



# Brown ghost electric fishes of the *Apteronotus leptorhynchus* species-group (Ostariophysi, Gymnotiformes); monophyly, major clades, and revision

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Neotropical brown ghost electric knifefishes of the *Apteronotus leptorhynchus* species-group are reviewed. A series of synapomorphies delimit the species-group and the two major subunits that comprise that clade. The phylogeny is concordant with the hypothesis of a primary division within the clade resultant from Andean uplift events 8 Mya and with the existence of ancestral components of the species-group 12 Mya. Species of the species-group are characterized by morphological stasis across that time frame. *Apteronotus leptorhynchus*, previously considered to be a widely distributed and morphologically variable species, was found to encompass five species. The description of the four new species is supplemented by the redescription of the five previously recognized forms within the species-group. Members of this clade are broadly distributed through the Essequibo River and Río Orinoco of the Atlantic slope of South America, the Ríos Aroa, Atrato, Cauca, Magdalena, and Yaracuy, and the rivers of the Lago Maracaibo basin of the Caribbean slope and drainages in northern Colombia and Panama along the Pacific versant.

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ADDITIONAL KEYWORDS: cladistics – Guyana Shield – historical biogeography – morphological stasis – phylogenetics – sexual dimorphism.

## INTRODUCTION

Ghost electric fishes of the genus *Apteronotus* inhabit rivers and streams across the expansive Atlantic drainages east of the Andean Cordilleras, the rivers of the Caribbean versant of north-western South America, and the rivers of the Pacific slope of Colombia and Panama (de Santana & Cox-Fernandes, 2012). One of the major subunits in the genus, the brown ghost electric fishes, or the *Apteronotus leptorhynchus* species-group of this paper, consists of small to medium-sized species inhabiting rivers and streams from the Pacific versant of Panama and Colombia across northern portions of South America and the Guyana Shield as far as the Essequibo River system in Guyana.

The first of the species now assigned to the *A. leptorhynchus* species-group was formally described by Ellis in Eigenmann (1912) as *Sternarchus leptorhynchus* based on material that originated in the lower Potaro and lower Essequibo rivers, Guyana. Soon thereafter Meek & Hildebrand (1913) described *Sternarchus rostratus* from the Río Grande of Panama and Regan (1914) proposed *Sternarchus spurrellii* from the Río San Juan, a river in western Colombia draining into the Pacific Ocean. Fowler (1943) subsequently described *Sternarchus macrostomus* from the Río Meta basin in eastern Colombia. In his summary analysis of the Gymnotiformes, Mago-Leccia (1994) assigned those four species to *Apteronotus*. A fifth species was added to the group after a six-decade hiatus with the description of *Apteronotus galvisi* by de Santana, Maldonado-Ocampo & Crampton (2007) from the portion of the Río Meta in the Cordillera Oriental piedmont of eastern Colombia.

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Ready availability of species of the *A. leptorhynchus* species-group in the European and North American aquarium trade in recent decades and their moderate body sizes and costs contributed to their incorporation into behavioural and neuroethological research programmes (e.g. Maler *et al.*, 1991; Moller, 1995; Thurston, 1996; Hupé & Lewis, 2008). Notwithstanding their frequent use in these analyses, the identity of these specimens was sometimes problematic (Hagedorn & Heiligenberg, 1985; see remarks in Cox-Fernandes, Lundberg & Riginos, 2002), and samples of the group with locality information remain relatively limited; a problem pervasive amongst many groups of Neotropical freshwater fishes (Vari & Malabarba, 1988). More critically, analysis revealed that what had previously been considered to represent local geographical variation in *A. leptorhynchus*, a reportedly widely distributed species (Myers, 1930; Schultz, 1949), instead encompassed cryptic and underestimated species level diversity. Unappreciated species richness has proved prevalent across the Apteronotidae (e.g. *Sternarchorhynchus*, de Santana & Vari, 2010) and the previously undetected species diversity in the *A. leptorhynchus* species-group highlights the need for revisionary and phylogenetic analyses across *Apteronotus*. As a first step in that endeavour, in this paper we herein:

1. Propose synapomorphies for the *A. leptorhynchus* species-group and for major units within the lineage;
2. Analyse and delimit the morphologically recognizable species within the species-group; and
3. Utilize the information from the revisionary and phylogenetic studies of the species to elucidate the historical biogeography and document the long-term morphological stasis of members of this species-group.

## MATERIAL AND METHODS

Morphological measurements were taken as point-to-point linear distances using digital callipers with a precision of 0.1 mm. Measurements taken included: total length (TL), from the tip of the snout to the posterior tip of the longest caudal-fin ray; length to the end of the anal fin (LEA), from the tip of the snout to the end of the anal fin; anal-fin length, from the anal-fin origin to the posterior end of the anal-fin base; preanal-fin distance, the distance from the tip of the snout to the base of the first anal-fin ray; snout to anus, from the tip of the snout to the anterior margin of the anus; pectoral-fin length, from the dorsal border of the fin base to the tip of the longest ray; greatest body depth, the vertical distance from the origin of the anal fin to the dorsal margin of the

body; tail length (CL), from the base of the last anal-fin ray to the tip of the longest caudal-fin ray; tail depth, between the dorsal and ventral margins of the caudal fin measured immediately after the last anal-fin ray; head length (HL), from the posterior margin of the dorsal limit of branchial opening to the tip of the snout; head depth at eye, between the dorsal and ventral margins of the head at the vertical through the eye; head width, the transverse dimension at the mid-opercle; length of mouth, measured from the tip of the snout to the rictus; branchial opening, from the dorsal to the ventral limits of the branchial opening; postorbital length, from the posterior margin of the branchial opening to the posterior margin of the eye; snout length, from the anterior margin of the eye to the tip of the snout; ocular diameter, between the anterior and posterior margins of the orbit; distance from posterior naris to eye, from the posterior margin of the posterior naris to the anterior margin of the eye; distance from tip of snout to posterior naris, from the tip of snout to the anterior margin of the eye; internarial distance, from the posterior margin of the anterior naris to the anterior border of the posterior naris; and interorbital distance, the linear distance between the medial margins of the orbits.

In the lists of material examined under each species, the institutional abbreviation and catalogue number for each lot is followed by the number of specimens in the lot and the size or size range of the specimen or specimens in the lot in mm. This is followed by specific locality information.

Specimens were cleared and double stained (c&s) following Taylor & Van Dyke (1985). Anal and caudal-fin ray and vertebral counts were taken from radiographs (R). Numbers of examined specimens with a particular meristic value are indicated in parentheses after each count in the text and meristic values for holotypes (when available) are designated by an asterisk \*. Sex and maturity were determined in a subset of the specimens that had undergone prior dissection or for which permission to do the appropriate dissection could be secured.

Principal components analysis (PCA) was used to determine differences amongst three sets of species, which although distinguishable using meristic and morphometric differences, nonetheless, demonstrate fewer such trenchant differences than those separating various other species. The analysis was carried out using PAST (Ryan, Harper & Whalley, 1995) with tail length and depth excluded because of the multiple individuals with damage to that portion of the body. Stepwise discriminant function analysis with jack-knife cross-validation was chosen to reduce our large set of variables. This analysis identifies a combination of variables that best separate the two

groups (Tabachnick & Fidell, 1989). Species descriptions are presented in alphabetical order.

#### INSTITUTIONAL ABBREVIATIONS

AUM, Auburn University Museum, Auburn; BMNH, The Natural History Museum, London; CAS, California Academy of Sciences, San Francisco; FMNH, Field Museum of Natural History, Chicago; IAvHP, Instituto Alexander von Humboldt, Colección de Peces, Villa de Leyva; INHS, Illinois Natural History Survey, Champaign; INPA, Instituto Nacional de Pesquisas da Amazônia, Manaus; MBUCV, Museo de Biología de la Universidad Central de Venezuela, Caracas; MCNG, Museum de Ciencias Naturales, Guanare; MCZ, Museum of Comparative Zoology, Harvard University, Cambridge; MNRJ, Museu Nacional, Rio de Janeiro; MPEG, Museu Paraense Emílio Goeldi, Belém; MZUSP, Museu de Zoologia da Universidade de São Paulo, São Paulo; USNM, National Museum of Natural History, Smithsonian Institution, Washington; ZMA, Zoologische Museum, Amsterdam (collections now at Netherlands Centre for Biodiversity, Naturalis, Leiden).

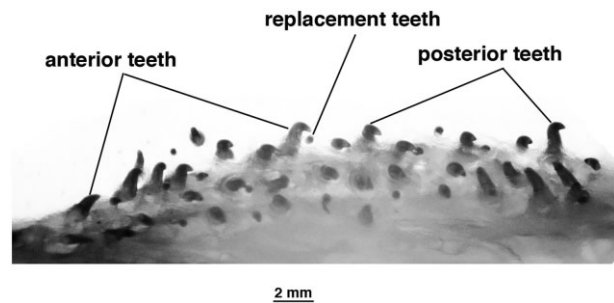
#### RESULTS

##### MONOPHYLY OF THE *APTERONOTUS LEPTORHYNCHUS* SPECIES-GROUP AND SYNAPOMORPHIES OF ITS SUBCLADES

For the purpose of character polarization, the other genera within the Apterontidae constituted the primary outgroup and the Sternopygidae (sister group of the Apterontidae; Albert, 2001) the secondary outgroup. The analysis revealed phylogenetically informative variation supporting the hypothesis of the monophyly of the *A. leptorhynchus* species-group and two major clades within that lineage. The first of these is composed of cis-Andean species (*Apteronotus baniwa*, *Apteronotus ferrarisi*, *A. galvisi*, *A. leptorhynchus*, *A. macrostomus*, and *Apteronotus pemon*) and the second of trans-Andean species (*Apteronotus anu*, *Apteronotus rostratus*, and *Apteronotus spurrellii*). Hereafter, we refer to the cis-Andean lineage as the *A. leptorhynchus* clade and the trans-Andean lineage as the *A. rostratus* clade.

##### *Synapomorphies of the Apteronotus leptorhynchus* species-group

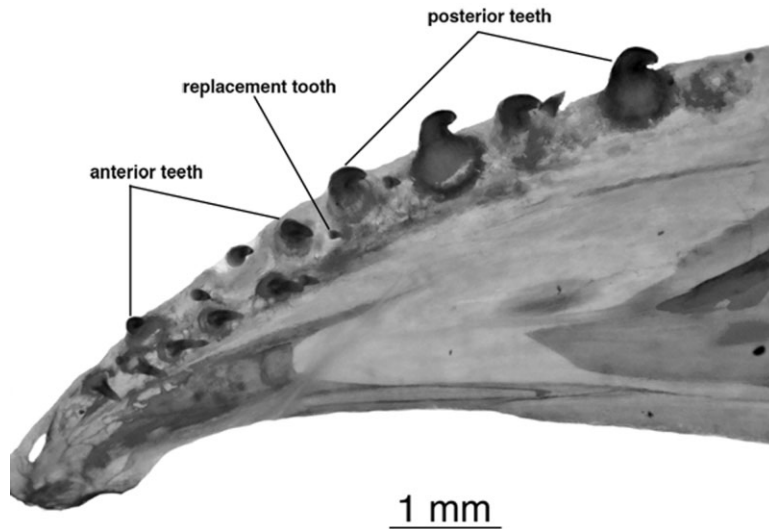
1. Presence of a pale median stripe commencing on the chin and extending mid-dorsally along the dorsal surface of the head and body to the posterodorsal portion of the body. Uniform dark pigmentation across the chin and dorsal portions of the head and body is prevalent across the Apteronti-



**Figure 1.** Cleared and stained dentary of *Apteronotus albifrons*, 114 mm total length, MCZ 52011. Left side, inverted, medial view, anterior to left, showing all teeth of approximately same size.

dae and Sternopygidae. Conversely, the species of the *A. leptorhynchus* species-group are characterized by a distinctly paler longitudinal median stripe extending from the chin dorsally onto the snout and continuing the length of the dorsal surface of the head and then posteriorly for varying distances along the body (for example see de Santana, Castillo & Taphorn, 2006: fig. 2). Comparable pigmentation patterns occur independently within the Apterontidae in some species of the *Apteronotus albifrons* species-group (de Santana, 2003) along with components of *Adontosternarchus* and *Sternarchorhynchus* (Lundberg, Mago-Leccia & Baskin, 1985; de Santana *et al.*, 2006; de Santana & Vari, 2010). Occurrence of this pigmentation pattern in these other lineages in the Apterontidae is judged homoplastic under hypotheses of relationships within *Apteronotus* (Alves-Gomes *et al.*, 1995) *Sternarchorhynchus* (de Santana & Vari, 2010), and the family (Albert, 2001).

2. Posterior teeth of the dentary approximately twice the size of the anterior teeth on that bone. Dentary teeth, when present, are of approximately comparable sizes along the dentigerous surface across the Sternopygidae and amongst most species in the Apterontidae (Fig. 1). Species of the *A. leptorhynchus* species-group conversely have the posterior teeth of the dentary approximately twice as large as the anterior teeth on that bone (Fig. 2).
3. Anterior elongation of the endopterygoid. The site of attachment of the pterygocranial ligament delimits the anterior versus posterior portions of the endopterygoid. Most species in the Apterontidae and Sternopygidae have an anterior portion of the endopterygoid of approximately the same size as the posterior portion of the ossification. Species of the *A. leptorhynchus* species-group alternatively have the portion of the endopterygoid anterior of the attachment site of the pterygocranial ligament



**Figure 2.** Cleared and stained dentary of *Apteronotus anu*, 149 mm total length, MCZ 52023. Left side, inverted, medial view, anterior to left, showing posterior functional teeth approximately twice size of anterior teeth.

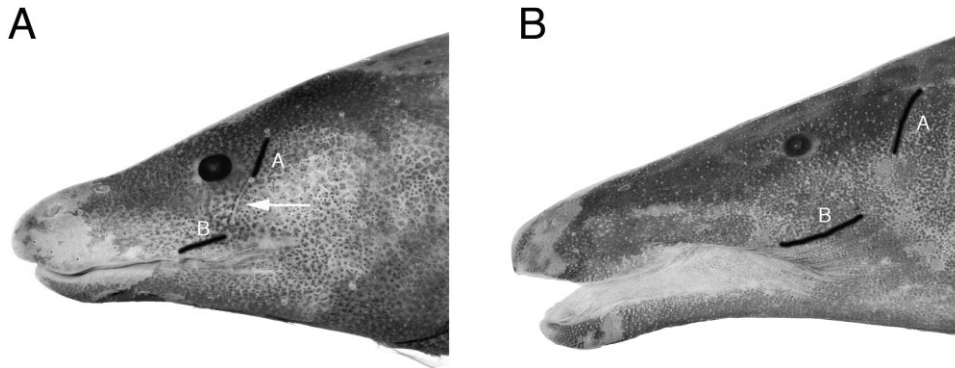
distinctly more elongate than the posterior portion of the bone (e.g. Hilton & Cox-Fernandes, 2006: fig. 5). A more pronounced elongation of this region of the endopterygoid occurs elsewhere within the Apteronotidae in some species of *Sternarchorhynchus* (de Santana & Vari, 2010: figs 9, 10). As with character 1, the presence of this condition within the latter genus is considered homoplastic relative to the endopterygoid elongation in the *A. leptorhynchus* species-group under present hypotheses of intrafamilial phylogenetic relationships (Albert, 2001; de Santana & Vari, 2010).

4. *Form of the quadrate.* The quadrate in the Apteronotidae and Sternopygidae is usually an anteriorly expanding, fan-shaped bone from a lateral view, with a posteroventral extension of the bone adjoining the anterior portion of the symplectic (Mago-Leccia, 1978: fig. 8; de Santana & Vari, 2010: fig. 8). Species of the *A. leptorhynchus* species-group, alternatively, have a rectangular quadrate.
5. *Position of the joint between the anguloarticular and quadrate.* In most species of the Apteronotidae and Sternopygidae the joint on the anguloarticular that articulates with the quadrate is located along the posterior-most portions of the anguloarticular at the margin between that ossification and the anterodorsal portion of the retroarticular. Variation from this general pattern in these two families includes a more posterior position of the joint formed by the anguloarticular plus retroarticular in *Megadontognathus kaitukaensis* in the Apteronotidae and in some members of the Sternopygidae (Mago-Leccia, 1978: fig. 8). Larger individuals

of all species of the *A. leptorhynchus* species-group have the anguloarticular-quadrate joint shifted distinctly anteriorly along the dorsal margin of the anguloarticular. This transition in position, which may correlate functionally with the elongation of the anguloarticular, occurs elsewhere in the Apteronotidae in *Platyurosternarchus* and *Sternarchorhynchus* (de Santana & Vari, 2010: figs 5–7). Present concepts of intrafamilial phylogenetic relationships (Albert, 2001) indicate that the shift of joint position in the latter genera is homoplastic relative to the transition in the *A. leptorhynchus* species-group.

6. *Ontogenetic elongation of the coronomeckelian bone.* The coronomeckelian bone is alternatively short and compact (as long as high) or somewhat longer than high across the Apteronotidae and Sternopygidae (de Santana & Vari, 2010; Vari, de Santana & Wosiacki, 2012). Even when the bone is elongate, its proportional length does not vary in post juveniles. The coronomeckelian bone in the species of the *A. leptorhynchus* species-group alternatively undergoes a progressive ontogenetic elongation yielding a distinctly elongate ossification in larger individuals. Comparable elongation characterizes sexually dimorphic males of various species of *Apteronotus* including *Apteronotus bonapartii* (Hilton & Cox-Fernandes, 2006: fig. 6). Those outgroup taxa are taxa not, however, closely related to the *A. leptorhynchus* species-group (Albert & Campos-da-Paz, 1998; Albert, 2001). Ontogenetic lengthening of the coronomeckelian bone in those taxa is consequently considered homoplastic relative to the restructuring of that element in the species-group.





**Figure 3.** Left lateral view of anterior and central portions of head of: A, *Apteronotus anu*, 132 mm total length (TL), holotype, MCNG 24991. A and B on figure positioned proximate to paths indicated in black of laterosensory canal segments in infraorbitals 6 and 4, respectively. Note presence of fifth infraorbital in form of paler tubular laterosensory canal segment between pores as indicated by white arrow; B, *Apteronotus pemon*, 165 mm TL, FMNH 70012. A and B on figure positioned proximate to paths indicated in black of laterosensory canal segments in infraorbitals 6 and 4 respectively. Note absence of tubular fifth infraorbital and associated pores between those canal segments.

7. *Ontogenetic reduction of the posterior dorsomedial cranial fontanel.* Two dorsomedial fontanels bordered by the frontals and parietals are prominent features of the neurocranium in the Apteronotidae and Sternopygidae. Separating the individual apertures is the transverse epiphyseal bar joining the contralateral frontals. The posterior fontanel is most often anteroposteriorly elongate across these families (Mago-Leccia, 1978: fig. 12; Hilton *et al.*, 2007: fig. 10a), albeit reduced to a circular opening delimited anteriorly and laterally by the parietals and posteriorly by the supraoccipital in the apteronotid genus *Platyurosternarchus* (de Santana & Vari, 2009), which is phylogenetically separated from *Apteronotus*. Smaller individuals of the species in the *A. leptorhynchus* species-group have an anteroposteriorly elongate posterior fontanel margined medially by the frontals and parietals. Ontogenetic medial expansion of the frontals and parietals lead to the progressive reduction and eventual elimination of the posterior fontanel in larger individuals of the species-group. The posterior fontanel is homoplastically absent in both small and large specimens of *Apteronotus cuchillo*, which is a member of a different lineage within *Apteronotus* (Albert & Campos-da-Paz, 1998; Albert, 2001).

