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Pariosternarchus amazonensis: a new genus and species of Neotropical electric fish (Gymnotiformes: Apteronotidae) from the Amazon River

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Pariosternarchus amazonensis, new genus and species, is described from the Amazon river of Brazil and Peru. It is unique among apteronotids in possessing a wide head that is flattened on its entire ventral surface, and in possessing highly expanded mandibular laterosensory canals. The phylogenetic position of *Pariosternarchus* is hypothesized by inclusion in a previously published data matrix of osteological and other morphological characters. Among apteronotids *Pariosternarchus* is inferred to be the sister taxon to *Sternarchella*, with which it shares several derived features associated with a life history as benthic foragers in large whitewater Amazonian rivers: a short gape, a large maxilla with a robust anterior process, gill rakers attached to gill arches, and flexible gill rakers that are not ossified to their tips.

Introduction

The weakly electric Neotropical fish family Apteronotidae is the most species rich family of gymnotiform fishes, with 53 valid species currently allotted to 14 genera. Many additional undescribed species are currently known in museum collections (e.g. Albert, 2003; Albert & Crampton, 2005; de Santana, 2003; de Santana & Maldonado-Ocampo, 2005; de Santana & Crampton, 2006). Apteronotids are readily distinguished from other gymnotiforms by the presence of three unique morphological features: a commissural tube of the laterosensory system behind the posterior nares connecting the infraorbital and supraorbital canals, a fleshy midsaggital dorsal electrosensory organ, and a caudal fin with segmented rays and a hypural plate. Apteronotids further differ from other gymnotiform fishes in a number of characters of cranial and post-cranial osteology and neuromorphology (Albert et al., 1998; Albert, 2001).

Apteronotids are medium sized gymnotiform fishes (100-560 mm adult total length) that occur in practically all major river drainages of tropical South America, ranging from Rio La Plata of Argentina (35 °S) to the Rio Tuyra on the Pacific slope of Panama (8 °N) (Albert, 2003). The Ama-

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zon basin is the area of highest apteronotid diversity, from where 61 % (34 of 53) of species representing all genera can be found, except the monotypic *Tembeassu marauna* from the Rio Parana (Triques, 1998; Campos-da-Paz, 2005). The majority of apteronotid species inhabit the deep channels (up to 25 m) of large lowland tropical rivers, a habitat only recently surveyed systematically (Lundberg et al., 1987; Mago-Leccia, 1994; Lundberg et al., 1996; Crampton, 1998; Albert, 2001; Cox-Fernandes et al., 2004; Crampton & Albert, 2006). As a result, many apteronotid species were, until recently, rare or unknown in museum collections.

Many deep channel apteronotids are members of the navajini, an informal species-rich suprageneric taxon within the Apteronotinae that possesses a suit of derived traits associate with foraging and locomotion in swiftly-flowing large river environments (Albert, 2001). Members of the navajini share two derived character states: scales rhomboid in shape (vs. ovoid); and anal-fin pterygiophores longer than length of hemal spines at same axial position (vs. shorter than hemal spines). In all species of navajini the entire body is strongly compressed laterally and the extent of endosekletal ossification is substantially reduced by one of several mechanisms, including delayed onset of mineralization (i.e., paedomorphosis) and active bone remodeling (Albert, 2001). As presently recognized (Albert, 2003) the navajini includes six genera (Adontosternarchus, Compsaraia, Magosternarchus, Porotergus, Sternarchella, Sternarchogiton) as well as several species of uncertain generic identity referred to in the literature as "Apteronotus" incertae cedis.

Here we describe a new genus and species of apteronotid fish, *Pariosternarchus amazonensis*, which inhabits the main channel of the Amazon River of Brazil and Peru, including areas near the mouths of some of the larger whitewater tributaries of the Central Amazon basin. The new taxon is characterized by a unique suite of morphological and osteological characters, especially associated with a pronounced broadening and flattening of the ventral surface of the head.

