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A new species of electric knifefish, genus *Compsaraia* (Gymnotiformes: Apteronotidae) from the Amazon River, with extreme sexual dimorphism in snout and jaw length

Abstract A new species of the neotropical electric fish genus *Compsaraia* is described from the western Amazon of Peru and Brazil. *Compsaraia samueli* is distinguishable from all other apteronotids by sexual dimorphism in which mature males exhibit extreme elongation and slenderness of the snout and jaws. *Compsaraia samueli* is readily distinguishable from its only congener, *C. compsa*, by more caudal-fin rays (17–18 vs. 13–16), a shorter caudal peduncle (mean length 9% vs. 34% body length to end of anal fin), a less tapering body shape in lateral profile (mean ratio of body depth at origins of anal fin and dorsal organ 93% vs. 75%), and a smaller maximum adult body size (230 vs. 305 mm). The genus *Compsaraia* is readily separated from other apteronotids by a pale antorbital stripe and a pale L-shaped patch over the supratemporal canal. The phylogenetic position of *C. samueli* is estimated by inclusion in a previously published data matrix of osteological and other morphological characters. Comparisons of the cranial bones in apteronotids shows the derived morphology of *C. samueli* to be a composite of three developmentally and phylogenetically discrete characters: (1) positive allometric growth before sexual maturity in both sexes of the pre-orbital region of the neurocranium, (2) positive allometric growth of the (oral) jaws, and (3) secondary sexual dimorphism of snout and jaw morphology. The genus *Compsaraia* represents one of at least three phylogenetically independent cases of snout elongation and one of at least four cases of jaw elongation within the Apteronotidae. *Compsaraia samueli* also represents one of at least four cases of secondary sexual dimorphism in snout and jaw length within the Apteronotidae. The phylogenetic distribution of snout and jaw characters within the Apteronotidae suggests the influence of both sexual and trophic functional influences on the evolution of head morphology.

Key words comparative morphology, mosaic evolution, neotropical biodiversity, osteology, phenotypic evolution, taxonomy

Introduction

The diversity and natural history of electric fishes (Gymnotiformes) from large river channels in the Neotropics has been underestimated because of the tremendous difficulty of sampling these habitats. As a result many species specialised to this environment have been historically rare in museum collections. In recent years however, gymnotiform electric fishes, in particular species of the family Apteronotidae, have come to be known as among the most diverse and abundant members of the deep channel fauna in large Neotropical rivers (Lundberg *et al.*, 1987; Cox Fernandes *et al.*, 2004; Albert & Crampton, 2005).

The genus *Compsaraia* represents one of many new taxa that have been discovered in the deep channels of neotropical rivers. The genus was established by Albert (2001) to separate *C. compsa* (Mago-Leccia, 1994) in the Orinoco basin, from the problematic taxon '*Porotergus*'. In the original description, *Compsaraia* was diagnosed as an apteronotid with six

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synapomorphies: pale stripe of low melanophore density in narrow band passing anterior to eyes and lateral to nares; long snout in which the pre-orbital region is greater than one third the head length in mature specimens; dorsal margin of frontals concave; supratemporal lateral line canal L-shaped; nasal capsule closer to tip of snout than to eye; basibranchial of the third gill arch unossified. Several character states in *Compsaraia* (elongate snout, concave dorsal margin of the frontals, anterior position of the nasal capsule) are similar to those in two other clades of Apteronotidae, *Parapteronotus* and *Sternarchorhamphus* + *Orthosternarchus*, which in a phylogenetic context were determined to be homoplastic (Albert, 2001).

The Apteronotidae is characterised by much greater diversity in head and skull morphology than other gymnotiform families, principally in structures of the snout (pre-orbital region of the neurocranium) and oral jaws, putatively related to trophic and agonistic sexual behaviours (Albert, 2003; Albert & Crampton, 2005; Crampton & Albert, 2006). Elongate snouts and jaws have evolved several times within the family, either as functional specialisations for feeding in benthic environments, or in association with larger jaws as midwater predators (Albert, 2001). Many tube-snouted apteronotids are ecologically specialised as benthic probers (Winemiller & Adite, 1997). The small terminal mouth of tube-snouted gymnotiforms functions in a grasp-suction feeding mode and is used for extracting immature stages of aquatic insects that burrow into the clay channel bottoms of many lowland neotropical rivers (Marrero & Winemiller, 1993). Many apteronotids also express secondary sexual dimorphism (SSD) in which males exhibit derived traits of snout and cranial morphology upon reaching sexual maturity. Secondary sexual dimorphism in snout and head shape has not been reported in other gymnotiform families. However, 6 of 15 (40%) apteronotid genera are currently known to exhibit some form of snout or head SSD (Mago-Leccia, 1994; Cox Fernandes, 1998; Cox Fernandes *et al.*, 2002; de Santana, 2003; Albert & Crampton, 2005; Rapp Py-Daniel & Cox Fernandes, 2005).

Here we describe a new species of *Compsaraia* from the western Amazon River of Peru and Brazil that possesses all of the derived traits of the genus. The new species is characterised by unique morphometric and meristic characters, an elongate snout and jaws, and pronounced SSD in snout and jaw length. The genus *Compsaraia* is determined to represent a third phylogenetically independent case of snout elongation within the Apteronotidae, and the new species represents a fourth case of SSD in snout and jaw morphology within the family.

Materials and methods

Specimens in the type series were captured by professional ornamental fish collectors near Iquitos, Peru. These fishermen used large (40 m) seine nets with 12 mm mesh, during the day, to catch these fishes on beaches of the Rio Amazonas. These seines were deployed to a maximum depth of 5 m. Body measurements are given in mm. Measurements include: (1) total length (TL), measured from snout (anterior margin of upper jaw at mid-axis of body) to posterior tip of longest caudal-fin rays; (2) length to the end of the anal fin (LEA), measured from the tip of snout to end of anal fin (where membrane posterior to last ray contacts the ventral surface of body); (3) length to the origin of the midsaggital dorsal organ (LOD); (4) length of anal fin (LAF), from origin of anal fin to posterior end of anal fin; (5) length of caudal peduncle (LCP), measured as the distance from the last anal-fin ray to the base of the caudal fin; (6) length to origin of the anal fin (LOA), measured as the distance from snout to base of first anal-fin ray; (7) length to the anus (LA), measured as the distance from the snout to the anterior margin of the anus; (8) head length (HL), measured from posterior margin of the opercle to tip of snout; (9) head width (HW), measured at mid opercle; (10) postorbital head length (PO), from posterior margin of the bony opercle to posterior margin of eye; (11) body depth anteriorly (BDA), vertical distance from origin of anal fin to dorsal body border; (12) body depth at midbody (BDM), vertical distance from origin of dorsal organ to ventral body border (contact of anal-fin pterygiophores with anal-fin rays); (13) body width (BW), measured at middle of body cavity; (14) head depth at occiput (HD), vertical distance at nape to ventral body border with lateral line held horizontal; (15) pre-orbital head length (PR), from anterior margin of eye to tip of snout; (16) eye diameter (ED), measured from postorbital to pre-orbital margins parallel with long axis; (17) length from eye to posterior nares (LPN), measured from pre-orbital margin to posterior margin of posterior nares; (18) length from eye to anterior nares (LAN), measured from pre-orbital margin to posterior margin of posterior nares; (19) interorbital distance (IO), measured as linear distance between medial margins of orbits; (20) pectoral-fin length (P1), from dorsal insertion of fin base where it contacts cleithrum to tip of the longest ray.

Measurements of TL and AF were taken with a ruler to the nearest millimetre. All other measurements were taken with a digital caliper to the nearest 0.1 mm. Morphometric data in diagnosis are reported as mean relative proportions, and ranges are reported in brackets for type series of *C. samueli* (n = 11) and *C. compsa* (n = 24) with both sexes combined. Meristic protocols follow Albert and Fink (1996). Skeletal counts obtained from cleared and stained specimens and radiographs, including the number of precaudal vertebrae (PCV) and those of the Weberian apparatus, which is a proxy for body cavity length (Albert, 2001); the total number of anal-fin rays (AFR); the number of pectoral-fin rays (P1R); and the number of caudal fin rays (CFR). Morphometric measurements and meristic counts were taken from the left side of specimens. Sex was determined by dissection. Sexually mature males have smooth, white testes. Sexually mature females have enlarged ovaries packed with yellow-white or yellow eggs.

