

***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**

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Abstract

Apteronotus caudimaculosus, a new species of ghost knifefish with males having greatly elongated snouts, is described from the Pantanal wetlands, Paraguay River basin in Western Brazil. It is distinguished from its congeners by two light bands encircling the caudal peduncle, the first caudal band with irregular spots throughout its development. The presence of two light bands can be used to identify a monophyletic clade in Gymnotiformes, the so-called *A. albifrons* species complex. This group comprises *A. albifrons*, *A. caudimaculosus* and at least six undescribed species. An artificial key to identification of species currently in *Apteronotus* (*sensu stricto*) is provided.

Key words: Fish, new species, Apteronotidae, Pantanal, black ghost knifefish, secondary sexual dimorphism

Introduction

Presently, fifteen species are included in the genus *Apteronotus*. They can be identified by the following features (Albert, 2001): (1) body surface deep brown or black with a white mid-dorsal stripe and white mental and caudal patches; (2) elongate posterior limb of the anguloarticular; (3) surface of cranial bones solid, not pitted; (4) behavior of inhabiting upland streams, small rivers and lagoons; (5) premaxilla gracile, scroll-shaped in adults, with two or fewer teeth.

Apteronotus albifrons (Linnaeus, 1766) is the most widespread apteronotid species, occurring from Napo River in Equador to rivers in the state of Maranhão, Brazil, and from the Orinoco River to the state of Rio Grande do Sul in Southern Brazil. There are no records of the species in the trans-Andean region (Albert, 2001) and eastern coastal rivers

of Brazil (Campos-da-Paz, 1997). All black ghost knifefish populations are referred to the specific name of *A. albifrons*, although there is a large variation in body shapes (de Santana, 2002). The aim of this paper is to describe a new species of *Apteronotus* related to *A. albifrons* from the Pantanal wetlands, Paraguay River basin, in the State of Mato Grosso do Sul, Central Brazil.

Materials and methods

Two lots with 37 specimens (4 males, 11 females and 22 immatures, identified by means of gonad inspection) from the MZUSP, and 2 females from the FMNH 108537, for a total of 39, originally misidentified as *A. albifrons* were analyzed. Measurements were taken with a digital caliper with a precision of 0.01 mm, and followed the methodology of Mago-Leccia (1994), Cox-Fernandes (1998) and Campos-da-Paz (1999). The abbreviations in Table 1 signify the following: total length (TL); length to end of anal fin (LEA); anal fin base (AFB); tail length (T); head length at gill opening (HL); head depth at nape (HDN); head width (HW); interorbital distance (IOD); distance from posterior naris to eye (DNE); orbital diameter (OD); postorbital distance at gill opening (POD); snout length (SNL); mouth length (ML); gill opening (GO); distance from snout to anus (DSA); pre-anal fin distance (PAFD).

Anal fin ray and vertebral counts were taken from radiographs. "Mouth rictus" is defined as the point where the tissues of upper and lower jaws meet (Cox-Fernandes, 1998). Counts of holotype are given in brackets (whenever possible). The word "light band" is preferred instead "white band", since some *A. albifrons* populations show yellow bands. Institution abbreviations followed Eschmeyer (1998), with the addition of the Georgia Museum of Natural History (GMNH). In the comparative material examined the abbreviation "cs" means cleared and stained. The key was produced by direct examination of type specimens, with the exceptions of *A. albifrons*, *A. brasiliensis* (Reinhardt, 1852), *A. ellisi* (Arámburu, 1957), *A. marauna* (Triques, 1998) and *A. spurrellii* (Regan, 1914). Other specimens of the former four species were examined from the type localities. For *A. spurrellii*, the character states were taken from the original description only; this species was excluded from the key due to the lack of detailed information.

Results

Apteronotus caudimaculosus - new species

Figs 1 - 2; Table 1

Holotype- MZUSP 79359, 286.8 mm TL, Mato Grosso do Sul. AQUARAP Pantanal 19° 36.64' S; 56°24.87' W, Aquidauna, Rio Novo, Brejo de Santa Sofia; A. Machado & B. Chernoff, 3 September 1998.

