
The Guiana Shield

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Highland areas that serve as sources and boundaries for the great rivers of South America can be broadly divided into two categories based on their geologic age and origin. As reviewed elsewhere in this volume (Chapters 15 and 16), the allochthonous terrains and massive crustal deformations of the Andes Mountains that comprise the extremely high-elevation western margin of South America have their origins in diastrophic (distortional) tectonic activity largely limited to the Late Paleogene and Neogene (<25 Ma; Gregory-Wodzicki 2000). In contrast, vast upland regions across much of the interior of the continent have been relatively tectonically quiescent since the Proterozoic (>550 Ma; Gibbs and Baron 1993) and exhibit a topography that is instead largely the result of nondeformational, epeirogenic uplift of the Guiana and Brazilian shields and subsequent erosion of overlying sedimentary formations.

Topographic and hydrologic evolution of both the Andes Mountains and the Amazon Platform advanced within the late Mesozoic to Cenozoic time frame recognized as largely encompassing the evolutionary radiations of Neotropical fishes (Lundberg et al. 1998); however, early uplifts of the Amazon Platform predate significant Andean orogeny by several hundred million years. Lundberg (1998), in his review of the temporal context for diversification of Neotropical freshwater fishes, made it clear that, despite the prevailing attention given to Andean orogeny and the various vicariant speciation events that it spawned, most major Neotropical fish lineages were already extant long before the Miocene surge in Andean uplift, and the search for geologic events relevant to basal nodes in the evolutionary history of Neotropical fish lineages should extend deeper in time.

In this chapter we describe the geologic, topographic, and hydrologic evolution of the Guiana Shield since at least the Cretaceous. We then compare these historical processes with evolution of the region's fishes. The primary taxonomic focus of this chapter is suckermouth armored catfishes (Loricariidae), because of their great diversity, comprising over 700 described species, their ancient ancestry as part of

a superfamily sister to all other Siluriformes, and their biogeographic tractability due to distributions across headwater habitats and associated allopatric distribution patterns among sister taxa. We conclude that the diverse loricariid fauna of the Guiana Shield accumulated gradually over tens of millions of years with major lineages being shaped by geologic evolution across the whole continent, and not as the result of a rapid, geographically restricted adaptive radiation. We demonstrate the role of the Guiana and Brazilian shields as ancient reservoirs of high-gradient lotic habitats influencing the origin of frequently rheophilic loricariid taxa. We also show how diversification was influenced by a restricted number of landscape scale features: especially dispersal and vicariance across several geologically persistent corridors, expansion and contraction of ranges due to tectonic alterations in prevailing slope, and patterns of local and regional climate change. Continued progress in this area will require increased sampling, especially in the southern and western portions of the Guiana Shield, both to more fully understand the alpha taxonomy and distribution of species, and for the reconstruction of detailed species-level phylogenies.

Geology and Hydrology

OVERVIEW

Surficial outcrops of the Amazon Platform can be observed as bedrock shoals in many northern and southern tributaries of the Amazon River, but rarely at elevations higher than 150 meters above sea level (m-asl). Topography higher than this is largely comprised by the Roraima Group, an aggregation of fluviolacustrine sediments deposited over much of the northern Amazon Platform during the Proterozoic and subsequently uplifted along with the basement. Portions of this formation resistant to erosion now comprise most of the striking topographic elements for which the shield regions are famous, including the fabled Mount Roraima (2,810 m-asl) and South America's highest non-Andean peak, Pico Neblina (3,014 m-asl) at the frontier with Brazil in the southwestern corner of Amazonas State, Venezuela. The relatively recent discovery of Pico Neblina in the mid-20th century illustrates both the long-standing inaccessibility of much of the Guiana Shield and the

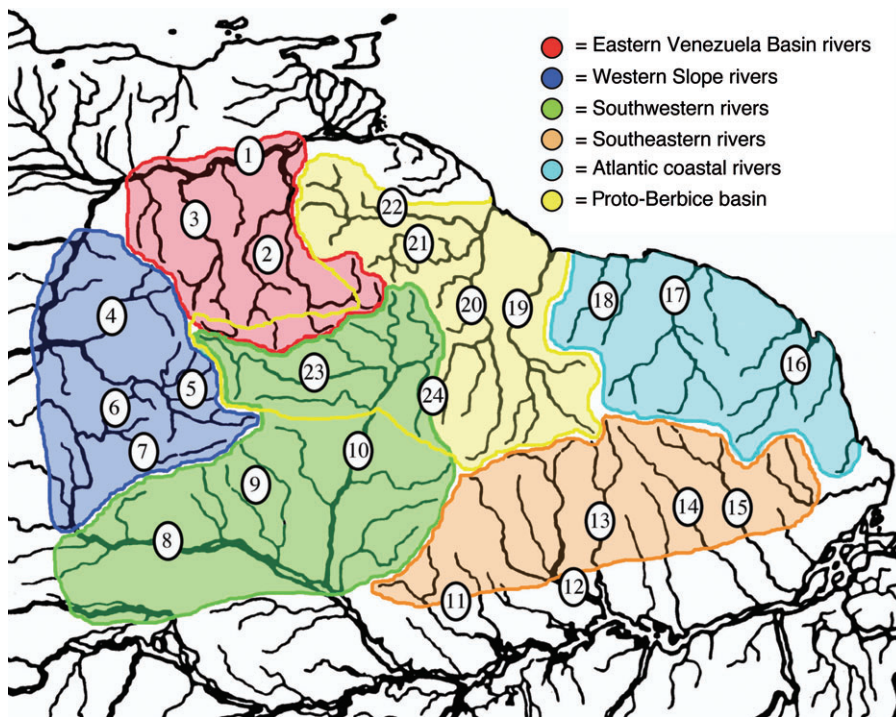


FIGURE 13.1 Major rivers and drainage basins of the Guiana Shield: 1, Orinoco River; 2, Caroni River with Paragua River as its western tributary; 3, Caura River; 4, Ventuari River; 5, Orinoco headwater rivers, from north to south: Padamo, Matacuni, Ocamo, Orinoco, Mavaca; 6, Casiquiare Canal; 7, Siapa River; 8, Negro River; 9, Demini River; 10, Branco River; 11, Uatuma River; 12, Trombetas River; 13, Paru do Oeste River; 14, Paru River; 15, Jari River; 16, Oyapok River; 17, Marone River; 18, Coppename River to the west and Surinam River to the east; 19, Corentyne River; 20, Essequibo River; 21, Potaro River; 22, Cuyuni River; 23, Uraricoera River; 24, Rupununi Savanna bordered on the west by the Takutu River and on the east by the Rupununi.

tremendous gaps in knowledge that still challenge summaries of Guiana Shield geology and biogeography.

Separating the Guiana Shield from the Brazilian Shield is the Amazon Graben, a structural downwarp underlying the Amazon Basin. This major divide is 300 to 1,000 km wide (from north to south) and is filled with sediments up to 7,000 m deep. South of the Amazon Graben to about 20° S latitude stretches the larger of the Amazon Platform's two subunits: the Brazilian (or Guaporé) Shield, whose highlands delineate watershed boundaries of the major southern Amazon River tributaries Tocantins, Tapajós, and Xingú, as well as northwestern headwaters of the south-flowing Paraná River. Middle reaches of the Madeira River are also interrupted by several major rapids as a result of their transect of a western arm of the Brazilian Shield.

The Guiana Shield, the smaller, more northern subunit of the Amazon Platform, is elongated nearly east to west and roughly oval in shape (Figure 13.1). From its eastern margin along the Atlantic coast, it stretches across French Guiana, Suriname, Guyana, and Venezuela, to southeastern Colombia in the west (approximately 2,000 km distance). Bounded by the Amazon Basin to its south and the Orinoco River to its north (approximately 1,000 km distance) and west, the Guiana Shield occupies some 2,288,000 km² (Hammond 2005). Average elevation of the Guiana Shield is approximately 270 m-asl, but disjunct and frequently shear-sided formations exceeding 2,000 m-asl, known variously as tepuis, cerros, massifs, sierras, and inselbergs, are common, particularly near Venezuela's frontier with Brazil in a region of concentrated high-elevation terrain known as Pantepui. The Pantepui region slopes more or less gently to the north but has a striking southern scarp boundary along the Venezuela-Brazil border. Ridges along

this border comprise the Sierras Pakaraima and Parima, which stretch some 800 km east-northeast–west-southwest and rarely drop below 1,000 m-asl. The Pakaraima and Parima ranges have their eastern origin in Mount Roraima at the tricorners between Guyana, Brazil, and Venezuela, and their western terminus in Sierra Neblina.

The name "Guiana" is believed to be derived from an Amerindian word meaning "water" or "many waters" (Hammond 2005). Indeed, as many as 47 medium to large rivers drain the greater Guiana Shield region (Figure 13.1), including the Negro, Orinoco, Essequibo, Trombetas, Caqueta (Japurá), Jatapu, Marone (Marowijne), and Corentyne (Correntijne). Discharge from rivers draining or traversing the Guiana Shield totals an estimated average of 2,792 km³ per year, which amounts to approximately a quarter of South America's total volume of freshwater exported to the oceans (Hammond 2005). This volume of water carries with it considerable erosive power, which, with sporadic periods of epeirogenic uplift, is a primary force responsible for the region's remarkable topography.

