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Diversity and Phylogeny of Neotropical Electric Fishes (Gymnotiformes)

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1. Introduction to Gymnotiform Diversity

The evolutionary radiations of Neotropical electric fishes (Gymnotiformes) provide unique materials for studies on the evolution of specialized sensory systems and the diversification of animals species in tropical ecosystems (Hopkins and Heiligenberg 1978; Heiligenberg 1980; Heiligenberg and Bastian 1986; Moller 1995a; Crampton 1998a; Stoddard 1999; Albert 2001, 2002). The teleost order Gymnotiformes is a clade of ostariophysan fishes most closely related to catfishes (Siluriformes), with which they share the presence of a passive electrosensory system (Fink and Fink 1981, 1996; Finger 1986). Gymnotiformes also possess a combined electrogenic–electroreceptive system that is employed for both active electrolocation, the detection of nearby objects that distort the self-generated electric field, and also electrocommunication, the signaling of identity or behavioral states and intentions to other fishes (Carr and Maler 1986). Active electroreception allows gymnotiforms to communicate, navigate, forage, and orient themselves relative to the substrate at night and in dark, sediment-laden waters, and contributes to their ecological success in Neotropical aquatic ecosystems (Crampton and Albert 2005). The species-specific electric signals of gymnotiform fishes allow investigations of behavior and ecology that are simply unavailable in other groups. Because these signals are used in both navigation and mate recognition (i.e., prezygotic reproductive isolation) they play central roles in the evolutionary diversification and ecological specialization of species, as well as the accumulation of species into local and regional assemblages.

The derived features of electrosensory and electrogenic structures not withstanding, patterns of diversity in gymnotiform fishes are similar to those of many diverse tropical taxa. Gymnotiform diversity is especially pronounced at the species level, and the group is considerably more diverse than has previously been recognized. About 78%, or 135 of the 173 known gymnotiform species, have been formally described, and perhaps half again as many species remain undiscovered in the wild. Gymnotiforms are widely distributed throughout the humid Neotropics, from southern Mexico (15°N) to northern Argentina (36°S), with representatives in Middle and South America, and in both cis- and trans-Andean basins. The Amazon–Orinoco–Guianas superbasin is the center of diversity for the group, from where the majority of gymnotiform genera (77%) and species (73%) may be found. These geographic distributions allow comparisons of divergence times calculated from independent molecular and geological datasets, and the testing of hypotheses regarding the role of geography in the origin and accumulation of species diversity. Gymnotiform clades are ancient and many genera are distributed in polyphyletic regional species assemblages.

A central theme of this chapter is that an evolutionary understanding of electric signaling in gymnotiform fishes requires knowledge of signal diversity, ecology, biogeography, and phylogenetic interrelationships—all at the species level. As in the evolutionary analysis of any taxon the main features in the phylogeny of electric signaling arise from patterns in cladogenesis (speciation) and anagenesis (adaptive change), processes that operate within and among species. In this chapter we review the current state of knowledge about gymnotiform taxonomic and species diversity and the diversity of phenotypic specializations associated with electrogenesis and active electroreception. These primary taxonomic and phylogenetic observations are used to examine patterns of evolution in body size and shape, of the electric organs and electric organ discharges (EODs), and of habitat use. We conclude this chapter with a review of recent work on the biogeography and historical ecology of gymnotiforms and a summary of recent findings on the origins and maintenance of species-rich gymnotiform faunas.

2. Taxonomic and Species Diversity

The order Gymnotiformes is considerably more diverse than has previously been recognized, with the number of valid species having increased from 94 to 135 in the past 10 years (Fig. 13.1). New methods of sampling, identifying, and collecting electric fishes in the wild have unveiled numerous species in previously unexplored habitats and regions (Crampton 1996a, 1998a; Hagedorn and Keller 1996; Lundberg et al. 1996; Albert and Crampton 2001; Albert et al. 2005a). The use of new techniques for characterizing morphology, and genetic differences have demonstrated that much of what was once regarded as intraspecific variation in fact represents interspecific differences (Albert and Miller 1995; Campos-da-Paz and Costa 1996; Fernandes-Matioli et al. 1998a; b, 2000; Albert et al. 1999; Albert and Crampton 2001, 2003a; Fernandes-Matioli and de Almeida-Toledo 2001; Crampton and Albert 2003; Crampton et al. 2004a, b, 2005). Compilations of the numbers of valid (described) and manuscript (undescribed) gymnotiform genera and species are provided in Tables 13.1 and 13.2. Many of the undescribed species known from museum collections are being described as of this writing. Extrapolating from current rates of discovery

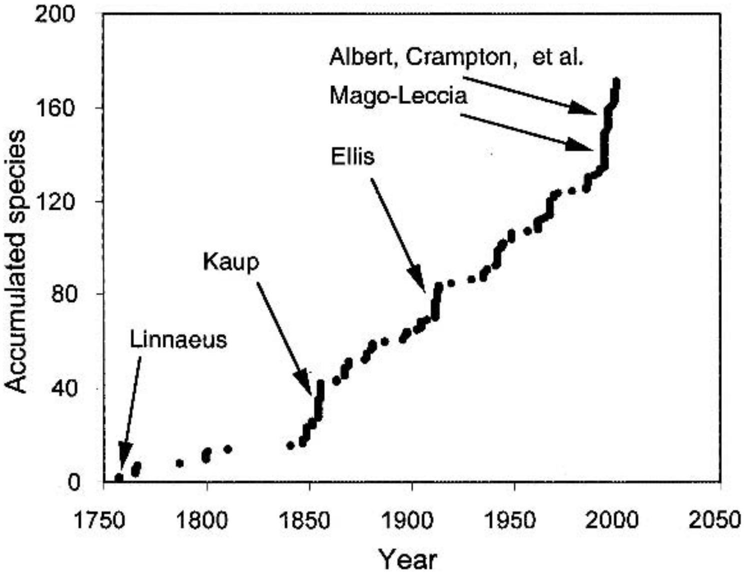


FIGURE 13.1. Accumulation of gymnotiform species from Linnaeus to the present. Note the curve is not approaching an asymptotic value, indicating the relatively incomplete state of knowledge of gymnotiform species diversity.

50 to 100 additional species are anticipated from newly explored field localities in tropical America.

Histories of the classification of gymnotiform fishes are provided in Campos-da-Paz and Albert (1998) and Albert (2001). A key to 28 genera is provided in Albert (2001) and diagnostic features of three genera subsequently recognized as valid are provided in the original citations (*Megadontognathus,* Mago-Leccia 1994; *Stegostenopos,* Triques 1997; *Humboldtichthys,* Gayet and Meunier 2000).

TABLE 13.1. Gymnotiform families with genus and species diversity estimates.

		Species			
Family	Genera	Valid	MS	Total	Spp./Genus
Apteronotidae	14	45	16	61	4.7
Gymnotidae	2	33	3	36	18.0
Hypopomidae	7	16	13	29	4.1
Rhamphichthyidae	3	12	0	12	4.0
Sternopygidae	6	29	6	35	5.8
Total	32	135	38	173	7.3

Valid, published and not junior synonym. MS, manuscript names (undescribed). Taxa are arranged alphabetically.

TABLE 13.2. Gymnotiform genera with original citation and species diversity estimates.

Family	Genus	Author	Date	Species		
				Valid	MS	Total
Apteronotidae	*Adontosternarchus*	Ellis	1912	4	2	6
	Apteronotus s.s.	Lacépède	1800	13	2	15
	"Apteronotus"	—	—	6	2	8
	Compsaraia	Albert	2001	1	2	3
	Magosternarchus	Lundberg, Cox, and Albert	1996	2	0	2
	Megadontognathus	Mago-Leccia	1994	2	0	2
	Orthosternarchus	Ellis	1912	1	0	1
	Parapteronotus	Albert	2001	1	0	1
	Platyurosternarchus	Mago-Leccia	1994	1	0	1
	Porotergus	Ellis	1912	2	0	2
	Sternarchella	Eigenmann	1905	4	2	6
	Sternarchogiton	Eigenmann and Ward	1905	1	2	3
	Sternarchorhamphus	Eigenmann	1905	1	0	1
	Sternarchorhynchus	Castelnau	1855	6	3	9
	n. Gen.	—	—	0	1	1
Gymnotidae	*Electrophorus*	Gill	1864	1	0	1
	Gymnotus	Linnaeus	1758	32	3	35
Hypopomidae	*Brachyhypopomus*	Mago-Leccia	1994	7	12	19
	Hypopomus	Gill	1864	1	0	1
	Hypopygus	Hoedeman	1962	2	1	3
	Microsternarchus	Fernàndez-Yépez	1968	1	0	1
	Racenisia	Mago-Leccia	1994	1	0	1
	Stegostenopos	Triques	1997	1	0	1
	Steatogenys	Boulenger	1898	3	0	3
Rhamphichthyidae	*Gymnorhamphichthys*	Ellis	1912	4	0	4
	Iracema	Triques	1996b	1	0	1
	Rhamphichthys	Müller and Troschel	1848	7	0	7
Sternopygidae	*Archolaemus*	Korringa	1970	1	0	1
	Distocyclus	Mago-Leccia	1978	2	0	2
	Eigenmannia	Jordan and Evermann	1896	8	3	11
	Humboldtichthys†	Gayet and Meunier	2000	1	0	1
	Rhabdolichops	Eigenmann and Allen	1942	8	2	10
	Sternopygus	Müller and Troschel	1849	9	1	10
Total				135	38	173

MS, manuscript names (undescribed). Taxa are arranged alphabetically by family and genus.

Gymnotiform families are recognized on the basis of the presence or absence of a caudal fin, dorsal organ (i.e., "dorsal thong"), oral teeth, and the shape of the head and snout. The families Gymnotidae and Electrophoridae were combined by Albert and Campos-da-Paz (1998). Salient diagnostic characters for families and genera are illustrated in Figure 13.2.

Many gymnotiform genera are recognized from features of head morphology and the oral jaws, especially the relative shape and proportions of the snout and mouth. As a result, the extent to which the current taxonomy of gymnotiform genera expresses morphological diversity strongly emphasizes trophic speciali-

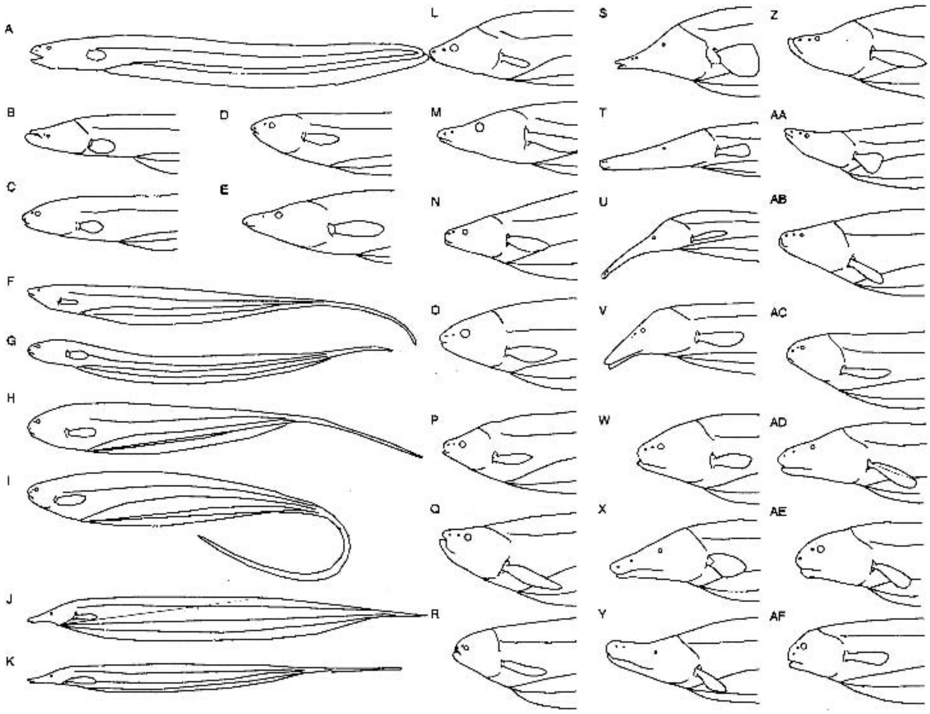


FIGURE 13.2. Line drawings of specimens representing 27 gymnotiform genera in profile, illustrating some important features used in identifications. Drawings not to scale. (**A**) *Electrophorus electricus*, (**B**) *Gymnotus mamiraua*, (**C**) *Microsternarchus bilineatus* (head), (**D**) *Brachyhypopomus occidentalis*, (**E**) *Hypopomus artedi*, (**F**) *M. bilineatus* (body), (**G**) *Racenisia fimbriipinna*, (**H**) *Hypopygus lepturus*, (**I**) *Steatogenys elegans*, (**J**) *Rhamphichthys marmoratus*, (**K**) *Gymnorhamphichthys rondoni*, (**L**) *Sternopygus xingu*, (**M**) *Archolaemus blax*, (**N**) *Distocyclus conirostris*, (**O**) *Eigenmannia humboldtii* (200 mm), (**P**) *E. humboldtii* (350 mm), (**Q**) *Rhabdolichops troscheli*, (**R**) *Adontosternarchus sachsi*, (**S**) *Sternarchorhamphus muelleri*, (**T**) *Orthosternarchus tamandua*, (**U**) *Sternarchorhynchus oxyrhynchus*, (**V**) *Platyurosternarchus macrostomus*, (**W**) *Apteronotus albifrons*, (**X**) *Apteronotus leptorhynchus*, (**Y**) *Parapteronotus hasemani* (mature male), (**Z**) *Magosternarchus duccis*, (**AA**) *Magosternarchus raptor*, (**AB**) *Sternarchella schotti*, (**AC**) *Sternarchella sima*, (**AD**) *Compsaraia compsa*, (**AE**) *Porotergus gimbeli*, (**AF**) *Sternarchogiton nattteri*.

zations. This bias may be observed in the numbers of species per genus among gymnotiform families, in which the Gymnotidae is much less divided into genera than are the other families (Table 13.1). Diversity of head and snout morphology also results from pronounced sexual dimorphism in many species of Apteronotidae in which individuals engage in male–male conflict. Sexual dimorphism in Apterontoidae has historically resulted in an overestimation of the number of certain apteronotid genera and species; for example, the nominal taxon *"Oedemognathus exodon"* is now known to a sexually mature male of *Sternarchogiton nattereri,* and the nominal taxon *"Apteronotus anas"* is a sexually mature male of *Parapteronotus hasemani* (Cox-Fernandes 1998a; Albert 2001; Cox-Fernandes et al. 2002).

