PROCEEDINGS OF THE BIOLOGICAL SOCIETY OF WASHINGTON
108(4):662–678. 1995

Gymnotus maculosus, a new species of electric fish (Chordata: Teleostei: Gymnotoidei) from Middle America, with a key to species of *Gymnotus*

James Spurling Albert and Robert Rush Miller

Museum of Zoology, University of Michigan, Ann Arbor, Michigan 48109-1079, U.S.A.

Abstract.—A new species of gymnotoid knifefish, *Gymnotus maculosus,* is described from Pacific drainages of Middle America, from Chiapas, Mexico, to Costa Rica, and an Atlantic drainage in Nicaragua. Morphological, meristic, and pigmentation features are compared with congeners. Variation among the species of *Gymnotus* from many localities in South America remains to be analyzed for a robust hypothesis about numbers of species and their interrelationships. A phylogenetic diagnosis of *Gymnotus,* and a key to the recognized species is provided.

Resumen.—Se describe una nueva especie de anguila electrica, *Gymnotus maculosus.* Esta especie se encuentra en las vertientes Pacíficas de Mesoamérica desde Chiapas, México, hasta Costa Rica, y en una cuenca Atlántica de Nicaragua. Se discuten y comparan características morfológicas, merísticas, y de pigmentación con otros miembros del género. Para poder establecer el número de especies de *Gymnotus* y sus relaciones, es necesario un análisis de la variabilidad entre especies de diversas localidades en Sudamérica. Se provee una diagnosis filogenética del género *Gymnotus* y una clave de identificación de las especies reconocidas.

Gymnotus is the most widely distributed genus of American electric knifefishes (Teleostei: Gymnotoidei). Members of the genus range from the Río San Nicolás of southeastern Chiapas, Mexico, south to the Río de la Plata, Argentina (Eigenmann & Ward 1905, Eigenmann & Fischer 1914, Eigenmann & Allen 1942, Miller 1966, Bussing 1985). Members of this lineage are aggressive, nocturnal predators who prefer small tributaries, lagoons, and backwater swamps, and in Middle America sometimes inhabit highland lakes.

The systematic position and organization of *Gymnotus* are problematic. *Gymnotus* was proposed by Peter Artedi in 1738 to include the type species *G. carapo* Linnaeus. According to Ellis (1913) the original specimens were collected in the Guyanas. Ellis (1913) was the first to propose a formal hypothesis of interrelationships among the major gymnotoid lineages, placing *Gymnotus* and *Electrophorus* as the sister lineage to all other gymnotoids (Ellis 1913, Eigenmann & Fischer 1914). Ellis synonymized all specimens of *Gymnotus* into the type species, *G. carapo.*

There are presently thirteen described species of *Gymnotus,* of which five have been synonymized with the type species (Mago-Leccia 1994). Several additional species are recognized in museum collections, however, so that the actual number of species may be substantially higher. Descriptions of several of these species await the acquisition of sufficient samples from populations across their geographical range (Mago-Leccia 1994). Most specimens of *Gymnotus* in museum collections are identified as *G. carapo,* regardless of their appearance or origin. This is due, in part, to the wide geographical extent of this puta-

Table 1.—Number of precaudal vertebrae in *Gymnotus* species. Counts from a total of 75 specimens are reported.

	30	32	34	36	38	40	42	44	46	48	50	*n*	Mode
anguillaris	0	0	0	0	5	0	0	0	0	0	0	5	38
carapo	0	0	0	0	6	0	0	0	0	0	0	6	38
catanaiapo	0	0	0	0	0	0	0	0	0	0	2	2	50
coatesi	0	0	0	0	0	3	1	0	0	0	0	4	40
cylindricus	2	15	6	0	0	0	0	0	0	0	0	23	32
maculosus	1	11	9	0	0	0	0	0	0	0	0	21	32
pedanopterus	0	0	0	7	0	0	0	0	0	0	0	7	36
stenoleucus	0	0	0	0	0	0	0	0	4	3	0	7	46
Total	3	26	15	7	7	3	1	0	4	3	2	75	

tive species, which is known from Guyana to the Río La Plata basin and many intervening sites. Furthermore, color patterns, and body shapes of specimens referred to *G. carapo* vary widely across the range.

The species diversity of *Gymnotus* is greatest in the Amazon basin, from where six species are recognized. Five of these species also inhabit the Upper Río Orinoco basin (Mago-Leccia 1994). *Gymnotus anguillaris* Hoedeman, originally described from Guyana, has also been collected from the Orinoco, Amazon, and La Plata basins. The other species have more restricted distributions. *Gymnotus coatesi* LaMonte is known only from the western Amazonian lowlands of Brazil and Perú, *G. inaequilabiatus* (Valenciennes) is from the Río de La Plata drainage, and *G. pantherinus* (Steindachner) from Atlantic drainages of southern Brazil.

Gymnotus also ranges into Middle America. Understanding the biogeographic history of *Gymnotus* in northwestern South America and Middle America is confounded by the complex geological history of the region (Bussing 1987, Pittman et al. 1993). Although the species diversity of *Gymnotus* has not been recently studied west of the Andes, there appear to be several unrecognized species inhabiting small coastal streams and rivers along the Pacific coast from Ecuador, north to Chiapas, Mexico. The purpose of this paper is to describe one of these species, discovered one of us (RRM).

Methods.—Methods used herein are modified or elaborated from Lundberg & Mago-Leccia (1986), Fink (1989), and Fink & Machado-Allison (1992). Specimens examined are listed in the Appendix. Museum acronyms are as presented by Leviton et al. (1985). Osteological data were taken from cleared and stained specimens using a modified version of the enzyme technique of Taylor & Van Dyke (1985). Standardized dissection methods of small teleosts were used (Weitzman 1974). We follow Fink & Fink (1981) for bone nomenclature. All drawings were made with the aid of a Zeiss dissecting microscope, equipped with a camera lucida, and edited by means of a PC graphics editor.

Counts of precaudal vertebrae (Table 1) and anal-fin rays (Table 2) were taken from radiographs. The number of precaudal vertebrae includes those of the Weberian apparatus; number of precaudal vertebrae is used here as a proxy for body-cavity length (Albert & Fink, in press). Body proportions reported include head length (HL), from posterior margin of bony operculum to tip of snout; postorbital head length (PO), from posterior margin of bony opercle to posterior margin of eye; preorbital head length (PR), from anterior margin of eye to tip of snout; body depth (BD), vertical distance from origin of anal fin to dorsal body bor-

Table 2.—Number of anal-fin rays in *Gymnotus* species. Counts from a total of 58 specimens are reported.

	155	165	175	185	195	205	215	225	235	245	255	*n*
anguillaris	0	0	0	0	0	1	0	2	1	1	0	5
carapo	0	0	0	0	2	1	2	1	0	0	0	6
catanaiapo	0	0	0	0	0	0	0	2	3	0	1	7
coatesi	0	0	0	0	0	2	1	1	0	0	0	4
cylindricus	0	1	1	5	0	3	3	1	0	0	0	14
maculosus	2	4	2	0	0	0	0	0	0	0	0	8
pedanopterus	0	0	0	0	0	0	1	1	1	1	0	7
stenoleucus	0	0	0	0	2	3	1	1	0	0	0	7
Total	2	5	3	5	4	10	8	9	5	2	1	58

der, with lateral line held horizontal; pectoral-fin length (P1), from dorsal border of fin base where it contacts cleithrum to tip of longest ray; interorbital distance (IO), between dorsomedial margins of eyes; size of branchial opening (BO), from posterodorsal to anteroventral extent of fold along anterior margin; pre-anal distance (PA), from anterior insertion of anal fin and posterior margin of anus. Body size is represented by head length (HL) in millimeters. The use of head length as a rough measure of overall body length is discussed by Albert & Fink (in press). Specimens in which the caudal filament was obviously damaged and unrepaired were excluded from measurements of total length.

Some measurements used in this report differ from those of earlier works on gymnotoids (Mago-Leccia 1978, 1994). Head length, for example, is defined as the distance between tip of snout and posterior extent of the bony opercle. Head length measured from the posterodorsal termination of the branchial opening (Mago-Leccia 1978) is subject to greater preservation-induced artifact and was not used. Measures of pectoral-fin length, postorbital length, and body depth reported here may also differ from results of previous studies. For these measurements, we attempted to use the unambiguous landmarks noted above to define endpoints.

This report is part of a larger research effort by the first author on systematics and evolution of the Gymnotoidei. A total of more than 2400 specimens representing at least 80 gymnotoid species have been examined (Albert 1995). Character polarities were determined from the hypothesis of relationships proposed by Albert (1995; see Discussion).

Monophyly and Nomenclature of *Gymnotus*

Gymnotus Linnaeus 1758

Gymnotus Linnaeus 1758:246 (type species, by original monotypy, *G. carapo* Linnaeus 1758).

Carapus Cuvier 1816 (nec Rafinesque): 237.

Giton Kaup *in* Duméril 1856:201 (type species, by original monotypy, *G. fasciatus* Pallas 1767:35).

Diagnosis.—Species of *Gymnotus* have multiple (13–50) pale oblique bands of reduced melanophore density along lateral surface of body (obscured in some species); anterior narial opening located within gape such that pore opening faces anteroventrally (also present in many rhamphichthyoids); anterior pharyngobranchial (associated with gill arch 3) unossified; all five basibranchials unossified; capacity to regenerate postcoelomic neural spines (Gayet & Meunier 1991); cylindrical or barrel shaped electrocytes, without a stalk, their long axis oriented longitudinally (Bass 1986, fig. 1).