Paratypes- ANSP 178659 (1 specimen, 145.9 mm); CAS 216788 (1, 127.6 mm); INHS 94260 (1, 137.5 mm); GMNH 3435 (1, 149.2 mm); INPA 20066 (1, 100.1 mm); MCZ 161831 (1, 126.0 mm); MZUSP 59295 (22, 71.7-165.8 mm); MZUSP 59296 (4, 175.4-231.1 mm); UMMZ 240259 (1, 107.1 mm); USNM 371234 (1, 106.2 mm); Locality data as for holotype. FMNH 108537 (2, 114.3-159.2 mm), Rio do Peixe on MS 080, 19° 23.15' S; 54° 48.47' W. 23 October 1998.

Diagnosis- *A. caudimaculosus* is included in the Apteronotidae by the presence of a dorsal-thong and caudal fin (Mago-Leccia, 1994; Albert & Campos-da-Paz, 1998; Albert, 2001). The new species shares the following diagnostic features within the Apteronotinae (Albert & Campos-da-Paz, 1998; Albert, 2001): gape of mouth large, extending to the edge of the eyes; maxilla rhomboid in lateral view; anterior surface of mesethmoid concave and lateral process of ventral ethmoid robust. It was included in the genus *Apteronotus* by the presence of three of the five synapomorphies proposed by Albert (2001): body surface deep brown or black with a white mid-dorsal stripe and white mental and caudal patches; elongated posterior limb of the anguloarticular; and surface of cranial bones solid, not pitted. *A. caudimaculosus* was included in *A. albifrons* species-group by the presence of a pale pigment patch on the caudal peduncle and a highly contrasting pale or white mid-dorsal stripe and mental patch. The new species can be recognized within the genus by the following derived characters: (1) two clear bands encircling the caudal peduncle (vs. one clear band encircling the base of caudal fin, except *A. albifrons*); (2) first caudal band with irregular dark spots throughout its development (vs. without spots in *A. albifrons*). Furthermore, shorter tail length can be used to separate *A. caudimaculosus* from *A. albifrons*, (10.4-19.2% vs. 22.3-23.1% of LEA).

Description- Morphometrics for holotype and paratypes are presented in Table 1. Body laterally compressed, with greatest body depth at abdominal cavity or a little posterior to this region. Dorsal profile straight. Lateral line extending to tail, absent in caudal fin. First perforated scale above pectoral fin origin.

Head laterally compressed, widest at opercular region and deepest at dorsal region; profile straight in males and slightly convex in females. Snout long in males, shorter in females and immature specimens. Eyes small, located laterally on head, completely covered by a thin membrane. Mesethmoid short and narrow, its anterior tip reduced, flexed ventrally, and concave. Lateral ethmoid present, ossified, small and slender, shaped as a tube. Premaxilla of moderate size, with two irregular rows of teeth. Maxilla crescent-shaped, with an ossified anterodorsal head and anteroventral shelf, the ventral margin of its descending blade curved. Dentary longer than deep, bearing two rows of teeth. Anguloarticular elongated. Mouth large, terminal, rictus passing a vertical through posterior border of eyes in both sexes. Endopterygoid narrow, without teeth, with ascending process connecting to the orbitosphenoid, its base ossified, and the remaining portion unossified; anterior portion narrow, extending to the midlength of dentary. Metapterygoid triangular, the posterior portion as an ascending process. Symplectic shorter than hyomandibula and artic-

ulated with it by a cartilage. Four branchiostegal rays, first and second almost filamentous, the remaining large and laminar. Anterior naris at the end of a small tube, close to the tip of snout; posterior naris ellipsoid, without a tube, closer to the tip of the snout than to the eyes. Branchial opening anterior to pectoral fin origin; branchial membranes joined to isthmus. Anus and urogenital papilla adjacent, ventral, located in a ventral posterior to eyes, but with a noticeable forward displacement with age. Pectoral fin somewhat elongated, broad and pointed distally, with $ii + 13-14$ [13]. Origin of anal fin slightly anterior to opercular region, anal fin rays 146-154 [151], with the 11-16 anterior rays unbranched. Small cycloid scales covering the body, 11 to 14 above lateral line. Number of black perforated scales on the lateral line before the first white scale equal to 64-66 [66].

Dorsal thong origin on posterior half of body, and inserted into a narrow middorsal groove, almost extending to, or slightly passing the end of the anal fin. Tail compressed and short, ending in a small and somewhat rounded caudal fin, with 18-22 rays [22].

Coloration in alcohol- Body, pectoral and anal fins black; caudal fin white on base and black posteriorly. Clear band from chin to the beginning of the dorsal thong. Two clear bands surrounding the caudal peduncle, the first with irregular dark spots during all stages of development.

