

Miocene tectonism and the separation of cis- and trans-Andean river basins: Evidence from Neotropical fishes

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Abstract

The fish fauna of *trans*-Andean river basins in northwestern South America is ancient and diverse, including 14% (558 of 4,085) of all Neotropical teleost species and representing 88% of the orders and 79% of the families. The evolutionary histories of these lineages provide many examples to test models of the tectonic uplift that isolated the *trans*-Andean basins. We report the results of two newly compiled data sets of phylogenetic and biogeographic information on the freshwater fishes of the region: (1) species-level phylogenies for 26 Neotropical freshwater teleost taxa, with a minimum of 37 *cis-trans*-Andean clades and (2) species distributions for 641 genera of Neotropical freshwater teleosts, with a minimum of 140 *cis-trans*-Andean clades. Although it provides only about one-quarter the total number of *cis-trans*-Andean clades, species phylogeny preserves a more accurate record of the temporal sequence of basin isolation. Phylogenies using gene sequences also may provide estimates on the timing of lineage divergences. However, the great majority (70%) of available species phylogenies for Neotropical freshwater teleosts employ comparative morphology alone, partly because species-level sampling for most taxa requires collections over large spatial (10^3 – 10^4 km) scales, and collections of whole specimens for morphological study are readily available for many taxa from natural history museums. Fish species phylogenies are partially concordant with patterns of drainage basin isolation generated from geological data on the Miocene of northwestern South America, which associate the initial rise of the Eastern Cordillera (~ 12 Ma) with the hydrological isolation of the Magdalena and Pacific Slope regions and the rise of the Merida Andes (~ 8 Ma) with the isolation of the modern Maracaibo and Orinoco basins. Although some phylogenies unite taxa from the Maracaibo and *cis*-Andean Orinoco, a more common set of area relationships occurs between clades exclusive to the Maracaibo and *trans*-Andean Magdalena basins. The compound origin of the Maracaibo ichthyofauna may be due to partial extinction of *cis*-Andean taxa that resulted from a marine incursion in the Late Miocene and subsequent invasion by congeners from the adjacent Magdalena Basin. In combination, the pooled data on species phylogenies and distributions suggest that the origins of the *trans*-Andean freshwater fish fauna predate the Miocene tectonic events that dissected the landscape. Among families of freshwater teleosts from northwestern South America, species diversity is significantly correlated with a minimum number of *cis-trans*-Andean clades, which indicates that the relative species diversity and biogeographic distributions of Amazonian fishes were effectively modern by the late Middle Miocene. The diverse taxonomic composition of the *trans*-Andean ichthyofauna further suggests that Miocene tectonism fragmented the entire aquatic fauna of northwestern South America, leaving a clear signal on all major taxa.

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1. Introduction

The geological history of river basins in northwestern South America (NSA) during the Neogene is complex and

incompletely understood. Data from fission track analysis (Kohn et al., 1984; Shagam et al., 1984), sedimentology (Mullins et al., 1987; Piper et al., 1997), palynology (Hoorn, 1994, 1996; Colinvaux and De Oliveira, 2001), and paleontology (Lundberg, 1998; Vonhof et al., 1998, 2003) suggest that until the Middle Miocene (~ 16 Ma), most of the area of what is the contemporary western Amazon drained northward to a delta located in the area of the modern Maracaibo Basin and that at this time, NSA was separated from southern Middle America by more than 200 km of open ocean (Galvis et al.,

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1979; Shagam et al., 1984; Kohn et al., 1984; Cooper et al., 1995; Hoorn et al., 1995; Dengo and Covey, 1993; Diaz de Gamero, 1996; Coates and Obando, 1996; Guerrero, 1997; Villamil, 1999; Gregory-Wodzicki, 2000; Costa et al., 2001). The Middle Miocene rise of the Eastern Cordillera (~12 Ma) and the Late Miocene rise of the Merida Andes (~8 Ma) were responsible for defining the boundaries of the modern drainages of NSA, including the western Amazon (west of the Purus Arch) and the Orinoco, Maracaibo, and Magdalena basins. Also during the Middle Miocene (11–16 Ma), the Choco Block underlying the modern San Juan, Baudo, and Atrato basins was accreted to the northwest corner of South America, resulting in the most recent uplift of the Western Cordillera (Duque-Caro, 1990; Colletta et al., 1990; Kellogg and Vega, 1995). The Isthmus of Panama emerged in the Pliocene (~3 Ma) to form the only fully terrestrial connection between Middle and South America during the Cenozoic (Coney, 1982; Ituralde-Vincent and MacPhee, 1999).

A simplified model for the sequential isolation of drainage basins in NSA resulting from Miocene tectonism is provided in Fig. 1. The principle events of this model are as follows: (1) the rise of the Eastern Cordillera (~12 Ma), which sets a minimum date for the hydrological isolation of the Magdalena and Pacific Slope of Colombia from the *cis*-Andean proto-Orinoco basin (modern western Amazon and Orinoco); (2) the initial formation of the modern Amazon sediment fan with a tenfold increase of terrigenous deposits in the Ceara Rise (~8–9 Ma), which sets a minimum date for the separation of the

western Amazon and Orinoco basins (Piper et al., 1997; Dobson et al., 1997, 2001); and (3) the rise of the Merida Andes (~8 Ma), which sets a minimum date for the isolation of the modern Maracaibo and Orinoco basins (Mullins et al., 1987; Hoorn et al., 1995; Lundberg et al., 1998).

Patterns in the historical biogeography of extant freshwater fishes provide unique opportunities to test alternative models of the evolution of hydrogeographic basins. The freshwater fish fauna of tropical South America is among the richest vertebrate faunas on Earth, with more than 6000 species representing about 46% of the world's 13,000 or so freshwater fish species and perhaps 10% of all known vertebrate species (Vari and Malabarba, 1998; Reis et al., 2003). This rich fauna provides copious examples of taxa with distributions on both slopes of the Andes. Documenting the alpha systematics and biogeography of this enormous diversity has consumed the attention of Neotropical ichthyologists for more than a century (Eigenmann and Fisher, 1914; Eigenmann, 1920; Eigenmann and Allen, 1942; Vari and Weitzman, 1990), and the actual dimensions of the fauna have only come to be fully known in the past decade. These advances in Neotropical ichthyology are summarized in two volumes that, in combination, have revolutionized our understanding of the species-level inter-relationships and biogeography of Neotropical freshwater fishes. *Phylogeny and Classification of Neotropical Fishes* (Malabarba et al., 1998) provided the first comprehensive review of phylogenetic data on which to evaluate alternative models of the tempo and mode of aquatic diversification in the region. *Checklist of the Freshwater Fishes of South and Central America* (CLOFFSCA; Reis et al., 2003) brought together contributions from 64 authors on 87 family and subfamily level taxa and provided the first clear image of Neotropical fish diversity at the species level.

