



Cranial morphology and osteology of the sexually dimorphic electric fish, *Compsaraia samueli* Albert & Crampton (Apteronotidae, Gymnotiformes), with comparisons to *C. compsa* (Mago-Leccia)

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Abstract

Sexual dimorphism of the snout has evolved independently in at least four separate clades of the gymnotiform family Apteronotidae. This phenomenon may help identify sex, except in the absence of mature individuals, and has led to confused taxonomy for several species. We examined a large collection of *Compsaraia samueli* collected during the breeding season from a remote stream in the Rio Negro drainage. This collection contains a wide range of sizes of both sexes, but most individuals were easily identified as mature. To quantify the sexual dimorphism of these specimens, 15 measurements were taken from the head and the body. In addition, some specimens were cleared-and-stained to study cranial osteology. We found that long-snouted males of *C. samueli* span a wide range of body sizes. As the snout length increases the distance between the eye and the occiput does not increase at the same rate, suggesting that it is only the anterior portion of the head that has an increased allometry. Skeletal anatomy differs between the sexes in that the lower jaw is more triangular in females and more linear in males. The coronomeckelian is small and round in females in contrast to being longer and pointed in males. There is strong interlacing of the dentary and anguloarticular bones in males, whereas this contact is not as extensive in females. We also discuss the implications of sexual dimorphism for identification of this species relative to its congener (*C. compsa*), and for the evolution of sexual dimorphism in the family.

Key words: Rio Negro, suspensorium, biodiversity, morphometrics, Apteronotidae, Gymnotiformes, osteology, dimorphism

Introduction

Sexual dimorphism encompasses secondary sexual characteristics that differ between males and females of a species, including variation in behavior, life history, and morphology, and is a primary source of morphological variation (Grande, 2004; Hilton & Bemis, 2012). Morphological sexual dimorphism has been studied extensively in fishes, such as for the caudal-fin extension in Poeciliidae (Basolo, 1990), and for the nuptial tubercles (Lachner, 1952) and body size (Pyrn, 1996) in cyprinids. Sexually dimorphic traits were a primary source for Darwin's (1859, 1871) ideas on sexual selection, and are typically expressed in reproductive contexts such as male-male combat and sexual ornamentation and display. In general, sexual dimorphism may develop from intrasexual and intersexual selection, variance within reproductive roles, and sex-specific ecological processes (Schultz, 1993). These processes can enhance phenotypic diversity and may lead to interspecific trait overlap, which sometimes can make taxonomic identification difficult in certain groups.

One group of Neotropical freshwater fishes in which sexual dimorphism is common is the Apteronotidae, the most species-rich family in the order Gymnotiformes (Neotropical weakly electric knifefishes). Sexual dimorphism in Apteronotidae manifests itself in a diversity of forms. For example, male *Sternarchogiton nattereri* (Steindachner) (a senior synonym of *Oedemognathus exodon* Myers) and some species of *Sternarchorhynchus* Castelnau develop teeth on the external surface of the jaw (Cox Fernandes *et al.*, 2009; Rapp Py-Daniel & Cox

Fernandes, 2005). *Sternarchella orinoco* Mago-Leccia develops cranial dimorphisms at maturity, at which point females have bulkier heads and larger interocular distances than their male counterparts (Mago-Leccia, 1994). Other examples include males of *Paraapteronotus hasemani* (Ellis) (Cox Fernandes, 1998; Cox Fernandes *et al.*, 2002), *Apteronotus rostratus* (Meek & Hildebrand) (Hagedorn & Heiligenberg, 1985), '*A. bonapartii*' (Castelnau) (Hilton & Cox Fernandes, 2006, 2017), and *Compsaraia* Albert (Albert & Crampton, 2009), which may possess elongate lower jaws and snouts. In one such case, male *Paraapteronotus hasemani* with long snouts were originally described as *Apteronotus anas* Eigenmann & Allen (Cox Fernandes *et al.*, 2002). *Oedomognathus exodon* was shown to be synonymous with *Sternarchogiton nattereri*; the former encompassing sexually dimorphic males of *S. nattereri*, with external teeth (de Santana & Crampton, 2007; Cox Fernandes *et al.*, 2009). Sexually dimorphic characters have not only led to problems in identifying species but have also hindered the correct identification of males and females within some species. In *C. samueli* Albert & Crampton, mature males are reported to grow elongated snouts of varying length (Albert & Crampton, 2009). *Compsaraia samueli* is similar morphologically to its sympatric sister species *C. compsa* (Mago-Leccia), which is not sexually dimorphic (Albert & Crampton, 2009). In the original description of *C. samueli*, of the specimens that were sexed, four were reported as females and seven as males. Albert & Crampton (2009) illustrated the osteology of a female and male, but their report did not capture the full range of variation in this species' anatomy.

A better understanding of the diversity of *Compsaraia* requires a more comprehensive study of sexual dimorphism. In the present study we aim to better document intraspecific variation related to sexual dimorphism in *Compsaraia*, using a large sample size of mature animals. Our analyses were conducted on specimens of both *C. samueli* and *C. compsa* collected during the breeding season in a remote secondary tributary of the Rio Negro (Fig. 1). This sample contains a wide range of sizes of both species and both sexes at maturity. Our goals are to (1) quantify facial variation in both sexes, (2) illustrate variation in cranial osteology, and (3) discuss implications of our findings for the evolution of sexual dimorphism.