Description.—The polarity of several

characters useful in identifying specimens of the genus *Gymnotus* are ambiguous. Mesethmoid short and broad. Frontals broad. Extrascapular firmly articulated with cranium. Lateral ethmoids absent. Mesopterygoid edentulous, bearing an ascending process. Infraorbital series represented by superficial bony tubes. Urohyal well developed. Four broad branchiostegal rays, two anterior branchiostegals narrower than the others. Basihyal elongate and hollow. Basibranchials not ossified. Three ossified pharyngobranchials. Five epibranchials, fifth one cartilaginous. Gill-rakers small, dentigerous plates, located on both margins of fourth branchial arch and on anterior margin of fifth arch, and covered by connective tissue. Branchial openings large, branchiostegal membrane united across isthmus. Posttemporal not fused with supracleithrum. Mesocoracoid present. Coracoid not bearing ventral process. Four pectoral radials. Lateral line complete. Presence of 30–51 precaudal vertebrae. No displaced hemal spines. Anus not growing anteriorly during ontogeny. Anterior insertion of anal fin not extending anterior to vertical through posterior margin of pectoral fin. Anal fin confluent with tip of tail (rays of the posterior portion of anal fin are tightly aggregated and lie horizontally caudally, making it difficult to count the exact number of rays other than in stained specimens or radiographs).

Species of *Gymnotus* mature at moderate body sizes (approximately 150 to 400 mm TL), possess a cylindrical or subcylindrical body, and are completely covered by cycloid scales on the postcranial part of their bodies. In many species, color pigmentation patterns are formed by alternating bands of dark and pale oblique bands along the body axis. The band-interband contrast increases ventrally, and is generally more pronounced in juveniles (less than 100 mm TL). Although the number, width, and shape of these bands are variable, banding patterns have diagnostic value for several species (Mago-Leccia 1994).

We follow Mago-Leccia (1994) in recognizing the following species of the genus and their synonyms:

Gymnotus carapo Linnaeus
- *G. carapo* Linnaeus, 1758:246 (type locality: America).
- *G. fasciatus* Pallas, 1767:35 (type locality: Brazil).
- *G. albus* Pallas, 1767:35 (type locality: Suriname).
- *G. brachiurus* Bloch, 1787:61, plate 157, fig. 1 (type locality: Brazil).
- *G. putaol* Lacépède, 1800:176 (type locality: Brazil).
- *G. cingulatus* Brind, 1935 (type locality: Brazil).

Gymnotus inaequilabiatus (Valenciennes)
- *Carapus inaequilabiatus* Valenciennes *in* D'Orbigny 1847:11, plate 14 (type locality: Río de La Plata, Argentina).

Gymnotus pantherinus (Steindachner)
- *Giton fasciatus* var. *pantherinus* Steindachner, 1908:129 (type locality: Santos, Brazil).

Gymnotus coatesi LaMonte
- *G. coatesi* LaMonte, 1935:1, fig. 1 (type locality: Rio Amazonas, Brazil).

Gymnotus cylindricus LaMonte
- *G. cylindricus* LaMonte, 1935:2 (type locality: Los Amates, Río Motagua Basin, Guatemala).

Gymnotus anguillaris Hoedeman
- *G. anguillaris* Hoedeman, 1962a:55, fig. 2 (type locality: Coropina Creek, Suriname).
- *G. coropinae* Hoedeman 1962a:55, fig. 1c (type locality: Coropina Creek, Suriname).

Gymnotus cataniapo Mago-Leccia
- *Gymnotus cataniapo* Mago-Leccia 1994: 90, fig. 100, table 9 (type locality: Río Cataniapo, Amazonas, Venezuela).

Gymnotus pedanopterus Mago-Leccia
- *Gymnotus pedanopterus* Mago-Leccia 1994:92, fig. 98, table 10 (type locality: Caño La Esmeralda, Río Orinoco, Amazonas, Venezuela).

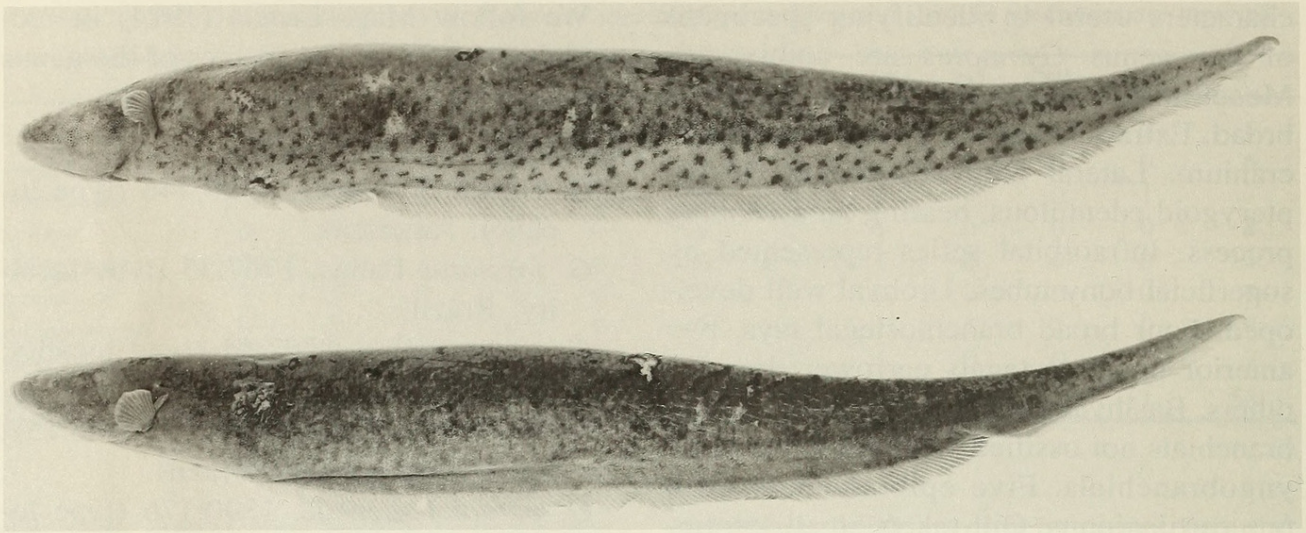

Fig. 1. Lateral view of *Gymnotus maculosus,* paratypes, USNM 134700, 185 and 195 mm TL, Río Buena Vista 8 km W of Pajal, Departamento Santa Rosa, Guatemala.

Gymnotus stenoleucus Mago-Leccia

Gymnotus stenoleucus Mago-Leccia 1994:94, figs. 99–101, table 11 (type locality: Río Cataniapo, Amazonas, Venezuela).

Gymnotus maculosus, new species
Fig. 1–6

Gymnotus carapo in part, Eigenmann & Fisher, 1914:235. Rivers and lakes on both slopes of Guatemala.

Gymnotus carapus Carr & Giovannoli, 1950:11–12. Río Choluteca, Honduras.

Gymnotus cylindricus Bussing, 1985, fig. 36.

Gymnotus sp. Miller, 1966:786 (Pacific slope of Middle America from Guatemala to the Gulf of Fonseca).

Gymnotus sp. Miller, 1986:129 (Pacific slope of Middle America between Tehuantepec and Guatemala).

Gymnotus sp. Espinosa Perez et al., 1993: 29 (Río Usumacinta).

Holotype.—UMMZ 230830, 191 mm TL. Diversion of channel from María Linda, 14°04′N; 90°37′W, c. 20 km. East of Escuintla, Departamento Santa Rosa, Guatemala; collected by D. E. Rosen and R. M. Bailey, 27 March 1971.

Paratypes.—UMMZ 190783, 3 specimens, 176–203 mm TL, type locality. UMMZ 224128, 5 specimens, 158–222 mm, Río Higuerón, Canas, Costa Rica. UMMZ 230354, 20 specimens, Río Buena Vista, trib. of Río Tigre, on road between Escuintla and Chiquimulilla, 8 km. West of Pajal, Departamento Santa Rosa, Guatemala, 128–230 mm, 1946.IV.18. USNM 134700, 49 specimens, Río Buena Vista, 8 km. West of Pajal, Departamento Santa Rosa, Guatemala, 67–195 mm TL, 1946.IV.18. TU 24965, 36 specimens, 60–260 mm TL, Boca del Río Sapoá at Sapoá, Nicaragua.

Diagnosis.—A gymnotid unique in possessing numerous small brown spots, varying in size from two to four times eye diameter, distributed over most of the body surface (Figs. 1, 2). The body lacks distinct oblique bands in both juveniles and adults. Scales above the lateral line large, 6–8 rows to the dorsal midline at about midbody.

Description.—Figure 3 illustrates body shape. Body subcylindrical (its greatest width 0.61–0.84% BD); BD = 10–13% TL; dorsal profile of body almost straight, ventral profile slightly convex; head small, depressed, HL = 9.8–12.7% TL; PO = 58–64.5% HL; anterior nares tubular, partially concealed in labial groove; posterior nares round, and positioned close to eye; mouth

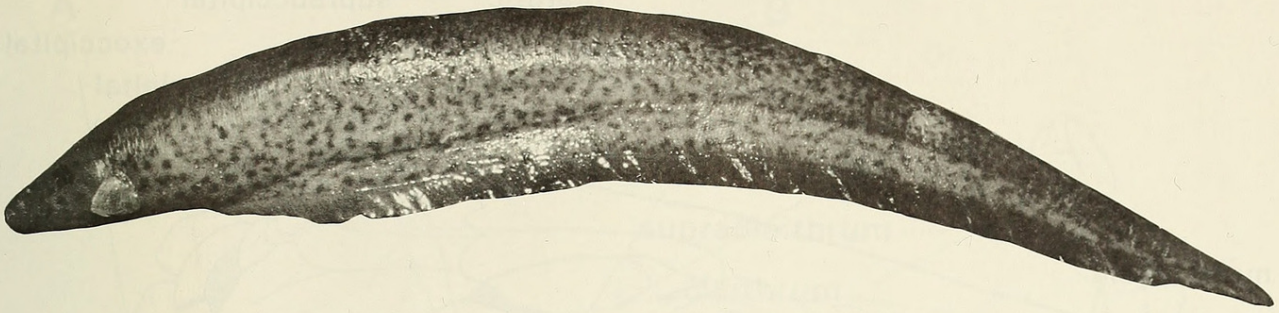

Fig. 2. Lateral view of *Gymnotus maculosus,* paratype, TU 24965, 238 mm TL, Río Sapoá at Sapoá, Nicaragua.

broad, gape large, rictus of mouth not reaching vertical through eyes; lower jaw protruding, teeth small, conical, in a single row in each jaw, with irregular second row; snout blunt, PR = 33.1–37.5% HL; IO = 37.0–41.0% HL; origin of anal fin posterior to tip of pectoral fin, PA = 7.4–11.1% TL; branchial opening large, B0 = 33.0–44.3% HL; nape without pale band; lateral line complete, paralleling main body axis; pectoral fin small, rounded, P1 = 43–48% HL; pectoral-fin rays ii+15–16 (n = 8); 30–34 precaudal vertebrae (Table 1, mode = 32, n = 21); anus near vertical through branchial opening; anal fin short, 155–182 anal-fin rays (Table 2, mode = 169, n = 8).

