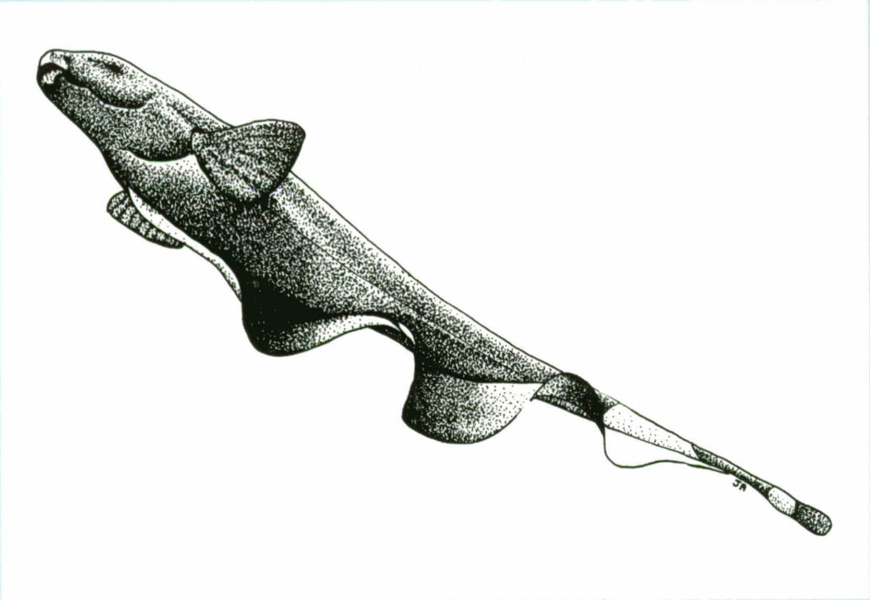
SPECIES DIVERSITY AND PHYLOGENETIC SYSTEMATICS OF AMERICAN KNIFEFISHES (GYMNOTIFORMES, TELEOSTEI)

BY

JAMES S. ALBERT



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THE REGENTS OF THE UNIVERSITY

Species Diversity and Phylogenetic Systematics of American Knifefishes (Gymnotiformes, Teleostei)

by

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ABSTRACT

Albert, J.S. 2000. Species diversity and phylogenetic systematics of American knifefishes (Gymnotiformes, Teleostei). Misc. Publ. Mus. Zool. Univ. Michigan, 190:1-127, 50 figs. Evolutionary relationships among American knifefishes are documented from comparative studies of morphological, physiological, and behavioral features. Materials were examined from more than 900 museum lots containing over 4200 gymnotiform specimens referred to 105 described and 32 undescribed species. Neural tissues were examined for 31 gymnotiform species, including representatives of 20 genera. These data were compiled into a matrix of 249 characters, including 45 characters of the nervous system, for 44 operational taxonomic units. The molecular sequence data of Alves-Gomes *et al.* (1995) were also analyzed, weighting transitions and transversions equally. Tree topologies from molecular sequence and morphological datasets analyzed independently using maximum parsimony are very similar, and to the topology resulting from a combined analysis.

These data are used to provide phylogenetic diagnoses for 75 clades and terminal taxa, including the Gymnotiformes, 5 families, and 29 genera. Two new genera and 14 additional supraspecific taxa are introduced. *Gymnotus* + *Electrophorus* are found to be monophyletic, and together form the sister group to all other gymnotiforms. Rhamphichthyidae + Hypopomidae and Sternopygidae + Apteronotidae are also monophyletic, the latter of which includes all species with a tone-type electric organ discharge (EOD). The fossil †*Ellisella* is determined to be a member of Sternopygidae. No evidence was found for the monophyly of the nominal genera *Iracema* (Triques), *Eigenmannia* (Jordan and Evermann), *Apteronotus sensu lato* (Lacépède) or *Porotergus* (Ellis). *Megadontognathus* (Mago-Leccia) and *Ubidia* (Miles) are regarded as junior synonyms of *Apteronotus sensu stricto* (new usage). An identification key to the recognized genera is provided.

The phylogenetic results permit several conclusions regarding character evolution. *Sternopygus astrabes* most closely resembles the ancestral gymnotiform phenotype. Two clades, Apteronotidae and *Eigenmannia* + *Rhabdolichops* possess numerous derived features, including two specializations of the central nervous system, related to the utilization of deep river channels. Gymnotidae, Rhamphichthyidae, and Hypopomidae retain the plesiomorphic pulse-type EOD and larval hypaxial electric organs into maturity. The tone-type EOD of Sternopygidae and Apteronotidae is derived, and the larval electric organ of these taxa degenerates at metamorphosis. Elongate snouts have evolved independently in at least four gymnotiform lineages, involving different sets of bones. The caudal fin of apteronotids is derived from the caudal appendage of other gymnotiforms, and is not an intermediate state in the loss of a caudal fin.

The actual number of gymnotiform species in the wild is much greater than has previously been recognized. There are currently 108 valid species of gymnotiforms in the literature and about 34 undescribed species recognized in museum collections. These species are distributed throughout the humid Neotropics, from the Rio Salado in the Pampas of Argentina to the Rio San Nicolás of Chiapas, Mexico. Species diversity is highest in the Amazon (89 species) followed by the Orinoco (61 species), the Guyanas (35 species), the Paraná (26 species), Northwestern South America (14 species), Southeast Brazil and Uruguay (12 species), Northeast Brazil (9 species), the Pacific slope of South America (7 species), Middle America (7 species), and the endorheic Rio Salí-Dulce of northwestern Argentina (1 species). There are at least seven trans-Andean gymnotiform clades.

Key words: *biodiversity, biogeography, cladistics, classification, comparative morphology, electric fishes, evolution, historical ecology, South America.*

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INTRODUCTION

> "*In the beginning the fishes were arranged according to external form and external characters. This served for considerable time until the attempt was made to go deeper and prove relationship by anatomy, particularly osteology. Generally the result was in the direction of improvement, especially if the internal characters were coordinated with the external ones* (Starks, 1926)."

American knifefishes or Neotropical electric fishes (Teleostei: Gymnotiformes) are an important component of the nocturnal ichthyofauna of Middle and South American freshwaters. Gymnotiformes range in latitude from Rio Salado in the Pampas of Argentina (36°S) to the Rio San Nicolas of southwestern Chiapas, Mexico (18°N) (Eigenmann and Allen, 1942; Mago-Leccia, 1994; Albert and Miller, 1995). An outstanding feature of gymnotiform biology, observed in all living species, is the capacity to produce and detect weak electric fields (Lissman, 1958). Gymnotiform fishes continually emit weak electric discharges, which they use in object location and communication. This electroreception is accomplished by detecting changes in the shape, amplitude, or frequency of the electric field (Hopkins, 1972; Bass, 1986).

The body shape of gymnotiform fishes is highly specialized in association with electroreception. Rather than swimming with alternating constrictions of the axial muscles, as do most fishes, gymnotiforms undulate their elongate anal fin, which extends along the majority of the ventral margin of the body (Fig. 1). The external surface of gymnotiforms is invested with numerous electroreceptor organs, and maintaining a somewhat rigid posture facilitates the use of the integument as a sensory sheet. The caudal (post-coelomic) portion of the body is also elongate, and the entire postcranial portion of the body is buttressed with numerous intermuscular bones. The anus, which lies anterior to the origin of the anal fin, grows anterior during ontogeny and is situated beneath the pectoral fins or even under the head in adult specimens. In gymnotiforms there are no dorsal, adipose, or pelvic fins. The caudal fin is either small (Apteronotidae) or absent (other families). A thin caudal appendage bearing electrocytes extends a variable length beyond the posterior-most anal-fin ray in gymnotiforms lacking a caudal fin, except *Electrophorus,* in which case the anal-fin extends to the tip of the tail.

In combination, these features give gymnotiform fishes a knife-like appearance, and are the source of their common names in many languages, including "knifefish" or "electric eel" in English, and "cuchillo" (knife) or "anguilla" (eel) in Spanish. They are also the source of many of the Latin names ascribed to these fishes, including *Gymnotus* (naked back), *Apteronotus (*without fin on back), and *Sternopygus* (breast rump). The shimmering appearance of the undulating anal fin, and their nocturnal habits, may have been the origin of the name "sarapó" (ghost) used by the Tupi-Guarani indigenous Amazonian peoples (Myers, 1943).

The motor effectors of the electrosensory system are specialized muscle or nerve cells called electrocytes, which generate the rhythmic electric organ discharge (EOD; Bass, 1986). Certain aspects of the frequency spectrum and wave form of the EOD appear to be unique to each species (Hopkins, 1973; 1974; Kramer *et al.,* 1981; Crampton, 1998a) while other aspects may be used to characterize more inclusive gymnotiform lineages (Sullivan, 1993; Sullivan and Lundberg, 1996). Electric organ discharges are also used as social signals, in both territorial and sexual behaviors (Black-Cleworth, 1970; Westby, 1988; McGregger and Westby, 1992). Depending on the form of thir EOD electric fishes may be regarded as either "pulse" or "tone" (= "wave") type species (Bennett, 1971). Pulse-type species emit discrete discharges of relatively lower frequencies (2-120 Hz) whereas tone-type species emit a continual series of discharges, generally with much higher repetition rates (60-1750 Hz; Crampton, 1998a). Since the closest relatives of knifefishes do not possess electrogenic organs it is not possible to use the

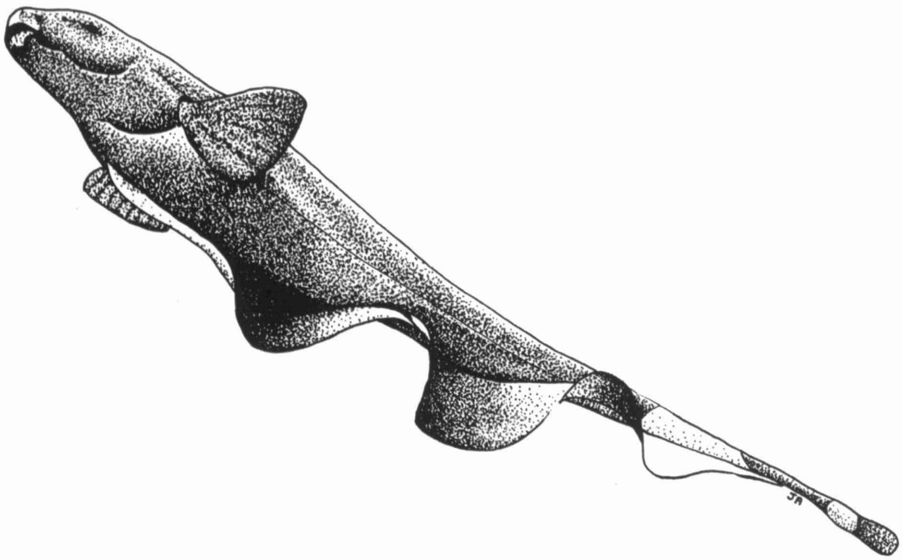

Fig. 1. Ventrolateral view of *Apteronotus albifrons* illustrating culteriform locomotion using anal-fin undulation. Drawing from photograph by Michael J. Lannoo.

outgroup criterion to determine which EOD mode is primitive (Hopkins and Heiligenberg, 1978; Bass, 1986).

The relative ease with which EOD signals and responses may be monitored has facilitated the use of gymnotiforms in numerous laboratory and field studies and resulted in a relatively large literature of comparative data. The electrosensory systems of several species have been the subject of intensive study, including physiology (Heiligenberg, 1989; 1991; Keller *et al.*, 1991; Rose and Canfield, 1993a, 1993b; Zakon *et al.*, 1995; Rasnow and Bower, 1996; Fortune and Rose, 1997; Assad *et al.*, 1998), anatomy (Johnston and Maler, 1992; Yamamoto *et al.*, 1992; Maler and Mugnaini 1994; Wong 1997; Corrêa *et al.*, 1998), behavior (Maler, 1987; Hopkins *et al.*, 1990; Fleishman, 1992; Fleishman *et al.*, 1992; Heiligenberg *et al.*, 1997), and development (Vischer *et al.*, 1990; Lannoo *et al.*, 1990; 1992; Viete, 1991; Kirschbaum 1994b; Zupanc and Horschke 1995; Unguez and Zakon, 1998). Several review volumes have been published in recent years summarizing the major discoveries of this research program (Bullock and Heiligenberg, 1986; Heiligenberg, 1991).

Data collected in both field (Hopkins, 1972; Crampton, 1998a) and laboratory settings (Black-Cleworth, 1970; Hagedorn, 1986) have documented the role of electroreception in trophic and social interactions. These investigations provoked interest into methods of breeding and raising gymnotiforms in captivity (Kirschbaum and Denizot, 1975; Kirschbaum and Westby, 1975, Kirschbaum, 1977; 1979; 1983). Gymnotiform fishes possess a unique capacity among vertebrates to regenerate the entire postcoelomic portion of the body as a natural and commonplace part of their natural history (Ellis, 1913). Understanding the details of gymnotiform regeneration facilitated the recognition of a fossil gymnotiform species, †*Ellisella kirschbaumi*, from the Upper Miocene (c. 10-12 mya) of Bolivia (Gayet and Meunier, 1991). In combination these studies have yielded detailed comparative information on an unconventional array of phenotypes for systematic analysis, including sexual and reproductive behaviors (Hagedorn, 1986), the behavior of larvae and juveniles (Kirschbaum and Westby, 1975; Bass, 1986, Vischer *et al.*, 1990), the development of the electric organs (Kirschbaum, 1977; 1983; Bass, 1986), and regeneration (Kirschbaum and Denizot, 1975; Kirschbaum and Meunier, 1981; 1988; Meunier and Kirschbaum, 1984; Anderson and Waxman, 1983; Waxman and Anderson, 1986; Anderson, 1987).

The actual number of gymnotiform species in the wild is much greater than has previously been recognized (Mago-Leccia, 1994). There are currently 108 valid species of gymnotiforms in the literature and about 34 additional undescribed species recognized in museum collections (Table 1, Appendix 1). Intensive surveys of deep river channels and flood-plain floating meadows in lowland Amazonia have produced many new species of gymnotiforms in recent years, some in enormous abundance (Lundberg *et al.*, 1987; Goulding *et al.*, 1988; Marrero, 1989; Gavis *et al.*, 1989; Machado-Allison, 1993; Lundberg *et al.*, 1996; Crampton, 1996). Much of this diversity has gone unnoticed before in large part because these habitats are difficult and expensive to sample. As a result, deep river channels and floating meadows have been neglected by commercial and aquarium fishermen, despite the fact that gymnotiforms generally constitute the majority of the fish biomass in these environments. Gymnotiform species diversity has also been overlooked because the fishes are often difficult to identify; differing by features that are cryptic to human senses. Aspects of gymnotiform diversity are now being documented from studies of the EOD, karyotypes, and genetics (Sullivan and Lundberg, 1996; Sullivan *et al.*, 1996; Albert *et al.*, 1999; Almeida-Toledo, 1998; Crampton 1998a; 1998b).

The present contribution provides evidence on the phylogenetic relationships of gymnotiforms from examination of specimens representing 133 species and all 29 recognized genera. Data presented here include the descriptions of external body morphology used in the pioneering works of gymnotiform systematics (*e.g.*, Kaup, 1856; Eigenmann and Ward, 1905; Ellis, 1913), osteological, neural, and physiological characters used in more recent comparative studies (*e.g.*, Mago-Leccia, 1978; 1994; Mago-Leccia *et al.*, 1985; Lundberg and Mago-Leccia, 1986; Triques, 1993; Gayet *et al.*, 1994; Alves-Gomes *et al.*, 1995; Sullivan, 1997a; 1997b), and numerous original observations. Combined with the availability of many species previously rare in museum collections (Lundberg *et al.*, 1987; 1996; Albert and Crampton, unpubl. data) the stage has been set for this comprehensive phylogenetic revision of the Gymnotiformes.

A BRIEF HISTORY OF GYMNOTIFORM SYSTEMATICS

> "*(O)rderings based on similarities of organisms... are so real, our mind is drawn to them by a propensity so necessary, that ordinary folk as well as naturalists have always had their genera* (Cuvier, 1828:282)."

Several ethnoichthyological studies include taxonomic information on gymnotiform fishes. The most complete reports are of the Kayapó, a Tupi-Guarani speaking people from the lower Rio Tocantins of Brazil (Posey; 1979; Beggosi and Garavello, 1990). The Kayapó classify knifefishes primarily on the basis of morphological criteria, using especially body shape, snout shape, and coloration. The names applied to gymnotiform species by the Cubéa, a Tikuna speaking people from the Rio Uaupes of Colombia, are outlined by da Silva (1977) and López and Hernández (1986). The Cubéa call the smaller knifefishes "calochi", recognizing at least seven different forms, and call *Electrophorus* "sà'à". They also recognize the deep channel habitat of apteronotid species (*i.e.* those with caudal fins) although they seem to have no specific term for these species. Other ethnoichthyological reports mentioning gymnotiforms include those of da Silva (1988) on the Piratininga in the State of Rio de Janeiro, Brazil, and Royero-Léon (1989) on the Piraoa from the upper Rio Orinoco in Venezuela. The naming systems used by these two peoples are roughly hierarchical, often employing a binomial system to identify different forms. Knifefishes are generally known as "eri" by the Piraoa, for example, and *Eigenmannia* species are called "te'a eri". *Electrophorus* is known by the single name "mejú". Many of the common names for gymnotiform species derive from words meaning "knife." These include "macána" in Perú, "cuchillo" in Venezuela, and "knifefish" in the aquarium trade. Throughout much of the Brazilian Amazon small-bodied electric fishes are collectively referred to as "sarapó", whereas *Electrophorus* is referred to specifically as "puraqué" (or poraquê). Many fishermen distinguish among the small-bodied species by color, referring to *Gymnotus* and

Table 1. Materials examined (numbers of specimens, museum lots, and species), and numbers of described (published) species presently recognized as valid, in each gymnotiform family. Materials examined listed by species in Appendix 1; species taxonomy and citations in Appendix 4. Note species totals derived from these Appendices differ.

Family	Materials Examined		Species		
	Specimens	Lots	Described	Undescribed	Valid
Apteronotidae	1047	283	40	8	43
Gymnotidae	936	217	17	5	17
Hypopomidae	895	178	13	10	15
Rhamphichthyidae	94	39	11	2	13
Sternopygidae	1247	199	24	7	24
Total	4223	915	105	32	112

Brachyhypopomus together as "sarapó pintura" (painted sarapó), *Eigenmannia* as "sarapó claro" (clear sarapó), and *Sternopygus* as "sarapó negro" (black sarapó).

The history of formal gymnotiform systematics is reviewed by Ellis (1913), Mago-Leccia (1978), and Campos-da-Paz and Albert (1998). Europeans were introduced to the electric eel and its peculiar properties by the friars C. d'Abbevile (1614), a capuchin monk serving with French troops in the area that is now known as São Luiz, Maranhão, and Cristobal Acuña (1641) in his account of Pedro de Teixeira's voyage into the Amazon (Faraday 1832; Smith, 1990). Gymnotiform taxonomy began with George Marcgraf (1648:170), who described as Carapó from Brazil the species named *Gymnotus carapo* by Peter Artedi (1738) (gymno = naked, noto = back, *carapo* presumably from the indiginous word sarapó). Artedi placed it in the "Malacopterygii" with the description "five ossified branchiostegal membranes, dorsal fin absent" (in translation). The Linnaean type (ZIU 56; Linnaeus, 1749, pl. 14, fig. 51), was collected by Pallberg near Paramaribo, Surinam, and desposited in King Adolf Fredrik's collection at Ulriksdal, now in the possession of the University of Uppsala and deposited in the Museum of Natural History in Stockholm. Linnaeus (1758; 1766) listed *Gymnotus carapo*, as well as three other species, *G. albifrons*, *G. rostratus*, and *G. electricus*, with the true eels under "Apodes." These other species were later elevated to be the types of different genera, and eventually of different families.

Bernard Germain Etienne Lacépède (1800) provided the first systematic arrangement of these fishes by placing *G. albifrons*, which has a caudal fin, into a separate taxon; *Apteronote.* Bloch and Schneider (1801) introduced the junior synonym *Sternarchus* to place the same species. Georges Cuvier (1817) extended the scheme of Lacépède by placing "*Carapus fasciatus*" (Pallas 1767, =*Gymnotus carapo* Linneus) and "*Gymnotus electricus*" into "Les Gymnotes", and *Sternarchus* (=*Apteronotus*) into "Les Apteronotes."

The broad outlines of gymnotiform diversity, like that of the Neotropical biota in general, came to be known after the opening of Spanish America to European scientists by Charles Marie la Condamine in 1735 (see Schaefer, 1994). Studies on the electric organs of *Electrophorus* by Richer (1729) and Hunter (1775) laid part of the foundation for Faraday (1832) to document electricity as a force of nature (Owen, 1837). The collections and publications of Alexander von Humboldt from his journeys to the Orinoco and Magdalena basins (Humboldt and Bonpland, 1811) stimulated interest among Europeans in the Amazon. Of outstanding attention was Humboldt's description of electric organs of *Electrophorus,* which he dissected at Calabozo, on a bank of the Rio Guárico in the Venezuelan llanos (Smith, 1990). Cuvier (1817) recognized the American knifefishes to be distinct from the eels and superficially similar forms in the old world. G. Valentin (1841) provided the first detailed study of the anatomy of the brain and cranial nerves.

Holland (1911) summarizes the most important of the eighteenth and nineteenth century voyages, of which several produced gymnotiform fishes. Traveling in the company of the well known naturalists Johann Baptist de Spix and Carl Friedrich von Martius in the years 1817-1820, the Austrian John Natterer made some of the earliest collections of knifefishes from the interior of the Brazilian shield. Natterer's specimens are the first recorded from the Guaporé-Maderia and Rio Negro drainages, and were deposited in the Vienna Museum. The Prussian Robert Schomburgk undertook the earliest ichthyological investigations of the Essequibo River in Guyana, and also visited the upper Rio Negro basin (Schomburgk, 1843). The first paper to begin sorting these materials was that of Müller and Troschel (1848), who grouped species partially on the basis of patterns in tooth morphology. The genus *Sternopygus* was introduced to group species with multiple rows of villiform teeth, and *Rhamphichthys* for species without teeth. Müller and Troschel also reported the first "tube snout" apteronotid, which they named *Sternarchus oxyrhynchus.*

In 1843, the Count Francis de Castelnau descended the Rio Tocantins of Brazil and the Rio Ucayali of Perú. The results of his expedition (Castelnau, 1855) described many new species and provided an early classification for the family. Castelnau's scheme, presented in the form of a branching key, is reproduced below (in translation).

"Gymnotoides"
- caudal fin present
  - mouth recurved .... *Sternarchorhynchus*
  - mouth normal .... *Sternarchus*
- caudal fin absent
  - scales absent .... *Gymnotus*
  - scales present
    - snout elongate .... *Rhamphichthys*
    - snout normal
      - anal-fin origin near mid-body...... *Carapus*
      - anal-fin origin near head .... *Sternopygus*

The specimens of knifefishes accrued from these and several smaller collections resulted in the publication of 50 species names by the end of the 19th century. Eigenmann and Ward (1905) recognized 29 of these as valid species, allotting them to 11 genera. These include material from the Brazilian collections of J.B. de Spix (Spix and Agassiz, 1829), and the Thayer Expedition (1865-1866) of Louis Agassiz to eastern Brazil, the Rio Tocantins, and the Rio Amazonas (Agassiz, 1886; Myers, 1943; Lurie, 1960; Dick, 1977; Higuchi, unpubl. manuscript). The contributions of several other collectors, notably Edward Bartlett who transmitted specimens to Günther at the British Museum, and James Orton whose specimens were described by Cope (1878), are detailed by Eigenmann and Allen (1942).

Gymnotiform systematics in the latter half of the nineteenth century was concerned primarily with the sorting and naming of this diversity. Castelnau's report (1855), along with that of Achille Valenciennes (1847), formed the basis of J.J. Kaup's (1856) "Catalogue of Apodal Fishes" of the British Museum. Kaup recognized 20 gymnotiform species, which he allotted to five genera, corresponding to the modern arrangement of families, but he provided no hypothesis of higher level relationships. This work was incorporated almost unmodified in to Günther's (1870) "Catalogue of the Fishes of the British Museum."

By comparison with the work describing gymnotiform species diversity, the systematic position and organization of gymnotiforms received relatively lesser attention in the latter half of the nineteenth century. The major advance of that period was that of Johann Reinhardt (1852), who recognized that the physostomous connection of the esophagus with the swim bladder was evidence that gymnotiforms are more like characins and salmonids than eels. C. Tate Regan's (1911) work was the first to use osteological characters in gymnotiform classification. Based on the presence of the Weberian ossicles of the anterior four vertebrae (Weber, 1820), Regan placed gymnotiforms in the Ostariophysi (Sagemehl, 1885). Regan was also the first to hypothesize a special affinity between the Sternarchidae (= Apteronotidae) and the Sternopygidae. As a nomenclatural aside, Kaup (1856) perpetuated the junior synonym *Sternarchus* (Bloch and Schneider, 1801) in place of *Apteronotus* (Lacépède, 1800). Regan (1911) propagated the error by using the name for the family Sternarchidae, and the mistake was finally repaired by Jordan (1923).

This period in the history of gymnotiform systematics was like that of other fish groups in being somewhat isolated from the writings of Darwin and Cope and the emerging theory of Organic Evolution. Although systematists of the day did understand the value of recognizing "natural taxa" (Starks, 1926), species were commonly grouped into higher categories on the basis of features useful in constructing identification keys, often without regard for the polarity of the characters or the creation of artificial groups. *Sternarchorhynchus* Castelnau (1855), for example, was designated for species of *Sternarchus* with elongate snouts, whereas Gill (1864) designated the name *Hypopomus* for species of *Rhamphichthys* with short snouts. The genus *Eigenmannia* was coined by Jordan and Evermann (1896) (replacing *Cryptops* Leach) for sternopygids lacking features of the other genera in that family. Although *Sternopygus* was regarded as a junior synonym of *Gymnotus* by Eigenmann and Ward (1905), it was reinstated by Ellis (1912) to place gymnotiforms with a free orbital rim, despite the fact that this character was regarded to be a primitive feature at the time. *Steatogenys* (Boulenger, 1898) however, was set aside to distinguish species of *Hypopomus* with a specialized "small, cylindrical filament of tissue in a groove on each side of the mental region (Ellis, 1913:132)".

Carl Eigenmann and his colleagues and students can be credited with organizing gymnotiforms into the modern taxonomy. Together with his wife Rosa Eigenmann, he began studying the Thayer collection in 1887, work which continued to his death in 1927 (Myers, 1943). Extending the reach of his studies by field work in Colombia and Panamá (Eigenmann and Eigenmann, 1891; Eigenmann, 1894; Eigenmann and Ward, 1905; Eigenmann, 1923), in the Guyanas (Ellis, 1912, Ellis, 1913), in Argentina and Paraguay (Eigenmann, 1910), and in Perú and Ecuador (Eigenmann and Fisher, 1914; Eigenmann and Allen, 1942), Eigenmann and his collaborators developed the outline of gymnotiform taxonomy and biogeography as it is understood today.

Eigenmann and Ward (1905) was the first review of the gymnotiforms since Kaup (1856), and the first to include a detailed biogeographic analysis of the genera. Their study was also the first to provide keys to all the species. In a series of reports describing material left by Natterer in the Vienna Museum, specimens provided by Agassiz from the Thayer expedition, and material from his own collections in Brazil in 1871-1872 (Myers, 1943), Franz Steindachner added six species to the literature (1868, 1878, 1880, 1881). From this diversity Eigenmann and Ward (1905) recognized three new genera. What are now recognized as *Sternarchella schotti* and *Adontosternarchus balenops* were separated from *Sternarchus* (= *Apteronotus*) by their short gape and snout. Eigenmann and Ward (1905) identified *Sternarchogiton*, including what is now recognized as *S. nattereri* and *Adontosternarchus sachsi*, by the absence of premaxillary teeth. *Sternarchorhamphus*, identified by the presence of a long, straight snout, included species that are recognized as *Sternarchorhamphus muelleri*, *Orthosternarchus tamandua*, and *Platyurosternarchus macrostomus* in this report.

One student of Eigenmann was John Haseman who spent the years 1907-1910 in South America collecting for the Carnegie Museum. The final year of his travels was spent in the lower stretches of the Amazon and its major southern tributaries, where he collected specimens later named for him by Ellis (1913). Haseman collected the type and four of the 10 paratypes used by Ellis to establish *Gymnorhamphichthys* (Ellis, 1912; 1913), which he distinguished from *Rhamphichthys* by the absence of scales over most of the body, as well as the type material of *"Apteronotus" hasemani* (Ellis, 1913). In addition, one of the two species used to designate *Porotergus* (Ellis, 1912) was based on material from Haseman's collections. As originally defined, *Porotergus* was recognized by the absence of scales along the dorsum, and the large scales along the lateral line, both characters of ambiguous utility. The monophyly of *Porotergus* and *Apteronotus* was further clouded by the subsequent designation of other genera (*e.g.*, *Oedemognathus* Myers, *Ubidia*, Miles, based on the presence of autapomorphic features.

Günther Schlessinger (1910) produced an early effort to synthesize the morphological data from these taxonomic studies with the ethological information reported by Carl Sachs (1879; 1881). Although this work produced little novel information of systematic importance, it did assemble the then available data into a single publication, and was the first to advance explicit hypotheses of primitive and derived characters states. Schlessinger depicted *Electrophorus* as the first branch of the gymnotiform tree, yet also regarded the caudal fin and dorsal organ (also called the dorsal thong or dorsal filament) of apteronotids to be primitive features.

Max Ellis's (1913) was the first to propose a formal hypothesis of interrelationships among all the known gymnotiform lineages. This hypothesis is presented in the form of a branching diagram, with the figure caption "Gymnotid Eels of South America. Generic Relationships, Parallelisms, and Convergences (1913: pl. XV)." In the papers documenting their progress in organizing gymnotiform diversity Eigenmann and his collaborators (Eigenmann and Ward, 1905; Eigenmann, 1912; Ellis, 1913) emphasized the division between *Gymnotus* and *Electrophorus* from other gymnotiforms, a view incorporated by Jordan (1923) and subsequent workers (Bertin and Arambourg, 1958; Lindberg, 1974; Mago-Leccia, 1976; 1978). Ellis notes many similarities between these two taxa, concluding that "it does not seem that *Electrophorus* should stand in a separate family (Ellis, 1913:112)."

The collections available to Ellis in Guyana (formerly British Guiana) included about 1300 specimens of gymnotiforms, within which he recognized 27 species. Many of these species, however, were poorly represented; six species were discussed from examination of less than 10 specimens each, six others from five or less, and five species from no material at all. Ellis studied 490 specimens of *Eigenmannia virescens*, 248 specimens of *Gymnotus carapo*, and 142 specimens of *Sternopygus macrurus*, all widely distributed throughout tropical South America (Mago-Leccia, unpublished manuscript).

The years between the world wars saw the last of the great museum-based expeditions to Amazonia. Under the direction of Carl Eigenmann, the University of Indiana undertook two expeditions from 1918-1921, and Harvard University undertook the Mulford expedition in 1923 (MacCreagh, 1927; Eigenmann and Allen, 1942). The decades immediately following the monographs of Eigenmann and Ward (1905) and Ellis (1913), were dedicated mainly to working up collections and describing new species. In the period from 1913 to 1962, 20 papers naming 34 species were published, of which all but four are recognized in this review. Among these was the recognition of *Rhabdolichops longicaudatus* (= *R. troscheli*), the type species of a new genus.

Carl Sachs was the first to describe the electric organs of gymnotiforms other than *Electrophorus* (Peters, 1877; see Ellis, 1913). The electrosensory capacity of gymnotiforms was first alluded to by Shaffer (1917). The discovery that electroreception is a normal sensory function in gymnotiform fishes by Hans Lissmann and his colleagues (Lissmann, 1958; Bennett and Grundfest, 1959; Bullock *et al.,* 1961; Fessard and Szabo, 1961) ushered in the modern era of research. In the following two decades, comparative studies were directed at many aspects of the electroreceptive biology of gymnotiforms, including the morphology and physiology of electric organs (Bullock, 1969; 1982; Bullock *et al.,* 1972; Bennett, 1971; Hopkins, 1974; Hopkins and Heiligenberg, 1978; Heiligenberg and Bastian, 1984), and electroreceptors (Szabo, 1965; Bennett, 1967; Hopkins, 1983; Zakon, 1986).

The growing interest in bioelectrogenesis facilitated the identification of *Hypopygus* (Hoedeman, 1962b) as distinct from the juveniles of its closets relatives, by the morphology of its accessory electric organs. *Hypopygus* includes the smallest gymnotiforms, and in addition to size and electric organ morphology differs from *Steatogenys* in meristics, color pattern, and the osteology of the ethmoid region (Nijssen and Isbrücker, 1972; Sullivan, 1997b). During this period Michel Chardon and Eduardo de la Hoz produced the first papers reporting more subtle details of variation in the osteology of representative gymnotiform species (Chardon and de la Hoz, 1974; 1977; de la Hoz and Chardon, 1973; 1975; 1984). Also at this time, ecological and geographical data were incorporated for the first time into our understanding of gymnotiform diversity (Hoedeman, 1962a, 1962b; Nijssen and Isbrücker, 1968; 1972; Nijssen *et al.,* 1976; Schwassmann 1984; 1989; Schwassmann and Carvalho, 1985; Hopkins, 1972, 1974; Britski, 1972; Britski *et al.,* 1988).

Knowledge of the phylogenetic and ecological diversity of gymnotiforms is presently undergoing dramatic changes. There have been several recent studies on the higher level systematics of the Gymnotiformes. In surveys of the lower Rio Orinoco in 1978 and 1979, and of the Brazilian Amazon from 1993-1996, John Lundberg and colleagues undertook a systematic exploration of the deep river channels in lowland Amazonia. Sampling with benthic trawl nets in these regions has produced many species of gymnotiforms, some in enormous abundance, with gymnotiforms often constituting the vast proportion of biomass in many localities (Lundberg *et al.,* 1987; Goulding *et al.,* 1988; Marrero, 1989; Gavis *et al.,* 1989; Rodriguez, 1990; Machado-Allison, 1993; Hagedorn and Keller, 1996). These surveys have demonstrated that many new forms of gymnotiforms await discovery. Extrapolating from present rates of discovery in the Brazilian and Venezuelan states of Amazonas, actual gymnotiform diversity may well be over 200 species (Mago-Leccia, pers. comm.).

The results of the Orinoco collections and subsequent field studies were published in the form of species descriptions and generic revisions (Mago-Leccia, 1978; Mago-Leccia *et al.,* 1985; Lundberg and Mago-Leccia, 1986; Mago-Leccia, 1994) or ecological reports (Mago-Leccia and Zaret, 1978; Brull, 1983; Marrero, 1983; 1987; 1989; Lundberg *et al.,* 1987; Machado-Allison, 1993). The result has mirrored the 19th century proliferation of taxonomic names with relatively less attention paid to systematic organization. The nomenclature used in these studies has largely emphasized unique derived features, and has resulted in a proliferation of generic names. More than one third (10 of 27) of the genera recognized by Mago-Leccia (1994) are monotypic (*i.e. Electrophorus* Gill, 1864, *Sternarchorhamphus* Eigenmann, 1905, *Orthosternarchus* Ellis, 1912, *Oedemognathus* Myers, 1936a, *Ubidia* Miles, 1945, *Microsternarchus* Fernández-Yépez, 1968, *Archolaemus* Korringa, 1970, *Racenisia* Mago-Leccia, 1994, *Platyurosternarchus* Mago-Leccia, 1994, and *Megadontognathus* Mago-Leccia, 1994). This type of taxonomy may indeed reflect the pattern of an ancient diversification of gymnotiform phenotypes with little subsequent speciation (*e.g.,* Lundberg, 1993), or it may be a taxonomic artifact resulting from an incomplete understanding of interrelationships.

Many groups remain poorly understood and may ultimately prove to represent several taxa (Sullivan and Lundberg, 1996). *Brachyhypopomus* Mago-Leccia (1994), for example, is defined by the presence of a short snout, no mesocoracoid, crescent-shaped maxilla, and posterior nares closer to eyes, all characters shared with plesiomorphic gymnotiforms. Additional studies on the alpha taxonomy and natural history of gymnotiforms are resolving many of these issues (*e.g.*, Brull 1983; Aguilera, 1986; Marrero, 1983; 1989; Campos-da-Paz, 1995; 1997; Cox-Fernandes, 1998a; 1998b; Albert and Crampton, unpubl. obs.).

Gymnotiforms have long been long known to be ostariophysans, not closely related to true eels (Reinhardt, 1852), and have generally been regarded as "without doubt connected by certain abdominal families to the order of *Physostomi*, namely by the *Characini* (Kaup, 1856:125)." This conclusion was based in part on the presence of the dorsal organ in apteronotids, regarded as an adipose fin, and the absence of several features of the dentition easily observed in cypriniforms and siluriforms. Both Boulenger (1904) and Ellis (1913) subscribed to this view, regarding gymnotids (as they were then called) to be "elongate Characins without dorsal or ventral fins (Ellis, 1913:113)." The perception that gymnotiforms were derived from a generalized characoid stock led Mago-Leccia and Zaret (1978) to conclude that the sternopygid *Rhabdolichops*, an elongate planktivore inhabiting deep river channels, represents the primitive gymnotiform phenotype.

The hypothesis that catfishes (Siluriformes) are the nearest evolutionary relatives of Gymnotiformes (Fink and Fink, 1981), now corroborated by numerous behavioral and neural features (Bullock and Northcutt, 1982; Striedter, 1990; 1992; Fink and Fink, 1996) has brought about a reassessment of character polarity and homology, and catalyzed renewed interest in gymnotiforms systematics.

There are several recent studies on higher level gymnotiform interrelationships. In the first published review of interfamily relationships since Ellis' (1913) classic monograph, Mauro Triques (1993) applied cladistic methodology to the traditional characters used in knifefish systematics, and added numerous new observations, especially from the ethmoid and branchial regions. The results of Triques study echoed those of the earlier literature (*e.g.*, Castelnau, 1855; Chardon and de la Hoz, 1974) in regarding the caudal fin of apteronotids as evidence for their basal position among gymnotiforms. Gayet *et al.* (1994) also separated apteronotids from other gymnotiforms on the basis of plesiomorphic characters, and united the remaining gymnotiform families into a separate taxon. Alves-Gomes *et al.* (1995) review characters of the electromotor system and provide data on ribosomal mitochondrial DNA sequences. A conclusion of Alves-Gomes *et al.* was that the low EOD repetition rate and lack of a jamming avoidance response (JAR) in *Sternopygus* are primitive features. Alves-Gomes *et al.* also concluded that species of gymnotiforms with a high EOD frequencies constitute a monophyletic group.

MATERIALS AND METHODS

"Fishing in South America is by far the most dangerous of all forms of scientific exploration. In order to maintain good health in the tropics my advice would be to eat anything you can get, whenever you can get it, and as much as you crave. Keep hard at work. Eternal vigilance is the price of a good collection. I am thoroughly convinced that the temperament of the individual has a great deal to do with health in the tropics. Ever-changing activities and a variety of interests tends to produce a frame of mind which is hostile to disease. Calmness in the face of grave danger is indispensable. Worry and fretfulness should be banished. Great faith should be placed in one's own arms, legs and head. I feel sure that most of the deaths of travelers in the tropics results either from inexcusable ignorance or from unnecessary fear.

"After the noises of the day the hush which comes at night-fall causes even the hardened traveler at time to shudder. No man over the age of fifty years of age should attempt to enter this region. A hard heart and cold blood are useful to him who invades it." (Haseman, 1911)

Material examined

Specimens were obtained from museums, field collections, and commercial dealers. A total of 915 museum lots containing 4223 specimens were examined, representing 105 described and 32 undescribed gymnotiform species (Table 1, Appendix 1). Specimens of uncertain specific identity are indicated with "sp." (*e.g., Gymnotus* sp.), and those representing undescribed species are indicated with Roman letters (*e.g., Gymnotus* sp. A). Specimens of unknown status which share similarities with the type material of a named species are referred to that species with "*cf.*" (*e.g., Gymnotus cf. carapo*) (Albert *et al.*, 1999). Museum acronyms are presented by Leviton *et al.* (1985), with the addition of the following: FML, Fundacion Miguel Lillo, Tucuman, Argentina; LGP, Laboratorio de Genetica de Peixes, Departamento de Biologia, Universidad de São Paulo, Brazil. This research was performed under guidelines established by the University of Michigan for the proper management and handling of vertebrate animals.

Osteology

Specimens were cleared and stained (C&S) for bone and cartilage using a modified version of the enzyme technique of Taylor and Van Dyke (1985). When sufficient material was available at least two specimens of each species were C&S. Skeletal preparations were also examined for several species, and observations of neural tissues were made for 21 knifefish species. Standard dissection methods for small teleosts were used (Weitzman, 1974). Drawings follow Mago-Leccia (1978), Fink and Fink (1981), and Mago-Leccia *et al.* (1985). Osteological characters describe conditions in mature specimens, with the exception of characters expressly pertaining to juveniles. Gymnotiforms possess the actinopterygian developmental pattern in which cartilages of the sphenoid region, the palatoquadrate arch, and the scapulocoracoid are among the last to ossify (Figs. 2-4; de Beer, 1937, plates 24-58; Arratia, 1992, figs. 4 and 24-25; Schultze, 1993, fig. 5.11). The presence of sutures between the orbitosphenoid and pterosphenoid, the quadrate and endopterygoid, and the scapula and cleithrum are fully formed, were used to assess the mature osteological condition. In the several taxa for which incomplete ossification is retained in adults, relative extent of ossification was used to assess maturity.

Nomenclature follows Patterson (1975) for bony elements of the skull, and Weitzman (1962) and Fink and Fink (1981) for the rest of the skeletal system; mesethmoid, anguloarticular and pharyngobranchials were preferred over ethmoid, angular and infrapharyngiobranchials, respectively. In this paper the ventral ethmoid refers to the endochondral ossification of the compound vomer of actinopterygians (Patterson, 1975). Topologically, the ventral ethmoid is the anterior portion of the compound vomer which articulates with the mesethmoid on the dorsal and anterior surfaces, and the ethmoid cartilage on the

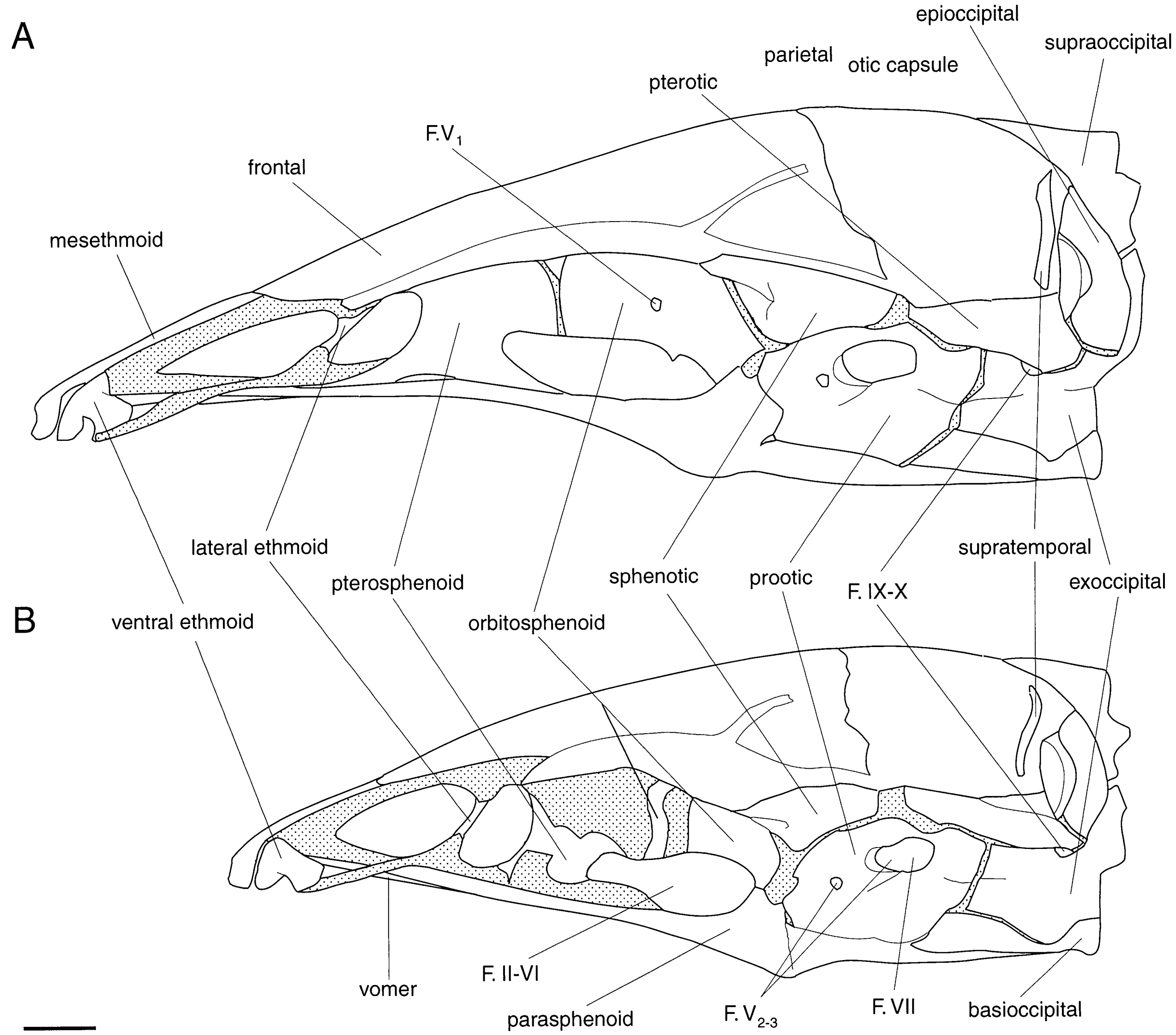

Fig. 2. Diagrammatic views of neurocranium of *Sternarchogiton* sp. B (UMMZ 211315) depicting two late ontogenetic stages. A. Morphologically mature specimen, 200 mm TL. B. Subadult specimen, 145 mm TL. Cartilage indicated by shading. Note the extent of ossification in the sphenoid region, and the relative lengths of the preorbital and basicranial regions. Scale bar equals 1 mm.

lateral surface. The ontogenetic fusion of the ventral ethmoid with the dermal vomer forms the compound vomer, equivalent to the vomer of previous authors (Fink and Fink, 1981; Mago-Leccia *et al.*, 1985, Lundberg and Mago-Leccia, 1986, Triques, 1993). The hypethmoid and prevomer of de la Hoz and Chardon (1975) are equivalent to the ventral ethmoid and dermal vomer, respectively, of this report. The prevomer of Weitzman (1962) is equivalent to the compound vomer used here.

Counts of vertebrae and anal-fin rays were taken from radiographs and cleared and stained specimens. The number of precaudal vertebrae includes those of the Weberian apparatus; precaudal vertebral number is used here as a proxy for body cavity length. In some cases meristic character states were established by simple gap-coding when discontinuities were observed in the ranges of values. Other methods to code continuous variation, either quantitative (*e.g.*, generalized gap-coding) or qualitative (*e.g.*, segment coding) have not been demonstrated to provide increased sensitivity to phylogenetic information (Pimentel and Riggins, 1987; Chappill, 1989).

Neuromorphology

Neuromorphological observations were taken from 35 knifefish species including representatives from each of the five recognized families and all 26 extant genera (Albert *et al.*, 1998). From this material specimens of 25 species were prepared for histological examination (Appendix 2). All living animals used in this study were anesthetized with 3-aminobenzoic acid ethyl ester (MS 222; Sigma, St. Louis), perfused intracardially or immersion-fixed with 10% formalin and stored in the same solution. Brains were carefully removed from the cranial vault by dissection from the dorsal aspect so as to inflict minimal damage to the rest of the head. Brains were uniformly trimmed of nerves (including optic tract), weighed, and postfixed in 10% formalin for at least 24 hours. After dehydration brains were embedded in paraffin wax and cut in 10 μm sections on a rotary microtome. Specimens subjected to medium term storage (12-36 months) in ethanol, and then to paraffin embedding, undergo approximately 10-15% shrinkage by volume. In order to

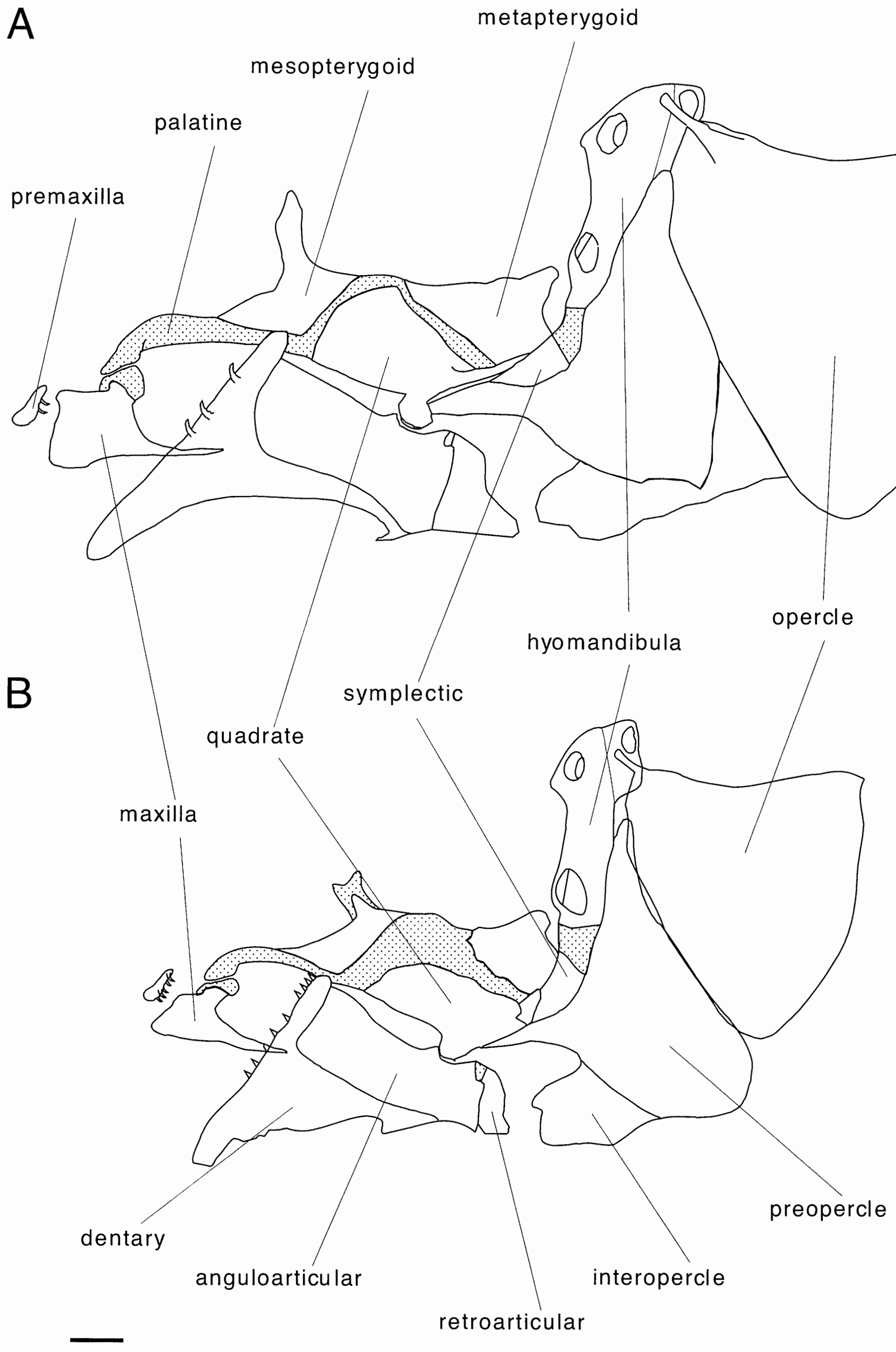

Fig. 3. Two late stages in the ontogeny of the suspensorium in *Sternarchogiton* sp. B. Panels A and B as in Fig. 1. Cartilage indicated by darker shading. Note the relative extent of ossification within the palatoquadrate arch and the reduced number of teeth in the dentary and premaxilla in A. Scale bar equals 1 mm.

assess the extent and nature of artifacts induced by these procedures, representatives of each family were prepared from specimens perfused intracardially in the field, preserved in 10% formalin, and later cut into 50 μm sections on a cryostat. Tissues subject to this procedure undergo approximately 2 - 5% shrinkage.

The histological organization of tracts and nuclei in one species, *Apteronotus albifrons* was examined in detail. The brains of four specimens were prepared using conventional cell body (Nissl) and tract staining (Luxol fast blue) procedures, and one specimen each was subjected to a modified version of the Bodian and Golgi silver impregnation methods (Ito and Yoshimoto, 1990). Electroreceptors, lateral line nerves, and nerve ganglia were visualized from seven specimens of *Apteronotus leptorhynchus*, cleared with trypsin and stained with Sudan Black B (Nishikawa, 1987). Whole mounts of the integument from the left side of the head were prepared for 16 gymnotiform species by staining with methylene green to visualize receptor organs. Additional and comparative slides of teleostean brains were examined from the collections of Drs. H. Ito, R.G. Northcutt, and M.J. Lannoo.

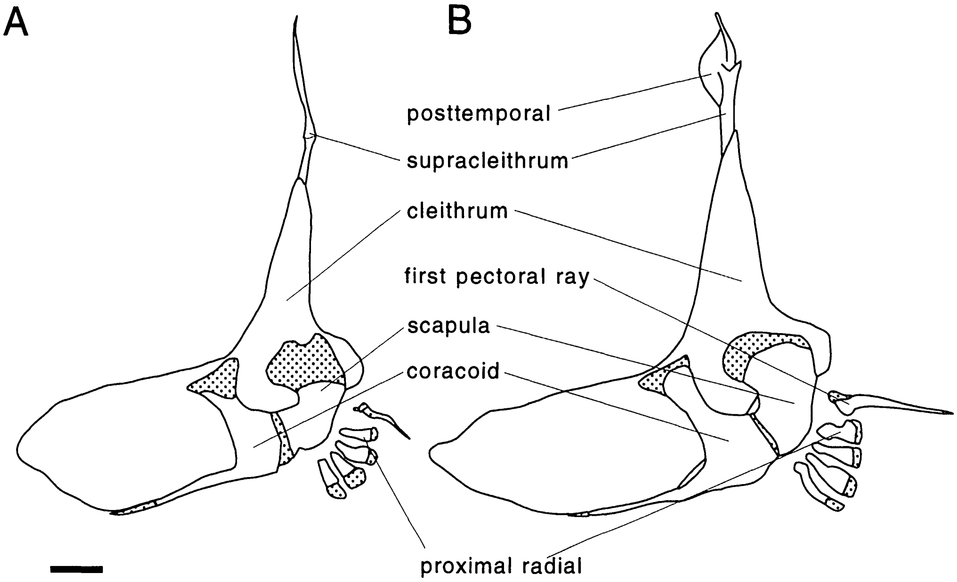

Fig. 4. Two late stages in the ontogeny of the pectoral girdle in *Sternarchogiton* sp. B. Panels A and B as in Fig. 1. Note the relative extent of ossification within the scapulocoracoid cartilage. Scale bar equals 1 mm.

Drawings of the gross brain morphology and representative histological sections were compiled into an atlas for each species following the format of Maler *et al.* (1990). Brains were sectioned at right angles to the neuraxis, such that dorsal structures in Maler *et al.* (1990) appear slightly more caudal than they do in similar transverse sections of this report. The plane of section used by Maler *et al.* (1990) was tilted 10 degrees from perpendicular with the neuraxis in order to simulate the orientation of animals in neurophysiological preparations. Drawings of nuclear organization were prepared using a Wild M20 compound microscope equipped with a camera lucida. Twelve transverse sections (T levels) were selected for detailed assignments of labels. These sections are separated by 600 μm, corresponding to every fourth level established by Maler *et al.* (1990), with the exception of a 300 micron gap between levels 28 and 30. Staggering the anterior three transverse sections in this manner permitted the sampling of several important diencephalic nuclei. Multiple criteria were used to assign sections to particular T levels, based on combinations of features regularly associated in their rostral-caudal extent and position (Albert *et al.*, 1998).

Polarity of neural characters was assessed by comparison with states observed in the siluriform and characiform taxa identified by Fink and Fink (1981), and in other teleosts (*e.g.*, Tuge *et al.*, 1968). Different patterns in the phylogenetic distribution of characters were regarded as *prima facia* evidence for their independence (Buckup, 1993). All neural characters describe conditions observed in morphologically mature specimens, although the brains of juvenile specimens in several species were also examined.

Taxa

Data were coded for 42 ingroup and two outgroup terminal taxa. The operational taxonomic units (OTUs) used this study are the nominal gymnotiform genera of Mago-Leccia (1994), as amended below, the fossil †*Ellisella* (Gayet and Meunier, 1991), and several undescribed species. In cases where the limits of recognized genera are uncertain, several species attributed to that taxon were included as separate terminal taxa. Although the authors of many genera intended to identify natural groups, the monophyly and/or limits of several gymnotiform taxa are problematic. As originally defined, the genera *Sternopygus*, *Eigenmannia*, *Hypopomus*, *Gymnorhamphichthys*, and *Apteronotus* were identified by the absence of characters thought to diagnose other members of their respective families (Eigenmann and Ward, 1905), and *Porotergus* by characters of ambiguous utility (Ellis, 1912; Mago-Leccia, 1994). The taxonomy employed here therefore differs from that of previous studies. Names of species-groups are given to the oldest valid species name. All taxa introduced here conform to the conventions of the International Commission on Zoological Nomenclature (1985).

The nominal taxa *Oedemognathus exodon* Myers and *Apteronotus anas* Eigenmann and Allen are sexually mature male specimens of *Sternarchogiton nattereri* and *"Apteronotus" hasemani* respectively (Cox Fernandes, 1998). Male specimens with varying degrees in the development of the secondary sexual phenotype exhibit continuous variation between the morphologies of the type specimens. These features may therefore be regarded as ontogenetically variable in these species.

Outgroup taxa were selected from previous studies on ostariophysan interrelationships (Fink and Fink, 1981). The two outgroup taxa were coded based on conditions in a multiple species. To estimate the plesiomorphic condition attention was given to character states in taxa thought to be relatively basal members of the two immediate outgroups; the characiform taxa *Distichodus*, *Citharinus*, and *Parodon* (Fink and Fink, 1981; Buckup, 1993), and the siluriform taxa *Diplomystes* (Arratia, 1987; Arratia and Schultze, 1990; 1992), *Helogenys*, and *Cetopsis* (Mo, 1991; de Pinna, 1993).

Characters

Data recovered from examination of morphological differences were compiled into a matrix of 249 characters for the 44

OTUs. Character descriptions include both plesiomorphic (0) and apomorphic (1) conditions. Characters were selected on the basis of their phylogenetic informativeness (Pimentel and Riggens, 1987; Eernisse *et al.*, 1992) and analyzed using maximum parsimony for congruence (Hennig, 1966; Wiley, 1981; Sober, 1988). No *a priori* assumptions were used to screen the selection of characters. Body proportions used in character definitions are defined by Albert and Fink (1996). Body size is represented by head length (HL) in millimeters. The use of head length as a measure of overall body size is discussed by Albert and Fink (1996).

Specimens in which the caudal fin or appendage was damaged and unregenerated were excluded from measurements of total length. Some of the measurements used in this report differ from those of earlier work on gymnotiforms (Mago-Leccia, 1978; 1994). Head length, for example, is defined as distance between the tip of the snout and the posterior extent of the bony opercle. Head length measured from the posterodorsal termination of the branchial opening (Mago-Leccia, 1978) is subject to preservation-induced artifact and was not used. Measures of pectoral-fin length, postorbital length, and body depth reported here may also differ from the results of previous studies; unambiguous landmarks were used to define endpoints.

Relevant data on phenotypic differences in gymnotiforms was assembled from published and unpublished sources, and from personal communication with various specialists. These sources include Fink and Fink (1981) for characters of the neurocranium and suspensorium; de la Hoz and Chardon (1973, 1975, 1984) for characters of the ethmoid region, pectoral girdle, and swim bladder; Chardon and de la Hoz (1977) and Arratia (1992) for characters of the suspensorium; Kirschbaum and Meunier (1981), Gayet and Meunier (1991), and Gayet *et al.* (1994) for data pertaining to caudal regeneration and the fossil †*Ellisella*; Mago-Leccia (1978) and Lundberg and Mago-Leccia (1986) for characters of the Sternopygidae; Sullivan (1993; pers. comm.) and Sullivan and Lundberg (1996) for data on electric organs, electric organ discharges, and characters of the Rhamphichthyoidea; and Triques (1993) for characters of the splanchnocranium. Other references are cited with the character descriptions. All character states reported in literature accounts were checked against specimens when material was available, and cases in which the data were coded differently from published accounts are noted in the character descriptions and in the footnotes to the data matrix.

Unless otherwise noted, each OTU was coded for the states observed in the type species as determined by reference to type material and/or collections from the type locality. Observations on types were taken from radiographs, C&S, and/or unprepared specimens. In several cases, previous and continuing work has identified species more plesiomorphic than the type species for an OTU (*e.g.*, *Rhabdolichops electrogrammus* by Lundberg and Mago-Leccia, 1986; *Adontosternarchus sachsi* by Mago-Leccia *et al.*, 1985; *Sternarchogiton* sp. B reported herein). When materials from these species were available they were used to represent their respective genera.

For several OTUs no single species could be identified which was unambiguously representative. Interspecific and intraspecific differences in *Gymnotus* and *Sternopygus* are treated separately (Albert and Miller, 1995; Albert and Fink, 1996). *Eigenmannia* was coded in consideration of the variation observed in all available specimens (noted in the text where appropriate). Variation within and differences between species was also recorded when applying discrete character states. Unpolarized character state variation within an OTU was treated as polymorphic, not as uncertain. The effects of alternative treatments for the coding of polymorphic OTUs are discussed under the section "Parsimony analysis" below.

An attempt was made to decompose all phylogenetically informative variation into binary characters. This study proceeded with the view that phylogenetic characters represent unitary hypotheses of anagenetic change. A goal of this study was to identify particular instances of phenotypic transformation, and under this view, it is not clear what multistate characters represent. The several cases of multistate characters employed represent instances in which a formal hypothesis of evolutionary transformation could not be provided. Multistate characters were coded and analyzed as unordered.

When more than two alternative states exist for a character, it is possible to allot the observable variation into a single character with multiple states, or to partition the variation into two or more characters. Although there is no computational difference in a maximum parsimony analysis between additive binary or ordered multistate characters (Farris *et al.*, 1970), the latter approach was avoided for three reasons. First, the author is unaware of any criteria for unambiguously ordering multistate characters. Second, the use of phenotypic similarity alone to order multistate characters undermines the efficacy of the tree topology to establish the sequence of evolutionary transformations. Last, the freedom allowed to unordered multistate characters renders the results non-comparable with those of binary coding (Hauser and Presch, 1991; Hauser, 1992; Lipscomb, 1992; Wilkinson, 1992).

Parsimony analysis

The principle of maximum parsimony (Hennig, 1966; Wiley, 1981; Sober, 1988) was used to find tree topologies that most economically summarized the results. The data matrix was assembled with the aid of MacClade 3.03 (Maddison and Maddison, 1993). The following options were employed in the parsimony analyses using a test version of PAUP 4.0, written by David L. Swofford (see Swofford, 1993). Due to the large size of the data matrix, heuristic searches were used with the MULPARS option set to save all minimum length trees. Inferred ancestral conditions at internal nodes include only those consistent with all three character optimization methods available in PAUP. Characters determined to be polymorphic on terminal taxa were treated alternatively as polymorphic and as missing data. Tree lengths were longer in the former case. Tree-bisection-reconnection (TBR) branch-swapping was performed with and without the steepest descent option, branches having maximum length zero were collapsed to yield polytomies, topological constraints were not enforced, and initial trees were unrooted. Due to the large number of missing character states the taxon †*Ellisella* was excluded from the parsimony analyses and added to the resulting trees post hoc in a position of maximum parsimony.

A PAUP command file was generated with a constraint statement for each node, and heuristic searches made for trees inconsistent with these constraint statements. Compared with the shortest unconstrained tree, the number of additional steps required on constrained trees inconsistent with a given node is the decay index for that node. For nodes with decay indices of more than a few steps, the constraint statement approach is more effective than enumerating all trees N steps longer than the shortest tree.

Parsimony analyses were replicated using the phylogenetic program Hennig86 version 1.5 (Farris, 1988) with polymorphic taxa coded as unknown, and employing the heuristic branch swapping options mhennig* and bb*. The topology and number of equally parsimonious trees generated by Hennig86 are the same as PAUP given the same assumptions. Although commonly used, bootstrapping and similar techniques were avoided because of the likelihood of deviations from the assumptions required to estimate confidence intervals (Eernisse *et al.*, 1992).

CHARACTER DESCRIPTIONS

The 249 characters and states described in this section are summarized in Appendix 3, and the character-state distributions among 44 OTUs are presented in Table 2. The morphological characters are grouped according to region of the body and organ system with which they are associated following Fink and Fink (1981). These character groups correspond to the association of bony elements that result from standardized dissection methods (Weitzman, 1974) and the developmental-functional units of the osteichthyan (Patterson, 1975; Jollie, 1986; Schultze, 1993), and otophysan skulls (Kindred, 1929; Weitzman, 1962; Fink and Fink, 1981; Arratia and Schultze, 1991, 1992). Within each heading characters are listed in a sequence corresponding to a survey from anterior to posterior, and dorsal to ventral. Developmentally or functionally associated features that are listed under different headings for descriptive purposes are noted where appropriate.

Body shape and integument. Characters of the external body surface not included under other character headings. These include features of gross body proportions, color patterns, and squamation.

1. Body shape. 0: Body laterally compressed, body width at pectoral fin base less than 70% its depth. 1: Body cylindrical or subcylindrical, roughly circular in cross section, body depth at pectoral girdle approximately equal to its width. The polarity of this character at the base of the gymnotiform tree is ambiguous due to different conditions in plesiomorphic Siluriformes and Characiformes.

2. Body depth. 0: Body relatively deep in profile, depth at pectoral girdle more than 11% total length. 1: Body elongate, slender, depth less than 11% total length.

3. Anal fin membrane. 0: Evenly pigmented. 1: With pale posterior patch.

4. Oblique stripes. 0: Body pigmentation evenly distributed along longitudinal axis. 1: Multiple (13 - 50) pale bands of alternating high and low melanophore density along lateral surface of body, oriented at an oblique angle to longitudinal body axis (Mago-Leccia, 1994, figs. 70-76, 81-84; Albert and Miller, 1995, fig. 1). Bands sometimes interrupted by patches of depigmented integument, resulting in a distribution of blotches arranged in oblique bands along the lateral surface of body (Albert and Miller, 1995).

5. Saddle-shaped bars. 0: Absent from dorsum. 1: 1 - 10 dark bars across mid-dorsal surface extending as vertical bands onto lateral surfaces.

6. Irregular blotches. 0: Pigments distributed homogeneously over body surface. 1: Irregular spots and blotches of dark pigment distributed over majority of body surface.

7. Caudal peduncle. 0: Even coloration in skin of caudal body region. 1: Depigmented or light patch at base of caudal fin.

8. Longitudinal lines. 0: Absent. 1: 2 - 3 thin dark lines extending posteriorly along the lateral body surface (Campos-da-Paz, 1997). 2: A white narrow stripe extending parallel to the base of the anal-fin pterygiophores, and then posteriorly along the lateral midline (Albert and Fink, 1996).

9. High contrast pigmentation. 0: Body surface yellow or pale brown, lacking high contrast dark brown or black and white pigments. 1: High contrast dark brown or black and white pigments on body surface.

10. Antorbital stripe. 0: Melanophores on snout distributed evenly. 1: Melanophores absent from narrow band passing lateral to nares (Mago-Leccia, 1994, fig. 90).

11. Marbled body coloration. 0: Pigments distributed homogeneously over body surface. 1: Black and white pigments distributed unevenly over body surface, darker and paler areas grading into one another; integument with a marbled or mottled appearance.

12. Body translucence. 0: Body opaque in living and formalin-fixed specimens, lateral body surface covered with brown melanophores. 1: Body translucent in living specimens, yellow or pink hue in living specimens, yellow or hyaline in formalin-fixed specimens, melanophores sparse or absent on lateral body surface. This character is variable within species. The degree of translucence may depend on environmental variables and ontogenetic stage. In species which exhibit circadian rhythmicity (*e.g., Apteronotus albifrons, Brachyhypopomus brevirostris*) the melanocytes contract at night so that the fishes become light brown or pink (Alves-Gomes, pers. comm.). Color intensity and hue may also be associated with water chemistry and clarity (*e.g.* Sullivan *et al.*, 1996). Pigment markings on specimens of *Eigenmannia virescens* and *Brachyhypopomus pinnicaudatus* are more pronounced in specimens collected in small, clear water streams than in the turbid water of confluence swamps in white-water rivers (pers. obs.). Species characterized by the derived state also vary in the degree to which the body is depigmented. *Eigenmannia limbata* for example, is not as translucent as *E. virescens.*

13. Branchial opening. 0: Branchial opening extends along entire posterior margin of opercle, from isthmus to pectoral fin insertion. 1: Vertical extent of branchial opening restricted to region around pectoral fin base; ventral portion reduced by a dorsolateral continuation of epidermis from isthmus (Lundberg and Mago-Leccia, 1986; Mago-Leccia, 1994; Albert and Fink, character 32, fig. 9).

14. Body squamation. 0: Scales present on body and head. 1: Body devoid of scales (Fink and Fink, 1981, character 124).

15. Cephalic scales. 0: Scales present on body and head. 1: No scales on head, anterior portion of dorsal midline, and area dorsal to pectoral fins. 2: Scales absent from entire mid-dorsal surface.

16. Body scales. 0: Scales present on posterolateral portion of body. 1: Scales absent on posterolateral portion of body.

17. Scales size. 0: Scales small, 9 - 11 scales rows from lateral line to mid-dorsal line at midbody. 1: Scales medium size, 5 - 8

Table 2. Matrix of 249 characters for 42 gymnotiform and two outgroup taxa. "P" indicates taxa polymorphic for 0&1, Q indicates taxa polymorphic for 1&2, and "?" indicates missing data or character state not pertinent. Character descriptions are provided by number in text, and in abbreviated form in Appendix 3.

1-10 81-90 161-170 241-249	11-20 91-100 171-180	21-30 101-110 181-190	31-40 111-120 191-200	41-50 121-130 201-210	51-60 131-140 211-220	61-70 141-150 221-230	71-80 151-160 231-240
Characiformes							
0000000000	0000000000	0000000000	0000000010	0000000000	0000000000	0000000000	0000000000
1000000000	0000000000	0000000000	00000000??	???000000?	?000000000	0000000000	0000000000
0000000000	0000000000	000000????	?0?0000000	0000000000	0000000000	000000????	?00?000??0
????00000							
Siluriformes							
1000000000	000121??00	2000000000	0100000100	0000000000	1100000000	0000000100	0000000000
0000100001	0010000001	0100100000	010001000?	?00100000?	?001000000	0102100001	0000000000
0000010010	0?00000000	000000????	?0?0000000	0000000000	0000000000	000000????	?00?000??0
????00000							
Gymnotus cylindricus							
10000P0000	0000001010	1000110010	1100001100	0000210000	1100011000	0001010100	1000010010
0000100001	001110010?	???110???1	11111?00??	????1?1110	0011100000	0100010101	0010000000
0110110001	1000100011	000010????	?0?1020100	1101202000	000101001?	11?0010010	000?000000
100000100							
Gymnotus carapo							
1011000000	0000001010	1000110010	1100001100	0000210000	1100011000	0001010100	1000010010
0000100001	0011110100	1101101001	11111?00??	????1?1110	0011100000	0100010101	0010000000
0110110001	1000100011	000010????	?0?1030100	1101202000	000101001?	11?0010010	000?000000
010100100							
Gymnotus anguillaris							
1101000000	0000001010	1000110010	1100001100	0000210000	1100011000	0001010100	1000010010
0000100001	001111010?	???110???1	11111?00??	????1?1110	0011100000	0100010101	0010000000
0110110001	1000100011	000010????	?0?1030100	1101202000	000101001?	11?0010010	000?000000
010100100							
Electrophorus electricus							
1100000000	000121??10	0000110010	1000001100	0000210000	1100001000	0001010100	1000010000
0000?00001	0010000000	1101101001	1111110?00	100110110?	?111100000	0110000?01	0010000000
0100010000	?000100111	0000?0????	?0?1040100	111?20?100	00?201001?	11?0011000	000?000000
100000100							
Rhamphichthys rostratus							
0000100000	0010000001	21??001011	11000001?0	0001010011	0111100100	0000000100	00110?0010
0000010111	0011001110	1101101001	1111110?01	1100001110	?111111101	0101110001	0010000000
0000010110	0000000011	0000011000	00?1240100	1100010000	000011111?	11?1110110	000?000000
0000001P0							
Gymnorhamphichthys hypostomus							
0000100000	0010110001	21??001011	11000001?0	0000010011	0111120100	0000000100	0011010000
0000010111	0011001110	1101101001	1111110?01	110000110?	?111111101	0101110001	0010000000
0000010010	0101000011	0000011000	00?1213100	1100010000	000001111?	11?1110110	?1?1000000
0001001P0							
Iracema caiana							
0000100000	0010110001	21?????0??	??????????	?????????1	0????3????	??????????	??????????
??????????	??1100111?	???110???1	11111?0???	??????110?	???????1??	??????????	??????????
??????????	??????0???	??????????	?0?12331??	??0???????	?????1110?	?1?1110??0	??0??00???
??????10?							
Steatogenys elegans							
0000100000	0010000001	21??000011	10000001?0	0010010000	1101100100	011?110100	0010010111
0000010111	0010000110	1101101001	1111111?11	100000110?	?011110001	1001010001	0010000010
0100010111	0000010011	0000010001	00?101?000	1100020000	000001102?	11?0010110	1111100000
0001001P0							
Hypopygus lepturus							
0000100000	0010000001	21??001011	11000001?0	0010010000	0101100100	011?110100	0010010111
0000010111	0010000110	1101101001	1111111?11	1000001110	?011110001	0000010101	1011000010
0100010101	0101100011	0000010001	00?101?000	1100020000	000001102?	11?0010110	1010000000
000100100							
Hypopomus artedi							
0000000000	0010000001	21??000011	11000011?0	0000010000	0101100100	0101000100	00100?0011
0000010111	001100011?	???110???1	1111111???	??????1110	0111110001	0001110001	0010000000
0100010000	0000100011	0000010001	00?1020000	1100010000	000001110?	11?0010110	000?000000
00??00100							

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Table 2. Continued

1-10 81-90 161-170 241-249	11-20 91-100 171-180	21-30 101-110 181-190	31-40 111-120 191-200	41-50 121-130 201-210	51-60 131-140 211-220	61-70 141-150 221-230	71-80 151-160 231-240
Brachyhypopomus brevirostris							
0000100000	0010000001	01??001011	11000001?0	1000010000	0101100100	0101010100	0010010011
0000010111	0010000110	1101101001	1111111?11	1000001110	0111110001	0001110001	0010000000
0100010000	0001110011	0000010001	00?1030000	1100001000	000001110?	11?0010110	PP0?000000
P01000100							
Racenisia fimbriipinna							
1100000000	0010102001	01??000011	11010111?0	0010010000	0101100100	010???0100	00100?0011
0000010111	001000011?	???110???1	111111???	??????1110	0?11110001	0001010001	0010000000
0110110000	0101110011	0000010001	00?1020000	1100100000	000001111?	11?0010110	110?000000
00?000100							
Microsternarchus bilineatus							
1100000000	0010102001	01??000011	11010101?0	0010010000	0101100100	010???0100	00100?0011
0000010111	0010000110	1101101001	1111121?11	1000001110	0?11110001	0000010001	0010000000
0100010000	0101110011	0000010001	00?1020000	1100010000	000001110?	11?0010110	110?000000
001000100							
†*Ellisella kirschbaumi*							
?0????????	???0?0????	??????????	??????????	??????????	??????????	??????????	??????????
?0????????	??????????	??????????	??????????	??????????	???????0?0	010???????	??????????
??????????	??????????	?11?1?????	???1??2000	1??0??00??	??????????	11?10?????	??????????
???????0?							
Sternopygus astrabes							
0000000200	0010000000	0001000011	1010000100	0000110000	0101000001	0001001110	0000010000
1000101000	0010000000	1200100001	1111010100	0011001110	0001100000	0101100001	1010001000
0000010000	010P000011	01101101PP	00?1132000	1000100000	000001100?	11?1010001	000?010012
201010001							
Archolaemus blax							
0000000000	0110000001	0001000011	1010001100	00001??000	0101???0??	0000001110	00001?0000
0000101000	001000100?	???010???1	1111010???	??????1110	0?01??0000	?101110001	0110001000
0000010010	1111000011	1??1110110	00?1131000	100?010001	000001100?	11??10001	000?000010
?0?010?0?							
Distocyclus conirostris							
0000000000	0P10000001	0001000011	1010001100	0000110000	0101100000	0001001110	0000110000
0P00101000	001000000?	1201100001	1111010?00	?011001110	00P1100000	0101110001	0110001010
0000010010	1111010011	1111110110	00?1131000	1000020011	000001100?	11?1010001	000?000010
?0?010?01							
Rhabdolichops electrogrammus							
0100000000	0110100001	0001010011	1100001100	0000110000	1101100000	0001001110	0000110110
1000101000	0010000000	1201100111	1111010?00	1011001110	0011100000	0101100001	0000001000
0000010010	1111010011	1111110100	10?1121100	1000020011	000001100?	11?1010011	000?020012
201010111							
Eigenmannia virescens							
0100000100	0110000001	0001000011	1010001100	0000110000	1101100000	001001110	0000110000
0000101000	0010000000	1201P00001	1111010100	1011101110	0011100000	0101110001	0000001000
0000010010	1111010011	1112110100	00?1121100	1000020011	000001100?	11?1010001	000?020011
2010101P1							
Eigenmannia humboldtii							
0000000000	0010000001	0001000011	1010001100	0000110000	1101100000	0001001110	0000110000
0000101000	0010000000	???1P0???1	1111010???	???10?1110	0011100000	0101110001	0000001000
0000010010	1111010011	1111110100	00?1131000	1000020011	000001100?	11?1010001	000?0?0011
?01010111							
Platyurosternarchus macrostomus							
0000000000	0010003010	2000001011	10?0102100	0000010011	0111000001	00011?0100	0000000000
1110100001	0010000000	1111101001	1111010?00	101101110?	?101110010	111011?111	1011010000
1000010011	1101000011	0110010110	0101231110	1000010000	1100011010	1011010001	000?001112
00?01?1P1							
Sternarchorhynchus oxyrhynchus							
0000000000	0010003001	2000001011	1100000100	0100010012	0111000001	00011?0100	0010000000
1110100001	0010001000	1111101001	1111010?00	101111110?	1111110010	1111110111	0011010000
1000010010	1101000011	0110010110	110122?110	1000010000	1100011010	1011010001	000?001113
0010111P1							
Sternarchorhamphus muelleri							
0000000000	0010103000	2000010011	1000100110	0000011001	0101000001	0001010101	0000010000
1111100001	0010001000	1111111001	1111010?00	101111110?	1111110010	1110110111	1011010000
1000010010	0100000011	0110010110	1111232111	1000010000	0010011001	1011010001	000?001013
10101?111							

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Table 2. Continued

1-10 81-90 161-170 241-249	11-20 91-100 171-180	21-30 101-110 181-190	31-40 111-120 191-200	41-50 121-130 201-210	51-60 131-140 211-220	61-70 141-150 221-230	71-80 151-160 231-240
Orthosternarchus tamandua							
0000000000	0010103000	2000010011	1010012110	000001?001	0101000001	000?1?0101	000001?000
1111100001	0010001000	1111111001	1111010?00	101111110?	?111110010	1120110111	1011010000
1000010000	0100000011	0110010110	1111232111	1000000000	0010011?0	1011010001	000?001013
10101?11?							
Paraptreronotus hasemani							
0000000000	0010000010	0000000011	1010010100	00000??001	0101101010	0001000100	0000010000
1111100001	001000000?	111110?001	1111010???	??????1110	0111100010	1110110111	1011010100
1000010010	1001000011	0110010100	1101121000	1000010000	1000011010	1011010001	000?001?13
00101011?							
Apteronotus cuyuniense							
0000000010	0010000010	2000001011	1010012100	0000010100	0101101010	0001000100	0000010000
1010??0001	001000000?	???110???1	1111010???	??????1?10	0111??0010	11101????1	1????????0
10000100?0	1?01000011	0110010110	?1011P1000	1000000000	1?00011000	1011010001	000?001?1?
001010101							
Apteronotus albifrons							
0000001010	0010000010	2000001111	1010012110	0000010100	0101101010	0001000100	0000010000
1010100001	0010000000	1111101001	1111010100	1011011110	0111100010	1110110111	1011010101
1000010010	1001000011	0110010110	11011P1000	1000010000	1100011000	1011010001	000?001112
001010101							
Apteronotus cuchillejo							
0000001010	0010200000	2000001111	1010011110	1000010100	0101101010	000?1?0100	0000011000
1010100001	001000000?	???1101001	1111010???	??????1110	0111100010	1110110111	1011010100
1001011?10	1001100011	0110010110	11011P1000	1000010000	1100011000	1011010001	000?001?1?
?0101010?							
Apteronotus leptorhynchus							
0000001010	0010000010	2000000P11	1010012110	0000010101	0101101010	0001000100	0100010000
1010100001	0010000000	1111101001	1111010100	1011011110	0111100010	1110110111	1011010101
1000010010	1001000011	0110010110	11011P1100	1000010000	1100011000	1011010001	000?001112
001010101							
Apteronotus cuchillo							
0000001010	1010000000	2000000111	1010012110	0000?10100	0101101010	0001000100	0200010000
10???????1	001000000?	???110???1	1111010???	??????110?	?111100010	111???????	1?????????
?????????0	??01?00011	011001011?	1101121000	1000000000	1100011000	1011010001	000?001?1?
?0101010?							
Apteronotus magdalenensis							
0000001010	101000??00	2000000?11	1010012110	0000???100	0101101010	0001000100	0200010000
10???????1	001000000?	???110???1	1111010???	??????111?	?111100010	111???????	1?????????
?????????0	??01?00011	?1??0101?0	?101121000	100000????	??00011000	1011010001	000?001?1?
?0101010?							
Magosternarchus raptor							
0000000000	0110100110	2000010011	1000000110	0000010001	01?1001000	0000000100	0000000000
1011100001	001000000?	???1101001	1111010???	??????1111	0011100010	1120110111	1?11?10100
1000110010	1001000011	0110010110	1101121100	1000010000	1100011010	1011010001	000?001?1?
00101011?							
Magosternarchus duccis							
0000000000	0110100100	1000010011	1000010110	0000010000	01?1001000	0000000100	0000000000
1111100001	001000000?	???1101001	1111010???	??????1111	0011100010	1120110111	1?11?10100
1000110010	1001000011	0110010110	1101121100	1000010000	1100011010	1011010001	000?001?13
00101011?							
Sternarchella schotti							
0000000000	0110200101	0000010011	1100001110	0000010000	0101101010	0001000100	0000010000
1111100001	0010000000	1111101001	1111010?00	1011011111	0011100010	1120101111	1011110100
1P00110010	1001000011	0110010110	1101121100	1000010000	1P01011010	1011010001	000?001113
001010111							
Sternarchella sima							
0000000000	0110200101	2000010011	1100001110	0000010000	0101101010	0001000100	0000010000
1111100001	0010000000	1111101001	1111010?00	1011011111	0011100010	1120101111	1011110100
1P00110010	1001000011	0110010110	1101121100	1000010000	1P00011010	1011010001	000?00111?
00101011?							
"Apteronotus" apurensis							
0000000000	0110201110	2000000011	1010012110	0000010?00	0101101010	0001000100	0000010000
1110100001	1010000000	1111101001	1111010?00	1011011110	0111100010	1110110111	1011010100
1000010010	1001000011	0110010110	1101121100	1000010000	1100011000	1011010001	000?001?13
00101011?							

(Continued on next page.)

Table 2. Continued.

1-10 81-90 161-170 241-249	11-20 91-100 171-180	21-30 101-110 181-190	31-40 111-120 191-200	41-50 121-130 201-210	51-60 131-140 211-220	61-70 141-150 221-230	71-80 151-160 231-240
Compsaraia sp. 1							
0000000001	0110201110	2000000011	1010112110	0000010001	0101101010	0001000101	00000?0000
1110100001	111000100?	???1101001	1111010???	??????1110	0111100010	111??10?11	1011010100
1001111010	1001001011	0110010110	1101121110	1000010000	1100011000	1011010001	000?001?13
?0101011?							
Compsaraia compsa							
0000000001	0110201110	2000000011	1010012110	0000010001	0101101010	0001000101	0000010000
1110100001	1110001000	111110???1	1111010?00	1011011110	0111100010	111??10111	1011010101
1001111010	1001001011	0110010110	1101121100	1000020000	1100011000	1011010001	000?001?13
00101011?							
"Porotergus" gimbeli							
0000000000	0110201110	2000001011	1010012101	0000???000	0101101010	1001010100	0010011000
11???0???1	001000000?	???110???1	1111010???	??????1110	0011100010	11101?????	1?????????
?????????0	??01001011	011?010110	0101121100	1000010000	1100011000	1011010001	020?001?13
?0101011?							
Sternarchogiton nattereri							
0000000000	0110201100	2000001011	1010011101	1000010000	1101101010	1001010100	0010011000
1110100001	1010000000	?111101001	1111010???	??????1110	0111100010	1110110111	1011010101
1000011000	1101001011	0110010110	P101121110	1000020000	1100011000	1011010001	000?001112
001010111							
Sternarchogiton sp. B							
0000000000	0110201100	2000001011	1010011101	1000010000	1101101010	1001010100	0010011000
1110100001	1010000000	?111101001	1111010???	??????1110	0111100010	1110110111	1011010101
1000011000	1101001011	0110010110	P101121110	1000020000	1100011000	1011010001	000?00111?
00101011?							
Adontosternarchus sachsi							
0000000000	0010001101	0010001011	1010002101	1000010000	1101100010	1001010100	0010011000
1111100001	0010000000	1111101001	1111010?00	1011011110	0011100010	1101110111	1011010100
1001011010	1001001011	0110010100	11011P1100	1000020000	10000110P0	1011010001	020?001112
001010111							

Footnotes to Table 2.