In this article, we review the current state of knowledge of species-level phylogenetics and geographical distributions of freshwater fishes in the *cis*- and *trans*-Andean drainages of NSA and consider the possible effects of Miocene tectonism on the evolution of the fish fauna of these regions. In particular, we examine the possibility that the uplift of the Eastern Cordillera and Merida Andes isolated *trans*-Andean basins and their resident fish faunas. This hypothesis involves several phylogenetic and biogeographic predictions, which we test using fish taxa for which appropriate data are available.

2. Methods

For this study, we compiled two data sets of phylogenetic and biogeographic data on the primary and secondary division freshwater teleost taxa of NSA. Primary freshwater fishes are those with little or no tolerance for brackish water (0.5 g or more total dissolved mineral salts per liter; Myers, 1938, 1951; Darlington, 1957). Saltwater is an important barrier for these fishes, and an extensive literature documents the impact of this physiological constraint on their geographic distributions (see Berra, 2001). Examples among Neotropical teleosts include Osteoglossiformes (e.g. arowana, arapaima), Characiformes (e.g. tetras), Gymnotiformes (Neotropical electric fishes), and

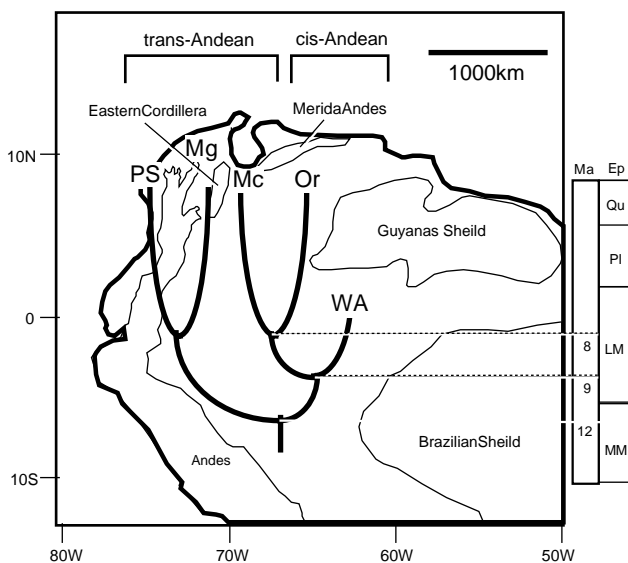


Fig. 1. Schematic model for the sequential isolation of drainage basins in northwestern South America resulting from Miocene tectonism. The rise of the Eastern Cordillera (~12 Ma) sets a minimum date for the isolation of the Magdalena (Mg) and Pacific Slope (PS) regions from *cis*-Andean basins; the initial formation of the Amazon fan (~9 Ma) sets a minimum date for the separation of the western Amazon (WA) and Orinoco (Or) basins; and the rise of the Merida Andes (~8 Ma) sets a minimum date for the separation of the Maracaibo (Mc) and Orinoco (Or) basins. Hydrogeographic regions from Reis (1998), Albert (2001), and Albert and Crampton (2005). Other abbreviations: Ma, millions of years ago; MM, Middle Miocene; LM, Late Miocene; Pl, Pliocene; Qu, Quaternary. Time scale is not proportional.

most families of Siluriformes (catfishes). Saltwater is thought to be a strong barrier to dispersal for primary freshwater fishes. Secondary freshwater fishes are tolerant of brackish waters but normally occur in inland aquatic systems rather than the sea; they are believed capable of occasionally crossing narrow marine barriers. Examples among Neotropical teleosts are most Cyprinodontidae (e.g. killifishes), Poeciliidae (e.g. guppies), Cichlidae, and Synbranchidae (swamp eels). Among Neotropical teleosts, most primary and secondary freshwater fish families originated from freshwater ancestors in the Cretaceous. We excluded from these data sets the so-called peripheral freshwater fish taxa, also known as the Marine Derived Lineages (see Lovejoy et al., 2006).

The first data set compiled for the present study is composed of 26 primary and secondary freshwater Neotropical teleost taxa (hereafter, Neotropical freshwater teleosts) for which species-level phylogenetic hypotheses are currently available (Table 1). The second data set compiles the geographic distributions of extant Neotropical freshwater teleosts from CLOFFSCA (Reis et al., 2003), including all 39 families (Table 2) and 123 generic or suprageneric taxa with *cis/trans*-Andean distributions (Table 3). Although species phylogenies are more useful for inferring biogeographic history than are raw species distributions, phylogenies are currently available for only a small proportion of the Neotropical freshwater fish fauna, especially curimatid characins and gymnotiform electric

fishes. The species-level interrelationships of many diverse catfish and characin taxa with *cis/trans*-Andean distributions remain poorly understood. The presence within a genus of species in both *cis*- and *trans*-Andean waters indicates at least a single cladogenetic event between these regions, assuming the genera are monophyletic and the presence and absence records from all regions are reliable.

3. Results

3.1. Number of *trans*-Andean clades

Published species phylogenies of Neotropical freshwater fish taxa provide 37 taxa with *cis/trans*-Andean distributions, of which 35 are presumed to result from vicariance due to Miocene tectonism (Table 1). These taxa include representatives of 57% (4 of 7) orders, 33% (13 of 39) families, and 19% (26 of 134) genera with *trans*-Andean distributions. The geographic distributions of all 39 Neotropical freshwater teleost families are summarized in Table 2 and those of genera with *cis/trans*-Andean distributions in Table 3. The number of *cis/trans*-Andean vicariance events with estimated minimum dates in the Miocene (marked 'Mioc.' in Table 2) differs from the total number of *trans*-Andean clades (TAC) for several reasons. For genera in six families (marked 'a' in Table 2), available phylogenetic information suggests some cladogenetic

Table 1
Twenty-six Neotropical freshwater teleost taxa with *cis/trans*-Andean distributions for which species-level phylogenies are available