TOPOGRAPHIC EVOLUTION

Granitic basement rocks that comprise most of the Amazon Platform formed during orogenic events of the Paleoproterozoic (1,700–2,200 Ma), although the Imataca Complex of northeastern Venezuela is exceptional for its Archean age (>2,500 Ma). For much of this time, it is hypothesized based on once-contiguous fault lines that the Amazon Platform was united with the West African craton, and that together they were part of a single tectonic plate forming parts of the supercontinents Gondwana, Pangea, and Columbia. Approximately 1,800 Ma, a major orogenic episode somewhere to the east

and north of the Guiana Shield, in what would have been the supercontinent Columbia, turned what is now the shield into a foreland basin and depositional zone (J. Santos et al. 2003). Over the course of a few hundred million years the northern Amazon Platform accumulated up to over 3,000 m (avg. 500 m; Gansser 1974) of sediment from rivers flowing off of this ancient mountain range into fluvio-deltaic and lacustrine environments (Edmond et al. 1995). The resulting sandstone formations, known as the Roraima Group, feature ripple marks and rounded pebbles indicating their fluvial origin and the original east-to-west direction of deposition (Gansser 1954; Ghosh 1985). Now uplifted at least 3,000 m and constituting highlands throughout the Guiana Shield, these sediments still cover a vast area but are much reduced from their original range, which surpassed 2,000,000 km² and stretched about 1,500 km from an eastern origin in or near Suriname (largely exclusive of French Guiana) to Colombia and across northern Brazil. Roraima formations in the eastern Guiana Shield, such as the Tafelberg in east-central Suriname and Cerro Roraima itself, are older and deeper than western Roraima sediments now evident as shallow sandstone caps of the central Colombian Macarena and Garzon massifs, and the southeastern Colombian mesas of Inirida, Mapiripán, and Yambi (Gansser 1974).

Transition from the once contiguous, fluvially deposited Roraima formation to the now disjunct Guiana Shield highlands required loss of an enormous volume of intervening sediment through erosion. The modern highlands constitute approximately 200,000 km³ of comparatively resistant sediment, but this is a small remnant of what was originally an approximately 1,000,000 km³ formation averaging approximately 500 m in depth (Gansser 1974). Erosional redistribution of Roraima Group sediments, along with younger Andean sediment, into structural basins encircling the shield has created peneplainer savannas north, west, and south of the highlands. To the north, the structure of the flat Eastern Venezuelan Llanos is that of a basin filled with sediments more than 12 km deep (Hedberg 1950). This Eastern Venezuela Basin is narrowly contiguous with the Apure-Barinas back-arc basin underlying the Apure Llanos northwest of the Guiana Shield (see later section "Eastern Venezuela Basin"). Around the western side of the Guiana Shield, the Apure-Barinas basin and a back-arc basin underlying the Colombian Llanos just southeast of the Andes are contiguous with a low-lying cratonic subduction or suture zone approximately coincident with the Colombia-Venezuela border (Gaudette and Olszewski 1985; Hammond 2005). Lowlands of the Amazon Graben form the shield's southern boundary, and the Rupununi Savannas in the middle of the Guiana Shield are made up of Cenozoic sediments filling a rift valley up to 5,400 m deep (see next section, "Proto-Berbice"). Basins as far as the Western Amazon have, since the Cretaceous, been filling with sediments from the Guiana and Brazilian shields (Räsänen et al. 1998). Despite the dramatic topographic results of a long history of erosion and sediment redistribution, the modern shield highlands are subject to chemical weathering almost exclusively, and shield rivers carry very little sediment (Lewis and Saunders 1990; see the section "Limnology and Geochemistry of Shield Rivers").

Nondeformational, epeirogenic uplift of the Guiana Shield has occurred sporadically almost since its formation in the Paleoproterozoic. Since at least the middle Paleozoic, when the region was first exposed at the surface, cycles of uplift and stasis during which erosion occurred have resulted in elevated erosional surfaces (pediplains or planation surfaces) that are now observed throughout the northern interior of South

America (C. Schaefer and do Vale 1997; Gibbs and Barron 1993; Table 13.1). At lower elevations, these appear as steps or stages of Roraima Formation sediments, vertically separated from each other by 60 to 200 m elevation. At higher elevations, collections of peaks can be identified that share similar elevations (Figure 13.2). Berrangé (1975, 813), for example, described the "remarkable concordance of summits" of the Kanuku Mountains, which are mostly between 900 and 946 m-asl. The heights of Kanuku peaks can be correlated with heights of the Pakaraima-Parima ranges to the northwest, Wassari Mountains to the south, and several other peaks to the north and east, each separated from the other by hundreds of kilometers. Five surfaces, one higher and four lower than that of the Kanuku Mountains, have been identified and assigned tentative ages (Schubert et al. 1986; Table 13.1).

The ages and history of Guiana Shield uplift provide important clues to the origin and evolution of topographic formations such as drainage divides and waterfalls particularly relevant to the distribution patterns of aquatic faunas. Kaieteur Falls (226 m) in Guyana, for example, isolates the only known habitats of *Lithogenes villosus*, a basal astroblepid or loricariid, and *Corymbophanes andersoni* and *C. kaiei*, the only two species in *Corymbophanes*, a lineage sister to all other hypostomine loricariids (Armbruster et al. 2000; Armbruster 2004). Fossil-calibrated relaxed molecular clock data (Lundberg et al. 2007) suggest that these relictual taxa predate the Oligocene uplift of the Kaieteur planation surface and may therefore owe their continued existence to isolation via shield uplift and consequent barrier formation (see later section "Relictual Fauna").

PROTO-BERBICE (CENTRAL SHIELD)

The hydrologic history of South America is a dynamic one, and a large body of evidence indicates that many of the paleofluvial predecessors of modern drainages were substantially different from rivers seen today. Regardless, the Guiana Shield has been embedded among headwaters of the Amazon, Orinoco, Essequibo, and their paleofluvial predecessors since their inception. Late Mesozoic and Paleogene terrigenous sediments recorded from the Caribbean Sea (Kasper and Larue 1986) and Atlantic Ocean (Dobson et al. 2001) are derived from Proterozoic- and Archean-age sources, indicating that, prior to Neogene acceleration of Andean uplift, the Guiana and Brazilian shields were the continent's major uplands, and likely the continent's most concentrated regions of high-gradient lotic habitat (Galvis 2006). One of the largest drainages of the central Guiana Shield during much of the Cenozoic was the proto-Berbice, a northeast-flowing river draining portions of Roraima state, Brazil, most of Guyana, and parts of southern and eastern Venezuela and western Suriname (Sinha 1968; C. Schaefer and do Vale 1997).

Central to the historical geography and hydrology of the proto-Berbice is the Takutu Graben, a deep structural divide between eastern and western lobes of the Guiana Shield approximately 280 km long by 40 km wide and up to 7 km deep, centered on the town of Lethem, Guyana. The modern graben is a valley between the Pakaraima and Kanuku mountains trending east-northeast to west-southwest and approximately equally divided between Brazil and Guyana. Early rifting of the graben resulted in volcanism in the Late Triassic to Early Jurassic, but the depression has received freshwater sediments since the Middle to Late Jurassic. Lake Maracanata, an endorheic lake approximately 75 to 100 m deep (though progressively shallower through time and fluctuating greatly

TABLE 13.1

Planation Surfaces, Their Age, Elevation, and Name in Each Country of the Guiana Shield

Age of Uplift	Country	Surface	Elevation (m asl)
Pre-Late Cretaceous	Venezuela	Auyantepui	2,000–2,900
	Brazil	Roraima Sedimentary Plateau	1,000–3,000
Pre-Late Cretaceous	Venezuela	Kamarata-Pakaraima	1,000–1,200
	Guyana	Kanuku	900–1,200
	Brazil	Gondwana	900–1,200
Late Cretaceous–Paleocene	Venezuela	Imataca-Nuria	600–700
	Guyana	Kopinang	600–700
	Surinam	E.T.S.-Brownsberg	700–750
	French Guiana	First Peneplain	525–550
	Brazil	Sul-Americana	700–750
Lower Eocene–Lower Oligocene	No uplifts (McConnell 1968)		
	Oligocene–Miocene	Venezuela	Caroni-Aro
Plio-Pleistocene	Guyana-North	Kaieteur	250–350
	Guyana-South	Marudi	400–500
	Surinam	Late Tertiary I	300–400
	French Guiana	Second to Third Peneplain	200–370
	Brazil	Early Velhas	200–450
	Venezuela	Llanos	80–150
Holocene	Guyana-North	Rupununi	110–160
	Guyana-South	Kuyuwini	up to 200
	Surinam	Late Tertiary II	80–150
	French Guiana	Fourth Peneplain	150–170
	Brazil	Late Velhas	80–150
	Venezuela	Orinoco floodplain	0–50
Guyana	Mazaruni	>80	
Surinam	Quaternary fluvial cycles	0–50	

NOTE: After Schubert et al. (1986), Briceño and Schubert (1990), and Gibbs and Barron (1993).

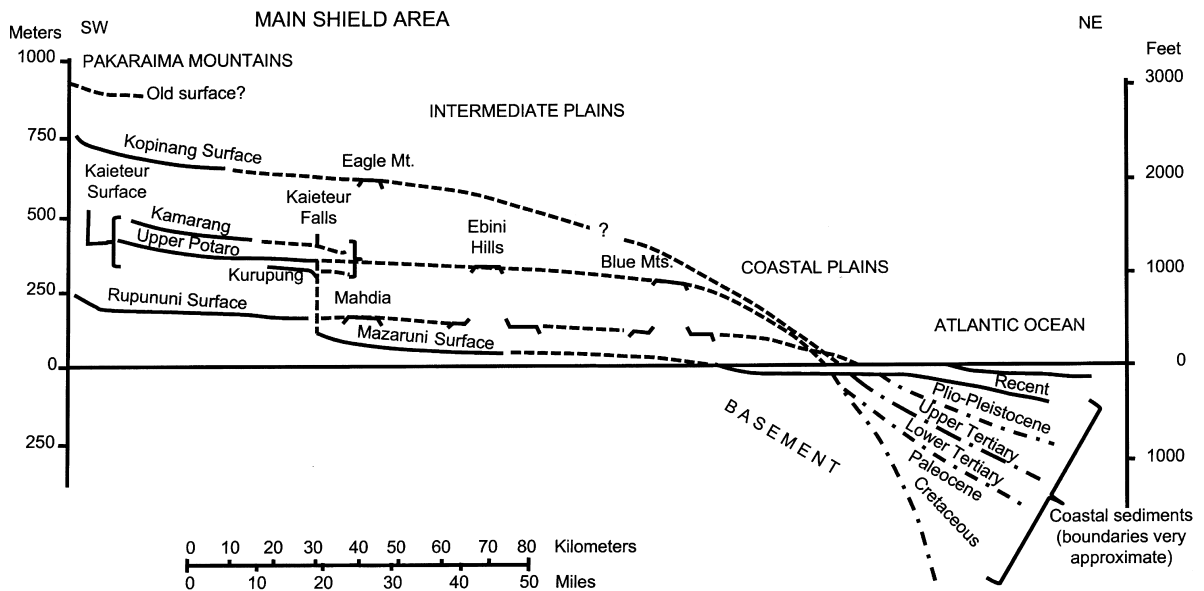


FIGURE 13.2 Schematic showing relationships among planation surfaces in Guyana, their historical contiguity (dashed lines), and their modern remnants (solid lines). Elevation of each surface relative to contemporary sea level in meters on the left and feet on the right (from McConnell 1968).

in depth through periods of aridity) occupied the graben until the Early Cretaceous (Crawford et al. 1985). This ancient lake received predecessors of the modern Ireng, Cotinga, Takutu, Uraricoera, Rupununi, Rewa, and Essequibo rivers (McConnell 1959; Sinha 1968; Berrangé 1975; Crawford et al. 1985).

