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ORIGINAL ARTICLE

Sexual dimorphism in the electric knifefish, *Gymnorhamphichthys rondoni* (Rhamphichthyidae: Gymnotiformes)

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ABSTRACT

Sexual dimorfism refers to morphological differences between males and females of a species. It may be a result of different selection pressures acting on either or both sexes and may occur in any sexually-reproducing dioecious species, including fishes. We analyzed 63 females and 63 adult males of *Gymnorhamphichthys rondoni* (Gymnotiformes) collected by us or deposited in museum collections. Sex was identified through abdominal dissection. We measured length from snout to posterior end of anal-fin, anal-fin length, distance from anus to anal-fin origin, distance from genital papilla to anal-fin origin, body width at beginning of anal-fin, and head length. Morphometric data submitted to a Principal Component Analysis (PCA) grouped males and females according to variables related to body size (along the first component) and to head length and body height along the second and third components. Females were larger than males, whereas males had proportionally larger heads and higher bodies than females. The urogenital papilla of males and females showed differences in shape, size and relative position on the body. The female papilla was elongated horizontally, larger than that of males, and was located on a vertical line below the eye, while the papilla of the males was vertically elongated and located on a vertical line below the operculum. To our knowledge, this is the first recorded case of sexual dimorphism in a species of Rhamphichthyidae, a condition that is now known in all the currently recognized families of Gymnotiformes.

KEYWORDS: electric fish, head morphology, morphological variation, sexual differences, urogenital papilla

Dimorfismo sexual no peixe elétrico, *Gymnorhamphichthys rondoni* (Rhamphichthyidae: Gymnotiformes)

RESUMO

Dimorfismo sexual é caracterizado por diferenças entre machos e fêmeas de uma espécie. Pode estar presente em qualquer ser vivo dioico que se reproduza sexualmente, inclusive peixes. Analisamos 63 fêmeas e 63 machos adultos de *Gymnorhamphichthys rondoni* (Gymnotiformes) coletados por nós ou obtidos em coleções. O sexo foi determinado por dissecção abdominal. Medimos o comprimento do focinho até o final da origem da nadadeira anal, comprimento da nadadeira anal, distância da papila genital até a origem da nadadeira anal, distância do ânus até a origem da nadadeira anal, altura do corpo e comprimento da cabeça. Dados morfométricos submetidos a uma Análise de Componentes Principais (PCA) agruparam machos e fêmeas de *G. rondoni* em função de variáveis relacionadas ao tamanho do corpo ao longo do primeiro componente, ao comprimento da cabeça e à altura do corpo ao longo do segundo e terceiro componentes. Fêmeas foram maiores que os machos, enquanto machos tiveram a cabeça proporcionalmente maior e o corpo mais alto que as fêmeas. A papila urogenital de machos e fêmeas diferiu no formato, tamanho e posição relativa no corpo. A papila das fêmeas foi alongada horizontalmente, maior que a dos machos e localizada na linha vertical abaixo do olho, enquanto que a papila dos machos foi alongada verticalmente e localizada na linha vertical abaixo do opérculo. Até onde sabemos, esse é o primeiro caso registrado de dimorfismo sexual em uma espécie de Rhamphichthyidae, uma condição que é agora conhecida para todas as famílias atualmente reconhecidas de Gymnotiformes.

PALAVRAS-CHAVE: peixe elétrico, morfologia da cabeça, variação morfológica, diferenças sexuais, papila urogenital

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INTRODUCTION

Sexual dimorphism refers to differences between males and females of a species in secondary sex-related features, like body size, color pattern, morphological details of specific body parts, and behavior. Sexual dimorphism may be present in any sexually-reproducing dioecious organism, including plants (e.g. Lloyd and Webb 1977; Barret 2002; Tsuji and Fukami 2018) and animals (e.g. Garcia *et al.* 2006; Loker and Brant 2006; Ceballos *et al.* 2013). Darwin (1871) described several examples of sexual dimorphism when proposing his theory of sexual selection, and Andersson (1994) postulated that sexual dimorphism would result from different sexual selection pressures acting on the two sexes.

For fish, secondary sexual dimorphism has been recorded in body size (e.g. Parker 1992; Erlandsson and Ribbink 1997; Neat *et al*. 1998; McMillan 1999; Morbey 2018), fin size and shape (e.g. Skjæraasen *et al*. 2006; Pires *et al*. 2016), color pattern (e.g. Robertson and Warner 1978; Karino and Someya 2007), and head morphology (e.g. Hastings 1991; Gramitto and Coen 1997; Cox Fernandes 1998; Cox Fernandes *et al*. 2002, 2009; de Santana and Vari 2010). In some species, jaws, mouth and snout are larger in males than in females (Goto 1984; Crabtree 1985). Dentition may also be sexually dimorphic, with differences between males and females in number, shape and arrangement of teeth (Gomes and Tomas 1991; Kajiura and Tricas 1996; Böhlke 1997; Rapp Py-Daniel and Cox Fernandes 2005; de Santana and Vari 2010). The shape of the urogenital papilla may also differ between males and females (Esmaeili *et al.* 2017).