Electric organ discharge (EOD) recording procedures follow Crampton *et al.* (2004). In brief: silver/silver-chloride electrodes were placed posterior and anterior to the fish, water temperature was controlled to within 0.5 °C of 27 °C, the signal amplified with a wide-band AC-coupled differential amplifier, and digitised to a computer file using an Edirol UA-5 analog-digital acquisition device at a sample rate of 96 kSs and a resolution of 24 bits.
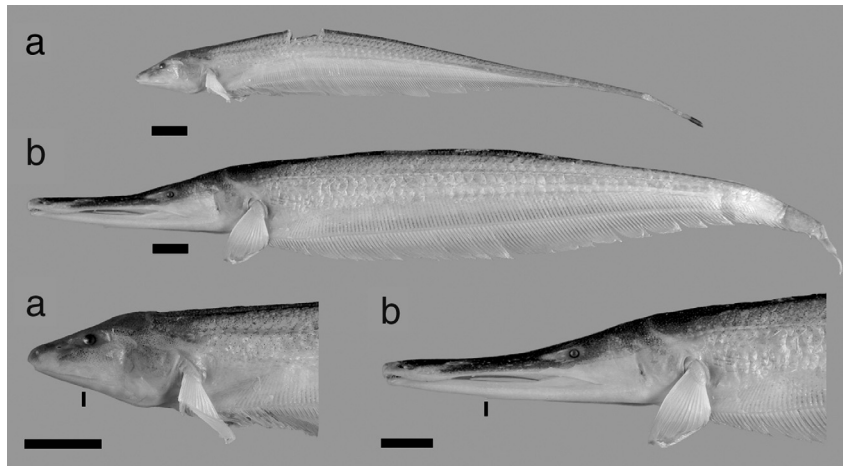
Figure 1 Photographs of a female and male in the type series of *Compsaraia samueli*. (a) MUSM 26094, female (paratype), 163 mm. (b) MUSM 26093, male (holotype), 226 mm. narrow vertical bars indicate position of anus. Scale bars = 1 mm.

In order to estimate the phylogenetic position of the new species we scored character states for all the characters employed in a recent morphologically based phylogenetic analysis of the Apteronotidae (Albert, 2001). The character analysis of the present study included all the currently recognised apteronotid genera except for the monotypic *Tembeassu* (Triques, 1998) and monotypic *Pariosternarchus* (Albert & Crampton, 2006) for which comparative osteological data are not available due to limited numbers of specimens. Neither *Tembeassu* (Campos-da-Paz, 2005) nor *Pariosternarchus* (Albert & Crampton, 2006) is known to possess SSD in aspects of head morphology. The taxonomic composition of the present study further differs from that of Albert (2001) by including a species '*A.*' *bonapartii* recently shown to be sexually dimorphic (Hilton & Cox Fernandes, 2006), and by substituting the species '*A.*' *macrolepis* for '*A.*' *apurensis* due to the availability of specimens cleared and stained for bone and cartilage. Following Albert (2003) and de Santana (2003) *Apteronotus sensu stricto* includes four species of the *A. albifrons* species group (including *A. albifrons*, *A. caudimaculosus*, *A. cuchillejo* and *A. mariae*) and five species of the *A. leptorhynchus* species group (*A. jurubidae*, *A. leptorhynchus*, *A. galvisi*, *A. rostratus* and *A. spurellii;* see de Santana *et al.*, 2007). Two other recently described apteronotids exhibit snout length SSD, *A. eschmeyeri* (de Santana *et al.*, 2004) and *A. milesi* (de Santana & Maldonado-Ocampo, 2005), and the phylogenetic positions of these species is currently unknown. Species referred to Apteronotidae *incertae sedis* include '*A.*' *macrolepis* and '*A.*' *bonapartii*. Species richness and character state data for *Sternarchorhynchus* were updated from recent reports by de Santana and colleagues (de Santana & Crampton, 2006; de Santana & Nogueira, 2006; de Santana & Taphorn, 2006).

Osteological data were taken from cleared and stained specimens prepared using the method of Taylor and Van Dyke (1985). Abbreviations of museum collections from which materials were examined follow Leviton *et al.* (1985). Comparative materials examined for phylogenetic portion of this study are reported in Albert (2001). We used standard micro-dissection methods of Weitzman (1962) to obtain osteological data, and followed Fink and Fink (1981) and Albert (2001) for morphological nomenclature. Drawings of cleared and stained specimens were made with the aid of a drawing tube, scanned into digital format, and then edited using Adobe Illustrator Creative Suite to prepare figures. Morphometric and other morphological data for *C. compsa* are presented from specimens in the Orinoco basin, the region of the type locality (see Comparative Materials Examined). Morphological data for *C. samueli* place this taxon in a unique position of maximum parsimony using MacClade 4.0 (Maddison & Maddison, 2000) within the context of the data matrix of Albert (2001), and using additional published information on other apteronotids (de Santana & Maldonado-Ocampo, 2004; Hilton & Cox Fernandes, 2006). Brief descriptions of these characters and states as coded for *C. samueli* are presented in the Appendix (which is available as 'Supplementary data' on Cambridge Journals Online: http://www.journals.cup.org/abstract_S1477200008002934). See Albert (2001) for lists of apteronotid specimens examined for external morphology and osteology.

Compsaraia samueli sp. nov

Samuel's ghost knifefish

Figs 1–4, Table 1

Apteronotus anas, Cox Fernandes, 1995: 63
Compsaraia sp. 1, Albert, 2001: 78, fig. 19C
Holotype. – MUSM 26093, male, 226 mm, Peru, Loreto, Rio Amazonas near Iquitos, Peru, 3.77° S, 73.25°W, S. Albert, 21.III.2004.

Paratypes. – ANSP 182209 (2), 122- 185 mm, 13.VIII.2005, Rio Amazonas near Iquitos, Loreto, Peru. ANSP 182214 (1), 156 mm, 08.VIII.2005, Rio Amazonas near Iquitos, Loreto, Peru. MUSM 26094 (5), 144–230 mm, 1 female c&s, same collection data as holotype. CAS 223382 (1), male c&s, 184

Figure 2   Photograph of head of the holotype (live) of *Compsaraia samueli* (MUSM 26093, male, 226 mm).
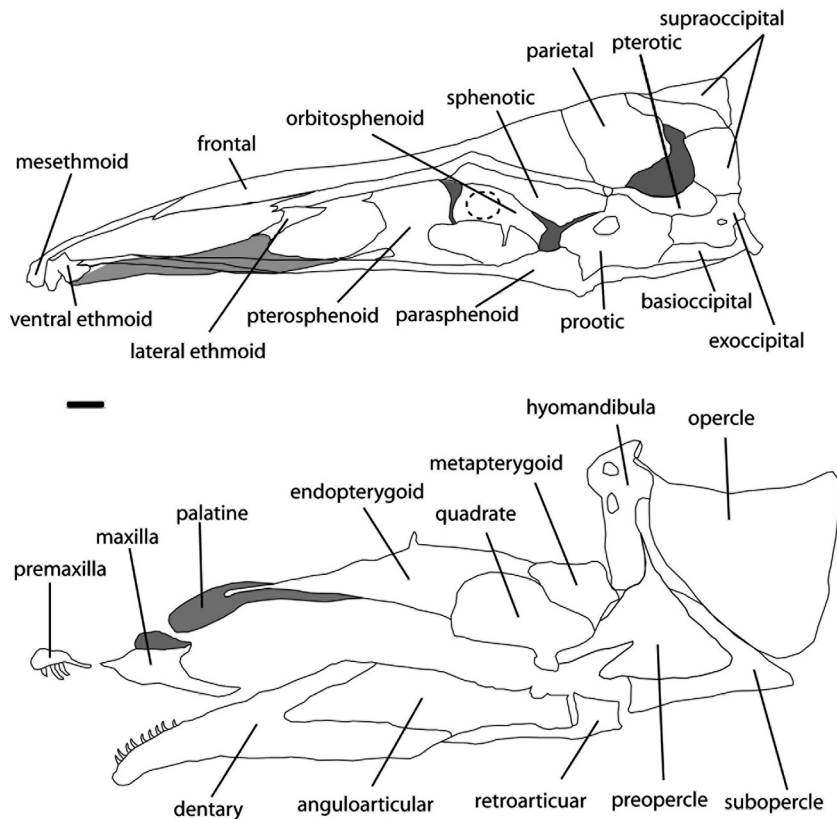

Figure 3   Illustration of the skull *Compsaraia samueli* in lateral view. Neurocranium (top) and suspensorium with oral jaws (bottom) of a mature female (MUSM 26094A, 144 mm). Scale bar = 1 mm. Grey = cartilage. Dashed circle over orbitosphenoid indicates position of eye.

mm, same collection data as holotype. CAS 223383 (1), male, 194 mm TL, same collection data as holotype. UF 122826 (1), male, 210 mm, 05.V.2002, Rio Amazonas near Iquitos, Loreto, Peru.

