

Sexual Dimorphism in *Apteronotus bonapartii* (Gymnotiformes: Apteronotidae)

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Here we document sexual dimorphism in both external measurements of the head and discrete features of the skull in *Apteronotus bonapartii*. To quantify morphological variation in *A. bonapartii*, ten external morphometric measurements were taken from the head and body of 58 individuals. By using Discriminant Function Analysis, we found that the best predictors for distinguishing sexes are the body depth, snout length, and the distance from the tip of the lower jaw to rictus (i.e., the gape length). Two measurements showed significant differences between males and females: supraoccipital to base of dorsal thong and tip of the lower jaw to rictus. Most skeletal elements were found to be similar between males and females; however, in males some elements of the skull roof (e.g., frontal) and suspensorium (e.g., endopterygoid) are elongate relative to females, and the lateral ethmoid is more obliquely positioned. In females, the dentary and anguloarticular are relatively deep and come together in a sharp angle dorsally, giving the lower jaw an almost triangular shape; in males the dorsal margin of the lower jaw is smoothly arched.

No presente trabalho nós documentamos o dimorfismo sexual em *Apteronotus bonapartii* utilizando medidas externas e características do crânio. Para quantificar a variação morfológica em *A. bonapartii*, dez medidas morfométricas foram obtidas da cabeça e corpo de 58 indivíduos. Através da Análise de Função Discriminante, os melhores preditores para distinguir machos e fêmeas foram a altura da cavidade abdominal, comprimento do focinho, e distância da mandíbula ao rictus. Na Análise de Covariância, duas medidas mostraram diferenças significativas entre machos e fêmeas: a altura do corpo na base do supraoccipital e mandíbula ao rictus. A maioria dos elementos do crânio dos machos e fêmeas são similares. Entretanto, em machos alguns elementos do crânio (e.g., frontal) e suspensório (e.g., endopterygóide) são alongados, em comparação com as fêmeas. Em machos, o etmóide lateral é posicionado mais obliquamente do que nas fêmeas. Em fêmeas o dentário e o ânguloarticular têm maior altura e proporcionam uma forma quase triangular na porção anterior da mandíbula, onde em machos a margem dorsal da mandíbula é levemente arqueada.

SEVERAL sexually dimorphic features have been detected in gymnotiform fishes, including the shape of the head region in several species of the family Apteronotidae (e.g., Cox Fernandes, 1998; Cox Fernandes et al., 2002; Santana, 2003) and the length and thickness of the caudal filament of several species of the family Hypopomidae (Hagedorn and Carr, 1985; Hopkins et al., 1990). Mago-Leccia (1994:99) reported sexual dimorphism in the color pattern of *Sternarchorhynchus roseni* and that females of *Sternarchella sima* have “bulkier heads, deeper bodies and larger interocular distances” than do males. Males of *Sternarchorhynchus mormyrus*, *S. curvirostris*, and *S. roseni* may have distended lower jaws with many more teeth than found in females, although this still remains to be demonstrated (see Py-Daniel and Cox Fernandes, 2005); Campos-da-Paz (2000) did not find any sexual dimorphism in the species of *Sternarchorhynchus* described in that study. Due to extreme

sexual dimorphism, males of *Parapteronotus hasemani* were described as *Apteronotus anas* (see Albert, 2001; Cox Fernandes et al., 2002) and Myers (1936) described male specimens of *Sternarchogiton nattereri* as members of a new genus *Oedemognathus* (e.g., Albert, 2001; CCF and Lundberg, pers. obs.). There is also pronounced sexual dimorphism in electrical organ discharges (EODs) of *Brachyhypopomus occidentalis*, *B. pinnicaudatus*, and *Sternopygus*, although the manner in which this dimorphism is manifest varies among taxa (e.g., Hagedorn and Heiligenberg, 1985; Hopkins et al., 1990; Dunlap et al., 1997). Although past studies on gymnotiform fishes have identified sexual dimorphism in external morphological traits, none have examined how this dimorphism may be reflected in the skeleton.