Characiformes: Rows of dentary teeth from *Distichodontus, Hepsetus,* Serrasalimines. Siluriformes: Anterior corpus cerebellum: *Diplomystes* = 1, *Helogenys* = 1. *Gymnotus cylindricus*: EOD monophasic in adults (Kirschbaum, 1994a, fig. 8.8). *Rhamphichthys*: habitat utilization from *R. apurensis,* lower Orinoco. *Steatogenys*: habitat utilization in *S. elegans* = 1, *S. cryptogenys* and *S. duidae* = 0. *Hypopomus:* Body cavity short in some *H. artedi.* Hypaxial electric organ length (Sullivan, pers. comm.). *Brachyhypopomus: B. beebei* mesocoracoid present; opercular accessory electric organ present in undescribed *Brachyhypopomus sp.* (Sullivan, pers. comm.). *Racenisia:* Lateral ethmoid not figured in Mago-Leccia (1994, fig. 77). *†Ellisella:* Cranial skeleton texture from opercle and preopercle of RL 1596; position of neural spines and vertebral morphology from several specimens; preservation of caudal intermusculars questionable; numerous unbranched anal-fin rays in several specimens; anal-fin ray morphology in holotype specimen RL 1596-4 = ?; RL 1596-1 (with regenerated caudal appendage) with deeply branched anal-fin rays; robust impression of caudal plate/rod inferred to indicate ossification; habitat inferred from gray marl matrix. *Sternopygus*: Branchial opening large in *S. xingu*; lateral ethmoid size in *S. xingu* = 0; basihyal dorsal groove in *S. xingu* = 1; mesocoracoid present in *S. aequilabiatus dariensis* (Lundberg and Mago-Leccia, 1986) and paratypes of *S. aequilabiatus pejeraton*, absent in *S. xingu* and *S. macrurus*, *S. astrabes* uncertain (Albert and Fink, 1996); pectoral fin small in *S. xingu*; position of neural spines and posterior chamber gas bladder in *S. macrurus* = 1; epaxial adult electric organ present in *S. macrurus* (Kirschbaum, 1994d). *Archolaemus*: Body translucence in life (Korringa, 1970; Gomes, pers. comm.); lateral ethmoid size (Campos-da-Paz, pers. comm.); anal-fin rays in *A. blax* = 202 - 218; body cavity length (Mago-Leccia, 1994); habitat in Rio Mucajai (Jegu, pers. comm.). *Distocyclus:* Body translucence in *D. goajira* = 0, *D. conirostris* = 1; cranial skeleton texture in *D. goajira* = 0, *D. conirostris* = 1; no. anal-fin rays in *D. conirostris* = 225 - 240, *D. goajira* = 242 - 271; anal-fin pterygiophore length *in D. conirostris* and *D. goajira* = 0; body cavity length in *D. goajira* = 1&2; habitat utilization in *D. conirostris* from large Orinoco and Amazon river channels, *D. goajira* from large Maracaibo river channels. *Rhabdolichops*: oral opening from adult *R. electrogrammus* = 0, *R. troscheli* = 1; no. anal-fin rays in *R. electrogrammus* = 175 - 191. *Eigenmannia humboldtii* body deep in specimens greater than 300 mm. *Eigenmannia virescens*:= 175 - 213, *E. macrops* = 181-239. *Eigenmannia humboldtii*: No. anal-fin rays: *E. nigra* = 220 - 240, *E. humboldtii* = 232 - 265. *Sternarchorhynchus:* No. anal-fin rays in *S. oxyrhynchus* 168-197; lower limit of *S. curvirostris* 164 (Campos-da-Paz, 1997:126); EOD frequencies: *Sternarchorhynchus* sp. 1300 - 1700 Hz (Langner and Scheich, 1978:236, not *Sternarchorhamphus*); EOD active phase coupling (Langner and Scheich, 1978). *Sternarchorhamphus:* EOD frequencies (Sullivan, pers. comm.). *Orthosternarchus*: EOD frequencies (Sullivan, pers. comm.). *Parapteronotus*: snout long in mature male specimens (= *Apteronotus anas*). *Apteronotus leptorhynchus*: Snout long in mature male specimens. *Sternarchogiton nattereri* coded for sexually immature specimens; premaxilla gracile, premaxillary teeth reduced, single row of dentary teeth, dentary gracile, snout short, ventral ethmoid deep, mandibular canal ossicles dumbbell shaped, no endopterygoid ascending process, fourth hypobranchial not ossified, single posterior DHS, AFP blades tapered. *Adontosternarchus*: Rows of dentary teeth in juveniles; locomotion-foraging coded from *A. devenanzii.*

rows above lateral line. 2: Scales large, 3 - 4 rows above lateral line. 3: Scales very small, more than 11 rows above lateral line.

18. Scale shape. 0: Scales dorsal to lateral line ovoid at midbody, their long axes oriented parallel with long axis of body. 1: Scales dorsal to lateral line rhomboid, their long axis oriented oblique to long axis of body, their dorsoventral axes longer than their longitudinal axes (Fig. 5; Myers, 1936a).

Oral jaws. As used here, the oral jaws compose the outer dental arcade of dermal bones of osteichthyans, as well as their associated dentition and ligaments.

19. Gape large. 0: Rictus of mouth extends ventral to nasal capsule, gape forming less than one-third total head length. 1: Rictus extends posterior to a vertical through eye, gape forming more than one-third total head length.

20. Gape short and oblique. 0: Rictus extends ventral to nasal capsule, gape more than three times eye diameter, oriented parallel with long axis of head. 1: Rictus extends to a vertical with mental symphysis, gape very small, less than twice diameter of eye, oriented oblique to long axis of head.

21. Oral opening in adults. 0: Upper and lower jaws of equal length, oral aperture terminal. 1: Lower jaw extends anterior to upper, oral aperture superior. 2: Upper jaw extends anterior to lower, oral aperture inferior. The polarity of this character at the base of the Gymnotiformes is ambiguous due to homoplasy among the outgroups. Whereas the characins *Xenocharax* and *Citharinis* possess a terminal mouth, a subterminal mouth is observed in the characins *Distichodontus* and *Parodon*, and in the plesiomorphic siluriform *Diplomystes.* The mouth is terminal in most sternopygids, variable among hypopomids, superior in the Gymnotidae, and subterminal in rhamphichthyids and most apteronotids.

22. Oral dentition. 0: Oral teeth present in juveniles and adults. 1: No oral teeth in juvenile or adults.

23. Adult dentition. 0: Oral teeth present in juveniles and adults. 1: Oral teeth present in juveniles, lost and not replaced during development.

24. Shape of teeth. 0: Teeth in both jaws conical, with a broad base tapering toward the cusp. 1: Teeth in both jaws villiform, each tooth a long cylindrical shaft with a narrow base (Lundberg and Mago-Leccia, 1986, character 2).

25. Premaxilla size, maxilla orientation. 0: Lateral margin of premaxilla approximately equal in length to lateral margin of maxilla, premaxilla terminating anterior to articulation of maxilla with autopalatine; articular surface of maxilla with autopalatine oriented posteriorly (posteromedially in

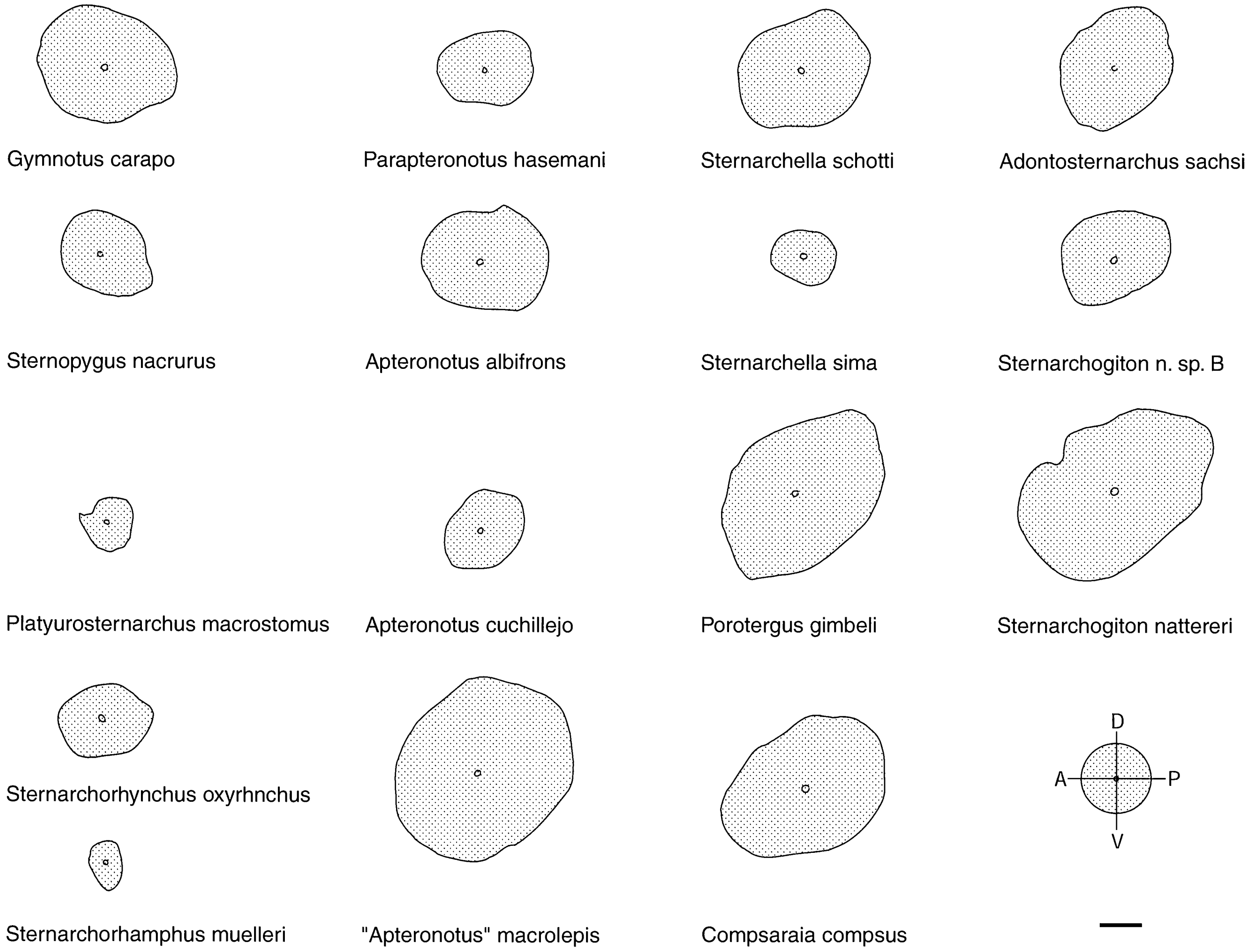


Fig. 5. Camera lucida tracings of gymnotiform scales. All scales from first row above lateral line at about midbody, from the left side of specimens between 150 and 200 mm TL. Orientation given by diagram in lower right (A = anterior, D = dorsal, P = posterior, V=ventral). Scale bar equals 1 mm.

plesiomorphic ostariophysans; Fink and Fink, 1981, fig. 3). 1: Lateral margin of premaxilla longer than lateral margin of maxilla, premaxilla extends posterodorsal to articulation of maxilla with autopalatine; articular surface of maxilla with autopalatine oriented anterodorsally (Fig. 6). The anterodorsal orientation of the articular surface of the maxilla with the autopalatine is a consequence of the large size of the premaxilla and the associated posterior position of the maxilla.

26. Premaxilla shape. 0: Premaxilla triangular in ventral aspect, its anterior margin equal to or longer than its lateral margin, main axis of premaxilla oriented perpendicular to main axis of head; premaxilla bearing three or four irregular rows of teeth at its mid-length, with less than nine teeth along its outer margin in mature specimens. 1: Premaxilla elongate in ventral aspect, its anterior margin less than its lateral margin, the main axis of premaxilla oriented parallel to main axis of body; premaxilla bearing one or two irregular rows of teeth at its midlength, with nine or more teeth along outer margin in mature specimens (Fig 6).

The relative lengths of the anterior and lateral margins of the premaxilla are used as a qualitative measure of premaxillary shape. Number of teeth is used here to quantify the length of the lateral margin of the premaxilla because use of the posterior extent of the premaxilla (*e.g.*, to posterior margin of ventral ethmoid) would require additional evidence for the phylogenetic constancy of the landmark. By contrast, tooth size and the relative spacing of teeth are conserved among plesiomorphic gymnotiforms. Reduction or enlargement of tooth size in several derived gymnotiform clades does not hinder the use of this criterion in assessing the size of the premaxilla among more plesiomorphic gymnotiforms. This definition of premaxillary size does not apply in juveniles because the number of premaxillary teeth varies with age in most gymnotiforms. For example, juvenile specimens of *Gymnotus cf. coatesi* at 48 - 75 mm TL (n = 3) have 6 - 11 premaxillary teeth, and specimens of 150 mm TL (n = 3) possess 13 or 14 premaxillary teeth. Similarly, *Sternarchorhamphus muelleri* specimens ranging from 63 to 233 mm TL (n = 3) have 5 - 23 premaxillary teeth.

27. Premaxilla gracile. 0: Premaxilla broad and triangular; three or four irregular rows of teeth at its midlength, 7-13 teeth along outer margin in mature specimens. 1: Premaxilla gracile in mature specimens, lateral margin concave, anterior margin laminar, curving smoothly into a dorsoposteriorly oriented ridge; fewer than three rows of teeth at its midlength, and never more

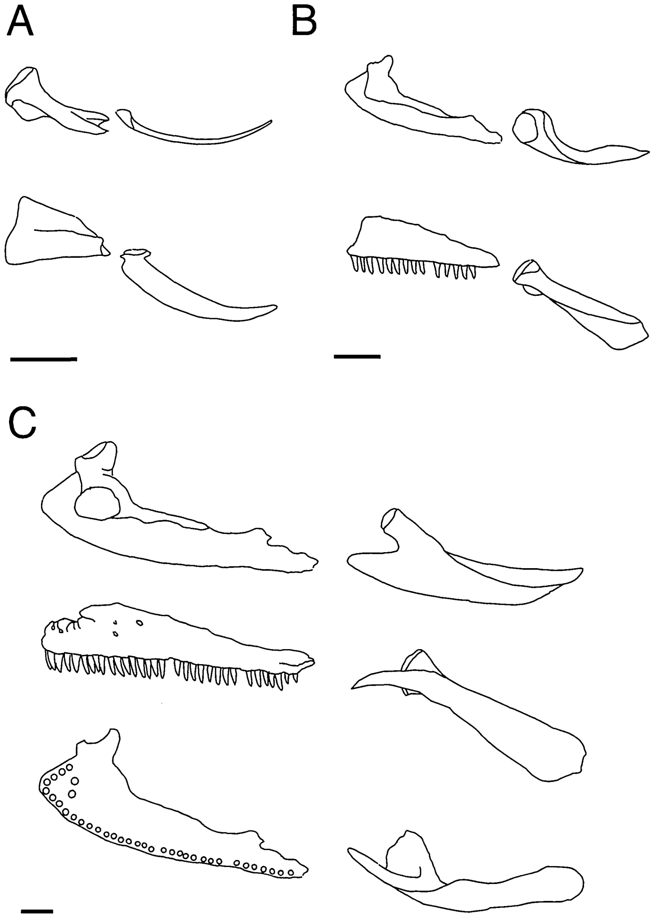


Fig. 6. Right premaxilla and maxilla of selected gymnotiform species. A. *Brachyhypopomus pinnicaudatus* (UMMZ 228984, 70 mm TL). B. *Gymnotus cylindricus* (UMMZ 194122, 105 mm TL). C. *Electrophorus electricus* (UMMZ 183710-S, 1000+ mm TL). For A and B, dorsal views above, lateral views below. For C, ventral view on bottom. The absence of teeth on the maxilla is a gymnotiform synapomorphy (character 22). Note length of lateral margin of premaxilla is larger than that of maxilla (character 19) and articular surface of maxilla is oriented anterodorsally (character 18) in the Gymnotidae (B and C). The derived orientation of maxilla in A is diagnostic of Sternopygoidei (character 23). Scale bars are 1 mm.

than four teeth along outer margin (Fig. 6; Lundberg and Mago-Leccia, 1986, fig. 9; Mago-Leccia, 1994, figs. 65 and 74). The polarity of this character within gymnotiforms is unambiguous. Plesiomorphic characiformes possess a relatively robust premaxilla, and in *Diplomystes* the premaxilla is small and triangular, bearing 7-9 teeth along the medial margin (Arratia, 1987, figs. 14, 23, and 36).

28. White mid-sagital pigments. 0: All mid-sagital surfaces brown. 1: Mid-sagital region of dorsal and mental surfaces bright white.

29. Maxillary dentition. 0: A single row of 6-10 conical teeth in along outer margin of maxilla. 1: No teeth on maxilla (Figs. 7 and 8). The polarity of this character may be determined by analyzing the phylogenetic distribution of teeth among ostariophysan lineages (Fig. 9). The presence of small conical teeth on the oral and branchial jaws is a general osteichthyan feature. Oral teeth are not present in Gonorhynchiformes, *Chanoides*, and Cypriniformes, and may therefore be inferred to have been lost in the ancestral species of Ostariophysi. Nevertheless, three ostariophysan groups possess maxillary teeth; Characiformes, *Diplomystes*, and †*Hypsidoris*. Grande (1987) presents evidence that the morphology and position of the teeth in *Diplomystes* and †*Hypsidoris* are similar to those of plesiomorphic ostariophysans, whereas Arratia (1992) cites positional differ-

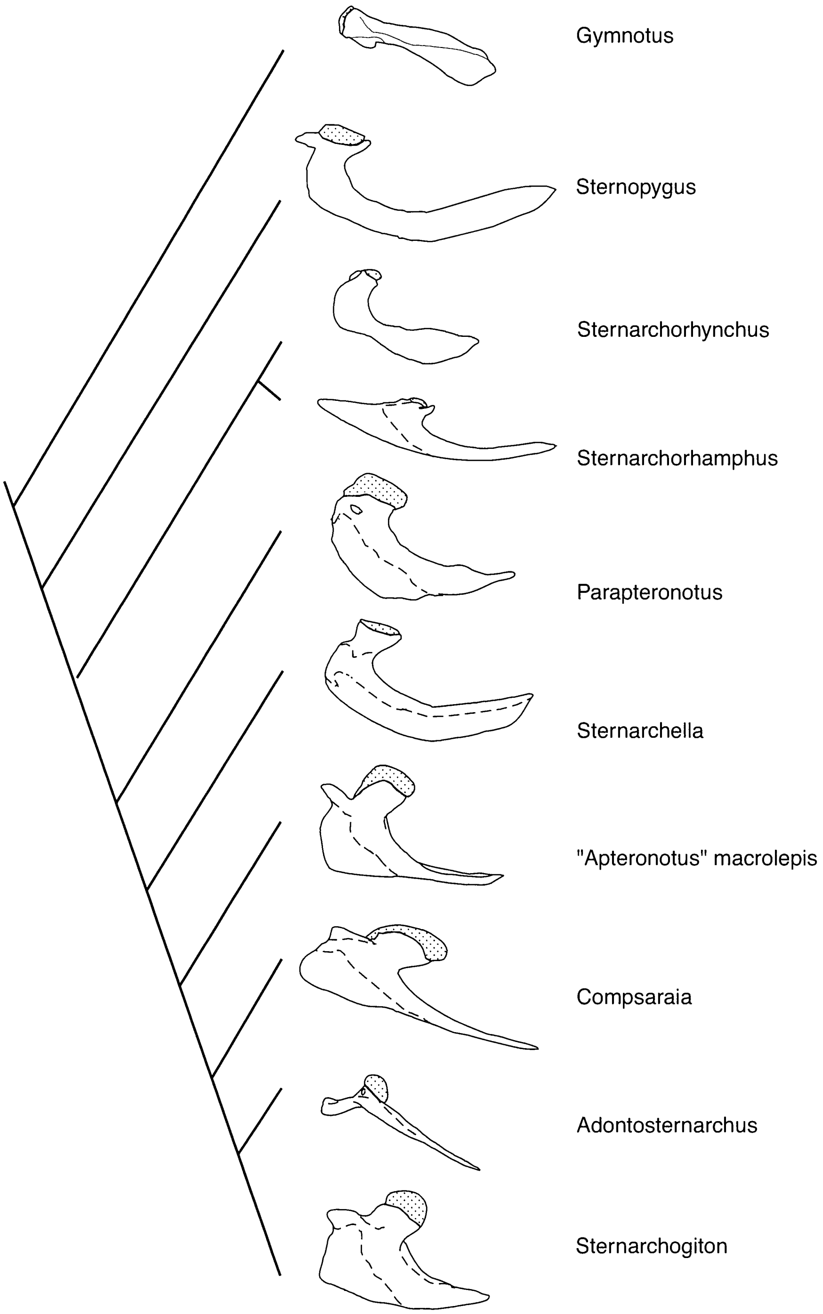


Fig. 7. Diagrammatic representations of the left maxilla in selected gymnotiform species superimposed on tree topology derived from the phylogenetic analysis of 249 characters. Dashed lines indicate margin of laminar bone.

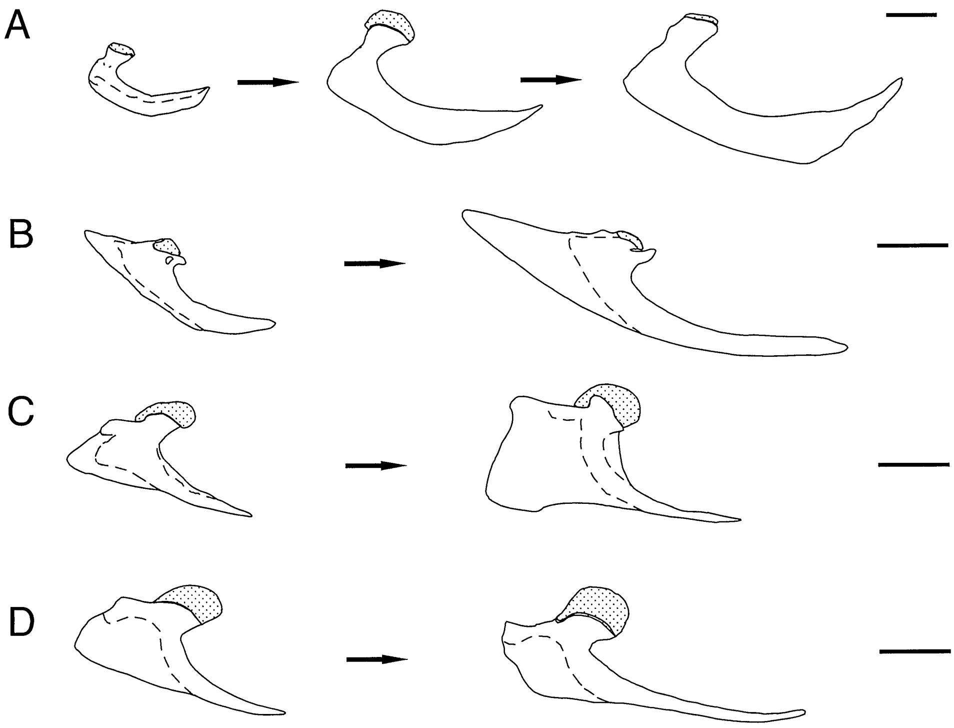
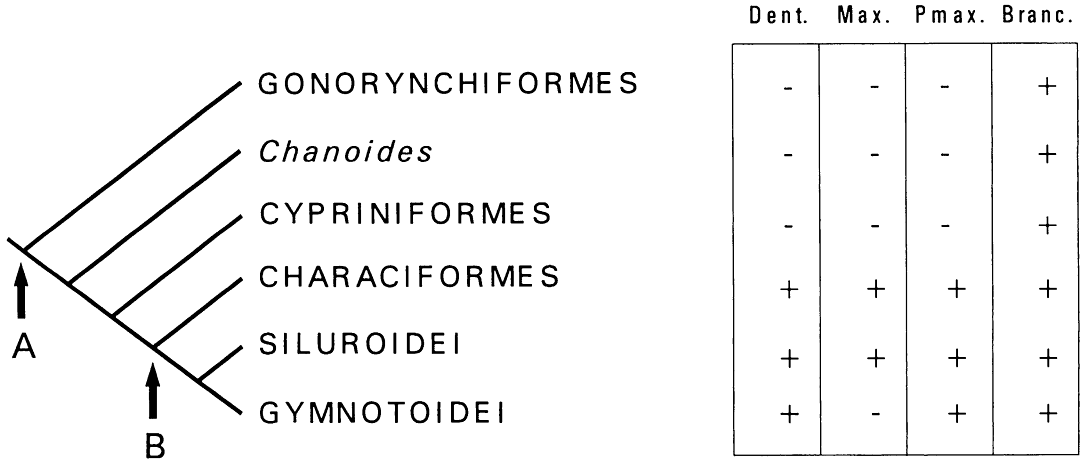


Fig. 8. Ontogenetic transformation of the maxilla in four apteronotid species. A. *Sternarchella orthos* (FMNH 100746, 216 - 226 mm TL). B. *Sternarchorhamphus muelleri* (USNM 228807, 135-220 mm TL). C. *Sternarchogiton* sp. B (UMMZ 211315, 145 - 200 mm TL). D. *Compsaraia compsa* (UMMZ uncat., 170-260 mm TL). Scale bar equals 1 mm.



	Dent.	Max.	Pmax.	Branc.
GONORYNCHIFORMES	-	-	-	+
Chanoides	-	-	-	+
CYPRINIFORMES	-	-	-	+
CHARACIFORMES	+	+	+	+
SILUROIDEI	+	+	+	+
GYMNOTOIDEI	+	-	+	+

Fig. 9. Phylogenetic and spatial distribution of teeth in ostariophysan lineages. Oral teeth may be either maxillary, premaxillary, or dentary. Abbreviations: Branc., branchial; Dent., dentary; Max., maxillary; Pmax., premaxillary. Character states from Fink and Fink (1981), Grande (1987), and Arratia (1992). Note the absence of oral teeth is inferred to be an ostariophysan apomorphy (A), and the presence of oral teeth a characiphysan apomorphy (B).

ences as evidence that they may not be homologous. The hypothesis that maxillary teeth were independently lost in Siluroidea (*sensu* de Pinna, 1993; Siluriformes excluding *Diplomystes* and *†Hypsidoris*) and Gymnotiformes, requires a third step positing the gain of maxillary teeth in Characiphysi (node B in Fig. 9). An equally parsimonious hypothesis is that maxillary teeth have been regained three times independently; in Characiformes, *Diplomystes*, and *†Hypsidoris*.

30. Orientation and shape of maxilla. 0: Maxilla robust, approximately as wide as deep at its midlength; descending blade at least twice as broad near posterior end as near articular surface with autopalatine; main axis straight in vertical plane, ventral margin straight in lateral view; articular surface with autopalatine facing dorsomedially. 1: Maxilla thin, more than twice as deep as wide at its midlength; descending blade relatively narrow, tapering evenly towards its distal tip; main axis curved in vertical plane, sickle-shaped in lateral view; articular surface with autopalatine facing dorsoposteriorly (Fig. 7).

31. Articular head of maxilla. 0: Articular surface of maxilla with autopalatine sessile, continuous with dorsal margin of maxilla; ethmopalatine cartilage forming a discrete quadrangular block bridging articulation of autopalatine and maxilla. 1: Articular surface of maxilla on a stalk, articulation with autopalatine at end of a bony process; ethmopalatine cartilage a small block attached firmly to articular head of maxilla (Figs. 6 and 7; Fink and Fink, 1981, fig. 3).

32. Anterior maxillary process. 0: Anterior process of maxilla extends anterior to articulation of maxilla and autopalatine, forming a tapered process, its ventral margin continuous with descending blade of maxilla; maxilla forked in lateral view. 1: Anterior process of maxilla not ossified; ventral margin of descending blade extends to articulation of maxilla with autopalatine, forming anterior border of maxilla; maxilla crescent shaped in lateral view (Figs. 6 and 7).

Although variable among the appropriate outgroups, the polarity of this character is unambiguous. Although the maxilla of the plesiomorphic characin *Xenocharax* does not have a portion anterior to the articulation with the autopalatine, the process is present in other characiforms (*e.g., Brycon, Rhoadsia*) and other ostariophysans (*Chanos, Opsariicthys*). The process is absent in siluriforms, *Gymnotus*, and some subadult *Electrophorus.*

33. Anterior maxillary process shape. 0: Anterior process of maxilla broad and triangular, its ventral margin continuous with descending blade of maxilla, tapering evenly to anterior tip. 1: Anterior process of maxilla extends as a narrow bar perpendicular to main axis of maxilla, its ventral margin not continuous with that of descending blade (Figs. 6 and 7; Lundberg and Mago-Leccia, 1986, character 4, figs. 6-7).

34. Anterior maxillary margin. 0: Anterior margin of maxilla broad and triangular. 1: Anterior margin cartilaginous, contacting posterior margin of premaxilla (Mago-Leccia, 1994, fig. 74).

35. Anterior maxillary shelf. 0: Anterior process of maxilla extending as a shelf of bone less than one-third the length of the descending blade. 1: Anterior process of maxilla large and broad, extending more than one half the length of the descending blade in mature specimens (Figs. 7 and 8).

36. Anteroventral shelf of descending maxillary blade. 0: Descending blade of maxilla broad and curved; maxilla sickle-shaped in lateral view (character 30, state 0). 1: Descending blade of maxilla broad, connective tissue membrane along its anteroventral margin ossified to form a thin shelf; anterior portion of maxilla rhomboid in lateral view (Figs. 7 and 8).

37. Ventral margin of descending maxillary blade. 0: Ventral margin of descending blade curves evenly towards its distal tip. 1: Ventral margin of descending blade with a sharp angle about two-thirds distance to its tip; ventral margin posterior to this angle relatively straight. 2: Anteroventral margin of descending blade not ossified; distal half of blade extending as a narrow process with a sharp point at its distal tip (Figs. 6 and 8).

38. Maxillary-anguloarticular ligament. 0: Ligament extends between maxilla, adjacent to its articulation with autopalatine, and a part of *Adductor mandibulae* muscle. 1: Ligament extends between maxilla and dorsal tip of anguloarticular at coronoid process of mandible (Gosline, 1971; Fink and Fink, 1981, character 45).

39. Rows of dentary teeth. 0: A single row of teeth on dentary. 1: Teeth on dentary arranged in two to three rows at its midlength. The plesiomorphic condition of tooth arrangement on the dentary of characiphysans is ambiguous. Plesiomorphic characiformes share with the Gymnotidae a single row of teeth on the dentary, with the addition of a single tooth medial to the outer dental arcade in characiformes (Weitzman, 1964). Plesiomorphic siluriforms and sternopygids possess a patch of teeth on the dentary with three to four irregular rows at its midlength (Arratia, 1987, figs. 15 and 26). Some apteronotids cease to replace their teeth during ontogeny (character 23) and rhamphichthyoids have no teeth at all (character 22).

40. Orientation and morphology of mandible. 0: Mandible longer than deep, oral margin of dentary longer than length of anguloarticular; posterodorsal tip of dentary extends posterior to midlength of mandible, its long axis oriented approximately parallel with long axis of head; articulation of dentary with quadrate approximately horizontal with mandibular symphysis. 1: Mandible shorter than deep, oral margin of dentary shorter than length of anguloarticular; posterodorsal tip of dentary extends to midlength of mandible, its long axis oriented at an oblique angle to long axis of head; articulation of dentary with quadrate ventral to a horizontal with mandibular symphysis (Fig. 10).

41. Dentary gracile. 0: Dentary robust, posterodorsal process rounded, ventral margin straight or slightly convex in lateral view. 1: Dentary gracile, posterodorsal process tapering to a point (except in *Adontosternarchus sachsi*), ventral margin concave (Fig. 10).

42. Dentary filamentous. 0: Dentary quadrangular, less than twice as long as deep. 1: Dentary elongate and filamentous, more than four times as long as deep.

43. Dentary process. 0: Ventral margin of dentary straight to its contact with anguloarticular. 1: Ventral margin of anterior portion of dentary bearing a posteriorly oriented process ("dentary hook"), a ventral extension of the medial surface of dentary where it covers the anterior portion of Meckel's cartilage (Mago-Leccia, 1994, fig. 66).

44. *M. Adductor mandibula.* 0: Belly of *Adductor mandibulae* muscle composed of muscle fibers and tendons. 1: Belly of *Adductor mandibulae* muscle invested with ossified intermuscular bones, oriented parallel to main axis of muscle fibers.

45. *M. Adductor mandibulae.* 0: Ventrolateral branch of *m. Adductor mandibulae* (ostariophysan A_1) inserts exclusively on maxilla; two discrete muscle bundles insert on oral jaws; A_1 inserts

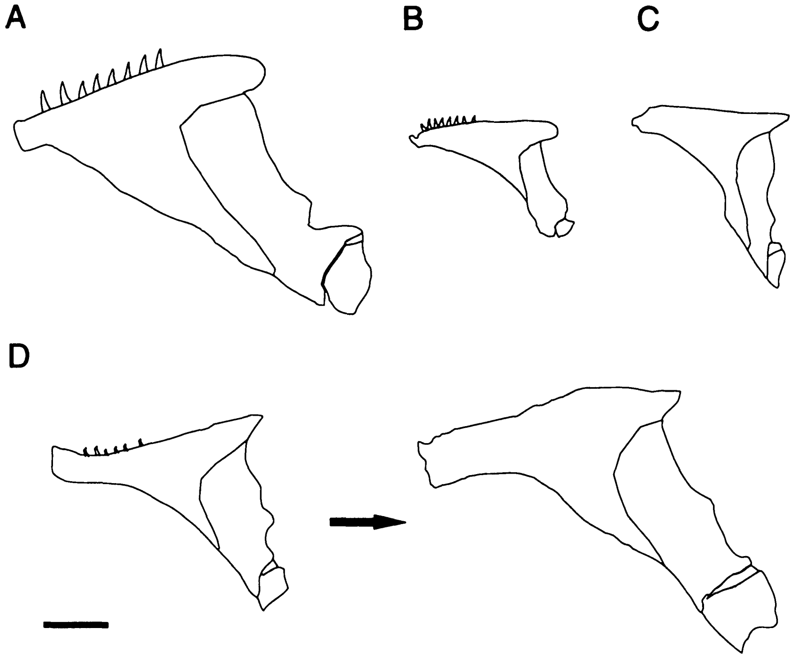


Fig. 10. Camera lucida tracings of the dentary in four apteronotid species. A. *Porotergus gimbeli* (UMMZ uncat., 150 mm TL). B. *Porotergus gymnotus* (CAS 062305, holotype, 30 mm TL). C. *Adontosternarchus sachsi* (UMMZ 204228, 65 mm TL). D. *Sternarchogiton nattereri* (UMMZ uncat., 115-145 mm TL). Scale bar equals 1 mm.

exclusively on maxilla, and A_2 on dentary. 1: Additional insertion of A_1 on first infraorbital (Chardon and de la Hoz, 1973, fig. 3; Aguilera, 1986, fig. 1; see Fink and Fink, 1981, character 127). 2: *M. Adductor mandibulae* undivided bundle, with distal rami inserting on oral jaws (Albert and Miller, 1995).

46. *M. Levator posterior.* 0: Present. 1: Absent.

47. *M. Sternobranchialis.* 0: Absent. 1: Present.

48. Anguloarticular, anterior limb. 0: Anterior limb of anguloarticular longer than posterior limb, measured as distance from dorsal-most point of contact with dentary to anterior and posterior margins. 1: Anterior limb of anguloarticular shorter than posterior limb.

49. Anguloarticular, posterior limb. 0: Posterior limb of anguloarticular small; its contribution to ventral margin of mandible shorter than that of retroarticular. 1: Posterior limb of anguloarticular large; its ventral margin longer than that of retroarticular (modified from Mago-Leccia, 1994).

Neurocranium. The bony and cartilaginous elements enclosing the craniate braincase and paired sensory capsules. A detailed comparative study of the gymnotiform neurocranium is provided by de la Hoz and Chardon (1975).

50. Snout (preorbital distance) long. 0: Length of the snout (preorbital length) about one-third total head length in mature specimens. 1: Snout elongate, frontal, vomer and anterior portion of parasphenoid elongate; preorbital length about one half total head length or greater in mature specimens (Figs. 11 - 17). 2: Snout very elongate, preorbital region more than twice postorbital region, snout gracile and recurved. The length of the preorbital region is negatively allometric during growth in the plesiomorphic gymnotiform condition. The relatively slower growth of the preorbital region in *Sternopygus* and *Gymnotus* (Figs. 11 and 12) results in a relatively shorter snout at larger body sizes (as measured by total head length; Albert and Fink, 1996).

51. Snout length short. 0: Preorbital length about one-third total head length in mature specimens. 1: Snout short, preorbital length less than one-third total head length (Fig. 13).

52. Mesethmoid narrow. 0: Entire length of mesethmoid broad in dorsal view, width of anterior tip approximately equal to width of region between nasal capsules. 1: Mesethmoid narrow near anterior end, forked in dorsal view, narrower between nasal capsules than in more posterior portions (Fink and Fink, 1981, character 5, fig. 3).

53. Length of mesethmoid. 0: Length of mesethmoid less than length of antorbital region of frontal. 1: Mesethmoid elongate, its length greater than antorbital region of frontal.

54. Tip of mesethmoid small. 0: Anterior tip of mesethmoid robust, anterodorsal surface (anterior to ventral ethmoid) broad and concave, with a medial groove located between two large anterolateral processes (forming articulation with premaxillae). 1: Anterior tip of mesethmoid small, anterodorsal surface narrow, with a median knob-shaped process directed anteriorly between two small lateral processes (Fink and Fink, 1981, fig 3E-F). The polarity of this character is ambiguous. Whereas *Diplomystes* and other basal siluriforms lack the medial mesethmoid process, *Xenocharax* and other basal characiformes possess the process. The condition in other ostariophysan groups is also variable (Fink and Fink, 1981). The morphological diversity encoded in this character is similar to character 1 of Triques (1993) which refers to the shape of the lateral processes of the mesethmoid. Variation in the morphology of the plesiomorphic state is discussed by Campos-da-Paz and Costa (1996) in relation to the diagnosis of *Gymnotus.*

55. Dorsal margin of mesethmoid. 0: Portion of mesethmoid anterior to ventral ethmoid horizontal; its dorsal surface anterior and posterior to ventral ethmoid approximately parallel;

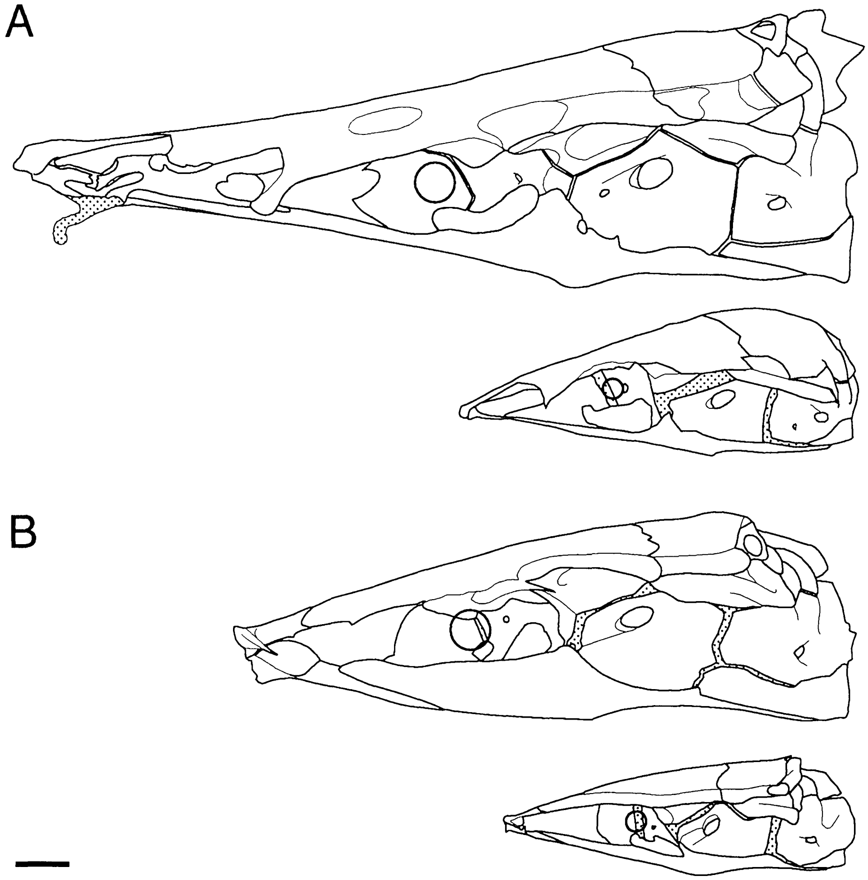


Fig. 11. Adult and juvenile neurocrania of two gymnotiform species. A. *Sternopygus xingu* (USNM 211830), adult on top. B. *Gymnotus maculosus* (UMMZ 190531), adult on top. Position of orbit indicated by circles. Scale bar equals 1 mm.

its ventral surface parallel with dorsal surface. 1: Portion of mesethmoid anterior to ventral ethmoid flexed ventrally in mature specimens; its dorsal surface anterior and posterior to ventral ethmoid at an oblique angle; its ventral surface oblique to dorsal surface (Chardon and de la Hoz, 1974, fig. 4; see Fig. 13). The description of the derived condition applies to all species in which the portion of the ethmoid cartilage anterior to the mesethmoid co-ossifies with the mesethmoid during ontogeny.

56. Mesethmoid anterolateral process. 0: Mesethmoid anterior tip rounded. 1: Mesethmoid with anterolateral process.

57. Anterior mesethmoid groove. 0: Anterior surface of mesethmoid flat or convex. 1: Anterior surface of mesethmoid concave (Figs. 13 and 14).

58. Lateral process of ventral ethmoid. 0: Lateral process of ventral ethmoid extends as a blunt posterolateral process articulating with lateral ethmoid cartilage. 1: No lateral process of ventral ethmoid; ventral ethmoid not contacting lateral ethmoid cartilage. This character is similar to character 12 of Triques (1993) but differs somewhat in definition and phylogenetic distribution. A posterolateral ridge articulating with the lateral ethmoid cartilage can be observed as a thin shelf on the ventral ethmoid of mature specimens of *Gymnotus* and *Electrophorus*.

59. Lateral process of ventral ethmoid. 0: Lateral process of ventral ethmoid narrow, flattened horizontally, posterior surface articulating with lateral ethmoid cartilage. 1: Lateral process of ventral ethmoid robust, posterior surface forming articulation with lateral ethmoid cartilage broad and rounded, covered by a cartilage cap (Fig. 13).

60. Median septum of ventral ethmoid. 0: Portion of ventral ethmoid ossified within medial nasal septum approximately as long as deep; posterior margins of median septum and lateral process of ventral ethmoid approximately equal. 1: Ossified median septum of ventral ethmoid elongate in mature specimens, longer than deep, extending posterior to posterior margin of lateral process (Figs 13 and 14).

61. Shape of ventral ethmoid. 0: Ventral ethmoid longer than deep, deepest at about midlength; anterior tip of snout flat, dorsal surface horizontal. 1: Ventral ethmoid deeper than long, foreshortened on its long axis, deepest posterior to its midlength; tip of snout curved, dorsal surface facing anterodorsal (Figs. 13 and 14).

62. Dermal vomer. 0: Dermal vomer extends from posterior margin of ventral ethmoid to parasphenoid. 1: Dermal vomer not ossified. The dermal portion of the compound vomer does not ossify in hypopomids. This is described as the loss of the "laminar portion of the vomer" by Triques (1993, character 10a); the drawing identified as the "vomer" of *Brachyhypopomus beebei* (Triques, 1993, fig. 4) is the ventral ethmoid component of the teleostean compound vomer. The absence of the dermal vomer in *Hypopomus artedi* is confirmed by de la Hoz and Chardon (1975,

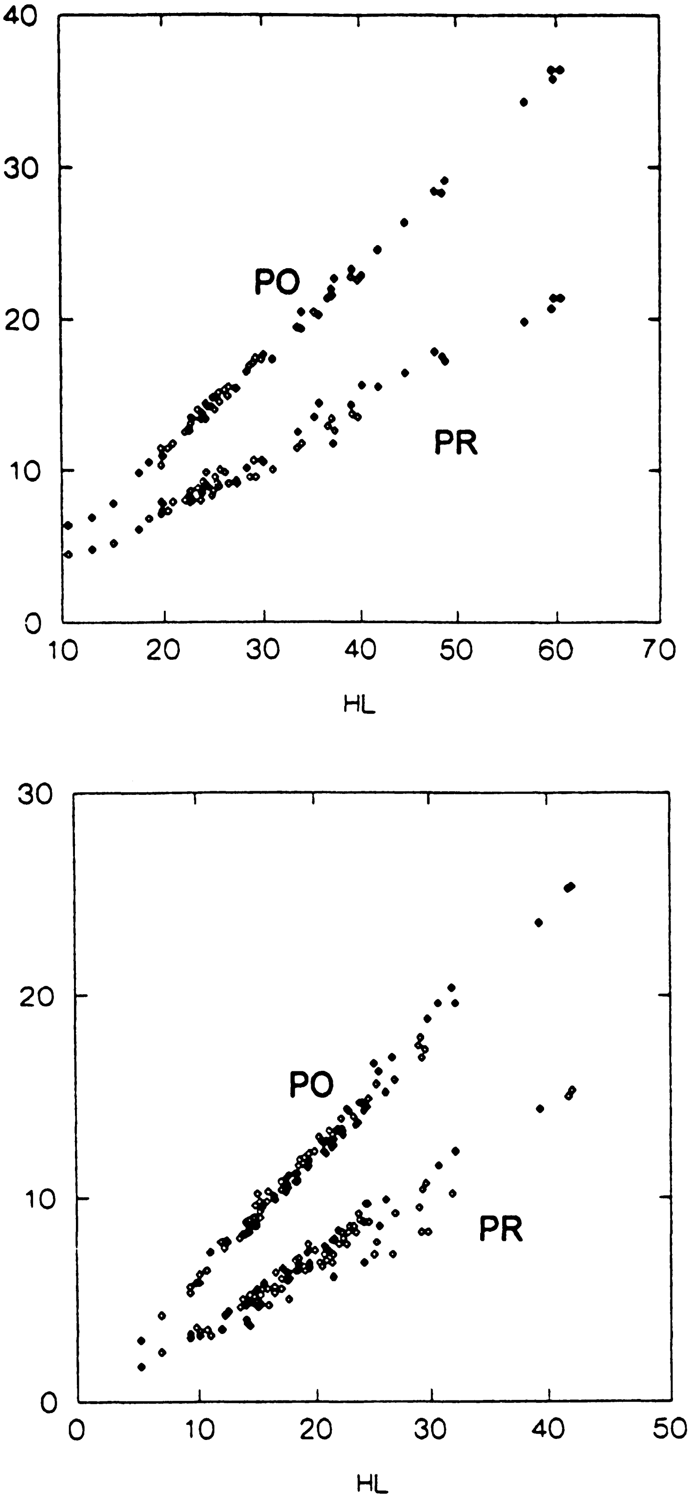


Fig. 12. Plots of preorbital (PR) and postorbital (PO) lengths against total head length (HL) in millimeters. Species of *Sternopygus* in top plot, species of *Gymnotus* in bottom plot. Note that growth in the preorbital region is slower than in the postorbital region.

fig. 4).

63. Ethmoid cartilage. 0: Ethmoid cartilage anterior to lateral ethmoid longer than deep; antorbital region of snout longer than deep. 1: Ethmoid cartilage deeper than long; antorbital region of snout about as deep as long (Chardon and de la Hoz, 1975, fig. 4).

64. Margins of lateral ethmoid. 0: Lateral ethmoid a large endochondral ossification in the antorbital region, arching laterally over profundus (V1) nerve, with four margins; anterolateral process contacting ventral ethmoid, posteromedial process contacting parasphenoid, dorsomedial margin contacting frontal, and anteromedial margin contacting mesethmoid (Fink and Fink, 1981, fig. 2; Albert and Fink, 1996, character 15, fig. 4). 1: Lateral ethmoid reduced in size; four peripheral margins not contacting other bony surfaces (Triques, 1993, character 6a, fig. 3). The distribution of this character is different from that reported by Triques (1993) for rhamphichthyids, and several sternopygid and apteronotid taxa. The lateral ethmoid is equivalent to the parethmoid of de la Hoz and Chardon (1975).

65. Lateral ethmoid ossification. 0: Lateral ethmoid ossified. 1: Lateral ethmoid not ossified (de la Hoz and Chardon, 1974, Triques, 1993, character 7a).

66. Shape of lateral ethmoid. 0: Lateral ethmoid broad; length of its ventral margin more than one half length of its anterior margin. 1: Lateral ethmoid narrow or tubular; length of its base less than one-third length of its anterior margin (Triques, 1993, character 7b; fig. 9).

67. Nasal. 0: Nasal narrow. 1: Nasal broad.

68. Sclerotic bones. 0: Eyes circumscribed by a series of sclerotic bones; 1: Sclerotic bones absent (Fink and Fink, 1981, character 17).

69. Antorbital process of frontal. 0: Lateral margin of frontal smooth in region anterior and dorsal to orbit. 1: Lateroventral process of frontals anterior to orbit (Albert and Fink, 1996, character 20, fig. 4).

70. Dorsal margin of frontal. 0: Dorsal margin of frontal straight or slightly convex in lateral profile. 1: Portion of frontal anterior to orbit concave in lateral profile (Figs. 16 and 17).

71. Cranial fontanels. 0: Paired frontals separated by two gaps along their medial borders; two large midsagittal openings present on dorsal surface of neurocranium. 1: Frontals in contact with each other along the entire extent of their medial margins in mature specimens (Ellis, 1913, plate 17, fig. 1).

72. Length of sphenoid region. 0: Sphenoid region of neurocranium less than one-third total head length in mature specimens, combined axial length of orbitosphenoid and pterosphenoid about equal to length of preorbital region. 1: Sphenoid region of neurocranium more than one-third total head length, combined axial length of the orbitosphenoid and pterosphenoid bones greater than preorbital region. 2: Sphenoid region of neurocranium more than one-third total head length, combined axial length of the orbitosphenoid and pterosphenoid bones greater than preorbital region, orbit positioned at anterior third of head (Figs. 2 and 15).

73. Extent of orbitosphenoid ossification. 0: Orbitosphenoid well ossified in median nasal septum, orbitosphenoid broad, its ventral margin longer than its dorsal margin. 1: Anterior margin of orbitosphenoid not ossified, orbitosphenoid narrow, its ventral margin about as long or shorter than its dorsal margin (Fig. 14 and 16; see also Triques, 1993, fig. 5).

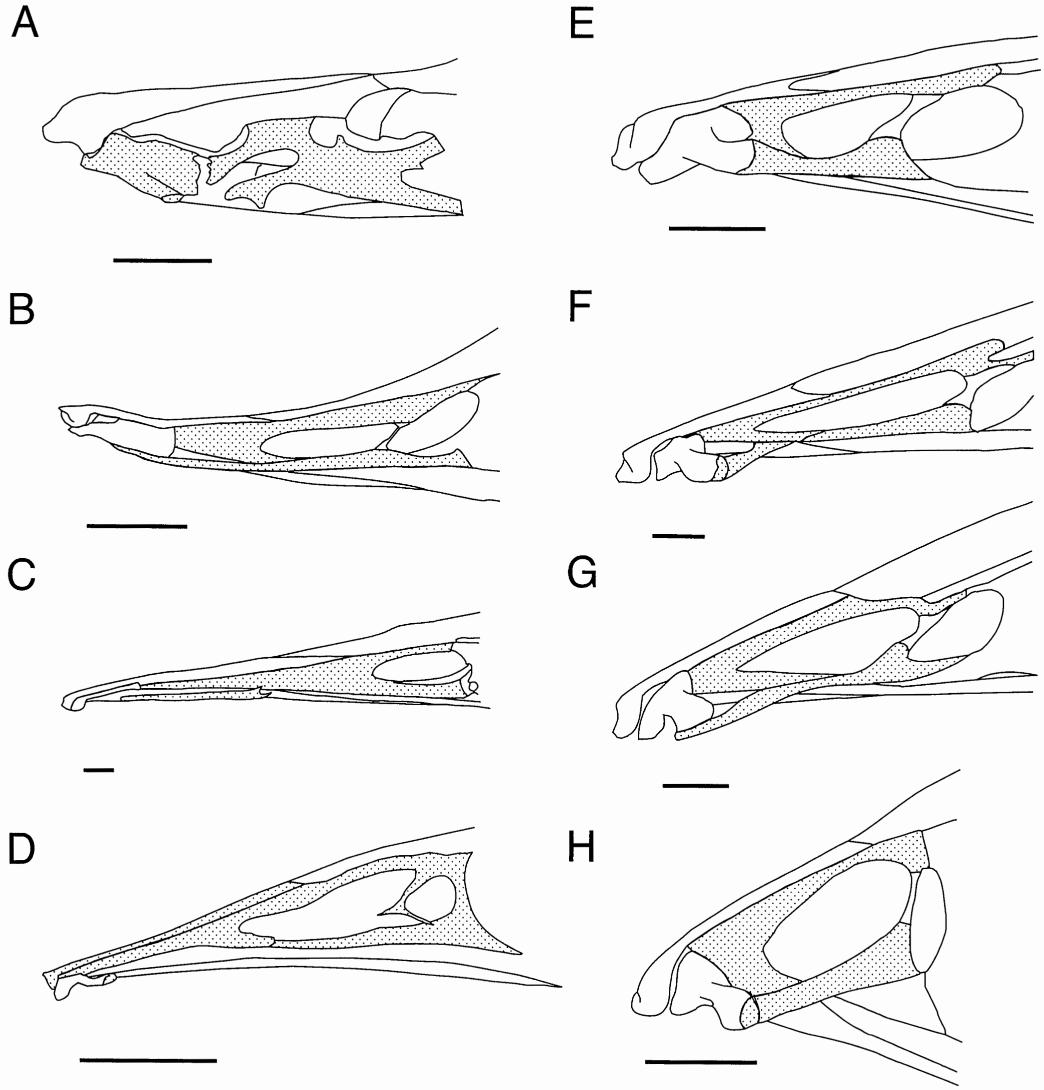


Fig. 13. Camera lucida tracings of the ethmoid region in seven apteronotid and one sternopygid species. A. *Sternopygus xingu.* B. *Sternarchorhamphus muelleri.* C. *Platyurosternarchus macrostomus.* D. *Sternarchorhynchus curvirostris.* E. *Sternarchella orthos.* F. *Parapteronotus hasemani.* G. *Sternarchogiton* sp. B. H. *Adontosternarchus sachsi.* Scale bars equal 1 mm.

74. Sphenoid fenestra. 0: Posterior margin of orbitosphenoid broadly contacting pterosphenoid, separated by means of a narrow block of cartilage in mature specimens. 1: Posterior margin of orbitosphenoid not contacting pterosphenoid, except between dorsal portion of their common margin; presence of an unmineralized fenestra between orbitosphenoid and pterosphenoid (Ellis, 1913, Pl. 17, fig. 2).

75. Sphenotic process. 0: Dorsolateral margin of sphenotic straight, anterior margin underlies frontal. 1: Dorsolateral margin of sphenotic bearing a transversely oriented crest or process exposed on dorsolateral edge, anterior margin not underlying frontal (Lundberg and Mago-Leccia, 1986, character 3, figs. 3 and 4).

76. Lateral processes of parasphenoid. 0: Lateral margins of parasphenoid extending as broad dorsolateral processes anterior to prootic, extending to a horizontal with trigeminal foramen. 1: Lateral margins of parasphenoid not extending to a horizontal with trigeminal foramen (Fig. 16).

77. Ventral margin of parasphenoid. 0: Ventral margin of parasphenoid straight in lateral profile in mature specimens; without a pronounced flexure at conjunction between otic and sphenoid regions of neurocranium. 1: Ventral margin of parasphenoid flexed sharply on either side of the basicranial region; ventral margin of sphenoid region oblique relative to long axis of neurocranium (Figs. 13).

78. Parasphenoid dorsal margin. 0: Dorsal margin broad. 1: Dorsal margin narrow.

79. Parasphenoid process. 0: Anteroventral margin of parasphenoid smooth. 1: Parasphenoid with anteroventral process.

80. Breadth of posterior parasphenoid. 0: Parasphenoid posterior to trigeminal foramen broad, occupying majority of ventral surface of neurocranium. 1: Posterior portion of parasphenoid narrow, occupying less half of ventral surface of neurocranium.

81. Posttemporal fossa. 0: Epioccipital, pterotic and parietal bones contact one another along their mutual margins, forming a bony surface in posttemporal region of neurocranium;

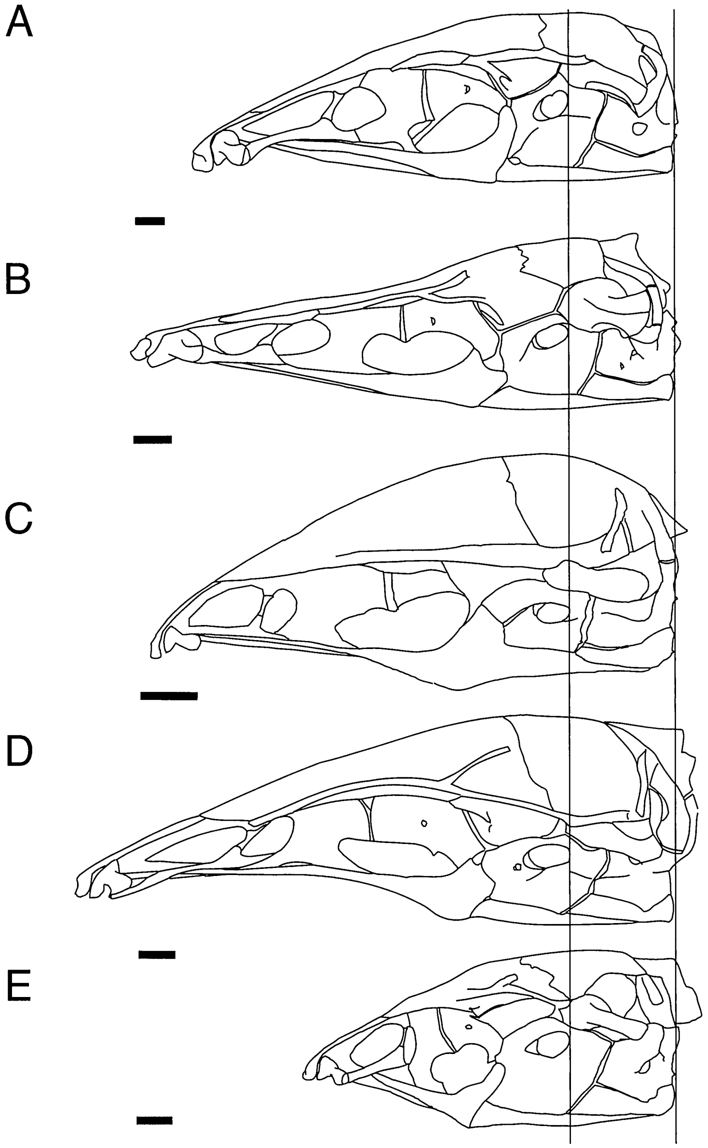


Fig. 14. Diagrammatic representations of the neurocranium in five species of Apteronotinae. A. *"Apteronotus" apurensis* (UMMZ 211315, 145 mm TL). B. *Sternarchella orthos* (FMNH 100746, 246 mm TL). C. *Porotergus gimbeli* (UMMZ uncat., 150 mm TL). D. *Sternarchogiton* sp. B (UMMZ 211315, 200 mm TL). E. *Adontosternarchus sachsi* (UMMZ 204228, 65 mm TL). Size of neurocrania standardized by distance between posterior margins of basioccipital and prootic foramen. Note in panels A, C, and D, the portion of frontals anterior to the orbit is convex in lateral profile, and the ventral margin of the parasphenoid is flexed on either side of sphenoid region. Scale bars equal 1 mm.

lateral surface of otic capsule enclosed. 1: Epioccipital, pterotic, and parietal bones not contacting one another along their mutual margins, forming a fossa in posttemporal region; lateral surface of otic capsule exposed (Mago-Leccia, 1978; Lundberg and Mago-Leccia, 1986, fig. 3). The polarity of this character is ambiguous due to the different conditions observed in the siluriform and characiform outgroups. Although a fossa in the posttemporal region is a plesiomorphic ostariophysan feature retained in most characins (Weitzman, 1962; Fink and Fink, 1981), the dermatoskeleton is entirely ossified in siluriforms, gymnotids, and rhamphichthyoids.

82. Texture of cranial skeleton. 0: Surface of endochondral and dermal ossifications of cranial skeleton composed of lamellar or cancellous bone. 1: Surface of many cranial bones pitted and/or reticular in appearance, excavated during ontogeny to form small pits and vesicles (Fig. 18; Triques, 1993, fig. 3). The apatite crystals of the bone in adult cleared and stained specimens appear aligned with the structure of the reticulate bone at the level of gross morphology, forming an interconnected network of arches and struts. This structure is possible to see at 40x magnification and with bottom illumination. The crystalline structure of juvenile specimens, by contrast, is lamellar or cancellous, like that of ordinary dermal and endochondral bone. These observations are taken as evidence for the action of active mineral remodeling and bone deposition during growth, and not just as the product of deossification alone.

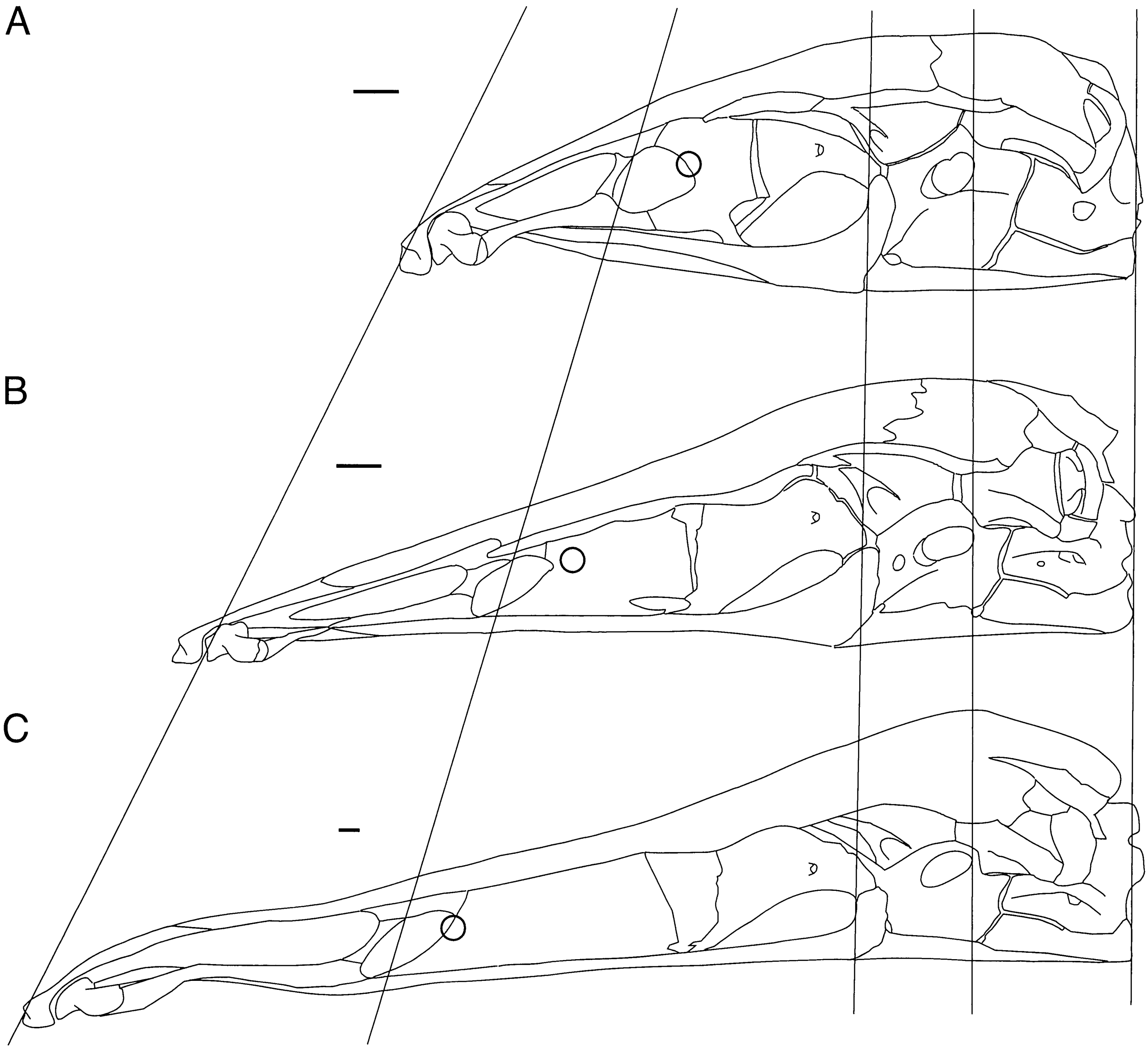


Fig. 15. Diagrammatic representations of the neurocranium in three species of *Apteronotus*. A. "*Apteronotus*" *apurensis* (UMMZ 228869, 145 mm TL). B. *Apteronotus leptorhynchus* (UMMZ 145761, 220 mm TL). C. *Apteronotus cuchillo* (UMMZ 157673, 215 mm TL). Size of neurocrania standardized as in Fig. 14. Note the elongate sphenoid region in B and C, where the combined axial extent of orbitosphenoid and pterosphenoid bones is longer than the preorbital length. Position of orbit indicated by circles. Scale bars equal 1 mm.

Laterosensory canals and bones. Ossified or membranous dermal elements associated with the lateralis sensory system.

83. Nasal loop. 0: Commissure connecting infraorbital and supraorbital laterosensory canals oriented vertically, embedded in integument immediately anterior to eye; antorbital and first infraorbital bones situated near posterior nares. 1: Commissure between infraorbital and supraorbital canals extended anteriorly, forming a loop ventrolateral to nasal capsule; antorbital and first infraorbital bones situated near anterior nares (Mago-Leccia, 1994, fig. 22; Fig. 5).

84. Anterior extension of infraorbital canal. 0: Anterior portion of infraorbital canal extending anterior from first infraorbital ventral to nasal capsule; anterior canal pore of infraorbital canal situated anterior to first infraorbital. 1: Anterior extension of infraorbital canal shorter than width of canal pore; anterior canal pore of infraorbital canal situated near first infraorbital (Fig. 19).

85. Antorbital bearing infraorbital canal. 0: Infraorbital canal not extending onto antorbital. 1: Infraorbital canal extending onto antorbital (Mago-Leccia, 1978, figs. 9 and 25; Fig. 19). The antorbital is usually not associated with the sensory canal; among teleosts in general it is the first infraorbital which "forms the bony anterior termination of the infraorbital laterosensory canal system (Weitzman, 1962:28)." Nevertheless, the antorbital may be identified in gymnotiforms (and siluriforms) as the anterior of the seven infraorbital ossifications and by its topographical position directly anterior to the orbit and forming the posteroventral border of the nasal capsule (Lundberg and Mago-Leccia, 1986, fig. 2). It is a broad dermal plate in the Sternopygidae.

86. Antorbital size. 0: Antorbital small, positioned directly anterior to orbit; its posteroventral process smaller than max-

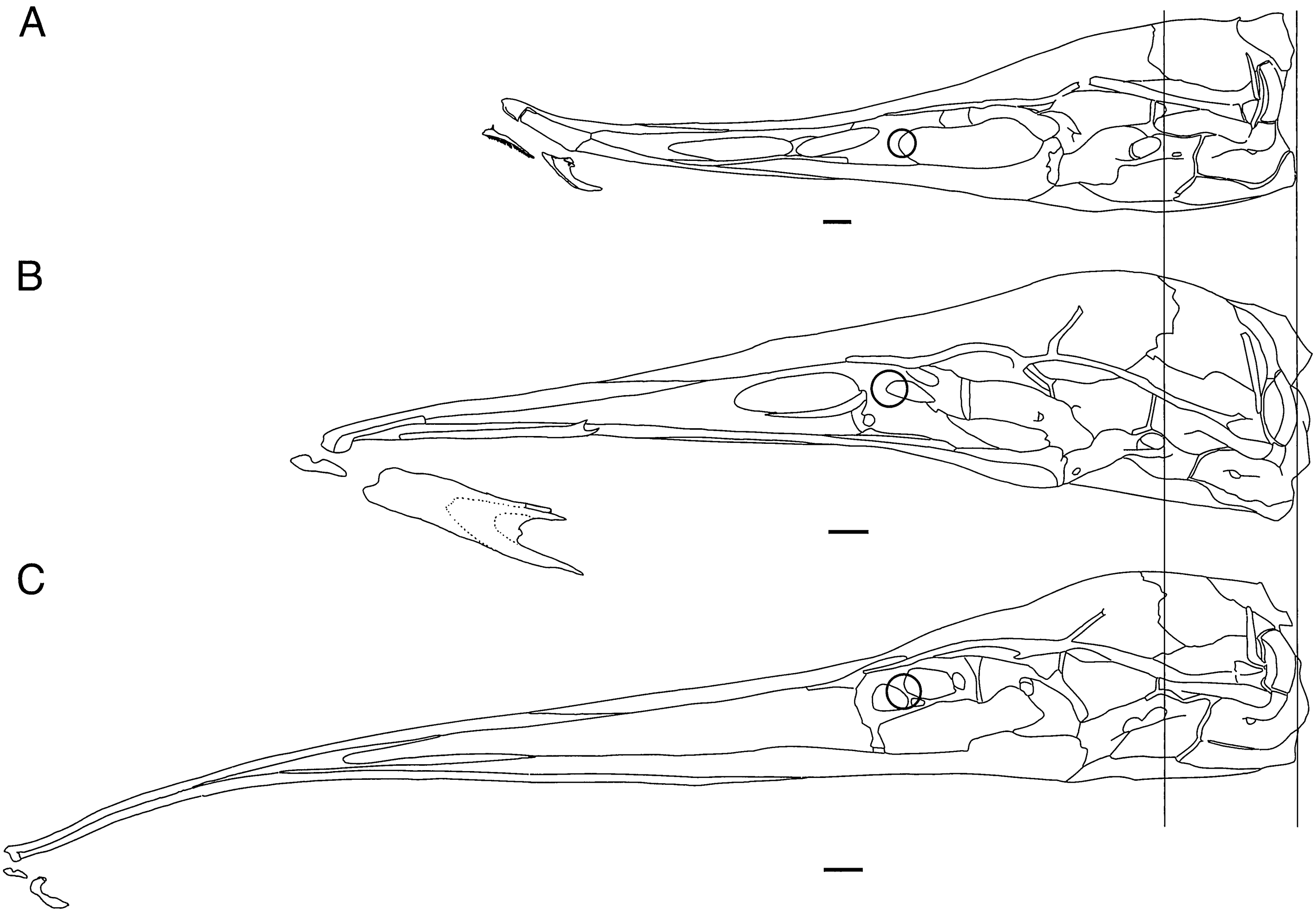


Fig. 16. Diagrammatic representations of the neurocranium and upper oral jaws in three species of the Sternarchorhynchinae. A. *Sternarchorhamphus muelleri*. B. *Platyurosternarchus macrostomus*. C. *Sternarchorhynchus oxyrhynchus*. Size of the neurocrania standardized as in Fig. 14. Scale bars equal 1 mm.

illa; does not contact autopalatine. 1: Antorbital large; its ventral portion larger than maxilla; expanded dorsal portion contacts autopalatine (Triques, 1993, character 18). The derived state of this character is present in several members of the Hypopomidae (*Brachyhypopomus*, *Steatogenys*) but not Rhamphichthyidae, *Electrophorus*, or *Gymnotus*.

87. Infraorbital canal plates. 0: Canal bearing portion of infraorbital bones slender and tubular. 1: Antorbital and infraorbitals 1-4 large, partial cylinders with slender osseous arches (Lundberg and Mago-Leccia, 1986, character 1, fig. 2; Albert and Fink, 1996, character 17). The infraorbital canal of plesiomorphic characiphysans is borne within the infraorbital series of canal bearing bones, whose dermal plates cover the cheek. In Siluriformes, only the canal bearing portions of the infraorbital bones are present, and the cheek is either partially or not covered by bony plates (Fink and Fink, 1981, character 18).

88. Infraorbital canal tube. 0: Canal bearing infraorbital bones present as six separate ossifications. 1: Infraorbital canal a single, lightly ossified continuous tube.

89. First infraorbital absent. 0: Anterior bone of infraorbital laterosensory canal present as a dermal ossification anterior to first infraorbital and dorsal to maxilla. 1: First infraorbital not present as a separate ossification.

90. Preopercular-mandibular laterosensory canal. 0: Canal bearing bones of preopercular-mandibular laterosensory canal long and slender ossifications embedded in dermis; diameter of canal slender. 1: Preopercular-mandibular laterosensory canal bones large and fused with mandible; diameter of canal wide (Mago-Leccia, 1978, figs. 8 and 25).

91. Mandibular canal bones. 0: Canal bearing bones of mandibular laterosensory canal long and slender tubes. 1: Canal bearing bones of mandibular laterosensory canal ossified as short, broad, dumbbell-shaped ossicles (Fig. 19).

92. Supratemporal laterosensory canal. 0: Supratemporal laterosensory canal straight, extending dorsally onto posterior portion of parietal; terminal pore oriented dorsoposteriorly; epidermis overlying supratemporal canal indistinguishable from general epidermis. 1: Supratemporal laterosensory canal curved at a sharp angle on surface of parietal, extending posterior onto epaxial surface of body; terminal canal pore oriented posteriorly; epidermis overlying supratemporal canal depigmented,

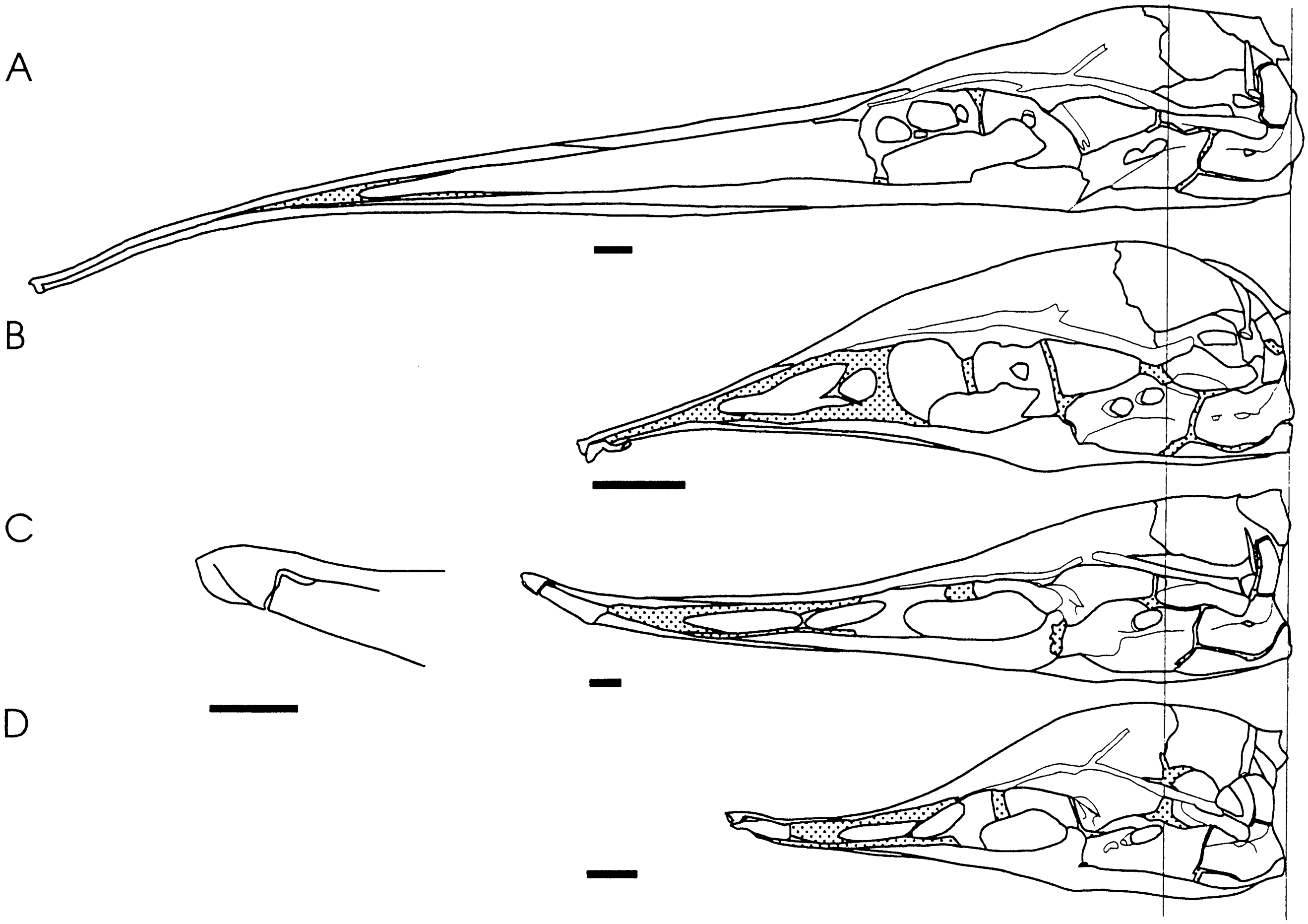


Fig. 17. Diagrammatic representations of the neurocranium in adult and juvenile specimens of two sternarchorhynchine taxa. A. *Sternarchorhynchus* (adult *S. oxyrhynchus* USNM 228987, 255 mm TL, juvenile specimen identified to genus only, FMNH 96983, 44 mm TL). B. *Sternarchorhamphus muelleri*, adult specimen USNM 228807, 233 mm TL, juvenile specimen USNM 228807, 162 mm TL). Size of the neurocrania standardized as in Fig. 14. Scale bars equal 1mm.

forming a pale inverted L shaped patch (Mago-Leccia, 1994, fig. 90; Figs. 19 and 20).

93. Intercalar. 0: Intercalar present on surface of endochondral cranium in region where pterotic, epioccipital, and exoccipitals meet. 1: Intercalar absent (Fink and Fink, 1981, character 13, figs. 5D-E).

94. Lateral line pores. 0: Posterior lateral line canal pores short; tube length less than three pore diameters. 1: Posterior lateral line pores tubular; tube length more than three times pore diameter.

95. Lateral line ventral rami. 0: No ventral rami of lateral line. 1: Numerous ventral rami extending parallel with lateral line.

96. Number ventral rami. 0: less than 16. 1: more than 16.

Sensory and neural. Characters of the central and peripheral nervous systems including the anatomical substrates of sensory and motor systems (*e.g.*, nerves, brain nuclei), and their physiological manifestations (*e.g.*, functions, behaviors). Data on the gross morphology and histology of gymnotiform neural structures have been studied in species representing several gymnotiform lineages (Lazar *et al.*, 1987; Shumway, 1989a; 1989b; Lannoo *et al.*, 1989; Losier and Matsubara, 1990; Lannoo *et al.*, 1990; 1991a; 1991b; 1992; Heiligenberg, 1989; 1991). Drawings of external brain morphology are provided in Figs. 21 - 27, and of standard histological sections in Figs. 28 and 29 (Albert *et al.*, 1998b).

97. Position of nasal capsule. 0: Nasal capsule, including olfactory epithelium and olfactory sensory neurons, positioned relatively posteriorly on snout; located closer to eye than to anterior tip of snout; posterior nares closer to anterior margin of eye than to anterior nares. 1: Anterior position of nasal capsule; located closer to tip of snout than to eye; posterior nares closer to anterior nares than to anterior margin of eye (Fig. 19).

98. Position of anterior nares. 0: Anterior nares situated on dorsal surface of snout, narial opening oriented dorsally. 1: Anterior nares located very close to or within gape, narial opening oriented anteroventrally (Mago-Leccia, 1994, figs. 69-B and 78-B).

99. Anterior narial pore. 0: Anterior narial opening situated at end of a short tube. 1: Anterior narial opening sessile, its rim flush with surrounding integument.

100. Olfactory bulb. 0: Olfactory bulb remote from rest of forebrain; olfactory tract longer than length of olfactory lobe.

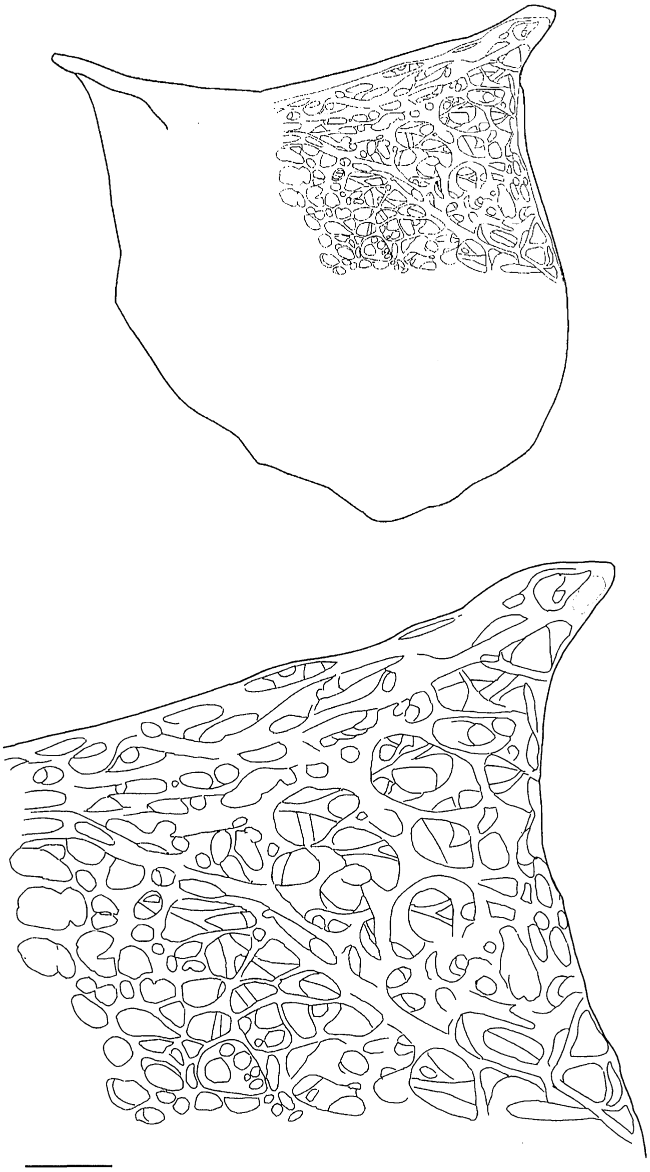


Fig. 18. Portion of the opercle of *Sternarchella sima* showing detail of reticulate ossification. Scale bar equals 1 mm.

1: Olfactory bulb sessile, positioned directly ventral to anterior pole of forebrain; olfactory tract shorter length of olfactory lobe (Vari, 1979; Fink and Fink, 1981, character 123).

101. Telencephalic area Dorsalis. 0: Anterior division of telencephalic area Dorsalis centralis (Dca) about equal in cross sectional area to dorsal division of telencephalic area Dorsalis lateralis (Dld); area Dorsalis medialis (Dm) about equal in cross sectional area to Dld; area Dm3 not separated into rostral and caudal divisions; ventral division of telencephalic area Dorsalis lateralis (Dlv) not segregated into dorsal and ventral divisions. 1: Dca larger in cross sectional area than Dld; Dm smaller in cross sectional area than Dld; rostral and caudal portions of Dm3 segregated; Dlvd and Dlvv segregated (Albert *et al.*, 1998; Striedter, 1992, figs. 5-7; Figs. 28 and 29). The three features described are unique and unreversed diagnostic characters of the Gymnotiformes.

102. Posterior division of telencephalic area Dorsalis. 0: Posterior pole of the posterior division of telencephalic area dorsalis (Dp) small, not distinct from more medial nuclei; posterior and anterior poles of Dp approximately equal in cross sectional area. 1: Posterior portion of Dp large and distinct from more medial nuclei, forming a discrete lobe on side of posterior forebrain; posterior pole larger than anterior pole in cross sectional area (Albert *et al.*, 1998).

103. Central division of telencephalic area Dorsalis. 0: Cells of lateral portion of the central division of telencephalic area Dorsalis (Dcl) all of similar size, at least some cells receiving direct afferent input from the lateral preglomerular nucleus of the diencephalon (PGl). 1: Large, histologically distinct population of cells in Dcl (Maler *et al.*, 1990); without afferent input from PGl (Striedter, 1992, figs. 6 and 7). Plesiomorphic condition demonstrated by Corrêa *et al.* (1998, fig. 8).

104. Position of eye. 0: Surface of eye not covered by epidermis in adults; free orbital margin. 1: Eye completely covered by epidermis in adults; orbital margin not free (Lundberg and Mago-Leccia, 1986, character 17).

105. Eye size. 0: Eye and optic tract large; about two eye diameters into postorbital head length. 1: Eye and optic tract small; more than five eye diameters into postorbital head length (Fink and Fink, 1981, character 17).

106. Extrinsic eyeball muscles. 0: Extrinsic eyeball muscles and fibers of nervous innervation robust, their diameters greater than that of *in situ* collagen fibers. 1: Extrinsic eyeball muscles and innervating nerves small or absent, their diameters about the same as collagen fibers (Albert *et al.*, 1998).

107. Accessory optic tract and nucleus. 0: Accessory optic tract large, easily visible in histological sections; neurons of tract organized into a distinct tegmental cell cluster (*i.e.*, accessory optic nucleus; Peyrichoux *et al.*, 1977; Ito *et al.*, 1986). 1: Accessory optic tract reduced or absent; discrete accessory optic nucleus not visible in sections (Finger and Karten, 1978; Sas and Maler, 1986, Lazar *et al.*, 1987). The size of the accessory optic tract and nucleus is correlated with retinal diameter, both of which are large in Sternopygidae, especially *Sternopygus.*

108. Optic tectum. 0: Large, posterior pole extending posterior to trigeminal nerve root. 1: Small, posterior pole extending anterior to trigeminal nerve root.

109. Hypothalamus. 0: Small, less deep than long. 1: Large, deeper than long.

110. Taste buds. 0: Taste buds present on head in characiforms, and over entire integumental surface in siluriforms; diameters of nerves V and VII equal to or larger than that of other cranial nerves in isthmal region; primary facial and vagal sensory nuclei larger than medial octaval nucleus. 1: Taste buds entirely absent from extra-oral integument; nerves V and VII smaller than other cranial nerves of isthmal region; primary facial and vagal sensory nuclei smaller than medial octaval nucleus.