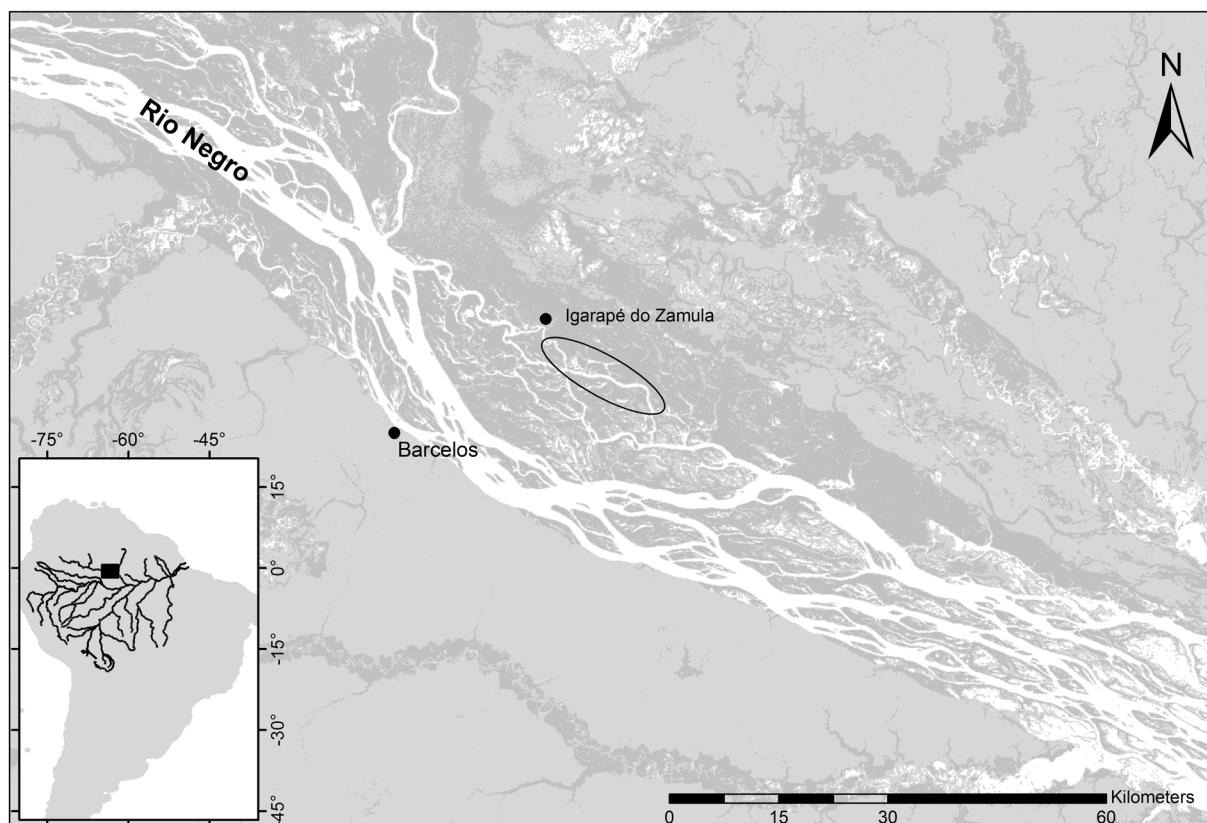


FIGURE 1. Map of the Rio Negro area, the black ellipse indicates the approximate geographic location of sampling near the mouth of the Igarapé do Zamula (0°50'24"S, 62°45'67"W). The dark gray areas represent the floodplain and the white represents open water. The map is the adaptation of the eight bit L-band radar images acquired in April of 1996 from Japanese Earth Resources Satellite 1 (JERS-1) with a spatial resolution of ~90 m (NASDA, 1993).

Materials and methods

In April 2002, Dr. Labbish Chao and his research group at the Universidade Federal do Amazonas collected individuals of *Compsaraia samueli* and *C. compsa* with trawl nets. The specimens (Fig. 2) were captured close to the mouth of the Igarapé do Zamula, a tributary of the Rio Negro drainage near Barcelos, Amazonas State, Brazil (0°50'24"S, 62°45'67"W). This portion of the basin has several islands and canals that inundate annually. Water levels can vary 5 m between wet and dry seasons (Chao, 2001). The black water of this area exhibited the following mean year parameters: 4.9 pH, 12 mS.cm⁻¹ conductivity, 1.0–1.6 m water transparency, 29°C, 4.5 mg.l⁻¹ dissolved oxygen near the surface and 3.8 mg.l⁻¹ at the bottom. The depth of the canals during the samples varied between 8–14 m. All specimens studied are listed in Appendix 1. All individuals in our study were in advanced stages of maturity. Females were easily identified by large eggs visible without dissection through the abdominal cavity. Males were identified through dissections to determine presence of well-developed testes. Only two immature individuals were found in our sample.

Forty-three males and 33 females of *C. samueli*, and 18 males, 21 females, and 2 immature specimens of *C. compsa* were measured following Cox Fernandes (1998) and Hilton & Cox Fernandes (2017) using digital calipers to the nearest 0.01 mm: total length (TL); length from tip of the snout to end of anal fin (LEA); length from tip of snout to origin of dorsal filament (LOD); depth of abdominal cavity (AB); head length from tip of upper jaw to the posterior edge of opercle (H); head depth at occiput (SV); snout length (S); distance from tip of snout to the posterior edge of the occiput (SS); tip of mandible to rictus (M); distance from snout to origin of anal fin (SA); distance from anterior edge of the eye to posterior naris (NE); distance between the anterior and posterior naris (ID), eye diameter (ED), distance from posterior edge of eye to opercle (EO) and interorbital (IO).

Six specimens of *C. samueli* (three females and three males) and two specimens of *C. compsa* (one male and one female) were cleared and double-stained for bone and cartilage (Dingerkus & Uhler, 1977) and examined with a Wild M5 dissecting microscope. Final illustrations were made in Adobe Illustrator software based on images taken on a Zeiss Discovery v20 using an AxioCam high-resolution camera. Terminology for skeleton elements follows Hilton *et al.* (2007) and Hilton & Cox Fernandes (2006, 2017).