2.1 Gymnotidae

Gymnotids may be distinguished from other gymnotiforms by the following unique combination of characters: a cylindrical body with the adult body depth 55% to 90% the body width at the anal-fin origin, the absence of cranial fontanels on the dorsal surface of the head of adults, a very long body cavity with 31 to 51 (more than 100 in *Electrophorus*) precaudal vertebrae, and the absence of displaced hemal spines at the posterior end of the body cavity. The Gymnotidae is represented by two genera. *Gymnotus* is the most diverse gymnotiform genus, with 32 described and at least three additional undescribed species (Campos-da-Paz 2003; Albert and Crampton 2003a; Albert and Crampton 2003a; Albert et al. 2005b). *Gymnotus* species occur in all major river systems in the humid Neotropics and inhabit a wide variety of lowland aquatic habitats. *Gymnotus* is the most geographically widespread of all gymnotiform genera, including the full range of the order (Albert and Crampton 2003a). The type species *Gymnotus carapo* (L) is distributed throughout the Amazon and Orinoco Basins (below 500 m), the Island of Trinidad, the drainages of the Guyanas Shield, and the Atlantic drainages of northeastern Brazil. Adult body size in *Gymnotus* ranges almost an order of magnitude, from 80 to 160 mm in mature specimens of *G. coropinae* from the Amazon Basin, to 1 m in *G. inaequilabiatus* from the Rio Paraná drainage. *Gymnotus* species are all aggressive nocturnal predators of fishes and other small aquatic animals, and most are also territorial (Black-Cleworth 1970; personal observation). Adult males of the small-bodied species *G. coropinae* (90 to 120 mm total length) guard territories in undercut banks of small rainforest streams, spaced at intervals of about 1.0 to 1.5 m (J. Albert and P. Moller, personal observation). The males of at least three *Gymnotus* species form nests and guard larvae (Crampton and Hopkins 2005). *Gymnotus carapo* is reported to mouth brood its eggs and larvae (Kirschbaum and Wieczorek 2002). Most if not all *Gymnotus* species utilize aerial respiration in hypoxic conditions (Liem et al. 1984; Crampton 1998b).

The monotypic *Electrophorus electricus* is unique among gymnotiforms in possessing a strong electric discharge of up to 600 V in mature specimens (Bennett 1971). *Electrophorus electricus* is also unique among gymnotiforms in possessing a vascularized oral respiratory organ, a body cavity extending to the caudal tip of the body (i.e., no postcelomic "tail"), the continuous addition of vertebrae throughout life, and three anatomically distinct hypaxial electric organs; the Main, Hunter's, and Sachs organs. *Electrophorus electricus* grows to the largest body size among gymnotiforms, attaining a total length more than 2

m. A specimen of 7 feet 4 inches (2.24 m) is reported by Ellis (1913) from Guyana. Males achieve larger body size, attaining reproductive maturity at about 120 cm total length, whereas females mature at about 70 cm (Assunção and Schwassman 1995). Specimens of *Electrophorus* have been maintained alive in aquaria for more than 20 years.

2.2 Hypopomidae

Hypopomids may be distinguished from other gymnotiforms by the following unique combination of characters: short snout, no oral teeth, tubelike infraorbital bones, anterior nares located outside gape; anal-fin origin below or posterior to pectoral-fin base; no caudal fin or dorsal organ. The family Hypopomidae is represented by seven genera. *Brachyhypopomus* is the most diverse hypopomid genus, with 7 described and at least 12 additional species as yet undescribed from localities throughout tropical South America and Panama (Albert and Crampton 2003b). *Brachyhypopomus* species occur in all major river systems in the humid Neotropics and inhabit a wide variety of lowland aquatic habitats. *Hypopomus* is known from a single species, *H. artedi*, which is endemic to the Guyanas Shield. *Hypopygus* is represented by three species; *H. lepturus* from the Amazon, Orinoco, and Guianas regions; *H. neblinae* from the Guianas, Rio Negro, and Amazon Basins; and a recently discovered new species from the Venezuelan Amazon (Crampton and Albert, personal observation). *Hypopygus* is the smallest-bodied gymnotiform taxon, attaining reproductive maturity at 50 to 90 mm total length (Nijssen and Isbrücker 1972; Crampton and Albert, personal observation). *Microsternarchus* is known from a single described species, *M. bilineatus*, which is distributed in the Amazon, Orinoco, and Guianas basins. Substantial genetic variation has been reported in both *Hypopygus* and *Microsternarchus* and the actual species diversity of these taxa is underappreciated (Aadland et al. 2003). *Racenisia* is represented by a single described species, *R. fimbriipinna*, known only from the Guianas region of Venezuela and Brazil (Mago-Leccia 1994; F. Lima, personal communication). *Stegostenopos* is represented by a single described species, *S. cryptogenys*, which is known from the Rio Negro basin of Brazil (Triques 1997) and Venezuela (Crampton personal observation), and which has also been recently found in blackwater streams in the Western Amazon of Peru (Albert personal observation). All species of *Hypopygus*, *Microsternarchus*, *Racenisia*, and *Stegostenopos* are restricted to the slowly moving waters or pools of terra firme streams. *Steatogenys* is represented by three species, including *S. elegans*, which inhabits large rivers and whitewater and blackwater floodplain systems; *S. ocellatus*, which inhabits blackwater floodplain systems, and *S. duidae*, which is restricted to terra firme forest streams (Crampton et al. 2004a). Whereas *S. elegans* occurs in Amazon and Orinoco basins and parts of the Guianas, and *S. duidae* occurs in the Amazon and Orinoco Basins, *S. ocellatus* is restricted to the Upper Amazon basin (Crampton et al. 2004a).

2.3 *Rhamphichthyidae*

Rhamphichthyids may be distinguished from other gymnotiforms by the following unique combination of characters: a highly elongate snout, a small mouth, no teeth in oral jaws, infraorbital canal present as a single membranous tube, location of anterior nares entirely within gape, anterior narial pore sessile, and absence of a caudal fin or dorsal organ. The family Rhamphichthyidae is represented by three genera. *Rhamphichthys* is known from seven species, *Gymnorhamphichthys* from four described species, and *Iracema* from one described and one undescribed species (Ferraris 2003). The species-level taxonomy of *Rhamphichthys* is perhaps presently the least well understood among Gymnotiformes with confusions as to species boundaries and the nature of intraspecific variation versus interspecific differences (Campos-da-Paz and Paepke 1994; Triques 1999; Albert 2001).

2.4 *Sternopygidae*

Sternopygids may be distinguished from other gymnotiforms by the following unique combination of characters: multiple rows of small, villiform (brushlike) teeth on premaxilla and dentary; relatively large eye (diameter equal to or greater than distance between nares); large baglike infraorbital bones with expanded bony arches; anterior nares located outside the gape; anal-fin origin at isthmus; absence of urogenital papilla; no caudal fin or dorsal organ. The Sternopygidae is represented by five genera (Albert 2003b). *Archolaemus* is known from a single described species (*A. blax*) that inhabits rapids in Amazonian black and clear water rivers. *Distocyclus* is known from two species, *D. conirostris* from Amazonian white water rivers and *D. goajira* from the trans-Andean Maracaibo, Magdalena, and Baudo (Pacific slope) basins. *Eigenmannia* is the most species-rich nominal sternopygid genus, with eight described and at least three undescribed species currently known, ranging from the Pacific Slope and Magdalena basins of Colombia throughout the Orinoco–Amazon basin, to the La Plata basin of Argentina. The monophyly of *Eigenmannia* is uncertain and there is some evidence that the type species of the genus *E. virescens* is phylogenetically closer to *Rhabdolichops* than to *E. humboldtii* (Albert 2001). A species of *Eigenmannia* is the only gymnotiform known to inhabit caves (Triques 1996a). *Rhabdolichops* is known from eight described and at least two undescribed species, from the Amazon, Orinoco and Guyanas regions, all of which inhabit large rivers (Albert and Crampton, personal observation). Several *Rhabdolichops* species are planktivorous with well-developed gill rakers and others feed on small aquatic invertebrates (Lundberg and Mago-Leccia 1986; Crampton 1996b). *Sternopygus* is known from nine described at least one undescribed species. *Sternopygus* exhibits the largest geographical range of the family, extending beyond that of *Eigenmannia* into Panama and into the Rio Salgado basin in the State of Ceará in Northeastern Brazil (Albert 2001). *Sternopygus macrurus* is the most widely distributed and most eurytopic of all gymnotiform species, inhabiting all hydrogeographical regions of tropical South America and most lowland aquatic habitats (Hulen et al. 2005).

2.5 Apteronotidae

Apteronotids may be distinguished from other gymnotiforms by the presence of a caudal fin and a fleshy dorsal organ, the latter of which has often been interpreted as a modified adipose fin. These two features led previous workers to the conclusion that apteronotids are primitive gymnotiforms (Kaup 1856; Chardon and de la Hoz 1974; Triques 1993; Gayet et al. 1994). The family Apteronotidae is characterized by much greater morphological diversity than in other gymnotiform families (Fig. 13.2). This is expressed primarily as variation in head structure related to trophic specialization and, in part, to male–male aggression. In at least four separate apteronotid clades (*Parapteronotus hasemani*, *Apteronotus leptorhynchus* + *A. (Ubidia) magdalenensis*, *"Apteronotus" bonapartii*, and *Compsaraia* n. sp. A.) sexually mature males develop elongate jaws (Cox-Fernandes 1998a; Albert 2001; Cox-Fernandes et al. 2002). In *Sternarchogiton nattereri* and in some species of *Sternarchorhynchus*, males develop prominent external teeth on the jaws and snout.

The Apteronotidae is the most speciose family of gymnotiform fishes, with 45 species described at present, allocated to 14 genera, and at least an additional 16 undescribed forms known in museum collections (Albert 2003a). The majority of apteronotid species (47 of 61, 77%) inhabit the deep channels (up to 25 m) of large rivers, a habitat surveyed systematically only in recent years (Lundberg et al. 1987, 1996; Crampton 1996b, 1998a; Albert 2001, 2003a). As a result, many apteronotid species were until recently rare or unknown in museum collections.

3. Phylogenetic Overview of Gymnotiformes

There have been four cladistic studies of interfamily relationships among Gymnotiformes. Based on analyses of morphological data, Triques (1993) and Gayet et al. (1994) place Apteronotidae as basal among gymnotiforms, and regard the presence of the caudal fin in apteronotids as primitive. Alves-Gomes et al. (1995) present the first analysis of molecular data, using 718 aligned base pairs of ribosomal mitochondrial DNA, including 211 informative sites among 19 gymnotiform taxa. In combination with analysis of characters of the electromotor system they conclude that *Sternopygus* is the basal gymnotiform taxon, and that this taxon retains a primitive lack of a jamming avoidance response (JAR). The preferred topology of Alves-Gomes et al. (1995, fig. 6) is a strict consensus of 32 equally most parsimonious trees recovered using three weighting schemes. This topology is used in the analysis of Alves-Gomes (2001).

The phylogeny of Figure 13.3A is the result of a maximum parsimony anal-

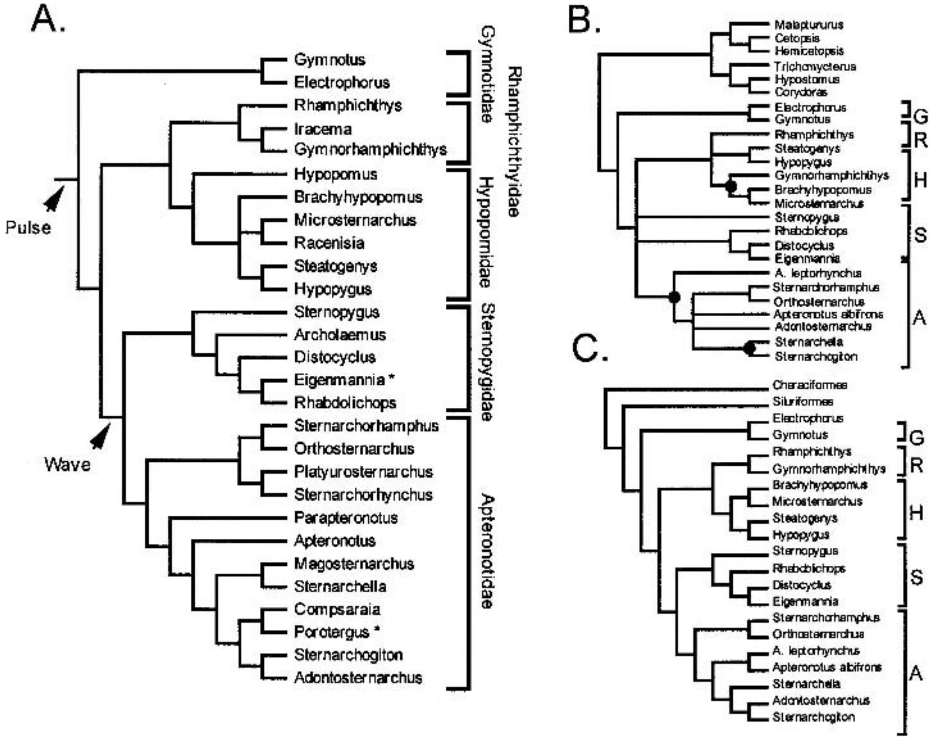


FIGURE 13.3. Alternative hypotheses of gymnotiform interrelationships. (**A**) Tree topology from maximum parsimony analysis of combined morphological and molecular data (Albert 2001). See text for details. *, Generic monophyly uncertain; A, Apteronotidae; G, Gymnotidae; H, Hypopomidae; Pulse, pulse-type EOD; R, Rhamphichthyidae; S, Sternopygidae; Wave, wave-type EOD. Note pulse-type EOD is plesiomorphic and wave-type EOD is derived. (**B**) Tree topology from maximum parsimony analysis of 12S + 16S rRNA (mt DNA). 25 OTUs, 718 bp, 178 informative sites, strict consensus of 9 trees, each l = 733, CI = 0.49, RC = 0.31. (Data from Alves-Gomes et al. 1995, topology from analysis of Albert 2001). *Black circles* indicate clades incongruent with topology of **C**. (**C**) Tree topology from maximum parsimony analysis of morphology + 12S/16S rRNA; 935 characters (CI = 0.57, RC = 0.39) (Albert 2001). Note family-level interrelationships and generic composition are the same in all three analyses.

ysis (Albert 2001) of combined morphological and molecular datasets, including all data then available (Triques 1993; Gayet et al. 1994; Alves-Gomes et al. 1995; Albert and Fink 1996; Sullivan 1997; Albert and Campos-da-Paz 1998). The morphological data in Albert (2001) include 249 characters of squamation, pigmentation, laterosensory canals, morphometrics, fin ray counts, osteology of the oral jaws and dentition, suspensorium, neurocranium, branchial skeleton, pectoral girdle, and axial skeleton, neuromorphology of the whole brain, sensory organs, developmentally defined brain regions, nuclei, tracts, and cranial nerves, and morphology of the musculature and electric organs.

