# Three New Species from a Diverse, Sympatric Assemblage of the Electric Fish Gymnotus (Gymnotiformes: Gymno....

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# Three New Species from a Diverse, Sympatric Assemblage of the Electric Fish *Gymnotus* (Gymnotiformes: Gymnotidae) in the Lowland Amazon Basin, with Notes on Ecology

William G. R. Crampton, Dean H. Thorsen, and James S. Albert

**Three new sympatric species of the Neotropical electric fish *Gymnotus* (Gymnotidae) are described from the lowland Amazon Basin at localities near Tefé (Brazil) and Iquitos and Jenaro Herrera (Peru). These taxa are described using features of external morphology, meristics, pigmentation, osteology, electric organ morphology, and the electric organ discharge. This paper concludes the documentation of the diversity of *Gymnotus* from the region of Tefé, near the confluence of the Rio Solimões (Amazon) with the Rio Japurá. The three new species described here bring to eight the number of species of *Gymnotus* originally described from the Tefé region, and to 11, the total number of species of *Gymnotus* in this region. Two of the new species described here, *Gymnotus obscurus* n. sp. and *Gymnotus varzea* n. sp., are known only from the Quaternary whitewater floodplain (várzea) of the Rio Amazon and/or Río Ucayali. The third new species reported, *Gymnotus curupira* n. sp., is restricted to the terra firme Tertiary peneplain and mainly inhabits isolated swamp pools in the rain forest, which it can reach by moving over-land through moist leaf litter.**

**Três espécies novas, e simpátricas, são descritas do gênero de peixes elétricos Neotropicais, *Gymnotus* (Gymnotidae). Estas espécies, provenientes de localidades próximas às cidades de Tefé (Brasil) e de Iquitos e Jenaro Herrera (Perú) na Bacía Amazônica, são descritas com base em características de morfologia externa, dados merísticos, pigmentação, osteologia e propriedades das descargas do órgão elétrico (DOE). Este artigo conclui a documentação da diversidade de *Gymnotus* da região de Tefé, próxima à confluência dos Rios Solimões e Japurá. Onze espécies de *Gymnotus* têm sido encontrada na região de Tefé, das quais oito foram descritas com base em material desta própria região. Duas das espécies descritas aqui, *Gymnotus obscurus* n. sp. e *Gymnotus varzea* n. sp., ocorrem exclusivamente em várzeas (planícies sazonalmente alagáveis de rios de água branca) do Rio Solimões e/ou do Río Ucayali. A terçeira espécie, *Gymnotus curupira* n. sp., é encontrada exclusivamente em sistemas de terra firme e é comum em poços isolados de água na floresta. *Gymnotus curupira* é capaz de percorrer distâncias pequenas entre igarapés e tais poços por terra, através de liteira húmida.**

THE Neotropical electric fish genus *Gymnotus* is the most diverse known of the gymnotiform genera, with 30 valid species including the three described in this report (Albert et al., 2004). It is also the most geographically widespread, occurring throughout lowland Middle and South America from southern Mexico to the Pampas of Argentina (Albert, 2001). Albert and Crampton (2003) summarize the diagnostic characters of *Gymnotus* and recognize three species groups within the genus: *Gymnotus cylindricus*, *Gymnotus pantherinus*, and *Gymnotus carapo* species-groups (Appendix 1). Members of the *G. carapo* group, including the three species described here, can be distinguished from species in the *G. pantherinus* and *G. cylindricus* species groups by the possession of a clear or pale patch near the caudal end of the anal fin and the presence of two (vs one) laterosensory canal pores in the preopercular-mandibular series of the dorso-posterior portion of the preopercle (Albert et al., 2004).

*Gymnotus* is the focus of intensive ongoing taxonomic attention and may now be the best known of all the Neotropical electric fish genera (Albert et al., 2004). The number of valid species increased from one to nine between 1758 and 1994 (Mago-Leccia, 1994) and, subsequently, to 30 (Appendix 1). This recent acceleration in the rate of species descriptions is attributable not only to a renewed interest in the alpha-taxonomy of this genus but also to the exploration of new regions of the Neotropics and to collecting in previously undersampled habitats such as the root mats of floating macrophytes

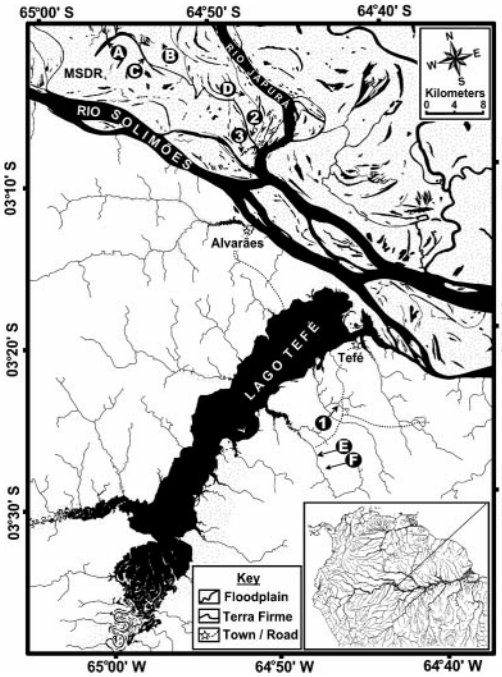

Fig. 1. Map of Tefé area, Brazil showing positions of the holotype localities of 1, *Gymnotus curupira* n. sp.; 2, *Gymnotus obscurus* n. sp.; 3, *Gymnotus varzea* n. sp. Areas exposed to an annual flood regime are stippled. Quaternary floodplain systems: (A) whitewater floodplain (várzea) lake; (B) seasonally inundated forest; (C) cano (seasonally flowing channel draining várzea); (D) paraná (channel connected at both ends to main river channel). Tertiary terra firme systems: (E) terra firme streams, (F) ephemeral rain-forest swamps. See Crampton (1998b) for detailed description of habitats A–E. MSDR = Mamirauá Sustainable Development Reserve. Base map traced from 1999 1: 150,000 Landsat TM5 images. Extent of annual flooding plotted from June 1995 NASDA JERS-1 image.

(Crampton, 1998a; Albert and Crampton, 2001).

Of the 30 valid species of *Gymnotus*, 18 are known from, and 13 are endemic to the Amazon Basin (Appendix 1). The Western Amazon hosts 15 species, of which nine are endemic. Ten of the Amazonian species of *Gymnotus* are known from the seasonally anoxic and perennially hypoxic várzea floodplains of major whitewater rivers, and of these, eight are apparently restricted to this habitat alone (Appendix 1). Nine Amazonian species are known from habitats in the Amazon's terra firme peneplain, and of these, three are restricted to this habitat.

Eleven species of *Gymnotus* are known to occur within 50 km of the town of Tefé, Brazil, near the confluence of the Rio Solimões (Amazon) with the Rio Japurá. (Fig. 1). These are *G. carapo* (redescription in Albert and Crampton, 2003), *Gymnotus coatesi* (redescription in Crampton and Albert, 2004), *G. coropinae* (redescription in Crampton and Albert, 2003), *Gymnotus arapaima*, *Gymnotus jonasi*, *Gymnotus mamiraua*, *Gymnotus onca*, *Gymnotus melanopleura* (described in Albert and Crampton, 2001), and the three new species described here. The description of the three new species reported here concludes the documentation of the species of *Gymnotus* in the Tefé region encountered during extensive sampling. This is the most diverse regional assemblage of *Gymnotus* known.

## MATERIALS AND METHODS

Specimens and their electric organ discharges (EODs) were captured as part of a long-term, multihabitat sampling program undertaken by one of us (WGRC) near the confluence of the Rio Solimões and the Rio Japurá in the Brazilian Amazon between 1993 and 2002 (Fig. 1). Additional specimens of *G. curupira* n. sp. and *Gymnotus varzea* n. sp. were collected by WGRC near the confluence of the Río Marañon and Río Ucayali in the Peruvian Amazon. Floating meadows of macrophytes in whitewater floodplains (várzeas) were sampled using a 30 × 4 mm seine-net with 5 mm stretched mesh or with a 0.3–0.4 m diameter dip-net with 3–4 mm stretched mesh. The leaf-litter and submerged roots of streams and swamp pools in terra firme rain forest were sampled with a similar dip-net. Sampling was sometimes assisted with a portable electric-fish detector comprising a custom-built differential amplifier and loud-speaker connected to electrodes on the end of a submersible pole. The following water quality parameters were measured at the collecting localities: conductivity using a Hanna 9033 electronic meter; dissolved oxygen using a Griffin 41 electronic meter or LaMotte Winkler Titration kit; pH using a Jenway 3071 electronic meter; temperature using an Oakton Temp-5 electronic meter or similar digital thermocouple/thermister device. Specimen sizes are all reported as total length (TL) in millimeters. Field numbers for specimens collected by the senior author follow a standard format: for example, WGRC 01.300498 (first specimen collected and recorded on 30 April 1998). The number prefix NR refers to specimens for which satisfactory EOD recordings are not available. A small number of specimens of *G. curupira* and *G. varzea* (but no further specimens of *Gymnotus obscurus* n. sp.) were encountered during a survey of around 3200 museum specimens of *Gymnotus*, including all the main Amazon basin holdings. The materials examined in this survey are mostly listed in Albert (2001), Albert and Crampton (2001, 2003), Crampton and Albert (2003), Crampton et al. (2003), Crampton and Albert (2004), and Albert et al. (2004). Institutional abbreviations presented here follow Reis et al. (2003) with the addition of IDSM (Instituto de Desenvolvimento Sustentável Mamirauá, Tefé), IIAP (Instituto de Investigaciones de la Amazonía Peruana, Iquitos), and UUZM (Uppsala University Zoological Museum, Uppsala).

Morphometric and meristic data, and descriptions of coloration for *G. curupira* and *G. varzea* are combined from populations collected near the confluence of the Rio Solimões and Rio Japurá in the Brazilian Amazon and from near the confluence of the Río Marañon and Río Ucayali in the Peruvian Amazon. Morphometric and meristic data and descriptions of pigmentation for *G. obscurus* are confined to the type series, which comprises all available specimens of this rare species. Morphometric data were taken as point-to-point linear distances from standardized landmarks on the left side of specimens using digital calipers to the nearest millimeter. Protocols for measurements follow those of Albert and Crampton (2001, 2003) and Crampton (2003), and abbreviations are given in Table 1. Morphometric data are used for comparative analyses between adult specimens alone. Adults are defined here as specimens with morphological, although not necessarily reproductive, maturity. This corresponds to 120 mm TL in all three species described here (see Fig. 2). Morphological measurements as a proportion of TL were not included for analysis in specimens with damage to the caudal appendage exceeding an estimated 5% of intact TL. Meristic and scale count procedures follow Albert and Crampton (2001), and abbreviations are given in Table 2. We refer to the vertical bars of *Gymnotus* as ''bands,'' as has become the standard in the literature on this genus. Descriptions of dentition and other osteological characters were taken from type-series specimens that were cleared and stained (denoted as c&s) and dissected following the methods outlined in Albert and Crampton (2001).

