Zootaxa 000: 1–54 (2003)
www.mapress.com/zootaxa/

ISSN 1175-5326 (print edition)
ZOOTAXA
ISSN 1175-5334 (online edition)

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Seven new species of the Neotropical electric fish *Gymnotus* (Teleostei, Gymnotiformes) with a redescription of *G. carapo* (Linnaeus)

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Abstract

Seven new species of *Gymnotus* are described, and a redescription of the type species *G. carapo sensu-stricto* Linnaeus (*G. carapo s.s.)* is provided, from examination of populations from throughout tropical South and Middle America. The new species are described on the basis of unique combinations of characters. Five of the new species are members of the *G. carapo* species-group: 1, *Gymnotus choco* n. sp., from the Baudó and Atrato basins on the Pacific and Caribbean slopes of Colombia; 2, *Gymnotus esmeraldas* n. sp., from the Esmeraldas and Guayaquil basins on the Pacific Slope of Ecuador; 3, *Gymnotus henni* n. sp., from the Calima and Juradó basins on the Pacific Slope of Colombia; 4, *Gymnotus paraguensis* n. sp., from the Paraguay basin; 5, *Gymnotus*

Accepted: 22 August 2003; published: ?? September 2003

tigre n. sp., from the Amazon basin of Ecuador, Peru and Brazil. Two of the new species are members of the *G. pantherinus* species-group: 1, *Gymnotus javari* n. sp., from the Amazon, Napo, Javarí, and Ucayali basins; 2, *Gymnotus panamensis* n. sp., from Atlantic slope of western Panama. *Gymnotus carapo s.s.* is restricted to the Amazon and Orinoco basins, the Island of Trinidad, the coastal basins of the Guianas, and the Brazilian state of Piauí. Six allopatric populations of *G. carapo s.s* are recognized from differences in the mean, modal or median values of morphometric and meristic traits: 1, Eastern Amazon; 2, Parnaíba and Itapicuru basins; 3, Branco basin; 4; Guiana Shield, Orinoco basin and Island of Trinidad; 5, Madeira basin of Brazil, Bolivia and Peru; 6, Western Amazon basin of Brazil, Colombia, Ecuador, and Peru. Four of the new species representing both the *G. carapo* and *G. pantherinus* species-groups inhabit waters to the west of the Andean Cordillera. The biogeographic distributions of these species-groups suggest origins and early diversification before the most recent Andean orogeny, c. 8–12 mya.

Key words: biodiversity, classification, comparative morphology, species descriptions, South America

Introduction

The Neotropical electric fish genus *Gymnotus* (Linnaeus 1758) is substantially more diverse than was previously recognized. New methods of sampling, identifying, and collecting electric fishes have unveiled numerous species in previously unexplored habitats and regions (Crampton 1996a; Lundberg *et al.*1996; Crampton 1998; Albert & Crampton 2001). Further, the use of new techniques for characterizing morphology, electric organ discharges, and genetic differences have demonstrated that much of what was once regarded as intraspecific variation represents interspecific differences (Campos-da-Paz & Costa 1996; Fernandes-Matioli *et al*. 1998a; Fernandes-Matioli *et al.* 1998b; Albert *et al.* 1999; Fernandes-Matioli *et al.* 2000; Fernandes-Matioli *et al.* 2001; Albert & Crampton 2001; Fernandes-Matioli & Almeida-Toledo, 2001).

Gymnotus species are aggressive nocturnal predators of fishes and other small aquatic animals, and most are territorial. The males of at least two *Gymnotus* species build and guard nests of foam and/or aquatic vegetation (Crampton & Hopkins pers. obs.). The type species *Gymnotus carapo* is reported to mouth brood its eggs and larvae (Kirschbaum & Wieczorek 2002). *Gymnotus* is the most geographically widespread of all gymnotiforms, extending from the Río Salado in the Pampas of Argentina (36°S) to the Río San Nicolás of southeastern Chiapas, Mexico (18°N), and is present in the continental waters of all South and Middle American countries except Chile and Belize (Albert 2001). Prior to this report, 25 species names were available for *Gymnotus*, of which five were synonymized with the type species *G. carapo* (Mago-Leccia 1994), and one with *G. coatesi* (Campos-da-Paz 2000). The geographical ranges of the currently valid *Gymnotus* species are summarized in Table 1. *Gymnotus* exhibits its greatest diversity in the western portion of the Amazon basin where 10 species are currently recognized. *Gymnotus anguillaris* Hoedeman is recognized here as distinct from *G. coropinae* Hoedeman with which it has been

synonymized (Nijssen & Isbrücker 1968). Data for and comparisons to *G. coropinae* will be presented in a forthcoming redescription of this species (Crampton & Albert unpubl. obs.).

TABLE 1. Valid species of *Gymnotus* with affiliation to species-group and geographical range (by drainage basin). Abbreviations: EA, Eastern Amazon (incl. lower Negro, Trombetas, Tapajós, Tocantins); GU, Guyanas - Orinoco (incl. Trinidad, upper Negro); MA, Middle America; MD, Madeira (incl. Mamoré, Guaporé, Beni, Madre de Dios); NE, Northeastern Brazil (from São Francisco to Jequitinhonha); PA, Paraguay-Paraná; PI, Piau' (incl. Itapicuru and Parnaíba); PS, Pacific Slope; RO, Roraima (incl. Branco); SE, southeast coast Brazil,Uruguay (include. Jacuí); WA, Western Amazon (incl. affluents west of mouth of Purus).

Group	Species	Geographical range
cylindricus	*Gymnotus cylindricus* LaMonte, 1935	MA
	Gymnotus maculosus Albert & Miller, 1995	MA
pantherinus	*Gymnotus anguillaris* Hoedeman, 1962	GU, MD, PA
	Gymnotus cataniapo Mago-Leccia, 1994	GU
	Gymnotus coatesi LaMonte, 1935	EA, WA
	Gymnotus coropinae Hoedeman, 1962	GU, EA, MD, WA
	Gymnotus javari n. sp.	WA
	Gymnotus jonasi Albert & Crampton, 2001	WA
	Gymnotus melanopleura Albert & Crampton, 2001	WA
	Gymnotus onca Albert & Crampton, 2001	WA
	Gymnotus panamensis n. sp.	MA
	Gymnotus pantherinus (Steindachner, 1908)	SE
	Gymnotus pedanopterus Mago-Leccia, 1994	EA, GU
	Gymnotus stenoleucus Mago-Leccia, 1994	GU
carapo	*Gymnotus arapaima* Albert & Crampton, 2001	MD, WA
	Gymnotus bahianus Campos da Paz & Costa, 1996	NE
	Gymnotus carapo s.s. Linnaeus, 1758	EA, GU, MD, PI, RO, WA
	Gymnotus choco n. sp.	PS
	Gymnotus diamantinensis Campos da Paz, 2002	EA
	Gymnotus esmeraldas n. sp.	PS
	Gymnotus henni n. sp.	PS
	Gymnotus inaequilabiatus (Valenciennes, 1847)	PA
	Gymnotus mamiraua Albert & Crampton, 2001	EA, MD, WA
	Gymnotus paraguensis n. sp.	PA
	Gymnotus sylvius Albert *et al.* 1999	PA, SE
	Gymnotus tigre n. sp.	EA, WA

Here we present evidence for the existence of seven new species of *Gymnotus* from examination of populations from throughout tropical South and Middle America. We

describe these new taxa on the basis of unique color patterns and unique combinations of morphometric, meristic, and osteological features. We also redescribe the geographically widespread species *G. carapo sensu stricto* (*G. carapo s.s.)* and distinguish six allopatric populations of *G. carapo s.s.* by differences in the mean and modal values of morphometric and meristic traits. The original description of *G. carapo* (Linnaeus, 1758) provides only enough information to identify specimens to the Order Gymnotiformes (sensu Mago-Leccia, 1994). Subsequent diagnoses and keys (Ellis 1913; Hoedeman 1962; Mago-Leccia 1994; Albert & Miller 1995) did not provide sufficient information to differentiate *G. carapo s.s.* from other member of the *G. carapo* species-group.

The material basis of these descriptions is 781 museum lots of *Gymnotus* bearing more than 2700 specimens from 32 museums. This study is to our knowledge the most thorough alpha-level review of morphological variation in any gymnotiform genus to date. The existence of so many previously unrecognized and undescribed taxa within existing museum collections is due in part to the cryptic nature of phenotypic diversity in *Gymnotus*. These fishes possess few external visual cues for species recognition. The lack of appreciation for diversity in *Gymnotus* has been compounded by a lack of published accounts of intraspecific variation. We predict that similarly high levels of cryptic diversity may exist in other gymnotiform groups with geographic distributions well represented in museum collections (e.g., *Brachyhypopomus*; *Gymnorhamphichthys*, *Eigenmannia*, *Sternarchorhynchus*).

Materials and Methods

Body size is represented by total length in millimeters (mm TL). Sex and sexual maturity can be assessed in *Gymnotus* only by dissection or histology. The ovaries of females are packed with eggs which are yellow and enlarged when mature. The testes of males are solid and white or pale pink when mature. Immature specimens cannot be reliably sexed without histological analysis of the developing gonads. Specimens in which the caudal appendage was obviously damaged and not, or only partially, regenerated were excluded from measurements of total length.

Morphometric data were captured as point-to-point linear distances from standardized landmarks using digital calipers to the nearest 0.1 mm. Body proportions reported include head length (HL), from posterior margin of bony operculum to tip of snout (dorsal midline of upper jaw); postorbital length (PO), from posterior margin of bony opercle to posterior margin of eye; preorbital length (PR), from anterior margin of eye to tip of snout; body depth (BD), vertical distance from origin of anal fin to dorsal body border (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 branchial fold; pre-anal distance (PA), from anterior insertion of anal fin to posterior margin of anus.

Scale, lateral-line pore, and pectoral-fin ray counts were taken directly from ethanol preserved and cleared-and-stained specimens under a dissecting microscope. Precaudal vertebrae and anal-fin ray counts were taken from radiographs or cleared-and-stained specimens under a dissecting microscope (Albert and Fink, 1996). Abbreviations used for meristic variables are: AFR, number of branched and unbranched anal-fin rays, rounded to the nearest multiple of five, and counted from radiographs only of specimens with little or no damage to the caudal appendage (10 repeated counts from a single radiograph differed by ±5 due to presence of numerous faint posterior anal-fin rays); APS, number of anal-fin pterygiophore scales counted as the number of scale rows over the pterygiophores (counted from an origin vertically below the base of the first lateral line ramus); BND, number of oblique lateral pigment bands; CEP, caudal electroplate rows counted as the number of horizontally aligned rows of electroplates in the electric organ at a distance of one head length from the tip of the caudal appendage (with the scales above the electric organ removed and the specimen placed under a stereoscopic microscope against strong backlighting, not counted from specimens with a heavily damaged caudal appendage); PCV, number of precaudal vertebrae including the five elements of the Weberian Apparatus; P1R, number of branched and unbranched pectoral-fin rays; PLL, number of pored lateral-line scales in posterior lateral line posterior to neurocranium; PLR, number of pored lateral line scales to first ventral ramus; SAL, number of scales above lateral line at midbody; VLR, number of ventrally oriented lateral line rami. Protocols for counting band numbers and lateral-line rami are described in Albert *et al.* (1999). Counts of bilaterally paired series (APS, CEP, P1R, PLL, PLR, SAL, VLR) were taken on the left side when possible. PLL were not counted from specimens with a damaged caudal appendage.

Morphological methods are described in detail in Northcutt *et al.* (2000), Albert (2001), and Albert & Crampton (2001). In brief, osteological data were taken from specimens cleared with KOH, trypsin, and glycerin, and stained with alizarin red and alcian blue, following Taylor & Van Dyke (1985) with reagent concentrations and reaction times adjusted to specimen size and preservation quality. Dissection methods and morphological nomenclature are described in Albert (2001). Bones were disarticulated to functional groups (e.g., neurocranium, suspensorium, pectoral girdle), or to individual elements, using microdissection tools under an Olympus SZ12 or SZ60 dissecting microscope. Outlines and standardized features (e.g., ridges, surface ornamentation) of each bone were traced from lateral and medial aspects with the aid of a camera lucida, and the line art scanned and edited using iGrafx Designer 8.0 on a PC. Laterosensory canals and pores were illustrated by integrating camera-lucida tracings of canal pores from ethanol preserved specimens and canal bones from cleared-and-stained specimens.

Diagnoses refer to conditions observed in adults and morphometric data in species descriptions are mean adult values. Size at morphological maturity is ascertained for each species at an asymptotic value of HL% in TL. Descriptions of some morphometric and pigmentation characters may apply to juveniles as well as adults in species paedomorphic

for these characters. Morphometric and pigmentation characteristics apply to morphologically (but not necessarily reproductively) mature specimens unless otherwise stated. Qualitative descriptions of body proportions (e.g., short, long) refer to codes in a data matrix to be published separately (Albert *et al*., in prep). Abbreviated descriptions of characters used to distinguish species in the *G. carapo* species-group are provided in the Appendix.

Institutional abbreviations follow Leviton *et al.* (1985), with the addition of: ICN-MHN (Instituto de Ciencias Naturales Museo de Historia Natural, Bogotá), IIAP (Instituto para la Investigaciones de la Amazonía Peruana, Iquitos), IAVHP (Instituto Alexander von Humboldt, Peces, Bogotá); IMCN (INCIVA Museo de Ciencias Naturales, Instituto para la Investigación y la Preservación del Patrimonio Cultural y Natural del Valle del Cauca, Cali); INPA (Instituto Nacional de Pesquisas da Amazônia, Manaus), MUSM (Museo de Historia Natural de la Universidad Nacional Mayor de San Marcos, Lima), NRM (Swedish Museum of Natural History, Stockholm), UUZM (Uppsala University, Museum of Evolution, Zoology Section, Uppsala). Locality names are provided in the local language; country names in English.

Monophyly and Species-Groups of *Gymnotus*

Gymnotus is unique among gymnotiform fishes in possessing a superior mouth with a prognathous lower jaw; a thick and fleshy pad of tuberous electroreceptor organs and insulating support tissues overlying the tip of the snout and oral jaws; a pair of dorsally oriented pipe-shaped anterior nares partially or entirely included within the gape; a ventrally curved rictus; a lateral position of the eye on the head, about horizontal with the anterior oral margin; numerous long rami of the posterior lateral line extending ventrally on the caudal portion of the body; and a very long body cavity, with 31–51 precaudal vertebrae (Albert 2001; Albert & Crampton 2001).

Albert & Miller (1995) and Albert (2001) recognize three species-groups within the genus based on color pattern and body proportions, the *G. cylindricus*, *G. pantherinus*, and *G. carapo* species-groups. The species composition and geographical range of these groups are summarized in Table 1. The *G. cylindricus* species-group is represented by two species endemic to the Atlantic and Pacific drainages of Middle America. The *G. pantherinus* species-group is represented by 12 species including those described herein, with distributions from Panama to Paraguay. Members of the *G. pantherinus* species-group can be distinguished from those in the other two species-groups by the possession of: a slender body (adult modal BD 6.1–9.0% TL [except *G. melanopleura*] vs. 9.1–11.7% in all other *Gymnotus* species except *G. henni* n. sp. and *G. esmeraldas* n. sp.); proximal portion of fifth rib with broad triangular ridge, more than three times width of sixth rib (vs. narrow ridge, less than three times width of sixth rib); dentary hook at mental symphysis composed of paired ventroposterior oriented processes. The *G. carapo* species-group is endemic to South America and is represented by 12 species, including those described

herein, with distributions from the Pacific slope of Colombia to the Pampas of Argentina. Members of the *G. carapo* species-group can be distinguished from those in the other two species-groups by the possession of: a clear or pale patch near the caudal end of the anal fin, most visible in juveniles and subadults (60–150 mm); two (vs. one) laterosensory pores in the dorso-posterior portion of preopercle, in the preopercular-mandibular canal. The classification of *Gymnotus* into three species groups is used as a basis for diagnosing the new species described herein.

Systematic Descriptions

Taxa are presented alphabetically within species-groups (Albert & Miller, 1995; Albert 2001). Two species from the Pacific Slope of Colombia are co-authored by Javier A. Maldonado, Instituto de Ciencias Naturales Museo de Historia Natural, Universidad Nacional de Colombia, Bogotá. One species from the Western Amazon is co-authored by Mary Hagedorn, Smithsonian Institution, Washington D.C.

Gymnotus carapo Species-Group (Albert 2001)

Gymnotus carapo sensu-stricto Linnaeus
(Fig. 1, Tables 2 and 3)

Gymnotus carapo sensu-stricto Linnaeus
Gymnotus carapo (Linnaeus1758): 246 (in part) [type locality: America].
Gymnotus albus (Pallas 1769): 35 [Surinam].
Gymnotus brachiurus (Bloch 1786): 61, plate 157, fig. 1 [Brazil].
Gymnotus fasciatus (Pallas 1767): 35 [Brazil: Roraima, Rio Branco].
Gymnotus putaol (Lacépède 1800): 145, 176 [Brazil].

Syntypes: Collected in the first half of the 18th Century near Paramaribo, Surinam (Lönnberg 1896:23; Fernholm & Wheeler 1983:216–217; Wheeler 1991:162–163, fig. 6): NRM 64 (1), 262 mm; NRM 8224 (1), 331 mm; UUZM Linn. coll. 56 (1), 293 mm.

Diagnosis. *Gymnotus carapo s.s.* differs from all members of the *G. carapo* species-group except *G. arapaima* in possessing a color pattern composed of 16–27 [mean 22] dark obliquely oriented pigment bands or band-pairs, with irregular wavy margins, often broken into spots above lateral line on anterior half of body (shared only with *G. arapaima* and *G. diamantinensis*), without large pale blotches on head. *Gymnotus carapo s.s.* further differs from all members of the *G. carapo* species group in the following unique combination of characters: 1, circular scales, about as long as wide above lateral line at midbody; 2, two laterosensory canal pores in dorso-posterior corner of preopercle (in specimens 120–400 mm); 3, deep body (BD 9.7–12.1% TL [mean 10.2%, n=101] vs. 5.5–9.4% [mean 6.3–9.0%); 5, head length moderate to long (HL 10.2–13.9% TL [mean 12.3%**,** n=99] vs. 7.9–

10.1% or 14.0–14.2%); 6, moderate size of scales over anal-fin pterygiophores (APS 7–12 [mode 8, n=50] vs. 5–7 or 12–16); 7, moderate number of lateral line scales to first ventral ramus (PLR 40–56 [mode 46, n=65] vs. 34–43 or 57–78); moderate number of precaudal vertebrae (PCV 33–37 [mode 33, n=50]; relatively few ventral lateral line rami (VLR 6–27 [mean 8, n=50] vs. mean 10–51); no dorsal lateral line rami. *Gymnotus carapo s.s.* can be distinguished from sympatric *G. arapaima* in the Western Amazon in possessing: 1, fewer pored lateral line scales to first ventral lateral line ramus (PLR 44–54 [mode 48, n=14] vs. 53–64 in *G. arapaima* [mode 57, n=27]); 2, fewer scales over anal fin pterygiophores (APS 8–10 [mode 9, n=14] vs. 10–13 in *G. arapaima* [mode 12, n=31]); and, 3, smaller size (maximum TL 418 mm, rarely more than 350 mm vs. 550 mm in *G. arapaima*).

Description. Fig. 1 illustrates head and body shape and pigment patterns. Morphometric data in Table 2, and meristic data in Table 3. Body size large, to 418 mm. Sexual maturity at about 280 mm in males and 270 mm in females. Sexually monomorphic in both immature and breeding condition. Scales circular or slightly ovoid, present on entire postcranial portion of body from nape to caudal appendage. Gape size in mature specimens large, extending to or beyond posterior nares. Mouth position superior, lower jaw longer than upper, rictus decurved. Chin fleshy and bulbous with thick pad of electroreceptor organs and support tissues overlying tip of snout and oral jaws. Anterior narial pore partially or entirely included within gape in large narial fold. Anterior nares large, subequal to diameter of eye. Circumorbital series ovoid to tear-drop shaped. Ethmoid region between anterior nares broad, its anterior margin rounded. Eye position lateral, lower margin of eye dorsal to horizontal with rictus.