TABLE 1. Morphometric data for holotype and paratypes (except FMNH 108537) of *Apteronotus caudimaculosus*, values in mm and as percent of LEA and HL.

Characters	Holotype (male)	Paratypes (males)			Paratypes (females)			Paratypes (immature)		
		Range	Mean+SD	n	Range	Mean+SD	n	range	Mean+SD	n
TL	286.8	113.8-231.1	-----	3	126.0-181.3	-----	11	71.7-114.5	-----	22
LEA	243.0	110.7-196.0	-----	2	106.2-160.0	-----	9	61.1-96.0	-----	22
HL	53.0	20.1-38.4	-----	3	18.7-29.4	-----	11	11.6-17.2	-----	22
HDN/HL	71.0	77.9-80.3	79.3+-1.3	3	80.3-92.5	85.7+-4.0	9	75.2-85.2	80.3+-2.6	22
HW /HL	39.1	44.2-48.3	46.3+-1.7	3	42.0-53.4	49.5+-3.2	11	42.1-49.2	45.3+-1.9	22
POD/HL	50.2	57.7-61.1	59.42+-1.7	3	54.8-66.7	60.9+-2.8	11	15.5-18.5	17.2+-0.8	22
IOD/ HL	22.4	21.4-25.7	23.0+-2.3	3	19.8-25.8	22.9+-1.9	10	18.8-29.1	24.0+-2.3	22
OD/ HL	3.5	5.2-8.6	7.1+-1.7	3	5.9-8.8	7.7+-0.9	10	7.6-11.0	9.3+-0.6	22
DNE/ HL	18.5	7.0-12.7	9.2+-3.0	3	6.7-9.9	8.2+-0.9	10	3.0-8.4	5.6+-1.2	22
SNL/ HL	41.9	31.1-36.0	33.0+-2.5	3	27.9-35.0	32.6+-1.9	11	21.2-34.4	30.7+-2.6	22
ML/ HL	59.2	39.5-46.6	42.7+-3.6	3	36.6-41.8	38.8+-1.6	11	32.5-43.4	38.2+-2.8	22
GO/ HL	12.9	17.3-18.6	17.8+-0.7	3	16.3-22.0	19.2+-1.7	10	13.7-20.1	17.0+-1.6	22
HL/ LEA	21.8	17.8-19.6	18.5+-0.9	3	16.9-19.3	18.0+-0.9	11	17.5-19.5	18.7+-0.5	22
AFB/ LEA	90.5	82.1-84.1	83.3+-1.0	3	81.9-87.0	85.1+-1.8	10	79.7-86.7	83.8+-1.5	22
DSA/ LEA	11.5	8.4-10.5	9.7+-1.1	3	7.8-10.2	9.1+-0.8	11	9.6-12.1	11.2+-0.7	22
PAFD/ LEA	20.3	14.8-17.5	16.4+-1.4	3	14.7-17.6	16.1+-0.9	11	15.5-18.5	17.2+-0.8	22
T/ LEA	18.0	14.7-17.9	16.3+-2.2	2	13.3-18.6	16.8+-1.6	9	10.4-19.2	16.8+-2.2	22

Secondary sexual dimorphism (SSD)- Secondary sexual dimorphism is an important issue in understanding intraspecific variation and species identification among apteronotids (e.g., Cox-Fernandes, 1998; Cox-Fernandes et al., 2002). Historically, populations of *A. albifrons* were treated as sexually monomorphic. For example, Ellis (1913) presented a taxonomic key using traits such as, short and blunt snout to diagnose *A. albifrons* and “*A. bonapartii* (Castelnau, 1855) from the remaining *Apteronotus* species. Mago-Leccia (1994) recognized two groups of species according to snout length, including *A. albifrons* among the species with a short snout. Dunlap et al. (1998), in a study of sexual dimorphism in *A. albifrons* and *A. leptorhynchus*, observed that “... *A. albifrons* shows relative little sexual dimorphism in both electrocommunication signals and morphology” and concluded that “... We found no obvious dimorphism in the body shape of *A. albifrons*.” Based on my observation and previous studies (Cox-Fernandes, 1998; Cox-Fernandes et al., 2002), it is possible to verify that males of *A. caudimaculosus* show SSD in head morphology and probably in body size as well (see Table 1 and Figure 2): head profile straight in males and slightly convex in females; snout straight and long in matures males, slightly curved in females and immature males and females. Based on gonad inspection, only four of 15 adults were males. It is possible that the greatly elongated snout in mature males of *A. caudimaculosus* offers some biological advantages in courtship and agonistics encounters as already suggested by Cox-Fernandes et al. (2002) in related apteronotids.