*Synapomorphy of the Apteronotus leptorhynchus clade*

8. *The absence of the fifth infraorbital.* Variation in the presence versus absence and morphology of the antorbital and infraorbitals is phylogenetically informative at multiple levels of inclusiveness across the Gymnotiformes (e.g. Lundberg &

Mago-Leccia, 1986; de Santana & Crampton, 2011). The homology of, and nomenclature applied to, elements around the orbital margin is the subject of dispute in some clades within the order (e.g. Hypopomidae and Ramphichthyidae; de Santana & Crampton, 2011: 1107), albeit established in the Sternopygidae (Lundberg & Mago-Leccia, 1986). That family has six ossifications in the series; five infraorbitals plus an anterior antorbital (Lundberg & Mago-Leccia, 1986: fig. 2). The morphologically diverse and speciose Apteronotidae demonstrates variation in the number and form of these elements (e.g. Hilton *et al.*, 2007), albeit with the condition in the Sternopygidae, its sister group, informative as to the homology of individual elements. Of particular note for this analysis is the variation involving the fifth infraorbital in the *A. leptorhynchus* species-group. A fifth infraorbital with an included laterosensory canal segment is present across *Apteronotus* (e.g. *A. anu*, Fig. 3A), but absent in the *A. leptorhynchus* clade (e.g. *A. pemon*, Fig. 3B). In light of the unique lack of this ossification in this clade within the Apteronotidae–Sternopygidae clade, this condition is hypothesized as derived.

*Synapomorphies of the Apteronotus rostratus clade*

9. *Bases of anterior teeth of the outer row of dentition on the premaxilla one and a half times wider than the bases of the posterior teeth on the bone.* Teeth on the premaxilla, when present, are usually of equal size and base width along the dentigerous margin of the bone in the Apteronotidae and Sternopygidae. Conversely, species of the *A. rostratus* clade have the anterior teeth of the

outer tooth row on the premaxilla approximately  $1.5 \times$  wider basally than the posterior teeth on the bone.

10. *Lateral ethmoid cartilaginous*. The lateral ethmoid is present as an ossified element across the Sternopygidae (e.g. Mago-Leccia, 1978: figs 6, 11, 25) but remains cartilaginous into adulthood in some species of the Apteronotidae (Hilton & Cox-Fernandes, 2006; de Santana & Vari, 2009, 2010) including species of the *A. rostratus* clade. A non-ossified lateral ethmoid is present elsewhere within *Apteronotus* in *Apteronotus cuchillejo* but this element is ossified in its closest relatives (Albert, 2001). The condition in *A. cuchillejo* is consequently hypothesized to be independent of the cartilaginous lateral ethmoid in the *A. rostratus* clade, with the condition a synapomorphy for the latter assemblage.

#### Phylogenetic biogeography

Overlay of species distributions on the phylogeny of the *A. leptorhynchus* species-group demonstrates complete allopatry between the two primary clades in that lineage; the *A. leptorhynchus* and *A. rostratus* clades. The *A. leptorhynchus* clade (*A. baniwa*, *A. ferrarisi*, *A. galvisi*, *A. leptorhynchus*, *A. macrostomus*, and *A. pemon*) inhabits a broad swath of cis-Andean northern South America including the Atlantic slope Essequibo and Orinoco river basins and two drainage systems of the Caribbean versant of northern Venezuela. The trans-Andean *A. rostratus* clade (*A. anu*, *A. rostratus*, and *A. spurrellii*) is restricted to the Caribbean versant Lago Maracaibo, Río Atrato, and Río Magdalena systems and a series of river systems of the Pacific slope of north-western Colombia and south-western Panama. Life history information for members of the *A. leptorhynchus* species-group is sparse, but indicates that the species do not occur in the precipitous river systems of the uplands of the Andean Cordilleras, albeit occurring at elevations of over 500 m asl in the Andean uplands of north-western Venezuela (Péfaur, 1988: 474). Their presence in the less energetic rivers of mid to low elevation settings make it likely that the Andean uplift events may have initiated the split into the cis- and trans-Andean *A. leptorhynchus* and *A. rostratus* clades. Even if preceded by earlier underlying vicariant events, the uplift of the northern Andean cordilleras serves as a minimum age for this division.

Under this biogeographical calibration, the minimum age for the division between the cis- and trans-Andean components of the *A. leptorhynchus* species-group is the closure of the then north-flowing Río Orinoco at the Maracaibo-Falcon outlet. This event minimally dates to approximately 8 Mya in the course of the final uplift sequences of northern com-

ponents of the cordilleras in the region of the Merida Andes. That sequence resulted in the isolation of the modern Lago Maracaibo basin from the proximate Río Orinoco basin (Hoorn, 1993; Hoorn *et al.*, 1995; Lundberg *et al.*, 1998).

Another yet earlier isolation event correlating with present species distributions in the *A. leptorhynchus* species-group is the uplift of the Eastern Cordillera of the northern Andes at 12 Mya, dividing the Magdalena basin and what is now the Pacific versant of north-western South America from regions to the east. This possibly accounts for allopatry between the members of the *A. rostratus* clade to the two sides of the Eastern Cordillera (*A. anu* in the Lago Maracaibo system to the east versus *A. rostratus* of the Ríos Atrato, Cauca, and Magdalena of the Caribbean slope and several rivers of the Pacific versant of Panama plus *A. spurrellii* of the Ríos Condoto and Dagua of the Pacific versant of Colombia in the west). Such concordance provides a minimum age of 12 Mya not only for the *A. leptorhynchus* species-group but also for *Apteronotus* and is a pattern common to multiple groups of fishes in northern South America (e.g. Albert, Lovejoy & Crampton, 2006).

#### Morphological stasis

Evolutionary stasis is the phenomenon of 'little or no net accrued species-wide morphological change during a species-lineage's existence up to millions of years' (Eldredge *et al.*, 2005). As noted by those authors, some taxa judged to be individual species in their analysis are thought to demonstrate this phenomenon on the scale of 16 to 2 Myr; a scale in keeping with the minimum ages discussed above for the possible vicariant events within the *A. leptorhynchus* species-group. Evolutionary stasis has been typically been invoked in the case of fossils; however, morphological stasis also applies in instances of supraspecific taxa such as the *A. leptorhynchus* species-group and its two major included lineages, the *A. leptorhynchus* clade and the *A. rostratus* clade, all of which lack any significant restructurings of the overall bauplan across the phylogeny (compare figures for each species). Modifications recognized herein as synapomorphies, although distinct, do not involve pronounced alterations of the pertinent, largely internal body complexes. Indeed, many if not all of the changes would be difficult to impossible to ascertain in fossil representatives if those exist. Thus, the clade would most likely be judged to reflect evolutionary stasis as traditionally defined. This may very well be a function of the 'phylogenetic niche conservatism' proposed by Wiens & Donoghue (2004). Occurrence of this phenomenon within gymnotiforms was analysed in an insightful discussion by Crampton (2011).

Morphological stasis has consequently been the norm post each of the major sequential cladogenic events within the *A. leptorhynchus* species-group discussed under Phylogenetic biogeography above (minimally 8 and 12 Mya). Comparisons with other components of *Apteronotus* make it clear that the basic bauplan is common across the genus and thus probably arose earlier than the cited cladogenic events with stasis of longer duration. In contrast, other groups of fishes from the same region have undergone more pronounced modifications between sister clades [e.g. in the Characiformes in *Rhoadsia* versus its sister taxa (Oliveira *et al.*, 2011); and *Boulengerella* versus *Ctenolucius* in the Ctenoluciidae (Vari, 1995)], thus demonstrating varying rates of morphological changes amongst different components of the ichthyofauna under the same biogeographical calibrations.

A pattern of apparent stasis based on effective bauplan uniformity amongst modern species was proposed for the characiform genus *Prochilodus* by Castro & Vari (2004) for a time period comparable to that for the *A. leptorhynchus* species-group. Fossil evidence indicates that such stasis similarly occurs in the characiform serrasalmid genus *Colossoma* (Lundberg, Machado-Alison & Kay, 1986) in which remains of the genus dating to the Miocene La Venta Formation in Colombia (approximately 15 Mya) are morphologically comparable to Recent members of *Colossoma*. Amongst New World ostariophysans this pattern of stasis extends beyond characiforms and gymnotiforms to the siluriforms as exemplified by Miocene era fossils of a large body-size catfish of the genus *Phractocephalus* of the family Pimelodidae (Lundberg & Aguilera, 2003).

## TAXONOMIC ACCOUNTS

### *APTERONOTUS LEPTORHYNCHUS* SPECIES-GROUP

**Diagnosis:** Species of the *A. leptorhynchus* species-group can be readily distinguished from the remaining genera of the Apteronotidae and within *Apteronotus* via the synapomorphies identified above. The species-group is externally recognizable by the stripe of distinctly paler pigmentation running from the chin along the mid-dorsal region of the head and body to the posterodorsal portion of the body, the pale band encircling the base of the caudal fin, the presence of scales on the dorsal portion of the body, and the possession of posterior dentary teeth two times as large as the anterior teeth on that bone.

**Distribution:** Species of the *A. leptorhynchus* species-group occur in the Essequibo River system in Guyana, various portions of the Río Orinoco basin, and two

coastal Caribbean drainages of northern Venezuela. Trans-Andean species inhabit various drainages of the Lago Maracaibo basin in north-western Venezuela and north-eastern Colombia, the Caribbean versant Rios Atrato, Cauca, and Magdalena of northern Colombia, and Pacific Ocean drainages in Colombia and Panama.

**Remarks:** Albert & Campos-da-Paz (1998) and Albert (2001), followed by de Santana & Cox-Fernandes (2012), proposed a slightly more encompassing assemblage than the *A. leptorhynchus* species-group of this analysis, which additionally incorporated *Apteronotus brasiliensis* and which they termed the *A. brasiliensis* species-group. In so far as the data matrices of the analyses Albert & Campos-da-Paz (1998) and Albert (2001) did not include *A. brasiliensis*, the basis for that assignment is uncertain. More pertinently, information collected in this study failed to support the placement of *A. brasiliensis* within the *A. leptorhynchus* species-group and we consequently did not include it here.

### *APTERONOTUS ANU* SP. NOV. (FIGS 4, 5; TABLE 1)

*Apteronotus leptorhynchus* (not of Ellis), Schultz, 1949: 69 [original description: Venezuela, Lago Maracaibo basin, Río San Juan, Río San Pedro, Río Negro]. – Galvis, Mojica & Camargo, 1997: 104, figs. [Colombia, Lago Maracaibo basin, Río Catatumbo; habitat]. – Péfaur, 1988: 471 [Venezuela, upper Andean areas]. – Albert, 2003: 498 [in part in listing of species; citations from Río Catatumbo]. – Lasso *et al.*, 2004a: 181 [Venezuela, Lago Maracaibo]. – Rodríguez-Olarte, Taphorn & Lobón-Cerviá, 2009: 67 [Venezuela, Perija Andes].

**Diagnosis:** *Apteronotus anu* is distinguished from *A. baniwa* by the condition of the fifth infraorbital (present as a tubular laterosensory canal segment versus absent), the number of caudal-fin rays (10–13 versus 14–17), the condition of the lateral ethmoid (cartilaginous versus ossified), and the number of precaudal vertebrae (18–19 versus 16–17). *Apteronotus anu* is differentiated from *A. ferrarisi* by the condition of the fifth infraorbital (present as a tubular laterosensory canal segment versus absent), the condition of the lateral ethmoid (cartilaginous versus ossified), the number of scales above the lateral line at the midbody (seven to nine versus 10–13), the number of scales along the lateral line (59–63 versus 73–80), the number of caudal-fin rays (10–13 versus 15–17), the extent of the mid-dorsal groove (extending seven to eight scales beyond the vertical through the posterior terminus of the anal fin versus two to six), and the tail length (17.1–37.5% of LEA versus 6.9–



KEY TO THE SPECIES OF *APTERONOTUS LEPTORHYNCHUS* SPECIES-GROUP

- 1a. Fifth infraorbital in form of externally obvious tubular laterosensory canal segment (Fig. 3A).....2
- 1b. Fifth infraorbital absent (Fig. 3B).....4
- 2a. Pectoral-fin rays 15–17; total anal-fin rays 137–164; posterior limit of mouth extending posteriorly distinctly beyond vertical through anterior margin of eye.....3
- 2b. Pectoral-fin rays 12–13; total anal-fin rays 171–173; posterior limit of mouth falling short of vertical through anterior margin of eye.....*Apteronotus spurrellii* (Ríos Condoto and Dagua, Pacific slope of Colombia)
- 3a. Tail length 17.1–37.5% of LEA; caudal-fin rays 10–13.....*Apteronotus anu* sp. nov. (Lago Maracaibo basin, Venezuela)
- 3b. Tail length 10.6–12.4% of LEA; caudal-fin rays 14–16.....*Apteronotus rostratus* (Río Magdalena, Río Cauca, and coastal rivers of Panamá)
- 4a. Tail length 11.3–24.3% of LEA; tail depth 6.8–19.0% of CL.....5
- 4b. Tail length 6.9–9.9% of LEA; tail depth 22.2–28.7% of CL.....*Apteronotus ferrarisi* sp. nov. (coastal Caribbean drainages of northernmost Venezuela)
- 5a. Scales above lateral line at midbody 7–10.....6
- 5b. Scales above lateral line at midbody 11–14.....7
- 6a. Scales along lateral line 61–70; scales above lateral line at midbody 7–8; caudal-fin rays 14–17.....*Apteronotus baniwa* sp. nov. (upper Río Orinoco, Venezuela)
- 6b. Scales along lateral line 74–83; scales above lateral line at midbody 9–10; caudal-fin rays 18–20.....*Apteronotus pemon* sp. nov. (Techine-Meru waterfall, upper Río Caroni basin, Venezuela)
- 7a. Caudal-fin rays 18–21.....8
- 7b. Caudal-fin rays 10–16.....*Apteronotus galvisi* (Ríos Cusiana, Cravo, Pauto, and Upia along piedmont of Cordillera Oriental, upper Río Meta, Colombia)
- 8a. Pectoral-fin rays 17–18; snout length in dimorphic male 41.9% of HL; mouth length in dimorphic male 48.8% of HL; branchial opening in dimorphic male 14.9% of HL.....*Apteronotus leptorhynchus* (Essequibo River basin, Guyana)
- 8b. Pectoral fin-rays 15–17; snout length in dimorphic male 44.7% of HL; mouth length in dimorphic male 56.2% of HL; branchial opening in dimorphic male 12.1% of HL....*Apteronotus macrostomus* (lower Río Meta, Colombia)

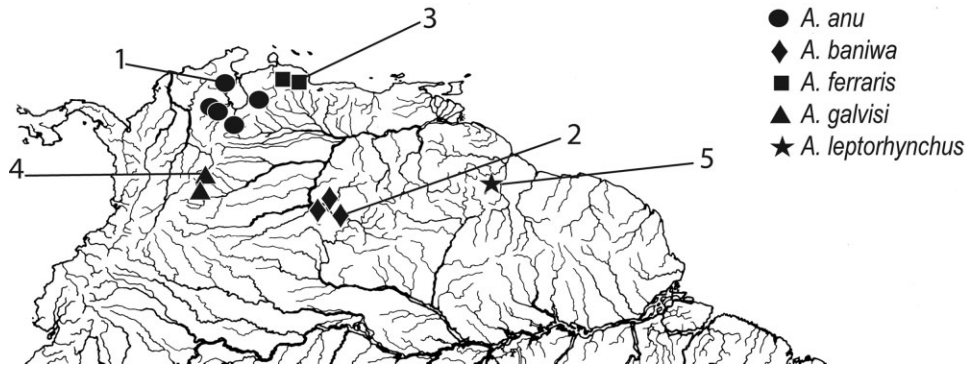


**Figure 4.** *Apteronotus anu*, 132 mm total length, male, holotype, MCNG 24991; Venezuela, Maracaibo, Rio Negro, at bridge, 12 km south of Machiques on road to Tokuko.

9.9%). *Apteronotus anu* differs from *A. galvisi* in the condition of the fifth infraorbital (present as a tubular laterosensory canal segment versus absent), the condition of the lateral ethmoid (cartilaginous versus

ossified), the number of scales above the lateral line at the midbody (seven to nine versus 11–12), and the tail length (17.1–37.5% of LEA versus 11.8–15.9%). *Apteronotus anu* is distinguished from *A. leptorhynchus*





**Figure 5.** Map of north portion of South America showing geographical distribution of *Apteronotus anu* (1 = holotype locality); *Apteronotus baniwa* (2 = holotype locality); *Apteronotus ferraris* (3 = holotype locality); *Apteronotus galvisi* (4 = holotype locality), and *Apteronotus leptorhynchus* (5 = holotype locality). Some symbols represent more than one locality and/or lot of specimens.

*chus* by the condition of the fifth infraorbital (present as a tubular laterosensory canal segment versus absent), the condition of the lateral ethmoid (cartilaginous versus ossified), the number of scales above the lateral line at the midbody (seven to nine versus 12–13), the number of pectoral-fin rays (14–16 versus 17–18), the number of anal-fin rays (159–176 versus 151–156), the number of caudal-fin rays (10–13 versus 17–21), and the number of scales along the lateral line (59–63 versus 78–82). *Apteronotus anu* is differentiated from *A. macrostomus* by the condition of the fifth infraorbital (present as a tubular laterosensory canal segment versus absent), the condition of the lateral ethmoid (cartilaginous versus ossified), the number of anal-fin rays (159–176 versus 140–152), the number of caudal-fin rays (10–13 versus 18–21), and the number of scales above the lateral line at the midbody (seven to nine versus 11–14). *Apteronotus anu* differs from *A. pemon* in the condition of the fifth infraorbital (present as a tubular laterosensory canal segment versus absent), the interorbital distance (14.7–36.5% of HL versus 9.7–14.6%), the number of caudal-fin rays (10–13 versus 18–20), the number of scales along the lateral line (59–63 versus 74–83), and the condition of the lateral ethmoid (cartilaginous versus ossified). *Apteronotus anu* is differentiated from *A. rostratus* by the tail length (17.1–37.5% of LEA versus 10.6–12.4%) and the number of caudal-fin rays (10–13 versus 14–16). *Apteronotus anu* is distinguished from *A. spurrellii* by the number of pectoral-fin rays (14–16 versus 12–13), the number of caudal-fin rays (10–13 versus 14), the number of scales along the lateral line (59–63 versus 73–76), the extent of the mid-dorsal groove (extending seven to eight scales beyond the vertical through the posterior terminus of the anal fin versus four) and the tail length (17.1–37.5% of LEA versus 12.5–13.7%).

*Description:* Head, body, and fin shape and pigmentation illustrated in Figure 4. Morphometrics for holotype and paratypes presented in Table 1. Body laterally compressed, greatest body depth located at, or slightly posterior to, abdominal cavity. Dorsal profile of body nearly straight. First perforated scale of lateral line located above pectoral-fin origin. Lateral line extending posteriorly to base of caudal fin. Scales along lateral line 59(6), 61(4), 62\*(5), or 63(3). Scales above lateral line to mid-dorsal line at midbody 7(4), 8(9), or 9\*(12).

Head laterally compressed, widest at opercular region and deepest at nape. Dorsal profile of snout and overall head nearly straight. Eye small, located laterally on head, and completely covered by thin membrane. Anterior naris located at end of small tube and close to tip of snout. Posterior naris ellipsoidal, without tube and positioned closer to tip of snout than to anterior margin of eye. Mouth inferior with rictus extending posterior of vertical through anterior border of eye. Branchial opening located at, or slightly posterior to, vertical through pectoral-fin insertion. Anus and urogenital papilla located posterior to vertical through eye; position not ontogenetically variable.

Pectoral fin elongate, with 14\*(10), 15(10), or 16(5) rays. Anal-fin origin located at, or slightly anterior to, vertical through posterior margin of opercle. Unbranched anal-fin rays 12(5), 15(3), 20(2), 23(5), 25\*(3), or 30(3). Total anal-fin rays 159(1), 160(1), 161(1), 162(2), 163\*(2), 164(1), 165(1), 167(1), 170(1), 171(4), 172(1), 173(1), or 176(1). Tail compressed and short; ending in small, elongate caudal fin. Caudal-fin rays 10(10), 11(2), or 13\*(6).