Nontypes. – MZUSP 57442 (1), 167 mm. Brazil, Amazonas, Rio Solimões, below Purus, 3° 35′ 11′ S, 61° 17′ 2' W, 28.VII.1996. UMMZ 230749 (2), 141–162 mm (1 c&s), Amazonas, lower Rio Iça, Brazil, 1994.IX.

Diagnosis. – *Compsaraia samueli* differs unambiguously from *C. compsa* by the presence of the following character states: more caudal-fin rays (17–18 [mode 18] vs. 13–16 [mode 14]); a shorter caudal peduncle (CP/LEA = 9% [0–23%] vs. 34% [18–46%]); a less tapering body shape in lateral profile, in which the ratio of body depth measurements at the anal fin and dorsal organ origins is greater (93% [80–116%] vs. 75% [67–82%]; Fig. 5E); and a smaller body size (minimum size at sexual maturity 144 mm [vs. 165 mm], maximum total
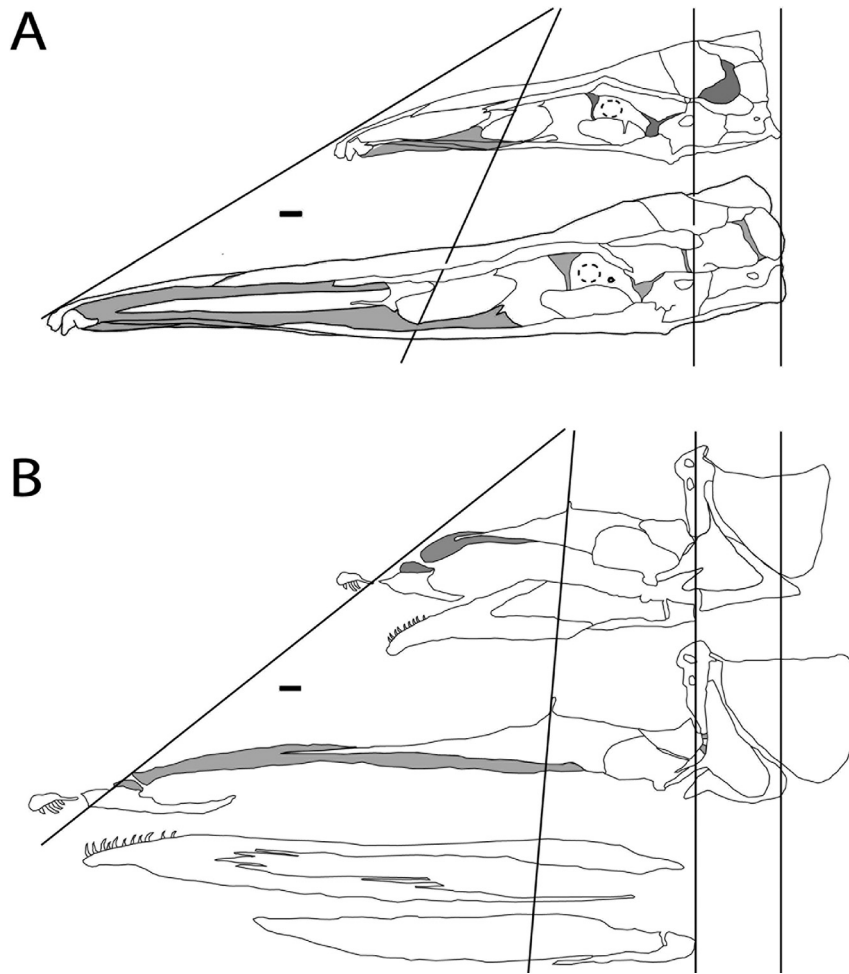
Figure 4 Comparisons of the neurocranium (a) and suspensorium (b) in *Compsaraia samueli*. In each panel a mature female (MUSM 26094A, 144 mm) is above, and a mature male (CAS 223382, 184 mm) is below. Scale bar = 1 mm. Grey = cartilage. Mandible of male presented as three disarticulated elements. Thin vertical and oblique lines superimposed to facilitate comparison following convention of Albert (2001). Dashed circles indicate position of eyes. Both sexes exhibit pre-orbital (snout) and jaw elongation, and this elongation is exaggerated in sexually mature males.

length of 230 mm [vs. 305 mm]). *Compsaraia samueli* may be further distinguished from *C. compsa* by secondary sexual dimorphisms in several features of snout and jaw morphology (see Discussion).

Description. – Minimum size of sexually mature males 184 mm, females 144 mm. Body compressed laterally. Origin of dorsal electroreceptive organ at about midbody. Scales large and ovoid, elongated obliquely along anteroventral-posterodorsal axis, scales absent from head, and from dorsum and flanks above lateral line on anterior half of body (Albert, 2001: 16, fig. 5). Eyes small, 12–17% post-orbital head length, without a free margin (sub-epidermal), and with small extrinsic eyeball muscles. Gape large, rictus reaching posterior to a vertical with eye (Figs 1 and 2). Mouth subterminal, upper jaw overhanging lower jaw in sexually mature males with a gap between the anterior margins of the dentary and premaxilla of 15% PR (5–29%, n = 7). Anterior and posterior nares well separated, nasal capsule elongate and located anteriorly, in some mature males a portion lying anterior to mental symphysis. Small conical teeth present at tip of both jaws. Premaxillae of moderate size in male and female (c&s) specimens, crescent-shaped in ventral view, with 4–5 small conical teeth and 1–3 even smaller replacement teeth of less than half the size of the conical teeth arranged irregularly on the anterior-medial premaxillary margin. Maxillae elongate with a broad anterodorsal–anteroventral lamella, without a curved anterior process (i.e. hook), and with a straight posterior process, the ventral margin of its descending blade straight (compare with *C. compsa*, Albert, 2001: 18–19, figs. 7 and 8). Anterior portion of dentary with 1–2 irregular rows of 10–13 recurved conical teeth along the outer margin, posterior 80% of its length without teeth (Figs 3 and 4). All three mandibular bones elongate (dentary, anguloarticular, retroarticular), especially so in sexually mature males. Dorsoposterior dentary process of mature males extends posterior to articulation of anguloarticular and quadrate; broader near its posterior tip than at its midlength. Dorsal and ventral margins of dentary posterior processes approximately straight and parallel. Dentary without extensive overlap with anguloarticular. Retroarticular with elongate anterior process contacting descending process of dentary. Mandibular