Distribution and habitat- *A. caudimaculosus* is known from the Rio Novo in the Middle Rio Negro and from Rio do Peixe in the Upper Rio Negro, Paraguay River basin in the state of Mato Grosso do Sul, Pantanal wetland, western Brazil (Willink, et al., 2000: map 3: 118). Following Strussmann et al. (2000), the type-locality showed the following characteristics: it is a small channel in a swamp, with turbid water, mud and sand at the bottom and moderate current. The borders of the channel are covered by thick aquatic vegetation extending across the rest of the marsh. The Middle Rio Negro swamp was characterized by abundant water hyacinths and other rooted and floating aquatic plants (Willink et al., 2000). The water characteristics in August and September of 1998 were: temperature 23.2-23.5°C; pH 5.85-5.82; conductivity 53.8 -55.0 $\mu\text{S}/\text{cm}$; dissolved oxygen 7.67-7.93 mg/cm. The specimens of *A. caudimaculosus* (cited as *A. albifrons*) were captured among water hyacinths (*Eichornia* sp.), which included also the following gymnotiforms: *Eigenmannia trilineata*, *E. virescens*, “*A. bonapartii*”; *Rhamphichthys* sp., *Brachyhypopomus* sp. and *Gymnotus* sp. (Willink et al., 2000). The following fish genera were caught in the same locality: *Apistogramma*, *Crenicichla*, *Cichlasoma* and *Bujurquina* (Cichlidae); *Hypostomus*, *Loricariichthys*, *Rineloricaria* and *Farlowella* (Loricariidae); *Pimelodella* (Pimelodidae).

Etymology- *Caudimaculosus*, with spots on tail. From the Latin, caudi and maculosus meaning, tail and spots, respectively.



FIGURE 1. Lateral view of *Apteronotus caudimaculosus* MZUSP 79359. Holotype, male, 286.8 mm TL.

Apteronotus albifrons species complex and its monophyly

Based on the description of *A. caudimaculosus* and previous studies (e.g., de Santana, 2002), it is hypothesized that the widespread populations of *A. albifrons*, represent a species complex. The pale bands on the tail, considered to be diagnostic character for a single species actually represent a synapomorphy for this monophyletic clade. This premise is reinforced by the presence in this group of some undescribed species, as illustrated in Planquette et al. (1996: 405, 407). A uniquely derived character among the Gymnotiformes, the presence of two clear bands encircling the caudal peduncle throughout its development defines the *A. albifrons* species complex. A similar feature is observed in individuals of *A. cuchillo*; however, it is only present in specimens below 140.0 mm TL. Currently, I am studying other putative species complexes, in nominal populations of *A. brasiliensis*, *A. leptorhynchus* and *A. rostratus* (e.g., de Santana, 2002). A study concerning the phylogenetic relationships of *Apteronotus* (*sensu stricto*) and a new classification of the genus is in preparation.

A dichotomous key to species of *Apteronotus* (*sensu stricto*)

(Specimens over 100.0 mm TL)

- 1 Body coloration even or finely spotted 3
- Body coloration blotchy or marbled..... 2
- 2 Mouth rictus passing imaginary vertical line at posterior naris; clear band on dorsal region of body; specimens less than 140.0 mm TL with two clear bands on caudal fin peduncle; those over 140.0 mm TL with one clear band encircling base of caudal fin. Distribution: Maracaibo basin, Venezuela.....*A. cuchillo* Schultz, 1949
- Mouth rictus not passing imaginary vertical line with posterior naris; dorsal region evenly colored; clear band encircling base of caudal fin in large specimens. Distribution: Magdalena basin, Colombia*A. magdalenensis* (Milles, 1945)