Results

Morphometric Analysis. In our sample, mature males and mature females of *C. samueli* overlap in snout/head vs. snout to end of anal fin (LEA) up to 120 mm. A histogram outlining the number of individuals at certain sizes (LEA) was unimodal, suggesting a lack of age classes (Fig. 3). After 120 mm, the growth trajectory for the snout of some males diverge from the trajectory of smaller males and females (Fig. 4). Overall, females tend to be smaller than males and have shorter snouts (Fig. 4). With increasing snout lengths, the distance between eye and opercle does not increase in the same proportion (Fig. 5). Large males show strong positive allometry ($r^2 = 0.836$) and variability of facial dimensions, whereas females show a positive isometry ($r^2 = 0.642$) similar to that of small males (<120 mm) (Fig. 5). In contrast, mature males and females of *C. compsa* were not seen to exhibit any difference of snout/head vs. snout to end of anal fin (LEA) related to sex (Fig. 6).

Cranial Osteology. For *C. samueli*, we compared female specimens with males with both elongate and shorter snouts, matched in size to some female specimens (Fig. 7). In both sexes, the hyomandibular, symplectic, quadrate, metapterygoid, and opercular elements are similarly shaped between the sexes. The opercle is slightly smaller in males, which aligns with our morphometric analysis above (Fig. 5). The endopterygoid and the associated *pars autopalatina* are elongated anterior to the quadrate in males. The *pars autopalatina* curves ventrally in the female, but projects straight anteriorly in the males. Both sexes have four small, conical teeth on the premaxilla and an edentulous maxilla. Although the premaxilla is similar between males and females, the posterior maxillary process of both males is relatively longer and narrower than that of the female.

The dorsal profile of the female lower jaw is markedly triangular in contrast to that of both long and short-snouted males, which have more linear lower jaws. The ventral margin of the lower jaw is straight to concave in the female, whereas the ventral margin in the males is convex. Further, the anguloarticular of the female spans from the anterior edge of the retroarticular to slightly beyond the anterior margin of the quadrate and its dorsal margin does not bow upwards. The anguloarticular of the male reaches from the anterior margin of the retroarticular to well past

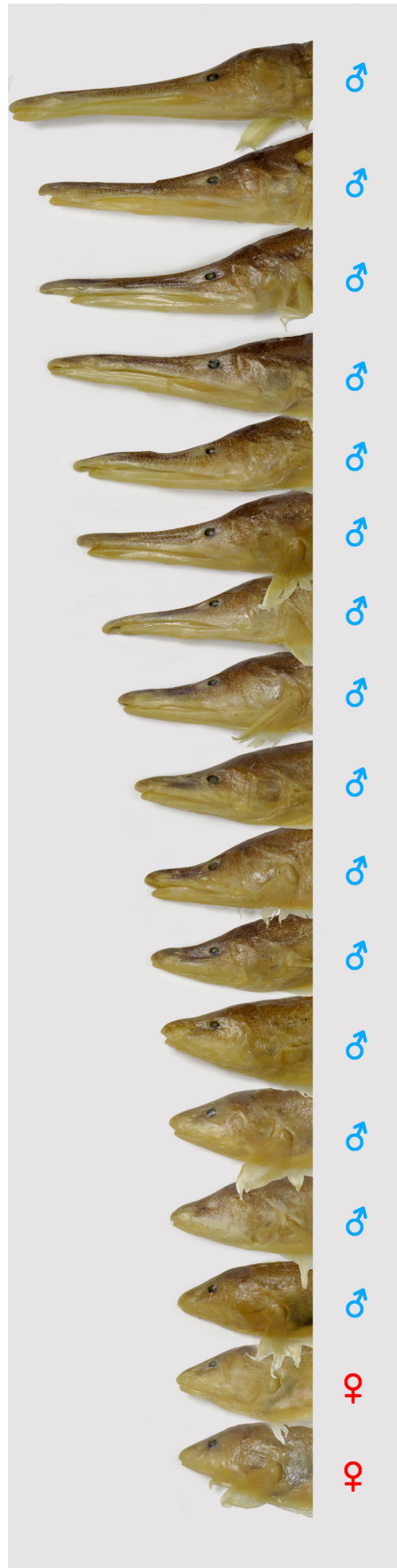


FIGURE 2. Head and pectoral regions of *C. samueli* (92.6–200.2 mm TL), showing the variation of snout length among 2 females and 15 males.

the quadrate and its dorsal margin is slightly curved. Both forms of males show strong interlacing of the dentary and anguloarticular; this is less pronounced in females. In males, thin elongate projections of bone from the dentary and anguloarticular fit together and overlap at their intersection; in the longer snouted male, gaps appear between these bones. Meckel's cartilage attaches in similar places on the dentary and anguloarticular in both sexes. The coronomeckelian is larger in both males than in the female, especially the thin lamella that sits between Meckel's cartilage and the bones of the lower jaw. In both males, this section is shaped like a posteriorly-facing arrowhead. In the female the coronomeckelian is small and circular. The retroarticular in males is slightly longer posteriorly and more rounded than in females. Both sexes have two rows of 12 small, conical teeth on the dentary, although they are angled more medially in the female than in the male. Both cleared and stained specimens of *C. compsa* (a male and female) that were examined have a lower jaw morphology that is similar to that of the female *C. samueli* (i.e., a triangular dorsal margin formed by the anguloarticular and dentary).

In general, mature male *Compsaraia samueli* share a similar cranial osteology, whether they have a long or a short snout, and there are only few differences between the two forms. The posterior process of the maxilla of the long-snouted male is relatively linear compared to the more curving posterior process of the short-snouted male. There is a distinct gap between the dentary and anguloarticular of the long-snouted male, but not in the short-snouted male. These differences most likely relate to the increased snout elongation in this individual.