Color in preservative.—Ground color yellow to pale brown laterally on preserved specimens. Dorsum dark brown due to densely concentrated melanophores. Dark brown dorsally and laterally. Ground color overlaid by numerous brown spots on head and body, ranging in size from about 2 to 4 eye diameters, and varying somewhat in

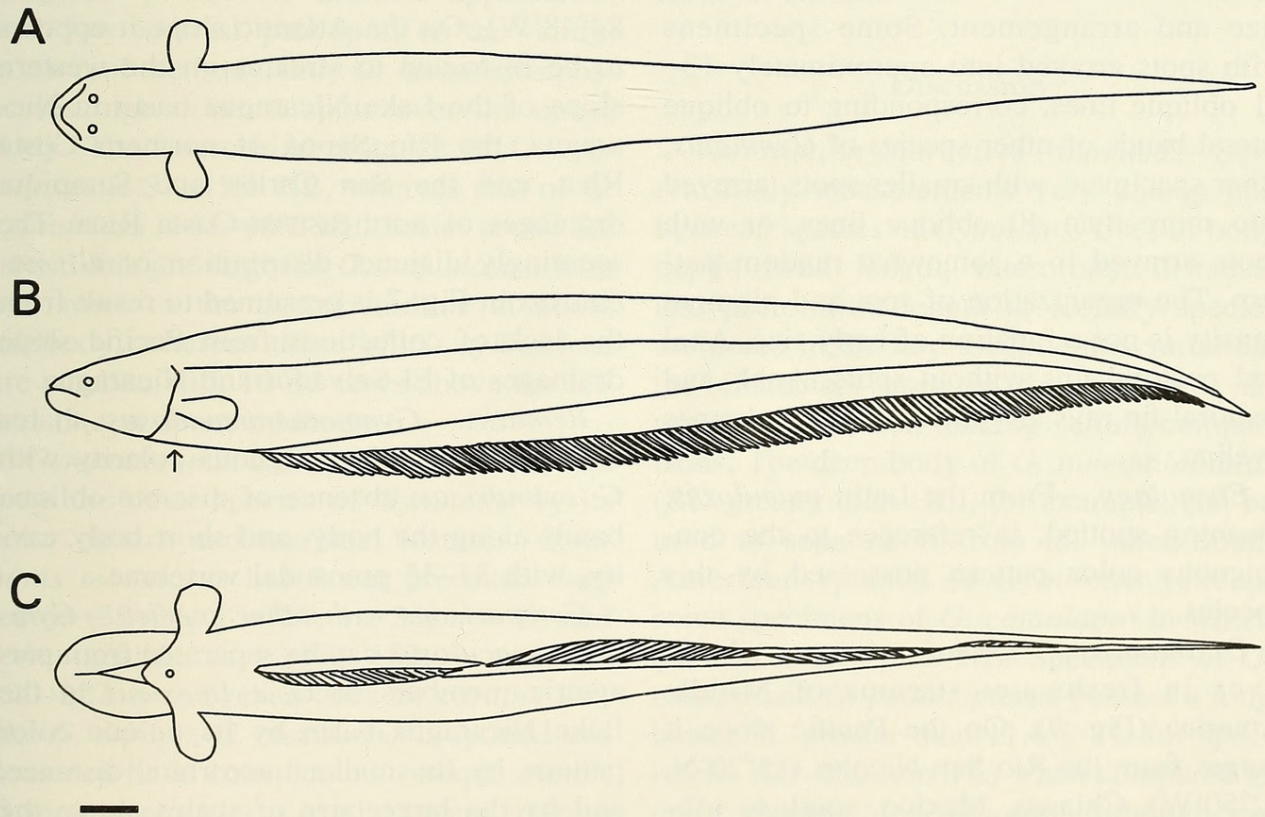

Fig. 3. Diagrammatic representation of *Gymnotus maculosus.* (A) dorsal, (B) lateral, and (C) ventral view. Arrow indicates position of the anus. Scale bar equals 10 mm.

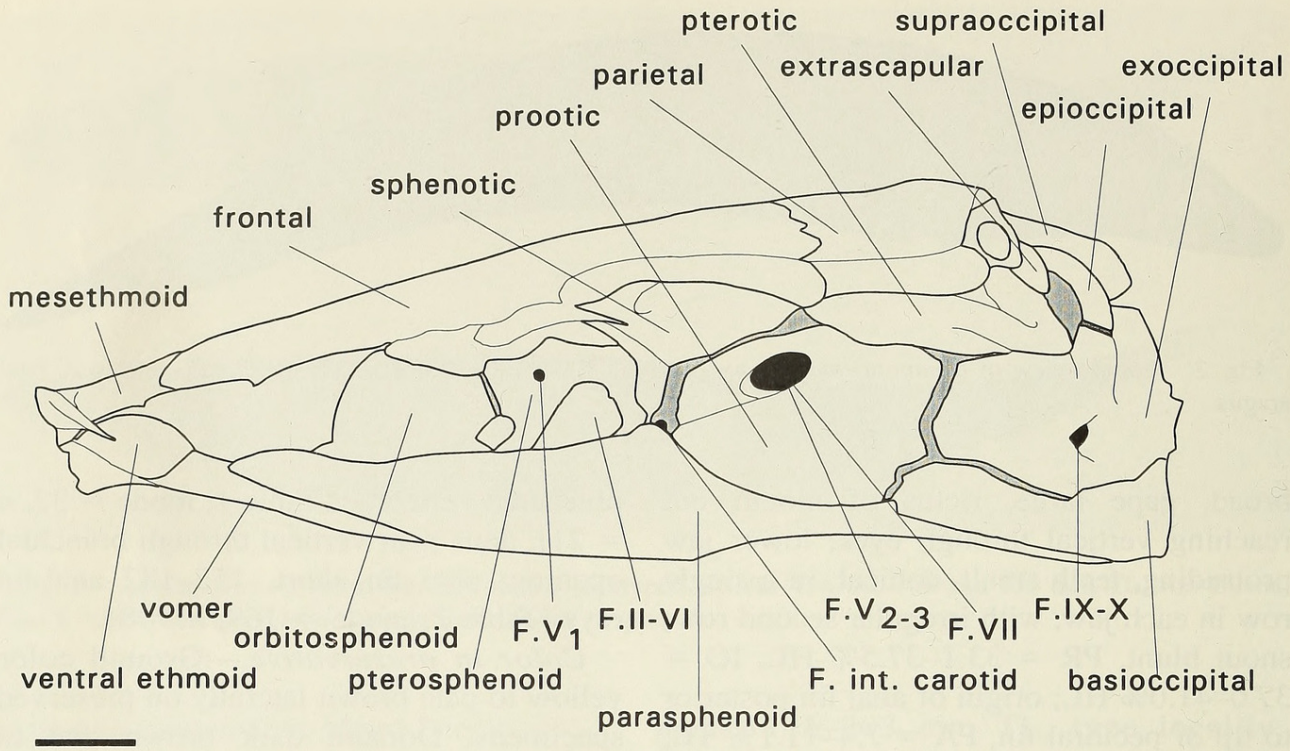

Fig. 4. Lateral view of neurocranium of *Gymnotus maculosus,* UMMZ 190531, 185 mm TL. Cartilage indicated by stippling. Abbreviations: F. V_1, foramen of cranial nerve V_1 (profundus); F. II–VI, foramen of optic tract and cranial nerves III (oculomotor), IV (trochlear), and VI (abducens); F. int. carotid, foramen of internal carotid artery; F. V_{2-3}, foramen of V_2 (superficial ophthalmic and maxillary) and V_3 (internal mandibular) rami of trigeminal nerve; F. VII, foramen of cranial nerve VII (facial); F. IX–X, foramen of cranial nerves IX (glossopharyngeal) and X (vagus). Scale bar equals 1 mm.

size and arrangement. Some specimens with spots arrayed into approximately 13–21 oblique lines, corresponding to oblique lateral bands of other species of *Gymnotus*; other specimens with smaller spots, arrayed into more than 40 oblique lines, or with spots arrayed in a somewhat random pattern. The organization of spot and pigment density is not a function of body size. Anal and pectoral fins without spots. Anal- and pectoral-fin rays and interradial membranes hyaline.

Etymology.—From the Latin *maculosus,* meaning spotted, in reference to the conspicuous color pattern possessed by this species.

Distribution.—*Gymnotus maculosus* lives in freshwater streams of Middle America (Fig. 7). On the Pacific slope it ranges from the Río San Nicolás (15°20′N, 92°50′W), Chiapas, Mexico, south to tributary streams to the Gulf of Nicoya in northwestern Costa Rica (9°47′N, 84°48′W). On the Atlantic slope it appears to be restricted to streams on the western slope of the Lake Nicaragua basin in Nicaragua, the Río Sapoá of northern Costa Rica, and the San Carlos and Sarapiqui drainages of northeastern Costa Rica. The seemingly disjunct distribution of *G. maculosus* in Fig. 7 is presumed to result from the lack of collections from Pacific slope drainages of El Salvador and Nicaragua.

