

## Nuclear Central America

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Nuclear Central America (NCA) is the northernmost region where Neotropical fishes dominate freshwater communities. This area and its fish fauna span numerous political boundaries and include present-day northern Costa Rica, Nicaragua, El Salvador, Honduras, Belize, Guatemala, and southeastern Mexico. In this region, fish with evolutionary links to South America, the Caribbean Antilles, North America, and the sea are distributed across a landscape structured by geologically intricate processes. The geological history of NCA is one of the most convoluted on Earth, with movements along major faults forming a rugged landscape ranging in elevation from sea level to over 5,700 meters. The topographic and latitudinal expanse, ranging from 7° to 19° N, together help to influence the area's substantial variation in climate. The numerous streams, rivers, and lakes lying between the Trans-Mexican Volcanic Belt (TMVB) and the Nicaraguan Depression contain a freshwater fish fauna with complex, and at times conflicting, patterns of distribution.

Because the distribution of freshwater fishes is largely dependent on connections between drainage basins, there is a significant interplay between the biological and geological evolution of a region such as NCA (Bermingham and Martin 1998; Lundberg et al. 1998). Freshwater fishes that do not have mostly marine relatives have been traditionally divided into two groups (G. Myers 1949; Chapter 1). Primary freshwater fishes, such as characiforms and siluriforms, have ancient and exclusive associations with freshwater habitats and are generally intolerant of saltwater conditions. Secondary freshwater fishes can commonly be found in brackish water and are more tolerant of saltwater conditions. Despite their tolerance of brackish conditions, vicariant events associated with the complex hydrogeology of this region have likely played a central role in promoting repeated allopatric divergence in the secondary freshwater cyprinodontiforms, cichlids, and groups of marine origin that collectively dominate the Central American fish fauna. The prevalence of secondary freshwater fishes in NCA (G. Myers 1949) stands in contrast to the South American

freshwater ichthyofauna that is dominated by Characiformes and Siluriformes (see Chapter 6) and also suggests that freshwater connections between NCA and South America may have been uncommon until the Plio-Pleistocene (R. Miller 1966; G. Myers 1966; Bussing 1985). The freshwater fish fauna of NCA also differs substantially from the South American fauna in that many species do not co-occur with congeners (R. Miller 1966; Perdices et al. 2002). The discrete, stepping-stone-like nature of species ranges up and down the Central American coasts is one of the reasons this area has played such a central role in the incorporation of phylogenetic information into studies of biogeography (D. Rosen 1975, 1978; Page 1988, 1990). Furthermore, the clear geographic boundaries that exist among closely related NCA fish species provide the means to test vicariant hypotheses and to delineate regions with diagnostic ichthyofaunas (R. Miller 1966; Bussing 1976).

The aquatic fauna of NCA can be grouped into four provinces (Figure 17.1), based largely on the scheme proposed by Bussing (1976). Three of these extend along the Atlantic coast: (1) the Usumacinta, (2) the Honduran, previously referred to as the Southern Usumacinta (Bussing 1976), and (3) the San Juan. A fourth region contains all the Pacific drainages and is called the Chiapas-Nicaraguan province. We follow this geographic classification to discuss the factors that influenced the spread of fishes across geological features that bound these provinces.

We examine fish biogeography within the NCA in five sections. First, we review the geologic history of the region to contextualize the processes that have generated pathways and barriers to fish diversification across this geologically complex region. Then, we use this framework to summarize the forces that structured the distribution of rivers and lakes across the dynamic NCA landscape. Next, we describe how climatic variation may have influenced the distribution of freshwater fishes across the many elevational gradients and environmentally distinct regions of NCA. Then, for groups of Central American fishes (Table 17.1), we summarize the phylogenetic information available in order to determine whether groups are most closely related to other groups from South America, the Caribbean, North America, or the sea. We also describe the geologic, climatic, and biotic factors that were critical in structuring fish biogeography among the major biotic

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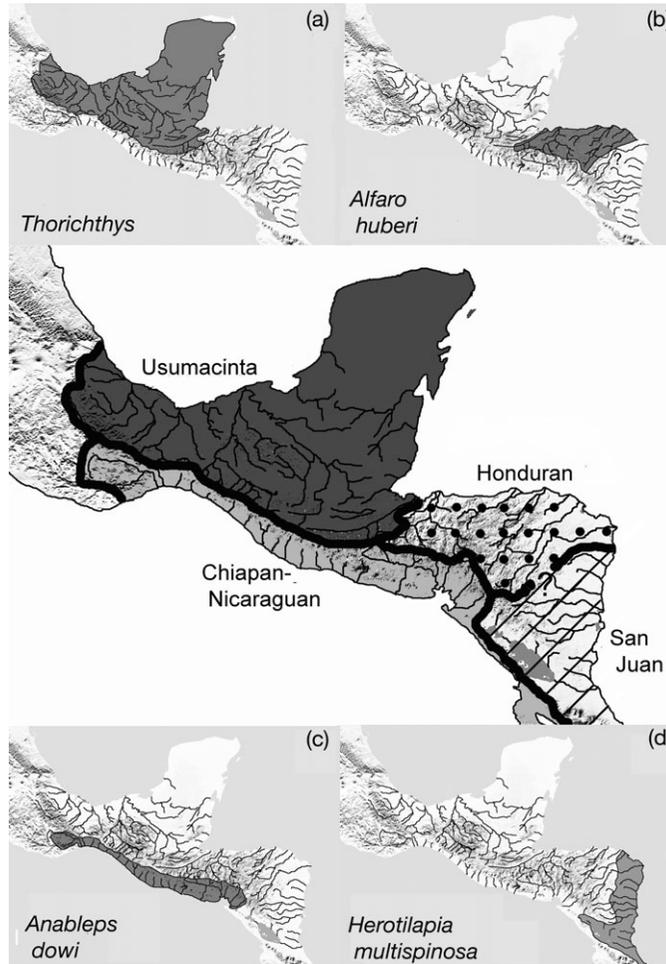


FIGURE 17.1 The aquatic provinces of NCA. The four major biotic provinces are depicted in the central panel. Distributions of species that are endemic to each province are shown. The distribution of the genus *Thorichthys* (a) spans the entirety of the Usumacinta drainage (dark gray). The distribution of the poeciliid *Alfaro huberi* (b) is characteristic of the Honduran province (black dots). The four-eyed fish, *Anableps dowi*, exhibits a range (c) typical of Chiapas-Nicaraguan (light gray) fishes. The cichlid *Herotilapia multispinosa* has a geographic distribution (d) that reflects species inhabiting the San Juan province (diagonal lines). The question mark depicted between the Honduran and San Juan provinces signifies our general lack of biogeographical understanding about the boundary between these two regions.

provinces. Finally, we discuss some areas where future studies will substantially increase our understanding of Central American fish biogeography.

### Geological History of Nuclear Central America

All of NCA resides near active tectonic boundaries (e.g., Burkhart 1994). The North American, South American, Caribbean, Cocos, and Nazca plates all converge in this region (Johnston and Thorkelson 1997), and their interaction has given rise to several displaced terranes. These terranes are regions of lithosphere that have moved horizontally along strike-slip faults (Dengo 1969; Donnelly et al. 1990; Burkhart 1994). One of the most important of these displaced terranes is the Chortis Block (Figure 17.2), which forms the northwestern edge of the Caribbean Plate (Giunta et al. 2006). The Chortis Block underlies parts of Nicaragua, El Salvador, Honduras, and southern Guatemala (Burkhart 1983; Pindell et al. 1988). Another major terrane is the Maya Block (Figure 17.2), which is bounded by the Polochic-Motagua fault of Guatemala to the south, by the Guerrero composite terrane to the west, and by offshore faults along the northern and eastern margins of the Yucatán

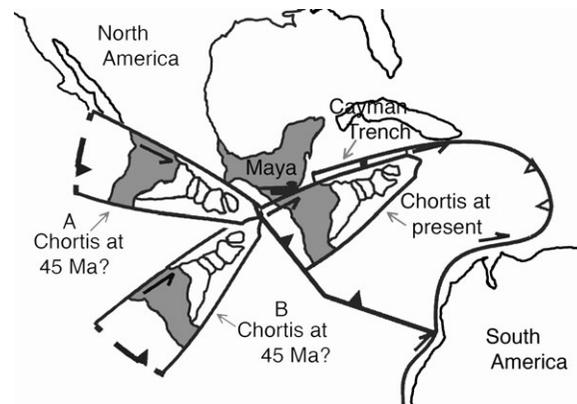


FIGURE 17.2 Debated locations of the Chortis Block before the Eocene (>56 Ma) as presented by Keppie and Morán-Zenteno (2005). The modern emergent Chortis is shown in gray. One set of reconstructions (A) places the Chortis Block against southern Mexico ~1,100 km from its present location during the Eocene. Another group of Cenozoic reconstructions (B) places its origin near the present-day Galápagos. Citations for alternative locations of the Chortis are given in the text.