From the Late Cretaceous to the Paleogene, Lake Maracanata transitioned to a fluvial environment with a trunk stream, the proto-Berbice, that flowed northeast through the North Savannas Gap and exited to the Atlantic between the modern towns of New Amsterdam, Guyana, and Nickerie, Suriname

(McConnell 1959). Head cutting by the Branco River, a south-flowing tributary of the Amazon River, into the western end of what had been Lake Maracaná robbed the proto-Berbice of the Cotinga and Uraricoera first, at the end of the Pliocene, then the Ireng and Takutu in the Pleistocene. The broader, flatter bed now apparent in the Takutu relative to the Ireng indicates that the former was captured and rejuvenated first, whereas the latter, with its entrenched, meandering bed, is still accommodating to its new slope (Sinha 1968). The modern Berbice River itself has withered and is now dwarfed by its former tributaries the Essequibo and Corentyne to its northwest and southeast, respectively. Evidence of a shift away from the lower Berbice as the more important trunk stream can be observed in an elbow of capture near Massara, at the eastern edge of the Maracaná Basin. This is the point at which the modern upper Essequibo shifts abruptly westward, away from a nearby north-flowing Berbice tributary, which has aggraded in response—raising the level of the stream bed (Gibbs and Baron 1993).

It seems likely, given their considerable endemism (see later section “Caroni (Orinoco) to Cuyuni/Mazaruni Corridors”), that the Mazaruni and Cuyuni rivers were also only recently linked with the Essequibo, and that they historically exited to the Atlantic via their own mouth, separate from that of the proto-Berbice. In the southern Guiana Shield highlands of Venezuela, strongly recurved elbows of capture are also regular features of the upper Caroni, Caura, and Erebató (Caura; Figure 13.1), which, along with biogeographic evidence (Lujan 2008), indicate historical confluence of these headwaters with the southeasterly flowing upper proto-Berbice, now the modern Uraricoera River.

The North Rupununi Savannas occupy the modern Maracaná depression and form a shallow continental divide between the northeastern versant of South America, drained in this area predominantly by the Essequibo, and a more southern versant that drains to the Amazon via the Branco and Negro. Seasonal (May to August) rains regularly flood this divide, forming a lentic connection extending to over 6,000 km² and centered between the north-flowing Rupununi River and headwaters of the Pirara River, a west-flowing tributary of the Ireng. Lake Amuku is the name sometimes applied to the broad areal extent of these floodwaters (Lowe-McConnell 1964), as well as to one or more restricted ponds into which floodwaters retreat (NKL, personal observation). Lacustrine sedimentation from the annual inundation continues to contribute to a shallowing of the Maracaná basin (Sinha 1968) and a possible long-term reduction of its role as a biogeographic portal between the Essequibo and Negro watersheds.

Tilting of the underlying basement both in the North Rupununi Savannas and across the Guiana Shield has occurred as recently as the Holocene (Gibbs and Baron 1993) and is likely a frequent driver of head cutting and stream capture. Evidence of this can be seen in the disproportionate incision of tributaries on one side of rivers flowing perpendicular to the direction of tilt, and aggradation of tributaries on the opposite side. Tilting to the west in the South Rupununi Savannas, for example, has led to rejuvenation and steepening of east-bank tributaries, and aggradation and sluggishness in west-bank tributaries of the north-flowing Takutu, Rupununi, and, in part, Kwitaro rivers (Gibbs and Baron 1993). In southeastern Venezuela, a gradual shift in the prevailing tilt of the Gran Sabana from north to south is thought by V. López and colleagues (1942) to be responsible for remarkably complex drainage patterns in the upper Caroni River. Abrupt and localized orthogonal

shifts in channel direction, with streams of the same drainage flowing in parallel but opposite directions, are common features, as are biogeographic patterns indicative of frequent stream capture (Lasso et al. 1990; see later section “Caroni (Orinoco) to Cuyuni/Mazaruni Corridors”).

PROTO-ORINOCO (WESTERN SHIELD)

The western Guiana Shield features one of the largest and most notable river capture events in the Neotropics: that of the ongoing piracy of the northwest-flowing Upper Orinoco River by the southeast-flowing Negro River, via the southwest-flowing Casiquiare Canal (i.e., Río Casiquiare). The Casiquiare Canal diverts up to 20% of the Upper Orinoco's discharge away from the Orinoco trunk and into the Amazon via the Negro. This is a relatively recent phenomenon, however, in the dynamic history of the Orinoco River, which has given rise to the upper Amazon and Magdalena rivers while its own main channel migrated progressively eastward from an ancestral north-south orientation. Prior to consolidation by any trunk stream, from at least the Campanian to the Maastriichtian, westward-flowing drainages from highlands of the Guiana and Brazilian shields likely followed short, anastomosing channels across a broad coastal plain, into shallow marine environments that occupied much of what is today Colombia, Ecuador, and Peru. The Panamanian Isthmus was not yet present, and the northern Andes were just beginning to form.

By the Middle Eocene, uplift of the Central Cordillera had progressed to the extent that it formed the western margin of a large south-to-north-trending valley, drained by a single fluvial system, then expanded by coalescence of both high-gradient left-bank tributaries draining the eastern slope of the young Central Cordillera and right-bank tributaries flowing west from Guiana Shield uplands. The mainstem of this proto-Orinoco was a large, low-energy, meandering river that deposited “vast amounts of sediment” (Villamil 1999, 245) in a geological formation called the Misoa Delta in what is now the Maracaibo Basin (Díaz de Gamero 1996). From the Late Eocene to the Oligocene, marine incursions pushed the mouth of the proto-Orinoco back as far south as the modern town of Villavicencio, Colombia, up to five times (Díaz de Gamero 1996; Villamil 1999). In the Late Oligocene, the proto-Orinoco expanded longitudinally to the north-northeast (Shagam et al. 1984; Villamil 1999), and by the Early Miocene it was flowing into the eastern end of the La Pascua-Roblecito marine basin, a deep seaway occupying much of modern-day Falcon state in northwest Venezuela. The proto-Orinoco and its mouth were isolated at this time from the Maracaibo Basin by uplift of the Merida Andes (Shagam et al. 1984; Villamil 1999) and from the Eastern Venezuela Basin by the El Baul structural arch (Kiser and Bass 1985; Díaz de Gamero 1996).

EASTERN VENEZUELA BASIN (NORTHERN SHIELD)

The Eastern Venezuela Basin is a structural depression located between the northern edge the Guiana Shield and the northern coast of South America that receives lower portions of the northern shield drainages Caura, Aro, and Caroni. The basin is asymmetric in bottom profile, growing shallower to the south and west and opening to the northeast, where the basement is over 12 km deep. The entire basin is filled and leveled with Mesozoic to Cenozoic sediments now zero to 50 m-asl and comprising the eastern half of the Venezuelan Llanos. Approximately 800 km east to west and 250 km

north to south, the basin is bounded in the east by the Sierra Imataca, a northern arm of the Guiana Shield, and in the south by the Guiana Shield proper. In the north, it is bounded by the Sierra del Interior and Coastal mountain ranges; and in the east, it has an opening to the Apure-Barinas Basin that is constricted as between a thumb and forefinger by the coastal mountain ranges in the north and the El Baul structural arch in the south.

From at least the Lower Cretaceous to the Early Eocene, the Eastern Venezuela Basin was a marine environment that received rivers draining the northern slope of the Guiana Shield directly. In the Early Eocene, however, tectonic convergence of the Caribbean Plate caused widespread emergence of the Eastern Venezuela Basin and northward expansion of the coastal plain. In response, the Caura extended its lower course north-northeast so that it formed a delta in the Sucre region of Venezuela between the modern islands of Margarita and Trinidad (Rohr 1991; Pindell et al. 1998). Emergent coastal plain conditions largely prevailed in the Eastern Venezuela Basin throughout the Eocene and into the Oligocene, but convergence of the Caribbean Plate in the Late Oligocene caused southeastward migration of the La Pascua-Roblecito seaway. While the proto-Orinoco continued to discharge into the seaway's closed southwestern end, the Caura and Caroni coalesced in a more restricted coastal plain and delta near the seaway's eastern opening, in the northern portion of Anzoategui state, Venezuela (Rohr 1991; Pindell et al. 1998).

In the Early Miocene, regression of the seaway and consequent eastward progradation of the proto-Orinoco placed deltas of the proto-Orinoco and Caura in close proximity at the western margin of the Eastern Venezuela Basin, but uplift of the El Baul Arch at this time ensured that they remained separate until at least the Middle Miocene (Pindell et al. 1998). In the Late Middle Miocene, southward propagation of rapid uplift in the Serrania del Interior, along with a possible decrease in the significance of the El Baul Arch, pushed the proto-Orinoco southward to capture the lower course of the Caura (Pindell et al. 1998). Further progradation and eastward movement of the Orinoco put its delta in the region of modern Trinidad in the mid-Pliocene. Final conformation of the Orinoco River to its modern course, adhering closely to the northern edge of the Guiana Shield, occurred in the Late Pliocene to Pleistocene (Rohr 1991; Hoorn et al. 1995; Díaz de Gamero 1996).