Order	Taxon	TAS	TAC	Mioc.	Refs.
Characiformes	<i>Characidium</i>	4	2	2	Buckup, 2003, pers. comm.
	Compsurini	3	1	1	Malabarba, 1998
	<i>Creagrutus</i>	7	3	2	Vari and Harold, 2001; Harold and Vari, 2001
	<i>Ctenoleucius</i>	2	1	1	Vari, 1995
	<i>Curimata</i>	1	1	1	Vari, 1989b
	<i>Cyphocharax</i>	2	1	1	Vari, 1992
	<i>Potamorhina</i>	1	1	1	Vari, 1984
	Prochilodontidae	3	1	1	Sivasundar et al., 2001
	<i>Pseudocurimata</i>	6	1	1	Vari, 1989a
	<i>Roeboides</i>	7	3	3	Bermingham and Martin, 1998
	Roestinae	3	1	1	Lucena and Menezes, 1998
<i>Steindachmerina</i>	1	1	1	Vari, 1991	
Cyprinodontiformes	<i>Rivulus</i>	22	1	1	Hrbek and Larson, 1999; Murphy et al., 1999
Gymnotiformes	<i>Apteronotus</i>	9	3	3	Albert, 2001, 2003b
	<i>Brachyhyopomus</i>	2	1	1	Bermingham and Martin, 1998; Albert and Crampton, 2003a
	<i>Distocyclus</i>	2	1	1	Albert, 2001
	<i>Eigenmannia</i>	3	2	2	Albert, 2001
	<i>Gymnotus</i>	7	4	3	Albert and Crampton, 2003b; Campos da Paz, 2003; Albert et al., 2005
	<i>Sternopygus</i>	4	2	2	Albert, 2003a; Hulen et al., in press
Siluriformes	<i>Centromochlus</i>	1	1	1	Soares-Porto, 1998
	<i>Farlowella</i>	2	1	1	Retzer and Page, 1997
	<i>Hemiancistrus</i>	3	1	1	Armbruster, 2004
	<i>Hoplosternum</i>	2	1	1	Reis, 1998
	<i>Hypostomus</i>	1	1	1	Montoya-Burgos, 2003; Armbruster, 2004
	<i>Pimelodella</i>	6	2	2	Martin and Bermingham, 2000
	<i>Rhamdia</i>	5	1	1	Perdices et al. 2000
Total		105	37	35	

TAC, minimum number of *trans*-Andean clades; TAS, number of *trans*-Andean species; Mioc., minimum number of TAC attributed to Miocene tectonism. Taxa are arranged alphabetically within orders. A total of 37 TACs are identified.

Table 2
Geographic distributions of all 39 primary and secondary freshwater Neotropical teleost families

Order	Family	Gen.	TAG	%TAG	Spp.	TAS	%TAS	TAC	Mioc.
Characiformes	Acestrorhynchidae	1	0	0	15	0	0	0	0
Characiformes	Anostomidae	12	3	25	138	3	2	3	3
	Characidae ^a	163	27	17	952	135	14	35	32
	Chilodontidae	2	0	0	7	0	0	0	0
	Crenuchidae ^a	12	1	8	73	6	8	2	2
	Ctenoluciidae ^a	2	1	50	7	2	29	1	1
	Curimatidae ^a	8	5	63	97	11	11	5	5
	Cynodontidae ^a	4	1	25	14	3	21	1	1
	Erythrinidae ^b	3	2	67	15	2	13	4	4
	Gasteropelecidae	3	1	33	9	1	11	1	1
	Hemiodontidae	5	0	0	28	0	0	0	0
	Lebiasinidae	7	2	29	61	8	13	2	2
	Parodontidae	3	1	67	23	2	9	1	1
	Prochilodontidae ^a	3	2	67	21	4	19	2	2
Cyprinodontiformes	Anablepidae	3	0	0	15	0	0	0	0
	Poeciliidae ^c	26	8	31	216	29	13	2	2
	Rivulidae ^a	27	3	11	235	26	11	3	3
Gymnotiformes	Apteronotidae ^a	13	1	8	52	9	17	3	3
	Gymnotidae ^a	2	1	50	33	7	21	4	3
	Hypopomidae ^a	7	1	14	25	2	8	1	1
	Rhamphichthyidae	3	0	0	13	0	0	0	0
	Sternopygidae ^a	5	3	60	27	9	33	6	6
Osteoglossiformes	Arapaimidae	1	0	0	1	0	0	0	0
	Osteoglossidae	1	0	0	2	0	0	0	0
Perciformes	Cichlidae ^d	51	17	33	406	112	28	5	5
Siluriformes	Aspredinidae	12	4	33	36	6	17	4	4
	Astroblepidae	1	1	100	54	34	63	1	1
	Auchenipteridae ^a	20	2	10	91	6	7	2	2
	Callichthyidae ^a	7	2	29	177	3	2	2	2
	Cetopsidae	7	2	29	20	6	30	2	2
	Scoloplacidae	1	0	0	4	0	0	0	0
	Doradidae	30	3	10	74	3	4	3	3
	Heptapteridae ^b	26	5	19	186	16	9	8	8
	Loricariidae ^a	93	20	22	673	81	12	20	20
	Pimelodidae ^a	30	7	23	83	10	12	8	8
	Pseudopimelodidae	5	3	60	26	4	15	3	3
	Trichomycteridae	41	4	10	171	16	9	4	4
Synbranchiformes	Synbranchidae	1	1	100	5	1	20	1	1
Total		641	134	21	4085	558	14	140	136

Data represent 91% (4079 of 4475) of all Neotropical freshwater fish species (Reis et al., 2003). TAC, *trans*-Andean clades; TAG, *trans*-Andean genera. Middle American heroines. Other abbreviations, symbols, and arrangement of taxa as in Table 1.

^a TAC from species phylogenies (see Table 1).

^b More than one species with *cis*-*trans*-Andean distributions.

^c Clades not rooted in *cis*-Andean basins.

^d 11 of 15 cichlid TAG are monophyletic (Middle American heroines).

events predate Miocene tectonism. For genera in another six families, more than one species is distributed in *cis*-*trans*-Andean basins (marked 'b' in Table 2), which suggests each species represents an independent TAC. In two families (Characidae and Cichlidae), multiple *trans*-Andean genera constitute monophyletic clades.

An analysis of species distributions patterns recovered a minimum of 136 presumed instances of vicariance resulting from Miocene tectonism in NSA (Table 2). These instances include representatives of 88% (7 of 8) of the orders of Neotropical freshwater teleosts, 79% (30 of 38) of the families, and 21% (134 of 641) of the genera (TAG; Table 2). Among

extant Neotropical freshwater teleost species, 14% (558 of 4085) inhabit *trans*-Andean waters (TAS; Table 2).