Character	*C. samueli* mature males	*C. samueli* females + juveniles	*C. samueli* pooled	*C. compsa* pooled
N	7	4	11	24
TL in mm	184–230	132–185	132–230	165–305
Morphometric				
LEA in mm	170–210	95–150	95–210	115–246
LOD in mm	105–144	55–84	55–144	75–145
LOD/LEA	0.63 (0.55–0.69)	0.59 (0.56–0.63)	0.61 (0.55–0.69)	0.63 (0.51–0.72)
L. anal-fin base/LOD	1.25 (1.05–1.40)	1.41 (1.30–1.53)	1.31 (1.05–1.53)	1.34 (1.12–1.64)
L. caudal peduncle/LEA	0.05 (0.00–0.08)	0.16 (0.09–0.23)	0.09 (0.00–0.23)	0.34 (0.18–0.46)
L. to origin anal fin/LEA	0.23 (0.21–0.26)	0.16 (0.15–0.18)	0.21 (0.15–0.26)	0.13 (0.05–0.17)
L. to anus/LEA	0.10 (0.08–0.12)	0.07 (0.06–0.08)	0.09 (0.06–0.12)	0.08 (0.05–0.12)
HL in mm	42.3 (35.2–53.4)	18.8 (16.6–20.6)	33.8 (16.6–53.4)	26.8 (18.0–38.4)
HL/LEA	0.22 (0.19–0.25)	0.15 (0.14–0.17)	0.20 (0.14–0.25)	0.15 (0.13–0.17)
PO/HL	0.42 (0.36–0.52)	0.58 (0.54–0.60)	0.47 (0.36–0.60)	0.58 (0.51–0.64)
PR/PO	1.45 (0.93–1.92)	0.39 (0.36–0.43)	0.52 (0.36–0.68)	0.39 (0.36–0.45)
ED/PO	0.13 (0.12–0.16)	0.17 (0.17–0.17)	0.15 (0.12–0.17)	0.15 (0.09–0.19)
BD at anal-fin origin/PO	0.99 (0.93–1.07)	1.19 (1.08–1.30)	1.06 (0.93–1.30)	1.16 (1.06–1.25)
BD at OD/PO	0.96 (0.74–1.22)	1.03 (0.92–1.17)	0.99 (0.74–1.22)	0.87 (0.75–0.99)
BD ratio: AFO/OD	0.96 (0.80–1.16)	0.87 (0.84–0.90)	0.93 (0.80–1.16)	0.75 (0.67–0.82)
BW/PO	0.32 (0.18–0.55)	0.35 (0.33–0.40)	0.33 (0.18–0.55)	0.31 (0.21–0.42)
HD/PO	0.97 (0.87–1.21)	1.02 (0.94–1.13)	0.99 (0.87–1.21)	0.98 (0.83–1.09)
HW/PO	0.60 (0.52–0.65)	0.61 (0.48–0.70)	0.61 (0.48–0.70)	0.65 (0.58–0.82)
Eye to post. nares/PO	0.79 (0.52–1.04)	0.27 (0.21–0.34)	0.60 (0.21–1.04)	0.28 (0.22–0.43)
Eye to ant. nares/PO	1.23 (0.83–1.56)	0.55 (0.45–0.63)	0.98 (0.45–1.56)	0.54 (0.45–0.71)
Internarial/PO	0.44 (0.37–0.53)	0.28 (0.24–0.32)	0.38 (0.24–0.53)	0.26 (0.17–0.34)
P1/PO	0.41 (0.36–0.47)	0.58 (0.54–0.60)	0.47 (0.36–0.60)	0.58 (0.51–0.64)
jaw gap/PO	0.15 (0.05–0.29)	0.00 (0.00–0.00)	0.09 (0.00–0.29)	0.00 (0.00–0.00)
IO/PO	0.30 (0.24–0.36)	0.26 (0.24–0.28)	0.29 (0.24–0.36)	0.27 (0.19–0.33)
Meristic				
AFR			170 (152–185)	195 (164–210)
P1R			14 (14–14)	14 (14–14)
CFR			18 (17–18)	14 (13–16)
PCV			14 (14–14)	14 (14–14)

Table 1 Morphometric and meristic data for the two species of *Compsaraia*. Data for *C. samueli* of mature males and of females + juveniles reported separately, and pooled. Linear values in mm reported as ranges; mean values for morphometric and median values for meristic traits followed by ranges in parentheses.

canal bones ossified as short, broad, dumbbell-shaped ossicles (Albert, 2001: 30, fig. 19C). Endopterygoid long, narrow and edentulous, with a small ascending process ossified within the ventral portion of the ethmopalatine ligament, the base of the ascending process positioned posterior to midlength of bone. Endopterygoid with elongate anterior process, especially so in mature males, and endopterygoid posterior margin abutting the metapterygoid. Metapterygoid with its dorsal (quadrangular) portion broad and completely ossified, its ventral (triangular portion) well ossified. Hyomandibula oriented vertically, approximately perpendicular to long axis of head, its proximal articulating head well ossified and broad, about twice the width of the distal hyomandibular tip. Preopercle broad and curved, oriented vertically, the ventral margin of its anterior limb not ossified. Opercle approximately triangular, with a straight to slightly concave dorsal margin and a vertical to slightly rounded posterior margin.

Preorbital region of snout elongate in adult males and females, exaggerated in sexually mature males (Figs 3 and 4). Mesethmoid elongate and narrow, its anterior tip small, concave, and flexed ventrally. Ventral ethmoid robust, slightly longer than deep, with a large lateral process articulating to lateral ethmoid cartilage. Lateral ethmoid bone relatively large compared with other apteronotids, with a broad base, its dorsal margin contacting ventrolateral margin of supraorbital canal. Frontal convex in lateral profile and thickened dorsoventrally in region above lateral ethmoid, thin and concave in lateral profile in region over orbitosphenoid-pterosphenoid junction. Orbitosphenoid shaped like a double-headed axe, broader dorsally and ventrally, its ventral margin with broad contact along parasphenoid. Position of eyeball lateral to anterior portion of pterosphenoid. Parasphenoid lateral margin small, not reaching to horizontal with ventral margin of prootic foramen. Sphenotic without posterior-lateral process. Prootic with
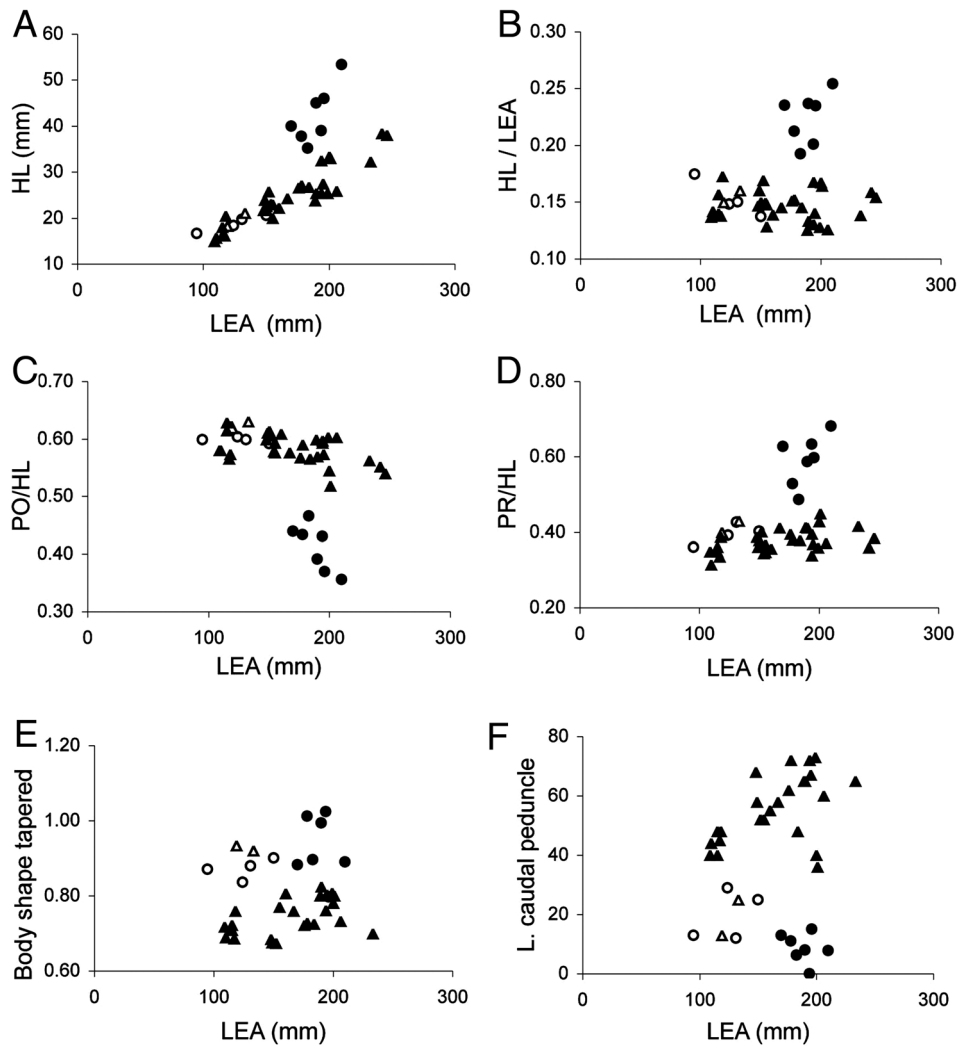
Figure 5 Morphometric comparisons of the two *Compsaraia* species. Solid circles are mature males of *C. samueli* (n = 7); open circles are females or juveniles of *C. samueli* (n = 4); closed triangles are *C. compsa* from the Orinoco (n = 24 or 30); open triangles are *Compsaraia* sp. from the western Amazon (n = 2). Head length (HL) includes postorbital (PO) basicranial and pre-orbital (PR) snout distances. Note patterns of allometric growth in the head (a, b), basicranial (c) and snout (d) regions are accelerated in mature males of *C. samueli*. Note also that in *C. samueli* relative snout length (PR/HL vs. LEA, r² = 0.69) is more variable than relative length of the basicranium (PO/HL vs. LEA, r² = 0.93; regressions linear and significant at *P* < 0.001, *t*-test for correlated samples). Note further that *C. samueli* has a more tapered body shape in lateral profile (e, larger ratio of body depths measured at origin of anal fin and dorsal organ), and a shorter caudal peduncle (f).