Premaxilla with 11–16 (mode 14, n=10) teeth disposed in single row along outer margin, arrow-head shaped anteriorly, conical posteriorly. Median margin of premaxilla curved. Maxilla-palatine articulation near anterior tip of mesopterygoid. Maxilla orientation vertical. Maxilla rod-shaped, narrow distally with a straight ventral margin. Maxilla length equal to about width of 4–6 dentary teeth. Dentary with one row of 16–19 (mode 17, n=4) teeth, 2–4 arrow-head shaped anteriorly, all others conical posteriorly. Dorsoposterior and ventroposterior dentary processes abut at midlength of bone. Dentary ventroposterior process almost as long as dorsoposterior process. Dentary dorsoposterior process narrow distally. Dentary ventral margin with a narrow lamella, its depth less than posterior process. Anteroventral margin of dentary rounded in lateral view, without a hook. Dorsal margin of opercle straight or slightly convex. Texture of dorsal operclar process lamellar or rugose. Dorsal opercular crest absent or small. Posterior margin of opercle smooth, entire, without spines or processes. Ventral ridge field of opercle broad. Dorsal ridge field of opercle long, more than half width of opercle. Dorsoposterior laterosensory ramus of preopercle with two superficial pores. Preopercle with anteroventral notch. Margin of preopercular medial shelf entire. Median shelf of preopercle large, more than half width of symplectic. Ascending process of mesopterygoid robust, long, its base shorter than its length. Mesopterygoid ascending process curved. Tip of mesopterygoid ascending process

simple. Metapterygoid superior and inferior portions approximately equal in size. Dorsal margin of interopercle with broad ascending process. Dorsal margin of subopercle concave. Posterior margin of retroarticular square. Retroarticular with an arched lamella posteriorly, forming a small canal. Anguloarticular process long, extending beyond ventral margin of dentary. Mandible long, extended, its length more than twice its depth. Hyomandibular trigeminal canals (supraorbital, infraorbitral), connected. Posterior lateral line fenestra contacting dorsoposterior margin of hyomandibula. Cranial fontanels closed in juveniles and adults. Anterior margin of frontal straight, continuous with margins of adjacent roofing bones. Frontal postorbital process broad, more than two times width of supraorbital canal. Frontal shape narrow, width at fourth infraorbital less than that of parietal. Lateral ethmoid absent. Parasphenoid posterior processes narrow. Parietal rectangular, its length less than width. Pterosphenoid anteroventral portion robust, extending ventral to lateral margin of parasphenoid. Prootic foramen Vp separate from V2–3+VII. Adductor mandibula undivided at insertion. Adductor mandibula intermusculars absent. All basibranchials unossified. Gill rakers not contacting gill bar. Basibranchial 5 unossified. Pectoral fin of moderate size, with 14–16 rays. Pectoral medial radial large. Mesocoracoid elongate, its length more than 4 times width. Postcleithrum thin, discoid or sickle-shaped. Cleithrum narrow, with a straight ventral margin. Anterior limb of cleithrum long, more than 1.8 times ascending limb. Cleithrum deeply incised on its anteroventral margin. Cleithrum without large facet for insertion of muscle from supracleithrum. Body cavity of moderate length, with 30–35 (mode 33) precaudal vertebrae. Rib 5 robust along its entire extent, less than 3 times width of rib 6. Hemal spines present. Displaced hemal spines absent. Anal fin of moderate length, with 217–260 rays. Multiple anal-fin ray branching posterior to rays 10–17. Lateral line ventral rami 4–27 (left or right). Lateral line dorsal rami absent in adults. Length anal-fin pterygiophores equal to or longer than hemal spines. Caudal appendage short, less 0.5 times length of pectoral fin. Single hypaxial electric organ, extending along entire ventral margin of body. Three or four (mode four) rows of electroplates near caudal insertion of anal fin.

Color in alcohol. Band appearance highly irregular in shape, width, arrangement, and color, both on and among individuals. All specimens share the following color features: ground color khaki yellow ventrally grading to pale brown dorsally in adults (200–300 mm), and pale yellow throughout in smaller specimens 16–23 (mode 21) obliquely oriented chocolate-colored bands on lateral surface extending from nape and pectoral-fin base to tip of caudal appendage. Bands occur singly and as band-pairs with bands becoming increasingly divided and irregular with size. Band-inter-band margins irregular and wavy. Bands divided dorsally or ventrally to form X or inverted Y-shaped patterns. Band-inter-band contrast increases ventrally and caudally and fades with growth; juveniles less than 150 mm clearly banded with distinct band margins, specimens 200–300 mm faintly banded, and some specimens over 250 mm unbanded except very faintly in posterior 1/3 of body. Pale inter-bands about 1/3 width of dark bands at mid-body. Bands of juveniles

more homogenous in shape and pigment intensity, with more clearly defined margins. Two to three bands from either side meet at ventral midline, between anus and anal-fin origin. One to three bands posterior to last anal-fin ray.

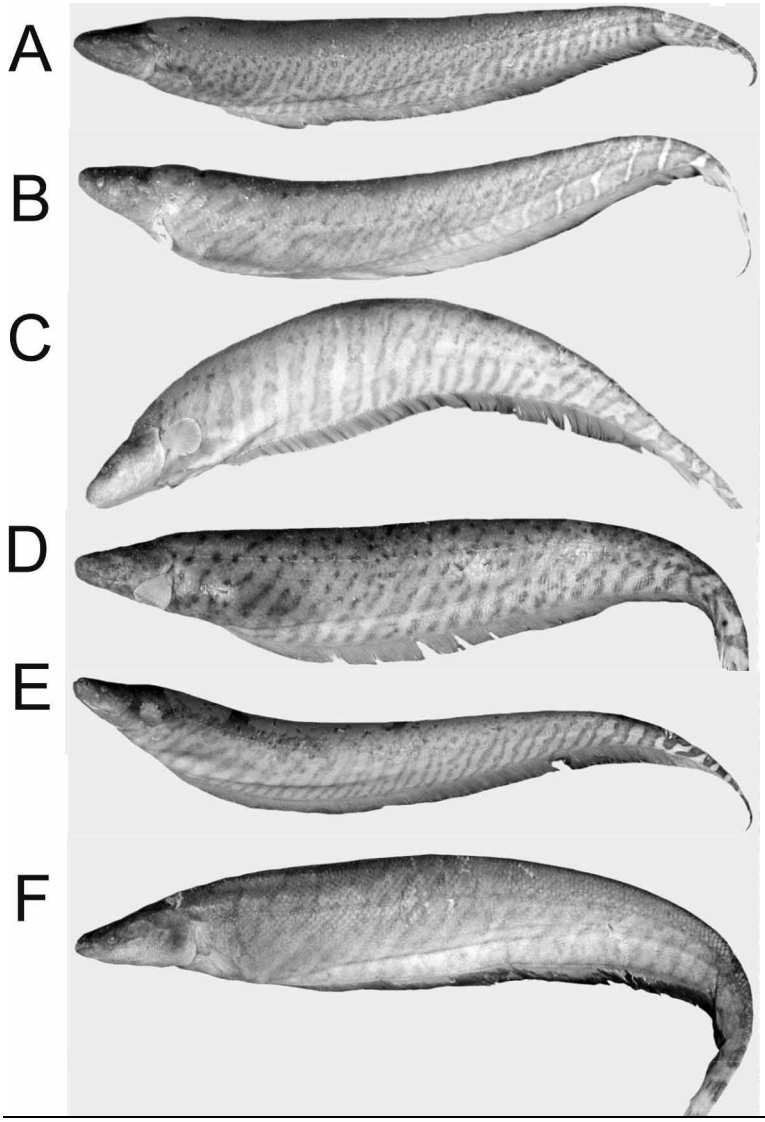

FIGURE 1. Specimens illustrating variation in color pattern and body shape in six allopatric populations of *Gymnotus carapo s.s.* A. *Gymnotus carapo* EA, MZUSP 30025, 237 mm. Brazil, Pará, Serra dos Carajás (06°00'S, 51°18'W). B. *Gymnotus carapo* GU, UMMZ 190414, 260 mm. Surinam, Brokopondo, Tapoeripa Creek (05°4'N, 54°58'W). C. *Gymnotus carapo* MD, UF 82485, 360 mm. Bolivia, Beni, San Javier, Río Ibare, Río Mamoré (14°37'S, 64°57'W). D. *Gymnotus carapo* PI, AUM 20624, 225 mm. Brazil, Piauí, Rio Gurgueia, Rio Parnaíba, nr. Bertolina (06°50'S, 43°24'W). E. *Gymnotus carapo* RO, MZUSP 30006, 200 mm, Brazil, Roraima, Rio Branco, Cachoeira do Bem Querer (approx. 01°00'N, 61°00'W). F. *Gymnotus carapo* WA, MZUSP 76061, 260 mm, Brazil, Amazonas, Tefé, Cabeçeira do Lago Tefé, Rio Tefé (03°35'S, 64°47'W). See Table 1 for abbreviations.

TABLE 2. Morphometric data for adults of 35 species and populations of Gymnotidae, including new taxa described in this paper. See Materials and Methods for morphometric abbreviations and Table 1 for geographic abbreviations. TL and head HL expressed in mm. Percentage measurements in HL, or TL for HL%, BW%, BD%, and AF%. BW/BD expressed as a ratio. *Gymnotus* n. sp. "cur", *G.* n. sp. "obs", and *G.* n. sp. "var" from Crampton *et al.* (in. prep.); *G.* n. sp. "pnt" from Fernandes-Matioli *et al.* (in prep.). N values vary because measurements were excluded from some specimens with damage (see text) or unusual preservation artifacts. *, new species described here; -, data not available. All data from specimens collected in region of type locality. Group A, *G. cylindricus* species-group; Group B, *G. pantherinus* species-group; Group C, *G. carapo* species-group. Character trait values used in diagnosis of *G. carapo s.s.* are pooled from six populations listed.

TABLE 2 (continued)**.**

Group	Species / population	TL		HL		HL %			PR %		
		n	range	n	range	n	range	mean	n	range	mean
	E. electricus	6	275–470	6	28.4–54.2	6	9.6–11.8	10.8	6	32.7–36.0	34.2
A	*G. cylindricus*	8	136–185	8	14.2–19.9	6	9.9–11.1	10.5	8	37.1–41.5	39.8
	G. maculosus	7	119–231	7	12.8–21.1	7	9.1–10.1	9.5	6	34.2–40.7	37.1
B	*G. anguillaris*	14	131–302	13	12.6–27.4	12	8.3–9.8	9.2	8	33.3–37.3	35.9
	G. cataniapo	7	179–316	7	16.2–29.0	7	8.8–10.0	9.4	2	36.0–37.0	36.5
	G. coatesi	4	81–180	4	9.4–18.0	4	10.0–11.7	10.9	4	30.9–37.0	34.8
	G. javari *	21	90–201	12	9.0–16.8	12	8.5–11.1	9.9	12	31.2–36.9	33.2
	G. jonasi	6	101–150	4	10.6–12.1	4	9.6–10.8	10.1	4	26.4–29.2	28.1
	G. melanopleura	1	99	1	11.6	1	11.7	11.7	1	32.8	32.8
	G. onca	1	116	1	10.2	1	8.8	8.8	1	30.4	30.4
	G. panamensis *	2	221–236	2	21.2–21.5	2	9.1–9.6	9.4	2	34.0–37.3	35.6
	G. n. sp. "pnt"	6	153–251	6	15.4–21.5	6	8.6–10.1	9.1	6	34.0–35.4	34.8
	G. pantherinus	9	105–205	9	11.1–20.6	9	8.5–10.5	9.2	8	33.4–36.8	34.5
	G. pedanopterus	8	135–337	8	17.8–27.0	8	8.0–13.2	10.9	8	32.9–35.9	34.1
	G. stenoleucus	9	84–142	9	9.2–15.2	9	8.4–11.1	10.4	4	29.3–36.4	31.5
C	*G. arapaima*	27	102–272	20	14.9–37.1	25	12.5–14.2	13.5	27	32.2–38.8	35.4
	G. bahianus	26	61–273	23	13.1–28.2	21	10.3–12.6	11.6	23	33.3–36.4	35.1
	G. carapo EA	16	165–253	16	21.0–34.5	15	11.7–13.6	12.7	16	32.9–35.7	34.2
	G. carapo GU	43	47–317	34	13.1–38.9	34	11.4–13.3	12.4	34	33.8–39.1	36.0
	G. carapo MD	17	99–360	15	11.1–42.8	14	10.4–13.7	11.8	15	32.3–39.4	35.9
	G. carapo PI	8	95–225	8	10.8–27.1	8	10.2–12.2	11.4	8	34.5–37.9	36.7
	G. carapo RO	10	120–375	10	15.6–39.3	10	10.5–13.2	12.2	10	34.5–37.5	35.9
	G. carapo WA	27	38–298	23	13.1–39.2	18	12.0–13.9	13.1	18	32.0–36.9	35.0
	G. choco *	9	142–260	9	21.7–33.1	9	11.1–13.3	12.3	9	31.9–35.9	34.7
	G. n. sp. "cur"	10	135–235	9	13.5–21.0	7	8.8–10.2	9.5	8	34.3–36.0	35.3
	G. diamantinensis	3	100–125	3	11.5–13.5	3	10.8–11.5	11.2	3	33.0–34.4	33.6
	G. esmeraldas *	8	200–309	8	21.5–30.3	7	9.1–10.8	10.2	8	36.0–39.6	37.7
	G. henni *	7	130–312	7	15.5–30.9	7	9.2–10.7	9.9	7	35.4–39.9	37.9
	G. inaequilabiatus	21	155–998	16	18.7–82.0	19	8.2–12.3	10.5	17	31.7–37.9	35.9
	G. mamiraua	10	121–228	9	18.1–22.4	8	9.7–10.7	10.4	9	31.3–35.5	33.2
	G. n. sp. "obs"	13	121–215	13	14.3–21.4	12	9.9–11.8	10.8	13	33.3–39.9	37.3
	G. paraguensis *	4	164–224	4	19.6–27.3	4	11.7–12.2	11.9	4	34.0–35.7	35.0
	G. sylvius	5	157–291	5	20.5–38.5	5	12.3–14.0	13.1	3	34.8–36.1	36.1
	G. tigre *	6	104–411	6	10.3–46.5	4	9.9–13.3	11.1	4	34.0–39.6	37.4
	G. n. sp. "var"	29	122–237	27	12.2–21.3	27	9.0–10.4	9.7	27	29.7–35.8	33.6
TOTAL		408		362		351			343		

TABLE 2 (continued)**.**

Species / population	MW %			PO %			IO %		
	n	range	mean	n	range	mean	n	range	mean
E. electricus	6	39.4–41.5	40.3	6	63.0–66.4	64.8	6	31.8–35.9	34.1
G. cylindricus	8	36.1–45.2	41.9	8	58.9–64.5	61.9	8	43.5–48.1	46.0
G. maculosus	6	36.1–40.8	38.8	7	59.0–65.6	62.2	7	39.8–48.5	44.9
G. anguillaris	8	41.4–55.1	47.0	8	59.6–63.5	61.6	8	42.9–56.3	45.6
G. cataniapo	2	42.2–44.4	43.3	2	59.8–63.5	61.6	2	41.2–41.3	41.3
G. coatesi	4	27.8–35.1	31.5	3	58.5–60.0	59.1	4	33.3–36.5	35.5
G. javari *	12	31.4–41.7	37.0	12	57.4–63.3	61.5	12	34.7–40.0	37.6
G. jonasi	4	30.6–33.0	31.9	4	62.0–62.7	62.3	4	36.4–38.5	37.7
G. melanopleura	1	38.8	38.8	1	61.2	61.2	1	38.8	38.8
G. onca	1	41.2	41.2	1	65.7	65.7	1	39.2	39.2
G. panamensis *	2	41.8–50.1	46.0	2	61.4–63.7	62.6	2	36.7–41.3	39.0
G. n. sp. "pnt"	6	34.6–48.4	44.6	6	57.1–66.0	61.8	6	35.9–44.4	39.6
G. pantherinus	9	36.8–47.4	42.1	9	60.1–65.8	63.2	9	37.2–42.6	40.1
G. pedanopterus	8	32.6–40.4	35.1	8	59.6–63.7	62.1	8	26.4–34.6	31.2
G. stenoleucus	4	30.4–40.6	36.3	4	61.0–64.1	62.5	4	30.4–38.8	33.3
G. arapaima	24	31.2–39.5	34.4	27	59.7–64.4	61.9	27	31.0–36.5	33.0
G. bahianus	23	35.2–44.8	40.2	23	59.3–63.5	61.1	23	33.9–42.5	38.1
G. carapo EA	8	41.0–46.1	43.7	16	60.0–65.5	62.3	16	34.4–40.6	37.1
G. carapo GU	26	34.4–46.6	40.2	34	59.1–63.7	61.6	34	35.1–42.5	39.0
G. carapo MD	15	37.2–49.0	42.2	15	57.9–64.3	60.8	15	36.3–44.8	40.3
G. carapo PI	8	41.7–45.7	43.8	8	63.2–67.6	65.5	8	35.8–39.8	37.6
G. carapo RO	10	32.3–38.2	35.1	10	61.4–64.6	62.8	10	34.8–38.1	36.5
G. carapo WA	17	32.3–37.8	35.3	18	58.7–62.7	61.3	18	31.4–37.6	34.4
G. choco *	9	28.3–37.2	33.2	9	57.3–65.8	59.8	9	28.6–31.9	30.1
G. n. sp. "cur"	9	41.4–56.8	48.8	8	59.3–66.7	63.6	9	42.1–47.4	44.1
G. diamantinensis	3	26.9–28.1	27.6	3	63.8–65.2	64.5	3	41.1–42.9	42.2
G. esmeraldas *	8	37.7–41.9	40.1	8	60.4–63.1	62.0	8	40.3–43.7	42.4
G. henni *	7	43.2–49.4	46.6	7	59.1–65.5	62.4	7	42.0–47.6	45.0
G. inaequilabiatus	17	39.8–47.3	42.5	17	59.4–63.7	62.2	12	37.0–45.7	42.6
G. mamiraua	9	34.8–41.6	37.5	9	61.5–64.5	63.2	9	36.3–40.8	37.7
G. n. sp. "obs"	13	37.3–46.3	42.7	13	59.9–64.5	62.1	13	35.2–43.3	39.5
G. paraguensis *	4	38.6–39.0	38.8	4	61.5–62.2	61.9	4	31.1–40.7	34.6
G. sylvius	4	32.2–39.3	35.5	3	58.7–60.9	59.8	3	36.4–38.2	37.5
G. tigre *	4	40.4–43.9	42.7	4	61.4–64.1	62.5	4	40.8–48.0	45.1
G. n. sp. "var"	25	35.0–45.9	40.4	28	58.7–66.3	62.4	27	32.5–44.3	39.6
TOTAL	324			345			341		

TABLE 2 (continued).

Species / population	BD %			BW %			BW/BD		
	n	range	mean	n	range	mean	n	range	mean
E. electricus	6	4.9–7.5	6.1	6	4.7–6.2	5.4	6	0.82–0.96	0.90
G. cylindricus	6	10.3–12.2	11.2	6	6.9–8.4	7.4	6	0.62–0.73	0.67
G. maculosus	5	7.7–10.1	9.4	5	5.7–7.7	7.0	5	0.70–0.79	0.75
G. anguillaris	8	6.7–9.8	8.3	8	5.7–6.7	6.3	8	0.70–0.83	0.74
G. cataniapo	7	8.0–9.4	8.7	7	5.4–7.3	6.4	7	0.57–0.83	0.74
G. coatesi	4	6.7–7.4	6.9	4	5.6–5.9	5.7	4.0	0.76–0.86	0.83
G. javari *	12	6.7–9.1	8.0	12	4.1–6.4	5.5	12	0.61–0.77	0.69
G. jonasi	4	6.5–8.0	7.5	4	4.7–5.2	5.0	4	0.60–0.75	0.66
G. melanopleura	1	10.6	10.6	1	6.2	6.2	1	0.58	0.58
G. onca	1	7.7	7.7	1	5	5.0	1	0.65	0.65
G. panamensis *	2	6.6–7.8	7.2	2	5.2–6.0	5.6	2	0.77–0.79	0.78
G. n. sp. "pnt"	6	8.2–9.9	9.0	6	6.2–7.6	6.7	6	0.70–0.83	0.75
G. pantherinus	9	6.7–8.9	7.4	9	4.1–6.5	5.4	9	0.60–0.081	0.73
G. pedanopterus	8	6.4–8.6	7.4	8	4.4–5.6	4.9	8	0.61–0.71	0.66
G. stenoleucus	9	7.1–8.9	8.0	9	4.5–5.6	5.0	9	0.58–0.65	0.62
G. arapaima	26	8.9–11.6	10.3	26	5.3–8.2	6.4	26	0.52–0.72	0.63
G. bahianus	21	9.3–13.3	11.1	21	6.1–8.7	7.0	21	0.54–0.84	0.65
G. carapo EA	16	8.7–12.4	10.1	16	6.2–8.6	7.2	16	0.67–0.76	0.72
G. carapo GU	34	8.7–11.8	10.8	34	6.7–8.3	7.5	34	0.60–0.85	0.70
G. carapo MD	15	8.8–12.6	10.8	15	6.2–9.4	7.3	15	0.59–0.84	0.68
G. carapo PI	8	8.4–10.3	9.5	8	6.4–7.8	7.1	8	0.68–0.76	0.74
G. carapo RO	10	8.9–9.8	9.2	10	6.7–7.6	7.3	10	0.69–0.83	0.79
G. carapo WA	18	8.8–12.1	10.6	18	5.7–8.3	7.0	17	0.52–0.76	0.67
G. choco *	9	8.8–11.3	10.0	9	7.1–8.2	7.6	9	0.68–0.83	0.77
G. n. sp. "cur"	9	7.4–8.6	8.1	9	5.7–6.6	6.1	9	0.68–0.83	0.76
G. diamantinensis	2	10.6–10.9	10.8	1	6.2	6.2	1	0.58	0.58
G. esmeraldas *	8	8.2–9.8	8.8	8	5.1–6.3	5.7	8	0.58–0.77	0.69
G. henni *	7	7.2–9.8	8.3	7	5.6–7.6	6.6	7	0.77–0.87	0.80
G. inaequilabiatus	12	7.5–12.0	10.6	12	5.8–8.6	6.8	12	0.54–0.77	0.64
G. mamiraua	9	9.3–12.6	10.7	9	5.0–7.1	6.3	9	0.53–0.72	0.58
G. n. sp. "obs"	12	9.0–10.8	9.5	12	5.3–6.3	5.9	12	0.51–0.68	0.62
G. paraguensis *	4	9.8–10.3	10.1	4	6.2–7.1	6.7	4	0.60–0.69	0.66
G. sylvius	4	10.3–13.1	11.7	3	7.2–7.8	7.5	3	0.61–0.70	0.67
G. tigre *	4	8.9–10.0	9.4	4	6.4–8.1	7.1	4	0.65–0.83	0.75
G. n. sp. "var"	27	8.3–10.8	9.4	27	4.6–6.4	5.6	27	0.47–0.69	0.60
TOTAL	343			341			340		