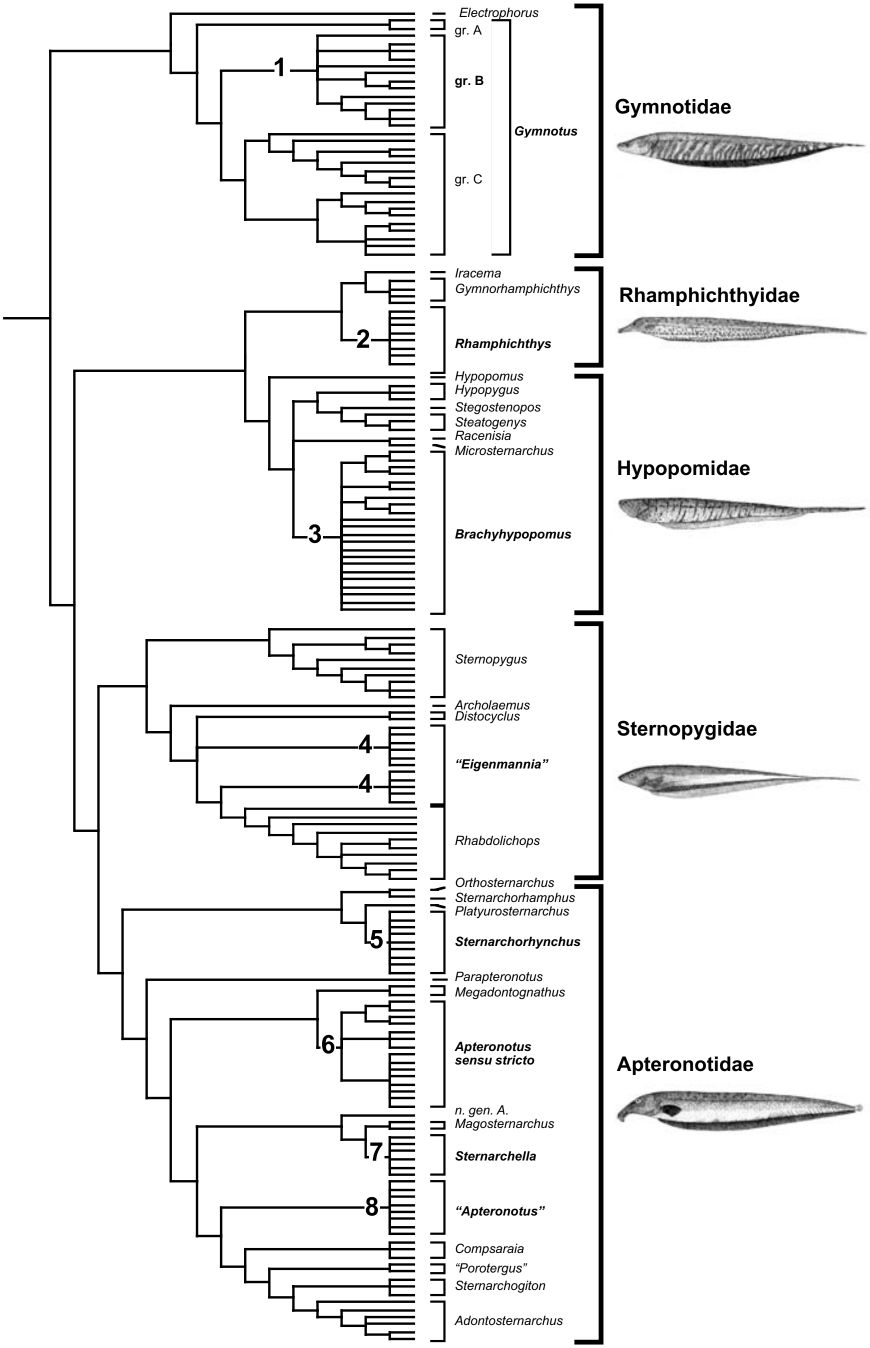
Albert (2001) also reanalyzed the sequence data presented by Alves-Gomes et al. (1995) using maximum parsimony regarding all characters as unordered and weighting transitions equal with transversions. Down-weighting transitions is common in molecular systematic studies when there is evidence that transitional changes are saturated. The rRNA data of Alves-Gomes et al. (1995), however, do not appear to be saturated at these sites (Alves-Gomes et al. 1995, figs. 4 and 5). A strict consensus tree of the nine most parsimonious topologies consistent with the equally weighted mitochondrial sequence data is presented in Figure 13.3B. The single most parsimonious tree resulting from analysis of a combined data matrix (Eernisse and Kluge 1993) of 935 morphological and molecular characters is presented in Figure 13.3C.

These results show strong agreement in the structure of the molecular and morphological datasets. All topologies presented in Figure 13.3A–C support the monophyly of Sternopygoidei, Rhamphichthyoidea, *Steatogenys* + *Hypopygus*, Eigenmannini, Apteronotidae, and Sternarchorhynchinae. The relative positions of *Sternopygus*, Eigenmanninae, and Apteronotidae are unresolved in Figure 13.3B. Nonetheless, the tree provided by the molecular data alone is consistent with the hypothesis that gymnotiform taxa with a wave-type EOD form a monophyletic group, the Sinusoidea (Apteronotidae + Sternopygidae). The trees derived from equally weighted sequence data are inconsistent with the morphological data with respect to the position of *Gymnorhamphichthys* and *Apteronotus leptorhynchus*.

Species diversity and systematics of the Hypopomidae are treated by Sullivan (1997) from a study of molecular sequence and morphological data. These data include 181 parsimony informative sites from 802 aligned base pairs of the 12S and 16S rRNA mitochondrial genes, sequenced from 33 specimens representing 18 rhamphichthyoid and a single gymnotiform outgroup species. Additional data were provided from 1065 aligned base pairs of the cytochrome *b* mitochondrial gene for 12 specimens representing 11 rhamphichthyoid and a single gymnotiform outgroup species. Sullivan (1997) also provides observations on color, external morphology, osteology, meristics, and electric organ morphology for 15 hypopomid species, including 6 undescribed species. The main difference between the topologies of Sullivan (1997) and that of Figure 13.3A is in the position of the Steatogenini (*Steatogenys* + *Hypopygus*); the Steatogenini is included within the Hypopomidae in Figure 13.3A and is the sister taxon to *Rhamphichthys* + *Gymnorhamphichthys* in Sullivan (1997). The monophyly and interrelationships of Hypopomidae is currently unresolved (Albert 2001).

Among gymnotiform family-level taxa there are abundant morphological and molecular data supporting the monophyly of the Rhamphichthyoidea (Rhamphichthyidae + Hypopomidae) and Sinusoidea (Sternopygidae + Apteronotidae). The interrelationships among Gymnotidae, Rhamphichthyoidea, and Sinusoidea are less well supported (Albert 2001). Among the characters used to place Gymnotidae as the sister taxon to other Gymnotiformes are several features that are unique and unreversed in the Sternopygoidei (Rhamphichthyoidea + Sinusoidea); for example, Gymnotidae lacks reduced oral jaws (Albert 2001), fasciculated laterosensory afferents (Albert et al. 1998), and displaced hemal spines at the posterior margin of the body cavity (Albert 2001). However, Sternopygidae is unique among gymnotiforms in possessing the highly developed (plesiomorphic) visual system of other teleost fishes, with large eyes and an accessory optic system (Lazar et al. 1987; Albert et al. 1998). Further, Apteronotidae possesses the plesiomorphic caudal fin of other teleost fishes with a hypural plate and segmented fin rays. Therefore, regardless of the tree topology, the phylogenetic distribution of these features requires a complex history of character evolution involving multiple losses and/or reversals. Maximum parsimony optimization of these features on the tree topology in Figure 13.1 suggests the developed visual system of Sternopygidae and caudal fin of Apteronotidae are atavistic (derived) reversals to the complex (plesiomorphic) teleostean condition. A less parsimonious but possible alternative is that the Sternopygidae retains a primitive (developed) visual system, and the reduced visual system of Gymnotidae, Rhamphichthyoidea, and Apteronotidae was derived independently. By a similar logic, the caudal fin of Apteronotidae could also be a plesiomorphic retention, having been lost independently in Gymnotidae, Rhamphichthyoidea, and Sternopygidae.

Investigations into the species-level diversity and phylogeny of Gymnotiformes are accelerating and the actual dimensions of the fauna are at last becoming clear. Phylogenetic revisions of eight species-rich gymnotiform clades are now being undertaken by the authors to complete the descriptive stage of this research program (Fig. 13.4): 1, *Gymnotus* species—group B (13 spp.); 2, *Rhamphichthys* (8 spp.); 3, *Brachyhypopomus* (22 spp.); 4, "*Eigenmannia*" (11 spp.); 5, *Sternarchorhynchus* (9 spp.); 6, *Apteronotus sensu stricto* (15 spp.); 7, *Sternarchella* (6 spp.); and 8, "*Apteronotus*" *sensu lato* (8 spp.). These eight clades represent 51% of known gymnotiform species and include 39 species with pulse- and 49 species with wave-type EODs. These investigations include: (1) monographic revisions of the alpha taxonomy, species diversity, and geographical distributions based on an exhaustive survey of existing museum materials and from new collections in remote regions; (2) phylogenetic hypotheses of species relationships using morphological and molecular data from all available species; (3) biogeographical analyses testing hypotheses on the role of geomorphology in the origin and accumulation of species diversity; (4) behavioral analyses of intra- and interspecific electric signal differences to test alternative hypotheses on the role of electric signals in the maintenance of species diversity; and (5) investigations into the diversity of electric organ morphology and cellular physiology that underlies EOD diversity.


Electrophorus
gr. A
1
gr. B
Gymnotus
gr. C
Gymnotidae
Iracema
Gymnorhamphichthys
2
Rhamphichthys
Rhamphichthyidae
Hypopomus
Hypopygus
Stegostenopos
Steatogenys
Racenisia
Microsternarchus
3
Brachyhypopomus
Hypopomidae
Sternopygus
Archolaemus
Distocyclus
4
4
"Eigenmannia"
Rhabdolichops
Sternopygidae
Orthosternarchus
Sternarchorhamphus
Platyurosternarchus
5
Sternarchorhynchus
Parapteronotus
Megadontognathus
6
Apteronotus sensu stricto
n. gen. A.
Magosternarchus
7
Sternarchella
8
"Apteronotus"
Compsaraia
"Porotergus"
Sternarchogiton
Adontosternarchus
Apteronotidae

3.1 Age of Taxa

Extant gymnotiform taxa are undoubtedly of considerably antiquity. Estimates of the minimum age of taxa may be inferred directly from fossil evidence and indirectly from age estimates of sister tax, molecular datasets, and biogeographic distributions. These sources of evidence suggest a chronology for gymnotiform evolution with origins and early divergence in the Upper Cretaceous and Lower Tertiary, and the acquisition of essentially modern phenotypic and species diversity by the late Middle Miocene. The following discussion combines information from each of these sources and presents information relevant to the timing of gymnotiform divergences.

The only known fossil gymnotiforms are 10 fragments from the Yecua Formation (Upper Miocene, c. 8 to 10 Ma) in Bolivia, ascribed to *Humboldtichthys* (formerly *Ellisella*) *kirschbaumi* (Gayet et al. 1994, Gayet and Meunier 2000). Although fragmentary, these fossil specimens can unambiguously be identified as Gymnotiformes by highly elongate body and anal fin, and specialized ball-and-socket anal-fin articulation with the pterygiophores (bony fin-ray supports). Because of incomplete preservation, many of these specimens cannot be ascribed to a modern family. In one specimen the caudal portion of the body is preserved with a regenerated caudal appendage and other aspect of morphology diagnostic of the extant sternopygid *Distocyclus*. The holotype of *H. kirschbaumi* shares the presence of a deeply striated opercle with some extant species of *Sternopygus* and *Distocyclus* and can also be placed in the Recent gymnotiform family Sternopygidae (Albert and Fink, in review).

Gymnotiformes is the sister taxon to Siluriformes, which is itself first known from fossil specimens ascribed to modern families (Ariidae, Diplomystidae) in the Campanean (83 to 73 Ma; Benton 1993), setting a minimum date for the origin of the line leading to modern Gymnotiformes. Gymnotiform taxa are entirely restricted to the Neotropics and it was once thought they originated after the final separation of South America from Africa in the Upper Cretaceous (c. 100 Ma; Lundberg 1993). Recent studies on the higher level interrelation-

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FIGURE 13.4. Composite species-level phylogenetic hypothesis of 173 gymnotiform species. Topology from multiple sources, using both morphological and molecular data; Gymnotidae (Albert et al. 2004; J. Albert, W. Crampton, N. Lovejoy, unpublished observations); Rhamphichthyoidea (Rhamphichthyidae + Hypopomidae) (Albert 2001; Sullivan 1997; J. Albert, W. Crampton, D. Thorsen, unpublished observations); Sternopygidae (Albert 2001; Hulen et al. 2004; J. Albert, W. Crampton, S. Correa, unpublished observations); Apteronotidae (Mago-Leccia et al. 1985; Albert 2001; J. Albert and W. Crampton, unpublished observations). Monophyly of *Eigenmannia* and *Porotergus* not confirmed. Numbered clades are polytomies (areas of phylogenetic uncertainty) prioritized for current and future studies: 1, *Gymnotus* species-group B; 2, *Rhamphichthys*; 3, *Brachyhypopomus*; 4, "*Eigenmannia*"; 5, *Sternarchorhynchus*; 6, *Apteronotus sensu stricto*; 7, *Sternarchella*; 8, "*Apteronotus*" *sensu lato*. Species in these eight clades represent of 88 of 173 (51%) known gymnotiforms, including 39 species with pulse- and 49 species with wave-type EODs.

ships of the first two outgroups (Siluriformes and Characiformes) have revealed numerous trans-Atlantic clades in both groups, suggesting origins predating the final breakup of Gondwana (de Pinna 1998; Lundberg 1998; Vari 1998). Because the line leading to modern Gymnotiformes originated before the final breakup of Gondwana the group may have originated in the western portion of Gondwana, in the area of modern northern South America (Albert 2001). It is also possible that gymnotiforms once exhibited a broader distribution, having since become extinct on the eastern portion of Gondwana, in the area of modern Central Africa, or that they were excluded from this region by the prior presence of electrosensory mormyrids.