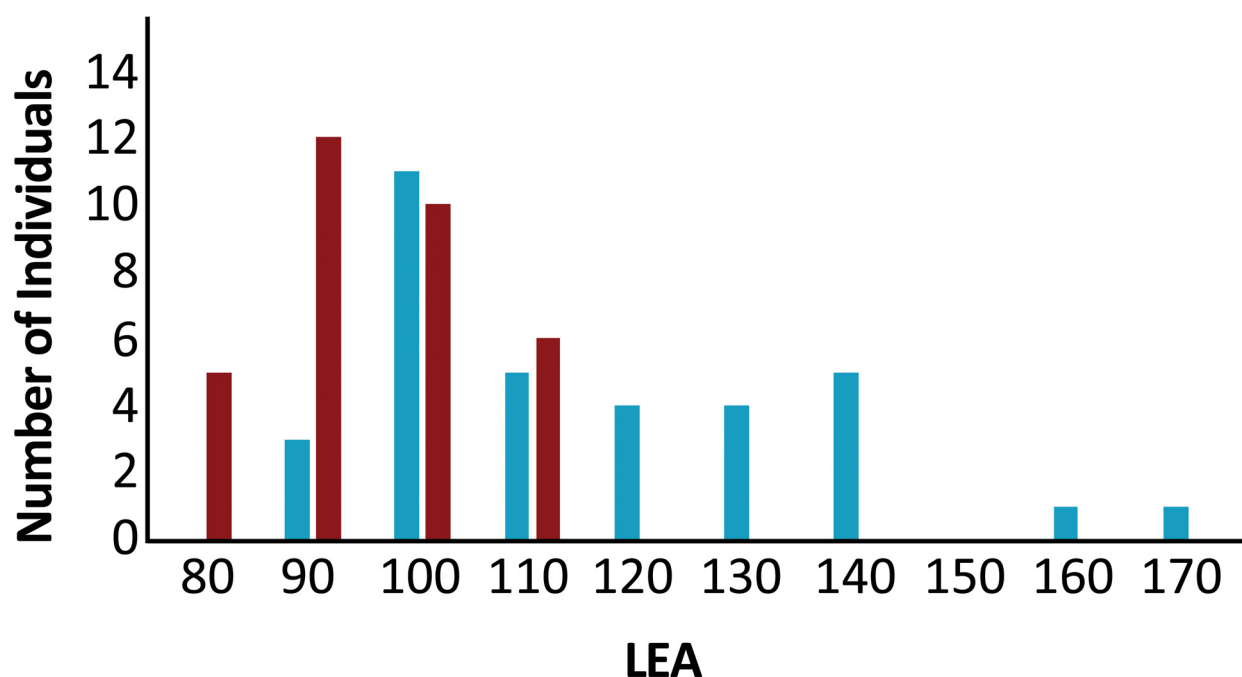


FIGURE 3. A histogram showing the number of individuals of *C. samueli* in our sample between certain size classes. Red bars are females, blue bars are males.

Discussion

Our results show that sexual dimorphism in *C. samueli* is tied to body length (LEA) and skull configuration. More precisely, we found that after a certain size (120 mm), mature males show more variation in snout length/head length compared to smaller males and females. We also found evidence of allometry between snout length (S) and the length of the posterior portion of the head (EO), especially in long-snouted males. Based on our analysis of skull osteology, short-snouted and long-snouted males are morphologically more similar to each other than to females. By extension, we discovered that mature males and females of *C. samueli* can easily be identified by skull anatomy, particularly in the overall shape of the lower jaw, coronomeckelian, and the *pars autopalatina* of the palatoquadrate cartilage.

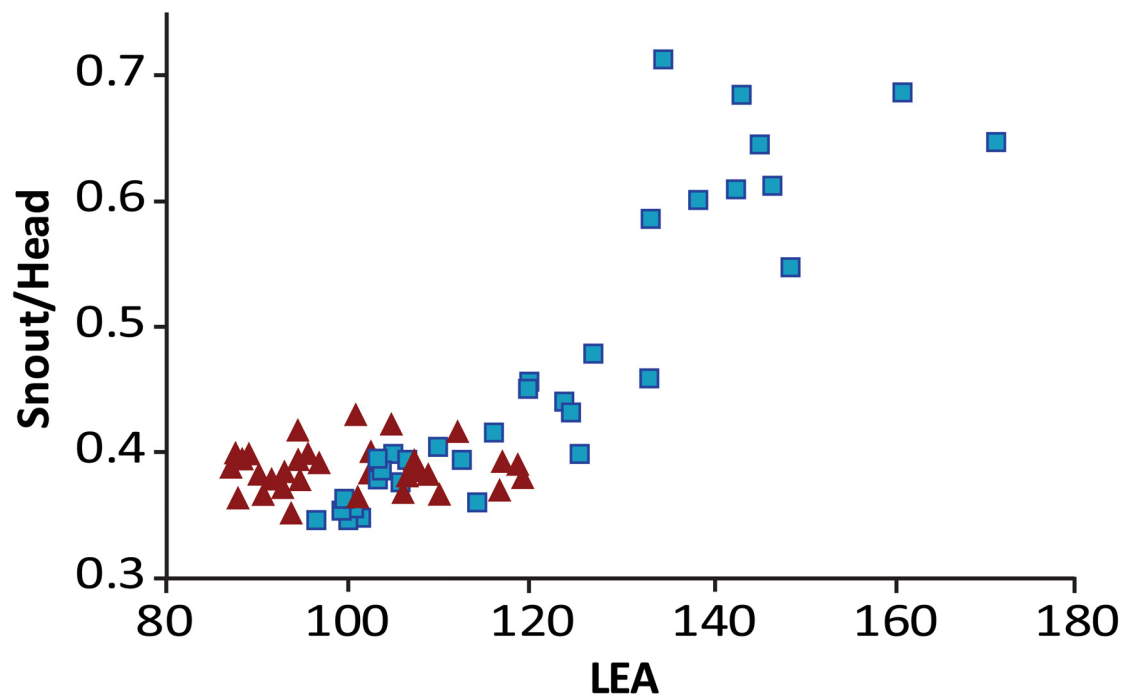


FIGURE 4. Scatterplot of length from the snout to end of anal fin (LEA) versus snout size relative to head size for *C. samueli* illustrating the relatively longer snout of mature males > 120 mm in LEA compared to mature males < 120 mm and the variability of snout/head within males of relatively the same size. In overall size, *C. samueli* mature females tend to be shorter than mature males. Red triangles are females (n=33), blue squares are males (n=43).