EOD recording were taken from single specimens restrained in a nylon cage and placed in a 5–20-liter plastic tank containing water from the capture site. Water temperature was held within ± 1 C of the temperature at the collecting locality. Signals were picked up from silver wire electrodes placed in front of and behind each fish and along the long axis of its body, with a ground electrode in the center. The electrodes were connected to an AC-coupled differential amplifier (custom built) with a frequency response of ± 3 dB from 0.2–110 kHz. Some amplified EODs were stored on digital audiotape using a Sony TC-D3 or D7 DAT recorder (sampling frequency 48 kHz) and later redigitized from the analog output using an Edirol UA5 A-D instrument (sampling rate 96 kHz, resolution 24 bits). Other EODs were digitized in the field directly using the Edirol UA5. EOD durations reported here are measured from the first and last points that deviated from the baseline by more than 1% of the normalized peak-to-peak amplitude using custom written Java software.

Sexual maturity and sex can be assessed reliably in *Gymnotus* only by dissection. The testes of mature males are pinkish-white and smooth, whereas the ovaries are packed with eggs which yellow when mature. Juveniles cannot be sexed reliably using morphology. Dietary preferences were determined by the qualitative visual analysis of stomach contents placed in a glass dish under a stereo microscope.

The differential diagnoses presented here are limited to salient characters that do not necessitate clearing and staining and, with the exception of meristic counts, refer to conditions observed in adults. We differentiate the new species presented reported here only from congeners known from the Amazon and Orinoco Basins and the Guyana Shield (sensu Albert, 2001). With the exception of *G. carapo* (also known from the North East of Brazil), none of the *Gymnotus* species in these regions is known elsewhere, and vice versa (Appendix 1). Comparative morphometric and meristic data for the differential diagnoses are from Albert and Crampton (2003) and Crampton et al. (2003).

### *Gymnotus curupira*, new species
Figures 3–4

*Holotype.*—MZUSP 60607, WGRC 05.160300, male, 235 mm, Brazil, Amazonas, Rio Tefé, Lago Tefé, Igarapé Curupira, terra firme swamp, 0.5 km west of Estrada Agrovila, Municipality of Tefé, 3°26′01″S, 64°43′47″W, collected by W. Crampton, 16 March 2000.

*Paratypes.*—IDSM 425, 1, WGRC NR03.210201, male, 172 mm, Brazil, Amazonas, Rio Tefé, Lago Tefé, Igarapé Repartimento, terra firme swamp 1.5 km downstream from bridge on Estrada Agrovila, Municipality of Tefé, 3°24′28″S, 64°44′10″W, 21 February 2001. INPA 18381, 1, WGRC 02.050600, 129 mm, locality as IDSM 425, 05 June 2000. INPA 18382, 1, WGRC 02.210201, female, 155 mm, 21 February 2001.

Table 1. Morphometric Data for Adult Specimens (Larger than 120 mm) of Three New Species of *Gymnotus* from the Amazon Basin. Data for *Gymnotus curupira* n. sp. and *Gymnotus varzea* n. sp. are pooled from populations near Tefé in the Brazilian Amazon and from localities in the Upper Amazon of Peru (see text). Data for *Gymnotus obscura* from type series near Tefé only. 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; BO, branchial opening; PA, preanal distance; P1, pectoral-fin length; AF, anal-fin base length; BD, body depth; BW, body width. TL and HL expressed in millimeters. 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. curupira* n. sp. | | *G. obscura* n. sp. | | *G. varzea* n. sp. | |
|---|---|---|---|---|---|---|
| | Range | Mean | Range | Mean | Range | Mean |
| TL | 135–235<br>(13) | — | 121–215<br>(13) | — | 122–285<br>(34) | — |
| HL | 13.5–21.0<br>(12) | — | 14.3–21.4<br>(13) | — | 12.2–26.3<br>(32) | — |
| HL %* | 8.8–10.2<br>(10) | 9.5 | 9.9–11.8<br>(12) | 10.8 | 9.0–10.4<br>(31) | 9.8 |
| PR % | 34.3–36.0<br>(11) | 35.8 | 33.3–39.9<br>(13) | 37.3 | 29.7–35.8<br>(31) | 33.5 |
| MW % | 41.4–56.8<br>(12) | 48.9 | 37.3–46.3<br>(13) | 42.7 | 35.0–45.9<br>(29) | 40.0 |
| PO % | 59.3–66.7<br>(11) | 63.5 | 59.9–64.5<br>(13) | 62.1 | 58.7–66.3<br>(32) | 63.0 |
| IO % | 42.1–47.4<br>(12) | 44.1 | 35.2–43.3<br>(13) | 39.5 | 32.5–44.3<br>(31) | 39.9 |
| BD %* | 7.4–8.6<br>(12) | 8.2 | 9.0–10.8<br>(12) | 9.5 | 8.3–10.8<br>(31) | 9.2 |
| BW %* | 5.7–6.6<br>(12) | 6.3 | 5.3–6.3<br>(12) | 5.9 | 4.6–6.4<br>(31) | 5.5 |
| BW/BD | 0.68–0.83<br>(9) | 0.76 | 0.51–0.68<br>(12) | 0.62 | 0.47–0.69<br>(31) | 0.61 |
| HD % | 54.4–59.6<br>(9) | 56.3 | 58.1–64.3<br>(13) | 61.7 | 59.9–73.9<br>(31) | 66.2 |
| HW % | 64.0–74.9<br>(9) | 70.1 | 55.9–68.3<br>(12) | 62.4 | 54.8–73.6<br>(31) | 63.0 |
| BO % | 29.1–39.7<br>(7) | 33.0 | 30.9–36.5<br>(6) | 34.5 | 32.7–46.4<br>(27) | 38.5 |
| PA % | 74.3–117.7<br>(9) | 96.7 | 71.3–94.2<br>(13) | 81.3 | 68.3–108.5<br>(30) | 92.0 |
| P1 % | 42.2–55.0<br>(9) | 48.2 | 40.6–55.0<br>(13) | 48.7 | 42.8–57.5<br>(28) | 50.0 |
| AF %* | 73.3–82.5<br>(7) | 78.3 | 70.1–83.1<br>(12) | 78.9 | 72.7–84.5<br>(26) | 81.0 |

INPA 60608, 3: WGRC 02.010200, 102 mm; WGRC 03.010200, female, 116 mm; WGRC 04.010200, female, 135 mm, locality as IDSM 425, 01 February 2000. INPA 60609, 3: WGRC 01.191199, 98 mm; WGRC 03.191199, 116mm; WGRC 04.191199, 87 mm, locality as IDSM 425, 19 November 1999. MZUSP 75143, 1, WGRC 04.210999, 102 mm, locality as IDSM 425, 21 September 1999. MZUSP 75144, 1, WGRC 05.210999, 99 mm, collected with MZUSP 75143. MZUSP 75149, 1, WGRC 01.050600, 194 mm, collected with INPA 18382. MZUSP 75150, 1, WGRC 01.291100, 143 mm, locality as IDSM 425, 29 November 2000. MZUSP 75151, 1, WGRC 02.291100, 121 mm, collected with MZUSP 75150. MZUSP 75145, 1, WGRC 01.040300, female, 150 mm (c&s), locality as holotype, 04 March 2000. MZUSP 75146, 1, WGRC 02.040300, 141 mm (c&s), collected with MZUSP 75145. MZUSP 75147, 1, WGRC 03.040300, female, 173 mm, collected with MZUSP 75145. MZUSP 75148, 1, WGRC 07.130300, female, 196 mm, locality as holotype, 13 March 2000.

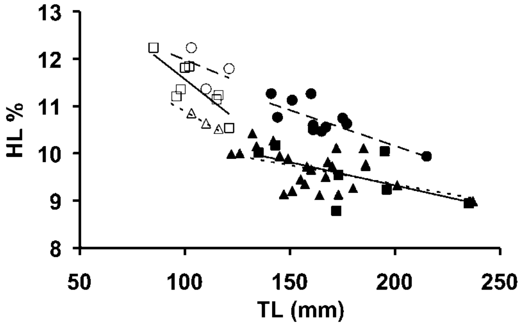

Fig. 2. Total length (TL) versus head length as a percentage of TL (HL%) for three species of *Gymnotus* from the Amazon Basin showing adult (solid symbol) and juvenile (open symbol) head proportions. Size of morphological maturity (adult size) is inferred from the inflection of these plots, which is in all species 120 mm TL. Most individuals achieved reproductive maturity at a larger size. *Gymnotus curupira* n. sp. = squares, solid line; *Gymnotus obscurus* n. sp. = circles, long dashes; *Gymnotus varzea* n. sp. = triangles, short dashes.

*Nontype material.*—MCZ 51710, 7, 89–197 mm, Ecuador, Napo, Río Napo, Río Payamino, Puerto Coca, approximately 00°29′S, 76°58′W, T. Roberts, 25 November 1971. UF 144627, 2, WGRC 01.120104, 164 mm; WGRC 02.120104, 148 mm, Peru, Loreto, Río Ucayali, small quebrada 3 km South of Jenaro Herrera, 04°55.63′S, 73°39.27′W, W. Crampton, H. Ortega, R. Reis, F. Lima, 12 January 2004. UF 144628, 2, WGRC 07.160104, 79 mm, WGRC 08.160104, 144 mm (c&s), Peru, Loreto, Río Ucayali, small quebrada 0.3 km north of km-3.9 on abandoned road from Jenaro Herrera to Colonia Angamos, 04°53.90′S, 73°38.36′W, W. Crampton, H. Ortega, R. Reis, F. Lima, 12 January 2004. NRM 27647, 1, 189 mm, Peru, Loreto, Río Putumayo, El Estrecho, 02°28′S, 72°42′W, S. Kullander, 21 July 1986.

