

Not So Fast

A New Take on the Great American Biotic Interchange

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The completion of the Middle American land bridge resulted in some limited interchange of freshwater fishes. Again, the predominant direction of dispersal was from south to north.

LOMOLINO ET AL. 2006, 379

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The prevailing biological view of the closure of the Isthmus of Panama is of a dominant South American fauna rapidly expanding northward via the newly formed land bridge between the continents (Stehli and Webb 1985; Bermingham and Martin 1998; Lomolino et al. 2006). The current diversity of Central American and tropical North American (together Middle American) freshwater fish lineages is largely explained to be the result of explosive radiations that were facilitated by the invasion of South American fishes into new and unoccupied habitats on and across the isthmus. To the contrary, we present data that suggest that the Isthmus acted as a “two-way street,” with an asymmetry favoring a dominant Central American freshwater fish fauna moving south. Our data show that much of the Central American species diversity can be explained by older biogeographic events between Central and South America, and that the faunal interchange made possible by the rise of the isthmus led to several Plio-Pleistocene reinvasions of Central American taxa back into northwestern South America.

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The native ichthyofauna of Central America is dominated by lineages of South American origin. These include about 246 species of obligate (i.e., primary and secondary) freshwater fishes (species estimates from Albert et al. 2006 based on the taxonomy of Reis et al. 2003). The principal families of southern derivation are Characidae, Pimelodidae, Gymnotidae, Hypopomidae, Cyprinodontidae, Poeciliidae, and Cichlidae. The only Central American freshwater fishes with living relatives in North America are species of Lepisosteidae, Catostomidae, and Ictaluridae (Minkley et al. 2005), and recent paleontological studies suggests that even Lepisosteidae has southern (i.e., Gondwanan) origins (Brito 2006; Brito et al. 2006, 2007). There are in addition several dozen species of predominantly marine fishes that have become permanent freshwater residents (i.e., *Dorosoma*, *Potamarius*, *Hyporhamphus*, *Atherinella*, *Diapterus*, *Ogilbia*).

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Based mainly on geographic distributions, Bussing (1976, 1985) broadly distinguished the Central American fish taxa

into two historical assemblages: members of an “Old Southern Element” (a Paleoiichthyofauna) of Cretaceous or Paleocene origins (including *Hyphessobrycon*, *Gymnotus*, *Rhamdia*, *Cichlasoma*, *Phallichthys*, *Alfaro*, *Rivulus*) and a Neoichthyofauna of Plio-Pleistocene origins (including *Astyanax*, *Brycon*, *Roeboides*, *Hypostomus*, *Trichomycterus*, *Brachyhypopomus*, *Apteronotus*, *Aequidens*, *Geophagus*, *Synbranchus*). Under this view, the current diversity of Central American fishes is the result of multiple temporally distinct waves of South American invasions. Members of the Paleoiichthyofauna may be regarded as the ecosystem incumbents (*sensu* Vermeij and Dudley 2000), which were resistant to being displaced by potential invaders from adjacent regions. Bussing’s Neoichthyofauna is dominated by catfish and characin species that are predominantly found in lower Central America, particularly in Costa Rica and Panama. Bussing and subsequent workers (R. Miller 1966; Bermingham and Martin 1998; Martin and Bermingham, 1998, 2000) regarded these catfishes and characins as part of a recent northerly expansion from South America linked to the closure of the Panamanian Isthmus.

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The geological and paleogeographical circumstances underlying the origin of Bussing’s Paleoiichthyofauna remain incompletely understood. D. Rosen (1975, 1978) suggested that South American lineages of some groups entered Central America via a land bridge or island chain during the Late Cretaceous or early Paleogene. G. Myers (1966) described the time before the invasion of catfishes and characids as an “ostariophysan vacuum,” ostariophysans (i.e., Cypriniformes, Characiformes, Siluriformes, Gymnotiformes) being the clade of teleost fishes that dominate the species richness of the world’s continental freshwaters. Myers suggested that a dearth of native ostariophysans allowed for the diversification of other fish groups, including especially cichlids (Perciformes) and poeciliids (Cyprinodontiformes). This conjecture was not framed in explicit phylogenetic contexts so much as based on raw biogeographic distributions and patterns of species richness.

In this chapter we review evidence from the past two decades of research on the phylogenetics and phylogeography of Central American freshwater fishes, to address the question of the timing of the origins of the major taxonomic components of the fauna. The available data indicate that most groups became established in Central America through the actions of ancient

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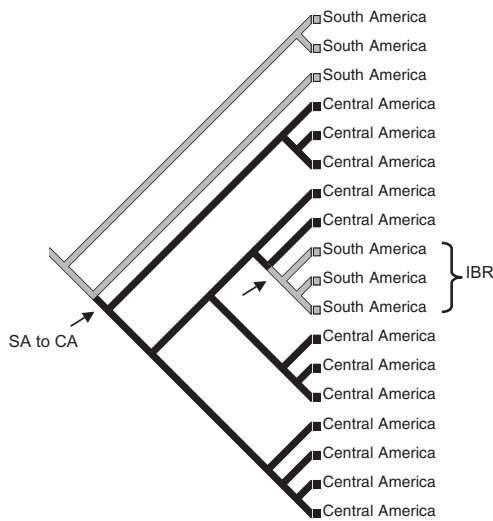


FIGURE 18.1 Example of a biogeographic pattern displayed on a parsimony optimization of Middle American and South American taxa. In this example an ancient dispersal event from South America (SA) to Central America (CA) is conjectured from the deep (basal) divergence. The more recent (apical) divergence is labeled as an “Isthmian biogeographic reversal” (IBR) conjectured to have taken place after closure of the Isthmus of Panama.

(Cretaceous or Paleogene) earth history events (Pindell et al. 1988; Pitman et al. 1993; Hoernle et al. 2002, 2004) or marine dispersal, perhaps assisted by freshwater plumes, and that the Isthmus of Panama allowed for Plio-Pleistocene expansions of several members of the Paleichthyofauna back into South America. Such returns of the older (originally South American derived) Central America lineages back to South America are referred to here as “Isthmian biogeographic reversals” (Figure 18.1).

Overview of Geology and Paleogeography

Modern Central America encompasses about 2.37 million km² in the land that lies between the Isthmus of Tehuantepec in southern Mexico and the Isthmus of Darien in southern Panama. Middle America is a more encompassing geographic region including the whole of Central America and Mexico north of the Isthmus of Tehuantepec to the Rio Grande on the U.S. border. The geology of Central America is dominated by three tectonic features. The oldest unit is the Chortis Block (also known as Nuclear Middle America), which includes parts of modern-day Honduras, Guatemala, El Salvador, and Nicaragua (Ross and Scotese 1988; Sedlock and Ortega-Gutiérrez 1993). The Chortis Block is a piece of continental crust that has been an emergent geological terrain since at least the Eocene and possibly as early as the Lower Cretaceous (Pindell and Kennan 2009). The two other major tectonic structures of Central America are volcanic arcs: Southern Central America, located in approximately the region of modern Costa Rica and southern Nicaragua, and the Isthmus of Panama. The trans-Andean lowlands (<300 m elevation) of northwestern South America are of Late Neogene age, including about 146,000 km² in the Pacific slope drainages of Colombia and Ecuador (from the Guayaquil to San Juan basins) and the

Caribbean drainages of northwestern Colombia (Atrato and Magdalena-Cauca basins).

The geology and paleogeography of lower Central America and northwestern South America during the Cenozoic have been well studied (see reviews in Coates et al. 2004, 2005; Iturralde-Vinent 2006; Doubrovine and Tarduno 2008; Pindell and Kennan 2009). Overland dispersal between western Laurasia (North America) and western Gondwana (South America) was interrupted in the Middle Jurassic Callovian (c. 165–162 Ma) when the continents became separated by a marine gap (Pindell and Barrett 1990; Iturralde-Vinent and MacPhee 1999). The Yucatan (Maya Block) was originally part of Gondwana prior to its collision with North America in the Late Carboniferous (Ross and Scotese 1988; Kerr et al. 1999; Pitman et al. 1993). Subsequently there have been several earth history events that may have potentially allowed the movement of freshwater taxa between the continents, including especially intermittent Cretaceous and Paleogene arcs that may have allowed sweepstakes dispersal across a narrow marine barrier, or even occasional complete terrestrial and freshwater continental routes between the American landmasses (e.g., proto-Greater Antilles arcs, Caribbean large igneous province; Figure 18.2; D. Rosen 1975, 1978).