a single large foramen for passage of trigeminal-facial-lateralis nerve complex. Supraoccipital with large crest, Posttemporal fossae present between epiotic and pterotic exposing lateral surface of cartilaginous otic capsule. Exoccipital with single large foramen for passage of basicranial nerve complex. Surfaces of dermal and endochondral cranial skeletal bones highly reticulate in mature specimens. Supratemporal laterosensory canal with an inverted L shape, curved at a sharp angle on posterolateral surface of parietal, extending posterior onto epaxial surface of body (Albert, 2001: fig. 19C).

Gill rakers of first arch small, ossified, not contacting gill bars. Pharyngobranchials 2–4 ossified, epibranchials 3–4 forked, not elongate and not contacting fifth epibranchials, ceratobranchials 5 with a small medial process, hypo-

branchials 2 broad at posterior margin, triangular in dorsal view, hypobranchials 3 without medial bridge, basihyal dorsal surface flat with weakly developed posterior ridge, basibranchial 2 arch hourglass-shaped, basibranchials 3–5 unossified, urohyal head broad, urohyal posterior blade unossified (compare with '*Apteronotus*' *macrolepis,* Albert, 2001: fig. 32B). Hypobranchial 2 without median bridge (compare with '*Apteronotus*' *macrolepis,* Albert, 2001: fig. 32B). Posttemporal fused with supracleithrum, three postcleithra, all thin and discoid, mesocoracoid not ossified, anterior coracoid process extending to flexion of ventral cleithral margin. Pectoral fin broad and of moderate size, extending not quite to eye when oriented anteriorly, pale and unpigmented. Males with a shorter relative pectoral-fin length than females (P1/PO = 0.41
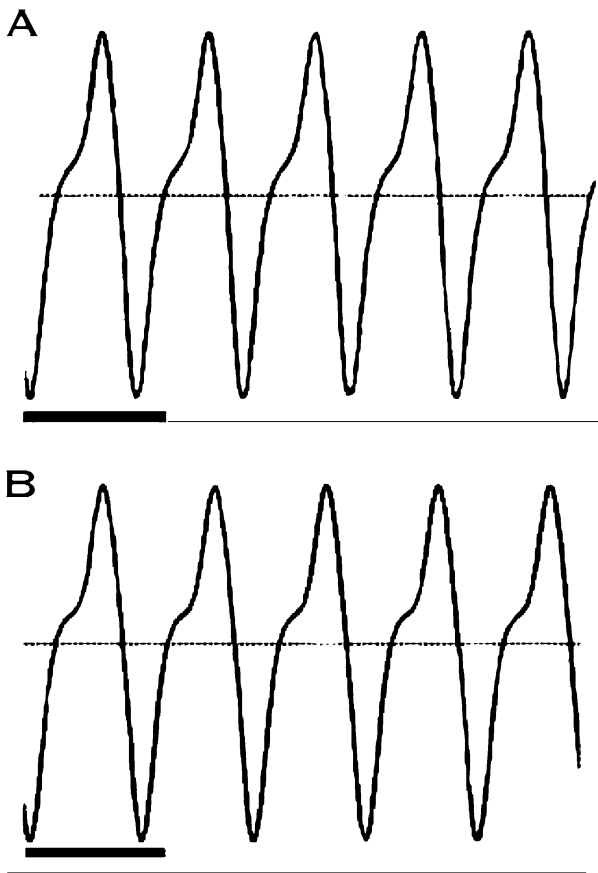
Figure 6 Electric organ discharge (EOD) waveform of *Compsaraia samueli*. (a) Male (holotype) MUSM 26093, 226 mm. (b) Female, MUSM 26094B, 144 mm. Electric organ discharge plotted with head-positivity upwards, voltage on the vertical axis (dashed line = 0 volts) and time on the horizontal axis (scale bar = 1 ms).

[0.36–0.47, n = 7] vs. 0.60 [n = 2]), or than either sex of *C. compsa* (0.58 [0.51–0.64], n = 10, sexes pooled]). Four independently ossified proximal pectoral radials, one fused to base of first pectoral-fin ray. Claustrum absent. Anterior displaced hemal spine large and strongly curved along ventral margin of body cavity, extending to about tip of 3rd rib, its dorsal head more than twice the width of its descending blade. One curved posterior displaced hemal spine. Anal-fin pterygiophores longer than hemal spines at midbody, their descending blades broad and tapered distally forming arrow-head shaped tips along majority of body axis. Body cavity short, with 14 vertebrae (n = 5). Anterior pleural ribs broad and robust, their width more than three times width of posterior ribs, the eight posterior ribs long and narrow. Posterior parapophyses longer than deep, their ventral margins parallel to long axis of body and not abutting along the midline. Parapophyses of last precaudal vertebra broad and squared.

Colour in life. – Ground colour of body semi-translucent white to pale grey on flanks, semi-translucent pink over anal-fin pterygiophores, and darker opaque grey along middorsum. Head and body weakly counter-shaded, grey dorsally and white ventrally. Scales with grey speckling of chromatophores along

trailing margins giving body low contrast mottled appearance; chromatophore density much higher above lateral line. Mid-dorsal area translucent-white along posterior 40% of body in area over dorsal midsaggital organ. Tuberous electroreceptors only readily visible under 5× or more magnification, as small pale spots, with higher densities over rostrum and dorsal surfaces of head and body. Antorbital stripe of pale yellow or white extending obliquely from eye to area between the nasal capsule and dorsal margin of gape, in skin over the infraorbital canal. Pectoral, anal, and caudal-fin membranes transparent, with light grey chromatophore speckling on fin rays. Caudal peduncle dark grey.

Colouration in alcohol. – Much as in life, but with grey pigmentation changed to faded brown and white ground colour changed to pale yellow. In brief: body colouration pale yellow with light brown mottling. Pectoral and anal fins hyaline.

Electric organ discharge. – Known from two sexually mature females and three sexually mature males. Continuous periodic wave-type EOD with biphasic waveform and stable repetition rate of 1242–1396 Hz (Fig. 6). The EOD of *C. samueli* has a harmonic spectral content, with energy concentrated into the fundamental frequency (F_0) and higher harmonics (at integer multiples of F_0). No spontaneous amplitude modulations ('chirps') or other EOD modulations were observed during the recordings. The two female specimens exhibited a lower F_0 (1.242–1.243 kHz) than the three male specimens (1.337, 1.387 and 1.396 kHz). Sexual differences in the EOD waveforms of apteronotid electric fishes are reviewed by Crampton and Albert (2006), with males of several species exhibiting higher fundamental frequencies than females.

Distribution. – Known from the western Amazon River basin of Peru and Brazil. Collection localities are in the Rio Amazonas, near Iquitos, Peru, the Rio Solimões below the confluence of the Rio Purus, Brazil, and the lower Rio Içá of Brazil.

Ecology. – Few specimens of *C. samueli* are known and the ecology of this species is poorly understood. *Compsaraia samueli* has been collected from flooded beaches and deep river channels using deep seines in the Rio Amazonas near its confluence with the Rio Nanay near Iquitos, and from the Rio Içá using trawls (Cox Fernandes, 1995; Cox Fernandes *et al.*, 2004). In the Iquitos region, the type series, which included sexually mature males and females, was collected during the periods of rising and high water (January–April). This corresponds with the typical pattern of apteronotids to breed during the early rising water phase (Crampton, 1996, 1998). Females were clearly identified as mature specimens from swollen ovaries packed with yellow eggs. Males were identified by swollen opaque white testes and sexually dimorphic exaggeration of snout and jaw length. Information on native diet was not available from stomach content analysis because these specimens were kept alive for several days to conduct electric organ discharge recordings.