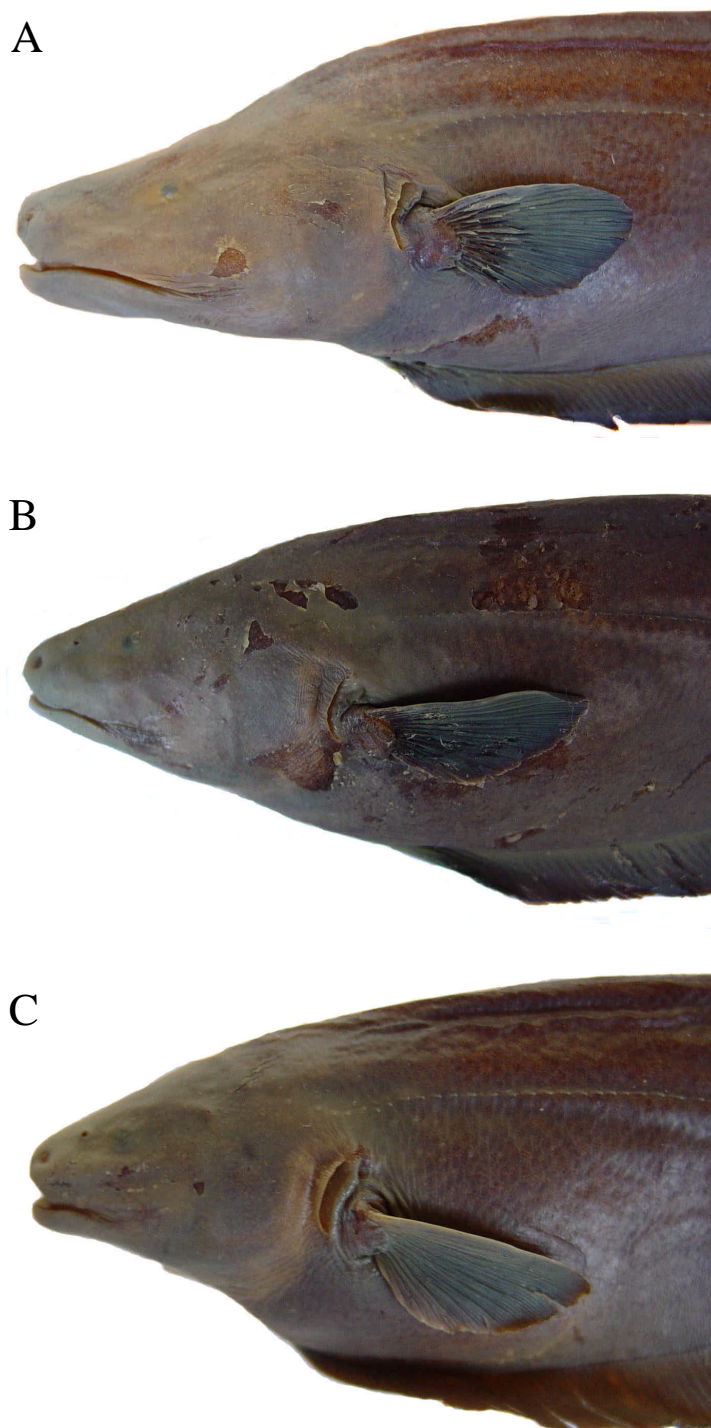


FIGURE 2. Close-up of the head of *Apteronotus caudimaculosus*: (A) holotype, male, 286.8 mm TL; (B) paratype, male 231.1 mm TL, MZUSP 59296; (C) paratype, mature female 175.0 mm TL, MZUSP 59296