PROTO-AMAZON AND EASTERN ATLANTIC DRAINAGES (SOUTHERN AND EASTERN SHIELD)

The Amazon River's birth as a distinctly South American, versus Gondwanan, river can be dated to at least the Middle Aptian, approximately 120 Ma. Fossil evidence indicates that by the Late Aptian, an equatorial seaway linked the North and South Atlantic, thereby dividing the once-contiguous landmass of Gondwana into South America and Africa (Maisey 2000). Given the much older Proterozoic structural evolution of the Amazon Graben as a regional lowland and its sediment fill dating at least to the Cambrian (Putzer 1984), it can be assumed that from the moment the South Atlantic Seaway opened, a paleofluvial predecessor of the Eastern Amazon drained the southeastern Guiana and northeastern Brazilian shields east through a mouth approximately coincident with its modern delta. This proto-Amazon was much smaller than the modern Amazon-Solimões system. For over 100 My following the breakup of Gondwana, upper and lower portions of the modern Amazon Basin (approximately coincident with

the modern Solimões and Amazonas reaches), were separated by the Purús Arch, a continental divide within the Amazon Graben located near the modern mouth of the Purús River. Lowland portions of those proto-Amazon tributaries draining the southern slope of the Guiana Shield would have also been separated by the Purús continental divide into western and southeastern paleodrainages. The upper Negro, Caqueta (Japurá), and upper Orinoco would have flowed west or northwest during this period, either directly into the Pacific or into the Caribbean via the proto-Orinoco (see previous section "Proto-Orinoco").

Southeastern drainages of the Guiana Shield would have been further limited in areal extent and distanced from the western lobe of the Guiana Shield relative to their modern pattern by the expanded proto-Berbice draining the central Guiana Shield region (see "Proto-Berbice"). Paleodrainages of the southeastern Guiana Shield that would have been south of the proto-Berbice's approximate watershed boundaries and east of the Purús Arch, and therefore still been northern tributaries of the proto-Amazon, would have included the lower Branco/Negro below the Mucujai River, and the Uatuma, Trombetas, and Paru rivers. A series of ridges with peaks in the range of 400 to 1,000 m extends east from the Kanuku Mountains and forms another continental divide within the eastern lobe of the Guiana Shield, in this case separating south-flowing Amazon tributaries from northeast-flowing Atlantic Coastal drainages. Headwaters of respective northern and southern rivers interdigitate across these highlands, rendering them largely porous to fish dispersal (Nijssen 1970; Cardoso and Montoya-Burgos 2009; see later section "Atlantic Coastal Corridors"). The westernmost of these east-to-west ranges, forming the border between Brazil and Guyana, are the Wasari and Acarai mountains, which give rise to the Trombetas, the fourth-largest watershed on the Guiana Shield (drainage area 136,400 km²). The easternmost of these ranges, forming the southern borders of Suriname and French Guiana, are the Tumucumaque Mountains, which give rise to the Paru River (44,250 km²). North of this divide, in order from west to east, flow the Correntyne (68,600 km²), Coppename (21,900 km²), Suriname (17,200 km²), and Marone (70,000 km²) rivers. Finally, draining the eastern slope of the eastern Guiana Shield is the Oyapok River (32,900 km²), which forms the border between French Guiana and Brazil, and the Approugue River (10,250 km²) just to its northwest inside French Guiana (Figure 13.1; drainage area data from Hammond 2005).

In the Late Miocene, paroxysms of Andean uplift shifted the prevailing slope of the Andean back-arc basin eastward and caused Andean-derived watercourses to breach the Purús Arch, vastly expanding the proto-Amazon's watershed westward. Regions joining the Amazon Basin included vast swaths of the modern western and southwestern Amazon Basin that had been tributary to the proto-Orinoco. New northern tributaries of the expanded Amazon included drainages of the western lobe of the Guiana Shield such as the Caqueta and upper Río Negro. Uplift of the Vaupes Arch and Macarena Massif contemporaneous with the Late Miocene Western Cordillera uplift also created a new drainage divide segregating the upper Negro from the upper Orinoco (Galvis 2006).

Orographic rainfall effects of the rapidly rising Andes Mountains further contributed to expansion of the Amazon in the Late Neogene by increasing its discharge beyond that predicted by areal expansion alone. With increased discharge came an increase in erosional potential and further watershed expansion via head cutting. The southeast flowing Branco River, for

example, sequentially captured headwater tributaries of the northeast flowing proto-Berbice throughout the Pliocene and Pleistocene. Indeed, the Amazon is still expanding, as seen in the ongoing capture of the upper Orinoco by the Rio Negro. Initiation of this capture and opening of this portal has been hypothesized to be fairly recent, possibly resulting from Late Pleistocene or even Holocene tilting (Stern 1970; Gibbs and Barron 1993). Under this scenario, the Orinoco is estimated to have been largely isolated from the Amazon for some 5–10 My, from the Late Miocene uplift of the Vaupes Arch to the Pleistocene-Holocene formation of the Casiquiare Canal. In the future, it is likely that a new drainage divide will form within the Orinoco downstream of the Tama-Tama bifurcation, and the current headwaters of the Orinoco will become entirely adopted by the Amazon (Stern 1970).

ARIDITY AND MARINE INCURSIONS

We have thus far described, in broad strokes, major trends and events in the drainage evolution of four hydrologic regions around the Guiana Shield, but we have done so at the expense of dwelling in too great detail on global cycles and climatological events that had periodic, widespread effects across all hydrologic units. Aridity and marine incursions are treated here together because of their similar effect on rivers and riverine biota—that of reducing and isolating habitats over a broad geographic range. The two phenomena are also correlated in their response to global cycles of glaciation with a periodicity of 20–100 thousand years (Milankovitch cycles; Bennett 1990). In general, warmer, interglacial climates correspond to higher sea levels, more extensive marine incursions, and higher levels of precipitation. Cooler, glacial periods result in reduced precipitation, retreat of the sea, expansion of the coastal plain, and incision of river channels.

Many lines of geological and biogeographical evidence indicate that the climate of South America was much drier in the recent past than it is today. The last major glacial period, the Würm or Wisconsin glaciation, lasted throughout the Late Pleistocene, from approximately 110,000 BP to between 10,000 and 15,000 BP. Several authors (e.g., Krock 1969; Hammen 1972; Tricart 1985; Schubert et al. 1986; Schubert 1988) describe the substantial paleobotanical and geomorphological evidence of aridity in South America during this period. Hammen (1972) states that within the overall trend of late Pleistocene aridity, the period from approximately 21,000 to 13,000 BP was the driest.

Terrestrial vegetation throughout much of the Guianas in the Late Pleistocene was of an open savanna or grassland type, with rainforests likely limited to a few highland refugia, including parts of the Pantepui highlands, and riparian margins. These refugia have featured heavily in explanations of patterns of terrestrial plant and animal diversity (e.g., Haffer 1969, 1997; Prance 1973; Vanzolini 1973; Brown and Ab'Sáber 1979; Kelloff and Funk 2004), but do not appear to be useful in explaining freshwater fish distributions (Weitzman and Weitzman 1982; see review in Chapter 1). Reduction in forest cover and decreases in sea level had major effects on the geomorphic evolution of South American rivers. Increased erosion due to loss of forest cover and lowered river base levels due to lower sea levels caused many rivers to cut deeply into their channels (Sternberg 1975; Tricart 1985; Latrubesse and Franzinelli 2005). Channel bottom in the lower reaches of lower Amazon tributaries, for example, can be up to 80 m below modern sea level (Sioli 1964; Latrubesse and Franzinelli

2005). During such arid periods, rapids would have been more widespread, and deep-channel habitats that may currently function as barriers to rheophilic taxa would have been reduced. Decreases in total discharge would have also led to shallowing, sedimentation, and aggradation or braiding of low-gradient habitats where they persisted (Schubert et al. 1986; Latrubesse and Franzinelli 2005). Garner (1966) suggests that the complex drainage pattern of the upper Caroni in the Gran Sabana may be the result of anastomosing channel development during a more arid climatic regime, and that the latest humid period has not lasted long enough for the Caroni to consolidate into a more stable drainage pattern.

Marine incursions have inundated much of northwestern South America during interglacial periods of globally high sea level since at least the Maastrichtian (Gayet et al. 1993; Hoorn 1993; see review in Chapter 8). During much of the Miocene, from approximately 23 to 11 Ma, the llanos basins of Colombia and Venezuela were dominated by coastal and lagunal conditions with occasional marine episodes (Hoorn et al. 1995). Given their similar elevations and exposure to the coast, it is likely that similar conditions prevailed in the Rupununi Savannas and coastal plain of Guyana. A more recent marine incursion, approximately 6–5 Ma, was hypothesized by Hubert and Renno (2006) to have affected the distribution and diversity of characiform fishes in northeastern South America by isolating a series of upland freshwater refuges in respective eastern and western portions of the eastern Guiana Shield highlands. Further support for vicariance resulting from such an incursion is provided by Noonan and Gaucher (2005, 2006), who recovered a temporally and spatially congruent vicariance pattern in their molecular phylogenetic studies of *Dendrobates* and *Atelopus* frogs.

LIMNOLOGY AND GEOCHEMISTRY OF SHIELD RIVERS

Rivers of the Guiana Shield are a heterogeneous mix of white, black, and clear water, with most tributaries initially trending toward black and clear water, then mixing to form intermediate main stems. In heavily forested and largely uninhabited regions such as the shields and the Amazon Basin of South America, topography, climate, geology, and a watershed's terrestrial vegetative cover are the main influences on riverine limnologies. Because of their origins in watersheds of ancient, highly weathered, and forest-covered basement rock, rivers of the Guiana Shield tend to be nutrient poor with very low levels of suspended solids and alkalinity but relatively high levels of dissolved silica. Limestones and evaporates are completely absent in the Guiana Shield, so the chemical signatures of its rivers are largely influenced by primary weathering of silica-rich felsic granitoids that are the dominant rock type (Edmond et al. 1995; Hammond 2005). Concentrations of major ions and nutrients in the Orinoco main stem and its Guiana Shield tributaries fall near or even below those expected in precipitation, though, indicating minimal contributions from geology and significant sequestration by forests (Lewis and Weibezahn 1981).