TABLE 17.1

Fish Groups that Occur in Freshwater in Nuclear Central America (NCA)  
 Divided into Primary, Secondary, and Marine-derived fishes

Order	Family	Genera	
PRIMARY			
Lepisosteiformes	Lepisosteidae	<i>Atractosteus</i>	
Siluriformes	Lacantunidae	<i>Lacantunia</i>	
	Heptapteridae	<i>Rhamdia</i>	
	Ictaluridae	<i>Ictalurus</i>	
Characiformes	Characidae	<i>Astyanax, Bramocharax, Brycon, Bryconamericus, Carlana, Hyphessobrycon, Roeboides</i>	
Cypriniformes	Cyprinidae	<i>Notropis</i>	
	Catostomidae	<i>Ictiobus</i>	
Gymnotiformes	Gymnotidae	<i>Gymnotus</i>	
SECONDARY			
Cyprinodontiformes	Anablepidae	<i>Anableps</i>	
	Cyprinodontidae	<i>Cyprinodon, Floridichthys, Garmanella</i>	
	Fundulidae	<i>Fundulus</i>	
	Poeciliidae	<i>Alfaro, Belonesox, Brachyrhaphis, Carlhubbsia, Gambusia, Girardinus, Heterandria, Heterophallus, Limia, Phallichthys, Poecilia, Poeciliopsis, Priapella, Priapichthys, Quintana, Scolichthys, Xenophallus, Xiphophorus</i>	
Perciformes	Profundulidae	<i>Profundulus</i>	
	Rivulidae	<i>Millerichthys, Rivulus</i>	
	Cichlidae	<i>Amatitlania, Amphilophus, Archocentrus, Astatheros, Herichthys, Heros, Herotilapia, Hypsophrys, Nandopsis, Parachromis, Paraneetroplus, Paratheraps, Petenia, Rocio, Theraps, Thorichthys, Tomocichla, Vieja</i>	
Synbranchiformes	Synbranchidae	<i>Ophisternon, Synbranchus</i>	
MARINE-DERIVED			
Carcharhiniformes	Carcharhinidae	<i>Carcharhinus</i>	
Pristiformes	Pristidae	<i>Pristis</i>	
Atheriniformes	Atherinopsidae	<i>Atherinella, Melaniris, Membras, Menidia, Xenatherina</i>	
Batrachoidiformes	Batrachoididae	<i>Batrachoides</i>	
Siluriformes	Ariidae	<i>Bagre, Cathorops, Potamariusathorops, Galeichthys, Notarius, Sciades</i>	
Beloniformes	Belonidae	<i>Strongylura</i>	
	Hemiramphidae	<i>Chriodorus, Hyporhamphus</i>	
Clupeiformes	Engraulidae	<i>Anchoa, Lycengraulus</i>	
	Clupeidae	<i>Dorosoma, Lile</i>	
Elopiformes	Megalopidae	<i>Megalops</i>	
Gobiesociformes	Gobiesocidae	<i>Gobiesox</i>	
Perciformes	Gobiidae	<i>Awaous, Bathygobius, Ctenogobius, Evorthodus, Gobiodes, Gobionellus, Gobiosoma, Lophogobius, Sicydium</i>	
	Carangidae	<i>Oligoplites</i>	
	Centropomidae	<i>Centropomus</i>	
	Eleotridae	<i>Dormitator, Eleotris, Erotilis, Gobiomorus, Hemieleotrus, Leptophilypnus</i>	
	Gerreidae	<i>Eucinostomus, Eugerres, Gerres</i>	
	Haemulidae	<i>Pomadasys</i>	
	Kuhliidae	<i>Kuhlia</i>	
	Sciaenidae	<i>Aplodinotus, Bairdiella</i>	
	Sparidae	<i>Archosargus, Lagodon</i>	
	Mugiliformes	Mugilidae	<i>Agonostomus, Joturus, Mugil</i>
	Ophidiiformes	Bythitidae	<i>Typhliasina</i>
	Pleuronectiformes	Achiridae	<i>Achirus</i>
		Cynoglossidae	<i>Symphurus</i>
	Paralichthyidae	<i>Citharichthys</i>	

NOTE: Group divisions from Myers 1949. Orders and families are listed with genera occurring in NCA or in geographically proximal regions.



FIGURE 17.3 Major terrestrial geologic features of Nuclear Central America (NCA). Major landforms referred to in the text are shown.

Peninsula (Burkhart 1983; Donnelly et al. 1990). The Maya Block represents the southeastern limit of the North American plate, and its western edge abuts the Isthmus of Tehuantepec. West of the Maya Block is a complex geological region that includes the Guerrero, Mixteca, and Oaxaquia terranes, among others that make up the highlands of the Sierra Madre del Sur (Keppie 2004). The Sierra Madre del Sur is delimited to the south by the Pacific Ocean and has high relief with few lowland areas containing fishes. Therefore, this region, although containing a few close relatives to NCA fish groups, will not be included in further discussions. All these terranes have ancient histories that minimally date to the middle Jurassic breakup of Pangea (Howell et al. 1985; Donnelly et al. 1990).

The oldest proposed ages of fish clades in NCA date to the Upper Cretaceous (Aptian age ~125 Ma; Hrbek, Seckinger, et al. 2007; see also Chapter 6). The evolutionary history of many groups like the Poeciliinae is therefore ancient, and likely to have been influenced by geological events extending over 100 Ma. For instance, during the Cretaceous, shallow seas covered much of NCA (Vinson 1962; T. Anderson et al. 1973), resulting in the deposition of limestones over wide areas and the formation of evaporites in restricted basins (e.g., Isthmus of Tehuantepec, Yucatán Peninsula, Petén of Guatemala; Weidie 1985). These regions form a large part of the Maya Block that had only occasional connections with South America and generally served as the southernmost extension of North America through most of the Cenozoic (Iturralde-Vinent and MacPhee 1999; and see the section “Connections, Phylogeny, and Geography”). Prior to the Cenozoic (>65 Ma), the proximity of the Maya Block to the Chortis Block, which is contiguous with and directly south of the Maya Block now, remains unclear (Keppie and Morán-Zenteno 2005). However, the interaction of these two terranes during the last 65 Ma has had important implications for fish biogeography in NCA.

The tectonic evolution of the Caribbean plate and the Chortis block is controversial (Dengo 1969; Donnelly et al. 1990; Burkhart 1994). There is no agreement upon the position and movement of the Chortis relative to the Maya Block (Keppie and Morán-Zenteno 2005). One set of reconstructions posits the Chortis terrane as moving at least 1,100 km, whereas the other reconstruction suggests a movement of only about 170

km. The positions and movement of the Maya and Chortis blocks relative to each other presumably influenced the ability of fish to move among provinces, and the low-lying fault zones between these two terranes has undoubtedly influenced fish distributions.

Those who agree that the Chortis terrane has moved at least 1,100 km nevertheless continue to debate its location before the Eocene (>56 Ma; Figure 17.2). One set of Cenozoic reconstructions places its origin near the present-day Galápagos using the rotation pole near Santiago, Chile (Ross and Scotese 1988), and an offset greater than 1,100 km on the Cayman transform fault (Pindell et al. 1988; Rosencranz et al. 1988; Pindell 1994). Alternative models assume a connection between the Cayman transform fault and the Acapulco Trench that could continue through the Motagua fault zone. Proponents of this reconstruction place the Chortis Block against southern Mexico ~1,100 km from its present location during the Eocene (Burkhart 1983; Meschede and Frisch 1998; Pindell et al. 1988; Ross and Scotese 1988; Donnelly et al. 1990). In addition to the potential movement and faulting between them, the interaction of the Maya and Chortis blocks has contributed to the extensive relief present in NCA (Figure 17.3).