TABLE 2 (continued)**.**

Species / population	HD %			HW %			BO %		
	n	range	mean	n	range	mean	n	range	mean
E. electricus	6	50.9–58.3	53.9	6	62.0–75.1	69.1	1	25.2	25.2
G. cylindricus	8	68.3–75.6	72.2	8	63.8–72.3	69.4	7	30.6–42.0	35.9
G. maculosus	7	65.3–76.9	70.5	5	68.3–72.2	70.3	5	36.4–48.5	41.9
G. anguillaris	8	60.1–67.7	64.1	8	66.1–76.6	70.3	8	28.9–36.0	32.8
G. cataniapo	2	59.6–63.6	61.6	2	62.1–62.7	62.4	2	30.6–38.9	34.7
G. coatesi	4	47.6–57.7	52.0	4	49.5–55.8	52.7	–	–	–
G. javari *	12	55.6–64.7	59.9	12	56.1–65.5	62.8	12	25.0–32.2	28.3
G. jonasi	4	53.7–59.6	57.7	4	61.2–63.6	62.4	5	30.0–32.6	31.9
G. melanopleura	1	69.8	69.8	1	56.9	56.9	1	31.9	31.9
G. onca	1	65.7	65.7	1	58.8	58.8	1	30.4	30.4
G. panamensis *	2	67.5–71.2	69.3	2	68.0–71.2	69.6	–	–	–
G. n. sp. “pnt”	6	64.1–73.1	68.2	6	67.9–74.7	70.1	6	39.7–45.4	42.5
G. pantherinus	9	60.1–65.6	63.4	9	58.3–69.5	64.6	9	30.4–41.2	35.7
G. pedanopterus	8	49.4–59.9	53.9	8	47.1–57.9	53.4	7	28.0–42.3	37.9
G. stenoleucus	4	56.8–61.7	59.2	4	53.2–58.7	56.4	3	32.1–40.8	36.7
G. arapaima	27	46.3–66.6	54.9	27	46.0–57.9	51.8	8	32.2–43.8	37.5
G. bahianus	23	55.4–66.7	60.9	23	56.9–65.2	61.5	20	27.7–38.2	33.0
G. carapo EA	16	50.8–60.9	55.2	16	53.3–64.4	56.3	5	34.7–38.1	36.5
G. carapo GU	34	54.6–67.2	60.9	34	56.6–64.6	60.9	25	30.5–40.6	34.9
G. carapo MD	13	57.1–72.4	62.9	15	53.5–67.7	61.7	12	30.4–47.0	38.6
G. carapo PI	8	58.3–64.8	61.0	8	58.3–64.8	61.4	5	32.0–33.2	32.6
G. carapo RO	10	51.6–57.5	53.3	10	52.3–55.8	54.1	10	31.2–41.4	35.1
G. carapo WA	18	50.3–60.1	56.4	18	50.0–63.4	56.9	18	28.8–38.3	33.6
G. choco *	9	54.4–59.6	56.6	9	53.9–62.2	58.6	9	38.4–43.8	41.6
G. n. sp. “cur”	9	54.4–59.6	56.6	9	64.0–74.9	70.2	7	29.1–39.7	33.2
G. diamantinensis	3	65.2–69.6	67.1	2	51.1–51.3	51.2	3	37.4–43.7	39.9
G. esmeraldas *	8	54.5–58.9	56.6	8	60.9–65.8	64.0	8	27.4–33.0	30.4
G. henni *	7	52.8–56.8	54.8	7	61.4–70.6	65.4	7	30.5–35.7	32.4
G. inaequilabiatus	12	63.4–69.0	66.3	12	65.3–72.0	67.8	12	24.4–45.2	37.3
G. mamiraua	9	60.9–70.7	67.2	9	55.4–68.6	59.3	5	38.2–43.6	41.0
G. n. sp. “obs”	13	58.1–64.3	61.7	12	55.9–68.3	62.4	6	30.9–36.5	34.5
G. paraguensis *	4	56.7–60.2	58.2	4	57.7–58.5	58.1	4	31.8–35.7	34.2
G. sylvius	3	60.5–61.8	61.4	3	59.5–63.8	61.7	3	40.4–47.3	43.8
G. tigre *	4	53.7–60.2	55.9	4	58.1–67.3	61.9	4	27.0–31.8	28.9
G. n. sp. “var”	27	59.9–73.9	66.2	27	54.8–73.6	62.8	23	32.7–46.4	38.1
TOTAL	339			337			261		

TABLE 2 (continued)**.**

Species / population	PA %			P1 %			AF %		
	n	range	mean	n	range	mean	n	range	mean
E. electricus	6	83.5–100.2	90.2	6	29.7–36.3	33.5	6	77.2–81.1	79.6
G. cylindricus	8	87.6–100.5	94.9	8	36.8–43.1	41.1	6	78.4–82.2	80.0
G. maculosus	7	94.8–109.6	102.3	7	35.5–44.5	40.3	5	78.6–81.4	79.9
G. anguillaris	8	83.9–122.3	99.4	8	42.1–56.3	48.0	8	77.1–83.3	81.3
G. cataniapo	2	102.3–109.6	105.9	7	29.3–41.5	34.1	5	79.0–82.0	81.0
G. coatesi	3	80.9–83.7	81.9	4	41.7–50.0	46.3	3	77.8–81.0	79.4
G. javari *	12	74.3–112.2	93.3	12	40.2–47.8	43.8	12	71.4–79.6	76.1
G. jonasi	4	72.6–92.8	84.4	4	51.9–56.9	53.8	4	68.8–76.2	72.9
G. melanopleura	1	72.4	72.4	1	50.0	50.0	1	74.7	74.7
G. onca	1	63.7	63.7	1	43.1	43.1	1	72.4	72.4
G. panamensis *	2	83.4–87.9	85.7	2	48.8–53.3	51.0	2	78.1–78.5	78.3
G. n. sp. "pnt"	6	78.8–96.3	87.7	6	48.0–55.8	50.7	6	78.1–81.3	79.5
G. pantherinus	8	120.6–136.0	128.4	9	32.6–39.8	37.0	9	74.7–79.6	77.9
G. pedanopterus	7	50.6–63.1	58.6	8	33.7–41.8	38.1	8	77.7–85.0	81.3
G. stenoleucus	4	77.2–80.7	78.7	7	34.5–51.8	39.6	4	62.9–69.9	66.9
G. arapaima	24	51.4–74.2	64.5	27	39.6–47.9	43.6	26	71.4–82.9	79.3
G. bahianus	22	75.8–96.8	84.8	16	42.4–55.8	49.4	20	67.6–85.3	77.9
G. carapo EA	16	76.5–99.2	89.0	16	42.7–49.1	45.7	16	69.4–86.6	75.9
G. carapo GU	34	66.8–88.3	77.1	34	40.3–52.2	46.0	33	75.4–86.2	79.6
G. carapo MD	15	64.7–91.9	74.4	15	41.1–51.7	46.0	15	73.6–84.9	80.2
G. carapo PI	8	71.8–96.0	82.7	8	46.2–58.0	52.0	8	70.9–80.1	75.9
G. carapo RO	10	62.3–84.6	69.0	10	38.6–49.0	45.7	10	71.2–81.6	76.4
G. carapo WA	18	60.1–82.7	71.7	18	40.1–50.3	44.0	18	76.5–86.8	80.1
G. choco *	9	76.7–90.7	83.9	9	43.7–55.4	48.6	9	75.8–82.7	79.0
G. n. sp. "cur"	9	74.3–117.7	96.9	9	42.2–55.0	48.2	7	73.3–82.5	78.9
G. diamantinensis	3	79.8–83.7	81.7	2	36.3–41.1	39.4	2	81.8–82.3	82.1
G. esmeraldas *	8	82.0–98.0	92.0	8	41.4–45.9	43.4	8	76.5–81.7	80.1
G. henni *	7	72.1–112.3	94.4	7	44.2–53.2	47.5	7	75.9–81.1	79.6
G. inaequilabiatus	12	67.3–90.1	79.1	11	36.8–51.0	44.7	9	77.8–85.2	81.7
G. mamiraua	9	63.7–81.5	73.3	9	41.6–51.2	45.4	9	72.4–87.7	81.2
G. n. sp. "obs"	13	71.3–94.2	81.3	13	40.6–55.0	48.7	12	70.1–83.1	78.9
G. paraguensis *	4	62.8–81.2	69.0	4	37.4–45.9	40.3	4	73.0–80.1	77.7
G. sylvius	4	48.3–67.2	56.4	3	41.6–46.7	44.9	4	76.0–80.4	77.5
G. tigre *	4	69.7–81.9	74.8	4	40.1–52.4	44.8	4	75.9–81.5	79.5
G. n. sp. "var"	26	68.3–108.5	89.1	24	42.8–57.5	50.5	22	72.7–84.5	81.9
TOTAL	334			337			323		

TABLE 3. Meristic data for adults and juveniles of 35 species and populations of Gymnotidae. Symbols, abbreviations and explanations as in Table 2. Mode, modal value (rounded up to nearest integer). Med., median value.

Group	Species / population	TL		BND			AFR			P1R		
		n	range	n	range	med.	n	range	med.	n	range	mode
	E. electricus	6	81–108	6	0	0	6	170–210	190	6	29–30	30
A	*G. cylindricus*	10	98–185	10	0	0	5	190–200	190	5	17–18	18
	G. maculosus	10	79–231	7	0	0	4	170–200	190	5	17–18	18
B	*G. anguillaris*	10	131–302	8	7–26	22	8	210–270	257	8	16–18	16
	G. cataniapo	7	179–316	7	23–35	29	7	240–300	245	7	13–15	13
	G. coatesi	4	81–180	4	15–17	16	4	214–223	217	3	15	15
	G. javari *	21	90–201	11	13–21	15	13	180–240	200	11	13–15	14
	G. jonasi	10	80–115	9	11–20	16	6	135–165	152	5	11–13	12
	G. melanopleura	1	99	1	12	12	1	160	160	1	14	14
	G. onca	1	116	1	0	0	1	180	180	1	13	13
	G. panamensis *	2	221–236	2	23–24	24	2	270	270	2	15–16	16
	G. n. sp. “pnt”	6	153–251	5	21–26	25	6	220–280	255	6	15–19	17
	G. pantherinus	9	105–205	9	0	0	5	220–240	230	6	17–18	18
	G. pedanopterus	19	87–337	15	18–27	22	12	220–310	257	16	12–14	12
	G. stenoleucus	9	84–142	9	18–24	22	8	190–245	216	8	12–14	13
C	*G. arapaima*	31	62–272	15	19–24	22	12	225–245	235	15	15–17	15
	G. bahianus	35	61–273	24	0–6	3	6	190–225	205	6	15–16	16
	G. carapo EA	16	165–253	15	21–25	23	10	190–235	222	16	13–15	14
	G. carapo GU	43	47–317	15	16–23	20	7	225–260	244	23	15–17	16
	G. carapo MD	17	99–360	10	16–25	23	7	205–260	235	14	13–17	15
	G. carapo PI	8	95–225	6	23	23	4	170–250	200	9	13–16	16
	G. carapo RO	10	120–375	10	23–27	25	5	260–285	270	9	13–16	14
	G. carapo WA	27	38–298	14	16–23	20	10	195–290	238	14	14–17	16
	G. choco *	9	142–260	9	18–22	21	5	210–255	235	9	14–16	16
	G. n. sp. “cur”	18	85–235	15	14–20	19	11	230–320	260	16	16–17	16
	G. diamantinensis	3	100–125	2	19–22	21	3	194–211	203	3	14–15	15
	G. esmeraldas *	8	200–309	8	6–10	8	3	226–260	253	8	17–19	17
	G. henni *	7	130–312	7	13–16	15	5	223–275	249	7	17–19	17
	G. inaequilabiatus	15	155–998	10	19–24	22	6	170–260	220	11	13–16	15
	G. mamiraua	10	121–228	9	18–21	20	8	195–245	216	11	14–15	15
	G. n. sp. “obs”	17	94–215	15	14–20	17	11	210–250	230	16	20–22	21
	G. paraguensis *	3	164–224	3	23–26	24	3	260–270	265	3	17–21	19
	G. sylvius	5	157–291	5	21–24	22	5	220–230	224	2	16	16
	G. tigre *	6	104–411	6	16–23	21	4	190–240	228	4	16–19	17
	G. n. sp. “var”	34	94–237	29	16–22	18	20	230–310	260	30	16–19	18
TOTAL		447		331			225			308		

TABLE 3 (continued)**.**

Species / population	SAL			CEP			APS		
	n	range	mode	n	range	mode	n	range	mode
E. electricus	6	0	0	6	8–9	8	6	0	0
G. cylindricus	2	11	11	5	4–5	4	5	5–6	6
G. maculosus	2	7	7	5	4–5	5	5	5–6	6
G. anguillaris	8	7–8	8	8	3	3	8	7–8	7
G. cataniapo	4	8	8	4	3	3	4	6–7	7
G. coatesi	3	6–8	6	3	2–3	2	3	6–7	7
G. javari	11	7–9	8	10	3	3	5	9–10	9
G. jonasi	5	6–7	7	6	3	3	6	5–6	5
G. melanopleura	1	8	8	1	3	3	1	7	7
G. onca	1	8	8	1	2	2	1	6	6
G. panamensis *	2	7–8	8	2	3	3	2	5–6	6
G. n. sp. “pnt”	6	8	8	6	3	3	6	7–8	8
G. pantherinus	6	8–9	8	4	3	3	6	5–6	6
G. pedanopterus	16	8–13	9	11	3	3	5	6–7	7
G. stenoleucus	9	8–9	9	4	3	3	5	5–6	6
G. arapaima	13	7–10	7	19	3–4	4	31	10–13	12
G. bahianus	6	6–7	7	6	3–4	4	6	9–10	9
G. carapo EA	16	6–7	7	12	3–4	3	7	7–8	8
G. carapo GU	16	6–8	7	14	3–4	4	14	7–9	8
G. carapo MD	13	5–7	6	13	3–4	4	4	10–12	11
G. carapo PI	6	5–6	6	8	3–4	4	5	7–8	7
G. carapo RO	10	5–8	7	8	3–4	3	6	7–8	8
G. carapo WA	14	5–8	6	14	3–4	3	14	8–10	9
G. choco *	9	6	6	9	3	3	3	8–9	8
G. n. sp. “cur”	15	5–8	6	15	3	3	4	7–8	7
G. diamantinensis	3	5–6	6	1	3	3	1	6	6
G. esmeraldas *	8	8–9	8	8	4–5	5	8	11–13	12
G. henni *	7	10–13	10	7	3–6	6	7	10–13	12
G. inaequilabiatus	10	6–9	6	10	3–5	4	5	6–7	6
G. mamiraua	9	5–7	5	9	3–4	4	9	5–6	6
G. n. sp. “obs”	15	5–7	6	14	3–4	4	6	6–7	6
G. paraguensis *	2	11–12	12	3	3–4	3	3	9–11	10
G. sylvius	2	8	8	3	3–4	3	5	6–7	6
G. tigre *	4	8–12	12	4	5–6	6	4	15–16	16
G. n. sp. “var”	29	5–8	6	27	4	4	10	4–6	6
TOTAL	289			277			220		

TABLE 3 (continued)**.**

Species / population	PCV			PLR			PLL			VLR		
	n	range	mode	n	range	med.	n	range	med.	n	range	med.
E. electricus	6	145–200	183	6	0	0	6	160–165	163	6	0	0
G. cylindricus	8	32–34	33	3	41–44	41	5	83–94	88	8	8–15	13
G. maculosus	5	34–36	34	3	35–44	42	5	80–86	83	8	3–19	17
G. anguillaris	8	37–38	38	8	51–62	58	8	102–130	124	2	8–12	10
G. cataniapo	4	47–51	50	2	60–69	63	4	114–120	117	2	17–18	17
G. coatesi	3	43	43	3	61–65	65	3	85–102	98	3	19–23	22
G. javari	14	40–44	42	11	52–67	59	5	88–108	98	5	10–15	13
G. jonasi	9	36–39	37	6	31–40	36	5	73–76	75	5	16–25	20
G. melanopleura	1	36	36	1	46	46	1	69	69	1	19	19
G. onca	1	35	35	1	44	44	1	80	80	1	20	20
G. panamensis *	2	36	36	2	54–57	56	2	88–92	90	2	11–15	13
G. n. sp. “pnt”	6	35–38	37	6	47–52	50	1	90	90	4	6–13	10
G. pantherinus	4	46–50	39	4	58–66	61	4	90–96	93	5	7–11	9
G. pedanopterus	14	31–32	32	10	50–60	55	10	94–111	103	5	7–13	10
G. stenoleucus	8	41–43	42	4	50–59	56	4	87–99	89	4	6–19	10
G. arapaima	16	34–37	35	27	53–64	57	12	99–108	103	11	10–22	17
G. bahianus	10	32–35	33	6	40–41	40	6	75–82	79	6	15–19	17
G. carapo EA	9	32–35	33	15	41–54	48	15	68–110	77	10	0–8	4
G. carapo GU	9	32–35	34	12	40–56	46	12	93–124	96	7	9–22	12
G. carapo MD	10	32–36	35	8	40–49	44	4	84–98	85	8	2–10	6
G. carapo PI	5	32–35	34	6	43–50	45	6	69–76	72	10	0–4	2
G. carapo RO	7	35–37	37	10	45–47	45	10	71–89	78	10	6–10	8
G. carapo WA	10	33–36	33	14	44–54	48	14	110–128	120	5	6–27	15
G. choco *	9	32–35	35	9	45–52	48	5	85–89	87	6	4–13	8
G. n. sp. “cur”	15	34–36	35	4	59–62	61	12	104–140	112	11	0–11	9
G. diamantinensis	1	34	34	1	49	49	1	71	71	1	8	8
G. esmeraldas *	5	41–46	44	8	52–56	54	5	115–119	117	8	14–18	15
G. henni *	7	43–44	44	7	59–68	62	7	95–125	105	7	16–22	18
G. inaequilabiatus	6	31–33	32	4	35–37	37	4	82–115	90	10	6–11	8
G. mamiraua	5	31–34	33	9	32–38	37	9	75–79	78	11	0–14	9
G. n. sp. “obs”	16	35–37	35	6	50–56	54	11	108–132	115	13	15–30	19
G. paraguensis *	3	32–35	34	3	40–48	48	2	114–135	125	3	49–55	51
G. sylvius	5	32–35	33	5	40–47	45	5	85–100	93	5	13–18	16
G. tigre *	4	46–48	47	4	62–78	70	4	125–140	131	4	29–55	33
G. n. sp. “var”	25	35–40	37	10	51–55	53	14	106–135	123	20	14–29	20
TOTAL	270			238			222			227		

TABLE 4. Summary of 27 character-states used to differentiate the 17 recognized taxa of the *Gymnotus carapo* species-group. *, new taxon described in this paper. Abbreviated character descriptions provided in the Appendix.

Species / population	Character													
	1	2	3	4	5	6	7	8	9	10	11	12	13	14
G. arapaima	0	2	2	2	0	0	0	1	0	1	0	1	0	0
G. bahianus	0	0	1	0	1	0	1	0	1	1	0	0	0	1
G. carapo EA	0	2	2	1	0	0	1	0	0	1	0	1	0	1
G. carapo GU	0	1	1	1	1	0	1	0	0	1	0	1	0	1
G. carapo MD	0	1	1	1	1	0	1	0	0	1	0	1	0	1
G. carapo PI	0	0	1	1	2	1	1	0	1	1	0	1	0	1
G. carapo RO	0	1	2	2	0	0	0	0	1	1	0	1	0	1
G. carapo WA	0	2	2	2	0	0	0	1	0	1	0	1	0	0
G. choco *	0	1	1	1	0	0	0	0	1	2	1	1	0	0
G. diamantinensis	0	0	0	?	1	0	?	?	0	1	0	1	0	1
G. esmeraldas *	0	0	1	1	1	0	1	0	1	0	1	1	1	0
G. henni *	0	0	1	1	1	0	1	0	1	1	1	1	1	0
G. inaequilabiatus	1	0	0	0	1	0	1	0	0	1	0	1	0	0
G. mamiraua	0	0	0	1	1	0	1	0	0	2	0	1	0	0
G. paraguensis *	0	1	1	1	0	0	0	1	0	2	1	1	0	0
G. sylvius	0	2	1	1	1	0	?	0	0	1	0	1	0	0
G. tigre *	0	1	1	1	2	1	0	1	1	1	1	1	1	0

Species	15	16	17	18	19	20	21	22	23	24	25	26	27
G. arapaima	1	1	0	0	1	1	1	1	2	1	3	0	1
G. bahianus	0	1	0	0	0	1	0	1	2	0	2	0	1
G. carapo EA	0	1	0	0	1	1	0	1	2	1	2	0	0
G. carapo GU	0	1	0	0	1	1	0	1	2	1	2	0	1
G. carapo MD	0	1	0	0	1	1	0	1	2	1	2	0	1
G. carapo PI	0	1	0	0	1	1	0	1	2	0	2	0	0
G. carapo RO	0	1	0	0	1	1	0	1	3	1	2	0	0
G. carapo WA	1	1	0	1	1	1	1	0	2	1	3	0	0
G. choco *	0	1	0	0	1	1	0	1	2	1	2	0	0
G. diamantinensis	0	1	0	0	0	1	0	1	2	1	2	0	?
G. esmeraldas *	0	0	1	1	2	1	0	0	4	1	1	1	2
G. henni *	0	0	1	1	2	1	0	0	4	1	1	1	2
G. inaequilabiatus	0	1	0	0	0	1	0	1	2	1	2	0	1
G. mamiraua	0	1	0	0	0	0	0	1	2	0	2	0	1
G. paraguensis *	0	1	0	0	1	1	0	0	2	1	2	0	0
G. sylvius	0	1	0	0	0	1	0	1	2	1	2	0	1
G. tigre *	0	0	1	1	2	0	0	0	4	0	1	0	2

Head never banded, spotted, or blotched, its ground color dark brown dorsally grading to lighter brown ventrally, with numerous minute chromatophores speckled over branchiostegal membranes and ventral surface of head. Operculum with a rosy hue from underlying gills in live juveniles. Pectoral-fin rays brown, interradial membranes hyaline. Anal-fin membrane divided into two parts along body axis in adults: anterior 80% dark brown, charcoal gray or black, posterior 20% translucent. Specimens fixed in 10% formalin and preserved for 1–5 years in 70% ethanol maintain approximate colors of life, although darker pigments tend to pale with time. Color variation not known to be correlated with sex or structure of electric organ discharge.