Alves-Gomes (1999) calculated absolute divergence times among 22 ostariophysan species representing 17 genera and all 5 orders, and including 13 gymnotiform species representing 8 genera and all 5 families. Sequence divergences among 810 base pairs of mitochondrial 12S + 16S rRNA genes were calibrated using data from the ostariophysan fossil record to estimate minimum times of divergence for four clades. Using a constant mutation rate of 0.13% 10^6 years^{-1} for the conserved stretches (stems), Alves-Gomes (1999) estimated minimal divergence times for Siluriphysi (Siluriformes + Gymnotiformes) of 79.39 to 117.56 Ma, and for the sternopygid *Eigenmannia* of 16.7 Ma. Examples of the use of historical biogeography to estimate minimum divergence times in gymnotiforms are provided in Section 6.3.

As in other Neotropical fish groups, the distribution of taxa with cis (east) and trans (west) Andean distributions have proven tremendously useful in estimating the phylogenetic age of taxa (Albert et al. 2005b). There are at least 12 trans-Andean gymnotiform clades, including examples in 6 genera and 4 of the 5 families. These clades are: 1, *Gymnotus cylindricus* + *G. maculosus*; 2, *G. panamensis*; 3, *G. choco* + *G. ardilai*; 4, *G. esmeraldas* + *G. henni*; 5, *Brachyhypopomus occidentalis* + *B. diazi*; 6, *Sternopygus macrurus* + *S. arenatus*; 7, *S. aequilabiatus* + *S. dariensis*; 8, *Eigenmannia virescens*; 9, *E. humboldtii*; 10, *Distocyclus goajira*; 11, *Apteronotus albifrons* + *A. mariae* group; and 12, *A. cuchillo* + *A. (Ubidia) magdalenensis* + *A. rostratus*.

4. Survey of Phenotypic Diversity

4.1 Culteriform Body Plan and Active Electroreception

The body plan of gymnotiform fishes is highly specialized in association with electrogenesis and active electroreception (Bastian 1986; Fink and Fink 1996; Albert 2001). A combination of derived features give gymnotiform fishes a knifelike or "culteriform" body shape. Gymnotiforms achieve propulsion by undulations of their elongate anal fin rather than swimming with alternating constrictions of the axial muscles, as do most fishes. Gymnotiforms also use their pectoral fin for fine adjustments of body position. All gymnotiform fishes possess a highly elongate body, with at least 50 (*Hypopygus*) and as many as

300 (*Electrophorus*) vertebrae, and an elongate anal fin containing 100 to 350 rays. The anal fin extends along the majority of the ventral portion of the body such that the position of the anus lies anterior to the body midlength in adults, often at the branchial isthmus, and sometimes at a vertical with the eye. Each anal-fin ray has a ball-and-socket articulation with the bony supports of the axial skeleton (pterygiophores) facilitating the use of anal-fin undulation in locomotion. All gymnotiform fishes entirely lack dorsal, adipose, and pectoral fins and their bony supports (i.e., pterygiophores, girdles).

All Gymnotiformes possess a unique capacity to regenerate the entire caudal (postcoelomic) portion of the body (Ellis 1913; Anderson and Waxman 1981; Anderson 1987). The postcranial portion of the body is buttressed with numerous and highly branched intermuscular bones. In Rhamphichthyoidea (Rhamphichthyidae + Hypopomidae) and Sternopygidae an elongate caudal appendage (sometimes called the "caudal filament" or "tail") extends beyond the last anal fin ray. This caudal appendage is a complex structure composed of electrocytes, and depending on taxon and extent of regeneration, may include axial and pterygiophore muscles, vertebral centra, neural and hemal spines, intermuscular bones, blood vessels, spinal cord, and spinal nerves (Kirschbaum and Meunier 1981; Albert 2001). In gymnotiforms the caudal fin is either small (Apteronotidae) or absent (other families).

The culteriform body shape facilitates the use of the external body surface as a sensory array. The integument of gymnotiforms is invested with numerous tuberous and ampullary electroreceptor organs, and in at least one species with a wave-type EOD (*A. leptorhynchus*) individuals learn to associate the proprioceptive feedback from bending the tail with increases in the activity of electroreceptors (Bell et al. 1997). Most of the body surface is covered with high frequency–tuned tuberous electroreceptor organs, which in most taxa are most densely arrayed on the surface of the snout (Zakon 1986; Albert 2001). In Apteronotidae tuberous organs are also densely arrayed on the midsagittal dorsal organ (Franchina and Hopkins 1996). In Gymnotiformes the low-frequency–tuned ampullary organs are less densely arrayed over the head and body, and in adults are organized in clusters called "rosettes" of 15 to 20 ampullary organs per cluster in which each cluster is innervated by a single afferent nerve fiber (Zakon 1986). The primary rhombencephalic electrosensory centers of the brain (i.e., the electrosensory lateral line lobe and corpus cerebellum) constitute approximately 50% of the total brain volume (Albert et al. 2000). This hypertrophy of electroreceptive brain structures is accompanied by a substantial reduction in other sensory systems. The eye is small and subdermal in all gymnotiform taxa except two sternopygids genera (*Sternopygus* and *Archolaemus*), and the accessory optic system is absent in all gymnotiforms except the Sternopygidae (Finger and Karten 1978; Lazar et al. 1987). Gymnotiformes do not possess extraoral taste buds, Schreckstoff, or integumental club cells (Albert 2001).

The culteriform body shape also facilitates production of a stereotyped three-dimensional electric field (Rasnow and Bower 1996; Assad et al. 1998). The hypaxial electric organ of gymnotiform fishes extends along 80% to 90% of the fish's body length and generates spatiotemporally complex electric fields and waveforms (Watson and Bastian 1979; Lorenzo et al. 1988; Caputi 1999; Stoddard et al. 1999). The external electric field approximates an oscillating dipole (a dumbbell-shaped field) that envelops the head and tail of the fish with alternating head-positive and head-negative phases that cycle with the EOD repetition rate. A transverse plane of zero voltage is located in the posterior region of the body, near the base of the caudal appendage (caudal end of the anal fin) in most taxa, and at about the level of the lateral-line rami in *Gymnotus*. The field amplitude decays from the body surface with the inverse cube of distance so that the effective range of sensory perception is 5–10 body lengths. Active electroreception is therefore sensitive to objects in the near field only. The electric field results from the weighted sum of individual electrocytes arranged in series and in parallel, with each electrocyte having a potentially different time-waveform and internal resistance (Caputi 1999; Aguilera et al. 2001; Aguilera and Caputi 2003).

4.2 Body Shape and Size Evolution

A combination of functional and phylogenetic considerations suggests that the active electrosensory system of Gymnotiformes has placed strong constraints on the evolution of adaptive diversity. Despite the substantial diversification of Gymnotiformes into numerous family and generic-level taxa and with significant adaptive changes in body size and trophic morphology, no gymnotiform lineage has deviated from the basic culteriform body plan. Active electroreception in Gymnotiformes involves physiological interactions between electrosensory and electrogenic structures in a stable geometric configuration (Caputi 1999). The culteriform body of Gymnotiformes with anal-fin locomotion and a semirigid body surface is required to form and maintain the electroptopic mapping of electroreceptors on the body surface to the primary electrosensory brain centers (Carr and Maler 1986).

Constraints on the phylogenetic diversification of Gymnotiformes are apparent in comparison with that of its sister taxon, Siluriformes (catfishes) (Fink and Fink 1981). There are approximately 3600 species of catfishes currently described, allocated to 436 genera and 37 families with a cosmopolitan distribution, including freshwaters of all continents except Antarctica, and two families that are found in coastal marine tropical and temperate waters worldwide (Eschmeyer 2003). Gymnotiformes, by contrast, are an order of magnitude less diverse in terms of species numbers, and much more conservative in terms of overall morphological and ecological disparity. Sister taxa are by definition of equal age and share the same unique common ancestor. Thus, the disparity species richness, morphological variety, and ecological breadth between Gymnotiformes and Siluriformes is not simply a result of differing clade ages or initial genetic variation.

Patterns of diversity in Gymnotiformes also suggest that the evolution of body size is influenced by EOD type. Adult body size in Gymnotiformes as a whole ranges over an order of magnitude, from as small as 50 mm total length in mature specimens of *Hypopygus* n. sp from the Venezuelan Amazon to more than 2 m in *Electrophorus electricus*. Gymnotiform species with pulse-type EODs are, on the whole, smaller and yet exhibit more size diversity than species with wave-type EODs (Fig. 13.5). The size distribution of species with pulse-type EODs is significantly skewed to smaller sizes (Kolmogorov-Smirnoff test, $p < 0.05$) whereas the size distribution of species with wave-type EODs does not differ significantly from a normal distribution. Constraints on size diversification in taxa with wave-type EODs may arise directly from the physiology of electrogenesis itself, or indirectly from epistatic factors associated with respiration, locomotion, navigation, and communication in the deep river channel habitats that characterize many species with wave-type EODs (Julian et al. 2003). Alternatively, the relatively higher size diversity of gymnotiforms with a pulse-type EOD may reflect the greater age and broader distribution of these taxa, in terms of both habitat and geographical region.

Nevertheless, there has been less net diversification (speciation minus extinction) in gymnotiforms with pulse-type EODs (77 species) as compared to wave-type EODs (96 species). In many deep-channel gymnotiforms with a wave-type EOD, notably species of Eigenmannini and Navajini, the entire body is modified for foraging and locomotion in a flowing environment. In these species the mouth is often terminal and the body cavity is relatively short and slender. The

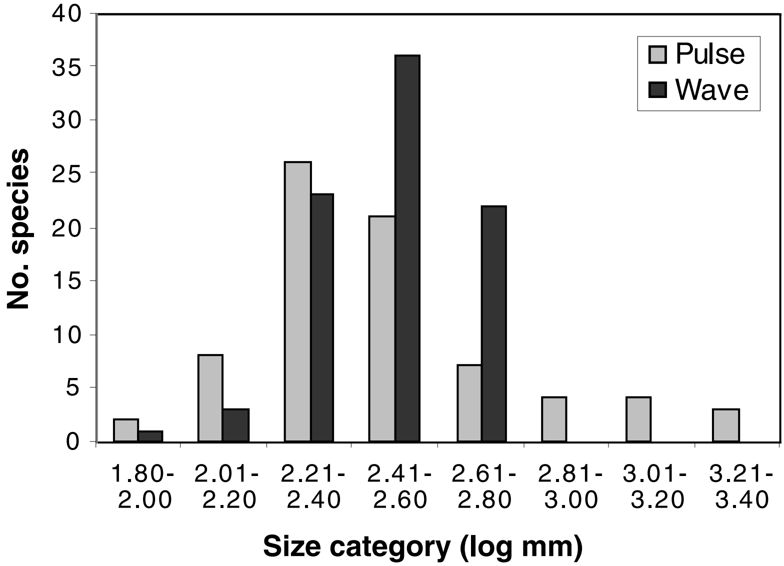

FIGURE 13.5. Size distributions for Gymnotiformes. Maximum total lengths for all described pulse- and wave-type gymnotiform species. Note species with a pulse-type EOD possess a smaller modal and median sizes and a larger body size range.

entire body is strongly compressed laterally, the lateral midbody scales are large, and the squamation is reduced anteriorly and dorsally. In addition, the extent of endosekletal ossification is substantially reduced, through one of several mechanisms including delayed onset of mineralization (i.e., paedomorphosis) and active bone remodeling (Albert 2001).

4.3 Electric Organ and Electric Signal Diversity

Gymnotiform fishes exhibit a wide range of electric organ and EOD specializations (Bennett 1971; Hopkins 1983; Bass 1986; Dye and Meyer 1986). Gymnotiform EODs fall into two main physiologically defined categories: pulse-type EODs comprising a train of relatively short and stereotyped pulses with one to six phases of alternating polarity separated by periods of silence; and wave-type EODs comprising a continuous periodic wave, with one to four phases. The EOD is itself the product of a temporal pattern of electrocyte activation across a regionally differentiated electric organ. Species-specific electric organ discharge patterns may result from differences in several morphological features of the electric organ and its constituent electrocytes: (1) neural innervation patterns and the coordinated activation of electrocyte faces; (2) size and shape of electrocytes at different positions along the body axis; (3) lengths, positions, and number of longitudinally arranged electrocyte tubes; and (4) orientation and position of insulating bands of connective tissue that channel ion flow across the electrocytes membranes within each tube. Of special interest for interspecific comparisons is the axial extent of double-innervated electrocytes (on both anterior and posterior faces) in relation to the magnitude of the first head-negative EOD phase (V1–V2 of Caputi 1999; P0 of Crampton et al. 2003).

The phylogenetic distributions of salient electric organ and EOD characters are summarized in Table 13.3. In two clades (Gymnotidae and Rhamphichthyoidea) electrogenic organs develop from paired bundles of the hypaxial muscle and extend along the entire ventral margin of the body, from below the pectoral fins to the tip of the caudal appendage. Members of these clades retain a plesiomorphic pulse-type EOD and larval hypaxial electric organs into maturity.

TABLE 13.3. Gymnotiform taxa with states of adult electric organ and EOD parameters.

Taxon	Main adult EO	EOD type	Accessory EOs
Apteronotidae	Spinal motoneurons	Wave	None
Gymnotidae	Hypaxial muscles	Pulse	None
Hypopomidae	Hypaxial muscles	Pulse	Several
Gymnorhamphichthys	Hypaxial muscles	Pulse	Mental
Sternopygus	Hypaxial and epaxial muscles	Wave	None
Eigenmanninae	Pterygiophore muscles	Wave	None

See text for descriptions of accessory electric organs.

In Sinusoidea (Apteronotidae + Sternopygidae) the larval hypaxial electric organ degenerates at metamorphosis to be replaced with a derived adult organ and a derived wave-type EOD (Mills et al. 1992; Unguez and Zakon 1998; Albert 2001).