Southern Central America originated as a volcanic island arc during the Upper Cretaceous (before 125 Ma), as a result of subduction along the eastern margin of the Cocos Plate under the trailing edge of the Caribbean Plate. This arc potentially may have facilitated biotic exchanges between North and South America during the latest Campanian/Maastrichtian (c. 75–65 Ma). From about the middle Miocene, Southern Central America was a peninsular extension of southern North America (Kirby and MacFadden 2005), after which a diversity gradient became established with fewer species southward (Taylor and Regal 1978; Zink 2002).

The formation of the Caribbean plate in the Pacific includes the origin of landmasses that are now Cuba, the Cayman Ridge, Hispaniola, Puerto Rico, and the Virgin Islands (Pindell and Barrett 1990). During the Late Cretaceous these landmasses collectively formed an island arc that drifted through the area between northern South America and Southern Central America (Iturralde-Vinent and MacPhee 1999). During periods of low eustatic sea levels (c. 80–70 Ma) this arc may have acted as a corridor for the movement of biotas between the two continents (Iturralde-Vinent and MacPhee 1999; Kerr et al. 1999). This arc began to break up at the end of the Cretaceous, and some geological reconstructions suggest direct but brief connections between the two continents in the Paleogene, at about 49 million years ago (Pitman et al. 1993). In addition, Hoernle and colleagues (2002, 2004) propose a Galapagos-hotspot-derived oceanic plateau called the Caribbean large igneous province (CLIP) that they suggest may have served as a land bridge or island chain connecting the continents in the Late Cretaceous or Early Paleogene.

There may also have been a transient land bridge between South America and the Greater Antilles in the Oligocene (c. 33 Ma) via an island ridge along the leading margin of the Caribbean Plate (i.e., Gaarlandia on the now submerged Aves ridge), although evidence for this hypothesis is currently ambiguous. Continued subduction along this trailing margin of the Caribbean Plate in the middle Cenozoic resulted in the Panama volcanic arc, which has maintained a relatively constant position between the North and South American plates from c. 46 Ma to Recent, and especially from c. 19 Ma. In other words, the plates and associated subduction arcs had attained their

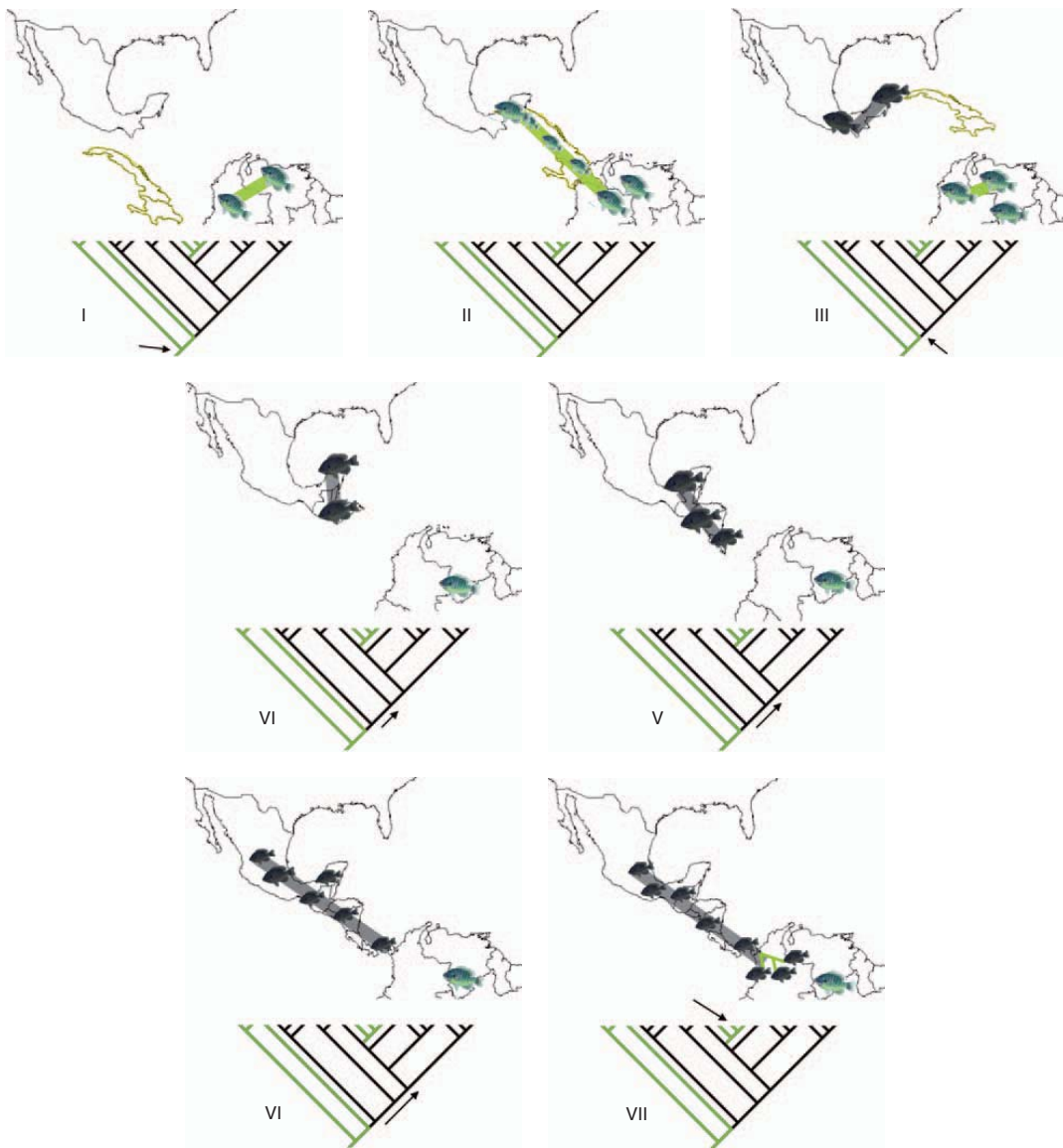


FIGURE 18.2 Hypothesis of dispersal events linked to earth history for Isthmian biogeographic reversals. (I) Cretaceous: Gondwanan (South American) taxa in green during the Cretaceous after the formation of the Cretaceous Island Arc (CIA) outlined in yellow in the Pacific. (II) Late Cretaceous: As the CIA drifted east to the Caribbean, it may have served as a land bridge creating a corridor between Middle and South America allowing South American taxa to disperse to Middle America. (III) Paleogene: After the CIA drifted to the Caribbean, Middle and South American taxa would have been isolated from each other (Black taxa: Middle American). (IV, V) After the formation of northern Central America from the addition of the Chortis Block, Southern Central America, the Nicaragua Rise, and other formations, taxa would be able to invade these new areas and diversify on them. (VI, VII) After the closure of the Isthmus of Panama, taxa would be able to “reinvade” South America as phylogenetically Middle American taxa.

modern configurations before the start of the Neogene, even if the modern land connections did not become fully emergent above the seas until the late Pliocene or early Pleistocene.

The Isthmus of Panama is geologically the youngest region of Central America, which rose in association with the Late Miocene to Pliocene collision of the Caribbean and South American plates and the closure of the Bolivar Trench (Coates

et al. 1992, 2004). The uplift of the isthmus took place over an extended period of more than 10 MY, beginning in the Late Miocene (c. 13 Ma) and concluding with the formation of a continuous land bridge in the late Pliocene or early Pleistocene (c. 3.5–2.6 Ma). Pliocene deposits are not known from the Darien or Panama Canal Basin, and no sediments younger than 4.8 Ma have been identified in the Atrato Basin

of Colombia. These observations suggest a rapid and extensive uplift along the Panama arc in the latest Miocene and early Pliocene.

Methods

Phylogenies for all taxa except Cichlidae were taken directly from published accounts; the phylogeny of cichlids is a new total-evidence analysis combining published morphological data (Chakrabarty 2007) and a newly generated molecular data set (see next section). Parsimony analyses for phylogenetic analysis were conducted using PAUP* 4.0b (Swofford 2003). Heuristic searches were performed with 1,000 random addition replicates for each analysis based on a single data partition. Jackknife resampling (100 replicates of 10 search replicates) was performed in NONA (Goloboff 1993) and WinClada (Nixon 1999). For combined analyses the parsimony ratchet (Nixon 1999) was implemented in PAUP* by using PAUPRat (Sikes and Lewis 2001) with 5% to 25% of the total characters perturbed (allowed to change weights) over 100 to 2,000 replicates until a stable solution was found (20 runs). A Malagasy cichlid, *Paratilapia polleni*, was used to root all trees. Area cladograms were examined in MacClade 4.0 (Maddison and Maddison 1992) using only unambiguously optimized characters (parsimony). Lesser Antillean islands such as Tobago were considered as South America in optimizations.