Color in life. Ellis (1913:120) provides an accurate description of living specimens of *G. carapo:* "In life the body is a translucent flesh-color or pale yellow, varying to a distinct pink in the parts rich in blood. The stripes and markings are blue or green, giving the fish a purplish or olive-green cast. The color may be deepened or lightened slightly by the expansion and contraction of the chromatophores."

Geographic variation. Six allopatric populations of *G. carapo s.s.* are recognized on the basis of the mean or modal values of several morphometric and meristic traits (Table 4). *Gymnotus carapo s.s.* from the Eastern Amazon (*G. carapo* EA) is found downstream from Manaus, in the lower-most region of the Rio Negro basin near Manaus, and in the Trombetas, Tapajós, and Tocantins basins. *Gymnotus carapo* EA is most similar in overall appearance to *G. carapo* from the Parnaíba and Itapicuru basins in the Brazilian state of Piauí (*G. carapo* PI), from which it differs on average by: 1, a longer head (HL 11.7–13.6% TL [mean 12.7%; n=15] vs. 10.2–12.2% [mean 11.4%, n=8]); 2, a flatter head (HD 50.8–60.9% HL [mean 55.2%, n=16] vs. 58.3–64.8% [mean 61.0%, n=8]); and 3, a shorter snout (PR 60.0–65.5% HL [mean 62.3%, n=16] vs. 63.2–67.6% [mean 65.5, n=8]). *Gymnotus carapo* PI can be distinguished from *G. bahianus* by possession of: 1, oblique pigment bands (vs. spots or no dark pigments) on the anterior portion of the body; 2, a longer snout (PR 35–38% HL [mean 37%, n=8] vs. 33–36% [mean 35%, n=23]); 3, a wider mouth (MW 42–46% HL [mean 44%, n=8] vs. 35–45% [mean 40%, n=23]); 4, a longer postorbital region (PO 63–68% HL [mean 66%, n=8] vs. 60–65% [mean 62%, n=16]).

Gymnotus carapo from the Rio Branco basin in the Brazilian state of Roraima (*G. carapo* RO) differs on average from other populations of *G. carapo s.s.* by: 1. a flatter head (mean HD 53% HL [n=10] vs. means 55–63% [n=89]); 2. a narrower head (mean HW 54% HL vs. means 56–61% [n=91]); and, 3. a longer body cavity (PCV 35–37 [mode 34, n=7] vs. modes 33–35 [n=40]). *Gymnotus carapo* from the rivers of the Guianas Shield, the Río Orinoco Basin and Island of Trinidad (*G. carapo* GU) is most similar in overall appearance to *G. carapo* RO, from which it differs on average by characters listed above.

Gymnotus carapo from the Western Amazon (*G. carapo* WA) is known from the Rio Tefé, Japurá and Javarí drainages of Brazil, the Río Napo drainage of Ecuador, and the Río Nanay, Pastaza and Ucayali drainages of Peru. *Gymnotus carapo* WA is readily distinguished from all other populations of *G. carapo* in that the anterior half of the anal fin is

black (vs. gray or brown; the anterior half of the anal fin is also black in *G. arapaima*). *Gymnotus carapo* from the Rio Madeira basin (*G. carapo* MD) is found in the Rio Jamarí and Machado drainages of Brazil, the Río Mamoré, Guaporé, and Beni drainages of Bolivia, and the Río Madre de Dios drainage of Peru. *Gymnotus carapo* MD is most similar in overall appearance to *G. carapo* WA, from which it differs on average by: 1, longer anal-fin pterygiophores and smaller overlying scales (APS 10–12 [mode 11, n=4] vs. 8–10 [mode 9, n=14]); 2, fewer posterior lateral line scales (to the first ventral lateral line ramus, PLR 40–49 [median 44, n=8] vs. 44–54 [median 48, n=14; total, PLL 84–98 [mean 85, n=4] vs. 110–128 [mean 120, n=14); 3, gray or brown (vs. black) color of the anterior half of the anal-fin.

Electric organ discharge. Electric organ discharge waveform with total duration of approximately 1.1 – 1.5 ms comprising four phases with low-voltage pre and post potentials either side of dominant, approximately symmetrical, biphasic component.

Distribution. A map with the distribution of identified lots of *G. carapo s.s.* is provided in Fig. 2. *Gymnotus carapo s.s.* is known from the Amazon and Orinoco Basins below c. 500 m elevation, the Island of Trinidad, drainages of the Guyanas Shield, and Atlantic drainages of northeastern Brazil (including the Ríos Pindaré, Itapicuru and Parnaíba). *Gymnotus carapo s.s.* is not known from Middle America, Trans-Andean (Pacific Slope, Ríos Atrato, Magdalena, Maracaibo), São Francisco, or Paraguay-Paraná river systems, the Rio Negro basin above Manaus (excl. Rio Branco), or the Atlantic drainages of Brazil east of Fortaleza or south of Recife.

Ecology. Gymnotus carapo s.s. occurs in shallow waters with little or no flow in both floodplain and non-floodplain habitats throughout its range. In floodplains, juvenile specimens are found in patches of floating macrophytes along channel and lake margins. Adults occur in floating macrophytes, shallow waters and seasonally flooded forests. *G. carapo s.s.* undertakes aerial respiration by gulping atmospheric air into the hypervascularized posterior chamber of the gas bladder (Liem *et al.* 1984). Juvenile *G. carapo s.s.* feed primarily on small aquatic insects and crustaceans; especially chironomid larvae, Odonata and Coleoptera larvae and choncostraca. Adults prey on larger animals such as shrimps and fishes. *Gymnotus carapo s.s.* breeds during the wet season or period of rising flood waters (pers. obs.) and has been reported to mouth brood (Kirschbaum & Wieczorek 2002). Populations from Trinidad are known to undertake nesting and paternal care (Hopkins pers. com.). Unlike most gymnotiform fishes, *G. carapo s.s.* is occasionally sold in fish markets due to its substantial size, abundance and its ease of capture with baited hooks. Further notes on the ecology of *G. carapo s.s.* are provided in Crampton (1996b) and Alves-Gomes (1997).

Remarks. The original description of *G. carapo* by Linnaeus (1758) was based in part on Artedi (1738), itself based on Marcgraf (1648), and in part on specimens in the Uppsala and Adolphi Friderici collections, now in the Ulriksdal Collection deposited at the NRM (Holthuis 1959; Hoogmoed 1973). Marcgraf's description was based on material from the

Dutch colonial region of northeastern Brazil; the current location of this material, if it still exists, is unknown (Ihering 1914). The overall species composition of South American fishes in the Uppsala and Adolphi Friderici collections indicates that these materials are from Surinam (S. Kullander pers. comm.). The specimens of *G. carapo* examined by Linnaeus are inferred to have been collected in the 18th Century near Paramaribo, Surinam, possibly by Dahlberg and Rolander. The type locality of *G. carapo* is here amended from "America" (Linnaeus 1758) to "Surinam."

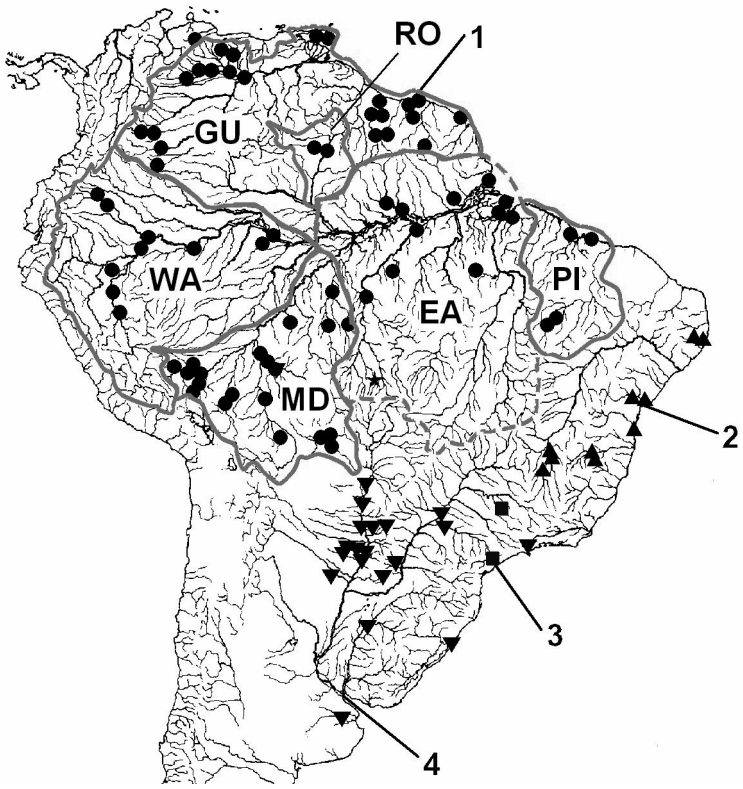

FIGURE 2. Part of South America showing collection records of *Gymnotus carapo s.s.* and some allied species from eastern Brazil and the Parana-Paraguay drainage. *Gymnotus carapo s.s.* (●, 1 = region of type locality), *G. diamantinensis* (★), *G. bahianus* (▲, 2 = type locality), *G. sylvius* (■, 3 = type locality), *G. inaequilabiatus* (▼, 4 = inferred area of type locality). Red lines (bold) indicate watershed boundaries for six allopatric populations of *G. carapo s.s.*; see Table 1 for abbreviations. Some symbols represent more than one locality or lot of specimens. Base map by M. Weitzman.

Materials examined. 57 lots bearing 170 specimens are presented by Albert (2001); an additional 128 lots bearing 575 specimens (33–418 mm) are presented here. BOLIVIA. *Beni*: UF 82470 (2), 170–218 mm, Río Mamoré, Río Ibaré, Cercado, Arroyo San Javier (14°38'S, 64°53'W). UF 82485 (1), 360 mm, Río Mamoré, Río Ibaré, Cercado, 20 km N San Javier (14°28'S, 64°56'W). UF 82510 (1), 241 mm, Río Mamoré, Río Ibaré, Cercado,

25 km N San Javier (14°24'S, 64°56'W). UMMZ 204771 (5), 44–51 mm, Río Guaporé, Rio Itenez, 3 km S. Costa Marquez, Brazil (12°30'S, 64°17'W). UMMZ 66433 (2), 215–331 mm, Río Beni, Lago Rogoagua (13°57'S, 66°58'W). *Santa Cruz*: UF 82191 (1), 187 mm, Río Guaporé, Río San Pablo, Río San Diablo, Velasco, 71 km N. San José de Chiquitos (17º18'S, 60º35'W). UF 82211 (2), 196–205 mm, Río Guaporé, Río San Pablo, Chiquitos, Comunidad La Esperanza, ca. 40 km N. San José de Chiquitos (17º25'S, 60º47'W). BRAZIL. *Amapá*: INPA uncat. (3), 33–81 mm, Rio Araguari, Bacapnari (01º15'N, 49º55'W). *Amazonas*: Alvarães: INPA 14227 (1, part), 385 mm, Presidente Figueiredo: Rio Urubu, Igarapé do Gavião, Fazenda Esteio (approx. 01º16'S, 59º49'W). INPA 21082 (1), 157 mm, Rio Japurá, Lago Amanã, Juá Grande (02º29'S, 64º49'W). MZUSP 75168 (1), 119 mm, Tefé: Rio Tefé, Ilha do Martelo (03°46'49"S, 64°59'29"W). MZUSP 76061 (1), 260 mm, Rio Tefé, Lago Tefé, Cabeçeira do Lago Tefé (03°34'35'S, 64°59'19"W). MZUSP 76062 (1), 94 mm, Rio Tefé, Lago Tefé, Ressaca do Socorro (03°19'11"S, 64°41'46"W). MZUSP 76063 (1), 298 mm, MSDR, Ressaca da Vila Alencar (03º07'42"S, 64°48'02"W). MZUSP 76064 (1), 253 mm, MSDR, Cano do Lago Mamirauá (03º04'26"S, 64º48'39"W). MZUSP 76066 (2), 97–136 mm, MSDR, Lago Secretaria (03º06'44"S, 64°48'01'W). Benjamin Constante: UMMZ 230734 (2), 190 – 210 mm, Rio Solimões, Rio Cayari (approx. 04°22'S, 70°02'W). *Mato Grosso*: Aripuanã: INPA 4383 (22), 42–188 mm, Rio Aripuanã, Igarapé do Aeroporto (approx. 10º10'S, 59º27'W). INPA 6383 (7), 139–197mm, same locality as INPA 4283. INPA 6388 (1, part), 292mm, same locality as INPA 4283. INPA 6392 (4), 140–190 mm, same locality as INPA 4283. INPA 6395 (2), 122–127 mm, same locality as INPA 6391. INPA 11554 (1), 145 mm, Rio Aripuanã, Praia Grande, 2 km below Cachoeira Dardanelos. INPA 6406 (26), 38–166 mm, same locality as INPA 4283. INPA 6407 (9), 107–313 mm, same locality as INPA 4283. INPA 6408a (9), 96–223 mm, same locality as INPA 4283. INPA 11549 (1), 230 mm, same locality as INPA 4283. INPA 11551 (4), 119–198 mm, same locality as INPA 4283. INPA 11552 (1), 182 mm, same locality as INPA 4283. INPA 11558 (1), 173 mm, Rio Aripuanã, Igarapé do Guaribal, 5 km below Cachoeira Dardanelos. INPA 11560 (11), 120–200 mm, same locality as INPA 4283. INPA 19954 (1), 135 mm, same locality as INPA 4283. INPA 6391 (8), 108–170 mm, Rio Aripuanã, 10 km above Cachoeira Dardanelos. *Pará*: Oriximiná: INPA 6379 (1), 229 mm, Rio Trombetas, Cachoeira Porteiro (01°05'S, 57°02'W). INPA 6385 (1), 164 mm, Rio Trombetas, Igarapé do Caxi-Pacoré. INPA 6393 (12), 97–220 mm, Rio Trombetas, BR 163, km 10–13. INPA 6400 (1), 96 mm, same locality as INPA 6379. INPA 6402 (1), 110 mm, same locality as INPA 6393. INPA uncat. (2), 89–107 mm, same locality as INPA 6393. MZUSP 30008 (8), 173–253 mm, Rio Trombetas, Rio Itacaiunas, Caldeirão, Igarapé do Pojuca (approx. 00°45'S, 56°13'W). MZUSP 30013 (1), 240 mm, Rio Trombetas, Igarapé do Paraíso. Parauapebas: MCZ 45189 (19), 133–210 mm, Ilha de Marajó, Rio Tocantins, Rio Arari, Cachoeira do Arari (01°01'S, 48°58'W). MZUSP 30025 (7), 165–237 mm, Rio Tocantins, Rio Itacaiuna, Serra Norte, Serra dos Carajás (approx. 05°05'S, 50°22'W. Tucurui: INPA 6378 (1), 315 mm, Rio Tocantins, Icangui. INPA 6380

(1), 246 mm, Rio Tocantins, Tucurui (04°25'S, 49°32'W). INPA 6386 (1), 157mm, same locality as INPA 6380. INPA 6382 (1), 418 mm, Rio Tocantins, Cameta (02°15'S, 49°30'W). INPA 6396 (1), 238 mm, Rio Tocantins, Jatubah. INPA 6405 (7), 65–125 mm, same locality as INPA 6382. *Piauí*: AUM 20624 (3), 179–225 mm, Piauí, Rio Gurgueia, Rio Parnaíba, 4 km E. Bertolina. AUM 20689 (2), 95–138 mm, Piauí, Rio Gurgueia, 25km SW Urucui. AUM 2079 (4), 156–192 mm, Piauí, Parnaíba, between Santa Filomena and Jurumenha. AUM 20624 (3), 179–225 mm, Piauí, Rio Gurgueia, Rio Parnaíba. AUM 20689 (3), 95–138 mm, Rio Gurgueia, Rio Parnaíba, Piauí. *Rondônia*: INPA 1152 (2), 165–175 mm, Ariquemes, Rio Cadeiras, Igarapé Tracoazinho, Serra Pacaas Novos. MZUSP 30006 (10), 125–200 mm, Rio Branco, Cachoeira do Bem Querer. *Roraima*: Mucajaí: INPA 6381 (5), 111–175 mm, Rio Mucajaí, Estação Fé-Esperança. INPA 6384 (2), 105–127 mm, Rio Mucajaí. COLOMBIA. *Meta*: NRM 27717 (1), 235 mm, Río Meta, Rio Ocoa, Laguna Santa Clara, ca. 5 km S Villavicencio (approx. 04°09'N, 73°39'W). UF 26178 (39), 134–239 mm, Río Guatiquia-Meta, Caños Negros, ca. 9 km Villavicencio on road to Puerto Porfia (approx. 04°09'N, 73°39'W). UF 33245 (1), 200 mm, Río Meta, Rio Guamal, 7 km E. Río Guayuriba, just N. Guamal (approx. 03°52'N, 73°45'W). ECUADOR. *Napo*: FMNH 103329 (10), 33–320 mm, Río Napo, Río Tiputini (approx. 00°49'S, 75°31'W). FMNH 103334 (2), 48–64 mm, Río Napo, Río Aguarico, Laguna Zancudococha (approx. 00°17'S, 75°52'W). PERU. *Loreto*: IAAP uncat. (1), 367 mm, Río Amazonas, Maynas, nr. Iquitos (no locality data). MUSM 9274 (1), 136 mm, Río Ucayali, Contamana, Aguas Calientes (07°02'S, 74°14'W). MUSM 14482 (7), 118–198 mm, Río Napo, Río Aguarico, Maynas, PV Castaña (00°48'13"S, 75°14'24"W). NRM 27650 (1), 305 mm, Río Samiria, Maynas, right bank stream tributary between Caño Pastos and Hamburgo (05°12'S, 75°08'W). NRM 40772 (1), 91 mm, Río Maniti, Maynas, 50 km NE of Iquitos (03°29'S, 72°44'W). UF 116573 (2), 189–279 mm, Río Amazonas, Maynas, Río Nanay . UF 122820 (1), 275 mm, same locality as UF 116573. UF 122822 (1), 330 mm, same locality as UF 116573. UF 122825 (1), 158 mm, same locality as UF 116573. UF 122847 (1), 188 mm, same locality as UF 116573. UF 122848 (1), 112 mm, same locality as UF 116573. UF 122849 (1), 132 mm, same locality as UF 116573. UF 122850 (1), 188 mm, same locality as UF 116573. UF 122851 (1), 107 mm, same locality as UF 116573. UF 122852 (1), 92 mm, same locality as UF 116573. UF 116665 (1), 298 mm, Río Nanay, Maynas, 3 km upstream Mishana, Reserva Allpahuayo-Mishana (03°52'05"S, 73°29'03"W). UF 126181 (2), 245–272 mm, Río Pacaya, Cocha Zapote (05°20'02"S, 74°29'05"W). UMMZ 228998 (4), 38–172 mm, Río Nanay, Río Momon, Amazon camp nr. Iquitos (approx. 03°42'S, 73°16'W). UMMZ 228999 (1), 162 mm Río Tahuayo (04°10'S, 73°12'W). UMMZ 230733 (1), 251 mm, Río Yavari, Buen Suceso, Quebrada Carana (approx. 04º08'S, 70º26'W). *Madre de Dios*: MUSM 3949 (1), 71 mm, Río Madre de Dios, Río Manu, Parque Nacional Manu, Aguajal (approx. 12°16'S, 70°51'W). MUSM 3961 (1), 202 mm, Río Manu, Parque Nacional Manu, Pakitza, Quebrada Picaflor (approx. 12°16'S, 70°51'W). MUSM 4519 (1), 141 mm, Río Manu, Parque Nacional Manu, Pak-