In NCA, a long history of mountain building has been critical in structuring the freshwater fish fauna. The Sierra Madre de Chiapas, Sierra de Chuacús, and Sierra de las Minas are mountain chains that run like a belt from the Pacific to the Atlantic along the Motagua-Polochic fault zone. These three ranges all contain Paleozoic (at least 290 Ma) metamorphics and sediments that are the oldest exposed rocks in NCA. The Sierra de los Cuchumatanes and Meseta Central of Chiapas that form parts of the Chiapan highlands are composed mostly of Mesozoic (290–144 Ma) sediments and are thought to have been uplifted during the late Cretaceous or early Cenozoic (Dengo 1969; T. Anderson et al. 1973). During the Laramide orogeny (Maldonado-Koerdell 1964), when the Sierra Madre Oriental and Rocky Mountains were elevated (80–40 Ma), there was also a period of intense mountain building in Central America. Coincident with the Laramide orogeny, the Trans-Mexican Volcanic Belt (TMVB) and the Sierra Madre del Sur began uplifting (Maldonado-Koerdell 1964; Byerly 1991; Ferrari et al. 1999). To what extent parts of NCA were elevated prior to the

early Cenozoic is controversial, but it appears that after these periods of mountain building ended, the region underwent a long period of erosion and subsidence (McBirney 1963). For much of the middle Cenozoic (~34–20 Ma), Central America might not have possessed extensive highland areas (Maldonado-Koerdell 1964; Dengo 1969).

The extensive highlands that currently lie between the Isthmus of Tehuantepec and the Nicaraguan Depression began to develop during the Miocene (~23 Ma, Williams and McBirney 1969; Rogers et al. 2002), and their elevations increased substantially well into the Pleistocene (beginning ~1.8 Ma). One illustration of this process is the Chortis highlands, which may have been uplifted as a single unit in the mid- to late Miocene (~14–5.3 Ma) resulting in the extreme high elevations present today (Rogers et al. 2002). Similar Miocene events also helped elevate the TMVB, a biogeographic wall that extends from the Pacific Ocean to the Gulf of Mexico roughly along latitude 19° N (Maldonado-Koerdell 1964; Ferrari et al. 1999). From the Pliocene (~5.3 Ma), the TMVB continued to rise and expand into the Recent forming large volcanoes, such as Volcán Orizaba, that remain active today (Dengo 1969; Ferrari et al. 1999). Critical to the distribution of the Neotropical fauna, the TMVB subdivided either the Maya Block (Sedlock et al. 1993) or the Oaxaquia terrane (Keppie 2004) into a northern part and a southern part, forming an important boundary to Neotropical freshwater environments.

During the late Miocene and Pliocene, a period of increased volcanism along a broad belt some 50–70 km wide, paralleling the Pacific (H. Williams 1960; H. Williams et al. 1964), began to extensively alter the topography of NCA. The continued formation of highland areas along the continental divide of NCA greatly contributed to the separation of fish faunas into Pacific- and Atlantic-draining rivers. The fact that the continental divide formed closer to the Pacific than to the Atlantic also had substantial influence on the hydrology and areal extents of the two NCA slopes, and thus on the evolution of their respective fish faunas (Stuart 1966).

The middle Pliocene was a time of volcanic quiescence and severe erosion creating the landscape largely evident today in the highlands of Central America (Williams et al. 1964). Deeply weathered erosional surfaces at about 2,000 m in the western portion of the Sierra de Las Minas are indications of the broad uplift and subsequent erosion that have occurred since the Pliocene (McBirney 1963). Erosion during the mid- to late Pliocene also resulted in the entrenchment of many Atlantic drainage systems that have their headwaters in the present-day continental divide. As the uplifted surroundings generated higher stream gradients, these streams carved ever-deeper river valleys (Rogers et al. 2002; J. Marshall 2007).

Several Pleistocene conditions likely also molded species ranges. Foremost among these were the renewal of intense and widespread volcanic activity reinitiated in the late Pliocene and fluctuations in climate brought on by advances and recessions of glaciers at high elevations. Much Pleistocene and recent volcanism in NCA has occurred near the Pacific slope of the Guatemalan Plateau (H. Williams 1960; McBirney 1963) and the Nicaraguan Depression (Kuteroff et al. 2007). The Central American volcanic front extends down the continental divide of NCA and still contains approximately 50 active volcanoes. The physiography of these highland regions was greatly modified by eruptions from these volcanoes that covered the intermontane basins, especially those formed by the parallel belt of eroded, fairly recent volcanic and sedimentary rocks (H. Williams 1960; McBirney 1963). The formation of

Quaternary volcanoes did not greatly increase the extent of the Central American highlands, but it did increase elevations along the southern portion of the Guatemalan Plateau. Volcanoes along the floor of the Nicaraguan depression have also been highly active into the Recent (Carr and Stoiber 1990).

The influence of much colder temperatures and extensive glaciation in the temperate zones during recent geological history had a debatable influence on tropical regions such as NCA. However, paleobotanical studies (Raven and Axelrod 1974) and paleoenvironmental reconstructions (Anselmetti et al. 2006) suggest that the glacio-pluvial periods in northern latitudes coincided with periods of increased tropical aridity. During the height of the temperate glacial advances, there is evidence for small glaciers forming on the highest peaks in Mexico, Guatemala, and Costa Rica (T. Anderson et al. 1973; West 1964; Horn 1990; Lachniet 2004, 2007). Glaciation and intense cold at high elevations likely substantially influenced the presence and altitudinal ranges of the largely warm-water-adapted Neotropical fish fauna of NCA.

## Hydrology of Nuclear Central America

### LAKES OF NUCLEAR CENTRAL AMERICA

The lakes and rivers of NCA (Figure 17.4) provide the geographical stage for diversification of its freshwater fishes. However, lakes in this region (Table 17.2) are frequently geologically ephemeral and contain few endemic species. In general, the largest lakes in Central America formed either in the calderas of recently erupted volcanoes or in low-lying areas subject to marine incursions during high sea-level stands. Many of these lakes also do not have imposing natural boundaries between them and their associated river drainages. Because of their transient nature, lakes in NCA have likely served only as temporary sinks for species diversity and rarely as major sources of freshwater fish lineages (but see Barluenga et al. 2006; Strecker 2006).

One of the most northerly lakes in NCA containing a robust Neotropical fauna is Lago Catemaco (Figure 17.4, location A). This lake formed in a caldera along the Gulf of Mexico coast less than 2 million years ago (West 1964). *Pociliopsis catemaco*, *Pocilia catemaconis*, and *Xiphophorus milleri* (D. Rosen 1960; R. Miller 1975) are endemic, but this lake also includes several cichlids such as *Thorichthys ellioti* and *Vieja fenestrata* that are found throughout the Veracruz and Tabasco lowlands. To the southeast of these lowlands, the marshy areas at the mouth of the Grijalva and Usumacinta (Figure 17.4, location 3) contain numerous lake-like habitats (R. Miller et al. 2005). However, the large amounts of flooding in this area likely have served to continually mix aquatic communities and prevented local differentiation of lineages.

The Yucatán Peninsula in contrast to the lowlands to its southwest is pocketed by numerous sinkholes (called cenotes) that are largely isolated at the surface (Covich and Stuiver 1974; Humphries and Miller 1981). However, this mostly river-free area that has developed across a flat sequence of Cenozoic marine carbonate rocks is heavily braided by underground connections that wind through the karst of the region (Troester et al. 1987). The freshwater fish fauna is composed of widespread species, species tolerant of brackish conditions, and a few species restricted to caves (Hubbs 1936b, 1938). One of the largest groups of cenotes is the Laguna Chichancanab (Figure 17.4, location B). This “laguna” is actually a series of eight lakes that contains an endemic radiation of the cyprinodontid genus

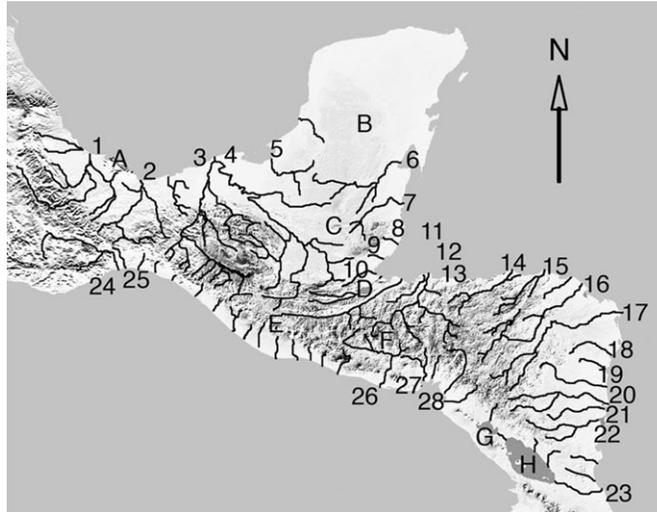


FIGURE 17.4 Major river drainages and lakes in NCA. Lake names indicated by capital letters (Table 17.2) and river drainages by Arabic numerals (Table 17.3).