111. Schreckstoff. 0: Schreckstoff (alarm substance), club cells, and fright response present in Ostariophysi. 1: Schreckstoff, club cells, and fright response absent (Pfeiffer, 1977; Fink and Fink, 1981, character 117).

112. Passive electroreception. 0: No ability to detect weak ambient electric fields. 1: Structures and behavioral capacity to detect weak low frequency ambient electric fields, used in predation; associated neural structures in peripheral (*e.g.*, ampul-

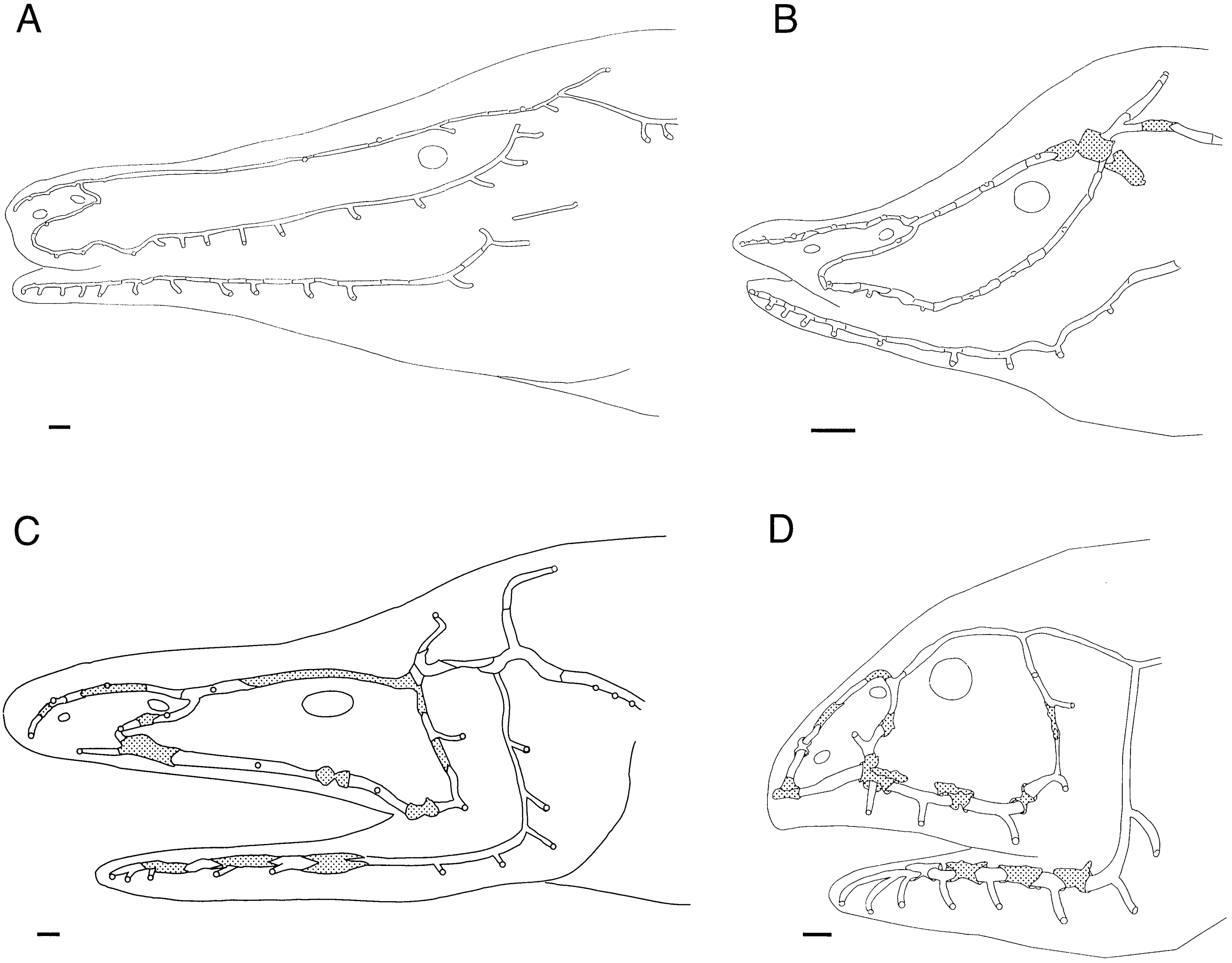


Fig. 19. Camera lucida tracings of cephalic laterosensory canals from four apteronotid species. A. *Orthosternarchus tamandua.* B. *Sternarchorhamphus muelleri.* C. *Compsaraia* sp. 1. D. *Sternarchogiton* sp. B. Note size and position of gape and nares and configuration of lateral sensory canals. Ossified cephalic sensory canal bones shaded. Scale bars equal 1 mm.

lary electroreceptor organs) and central (*e.g.*, electrosensory lateral line lobe, nucleus electrosensorius) nervous systems (Finger, 1986; Carr and Maler, 1986; Bastian, 1986). The homology of electrosensory structures in catfishes and gymnotiform electric fishes was first formalized by Fink and Fink (1981, character 119). The siluriphysan electrosensory system (SES) is diagnosed by a suit of 15 morphological features, listed below with Roman numerals, and organized into five developmental/spatial categories (Carr *et al.*, 1981; Heiligenberg and Dye, 1982; Finger and Tong, 1984; Carr and Maler, 1986).

Electroreceptive periphery.—Lateralis nerves and integumental receptor organs (Northcutt, 1990). i. Low frequency, ampullary-shaped electroreceptor organs, tuned to low frequency (less than 30 Hz) ambient electric fields (Zakon, 1986), with behavioral function in predation. There are no electroreceptor organs in pertinent outgroups; within neopterygians, electroreception has evolved independently in osteoglossomorphs. ii. Electrosensory afferents in the lateral line nerve(s). This feature is character 120 of Fink and Fink (1981). In siluriforms, the afferents are found in all six lateral line nerves (Tong and Finger, 1983); in gymnotiforms they are exclusively in the anteroventral lateral line nerve (Northcutt and Vischer, 1988). There are no electrosensory afferents in pertinent outgroup taxa. Electrosensory afferents terminate in the rhombencephalic electrosensory lateral line nucleus (ELL), and on the posterolateral surface of the cerebellum (EGp), preserving an electrotopic representation of the body surface (Tong and Finger, 1983; New and Singh, 1994). iii. Fusion of preotic lateral line nerve ganglia. During ontogeny, all three preotic lateral line nerve ganglia fuse such that the five anterior lateral line nerves enter the brain in a single bundle (Northcutt, 1992). In non-siluriforms the ganglia are spatially discrete.

Rhombencephalon. Features developing from neurectoderm of the rhombic lip (Lannoo *et al.*, 1990). iv. A primary electroreceptive medullary nucleus, the ELL, with cytoarchitectonic lamination into seven layers (Maler *et al.*, 1974, 1981; Maler,

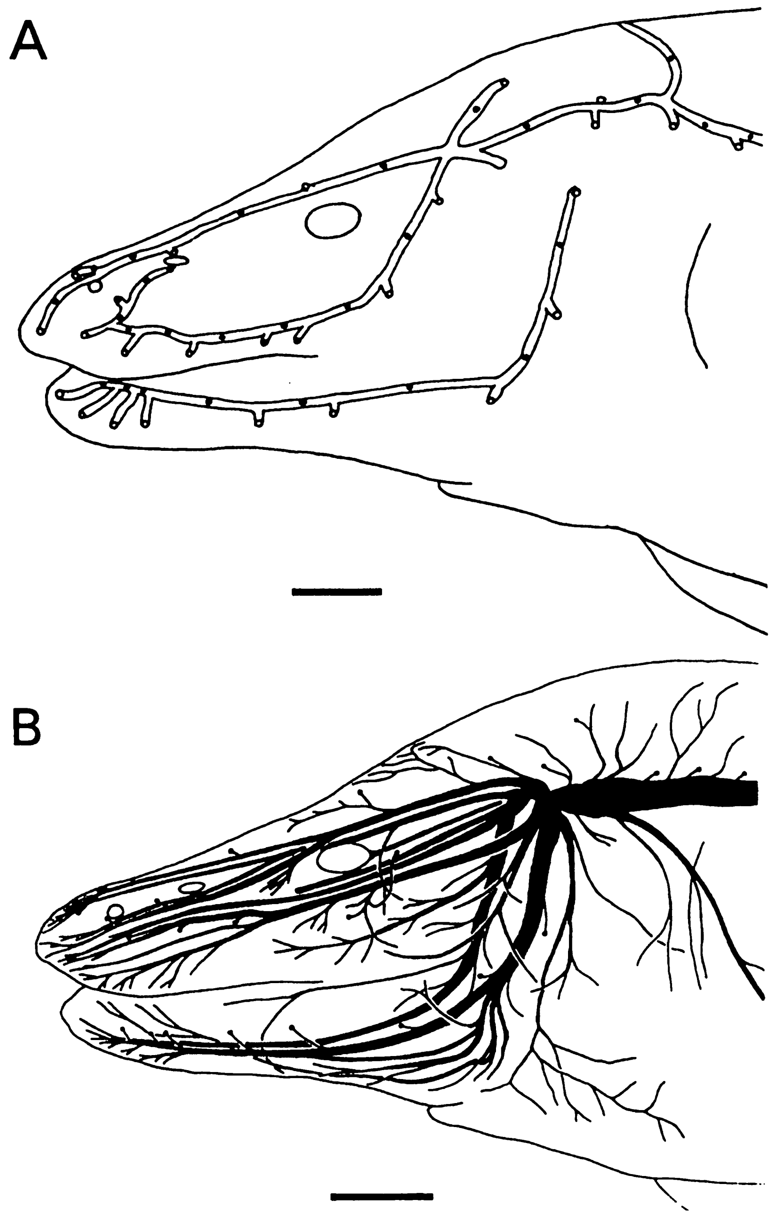


Fig. 20. Camera lucida tracings of the cephalic laterosensory canals (A) and cranial nerves (B) of *Apteronotus leptorhynchus (*Apteronotidae). Black circles represent position of neuromasts. Anterior to left, dorsal to top of page. Scale bars equal 1 mm.

1979; Finger and Tong, 1984; Finger *et al.,* 1986). The cytology and circuitry of the siluriform ELL is summarized by Finger *et al.* (1986, fig. 5) and Carr and Maler (1986, fig. 3), and differs from the electroreceptive medullary nucleus of notopteroids (Finger *et al.,* 1986). Features of the ELL in all siluriphysans are described below, from superficial to deep. Near the dorsal or lateral surface there is a dorsal molecular layer of of parasagittal fibers descending from the posterior eminentia granularis of the cerebellum; below that there is a ventral molecular layer of fibers descending from a midbrain electrosensory nucleus (the PEd). Below these fibers is a layer of efferent (pyramidal/crest) cells whose axonal projections to the lateral lemniscus are bundled into a more ventrally positoined plexiform layer. Siluriformes possess two populations of pyramidal cells recognized by the presence or absence of basilar dendrites. Two populations of granule cells reside in the layer deep to the plexiform layer. Situated in a deep neuropile layer of primary afferents are large (15-20 µm) cells, with dendritic extensions into the lower plexiform layer. The ventral lamina, the deep fiber layer, is the site of primary afferent inputs from the electrosensory periphery.

Similarities between the ELL of siluriforms and gymnotiforms extend beyond these cytological features. The electrotopic representation of the body surface in the ELL of all siluriform fishes is maintained along both the longitudinal and dorsoventral axes (Carr *et al.,* 1981; Carr and Maler, 1986; New and Singh, 1994).

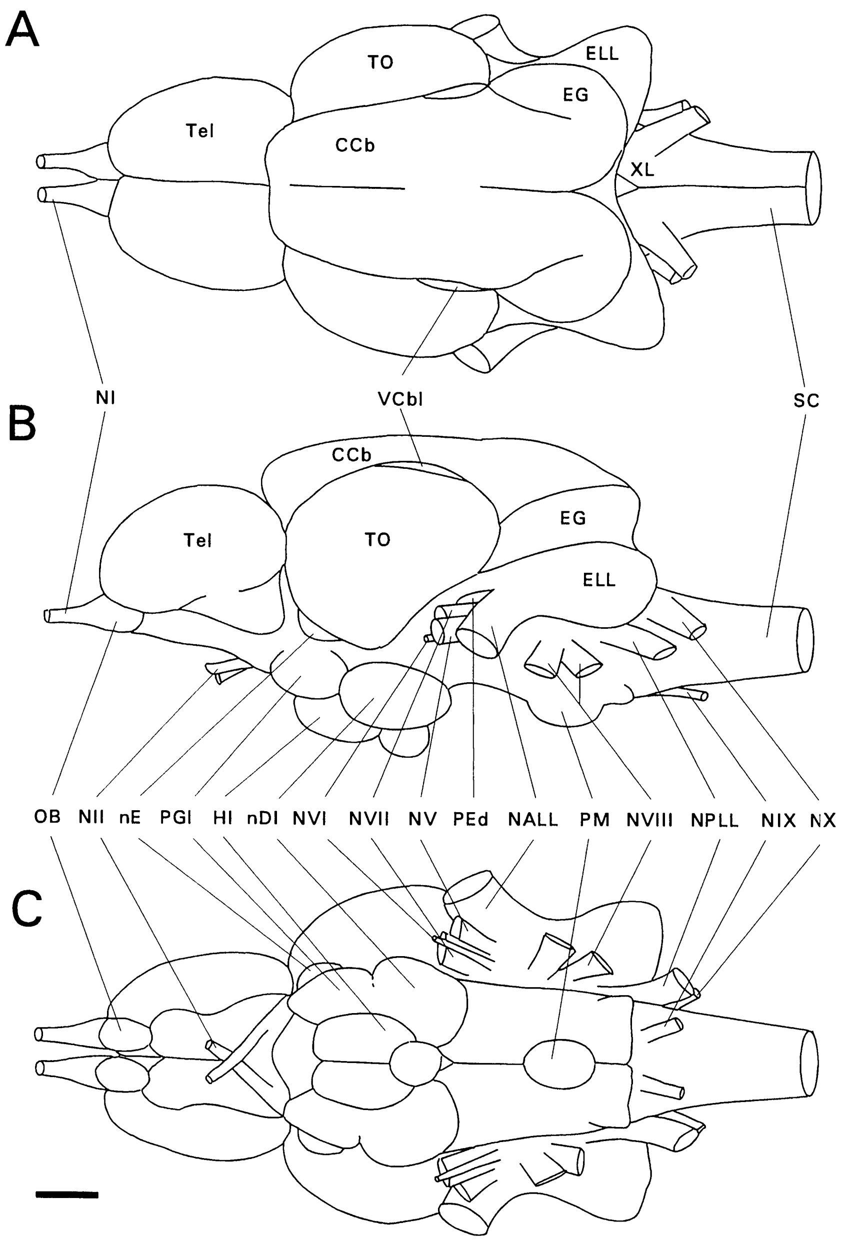


Fig. 21. Dorsal (A), lateral (B), and ventral (C) views of the brain of *Apteronotus leptorhynchus* (Apteronotidae), depicting boundaries of some structures used in descriptions of neural characters. Anterior to left, dorsal to top of page. Scale bar = 1 mm. Abbreviations: CCb, corpus cerebellum; EG, eminentia granularis; ELL, electrosensory lateral line lobe; Hl, lateral nucleus of hypothalamus; NI, olfactory nerve; NII, optic tract; NV, trigeminal and profundus nerves; NVI, abducens nerve; NVIII, eighth nerve; NIX, hypoglossal nerve; NX, vagal nerve; NALL, anterior lateral line nerves; nDl, lateral portion of nucleus diffusus; nE, nucleus electrosensorius; NPLL, posterior lateral line nerve; OB, olfactory bulb; PEd, dorsal praeeminential nucleus; PGl, lateral preglomerular nucleus; PM, pacemaker nucleus; Tel, telencephalon; TO, optic tectum; SC, spinal cord; VCb, valvula cerebellum; XL, vagal lobe. Scale bar equals 1 mm.

The pyramidal cells in the siluriform ELL and the medial segment of the gymnotiform ELL share the expression of a 36 kilodalton polypeptide which is immunoreactive to the monoclonal antibody zebrin II. In teleosts, this response is otherwise only known from cerebellar Purkinje cells and acousticolateralis pyramidal cells (Lannoo *et al.*, 1991a, 1991b, 1992; Hoggatt and Lannoo, 1994). v. The anterior lobe of the corpus cerebellum is large, extending anterior to midlength of the optic tectum (compare panels A and B in Fig. 24). Descriptions of variation in this feature accompany character 124. vi. There is a posterior lobe of the eminentia granularis (EGp), with associated toral, olivary, and cerebellar pathways. A portion of the cerebellar molecular layer receives direct lateral line efferents (exclusively electrosensory in gymnotiforms; Bass, 1982; Tong and Finger, 1983; Sas and Maler, 1987). These include descending toral efferents to the lateral inferior olive, ascending olivary efferents to posterior eminentia granularis, and the projection of cerebellar granule cells via the brachium conjuctivum to the torus semicircularis (Carr *et al.*, 1982).

Lemniscal nuclei. Nuclei and tracts of the lateral lemniscus.

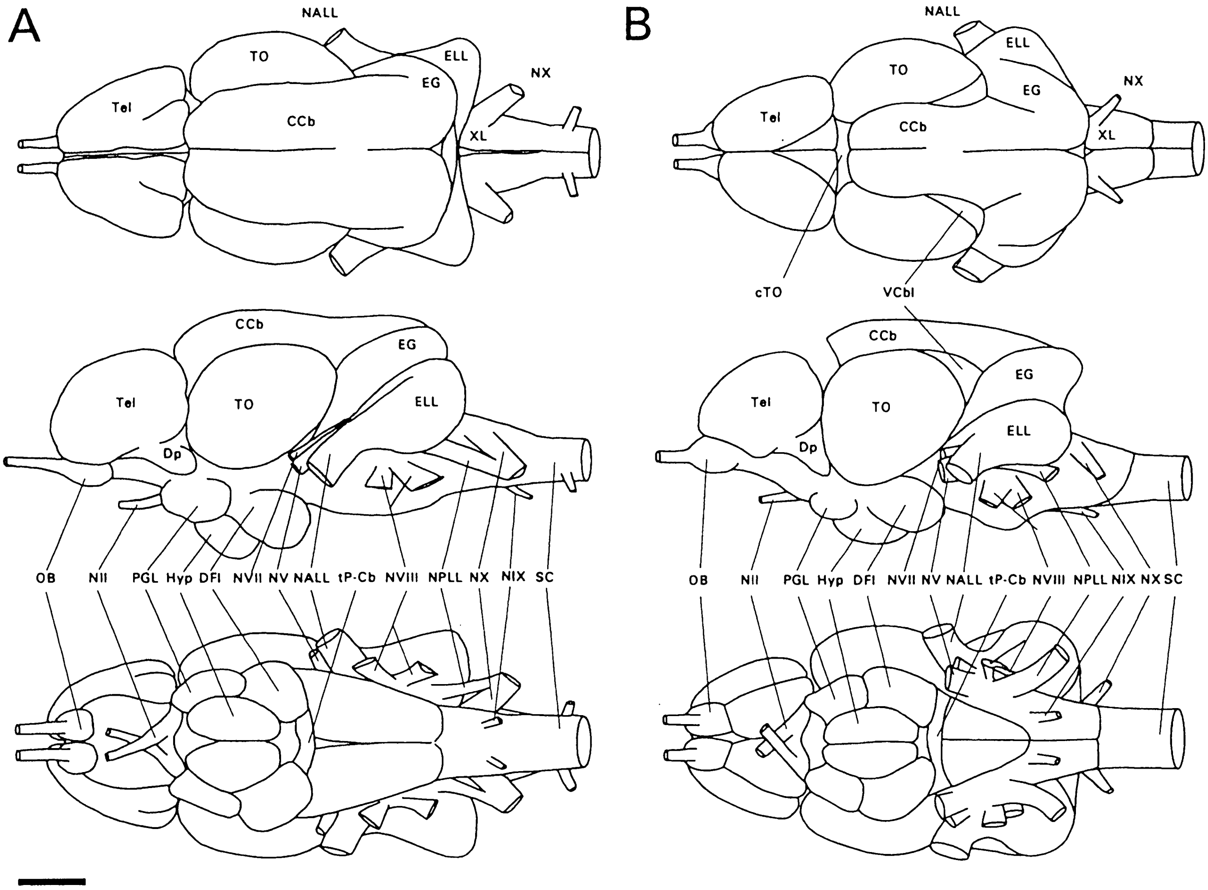


Fig. 22. Dorsal (top), lateral (middle), and ventral (bottom) views of the brains of two sternopygid species. A. *Sternopygus macrurus.* B. *Eigenmannia virescens.* Anterior to left, dorsal to top of page. Abbreviations as in Fig. 21. Scale bar equals 1 mm.

vii. A lateral (or dorsal) and a medial (or ventral) member representing each of the nuclei of the lateral lemniscus (*i.e.*, ELL, PE and TS). The lateral (or dorsal) member of each pair is electrosensory; the medial (or ventral) member is mechanosensory. In outgroups, there is no electrosensory component to the lateral lemniscus (and thus no nuclei). Each nucleus of the lateral lemniscus is a laminated body with somatotopic preservation of spatial information (Knudsen, 1976, 1977; Carr and Maler, 1986). viii. The torus semicircularis (TS) is large, occupying and almost entirely filling the mesencephalic (third) ventricle (Striedter, 1992). Both mono-and disynaptic electrosensory information pass to the lateral division in siluriforms (TSl), which is homologous with the dorsal division (TSd) in gymnotiforms. Mechanosensory and auditory input project to the medial portion of the TS in siluriforms (TSm and TSc; Finger and Tong, 1984) and the ventral portion in gymnotiforms (TSv; Striedter, 1992).

Diencephalon. Nuclei and tracts of the posterior prosencephalon. Identity of diencephalic nuclei is discussed by Northcutt and Braford (1980); a list of gymnotiform diencephalic nuclei is provided in Albert *et al.* (1998b). ix. Projections from the anterior diencephalic nucleus (nA) to the lateral nucleus preglomerulosus are not present (Striedter, 1991). x. A pretectal laterosensory structure, the nucleus electrosensorius (nE) complex, completes a feedback loop from the TS to the PGl (Striedter, 1990b, fig. 9a, 1991, fig. 14). The nE also projects to the CP in gymnotiforms (Keller *et al.,* 1990; Heiligenberg, 1991, fig. 4.39; Zupanc and Horschke, 1997) but comparative data are unavailable in siluriforms. There is no structure with these connections in other teleosts. xi. The superficial pretectum (PS) is reduced; there are no discrete parvocellular (PSp) or intermediate (PSi) nuclei, as there are in most other teleosts (Northcutt and Wullimann, 1988).

Telencephalon.—The identity of telencephalic nuclei is discussed by Northcutt and Davis (1983, fig. 16) and Murakami *et al.* (1983, 1986). Evolution of the connectivity between diencephalic and telencephalic nuclei in otophysans is summarized by Striedter (1991, fig. 14, 1992, fig. 7) and Butler and Northcutt (1993). xii. The posterior division of telencephalic area dorsalis (Dp) is large, forming a discrete lobe on the side of posterior portion of the forebrain, and contacting the lateral margin. xiii. Projections from division 2 of the medial division of telencephalic area dorsalis (Dm) to PGl are lacking (Striedter, 1992). Such projections are present in the outgroups examined. xiv. There is a lateral portion of the central division of telencephalic area dorsalis (Dcl) (Striedter, 1992). In outgroups, there is no such division. xv. The posterior portion of the central division of telencephalic area dorsalis (Dcp) is large. This portion of the division is small in outgroups (Striedter, 1992).

113. Ampullary rosettes. 0: Ampullary organs distributed individually in integument. 1: Ampullary organs clustered in rosettes (Wachtel and Szamier, 1966; Zakon, 1984).

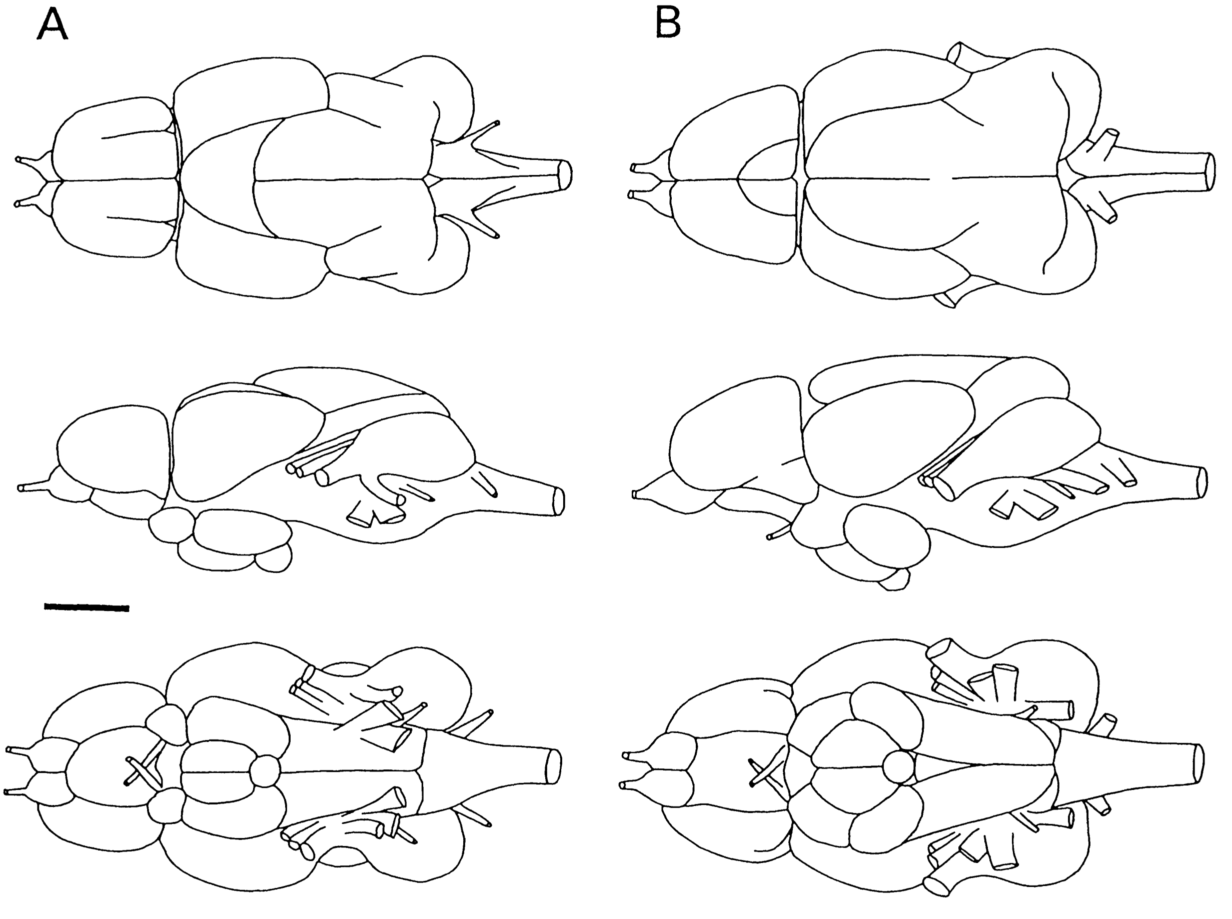


Fig. 23. Dorsal (top), lateral (middle), and ventral (bottom) views of the brains of two gymnotiform species. A. *Gymnotus carapo*. B. *Brachyhypopomus brevirostris*. Anterior to left, dorsal to top of page. Labels omitted for clarity. Scale bar equals 1 mm.

114. Electrogeneration and active electroreception. 0: Passive, low frequency electroreception, used in predation; neural apparatus for detecting low frequency electric currents. 1: Electrogeneration and high frequency electroreception, used in communication and navigation (in addition to predation); neural apparatus for producing and detecting high frequency electric currents (Heiligenberg, 1991; Metzner and Heiligenberg, 1992; Fleishman, 1992; Fleishman *et al.*, 1992).

The use of active electroreception in predation is discussed by Lannoo and Lannoo (1993). The suite of neural features which constitutes the gymnotiform electrosensory system is summarized by Carr and Maler (1986) and Heiligenberg (1991). Derived features are known from all major divisions of the nervous system. Features of the sensory periphery (*e.g.*, tuberous electroreceptor organs) are reviewed by Zakon (1986) and of the motor periphery (*e.g.*, electromotor neurons) by Dye and Meyer (1986). Features of the rhombencephalon (*e.g.*, ELL, EGp, IOl) and mesencephalon (*e.g.*, PEd, PPn, and TSl) are reviewed by Dye and Meyer (1986) and Carr and Maler (1986). Features of the prosencephalon include lack of differentiation in the migrated portion of the posterior tuberculum (*i.e.*, SG and CM not segregated from other preglomerular nuclei), and no projection from CP to PGl (Striedter, 1992, figs. 5-7). Derived features of the gymnotiform telencephalon not directly linked to electroreception are described separately as characters 5-7. Correlated with the large electrosensory nuclei of gymnotiforms is the reduction of several structures mediating other sensory modalities. Compared with outgroup taxa lacking a pronounced gustatory system (*e.g.*, *Pygocentrus*; *Esox*), the facial lobe and secondary gustatory nucleus of gymnotiforms are reduced (unpubl. obs.). Reduced characters in sensory systems exhibiting different phylogenetic distributions are treated separately.

Alves-Gomes *et al.* (1995) describe five features associated with the plesiomorphic mode of gymnotiform electrogeneration. i. Individual electric organ discharges produced as non-overlapping pulses; ii. cells of the medullary pacemaker nucleus (PM) organized into two distinct nuclei, such that pacemaker cells are segregated from relay cells; iii. prepacemaker nucleus of tegmentum with synaptic contact on relay cells (Zupanc and Horschke, 1997); iv. gradual rises in EOD excitatory synapses on pacemaker cells; v. long interruptions of EOD-inhibitory synapses on pacemaker cells (Hopkins *et al.*, 1990).

115. Tuberous electroreceptor organs. 0: One class of tuberous electroreceptor organs. 1: Two classes of morphologically distinct tuberous electroreceptor organs (Szabo, 1965; Zakon, 1986).

116. Preotic lateral line nerves. 0: All preotic lateral line nerve

ganglia form from separate placodes, their axonal bundles entering brain separately (Northcutt, 1992). 1: Anterodorsal, anteroventral, and preopercular-mandibular lateral line nerve ganglia fused during ontogeny, their axons entering brain in a single bundle (Albert *et al.,* 1998).

117. Dorsal branch of posterior lateral line nerve. 0: Dorsal branch of posterior lateral line nerve joined with recurrent ramus of anteroventral lateral line nerve; nerve composed of both sets of axons extending along dorsal portion of trunk. 1: Dorsal branch of posterior lateral line nerve separate from recurrent ramus of anteroventral lateral line nerve (Sullivan, 1993).

118. Lateral line nerve afferents. 0: Lateral line afferents from electrosensory periphery intermingled as they course into the electrosensory lateral line lobe (ELL); fibers from different lateral line nerves not segregated. 1: Lateral line afferents fasciculated into discrete bundles; fibers from each lateral line nerve segregated from those of other lateral line nerves (Lannoo and Maler, 1990).

119. Size of ELL. 0: ELL relatively small, its posterior margin perpendicular to neuraxis; its lateral margin convex and rounded in frontal view. 1: ELL relatively large, its posterior margin curved in dorsal aspect, reflected laterally; its lateral margin concave in frontal view (Albert *et al.,* 1998).

120. Shape of ELL. 0: Ventral margin of ELL flat, angle between medial and lateral segments obtuse (more than 90°); lateral segment positioned ventral to lateral margin of cerebellar-medullary cistern, depth of cistern about equal to that of medial octavolateral nucleus. 1: Ventral margin of ELL curved, angle between medial and lateral segments acute (less than 90°); lateral segment dorsal to cerebellar-medullary cistern, cistern compressed, its depth less than that of medial octavolateral nucleus (Albert *et al.,* 1998; Fig. 29).

121. Basilar dendrites of ELL spherical cells. 0: Round spherical cells in ELL tuberous segments, not bearing a basilar dendrite; contacting primary afferents by gap junctions. 1: Oblong spherical cells in ELL tuberous segments, with a single, large basilar dendrite; contacting primary afferents by asymmetrical chemical synapses (Losier and Matsubara, 1990; Albert and Fink, 1996).

122. Anterior extent of eminentia granularis. 0: Eminentia granularis (EG) of dorsal medulla well developed, extending to posterior pole of optic tectum. 1: EG small, its anterior margin not extending to contact optic tectum (Albert *et al.,* 1998).

123. Posterior extent of EG. 0: Posterior margin of EG not extending to posterior margin of ELL. 1: Posterior lobe of EG well developed, wrapped around caudal lobe of cerebellum, its posterior margin extending to a vertical with posterior margin of ELL (Albert *et al.,* 1998).

124. Anterior extent of corpus cerebellum. 0: Anterior lobe of corpus cerebellum extending to midlength of optic tectum; commissure of optic tectum exposed on dorsal surface. 1: Anterior lobe of corpus cerebellum large, extending anterior to midlength of optic tectum; cerebellum overlying commissure of optic tectum (Valentin, 1841, plates 1 and 2, figs. 2-8).

125. Lateral valvula cerebellum. 0: Lateral division of valvula of cerebellum relatively small; less cross sectional area than medial portion of valvula at isthmus; not exposed at superficial margin on lateral surfaces of brain. 1: Lateral division of valvula of cerebellum large; roughly equal in cross sectional area to medial portion of valvula at isthmus; broadly exposed at superficial margin on lateral surfaces of brain (Albert *et al.,* 1998).

126. Pacemaker nucleus. 0: Pacemaker nucleus of medulla oblongata small, positioned on midline of neuraxis, adjacent to medial longitudinal fasciculus; its ventral margin not contacting ventral aspect of medulla. 1: Pacemaker nucleus large, visible as a median, ovoid eminence on ventral surface of medulla; its ventral margin extending to medullary surface (Dye and Meyer, 1986, figs. 3-6; Fig. 29).

Suspensorium. The bony bridge of mandiblulular and opercular bones suspended from the neurocranium. Several suspensorial elements ossify as dermal or endochondral bone, others develop from both dermal and endochondral ossifications, and at least the autopalatine does not ossify in gymnotiforms, except partially in some species of *Brachyhypopomus.* Due to their topographic association with the suspensorium characters of the opercular series is included in this section. The first comparative study of the suspensorium in gymnotiforms is that of Chardon and de la Hoz (1974). A comparative review of the suspensorium in ostariophysans is provided by Arratia (1992), and of the palatoquadrate and its ossifications in osteichthyans by Arratia (1991).

127. Autopalatine. 0: Autopalatine ossified, straight. 1: Autopalatine unossified, arched. Chardon and de la Hoz (1974) report the presence of chondroidal osteogenesis in the autopalatines of some specimens of *Sternopygus* and *Gymnotus.* Arratia (1992, fig. 12B) also reports an endochondral ossification in *Brachyhypopomus cf. brevirostris.* Specimens of *Brachyhypopomus* used in this study exhibited very little uptake of alizarin stain in the autopalatine, and then only in the core of the anterior portion which forms the articulation with the maxilla. All gymnotiform species lack ossification in the posterior portion of the autopalatine.

128. Ectopterygoid. 0: Ectopterygoid ossified as a dentigerous element in membrane overlying ventral portion of endopterygoid. 1: Ectopterygoid and associated teeth absent (Fink and Fink, 1981, character 26, figs. 8-12).

129. Ascending process of endopterygoid. 0: Lateral surface of endopterygoid smooth; no ascending process ossified in pterygocranial ligament (connecting endopterygoid with neurocranium). 1: Ascending process on lateral surface of endopterygoid; pterygocranial ligament ossified; base of ascending process situated approximately dorsal to articulation of quadrate with anguloarticular (Fig. 30; Chardon and de la Hoz, 1974, figs. 1-6; Fink and Fink, 1981, character 28). The endopterygoid of this report is equivalent to the entopterygoid of Chardon and de la Hoz (1974). The degree of ossification within the pterygocranial ligament is ontogenetically variable. Characters 130 and 131 code two aspects of this variation.

130. Ontogeny of ascending process of endopterygoid. 0: Ascending process of endopterygoid developed in juvenile stages of growth and retained into adult. 1: Small ascending process of endopterygoid in juveniles obliterated by growth along dorsal margin of bone; no endopterygoid process in adults (Fig. 31).

131. Size of endopterygoid process. 0: Dorsal portion of pterygocranial ligament not ossified; base of ascending process of endopterygoid broader than its tip. 1: Entire extent of ligament ossified, forming a bony strut anterior to orbit; process equally as wide along most of its length (Figs. 3, 30 and 31).

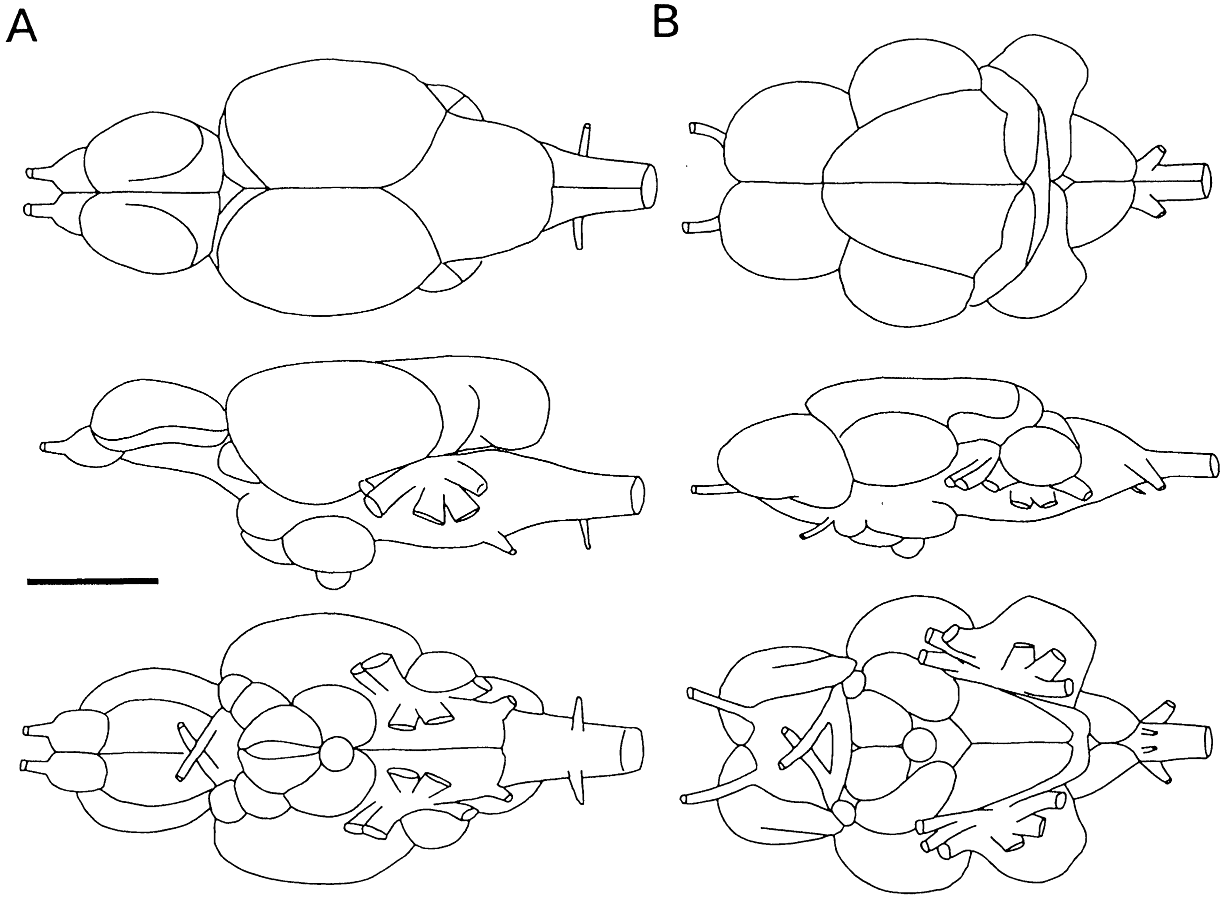


Fig. 24. Dorsal (top), lateral (middle), and ventral (bottom) views of the brains of two outgroup taxa. A. *Parodon gesteri* (Characiformes: Parodontidae). B. *Helogenys marmoratus* (Siluriformes: Cetopsidae). Anterior to left, dorsal to top of page. Labels omitted for clarity. Scale bar equals 1 mm.

132. Shape of endopterygoid. 0: Endopterygoid relatively short and deep; position of ascending process (or ligament) at about midlength of endopterygoid; anterior tip of endopterygoid blunt. 1: Endopterygoid long and narrow; position of ascending process posterior to midlength of endopterygoid; anterior tip pointed (Chardon and de la Hoz, 1974, figs. 2 and 3, Figs. 30 and 31).

133. Endopterygoid dentition. 0: Numerous small teeth distributed in an irregular field on anterior portion of ventral surface of endopterygoid. 1: Few or no teeth on endopterygoid (Chardon and de la Hoz, 1974; Albert and Fink, 1996, character 22, fig. 5).

134. Posterior margin of metapterygoid. 0: Posterior border of metapterygoid separated from hyomandibula by an unossified gap or with a cartilaginous margin. 1: Posterior margin of metapterygoid directly abutting hyomandibula (Fink and Fink, 1981, character 31, figs. 8-12).

135. Metapterygoid triangular. 0: Metapterygoid shaped like head of a double-headed ax; dorsal and ventral margins concave. 1: Metapterygoid triangular in lateral view (Fink and Fink, 1981, figs. 8-12; Arratia, 1992, fig. 12).

136. Metapterygoid narrow. 0: Metapterygoid broad, its width at midlength greater than its total length. 1: Metapterygoid elongate and narrow, longer than wide at its midlength (Chardon and de la Hoz, 1974, figs. 2-6; Triques, 1993, character 15b, fig. 6). Observations on the material available for this investigation agree with the states described as character 15b of Triques (1993) for rhamphichthyoids and *Electrophorus*, but not for *Gymnotus* (Albert and Miller, 1995, fig. 6). Although specimens of *G. pantherinus* were not examined, observations were available for the closely related *G. inaequilabiatus*, and other species of *Gymnotus*.

137. Size of symplectic. 0: Length of symplectic less than hyomandibula. 1: Length of symplectic greater than hyomandibula (Chardon and de la Hoz, 1974, figs. 2-6).

138. Orientation of hyomandibula. 0: Main axis of hyomandibula oblique to main axis of neurocranium. 1: Main axis of hyomandibula oriented horizontally, parallel to main axis of neurocranium (Fig. 31; Chardon and de la Hoz, 1974, figs. 2-6).

139. Proximal articulating head of hyomandibula. 0: Proximal portion of hyomandibula broad; articulating surface facing anterodorsally. 1: Proximal portion of hyomandibula narrow; articulating surface facing dorsally (Fig. 31; Chardon and de la Hoz, 1974, figs. 2-6).

140. Orientation of preopercle. 0: Long axis of preopercle oriented at an oblique angle to main axis of neurocranium. 1: Long axis of preopercle horizontal, roughly parallel with main axis of neurocranium (Chardon and de la Hoz, 1974, figs. 2-6; Triques, 1993, figs. 5 and 6).

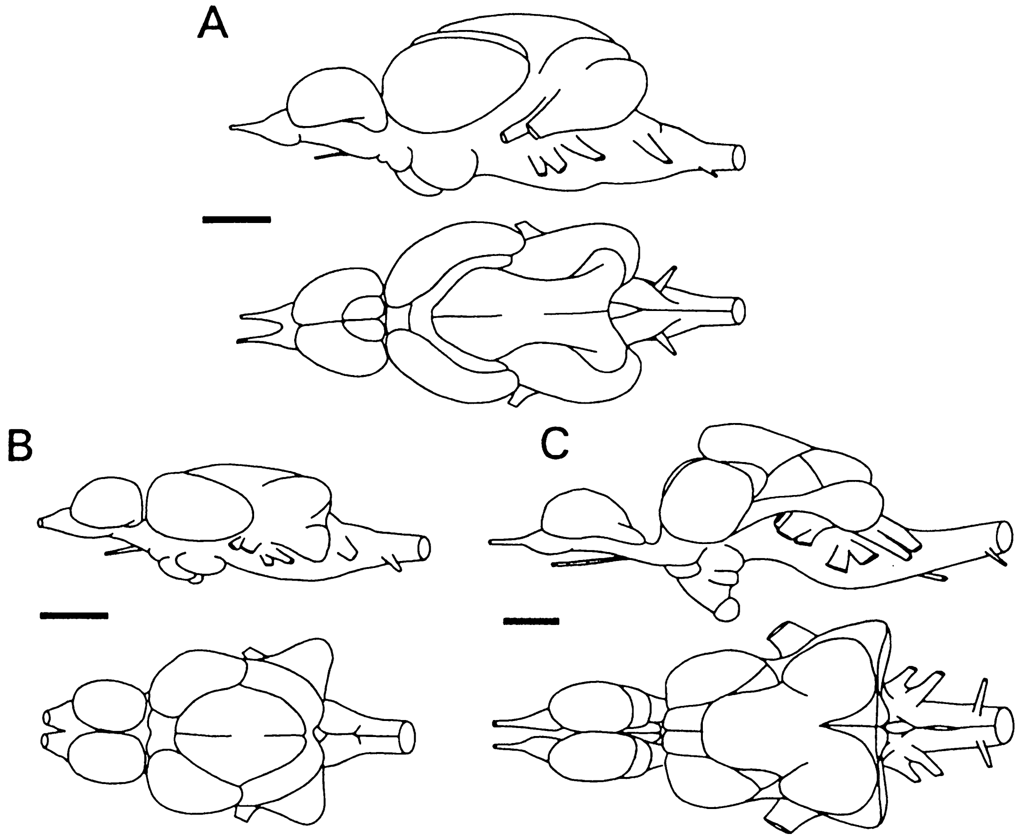


Fig. 25. Lateral (top) and dorsal (bottom) views of the brains of species representing three gymnotiform taxa. A. *Rhamphichthys rostratus* (Rhamphicthyidae). B. *Hypopygus lepturus* (Hypopomidae). C. *Rhabdolichops eastwardi* (Sternopygidae). Note the large size of the hypothalamus (character 109), and the reduced extent of the posterior margin of the optic tectum (character 108) in C. Anterior to left, dorsal to top of page. Labels omitted for clarity. Scale bars equal 1 mm.

141. Anterior limb of preopercle. 0: Preopercle broad, crescent-shaped; ventral margin of anterior limb of preopercle curving smoothly to anterior tip. 1: Preopercle narrow, curved; ventral margin of anterior limb not ossified (Chardon and de la Hoz, 1974, figs. 2-6; Fink and Fink, 1981, figs. 8-12; Figs. 30 and 31). The derived condition observed in apteronotids contrasts with that of other gymnotiforms, in which the axes of anterior and dorsal portions of preopercle are situated at right angles to each other, such that the anterodorsal margin of preopercle is interrupted by an angle immediately ventral to posterior margin of symplectic and is separated by gap from posterior margin of symplectic (Chardon and de la Hoz, 1974, figs. 2-6; Fink and Fink, 1981, figs. 8-12).

142. Shape of opercle. 0: Outline of opercle approximately rectangular; dorsal margin shorter than posterior margin, and interrupted by a pronounced angle. 1: Opercle approximately triangular; dorsal margin about as long as posterior margin, and either slightly curved or straight (Fink and Fink, 1981, character 36, figs. 8-12; see Triques, 1993).

143. Dorsal margin of opercle. 0: Dorsal margin of opercle convex. 1: Dorsal margin of opercle straight. 2: Dorsal margin of opercle concave (Fink and Fink, 1981, figs. 8-12; Lundberg *et al.*, 1996).

Splanchnocranium. The skeletal support of the gills and associated elements, including the basihyal, urohyal and branchiostegal rays. The numbering system used here follows Goodrich (1918) in identifying the mandibular arch with the first branchial pouch. The numbering system used here for all posterior elements identifies each branchial element by its gill arch, regardless of the actual number of elements in the series to which it belongs. For example, the five epibranchial elements of characiphysans are numbered 3 through 7. This numbering scheme is different that from other published accounts (Nelson, 1969; Fink and Fink, 1981; Triques, 1993). A comparative review of the urohyal and anterior basibranchial elements in teleosts is provided by Arratia and Schultze (1990).

144. Number branchiostegal rays. 0: 3 - 4 rays. 1: 5 - 6 rays. 2: more than 7 rays.

145. Shape of branchiostegal rays. 0: Anterior 1 - 2 rays broad. 1: Anterior rays narrow.

146. Base of gill rakers. 0: Gill rakers directly attached to gill arches. 1: Base of gill rakers not mineralized, rakers (when present) not attached to gill arches. The morphology of the gill rakers in *Sternopygus* is described by Mago-Leccia (1978) and Lundberg and Mago-Leccia (1986, character 24, fig. 11). The phylogenetic distribution of gill raker attachment is discussed in Albert and Fink (1996, character 34).

147. Gill raker tips. 0: Gill rakers ossified to distal tips. 1: Distal tips of gill rakers cartilaginous (Mago-Leccia, 1978, Lundberg and Mago-Leccia, 1986, character 24, fig. 11).

148. Anterior pharyngobranchial. 0: Anterior

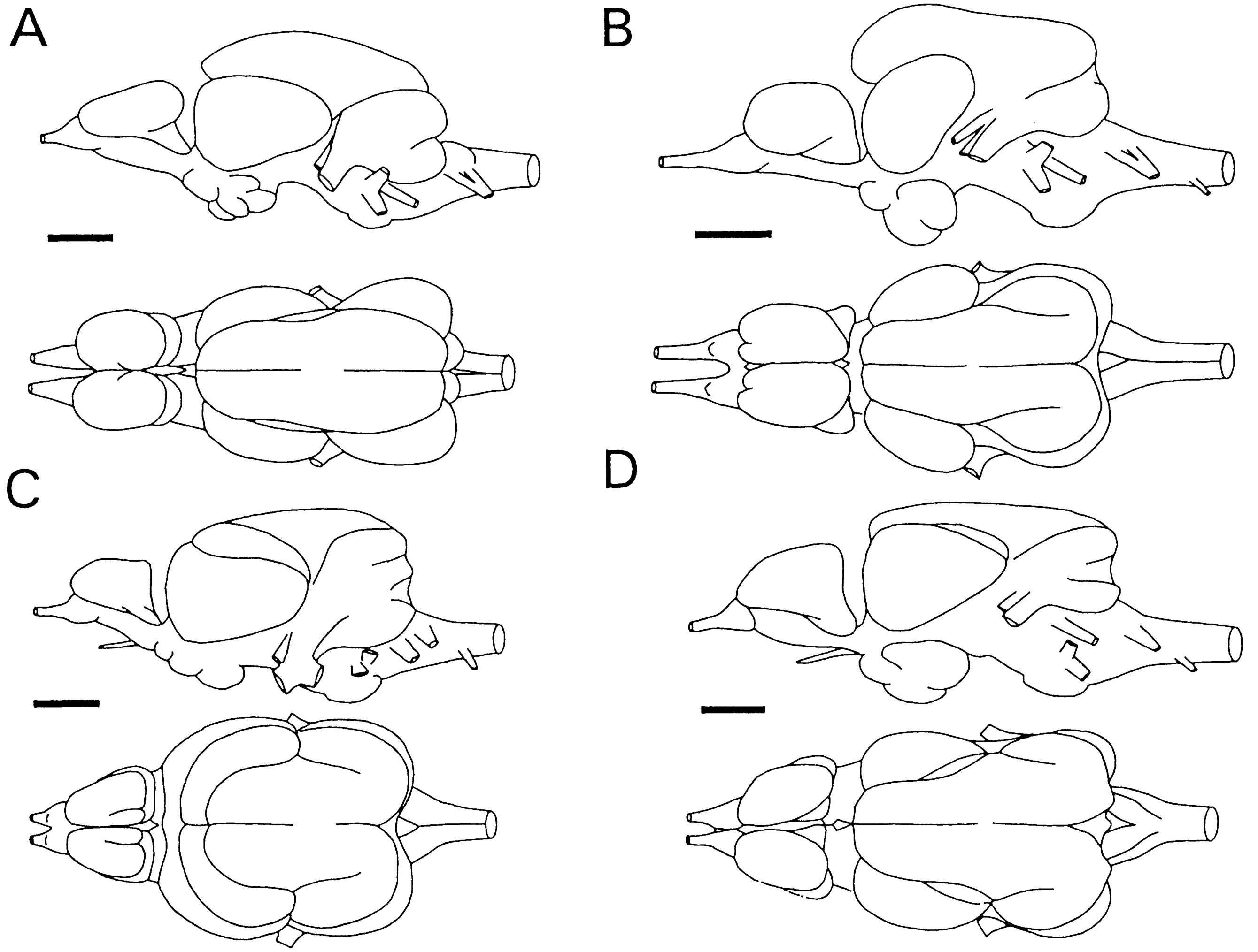


Fig. 26. Lateral (top) and dorsal (bottom) views of the brains of representative apteronotid species. A. *Platyurosternarchus macrostomus*. B. *Sternarchella orthos*. C. *Sternarchorhamphus muelleri*. D. *Sternarchorhynchus oxyrhynchus*. Anterior to left, dorsal to top of page. Labels omitted for clarity. Scale bars equal 1mm.

pharyngobranchial (associated with gill arch two) ossified, articulating with parasphenoid (Fink and Fink, 1981, fig. 13). 1: Anterior pharyngobranchial unossified (Triques, 1993, character 40).

149. Third and fourth pharyngobranchials. 0: Pharyngobranchials of third and fourth arches cartilaginous. 1: Pharyngobranchials of third and fourth arches ossified.

150. Pharyngobranchial tooth plates. 0: Four dentigerous plates present on posterior gill arches. 1: One dentigerous plate present on posterior gill arch (Fink and Fink, 1981, character 51).

151. Shape of fifth epibranchial. 0: Anterior portion of fifth epibranchial straight (Fink and Fink, 1981, fig. 13). 1: Shape of anterior portion of fifth epibranchial sinuous (Triques, 1993, character 43, fig. 21).

152. Ascending ramus of sixth epibranchial. 0: Ascending ramus of sixth epibranchial short, not contacting posterior face of fifth epibranchial. 1: Ascending ramus of sixth epibranchial elongate, contacting fifth epibranchial (Triques, 1993, character 41, fig. 20).

153. Sixth epibranchial shape. 0: With short ascending process. 1: With elongate ascending process.

154. Process of seventh epibranchial. 0: Posterior surface of seventh epibranchial flat. 1: Posterior surface of seventh epibranchial with a dorsomedially oriented process (Triques, 1993, character 42a, figs. 18 and 20).

155. Orientation of process on seventh epibranchial. 0: Posterior surface of seventh epibranchial with a dorsomedially oriented process. 1: Posterior surface of seventh epibranchial with a dorsoventrally oriented process (Triques, 1993, character 42b, figs. 18 and 20).

156. Posterior process of fourth ceratobranchial. 0: Posterior surface of fourth ceratobranchial smooth. 1: Posterior surface of fourth ceratobranchial with a medially oriented process (Triques, 1993, character 39, figs. 17 and 19).

157. Lateral process of sixth ceratobranchial. 0: Lateral surface of sixth ceratobranchial smooth. 1: Lateral surface of sixth ceratobranchial with an anterolaterally oriented process (Triques, 1993, character 38, figs. 17 and 19).

158. Posterior margin of third hypobranchial. 0: Third hypobranchial rod-like, elongate and rectangular in dorsal view.

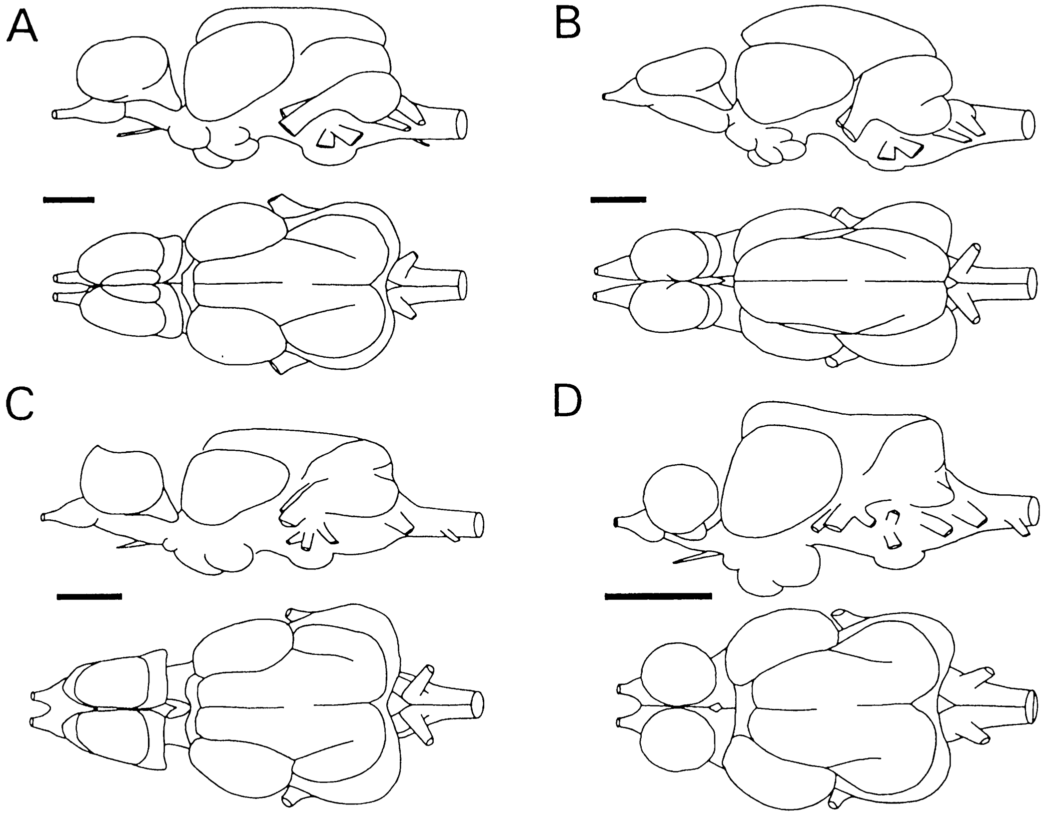


Fig. 27. Lateral (top) and dorsal (bottom) views of the brains of representative apteronotid species. A. *"Apteronotus" apurensis*. B. *Compsaraia compsus*. C. *Sternarchogiton* n. sp. B. D. *Adontosternarchus devenanzii*. Anterior to left, dorsal to top of page. Labels omitted for clarity. Scale bars equal 1 mm.

1: Third hypobranchial broad at posterior margin, triangular in horizontal view (Triques, 1993, character 33a, fig 16; Fig. 32).

159. Anterior margin of third hypobranchial. 0: Third hypobranchial rectangular in dorsal view; anterior margin straight. 1: Third hypobranchial pentagonal in dorsal view; anterior margin interrupted by a sharp angle (Triques, 1993, character 33b, fig. 15).

160. Medial bridge of third hypobranchial. 0: Medial surface of third hypobranchial flat; anterior tip symmetrically conical or flat. 1: Anterior tip of third hypobranchial with a large medially oriented process, contacting contralateral third hypobranchial across midline by means of a cartilaginous bridge (Triques, 1993, character 34a, fig. 16; Fig. 32).

161. Posterior ridge of basihyal. 0: Dorsal surface of basihyal flat or rounded. 1: Dorsal surface of basihyal convex along its long axis, forming a ridge (Triques, 1993, character 29, fig. 12).

162. Dorsal surface of basihyal. 0: Dorsal surface of basihyal flat or convex. 1: Dorsal surface of basihyal concave along its long axis, forming a shallow trough (Triques, 1993, character 30a).

163. Basibranchial ossification. 0: All five basibranchial elements (including basihyal) ossified. 1: All five elements of basibranchial series (including basihyal) unossified.

164. Shape of third basibranchial. 0: Third (anterior) basibranchial elongate, width at midlength about same as at anterior and posterior ends. 1: Third basibranchial foreshortened and broad, hourglass shaped, breadth at midlength narrower than at either end (Fig. 32).

165. Fifth basibranchial ossification. 0: Fifth basibranchial ossified. 1: Fifth basibranchial not ossified; developmental precursor cartilage maintained or fused with cartilages of posterior basibranchials.

166. Urohyal head. 0: Anterior head of urohyal narrow, lateral surfaces flat. 1: Anterior head of urohyal large, with lateral ridges (Weitzman, 1962, fig. 11; Fig. 32).

167. Urohyal blade. 0: Posterior blade of urohyal ossified, extending posterior to fourth basibranchial. 1: Posterior blade of urohyal unossified, anterior head of urohyal positioned ventral to second basibranchial (Fig. 32).

168. Urohyal blade hyperossified. 0: Urohyal blade short, ossified to level of third basibranchial. 1: Urohyal blade long, ossified to level of fourth basibranchial.

Paired fins. The skeletal support of the paired fins, including elements ossifying within the scapulocoracoid cartilage, its rays and radials, its connection with the posterior portion of the neurocranium, and associated dermal ossifications.

169. Posttemporal. 0: Posttemporal independent from supracleithrum in mature specimens. 1: Posttemporal fused with supracleithrum in mature specimens (Mago-Leccia *et al.*, 1985, fig. 6; Lundberg and Mago-Leccia, 1986, character 10, fig. 4; Figs. 33 and 34).

170. Extrascapular. 0: Independent ossification. 1: Fused with neurocranium.

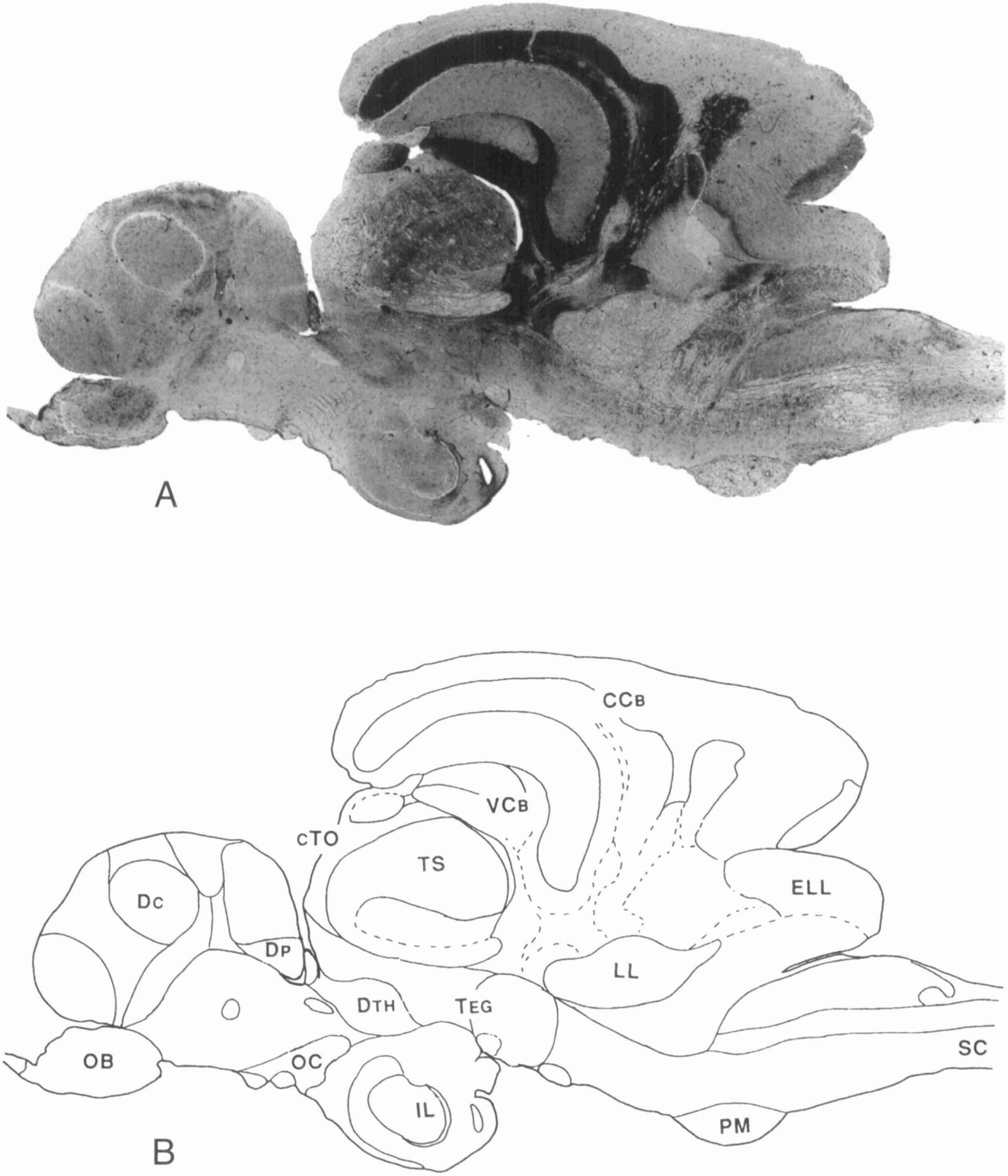


Fig. 28. A. Photomicrograph of a parasagittal section of the brain of *Apteronotus albifrons* (Apteronotidae). Luxol blue and Nissl stain. B. Drawing of the same section depicting boundaries of some structures used in descriptions of neural characters. Anterior to left, dorsal to top. Abbreviations: DT = dorsal thalamus (including nucleus electrosensorius and sublemniscal prepacemaker nucleus); CA = commissure ansulata; CC = corpus cerebellum; Dc= telencephalic area dorsalis centralis; Dp= telencephalic area dorsalis posterior; EG= eminentia granularis; ELL= electrosensory lateral line lobe; FL = facial lobe; ON = optic nerve; PM = pacemaker nucleus; TO= tectum opticum; TS = torus semicircularis; VC = valvula cerebellum. See Fig. 21 for location of more laterally positioned structures (e.g., PGl = lateral preglomerular nucleus; NV = trigeminal nerve root). Scale bar equals 1 mm.

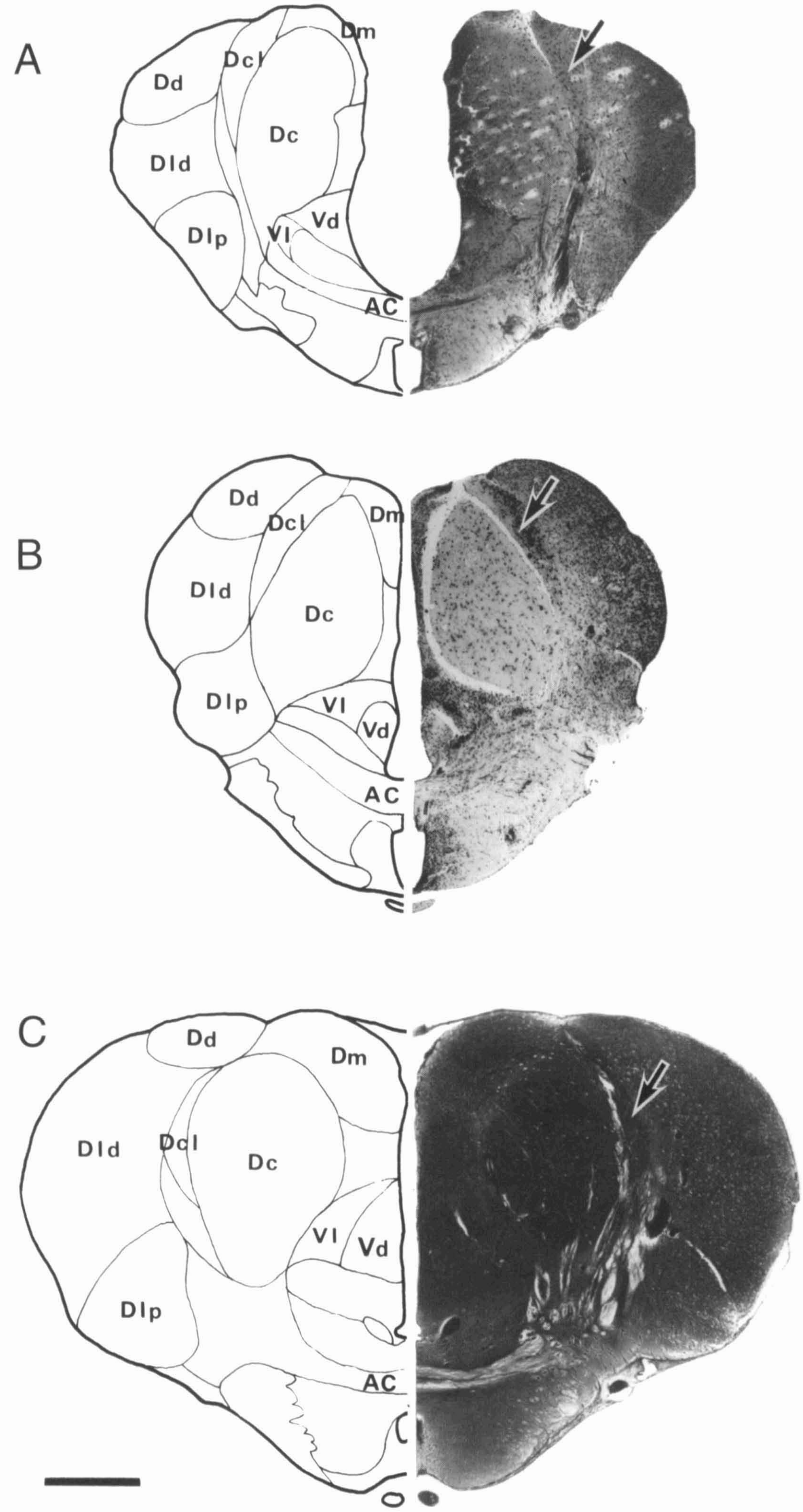


Fig. 29. Photomicrographs (right) and nuclear boundaries (left) of transverse sections through the brain of gymnotiform species. Left column: sections through the telencephalon at transverse level 34 depicting alternative states of character 101. A. *Gymnotus carapo* (Gymnotidae), Nissl stain. B. "*Apteronotus*" *apurensis* (Apteronotidae), Nissl stain. C. *Apteronotus albifrons* (Apteronotidae), Bodian stain. Note large cells in Dcl in B compared to A (arrows). Effects of medium-term ethanol storage may be noted in comparing panels A and B with C. Note the separation of nucleus Dc in panels A and B from surrounding structures. Middle column: midbrain sections at transverse level 12 depicting alternative states of character 123.

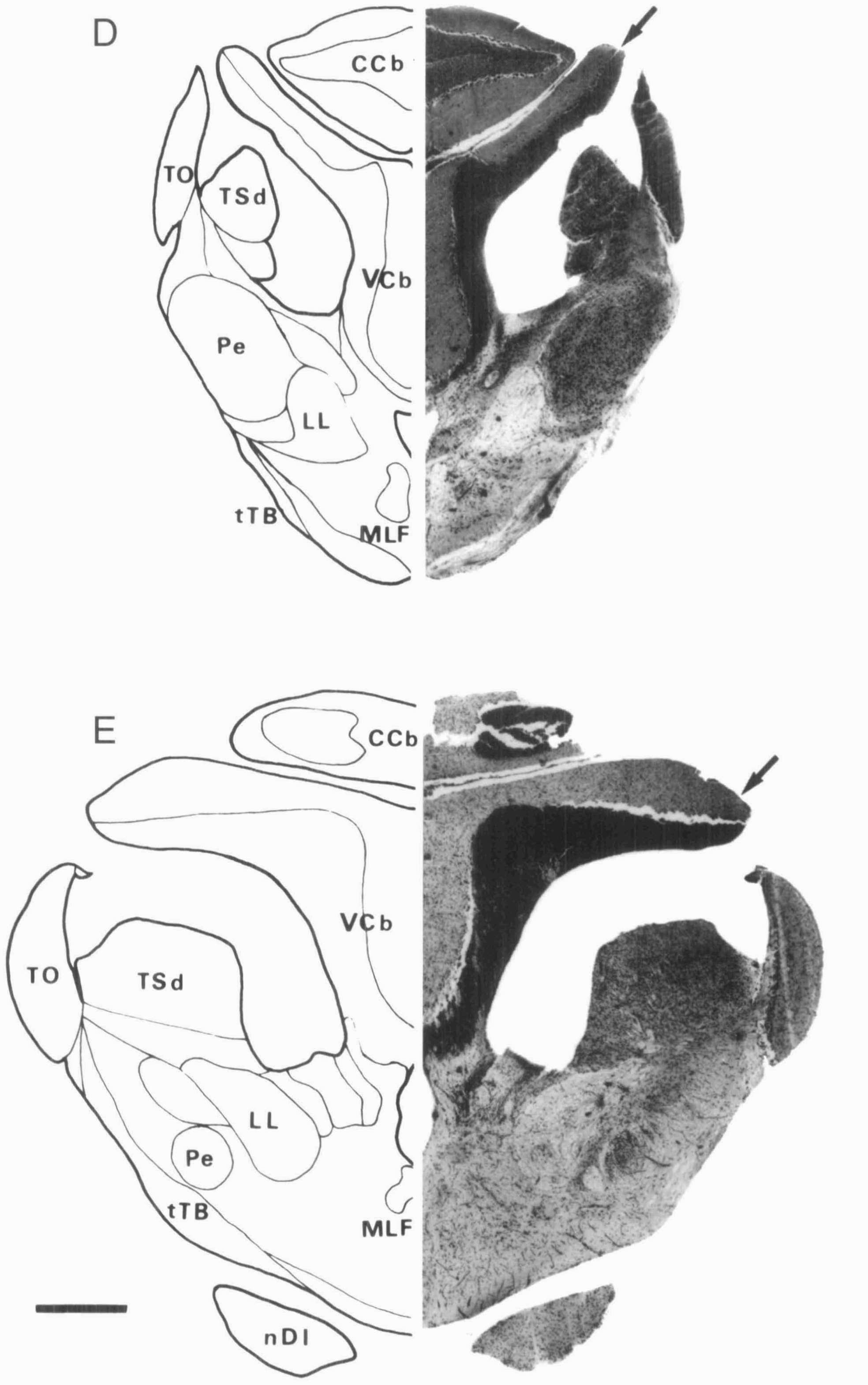


Fig. 29 (continued). Photomicrographs (right) and nuclear boundaries (left) of transverse sections through the brain of gymnotiform species. Left column: sections through the telencephalon at transverse level 34 depicting alternative states of character 101. D. *Sternopygus macrurus* (Sternopygidae). E. *Sternarchorhamphus muelleri* (Apteronotidae). Note the large lateral portion of the valvula cerebellum (VCb) in B compared to A (arrows). Right column: hindbrain sections at transverse level -8 depicting alternative states of character 120.

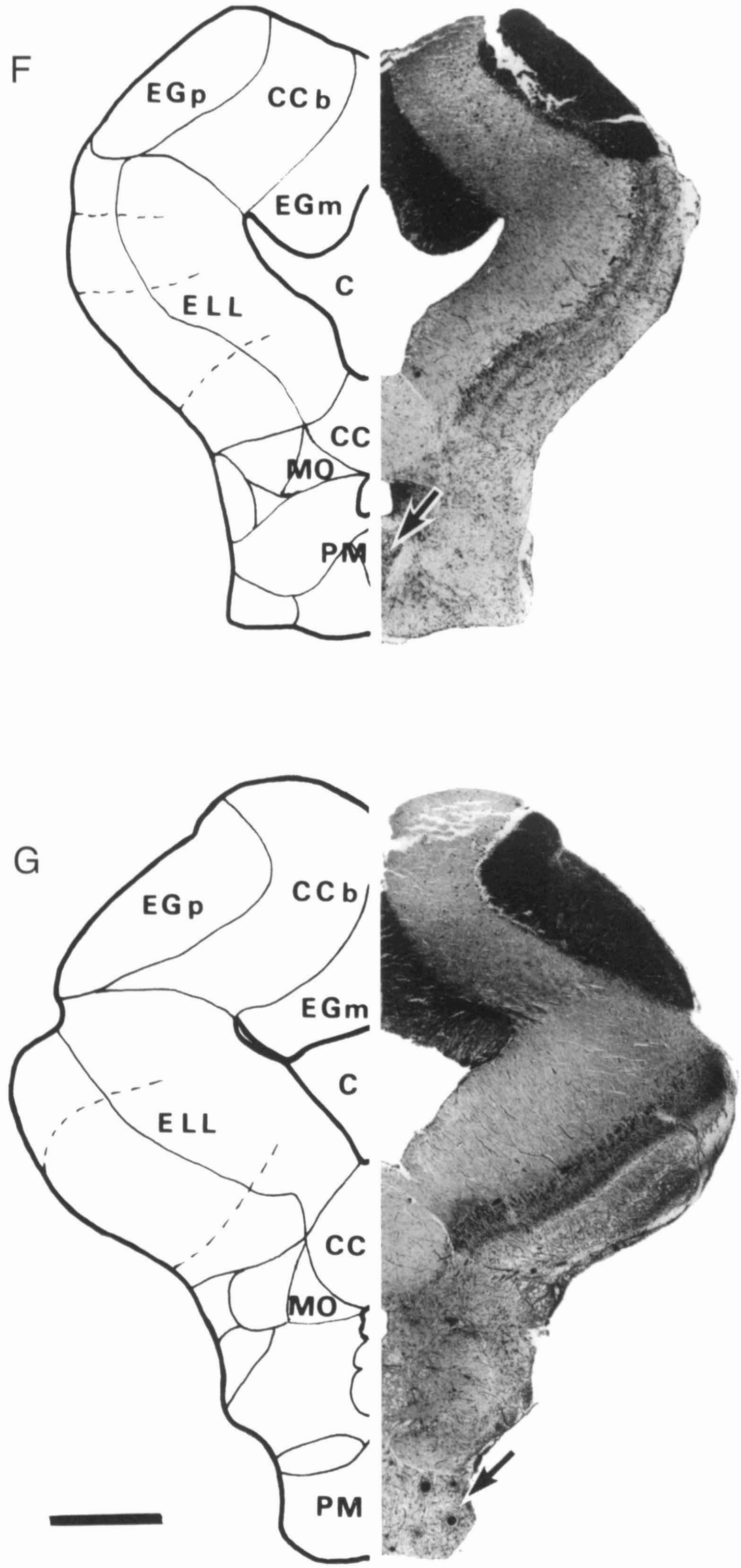


Fig. 29 (continued). Photomicrographs (right) and nuclear boundaries (left) of transverse sections through the brain of gymnotiform species. Left column: sections through the telencephalon at transverse level 34 depicting alternative states of character 101. F. *Eigenmannia virescens* (Sternopygidae). G. *Sternarchella sima* (Apteronotidae). Note the pacemaker nucleus (PM) is large and positioned ventrally in G compared to F (arrows). Other abbreviations as in Fig. 28.

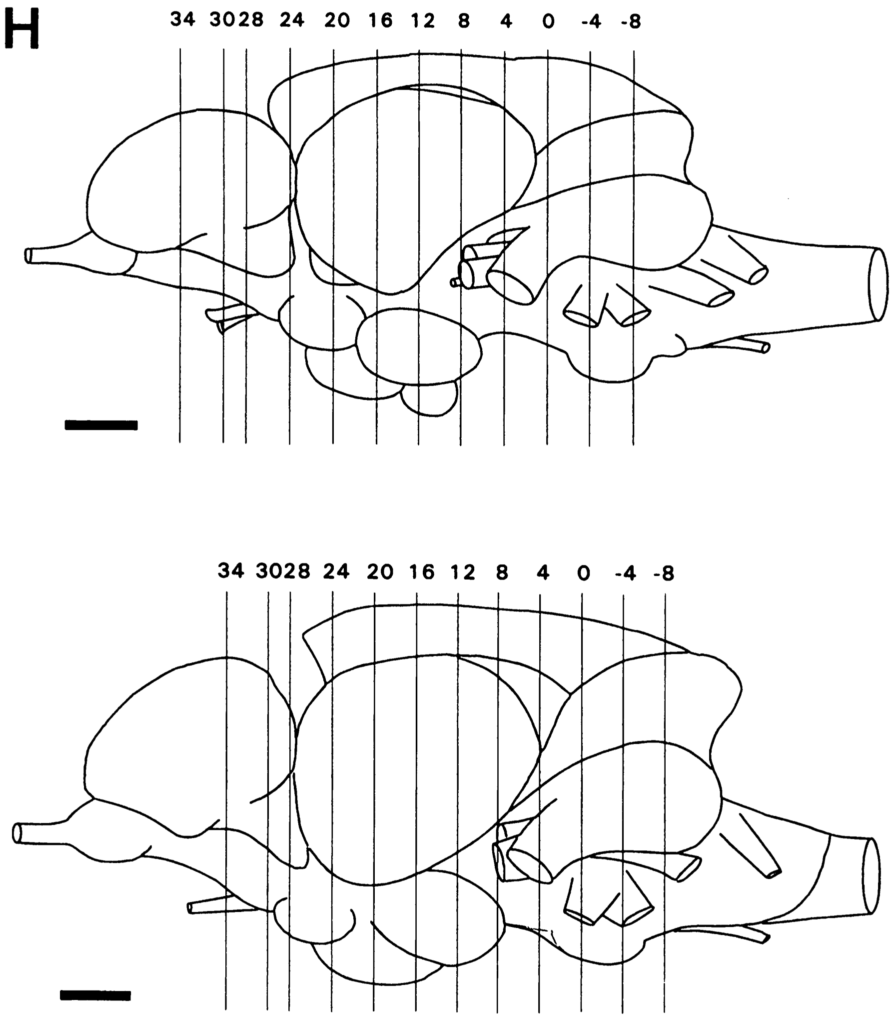


Fig. 29 (continued). H. Comparable transverse levels from Maler *et al.* (1990) in *Apteronotus leptorhynchus* (top) and *Eigenmannia virescens* (bottom). Scale bars equal 1 mm.

171. Shape of postcleithra. 0: Postcleithra robust, posterior margins straight; main axes of postcleithra aligned with that of supracleithrum. 1: Postcleithra thin and discoid, posterior margins curved; main axes of postcleithra oblique with that of supracleithrum (Weitzman, 1962, fig. 18; Mago-Leccia *et al.*, 1985, fig. 6; Lundberg and Mago-Leccia, 1986, character 11 in part).

172. Third postcleithrum. 0: Three postcleithra ossified; third postcleithrum sickle shaped. 1: Posterior (third) postcleithrum not ossified (Mago-Leccia *et al.*, 1985, fig. 6; Lundberg and Mago-Leccia, 1986, character 11 in part, fig. 8).

173. Scapular foramen. 0: Unossified area along medial margin in scapulocoracoid cartilage separating coracoid and scapular ossifications. 1: Unossified region of scapulocoracoid cartilage included entirely within the scapula, forming a large foramen (Lundberg *et al.*, 1986, character 9, fig. 7).

174. Mesocoracoid. 0: Mesocoracoid ossified within scapulocoracoid cartilage, forming a bridge between medial surface of coracoid and cleithrum. 1: Mesocoracoid not ossified (Albert and Miller, 1995, fig. 6; Figs 33 and 34).

175. Anterior process of coracoid. 0: Anterior coracoid process extending anterior towards cleithral symphysis, paralleling ventral margin of cleithrum. 1: Anterior coracoid process not extending to a vertical with contact of dorsomedial limb of coracoid with cleithrum (Fig. 33).

176. Proximal pectoral radials. 0: : Proximal radials three and four seperate. 1: Proximal radials three and four co-osified in adult specimens (Lundberg and Mago-Leccia, 1986, character 15, fig. 7).

177. Pectoral fin. 0: Pectoral fin large and pigmented; more than 43% head length; membrane infused with numerous small chromatophores. 1: Pectoral fin small and unpigmented; less than 43% head length; membrane without chromatophores (Albert and Fink, 1996, character 29).

178. Number of pectoral radials. 0: Four proximal pectoral radials. 1: Eight proximal pectoral radials.

179. Pelvic girdles and fins. 0: Pelvic girdles and fins present. 1: No pelvic girdles or fins (Fink and Fink, 1981, character 103).

Axial structures. The vertebral column and associated mesodermal elements. Precaudal vertebrae and ribs are included in the section *Body cavity.*

180. Claustrum. 0: Dissociated dorsomedial portion of first

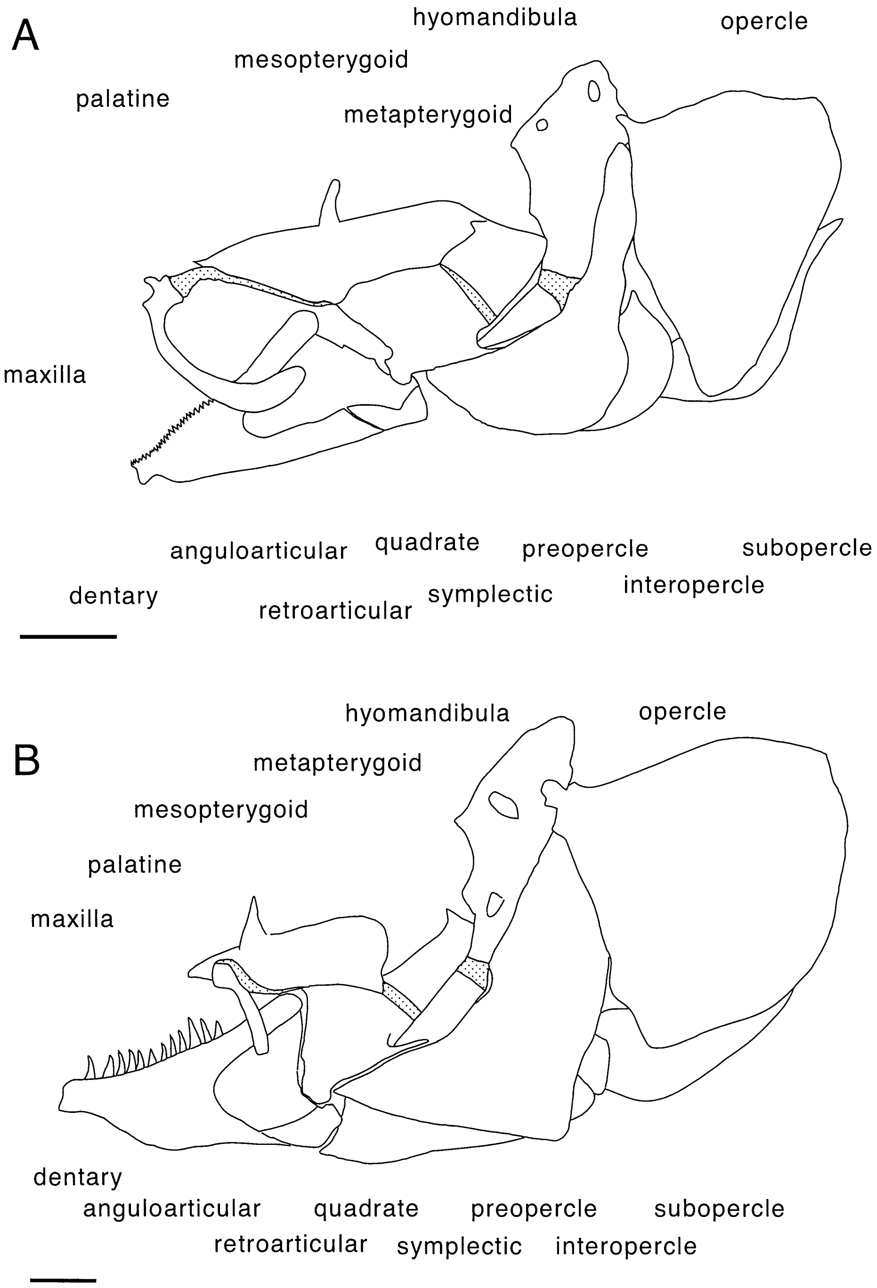


Fig. 30. The suspensorium of two gymnotiform species. A. *Sternopygus xingu* (USNM 211830). B. *Gymnotus maculosus* (UMMZ 190531). Cartilage indicated by shading. Note the cartilaginous autopalatine (character 103) and the ascending process of endopterygoid (character 105). Scale bars equal 1 mm.

neural arch modified to form claustrum. 1: Claustrum absent as an ossified element (Fink and Fink, 1981, character 67, figs. 14-18).