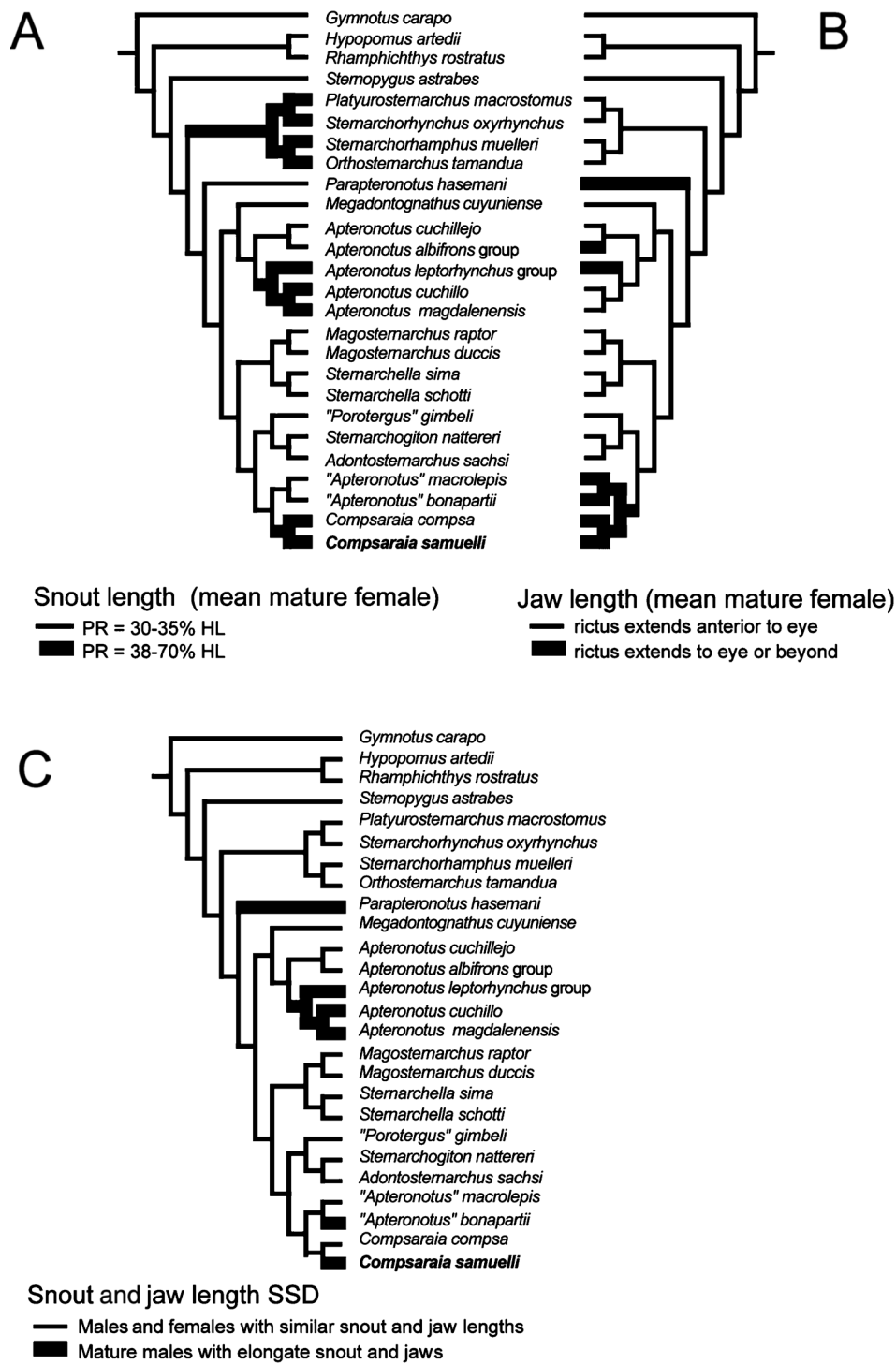*Etymology.* – Patronym in honour of Dr Samuel Albert, who provided the authors with specimens of the type series.

Figure 7 Phylogenetic position of *Compsaraia samueli* (bold) and evolution of snout and jaw morphologies in Apteronotidae. Tree topology from Albert (2001) with addition of *C. samueli* in a unique position of maximum parsimony. Tree from data matrix of 141 characters for 27 taxa (steps = 310, CI = 0.52, RC = 0.36). (a) Snout length (mean mature female). (b) Jaw length (mean mature female). (c) Snout and jaw elongation as a secondary sexual dimorphism (SSD). Note the phylogenetic distributions of snout length, jaw length, and SSD in snout and jaw elongation are different, indicating distinct developmental and genetic bases for these three characters. Note also that SSD in snout and jaw morphologies exactly coincide, suggesting these characters may be functionally and/or developmentally coupled.

Genus	Author	Date	Species			#SSD
			Valid	MS	Total	
Adontosternarchus	Ellis	1912	5	0	5	0
Apteronotus s.s.	Lacépède	1800	18	2	20	6
'Apteronotus' i.c.	–	–	4	2	6	1
Compsaraia	Albert	2001	2	0	2	1
Magosternarchus	Lundberg, Cox & Albert	1996	2	0	2	0
Megadontognathus	Mago-Leccia	1994	2	0	2	?
Orthosternarchus	Ellis	1912	1	0	1	0
Parapteronotus	Albert	2001	1	0	1	1
Pariosternarchus	Albert & Crampton	2006	1	0	1	0
Platyurosternarchus	Mago-Leccia	1994	1	1	2	0
Porotergus	Ellis	1912	3	0	3	0
Sternarchella	Eigenmann	1905	4	2	6	1*
Sternarchogiton	Eigenmann & Ward	1905	4	0	3	1
Sternarchorhamphus	Eigenmann	1905	1	0	1	0
Sternarchorhynchus	Castelnau	1855	10	2	12	1
Tembeassu	Triques	1998	1	0	1	0
Total			60	9	69	11

Table 2 Apteronotid genera with diversity estimates for total numbers of species and those with SSD. Data modified from Albert and Crampton (2005), de Santana and Maldonado-Ocampo (2004), and Lundberg and Cox Fernandes (2007). MS, manuscript names (i.e., undescribed). Taxa arranged alphabetically. *i.c.*, *incertae sedis*; *s.s., sensu stricto*; #SSD, minimum number of species with secondary sexual dimorphism. ?, SSD status uncertain.*, *Sternarchella sima* from the Rio Orinoco (Mago-Leccia, 1994).

Discussion

Comparisons with other apteronotids

Compsaraia samueli is readily distinguished from other apteronotids (except '*A.*' *bonapartii*, *A. leptorhynchus* group and *P. hasemani*) by the presence of SSD snout elongation, in which mature males develop a highly elongate snout and jaws, with lengthening of pre-orbital distance and head length, compared with females or immature specimens at a given body size. This elongation of the snout and jaw in sexually mature males compared with females is manifested in several measurements, including relative head length (HL/LEA = 0.22 [0.19–0.25] vs. 0.15 [0.14–0.17]), snout length (PR/PO = 1.45 [0.93–1.92] vs. 0.39 [0.36–0.43]); eye to anterior nares/PO (1.23 [0.83–1.56] vs. 0.27 [0.21–0.34]); and a longer nasal capsule (inter-narial distance/PO = 0.44 [0.37–0.53] vs. 0.28 [0.24–0.32]).

Compsaraia samueli is further distinguished from other apteronotids (except *A. albifrons* group, *A. leptorhynchus* group, '*A.*' *bonapartii*, '*A.*' *macrolepis*, *C. compsus* and *P. hasemani*) by a large gape in which the rictus is located at about or posterior to a vertical with the eye (vs. anterior to eye; Albert, 2001: figs. 19 and 20). *Compsaraia samueli* is readily distinguished from other apteronotids with SSD in snout length by its overall colour pattern (pale mottled white laterally and grey dorsally in life, pale yellow laterally and light brown dorsally when preserved vs. dark brown laterally and dorsally in *P. hasemani*, '*A.*' *bonapartii*, and *A. leptorhynchus* group) and by the colouration characters used to recognise *Compsaraia* (e.g. pale antorbital stripe, pale inverted L-shaped patch over the supratemporal canal).