Origin of dorsal sagittal electroreceptive filament situated on posterior half of body. Filament inserted into narrow mid-dorsal groove extending 7\*(13) or

**Table 1.** Morphometrics for examined specimens of *Apteronotus anu*, *Apteronotus baniwa*, and *Apteronotus ferrarisi*

	<i>A. anu</i>				<i>A. baniwa</i>				<i>A. ferrarisi</i>			
	H	Range	N	Mean	H	Range	N	Mean	H	Range	N	Mean
Total length (mm)	132.0	45.6–271	25	–	155.0	71.1–155	6	–	231.0	160–274	5	–
Length to end of anal fin (mm)	109.0	36.9–225	25	–	130.0	56.6–130	6	–	212.0	146–212	4	–
Tail length (mm)	17.9	13–55	24	–	26.0	11.0–26.0	5	–	18.8	11.5–18.8	4	–
Head length (mm)	19.1	7.3–46.9	25	–	28.4	11.8–28.4	6	–	46.8	30.0–67.7	5	–
Per cent of length to end of anal fin												
Anal-fin length	84.3	75.9–84.3	25	80.3	80.0	80.0–85.4	6	82.1	82.5	78.7–82.5	4	81.0
Snout to anus	12.9	11.3–18.4	25	13.8	14.5	11.2–15.7	6	12.7	12.5	11.6–13.2	4	12.4
Greatest body depth	11.1	11.1–15.3	25	12.9	12.7	12.7–15.1	6	13.9	15.2	15.1–16.2	4	13.5
Prenal-fin distance	16.2	16.2–23.0	25	18.9	19.7	15.8–19.7	6	17.4	18.9	18.0–19.0	4	17.0
Tail length	17.1	17.1–37.5	24	24.9	20.0	13.3–24.2	5	19.8	8.9	6.9–9.9	4	8.3
Head length	17.4	9.4–20.8	25	18.3	21.8	18.4–21.8	6	19.5	22.1	20.0–22.1	4	19.0
Per cent of head length												
Head depth at eye	40.1	33.9–69.5	25	41.9	30.5	30.5–38.7	6	36.4	38.4	34.6–41.9	5	38.2
Head width	34.6	34.6–68.8	25	38.8	28.6	28.6–30.0	6	32.2	34.0	30.1–38.9	5	35.1
Ocular diameter	7.4	4.4–8.7	25	6.0	4.8	4.8–6.9	6	6.3	4.1	4.0–5.9	5	4.7
Interorbital distance	23.8	14.7–36.5	25	20.4	13.0	13.0	1	–	17.8	15.7–18.7	5	17.6
Internarial distance	10.6	7.6–12.8	25	9.2	10.3	10.3	1	–	9.9	9.1–10.7	5	9.9
Snout length	39.6	29.8–64.2	25	36.5	43.6	43.6	1	–	43.5	43.5–45.1	2	44.3
Snout to posterior naris	18.3	16.9–23.5	25	20.0	20.9	18.6–21.9	6	20.7	19.3	19.3–23.2	5	21.2
Posterior naris to eye	18.2	15.5–24.7	25	19.5	19.4	19.4	1	–	22.0	22.0–23.6	2	22.8
Mouth length	51.3	35.2–61.6	25	46.4	47.1	47.1	1	–	55.0	55.0–56.4	2	55.7
Branchial opening	14.9	8.7–19.1	25	11.3	12.0	12.0–15.9	6	14.8	12.7	11.3–15.7	5	13.3
Pectoral-fin length	36.0	11.2–36.6	25	26.8	50.8	31.8–50.8	6	44.7	33.4	18–22.5	4	20.5
Postorbital length	54.8	46.9–58.1	25	55.7	52.8	52.8–55.6	6	54.0	53.7	53.4–55.1	5	54.3
Per cent of tail length												
Tail depth	6.3	6.3–9.5	24	7.4	9.5	8.2–15.3	5	10.1	25.3	22.2–28.7	4	25.4

*N*, number of specimens; H, holotype. Range includes holotype. Sexually dimorphic features for *A. baniwa* and *A. ferrarisi* are presented as two entries. First entry is for sexually dimorphic males with information for females and immatures in second entry.

8(5) scales posterior to vertical through posterior terminus of anal-fin base. Precaudal vertebrae 18(3), 19\*(2). Total vertebrae 70(2), 73\*(2) or 83(1).

**Coloration in life:** Galvis *et al.* (1997: 104) provided a life photo of *A. anu* (identified in that paper as *A. leptorhynchus*), which shows the head and body to be dark brown from a lateral view with the fins apparently hyaline.

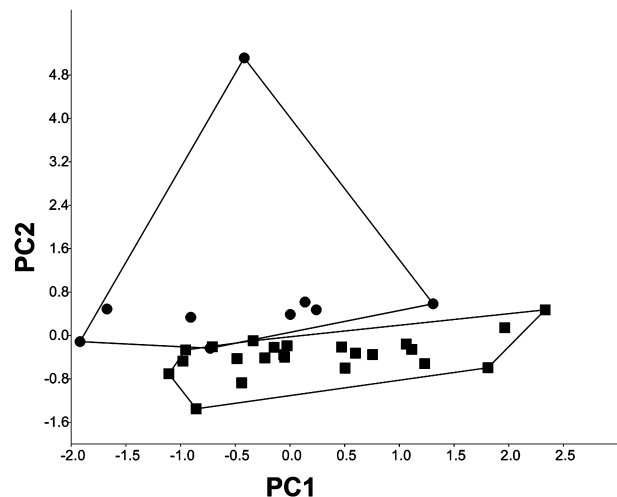
**Coloration in alcohol:** Body and head light brown to black. Prominent pale, broad, longitudinal band extends from chin along dorsal midline of head and body to over dorsal filament. Pectoral and anal-fin rays ranging from translucent to dark brown. Inter-radial membranes translucent. Pale band encircling base of caudal fin. Caudal fin pale at base, pale to black on central portion and translucent posteriorly.

**Distribution:** *Apteronotus anu* is known from several rivers draining into Lago Maracaibo in north-eastern Colombia and north-western Venezuela (Fig. 5). The apparent restriction of this species to the rivers draining that basin conforms to a pattern general in the Lago Maracaibo ichthyofauna in which two-thirds of the freshwater fish species in the basin are endemics (Rodríguez-Olarte *et al.*, 2009: 87).

**Habitat:** According to Galvis *et al.* (1997: 104), *A. anu* (identified in that study as *A. leptorhynchus*) occurs in swift current habitats over substrates of rounded stones in the portion of Río Catatumbo in Colombia. Their observations indicate that *A. anu* is a voracious nocturnal predator. Péfaur (1988: 474) reported that the species (identified by him as *A. leptorhynchus*) occurs at elevations of over 500 m asl in the Río Chama, a tributary to Lago Maracaibo.

**Etymology:** The species name, *anu*, is in reference to the Añu indigenous peoples who lived along the shores of Lago Maracaibo in traditional houses termed Palafitos, which they built above the lake. Such housing reminded early European explorers of Venice, Italy, and may have been the basis for the application of the name Venezuela to the region.

**Remarks:** *Apteronotus anu* is trenchantly differentiated from *A. spurrellii*, one of two other species of the *A. rostratus* clade, in the numbers of pectoral- and total anal-fin rays in addition to the position of the posterior limit of the mouth. *Apteronotus anu* and *A. rostratus*, the other member of the clade, are not separated to a comparable degree, but differ in the length of the tail (17.1–37.5% of LEA versus 10.6–12.4%, respectively) and in the number of caudal-fin rays (10–13 versus 14–16). The results of the PCA showed separation



**Figure 6.** Principal components analysis on covariance matrix of log-transformed measurements of *Apteronotus anu* (squares) and *Apteronotus rostratus* (circles). Scatter plot of scores on first (PC1) and second (PC2) principal components.

between *A. anu* and *A. rostratus* along the first and second principal components (PC1 and PC2; Fig. 6). PC1 and PC2 reflected 89.7 and 3.8%, of the variation respectively. The best predictors of the differences between the two species were: the distance from the posterior snout to the eye (0.38), the mouth length (0.30), and the internarial distance (0.89). A jack-knife cross-validation procedure correctly classified 100% of the specimens by species, further supporting the hypothesis of the differences of *A. anu* and *A. rostratus*.

As noted in the Introduction, samples of the *A. leptorhynchus* clade from across vast expanses were identified as *A. leptorhynchus* in the prior literature. Populations previously identified as *A. leptorhynchus* by Schultz (1949: 69), Galvis *et al.* (1997: 104), Péfaur (1988: 471), Lasso *et al.* (2004a: 181), and Rodríguez-Olarte *et al.* (2009) based on samples originating in various rivers draining into Lago Maracaibo in both Colombia and Venezuela were found here to be *A. anu* based on the collecting localities.

**Material examined:** Holotype: Venezuela. Zulia. MCNG 24991, holotype, 132; Rio Negro, 12 km south of Machiques on way to Tokuko at the bridge, Taphorn *et al.*, 1.viii.1991.

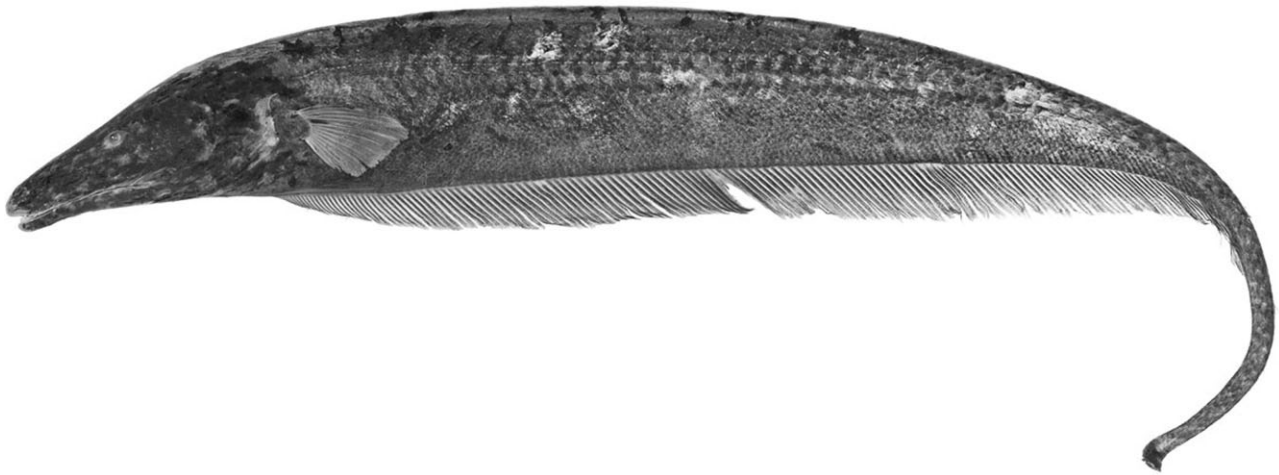
Paratypes: Venezuela. Mérida. INHS 34978, 1, 231; Rio Chama, Lago Maracaibo, El Vigia, 08°25'54"N, 71°37'31"W, 31.i.1995. INHS 59885, 1, 174; tributary of Río Gavilan, Lago Maracaibo basin, 3 km east of Capazon, 08°49'04"N, 71°25'03"W, 6.i.1991. Zulia. INHS 35364, 16, 35–118, Caño Taguara, Rio Santa

Ana, Lago Maracaibo basin, 18 km north of Puerto Catatumbo along highway at bridge, 09°17'22"N, 72°32'49"W, 2.ii.1995. INHS 35443, 1, Río Santa Ana, Lago Maracaibo basin, bridge approximately 8 km south-west of Alturistas, 09°41'30"N, 72°25'47"W. INHS 59949, 1, 182; Río Negro, Río Santa Ana, Lago Maracaibo basin, 12 km south of Machiques on road to Tucuco, collected 8.i.1991. INHS 60284, 6, 90–115; Caño off Río Zulia, Lago Maracaibo basin, 12 km south of intersection of Highways 2 and 6, 8.i.1991. INHS 60468, 1, 117, Río Yasa, Río Palmar, Lago Maracaibo, 5 km south of Machiques on road to Tucuco, 9.i.1991. MCZ 52023, 1 c&s, 149; Río San Juan, near bridge south of Mene Grande, Río Motatán basin, 09°49'N, 56°00'W, 17.iii.1942. USNM 121592, 1, 60; Río San Juan 12 km south of Rosario, Lago Maracaibo basin, 26.ii.1942. USNM 121593, 3, 97–147; Río San Pedro at bridge, tributary of Río Motatán, Lago Maracaibo basin, 20.iii.1942. USNM 121595, 6, 112–175; Río San Juan, near bridge close to Mene Grande, tributary of Río Motatán, Lago Maracaibo basin, 17–20.iii.1942.

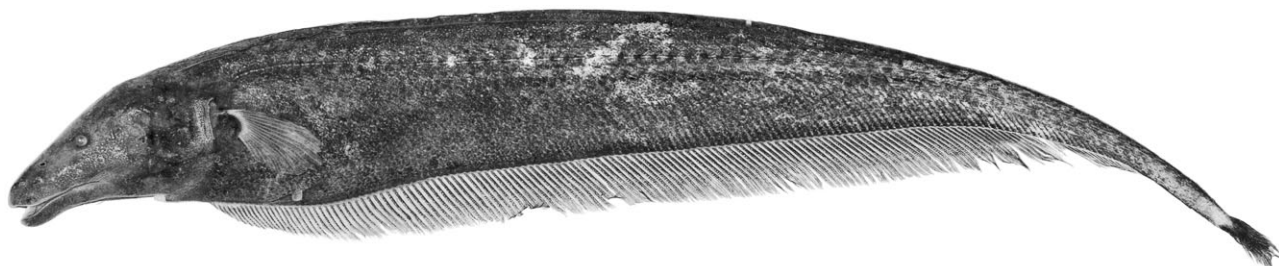
**APTERONOTUS BANIWA SP. NOV.**

(FIGS 5, 7, 8; TABLE 1)

*Diagnosis:* *Apteronotus baniwa* is distinguished from *A. anu* by the condition of the fifth infraorbital (present as a tubular laterosensory canal segment versus absent), the number of caudal-fin rays (14–17 versus 10–13), the condition of the lateral ethmoid (ossified versus cartilaginous), and the number of precaudal vertebrae (16–17 versus 18–19). *Apteronotus baniwa* is differentiated from *A. ferrarisi* by the number of scales above the lateral line at the midbody (seven to eight versus 10–13), the number of scales along the lateral line (61–70 versus 73–80), the mouth length (36.6–47.2% of HL versus 49.4–56.4%), the tail length (13.3–24.2% of LEA versus 6.9–9.9%) and the tail depth (8.2–15.3% of CL versus 22.2–28.7%). *Apteronotus baniwa* differs from *A. galvisi* in the number of scales above the lateral line at the midbody (seven to eight versus 11–12). *Apteronotus baniwa* is distinguished from *A. leptorhynchus* by the number of scales above the lateral line at the midbody



**Figure 7.** *Apteronotus baniwa*, 155 mm total length, male, holotype, AUM 43275; Venezuela, Amazonas, Río Orinoco, 147 km east-south-east of San Fernando de Atabapo, 03°18'23"N, 66°36'12"W.



**Figure 8.** *Apteronotus baniwa*, 101 mm total length, female, paratype, MGNC 52994; Venezuela, Amazonas, Río Orinoco, 147 km east-south-east of San Fernando de Atabapo, 03°18'23"N, 66°36'12"W.



(seven to eight versus 12–13), the number of scales along the lateral line (61–70 versus 78–82), the number of pectoral-fin rays (14–16 versus 17–18), the number of precaudal vertebrae (16–17 versus 18), and the number of total vertebrae (68–77 versus 78–81). *Apteronotus baniwa* is differentiated from *A. macrotomus* by the number of scales above the lateral line at the midbody (seven to eight versus 11–14), the number of caudal-fin rays (14–17 versus 18–21), and the number of precaudal vertebrae (16–17 versus 18). *Apteronotus baniwa* differs from *A. pemon* in the number of scales above the lateral line at the midbody (seven to eight versus nine to ten), the number of scales along the lateral line (61–70 versus 74–83), the number of caudal-fin rays (14–17 versus 18–20), and the number of precaudal vertebrae (16–17 versus 18–19). *Apteronotus baniwa* is distinguished from *A. rostratus* by the condition of the fifth infraorbital (absent versus present as a tubular laterosensory canal segment), the condition of the lateral ethmoid (ossified versus cartilaginous), the number of precaudal vertebrae (16–17 versus 18–19) and the tail length (13.3–24.3% of LEA versus 10.6–12.4%). *Apteronotus baniwa* is differentiated from *A. spurrellii* by the condition of the fifth infraorbital (absent versus present as a tubular laterosensory canal segment), the condition of the lateral ethmoid (ossified versus cartilaginous), and the number of scales along the lateral line (61–70 versus 73–76).

**Description:** Head, body, and fin shape and pigmentation illustrated in Figures 7 and 8. Morphometrics for holotype and paratypes presented in Table 1. Body laterally compressed, greatest body depth located at, or slightly posterior to, abdominal cavity. Dorsal profile of body nearly straight. First perforated scale of lateral line located above pectoral-fin origin. Lateral line extending posteriorly to base of caudal fin. Scales along lateral line 61(1), 63(1), 66(1), 67(1), 70\*(1). Scales above lateral line to mid-dorsal line at midbody 7(1), 8\*(5).

Head laterally compressed, widest at opercular region and deepest at nape. Dorsal profile of head overall slightly convex. Dorsal margin of snout straight in single examined mature male but slightly convex in mature female and immatures. Eye small, located laterally on head and completely covered by thin membrane. Anterior naris located at end of small tube and close to tip of snout. Posterior naris ellipsoidal, without tube and positioned closer to tip of snout than to anterior margin of eye. Mouth terminal with rictus extending posterior of vertical through anterior margin of eye. Branchial opening located anterior to vertical through pectoral-fin insertion. Anus and urogenital papillae located posterior to vertical through eye and without ontogenetic variation in position.

Pectoral fin elongate, with 14\*(4) or 16(2) rays. Anal-fin origin located anterior to vertical through posterior margin of opercle. Unbranched anal-fin rays 16(1), 20\*(1), 22(2) or 31(1); total anal-fin rays 136(1), 142(1), 143(1), 144(1), 151\*(1) or 159(1). Tail compressed and short; ending in small, elongate, caudal fin. Caudal-fin rays 14(1), 15\*(2), 16(1) or 17(1).

Origin of dorsal sagittal electroreceptive filament located on posterior half of body. Filament inserted into narrow mid-dorsal groove and extending 6(2), 9\*(3) scales posterior of vertical through posterior terminus of anal fin. Precaudal vertebrae 16\*(2) or 17(4). Total vertebrae 68(2), 72(1), 73(1) or 77\*(2).

**Secondary sexual dimorphism:** The single examined sexually mature male ( $N = 1$ , 155 mm TL) of *A. baniwa* differs from mature females ( $N = 4$ , 94–111 mm TL) in diverse aspects of head morphology. The dorsal margin of snout is nearly straight in the male (Fig. 7) versus slightly convex in mature females (Fig. 8) and immature specimens. The snout length, the distance from the posterior naris to the eye, the internarial distance, and the length of the mouth are proportionally greater in the male than in the females and immatures (Table 1). The proportional interorbital distance is smaller in the male than in females and immatures, with this reflecting the more elongate head in the male (Table 1).

**Coloration in alcohol:** Body and head dark brown. Narrow, pale, longitudinal band extending from chin along mid-dorsal surface of head and body to, or slightly posterior of, vertical through tip of pectoral fin. Pectoral- and anal-fins rays dark brown with inter-radial membranes translucent. Pale band encircling base of caudal fin. Caudal fin pale at base and dark brown posteriorly.

**Distribution:** *Apteronotus baniwa* is known from the Ríos Orinoco and Ventuari in the southern portions of the Río Orinoco basin, Venezuela (Fig. 5).

**Etymology:** The species name, *baniwa*, is based on the name of the indigenous people whose home territory is in the vicinity of the type-locality for the species.