181. Anterior vertebrae. 0: Close proximity between parapophyses of second vertebrae and *os suspensorium.* 1: Parapophyses of second vertebrae separated by distinct gap from the *os suspensorium* (modified from Lundberg and Mago-Leccia, 1986, character 8; Fink and Fink, 1981, characters 74 and 92, figs. 17-18; Albert and Fink, 1996, character 39).

182. Position of neural spine. 0: Neural spines inserting on middle of caudal vertebral centra. 1: Neural spine inserting on posterior margin of caudal vertebral centra (Fig. 35). The neural spines of anterior thoracic vertebrae have expanded bases and establish a relatively broad contact with their corresponding vertebral centra. The position at which the more narrow bases of caudal neural arches insert on their associated vertebral centra is variable. In Apteronotidae and Sternopygidae the neural arches contact the middle of centra in more anterior segments, and more posterior portions of the centra more posteriorly. The axial position at which the insertion of neural spines changes is variable, ranging from vertebra 32 to 46 in apteronotids, to vertebra 40 to 57 in sternopygids. Using this

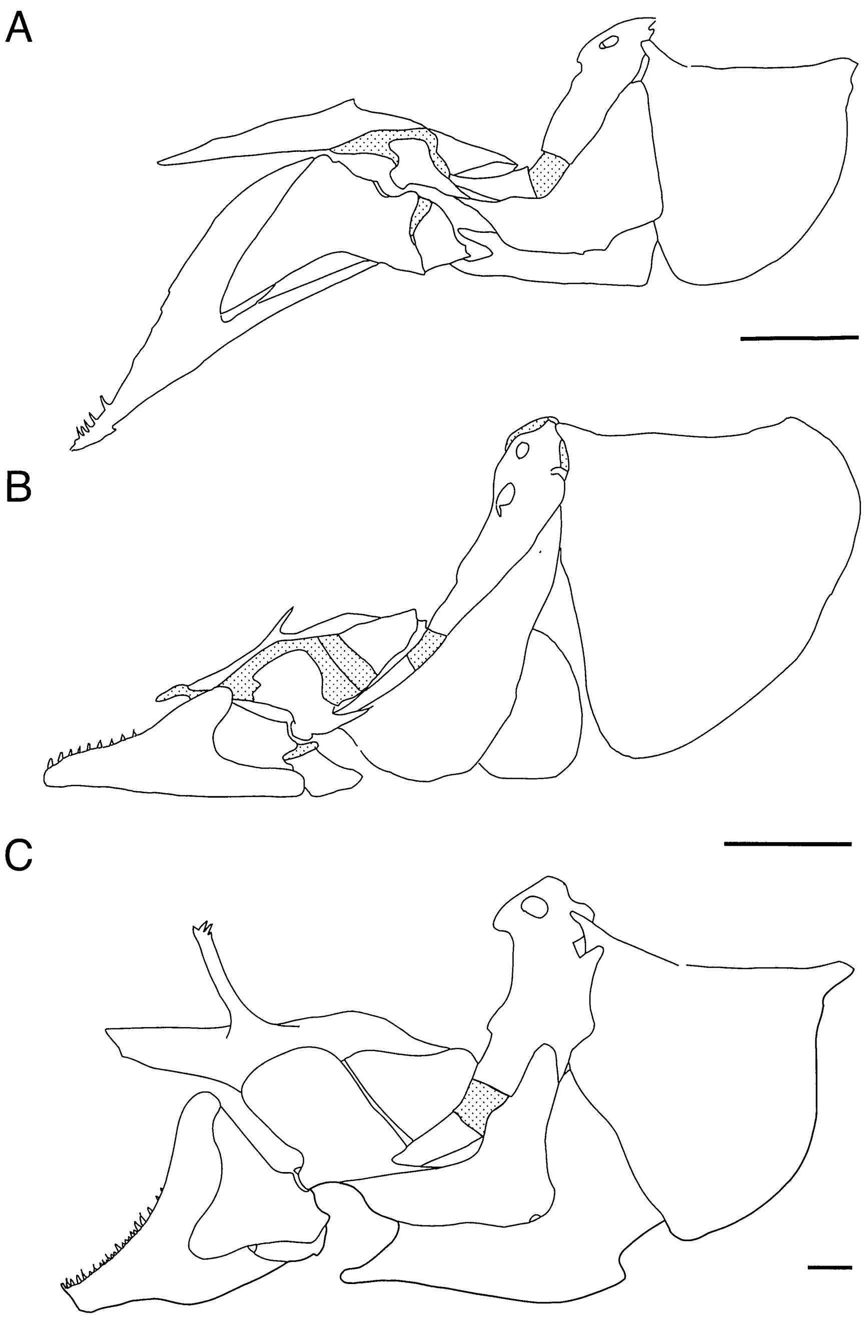


Fig. 31. Diagrammatic representations of the suspensorium in three apteronotid species. A. *Platyurosternarchus macrostomus* (FMNH 100730, 212 mm TL). B. *Sternarchorhamphus muelleri* (USNM 228807, 220 mm TL). C. *Sternarchella sima* (UMMZ 211329, 225mm TL). Cartilage indicated by shading. Scale bars equal 1 mm.

criterion, it is possible to assess the axial position of the †*Ellisella* RL 1596-1 (Meunier and Gayet, 1991, fig. 1.2) as representing this transitional zone (Albert *et al.*, in press).

183. Vertebral fenestrae. 0: Lateral walls of neural arches completely ossified; dorsal margin straight. 1: Lateral walls of neural arches with several small fenestrae; dorsal margin uneven, with several evaginations (Figs. 36 and 37; Meunier and Gayet, 1991, figs. 3-5; Gayet *et al.*, 1994, fig. 6). In order to control for axial position, ontogenetic stage, and the effects of regeneration, observations were made on several specimens of different total lengths for each species, and the characters were coded for the condition represented at the posterior precaudal vertebrae.

184. Anterior intermuscular bones. 0: Simple or little branched. 1: Anterior epipleurals branched, with 2 - 4 rami each. 2: Anterior epipleurals highly branched, with 6 - 20 rami each at the level of the seventh to ninth precaudal vertebrae (Lundberg and Mago-Leccia, 1986, character 7, fig. 6).

185. Regeneration of intermuscular bones. 0: Inability to regenerate intermuscular bones. 1: Capacity to regenerate ossi-

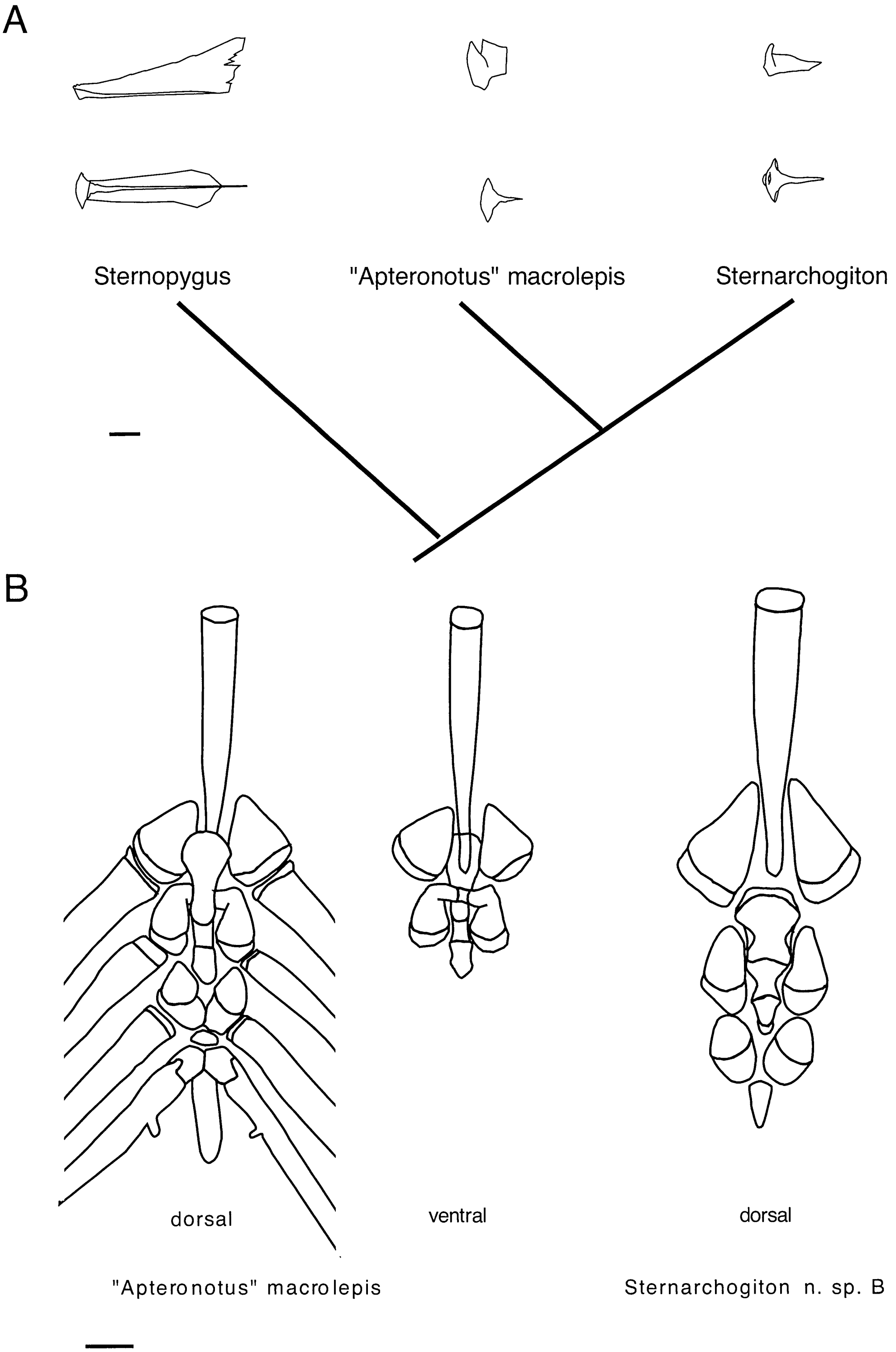


Fig. 32. Portions of the splanchnocranium in representative apteronotine taxa. A. Lateral (top) and dorsal (bottom) views of the urohyal in three species, superimposed on a topology isomorphic that of Fig. 33. Note only the anterior head of the urohyal ossifies in *"Apteronotus" macrolepis* and *Sternarchogiton* sp. B. Anterior branchial arches of *"Apteronotus" macrolepis* (FMNH 96040, 135 mm TL; left) and *Sternarchogiton* sp. B (UMMZ 211315, 200 mm TL; right). Note the contact between the fourth basibranchials ventral to the second gill arch in *"Apteronotus" macrolepis.* Scale bars equal 1 mm.

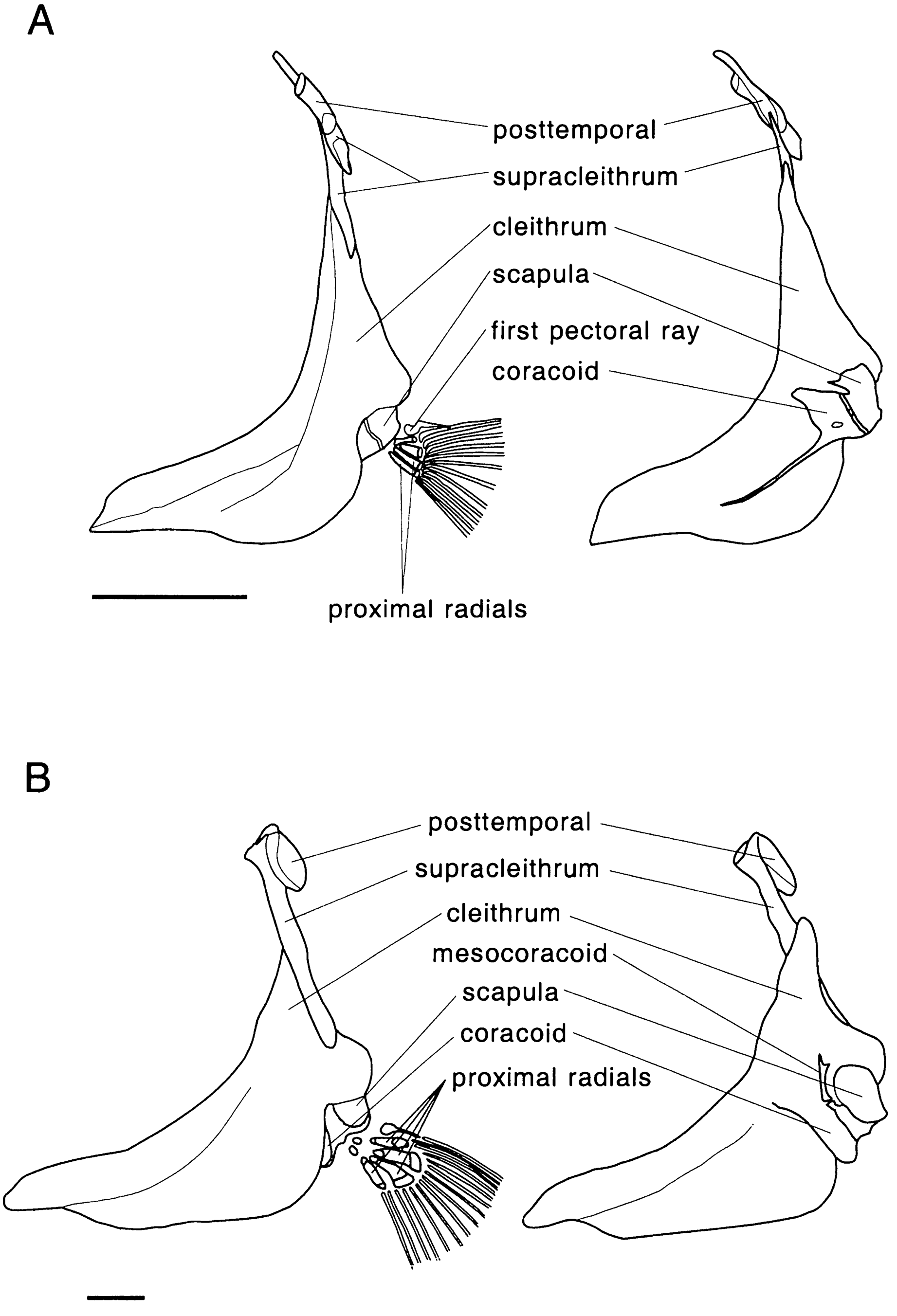


Fig. 33. The pectoral girdle of two gymnotiform species. A. *Sternopygus xingu*. B. *Gymnotus maculosus*. Note the ventral process of the coracoid does not extend anterior to a vertical line through the contact of the dorsomedial limb of the coracoid with the cleithrum (character 151). Scale bars equal 1 mm.

fied intermuscular bones (Meunier and Gayet, 1991, figs. 3-5; Gayet *et al.*, 1994, character 32). Lightly ossified intermuscular bones are present in the regenerated caudal appendage of Sternopygidae and Gymnotidae, but they are distinctly thinner and less dense than unregenerated intermuscular bones. Intermuscular bones are not evident in the regenerated caudal region of †*Ellisella*, and are not present in Apteronotidae or Rhamphichthyoidea. More precise identification of which intermuscular series are regenerated would require data on their articulation and orientation with elements of the neuraxis (Patterson and Johnson, 1995), neither of which pertain.

186. Displaced hemal spines. 0: All hemal spines medial, fused with hemal arches in adult specimens; one to one correspondence between caudal vertebrae and associated hemal spines. 1: Three additional hemal spines positioned in hypaxial musculature posterior to body cavity, often lateral to unmodified hemal spines, rarely fused with hemal arches or parapophyses; irregular association with posterior thoracic and anterior caudal

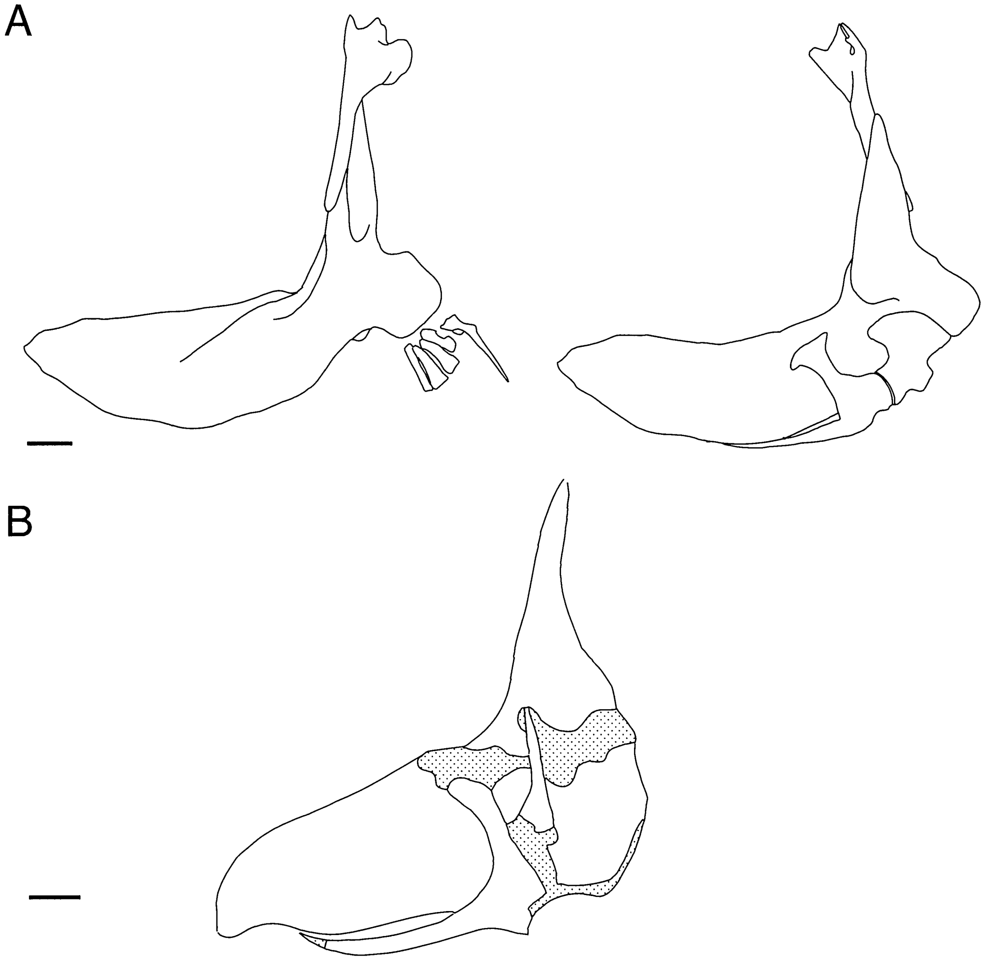


Fig. 34. Diagrammatic representations of the pectoral girdle in two apteronotid species. A. *Sternarchella orinoco*, lateral view at left, medial view at right. B. *Orthosternarchus tamandua*, medial view. Cartilage indicated by shading. Note the presence of the mesocoracoid in B. Scale bar equals 1 mm.

vertebrae (Figs. 35 and 36). The anterior displaced hemal spine (DHS) extends from the region immediately ventral to the hemal arches of the first caudal vertebra anteroventrally towards the origin of the anal fin. The two posterior DHSs are shorter and usually less robust, oriented in the same direction, commonly lying to the left of the midline, often crossing one another or the anterior DHS. The shape and position of the posterior DHS is variable (see the Discussion). Phylogenetic structure in some aspects of this diversity is reported as separate character descriptions.

187. Anterior series of displaced hemal spines. 0: Three DHSs in hypaxial musculature immediately posterior to body cavity. 1: Anterior series of 8-14 DHSs in hypaxial musculature lateral to body cavity (Fig. 35E). The anterior series extends along the anal-fin base supporting the anal-fin pterygiophores anterior to the region of the pectoral girdle.

188. Size of anterior displaced hemal spine. 0: Anterior DHS approximately as straight and as wide as other hemal spines. 1: Anterior DHS large, two to three times as broad as other hemal spines, often exhibiting additional distal tips (Figs. 35 and 36). In the derived state the anterior DHS is curved and scythe shaped. It extends from between the parapophyses of the last thoracic vertebrae, or sometimes just ventral to the hemal arches of the first caudal vertebrae, anteroventrally around the posterior margin of the body cavity and towards the origin of the anal fin. The ventral margin of the anterior DHS supports the anal-fin pterygiophores near the insertion of the anal-fin. A second distal tip observed in some specimens, is present juveniles of 20 - 30 mm TL (see Discussion on the phylogenetic origin of the DHSs).

189. Dorsal head of anterior displaced hemal spine. 0: Dorsal head of anterior DHS as wide as that of its descending blade; anterior margin of descending blade straight, continuous with proximal (dorsal) head; dorsal head extending ventral to parapophyses of anterior caudal vertebrae. 1: Dorsal head of anterior DHS more than twice the width of its descending blade; anterior margin of descending blade curved around posterior margin of body cavity, anterior margin of dorsal head expanded, forming an angle with that of its descending blade; dorsal head extending ventral to or inserting between parapophyses of posterior thoracic vertebrae (Fig. 36).

190. Second posterior displaced hemal spine. 0: Second posterior DHS straight. 1: Second posterior DHS curved (Lundberg and Mago-Leccia, 1986, fig. 10; Fig. 36).

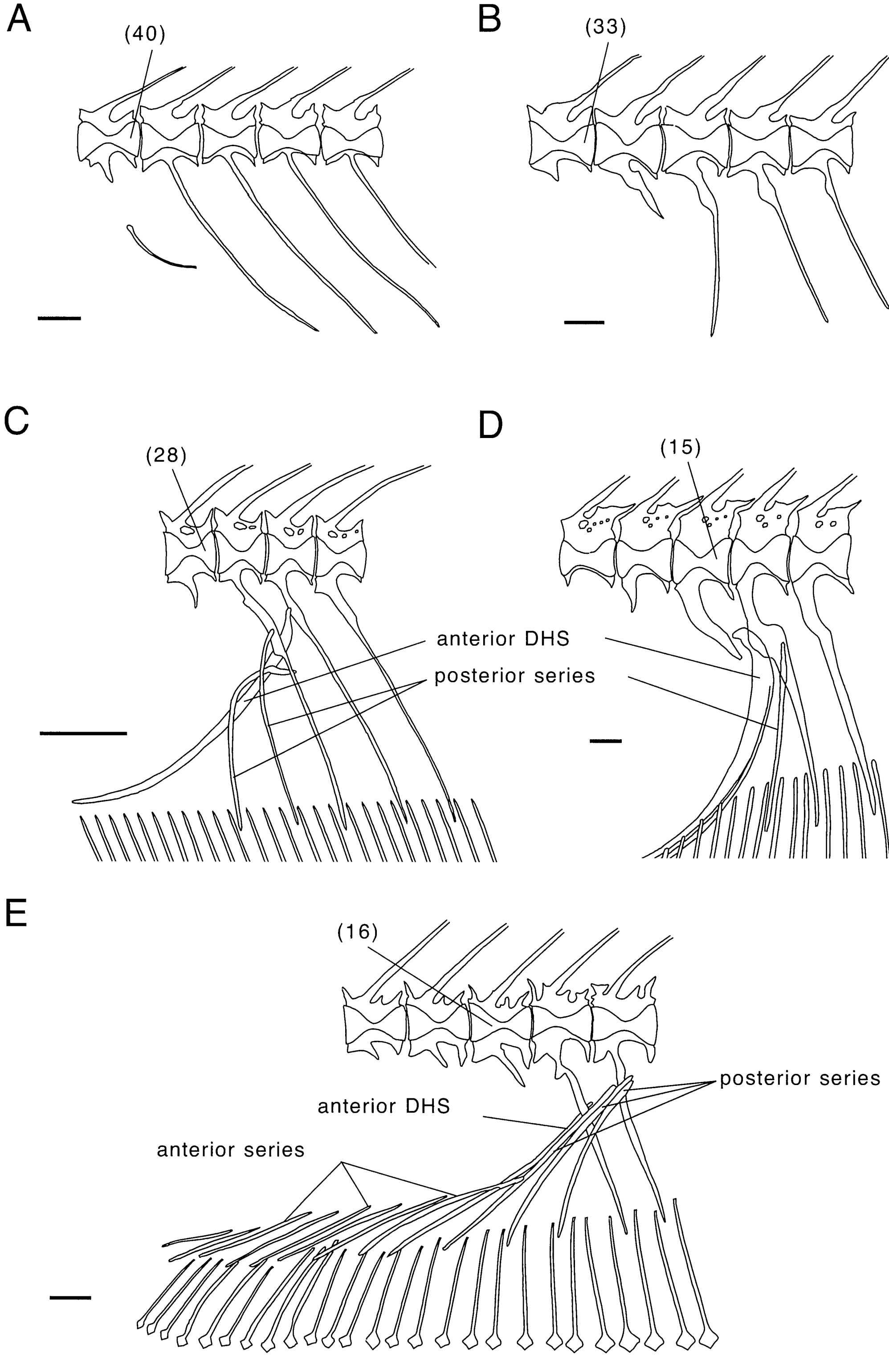


Fig. 35. Diagrammatic representation of skeleton of posterior body cavity in selected gymnotiform species. A. *Gymnotus carapo* UMMZ 206096 (142 mm TL). B. *Gymnotus maculosus* UMMZ 190531. C. *Sternopygus xingu* USNM 211830. D. *Sternarchella sima* UMMZ 211329. E. *Gymnorhamphichthys hypostomus* FMNH 100744. The last precaudal vertebrae is indicated in parentheses. Note the position and number of displaced hemal spines (DHS). Scale bars equal 2 mm in A, B, D, and E, and 1 mm in C.

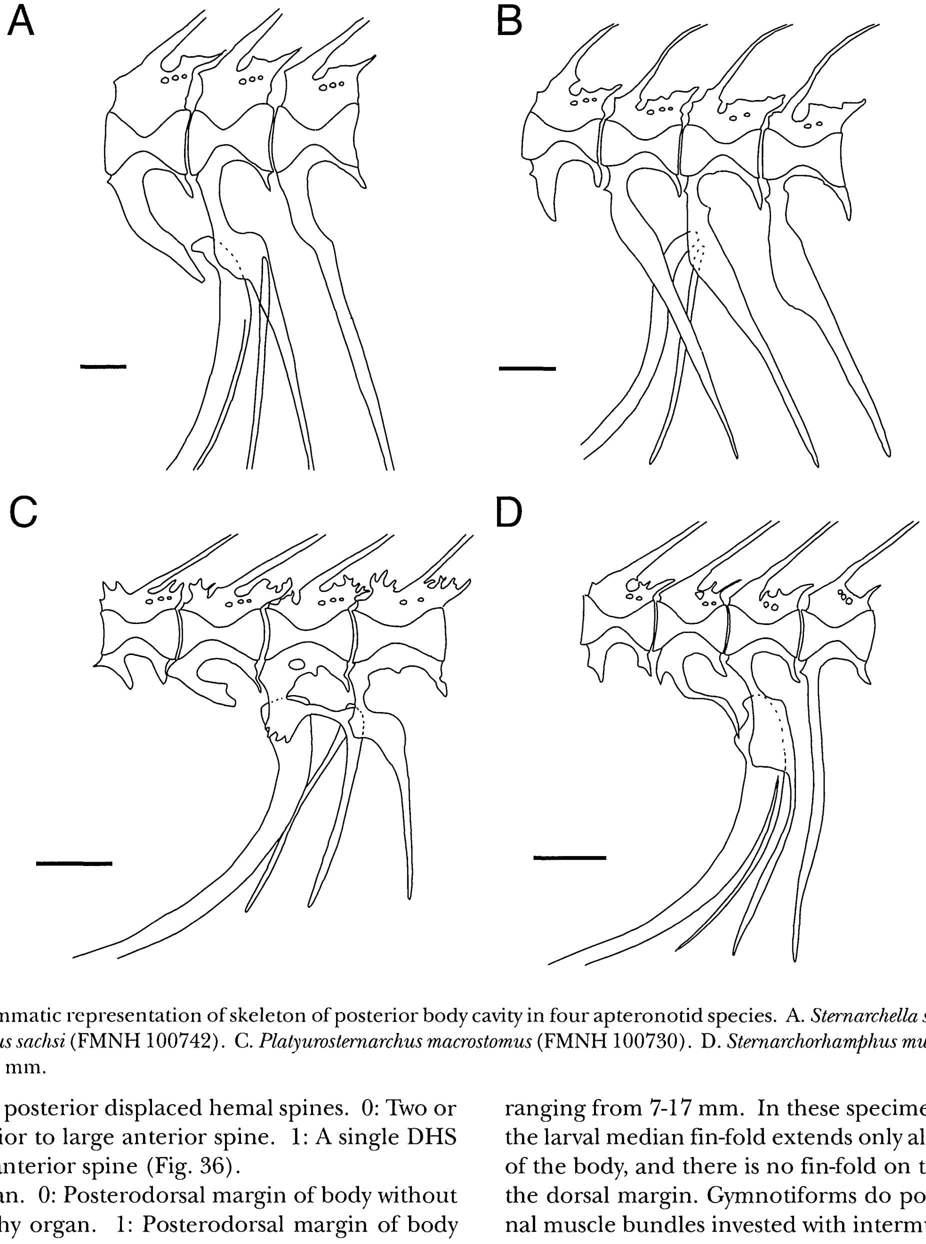


Fig. 36. Diagrammatic representation of skeleton of posterior body cavity in four apteronotid species. A. *Sternarchella sima* (UMMZ 211329). B. *Adontosternarchus sachsi* (FMNH 100742). C. *Platyurosternarchus macrostomus* (FMNH 100730). D. *Sternarchorhamphus muelleri* (USNM 228807). Scale bars equal 2 mm.

191. Number of posterior displaced hemal spines. 0: Two or three DHSs posterior to large anterior spine. 1: A single DHS posterior to large anterior spine (Fig. 36).

192. Dorsal organ. 0: Posterodorsal margin of body without a longitudinal fleshy organ. 1: Posterodorsal margin of body with a median flap or bar of fleshy tissue, extending parallel to the dorsal margin of epaxial musculature (Franchina *et al.*, 1990; Franchina and Hopkins, 1996; Figs. 37 and 38).

193. Dorsal organ length. 0: Dorsal organ extending along dorsal margin posterior to midlength of body. 1: Dorsal organ extends along entire dorsal margin of body, from nape to caudal peduncle (Franchina and Hopkins, 1996; Albert, unpubl. obs.).

Median fins. Dorsal, caudal, and anal fins, which develop within the median (midsagittal) fin fold.

194. Dorsal and adipose fins. 0: Dorsal and adipose fins present. 1: Dorsal and adipose fins absent (Fink and Fink, 1981, characters 104 and 125). The absence of the two median fins of the dorsal margin co-occur, and are treated as a single character. The absence of these fins in Gymnotiformes was confirmed in larval specimens of *Apteronotus*, *Eigenmannia* and *Gymnotus*, ranging from 7-17 mm. In these specimens, the dorsal ridge of the larval median fin-fold extends only along the posterior 25% of the body, and there is no fin-fold on the anterior portion of the dorsal margin. Gymnotiforms do possess paired longitudinal muscle bundles invested with intermuscular bones, extending along the dorsal and ventral body margins (Figs. 37 and 38; Winterbottom, 1974, fig. 47). The presence of an adipose fin in †*Ellisella* (Meunier and Gayet, 1991, fig. 1) is interpreted here as a taphonomic artifact resulting from compressing the body outline of a three-dimensional animal into two dimensions (Albert *et al.*, in press; see Discussion).

195. Anal fin origin. 0: Anal-fin origin posterior to cleithrum of pectoral girdle. 1: Anal-fin origin ventral to posterior margin of cleithrum. 2: Anal fin origin near branchial isthmus.

196. Length of anal fin. 0: Anal fin short, extending less than 0.2 times total length of body; fewer than 20 rays. 1: Anal fin long, extending along majority of ventral body margin; 100 - 159 rays. 2: 160 - 199 rays. 3: 200 - 299 rays. 4: 300 or more rays. Taxa coded by modal number of anal-fin rays (Figs. 39 - 42, Tables 3 and 4).

197. Number unbranched anal-fin rays. 0: 10 - 15 anal-fin rays branched into two rami about half distance to their tips. 1:

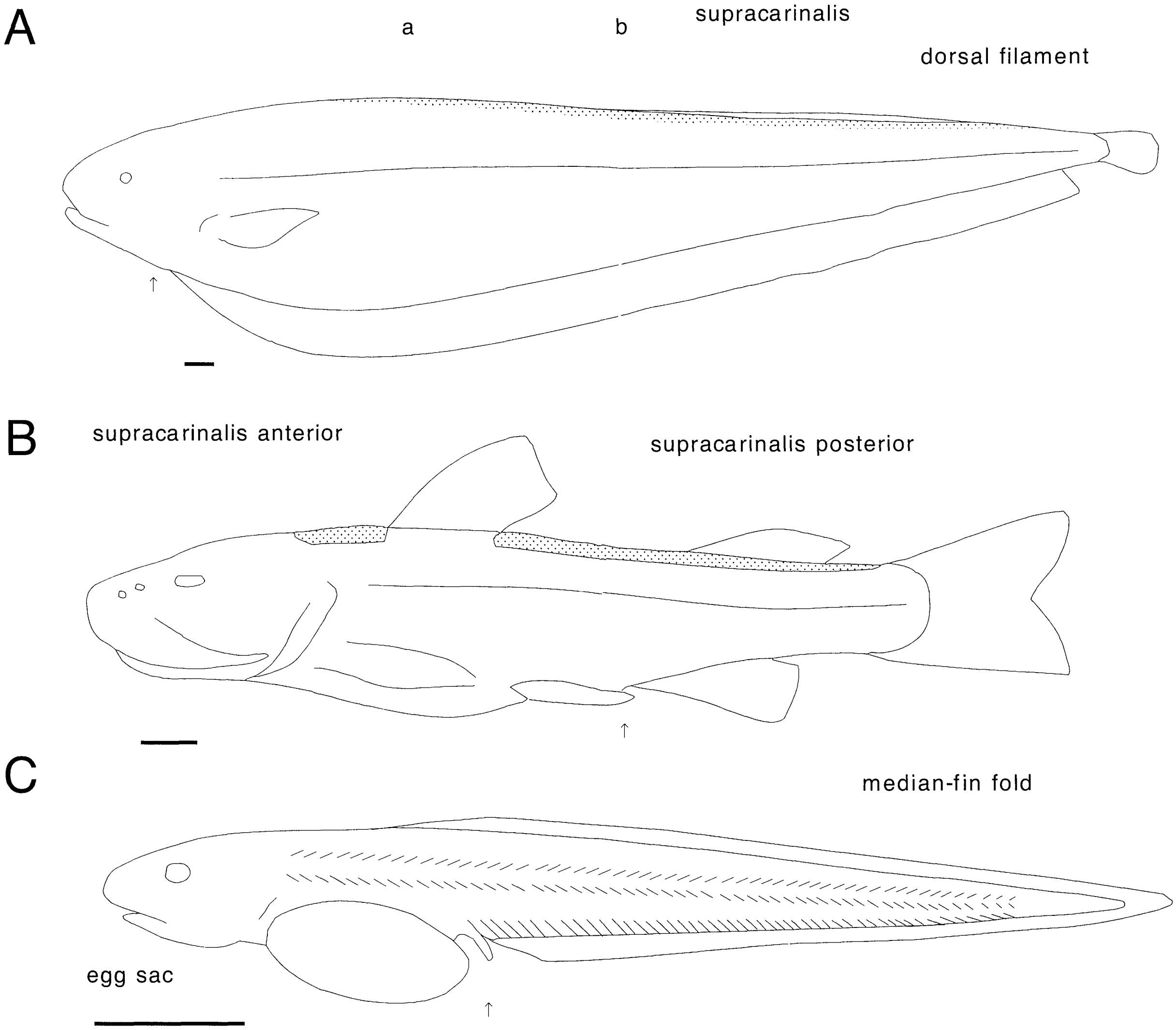


Fig. 37. Schematic drawings of body profiles. A. *Apteronotus albifrons*, adult. B. *Diplomystes nahuelbutaensis*. C. *Apteronotus leptorhynchus*, posthatching juvenile. Vertical lines labeled "a" and "b" indicate the positions of the transverse sections diagrammed in panels A and B of Fig. 38. Arrows indicate position of anus. Scale bars equal 10 mm.

Anterior 15 - 25 rays anal-fin rays unbranched to their tips (modified from Albert and Fink, 1996, character 49). 2: 30 - 60 unbranched anal-fin rays. 3: all anal-fin rays unbranched.

198. Anal-fin pterygiophore length. 0: Anal-fin pterygiophores shorter than hemal spines at midbody; less than one-third total body depth (more than 1.5 times into depth of axial musculature). 1: Anal-fin pterygiophores longer than hemal spines at midbody; more than one-third total body depth (less than 1.5 times into depth of axial musculature).

199. Shape of anal-fin pterygiophore blades. 0: Descending blades of proximal anal-fin pterygiophores slender, approximately cylindrical in cross section. 1: Descending blades of anal-fin pterygiophores broad, anterior and posterior margins extending into ventral median septum in cross section.

200. Shape of anal-fin pterygiophore tips. 0: Anal-fin pterygiophores tapering smoothly to tips. 1: Tips of pterygiophores shaped like an arrow-head; axial series of pterygiophores providing the ventral margin of the anal-fin base a scalloped appearance (Lundberg *et al.,* 1996).

201. Anal-fin ray articulation. 0: Anal-fin rays articulate with distal anal-fin pterygiophores. 1: Anal-fin rays articulate with proximal anal-fin pterygiophores (Fink and Fink, 1981, character 107, fig. 22).

202. Distal anal-fin pterygiophores. 0: Distal anal-fin pterygiophores present. 1: No distal anal-fin pterygiophores. The distal anal-fin pterygiophores of apteronotids and sternopygids are present as small cartilaginous blocks interdigitating with the articulation of the anal-fin rays and proximal pterygiophores along the dorsal margin of the anal fin.

203. AFR posterior rays. 0: not to tip of tail. 1: to tip of tail.

204. Free neural and hemal spines. 0: No capacity to regenerate axial structures. 1: Capacity to generate series of free neural and hemal spines associated with regenerated cartilaginous rod (Gayet *et al.,* 1994, character 2.2; Gayet *et al.,* 1994, characters 43 and 56). The phylogenetic distribution of character 204 is *prima facia* evidence for its independence from characters 185 and 221. Although not associated with individual vertebral centra, free neural and hemal spines are similar to unregenerated

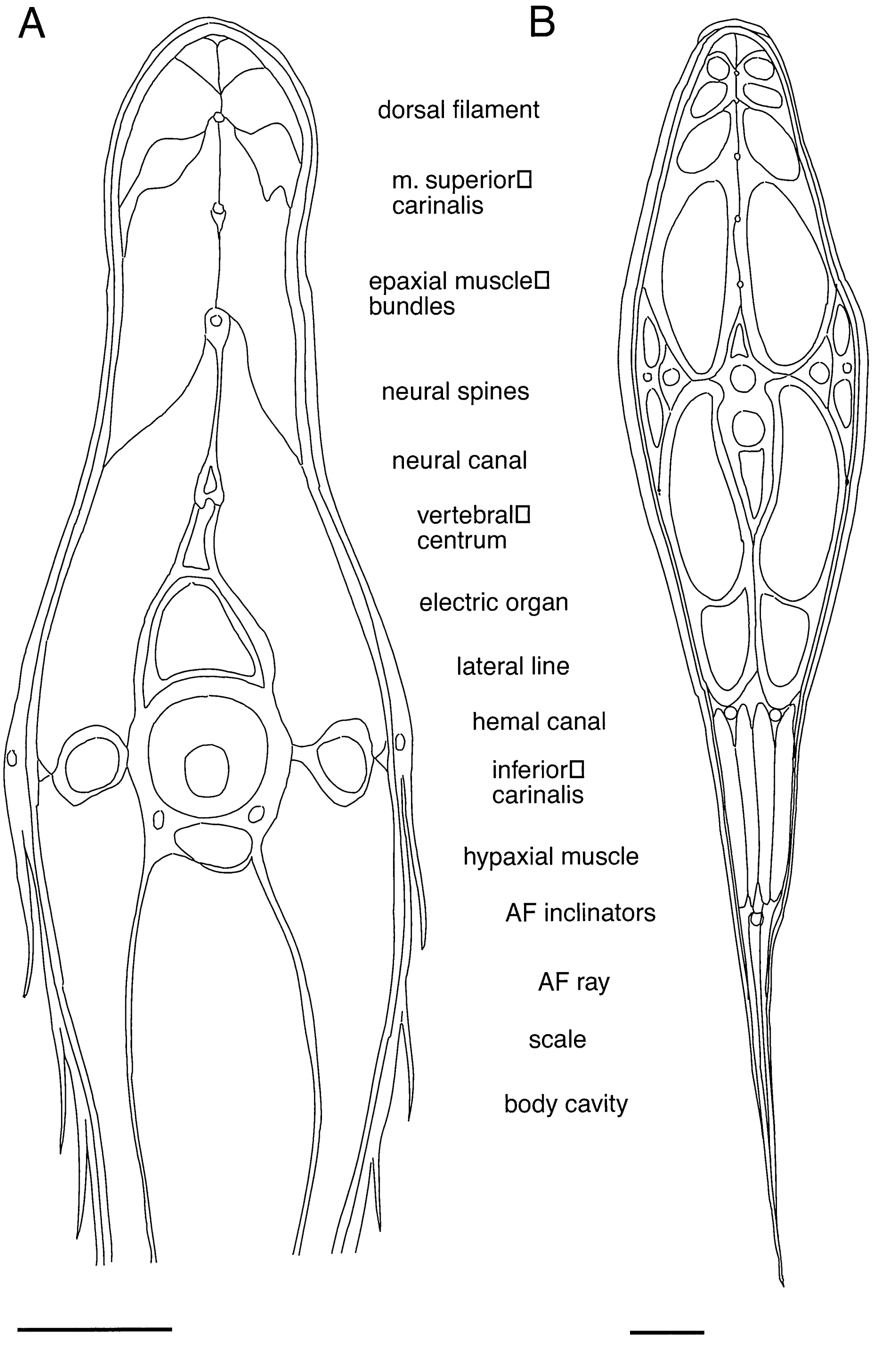


Fig. 38. Camera lucida tracings of transverse sections through the body of *Apteronotus albifrons*. Panels A and B are indicated by "a" and "b" in panel A of Fig. 37. Note in B the dorsal organ is a median, longitudinal, ectodermal structure. Scale bars equal 1 mm.

neurapophyses in size, shape, and position, as well as by being arranged in series (Meunier and Gayet, 1991, fig. 4). Free neural and hemal spines are present in both radiographed and cleared and stained specimens of all *Gymnotus* species examined with regenerated caudal regions. Newly generated free neural or hemal spines have not been observed in radiographed or cleared and stained specimens of the other gymnotiforms. No rhamphichthyoids were observed with newly generated free hemal spines (contra Gayet *et al.*, 1994, character 43).

The capacity to regenerate damaged portions of neural and hemal spines has been reported for †*Ellisella* by Meunier and Gayet 1991 (fig. 1.2), who also report regenerated portions of damaged hemal spines for *Eigenmannia virescens* (fig. 3), *Gymnotus carapo* (fig. 4), and *Apteronotus leptorhynchus* (fig. 5). I observed regenerated neural and hemal spines in species of *Sternopygus* and *Apteronotus s.s.*; *Electrophorus* have no hemal spines. The inferred capacity of †*Ellisella* to regenerate the damaged posterior vertebral centrum (fig. 1.2) is enigmatic; if confirmed such a capacity would be unique among gymnotiforms. In their regeneration experiments Meunier and Gayet (1991) did not sever

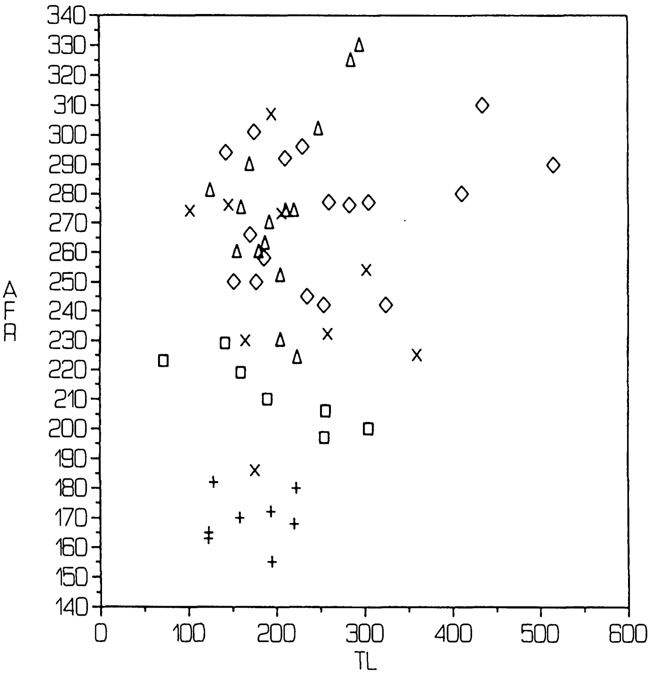


Fig. 39. Number of anal-fin rays AFR and precaudal vertebrae (PCV) in specimens representing each rhamphichthyoid lineage. *Brachyhypopomus* (◊), *Gymnorhamphichthys* (□), *Gymnotus* (x), *Hypopomus* (+), *Rhamphichthys* (Δ), Steatogini (—).

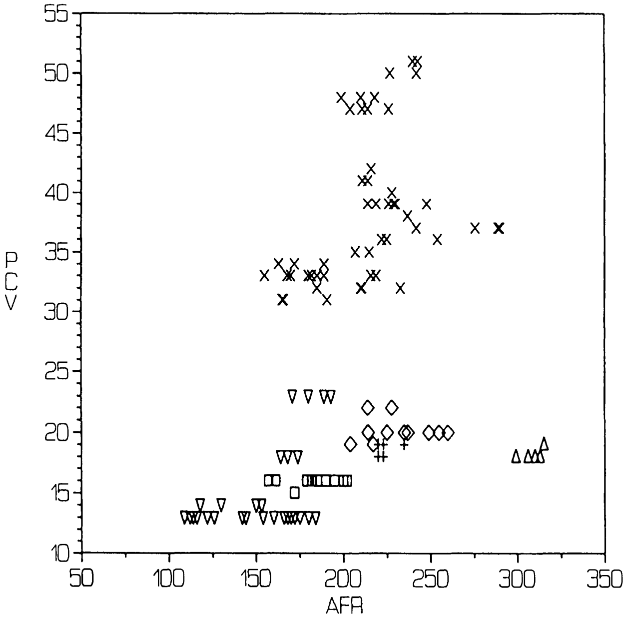


Fig. 40. Number of AFR and PCV in specimens representing each sinusoid lineage. Apteronotinae (◊), Sternarchorhynchinae (x), Eigenmanninae (□), Sternopyginae (+).

a vertebral centrum, and no specimen from field collections have been observed exhibiting regeneration of a damaged posterior vertebra. The capacity to regenerate lost anal-fin pterygiophores (Gayet *et al.*, 1994, character 22), and portions of the caudal appendage or peduncle, has been observed in all gymnotiforms except Apteronotidae. The morphology of regenerated anal-fin rays, however, varies by taxon; they are predominantly branched (like unregenerated rays) in gymnotids, whereas in †*Ellisella* and sternopygids they are predominantly unbranched (Albert and Fink, 1996).

Body cavity. Characters associated with the coelomic cavity including the gas bladder, anus, precaudal vertebrae, and ribs.

205. Body cavity long. 0: Body cavity associated with 16-19 precaudal vertebrae (including Weberian ossicles). 1: Body cavity associated with 23-29 precaudal vertebrae (Figs. 39 and 40, Tables 5 and 6). 2: Body cavity associated with 30 or more precaudal vertebrae.

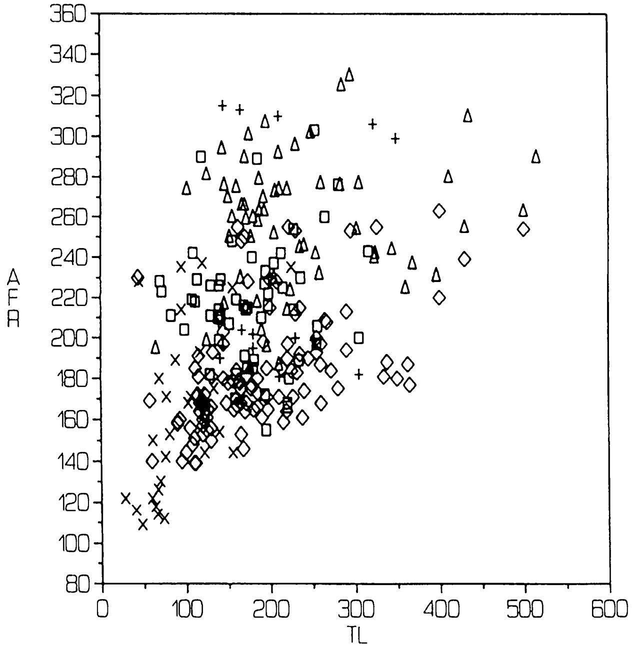


Fig. 41. Number of anal-fin rays (AFR) versus TL in species of *Sternopygus* and *Gymnotus*: *S. aequilabiatus aequilabiatus* (◊), *S. aequilabiatus pejeraton* (Δ), *S. macrurus* (x), *S. xingu* (—), *G. carapo* (□) *G. maculosus* (+). Note that species in which individuals possess a larger adult body size also possess more anal-fin rays.

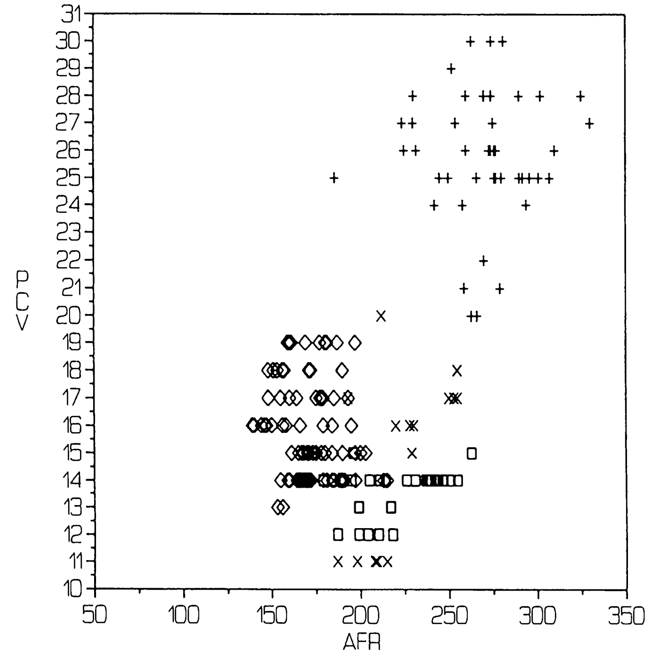


Fig. 42. Number of AFR versus TL in selected sternopygid and gymnotid species; *Sternopygus aequilabiatus* (◊), *S. macrurus* (x), *S. aequilabiatus pejeraton* (Δ), *Gymnotus carapo* (□), *G. maculosus* (+), *S. xingu* (—). Note individuals of a single gymnotiform species possess approximately the same number anal-fin rays throughout their ontogeny.

206. Body cavity short. 0: Body cavity associated with 16-19 vertebrae. 1: Body cavity short; associated with 12-15 precaudal vertebrae. 2: Body cavity very short; associated with 11 or fewer precaudal vertebrae (Figs. 39 and 40, Tables 5 and 6; Lundberg and Mago-Leccia, 1986, character 5; Mago-Leccia, 1994; Albert and Fink, 1996, character 41).

207. Number of transitional vertebrae. 0: Presence of two to eight transitional vertebrae. 1: Presence of a single transitional vertebra. 2: Presence of 20 or more transitional vertebrae.

208. Hemal spines. 0: Hemal spines present; body cavity associated with 16-19 vertebrae lacking hemal spines, and 8-10 vertebrae with paired ribs; caudal (post-coelomic) vertebrae

Table 3. An indented sequenced classification of gymnotiform taxa. New taxa in bold-face type.

- Gymnotiformes
  - Gymnotidae
    - *Gymnotus*
    - *Electrophorus*
  - Sternopygoidei
    - Rhamphichthyoidea
      - Rhamphichthyidae
      - *Rhamphichthys*
      - *Gymnorhamphichthys*
      - *Iracema*
    - Hypopomidae
      - *Hypopomus*
      - **Brachyhypopominae**
        - *Brachyhypopomus*
        - **Microsternarchini**
          - *Microsternarchus*
          - *Racenisia*
        - **Steatogini**
          - *Steatogenys*
          - *Hypopygus*
  - **Sinusoidea**
    - Sternopygidae
      - Sternopyginae
        - *†Ellisella*
        - *Sternopygus*
      - Eigenmanninae
        - *Archolaemus*
        - **Eigenmannini**
          - *Distocyclus*
          - "*Eigenmannia*"
          - *Rhabdolichops*
    - Apteronotidae
      - Sternarchorhynchinae
        - **Sternarchorhamphini**
          - *Sternarchorhamphus*
          - *Orthosternarchus*
        - **Sternarchorhynchini**
          - *Sternarchorhynchus*
          - *Platyurosternarchus*
    - Apteronotinae
      - ***Parapteronotus***
      - *Apteronotus sensu stricto*
      - **Navajini**
        - **Sternarchellini**
          - *Sternarchella*
          - *Magosternarchus*
        - ***Compsaraia***
        - **Porotergini**
          - "*Porotergus*"
          - *Sternarchogiton*
          - *Adontosternarchus*

bearing hemal spines present. 1: Hemal spines absent, body cavity extending almost to tip of the tail; no caudal (post-coelomic) vertebrae (Evans, 1929).

209. Number of pleural ribs. 0: Eight or more pairs of pleural ribs. 1: Seven or fewer pairs of pleural ribs (Lundberg and Mago-Leccia, 1986, characters 5 and 13).

210. Length of anterior ribs. 0: Anterior two or three ribs relatively short, their lengths less than 80% body depth at pectoral girdle. 1: Length of anterior two ribs greater than 80% body depth at pectoral girdle (Lundberg and Mago-Leccia, 1986, character 6).

211. Shape of anterior ribs. 0: Anterior pair of pleural ribs narrow; breadth approximately equal to width. 1: Anterior ribs broad, breadth two to three times width.

212. Size of posterior precaudal parapophyses. 0: Parapophyses of posterior precaudal vertebra small, their ventral margins oblique to long axis of body, not contacting one another along midline. 1: Parapophyses of posterior precaudal vertebra longer than wide, their ventral margins parallel with long axis of body, abutting at midline (Fig. 36-C).

213. Shape of last precaudal parapophyses. 0: Parapophyses of last precaudal vertebra broad and triangular, their tips rounded. 1: Parapophyses of last precaudal vertebra slender and sinuous, their tips pointed (Fig. 36-D).

214. Size of posterior chamber of gas bladder. 0: Gas bladder divided into two unequal chambers; anterior chamber larger in diameter and shorter in length than posterior chamber. 1: Posterior chamber of gas bladder elongate, passing between hemal arches of postcoelomic axial skeleton and musculature (Reinhardt, 1852; Kaup, 1856; Evans, 1929; Albert and Fink, 1996, character 46, fig. 14). 2: Posterior chamber of gas bladder extending to tip of tail.

215. Anterior chamber of gas bladder. 0: Anterior and posterior chambers of gas bladder thin and translucent. 1: Anterior chamber of gas bladder encapsulated in a thick, opaque layer of tissue.

216. Position of anus. 0: Anus located posterior to midlength of body. 1: Anus located anterior to midlength of body (Fink and Fink, 1981, character 122).

217. Allometry of anus position. 0: Position of anus relatively fixed during post-larval development; anus located posterior to tip of pectoral fin. 1: Position of anus changing allometrically during ontogeny, starting near posterior end of coelomic cavity and growing anterior to pectoral girdle; anus located near isthmus.

218. Urogenital papilla. 0: Urogenital pore sessile, opening flush with ventral margin of body wall in sexually mature specimens. 1: Urogenital pore elevated onto a papilla in sexually mature specimens (Mago-Leccia, 1994).

219. Tail length. 0: Length of tail posterior to anal-fin 17 - 45% total length. 1: Tail short, 0 - 16% total length. 2: Tail long, more than 45% total length.

220. Number caudal-fin rays. 0: 7 - 15 caudal-fin rays. 1: Six or fewer caudal-fin rays.

221. Regeneration of caudal axial structures. 0: No capacity to regenerate axial sclerotomal and neural structures. 1: Capacity to regenerate sclerotomal structures (*e.g.*, caudal plate or rod; Meunier and Gayet, 1991, figs. 3-5) and spinal cord (Anderson and Waxman, 1983). This character is similar to character 28 of Gayet *et al.* (1994). As defined here, however, it also applies to the Apteronotidae, which possess the capacity to regenerate spinal neurons, muscles, and tendons, and the hypural plate, rays, and scales of the caudal fin. Apteronotids also regenerate damaged anal-fin rays and anal-fin pterygiophores (pers. obs.).

222. Caudal rod. 0: Caudal fin present with hypural plate and segmented rays. 1: No caudal fin, hypural plate, or segmented rays; cartilaginous hypural-opisthural bar, rod, or filament, regenerated in place of caudal vertebrae (see character 157; Fink and Fink, 1981, character 109, fig. 23; Gayet *et al.*, 1994, characters 26 and 27); sometimes ossified (see character

Table 4. Ranges of anal-fin ray counts for 359 specimens in 26 gymnotiform genera. Taxa in quotations represent species assigned to genera not demonstrated to be monophyletic; *s.s.* = *sensu stricto*; *s.m.* = *sedis mutabilis.* Numbers grouped by twenties, beginning with number at column head. When available, data were taken from specimens in Appendix 1; other data from citations in Appendix 4.

Genus	100	120	140	160	180	200	220	240	260	280	300	320+	N
Adontosternarchus	-	-	4	5	1	-	-	-	-	-	-	-	10
Apteronotus s.s.	-	2	15	12	7	-	-	-	-	-	-	-	36
"Apteronotus" s.m.	-	-	-	2	3	-	-	-	-	-	-	-	5
Brachyhypopomus	-	-	-	2	1	16	9	2	1	-	-	-	31
Compsaraia	-	-	-	9	5	1	-	-	-	-	-	-	15
Distocyclus	-	-	-	-	-	2	2	2	1	-	-	-	7
Eigenmannia	-	-	-	1	5	3	3	5	-	-	-	-	17
Electrophorus	-	-	-	-	-	-	-	-	-	-	-	2	2
Gymnorhamphichthys	-	-	1	3	7	4	-	-	-	-	-	-	15
Gymnotus	-	-	1	6	9	16	10	6	1	2	-	-	50
Hypopomus	-	-	-	-	-	-	5	-	1	-	-	-	6
Hypopygus	5	4	4	-	-	-	-	-	-	-	-	-	13
Iracema	-	-	-	-	-	-	-	1	1	-	-	-	2
Magosternarchus	-	-	-	-	12	2	-	-	-	-	-	-	14
Microsternarchus	-	-	-	3	-	-	-	-	-	-	-	-	3
Orthosternarchus	-	-	-	-	-	1	1	-	-	-	-	-	2
Parapteronotus	-	-	-	3	1	-	-	-	-	-	-	-	4
Platyurosternarchus	-	-	-	-	-	1	3	-	-	-	-	-	4
"Porotergus"	-	-	1	2	1	-	-	-	-	-	-	-	4
Racenisia	-	-	-	2	3	-	-	-	-	-	-	-	5
Rhabdolichops	-	-	-	-	2	3	-	-	-	-	-	-	5
Rhamphichthys	-	-	-	-	-	-	-	-	-	1	4	-	5
Steatogenys	-	-	2	7	2	-	-	-	-	-	-	-	11
Sternarchella	-	-	1	10	2	1	-	-	-	-	-	-	14
Sternarchogiton	-	-	-	1	6	2	-	-	-	-	-	-	9
Sternarchorhamphus	-	-	-	-	-	-	1	8	1	-	-	-	10
Sternarchorhynchus	-	-	-	4	6	3	2	-	-	-	-	-	15
Sternopygus	-	-	-	-	1	-	5	9	18	7	4	-	44
Total	5	6	29	71	74	55	41	33	24	10	8	2	359

224). Among gymnotiforms only apteronotids possess a caudal fin, including a hypural plate and segmented fin rays. Contrary to previous reports (Mago-Leccia, 1994: 14) segmented caudal-fin rays and a hypural plate are not present in juvenile *Eigenmannia virescens.* Specimens examined ranging from 7.0 to 9.0 mm TL (8 -10 days old) possess short, unsegmented actinotrichia at regular intervals within the median fin fold enveloping the caudal region. True anal-fin pterygiophores and segmented anal-fin rays were not observed until 15 mm TL (18 days old), at which point the posterior and dorsal portions of the fin fold had already degenerated. Segmented caudal-fin rays or a hypural plate are not present in specimens of *Apteronotus leptorhynchus* of similar body size (9.5 - 15.0 mm TL). Caudal fin elements are not present in specimens of *Gymnotus cf. coatesi* at 17 - 20 mm TL (N = 6).

223. Caudal fin shape. 0: Caudal fin deeply forked; distinct dorsal and ventral lobes. 1: Caudal fin rounded; longest rays extend from middle of caudal fin.

224. Ossified caudal rod or plate. 0: Axial skeleton of caudal region regenerated as a an elongate cartilaginous rod or filament. 1: Caudal rod or plate of regenerated axial skeleton ossified (modified from Albert and Fink, 1996, character 50).

225. Caudal rod ossification. 0: Bony core of caudal appendage regenerated as a thin elongate bony or cartilaginous rod. 1: Ossification of caudal rod restricted to outer membrane; rod appearing translucent in profile, except the thicker dorsal and ventral margins (Redescription of character 46, Gayet *et al.*, 1994).

Electric organs. Comparative studies of gymnotiform electric organs have examined the morphology and physiology of electrocytes, electric organs, and electric organ discharges. This category includes characters of electric organ morphology, and behavioral characters associated with electrogenesis. The morphology and nervous innervation of the mental and humeral electric organs among hypopomids is treated by Sullivan (1993; pers. comm.).

226. Electric organs. 0: All axial muscle fibers unmodified; no organs capable of generating rhythmic electric discharges. 1: Paired electrogenic organs developing in larval hypaxial musculature; electric organ composed of rows of modified elongate myofibrils (electrocytes; Bennett, 1971; Fink and Fink, 1981, character 121). Development of the electric organ varies by taxon (Kirschbaum, 1977; Mills *et al.*, 1992; Unguez and Zakon, 1998).

Electric organs are present in members of several derived siluriform groups. Some species of the African *Synodontus* and *Clarias* produce weak electric discharges from extrinsic gas bladder muscles for use in social communication (Hagedorn *et al.*, 1990; Baron *et al.*, 1994; 1996). The African electric catfish

Table 5. Ranges of anal-fin ray counts for 359 specimens in 72 gymnotiform species. Numbers grouped by twenties, beginning with number at column head. Specimens examined as in Table 4.

Species	100	120	140	160	180	200	220	240	260	280	300+	N
Apteronotidae (30 species)												
Adontosternarchus devenanzii	-	-	2	3	-	-	-	-	-	-	-	5
Adontosternarchus sachsi	-	-	2	2	1	-	-	-	-	-	-	5
Apteronotus albifrons	-	-	6	4	-	-	-	-	-	-	-	10
"Apteronotus" apurensis	-	-	-	1	2	-	-	-	-	-	-	3
Apteronotus brasiliensis	-	-	-	1	1	-	-	-	-	-	-	2
Apteronotus cuchillejo	-	1	4	-	-	-	-	-	-	-	-	5
Apteronotus cuchillo	-	-	-	1	4	-	-	-	-	-	-	5
Apteronotus cuyuniense	-	-	1	4	-	-	-	-	-	-	-	5
Apteronotus ellisi	-	-	-	-	1	-	-	-	-	-	-	1
Apteronotus leptorhynchus	-	1	4	-	1	-	-	-	-	-	-	6
"Apteronotus" macrolepis	-	-	-	1	1	-	-	-	-	-	-	2
Apteronotus mariae	-	-	-	1	-	-	-	-	-	-	-	1
Parapteronotus hasemani	-	-	-	3	1	-	-	-	-	-	-	4
Compsaraia compsa	-	-	-	7	4	1	-	-	-	-	-	12
Compsaraia sp. 1	-	-	-	2	1	-	-	-	-	-	-	3
Magosternarchus duccis	-	-	-	-	-	2	-	-	-	-	-	2
Magosternarchus raptor	-	-	-	-	12	-	-	-	-	-	-	12
Orthosternarchus tamandua	-	-	-	-	-	1	1	-	-	-	-	2
"Porotergus" gimbeli	-	-	-	2	1	-	-	-	-	-	-	3
"Porotergus" sp. 1	-	-	1	-	-	-	-	-	-	-	-	1
Sternarchogiton sp. B	-	-	-	1	2	2	-	-	-	-	-	5
Sternarchogiton nattereri	-	-	-	-	4	-	-	-	-	-	-	4
Sternarchella curvioperculata	-	-	1	-	-	-	-	-	-	-	-	1
Sternarchella orinoco	-	-	-	-	2	-	-	-	-	-	-	2
Sternarchella orthos	-	-	-	10	-	1	-	-	-	-	-	11
Platyurosternarchus macrostomus	-	-	-	-	-	1	3	-	-	-	-	4
Sternarchorhamphus muelleri	-	-	-	-	-	-	1	8	1	-	-	10
Sternarchorhynchus curvirostris	-	-	-	-	-	-	2	-	-	-	-	2
Sternarchorhynchus oxyrhynchus	-	-	-	4	6	-	-	-	-	-	-	10
Sternarchorhynchus roseni	-	-	-	-	2	3	-	-	-	-	-	5
Subtotal	-	2	21	47	46	11	7	8	1	-	-	143
Sternopygidae (11 species)												
Distocyclus conirostris	-	-	-	-	-	2	2	1	-	-	-	5
Distocyclus goajira	-	-	-	-	-	-	-	1	1	-	-	2
Eigenmannia humboldti	-	-	-	-	-	-	1	2	-	-	-	3
Eigenmannia sp. G	-	-	-	-	2	-	-	-	-	-	-	2
Eigenmannia nigra	-	-	-	-	-	-	2	3	-	-	-	5
Eigenmannia virescens	-	-	-	1	3	3	-	-	-	-	-	7
Rhabdolichops eastwardi	-	-	-	-	2	3	-	-	-	-	-	5
Sternopygus aequilabiatus	-	-	-	-	-	-	-	6	4	5	2	17
Sternopygus astrabes	-	-	-	-	-	-	-	1	4	-	-	5
Sternopygus macrurus	-	-	-	-	1	-	3	1	3	-	1	9
Sternopygus xingu	-	-	-	-	-	-	2	1	7	2	1	13
Subtotal	-	-	-	1	8	8	10	16	19	7	4	73
Hypopomidae (17 species)												
Brachyhypopomus beebei	-	-	-	-	-	1	1	-	-	-	-	2
Brachyhypopomus brevirostris	-	-	-	-	-	-	-	2	1	-	-	3
Brachyhypopomus occidentalis	-	-	-	-	-	2	-	-	-	-	-	2
Brachyhypopomus pinnicaudatus	-	-	-	-	-	1	3	-	-	-	-	4
Brachyhypopomus sp. B	-	-	-	-	-	5	-	-	-	-	-	5
Brachyhypopomus sp. E	-	-	-	2	-	-	-	-	-	-	-	2
Brachyhypopomus sp. M	-	-	-	-	-	-	5	-	-	-	-	5
Brachyhypopomus sp. R	-	-	-	-	1	2	-	-	-	-	-	3
Brachyhypopomus sp. W	-	-	-	-	-	5	-	-	-	-	-	5
Microsternarchus bilineatus	-	-	-	3	-	-	-	-	-	-	-	3
Hypopomus artedi	-	-	-	-	-	-	5	-	-	-	-	5

(Continued on next page)

Table 5. Continued.

Species	100	120	140	160	180	200	220	240	260	280	300+	N
Hypopomus sp. Z	-	-	-	-	-	-	-	-	1	-	-	1
Hypopygus lepturus	5	3	-	-	-	-	-	-	-	-	-	8
Hypopygus neblinae	-	1	4	-	-	-	-	-	-	-	-	5
Racenisia fimbriipinna	-	-	-	2	3	-	-	-	-	-	-	5
Steatogenys duidae	-	-	2	2	-	-	-	-	-	-	-	4
Steatogenys elegans	-	-	-	5	2	-	-	-	-	-	-	7
Subtotal	5	4	6	14	6	16	14	2	1	-	-	68
Rhamphichthyidae (5 species)												
Gymnorhamphichthys hypostomus	-	-	-	-	3	3	-	-	-	-	-	6
Gymnorhamphichthys rondoni	-	-	1	2	2	1	-	-	-	-	-	6
Gymnorhamphichthys rosamariae	-	-	-	1	2	-	-	-	-	-	-	3
Iracema caiana	-	-	-	-	-	-	-	1	1	-	-	2
Rhamphichthys rostratus	-	-	-	-	-	-	-	-	-	1	4	5
Subtotal	-	-	1	3	7	4	-	1	1	1	4	22
Gymnotidae (9 species)												
Gymnotus anguillaris	-	-	-	-	-	1	3	1	-	-	-	5
Gymnotus carapo	-	-	-	-	-	1	1	-	-	-	-	2
Gymnotus cataniapo	-	-	-	-	-	-	1	3	-	-	-	4
Gymnotus coatesi	-	-	-	-	-	3	1	-	-	-	-	4
Gymnotus cylindricus	-	-	-	1	6	6	1	-	-	-	-	14
Gymnotus maculosus	-	-	1	5	2	-	-	-	-	-	-	8
Gymnotus pedanopterus	-	-	-	-	-	-	2	2	1	2	-	7
Gymnotus stenoleucus	-	-	-	-	1	5	1	-	-	-	-	7
Electrophorus electricus	-	-	-	-	-	-	-	-	-	-	2	2
Subtotal	-	-	1	6	9	16	10	6	1	2	2	53
Total	5	6	29	71	75	55	41	33	24	10	10	359

Malapturus (Malapteruridae) emits strong biphasic electric discharges of up to 350 volts for use in predation and predator avoidance (Bennett, 1971). The phylogenetic position of these electrogenic catfishes is nested within the Siluriformes (de Pinna, 1993), and is therefore not relevant in considering the plesiomorphic condition of gymnotiforms. Electrogenesis has not been reported in any characiform species. The retention of hypaxial electric organs into maturity in gymnotiforms represents the plesiomorphic condition.

227. Number of hypaxial electric organs. 0: Single hypaxial electric organ. 1: Three anatomically distinct hypaxial electric organs (*i.e.* Sachs', Hunter's, and Main electric organs).

228. Posterior surface of electrocytes. 0: Nervous innervation of electrocytes on microvilli of posterior surface. 1: Electrocytes innervation on a short stalk emanating from posterior surface of the cell (Bass, 1986, fig. 1).

229. Shape of electrocytes. 0: Electrocytes cigar shaped, elongate; longitudinal axis parallel with neuraxis. 1: Electrocytes barrel shaped, cylindrical; long axis oriented vertically (Bass, 1986, fig. 1). The plesiomorphic morphology of electrocytes is retained in the larvae of all gymnotiforms examined, and in the mature electric organ of many sternopygid species (not in *Rhabdolichops* or *Eigenmannia virescens*).

230. Electric organ replacement. 0: Main electric organ of mature specimens developing from a medial portion of hypaxial musculature, extending along ventral margin of hypaxial musculature. 1: Hypaxial electric organ replaced during development, adult organ not derived from hypaxial musculature (Kirschbaum, 1977; Franchina, 1997). Bennett (1971:417, fig. 32) suggests that the nerve plexus present above the larval electric organs in rhamphichthyoids and *Gymnotus* is homologous to the electric organ of apteronotids. The plexus is absent in *Electrophorus*, *Sternopygus* and *Eigenmannia*, and present in rhamphichthyoids and *Gymnotus*. The relationship of this plexus to the degeneration/retention of the larval organ is unclear. The adult organ begins differentiating at about 13 mm TL in *Eigenmannia virescens* (Bass, 1986) and is fully formed by 55 mm TL. An EOD is emitted as soon as the organ forms (Hagedorn, 1986) and rises in frequency during the transformation to the adult organ from about 150 to about 400 Hz. In *Apteronotus leptorhynchus*, the EOD frequency changes from 300 to 700 Hz in females, and to 800 Hz in males (Kirschbaum and Westby, 1975).

231. Hypaxial electric organ length. 0: Electric organ extending from anus to tip of tail, along ventral margin of hypaxial musculature. 1: Electric organ extending anterior to position of anal pore. The position of the anus is at the posterior end of the body cavity when the electric organ first develops in juvenile *Eigenmannia* and *Apteronotus* at c. 7 - 9 mm TL (Kirschbaum, 1977; pers. obs.).

232. Mental accessory organ. 0: No electrocytes on ventral surface of head; EOD biphasic with each pulse compsed of a head-positive followed by a head-negative discharge. 1: Electrocytes extend anterior to anus onto ventral surface of head; EOD tetraphasic with two head-positive and two head-negative discharges and a complex power spectrum (Bennett, 1962; 1971; Bass, 1986; Crampton, 1998a). 2: Mental swelling composed of electrosensory organs.

Table 6. Ranges precaudal vertebrae counts for for 481 specimens in 26 gymnotiform genera. Numbers grouped by fours, beginning with number at column head. Specimens examined and nomenclature in Table 4.

Genus	11	15	19	23	27	31	35	39	43	47+	N
Adontosternarchus	10	-	-	-	-	-	-	-	-	-	10
Apteronotus s.s.	-	24	10	-	-	-	-	-	-	-	34
"Apteronotus" s.m.	-	5	-	-	-	-	-	-	-	-	5
Archlaemus	-	5	-	-	-	-	-	-	-	-	5
Brachyhypopomus	23	40	-	-	-	-	-	-	-	-	63
Compsaraia	15	3	-	-	-	-	-	-	-	-	18
Distocyclus	6	1	-	-	-	-	-	-	-	-	7
Eigenmannia	22	1	-	-	-	-	-	-	-	-	23
Electrophorus	-	-	-	-	-	-	-	-	-	3	3
Gymnorhamphichthys	-	2	-	-	-	-	-	-	-	-	25
Gymnotus	-	-	-	-	-	42	10	10	-	11	73
Hypopomus	-	13	-	-	-	-	-	-	-	-	13
Hypopygus	13	-	-	-	-	-	-	-	-	-	13
Magosternarchus	-	10	-	-	-	-	-	-	-	-	10
Microsternarchus	-	7	-	-	-	-	-	-	-	-	7
Parapteronotus	-	4	-	-	-	-	-	-	-	-	4
Platyurosternarchus	-	3	-	-	-	-	-	-	-	-	3
"Porotergus"	1	3	-	-	-	-	-	-	-	-	4
Racenisia	-	-	-	6	-	-	-	-	-	-	6
Rhabdolichops	5	-	-	-	-	-	-	-	-	-	5
Rhamphichthys	-	4	1	-	-	-	-	-	-	-	5
Steatogenys	11	-	-	-	-	-	-	-	-	-	11
Sternarchella	-	13	-	-	-	-	-	-	-	-	13
Sternarchogiton	7	2	-	-	-	-	-	-	-	-	9
Sternarchorhamphus	-	6	3	-	-	-	-	-	-	-	9
Sternarchorhynchus	5	5	-	-	-	-	-	-	-	-	10
Sternopygus	-	-	5	25	53	-	-	-	-	-	83
Total	118	184	19	31	53	42	10	10	-	14	481

233. Humeral accessory organ. 0: No humeral electric organ. 1: Humeral electric organ extending dorsally from pectoral fin base, and then posteriorly along horizontal myoseptum a distance less than length of pectoral fin (Schwassmann, 1984, fig, 6).

234. Position of humeral electric organ. 0: Axillary, dorsal to pectoral fin. 1: Posterior to pectoral fin.

235. Opercular accessory electric organ. 0: Absent. 1: Present on head over operculum.

236. Myogenic electric organ. 0: Main electric organ of mature specimens derived exclusively from hypaxial musculature. 1: Main electric organ also derived from epaxial musculature. 2: Main electric organ also derived from medial portion of anal-fin pterygiophore muscles (Kirschbaum, 1977; Mills *et al.*, 1992; Unguez and Zakon; 1998).

237. Neurogenic electric organ. 0: Main electric organ of mature specimens ontogenetically derived from hypaxial musculature. 1: Main electric organ of mature specimens derived from electromotor neurons which innervate larval hypaxial organ (Kirschbaum, 1983; Franchina, 1997).

238. Electromotoneuron morphology. 0: Motor neurons innervating larval electric organs and/or adult electromotor neurons straight, extending posteriorly in parallel with neuraxis. 1: Electromotor neurons U-shaped, with rostral and caudal extensions, curving on themselves in axial extent (Anderson and Waxman, 1981; Bass, 1986).

239. EOD form. 0: EOD of mature specimens produced as discrete non-overlapping pulses with alternating periods of current flow and no current flow; capacity for EOD frequency modulations present; cells of pacemaker nucleus organized into two separate clusters. 1: EOD produced as a continual series of discharges to form a quasi-sinusoidal pattern of current emission; no capacity for EOD frequency modulations; relay and pacemaker cells mingled in a single medullary nucleus (Bennett 1971; Dye and Meyer, 1986, figs. 3-5; Franchina and Stoddard, 1998).

240. EOD repetition rate (frequency). 0: Mean EOD of mature specimens with a fundamental frequency less than 250 Hz. 1: EOD frequency 251- 750 Hz. 2: EOD frequency 751 - 1200 Hz. 3: EOD frequency 1200 - 1750 Hz (Langner and Scheich, 1978; Bass, 1986; Kirschbaum, 1994c; Crampton, 1998a).

241. EOD monophasic. 0: EOD of mature specimens with two (sometimes three or four) phases; EOD characterized by both head-positive and head-negative depolarizations. 1: Monophasic EOD of juveniles retained into maturity; EOD characterized exclusively by head-positive depolarizations. 2: Monophasic hyperpolarization from negative baseline (Bennett, 1971; Bass, 1986; Alves-Gomes *et al.*, 1995; Stoddard *et al.*, 1999).

242. EOD pulse power spectrum. 0: EOD of mature specimens simple, with one or no higher harmonics. 1: EOD complex, with two or more harmonics.

243. EOD duration / shape. 0: EOD of mature specimens a short biphasic pulse of about 1.0 milliseconds in duration, with a small amplitude negative pulse immediately preceding larger amplitude positive pulse. 1: EOD greater than 2 milliseconds in duration, without small amplitude negative pulse preceding large positive pulse (Alves-Gomes *et al.*, 1995, fig. 9; Crampton, 1998a,

Table 7. Ranges of precaudal vertebrae counts for 481 specimens in 71 gymnotiform species. Numbers grouped by fours, beginning with number at column head. Specimens examined and nomenclature as in Table 4.

Species	11	15	19	23	27	31	35	39	43	47+	N
Apteronotidae (28 species)											
Adontosternarchus devenanzii	5	-	-	-	-	-	-	-	-	-	5
Adontosternarchus sachsi	5	-	-	-	-	-	-	-	-	-	5
Apteronotus albifrons	-	10	-	-	-	-	-	-	-	-	10
"Apteronotus" apurensis	-	3	-	-	-	-	-	-	-	-	3
Apteronotus brasiliensis	-	2	-	-	-	-	-	-	-	-	2
Apteronotus cuchillejo	-	5	-	-	-	-	-	-	-	-	5
Apteronotus cuchillo	-	-	5	-	-	-	-	-	-	-	5
Apteronotus cuyuniense	-	-	5	-	-	-	-	-	-	-	5
Apteronotus leptorhynchus	-	6	-	-	-	-	-	-	-	-	6
"Apteronotus" macrolepis	-	2	-	-	-	-	-	-	-	-	2
Apteronotus mariae	-	1	-	-	-	-	-	-	-	-	1
Compsaraia compsa	15	-	-	-	-	-	-	-	-	-	15
Compsaraia sp. 1	-	3	-	-	-	-	-	-	-	-	3
Magosternarchus raptor	-	7	-	-	-	-	-	-	-	-	7
Magosternarchus duccis	-	3	-	-	-	-	-	-	-	-	3
Orthosternarchus tamandua	-	-	3	-	-	-	-	-	-	-	3
Parapteronotus hasemani	-	4	-	-	-	-	-	-	-	-	4
"Porotergus" gimbeli	1	2	-	-	-	-	-	-	-	-	3
"Porotergus" sp. 1	-	1	-	-	-	-	-	-	-	-	1
Sternarchogiton sp. B	3	2	-	-	-	-	-	-	-	-	5
Sternarchogiton nattereri	4	-	-	-	-	-	-	-	-	-	4
Sternarchella orinoco	-	2	-	-	-	-	-	-	-	-	2
Sternarchella orthos	-	11	-	-	-	-	-	-	-	-	11
Platyurosternarchus macrostomus	-	3	-	-	-	-	-	-	-	-	3
Sternarchorhamphus muelleri	-	6	-	-	-	-	-	-	-	-	6
Sternarchorhynchus curvirostris	-	2	-	-	-	-	-	-	-	-	2
Sternarchorhynchus oxyrhynchus	-	3	-	-	-	-	-	-	-	-	3
Sternarchorhynchus roseni	5	-	-	-	-	-	-	-	-	-	5
Subtotal	38	78	13	-	-	-	-	-	-	-	129
Sternopygidae (12 species)											
Archolaemus blax	-	5	-	-	-	-	-	-	-	-	5
Distocyclus conirostris	5	-	-	-	-	-	-	-	-	-	5
Distocyclus goajira	1	1	-	-	-	-	-	-	-	-	2
Eigenmannia humboldti	8	-	-	-	-	-	-	-	-	-	8
Eigenmannia sp. G	1	1	-	-	-	-	-	-	-	-	2
Eigenmannia nigra	6	-	-	-	-	-	-	-	-	-	6
Eigenmannia virescens	7	-	-	-	-	-	-	-	-	-	7
Rhabdolichops eastwardi	5	-	-	-	-	-	-	-	-	-	5
Sternopygus aequilabiatus	-	-	-	17	-	-	-	-	-	-	17
Sternopygus astrabes	-	-	5	-	-	-	-	-	-	-	5
Sternopygus macrurus	-	-	-	7	2	-	-	-	-	-	9
Sternopygus xingu	-	-	-	1	51	-	-	-	-	-	52
Subtotal	33	7	5	25	53	-	-	-	-	-	123
Hypopomidae (18 species)											
Brachyhypopomus beebei	-	5	-	-	-	-	-	-	-	-	5
Brachyhypopomus brevirostris	-	5	-	-	-	-	-	-	-	-	5
Brachyhypopomus diazi	4	1	-	-	-	-	-	-	-	-	5
Brachyhypopomus occidentalis	-	7	-	-	-	-	-	-	-	-	7
Brachyhypopomus pinnicaudatus	1	20	-	-	-	-	-	-	-	-	21
Brachyhypopomus sp. B	5	-	-	-	-	-	-	-	-	-	5
Brachyhypopomus sp. E	2	-	-	-	-	-	-	-	-	-	2
Brachyhypopomus sp. M	3	2	-	-	-	-	-	-	-	-	5
Brachyhypopomus sp. R	3	-	-	-	-	-	-	-	-	-	3
Brachyhypopomus sp. W	5	-	-	-	-	-	-	-	-	-	5
Microsternarchus bilineatus	-	7	-	-	-	-	-	-	-	-	7
Hypopomus artedi	-	12	-	-	-	-	-	-	-	-	12
Hypopomus sp. Z	-	1	-	-	-	-	-	-	-	-	1

(*Continued on next page*)

Table 7. Continued.

Species	11	15	19	23	27	31	35	39	43	47+	N
Hypopygus lepturus	8	-	-	-	-	-	-	-	-	-	8
Hypopygus neblinae	5	-	-	-	-	-	-	-	-	-	5
Racenisia fimbriipinna	-	-	-	6	-	-	-	-	-	-	6
Steatogenys duidae	4	-	-	-	-	-	-	-	-	-	4
Steatogenys elegans	7	-	-	-	-	-	-	-	-	-	7
Subtotal	47	70	-	6	-	-	-	-	-	-	113
Rhamphichthyidae (4 species)											
Gymnorhamphichthys hypostomus	-	6	-	-	-	-	-	-	-	-	6
Gymnorhamphichthys rondoni	-	16	-	-	-	-	-	-	-	-	16
Gymnorhamphichthys rosamariae	-	3	-	-	-	-	-	-	-	-	3
Rhamphichthys rostratus	-	4	1	-	-	-	-	-	-	-	5
Subtotal	-	29	1	-	-	-	-	-	-	-	30
Gymnotidae (9 species)											
Gymnotus anguillaris	-	-	-	-	-	-	1	4	-	-	5
Gymnotus carapo	-	-	-	-	-	-	-	2	-	-	2
Gymnotus cataniapo	-	-	-	-	-	-	-	-	-	4	4
Gymnotus coatesi	-	-	-	-	-	-	-	4	-	-	4
Gymnotus cylindricus	-	-	-	-	-	21	2	-	-	-	23
Gymnotus maculosus	-	-	-	-	-	21	-	-	-	-	21
Gymnotus pedanopterus	-	-	-	-	-	-	7	-	-	-	7
Gymnotus stenoleucus	-	-	-	-	-	-	-	-	-	7	7
Electrophorus electricus	-	-	-	-	-	-	-	-	-	3	3
Subtotal	-	-	-	-	-	42	10	10	-	14	76
Total	118	184	19	31	53	42	10	10	-	14	481

figs. 4 - 6).

