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Redescription of *Gymnotus coropinae* (Gymnotiformes, Gymnotidae), an often misidentified species of Neotropical electric fish, with notes on natural history and electric signals

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Abstract

Gymnotus coropinae, a diminutive species of Neotropical electric fish, was originally described by Hoedeman from Surinam. Shortly after its description, *G. coropinae* was synonymized with a syntopic congener, *G. anguillaris*. Here we redescribe *G. coropinae* as a valid species distinguishable from all congeners by a unique color pattern comprised of a dark brown background color marked by 8–18 white or pale yellow bands that in the anterior 1/3 to 2/3 of body are absent or largely restricted to the ventral part of the lateral surface. *Gymnotus coropinae* is further distinguishable from *G. anguillaris* and other congeners on the basis of several meristic and morphometric characters. *Gymnotus coropinae* is widely distributed throughout the Amazon and Orinoco Basins and the Guyana Shield. It inhabits small terra firme forest streams and swamps containing acidic, low-conductivity water.

Key words: Amazon, biodiversity, electrogenesis

Introduction

Gymnotus is the focus of intensive ongoing taxonomic attention and may now be the best known of all the Neotropical electric fish genera (Mago-Leccia 1994; Albert & Miller 1995; Campos da Paz 1996; Campos da Paz & Costa 1996; Fernandes-Matioli & Almeida-Toledo 1998; Fernandes-Matioli *et al.* 1998; Albert *et al.* 1999; Campos da Paz 2000; Fernandes-Matioli *et al.* 2000; Albert 2001; Albert & Crampton 2001; Fernandes-Matioli & Almeida-Toledo 2001; Campos da Paz 2002; Albert & Crampton 2003; Campos da Paz 2003; Crampton *et al.* 2003). *Gymnotus* is the most diverse of the gymnotiform genera, with 27 valid species including the species redescribed herein (Table 1). It is also the most geographically widespread, occurring throughout lowland Middle and South America from southern Mexico to the Pampas of Argentina (Albert 2001).

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TABLE 1. Twenty seven valid species of *Gymnotus* with affiliation to species-groups (see text) and geographical range: Geographical areas follow Albert and Crampton (2003): EA, Eastern Amazon; GU, Guyana Shield and Orinoco basin; MA, Middle America; MD, Madeira; NE, northeastern Brazil; PA, Paraguay-Paraná; PI, Piauí; PS, Pacific Slope; RO, Roraima; SE, southeast coast Brazil, Uruguay; WA, Western Amazon.

Group	Species	Geographical Range
cylindricus	*G. cylindricus* LaMonte, 1935	MA
	G. maculosus Albert & Miller, 1995	MA
pantherinus	*G. anguillaris* Hoedeman, 1962	GU, MD
	G. cataniapo Mago-Leccia, 1994	GU
	G. coatesi LaMonte, 1935	EA, WA
	G. coropinae Hoedeman, 1962	GU, EA, MD, WA
	G. javari Albert, Crampton & Hagedorn, 2003	WA
	G. jonasi Albert & Crampton, 2001	WA
	G. melanopleura Albert & Crampton, 2001	WA
	G. onca Albert & Crampton, 2001	WA
	G. panamensis Albert & Crampton, 2003	MA
	G. pantherinus (Steindachner, 1908)	SE
	G. pedanopterus Mago-Leccia, 1994	EA, GU
	G. stenoleucus Mago-Leccia, 1994	GU
carapo	*G. arapaima* Albert & Crampton, 2001	MD, WA
	G. bahianus Campos-da-Paz & Costa, 1996	NE
	G. carapo Linnaeus, 1758	EA, GU, MD, PI, RO, WA
	G. choco Albert, Crampton & Maldonado, 2003	PS
	G. diamantinensis Campos da Paz, 2002	EA
	G. esmeraldas Albert & Crampton, 2003	PS
	G. henni Albert, Crampton & Maldonado, 2003	PS
	G. inaequilabiatus (Valenciennes, 1847)	PA
	G. mamiraua Albert & Crampton, 2001	MD, WA
	G. paraguensis Albert & Crampton, 2003	PA
	G. sylvius Albert *et al.* 1999	PA, SE
	G. tigre Albert & Crampton, 2003	EA, WA
	G. ucamara Crampton, Lovejoy & Albert, 2003	WA

Hoedeman (1962) described *G. coropinae* from Surinam on the basis of a single 49.3 mm-specimen with a broken caudal appendage. In the same paper, Hoedeman described the sympatric and syntopic congener, *G. anguillaris*. Nijssen and Isbrücker (1968) noted that the single holotype specimen of *G. coropinae* had the "same appearance as young

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damaged, dried out specimens of *G. anguillaris*" and placed *G. coropinae* as a synonym of *G. anguillaris*. As part of a revision of *Gymnotus*, we examined the holotype of *G. coropinae*, the single paratype of *G. anguillaris*, and other collections of *Gymnotus* from Surinam and concluded that *G. coropinae* is a valid species. Here we present a redescription of this species based on features of external morphology, meristics, squamation, pigmentation, and osteology. We also describe its geographical range and provide ecological notes, with emphasis on populations from the Tefé region of the Central Amazon basin of Brazil. This region is the subject of an ongoing evolutionary study of the species and electric signal diversity of gymnotiform fishes (Crampton 1996a; b; 1998a; b; Albert & Crampton 2001).

Albert and Crampton (2003) summarize the diagnostic characters of *Gymnotus* and recognize three species-groups within the genus: *G. cylindricus*, *G. pantherinus* and *G. carapo* species-groups. The species composition and geographical range of these groups are summarized in Table 1. We use this classification of *Gymnotus* as a basis for the differential diagnoses presented here.

Materials and Methods

Specimens and their electric organ discharges (EODs) were captured as part of a long-term, multi-habitat sampling program undertaken by one of us (WGRC) near the town of Tefé, Amazonas, Brazil between 1993 and 2002 (Fig. 1). Sampling was undertaken with a dip-net (0.3–0.4 m diameter, 2–4 mm mesh) in terra firme forest streams and swamps, and often involved the use of a portable electric-fish detector. This device consisted of an amplifier and loud speaker connected to electrodes on the end of a submersible pole. Additional material was examined from museum collections. Institutional abbreviations presented here follow Leviton et al. (1985) with the addition of IDSM (Instituto de Desenvolvimento Sustentável Mamirauá, Tefé), INPA (Instituto Nacional de Pesquisas da Amazônia, Manaus), MUSM (Museo de Historia Nacional de la Universidad Nacional Mayor de San Marcos, Lima), and NRM (Swedish Museum of Natural History, Stockholm). Methods for sex determination follow Albert and Crampton (2001). Specimen sizes are all reported as total length (TL) in mm.

Morphometric data were measured as point-to-point linear distances from standardized landmarks on the left side of specimens using digital calipers to the nearest mm. Protocols for measurements follow those of Albert and Crampton (2001; 2003) and Crampton *et al*. (2003), and abbreviations are given in Table 2. Meristic and scale counts follow Albert and Crampton (2003), and abbreviations are given in Table 3. For descriptive purposes we report band number as the number of pale bands superimposed over the predominantly dark background coloration. For the differential diagnosis, dark inter-bands (dark background pigmentation between pale bands) were counted (see protocol in Fig. 2). This was done in order to standardize this count with congeners, where dark body pigmentation forms bands which are often narrower than a pale background coloration. 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. Osteological data were taken from specimens cleared and stained and dissected following Albert and Crampton (2003). EOD recording techniques follow Crampton (1998b) and Crampton *et al*. (2003) but recordings were taken in water from source at ambient stream temperatures of 24–26 ºC.