The goal of this paper is to describe aspects of the sexual dimorphism in *Apteronotus bonapartii*. We did this by quantifying the external morpho-

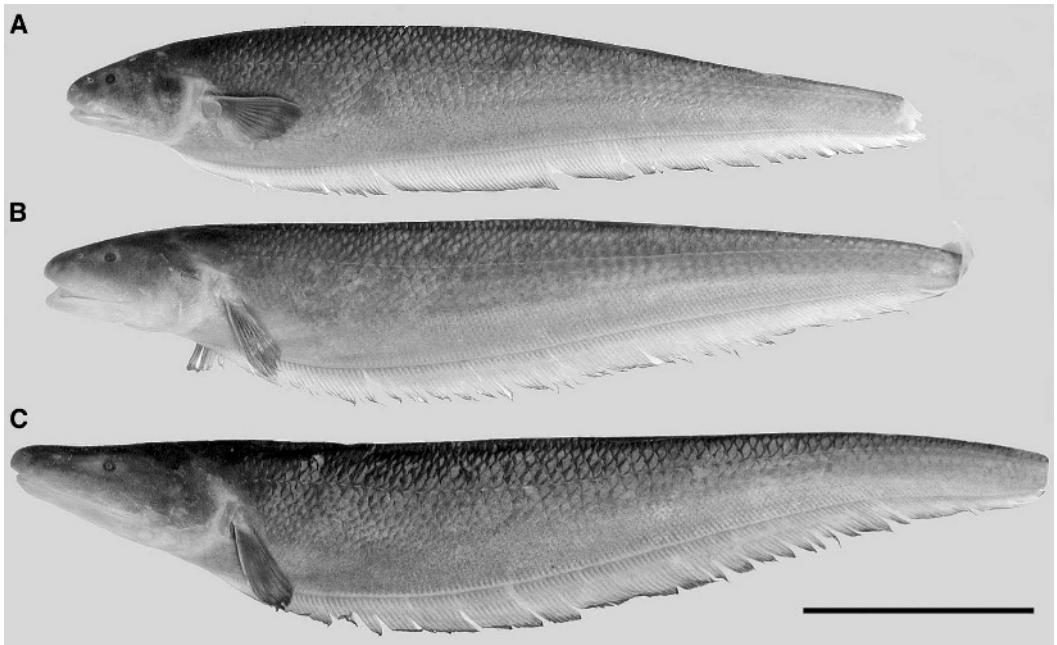


Fig. 1. Specimens of *Apteronotus bonapartii* shown in left lateral view. (A) Female (INPA 16067). (B) Short snouted male (INPA 16058). (C) Long snouted male (INPA 13997). Scale bar equals 5 cm. Anterior facing left in all.

logical variation we discovered between the sexes and qualitatively describing and illustrating skeletal differences we found in the skull. *Apteronotus bonapartii* (Fig. 1) belongs to the family Apteronotidae, which comprises 14 genera and more than 60 species, at least 16 of which are undescribed (Albert and Crampton, 2005). The family is distributed throughout Central and South America (Albert, 2003; Albert and Crampton, 2005), with its highest diversity in the Amazon Basin (Cox Fernandes, 1999; Cox Fernandes et al., 2004). *Apteronotus bonapartii* is one of four species regarded by Albert and Campos-da-Paz (1998) to be “*Apteronotus*” *sedis mutabilis*; the others are *A. apurensis* (Fernández-Yépez, 1968), *A. macrostomus* (Fowler, 1943), and *A. macrolepis* (Steindachner, 1881). These authors found that these species (“Unnamed clade AH” of Albert, 2001) did not form a monophyletic group with the genus *Apteronotus sensu stricto*, and, consequently, questioned their generic assignment (i.e., “*Apteronotus*”). Albert (2001:77) identified the taxon he studied as “*A.*” *cf. bonapartii* and suggested that his specimens, those considered by Ellis (1913), as well as “many specimens labeled as such in museum collections” may not be *A. bonapartii*. *Apteronotus bonapartii* may be distinguished from other members of this group by a uniform, dark body coloration and pectoral fins that are entirely

pigmented (in contrast to only being pigmented distally). Species delineation of these species and their relationships, however, are beyond the scope of this paper and are in need of further study.

MATERIALS AND METHODS

Specimens were obtained by CCF between 1997 and 2000 with seine nets as described in detail in Cox Fernandes et al. (2002) from localities between the lower part of the Rio Solimões to Careiro Island 3°04' to 3°18'S and 59°30' to 60°06'W, downriver of the confluence of Rio Solimões and Rio Negro (Cox Fernandes, 1998:fig. 1).

