (2003a); Myers (1927)
Achiridae (American soles)	*Achiropsis*, *Achirus*, *Apionichthys*, *Hypoclinemus*, *Pnictes*, *Soleonasus*	Probably types 1, 2, 3; possibly type 4	Ramos (2003)
Tetraodontidae (Pufferfishes)	*Colomesus asellus*, *Colomesus psittacus*	Type 1 (C. psittacus), type 3 (C. asellus)	Kullander (2003b)

orogeny, becoming an inland sea and eventually opening to the Atlantic' (Brooks, 1992: 592) is not accurate (Lundberg et al., 1998). More recently, it has been proposed that fish MDLs may have originated as a result of Miocene marine incursions that extended to the upper Amazon (Webb, 1995; Lovejoy et al., 1998; Boeger and Kritsky, 2003).

The upper Amazon was affected by marine incursions at least twice during the Neogene (Hoorn, 1993, 1994a,b, 1996; Lundberg et al., 1998). These were not the first marine influences in the region; earlier incursions have been documented during the Paleocene and Eocene (for a review, see Lundberg et al., 1998). The extent and timing of Neogene marine incursions in Amazonia is currently controversial. Some authors have suggested that marine incursions were relatively long lasting and widespread (e.g. Räsänen et al., 1995, 1998; Webb, 1995; Gingras et al., 2002). Others imply that the predominant depositional context of Miocene Amazonia was freshwater, interspersed with brief and geographically limited bouts of marine influence (e.g. Hoorn, 1996, Vonhof et al., 1998; 2003; Wesselingh et al., 2002). However, there is general agreement that some form of connection existed between the upper Amazon and the Caribbean (probably via the Los Llanos Basin of Venezuela), as evidenced by fossil marine fishes (Monsch, 1998), mangroves (Hoorn, 1993, 1994a,b), and ichnofossils (Gingras et al., 2002). In addition, mollusc fossils and isotope data confirm the presence of saline waters in the upper Amazon, particularly during the Late Middle Miocene (~12–11 Ma in the *Grimsdalea* pollen zone) (Hoorn, 1993; Vonhof et al., 1998, 2003; Monsch, 1998; Wesselingh et al., 2002) and the Late Early Miocene (~22–16.5 Ma) (Hoorn, 1994a; Wesselingh et al., 2002).

Wesselingh et al. (2002) document a long-standing (25–8 Ma), immense wetland complex in the upper Amazon (often referred to as 'Lake Pebas' or 'Pebas system') that was connected, via the Los Llanos Basin, to the marine waters of the Caribbean. Several invertebrate taxa that diversified in this wetland system were marine derived (Nuttall, 1990; Vermeij and Wesselingh, 2002; Wesselingh et al., 2002). Nuttall (1990: 351) provides a scenario to explain the evolutionary transition from marine to freshwater habitats: 'It would not seem to be necessary for the connection between the sea and the heart of the basin to be direct at any one time. A series of lakes continually splitting and merging with each other, or perhaps becoming reconnected by streams, would enable taxa to progress gradually from one area to another.' Thus, freshwater species could have evolved from marine ancestors by a complex series of interconnected water bodies of varying salinity. The transition might also have been more abrupt, with marine species transported far inland during one of the more extensive marine incursions and 'stranded' in progressively desalinized habitats.

If MDLs originated as a result of marine incursions or connections with the Miocene upper Amazon wetland system, distinct patterns should appear in analyses of phylogenies, distributions, fossils, and molecular estimates of clade age. First, phylogenetic analyses of MDLs should show that their sister taxa are distributed in marine areas that are near the source(s) of the marine incursions. The Caribbean is considered the most likely source of the Miocene marine

Fig. 2. Map of South America, showing hypothesized sources of marine incursions during the Miocene. The Caribbean is considered the most likely source.

influences and incursions into the upper Amazon (Hoorn et al., 1995; Wesselingh et al., 2002; Vermeij and Wesselingh, 2002), though Nuttall (1990) also considered three other possible sources: an eastern connection along the course of the current Amazon River, a southern connection via the Río Paraná Basin, and a western connection across the Andes to the Pacific (Fig. 2). For a variety of reasons, these alternative routes of marine incursions are considered unlikely during the Miocene (e.g. Hoorn et al., 1995; Lundberg et al., 1998), but we make note of the presence of marine sister taxa in these areas. Second, estimates of the age of divergence between MDLs and their marine sister clades should fall within the Miocene. Age can be estimated using a variety of approaches, including analyses of fossils, molecular divergences, and biogeography (Lundberg, 1998). Third, because a particular paleogeographic event may be responsible for the origin of several different groups in freshwater, we expect phylogenetic and biogeographic congruence between unrelated lineages. We consider these predictions for four groups of fishes for which appropriate data are available: stingrays, drums, anchovies, and needlefishes. We consider congruence after we summarize the patterns from all taxa.