Extreme black-water conditions of low acidity (pH <5.5), negative to low alkalinity, and low conductivity (<25 μ ohms) prevail in the Atabapo, Guainia, Negro, Pasimoni, and other tributaries of the Casiquiare that drain low-lying peneplains between the upper Orinoco and Negro. Adjacent higher-gradient headwaters of the Orinoco such as the Ventuari, Ocamo, Mavaca, and Guaviare are white to clear water, with near neutral pH, alkalinity up to 85 μ eq/kg, and up to

29 μ ohms conductance (Thornes 1969; Edmond et al. 1995). Rivers draining the northern slope of the Guiana Shield, such as the Caura, Caroni, and Cuyuni, as well as rivers further east in Suriname and French Guiana, trend toward black-water conditions despite also having higher gradients. Drainages in the central, south, and southeast of the Guiana Shield, such as the Essequibo, Branco, Trombetas, and Paru rivers are clear to white water. Guiana Shield white-water rivers, it should be noted, are defined based largely on alkalinity and pH, being considerably lower in suspended solid load than those Andean drainages on which the traditional definition of white-water rivers is based (Sioli 1964).

Biogeography of Guiana Shield Fishes

MODERN CORRIDORS: THE PRONE-8

Phylogeography of South American fishes is hampered by a lack of collections and a lack of studies, and the problems of amassing specimens for phylogeographic studies have been particularly acute in the Guiana Shield. Most of the region is difficult to access, with few or no roads to important habitats. Among the better-sampled areas are lowlands of Amazonas, Venezuela, the lower and upper Caroni of Venezuela (although not the middle reaches or the Paragua, a large tributary), the Cuyuni of Venezuela, the Rupununi and Takutu of Guyana, and much of French Guiana. The western highlands, the Mazaruni, the Corantijne, and most rivers of the southern edge of the Guiana Shield have been poorly sampled. Biogeographic studies have been especially hampered by the scarcity of collections from headwaters throughout the Guiana Shield. Most molecular phylogenetic studies inclusive of Guiana Shield populations, including those of *Potamorrhaphis* (Lovejoy and Araújo 2000), prochilodontids (Turner et al. 2004; Moyer et al. 2005), and *Cichla* (S. Willis et al. 2007), are based on lowland taxa that are potentially highly vagile and therefore less likely to resolve fine-scale biogeographic patterns within the Guiana Shield.

To observe fine-scale biogeographic patterns within and between drainages, low-vagility taxa that are less likely to have biogeographic patterns erased via migration and panmixis should be examined. Headwater and rheophilic fishes are especially good candidates because their movements between drainages and habitats would be expected to be hindered by deep, main-channel habitats, but facilitated by stream captures or reductions in river base level during oceanic low stands. Phylogenetic patterns of rheophilic taxa distributed allopatrically across isolated headwaters may be particularly informative when trying to understand the biogeographic significance of such historical events (Cardoso and Montoya-Burgos 2009). Among rheophilic Neotropical fishes, loricariid catfishes of the tribe Ancistrini (Hypostominae) are a group with several genera and species that appear to be both most common and most diverse in shield uplands. Ancistrin catfishes are, as a whole, also highly territorial with relatively low vagility (see Power 1984). As a result, and because they are a group we have studied most, we will focus on them in the following discussion.

For the purpose of our discussion, we refer to taxa known only from the Guiana and/or Brazilian shields as *shield endemic taxa*. Taxa that are only most common within the Guiana and/or Brazilian shields, but have ranges extending beyond these regions, are considered *shield specialist taxa*. Although our discussion of biogeographic patterns will focus on the tribes

Ancistrini and Hypostomini, which we have studied most, published examples from other taxa will also be discussed.

Problematically, the phylogeny and taxonomy of Loricariidae are in their infancy and are complicated by gross morphological similarity. In many of our studies (Armbruster 2005, 2008; Armbruster et al. 2007), we have found little morphological variability within genera upon which to base phylogenies; however, by using what is known about historical and current corridors between river systems and ancistrin phylogenetics and distributions, we will support a conceptual model of biogeographically significant hydrologic corridors around the Guiana Shield. This model approximates the appearance of a prone number 8 (Figure 13.3). Corridors between hydrologically contiguous segments of this Prone-8 consist of both recently formed portals such as the Casiquiare Canal (see "Proto-Orinoco"), recently closed or altered corridors such as the Rupununi Savannas, and numerous intermittent corridors that have likely been present in the recent past. These corridors allow for dispersal around the shield, and their intermittent nature serves as the basis for allopatric speciation. Given that our understanding of the geologic and hydrologic evolution of the Guiana Shield extends beyond the node-age estimates for most Neotropical taxa, especially ancistrin loricariids, we assume that such geophysical evolution has been relevant to the dispersal and evolution of extant taxa. The alternative argument that modern Neotropical fish distributions are the result of widespread extinction versus dispersal will be discussed under "Relictual Fauna," but will not be considered in the majority of our discussion.

CARONI (ORINOCO) TO CUYUNI/MAZARUNI CORRIDORS

Headwaters tributary to the lower Caroni interdigitate with headwaters of the upper Cuyuni, and headwaters of the upper Caroni interdigitate with the upper Mazaruni, making it likely that stream capture would facilitate an exchange of fish fauna between Orinoco and Essequibo drainages. Lasso and colleagues (1990) found a close similarity between whole fish communities of the Caroni in the Gran Sabana and those of the Cuyuni-Essequibo system and hypothesized frequent stream capture as a cause. Despite the relative richness of the loricariid fauna in the Orinoco and Essequibo basins, there seems to be little evidence that the Caroni to Cuyuni and Caroni to Mazaruni corridors are particularly important for loricariids. Armbruster and Taphorn (2008) suggest that the ancestor of *Pseudancistrus reus* (Ancistrini) may have entered the Caroni from the Cuyuni, as it is the only member of *Pseudancistrus sensu stricto* currently known from the Orinoco (all other Orinoco *Pseudancistrus* are basal species); however, *P. reus* has some unique characteristics that make its relationship to other *Pseudancistrus* unclear. The only species of *Pseudancistrus* we know of in the Cuyuni is a species with large white blotches that may be undescribed, and that is relatively common in the Essequibo.

Exchange of loricariids between the upper Caroni and upper Mazaruni also seems to be rare, and consistent with a general pattern of Mazaruni endemism. An undescribed species of *Exastilithoxus* (Ancistrini) from the upper Mazaruni has been reported in aquarium literature, although we have not examined specimens, and *E. fimbriatus* is restricted to the upper Caroni. Two undescribed species of *Neblinichthys* (Loricariidae: Ancistrini) were collected during recent fieldwork in the upper Mazaruni by H. Lopez and D. Taphorn (personal communication), while the congeneric *N. yaravi* is only known

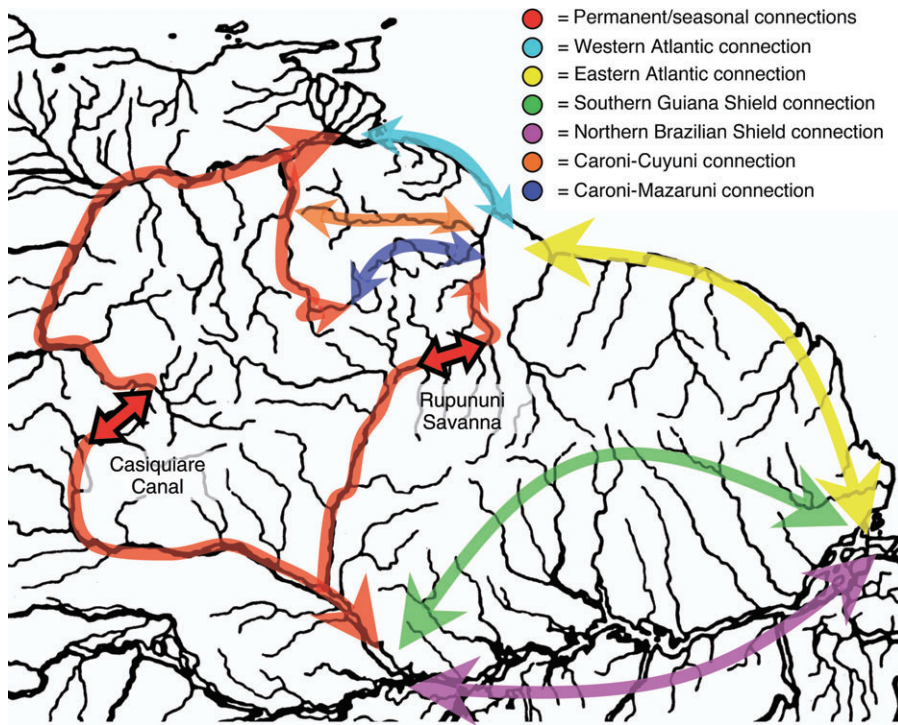


FIGURE 13.3 The Prone-8: Hypothesized areas of movement between basins of the Guiana Shield. Areas of some connections are approximate.

from the upper Caroni. Nonloricariid taxa endemic to the Mazaruni include a recently described new species, possibly new genus, of parodontid (*Apareiodon agmatos*; Taphorn et al. 2008), a basal crenicarinid cichlid (*Mazarunia mazarunii*; Kullander 1990), a lebiasinid, possibly sister to the Pyrrhulininae (*Derhamia hoffmannorum*; Géry and Zarske 2002), and a basal *Nannostomus* (*N. espeii*; Weitzman and Cobb 1975). The basal crenuchid *Skiotocharax meizon* was also described largely from the Mazaruni (Presswell et al. 2000). Taken together, these taxa provide strong evidence of long-term isolation of the Mazaruni River. Indeed, if the proto-Berbice paleodrainage hypothesis is correct, it seems likely that the Mazaruni would have maintained its own mouth to the Atlantic through much of the Miocene-Pliocene when the proto-Berbice is thought to have exited farther to the east.