**Material examined:** Holotype: Venezuela. Amazonas. AUM 43275, male, 155 mm; Río Orinoco, 147 km east-south-east of San Fernando de Atabapo, 03°18'23"N, 66°36'12"W, N. Lujan *et al.*, 4.iii.2005. Paratypes: Venezuela. Amazonas. AUM 44075, 1 (immature), 71.1 mm; USNM 406841, 1 (female), 111 mm; Río Ventuari, near ornamental fish market, 04°45'23"N, 66°53'34"W, N. Lujan *et al.*, 3.iv.2005. MCNG 52994, 3 (females), 94–101 mm; AUM 43276, 2, 82–103; same data as holotype. Nontype: Ven-

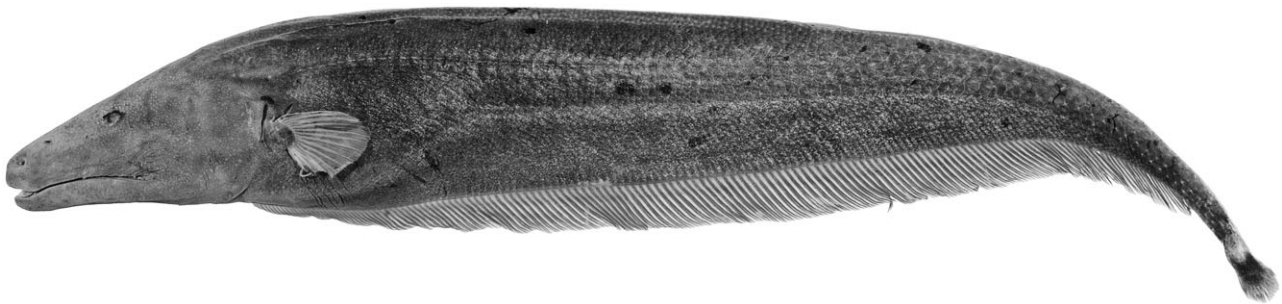
ezuela. Amazonas. FMNH 102100, 8, 48–131 mm; rocks and rapids in Río Orinoco at Isla Cupaven, approximately 03°05'N, 67°40'W.

**APTERONOTUS FERRARISI SP. NOV.**

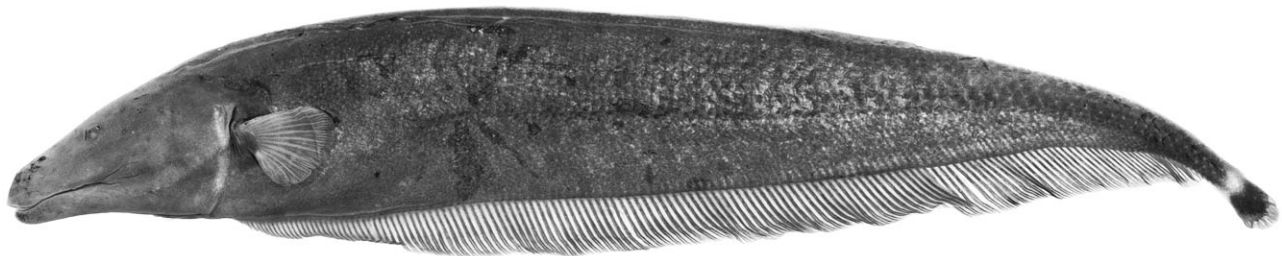
(FIGS 5, 9, 10; TABLE 1)

**Diagnosis:** *Apteronotus ferrarisi* is distinguished from *A. anu* by the condition of the fifth infraorbital (absent versus present as a tubular laterosensory canal segment), the condition of the lateral ethmoid (ossified versus cartilaginous), the number of scales above the lateral line at the midbody (10–13 versus seven to nine), the number of scales along the lateral line (73–80 versus 59–63), the number of caudal-fin rays (15–17 versus 10–13), the extent of the mid-dorsal groove (extending two to six scales beyond the vertical through the posterior terminus of the anal fin versus seven to eight) and the tail length (6.9–9.9% of LEA versus 17.1–37.5%). *Apteronotus ferrarisi* differs from *A. baniwa* in the number of scales above the lateral line at the midbody (10–13 versus seven to eight), the number of scales along the lateral line (73–80 versus 61–70), the mouth length (49.4–56.4% of HL versus 36.6–47.2%), the tail length (6.9–9.9% of LEA versus 13.3–24.2%), and the tail depth (22.2–28.7% of CL versus 8.2–15.3%). *Apteronotus ferrarisi* is differentiated from *A. galvisi* by the orbital diameter (4.0–5.9% of HL versus 6.4–11.3%) and the tail

length (6.9–9.9% of LEA versus 11.8–15.9%). *Apteronotus ferrarisi* is distinguished from *A. leptorhynchus* by the mouth length (49.4–56.3% of HL versus 35.1–48.8) and the tail length (6.9–9.9% of LEA versus 17.1–18.6%). *Apteronotus ferrarisi* differs from *A. macrostomus* in the tail length (6.9–9.9% of LEA versus 13.9–20.6%), the number of caudal-fin rays (15–17 versus 18–21), and the number of total vertebrae (61–71 versus 75). *Apteronotus ferrarisi* is differentiated from *A. pemon* by the mouth length (49.4–56.3% of HL versus 30–44.5%), the tail length (6.9–9.9% of LEA versus 13.0–17.5%), the tail depth (22.2–28.7% of CL versus 9.9–15.4%), and the number of caudal-fin rays (15–17 versus 18–20). *Apteronotus ferrarisi* is distinguished from *A. rostratus* by the condition of the fifth infraorbital (absent versus present as a tubular laterosensory canal segment), the condition of the lateral ethmoid (ossified versus cartilaginous), the tail length (6.9–9.9% of LEA versus 10.6–12.4%), and the number of scales along the lateral line (73–80 versus 63–67). *Apteronotus ferrarisi* differs from *A. spurrellii* in the condition of the fifth infraorbital (absent versus present as a tubular laterosensory canal segment), the condition of the lateral ethmoid (ossified versus cartilaginous), the mouth length (49.4–56.3% of HL versus 42.9–48.4%), the tail length (6.9–9.9% of LEA versus 12.4–28.7%), the number of scales above the lateral line at the midbody (10–13 versus eight to nine), the number of



**Figure 9.** *Apteronotus ferrarisi*, 231 mm total length, male, holotype, MCNG 55635; Venezuela, Yaracuy, Río Yaracuy basin, Quebrada Guaquira on Hacienda Guaquira, south-east of El Peñon Reservoir, 10°17'40"N, 68°39'35"W.



**Figure 10.** *Apteronotus ferrarisi*, 196 mm total length, female, paratype, MCNG 54597; Venezuela, Yaracuy, Río Yaracuy basin, Quebrada Guaquira on Hacienda Guaquira, south-east of El Peñon Reservoir, 10°17'40"N, 68°39'35"W.

anal-fin rays (150–167 versus 171–173), and the number of caudal-fin rays (15–17 versus 14).

*Description:* Head and body shape and pigmentation illustrated in Figures 9 and 10. Morphometrics for holotype and paratypes presented in Table 1. Body laterally compressed, greatest body depth located at, or slightly posterior to, abdominal cavity. Dorsal profile of body nearly straight. First perforated scale of lateral line located above pectoral-fin origin. Lateral line extending posteriorly to base of caudal fin. Scales along lateral line 73(1), 74(1), 77\*(2), or 80(1). Scales above lateral line to mid-dorsal line at midbody 10(2), 11\*(2), or 13(1).

Head laterally compressed, widest at opercular region and deepest at nape. Dorsal profile of head nearly straight but with snout longer in mature males (Fig. 9) than mature females (Fig. 10). Eye small, located laterally on head and completely covered by thin membrane. Anterior naris located at end of small tube and close to tip of snout. Posterior naris ellipsoidal, without tube and positioned closer to tip of snout than to anterior margin of eye. Mouth terminal with rictus extending posterior of vertical through anterior border of eye. Branchial opening located anterior to vertical through pectoral-fin insertion. Anus and urogenital papillae located posterior to vertical through eye and not varying ontogenetically in position.

Pectoral fin elongate, with 13(1), 15\*(1), 16(2), or 17(1) rays. Anal-fin origin located anterior to vertical through posterior margin of opercle. Unbranched anal-fin rays 21(1), 23(1), 24(1), 25\*(1), or 33(1); total anal-fin rays 150(1), 153\*(1), 156(1), or 167(1). Tail compressed and short; ending in small, elongate, caudal fin. Caudal-fin rays 15\*(3) or 17(1).

Origin of dorsal sagittal electroreceptive filament located on posterior half of body. Filament inserted into narrow mid-dorsal groove and extending 2(3), 4\*(1), or 6(1) scales posterior of vertical through posterior terminus of anal fin. Precaudal vertebrae 17(2) or 18\*(3). Total vertebrae 61(1), 68\*(1), 70(2), or 71(1).

*Secondary sexual dimorphism:* Sexually mature males ( $N = 2$ , 231–274 mm TL; Fig. 9) and females ( $N = 3$ , 94–111 mm TL, Fig. 10) of *A. ferrarisi* differ in diverse components of head morphology. The length of the snout, mouth length, and the distance from the posterior naris to the eye are proportionally longer in mature males than in mature females (Table 1).

*Coloration in alcohol:* Body dark and head dark brown. Prominent pale, broad, longitudinal band extending from chin along dorsal midline of head and body to beginning of dorsal filament. Pectoral and anal-fin rays dark brown and inter-radial membranes

translucent. Pale band encircling base of caudal fin. Caudal fin pale at base and dark brown posteriorly.

*Distribution:* *Apteronotus ferrarisi* is known from the type locality in the Río Yaracuy and also occurs in the adjoining Río Aroa, both of which are coastal Caribbean versant drainages of northern Venezuela (Fig. 5). These rivers are a centre of endemism within the Tocuyo-Yaracuy subprovince as defined by Rodríguez-Olarte *et al.* (2009: 87), with 24 endemic fish species previously reported in these basins.

*Etymology:* The species name, *ferrarisi*, is in honour of Carl J. Ferraris Jr, in recognition of his many contributions to our knowledge of tropical freshwater fishes worldwide and his invaluable assistance to the authors, particularly the second author, over the years.

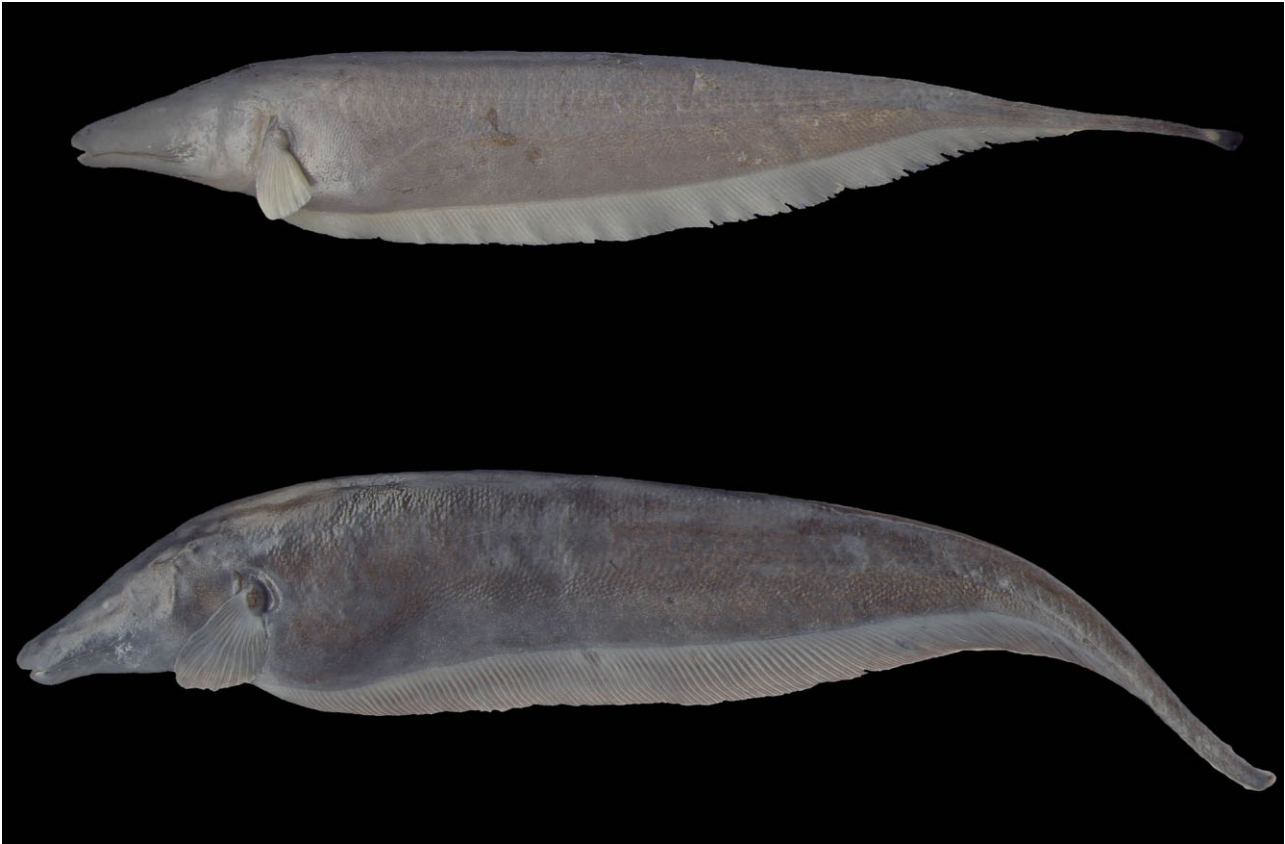
*Remarks:* The report of *Apteronotus* sp. from the Tocuyo-Yaracuy region by Rodríguez-Olarte *et al.* (2009: 73) is presumably based on *A. ferrarisi*, which is the only member of the genus known to occur in those basins.

*Material examined:* Holotype: Venezuela. Yaracuy. MCNG 55635, male, 231 mm; Río Yaracuy basin (Caribbean coast), Quebrada Guaquirá on Hacienda Guaquirá, south-east of El Peñón Reservoir, 10°17'40"N, 68°39'35"W, collected by D. Rodríguez, A. Amaro, H. Aguldelho, J. Coronel & D. Taphorn, 23.x.2005. Paratypes: Venezuela. Yaracuy. MCNG 54584, 1 (male), 160 mm; collected at holotype locality, 21.x.2005. MCNG 54597, 2 (females), 176–196 mm; collected at holotype locality. MCNG 52077, 1 (male), 274 mm; Río Carabobo, Río Aroa drainage (Caribbean coast), 10°30'08"N, 68°47'02"W, D. Taphorn *et al.*, 15.i.2004.

*APTERONOTUS GALVISI* DE SANTANA,  
MALDONADO-OCAMPO & CRAMPTON  
(FIGS 5, 11; TABLE 2)

*Apteronotus galvisi* de Santana, Maldonado-Ocampo & Crampton, 2007: 118, fig. 1 [original description; type-locality Río Cusiana, piedmont of Cordillera Oriental, 305–424 m asl, upper Río Meta; secondary sexual dimorphism]. – Maldonado-Ocampo *et al.*, 2008: 213 [Colombia]. – Urbano-Bonilla *et al.*, 2009: 162 [Colombia, Departamento de Casanare, Ríos Pauto, Cravo Sur, Cusiana, Upiá]. – Machado-Allison *et al.* 2010: 242 [Río Meta]. – de Santana & Cox-Fernandes, 2012: 284 [Río Orinoco basin; occurrence in streams; presence of secondary sexual dimorphism].





**Figure 11.** *Apteronotus galvisi*, top, 184.4 mm total length, male, holotype, IAvHP 8133; bottom, 162.6 mm total length, female (missing caudal fin), paratype, IAvHP 8131. Colombia. Casanare, Río Meta drainage, Río Cusiana, at El Venado bridge, 305 m asl, 05°00'50"N, 72°41'30"W.

**Diagnosis:** *Apteronotus galvisi* is differentiated from *A. anu* by the condition of the fifth infraorbital (present as a tubular laterosensory canal segment versus absent), the condition of the lateral ethmoid (ossified versus cartilaginous), the number of scales above the lateral line at the midbody (11–12 versus seven to nine), and the tail length (11.8–15.9% of LEA versus 17.1–37.5%). *Apteronotus galvisi* is distinguished from *A. baniwa* by the number of scales above the lateral line at the midbody (11–12 versus seven to eight). *Apteronotus galvisi* differs from *A. ferrarisi* in the orbital diameter (6.4–11.3% of HL versus 4.0–5.9%) and the tail length (11.8–15.9% of LEA versus 6.9–9.9%). *Apteronotus galvisi* is differentiated from *A. leptorhynchus* by the number of caudal-fin rays (10–16 versus 17–21), the length of the anal-fin base (69.4–81.1% of LEA versus 81.7–83.7%), and the tail length (11.8–15.9% of LEA versus 17.1–18.6%). *Apteronotus galvisi* is distinguished from *A. macrosotomus* by the number of caudal-fin rays (10–16 versus 18–21). *Apteronotus galvisi* differs from *A. pemon* in the ocular diameter (6.4–11.3% of HL versus 4.0–6.3%), the number of scales above the lateral line at

the midbody (11–12 versus eight to nine), and the number of caudal-fin rays (10–16 versus 18–20). *Apteronotus galvisi* is differentiated from *A. rostratus* by the condition of the fifth infraorbital (present as a tubular laterosensory canal segment versus absent), the condition of the lateral ethmoid (ossified versus cartilaginous), and the number of scales above the lateral line at the midbody (11–12 versus nine to ten). *Apteronotus galvisi* is distinguished from *A. spurrellii* by the ocular diameter (6.4–11.3% of HL versus 3.7–5.8%), the condition of the fifth infraorbital (present as a tubular laterosensory canal segment versus absent), the number of scales above the lateral line at the midbody (11–12 versus eight to nine), the number of anal-fin rays (145–165 versus 171–173), and the condition of the lateral ethmoid (ossified versus cartilaginous).

**Description:** Head, body, and fin shape and pigmentation illustrated in Figure 11. Morphometrics for holotype and paratypes presented in Table 2. Body laterally compressed, greatest body depth located at, or slightly posterior to, abdominal cavity. Dorsal



**Table 2.** Morphometrics for examined specimens of *Apteronotus galvisi*, *Apteronotus leptorhynchus*, and *Apteronotus macrostomus*

	<i>A. galvisi</i>				<i>A. leptorhynchus</i>				<i>A. macrostomus</i>			
	H	Range	N	Mean	H	Range	N	Mean	H	Range	N	Mean
Total length (mm)	184.4	97.5–189	16	–	260.0	93.1–260	4	–	265.0	83–265	13	–
Length to end of anal fin (mm)	157.0	82.0–163	15	–	221.0	78.7–221	3	–	230.0	70–230	10	–
Tail length (mm)	27.3	14.4–27.3	11	–	13.0	13.0–20.7	3	–	22.0	8.0–22.0	9	–
Head length (mm)	32.0	16.0–32.0	16	–	46.7	15.0–46.7	4	–	44.0	13.9–44.0	13	–
Per cent of length to end of anal fin												
Anal-fin length	70.0	69.4–81.1	15	73.2	81.7	81.7–83.7	2	82.7	82.7	71.7–82.7	9	80.0
Snout to anus	11.9	9.8–13.8	15	11.2	12.7	12.7–13.5	3	13.7	14.0	12.5–14.0	9	13.1
Greatest body depth	13.8	11.0–16.1	15	13.0	14.1	13.5–14.1	3	13.7	12.4	12.4–16.6	10	14.7
Preal-fin distance	15.1	13.6–19.5	15	15.5	17.0	17.0–17.9	3	17.4	17.3	17.3–19.1	9	18.4
Tail length	14.8	11.8–15.9	11	13.9	18.6	17.1–18.6	3	17.8	13.9	13.9–20.6	9	17.1
Head length	20.3	17.1–20.3	14	18.6	21.0	9.0–21.0	3	19.8	21.4	19.1–21.4	10	20.6
Per cent of head length												
Head depth at eye	38.3	35.6–43.8	15	39.5	43.6	32.0–43.6	4	38.5	32.5	32.5–50.1	13	39.7
Head width	34.7	25.3–39.2	15	34.4	37.3	27.4–37.3	4	32.9	30.0	30.0–39.3	13	34.3
Ocular diameter	9.0	6.4–11.3	15	8.8	3.9	3.9–7.0	4	5.6	3.9	3.9–8.1	13	6.3
Interorbital distance	18.1	12.7–19.3	15	16.1	9.6	9.6–16.2	4	13.6	12.2	12.2–19.9	13	14.7
Internarial distance	10.9	8.6–14.4	15	11.1	7.6	7.6–9.4	4	8.4	7.7	7.7–11.4	12	9.5
Snout length	43.8	34.8–44.8	15	39.2	41.9	34.9–41.9	4	38.3	44.7	22.5–44.7	13	37.2
Snout to posterior naris	22.5	19.1–22.9	15	21.9	22.1	15.9–22.1	4	19.7	19.0	19.0–21.3	11	20.3
Posterior naris to eye	20.3	11.2–22.3	15	17.1	22.5	11.5–22.5	4	15.7	23.6	10.3–23.6	11	15.2
Mouth length	40.6	38.6–50.1	15	44.3	48.8	35.1–48.8	4	40.2	56.2	38.6–56.2	13	44.3
Branchial opening	20.9	13.4–20.9	15	18.0	11.0	11.0–16.4	4	14.9	12.1	12.1–16.3	13	14.1
Pectoral-fin length	43.4	39.6–57.8	15	46.4	40.2	37.7–40.2	4	39.5	40.7	33.1–40.7	13	36.5
Postorbital length	49.2	49.2–58.6	15	55.8	52.9	52.9–57.9	4	55.9	48.7	48.7–62.1	12	55.0
Per cent of tail length												
Tail depth	–	–	–	–	5.3	5.3–9.6	3	5.9	4.2	4.2–10.5	9	6.3

*N*, number of specimens; H, holotype. Range includes holotype. Tail depth data unavailable for *A. galvisi*.

profile of body nearly straight. First perforated scale of lateral line located above pectoral-fin origin. Lateral line extending posteriorly to base of caudal fin. Scales above lateral line to mid-dorsal line at midbody 11(11) or 12\*(4).