Materials and methods

All body distance measurements are reported in mm. Measurements reported include: (1) total length, measured from snout (anterior margin of upper jaw at mid-axis of body) to posterior tip of longest caudal-fin rays; (2) standard length, measured from snout to base of caudal fin; (3) length to end of the anal fin, measured from tip of snout to end of anal fin (where membrane posterior to last ray contacts ventral surface of body); (4) distance from nape to origin of midsagittal dorsal organ; (5) length of anal-fin base, from origin of anal fin to posterior end of anal fin; (6) length to origin of anal-fin, measured as distance from snout to base of first anal-fin ray; (7) length to anus, measured as distance from snout to anterior margin of anus; (8) head length, measured from posterior margin of bony opercle to tip of snout; (9) head length measured from snout to branchial opening; (10) distance from snout to nape; (11) head width, measured at mid opercle; (12) head depth at nape, vertical distance at nape to ventral body border with lateral line held horizontal; (13) head depth at eye; (14) mouth length, from middle of gape to rictus; (15) mouth width, between ricti; (16) distance from snout to posterior nares; (17) pre-orbital head length, from anterior margin of eye to tip of snout; (18) distance from posterior margin of eye to branchial opening; (19) eye diameter, measured from postorbital to pre-orbital margins parallel with long axis; (20) postorbital head length, from posterior margin of the bony opercle to posterior margin of eye; (21) length from eye to posterior nares, measured from pre-orbital margin to posterior margin of posterior nares; (22) internarial distance; (23) interorbital distance, measured as linear distance between medial margins of orbits; (24) length of the branchial opening; (25) pectoral-fin length, from dorsal border of fin base where it contacts cleithrum to tip of longest ray; (26) width pectoral fin base; (27) pre-pectoral distance; (28) greatest body depth; (29) caudal peduncle depth; (30) length longest anal-fin ray; (31) length of caudal peduncle and caudal fin, measured as the distance from the last anal-fin ray to the tip of longest caudal-fin ray.

Measurements of total length and anal-fin length were taken with a ruler to the nearest millimeter. All other measurements were taken with a digital caliper to the nearest 0.1 mm. Morphometric data in diagnosis are reported as mean relative proportions, and ranges are reported in brackets. Meristic protocols follow Albert & Fink (1996). Skeletal counts obtained from cleared and stained specimens and radiographs include: number of precaudal vertebrae, which include those of the Weberian apparatus, and is a proxy for body cavity length (Albert, 2001); total number of anal-fin rays; number of pectoral-fin rays; scale rows above the lateral line at midbody; number of caudal fin rays. Measurements and counts were taken from the left side of specimens. Sex was determined by dissection. Sexually mature males have smooth, white testes. Sexually mature females have enlarged ovaries packed with yellowwhite or yellow eggs. Specimens from the area of the type locality were captured using 50×6 m beach seines (10 mm mesh) as part of a long-term (1993-2001) multi-habitat sampling program undertaken by one of us (WGRC) near the town of Tefé, Amazonas, Brazil. Museum lot records indicate that all non-type specimens were captured with trawl nets to depths of 15 m. Abbreviations of museum collections from which materials were examined follow Leviton et al. (1985).

Osteological data were taken from cleared and stained specimens using the techniques of Taylor & Van Dyke (1985). We used standardized micro-dissection methods of small teleosts (Weitzman, 1962) and follow Fink & Fink (1981) and Albert (2001) for morphological nomenclature. See Albert (2001) for lists of apteronotid specimens examined for external morphology and osteology.

Pariosternarchus, new genus

Diagnosis. An apteronotid unique in possessing a wide head (head width 51-69 % HL [mean 58 %] vs. 30-40 % in other apteronotid genera) whose entire ventral surface is flat (vs. convex) from the mental to gular regions, and in possessing greatly expanded mandibular laterosensory canal ossicles, which extend more than half the distance from the lateral margin of the head to the ventral midline (vs. slender ossicles).