244. EOD tetraphasic. 0: EOD of mature specimens with two (sometimes one or three) phases. 1: EOD with four phases, two alternating positive and negative phases (Alves-Gomes *et al.*, 1995, fig. 9; Crampton, 1998a, figs. 4 - 6).

245. EOD frequency shift. 0: EOD frequency not changing during ontogeny. 1: EOD of mature males changing during transition from juveniles to adults (Albert and Fink, 1996; Franchina, 1997).

246. EOD active phase coupling. 0: Absent. 1: Present.

247. EOD jamming avoidance response. 0: An inability to alter EOD in response to electrical interference. 1: Jamming avoidance response and associated neural structures; capacity to alter EOD output in response to presence of conspecifics discharging at same frequency (Heiligenberg, 1973; Matsubara, 1981; Losier and Matsubara, 1990).

248. Habitat utilization. 0: Behavioral capacity to inhabit terre firme (upland) forest streams, small rivers, lagoons, or standing water on flood plains. 1: Behavioral capacity to inahbit the bottoms of large river channels. Habitat utilization is a consequence of behaviors arising from the organization of the nervous system (Wenzel, 1992; see Discussion). As in any hypothesis of homology, variation in behavioral phenotypes is assumed to be heritable (Buckup, 1993). In several gymnotiform taxa, the capacity to dwell in deep river channels is correlated to differing extents with a suit of morphological characters (*e.g.*, reticulate skeletal morphology, shorter body cavity, longer total body and anal fin lengths, higher maximum EOD frequencies, large pacemaker nucleus, small lateral portion of the valvula cerebellum).

249. Locomotion - foraging. 0: Rostral probing; swims forward to position mouth near prey object; approaches objects head first, detecting prey objects near or in front of head; does not swim backwards easily or frequently during foraging. 1: Lateral scanning; swims backwards to position mouth near prey object; approaches objects tail first along trajectories that maintain constant distance, scans objects across axial electroreceptor array; moves forwards and backwards frequently and with equal facility during foraging (Mago-Leccia and Zaret, 1978; Lannoo and Lannoo, 1993; Rasnow and Bower, 1996; Assad *et al.*, 1998; Stoddard *et al.*, 1999; Nanjappa *et al.*, unpubl. obs.).

PHYLOGENETIC RELATIONSHIPS

> "*It is in the descriptions themselves... that one must seek the proper idea of the degree of organization, and not in the positions we are obliged to assign to the species* (Cuvier, 1828:281-282)."

The systematic results of this study are summarized in the form of phylogenetic trees. Figure 43 is a strict consensus of 6 equally parsimonious trees congruent with the data matrix of Table 2. Each of the trees used to make this consensus has a treelength of 598 steps (ci = 0.52, ri = 0.82, rc = 0.42). Figure 44 is a summary of these relationships for the 29 recognized gymnotiform genera. Figure 45 is a summary of the relationships among the five family-level taxa recognized.

The taxonomy of gymnotiform genera proposed in this study is summarized in Table 3. A detailed taxonomy and list of the species recognized is provided in Appendix 4. This nomenclature is derived directly from the topology of the cladograms.

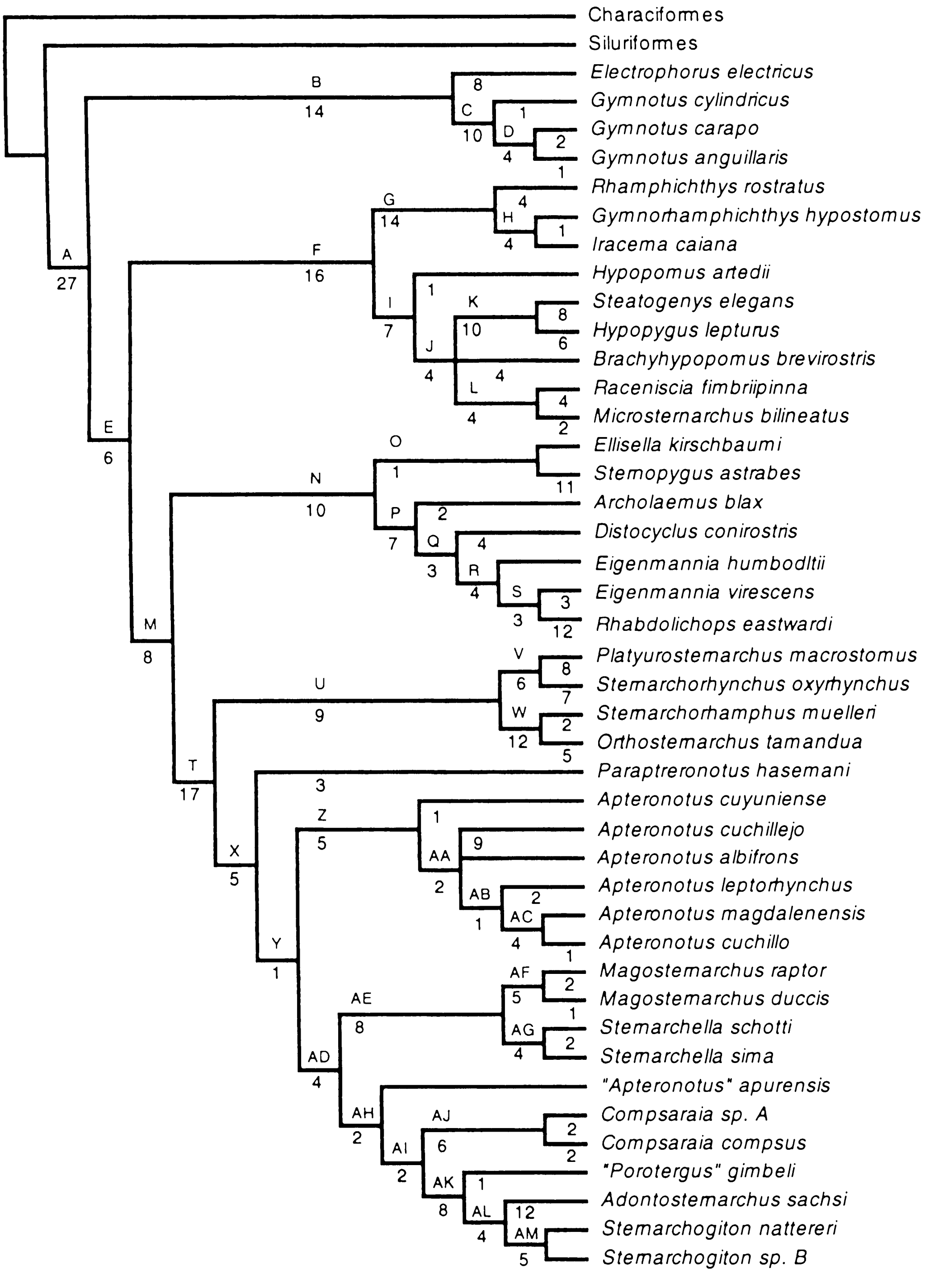


Fig. 43. Phylogenetic hypothesis of interrelationships among 44 OTUs represented in Table 2, with †*Ellisella* added in a position of maximum parsimony. Numbers of unambiguous steps blow branch, clade designation by Roman letter above branch. The topology is a strict consensus of 6 equally parsimonious trees, each of 598 steps (ci = 0.52, ri = 0.82, rc = 0.42). Terminal taxa are identified in Methods.

With several exceptions this system maintains the traditional names attributed to species groups outlined by Eigenmann and Ward (1905), Ellis (1913), and Mago-Leccia (1978; 1994). Whenever possible species and characters used in the original definitions of genera are maintained. The systematic positions of several species for which character data are ambiguous are listed as *sedis mutabilis* (Wiley, 1981).

The diagnoses provided in this section are restricted to characters of unambiguous optimization. Character states were reconstructed at resolved nodes of the strict consensus cladogram (Fig. 43), on an arbitrarily resolved topology to avoid loss of information regarding character state transformations. Each character is accompanied by its numerical position in the data matrix (Table 2).

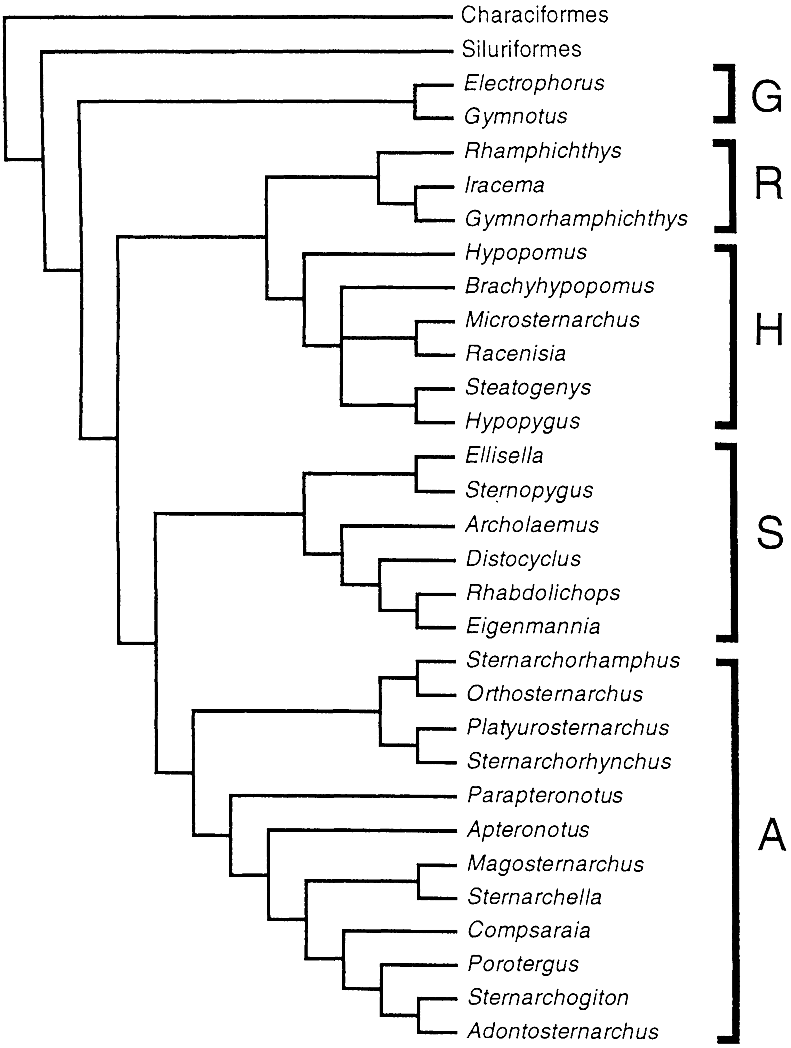


Fig. 44. Simplified diagram of interrelationships among the 29 recognized gymnotiform genera. The classification used in this report (Table 3, Appendix 4) is isomorphic with the branching order presented. G, Gymnotidae; R, Rhamphichthyidae; H, Hypopomidae; S, Sternopygidae; A, Apteronotidae.

GYMNOTIFORMES (CLADE A)

The monophyly of the Gymnotiformes is well documented (Fink and Fink, 1981; Mago-Leccia, 1978; 1994). This study reports 27 characters which unambiguously diagnose the Gymnotiformes, 16 of which are unique and unreversed among otophysan fishes: No maxillary teeth (29). Maxillary head on stalk (31). *M. levator posterior* not differentiated (46). Lateral ethmoid small, not contacting neurocranium (except Rhamphichthyidae, *Archolaemus*, *Sternopygus xingu*, and *Magosternarchus*, 64). Parasphenoid lateral margins not extending to horizontal with trigeminal foramen (76). Dorsal telencephalic area Dca large, Dm small (101). Eye subdermal (104). Accessory optic system absent (except sternopygids, 107). Extra-oral taste buds absent (110). Schreckstoff/club cells absent (111). Ampullary organs organized into rosettes (113). Suite of characters associated with active, high frequency electroreception (114, Carr and Maler, 1986; Albert *et al.,* 1998). Autopalatines arched, not ossified (127). Ectopterygoid absent (128). Endopterygoid teeth few or none (present in most Sternopygidae excluding some species of *Distocyclus*, *Eigenmannia*, and the *Rhabdolichops stewarti* species-group, and also present in *Platyurosternarchus*, 133). Metapterygoid triangular (135). Sixth epibranchial with elongate ascending process (153). No pelvic girdles or fins (179). No claustrum (180). No dorsal or adipose fins (194). Anal fin elongate, with more than 100 rays (196). Anal-fin ray articulation with distal pterygiophores (201). Position of anus anterior to body midlength (216). Caudal regeneration (221). Cartilaginous hypural-opisthural rod (222). Electric organs (226). EOD jamming avoidance response (except *Sternopygus*, 247).

GYMNOTIDAE (CLADE B)

The results of this study support Ellis's (1913) hypothesis that *Gymnotus* and *Electrophorus* form a natural taxon, the Gymnotidae, which is the sister lineage to the Sternopygoidei (Mago-Leccia, 1978). The later taxon includes all remaining gymnotiform species. Gymnotidae is diagnosed by 14 characters: Gape large, more than one third head length (19). Premaxilla large (25).

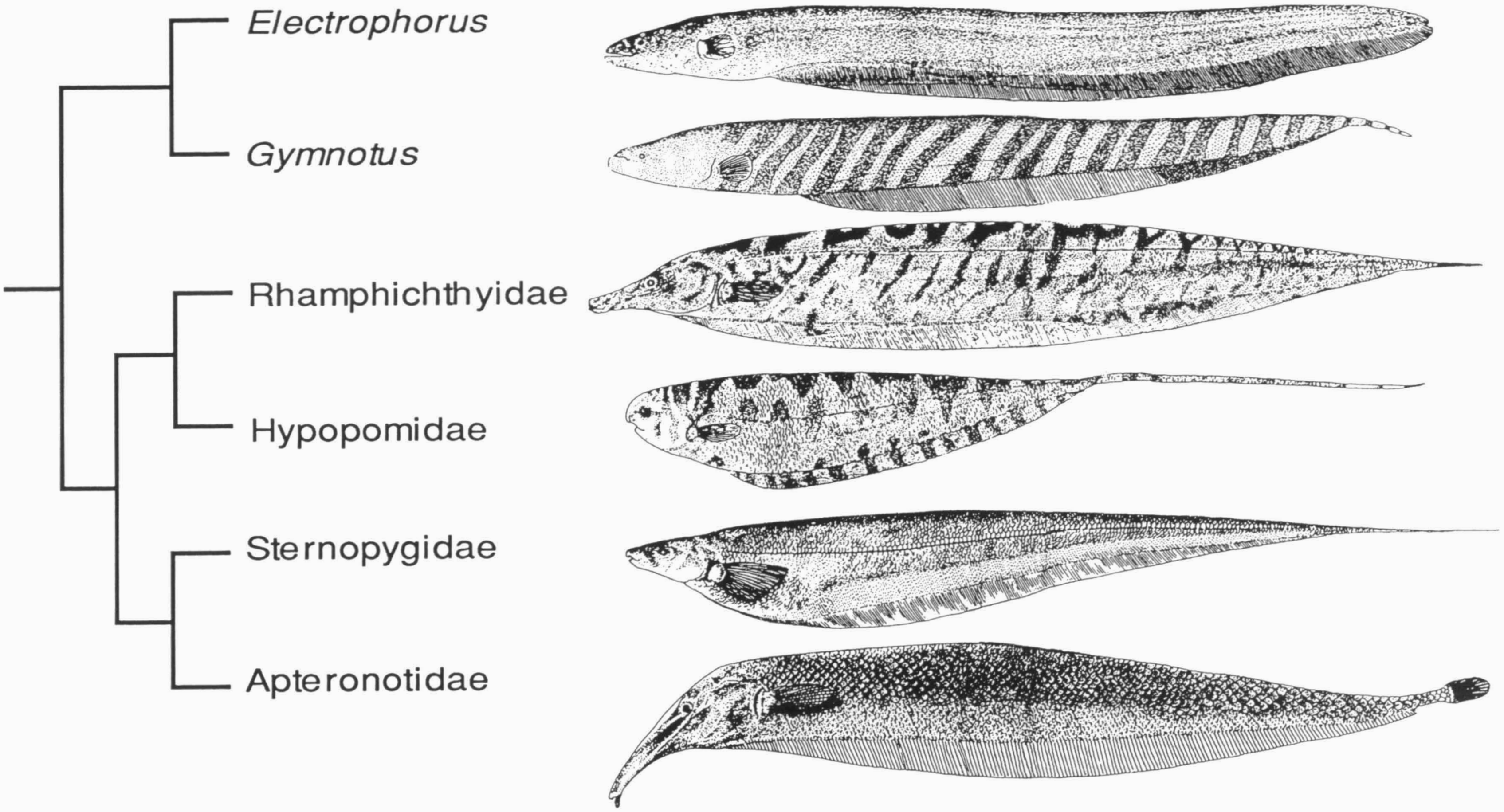


Fig. 45. Summary of relationships for the five family-level taxa recognized. Note drawings are not to scale. Drawings modified from Mago-Leccia (1994).

Premaxilla elongate, articulation with maxilla oriented anteriorly (26). Ventral margin of descending maxillary blade with a pronounced angle about two-thirds distance to its tip (37). *M. adductor mandibula* insertion on maxilla, undivided bundle at origin (45). Mesethmoid tip concave (57). Base lateral ethmoid narrow (66). Cranial fontanels closed in adults (71). Lateral valvula cerebellum large (125). Basihyal with dorsal groove (162). Anterior coracoid process absent (175). Anal-fin pterygiophores longer than hemal spines (198). Body cavity very long, with 30 or more precaudal vertebrae (205). Tail short, 0 - 16% total length (219). Gymnotids are aggressive nocturnal predators of fishes and other small aquatic animals, and most are also territorial. Gymnotids are the only gymnotiforms known to build and guard nests of foam and/or aquatic vegetation, and to brood their eggs and larvae (*Electrophorus*, Assunção and Schwassman, 1995; *Gymnotus*, Crampton, pers. comm.).

ELECTROPHORUS GILL

The monotypic *Electrophorus* possesses eight characters unique among gymnotiforms: Thick integument, with large lateral sensory pores. Vascularized oral respiratory organ. Broad parasphenoid, enveloping orbitosphenoid and pterosphenoid. Eight pectoral radials, and an elongate curved cleithrum (178). Anal-fin rays extending to tip of tail (203). Hemal spines absent, body cavity extending to tip of tail (208). Continuous addition of vertebrae throughout life. Three anatomically separate hypaxial electric organs (227).

An additional 4 characters variable among Gymnotiformes are diagnostic of *Electrophorus*: Body elongate, body depth less than 11% total length (2). Scales absent (14). Opercular dorsal margin concave (143, also in *Magosternarchus*). More than 400 anal-fin rays (196).

Electrophorus electricus grows to the largest body size among gymnotiforms, attaining a total length more than two meters. A specimen of 7 feet 4 inches (2.24 meters) 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 in aquaria for more than 20 years.

GYMNOTUS LINNAEUS (CLADE C)

Species of *Gymnotus* are moderate to large-sized gymnotiforms (120 to 1000 mm TL) which share 10 characters: Mouth superior, lower jaw prognathus, rictus curved ventrally. Eye positioned ventrally on head, on horizontal with gape. Mesethmoid tip with paired anterior processes on either side a median notch (56). Parasphenoid with anteroventral process (79). Some long posterior lateral line pores (94). Lateral line ventral rami in specimens less than 150 mm (95). Anterior nares pipe-shaped, entirely included within a narial groove within gape, narial pore located within gape, facing anteroventrally (a similar condition but without narial groove in Rhamphichthyoidea, 98). All five basibranchials unossified (163). Extrascapular fused with neurocranium (170). The capacity to regenerate postcoelomic neural and hemal spines is only known in *Gymnotus* (204). *Gymnotus* also possesses cylindrical or barrel shaped electrocytes, without a stalk (also in rhamphichthyoids and some species of *Rhabdolichops*, 229). Interrelationships and monophyly of *Gymnotus* species are discussed by Albert and Miller (1995) and Campos-da-Paz and Costa (1996).

GYMNOTUS CARAPO + *G. ANGUILLARIS* (CLADE D)

Species of *Gymnotus* from South America share four characters: Multiple (13-50) oblique bands along lateral surface of body (4). More than 16 ventral lateral line rami (96). EOD pulse with complex power spectrum (242). EOD with 3 or 4 phases (244 in part).

GYMNOTUS CYLINDRICUS SPECIES-GROUP ALBERT AND MILLER

The two species of *Gymnotus* from Middle America share a single unambiguous character, reduction in the number anal-fin rays, to less than 200 (196).

GYMNOTUS CARAPO SPECIES-GROUP ALBERT AND MILLER

Several species of *Gymnotus* share two characters of color pattern with the type of the genus *G. carapo*: Dark oblique bands with irregular, wavy margins. Anal-fin membrane with pale posterior patch (3).

GYMNOTUS ANGUILLARIS SPECIES-GROUP ALBERT AND MILLER

Several species of *Gymnotus* share a character of body shape with *G. anguillaris*, body elongate, body depth less than 11% total length (2).

STERNOPYGOIDEI (CLADE E)

The Sternopygoidei was proposed by Mago-Leccia (1978) to include Rhamphichthyidae, Hypopomidae, Sternopygidae, and Apteronotidae. The present study provides six characters in support of this hypothesis: Branchial opening small (13). Maxilla thin, more than twice as deep as wide (30). Mesethmoid tip gracile (54). Displaced hemal spines (186). Body cavity short, 12 - 15 PCV (206). Position of anus allometric in juvenile growth (217). In addition the mesocoracoid is not ossified in most members of the Sternopygoidei (except in *Rhamphichthys, Hypopomus, Steatogenys, Sternopygus aequilabiatus,* and *Sternarchorhamphus* + *Orthosternarchus*, 149).

An alternative hypothesis of relationships, uniting Rhamphichthyoidea with Gymnotidae, requires 604 steps, or 6 steps more than the most parsimonious set of trees (Fig. 46). This topology is supported however by two unique and unreversed characters: morphologically distinct P and T type tuberous electroreceptor organs (115), and the absence of distal anal-fin pterygiophores (202). On the most parsimonious tree (Fig. 43) these characters may be interpreted to be either homoplastic in Rhamphichthyoidea and Gymnotidae, or as plesiomorphic with respect to Gymnotiformes, with a reversal in the common ancestor of Apteronotidae and Sternopygidae. The polarity of the pulse-type EOD and associated neural characters (239) is ambiguous under the hypothesis of relationships of Fig. 43. The phylogenetic distribution of the ascending pro-

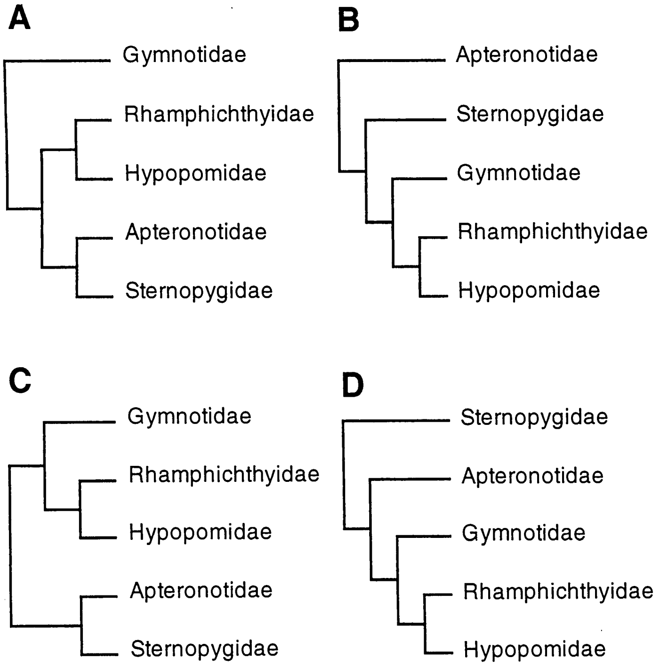


Fig. 46. Alternative hypotheses of relationships among the five gymnotiform families. A. Gymnotidae as the sister group to other Gymnotiformes (598 steps; Ellis, 1913; Mago-Leccia, 1978, shortest tree from data in Table 2). B. Apteronotidae as the sister group to other Gymnotiformes requires 13 additional steps (Castelnau, 1855; Chardon and de la Hoz, 1974; Triques, 1993, Gayet et al., 1994). C. Apteronotidae + Sternopygidae as sister group to Gymnotidae + Rhamphichthyoidei requires 6 additional steps. *Sternopygus* + *Ellisella* as the sister group to other Gymnotiformes requires 19 additional steps (Alves-Gomes, 1995). D. Sternopygidae as the sister group to other Gymnotiformes requires 10 additional steps (Mago-Leccia and Zaret, 1978).

cess of the metapterygoid (130) also depends on relationships among basal gymnotiform taxa. Although optimized as present at the root of the Sternopygoidei, the presence of both states within the Gymnotidae renders the condition at the root of the Gymnotiformes ambiguous. If the Rhamphichthyoidea is in fact the sister taxon to the Gymnotidae the ascending process of the metapterygoid is an additional diagnostic feature of Gymnotiformes.

Rhamphichthyoidea (Clade F)

The monophyly of a clade constituting Rhamphichthyidae and Hypopomidae is corroborated by 16 diagnostic characters: Mouth small, gape short (20, also in Eigenmannini, *Sternarchorhynchus*, *Sternarchella*, and *Adontosternarchus*). No teeth in oral jaws (22). Lateral margin of ventral ethmoid without posterolateral ridge (58). Orbitosphenoid narrow (73). Antorbital without infraorbital canal (85). Antorbital large, contacting autopalatine (86). Infraorbital canal tube single membranous tube (88). First infraorbital absent (89). Anterior nares located entirely within gape (98). Anterior narial pore sessile (99). Ventral margin of ELL curved (120). Anterior corpus cerebellum small (124). Metapterygoid posterior wing narrow (136). Preopercular orientation parallel to head axis (140). Urogenital papilla (except Steatogini, 218). Electrocyte posterior surface stalked (228). Species of Rhamphichthyoidei also possess barrel-shaped electrocytes (also in *Gymnotus* and *Rhabdolichops*, 229).

Interrelationships among basal rhamphichthyoid taxa are poorly resolved. Recent work by Sullivan and Lundberg (1996; pers. comm.) indicates the two widely recognized family level taxa may not be monophyletic. The following diagnoses based on data presented in Table 2 are therefore tentative.

Rhamphichthyidae (Clade G)

The monophyly of the Rhamphichthyidae is supported by 14 characters: Premaxilla gracile (27). Posterior limb of anguloarticular longer than retroarticular (49). Snout long, more than one third head length (50, also in some apteronotids). Mesethmoid long, greater than antorbital region of frontal (53). Lateral ethmoid robust, contacting other neurocranial bones (64). Orbitosphenoid margin not contacting pterosphenoid (74). Nasal capsule near tip of snout (also in *Archolaemus*, Sternarchorhynchinae except *Platyurosternarchus*, and some apteronotids, 97). Anterior eminentia granularis of cerebellum small (122). Sympletic larger than hyomandibula (137). Hyomandibula oriented parallel with long axis of head (138). Anterior series of 12-14 laterally displaced hemal spines (187). Anal-fin origin at isthmus (195). Anal-fin pterygiophores longer than hemal spines (198, also in Gymnotidae, some sternopygids, and some apteronotids). Caudal rod with double ossification (225).

Rhamphichthys Müller and Troschel

Species of *Rhamphichthys* share four characters: *M. adductor mandibula* with ossified intermuscular bones (44). Urohyal blade large, ossified to 4th basibranchial (168). More than 300 anal-fin rays (196). Gas bladder thick, fibrous, and opaque (215).

GYMNORHAMPHICHTHYS + *IRACEMA* (CLADE H)

Gymnorhamphichthys and *Iracema* share four characters: Scales absent on anterior middorsum (15). Scales absent on posterolateral body (16). Ascending process metapterygoid absent (129). All anal-fin rays unbranched (197).

GYMNORHAMPHICHTHYS ELLIS

Gymnorhamphichthys is diagnosed by a relatively small number of anal-fin rays, ranging from 140 - 200 (196). *Gymnorhamphichthys* may also be differentiated from *Rhamphichthys* by several characters of ambiguous optimization: no scales on the anterior body surface (present on tail (9), no ascending process of endopterygoid (109), no third postcleithrum (147), an EOD with four phases (also in *Steatogenys* and *Hypopygus,* 244), a long caudal filament extending posterior to the anal fin (219), no mesocoracoid (174), presence of a condyle on the supraoccipital articulating with the first supraneural (Mago-Leccia, 1994), and the origin of the anal fin near the branchial opening rather than under the eyes.

IRACEMA TRIQUES

No unambiguous changes were recovered diagnosing *Iracema. Iracema* differs from *Gymnorhamphichthys* by its color pattern, composed of a series of irregular, round blotches on the sides of the body, a higher number of anal-fin rays (240 - 266), and its large body size, growing to total more than 400 mm TL. Osteological data on *Iracema* are not presently available.

HYPOPOMIDAE (CLADE I)

The present work considers only the relative positions of type species for each of the five nominal genera. The monophyly of the Hypopomidae is supported by seven characters: Dermal component of compound vomer not ossified (62). Posterior portion of parasphenoid narrow, occupying less than half ventral surface of neurocranium (80). A branch of posterior lateral line nerve coursing trogether with a recurrent ramus of anterior-ventral lateral line nerve (117). Shape of operculum trapezoidal (142). Dorsal surface of basihyal concave (162, also in Gymnotidae). Reduced size of anteroventral process of coracoid (175, except *Steatogenys*). Second posterior DHS curved (190). Hypopomids also differ from rhamphichthyids in that the posttemporal and supracleithrum are fused (169) in rhamphichthyids and *Steatogenys* and not fused in the other hypopomids, other gymnotiforms and relevant outgroups.

HYPOPOMUS GILL

In this study *Hypopomus* is hypothesized to be sister group to the other hypopomids. The two currently recognized species of *Hypopomus* share a single derived character state among the data provided in Table 2. The ventral margin of descending maxillary blade is angled (37). Sullivan (1997b) provides three characters diagnostic of *Hypopomus*: Body covered with brown pigment spots or blotches, pigments distributed along anal-fin rays, interadial membranes hyaline. Head narrow and shallow, headwidth at opercle 42 - 48 % head length, head width at eyes about 63% width at opercle, head depth at occiput 53 - 63% head length. Long anal-fin with many (217 - 237) rays. Mago-Leccia (1994) provides two characters of ambiguous polarity to distinguish *Hypopomus* from other hypopomids. The snout is longer in *Hypopomus,* about 2.6 to 2.8 times into the length of the head, and the position of the posterior nares is about equidistant between the tip of the snout and the anterior margin of the eye.

BRACHYHYPOPOMINAE (CLADE J, NEW TAXON)

The monophyly of the Brachyhypopominae is supported by four characters: Base of lateral ethmoid narrow (66). Proximal pectoral radials 3 and 4 fused (176, except *Hypopygus*). Anterior extension of hypaxial electric organ (231, except some *Brachyhypopomus* species). Mental accessory electric organs (232, except some *Brachyhypopomus* species). Also, there is no ossified mesocoracoid (174) in all members of the Brachyhypopominae except *Brachyhypopomus brevirostris, B.* sp. B, and*Steatogenys* (Sullivan, 1997b). The mesocoracoid is also absent in *Gymnorhamphichthys* and most sternopygids and apteronotids.

BRACHYHYPOPOMUS MAGO-LECCIA

Mago-Leccia (1994:47) diagnosed *Brachyhypopomus* species by the presence of "short snouts and included mouths, absence of mesocoracoid bridge, short and crescent-shaped maxillary bone, and posterior nares closer to eyes." These characters are not optimized unambiguously in this analysis as derived features of *Brachyhypopomus. Brachyhypopomus* is diagnosed here by four other characters: Premaxilla gracile with a curved anterior margin and forming a distinct angle with the maxilla in lateral view (27, except *B. beebei;* also present in *Steatogenys,* Sullivan, 1997b). Dentary gracile (41). Body cavity with 16 - 17 PCV (206). Single transitional vertebrae (207).

From a study of both morphological and molecular sequence and data Sullivan (1997b) provides diagnoses for five clades within *Brachyhypopomus.* There is a *B.brevirostris* species-group consisting of *B. brevirostris* and *B.* sp. B, which share three characters: a very long caudal appendage in reproductively mature males (up to 45% total length); wide, regular saddle-shaped pigment bands over the dorsum; and an ossified mesocoracoid. *Brachyhypopomus beebei, B. pinnicaudatus, B. janeiroensis, B.* sp. E, *B.* sp. R, *B.* sp. M, and *B.* sp. W constitute the*B. beebei* species group, diagnosed by four characters; lower jaw equal to upper jaw; ventral ethmoid reduced; fourth supraorbital lateral line pore close to vertical through posterior nares; and supraorbital lateral line canal not attached to frontal rostral to the orbit. Within the *B. beebei* species group is a clade consisting of *B.* sp. M and *B.* sp. W, which together share four derived characters; two small conical teeth on the lateral portion of the premaxilla; medial two branchiostegal rays thin, oriented more vertically than other rays; EOD of long duration and a slow repetition rate, second head-negative phase reduced or absent; and yellow ground color in life, head and sides peppered with small, widely-spaced very dark brown stellate chromatophores. Also within the *B. beebei* species group is a clade consisting of *B. beebei* and *B. pinnicaudatus*, which share one character; 2nd branchiostegal ray small and hook-shaped, or absent (polymorphic in *B. pinnicaudatus*). The final clade is the *Brachyhypopomus occidentalis* species-group consisting of two species from Northwest South America, *B occidentalis* and *B. diazi*, which share three diagnostic characters; anterodorsal process of maxilla broad; epidermal laterosensory canals depigmented and elaborated along middle two-thirds of body; and caudal appendage deep, with four rows of electrocytes at the caudal peduncle.

STEATOGINI (CLADE K, NEW TAXON)

A sister-group relationship between *Steatogenys* and *Hypopygus* is supported by 10 characters: Ethmoid cartilage deep (63). Parasphenoid dorsal margin narrow (78). Hypobranchial 3 pentagonal (159). Urohyal blade ossified to 4th basibranchial (168). Extrascapular fused with neurocranium (170). Body cavity short, with 10 - 11 PCV (206). Urogenital papilla absent (218). Tail long, more than 45% total length (219). Humeral accessory electric organ (233). EOD with 4 phases (also in *Gymnorhamphichthys*, 244).

STEATOGENYS BOULENGER

The four described species of *Steatogenys* share eight characters: Anterior process of maxilla absent (32). Snout short, less than one third head length (51). Ascending process metapterygoid absent (129). Anterior limb preoperculum narrow, curved (141). Posttemporal fused with supracleithrum (169). Mesocoracoid (174). Anterior coracoid process (175). Opercular accessory electric organ (235).

HYPOPYGUS HOEDEMAN

Hypopygus species are the smallest gymnotiforms, attaining full maturity at 60 - 90 mm total length (Nijssen and Isbrücker, 1972). The two described species of *Hypopygus* share six characters. Premaxilla small, laminar and concave (27, premaxilla gracil but with different shape in *Brachyhypopomus* except *B. beebei*). Three or four branchiostegal rays (144). Anterior pharyngobranchial unossified (148). Fifth epibranchial with short posterior process (151). Seventh epibranchial with posterior process (154). Proximal pectoral radials 3 and 4 separate (176). Small adult body size.

The "subepidermal organ ancillary to the pectoral fin (Mago-Leccia, 1994:50)" of *Hypopygus* is regarded here to be homologous with the humeral organ of *Steatogenys* (see Myers, 1951). Both organs are situated anterior to the origin of the pectoral girdle, are derived developmentally from dorsal extensions of the hypaxial organ, and are innervated by anterodorsal extensions of post-pectoral (spinal) motor neurons (Sullivan, pers. comm.).

MICROSTERNARCHINI (CLADE L, NEW TAXON)

Microsternarchus bilineatus and *Racenisia fimbriipinna* share four characters: Body cylindrical (1). Body elongate, depth less than 11% total length (2). Scales absent from anterior portion of dorsal midline (15). Scales large, 3 - 4 above lateral line (17). Anterior process of maxilla cartilaginous, forming a connection with posterior margin of premaxilla (34). Descending blade maxilla broad, with anteroventral shelf (36).

MICROSTERNARCHUS FERNÀNDEZ-YÉPEZ

The monotypic *Microsternarchus* is diagnosed by two characters in the data reported in Table 2: Recurrent branch of posterior lateral line nerve superficial and pigmented darkly, appearing as paired parallel brown lines on either side of dorsal surface (117). 3 - 4 branchiostegal rays (144). The following additional four characters modified from Sullivan (1997b) also diagnose *Microsternarchus*: Dorsomedial hook-shaped process on posterodorsal portion of dentary. Endopterygoid process small. Foramen of opthalmic ramus of facial nerve in hyomandibula bordred dorsally by sphenotic and pterotic. No gill rakers.

RACENISIA MAGO-LECCIA

The monotypic *Racenisia* is diagnosed by four characters: Ventral margin of descending maxillary blade angled (37). Basibranchials unossified (163). Body cavity long, with 23 - 29 vertebrae (205), body attenuated caudally. Tail posterior to anal-fin short, less than 16% total length (219). In addition, *Racenisia* has a uniform pigment distribution.

SINUSOIDEA (CLADE M, NEW TAXON)

The Sinusoidea is proposed here as a taxon including the Sternopygidae and the Apteronotidae. Considering the Sternopygidae and Apteronotidae as sister taxa indicates a single origin of the tone-type EOD. This study is the first to propose character evidence from multiple organ systems supporting the monophyly of the tone-type EOD electric knifefishes. Although there are differences in the physiological mechanisms by which members of these two groups generate a tone-type EOD (Sullivan, 1993; Lundberg *et al.*, unpubl. data), there are also similarities. The EODs of all tone-type gymnotiforms possess a high repetition rate in which individual pulses overlap to form a quasi-sinusoidal discharge pattern. In species exhibiting the pulse-type EOD, individual EODs are produced at low frequencies as non-overlapping pulses. The monophyly of the Sinusoidea is incompatible with the hypotheses that sternopygids (Mago-Leccia and Zaret, 1978) or apteronotids (Triques, 1993; Gayet *et al.*, 1994) are the sister lineage to other Gymnotiformes (Fig. 46).

This study reports nine characters that diagnose the Sinusoidea: Posterior eminentia granularis of cerebellum well developed, extending to posterior margin of ELL large (123). Neural spines originate from posterior end of caudal vertebral centra (182). Several (1-3) small fenestrae in lateral wall of neural arches (183). Anal fin origin at pectoral girdle (195, also in Rhamphichthyidae). 15 - 25 unbranched anal-fin rays (197). Ontogenetic replacement of larval hypaxial electric organ with adult organ (230). High frequency tone-type EOD and associated neural substrates (239). EOD frequency shift in ontogeny (245). Foraging using lateral scanning locomotion (249). The large crescent anterior DHS (188) of sinusoids is unique and unreversed, although optimized ambiguously due to the absence of DHSs in Gymnotidae. The independence of the neural characters supporting the monophyly of the Sinusoidea is discussed in Albert *et al.* (1998b).

An additional six characters of ambiguous optimization further distinguish members of the Sinusoidea from other gymnotiforms. The anterior process of the maxilla is hook-shaped (32) in all sinusoids except *Sternarchella, Sternarchorhynchus,* and *Rhabdolichops.* An ossified laminar ridge obscures the morphology of this region in *Rhabdolichops* and juvenile specimens of most apteronotids (except some *Sternarchella*). A posttemporal fenestra (81, except some Sternopygidae). No morphologically distinct classes of tuberous electroreceptor organs (115). Retention of the distal anal-fin pterygiophores (202). Fasciculated laterosensory afferents (118). No mesocoracoid (except *Sternarchorhamphus* and some populations of *Sternopygus aequilabiatus,* 174). Sinusoids may be distinguished from Hypopomidae and Gymnotidae by the presence of an ossified caudal rod (224).

STERNOPYGIDAE (CLADE N)

Species diversity and systematics of the Sternopygidae has been reviewed by Mago-Leccia (1978), Lundberg and Mago-Leccia (1986), and Albert and Fink (1996). The monophyly of the Sternopygidae is supported by 11 characters: Teeth villiform (24). *M. adductor mandibula* insertion in 1st infraorbital (45, also in *Rhamphichthys*). Nasal broad (67). Antorbital process of frontals (69). Antorbital and infraorbital bones 1-4 large, partial cylinders with slender osseous arches (87). Mandibular canal not fused with mandible (90). Telencephalic area Dp (primary olfactory center) very large (102). Accessory optic tract and brain centers present (107). Ceratobranchial 6 with lateral process (157). Caudal intermuscular bones regenerated (185). In sternopygids for which data are available the adult EOD is monophasic due to hyperpolarization from negative baseline (241). The monophyly of the Sternopygidae is also consistent with two additional characters of ambiguous polarity: hook-shaped anterior process of maxilla (26, discussed above), and the lack of the third postcleithrum (147, also in Clade U among sinusoids).

Alternative placements of the Sternopygidae within the Gymnotiformes adds additional steps to the overall tree, but do not alter its monophyly or internal topology. Placing Sternopygidae as the sister taxon to a monophyletic group consisting of all other gymnotiforms requires a minimum of 10 steps more than the most parsimonious set of trees (Fig. 46D).

STERNOPYGINAE (CLADE O)

The Sternopyginae is proposed here as a taxon including †*Ellisella* and *Sternopygus.* These taxa share a single character: Anal-fin rays unbranched, with the exception of about 10 - 20 fin-ray tips at midbody (197). Several mid-body fragments of †*Ellisella* possess numerous unbranched anal-fin rays and no branched fin-rays, but specimen RL 1596-1 with a regenerated caudal region possesses a series of deeply branched anal-fin rays.

†*Ellisella* GAYET AND MEUNIER

No unambiguous changes were recovered diagnosing †*Ellisella.* The morphological data available for specimens attributed to †*Ellisella* are limited to the region of the opercle and preopercle, the posterior portion of the axial skeleton, and the anal fin (Meunier and Gayet, 1991; Gayet *et al.,* 1994). This material is sufficient to code 26 characters in Table 2. Several observations suggest the placement of †*Ellisella* within the Sternopygidae (Albert *et al.,* in press). Two of the diagnostic characters of Sinusoidea appear to be present in †*Ellisella* specimen RL 1596-1: posterior insertion of neural spines on posterior margin of caudal vertebral centra (158); and fenestrated neural arches (159). Among sternopygids †*Ellisella* resembles the large bodied and heavily ossified species *Sternopygus macrurus* and *Distocyclus goajira,* which also have tuberculate striations on the underside of the opercle. The numerous unbranched anal-fin rays of fragment RL 1596-7 is similar to *Sternopygus.* Specimen RL 1596-1 possesses one bifurcation per ray, and the anal-fin rays are approximately as long as the anal-fin pterygiophores, characters which suggest a closer affinity with *Distocyclus.*

Ellisella (Gayet and Meunier, 1991) is replaced by *Humboldtichthys* (Gayet and Meunier, 2000), and is regarded by Albert and Fink (submitted) as a junior synonym of *Sternopygus.* [Gayet, M. and F. Meunier. 2000. Rectification of the nomenclature of the genus name *Ellisella* Gayet and Meunier, 1991 (Teleostei, Ostariophysi, Gymnotiformes) in *Humboldtichthys Nom. Nov.* Cymbium 24(1): 104.]

†*Ellisella* does not possess diagnostic characters of the other gymnotiform taxa. The presence of a caudal rod and the absence of a hypural plate (224) excludes this taxon from the Apteronotidae, and the absence of regenerated neural and hemal spines (204) excludes it from *Gymnotus* (Meunier and Gayet, 1991). †*Ellisella* does not possess two derived characters of *Electrophorus;* the dorsal of margin if the opercle is not concave (142) and hemal spines are present (204). The orientation and morphology of the preopercle (140) is unlike that of the Rhamphichthyoidea.

STERNOPYGUS MÜLLER AND TROSCHEL

The six species of *Sternopygus* recognized here share 11 derived characters: Dorsal portion of ventral ethmoid long, extending more posterior than lateral process of the ventral ethmoid (also in Sternarchorhynchinae). No postcleithra. Gill rakers comprised of three bony elements firmly attached to branchial arches, including two small concave bones, each with 1-3 minute teeth on the larger rakers (146, a similar condition is observed in *Electrophorus*). Large black humeral spot (absent in *S. aequilabiatus*). Pale yellow or white longitudinal stripe along the base of the anal-fin pterygiophores and lateral midline posteriorly (8). Gap between parapophyses of second vertebrae and *os suspensorium* (181). Body cavity long, with 23 - 30 precaudal vertebrae (205). Anal fin very long, more than 220 anal-fin rays (196, also in *Distocyclus* and *Eigenmannia humboldti* among sternopygids). Developmental origin of adult electric organ from both hypaxial and epaxial muscles (236). EOD lower than 60 Hz in adult males, and partial segregation between populations of pacemaker and relay cells in pacemaker nucleus (240). No jamming avoidance response (JAR) or associated neural substrates (247).

Sternopygus can be also distinguished from other sternopygids by four additional characters of ambiguous optimization: Orbital margin free in adults (104, also in *Archolaemus*). Maxilla long, without connective tissue on the ventral border, anterior border of the descending blade of maxilla smoothly and evenly curved (36, also in some *Sternarchella*). Posttemporal fossa present between the pterotic and epioccipital (64, also in *Rhabdolichops*). Posttemporal bone not fused with supracleithrum (169). Albert and Fink (1996) discuss interrelationships among the recognized species of *Sternopygus*.

EIGENMANNINAE (CLADE P)

The Eigenmanninae of this report includes the same taxa as the Eigenmannidae of Alves-Gomes *et al.* (1995). Eigenmanninae is here diagnosed by seven characters: Gape small, less than twice diameter of orbit (20). Ventral margin of descending maxillary blade angled (37). Sphenotic process (75). Scapular foramen (173). Foreshortening of anterior vertebrae, anterior vertebral parapophyses separated by small gap (181). Anterior intermusculars highly branched with 6-20 rami each (184). Length of anterior ribs long, more than 0.80 body depth (210). Eigenmanninae may also be separated from Sternopyginae by the fusion of the posttemporal with the supracleithrum (169, also in many apteronotids and in Rhamphichthyidae), and thin, discoid postcleithra (146, also in Apteronotidae except *Sternarchorhamphus*). Data on the jamming avoidance response in *Archolaemus* or *Distocyclus* have not been published.

ARCHOLAEMUS KORRINGA

The monotypic *Archolaemus* is diagnosed here by two characters: Lateral ethmoid large, contacting 4 bones (64). Nasal capsule closer to tip of snout than to eye (97). *Archolaemus blax* shares with *Sternopygus* a large eye with a free orbital margin (104), and with *Distocyclus* a conical snout and the sinuous shape of the anterior portion of sixth epibranchial (152).

EIGENMANNINI (CLADE Q, NEW TAXON)

Three characters are proposed to diagnose a taxon including *Distocyclus, Eigenmannia* and *Rhabdolichops*: Proximal pectoral radials 3 and 4 fused (176). Body cavity very short, with 10 - 11 PCV (206). Number of pleural ribs 7 or less (209). The character of inhabiting large river channels (248) is ambiguous due to the presence of *D. goajira* in the coastal rivers of the Maracaibo basin. The presence of some species of the *Eigenmannia virescens* group from a wide range of habitats, including small streams, is regarded as derived (Lundberg and Stager, 1985; Lundberg *et al.*, 1987; Albert, unpub. data).

DISTOCYCLUS MAGO-LECCIA

The genus *Distocyclus* was designated to place certain species previously referred to the genus *Eigenmannia* with two characters, including small nasal capsules (nares placed close together) and a conical snout (Mago-Leccia, 1978). There are two additional characters which support this hypothesis; few or no teeth on endopterygoid (113, reversal to the general gymnotiform condition), and more than 220 rays in the anal fin (also in *Sternopygus* among sternopygids, 173).

EIGENMANNIA + *RHABDOLICHOPS* (CLADE R)

Species of *Eigenmannia* and *Rhabdolichops* examined in this study share four characters: Snout short, less than one third head length (51). Sixth epibranchial with short ascending process (153). Anterior DHS as large and straight as unmodified (posterior) hemal spines (189). Developmental origin of adult electric organ from portions of both the hypaxial and anal-fin pterygiophore muscles (236).

EIGENMANNIA JORDAN AND EVERMANN

The monophyly of the genus *Eigenmannia* (Jordan and Evermann, 1896) is not diagnosed in this or previous studies (Lundberg and Mago-Leccia, 1986; Mago-Leccia, 1994). The two species of *Eigenmannia* (*E. humboldtii* and *E. virescens*) used in the phylogenetic analysis depicted in Fig. 43 do not constitute a monophyletic group. Some of the species of *Eigenmannia* examined in this study are grouped into two species-groups.

***EIGENMANNIA MICROSTOMA* SPECIES-GROUP (NEW TAXON)**

Five species of *Eigenmannia* possess a relatively deep body (more than 11% TL) at maturity and large adult body size (more than 350 mm). Members of the *E. microstoma* species-group are widely distributed in South America, including *Eigenmannia humboldtii* from the Rio Magdalena, *Eigenmannia limbata* from Amazonas of Brazil and Venezuela, *Eigenmannia microstoma* from the Rio das Velhas of northeast Brazil, *Eigenmannia nigra* from the Rio Negro of Brazil and Venezuela, and an undescribed species (*Eigenmannia* sp. J) from the Rio Paraiba in Rio de Janeiro (southeast Brazil).

***EIGENMANNIA VIRESCENS* + *RHABDOLICHOPS* (CLADE S, NEW TAXON)**

Eigenmannia virescens, the type of the genus, shares three characters with *Rhabdolichops*: Body elongate, body depth less than 11% total length (2). 160 - 199 anal-fin rays (196). Anal-fin pterygiophores longer than hemal spines (198).

***EIGENMANNIA VIRESCENS* SPECIES-GROUP (NEW TAXON)**

Eigenmannia virescens and two congeners share three characters: Two or three thin dark longitudinal lines on either side of the body (also in some *E. microstoma*, 8). Lateral valvula cerebellum large (125). Anterior intermusculars highly branched (184). Members of the *E. virescens* species-group also include *Eigenmannia trilineata* from the Rio de la Plata, and an undescribed species (*Eigenmannia* sp. D) from the Rio Salí, Tucumán, Argentina.

RHABDOLICHOPS EIGENMANN AND ALLEN

The monophyly, species diversity, and relationships of *Rhabdolichops* are treated by Lundberg and Mago-Leccia (1986).

This study reports 12 derived characters: Scales on anterior middorsum absent (15). Premaxilla elongate, extending laterally and posteriorly around the oral margin (26). Anterior process of maxilla absent (32). Anterior hook of maxilla absent (33). Parasphenoid dorsal margin narrow (78). Parasphenoid process anteroventral process (79). Posttemporal fossae (81). Optic tectum large (108). Hypothalamus large and deep (109). Gill rakers firmly attached to gill arches (146). Single posterior DHS (191). Electrocytes enlarged and barrel-shaped (229).

APTERONOTIDAE (CLADE T)

The Apteronotidae is the most speciose family of gymnotiform fishes, with 41 species presently described and at least eight undescribed forms known in museum collections (Appendix 1; Table 1). These species range from Rio La Plata of Argentina (35°S) to the Rio Tuyra of the Pacific slope of Panamá (8°N) (Eigenmann and Allen, 1942; Mago-Leccia, 1994). Many apteronotid species inhabit the deep channels of large Amazonian rivers, a habitat only recently surveyed systematically (Lundberg *et al.*, 1986; Lundberg *et al.*, 1996). As a result, many apteronotid species were until recently rare or unknown in museum collections. Systematic treatments to date have therefore been limited to species lists and identification keys (Eigenmann and Ward, 1905; Eigenmann and Allen, 1942; Mago-Leccia, 1994).

Apteronotids are easily 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). Adult apteronotids also possess a neurogenic electric organ, a high frequency tone-type electric organ discharge (EOD), and other specialized features of the gymnotiform electrosensory system (Heiligenberg, 1991; Albert *et al.*, 1998).

Relationships of the Apteronotidae have been discussed in several recent papers. Triques (1993) applied cladistic methodology to the traditional characters used in knifefish classification and added new observations from the ethmoid and branchial regions. Triques examined specimens of 18 gymnotiform species, including six apteronotid species, providing nine characters used in the present study. Triques (1993) concludes that *Apteronotus albifrons* is the plesiomorphic apteronotid taxon, that the Sternarchorhynchini is paraphyletic, and that the short-snouted taxa *Adontosternarchus* and *Sternarchella* are sister groups. Gayet *et al.* (1994) assumed the monophyly of six gymnotiform families and did not discuss relationships within each terminal taxon. Gayet *et al.* (1994) concur with Triques (1993) in separating apteronotids from other gymnotiforms. Both Triques (1993) and Gayet *et al.* (1994) conclude that the caudal fin of apteronotids is a primitive feature. Placing apteronotids as the sister taxon to a monophyletic group consisting of all other gymnotiforms requires 13 steps more than the most parsimonious set of trees.

Alves-Gomes *et al.* (1995) analyzed 718 aligned base pairs of ribosomal mitochondrial DNA. Of the 211 informative sites among gymnotiforms, 27 loci proved informative in resolving apteronotid relationships, of which 19 were shared by the two species of *Sternarchorhamphus*. Congruence in the phylogenetic distribution of the remaining eight base pair changes provides support for the monophyly of a clade including *Sternarchella* and *Sternarchogiton* to the exclusion of *Adontosternarchus*, *Apteronotus albifrons*, *A. leptorhynchus*, and *Sternarchorhamphus*. With the exception of these two clades, the strict consensus of the nine equally parsimonious trees consistent with these data shows no resolution. The topologies of the morphological and molecular trees differ in the position of *Adontosternarchus* and in the monophyly of *Apteronotus*. The trees based on morphological and molecular data analyzed separately are congruent with respect to the monophyly of the Apteronotidae, the Sternarchorhynchinae, and a clade composed of *Sternarchogiton* and *Sternarchella*.

In the present study, the monophyly of the Apteronotidae is supported by 16 characters: Surface of many dermal and endochondral bones pitted, spongy, or reticulate (82, except *Apteronotus sensu stricto*). Nasal loop of infraorbital cephalic line (83). Histologically distinct population of large neurons in lateral portion of telencephalic nucleus Dc (103). Pacemaker nucleus large and visible on ventral surface of medulla (126). Proximal portion of hyomandibula narrow, articulating surface facing dorsal (139). Anterior limb of preopercle narrow, curved, ventral margin of anterior limb not ossified (141). Dorsal margin of opercle straight or slightly concave (143). Pharyngobranchial 3 absent (148). Epibranchial 7 with posterior process (154). Ceratobranchial 4 with posterior process (156). Basihyal with dorsoposterior crest (161). Single posterior DHS (191). Dorsal organ present (192). Caudal fin with segmented rays and a hypural plate, posterior margin of caudal fin rounded, no elongate caudal rod (222). Neurogenic electric organ derived from spinal motor neurons which innervate larval myogenic organ (237). Behavioral capacity to dwell in deep channels of large rivers (248). Apteronotid species also possess a subterminal mouth (21) in the plesiomorphic condition, although the mouth is terminal or superior in members of several derived apteronotid clades.

STERNARCHORHYNCHINAE (CLADE U)

The seven species of Sternarchorhynchinae recognized here share eight characters: Scales above lateral line very small, more than 11 to dorsal midline (17). Ventral ethmoid septum longer than deep (60). Ascending process metapterygoid absent (129). Endopterygoid process lost in ontogeny (131, also in *Apteronotus cuchillo* and *A. magdalenensis*). Metapterygoid posterior wing narrow (136). Anal fin origin at isthmus (195). Anal-fin pterygiophores longer than hemal spines (198). AFP blades broad (199). Sternarchorhynchinae also differs from other apteronotids by the presence of an elongate preorbital region (snout) (50, also in some other apteronotids), and by the presence of more than 200 anal-fin rays (196, except in *S. oxyrhynchus* and some populations of *S. curvirostris*).

STERNARCHORHYNCHINI (CLADE V, NEW TAXON)

Sternarchorhynchus and *Platyurosternarchus* share seven characters: Premaxilla gracile (27). Premaxillary teeth not retained in adults (28). Posterior limb anguloarticular longer than retroarticular (49). Mesethmoid elongate (53). Parasphenoid lateral wing not extending to a horizontal with trigeminal foramen (76). Posterior parapophyses (or anterior hemal arches) long, abutting at midline to form a keel (212). Tail short, less than 16% total length (219). Three additional characters of ambiguous optimization may be used to separate *Sternarchorhynchus* and *Platyurosternarchus* from other apteronotids. The lateral ethmoid is absent (65, also in *Orthosternarchus*), the postcleithra are thin and discoid (171, also in Apteronotinae and Eigenmanninae), and the neural spine associated with the posterior thoracic vertebra is positioned over the midlength of the centrum (182, also in other gymnotiforms).

PLATYUROSTERNARCHUS MAGO-LECCIA

The monotypic *Platyurosternarchus* is diagnosed by seven characters: Gape large, more than one third head length (19). Maxilla large and quadrangular, anterior process of maxilla extremely large and broad, extending more than length of descending blade in mature specimens (35). Anteroventral margin of descending maxillary blade not ossified (37, also in *Orthosternarchus*). Numerous endopterygoid teeth (133). Extrascapular fused with neurocranium (170). Two or three posterior DHS (191). Caudal peduncle deep. *Platyurosternarchus macrostomus* possesses a unique color pattern composed of large and irregular dark brown and black blotches and a broad black longitudinal band extending ventral to the lateral line.

STERNARCHORHYNCHUS CASTELNAU

The six recognized species of *Sternarchorhynchus* (Campos-da-Paz, 1999b) share eight characters: Gape short, rictus extending to vertical with mental symphysis (20). Maxilla small, sickle-shaped, anterior process of maxilla not ossified (32). Dentary filamentous (42). Snout highly elongate, gracile, tubular, and recurved (50). Orbitosphenoid narrow, its anterior margin not ossified (73). Five or six branchiostegal rays (144). Epibranchial 5 without posterior process (151). 160 - 199 anal-fin rays (196). Active phase coupling of the EOD has been reported only in *Sternarchorhynchus* (Langner and Scheich, 1978).

STERNARCHORHAMPHINI (CLADE W, NEW TAXON)

The monotypic genera *Sternarchorhamphus* and *Orthosternarchus* share 12 derived characters: No scales on anterior mid-dorsum (15). Premaxilla elongate (26). Teeth on dentary arranged in two-three rows at midlength of bone (39). Anterior portion of frontal concave in lateral profile (70). Anterior infraorbital canal pore remote from 1st infraorbital (84). Eyeball minute, no extrinsic eyeball muscles (106). Mesocoracoid ossified (174). Dorsal organ extending from nape to caudal peduncle (193). Numerous (30 - 60) anterior anal-fin rays unbranched to tip (197). Anal-fin pterygiophore tips shaped like arrow-heads (200). Posterior-most precaudal parapophyses slender, sinuous (213). Electric organ discharges expressed as a monophasic depolarization (241).

Species of Sternarchorhamphini may also be distinguished from other apteronotids by several share characters of ambiguous optimization: Posterior postcleithra robust, not discoid, their posterior margins curve medially (171). A single displaced hemal spine posterior to the large anterior spine (191). Anterior ribs narrow (211). Electromotor neurons of neurogenic electric organ straight (238). *Sternarchorhamphus* and *Orthosternarchus* also share two characters with *Sternarchorhynchus* not present in *Platyurosternarchus*: anterior position of nasal capsule (97), and large size of lateral valvula of cerebellum (125). *Sternarchorhamphus* shares the absence of scales from head and back (15) with *Sternarchorhynchus oxyrhynchus*.

STERNARCHORHAMPHUS EIGENMANN

Sternarchorhamphus is diagnosed here by four characters, two of which are coded in Table 2: Snout tip decurved anterior to nasal capsule. Black pectoral and anal-fin margins. Anterior shelf of maxilla ossified (35). Six or fewer caudal-fin rays (220).

ORTHOSTERNARCHUS ELLIS

Orthosternarchus is diagnosed here by nine characters, five of which are coded in Table 2: Snout long and straight. Head conical, tapering evenly to anterior tip. Nasal capsule positioned at tip of snout. Eye extremely minute. Descending blade of maxilla with strongly ossified anterior shelf (36). Ventral margin of descending maxillary blade not ossified (37). Opercular dorsal margin concave (143). Posttemporal not fused with supracleithrum (169). Body cavity with 16 - 17 PCV (206). All derived characters are present in a juvenile specimen of 145 mm TL (MZUSP uncat. AMZ 96-87).

APTERONOTINAE (CLADE X)

The 32 species of Apteronotinae recognized here exhibit sizable diversity in most aspects of their morphology. These species share five unambiguous characters, only one of which is unreversed: Gape large, rictus extending more posterior than a vertical with anterior margin of eye (19, also in *Platyurosternarchus*, not in several clades within Apteronotinae). Descending blade of maxilla broad and rhomboid, with anterior shelf (36, except *Sternarchella*, *Magosternarchus duccis*, and *Adontosternarchus*). Anterior surface of mesethmoid tip concave (57, except in *Adontosternarchus*). Lateral process of ventral ethmoid robust, its posterior surface broad and rounded (59, except *Magosternarchus*). Posterior margin of third hypobranchial broad, triangular in horizontal view (158).

***PARAPTERONOTUS* (NEW GENUS)**
FIGURE 47A, 47B

Type species.—A single species is recognized, *Parapteronotus hasemani* (Ellis, 1912). Holotype: FMNH 54562, Santarem, Rio Amazonas, 177 mm TL, 1910.

Diagnosis. —An apteronotid possessing the following six characters: Body covered with numerous fine dark chromatophores. Oral margin of upper lip is fleshy and square at anterior end of gape. Preorbital region increasingly elongate in male specimens greater than about 250 mm TL. No anterior extension of the infraorbital canal, anterior canal pore of infraorbital canal situated near first infraorbital (84, also in Sternarchorhamphini,

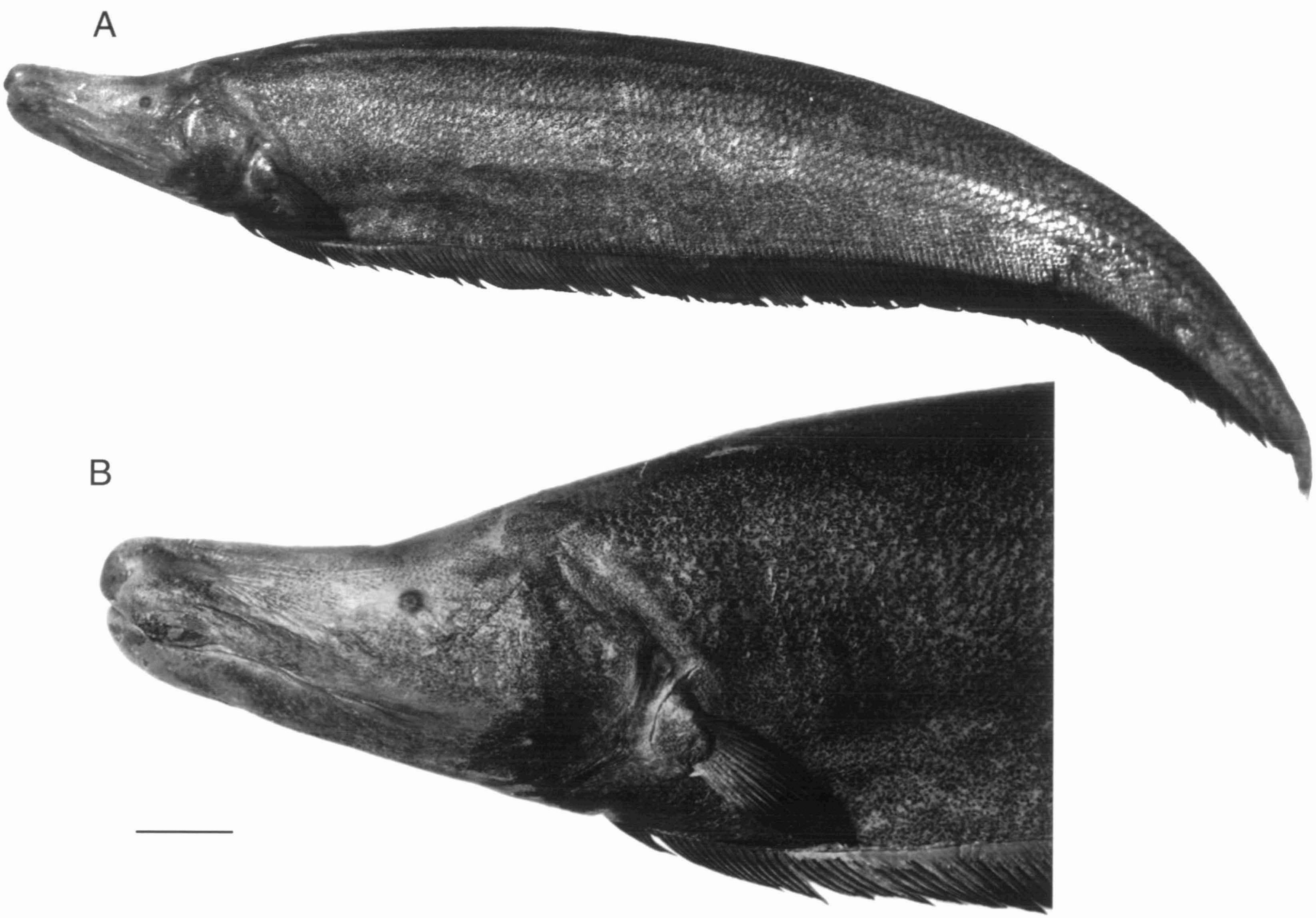


Fig. 47. Photographs of *Parapteronotus hasemani* showing sexual dimorphism of snout-length. A. Whole body of male specimen, 305 mm TL, collected near Manaus, Brazil (FK uncat.). B. Enlarged view of head of specimen in A (head-length = 60 mm).

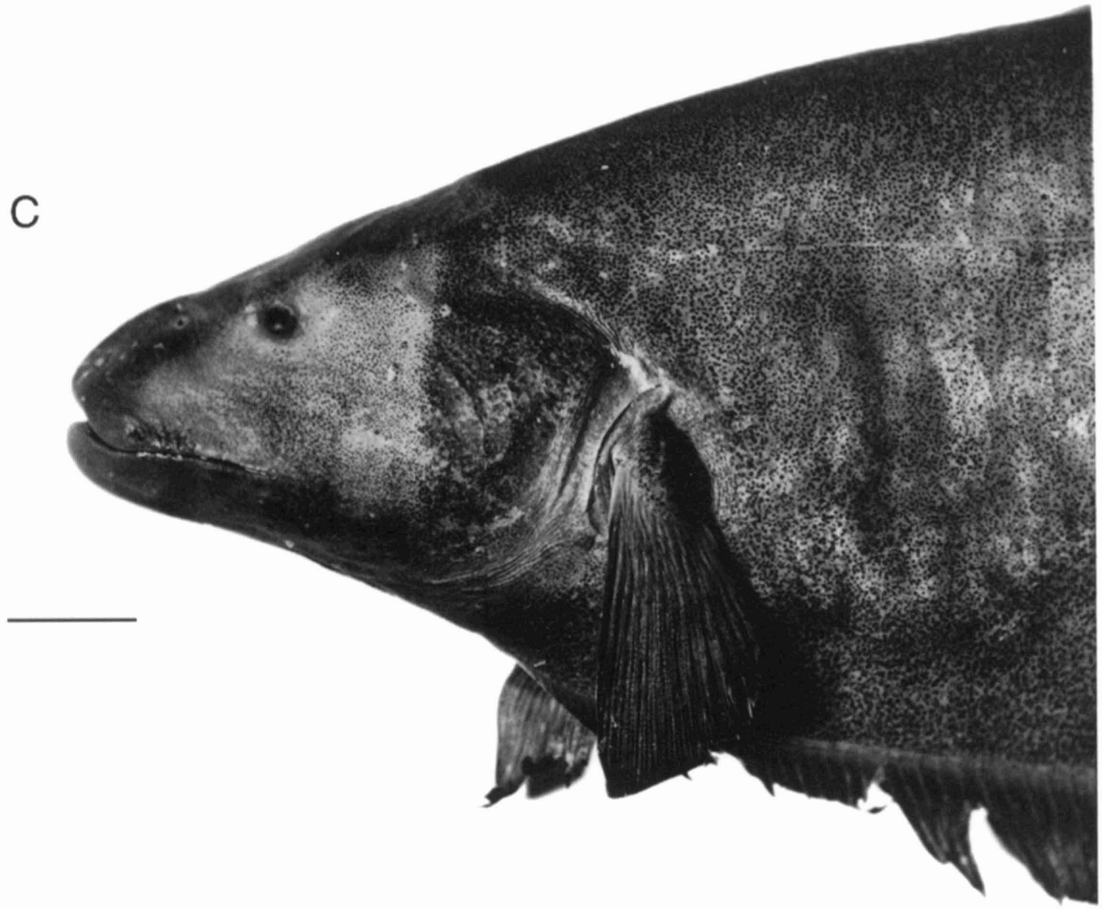


Fig. 47 (continued). C. Head of female specimen, 270 mm TL (head-length = 45 mm) collected with specimen in A. Scale bars = 10 mm. Note the elongate preorbital region in B, and deep body and long pectoral fin in C.

Sternarchella, *Magosternarchus*, and *Adontosternarchus*). Dorsal head of the anterior DHS narrow, approximately as wide as descending blade, anterior margin straight and continuous with proximal (dorsal) head, extending ventral to the parapophyses of the anterior caudal vertebrae (165). Caudal fin truncate, caudal peduncle short, caudal region posterior to last anal-fin ray less than 10% total length (219).

Description.—Color in ethanol light brown to gray, body opaque, weakly compressed laterally, covered entirely with small, cycloid scales, including head and dorsum, 10-12 scales above lateral line at midbody. Pectoral fins large, distal half of pectoral- and anal-fin membranes dark. Gape large, reaching to vertical with eye, mouth subterminal, small conical teeth present in both jaws. Premaxilla moderate size, with small conical teeth. Maxilla crescent-shaped, with an ossified anterodorsal head and anteroventral shelf, without an anterior process and without a straight posterior process, the ventral margin of its descending blade curved. One row of dentary teeth, dentary horizontal, its ventral margin straight, the anterior and posterior limbs of anguloarticular short.

Snout short (preporbital length about 0.30 head length) in juveniles and females, increasingly elongate in adult males beginning from about 250 mm TL. Mesethmoid short and narrow, its anterior tip reduced, flexed ventrally, and concave. Lateral process of ventral ethmoid extending as a blunt posterolateral process, articulating with lateral ethmoid cartilage. Lateral process of ventral ethmoid robust, its posterior surface forming an articulation with lateral ethmoid cartilage. Antorbital region of snout deeper than long, ethmoid cartilage anterior to lateral ethmoid longer than deep. Lateral ethmoid unossified. Posttemporal fossae present, cranial skeleton reticulate. Eyes small, without free margin, with small extrinsic eyeball muscles. Nasal loop of infraorbital laterosensory canal present, without subnasal extension, antorbital bearing infraorbital canal. Mandibular canal ossicles long and slender tubes. Supratemporal laterosensory canal straight, extending dorsoposteriorly onto posterior portion of parietal.

Endopterygoid narrow, without teeth, with weakly ossified ascending process at about its midlength, its posterior margin abutting hyomandibula. Metapterygoid triangular, its posterior wing broad. Symplectic shorter than hyomandibula, hyomandibula oriented oblique to head axis, its proximal articulating head narrow. Preopercle narrow and curved, oriented oblique to head axis, ventral margin of its anterior limb not ossified. Opercle triangular, its dorsal margin straight. Gill rakers not contacting gill bar, fourth and fifth pharyngobranchials ossified. Sixth epibranchial elongate, contacting fifth epibranchial, with posterior process. Sixth ceratobranchial with a medial process. Third hypobranchial triangular, fourth hypobranchial without bridge. Basihyal dorsal surface flat, with posterior ridge, third basibranchial hourglass-shaped, fourth basibranchial ossified, urohyal head expanded, urohyal blade ossified. Posttemporal fused with supracleithrum, third postcleithrum not ossified. Mesocoracoid not ossified, no anterior coracoid process.

Four proximal pectoral radials. Claustrum absent. Neural spine inserting on posterior margin of caudal vertebral centra. Origin of dorsal organ at about midbody. 160-180 anal-fin rays. Anal-fin pterygiophores shorter than hemal spines at midbody, their descending blades narrow and tapered. Body cavity with 15-18 precaudal vertebrae, and eight narrow, long pleural ribs. Posterior parapophyses small, broad and triangular. Caudal fin and adjacent portion of caudal region truncate, resembling regenerated caudal fin of other apteronotids.

Etymology.—From the Greek *para*, meaning beside or near, referring to the phylogenetic position of this lineage as the sister taxon to other members of the Apteronotinae, plus *apteronotus*, the genus for which the family is named. Gender masculine.

Unnamed clade (Clade Y)

Although supported in the maximum parsimony analysis, there are no unique and unreversed characters supporting Clade Y. Species of Clade Y (Apteronotinae except *Parapteronotus*) possess a single shared character: Parapophyses of posterior thoracic vertebrae and/or anterior hemal arches broad and long (193, except *Adontosternarchus*, also in Sternarchorhynchini). An additional character of ambiguous optimization may be derived at this node, dentary arranged in two-three rows at midlength of bone (39, not in *Apteronotus cuyuniense*, "*Porotergus*", most *Sternarchogiton*, or *Adontosternarchus*).

Apteronotus sensu lato Lacépède

No characters were recovered supporting the monophyly of all species previously referred to *Apteronotus sensu lato* (Mago-Leccia, 1994). The criteria used to recognize *Apteronotus* Lacépède (= *Sternarchus* Bloch and Schneider) by Ellis (1913) and later workers are determined here to be plesiomorphic among apteronotids; *i.e. Apteronotus* has been used as a "wastebasket" taxon to place species not allotted to other apteronotid genera. Mago-Leccia (1994) provides 14 characters used in combination to recognize *Apteronotus*, none which optimize unambiguously in this analysis.

Apteronotus sensu stricto (Clade Z, new taxon)

Monophyly of *Apteronotus sensu stricto (Apteronotus s.s.)* is supported by five characters: Color of body surface deep brown or black (9). Premaxilla gracile, scroll-shaped in adults, with 2 or fewer teeth (27). Anterior limb of anguloarticular shorter than posterior limb (48). Surface of cranial bones smooth and laminar, not pitted (82, reversal). Behavioral capacity to inhabit small rivers, swamps, estuaries, or upland streams (248, reversal). According to this diagnosis, *Apteronotus s.s.* includes several species previously assigned to other genera; *A. (Sternarchogiton) cuchillejo* (Schultz, 1949) from the Maracaibo basin of Venezuela, *A.* (*Megadontognathus*) *cuyuniense* (Mago-Leccia, 1994) from the Guyanas of Venezuela, *Apteronotus (Porotergus) ellisi* (Arámburu, 1957) from the Rio de La Plata and Rio Paraná of Argentina, Brazil, and Paraguay, and *A. (Ubidia) magdalenensis* (Miles, 1945) from the Rio Magdalena and Choco basins of Colombia.

The osteology of several species of *Apteronotus s.s.* was examined from cleared and stained material and radiographs, including type material of *A. brasiliensis, A. cuyuniense, A. cuchillejo, A. leptorhynchus, A. mariae, A. rostratus*, and specimens of *A. albifrons* from across its geographical range. Although specimens of *A. jurubidae* were not examined for this report, the published description this species indicates it may be a synonym of *A. mariae. Apteronotus maximiliani* (Castelnau, 1855) from the Rio Urubamba of Perú is regarded as a synonym of *A. albifrons* by Mago-Leccia (1994).

Apteronotus cuyuniense (Mago-Leccia)

Apteronotus cuyuniense is diagnosed by the presence of 2-3 large conical teeth on the posterior end of the dentary (Mago-Leccia, 1994, fig. 58), a single row of teeth on dentary (also in *Porotergus* and *Sternarchogiton*), and a short body cavity, with 16 - 18 PCV (206). *Apteronotus cuyuniense* is known from the Rio Cuyuní and Caroní drainages of the Sate of Bolivar, Venezuela.

Apteronotus albifrons species-group (Clade AA, new taxon)

Apteronotus albifrons species-group includes species of *Apteronotus s.s.* with two unique features of the color pattern: Pale pigment patch on caudal peduncle (7). High contrast pale or white mid-dorsal stripe and mental patch (28). These color pattern characters are obscured by pigment mottling (11) in larger specimens of *A. leptorhynchus* and *A. cuchillejo*, and not observed in the large-bodied specimens of *A. magdalenensis.*

Five species are recognized in the *Apteronotus albifrons* species-group. *Apteronotus albifrons* (Linnaeus, 1766) is distributed widely across tropical South America. The type locality is "Surinam" and specimens pertaining to this species have been collected throughout the Paraná, Amazon, and Orinoco basins (Appendix 1). *Apteronotus cuchillejo* (Schultz, 1949) was described from the Maracaibo basin of Venezuela, *A. jurubidae* (Fowler, 1944) from the Pacific slope of Colombia, *A. mariae* Eigenmann and Fisher (1914) from the Magdalena drainage of Colombia, and *A. spurrellii* (Regan, 1914) from the Rio San Juan drainage on the Pacific slope of Colombia.

Apteronotus brasiliensis species-group (Clade AB, new taxon)

Species of the *Apteronotus brasiliensis* species-group includes species of *Apteronotus s.s.* with a hypermorphosis of the sphenoid region of the neurocranium (57). This growth is an ontogenetic extension of the plesiomorphic gymnotiform growth pattern, and produces an elongate head in larger specimens (more than 160 mm TL), in which the orbit lies at about (or in advance of) the midlength of the head. The species composition of the *A. brasiliensis* species-group is similar to the *Apteronotus* group 1 of Mago-Leccia (1994: 28).

Four of the species in the *A. brasiliensis* group are distributed across northern South America and Panamá. *Apteronotus leptorhynchus* (Ellis, 1912) was originally described from Amatuk, Guyana, and is known from across the Guyanas, as well the Orinoco and Maracaibo basins of Venezuela. *Apteronotus rostratus* (Meek and Hildebrand, 1913) was described from the Rio Grande of Panamá, and is also known from Pacific and Atlantic drainages of Colombia. *Apteronotus (Ubidia) magdalenensis* (Miles, 1945) was described from the Magdalena drainage, and *Apteronotus cuchillo* (Schultz, 1949) from the Maracaibo basin. The two southern species in this species-group are *A. brasiliensis* (Reinhardt, 1852) from the Rio das Velhas of Brazil, and *Apteronotus* sp. S from the Rio Parana, State of Mato Grosso do Sul, Brazil.

Apteronotus magdalenensis species-group (Clade AC, new taxon)

Within the *A. brasiliensis* species-group, the species *A. cuchillo* and *A. magdalenensis* are unique in attaining a large body size, with total lengths greater than 300 mm. These species also share four derived characters: Pigment distribution blotchy, marbled or mottled appearance (11). Gape small, not reaching a vertical through anterior margin of eye (19). Sphenoid region highly elongate, eye positioned anterior to head midlength (72). Body cavity long, with 16 - 19 precaudal vertebrae (206, also in *A. cuyuniense* and *Orthosternarchus tamandua*).

Navajini (Clade AD, new taxon)

All other lineages of the Apteronotinae constitute a clade designated the Navajini, from the Spanish *navaja* ("blade"), in reference to the derived body shape shared by member species. Four characters support the monophyly of the Navajini: Body translucent with a yellow or pink hue in living specimens, yellow or hyaline in formalin-fixed specimens, melanophores scarce or absent on lateral body surface (12, except *Adontosternarchus*). No scales on surface of head and back (except *Sternarchogiton nattereri* and *Adontosternarchus*, 15). Large rhomboid scales above lateral line (18). Anal-fin pterygiophores long, less than 1.5 times into depth of epaxial musculature (also in *Apteronotus leptorhynchus*, 198).

Sternarchellini (Clade AE, new taxon)

The Sternarchellini is composed of two genera, *Sternarchella* and *Magosternarchus*, which is diagnosed by eight characters: Lateral margin of premaxilla elongate, with more than 13 teeth (26). Anterior hook of maxilla absent (26, also in some species of Sternarchorhynchinae). Anterior infraorbital canal pore remote from 1st infraorbital (84, also in *Adontosternarchus* and *Parapteronotus*). Endopterygoid process robustly ossified (110). Endopterygoid short and deep, without anterior process (132, also in *"Porotergus"* + *Sternarchogiton* + *Adontosternarchus*). Dorsal margin of opercle straight or slightly concave (143). Basibranchial of fourth arch not ossified (165). Tail short, less than 16% total length (219).

Sternarchella Eigenmann (Clade AG)

The seven recognized species of *Sternarchella* are diagnosed by four unambiguous characters: Gape of mouth very small, length less than twice diameter of eye (20). Maxilla crescent-shaped, anterior process and anteroventral margins not ossified (32). Gill rakers firmly attached to gill arches (146). Gill raker tips not ossified, covered with cartilage caps (147).

Species of the *Sternarchella schotti* species-group possess a terminal or slightly superior mouth as adults (21). *Sternarchella schotti* possesses a gas bladder which extends posteriorly into the caudal region behind the body cavity (214). *Sternarchella terminalis* possesses the deepest body of any apteronotid. Species of the *Sternarchella sima* species-group possess a ventral mouth, a strongly rounded forehead, and large scales, 5 - 8 above lateral line (17).

Magosternarchus Lundberg, Cox Fernandes, and Albert (Clade AG)

This taxon and its two member species are diagnosed by Lundberg *et al.* (1996). *Magosternarchus* is diagnosed here by five characters: Premaxilla robust, elongate, extending medial and posterior to maxilla, ventral to autopalatine cartilage, and dorsal to posterior dentary teeth, and with a correspondingly elongate articulation with mesethmoid (Lundberg *et al.*, 1996, figs. 3, 4); premaxilla heavily dentigerous, with two-three rows of teeth, and at least 9 to 14 teeth in outer row; anterior surface of mesethmoid flexed ventrally (25, 55). Elongate dentary; length about 1.5 times depth at coronoid process, with rows of teeth, the outer row with 15 to 19 teeth, extending more than half way up coronoid process. Scales absent on anterior mid-dorsum (15). Lateral ventral ethmoid process flat, gracil (59). Lateral ethmoid large, contacting other bones of neurocranium (64). Parasphenoid lateral wing present (76).

Unnamed clade (Clade AH)

Several species previously included within *Apteronotus* (Mago-Leccia, 1994) on the basis of primitive features share derived features with members of the Navajini. These species include *"Apteronotus" bonapartii* (Castelnau, 1855), *"Apteronotus" macrostomus* (Fowler, 1943) from the Rio Meta (Villavicencio) of Colombia, and *"Apteronotus" apurensis* (Fernàndez-Yépez, 1968) from the Rio Apuré of Venezuela. *"Apteronotus" bonapartii* was described from the Ucayale of Perú. The holotype of this species (MNHN 82.9.2.1; Castelnau, 1855, plate 45, no. 2; Mago-Leccia, 1994, fig. 27) has an elongate snout and a large gape, and may be distinct from the specimens recognized as *Apteronotus bonapartii* by Ellis (1913), and also from many specimens labeled as such in museums collections. Specimens referred to in this study as *"Apteronotus" cf. bonapartii* possess a black margin on the pectoral and anal fins, have rounded heads with short snouts, and have been collected from the Paraná, Meta, Napo, and Amazon Rivers (Appendix 1).

"Apteronotus" macrolepis and *"A". apurensis* share two characters with *"Porotergus" sensu lato*; an anterior hook of maxilla (26) and curved supratemporal laterosensory canal (76). *"Apteronotus" macrolepis* shares the absence of the posterior blade of the urohyal (144) and the large medially directed process of

the third hypobranchial (137) with some members of the Porotergini, but this character is also present in some species of *Apteronotus s.s.* "*Apteronotus*" *macrolepis* and "*A.*" *apurensis* also share with *Sternarchorhynchus* the possession of three or more DHS posterior to the large, saber shaped anterior DHS (167); this character is polymorphic in *A. albifrons* and *A. leptorhynchus.*

UNNAMED CLADE (CLADE AI)

Species of Clade AI possess two diagnostic characters: Urohyal blade unossified (167). Pectoral fin small and unpigmented (177).

COMPSARAIA (CLADE AJ, NEW GENUS)

Type species.—*Compsaraia compsa* (Mago-Leccia, 1994, figs. 90 - 91). Holotype: MBUCV 11010, Isla Iguana, Delta Amacura, Rio Orinoco, 339 mm, 1978.II.18.

Diagnosis.—Apteronotid fishes possessing the following six characters: Pale stripe of low melanophore density in narrow band passing anterior to eyes and lateral to nares (10). Snout long, preorbital region more than one third head length in adults specimens (50). Dorsal margin of frontals concave (70, also in *Parapteronotus* and Sternarchorhamphini). Supratemporal lateralis canal L-shaped (92). Nasal capsule closer to tip of snout than to eye (97, also in *Parapteronotus* and Sternarchorhamphini). Fifth basibranchial unossified (165).

Description.—Body compressed laterally, semitranslucent in living specimens. Scales large and rhomboid, absent from head and dorsum. Pectoral fin small and unpigmented. Gape large, reaching to vertical with eye, mouth subterminal, small conical teeth present in both jaws. Premaxilla moderate size. Maxilla quadrangular, with ossified anterodorsal head and anteroventral shelf, without an anterior process and with a straight posterior process, the ventral margin of its descending blade straight. Two to three rows of dentary teeth, dentary horizontal, its ventral margin straight. Anterior and posterior limbs of anguloarticular short, mandibular canal ossicles canal ossified as short, broad, dumbbell-shaped ossicles.

Preorbital region of snout elongate in adult males and females. Mesethmoid elongate and narrow, its anterior tip small, concave and flexed ventrally. Ventral ethmoid longer than deep, without lateral process, lateral margin articulating with lateral ethmoid cartilage. Ethmoid cartilage small and narrow. Lateral ethmoid small with a broad base, not contacting other bones of neurocranium. Posttemporal fossae present. Cranial skeleton reticulate. Eyes small, without free margin, with small extrinsic eyeball muscles. Supratemporal laterosensory canal curved at a sharp angle on surface of parietal, extending posterior onto epaxial surface of body.