Species diversity is significantly correlated with a minimum number of *cis*-*trans*-Andean clades in extant families of Neotropical freshwater teleost fishes (Fig. 2). This high correlation is due in part to a single taxon: loricariid catfishes. Removing this taxon reduces the R^2 correlation value to 0.63, which is significant ($p < 0.01$). The correlation between species and cladal diversity remains robust with the subsequent removal of the most species-rich taxa, with R^2 values of 0.23 for the removal of two taxa, 0.21 for the removal of three taxa, and 0.24 for the removal of four taxa, all of which are

Table 3 (continued)

Taxon	MA	PS	Atr.	Mag.	Mar.	cis	Refs.
<i>Caquetaia</i>	X	X	X	X	X	X	Kullander, 2003
<i>Cichlasoma</i>	X	X				X	Kullander, 2003
<i>Geophagus</i>	X	X	X	X	X	X	Kullander, 2003
MA heroines ^b	X						Kullander, 2003
<i>Plagioscion</i>					X	X	Friel, 2003
<i>Bunocephalus</i>			X	X		X	Friel, 2003
<i>Dupouyichthys</i>				X	X		Friel, 2003
<i>Hoplomyzon</i>					X	X	Friel, 2003
<i>Xylophius</i>				X	X	X	Schaefer, 2003a,b
<i>Astroblepus</i>	X	X	X	X	X		Ferraris, 2003
<i>Centromochlus</i>				X		X	Ferraris, 2003
<i>Trachelyopterus</i>	X		X	X	X	X	Reis, 2003
<i>Callichthys</i>				X		X	Reis, 2003
<i>Hoplosternum</i>	X	X	X	X		X	Vari and Ferraris, 2003
<i>Paracetopsis</i>		X					Vari and Ferraris, 2003
<i>Pseudocetopsis</i>		X	X	X	X	X	Sabaj and Ferraris, 2003
<i>Centrochir</i>				X			Sabaj and Ferraris, 2003
<i>Doraops</i>					X		Sabaj and Ferraris, 2003
<i>Rhinodoras</i>					X	X	Bockmann and Guazelli, 2003
<i>Cetopsorhamdia</i>				X	X	X	Bockmann and Guazelli, 2003
<i>Imparales</i>	X					X	Bockmann and Guazelli, 2003
<i>Imparfinis</i>	X	X				X	Bockmann and Guazelli, 2003
<i>Pimelodella</i> ^c	X	X	X	X	X	X	Martin and Bermingham, 2000
<i>Rhamdia</i> ^c	X	X	X	X	X	X	Perdices et al., 2002
<i>Ancistrus</i>	X	X	X	X	X	X	Fisch-Muller, 2003
<i>Chaetostoma</i>	X	X	X	X	X	X	Fisch-Muller, 2003
<i>Cordylancistrus</i>		X			X	X	Ferraris, 2003
<i>Crossoloricaria</i>	X	X		X			Ferraris, 2003
<i>Dasylicaria</i>	X	X		X			Fisch-Muller, 2003
<i>Dolichancistrus</i>		X	X	X	X	X	Fisch-Muller, 2003
<i>Farlowella</i>					X	X	Retzer and Page, 1997
<i>Hemiancistrus</i>	X	X	X		X	X	Montoya-Burgos, 2003
<i>Hypostomus</i>					X	X	Weber, 2003; Armbruster, 2004
<i>Isorhineloricaria</i>	X						Ferraris, 2003
<i>Lamontichthys</i>					X	X	Fisch-Muller, 2003
<i>Lasiancistrus</i>	X	X		X	X	X	Fisch-Muller, 2003
<i>Leptoancistrus</i>	X			X			Fisch-Muller, 2003
<i>Panaque</i>				X		X	Weber, 2003
<i>Pterygoplichthys</i>				X	X	X	Ferraris, 2003
<i>Rhinloricaria</i>	X	X		X	X	X	Ferraris, 2003
<i>Spatuloricaria</i>	X		X	X	X	X	Weber, 2003
<i>Squaliforma</i>				X			Ferraris, 2003
<i>Sturisoma</i>	X	X	X	X	X	X	Ferraris, 2003
<i>Sturisomatichthys</i>	X	X		X			Lundberg and Littmann, 2003
<i>Cheirocerus</i>					X	X	Lundberg and Littmann, 2003
<i>Megalonema</i>				X	X	X	Lundberg and Littmann, 2003
<i>Perrnichthys</i>					X		Lundberg and Aguilera, 2003
<i>Phractocephalus</i> ^a			X	X	X	X	Lundberg and Aguilera, 2003
<i>Pimelodus</i>	X			X	X	X	Lundberg and Aguilera, 2003
<i>Platysilurus</i>					X	X	Lundberg and Aguilera, 2003
<i>Sorubim</i>			X	X	X	X	Shibatta, 2003
<i>Batrochoglanis</i>		X		X	X		Shibatta, 2003
<i>Microglanis</i>		X					Shibatta, 2003
<i>Pseudopimelodus</i>			X		X	X	de Pinna and Wosiaki, 2003
<i>Eremophilus</i>				X			de Pinna and Wosiaki, 2003
<i>Paravandellia</i>				X			de Pinna and Wosiaki, 2003
<i>Rhizosomichthys</i>				X			de Pinna and Wosiaki, 2003
<i>Trichomycterus</i>		X		X		X	Kullander, 2003
<i>Synbranchus</i>	X	X	X	X	X	X	Kullander, 2003
Total	54	55	48	83	64	87	

Hydrogeographic regions: MA, Middle America; PS, Pacific Slope Colombia and Ecuador; Atr., Atrato and Salí basins; Mag., Magdalena and Cauca basins; Mar., Maracaibo Basin; cis, cis-Andean Amazon-Orinoco basins. Taxa arranged as in Table 2.

^a Including fossils.

^b Supra-generic clades: Compsurini and Roestinae with 2 genera each; Cnesterodontini with 4 genera; Middle American heroine cichlids with 11 genera.

^c Taxa with multiple trans-Andean clades.

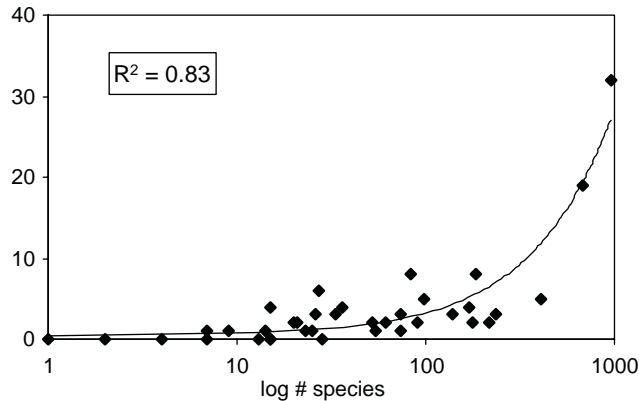


Fig. 2. Species diversity is significantly correlated with minimum number of *trans*-Andean clades among extant families of Neotropical freshwater fishes ($n=39$). This correlation indicates that the relationship between species and cladal diversity predates the isolation of the *cis*- and *trans*-Andean faunas in the Late Miocene and that the relative species diversity of Amazonian fish clades was modern by this time.

significant ($p < 0.05$). Conventional statistics may be applied if we assume each TAC is historically independent, regardless of the position of that clade in the phylogenetic hierarchy. This logic underlies all methods used to assess the relationships of variables in a phylogenetic context (Felsenstein, 1985).