CICHLID PHYLOGENETIC ANALYSIS

The cichlid phylogeny is a total evidence phylogeny from Chakrabarty (2006b). This phylogeny combines morphological characters from Chakrabarty (2007); molecular data of Chakrabarty (2006a) for 16S, COI, S7, and Tmo-4C4; and *cyt-b* data from Genbank. Primers S7RPEX1F 5'-TGGCCTCTTCCTT-GGCCGTC-3' and S7RPEX2R 5'-AACTCGTCTGGCTTTTCGCC-3' were used to amplify and sequence the first intron in the nuclear S7 ribosomal protein gene, yielding sequences of 774 aligned positions (Chow and Hazama 1998; Lavoué et al. 2003). Primers Tmo-f2-5' 5'-ATCTGTGAGGCTGTGAACATA-3' (Lovejoy 2000) and Tmo-r1-3' 5'-CATCGTGCTCTGGGT-GACAAAGT-3' (Streelman and Karl 1997) were used to amplify and sequence a portion of the nuclear gene Tmo-4C4, yielding sequences of 299 aligned positions. Primers 16S ar-L 5'-CGCCTGTTTATCAAAAACAT-3' and 16S br-H 5'-CCGGTCTGAACCTCAGATCACGT-3' (Koucher et al. 1989; Palumbi 1996) were used to amplify and sequence a fragment of mitochondrial large ribosomal subunit 16S, yielding sequences of 614 aligned positions. Primers COI for 5'-TTCTCGACTAATCACAAAGACATYGG-3' and COI rev 5'-TCAAARAAGTTGTGTTAGGTYC-3' were modified from the primers of Folmer and colleagues (1994) to amplify and sequence a segment of mitochondrial gene COI, yielding sequences of 591 aligned positions.

Tissue samples were taken from specimens preserved as vouchers in the University of Michigan Museum of Zoology (UMMZ) Fish Division (Table 18.1). Voucher and GenBank accession numbers are listed in Table 18.1. Locality data for specimens can be obtained by searching the UMMZ fish collection catalog. All specimens are either wild-caught or purchased from a breeder raising wild-caught individuals and selling their young (Jeff Rapps; www.tangledupincichlids.com). Fish tissues are preserved in 95% ETOH and stored at -80°C. Tissue extraction was done using a Qiagen Tissue Extraction Kit following the manufacturer's protocol. PCR amplifications were

done for 30–35 cycles. Denaturation of 20 seconds at 95°C was followed by annealing for 15 seconds at temperatures of 60°C (S7), 50°C (Tmo-4C4), 45°C (COI). Extension times varied from 1 min 30 seconds, to 2 minutes. This extension was followed by a terminal extension for 7 minutes at 72°C. PCR amplification of 16S follows the protocol of Sparks (2004). PCR product was isolated on 1% agarose gels. Bands were removed from the gel under a UV light and extracted using Qiagen Gel Extraction Kits following the manufacturer's protocol. Sequencing was completed by the University of Michigan Sequencing Core Facility. DNA sequences were edited from chromatograms and aligned manually in Sequence Navigator (Elmer 1995). Species that appeared either paraphyletic or polyphyletic in Hulsey et al. (2004) were not sampled here. One representative sequence was selected if multiple copies were available. All S7 sequences are from Chakrabarty (2006a). TMO-4C4, 16S, and COI sequencing and extraction follow the procedure in Chakrabarty (2006a). Novel sampling of TMO-4C4, 16S, and COI sequence are listed in Table 18.1. *Cichla ocellaris* and *Crenicichla saxatilis* were sampled only for morphological features. *Cichla temensis* and *Crenicichla acutirostris* were sampled only for molecular characters. These species were used to make composite taxa to represent their respective genera, *Cichla* and *Crenicichla*. Because these genera are important outgroups, creating composites was favored over deletion.

Interpreting Biogeographic Patterns of Major Lineages

Freshwater fish taxa with Central American and South American representatives that may potentially reveal Isthmian biogeographic reversals are listed in Table 18.2. The phylogenetic histories of these groups are discussed and tested when possible to reveal each biogeographic history as it pertains to the Isthmus of Panama.

CHARACIFORMES: ROEBOIDES, CYPHOCHARAX, CTENOLUCIIDAE, CHARACIDIUM, COMPSURINI

The order Characiformes contains five clades whose interrelationships may have important biogeographic implications pertaining to the rise of the Isthmus of Panama. The phylogeny of the Characiform genus *Roeboides* by Bermingham and Martin (1998) contains 38 taxa representing five species: *Roeboides dayi*, *R. magdalenae*, *R. meeki*, *R. occidentalis*, and *R. guatemalensis*. The clade of *R. meeki*, from the Rio Atrato in Colombia, is optimized as an Isthmian biogeographic reversal (Figure 18.3C). *Roeboides meeki* was recovered as the sister group to a clade comprising three individuals of *R. occidentalis* from Rio Pirre and Rio Caimito. *Roeboides occidentalis* is recovered as a polyphyletic species. This result potentially indicates the recent dispersal of the lineage containing *R. meeki* from Central America to South America. Vari (1992) recognized 33 species in *Cyphocharax*; unfortunately, this clade lacks a phylogenetic treatment. This genus has the greatest north-to-south range of any Curimatidae and includes one species, *Cyphocharax magdalenae*, that is found in Costa Rica and Panama (Vari 1992). Lacking a phylogenetic analysis of this group, it is impossible to study the dispersal history of this group in relation to the rise of the Isthmus of Panama. The family Ctenoluciidae is a widespread Neotropical family of characiforms, including *Ctenolucius*, that ranges from western Panama to Colombia and Venezuela. Vari (1995) recovered the Panamanian/Colombian species *Ctenolucius beani* as sister to its South

TABLE 18.1

Genbank Accession Numbers for Cichlid Species Used in the Phylogenetic Analysis
Data for 112 Species