TABLE 17.2  
Major Lakes of NCA  
Location letters refer to Figure 17.4

Location	Lake	Lake Area (km <sup>2</sup> )	Maximum Depth (m)	Source
A	Lago Catemaco	73	22	Torres-Orozco et al. 1996
B	Laguna Chichancanab	~20	13	Covich and Stuver 1974
C	Lago Peten-Itza	100	160	Anselmetti et al. 2006
D	Lago Izabal	717	17	Brinson and Nordlie 1975
E	Lago Atitlan	126	340	H. Williams 1960
F	Lago Yojoa	285	29	Vevey et al. 1993
G	Lago Managua	1,016	26	Freundt et al. 2007
H	Lago Nicaragua	8,150	70	Freundt et al. 2007

NOTE: The lake area and maximum depth are given to facilitate comparisons of lake sizes.

*Cyprinodon* (Humphries and Miller 1981; U. Strecker 2006) but few other fishes. Like many Yucatán water bodies, these shallow lakes are brackish and exhibit virtually constant temperature (Covich and Stuver 1974; U. Strecker 2006).

Moving south into present-day Guatemala, the more rugged karst terrain of the Petén becomes prevalent. Surface drainages across this hilly region are poorly developed and feed extensive networks of sinkholes and caverns (J. Marshall, 2007). Lago Petén-Itzá (Figure 17.4, location C) is the largest of a group of karstic lakes in the Petén region and the deepest lake in lowland Central America (Anselmetti et al. 2006) having formed through a combination of faulting and dissolution of limestone bedrock (Anselmetti et al. 2006). The fish faunas of Petén-Itzá and associated lakes are some of the most diverse in NCA (Valdez-Moreno et al. 2005).

Lago Izabal (Figure 17.4, location D), at 717 km<sup>2</sup>, is the largest inland body of water in northern Central America and forms part of the Río Polochic drainage (Brinson and Nordlie 1975). This lake is found at the faulted meeting of the Maya and Chortis blocks, where a marine embayment of the Gulf of Honduras ancestrally extended into mainland Guatemala (Bussing 1985). The suture between the Maya and Chortis blocks containing Lago Izabal continues offshore to form the Cayman trench that ultimately separates Cuba and Hispaniola

(Rosencrantz et al. 1988). Lago Izabal contains many marine invaders and brackish water species (Thorson et al. 1966; Betancur et al. 2007), but also contains some virtually endemic freshwater species such as '*Cichlasoma*' *bocourti* and the catfish *Potamarius izabalensis* (Hubbs and Miller 1960).

Moving inland, there are numerous lakes in the high-altitude region where the Maya and Chortis blocks meet. Many of these water bodies were formed in volcanic calderas and have depauperate fish faunas (Meek 1908; D. Rosen 1979). One of the largest is Lago Atitlán (Figure 17.4, location E), which formed from a volcanic explosion within the last 100,000 years and is the deepest lake in Central America at approximately 340 m (H. Williams 1960). Moving southwest into the Chortis Block there are several other large, deep lakes formed in calderas such as Lago Yojoa (Figure 17.3, location F; Vevey et al. 1993). This lake in present-day Honduras was formed recently and contains few endemic or wide-ranging freshwater fishes.

Although the low-gradient Mosquito region along the Caribbean coast contains a series of extensive wetlands and lagoons (J. Marshall, 2007), it is not until the Nicaraguan Depression that true lake habitats are encountered. Serving as a major link between the Caribbean and Pacific coasts, the Nicaraguan Depression is an approximately 50 km wide trough that

TABLE 17.3  
Major Drainages of NCA  
Location numbers refer to Figure 17.4

Location	Drainage	Basin Area (km <sup>2</sup> )	Discharge	Citation
ATLANTIC SLOPE				
1	Río Papaloapan	37,380	37,290	Tamayo and West 1964
2	Río Coatzacoalcos	21,120	22,394	Tamayo and West 1964
3	Grijalva	121,930	105,200	Tamayo and West 1964
4	Usumacinta			
5	Río Candelaria	7,790	1,692	Tamayo and West 1964
6	Río Hondo	13,465	15,000	Yáñez-Arancibia and Day 2004
7	Belize River	9,434	4,888	Environment <sup>a</sup>
8	Monkey River	1,292	1,545	Thattai et al. 2003
9	Moho River	1,583	3,090	Thattai et al. 2003
10	Sarstun River	2,117	4,604	Thattai et al. 2003
11	Río Polochic	5,832	9,870	Thattai et al. 2003
12	Río Motagua	13,168	5,865	Thattai et al. 2003
13	Río Ceme'locon	16,880	11,668	Thattai et al. 2003
14	Río Aguan	10,386	7,329	AQUASTAT <sup>b</sup>
15	Río Negro	7,090	5,908	AQUASTAT
16	Río Patuca	24,762	23,706	AQUASTAT
17	Río Coco	6,830	26,088	UCAR <sup>c</sup>
18	Río Huahua	?	?	
19	Río Prinzapolka	?	?	
20	Río Grande de Matagalpa	15,073	?	UCAR
21	Río Curinhuas	?	?	
22	Río Escondido	?	?	
23	Río San Juan	42,200	?	Wolf et al. 1999
PACIFIC SLOPE				
24	Río Tehautepec	10,520	1,439	Tamayo and West 1964
25	Río de los Perros	1,010	89	Tamayo and West 1964
26	Río Lempa	18,240	6,214	AQUASTAT
27	Río Goascoran	3,080	1,110	AQUASTAT
28	Río Choluteca	7,681	3,032	AQUASTAT

NOTE: Basin area and mean annual discharge are given to facilitate comparisons of drainage sizes. Discharges as mean annual discharge (millions of cubic meters per year). Little information is available for the rivers in the Mosquitia.

<sup>a</sup>Biodiversity and Environmental Resource Data System of Belize 2010. [http://www.biodiversity.bz/find/watershed/profile.phtml?watershed\\_id=3](http://www.biodiversity.bz/find/watershed/profile.phtml?watershed_id=3).

<sup>b</sup>AQUASTAT. 2000. Food and Agriculture Organization of the United Nation's on-line global information system on water and agriculture. <http://www.fao.org/nr/water/aquastat/countries/honduras/indexesp.stm>.

<sup>c</sup>Bodo, B. 2001. University Corporation for Atmospheric Research data set on Flow Rates of World Rivers (excluding former Soviet Union countries). <http://dss.ucar.edu/datasets/ds552.0/>.

extends from the Gulf of Fonseca in southern Honduras to the Northern Costa Rican Tortuguero lowlands on the Caribbean (McBirney and Williams 1965; Weinberg 1992). This shallow basin is most pronounced where it contains Central America's largest lakes (Freundt et al. 2007; J. Marshall 2007), Lagos Managua and Nicaragua (Figure 17.4, locations G and H), which house one of the few lake-centered cichlid radiations in Central America (Regan 1906–1908; Barluenga et al. 2006).

There are no lakes of any size along the entire Pacific coast of NCA (R. Miller 1966; Bussing 1985). This lack of lentic habitats is primarily due to the short, high-gradient transition between the continental divide and the ocean (Stuart 1966) that ranges only from about 20 to 50 km (Short 1986). The large number of Pleistocene and Quaternary deposits resulting from extensive volcanism along the continental divide (Vallance et al. 1995) suggests that the aquatic habitats on the Pacific coast have had a disturbed and dynamic tectonic history.

#### RIVERS OF NUCLEAR CENTRAL AMERICA

Rivers are the cradle of freshwater fish diversification in NCA. When contrasted with lakes, the flow of river systems across the landscape misleadingly confers a sense of geologic transience. However, in NCA, perennial rivers are frequently old and deeply embedded in ancient geologic terrains where years of erosion lowered valleys below the water table (Bethune et al. 2007). Freshwater fish have moved among these drainages primarily through connections at river mouths where adjacent river systems merge at low sea-level stands or via stream capture at upland headwaters. Understanding the geography of rivers (Table 17.3; Figure 17.4) is critical to understanding NCA fish distributions among the four major aquatic provinces.

The Usumacinta province begins south of the TMVB along the Gulf of Mexico coast in a lowland region of large rivers nested in huge floodplains (R. Miller et al. 2005). The Río Papaloapan is the northernmost major drainage that

contains predominantly Neotropical species (Obregón-Barboza et al. 1994). This river system is the outlet for Lago Catemaco and has strong affinities with the Río Coatzacoalcos to the southeast. The headwaters of the Río Coatzacoalcos begin very close to the Pacific slope of the Isthmus of Tehuantepec and have served as an important biogeographic route across the NCA continental divide (Mateos et al. 2002; Mulcahy and Mendelson 2000). To the east of this region, a series of small drainages empty into the Gulf of Mexico before the expansive Grijalva-Usumacinta delta is encountered.