*Diagnosis.*—*Gymnotus curupira* is unique among congeners endemic to the Amazon and Orinoco Basins, and the Guyana Shield in possessing a color pattern of 14–20 oblique, dark, pigment bands with wavy and irregular margins in which the majority of bands are branched ventrally to form inverted Y-shaped patterns (in adults), in which the dark bands are about twice as broad as the pale interbands, and in which the bands rarely form X-shaped patterns at midbody (Fig. 4). *Gymnotus curupira* can be further distinguished from congeners endemic to the Amazon-Orinoco Basins and the Guyana Shield in possessing the following unique combination of characters: 1, clear (unpigmented) patch at the

TABLE 2. MERISTIC DATA FOR THREE NEW SPECIES OF *Gymnotus* FROM THE AMAZON BASIN. Data for *Gymnotus curupira* n. sp. and *Gymnotus varzea* n. sp are pooled from populations near Tefé in the Brazilian Amazon and from localities in the Upper Amazon of Peru (see text). Data for *Gymnotus obscura* from type series near Tefé only. 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). *N*-values (in parentheses) vary because counts were excluded from specimens with damage or unusual preservation artifacts.

| | BND | | AFR | | P1R | | SAL | | CEP | | APS | | PCV | | PLR | | PLL | | VLR | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Range | Med. | Range | Med. | Range | Mode | Range | Mode | Range | Mode | Range | Mode | Range | Mode | Range | Med. | Range | Med. | Range | Med. |
| *G. curupira* n. sp. | 14–20<br>(19) | 19 | 230–320<br>(15) | 255 | 16–17<br>(19) | 16 | 5–8<br>(19) | 6 | 3<br>(19) | 3 | 7–8<br>(7) | 7 | 34–36<br>(19) | 35 | 59–62<br>(8) | 60 | 104–140<br>(16) | 114 | 0–11<br>(15) | 8 |
| *G. obscura* n. sp. | 14–20<br>(16) | 17 | 210–250<br>(11) | 230 | 20–22<br>(16) | 21 | 5–7<br>(15) | 6 | 3–4<br>(14) | 4 | 6–7<br>(6) | 6 | 35–37<br>(16) | 35 | 50–56<br>(6) | 54 | 108–132<br>(11) | 115 | 15–30<br>(13) | 19 |
| *G. varzea* n. sp. | 16–22<br>(37) | 18 | 230–310<br>(28) | 255 | 16–19<br>(38) | 18 | 5–8<br>(37) | 6 | 4<br>(37) | 4 | 4–6<br>(18) | 6 | 35–40<br>(33) | 37 | 51–55<br>(18) | 53 | 106–135<br>(20) | 121 | 14–29<br>(25) | 20 |

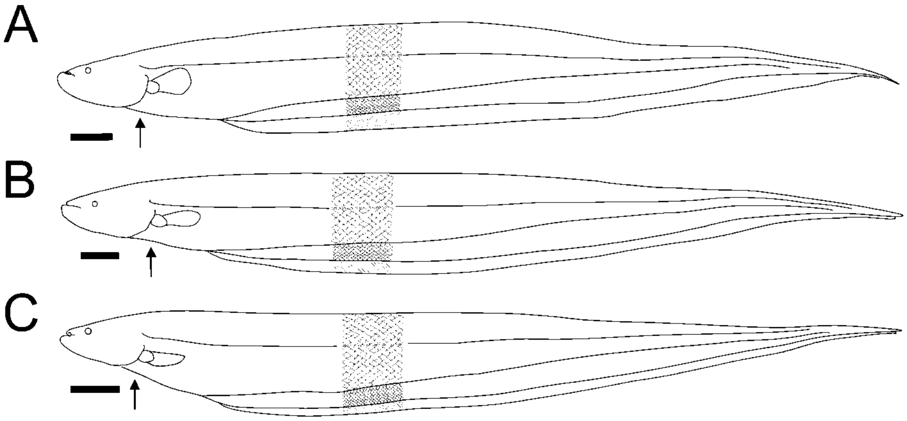

Fig. 3. Diagrammatic representation of body outlines and squamation of the holotypes of three new species of *Gymnotus*: (A) *Gymnotus curupira* n. sp., MZUSP 60607; (B) *Gymnotus obscurus* n. sp. MZUSP 60604; (C) *Gymnotus varzea* n. sp. MZUSP 60601. Arrows indicate position of anus. Scale bars = 10 mm.

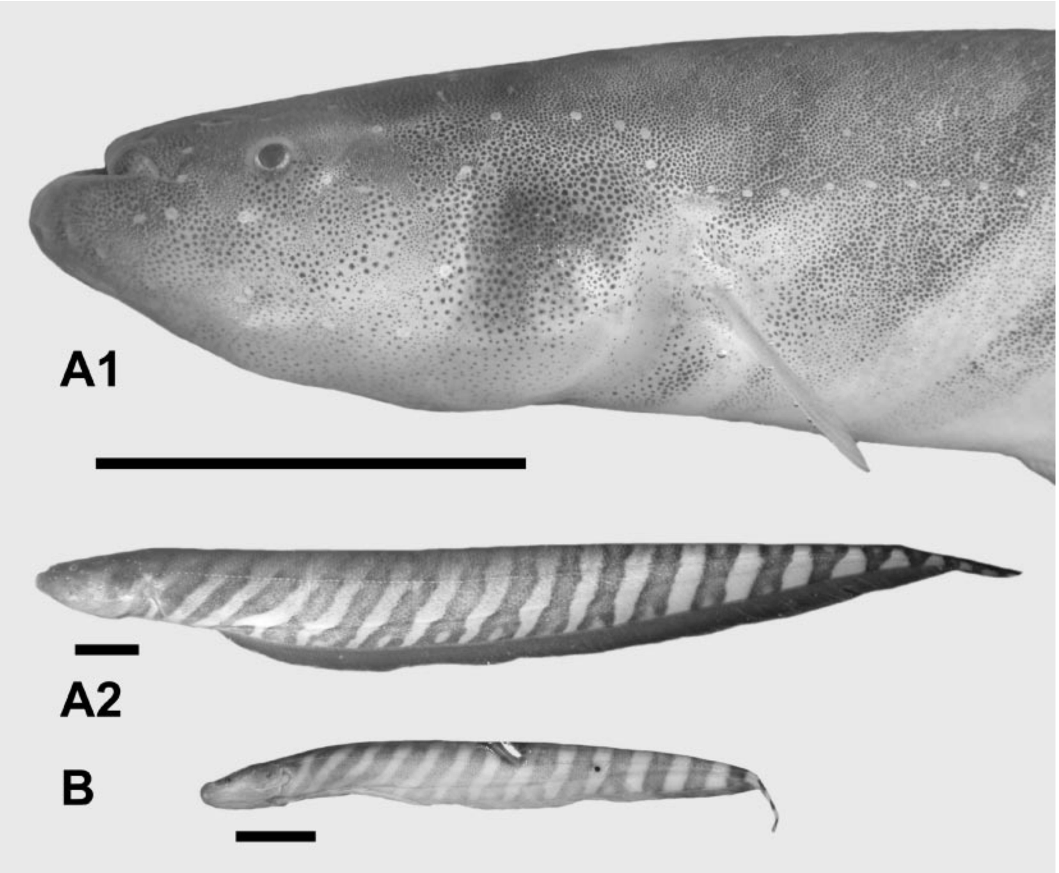

Fig. 4. *Gymnotus curupira* n. sp. A1 (head) and A2 (body), MZUSP 75150; B, MZUSP 60609, WGRC 01.191199. Scale bars = 10 mm.

caudal end of the anal-fin membrane in specimens 60–235 mm (not present in all members of *G. pantherinus* species-group, hence diagnosing *G. curupira* as member of *G. carapo* species group); 2, bands never divided to form band pairs, sensu Albert et al. (1999), in contrast to *G. arapaima*, *G. carapo* and *Gymnotus diamantinensis*; 3, body depth 7.4–8.6% TL versus 8.7–12.6 in all other species from *G. carapo* species group except *G. varzea* (8.3–10.8), versus 5.5–8.5 in *G. coropinae*, and versus 6.7–7.4 in *G. coatesi*; 4, head length 8.8–10.2% TL versus 10.2–14.2 in *G. arapaima*, *G. carapo*, *G. diamantinensis*, *Gymnotus ucamara*, and *G. melanopleura*; 5, preorbital length 34.3–36.0% HL versus 26.4–29.2 in *G. jonasi*; 6, mouth width 41.4–56.8% HL versus 26.9–39.5 in *G. arapaima* and *G. diamantinensis* and versus 27.8–40.6 in all members of the *G. pantherinus* species group except *Gymnotus anguillaris*, *Gymnotus cataniapo*, and *Gymnotus javari*; 7, interorbital length 42.1–47.4% HL versus 26.4–41.3 in all members of the *G. pantherinus* species group except *Gymnotus anguillaris*, and versus 31.0–40.8 in *G. arapaima* and *Gymnotus mamiraua*; 8, body width 5.7–6.6% TL versus 3.5–5.6 in *Gymnotus coropinae*, *G. jonasi*, *G. onca*, *G. pedanopterus*, and *Gymnotus stenoleucus*, and versus 7.0–8.7 in *G. ucamara*; 9, body width/body depth ratio 0.68–0.83 versus 0.47–0.68 in *G. diamantinensis*, *G. obscurus*, *G. melanopleura*, and *G. stenoleucus*, and versus 0.47–0.69 in *G. varzea*; 10, head depth 54.4–59.6% HL versus 59.6–73.9 in *G. anguillaris*, *Gymnotus cataniapo*, *Gymnotus onca*, *G. diamantinensis*, *Gymnotus mamiraua*, and *G. varzea*; 11, head width 64.0–74.9% HL versus 47.1–63.6 in *G. diamantinensis*, *G. coatesi*, *G. jonasi*, *G. onca*, *G. pedanopterus*, and *G. stenoleucus*; 12, preanal length 74.3–117.7% HL versus 50.6–74.2 in *G. arapaima* and *G. pedanopterus*, and versus 64.5–75.0 in *G. ucamara*; 13, pectoral-fin length 42.2–55.0% HL versus 29.3–41.8 in *G. diamantinensis*, *G. cataniapo*, and *G. pedanopterus*; 14, dark bands 14–20 versus 23–35 in *G. cataniapo* and versus none in *G. onca* (spotted); 15, anal-fin rays 230–320 versus 135–211 in *G. jonasi*, *G. onca*, and *G. diamantinensis*; 16, pectoral-fin rays 14–17 versus 20–22 in *G. obscurus*, and versus 11–15 in *G. diamantinensis*, *G. mamiraua*, and all members of *G. pantherinus* species group except *G. anguillaris* and *G. coropinae*; 17, scales above lateral line 5–8 versus 8–13 in *G. pedanopterus* and *Gymnotus tigre*; 18, caudal electroplate rows invariably 3, versus 2–3 in all members of *G. pantherinus* species group, versus 3–4 in *G. arapaima*, *G. carapo*, *G. mamiraua*, and *G. obscurus*, versus invariably 4 in *G. ucamara* and *G. varzea*, and versus 5–6 in *G. tigre*; 19, scales over anal-fin pterygiophores 7–8 versus 4–6 in *G. diamantinensis*, *G. mamiraua*, *G. varzea*, *G. jonasi*, *G. onca*, and *G. stenoleucus*, and versus 9–16 in *G. arapaima*, *G. tigre*, *G. ucamara*, and *G. javari*; 20, precaudal vertebrae 34–36 versus 31–32 in *G. pedanopterus*, versus 31–34 in *G. mamiraua* and *G. ucamara*, versus 36–39 in *G. jonasi*, and versus 37–51 in *G. tigre*, *G. anguillaris*, *G. cataniapo*, *G. coatesi*, *G. coropinae*, *G. javari*, and *G. stenoleucus*; 21, pored lateral-line scales to first ventral ramus 59–62 versus 31–61 in *G. diamantinensis*, *G. mamiraua*, *G. obscurus*, *G. ucamara*, *G. varzea*, *G. coropinae*, *G. jonasi*, and *G. onca*, and versus 62–78 in *G. tigre*; 22, total pored lateral-line scales 104–140 versus 71–102 in *G. diamantinensis*, *G. mamiraua*, *G. ucamara*, *G. coatesi*, *G. coropinae*, *G. jonasi*, *G. onca*, and *G. stenoleucus*; 23, ventrally oriented lateral-line rami 0–11 versus 10–22 in *G. arapaima*, versus 11–19 in *G. ucamara*, and versus 14–55 in *G. obscurus*, *G. tigre*, *G. varzea*, *G. cataniapo*, *G. coatesi*, *G. jonasi*, *G. melanopleura*, and *G. onca*.