itza, Quebrada Carpinteiro (approx. 12°16'S, 70°51'W). MUSM 4567 (2), 106–151 mm, same locality as MUSM 4519. MUSM 14235 (2), 51–157 mm, same locality as MUSM 4519. MUSM 7593 (1), 116 mm, Río Madre de Dios, Río Tambopata, Río Palma Real, Enahuipa (approx. 12°36'S, 69°11'W). MUSM 7673 (2), 125–183 mm, Río Manu, Parque Nacional Manu, Cocha Salvador (approx. 12°16'S, 70°51'W). MUSM 8601 (1), 131 mm, Río Madre de Dios, Puerto Maldonado, La Cachuela (approx. 12°36'S, 69°11'W). MUSM 14021 (1), 183 mm, Río Manu, Parque Nacional Manu, Quebrada Pachija (approx. 12°16'S, 70°51'W). MUSM 14241 (4), 114–148 mm, Río Manu, Parque Nacional Manu, Quebrada Martin Pescador (approx. 12°16'S, 70°51'W). MUSM 16662 (1), 325 mm, Río Madre de Dios, Tambopata, Lago Copamanu (approx. 12°36'S, 69°11'W). *Puno:* MUSM 10380 (1), 145 mm, Sandia, Río Candamo (approx. 13°31'S, 69°41'W). MUSM 10969 (2), 142–182 mm, same locality as MUSM 10380. MUSM 11000 (1), 77 mm, same locality as MUSM 10380. MUSM 12949 (3), 101–227 mm, same locality as MUSM 10380. MUSM 11590 (5), 193–211 mm, Cuenca Ebehuabaeji, Sandia. MUSM 11639 (2), 123–159 mm, same locality as MUSM 11590. MUSM 11784 (3), 134–191 mm, Río Candamo, Carabaya, Quebrada Pacal (12°37'S, 70°19'W). MUSM 11891 (1), 82 mm, Río Candamo, Carabaya, Quebrada Bujurqui. MUSM 12949 (4), 101–227mm, Puno, Sandia, Río Candamo, (13°25' S, 70°01'W). *Ucayali*: MUSM 529 (7), 83–109 mm, Río Ucayali, Pucallpa, Estación del IVITA, Quebrada Piscigranja (approx. 08°23'S, 74°32'W). MUSM 532 (1), 181 mm, same locality as MUSM 529. MUSM 537 (2), 222–260 mm, same locality as MUSM 529. MUSM 2691 (5), 132–222 mm, same locality as MUSM 529. MUSM 2971 (1), 187 mm, same locality as MUSM 529. MUSM 1547 (1), 122 mm, Río Ucayali, Río Huacamayo km 155 (approx. 12°46'S, 69°52'W). MUSM 1757 (3), 154–267 mm, Río Ucayali, Pucallpa, Utuguinia (08°23'S, 74°32'W). SURINAM. *Brokopondo District*: UMMZ 190414 (6), 71–260 mm, Suriname River, Tapeoeripa creek nr. Brokopondo village (approx. 05°04'N, 54°58'W). *Nickerie District*: USNM 225274 (8), 81–318 mm, Lucie River, creek, upstream of Amotopo-Camp Geologie Rd. (03º36'N, 57º37'W). USNM 225275 (11), 81–270 mm, Corantijn River, E bank creek, 350 m downstream from Wilhelm II falls (03º34'N, 57º15'W). USNM 225276 (16), 75–148 mm, Corantijn River, Dalbana Creek, ca. 3 km upstream from Amotopo-Camp Geologie Rd. (04º20'N, 57º37'W). USNM 225284 (10), 54–143 mm, Corantijn River, Lana Creek, ca. 4 km from intersection with W. Corantijn River (05º28'N, 57º15'W). USNM 225285 (12), 85–257 mm, Corantijn River, creek south of Matapi, approx. 2 km downstream of Cow Falls (04º59'N, 57º38'W). USNM 225286 (15), 80–319 mm, Corantijn River, Koekwie creek (05º31'N, 57º10'W). USNM 225290 (19), 14–157 mm, Corantijn River, Dalibane Creek, Camp Dacclemmen (05º34'N, 57º11'W). USNM 225297 (14), 53–137 mm, Corantijn River, stream on S. side Lucie River (03º35'N, 57º39'W). TRINIDAD & TOBAGO. *Mayaro*: UMMZ 169080 (5), 46–71 mm, Gunupia, Mt. Plaisance Village (10°16'N, 61°00'W). VENEZUELA. *Apure:* UF 37030 (20), 101–176 mm, Río Apure, Río Guaritico, Hato El Frio (approx. 09°03'N, 68°20'W). UF 77334 (1), 173 mm, Río Apure, Cano Caicara, ca. 30 km SW La Ye

(approx. 07°40'N, 72°22'W). UF 80734 (47), 165–262 mm, Río Apure, E. dike in UNELLEZ module. UF 80734 (6), 165–262 mm, Río Apure, E dike in UNELLEZ module. *Guarico*: UF 35402 (3), 148–178 mm, Río Apure, ca. 50 km N San Fernando de Apure (approx. 07°54'N, 67°28'W). UF 78069 (3), 151–190 mm, Rio Apure, 2. 3 km N San Fernando de Apure (approx. 07°54'N, 67°28'W).

***Gymnotus choco* n. sp. Albert, Crampton, and Maldonado**
(Fig. 3, Tables 2 and 3)

Holotype: ICNMHN 6621, 237 mm, collected 28 February 1993, at Boca de Pepé, Río Baudó, Chocó Department, Colombia (05°03'N, 77°03'W) by S. Kullander and A. Silfvergrip.

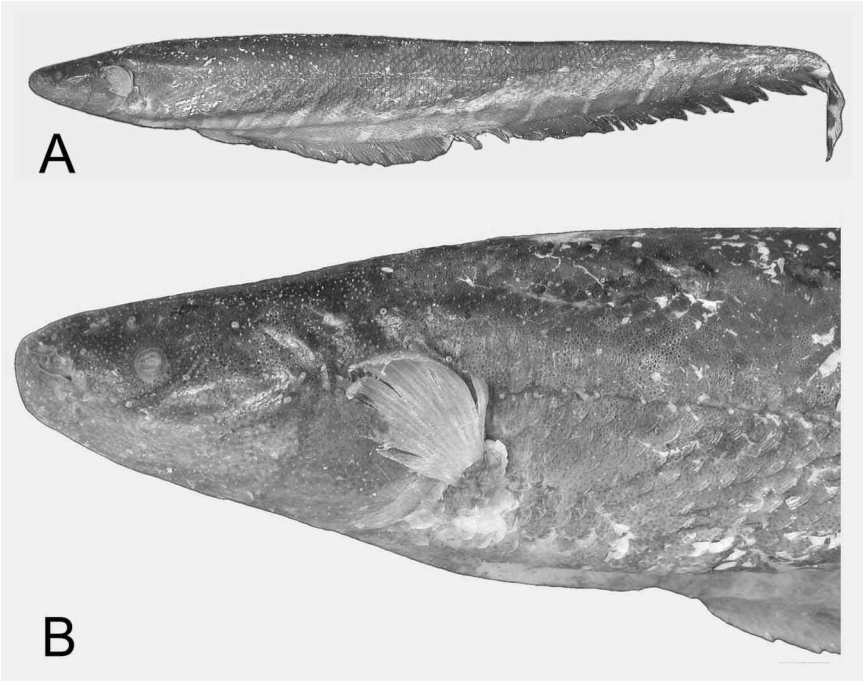

FIGURE 3. *Gymnotus choco* n. sp., holotype, ICNMHN 6621, 237 mm, Colombia, Chocó, Río Baudó, Boca de Pepé (05°03'N, 77°03'W). A, whole body. B, head.

Paratypes: NRM 27734 (6), 142–260 mm. Collected with holotype.

Nontypes: 7 lots with 14 specimens, all collected in Colombia. CAS 72192 (2), 150–179 mm, 1913, Río Sucio, Río Truando, Chocó Department, Atrato basin (07°09'N, 77°12'W). ICNMHN 6686 (1), 321 mm, March 1994, Upper Río San Juan, Pueblo Rico, Risaralda Department. IMCN 1050 (2), 208–239 mm, June 01, 2002, Resguardo Puerto

Pizarro, Río San Juan, Litoral del San Juan, Chocó Department. IMCN 1370 (1), 215 mm, same collection data as IMCN 1050. FMNH 70511 (5), 124–247 mm, November 1945, at Pizarro (Baja Baudó), Río Baudó, Chocó Department (04°58'N, 77°22'W). FMNH 56794 (2), 174–175 mm, same collection data as CAS 72192. NRM 27744 (1), 350 mm, 07 February 1989, at Quebrada Piscindé, close to Pan-American bridge across Río San Pablo, Atrato basin, Chocó Department (05°42'N, 76°37'W).

Diagnosis. *Gymnotus choco* can be distinguished from other species of the *G. carapo* species-group by a color pattern with obliquely oriented pale-yellow bands in which the band-interband margins are irregular and wavy, in which there are one to three inverted Y-shaped (divided ventrally) dark bands in the posterior portion of body (at bands 6–9 from posterior tip of tail), and in which the pale bands do not extend above the lateral line on the anterior 2/3 of body. *Gymnotus choco* is most similar to *G. paraguensis* n. sp. (described below*)* from the Pantanal of Brazil and Paraguay from which it can be distinguished by: 1, a more narrow mouth (MW 28.3–29.7% HL [mean 33%, n=9] vs. 38.6–39.0% [mean 39%, n=4]); 2, a more cylindrical body (BW 0.68–0.83% BD [mean 77%, n=9] vs. 0.60–0.69 [mean 66%, n=4]); 3, a longer preanal distance (PA 76.7–90.7% HL [mean 84%, n=9 vs. 62.9–81.2% [mean 69%, n=4]). *Gymnotus choco* can be further distinguished from other taxa of the *G. carapo* species-group by the unique combination of character states provided in Table 4.

Description. Fig. 3 illustrates head and body shape and pigment patterns. Morphometric data in Table 2, and meristic data in Table 3. Body size moderate, up to 260 mm. Size at reproductive maturity and sexual dimorphism unknown. Scales circular or slightly ovoid, present on entire post-cranial portion of body from nape to caudal appendage. Gape size in mature specimens large, extending to or beyond posterior nares. Mouth position superior, lower jaw longer than upper, rictus decurved. Chin fleshy and bulbous. Anterior narial pore partially or entirely included within gape in large narial fold. Anterior nares large, subequal to diameter of eye. Mesethmoid anterior margin concave with short paired anterolateral processes. Mesethmoid neck broad, more than width of ventral ethmoid. Ethmoid region between anterior nares broad, its anterior margin rounded. Circumorbital series ovoid. Eye position lateral, lower margin of eye dorsal to rictus.

Premaxilla with 13–15 teeth disposed in single row along outer margin, arrow-head shaped anteriorly, conical posteriorly. Median margin of premaxilla curved. Maxilla-palatine articulation near anterior tip of mesopterygoid. Maxilla orientation vertical. Maxilla rod-shaped, narrow distally with straight ventral margin. Maxilla length equal to about width of 4–6 dentary teeth. Dentary with one row of 16–17 teeth (n=2), 2–3 arrow-shaped teeth anteriorly, all others conical posteriorly. Dorsoposterior and ventroposterior dentary processes abut at midlength of dentary. Dentary ventroposterior process almost as long as dorsoposterior process. Dentary dorsoposterior process narrow distally. Dentary ventral margin with a narrow lamella, less than posterior process. Anteroventral margin of dentary rounded in lateral view, without a hook. Dorsal margin of opercle straight or slightly con-

vex. Texture of dorsal opercle process deeply pitted and cancellous. Dorsal opercular crest longer than dorsal opercle process. Posterior margin of opercle smooth, entire, without spines or processes. Ventral ridge field of opercle broad. Dorsal ridge field of opercle long, more than half width of opercle. Dorsoposterior laterosensory ramus of preopercle with two superficial pores. Preopercle with anteroventral notch. Margin of preopercular medial shelf entire. Median shelf of preopercle small, less than half width of symplectic. Ascending process of mesopterygoid robust, long, its base shorter than its length. Mesopterygoid ascending process curved. Tip of mesopterygoid ascending process simple. Metapterygoid superior and inferior portions approximately equal in size. Dorsal margin of interopercle with broad ascending process. Dorsal margin of subopercle concave. Posterior margin of retroarticular square. Retroarticular with an arched lamella posteriorly, forming a small canal. Anguloarticular process short, to ventral margin poster. Mandible long, extended, its length more than twice its depth. Trigeminal canals (supraorbital, infraorbitral) with separate fenestrae on outer surface of hyomandibula. Posterior lateral line fenestra contacting dorsoposterior margin of hyomandibula. Cranial fontanels closed in juveniles and adults. Anterior margin of frontal straight, continuous with margins of adjacent roofing bones. Frontal postorbital process broad, more than two times width of supraorbital canal. Frontal shape narrow, width at fourth infraorbital less than that of parietal. Lateral ethmoid absent. Parasphenoid posterior process broad. Parasphenoid lateral process broad, triangular. Parietal rectangular, its length less than width. Pterosphenoid anteroventral portion robust, extending ventral to lateral margin of parasphenoid. Prootic foramen Vp combined with V2–3+VII. Adductor mandibula undivided at insertion. Adductor mandibula intermuscular absent. All basibranchials unossified. Gill rakers not contacting gill bar. Basibranchial 5 unossified. Pectoral medial radial large. Mesocoracoid elongate, its length more than 4 times width. Postcleithrum thin, discoid or sickle-shaped. Cleithrum narrow, with a straight ventral margin. Anterior limb of cleithrum long, more than 1.8 times ascending limb. Cleithrum deeply incised on its anteroventral margin. Cleithrum without large facet for insertion of muscle from supracleithrum. Rib 5 robust along its entire extent, less than 3 times width of rib 6. Hemal spines present. Displaced hemal spines absent. Multiple anal-fin ray branching posterior to rays 10–17. Length anal-fin pterygiophores equal to or longer than hemal spines. Single hypaxial electric organ, extending along entire ventral margin of body. Electric organ discharge not known.

Color in alcohol. Ground color of body dark brown dorsally grading to pale brown ventrally. Chromatophores most densely concentrated along dorsum near midline. Body with 21 or 22 (median 21) obliquely oriented pale-yellow bands on ventrolateral surface extending from tip of tail to pectoral-fin base. Band appearance variable in shape, width, and arrangement, both on and among individuals. Band-interband margins irregular and wavy. One to three inverted Y-shaped (divided ventrally) dark bands in posterior portion of body, at bands 6–9 from posterior tip of tail. Pale bands do not extend above lateral line along anterior 2/3 of body. Interband contrast increases ventrally and caudally, and more

pronounced in smaller specimens. Anterior 80% of dorsum (anterior to anal-fin clear patch) without banding. Three bands from either side meet on ventral midline, between anus and anal-fin origin. A single band posterior to last anal-fin ray.

Head not banded, its ground color dark brown dorsally grading to lighter brown ventrally, without freckles and with numerous speckles distributed over branchiostegal membranes and ventral surface of head. Pectoral-fin rays brown, interradial membranes hyaline. Anal-fin membrane divided into three parts along body axis: anterior 40% brown, mid 40% black, posterior 20% translucent.

Distribution. Known from the Río Baudó drainage on the Pacific Slope of Colombia, and the Río Atrato, a Caribbean drainage in northern Colombia (Fig. 4).

FIGURE 4. Part of South America showing collection records of five new species of the *Gymnotus carapo*-species group. *G. choco* n. sp. (★, 1 = type locality), *G. esmeraldas* n. sp. (■, 2 = type locality), *G. henni* n. sp. (▼, 1 = type locality), *G. paraguensis* n. sp. (●, 3 = type locality), *G. tigre* n. sp. (▲, 4 = type locality). Some symbols represent more than one locality or lot of specimens. Base map by M. Weitzman.

Common name. Cuchillo.

Etymology. Specific epithet for the Chocó region on the Pacific slope of Colombia. A noun in apposition.

***Gymnotus esmeraldas* n. sp. Albert and Crampton**
(Fig. 5, Tables 2 and 3)

Holotype: MCZ 58729, 296 mm, collected 18 June, 1977, at Hoja Blanca nr. San Miguel, Ríos Cayapas, Río Esmeraldas drainage, Ecuador (01°05'N, 79°03'W) by K. Miyata and A. Rankis.

Paratypes: MCZ 162745 (4), 200–309 mm; collected with holotype.

Nontypes: 2 lots with 3 specimens, all collected in Ecuador. CAS 164103 (1), 355 mm, 01 December, 1949, nr. mouth of Río Quinide, Río Toachi, Río Blanco, Río Esmeraldas drainage. FMNH 92041 (2), 229–288 mm, 31 July, 1974 nr. Station 16, Río Palenque Biological Station, Los Rios Department, Río Guayaquil drainage.

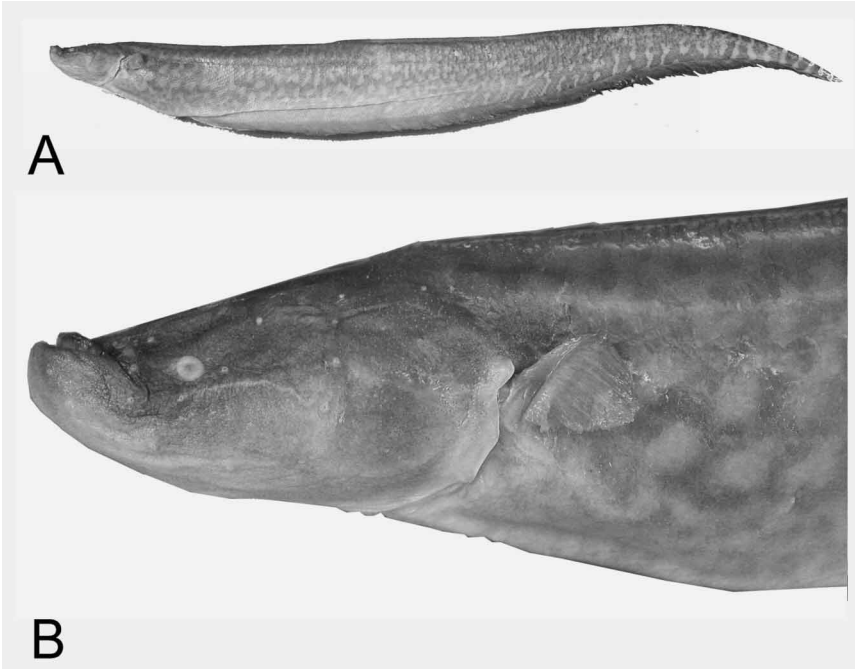

FIGURE 5. *Gymnotus esmeraldas* n. sp., holotype, MCZ 58729, 296 mm, Ecuador, Esmeraldas, Ríos Cayapas, Hoja Blanca nr. San Miguel (01°05'N, 79°03'W). A, whole body. B, head.

Diagnosis. *Gymnotus esmeraldas* can be distinguished from all species of the *G. carapo* species-group except *G. bahianus* by the absence of alternating dark and light pigment bands on the anterior 80% of the body. Specimens in the type series of *G. esmeraldas* from the Río Esmeraldas basin possess a unique speckled color pattern composed of irregular pale yellow or cream-colored patches interspersed on a dark brown ground color over most body and anal-fin surfaces, in which the pale pigment patches are about 2–3 scales in width and height. *Gymnotus esmeraldas* is most similar to *G. henni* n. sp. (see below) from

the Río Calima on the Pacific Slope of Colombia, from which it can be distinguished by: 1, reticulated color pattern without bands on the majority of the body surface and without pale blotches on the head (vs. presence of 13–16 pigment bands and pale blotches on the head]; 2, body shape laterally compressed (BW 58–77% BD [mean 69%, n=8] vs. 77–87% [mean 80%, n=7]); 3, moderate number of pored lateral-line scales to first ventral ramus (PLR 51–54 [median 52, n=8] vs. 59–68 [median 62, n=7]). In addition to color differences, *G. esmeraldas* can be distinguished from *G. bahianus* by: 1, a more slender body (BD 8.2–9.8% HL [mean 8.8%, n=8] vs. 9.3–13.3% [mean 11.1, n=21]); 2, more pectoral-fin rays (P1R 17–19 [mode 17, n=8] vs. 15–16 [mode 16, n=6]); 3, a longer preanal region (PA 82–98% HL [mean 92%, n=8] vs. 76–97% [mean 85%, n=22]); 4, elongate (vs. circular) scales (SAL 8–9 [mode 8, n=8] vs. 6–7 [mode 7, n=16]); and 5, broader electric organ with more rows of electroplates (CEP 4–5 [mode 5, n=8] vs. 3–4 [mode 4, n=6]). *Gymnotus esmeraldas* can further be distinguished from congeners by the unique combination of character states provided in Table 4.

Description. Fig. 5 illustrates head and body shape and pigment patterns. Morphometric data in Table 2 and meristic data in Table 3. Size up to 309 mm. Size at reproductive maturity and sexual dimorphism unknown. Scales present on entire post-cranial portion of body from nape to caudal appendage. Scales above lateral line large, 8–9 to dorsal midline at midbody. Most scales on body moderately elongate, scales above lateral line at midbody approximately 2–3 times as long as deep, their proportional elongation increasing with body size. Gape size in mature specimens large, extending to or beyond posterior nares. Mouth position superior, rictus decurved. Eye position below horizontal with front of mouth. Anterior narial pore partially or entirely included within gape. Circumorbital series ovoid. Caudal appendage short, less 0.5 times length of pectoral fin. Single hypaxial electric organ, extending along entire ventral margin of body. Electric organ discharge not known. Many osteological features not known due to paucity of specimens for clearing and staining; some character states were determined from radiographs. Dorsoposterior laterosensory ramus of preopercle with two superficial pores. Displaced hemal spines absent. Multiple anal-fin ray branching posterior to rays 10–17. Length of anal-fin pterygiophores equal to or longer than hemal spines.