Endopterygoid long and narrow and edentulous, with a small ascending process positioned posterior to midlength of bone, its posterior margin abutting hyomandibula. Metapterygoid triangular, its posterior wing broad. Hyomandibula oriented oblique to head axis, its proximal articulating head narrow. Preopercle narrow and curved, oriented oblique to head axis, the ventral margin of its anterior limb not ossified. Opercle triangular, with straight dorsal margin. Gill rakers not contacting gill bar. Fourth and fifth pharyngobranchials ossified, sixth epibranchial elongate, contacting fifth epibranchial, with posterior process, sixth ceratobranchial with a medial process, third hypobranchial broad at posterior margin, triangular in horizontal view, fourth hypobranchial without bridge. Basihyal dorsal surface flat with posterior ridge, third basibranchial hourglass-shaped, fourth basibranchial unossified. Urohyal head expanded, urohyal blade unossified. Posttemporal fused with supracleithrum. Three postcleithra, all thin and discoid. Mesocoracoid not ossified, no anterior coracoid process.

Four proximal pectoral radials. Claustrum absent. Anterior displaced hemal spine large and curved, its dorsal head more than twice the width of its descending blade. Two curved posterior, displaced hemal spines. Origin of dorsal organ at about midbody. 160-200 anal-fin rays. Anal-fin pterygiophores longer than hemal spines at midbody, their descending blades broad and tapered. Body cavity short, with 11-15 PCV. Eight long, narrow pleural ribs. Posterior parapophyses longer than wide, their ventral margins parallel with long axis of body and abutting along the midline. Parapophyses of last precaudal vertebra broad and triangular, their tips rounded.

Etymology.—From the Greek *compso*, meaning neat or elegant, plus *raia*, meaning ray, in reference to the anal-fin. Gender feminine.

Two species of *Compsaraia* are recognized. 1. *Compsaraia compsa* (Mago-Leccia, 1994, figs. 90 and 91). Holotype: MCUCV-V-11010, Venezuela, Isla Iguana, Delta Amacura, Rio Orinoco, 339 mm TL. 2. *Compsaraia* sp. *1* (MZUSP uncat.), Rio Solimões, Amazonas, Brazil.

POROTERGINI (CLADE AK, NEW TAXON)

The taxa "*Porotergus*," *Sternarchogiton*, and *Adontosternarchus* constitute a clade diagnosed by eight characters: Premaxilla gracile, lateral margin concave, anterior margin laminar (27, also in *Apteronotus albifrons* species-group). Some or all premaxillary teeth lost without replacement during development, adults with fewer teeth than juveniles (28). Single row of dentary teeth (39). Mandible shorter than deep; oral margin of dentary shorter than length of anguloarticular (40). Tip of snout curved, the ventral ethmoid foreshortened on its long axis, and deepest posterior to its midlength (61). Lateral ethmoid narrow, its base shorter than its height (66). Orbitosphenoid narrow, its ventral margin as long or shorter than its dorsal margin (73, except *Sternarchogiton* sp. B). ventral margin of parasphenoid flexed sharply on either side of the basicranial region (77, also in *Apteronotus cuchillejo*).

POROTERGUS ELLIS

This study was unable to recover unambiguous characters supporting the monophyly of the several species of *Porotergus* recognized by Mago-Leccia (1994). The genus *Porotergus* was originally defined as apteronotids lacking scales along the anterior portion of the dorsal surface, to include *P. gymnotus* and *P. gimbeli* (Ellis, 1912). This character, however, is observed in many apteronotid species, including "*Apteronotus*" *apurensis*, Sternarchorhamphini, and many members of the Navajini. Furthermore, scales are present on the back in some species previously referred to "*Porotergus.*"

STERNARCHOGITON + *ADONTOSTERNARCHUS* (CLADE AL)

The taxa *Sternarchogiton* and *Adontosternarchus* constitute a clade diagnosed by four characters: Gape small, less than one third head length (19). Dentary gracile, its posterior margin tapering to a point and its ventral margin concave (41, posterior margin not tapered in *Adontosternarchus sachsi*). Snout short, less than one third head length (51). Body cavity short, with 10 - 11 PCV (206). *Sternarchogiton nattereri* and *Adontosternarchus sachsi* were included within *Sternarchogiton* by Eigenmann and Ward (1905) on the basis of their lacking premaxillary teeth, although juvenile and some adult specimens of *Sternarchogiton* do possess premaxillary teeth (27, also in *Apteronotus albifrons* species-group and Sternarchorhynchini).

***STERNARCHOGITON* EIGENMANN, CLADE AM**

The three species of *Sternarchogiton* examined in this study share five characters: Ventral margin of descending maxillary blade with a sharp angle about two thirds distance to its tip (37, also in *Apteronotus cuchillejo*). Fourth hypobranchial with medial bridge (160). Posttemporal not fused with supracleithrum (169). 3rd postcleithrum not ossified (172). Descending blades of anal-fin pterygiophores broad (199, also in *Sternarchorhamphus*).

Oedemognathus exodon appears to represent the sexually mature male morphology of *Sternarchogiton nattereri.* Male specimens exhibiting a continuous variation in the development of the oral jaws and cranial bones are now known (Lundberg, pers. comm.). *Oedemognathus* was named by Myers (1936a) on the basis of a single specimen (USNM 102040, 92mm TL) with hypertrophied oral dentition. All specimens resembling the holotype of *Oedemognathus* examined in this study are male, as indicated by examination of their gonads (Cox-Fernandes, pers. comm.). These specimens also possess the hypertrophied oral dentition of the holotype. These specimens differ from other members of the Porotergini in several regards, none of which are unambiguously optimized.

Schultz (1944) regarded *Apteronotus cuchillejo* as a member of *Sternarchogiton* based on the absence of premaxillary teeth and on the presence of a short snout, neither of which is unique to these taxa among apteronotids. *Sternarchogiton nattereri* and *Apteronotus cuchillejo* do possess several other similarities, possibly associated with shared possession of a short snout; the shape of the maxilla (37), orbitosphenoid (broad and well ossified), and endopterygoid (long and narrow, with a posterior position of the ascending process). *Apteronotus cuchillejo* also possesses the mid-dorsal scales and the gracile dentary of *Sternarchogiton* and *Adontosternarchus*, and the hourglass anterior basibranchial and unossified urohyal blade of Porotergini and *"Apteronotus" macrolepis.* Placing *Apteronotus cuchillejo* within *Sternarchogiton* or as the sister to Porotergini requires an additional six steps to the total tree length, and placing it as the sister to the Navajini requires an additional five steps.

ADONTOSTERNARCHUS ELLIS

Four species of *Adontosternarchus* are recognized in the review of Mago-Leccia *et al.* (1985). This study reports 13 diagnostic characters of this clade, of which 10 are optimized as derived reversals according to the character definitions, but many of which represent uniquely derived morphologies: Black and yellow chromatophores (body opaque, 12). Mental organ consisting of a thick pad of electroreceptor organs. Scales present on mid-dorsum (15). Gape of mouth very small (20, also in *Sternarchella* and *Sternarchorhynchus*). Oral opening terminal, mouth V-shaped, upper jaw inserting in groove formed by mandible (21). Oral teeth not retained in adults (23). Ethmoid region deep, descending blade of maxilla straight and narrow, without anterior shelf (36). Mesethmoid tip flat, without groove (57). Infraorbital subnasal extension remote from anterior pore (84). Opercular dorsal margin convex (143). Five or 6 branchiostegal rays (144). Dorsal head of anterior DHS as narrow as descending blade, its anterior margin continuous with curve of descending blade (189). Parapophyses of posterior precaudal vertebra not contacting one another (212).

The several plesiomorphic features of *Adontosternarchus* are regarded as derived in the topology of Fig. 43, and the distribution of these character states among apteronotids indicates that the morphologies represented are phylogenetically independent. Placing *Adontosternarchus* as the sister taxon to the Porotergini or Apteronotidae requires the addition of five steps to the total tree length.

COMPARISONS WITH PREVIOUS STUDIES

Some of the characters used in this report were modified from three previous studies on phylogenetic differences among gymnotiform taxa (Triques, 1993; Gayet *et al.*, 1994; Alves-Gomes *et al.,* 1995). The branching order of the major lineages presented by Triques (1993, fig. 24) and Gayet *et al.* (1994, fig. 11-A) are similar in the position of Apteronotidae as the sister taxon to other gymnotiforms, and in placing Sternopygidae as the sister taxon to a clade consisting of Gymnotidae and Rhamphichthyoidea (Alves-Gomes *et al.,* 1995, fig. 2-B). The topology preferred by Alves-Gomes *et al.* (1995, fig. 10) concurs with the present study with regards to the monophyly of high frequency, tone-type EODs (in Apteronotidae and Eigenmanninae), and the position of the Gymnotidae as a relatively basal member of the Gymnotiformes.

The following discussion presents several alternative definitions, polarities, or phylogenetic distributions of characters modified from these studies for use for use in the present analysis. The definition and distribution of three characters used in the present study were modified from Triques (1993). The lateral process of the ventral ethmoid (the vomer of Triques, 1993, character 12) is present in Gymnotidae (character 59 of the present study); the contact between the autopalatine cartilage and the antorbital (Triques, 1993, characters 18 and 19) is not regarded as two independent characters (character 127 of the present study), and the concave dorsal margin of the basihyal (Triques, 1993, character 30a) is not observed in Rhamphichthyidae (character 162 of the present study). Other differences in the character-coding of the present analysis from that of Triques (1993) include the lack of an ascending process of the posterodorsal margin of the parasphenoid (Triques, 1993, character 14a) in Gymnotidae and Rhamphichthyoidea, and the lack of fusion between suspensorial elements in *Adontosternarchus* and *Sternarchella* (Mago-Leccia *et al.,* 1985).

Two concerns arise from Triques' (1993) choice of terminal taxa. The polarity of three characters (*i.e.*, reticulate skeleton, size and shape of premaxilla) among apteronotids and sternopygids is problematic due to the use of *Apteronotus albifrons* to represent the basal apteronotid condition. Additionally, specimens of " *"Porotergus" terminalis*" (USNM 228643) from the lower Orinoco are presumably *Sternarchella orthos* (Mago-Leccia, 1994; see Lundberg *et al.*, 1996). It is therefore not unexpected that these specimens share many features with specimens of *S. sima* examined.

The following comments will help the reader compare the results of this study with those of Gayet *et al.* (1994). Characters 26 - 34 of Gayet *et al.* (1994) purporting to unite Sternopygidae with "Gymnotia" are represented in the present study, but morphologies resembling the descriptions of four characters (30, 33, 34, and 41 of Gayet *et al.* 1994) were not observed in the material examined for the present study. For example, observations on specimens from all gymnotiform genera indicate that the neural arches of gymnotiforms do not establish contact along the majority of the length of the centrum in vertebrae of the anterior half of the body. The neural canal does, however, become closed on its dorsal aspect posteriorly in all gymnotiform groups. Lack of an adipose fin is not used here because the dorsal organ of apteronotids is not similar to the adipose fin of other euteleosts (Franchina and Hopkins, 1996; character 192). The impression along the dorsal margin of the body in *†Ellisella*, regarded as an adipose fin by Gayet *et al.* (1994, fig. 1), is interpreted here to be a taphonomic artifact (see Albert *et al.*, in press).

Definitions and/or distributions of several other characters proposed by Gayet *et al.* (1994) are amended for use in the present study. Comments on the phylogenetic distribution of characters related to regeneration are provided with the description of characters 185, 204 and 221. The phylogenetic distribution of the mesocoracoid, the loss of which is employed to diagnose "Gymnotia" (Gayet *et al.*, 1994, character 42, equivalent with Gymnotidae + Rhamphichthyoidea), is somewhat more complex (see character 174 of the present report). The mobile premaxilla (Gayet *et al.*, 1994, character 47) used to diagnose the Hypopomidae is not used in the present study because similar conditions are observed in other members of the Sternopygoidei. The absence of the dermal vomer (character 62 of this study) is, however, a unique feature of the ethmoid region of hypopomids associated with reduced ossification and greater mobility. Lastly, the "epicentrals" of Gayet *et al.* (1994, fig. 1.2-2) are the medial branch of the epipleurals (Patterson and Johnson, 1995).

Several additional comments will aid in the comparison of the data reported here with those of Gayet *et al.* (1994). Differences in the polarity of some characters may be due to the use of different outgroups. Although Gayet *et al.* (1994) do not present a formal data matrix, outgroup conditions may be inferred from the specimens listed in their Materials Examined, representing five South American characiform families and three groups of siluriforms. Specimens of the plesiomorphic characiphysan taxa used by Fink and Fink (1981) are not reported. Gayet *et al.* (1994) report examining 22 gymnotiform species representing 13 of the OTUs used in the present study. Since museum numbers and a data matrix were not presented by Gayet *et al.* it is not possible to determine which specimens were coded to represent individual taxa. Finally, it is helpful to note that figure 11 of Gayet *et al.* (1994) omits character 20 (pulse-type EOD) from the character list, such that the remaining characters are misnumbered.

Alves-Gomes *et al.* (1995) provide a phylogenetic analysis of 302 aligned bases of mitochondrial 12S rRNA, and 416 bases of 16S rRNA. For that study, 19 ingroup OTUs were coded for a total of 178 informative sites among the gymnotiform taxa. Of the nine electrophysiological/ morphological characters employed (Alves-Gomes *et al.*, 1995, table 2), characters 1-4 and 9 are regarded in the present report as different aspects of the gymnotiform electromotor system (character 114). The preferred topology of Alves-Gomes *et al.* (1995, fig. 6) is a strict consensus of 32 most parsimonious trees recovered using three weighting schemes.

The sequence data presented by Alves-Gomes *et al.* (1995) were reanalyzed using PAUP 4.0, regarding all characters as unordered and weighting transitions equal with transversions. Weighting transitions less than transversions is a common procedure in molecular systematic studies when there is evidence that transitional changes are saturated. These data, however, do not appear to be saturated at these sites (Alves-Gomes *et al.*, 1995, figs. 4-5). A single siluriform outgroup taxon (*Cetopsis*) was used in combination with the morphological characters in a total evidence analysis. A strict consensus of the nine most parsimonious trees consistent with the equally weighted mitochondrial sequence data is presented in Fig. 43. The single most parsimonious tree resulting from a combined data matrix of 935 morphological and molecular characters is presented in Fig. 48-B.

These results show strong agreement in the structure of the molecular and morphological data sets. Both of the topologies presented in Figs. 48-A and 48-B support the monophyly of Sternopygoidei, Rhamphichthyoidea, *Steatogenys* + *Hypopygus*, Eigenmannini, Apteronotidae, and Sternarchorhynchinae. Although the relative positions of *Sternopygus*, Eigenmanninae, and Apteronotidae are unresolved in Fig. 48-A, the tree provided by the molecular data alone is not inconsistent with the hypothesis of a monophyletic Sinusoidea. The trees derived from equally weighted sequence data are, however, inconsistent with the morphological data with respect to the position of *Gymnorhamphichthys* and *Apteronotus leptorhynchus*.

Species diversity and systematics of hypopomids is treated by Sullivan (1997a, 1997b) 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 (1997b) 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 (1997b) and that reported in the present study is in the position of Steatogini. Whereas *Steatogenys* + *Hypopygus* are included within the Hypopomidae in the present study, they are the immediate sister group to *Rhamphichthys* + *Gymnorhamphichthys* in Sullivan (1997b). The data reported in Table 2

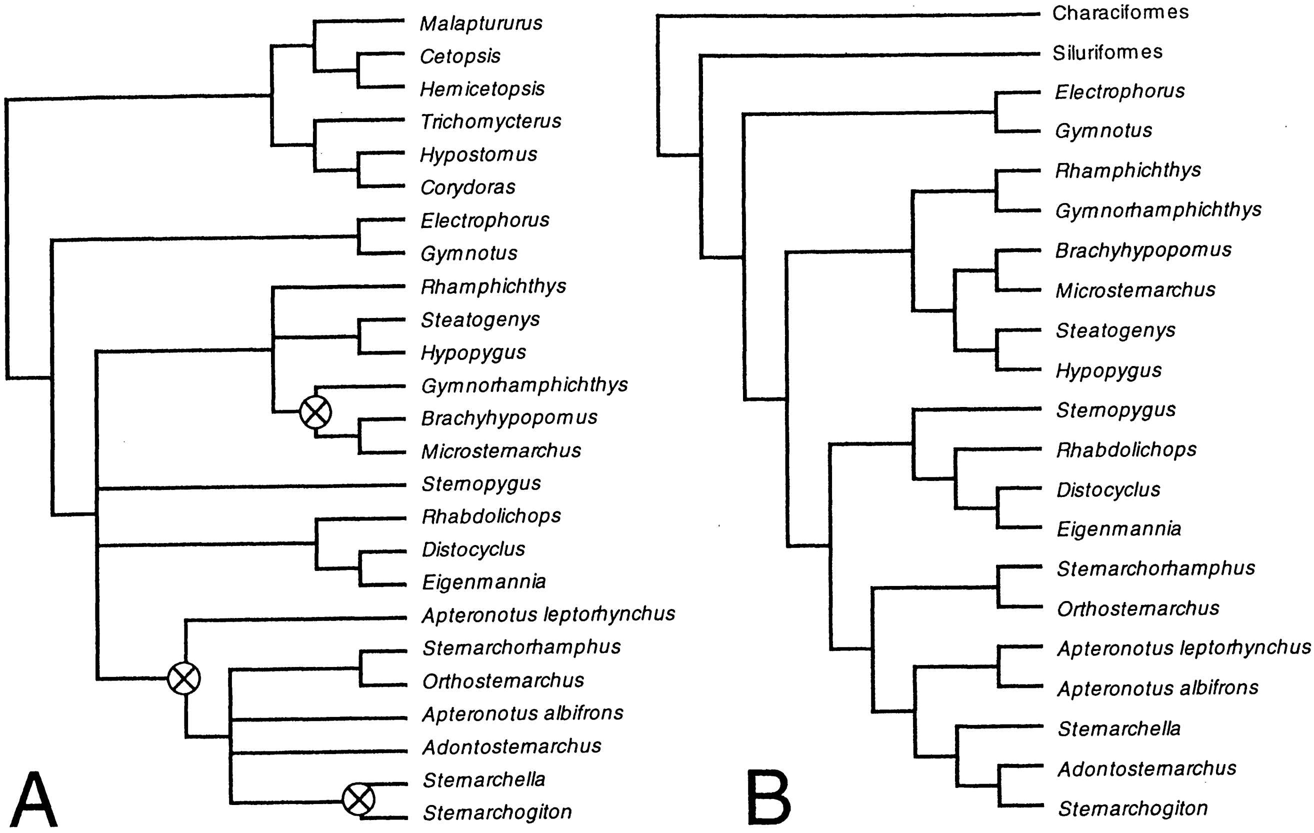


Fig. 48. A. Phylogenetic hypothesis of gymnotiform interrelationships based on mitochondrial DNA sequence data of Alves-Gomes *et al.* (1995). The data include 178 informative sites. This topology is a strict consensus of nine equally parsimonious trees, each of 733 steps (ci = 0.49, rc = 0.31). Terminal taxa are those of Alves-Gomes *et al.* (1995). B. Phylogenetic relationships of 19 gymnotiform taxa based on 935 morphological and mitochondrial DNA sequence characters. This tree is the single most parsimonious topology, requiring 933 steps (ci = 0.57, rc = 0.39). Ingroup topology is insensitive to choice of siluriform taxon employed as outgroup. Points of incongruent between the topologies indicated with ⊗; note the phylogenetic positions of *Gymnorhamphichthys*, *Apteronotus leptorhynchus* and *Adontosternarchus* in B differ from A. Terminal taxa are identified in Methods.

do not include a systematic review of Sullivan (1997b), the analysis of which is work in progress.

NOTES ON CHARACTER EVOLUTION

GENERAL BODY FORM.—A "knife-shaped" or culteriform body morphology has evolved independently in at least seven different teleost groups (Table 8). Fishes with a culteriform morphology achieved propulsion by undulating an elongate median fin; either the anal fin (*e.g.*, notopterids, gymnotiforms) or dorsal fin (*e.g.*, *Gymnarchus*). Culteriform bodies are generally compressed laterally, and the posture is rigid, the body often being reinforced by ossified intermuscular bones (Schlessinger, 1910). In fishes with a culteriform body the other median fins are either highly reduced or entirely absent. Culteriform locomotion derived from pterygiophore muscles may be contrasted with anguilliform locomotion, in which propulsion is achieved by axial muscles (Webb and Weihs, 1983). The later is associated more frequently with body elongation in teleosts, and is observed in true anguilliform eels, halosaurs, plotosid catfishes, macrourids, carapids, and numerous derived groups of spiny-rayed acanthopterygians. Culteriform locomotion is commonly associated with mesopelagic and benthic habitats and anguilliform locomotion with infaunal habitats.

Although the culteriform body of gymnotiforms is functionally coupled with active electroreception, the evolution of culteriform morphology among teleosts is associated with passive electroreception. Of the seven independent origins of culteriform body shape in teleosts listed in Table 8, all occur within electroreceptive clades. Whereas, only electroreceptive fishes have evolved a culteriform body, only two of the five groups which have independently acquired electrogeneration possess a culteriform body. That is, electrogeneration is not required to evolve a culteriform morphology.

Based on the distribution of character states in Table 2 it is possible to reconstruct several aspects of the gross body form of plesiomorphic gymnotiforms. In several important regards the sternopygid *Sternopygus astrabes*, recently described from the Venezuelan Amazon (Mago-Leccia, 1994), resembles this condition. In this species the body is moderately compressed, the coelomic cavity contains 18 to 20 vertebrae, and the snout (preorbital) length is about one third the total length of the head in mature specimens (Figs. 11 and 12). It must be emphasized, however, that *S. astrabes* is nested several nodes within the gymnotiform hierarchy of relationships, and therefore also pos-

Table 8. The phylogenetic distributions of culteriform (knife-shaped) body morphology, electroreception, and electrogeneration in teleost fishes. Abbreviations: AF = anal-fin; AM = axial muscles; DF = dorsal-fin; EM = extrinsic eye-ball muscles; ER = electroreception; EG = electrogeneration; NP = notopteroid passive electroreception; SP = siluriphysan passive electroreception (character 112); SB = swim-bladder muscle; * = gymnotiform electrogeneration and active electroreception (character 114); ** = mormyriform electrogeneration and active electroreception; "—" = character absent. Note the seven independent origins of a culteriform body morphology in teleosts all occur within electroreceptive clades. Note also that only two of the five independently derived electrogenerative groups possess a culteriform morphology (i.e., Gymnotiformes, Gymnarchidae).

Taxon		Culteriform	ER	EG
Gymnotiformes		AF	SP	AM*
Aegeniosidae	Siluriformes	AM+AF	SP	—
Auchenipteridae	Siluriformes	AM+AF	SP	—
Schilbeidae	Siluriformes	AM+AF	SP	—
Siluridae	Siluriformes	AM+AF	SP	—
Mochokidae	Siluriformes	—	SP	SB
Malapteruridae	Siluriformes	—	SP	AM
Notopteridae	Notopteroidei	AF	NP	—
Gymnarchidae	Notopteroidei	DF	NP	AM
Mormyridae	Notopteroidei	—	NP	AM**
Uranoscopidae	Percomorpha	—	—	EM

sesses many derived features (Albert and Fink, 1996). Other plesiomorphic gymnotiform features retained by *Sternopygus* species are discussed by Albert and Fink (1996). The single known fossil gymnotiform †*Ellisella* possesses several derived traits associated with culteriform locomotion, including an elongate anal fin, regeneration of the caudal appendage, and intermuscular bones.

Osteology.—In the plesiomorphic condition, gymnotiforms possess moderately developed oral jaws, a well-ossified neurocranium, suspensorium, splanchnocranium, and pectoral girdle, and tubular cephalic laterosensory canals. In various combinations these features are retained in certain gymnotiform species in association with a generalized omnivorous diet of small (0.1 - 1.0 mm) autochthonous aquatic animals and detritus, and allochthonous vegetable matter (Goulding *et al.*, 1988). Robust oral dentition and jaws characterize the plesiomorphic condition among sinusoids (*e.g., Sternopygus, Parapteronotus*) and in the Gymnotidae.

In several gymnotiform clades there has been an overall reduction in the ossification of bony elements. Reduced ossification is observed in many aspects of the skeleton of the small-bodied gymnotiform *Hypopygus* which attains adult total body length of about 60 mm. *Rhamphichthys*, however, also exhibits the reduced oral jaws and complete absence of teeth which characterize the Rhamphichthyoidea, despite the large size of some species (c.1000 mm in *R. rostratus*), indicating the reduction may not be ascribed to a single event of paedomorphosis. Reduced ossification is associated with paedomorphosis of the cranial region in several sinusoid taxa (*e.g.,* Eigenmannini, Porotergini), both in terms of the shape and extent of ossification of the ethmoid, sphenoid, and otic regions of the endocranium. Some species in these lineages also exhibit specialized remodeling of the bone during post-larval development to produce a reticulated skeleton (character 82).

Snout elongation.—Independent derivation of elongate snouts has long been recognized as a feature of evolution in electric fishes (Ellis, 1913; Bullock *et al.*, 1975; Marrero 1989; Winemiller and Alphonse, 1997). Elongation of the snout appears to have evolved independently in Rhamphichthyidae and in at least three separate apteronotid lineages, each time involving different sets of bones. In the Sternarchorhynchinae the entire orbital and ethmoid regions of the head elongate during postjuvenile growth, such that the eyes are positioned relatively anteriorly and the nares are positioned at the extreme anterior end of an elongate snout. In the *Apteronotus brasiliensis* species-group snout elongation results from hypertrophy of the sphenoid region of neurocranium, so that the combined axial length of the orbitosphenoid and pterosphenoid bones is greater than preorbital region, and the orbit is positioned in anterior third of head (Figs. 11 and 12). This growth of the sphenoid region is an extension of the plesiomorphic ontogenetic trajectory observed in other apteronotid species (Fig. 1). In *Parapteronotus* and *Compsaraia* it is the preorbital region of the neurocranium which undergoes hypertrophy.

Anal-fin rays.—Although anal-fin ray counts vary considerably in natural populations, several gymnotiform clades are diagnosed by high anal-fin ray counts (character 196). In gymnotiforms the number of anal-fin rays and precaudal vertebrae is not correlated. The high number of anal-fin rays observed in Gymnotidae, *Rhamphichthys*, *Sternopygus* and sternarchorhynchine apteronotids does not accompany a longer body cavity (Figs. 40 and 41) or more displaced hemal spines. There is a weak correlation between the number of anal-fin rays and total body length among species (Fig. 42) and there does not appear be a direct correlation between the number of anal-fin rays and habitat.

Gymnotiform species with larger bodies have longer anal fins and more anal-fin rays (Fig. 41). Individual knifefishes, however, bear the same number of anal-fin rays throughout their post-larval ontogeny (Fig. 42). In other words, species which attain larger body sizes start out life with more anal-fin rays. An exception may be *Electrophorus*, which appears to lose rays as it grows, possibly due to incomplete regeneration of lost rays (Mago-Leccia, 1994). With respect to this meristic variable different patterns are exhibited within and between species. That is, the distribution of anal-fin ray differences among species is not accounted for by allometry alone. Instances such as this, in which the macroevolutionary pattern is not a direct extension of microevolutionary variation, may be probed for additional causes. These data are not inconsistent with the hypothesis that some gymnotiform clades have experienced selection to match anal-fin ray number with adult body size.

DISPLACED HEMAL SPINES.—The series of spines lying posterior to the coelomic cavity in the Sternopygoidei are enigmatic structures of uncertain phylogenetic origin (Lundberg and Mago-Leccia, 1986, Lundberg *et al.,* 1996). Due to their position and they have been thought to be homologous with proximal anal-fin pterygiophores, ribs, or hemal spines (Lundberg and Mago-Leccia, 1986; Chardon and de la Hoz, 1974; de la Hoz and Chardon, 1984). Although the function of these bone has not been studied systematically, they may act to reduce torsion about the posterior end of the body cavity or as additional sites for the insertion of anal-fin pterygiophore muscles.

Lundberg and Mago-Leccia (1986) suggest that different elements of the series may be derived from different ontogenetic and phylogenetic sources. Several observations, however, support the hypothesis that the entire series of medial elements posterior to the body cavity are hemal spines. Serial repetition along the longitudinal axis is an aspect of similarity shared by the DHS and unmodified hemal spines. All are elongate vertical bony elements, ossifying from the middle of hypaxial vertical myosepta, dorsally towards their articulations with the hemal arches, and ventrally towards the insertion of their distal tips (Gadow, 1933). Whereas the unmodified hemal spines maintain a one-to-one connection with the hemal arches to which they are fused, the position of one or sometimes two DHS corresponds with the hemal arch of the anterior caudal vertebra or the parapophyses of the last precaudal vertebrae. The distal tips of both unmodified and modified hemal spines insert between each third (sometimes fourth) anal-fin pterygiophore (Fig. 35). There is no evidence that any of the DHS elements are bilaterally paired structures, undermining hypotheses that they are homologous with ribs, pelvic girdle elements, intermuscular bones, parapophyses, or hemal arches.

The anterior, scythe-shaped spine is regarded as a member of this series based on its shape, position, and orientation. The scythe shape results from perichondral ossification on the proximal surface which is expanded and rounded, and in which the main axis of the spine continues to curve anterodorsally. With few exceptions, the spine is a medial ossification, the dorsal margin of the proximal surface is positioned either between or immediately ventral to the parapophyses of the anterior caudal vertebra, and the ventral margin is oriented in parallel with the ventral margin of the parapophyses of the last precaudal vertebra. Additional evidence on the identity of the scythe-shaped spine is provided by certain specimens of apteronotid species (*e.g., Apteronotus albifrons, Sternarchella sima*) in which this spine is composed of two descending blades (Fig. 36), indicating a phylogenetic origin from the fusion of multiple posterior elements. Observations on an ontogenetic series of *Apteronotus leptorhynchus* reveal that the scythe-shaped spine in fully formed in cartilage before ossification commences. There is no indication of ontogenetic fusion. In certain species (*e.g., Apteronotus leptorhynchus, Platyurosternarchus macrostomus, Sternarchogiton nattereri*), a collagenous or lightly ossified connection sometimes exists between the parapophyses of the anterior caudal vertebra and the posterior DHS.

The anterior DHS is shaped like a scythe in all species of apteronotids and in many sternopygids (character 187; Mago-Leccia, 1976; Lundberg and Mago-Leccia, 1986; Fig. 35). In these species the anterior spine is large, about three times as broad as other hemal spines, and curved, extending from between the parapophyses of the last precaudal vertebrae, or sometimes just ventral to the hemal arches of the anterior caudal vertebrae, anteroventrally around the posterior margin of the body cavity towards the origin of the anal fin. In some species of apteronotids, and in *Eigenmannia* and *Rhabdolichops,* the spine is as straight and as wide as other hemal spines. All three species of *Sternopygus* for which radiographic data were collected are polymorphic for this character (Albert and Fink, 1996). *Sternopygus xingu* is unique in that the absence of a scythe-like element is the predominant condition (76.4%; N = 53), in which case it is regarded as derived. Displaced hemal spines are not present in *Gymnotus,* or in *Electrophorus* which has no hemal spines at all.

Variation the morphology and position of the DHS and other axial elements undermines conventional definitions of thoracic and caudal vertebrae in gymnotiforms. In many percomorph teleosts the development of the vertebral skeleton is integrated such that thoracic and caudal vertebrae may be identified relatively unambiguously (Gadow, 1933; Mabee, 1993). In caudal vertebrae, the hemal arches typically contact one another along the ventral midline forming the hemal canal, and contact the hemal spine ventrally, which ossifies within the vertical myoseptum. Precaudal (or thoracic) vertebrae are characterized by the presence of ventrolateral hemapophyses (or basiventrals, Rosa-Molinar *et al.,* 1994, figs. 1C and 1D) and parapophyses, and associated pleural ribs (Romer and Parsons, 1986).

These criteria do not absolutely distinguish caudal and precaudal vertebrae in gymnotiforms, or in many other teleost groups (Ford, 1937; Clothier, 1950; White, 1985; Dyer and de la Hoz, 1988; McKay, 1992; Rosa-Molinar *et al.,* 1994; Tominaga *et al.,* 1996). In gymnotiforms, the position of the anterior hemal spine varies with respect to the posterior margin of the thoracic cavity and with the position of the posterior parapophyses. In *Gymnotus,* the parapophyses of the posterior thoracic vertebrae may lie posterior to the most anterior hemal spine or fuse ventrally to enclose the dorsal aorta (Albert and Miller, 1995). One of the paired parapophyses may extend ventrally to ossify within the medial myoseptum forming the anterior hemal spine. The position of the anterior DHS in the Sternopygoidei is more regularly associated with the posterior margin of the body cavity than with any bony landmark of the axial skeleton.

One conclusion of these observations is that the ontogeny of the sclerotome which forms the axial skeleton (including vertebrae, ribs, the medial fins and their supports) has been modified in gymnotiforms. The large amount of variation in the position and morphology of axial elements within and between gymnotiform species may result from decreased canalization in the development of serially repeated sclerotomal elements. The mere existence of the DHS clustered posterior to the body cavity suggests a breakdown of the one-to-one association of serially arranged sclerotomal elements found in outgroups. These observations support the hypothesis that there is a change in the mechanisms underlying patterning in the sclerotome of gymnotiforms, resulting in transformations resembling homeosis.

ELECTRIC ORGANS.—Understanding the phylogenetic origin of gymnotiform electrogeneration is clouded by the lack of electric organs (EOs) in plesiomorphic members of the relevant outgroup taxa. The plesiomorphic condition within gymnotiforms can be estimated from the distribution of EOs among extant species. The ancestral condition is inferred to be the presence of a single hypaxial organ extending along the majority of the ventral body margin. This EO is enervated by serially repeated spinal motor neurons, which receive descending input from pacemaker cells located in a discrete medullary nucleus. The identity of the primary EO efferents is not known beyond their general homology with spinal motor neurons of other otophysans. In terms of position and function, the medullary pacemaker cells resemble the sonic motor neurons of some catfishes (Ladich and Bass, 1998). Both of these neuronal classes generate repetitive bursts of action potentials used in communication. Further, in the plesiomorphic condition, both of these groups of neurons are located on or close to the midline of the caudal medulla, adjacent to the medial longitudinal fasciculus. Gymnotiforms are unique in the high degree of electrical coupling among pacemaker cells, in the location of innervating neurons along the length of the spinal cord, and in the fact that the innervating muscle is hypaxial (Dye and Meyer, 1986).

Discussions on the evolution of multiple EOs within gymnotiformes are treated by Kirschbaum (1977; 1983), Bass (1986), and Sullivan (1993). With regard to features of gross morphology, the EO of some *Gymnotus* species most closely approximates the plesiomorphic gymnotiform condition. In gymnotids and rhamphichthyoids the larval hypaxial electric organ is retained into the adult state, becoming enveloped by the ventral myorhabdos posteriorly. The larval electric organ of sinusoids degenerates at metamorphosis. In sternopygids the hypaxial electric organ is replaced by an adult EO derived at least in part from anal-fin pterygiophore-muscles. The EO of mature apteronotids forms from a proliferation and elongation of the spinal electromotor neurons which innervate the larval EO (Kirschbaum, 1977).

Gymnotus is polymorphic for a monophasic discharge, with the Middle American species *G. maculosus* and *G. cylindricus* possessing a simple, monophasic EOD and almost no spatial variability in its electric-field (P. Stoddard and B. Rasnow, pers. comm.). *Electrophorus*, sternopygids, and *Sternarchorhamphus* also possess a monophasic discharge, and the number of EOD phases is optimized with ambiguous polarity at the root of the gymnotiform tree. Depending on relationships within *Gymnotus* itself, therefore, the condition in *G. maculosus* and *G. cylindricus* may reverse the evolutionary order of the character among all gymnotiforms. If a complex, tetraphasic EOD is a derived character of a monophyletic clade of South American *Gymnotus*, then *G. maculosus* and *G. cylindricus* are the primitive sister group, and their monophasic discharge is also primitive. If on the other hand, *G. maculosus* and *G. cylindricus* are demonstrated to be closer to some South American *Gymnotus* then others (*e.g.*, the spotted *G. bahianus* and *G. pantherinus*), then the monophasic discharge may be derived.

CAUDAL FIN.—The tree topology emerging from the analysis of all available data produces the seemingly counterintuitive result that the caudal fin of apteronotids is a derived structure. This pattern is an apparent exception to Dollo's Law, which states that complex organs, once lost in phylogeny, can never be regained (Dollo, 1893; Bull and Charnov, 1985). Dollo's law supposes that the complex genetic and developmental bases underlying morphogenesis soon decay once a pathway is lost from an ontogeny.

Several observations may contribute to understanding this problematic character-state polarity. First, it is useful to recognize that Dollo's Law is more of a trend than a universal generalization. The existence of numerous atavisms in the literature demonstrates that genetic and developmental information may be retained for long periods even when unexpressed as morphology (Lande, 1978). In addition, many complex morphological structures are known which have relatively simple developmental bases (Raff, 1996). Second, under any tree topology, the cartilage forming the hypural plate of apteronotids may reasonably be concluded to be homologous with the caudal rod of other gymnotiforms and with the hypural plate of other teleosts. The caudal fin of apteronotids may therefore develop by combining the developmental program underlying the specialized axial regeneration system of gymnotiforms with the more plesiomorphic program underlying teleost caudal-fin morphogenesis. Because the caudal fin of apteronotids is a derived structure it should not be regarded as an intermediate condition in the transition to a complete absence of a caudal fin in other gymnotiforms.

HABITAT UTILIZATION.—Habitat utilization arises from behavioral properties of the nervous system and is subjected to phylogenetic analysis like other aspects of the phenotype (Wenzel, 1992). Three observations indicate that the behavioral capacity to forage and seek refuge on the bottom of large Amazonian rivers channels (character 248) is a derived feature of certain gymnotiform clades. First, most or all species in three monophyletic groups of gymnotiforms are abundant in this habitat, both in terms of biomass and diversity (Lundberg *et al.*, 1987, 1996). Second, many species of these lineages are only known from this habitat. Third, few other fish taxa are present in this habitat. The characteristic behavior of apteronotids to inhabit the depths of large rivers is recognized by several indigenous Amazonian peoples (López and Hernández, 1986; Royero-Léon, 1989).

The use of habitat utilization as a phylogenetic character is problematic in several regards. Habitat variables are difficult to identify in the Amazon basin where the natural history of many fishes is complex and poorly known (Goulding *et al.*, 1988; Lowe-McConnell, 1975; 1991). Assigning taxa to particular habitats may be obscured my the fact that many species undergo seasonal migrations from deep river channels to várzea (white-water flood-plain) channels and flooded forests for breeding and foraging (Cox Fernandes, 1996a; Lundberg *et al.*, 1996; Cox Fernandes, 1998b). Several species also undergo ontogenetic shifts in habitat (Schwassmann, 1978; Albert and Royero-Léon, unpubl. data). Finally, coding taxa as inabiting discrete habitats often relies on the negative evidence that species not sampled from a habitat are actually not present, an assumption of varying veracity in many Amazonian localities.

Although the neural basis for habitat utilization in fishes in poorly understood, the telencephalon is thought to participate in complex activities such as sensorimotor integration, premotor planning, motivation, and the suppression of behavioral inhibitions (Northcutt and Davis, 1983; Ito *et al.*, 1986). The dorsal area of the telencephalon in actinopterygian fishes is homologous in large part to the pallium of other vertebrates, including the cerebrum of mammals (Northcutt, 1995; Yoshimoto *et al.*, 1997). The telencephalic neurons of area Dcl described in character 103 lack input from the lateral preglomerular nucleus of the diencephalon in apteronotids, a structure which serves as a relay of laterosensory information to the telencephalon in other teleosts. Telencephalic area Dcl also receives projections from several sensory systems and projects to the neuroendocrine system in gymnotiforms (Striedter, 1992; Wong, 1997; Corrêa *et al.*, 1998). These sensory and neuroendocrine structures are in turn part of a diencephalic neural network which regulates the pacemaker cells of the medulla (Heiligenberg, 1991; Zupanc and Horschke, 1997; Zupanc and Maler, 1997). The phylogenetic origin of these neural specializations is congruent with the derived condition of habitat utilization defined in character 248. These data are consistent with the hypothesis that the derived states of characters 103 and 126 participate in the construction of behaviors related to the utilization of deep rivers channels.

Several gymnotiform lineages exhibit additional morphological characters associated with a life history in the deep-channel benthic habitats. Some of these characters resemble conditions observed in troglodytes, including reduced eyes and pigmentation (Lundberg and Rapp Py-Daniel, 1994). In many deep-channel gymnotiforms, notably species of Eigenmannini and Navajini, the entire body is modified for foraging and locomotion in the swiftly flowing river channels. In these species the mouth is often terminal and the body cavity is relatively short and slender. The 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 endoskeletal ossification is substantially reduced, through one of several mechanisms including delayed onset of mineralization (*i.e.*, paedomorphosis) and active bone remodeling.

The derived members of *Apteronotus s.s.* which inhabit smaller rivers and streams possess a complimentary suit of characters; they have a longer, deeper body cavity and an opaque body, with more completely ossified bones and more complete squamation than their relatives which inhabit large rivers (*e.g.*, "*Apteronotus*" *bonapartii*). A similar contrast is observed when comparing the strictly channel dwelling *Adontosternarchus balenops* with its derived congener *A. devenanzii*, the latter possessing a shorter, deeper body, and which is collected in a wider range of fluvial habitats (Mago-Leccia *et al.*, 1985). This pattern is also observed in *Rhabdolichops*, with *R. electrogrammus* possessing a relatively larger head (HL more than 13% TL) and shorter anal fin (with fewer anal-fin rays; 173 - 193) than ""the more specialized and planktivorous *R. troscheli* (HL less than 8% TL, anal-fin rays = 225 - 274).

DESCRIPTIVE BIOGEOGRAPHY

All known fossil and extant gymnotiform species are restricted to Neotropical freshwaters (Fig. 49). Gymnotiforms range from the Rio Salado in the Pampas of Argentina (36∞ S) to the Rio San Nicolás of southeastern Chiapas, Mexico (18°N), and are known from the continental waters of all South and Middle American countries except Chile and Belize (Eigenmann and Ward, 1905; Ellis, 1913; Eigenmann and Fischer, 1914; Eigenmann and Allen, 1942; Miller, 1966; Bussing, 1985; Lopez *et al.*, 1984). The biogeographic distributions of gymnotiform genera are summarized in Table 9A by hydrological region; Table 9B summarizes the biogeographic distributions of the currently recognized gymnotiform species.

The hydrological regions depicted in Fig. 49 are defined from results of previous biogeographic studies of the Neotropical ichthyofauna (see Bermingham and Martin, 1998; Lundberg, 1998; and references therein). The Amazon region (AM) includes the Rio Amazonas-Solimões basin, the Rio Tocantins, the entire extent of the south-bank tributaries, the Andean headwater tributaries below about 500 meters elevation, and the north-bank tributaries below the Guyana fall-line (*i.e.*, Rio Negro below Barcelos and Rio Branco below Catrimani). The Guyanas region (GU) includes the waters of the Guyana shield above the fall-line, including but not restricted to the Rio Caroni, Rio Cuyuni, Upper Rio Orinoco (above San Fernando de Atabapo) and Casiquiare canal, Rio Uaupes, upper Rio Negro (above Barcelos), upper Rio Branco and Rio Tacutu basins, Rio Essequibo, Rio Maroni, and Rio Oyapok. The Orinoco region (OR) includes the east-flowing drainages of the Coridillera Oriental and the south-flowing drainages of the Cordillera Merdia, including the Apure, Meta, and Guaviare rivers. The Pacific slope region (PS) includes the west-flowing drainages of coastal northeastern South America, from the Rio San Juan and Rio Baudó of Colombia to the Rio Guayaquil of Ecuador. The Middle America region (MA) includes the coastal drainages of both slopes, from the Rio Atrato of Colombia to the Rio Motagua of Guatemala on the Atlantic slope, and from the Rio Tuyra of Panamá to the Rio San Nicolas of Chiapas, Mexico on the Pacific slope. The Northwest (NW) region includes the north-flowing Atlantic drainages of Colombia and Venezuela, including Rio Magdalena of Colombia and Maracaibo basin of Venezuela and Colombia. The Northeast region (NE) includes the north and east-flowing coastal drainages of northeastern Brazil, from the Rio Parnaíba in the north to the Rio Jequitinhonha in the south, including the Rio São Francisco basin. The Paraná-Paraguay region (PA) includes the entire Paraná-Paraguay-Uruguay-La Plata basin, the endorheic Dulce-Salí basin in Tucuman state, Argentina, and the Rio Salado basin in Buenos Aires state, Argentina. The Southeast region (SE) includes the Atlantic coastal drainages of southeastern Brazil and Uruguay, extending from the Rio Docé in Espiríto Santo state to the Lagoa Mirim basin in Rio Grande do Sul state of Brazil and Uruguay.

By any measure the Amazon basin is the region of highest gymnotiform diversity. There are about 89 species currently known in this region, constituting 62% of the total gymnotiform fauna. Among these are 42 species endemic to the Amazon. The Orinoco basin, with 56 species currently recognized, is also an important area of gymnotiform diversity, constituting 40% of the total species. At least 44 gymnotiform species are common to the Amazon and Orinoco drainages, which is largest shared-fauna among the major drainage basins in South America. About 35 gymnotiform species are currently known from the clear and black waters of the Guyanas, of which five

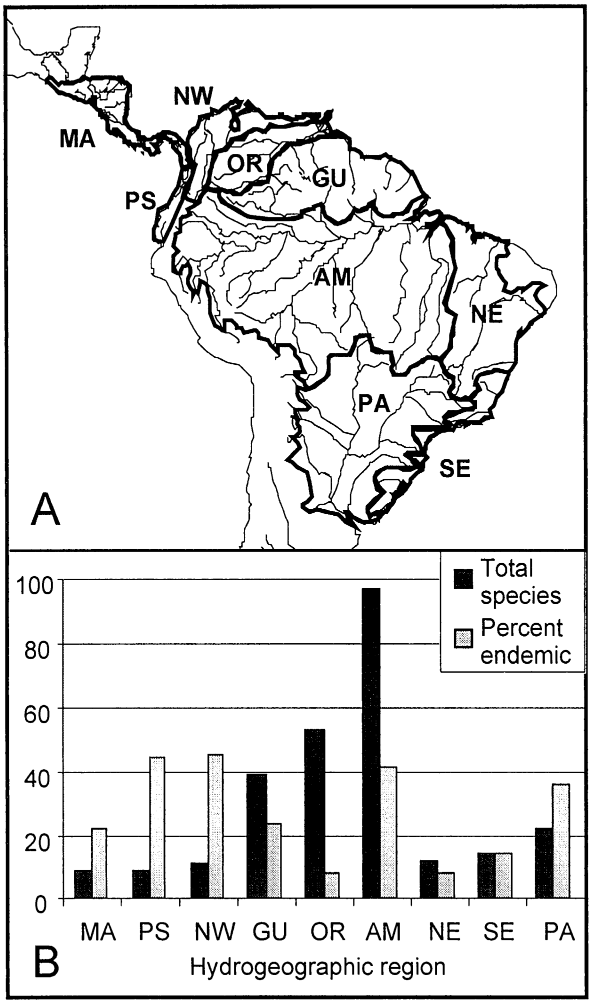


Fig. 49. **A**. Geographic distributions of gymnotiform species. Hydrological regions defined in the text. MA = Atlantic and Pacific slopes of Middle America. PS = Pacific slopes of Colombia and Ecuador. NW = Northwestern South America including the Atrato, Magdalena and Maracaibo basins, and the north slope of Venezuela. OR = Orinoco basin including the island of Trinidad. GU = Guyanas and Upper Rio Negro. AM = Amazon basin below about 500 meters elevation. NE = coastal drainages of northeast Brazil including the Rio Parnaíba, Rio São Francisco, and Rio Jequitinhonha basins. SE = coastal drainages of southeast Brazil and Uruguay from the Rio Doce to the Lagoa Mirim basins. PA = Paraguay-Paraná basin including endorheic Rio Dulce-Salí basin of northeastern Argentina. **B**. Total number of gymnotiform species and number of endemic gymnotiform species in each of the nine hydrological regions depicted in A. Data from Table 9.

are endemic. Gymnotiforms are known from Andean white waters of Bolivia, Colombia, Ecuador, and Perú below about 500 meters elevation.

Outside the Amazon-Orinoco drainage system the gymnotiform fauna is less diverse. There are 25 gymnotiform species known in the La Plata-Paraná basin, and one species from the endorheic Dulce-Salí basin of Northwestern Argentina (*Eigenmannia* sp. D). Only nine gymnotiform species have been reported from the relatively arid Northeast region of Brazil (including the São Francisco basin), among which is a single apteronotid (*Apteronotus brasiliensis*) (Britski, 1972; Britski *et al.*, 1988; Triques, pers. comm.). There are 12 species inhabiting the small rivers of Southeastern Brazil and Uruguay (Travassos, 1960; Campos-da-Paz, 1997). According to the current taxonomy, both the Northeast and Southeast regions of Brazil exhibit relatively low levels of endemism, with only three species restricted to one or the other of these regions. This pattern may reflect a real history of extensive faunal exchanges with the Amazon and Paraná, or it may indicate a poor understanding of species differences in these areas (Albert *et al.*, 1998a).

The Pacific and Atlantic slopes of northwestern South America and Middle America also have a gymnotiform fauna (Eigenmann and Fisher, 1914), assigned to at least seven trans-Andean clades; 1. *Apteronotus rostratus - leptorhynchus*, 2. *Apteronotus cuchillo - magdalenensis*, 3. *Brachyhypopomus occidentalis - diazi*, 4. *Eigenmannia humboldti - limbata*, 5. *Gymnotus cf. carapo* spp, 6. *G. cf. anguillaris* spp., 7. *Sternopygus aequilabitaus - arenatus*. Fourteen gymnotiform species inhabit the Caribbean catchment area, excluding the Orinoco, from the Atlantic slopes of Guyana to Guatemala, including the Maracaibo and Magdalena drainages and the Island of Trinidad. Gymnotiform fishes are much less diverse west of the Andes (Eigenmann and Allen, 1942), with only seven species recognized from the Pacific coast of South America, and another seven species from Middle America (Albert and Miller, 1995). The Pacific slopes of Middle and South America share three species (*Brachyhypopomus occidentalis*, *Sternopygus aequilabitaus*, and *Apteronotus rostratus*). Gymnotiforms have not been reported from the Usumacinta basin of Guatemala and Mexico, or from the Pacific slope of Perú.

The geographic patterns of taxic richness observed among species are also present among higher gymnotiform taxa. The Amazon is the center of diversity at the generic level, with species representing 27 genera, four of which are not found elsewhere. The Guyanas is the only other region with an endemic genus (*i.e., Racenisia*). *Gymnotus* is the most widely distributed gymnotiform genus, inhabiting almost the entire range of all other groups combined. Members of this lineage inhabit the Pacific (*G. maculosus*) and Atlantic (*G. cylindricus*) slopes of Middle America, the Pacific slopes of Colombia and Ecuador, including the Atrato, Magdalena and Maracaibo basins of Colombia and the north slope of Venezuela (*G. cf. carapo* and *G. anguillaris*), the island of Trinidad (*G. cf. carapo*), the North Atlantic drainages of the Guyanas (*G. cf. carapo*), the Orinoco-Amazon basin east of the Andes (six species), the Parnaíba of northwest Brazil (*G. cf. carapo*), the South Atlantic drainages of southeast Brazil, from the São Francisco to Uruguay (*G. pantherinus*), and the Pilcomayo, Paraguay, Paraná, and Uruguay drainages of the La Plata basin (*G. inaequilabiatus*). *Brachyhypopomus*, *Sternopygus*, and *Apteronotus s.s* are also recorded from all regions defined in Table 9. *Rhamphichthys* is the most widely distributed member of Rhamphichthyidae, but is restricted to waters east of the Andes. Gymnotiform species diversity is not strongly correlated with geographical area. The Amazon is the largest of the regions defined, covering approximately 7.05 million km^2 (excluding the Rio Tocantins). The highly diverse Orinoco basin, however, is substantially smaller, covering about 0.94 million km^2 (including the Caroni-Cuyuni basin), whereas the much less diverse Paraná basin is realtively large, covering 3.1 million km^2.

HISTORICAL ECOLOGY

From the available systematic and biogeographic data, gymnotiforms are inferred to have originated in the Western (South American) part of the African-South American continent (northern Western Gondwana) during the Upper Cretaceous (Lundberg, 1993; Lundberg, 1998). The origin of gymnotiforms coincides with the initial development of the Neotropical biota, approximately at the time of separation of South America and Africa about 100 million years ago (Pittman *et al.*, 1993; Romero, 1993). A minimum date for the origin of the gymnotiform clade can be established by dating the earliest fossil representative of their closest relatives the catfishes (Fink and Fink, 1981; Maisey, 1993). Fossilized partial skulls and anterior vertebrae of catfishes are known from the late Cretaceous or Paleocene of Bolivia and isolated arioid catfish otoliths have been reported from the Maastrichtian (Late Cretaceous) of South Dakota (Lundberg, 1993). The presence of *†Ellisella*, with an elongate anal-fin, reduced distal anal-fin pterygiophores, and a regenerated caudal appendage, from the Upper Miocene (Gayet and Meunier, 1991), establishes an minimum date for the origin of the specialized gymnotiform anal-fin undulatory locomotion.

During the Tertiary period, when South America was an isolated island continent and the modern Amazon basin was formed, gymnotiform knifefishes diversified into the habitats in which they exist today. The phylogenetic distribution of habitat preferences among the basal lineages of gymnotiforms and the immediate outgroup taxa indicates that gymnotiforms originated in small upland (*terra firme*) forest streams (*i.e., quebradas, igarapés*). This habitat is shared by basal members of four of the five gymnotiform families (except Apteronotidae), including some or all extant species of *Electrophorus*, *Gymnotus*, *Gymnorhamphichthys*, *Hypopomus*, and *Sternopygus*. Gymnotiform taxa inhabiting other habitats are regarded to be derived.

The great South American rivers were an important site of gymnotiform diversification during the Tertiary period. In terms of relative abundance and ecological importance, knifefishes are a predominant component the deep river channels (Lundberg *et al.*, 1987; Goulding *et al.*, 1988; Marero, 1989; 1993; Gavis *et al.*, 1989; Lundberg *et al.*, 1996). Approximately half of the recognized species of gymnotiforms dwell in the deep voluminous waters of the Amazon and Orinoco rivers and their larger tributaries. Collections from the channels of these rivers produce primarily three lineages of gymnotiform fishes, approximately 30 species of Apteronotidae, six species of Eigenmannini (Lundberg *et al.*, 1987; Campos-da-Paz, 1996), one species *Steatogenys* and two species of *Rhamphichthys* (pers. obs).

Surveys of Amazonian river channels from the Orinoco drainage of Venezuela (Mago-Leccia *et al.*, 1985; Lundberg and Mago-Leccia, 1986; Lundberg *et al.*, 1987) and Amazon drainages of Brazil (Lundberg *et al.*, 1991; 1996) have produced many species of gymnotiforms new to ichthyology. These high volume waters, rich in sediments and debris, constitute a major component of the ecology of the entire region (Humboldt and Bonpland, 1811; Goulding *et al.*, 1988; Lundberg *et al.*, 1987; Machado-Allison, 1993).

Characteristic gymnotiform faunas may also be recognized in several other habitats, where their presence is inferred to be derived. These habitats include the species-rich gymnotiform assemblages of the *várzea* floating meadows, flood-plain lakes, confluence and coastal estuaries, cataracts of Andean and Guyanan escarpments, and upland seasonal ponds (Goulding *et al.*, 1988; Schwassmann, 1989; Crampton, 1996; Crampton, 1998a). Many rhamphichthyoids (*e.g., Brachyhypopomus, Hypopygus, Microsternarchus, Gymnorhamphichthys)* are an important component of the ichthyofauna in seasonal streams of several South American savannas, including the Gran Sabana (Lavrado) of the Guyanas (Planquette *et al.*, 1996; Alves-Gomes, 1997), and the cerrado of the Brazilian shield. Species of *Brachyhypopomus* are also widespread in relatively xeric areas, including the desertified regions of northwest of Venezuela and northeast Brazil, the coastal drainages of southeast Brazil and Uruguay, and the Chaco of northern Argentina (Costa and Campos-da-Paz, 1992; Mago-Leccia, 1994; Butí and Miquelarena. 1995; Campos-da-Paz and Costa, 1996; Sullivan, 1997b). There are also two species of troglodytic gymnotiforms (*sensu* Eleonora, 1997) from the Rio Tocantins basin of central Brazil; *Eigenmannia vicentespelae* (Triques, 1996), and *Sternarchorhynchus mesaensis* (Campos-da-Paz, 1999b).

IDENTIFICATION KEY TO GYMNOTIFORM GENERA

The following identification key applies to mature specimens of 27 gymnotiform genera. Mature specimens of most gymnotiform species are more than 140 mm total length, with some exceptions (see footnote 1). The key is artificial; *i.e.,* the branching order presented is for convenience of identification only. Exceptions to certain character-state couplets are appendedas footnotes. The features employed are mainly of external morphology and color, although some useful characters are provided that are observable only from radiographs or cleared-and-stained specimens. Simple line-drawings of each genus in profile are provided to illustrate some of the characters (Fig. 50). Specimens used in construction of the key are listed in Appendix 1. Geographic distributions from Table 9A.

1a. No scales visible on body surface. Thick skin, large lateral line canal pores. Vascularized respiratory organ in mouth. Body cavity extending to tip of tail, no hemal spines or caudal vertebrae. Anal-fin rays to tip of tail. Attains large body size, more than two meters. Color uniform dark brown dorsally, pale yellow or red ventrally. Range: Amazon, Guyanas, Orinoco .... *Electrophorus* (Fig. 50-A)

1b. Scales present on body surface. Thin skin, small lateral line canal pores. No vascularized respiratory organ in mouth. Body cavity not extending to tip of tail, hemal spines and caudal vertebrae present. Caudal appendage extending posterior to anal-fin. Variable adult body sizes, 120 - 1000 mm. Color variable, not uniform dark brown dorsally and pale yellow or red ventrally 2

2a. Mouth superior with prognathous chin, rictus curved ventrally. Eye positioned below middle of head, horizontal with rictus of gape. Anterior nares pipe-shaped, with elevated rim opened dorsally, entirely included within gape. No cranial fontanels. Branchial opening along entire posterior mar-

Table 9A. Geographic distributions of gymnotiform genera, arranged according to classification in Appendix 4. Hydrological regions: AM = Amazon (incl. Branco, Tocantins); GU = Guyanas (incl. Caroni, Cuyuni, Upper Orinoco, Cassiqiare, upper Negro, Tacutu, Essequibo, Maroni, Oyapok); MA = Middle America (incl. Tuyra, Atrato); NW = Northwest South America (incl. Magdalena, Maracaibo); NE = Northeast Brazil (incl. Parnaíba, São Fransico, Jequitinhonha); OR = Orinoco-Meta (incl. Guaviare); PA = Parana-Paraguay (incl. Uruguay, Dulce-Salí); PS = Pacific slope South America (incl. San Jaun, Guayaquil); SE = Southeast Brazil (incl. Doce, Lagoa Mirim). ⊗ = region with type locality of type species; X = species from other region; underlined symbols represent genera endemic to region. Data from Appendix 1.

Genus	MA	PS	NW	GU	OR	AM	NE	SE	PA
Gymnotus	X	X	X	X	X	X	X	X	X
Electrophorus				⊗	X	X			
Rhamphichthys				X	X	X	X	X	X
Gymnorhamphichthys				X	X	⊗			X
Iracema						$\underline{\otimes}$			
Hypopomus				⊗		X			
Brachyhypopomus	X	X	X	X	X	⊗	X	X	X
Microsternarchus				X	⊗	X			
Racenisia				$\underline{\otimes}$					
Steatogenys			X	X	X	⊗			
Hypopygus				⊗	X	X			
Sternopygus	X	X	X	X	X	⊗	X	X	X
Archolaemus				X		⊗			
Distocyclus			X	X	X	⊗			
Rhabdolichops				⊗	X	X			
Eigenmannia	X		X	X	X	X	X	X	X
Sternarchorhamphus				X	X	⊗			
Orthosternarchus						$\underline{\otimes}$			
Sternarchorhynchus				⊗	X	X			X
Platyurosternarchus				X	X	⊗			
Parapteronotus						$\underline{\otimes}$			
Apteronotus s.s.	X	X	X	⊗	X	X	X	X	X
Sternarchella					X	⊗			X
Magosternarchus						$\underline{\otimes}$			
Compsaraia					⊗	X			
Porotergus				⊗	X	X			
Sternarchogiton					X	⊗			
Adontosternarchus					⊗	X			
Total	5	4	7	20	21	27	6	6	9
Endemic	-	-	-	1	-	4	-	-	-

gin of opercle. Body cavity long, more than 30 precaudal vertebrae. No displaced hemal spines. Color oblique bands on lateral surfaces with highest contrast ventrally and caudally[2]. Range: all regions .... *Gymnotus* (Fig. 50-B)

2b. Mouth subterminal or terminal, without prognathus chin, rictus horizontal, parallel with rest of gape[3]. Eye positioned in middle of head, horizontal or dorsal to nares. Anterior nares without elevated rim, positioned on dorsal surface of head (or if partially within gape, opening anteriorly[4]). Cranial fontanels open. Branchial opening restricted to region around pectoral fin base. Body cavity short, less than 30 precaudal vertebrae. Displaced hemal spines present. Color variable, no bands with highest contrast ventrally and caudally 3

3a. Infraorbital and supraorbital laterosensory lines connected anterior to eye. Longitudinal bar or strip of fleshy tissue firmly attached to posterodorsal midline. Caudal fin present. Neurogenic electric organ medial (deep) to lateral line. EOD frequency more than 750 Hz. .... APTERONOTIDAE (15)

3b. No connection between infraorbital and supraorbital laterosensory lines anterior to eye. No bar or strip of fleshy tissue on posterodorsal midline. No caudal fin. Electric organ in axial or pterygiophore muscles. EOD frequency less than 750 Hz 4

4a. No teeth in oral jaws[6]. Eye small, diameter of orbit less than distance between nares. Infraorbital bones thin cylinders, without bony arches. Anterior nares located near or within gape. Urogenital papilla present[7A]. Pulse-type EOD 5

4b. Small villiform teeth present in both jaws. Eye large, diameter of orbit equal to or greater than distance between nares. Infraorbital bones large and bag-like, with expanded bony arches. Anterior nares located outside gape. No urogenital papilla. Tone-type EOD .... STERNOPYGIDAE (11)

5a. Snout long, preorbital region more than 38% head length. Nasal capsule near tip of snout. Operculum triangular. Hyomandibula oriented parallel to long axis of head. Anal-fin base without fold of tissue. Anal-fin origin at branchial

Table 9B. Geographic distributions of 142 gymnotiform species, arranged according to classification in Appendix 4. Regions as in Table 9A. ⊗ = region with type locality; X = specimens from other region; Y = specimens of unknown specific status (= *cf.*). Underlined symbols represent species endemic to region. Data from Appendix 1; additional records from Sullivan (1997b) [1]; Alves-Gomes (1997) [2]; Bermingham and Martin (1998) [3]; J.G. Lundberg, (unpubl. obs.) [4] Original citation [5]

Species	MA	PS	NW	GU	OR	AM	NE	SE	PA
Gymnotus cylindricus	⊗								
Gymnotus maculosus	⊗								
Gymnotus carapo		Y	Y	X	X	X	Y	X	
Gymnotus bahianus							⊗		
Gymnotus inaequilabeatus						Y	Y	X	⊗
Gymnotus silvius								⊗	X
Gymnotus mamiraua						⊗			
Gymnotus arapaima						⊗			
Gymnotus anguillaris	Y		Y	⊗	X	X			Y
Gymnotus cataniapo					⊗	X			
Gymnotus coatesi						⊗			Y
Gymnotus melanopleurus						⊗			
Gymnotus onca						⊗			
Gymnotus pantherinus							Y	⊗	
Gymnotus pedanopterus					⊗	Y			
Gymnotus jonasi						⊗			
Gymnotus sp. J						X			
Gymnotus sp. *P*									*X*
Gymnotus stenoleucus						⊗			
Electrophorus electricus				⊗	X	X			
Rhamphichthys apurensis				⊗					
Rhamphichthys hahni									⊗
Rhamphichthys lineatus						⊗			
Rhamphichthys rostratus				X	X	⊗	Y	X	Y
Rhamphichthys marmoratus						⊗			
Rhamphichthys pantherinus						⊗[5]			
Rhamphichthys reinhardti						⊗			
Rhamphichthys schomburgki				⊗[5]					
Gymnorhamphichthys hypostomus				X	X	⊗			X
Gymnorhamphichthys sp. P					X	X			
Gymnorhamphichthys petiti						⊗			
Gymnorhamphichthys rondoni				X		⊗			
Gymnorhamphichthys rosamariae				⊗					
Iracema caiana						⊗			
Iracema sp. C						X			
Hypopomus artedi				⊗					
Hypopomus sp. Z						X[1]			
Brachyhypopomus beebei				X	⊗	X	Y	Y	
Brachyhypopomus brevirostrus				X	X	⊗	Y		X
Brachyhypopomus diazi			⊗		X				
Brachyhypopomus janeiroensis								⊗	
Brachyhyp. occidentalis	X[1,3]	⊗	Y						
Brachyhypopomus pinnicaudatus				⊗		X		Y	Y
Brachyhypopomus sp. B				X	X	X			
Brachyhypopomus sp. E				X[1,2]	X[1]	X		X	X
Brachyhypopomus sp. F						X			
Brachyhypopomus sp. M						X			
Brachyhypopomus sp. R				X[1,2]	X	X			X
Brachyhypopomus sp. T						X			
Brachyhypopomus sp. W						X			
Microsternarchus bilineatus				⊗	X	Y			
Microsternarchus sp. A				X[2]		X			
Racenisia fibriipinna				⊗					
Steatogenys cryptogenys						⊗			
Steatogenys duidae				X	⊗	X			
Steatogenys elegans					X	⊗			
Steatogenys mirabilis				⊗[5]					
Steatogenys sp. N						X			
Steatogenys sp. O						X			

(Continued on next page)

Table 9B. Continued.

Species	MA	PS	NW	GU	OR	AM	NE	SE	PA
Hypopygus lepturus				⊗	X	X			
Hypopygus neblinae					⊗	X			
Sternopygus astrabes				⊗		Y			
Sternopygus aequilabeatus	X	X	⊗						
Sternopygus arenatus		$\underline{\otimes}$							
Sternopygus macrurus				X	X	⊗	X	X	X
Sternopygus castroi						$\underline{\otimes}$			
Sternopygus sp. B				$\underline{\text{X}}$					
Sternopygus sp. G				$\underline{\text{X}}$					
Archolaemus blax				X		⊗			
Distocyclus conirostrus					X	⊗			
Distocyclus goajira			$\underline{\otimes}$						
Eigenmannia humboldti	Y		⊗		Y	Y			
Eigenmannia microstoma						X	⊗		
Eigenmannia limbata					X	⊗			
Eigenmannia nigra				⊗	X				
Eigenmannia sp. J.								$\underline{\text{X}}$	
Eigenmannia macrops				⊗	X	X			
Eigenmannia cf. macrops B						$\underline{\text{X}}$			
Eigenmannia trilineata								Y	⊗
Eigenmannia virescens				X	X	X	Y	Y	
Eigenmannia cf. virescens D									$\underline{\text{X}}$
Eigenmannia sp. I						$\underline{\text{X}}$			
Eigenmannia sp. N						$\underline{\text{X}}$			
Eigenmannia vicentespelaea						$\underline{\otimes}$			
Rhabdolichops electrogrammus					⊗	X			
Rhabdolichops zareti					$\underline{\otimes}$				
Rhabdolichops eastwardi					⊗	X			
Rhabdolichops stewarti					X	⊗			
Rhabdolichops caviceps					⊗	X			
Rhabdolichops troscheli				⊗	X	X			
Sternarchorhamphus muelleri				X^2	X	⊗			
Orthosternarchus tamandua						$\underline{\otimes}$			
Sternarchorhynchus britskii									$\underline{\otimes}$
Sternarchorhynchus curvirostris				X	X	⊗	Y		
Sternarchorhynchus mesaensis						$\underline{\otimes}$			
Sternarchorhynchus mormyrus					X	⊗			
Sternarchorhynchus oxyrhynchus				⊗	X	X			
Sternarchorhynchus roseni					⊗	X			
Platyurosternarchus macrostomus				X^2	X	⊗			
Parapteronotus hasemani						$\underline{\otimes}$			
Apteronotus s.s. albifrons				⊗	X	X	X	X	
Apteronotus s.s. cuchillejo			$\underline{\otimes}$						
Apteronotus s.s. jurubidae		$\underline{\otimes}$^{5}							
Apteronotus s.s. mariae		$\underline{\otimes}$							
Apteronotus s.s. spurrellii		$\underline{\otimes}$							
Apteronotus s.s. brasiliensis							⊗		Y
Apteronotus s.s. marauna									$\underline{\otimes}$
Apteronotus s.s. sp. S									$\underline{\text{X}}$
Apteronotus s.s. sp. T				X^2					
Apteronotus s.s. cuchillo			$\underline{\otimes}$						
Apteronotus s.s. leptorhynchus				⊗	X				
Apteronotus s.s. rostratus	⊗	X							
Apteronotus s.s. magdalenensis			$\underline{\otimes}$						
Megadontognathus cuyuniense				$\underline{\otimes}$					
Megadontognathus kaitukaensis						$\underline{\otimes}$			
Apteronotus s.l. ellisi									$\underline{\otimes}$
Apteronotus s.l. apurensis					$\underline{\otimes}$				
Apteronotus s.l. bonapartii					Y	⊗			Y
Apteronotus s.l. macrostomus					$\underline{\otimes}$	X			
Apteronotus s.l. macrolepis						$\underline{\otimes}$			
Sternarchella orthos					$\underline{\otimes}$				

(Continued on next page)

Table 9B. Continued.

Species	MA	PS	NW	GU	OR	AM	NE	SE	PA
Sternarchella schotti						$\underline{\otimes}$			
Sternarchella terminalis						$\underline{\otimes}$			
Sternarchella curvioperculata									$\underline{\otimes}$
Sternarchella sp. S						$\underline{X}$			
Sternarchella sima					X	⊗			
Magosternarchus duccis						$\underline{\otimes}$			
Magosternarchus raptor						$\underline{\otimes}$			
Compsaraia compsa					⊗	X			
Compsaraia sp. A						$\underline{\otimes}$			
Porotergus gimbeli						$\underline{\otimes}$			
Porotergus gymnotus				⊗		X			
Porotergus sp. 1					X^4	X			
Porotergus sp. 2						$\underline{X}$			
Sternarchogiton sp. B					$\underline{X}$				
Sternarchogiton nattereri					X	⊗			
Sternarchogiton porcinum						$\underline{\otimes}$			
Adontosternarchus balaenops					X	⊗			
Adontosternarchus clarkae					X	⊗			
Adontosternarchus devenanzii					⊗	X			
Adontosternarchus sachsi					⊗	X			
Adontosternarchus sp. A						$\underline{X}$			
Total	9	9	11	39	53	97	12	14	22
Endemic	2	4	5	9	4	40	1	2	8
Percent endemic	22	44	45	23	8	41	8	14	36

isthmus. Anal-fin pterygiophores longer than hemal spines. More than 10 displaced hemal spines lateral to body cavity .... RHAMPHICHTHYIDAE (6)

5b. Snout moderate to short, preorbital region less than 38% head length. Nasal capsule near eye. Operculum trapezoidal. Hyomandibula oriented oblique to long axis of head. Thick fold of semitransparent tissue over anal-fin base. Anal-fin origin ventral or posterior to pectoral fin. Anal-fin pterygiophores shorter than hemal spines. Three displaced hemal spines lateral to body cavity ... HYPOPOMIDAE (7)

6a. Scales present over most of body. Long anal fin with more than 300 rays. Some anal-fin rays branched. Origin of anal fin under eyes. Short caudal filament extending posterior to anal fin^{7B}. Gas bladder thick, fibrous, and opaque^{7C}. Adductor mandibula with ossified intermuscular bones. Large body size, 400 - 1000 mm total length. Color consists of broad incomplete oblique lateral bands with irregular margins; never even ground color or translucent. Range: all regions east of Andes .... *Rhamphichthys* (Fig. 50-J)

6b. Scales absent from anterior 2/3 of body. Moderate anal-fin length with fewer than 200 anal-fin rays. All anal-fin rays unbranched. Origin of anal fin near branchial opening. Long caudal filament extending posterior to anal fin. Gas bladder thin and membranous. Adductor mandibula without ossified intermuscular bones. Small to moderate body size, less than 300 mm total length. Color variable, including saddles over dorsal midline, irregular spots on lateral surfaces, or translucent with little or no pigmentation; no oblique lateral bands. Range: Amazon, Guyanas, Orinoco, Paraná .... *Gymnorhamphichthys* (Fig. 50-K)

6c. Scales absent from anterior mid-dorsum and posterolateral surfaces. Anal-fin with 200 - 300 rays. All anal-fin rays unbranched. Origin of anal fin near branchial opening. Long caudal filament extending posterior to anal fin. Moderate body size, to about 400 mm total length. Color consists of irregular, round blotches arranged as irregular lateral bands. Range: Rio Solimões and Rio Negro .... *Iracema*

7a. Snout more than one third head length. Posterior nares about equidistant between tip of snout and anterior margin of eye. Head long, narrow, and depressed, head-width at opercle less than 48% head length, head depth at occiput less than 63% head length. Long anal-fin (mode = 220 - 240 rays). Color consists of large brown pigment spots or blotches. Range: Amazon, Guyanas .... *Hypopomus* (Fig. 50-E)

7b. Snout about one third head length. Posterior nares closer to tip of snout than anterior margin of eye. Head short, broad and deep, head-width at opercle more than 48% head length, head depth at occiput more than 63% head length. Moderate length anal-fin (mode = 200 - 220 rays). Color variable, including saddles over dorsum and irregular oblique bands or uniform speckling; no large pigment spots or blotches 8

8a. Snout slender, longer than deep. Scales present on anterior dorsal midline; scales small, four or more to dorsal midline. Body compressed laterally. Body cavity length not short, 11 - 17 PCV. No humeral accessory electric organ. EOD with 1 - 3 phases. Tail length less than 45% total length. Moderate adult body sizes (140 - 350 mm). Color variable, including saddles over dorsum and irregular oblique bands, or

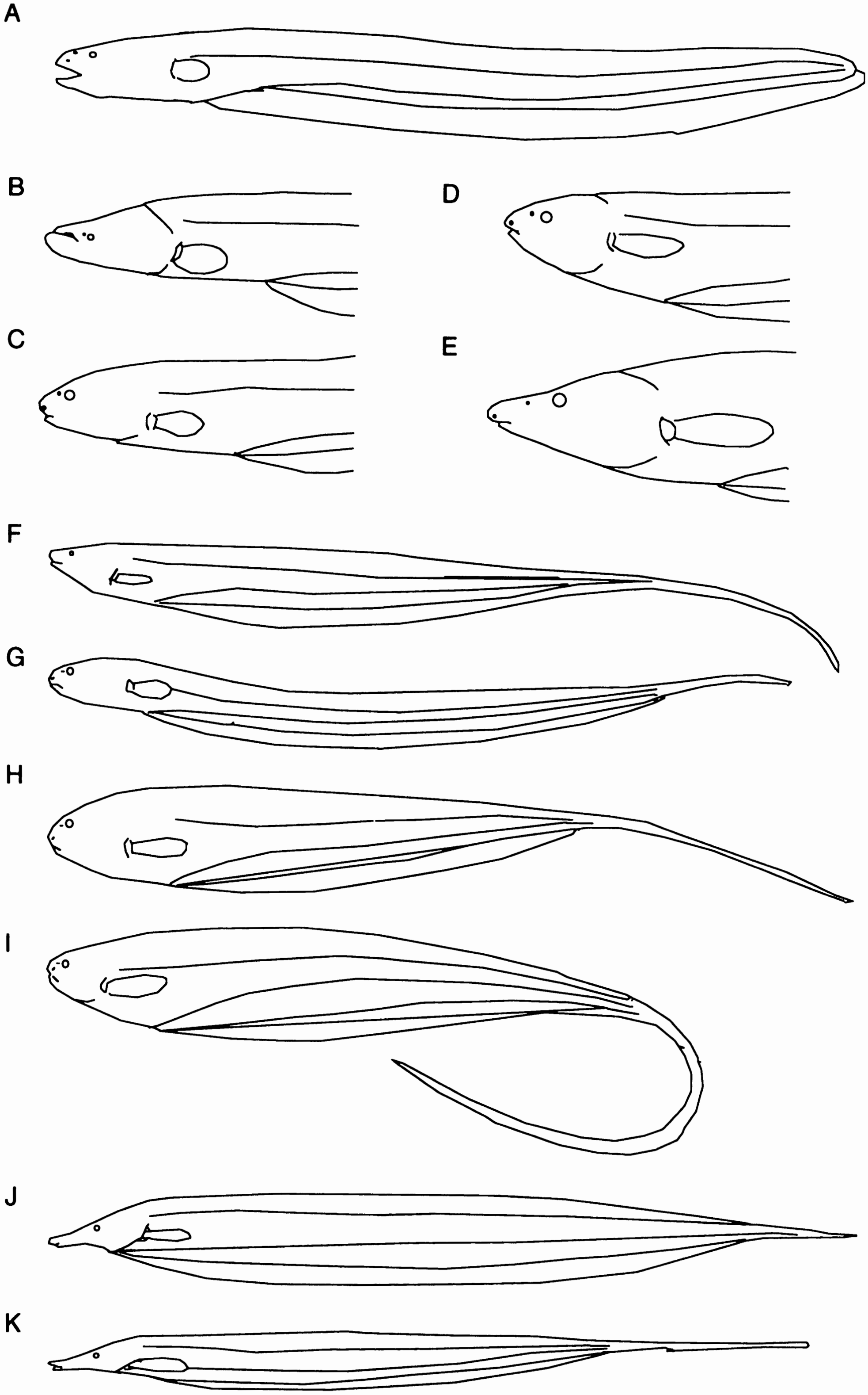


Fig. 50A. Line-drawings of specimens representing 27 gymnotiform genera in profile, illustrating some important features used in the identification key. Drawings not to scale. A. *Electrophorus electricus.* B. *Gymnotus mamiraua.* C. *Microsternarchus bilineatus* (head). D. *Brachyhypopomus occidentalis.* E. *Hypopomus artedi.* F. *Microsternarchus bilineatus* (body). G. *Racenisia fimbriipinna.* H. *Hypopygus lepturus.* I. *Steatogenys elegans.* J. *Rhamphichthys marmoratus.* K. *Gymnorhamphichthys rondoni.*

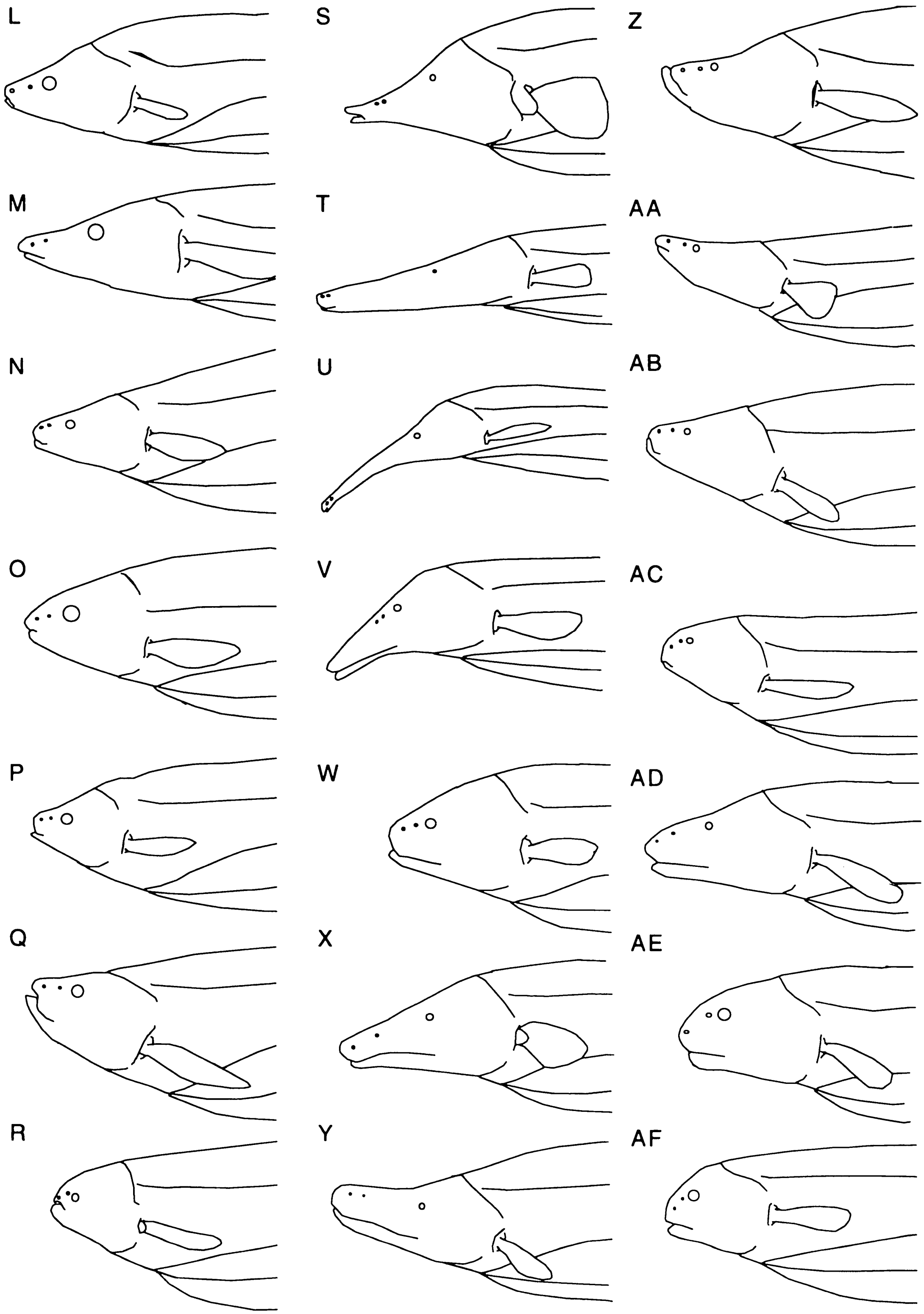


Fig. 50B. Line-drawings of specimens representing 27 gymnotiform genera in profile, illustrating some important features used in the identification key. Drawings not to scale. L. *Sternopygus xingu.* M. *Archolaemus blax.* N. *Distocyclus conirostris.* O. *Eigenmannia humboldtii* (200 mm). P. *Eigenmannia humboldii* (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.*

even brown chromatophore speckling. Range: all regions .... *Brachyhypopomus* (Figs. 50-C & D)

8b. Snout slender, longer than deep. Scales absent from anterior dorsal midline; other scales above lateral line large, 3 - 4 to dorsal midline. Body cylindrical, its depth less than 11% total length. Body cavity length not short, 13 - 23 PCV. No humeral accessory electric organ. Tail length less than 45% total length. EOD with 2 phases. Small adult body sizes (to 120 mm total length). Color consists of even and dense brown pigment distribution; no bands or saddles 9

8c. Snout deeper than long. Scales present on anterior dorsal midline; scales small, 4 or more to dorsal midline. Body compressed laterally. Body cavity short, 9 - 10 PCV. Humeral accessory electric organ present. Tail long, more than 45% total length. EOD with 4 phases. Small to moderate adult body sizes (60 - 325 mm). Color consists of saddles over dorsum and irregular oblique bands. 10

9a. Recurrent branch of posterior lateral line nerve superficial and pigmented, visible as parallel brown lines on dorsal surface. Gill rakers absent. Body slightly deeper than wide, not strongly attenuated caudally. Body cavity with 12 - 15 PCV. Tail posterior to anal-fin longer than 16% total length. Color variable pigment intensity from light to medium brown, with brown spots of variable intensity, sometimes pale or absent. Range: Amazon, Guyanas, Orinoco .... *Microsternarchus* (Fig. 50-F)

9b. Recurrent branch of posterior lateral line not visible on dorsal surface. Gill rakers present. Body cylindrical, as deep as wide, girth strongly attenuated caudally. Body cavity long, with 20 - 23 PCV. Tail posterior to anal-fin short, less than 16% total length. Color uniform dark brown; no spots. Range: Guyanas. .... *Racenisia* (Fig. 50-G)

10a. Snout short, less than one third head length. Anal fin moderate length, 140 - 200 rays. Mental accessory electric organ present. Moderate adult body size (130 - 325 mm). Range: Amazon, Guyanas, Orinoco, Magdalena .... *Steatogenys* (Fig. 50-I)

10b. Snout about one third head length. Anal fin short, 110 - 140 rays. Mental accessory electric organ absent. Small adult body sizes (60 - 90 mm). Range: Amazon, Guyanas, Orinoco .... *Hypopygus* (Fig. 50-H)

11a. Orbital margin free, eye not covered by skin, eye surrounded by groove. Body cavity not short, more than 12 precaudal vertebrae. Color brown or gray ground color composed of dense speckling of fine dark chromatophores. 12

11b. Orbital margin covered by skin continuous with skin of head. Body cavity short, less than 12 precaudal vertebrae. Color white, yellow, or translucent in life, creamy-white to tan in ethanol; dark pigments scarce or absent on lateral surfaces[8] 13

12a. Snout length moderate, about one third head length. Nasal capsule not closer to tip of snout than to eye. Body cavity very long, with 23 - 30 precaudal vertebrae. All anal-fin rays unbranched. EOD lower than 60 Hz in adult males. Color brown or gray, usually with large black humeral spot[9] and a pale yellow or white thin longitudinal stripe along the base of the anal-fin pterygiophores and lateral midline posteriorly; no broad yellow longitudinal band. Range: all regions .... *Sternopygus* (Fig. 50-L)

12b. Snout long, more than one third head length. Nasal capsule closer to tip of snout than to eye. Body cavity length moderate, with 14 - 15 precaudal vertebrae. Anal-fin rays mostly branched. EOD higher than 60 Hz. Color Dark brown ground color over epaxial muscles and anal-fin pterygiophores; broad yellow longitudinal band overlaying hypaxial muscles; anal fin yellow. No dark humeral spot or thin white longitudinal stripe. Range: Amazon, Guyanas . ... *Archolaemus* (Fig. 50-M)

13a. Snout conical, of moderate length, about one third head length. Small nasal capsules, nares placed close together. Anal fin long, with more than 220 rays. Electric organ not visible over anal-fin pterygiophores caudally. Range: Amazon, Guyanas, Orinoco, Maracaibo .... *Distocyclus* (Fig. 50-N)

13b. Snout blunt, short, less than one third head length. Moderate size nasal capsules, nares not close together. Anal-fin length moderate, less than 220 rays. Electric organ visible as translucent brick-like array over anal-fin pterygiophores caudally 14

14a. Scales present on anterior mid-dorsum. Branchial opening small, less than length of snout. Gill rakers not attached to gill arches. Electrocytes small, square in profile. Range: all regions except Pacific slope of South America .... *Eigenmannia* (Figs. 50-O & P)

14b. No scales on anterior mid-dorsum. Branchial opening large, more than length of snout. Gill rakers firmly attached to gill arches. Electrocytes large, rectangular, longer than deep. Range: Amazon, Guyanas, Orinoco .... *Rhabdolichops* (Fig. 50-Q)

15a. Snout elongate, longer than postorbital region of head. Snout tubular, about as deep as wide at tip. Small scales above lateral line, 11 or more scales to dorsal midline at midbody. Anal fin origin at branchial isthmus 16

15b. Snout short, about the same length as postorbital region[10]. Snout not tubular, deeper than wide at anterior nares[11]. Scales above lateral line moderate to large size, less than 11 scales to dorsal midline at midbody. Anal fin origin ventral to pectoral fin 19

16a. Scales present on nape. Anterior portion of frontal straight or convex in lateral profile. Eyeball small, extrinsic eyeball muscles present. Dorsal organ extending from midbody to caudal peduncle. Almost all anal-fin rays branched. Tail short, less than 16% total length. Biphasic EOD 17

16b. No scales on nape. Anterior portion of frontal concave in lateral profile. Eyeball minute, no extrinsic eyeball muscles. Dorsal organ extending from nape to caudal peduncle. Numerous (30 - 60) anterior unbranched anal-fin rays. Tail longer than 16% total length. Monophasic EOD 18

17a. Snout decurved anterior to nasal capsule. Head slender, conical, depth at eye less than three times depth at snout tip. Nasal capsule not located at tip, separated by more than one of its own diameters. Pectoral fin broad. Six or fewer caudal-fin rays. Color yellow-white ground color in life with a dark pigments along dorsum, and black pectoral and anal-fin margins; pale yellow or tan in ethanol. Range: Amazon, Guyanas, Orinoco .... *Sternarchorhamphus* (Fig. 50-S)

17b. Snout straight anterior to nasal capsule. Head deep, tapering, depth at eye more than three times depth at snout tip. Nasal capsule at tip of snout. Pectoral fin narrow. Seven or more caudal-fin rays. Color no pigments; translucent pink in life, pale yellow or tan in ethanol. Range: Amazon .... *Orthosternarchus* (Fig. 50-T)

18a. Snout elongate, gracile, tubular, and recurved. Gape short, much less than one third head length. Anal fin with less than 200 rays. Caudal peduncle slender. Color uniform dark ground color, sometimes with white middorsal stripe; no broad lateral band or blotches. Range: Amazon, Guyanas, Orinoco, Paraná .... *Sternarchorhynchus* (Fig. 50-U)

18b. Snout not elongate, about as long as postorbital distance. Gape large, more than one third head length. Anal fin with more than 200 rays. Caudal peduncle deep. Color broad longitudinal lateral band ventral to lateral line, large irregular dark brown or black blotches. Range: Amazon, Guyanas, Orinoco .... *Platyurosternarchus* (Fig. 50-V)

19a. Mouth V-shaped viewed face on, upper jaw narrow, beak-like, inserting in groove formed by mandible. No oral teeth. Chin bulbous. Color black and bright yellow chromatophore speckling in life; back and pale yellow or white in ethanol. Range: Amazon, Orinoco .... *Adontosternarchus* (Fig. 50-R)

19b. Mouth arched viewed face on, upper jaw broad, with a straight or evenly curved margin, not beak-like. Teeth present on dentary. Chin not bulbous[12]. Color variable; no black and yellow speckling 20

20a. Scales present on nape. Small circular scales at midbody, more than 5 scales from lateral line to dorsal midline. Snout square, upper lip sharply angled. Margin of upper lip fleshy. Snout elongate in mature males (greater than 250 mm), longer than postorbital length. Snout angled up in mature males, nares above horizontal with eye. Anal-fin pterygiophores short, more than 1.5 times into depth of epaxial musculature. Color even brown composed of dense speckling of fine dark chromatophores. Range: Amazon . ... *Parapteronotus* (Fig. 50-Y)

20b. Scales present on nape. Small circular scales at midbody, more than 5 scales from lateral line to dorsal midline. Snout square or rounded, upper lip angled. Margin of upper lip fleshy. Snout length variable, snout not longer than postorbital length. When elongate, snout angled down, nares at or below horizontal with eye. Anal-fin pterygiophores short, more than 1.5 times into depth of epaxial musculature[13]. Color high contrast pigments; dark brown or black ground color, with either white middorsal stripe and/or patches on chin and caudal peduncle, and/or white mottling over whole body surface; no speckling of fine dark chromatophores; not white, yellow, or translucent. Range: all regions .... *Apteronotus* (Figs. 50-W & X)

20c. No scales on nape. Large rhomboid scales at midbody, 5 or fewer scales from lateral line to dorsal midline. Snout pointed or rounded, upper lip straight or curved. Margin of upper lip thin[12]. Snout length variable, preorbital region not longer than postorbital region[14]. Snout straight or down, nares at or blow horizontal with eye. Anal-fin pterygiophores long, less than 1.5 times into depth of epaxial musculature. Color variable; white, pink, or translucent in life, creamy-white to tan in ethanol; dark pigments scarce or absent on lateral surfaces; no speckling of fine dark chromatophores; no high contrast pigments 21

21a. Snout long, preorbital region more than one third head length in mature specimens. Nasal capsule positioned anteriorly, closer to tip of snout than to eye. Supratemporal canal angled sharply, forming an inverted L-shape. Color narrow pale stripe anterior to eyes and lateral to nares. Range: Amazon, Orinoco .... *Compsaraia.* (Fig. 50-AD)

21b. Snout short to moderate length, not more than one third head length. Nasal capsule near eye, not closer to tip of snout than to eye. Supratemporal canal straight or curved, not L-shaped. Color no pale stripe anterior to eyes....... 22

22a. Gape large, rictus to eye. Jaws thin, with few teeth........ 23

22b. Gape moderate to small, rictus not posterior to nares. Jaws robust, with many teeth 24

23a. Snout moderate length, not less than one third head length. Mouth position either strongly superior or inferior, with upper or lower jaw prognathic. Gape moderate, rictus to posterior nares or eye. Gill rakers not attached to gill arches. Gill rakers ossified to tips. No scales on dorsal midline of anterior half of body. Range: Amazon .... *Magosternarchus* (Fig. 50-Z & AA)

23b. Snout short, preorbital region less than one third head length. Mouth position either terminal or subterminal, neither jaw prognathic. Gape small, rictus to anterior nares. Gill rakers firmly attached to gill arches. Gill raker tips not ossified, covered with cartilage caps. Scales present on dorsal midline of anterior half of body. Range: Amazon, Orinoco, Paraná .... *Sternarchella* (Fig. 50-AB & AC)

24a. Snout moderate length, not less than one third head length. Head rounded, snout deeper than long. No scales on dorsal midline of anterior half of body. Range: Amazon, Guyanas, Orinoco .... *Porotergus* (Fig. 50-AE)

24b. Snout short, preorbital region less than one third head length. Snout blunt, forehead straight in profile above eyes. Scales present on dorsal midline of anterior half of body. Range: Amazon, Orinoco .... *Sternarchogiton* (Fig. 50-AF)

Footnotes to Key: [1]Reproductively mature specimens greater than about 140 mm total length, except *Gymnotus anguillaris, Gymnotus* sp. B, *Brachyhypopomus* sp. R, *Hypopygus, Microsternarchus,* and *Racenisia.* [2]Except *Gymnotus bahianus, G. cylindricus, G. maculosus,* and *G. pantherinus.* [3]Except some species of *Rhabdolichops, Magosternarchus,* and *Sternarchella.* [4]Rhamphichthyidae. [5]Except *Rhabdolichops eastwardi.* [6]Several small premaxillary teeth present in two *Brachyhypopomus* species. Adult *Adontosternarchus* and *Sternarchogiton nattereri* without oral teeth. [7A]Except *Steatogenys* and *Hypopygus.* [7B]Caudal filament long in *Rhamphichthys rostratus and R. apurensis.* [7C]Gas bladder thin in *Rhamphichthys hahni.* [8]Except *Distocyclus goajira.* [9]No humeral spot in *Sternopygus aequilabiatus* or *S. astrabes.* [10]Except breeding males of *Parapteronotus* and *Compsaraia* sp. 1. [11]Except largest specimens of *Apteronotus magdalenensis.* [12]Except breeding *Porotergus gimbeli.* [13]Except some *Apteronotus leptorhynchus.* [14]Except *Compsaraia* sp. 1.