Heroines	Morphology	16S	COI	Tmo-4c4	S7	Cyt b
MIDDLE AMERICA HEROINES						
<i>Amphilophus altifrons</i>						AF145127
<i>Amphilophus bussingi</i>						AF145129
<i>Amphilophus calobrense</i>		GU817207	GU817255			
<i>Amphilophus citrinellus</i>		DQ119169	DQ119198	DQ119227	DQ119256	AB018985
<i>Amphilophus diquis</i>						AF009945
<i>Amphilophus hogaboomorus</i>	C 2007					
<i>Amphilophus labiatus</i>				GU817298		AF370662
<i>Amphilophus longimanus</i>						AF009943
<i>Amphilophus lyonsi</i>		DQ119170	DQ119199	DQ119228	DQ119257	
<i>Amphilophus macracanthus</i>	C 2007					U97160
<i>Amphilophus rhytisma</i>						AF009946
<i>Amphilophus robertsoni</i>	C 2007	GU817208	GU817256			U97163
<i>Amphilophus rostratus</i>						AF141319
<i>Archocentrus centrarchus</i>		DQ119162	DQ119163	DQ119164	DQ119165	AF009931
<i>Archocentrus multispinosus</i>		DQ119166	DQ119195	DQ119224	DQ119253	AF009942
<i>Archocentrus myrmae</i>		GU817209	GU817257			AF009927
<i>Archocentrus nanoluteus</i>		GU817210				
<i>Archocentrus panamensis</i>		GU817211	GU817258			
<i>Archocentrus nigrofasciatus</i>	C 2007	DQ119167	DQ119196	DQ119225	DQ119254	AF009935
<i>Archocentrus sajica</i>		GU817212	GU817259			AF009925
<i>Archocentrus septemfasciatus</i>	C 2007	GU817213	GU817260	GU817299		AF009932
<i>Archocentrus spilurus</i>	C 2007	GU817214	GU817261	GU817300		AY050620
<i>Archocentrus spinosissimus</i>		GU817215	GU817262			
<i>Caquetaia umbrifera</i>		GU817216	GU817263			AF009940
" <i>Cichlasoma</i> " <i>beani</i>	C 2007					
" <i>Cichlasoma</i> " <i>deppii</i>		GU817217	GU817264	GU817301		
" <i>Cichlasoma</i> " <i>grammodes</i>	C 2007	GU817218	GU817265	GU817302		
" <i>Cichlasoma</i> " <i>istlanum</i>	C 2007					
" <i>Cichlasoma</i> " <i>cf. facetum-oblongus</i>		GU817219	GU817266			
" <i>Cichlasoma</i> " <i>trimaculatum</i>	C 2007	GU817220	GU817267			AY324031
" <i>Cichlasoma</i> " <i>octofasciatum</i>	C 2007	GU817221	GU817268	DQ119226	DQ119255	AY050616
" <i>Cichlasoma</i> " <i>urophthalmum</i>	C 2007	GU817222				AY050624
" <i>Cichlasoma</i> " <i>salvini</i>	C 2007	GU817223	DQ119200	DQ119229	DQ119258	
<i>Herichthys bartoni</i>	C 2007					AY324014
<i>Herichthys carpintis</i>		DQ119172	DQ119201	DQ119230	DQ119259	
<i>Herichthys cyanoguttatus</i>	C 2007					AY323982
<i>Herichthys labridens</i>		GU817224	GU817269			
<i>Herichthys minckleyi</i>						AY323994
<i>Herichthys pantostictus</i>						AY323988
<i>Herichthys steindachneri</i>	C 2007					AY324012
<i>Herichthys tamasopoensis</i>		GU817225	GU817270			AY324000
<i>Hypsophrys nicaraguensis</i>	C 2007	DQ119173	DQ119202	DQ119231	DQ119260	AF009930
<i>Neotroplus nematopus</i>						AF009928
<i>Parachromis dovii</i>	C 2007	DQ119175	DQ119204	DQ119233	DQ119262	U88864
<i>Parachromis friedrichsthalii</i>	C 2007	GU817226	GU817271			
<i>Parachromis loisellei</i>	C 2007	GU817227	GU817272			AF009926
<i>Parachromis managuense</i>	C 2007	DQ119174	DQ119203	DQ119232	DQ119261	AY050613
<i>Parachromis motaguense</i>	C 2007	DQ119176	DQ119205	DQ119234	DQ119263	
<i>Paraneotroplus bulleri</i>						AY324004
<i>Theraps wesseli</i>		GU817228	GU817273			
<i>Thorichthys affinis</i>	C 2007					
<i>Thorichthys aureus</i>		DQ119178	DQ119207	DQ119236	DQ119265	
<i>Thorichthys callolepis</i>						AY324005
<i>Thorichthys ellioti</i>		GU817229	GU817274			AY324009
<i>Thorichthys helleri</i>						AY324021
<i>Thorichthys meeki</i>	C 2007	GU817230	GU817275	GU817303		U88860
<i>Thorichthys pasionis</i>	C 2007	GU817231	GU817276			
<i>Tomocichla asfraci</i>		AY662735	AY662786			
<i>Tomocichla sieboldi</i>	C 2007	DQ119179	DQ119208	DQ119237	DQ119266	AF009937
<i>Tomocichla tuba</i>	C 2007					AF009941
<i>Vieja argentea</i>		GU817232	GU817277	GU817304		
<i>Vieja bifasciata</i>		GU817233	GU817278	GU817305		

1

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TABLE 18.I (continued)

<i>Heroines</i>	<i>Morphology</i>	<i>16S</i>	<i>COI</i>	<i>Tmo-4c4</i>	<i>S7</i>	<i>Cyt b</i>
<i>Vieja breidohri</i>						AY050626
<i>Vieja fenestrata</i>	C 2007					AY324002
<i>Vieja godmanni</i>		GU817234	GU817279			
<i>Vieja guttulata</i>						AY324023
<i>Vieja heterospilus</i>		GU817235	GU817280	GU817306		
<i>Vieja intermedia</i>		GU817236	GU817281			
<i>Vieja regani</i>		GU817237	GU817282			AF370646
<i>Vieja synspila</i>	C 2007	GU817238	GU817283	DQ119238	DQ119267	AY050625
<i>Vieja maculicauda</i>	C 2007	GU817239	GU817284			U97165
<i>Vieja 'Belize' melanurus</i>		GU817240	GU817285			
<i>Vieja tuyrense</i>		DQ119181	DQ119210	DQ119239	DQ119268	
<i>Vieja ufermanni</i>		GU817241	GU817286			
<i>Vieja zonata</i>	C 2007					
GREATER ANTILLES HEROINES						
<i>Nandopsis ramsdeni</i>	C 2007	DQ119182	DQ119211	DQ119240	DQ119269	
<i>Nandopsis tetracanthus</i>	C 2007	DQ119183	DQ119212	DQ119241	DQ119270	
<i>Nandopsis haitiensis</i>	C 2007	DQ119184	DQ119213	DQ119242	DQ119271	
SOUTH AMERICAN HEROINES						
<i>Caquetaia kraussii</i>		GU817242	GU817287	GU817307		AF009938
<i>Caquetaia myersi</i>		GU817243	GU817288	GU817308		AY050615
<i>Caquetaia spectabilis</i>		GU817244	GU817289	GU817309		AF370671
" <i>Cichlasoma</i> " <i>atromaculatum</i>	C 2007					AF009939
" <i>Cichlasoma</i> " <i>facetum</i>	C 2007	GU817245	GU817290	GU817310		
" <i>Cichlasoma</i> " <i>festae</i>	C 2007	DQ119187	DQ119216	DQ119245	DQ119274	AY050610
" <i>Cichlasoma</i> " <i>ornatum</i>	C 2007					
<i>Heros appendiculatus</i>		DQ119189	DQ119218	DQ119247	DQ119276	AF009951
<i>Hypselecara coryphaenoides</i>						AF370674
<i>Hypselecara temporalis</i>		DQ119190	DQ119219	DQ119248	DQ119277	
<i>Mesonauta insignis</i>						AF370675
<i>Symphysodon aequifasciatus</i>						AF370677
<i>Uaru amphiacanthoides</i>		DQ119191	DQ119220	DQ11924	DQ119278	AY050622
SOUTH AMERICAN OUTGROUPS						
<i>Aequidens diadema</i>		GU817246	GU817291			
<i>Apistogramma bitaeniata</i>		DQ119185	DQ119214	DQ119243	DQ119272	
<i>Bujurquina vittata</i>		DQ119186	DQ119215	DQ119244	DQ119273	
<i>Cichla ocellaris</i>	C 2007					
<i>Cichla temensis</i>		GU817247		GU817311		AF370644
<i>Crenicichla acutirostris</i>		GU817248	GU817292	GU817312		
<i>Crenicichla saxatilis</i>	C 2007					
<i>Geophagus steindachneri</i>		DQ119188	DQ119217	DQ119246	DQ119275	
<i>Gymnogeophagus gymnogynys</i>		GU817249	GU817293	GU817313		
<i>Satanoperca jurupari</i>		GU817250		GU817314		
<i>Tahuantinsuyoa macantzatzta</i>		GU817251	GU817294	GU817315		
<i>Teleocichla monogramma</i>		GU817252	GU817295	GU817316		
MADAGASCAR-INDIA OUTGROUPS						
<i>Etroplus maculatus</i>		DQ119192	DQ119221	DQ119250	DQ119279	
<i>Paretroplus kieneri</i>		DQ119194	DQ119223	DQ119252	DQ119281	
<i>Paratilapia polleni</i>		DQ119193	DQ119222	DQ119251	DQ119280	
AFRICAN OUTGROUPS						
<i>Etia nguti</i>		GU817253	GU817296			
<i>Hemichromis letourneuxi</i>		GU817254	GU817297			

NOTE: All vouchers and a complete list of specimens examined are reported in Chakrabarty (2006b) and Chakrabarty (2007).

TABLE 18.2

Freshwater Fish Taxa with Central American and South American Representatives That Include Isthmian Biogeographic Reversals

Order	Taxon	MA	PS	Atr.	Mag.	Mar.	SA	References
Characiformes	<i>Characidium</i>	1	2	0	2	1	0	Buckup 2003; personal communication
	Compsurini	3	1	1	1	1	0	Malabarba 1998
	<i>Roeboidea</i>	4	2	1	1	1	0	Bermingham and Martins 1998
	Ctenoleucidae	1	1	1	1	1	0	Vari 1995
	<i>Cyphocharax</i>	1	0	1	1	2	0	Vari 1992
Cyprinodontiformes	<i>Rivulus</i>	17	3	0	2	0	0	Hrbek and Larson 1999; Murphy et al. 1999
	<i>Neoheterandria</i>	4	0	1	0	0	0	Hrbek et al. 2006
	<i>Pseudopocilia</i>	1	1	0	0	0	2	Hrbek et al. 2006
	<i>Priapichthys</i>	4	3	0	0	0	0	Mateos et al. 2002; Hrbek et al. 2006
Gymnotiformes	<i>Apteronotus</i>	1	4	2	3	3	0	Albert 2001
	<i>Gymnotus</i>	3	3	1	1	0	0	Albert et al. 2003
	<i>Brachyhyopomus</i>	1	1	1	1	1	0	Bermingham and Martins 1998; Albert 2001
Perciformes-Cichlinae	<i>Caquetaia</i>	1	0	0	1	0	2	Chakrabarty 2006, this study, referenced within
	<i>Cichlasoma</i>	109	0	1	0	0	3	Chakrabarty 2006, this study, referenced within
Siluriformes	<i>Hoplosternum</i>	1	1	1	1	1	0	Reis 1998
	<i>Pimelodella</i>	2	4	1	1	1	0	Martin and Bermingham 2000
	<i>Rhamdia</i>	2	1	1	1	1	0	Perdices et al. 2000
Total		156	27	13	17	13	7	233

NOTE: Taxa distributed in Middle America (MA) and trans-Andean northwestern South America. PS, Pacific Slope Colombia and Ecuador; Atr., Atrato and Salí basins; Mag., Magdalena-Cauca Basin; Mar., Maracaibo Basin; SA, other South America/Amazonian.