Morphological analysis.—Morphometric sampling followed the methods outlined in Cox Fernandes (1998) and Cox Fernandes et al. (2002). Ten body measurements were recorded for 58 individuals (see Cox Fernandes, 1998:fig. 1) that were sexed by examination of gonads; one immature individual was excluded from statistical analyses. These measurements included: body depth at the posterior end of abdominal cavity (AB); distance from posterior edge of eye to posterior margin of opercle (EO); head length, measured from the tip of upper jaw to posterior edge of opercle (H); internarial distance (ID);

distance from the tip of lower jaw to the rictus (i.e., the gape length; M); distance from the anterior edge of the eye to the posterior border of the posterior nares (NE); distance from the tip of snout to the anterior edge of the eye (S); distance from the tip of snout to the posterior edge of the supraoccipital (SS); distance between the posterior edge of supraoccipital to dorsal thong (ST); and body depth at the supraoccipital spine (SV). We use ST as a standardized body length because damage to the posterior caudal region in much of our sample prevents standard lengths from being measured.

Fourteen specimens (six females and eight males) were cleared and double stained for bone and cartilage (e.g., Dingerkus and Uhler, 1977; Hanken and Wassersug, 1981) and examined with a Wild M5 dissecting microscope with substage illumination and camera lucida attachment. Our osteological study emphasized the skull although cursory study suggests that little if any sexual dimorphism occurs in the post-cranial skeleton.

Statistical analysis.—Discriminant Function Analysis (DFA) was performed on the 57 mature specimens using the ten body variables as predictors of sex. Jackknifed classification was used to eliminate the bias that enters the analysis when the coefficients used to assign a case to a group are derived from that case, thereby giving a more realistic estimate of the ability of predictors to separate groups (Tabachnick and Fidell, 1989). To graphically visualize sexual dimorphism along the discriminant axis, we plotted canonical discriminant scores.

We also tested for differences between the sexes by following the approach of Cox Fernandes (1998), in which one-way analysis of covariance (ANCOVA) and *t*-tests were employed. Examination of the residual plots provided a test of assumptions of normality, linearity, and variance; data were log-transformed. To generate a size component from our measurements, Principal Component Analysis was performed on the covariance matrix of log-transformed measurements and PC1 extracted. ANCOVA can only be performed on variables with no significant interaction between sex and PC1 (size), which is determined by the parallelism of slopes test (Sokal and Rohlf, 1995). For variables with significant interaction, residuals from the regression between PC1 and these variables were saved and differences were tested using independent sample *t*-tests. To avoid Type I error in analysis (ANCOVA and *t*-tests), we adjusted the *P*-values using a Bonferroni correction.

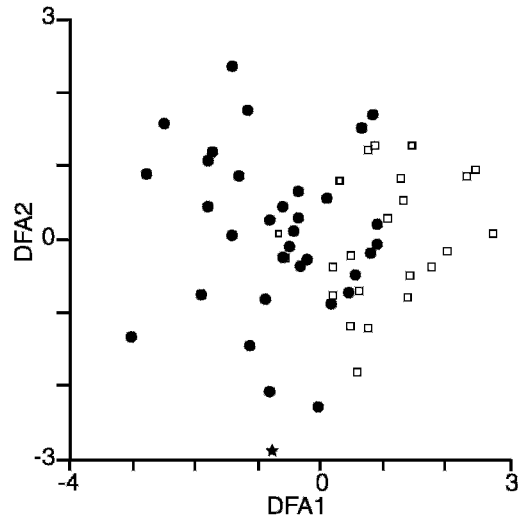


Fig. 2. Discriminant Function Axis 1 and Discriminant Function Axis 2 of 58 specimens of *Apteronotus bonapartii* derived from DFA of the ten morphometric body measurements. Males are indicated by filled circles, females by open squares, and the immature specimen by a star.

RESULTS

Morphometric analysis.—Mean measurements of males tend to be slightly larger for all variables although the largest individual in our sample is a female. DFA resulted in significant separation between males and females (Wilk's lambda = 0.588, approximate $F_{1,55} = 3.22$, $P < 0.01$) and male, female, and immature groups (Wilk's lambda = 0.508, approximate $F_{2,55} = 1.85$, $P < 0.05$). The separation of the two sexes occurs maximally along the first canonical axis (Fig. 2), although there is overlap between males and females. The first canonical discriminant function suggests that the best predictors for distinguishing between sexes are body depth (AB), snout length (S), and mandible to rictus (M). Based on the ten external body variables, classification revealed a high degree of correct separation for the two sexes (91% females, 76% males, and 82% combined). Values from the Jackknife classification analysis were lower, with 67% of all specimens classified correctly (65% females and 68% males).