*Description.*—Body shape and pigment patterns illustrated in Figures 3 and 4. Morphological and meristic data (Tables 1 and 2, respectively) pooled from 15 specimens of type-series (from Brazilian Amazon) and four specimens of nontype material from Peruvian Amazon (lots UF 144627, 144628). Morphometric and meristic data not taken from nontype lots MCZ 51710 and NRM 27647 because of poor preservation status. Size up to 235 mm and 30g in life. Maturity at about 170 mm in males and 150 mm in females. Sexually monomorphic other than size differences in both immature and breeding condition.

Scales cycloid, ovoid, present on entire postcranial portion of body from nape to tip of caudal appendage. Lateral-line scales in 150 mm specimen (MZUSP 75145, WGRC 01.040300) 1.3 mm high by 1.7 mm long in humeral region, 2.0 mm high by 2.1 mm long at midbody, 1.4 mm high by 2.1 mm long dorsal to anterior margin of clear patch on anal fin. Gape size in mature specimens very large, extending to or beyond posterior nares. Mouth position superior, lower jaw extending beyond 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. Ethmoid region between anterior nares broad, its anterior margin straight. Eye without free orbital margin, position lateral, lower margin of eye dorsal to rictus.

Premaxilla with 11–13 (mode 12, $N = 4$)

teeth in single row along outer margin, the anterior 8–10 arrow-head shaped, the posterior 3–5 conical. Dentary with 12–15 (mode 13, $N$ = 4) teeth in single row, the anterior 3–4 arrow-shaped, the posterior 8–11 conical or flattened posteriorly. Rib 5 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 all specimens. Anal-fin pterygiophores at posterior end of body cavity equal to or longer than first hemal spine. Caudal appendage long, more than 0.5 times pectoral-fin length in undamaged and unregenerated specimens. Single hypaxial electric organ, extending along entire ventral margin of body and caudal appendage. Three rows of electroplates at one HL distance from end of caudal appendage.

*Color in life.*—Ground color pale brown to yellow in adults and juveniles. Fourteen to 20 dark brown or gray bands on lateral surface extending from nape and pectoral-fin base to tip of caudal appendage and oriented either vertically or obliquely in an anterio-ventral to posterio-dorsal diagonal. No bands divided into double bands. Bands less distinct on the dorsum where they almost merge with darker ground color. Pigment density greater at band margins than in middle. Band-interband contrast sharper caudally and bands thinner and more oblique anteriorly. Most bands completely undivided, 7–9 bands divided ventrally in the region over the pterygiophores at midbody in specimens greater than 100 mm. In some specimens, several bands branch dorsally posterior to midbody (but do not form double bands). All band margins wavy and approximately parallel, although bands broader ventrally in the midbody region and broader dorsally in caudal regions. Three dark bands meet irregularly at ventral midline in region anterior to anal-fin origin. Juveniles possess more regularly arrayed alternating pigment bands with sharper band-interband contrast.

Head never banded, spotted or blotched, dark-brown dorsally and over opercle, grading to pale yellow ventrally at branchial isthmus, numerous minute chromatophores speckled over branchiostegal membranes and ventral surface of head. Rosy hue to operculum from underlying gills in juveniles. Pectoral-fin rays and interradial membranes uniform dark gray. Anal-fin rays gray. Anal-fin membrane never blotched, spotted or marked, divided into three parts along body axis: in adults anterior 50% light gray or brown, middle 30% dark gray, posterior 20% hyaline. In juveniles, anterior 50% hyaline, middle 30% light gray, posterior 20% hyaline. Specimens fixed in 10% formalin and preserved for up to six years in 70% ethanol maintain approximate colors of life, although the darker pigments tend to pale with time.

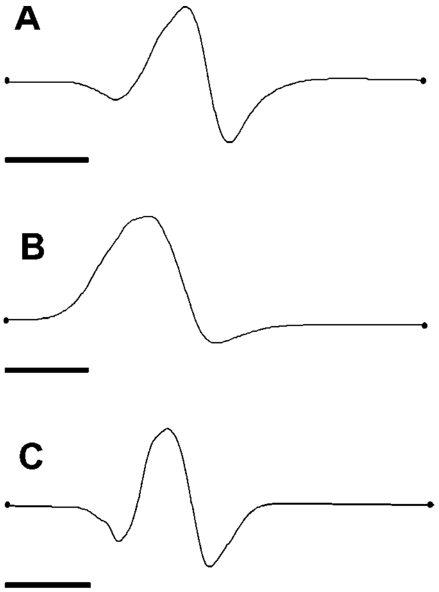

Fig. 5. Electric Organ Discharge (EOD) waveforms of sexually immature adult specimens of three new species of *Gymnotus.* EODs plotted head-positive upwards and scaled to the same peak-to-peak height and time base. Scale bar = 5 mm. (A) *Gymnotus curupira* n. sp. MZUSP 75145; (B) *Gymnotus obscurus* n. sp. UF 118836; (C) *Gymnotus varzea* n. sp. BMNH 1998.3.12.11.

*Electric organ discharge.*—EOD waveform with total duration of 1.1–1.5 msec ($N$ = 20) and invariably comprising three phases. EOD waveform similar in all recorded specimens, with no sexual differences. A typical example is illustrated in Figure 5.

*Intraspecific variation.*—Unlike some species of *Gymnotus* that display polymorphism of banding (e.g. *G. stenoleucus*; Mago-Leccia, 1994) and *G. jonasi* (Albert and Crampton, 2001), intraspecific color variation in *G. curupira* is apparently restricted to growth-related changes (see above), with specimens of the same size strongly resembling each other. We observed no sexual differences in pigmentation, EOD waveform or non-reproductive morphology, other than a slight difference in maximum size (see Description). We also observed no salient interpopulation differences in pigmentation between specimens of the type series from the Brazilian Amazon and

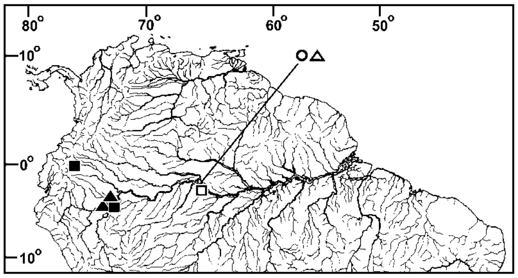

Fig. 6. Part of South America showing collection records of three new species of *Gymnotus*: *Gymnotus curupira* n. sp. = squares; *Gymnotus obscurus* n. sp. = circles; *Gymnotus varzea* n. sp. = triangles. Open symbols are type localities. Some symbols represent more than one lot or locality. Base map by M. Weitzman.

nontype specimens from the Peruvian Amazon. Likewise, morphometric and meristic data for specimens from the Peruvian Amazon all fell well within the range of those from Brazilian Amazon. A single cleared-and-stained specimen from the Peruvian Amazon (UF 144628, WGRC 08.160104) exhibited no salient osteological differences to specimens from the Brazilian Amazon. EOD waveforms from the Brazilian Amazon and Peruvian Amazon were similar, with no quantifiable consistent differences in the Peak Power Frequency of the Fast Fourier Transform, nor in the relative amplitude or duration of the three phases of the waveform.

*Distribution.*—The type series is from terra firme forest swamps and stream pools of the Rio Tefé drainage near the town of Tefé, Amazonas, Brazil (Fig. 1). *Gymnotus curupira* n. sp is also known from terra firme stream pools near the town of Jenaro Herrera in the Upper Amazon of Peru (near the confluence of the Río Marañon and Río Ucayali), and from localities in the Napo and Putumayo basins of Peru (Fig. 6).

*Ecology.*—In the region of the type locality, *G. curupira* occurs almost exclusively in shallow, often ephemeral swamps in terra firme forests above the Amazon floodplain. These swamps are not inundated by the seasonal rise of the Amazon and its tributaries but by groundwater and rainwater or, sometimes, from the flash-flooding of adjacent streams. Terra firme swamps are usually found in poorly drained depressions and shallow valleys. Water depth rarely exceeds more than 30 cm, and the substrate consists of a tangle of leaf litter, palm fronds, and branches. The standing water is usually overgrown with a variety of rooted nonwoody plants including *Philodendron* spp., *Montrichardia arborescens* (Araceae), and *Ischnosiphon* spp. (Marantaceae). The understory and canopy are dominated by palms and riparian angiosperm trees (Prance, 1979). There are no published accounts of the water chemistry or ichthyofauna of Amazonian terra firme swamps, despite the fact that satellite images reveal that they cover a large area of the Amazon Basin (Junk, 1997). In the Tefé region, terra firme swamp water is cool (23–25 C), unsedimented, clear or tannin-stained, and characterized by extremely low pH (2.5–5). The electrical conductivity is low throughout the year (5–15 $\mu$Scm$^{-1}$), reflecting its rainwater origin. Dissolved oxygen concentrations are usually extremely low (0–0.5mg/l), although they may rise to 1–2mg/liter following heavy rain. *Gymnotus curupira* undertakes aerial respiration by gulping atmospheric air into the hypervascularized posterior chamber of the gas bladder (Liem et al., 1984; Crampton, 1998a). Specimens held in poorly oxygenated water from the capture locality rose to the surface and gulped air about once every 30 sec to 3 min. Air breathing frequency rose with an increase in swimming activity.