Pariosternarchus further differs from other apteronotid genera in possessing the following unique combination of characters: scales absent from dorsal surface of head and body (shared with other navajini except Sternarchogiton nattereri and Adontosternarchus; also shared with Apteronotus cuchillejo and Orthosternarchus; vs. scales present on middorsum in other Apteronotidae); scales large and rhomboid with 5-6 rows above lateral line at midbody (shared with other navajini; vs. scales small and ovoid in other Apteronotidae, with 6-12 rows); anterior infraorbital canal pore remote from first infraorbital bone (shared with Magosternarchus, Sternarchella, Adontosternarchus, Parapteronotus, Sternarchorhamphus and Orthosternarchus: vs. close to first infraorbital bone in other Apteronotidae); endopterygoid ascending process robustly ossified within the anterior pterygoid ligament (shared with Magosternarchus, Sternarchella; vs. slender or absent in other Apteronotidae); endopterygoid with an elongate anterior process (shared with most Apteronotidae; vs. short and deep, without an elongate anterior process in Magosternarchus, Sternarchella, Porotergus and Adontosternarchus); opercle dorsal margin slightly concave (shared with Magosternarchus, Sternarchella and Orthosternarchus; vs. convex in other Apteronotidae); basibranchial of fifth arch not ossified (shared with Magosternarchus and Sternarchella; vs. ossified in other Apteronotidae); anal-fin pterygiophores long, 1.0-1.5 times into depth of epaxial musculature (shared with most Apteronotidae; vs. 0.7-0.9 in Apteronotus sensu stricto, Parapteronotus, and Megadontognathus); tail short, mean caudal peduncle + fin length 14 % TL [range 8-17 %] (shared with Sternarchella, Magosternarchus, Parapteronotus, Sternarchorhynchus and Platyurosternarchus; vs. mean caudal peduncle + fin lengths 17-45 % TL in other Apteronotidae).

Pariosternarchus further differs from all apteronotids outside navajini (except Sternarchorhamphus and Orthosternarchus) in exhibiting very reduced pigmentation such that live specimens have a pale white-pink appearance (opaque yellow or hyaline in preserved specimens) within navajini, Compsaraia, Magosternarchus and some Sternarchogiton species share this reduced pigmentation. Among apteronotids Pariosternarchus is most similar to Sternarchella from which it readily separated by the broad head with flattened ventral surface (vs. narrow and rounded), expanded mandibular laterosensory canals (vs. narrow and slender), and in the shape maxilla (ventral margin evenly rounded vs. sharply angled).

Etymology. The genus name is from the Greek pario, cheek, in reference to the expanded vent-rolateral surface of the head, and sternarchus, a commonly used name in apteronotid taxonomy. Gender masculine.

Pariosternarchus amazonensis, new species (Fig. 1)

Holotype. MCP 34916, 121 mm; Brazil: Amazonas: Paraná Maiana, Mamirauá Lake System, municipality of Alvarães, 3°06.74'S 64°47.53'W; W. G. R. Crampton, 1 Feb 1999,

Paratype. MCP 34917, 1, 106 mm, cleared and stained; collected with holotype.

Non-types. ANSP 182281, 1, 145 mm, female; Peru: Dept. Loreto: Prov. Maynas: Rio Amazonas near Iquitos; A. Bullard et al., 14 Aug 2005. - MZUSP 57061, 1, 153 mm, male; Brazil: Amazonas: Rio Amazonas near mouth of Rio Negro and Preto da Eva, 3°04'31"S 59°47'23"W; Jewett et al., 22 Oct 1993. - MZUSP 57244, 1, 106 mm, male; Brazil: Amazonas: Rio Amazonas, below confluence with Rio Madeira; A. Zanata et al., 10 Aug 1996. - MZUSP 57342., 1, 101 mm, immature; Brazil: Amazonas: near confluence with Rio Madeira; A. Zanata et al., 6 Aug 1996. - MZUSP 57345, 1, 57 mm, immature; Brazil: Amazonas: Rio Amazonas, near confluence with Rio Purus; A. Zanata et al., 30 Jul 1996. - MZUSP 57352, 1, 105 mm, immature; Brazil: Amazonas: near mouth of Rio Madeira; Zanata et al., 6 Aug 1996. - MZUSP 57964, 1, 74 mm, immature; Brazil: Amazonas: 191 km below confluence with Rio Purus; C. Cox-Fernandes et al., 20 Jul 1996. - MZUSP 57966., 1,60 mm, immature; Brazil: Amazonas: Rio Amazonas, 61 miles below confluence with Rio Negro; C. Cox-Fernandes et al., 5 Aug 1996. - MZUSP 58243, 1, 84 mm, immature; Brazil: Amazonas: Rio Madeira near mouth; M. Toledo-Piza et al., 7 Aug 1996. - MZUSP 58249, 1, 101 mm, immature; Brazil: Amazonas: Rio Amazonas, near confluence with Rio Madeira; M. Toledo-Piza et al., 7 Aug 1996. - MZUSP 58250, 1, 116 mm, immature; Brazil: Amazonas: near confluence with Rio Madeira; M. Toledo-Piza et al., 1 Aug 1996. - MZUSP 58521, 2, 91-106 mm, immatures; Brazil: Amazonas: Rio Amazonas, 18 km below near confluence with Rio Madeira; C. Cox-Fernandes et al., 10 Aug 1996.