Gymnotids possess hypaxial myogenic electric organs with barrel- or coin-shaped electrocytes. The plesiomorphic condition for gymnotids is a head-positive monophasic pulse type EOD as seen in *E. electricus* (the most basal species) and the two Middle American species of *Gymnotus, G. cylindricus* and *G. maculosus* (Albert and Miller 1995; Kirschbaum 1995; Moller 1995a, fig. 8.8). All South American species of *Gymnotus* possess a derived EOD with two to five phases (Albert 2001; Albert et al. 2003, 2005b). The electric organ of *Gymnotus*, although physically not compartmentalized, exhibits regional specialization in patterns of nervous innervation, size and shape of individual electrocytes, and the rostral extent and number of electrocyte tubes, all of which yield physiological heterogeneities in the electric field. During two decades of laboratory investigations Caputi and colleagues have generated a detailed cellular-level functional model for the physiological and anatomical basis of the complex multiphasic EOD waveform in one species of *Gymnotus*, *G. inaequilabiatus* (Trujillo-Cenóz et al. 1984; Caputi et al. 1989, 1994; Caputi and Aguilera 1996, 2003; Aguilera et al. 2001). This model is summarized by Caputi (1999) and has been used as the basis for understanding the diversity of EOD waveforms observed in other gymnotiform taxa (Caputi et al. 1994; 1998). The electromotor system is repetitively activated by impulselike signals generated by the pacemaker nucleus in the brain stem medulla. This nucleus activates a set of relay cells whose axons descend along the spinal cord and project to electromotor neurons, which, in turn, project to the electrocytes of the electric organ. These relay neurons, electromotor neurons, and electrocytes are layers of a network arranged in a lattice hierarchy, which coordinates the spatiotemporal pattern of postsynaptic and action currents generated by the electrocyte membranes. The size, shape, and configuration of electrocytes within the electric organ vary dorsoventrally and anteroposteriorly, and in some cases are differentiated into morphologically discrete compartments. Neural innervation of the electrocytes may be at either their rostral or caudal faces, or at both faces, depending on the site within the organ and on the species. The depolarization activity of electrocyte faces is synchronized by a synergistic combination of delay lines and coordinated in a precise sequence to produce the orderly recruitment of electromotor neurons according to their position along the spinal cord. The body of the animal filters the electric organ output electrically, and the whole fish is transformed into a distributed electric source.

Electrophorus electricus is unique among gymnotiform fishes in possessing three anatomically distinct electric organs (i.e., Sachs, Hunter's, and Main electric organs), all of which are derived developmentally from a germinal zone located on the ventral margin of the hypaxial musculature (Bennett 1971; Schwassman, personal communication). The specialized electric tissues of *E. electricus* are used as a model system in membrane electrophysiology and biochemistry (Gotter et al. 1998). The Main electric organ and the anterior two thirds of the more ventral Hunter's electric organ generate occasional trains of strong (up to 600 V) discharges. These trains of strong discharges are under voluntary control and are used in aggressive and predatory behaviors. The posterior one third of the Hunter's organ, together with the organ of Sachs lying dorsal and posterior to the other two electric organs, generate a continuous, variable, low-frequency (1 to 5 Hz) weak (1 to 10 V) electric discharge. The continuous weak EOD of *Electrophorus* is a head-positive monophasic pulse that generates the electric field used in navigation and sexual communication (Bass 1986).

Hypopomids possess a single hypaxial myogenic electric organ with barrel-shaped to cigar-shaped electrocytes, and a pulse-type EOD with one to three phases in *Brachyhypopomus*, two phases in *Microsternarchus* and *Racenisia*, and three to five phases in *Hypopygus*, *Steatogenys*, and *Stegostenopos*. Several hypopomids have evolved accessory electric organs that increase the complexity and presumably species specificity of the waveform generated by the summed discharges of the electric organs. Members of the Steatogenini (*Steatogenys*, *Stegostenopos*, *Hypopygus*) are characterized by paired postpectoral organs, which assume different configurations in each genus. *Steatogenys* also has paired villiform mental organs. Both the postpectoral and villiform mental organs are innervated by spinal nerves emerging from the region immediately behind the pectoral fin (Bennett 1971; Moller 1995b, fig. 16.7; D. Thorsen, personal communication). The EOD repetition rate is more stable, and the medullary pacemaker nucleus is larger, in *Steatogenys elegans* which inhabits swiftly flowing large rivers, than in *S. duidae*, which inhabits small, slowly moving streams (Crampton and Albert 2005). At least one (undescribed) species of *Brachyhypopomus* possesses paired accessory electric organs in the opercular region. This appears, however, to be unusual in *Brachyhypopomus*. Accessory electric organs are not known from *Hypopomus*, *Racenisia*, and *Microsternarchus*. Many species of *Brachyhypopomus* display sex differences in the EOD (Hopkins 1972; Stoddard et al. 1999). In *B. pinnicaudatus*, for example, the EOD is different in shape and up to twice as long in mature males as in females or immature males with the peak frequency of the Fourier transform hence being lower. The tail filament also becomes elongated (Hopkins et al. 1990). Hopkins et al. (1990) suggested that the sex difference in EODs has arisen because of female choice for long duration signals. They also observed a proportional decrease in the amplitude of the electric discharge of males of a given body size compared to females and suggested that the production of a long EOD causes a reduction in amplitude. The concluded that males may have evolved longer electric organs with more electrocytes to compensate for the loss of signal amplitude. Recently, it has become clear that some species of *Brachyhypopomus* (Hypopomidae) can rapidly modulate both the duration and amplitude of their EODs. These modulations can occur transiently, in response to a fright stimulus, and, in breeding males, under the influence of the natural circadian rhythm

(Franchina and Stoddard 1998). The presence of males rather than females appeared to stimulate these changes, a pattern observed independently for *B. brevirostris* and *B. beebei* (W.G.R.C., unpublished observation).

Rhamphichthyids possess a hypaxial myogenic electric organ with barrel-shaped to cigar-shaped electrocytes, and a pulse-type EOD with three to five phases. Individual specimens of *Gymnorhamphichthys* also possess a mental accessory electric organ that develops as an anterior extension of the hypaxial musculature along the ventral margin of the head.

Juvenile sternopygids possess the larval hypaxial organ characteristic of other gymnotiforms. *Sternopygus* has in addition to the hypaxial an epaxial organ. Both of these organs extend along the majority of the length of the body and caudal appendage. In the Eigenmanninae the larval hypaxial organ degenerates at metamorphosis and is replaced by an adult electric organ derived from anal-fin pterygiophore muscles. The individual electrocytes of adult sternopygid electric organs are cigar shaped (elongate on the body axis) and innervated on their posterior margin. Sternopygids possess a wave-type EOD characterized by a monophasic hyperpolarization from a negative baseline. Transient and spontaneous modulations of EOD amplitude have been observed in at least two species: *Sternopygus macrurus* (McAnelly et al. 2003) and *S. branco* (Crampton et al. 2004b).

There is considerable variation in EOD repetition rate in the sternopygids. *Sternopygus* generate the lowest rates. One recently described species, *S. branco* (Crampton et al. 2004b), generates EODs at a rate of 24 to 35 Hz, the lowest rate known for any gymnotiform with a wave-type EOD. Other *Sternopygus* species generate EODs from around 40 to 300 Hz (Crampton 1998a). *Sternopygus macrurus* has sexually dimorphic EODs, with females generating EODs at approximately twice the frequency of males (approximately 40 to 80 Hz in males, 80 to 160 Hz in females). EOD sexual dimorphism was not noted in *S. branco* (Crampton et al. 2004b). All Sternopygidae have simple sinusoid-like discharges with no complex inflections or extra phases contained within each discharge cycle. The dominant component of the Fourier power spectra of sternopygids is invariably the fundamental frequency.

In Apteronotidae the larval hypaxial organ also degenerates at metamorphosis, where it is replaced in adults by proliferation and elongation of the spinal electromotor neurons that innervated the larval organ (Kirschbaum 1977). The neurogenic electric organ of adult apteronotids facilitates a high frequency wave-type EOD. Apteronotidae generate the highest EOD repetition rates (up to 2200 Hz), have the largest medullary pacemaker nucleus, and possess many other derived features of the nervous system associated with living in deep river channels and other fast-flowing environments (Crampton 1998a; Albert 2001). Waveform shape varies considerably in the Apteronotidae, from a simple sinusoid-like cycle to complex waveforms with more than one peak in a single cycle. In many but not all species the dominant component of the Fourier power spectrum is the fundamental frequency.

4.4 Gymnotiform Chromosomal Diversity

Karyotypic diversity is most well known in two species-rich genera, the pulse-type *Gymnotus* and wave-type *Eigenmannia*. A systematic survey of chromosomal diversity has not yet been undertaken in Gymnotiformes. Karyotype work shows the following diploid number ($2n$) for selected taxa: *Gymnotus* (*G. carapo*, $2n = 54$, *G. pantherinus* $2n = 52$, *G. inaequilabiatus* $2n = 52$, Fernandes-Matioli et al. 1998; *G. sylvius*, $2n = 40$, Albert et al. 1999; *G.* n. sp. "pan," $2n = 40$, Fernandes et al., unpublished observations), *Electrophorus* ($2n = 52$, Fonteles-Santos et al. 2002), *Eigenmannia* ($2n = 28$, 36, 38, and 31/32, de Almeida-Toledo et al. 2002), and *Brachyhypopomus* ($2n = 42/41$, de Almeida-Toledo et al. 2000a). High intraspecific conservatism in karyotypes was detected in four species of the genus *Gymnotus* from Southeastern Brazil and the karyotypes are species specific in relation to diploid number, NOR-bearing chromosomes, and C-band pattern (Fernandes-Matioli et al. 1998b). There is also a natural case of triploidy in *G. carapo* (Fernandes-Matioli et al. 1998). No geographic chromosome races have yet been reported in *Gymnotus*. A multiple sex chromosome system has been reported in species representing two gymnotiform families, the hypopomid *Brachyhypopomus pinnicaudatus* and the sternopygid *Eigenmannia gr. virescens* (de Almeida-Toledo et al. 1998, 2000a,b). Five distinct karyotypes are known from *E. gr. virescens* living in sympatry in Southeastern Brazil, with $2n = 36$, and $2n = 38$, a $2n = 36–38$ (de Almeida-Toledo et al. 2002). This karyotypic diversity may result in part from the presence of sexual chromosomes, hybridization, or multiple (cryptic) species (de Almeida-Toledo 1998).

5. Gymnotiform Species Assemblages

Gymnotiforms occur in most lowland Neotropical aquatic habitats, including rainforest streams and swamps, xeric coastal streams and estuaries, caves, flooded forests and grasslands, and large river channels and cataracts. There have been significant advances in the understanding of gymnotiform species assemblages over the last two decades, with an emphasis on the study of the Amazon and Orinoco basins (Henderson and Walker 1986; Crampton 1996a,b, 1998a,b, 1999; Cox-Fernandes 1998b; Motta-Bührnheim and Cox-Fernandes 2001; Stewart et al. 2002), and the smaller coastal drainages of Central and South America (Westby 1988; Hagedorn 1985; Castro and Casatti 1997; Giora 2004). In terms of relative abundance and ecological importance, Gymnotiformes are a predominant component of the fauna in flooded forests and floating aquatic macrophytes of Amazonian floodplains (Crampton 1996a,b). Two genera in particular with pulse-type EODs (i.e., *Gymnotus* and *Brachyhypopomus*), are especially diverse and abundant in floodplain aquatic macrophytes (floating meadows). Gymnotiformes with wave-type EODs, notably species of Eigenmannini and Navajini, dominate the benthos of deep river channels with more than 75% of the biomass in trawl samples from both blackwater and whitewater rivers (Lundberg et al. 1987, 1996; Marrero 1987, 1993; Goulding et al. 1988).

Three distinct gymnotiform communities can be delineated, the exact species composition of which may vary from region to region, but which are similar in terms of species numbers, generic composition, and morphological diversity (Crampton 1998a; Crampton and Albert 2005): (1) terra firme streams and small rivers not exposed to seasonal flooding; (2) seasonally inundated floodplains, including lakes and flooded forests; and (3), deep, swiftly flowing river channels.

5.1 Terra Firme Systems

Terra firme forest streams of the Amazon and Orinoco Basins and the Guyanas host specialized communities of miniaturized gymnotiform species that shelter in submerged vegetation, root mats, and leaf litter. Larger species often hide in holes or caverns in undercut banks. One species, *Gymnorhamphichthys rondoni*, burrows into sand during the day—emerging to forage at night. This species forms small communities on submerged sand banks. In the Tefé region of the Brazilian Amazon streams host a fauna of four *Gymnotus*, four *Brachyhypopomus*, two *Hypopygus*, one *Microsternarchus*, one *Gymnorhamphichthys*, two *Sternopygus*, and one *Eigenmannia*. As with deep river channel and varzea floodplains, gymnotiforms represent a dominant component of the numbers and biomass of stream-dwelling fishes. Some stream dwelling fishes are able to move over land to inhabit ephemeral rainwater pools. In addition to the well-known land-walkers such as *Rivulus* spp. *Erythrinus erythrinus* and *Callichthys callichthys*, one species of *Gymnotus* (*G. curupira*) from the Western Amazon basin of Brazil and Peru can move over land on rainy nights from streams to pools. Terra firme forest streams and their flooded lower reaches are typified by very-low-conductivity water. Conductivity, as a metric of the concentration of nutrients (salts), is often correlated to fish distributions owing to its influence on primary productivity and correlation to other important water quality variables such as pH. Conductivity is also a measure of the external resistance through which electric fishes must drive electric current. As such it could also impose direct effects on the biology of electric fishes—either on the physiology of their electric organs and electroreceptors, or on their biogeographical distribution. One genus, *Brachyhypopomus*, exhibits clear correlations between the structure of the electric organ (and therefore the shape of the caudal appendage) and the ambient conductivity. First, the caudal portion of the electric organ tends to be long and slender in fishes that inhabit low conductivity water (less than 20 µs/cm); and short and thick in fish from higher conductivity waters (100 µs/cm or more). Second, there are structural differences in electric organs related to water conductivity, with those species occurring in low-conductivity waters having only two to three parallel columns of electrocytes on each side of the midline, whereas those from higher conductivity waters having up to five columns on each side.

Long, thin tails represent a predominantly serial configuration of the electrocytes, whereas short, thick tails represent a predominantly parallel configuration. Hopkins (1999) used a mathematic model to demonstrate that a deployment of electrocytes in series should theoretically maximise power output where the external resistance is high. In contrast, a deployment of electrocytes in parallel should theoretically maximise power output where the external resistance is low. Therefore, the electric organ structure and associated morphology of the caudal appendage in *Brachyhypopomus* appears to be adapted to the conductivity of the environment.