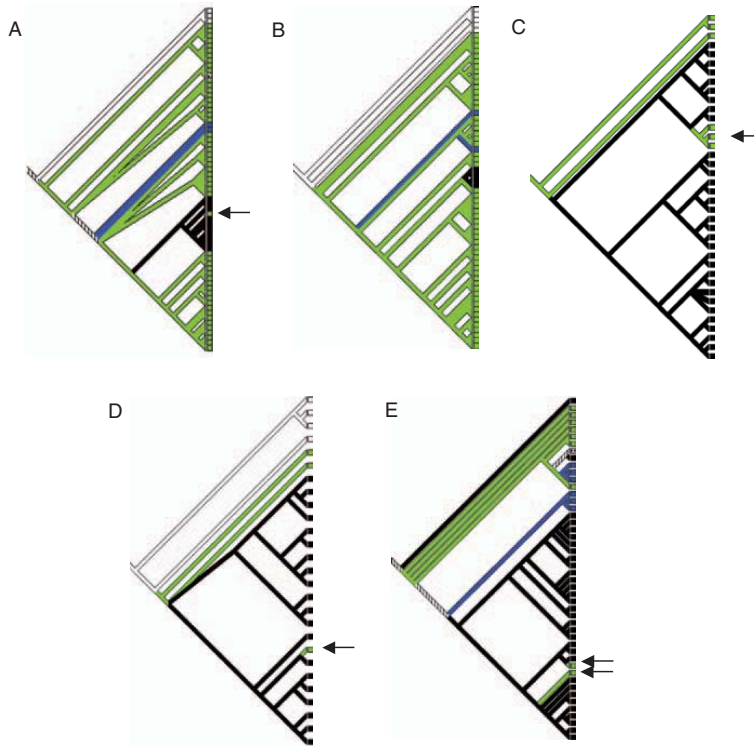


FIGURE 18.3 Phylogeny of Central American taxa. White clades are outgroups, green clades are South American, blue clades are Greater Antillean, and black clades are South American. All optimizations are unambiguous. **A.** Phylogeny of Rivalidae from Murphy et al. (1999). **B.** Phylogeny of Rivalidae based on Hrbek and Larson (1999). **C.** Phylogeny of *Roboidea* from Bermingham and Martin (1998). **D.** Phylogeny of *Rhamdia* from Perdices et al. (2002). **E.** Phylogeny of Poeciliidae from Hrbek et al. (2007). Arrows indicate Isthmian Biogeographic Reversals.

American congener *C. hujeta* and nested within other South American clades. Therefore, *Ctenolucius beani* is likely the result of dispersal event from South America to Central America. However, without a species-level analysis of *C. beani* it remains unresolved whether there may have been recent dispersal events from the northern populations of *C. beani* from Panama to the Atrato River in Colombia. *Characidium* is a poorly studied genus of Crenuchidae (the South American darters). Buckup (2003) listed 47 species in his checklist of *Characidium* that included only South American taxa. However, an undescribed species is known from Central America (Buckup, personal communication). Unfortunately, without a phylogenetic analysis of this group that includes this undescribed species little can be said about the historical biogeography of this group. Compusurini is a tribe of Cheirodontinae defined by the presence of spermatozoa in the ovaries of mature females (Burns et al. 1997; Malabarba 1998). Two genera in this tribe *Odontostilbe* and *Compsura*, contain members that are found in Panama and Costa Rica. Unfortunately, the only phylogeny to date that includes these species (Malabarba 1998) lacks sufficient resolution to be useful in our biogeographic analyses.

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SILURIFORMES: *HOPLOSTERNUM*,
RHAMDIA, *PIMELODELLA*

The catfish order Siluriformes contains three genera whose relationships potentially have important biogeographic implications related to the rise of the Isthmus of Panama. The armored catfish *Hoplosternum* (Callichthyidae) possesses both cis- and trans-Andean distributions—that is, on the eastern and western slopes, respectively (Reis 1998). *Hoplosternum punctatum* is found in both the Rio Atrato and in Panama, whereas all other *Hoplosternum* species inhabit South American waters. Therefore, a species-level phylogeny of *Hoplosternum punctatum* will be required to see if there are any dispersal events that can be revealed between the Colombian and Panamanian populations. The phylogeny of the genus *Rhamdia* by Perdices and colleagues (2002) includes a potential Isthmian biogeographic reversal (Figure 18.3D). Individuals of *Rhamdia guatemalensis* are found throughout Central America as well as northern South America. The northern South American individuals from the Magdalena, Colombia, and Lake Maracaibo, Venezuela, both optimize as phylogenetically Central American. The larger radiation that includes the sister-group relationship between *Rhamdia laticauda* and *R. guatemalensis* optimizes as phylogenetically South American, which represents an older radiation than that within the *R. guatemalensis* clade. A phylogeny of *Pimelodella chagresi* by Bermingham and Martin (1998) and Martin and Bermingham (2000) recovered multiple invasions of populations of this species from South America to Panama and more northern regions. However, no evidence of northern lineages dispersing into South America was revealed in this population-level study.

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GYMNOTIFORMES: *GYMNOTUS*,
BRACHYHYPOPOMUS, *APTERONOTUS*

There is a single gymnotiform lineage in the Central American Paleioichthyofauna, and at least three lineages in the Neioichthyofauna (Albert 2001; Albert et al. 2005; Lovejoy et al. 2010). *Gymnotus* (Gymnotidae) is the most species-rich gymnotiform genus in Central America, with three species in two clades: *G. cylindricus* and *G. maculosus* are sister species

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of a single lineage, which inhabit the Atlantic and Pacific slopes respectively of the Chortis Block and Southern Central America; *G. panamensis* represents a distinct lineage endemic to the Isthmus of Panama, whose closest relatives inhabit cis-Andean regions of South America. *Brachyhyppopomus occidentalis* (Hypopomidae) is known from Panama and northern Colombia, and although the phylogenetics of this species are unresolved, all other congeners are South American. *Apteronotus rostratus* (Apteronotidae) is endemic to Panama with nearest relatives in trans-Andean South America (*A. spurrellii*, *A. leptorhynchus*).

CYPRINODONTIFORMES: *RIVULIDAE*

The biogeographic area relationships of rivulids were analyzed from the phylogenetic analyses of Hrbek and Larson (1999) and Murphy and colleagues (1999) and shown as unambiguously optimized area cladograms in Figure 18.3A. The phylogeny of Murphy and colleagues (1999) recovers a single lineage of Central American taxa that are nested within other South American taxa. A single species, *Rivulus magdalenae*, from Colombia is optimized as an Isthmian biogeographic reversal—that is, a South American species optimizing as phylogenetically Central American. This result potentially indicates the recent dispersal of this lineage from Central America to South America. Therefore, the entire Central American lineage recovered in this phylogeny may represent a pre-Isthmian radiation from South America. However, one would draw a different conclusion based on the phylogeny of Hrbek and Larson (1999; Figure 18.3B). The placement of *Rivulus magdalenae* in this phylogeny optimizes it as a South American species sister to an apical clade of Central American taxa. The results for this family are therefore equivocal.

CYPRINODONTIFORMES: *POECILIIDAE*

A biogeographic phylogenetic analysis of the killifish family Poeciliidae by Hrbek and colleagues (2007; redrawn in Figure 18.3E) recovers several potential Isthmian biogeographic reversals. The South American taxon *Neoheterandria elegans* from the Trundo River of Colombia is nested within Middle American taxa. This species is sister to *Neoheterandria tridentiger* of Panama. *Priapichthys (Pseudopoecilia) festae*, which can be found as far as Ecuador, is also recovered as having Middle American origins independent of *Neoheterandria*. Poeciliids are among the most abundant and diverse families of Middle American fishes and include over 200 species. Notably the phylogeny of Hrbek and colleagues (2007) recovered several potentially recent invasions of South American fishes into Central America (*Poecilia*) and the Greater Antilles (*Limia*). The Middle American taxon *Xenodexia ctenolepis* is sister to the remaining South American and Middle American in-group taxa sampled by Hrbek and colleagues (2007). The authors interpret this relationship as the earliest Central American invasion of poeciliids from South America, and because of its basal phylogenetic position we do not interpret this relationship to represent an Isthmian biogeographic reversal.