- 3 Presence of one clear band encircling caudal fin peduncle throughout development .. 5
 - Presence of two clear bands encircling caudal fin peduncle throughout development...
 4 (*A. albifrons* species complex)
- 4 Absence of spots on first clear band on caudal peduncle; long tail 22.3-23.1% of LEA.
 Distribution: Surinam..... *A. albifrons* (Linnaeus, 1766)
 - Irregular spots on first clear band on caudal peduncle throughout development; short
 tail 10.4-19.2% of LEA. Distribution: Pantanal, central Brazil
 *A. caudimaculosus* n. sp.
- 5 Presence of clear band on dorsal region of body 6
 - Absence of clear band on dorsal region of body 9
- 6 Seven transitional vertebrae. Distribution: Maracaibo basin, Venezuela.....
 *A. cuchillejo* (Schultz, 1949)
 - Three to four transitional vertebrae 7
- 7 Presence of clear band on chin 8
 - Absence of clear band on chin. Distribution: Magdalena basin, Colombia.....
 *A. mariae* (Eigenmann and Fisher, 1914)
- 8 Two rows of teeth on dentary; maxilla without conspicuous ascending process in dor-
 soposterior region; twelve scales above lateral line at mid-body. Distribution: Basins
 of the Guyana shield..... *A. leptorhynchus* species complex (Ellis, 1912)
 - Two rows of teeth on anterior part of dentary and one row on posterior portion; max-
 illa with conspicuous ascending process in dorsoposterior region; nine to ten scales
 above lateral line at mid-body. Distribution: Magdalena basin, Northern basins of
 Colombia and Panama..... *A. rostratus* species complex (Meek and Hildebrand, 1913)
- 9 Mouth rictus reaching an imaginary vertical line with eyes 10
 - Mouth rictus not reaching an imaginary vertical line with eyes 11
- 10 Five to eight scales above lateral line at mid-body. Distribution: Paraná and Paraguay
 River basins..... *A. ellisi* (Arámburu, 1957)
 - More than nine scales above lateral line at mid-body. Distribution: Rio Jurubidá,
 Nuquí (Colombia) *A. jurubidae* (Fowler, 1944)
- 11 Mouth rictus passing an imaginary vertical line at posterior naris; dorsum covered by
 scales; 12 to 16 scales above lateral line at mid-body; two rows of teeth on dentary.
 Distribution: São Francisco, Paraná and Parnaíba river basins.....
 *A. brasiliensis* species complex (Reinhardt, 1852)
 - Mouth rictus not passing an imaginary vertical line at posterior naris; absence of scales
 on dorsal region of body; presence of enlarged fleshy lateral lobe on chin; eight scales
 above lateral line at mid-body; two to three rows of teeth on dentary. Distribution: Rio
 Paraná, Mato Grosso do Sul, Brazil..... *A. marauna* (Triques, 1998)

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Comparative material examined

Apteronotus albifrons- Bolívia- FMNH 106642, 1 ex. Brazil-INPA 6813, 5 ex.; INPA 2037, 2 ex.; INPA 7374, 1 ex.; INPA 765, 4 ex.; INPA 4728, 2 ex.; INPA 3080, 1 ex.; INPA 3959, 1 ex.; INPA 3926, 2 ex.; INPA 3927, 3 ex.; INPA 3928, 12 ex.; INPA 9059, 1 ex.; MCZ 52011, 1 cs ex.; MCZ 52012, 1 cs ex.; MCZ 52013, 1 cs ex.; MNRJ 1202, 2 ex.; MNRJ 1204, 1 ex. MNRJ 8919, 1 ex.; MNRJ 12224, 1 ex.; MNRJ 15736, 2 ex.; MNRJ 18247, 1 ex.; MPEG 3010, 1 ex.; MPEG 4515, 1 ex.; MPEG 3707, 1 ex.; MZUSP 3782, 1 ex.; MZUSP 30080, 2 ex.; MZUSP 30081, 3 ex.; MZUSP 30083, 5 ex.; MZUSP 30084, 4 ex.; MZUSP 22243, 2 ex.; MZUSP 22285, 2 ex.; MZUSP 23391, 1 ex.; MZUSP 24003, 2 ex.; MZUSP 24037, 2 ex.; MZUSP 24190, 1 ex.; MZUSP 24057, 1 ex.; MZUSP 24274, 1 ex.; MZUSP 27700, 1 ex.; MZUSP 31025, 1 ex.; MZUSP 53996, 1 ex.; MZUSP 57350, 1 ex.; USNM 330513, 5 ex.; USNM 191594, 1 ex.; Colombia- ANSP 131645, 2 ex.; ANSP 128200, 5 ex.; ANSP 131644, 2 ex.; ANSP 131466, 2 ex.; Ecuador- ANSP 121617, 1 ex.; FMNH 100614, 1 ex.; USNM 163888, 2 ex.; Guyana- ANSP 177418, 1 ex.; ANSP 39830, 1 ex.; ANSP 39831, 1 ex.; CAS 72122, 3 ex.; FMNH 53292, 2 ex.; USNM 209186, 1 ex.; Paraguay- CAS 72120 [IU 10058], 1 ex.; Peru- CAS 15432 [IU 15432], 1 ex.; CAS (SU) 67968, 1 ex.; FMNH 97013, 2 ex.; MZUSP 26091, 1 ex.; MZUSP 26683, 2 ex.; MZUSP 26732, 1 ex.; UMMZ 207459, 1 cs ex.; USNM 280422, 1 ex.; SIUC 29322, 1 ex.; Surinam- NRM 31667, 1 ex.; Venezuela- ANSP 1668101, 2 ex.; ANSP 177416, 1 ex.; CAS 64413, 2 ex.; CAS 64333, 1 ex.; CU 54661, 3 ex.; CU 72159 5 ex.; CU 72374, 7 ex.; CU 82351, 1 ex.; USNM 233388, 2 ex.; USNM 233250, 1 ex.; USNM 228877, 3 ex.; FMNH 100729,