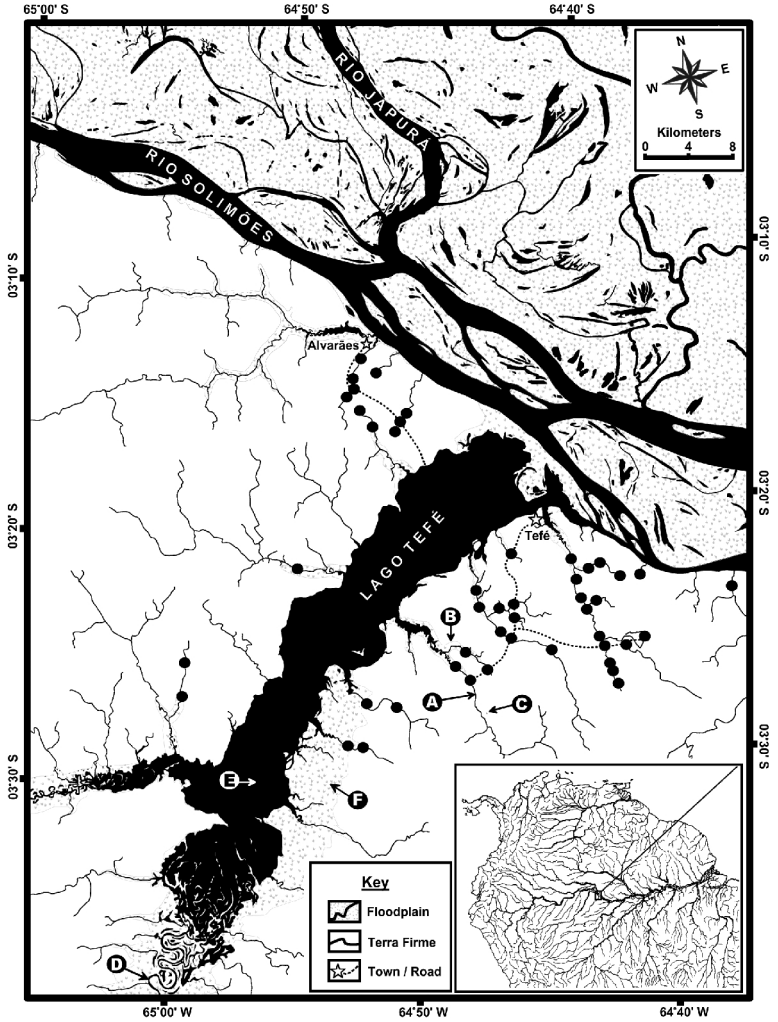

FIGURE 1. Map of Tefé area, Brazil, showing collecting sites (small black circles) where *Gymnotus coropinae* was collected. Areas exposed to an annual flood regime are stippled. Low-conductivity blackwater systems are labeled: A, terra firme stream (*igarapé*); B, lower, seasonally-flooded stretch of igarapé; C, ephemeral terra firme swamps; D, blackwater river, E, mouth bay lake; F, seasonally-flooded blackwater *igapó* forest. The area to the north of the Rio Solimões is high-conductivity whitewater várzea floodplain. Base map traced from 1999 1:150,000 Landsat TM5 images. Extent of annual flooding plotted from June 1995 NASDA JERS-1 image.

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TABLE 2. Morphometric data for adult specimens of three geographical populations of *Gymnotus coropinae* (separated and pooled) and *G. anguillaris*. GU = Guyana Shield of Surinam (region of type locality for *G. coropinae* and *G. anguillaris*). MD = Upper Madeira basin of Peru. WA = Western Amazon in Tefé region. Abbreviations: TL, total length; HL, head length; PR, preorbital length; MW, mouth width; PO, postorbital length; IO, interorbital distance; HD, head depth; HW, head width; PA, preanal distance; P1, pectoral-fin length; AF, anal fin base length; BD, body depth; BW, body width. TL and HL expressed in mm. Percentage measurements in HL or, if marked with an asterisk, in TL. BW/BD expressed as a ratio. N values (in parentheses) vary because measurements were excluded from specimens with damage or unusual preservation artifacts.

	G. coropinae (GU)		*G. coropinae* (MD)		*G. coropinae* (WA)		*G. coropinae* (pooled)		*G. anguillaris* (GU)	
	Range	Mean	Range	Mean	Range	Mean	Range	Mean	Range	Mean
TL	107–160 (17)	–	84–162 (13)	–	112–156 (12)	–	84–162 (42)	–	131–302 (14)	–
HL	10.7–14.4 (17)	–	7.0–11.6 (12)	–	9.7–13.1 (11)	–	7.0–14.4 (40)	–	12.6–27.4 (12)	–
HL %*	9.0–10.6 (17)	9.8	7.9–9.5 (12)	8.4	8.4–9.3 (11)	8.9	7.9–10.6 (40)	9.1	8.3–9.8 (12)	9.2
PR %	32.1–37.7 (9)	35.2	29.3–34.5 (12)	31.7	31.0–38.2 (11)	34.0	29.3–38.2 (32)	33.5	33.3–37.3 (8)	35.9
MW %	36.7–44.7 (7)	40.5	36.1–46.1 (12)	40.2	35.2–46.6 (11)	41.3	35.2–46.6 (30)	40.7	41.4–55.1 (8)	47.0
PO %	59.7–65.3 (7)	62.4	60.4–65.7 (12)	62.6	62.4–67.1 (11)	65.1	59.7–67.1 (30)	63.5	59.6–63.5 (8)	61.6
IO %	39.0 –43.2 (7)	40.5	38.1–45.6 (12)	41.4	39.5–47.5 (11)	43.3	30.5–43.2 (32)	41.5	42.9–56.3 (8)	45.6
BD %*	7.0–8.5 (17)	7.8	5.9–6.7 (12)	6.3	5.5–7.5 (11)	6.6	5.5–8.5 (40)	7.0	6.7–9.8 (8)	8.3
BW %*	4.8–5.4 (7)	5.1	4.5–5.1 (12)	4.8	3.5–5.1 (11)	4.6	3.5–5.4 (30)	4.8	5.7–6.7 (8)	6.3
BW/BD	0.60–0.73 (7)	0.66	0.70–0.82 (12)	0.76	0.53–0.83 (11)	0.70	0.53–0.83 (30)	0.71	0.70–0.83 (8)	0.74
HD %	55.6–65.1 (7)	60.0	53.8–65.3 (12)	59.7	53.8–61.5 (11)	56.7	53.8–65.3 (30)	58.7	60.1–67.7 (8)	64.1
HW %	58.0–63.7 (7)	61.7	58.3–73.3 (12)	64.9	53.8–62.7 (11)	59.1	53.8–73.3 (30)	62.0	66.1–76.6 (8)	70.3
PA %	82.2–102.8 (7)	91.3	88.4–120.3 (12)	107.7	97.1–123.8 (11)	108.2	82.2–123.8 (30)	104.1	83.9–122.3 (8)	99.4
P1 %	41.2–49.1 (6)	45.9	42.9–54.4 (12)	47.5	38.4–54.8 (11)	44.6	38.4–54.8 (29)	46.1	42.1–56.3 (8)	48.0
AF %*	73.4–79.5 (7)	76.1	71.4–84.2 (12)	78.9	75.2–84.3 (11)	82.0	71.4–84.3 (30)	79.4	77.1–83.3 (8)	81.3