Diagnosis. As for the genus.

Description. Body shape and pigment patterns illustrated in Fig. 1. Morphological and meristic data presented in Table 1. Known size up to 153 mm TL. Sexually mature males with 106-153 mm TL (n=2). Single mature female with 145 mm TL. No cranial or post-cranial sexual dimorphism observed among sexually mature specimens (n=2 males, 1 female) although we acknowledge the small sample size is not enough to exclude dimorphism. Scales cycloid, ovoid, present on entire post-cranial portion of body

from nape to tip of caudal appendage. Scales small, 6-8 (mode 6) rows above lateral line at midbody. Oral teeth conical. Premaxilla small, elongate, premaxillary teeth retained to adult.

Table 1. Morphometric and meristic data for *Parioster*narchus amazonensis (n=9). All data reported for adult specimens (males n=2, females n=1) and immature specimens (n=6) combined. Hence, n=9 unless otherwise stated.

| | mean | range |
|---------------------------------------|-------|----------|
| Total length (mm) | | 74-157 |
| Standard length (mm) | | 72-152 |
| Length to end of anal fin (mm) | | 65-132 |
| Head length to posterior margin | | |
| of opercle (mm) | | 9.9-19.3 |
| In % of standard length | | |
| Nape-origin dorsal organ | 42 | 35-48 |
| Anal fin base | 75 | 72-79 |
| In % of total length | | |
| Caudal peduncle + fin length | 14 | 8-17 |
| Snout to nape | 83 | 74-96 |
| In % of head length | | |
| Greatest body depth | 99 | 79-112 |
| Head length at branchial opening | 107 | 102-114 |
| Head depth at eye | 43 | 38-52 |
| Head depth at nape | 69 | 59-81 |
| Head width | 58 | 51-69 |
| Interocular distance | 25 | 21-30 |
| Eye diameter | 5 | 4-8 |
| Internarial distance | 15 | 13-18 |
| Postorbital distance at branchial ope | ening | |
| | 72 | 65-81 |
| Postorbital distance to opercle | 71 | 58-105 |
| Snout to posterior nares | 25 | 22-31 |
| Length eye to posterior nares | 59 | 44-83 |
| Preorbital length | 35 | 30-40 |
| Mouth length | 26 | 18-33 |
| Branchial opening | 18 | 14-23 |
| Length to anus | 81 | 68-97 |
| Length to origin of anal fin | 127 | 109-143 |
| Pre-pectoral distance | 115 | 109-125 |
| Mouth width | 26 | 22-30 |
| Pectoral fin length | 72 | 66-81 |
| Pectoral fin base (width) | 16 | 13-19 |
| Longest anal-fin ray | 45 | 34-54 |
| Caudal peduncle depth | 10 | 7-15 |
| meristics | mode | range |
| Anal fin rays | 162 | 155-168 |
| Pectoral fin rays | 14 | 14-15 |
| Caudal fin rays | 16 | 16-17 |
| Scale rows above lateral line | 6 | 6-8 |
| Posterior lateral line scales | 73 | 68-76 |
| Precaudal vertebrae (n=2) | | 12-14 |



Fig. 1. Pariosternarchus amazonensis, MCP 34916, holotype, 121 mm total length; Brazil, Amazonas: Paraná Maiana. Scale bars 10 mm.

Maxilla thin, more than twice as deep as wide, with a small straight and thin anterior process, and crescent-shaped, descending blade of maxilla curved, its ventral margin rounded. Dentary with 2-3 rows of teeth; dentary robustly ossified and somewhat elongate, its length greater than its depth. Anterior limb of anguloarticular longer than posterior limb. Posterior limb of anguloarticular shorter than retroarticular. Snout moderate length, preorbital distance about one third head length (mean preorbital distance 30-40 % head length [mean 35 %, n=9]).