All variables loaded positively for PC1 (which reflects overall size) for analysis of the body measurements. PC1 for body measurements of all individuals, which was used for the ANCOVA to test for sex differences of individual morphometric variables, accounted for 92.5% of the variation.

TABLE 1. TESTS FOR HOMOGENEITY OF SLOPE OF 57 MATURE *Apteronotus bonapartii* FOR SEX AND PC1 SCORES. Asterisks indicate the level of significance: *, $P < 0.05$; **, $P < 0.01$; and ***, $P < 0.001$.

Variable	F		
	Sex	PC1	Interaction
Log depth of abdominal cavity (AB)	8.26**	201.72***	5.26*
Log depth at occiput (SV)	11.52**	332.47***	28.77***
Log supraoccipital to base of dorsal thong (ST)	36.50***	405.91***	19.88***
Log snout to edge of eye (S)	4.52*	1505.37***	5.94*
Log mandible to rictus (M)	21.47***	444.50***	5.40*
Log upper jaw to edge of opercle (H)	0.83	2548.84***	1.21
Log edge of eye to posterior nares (NE)	3.35	915.57***	19.31***
Log edge of eye to opercle (EO)	6.28*	770.76***	1.61
Log snout to supraoccipital (SS)	0.60	559.37***	5.59*
Log anterior to posterior nares distance (ID)	0.32	423.72***	6.68*

Covariance analysis was performed on two body measurements that tested affirmatively for homogeneity of slopes: log of eye to opercle (EO) and log of head (H; Table 1). Neither of these exhibited statistically significant differences between males and females after the Bonferroni corrections ($P > 0.005$). In the t -tests of residuals on the remaining eight variables, two exhibited significant differences between males and females after Bonferroni correction: log of supraoccipital to base of dorsal thong (ST; $P < 0.001$, Fig. 3A) and log mandible to rictus (M; $P < 0.001$ Fig. 3B).

Skeletal anatomy.—Most elements of the skull roof and braincase are similar in the two sexes in their size, position, and form. A notable exception is the orientation of the lateral ethmoid (Fig. 4). In both sexes this bone is dorsoventrally inclined, although in males it is more oblique relative to the body axis; in small females (e.g., INPA 16052, 59 mm ST) the lateral ethmoid is nearly vertical. The frontals, vomer, and parasphenoid of males are slightly more elongate than those of females. The posterior rami of the mesethmoid, which form the left and right margins of the anterior fontanelle, are more elongate in males than in females, although in both sexes they reach approximately the same level of the skull (i.e., they extend posteriorly to about the level of the orbitosphenoid-pterosphenoid suture). There were no differences noticed in the anterior portion of the mesethmoid or the ventral ethmoid (i.e., the elements anterior to the nares).

The only element of the suspensorium that we found to differ between the two sexes was the endopterygoid, which is more elongate and slender anteriorly in males than in females (Fig. 5). We did not detect any appreciable differences in the bones of the opercular series,

the ventral hyoid arch (e.g., hypohyals and ceratohyal), or the branchial arches.

In long snouted males, the anterolateral process of the anguloarticular that overlaps the dentary is well developed (Fig. 6C); in females this process is much smaller (Fig. 6A), and in short snouted males it is intermediate (Fig. 6B). The lower jaw of females appears to be relatively deeper than that of males and is roughly triangular in lateral view (Fig. 6A), whereas in males the lower jaw is elongate and its dorsal margin is smoothly arched (Fig. 6B, C). There was no discernable sexual dimorphism in the upper jaws.

DISCUSSION

Adult specimens of *Apteronotus bonapartii* were found to be sexually dimorphic in a number of anatomical characteristics. Cox Fernandes (1998) previously reported that no sexual dimorphism was found in *A. bonapartii*. However, the specimens that this statement was based upon are not *A. bonapartii*, but perhaps an undescribed species from the Amazon that are probably the same as Albert's (2001) "A." *cf. bonapartii*.