The Usumacinta and Grijalva watersheds clearly harbor the greatest fish diversity in NCA (R. Miller 1966; Lozano-Vilano and Contreras-Balderas 1987; Rodiles-Hernández et al. 1999). The headwaters of the Grijalva are largely confined to the Maya highlands, but the headwaters of the Usumacinta extend deep into the Petén lowlands and drain the highlands of Guatemala. The relative age and size of these rivers has likely contributed to both the large number of endemic species and the presence of many wide-ranging taxa. The geographic span of the Usumacinta may have provided ample opportunity for the transfer of species among regions as seemingly disparate as the Motagua fault zone, the Tabasco Lowlands, and the Yucatán Peninsula (Lozano-Vilano and Contreras-Balderas 1987; Valdez-Moreno et al. 2005).

Draining the southern Yucatán Peninsula, the Río Candelaria is one of the few large perennial rivers in this region (Tamayo and West 1964). The tortuous path of the Río Candelaria through the karstic landscape is indicative of the ever smaller and hydrologically complicated lotic systems that characterize the Yucatán Peninsula (Hubbs 1936a). The proximity of the Río Candelaria headwaters to the upper Río Hondo that empties into the Caribbean could have facilitated freshwater exchange between these two sides of the Yucatán. Moving south from the Río Hondo into present-day Belize, several rivers that run short distances from the Maya mountains to the Caribbean coast are encountered (Hubbs 1936b; Thattai et al. 2003). The Belize, Monkey, Moho, and Sarstun rivers all experience sharp changes in hydrogeology as their basins transition from the Maya massif to the carbonate platform of the Caribbean lowlands (Esselman et al. 2006). The fish fauna of these regions is fairly similar among drainages (Greenfield and Thomerson 1997) but reflects this geologic transition (Esselman et al. 2006).

Many of the major river systems in NCA follow ancient geologic faults, and this fact becomes increasingly evident south of the Yucatán Peninsula. For instance, the Río Hondo follows the Río Hondo–Bacalar fault zone (Donnelly et al. 1990), and the Río Motagua follows the Motagua fault zone (Harlow et al. 2004). The Río Polochic to the north and the Río Chamelocón to the south of the Río Motagua were likely formed along faults parallel to the Motagua fault (Keppie and Morán-Zenteno, 2005). All these river systems may have once been the location of plate-boundary slip between the Maya and Chortis terranes (J. Marshall, 2007), and they represent the transition between the Usumacinta and Honduran provinces.

The Honduran province is largely composed of drainages running off the uplifted Chortis Block that lie along faults. The Río Aguán, Río Negro, and Río Patuca all lie in basins running primarily east to west that are bounded by the Nombre de Dios, La Esperanza, and Patuca mountain ranges (Finch and Ritchie 1991; Rogers et al. 2005). One of the geologically clearest examples of Pleistocene stream piracy in Central America likely occurred within the southern highlands of present-day Honduras where the Patuca River captured flow from the

paleo-Coco drainage (Rogers 1998) that may mark the southern boundary of the Honduran province. Many fish species that are common in the Usumacinta intrude into the Honduran region (R. Miller 1966; Bussing 1985). However, the phylogenetic affinities of the fish faunas in these major drainages are unclear, and as the region is further explored the fauna might be found to be more closely allied to Mosquito rivers to the south (R. Miller and Carr 1974).

The San Juan province begins along the Mosquito coast, which is up to 150 km wide and is bordered by the Caribbean Sea (J. Marshall 2007). The uplift of the Chortis highlands and the subsequent erosion from these areas contributed to the extensive deposition forming this area (Rogers 1998). This huge alluvial plane contains numerous low-gradient rivers running through some of the wettest regions (>5,000 mm of rain a year) on earth and represents a true flooded forest similar to the Amazon (Stuart 1966). Large rivers such as Río Cusalaya, Río Prinzapolka, Río Grande de Matagalpa, Río Curinhuas, and Río Escondido all drain extensive watersheds. The biogeographic independence of these drainages could be minor as the broad wetlands at the mouth of these rivers frequently coalesce during wet periods. Basic information on the presence and absence of fish would facilitate an understanding of the connectivity among these drainages and their connection to the Río San Juan. The Río San Juan provides the outlet of Lagos Managua and Nicaragua to the Caribbean Sea and lies within the Nicaraguan Depression, which is bounded on the northeast by the 500 m high mountain front of the Chortis highlands (McBirney and Williams 1965). To its southwest, the Matearas fault forms a prominent 900 m high escarpment (Weinberg 1992). Faunistically, the Río San Juan has much in common with Costa Rican rivers to the south (R. Miller 1966; Bussing 1976), and it may have served as a pathway for movement both northward and from Pacific to Atlantic drainages (Bussing 1985).

Following the Nicaraguan Depression northwest to the Gulf of Fonseca, rivers begin draining into the Pacific. Along the Pacific, a narrow coastal plain of deeply incised rivers runs virtually uninterrupted from the Gulf of Fonseca to the Isthmus of Tehuantepec (J. Marshall, 2007). Some of the bigger southern rivers in this region, such as the Choluteca and the Río Lempa, may have served as faunal exchange sites across the continental divide (Hildebrand 1925; Carr and Giovannoli 1950; R. Miller 1966; Bussing 1976). Eruptions and landslides along the Central American volcanic front (Vallance et al. 1995) have likely frequently degraded these rivers as fish habitats. Many of the river systems are also intermittent because of the relatively low rainfall on the Pacific coast. As one moves north only small drainages are encountered until the Gulf of Tehuantepec, where the Río de los Perros and Río Tehuantepec border the Atlantic-draining headwaters of the Río Coatzacoalcos (R. Miller et al. 2005).

### Climate and the Distribution of NCA Fishes

The interactions between climatic factors and geology help to determine the distribution of fishes in the complex configuration of lakes and rivers across the NCA landscape. Precipitation and temperature regimes in NCA can be classified into three major climatic zones: (1) the tropical lowlands of the Caribbean, (2) the interior highlands, and (3) the narrow Pacific slope (Schwerdtfeger 1976). Precipitation over the entirety of NCA is seasonal, but the degree of seasonality varies widely (Stuart 1966). Temperature in each of the three zones is

largely a function of elevation. The two lowland areas average daytime highs of 29–32°C and average annual temperatures of 24–27°C. Temperatures on the Gulf of Mexico and Caribbean lowlands are warm and vary relatively little throughout the year. Temperatures in the Pacific lowlands generally range from warm to intensely hot (Stuart 1966). At elevations above 3,000 m the mean annual temperature may be less than 10°C.

The sharp division that the continental divide apparently creates for the distribution of many NCA fishes may indicate that few aquatic connections have ever existed between Atlantic and Pacific drainages. However, it is also possible that cool temperatures at higher elevations have limited the ability of lowland groups to exploit the connections that have existed. Unlike the TMVB region where there have been several high-altitude radiations of fishes in the Atherinidae and Goodeidae, fish taxa are generally uncommon in the Central America highlands above 1,500 m (Barbour 1973; R. Miller 1955; Miller et al. 2005). Few NCA fish have likely adapted to the cold present at high elevations (R. Miller 1966), as *Profundulus* is the only genus that commonly occurs above 1,500 m (R. Miller 1955), and high-elevation areas may not have been extensive prior to the Miocene (Dengo 1968, Maldonado-Koerdell 1964). Glaciers might have also recently served to effectively remove many groups of tropical freshwater fish from higher altitudes (T. Anderson et al. 1973; West 1964; Horn 1990; Lachniet 2004, 2007). In contrast, the small differences in temperatures along the Atlantic and Pacific have not likely impeded movements among drainages, although cooler temperatures could have determined the northern distribution of some groups (Perdices et al. 2002; R. Miller et al. 2005).