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TABLE 3. Meristic data for three geographical populations of *Gymnotus coropinae* (separated and pooled) and *G. anguillaris*. Abbreviations for populations in Table 2. Other abbreviations: BND, dark bands; AFR, anal-fin rays; P1R, pectoral-fin rays; SAL, scales above lateral line; CEP, caudal electroplate rows; APS, anal-fin pterygiophore scales; PCV, precaudal vertebrae; PLR, pored lateral-line scales to first ramus; PLL, total pored lateral-line scales; VLR, lateral-line ventral rami (left or right). Med. = Median. N values (in parentheses) vary because counts were excluded from specimens with damage or unusual preservation artifacts.

	BND		AFR		P1R		SAL		CEP	
	Range	Med.	Range	Med.	Range	Mode	Range	Mode	Range	Mode
G. coropinae GU	7–22 (24)	14	195–245 (14)	220	13–14 (23)	14	6–8 (28)	7	2–3 (27)	3
G. coropinae MD	4–20 (6)	17	210–230 (4)	223	13–14 (6)	13	7–8 (7)	7	2–3 (7)	3
G. coropinae WA	8–18 (15)	14	185–215 (10)	208	12–13 (15)	12	6–7 (14)	7	2–3 (13)	3
G. coropinae (pooled)	4–22 (45)	14	185–245 (28)	212	12–14 (44)	14	6–8 (49)	7	2–3 (47)	3
G. anguillaris GU	7–26 (8)	22	210–270 (8)	257	16–18 (8)	16	7–8 (8)	8	3 (8)	3

	APS		PCV		PLR		PLL		VLR	
	Range	Mode	Range	Mode	Range	Med.	Range	Med.	Range	Med.
G. coropinae GU	5–7 (14)	6	39–43 (18)	41	48–61 (20)	55	83–102 (10)	91	11–16 (7)	14
G. coropinae MD	6–7 (7)	6	40–42 (5)	41	44–53 (7)	48	85–100 (7)	94	8–15 (7)	12
G. coropinae WA	5–6 (6)	6	39–43 (16)	41	45–56 10)	48	72–92 (10)	80	11–27 (11)	22
G. coropinae (pooled)	5–7 (27)	6	39–43 (39)	41	44–61 (37)	52	72–102 (27)	86	8–27 (24)	15
G. anguillaris GU	7–8 (8)	7	37–38 (8)	38	51–62 (8)	58	102–130 (8)	124	8–12 (2)	10

The differential diagnosis presented here is limited to salient characters that do not necessitate clearing and staining. Mean, median, or modal values are given for diagnostic characters that have slightly overlapping ranges but divergent measures of central tendency. Morphometric and meristic data for diagnoses are from data pooled from three geographical populations of *G. coropinae*, and from specimens of *G. anguillaris* from the region of the type locality in Surinam (Tables 2–3). We distinguish *G. coropinae* from members of the *G. carapo* and *G. pantherinus* species-groups endemic to the Amazon and

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Orinoco Basins and to the Guyana Shield (species-groups and geographical areas *sensu* Albert and Crampton, 2003). Species in the *G. cylindricus* species-group are confined to Middle America where *G. coropinae* does not occur.

Gymnotus coropinae **Hoedeman**
(Figs. 2–5)

Gymnotus coropinae. — Hoedeman (1962): 55, fig. 1c [type locality: Surinam: Coropina Creek, sta. 17, May 20, 1956].

Gymnotus anguillaris. — Nijssen & Isbrücker (1968): 162, fig. 1 [in part, places *G. coropinae* as a synonym of *G. anguillaris*, Surinam: Marowijne, Suriname, Saramacca, Coppename, Nickerie rivers]. — Knöppel (1970): 257 [Brazil: Rio Negro]. — Mago-Leccia (1994): 56, fig. 84 [in part, regards *G. coropinae* as synonym of *G. anguillaris*]. — Planquette *et al.* (1996): 410, fig. and distribution map. pp. 411 (map may also contain records for *G. anguillaris sensu stricto*) [French Guyana]. — Crampton (1998a): 817 [Brazil: Rio Tefé]. — Crampton (1998b): 314 [Brazil: Rio Tefé]. — Crampton (1999): 17 [Brazil: Rio Tefé]. — Albert (2001): 112 [in part, regards *G. coropinae* as synonym of *G. anguillaris*: Guyana, Surinam, Amazon drainages of Brazil, Bolivia, Peru]. — Campos-da-Paz (2003): 484 [in part, regards *G. coropinae* as synonym of *G. anguillaris*].

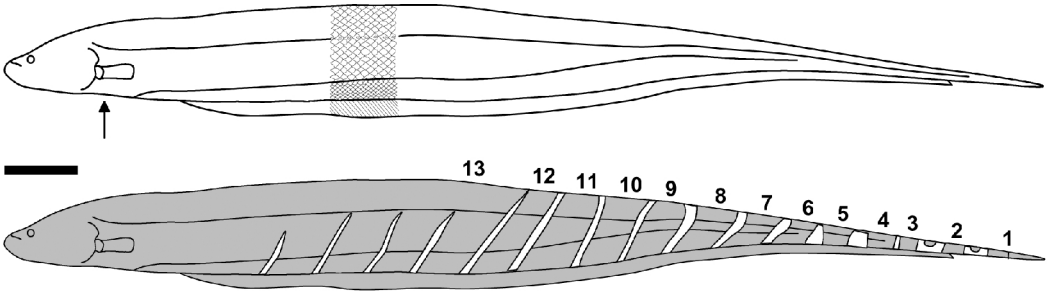

FIGURE 2. Diagrammatic representation of proportions and squamation (above) and banding pattern (below) of *Gymnotus coropinae*. Dark bands are counted from the caudal appendage in an anterior direction; the last one is anterior to the last pale band band reaching the midline of the dorsum. Arrow indicates position of anus. Scale bar = 10 mm.