5.2 Floodplains

The expansive and productive whitewater floodplains or "várzeas" of the Amazon and Orinoco basins, and parts of the Paraguay–Paraná basins, contain diverse and abundant communities of gymnotiforms dominated by taxa that are able to withstand prolonged periods of hypoxia or anoxia. The decomposition of leaf litter in seasonally flooded forests causes seasonal anoxia throughout the water column of Amazonian várzeas and excludes all species that are intolerant of such conditions. Consequently only gymnotiforms with air breathing adaptations are able to take advantage of the exceptional productivity of these ecosystems. *Electrophorus electricus* is an obligate air breather, employing the hypervascularized and convoluted lining of its mouth as an air-breathing organ (Evans 1929). *Gymnotus* species breathe air using the gas bladder, an accessory air-breathing organ (Liem et al. 1984). Some species of *Brachyhypopomus* take up atmospheric oxygen via their gills by inflating the opercular chambers with air and floating at the water surface (Carter and Beadle 1931; Hopkins et al. 1990; Crampton 1998b). Many gymnotiform fishes enter varzea systems via paraná channels that transport well-oxygenated river water from the adjacent parent river(s). Floating rafts of macrophytes along the borders of these channels are important spawning sites for many apteronotid and sternopygid species that are intolerant of hypoxia. As water levels rise and oxygen levels decline at the onset of the high water season, juvenile apteronotids and sternopygids hitch rides out of the varzea in drifting meadows, while the adults retreat to the main river channels, which remain well oxygenated throughout the year.

Floating meadows of macrophytes in várzeas lakes are extremely productive habitats that support diverse communities of two pulse-generating genera: *Gymnotus* and *Brachyhypopomus*. In the Tefé region a syntopic breeding assemblage of eight permanently resident species of *Brachyhypopomus* and seven resident species of *Gymnotus* occurs in whitewater floodplain habitats. Only two other resident species occur, including *Eigenmannia gr. virescens* and *Rhamphichthys marmoratus*. A further three species of *Brachyhypopomus* and three species of *Gymnotus* occur sympatrically in low-conductivity systems of the Tefé region. The electric organ discharge waveforms of syntopic (but not necessarily allotropic) species of *Brachyhypopomus* and *Gymnotus* show clear species differences, which presumably mediate reproductive isolation (Crampton et al. 2003).

Gymnotiform fishes with wave-type EODs are less hypoxia tolerant and are less likely to be found in hypoxic habitats than weakly electric gymnotiforms with pulse-type EOD, suggesting that differences in metabolism resulting from EOD type affects habitat choice. Julian et al. (2002) report O_2 consumption rates during EOD generation for 34 gymnotiforms representing 23 species, all 5 families and 17 (59%) of the 28 genera. Over the size range sampled (0.4 g to 125 g), O_2 consumption of gymnotiform fishes was found to be dependent on body mass, fitting a power function with a scaling exponent of 0.74, but the O_2 consumption rate was generally about 50% of that expected by extrapolation of temperate teleost metabolic rates to a similar ambient temperature (26°C). The O_2 consumption rate was not found to be dependent on EOD type, but rather on maintenance of active scan swimming, suggesting that the locomotor costs of amplitude modulations underlie the exclusion of wave-type gymotiforms from hypoxic floodplain environments. Scan-swimming is a behavior observed only in fishes with wave-type EODs, in which the fish continually moves forwards and backwards near the substrate, thereby creating amplitude-modulated changes in the voltage detected by the electroreceptors (Julian et al. 2003).

Gymnotiform fishes form a dominant component of the biomass and numbers of fishes living in floating meadows (Crampton 1996a; Albert 2002). Likewise, the electric eel, *E. electricus*, is a dominant predator in seasonally flooded forests of varzea habitats (Crampton 1996a). The abundance of gymnotiform fishes has also been noted in seasonally flooded grassland habitats of the Venezuelan llanos (Marrero 1987; Lasso et al. 1997) and savannahs of Roraima, Brazil (Alves-Gomes 1997). In the Central Amazon basin nutrient-poor and relatively sediment-free rivers form smaller areas of seasonally inundated floodplain. In the Tefé region of the Brazilian Amazon, small patches of floating meadows in oxbow lakes support breeding communities of three species of *Brachyhypopomus*, one *Gymnotus* and two *Sternopygus* species. The diversity of *Brachyhypopomus* and *Gymnotus* is substantially lower than in whitewater floodplain systems, a pattern repeated at the generic level in several other fish groups. These discrepancies in species diversity are probably related to productivity, habitat size and availability, the amount of interconnectance, differential immigration/emigration levels, and, perhaps most importantly, differential levels of disturbance.

5.3 Deep River Channels

The benthos of large, swiftly flowing and deep (up to 25 m) river channels of the Amazon basin host diverse and specialized communities of gymnotiforms with species that are rarely found in other habitats. These communities are dominated by apteronotids and sternopygids generating wave-type discharges. Few deep river channel gymnotiform species generate pulse-type discharges but these can be abundant in terms of numbers and biomass. Common pulse-type species include *Steatogenys elegans, Rhamphichthys* spp., and *Gymnorhamphichthys* spp. Gymnotids are entirely absent. Pioneering studies by John Lundberg and colleagues used trawling equipment to investigate the species diversity of deep channel gymnotiform communities in the Orinoco and Amazon basins and revealed a plethora of new species including two species of the new genus *Magosternarchus* (Lundberg et al. 1996), two new species of *Adontosternarchus* (Mago-Leccia et al. 1985), and four new species of *Rhabdolichops* (Lundberg and Mago-Leccia 1986). Although there are some correlations between water quality and species occurrences (Cox-Fernandes 1998b), the deep-channel fauna of turbid, nutrient rich whitewater rivers is similar to those of relatively sediment free and nutrient poor blackwaters in terms of species composition (Garcia 1995; Crampton 1996a, 1998a; personal observation). Three apteronotid genera are restricted to large river channels of the Amazon Basin: *Magosternarchus* with two species, and the monotypic *Orthosternarchus* and *Parapteronotus*.

Intensive studies of deep river channels communities in the Tefé region of the lowland Amazon basin revealed a fauna of 55 species comprising one *Distocyclus*, three *Eigenmannia*, seven *Rhabdolichops*, three *Sternopygus*, two *Gymnorhamphichthys*, three *Rhamphichthys*, one *Steatogenys*, five *Adontosternarchus*, five *Apteronotus*, three *Compsaraia*, two *Magosternarchus*, one *Orthosternarchus*, one *Parapteronotus*, one *Platyurosternarchus*, two *Porotergus*, four *Sternarchella*, three *Sternarchogiton*, one *Sternarchorhamphus*, six *Sternarchorhynchus*, and one undescribed genus and species (Crampton 1996b; 1998a,b; 1999; Crampton and Albert 2005). All species, with the exception of the following, are found in both whitewater and blackwater channels: *Sternopygus branco*, *Adontosternarchus* n. sp. A and n. sp. B, *Orthosternarchus tamandua*, *Platyurosternarchus macrostomus*, *Sternarchella schotti*, and *Sternarchella* sp. A are known from whitewaters only. *Gymnorhamphichthys rosamariae* is known from blackwaters only. In terms of species diversity, gymnotiforms represent the dominant group in deep river channels, catfishes being the other main groups with some 30 species specialized for life on the benthos of deep river channels. More than 75% of the biomass of trawl samples from both blackwater and whitewater rivers during the low-water season in the Tefé region was represented by gymnotiform fishes. These samples did not intercept large pimelodid catfishes, which are also expected to form a large biomass component of these communities. Gymnotiform fishes are a dominant component of the diet of large and commercially important pimelodid catfishes, notably *Pseudoplatystoma* spp. (Reid 1983; Lundberg et al. 1987). It is unlikely that the biomass of large pimelodid catfishes in these systems outweighs that of their principal food source. Some deep channel electric fishes (e.g., *Sternarchella* spp.) are found in the lower estuarine reaches of the Amazon River around Ilha do Marajó and in tidal channels that connect the Amazon and lower Rio Tocantins. During the flood season, these species can occur many miles offshore. During the dry season wedges of brackish water push further inland and displace gymnotiform fishes (Barthem 1985).

Some physical aspects of deep river channel habitats have resulted in the evolution of a number of morphological and physiological adaptations unique to gymnotiforms (Albert et al. 1998; Albert 2001). The absence of light at the bottom of deep river channels has resulted in a number of taxa with highly reduced eyes and pigmentation and a greatly increased dependence on the electric sense. Elongate snouts with small terminal mouths have evolved independently in at least three gymnotiform lineages (Rhamphichthyidae, Sternarchorhynchinae, *Apteronotus sensu stricto* [including *Ubidia*]), in each case involving different sets of bones (Albert 2001; figs. 15 and 16). These elongate and sometimes decurved snouts are used for extracting larvae of Chironomidae, Plecoptera, Ephemeroptera, and other insects from small burrows in the clay substrates of river beds (Marrero 1987; Winemiller and Adite 1997; Crampton 1998a). In many places the clay beds of the Amazon River and its major whitewater tributaries are riddled with insect burrows, and the biomass of benthic insect larvae is substantial (Junk and Robertson 1997). Many deep-channel gymnotiforms, notably species of Eigenmannini and Navajini, are highly specialized for life at the bottom of deep Amazonian rivers. Some derived species of *Rhabdolichops* have long, ossified gill rakers used to filter plankton. Many apteronotids (e.g., *Sternarchella*) are aggressive predators with short, strong jaws and robust oral teeth. *Magosternarchus* is specialized to nip the tails off of other gymnotiforms. Other apteronotids have gracile jaws in which the oral teeth are reduced (*Sternarchogiton*) or absent (*Adontosternarchus*). These species forage on small aquatic animals, and one species (*Sternarchogiton nattereri*) eats sponge spicules.

6. Macroevolutionary Patterns

6.1 Descriptive Biogeography

Extant gymnotiform species are distributed in the continental waters of all South and Middle American countries except Chile and Belize, ranging from the Rio Salado of Argentina (36°S) to the Rio San Nicolás of southern Chiapas, Mexico (15°N) (Albert 2001). The nine hydrogeographic regions defined in Figure 13.6A are circumscribed by watershed divides and other geomorphological features (i.e., fall line of the Guyanas Shield, Purus Arch). These boundaries were selected to best represent the species composition of regional gymnotiform faunas (Albert 2001). Numbers of gymnotiform species in each genus for these nine hydrogeographic regions are summarized in Table 13.4.

As with most Neotropical taxa the Amazon Basin is the center of diversity for gymnotiforms, with 99 species (57%) in the Western Amazon (WA), and 79 species (46%) in the Eastern Amazon (EA) regions, and 128 species (74%) in these two regions combined. The Guyanas–Orinoco region (GO) has 62 species (35%). The disproportionately high species richness of this region for its size is due in part to its historical and current hydrological connections to the Amazon basin. The Paraguay–Paraná region (PA) has 23 species (13%), which is disproportionately low for its area owing in part to its relatively high latitude and cool temperatures (Silva et al. 2003). The Northeast region of Brazil (NE) with only 10 known species (5%) is also relatively depauperate for its size, largely as a result of the aridity of this region. The three trans-Andean regions

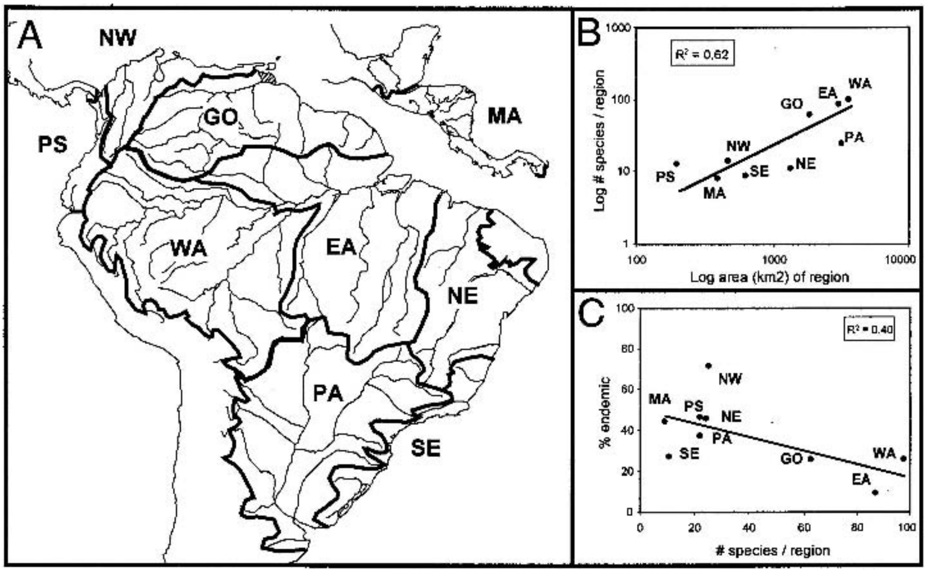

FIGURE 13.6. Descriptive biogeography of Gymnotiformes. (**A**), Neotropical hydrogeographic regions used in biogeographic analysis of Gymnotiformes. (Regions modified from Albert 2001.) EA, Eastern Amazon Basin, east of Purus Arch and all tributaries below fall-line of Guyana Shield (2,985,000 km^2); GO, Guyanas–Orinoco Region, including island of Trinidad and Upper Rio Negro drainages above fall line (1,843,000 km^2); MA, Middle America, Atlantic and Pacific slopes, from the Motagua to Tuyra Basins (393,000 km^2); NE, Northeast Brazil coastal drainages, including Parnaíba, Piaui, São Francisco, and Jequitinhonha Basins (1,357,000 km^2); NW, northwestern South America including the Magdalena and Maracaibo Basins, and the north slope of Venezuela (471,000 km^2); PA, Paraguay–Paraná Basin including Dulce-Salí and Salado Basins of Argentina (3,185,000 km^2); PS, Pacific Slope of Colombia and Ecuador, from Baudó to Guayaquil Basins, including the Atrato (Caribbean) Basin (200,000 km^2); SE, Southeast Brazil and Uruguay, coastal drainages from the Docé to Lagoa Mirim Basins (628,000 km^2); WA, Western Amazon Basin, west of Purus Arch, below about 500 m elevation (3,556,000 km^2). (**B**) Species-area relationship of Gymnotiformes in the hydrogeographic regions of **A**. (**C**) Species-endemism relationships of Gymnotiformes in the hydrogeographic regions of **A**. Note the regions with highest species diversity (EA, GO, WA) have the lowest levels of species endemicity, indicating a history of extensive faunal exchange.

(MA, NW, PS) contribute 32 species (19%) to the gymnotiform total, and include numerous examples of taxa with cis-trans Andean distributions useful for estimating the phylogenetic age of taxa. Examples of dating clades are provided for two taxa in Section 6.3 (*Gymnotus* and *Sternopygus*).