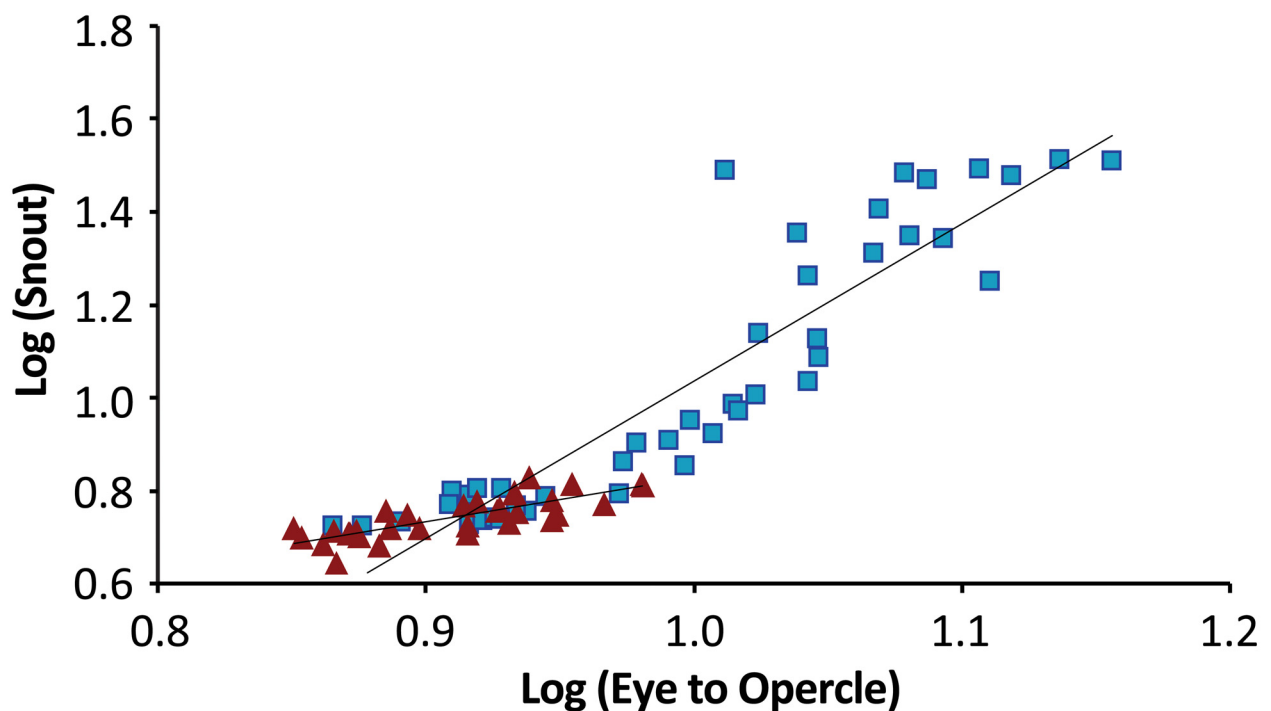


FIGURE 5. Scatterplot of log distance from eye to opercle versus log snout length for *C. samueli*, with least squared regression lines fitted separately to 33 mature females and 43 mature males. The curves were fitted by: (blue squares = males) $y = 2.35 + 3.38x$; (red triangles=females) $y = 0.11 + 0.94x$. Note that the variables are not increasing at the same rate.

Our study reinforces the importance of quantifying sexual dimorphism in apteronotid fishes, especially in their osteology. The extreme variability we see in male *C. samueli* may have led to the misidentification in Albert & Crampton (2009: fig. 4), in which a short-snouted male *C. samueli* was apparently mislabeled as a female. In that figure, the putative female has a linear dentary, straightened *pars autopalatina*, and a dentary-anguloarticular suture well anterior to the anterior margin of the quadrate. Based on our study, this fish can be identified as a short-snouted male. It is important to recognize that apteronotids are highly variable in their morphology. Small sample sizes can thus mask important information about sexually dimorphic features.

Another potential source of misidentification with this group is the similar appearance of *C. samueli* and *C. compsa*. In our study, both species were collected in the same habitat and experience similar environmental pressures. Both species were collected in advanced reproductive stages at the end of the rainy season (April). Since both species are primarily diagnosed from each other based on the number caudal-fin rays and caudal-peduncle length (Albert & Crampton, 2009), *C. samueli* and *C. compsa* can look nearly identical if their caudal fin and peduncle are damaged, which is a common situation in these fishes. If *C. samueli* males have a short snout, it is difficult to distinguish the two species. Unlike *C. samueli*, however, *C. compsa* does not exhibit sexual dimorphism despite occurring sympatrically and belonging to the same genus. One measurement that helps to distinguish females of *C. samueli* from females and males of *C. compsa* is the interorbital distance, which tends to be larger in *C. samueli* females when compared to other specimens of the same size (Fig. 8). Also, in our sample, female *C. samueli*, tend to have a smaller maximum LEA than all others. We are not aware of EOD information available for *C. compsa*. More osteological work for *C. compsa* is needed to identify any additional differences within the skeletons of these sister species. In addition, the newly described *Melanosternarchus amaru* Bernt, Crampton, Orfinger & Albert is now considered sister to the genus *Compsaraia* and appears similar but can be distinguished from *Compsaraia* by the morphology of its lateral-line canal and melanophore density (Bernt *et al.*, 2018). It is not known to be sexually dimorphic.