### Connections, Phylogeny, and Geography: NCA Fishes at a Crossroads

#### SOUTH AMERICAN CONNECTIONS

The history of NCA faunas is complex because the region lies at a crossroads of biogeographic influences and geological units (Stehli and Webb 1985). Most NCA freshwater fish groups are phylogenetically nested within clades from South America. The relatively few characiforms (e.g., *Astyanax*) that occupy NCA are derived from wide-ranging South American groups (Reeves and Bermingham 2006). Other ostariophysan fishes such as *Gymnotus* (Albert et al. 2005) and *Rhamdia* (Perdices et al. 2002) are also clearly descended from lineages with South American sister taxa. With the exception of '*Aequidens coeruleopunctatus*' and two '*Geophagus*' species in southern Central America, the 100+ species of heroines are the only Neotropical cichlid group found outside of South America (Conkel 1993; Chakrabarty 2004). Phylogenetic studies by Farias and colleagues (2000, 2001) have demonstrated that the heroine cichlids in Central America are nested within the South American radiation (and see also Roe et al. 1997; Martin and Bermingham 1998; Hulsey et al. 2004; Chakrabarty 2006a; Concheiro-Pérez et al. 2007). Similarly, the Poeciliinae that dominates the Central American fauna with approximately 200 species is also descended from South American groups (Lucinda and Reis 2005; Hrbek, Seckinger, et al. 2007).

Fish biogeographers have long recognized the contrast between "old" groups that likely colonized NCA before the rise of the Isthmus of Panama and "recent" groups that did it in the last 3 Ma (Bussing 1985). Unequal species diversity and the limited fossil record in NCA were originally used to make

these inferences, but the advent of extensive phylogenies and explicit time frames from molecular dating has allowed these hypotheses to be more rigorously evaluated. Molecular dating has generally been based on a so-called standard fish mtDNA molecular clock estimate: 1.1–1.3% uncorrected distance per million years (Bermingham et al. 1997; Near et al. 2003). All studies using molecular clocks should be evaluated with the caveat that the dates obtained are susceptible to significant estimation bias when the rates of molecular evolution are variable within a phylogeny or the calibrations are poor (Yoder and Yang 2000; Avise 2000).

Based on sequence divergence, Perdices and colleagues (2005) place synbranchid eels in NCA beginning in the lower-middle Miocene (~16 Ma). Their reanalysis of Murphy and colleagues' (1999) cytochrome *b* data for *Rivulus* using a 1% divergence rate places *Rivulus* in Central America beginning around 18–20 Ma (Perdices et al. 2005). Using Bayesian dating methods that account for heterogeneous rates of molecular evolution, Hrbek, Seckinger, and colleagues (2007) found strong evidence of a late Cretaceous (~68 Ma) dispersal from South to Central America in the Poeciliinae. Similarly, Cretaceous (~68 Ma) and Paleogene (~50 Ma) movements among South and Central America and the Caribbean have been proposed for heroine cichlids (Chakrabarty 2006a), but alternative younger dates (~20 Ma) for cichlid diversification in Central America have also been proposed (Martin and Bermingham 1998; Concheiro-Pérez et al. 2007). These studies highlight the need for further research and suggest that some NCA freshwater fish clades may be much older than previously thought. This suggestion is compatible with the emerging notion that modern South American fishes are likely of Cretaceous origin (Chapter 5) and that Neotropical fish diversification was under way by the Paleogene (65–23 Ma; see Chapter 6). A general lack of phylogenetic hypotheses and molecular data for many relevant groups hinders further understanding of the time frames for fish diversification in NCA.

Recently arrived South American fish groups appear to have had little impact on the diversity of NCA, especially north of the Nicaraguan Depression (R. Miller 1966; Bussing 1985; S. Smith and Bermingham 2005). The vast majority of freshwater fish lineages were present in NCA prior to the rising of the Isthmus of Panama. Some groups may have occupied NCA tens of millions of years ago, before the current connection between the continents was established (c. 3 Ma, see Chapters 6 and 18). Several links older than 3 Ma have been proposed to have had existed between Central and South America based on biological inference (G. Myers 1966; Bussing 1985) or on elaborate geological models (Haq et al. 1987; Pindell 1994; Iturralde-Vinent and MacPhee 1999). For instance, Bermingham and Martin (1998) proposed a short-lived connection during a late Miocene low sea-level stand (5.7–5.3 Ma). Coates and Obando (1996) proposed that the deep-water trench separating Central and South America might have become shallow enough to permit faunal exchange in the middle to late Miocene (15–6 Ma). According to Haq and colleagues (1987), in the lower-middle Miocene, sea levels were generally very high, but two sea-level drops of almost 100 m may have occurred between 17 and 15 Ma. A Cretaceous Island Arc (Iturralde-Vinent and MacPhee 1999) has also been proposed to have linked Central America, the Greater Antilles, and South America 80–70 Ma. Some have argued that this Cretaceous Island Arc connection may have lasted until 49 Ma (Pitman et al. 1993). A final hypothesis proposes a geological connection between NCA and South America via a land bridge through the Greater Antilles

and the Aves Islands Ridge as recently as 32 Ma (GAARlandia hypothesis; Iturralde-Vinent and MacPhee 1999). Problematically, the alleged age of this connection between South America and the Greater Antilles is more recent than any connection posited between any Antillean island and Central America. Sea levels may also not have dropped low enough to allow fish to disperse between land-masses separated by marine habitats (K. Miller et al. 2005). However, recent phylogenetic patterns and age estimates for freshwater fishes suggest that the Greater Antilles may have played a larger role than previously thought in connecting the fish faunas of NCA and South America (Chakrabarty 2006a; Hrbek, Seckinger, et al. 2007).

#### GREATER ANTILLEAN CONNECTIONS

The Greater Antilles (i.e., Cuba, Hispaniola, Jamaica, and Puerto Rico) have relatively few freshwater fish species, and may have acted as sink locations for wide-ranging fish groups from Central America, South America, or regions such as the Florida Peninsula of North America (G. Myers 1938a; Fowler 1952; Rivas 1958; Hedges 1960; D. Rosen and Bailey 1963; W. Fink 1971; Briggs 1984; Rauchenberger 1988, 1989; Burgess and Franz 1989). For instance, Puerto Rico with 9,104 km<sup>2</sup> has no native primary or secondary freshwater fishes, and Jamaica with 11,100 km<sup>2</sup> has only six such species. However, a low number of species in the Greater Antilles might be expected based on species-area curves given the island sizes (MacArthur and Wilson 1967; Losos and Schluter 2000) and the paucity of perennial freshwater habitats (Burgess and Franz 1989). The low number of species in the Greater Antilles has likely contributed to the notion that these faunas were not sources for the assemblage of the more species-rich Central American fauna and could indicate that any divergence between Antillean Islands and mainland NCA was fairly recent.

Despite the preceding considerations, increasing phylogenetic evidence suggests that the sister lineages to several NCA groups are Caribbean taxa (Murphy et al. 1999; Perdices et al. 2005; Chakrabarty 2006a; Hulsey et al. 2006; Hrbek, Seckinger, et al. 2007). For instance, a highly suggestive result is the sister-group relationship between NCA heroine cichlids and a small Antillean endemic clade assigned to *Nandopsis* (Hulsey et al. 2006; Chakrabarty 2006a; Concheiro-Pérez et al. 2007). Interestingly, the only known heroine cichlid fossil is *Nandopsis woodringi* (Cockerell 1923), found on the Caribbean island of Hispaniola (Haiti). This fossil is from upper or middle Miocene (minimum age ~15 Ma; Tee-Van 1935; and see Chakrabarty 2006b). Further testing of the sister-group relationship between *Nandopsis* and the NCA cichlids (Hulsey et al. 2006; Concheiro-Pérez et al. 2007; but see Chakrabarty 2006a) would provide a test of shared history between the Caribbean and mainland NCA extending back to at least the Miocene.

As in cichlids, some phylogenetic evidence suggests the Greater Antilles genera *Girardinus* and *Quintana* form the sister clade to the majority of Central American poeciliid genera. Hrbek, Seckinger, and colleagues (2007, fig. 2) postulate movement between Central America and the Greater Antilles between 20 and 13 Ma. Likewise, they suggest the genus *Gambusia* may have descended from groups inhabiting NCA and Mexico (Hrbek, Seckinger, et al. 2007). Similarly, sister-group relationships between synbranchid eels from Cuba and the Yucatán Peninsula (Perdices et al. 2005) and the split between *Rivulus* in the Greater Antilles and Central American species suggest an old divergence between the Caribbean and NCA (Murphy et al. 1999). The basal divergence between two extant

gars *Atractosteus tristoechus* (from Cuba) and *A. tropicus* (from Central America) offers a yet-unresolved further test of this putatively ancient connection (Wiley 1976).

Phylogenetic relationships of several cyprinodontiform taxa in the Yucatán to taxa in Florida also indicate important biogeographic links between Central American and Caribbean fishes (R. Miller et al. 2005). Seven endemic or near-endemic coastal cyprinodontiform taxa in the genera *Poecilia*, *Cyprinodon*, *Floridichthys*, *Fundulus*, and *Garmanella* have close southeastern United States relatives in *Poecilia*, *Cyprinodon*, *Floridichthys*, *Fundulus*, and *Jordanella* (Miller et al. 2005). However, whether these groups are actually sister groups has been questioned by recent molecular phylogenies (Echelle et al. 2005; Parker and Kornfield 1995). Nevertheless, phylogenetic information suggests *Poecilia latipinna* from southeastern North America and *P. velifera* from the Yucatán are closely related (Ptacek and Breden 1998).