3.2. Area relationships

Alternative area relationships of NSA basins, based on species phylogenies of freshwater fishes, are provided in Table 4 and Fig. 3. Species-level phylogenetic information is currently available for 11 Neotropical freshwater teleost taxa that inhabit all NSA basins, including five characins (*Creagrutus*, *Roeboides*, *Ctenoluciidae*, *Cyphocharax*, *Roestinae*), three gymnotiforms (*Apteronotus*, *Brachyhyppopomus*, *Sternopygus*), and three catfishes (*Hoplosternum*, *Pimelodella*, *Rhamdia*) (for references, see Table 1). The main result of this analysis is that 7 of the 19 TAC recovered are exclusive to the Maracaibo and Magdalena, four to the Magdalena and Pacific

Table 4
Area relationships for 12 Neotropical freshwater teleost clades with species in the Maracaibo, Magdalena, and *cis*-Andean regions

Taxon	TAC	Mar. + Mag.	Mag. + PS	Mar. + Cis
<i>Creagrutus</i>	3	1		
<i>Roeboides</i>	3		1	1
<i>Ctenoluciidae</i>	1	1		
<i>Cyphocharax</i>	1	1		
<i>Roestinae</i>	1	1		
<i>Apteronotus</i>	3	1		1
<i>Brachyhyppopomus</i>	1			1
<i>Sternopygus</i>	2		1	
<i>Hoplosternum</i>	1	1		
<i>Pimelodella</i>	2		2	
<i>Rhamdia</i>	1	1		
	19	7	4	3

Data sources and arrangement of taxa from Table 1; abbreviations of regions from Table 3.

Slope, and three to the Maracaibo and *cis*-Andean region. In other words, the Maracaibo and Magdalena share the most exclusive clades among the basins of NSA (see Reis, 1998). Data about the species composition of freshwater fishes in the Maracaibo and adjacent basins show a slightly different pattern (Fig. 4). Whereas the results of the phylogenetic studies show that more taxa in the Maracaibo are related to (*trans*-Andean) Magdalena than to *cis*-Andean taxa (Reis, 1998), the Maracaibo actually shares more genera of freshwater fishes with the (*cis*-Andean) Orinoco than with the (*trans*-Andean) Magdalena.

4. Discussion

4.1. A synthetic model of NSA basin evolution

The pooled data from species phylogenies and composition of freshwater fishes in NSA are summarized in a synthetic model of river basin isolation and aquatic faunal division (Fig. 5). The most common set of area relationships (Fig. 3C) is concordant with the model of drainage history derived from geological information, which associates the rise of the Eastern Cordillera (~12 Ma) with the hydrological isolation of the Magdalena and Pacific Slope regions and the rise of the Merida Andes (~8 Ma) with the isolation the modern Maracaibo and Orinoco basins (Fig. 1). However, the preponderance of clades exclusive to the Maracaibo and Magdalena basins is not anticipated from the geological model.

We propose two nonexclusive explanations for the compound origin of the Maracaibo ichthyofauna. One explanation involves a partial extinction of the original (*cis*-Andean) Maracaibo aquatic fauna in the Late Miocene (Lundberg et al., 1998; Lundberg and Aguilera, 2003). The rise of the Merida Andes may have been associated with backarc deformation, such that the area of the modern Maracaibo Basin was inundated with a local marine incursion (Gregory-Wodzicki, 2000). Marine transgressions are recorded from the early Pliocene of Panama, thus reflecting backarc deformation associated with regional tectonism (Diaz de Gamero, 1996; Guerrero, 1997; Gregory-Wodzicki, 2000; Costa et al., 2001).

The other explanation includes secondary replacement of freshwater fish taxa from the adjacent (*trans*-Andean) Magdalena Basin. Colonization of newly exposed freshwater habitats in the Maracaibo by Magdalena taxa could have occurred by coastal stream capture along their common Caribbean shorelines, especially during periods of marine regression. Exchanges also could have occurred by headwater stream capture or dispersal across the Sierra de Perija, the range of hills that currently separates the two basins. Contemporary passes in these hills are less than 500 m elevation and would have been lower in the past, given the geological history of uplift in the region (Galvis et al., 1979; Cooper et al., 1995; Gregory-Wodzicki, 2000). According to this model, Maracaibo taxa with Magdalena affinities (e.g. clades within *Creagrutus*, *Ctenolucius*, *Cyphocharax*, *Gilbertolus*, *Apteronotus*, *Hoplosternum*, and *Rhamdia*) date perhaps

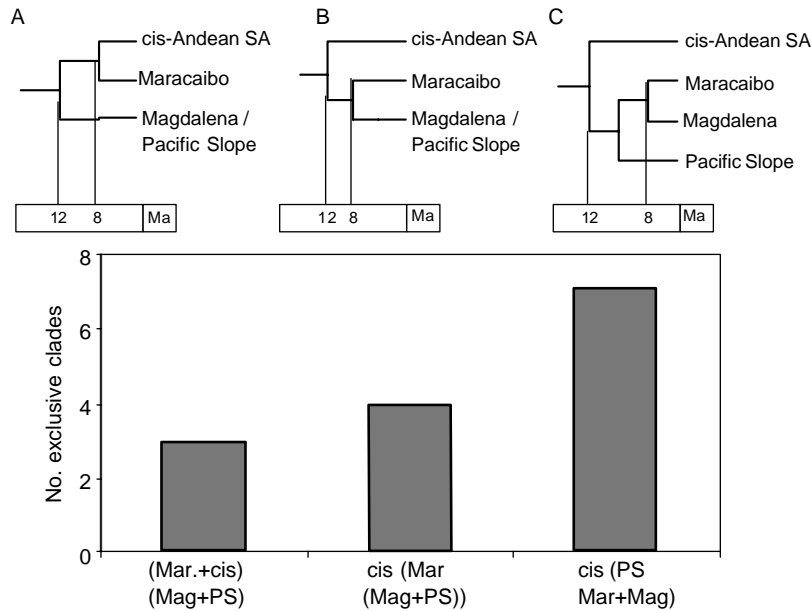


Fig. 3. Alternative area relationships of NSA basins based on species-level phylogenies of freshwater fishes. Dates at internal tree nodes from Fig. 1. Time scale not proportional. (A) Area relationships for three clades, including one each in *Roeboides*, *Apteronotus*, and *Brachyhypopomus*. (B) Area relationships for four clades, including one each in *Roeboides* and *Sternopygus* and two in *Pimelodella*. (C) Area relationships for seven clades, including one each in *Creagrutus*, *Ctenoluciidae*, *Cyphocharax*, Roestinae, *Apteronotus*, *Hoplosternum*, and *Rhamdia*. See Table 3 for references. Note the preponderance of clades exclusive to the Maracaibo and Magdalena basins.