Diagnosis. *Gymnotus coropinae* is unique among all congeners endemic to the Amazon-Orinoco basins and the Guyana Shield in possessing a dark brown background color marked by 8–18 white or pale yellowish bands (or 4–22 dark inter-bands, see Fig. 2) which in anterior 1/3 to 2/3 of body are absent or largely restricted to the ventral part of the lateral surface (Figs. 2, 4). *Gymnotus coropinae* and all congeners in the *G. pantherinus* species-group can be distinguished from species in the *G. carapo* species-group by the absence of a clear or pale patch near the caudal end of the anal fin and by the presence of one (vs. two) laterosensory canal pores in the preopercular-mandibular series at the dorsoposterior

portion of the preopercle. *Gymnotus coropinae* can be distinguished from congeners of the *G. pantherinus* species-group endemic to the Amazon-Orinoco basins and the Guyana Shield in possessing the following unique combination of characters: 1, maximum known body size 162 mm (vs. more than 300 mm in *G. anguillaris*, *G. cataniapo* and *G. pedanopterus*); 2, precaudal vertebrate (PCV) 39–43 [mode 41] (vs. 31–32 in *G. pedanopterus*, vs. 37–38 in *G. anguillaris*, *G. melanopleura*, and *G. onca*, vs. 36–39 [mode 37] in *G. jonasi*, and vs. 47–51 in *G. cataniapo*); 3, pectoral-fin rays (P1R) 12–14 (vs. 16–18 in *G. anguillaris*, and vs. 15 in *G. coatesi*); 4, scales above lateral line (SAL) 6–8 [mode 7] (vs. 8–13 [mode 9] in *G. pedanopterus*); 5, pored lateral-line scales to first ramus (PLR) 44–61 [median 52] (vs. 31–40 in *G. jonasi*, vs. 60–69 [median 63] in *G. cataniapo*, and vs. 61–65 [mode 65] in *G. coatesi*); 6, total number of pored lateral-line scales (PLL) 72–102 [median 86] (vs. 102–130 [median 124] in *G. anguillaris*, and vs. 114–120 in *G. cataniapo*); 7, anal-fin pterygiophore scales (APS) 5–7 (vs. 9–10 in *G. javari*); 8, adult preorbital length (PR) 29.3–38.2 % HL (vs. 26.4–29.2 in *G. jonasi*); 9, adult mouth width (MW) 35.2–46.6 % HL (vs. 27.8–35.1 in *G. coatesi* and *G. jonasi*); 10, adult body width (BW) 3.5–5.4 [mean 4.8] % TL (vs. 5.6–6.7 in *G. anguillaris* and *G. coatesi*, and vs. 5.4–7.3 [mean 6.4] in *G. cataniapo*).

FIGURE 3. Photograph of *Gymnotus coropinae*, AMNH 55000, from region of the type locality, River Corantijn, Surinam. Scale bar = 10 mm.

FIGURE 4. Photograph of head and body of *Gymnotus coropinae*, MZUSP 75188, from the vicinity of Tefé, Brazil. Scale bars = 10 mm.

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Description. Figs. 2–4 illustrate body shape and pigment patterns. Fig. 3 illustrates a preserved specimen from the region of the type locality in Surinam. Fig. 4 illustrates a live specimen from the vicinity of Tefé, Brazil. Nijssen and Isbrücker (1968, fig. 1) also provide a photograph of a specimen from the region of the type locality in Surinam (ZMA 105.904, 125 mm). Morphometric and meristic data presented in Tables 2 and 3. Cephalic sensory canal pore configurations illustrated in Fig. 5. Size up to 162 mm in males and 140 mm in females. Maturity at about 90–120 mm in males and females. Sexually monomorphic other than size differences. Scales cycloid, ovoid, present on entire post-cranial portion of body from nape to tip of caudal appendage. Scales on dorsal surface relatively large at midbody; 6–8 rows from lateral line to dorsal midline. In adult specimen, 150 mm, lateral-line scales approximately 1.5 mm high by 1.3 mm long at midbody, 1 mm high by 1.3 mm long at one head length anterior to distal end of caudal appendage. Gape size in mature specimens moderate, extending three quarters distance from anterior tip of snout to 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, half diameter of eye. Branchial opening moderate, 24.0–30.4% HL. Circumorbital series ovoid. Anterior margin of ethmoid region rounded. Eye position lateral, lower margin of eye dorsal to rictus.

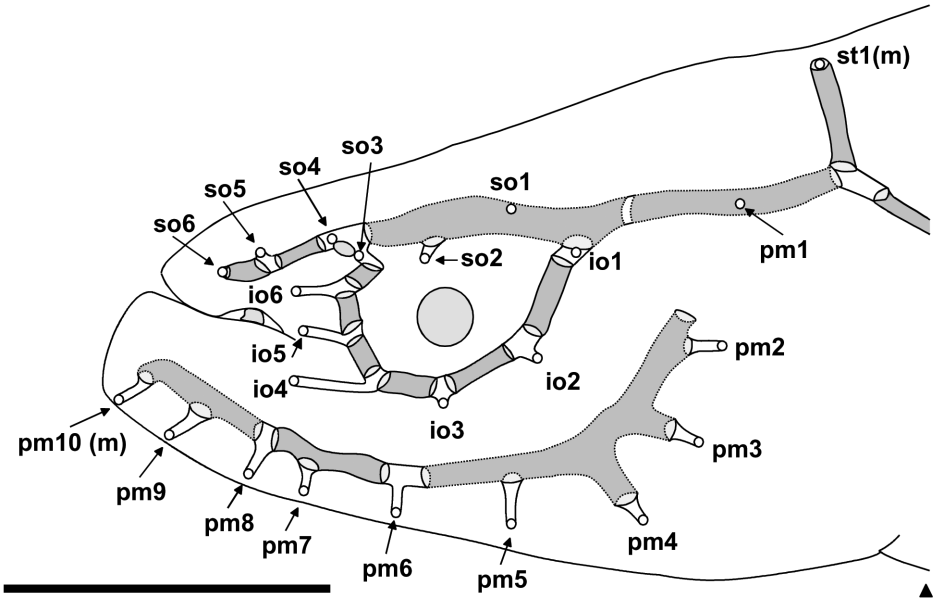

FIGURE 5. Head of *Gymnotus coropinae*, MZUSP 75188, illustrating organization of cephalic sensory canals and pores. Ossified portions of canals shaded gray. Unossified portions white. Pores indicated by small circles. Eye and anterior and posterior nares shaded gray. Abbreviations: so, supraorbital; io, infraorbital; pm, preopercular-mandibular; st, supratemporal; m, medial. Arrow in bottom right indicates position of anus. Scale bar = 5 mm.

Premaxilla triangular in ventral view, with 11–12 teeth (mode 12, n = 2) teeth disposed in single row along outer edge, and 4–5 (mode 5, n = 2) in inner row. Outer row teeth large and needle shaped. Inner teeth short and needle shaped. Dentary with 19–21 (mode 21, n = 2) teeth disposed in single row along outer edge, and 10–12 (mode 11, n = 2) teeth in inner row. Outer row with 1–10 slender recurved needle-shaped teeth anteriorly, those posteriorly larger and less slender. Inner tooth row extends about two-thirds along the tooth-bearing portion of dentary bone, teeth long, needle shaped and closely spaced anteriorly; smaller, less slender and more distantly spaced posteriorly. Rib 5 triangular in lateral view, narrow proximally and distally, broad in middle, more than 3 times width of rib 6, with a large medial triangular shelf. Hemal spines present. Displaced hemal spines absent. Multiple anal-fin ray branching posterior to ray 18. Variable number (8–27) of asymmetrically arranged lateral-line rami extending posteroventrally at posterior end of lateral line. Dorsal lateral-line rami absent in all specimens. Anal-fin pterygiophores at posterior end of body cavity equal to or longer than first hemal spine. Caudal appendage short, less than half pectoral-fin length in undamaged and unregenerated specimens. Single hypaxial electric organ, extending along entire ventral margin of body. Two or 3 (mode 3) rows of electroplates at one head length from distal end of caudal appendage.