Remarks.—*Gymnotus maculosus* shares two characters of ambiguous polarity with *G. cylindricus*; absence of discrete oblique bands along the body, and short body cavity, with 31–35 precaudal vertebrae.

Comparisons with other species.—*Gymnotus maculosus* can be separated from parapatric members of *G. cylindricus* in the Lake Nicaragua basin by its unique color pattern, by its smaller interorbital distance, and by the larger size of scales above the lateral line. Specimens of *G. cylindricus* possess few if any small brown spots on the

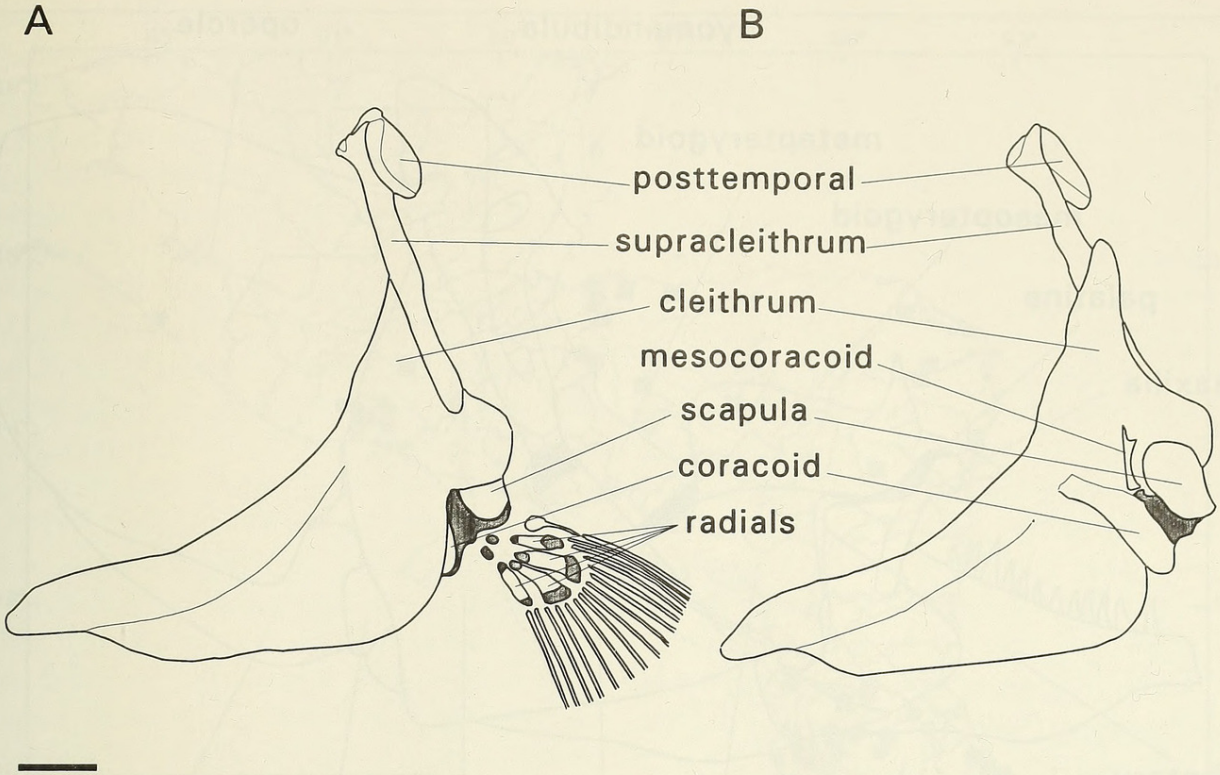

Fig. 5. Pectoral girdle of *Gymnotus maculosus,* UMMZ 190531. (A) lateral view. (B) medial view. Cartilage indicated by stippling. Scale bar equals 1 mm.

body. Although some specimens of *G. cylindricus* possess a mottled appearance, with low contrast, pale spots on the ventral portion of the body, only *G. maculosus* possesses high contrast spots over the entire body. The interorbital distance of *G. maculosus* is 37–41% HL, whereas that of *G. cylindricus* is 41–46% HL. Scales above the lateral line are larger in *G. maculosus,* with 6–8 rows to the dorsal midline at about midbody, whereas those of *G. cylindricus* are smaller, with 10–12 rows above the lateral line at about midbody.

Gymnotus maculosus can be separated from the other species of *Gymnotus* by its color pattern and meristic, features. *Gymnotus maculosus* has fewer precaudal vertebrae (30–34, $n = 21$; vs. 38, $n = 6$) and fewer anal-fin rays (155–182, $n = 8$; vs. 190–222, $n = 6$) than does *G. carapo.* Unlike *G. carapo, G. maculosus* is spotted and does not have conspicuous oblique bands. *Gymnotus maculosus* can be separated from other spotted species of *Gymnotus, G. inaequilabiatus* and *G. pantherinus,* by the same meristic characters used to separate it from *G. carapo.*

Discussion

Variation in characters examined.—Several body measurements vary among and between species of *Gymnotus.* Uses of body depth, head length, interorbital distance, and pectoral-fin length to identify species are noted in the key. Despite this variation, the characters used in the diagnoses do prove useful when making certain comparisons. The deep body of *G. inaequilabiatus* (BD greater than HL), for example, can be used to separate it from all other South American species of *Gymnotus* (except some specimens of *G. cataniapo*) in which the BD is less than HL. Specimens of *G. carapo* and *G. pedanopterus* possess a long head (HL greater than 11.8% TL for specimens 100–250 mm TL) when compared to other species of *Gymnotus.* Although the snout length of most *Gymnotus* species ranges from PR = 32.5–38.0% HL, speci-

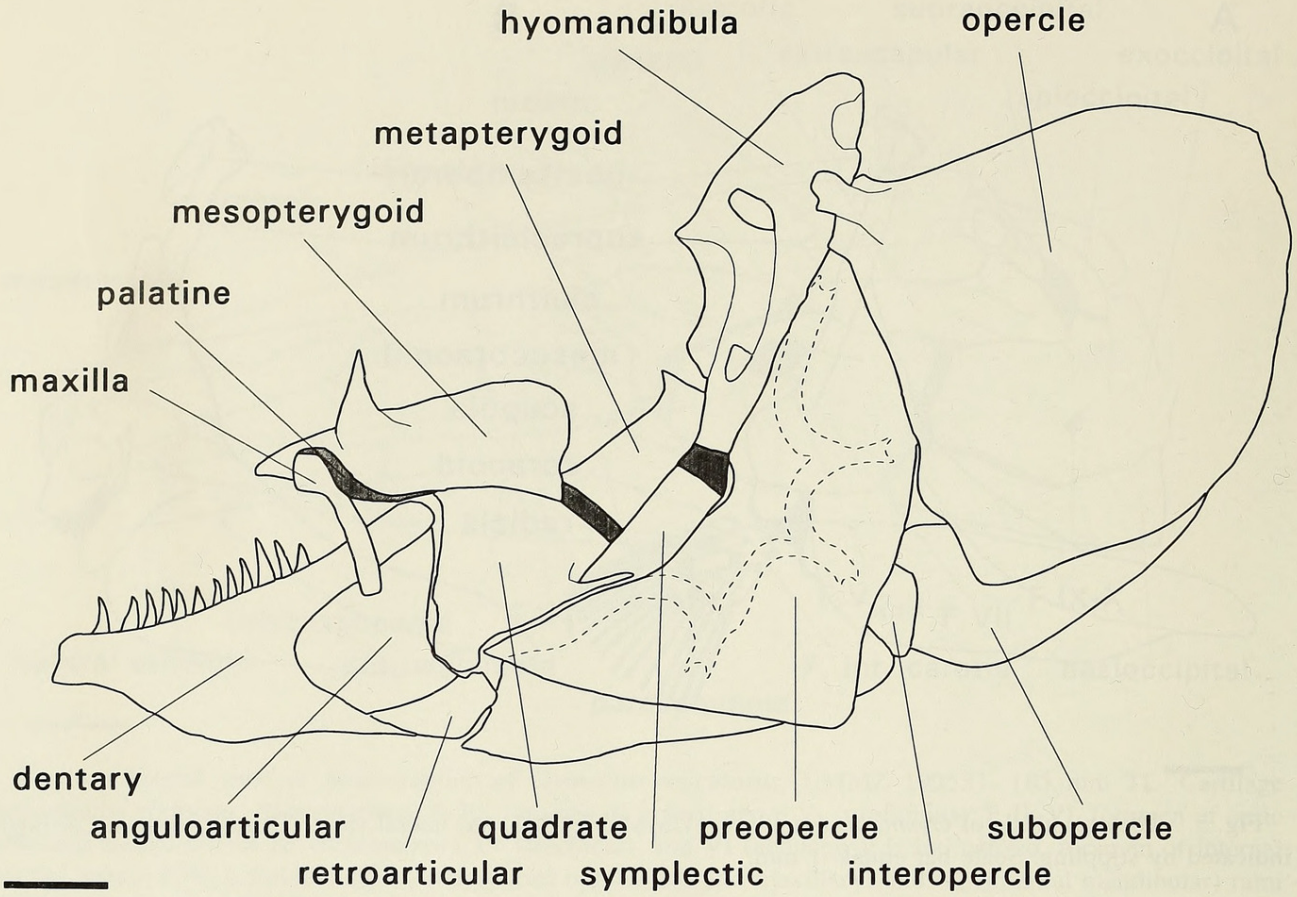

Fig. 6. Lateral view of suspensorium of *Gymnotus maculosus,* UMMZ 190531. Cartilage indicated by stippling. Scale bar equals 1 mm.