Mesethmoid length moderate, its anterior tip small and flexed ventrally, with a median concave groove. Ventral ethmoid deepest at about midlength, with blunt, rounded lateral processes, and medium septum approximately as long as deep. Dermal vomer ossified and overlapping anterior limb of parasphenoid. Lateral ethmoid ossified, small with broad base but not contacting other cranial bones. Frontals without antorbital process. Dorsal margin of frontals flat or convex. Two



Fig. 2. Part of South America showing collection localities of *Pariosternarchus amazonensis*. 1, type locality. Some symbols represent more than one collecting record.

cranial fontanels present. Sphenoid region short. Orbitosphenoid shape broad. Orbitosphenoid margin contact pterosphenoid. Parasphenoid lateral wing absent. Parasphenoid ventral margin flat. Posterior portion of parasphenoid broad. Posttemporal fossae present. Cranial skeleton texture deeply pitted to reticulate. Infraorbital subnasal extension remote from anterior pore. Antorbital small, with infraorbital canal. Infraorbital canal plates narrow. Infraorbital canal tube with six bones. First infraorbital present. Mandibular canal fused with mandible. Supratemporal lateral line canal straight.

Position of nasal capsule near eye. Anterior narial pore at end of short tube. Eye subdermal. Ascending process endopterygoid robust. Mesopterygoid without teeth. Metapterygoid posterior wing broad. Size of sympletic smaller than hyomandibula. Orientation of hyomandibula oblique to head. Hyomandibular proximal articulation narrow. Preopercular orientation oblique to head axis. Anterior limb of preopercle narrow and curved. Opercle triangular, with a slightly concave dorsal margin. All pharyngobranchials ossified except those of third arch. Epibranchials of fifth arch with short posterior process. Epibranchials of seventh arch with short posterior-medial process. Ceratobranchials of fourth arch with posterior process, ceratobranchials of sixth arch smooth. Hypobranchial of third arch triangular. Hypobranchial of fourth arch with a smooth medial surface. Basihyal with a middorsal ridge. Basibranchial of fourth arch rod-shaped. Basibranchial of fifth arch cartilaginous (unossified). Urohyal blade robustly ossified.

Posttemporal fused with supracleithrum. Postcleithra thin and discoid. Third postcleithrum ossified. Mesocoracoid not ossified. Anterior coracoid process present. Pectoral fin large. Position of neural spines on posterior portion of posterior (caudal) centra. Vertebral fenestrae present. Caudal intermuscular bones not regenerated. Two displaced hemal spines present, with an anterior large saber-shaped bone, its proximal surface about as broad as descending blade, and a posterior bone short and straight. Dorsal organ located on posterior half of body. Anal fin origin at about vertical with pectoral girdle. Anal-fin pterygiophore length longer than hemal spines. Shape of anal-fin pterygiophore blades long and slender, their tips tapered. No distal anal-fin pterygiophore. Body cavity short with 12-14 precaudal vertebrae. Size of anterior ribs broad. Posterior parapophyses small, not contacting and long, contacting on midline. Shape of last precaudal parapophyses broad, triangular. Urogenital papilla absent.

Color in life. Body very pale white-pink in life. Pigment reduced with even distribution. No stripes, bars or irregular blotches. Head never banded, spotted or blotched, uniformly light gray but slightly paler in gular region. Numerous minute chromatophores speckled over branchiostegal membranes and ventral surface of head. Pectoral-fin and anal-fin rays and membranes hyaline or translucent. Color variation was not correlated with size or sex in the specimens examined. **Coloration in alcohol.** Much as in life, but with gray pigmentation changed to faded brown and white ground color changed to pale yellow. In brief: body coloration pale yellow with light brown mottling. Pectoral and anal fins hyaline.

Electric organ discharge. Not known.

Distribution. Known from localities along the main Amazon River channel in Brazil and Peru. Collection localities are in the Rio Amazonas (Amazon River), near Iquitos, Peru, and along the Rio Solimões (Amazon River) in Brazil from near the confluence of the Rio Japurá to near the confluence of the Rio Madeira (Fig. 2).

Ecology. *Pariosternarchus amazonensis* has been collected from flooded beaches and deep river channels using seines and trawl nets in the Amazon River, and the mouths of some of its larger whitewater tributaries (inferred from museum labels). *Pariosternarchus* exhibits a mosaic of traits associated with a life history in large river habitats, including reduced squamation and pigmentation, a laterally compressed body with a short body cavity, a small eye, and a small subterminal mouth with robust tooth-bearing bones of the oral jaws.

Etymology. Species named for the Amazon River.

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