Head laterally compressed, widest at opercular region and deepest at nape. Dorsal profile of snout and overall head nearly straight with snout longer in mature males than mature females. Eye small, located laterally on head, and completely covered by thin membrane. Anterior naris located at end of small tube and close to tip of snout. Posterior naris ellipsoidal, without tube and positioned closer to tip of snout than to anterior margin of eye. Mouth terminal with rictus extending posterior of vertical through anterior border of eye. Branchial opening located anterior to vertical through pectoral-fin insertion. Anus and urogenital papillae located posterior to vertical through eye without ontogenetic variation in position.

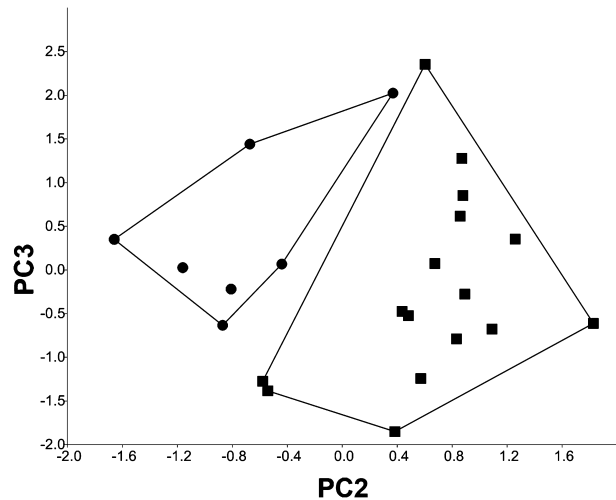
Pectoral fin elongate, with 13\*(3), 14(3), 15(7), 16(2), or 17(1) rays. Anal-fin origin located anterior to vertical through posterior margin of opercle. Total anal-fin rays 145(1), 146(2), 147(1), 148(2), 152\*(3), 153(1), 155(1), 156(1), 161(1), or 165(2). Tail compressed and short; ending in small, elongate caudal fin. Caudal-fin rays 10 (2), 11(1), 12\*(6), 14(2), or 16(1).

Origin of dorsal sagittal electroreceptive filament situated on posterior half of body. Filament inserted into narrow mid-dorsal groove and almost extending to, or slightly beyond, vertical through posterior terminus of anal-fin base.

**Secondary sexual dimorphism:** Sexually mature males ( $N = 3$ , 160–174 mm TL) and females ( $N = 9$ , 124–189 mm TL) of *A. galvisi* differ in overall head morphology with the dorsal profile of head straight in mature males versus slightly curved ventrally in immature and mature females (Fig. 11; de Santana *et al.*, 2007: fig. 1).

**Coloration in alcohol:** Body and head grey to light brown. Prominent, broad, cream-coloured or yellow band extending from chin along dorsal midline of head and body to beginning of dorsal filament. Pectoral and anal-fin rays brown with inter-radial membranes hyaline. Pale band encircling base of caudal fin. Caudal fin light coloured basally and brown distally.

**Distribution:** *Apteronotus galvisi* is known from the Ríos Cusiana, Cravo, Pauto, and Upia in the piedmont of the Cordillera Oriental, 305–424 m asl, in the upper Río Meta system, Colombia (Fig. 5).



**Figure 12.** Principal components analysis on covariance matrix of log-transformed measurements of *Apteronotus galvisi* (squares) and *Apteronotus macrostomus* (circles). Scatter plot of scores on second (PC2) and third (PC3) principal components.

**Electric organ discharges (EODs):** As is the case in all other recorded species of the Apterotonidae, *A. galvisi* generates wave-type EOD with frequencies in the species ranging from 700–957 Hz, without overlapping frequencies between mature males and females (de Santana *et al.*, 2007).

**Remarks:** The Río Orinoco basin is home to four of the nine species in the *A. leptorhynchus* species-group. This high percentage correlates with this river system being by far the largest basin within the range of the species-group. Two of the species, *A. baniwa* and *A. pemon*, are limited to southern portions of the Orinoco basin with known areas of occurrence distant from both each other and from *A. galvisi* and *A. macrostomus*, the two other members of the species-group in the system. *Apteronotus galvisi* and *A. macrostomus*, in contrast, both occur within a relatively limited region in the western portion of the Orinoco basin.

Notwithstanding their geographical proximity, *A. galvisi* and *A. macrostomus* have a distinct separation in the ranges of caudal-fin rays (10–16 versus 18–21, respectively); a difference all the more noteworthy because the samples of these two species are the largest available in the *A. leptorhynchus* species-group. The results of the PCA showed the separation between *A. galvisi* and *A. macrostomus* along the second and third principal components (Fig. 12). PC2 and PC3 reflected 4.6 and 1.4% of the variation, respectively. The best predictors of the differences between the two species were: the internarial dis-

tance (0.54), the ocular diameter (0.76), the interorbital distance (0.58), the branchial opening (0.44), and the pectoral fin length (0.35). The jack-knife cross-validation procedure classified 100% of the specimens between these species, further supporting the recognition of these as valid species. Finally, although mature males of both species are relatively rare, it is noteworthy that mature males of *A. galvisi* (three specimens, 160–174 mm TL) can be distinguished from the only known mature male of *A. macrostomus* (the holotype, 265 mm TL) by the head length (18.6–20.3% of LEA versus 21.4%), the head width (25.3–36.5% of HL versus 39.3%), the head depth (37.9–39.4% of HL versus 50.1%), the snout length (40.0–43.8% of HL versus 44.7%), the distance from the posterior naris to the eye (17.8–20.3% of HL versus 23.6%), the width of the mouth (40.6–50.1% of HL versus 56.2%), the intraocular width (14.1–18.6% of HL versus 19.9%), and the postocular distance (49.2–58% of HL versus 62.1%). Many of these differences are more pronounced than those between mature males of different species in other groups within the Apteronotidae; however, additional material is necessary to test whether these differences, or some subset of them, serve to unambiguously delimit the two species.

**Material examined:** Colombia. Casanare. IAvHP 8133, holotype, male, 184.4 mm TL; Río Meta drainage, Río Cusiana, at El Venado bridge, 305 m asl, 05°00'50"N, 72°41'30"W. Paratypes: IAvHP 8130, two immatures, 97.5–99.2 mm TL; same data as holotype. IAvHP 8129, three males, 125–174.2 mm TL, three females 132.8–163.3 mm TL; Yopal, Quebrada La Aguatoca at

bridge on road to Morro, 357 m asl, 05°26'21"N, 72°27'09"W. IAvHP 8131, two females, 124.8–162.6 mm TL; Río Pauto at bridge on road to Yopal-Pore, 306 m asl, 05°33'44"N, 72°08'44"W. IAvHP 8132, one immature, 98.3 mm TL, one female, 158.4 mm TL, Río Upia at bridge on road to Sisga, 327 m asl, 04°49'09"N, 73°04'57"W. IAvHP 8167, three females, 170.6–189.8 mm TL; Yopal, Río Cravo Sur at Colgante bridge, 424 m asl, 05°25'37"N, 72°27'11"W.

*APTERONOTUS LEPTORHYNCHUS* (ELLIS)  
(FIGS 5, 13; TABLE 2)

*Sternarchus leptorhynchus* Ellis in Eigenmann, 1912: 439 [original description; type-locality Amatuk, Guyana]. – Ellis, 1913: 147, pl. 23, fig. 4 [redescription based on Ellis, in Eigenmann, 1912; first illustration of species].

*Apteronotus leptorhynchus*, Fowler, 1951: 426 [comb. nov.; in part, citations from Guyana; not citations from upper Amazon]. – Lasso, Machado-Allison & Pérez Hernández, 1989: 122 [Essequibo River]. – Mago-Leccia, 1994: 29 [in listing of species; not illustrated specimen from Río Orinoco basin]. – Albert, 2003: 498 [in part; in listing of species; Guyana; not citations from other regions of South America]. – Albert, 2009: 46 [in part; Guyana; not citations from other regions of Guiana Shield]. – de Santana & Cox-Fernandes, 2012: 284 [Essequibo River basin; occurrence in streams].

**Diagnosis:** *Apteronotus leptorhynchus* is differentiated from *A. anu* by the condition of the fifth infraor-



**Figure 13.** *Apteronotus leptorhynchus*, 260 mm total length, male, holotype, FMNH 53294; Guyana, Amatuk.

bital (present as a tubular laterosensory canal segment versus absent), the condition of the lateral ethmoid (ossified versus cartilaginous), the number of scales above the lateral line at the midbody (12–13 versus seven to nine), the number of pectoral-fin rays (17–18 versus 14–16), the number of anal-fin rays (151–156 versus 159–176), the number of caudal-fin rays (17–21 versus 10–13), and the number of scales along the lateral line (78–82 versus 59–63). *Apteronotus leptorhynchus* differs from *A. baniwa* in the number of scales above the lateral line at the midbody (12–13 versus seven to eight), the number of scales along the lateral line (78–82 versus 61–70), the number of pectoral-fin rays (17–18 versus 14–16), the number of precaudal vertebrae (18 versus 16–17), and the number of total vertebrae (78–81 versus 68–77). *Apteronotus leptorhynchus* is distinguished from *A. ferrarisi* by the mouth length (35.1–48.8% of HL versus 49.4–56.3%) and the tail length (17.1–18.6% of LEA versus 6.9–9.9%). *Apteronotus leptorhynchus* is differentiated from *A. galvisi* by the number of caudal-fin rays (17–21 versus 10–16), the length of the anal-fin base (81.7–83.7% of LEA versus 69.4–81.1%), and the tail length (17.1–18.6% of LEA versus 11.8–15.9%). *Apteronotus leptorhynchus* differs from *A. macrostomus* in the number of pectoral-fin rays [17–18 (17 pectoral-fin rays present in one of four specimens examined) versus 14–17 (17 pectoral-fin rays present in two of 13 specimens examined)]; in addition, the holotypes of *A. leptorhynchus* and *A. macrostomus*, mature males of nearly identical sizes, differ from each other in the head depth (43.6% of HL versus 32.5%), the snout length (41.9% of HL versus 44.7%), the mouth length (48.8% of HL versus 56.2%), and the postorbital distance (57.9% of HL versus 48.7%). *Apteronotus leptorhynchus* is distinguished from *A. pemon* by the number of scales above the lateral line at the midbody (12–13 versus eight to nine) and the number of pectoral-fin rays (17–18 versus 16). *Apteronotus leptorhynchus* is differentiated from *A. rostratus* by the condition of the fifth infraorbital (present as a tubular laterosensory canal segment versus absent), the number of scales above the lateral line at the midbody (12–13 versus nine to ten), the number of caudal-fin rays (17–21 versus 14–16), the number of scales along the lateral line (78–82 versus 63–67), the tail length (17.1–18.6% of LEA versus 10.6–12.4%), and the condition of the lateral ethmoid (ossified versus cartilaginous). *Apteronotus leptorhynchus* differs from *A. spurrellii* in the condition of the fifth infraorbital (present as a tubular laterosensory canal segment versus absent), the condition of the lateral ethmoid (ossified versus cartilaginous), the number of pectoral-fin rays (17–18 versus 12–13), the number of anal-fin rays (151–156 versus 171–173), the number of scales along the

lateral line (78–82 versus 73–76), and the extent of the mid-dorsal groove (extending eight scales beyond the vertical through the posterior terminus of the anal fin versus four scales).

**Description:** Head, body, and fin shape and pigmentation illustrated in Figure 13. Morphometrics for holotype and paratypes presented in Table 2. Body laterally compressed, greatest body depth located at, or slightly posterior to, abdominal cavity. Dorsal profile of body nearly straight. First perforated scale of lateral line located above pectoral-fin origin. Lateral line extending posteriorly to base of caudal fin. Scales along lateral line 78(1), 80(1), or 82\*(1). Scales above lateral line to mid-dorsal line at midbody 12\*(3) or 13(1).

Head laterally compressed, widest at opercular region and deepest at nape. Dorsal profile of snout and overall head nearly straight. Eye small, located laterally on head, and completely covered by thin membrane. Anterior naris located at end of small tube and close to tip of snout. Posterior naris ellipsoidal, without tube and positioned closer to tip of snout than to anterior margin of eye. Mouth terminal with rictus situated posterior of vertical through anterior margin of eye. Branchial opening located slightly anterior to vertical through pectoral-fin insertion. Anus and urogenital papillae located posterior to vertical through eye and without ontogenetic variation in position.

Pectoral fin elongate, with 17(2) or 18\*(2) rays. Anal-fin origin located at, or slightly anterior to, vertical through posterior margin of opercle. Unbranched anal-fin rays 19\*(1) or 22(2); total anal-fin rays 151(1), 152\*(1), or 156(1). Tail compressed and short; ending in small, elongate caudal fin. Caudal-fin rays 17(1), 19(1), or 21\*(1).

Origin of dorsal sagittal electroreceptive filament located on posterior half of body. Filament inserted into narrow mid-dorsal groove extending 8\*(2) scales beyond vertical through posterior terminus of anal fin. Precaudal vertebrae 18\*(4). Total vertebrae 78(2) or 81\*(1).

**Coloration in alcohol:** Body and head light to dark brown. Prominent, pale band extending from chin along dorsal midline of head and body to beginning of dorsal filament. Pectoral- and anal-fin rays dark brown with inter-radial membranes translucent. Pale band encircling base of caudal fin. Caudal fin pale at base and dark brown posteriorly.

**Distribution:** *Apteronotus leptorhynchus* is known only from the Essequibo River drainage in Guyana (Fig. 5).

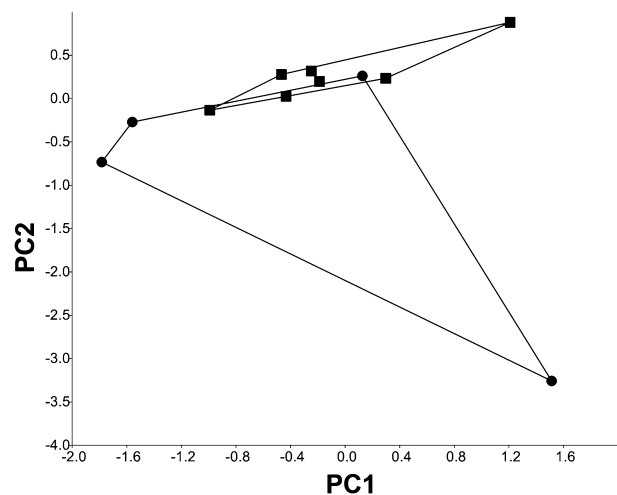
**Remarks:** *Apteronotus leptorhynchus* has been reported from broad regions of northern South



America (cis- and trans-Andean regions of Colombia – Mojica-C, 1999: 563; Lago Maracaibo – Mago-Leccia, 1970: 77; Taphorn *et al.*, 1997: 80; Río Caura, Rodríguez-Olarte *et al.*, 2003: 198; Lasso *et al.*, 2003: 238; Lasso *et al.*, 2010: 70; Río Orinoco basin and Río Paria – Cala, 1977: 10; Lasso *et al.*, 2004a: 181, 2004b: 142; Pacific and Caribbean drainages of Colombia – Maldonado-Ocampo *et al.*, 2008: 213; Peru – Fowler, 1945: 182, 1951: 426; and Venezuela – Lasso *et al.*, 2004a: 181). Available information, however, indicates that *A. leptorhynchus* is endemic to the parts of the Essequibo River basin in Guyana. The above records are either misidentifications of specimens of other species-groups or may be based on species described as new herein. Lasso *et al.* (2010: 70) reported *A. leptorhynchus* from the Río San Juan, a river draining into the Golfo de Paria north of the mouth of the Río Orinoco. Owing to lack of access to the voucher specimen we were unable to evaluate this record.

Although the primary diagnostic feature discriminating *A. leptorhynchus* from *A. macrostomus*, the number of pectoral-fin rays, shows a limited degree of overlap in the available samples of the species, the holotypes of the two species, both mature males of approximately the same body size, show trenchant differences in various details (see Diagnosis for each species). In addition, various features of mature males not readily expressed via standard meristics and morphometrics differ notably between mature males of the two species. Most obvious of these is the form of the snout and dorsal surface of the head, which is straight in the case of *A. leptorhynchus* versus notably convex in *A. macrostomus* (see Figs 13, 15). Furthermore, the results of the PCA showed partial notable, albeit not absolute, separation between *A. leptorhynchus* and *A. macrostomus* along the first and second principal components (Fig. 14). PC1 and PC2 reflected 91.6 and 5.8% of the variation, respectively. The best predictors of the differences between the two species were: the distance from the posterior snout to the eye (0.36) and the head depth (–0.94). A jack-knife cross-validation procedure correctly classified 86.6% of the specimens by species, further supporting the hypothesis of the differences between the two species. Those morphological differences, supplemented by the distinct gap in the known distributions of the two species, support the recognition of the two nominal forms as valid.

*Material examined:* Guyana. BMNH 1974.5.22.136, 1, 124; Potaro River. CAS 62333, 1, 100; Essequibo River, Potaro River at Amatuk, 1908. FMNH 53294, 1, 260; holotype, Amatuk, 1908. FMNH 53295, 1, 95, Warraputa, 1908. INHS 49524, 1, 94; Potaro River, Essequibo River basin, Amatuk Cataract, Macaroni-Potaro 05°18'13"N, 59°18'40"W.



**Figure 14.** Principal components analysis on covariance matrix of log-transformed measurements of *Apterotonus leptorhynchus* (circles) and *Apterotonus macrostomus* (squares). Scatter plot of scores on first (PC1) and second (PC2) principal components.

*APTERONOTUS MACROSTOMUS* (FOWLER)  
(FIGS 15, 16; TABLE 2)

*Sternarchus macrostomus* Fowler, 1943: 263, fig. 63 [original description; type-locality: Villavicencio, Río Meta basin, Colombia].

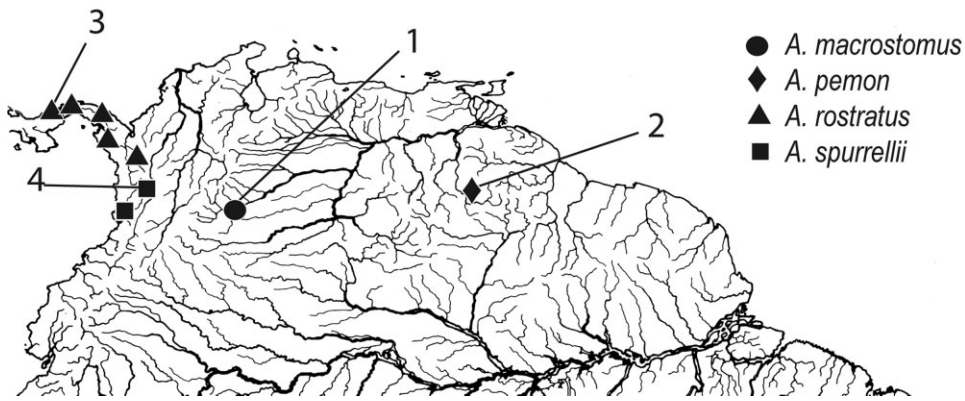
*Apterotonus macrostomus*, Mago-Leccia, 1994: 30, fig. 35 [comb. nov.; in listing of species]. – Albert, 2003: 499 [in listing of species; Río Meta basin, Colombia]. – Lasso *et al.*, 2004a: 181 [Orinoco basin]. – Lasso *et al.*, 2004b: 142 [western Orinoco basin]. – de Santana & Cox-Fernandes, 2012: 284 [Río Orinoco basin; occurrence in rivers].