mens of *G. anguillaris* tend to have a longer snout (PR = 36.0–41.0% HL), and specimens of *G. coatesi, G. cataniapo, G. pedanopterus,* and *G. stenoleucus* tend to have shorter snouts (PR = 28.5–36.5% HL). The anal fin of *G. carapo* and *G. inaequilabiatus* tends to insert more anteriorly than in other *Gymnotus* species (PA = 55–86% HL vs. 72–112% HL). These measurements exclude two specimens of *G. cylindricus* with abnormally short PA distances (31% and 46% HL). PA data for *G. pedanopterus* and *G. stenoleucus* were not available for this study. The two species of *Gymnotus* from Middle America share a short pectoral fin (P1 = 38.0–47.5% HL) with the Suriname specimens of *G. carapo,* and with the slender species *G. cataniapo, G. pedanopterus,* and *G. stenoleucus.*

Body proportions of *Gymnotus carapo* in South America vary considerably. Specimens examined from Suriname can be distinguished from those in the Amazon basin by having a deeper body (BD = 11.5–12.5% TL vs. 10–11% TL) and a shorter pectoral fin (P1 = 38–45% HL vs. 46–57% HL). The anal-fin origin also tends to be more remote from the anus in the Suriname specimens (PA = 9.5–11.0% HL vs. 6.5–10.0% TL). Specimens collected west of the Andean cordillera in Colombia, from the Río Atrato basin and the Pacific drainage at Pizarro, possess the two diagnostic traits of *G. carapo:* a long head (HL = 11.8–12.5% TL) and a clear anal-fin membrane at the posterior end of the fin. Measurements of these specimens (N = 5) reveal that they have the more slender body (BD = 10.0–10.2% TL) and longer pectoral fin (P1 = 45.2–58.3% HL) of *G. carapo* from the Amazon, and the posterior origin of the anal fin (PA = 9.0–11.2% TL) of *G. carapo* from Suriname, and of the other *Gymnotus* species.

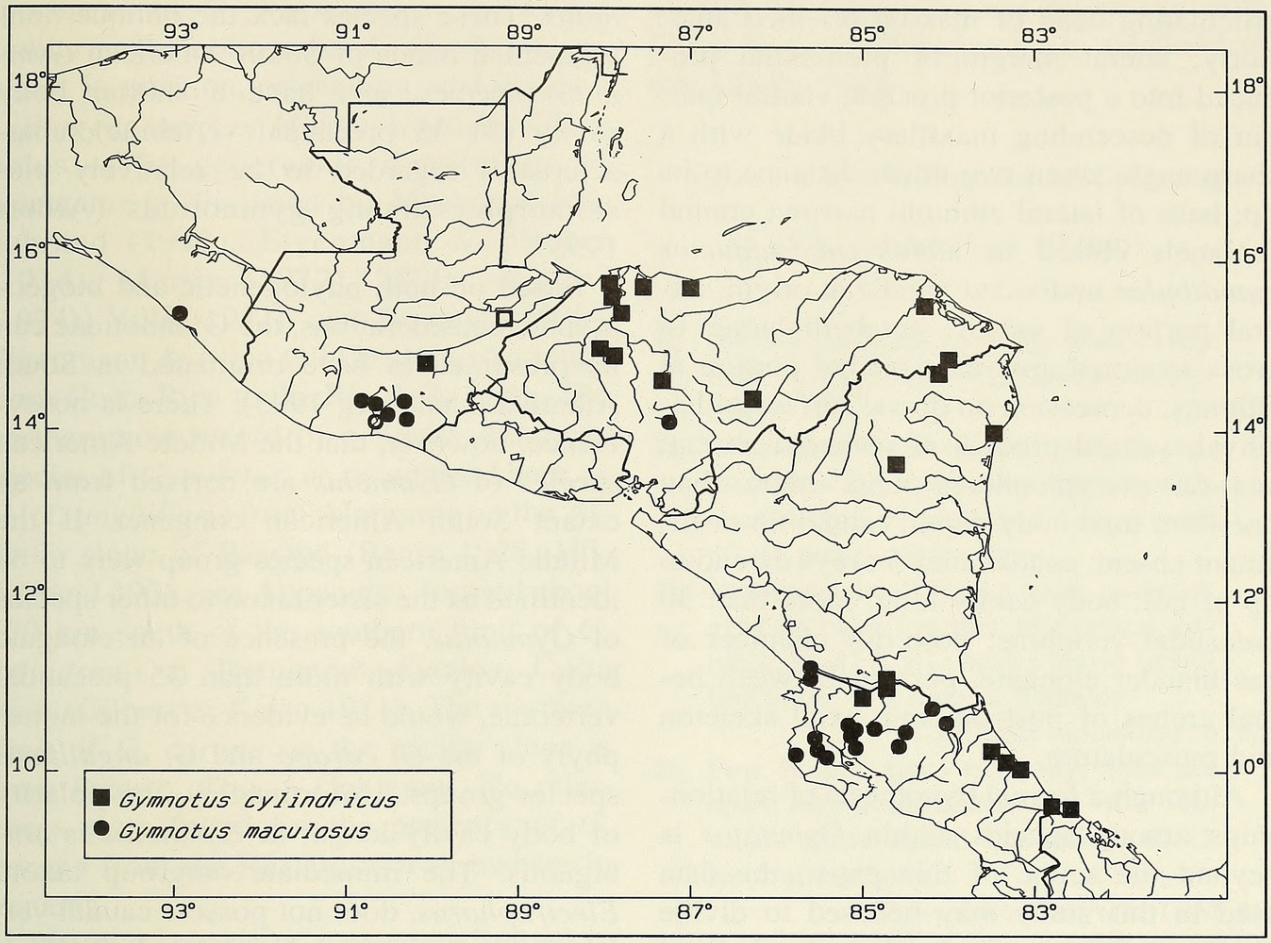

Fig. 7. Geographic distribution of the two Middle American species of *Gymnotus*. Type localities indicated by hollow symbols. The absence of *G. maculosus* from the Pacific slope of El Salvador and Nicaragua is due to sampling bias.

Although color patterns are of use in identifying species of *Gymnotus,* certain aspects are variable (Nijssen & Isbrücker 1968, Mago-Leccia 1994). The trans-Andean specimens of *G. carapo,* for example, differ from other populations *G. carapo* in possessing narrow pale bands. This aspect of coloration is otherwise only observed in elongate, slender species of *Gymnotus* (see below). Another example of variable color pattern is *G. anguillaris* from the Lawa River, Suriname, which resemble *G. carapo* in their dusky brown ground color and in possessing more than 23 alternating pale and dark bands. The pale bands are narrower than the dark bands only on the posterior end of the body. Specimens of *G. anguillaris* from other localities, however, ranging from Guyana to Paraguay, more closely resemble the description of the type specimen in which the pale bands are more narrow along the entire length of the body (Hoedeman 1962a).

Comments on the interrelationships of Gymnotus.—Species diversity and systematics of the Gymnotoidei have received considerable attention in recent years (Mago-Leccia 1978, 1994; Lundberg and Mago-Leccia 1986; Triques 1993; Gayet et al. 1994; Alves-Gomes et al. 1995; Albert 1995). The results of Albert's (1995) study support Ellis's (1913) hypothesis that *Gymnotus* and *Electrophorus* form a monophyletic group, the Gymnotoidea (Gymnotoidei of Mago-Leccia 1978), which is itself the sister lineage to other gymnotoids (Albert 1995, fig. 1; Albert & Fink 1995, fig. 2). The Gymnotoidea is diagnosed by 14 characters. Gape large, extending to vertical through posterior nares; premaxilla large,

articulating head of maxilla oriented anteriorly; lateral margin of premaxilla produced into a posterior process; ventral margin of descending maxillary blade with a sharp angle about two-thirds distance to its tip; base of lateral ethmoid narrow; cranial fontanels closed in adults; *m. adductor mandibulae* undivided bundle at origin; lateral portion of valvula cerebelli larger in cross sectional area than medial portion at isthmus; depression on dorsal surface of basihyal; ventral process of coracoid absent; anal-fin pterygiophores long, more than one-third total body depth; caudal fin or filament absent, caudal anal-fin rays extend to tip of tail; body cavity long, more than 30 precaudal vertebrae; posterior chamber of gas bladder elongate, passing between hemal arches of postcoelomic axial skeleton and musculature.

Although a formal hypothesis of relationships among species within *Gymnotus* is beyond the scope of this paper, the data used in this study may be used to divide *Gymnotus* into three species-groups, on the basis of color pattern and general body proportions. Because the characters used to recognize these species-groups are not polarized, the monophyly of these groups and their interrelationships are ambiguous.

One species-group is composed of elongate, slender species, with a BD less than 11% TL. Members of this group also possess a color pattern consisting of alternating dark and pale bands, in which the pale bands are narrower than the dark bands, and the dense brown or grey dark bands extend onto the dorsum. *Gymnotus anguillaris* is the most widely distributed member of this group and exhibits the greatest variation in these characters. Members of the second species-group have deeper bodies, with a BD greater than 11% TL, and the alternating bands of heavy and light pigmentation are of about equal width, grading to a dusky brown on the dorsum. This group includes the type species *G. carapo*. The third species-group is composed of the two exclusively Middle American species of *Gymnotus*. These species lack the oblique nonpigmented bands of South American *Gymnotus* species, and have a shorter body cavity (31–35 precaudal vertebrae), characteristics regarded to be relatively plesiomorphic among gymnotoids (Albert 1995).

Based on both phylogenetic and biogeographic considerations, the Gymnotidae can be presumed to have originated in South America (Lundberg 1993). There is no evidence, however, that the Middle American species of *Gymnotus* are derived from an extant South American congener. If the Middle American species-group were to be identified as the sister taxon to other species of *Gymnotus,* the presence of an elongate body cavity with more than 35 precaudal vertebrae, would be evidence for the monophyly of the *G. carapo* and *G. anguillaris* species-groups. Unfortunately, the polarity of body cavity length in *Gymnotus* is ambiguous. The immediate outgroup taxon, *Electrophorus,* does not possess caudal vertebrae at all; the body cavity and gas bladder extend to the caudal end of the animal, hemal spines do not form, and the hemal arches do not meet along the midline. The next outgroup is not elongate; species of *Sternopygus,* which retain a relatively plesiomorphic gymnotoid morphology, possess fewer precaudal vertebrae than any species of *Gymnotus.* In fact, the phylogenetic distribution of the number of precaudal vertebrae among extant gymnotoid taxa indicates that the plesiomorphic condition for the group is 17–19 (Albert 1995).