2. Stingrays

The more than 20 species of freshwater stingrays that make up the family Potamotrygonidae have a wide distribution that includes most Atlantic drainages of South America (de Carvalho et al., 2003). Lovejoy (1996) and McEachran et al. (1996) present stingray phylogenies based on morphological data, and Lovejoy et al. (1998), Marques (2000), and Dunn et al. (2003) propose molecular-based trees. These studies support the monophyly of the Neotropical freshwater stingrays and identify a pair of marine stingrays, *Himantura schmardae* from the western Atlantic (WA) and *H. pacifica* from the eastern Pacific (EP), as the sister taxon of freshwater potamotrygonids. This biogeographic pattern—a freshwater South American group with a marine sister lineage with representatives in both the Atlantic and Pacific—is repeated in several clades of stingray helminth parasites (Brooks et al., 1981; Lovejoy, 1997; Hoberg et al., 1998).

The current distribution of *H. schmardae* and *H. pacifica* includes, respectively, the Caribbean coast of South America and the Pacific coast of Central America (Lovejoy et al., 1998). The distribution does not overlap the putative source of Pacific marine incursions (the 'Marañon portal'), nor does it include the mouths of the Amazon or the Paraná, which could be likely sources of recent invasions (Table 2). Of course, the current distribution of these *Himantura* species may not accurately reflect their distributional range when they split from freshwater forms in the distant past. Also, further sampling of these poorly known species may result in range extensions. However, our current understanding of the distribution of the marine sister clade is most compatible with a Caribbean ancestry for freshwater forms.

Data pertaining to the origins of potamotrygonids are available from analyses of DNA sequences, geographic distributions, and fossils (Table 2). Lovejoy et al. (1998) use a mitochondrial cytochrome *b* sequence data set to estimate the time of divergence between potamotrygonids and their marine sister taxon. The result was an Early Miocene age for Potamotrygonidae. More recently, cytochrome *b* sequences from additional species have been collected and analyzed in detail by Marques (2000), who determined a similar age of divergence for potamotrygonids (19 Ma), though the inclusion of confidence limits places the range of possible divergence at 6–38 Ma. (Late Miocene–Early Oligocene/Late Eocene).

Additional data regarding the minimum age of potamotrygonids can be inferred from the geographic distribution of relevant taxa on either side of geographic barriers with known ages. The distribution of *H. schmardae* and *H. pacifica* on either side of the Isthmus of Panama indicates that the divergence of potamotrygonids from their marine sister taxon took place before the Late Pliocene emergence of the Isthmus. One *Potamotrygon* species occurs in the Magdalena Basin of northern South America, which was isolated from the rest of the Atlantic drainages of South America by the Colombian/Venezuelan Eastern Cordillera of the Andes at approximately 12 Ma (Lundberg et al., 1998). Thus, the genus *Potamotrygon* (and by extension, potamotrygonids) must have originated prior to 12 Ma, which extends the minimum age of the clade to the Middle Miocene. Because *Potamotrygon* is not the basal genus within Potamotrygonidae, we can infer that the basal diversification of freshwater stingrays took place during or before the Middle Miocene. Thus, biogeographic information is compatible with molecular estimates of an Early–Middle Miocene origin of potamotrygonids.