In combination, these results suggest that the Greater Antilles may have served as stepping-stones for North and South American fish groups on their way to colonizing NCA. Interestingly, today's western tip of Cuba is approximately 200 km from the northeastern tip of the Yucatán Peninsula. The Nicaraguan rise is a shallow offshore continuation of the Chortis Block connecting Jamaica to Nicaragua and could have also historically linked NCA and the Greater Antilles (Rauchenberger 1989). Conversely, the depauperate fish fauna of Jamaica suggests it likely never exhibited faunistic elements shared between NCA and the Antilles. Regardless, it seems plausible that the Greater Antilles could have harbored fish lineages from South America for extensive periods of time, allowing them to subsequently colonize Central America. A GAARlandia colonization of the Greater Antilles coupled with large sea-level drops (Haq et al. 1987) may have permitted groups to indirectly make their way from South America to the Greater Antilles and into NCA. However, recent reconstructions of sea levels suggest that drops of 100 m were unlikely before the Eocene (R. Miller et al. 2005), and drops of this extent would not allow the formation of a terrestrial connection between NCA and Cuba given the current bathymetry of the intervening sea floor.

#### NORTH AMERICAN CONNECTIONS

Several groups present south of the TMVB have phylogenetic affinities with North American taxa and no relatives in South America or the Antilles. The catfish *Ictalurus meridionalis* reaches as far south as the Belize River (Greenfield and Thomerson 1997). In the family Catostomidae, species of *Ictiobus* reach to the Papaloapan and Usumacinta basins (R. Miller et al. 2005). Gars in NCA also have close affiliations with extant groups in North America (Wiley 1976). A monophyletic group of cyprinids closely allied to the genus *Notropis* also has undergone restricted diversification south of the TMVB (Schonhuth and Doadrio 2003), representing the southernmost extension of this species-rich group into the Neotropics. Future biogeographic analyses of these North American groups in NCA could benefit from their well-documented fossil records to determine time frames for their arrival into Central America.

Highly diverse North American groups such as Percidae and Centrarchidae are absent from the river systems south of the TMVB, coinciding with an abrupt faunal transition along the Atlantic coast of Mexico (R. Miller 1966; R. Miller et al. 2005). Extensive faunal turnover has been repeatedly found at this location, suggesting the TMVB has had a profound

biogeographic influence on other vertebrate groups as well (Pérez-Higaredera and Navarro 1980; Mulcahy and Mendelson 2000; Mateos et al. 2002). The northern reaches of the Neotropical fish fauna are likewise largely shut off by the TMVB. Fishes in the genera *Rivulus*, *Thorichthys*, *Vieja*, *Ophisternon*, *Hyphessobrycon*, *Rhamdia*, *Priapella*, *Poeciliopsis*, *Belonesox*, *Hyporhamphus*, and *Atherinella* have their northernmost distribution on the Atlantic slope just south of the TMVB at the Punta Del Morro (Bussing 1976; Savage 1966; Obregón-Barboza et al. 1994). Exceptions include the cichlid genus *Herichthys* and the characiform *Astyanax* that belong to larger clades ancestrally present south of this biogeographic boundary but that have spread north of it (Miller et al. 2005). The timing of the divergence between *Herichthys* and other heroine cichlids suggests that cichlid distributions both north and south of this region have been constrained by the TMVB (Hulsey et al. 2004). *Astyanax* likely invaded the region north of the TMVB twice (Strecker et al. 2004), although the time frame for these events is unclear. The poeciliid genera *Gambusia*, *Heterandria*, *Poecilia*, and *Xiphophorus* are also represented north of this boundary (Rauchenberger 1988, 1989), but based on our current understanding of their phylogenies, clades in these genera south of the TMVB may actually represent invasions from the north (Rauchenberger 1989; Lydeard et al. 1995).

#### POLOCHIC-MOTAGUA FAULT

The Usumacinta province extends from the TMVB to the Polochic-Motagua fault zone. The boundary between the Usumacinta and Honduras provinces represented by the Polochic-Motagua fault in Guatemala has long been recognized (Bussing 1976, 1985; G. Myers 1966; Perdices et al. 2002, 2005). The Motagua region is where the Chortis and Maya blocks meet, and a significant biogeographic break is clearly reflected in the fish fauna. It has also been suggested that this narrow, low-lying region has been subjected to repeated marine incursions since at least the lower Miocene (Bussing 1985; K. Miller et al. 2005). This infusion of saltwater likely eliminated freshwater faunas that occurred there and limited exchange via one of the narrowest regions along the Atlantic Coast. Marine regressions also should have created new habitat for freshwater fishes and opened areas for range expansion (see also Chapter 6).

The southern distribution of many freshwater groups ends near the Río Motagua valley (Bussing 1976, 1985). The cichlids *Rocio octofasciata*, the '*Cichlasoma*' *urophthalmum* species group, and *Thorichthys*, as well as the poeciliids *Gambusia*, *Xiphophorus*, and *Heterandria*, are absent or rare south of the Motagua fault (Figure 17.1). This fault zone has also likely influenced the distribution of the synbranchids *Ophisternon* and *Synbranchus* (Perdices et al. 2005). Phylogeographic analyses of species spanning the fault would be interesting as, for example, *Rhamdia quelen* shows a distributional break at the Río Motagua (Perdices et al. 2002). The genera *Phallichthys*, *Belonesox* and *Astatheros* are present on both sides of the Motagua (R. Miller 1966) and could be examined to test the timing of species-level divergence across the region.

#### HONDURAN-SAN JUAN PROVINCES

Further distributional, phylogenetic, and phylogeographic information on groups in the Honduran province whose northern distributions about the Motagua fault would clarify the biogeographic boundaries of the Usumacinta and Honduran provinces. The Honduran region has few endemic species

and instead contains some fish with peripheral distributions that cross the Polochic-Motagua fault or that are also present in the San Juan province. Wide-ranging northern species such as *Astatheros robertsoni* and *Belonesox belizanus* occur in several drainages in this region (R. Miller 1966; Bussing and Martin 1975). In contrast, there are some fish endemic to this region such as the poeciliid *Alfaro huberi* and likely several more (R. Miller and Carr 1974). Generally, it is unclear where the Honduran province ends and the San Juan province begins. Several species in the Honduran province reach their southern distribution in the Río San Juan. The clupeid *Dorosoma* and the gar *Atractosteus tropicus* are examples and have clear recent affinities with fishes farther north (R. Miller 1966). The San Juan province also shares a substantial number of species with Costa Rica to the south (Bussing 1976). Groups such as *Herotilapia multispinosa*, *Bryconamericus*, and *Carlana eigenmanni* make it only as far north as this region but are present much farther south. Generally, extensive collections between the Motagua and San Juan rivers are needed to better define biogeographic boundaries in the region.

#### CROSSING THE CONTINENTAL DIVIDE

The Chiapas-Nicaraguan province is relatively species poor, with almost one-third of the fish fauna present on the NCA Pacific Slope shared with Atlantic drainages (Bussing 1976). Understanding where fish have crossed the continental divide could shed light on why this region is depauperate and also point to shared geologic linkages among NCA provinces. Distributions of freshwater fish groups suggest several historical routes permitting the exchange of fish groups across the continental divide. For instance, *Atractosteus tropicus* is present in a disjunct ring ranging from the Río San Juan on the Atlantic slope of the Nicaraguan Depression to the Río Coatzacoalcos in southern Mexico and is also found on the Pacific slope from southern Chiapas to the Gulf of Fonseca (R. Miller 1966). That the divide separating Pacific and Atlantic drainages may commonly be crossed is indicated by phylogeographic analyses of species in the catfish genus *Rhamdia* that have apparently crossed the divide into the Chiapas-Nicaraguan province several times and possibly at four different locations (Perdices et al. 2002). The primary avenues for fish crossing of the NCA continental divide include the Isthmus of Tehuantepec, potentially two different regions across the Chortis highlands, and the Nicaraguan Depression.