Evolution of apteronotid snout and jaw elongation

Snout and jaw elongation in Apteronotidae is polyphyletic, having evolved in at least three developmentally distinct character systems under the functional influences of both trophic and sexual behaviours (Fig. 7). (1) Positive allometric growth before sexual maturity in both sexes of the pre-orbital region of the neurocranium. (2) Positive allometric growth of the jaws. (3) Snout and jaw SSD in sexually mature males in which snout and jaw lengths are isometrically extended by means of hypermorphic growth. In most Gymnotiformes snout growth as a proportion of head length (PR/HL) is negatively allometric (Albert, 2001: 23, fig. 21), such that larger specimens have proportionately shorter snouts. Allometry is departure from geometric similarity, or differences in proportions correlated with changes in size (Gould, 1966).

Among gymnotiforms, only *C. samueli* and species of the *A. leptorhynchus* group exhibit the simultaneous presence of all three of these characters. The identical phylogenetic distributions of SSD in snout and jaw elongation suggest that these two phenotypes may be developmentally coupled; i.e. the presence of large jaws and long snouts have independent histories, while SSD in jaw and snout length are functionally and/or developmentally coupled.

A summary of apteronotid genera with known instances of SSD in any phenotype (snout, jaw, or otherwise) is provided in Table 2. An elongate snout is present in both sexes of the two species of *Compsaraia*, in a clade composed of species in the *A. leptorhynchus* group + *A. cuchillo* + *A. magdalenensis*, and in the Sternarchorhynchinae. An elongate set of jaws, in which the rictus extends to or beyond a vertical with the eye,

is present in a clade composed of *Compsaraia* + '*A.*' *bona-partii* + '*A.*' *macrolepis*, in the *A. leptorhynchus* group, in the *A. albifrons* group, and in *P. hasemani*. Snout and jaw SSD is present in yet another distinct set of taxa; in *C. samueli*, in '*A.*' *bonapartii*, in the *A. leptorhynchus* group and in *P. hasemani*. The snout lengths of species in the *A. albifrons* group are not here regarded to be instances of SSD because both sexes have a mean snout length of about 33% head length (which is the plesiomorphic gymnotiform condition; Albert, 2001), and be-cause standard deviations in snout length are larger than the differences between the mean values of the sexes (De Santana, 2003: 4, table 1). At least two apteronotid species (*Sternarcho-rhynchus roseni* and *Sternarchogiton nattereri*) possess SSD in the presence of external dentition (i.e. teeth distributed over the outer surface of the jaws; Mago-Leccia, 1994; Rapp Py-Daniel & Cox Fernandes, 2005). Secondary sexual dimorphism in body size or snout length has not been observed in *C. compsa* from the Orinoco basin (124 specimens in 14 lots examined, collections at low water November–February), or from *C. cf. compsa* from the Amazon basin (20 specimens in 8 lots, collec-tion dates in February, March, July, October and November).

The qualitative results of this analysis tracing SSD char-acter history on the apteronotid tree topology of Albert (2001) are similar to the results of tracing the same characters on the apteronotid tree topology of Triques (2005). Triques (2005) ex-amined 127 morphological characters among 37 apteronotid species. The tree topology of Triques (2005) is partially similar to that of Albert (2001) in terms of the relationships among the terminal taxa, and recovered little resolution among the basal nodes. The tree topologies of Albert (2001) and Triques (2005) differ at two nodes. Importantly, the phylogenetic distribution of snout elongation, jaw elongation, and SSD in snout and jaw length are disassociated on both these tree topologies, and these characters exhibit mosaic patterns of evolution.

Functions of apteronotid snout and jaw elongation

Observations on the morphology and behaviour of *C. samueli* suggest that the primary functional role of SSD in snout length is male aggression. As in many apteronotid species sexually mature individuals in both sexes of *C. samueli* are highly ag-gressive and prone to fight when kept together in small (40 gallon) aquaria (JSA pers. obs.; E. Panduro, pers. comm.). Adult males spar with repeated aggressive non-contact pos-tures when introduced to a common tank, and the aggression usually escalates to biting and jaw-locking within minutes. In another apteronotid species, *A. leptorhynchus* (the brown ghost knifefish) with non-homologous snout and jaw SSD, sexually mature males use their elongate jaws in male–male agonistic displays and jaw-locking behaviours, which are ac-companied by agonistic electric signal displays (Tallarovic & Zakon, 2005). Jaw-locking behaviours have evolved in a vari-ety of teleost species with disparate taxonomic backgrounds (e.g. ictalurid catfishes, anabantoids, cichlids, gobiids) where it is often used by sexually mature males to assess dominance in competing for nest sites and/or females (Figler & Klauenberg, 1980; Neat, 1998; Hendrickson *et al.*, 2001; Gaisner, 2005). In *C. samueli* this behaviour is associated with the formation of a deep and robust middle portion of the frontal bone in

sexually mature males, which in the region above the ethmoid cartilage is more than twice its depth above the orbit (Figs 3 and 4). Further, the jaws are more robust in sexually mature males, with a larger maxilla and dentary. An alternative or additional hypothesis is that SSD in snout length is a trophic specialisation. The latter hypothesis is amenable to evaluation by detailed studies of trophic ecology.

The phylogenetic history of snout and jaw characters within the Apteronotidae suggests a complex history in which developmental elongation of the pre-orbital region occurs in at least three distinct ecophenotypic circumstances (Albert, 2001). The first circumstance is snout elongation accompanied by a relatively small, terminal mouth, as occurs in *Sternarch-orhynchus* and in S*ternarchorhamphus* + *Orthosternarchus*, where it is used for grasp-suction feeding in submerged ve-getation and benthic riverine environments (Marrero & Wine-miller, 1993). The second circumstance is allometric elong-ation of the entire pre-otic portion of the neurocranium (i.e. the sphenoid and pre-orbital regions) accompanied by a small mouth. This suite of phenotypes is unique to a clade of geographically isolated trans-Andean species (*A. cuchillo* + *A. magdalenensis*), where at least in *A. magdalenensis* it functions in benthic probing in deep river channels (WGRC, pers. obs.). The third circumstance is elongation of the jaws accompanied by pre-orbital cranial elongation, where the primary function is social, mainly in male–male aggression, but possibly also in male–female interactions. Elongation of the jaws is the most phylogenetically plastic form of snout elongation in the Apteronotidae, being observed in at least four clades; the *A. leptorhynchus* group, '*A.*' *bonapartii*', *P. hasemani* and *Compsaraia*. The presence of large jaws and an elongate snout in both sexes of *Compsaraia* suggests that these features also function to aid in specialised trophic behaviours.

References

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

ALBERT, J.S. 2003. Family Apterontoidae. In: REIS R.E., KULLANDER S.O. & FERRARIS C. J., JR., Eds., *Checklist of the Freshwater Fishes of South and Central America*. Edipucrs, Porto Alegre, pp. 503–508.

ALBERT, J.S. & CRAMPTON, W.G.R. 2005. Diversity and phylogeny of Neotropical electric fishes (Gymnotiformes). In: BULLOCK T.H., HOPKINS C. D., POPPER A. N. & FAY R. R., Eds., *Electroreception. Springer Handbook of Auditory Research*, Volume 21 (R.R. Fay & A. N. Popper, eds.), pp. 360–409, Springer, New York.

ALBERT, J.S. & CRAMPTON, W.G.R. 2006. *Pariosternarchus amazon-ensis*: a new genus and species of Neotropical electric fish (Gymnotiformes: Apteronotidae) from the Amazon River. *Ich-thyological Explorations Freshwaters* **17**(3), 267–274.

ALBERT, J. S. & FINK, W.L. 1996. *Sternopygus xingu,* a new species of electric fish (Gymnotoidei, Teleostei) from South America, with comments on the phylogenetic position of *Sternopygus. Copeia* **1996**(1), 85–102.

CAMPOS-DA-PAZ, R. 2005. Previously undescribed dental arrangement among electric knifefishes, with comments on the taxonomic and conservation status of *Tembeassu marauna* Triques (Otophysi: Gymnotiformes: Apteronotidae). *Neotropical Ichthyology* **3**(3), 395–400.

COX FERNANDES, C. 1995. Diversity, distribution and community structure of electric fishes (Gymnotiformes) in the channels of the Amazon River System, Brazil. Unpubl. Ph.D. thesis, Duke University, 394 pp.