Fossil remains of potamotrygonids or their sister taxon, *H. schmardae* and *H. pacifica*, can be used to infer a minimum

Table 2
Summary of distribution data for marine sister groups of marine-derived lineages (MDLs) and age estimates of MDLs

	Distribution of Marine Sister Taxon				Age of Freshwater Taxon		
	Caribbean	Marañon Portal	Mouth of Amazon	Mouth of Paraná	Molecular estimate	Biogeographic estimate (minimum)	Fossil estimate (minimum)
Stingrays (Potamotrygonidae)	Yes	No	No	No	19 (8–38) Ma	Pre-Magdalena	Late Miocene
Drums (*Plagioscion*)	Yes?[a]	Yes?	Yes?	Yes?	None	Pre-Magdalena	Middle Miocene
Anchovies (*Jurengraulis*)	Yes	Yes	Yes	No	None	Pre-Isthmus	None
Anchovies (*Anchovia*)	Yes	Yes	Yes	No	None	Pre-Isthmus	None
Needlefishes (*Potamorrhaphis*/*Belonion*)	Yes	Yes	No	No	17 Ma	Pre-Isthmus	None
Needlefishes (*Pseudotylosurus*)	Yes	No	Yes	No	14 Ma	None	None

[a] '?' for distribution of *Plagioscion* sister taxon refers to phylogenetic uncertainty. See text for details.

age for Potamotrygonidae. Unfortunately, fossils belonging to the *H. schmardae* and *H. pacifica* lineage are unknown. Putative fossil potamotrygonids have been reported from Miocene deposits of the Magdalena Basin (the La Venta fauna; Lundberg, 1997), the Paraná Basin (Deynat and Brito, 1994), and the upper Amazon (Pebas/Solimões Formation; Monsch, 1998). However, clear diagnostic synapomorphies that identify these spines, teeth, or tubercles as belonging to potamotrygonids have not been published. Also, it is impossible to assume that fossil stingray remains represent potamotrygonids simply because they occur in freshwater deposits, because several marine stingray taxa are known to enter freshwater environments. The Pebas/Solimões Formation is particularly troublesome in this regard, because marine stingray taxa, including *Myliobatis*, *Rhinoptera*, and possibly *Dasyatis* have been recorded therein (Monsch, 1998). Both Lundberg (1997, 1998) and Monsch (1998) admit the difficulties of clearly differentiating spines, teeth, and denticles between Potamotrygonidae and marine Dasyatidae. Deynat and Brito (1994) present a more complete analysis of fossil stingray denticles from Late Miocene deposits in the Paraná Basin. Although their study must also be regarded with caution for the same reasons, we tentatively consider the earliest fossil evidence of potamotrygonids to be Late Miocene in age. Thus, available fossil information is compatible with molecular estimates of an Early Miocene origin of Potamotrygonidae.

3. Drums

The Sciaenidae is a species-rich family of primarily marine fishes with particularly high diversity in estuaries of the Atlantic, Pacific, and Indian oceans (Chao, 1978). Four endemic genera occur in South American freshwaters: *Plagioscion*, *Pachypops*, *Pachyurus,* and the newly described *Petilipinnis* (Casatti, 2003). Sazaki (1989) and Casatti (2000; see also Boeger and Kritsky, 2003) have presented drum phylogenies, both of which indicate that the *Plagioscion* and *Pachypops*/*Pachyurus Petilipinnis* lineages separately entered freshwater. We focus on *Plagioscion* here because of the recent studies of the parasites, evolution, and biogeography of this genus (Boeger and Kritsky, 2003).

The phylogenetic placement of *Plagioscion* is unclear. Sazaki (1989) includes it in a clade with several amphi-American taxa, whereas Casatti (2000) groups it with two Indo-Pacific genera. On the basis of the phylogeny of dactylogyrid parasites of the genus *Euryhaliotrema*, Boeger and Kritsky (2003) suggest a relationship between *Plagioscion* and the amphi-American marine drum genus *Paralonchurus*. Distributional information in Table 2 is based on the distribution of *Paralonchurus* but must be regarded with caution, because *Euryhaliotrema* parasites were not sampled from all possible marine sister taxa. Nonetheless, it is notable that the parasite phylogeny repeats the biogeographic pattern found in other taxa; namely, a freshwater lineage is most closely related to a clade of WA/EP sister species.

The distribution of the putative marine sister taxon to *Plagioscion* (and the marine sister taxon to *Plagioscion*'s parasites) on either side of the Isthmus of Panama provides a minimum Pliocene age for *Plagioscion*. The presence of *Plagioscion* in the Rio Magadalena extends this age to the Middle Miocene, as was the case for Potamotrygonidae. Fossil *Plagioscion* otoliths have been reported by Monsch (1998) from Middle Miocene deposits of the Pebas Formation and by Aguilera and Rodrigues de Aguilera (2003) from Neogene marine sediments of Venezuela. Available fossil and biogeographic data appear to support Boeger and Kritsky's (2003) hypothesis that *Plagioscion* evolved sometime in the Early Miocene, probably in association with marine transgressions from western Venezuela that extended to the upper Amazon.