The Isthmus of Tehuantepec has undoubtedly been an important avenue for fish movement from Atlantic to Pacific drainages. This low-altitude, narrow (<200 km) passage is nearly traversed by the Río Coatzacoalcos and is the only region in Mexico where multiple groups of aquatic and riparian animals appear to have spread between the Gulf of Mexico and Pacific drainages (Mulcahy and Mendelson 2000; Savage and Wake 2001). For instance, *Ophisternon* spp. from the Pacific Coast of Guatemala and the Atlantic Río Papaloapan on the Atlantic slope of the Isthmus of Tehuantepec are more closely related to each other than to *Ophisternon* lineages in other Atlantic slope populations (Perdices et al. 2005). *Poeciliopsis* species show fairly recent mitochondrial divergence (2.5% or less) across the Isthmus of Tehuantepec (Mateos et al. 2002), although boundaries between some species in the genus may not be well defined (Mateos et al. 2002). Likewise the cichlid *Vieja guttulata* is present in the Pacific Río Tehuantepec and Río de los Perros and is also found in the Atlantic Río Coatzacoalcos basin, with scant genetic divergence

across the divide (Hulsey et al. 2004). *Profundulus punctatus* is present in both the Río Coatzacoalcos and Pacific slope drainages, ranging south of the Isthmus of Tehuantepec to El Salvador (R. Miller 1966). *Rhamdia laticauda* may also have crossed the Isthmus during its initial diversification in Central America (Perdices et al. 2002). Nonetheless, crossing the continental divide is clearly not trivial because there are several groups such as *Xiphophorus*, *Gambusia*, *Thorichthys*, and *Paraneotroplus* that are present in the headwaters of the Río Coatzacoalcos but do not cross into Pacific drainages.

There may be several areas of faunal exchange across the continental divide in the Chortis highlands (Hildebrand 1925; Boseman 1956; R. Miller 1966). *Profundulus guatemalensis* occurs both in tributaries to the Río Motagua on the Atlantic and in the Río Lempa on the Pacific (R. Miller 1966), and a haplotype group of *Rhamdia quelen* shows a fairly similar distribution (Perdices et al. 2002). Phylogeographic data of *Rhamdia laticauda* also suggest this species may have utilized connections between Atlantic slope drainages and the Río Choluteca (Perdices et al. 2002). The heroine cichlid *Parachromis motaguense* is present in the Atlantic-flowing Río Motagua basin and is also present in the Río Choluteca and several other Pacific drainages (R. Miller 1966). Detailed phylogeographic studies of more of these species that have crossed the continental divide in the Chortis highlands could provide insight into the hydrogeological processes governing stream capture in this region.

The Nicaraguan Depression also likely serves as a major link between the Caribbean and Pacific coasts (R. Miller 1966; 1976; Stuart 1966; Bussing 1976, 1985); this lowland area extends virtually continuously from the Gulf of Fonseca to the Tortuguero lowlands in Northern Costa Rica on the Caribbean coast (McBirney and Williams 1965). According to phylogeographic data, *Rhamdia quelen* and *R. laticauda* may have crossed the continental divide via the Nicaraguan Depression (Perdices et al. 2002). The cichlid clade *Astatheros* has a continuous distribution through this region on both the Atlantic and Pacific slopes and a more robust phylogeny and phylogeography of a few key species could shed light on the colonization route of these fishes. The cichlid *Amatitlania nigrofasciata* species group likewise has probably used this region to cross from the San Juan biotic province to the Pacific coast (Schmitter-Soto 2007). The disjunct distribution of the poeciliid *Brachyrhaphis*, in which most species occur in Costa Rica and Panama, but one species occurs along the Pacific coast of Guatemala and Honduras, is likely a result of movement through the Nicaraguan Depression. However, this group is interestingly absent from the depression itself (Mojica et al. 1997).

#### MARINE INFLUENCES ON THE NCA FAUNA

The presence of marine habitats has exerted a strong influence on NCA fish biogeography. Fluctuating sea levels have likely resulted in repeated marine regressions and incursions into mainland Central America. It is probable that the marine embayment into the Polochic region of Guatemala, indicated today by Lago Izabal, influenced distributions to the north and south of the region (Perdices et al. 2005). The barrier presented by the embayment across the Nicaraguan Depression persisted until the late Pliocene, dissecting Central America from about the Río San Juan almost to the Gulf of Fonseca on the Pacific (Lloyd 1963; J. Campbell 1999). The Yucatán Peninsula has also been heavily influenced by marine incursions. There are very few freshwater species endemic to this region (R. Miller

et al. 2005), and most groups have likely only recently invaded this area.

Marine incursions have also contributed positively to the freshwater fish fauna in Central America, as many saltwater groups have invaded freshwater habitats and constitute a substantial component of the Central American fish fauna (Gunter 1956; R. Miller 1966; Hubbs and Miller 1960; R. Miller et al. 2005; Marceniuk and Betancur 2008; and see Table 17.1). For example, Lago Izabal and Lago Nicaragua are low-elevation, largely freshwater lakes that contain resident marine components such as the sawfish *Pristis pristis* and *P. pectinata*, a shark (*Carcharhinus leucas*), and the normally estuarine tarpon (*Megalops atlanticus*) (Thorson et al. 1966; Thorson 1976; Astorqui 1972). Ariid catfish in the genus *Potamarius* have become restricted to freshwater and range from Lago Izabal to the Usumacinta basin (R. Miller 1966; Betancur et al. 2007). The dominance of marine invaders and secondary fish groups suggests that the interplay between marine and freshwater has been fundamental in structuring NCA fish diversity.

#### Future Directions

We have attempted to summarize the current understanding of how geology, hydrology, and fish systematics interact to influence the historical biogeography of NCA fishes. However, we need a better understanding of the basic presence and absence of fish taxa from drainages in Central America. There are certain undercollected regions such as the Pacific coast and Atlantic drainages of the Mosquitia of Honduras and Nicaragua where the lack of attention makes discovery of common biogeographic patterns difficult. A striking example highlighting the need for further field collections is the recent discovery of the most mysterious taxon in NCA, the endemic catfish *Lacantunia enigmatica* in the Usumacinta region (Rodiles-Hernández et al. 2005). Belonging to its own family, Lacantunidae has closer phylogenetic affinities with African rather than South or North American catfishes (Sullivan et al. 2006). Mapping the geographic range, the fundamental unit of biogeography (Brown et al. 1996), for known and undiscovered species will remain key to understanding NCA freshwater fish biogeography.

With the advent of molecular phylogenetics, our understanding of the evolution of fish faunas across the Central American landscape has substantially progressed. However, phylogenies for groups like *Fundulus* and many genera in the Poeciliinae and Cichlidae would provide a firmer framework against which to test future evolutionary and biogeographic hypotheses. Most phylogenies and age-estimation efforts to date have been based on mitochondrial DNA (but see Chakrabarty 2006a; Hrbek, Seckinger, et al. 2007) and would improve substantially with added information from the nuclear genome and the incorporation of methods based on more realistic models of molecular evolution. The few phylogeographic studies on fishes in NCA (Perdices et al. 2002, 2005) also vividly demonstrate how population-level variation can both confirm broad-scale patterns and provide surprising results that can only be recovered using within-species genetic information.

Further paleontological discoveries would provide invaluable additions to our understanding of NCA fish evolution. NCA fossils collected from any site older than 3 Ma would provide substantial insight into the composition of the Central American freshwater fish fauna prior to the formation of the Isthmus of Panama. Refinement of our geological understanding of NCA would also clarify the timeline of NCA fish

evolution. Geographic calibration of molecular phylogenies could provide a valid alternative for estimating the age of clades based on their distribution and assumed vicariant patterns. There is also a growing consensus from phylogenetics, molecular dating, and the fossil record that Neotropical fishes are older than previously believed (e.g., Lundberg et al. 1998; Chapter 6), and multiple sources of information should be increasingly used to determine the time frame for NCA fish diversification.

Negative interactions among organisms may have played a prominent role in determining species distributions in NCA, but there is little but conjecture that confirms this. Ecologically equivalent groups like centrarchids might have limited the northward dispersal of cichlids by means of competition (R. Miller 1966), and the substantial trophic diversification of heroine cichlids could be due to the absence of benthic-feeding ostariophysan fishes (Winemiller et al. 1995). The absence of small fish groups like North American darters and South American characiforms and catfish may have created conditions of “ecological release” (Schluter 2000)

allowing cichlids and poeciliids to occupy niches beyond those they normally utilize in more diverse communities (Winemiller et al. 1995). Parasites and predators may have also greatly structured fish distributions, but again there is little evidence for their influence on NCA fish biogeography. Documenting how biotic interactions, abiotic factors, and our continually emerging geological understanding of how Central America was constructed should provide substantial future insight into the factors governing the biogeography of Neotropical freshwater fishes.

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