The differences described here, including those between male specimens, were found in specimens collected in a relatively limited area and therefore do not represent geographic variation. All were collected during the reproductive season (from November to April; most of them in 1998), so the differences do not represent seasonal or temporal variation. Our results indicate that males reach a slightly larger mean body size than do females but body size does not fully explain the anatomical variation we observed, either between sexes or among male specimens. Large males of roughly similar size have considerable variation in head dimensions (e.g., mouth and snout size)

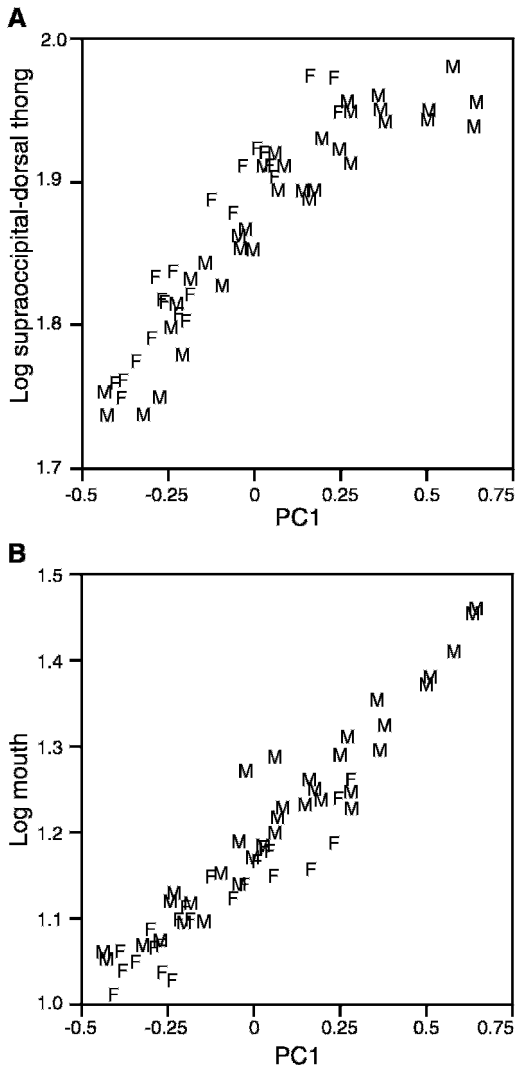


Fig. 3. Two variables plotted against the first principal component for 58 specimens of *Apteronotus bonapartii*.

similar to, but not as dramatic as, the variation observed in *Paraapteronotus hasemani* by Cox Fernandes et al. (2002). Females were found to be as large as males but without the variation in head dimensions.

Here we have demonstrated through both morphometric analysis and descriptive osteology that there is a difference between the sexes of *Apteronotus bonapartii*. Differences in head shape are often reflected in skull structure (e.g., see discussion of the skulls of fishes as a “natural mechanism” reflective of the “more active parts of the head” by Gregory, 1933:431). However, until now the details of this skeletal variation have not been described for any sexually di-

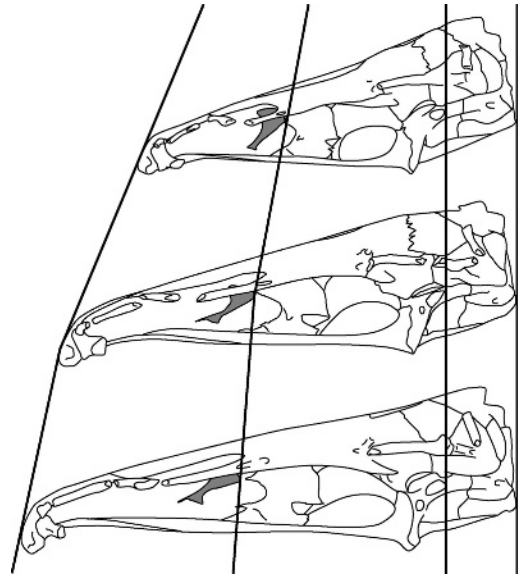


Fig. 4. Schematic representations of the skull roof and neurocranium of *Apteronotus bonapartii* in lateral view, standardized for the distance between the basioccipital and the posterior margin of the foramen cranial nerve VII (following Albert, 2001:figs. 14–17); anterior facing left. From top to bottom, specimens are a female, a short snouted male, and a long snouted male. The two lines toward the front of the specimens connect the very anterior tip of the ethmoid region and the posterior extent of the lateral ethmoid (highlighted in gray). The obliqueness of these lines graphically indicates the degree of difference between specimens.

morphic apteronotid species. In *A. bonapartii* it is the bones positioned between the orbit and the posterior nares (e.g., the frontals, vomer, lateral ethmoids, mesethmoid, and endopterygoids) and the lower jaw that are dimorphic, whereas those of the more posterior regions of the skull (e.g., the braincase, posterior suspensorium, opercular series, and gill arches) are not. In effect, the skull of the male resembles that of a female that has been stretched between the posterior nares and the eye. Such differences are similar to the interspecific variation described by Albert (2001) and may suggest common craniofacial developmental plasticity underlying both sexual and phylogenetic variation.