4. Anchovies

The Engraulididae are a diverse family of predominantly plankton-feeding fishes. Approximately 100 species occur in the Western Hemisphere, with at least 10 species in South America freshwaters (Whitehead et al., 1988). Phylogenetic relationships of engraulidids are poorly known, though trees have been proposed for some sets of species. Current generic classifications suggest that multiple transitions to freshwater have occurred. Nelson (1984) proposes that the freshwater species *Jurengraulis juruensis* is most closely related to the two marine species of *Cetengraulis* (Atlantic and Pacific). He also notes that *Anchovia* share the same biogeographic pattern with a freshwater species most closely related to a sister species pair distributed on either side of the Isthmus of Panama. A third genus, *Lycengraulis*, may show the same pattern; however, a hypothesis of relationships is unavailable, and *Lycengraulis* is not included in Table 2.

For both *Jurengraulis* and *Anchovia*, marine sister groups have wide distributions but do not occur at the mouth of Río Paraná (Whitehead et al., 1988). No fossils are available, and biogeographic data indicate only that the freshwater species originated prior to the emergence of the Isthmus of Panama.

5. Needlefishes

The Belonidae are a family of more than 30 primarily piscivorous species distributed worldwide in tropical marine habitats and some freshwater systems. Eight freshwater species are known from South America, and phylogenetic analysis based on molecular data sets indicates that three separate transitions to freshwater have occurred (Lovejoy and Collette, 2001). One of these is restricted to the Pacific slope drainages of Ecuador and Colombia and is not discussed further. The other two freshwater lineages are widespread in the Amazon, Orinoco, Guyana, and Paraná drainages and have separate sister clades in coastal marine waters.

The freshwater *Potamorrhaphis*/*Belonion* lineage fits the pattern of several other groups: the freshwater species are related to a clade that includes WA/EP species. However, the freshwater *Pseudotylosurus* lineage is most closely related to a pair of species that occur on either side of the Atlantic: *Strongylura timucu* is found in the Caribbean, while *S. senegalensis* is distributed along the coast of west Africa (Lovejoy and Collette, 2001). Small amounts of sequence divergence between these sister species suggest a relatively recent trans-Atlantic dispersal. Neither marine clade has a distribution that extends as far as the mouth of the Paraná.

Banford et al. (2004) have provided a molecular biogeographic study of New World needlefishes, with particular emphasis on trans-Isthmian calibrations of rates of molecular evolution. In comparing multiple trans-Isthmian clades, they propose that the *Strongylura marina* (WA)/*S. exilis* (EP) split likely occurred during the Late Miocene (5–7 Ma), coincident with extensive shoaling and the earliest emergence of Central American Isthmian landmasses. We use this date to calibrate a rate of molecular evolution for the third-position transversions in the cytochrome-b gene (directly comparable to the approach used by Lovejoy et al., 1998). Branch lengths were derived from a needlefish phylogram using the data set of Lovejoy and Collette (2001). The average distance was calculated from the tips of the phylogram to the divergence point between freshwater and marine taxa. Only the distances for marine taxa were used because preliminary analyses showed that the freshwater lineages likely were evolving at a different rate, and our calibration was derived from marine species. The calculated rate was approximately 1.1 transversions per million years, which provides age estimates of 17 Ma for the *Potamorrhaphis*/*Belonion* lineages and 14 Ma for the *Pseudotylosurus* lineage. Unfortunately, fossil evidence to confirm these dates is unavailable, and biogeographic calibrations are not highly informative because needlefishes do not occur in the Magdalena or Maracaibo basins.

6. Discussion

Our analysis shows that for Amazonian marine-derived fishes, available data are consistent with the hypothesis that Miocene marine incursions and connections played a role in the transition to freshwater habitats. The first prediction for this hypothesis was that the geographic distribution of marine sister groups of freshwater endemics should include the Caribbean, the most likely source of Miocene incursions (Hoorn et al., 1995; Vermeij and Wesselingh, 2002). For all taxa examined (Table 2), this hypothesis is supported. Marine sister taxa of MDLs were less frequently distributed at other putative sources of marine incursions. The connections via both the current course of the Amazon and the Paraná are considered unlikely according to paleogeographical and paleontological evidence (Hoorn et al., 1995; Lundberg et al., 1998; Marshall and Lundberg, 1996), and our data are consistent with these findings. Only a single taxon (*Plagioscion*) has a marine sister group whose distribution includes the mouth of Río Paraná. A Pacific source for Early Miocene marine incursions has been considered a possibility by some authors, but the pre-Pliocene northern South American coastline was not divided by the Isthmus of Panama and likely represented a single biogeographic province (Rosa, 1985; Nuttall, 1990; Lovejoy, 1996). Thus, a marine ancestor could have entered the upper Amazon from either the Caribbean or the Pacific—or both.