CASIQUIARE PORTAL

The Casiquiare Canal is a large and permanently navigable corridor between the upper Orinoco and the upper Rio Negro (Amazon). Distributions of species across the Casiquiare have been studied by Chernoff and colleagues (1991), Buckup (1993), Schaefer and Provenzano (1993), Lovejoy and Araújo (2000), Turner and colleagues (2004), Moyer and colleagues (2005), and S. Willis and colleagues (2007). Winemiller, López-Fernández, and colleagues (2008) and Winemiller and Willis (Chapter 14 in this volume) review this literature and supplement it with fish community ecology data transecting the entire Casiquiare. They describe three common patterns of distribution: broad distribution in the Orinoco and Negro, distribution in the upper Orinoco and upper Casiquiare (but not lower Casiquiare or Negro), and distribution in the lower Casiquiare and the Negro (but not upper Casiquiare or Orinoco). They attribute the second two distributional patterns to an environmental gradient from clear water (Upper

Orinoco) to black water (Negro). In addition to this limnological gradient, upper portions of the Orinoco and Negro are isolated from lower portions of their respective drainages by the high-energy rapids Atures and Maipures (Orinoco) and São Gabriel (Negro). Several Amazonian species conspicuously absent from the Orinoco basin (e.g., *Osteoglossum* spp., *Arapaima gigas*, *Parapteronotus hasemani*, *Orthosternarchus tamandua*, *Symphysodon* spp.) are more likely subject to exclusion by the São Gabriel rapids than by shifts in limnology.

Turner and colleagues (2004) and Moyer and colleagues (2005) reported complete segregation between mitochondrial genotypes of *Prochilodus mariae* and *P. rubrotaineatus* in the Orinoco and *P. rubrotaineatus* in the Negro and Essequibo. Likewise Lovejoy and Araújo (2000) identified basal haplotypes of *Potamorhaphis* that were isolated in the upper Orinoco and not shared with Negro populations, indicating a barrier at the Casiquiare. S. Willis and colleagues (2007), however, observed that three of the four *Cichla* taxa present in the upper Orinoco (*C. monoculus*, *C. orinocensis*, *C. temensis*) were genetically similar to conspecifics in the upper Negro. Chernoff and colleagues (1991) list 16 species (11 Characiformes, four Siluriformes, one Gymnotiform) distributed from the upper Orinoco, across the Casiquiare, into the upper Negro; and Buckup's (1993) revision of characidiin fishes lists eight more species whose distribution encompasses at least this divide.

Several loricariids have broad distribution patterns that include the Orinoco, Casiquiare, Negro, and possibly even northern tributaries of the Brazilian Shield. We have studied five species (two shield endemics and three shield specialists) of hypostomines that occur in the Orinoco, Casiquiare/Negro, and drainages of the Brazilian Shield: shield endemics: *Hemiancistrus sabaji* (Armbruster 2008) and *Leporacanthicus galaxias*; shield specialists: *Hypostomus hemicochliodon* (Armbruster 2003), *Lasiancistrus schomburgkii* (Armbruster 2005), and *Peckoltia vittata* (Armbruster 2008). Two of these species

(*H. sabaji* and *L. schomburgkii*) are also found in the Essequibo. These species may offer the best insights into potentially recent movements of taxa among drainages of the Guiana Shield and between the Brazilian and Guiana shields; however, intrataxon relationships must be explored with genetic techniques to determine the relative timing of dispersal and degree of population structure. Three shield endemic genera have ranges similar to those outlined for the species mentioned previously (*Baryancistrus*, *Hypancistrus*, and *Leporacanthicus*; Werneke, Sabaj, et al. 2005; Armbruster et al. 2007, Lujan et al. 2009), as do two shield specialist genera (*Hemiancistrus* and *Peckoltia*; Armbruster 2008).

Several loricariids have distributions limited to the Upper Orinoco and upper Casiquiare. *Hemiancistrus guahiborum*, *H. subviridis*, *Hypostomus sculpodon*, *Pseudancistrus orinoco*, *P. pectegenitor*, and *P. sidereus* all occur in the upper Orinoco and Casiquiare but are not currently known from elsewhere in the Amazon. A few recently described species from the Orinoco have putative sister species in the Casiquiare: *Hypancistrus inspector* (Casiquiare) versus *H. contradens* and *H. lunao-rum* (Orinoco) and *Pseudolithoxus nicoi* (Casiquiare) versus *P. anthrax* (Orinoco). Given the relatively recent formation of the Casiquiare Portal (Late Pleistocene to Holocene; see "Proto-Amazon"), these species may represent recent invasions from the Orinoco to the Casiquiare and/or relatively recent speciation events. Aside from a few widespread black-water adapted species (e.g., *Dekeyseria niveata*, *D. pulchra*), most ancistrin loricariids appear to be excluded from the lower Casiquiare and upper Negro by their extremely black-water limnology.

SOUTHERN GUIANA SHIELD AND NORTHERN BRAZILIAN SHIELD CORRIDORS

The mainstem Amazon River likely acts as a partial barrier for both shield endemic and shield specialist taxa on the respective Guiana and Brazilian shields. Genera known to tolerate more lowland conditions (e.g., *Ancistrus*, *Lasiancistrus*, and *Hypostomus*) may be able to cross the Amazon Basin, but such dispersal is unlikely among most ancistrins. East-west dispersal around the southern part of the Guiana Shield may be via either southern Guiana Shield drainages or drainages of the northern part of the Brazilian Shield. Currently, the fauna of the northern Brazilian Shield is much better known than that of the southern part of the Guiana Shield. Species and genera mentioned previously from both the Guiana and Brazilian shields offer potential examples of movement across the northern Brazilian Shield at least to the Tocantins. Dispersal along the southern flank of the Guiana Shield may be exemplified by *Pseudancistrus sensu stricto*, as several undescribed species are known from these drainages; however, undescribed species are also known from the northern Brazilian Shield. Demonstration of ancistrin biogeographic patterns across the southern Guiana Shield and northern Brazilian Shield must, therefore, await further collections and analyses of genetic data. Among other fishes, the range of *Psectrogaster essequeibensis* (Characiformes: Curimatidae; Vari 1987) and *Parotocinclus ariapuanensis* and *P. britskii* (Loricariidae: Hypoptopomatinae) support dispersal via the northern Brazilian Shield, although we reiterate that collection data in this region are poor.

RUPUNUNI PORTAL

The Rupununi Savanna floods seasonally, creating a lentic corridor between the Essequibo and Takutu rivers, the

latter of which was lost to the Negro through stream capture as recently as the Pleistocene (see "Proto-Berbice"). Loricariids of the Essequibo are nearly identical to those of the Takutu, indicating either regular, recent dispersal across the flooded savanna or insufficient time for differentiation since stream capture. Among hypostomines we have examined, *Hemiancistrus sabaji*, *Hypostomus squalinus*, *H. macushi*, *Lasiancistrus schomburgkii*, *Lithoxus lithoides*, and *Pseudacanthicus leopardus* are well represented in collections on either side of the Rupununi Portal and show no morphological differentiation between drainages. Many other fishes also have ranges that extend across the Rupununi Portal, including *Osteoglossum bicirrhosum*, *Arapaima gigas*, *Psectrogaster essequeibensis* (Vari 1987), and *Rhinodoras armbrusteri* (Sabaj et al. 2008). Molecular phylogenetic studies by Lovejoy and Araújo (2000), Turner and colleagues (2004), and S. Willis and colleagues (2007) support transparency of the Rupununi Portal for *Potamorhaphis*, *Prochilodus rubrotaeniatus*, and *Cichla ocellaris*, respectively.

The relative importance of the Rupununi Savannas as either portal or barrier is difficult to demonstrate. Collections of *Hypostomus taphorni* have been made from throughout the Essequibo, but from only one location in the Pirara River, a tributary of the Ireng (Negro) near the drainage divide, perhaps suggestive of recent immigration. Existence of sister species *Peckoltia braueri* (Takutu) and *P. cavatica* (Essequibo) on opposite sides of the divide seems to support the Rupununi's role as a barrier. Undescribed species of both *Hypancistrus* and *Panaque* (*Panaqolus*) have only been collected on the Takutu River side, as has *Cichla temensis* (S. Willis et al. 2007), further supporting its role as barrier. JWA's lab is currently investigating gene flow across the Rupununi Portal in several fish groups to determine both relative transparency of this portal for various taxa and its timing of closure to rheophilic species intolerant of conditions in the flooded savanna.

ATLANTIC COASTAL CORRIDORS

The exchange of fishes between Atlantic coastal drainages of the eastern Guianas (Guyana, Suriname, French Guiana) and the eastern Amazon Basin may be accomplished via either a coastal marine corridor with reduced salinity due to the westerly deflected Amazon River discharge, coastal confluences during times of lower sea level and expanded coastal plains, and/or headwater interdigitation and stream capture. The region can be broadly divided into the Western Atlantic Coastal Corridor (from the mouth of the Orinoco to the mouth of the Essequibo) and the Eastern Atlantic Coastal Corridor (from the mouth of the Essequibo to (and possibly beyond) the mouth of the Amazon).

The Atlantic Coastal region is poorly represented in molecular biogeographic studies of northern South America. S. Willis and colleagues (2007) report a single species of *Cichla* (*C. ocellaris*) distributed from the Essequibo in the west to the Oyapock in the east, but the aforementioned studies of *Potamorhaphis* and *Prochilodus* do not cover this region. In a morphology-based taxonomic revision demonstrating a similar pattern to that of *C. ocellaris*, Mattox and colleagues (2006) identified the single species *Hoplias aimara* in Atlantic coastal drainages from the eastern Amazon Basin as far west as the northern Guiana Shield drainages entering the Eastern Venezuela Basin, but not entering the upper Orinoco. Renno and colleagues (1990, 1991) investigated the population structure of *Leporinus friderici* using genetic markers and interpreted their data as providing support for the existence of an eastern and

western Pleistocene refuge from which this species has more recently expanded its range. Their data identify the Kourou River in French Guiana as the point of convergence between populations historically isolated east and west of the Kourou.