Color in life. Ground color dark brown in adults and juveniles. 8–18 (median 14, n = 15) pale yellow or white bands on lateral surface which in anterior 1/3 to 2/3 of body of adults are either absent or largely restricted to the ventral part of the lateral surface (Figs. 2, 3) such that the dark inter-bands (ground color between pale bands) in the anterior portion of the body fuse into a uniform dark coloration. Occasionally some bands in the anterior portion of the body extend onto the dorsal part of the lateral surface but never connect with bands from the other side of the body at the dorsal midline. Pale bands are oriented vertically or obliquely in anterior-inferior to posterior-superior orientation. Pale band appearance irregular in shape, width, and arrangement, both on and among individuals. Pale bands progressively more narrow and short anteriorly, only rarely extending dorsal to midline on anterior half of body. Pale band margins highly contrasted with dark ground color. Pale bands never completely divided, although posterior-most 3–6 bands have less intense dark coloration in their middle. Dark area between pale bands sometimes marked by small white or pale yellow pigment patch near ventral margin of anal-fin pterygiophores, especially in posterior portion of body. Pale bands extend to mid-dorsum along posterior 1/4 of body. Pale bands of juveniles resemble adults but sometimes extend further dorsally in anterior portion of body. No pale bands from either side meet on ventral midline, between the anus and anal-fin origin. Two to 3 pale bands lie posterior to last anal-fin ray.

Head never banded, spotted or blotched, dark brown dorsally grading to a slightly lighter brown ventrally, with numerous minute chromatophore speckled over branchiostegal membranes and ventral surface of head. In life the operculum is dark. Pectoral-fin rays dark brown, inter-radial membranes hyaline. Anal-fin membrane grading from charcoal

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gray anteriorly to black posteriorly with no unpigmented patch at the caudal end. Fin colors similar in juveniles and adults. Specimens fixed in 10% formalin and preserved for 1–5 years in 70% ethanol maintain approximate colors of life, although the darker pigments tend to pale with time. Color variation is not known to be correlated with sex or EOD structure.

Electric organ discharges. EOD waveform with total duration of approximately 0.85–1.30 ms (with beginnings and ends of EOD, i.e. zero crossovers taken at threshold 1% of peak-to-peak amplitude). EOD comprises four phases with low-voltage pre- and post potentials preceding (P0) and following (P3) a dominant, approximately symmetrical biphasic component (P1, P2) (Fig. 6-A). A very low-amplitude initial positive phase (P-1) precedes P0 in some specimens (e.g. in Fig. 6-A). The Peak Power Frequency (PPF) (Fig. 6-B) of the Fourier Transform of EODs of *G. coropinae* ranges from 2.1 to 2.7 kHz (mean 2.4, n = 20). The EOD pulse repetition rate of *G. coropinae* is relatively low and less variable during the day when this species lodges itself into submerged roots or leaf litter (approx. 45–55 Hz). The EOD pulse repetition rate is usually higher and more variable at night, when *G. coropinae* is active (approx. 50–65 Hz).

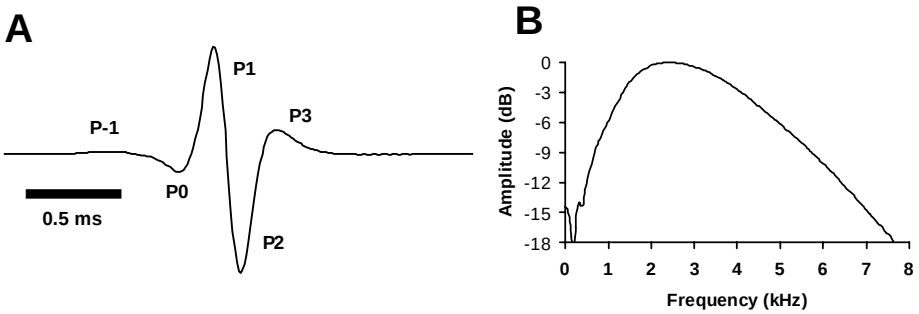

FIGURE 6. EOD waveform (A) and Fourier Power Spectrum (B) of *Gymnotus coropinae*, MZUSP 60601. The EOD is plotted with head-positivity upwards and its component phases labeled P-1 through P3. P1 represents the dominant positive component. The power spectrum was computed from a 2048 point Fast-Fourier-Transform and the Peak-Power-Frequency scaled to 0 dB.

Remarks and comparisons. Hoedeman (1962, p. 55, fig. 1c) described *G. coropinae* from Surinam on the basis of a single 49.3 mm-specimen with a broken caudal appendage. On the basis of a distinct pigmentation pattern comprising only "10 faint, narrow yellowish streaks on the posterior part of the tail, otherwise the fish is dark tan (in alcohol)" and a low anal-fin ray count (142), Hoedeman opted to "provisionally describe it as a new species". Nijssen and Isbrücker (1968, p. 164) examined the holotype of *G. coropinae* and noted that it had the "same appearance as young damaged, dried out specimens of *G. anguillaris*." They also observed that the low anal-fin ray count was a consequence of its broken caudal appendage and concluded that *G. coropinae* is a synonym of *G. anguillaris*.

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We examined the holotype of *G. coropinae*, the single paratype of *G. anguillaris*, and other collections of *Gymnotus* from Surinam and concluded that *G. coropinae* is a valid species.

Specimens of *G. coropinae* can be unambiguously distinguished from *G. anguillaris* on the basis of several characters: 1, pale white or yellow bands usually complete only in posterior 1/3 to 2/3 of body (vs. usually complete along entire body length although more pronounced in posterior part of body in adult *G. anguillaris*); 2, body length small, maximum 162 mm (vs. maximum 302 mm in *G. anguillaris*); 3, pectoral-fin rays 12–14 [mode 14] (vs. 16–18 [mode 16] in *G. anguillaris*); 4, body cavity relatively long, with 39–43 [mode 41] precaudal vertebrae (vs. 37–38 [mode 38] in *G. anguillaris*); total number of pored lateral-line scales 72–102 [median 86] (vs. 102–130 [median 124] in *G. anguillaris*). Juvenile *G. anguillaris* have a similar pigmentation pattern to juveniles and adults of *G. coropinae*, with the pale inter-bands being very faint to absent in the anterior portion of the body. Nonetheless, pectoral-fin ray and precaudal vertebrae counts allow unambiguous recognition. The holotype of *G. coropinae* has 12 pectoral-fin rays and 39 precaudal vertebrae, well within the range of other specimens from the region of the type locality.

Gymnotus coropinae can be readily distinguished from all other species of *Gymnotus* on the basis of the unique color pattern described above. It can be further distinguished from congeners of the *G. pantherinus* species-group endemic to the Amazon and Orinoco basins to the Guyana Shield on the basis of the unique combination of characters described in the diagnosis.

Geographical variation. Populations of *G. coropinae* from the upper Madeira and upper Amazon (see Tables 2 and 3) and also from other areas of the Amazon-Orinoco Basins and the Guyana Shield cannot be unambiguously distinguished from *G. coropinae* specimens from the region of the type locality in Surinam on the basis of color, morphometric, meristic or osteological characters. The averages of certain morphometric and meristic characters do differ slightly between populations of these regions, although the ranges of all these characters overlap considerably (Table 2 and 3). EOD data is presently unavailable for specimens outside the Tefé region.

Distribution. *Gymnotus coropinae* is widely distributed throughout the Amazon-Orinoco Basins and the Guyana Shield (Fig. 7).