10 ex., 1 of these cs; FMNH 102102, 3 ex.; FMNH 102106, 1 ex.; FMNH 85490, 2 ex.; *A. anas*.- CAS 56510, 1 ex., holotype; *A. bonapartii*- Peru- SIUC 26941, 1 ex.; SIUC 27974, 1 ex.; SIUC 29321, 3 ex.; SIUC 29429, 3 ex.; *Apteronotus leptorhynchus*- Venezuela- AMNH 91010, 4 ex.; AMNH 91011, 1 ex.; FMNH 70012, 5 ex., 1 cs; FMNH 102100, 8 ex.; INHS 28280, 1 ex.; INHS 31842, 4 ex.; INHS 31863, 4 ex.; USNM 194141, 2 ex.; Guyana- CAS 62333, 1 ex. paratype; FMNH 53294, holotype; FMNH 53295, 1 ex. paratype; INHS 49524, 1 ex.; *Apteronotus cf. leptorhynchus*- Colombia- CAS 72124, 1 ex.; NRM 19739, 1 ex.; NRM 27748, 1 ex.; *Apteronotus rostratus*- Colombia- CAS 72124 [IU 13374], 1 ex.; FMNH 71201, 3 ex.; USNM 317229, 3 ex.; USNM 324044, 1 ex.; USNM 317230, 1 ex.; Panama- AUM 31623, 1 ex.; FMNH 7592, holotype; USNM 324045, 2 ex.; Venezuela- INHS 34978, 1 ex.; INHS 35364, 16 ex.; INHS 35443, 1 ex.; INHS 59949, 1 ex.; INHS 59885, 1 ex.; INHS 60284, 6 ex.; INHS 60468, 1 ex.; MCZ 48686, 2 ex.; MCZ 121595, 6 ex.; USNM 121593, 3 ex.; *Apteronotus brasiliensis*- MNRJ 8991, 1 ex.; MNRJ 8982, 2 ex.; MNRJ 17037, 1 ex.; MNRJ 19185, 1 ex.; MZUSP 22512, 2 ex.; MZUSP 45663, 1 ex.; *Apteronotus cuchillo*- CU 82193, 4 ex.; USNM 121587, paratypes, 13 ex.; USNM 121588, paratypes, 3 ex.; USNM 121589, paratypes, 11 ex.; USNM 121590, paratypes, 7 ex.; USNM 121591, holotype; *Apteronotus macrostomus*- ANSP 70528, holotype; CAS 123728, 1 ex.; UF 36604, 5 ex.; *Apteronotus magdalenensis*- USNM 123795, paratype, 1 ex.; *Sternachogiton cuchillejo*- USNM 121598, paratypes, 7 ex.; USNM 121599, paratypes, 39 ex.; USNM 121600, holotype; USNM 121601, paratypes, 5 ex.; USNM 121602, paratypes, 10 ex.; *Apteronotus mariae*- FMNH 56774, holotype; CAS 62345, paratype, 1 ex.; *Apteronotus jurubidae*- ANSP 71435, holotype; *Apteronotus cf. jurubidae*- NRM 27739, 2 ex. *Apteronotus* sp.- Brazil- MZUSP 23095, 24 ex.; MZUSP 24463, 11 ex.; Venezuela- CU 72164, 2 ex.; CU 78520, 1 ex.; CU 78556, 3 ex.; CU 78564, 5 ex.; CU 78616, 1 ex.; CU 78631, 1 ex.; CU 78679, 2 ex.; CU 78722, 2 ex.; CU 78778, 2 ex.; CU 82349, 11 ex.; CU 82441, 2 ex.; CU 82442, 1 ex.; CU 82443, 10 ex.; CU 82446, 2 ex.; Colombia- UF 23847, 1 ex.; UF 23848, 1 ex.; UF 23849, 1 ex.; UF 23850, 1 ex.; UF 23851, 1 ex.; UF 23852, 1 ex.; UF 23854, 2 ex.; UF 33218, 1 ex.; UF 33310, 1 ex. *Parapteronotus hasemani*- FMNH 54562, holotype; FMNH 15199, 1 ex., paratype; FMNH 15200, 1 ex., paratype; FMNH 92070, 13 ex., paratypes; Brazil- MZUSP 6557, 3 ex.; MZUSP 24928, 4 ex.; MZUSP 32203, 1 ex.; MZUSP 44497, 5 ex.