'*Apterotonus*' *macrostomus*, Albert & Campos-da-Paz, 1998: 431 [phylogenetic position].

*Diagnosis:* *Apterotonus macrostomus* is distinguished from *A. anu* by the condition of the fifth infraorbital (present as a tubular laterosensory canal segment versus absent), the condition of the lateral ethmoid (ossified versus cartilaginous), the number of anal-fin rays (140–152 versus 159–176), the number of caudal-fin rays (18–21 versus 10–13), and the number of scales above the lateral line at the midbody (11–14 versus seven to nine). *Apterotonus macrostomus* is differentiated from *A. baniwa* by the number of scales above the lateral line at the midbody (11–14 versus seven to eight), the number of caudal-fin rays (18–21 versus 14–17), and the number of precaudal vertebrae (18 versus 16–17). *Apterotonus macrostomus* differs from *A. ferrarisi* in the tail length (13.9–20.6% of LEA versus 6.9–9.9%), the number of caudal-fin rays (18–21 versus 15–17), and the number of total vertebrae (75 versus 61–71). *Apterotonus macrostomus* is distin-



**Figure 15.** *Apteronotus macrostomus*, 265 mm total length, male, holotype, ANSP 70528; Colombia, Meta, Río Meta at Villavicencio.



**Figure 16.** Map of north portion of South America showing geographical distribution of *Apteronotus macrostomus* (1 = holotype locality); *Apteronotus pemon* (2 = holotype locality); *Apteronotus rostratus* (3 = holotype locality); and *Apteronotus spurrellii* (4 = type locality). Some symbols represent more than one locality and/or lot of specimens.

guished from *A. galvisi* by the number of caudal-fin rays (18–21 versus 10–16). *Apteronotus macrostomus* is differentiated from *A. leptorhynchus* by the number of pectoral-fin rays [14–17 (17 pectoral-fin rays present in two of 13 specimens examined) versus 17–18 (17 pectoral-fin rays present in one of four specimens examined)]; in addition, the holotypes of *A. macrostomus* and *A. leptorhynchus*, both mature males of nearly identical sizes, differ from each other in the head depth (32.5% of HL versus 43.6%), the snout length (44.7% of HL versus 41.9%), the mouth length (56.2% of HL versus 48.8%), and the postorbital distance (48.7% of HL versus 57.9%). *Apteronotus macrostomus* is distinguished from *A. pemon* by the number of scales above the lateral line at the midbody (11–14 versus eight to nine). *Apteronotus macrostomus* is distinguished from *A. rostratus* by the condition of the fifth infraorbital (present as a tubular laterosensory canal segment versus absent), the condition of the lateral ethmoid (ossified versus cartilaginous), the number of scales above the lateral line at the midbody (11–14 versus nine to ten), the number of anal-fin rays (140–152 versus 153–162), the number of caudal-fin

rays (18–21 versus 14–16), and the tail length (13.9–20.6% of LEA versus 10.6–12.4%). *Apteronotus macrostomus* is differentiated from *A. spurrellii* by the condition of the fifth infraorbital (present as a tubular laterosensory canal segment versus absent), the condition of the lateral ethmoid (ossified versus cartilaginous), the number of pectoral-fin rays (15–17 versus 12–13), the number of scales above the lateral line at the midbody (11–14 versus eight to nine), the number of anal-fin rays (140–152 versus 171–173), and the number of caudal-fin rays (18–21 versus 14).

*Description:* Head, body, and fin shape and pigmentation illustrated in Figure 15. Morphometrics for holotype and paratypes presented in Table 2. Body laterally compressed with greatest body depth located at, or slightly posterior to, abdominal cavity. Dorsal profile of body nearly straight. First perforated scale of lateral line located above pectoral-fin origin. Lateral line extending posteriorly to base of caudal fin. Scales along lateral line 79(3), 80(4), or 81\*(5). Scales above lateral line to mid-dorsal line at midbody 11(5), 12\*(3), 13(1), or 14(3).

Head laterally compressed, widest at opercular region and deepest at nape. Dorsal profile of head nearly straight. Eye small, located laterally on head, and completely covered by thin membrane. Anterior naris located at end of small tube and close to tip of snout. Posterior naris ellipsoidal, without tube and positioned closer to tip of snout than to anterior margin of eye. Mouth terminal with rictus extending posterior of vertical through anterior border of eye. Branchial opening located slightly anterior to vertical through pectoral-fin insertion. Anus and urogenital papillae located posterior to vertical through eye without ontogenetic variation in position.

Pectoral fin elongate, with 14\*(3), 15(2), 16(2), or 17(5) rays. Anal-fin origin located at, or slightly anterior to, vertical through posterior margin of opercle. Unbranched anal-fin rays 19\*(1), 22(4), 23(2), 25(3), or 27(2); total anal-fin rays 140(1), 141(1), 143(2), 146\*(3), 148(1), or 152(1). Tail compressed and short; ending in small, elongate caudal fin. Caudal-fin rays 18(3), 19(4), or 21\*(3).

Origin of dorsal sagittal electroreceptive filament located on posterior half of body. Filament inserted into narrow mid-dorsal groove ranging from slightly anterior to slightly posterior of vertical through posterior terminus of anal fin. Precaudal vertebrae 17(3) or 18\*(2). Total vertebrae 71(1), 73(2), 74(2), or 75(1).

*Coloration in alcohol:* Body and head lightly coloured to dark brown. Pale, broad, longitudinal band extending from chin along dorsal midline of head and body to beginning of dorsal filament. Pectoral- and anal-fin rays dark brown with inter-radial membranes translucent. Pale band encircling base of caudal fin. Caudal fin pale basally and dark brown distally.

*Distribution:* *Apteronotus macrostomus* is known from the Río Meta at Villavicencio, Colombia (Fig. 16).

*Remarks:* See under Remarks for *A. galvisi* concerning differences between that species and *A. macrostomus* and the diagnostic features discriminating the single available mature male (holotype) of *A. macrostomus* from mature males of *A. galvisi*. Features distinguishing *A. galvisi* from *A. leptorhynchus* are discussed in the Remarks for the latter species.

*Material examined:* Colombia. Meta. ANSP 70528, 1, holotype, 265; Río Meta at Villavicencio (4°08'S, 73°40'W). CAS [SU 23728], 1, 205; Guaicaramo. FMNH 92638, 8, 83–145; Caño Negro on road to Puerto Porfia, east of Villavicencio. FMNH 92715, 1, 85, Campo Alegre, Campo Aguasclaras east of Villavicencio. USNM 100808, 1, 172, Villavicencio, Río Meta basin. UF 33218, 1, 157; Río Meta, Caño Quenane (4°02'S, 73°10'W). UF 36604, 5, 71–230, Río Guatiguia, near Villavicencio.

#### ***APTERONOTUS PEMON* SP. NOV.**

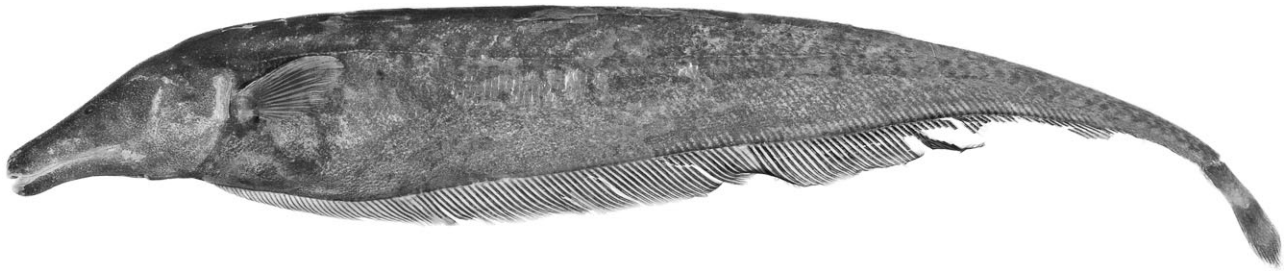
(FIGS 16–18; TABLE 3)

*Diagnosis:* *Apteronotus pemon* is distinguished from *A. anu* by the condition of the fifth infraorbital (present as a tubular laterosensory canal segment versus absent), the interorbital distance (9.7–14.6% of HL versus 14.7–36.5%), the number of caudal-fin rays (18–20 versus 10–13), the number of scales along the lateral line (74–83 versus 59–63), and the condition of the lateral ethmoid (ossified versus cartilaginous). *Apteronotus pemon* differs from *A. baniwa* in the number of scales above the lateral line at the midbody



**Figure 17.** *Apteronotus pemon*, 206 mm total length, male, holotype, FMNH 70012; Venezuela, Bolivar, Techiné-meru waterfall, tributary of Río Caroni, approximately 05°01'N, 62°03'W.





**Figure 18.** *Apteronotus pemon*, 165 mm total length, female, FMNH 121159; Venezuela, Bolivar, Techiné-meru, tributary of Rio Caroni, approximately 05°01'N, 62°03'W.

**Table 3.** Morphometrics for examined specimens of *Apteronotus pemon*, *Apteronotus rostratus*, and syntypes of *Apteronotus spurrellii*

	H	<i>A. pemon</i>			<i>A. rostratus</i>			<i>A. spurrellii</i>		
		Range	N	Mean	Range	N	Mean	Range	N	Mean
Total length (mm)	206.0	95–206	4	–	74–182	12	–	142–189	4	–
Length to end of anal fin (mm)	183.0	80–183	4	–	63.9–165	8	–	128–168	4	–
Tail length (mm)	23.8	10.2–23.8	4	–	11.5–25.2	5	–	10.9–12.4	3	–
Head length (mm)	41.9	15.0–41.9	4	–	12.2–32.9	12	–	21.6–25.0	4	–
Per cent of length to end of anal fin										
Anal-fin length	80.3	80.0–89.4	4	83.3	76.3–83.9	8	81.2	82.8–85.1	4	83.8
Snout to anus	14.5	9.3–14.5	4	11.7	12.3–13.4	5	12.6	12.1–16.4	4	14.2
Greatest body depth	14.1	12.1–14.7	4	13.6	11.7–18.6	8	14.4	12.8–13.7	4	13.2
Preal-anal-fin distance	19.3	10.9–19.3	4	13.5	16.7–18.8	8	17.8	16.0–18.7	4	17.8
Tail length	13.0	13.0–17.5	3	15.7	12.4–28.7	5	18.3	12.5–13.7	3	12.9
Head length	22.9	18.4–22.9	4	29.8	17.5–19.6	8	18.8	14.8–16.8	4	16.1
Per cent of head length										
Head depth at eye	21.5	21.5–40.9	4	33.6	29.5–41.3	6	38.2	32.1–36.5	4	34.3
Head width	34.5	31.3–37.3	4	34.2	31.4–37.3	6	35.3	31.5–33.8	4	32.6
Ocular diameter	4.0	4.0–6.3	4	5.5	4.1–8.3	11	6.7	3.7–5.8	4	4.8
Interorbital distance	9.7	9.7	1	–	13.4–22.9	10	17.6	22.2–24.0	4	23.1
		11.7–14.6	3	13.3						
Internarial distance	7.2	7.2–10.0	4	8.5	3.3–8.0	10	6.8	6.7–8.2	4	7.4
Snout length	34.5	34.5–41.0	4	39.1	32.9–44.0	11	38.8	42.5–44.1	4	43.2
Snout to posterior naris	18.1	18.1–22.9	4	20.4	16.1–20.0	10	17.6	17.4–18.5	4	17.7
Posterior naris to eye	21.1	21.1	1	–	16.7–21.9	10	19.0	19.7–24.8	4	21.0
		13.3–20.8	3	16.4						
Mouth length	44.5	44.5	1	–	39.9–51.2	11	45.9	42.9–48.4	4	45.7
		30.0–39.7	3	36.2						
Branchial opening	15.9	14.9–18.2	4	16.1	8.2–12.4	10	10.5	6.0–9.6	4	7.5
Pectoral-fin length	40.9	40.9–49.5	3	43.9	37.2–51.6	12	42.2	38.2–46.0	4	43.1
Postorbital length	54.2	54.2–55.8	4	54.9	48.1–56.5	10	52.3	34.6–60.0	4	56.9
Per cent of tail length										
Tail depth	15.4	9.9–15.4	3	11.8	5.1–9.5	5	5.8	7.1–10.2	3	8.3

N, number of specimens; H, holotype. Range includes holotypes if examined.

Sexually dimorphic features for *A. pemon* are presented as two entries. First entry is for sexually dimorphic males with information for females and immatures in second entry. Holotypes for *A. rostratus* or *A. spurrellii* are not available for examination.

(nine to ten versus seven to eight), the number of scales along the lateral line (74–83 versus 61–70), and the number of precaudal vertebrae (18–19 versus 16–17). *Apteronotus pemon* is differentiated from *A. ferrarisi* by the mouth length (30–44.5% of HL versus 49.4–56.3%), the tail length (13.0–17.5% of LEA versus 6.9–9.9%), the tail depth (9.9–15.4% of CL versus 22.2–28.7%), the number of scales above the lateral line at the midbody (nine to ten versus 10–13), and the number of caudal-fin rays (18–20 versus 15–17). *Apteronotus pemon* is distinguished from *A. galvisi* by the ocular diameter (4.0–6.3% of HL versus 6.4–11.3%), the number of scales above the lateral line at the midbody (nine to ten versus 11–12), and the number of caudal-fin rays (18–20 versus 10–16). *Apteronotus pemon* differs from *A. leptorhynchus* in the number of scales above the lateral line at the midbody (nine to ten versus 12–13) and the number of pectoral-fin rays (16 versus 17–18). *Apteronotus pemon* is differentiated from *A. macrostomus* by the number of scales above the lateral line at the midbody (nine to ten versus 11–14). *Apteronotus pemon* is distinguished from *A. rostratus* by the condition of the fifth infraorbital (present as a tubular laterosensory canal segment versus absent), the number of scales along the lateral line (74–83 versus 63–67), the number of caudal-fin rays (18–20 versus 14–16), and the condition of the lateral ethmoid (ossified versus cartilaginous). *Apteronotus pemon* can be differentiated from *A. spurrellii* by the condition of the fifth infraorbital (present as a tubular laterosensory canal segment versus absent), the number of pectoral-fin rays (16 versus 12–13), the number of anal-fin rays (152–160 versus 171–173), the number of caudal-fin rays (18–20 versus 14), and the condition of the lateral ethmoid (ossified versus cartilaginous).

**Description:** Head, body, and fin shape and pigmentation illustrated in Figures 17 and 18. Morphometrics for holotype and paratypes presented in Table 3. Body laterally compressed, greatest body depth located at, or slightly posterior to, abdominal cavity. Dorsal profile of body nearly straight. First perforated scale of lateral line located above pectoral-fin origin. Lateral line extending posteriorly to base of caudal fin. Scales along lateral line 74\*(1), 79(1), 82(1), or 83(1). Scales above lateral line to mid-dorsal line at midbody 9(2) or 10\*(2).

Head laterally compressed, widest at opercular region and deepest at nape. Dorsal profile of head slightly convex. Snout longer in sexually mature male than in mature female and immatures. Eye small, located laterally on head and completely covered by thin membrane. Anterior naris located at end of small tube and close to tip of snout. Posterior naris ellipsoidal, without tube and positioned closer to tip of snout

than to anterior margin of eye. Mouth terminal with rictus reaching vertical through anterior border of eye in small individuals and extending posterior of that vertical in adults. Branchial opening located anterior to vertical through pectoral-fin insertion. Anus and urogenital papillae located posterior to vertical through eye without ontogenetic variation in position.

Pectoral fin elongate, with 16\*(3) rays. Anal-fin origin located anterior to vertical through posterior margin of opercle. Unbranched anal-fin rays 22\*(1), 24(1), or 32(1); total anal-fin rays 152(1), 157(1), 160(1), or 162\*(1). Tail compressed and short; ending in small, elongate caudal fin. Caudal-fin rays 18(1), 19(1), or 20\*(2).

Origin of dorsal sagittal electroreceptive filament located on posterior half of body. Filament inserted into narrow mid-dorsal groove extending 4\*(3) or 9(1) scales beyond vertical through posterior terminus of anal-fin base. Precaudal vertebrae 18\*(2) or 19(2). Total vertebrae 63(1), 67\*(1), 73(1), or 82(1).

**Secondary sexual dimorphism:** The single examined sexually mature male (206 mm TL; Fig. 17) and female of *A. pemon* (165 mm TL; Fig. 18) differ in several aspects of head morphology, with the distance from the posterior naris to the eye and mouth greater in the male than in the female and immatures (Table 3). In addition, the interorbital distance is narrower in the male than in the female and immatures (Table 3).

**Coloration in alcohol:** Body and head brown. Prominent, broad, lightly coloured longitudinal band extending from chin along dorsal midline of head and body to beginning of dorsal filament. Pectoral- and anal-fin rays dark brown with inter-radial membranes translucent. Light band encircling base of caudal fin. Caudal fin pale at base, dark brown posteriorly.

**Distribution:** *Apteronotus pemon* is only known from the type locality at the Techiné-meru waterfall along a tributary of the upper Río Caroni basin, Venezuela (Fig. 16).

**Etymology:** The species name, *pemon*, is in reference to the Pemon indigenous group whose traditional lands included much of the Río Caroni basin, which includes the type locality of the species.

**Remarks:** The report of *A. leptorhynchus* from the Río Claro, a left bank tributary of the lower Río Caroni, by Taphorn & García Tenía (1991: 35) may be based on samples of *A. pemon*, which is the only member of the species-group known from that river system. The same may be the case with the report of *A. leptorhynchus* from the Gran Sabana region of the upper Río Caroni basin by Lasso *et al.* (1989: 116).

*Material examined:* Holotype: Venezuela. Bolivar. FMNH 70012, male, 206 mm; Techiné-meru waterfall, along tributary of Río Caroni, approximately 05°01'N, 62°17'60"W, J. Steyermark, 16.iii.1955. Paratypes: Venezuela. Bolivar. FMNH 121159, 4 (one female, two immature), 1 c&s, 121–165 mm; same locality as holotype.

*APTERONOTUS ROSTRATUS* (MEEK & HILDEBRAND)  
(FIGS 16, 19; TABLE 3)

*Sternarchus rostratus* Meek & Hildebrand, 1913: 85 [original description; type-locality: Río Grande near Cana, Panama]. – Eigenmann & Fisher, 1914: 236 [Colombia, Girardot, Apulo, Cartago, Río Cauca at Cali]. – Meek & Hildebrand, 1916: pl. 27 [based on Meek & Hildebrand, 1913; first illustration of species; Río Grande near Cana, Panama; Río Cauca at Cali, Colombia]. – Eigenmann, 1922: 176, pl. 35, figs 3–5 [Colombia, Río Magdalena; Panama, Río Tuyra]. – Hildebrand, 1938: 292 [Colombia, Río Magdalena; Panama, Río Tuyra]. – Dahl, 1971: 99, unnumbered fig. [Colombia, Río Cauca, Río Magdalena and Río Sinú; maximum size and habitat].

*Apteronotus rostratus*, Miles, 1947: 185 [comb. nov.; Colombia, Río Magdalena and upper Río Cauca; Panama, Río Tuyra]. – Mago-Leccia, 1994: 29, fig. 30 [in listing of species]. – Roman-Valencia, 1995: 4 [Colombia, Alto Cauca, Río La Vieja]. – Mojica-C, 1999: 563 [Colombia]. – Cardona, Roman-Valencia, Jimenez & Hurtado T., 1998: 17 [Colombia, upper Río Cauca]. – Albert, 2003: 499 [in listing of species; Río Grande basin, Panama]. – Maldonado-Ocampo *et al.*, 2008: 213 [Colombia, Pacific and Caribbean drainages]. – de Santana & Cox-Fernandes, 2012: 284 [Río Magdalena basin; occurrence in streams].