Ecology. Detailed ecological notes on *Gymnotus coropinae* were compiled from studies in the Tefé region of Amazonas, Brazil (see Fig. 1 for notes on aquatic habitats). Here, this species is found in small streams (igarapés) that drain the rainforests of the terra firme peneplain above the Amazonís floodplain (Fig. 8), and also in the lower, seasonally inundated reaches of these streams where they drain into floodplain habitats. *Gymnotus coropinae* occurs sympatrically in this habitat with three other species of *Gymnotus*: *G. arapaima*, *G. coatesi* and, rarely, *G.* n. sp. "cur". Igarapés of the lowland Amazon Basin flow with cool (23–26 °C), low-conductivity (5–25 μScm^{-1}) water. Where igarapés drain sandy soils, leached tannic and folic acids impart a dark tea-like coloration to the water. Where igarapés drain clay-dominated soils these humic substances are sequestered by the

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soil and the water tends to be clearer. In either case suspended sediment loads are usually low (visibility with Sechi disk 1.5–2.5 m) except following heavy rainfall or disturbance. pH values in igarapés of the Tefé region vary from 3 to 5.

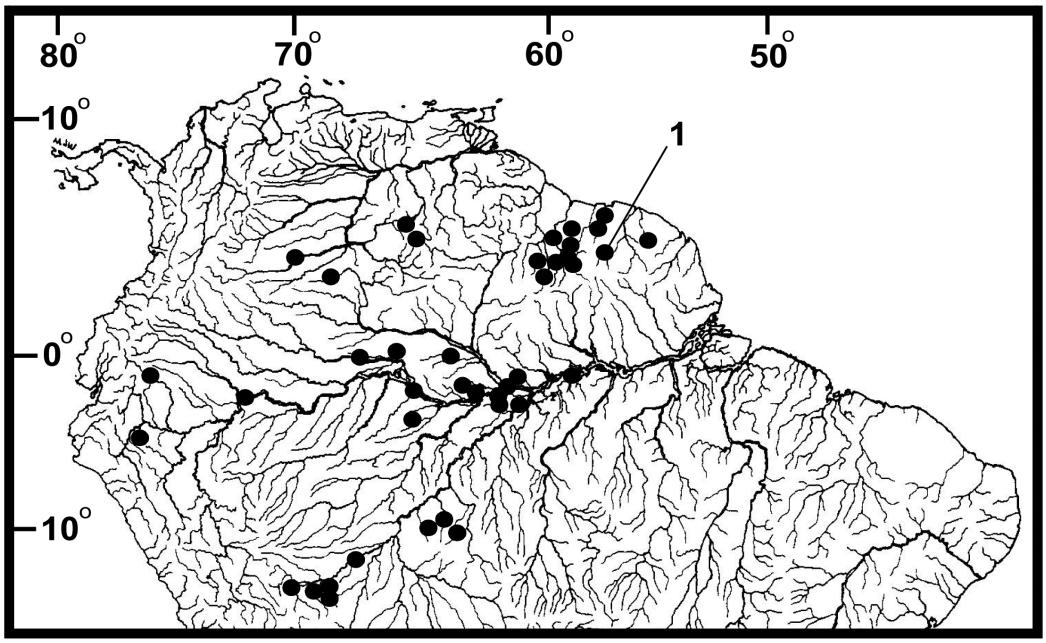

FIGURE 7. Part of northern South America showing collection records of *Gymnotus coropinae*. 1 = holotype locality. Some symbols represent more than one lot or locality. Base map by M. Weitzman.

FIGURE 8. Terra firme stream in rainforest near Tefé, Amazonas, Brazil. *Gymnotus coropinae* occurs in hanging roots along the banks and in banks of submerged leaf litter.

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Terra firme streams of the Central Amazon basin are usually devoid of macrophytes, except in forest gaps or clearings, and are choked with leaf litter and submerged branches. *Gymnotus coropinae* shelters during the day in curtains of dense rootmats that festoon the banks of terra firme streams or within the interstices of submerged banks of leaf litter. The diminutive size and eel-like shape of *G. coropinae* are well adapted for foraging in these microhabitats. Here *G. coropinae* prey on aquatic invertebrates of primarily autochthonous origin including small freshwater crustaceans and the nymphs or larvae of a variety of aquatic insects. Chironomidae larvae are often the dominant food. Breeding occurs primarily during the months of most rainfall (December–April) when streams are often swollen with flood waters and flood adjacent areas of low-lying forest. *Gymnotus coropinae* also colonizes shallow, often ephemeral, swamp-pools in terra firme forest which are temporarily connected to streams following heavy rainfall and flash flooding. *Gymnotus* n. sp. "cur" is also found in these swamp pools.

Gymnotus coropinae has been documented in ecological studies of small forest streams in other areas of the lowland Amazon Basin, including the Rio Negro drainage (Henderson & Walker, 1990; Knöppel, 1970; pers. obs.) where it occurs sympatrically with *G. arapaima*, *G. pedanopterus*, and *G. stenoleucus*. *Gymnotus coropinae* is also found in forest streams in the Guyanas where it occurs sympatrically with *G. anguillaris* and *G. carapo*: Surinam (Hoedeman, 1962; Hopkins & Heiligenberg, 1978; Nijssen & Isbrücker, 1968; Hopkins pers. comm.), French Guyana (Planquette *et al*. 1996), and Guyana (G. Watkins, R. Lowe-McConnell pers. comm.). Nijssen and Isbrücker (1968:164) describe *G. coropinae*'s habitat in Surinam as "limpid, dark brown—coca-cola colored—, acid water."

Etymology. Named for the collecting locality of the holotype, at Coropina Creek, Surinam.

Materials Examined. Over 2795 specimens from 822 museum lots and 32 museums were examined as part of an ongoing revision of *Gymnotus*. Comparative materials examined follow Albert *et al.* (1999), Albert (2001), Albert and Crampton (2001; 2003), and Crampton *et al*. (2003), with the addition of that listed below. Data are arranged alphabetically by country, state and municipality (when known), and then alphanumerically by museum acronym and museum lot number. Lot numbers followed by number of specimens and total length (mm). All material from the Brazilian municipality of Tefé collected by W. Crampton.

Gymnotus anguillaris (5 specimens, 131–289 mm) — Surinam: Brokopondo: Marowijne River, 04°22'N, 54°26'W, UMMZ 190413 (3, 131–289). Commewijne: Coropina Creek, 05°32'N, 55°10'W, ZMA 100.338a (1, paratype, 233); locality unknown: MCZ 31219 (1, 262).

Gymnotus cataniapo (3 specimens, 97–184 mm) — Venezuela: Amazonas: Río Orinoco, Río Cataniapo, Caño Las Pavas, approx. 05°36'N, 67°36'W, AMNH 58650 (1, paratype, 179); AMNH 58668 (1, paratype 184). Río Orinoco, Río Cataniapo, nr. Puerto Ayacucho, 05°39'N, 67°37'W, UMMZ 230735 (1, 97).