SUMMARY

Evolutionary relationships of the gymnotiform knifefishes are documented from a study of phenotypic diversity. More than 4200 knifefish specimens representing 105 described and 32 undescribed species were examined. Observations of neural tissues were made for 31 knifefish species, including representatives of 20 recognized genera. Data were compiled into a matrix of 249 characters, including 39 characters of the central nervous system, coded for 44 operational taxonomic units. Phylogenetic diagnoses for 75 gymnotiform clades and terminal taxa are provided, including 29 genera and five families. Eighteen supraspecific taxa are introduced, including two new apteronotid genera; *Parapteronotus* and *Compsaraia.* Two previously named monotypic gymnotiform genera, *Ubidia* and *Megadontognathus* are regarded as junior synonyms of *Apteronotus s.s. Gymnotus* and *Electrophorus* are determined to form a natural taxon, the Gymnotidae, which is the sister lineage to all other gymnotiforms, referred to as Sternopygoidei. The monophyly of Rhamphichthyoidea (Rhamphichthyidae + Hypopomidae) is supported, as is the monophyly of the tone-type EOD electric knifefishes (Sternopygidae and Apteronotidae), referred to as Sinusoidea. Within the Apteronotidae two monophyletic subfamilies are recognized: Sternarchorhynchinae, composed exclusively of forms with elongate snouts, and Apteronotinae, composed mainly of forms with short snouts, but also with at least two clades in which long snouts have evolved.

The patterns of relationships recovered permit several conclusions regarding the evolution of gymnotiform morphology. The "knife-shaped" or culteriform body of gymnotiforms is functionally associated with active electroreception, but among teleosts only two of the five groups which have independently acquired electrogeneration are culteriform. Nonetheless, all seven independent origins of culteriform body shapes are known to occur within electroreceptive clades. That is, culteriform morphologies are only observed in groups with passive electroreception. The general body shape of plesiomorphic gymnotiforms is determined to resemble the sternopygid *Sternopygus astrabes* in several regards. The body is moderately compressed, the coelomic cavity contains 18 to 20 vertebrae, the snout (preorbital) length is about one third the total length of the head in mature specimens, and the oral jaws, neurocranium, suspensorium, splanchnocranium, and pectoral girdle are both well ossified and moderately robust. These features are retained in many gymnotiform species in association with a generalized omnivorous diet.

A series of displaced hemal spines are present at the posterior margin of the body cavity in all members of the Sternopygoidea. The diversity in the position and morphology of these elements may result from decreased canalization in the development of serially repeated structures of the sclerotome. These observations suggest there has been a change in the mechanisms underlying patterning in the sclerotome of gymnotiforms, resulting in transformations resembling homeosis. Although gymnotiform species with larger bodies have more anal-fin rays, individual knifefishes possess the same number of anal-fin rays throughout their life. These differential patterns within and between species highlight instances of selection based on functional criteria.

All extant gymnotiform taxa possess derived characters of the electric organs. In terms of gross morphology the electric organ of the Middle American species of *Gymnotus* retains a relatively plesiomorphic suite of characters. The larval hypaxial electric organ is retained into the adult state in gymnotids and rhamphichthyoids, and the larval electric organ of sinusoids degenerates at metamorphosis. The larval electric organ of sinusoids is replaced by an adult organ derived from anal-fin pterygiophore-muscles in sternopygids, and from the spinal electromotor neurons which innervate the larval electric organ in apteronotids. Sinusoids also possess a continuous EOD in which the pulses form a quasi-sinusoidal tone-type discharge. A neural correlate of this behavior has been found in the morphology of relay and pacemaker cells in the pacemaker nucleus.

Apteronotidae and Eigenmannini possess several derived characters associated with life in large Amazonian rivers. In derived members of these taxa the mouth is terminal, the body is relatively short, stout, lateral compressed, and translucent, lateral midbody scales are large, anterior and dorsal squamation is reduced, and the extent of endoskeletal ossification is also reduced. Mechanisms to reduce ossification include a general paedomorphosis of the cranial region, and a specialized remodeling of bone to produce reticulated endo- and dermatoskeletal elements. Specializations in the telencephalon and medulla of the brain in apteronotids are congruent with the derived condition of habitat utilization, and may participate in the construction of behaviors related to the utilization of deep rivers channels.

Elongate snout morphologies are inferred to have evolved independently within at least three apteronotid lineages, each involving different sets of bones. The caudal fin of apteronotids is inferred to be a specialized feature, not an intermediate state in the loss of a caudal fin. The cartilaginous hypural plate of apteronotids is inferrred to be homologous with the caudal rod of other gymnotiforms. The caudal fin of apteronotids is inferred to develop by combining the specialized axial regeneration system of gymnotiforms with normal osteichthyan caudal-fin morphogenesis.

The actual number of gymnotiform species in the wild is much greater than has previously been recognized. There are currently 112 valid species of gymnotiforms in the literature and about 32 additional undescribed species recognized in museum collections. These species are distributed throughout the humid Neotropics, from the Rio Salado of Buenos Aires state, Argentina, to the Rio San Nicolás of Chiapas state, Mexico. Gymnotiform species diversity is greatest in the Amazon region with 89 species constituting 62% of the total gymnotiform fauna. It is followed by the Orinoco region with 61 species, the Guyanas region with 35 species, the Paraná region with 26 species, the Northwestern region of South America with 14 species, the Southeast region of Brazil and Uruguay with 12 species, the Northeast region of Brazil with 9 species, the Pacific slope region of South America with 7 species, and the Middle American region also with 7 species. *Gymnotus* is the most widely distributed gymnotiform genus, inhabiting all regions defined in this analysis and almost the entire range of all other groups combined. *Apteronotus s.s.*, *Brachyhypopomus*, and *Sternopygus* are also recorded from all regions defined. The presence of *Distocyclus* in the Maracaibo, *Steatogenys* in the Magdalena, and *Eigenmannia* in the Rio Tuyra indicates that there are at least seven trans-Andean gymnotiform clades.

Gymnotiformes are inferred to have originated in the Upper Cretaceous, approximately at the time of separation of South America and Africa and the origin of the Neotropical biota. The Upper Miocene fossil gymnotiform *†Ellisella*, with an elongate anal-fin and reduced distal anal-fin pterygiophores, establishes a minimum age for the origin of the specialized culteriform locomotion. Gymnotiforms are inferred to have originated in small rainforest rivers and/or upland streams, and to have diversified into other habitats. Derived gymnotiform habitats include the large and deep rivers of the Amazon and Orinoco basins, *várzea* floating meadows, flood-plain lakes, confluence and coastal estuaries, cataracts of Andean and Guyanan escarpments, and upland ponds and streams of seasonally dry savannas and coastal regions.

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Appendix 1. List of materials examined. Data are arranged by country, then alphabetically by museum acronym and number. Museum number is followed in parentheses by number of specimens, and then by locality, size (range) in millimeters total length, and date of capture (data presented when available). HT and PT indicate holotype and paratypes respectively. Species assigned to genera in quotations do not conform to the generic diagnosis of this report. Abbreviations for some field numbers of uncatelogued lots: JSA, James S. Albert; JAG, Jose Alves-Gomes; WGRC, William G.R. Crampton; CCF, Cristina Cox-Fernandes; JGL, John G. Lundberg.

APTERONOTIDAE

Adontosternarchus balaenops.—**Bolivia**: UMMZ 204705 (4), mouth of Rio Baures at Rio Itenez, Rio Mamore, near Costa Marquez, Beni, 1964.IX.29. **Brazil**: MBUCV 13219 (1), Lago Camaleo on Ilha Marchanteria, 25 km SE Manaus, Rio Solimões, 169 mm. UMMZ uncat. JSA (1), Rio Solimões, Amazonas, 175 mm, 1993.IX.

Adontosternarchus clarkae.—**Venezuela**: MBUCV 12703 (HT 1), Raudal de Mavahate, near San Carlos de Rio Negro, Amazonas, Rio Negro, 172 mm, 1981.V.6. MBUCV 11218 (PT, 2), collected with HT, 159 - 172 mm.

Adontosternarchus devenanzii.—**Venezuela**: FMNH 100731 (1), Caño Socopo, Rio Suripa, Barinas, Apuré, 120 mm, 1991.I.12. FMNH 100741 (42), Rio Suripa near mouth of Rio Anero, Apuré, 1991.I.14. UMMZ uncat. JSA A&R94-1 (3), mouth of Rio Guaviare, Alta Orinoco, Amazonas, 1994.I.2. UMMZ uncat. JSA A&R94-2 (4), same collection data as UMMZ uncat. JSA A&R94-1. UMMZ uncat. JSA A&R94-3 (37), same collection data as UMMZ uncat. JSA A&R94-1. UMMZ uncat. JSA A&R94-5 (4), same collection data as UMMZ uncat. JSA A&R94-1. UMMZ uncat. JSA A&R94-6 (6), mouth of Upper Orinoco, Alta Orinoco, 1993.XII.28.

Adontosternarchus sachsi.—**Venezuela**: FMNH 100742 (9), Rio Suripa, Rio Anero, Apuré, 110 - 138 mm, 1991.I.14. UMMZ uncat. JSA (3), mouth of Rio Guaviare, Alta Orinoco, 1994.I.2. UMMZ uncat. JSA (1), mouth of Upper Orinoco, Alta Orinoco, 1993.XII.28. UMMZ uncat. JSA A&R94-7 (1), San Fernando de Atabapo, Rio Atabapo, Alta Orinoco, Amazonas, 1993.XII.25.

Adontosternarchus sp. A.—**Brazil**: MZUSP uncat. CCF 96-102 (2), Rio Solimões, Amazonas, 150 mm, 1996.

Apteronotus albifrons.—**Brazil**: FMNH 54757 (1), Rio Tocantins, Pará, 1910.I.22. FURG 730010 (2), Banhados do rio Camaqua, Rio Grande do Sul, 1973. MCP 15736 (2) Rio Paraguai em Caceres e arredores, Mato Grosso, 1991.VIII.11. MZUSP 43273 (2), Rio Itacaiunas, Caldeirao, igarape do Pojuca, Para, 19083.X.15. MZUSP 27700 (1) Rio Taquari, Mato Grosso do Sul, 1978.III.11. **Colombia**: UMMZ 179239 (2), Rio Meta, Meta, 109 - 270 mm, 1936. **Ecuador**: MNH 100614 (1), 10 km N. Marian, 1 km N. Rio Cuyabeno, Rio Napo, 245 mm, 1981.XI.30. **Guyana**: CAS 72121 (1), Potaro Landing, Essequibo River. CAS 72122 (3), Potaro Landing, Essequibo River. FMNH 53292 (2), Potaro Landing, Essequibo River. UMMZ uncat. JSA (6), 70 - 190 mm, 1990.V.1. **Paraguay**: UMMZ 207459, (5), side channel and bay, Rio Paraná, 90 - 225 mm, 1979.VIII.26. **Peru**: FMNH 97013, (2), Station Maria de Nieva near confluence with Marañon, Loreto, 1980.IV.16. UMMZ 187218, (1), Rio Curanja, Loreto, 180 mm, 1966.VII. **Venezuela**: FMNH 85490 (2), Rio Aruaca, 32.5 km S Biruaca, Apuré, 1975.I.07. FMNH 100729 (10), Caño Socopo, Rio Suripa, Barinas, 1991.I.12. MBUCV 10875 (1), Guarico, Rio Orituco, 400 mm. MBUCV 15703 (1), Rio Guarico, Guarico, 120 mm. USNM 260256 (1), Rio Caracol at bridge, Rio Guarico, 106 mm, 1983.I.19.

"Apteronotus" apurensis.—**Venezuela**: FMNH 85499 (32), Rio Aruaca, 32.5 km S Biruaca, Rio Apuré, Apuré, 38 - 188 mm, 1975.I.07. FMNH 100738 (6), Rio Suripa, Rio Anero, Rio Apuré, Barinas, 146 - 308 mm, 1991.I.14. FMNH 100739 (1), Rio Suripa, Rio Anero, Rio Apuré, 1991.I.14. UMMZ 211318 (1), nautical mile 180, Rio Orinoco, Delta Amacuro, 137 mm, 1979.XI.23. USNM 228869 (2), Isla Tres Caños, shallow river, Rio Orinoco, Delta Amacuro, 1979.XI.14.

"Apteronotus" cf. apurensis.—**Colombia**: FMNH 56778 (3), Cali, Rio Cauca, Rio Magdelena, 95 - 115 mm, 1912.III.01.

"Apteronotus" cf. bonapartii.—**Brazil**: FMNH 54564 (1), Santarem, Rio Amazonas, 113 mm, 1910. MZUSP 49827 (1), Rio Acre, Colocaçao, Boa Unitão, 270 mm, 1994.IX. UMMZ uncat. JSA (5), Rio Amazonas, 1 mm, 1994.IX. **Ecuador**: FMNH 100613 (1), Rio Anzu, near el Capricho, Rio Napo, 13 mm, 1981.XI.15. **Paraguay**: UMMZ 207460 (9), side channel and bay, Rio Paraná, 80 - 125 mm, 1979.VIII.26. **Peru**: CAS 52834 (1), Rio Amazonas, 100 mm.

Apteronotus brasiliensis.—**Brazil**: CAS 31249 (10), Piracicaba, São Paulo, no date. FMNH 54561 (2), Pirapora, 250 - 290 mm, 1907.XII.15. MZUSP 22513 (2), Rio Paraná, frente a Jupiá, 15-23.IX.1962. MZUSP 24460 (9), Ilha Solteira, Rio Paraná, 25-28.V.1972. MZUSP 39605 (2), Rio Abaeté, Malhada, faz. Macaúba, Major Porto, Minas Gerais, 17.III.1988. MZUSP 39659 (1), cachoeira do Abaeté, Rio Abaeté, Malhada, Minas Gerais, VIII.1988. MZUSP 39955 (1), represa de Água Vermelha, Rio Grande, 27.VI.1978. USNM 44968 (1), Rio das Velhas.

Apteronotus cf. brasiliensis.—**Paraguay**: UMMZ 207460 (9), side channel and bay of Rio Paraná, ca. 2 km E of Ayolas, 80 - 125 mm, 1979.VIII.26.

Apteronotus cuchillejo.—**Venezuela**: CAS 51069 (PT, 1), Rio Orinoco, Delta Amacuro. UMMZ 157672 (PT, 2), Rio Machaugo, 20 km S Lagunillas, Zulia, 120 - 156 mm, 1942.III.21. USNM 121598 (PT, 7), Rio Yasa, Rio Negro, Zulia, 60 - 147 mm, 1942.III.02. USNM 121599 (PT, 39), Rio Motatan, Zulia, 92 - 189 mm, 1943.IX.13. USNM 121600 (HT, 1), same collection locality as USNM 121599, 168 mm, 1942.III.24. USNM 121601 (PT, 5), same collection locality as USNM 121599, 148 - 177 mm, 1942.III.24. USNM 121602 (10), Rio San Pedro, Rio Motatan, Zulia, 80 - 115 mm, 1942.III.20.

Apteronotus cuchillo.—**Venezuela**: UMMZ 157673 (PT, 3), Rio Palmar 70 km SW Maracaibo, Zulia, 215 - 375 mm, 1942.III.06. USNM 121587 (PT, 13), Rio Socuy, Zulia, 156 - 385 mm, 1942.II.24. USNM 121588 (3), Rio Palmar, 70 km southwest of Maracaibo, Zulia, 215 - 375 mm, 1942.III.06. USNM 121589 (11), Rio Motatan at bridge, 22 km north of Motatan, Zulia, 164 - 390 mm, 1942.III.17. USNM 121590 (7), Rio Apon, 35 km south of Rosario, Zulia, 132 - 194 mm, 1942.II.24. USNM 121591 (HT, 1), Rio Socuy, 3 km from mouth, Zulia, 352 mm, 1942.II.24.

Apteronotus cf. cuchillo.—**Colombia**: NRM 27739 (2), Boca de Pepé, Rio Baudo, Choco, 260 - 280 mm, 1989.II.22.

Apteronotus cuyuniense.—**Venezuela**: MBUCV 09499 (HT, 1), Rio Cuyuní, Rio Caroní, Bolivar, 57 mm, 1977.I.25. MBUCV 17940 (PT, 1), Raudles de Atures, Puerto Ayacucho, Rio Orinoco, Amazonas, 238 mm, 1985.XI.11. FMNH 93459 (2), Rio Cuyuní, Rio Caroní, Bolivar, 223 - 289 mm, 1973. FMNH 96219 (2), Rio

Caroní Bolivar, 1973.

Apteronotus ellisi.—**Brazil**: MZUSP 23095 (24, 1 C&S), Rio Paraná, Ilha Solteira, IX.1965. MZUSP 24462 (23), Rio Paraná, Ilha Solteira, 25-28.V.1972. MZUSP 25672 (1), Rio Taquari, Coxim, Mato Grosso, X.1981. MZUSP 45080 (1), Rio Taquari, Coxim, Mato Grosso, XII.1967. **Paraguay**: UMMZ 207460 (9, 1 C&S), side channel and bay of Rio Paraná, *ca.* 2 km E Ayolas, Rio de La Plata, Misiones, 26.VIII.1979.

Apteronotus leptorhynchus.—**Aquarium**: UMMZ 190905 (215 mm), UMMZ uncat. JSA (9) 90 - 135 mm, 1992.VI.3. UMMZ uncat. JSA (6), 88 - 140 mm, 1992.VII.6. **Colombia**: FMNH 92638 (8), Caño Negro on road to Puerto Porfia, E Villavicencio, Rio Meta, 1974.III.27. UMMZ 145761 (5), Villavicencio, Rio Meta, 127 - 226 mm, 1935. **Guyana**: FMNH 53294 (HT, 1), Amatuk, Essequibo River, 269 mm, 1908. FMNH 53295 (PT, 1), Warraputa, Essequibo River, 1908. **Panamá**: FMNH 7592 (HT, 1), Rio Grande, Cana, Rio Tuyra, 114 mm, 1912.III.03. **Venezuela**: FMNH 77039 (1), Rio Caroni, 1973. FMNH 77040 (1), Rio Caroni, 1973. USNM 121592 (1), Rio San Juan, 12 km south of Rosario, Zulia, 57 mm, 1942.II.26. USNM 121593 (3), Rio San Juan, near Mene Grande, Rio Motatan, Zulia, 94 - 151 mm, 1942.III.20. USNM 121594 (1), Rio Negro, near mouth of Rio Yasa, Zulia, 43 mm, 1942.III.2. USNM 121595 (10), Rio San Juan, Rio Motatan, Zulia, 103 - 178 mm, 1942.III.17.

"Apteronotus" macrolepis.—**Colombia**: FMNH 85356 (15), Rio Amazonas near Leticia, Rio Amazonas, 85 - 180 mm, 1973.XI.13. FMNH 96040 (58), Rio Amazonas near Leticia, Rio Amazonas, 92 - 163 mm, 1973.XI.11.

Apteronotus macrostomus.—**Ecuador**: FMNH 100612 (1), Mouth of Rio Tiputuni, Rio Napo, 125 mm, 1981.X.28. FMNH 100615 (1), Rio Jivino, Rio Napo, 1981.X.08. FMNH 100618 (1), Rio Tiputuni mouth, Rio Napo, 111 mm, 1981.X.28. **Venezuela**: FMNH 100728 (1), Caño Socopo, Rio Suripa, Rio Apuré, Barinas, 88 mm, 1991.I.12.

Apteronotus cf. macrostomus.—**Venezuela**: FMNH 84596 (2), Rio Caroni, Bolivar, 210 - 268 mm, 1973. FMNH 100724 (6), Caño La Indiaolta, near mouth of Rio Suripa, Rio Apuré, 50 - 86 mm, 1991.I.11.

Apteronotus magdalenensis.—**Colombia**: USNM 39749 (PT, 1), Honda, Tolima, Rio Magdalena, 280 mm, 1945.IX.

Apteronotus mariae.—**Colombia**: FMNH 56774 (HT, 1), Girardot, Rio Magdelena, 204 mm, 1912.II.01. FMNH 56775 (2), Girardot, Rio Magdelena, 1912.II.01.

Apteronotus marauna.—**Brazil:** MZUSP 48510 (1, HT), Ilha Solteira, Rio Paraná, Mato Grosso do Sul, 194 mm, 1965.IX. MZUSP 23090 (2, PT), collected with HT, 188 - 196 mm.

Apteronotus cf. spurrelii.—**Colombia**: NRM 25707 (1), La Guayacana, Rio Güiza, Rio Mira, Nariño, 270 mm, 1947.V.

Apteronotus sp. (unidentified).—**Ecuador**: FMNH 100617 (1), Rio Arajuno, Rio Napo, 23 mm, 1981.XI.08. **Colombia**: FMNH 92715 (1), Camp Alegre, Caño Aguascolarae, E. Villavicencio, Rio Meta, 1974.III.27.

Apteronotus sp. S.—**Brazil**: MZUSP 2646 (1), Rio Mogi-Guaçu, 1908.I. MZUSP 22944 (1), Rio Mogi-Guaçu, 1964.II. MZUSP 23094 (5), Ilha Solteira, Rio Paraná, 1965.IX. MZUSP 24463 (4), Ilha Solteira, Rio Paraná, 1972.V.25-28. MZUSP 43280 (2, C&S), Ilha Solteira, Rio Paraná, 1972.V.25-28. MZUSP 45685 (1), Ilha Solteira, Rio Paraná, Mato Grosso do Sul, 399 mm, 1965.IX.

Apteronotus sp. T.—Brazil: INPA uncat. JAG-91-1 (1), Rio Tacutu near Lethem, Rio Branco, Roraima, 140 mm, XII.1991.

Apteronotus rostratus.—**Colombia**: FMNH 56773 (1), creek near mouth of Calima, Rio Calima, 130 mm, 1913. FMNH 56773 (1), Calima, Rio Calima, 130 mm, 1913. FMNH 56775 (2), Girardot, Rio Magdalena, 193 - 218 mm, 1912.II.01. FMNH 56776 (1), Apulo, Rio Magdelena, 203 mm. FMNH 56776 (1), Apulo, Rio Magdalena, 203. FMNH 71201 (3), Pangola, 40 km N Palestine, Choco, Rio San Juan, 120 - 160 mm, 1972.I.12. **Panamá**: FMNH 7592 (HT, 1), Rio Grande, Darien, Rio Grande, 116 mm, 1912.III.03.

Compsaraia compsa.—**Brazil**: MZUSP uncat. AMZ 96-08 (2), Rio Solimões, Amazonas, 180 mm, 1996. UMMZ uncat. JSA (2), Rio Solimões, Amazonas, 145 - 312 mm, 1994.IX. **Ecuador**: FMNH 94417 (PT, 7), Rio Napo at mouth of Rio Tupitini, Rio Napo, 1981.X.28. FMNH 100619 (2), Rio Aguarico near mouth of Rio Lagartococha, Rio Napo, 112 - 135 mm, 1983.XI.02. **Venezuela**: FMNH 100736 (2), Playa in Rio Suripa, 15 km above pump station, Rio Apuré, Apuré, 1991.I.13. FMNH 100737 (5), Rio Suripa near mouth of Rio Anero, Rio Apuré, Apuré, 1991.I.14. MBUCV 10425 (PT, 2), Isla Iguana, Rio Orinoco, Delta Amacuro, 203 - 247 mm, 1978.II.18. MBUCV 11010 (HT, 1), Isla Iguana, Delta Amacura, Rio Orinoco, 339 mm, 1978.II.18. UMMZ 211308 (13), Playa Iguana, Punta Cabrian, Rio Orinoco, Delta Amacuro, 196 - 311 mm, 1978. UMMZ 211314 (5), near Curiapo, km 60, Rio Orinoco, Delta Amacuro, 149 - 189 mm, 1978.II.23. UMMZ uncat. JSA (5), mouth of Upper Orinoco, near San Fernando de Atabapo, Amazonas, 1993.XII.28. UMMZ uncat. JSA (5), mouth of Guaviare, Rio Orinoco near San Fernando de Atabapo, 1993.XII.25. UMMZ uncat. JSA (5), mouth of Rio Guaviare, Rio Orinoco near San Fernando de Atabapo, 1993.XII.25. UMMZ uncat. JSA (7), mouth of Rio Guaviare, mouth of Rio Guaviare, Rio Orinoco near San Fernando de Atabapo, 1993.XII.25. UMMZ uncat. JSA (18), San Fernando de Atabapo, Rio Atabapo, Amazonas, 1993.XII.25. UMMZ uncat. JSA (43), San Fernando de Atabapo, Rio Atabapo, Amazonas, 10 - 255 mm, 1993.XII.25.

Compsaraia sp. 1.—**Brazil**: MZUSP uncat., JGL-94, (2), Rio Ica, Amazonas state, 130 - 174 mm, 1994. INPA uncat. WGRC (1), Rio Solimões, Mamirauá Ecological Reserve, Amazonas state, 1999.I. INPA uncat. WGRC (1), WGRC (1), Rio Solimões, Mamirauá Ecological Reserve, Amazonas state, 1999.I.

Magosternarchus duccis.—**Brazil**: INPA 8533 (PT, 2), Paraná do Prato, Anavilhanas Archipelago, 14 m depth, Rio Negro, Amazonas, 130 - 226 mm, 1992.VI.10. MZUSP 48436 (HT), Rio Branco, 3-11 km upstream from confluence with Rio Negro, Roraima, 187 mm, 1993.X.08.

Magosternarchus raptor.—**Brazil**: INPA 8534 (PT, 2), Lago do Prato, Anavilhanas Archipelago, 9.5 m depth, Rio Negro, Amazonas, 130 - 150 mm, 1991.V.17. INPA 8535 (PT, 2), Lago do Prato, Anavilhanas Archipelago, 11 m depth, Rio Negro, Amazonas, 100 - 120 mm, 1991.V.16. MZUSP 48436 (HT), Rio Solimões, 17 km downstream from confluence with Rio Purus, Amazonas, 161 mm, 1993.IX.29.

Orthosternarchus tamandua.—**Brazil**: MZUSP uncat. AMZ 96-87 (1), Rio Solimões, Amazonas, 260 mm, 1996. MZUSP uncat. AMZ 96-87 (1), Rio Solimões, Amazonas, 145 mm, 1996. UMMZ uncat. JSA (1), 230 mm, 1993.IX. UMMZ uncat. JSA (1), Rio Solimões, Amazonas, 1993.IX.

Parapteronotus hasemani.—**Brazil**: CAS 62555 (PT, 1), Rio Amazonas, 170 mm. FMNH 15199 (PT, 1), Santarem, Rio

Amazonas, 176 mm. FMNH 15200 (PT, 1), Santarem, Rio Amazonas. FMNH 54562 (HT, 1), Santarem, Rio Amazonas, 177 mm, 1909.XII.15. FMNH 92070 (PT, 13), Santarem, Gran Para, between Belém and Salinas, mouth of Rio Caete, Rio Amazonas, 150 - 252 mm, 1909.XII.09. **Colombia**: FMNH 85362 (3), Amazon river near Leticia, Amazonas, 1973.XI.13. FMNH 96039 (5), Amazon river near Leticia, Amazonas, 1973.XI.11. MZUSP 23320 (1), Boca de Paraná do Catito, Rio Solimões below mouth Rio Jurua, 274 mm. 1968.X.4. MZUSP 24928 (4), Lago Janauacá, Amazonas, 154 - 185 mm, 1976.IX. MZUSP 32203 (1), Rio Madeira, Calama, 251 mm, 1981.II.11. MZUSP 44497 (5), Lago Janauacá, Amazonas, 224 - 381 mm, 1976.XII. **Peru**: CAS 15425 (2), Iquitos, Rio Amazonas, Loreto, 294 - 318 mm, 1922. CAS 15433 (1), Iquitos, Rio Amazonas, Loreto, 367 mm, 1922 ("*Apteronotus anas*" HT). CAS 15434 (1), Iquitos, Rio Amazonas, Loreto, 340 mm, 1922. NRM 27755 (2), market, Iquitos, 245 - 252 mm, 1984.VI.26.

Platyurosternarchus macrostomus.—**Bolivia**: UMMZ 204887 (1), Rio Baures, Rio Madeira, Beni, 233 mm, 1964.X.07. **Ecuador**: FMNH 100615 (1), Rio Jivino near Limoucocha, Rio Napo, 180 mm, 1981.VIII.8. **Venezuela**: FMNH 100721 (2), Caño La Indiaolta, near mouth of Rio Suripa, Rio Apuré, Apuré, 1991.I.11. FMNH 100730 (2), Caño Socopo, Rio Suripa, Rio Apuré, Barinas, 156 - 212 mm, 1991.I.12.

"Porotergus" gimbeli.—**Brazil**: FMNH 54327 (1), Santarem, Rio Amazonas. FMNH 54566 (HT, 1), Rio Tocantins, Pará, 1910.I. FMNH 54567 (PT, 2), Pará, Rio Tocantins, 170 - 240 mm, 1910.I.22. MZUSP uncat. JGL 94-1 (5), Rio Solimões, Amazonas, 140 - 190 mm, 1994:IX. MZUSP uncat. JGL 95.1 (5), Rio Solimões, Amazonas, 1993.IX. UMMZ uncat. JSA JGL 95.1 (6), Rio Solimões, Amazonas, 150 - 205 mm, 1993.IX. UMMZ uncat. JSA JGL 95.1 (2), Rio Solimões, Amazonas, 1993.IX.

Porotergus gymnotus.—**Guyana**: CAS 62305 (PT, 1), Potaro at Amatuk Essequibo River, 30 mm. CAS 31237 (2), Warraputa, Essequibo River, 1908. CAS 72234 (2), Potaro at Amatuk, Essequibo River, 1908.X.08. FMNH 53291 (PT, 1), Amatuk, Essequibo River, 61 mm, 1908. FMNH 53575 (HT, 1), Amatuk, Essequibo River, 60 mm, 1908.

"Porotergus" sp. 1.—**Brazil**: MZUSP uncat. JGL 94-1 (5), Rio Solimões, Amazonas, 140 - 190 mm, 1994:IX. MZUSP uncat. AMZ 96-87 (1), Rio Solimões, Amazonas, c. 200 mm, 1996.

"Porotergus" sp. 2.—**Brazil**: MZUSP uncat. AMZ 96-97 (1), Rio Solimões, Amazonas, c. 200 mm, 1996.

Sternarchella curvioperculata.—**Brazil**: MZUSP 22514 (2), Rio Paraná, frente à Jupiá, 15-23.IX.1962. MZUSP 23098 (7), Ilha Solteira, Rio Paraná, IX.1965. MZUSP 23099 (5), Ilha Solteira, Rio Paraná, IX.1965. MZUSP 24465 (16), Ilha Solteira, Rio Paraná, 25-28.V.1972. MZUSP 24466 (1), Ilha Solteira, Rio Paraná, 25-28.V.1972. MZUSP 39952 (1), represa de Água Vermelha, bacia do Rio Grande, 27.VI.1978. MZUSP 39952 (1), represa de Água Vermelha, Rio Grande, 27.VI.1978. MZUSP 39953 (2), represa de Água Vermelha, Rio Grande, 27.VI.1978. MZUSP 43279 (2, C&S), Ilha Solteira, Rio Paraná, 25-28.V.1972.

Sternarchella sp. S.—**Brazil**: MZUSP uncat. AMZ 93-03 (1), 160 mm, 1996. UMMZ uncat. JSA (2), Rio Solimões, Amazonas, 109 - 220 mm, 1993.IX.

Sternarchella orthos.—**Venezuela**: CAS 50801 (1), Rio Orinoco, 70 mm. CAS 52833 (1), Rio Orinoco, 300 mm. FMNH 100746 (11), Rio Suripa, near mouth of Rio Anero, Rio Apuré, Apuré, 1991.I.14. MBUCV 10429 (PT, 3), main channel, Kms. 152 - 153, Rio Orinoco, Delta Amacuro, 101-172, 1978.II.18. MBUCV 14173 (HT, 1), mouth of Rio Boquerones, east of San Fernando de Apuré, Rio Apuré, Apuré, 169 mm, 1978.II.19. MBUCV 14174 (PT, 5), mouth of Rio Boquerones, east of San Fernando de Apuré, Rio Apuré, Apuré, 95 - 170, 1978.II.19. UMMZ 211323 (3), nautical mile 116, Rio Orinoco, Delta Amacuro, 157 - 183 mm, 1979.XI.14. UMMZ 211327 (16), 2 km E. Barrancas, Rio Orinoco, Delta Amacuro, 228 - 291 mm, 1978.II.17. UMMZ 211328 (1), nautical mile 152, Rio Orinoco, Delta Amacuro, 162 mm, 1978.II.18. UMMZ uncat. JSA (1), mouth of Rio Guaviare, Rio Orinoco, near San Fernando de Atabapo, 1994.I.2. USNM 228723 (29), nautical mile 116, Rio Orinoco, Delta Amacuro, 1978.II.22.

Sternarchella schotti.—**Brazil**: CAS 50794 (1), Rio Amazonas, 170 mm. FMNH 54565 (5), Santarem, Rio Amazonas. MZUSP uncat. AMZ 96-131 (19), 1996. MBUCV 10908 (1), Manaus, Amazonas, Rio Negro.

Sternarchella sima.—**Brazil**: AMNH 3864 (HT, 1), Rio Amazonas, Pará, 1911. CAS 122220 (1), Rio Amazonas, Pará, 1911. **Peru**: AMNH 139073 (1), Iquitos, Rio Amazonas, Loreto, 1955.X. **Venezuela**: CAS 51078 (1), 400 mm. FMNH 100734 (1), Playa in Rio Suripa, 15 km above pump station, Rio Apuré, Apuré, 1991.I.13. FMNH 100740 (2), Rio Suripa, Rio Anero, Rio Apuré, Apuré, 1991.I.14. FMNH 100747 (1), Rio Suripa, mouth of Rio Anero, Rio Apuré, Apuré, 1991.I.14. MBUCV uncat. JGL (1), mouth of Upper Orinoco, Rio Alta Orinoco, 214 mm, 1993.XII.28. MBUCV 10420 (PT, 1), shipping channel, south of Isla Portuguesa, Rio Orinoco, Delta Amacuro, 240 mm, 1978.II.20. MBUCV 10514 (1), Isla Iguana, Delta Amacuro, Rio Orinoco, 201 mm, 1978.II.18 (HT *S. orinoco*). MBUCV 10551 (1), shipping channel, south of Isla Portuguesa, Rio Orinoco, Delta Amacuro, 234 mm, 1978.II.20 (PT *S. orinoco*). UMMZ 211339 (5), nautical mile 87, Rio Orinoco, Delta Amacuro, 157 - 250 mm, 1978.II.21. UMMZ uncat. JSA (1), mouth of Rio Guaviare, Rio Orinoco, near San Fernando de Atabapo, 1994.I.2. UMMZ uncat. JSA (1), mouth of Upper Orinoco, Rio Alta Orinoco, 1993.XII.28. UMMZ uncat. JSA (2), mouth of Rio Guaviare, Rio Orinoco, near San Fernando de Atabapo, 1994.I.2. UMMZ uncat. JSA (1), mouth of Upper Orinoco Rio Alta Orinoco, 1993.XII.28. UMMZ uncat. JSA (1), San Fernando de Atabapo, Rio Atabapo, 1993.XII.25.

Sternarchogiton porcinum.—**Brazil**: MZUSP uncat. MG 93-36 (2), c. 155 mm, 1993. **Peru:** CAS 28810 (1, HT), Rio Huallaga, Yurimaguas, 300 mm.

Sternarchogiton nattereri.—**Brazil**: SU 22452, Rio Madeira, 180 mm. UMMZ uncat. JSA (1), Rio Solimões, Amazonas, 220 mm, 1993.IX. USNM 102040 (1), Rio Amazonas. **Peru**: CAS 31236 (1), Iquitos, Rio Amazonas, Loreto. **Venezuela:** MBUCV 12831 (1), near airport, Sna Fernando de Apure, Rio Apure, Rio Oinoco. 230 mm.

Sternarchogiton sp. B.—**Venezuela**: CAS 50736, Porteguesa, Rio Orinoco, 150 mm. UMMZ 211307 (3), nautical mile 118, Rio Orinoco, Delta Amacuro, 192 - 200 mm, 1979.XI.14. UMMZ 211313 (2), El Torro, km 96, Rio Orinoco, Delta Amacuro, 184 - 256 mm, 1978.II.21. UMMZ 211315 (4), nautical mile 182, Rio Orinoco, Delta Amacuro, 1979.XI.09. UMMZ 211316 (2), nautical mile 182, Rio Orinoco, Delta Amacuro, 157 - 168 mm, 1979.XI.09. UMMZ uncat. JSA (4), Puerto Miranda, Apuré, Rio Apuré, 1986.II.13. UMMZ 211330 (1), nautical mile 182, Rio

Orinoco, 111 mm, 1979.XI.09. UMMZ uncat. JSA (2), San Fernando de Atabapo, Rio Atabapo, Amazonas, 1993.XII.25. USNM 233363 (2), La Providencia Rio Orinoco, 1979.XI.6. USNM 233367 (3), Isla Isabel, Rio Orinoco, Delta Amacuro, 1979.XI.7. USNM 233391 (1), Arature, Rio Orinoco, 1979.XI.18. USNM 233393 (1), Isla Portuguesa, Rio Orinoco, 1978.II.20. USNM 233790 (1), Los Castillos, Rio Orinoco, 343 mm, 1978.II.16. USNM 233823 (1), Islote de Fajardo, Rio Orinoco, 360 mm, 1978.II.14.

Sternarchorhamphus muelleri.—**Brazil**: FMNH 54560 (2), Alcobaca, Rio Tocantins, Pará, 1910.I.10. UMMZ uncat. JSA (1), Rio Amazonas, 310 mm, 1994.IX. UMMZ uncat. JSA (1), Rio Amazonas, 63 mm, 1994.IX. **Peru**: FMNH 96982 (1), Rio Santiago, La Poza, Rio Marañon, Loreto, 1979.X.17. **Venezuela**: FMNH 100745 (1), Rio Suripa, mouth of Rio Anero, Barinas, Rio Apuré, 1991.I.14. UMMZ 211331 (1), Punta Cabrian, km 150, Rio Orinoco, Delta Amacuro, 388 mm, 1978.II.18. UMMZ uncat. JSA (1), mouth of Upper Orinoco, Amazonas, Rio Alta Orinoco, 1993.XII.28. USNM 228807 (16), La Providencia, North side of Isla Fajardo, 182 km from Sea Buoy, Rio Orinoco, Delta Amacuro, 163 - 455 mm, 1979.XI.06. USNM 228878 (2), Isla Tres Caños, 131.8 nautical mile from sea buoy, Rio Orinoco, Delta Amacuro, 220 - 300 mm, 1979.XI.14.

Sternarchorhynchus curvirostris.—**Brazil**: FMNH 54558 (2), Santarem Rio Amazonas, 1910.XII.12. FMNH 59064 (2), Rio Tocantins, Pará, 1911. UMMZ uncat. JSA (1), Rio Amazonas, 256 mm, 1994.IX. MZUSP 2647 (1), Rio Jurua, 406 mm, 1902. **Ecuador**: FMNH 100616 (1), Rio Aguarico near mouth Rio Eno, Rio Napo, 1983.XI.25. **Peru**: FMNH 96983 (3), Rio Santiago at Pinglo, confluence of Rio Santiago and Rio Marañon, Loreto,1980.IV.08. FMNH 100722 (1), Caño La Indiaolta, near mouth of Rio Suripa, Rio Apuré, Barinas, 1991.I.11. USNM 228786 (1), Isla Tres Caños, Rio Orinoco, Delta Amacuro, 225 mm, 1979.XI.14.

Sternarchorhynchus cf. curvirostris.—**Brazil**: MZUSP 28570 (1), Rio Taquari, junto à cidade de Coxim, bacia do Rio Paraguai, Mato Grosso, X.1983.

Sternarchorhynchus britskii.—**Brazil**: MZUSP 23097 (3), Rio Paraná, Ilha Solteira, São Paulo, IX.1965. MZUSP 24464 (6, PT), Rio Paraná, Ilha Solteira, 25-28.V.1972. MZUSP 39956 (7), Rio Grande, represa de Água Vermelha, São Paulo/Minas Gerais. MZUSP 43277 (3, PT, 3 C&S), Rio Paraná, Ilha Solteira, 25-28.V.1972. MZUSP 50188 (1), Fernandópolis, bacia do Rio Paraná, São Paulo, 09.I.1968. MZUSP 52923 (1, HT), Rio Paraná, Ilha Solteira, 243 mm, 25-28.V.1972.

Sternarchorhynchus mormyrus.—**Brazil**: MZUSP 50187 (3), São Gabriel da Rio Negro, São Gabriel da Cachoeira, - 450 mm, 1979.V.18. MZUSP uncat. MTP 96-59 (1), Rio Solimões, Amazonas, 290 mm, 1996. **Venezuela**: MBUCV 8994 (1), muddy creek connecting Rio Teté with blackwater lake, c. 15 mi. west of Corri, Amazonas, 1974.III.

Sternarchorhynchus oxyrhynchus.—**Brazil**: FMNH 54559 (1), Pará, Rio Tocantins, 1910.I.22. FMNH 85497 (1), Rio Aruaca, 32.5 km S Biruaca, Rio Apuré, 1975.I.07. MZUSP uncat. MTP 96-59 (1), Rio Solimões, Amazonas, 280 mm, 1996. **Venezuela**: UMMZ uncat. JSA (1), mouth of Alta Orinoco, Amazonas, 1994.I.2. USNM 228787 (1), Isla Tres Caños, 131.8 nautical mile from sea buoy, Rio Orinoco, Delta Amacuro, 260 mm, 1979.XI.14.

Sternarchorhynchus roseni.—**Venezuela**: ANSP 165222 (1), Rio Apuré, Orinoco. MBUCV 10411 (PT, 1), Los Castillos, Rio Orinoco, Delta Amacuro, 235 mm, 1978.II.16. MBUCV 10622 (PT, 1), old shipping channel, south of Isla Portuguesa, Rio Orinoco, Delta Amacuro, 266 mm, 1978.II.20. MBUCV 12201 (PT, 3), El Concejo, mouth of Caño Guine, Delta Amacuro, 228 - 258 mm, 1979.XI.13. MBUCV 20037 (HT, 1), Jarina, San Fernando de Apuré, Rio Apuré, Apuré, 267 mm, 1984.IV.17. MBUCV 5491 (PT, 1), Rio Orituco, Guarico, 192 mm, 1968.VII.20. MBUCV 7562 (PT, 1), Rio Apuré at confluence with Rio Portuguesa, Rio Apuré, 143 mm, 1975.V.9.

Sternarchorhynchus mesaensis.—**Brazil**: MZUSP 24497 (2) Lagoa do Ribeirão do Bezerra, Rio Tocantins drainage near São Domingo, Goiás, 1977.II.23.

GYMNOTIDAE

Electrophorus electricus.—**Bolivia**: UMMZ 204426 (1), Costa Marquez, Rio Itenez, Rio Madeira, 940 mm, 1961.VII.1. **Brazil**: MZUSP 19272 (1), Rio Araguaia e Tocantins, Goias. **Colombia**: NRM 26263 (1), Guainia, Porto Inirida, Amazon, 1976.VII. **Ecuador**: FMNH 103373 (1), Rio Teteya, Aguarico drainage, Napo, 1983.XI.21. CAS 72183 (3), Rio Pichis near Puerto Bermudez, Amazon, 1920.VII.12. **Guyana**: USNM 228883 (3), Essequibo, 1000+ mm, 1992.XII.12. **Peru**: CAS 136681 (1), Rio Ampiyacu., near Pebas, Loreto, 1936.IX.14. NRM 27643 (1), quebradita tributary to Quebrada Santa Elena, Rio Samiria drainage, Loreto. NRM 27649 (3), Colonia Angamos, near Cocha Palometal, Rio Yauerana, Rio Javari, 1984.VII.29. **Suriname**: USNM 225669 (1), Amotopa landing, Nickerie District, Rio Corantijn, 511 mm, 1980.VII.19. USNM 225671 (1), Nickerie District, pool in front of Camp Hydro, 1980.IX.17. **Venezuela**: MBUCV 10064 (1), Rio Cuyuni, raudal de Kinotovaca, c. 40 Km S De El Dorado, Bolivar, 1977.I.23. MBUCV2643 (1), Guaimaral, tributario del Rio Capara, Orinoco drainage, Apure, 1965.I.6. MBUCV3463 (2), Cano Iguapo, Al E De La Esmeralda, Alto Orinoco, 1966.I.19.

Gymnotus anguillaris.—**Brazil**: INPA 9841 (2), Igarape Jatuarana, UHE Samuel, Rôndonia, 110 - 115 mm, 06.V.1985. INPA uncat. WGRC 94-4 (1), Igarapé Repartimento, stream 6 km SW Tefé Airport, Amazonas, 03°24'55"S, 64°45'00"W, 97 mm, 1994.I. **Bolivia**: MNHN 1988 1024 (10), San Juanito, Yacuma, Rio Mamore, 75 - 145 mm, 1982. French Guiana: NRM 28326 (2), Crique Soumouro, Kourou River, Cayenne, 1994.III.20. **Guyana**: FAU uncat. (2), Madewini River, 132 - 165 mm, 1994.IV.20. **Peru**: FMNH 96980 (1) 500 m upstream from Caterpiza, Loreto, 1980.II.02. **Suriname**: UMMZ 190413 (6), Maka Creek, Lawa River, Morowyne, 1967.IV.21. ZMA 100338 (2), Coropina Creek, 228 - 236 mm, 1956.V.20. **Venezuela**: MBUCV 9805 (3), Igarape Manaus, Reserva Duque, Amazonas, 1977.II.

Gymnotus cf. anguillaris .—**Panamá**: CAS 72209 (2), small creek in Rio Cricamola, Konkintu, Boca del Toro, 225 - 239 mm, 1923.II.25.

Gymnotus cf. anguillaris sp. P.—**Argentina**: CAS 167969 (1), off Patagonia, 1960.II.24. **Paraguay**: UMMZ 206080 (21), Arroyo in Parque Nacional Ybycui, Rio Paraguay, 82 - 260 mm, 1979.VI.20.

Gymnotus arapaima.—**Brazil**: INPA uncat. WGRC 94-3.1 (1), Paraná Apara, 10 km NW confluence Rios Jurua and Solimões, Mamirauá Ecological Reserve, Amazonas, 03°09'52"S, 64°47'00"W, 192 mm, 1994.I.4. INPA uncat. WGRC 94-3.2 (2), same collection data as INPA uncat. WGRC 94-3.1, 127 - 222 mm, (1 C&S, 222 mm), 1994.I.4.

Gymnotus cf. arapaima.—**Brazil**: MZUSP 52660 (1) Para Porto, Igarape Papagaio, Rio Trombetas, 155 mm, 15.III.1997.

Gymnotus bahianus.—**Brazil**: MZUSP 12316 (1, HT), fazenda Almada, Ilheus, Rio Almada, Bahia, 177 mm, 1945.II.16-23. MZUSP 18311 (2, PT), same collection data as MZUSP 12316, 84 - 108 mm.

Gymnotus cf. bahiensis.—**Brazil**: MCP 18110 (2), Padre Paraiso, Minas Gereis, 90 - 92 mm, 1995.I.20.

Gymnotus carapo.—**Bolivia**: UMMZ 066433 (2), Lake Rogoagua, Rio Beni, 214 - 338 mm, 1921.IX. UMMZ 066462 (2), Reyes, Rio Beni, 205 - 245 mm, 1921.IX. UMMZ 204299 (1), Costa Marquez, Rio Itenez, Guapore, Madeira, 164 mm, 1964.IX.02. UMMZ 204771 (5), same locality data as UMMZ 204299, 44 - 51 mm, 1964.X.1. UMMZ 204886 (3), Rio Baures, Rio Itenez, 145 - 345 mm, 1964.X.7. **Brazil**: MCZ 45189 (19), Ilha de Marajo, Rio Arari at Cachoeira do Arari, Parà, VII.1965. MCZ 45190 (4) Belém, Igarapé Paracuri near Icoraci, Parà, VII-1965. UMMZ 143282 (2), Lagoa dos Quadros, Tramandai, Rio Grande do Sul, 55 - 129 mm, 1941.VIII. UMMZ 230732 (2), Agassiz collections, presumably Brazil, 174 - 202 mm, 1876.V.9. UMMZ 230734 (2), Rio Cayari near Benjamin Constant, Amazonas, 190 - 210 mm, 1993.V.11. USNM 199215 (1), Upper Yuruena, Mato Grosso, 85 mm, 1964.VII.20. USNM 199219 (2), same locality data as USNM 199219, 1965.IV.9. **Colombia**: CAS 153799 (3), Cordillera Macarena; small brook 3 mi. below El Refugio on Rio Guayabero, elev. 925 ft., Rio Orinoco, Meta, 1960.II.24. FMNH 94759 (1) Cano Ti, white water creek near Pamopeta, Vaupes, 1992.V.07. **Ecuador**: FMNH 103329 (18), Quebrada to the Rio Tiputini, Napo, 1981.X.29. FMNH 103334 (2), Laguna Zancudococha, flooded forest edge, Rio Aguarico, Napo, 1983.X.29. MCZ 51710 (7), Rio Payamino, 1 mi. upriver from mouth at Puerto Coca, 1971.IX.25. NRM 39636 (1), Río Pastaza, Amazonas, 1937. **Paraguay**: NRM 23121 (1), Estancia Laguna Negra, 275 mm, 1983.VIII.22 . **Peru**: UMMZ 072636 (2), Yurimaguas, Rio Maranon, 148 - 214 mm, 1920.IX. UMMZ 230733 (1), Quebrada near Buen Sucesso, Rio Javari, Loreto, 250 mm, 1993.V.15. UMMZ 228998 (2), Rio Momon, near Iquitos, Rio Nanay, Loreto, 38 - 172 mm, 1993.V.5. UMMZ 228999 (1), Rio Tapira, Rio Tahuayo, Loreto, 161 mm, 1993.V.7. **Suriname**: ZIU 56 (1, HT), no locality on label, from King Adolf Fredrik's collection at Ulriksdal, figured in Linnaeus (1749, pl. 14, fig. 51), probably collected by Pallberg near Paramaribo. UMMZ 187499 (1), Brokopondo, 195 mm, 1966.IX.15. UMMZ 190414 (6), same collection data as UMMZ 187499, 71 - 22 mm. ZMA 100409 (1), Aloike, Litany River, 71 mm, 1957.XI.27. ZMA 100430 (1), Ile de Cayenne, 305 mm, 1957.X.6. ZMA 100434 (2), Degrad Cacao, 190 - 255 mm, 1957.XI.10. ZMA 100439 (1), same locality data as ZMA 100434, 256 mm, 1957.X.5. **Trinidad**: CU 54984 (1) Nariva Swamp, B1/19 Cunapo Southern Road, Trinidad Is., 300 mm, 1977.I12. UMMZ 169080 (2), Gunupia, Mt. Plaisance, Trinidad Is., 46 - 74 mm, 1953.III.12. **Venezuela**: UMMZ 212345 (1), Esteros de Camaguan, Guarico, Apure, 45 mm, 1981.VIII. UMMZ 214766 (1), Cano Falcon, Portuguesa, 241 mm, 1987.II.19.

Gymnotus cf. carapo.—**Argentina**: FML 223 (2), Ayo. Pilagás, Pirané, Formosa, Paraguay, 1950.VIII.19. FML 258 (3), Isla Apipé Gde, Ituzaingó Corrientes, Paraná, 1950.X.15. FML 1037 (1), no collection data. **Brazil**: MCZ 2414 (16), Pernambuco, Ipojuca, 1863. MCZ 9349 (4), Pernambuco, Probably Recife and environs, received in 1864. MCZ 9351 (3), Minas Gerais/Bahia, Rio São Francisco, between Guaicu and Januria, 28.VIII.1865. MCZ 9371 (6), Rio de Janeiro, Rio Muria at Campos, 3 mi from town, 1865. MCZ 9372 (1), Espírito Santo, Rio São Mateus at São Mateus, XII.1865. MCZ 9375 (1), Minas Gerais, Lagoa Santa and environs, VII.1865. MCZ 9383 (2), Bahia, Salvador & environs, 28.VII.1865. MCZ 9384 (1), Bahia, Salvador & environs, 28.VII.1865. MZUSP 22952 (1), Rio São Fancisco at Tres Marias, Minas Gereis. No date. MZUSP 521500 (3), Rio Paraopeba at Fortuna de Minas, Lagoa Massaracá, Rio São Fancisco, Minas Gereis, 41 - 555 mm. No date. **Colombia**: CAS 072192 (2), Rio Sucio, Rio Truando, Rio Atrato, 150 - 179 mm, 1913. FMNH 56793 (2), mouth of Rio Calima, Rio Atrato, 1913. FMNH 56794 (2), same collection data as CAS 072192, 174 - 175 mm. FMNH 70511 (5), Pizarro, Choco, Pacific slope, 124 - 247 mm, 1945.IX. FMNH 94776 (2), Pamopeta Cano Ti, Vaupes, 1979.IV.18. NRM 27717 (1), Laguna Santa Clara, Rio Ococa, Near Villavicencio, Rio Meta, 245 mm, 1988.I.16. NRM 27734 (7), Boca de Pepé, Baudó, Dept. Chocó, 1989.II.22. NRM 27744 (1), Quebrada Piscindé, Río San Pablo, Río Atrato, Chocó, 1989.II.07. **Ecuador**: CAS 164103 (1), Rio Toachi, Rio Blanco, near mouth of Quinide, Rio Esmeraldas, 1949.XII. FMNH 97389 (1), Canelos, Rio Babonaza, Rio Pastaza, Pastaza, 1956.IX.

Gymnotus cataniapo.—**Brazil**: INPA 9808 (1), Igarape Paso, Rio Jamari, UHE Samuel, Rôndonia, 110 mm, 21.VI.1988. INPA 9834 (13), Rio Aripuaná, Igarape do Castanhal, MT, 90 - 215 mm, 22.VIII.1976. **Venezuela**: MBUCV 14154 (3, PT), cano near Salto Nieve, Rio Orinoco, Amazonas, 75 - 194 mm, 1983.XII.22. MBUCV 14300 (1, PT), Cano Merete, Rio Casiquiare, Amazonas, 213 mm, 1984.VIII.20. MBUCV 14736 (1, HT), San Carlos de Rio Negro, Amazonas, 253 mm, 1984.X.4. MBUCV 14757 (1, PT), Cano Guayabal, near Puerto Ayacucho, Rio Orinoco, Amazonas, 114 mm, 1984.XII.12. MBUCV 14781 (15, PT), Cano Las Pevas, Rio Casiquiare, Amazonas, 143 - 316 mm, 1984.VIII.2.

Gymnotus coatesi.—**Brazil**: AMNH 12624 (1, HT), near mouth of Rio Moju, 50 miles upstream from Santarem, Para, Brazil, 180 mm, 1934.

Gymnotus cf. coatesi.—**Bolivia**: UMMZ 205149 (7), near Guayaramerin, Arroyo Grande, 45 - 175 mm, 1964.X.23. **Brazil**: INPA uncat. WGRC 97-1 (1), 116 mm. Várzea lake, between Rio Solimões and Japurá, Mamirauá Ecological Reserve, Amazonas, 03°09'52"S, 64°47'00"W, 1996. **Ecuador**: FMNH 103345 (2) Qbda Apoalla, tributary to lower Rio Shushufindi, Napo, 1983.XI.24. FMNH 103343 (6) Rio Yasuni, Quebrada to Rio Jatuncocha, est. 2 km upstream from Laguna Jatuncocha, Napo, 1981.X.26. **Peru**: UMMZ 224601 (1), cano near Santa Ana, Rio Tahwayo, Loreto, 133 mm, 1993.V.4. UMMZ 224607 (6), near Iquitos, Rio Nanay, 30 - 144 mm, 1993.V.4.

Gymnotus cylindricus.—**Costa Rica**: UCR 280-2 (3), Rio Escondido, Limon, Rio Sixaola, 1968.X.3. UCR 1014-1 (12), Rio Escondido, Limon, Rio Sixaola, 123 - 249 mm, 1976.IX.17. UMMZ 224129 (10), Rio Escondido, Limon, Rio Sixaola, 131 - 205 mm, 1968.X.3. **Guatemala**: AMNH 1358 (1, HT), brook E Los Amates, Rio Motagua, 187 mm. 1905.II.17. UMMZ 193873 (2), el Progresso, Morazin, Rio Yeguare, 192 - 210 mm, 1973.III.24. UMMZ 193986 (14), Quebrada de Vegega, Los Amates, Rio Izabal, 26 - 183 mm, 1973.IV.5. **Honduras**: UMMZ 155831 (1), bridge on Tegucigalpa-Danli road, Rio Yeguare, 174 mm, 1948.I.30. UMMZ 155832 (2), Quebrada near Los Flores, Rio Yeguare, 161 - 204 mm, 1947.VII.23. UMMZ 188110 (2), Pito Solo, Cortez, Rio Jaitique, 93 - 191 mm, 1948.V.23. UMMZ 188273 (1), Lago Yoyoa, Santa Barbara, Rio Yeguare, 135 mm, 1949.VIII.1. UMMZ 188274 (5), Lago Yoyoa, Santa Barbara, Rio Yeguare, 97 - 175 mm, 1948.IV.14. UMMZ 188275 (16), Lago Yojoa, Rio Yeguare, 166 - 224 mm, 1949.VIII.10. UMMZ 188296 (2), Quebrada Lagunita, Morazin, Rio Yeguare, 120 - 138 mm, 1947.VII.29. UMMZ 188297 (5), Quebrada behind finca de Rudolfo Rosales, Rio Yeguare, 69 - 129 mm, 1947.XI. UMMZ 199598 (1), Laguna Sikalanka, Rio Sucre, 215 mm, 1975.V.11. **Nicaragua**: CAS 161383 (3), Rio Frio, about 1.5 mi. above San Carlos, Lago Nicaragua, Rio San Juan, 1963.II.12. TU uncat. (1), San Carlos, Lago Nicaragua, Rio San Juan. No date. UMMZ 199622 (13), SE of Bilwaskarma, Rio Kurnog, 1975.V.13. UMMZ 199633 (2), Rio Putkrukira near Waspán, Rio Coco, 121 - 194 mm, 1975.V.27.

Gymnotus inaequilabeatus.—**Bolivia**: UMMZ 231097 (1), Rio Baures, 2 km above mouth, Rio Itenez, Rio Mamore, Rio Madeira, Amazon, Beni, 1964.X.07. **Brazil**: MCP 6956 (2), Rio Uruguai Santana Velha, Uruguaiana, Rio Grande do Sul, 25.X.1985. MCP 7155 (1), Rio Maquine, Osorio, 254 mm, 1984.IX.26. MZUSP 46001 (1), Porto Primavera, Rio Paraná, São Paulo, 998 mm, 1993.VIII. MZUSP 51667 (1), small creek, Paraibo do Sul, Jacarei, São Paulo, 1993.I.24. MZUSP 51268 (1), Rio Capivara, affluent do Rio Paranapanema, São Paulo, c. 370 mm, 1994.III. USNM 1643 (1), Rio Paraguay, 791 mm. **Paraguay**: UMMZ 206939 (1), near Pto. Stroessner, Arroyo Venecia, 154 mm, 1979.VIII.5. UMMZ 206703 (4), Pedro Juan Caballero, Paraná, 113 - 280 mm, 1979.VI.24. UMMZ 206971 (2), Estancia la Golondrina, Presidente Hayes, Confuso, 255 - 261 mm, 1979.VIII. UMMZ 207025 (17), marsh 34 km NW Pt. Remaro bridge, Rio Confuso, 485 mm, 1979.VIII.9. UMMZ 207096 (3), same collection data as UMMZ 206971, 132 - 210 mm. UMMZ 207564 (2), Rio Pilcomayo near Peurto Falcon, Rio Paraguay, 220 - 242 mm, 1979.VIII.29. UMMZ 207619 (1), Riachuelo Pilco, Presidente Hayes, 144 mm, 1979.VIII.31. UMMZ 207760 (2), Arroyo Peguajho, Ypane, 77 mm, 1979.IX.04. UMMZ 207893 (6), Rio Aequidaban near Paso Hasqueta, Rio Paraná, 16 - 390 mm, 1979.IX.6. UMMZ 215183 (1), Estancia la Golondrina, Presidente Hayes, Confuso, 170 mm, 1981.X.02. UMMZ 216576 (1), Estancia la Golondrina, Presidente Hayes, Rio Confuso, 322 mm, 1981.X.02. UMMZ 216576 (1), near Trans Chaco-Villa, Presidente Hayes, 322 mm, 1981.X.2.

Gymnotus cf. inaequilabeatus sp. A.—**Brazil**: INPA 6378 (1) Iconqui, Tocantins, SA, 315 mm, 29.XI.1980. INPA 6390 (24), 170 - 445 mm, Rio Aripuaná, Igarape do Castanhal, MT, 26.VIII.1976. INPA 11549 (1), Rio Orijuaná, Igarape Orojoto, cidade Humboldt, MT, 230 mm, 09.XI.1976. INPA uncat. Polo 482 (2), Lagoa Boa Viajen, Rôndonia, 440 - 475, 17.VI.1985. MZUSP 50105 (4), Rio Purus at Manoel Urbano, Acre, 115 - 270, 7.IX.1973. **Colombia**: NRM 27717 (1) Laguna Santa Clara tributary to Río Ocoa, 5 km S Villavicencio, Río Meta, Meta, 1988.I.16.

Gymnotus jonasi.—**Brazil**: INPA uncat. WGRC 94-2.1 (1), same collection data as INPA uncat. WGRC 94-1.1, 114 mm. INPA uncat. WGRC 94-2.2 (6) same collection data as INPA uncat. WGRC 94-1.1, 70 - 99 mm, (1 C&S, 99 mm).

Gymnotus maculosus.—**Costa Rica**: TU 24935 (16), La Virgin, Rio Sarapiqui, 1960.II.22. TU 25063 (3), Rio Tempisque, near Liberia, Guanacaste, 193 - 218 mm, 1961.I.21. UCR 969-9 (20), Santa Cruz, Rio Garzon, Guanacaste, 123 - 195 mm, 1976.I.25. UCR 980-9 (5), Arenal, Rio Dos Bocas, Guanacaste, Rio San Carlos, 1968.VI.10. UMMZ 158451 (1), Finca la Trinidad, Guanacaste, 179 mm, 1949.X.21. UMMZ 224128 (5), Rio Higueron, near Canas, Guanacaste, 158 - 222 mm, 1968.VI.10. **Guatemala**: UMMZ 188072 (1), Rio Bravo, Rio Nahualate, 1968.IV.3. UMMZ 190531 (7), El Obraje, Jutiapa, Rio Grande de Pasaco, 146 - 200 mm, 1971.III.9. UMMZ 190783 (3, paratypes), diversion of channel from Rio Maria Linda, 20 km east of Escuintla, Departamento Santa Rosa, 176 - 203 mm, _1971.III.27. UMMZ 194122 (6), 2.6 km ESE Eca Cocales, Rio La Primavera, 105 - 135 mm, 1973.IV.20. UMMZ 194150 (2), Rio Siguacan, near Escuintla, Santa Rosa, 141 - 172 mm, 1973.IV.24. UMMZ 197103 (20), Taxisco, Santa Rosa, 78 - 227 mm, 1974.IV.6. UMMZ 230354 (20, PT), Rio Buena Vista, Rio Tigre, on road between Escuintla and Chiquimulilla, 8 km west of Pajal, Santa Rosa, 128 - 230 mm, 1946.IV.18. UMMZ 230830, (1, HT), diversion of channel from Rio Maria Linda, 20 km east of Escuintla, Santa Rosa, 191 mm, 1971.III.27. USNM 114235 (2), Rio Colojate, 1947. USNM 114539 (22), near Malacatan, Rio Gramal, 1956.VII.6. USNM 134700 (49, PT), near Pajal, Rio Buen Vista, 138 - 226 mm, 1946.IV.18. USNM 225435 (1), Rio Chiquimulilla, 1946. USNM uncat. (1), Rio Hondo, 1946. USNM uncat. (8), Rio Lato, 1946. USNM uncat. (23), Rio Gramal, 1947. **Mexico**: UMMZ 191702 (2), Tapachula, Rio San Nicolas, Chiapas, 163 - 189 mm, 1971.III.13. UMMZ 191712 (3), same locality data as UMMZ 191702, 184 - 228, 1971.II.27. **Honduras**: TU 24965 (38, PT), Boca de Rio Sapoi, Sapoi, Lago Nicaragua, Rivas Province, 1960.IV.23. TU 25032 (1), same collection data as TU 24965, 43 mm.

Gymnotus mamiraua.—**Brazil**: INPA 9962 (12), 65 - 220 mm, Lago Rato, Lago Mamirauá, Mamirauá Ecological Reserve, near Tefé, Amazonas, 20.V.94. INPA uncat. WGRC 94-1.1 (1), várzea lake, between Rio Solimões and Japurá, Mamirauá Ecological Reserve, Amazonas, 03°09'52"S, 64°47'00"W, 178 mm. 1994.I. INPA uncat. WGRC 94-1.2 (6), same collection data as INPA uncat. WGRC 94-1.1, 99 - 219 mm, (1 C&S, 120 mm).

Gymnotus melanopleura.—**Brazil:** INPA 9966 (1, HT), várzea lake between Rio Solimões and Japurá, Mamirauá Reserve, Amazonas, 03∞02'36"S, 64∞51'02"W, 99 mm, 1994.IV.30.

Gymnotus pantherinus.—**Brazil**: LGP 0932 (1), P2104, near Itanhaem, affluent of Rio Preto, São Paulo, 46°46'00" Wß, 24°14'17"Sß, 133 mm, 1997.V.15. LGP 0939 (1), same collection data as LGP 0932, 222 mm. MCP 10628 (2), Joinville, Santa Catarina. MCP 13257 (1), Porto de Santo Izidro at S Nicolau, Rio Uruguay, Rio Grande do Sul, 360 mm. MCP 17327 (1) Rio Jacuí, Rio Grande do Sul, 71 mm. MCP 18108 (1), Lumiar, Rio de Janeiro, 177 mm, 1995.I.28. MCP uncat. (6) Macaé near Lumiar at road to Casemiro, Rio de Janeiro, 139 - 171 mm. MZUSP 22792 (1) Rio Paraíba at São João da Barra, Rio de Janeiro, 200 mm. MZUSP 2649 (1) Rio Doce, Espírito Stanto, 172 mm. MZUSP 51670 (2), Santa Fe, affluent Paraibo do Sul, Jacarei, São Paulo, 190 - 220 mm, 1993.I.24. USNM 297933 (20), Naneia, São Paulo, 1988.II.21. USNM 297939 (12), Guaratuba, Rio da Praia, 1988.X.3.

Gymnotus cf. pantherinus.—**Brazil**: MZUSP 48549 (1) Rio Pium at bridge, Parnamirim, Rio Grande do Norte, 123 mm.

Gymnotus pedanopterus.—**Venezuela**: MBUCV 4860 (1, PT), Cano Esmeralda, Rio Orinoco, Amazonas, 281 mm, 1966.XI.6. MBUCV 7135 (2, PT), El Pozo de Lucas, near San Fernando de Atabapo, Rio Orinoco, Amazonas, 109 - 119 mm, 1973. MBUCV

7310 (3, PT), same locality data as MBUCV 7135, 92 - 185 mm, 1972.IV.14. MBUCV 14737 (2, PT), Cano Chola, near San Carlos de Rio Negro, Rio Casiquiare, Amazonas, 198 - 228 mm, 1984.XI. MBUCV 14738 (1, HT), Cano Temblador, Rio Casiquiare, Amazonas, 215 mm, _1984.XII.5.

Gymnotus onca.—**Brazil**: INPA 11512 (1 HT), Cano do Lago Rato, várzea lake between Rio Solimões and Japurá, Mamirauá Reserve, Amazonas, 03∞02'36''S, 64∞51'02''W, 116 mm, 1994.V. 5.

Gymnotus cf. pedanopterus.—**Brazil**: INPA uncat. WGRC 97-2 (1), 99 mm, Várzea lake, between Rio Solimões and Japurá, Mamirauá Ecological Reserve, Amazonas, 03°09'52"S, 64°47'00"W, 1996. MZUSP uncat. (1), Acima do Rio Urumbari, lago central da ilha de Buiu-açu, 150 mm, 1990.II.06. **Ecuador**: MZUSP uncat. RBS 96-19 (1), Rio Tatumcocha, Napo, 110 mm, 1996.

Gymnotus silvius.—**Brazil**: LGP 0925.1 (1, HT), 291 mm, Miracatu, Rio Ribeira de Iguape, São Paulo, 24ß32'50" Sß, 47ß26'13" Wß, 1995.IX.15. LGP 0925.2 (2, PT), 251 - 307 mm, same collection data as HT. LGP 0931 (1), 157 mm, São Simão, São Paulo, Rio Tamandua, Rio Pardo, 21ß30'00" Sß, 47ß31'11" Wß, 1996.VI.30. UMMZ 234347 (2), same collection data as HT, 255 - 271 mm.

Gymnotus sp. J.—**Peru**: UMMZ 224596 (10), Buen Sucesso, Rio Javari, Loreto, 45 - 175 mm, 1993.V.15. UMMZ 224599 (2), Quebrada near Buen Sucesso, Rio Javari, Loreto, 163 - 196 mm, 1993.V.15.

Gymnotus sp. N.—**Ecuador**: FMNH uncat. (46), Aguarico, Rio Napo, 1983.XI.21.

Gymnotus sp. P.—**Paraguay**: UMMZ 206155 (2), near San Rafael, Arroyo Tembley, 194 - 225 mm, 1979.VI.26.

Gymnotus sp. R.—**Brazil**: INPA 9841 (1), Igarape Jatuarana, UHE Samuel, Rôndonia, 235 mm, 06.V.1985.

Gymnotus stenoleucus.—**Brazil**: MZUSP 43356 (1), Piractuba, Rio Negro, Amazonas, 222 mm, 11.XI.1972. **Venezuela**: MBUCV 4644 (2, PT), Rio Quiritare, Rio Orinoco, Amazonas, 91 - 95 mm, 1966.X.30. MBUCV 6218 (1, HT), Cano Caripo, Rio Casiquiare, Amazonas, 140 mm, 1969.I.26. MBUCV 9417 (4, PT), same collection data as MBUCV 6218, 91 - 142 mm. MBUCV 14028 (15, PT), Rio Cataniapo, Rio Orinoco, Amazonas, 80 - 171 mm, 1983.III.30. MBUCV 14747 (1, PT), Cano Guayabal, near Peurto Ayacucho, Rio Orinoco, Amazonas, 140 mm, 1984.XII.12.

HYPOPOMIDAE

Brachyhypopomus beebei.—**Venezuela**: USNM 120753 (1, HT), Rio Caripe, near Caripito, Monagas, 136 mm. **Brazil**: INPA 1154 (2), Mamirauá Ecological Reserve, near Tefé, Amazonas. INPA 9943 (14), 90 - 150 mm, Mamirauá Ecological Reserve, near Tefé, Amazonas. INPA uncat. WGRC (40), Mamirauá Ecological Reserve, near Tefé, Amazonas, 60 - 170 mm.

Brachyhypopomus cf. beebei.—**Brazil**: MZUSP 25138 (2), ilha de Taiamã (Sema), Rio Paraguay, Mato Grosso, 8.VIII.1980. MZUSP 23630 (3), banhado Schreck, São Leopoldo, Rio Grande do Sul, 1969.V.1. MZUSP 25165 (6), fazenda dentro da bacia dos rios Jacuí e Guaíba, Camaquã, Rio Grande do Sul, VI.1979. NRM 22480 (2), Silvia Jardim, Japubia, Gavioes, Rio São João, Rio Janeiro, 22° 25' Sß, 42° 32' Wß, 89 mm, 1992.IX.22. **Paraguay**: NRM 22601 (1), Presedente Hayes, Rio Pilcomayo, 1994.V.30. NRM 33622 (1), 115 mm. UMMZ 205767 (1), Arroyo Tabati, Rio Paraná, 1979.VI.3. UMMZ 206252 (5), Carayao, Rio Paraná, 1979.VII.4. UMMZ 207098 (4), Puente Remano Bridge, Rio Paraná, 1979.VIII.11. UMMZ 208106 (2), Puente Remano Bridge, Rio Paraná, 1979.IX.15.

Brachyhypopomus brevirostris.—**Bolivia**: UMMZ 204229 (1), Rio Iteneg near Costa Marquez, Rio Madeira, Beni, 1964.VIII.30. UMMZ 204298 (2), Rio Iteneg near Costa Marquez, Rio Madeira, Beni, 1964.IX.2. UMMZ 204513 (4), Rio Iteneg near Costa Marquez, Rio Madeira, Beni, 1964.IX.15. **Brazil**: INPA 9947 (20), 62 - 315 mm, Mamirauá Ecological Reserve, near Tefé, Amazonas. INPA 9949 (3), Mamirauá Ecological Reserve, near Tefé, Amazaonas. MZUSP 19243 (1), Poconé, Mato Grosso, 1978. MZUSP 25137 (2), ilha de Taiamã, Rio Paraguay, Mato Grosso, 8.VIII.1980. MZUSP 25257 (1), Santo Antônio do Paraíso, Itiquira, Mato Grosso, 24-29.X.1978. MZUSP 36341 (2), Ladário, próximo a Corumbá, Mato Grosso, IX.1985. MZUSP 36436 (1), Corumbá, bacia do Rio Paraguay. MZUSP 43681 (26), Descalvados, Rio Paraguay, Mato Grosso, 9.VIII.1980. MZUSP 45032 (1), Descalvados, Rio Paraguay, Mato Grosso, 9.VIII.1980. UMMZ 224598 (3), Rio Cayari near Benjamin Constant, Rio Cayari, Amazonas, 1993.V.11. **Guyana**: UMMZ 215583 (1), Shebe Pond, Essequibo River, Rupununi, 244 mm, 1971.V.11. UMMZ 215603 (1), Juari Ranch, E. of Takatu River, Essequibo River, 225 mm, 1971.V.13. UMMZ 215603 (1), Juari, Takatu River, Essequibo River, Rupununi, 225 mm, 1971.V.13. UMMZ 215911 (20), Daiga Creek, Barama River, Rio Waini, 1971.IX.1. **Venezuela**: UMMZ uncat. JSA (1), Puerto Ayacucho, Rio Orinoco, Amazonas, 1991.VIII.25.

Brachyhypopomus cf. brevirostris.—**Argentina**: FML 47 (39), Pirá Virá, Río Inglés, Santa Catalina, Formosa, Paraguay, 1944.XI.02. FML 250 (62), Destacamento Potrero No. 6, Formosa, 1950.VIII.18. FML 320 (19), Laguna Oca, Formosa, 1950.XI.10. FML 481 (34), Río San Hilario, Formosa, 622, Bermejo, 1951.XI.20. FML 1743 (2), San José del Rincón, Capital, Santa Fe, 2., no date. FML 2011 (1), Pozo de Las Conchas, San Martín, Salta, Paraná, 1991.XII.03. FML 2034 (46), Bermejo, 1951.X.15. FML 2708 (1) Tres Cruces, cerca de La Cienaga, El Carmen, Jujuy, Río Bermejo. 24° 30' S, 65° 15' W, 1958.III. FML 2034 (46), Bermejo, 1951.X.15. FML 2284 (1), 7 km Resistencia, San Fernando Chaco, 1973.XI.11. FML 2469 (1), Antequera, Resistencia, Chaco, 1997.VI.15. **Brazil**: MZUSP 40190 (1), Rio Icatu (bacia do Rio São Francisco), próximo à foz, Ibiaba, Bahia, IX.1988.

Brachyhypopomus diazi.—**Venezuela**: UMMZ 217073 (1), Maria's Bodego, Paso de Caballo, Rio Guariquito, 1987.II.20.

Brachyhypopomus janeiroensis.—**Brazil**: MZUSP 43130 (1, HT), córrego Salto d'Água, afluente do Rio São João, 6 km N de Silva Jardim, Rio de Janeiro, 92 mm, 7.VIII.1991. MZUSP 43131 (7, PT), collected with HT, 75 - 84 mm.

Brachyhypopomus occidentalis.—**Colombia**: CAS 72219 (3), upper Quibo basin, Rio Atrato, Choco, 1913. CAS 72229 (2), Rio Calima near Boca del Guineo, Rio San Juan Basin, Choco, IV-V.1913.

Brachyhypopomus pinnicaudatus.—**Bolivia**: UMMZ 204297 (2), Rio Iteneg near Costa Marquez, Rio Madeira, Beni, 1964.IX.2. UMMZ 204512 (1), Rio Iteneg near Costa Marquez, Rio Madeira, Beni, 1964.IX.15. UMMZ 204632 (6), Rio Iteneg near Costa Marquez, Rio Madeira, Beni, 1964.IX.25. UMMZ 204743 (3), Rio Iteneg near Costa Marquez, Rio Madeira, Beni, 1964.IX.30. UMMZ 204829 (5), Rio Baures, Rio Madeira, Beni, 1964.X.5. UMMZ 205102 (1), Guayaramerin, Rio Madeira, Beni, 1964.X.22. UMMZ 205163 (6), Rio Iteneg near Costa Marquez, Rio Madeira, Beni, 1964.IX.10. **French Guyana:** ANSP 163463 (1, HT), Grand Prispris swamp, near old Kourou, 8.VI.1986. **Guyana**: UMMZ 216032 (3), Kourou, Essequibo River, 1988.VI.8. **Paraguay**: UMMZ 206001 (5), Rio Salado, Rio Paraná, 1979.VI.16. UMMZ 207369 (6), Riacho San Carlos, near Estancia Juan Zalazar, Rio Paraná, 1979.VIII.22. UMMZ 207463 (1), Ayolas, Rio Paraná, 1979.VIII.25. UMMZ 207620 (1), Rio Pilco, Rio Paraná, 1979.VIII.31. **Peru**: UMMZ uncat. JSA (3), 1993.IX.20. UMMZ 224602 (1), near Santa Ana, Rio Tahwayo, Loreto, 1993.V.6. UMMZ 224603 (1), Rio Tapira, Rio Tahwayo, Loreto, 1993.V.5. UMMZ 224604 (1), Rio Momon near Iquitos, Rio Nanay, Loreto, 1993.V.5. UMMZ 224606 (1), Pebas, Rio Ampiyacu, Loreto, 1993.V.5. UMMZ uncat. JSA (2), Quebrada near Buen Suceso, Rio Javari, Loreto, 1993.V.15. UMMZ uncat. JSA (12), Rio Momon near Iquitos, Rio Nanay, Loreto, 1993.V.7.