*Diagnosis:* *Apteronotus rostratus* is distinguished from *A. anu* by the tail length (10.6–12.4% of LEA versus 17.1–37.5%) and the number of caudal-fin rays (14–16 versus 10–13). *Apteronotus rostratus* is differentiated from *A. baniwa* by the condition of the fifth infraorbital (absent versus present as a tubular laterosensory canal segment), the condition of the lateral ethmoid (cartilaginous versus ossified), the number of precaudal vertebrae (18–19 versus 16–17), and the tail length (10.6–12.4% of LEA versus 13.0–24.3%). *Apteronotus rostratus* differs from *A. ferrarisi* in the condition of the fifth infraorbital (absent versus present as a tubular laterosensory canal segment), the condition of the lateral ethmoid (cartilaginous versus ossified), the tail length (10.6–12.4% of LEA versus 6.9–9.9%), and the number of scales along the lateral line (63–67 versus 73–80). *Apteronotus rostratus* is distinguished from *A. galvisi* by the condition of the fifth infraorbital (absent versus present as a tubular laterosensory canal segment), the condition of the lateral ethmoid (cartilaginous versus ossified), and the number of scales above the lateral line at the midbody (nine to ten versus 11–12). *Apteronotus rostratus* is differentiated from *A. leptorhynchus* by the condition of the fifth infraorbital (absent versus present as a tubular laterosensory canal segment), the condition of the lateral ethmoid (cartilaginous versus ossified), the number of scales above the lateral line at the midbody (nine to ten versus 12–13), the number of caudal-fin rays (14–16 versus 17–21), the number of scales along the lateral line (63–67 versus 78–82), and the tail length (10.6–12.4% of LEA versus 17.1–18.6%). *Apteronotus rostratus* differs from *A. macrostomus* in the condition of the fifth infraorbital (absent versus present as a tubular laterosensory canal segment), the condition of the lateral ethmoid (cartilaginous versus ossified), the



**Figure 19.** *Apteronotus rostratus*, 132 mm total length, MBUCV V-10926; Panama, Río Pirre, tributary of Río Tuyra.



number of scales above the lateral line at the midbody (nine to ten versus 11–14), the number of anal-fin rays (153–162 versus 140–152), the number of caudal-fin rays (14–16 versus 18–21), and the tail length (10.6–12.4% of LEA versus 13.9–20.6%). *Apteronotus rostratus* is distinguished from *A. pemon* by the condition of the fifth infraorbital (absent versus present as a tubular laterosensory canal segment), the number of scales along the lateral line (63–67 versus 74–83), the number of caudal-fin rays (14–16 versus 18–20), and the condition of the lateral ethmoid (cartilaginous versus ossified). *Apteronotus rostratus* is differentiated from *A. spurrellii* by the number of pectoral-fin rays (15–17 versus 12–13), the number of total anal-fin rays (153–162 versus 171–173), the number of scales along the lateral line (63–67 versus 73–76), and the tail length (10.6–12.4% of LEA versus 12.5–13.7%).

**Description:** Head, body, and fin shape and pigmentation illustrated in Figure 19. Morphometrics for holotype and paratypes presented in Table 3. Body laterally compressed, greatest body depth located at, or slightly posterior to, abdominal cavity. Dorsal profile of body nearly straight. First perforated scale of lateral line located above pectoral-fin origin. Lateral line extending posteriorly to base of caudal fin. Scales along lateral line 63(1), 64(2), 66(2), or 67(3). Scales above lateral line to mid-dorsal line at midbody 9(6) or 10(6).

Head laterally compressed, widest at opercular region and deepest at nape. Dorsal profile of head nearly straight. Eye small, located laterally on head, and completely covered by thin membrane. Anterior naris located at end of small tube and close to tip of snout. Posterior naris ellipsoidal, without tube and positioned closer to tip of snout than to anterior margin of eye. Mouth terminal with rictus located posterior of vertical through anterior border of eye. Branchial opening located slightly anterior to vertical through pectoral-fin insertion. Anus and urogenital papillae located posterior to vertical through eye and without ontogenetic variation in position.

Pectoral fin elongate, with 15(10) or 17(2) rays. Anal-fin origin located at, or slightly anterior to, vertical through posterior margin of opercle. Unbranched anal-fin rays 14(3), 18(5), 23(2), or 27(2); total anal-fin rays 153(2), 154(2), 156(1), 157(1), 160(1), or 162(1). Tail compressed and short; ending in small, elongate caudal fin. Caudal-fin rays 14(3), 15(1), or 16(1).

Origin of dorsal sagittal electroreceptive filament located on posterior half of body. Filament inserted into narrow mid-dorsal groove extending 2(2), 3(1), 8(2), or 11(4) scales beyond vertical through posterior terminus of anal fin. Precaudal vertebrae 18(3) or 19(3). Total vertebrae 72(1), 74(2), 75(1), or 77(1).

**Coloration in alcohol:** Body and head grey to dark brown. Prominent, broad, lightly coloured longitudinal band extending from chin along dorsal midline of head and body to over dorsal filament. Pectoral- and anal-fin rays dark brown with inter-radial membranes translucent. Lightly coloured band encircling base of caudal fin. Caudal fin pale basally, grey to dark brown in central portion and translucent posteriorly.

**Distribution:** *Apteronotus rostratus* is known from the Ríos Magdalena and Cauca, Colombia, and several rivers of the Pacific versant of Panama (Fig. 16).

**Common name:** Cardona *et al.* (1998: 17) reported that *A. rostratus* has a common name of 'Boca da perra' in the upper Río Cauca, Colombia.

**Remarks:** *Apteronotus anu* and *A. rostratus* are morphologically the most similar members of the *A. rostratus*-clade but can be differentiated on the basis of various features (see Remarks for *A. anu*).

**Geographical variation:** *Apteronotus rostratus* demonstrates considerable variation in some features across its geographical range; most notably differences in the posterior extent of the dorsal sagittal electroreceptive filament. Whereas the filament extends only two scales beyond the vertical through the posterior terminus of the anal fin in some examined specimens from the Río Pirre, Panama, in the northern portion of the species range, it continues up to 11 scales beyond that point in a specimen that originated in the Río Cauca in the southern portion of the range. Continuity between these extremes occurs in intervening populations. Such variation is expected given the highly dissected geographical isolation of the river basins and parallels variation previously reported in other groups of fishes from the region (Birmingham & Martin, 1998). The report by Cala (1986) of *A. rostratus* from the Río Meta basin is erroneous under available information as to the distribution of the species and most likely is based on congeners inhabiting that river basin.

**Material examined:** Colombia. Choco. USNM 317229, 3, 109–157; Río Salado near Teresita (approximately 7°06'N, 77°23'W). USNM 324044, 1, 112; Río Pavarando, tributary of Río Salaquí. USNM 317230, 1, 183; creek of Río Parado, approximately 10 min by helicopter from village of Parado. Panamá. Chepo. AUM 31623, 1, Bahía de Panamá, Pan American Highway, 17.7 km north-east of Chepo. FMNH 7592, 1, 94, holotype (specimen in poor condition and morphometrics not included in Table 3); Río Grande near Cana, Panama. MBUCV-V 10926, 4 (2 c&s), 115–162; Río

Pirre, tributary of Río Tuyra. Colon. USNM 324045, 2, 108–132, Río Membrillo, 08°41'N, 77°41'W.

*APTERONOTUS SPURRELLII* (REGAN)  
(FIGS 16, 20; TABLE 3)

*Sternarchus spurrellii* Regan, 1914: 32 [original description; type locality: Río Condoto, Colombia].

*Sternarchus leptorhynchus*, (not of Eigenmann, 1912), Eigenmann & Fisher, 1914: 236 [Colombia, Pacific Slope, Calima, Río Dagua at Cordova]. – Eigenmann, 1922: 177, pl. XXXV, fig. 1 [illustration].

*Apteronotus spurrellii*, Albert, 2003: 499 [comb. nov.; in listing of species; Colombia, Río San Juan basin]. – de Santana & Crampton, 2006: 116 [Río Condoto, Colombia]. – Maldonado-Ocampo *et al.*, 2008: 213 [Colombia, Pacific drainages]. – de Santana & Cox-Fernandes, 2012: 284 [Río San Juan basin; occurrence in streams].

**Diagnosis:** *Apteronotus spurrellii* is distinguished from *A. anu* by the number of pectoral-fin rays (12–13 versus 14–16), the number of caudal-fin rays (14 versus 10–13), the number of scales along the lateral line (73–76 versus 59–63), the extent of the mid-dorsal groove (extending four scales beyond the vertical through the posterior terminus of the anal fin versus seven to eight scales) and the tail length (12.5–13.7% of LEA versus 17.1–37.5%). *Apteronotus spurrellii* differs from *A. baniwa* in the condition of the fifth infraorbital (absent versus present as a tubular laterosensory canal segment), the condition of the lateral ethmoid (cartilaginous versus ossified), the number of scales along the lateral line (73–76 versus 61–70), and the number of pectoral-fin rays (12–13 versus 14–16). *Apteronotus spurrellii* is differentiated from *A. ferrarisi* by the condition of the fifth infraorbital (absent versus present as a tubular laterosensory canal segment), the condition of the lateral ethmoid (cartilaginous versus ossified), the mouth length (42.9–48.4% of HL versus 49.4–56.3%), the tail

length (12.5–13.7% of LEA versus 6.9–9.9%), the number of scales above the lateral line at the midbody (eight to nine versus 10–13), the number of anal-fin rays (171–173 versus 150–167), and the number of caudal-fin rays (14 versus 15–17). *Apteronotus spurrellii* is distinguished from *A. galvisi* by the ocular diameter (3.7–5.8% of HL versus 6.4–11.3%), the condition of the fifth infraorbital (absent versus present as a tubular laterosensory canal segment), the number of scales above the lateral line at the midbody (eight to nine versus 11–12), the number of anal-fin rays (171–173 versus 145–165), and the condition of the lateral ethmoid (cartilaginous versus ossified). *Apteronotus spurrellii* differs from *A. leptorhynchus* in the condition of the fifth infraorbital (absent versus present as a tubular laterosensory canal segment), the condition of the lateral ethmoid (cartilaginous versus ossified), the number of pectoral-fin rays (12–13 versus 17–18), the number of anal-fin rays (171–173 versus 151–156), the number of scales along the lateral line (73–76 versus 78–82), and the extent of the mid-dorsal groove (extending four scales beyond the vertical through the posterior terminus of the anal fin versus eight scales). *Apteronotus spurrellii* is differentiated from *A. macrotomus* by the condition of the fifth infraorbital (absent versus present as a tubular laterosensory canal segment), the condition of the lateral ethmoid (cartilaginous versus ossified), the number of pectoral-fin rays (12–13 versus 15–17), the number of scales above the lateral line at the midbody (eight to nine versus 11–14), the number of anal-fin rays (171–173 versus 140–152), and the number of caudal-fin rays (14 versus 18–21). *Apteronotus spurrellii* is distinguished from *A. pemon* by the condition of the fifth infraorbital (absent versus present as a tubular laterosensory canal segment), the number of pectoral-fin rays (12–13 versus 16), the number of anal-fin rays (171–173 versus 152–160), the number of caudal-fin rays (14 versus 18–20), and the condition of the



**Figure 20.** *Apteronotus spurrellii*, 189 mm total length, syntype, BMNH 1914.5.18:90-3; Colombia, Choco.

lateral ethmoid (cartilaginous versus ossified). *Apteronotus spurrellii* differs from *A. rostratus* in the number of pectoral-fin rays (12–13 versus 15–17), the number of scales along the lateral line (73–76 versus 63–67), the total number of anal-fin rays (171–173 versus 153–162), and the tail length (12.5–13.7% of LEA versus 10.6–12.4%).

*Description:* Head, body, and fin shape and pigmentation illustrated in Figure 20. Morphometrics for holotype and paratypes presented in Table 3. Body laterally compressed; greatest body depth located at, or slightly posterior to, abdominal cavity. Dorsal profile of body nearly straight. First perforated scale of lateral line located above pectoral-fin origin. Lateral line extending posteriorly to base of caudal fin. Scales along lateral line 73(1) or 76(1). Scales above lateral line to mid-dorsal line at midbody 8(2) or 9(2).

Head laterally compressed, widest at opercular region and deepest at nape. Dorsal profile of head nearly straight. Eye small, located laterally on head, and completely covered by thin membrane. Anterior naris located at end of small tube and close to tip of snout. Posterior naris ellipsoidal, without tube and positioned closer to tip of snout than to anterior margin of eye. Mouth terminal with rictus extending posteriorly beyond vertical through anterior border of eye. Branchial opening located slightly anterior to vertical through pectoral-fin insertion. Anus and urogenital papillae located posterior to vertical through eye and without ontogenetic variation in position.

Pectoral fin elongate, with 12(3) or 13(1) rays. Anal-fin origin located at, or slightly anterior to, vertical through posterior margin of opercle. Total anal-fin rays 171(1) or 173(2). Tail compressed and short; ending in small, elongate caudal fin. Caudal-fin rays 14 (1).

Origin of dorsal sagittal electroreceptive filament located on posterior half of body. Filament inserted into narrow mid-dorsal groove extending 4(2) scales beyond vertical through posterior terminus of anal fin. Precaudal vertebrae 17(2) or 18(2). Total vertebrae 74 (1).

*Coloration in alcohol:* Body dark brown. Prominent, lightly coloured, broad longitudinal band extending from chin along dorsal midline of head and body to beginning of dorsal filament. Pectoral- and anal-fin rays dark brown, with inter-radial membranes translucent. Lightly coloured band encircling base of caudal fin. Caudal fin pale basally and dark brown distally.

*Distribution:* *Apteronotus spurrellii* inhabits the Ríos Condoto and Dagua of the Pacific versant of Colombia (Fig. 16).

*Material examined:* Colombia. Choco. BMNH 1914.5.18:90-3, 4, syntypes, 142–189; Río Condoto. Valle del Cauca. CAS 72124 [IU 13374], 1, 185; Río Dagua, 19.3 km above its mouth at Buenaventura, 36.6 m elevation. FMNH 56773, 1, 128, creek near mouth of Río Calima.

#### COMPARATIVE MATERIAL EXAMINED

##### *Apteronotidae*

*Apteronotus albifrons.* Suriname. Nickerie: ZMA 106.041, 1, 233; Stondansie Falls, Nickerie River. ZMA 106.042, 3, 62–152; Marowijne Creek, Brokopondo. ZMA 106.043, 1, 160; Coppename River, Saramacca. *Apteronotus* cf. *albifrons.* Venezuela. Amazonas: MCNG 2658, 1, 195; Caño Yatuje, Río Orinoco basin. MCNG 38192, 1, 130; Río Manipitare. MCNG 38288, 1, 101; Río Emoni. MCNG 52993, 1, 114; Río Orinoco basin. Anzoatgui: MCNG 30845, 1, 327; Río Orinoco, Laguna El Venado. Apure: MCNG 1496, 14, 87–146; El Frio, Río Apure basin. MCNG 2893, 1, 103; 1.2 km south of Bruzual, Río Apure basin. MCNG 19912, 3, 138–175; MCNG 20351, 3, 137–157; MCNG 20359, 1, 134; MCNG 20375, 1, 144; MCNG 20712, 1, 132; Río Arauca. MCNG 39100, 3, 128–203; Río Manglar, 1 km from Río Apure. MCNG 51412, 1, 158; Caño Portrerito. MCNG 52333, 2, 123–174; Caño Maporal. MCNG 52588, 6, 204–273; Caño Bucural. Barinas: MCNG 3388, 2, 133–154; 100 m from Puente Bruzual, Río Apure basin. MCNG 4404, 3, 145–222; 100 m from Puente Bruzual, Río Apure basin. MCNG 10796, 3, 103–160; Río Apure. MCNG 21291, 3, 153–233; Laguna La Pildora, Río Apure basin. MCNG 21298, 1, 141; Río Suripá, Río Apure basin. MCNG 51748, 7, 117–182; MCNG 51800, 1, 115; Caño Bravo, Río Apure basin. MCNG 52544, 1, 161; mouth of Río Portuguesa. Guárico: MCNG 13107, 1, 133; MCNG 14486, 1, 162; Río Apure basin. Monagas: MCNG 11086, 2, 118–136; Caño Agua Clarita. MCNG 11199, 1, 166; Río Uraoa. MCNG 15933, 1, 101; Río Yabo. MCNG 17349, 1, 65; Río Tigre. MCNG 29128, 3, 85–124; Río Guanipa, Río Apure basin. MCNG 29282, 1, 160; Río Yabo, Río Apure basin. Portuguesa: MCNG 1180, 1, 118; MCNG 6168, 3, 117–130; MCNG 11885, 1, 120; MCNG 35748, 3, 26–212; Caño Maraca, Río Apure basin. MCNG 49283, 3, 117–130; MCNG 49315, 1, 135; MCNG 49365, 1, 147; MCNG 49404, 1, 145; Caño MCNG 49543, 1, 153; Caño Bravo, Río Apure basin. *Apteronotus caudimaculosus.* Brazil. Mato Grosso do Sul: ANSP 178659, one paratype, 145. CAS 216788, one paratype, 127. INHS 94260, one paratype, 137. UGAMNH 3435, one paratype, 149. INPA 20066, one paratype, 100. MCZ 161831, one paratype, 126. MZUSP 59295, 22 paratypes, 71–165. MZUSP 59296, four paratypes, 175–231. MZUSP 79359, holotype,



286. UMMZ 240259, one paratype, 107. USNM 371234, one paratype, 106; Rio Novo, brejo de Santa Sofia. *Apteronotus* cf. *camposdapazi*. French Guyana. ZMA 107.818, 4 (R), 90–151; upper Fleuve Oyapock, Trois Sauts rapids. *Apteronotus cuchillejo*. Venezuela. Zulia: USNM 121598, seven paratypes (R), 60–149; Río Yasa, Río Negro. USNM 121599, 39 paratypes (R), 90–190; USNM 121600, holotype (R), 168; USNM 121601, five paratypes (R), 145–169; Río Motatán. USNM 121602, ten paratypes (R), 81–115; Río San Pedro, Río Motatán. *Apteronotus cuchillo*. Venezuela. Zulia: MBUCV 389 (formerly USNM 121590), 1 c&s. MCZ 52010, 1 c&s, paratype; Río Motatán at bridge, 22 km from Motatán, Lago Maracaibo basin. USNM 121587, 13 paratypes (R), 157–385; Río Socuy. USNM 121588, three paratypes (R), 215–315; Río Palmar, 70 km south-west of Maracaibo. USNM 121589, 11 paratypes (R), 164–390; Río Motatán at bridge, 22 km north of Motatán. USNM 121590, seven paratypes (R), 132–194; Río Apon, 35 km south of Rosário. USNM 121591, holotype (R), 352; Río Socuy, 3 km from mouth. *Apteronotus eschmeyerii*. Colombia. Tolima: CAS 721 15 (IU 13377), holotype (R), 303.7; Río Magdalena basin, Las Juntas de Apulo, Río Bogotá along railway between Girardot and Facatativa. FMNH 56775, two paratypes (R), 195–213; Girardot. USNM 120473, one (R) paratype, 270; Río Luisa. *Apteronotus jurubidae*. Colombia. Chocó: ANSP 71435, holotype (R), 253. *Apteronotus magdalenensis*. Colombia. Tolima: IAvHP 7829, 3 (R), 225–317. IAvHP 7831, 2 (R), 301–357. IAvHP 7833, 5 (R), 284–383. IAvHP 7834, 6 (R), 308–389. USNM 123795, 1 (R), 287, paratype; Honda, Río Magdalena basin. *Apteronotus mariae*. Colombia. Tolima: FMNH 56774, holotype (R), 195; Girardot. CAS 62345 (IU 13375), one paratype (R), 274; Apulo. *Apteronotus milesi*. Colombia. Cauca: CAS 72249 (IU 13378), 4 (R), 91–178; Río Magdalena, Cartago, town on River Viejo, 6 miles from Río Cauca. CAS 72250 (IU 13379), 2 (R), 113–147; Río Cauca at Cali, 3312 ft asl. IAvHP 3936, holotype, 160; IAvHP 3997, 13 paratypes, 125–211; Río Chanco, 950 m asl, Municipio de Ancermanuevo, Hacienda El Amparo. *Megadontognathus kaitukaensis*, INPA 3936, 2 c&s, 90–116; Brazil, Rio Xingu, Pará.