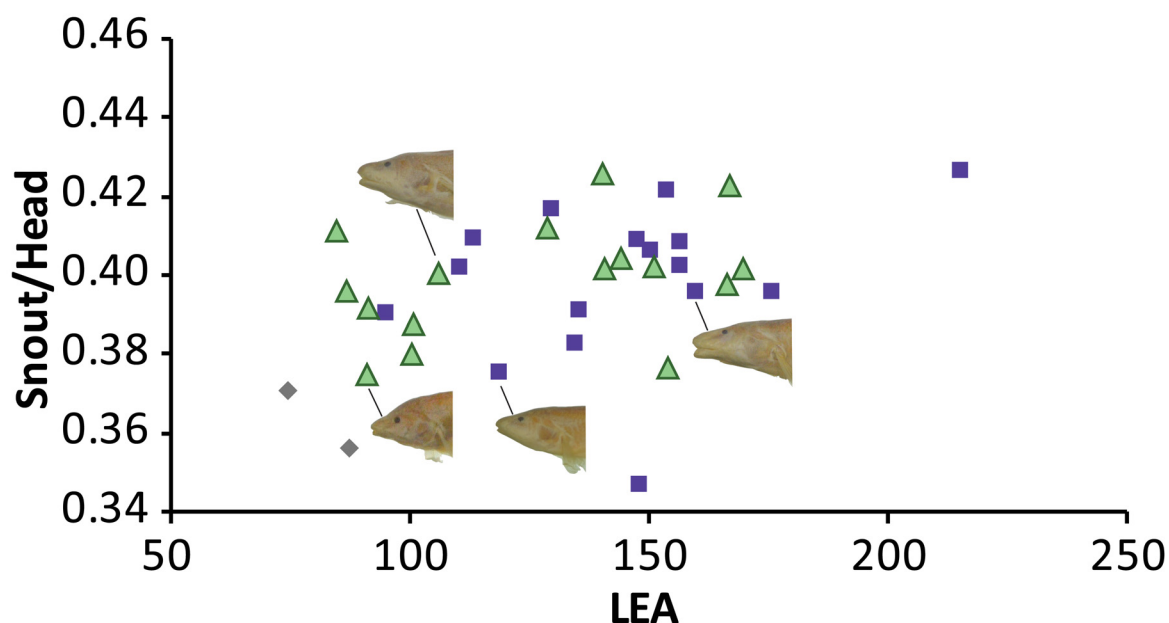


FIGURE 6. Scatterplot of length from the snout to end of anal fin (LEA) versus snout size relative to head size of *C. compsa*. Green triangles are females (n=21), purple squares are males (n=18), and gray diamonds are immature (n=2). Headshots of four individuals (INPA 27587, INPA 27488, INPA 27589, INPA 27591) are associated with the appropriate points to illustrate cranial morphology.

More broadly, elongate snouts occur in at least four apteronotid lineages (*Apteronotus*, *Orthosternarchus*, *Parapteronotus*, and *Sternarchorhynchus*). Each involves different sets of bones and thus have likely evolved independently (Albert, 2001). Of the above clades, *Apteronotus* is most closely related to *Compsaraia* (Albert & Crampton, 2005). *Apteronotus* exhibits sexually dimorphic snout elongation (Cox Fernandes *et al.*, 2002; Hilton &

Cox Fernandes, 2006) and males exhibit a wide range of phenotypes like *C. samueli*, although perhaps not as extreme. Like *Compsaraia*, the cranial bones responsible for snout elongation in *Apteronotus* are positioned between the orbit and the posterior nares. The dentary and anguloarticular bones in *C. samueli* and “*A.*” *bonapartii* are similar in shape between females, but in long-snouted *C. samueli* males there is more extreme interlacing between these bones. The coronomeckelian also tends to be smaller in male and female *C. samueli* than in their “*A.*” *bonapartii* counterparts. *Parapteronotus*, sister to *Apteronotus* and *Compsaraia*, is also known to have distinct short and long male snout phenotypes (Petzold & Smith, 2016; Cox Fernandes *et al.*, 2002) and to have an elongate lower jaw spanning most of the preorbital region.