We have no explanation for what causes or maintains the dimorphism within *Apteronotus bonapartii* or other apteronotid fishes. Virtually nothing is known about the natural history and reproductive ecology of apteronotids, so we can only speculate that the underlying basis for the maintenance of sexual dimorphism in this

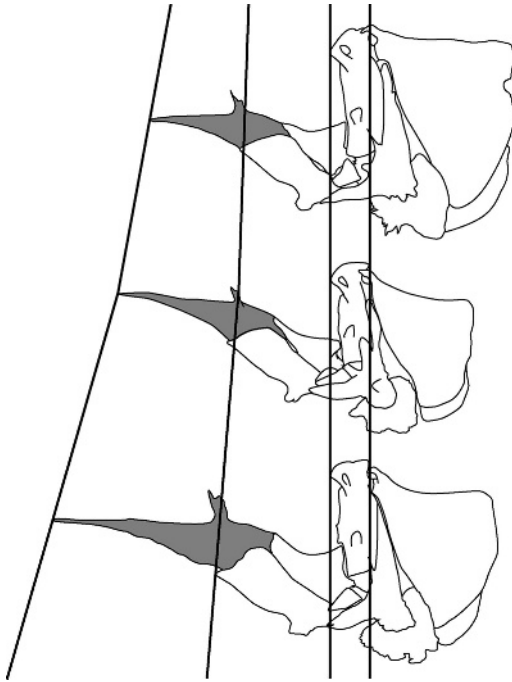


Fig. 5. Schematic representation of the suspensorium and opercular series of *Aptereronotus bonapartii* in lateral view, standardized for the width of the dorsal head of the hyomandibula, anterior facing left. From top to bottom, specimens are a female, a short snouted male, and a long snouted male. The two lines toward the front of the specimens connect the very anterior tip of the endopterygoid (highlighted in gray) and the posterodorsal tip of the endopterygoid process. The obliqueness of these lines graphically indicates the degree of difference between specimens.

species may involve a complex reproductive system (e.g., see Cox Fernandes et al., 2002). Until direct field observations are made, behavioral data collected, and the function of steroids in establishing this dimorphism is studied, our understanding of this phenomenon will remain speculative.

MATERIAL EXAMINED

The following specimens were examined. Numbers in parentheses refer to number of specimens; if determined, sex is indicated (F = female, M = male, I = immature). All specimens are alcohol-stored specimens unless indicated as cleared-and-stained (CS) specimens. Institutional abbreviations follow Leviton et al. (1985); CCF = uncatalogued specimens.

Aptereronotus bonapartii.—Digital photo of the holotype, Rio Ucayali (Peru) MNHN 3807. Rio