COX FERNANDES, C. 1998. Sex-related morphological variation in two species of apteronotid fishes (Gymnotiformes) from the Amazon river basin. *Copeia* **1998**, 730–735.

COX FERNANDES, C., LUNDBERG, J.G. & RIGINOS, C. 2002. Largest of all electric-fish snouts: hypermorphic facial growth in *Apteronotus hasemani* and the identity of *Apteronotus anas* (Gymnotiformes: Apteronotidae). *Copeia* **2002**, 52–61.

COX FERNANDES, C., PODOS, J. & LUNDBERG, J.G. 2004. Amazonian ecology: tributaries enhance the diversity of electric fishes. *Science* **305**, 1960–1962.

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

CRAMPTON, W.G.R. 1998. Effects of anoxia on the distribution, respiratory strategies and electric signal diversity of gymnotiform fishes. *Journal of Fish Biology* **53** (Supplement A), 307–330.

CRAMPTON, W.G.R. & ALBERT, J.S. 2006. Evolution of electric signal diversity in gymnotiform fishes. In: LADICH F., COLLIN S.P., MOLLER P. & KAPOOR B.G., Eds., *Communication in Fishes.* Science Publishers Inc., Enfield, NH, pp. 641–725.

CRAMPTON, W.G.R., THORSEN, D.H. & ALBERT, J.S. 2004. Three new species from a diverse, sympatric assemblage of the electric fish *Gymnotus* (Gymnotiformes, Gymnotidae) in the lowland Amazon basin, with notes on ecology. *Copeia* **2004**, 82–99.

DE SANTANA, C.D. 2003. *Apteronotus caudimaculosus* n. sp. (Gymnotiformes: Apteronotidae), 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, C.D. & CRAMPTON, W.G.R. 2006. *Sternarchorhynchus curumim* (Gymnotiformes: Apteronotidae), a new species of tube-snouted ghost electric knifefish from the lowland Amazon basin, Brazil. *Zootaxa* **1166**, 57–68.

DE SANTANA, C.D. & MALDONADO-OCAMPO, J.A. 2004. Redescription of *Apteronotus mariae* (Eigenmann AND Fisher, 1914) and the taxonomic status of *Apteronotus jurubidae* (Fowler, 1944) (Gymnotiformes: Apteronotidae). *Zootaxa* **632**, 1–14.

DE SANTANA, C.D. & MALDONADO-OCAMPO, J.A. 2005. *Apteronotus milesi*, new species of ghost knifefish (Gymnotiformes: Apteronotidae) from the Cauca River, with a key to apteronotids from the Magdalena-Cauca basin, Colombia. *Ichthyological Exploration of Freshwaters* **16**(3), 223–230.

DE SANTANA, C.D. & NOGUEIRA, A. 2006. Two new species of *Sternarchorhynchus* Castelnau from the Amazon Basin, Brazil (Gymnotiformes: Apteronotidae). *Ichthyological Exploration of Freshwaters* **17**(1), 85–92.

DE SANTANA, C.D. & TAPHORN, D.C. 2006. *Sternarchorhynchus gnomus*, a new species of electric knifefish from the Lower Rio Caroni, Venezuela (Gymnotiformes: Apteronotidae). *Ichthyological Exploration of Freshwaters* **17**(1), 1–8.

DE SANTANA, C.D., MALDONADO-OCAMPO, J.A. & CRAMPTON, W.G.R. 2007. *Apteronotus galvisi*, a new species of electric ghost knifefish from the Rio Meta basin, Colombia (Gymnotiformes: Apteronotidae). *Ichthyological Exploration of Freshwaters* **18**(2), 117–124.

DE SANTANA, C.D., MALDONADO-OCAMPO, J.A., SEVERI, W. & MENDES, G.N. 2004. *Apteronotus eschmeyeri*, a new species of ghost knifefish from the Magdalena Basin, Colombia (Gymnotiformes: Apteronotidae). *Zootaxa* **410**, 1–11.

FIGLER, M.H. & KLAUENBERG, B.J. 1980. Pentobarbital sodium and attack behavior in male Siamese fighting fish. *Psychopharmacology* **69**(2), 207–208.

FINK, S.V. & FINK, W.L. 1981. Interrelationships of the ostariophysan fishes (Teleostei). *Zoological Journal of the Linnean Society* **72**(4), 297–353.

GAISNER, A. 2005. Parental care and reproductive behavior of the clown goby, *Microgobius gulosus*, with observations on predator interactions, *Environmental Biology of Fishes* **73**(4), 341–356.

GOULD, S.J. 1966. Allometry and size in ontogeny and phylogeny. *Biological Review* **41**, 587–640.

HENDRICKSON, D.A., KREJCA, J.K. & RODRIGUEZ MARTINEZ, J.M. 2001. Mexican blindcats Genus *Prietella* (Siluriformes: Ictaluridae): an overview of recent explorations. *Environmental Biology of Fishes* **62**(1–3), 315–337.

HILTON, E. & COX FERNANDES, C.C. 2006. Sexual dimorphism in '*Apteronotus*' *bonapartii* (Castelnau, 1855) (Gymnotiformes: Apteronotidae). *Copeia* **2006**, 826–833.

LEVITON, A.E., GIBBS, JR., R.H., HEAL, E. & DAWSON, C.E. 1985. Standards in herpetology and ichthyology: Part I. Standard symbolic codes for institutional resource collections in herpetology and ichthyology. *Copeia* **1985**, 802–832.

LUNDBERG, J.G., LEWIS, W.M., SAUNDERS, J.F. & MAGO-LECCIA, F. 1987. A major food web component in the Orinoco River channel: evidence from planktivorous electric fishes. *Science* **237**, 81–83.

LUNDBERG, J.G. & COX FERNANDES, C. 2007. A new species of South American ghost knifefish (Apteronotidae: *Adontosternarchus*) from the Amazon Basin. *Proceedings of the Academy of Natural Sciences of Philadelphia* **156**, 27–37.

MADDISON, W.P. & MADDISON, D.R. 2000. *MacClade, Analysis of Phylogeny and Character Evolution, version 4.0*, Sunderland, Sunderland Associates, Inc. Massachusetts.

MAGO-LECCIA, F. 1994. *Electric Fishes of the Continental Waters of America*. Peces Eléctricos de las aguas continentales de América. Biblioteca de la Academia de Ciencias Fisicas, Matematicas, y Naturales, Caracas, Venezuela 29, 1–206.

MARRERO, C. & WINEMILLER, K.O. 1993. Tube-snouted gymnotiform and mormyriform fishes – convergence of a specialized foraging mode in teleosts. *Environmental Biology of Fishes* **38**, 299–309.

NEAT, F.C. 1998. Mouth morphology, testes size and body size in male *Tilapia zillii*: implications for fighting and assessment. *Journal of Fish Biology* **53**(4), 890–892.

RAPP PY-DANIEL, L. & COX-FERNANDES, C. 2005. Dimorfismo sexual em Siluriformes e Gymnotiformes (Ostariophysi) da Amazonia. *Acta Amazonica* **35**(1), 97–110.

TALLAROVIC, S.K. & ZAKON, H.H. 2005. Electric organ discharge frequency jamming during social interactions in brown ghost knifefish, *Apteronotus leptorhynchus. Animal Behaviour* **70**, 1355–1365.

TAYLOR, W.R. & VAN DYKE, G.C. 1985. Revised procedures for staining and clearing small fishes and other vertebrates for bone and cartilage study. *Cybium* **9**(2), 107–119.

TRIQUES, M.L. 1998. *Tembeassu marauna*, a new genus and species of electrogenic neotropical fish (Ostariophysi: Gymnotiformes: Apteronotidae). *Revue Français d'Aquariologie* **25**, 1–22.

TRIQUES, M.L. 2005. Analise cladistica dos caracteres de anatomica externa e esqueletica de Apteronotidae (Teleostei: Gymnotiformes). *Lundiana* **6**(2), 21–149.

WEITZMAN, S.H. 1962. The osteology of *Brycon meeki*, a generalized characid fish, with an osteological definition of the family. *Stanford Ichthyological Bulletin* **8**(1), 1–77.

WINEMILLER, K.O. & ADITE, A. 1997. Convergent evolution of weakly electric fishes from floodplain habitats in Africa and South America. *Environmental Biology of Fishes* **49**, 175–186.