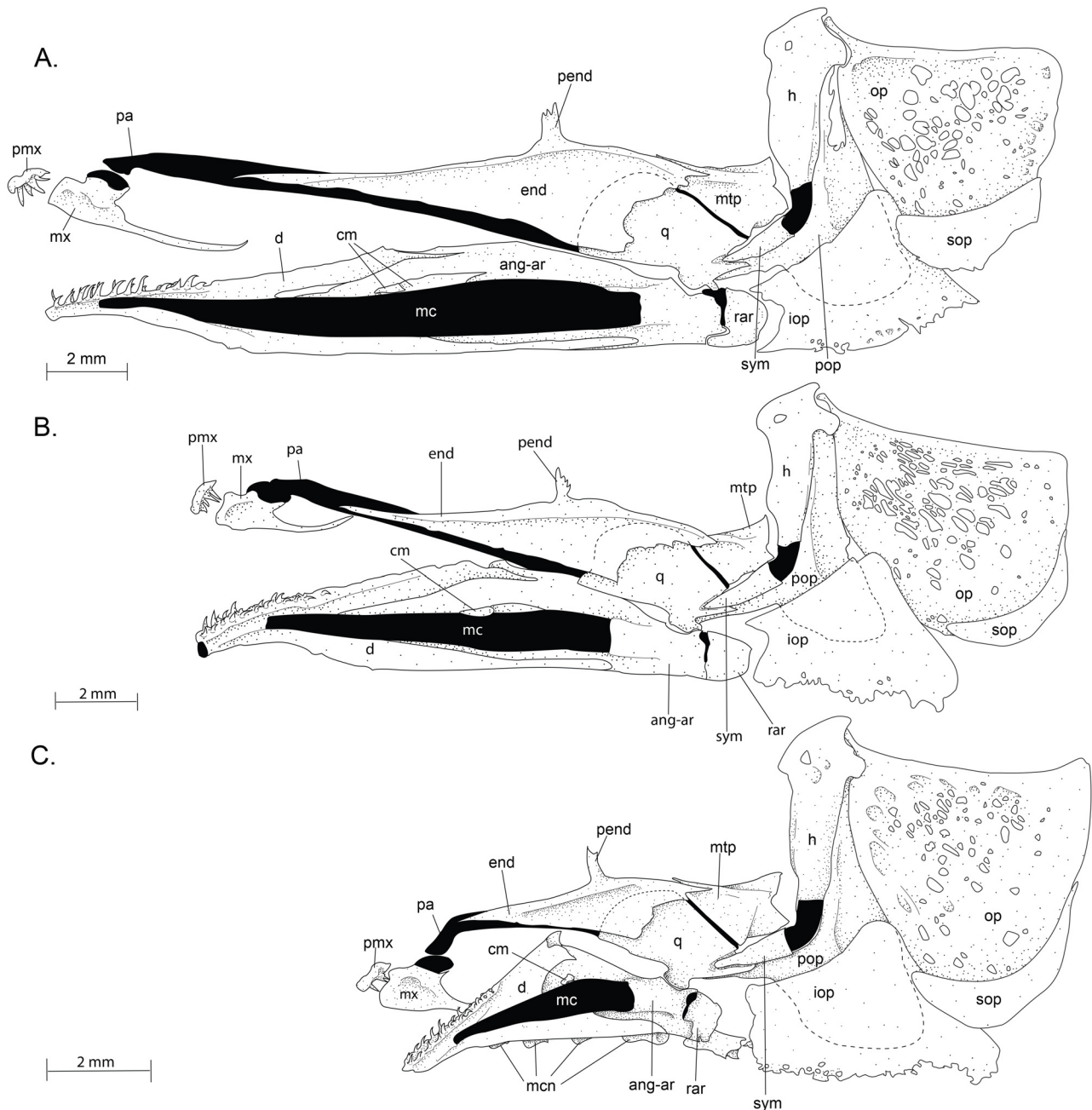


FIGURE 7. Suspensorium and oral jaws of *C. samueli* in medial view. A, a long-snouted male (172 mm TL), B, a short-snouted male (132 mm TL), and C, a female (132 mm TL) specimen (all from INPA 27585). Abbreviations: ang-ar, anguloarticular; cm, coronomeckelian; d, dentary; end, endopterygoid; h, hyomandibular; iop, interopercle; mc, Meckel's cartilage; mcn, mandibular sensory canal ossicles; mx, maxilla; mtp, metapterygoid; pa, pars autopalatina; pend, endopterygoid process; pmx, premaxilla; pop, preopercle; q, quadrate; rar, retroarticular; sym, symplectic.

Comparisons of *C. samueli* to other gymnotid groups are also informative. The Sternarchorhynchini (to which *Sternarchorhynchus* belongs) possess elongate snouts that are seen in both males and females. Unlike *C. samueli*, the gape is short and the lower jaw is more recurved and filamentous. The endopterygoid and metapterygoid do not overlap, and the elongation of the snout is caused more from the extension of the endopterygoid than from the palatoquadrate cartilage (de Santana & Vari, 2010). As described in Hilton *et al.* (2007), the monotypic genus *Orthosternarchus* is part of a clade that is sister to all other apteronotids (Sternarchorhamphini) and snout elongation is achieved differently than in other apteronotids. *Orthosternarchus tamandua* does not exhibit sexual dimorphism but has a long snout and a short gape as found in *Sternarchorhynchus*. Unlike *Sternarchorhynchus*, the jaw joint of *Orthosternarchus* is positioned more anteriorly, resulting in a lower jaw that is not as greatly elongate as in the other groups mentioned here. In comparison to *C. samueli*, the hyomandibular and the opercular chain are greatly elongate, much more than the palatoquadrate and its associated cartilage.

More study is needed to fully understand mechanisms of snout elongation across the apteronotids. It is possible that males with longer snouts are older than those with short snouts. However, this hypothesis is not supported by our data. For instance, the male with the longest snout in our sample is of only average body length. Another possibility is that sex hormones are affecting mature males of all body sizes at the same time. Previous work has shown that androgen levels control sexual dimorphism in other gymnotiforms (e.g., the external teeth seen in *Sternarchogiton nattereri*) and can vary within and across reproductive seasons (Cox Fernandes *et al.*, 2010). This may explain the discrepancy between LEA and snout length in our data (Fig. 2). For any of these scenarios, it would be helpful to learn more about the natural history of *C. samueli*, including whether these fish survive multiple breeding seasons, as well as basic data on patterns of growth as they related to age.