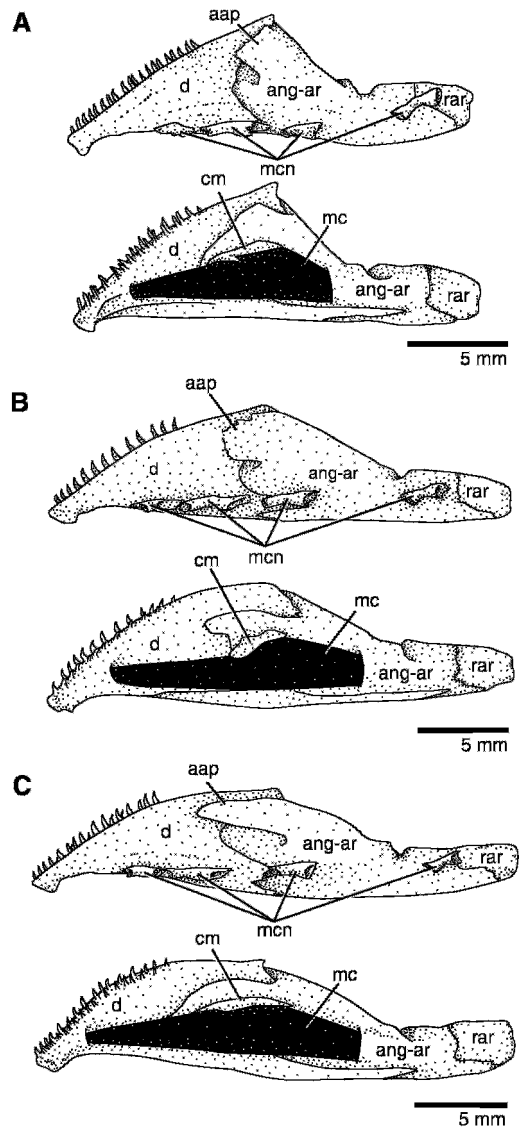


Fig. 6. Left lower jaws of *Aptereronotus bonapartii* in lateral (above) and medial (below) views. (A) Female (INPA 16069). (B) Short snouted male (INPA 16067). (C) Long snouted male (INPA 16062a). Cartilage shown in black. Anterior facing left in all (medial views reversed). Abbreviations: aap, anterolateral process of the anguloarticular; ang-art, anguloarticular; cm, coronomeckelian; d, dentary; mc, Meckel's cartilage; mcn, bony ossicles of the mandibular sensory canal; rar, retroarticular.

Solimões (Brazil)—Canal da Xiborena: INPA 13997 (8 M, 1F), INPA 16052 (2F, 1F CS), INPA 16056 (2F), INPA 16058 (3M, 2M CS), INPA 16064 (1M), INPA 16070 (1M CS), INPA 16071 (1M), INPA 16072 (1F and 1M CS, 1M, 1F), INPA 16073 (1M), INPA 16074 (1M, 1F); at the

meeting of the waters with Rio Negro: INPA 16069 (5M, 1F CS); Parana do Curari: INPA 16059 (1M); Ilha da Marchantaria: INPA 16053 (1F), INPA 16054 (1M), INPA 16055 (1F), INPA 16062 (2F). Rio Amazonas (Brazil)—Parana do Rei, Ilha do Careiro: INPA 16051 (1M, 1F, 1I), INPA 16066 (1M CS), INPA 16067 (1M and 1F CS, 1M, 1F), INPA 16068 (1M, 3F); Lago do Catalão: INPA16060 (1M, 1F), INPA 16063 (1F CS), INPA 16065 (1M, 1F). Rio Apure (Venezuela)—Guarico: FMNH 102107 (3); ANSP 165220 (4). Rio Orinoco (Venezuela)—Delta Amacuro: ANSP 149507 (1); ANSP 149540 (5); ANSP 151952 (2); Bolivar: ANSP 163036 (2). Rio Metica (Colombia)—Meta: ANSP 151954 (2). Rio Ucayali (Peru): ANSP 86722 (1). Rio Napo (Peru): ANSP 178182 (3). Rupununi River (Guyana): ANSP 180283 (1).

Apteronotus macrolepis.—Rio Amazonas (upstream Leticia, Colombia): FMNH 85356 (25).

Apteronotus apurensis.—Digital photo of the holotype, MBUCV-V-10840. Rio Suripa (Barinas, Venezuela): FMNH 100738 (6).

Apteronotus sp. 1.—Rio Amazonas (Brazil)—Costa do Marimba, Ilha do Careiro: INPA 16057 (3); Gambôa, Ilha do Careiro: INPA 16061 (1), above the mouth of Rio Tapajós: CCF 92.24 (1). Rio Solimões (Brazil)—above the mouth of Rio Purus: CCF 92.9 (3). Rio Purus (Brazil): CCF 92.7 (3).

Apteronotus sp. 2.—Rio Negro (Brazil)—Lago do Prato: INPA 7687 (2).

Apteronotus sp. 3.—Rio Paraná (Brazil): INPA 16075 (6).

Apteronotus sp. 4.—Rio Meta (Venezuela)—Apure: ASNP 160193 (6).

Apteronotus albifrons.—Rio Suripa (Venezuela): Barinas: FMNH 100729 (1 CS).

Paraapteronotus hasemani.—Rio Amazonas (Colombia): FMNH 960391 (1 CS).

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