The polarity of oblique depigmented bands in *Gymnotus* is also ambiguous. Many rhamphichthyoid species possess alternating color bands, but these bands are vertical regions of pigment investing a nonpigmented background. Narrow bands are not present in *Electrophorus, Sternopygus,* or the plesiomorphic hypopomid *Hypopomus* (Albert 1995). Furthermore, the presumed absence of oblique bands in the Middle American species of *Gymnotus* is not entirely clear; the pattern of spots in some

specimens of *G. maculosus* is somewhat similar to the oblique bands of other *Gymnotus,* in position, orientation, and number.

Biogeography of Middle American Gymnotus.—The geographic distribution of *Gymnotus* is discussed by Meek and Hildebrand (1913), Eigenmann & Fischer (1914), Martin (1972), Miller & Carr (1974), Villa (1982), and Bussing (1987). Eigenmann & Allen (1942) claimed a range from Costa Rica to the Río de la Plata. The northernmost record of a South American species of *Gymnotus,* as recognized here, is *G.* cf. *anguillaris* from Almirante on the Atlantic slope of Panamá (Behre 1928, Hildebrand 1938, see Appendix), located about 170 km south of the southern limit of *G. cylindricus* at Tortuguero, Sixaloa, Costa Rica (Gilbert & Kelso 1971). The northern limit of *G. carapo* on the pacific slope is from Pizarro, Choco, Colombia. No references were found for the presence of *G. carapo* from the Río Tuira or elsewhere in Panamá.

The two species of *Gymnotus* limited to Middle America come into closest contact in small streams on opposite sides of Lake Nicaragua, and in several tributaries of the Río San Juan in Northern Costa Rica, an Atlantic drainage. The presence of *G. maculosus* in these localities may have resulted from stream capture due to tectonic uplift of the region in the past several million years (Durham 1944; Miller 1950, 1986). Geologic evidence for the uplift of the Nicaraguan graben is discussed by Riedel (1972).

The parapatric distribution of species of *Gymnotus* is similar to that of some other fishes in the lake Nicaragua basin. The shad *Dorosoma chavesi,* the poeciliid *Poeciliopsis* cf. *turrubarensis,* and the gar *Atractosteus tropicus* found in this basin are otherwise only known from Pacific-slope drainages. A second species of poeciliid recorded from the Lake Nicaragua basin, *P.* cf. *gracilis,* also occurs on the Atlantic slope in southern Mexico and in the Río Motagua of Guatemala. The sawfish *Pristis pectinata,* and the tarpon *Tarpon atlanticus,* both found in Lake Nicaragua, are confined to the Atlantic basin.

Key to adults of species of *Gymnotus*

(HL greater than 10 mm)

1a. No oblique bands on body; body cavity with 31–35 (mode = 32) precaudal vertebrae 2

1b. Alternating bands of dark and pale pigmentation arranged at an oblique angle along length of body; body cavity with 36–51 precaudal vertebrae 3

2a. Numerous small brown spots on body; eyes set close together, interorbital distance 37–41% HL; scales above lateral line large, 6–8 rows at midbody .... *Gymnotus maculosus,* n. sp.

2b. Few if any spots on body; eyes set apart, interorbital distance 41–46% HL; scales above lateral line small, 10–12 rows at midbody .... *Gymnotus cylindricus* LaMonte

3a. Body deep, depth at anal-fin origin more than about 9% TL (except *G. pantherinus*); alternating dark and pale oblique bands of equal width at midbody, or pale bands broader; ground color dusky brown on dorsum; anal fin hyaline posteriorly 4

3b. Body slender, depth at anal-fin origin less than about 9% TL; dark oblique bands broader than pale bands at midbody; ground color dark brown or dark grey on dorsum; anal fin pigmented posteriorly 6

4a. Head long, HL greater than about 11% TL for specimens 100–250 mm TL); no spots on body, dark oblique bands uninterrupted; pigment density in middle part of dark bands less dense than near margins; bands present on anterior portion of body .. *Gymnotus carapo* (Linneus)

4b. Head short, HL less than about 11% TL; spots on head and back, dorsal part of dark oblique bands interrupted; dark oblique bands of uniform pigment density; bands not present on anterior half of body in specimens larger than 220 mm TL 5

5a. Body deep, BD greater than 9% TL . *Gymnotus inaequilabiatus* (Valenciennes)

5b. Body shallow, BD less than 9% TL .... *Gymnotus pantherinus* (Steindachner)

6a. Eyes set further apart, IO 39–44% HL; nape dark, pale bands not extending above lateral line on anterior half of the body .. *Gymnotus anguillaris* Hoedeman

6b. Eyes set closer together, IO 25–38% HL (except some *G. cataniapo*); white band at nape, pale bands extending to dorsal midline on anterior half of body 7

7a. 13–23 oblique bands; pectoral fin longer, 38–54% HL 8

7b. 23–50 oblique bands; pectoral fin shorter, 28–37% HL 9

8a. Body cavity shorter, 40–42 precaudal vertebrae; alternate pale bands incomplete ..... *Gymnotus coatesi* LaMonte

8b. Body cavity longer, 47–48 precaudal vertebrae; all pale bands complete ..... *Gymnotus stenoleucus* Mago-Leccia

9a. Head shorter, HL 8–10% TL; body cavity shorter, 50–51 precaudal vertebrae; posterior end of anal fin dark .... *Gymnotus cataniapo* Mago-Leccia

9b. Head longer, HL 12–14% TL; body cavity shorter, 36–37 precaudal vertebrae; posterior end of anal fin pale .... *Gymnotus pedanopterus* Mago-Leccia

Acknowledgments

William Bussing, David Catania, Mary Anne Rogers, Bill Saul, and Richard Vari provided many specimens used in this study. Sara Fink helped interpret the morphology of the ethmoid region. Tamaki Yuri helped with construction of the key. Ricardo Campos-da-Paz and John Sullivan provided useful comments on the characters. William Bussing, John Lundberg, and Richard Vari made many useful suggestions on earlier drafts of the manuscript. We thank the Smithsonian Institution photographic laboratory for the photograph reproduced in Fig. 1, and Margaret Van Bolt who retouched the background. Brian Dyer provided the Spanish abstract. We acknowledge the NEODAT project (NSF/AID DEB grant 90-24797) for collection information. We thank Doug Nelson for curatorial assistance, and the Secretaría, Departamento de Pesca, for permission to collect in Mexico. Part of the research reported was conducted in facilities provided by NSF grant BSR 9015158 to Willim Fink.

Literature Cited

Albert, J. S. 1995. Phylogenetic systematics of the American Knifefishes (Teleostei: Gymnotoidei). Unpublished Ph.D. Thesis, University of Michigan, 528 pp.

———, & W. L. Fink. 1995. *Sternopygus xingu,* a new species of electric fish from South America (Gymnotoidei, Teleostei), with comments on the phylogenetic position of *Sternopygus.*—Copeia (in press).

Alves-Gomes, J. A., G. Orti, M. Haygood, A. Meyer, & W. Heiligenberg. 1995. Phylogenetic analysis of the South American electric fishes (Order Gymnotiformes) and the evolution of their electrogenic system: a synthesis based on morphology, electrophysiology, and mitochondrial sequence data.—Molecular Biology and Evolution 12(2):298–318.

Artedi, P. 1738. Ichthyologia sive Opera Omnia de Piscibus, *in* Carolus Linneaus, ed., Lugdini Batavorum.

Behre, E. H. 1928. A list of the freshwater fishes of western Panama, between long. 81°45′ and 83°15′ W.—Annals of the Carnegie Museum 18(2):305–328.

Bloch, M. E. 1787. Naturgeschichte der Ausländischen Fische, Berlin.

Brind, W. L. 1935. Hunting the "Tiger Knife Fish" in the Amazons.—Aquarium News, New York 2(2):5, 8–10.

Breder, C. M. Jr. 1927. The fishes of the Rio Chucunaque Drainage, Eastern Panama.—Bulletin of the American Museum of Natural History 52(3):91–176.

Bussing, W. A. 1985. Patterns of distribution of the Central American ichthyofauna. Pp. 453–473 *in* F. G. Stehli and S. D. Webb, eds., The Great American Biotic Interchange. Plenum, New York.

———. 1987. Peces de las aguas continentales de Costa Rica. Editorial de la Universidad de Costa Rica. San José, 271 pp.

Carr, A., & L. Giovannoli. 1950. The fishes of the Choluteca drainage of southern Honduras.—Occasional Papers of the Museum of Zoology, University of Michigan 523:1–37.

Cuvier, G. 1816. Le Regne Animal distribué d'apres son organisation pour servir de base à l'histoire

naturelle des animaux et d'introduction à l'anatomie compareé, Edition 1. v.2i–xviii+1–532.

Duméril, M. C. 1856. Ichthyologie Analytique ou Essai d'une classification naturelle des Poissons a l'aide de Tableaux Synoptiques.—Memiores Academie France 27, Paris.

Durham, H. W. 1944. New volcanoes and new mountain ranges.—Science 100:49–50.

Eigenmann, C. H., & W. R. Allen. 1942. Fishes of Western South America, University of Kentucky, Lexington, 494 pp.

———, & H. G. Fischer. 1914. The Gymnotidae of Trans-Andean Colombia and Ecuador.—Indiana University studies no. 25, 141:235–237.

———, & D. P. Ward. 1905. The Gymnotidae.—Proceedings of the Washington Academy of Science 7:157–86.

Ellis, M. M. 1913. The gymnotid eels of South America.—Memiores of the Carnegie Museum 6(3): 109–195.

Espinosa-Pérez, H., M. T. Gaspar-Dillanes, & P. Fuentes-Mata. 1993. Listados faunísticos de México. III. Los peces dulceacuícolas Mexicanos.—Universidad Nacional Autónoma de México 1993:1–98.