Low-gradient streams of the Western Atlantic coastal plain's lower drainages are unsuitable for most anacistrins. *Hypostomus plecostomus* and *H. watwata*, coastal plain species that can be found in some estuaries, may use the low-gradient streams and near-shore marine habitats to move between drainages along the whole Atlantic Coastal Corridor (Eigenmann 1912; Boeseman 1968). Several more rheophilic loricariid species are restricted to upland habitats across the Eastern Atlantic versant. *Lithoxus* spp. are found in upland habitats throughout the eastern Guiana Shield, and morphological characters suggest they are divided into a western, proto-Berbice subgenus (*Lithoxus*, 2 spp.), and an Eastern Atlantic Coastal subgenus (*Paralithoxus*, 5 spp.; Boeseman 1982; Lujan 2008). *Pseudancistrus sensu stricto* is distributed throughout the eastern Guiana and northern Brazilian shields, with only a single Orinoco species, *P. reus*, restricted to the Caroni River (Armbruster and Taphorn 2008). *Pseudancistrus barbatus* and *P. nigrescens* are distributed from the Essequibo to French Guiana (Eigenmann 1912; Le Bail et al. 2000), *P. megacephalus* is in at least the Essequibo and Suriname rivers (Eigenmann 1912), and *P. brevispinnis* is found from the Corantijn to the Oyapock and in several northern tributaries of the Amazon (Cardoso and Montoya-Burgos 2009). Several species of *Pseudacanthicus* are also found across the eastern Atlantic Coastal drainages of the Guianas, but specimens of these are rare in collections and they appear to be largely restricted to main river channels. *Pseudacanthicus* and *Pseudancistrus* are both shield specialists, with ranges throughout the eastern Guiana and northern Brazilian shields, and *Lithoxus* is a shield endemic, making these groups excellent subjects for biogeographic studies of the eastern Guiana Shield and adjacent areas.

Cardoso and Montoya-Burgos (2009) conducted a molecular phylogeographic study of *Pseudancistrus brevispinnis* and found support for the hypothesis that this species invaded the Atlantic Coastal river system from the Jari River, a south-flowing tributary of the Amazon, via headwater interdigitation and stream capture with the north-flowing Marone River. From the Marone, *P. brevispinnis* dispersed eastward as far as the Oyapock River and westward as far as the Corantijn River (Cardoso and Montoya-Burgos, 2009). Similarly, Nijssen (1970) suggests a seasonal portal between the Sipalawini River (Corantijn River basin) and the Paru do Oeste River (Amazon River basin) across the potentially flooded Sipalawini-Paru Savanna. He used as support the range of *Corydoras bondi bondi*, which is found through much of Suriname, the Essequibo of Guyana, and the Yuruari (Cuyuni-Essequibo) of Venezuela; however, given the westward extent of the range of *C. bondi bondi*, the proto-Berbice or Eastern Atlantic Coastal Corridor might provide a better explanation. Regardless, Nijssen (1970) describes a variety of potential corridors between north-northeast-flowing Atlantic Coastal rivers and south-flowing Amazon Rivers, and Cardoso and Montoya-Burgos (2009) provide strong support for transit of at least the species *Pseudancistrus brevispinnis* through these corridors.

Availability of the Eastern Atlantic Coastal Corridor as a means of distribution between mouths of the Essequibo and the Amazon is suggested by ranges of *Curimata cyprinoides*, which is a lowland species that is widely distributed throughout Atlantic Coast drainages from the Orinoco to the Amazon (Vari 1987), *Parotocinclus britskii*, which ranges across Atlantic

Coast drainages from the Essequibo to the Amazon (Schaefer and Provenzano 1993), and several serrasalmin species with ranges extending from the Oyapock to the Amazon (Jégu and Keith 1999).

RELICTUAL FAUNA

Inspired by Thurn's (1885) first ascent of Mount Roraima, Doyle (1912) wrote his fictional novel *The Lost World* about a prehistoric landscape isolated atop a table mountain and populated with ape-men and dinosaurs. Although no such archaic member of the terrestrial fauna has yet been discovered, the Guiana Shield does harbor at least one aquatic taxon among the Loricarioidea that may have been swimming with dinosaurs of the Cretaceous. The genus *Lithogenes* includes three species that currently comprise the Lithogeninae of either the Astroblepidae or Loricariidae. *Lithogenes* is similar in external appearance to basal astroblepids and loricariids (Schaefer and Provenzano 2008), but has a morphology so distinct that it does not fit comfortably into either of these loricarioid families. Armbruster (2004, 2008) and Hardman (2005) hypothesize that *Lithogenes* is sister to astroblepids, while Schaefer (2003a) hypothesizes that the genus is sister to loricariids. In a phylogeny with nodes dated by a fossil-calibrated relaxed molecular clock, Lundberg and colleagues (2007) hypothesize that the split between the Astroblepidae and Loricariidae occurred approximately 85–90 Ma (*Lithogenes* was not included in the analysis). If *Lithogenes* is sister to all other loricariids, it must also be at least 65–70 million years old (age of deepest node in the Loricariidae), but if *Lithogenes* is sister to astroblepids, it may be as young as 20 million years (age of basal node in the Astroblepidae).

Two *Lithogenes* species, *L. villosus* (Potaro-Essequibo) and *L. wahari* (Cua-Orinoco), are found in the Guiana Shield, and the third species, *L. valencia*, is thought to be from the Lago Valencia drainage in the coastal mountains of northern Venezuela (date and collector of *L. valencia* types are unknown, and the species is currently thought extinct; Provenzano et al. 2003). The disjunct distribution of *L. villosus* and *L. wahari* on opposite sides of the western Guiana Shield is shared by a number of other rheophilic taxa, and may be the product of sequential capture of proto-Berbice headwaters by north- and west-flowing tributaries of the Orinoco. Dispersal via headwater capture seems a likely avenue for *Lithogenes*, which live in clear, swift-flowing streams and have a specialized pelvic fin morphology enabling them to cling to surfaces and climb vertically (Schaefer and Provenzano 2008).

Other rheophilic loricariid taxa that seem to represent disjunct east-west relicts of a more widespread proto-Berbice distribution include *Lithoxus*, *Exastilithoxus*, *Neblinichthys*, and *Harttia*. *Lithoxus* is represented in the west by *L. jantjæ* in the upper Ventuari River (Orinoco) and in the east by *L. lithoides*, its likely sister species (Lujan 2008) in the Essequibo, upper Branco, and Trombetas. *Exastilithoxus*, the sister of *Lithoxus*, is represented in the west by *E. hoedemani* in the Marauíá River (upper Negro), and in the east by *E. fimbriatus* in the upper Caroni. *Neblinichthys* is represented by *N. pillosus* from the Baria River (lower Casiquiare) and by *N. yekuana* from tributaries of the upper Caroni River. *Harttia* is represented by *H. merevari* in the upper Caura and upper Ventuari Rivers and by *H. platystoma* in the Essequibo River.

Occurrence of *Lithogenes valencia* in the Coastal Range, across the Eastern Venezuela Basin from the Guiana Shield, is more difficult to explain. At no point in the hydrologic

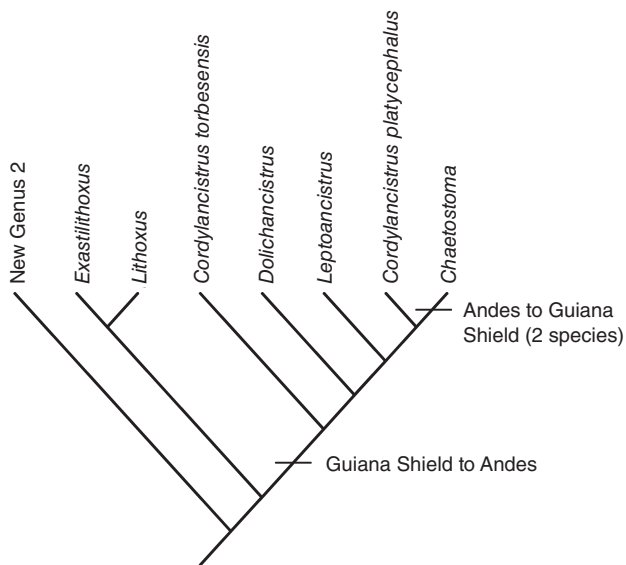


FIGURE 13.4 Hypothesis of generic relationships within the *Chaetostoma* group showing the relative timing of dispersal events between the Guiana Shield and Andean uplands (cladogram modified from Armbruster 2008).

history of the Eastern Venezuela Basin (discussed earlier) was there a period in which high-gradient habitat of the coastal mountain range seems to have been contiguous with that of the Guiana Shield. Periods of low sea level during the Middle Miocene eastward expansion of the Orinoco may be one period in which such contiguity existed. Dispersal from the shield, across the Apure Llanos to the Merida Andes and from there northeast via headwaters to the Coastal Mountain range, represents another possibility. Regardless, the genus seems to have had a much wider distribution at one time, of which the three known localities represent relicts (Schaefer and Provenzano 2008).

If *Lithogenes* is the sister lineage to astroblepids, a Guiana Shield origin is indicated for Astroblepidae, a diverse group of Andean-restricted loricarioids. Likewise, competition with and replacement by more highly derived astroblepids throughout the Merida Andes provides a compelling explanation for the possible extirpation of *Lithogenes* from Andean habitat between the Guiana Shield and the Coastal Mountains. Dispersal of rheophilic taxa from the Guiana Shield to the Andes, followed by radiation along the Andean flanks, is a pattern also apparent in the ancistrin clade comprising *Chaetostoma*, *Cordylancistrus*, *Dolichancistrus*, *Leptoancistrus*, *Exastilithoxus*, *Lithoxus*, and New Genus 2. New Genus 2 is known only from the upper Orinoco of Venezuela. In a phylogenetic study of morphological characters (Armbruster 2008), it was recovered as sister to two clades: *Exastilithoxus* + *Lithoxus* and the *Chaetostoma* group (*Chaetostoma* + *Cordylancistrus* + *Dolichancistrus* + *Leptoancistrus*; Figure 13.4).