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PERCIFORMES: *CICHLIDAE*

Aligned sequences and morphological characters yielded 3,523 characters for each of the 109 taxa. S7 primers yielded 774 aligned positions, Tmo-4C4 primers yielded 299 aligned

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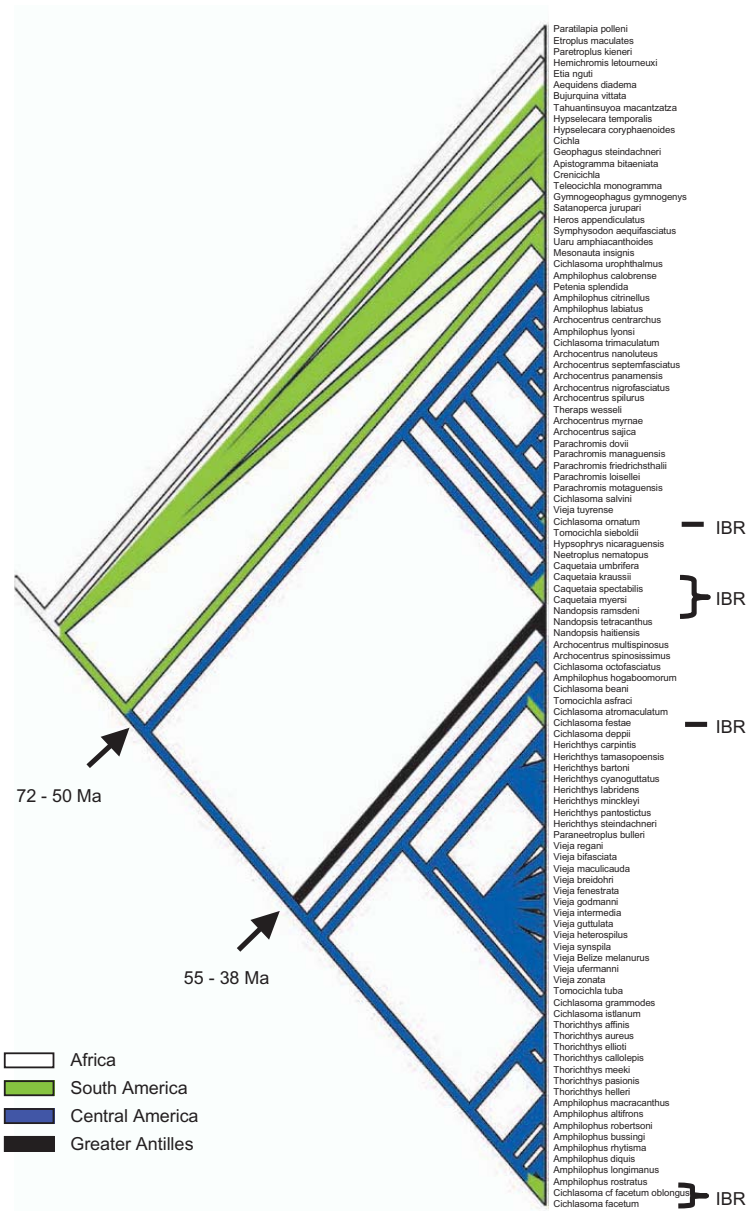


FIGURE 18.4 Phylogeny of Middle American cichlids from Chakrabarty (2006b) based on S7, Tmo-4C4, 16S, COI, cyt-*b*, and morphological characters. A parsimony optimization of area is shown. Dates based on estimated divergence times from Chakrabarty (2006a). Green clades are South American, blue clades Greater Antillean, pink taxa are found in both Middle and South America, and black clades are Middle American.

positions, 16S primers yielded 614 aligned positions, COI primers yielded 591 aligned positions, and cytochrome *b* sequences totaled 1,148 aligned positions; there were 89 morphological characters. Figure 18.4 show the total evidence analyses based on those gene fragments and characters from the morphological study of Chakrabarty (2007), in which the clade of Central American cichlids is nested within a South American clade. Central American cichlids are more closely related to each other than to South American lineages in all

cases. Four geographically South American species were found to be phylogenetically Central American with this optimization. Two large clades of Central American cichlids were recovered. One clade is sister to the mainly South American *Caquetaia*. The other Central American clade is sister to the Greater Antillean *Nandopsis*. Within each Central American group are several geographically South American cichlid taxa including "*Cichlasoma*" *ornatum* (Ecuador and Colombia), *C. festae* (Ecuador and Peru), *C. atromaculatum* (Colombia), and

C. facetum (middle South America). However, the parsimony optimization reveals that these species are phylogenetically Central American (blue). These species are therefore Central American taxa that have dispersed onto South America. The dispersal is apparently recent because they are distally located on the phylogeny (an example of a more ancient divergence would be *Nandopsis*, which is sister to a large clade of Central American cichlids). These results are congruent with those of other recent analysis on Central American cichlids. The analyses of W. Smith and colleagues (2008), Rícan and colleagues (2008), Concheiro-Pérez and colleagues (2007), Hulseley and colleagues (2006), and Chakrabarty (2006) all recover the same South American taxa (*Caquetaia* spp., "*Cichlasoma*" *ornatum*, *C. festae*, *C. atromaculatum*, and *C. facetum*) nested within Central American endemics whenever they are sampled in analyses.

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TERRESTRIAL TAXA

Dispersal between northern South America and Central America has been shown in several terrestrial taxa before the Pliocene. Some well-studied north-to-south taxa include cricetine rodents (Marshall 1979), howler monkeys (Atelidae: *Alouatta*) (Cortes-Ortiz et al. 2003), and procyonid mammals (Koepfli et al. 2007). Taxa that moved south to north include recluse spiders (Sicariidae: *Loxosceles*; Binford et al. 2008) and valerian plants (Valerianaceae; C. Bell and Donoghue 2005). At least three dispersal events are hypothesized for Central American *Eleutherodactylus* (Anura: Leptodactylidae) from South America: in the early Paleocene, at the end of the Eocene, and multiple dispersal events from South America during the Pliocene (Crawford and Smith 2005). *Guatertia* (Annonaceae), the third most species-rich genus of Neotropical trees, arrived in Central America before the closing of the Isthmus of Panama, and several Isthmian biogeographic reversals have been documented within this clade (Erkens et al. 2007).

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Reversals and Gradients before the Isthmus

ISTHMIAN BIOGEOGRAPHIC REVERSALS

The general impression that arises from the study of freshwater fishes is that the biotic interchange that resulted from the rise of the Isthmus of Panama was less important to the formation of the modern ichthyofaunas than were the earlier interchanges (Figure 18.2) during the Upper Cretaceous (Iturralde-Vinent and MacPhee 1999), Paleogene (Hoernle et al. 2002, 2004; Mann et al. 2007), or Middle Neogene. In addition, and contrary to previous interpretations, the Pliocene event facilitated a reciprocal and asymmetrical interchange among the ichthyofaunas of Central and South America, with more species moving south than north.

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Despite a lack of well-resolved species-level phylogenies for most groups of Central American freshwater fishes, the available phylogenetic and biogeographic information suggests multiple instances of Isthmian biogeographic reversals (Figures 18.3 and 18.4). There are several examples of populations or species inhabiting the trans-Andean region of northern South America whose closest relatives live in Panama, including *Roebooides meeki*, *Characidium* spp. and *Compsurini* spp. (Characidae), *Cyphocharax* spp. (Ctenoluciidae), *Brachyhyopomus occidentalis* (Hypopomidae), *Apteronotus spurrellii* and *A. leptorhynchus* (Apteronotidae), and *Rivulus magdalenae* (Rivulidae).

Populations of the catfish *Rhamdia guatemalensis* (Pimelodidae) in the Magdalena basin of northern South America are phylogenetically of Central American origin (Perdices et al. 2002).