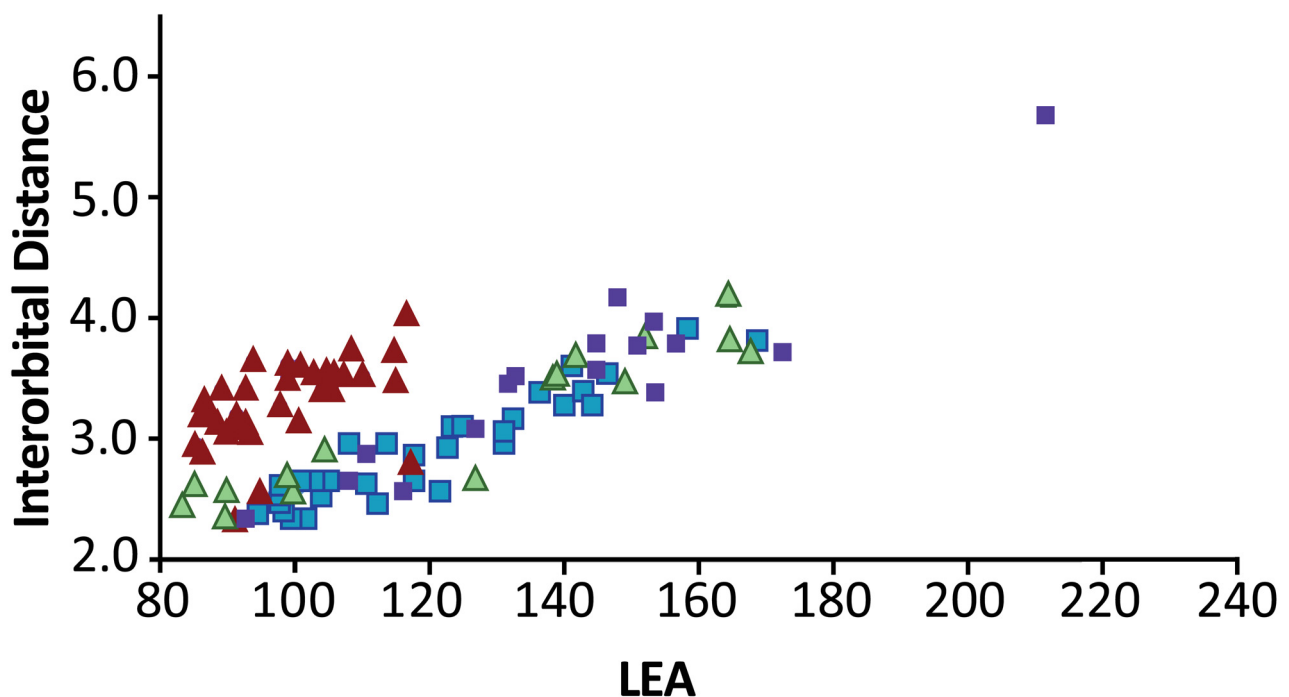


FIGURE 8. Scatterplot of interorbital distance (IO) versus length from the snout to end of anal fin (LEA) of *C. compsa* and *C. samueli*. Red triangles are female *C. samueli* (n=33), blue squares are male *C. samueli* (n=34), green triangles are female *C. compsa* (n=16), and purple squares are male *C. compsa* (n=16).

Sexual dimorphism of the snout may serve several functional purposes in *C. samueli*. Captive individuals of this species engage in male vs. male combat, wherein males will joust and/or ram into one another with their snouts. Long-snouted males exhibit weaker bite forces than their short-snouted counterparts (Evans *et al.*, 2018). Our results support this finding. During dissection, we found the jaws of long-snouted males poorly ossified and easily warped. These are not traits that would facilitate combat or even feeding ability. Dissecting the stomachs of four long-snouted males in our study did not yield any food items, and instead we found an abundance of nematode

parasites as well as fat deposits around the intestinal areas. This suggests that the elongated snout condition is terminal for these fish. The long snout is likely more of a sexual ornament than a weapon and may be a way for fish to superficially appear larger. Body size may be more relevant for these fish, which are nocturnal and live in dark waters, than colors and ornaments as they rely less on vision and more on electroreception and tactile senses. Only testing female mate choices and behavior will help to better understand these potential intra- and inter-specific trade-offs.

In conclusion, this study describes the morphological sexual dimorphism in *C. samueli* to serve as a basis for further study on this group. We quantified cranial allometric variation, illustrated skull osteology, and discussed the relationship between *C. samueli* and *C. compsa*. We found that mature male and female *C. samueli* can be distinguished by their cranial osteology and that males display a wide variation of sexually dimorphic snout phenotypes. This work will benefit future researchers in the identification of these species and serve as an example for future descriptions of sexual dimorphism within Aptereronotidae.

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APPENDIX 1. Material examined

Compsaraia samueli—Brazil, Rio Negro drainage, Rio Zamula: INPA 27585, 51 (33 males, 92.6–173.4 mm TL and 12 females, 104.6–136 mm TL) and 17 not sexed; 6 C&S (3 males, 132–172 mm TL and 3 females, 127–132 mm TL). INPA 26983, 26 (7 males, 102.1–146.2 mm TL and 19 females, 103.5–137.8 mm TL) and 23 not sexed, INPA 27589, 3 (male, 125.6 mm TL, 2 females, 104.9–123 mm TL). Rio Demini: INPA 18615, 2 (males, 159.7–172.8 mm TL), INPA 018616, 1 (male, 137.4). Rio Amazonas drainage, Rio Trombetas: INPA 34408, 1 (male, 182 mm).

Compsaraia compsa—Brazil, Rio Negro drainage, Rio Zamula: INPA 27586, 14 (8 males, 154.3–195.5 mm TL, 2 indeterminate sex, 97.1–104.9 mm TL, and 4 females, 132–196.2 mm TL), INPA 27587, 2 (males, 136–178 mm TL and female, 165.4 mm TL), INPA 27590, 13 (2 males, 140–169.1 mm TL and 9 females, 111.7–209.4 mm TL) and 2 C&S (male, 187 mm TL and female, 117 mm TL) and 25 not sexed, INPA 27588, 1 (male, 189 mm TL), INPA 27589 1 (female 121.6 mm TL), INPA 27591 1 (female, 145 mm TL) .

Rio Negro, above Rio Branco: JGL 93–187, 3 (2 females, 166–170.5 mm TL and male, 178.4 mm TL), 10°22'20.7"S 61°54'32.1"W and JGL 93–190, 1 (female, 209.4 mm TL), 10°22'44.1"S 61° 54'7.3"W; below Rio Branco: JPF 93–158, 8 (4 males, 107.3–234.2 mm TL and 4 females, 105.8–149.6 mm TL), 10°57'54.5"S 61°15'48.4"W and MG 93–38, 1 (male, 178.6 mm TL), 10°13'32.6" S 62°13' 54.8" W.