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Gymnotus coropinae (330 specimens, 19–162 mm) — Bolivia: Pando: Río Abuna, Río Nareuda, approx. 11°18'S, 68°46'W, FMNH 106694 (1, 68). — Brazil: Amazonas: Barcelos: Rio Demini, 00º16'S, 62º46'W, UF 127275 (1, 141); UF 127323 (1, 127). Itacoatiara: Rio Preta da Eva, Manaus-Itacoatiara km 15, 02º45'S, 59º35'W, INPA 9811 (1, 73). Manaus: Rio Negro, Rio Tarumã-Açu, 03º00'S, 60º04'W, INPA 16004 (1, 82); Rio Negro, Igarapé Tarumã-Mirim, 03°02'S, 60°09'W, INPA 13427 (3, 54–67); INPA 13428 (3, 60–115); INPA 14993 (3, 41–58). Novo Airão: Rio Negro: Rio Jaú, Igarapé Miratuca, approx. 01º54'S, 61º26'W, INPA 9739 (1, 65); INPA uncat. (1, 59); Rio Jaú, Rio Carabinani, 01º58'S, 61º31'W, INPA 9743 (1, 58). Presidente Figueiredo: Rio Uatamã, approx. 01º52'S, 60º08'W, INPA 9807 (1, 126); Rio Urubú, approx. 01º16'S, 59º49'W, INPA 14214 (3, 46–76); Rio Urubú, Igarapé Gavião, approx. 01º16'S, 59º49'W, INPA 14227 (part, 3, 41–55); Rio Urubú, Igarapé Porto Alegre, approx. 01º16'S, 59º49'W, INPA 14258 (2, 81–86). Santa Isabel do Rio Negro: Rio Negro, Igarapé Santo Antônio, 01º60'S, 67º14'W, INPA 6594 (1, 84). São Gabriel da Cachoeira: Rio Negro, approx. 00°07'S, 67°05'W, INPA 9131 (1, 60). Tefé: Rio Tefé, Lago Tefé, Igarapé Curupira, 03º26'01"S, 64º43'47"W, BMNH 1998.3.12.211 (1, 52); BMNH 1998.3.12.212 (1, 93); BMNH 1998.3.12.213–214 (2, 84–87); BMNH 1998.3.12.215 (1, 84); BMNH 1998.3.12.216 (1, 76); BMNH 1998.3.12.217 (1, 90); IDSM 426 (8, 55–73); INPA 9964 (1, 92); INPA 9965A (1, 74); INPA 15831 (4, 74–109); INPA 18182 (3, 87–100); INPA 18385 (1, 49); MZUSP 60610 (1, 145); MZUSP 60611 (4, 113–122); MZUSP 60612 (2, 112–123); MZUSP 75188 (1, 113); Rio Tefé, Lago Tefé, Igarapé Curupira, swamp pools, 03º26'01"S, 64º43'52"W, INPA 18184 (4, 87–107); INPA 18185 (5, 98–112); MCP 30679 (3, 80–93); MZUSP 60613 (1, 101); MZUSP 75181 (1, 132); MZUSP 75182 (1, 100); MZUSP 75183 (1, 112); MZUSP 75184 (1, 106); MZUSP 75185 (1, 156); MZUSP 75186 (1, 137); MZUSP 75187 (1, 125); Rio Tefé, Lago Tefé, Igarapé Repartimento, 03º24'28"S, 64º44'10"W, INPA 9965B (2, 87–98); INPA 18181 (1, 117); INPA 18183 (3, 79–97); INPA 18186 (3, 28–105); INPA 18187 (12, 47–127); INPA 18384 (1, 85); INPA 18386 (3, 52–128); INPA 18387 (1, 45); MCP 30673 (1, 90); MCP 30674 (2, 95–102); MCP 30675 (6, 70–122); MCP 30676 (6, 83–98); MCP 30677 (3, 75–128); MCP 30678 (2, 54–77); MCP 30680 (2, 94–109); MCP 30681 (1, 97); MCP 30682 (2, 112–118); UF 118840 (1, 97). Pará: Oriximiñã: Rio Trombetas, Rio Mapuera, Igarapé do Patauá, approx. 01°05'S, 57°02'W, INPA 9806 (1, 84); INPA 9809 (21, 51–126); Rio Trombetas, Igarapé Porteiro, Cachoeira Porteiro, approx. 01°05'"S, 57°01'W, INPA 9819 (1, 39). Rondônia: Ariquemes: Rio Madeira, Bacia do Igarapé Agua Azul, 09°46'S, 62°22'W, INPA 1153 (2, 36–41). Porto Velho: Rio Madeira, Rio Jamari, Igarapé Jatuarana, 08°45'S, 63°28'W, INPA 9839 (4, 55–130); INPA 9841 (2, 115–116); INPA uncat. (POLO 879) (1, 127). Rio Madeira, Rio Candeias, Rio Preto do Candeias, approx. 08º39'S, 63º31'W, INPA 841 (1, 71). — Colombia: Vichada: Río Orinoco, Río Guaviare, Río Guayabero, approx. 05º54'N, 68º28'W, CAS 167969 (1, 108); Río Orinoco, Río Meta, RíoYucao, 04°19'N, 72°04'W, UF 19471 (1, 112); UF 33470 (1, 87). — Ecuador: Napo: Río Payamino, 00º30'S, 77º15'W, FMNH 103352 (3, 19–155). — Guyana:

Demerara: Essequibo River, 04º45'N, 58º42'W, ANSP 177445 (1, 50); Essequibo River, Kumaka, 05°38'N, 57°52'W, FMNH 97300 (1, 124). Rupunini: Moco-Moco creek, 3°21'N, 59°47'59W, USNM (3, 35–118); USNM (1, 157). Siparuni: Siparuni River, Tumbledown Creek/Falls, 04º48'N, 58º51'W, ANSP 17746 (1, 107); Tiger Creek, 3 km Kurupukari, 04º38'N, 58º43'W, Dog Falls (no coordinates available), ANSP 177444 (1, 170); Turtle Pond (no coordinates available), ANSP 175947 (2, 88–93); ANSP 175949 (1, 126); nr. Kurupukari (no coordinates available), ANSP 17591 (1, 131); nr. Burro Burro (no coordinates available), ANSP 175950 (1, 63). — Peru: Amazonas: Río Marañon, Río Santiago, Quebrada Caterpiza, 03°50'S, 77°42'W, FMNH 96980 (1, 98). Loreto: Río Putumayo, El Estrecho, 02°28'S, 72°42'W, NRM 5282, 1 (not measured). Madre de Dios: Río Madre de Dios, 12°36'S, 69°11'W, MUSM 17596 (3, 90–112); Río Madre de Dios, Parque Nacional Manu, Río de los Amigos, 12°34'36"S, 70°04'14"W, MUSM 20146 (1, 76); Río Madre de Dios, Río Tambopata, approx. 12°44'S, 69°11'W, MUSM 4176 (1, 81); MUSM 7594 (1, 76); Río Tambopata, cuenca del Río Heath, Quebrada San Antonio, approx. 12°44'S, 69°11'W, MUSM 4503 (2, 66–70); Río Tambopata, Cochachica, approx. 12°44'S, 69°11'W, MUSM 3013 (1, 105); MUSM 535 (13, 79–136). Río Tambopata, nr. Cochachica, 12°50'30"S, 69°17'31"W, USNM 264102 (2, 112–114); Río Tambopata, nr. Río la Torre, 12°49'40"S, 69°18'00"W, USNM 264108 (2, 117–121); Río Tambopata, nr. Cochachica, 12°49'45"S, 69°16'15"W, USNM 366207 (3, 86–142); Río Tambopata, nr. Río la Torre, 12°50'S, 69°18'W, USNM 366208 (1, 97). —Surinam: Commewijne: Coropina Creek, 05°32'N, 55°10'W, ZMA 100.185 (1, holotype, 49). Nickerie: stream nr. Devis Falls, nr. Avanavero, 04°50'N, 57°14'W, AMNH 54843 (4, 63–94). Corantijn River, no locality data, FMNH 84584 (3, 127–160); Mataway Creek, no locality data, AMNH 54888 (2, 65–79); Kapoeri Creek, 05°16'N, 57°13'W, AMNH 54758 (2, 71–112); Toeboeroe Creek, 05°00'N, 57°31íW, AMNH 54875 (1, 46); Lucie River, Paramaribo River Road, km 212, AMNH 55000 (2, 58–96); Corantijn River, stream S. Tiger Falls (no coordinates available), AMNH 5496 (1, 73); Corantijn River (no coordinates available), USNM 225272 (part, 8, 86–127); Lucie River, approx. 3°35'N, 57°40'W, USNM 225263 (2, 44–51); Lana Creek, 05°26'N, 57°15'0"W, USNM 225264 (9, 58–87); nr. Mataway, approx. 05°1'N, 55°42'W, USNM 225265 (2, 91–113); Lucie River, approx. 3°35'N, 57°40'W, USNM 225277 (3, 72–93); nr. Cow Falls, approx. 05°0'N, 57°38'W, USNM 225278 (19, 33–138); nr. Amotopo, approx. 05°33'N, 57°38'W, USNM 225279 (4, 52–81); nr. Mataway, approx. 05°1'N, 55°42'W, USNM 225281 (2, 54–67); Dalibane Creek, approx. 05°34'N, 57°10'W, USNM 225282 (10, 44–68); nr. Tiger Falls, approx. 05°16'N, 58°57'W, USNM 225287 (25, 47–114); nr. Dalibane Creek approx. 05°34'N, 57°10'W, USNM 225298 (1, 67). — Venezuela: Bolivar: Río Mato, 07º08'N, 65º10'W, ANSP 139849 (8, 97–144). Río Caura, 06º38'N, 64º37'W, UF 97641 (3, 131–132).

Gymnotus javari (42 specimens, 27–221 mm) — Ecuador: Napo: Río Yasuni, nr. Laguna Jatuncocha, 01°01'S, 75°32'W, FMNH 103342 (8, 72–152); FMNH 103343 (6, 85–200); Río Aguarico, Trib. Río Cuyabeno, nr. Laguna Grande de Cuyabeno, 01°01'30"S,

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75°13'12"W, FMNH 103344 (2, 48–62); Quebrada Apoalla, Trib. Lower Río Shushufindi, 01°17'S, 76°27'W, FMNH 103345 (1, 157); Trib. Río Cuyabeno (no coordinates available), FMNH 103346 (8, 68–221); FMNH 103347 (1, 207); Río Cuyabeno, Río Aguas Negras (no coordinates given), FMNH 103348 (4, 27–90). Río Cuyabeno, Trib. Río Tarapuy (no coordinates given), FMNH 103349 (5, 59–145). Cicherota, nr. mouth of Río Bobonaza, approx. 02°36'S, 76°38'W, USNM 177214 (8, 88–205).

Gymnotus jonasi (29 specimens, 41–133 mm) — Brazil: Amazonas: Alvarães: Cano Lago Rato, nr. confluence of Rio Solimões and Rio Japurá, 03º06'37"S, 64º47'49"W, MCP uncat. (15, 41–97). Peru: Loreto: Maynas: Río Ucayali. Río Pacaya, Caño Yarina, 05º21'52"S, 74º30'41"W, UF 131407 (4, 67–94). Maynas. Río Ucayali. Río Pacaya, 05º16'43"S, 74º31'06", UF 131408 (1, 103). Maynas. Río Ucayali. Río Pacaya, 05º18'14"S, 74º30'05", UF 131409 (2, 79–92). Maynas: Río Ucayali. Río Pacaya, Cocha Yarina, 05º24'37"S, 74º30'15"W, UF 131410 (1, 129). Maynas: Río Ucayali. Río Pacaya, Caño Yarina, 05º19'20"S, 74º30'14"W, UF 131411 (1, 92). Maynas: Río Ucayali. Río Pacaya, Cocha Shitari, 05º20'S, 74º30'W, UF 131413 (1, 96). Maynas: Río Ucayali. Río Pacaya, Caño Yarina, 05º23'05"S, 74º30'48"W, UF 131414 (1, 93). Peru: Loreto: Maynas: Río Ucayali. Río Pacaya, Cocha Yarina, 05º21'52"S, 74º30'41"W, UF 131415 (3, 105–133).

Gymnotus pedanopterus (29 specimens, 43–340 mm) — Brazil: Amazonas: Barcelos: Rio Negro, Rio Demini, approx. 00°23'N, 62°51'W, MCP uncat. (1, 85); MCP uncat. (1, 103); MCP uncat. (1, 90). Manaus: Rio Negro, Rio Tarumã-Açu, approx. 03°02'S, 60°07'W, INPA 15907 (1, 47). Novo Airão: Rio Jaú, Rio Carabinani, approx. 01°58'S, 61°30'W, INPA 9742 (1, 67). Presidente Figueiredo: Rio Negro, Rio Cueiras, approx. 02°41'N, 60°21'W, INPA 6398 (2, 43–208). — Guyana: Potaro-Siparuni: Lower Potaro River, Tukeit, 05°12'N, 59°27'W, FMNH 105324 (3, 69–79). — Venezuela: Amazonas: Río Orinoco, Río Casiquiare, Caño Manu, 02°00'N, 66°57'W, AMNH 58651 (1, paratype, 153); Río Orinoco, Río Casiquiare, nr. mouth Río Pamoni, 02°48'N, 65°58'W, ANSP 162606 (2, 86–129). Río Negro, Caño Adabo (no coordinates), NRM 27283 (2, 135–175). Bolivar: Jabillal, 06°57'N, 64°50'W, ANSP 141596 (14, 76–340).

Gymnotus stenoleucus (7 specimens, 60–136 mm). Colombia: Vaupes: Pamopeta, Caño Ti (no coordinates), FMNH 94776 (2, 76–114). Venezuela. Amazonas: Río Orinoco, Río Cataniapo, approx. 5°36'N, 67°36'W, AMNH 59047 (1, paratype, 84); Río Orinoco, Río Cunucunuma, 03°30'N, 65°56'W, ANSP 162127 (1, paratype, 136); Río Orinoco, Río Casiquiare, 03°05'N, 65°55'W, ANSP 162607 (1, 105); Río Orinoco, Río Casiquiare, Caño Caripo, 03°06'N, 65°50'W, ANSP 162608 (1, 89); Río Orinoco, nr. Puerto Ayacucho, approx. 05°39'N, 67°37'W, FMNH 85592 (1, 60).

Gymnotus sp. indet. (10 specimens, 106–187). — Brazil: Amazonas: Lago Codajás, 03°24'S, 62°38'W, MCZ 60007 (5 of 8, 106–127); Lago Curupira, 03°46'S, 58°33'W, MCZ 60009 (5 of 7, 130–187).

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