*Gymnotus curupira* must colonize terra firme swamps from nearby streams where they are found very seldomly in static side branches and cut-off meanders. Most terra firme swamps are constantly replenished from ground water but experience the occasional influx of water from the flooding of nearby streams. These events may allow dispersal from streams to swamps and vice versa. Nonetheless, *G. curupira* is also found in small swamp pools that are never connected to streams and that dry out completely during periods of draught. A small (98 mm) specimen of *G. curupira* was observed on a rainy night crossing waterlogged leaf litter between the swamp from which the holotype is described and a smaller, ephemeral pool about 15 m away. It moved by wriggling and flipping in short jumps. *Gymnotus curupira* is able to survive out of water for many hours on a moist substrate (pers. obs). Two other gymnotiform species are found in terra firme swamps: *G. coropinae* and *G. arapaima*, although only in swamps that are permanently or intermittently connected to streams. In the Peruvian Amazon near the confluence of the Río Marañon and Río Ucayali, *G. curupira* was found in still pools of slow-flowing terra firme forest streams that resembled those of the Tefé region in terms of soil and substrate structure, water chemistry, forest structure and floral composition and also the ichthyofauna in general.

The diet of *G. curupira* is dominated by chironomid larvae, insect nymphs, and allochthonous invertebrates that fall from the forest canopy. In the Tefé region, sexually mature male and female *G. curupira* as well as juveniles are found in terra firme swamps, indicating that this species breeds and spends its entire lifecycle in this habitat.

*Etymology.*—Named for the Igarapé Curupira, a forest stream near Tefé and location of the holotype. The Curupira is a mythical spirit of the Amazon rain forest (Smith, 1996). Name applied as a noun in apposition.

### *Gymnotus obscurus* new species

Figures 3, 7

*Holotype.*—MZUSP 60604, WGRC 02.100599, 215 mm, Brazil, Amazonas, Municipality of Alvarães: Mamirauá Sustainable Development Reserve (Mamirauá Reserve), Cano do Lago Mamirauá at Comunidade Boca do Mamirauá, 3°06′37″S, 64°47′49″W, collected by W. Crampton, 10 May 1999.

*Paratypes.*—BMNH. 1998.3.12.19, 1, WGRC 10.070597, female, 161 mm, Brazil, Amazonas, Municipality of Alvarães, Mamirauá Reserve, Ressaca da Vila Alencar, 3°07′42″S, 64°48′02″W, 07 May 1997. BMNH 1998.3.12.20, 1, WGRC 11.070597, 151 mm, collected with BMNH. 1998.3.12.19. BMNH 1998.3.12.21, 1, WGRC 16.070597, 94 mm (c&s), collected with BMNH. 1998.3.12.19. IDSM 432, 1, WGRC 01.220500, 110 mm, locality as BMNH. 1998.3.12.19, 22 May 2000. INPA 18388, 2: WGRC 01.190500, 111 mm; WGRC 04.190500, 154 mm, Mamirauá Reserve, Cano do Lago Sapucaia, 3°04′07″S, 64°48′32″W, 19 May 2000. MZUSP 75152, 1, WGRC 03.190500, 160 mm, collected with INPA 18388. MZUSP 60605, 1, WGRC 08.170597, male 161 mm (c&s), locality as BMNH. 1998.3.12.19, 17 May 1997. MZUSP 60606, 1, WGRC 03.160698, 122 mm, Mamirauá Reserve, Cano do Lago Mamirauá nr. Cano do Lago Arauaé, 3°01′38″S, 64°52′35″W, 16 June 1998. MZUSP 75153, 1, WGRC 03.070600, 167 mm, Mamirauá Reserve, Lago Secretaria, 3°06′44″S, 64°48′01″W, 07 June 2000. MZUSP 75154, 1, WGRC 01.120401, 177 mm, locality as holotype, 12 April 2001. MZUSP 75155, 1, WGRC 03.170401, 141 mm, Mamirauá Reserve, Ressaca do Pau, 3°02′18″S, 64°51′58″W, 17 April 2001. MZUSP 75156, 1, WGRC 05.170401, 175 mm, collected with MZUSP 75155. MZUSP 75157, 1, WGRC 07.170401, 165 mm, collected with MZUSP 75155. UF 118833, 2: WGRC 11.030597, 103mm; WGRC 19.030597, 112 mm, locality as BMNH. 1998.3.12.19, 03 May 1997. UF 118837, 1, WGRC NR08.070597, 171 mm, collected with BMNH. 1998.3.12.19. UF 118836, 1, WGRC 06.300497, 144 mm, Mamirauá Reserve, Cano do Lago Rato, 3°02′58″S, 64°51′31″W, 30 April 1997.

*Diagnosis.*—*Gymnotus obscurus* is unique among congeners endemic to the Amazon and Orinoco Basins and the Guyana Shield in possessing: 1, many pectoral-fin rays (20–22 vs 11–19 in other species), and; 2, a color pattern of oblique and undivided thin pale bands, less than one-quarter width of dark bands, with straight high-contrast margins, which extend to the dorsal midline on the anterior half of the body, and of which many are interrupted at the ventral margin of the hypaxial muscles along the anterior two-thirds of the body. *Gymnotus obscurus* may be further distinguished from congeners endemic to the Amazon-Orinoco Basins and the Guyana Shield in possessing the following unique combination of characters: 1, clear (unpigmented) patch at the caudal end of the anal-fin membrane in specimens 60–235 mm (not present in members of *G. pantherinus* species-group, hence diagnosing *G. obscurus* as member of *G. carapo* species group); 2, bands never divided to form band pairs (in contrast to *G. arapaima*, *G. carapo*, and *G. diamantinensis*); 3, 6–27 dorsal lateral-line rami (absent in all species except occasionally in *G. varzea*); 4, body depth 9.0–10.8% TL versus 5.5–.9 in *G. curupira* and all members of *G. pantherinus* species group except *G. anguillaris* and *G. cataniapo*); 5, head length 9.9–11.8% TL versus 39.8 in *G. anguillaris* and *G. onca*, and versus 12.2–14.2 in *G. arapaima* and *G. ucamara*; 6, preorbital length 33.3–39.9% HL versus 26.4–32.8 in *G. jonasi*, *G. melanopleura*, and *G. onca*; 7, mouth width 37.3–46.3% HL versus 26.9–35.1 in *G. coatesi*, *G. jonasi*, and *G. diamantinensis*; 8, body width 5.3–6.3% TL versus 4.7–5.2 in *G. jonasi* and *G. onca*, versus 3.5–5.4 in *G. coropinae*, versus 6.2–9.4 in *G. carapo*, and versus 6.4–8.7 in *G. tigre* and *G. ucamara*; 9, body width/body depth ratio 0.51–0.68 versus 0.68–0.83 in *G. curupira*, *G. anguillaris*, and *G. coatesi*; 10, head depth 58.1–64.3% HL versus 47.6–57.7 in *G. coatesi*; 11, head width 55.9–68.3% HL versus 49.5–55.8 in *G. coatesi* and *G. diamantinensis*; 12, preanal length 71.3–94.2% HL versus 50.6–63.7 in *G. onca* and *G. pedanopterus* and versus 102.3–109.6 in *G. cataniapo*; 13, anal-fin length 70.1–83.1% TL versus 62.9–69.9 in *G. stenoleucus*; 14, 14–20 dark bands versus 23–35 in *G. cataniapo* and versus 0 in *G. onca* (spotted); 15, anal-fin rays 210–250 versus 135–211 in *G. jonasi*, *G. onca*, *G. melanopleura*, and *G. diamantinensis*; 16, scales above lateral line 5–7 versus 8–13 in *G.*

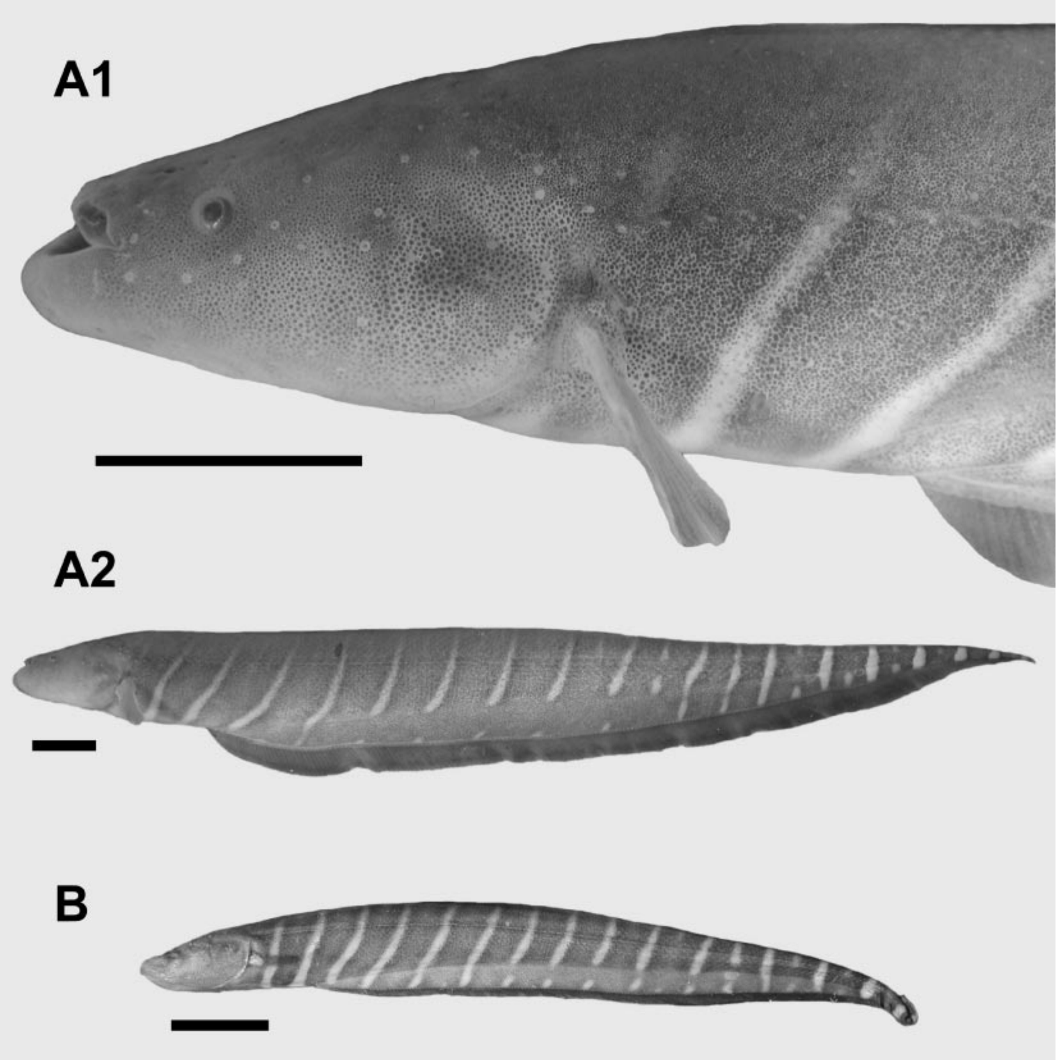

Fig. 7. *Gymnotus obscurus* n. sp. A1 (head) A2 (body), MZUSP 75152; B, UF 118833, WGRC 11.030597. Scale bars = 10 mm.