to the Late Miocene or Pliocene, whereas other taxa (e.g. clades within *Roeboides*, *Apteronotus*, and *Brachyhypopomus*) with *cis*-Andean affinities date to before the Late Miocene and somehow persisted through the early Late Miocene marine incursion into the Maracaibo Basin in freshwater refugia. Some genera (e.g. *Roeboides*, *Apteronotus*) exhibit clades with both patterns of phylogenetic affinities.

A hybrid origin of the Maracaibo ichthyofauna is consistent with data about the species composition of the basin, which shares more genera of freshwater fishes with the (*cis*-Andean) Orinoco than with the (*trans*-Andean) Magdalena (Fig. 4). Because the majority of freshwater fish genera are present throughout the region (i.e. Maracaibo, Magdalena, and Orinoco basins), the regional ichthyofauna may predate the Miocene tectonic events that isolated these basins. The number of shared genera in these basins therefore may be attributed, at least in part, to widespread extinction of freshwater fishes in the Magdalena Basin since the Miocene (Lundberg, 1997).

4.2. Minimum divergence times for TAC

Estimates for the minimum time of origin of TACs come from three main sources: direct evidence from radiometric and stratigraphic dating of fossils and indirect evidence from molecular sequence and biogeographic divergence times (Lundberg, 1998; Lovejoy et al., 2006). At least 25 freshwater teleost genera were present in NSA by the Late Miocene (Table 5). Branch lengths (i.e. number of nucleotide substitutions) on phylogenies generated from molecular data sets have been used to estimate divergence times by calibration with geological events, such as the rise of the Panamanian landbridge (Martin and Bermingham, 2000) and the rise of the

Merida Andes (Sivasundar et al., 2001), or divergence rates in other taxa (e.g. Zamudio and Green, 1997). The divergence time estimates from the taxa in Table 1 suggest that most *trans*-Andean and Middle American freshwater fish clades of South American origin predate the Pliocene rise of the Isthmus of Panama and date to approximately the Middle–Late Miocene (8–15 Ma; Bermingham and Martin, 1998; Montoya-Burgos et al., 1998; Perdices et al., 2002; Sivasundar et al., 2001). Only some of the primary freshwater fishes in Middle America are believed to have invaded after the Pliocene rise of the Isthmus of Panama (e.g. characin *Roeboides*, catfish *Pimelodella*) (Bermingham and Martin, 1998; Martin and Bermingham, 1998, 2000).

The diverse taxonomic composition of the *trans*-Andean ichthyofauna (88% of Neotropical freshwater fish orders, 79% of families) suggests that the Late Miocene tectonism that

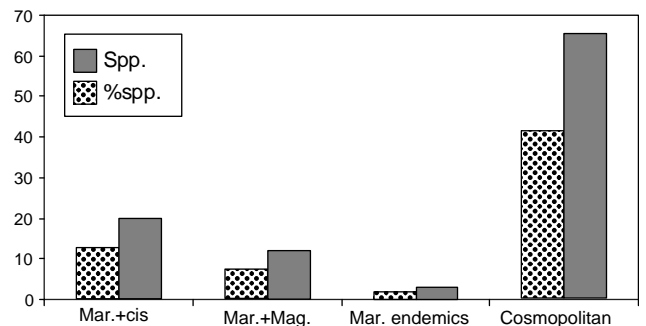


Fig. 4. Distribution of 62 genera of freshwater fishes in Maracaibo and adjacent basins. Data and abbreviations of regions from Table 3. Note that the Maracaibo Basin shares more genera of freshwater fishes with the Orinoco than the Magdalena Basin, and the majority of freshwater fish genera are present in all three.

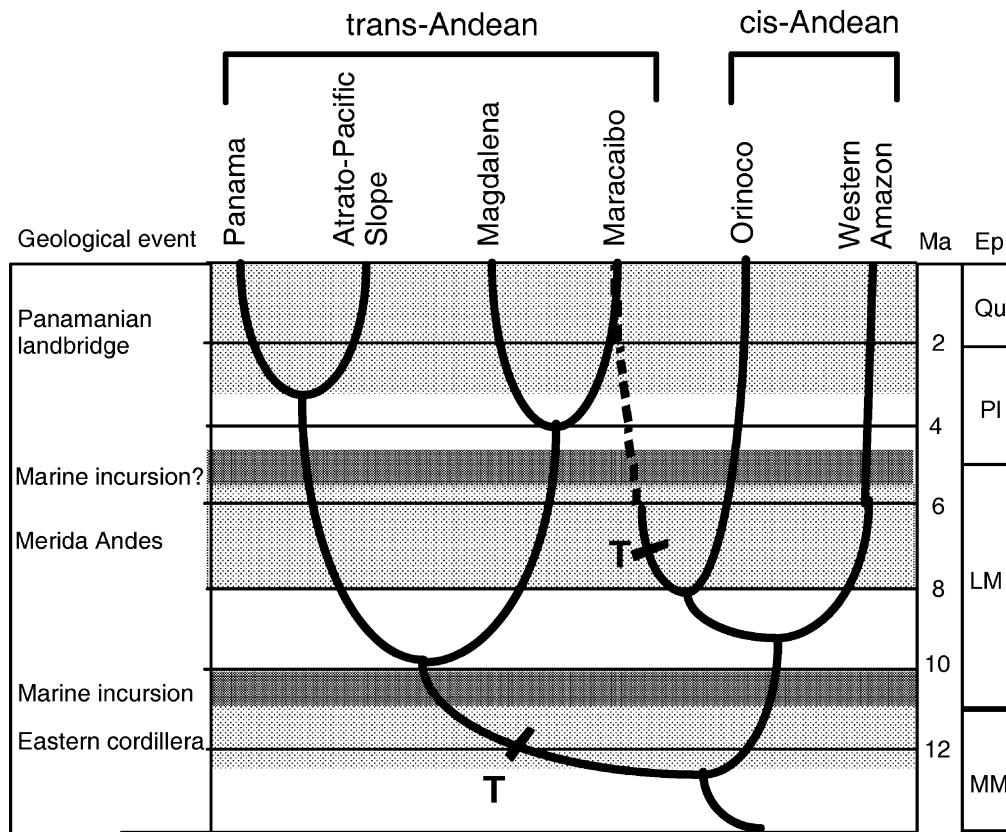


Fig. 5. Synthetic model of river basin isolation and aquatic faunal division based on species-level phylogenies and species composition of freshwater fishes. T, *trans*-Andean. Dashed line indicates partial faunal extinction. Hydrogeographic regions as in Table 3. Abbreviations as in Fig. 1. Note the dual origin of the *trans*-Andean ichthyofauna and the hybrid origin of the Maracaibo ichthyofauna.