Color in alcohol. Ground color of body pale brown with slight countershading, and chromatophores concentrated along dorsum near midline. Body with 6–10 very irregular dark bands with wavy margins or broken to blotches restricted to the posterior 20% of body. Pigment bands not apparent on anterior 80% of post-cranial body, coloration composed here of irregularly distributed pigment patches in a reticulate pattern of cream-colored and dark brown areas over body and anal-fin surfaces. Pigment patches about 2–4 scale-diameters across, with dark and light patches summing to approximately equal total surface areas in region over hypaxial musculature.

Head ground-color dark chocolate dorsally, without blotches, pale yellow ventrally. Dark regions on dorsal surface of head composed of numerous dark brown chromato-

phores with even pigment densities. Branchiostegal membranes and ventral surface of head almost without pigments. Pectoral-fin interradial membranes dusky or hyaline. Color of anal-fin membrane graded along body axis, from light brown or hyaline anteriorly to dark brown or black posteriorly, with short, obliquely oriented hyaline and dark stripes near fin base in posterior-most region.

Distribution. Known from two river basins on Pacific Slope of Ecuador; the Río Esmeraldas and Río Palenqué, Guayaquil basin (Fig. 4).

Common name. Unknown.

Etymology. Specific epithet in allusion to the Río Esmeraldas. A noun in apposition.

Remarks. Specimens referred to *G. esmeraldas* from the Río Guayaquil basin are uniformly dark brown (without speckles or reticulated pattern).

***Gymnotus henni* n. sp. Albert, Crampton, and Maldonado**

(Fig. 6, Tables 2 and 3)

Holotype: CAS 47290, 308 mm, collected in 1913, at a creek nr. mouth of Río Calima, Río San Juan drainage, north of Buenaventura, Valle de Cauca Department, Colombia (03°53'N, 77°04'W) by A. Henn.

FIGURE 6. *Gymnotus henni* n. sp., holotype, CAS 47290, 308 mm, Colombia, Valle de Cauca, Río Calima, north of Buenaventura (03°53'N, 77°04'W). A, whole body. B, head.

Paratypes: CAS 217162, collected with holotype, 145 mm. FMNH 56793 (2), 254–273 mm, collected with holotype.

Nontypes: 5 lots with 13 specimens, all collected in Colombia: ICNMHN 96 (7), 127–371 mm (all with regenerated caudal appendages), November, 1959, Río Baudó, Chocó Department. ICNMHN 102, (1), 237 mm (damaged caudal appendage), November, 1959, Río Baudó nr. Pavarandó, Chocó Department. ICNMHN 2284 (1), 346 mm, March, 1994, Río Baudó over road to Pie de Pepe, Upper Río San Juan, Pueblo Rico, Risaralda Department (05°07'N, 76°50'W). IMCN 1369 (1), 333 mm, 01 June, 2002, Resguardo Puerto Pizarro, Río San Juan, Litoral del San Juan, Chocó Department. USNM 246793 (3), 131–314 mm, 31 August, 1967, at creek off Río Juradó, Chocó Department (07°06'N, 77°46'W).

Diagnosis. *Gymnotus henni* differs from other species in the *Gymnotus carapo* species-group except *G. tigre* n. sp. (see below) in the following aspects of pigmentation: 1, head with brown ground color and irregularly shaped pale-yellow blotches located on chin, gular area, behind and under eyes, over opercle, and between eyes; 2, pale yellow bands as broad or broader than dark brown bands on anterior half of body; 3, obliquely oriented hyaline and dark stripes at caudal end of anal fin. *Gymnotus henni* is most similar to *G. tigre* n. sp. from the Amazon basin from which it can be distinguished by: 1, fewer pigment band-pairs (BND 13–16 [median 15, n=7] vs. 16–23 [median 21, n=6]); 2, a wider mouth (MW 43.2–49.4% HL [mean 46.6%, n=7] vs. 40.4–43.9% [mean 42.7%, n=6]); 3, more slender body (BD 7.2–9.8% HL [mean 8.3%, n=7] vs. 8.9–10.0% [mean 9.4%, n=6]); 4, shorter head (HL 9.2–10.7% TL [mean 9.9%, n=7] vs. 9.9–13.3% [mean 11.1%, n=6]); 5, longer preanal distance (PA 72.1–112.3% HL [mean 94.4%, n=7] vs. 69.7–81.9% [mean 74.8%, n=6]); 6, presence of dorsal lateral line rami (vs. absent in *G. tigre* n. sp.). *Gymnotus henni* can be further distinguished from other taxa of the *G. carapo* species-group by the unique combination of character states provided in Table 4.

Description. Fig. 6 illustrates head and body shape and pigment patterns. Morphometric data in Table 2 and meristic data in Table 3. Size up to 312 mm. Size at reproductive maturity and sexual dimorphism unknown. Scales present on entire post-cranial portion of body from nape to caudal appendage. Scales above lateral line large, 6 to dorsal midline at midbody. Scales on body elongate, approximately 3–5 times as long as deep at midbody, 1.5–2 times as long as deep at posterior region of caudal filament, their proportional elongation increasing with body size. Gape in mature specimens large, extending to or beyond posterior nares. Mouth position superior, rictus decurved. Eye position below horizontal with front of mouth. Anterior narial pore partially or entirely included within gape. Circumorbital series ovoid. Caudal appendage short, less 0.5 times length of pectoral fin. Single hypaxial electric organ, extending along entire ventral margin of body. Electric organ discharge not known.

Many osteological features not known due to unavailability of specimens for clearing and staining; some character states were determined from radiographs. Dorsoposterior lat-

erosensory ramus of preopercle with two superficial pores. Anterior margin of frontal straight, continuous with margins of adjacent roofing bones. Displaced hemal spines absent. Multiple anal-fin ray branching posterior to rays 10–17. Length anal-fin pterygiophores equal to or longer than hemal spines.

Color in alcohol. Ground color of body pale yellow without countershading. Chromatophores not concentrated along dorsum near midline. Body with 14–16 (median 16) pairs of dark band-pairs extending from nape to tip of tail head. Band-pairs vertical above lateral line and obliquely oriented below lateral line. Band-interband margins irregular and wavy. Bands completely divided forming band-pairs on anterior half of body, and 2–4 H- or X-shaped band-pairs connected by dark cross-bars in pale-yellow interband regions posteriorly. Bands meet on mid-dorsum along entire body length. Interband contrast similar along entire body axis. Two to four dark bands from either side meet on ventral midline, between anus and anal-fin origin.

Head ground-color dark chocolate with irregular pale-yellow blotches on side of chin, behind and under eyes, over opercle, and between eyes. Dark regions on head composed of numerous dark brown chromatophores with even pigment densities. Branchiostegal membranes and ventral surface of head lightly speckled. Pectoral-fin interradial membranes dusky or hyaline. Color of anal-fin membrane graded along body axis, from light brown or hyaline anteriorly to dark brown or black posteriorly, with an irregularly arranged set of hyaline and dark stripes extending obliquely to fin base along posterior most 10% of anal fin.

Distribution. Known from two rivers on the Pacific Slope of Colombia; the Río Calima, Valle de Cauca Department, and the Río Juradó, Chocó Department (Fig. 4).

Common name. Mayupa.

Etymology. Named for Arthur W. Henn, a pioneer in Neotropical ichthyology, who collected the types specimens of this species. An adjective.

Gymnotus paraguensis n. sp. Albert and Crampton

(Fig. 7; Tables 2 and 3)

Holotype: UMMZ 206155 (1), 222 mm, collected 27 June, 1983, at Itapua, Arroyo Tembey, 7.4 km SW of San Rafael, Río Parana drainage, Paraguay (26°35'S, 55°34'W) by R. Bailey, J. Taylor, T. Grimshaw, P. Myers, and L. Creighton.

Paratype: UMMZ 240700, 193 mm, collected with holotype.

Nontypes: 3 lots, 3 specimens. FMNH 108546 (1), 164 mm, 03 November, 1998, at Río Nueva in Brejo do Santo Sofia, Mato Grosso do Sul, Brazil. NRM 42380 (in part) (1 of 2), 240 mm, 28 February, 1988, at Saltos da Guaira, Mulle Ytaipú, Canindeyú, Río Paraná drainage, Paraguay (24°03'44" S, 54°18'W).

Diagnosis. *Gymnotus paraguensis* can be distinguished from other species of the *G. carapo* species-group by: 1, a color pattern composed of regularly arranged, unpaired

(evenly pigmented), dark bands with straight, high contrast margins, with 4–7 inverted Y-shaped, or sometimes X-shaped, or discontinuous dark pigment bands in middle to posterior portions of body; 2, many short lateral line ventral rami (49–55 [median 51, n=3]). *Gymnotus paraguensis* is most similar to *G. choco* from the Pacific slope of Colombia, from which it can be distinguished by characters provided in the diagnosis of *G. choco* (above). *Gymnotus paraguensis* can be further distinguished from other taxa of the *G. carapo* species-group by the unique combination of character states provided in Table 4.

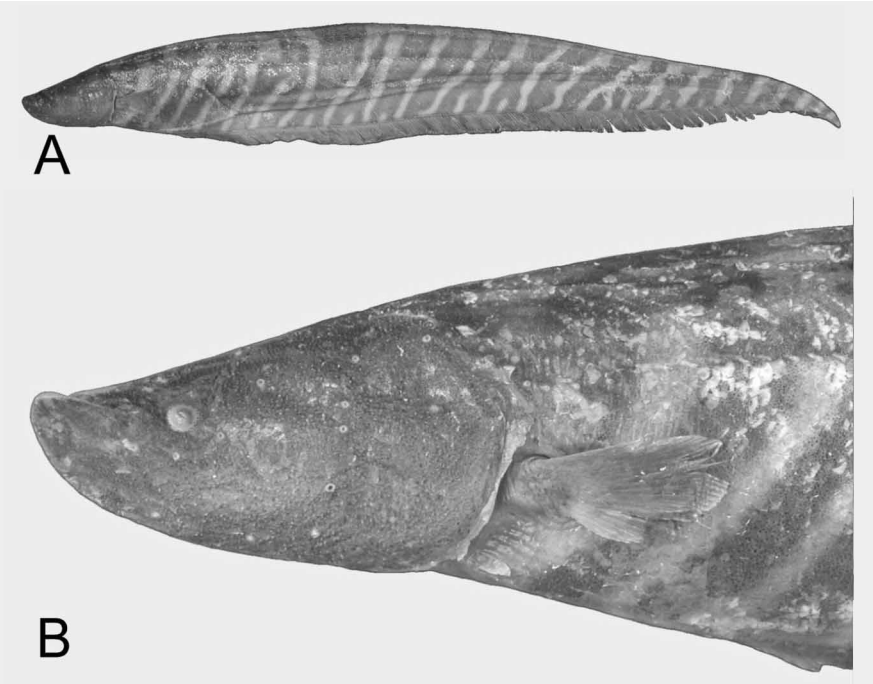

FIGURE 7. *Gymnotus paraguensis* n. sp., holotype, UMMZ 206155, 222 mm, Paraguay, Paraná, Arroyo Tembley, nr. San Rafael (26°35'S, 55°34'W). A, whole body. B, head.

Description. Fig. 7 illustrates head and body shape and pigment patterns. Morphometric data in Table 2 and meristic data in Table 3. Size up to 224 mm. Size at reproductive maturity and sexual dimorphism unknown. Scales present on entire post-cranial portion of body from nape to caudal appendage. Scales above lateral line large, 6 to dorsal midline at midbody. Scales ovoid over most of body, 1.5 times as long as deep. Gape size in mature specimens large, extending to or beyond posterior nares. Mouth position superior, rictus decurved. Eye position below horizontal line from front of mouth. Anterior narial pore partially or entirely included within gape. Circumorbital series ovoid. Caudal appendage short, less 0.5 times length of pectoral fin. Single hypaxial electric organ, extending along entire ventral margin of body. Electric organ discharge not known.

Many osteological features not known due to paucity of specimens for clearing and staining; some character states were determined from radiographs. Dorsoposterior lat-

erosensory ramus of preopercle with two superficial pores. Cranial fontanels closed in juveniles and adults. Anterior margin of frontal straight, continuous with margins of adjacent roofing bones. Frontal shape narrow, width at fourth infraorbital less than that of parietal. Anterior limb of cleithrum long, more than 1.8 times ascending limb. Rib 5 robust along its entire extent, less than 3 times width of rib 6. Hemal spines present. Displaced hemal spines absent. Multiple anal-fin ray branching posterior to rays 10–17. Lateral line dorsal rami absent in adults. Length anal-fin pterygiophores equal to or longer than hemal spines.

Color in alcohol. Ground color of body pale brown without countershading. Chromatophores not concentrated along dorsum near midline. Body with 23–26 (median 24, n=3) dark brown obliquely oriented pigment bands (or band-pairs) extending from tip of tail to nape. Dark bands evenly pigmented along entire body with band margins as dark as band middles. Bands meet on mid-dorsum along entire body length. Interband contrast similar along entire body axis. Three dark bands from either side meet on ventral midline, between anus and anal-fin origin.

Head not banded, its ground color dark brown dorsally grading to lighter brown ventrally, without freckles and with numerous speckles distributed over branchiostegal membranes and ventral surface of head. Pectoral-fin rays brown, interradial membranes hyaline. Anal-fin membrane divided into three parts along body axis: anterior 40% brown, mid 40% black, posterior 20% translucent.

Distribution. Known only from the Río Paraguay basin; in Paraguay from the Río Itapua, and Brazil from the Rio Nueva, Mato Grosso do Sul (Fig. 4).

Common name. Tuvira (Brazil), morenita (Argentina).

Etymology. The specific epithet is named for the Río Paraguay. An adjective.

***Gymnotus tigre* n. sp. Albert and Crampton**
(Fig. 8; Tables 2 and 3)

Holotype: UF 25552, 411 mm, collected 11 November, 1973, in floating macrophytes along north shore of Río Amazonas nr. Leticia, Colombia (04°09'S, 69°57'W) by D. Taphorn.

Paratypes: UF 128412 (1), 332 mm, collected with holotype. ICNMHN 6690 (1), 340 mm, 26 July, 1992, same locality data as holotype by L. Jimenez.

Nontypes: 5 lots with 5 specimens. IAVHP 0615 (1), 179 mm, regenerated caudal appendage, 19 September, 1973, nr. Leticia, Amazonas Department, Rio Amazonas, Colombia (04°09'S, 69°57'W). INPA 6814 (1), 113 mm, 20 October, 1991, at Ilha Terra Grande, Rio Jamanxim, Rio Tapajós drainage, Pará State, Brazil. FMNH 97389 (1), 292 mm, November, 1956, at Río Bobonaza, nr. Canelos, Río Pastaza drainage, Pastaza Department, Peru (01°39'S, 77°46'W). UF 117112 (5), 89–171 mm, acquired from fishermen 04 January 1993, Río Amazonas nr. Iquitos, Loreto Department, Peru (03°46'S,

73°15'W). UF 122821 (1), 331 mm, acquired from fishermen 28 May, 2002, same locality data as UF 117112. NRM 27644 (1), 104 mm, 02 July 1986 at El Estrecho, Río Putumayo, Loreto Department, Peru (02°28'S, 72°42'W).

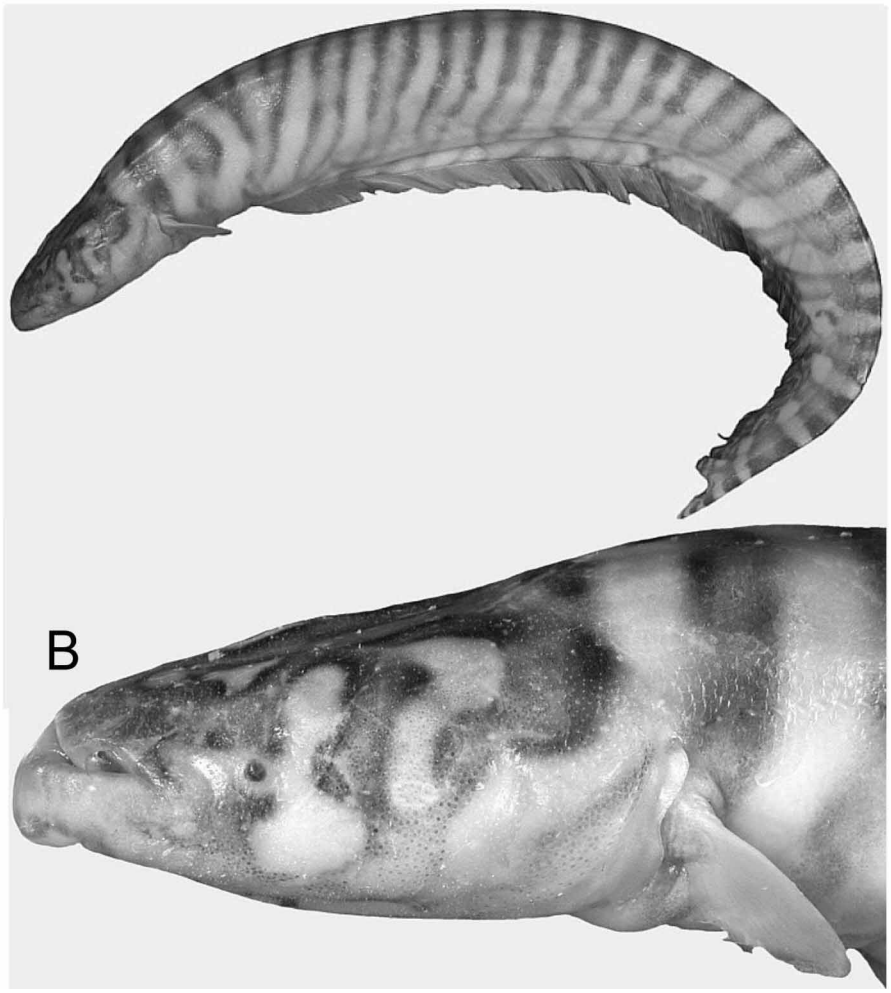

FIGURE 8. *Gymnotus tigre* n. sp., holotype, UF 25552, 411 mm, Colombia, Amazonas, N shore of the Río Amazonas nr. Leticia (04°09'S, 69°57'W). A, whole body. B, head.

Diagnosis. Gymnotus tigre can be distinguished from all congeners except *G. henni* (from the Pacific Slope of Colombia) by the presence of irregular pale-yellow blotches on chin, behind and under eyes, over opercle, and between eyes. *Gymnotus tigre* can be further distinguished from other species of the *G. carapo* species-group (except *G. henni*) by: 1, pale yellow bands on body with straight, high contrast margins, as broad or broader than brown bands anteriorly; 2, obliquely oriented hyaline and dark stripes at caudal end of anal fin. *Gymnotus tigre* can be distinguished from other species of the *G. carapo* species-group except *G. esmeraldas* (from the Pacific Slope of Ecuador) by the presence of more (46–48;

mode 47 vs. 32–44) precaudal vertebrae, and from *G. esmeraldas* by the presence of pigment bands. *Gymnotus tigre* can be further distinguished from other taxa of the *G. carapo* species-group by the unique combination of character states provided in Table 4.

Description. Fig. 8 illustrates head and body shape and pigment patterns. Morphometric data in Table 2 and meristic data in Table 3. Size up to 411 mm. Size at reproductive maturity and sexual dimorphism unknown. All scales highly elongate on their anteroposterior axis; approximately 3–5 times as long as deep at midbody, 1.5–2 times as long as deep at posterior region of caudal filament, their proportional elongation increasing with body size. Gape size in mature specimens small, not to anterior nares. Mouth position superior, rictus decurved. Eye position below horizontal line with front of mouth. Anterior narial pore partially or entirely included within gape. Circumorbital series ovoid. Caudal appendage short, less 0.5 times length of pectoral fin. Single hypaxial electric organ, extending along entire ventral margin of body. Electric organ discharge not known.

Many osteological features not known due to unavailability of specimens for clearing and staining; some character states were determined from radiographs. Dorsoposterior laterosensory ramus of preopercle with two superficial pores. Cranial fontanels closed in juveniles and adults. Anterior margin of frontal straight, continuous with margins of adjacent roofing bones. Frontal shape narrow, width at fourth infraorbital less than that of parietal. Anterior limb of cleithrum long, more than 1.8 times ascending limb. Rib 5 robust along its entire extent, less than 3 times width of rib 6. Displaced hemal spines absent. Multiple anal-fin ray branching posterior to rays 10–17. Lateral line dorsal rami absent in adults. Length anal-fin pterygiophores equal to or longer than hemal spines.

Color in alcohol. Ground color of body pale yellow without countershading. Chromatophores not concentrated along dorsum near midline. Body with 16–23 (mode 23) pairs of dark bands on extending from tip of tail onto head. Band-pairs vertical above lateral line and obliquely oriented below lateral line. Band appearance more regular anteriorly with 4–5 X or Y-shaped pale-yellow interband regions posteriorly. Band-interband margins irregular and wavy. Bands divided along entire body with margins much darker than middles, with greatest pigment densities along the outer edge of band margins. Bands meet on mid-dorsum along entire body length. Interband contrast similar along entire body axis. Three faint dark bands from either side meet on ventral midline, between anus and anal-fin origin.

Head ground-color dark chocolate with irregular pale-yellow blotches on chin, behind and under eyes, over opercle, and between eyes. Dark regions on head composed of numerous dark brown chromatophores with greatest pigment densities along outer edge of pale blotches. Branchiostegal membranes and ventral surface of head lightly speckled. Pectoral-fin interradial membranes dusky or hyaline. Color of anal-fin membrane graded along body axis, from light brown or hyaline anteriorly to dark brown or black posteriorly. Irregularly arranged hyaline and dark stripes extending obliquely to fin base along posterior most 10% of anal fin.

Distribution. Known from the Río Amazon basin, from the Río Pastaza basin in Ecuador to the Tapajós basin in Brazil (Fig. 4).