*Sternopygidae*

*Archolaemus blax*, INPA 4828, 11, 45–340; Brazil, Rio Tocantins, Pará. *Distocyclus conirostris*, INPA 28879, 2, 142–239; INPA 28915, 2135–158, Brazil, Rio Negro. *Eigenmannia limbata*, INPA 18288, 2, 137–176; Brazil, Rio Japura. *Eigenmannia macrops*, INPA 33259, 2, 67.7–94.1; Brazil, Rio Solimões. *Japigny kirschbaum*, FMNH 50185, 3, 100–130; Guyana, New River. *Rhabdolichops eastwardi*, INPA 12361, 2, 60–172; Brazil, Rio Negro. *Rhabdolichops troscheli*,

INPA 12363, 3, 70–174; Brazil, Rio Negro. *Sternopygus astrabes*, INPA 30502, 2, 112–156; Brazil, Rio Negro. *Sternopygus macrurus*, INPA 4869, 4, 31.9–84.1; Brazil, Rio Solimões, Lago Castanho, INPA 16001, 1, 27; Brazil, Rio Urubu.

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REFERENCES

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

**Albert JS. 2003.** Family Apterontidae – ghost knifefishes. In: Reis RE, Kullander SO, Ferraris CJ Jr, eds. *Check list of the freshwater fishes of South and Central America*. Porto Alegre, Brazil: EDIPUCRS, 497–502.

**Albert JS. 2009.** Family Apterontidae. In: Vari RP, Ferraris CJ Jr, Radosavljevic A, Funk VA, eds, Checklist of the freshwater fishes of the Guiana Shield. *Bulletin of the Biological Society of Washington* **17**: 1–95.

**Albert JS, Campos-da-Paz R. 1998.** Phylogenetic systematics of Gymnotiformes with diagnoses of 58 clades: a review of available data. In: Malabarba LR, Reis RE, Vari RP, Lucena ZM, Lucena C, eds. *Phylogeny and classification of Neotropical fishes*. Porto Alegre, Brazil: EDIPUCRS, 419–446.

**Albert JS, Lovejoy NR, Crampton WGR. 2006.** Miocene tectonism and the separation of cis- and trans-Andean river

- basins: evidence from Neotropical fishes. *Journal of South American Earth Sciences* **21**: 14–27.
- Alves-Gomes JA, Ortí G, Haygood M, Heiligenberg H, Meyer A. 1995.** Phylogenetic analysis of the South American electric fishes (order Gymnotiformes) and the evolution of their electrogenic system: a synthesis based on morphology, electrophysiology, and mitochondrial sequence data. *Molecular Biology and Evolution* **12**: 298–318.
- Bermingham E, Martin AP. 1998.** Comparative mtDNA phylogeography of neotropical freshwater fishes: Testing shared history to infer the evolutionary landscape of lower Central America. *Molecular Ecology* **7**: 499–517.
- Cala P. 1977.** Los peces de la Orinoquia Colombiana. *Lozania (Acta Zoologica Colombiana)* **24**: 1–21.
- Cala P. 1986.** Nuevos registros de peces para la Orinoquia Colombiana, I. Los Rajiformes, Clupeiformes, Characiformes, y Gymnotiformes. *Revista Unellez de Ciencia y Tecnología* **4**: 89–99.
- Cardona M, Roman-Valencia C, Jimenez JL, Hurtado TH. 1998.** Compasión y diversidad de los peces de la Quebrada San Pablo en Alto Cauca, Colombia. *Boletín Ecológico: Ecosystemas Tropicales* **32**: 11–24.
- Castro RMC, Vari RP. 2004.** Detritivores of the South American fish family Prochilodontidae (Teleostei: Ostariophysi: Characiformes): a phylogenetic and revisionary study. *Smithsonian Contributions to Zoology* **622**: 1–189.
- Cox-Fernandes C, Lundberg JG, Riginos C. 2002.** Largest of all electric-fishes snouts: hypermorphic facial growth in male *Apteronotus hasemani* and the identity of *Apteronotus anas* (Gymnotiformes: Apteronotidae). *Copeia* **2002**: 52–61.
- Crampton WGR. 2011.** An ecological perspective on diversity and distributions. In: Albert JS, Reis RE, eds. *Historical biogeography of Neotropical freshwater fishes*. Berkeley: University of California Press, 165–189.
- Dahl G. 1971.** *Los peces del norte de Colombia*. Bogotá, Colombia: Instituto de Desarrollo de los Recursos Naturales Renovables.
- Eigenmann CH. 1912.** The freshwater fishes of British Guiana, including a study of the ecological grouping of species, and the relation of the fauna of the plateau to that of the lowlands. *Memoirs of the Carnegie Museum* **5**: 1–578.
- Eigenmann CH. 1922.** The fishes of western South America, part I. The fresh-water fishes of northwestern South America, including Colombia, Panama, and Pacific slopes of Ecuador and Peru, together with an appendix upon the fishes of the Rio Meta in Colombia. *Memoirs of the Carnegie Museum* **9**: 1–346.
- Eigenmann CH, Fisher HG. 1914.** The Gymnotidae of trans-Andean Colombia and Ecuador. *Indiana University Studies* **25**: 235–237.
- Eldredge N, Thompson JN, Brakefield PM, Gavrillets S, Jablonski D, Jackson JBC, Lenski RE, Lieberman BS, McPeck MA, Miller W. 2005.** The dynamics of evolutionary stasis. *Paleobiology* **31**: 133–145.
- Ellis MM. 1913.** The gymnotid eels of tropical America. *Memoirs of the Carnegie Museum* **6**: 109–195.
- Fowler HW. 1943.** A collection of fresh-water fishes from Colombia, obtained chiefly by brother Nicéforo Maria. *Proceedings of Academy of Natural Sciences of Philadelphia* **95**: 223–266.
- Fowler HW. 1945.** *Los peces del Peru. Catálogo sistemático de los peces que habitan en aguas peruanas*. Lima: Museo de Historia Natural 'Javier Prado'.
- Fowler HW. 1951.** Os peixes de água doce do Brasil (3.<sup>a</sup> entrega). *Arquivos de Zoologia* **6**: 404–625.
- Galvis G, Mojica JI, Camargo M. 1997.** *Peces del Catatumbo*. Bogotá, Colombia: D'Vinni Editorial.
- Hagedorn M, Heiligenberg W. 1985.** Court and spark: electric signals in the courtship and mating of gymnotoid fish. *Animal Behaviour* **33**: 254–265.
- Hildebrand SF. 1938.** A new catalogue of the fresh-water fishes of Panama. *Field Museum of Natural History, Zoological Series* **12**: 219–359.
- Hilton EJ, Cox-Fernandes C. 2006.** Sexual dimorphism in *Apteronotus bonapartii* (Gymnotiformes: Apteronotidae). *Copeia* **2006**: 826–833.
- Hilton EJ, Cox-Fernandes C, Sullivan JP, Lundberg JG, Campos-da-Paz R. 2007.** Redescription of *Orthosternarchus tamandua* (Boulenger, 1898) (Gymnotiformes, Apteronotidae), with reviews of its ecology, electric organ discharges, external morphology, osteology, and phylogenetic affinities. *Proceedings of the Academy of Natural Sciences of Philadelphia* **156**: 1–25.
- Hoorn C. 1993.** Marine incursion and the influence of Andean tectonics on the Miocene depositional history of northwestern Amazonia: results of a palynostratigraphic study. *Palaeogeography, Palaeoclimatology and Palaeoecology* **112**: 187–238.
- Hoorn C, Guerrero J, Sarmiento FA, Lorente MA. 1995.** Andean tectonics as a cause for changing drainage patterns in Miocene northern South America. *Geology* **23**: 237–240.
- Hupé GJ, Lewis JE. 2008.** Electrocommunication signals in free swimming brown ghost knifefish, *Apteronotus leptorhynchus*. *Journal of Experimental Biology* **21**: 1657–1667.
- Lasso CA, Lew D, Taphorn DC, DoNascimento C, Lasso-Alcalá O, Provenzano F, Machado-Allison A. 2004a.** Biodiversidad ictológico continental de Venezuela. Parte 1. Lista de especies y distribución por cuencas. *Memoria de la Fundación La Salle de Ciencias Naturales* **159–160** (for 2003): 105–195.
- Lasso CA, Machado-Allison A, Pérez Hernández R. 1989.** Consideraciones zoogeográficas de los peces de La Gran Sabana (Alton Caroni) Venezuela, y sus relaciones con las cuencas vecinas. *Memoria de la Fundación La Salle de Ciencias Naturales* **131–132**: 109–129.
- Lasso CA, Machado-Allison A, Taphorn D, Rodríguez-Oldarte D, Vispo CR, Chernoff B, Provenzano F, Lasso-Alcalá O, Cervó A, Nakamura K, González N, Meri J, Silvera C, Bonilla A, López-Rojas H, Machado-Aranda D. 2003.** The fishes of the Caura River basin, Orinoco drainage, Venezuela. Annotated checklist. *Scientia Guianae* **12**: 223–245.
- Lasso CA, Mojica JI, Usma JS, Maldonado JA, DoNascimento C, Taphorn DC, Provenzano F, Lasso-Alcalá OM, Galvis G, Vásquez L, Lugo M, Machado-Allison A, Royero R, Suárez C, Ortega-Lara A. 2004b.** Peces de las

- cuencas del río Orinoco. Parte I: lista de especies y distribución por subcuencas. *Biota Colombiana* **5**: 95–158.
- Lasso CA, Provenzano F, Lasso-Alcalá OM, Marcano A. 2010.** Ictiofauna dulceacuícola y estuarina de la cuenca del golfo de Paria, Venezuela: composición y relaciones biogeográficas con la cuenca del Orinoco. *Biota Colombiana* **11**: 53–73.
- Lundberg JG, Aguilera O. 2003.** The late Miocene *Phractocephalus* catfish (Siluriformes: Pimelodidae) from Urumaco, Venezuela: additional specimens and reinterpretation as a distinct species. *Neotropical Ichthyology* **1**: 97–109.
- Lundberg JG, Machado-Alison A, Kay RF. 1986.** Miocene characid fishes from Colombia: evolutionary stasis and extirpation. *Science* **234**: 208–209.
- Lundberg JG, Mago-Leccia F. 1986.** A review of *Rhabdoli-chops* (Gymnotiformes, Sternopygidae), a genus of South American freshwater fishes, with description of four new species. *Proceedings of the Academy of Natural Sciences of Philadelphia* **138**: 53–85.
- Lundberg JG, Mago-Leccia F, Baskin JN. 1985.** Systematics of the South American freshwater fish genus *Adontosternarchus* (Gymnotiformes, Apterontidae). *Contributions in Science, Natural History Museum, Los Angeles County* **358**: 1–19.
- Lundberg JG, Marshall LG, Guerrero J, Horton B, Malabarba MC, Wessling F. 1998.** The stage for Neotropical fish diversification: a history of tropical South American rivers. In: Malabarba LR, Reis RE, Vari RP, Lucena ZM, Lucena C, eds. *Phylogeny and classification of Neotropical fishes*. Porto Alegre, Brazil: EDIPUCRS, 13–48.
- Machado-Alison A, Lasso CA, Usma JS, Sánchez-Duarte P, Lasso-Alcalá OM. 2010.** Chapter 7. Peces. In: Lasso CA, Usma JS, Trujillo F, Rial A, eds. *Biodiversidad de la Cuenca del Orinoco. Bases científicas para la identificación de áreas prioritarias para la conservación y uso sostenible de la biodiversidad*. Bogotá, Colombia: Instituto de Investigación Biológicas Alexander von Humboldt; WWF Colombia, Fundación Omacha, Fundación La Salle, Instituto de Estudios de la Orinoquia, 217–257.
- Mago-Leccia F. 1970.** *Lista de los peces de Venezuela incluyendo un estudio preliminar sobre la ictiogeografía del país*. Caracas: Ministerio de Agricultura y Cria, Oficina Nacional de Pesca.
- Mago-Leccia F. 1978.** Los peces de la familia Sternopygidae de Venezuela. *Acta Scientifica Venezuelana* **29** (suplemento): 1–89.
- Mago-Leccia F. 1994.** *Electric fishes of the continental waters of America*. Caracas, Venezuela: Biblioteca de la Academia de Ciencias Físicas, Matemáticas y Naturales.
- Maldonado-Ocampo JA, Vari RP, Usma JS. 2008.** Checklist of the freshwater fishes of Colombia. *Biota Colombiana* **9**: 143–237.
- Maler L, Sas E, Johnston S, Ellis W. 1991.** An atlas of the brain of the electric fish *Aptereronotus leptorhynchus*. *Journal of Chemical Neuroanatomy* **4**: 1–38.
- Meek SE, Hildebrand SF. 1913.** New species of fishes from Panama. *Field Museum of Natural History Publications, Zoological Series* **10**: 77–91.
- Meek SE, Hildebrand SF. 1916.** The fishes of fresh-water of Panama. *Field Museum of Natural History Publications, Zoological Series* **15**: 217–374.
- Miles C. 1947.** *Los peces del Río Magdalena*. ('A field book of Magdalena fishes'). Bogotá, Colombia: Ministerio de la economía nacional, secció de piscicultura, pesca y caza.
- Mojica-C JI. 1999.** Lista preliminar de las especies de peces dulceacuícolas de Colombia. *Revista de la Academia Colombiana de Ciencias Exactas, Físicas y Naturales* **23**: 547–566.
- Moller P. 1995.** *Electric fish: history and behavior*. London: Chapman & Hall.
- Myers GS. 1930.** Fishes from the upper Rio Meta basin, Colombia. *Proceedings of the Biological Society of Washington* **43**: 65–72.
- Oliveira C, Avelino GS, Abe KT, Mariguela TC, Benine RC, Ortí G, Vari RP, Castro e Castro RM. 2011.** Phylogenetic relationships within the speciose family Characidae (Teleostei: Ostariophysi: Characiformes) based on multilocus analysis and extensive ingroup sampling. *BMC Evolutionary Biology* **11**: 275.
- Péfaur JE. 1988.** Catalogación económica de la ictiofauna alto-andina venezolana. *Memoria Sociedad de Ciencias Naturales La Salle* **48** (Supplement): 471–492.
- Regan CT. 1914.** Fishes from the Condoto River, Colombia, collected by Dr. H. G. F. Spurrell. *Annals and Magazine of Natural History* **14**: 31–33.
- Rodríguez-Olarte D, Taphorn DC, Lasso C, Vispo CR. 2003.** Fishes of the lower Caura, Orinoco basin, Venezuela. *Scientia Guianae* **12**: 181–221.
- Rodríguez-Olarte D, Taphorn DC, Lobón-Cervía J. 2009.** Patterns of freshwater fishes on the Caribbean versant of Venezuela. *International Review of Hydrobiology* **94**: 67–90.
- Roman-Valencia C. 1995.** Lista anotada de los peces de la Cuenca del Río La Vieja, Alto Cauca, Colombia. *Boletín Ecotropía* **29**: 1–10.
- Ryan PD, Harper DAT, Whalley JS. 1995.** *PALSTAT, Statistics for palaeontologists*. London: Chapman & Hall (now Kluwer Academic Publishers).
- de Santana CD. 2003.** *Aptereronotus caudimaculosus* n. sp. (Gymnotiformes: Apterontidae), a sexually dimorphic black ghost knifefish from the Pantanal, western Brazil, with a note on the monophyly of the *A. albifrons* species-complex. *Zootaxa* **252**: 1–11.
- de Santana CD, Castillo O, Taphorn D. 2006.** *Aptereronotus magoi*, a new species of ghost electric knifefish from the Orinoco basin Venezuela (Gymnotiformes: Apterontidae). *Ichthyological Exploration of Freshwaters* **3**: 275–280.
- de Santana CD, Cox-Fernandes C. 2012.** A new sexually dimorphic electric knifefish from the Amazon basin, Brazil (Gymnotiformes: Apterontidae). *Copeia* **2012**: 284–293.
- de Santana CD, Crampton WGR. 2006.** Redescription of the ghost knifefish *Aptereronotus spurrellii* from trans-Andean Colombia (Gymnotiformes: Apterontidae). *Ichthyological Exploration of Freshwaters* **2**: 115–120.
- de Santana CD, Crampton WGR. 2011.** Phylogenetic interrelationships, taxonomy and reductive evolution in the



- Neotropical electric fish genus *Hypopygus* (Teleostei, Ostariophysi, Gymnotiformes). *Zoological Journal of the Linnean Society* **163**: 1096–1156.
- de Santana CD, Maldonado-Ocampo J, Crampton WGR. 2007.** *Apteronotus galvisi*, a new species of electric ghost knifefish from the Río Meta basin, Colombia (Gymnotiformes: Apteronotidae). *Ichthyological Exploration of Freshwaters* **2**: 117–124.
- de Santana CD, Vari RP. 2009.** The South American electric fish genus *Platyurosternarchus* (Gymnotiformes: Apteronotidae). *Copeia* **2009**: 233–244.
- de Santana CD, Vari RP. 2010.** Electric fishes of the genus *Sternarchorhynchus*; phylogenetic and revisionary studies (Teleostei, Ostariophysi, Gymnotiformes). *Zoological Journal of the Linnean Society* **159**: 223–371.
- Schultz LP. 1949.** A further contribution to the ichthyology of Venezuela. *Proceedings of the United States National Museum* **99**: 1–211.
- Tabachnick B, Fidell L. 1989.** *Using multivariate statistics*. New York: Harper & Row Publishers.
- Taphorn D, García Tenía JG. 1991.** El Río Claro y sus peces, con consideraciones de los impactos ambientales de las presas sobre la ictiofauna del bajo Río Caroni. *Biollania (Museo de Ciencias Naturales)*, Universidad Nacional Experimental de los Llanos Occidentales Ezequiel Zamor **8**: 23–45.
- Taphorn D, Royero R, Machado-Allison A, Mago Leccia F. 1997.** Lista actualizada de los peces de agua dulce de Venezuela. In: La Marcha E, ed. *Vertebrados actuales y Fósiles de Venezuela*. Merida, Venezuela: Museo de Ciencia y Tecnología de Merida, 55–100.
- Taylor WR, Van Dyke GC. 1985.** Revised procedures for staining and clearing small fishes and other vertebrates for bone and cartilage study. *Cybium* **9**: 107–119.
- Thurston K. 1996.** The black ghost. *Tropical Fish Hobbyist* **462**: 16–22.
- Urbano-Bonilla A, Zamudio J, Maldonado-Ocampo JA, Bogotá-Grégory JD, Cortes-Millán GC, López Y. 2009.** Peces del piedemonte del Departamento do Casanare, Colombia. *Biota Colombiana* **10**: 149–162.
- Vari RP. 1995.** The Neotropical fish family Ctenoluciidae (Teleostei: Ostariophysi: Characiformes): supra and intrafamilial phylogenetic relationships with a revisionary study. *Smithsonian Contributions to Zoology* **564**: 1–97.
- Vari RP, Malabarba LR. 1988.** Neotropical ichthyology: an overview. In: Malabarba LR, Reis RE, Vari RP, Lucena ZMS, Lucena CA, eds. *Phylogeny and classification of neotropical fishes*. Porto Alegre: EDIPUCRS, 1–11.
- Vari RP, de Santana CD, Wosiacki WB. 2012.** The South American electric knifefishes of the genus *Archolaemus* (Ostariophysi, Gymnotiformes): undetected diversity in a clade of rheophiles. *Zoological Journal of the Linnean Society* **165**: 670–699.
- Wiens JJ, Donoghue MJ. 2004.** Historical biogeography, ecology and species richness. *Trends in Ecology and Evolution* **19**: 639–644.