formed the modern basins of NSA fragmented the entire aquatic fauna, leaving a clear signal on all major taxa. The significant correlation between species and cladal diversity (Fig. 2) suggests that the relative species diversity and biogeographic distributions of Amazonian fish taxa were modern by the late Middle Miocene. That is, species and cladal diversity had achieved approximately extant values before this vicariance event. An alternative explanation, which suggests that postvicariant species and cladal diversification has been equal on both slopes, may be regarded as less likely because of the vastly different sizes of these regions and the many known extinctions in *trans*-Andean basins (Lundberg, 1997).

Among the taxa with *cis*-*trans*-Andean distributions (Table 1), species phylogenies are available for only three genera with a diversity of more than 30 species: *Rivulus* (Hrbek and Larson, 1999; Murphy et al., 1999), *Creagrutus* (Vari and Harold, 2001), and *Gymnotus* (Albert et al., 2005). According to the two analyses of *Rivulus* using mt DNA, the *trans*-Andean species (including 8 spp. from nuclear and southern Middle America and one from the Magdalena) are monophyletic, and the basal nodes of the genus are all optimized in *cis*-Andean basins. In *Creagrutus* and *Gymnotus*, the *trans*-Andean assemblage of species was not found to be monophyletic according to morphological (mainly osteological) data (Vari and Harold, 2001; Albert et al., 2005). In both of these genera, the basal divisions are between *cis*- and *trans*-Andean clades,

and there are additional instances of taxa with *cis*- and *trans*-Andean species located at distal positions within the phylogeny. These phylogenetic patterns suggest a cladogenetic history that transcends multiple, geologically imposed vicariance events. In the case of *Gymnotus*, three terminal clades with *cis*-*trans*-Andean distributions are inferred to result from Late Miocene tectonism.

4.3. Ichthyofaunal isolation of Orinoco and western Amazon basins

At the species level, the electric fish (gymnotiform) fauna of the Orinoco Basin is much more similar to that of the western Amazon, from which it is currently isolated hydrologically, than it is to the drainages of the Guyanas Shield or eastern Amazon, with which it is now connected (Fig. 6). This result is surprising because the Upper Orinoco itself, as well as several of its large tributaries (e.g. Ventuari, Caroni, Cuyuni), emerge directly from the Guyanas Shield. Furthermore, the Upper Orinoco is directly connected to the Rio Negro basins of the eastern Amazon by means of the Casiquiare Canal. Clearly, the current levels of species migration in electric fishes between these adjacent basins are relatively low. The rivers of the Guyanas and Casiquiare Canal are apparently poor routes for dispersal in electric fishes, possibly because of the physical barriers (i.e. rapids) at Pto. Ayacucho and Sao Gabriel de Cachoeira and the chemical barriers (e.g. differences in pH,

Table 5
Summary of fossil record for Neotropical primary and secondary freshwater fishes

Order	Genus	Epoch	Age	Reference
Characif.	<i>Colossoma</i>	Middle Miocene	13.5	Lundberg et al., 1998
Characif.	<i>Cyphocharax</i>	Late Oligocene	22.5	Malabarba, 1998
Characif.	<i>Hoplias</i>	Late Paleocene	58.5	Gayet, 1991
Characif.	<i>Hoplias</i>	Middle Miocene	13.5	Roberts, 1975; Lundberg, 1997
Characif.	<i>Hydrolycus</i>	Middle Miocene	13.5	Lundberg et al., 1998
Characif.	<i>Leporinus</i>	Middle Miocene	13.5	Roberts, 1975; Lundberg, 1997
Characif.	<i>Lignobrycon</i>	Late Oligocene	22.5	Malabarba, 1998
Characif.	<i>Megacheirodon</i>	Late Oligocene	22.5	Malabarba, 1998
Characif.	<i>Myleinae</i>	Late Paleocene	58.5	Gayet, 1991
Characif.	<i>Parodon</i>	Middle Miocene	13.5	Roberts, 1975; Lundberg, 1997
Characif.	<i>Serrasalminae indet.</i>	Middle Miocene	13.5	Lundberg et al., 1998
Cichlidae	<i>Geophaginae indet.</i>	Miocene	8-22	Arratia and Cione, 1996
Cichlidae	<i>Maracara</i>	Paleogene	60-23	Lundberg, 1998
Cichlidae	<i>Paleocichla</i>	Miocene	8-22	Lundberg, 1998
Gymnotif.	<i>Sternopygus</i>	Late Miocene	8.0	Gayet and Meunier, 1991
Osteogl.	<i>Arapaima</i>	Middle Miocene	13.5	Lundberg et al., 1998
Silurif.	<i>Acanthicus</i>	Middle Miocene	13.5	Lundberg et al., 1998; Reis, 1998
Silurif.	<i>Brachyplatystoma</i>	Middle Miocene	13.5	Lundberg et al., 1998
Silurif.	<i>Corydoras</i>	Late Paleocene	58.5	Cockerell, 1925
Silurif.	<i>Hoplosternum</i>	Middle Miocene	13.5	Lundberg et al., 1998
Silurif.	<i>Nematogenys</i>	Middle Miocene	13.5	Lundberg et al., 1998; Reis, 1998
Silurif.	<i>Oxydoras</i>	Late Miocene	8.0	Aguilera, 1994; Lundberg, 1998
Silurif.	<i>Phractocephalus</i>	Middle Miocene	13.5	Lundberg et al., 1998
Silurif.	<i>Pseudopimelodus</i>	Middle Miocene	13.5	Lundberg, 1998
Silurif.	<i>Steindachneridion</i>	Late Oligocene	22.5	Malabarba, 1998

Taxa arranged alphabetically by order and genus.

temperature, conductivity) between the black water Rio Negro and Casiquiare Canal and the white water Orinoco and Amazon rivers. The very similar electric fish faunas of the Orinoco and Amazon basins may be explained by historical connections, perhaps through the north-flowing, Miocene, proto-Orinoco basin (Lundberg et al., 1998; Wesselingh et al., 2002). The timing of isolation between the Orinoco and western Amazon basins can be tested by phylogenetic data on electric fishes, as well as other groups of Neotropical fishes that inhabit these regions.