Common name. Macana tigre (Peru).

Etymology. Specific epithet from the common name used in the local aquarium trade referring to the tiger-like markings. A noun in apposition.

Gymnotus pantherinus Species-Group (Albert 2001)

Gymnotus javari n. sp. Albert, Crampton and Hagedorn
(Fig. 9; Tables 2 and 3)

Holotype: UMMZ 224599, 197 mm, collected 15 May, 1993 at Quebrada Caraná nr. Buen Sucesso, Río Yavari (Rio Javarí), Loreto Department, Peru (04°22'S, 70°31'W) by J. Albert and T. DiBenedetto.

FIGURE 9. *Gymnotus javari* n. sp., holotype, UMMZ 224599, 197 mm, Peru, Loreto, Buen Sucesso, Quebrada Caraná, Río Yavari (Rio Javarí) (04°22'S, 70°31'W). A, whole body. B, head.

Paratypes: UMMZ 224596 (10), 45–175 mm, collected with holotype. UMMZ 240971, 162 mm, collected with holotype.

Nontypes: 11 lots with 40 specimens. IIAP uncat. (1), 201 mm, no date, nr. Iquitos Loreto Department, Peru (03°46'S, 73°15'W). MCZ 60005 (8), 70-208 mm, 19 September 1865, at Tabatinga, Rio Solimões, Amazonas State, Brazil (04°16'S, 69°56'W). MUSM

14480b (1), 85 mm, October 1993, at Río Aguarico, Río Napo drainage, Napo State, Ecuador (01°00'S, 75°12'W). MUSM 14481 (8), 72–124 mm, no date, same locality data as MUSM 14480b. MUSM 3234 (2), 51–102 mm, 16 February, 1992, at Jenaro Herrera, Río Ucayali, Loreto Department, Peru (05°03'S, 73°50'W). NRM 13521 (1), 93 mm, 12 July 1981, nr. Pebas in floating meadows, Río Ampiyacu, Loreto Department, Peru (03°20'S, 71°49'W). NRM 27702 (2), 47–51 mm, 31 July, 1984, at stream nr. Colonia Angamos, Río Yavari, Loreto Department, Peru (05°11'S, 72°53'W). UF 122824 (1), 141 mm, 21–28 May, 2002, nr. Iquitos, Loreto Department, Peru (03°46'S, 73°15'W). UMMZ 224601 (1), 132 mm, 4 May, 1993, at Río Tahwayo nr. Santa Ana, Loreto Department, Peru (04°5'S, 73°0'W). UMMZ 224607 (5, in part), 29–106 mm, 4 May, 1993, at Bora Indian village nr. Amazon camp, Río Momon, nr. Iquitos, Loreto Department, Peru (03°46'S, 73°15'W).

Diagnosis. Gymnotus javari can be distinguished from other species of the *G. pantherinus* species-group by a unique color pattern composed of narrow pale bands (about 1/4 width of dark bands) on anterior half of body, approximately equally narrow dorsally and ventrally, and 5–8 partially divided, often H-shaped dark bands on posterior half of body. *Gymnotus javari* can be further distinguished from other species of the *G. pantherinus* species-group by the following unique combination of characters: head depth moderate (HD 55.6–64.7% HL [mean 59.9, n=12] vs. 53–55% or 66–75%); and large scales, with 7–9 (mode 8, n=11) scale rows above lateral line to dorsal midline at midbody.

Gymnotus javari is most similar to *G. coatesi* from which it can be distinguished by: 1, a unique color pattern (see above) (vs. pale bands as broad as dark bands on anterior half of body, pale bands broader dorsally, and dark bands undivided on posterior half of body); 2, a more laterally compressed adult body (BW 61–77% BD [mean 69%, n=12] vs. 76–86% [mean 83%, n=4]); 3, a wider head (HW 56–66% HL [mean 63%] vs. 50–56% [mean 53%]); 4, more scales over the anal-fin pterygiophores (APS 9–10 rows [mode 9, n=5] vs. 6–7 rows [mode 7, n=3]); and 5, fewer ventral lateral line rami (VLR 10–15 [mode 13, n=5] vs. 19–23 [mode 22, n=3]).

Gymnotus javari is also similar to *G. jonasi* from the Western Amazon and Rio Madeira basin, from which it can be distinguished by: 1, a unique color pattern (see above); 2, a larger maximum body size (201 mm vs. 150 mm); 3, a wider mouth (MW 32–42% HL [mean 37%, n=12] vs. 31–33% [mean 33%, n=4]; 4, a shorter pectoral fin (P1R 40–48% [mean 42, n=12] vs. 52–55% [mean 54%, n=4]); 5, more anal-fin rays (AFR 180–240 [mean 200, n=13] vs. 135–165 [mean 152, n=6]); 6, more scales above the anal-fin pterygiophores (AFP 9–10 [mode 9, n=2] vs. 5–6 [mode 5, n=6]); 7, more precaudal vertebrae (PCV 40–44 [mode 42, n=14] vs. 36–39 [mode 37, n=9]); 8, more pored scales to the first ventral lateral line ramus (PLR 52–67 [mean 59, n=11] vs. 31–40 [mean 36, n=6]); 9, more pored lateral line scales (PLL 88–108 [mean 98, n=5] vs. 73–76 [mean 75, n=5]); 10, fewer ventral lateral line rami (VLR 10–15 [mean 13, n=5] vs. 16–25 [mean 20, n=5]).

Gymnotus javari is also similar to *G. stenoleucus* from the Venezuelan Amazon, from which it can be distinguished by: 1, a unique color pattern (see above); 2, a larger maxi-

mum body size (201 mm [n=21] vs. 142 mm [n=9]); 3, fewer pale lateral bands (BND 13–21 [mode 15, n=11] vs. 18–24 [mode 22, n=9]); 4, more pectoral-fin rays (P1R 12–14 [mode 13, n=8] vs. 13–15 [mode 14, n=11]); 5, more scales over anal-fin pterygiophores (AFP 9–10 vs. 7–8 rows).

Description. Fig. 9 illustrates head and body shape and pigment patterns. Morphometric data in Table 2 and meristic data in Table 3. Size up to 201 mm. Size at reproductive maturity and sexual dimorphism unknown. Circular scales present on entire post-cranial portion of body from nape to tip of caudal appendage. Gape size in mature specimens large, extending to or beyond posterior nares. Mouth position superior, rictus decurved. Eye position lateral, lower margin of eye dorsal to horizontal with rictus. Circumorbital series ovoid.

Mesethmoid anterior margin concave with small paired anterolateral processes. Mesethmoid neck broad, more than width of ventral ethmoid. Anterior narial pore partially or entirely included within gape. Maxilla-palatine articulation near anterior tip of mesopterygoid. Maxilla orientation vertical. Maxilla rod- or paddle-shaped with straight ventral margin. Maxilla length equal to width of 7–9 dentary teeth. Maxilla broad distally, paddle-shaped. Premaxilla with 11–16 teeth along outer margin. Median margin of premaxilla curved. Premaxilla with two tooth rows, or one row with an inner patch anteriorly. Dentary with one or two tooth rows, including 5 or more needle-shaped teeth. Dentary outer tooth row with 16 or more teeth. Dentary with short inner row or patch of teeth anteriorly. Dorso- and ventro-posterior dentary processes abut, ventro- shorter than dorsoposterior process. Dentary dorsoposterior process narrow distally. Dentary ventral margin with a narrow lamella, less than posterior process. Dentary with pronounced ventroposteriorly oriented hook at mental symphysis. Dorsal margin of opercle straight or slightly convex. Texture of dorsal opercle process deeply pitted and cancellous. Dorsal opercular crest absent or small. Posterior margin of opercle smooth, entire, without spines or processes. Ventral ridge field of opercle broad. Dorsal ridge field of opercle short, less half opercular width. Dorsoposterior laterosensory ramus of preopercle with single superficial pore. Preopercle with anteroventral notch. Margin of preopercular medial shelf entire. Median shelf of preopercle small, less than half width of symplectic. Ascending process of mesopterygoid robust, long, its base shorter than its length. Mesopterygoid ascending process straight. Tip of mesopterygoid ascending process simple. Metapterygoid small, its superior portion less ossified than its inferior portion. Dorsal margin of interopercle with broad ascending process. Dorsal margin of subopercle concave. Posterior margin of retroarticular square. Retroarticular with an arched lamella posteriorly, forming a small canal. Anguloarticular process short, to ventral margin poster. Mandible long, extended, its length more than twice its depth. Hyomandibular trigeminal canals (supraorbital, infraorbitral), connected. Posterior lateral line fenestra contacting dorsoposterior margin of hyomandibula. Cranial fontanels closed in juveniles and adults. Anterior margin of frontal straight, continuous with margins of adjacent roofing bones. Frontal postorbital process narrow,

less than two times width of supraorbital canal. Frontal broad, its width at fourth infraorbital subequal to that of parietal. Lateral ethmoid absent. Parasphenoid posterior processes narrow. Parasphenoid lateral process broad, triangular. Parietal rectangular, its length less than width. Pterosphenoid anteroventral portion robust, extending ventral to lateral margin of parasphenoid. Prootic foramen Vp combined with V2–3+VII. Adductor mandibula undivided at insertion. Adductor mandibula intermusculars absent. All basibranchials unossified. Gill rakers not contacting gill bar. Basibranchial 5 unossified. Pectoral fin of moderate size, with 14–16 rays. Pectoral fin, medial radial small. Mesocoracoid elongate, its length more than 4 times width. Postcleithrum thin, discoid or sickle-shaped. Cleithrum very narrow, ventral margin straight. Anterior limb of cleithrum long, more than 1.8 times ascending limb. Cleithrum anterior notch absent. Cleithrum without large facet for insertion of muscle from supracleithrum. Rib 5 broad, with a large medial triangular shelf. Hemal spines present. Displaced hemal spines absent. Multiple anal-fin ray branching posterior to rays 18 or more. Lateral line dorsal rami absent in adults. Length anal-fin pterygiophores equal to or longer than hemal spines. Caudal appendage short, less 0.5 times length of pectoral fin. Single hypaxial electric organ, extending along entire ventral margin of body. Electric organ discharge with four phases away from baseline in adults.

Color in life and in alcohol. Ground color of body dark brown. Body with 13 to 21 (median 15, n=11) alternating pale-yellow (or cream) and dark chocolate brown pigment bands, vertically oriented on posterior half of body and slightly oblique on anterior half of body. Pale bands generally regular in form, width, and arrangement, although variable in number among individuals. Band-interband margins regular and straight. 5–8 dark bands partially or completely divided (H-shaped) on posterior half of body. Dark bands about four times as broad as pale bands on anterior half of body. Pale bands never branched, and extending to dorsal midline along entire extent of body. One or rarely two pale bands meet at ventral midline between anus and anal-fin origin. One or two pale bands posterior to last anal-fin ray.

Head not banded or blotched, its ground color dark brown dorsally grading to lighter brown ventrally, with numerous freckles and speckles distributed over entire surface. Pectoral-fin rays brown or gray, interradial membranes hyaline. Anal-fin membrane hyaline, anal-fin rays brown.

Ecology. The types of *G. javari* were collected from the lower reaches of meandering upland (non-floodplain) streams, in undercut banks and submerged vegetation. Other specimens pertaining to *G. javari* were collected from rootmats of whitewater floodplain floating meadows, near the margins of rivers channels and lakes. Specimens from the Río Aguarico, Ecuador, were caught in small streams with clay sides, silt or vegetation bottom, pH 5.5–6.0, conductivity 15 microsemens/cm, air temp, 34.8 °C, water temp 24.6°C, surface flow 4.6 cm/s, secchi depth 120 cm, stream depth, 1–4 m, width 4–8 m (M. Hagedorn pers. obs.).

Distribution. Known from the Western Amazon, from the Río Amazonas, the lower portions of the Napo, Javarí, and Ucayali basins (Fig. 10).

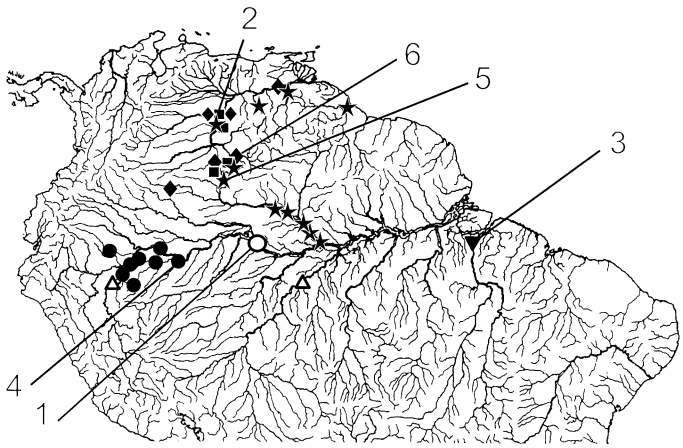

FIGURE 10. Part of South America showing collection records of *G. javari* n. sp. and allied species from the Amazon. *G. jonasi, G. melanopleura, G. onca, G. coatesi (*○, 1 = type locality *G. jonasi, G. melanopleura, G. onca*), *G. cataniapo* (■, 2 = type locality), *G. coatesi* (▼, 3 = type locality), *G. javari* n. sp. (●, 4 = type locality), *G. jonasi* (△), *G. pedanopterus* (★, 5 = type locality), *G. stenoleucus* (◆, 6 = type locality). Some symbols represent more than one locality or lot of specimens. Base map by M. Weitzman. Note *G. javari* n. sp. is restricted to Western Amazon.

Common name. Macana (Peru), sarapó (Brazil).

Etymology. Named for the Rio Javarí. A noun in apposition.

Gymnotus panamensis n. sp. Albert and Crampton

(Fig. 11; Tables 2 and 3)

Holotype: CAS 72209, 236 mm, collected 25 February, 1923 in a small creek into the Río Cricamola, nr. Konkitu, Bocas del Toro Province, Panama (08°59'N, 81°55'W) by E. Behre and J. Chambers.

Paratype: CAS 217109, 221 mm, collected with holotype.

Diagnosis: *Gymnotus panamensis* can be distinguished from all congeners by a unique color pattern in which the dark pigment bands on the anterior 2/3 of body are mottled and blotched with numerous, small (1–2 scales wide), irregularly-formed cream-colored patches, such that the pattern of alternating pale and dark bands is highly obscured. *Gymnotus panamensis* further differs from other members of the *G. pantherinus* species-group except *G. anguillaris* by: 1, restriction of pigment bands to ventral portion of body (rarely extending above lateral line) on anterior half of body; 2, a broader head (mean HW 70% HL vs. mean 53–65%); and 3, a wider mouth (mean MW 46% HL vs. mean 32–43%).

Gymnotus panamensis is most similar to *G. anguillaris* from which it can be distinguished by: 1, more narrowly set eyes (IO 37–41% HL [mean 39%, n=2] vs. 43–56% [mean 46%, n=8]); 2, a deeper head (HD 68–71% HL [mean 69%,, n=2] vs. 61–68% [mean 64%, n=8]); 3, shorter pre-anal distance (PA 83–89% HL [mean 86%, n=2] vs. 84–122% [mean 99%, n=8]; 4, fewer pored posterior lateral line scales (88–92 [mean 90, n=2] vs. 102–130 [mean 124, n=8]).

Description. Figure 11 illustrates head and body shape and pigment patterns. Morphometric data in Table 2 and meristic data in Table 3. Size up to 236 mm. Size at reproductive maturity and sexual dimorphism unknown. Circular scales present on entire postcranial portion of body from nape to caudal appendage. Gape size in mature specimens large, extending to or beyond posterior nares. Mouth position superior, rictus decurved. Eye position lateral, lower margin of eye dorsal to horizontal with rictus. Anterior narial pore partially or entirely included within gape. Circumorbital series ovoid. Caudal appendage long, more than 0.5 time pectoral-fin length in undamaged and unregenerated specimens. Single hypaxial electric organ, extending along entire ventral margin of body. Electric organ discharge unknown.

FIGURE 11. *Gymnotus panamensis* n. sp., holotype, CAS 72209, 236 mm, Panama, Bocas del Toro, Río Cricamola nr. Konkitu (08°59'N, 81°55'W). A, whole body. B, head.

Many osteological features not known due to unavailability of specimens for clearing and staining; some character states were determined from radiographs. Dorsoposterior laterosensory ramus of preopercle with single superficial pore. Cranial fontanels closed in juveniles and adults. Anterior margin of frontal straight, continuous with margins of adja-

cent roofing bones. Frontal postorbital process narrow, less than two times width of supraorbital canal. Frontal broad, its width at fourth infraorbital subequal to that of parietal. Pectoral fin of moderate size, with 14–16 rays. Postcleithrum thin, discoid or sickle-shaped. Rib 5 broad, with a large medial triangular shelf. Hemal spines present. Displaced hemal spines absent. Multiple anal-fin ray branching posterior to rays 10–17. Lateral line dorsal rami absent in adults. Length anal-fin pterygiophores equal to or longer than hemal spines.

Color in alcohol. Ground color of body pale brown, with 23 or 24 (n=2) pale-yellow bands on lateral body surface extending from tip of tail to pectoral-fin base. Band appearance obscured by wavy margins and numerous pale patches within dark bands, body surface with a mottled or blotched appearance. Anterior 80% of mid-dorsum without banding. Three bands from either side meet on ventral midline, between anus and anal-fin origin. Two of three bands posterior to last anal-fin ray.

Head not banded, its ground color light brown dorsally grading to pale yellow ventrally, with blotches on cheeks and numerous speckles distributed over branchiostegal membranes and ventral surface of head. Pectoral-fin rays brown or gray, interradial membranes hyaline. Anal-fin rays light brown, anal-fin membrane hyaline.

Distribution. Known only from the type locality in the Río Cricamola on the Atlantic slope of western Panama (Fig. 12). Collected by E. Bermingham and A. Martin in the Río Cricamola in 1993 and 2000 (E.B. pers. comm., specimens not preserved).

FIGURE 12. Part of South America showing collection records of *G. panamensis* n. sp. and allied species. *G. anguillaris* (●, 1 = type locality), *G. cf. anguillaris* (■); *G.* n. sp. "pnt" (▲, 2 = locality of MZUSP 67874), *G. panamensis* n. sp. (▼). Some symbols represent more than one locality or lot of specimens. Base map by M. Weitzman. Note absence of *G. anguillaris* from central Amazon.

Common name. Unknown

Etymology. The specific epithet is named for the country of Panama. An adjective.

Discussion

Species and populations. The new taxa described in this report are advanced as hypotheses of species or populations, to be tested with additional morphological, molecular sequence, and electric organ discharge data. Here we regard species as taxa representing separate evolutionary lineages, and populations as taxa representing geographic variants of a single evolutionary lineage (Ricklefs 1989; Moritz 1994; Da Silva & Patton 1998). Maintaining distinct phenotypes in sympatry is regarded as direct evidence that populations represent different species. Several morphological traits found useful in diagnosing sympatric species also provided information on the amount and quality of interspecific phenotypic differences observed in allopatry. In *Gymnotus* these are differences of four or more precaudal vertebrae, 3–5% head length (as percentage total length), and the appearance of dark bands (continuous vs. broken) above the lateral line at midbody. Discontinuities in the geographic variation of these meristic, morphometric, and color traits distinguish *G. carapo* from several allopatric species (i.e., *G. bahianus*, *G. diamantinensis*, *G. inaequilabiatus*, and *G. sylvius*). None of these traits differ among the six allopatric populations of *G. carapo s.s.* recognized here. The six allopatric populations of *G. carapo s.s.* recognized here do not possess diagnostic characters, but they do differ in the mean values of several morphological traits exhibiting overlapping values (Tables 2 and 3).

Locality sampling density of *G. carapo s.s.* across the landscape to date is too poor to apply the criterion of continuity in morphological variation to distinguish species from subspecies (Fig. 2). In comparison to previous studies of gymnotiform fishes the materials examined for this study are relatively extensive, including 781 lots collected over the whole of tropical South America over a period of 137 years (1865 to 2002). Nevertheless, the geographic sampling density remains too sparse to assess the nature of phenotypic intergrades between allopatric populations of *G. carapo s.s.* These collections are concentrated near or on the main axis of the Amazon river and some of its major tributaries, the Western Amazon, the llanos of Venezuela, and the Atlantic coast of the Guyanas. There are large areas of little or no information in the interior basins of the Guyanas and Brazilian shields, the Rio Negro, Rio Juruá and Rio Purus basins. This distribution apparently reflects a bias in the distribution of gymnotiform collections. A search using the NEODAT online database for several widespread nominal gymnotiform species in South America returned 324 georeferenced records for "*Gymnotus carapo*", 332 records for "*Sternopygus macrurus*", 75 records for "*Apteronotus albifrons*", and 82 records for "*Brachyhypopomus brevirostris*" or "*Hypopomus brevirostris*". With very few exceptions the distributions of these nominal species are qualitatively similar to that of *G. carapo*.

Trans-Andean distributions. The biogeographic distributions of the *G. carapo* and *G. pantherinus* species-groups suggest relatively ancient origins for these taxa (Figs. 2, 4, 12). The *G. carapo* species-group is widespread and diverse on both slopes of the Andes; in all cis-Andean watersheds of Neotropical South America, except several isolated coastal basins in the extreme northeast of Brazil (e.g., Salgado, Piranhas), and several trans-Andean drainages on the Pacific slope of Ecuador and Colombia (e.g., Guayaquil, Esmeraldas, San Juan, Baudó) and the Caribbean (Atrato). Many species within the *G. carapo* species-group are sympatric; *G. carapo*, *G. arapaima*, *G. mamiraua*, and *G. tigre* exhibit zones of sympatry in the Amazon basin, *G. choco* and *G. henni* in the Chocó region of Colombia, and *G. inaequilabiatus*, *G. sylvius* and *G. paraguensis in* the Paraguay basin. The *G. pantherinus* species-group is also widespread and diverse in cis-Andean watersheds, and is also present in Panama. These observations suggest that the origins and early divergence of these two species-groups minimally predate the most recent Andean orogeny, c. 8–12 mya (Lundberg 1998).