*tigre*, *G. cataniapo*, *G. melanopleura*, *G. pedanopterus*, and *G. stenoleucus*; 17, caudal electroplate rows 3–4 versus 2–3 in all members of *G. pantherinus* species-group, versus invariably 3 in *G. curupira* and versus 5–6 in *G. tigre*; 18, scales over anal-fin pterygiophores 6–7 versus 7–12 in *G. carapo*, and versus 9–16 in *G. arapaima*, *G. tigre*, *G. ucamara*, and *G. javari*; 19, precaudal vertebrae 35–37 versus 31–34 in *G. diamantinensis*, *G. mamiraua*, *G. ucamara*, and *G. pedanopterus*, versus 37–38 in *G. anguillaris*, and versus 39–51 in *G. tigre*, *G. cataniapo*, *G. coatesi*, *G. coropinae*, *G. javari*, and *G. stenoleucus*; 20, pored lateral-line scales to first ventral ramus 50–56 versus 31–49 in *G. jonasi*, *G. onca*, *G. diamantinensis*, *G. mamiraua*, and *G. ucamara*, and versus 60–78 in *G. tigre*, and *G. cataniapo*; 21, total pored lateral-line scales 108–132 versus 71–102 in *G. diamantinensis*, *G. mamiraua*, *G. ucamara*, *G. coatesi*, *G. coropinae*, *G. jonasi*, *G. onca*, and *G. stenoleucus*, and versus 88–108 in *G. arapaima* and *G. javari*; 22, ventrally oriented lateral-line rami 15–30 versus 0–14 in *G. curupira*, *G. diamantinensis*, *G. mamiraua*, *G. anguillaris*, and *G. pedanopterus*, versus 10–15 in *G. javari*, and versus 29–55 in *G. tigre*.

*Description.*—Body shape and pigment patterns illustrated in Figures 3 and 7. Morphological and meristic data are presented in Tables 1 and 2. Size up to 215 mm and 25 g in life. Maturity at about 160 mm in males and females. Sexually monomorphic in both immature and breeding condition.

Scales cycloid, ovoid, present on entire postcranial portion of body from nape to tip of caudal appendage. Lateral-line scales in 151 mm specimen (BMNH 1998.3.12.20, 1, WGRC 11.070597) approximately 1.5 mm high by 1.8 mm long in humeral region, 2.4 mm high by 2.7 mm long at midbody, 1.6 mm high by 2.1 mm long dorsal to anterior margin of clear patch on anal fin. Gape size in mature specimens large, extending to or beyond posterior nares. Mouth position dorsal, lower jaw extends beyond 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. Ethmoid region between anterior nares moderately broad, its anterior margin straight in adult specimens, rounded in juvenile specimens. Eye without free orbital margin, position lateral, lower margin of eye dorsal to rictus.

Premaxilla with 9–10 (mode 9, $N = 2$) teeth in single row along outer margin, and 5–6 (mode 5, $N = 2$) teeth in inner row. Outer row teeth large and arrow-head shaped. Inner teeth small, recurved conical shape. Dentary with 19 ($N = 2$) teeth in single row along outer margin and 5 widely spaced teeth in inner row. Outer row with large teeth, 1–3 arrow-head shaped, those posterior with flattened conical shape. Inner row with small conical teeth. Rib 5 less than three 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 present in all specimens examined, 6–27 (left or right). Anal-fin pterygiophores at posterior end of body cavity equal to or longer than first hemal spine. Caudal appendage long, more than 0.5 times pectoral-fin length in undamaged and unregenerated specimens. Single hypaxial electric organ, extending along entire ventral margin of body and caudal appendage. Three or four (mode 4) rows of electroplates at one HL distance from end of caudal appendage.

*Color in life.*—Ground color dark chocolate brown and without countershading in adults and juveniles. Fourteen to 20 thin pale yellowish or whitish interbands on lateral surface extending from nape and pectoral-fin base to tip of caudal appendage and oriented either vertically or obliquely in an anterio-ventral to posterio-dorsal diagonal. Dark bands occur singly and are not divided into Y or X shapes or into double bands along entire body length. Pigment density greater at the dark band margins than in the middle. Pale interbands regular in shape, width, arrangement and color both on and among individuals. Band-interband margins straight and with high contrast. Band-interband contrast increases ventrally but not caudally. Pale interbands do not extend to middorsum along anterior two-thirds of body. Incomplete pale interband present in middle of dark bands 4–8 from tip of caudal appendage. Two pale interbands from either side meet on ventral midline, between the anus and anal-fin origin. One to two bands lie posterior to last anal-fin ray. Banding of juveniles resemble that of adults but is more homogenous in pattern and pigment intensity and the pale interbands of juveniles are wider relative to the dark bands than in adults.

Head never banded, spotted, or blotched, dark brown dorsally and over the operculum grading to lighter brown ventrally, with numerous minute chromatophores speckled over branchiostegal membranes and ventral surface of head. Head coloration too dark to see rosy hue of gills beneath operculum. Pectoral-fin rays brown, interradial membranes hyaline. Anal-fin membrane never blotched, spotted or marked, divided into two parts along body axis: anterior 80% light gray, posterior 20% translucent. Fin colors in juveniles and adults are similar. Specimens fixed in 10% formalin and preserved for up to six years in 70% ethanol maintain approximate colors of life, although the darker pigments tend to pale with time.

*Electric organ discharges.*—EOD waveform with total duration of 1.3–1.5 msec ($N = 16$) Comprises two phases with a dominant positive phase followed by a low-voltage negative phase. EOD waveform similar in all recorded specimens, with no sexual differences. A typical example is illustrated in Figure 5.

*Intraspecific variation.*—*Gymnotus obscurus* does not exhibit polymorphism of banding pattern. On the contrary, specimens of the same size strongly resembled each other, with variation in pigmentation apparently restricted to growth-related changes (see above). We observed no sexual difference in size, pigmentation, nonreproductive morphology or EOD waveform. The absence of specimens from outside the region of the type series rule out any interpopulation comparisons.

*Distribution.*—Known only from the type series in várzea floodplain at the confluence of the Rio Solimões (Amazon) and the Rio Japurá in the Mamirauá Reserve near Tefé, Amazonas, Brazil (Figs 1, 6).

*Ecology.*—*Gymnotus obscurus* is known only from the root mats of floating meadows in várzea floodplains at the confluence of the Rio Solimões and Rio Japurá near Tefé (Fig. 1) where it occurs sympatrically with *G. arapaima*, *G. carapo*, *G. jonasi*, *G. mamiraua*, *G. melanopleura*, *G. onca*, and *G. varzea*. Henderson and Crampton (1997), Crampton (1998b), and Henderson et al. (1998) describe the aquatic habitats and water quality of várzea floodplains of the Tefé region. Ayres (1993) describes the floodplain ecosystems of the Rio Solimões Japurá. In the whitewater floodplain, juvenile specimens of *G. obscurus* are found in patches of floating macrophytes along lakes margins and along the edge of *canos* (drainage channels from lakes to the main river channels) and *paranás* (channels connected at both ends to the main river channel that transport whitewater through the floodplain; Fig. 1). Floating macrophytes form extensive floating meadows dominated by the grasses *Paspalum repens* and *Echinochloa polystachya* (Poaceae) and by smaller floating plants such as *Eichornia crassipes* (Pontederiaceae), *Pistia stratiotes* (Araceaea), *Salvinia* spp., and *Azolla* spp. (Salviniaceae). The root substrate of these meadows hosts a rich infauna of insect larvae, crustaceans and other aquatic invertebrates. All whitewater floodplain habitats are subject to extended periods of hypoxia, especially during the high-water period (Crampton, 1998a). *Gymnotus obscurus* like other species of *Gymnotus* from the Amazonian floodplains, undertakes aerial respiration by gulping atmospheric air into the hypervascularized posterior chamber of the gas bladder (Liem et al., 1984; Crampton, 1998a). Specimens held in poorly oxygenated water from the capture locality rose to the surface and gulped air about once every 30 sec to 5 min. Air breathing frequency rose with an increase in swimming activity.

Stomach content analysis of this species reveals that it feeds primarily upon chironomid larvae, small insect nymphs and small crustaceans such as Conchostraca. Although only one mature female and one mature male of this species were encountered in the type series, the presence of small immature specimens suggests that this species breeds within the floating meadow. The sympatric species *Gymnotus arapaima*, *G. jonasi*, and *G. mamiraua* are also known to spawn in the rootmats of floating meadows (WGRC, pers. obs.).

*Etymology.*—Named obscurus from the Latin adjective dark for its predominantly dark coloration.

### *Gymnotus varzea* new species

Figures 3, 8

*Holotype.*—MZUSP 60601, WGRC 15.170597, 173 mm, Brazil, Amazonas, Municipality of Alvarães, Mamirauá Sustainable Development Reserve (Mamirauá Reserve), Ressaca da Vila Alencar, 3°07′42″S, 64°48′02″W, collected by W. Crampton, 17 May 1997.