Several gymnotiform species are distributed over remarkably large areas of South America. A single morphospecies (*Eigenmannia virescens*) is known

TABLE 13.4. Gymnotiform species diversity by genus for the nine hydrogeographic regions of Figure 13.6A.

Family	Genus	MA	PS	NW	GO	WA	EA	NE	SE	PA
Apteronotidae	*Adontosternarchus*	0	0	0	4	6	5	0	0	0
	Apteronotus s.s.	1	4	4	3	1	1	2	1	4
	“Apteronotus”	0	0	0	2	4	2	0	0	3
	Compsaraia	0	0	0	1	3	1	0	0	0
	Magosternarchus	0	0	0	0	2	2	0	0	0
	Megadontognathus	0	0	0	1	0	1	0	0	0
	Orthosternarchus	0	0	0	0	1	1	0	0	0
	Parapteronotus	0	0	0	0	1	1	0	0	0
	Platyurosternarchus	0	0	0	1	1	1	0	0	0
	Porotergus	0	0	0	1	2	2	0	0	0
	Sternarchella	0	0	0	1	5	3	0	0	1
	Sternarchogiton	0	0	0	2	3	2	0	0	0
	Sternarchorhamphus	0	0	0	1	1	1	0	0	0
	Sternarchorhynchus	0	0	0	1	8	5	1	0	1
	n. Gen.	0	0	0	0	1	0	0	0	0
Gymnotidae	*Electrophorus*	0	0	0	1	1	1	0	0	0
	Gymnotus	3	3	1	5	14	8	1	3	4
Hypopomidae	*Brachyhypopomus*	1	1	2	8	11	9	2	3	4
	Hypopomus	0	0	0	1	0	0	0	0	0
	Hypopygus	0	0	0	2	2	2	0	0	0
	Microsternarchus	0	0	0	1	1	1	0	0	0
	Racenisia	0	0	0	1	0	0	0	0	0
	Steatogenys	0	0	0	1	3	2	0	0	0
	Stegostenopos	0	0	0	0	1	1	0	0	0
Rhamphichthyid.	*Gymnorhamphichthys*	0	0	0	3	3	2	0	0	1
	Iracema	0	0	0	0	0	2	0	0	0
	Rhamphichthys	0	0	0	3	3	5	1	0	2
Sternopygidae	*Archolaemus*	0	0	0	1	0	1	0	0	0
	Distocyclus	0	0	1	1	1	1	0	0	0
	Eigenmannia	2	2	2	5	6	5	2	2	2
	Humboldtichthys†	0	0	0	0	1	0	0	0	0
	Rhabdolichops	0	0	0	7	9	6	0	0	0
	Sternopygus	1	3	3	4	4	5	1	1	1
No. of species		8	13	13	62	99	79	10	10	23
Percentage of Gymnotiformes		5	8	8	36	57	46	6	6	13
No. of endemics		3	8	9	15	32	8	3	5	11
Percentage endemic		38	62	64	23	32	11	33	50	48

Taxa arranged alphabetically by family and genus.

from populations in all nine hydrogeographic region of Figure 13.6A, although the conspecific nature of these populations remains to be validated with molecular data. *Sternopygus macrurus* is known from all eight regions in South America (Hulen et al. 2005), including populations on both the Pacific and Atlantic slopes of the Colombian Andes. Three gymnotiform species are known from five regions (*Apteronotus albifrons*, *Brachyhypopomus pinnicaudatus*, *Brachyhypopomus* n. sp. E), 32 of 173 (18%) species in three regions, 38 of 173 (22%) species in two regions, and 95 of 173 (55%) species are endemic to a single region.

In general most gymnotiform clades have broad geographical distributions, occurring in two or more of the hydrogeographic regions in Figure 13.6A. Five gymnotiform genera are known from all nine regions (*Gymnotus*, *Brachyhypopomus*, *Sternopygus*, *Eigenmannia*, and *Apteronotus sensu stricto*), and 24 genera are present in two to eight regions. The Amazon–Orinoco–Guianas superbasin (WA + EA + GO) is the center of diversity at the generic level, and the majority of gymnotiform genera (24 of 32, 75%) are known from this region. The pattern of gymnotiform clades having broad geographical distributions is so strong that no gymnotiform clade comprising more than one species is restricted to a single hydrogeographic region. Five genera are restricted to a single biogeographic region, all of which are monotypic, and of which only two (the terra firme stream hypopomids *Hypopomus* and *Racenisia*) are known sufficiently to be able to have confidence in these restricted distributions. Most closely related species are allopatric; in only one genus (*Hypopygus*) are all the extant species both sympatric and syntopic in at least part of their range (Upper Orinoco basin). Rhamphichthyidae is the only gymnotiform family that is entirely restricted to Atlantic (cis-Andean) drainages.

The production of electric fields in freshwaters is highly sensitive to water quality parameters such as temperature and conductivity, and gymnotiforms are strictly excluded from marine or brackish waters. Similarly most gymnotiform species are physiologically intolerant of temperatures below approximately 17°C, and this may be the reason why they are restricted to altitudes below about 500 m elevation and to tropical or subtropical latitudes (Silva et al. 2003; see Section 6.3). A few species have adapted locally to cooler winter temperatures (c. 8°C) in the Brazilian state of Rio Grande do Sul, and in Uruguay and Argentina. One species of *Gymnotus* inhabits whitewater rivers in the Magdalena basin of the Colombian Andes at about 1000 m elevation (Maldonado-Ocampo and Albert 2003), and one (undescribed) species of *Sternarchorhynchus* is known from about 500 m in the Huallaga basin of Peru (H. Ortega, personal communication).

6.2 Polyphyletic Species Assemblages

A prominent feature of gymnotiform evolution and ecology is the absence of monophyletic regional species assemblages. In all genera, regional assemblages are polyphyletic and composed of species with disparate phylogenetic affinities and widespread geographical distributions. This feature is exemplified by the case of the gymnotiform fauna of the Tefé region, in the Western Amazon, from where 25/32 (78%) genera are known, representing all five families and nearly every major gymnotiform clade (Crampton 1998a; Crampton and Albert 2005). Of the species in the Tefé region 66 of 89 (74%) also occur outside the Western Amazon.

Sharing of species between the Amazon–Orinoco–Guianas superbasin (WA + EA + GO) is very extensive. Although these regions have the highest gymnotiform species diversity they exhibit the lowest levels of species endemism (32%, 11%, and 23% respectively). These patterns are illustrated by the positive regression in Figure 13.6B and the negative regression in Figure 13.6C. The Western Amazon, Eastern Amazon, and Guyanas–Orinoco are interlinked by two major modern hydrological connections: the Casiquiare canal (Amazon–Orinoco), and the Rupununi wetlands (Rio Branco–Essequibo), and have probably been subject to more intimate connections in recent geological history (Hoorn et al. 1995; Lovejoy et al. 1998; Lundberg et al. 1998; Lovejoy and deAraújo 2000). The Paraná–Paraguay drainages (PA), Southeast Brazilian drainages (SE), and Northeast Brazilian drainages (NE) all have considerably higher levels of endemicity despite their lower diversity (48%, 50%, and 33%, respectively). This is undoubtedly related to a longer history of isolation and a lack of hydrological interconnections. The upper Paraná is hydrologically linked only intermittently to the Upper Madeira at the Pantanal wetlands. Middle America, and the Pacific slope and North Western regions of South America have comparatively high levels of endemicity (38%, 57%, and 69%, respectively) owing to their complete isolation by high mountain ranges (4000 m +) since the late Middle Miocene (c. 12 Ma) or the narrow Isthmus of Panama since the Pliocene (c. 3 Ma).

The distribution of species among the three structurally defined Neotropical aquatic ecosystems is summarized in Table 13.5A. The two main patterns that emerge from this analysis relate to diversity and ecosystem endemism (specificity). The first observation is that species with wave-type EODs are more diverse in deep river channels, and much less so in streams and floodplains. In contrast, species with pulse-type EODs are most diverse in streams and floodplains, and substantially less so in deep river channels. The second observation is that the great majority (81%) of gymnotiform species occur in just one of these three ecosystems and, remarkably, only two species (*Sternopygus macrurus* and *Apteronotus albifrons* with wave-type EODs), representing only about 1% of gym-

TABLE 13.5. Ecological distribution of pulse- and wave-type gymnotiform species among three structurally defined lowland aquatic ecosystems in the Neotropics.

	Pulse-type EOD	Wave-type EOD
Terra firme streams	49/67 (73%)	18/67 (27%)
Floodplains	35/51 (69%)	16/51 (31%)
River channels	12/90 (13%)	78/90 (87%)

Number of species with a given EOD type in a given ecosystem is followed by the total number of species in that ecosystem (with percentage in parentheses). For example, 49 of 67 (73%) gymnotiforms living in terra firme streams have a pulse-type EOD.

notiforms, occur in all three ecosystems. A more complete analysis of habitat and electric signal diversity is provided by Crampton and Albert (2005).

The polyphyletic nature of regional gymnotiform species assemblages is the result of evolutionary diversification at a continental scale. The gymnotid *Gymnotus* is currently the best understood gymnotiform genus in terms of species-level interrelationships and geographic variation. The most species-rich local assemblage of *Gymnotus* is the area of Tefé in the Western Amazon from where 11 species occur in sympatry (Crampton et al. 1998a, b, 2005; Albert and Crampton 2001; Albert et al. 2003a; Crampton and Albert 2003). Species in this assemblage are members of at least four distinct clades, each with a sister taxon in another part of South America (Albert et al. 2005b). The capacity of this region to permit the coexistence of so many *Gymnotus* species in sympatry involves multiple ecological and historical factors, as well as the species-specific nature of their electric signals (Crampton and Albert 2005). Similarly, the assemblages of *Gymnotus* species in all nine hydrogeographic regions are not monophyletic. In other words, the species present in each of these regions do not represent the result of local or regional radiations, but rather were assembled incrementally over a lengthy history by means of a combination of processes. These include in situ speciation, extinction, immigration, and ecological factors allowing coexistence in sympatry. In this regard Amazonian species richness is not strictly a consequence of local or regional processes. These patterns are representative of other highly diverse groups of Neotropical fishes, and do not resemble those of monophyletic, rapidly generated species flocks in isolated aquatic systems (Greenwood 1984; Kornfield and Smith 2000).

6.3 Historical Biogeography and Ecology

The lineage leading to modern Gymnotiformes originated before the final breakup of Gondwana into South America and Africa some 100 Ma. During the Upper Cretaceous and early Cenozoic the gymnotiform line acquired the suite of derived phenotypes associated with bioelectrogenesis and active electroreception (e.g., electric organs, tuberous electroreceptors, anal-fin locomotion, caudal regeneration). It was during this early period, when South America was an isolated island continent and large river basins were being formed, that Gymnotiformes radiated into the full range of body plans (e.g., family and genera), habitats, and EOD types known today.

Dating by vicariance biogeography and molecular clocks combined with the phylogenetic distribution of modern habitat preferences suggests that the origins of pulse-type electric signals occurred before 80 Ma in terra firme (non-floodplain) forest streams and small rivers (Albert 2001). The transition from pulse to wave-type EODs can be inferred to have occurred in the Sinusoidea (Sternopygidae + Apteronotidae) within the giant rivers of northern South America between 20 and 80 Ma. The early gymnotiform radiations coincided in time and space with the development of the extraordinarily diverse Neotropical biota as a whole, including other ostariophysan fishes, the modern angiosperm-dominated tropical rainforests, and the radiations of insects and other sources of food for modern Gymnotiformes.

With the uplift of the Eastern Cordillera (c. 11.8 to 12.2 Ma) the Amazon–Orinoco, Maracaibo, Magdalena, and Atrato–Pacific Slope regions became isolated (Hoorn et al. 1995; Hoorn 1996; Diaz de Gamero 1996; Guerrero 1997; Gregory-Wodzicki 2000). According to a simple vicariance model this event would have separated sister taxa with existing distributions across northwestern South America, or caused the split. Such Miocene origins of multiple gymnotiform taxa with cis-trans Andean distributions resemble other groups of Neotropical fishes for which species level phylogenies have been proposed (Vari 1988, 1995; Vari and Weitzman 1990; Bermingham et al. 1997; Bermingham and Martin 1998; Martin and Bermingham 2000; Albert et al. 2005a).

The existence of at least 12 trans-Andean gymnotiform clades, including examples within six genera, suggests origins for this level of phenotypic diversity before the most recent geological isolation of the trans-Andean regions. Miocene tectonism in the northeastern Andes resulted in the formation of the modern watersheds of northwestern South America, including the Western Amazon, Orinoco, Maracaibo, and Magdalena Basins (Hoorn et al. 1995; Paxton et al. 1996; Guerrero 1997; Lundberg et al. 1998; Gregory-Wodzicki 2000). Also during the Middle Miocene the Choco Block underlying the modern San Juan and Atrato Basins was accreted to the northwest corner of South America (Duque-Caro 1990). Before the Middle Miocene most of the area of the modern Western Amazon drained northward to a delta located in the area of the modern Maracaibo Basin, and lowland Amazonian ichthyofaunas were present throughout much of northwestern South America (Lundberg 1997, 1998; Lundberg et al. 1998).