Fink, S. V., & W. L. Fink. 1981. Interrelationships of the ostariophysan fishes (Teleostei).—Zoological Journal Linnean Society 72(4):297–353.

Fink, W. L. 1989. Ontogeny and phylogeny of shape change and diet in the South American fishes called piranhas. *In* B. David et al., eds., Ontogenèse et évolution.—Geobios, mémiore spécial 12:167–172.

———, & A. Machado-Allison. 1993. Three new species of piranhas from Brazil and Venezuela (Teleostei: Characiformes).—Ichthyological Explorations of Freshwaters 3(1):55–71.

Gayet, M., & F. J. Meunier. 1991. Première découverte de Gymnotiformes fossiles (Miocène supérieur, Bolivie).—C. R. Academie Sciences Paris, Série II:471–476.

———, ———, & F. Kirschbaum. 1994. *Ellisella kirschbaumi* Gayet & Meunier, 1991, gymnotiforme fossile de Bolivie et ses relations phylogénétiques au sein des formes actuelles.—Cybium 18(3):273–306.

Gilbert, C. R., & D. P. Kelso. 1971. Fishes of the Tortuguero area, Caribbean Costa Rica.—Bulletin of the Florida State Museum of Biological Science 16:1–54.

Hildebrand, S. F. 1938. A new catalogue of the freshwater fishes of Panama.—Field Museum of Natural History, Zoological Series 22(4), Publication 425:219–359.

Hoedeman, J. J. 1962a. Notes on the ichthyology of Suriname and other Guyanas, 9. New records of gymnotid fishes.—Bulletin Aquatic Biology, Amsterdam 3(26):53–60.

———. 1962b. Notes on the ichthyology of Suriname and other Guyanas, 11. New gymnotoid fishes from Suriname and French Guyana, with additional records and a key to the groups and species from Guyana.—Bulletin Aquatic Biology, Amsterdam 3(30):97–107.

Lacépède, B. G. E. 1800. Histoire Naturelle des Poissons. Vol. 2, Chez Plassan, Imprimeur-Libraire, Paris.

LaMonte, F. 1935. Two new species of *Gymnotus*.—American Museum Novitates No. 781:1–3.

Leviton, A. E., R. H. Gibbs, Jr., E. Heal, & C. E. Dawson. 1985. Standards in herpetology and ichthyology: Part I. Standard symbolic codes for institutional resource collections in herpetology and ichthyology.—Copeia 1985(3):802–832.

Linnaeus, C. 1758. Systema Naturae, 10th edition, Vol. 1. Laurentii Salvii, Holmiae, 824 pp.

Lundberg, J. G. 1993. African-South American freshwater fish clades and continental drift: problems with a paradigm. Pp. 156–199 *in* P. Goldblatt, ed., Biological relationships between Africa and South America. Yale University Press, New Haven.

———, & F. Mago-Leccia. 1986. A review of *Rhabdolichops* (Gymnotiformes, Sternopygidae), a genus of South American freshwater fishes, with descriptions of four new species.—Proceedings of the Academy Natural Sciences Philalephia 138:53–85.

Mago-Leccia, F. 1978. Los peces de la familia Sternopygidae de Venezuela.—Acta Científica Venezolana 29:1–51.

———. 1994. Electric fishes of the continental waters of America. Biblioteca de la Academia de Ciencias Físicas, Matematicas, y Naturales, Vol. 29, Caracas, Venezuela, 206 pp.

Martin, M. 1972. A biogeographic analysis of the freshwater fishes of Honduras. Unpublished Ph.D. Thesis, University of Southern California, 456 pp.

Meek, S. E., & S. F. Hildebrand. 1913. New species of fishes from Panama. Family Gymnotidae.—Field Museum of Natural History, Zoological series, 10(8), Publication 166:305–313.

Miller, R. R. 1950. A review of the American clupeid fishes of the genus *Dorosoma*.—Proceedings of the U.S. National Museum 100:387–410.

———. 1966. Geographical distribution of Central American freshwater fishes.—Copeia 1966: 773–802.

———. 1986. Composition and derivation of the freshwater fish fauna of Mexico.—Anales de la Escuela Nacional de Ciencias Biológicas, México 30(1–4):121–153.

Miller, R. R., & A. Carr. 1974. Systematics and dis-

tribution of some freshwater fishes from Honduras and Nicaragua.—Copeia 1974:120–125.

Nijssen, H., & I. J. H. Isbrücker. 1968. *Gymnotus carapo* and *G. anguillaris* (syn. *G. coropinae*), two often confused species of gymnotid fishes. Pisces, Cypriniformes.—Beaufortia 15(203):161–168.

Pallas, P. S. 1767. Spicilegia Zoologica, Petrop., 1769–79.

Pittman, W. C. III., S. Cande, J. LaBrecque, & J. Pindell. 1993. Fragmentation of Gondwana: The separation of Africa from South America. Pp. 15–61 *In* P. Goldblatt, ed., Biological relationships between Africa and South America. Yale University Press, New Haven.

Putzer, H. 1984. The geological evolution of the Amazon Basin and its mineral resources. Pp. 14–46 *in* H. Sioli, ed., The Amazon. Limnology and landscape ecology of a mighty tropical river and its basin. Dr. W. Junk Publisher, The Netherlands, ix + 763 pp.

Riedel, D. 1972. Die Genesis der nicaraguensischen Grabenseen (Teil I) und des mesoamerickanischen (Teil II) aus der Sicht des Fischereibiologen.—Archives Hydrobiologia 70:82–107.

Steindachner, F. 1908. *Brachyplatystoma* -Art aus dem Río Parnahyba un über eine ditch gefleckte und gestrichelte Varietaet von *Giton fasciatus* aus dem Gewassern von Santos. Staat São Paulo.—Anzeiger der Akademie der Wissenschafften, Wien 45(9):123–130.

Taylor, W. R., & G. C. Van Dyke. 1985. Revised proceedures for staining and clearing small fishes and other vertebrates for bone and cartilage study.—Cybium 9:107–119.

Triques, M. L. 1993. Filogenia dos gêneros de Gymnotiformes (Actinopterygii, Ostariophysi), com base em characters esqueleticos.—Comunicações do Museu Ciências da PURCS, série Zoologia, Porto Alegre, 6:85–130.

Valenciennes, A. 1847. Poissons. Pp. 5–11 *in* D'Orbigny, Voyage dans l'Amérique Meridionale Vol. 5, 2nd part, Paris.

Villa, J. 1982. Peces nicaraguenses de agua dulce.—Banco de América, serie geografia y naturaleza 3:i–xiv, 1–253.

Weitzman, S. H. 1974. Osteology and evolutionary relationships of the Sternoptychidae, with a new classification of stomiatoid families.—Bulletin of the American Museum of Natural History 153:327–478.

Appendix 1

List of 125 lots containing 698 specimens of gymnotids examined. Data are arranged by country, then alphabetically by museum acronym and number. Catalogue numbers are followed in parentheses by number of specimens, and then by locality, size range in millimeters total length (mm), and date of capture.

Gymnotus anguillaris.—Guyana: FAU uncat. (2), Madewini River, 132–165 mm, 1994.IV.20. Paraguay: UMMZ 206080 (21), Arroyo in Parque Nacional Ybycui, 82–260 mm, 1979.VI.20. Suriname: UMMZ 190413 (6), Maka Creek, Lawa River, Morowyne, 1967.IV.21. ZMA 100338 (2), Coropina Creek, 228–236 mm, 1956.V.20.

Gymnotus cf. *anguillaris.*—Panama: CAS 72209 (2), small creek into Río Cricamola, behind Konkintu, Boca del Toro Province, 225–239 mm, 1923.II.25.

Gymnotus carapo.—Bolivia: UMMZ 066433 (2), Lake Rogoagua, Río Beni, 214–338 mm, 1921.IX. UMMZ 066462 (2), Reyes, Río Beni, 205–245 mm, 1921.IX. UMMZ 204299 (1), Costa Marquez, Río Itenez (Guapore), Madeira, 164 mm, 1964.IX.02. UMMZ 204771 (5), Costa Marquez, Río Itenez, 44–51 mm, 1964.X.1. UMMZ 204886 (3), Río Baures, Río Itenez, 145–345 mm, 1964.X.7. Brazil: UMMZ 143282 (2), Lagoa dos Quadros, Rio Grande do Sul, Tramandai, 55–129 mm, 1941.VIII. UMMZ 230732 (2), Aggassiz collections, presumably Brazil, 174–202 mm, Acc. 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), Upper Yuruena, Mato Grosso, 1965.IV.9. Colombia: CAS 072192 (2), Río Sucio, Río Truando, Río Atrato, 150–179 mm, 1913. FMNH 56793 (2), mouth of Río Calima, Río Atrato, 1913. FMNH 56794 (2), Río Sucio, Río Truando, Río Atrato, 174–175 mm, 1913. FMNH 70511 (5), Pizarro, Choco, Pacific drainage, 124–247 mm, 1945.IX. Perú: UMMZ 072636 (2), Yurimaguas, Río Maranon, 148–214 mm, 1920.IX. UMMZ 230733 (1), Quebrada near Buen Sucesso, Rio Javari, Loreto, 250 mm, 1993.V.15. UMMZ 228998 (2), Río Momon, near Iquitos, Río Nanay, Loreto, 38–172 mm, 1993.V.5. UMMZ 228999 (1), Río Tapira, Río Tahuayo, Loreto, 161 mm, 1993.V.7. Suriname: UMMZ 187499 (1), Brokopondo, 195 mm, 1966.IX.15. UMMZ 190414 (6), Brokopondo, 71–225 mm, 1966.IX.15. 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), 256 mm, 1957.X.5. Trinidad: UMMZ 169080 (2), Gunupia, Mt. Plaisance, 46–74 mm, 1953.III.12. Venezuela: UMMZ 212345 (1), Esteros de Camaguan, Guarico, Apure, 45 mm, 1981.VIII. UMMZ 214766 (1), Caño Falcón, Portuguesa, 241 mm, 1987.II.19.