*Paratypes.*—BMNH 1998.3.12.7, 1, WGRC 01.010497, 176 mm, Brazil, Amazonas, Municipality of Alvarães, Mamirauá Reserve, Lago Araçazinho, 2°59′16″S, 64°51′28″W, 1 April 1997. BMNH 1998.3.12.11, 1, WGRC 16.300497, 160 mm, Mamirauá Reserve, Cano do Lago Rato, 3°02′58″S, 64°51′31″W, 30 April 1997. BMNH 1998.3.12.15–18, 4: WGRC 12.070597, 151 mm; WGRC 13.070597, 134 mm (c&s); WGRC 14.070597, 126 mm, WGRC 15.070597, 132 mm, locality as holotype, 7 May 1997. IDSM 433, 1, WGRC NR06.070597, 158 mm, collected with BMNH 1998.3.12.15–18. INPA 18422, 1, WGRC 07.310598, 66 mm, Mamirauá Reserve, Lago Geraldo, 3°06′57″S, 64°49′10″W, 31 May 1998. INPA 18423, 1, WGRC 02.220500, 152 mm, locality as holotype, 22 May 2000. INPA 18424, 1, WGRC 05.090600, 89 mm, Mamirauá Reserve, Lago Secretaria, 3°06′44″S, 64°48′01″W, 9 June 2000. MZUSP 75158, 1, WGRC 03.300498, 237 mm, Mamirauá Reserve, Cano do Lago Sapucaia, 3°04′07″S, 64°48.53′32″W, 30 April 1998. MZUSP 75159, 1, WGRC 06.290598, 149 mm, locality as INPA 18422, 29 May 1998. MZUSP 75160, 1, WGRC 02.190500, 110 mm, locality as MZUSP 75158, 19 May 2000. MZUSP 75161, 1, WGRC 01.230500, 142 mm, locality as MZUSP 75158, 23 May 2000. MZUSP 75163, 1, WGRC 02.170401, 94 mm, Mamirauá Reserve, Lago Mamirauá, 3°02′18″S, 64°51′58″W, 17 April 2001. MZUSP 75164, 1, WGRC 04.170401, 190 mm, collected with MZUSP 75163. MZUSP 60602, 8: WGRC 02.070597, 116 mm; WGRC NR01–05.070597, 155–201 mm; WGRC NR 07.070597, 103, WGRC NR09.070597, 172 mm, collected with BMNH 1998.3.12.15–18. MZUSP 60603, 6: WGRC 09.170597, 164 mm, WGRC 10.170597, 150mm, WGRC 11.170597, 147 mm, WGRC 12.170597, 145 mm, WGRC 13.170597, 186 mm, WGRC 14.170597, 157 mm, collected with holotype. MZUSP 75162, 1, WGRC

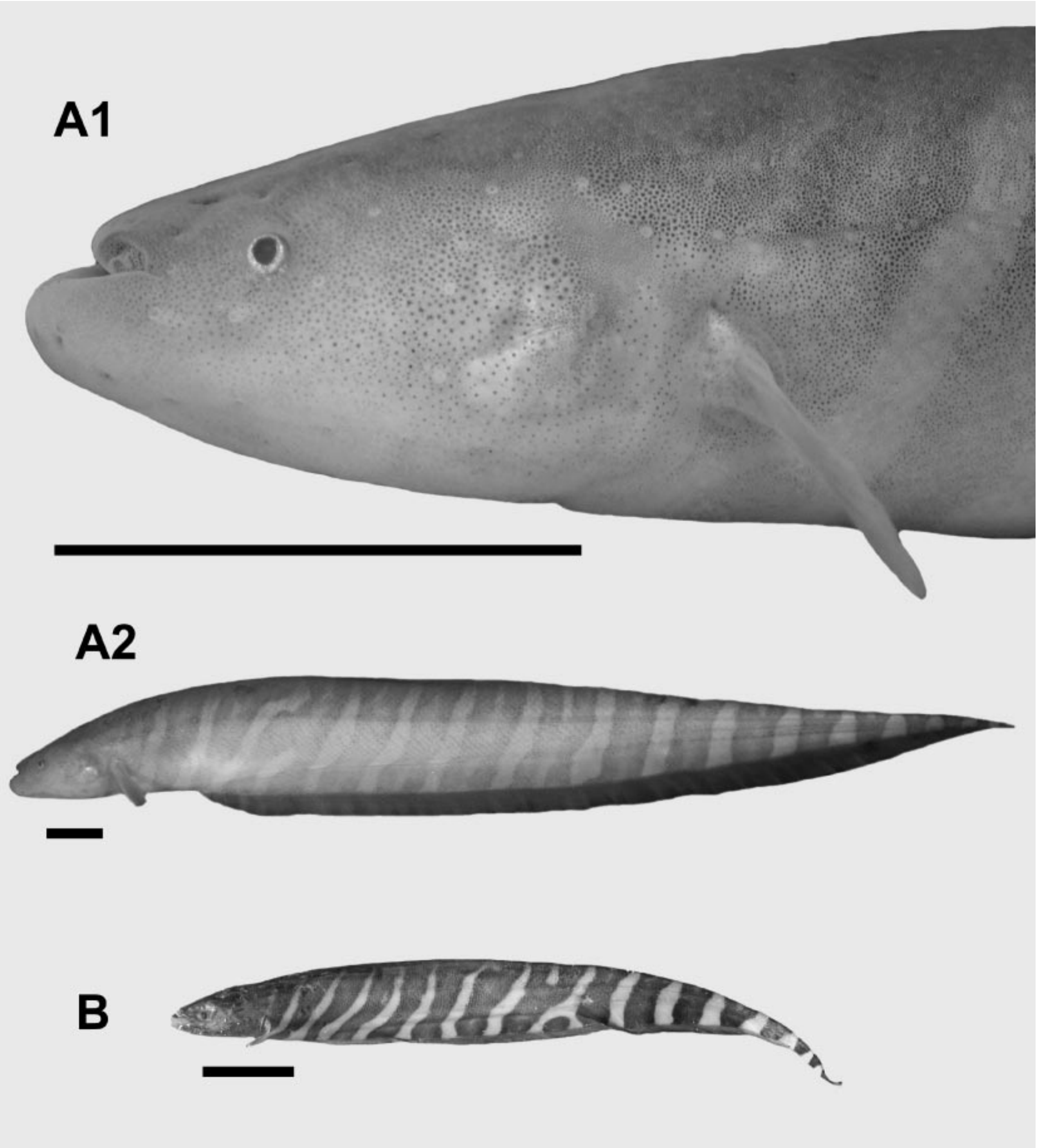

Fig. 8. *Gymnotus varzea* n. sp. A1 (head) and A2 (body), INPA 18423; B, MZUSP 75160. Scale bars = 10 mm.

02.070600, 170 mm, locality as holotype, 7 June 2000. UF 118834, 2: WGRC 10.030597, 140mm (c&s); WGRC 13.030597, 135 mm (slide mounts of cross sections of body), locality as holotype, 03 May 1997. UF 118835, 2: WGRC 02.010497, 185 mm; WGRC 06.010497, 168 mm, collected with BMNH 1998.3.12.7. UF 118838, 1, WGRC 10.100497, 116 mm, Mamirauá Reserve, Lago Arauaé, 3°02′52″S, 64°50′05″W, 10 April 1997. UF 118839, 1, WGRC 10.240497, 122 mm, locality as MZUSP 75158, 24 April 1997.

*Nontype material.*—UF 116553, 3: WGRC 15.310301, 108 mm; WGRC 27.310301, 98 mm; WGRC 28.310301, 96 mm, Peru, Loreto, Maynas, Río Amazon, unspecified Amazon river drainage nr. Iquitos (procured from ornamental fish catchers), J. Albert and W. Crampton, 31 March 2001. UF 133582, 4: WGRC 05.130503 198 mm, WGRC 06.130503, 111 mm; WGRC 07.130503, male, 141 mm, WGRC 08.130503, male, 217 mm, Peru, Loreto, Río Pacaya, Caño Yarina, Reserva Nacional Pacaya Samiria

(RNPS) nr. confluence of Río Marañon and Río Ucayali, 5°18′07″S, 74°30′36″W, W. Crampton and J. Albert, 13 May 2003. UF 133583, 1, WGRC 02.200503, 171 mm, Peru, Loreto, Río Pacaya, Cocha Sapote (RNPS), 5°20′15″S, 74°29′40″W, W. Crampton and J. Albert, 20 May 2003. UF 146953, 285 mm, Peru, Loreto, Río Pacaya, Caño Yarina (RNPS), 5°20′46″S, 74°30′12″W, S. Correa and W. Crampton, 10 May 2003. UMMZ 224607 (part), 1, 142 mm, Peru, Loreto, Río Momon, Maynas, Bora village nr. Amazon camp, approximately 03°42′S, 73°16′W, J. Albert and T. DiBenedetto, 04 May 1993.

*Diagnosis.*—*Gymnotus varzea* is unique among congeners endemic to the Amazon and Orinoco Basins and the Guyana Shield in possessing a color pattern of 16–22 oblique dark pigment bands with wavy and irregular margins in which the majority of bands at midbody form X-shaped patterns (resembling metaphase chromosomes) and in which the dark bands are about twice as broad as the pale interbands. *Gymnotus varzea* may be further distinguished from congeners in possessing the following unique combination of characters: 1, clear (unpigmented) patch at the caudal end of the anal-fin membrane in specimens 60–237 mm (not present in *G. pantherinus* species group, hence diagnosing *G. varzea* as member of *G. carapo* species group); 2, bands never divided to form band pairs (in contrast to *G. arapaima*, *G. carapo*, and *G. diamantinensis*); 3, head length 9.0–10.4 versus 10.4–13.9 in *G. carapo*, and versus 10.8–14.2 in *G. arapaima*, *G. diamantinensis*, and *G. ucamara*; 4, preorbital length 29.7–35.8% HL versus 26.4–29.2 in *G. jonasi* and 36.0–37.0 in *G. cataniapo*; 5, mouth width 35.0–45.9% HL versus 30.6–33.0 in *G. jonasi*; 6, body depth 8.3–10.8% HL versus 6.7–8.0 in *G. coatesi*, *G. jonasi*, and *G. onca*; 7, body width 4.6–6.4 versus 6.4–8.1 in *G. tigre* and *G. ucamara*; 8, body width/body depth ratio 0.47–0.69% TL versus 0.70–0.86 in *G. anguillaris* and *G. coatesi*; 9, head depth 59.9–73.9 versus 47.6–59.6 in *G. coatesi*, *G. jonasi*, and *G. curupira*, and versus 49.4–59.9 in *G. stenoleucus*; 10, head width 54.8–73.6% HL versus 51.1–51.3 in *G. diamantinensis*; 11, branchial opening 32.7–46.4% HL versus 25.0–32.6 in *G. tigre*, *G. javari*, and *G. jonasi*; 12, preanal length 68.3–108.5% HL, versus 50.6–63.1 in *G. pedanopterus*; 13, pectoral-fin length 42.8–57.5% HL versus 29.3–41.8 in *G. cataniapo* and *G. pedanopterus*; 14, anal-fin length 72.7–84.5% TL versus 62.9–69.9 in *G. stenoleucus*; dark bands 16–22 versus 23–35 in *G. cataniapo* and versus 0 in *G. onca* (spotted); 15, anal-fin rays 230–310 versus 135–223 in *G. coatesi*, *G. jonasi*, *G. onca*, *G. melanopleura*, and *G. diamantinensis*; 16, pectoral-fin rays 16–19 versus 11–15 in all members of *G. pantherinus* species group except *G. anguillaris*, and versus 14–15 in *G. diamantinensis* and *G. mamiraua*; 17, scales above lateral line 5–8 versus 8–13 in *G. tigre*, *G. pedanopterus*, and *G. stenoleucus*; 18, caudal electroplate rows invariably 4 versus 2–3 in all members of *G. pantherinus* species group, versus invariably 3 in *G. curupira* and versus 5–6 in *G. tigre*; 19, scales over anal-fin pterygiophores 4–6 versus 7–16 in *G. arapaima*, *G. carapo*, *G. curupira*, *G. tigre*, *G. ucamara*, *G. anguillaris*, and *G. javari*; 20, precaudal vertebrae 35–40 versus 31–34 in *G. diamantinensis*, *G. mamiraua*, *G. ucamara*, and *G. pedanopterus*, versus 40–43 in *G. javari*, and versus 41–51 in *G. tigre*, *G. cataniapo*, *G. coatesi*, and *G. stenoleucus*; 21, pored lateral-line scales to first ventral ramus 51–55 versus 31–49 in *G. diamantinensis*, *G. mamiraua*, *G. ucamara*, *G. jonasi*, *G. melanopleura*, and *G. onca*, and versus 60–78 in *G. tigre*, and *G. cataniapo*; 22, total pored lateral-line scales 106–135 versus 71–102 in *G. diamantinensis*, *G. mamiraua*, *G. ucamara*, *G. coatesi*, *G. coropinae*, *G. jonasi*, *G. onca*, and *G. stenoleucus*, and versus 88–108 in *G. javari*; 23, ventrally oriented lateral-line rami 14–29 versus 0–13 in *G. curupira*, *G. diamantinensis*, *G. anguillaris*, and *G. pedanopterus*, versus 0–14 in *G. mamiraua*, and versus 29–55 in *G. tigre*.