Phylogenetic data on at least two gymnotiform genera support the general chronology of generic diversification by the late Middle Miocene (c. 12 Ma). Both the genera *Gymnotus* and *Sternopygus* include multiple sister-taxon pairs on the Pacific (trans-Andean) and Atlantic (cis-Andean) slopes of northwestern South America (Albert et al. 2005b; Hulen et al. 2005). In both of these genera the cis–trans-Andean sister taxa occupy terminal positions within the phylogeny, suggesting minimum dates for the origins of these clades in the late Middle Miocene (Hoorn et al. 1995; Lundberg et al. 1998). In the case of *Gymnotus*, the basal division is between clades endemic to Middle and South America, suggesting an origin before the Pliocene Panamanian landbridge (Fig. 13.7). Under a vicariance model *Gymnotus* clade E dispersed to Middle America before the speciation of *Gymnotus* clades D and E; under a dispersal model *Gymnotus* clade E dispersed to Middle America after speciation of *Gymnotus* clades D and E within South America. In combination these geographic and phylogenetic patterns suggest that *Gymnotus* and *Sternopygus* predate the uplift of the Eastern Cordillera c. 12 Ma, and that *Gymnotus* became emplaced in Middle America long before the Pleistocene landbridge. These patterns of diversity and biogeography are consistent with those of other groups of Neotropical freshwater fishes indicating a long history extending for tens of millions of years (Lundberg

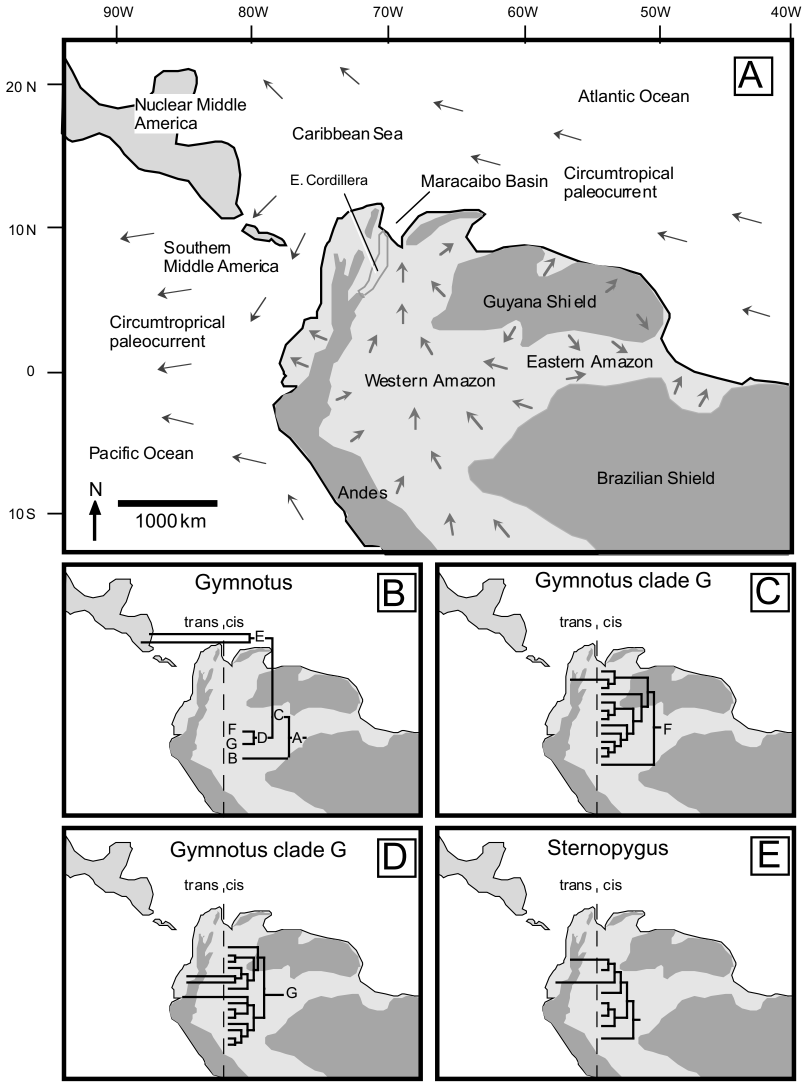

FIGURE 13.7. Historical biogeography of trans-Andean Gymnotiformes. (**A**) Paleogeographic reconstruction of northern South America and southern Middle America immediately before the uplift of the Eastern Cordillera in the late Middle Miocene (c. 12 Ma). (Map redrawn from Hoorn et al. 1995 and Ituralde-Vincent and MacPhee 1999. *Long arrows* indicate prevailing directions of marine paleocurrents; *short arrows* indicate direction of continental sediment paleotransport. *Dark shading* indicates highlands, *light shading*, lowlands. Note mouth of paleo-Amazon in area of modern Maracaibo Basin. (**B**) Basal four nodes of Gymnotidae (clade A) superimposed on paleogeographic recon-

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1993, 1997; Bermingham et al. 1997; Bermingham and Martin 1998; Lundberg 1998; Reis 1998; Lovejoy et al. 1998; Lovejoy and deAraújo 2000; Albert 2001).

The last 12 million years of active tectonism in the northern Andes resulted in dramatic geomorphological changes to the region and the closures of the modern watersheds of northwestern South America. Paramount among these changes was the capture of the Western Amazon basin by the Eastern Amazon basin, forming the modern Atlantic draining Amazon (c. 8 to 10 Ma), the largest freshwater basin on earth with by far the largest hydrological discharge (Goulding et al. 2003). This period also witnessed additional multiple changes in the hydrogeographic connections of the Amazon, Orinoco, and Paraná–Paraguay systems and other basins of northern South America. Extensive interbasin exchanges of species during these hydrological upheavals are reflected today by the low levels of geographical endemism in the Atlantic drainages of South America. The time frame represented by these late Tertiary events represents a relatively recent portion (less than 12%) of the whole history of Gymnotiformes.

7. Summary and Prospectus

Recent years have seen tremendous advances in our understanding of the diversity and phylogeny of gymnotiform fishes, opening new avenues of research into ecology and ethology of electric signaling and the evolution of diverse tropical animal species assemblages. The continuous, stereotyped, species-specific EODs of gymnotiform fishes play a role in sexual communication and reproductive isolation. These signals are easy to record and quantify, facilitate the identification of morphologically cryptic species, and provide an unparalleled window on communication and species recognition that is simply unavailable in most other fish groups. New methods of sampling, identifying, and collecting gymnotiform in the wild have unveiled numerous species in previously unexplored habitats and regions. Gymnotiformes is a considerably more diverse order than was previously recognized, with 135 valid species as of this writing, assigned to 32 genera in 5 families, and an additional 38 undescribed species currently known in museum collections. The actual number of gymnotiform species in the wild probably lies between 200 and 300.

FIGURE 13.7. *Continued*
struction (Albert et al. 2004b). Note basal split in *Gymnotus* (clade C) between clades endemic to South America (clade D) and Middle America (clade E). (**C**) Phylogenetic relationships of *Gymnotus* clade F. Note the single cis–trans–Andean species pair nested at a terminal position in the phylogeny. (**D**) Phylogenetic relationships of *Gymnotus* clade G. Note the two cis–trans–Andean taxa nested at terminal positions. (**E**) Phylogenetic relationships of *Sternopygus* (Hulen et al. 2004). Note the two cis–trans–Andean taxa nested at terminal positions in the phylogeny. Physical position of terminals on maps only informative with respect to locations in Middle America and South America, or cis- and trans-Andean watersheds.

Gymnotiform fishes are an important component of the nocturnal ichthyofauna of Neotropical freshwaters, both in terms of relative abundance and ecological importance. Gymnotiforms occur in most lowland Neotropical aquatic habitats and are especially diverse and abundant in floodplain aquatic macrophytes and deep river channels. Gymnotiform species diversity may be roughly divided eqally between those with pulse-type (45%) and wave-type (56%) electric signals. Species with pulse-type EODs are most diverse in streams and floodplains whereas species with wave-type EODs are more diverse in deep river channels. In terms of biomass and numbers of individuals two clades with pulse-type EODs (*Gymnotus* and *Brachyhypopomus*) dominate floodplain aquatic macrophytes, and two clades with wave-type EODs (Eigenmannini and Navajini) dominate deep river channels. The majority (81%) of gymnotiform species are specialized to occur in just one of these three ecosystems, and only two species (both with wave-type EODs) are generalized to occur in all three ecosystems. Adult body size in Gymnotiformes ranges over an order of magnitude (from about 5 to 200 cm total length). Gymnotiform species with pulse-type EODs are smaller on average than species with wave-type EODs, and exhibit more size and habitat diversity.

A combination of functional and phylogenetic considerations suggests that the active electrosensory system of Gymnotiformes, which on the one hand has allowed these fishes to exploit new habitats and dominate whole ecosystems, has also placed strong constraints on the evolution of adaptive diversity. Overall phenotypic diversity in Gymnotiformes is relatively conservative compared to other Neotropical taxa of comparable geological age and geographical range. Active electroreception in Gymnotiformes involves a physiological coupling of electrosensory and electrogenic structures interacting in a fixed geometry.

Many of the diagnostic characters of Gymnotiformes are salient features of body form and are functionally coupled with active electroreception. The elongate, knife-shaped culteriform body plan of Gymnotiformes with anal-fin locomotion and a semirigid body surface facilitates the ontogenetic formation of two-dimensional electroptopic maps on the surface on the body and primary electrosensory brain centers. The culteriform body shape also facilitates production of a stereotyped three-dimensional electric field from the electric organ. Despite the substantial diversification of Gymnotiformes into numerous family and generic-level taxa with more than a hundred species and significant adaptive changes in body size and trophic morphology, no gymnotiform lineage has deviated from the basic culteriform body plan.

Despite or perhaps because of these constraints, the gymnotiform radiations have produced substantial diversity in the organization and development of the electrogenic and electrosensory systems. Two clades, the Gymnotidae and Rhamphichthyoidea (Rhamphichthyidae + Hypopomidae), retain the plesiomorphic pulse-type EOD, and also retain the larval hypaxial electric organ into maturity. Myogenic accessory electric organs have evolved in at least four species-rich clades of rhamphichthyoid fishes with a pulse-type EOD, in each case on or around the head; a neurogenic mental accessory electric organ is known in one species-rich clade with a wave-type EOD (*Adontosternarchus*). Sinusoidea (Sternopygidae + Apteronotidae) possess a derived wave-type EOD, and the larval electric organ of these taxa degenerates at metamorphosis to be replaced by an adult organ derived from anal-fin pterygiophore muscles (Sternopygidae) or the electromotor neurons (Apteronotidae) that innervated the larval organ. Sinusoids also possess numerous derived features related to the utilization of deep rivers channels, including specializations of the central nervous system. Approximately half of total brain volume in gymnotiform fishes is dedicated to primary electrosensory structures. Apteronotids have the largest pacemaker nucleus of all gymnotiforms, the group of medullary neurons that regulates the rhythmic EOD rate. The EOD of some apteronotid species is the fastest and most stable known biological oscillator, achieving a maximum repetition rate of 2179 Hz in *Sternarchella schotti*. In terms of waveform diversity the Sternopygidae with a wave-type EOD is the most conservative gymnotiform taxon. Waveform diversity is highest in two clades with a pulse-type EOD (*Gymnotus* and *Brachyhypopomus*), which together include 54 known species, or about 31% of all gymnotiform species. Species assemblages of these two genera are most diverse in floodplains of the Western Amazon, where up to 11 species of each may occur in sympatry.

Two species-rich clades (i.e., Rhamphichthyidae and Sternarchorhynchinae) have independently evolved elongate tubular snouts with small mouths for foraging on insect larvae in the benthos of deep river channels. Apteronotidae is characterized by much greater morphological diversity than other gymnotiform families, which is expressed primarily as variation in head structure related to trophic specialization and, in part, to male–male aggression. In at least four separate apteronotid clades (*Parapteronotus, Apteronotus sensu stricto*, *"Apteronotus" sensu lato*, and *Compsaraia*) sexually mature males develop elongate jaws. In *Sternarchogiton nattereri* and in some *Sternarchorhynchus*, males develop prominent external teeth.

The lineage leading to modern Gymnotiformes originated before the final breakup of Gondwana into South America and Africa some 100 Ma. During the Upper Cretaceous and early Cenozoic the gymnotiform line acquired the suite of derived phenotypes associated with bioelectrogenesis and active electroreception (e.g., electric organs, tuberous electroreceptors, anal-fin locomotion, caudal regeneration). It was during this early period, when South America was an isolated island continent and large river basins were being formed, that Gymnotiformes radiated into the full range of body plans (e.g., family and genera), habitats, and EOD types known today. Dating by vicariance biogeography and molecular clocks suggest that the origins of pulse-type electric signals occurred before c. 80 Ma. in terra firme (non-floodplain) forest streams and small rivers. Given the phylogenetic distribution of modern habitat preferences, the transition from pulse to wave-type EODs can be inferred to have occurred in the Sinusoidea (Sternopygidae + Apteronotidae) within the giant rivers of northern South America between 20 and 80 Ma. The early gymnotiform radiations coincided in time and space with the development of the extraordinarily diverse

Neotropical biota as a whole, including other ostariophysan fishes, the modern angiosperm-dominated tropical rainforests, and the radiations of insects and other sources of food for modern Gymnotiformes.

Most if not all gymnotiform lineages were essentially modern in terms of phenotypic and species diversity by the late Middle Miocene (c. 12 Ma). There are at least 12 gymnotiform clades, in 6 genera and 4 of the 5 gymnotiform families, with cis–trans-Andean distributions, suggesting minimum dates for the origins of these clades by 12 Ma as a consequence of the final closure of the Andean cordillera during the Magdalenian orogeny. Moreover, in several of these clades the cis–trans-Andean sister taxa occupy terminal positions within the phylogeny, indicating that many modern species-level taxa had evolved by the late Middle Miocene. The only known fossil gymnotiforms are from the Late Miocene of Bolivia. These fossils resemble modern sternopygids and set a minimum date for the origin several derived features associated with active electroreception, including the specialized culteriform body shape, ball-and-socket anal-fin ray articulation, and regeneration of the caudal appendage. Since the Middle Miocene the South American river basins have undergone massive modifications and sharing of faunas resulting in very extensive exchanges of species. This is reflected by low levels of geographical endemism in the area corresponding to the highest electric fish diversity, and by the polyphyletic structure of regional assemblages.

Understanding the forces governing the number and identity of gymnotiform species in a regional assemblage requires phylogenetic, biogeographic, and ecological data as well as information about electric signals. These phylogenetic and biogeographic patterns suggest that diversification in most gymnotiform taxa has been a continental, not basin-wide, phenomenon, occurring over periods of tens of millions of years. In this regard Amazonian species richness is not strictly a consequence of local or regional processes. These patterns are representative of other highly diverse groups of Neotropical fishes, and do not resemble those of monophyletic, rapidly generated species flocks in isolated aquatic systems.

Investigations into phylogenetic, biogeographic, and ecological aspects of gymnotiform diversity are accelerating and the actual dimensions of the fauna now coming to be more fully appreciated. Current projects to complete the descriptive stage of this research program include phylogenetic revisions of eight species-rich gymnotiform clades including 51% of known gymnotiform species. Species-level understanding of these geographically widespread and diverse taxa is advancing the use of Neotropical electric fishes as a model group for studies on the origins and maintenance of species and signal diversity. The results of these systematically based studies, combined with comparative studies of electric organ and electrocyte morphology and electrocyte membrane physiology, are advancing understanding how gymnotiform fishes generate stereotyped, species-specific signals. These results are also contributing to the general area of vertebrate neurophysiology concerned the coordination of complex motor output patterns. The wealth of knowledge accumulated from comparative studies of electric fish phylogeny, biogeography, ecology, and ethology is allowing perhaps for the first time a synthetic understanding of animal communication in the evolutionary context.

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