4.4. Proto-Orinoco freshwater plume and Middle American ichthyofauna

The emergence of the Isthmus of Panama, beginning in the Late Pliocene (~3 Ma), formed the only fully terrestrial connection between Middle and South America during the Cenozoic (Coney, 1982; Ituralde-Vincent and MacPhee, 1999). The pre-Pleistocene paleogeography of NSA therefore favored emplacement (i.e. origins by speciation or dispersal) of freshwater taxa to Middle America over the ocean, not land (Hoorn et al., 1995; Lundberg et al., 1998; Ituralde-Vincent and MacPhee, 1999). The presence of many freshwater fish taxa in Middle America before rise of the landbridge (Bussing, 1985; Bermingham et al., 1997; Bermingham and Martin, 1998; Martin and Bermingham, 1998, 2000) suggests a common mechanism of dispersal across the marine barrier. In this regard, it is interesting to compare the hydrological and biotic influences of the modern Amazon freshwater discharge into the Atlantic with that of the Miocene proto-Orinoco discharge into

the Caribbean. The freshwater plume of the modern Amazon is approximately 6700 km³ per year, or 214 million liters per second, averaged over the annual cycle (Goulding et al., 2003). This freshwater is distributed by the southern equatorial current northwest along the coast of the Brazilian state of Amapá and French Guyana a distance of 600–800 km, depending on the season. Not coincidentally, the freshwater fish fauna of these regions is strongly Amazonian in species composition compared with other parts of the Guyanas or northeastern Brazil (Planquette et al., 1996; Jégu and Keith, 1999; Albert, 2001; Hardman et al., 2002).

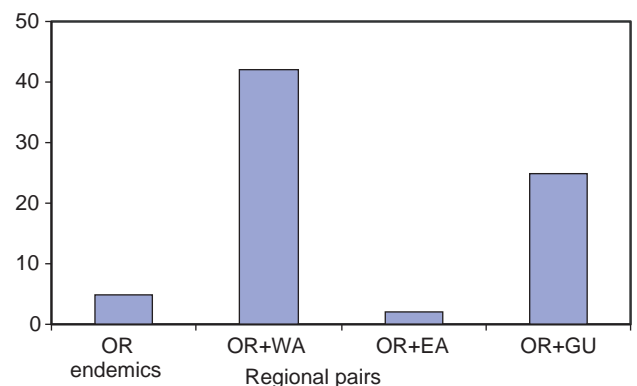


Fig. 6. Number of gymnotiform electric fish species shared between three cis-Andean hydrogeographic regions; Eastern Amazon (EA), Guyanas (GU), Orinoco (OR), western Amazon (WA). Geographic data and boundaries of hydrogeographic regions from Albert (2001) and Albert and Crampton (2005). Note that at the species level, the electric fish fauna of OR is more similar to WA than to GU or EA, which indicates higher levels of current or historical interchange.

There is no direct evidence bearing on the extent of the freshwater plume emerging from the Miocene proto-Orinoco River. Comparison of the sediment fans of the modern and proto-Orinoco rivers indicates similar total discharge volumes from these basins. The modern Amazon fan, accumulated over the past 9–10 million years, extends over an area of approximately 200,000 km² (Piper et al., 1997). As with the freshwater plume, much of the Amazon sediment load is distributed along the coast of the Guyanas, approximately 1500 km. Evidence for a wide geographic influence of the proto-Orinoco is provided by the Middle Miocene Napipi Formation of hemipelagic mudstones in the Atrato Basin (Duque-Caro, 1990). An important source of these mudstones was sediment from the proto-Orinoco that emerged from area of the modern Maracaibo Basin and was carried westward approximately 800 km by the prevailing circumtropical paleocurrent (Mullins et al., 1987). The northern coast of Colombia in the Middle Miocene may therefore be inferred to have been predominantly freshwater or brackish. The several marine transgressions and regressions in the Middle–Upper Miocene (Rasänen et al., 1995; Paxton et al., 1996; Lovejoy et al., 1998) would have substantially altered the coastline, episodically isolating and uniting the mouths of coastal rivers, altering the distance between freshwaters of Middle and South America, and strongly affecting opportunities for transoceanic dispersal during this interval.

4.5. Phylogenetic resolution from morphology and molecules

The data used to construct Table 1 were compiled from 24 published phylogenetic studies. Of these, 67% (16) examined morphological data only, 17% (4) molecular sequence data only, and 21% (5) considered both morphological and molecular data. Among the 37 *cis-trans*-Andean vicariance events attributed to Miocene tectonism in Table 1, 51% (19) were identified from studies using morphological data only, 22% (8) from molecular data only, and 22% (8) from studies using both morphological and molecular data. Our current understanding of phylogenetic relationships among freshwater fishes with *cis-trans*-Andean distributions is therefore largely the result of studies in comparative morphology, which arises partly because species-level sampling for most taxa requires collections made across large spatial (10³–10⁴ km) scales, and collections of whole specimens for morphological study are readily available for many taxa from natural history museums.

5. Conclusions

Patterns in the phylogenetic history of fishes from the rivers of NSA are largely concordant with geological information about the timing of drainage basin isolation. The effects of four prominent geological events in the Neogene left a strong phylogenetic signal on many fish taxa: (1) the rise of the Eastern Cordillera (~12 Ma), which hydrologically isolated the Magdalena and Pacific Slope ichthyofaunas from that of the north-flowing proto-Orinoco River; (2) the hydrological capture of the western Amazon Basin by the eastern Amazon

Basin (~9 Ma), which allowed extensive exchanges of species between these two regions and the formation of modern Amazon fish species assemblages, and the formation of the modern east-flowing modern Amazon River, which isolated the Orinoco and western Amazon ichthyofaunas; (3) the rise of the western portion of the Merida Andes (~8 Ma), which isolated the modern Maracaibo and Orinoco ichthyofaunas. The ichthyofauna of the Maracaibo Basin has a compound origin due to a partial extinction of *cis*-Andean taxa in the Late Miocene and to subsequent invasion by taxa from the adjacent Magdalena Basin; and (4) the rise of the Isthmus of Panama (~3 Ma), which formed the first terrestrial connection between Middle and South America. In terms of species composition, the ichthyofaunas of all river basins in NSA were largely modern by the time of the Late Miocene tectonic events that dissected the landscape.

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