Unequivocal examples of Isthmian biogeographic reversals are found in the phylogeny of Central American heroine cichlids. There are two divisions of Central American cichlids. Division I is a clade of 27 species, and its sister group is the primarily South American *Caquetaia*. Division II is a clade composed of 51 Central American species and its sister group *Nandopsis*, itself an endemic to the Greater Antilles. These two divisions are sister taxa (Figure 18.4). The parsimony-based optimization is equivocal about the origins of each of these divisions, but together as a clade they are nested within a more inclusive clade of South American origin. Nested within the Central American heroine species are several South American species (Figure 18.4).

There are several Isthmian biogeographic reversals within Central American cichlids, based on the phylogenies presented here. "*Cichlasoma*" *ornatum*, *C. festae*, *C. atromaculatum*, and *C. facetum* all are phylogenetically Central American cichlids found in South America. These species are all found on apical positions on the phylogeny, and are therefore likely the product of dispersal. The monophyletic *Caquetaia* is a South American lineage with one species, *Caquetaia umbrifera*, that is present in both South America and Panama. *Caquetaia* is the sister lineage to a large clade of Central American cichlids. "*Cichlasoma*" *atromaculatum* is one of only a few species that are found in both Central America (Panama) and South America. Notably, all the species that are phylogenetically Central American but native to South America were determined to be Central American much earlier by C. Tate Regan. Regan (1906–1908) stated that "*Cichlasoma*" *festae*, *C. ornatum*, *C. atromaculatum*, and *Caquetaia* were members of his Central American section "*Nandopsis*" and that "the South American species of this section are probably derived from immigrants from Central America." Two South American cichlids recently invaded Central America: *Geophagus crassilabris* and *Aequidens coeruleopunctatus*; unfortunately neither was available for sampling here. Both taxa are endemic to lower Central America, and neither is a heroine cichlid (the only nonheroine cichlids in Central or North America), nor are they closely related to these Central American taxa (Kullander 1998).

If all the 115 species of cichlids that currently inhabit Central America had invaded the region recently (e.g., after the rise of the Isthmus of Panama), it would be expected that there would be evidence of multiple invasions by different South American lineages, instead of only one. A representative phylogeny in this case would show some geographically Central American cichlids being more closely related to South American lineages. The phylogeny of cichlids recovered here falsifies the notion that multiple South American lineages are responsible for the radiation of more than 100 species currently found in Central America.

Bussing (1985) interpreted the Central American cichlids as part of an ancient South American radiation that dispersed into Central America in the Late Cretaceous or Paleogene. These cichlids were subsequently stranded in this area during the Tertiary and were only reunited with their ancestral source during the Pliocene closure of the Isthmus of Panama. Among the members of this Paleochthyofauna, Bussing placed several cyprinodontiforms (*Poecilia*, *Poeciliopsis*, *Cyprinodon*, *Floridaichthys*, *Heterandria*, *Profundulus*, and *Fundulus*). His conclusions were derived from distributions and not phylogenetic analyses. The phylogenetic data for the Central American cichlids

TABLE 18.3

Species-Area Analysis of Freshwater Fishes from Central and Trans-Andean South America

Region	Area (km ²)	Expected Number of Species	Observed Number of Species	Expected/Observed
CA	2,368,000	514	426	1.21
TSA	146,000	217	520	0.42

NOTE: Geographic areas estimated from scanned maps using NIH Image. CA, Central America (excluding the Panamanian landbridge). TSA, trans-Andean northwestern South America (Pacific Slope + Atrato + Magdalena) below 300 m. Expected number species from species-area regions of 44 ecoregions of the Neotropical freshwater ichthyofauna (Chapter 2). Observed numbers of species tabulated by Albert et al. (2006) from raw data in Reis et al. (2003).

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supported this view. Chakrabarty (2006a) dated the Central American heroine radiation to be between 72 and 50 Ma. This period in the Late Cretaceous/ Paleocene corresponds to a time when the Greater Antillean island arc passed between South America and the Chortis Block (Iturralde-Vinent and MacPhee 1999; Pitman et al. 1993; Figure 18.2).

Martin and Bermingham (1998) sampled 17 Costa Rican cichlid species and concluded that the heroine radiation of cichlids was Middle to Late Miocene age (18–15 Ma), a significantly younger age than found by Chakrabarty (2006a). The estimate by Martin and Bermingham (1998) is based on cytochrome *b* sequence divergence rates from “marine fishes.” Their approach of taking the average divergence from distantly related and taxonomically diverse marine species and applying it to Central American cichlids is problematic because it assumes that all taxa (at least all teleosts) have the same rate of evolution for *cyt b*. Their analysis is flawed because they did not estimate rates, and variability in rates, within their cichlid phylogeny.

SPECIES GRADIENTS AND PALEOGEOGRAPHY

The predominance of taxa moving south during the Isthmian interchange is puzzling given the contemporary species gradient, in which the trans-Andean region of northern South America has more fish species than Central America. Neutral models of biogeography and biodiversity predict higher rates of dispersal down species gradients (MacArthur and Wilson 1967; Hubbell 2001; K. Roy and Goldberg 2007). Under neutral expectations, species do not differ significantly in their rates of speciation, extinction, and dispersal, and all regions have similar effects on rates of speciation, extinction, and dispersal. Therefore, the removal of a barrier to dispersal among adjacent biotas is expected to result in an asymmetric exchange down the gradient of species density.

The number of extant species in Central America ($n = 426$) is somewhat less than the number predicted ($n = 514$) from the species-area relationship ($S = cA^b$), based on empirically defined values of $c = 2.85$ and $b = 0.354$ obtained from an analysis of 39 freshwater ecoregions of tropical South America (Table 18.3; see also Chapter 2). By contrast, the observed number of species in trans-Andean South America ($n = 520$) is 2.4 times greater than the equilibrium number ($n = 217$) predicted from its geographic area alone. Indeed, in a pre-Isthmian geographic context, Central America had about 16 times as much land area as trans-Andean South America (Pacific Slope, Atrato, and Magdalena basins). Therefore, based on species-area considerations alone, and in both the modern and Plio-Pleistocene geographic contexts, Central America is expected to have more species than trans-Andean South America, an imbalance which would predict a “north over south” asymmetrical interchange.

The unexpectedly high diversity of fishes in the trans-Andean region derives from its geographic and historical proximity to the megadiverse ichthyofaunas of the cis-Andean Orinoco and Amazon basins. The trans-Andean region has long been recognized as a faunistically distinct province of Neotropical freshwater fishes (Eigenmann 1923; Eigenmann and Allen 1942; Vari 1988). On the modern landscape the region is completely separated from cis-Andean basins by lofty mountains of the northern Andes, where the lowest mountain passes are well above 3,000 m, an impermeable barrier for lowland tropical fishes (Chapter 16). The cis- and trans-Andean regions became hydrologically isolated with the rise of the Eastern Cordillera of Colombia and Merida Andes of western Venezuela during the Late Miocene c. 12–10 Ma (see Albert et al. 2006 and references therein). In other words, the geological isolation of trans-Andean waters took place about 10 million years before the rise of the Panamanian Isthmus. As a result, the Plio-Pleistocene interchange of freshwater fishes was restricted to the faunas of Central America and the relatively small area of trans-Andean northwestern South America.

In contrast, Nuclear (Northern) and Southern Central America were largely isolated for most of the Cenozoic from the large pools of freshwater fish species in North and South America. The fauna of this region is therefore of compound origin, assembled by long-distance dispersal across land bridges, island chains, or open seas, and composed of taxa descended from vagile and possibly eurytopic founders. From this perspective it is not surprising that the Central American ichthyofauna more closely matches the equilibrium expectations of island biogeography.

The rise of the isthmus eroded the barriers to dispersal between the adjacent Central American and trans-Andean faunas. As in most dispersal corridors, the emerging isthmus itself was only semipermeable to the movements of taxa and served more as an ecological filter than a highway between the two regions (Webb 1991; S. Smith and Bermingham 2005). The Isthmian interchange was therefore not between the whole species pools of Central America and trans-Andean South America, but rather between the subset of species that disperse readily and can tolerate marginal habitats (e.g., small seasonal streams, xeric savannas). Many of the highly specialized, stenotopic taxa of Neotropical lowlands (e.g., those restricted to floodplains and river channels) were not good candidates for dispersal across the most recently formed Pleistocene land bridge.

HOW DID CENTRAL AMERICAN FISHES ARRIVE BEFORE THE PANAMANIAN BRIDGE?