*Description.*—Figures 3 and 8 illustrate body shape and pigment patterns. Morphological and meristic (Tables 1 and 2, respectively) pooled from 29 specimens of type series (from Brazilian Amazon), and eight specimens of nontype material from Peruvian Amazon (lots UF 116553, UF 133582, UF 133583). Morphometric and meristic data not taken from nontype lot UMMZ 224607 because of poor preservation status. Size up to 285 mm and 65 g. Size of sexual maturity 141 mm in male, unknown in female.

Scales cycloid, ovoid, present on entire postcranial portion of body from nape to tip of caudal appendage. Lateral-line scales in 150 mm specimen (MZUSP 60602, WGRC 10.170597) 1.5 mm high by 1.9 mm long in humeral region, 1.8 mm high by 2.3 mm long at midbody, and 0.8 mm by 1.9 mm high dorsal to anterior margin of clear patch on anal fin. Gape size in mature specimens moderate, extending to posterior nares. Mouth position superior, lower jaw extends beyond upper, rictus decurved. Chin fleshy and bulbous with thick pad of electroreceptors 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. Ethmoid region between anterior nares broad, its anterior margin straight. Eye without free orbital margin, position lateral, lower margin of eye dorsal to rictus.

Premaxilla with 6–7 (mode 6, $N = 2$) teeth in single row along outer margin, all arrow-head shaped. Dentary with 10–11 (mode 10, $N = 2$) teeth in single row along outer margin, all arrow-head shaped. Rib 5 robust along its entire extent, less than three 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 present in 9/37 specimens examined, 0–10 rami (left or right). Anal-fin pterygiophores at posterior end of body cavity equal to or longer than first hemal spine. 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. Four rows of electroplates at one HL distance from end of caudal appendage.

*Color in life.*—Ground color pale yellow ventrally grading to pale brown dorsally in adults (larger than 100 mm) and yellow or pale pink in juveniles. Sixteen to 22 light or dark brown bands on lateral surface extending from nape and pectoral-fin base to tip of caudal appendage and oriented either vertically or obliquely in an anterio-ventral to posterio-dorsal diagonal. Bands occur singly or in band-pairs. Band appearance somewhat irregular in shape, width, and arrangement, both on and among individuals. Band-interband margins irregular and wavy. Most band pairs along the middle to posterior portions of the body are incompletely divided, merging near the base of the hypaxial musculature, to form X-shaped patterns resembling stained chromosomes on the metaphase plate (Fig. 8). Pale interbands areas extend to middorsum along posterior one-third of body. Interband contrast increases slightly ventrally and caudally and is more pronounced in smaller specimens. Three (seldom four) bands from either side meet on ventral midline, between the anus and anal-fin origin. One to three bands lie posterior to last anal-fin ray. Bands of juveniles resemble adults except that they are less divided and more homogenous.

Head never banded, spotted or blotched, dark brown dorsally grading to lighter brown ventrally, with numerous minute chromatophore speckled over branchiostegal membranes and ventral surface of head. A rosy hue to operculum from the underlying gills in juveniles. Pectoral-fin rays brown, interradial membranes hyaline. Anal-fin rays brown, membrane divided into three parts along body axis: anterior 40% light gray, middle 40% dark charcoal gray, posterior 20% translucent. Fins lighter in juveniles. Specimens fixed in 10% formalin and preserved for up to six years in 70% ethanol maintain approximate colors of life, although the darker pigments tend to pale with time.

*Electric organ discharges.*—EOD waveform with total duration of 1.0–1.3 msec ($N = 38$). Comprises three phases with a dominant head-positive biphasic phase preceded by a negative phase, which reaches about half the voltage of the final negative phase. EOD waveform similar in all recorded specimens. A typical example is illustrated in Figure 5.

*Intraspecific variation.*—*Gymnotus varzea* does not exhibit polymorphism of banding pattern. Specimens of the same size resembled each other, with variation in pigmentation apparently restricted to growth-related changes (see above). We were unable to assess sexual differences in size, pigmentation, nonreproductive morphology, or EOD waveform because of the absence of mature female specimens. We observed no salient interpopulation differences in pigmentation between specimens of the type series from the Brazilian Amazon and nontype specimens from the Peruvian Amazon. Likewise, morphometric and meristic data for specimens from the Peruvian Amazon all fell well within the range of those from Brazilian Amazon. A single cleared and stained specimen from the Peruvian Amazon (UF 133582, WGRC 07.130503) exhibited no salient osteological differences to specimens from the Brazilian Amazon. EOD waveforms from the Brazilian Amazon and Peruvian Amazon were similar, with no quantifiable consistent differences in the Peak Power Frequency of the Fast Fourier Transform, nor in the relative amplitude or duration of the three phases of the waveform.

*Distribution.*—The type series comes from várzea floodplains at the confluence of the Rio Solimões (Amazon) and the Rio Japurá in the Mamirauá Reserve near Tefé, Amazonas, Brazil (Fig. 1). *Gymnotus varzea* is also known from localities in the Peruvian Amazon near the confluence of the Río Marañon and Río Ucayali, and near the town of Iquitos on the Río Amazonas (Fig. 6).

*Ecology.*—Like *G. obscurus*, *G. varzea* is apparently restricted to whitewater várzea floodplains (see description of habitat under *G. obscurus*). As with other species of *Gymnotus* from the perennially hypoxic várzea floodplain, *G. varzea* gulps air into the hypervascularized posterior chamber of its gas bladder. The gas bladder of *G. varzea* extends to the posterior end of the body cavity, which is itself longer than that of other described members of the *G. carapo* species group (extending to precaudal vertebra 36–40). Specimens held in poorly oxygenated water from the capture locality rose to the surface and gulped air about once every 1–7 min. Air breathing frequency rose with an increase in swimming activity. The diet of *G. varzea* comprises small aquatic invertebrates such as chironomid larvae, insect nymphs and micro crustaceans. Although no sexually mature male or female specimens of this species were encountered from floodplains at the confluence of the Rio Solimões and Japurá (two mature males were captured in floodplains of the Río Ucayali in Peru), the occasional capture of small juvenile specimens indicates that this species forms breeding populations in floating meadows. One specimen was captured in a gill net set in flooded forest (UF 149653).

*Etymology.*—Named for the whitewater várzea floodplain, which this species is restricted to. Name applied as a noun in apposition.

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## APPENDIX 1

### LIST OF VALID SPECIES OF *GYMNOTUS*

Thirty valid species of *Gymnotus* with affiliation to species groups, geographical range and habitat are listed below. Geographical regions (in parentheses and followed after hyphen by habitat): EA, Eastern Amazon; GU, Guyana Shield, OR, Orinoco Basin, MA, Middle America; NE, northeastern Brazil; PA, Paraguay-Paraná; PS, Pacific Slope; SE, southeast coast Brazil and Uruguay; WA, Western Amazon (division of the Amazon into Eastern and Western portions at the watersheds of the Rio Negro-Rio Solimões and the Rio Madeira-Tapajós). Habitats: TS, terra firme systems and their seasonally flooded lower reaches or coastal streams/rivers; BF, blackwater or other nutrient poor rivers with seasonal flood cycle; WF, whitewater várzea floodplain. Habitat data from museum records and field observations.

*Gymnotus cylindricus species group.—Gymnotus cylindricus* LaMonte, 1935, (MA-TS); *G. maculosus* Albert and Miller, 1995 (MA-TS).

*Gymnotus pantherinus species group.—Gymnotus anguillaris* Hoedeman, 1962 (GU, OR-TS); *G. cataniapo* Mago-Leccia, 1994 (GU, OR-TS, BF); *G. coatesi* LaMonte, 1935 (EA, WA-TS); *G. coropinae* Hoedeman, 1962 (EA, GU, OR, WA-TS); *G. javari* Albert, Crampton, and Hagedorn, 2003 (WA-TS, BF); *G. jonasi* Albert and Crampton, 2001 (WA-WF); *G. melanopleura* Albert and Crampton, 2001 (WA-WF); *G. onca* Albert and Crampton, 2001 (WA-WF); *G. panamensis*, Albert and Crampton, 2003 (MA-TS); *G. pantherinus* (Steindachner, 1908) (SE-TS); *G. pedanopterus* Mago-Leccia, 1994 (EA, GU, OR-TS, BF); *G. stenoleucus* Mago-Leccia, 1994 (EA, GU-TS, BF).

*Gymnotus pantherinus species group.—Gymnotus arapaima* Albert and Crampton, 2001 (WA-TS, BF, WF); *G. bahianus* Campos-da-Paz and Costa, 1996 (NE-TS); *G. carapo* Linnaeus, 1758 (EA, GU, NE, OR, WA-TS, BF, WF); *G. choco* Albert, Crampton and Maldonado, 2003 (PS-?); *G. curupira* (WA-TS); *G. diamantinensis* Campos-da-Paz, 2002 (EA-BF); *G. esmeraldas* Albert and Crampton, 2003 (PS-?); *G. henni* Albert, Crampton and Maldonado, 2003 (PS-?); *G. inaequilabiatus* (Valenciennes, 1847) (PA -WF); *G. mamiraua* Albert and Crampton, 2001 (WA-WF); *G. obscurus* (WA-WF); *G. paraguensis* Albert and Crampton, 2003 (PA-WF); *G. sylvius* Albert and Fernandes-Matioli, 1999 (PA, SE-TS, WF); *G. tigre* Albert and Crampton, 2003 (EA, WA-WF); *G. ucamara* Crampton, Lovejoy, and Albert, 2003 (WA-WF); *G. varzea* (WA-WF).