Exastilithoxus and *Lithoxus* are endemic to the Guiana Shield, but all except two species of *Chaetostoma* are distributed across Andean drainages ranging from Panama to southeastern Peru. Species of *Cordylancistrus*, *Dolichancistrus*, and *Leptoancistrus* are distributed largely across the Northern Andes of Panama, Colombia, and Venezuela, although two species currently placed in *Cordylancistrus* (*C. platycephalus* and an undescribed species) are known from the Napo and Marañón of Ecuador and Peru. *Cordylancistrus torbesensis* is basal within the *Chaetostoma* group (Figure 13.4), and it hails from southeastern

slopes of the Merida Andes, across the Apure Llanos from the northwestern corner of the Guiana Shield. The distribution of sister clades across the Guiana Shield, a basal species in an adjacent region of the Andes, an intermediate radiation in the Northern Andes, and derived taxa across the Andes from north to south, support a Guiana Shield origin for the *Chaetostoma* group. This largely Andean radiation has even contributed two species back to the ancistrin fauna of the Guiana Shield. *Chaetostoma jegui* and *C. vasquezi* are the only two non-Andean *Chaetostoma*, and they are present on the respective southern and northern slopes of the western Guiana Shield. *Chaetostoma jegui* was described from the Uraricoera River (Branco) and *C. vasquezi* from the Caura and Caroni (Orinoco). Derived placement of both these species within *Chaetostoma* is supported by the presence of a fleshy excrescence behind the head (Armbruster 2004; Salcedo 2006).

Corymbophanes is another genus whose basal relationships within Loricariidae and narrowly endemic range suggest that it might be a relict. Armbruster (2004, 2008) recovered *Corymbophanes* as sister to all other hypostomines, and the two known species of *Corymbophanes* are known only from the Potaro River above Kaieteur Falls, where they are sympatric with *Lithogenes villosus* (Armbruster et al. 2000). No ancistrins are present in the upper Potaro, likely because of their restriction to downstream habitats by Kaieteur Falls, a 226 m drop in the Potaro River over a scarp of the Guiana Shield uplifted in the Oligocene (Table 13.1).

The most basal loricariid subfamily (if *Lithogenes* is not a loricariid) is the Delturinae (Montoya-Burgos et al. 1997; Armbruster 2004, 2008), which is known only from swift rivers of the southeastern Brazilian tributaries of the Brazilian Shield (Reis et al. 2006). With *Lithogenes* and the Delturinae in shield regions, it could be speculated that at least the loricariids (or loricariids + astroblepids) originated in the shields and subsequently spread through the rest of northern South and southern Central America. We doubt that the current ranges of the Lithogeninae and Delturinae represent the full historical distributions of these taxa, and suggest that the modern ranges represent relictual distributions. The fact that these two basal taxa are on opposite sides of the shield regions suggest that they or their ancestors had a range that may have included at least both shields. Origin of the Loricariidae in the shield regions is consistent with the hypothesis (e.g., Galvis, 2006) that shield areas were the most concentrated areas of high-gradient aquatic habitat prior to significant uplift of the Andes. Loricariids share many elements of their highly derived morphology with rheophilic specialist taxa in other parts of the world (e.g., sucker-like mouth with *Garra* and balitorid species in Asia and *Chiloglanis* in Africa, and encapsulated swim bladders with *Glyptothorax*, *Glyptosternum*, and *Pseudocheneis* in Asia; Hora 1922), indicating the selective pressures required for origination of these structures and supporting the origin of Loricariidae in high-gradient habitats (Schaefer and Provenzano 2008).

Conclusions

The Prone-8 biogeographic patterns of the Guiana Shield, coupled with more ancient drainage patterns within the Amazon and Orinoco basins, provide a conceptual framework upon which to build phylogeographic hypotheses for stream organisms in northern South America. The Guiana Shield not only is an island of upland habitat, but also shares extensive biogeographic connections with upland habitats of the Brazil-

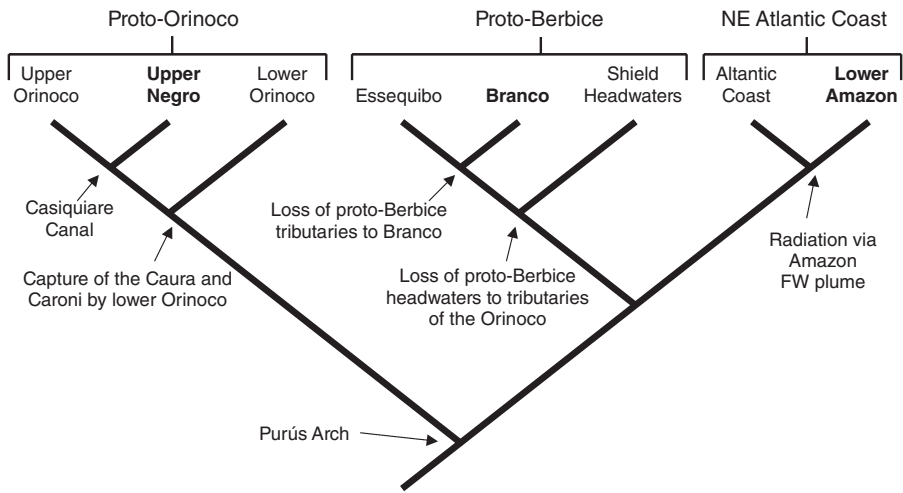


FIGURE 13.5 Null hypothesis of areal relationships among Guiana Shield fishes based only upon hydrologic history. Basal node represents the historical continental divide between eastern and western drainages at the Purús Arch. Terminal nodes represent modern river drainages, with typeface indicating major modern drainage basin: boldface, Amazon River; lightface, Orinoco River. Three major clades of modern river drainages (proto-Orinoco, proto-Berbice, and Northeast Atlantic Coast) represent historical contiguity and regional affinities. Historical geologic and hydrologic events at internal nodes labeled accordingly.

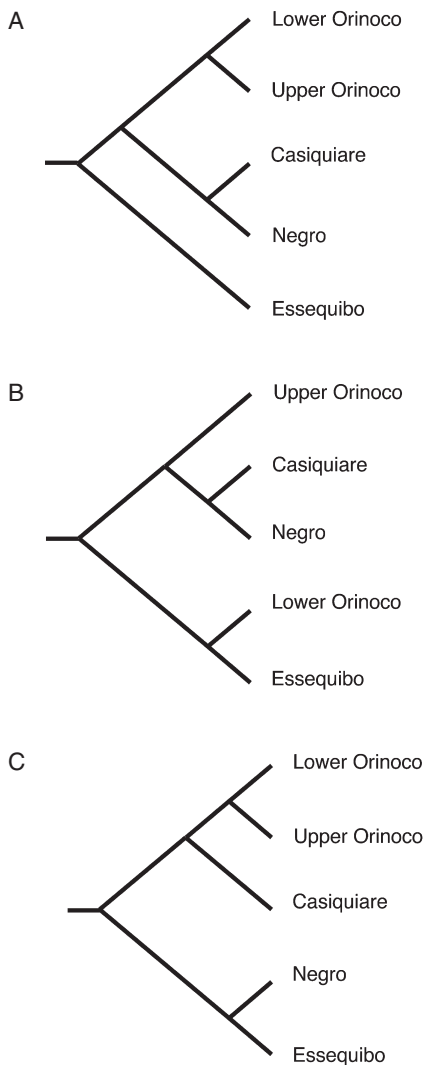


FIGURE 13.6 Three different biogeographic hypotheses based on differential use of connections in the Prone-8. A. Hypothesis based on current drainage patterns. B. Hypothesis if the Mazaruni-Caroni, Cuyuni-Caroni, or Western Atlantic Coastal Connections were used. C. Hypothesis considering the Casiquiare to be Orinoco in origin.

ian Shield, the Andes, and the Coastal Mountains. Distributions of loricariid taxa suggest that connections to these other areas have been important, but that within the Guiana Shield there has been little mixing of upland faunas via the Western Atlantic Coastal and Caroni–Cuyuni/Mazaruni corridors. Most distributions within the Guiana Shield can be explained via current watershed boundaries, stream-capture events in the uplands of larger systems, and/or ancient river systems such as the proto-Berbice.

Because of temporal fluctuations in these connections and their differential use by various taxa, there is no single hypothesis explaining biogeographic patterns across the Guiana Shield and neighboring uplands. We present a null hypothesis for biogeographic patterns based solely on our descriptions of basin evolution and geologic evidence of historical watershed boundaries (Figure 13.5). Differential use of modern corridors of the Prone-8 can obscure these relationships, however, and give rise to a variety of divergent phylogeographic patterns. The disjunct distribution of *Lithogenes*, for example, could represent relicts from a broader Oligocene distribution, or it could be due to more recent distribution via the proto-Orinoco, proto-Caura, or proto-Berbice. Figure 13.6 provides examples of three such alternative phylogeographic patterns.

Multiple biogeographic hypotheses described herein work for most taxa of the Guiana Shield, but no single explanation works for all taxa. Diverse, species-level phylogenies will be required to work out the timing and relative importance of

proposed corridors. Further investigations of Guiana Shield biogeographic patterns will require genetic data sets that can be subjected to molecular-clock analyses, and studies of upland taxa are especially important because of their frequently smaller ranges and corresponding potential for finer-scale resolution. The timing and dispersal rates of the *Chaetostoma* group, for example, from the Guiana Shield to the Andes and back again offer an intriguing opportunity to understand not only the relative importance of the Andes as a novel upland habitat, but also more general mechanisms of upland fish dispersal and evolutionary radiation. In the modern era of advanced scientific understanding, many discoveries of primitive taxa and ancient biogeographic patterns are still waiting to be made in the Guiana Shield, each of which is as exciting as the fantastic visions in Doyle's *The Lost World* (1912).

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