Summary

The geographically widespread taxon *G. carapo s.s.* Linnaeus is redescribed and six allopatric populations are recognized. *Gymnotus carapo s.s.* differs from all congeners except *G. arapaima* in the following unique combination of characters: clear patch at caudal end of anal fin without oblique hyaline and dark stripes; two laterosensory canal pores in dorso-posterior corner of preopercle; 16–27 [mean 22] dark pigment band-pairs with irregular margins often broken into spots above lateral line on anterior half of body; no pale blotches on head; circular scales, about as long as wide above lateral line at midbody; deep body, its depth 9.7–12.1% total length (mean 10.2%); long head, its length 10.2–13.7% total length (mean 12.3%); 33–37 (mode 33) precaudal vertebrae; 6–27 ventral lateral line rami (mean 15); and no dorsal lateral line rami. *Gymnotus carapo s.s.* from the Western Amazon can be distinguished from sympatric *G. arapaima* by: 1, fewer pored lateral line scales to the first ventral lateral line ramus (44–54 [mode 48] vs. 53–64 [mode 57]); 2, fewer scales over the anal fin pterygiophores (8–10 [mode 9] vs. 10–13 [mode 12]); 3, smaller size (maximum total length 418 mm vs. 550 mm). Six allopatric populations of *G. carapo s.s.* are recognized from differences in the mean values of morphometric and meristic traits: 1, Eastern Amazon, including the lower-most Negro, and the Trombetas, Tapajos, and Tocantins basins; 2, Parnaíba and Itapicuru basins in the Brazilian state of Piauí; 3, Branco basin in the Brazilian sate of Roraima; 4; Guianas Shield, Orinoco basin and Island of Trinidad, 5, Madeira basin of Brazil, Bolivia and Peru; and 6, Western Amazon, including Tefé, Japurá and Javarí basins of Brazil, Napo basin of Ecuador, and Nanay, Pastaza and Ucayali basins of Peru.

Seven new species of *Gymnotus* are described from cis- and trans-Andean basins in South America on the basis of unique combinations of characters. 1. *Gymnotus choco* n.

sp., from the Baudó and Atrato basins on the Pacific and Caribbean slopes of Colombia, respectively, differs from congeners by: posterior portion of anal fin without stripes and with clear patch; two canal pores in dorso-posterior preopercle; 18–22 (median 21) thin pale bands with wavy margins restricted to area below lateral line on anterior 2/3 body; 1–3 dark bands divided ventrally on posterior portion of body; circular scales; deep body, its depth 8.8–11.3% total length (mean 10.8%); 32–35 (mode 35) precaudal vertebrae; 4–13 (median 8) ventral lateral line rami; and no dorsal lateral line rami. 2. *Gymnotus esmeraldas* n. sp., from Esmeraldas and Guayaquil basins on the Pacific Slope of Ecuador, differs from congeners by: anal fin striped posteriorly and with clear patch at caudal end; two canal pores in dorso-posterior preopercle; no bands on majority of body surface and no pale blotches on head; elongate scales, 2–3 times as long as deep above lateral line at midbody; slender body, depth 8.2–9.8% total length (mean 8.8%); 41–46 (mode 44) precaudal vertebrae; 14–18 (median 15) ventral lateral line rami; and no dorsal lateral line rami. 3. *Gymnotus henni* n. sp., from the Calima and Juradó basins on the Pacific Slope of Colombia, differs from congeners by: anal fin striped posteriorly and with clear patch at caudal end; two canal pores in dorso-posterior preopercle; irregularly shaped pale-yellow blotches on chin and gular regions, behind and under eyes, over opercle, and between eyes; 13–16 (median 15) dark band-pairs with pale yellow interbands are as broad or broader than dark bands on anterior half of body; elongate scales, 3–5 times as long as deep above lateral line at midbody; slender body, its depth 7.2–9.8% total length (mean 8.8%); 43–44 (mode 44) precaudal vertebrae; 16–22 (median 18) ventral lateral line rami; and no dorsal lateral line rami. 4. *Gymnotus paraguensis* n. sp., from the Paraguay basin, differs from congeners by: posterior portion of anal fin without stripes and with clear patch; two canal pores in dorso-posterior corner of preopercle; regularly arranged, 23–26 (median 24) unpaired dark bands with straight, high contrast margins; circular scales; deep body, its depth 9.8–10.3% total length (mean 10.1%); many (49–55, median 51), short ventral lateral line rami; and no dorsal lateral line rami. 5. *Gymnotus tigre* n. sp., from the Amazon basin of Ecuador, Peru and Brazil, differs from congeners by: anal fin striped posteriorly and with clear patch at caudal end; two canal pores in dorso-posterior preopercle; irregularly shaped pale-yellow blotches on chin and gular regions, behind and under eyes, over opercle, and between eyes; 16–23 (median 21) dark band-pairs with pale yellow interbands as broad or broader than dark bands on anterior half of body; elongate scales, 3–5 times as long as deep above lateral line at midbody; 46–48 (mode 47) precaudal vertebrae; 29–55 (median 51) ventral lateral line rami; and no dorsal lateral line rami. 6. *Gymnotus javari* n. sp., from the Amazonas, Napo, Javarí, and Ucayali basins, differs from congeners by: brown anal fin without stripes or clear patch posteriorly; one canal pore in dorso-posterior preopercle; 13–21 (mode 15) thin pale bands less than one-fourth width of dark bands; 5–8 dark H-shaped bands on the posterior part of the body; head depth 60–65% its length; large circular scales, 7–9 (mode 8) rows to dorsal midline at midbody; slender body, its depth 6.7–9.1% total length (mean 8.9%); 40–44 (mode 42) precaudal vertebrae; 1–15

(median 13) ventral lateral line rami; and no dorsal lateral line rami. 7. *Gymnotus panamensis* n. sp., from Atlantic slope of western Panama, differs from congeners by: anal fin mottled, without stripes or clear patch posteriorly; one canal pore in dorso-posterior preopercle; pale bands restricted to area below lateral line on anterior half body; dark interbands heavily mottled, obscuring banding pattern; scales large and circular, with 7–9 (mode 8) rows to dorsal midline at midbody; slender body, its depth 6.6–7.8% total length (mean 7.2%); 36 precaudal vertebrae; 11–15 (median 13) ventral lateral line rami; and no dorsal lateral line rami.

The existence of so many previously unrecognized and undescribed taxa is due in part to the cryptic nature of many *Gymnotus* species, and in part to a poor understanding of intraspecific variation and interspecific character-state diversity in the group.

Acknowledgements

We acknowledge the following for access to specimens and information; B. Brown, X. Freilich, S. Schaefer (AMNH); J. Lundberg, M. Sabaj (ANSP); J. Armbruster (AUM); O. Crimmen, D. Siebert (BMNH); D. Catania, W. Eschmeyer (CAS); P. Stoddard (FIU); R. Robins, G. Sheehy, A. Varandas (FLMNH); C. Buti (FML); B. Chernoff, M. Rogers, K. Swagel (FMNH); R. Royero-Léon (FUDECI); J. Maldonado, I. Mojica (ICNMHN); F. Kirschbaum (IGB); H. Sanchez (IIAP); M. Retzer (INHS); J. Alves-Gomes, E. Ferreira, L. Rapp Y Daniel (INPA); A. Machado, F. Provenzano, R. Royero (MBUCV); R. Reis (MCP); K. Hartel (MCZ); M. Azpelicueta (MLP); P. Buckup, R. Campos-da-Paz (MNRJ); H. Britski, M. de Pinna, J. Lima De Figueiredo, O. Oyakawa, (MZUSP); E. Ahlander, S. Kullander (NRM); R. Winterbottom (ROM); W. Bussing (UCR); W. Fink, D. Nelson (UMMZ); H. Ortega (MUSM); M. Hagedorn, S. Jewett, L. Parenti, R. Vari (USNM); F. Fernandes-Matioli (USP); and I. Isbrücker (ZMA). We appreciate additional exchanges of data and ideas with R. Barriga, E. Bermingham, T. Berra, T. DiBenedetto, M. Goulding, C. Hopkins, K. Lester, N. Lovejoy, R. Miller, L. Page, D. Taphorn, D. Thorsen, M. Triques, and L. Verdi. Special thanks to K. Aviles and J. Hill for laboratory assistance. We acknowledge the NEODAT project (NSF DEB 90-24797) for collection information, and the Alexandria Digital Library Gazetteer for georeferencing data. Aspects of this research were supported by grants from Fisheries Society of the British Isles, Brazilian National Council for Scientific and Technological Development (CNPq), U.S. National Science Foundation (NSF-DEB 0084704, 0102593, 0138633), University of Florida Research Opportunity Fund, and Florida Museum of Natural History.

References

Albert, J.S. (2001) Species diversity and phylogenetic systematics of American knifefishes (Gymnotiformes, Teleostei). *Miscellaneous Publications Museum Zoology, University of Michigan*, 190, 1–127.

Albert, J.S. & Crampton, W.G.R. (2001) Five new species of *Gymnotus* (Gymnotiformes, Teleostei) from an Upper Amazonian floodplain, with descriptions of electric organ discharges and ecology. *Ichthyological Exploration Freshwaters*, 12, 241–266.

Albert, J.S., Fernandes-Matioli, F.M. & de Almeida-Toledo, L.F. (1999) A new species of *Gymnotus* (Gymnotiformes, Teleostei) from southeastern Brazil: Towards the deconstruction of *Gymnotus carapo*. *Copeia*, 1999, 410–421.

Albert, J.S. & Fink, W.L. (1996) *Sternopygus xingu*, a new species of electric fish (Gymnotoidei, Teleostei), from South America, with comments on the phylogenetic position of *Sternopygus*. *Copeia*, 1996, 85–102.

Albert, J.S. & Miller, R.R. (1995) *Gymnotus maculosus*: a new species of electric fish from Middle America (Teleostei: Gymnotoidei), with a key to the species of Gymnotus. *Proceedings Biological Society Washington*, 108, 662–678.

Alves-Gomes, J.A. (1997) Informações preliminares sobre a bio-ecologia de peixes elétricos (Ordem Gymnotiformes) em Roraima. *In*: Barbosa, R.I., Ferreira, E.F., & Castellón, E.G. (Ed) *Homen, Ambiente e Ecologia no Estado de Roraima*, INPA, Manaus, pp. 509–553.

Artedi, P. (1738) *Ichthyologia sive Opera Omnia de Piscibus*.

Bloch, M.E. (1786) *Naturgeschichte der Auslandischen Fische*. Berlin. v. 3: i-xii + 1–146, Pls. 181–216.

Campos-da-Paz, R. (2000) Taxonomic status of *Rhamphichthys cingulatus* Brind and a more precise assignment of the type-locality of *Gymnotus coatesi* LaMonte (Ostariophysi : Gymnotiformes). *Copeia*, 2000, 1114–1117.

Campos-da-Paz, R. (2002) *Gymnotus diamantinensis*, a new species of electric knifefish from upper rio Arinos basin, Brazil (Ostariophysi: Gymnotidae). *Ichthyological Exploration Freshwaters*, 13, 185–192.

Campos-da-Paz, R. & Costa, W.J.E.M. (1996) *Gymnotus bahianus* n. sp., a new gymnotid fish from eastern Brazil (Teleostei: Ostariophysi: Gymnotiforms), with evidence for the monophyly of the genus. *Copeia*, 1996, 937–944.

Crampton, W.G.R. (1996a) Gymnotiform fish: an important component of Amazonian flood plain fish communities. *Journal of Fish Biology*, 48, 298–301.

Crampton, W.G.R. (1996b) *The Electric Fish of the Upper Amazon: Ecology and Signal Diversity*, unpublished Doctoral thesis. Department of Zoology. The University of Oxford, Oxford, pp. 1–223.

Crampton, W.G.R. (1998) Electric signal design and habitat preferences in a species rich assemblage of gymnotiform fishes from the Upper Amazon Basin. *Anais da Academia Brasileira de Ciências*, 70, 805–847.

Da Silva, M.N.F. & Patton, J.L. (1998) Molecular phylogeography and the evolution and conservation of Amazonian mammals. *Molecular Ecology*, 7, 475–486.

Ellis, M.M. (1913) The gymnotid eels of tropical America. *Memoirs of the Carnegie Museum*, 6, 109–195.

Fernandes-Matioli, F.M.C. & Almeida-Toledo, L.F. (2001) A molecular phylogenetic analysis in *Gymnotus* species (Pisces: Gymnotiformes) with inferences on chromosome evolution. *Caryologia*, 54, 23–30.

Fernandes-Matioli, F.M.C., Almeida-Toledo, L.F. & Toledo, S.A. (1998a) Natural triploidy in the Neotropical species *Gymnotus carapo* (Pisces : Gymnotiformes). *Caryologia*, 51, 319–322.

Fernandes-Matioli, F.M.C., Marchetto, M.C.N., Almeida-Toledo, L.F. & Toledo, S.A. (1998b) High

intraspecific karyological conservation in four species of *Gymnotus* (Pisces : Gymnotiformes) from southeastern Brazilian basins. *Caryologia*, 51, 221–234.

Fernandes-Matioli, F.M.C., Matioli, S.R. & Almeida-Toledo, L.F. (2000) Species diversity and geographic distribution of *Gymnotus* (Pisces: Gymnotiformes) by nuclear (GGAC)(n) microsatellite analysis. *Genetics and Molecular Biology*, 23(4), 803–807.

Fernholm, B. & Wheeler, A. (1983) Linnaean fish specimens in the Swedish Museum of Natural History, Stockholm. *Zoological Journal Linnean Society*, 78, 199–286.

Hoedeman, J.J. (1962) Notes on the ichthyology of Surinam and other Guianas. 11. New gymnotiform fishes from Surinam and French Guiana, with additional records and a key to the groups and species from Guiana. *Bulletin Aquatic Biology Amsterdam*, 3, 97–107.

Holthuis, L.B. (1959) The Crustacea Decapoda of Suriname (Dutch Guiana). Leiden.

Hoogmoed, M.S. (1973) *Notes on the Herpetofauna of Surinam IV - The Lizards and Amphisbaenians of Surinam*. Biogeographica, The Hague, Dr. W. Junk, 419 pp.

Ihering, R. von. (1914) Duas especies novas de Peixes da Fam. Cichlidae. *Revista Museu São Paulo* 9, 333–337.

Kirschbaum, F. & Wieczorek, L. (2002) Entdeckung einer neuen Fortpflanzungs-strategie bei südamerikainischen Messerfischen (Teleostei: Gymnotiformes: Gymnotidae): Maulbrüten bei *Gymnotus carapo*. *Verhalten der Aquarienfische*, 2, 99–107.

LaMonte, F.R. (1935) Two new species of *Gymnotus*. *American Museum Novitates*, 781, 1–3.

Lacépède, B.G.E. (1800) Histoire Naturelle des Poissons. Paris, v.2, 632 pp.

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

Liem K.F., Eclancher, B., & Fink W.L. (1984) Aerial respiration in the banded knife fish *Gymnotus carapo* (Teleostei, Gymnotoidei). *Physiological Zoology*, 57, 185–195.

Linnaeus, C. (1758) Systema Naturae, Ed. X. (Systema naturae per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis. Tomus I. Editio decima, reformata.) Holmiae.

Lundberg, J.G. (1998). The temporal context for the diversification of Neotropical fishes. *In*: Malabarba, L., Reis, R.E., Vari, R.P., de Lucena, C.A.S. & de Lucena, Z.M.S. (Ed) *Phylogeny and Classification of Neotropical Fishes*, Porto Alegre, Museu de Ciências e Tecnologia, pp. 49–68.

Lundberg, J.G., Cox Fernandes, C., Albert, J.S., & Garcia, M. (1996) *Magosternarchus*, a new genus with two new species of electric fish (Gymnotiformes: Apteronotidae) from the Amazon River basin, South America. *Copeia*, 1996, 657–670.

Lönnberg, E. (1896) Linnean type-specimens of birds, reptiles, batrachians and fishes in the Zoological Museum of the R. University in Upsala. Bihang Kongl. Svenska Vet.-Akad. Handl. v. 22, afd. 4, 1–45.

Mago-Leccia, F. (1994) *Electric Fishes of the Continental Waters of America*. Biblioteca de la Academia de Ciencias Fisicas, Matematicas, y Naturales, Caracas, 206 pp.

Marcgraf, G. (1648) *Historiae rerum naturalium Brasiliae*. Haak en Elsevier, Leiden and Amsterdam.

Moritz, C. (1994) Applications of mitochondrial DNA analysis in conservation: a critical review. *Molecular Ecology*, 3, 401–411.

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

Northcutt, R.G., Holmes, P.H. & Albert, J.S. (2000) Distribution and innervation of lateral line organs of the Channel Catfish. *Journal of Comparative Neurology*, 421, 570–592.

Pallas, P.S. (1769) Spicilegia Zoologica quibus novae imprimis et obscurae animalium species iconibus, descriptionibus atque commentariis illustrantur. Berolini, 1, 1–42.

Ricklefs, R.E. (1989). Speciation and Diversity: The Integration of Local and Regional Processes. *In:* Otte, D. & Endler, J.A. (Ed) *Speciation and Its Consequences*, Sunderland, Sinauer Associates, pp. 599–624.

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

Wheeler, A. (1991) The Linnaean fish collection in the Zoological Museum of the University of Uppsala. *Zoological Journal Linnean Society*, 103, 145–195.

Appendix. Abbreviated descriptions of field characters and states used in combination to differentiate taxa of the *Gymnotus carapo* species-group (Table 4). Abbreviations: AFR, anal-fin rays; BD, body depth; BO, branchial opening; BW, body width; HD, head depth; HL, head length; HW, head width; IO, interorbital distance; P1, pectoral–fin length; PA, preanal distance; PCV, pre-caudal vertebrae; TL, total length.

1. Body size. 0: grows to maximum total length of 800 mm or less. 1: grows to more than 800 mm.
2. Head length. 0: short, mean HL 9.5–11.4% TL. 1: moderate, mean HL 11.5–12.4% TL. 2: long, mean HL 12.5–13.5% TL.
3. Head depth. 0: very deep, mean adult HD= 66–75%HL. 1: moderate, HD = 60–65% HL. 2: shallow, HD 53–59% HL,
4. Head width. 0: wide, mean adult HW= 68–70% HL. 1: moderate, HD = 56–65% HL. 2: narrow, HD 52–55% HL,
5. Interorbital distance. 0: narrow, mean adult IO: 31–37% H. 1: broad, IO: 38–43% HL. 2: very broad, IO: 44–50% HL,
6. Branchial opening. 0: broad, mean adult BO: 33–47% HL. 1: narrow, IO: 25–32% HL.
7. Preanal distance. 0: long, mean adult PA 121–130%HL. 1: short, PA 61–120% HL.
8. Pectoral fin length. 0: large, mean adult P1= 45–55% HL. 1: small, P1 25–44% HL.
9. Body shape, transverse section at anal-fin origin. 0: laterally compressed, mean adult BD 0.50–0.72% BW. 1: cylindrical, 0.73–0.90%.
10. Band pigment density. 0: no bands. 1: dark bands paired, pale middle. 2: dark bands evenly pigmented.
11. Dark bands above lateral line at midbody. 0: continuous (or unbanded). 1: bands broken into irregular patches or spots.
12. Band (pair) number. 0: mode = 0–16. 1: mode = 17 or more.
13. Head color pattern. 0: evenly pigmented with slight dorsoventral countershading. 1: blotched.
14. Color mid-dorsum at midbody. 0: dark. 1: light.
15. Anal-fin color. 0: anterior half hyaline to brown. 1: all black (except clear patch posteriorly).
16. Scales above lateral line. 0: small, mode 9–13. 1: large, mode 5–8.
17. Scale shape. 0: circular to slightly ovoid. 1: elongate in mature specimens, length more than four times depth.
18. Posterior lateral line scales. 0: mode less than 110. 1: mode 110 or more.
19. Scales to first ventral ramus. 0: moderate: 34–43. 1: few: 44–65. 2: many: 66–78,
20. Scales over anal-fin pterygiophores. 0: large, mode 5–6 rows. 1: small, mode 7–9 rows.
21. Circumorbital series. 0: ovoid, angle between supraorbital and infraorbital canals right or slightly acute (60–90°). 1: tear-drop shaped, angle between supraorbital and infraorbital canals strongly acute (40–60°).

22. Pectoral-fin rays. 0: many, mode = 17–21. 1: few, mode = 14–16.
23. Body cavity length. 0: mode = 22–29 PCV. 1: 30–35 PCV. 2: 36–39 PCV. 3: 40–44 PCV.
24. Anal-fin rays. 0: few, median 150–216 AFR. 1: many, median 217–260 AFR.
25. Ventral lateral line rami (modal number in adults). 0: none. 1: 1–6. 2: 7–18. 3: 19–30.
26. Dorsal lateral line rami (modal number in adults). 0: 0–2. 1: 3–6.
27. Electric organ depth; number of electroplate rows above caudal end of anal fin (modal number in adults). 0: 2 rows. 1: 3–4 rows. 2: 5–6 rows.