Brachyhypopomus cf. pinnicaudatus.—**Brazil**: MZUSP 25149 (2), Ilha de Taiamão, Rio Paraguay, Mato Grosso, 12.VIII.1980. MZUSP 36385 (5), fazenda Nhumirim, Nhecolândia, Corumbá, Mato Grosso, VII.1984. MZUSP 49201 (9), represa de Santa Maria da Serra, Americana, São Paulo, 07.III.1995.

Brachyhypopomus sp. B.—**Colombia**: ANSP 138042 (1, HT), Rancho Llano Grande, Rio Metica, Rio Meta, Dept. Meta, 221 mm, 23.V.1969. ANSP 138024 (9, PT), collected with HT.

Brachyhypopomus sp. E.—**Brazil**: MZUSP 45032 (1, HT), Descalvados, tributary to Rio Paraguay, upper Pantanal, Mato Grosso, 9.VIII.1980. MZUSP 43681 (26, PT), collected with HT). INPA uncat. WGRC (15), Mamirauá Ecological Reserve, near Tefé, Amazonas, 140 - 165 mm.

Brachyhypopomus sp. F.—**Brazil**: INPA uncat. WGRC (15), Mamirauá Ecological Reserve, near Tefé, Amazonas, 140 - 160 mm.

Brachyhypopomus sp. M.—**Brazil**: INPA 8941 (1, HT), Paraná do Paracuúba, near mouth of Lago Januari, Rio Negro, Amazonas, 215 mm, 23.IV.1993. INPA 8939 (9, PT), same collection data as HT. INPA uncat. WGRC (40), Mamirauá Ecological Reserve, near Tefé, Amazonas, 160 - 260 mm.

Brachyhypopomus sp. R.—**Brazil**: INPA uncat. WGRC (5), Mamirauá Ecological Reserve, near Tefé, Amazonas, 85 - 140 mm.

Brachyhypopomus sp. T.—**Brazil**: INPA 9950 (10), Mamirauá Ecological Reserve, near Tefé, Amazonas, 140 - 155 mm. INPA uncat. WGRC (35), Mamirauá Ecological Reserve, near Tefé, Amazonas, 140 - 220 mm.

Brachyhypopomus sp. W.—**Brazil**: INPA 8941 (1, HT), Parana do Paracuúba, near mouth of Lago Januari, Rio Negro, Amazonas, 163 mm, 23.IV.1993. INPA 8896 (10, PT), collected with HT. INPA uncat. WGRC (30), Mamirauá Ecological Reserve, near Tefé, Amazonas, 155 - 280 mm.

Hypopomus artedi.—**Guyana**: UMMZ 187500 (3), 117 - 152 mm, no date (determined 1965). UMMZ 215603 (1), Juari Ranch, east of Takatu, Rupununi, 225 mm, 1971.V.13.

Hypopomus sp. Z.—**Brazil**: INPA 9730 (1), Rio Abonari, Rio Uatamá, Amazonas, Brazil, 261 mm, 1983.VIII.18.

Hypopygus lepturus.—**Brazil**: INPA uncat. WGRC (25), Mamirauá Ecological Reserve, near Tefé, Amazonas, 45 - 160 mm. **Bolivia**: UMMZ 205162 (12), Rio Itenez near Costa Marquez, Rio Madeira, Beni, 1964.IX.10. **Guyana**: UMMZ 216853 (1), Yarakabra, Madewini River near Thimeri, Rio Demerara, 1989.II.28. **Peru**: UMMZ uncat. JSA (5), Quebrada near Buen Suceso, Rio Javari, Loreto, 1993.V.15. **Venezuela**: UMMZ uncat. JSA (8), Caño Viejita, Rio Atabapo, Amazonas, 1993.XII.30. UMMZ uncat. JSA (1), El Pozo, Rio Alta Orinoco, Amazonas, 1994.I.1. UMMZ uncat. JSA (2), Isla Sapo, Rio Atabapo, Amazonas, 1993.XII.23. UMMZ uncat. JSA (2), Puerto Ayacucho, Rio Orinoco, Amazonas, 1991.VIII.26.

Hypopygus neblinae.—**Venezuela**: MBUCV 08077 (PT, 1), Caño Moriche, near San Fernando de Atabapo, Rio Atababo, 58 mm, 1974.II.12. MBUCV 12998 (PT, 14), Caño near mouth of Isla Chamuchima, Rio Atababo, Amazonas, 65 - 78 mm, 1982.IV.8. MBUCV 14694 (HT, 1), 3 km from La Neblina camp, Rio Baria, Amazonas, 122 mm, 1984.II.6. MBUCV 14741 (PT, 79), Caño Manu, 250 meters from Solano, Rio Casiquiare, Amazonas, 55 - 76, 1984.XII.7.

Microsternarchus bilineatus.—**Bolivia**: UMMZ 205150 (2), Arroyo Grande, near Guayaramerin, Rio Madeira, Beni, 58 - 65 mm, 1964.X.23. **Peru**: UMMZ 224600 (1), Chino, Rio Tahwayo, Loreto, 1993.V.7. UMMZ 224602 (3), Santa Ana, Rio Tahwayo, Loreto, 1993.V.6. UMMZ uncat. JSA (1), Rio Momon near Iquitos, Rio Nanay, Loreto, 1993.V.5. **Venezuela**: UMMZ uncat. JSA (15), Caño Viejita, Rio Atabapo, Loreto, 1993.XII.30. UMMZ uncat. JSA (6), El Pozo, Rio Alta Orinoco, Amazonas, 1994.I.1. UMMZ uncat. JSA (1), Isla Sapo, Rio Atabapo, Amazonas, 1993.XII.23.

Microsternarchus sp. A.—**Brazil**: INPA uncat. WGRC (5), Mamirauá Ecological Reserve, near Tefé, Amazonas, 70 - 110 mm.

Racenisia fimbriipinna.—**Venezuela**: MBUCV 07127 (PT, 25), El Pozo, Rio Alta Orinoco, Amazonas, 49-107 mm, 1973.VII.31. MBUCV 07142 (PT, 2), El Pozo, Rio Alta Orinoco, 51-56 mm, 1972.IV.14. MBUCV 07540 (HT, 1), El Pozo, Rio Alta Orinoco, 117 mm, 1973.VII.31. UMMZ uncat. JSA (1), El Pozo, Rio Alta Orinoco, 1994.I.1.

Steatogenys cryptogenes.—**Brazil**: MZUSP 47985 (HT), Igarape Sirinau, right margin Rio Cuieiras, c. 25 Km from mouth of Rio Negro, 93 mm, 1977.I.30. MZUSP 47986 (12 PT), collected with HT, 65 - 98 mm.

Steatogenys duidae.—**Brazil**: INPA uncat. WGRC (10), Mamirauá Ecological Reserve, near Tefé, Amazonas, 130 - 190 mm. **Venezuela**: UMMZ uncat. JSA (1), El Pozo, Upper Rio Orinoco, 1992.XI.11. UMMZ uncat. JSA (3), El Pozo, Upper Rio Orinoco, 1994.I.1.

Steatogenys elegans.—**Brazil**: INPA uncat. WGRC (35), Mamirauá Ecological Reserve, near Tefé, Amazonas, 110 - 210 mm. UMMZ uncat. JSA (1), Rio Solimões, Amazonas, 130 mm, 1994.IX. **Venezuela**: UMMZ 211325 (1), near Isla Porteguesa, Rio Orinoco, Delta Amacuro, 181 mm, 1978.II.20. UMMZ uncat. JSA (3), mouth of Rio Guaviare, near San Fernando de Atabapo, Rio Orinoco, Amazonas, 1994.I.2. UMMZ uncat. JSA (4), mouth of Rio Guaviare, near San Fernando de Atabapo, Rio Orinoco, Amazonas, 1994.I.2. UMMZ uncat. JSA (4), mouth of Upper Orinoco, Amazonas, 1993.XII.28.

Steatogenys sp. N.—**Ecuador**. MZUSP uncat. RBS 96-31 (1), Rio Tambococha, Napo, 160 mm, 1996.IX.14.

Steatogenys sp. O.—**Brazil:** INPA uncat. WGRC (3), Mamirauá Ecological Reserve, near Tefé, Amazonas, 230 - 325 mm.

Rhamphichthyidae

Gymnorhamphichthys hypostomus.— **Brazil**: MZUSP 27701 (1), Rio Taquari, Coxim, Mato Grosso, 3.XI.1978. MZUSP uncat. MTP 96-135 (4), Rio Solimões, Amazonas, 210 mm, 1996. **Bolivia**: FMNH 54554 (1, HT), Rio Machupo San Joaquin, Beni, bacia do Rio Guaporé, 5.IX.1909. **Paraguay**: CAS 31185 (1), Puerto Bertoni, "Alto Paraguay", 1910. **Venezuela**: FMNH 100744 (1), Rio Suripa, mouth of Rio Anero, Rio Apuré, Apuré, 1991.I.14. MBUCV V uncat. (1), mouth of Rio Guaviare, near San Fernando de Atabapo, Rio Orinoco, Amazonas, 40 mm, 1994.I.2.

Gymnorhamphichthys petiti.—Brazil: INPA 13050 (2), 150 - 180 mm, Ilha da Marchantaria, Amazonas, 10.VIII.1978.

Gymnorhamphichthys sp. O.—**Brazil**: INPA 9669 (3), Boca do Rio Ja Jaú, Rio Negro, Amazonas, 140 - 180 mm, 26.VI.94. MZUSP uncat. MTP 96-126 (1), Amazonas, 120 mm, 1996. **Venezuela**: MBUCV V uncat. (1), mouth of Rio Guaviare, near San Fernando de Atabapo, Rio Orinoco, Amazonas, 140 mm, 1994.I.2.

Gymnorhamphichthys rondoni.—**Brazil**: INPA 9382 (4), Ilha da Marchantaria, Amazonas, 90 - 170 mm, 10.VIII.1978. **Venezuela**: MBUCV V uncat. (2), mouth of Rio Guaviare, near San Fernando de Atabapo, Rio Orinoco, Amazonas, 220 - 290 mm, 1994.I.2. UMMZ uncat. JSA (1), 5 km SE San Fernando de Atabapo, Rio Orinoco, Amazonas, 1993.XII.27. UMMZ uncat. JSA (1), 5 km SE San Fernando de Atabapo, Rio Orinoco, Amazonas, 1993.XII.27. UMMZ uncat. JSA (20), Caño Viejita, Rio Atabapo, Amazonas, 1993.XII.30.

Gymnorhamphichthys rosamaraie.—**Bolivia**: UMMZ 204885 (3), Rio Baures, Rio Madeira, Beni, 1964.X.7. **Brazil**: MZUSP 30202 (HT, 1), Rosa Maria, Rio Negro, Amazonas, 225 mm, 1979.X.24. MZUSP uncat. CCF 96-09 (4), Rio Solimões, Amazonas, - 180 mm, 1996.

Iracema caiana.—**Brazil**: MZUSP 8952 (5), Rio Jauapari, c. 50 km above mouth of Rio Negro, 120 - 330 mm, 1968.IX.19.

Iracema sp. C.—**Brazil**: INPA 4725 (1), Janauacá, Lago da Castanho, Rio Solimões, 170 mm, 17.III.1978.

Rhamphichthys apurensis.—**Venezuela**: MBUCV V uncat. (1), mouth of Rio Guaviare, near San Fernando de Atabapo, Rio Orinoco, Amazonas, 382 mm, 1994.I.2.

Rhamphichthys hahni.—**Argentina**: MZUSP 23133 (1), Rio de La Plata, Buenos Aires, 16.III.1966. **Brazil**: MZUSP 24736 (1), Rio Coxipó da Ponte, Coxipó da Ponte, Mato Grosso, 28.X.1975. MZUSP 24863 (1), Rio Cuiabá, Bocaiuval, Barão de Melgaço, Mato Grosso, 10.VIII.1976. MZUSP 26918 (1), fazenda Jofre, Transpantaneira, Mato Grosso, III.1979. MZUSP 44062 (4), Rio Paranapanema. MZUSP 44679 (1), Rio Cuiabá, 16-22.IX.1981.

Rhamphichthys lineatus.—**Peru**: UMMZ uncat. JSA (1), Rio Momon near Iquitos, Rio Nanay, Loreto, 1993.V.4.

Rhamphichthys cf. marmoratus.—**Brazil**: INPA 3925 (1) Ilha de Careiro, Parana do Rú, Rio Amazonas, Amazonas, 930 mm, XII.1986. INPA 9904 (1), Igarape Miratuca, Rio Jaú, Rio Negro, 680 mm, 30.X.1994. INPA uncat. WGRC (8), Mamirauá Ecological Reserve, near Tefé, Amazonas, 310 - 1130 mm. INPA uncat. WGRC (3), Mamirauá Ecological Reserve, near Tefé, Amazonas, 440 - 1125 mm.

Rhamphichthys reinhardti.—**Brazil:** INPA 9354 (1), Itupiranga, Tocantins, SA, 305 mm, XI.1980.

Rhamphichthys rostratus.—**Brazil**: UMMZ uncat. JSA (1), Rosa Maria, Rio Negro, 1991. **Ecuador**: MZUSP uncat. RBS596-31 (1), Rio Tambocoda, c.500 mm, Rio Napo, 1996.IX.14. **Peru**: NRM 12900 (2), market, Iquitos, 475-535 mm, 1984.VI.26. **Venezuela**: UMMZ uncat. JSA (2), mouth of Rio Guaviare, near San Fernando de Atabapo, Rio Orinoco, Amazonas, 1993.IX.20. UMMZ 211324 (2), nautical mile 132, Rio Orinoco, Delta Amacuro, 322-349 mm, 1979.XI.14.

Rhamphichthys cf. rostratus.—**Argentina**: FML 272 (1), I. Apipa Grande, Ituzaingo Corrientes Paraná, 1950.XI.15.

STERNOPYGIDAE

Archolaemus blax.—**Brazil**: INPA 6422 (11), Rio Mucajai, near mouth Igarape Traira, 175 - 270 mm, 21.I.1987. INPA uncat. (26) Rio Timbo, Rio Trombetas, 65 - 215 mm, 19.IV.1985. MZUSP 24268 (1), 270 mm. MZUSP uncat. (1), Serra da Carajas, Rio Negro, c. 200 mm, 1983.X.16.

Distocyclus conirostris.—**Bolivia**: UMMZ 205080 (1), Rio Mamore at Cachuela, 221 mm, 1964.X.21. **Peru**: UMMZ 216887 (1), Rio Itaya, Loreto, 210 mm, 1947.II.01. **Ecuador**: MZUSP uncat. RBS96 (1), Rio Tambocoda, c. 500 mm, Napo, 1996.IX.14. **Venezuela**: UMMZ 211319 (1), Los Castillos, Delta Amacuro, 266 mm, 1978.II.16. UMMZ 228966 (1), mouth of Guaviare, near San Fernando de Atabapo, Amazonas, 214 mm, 1994.I.02. UMMZ 230815 (2), mouth of upper Rio Orinoco, near San Fernando de Atabapo, Amazonas, 190-205 mm, 1993.XII.25.

Distocyclus goajira.—**Colombia**: NRM 27741 (1), Cano Ponelaolla, Buchado, Rio Atrato, Antioquia, 390 mm, 1989.I.28. **Venezuela**: USNM 121596 (2), Rio Socuy, Maracaibo, 496 mm, 1942.II.24. USNM 121597 (1), Rio Socuy, Maracaibo, 430 mm, 1943.IX.13.

Eigenmannia humboldti.—**Venezuela**: USNM 260240 (22), San Fernando de Apuré, Apuré, 115 - 305 mm, 1983.I.25. USNM 260242 (15), San Fernando de Apuré, Apuré, 116 - 305 mm, 1983.VII.26.

Eigenmannia cf. humboldti .—**Panamá**: MBUCV 14995 (1), Rio Tuyra, 191 mm.

Eigenmannia limbata.—**Brazil**: INPA 4866 (13), Lago de Castonho, Januari, Rio Negro, Amazonas, 75 - 485 mm, 25.II.78. INPA 9976 (6), Parana Apará, Mamirauá Ecological Reserve, Alvarãos, Amazonas, 215 - 385 mm, 11.X.1994. INPA 11539 (2) 325 - 360 mm, Rio Oajaunã, Igarape Jaiau Grande, near base of cachoeira Dardane, MT, 09.XI.1976. INPA uncat. WGRC (10), Mamirauá Ecological Reserve, near Tefé, Amazonas, 170 - 340 mm. **Venezuela**: UMMZ 211320 (2), lagoon at nautical mile 163, Rio Orinoco, Delta Amacuro, 196 - 373 mm,1979.XI.10.

Eigenmannia macrops.—**Brazil**: INPA uncat. WGRC (1), Mamirauá Ecological Reserve, near Tefé, Amazonas, 160 mm. **Guyana**: UMMZ 216212 (2), Bartica, Essequibo River, 140 - 190 mm, 1972.V.20. UMMZ 216503 (17), Bartica, Essequibo River, 139 - 205 mm, 1972.VI.04. **Venezuela**: FMNH 100735 (3), Playa in Rio Suripa, Rio Apuré, Apuré, 90 - 252 mm, 1991.I.13. FMNH 100743 (3), Rio Suripa, Rio Anero, Rio Apuré, Apuré, 100 - 245 mm, 1991.I.14. UMMZ 228963 (4), Isla Buenos Aires in Rio Orinoco 30 km south of Samariapo, Amazonas, 116-230 mm, 1993.XII.23. UMMZ 203807 (3), Pto. Ayacucho, 102-122 mm, 1991.VIII.25. UMMZ 230816 (3), mouth of upper Rio Orinoco, Amazonas, 140-150 mm, 1993.XII.28. UMMZ 230817(2), mouth of Rio Guaviare, Amazonas, 66-180 mm, 1994.I.02. UMMZ 230818 (3), near San Fernando de Atabapo, Amazonas, 138-160 mm, 1993.XII.25.

Eigenmannia cf. macrops sp. B.—**Brazil**: INPA 11516 (3), Parana Apará, Mamirauá Ecological Reserve, Alvarãos, Amazonas, 85 - 115 mm, 02.II.1995. INPA uncat. WGRC (3), Mamirauá Ecological Reserve, near Tefé, Amazonas, 60 - 130 mm.

Eigenmannia microstoma.— **Brazil**: MZUSP 22955 (2), Tres Marias, Rio São Francisco, Minas Gereis, 1964. MZUSP uncat. FCL 9707060 (2), Rio Agua Fria, Araguaçú, Tocantins, 86-96 mm, 1997.XII.7. **Peru**: UMMZ 224597 (1), Rio Cayari, Loreto, 90 mm, 1991.V.15.MZUSP 24643 (2), Três Marias, Rio São Francisco, Minas Gerais, 1978. MZUSP 39472 (4), Rio São Francisco, barra do Rio Formoso, Minas Gerais, 8-10.II.1988.

Eigenmannia cf. microstoma sp. J.—**Brazil**: CAS 1774 (2), Rio Paraiba, Rio de Janeiro, 300-340 mm, 1911.XII.

Eigenmannia nigra.— **Venezuela**: MBUCV 14184 (1, HT), Cano Urama, near Santa Lucía, Rio Negro, Amazonas, 476 mm, 1984.II.4. MBUCV 13437 (1, PT), Mavahate raipids, Guainía, nea San Carlos de Rio Negro, Amazonas, 1981.V.6. MBUCV 14185 (15, PT), collected with HT).

Eigenmannia sp. D.—**Argentina**: FML 1398 (1), Ayo. Rio Salí, Trancas, Tucumán, Salí-Dulce, 1985.XII.19. FML 1467 (2), Qda. de Lules-La Usina, Lules, Tucumán, Salí-Dulce, 1988.VI.13. FML 1644 (3), Ayo. India Muerta, Trancas, Tucumán, Salí-Dulce, 1987.IV.01. FML 1675 (3), Ayo. Rey-Bella Vista, Famaillá, Tucumán, Salí-Dulce, 1991.VII.26. FML 1883 (1), Bahía-Emb. Río Hondo, Río Hondo S. del Estero, Salí-Dulce, 1992.VI.09. FML 1905 (2), Río Medina-Emb. Río Hondo Simoca, Tucumán, Salí-Dulce, 1993.VI.06. FML 2065 (1), Embalse Río Hondo, Río Hondo S. del Estero, Salí-Dulce, 1986.II.16.

Eigenmannia sp. N.—**Brazil**: INPA 9579 (5), Lago Janema, near mouth of Rio Jaú, Rio Negro, 155 - 185 mm, 10.VII.1994. INPA 11406 (111), Lago Coarí, Rio Negro, Amazonas, 190 - 270 mm, 23.X.1992. INPA uncat. WGRC (25), Mamirauá Ecological Reserve, near Tefé, Amazonas, 90 - 360 mm.

Eigenmannia sp. I.—**Brazil**: INPA uncat. WGRC (4), Mamirauá Ecological Reserve, near Tefé, Amazonas, 110 - 260 mm.

Eigenmannia trilineata.—**Argentina**: FML 310 (5) Esteros Laguna Oca, Formosa, 1950.XI.10. FML 343 (6) virescens, Isla Apipé Grande, Ituzaingó Ctes, Bermejo, 1950.X.15. FML 450 (28), Río Paraguay, Formosa,1951.XI.21. FML 503 (2), Laguna López, Formosa, 1951.XI.24. FML 508 (7), Riacho Paz, Formosa, Formosa, Bermejo, 1951.XI.19. FML 550 (1), Rio San Hilario, Formosa, Formosa, Bermejo, 1951.XI.25. FML 623 (5), no collection data. FML 660 (1), no collection data. FML 1036 (13), no collection data. FML 1062 (2), Isla del Paraná, no collection date. FML 1619 (5), Caño Catí, Gral. Paz Corrientes, Paraná, 1987.XII.26. FML 1804 (2), same collection data as FML 1675. FML 2481 (4), Misión La Paz, Rivadavia, Salta, Río Pilcomayo, 1997.XII.01. FML 2490 (8), same locality data as FML 2481, 1998.I.04. FML 2670 (12), same locality data as FML 2481, 1998.VII.24. **Brazil**: MZUSP 25135 (75), ilha de Taiamã (Sema), Rio Paraguay, Mato Grosso, 8.VIII.1980. MZUSP 27740 (3), represa de Furnas, Rio Grande, Alfenas, Minas Gerais, 2-3.X.1975. MZUSP 38169 (13), Rio Paraguay, Descalvados, Cáceres, Mato Grosso, 22.I.1977. **Paraguay**: UMMZ 206286 (8), Arroyo Curimbatay, ca. 15.6 km WSW Curuguaty, Rio Paraná, 50-135 mm, 1979.VII.06. UMMZ 207408 (2), Lago Ypacari, Rio Paraná, 239-250 mm, 1979.VIII.23.

Eigenmannia vicentespelaea.—**Brazil**: MZUSP 42605 (HT, 1), Gruta São Vicente, Rio Tocantins, Goiás, 120 mm, 1978.VII. MZUSP 47984 (PT, 1), Gruta São Vicente, Rio Tocantins, Goiás, 1978.VII.

Eigenmannia virescens.—**Bolivia**: UMMZ 204706 (21), Rio Baures, Beni, 72-182 mm, 1964.IX.29. **Brazil**: INPA 9975 (18), Parana Apará, Mamirauá Ecological Reserve, Alvarãos, Amazonas, 25 - 165 mm. X.1994. INPA uncat. WGRC (17), Mamirauá Ecological Reserve, near Tefé, Amazonas, 60 - 130 mm. **Venezuela**: FMNH 100720 (7), Rio Anarco near mouth of Rio Suripa, Rio Apuré, Apuré, 89-152 mm, 1991.I.01. FMNH 100723 (12), Caño La Indiaolta, near mouth of Rio Suripa, Rio Apuré, Apuré, 70-160 mm, 1991.I.11. FMNH 100727 (34), Caño Socopo, Rio Suripa, Rio Apuré, Apuré, 92-145 mm, 1991.I.12. FMNH 100732 (1), same collection data as FMNH 100727. 108 mm. FMNH 100733 (20), playa in Rio Suripa, 15 km above pump station, Rio Apuré, Apuré, 71-117 mm, 1991.I.13.

Eigenmannia cf. virescens.— **Argentina**: MLP 6071 (1), Rio de La Plata, Punta Lara, Buenos Aires, 29.VI.1959. MLP 6127 (2), San Nicolas, Buenos Aires, III.1953. USNM 126847 (1), 1903-4. USNM 176010 (1), Buenos Aires, VII.1931. **Brazil**: INPA 99832 (3), Lago Amaná, Marão, Rio Japará, Amazonas, 1.V.1995, 150 - 180 mm. MZUSP 3797 (2), Rio São Francisco, Bahia, 1941. MZUSP 24722 (1), Rio Coxipó Mirim, Cuiabá, Mato Grosso, 2.IX.1975. MZUSP 27723 (1), Rio Taquari, Coxim, Mato Grosso, 22.X-2.XI.1980. MZUSP 28567 (1), Rio Taquari, junto à cidade de Coxim, Mato Grosso, X.1983. MZUSP 39162 (2), córrego Tapera, afl. Rio São Francisco, Minas Gerais, 23.XI.1987. MZUSP 39472 (4), barra do Rio Formoso, Rio São Francisco, Minas Gerais, 8-10.II.1988. MZUSP 44386 (20), Rio Paraguay Cáceres e arredores, Cáceres, Mato Grosso, 11-12.VIII.1991. MZUSP 47364 (2), riacho afluente do Rio Correntina, na faz. São José, próximo à Barra de São José, 22.VII.1994. INPA uncat. WGRC (5), Mamirauá Ecological Reserve, near Tefé, Amazonas, 65 - 160 mm.

†*Ellisella kirschbaumi*.—**Bolivia**: RL 1596-01 (1), Río Alto Moile, 95 km WNW Santa Cruz de la Sierra. Collected before 1973. RL 1596-03 (1), same collection data as RL 1596-01. RL 1596-04 (1), same collection data as RL 1596-01. 1596-05 (1), same collection data as RL 1596-01. 1596-07 (1), same collection data as RL 1596-01. RL 1596-13 (1), same collection data as RL 1596-01. RL 1596-15 (1), same collection data as RL 1596-01. RL-uncat. 1 (1), same collection data as RL 1596-01. RL-uncat. 2 (1), same collection data as RL 1596-01. RL-uncat. 3 (1), same collection data as RL 1596-01.

Rhabdolichops caviceps.—**Venezuela**: UMMZ 214592 (2), Rio Orinoco, above Barrancas, Delta Amacuro, 203-208 mm, 1976.II.18. UMMZ 214593 (12), Rio Orinoco, Isla Tres Caños, Delta Amacuro, 90 - 222 mm, 1979.IX.24. UMMZ 214594 (3), Rio Orinoco, Braza Imataca, Delta Amacuro, 183 - 213 mm, 1978.II.23. UMMZ 214597 (2), Rio Orinoco, at Palua, Delta Amacuro 160 - 273 mm, 1979.IX.09. UMMZ 230812 (3), mouth of Rio Guaviare, San Fernando de Atabapo, Amazonas, 151 - 165 mm, 1994.I.02.

Rhabdolichops eastwardi.—**Venezuela**: FMNH 100748 (14), Rio Suripa, mouth of Rio Anero, 118 - 256 mm, 1991.I.14. UMMZ 214598 (12), Lagoon of Rio Orinoco, Delta Amacuro, naut. mi. 201, on south side of Isla Isabela, 114 - 213 mm, 1979.IX.07. UMMZ 228968 (23), mouth of Rio Guaviare, San Fernando de Atabapo, Amazonas, 170 - 276 mm, 1994.I.2. UMMZ 230813 (30), mouth of Rio Guaviare, San Fernando de Atabapo, Amazonas, 125 - 256 mm, 1994.I.02.

Rhabdolichops electrogrammus.—**Venezuela**: MBUCV 10489

1964.VIII, 182 mm, from USNM 218830. MZUSP 48375 (4, PT), same locality as HT, 162 - 260 mm. USNM 218830 (15; PT, 2 C&S), same locality as HT, 175 - 265 mm. USNM 326120 (3), Rio Batovi, Rio Xingu, Mato Grosso do Sul, Sta. B, 380 - 525 (1, HT), Isla Tres Caños, near Caño Araguaito, Delta Amacuro, 225.7 mm, 1978.II.19. FMNH 97070 (3), Isla Portuguesa, 116 nautical miles from sea buoy, Delta Amacuro, 125 - 142 mm, 1978:II.16. MBUCV 14666 (1), Rio Cataniapo, near Puerto Ayacucho, Amazonas, 292 mm, 1984.XII.26. UMMZ 214599 (1), Rio Orinoco, Delta Amacuro, downstream of Isla Portuguesa, ca. naut. mi. 116.5, 212 mm, 1979.IX.14.

Rhabdolichops sp. (unidentified).—**Suriname**: NRM 64 (ST), no locality on label, from King Adolf Fredrik's collection at Ulriksdal, probably from near Paramaribo.

Rhabdolichops sp.—**Venezuela**: UMMZ 230832 (6), mouth of Rio Guaviare, across from San Fernando de Atabapo, Amazonas, 56 - 122 mm, 1994.I.2. UMMZ 228969 (1), mouth of Rio Guaviare, across from San Fernando de Atabapo, Amazonas, 190 mm, 1993.XII.25. UMMZ 230833 (1), mouth of Rio Guaviare, across from San Fernando de Atabapo, Amazonas, 89 mm, 1993.XII.28.

Rhabdolichops stewarti.—**Brazil**: ANSP 158678 (1, HT), 26 km E Jacaréacanga, Rio Tapajos, Pará, 98 mm. **Venezuela**: MBUCV 7541 (1, PT), Quiritare, near mouth Rio Cuncunuma, Rio Orinoco, Amazonas, 110 mm.

Rhabdolichops troscheli.—**Bolivia**: UMMZ 204707 (3), 6 km SW Costa Marques, Rio Itenez, Rio Baures, Beni, 93 - 152 mm, 1964.IX.29. UMMZ 205078 (1), Rio Mamore at Cachuela, just below Guayaramerin, Dept. Beni, 85 mm, 1964.X.21. **Brazil**: MBUCV 9772 (6), Rio Amazonas, near Manaus, 1977.II. MCZ 54336 (4), south bank Rio Solimoes, 0.5 km mouth Parana de Januaca, Amazonas, 1976.XII.9. INPA 4827 (46), Rio Uatumá, Balbina, Barquem, Amazonas, c. 100 - 490 mm, 24.X.1987. **Venezuela**: MBUCV 10625 (1), Delta Amacuro, 1993.III.15.

Rhabdolichops zareti.—**Venezuela**: UMMZ 214569 (94), Lagoon of Rio Orinoco, naut. mi. 210, on south side of Isla Isabela, between Paula and Ciudad Bolivar, 85 - 225 mm, 1979.IX.07.

Sternopygus aequilabiatus dariensis.—**Colombia**: FSUC uncat. (2), upper Rio Nercua, Rio Truando, Choco, 145 - 252 mm, 1967.VIII.28. FSUC uncat. (11), Rio Solado, near Teresita, Rio Solando, Choco, 103 - 320 mm 1968.II.08. NRM 10697 (1), Rio Saija, Choco, 170 mm, 1939. NRM 10698 (3), Rio San Juan, Choco, 1939. **Panamá**: CAS 14037 (1), Rio Tuyra, Marrigante, Darien, 1912.III. FMNH 8949 (1, HT), Rio Tuyra, Marrigante, Darien, 1912.III.08. FMNH 8829 (1, PT), collected with HT. USNM 329425 (2), Rio Mebrillo, Colon, 180 - 185 mm, 1967.III.22.

Sternopygus aequilabiatus pejeraton.—**Venezuela**: UMMZ 157671 (2), Rio Palmar, near Totuma, Lago Maracaibo, Zulia, 195-228 mm, 1942.II.21. USNM 121567 (17), Rio Socuy, Lago Maracaibo, Zulia, 160 - 426 mm, 1942.II.24.

Sternopygus arenatus.—**Ecuador**: NRM 28178 (2), market, Guayaquil, 490 - 595 mm, 1934.XI.26. UMMZ 205390 (4), Guayaquil, 260 - 525 mm, date unknown.

Sternopygus astrabes.— **Brazil**: INPA 9981 (1), Lago Amanã, Marão, Rio Japará, Amazonas, 620 mm, V.1995. INPA uncat. WGRC (1), Igarapé on road past airport, Tefé, Amazonas, 160 mm, 1998.XII.30. **Venezuela**: MZUCV 14182 (1, HT), cano Poxo Azul, Agua Linda, c. 23 km. NE Puerto Ayacucho, Rio Orinoco, Amazonas, 196 mm, 1983.III.30. MZUCV 13896 (6, PT), collected with HT.

Sternopygus castroi.—**Brazil**: MZUSP 48912 (1, HT), Igarape Jaradá, Rio Cuieiras, 40 km from mouth of Rio Negro, Amazonas, 178 mm, 1977.II.1. MZUSP 48191 (1, PT), collected with HT, 117 mm. MZUSP 49788 (1, PT), collected with HT, 142 mm.

Sternopygus macrurus.—**Brazil**: MCZ 9453 (1), Lago Aleixo, Rio Negro, Amazonas, 212 mm, 1865.XI.27. MZUSP 2644 (1), Rio São Francisco, Bahia, 1908. MZUSP 24476 (1), Rio São Francisco, Propriá, Sergipe, 18.XII.1975. MZUSP 24652 (1), Pedra Ponte, Três Marias, Minas Gerais, 23.VIII.1978. MZUSP 25136 (1), ilha de Taiamã (Sema), Rio Paraguay, Mato Grosso, 8.VIII.1980. MZUSP 27740 (1), Rio Taquari, Coxim, Mato Grosso do Sul. MZUSP 28568 (1), Rio Taquari, junto à cidade de Coxim, Mato Grosso, X.1983. MZUSP 36339 (2), Ladá Rio Corumbá, Mato Grosso, IX.1985. MZUSP 39474 (3), Rio São Francisco, barra do Rio Formoso, Minas Gerais, 8-10.II.1988. MZUSP 39640 (1), Rio Abaeté, Tiros, Minas Gerais, 18.III.1988. MZUSP 39951 (1), Água Vermelha, Rio Grande, São Paulo e Minas Gerais, 27.VI.1978. MZUSP 44418 (3), Cáceres, Rio Paraguay, Mato Grosso, 11-12.VIII.1991. MZUSP 45345 (2), riacho Monjolinho, Rio Preto, São Francisco, Mato Grosso, 24.X.1992. MZUSP 47447 (1), Rio Verde, entre Francisco Sá e Montes Claros, Minas Gerais, 23.VII.1994. NRM 14073 (1), Joapoary, Amazonas, 505 mm, 1924.XI.30. UMMZ 203393 (1), Rio Tocantins, Belem, Pará, 355 mm, 1935.VII.19. UMMZ 216316 (1), Barreiras, mouth of Rio Grande, Bahia, 275 mm, 1942.III.28. USNM 326121 (3), Waura, Rio Batovi, Rio Xingu, Mato Grosso do Sul, Sta. S, 133 - 368 mm, 1964.VIII. USNM 44967 (1), Rio das Velhas, São Francisco, 354 mm, 1895.II.15. USNM uncat. (6), Waura, Rio Batovi, Rio Xingu, Mato Grosso do Sul, Sta. X, 125 - 215 mm, 1964.VIII. USNM uncat. (2), Waura, Rio Batovi, Rio Xingu, Mato Grosso do Sul, Sta. J, 161 - 164 mm, 1964.VIII. **Colombia**: UMMZ 179240 (1) Rio Meta, 312 mm, 1936. **Guyana**: UMMZ 13054 (1), Botami Gardens, Georgetown, 308 mm, no date. UMMZ 215184 (1), Mahida Creek, Potaro River, Essequibo River, 180 mm, 1971.VIII.20. UMMZ 215834 (2), canal at Anna Regima, Essequibo coast, tidal influence, 138 - 461 mm, 1971.VIII.27. UMMZ 215916 (1), Barana River at Kokerite Village, 57.5 km from mouth of Barama River, 384 mm, 1971.IX.01. USNM 209204 (1), Crusa Creek, Rupununi District, 160 mm, 1970.V.15. **Paraguay**: UMMZ 206424 (1), 3 km N Salto del Guaira, 143 mm, 1979.VII.13. UMMZ 208004 (1), Arroyo Guarico, 33 km S Hwy. #5, at Yhy-yan, 102 mm, 1979.IX.11. **Peru**: UMMZ 228964 (2), Buen Suceso, Rio Javari, Loreto, 270 - 285 mm, 1993.V.15. UMMZ 228965 (1), Santa Ana, Rio Tahwayo, Loreto, 224 mm, 1993.V.6. USNM 86835 (1), Rio Pichis, Loreto, 176 mm, 1920. **Venezuela**: FMNH 100719 (1), Rio Anarco near Rio Suripa, Rio Apuré, Apuré, 175 mm, 1991.I.01. FMNH 100725 (5), Caño Socopo, Rio Suripa, Rio Apuré, Apuré, 1991.I.07. FMNH 100726 (1), same locality data as FMNH 100725, 197 mm, 1991.I.12. UMMZ 212346 (1), Esteros de Camaguan, Guarico, Rio Apuré, Apuré, 36 mm, 1981.VIII.21. USNM 194179 (1), Rio Las Palmas, Barinas, 306 mm, 1958.VI.15.

Sternopygus sp. B.—**Bolivia**: UMMZ 204744 (22), 6 km SW Costa Marques, Rio Itenez, Rio Baures, Beni, 124 - 415 mm, 1964.IX.30. UMMZ 204888 (11), same locality data as UMMZ 204744, 145 - 411 mm, 1964.X.07.

Sternopygus sp. G.—**Guyana**: FMNH 50185 (1), creek near border, New River, 170 mm, 1938.X. NRM 29502 (3), Iracoubo, Cayenne, 24 - 178 mm, 1986.IV.22.

Sternopygus xingu.—**Brazil**: INPA 6918 (1), Lago Touá, Tocantins, Para, 360 mm, XI.1980. INPA 6426 (1), Lago Touá, Tocantins, Para, 445 mm, XI.1980. MZUSP 48374 (1, HT), Waura Indian village, Rio Batovi, Rio Xingu, Mato Grosso do Sul, Sta.X, 1964.VIII, 182 mm, from USNM 218830. MZUSP 48375 (4, PT), same locality as HT, 162 - 260 mm. USNM 218830 (15; PT, 2 C&S), same locality as HT, 175 - 265 mm. USNM 326120 (3), Rio Batovi, Rio Xingu, Mato Grosso do Sul, Sta. B, 380 - 525 mm, 1964.VIII, paratypes. USNM uncat. (28, PT, 2 C&S), Rio Batovi, Rio Xingu, Mato Grosso do Sul, 91 - 240 mm, Sta. S, 1964.VIII. USNM 338273 (14, PT), Waura, Rio Batovi, Rio Xingu, Mato Grosso do Sul, 72 - 304 mm, 1964.VIII. UMMZ 228961 (PT, 4) 2 C&S, same data as HT, 206 - 265 mm.

Appendix 2. Materials examined for neuromorphological character data. Specimens from museum lots representing 35 gymnotiform species were examined, including the brains of 138 specimens. These include serially sectioned brains of 25 species, of which 10 species are represented by perfused specimens. Data are arranged alphabetically by family, genus, and species. Museum acronym and number is followed in parentheses by number of specimens examined, then numbers of specimens perfused and brains sectioned, and then size range in millimeters total length.

Apteronotidae. *Adontosternarchus balaenops*. UMMZ uncat. JSA JGL-93 (1) 0-0, 175 mm. *Adontosternarchus devenanzii*. FMNH 100741 (1) 0-1. UMMZ 228972 (1) 1-1. *Adontosternarchus sachsi*. FMNH 100742 (1) 0-0, 110-138 mm. UMMZ 228979 (1) 1-1. *Apteronotus albifrons*. UMMZ uncat. JSA (6) 6-6, 70-190 mm. *"Apteronotus" apurensis*. FMNH 085499 (1) 0-1, 38-188 mm. *Apteronotus leptorhynchus*. UMMZ uncat. JSA (10) 0-1, 90-135 mm. UMMZ uncat. JSA (6) 2-2, 88-140 mm. *Compsaraia compsa*. UMMZ 211308 (1) 0-1, 196-311 mm. UMMZ 228981 (2) 1-0. UMMZ 228982 (2) 0-0, 110-255 mm. *Orthosternarchus tamandua*. UMMZ uncat. JSA JGL-94 (1) 0-0, 230 mm. *Platyurosternarchus macrostomus*. FMNH 100730 (2) 0-2, 156-212 mm. *"Porotergus" gimbeli*. UMMZ uncat. JSA JGL-94 (2) 0-0, 150-205 mm. *Sternarchella orinoco*. UMMZ 228975 (1) 0-0. UMMZ 228976 (1) 1-0. _*Sternarchella orthos*. FMNH 100746 (3) 0-3, 94-204 mm. UMMZ 228977 (1) 1-0. UMMZ 228978 (1) 1-0. *Sternarchogiton sp*. B. UMMZ 211315 (3) 0-1, 149-193 mm. *Sternarchogiton nattereri*. UMMZ 211330 (1) 0-1, 111 mm. UMMZ uncat. JSA (2) 0-0. *Sternarchorhamphus muelleri*. UMMZ uncat. JSA JGL-94 (1) 0-0, 310 mm. UMMZ 228973 (1) 0-1. USNM 228807 (3) 0-1, 163-455 mm. *Sternarchorhynchus curvirostris*. UMMZ uncat. JSA JGL-94 (1) 0-0, 256 mm. FMNH 100722 (1) 0-1. *Sternarchorhynchus oxyrhynchus*. UMMZ 228974 (1) 1-1, 270 mm.

Gymnotidae. *Electrophorus electricus*. UMMZ uncat. JSA CC-92 (1) 1-1. Yokohama City University no. 32 (1) 0-0. *Gymnotus carapo*. UMMZ 228998 (2) 0-1. UMMZ 228999 (1) 0-0, 166 mm. UMMZ 230734 (2) 0-0, 191-211 mm. *Gymnotus inaequilibeatus*. UMMZ 207025 (2) 0-2.

Hypopomidae. *Brachyhypopomus pinnicaudatus*. Perú. UMMZ 224602 (1) 0-0. UMMZ uncat. JSA (1) 0-0. UMMZ uncat. JSA A&D 94-1 (1) 0-0. UMMZ uncat. JSA A&R 93-1 (3) 0-1. *Hypopygus lepturus*. UMMZ uncat. JSA (2) 0-0. UMMZ uncat. JSA A&R 93-2 (2) 0-1. *Microsternarchus bilineatus*. UMMZ uncat. JSA A&R 93-1 (2) 0-0. *Steatogenys duidae*. UMMZ uncat. JSA (1) 0-1. UMMZ 228994 (3) 1-0. *Steatogenys elegans*. UMMZ 228996 (3) 0-0.

Rhamphichthyidae. *Gymnorhamphichthys hypostomus*. FMNH 100744 (1) 0-1. *Gymnorhamphichthys rondoni*. UMMZ 228997 (10) 0-3. *Rhamphichthys rostratus*. UMMZ uncat. JSA A93-1 (2) 0-2, 180-265 mm.

Sternopygidae. *Distocyclus conirostris*. UMMZ uncat. JSA A&R 94-1 (1) 0-0. *Eigenmannia macrops*. UMMZ uncat. JSA A&R 93-3 (4) 0-0, 155-190 mm. *Eigenmannia virescens*. UMMZ uncat. JSA A 91-1 (3) 0-1, 140-170 mm. Perú. UMMZ uncat. JSA A&D 93-3 (10) 0-1, 125-216 mm. *Rhabdolichops caviceps*. UMMZ uncat. JSA A&R93-3 (1) 0-0. *Rhabdolichops eastwardi*. FMNH 100748 (10) 0-1. UMMZ uncat. JSA A&R94-1 (2) 0-1. *Sternopygus macrurus*. UMMZ 204744 (3) 0-1. Perú. UMMZ uncat. JSA A&D 93-3 (2) 0-0, 260-285 mm.

Appendix 3. Abbreviated descriptions of 249 gymnotiform characters and states used in Table 2. Complete descriptions in text. Abbreviations: AFP = anal-fin pterygiophores; AFR = anal-fin rays; Dc= telencephalic nucleus dorsalis centralis; Dca= telencephalic dorsalis centralis anterior; DHS = displaced hemal spines; Dm= telencephalic dorsalis medialis; Dp= telencephalic dorsalis posterior; EOD= electric organ discharge; EG= eminentia granularis; ELL= electrosensory lateral line lobe; PCV = precaudal vertebrae.

1. Body girth. 0: laterally compressed; width less than 70% depth at pectoral girdle. 1: cylindrical or subcylindrical, width more than 70% depth.
2. Body depth. 0: thin, depth at pectoral girdle more than 11% total length. 1: elongate, depth less than 11% total length.
3. Anal fin membrane. 0: evenly pigmented. 1: with pale posterior patch.
4. Oblique stripes. 0: absent. 1: present.
5. Saddle - shaped bars. 0: absent. 1: present.
6. Irregular blotches. 0: absent. 1: present.
7. Clear area at base of caudal fin. 0: absent. 1: present.
8. Longitudinal lines. 0: absent. 1: 2 - 3 thin dark lines. 2: white line.
9. Pigments. 0: low contrast. 1: high contrast.
10. Antorbital stripe. 0: absent. 1: present.
11. Pigment distribution. 0: even. 1: blotchy, marbled.
12. Body translucence. 0: absent. 1: present.
13. Branchial opening. 0: large. 1: small.
14. Body squamation. 0: absent. 1: present.
15. Scales on middorsum. 0: present. 1: absent anteriorly. 2: absent on whole middorsum.
16. Scales posterolateral body. 0: present. 1: absent.
17. Scales size, Number above lateral line at midbody. 0: small, 9 - 11. 1: medium, 5 - 8. 2: large, 3 - 4. 3: very small, more than 11.
18. Scale shape. 0: ovoid. 1: rhomboid.
19. Gape large. 0: less than one third head length. 1: more than one third head length.
20. Gape short. 0: absent. 1: present.
21. Oral opening in adults. 0: terminal. 1: superior. 2: inferior.
22. Oral dentition. 0: present. 1: absent.
23. Adult dentition. 0: present. 1: absent.
24. Shape of teeth. 0: conical. 1: villiform.
25. Premaxilla large. 0: triangular. 1: elongate lateral margin.
26. Premaxilla shape. 0: triangular. 1: trapezoidal, elongate.
27. Premaxilla gracile. 0: triangular. 1: thin and scroll-shaped in adults, 0 - 2 teeth.
28. White sagital pigments. 0: absent. 1: present in mid-dorsal and mental surfaces.
29. Maxillary dentition. 0: 6 - 10. 1: none.
30. Maxillary shape. 0: robust, wide as deep. 1: thin, less than twice deep as wide.
31. Maxillary head. 0: sessile. 1: on stalk.
32. Anterior process of maxilla. 0: absent. 1: present.
33. Anterior hook of maxilla. 0: absent. 1: present.
34. Anterior maxillary margin. 0: broad, triangular. 1: cartilaginous.
35. Anterior shelf of maxilla. 0: absent. 1: present.
36. Descending blade maxilla. 0: thin, curved. 1: broad, with anterior shelf.
37. Descending blade maxilla. 0: ventral margin rounded. 1: ventral margin angled. 2: ventral margin not ossified.
38. Maxillary - anguloarticular ligament. 0: absent. 1: present.
39. Rows of dentary teeth. 0: 1 row. 1: 2 - 3 rows.
40. Dentary shape. 0: longer than deep. 1: deeper than long.
41. Dentary gracile. 0: absent. 1: present.
42. Dentary filamentous. 0: absent. 1: present.
43. Dentary hook. 0: absent. 1: present.
44. *M. adductor mandibula.* 0: no intermusculars. 1: intermusculars present.
45. *M. adductor mandibula* insertion. 0: to maxilla. 1: also to 1st infraorbital.
46. *M. levator posterior.* 0: present. 1: absent.
47. *M. sternobrachialis.* 0: absent. 1: present.
48. Anterior limb anguloarticular. 0: longer than posterior limb. 1: shorter than posterior limb.
49. Posterior limb anguloarticular. 0: shorter than retroarticular. 1: longer than retroarticular.
50. Snout (preorbital distance) long. 0: about one third head length. 1: long, more than one third head length. 2: elongate, gracile, recurved.
51. Snout short. 0: one third head length. 1: less than one third head length.
52. Mesethmoid shape. 0: broad. 1: narrow.
53. Mesethmoid length. 0: Absent. 1: Present.
54. Mesethmoid, tip size. 0: robust. 1: reduced.
55. Mesethmoid, tip shape. 0: straight. 1: flexed.
56. Mesethmoid tip process. 0: absent. 1: anterolateral process.
57. Mesethmoid tip groove. 0: flat. 1: concave.
58. Ventral ethmoid. 0: with blunt lateral process. 1: without process.
59. Ventral ethmoid process. 0: lateral process flat, gracil. 1: lateral process blunt, rounded.
60. Ventral ethmoid septum. 0: long as deep. 1: longer than deep.
61. Ventral ethmoid shape. 0: deepest at midlength. 1: deepest posterior to midlength.
62. Dermal vomer. 0: ossified. 1: not ossified.
63. Ethmoid cartilage. 0: narrow. 1: deep.
64. Lateral ethmoid size. 0: large, contacting other cranial bones. 1: small, not contacting other bones.
65. Lateral ethmoid. 0: ossified. 1: unossified.
66. Base lateral ethmoid. 0: broad. 1: narrow.
67. Nasal. 0: narrow. 1: broad.
68. Sclerotic bones. 0: present. 1: absent.
69. Antorbital process frontals. 0: absent. 1: present.
70. Dorsal margin of frontals. 0: flat or convex. 1: concave.
71. Cranial fontanels. 0: present. 1: absent.
72. Sphenoid region. 0: short, preorbital distance about 0.3 total head length. 1: elongate, orbit in advance of middle of head. 2: very elongate, distance from orbit to tip of snout less than 0.3 post-orbital distance.
73. Orbitosphenoid shape. 0: broad. 1: narrow.
74. Orbitosphenoid margin. 0: contact pterosphenoid. 1: not contact pterosphenoid.
75. Sphenotic process. 0: absent. 1: present.
76. Parasphenoid lateral wing. 0: present. 1: absent.
77. Parasphenoid ventral margin. 0: flat. 1: angled at about midlength.
78. Parasphenoid dorsal margin. 0: broad. 1: narrow.
79. Parasphenoid process. 0: absent. 1: anteroventral process.

80. Posterior parasphenoid. 0: broad. 1: narrow.
81. Posttemporal fossae. 0: absent. 1: present.
82. Cranial skeleton texture. 0: laminar. 1: reticulate.
83. Nasal loop. 0: Vertical commissure. 1: rostral loop of commissure.
84. Infraorbital canal. 0: anterior pore near 1st infraorbital. 1: subnasal extension, anterior pore remote from 1st infraorbital.
85. Antorbital. 0: without infraorbital canal. 1: bearing portion of infraorbital canal.
86. Antorbital size. 0: small. 1: large.
87. Infraorbital canal plates. 0: narrow. 1: broad.
88. Infraorbital canal tube. 0: Six separate bones. 1: single tube.
89. First infraorbital. 0: present. 1: absent.
90. Mandibular canal. 0: free. 1: fused with mandible.
91. Mandibular canal ossicles. 0: long slender tubes. 1: dumbbell - shaped ossicles.
92. Supratemporal lateralis canal. 0: straight. 1: L - shaped.
93. Intercalar. 0: present. 1: absent.
94. Lateral line pores. 0: all short. 1: some posterior pores long.
95. Lateral line ventral rami. 0: absent. 1: present.
96. Number ventral rami. 0: less than 16. 1: more than 16.
97. Position of nasal capsule. 0: near eye. 1: near tip of snout.
98. Position of anterior nares. 0: dorsal surface. 1: within gape.
99. Anterior narial pore. 0: at end of tube. 1: sessile.
100. Olfactory bulb. 0: sessile. 1: pedunculate.
101. Dorsal telencephalic nuclei. 0: Dca small, Dm large. 1: Dca large, Dm small.
102. Telencephalic area Dp. 0: small. 1: large. 2: very large.
103. Telencephalic nucleus Dcl. 0: cells uniform. 1: magnocellular portion.
104. Position of eye. 0: free orbital margin. 1: subdermal.
105. Eye size. 0: large, 2 diameters in postorbital distance. 1: small, less than 5 diameters in postorbital distance.
106. Eyeball and muscles. 0: robust. 1: eyeball minute, no muscles.
107. Accessory optic system. 0: present. 1: absent.
108. Optic tectum. 0: posterior pole large. 1: posterior pole small.
109. Hypothalamus. 0: short. 1: deep.
110. Integumental taste buds. 0: present. 1: absent.
111. Schreckstoff/club cells. 0: present. 1: absent.
112. Passive electroreception. 0: absent. 1: present.
113. Ampullary organ rosettes. 0: absent. 1: present.
114. Active electroreception. 0: absent. 1: present.
115. Tuberous electroreceptors. 0: monomorphic. 1: two morphological classes.
116. Preotic lateralis ganglia. 0: separate. 1: fused.
117. Posterior lateral line nerve. 0: no accessory rami. 1: with dorsal ramus. 2: superficial dorsal ramus.
118. Lateral line afferents. 0: not segregated. 1: fasciculated.
119. ELL size. 0: small. 1: large.
120. ELL ventral margin. 0: flat. 1: curved.
121. ELL spherical cells. 0: no basal dendrites. 1: with basal dendrites.
122. Anterior EG. 0: large. 1: small.
123. Posterior EG. 0: small. 1: large.
124. Anterior corpus cerebellum. 0: large. 1: small.
125. Lateral valvula cerebellum. 0: small. 1: large.
126. Pacemaker nucleus. 0: small. 1: large.
127. Autopalatines. 0: ossified, straight. 1: cartilaginous, arched.
128. Ectopterygoid. 0: present. 1: absent.
129. Ascending process metapterygoid. 0: absent. 1: present.
130. Endopterygoid process. 0: absent. 1: present.
131. Endopterygoid process. 0: retained to adult. 1: lost in ontogeny.
132. Endopterygoid shape. 0: no anterior process. 1: with anterior process.
133. Endopterygoid dentition. 0: numerous. 1: few or none.
134. Metapterygoid posterior margin. 0: separate from hyomandibula. 1: contacting hyomandibula.
135. Metapterygoid shape. 0: double - headed ax. 1: triangular.
136. Metapterygoid posterior wing. 0: broad. 1: narrow.
137. Size of sympletic. 0: smaller than hyomandibula. 1: larger than hyomandibula.
138. Orientation of hyomandibula. 0: oblique to head. 1: parallel to head.
139. Hyomandibular proximal articulation. 0: broad. 1: narrow.
140. Preopercular orientation. 0: oblique to head axis. 1: parallel to head axis.
141. Anterior limb preoperculum. 0: broad, crescent. 1: narrow, curved.
142. Shape of operculum. 0: rectangular, trapezoidal. 1: triangular.
143. Opercular dorsal margin. 0: convex. 1: straight. 2: concave.
144. Number branchiostegal rays. 0: 3 - 4. 1: 5 - 6. 2: more than 7.
145. Shape of branchiostegal rays. 0: anterior 1 - 2 rays broad. 1: anterior rays narrow.
146. Gill raker configuration. 0: contacting gill bar. 1: not contacting gill bar.
147. Gill raker tips. 0: ossified. 1: not ossified.
148. Pharyngobranchial 3. 0: present. 1: absent.
149. Pharyngobranchials. 0: cartilaginous. 1: ossified.
150. Pharyngobranchial plates. 0: present. 1: absent.
151. Epibranchial 5. 0: posterior margin flat. 1: with short posterior process.
152. Epibranchial 6. 0: straight. 1: sinuous.
153. Epibranchial 6 shape. 0: short ascending process. 1: elongate ascending process.
154. Epibranchial 7. 0: posterior surface flat. 1: posterior process.
155. Epibranchial 7 posteromedial process. 0: absent. 1: present.
156. Ceratobranchial 4. 0: no posterior process. 1: posterior process present.
157. Ceratobranchial 6. 0: smooth. 1: with lateral process.
158. Hypobranchial 3. 0: rod - shaped. 1: triangular.
159. Hypobranchial 3. 0: rectangular. 1: pentagonal.
160. Hypobranchial 4. 0: medial surface smooth. 1: medial bridge.
161. Basihyal dorsal ridge. 0: flat. 1: dorsoposterior crest.
162. Basihyal dorsal groove. 0: absent. 1: present.
163. Basibranchials. 0: ossified. 1: unossified.
164. Basibranchial 4. 0: rod - shaped. 1: hourglass - shaped.
165. Basibranchial 5. 0: ossified. 1: unossified.
166. Urohyal head. 0: small. 1: large.
167. Urohyal posterior blade. 0: ossified. 1: unossified.
168. Urohyal blade hyperossified. 0: to 3rd basibranchial. 1: to 4th basibranchial.
169. Posttemporal. 0: independent. 1: fused with supracleithrum.
170. Extrascapular. 0: independent ossification. 1: fused with neurocranium.

171. Postcleithra. 0: robust. 1: thin, discoid.
172. 3rd postcleithrum. 0: ossified. 1: not ossified.
173. Scapular foramen. 0: absent. 1: present.
174. Mesocoracoid. 0: present. 1: absent.
175. Anterior coracoid process. 0: present. 1: absent.
176. Proximal pectoral radials. 0: 3 and 4 separate. 1: 3 and 4 fused.
177. Pectoral fin size. 0: large. 1: small.
178. Number pectoral radials. 0: 4. 1: 8.
179. Pelvic girdle and fin. 0: present. 1: absent.
180. Claustrum. 0: present. 1: absent.
181. Anterior vertebral parapophyses. 0: near *os suspensorium.* 1: separated by gap.
182. Position of neural spines. 0: middle of caudal centra. 1: posterior of caudal centra.
183. Vertebral fenestrae. 0: absent. 1: present.
184. Shape anterior intermusculars. 0: simple or little branched. 1: branched. 2: highly branched at PCV 7 - 9.
185. Caudal intermusculars. 0: not regenerated. 1: regenerated.
186. Displaced hemal spines. 0: Absent. 1: Present.
187. DHS anterior series. 0: absent. 1: present.
188. DHS 1. 0: narrow, straight. 1: saber - shaped.
189. DHS 1 proximal surface. 0: narrow. 1: broad as blade.
190. DHS 2 shape. 0: straight. 1: curved.
191. Number posterior DHS. 0: 2 - 3. 1: 1.
192. Dorsal organ. 0: absent. 1: epidermal structure along dorsal body margin.
193. Dorsal organ length. 0: posterior half of body. 1: entire dorsum.
194. Dorsal and adipose fins. 0: present. 1: absent.
195. Anal fin origin. 0: posterior to pectoral girdle. 1: at pectoral girdle. 2: at isthmus.
196. Number anal-fin rays. 0: less than 100. 1: 100 - 159. 2: 160 - 199. 3: 200 - 299. 4: 300 or more.
197. Number unbranched anal-fin rays. 0: 10 - 15. 1: 15 - 25. 2: 30 - 60. 3: all.
198. Anal - fin pterygiophore length. 0: shorter than hemal spines. 1: longer than hemal spines.
199. Shape of AFP blades. 0: slender. 1: broad.
200. Shape of AFP tips. 0: tapered. 1: arrow - head shaped.
201. AFR articulation. 0: proximal pterygiophores. 1: distal pterygiophores.
202. Distal AFP. 0: present. 1: absent.
203. AFR posterior rays. 0: not to tip of tail. 1: to tip of tail.
204. Regenerated hemal and neural spines. 0: absent. 1: present.
205. Body cavity long. 0: 22 or less PCV. 1: 23 - 29 PCV. 2: 30 or more PCV.
206. Body cavity short. 0: 16 or more PCV. 1: 12 - 15 PCV. 2: 10 - 11 PCV.
207. Number transitional vertebrae. 0: 2 - 8. 1: 1. 2: 20 or more.
208. Hemal spines. 0: present. 1: absent.
209. Number of pleural ribs. 0: 8 or more. 1: 7 or less.
210. Length of anterior ribs. 0: short, less than 0.80 body depth. 1: long, more than 0.80 body depth.
211. Size of anterior ribs. 0: narrow. 1: broad.
212. Posterior parapophyses. 0: small, not contacting. 1: long, contacting on midline.
213. Shape last precaudal parapophyses. 0: broad, triangular. 1: slender, sinuous.
214. Posterior chamber gas bladder. 0: entirely within body cavity. 1: posterior extension. 2: extending to tip of tail.
215. Gas bladder. 0: thin, translucent. 1: thick, fibrous, opaque.
216. Position of anus. 0: posterior to body midlength. 1: anterior to body midlength.
217. Anal position. 0: isometric in post juveniles. 1: allometric in post juveniles.
218. Urogenital papilla. 0: absent. 1: present.
219. Tail length. 0: post anal-fin 17 - 45% total length. 1: short. 0 - 16% total length. 2: long, more than 45% total length.
220. Number caudal fin rays. 0: 7 - 15. 1: less than 6.
221. Caudal regeneration. 0: absent. 1: present.
222. Elongate caudal rod. 0: absent. 1: present.
223. Caudal fin. 0: forked. 1: rounded.
224. Caudal plate/rod . 0: not ossified. 1: ossified.
225. Caudal rod. 0: not ossified, or single ossification. 1: double ossification.
226. Electric organs. 0: absent. 1: present.
227. Number hypaxial electric organ. 0: 1. 1: 3.
228. Electrocyte posterior surface e. 0: with microvilli. 1: stalked.
229. Electrocyte morphology. 0: cigar - shaped. 1: barrel - shaped.
230. Hypaxial electric organ ontogeny. 0: retained to adult. 1: replaced at metamorphosis.
231. Hypaxial electric organ length. 0: anterior to anus. 1: anterior to mental area.
232. Mental accessory electric organ. 0: absent. 1: present. 2: mental swelling composed of electrosensory organs.
233. Humeral accessory electric organ. 0: absent. 1: present.
234. Humeral electric organ position. 0: axillary. 1: post - pectoral.
235. Opercular accessory electric organ. 0: absent. 1: present.
236. Myogenic electric organ. 0: hypaxial only. 1: hypaxial and epaxial. 2: hypaxial and pterygiophore.
237. Neurogenic electric organ. 0: Ault EO from hypaxial muscles. 1: Adult EO from spinal motor neurons.
238. Electromotoneuron morphology. 0: straight. 1: U - shaped.
239. EOD form. 0: pulse-type discharge with period of no current flow. 1: tone-type discharge continual current flow.
240. EOD adult mean repetition rate (frequency). 0: less than 250 Hz. 1: 251- 750 Hz. 2: 751 - 1200 Hz. 3: 1200 - 1750 Hz.
241. EOD monophasic. 0: biphasic. 1: monophasic depolarization. 2: monophasic hyperpolarization from negative baseline.
242. EOD pulse power spectrum. 0: simple, few harmonics. 1: complex, multiple harmonics.
243. EOD duration / shape. 0: 1 ms with prepulse. 1: 2 ms without prepulse.
244. EOD tetraphasic. 0: absent. 1: present.
245. EOD frequency shift. 0: absent. 1: present.
246. EOD active phase coupling. 0: absent. 1: present.
247. EOD jamming avoidance response. 0: absent. 1: present.
248. Habitat utilization. 0: small streams. 1: large river channels.
249. Foraging locomotion. 0: rostral probing. 1: lateral scanning.

Appendix 4. A classification of 112 described and 32 undescribed gymnotiform species recognized in this report. Literature citations are provided for families, genera, and species; genera in bold font. Species are numbered within each genus alphabetically, except for those organized phylogenetically into species-groups. Type localities and synonyms for each species are provided, as well as the type species for genera represented by more than one species. Materials from Appendix 1.

Gymnotiformes

GYMNOTIDAE Bonaparte, 1846 (17 described, 5 undescribed species)

***Gymnotus* Linnaeus, 1758**

Gymnotus carapo species-group

1. *Gymnotus carapo* Linnaeus, 1758, America, type species

Gymnotus albus Pallas, 1767, Surinam

Gymnotus brachiurus Bloch, 1787, Brazil

Gymnotus fasciatus Pallas, 1767, Rio Branco, Roraima, Brazil

Gymnotus putaol Lacépède, 1800, Brazil

2. *Gymnotus bahianus* Campos-da-Paz and Costa, 1996, Bahia, Brazil.
3. *Gymnotus inaequilabeatus* (Valenciennes, 1847), Rio de la Plata, Argentina
4. *Gymnotus silvius*, Albert, Fernandes-Matioli, and de Almeida-Toledo 1999, Rio Ribeira de Iguape, São Paulo, Brazil
5. *Gymnotus mamiraua* Albert and Crampton, 2000, Mamirauá Ecological Reserve, near Tefé, Amazonas, Brazil
6. *Gymnotus arapaima* Albert and Crampton, 2000, Mamirauá Ecological Reserve, near Tefé, Amazonas, Brazil
7. *Gymnotus* sp. D, Mamirauá Ecological Reserve, near Tefé, Amazonas, Brazil
8. *Gymnotus* sp. E, Mamirauá Ecological Reserve, near Tefé, Amazonas, Brazil

Gymnotus cylindricus species-group

9. *Gymnotus cylindricus* La Monte, 1935, Rio Motagua, near Los Amates, Guatemala
10. *Gymnotus maculosus* Albert and Miller, 1995, Rio Maria Linda, Santa Rosa, Guatemala

Gymnotus pantherinus species-group

11. *Gymnotus anguillaris* Hoedeman, 1962, Coropina creek, Surinam

Gymnotus coropinae Hoedeman, 1962, Coropina creek, Surinam

12. *Gymnotus* sp. P, Parque Nacional Ybycui, Rio Paraguay, Paraguay
13. *Gymnotus cataniapo* Mago-Leccia, 1994, San Carlos de Rio Negro, Venezuela
14. *Gymnotus coatesi* La Monte, 1935, near Santarem, Para, Brazil

Gymnotus cingulatus (Brind), 1935

15. *Gymnotus melanopleurus* Albert and Crampton, 2000, Mamirauá Ecological Reserve, near Tefé, Amazonas, Brazil
16. *Gymnotus onca* Albert and Crampton, 2000, Mamirauá Ecological Reserve, near Tefé, Amazonas, Brazil
17. *Gymnotus pantherinus* (Steindachner, 1908), Santos, São Paulo, Brazil
18. *Gymnotus pedanopterus* Mago-Leccia, 1994, Caño Temblador, Amazonas, Venezuela
19. *Gymnotus jonasi* Albert and Crampton, 2000, Mamirauá Ecological Reserve, near Tefé, Amazonas, Brazil
20. *Gymnotus* sp. J, Buen Sucesso, Rio Javari, Loreto, Perú
21. *Gymnotus* sp. R, Igarape Jatuarana, Rôndonia, Brazil
22. *Gymnotus stenoleucus* Mago-Leccia, 1994, Casiquiare, Amazonas, Venezuela

***Electrophorus* Gill, 1864**

1. *Electrophorus electricus* (Linnaeus, 1766), Surinam

Electrophorus multivalvulatus Nakashima, 1941, Amazonas, Perú

Electrophorus regius (Chiaje, 1847), America

Sternopygoidei

Rhamphichthyoidea

RHAMPHICHTHYIDAE Regan, 1911 (13 described, 2 undescribed species)

***Rhamphichthys* Müller and Troschel, 1849**

1. *Rhamphichthys apurensis* (Fernàndez-Yépez, 1968), Rio Bucaral, Apuré, Venezuela
2. *Rhamphichthys lineatus* Castelnau, 1855, Lake near Rio Ucayali, Perú
3. *Rhamphichthys rostratus* (Linnaeus, 1766), America, type species

Rhamphichthys blochii (Kaup, 1856)

Rhamphichthys longirostratus (Lacépède, 1800)

Rhamphichthys schneideri Kaup, 1856, Cayenne, French Guyana

4. *Rhamphichthys hahni* (Meinken, 1937), Corrientes, Rio Paraná, Argentina
5. *Rhamphichthys marmoratus* Castelnau, 1855, Itaituba, Rio Araguaia, Pará, Brazil
6. *Rhamphichthys pantherinus* Castelnau, 1855, Lake near Rio Ucayali, Perú
7. *Rhamphichthys reinhardti* Kaup, 1856
8. *Rhamphichthys schomburgki* (Kaup, 1856), Demerara River, Georgetown, Guyana

***Gymnorhamphichthys* Ellis, 1912**

1. *Gymnorhamphichthys hypostomus* Ellis, 1912, Rio Machupo, San Joaquin, Beni, Bolivia, type species
2. *Gymnorhamphichthys* sp. P, Rio Orinoco, Venezuela
3. *Gymnorhamphichthys petiti* Géry & Vu, 1964, Ilha do Bananal, Upper Rio Araguaia, Brazil

4 *Gymnorhamphichthys rondoni* (A. Miranda-Ribeiro, 1920), Rio Dezessete de Setembro, Guaporé, Rôndonia, Brazil

5. *Gymnorhamphichthys rosamariae* Schwassmann, 1989, Rio Negro at Rosa Maria, Brazil

***Iracema* Triques, 1996**

1. *Iracema caiana* Triques, 1996, Rio Jauaperi, Rio Negro, Amazonas, Brazil, type species
2. *Iracema* sp. C, Janauacá, Lago da Castanho, Rio Solimões, Amazonas, Brazil

HYPOPOMIDAE Mago-Leccia, 1978 (15 described, 10 undescribed species)

***Hypopomus* Gill, 1864**

1. *Hypopomus artedi* (Kaup, 1856), Mana River, French Guyana, type species

Rhamphichthys mulleri Kaup, 1856, Cayenne, French Guyana

Parupygus savannensis Hoedeman, 1962a, Sipaliwini, Paru savannah, Surinam

Parupygus litaniensis Hoedeman, 1962b, Litani River and Sant-Patawa, La Mana River, Surinam

2. *Hypopomus* sp. Z, Rio Abonari, Rio Uatamá, Amazonas, Brazil.

Brachyhypopominae

***Brachyhypopomus* Mago-Leccia, 1994**

Brachyhypopomus brevirostris species-group

1. *Brachyhypopomus brevirostris* (Steindachner, 1868), Rio Guaporé, Rondônia, Brazil, type species

2. *Brachyhypopomus* sp. B, Rio Metica, Rio Meta, Colombia

Brachyhypopomus beebei species-group

3. *Brachyhypopomus beebei* (Schultz, 1944), Rio Caripe, Caripito, Monagas, Venezuela

4. *Brachyhypopomus pinnicaudatus* (Hopkins, 1991), Grand Pripris, French Guyana

5. *Brachyhypopomus janeiroensis* (Costa and Campos-da-Paz, 1992), Rio São João, Brazil

6. *Brachyhypopomus* sp. E, Descalvados, Rio Paraguay, Mato Grosso, Brazil

7. *Brachyhypopomus* sp. R, Pozo de Lucas, near San Fernando de Atabapo, Amazonas, Venezeula

8. *Brachyhypopomus* sp. M, Parana do Paracuúba, Lago Januari, Rio Negro, Amazonas, Brazil

9. *Brachyhypopomus* sp. W, Parana do Paracuúba, Lago Januari, Rio Negro, Amazonas, Brazil

Brachyhypopomus occidentalis species-group

10. *Brachyhypopomus diazi* (Fernández-Yépez, 1972), Rio Alpargatin, Carabobo State, Venezuela

11. *Brachyhypopomus occidentalis* (Regan, 1914), Rio Condoto, Rio San Juan, Colombia

Brachyhypopomus incertae sedis

12. *Brachyhypopomus* sp. F, Mamirauá Ecological Reserve, near Tefé, Amazonas, Brazil

13. *Brachyhypopomus* sp. T, Mamirauá Ecological Reserve, near Tefé, Amazonas, Brazil

Microsternarchini

***Microsternarchus* Fernàndez-Yépez, 1968**

1. *Microsternarchus bilineatus* Fernández-Yépez, 1968, Rio San Jose, Guarico, Venezuela

***Racenisia* Mago-Leccia, 1994**

1. *Racenisia fimbriipinna* Mago-Leccia, 1994, San Fernando de Atabapo, Amazonas, Venezuela

Steatogini

***Steatogenys* Boulenger, 1898**

1. *Steatogenys cryptogenes* (Triques, 1997), Igarape Sirinau, Rio Cuieiras, Rio Negro, Brazil

2. *Steatogenys duidae* (La Monte, 1929), Caño Pescado, Amazonas, Venezuela

3. *Steatogenys elegans* (Steindachner, 1880), Rio Negro, Amazonas, Brazil, type species

4. *Steatogenys mirabilis* (Steindachner, 1878), Rio Cauca, Colombia

5. *Steatogenys* sp. N, Rio Tambocochа, Rio Napo, Ecuador

6. *Steatogenys* sp. O, Mamirauá Ecological Reserve, near Tefé, Amazonas, Brazil

***Hypopygus* Hoedeman, 1962**

1. *Hypopygus lepturus* Hoedeman, 1962, Marowinje, Maroni River, Surinam, type species

2. *Hypopygus neblinae* Mago-Leccia, 1994, Rio Barana, Casiquiari, Amazonas, Venezuela

Sinusoidea

STERNOPYGIDAE Cope, 1871 (24 described, 8 undescribed species)

†*Ellisella* Gayet and Meunier, 1991

1. †*Ellisella kirschbaumi* Gayet and Meunier, 1991, Rio Moile, Rio Paraguay, Bolivia

***Sternopygus* Müller and Troschel, 1849**

1. *Sternopygus astrabes* Mago-Leccia, 1994, Pozo Azul, Puerto Ayacucho, Amazonas, Venezuela

Sternopygus aequilabeatus species-group

2. *Sternopygus aequilabeatus* (Humboldt and Bonpland, 1811), Rio Magdalena, Colombia

Sternopygus dariensis Meek and Hildebrand, 1913, Rio Tuyra, Marrigante, Darien, Panamá

Sternopygus pejeraton Schultz, 1949, Rio Apón, Villa de Rosario, Maracaibo, Zulia, Venezuela

3. *Sternopygus arenatus* (Eydoux and Souleyet, 1841), Rio Guyaquil, Ecuador

4. *Sternopygus xingu* Albert and Fink, 1996, Rio Batovi, Rio Xingu, Brazil

Sternopygus macrurus species-group

5. *Sternopygus castroi* Triques 1999, Rio Cuieiras, Rio Negro, Amazonas, Brazil

6. *Sternopygus macrurus* (Bloch and Schneider, 1801), Brazil, type species

Sternopygus brasiliensis (Fernàndez-Yépez, 1968), Sarapó Piaui, Parnaíba, Brazil

Sternopygus marcgravii (Reinhardt, 1852), Rio das Velhas, Minas Gerais, Brazil

Sternopygus sanguinolentus (Castelnau, 1855), Rio Urubamba, Loreto, Perú

Sternopygus obtusirostris Steindachner, 1881, Lago Aleixo, Manacapurú, near Manaus, Brazil.

7. *Sternopygus* sp. B, near Costa Marques, Rio Itenez, Rio Baures, Beni, Bolivia

8. *Sternopygus* sp. G, New River, Guyana

Eigenmanninae

***Archolaemus* Korringa, 1970**

1. *Archolaemus blax* Korringa, 1970, Porto Nacional, Rio Tocantins, Goiás, Brazil

Eigenmannini

***Distocyclus* Mago-Leccia, 1978**

1. *Distocyclus conirostrus* (Eigenmann and Allen, 1942), Iquitos, Loreto, Perú, type species

2. *Distocyclus goajira* (Schutlz, 1949), Rio Socuy, Maracaibo Basin, Zulia, Venezuela

***Eigenmannia* Jordan and Evermann, 1896**

Eigenmannia microstoma species-group

1. *Eigenmannia humboldtii* (Steindachner, 1878), Rio Magdalena, Colombia

2. *Eigenmannia limbata* (Schreiner and Miranda-Rebeiro, 1903), Amazonas, Brazil

3. *Eigenmannia microstoma* (Reinhardt, 1852), Lagoa Santa, Rio das Velhas, Minas Gerais, Brazil

4. *Eigenmannia* sp. J, Rio Paraiba, Rio de Janeiro, Brazil

5. *Eigenmannia nigra* Mago-Leccia, 1994, Rio Guainia, Mahavate, San Carlos de Rio Negro, Amazonas, Venezuela

Eigenmannia macrops species-group

6. *Eigenmannia macrops* (Boulenger, 1897), Potaro River, Essequibo, Guyana

7. *Eigenmannia* sp. B, Mamirauá Ecological Reserve, near Tefé, Amazonas, Brazil

Eigenmannia virescens species-group

8. *Eigenmannia trilineata* Lopez and Castello, 1966, Rio de la Plata, de Nuñez, Argentina

9. *Eigenmannia virescens* (Valenciennes, 1847), Amerique Meridionale, type species

Eigenmannia lineata (Müller and Troschel, 1849), Lake Amucu, Guyana

Eigenmannia tumifrons (Müller and Troschel, 1849), South America
10. *Eigenmannia sp.* D, Rio Salí-Trancas, Tucumán, Argentina
Eigenmannia incertae cedis
11. *Eigenmannia* sp. I, Mamirauá Ecological Reserve, near Tefé, Amazonas, Brazil
12. *Eigenmannia* sp. N, Mamirauá Ecological Reserve, near Tefé, Amazonas, Brazil
13. *Eigenmannia vicentespelaea* Triques 1996, Gruta São Vicente, Rio Tocantins, Goiás, Brazil
***Rhabdolichops* Eigenmann and Allen, 1942**
1. *Rhabdolichops electrogrammus* Lundberg and Mago-Leccia, 1986, Isla Tres Caños, Delta Amacuro, Venezuela
2. *Rhabdolichops zareti* Lundberg and Mago-Leccia, 1986, Isla Tres Caños, Delta Amacuro, Venezuela
3. *Rhabdolichops eastwardi* Lundberg and Mago-Leccia, 1986, Isla Porteguesa, Delta Amacuro, Venezuela
4. *Rhabdolichops stewarti* Lundberg and Mago-Leccia, 1986 Rio Tapajós, Pará, Brazil
5. *Rhabdolichops caviceps* (Fernández-Yépez, 1968), Rio Apuré, Apuré, Venezuela
6. *Rhabdolichops troscheli* (Kaup, 1856), Guyana, type species
Rhabdolichops axillaris (Guenther, 1870), Belém, Pará, Brazil
Rhabdolichops longicaudatus Eigenmann and Allen, 1942, Iquitos, Perú
APTERONOTIDAE Jordan, 1923 (43 described, 8 undescribed species)
Sternarchorhynchinae
Sternarchorhamphini
***Sternarchorhamphus* Eigenmann, 1905**
1. *Sternarchorhamphus muelleri* (Steindachner, 1881), Belém, Pará, Brazil
***Orthosternarchus* Ellis 1912**
1. *Orthosternarchus tamandua* (Boulenger, 1898), Rio Juruà, Amazonas, Brazil
Sternarchorhynchini
***Sternarchorhynchus* Castelnau, 1855**
1. *Sternarchorhynchus britskii* Campos-da-Paz, 1999b, Ilha Solteira, Rio Paraná, Mato Grosso do Sul, Brazil
2. *Sternarchorhynchus curvirostris* (Boulenger, 1887), Canelos, Rio Pastaza, Ecuador
3. *Sternarchorhynchus mesaensis* Campos-da-Paz, 1999b, Serra da Mesa, Rio Tocantins, Goiás, Brazil
4. *Sternarchorhynchus mormyrus* Steindachner, 1868, Marabitanos, Amazonas, Brazil
5. *Sternarchorhynchus oxyrhynchus* (Müller and Troschel, 1849), Essequibo River, Guyana, type species
6. *Sternarchorhynchus roseni* Mago-Leccia, 1994, Jarina, Rio Apuré, Apuré, Venezuela
***Platyurosternarchus* Mago-Leccia, 1994**
1. *Platyurosternarchus macrostomus* (Günther, 1870), Xeberos (Jeberos), Perú
Apteronotinae
***Parapteronotus* n. gen.**
1. *Parapteronotus hasemani* (Ellis, 1913), Santarem, Pará, Brazil
Apteronotus anas (Eigenmann and Allen, 1942), Rio Marañon, Iquitos, Perú
***Apteronotus sensu stricto* (Lacépède, 1800)**
Apteronotus albifrons species-group
1. *Apteronotus albifrons* (Linnaeus, 1766), Surinam, type species
Apteronotus lacepedi (Castelnau, 1855), Surinam
Apteronotus maximiliani (Castelnau, 1855), Rio Urubamba, Cuzco, Perú
Apteronotus passan Lacépède, 1800, Surinam
2. *Apteronotus cuchillejo* (Schultz, 1949), Rio Motatan, Zulia, Venezuela
3. *Apteronotus jurubidae* (Fowler, 1944), Rio Jurubida, Nuqui, Choco, Colombia
4. *Apteronotus mariae* Eigenmann and Fisher, 1914, Girardot, Apulo, Colombia
5. *Apteronotus spurrellii* (Regan, 1914), Rio Condoto, Colombia
6. *Apteronotus* sp. T, Rio Tacutu near Lethem, Rio Branco, Roraima, Brazil
Apteronotus brasiliensis species-group
7. *Apteronotus brasiliensis* (Reinhardt, 1852), Rio das Velhas, Minas Gerais, Brazil
8. *Apteronotus cuchillo* Schultz, 1949, Rio Socay, Zulia, Venezuela
9. *Apteronotus leptorhynchus* (Ellis, 1912), Amatuk, Warraputa, Guyana
10. *Apteronotus (Ubidia) magdalenensis* (Miles, 1945), Honda, Colombia
11. *Apteronotus marauna* (Triques, 1998), Ilha Solteira, Rio Paraná, Mato Grosso do Sul, Brazil
12. *Apteronotus rostratus* (Meek and Hildebrand, 1913), Rio Grande, near Cana, Panamá
13. *Apteronotus* sp. S, Ilha Solteira, Rio Paraná, Mato Grosso do Sul, Brazil
Apteronotus incertae cedis
14. *Apteronotus (Megadontognathus) cuyuniense* (Mago-Leccia, 1994), Rio Cuyuní, Bolivar, Venezuela
15. *Apteronotus ellisi* (Arámburu, 1957), San Pedro, Delta Paraná, Buenos Aires, Argentina
Navajini
Sternarchellini
***Sternarchella* Eigenmann, 1905**
Sternarchella schotti species-group
1. *Sternarchella orthos* Mago-Leccia, 1994, Rio Boquerones, Apuré, Venezuela
2. *Sternarchella schotti* (Steindachner, 1868), Manaus, Amazonas, Brazil, type species
Sternarchella capanemae (Steindachner, 1868), Manaus, Amazonas, Brazil
3. *Sternarchella terminalis* (Eigenmann and Allen, 1942), Iquitos, Loreto, Perú
Sternarchella sima species-group
4. *Sternarchella curvioperculata* (de Godoy, 1968), Rio Mogi Guassu, São Paulo, Brazil.
5. *Sternarchella sima* Starks, 1913, Belém, Pará, Brazil
Sternarchella orinoco Mago-Leccia, 1994, Rio Boquerones, Apuré, Venezuela
6. *Sternarchella* sp. S, Rio Solimões, Amazonas, Brazil
***Magosternarchus* Lundberg, Cox Fernandes, and Albert, 1996**
1. *Magosternarchus duccis* Lundberg, Cox Fernandes, and Albert, 1996, Rio Branco, near confluence with Rio Negro, Roraima State, Brazil
2. *Magosternarchus raptor* Lundberg, Cox Fernandes, and Albert, 1996, Rio Solimões, near confluence of Rio Purus, Amazonas State, Brazil, type species
Unnamed Clade AH
1. *"Apteronotus" apurensis* (Fernàndez-Yépez, 1968), Rio Bucaral,

Apuré, Venezuela
2. *"Apteronotus" bonapartii* (Castelnau, 1855), Lake near the Ucayale, Perú
Apteronotus lacepedii (Castelnau, 1855), Surinam
3. *"Apteronotus" macrostomus* (Fowler, 1943), Villavicencio, Colombia
4. *"Apteronotus" macrolepis* Steindachner, 1881, Lago Manacapurú, near Manaus, Brazil
Unnamed Clade AI
***Compsaraia* n. gen.**
1. *Compsaraia compsa* (Mago-Leccia, 1994), Isla Iguana, Delta Amacuro, Venezuela, type species
2. *Compsaraia* sp. *1*, Rio Solimões, Amazonas, Brazil
Porotergini
***Porotergus* Ellis, 1912**
1. *Porotergus gimbeli* Ellis, 1912, Belém, Pará, Brazil
2. *Porotergus gymnotus* Ellis, 1912, Amatuk, Warraputa, Guyana, type species
3. *Porotergus* sp. 1, Rio Solimões, Amazonas, Brazil
4. *Porotergus* sp. 2, Rio Solimões, Amazonas, Brazil
***Sternarchogiton* Eigenmann and Ward, 1905**
1. *Sternarchogiton nattereri* (Steindachner, 1868), Manaus, Amazonas, Brazil, type species
Oedemognathus exodon Meyers, 1936, Rio Ampiyacu, Loreto, Perú
2. *Sternarchogiton porcinum* Eigenmann and Allen, 1942, Rio Huallaga, Yurimaguas, Perú
3. *Sternarchogiton* sp. B, Rio Orinoco, Amazonas, Venezuela
***Adontosternarchus* Ellis, 1912**
1. *Adontosternarchus balaenops* (Cope, 1878), Pebas, Loreto, Perú
2. *Adontosternarchus clarkae* Mago-Leccia *et al.*, 1985, Mahavaté, San Carlos de Rio Negro, Venezuela
3. *Adontosternarchus devenanzii* Mago-Leccia *et al.*, 1985, Caño Caujarito, Rio Porteguesa, Guarico, Venezuela
4. *Adontosternarchus sachsi* (Peters, 1877), Venezuela, type species
5. *Adontosternarchus sp.* A, Rio Solimões, Amazonas, Brazil.