Gymnotus cataniapo.—Venezuela: MBUCV-V-14154 (3), caño near Salto Nieve, Río Orinoco, 75–194 mm, 1983.XII.22. MBUCV-V-14300 (1), Caño Merete, Río Casiquiare, 213 mm, 1984.VIII.20. MBUCV-V-14736 (1), San Carlos de Río Negro, Río Orinoco, 253 mm, 1984.X.4. MCUCV-V-14757 (1), Caño Guayabal, near Puerto Ayacuchu, Río Orinoco, 114 mm, 1984.XII.12. MBUCV-V-14781 (15), Caño Las Pevas, Río Casiquiare, 143–316 mm, 1984.VIII.2.

Gymnotus coatesi.—Bolivia: UMMZ 205149 (7), near Guayaramerin, Arroyo Grande, 45–175 mm, 1964.X.23. Paraguay: UMMZ 206155 (2), near San Rafael, Arroyo Tembley, 194–225 mm, 1979.VI.26. Perú: UMMZ 224596 (10), Buen Sucesso, Rio Javari, Loreto, 45–167 mm, 1993.V.15. UMMZ 224599 (2), Quebrada near Buen Sucesso, Rio Javari, Loreto, 1993.V.15. UMMZ 224601 (1), caño near Santa Ana, Río Tahwayo, Loreto, 1993.V.4. UMMZ 224607 (6), near Iquitos, Río Nanay, 30–144 mm, 1993.V.4.

Gymnotus cylindricus.—Costa Rica: UCR 1014-1 (12), Río Escondido, Limon, Río Sixaola, 123–249 mm, 1976.IX..17. UCR 280-2 (3), Río Escondido, Limon, Río Sixaola, 1968.X.3. UMMZ 224129 (10), Río Escondido, Limon, Río Sixaola, 131–205 mm, 1968.X.3. Guatemala: UMMZ 193873 (2), el Progresso, Morazán, Río Yeguare, 192–210 mm, 1973.III.24. UMMZ 193986 (14), Quebrada de Vegega, Los Amates, Río Izabal, 26–183 mm, 1973.IV.5. Honduras: UMMZ 155831 (1), bridge on Tegucigalpa-Danli road, Río Yeguare, 174 mm, 1948.I.30. UMMZ 155832 (2), Quebrada near Los Flores, Río Yeguare, 161–204 mm, 1947.VII.23. UMMZ 188110 (2), Pito Solo, Cortez, Río Jaitique, 93–191 mm, 1948.V.23. UMMZ 188273 (1), Lago Yoyoa, Santa Barbara, Río Yeguare, 135 mm, 1949.VIII.1. UMMZ 188274 (5), Lago Yojoa, Santa Barbara, Río Yeguare, 97–175 mm, 1948.IV.14. UMMZ 188275 (16), Lago Yojoa, Río Yeguare, 166–224 mm, 1949.VIII.10. UMMZ 188296 (2), Quebrada Lagunita, Morazán, Río Yeguare, 120–138 mm, 1947.VII.29. UMMZ 188297 (5) Quebrada behind finca de Rudolfo Rosales, Río Yeguare, 69–129 mm, 1947.XI. UMMZ 199598 (1), Laguna Sikalanka, Río Sucre, 215 mm, 1975.V.11. Nicaragua: CAS 161383 (3), Rio Frio, about 1.5 mi. above San Carlos, in bayou with sluggish current, Lago Nicuaragua drainage, Río San Juan state, 1963.II.12. TU uncat. (1), San Carlos, Lago Nicuaragua drainage, Río San Juan state. UMMZ 199622 (13), SE of Bilwaskarma, Río Kurnog, 1975.V.13. UMMZ 199633 (2), Río Putkrukira near Waspán, Río Coco, 121–194 mm, 1975.V.27.

Gymnotus inaequilabeatus.—Brazil: USNM 1643 (1), Río Paraguay, 791 mm. USNM 1644 (1), Río Paraguay. USNM 1645 (1), Río Paraguay. 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 N.W. Pt. Remaro bridge, Río Confuso, 485 mm, 1979.VIII.9. UMMZ 207096 (3), Estancia la Golondrina, Presidente Hayes, Confuso, 132–210 mm, 1979.VIII. UMMZ 207564 (2), Río Pilcomayo near Peurto Falcón, Río Paraguay, 220–242 mm, 1979.VIII.29. UMMZ 207619 (1), Riachúelo Pilco, Presidente Hayes, 144 mm, 1979.VIII.31. UMMZ 207760 (2), Arroyo Peguajho, Ypane, 77 mm, 1979.IX.04. UMMZ 207893 (6), Río Aequidaban near Paso Hasqueta, Río 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, Río Confuso, 322 mm, 1981.X.02. UMMZ 216576 (1), near Trans Chaco-Villa, Presedente Hayes, 322 mm, 1981.X.2.

Gymnotus maculosus.—Costa Rica: TU 24935 (16), La Virgin, Río Sarapiqui, 1960.II.22. TU 25063 (3), Río Tempisque, near Liberia, Guanacaste, 193–218 mm, 1961.I.21. UCR 969-9 (20), Santa Cruz, Río Garzón, Guanacaste, 123–195 mm, 1976.I.25. UCR 980-9 (5), Arenal, Río Dos Bocas, Guanacaste, Río San Carlos drainage, 1968.VI.10. UMMZ 158451 (1), Finca la Trinidad, Guanacaste, 179 mm, 1949.X.21. UMMZ 224128 (5), Río Higuerón, near Canas, Guanacaste, 158–222 mm, 1968.VI.10. Guatemala: UMMZ 188072 (1), Río Bravo, Río Nahualate, 1968.IV.3. UMMZ 190531 (7), El Obraje, Jutiapa, Río Grande de Pasaco, 146–200 mm, 1971.III.9. UMMZ 190783 (3, paratypes), diversion of channel from Rio María Linda, 20 km East of Escuintla, Departamento Santa Rosa, 176–203 mm, 1971.III.27. UMMZ 194122 (6), 2.6 km ESE Eca Cocales, Río La Primavera, 105–135 mm, 1973.IV.20. UMMZ 194150 (2), Río Siguacan, near Escuintla, Santa Rosa, 141–172 mm, 1973.IV.24. UMMZ 197103 (17), near Taxisco, Santa Rosa, 1974.IV.26. UMMZ 197103 (20), Taxisco, Santa Rosa, 78–227 mm, 1974.IV.6. UMMZ 230354 (20, paratypes), Río Buena Vista, trib. of Río Tigre, on road between Escuintla and Chiquimulilla, 8 km West of Pajal, Departamento Santa Rosa, Guatemala, 128–230 mm, 1946.IV.18. UMMZ 230830, (1, holotype), diversion of channel from Rio María Linda, 20 km East of Escuintla, Departamento Santa Rosa, 191 mm, 1971.III.27. USNM 114235 (2), Río Colojate, 1947. USNM 114539 (22), near Malacatan, Río Gramal, 1956.VII.6. USNM 134700 (49, paratypes), near Pajal, Río Buen Vista, 138–226 mm, 1946.IV.18. USNM 225435 (1), Río Chiquimulilla, 1946. USNM uncat. Río Hondo, 1946. USNM uncat. (8), Río Lato, 1946. USNM uncat. (23), Río Grammal, 1947. Mexico: UMMZ 191702 (2), Tapachula, Río San Nicolás, Chiapas, 163–189 mm, 1971.III.13. UMMZ 191712 (3), Tapachula, Río San Nicolás, Chiapas, 184-228, 1971.II.27. Nicaragua: TU 24965 (38, paratypes), Boca de Río Sapoá, Sapoá, Lago Nicaragua drainage, Rivas Province, 1960.IV.23. TU 25032 (1), Boca de Río Sapoá, Sapoá, Lago Nicaragua drainage, Rivas Province, 43 mm, 1961.I.21.

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

Gymnotus pantherinus.—Brazil: USMN 297933 (20), Naneia, São Paulo, 1988.ii.21. USMN 297939 (12), Guaratuba, Río da Praia, 1988.X.3.

Gymnotus pedanopterus.—Venezuela: MBUCV-V-14737 (2), Caño Chola, near San Carlos de Río Negro, Río Casiquiare, 198–228 mm, 1984.XI. MBUCV-V-

14738 (1), Caño Temblador, Río Casiquiare, 215 mm, 1984.XII.5. MBUCV-V-4860 (1), Caño Esmeralda, Río Orinoco, 281 mm, 1966.XI.6. MBUCV-V-7135 (2), El Pozo de Lucas, near San Fernando de Atabapo, Río Orinoco, 109–119 mm, 1973. MBUCV-V-7310 (3), caño near San Fernando de Atabapo, Río Orinoco, 92–185 mm, 1972.IV.14.

Gymnotus stenoleucus.—Venezuela: MBUCV-V-14028 (15), Río Cataniapo, Río Orinoco, 80–171 mm, 1983.III.30. MBUCV-V-14747 (1), Caño Guayabal, near Peurto Ayacuchu, Río Orinoco, 140 mm, 1984.XII.12. MBUCV-V-4644 (2), Río Quiritare, Río Orinoco, 91–95 mm, 1966.X.30. MBUCV-V-6218 (1), Caño Caripo, Río Casiquiare, 140 mm, 1969.I.26. MBUCV-V-9417 (4), Caño Caripo, Río Casiquiare, 91–142 mm, 1969.I.26.

Electrophorus electricus.—Aquarium: UMMZ 183710-S (1), 100 mm+, 1961.VII.1. Bolivia: UMMZ 204426-S (2), Costa Marques, Rio Itenez, Rio Madeira, 940 mm, 1964.IX.12. Guyana: USNM 228883 (3), Essequibo River. UMMZ uncat. (1), 1000+ mm, 1992.XII.12. Suriname: USNM 225669 (1), Amotopa landing, Nickerie District, Rio Corantijn, 511 mm, 1980.VII.19.