Thus the North American–Caribbean track and the South American–Caribbean track represent extensions of the original

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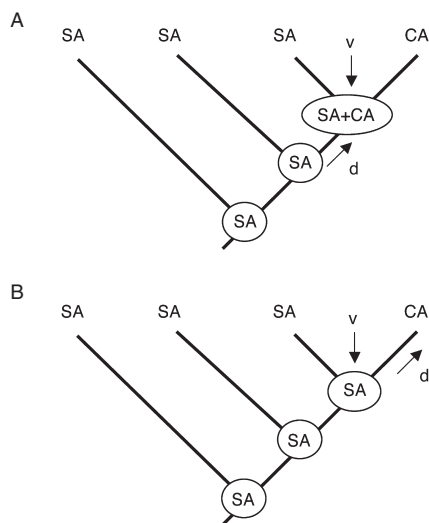


FIGURE 18.5 Alternative biogeographic scenarios for the occurrence of species in South America (SA) and Central America (CA). **A.** Dispersal (d) followed by vicariance (v). **B.** Dispersal following vicariance. Note that an origin in SA requires both dispersal and vicariance events, regardless of their sequence, to explain the occurrence in CA.

biotas into the Caribbean region, where they overlap in Central America and the Antilles. This biotic sympatry clearly implies that the earliest history of the area must have witnessed a dispersal of one or both components. If elements of both the northern and southern biotas had dispersed, the predominance of South American representation in both the areas of track sympatry . . . suggests that these early dispersals might have been primarily from the south northwards. [A]nother indication of an early history of dispersal prior to vicariance is the existence in the Antilles and in Nuclear Central America of groups . . . that have their primary affinities with South American assemblages. (D. Rosen 1975, 447)

From these phylogenetic and paleogeographic considerations, it is evident that the modern ichthyofaunas of Central America and trans-Andean South America were largely established long before the Plio-Pleistocene rise of the Panamanian Isthmus. Throughout the Upper Cretaceous and most of the Cenozoic, Central America was widely separated from South America by open ocean, so the presence of freshwater taxa of South American origin in Central America before the rise of the Panamanian Isthmus necessarily implies dispersal (Figure 18.5). Further, the presence of so many obligatory freshwater fish taxa in Central America before rise of the Panamanian land bridge suggests a shared mechanism of dispersal across the marine barrier, either by means of transient land bridges, island chains, or simply across the open sea. Hypothesized pre-Isthmian dispersal corridors between North and South America include connections such as the CLIP (Hoernle et al. 2002; 2004) or drifting proto-Greater Antillean arcs (D. Rosen 1975, 1978; Pindell and Barrett 1990; Pitman et al. 1993), events thought to date to the Lower Paleogene or Upper Cretaceous.

Additional contributing factors to patterns of dispersal between the continents were the prevailing directions of wind and water currents on pre-Pliocene landscapes and seascapes. Throughout the great majority of the history of Neotropical fishes (i.e., 120–10 Ma), the main flow of the proto-

Orinoco-Amazon was directed into the Caribbean Basin through a mouth located in the region of the modern Maracaibo Basin (Hoorn et al. 1995; Lundberg 1998). Further, the prevailing oceanic and atmospheric conditions reconstructed for this time (i.e., the Circumtropical Paleocurrent and North Atlantic hurricane tracks) were permanent and perennial vectors trending west and northwest, from the area of the mouth of the proto-Orinoco-Amazon, and toward the emergent (terrestrial) coasts of southern Central America (Albert et al. 2006).

In this regard it is interesting to compare the hydrological and biotic influences of the modern Amazon freshwater discharge into the Atlantic with those of the Miocene proto-Orinoco discharge into the Caribbean. The plume of freshwater discharged from the mouth of the modern Amazon River is about 6,700 km³ per year, or 214 million liters per second averaged over the annual cycle (Goulding et al. 2003). This volume of low-salinity water floats on the more salty marine water and is distributed by the Southern Equatorial Current northwest along the coast of the Brazilian state of Amapá and French Guiana a distance of c. 600–800 km, depending on the season. Not coincidentally, the species composition of fishes in these coastal regions is strongly Amazonian in comparison with the interior of the Guianas or with northeastern Brazil (Albert et al. 2006 and references therein).

The extent and depth of the sediment fan produced by the Miocene proto-Amazon-Orinoco River indicates a very large discharge volume, on the order of that of the modern Amazon. The modern Amazon fan accumulated over the past 9–10 million years over an area of c. 200,000 km², and the Amazon sediment load like the freshwater plume is distributed along the coast of the Guianas c. 1,500 km. Evidence for a wide geographic influence of the proto-Orinoco is provided by the Middle Miocene Napipi Formation of hemipelagic mudstones in what is now the Atrato Basin (Duque-Caro, 1990). An important source of these mudstones was sediment from the proto-Orinoco emerging from the area of the modern Maracaibo Basin and carried westward c. 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 to Upper Miocene (Lovejoy et al. 2006) would have substantially altered the coastline, episodically isolating and uniting the mouths of coastal rivers, altering the distance between freshwaters of southern Central and South America, and strongly affecting opportunities for transoceanic dispersal during this time interval.

Although individual dispersal events of strictly freshwater taxa over open ocean are presumably rare, the probabilities of such events are additive. Given the enormous amount of time involved (>100 Ma) the aggregate probability of successful dispersal and establishment of a new population may be considered to be not negligible. Indeed, all the members of the Central American paleoichthyofauna necessarily arrived before the rise of the isthmus, and these taxa are de facto examples of successful long-distance dispersal. Rare events such as these can have profound consequences on the formation of biotas, although because of their infrequency, the effects are often idiosyncratic. Such sweepstakes dispersal is similar to other low-frequency yet high-impact evolutionary events such as mass extinctions or adaptive radiations, which although rarely observed in the ecological time frames of human observation, are thought to structure some of the main features of phylogenetic diversification (Simpson 1944; Stanley 1998).

Understanding the biogeographic consequences of geologically persistent and stable features of the physical environment, such as geologically persistent vectors of mass water movement across continents or oceanic currents, is very much in the intellectual tradition of historical biogeography. Just as vicariance is the formation of barriers to dispersal due to earth-history events (e.g., tectonic or climatic change) that results in congruent phylogenetic patterns (D. Rosen 1975; G. Nelson and Platnick 1981; G. Nelson and Rosen 1981), geodispersal refers to the removal of such barriers, resulting in temporally correlated range expansions among multiple independent clades within a biota (Lieberman and Eldredge 1996). Geologically long-lived agents of dispersal that persisted for tens of millions of years also have explanatory power and generality of prediction regarding the diversification of biotas. Uncovering the divergence times of the numerous Isthmian biogeographic reversals may lead to support of a singular congruent geological explanation (such as a Paleogene land bridge) or it may require multiple diverse explanations from several time periods. Only more detailed analyses will be able to discriminate between these hypotheses.

Conclusions

The traditional interpretation of "The Great American Biotic Interchange" (Stehli and Webb 1985) is inconsistent with the newly available phylogenetic and paleogeographic information on freshwater fishes. Certainly the prevailing view of a predominantly south-to-north faunal exchange starting about 3 Ma that was the source of much of the current Central American ichthyofauna is an overly simplistic interpretation. The formation of the Central American and trans-Andean faunas was constrained by many events and conditions over a lengthy interval of more than 100 million years, including

several transient land bridges or island chains, marine dispersals by prevailing vectors of atmospheric and oceanic circulation, and regional biogeographic factors affecting the size, taxonomic composition, and ecological characteristics of the pre-Isthmian regional species pools. The result was a highly asymmetric Isthmian interchange, with more taxa dispersing south than north, despite the fact that most of the pre-Isthmian fish fauna of Central America was itself of southern (South American) derivation. Further, many of the historical and geographic factors involved in the assembly of pre-Isthmian regional species pools, as well as the prevailing ecological conditions on, and on either side of, the emerging Isthmus, presumably applied to other dispersal-limited freshwater and terrestrial taxa (e.g., frogs, mollusks). The Pliocene rise of the Panamanian Isthmus must therefore be seen as the most recent of many geological and geographic phenomena involved in the formation of the modern Central American and trans-Andean ichthyofaunas. The Panamanian Isthmus is only one piece of a richly complex puzzle that is the biogeographic history of this region.

ACKNOWLEDGMENTS

We acknowledge the following people for generously sharing information and ideas: Sara Albert, Eldridge Bermingham, Paulo Buckup, Tiago Carvalho, Tim Collins, William Crampton, William Fink, German Galvis, William Gosline, Michael Goulding, Carina Hoorn, Hernán López-Fernández, Nathan Lovejoy, John Lundberg, Luiz Malabarba, Robert Miller, Joseph Neigel, Gustav Paulay, Gerald Smith, Roberto Reis, John Sparks, Richard Vari, and Kirk Winemiller. Aspects of this research were supported by grants from the U.S. National Science Foundation including NSF 0215388, 0317278, and 0138633 to JSA.