Fig. 3 presents the age estimates combined with Neogene paleogeographic events. When available, age data for MDLs are consistent with the Miocene incursion/connection hypothesis. Molecular estimates of age can be problematic for several reasons and are subject to wide confidence intervals, fossil estimates depend on the vagaries of fossil preservation, and biogeographic analyses provide only minimum age estimates (Hillis et al., 1996; Lundberg, 1998). Despite such difficulties, it seems significant that all estimated ages for MDLs are Miocene or younger. Also, excepting anchovies (for which very limited age data are available), age estimates for MDLs from a variety of approaches are all older than Pliocene. Despite this rather broad range of possible ages, these data falsify the idea that Cretaceous or Paleocene events (Brooks et al., 1981) were responsible for the origin of the examined MDLs (Lovejoy et al., 1998; Marques, 2000). Lundberg et al. (1998) discuss a period of marine incursion that took place sometime during 43–30 Ma, which slightly overlaps with the upper limits of the potamotrygonid molecular estimate confidence intervals. However, the preponderance of data suggest that MDLs originated more recently during Miocene marine incursions and connections.

The third prediction of the Miocene marine incursion/connection hypothesis is that clades containing MDLs would show congruent biogeographic and phylogenetic patterns, due to their shared responses to the same paleogeographic event.

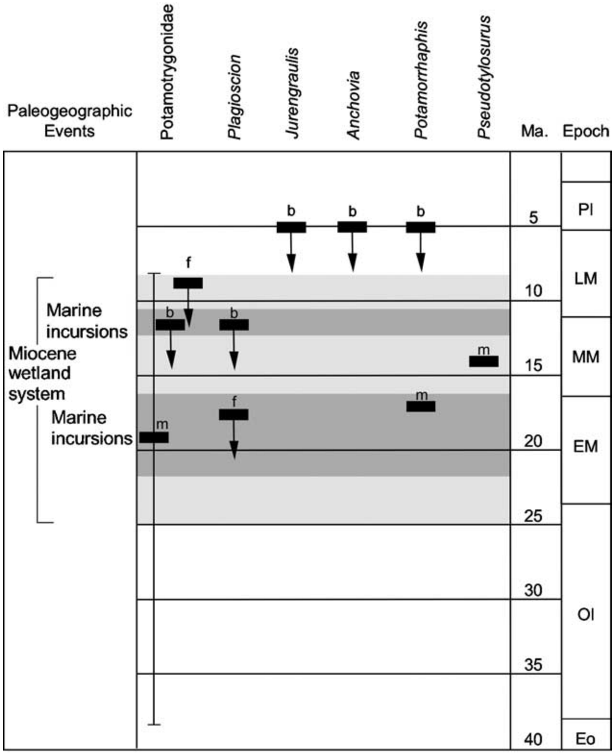

Fig. 3. Age estimates for marine-derived lineages (MDLs) in relation to paleogeographic events in the upper Amazon. Duration of the upper Amazon wetland system is from Wesselingh et al. (2002); possible intervals of marine incursions in dark grey from Hoorn (1993, 1994a), Lundberg et al. (1998), and Wesselingh et al. (2002). Abbreviations m, b, and f represent age estimates based on, respectively, molecular data, biogeography, and fossils. Arrows on estimates from fossils and biogeography show that these are minimal age estimates. Molecular estimate for potamotrygonids shows confidence intervals estimated by Marques (2000).