References cited

- Albert, J.S. (2001) Species diversity and phylogenetical systematics of American knifefishes (Gymnotiformes, Teleostei). *Miscellaneous Publications, Museum of Zoology, University of Michigan*, 190, 1-129.
- Albert, J.S. & Campos-da-Paz, R. (1998) Phylogenetic systematics of Gymnotiformes with diagnoses of 58 clades: a review of available data. In: Malabarba, L.R., Reis, R.E., Vari, R.P., Lucena, Z.M. S. & Lucena, C.A.S. (Eds). *Phylogeny and Classification of Neotropical Fishes*. Edipucrs, Porto Alegre, Brazil, pp. 419-446.

- Campos-da-Paz, R. (1997) *Sistemática e Taxonomia dos Peixes Elétricos das Bacias dos Rios Paraguai, Paraná e São Francisco, com Notas Sobre espécies Presentes em Rios Costeiros do Leste do Brasil (Teleostei: Ostariophysi: Gymnotiformes)*. Tese de Doutorado. Não Publicado. Instituto de Biociências da Universidade de São Paulo, 314 pp.
- Campos-da-Paz, R. (1999) New species of *Megadontognathus* from the Amazon Basin, with phylogenetic and taxonomic discussions on the genus (Gymnotiformes: Apterontidae). *Copeia* 1999, 1041-1049.
- Cox-Fernandes, C. (1998) Sex-related morphological variation in two 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-fishes snouts: hypermorphic facial growth in male *Apterontus hasemani* and the identity of *Apterontus anas* (Gymnotiformes: Apterontidae). *Copeia*, 2002, 52-61.
- Dunlap, K.D., Thomas, P. & Zakon, H.H. (1998) Diversity of sexual dimorphism in electrocommunication signals and its androgen regulation in a genus of electric fish, *Apterontus*. *Journal of Comparative Physiology A*, 183, 77-86.
- Ellis, M.M. (1913) The gymnotid eels of tropical America. *Memoirs of the Carnegie Museum*, 6(3), 109-195.
- Eschmeyer, W.N. (1998) *Catalog of fishes*. San Francisco. California Academy of Sciences, 1, 956 pp.
- Mago-Leccia, F. (1994) *Electric Fishes of Continental Waters of America*. Fundacion para el Desarrollo de las Ciencias Fisicas, Matematicas y Naturales, 207 pp.
- Planquette, P., Keith P. & Le Bail, P.Y. (1996) *Atlas des poisons d'Eau douce de Guyane*. Paris. Tome 1. Patrimoines Naturels, 22, 429pp.
- de Santana, C.D. (2002) "*Apterontus*" (*sensu stricto*) (Gymnotiformes: Apterontidae): *Monofiletismo, Sistemática, e Diversidade Subestimada em Peixes Elétricos Neotropicais*. Unpubl. Master's thesis, Universidade Federal de Pernambuco, Pernambuco, Brazil, 394pp.
- Strussmann, C., Prado, C.P.A., Utenabaro, M., Ferreira, V.L. & Willink, P. W. (2000) Gazetteer. In: Willink, P.W., Chernoff, B., Alonso, L.E., Montalbault, J.R. & Lourival, R. (Ed) *A Biological Assessment of the Aquatic Ecosystems of Pantanal, Mato Grosso do Sul, Brasil*. RAP Bulletin of Biological Assessment 18, Conservation International, Washington, DC, pp. 109-121.
- Willink, P. W., Froelich, O., Machado-Alison, A., Menezes, N. A., Oyakawa, Catella, O. A. C., Chernoff, B., Lima, F. C. T., Toledo-Piza, M., Ortega, H., Zanata, A. & Barriga, R. (2000) Fishes of the rios Negro, Negrinho, Taboco, Aquidauana, Taquari and Miranda, Pantanal, Brasil: diversity, distribution, critical habitats, and value. In: Willink, P. W., Chernoff, B., Alonso, L. E., Montalbault, J. R. & Lourival, R. (Ed). *A biological Assessment of the Aquatic Ecosystems of Pantanal, Mato Grosso do Sul, Brasil*. RAP Bulletin of Biological Assessment 18, Conservation International, Washington, DC, pp. 63-81.