Quantifying congruence is difficult, but several shared patterns characterize the examined MDLs. As we discussed, all examined MDLs have marine sister taxa with distributions that include the Caribbean, and all available age estimates point to a Miocene date of divergence between marine and freshwater lineages. In addition, nearly all examined fish MDLs (and often their parasites) exhibit a phylogenetic pattern in which the freshwater lineage is the sister group to a clade that contains WA/EP species (Lovejoy, 1997; Lovejoy and Collette, 2001; Boeger and Kritsky, 2003). The frequent repetition of these shared patterns suggests the effect of a major paleogeographic event with particular geographical and temporal boundaries. We hypothesize that this event was the occurrence of a para-marine wetland system that characterized the upper Amazon during the Miocene (Wesselingh et al., 2002).

Miocene marine incursions and connections will not explain the origin of all South American MDLs. Some MDLs have evolved more recently; for example, the *Odontesthes* silverside radiation of coastal southern Brazil originated during Pleistocene and Holocene sea-level changes (Beheregaray et al., 2002). Other MDLs may be older than the Miocene and products of earlier marine incursions or freshwater invasions. Also, it is difficult to disregard the dispersal hypothesis that the MDLs examined here opportunistically and independently invaded freshwater habitats rather than responding to a shared paleogeographic event. For example, in criticizing Webb's (1995) suggestion that Miocene marine seaways explain the richness of marine-derived endemics in the Amazon, Marshall and Lundberg (1996: 123) argue that 'there is no compelling evidence that the ancestors of these groups could not have entered freshwater rivers directly, as related taxa do today around the world.' However, dispersal explanations can be devised for any distribution pattern and are always difficult to test. Historical biogeographers prefer to explain similar biogeographic patterns by shared responses to the same earth history event, thereby minimizing the number of ad hoc dispersal explanations (Nelson and Platnick, 1981; Humphries and Parenti, 1999). For the MDLs examined herein, the clear evidence of shared biogeographic patterns argues for a common paleogeographic explanation.

Miocene South America probably was affected by several separate marine incursions, including events during the Late Middle Miocene and the Late Early Miocene. However, associating the origin of the MDLs considered here with a particular Miocene incursion would be extremely difficult, owing to the relatively poor resolution of molecular clocks, fossil remains, and biogeographic indicators. Barring the discovery of fossil beds with extremely well-preserved fishes and broad temporal scales, estimates of the origin age probably will be limited to the epoch level. In any case, it is not unlikely that multiple MDLs originated concomitantly but over a somewhat extended period of time. An important ecological aspect of the Miocene upper Amazon wetland system appears to be its long-standing connection to marine waters (Wesselingh et al., 2002), offering habitats with shifting salinity levels and intermittent barriers. Such conditions may have presented ideal conditions for the evolution of freshwater tolerance and the isolation of incipient freshwater lineages from their marine relatives. Perhaps the Miocene upper Amazon wetlands could be considered a lineage pump that acted to 'inject' marine taxa into freshwater habitats over an extended period of time.

Despite the distribution of marine and estuarine taxa, such as drum, needlefish, and stingrays, along the South American coastline and at the mouths of the major river systems during the span of the Neogene, only a few lineages successfully transitioned to freshwater. Vermeij and Wesselingh (2002: 265) have commented on a similar pattern in molluscs and suggest that ecological barriers presented by 'well-adapted incumbents' may be partly responsible. This barrier may be particularly relevant for fishes, because the incredibly diverse fish fauna of South America must represent a formidable community for prospective invaders. However, the majority of South American fish lineages are classified as primary division fishes and thus should show limited tolerance to marine conditions (Gayet, 1991). Wesselingh et al. (2002: 44) note that 97% of examined Pebas/Solimões Formation molluscs can be considered 'freshwater to oligohaline taxa,' whereas only 2.5% can be considered 'obligate freshwater taxa,' a distinction that highlights the potential impact of salinity on this community. The common occurrence of marine sciaenids (a family that includes many estuary specialists) and marine chondrichthyans in the Pebas/Solimões fauna support the pattern found in molluscs (Monsch, 1998). If slightly increased salinity was common, we might expect a relatively depauperate fish community. Vermeij and Wesselingh (2002: 269) discuss a possible 'evolutionary predation trough' that might occur 'in environments of strongly reduced salinity during Pebas times, between more typically marine and fully freshwater environments.' If Miocene upper Amazon wetlands experienced a depauperate fish community due to intermediate salinity conditions, it may have been a 'competition trough' that could be exploited by newly arriving marine lineages. We therefore propose that the Miocene upper Amazon provided a unique set of conditions for the evolution of MDLs, which explains the concentration of marine to freshwater transitions in time and space.

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