Secondary sexual dimorphism may also be expressed in communication systems, such as in sound-producing mechanisms (Ali *et al.* 2016; Parmentier *et al*. 2018) or as differences in electrical signal repertoires of male and female electric fishes (Fugere and Krake 2009; Ho *et al.* 2010, 2013). Among Neotropical electric fishes of the order Gymnotiformes, the most common forms of sexual dimorphism occur in body size (Hilton and Cox Fernandes 2006; de Santana and Cox Fernandes 2012), snout shape (de Santana 2003; Albert and Crampton 2009; Evans *et al.* 2018), and caudal filament size and shape (Hopkins *et al.* 1990; Giora *et al.* 2008). Differences in mouth shape, position and shape of teeth (de Santana and Vari 2010; Cox Fernandes *et al*. 2010), and electric organ discharge (Nogueira 2006; de Santana and Crampton 2007; Smith and Combs 2008; Fugere and Krake 2009; Ho *et al.* 2010, 2013) have also been reported.

Rapp Py-Daniel and Cox Fernandes (2005) discuss the evolution of sexual dimorphism in Gymnotiformes by mapping sex-related features on phylogenetic hypotheses and presenting evidences that secondary sexual differences arose independently both among the gymnotiform families and inside Apteronotidae, where most cases of sexual dimorphism in electric knifefishes were reported (de Santana 2003; Hilton and Cox Fernandes 2006; Albert and Crampton 2009; Cox Fernandes *et al.* 2010; de Santana and Vari 2010; Ho *et al.* 2013). Sexual dimorphism in Hypopomidae (Hopkins *et al.* 1990; Hopkins 1999; Giora *et al.* 2008; Gavassa *et al.* 2013), Gymnotidae (Mendes-Júnior 2015) and in Sternopygidae (Zakon *et al.* 1991; Giora and Fialho 2009; Vari *et al.* 2012) has also been reported. However, for Rhamphichthyidae (*Ramphichthys* + *Gymnorhamphicthys* + *Iracema* + *Hypopygus* + *Steatogenys*; Carvalho 2013; Tagliacollo *et al.* 2015) we have found no recorded instances of sexual dimorphism in the literature.

Recently, we had the opportunity to study the reproductive biology and spatial distribution of individuals of *Gymnorhamphichthys rondoni* (Miranda Ribeiro, 1920), a strictly psammophilous electric knifefish widely distributed in the Amazon Basin and a common inhabitant of upland forest streams of the Brazilian Amazon (Zuanon *et al*. 2006; Carvalho 2013). During the study, we noted differences in the proportional size of the head, as well as in the conspicuousness of the urogenital papilla between male and female specimens, which suggested a possible case of sexual dimorphism. Therefore, our objective was to evaluate the occurrence of secondary sexual dimorphism in a population of *G. rondoni* in a Central Amazon forest stream by analyzing external morphometric parameters.

MATERIAL AND METHODS

We collected 45 adult individuals (36 females and nine males) of *Gymnorhamphichthys rondoni* using an electric fish detector (Crampton *et al.* 2007) and hand nets in a *terra firme* forest stream at Fazenda Dimona of the Biological Dynamics of Forest Fragments Project (BDFFP - http://pdbff.inpa.gov.br/), located about 80 km north of Manaus, Amazonas state, Brazil. The studied forest stream is a tributary of the Cuieiras River in the Negro River basin, in the central Brazilian Amazon. The studied stream section (2°21'1.41"S, 60°5'44.31"W) has a width of 3 – 5 m, maximum depth of 1.5 m, a predominantly sandy substrate with coarse litter deposits, and the channel almost completely shaded by riparian forest canopy. The water was clear, acidic (pH ~5.0), with low electric conductivity (~10 $\mu S*cm^{-1}$), and temperature of 23-24 °C. In addition to the collected fish, we also used preserved specimens from the Fish Collection of the Instituto Nacional de Pesquisas da Amazônia (INPA-ICT). All specimens had the abdominal cavity opened for identification of sex via gonadal examination. We retained for subsequent analyzes only the adult specimens (i.e. those with gonads classified as in late maturation, spawning or regenerating, according to definitions by Brown-Peterson *et al.* 2011). Combining the 45 specimens collected by us with 81 adult specimens from INPA's Fish Collection we had a final sample of 63 females and 63 males (Supplementary Material, Table S1).

To quantify morphological characteristics, we used digital calipers and measured (in mm) the length of snout to posterior end of anal-fin (LEA), length of anal-fin length (LAF), distance from anus to anal-fin origin (DAAF), distance from the genital papilla to anal-fin origin (DPAF), body height (BH), and head length (HL) (Figure 1). Morphometric differences between males and females were tested with a Kruskal-Wallis test, as the data distribution lacked normality. The morphometric variables were also analyzed using Principal Component Analysis (PCA) via R statistical software (R Core Team 2016). Since the first component usually is strongly influenced by the size of the specimens, we plotted the data considering the first principal component (PC1 x PC2) and the next two components (PC2 x PC3) to depict the ordination without the effect of body size.

To check for occurrence of sexual dimorphism in the urogenital papilla, we used an extended focus stereomicroscope to produce lateral and ventral images of the papillae of adult male and female *G. rondoni*. All the procedures in this study involving animals were in accordance with and duly approved by the Ethics Committee on Animal Use (CEUA/INPA, protocol #022/2016).

RESULTS

The morphometric analysis showed that female *G. rondoni* had a longer anal-fin (LAF), a larger distance between the urogenital papilla and the anal-fin origin (DPAF) and a larger distance from the anus to the anal-fin origin (DAAF), whereas males presented a longer head (HL) (Figure 2, Table 1).

The first three morphometric-based PCA components explained 64.5%, 21% and 8.4% of observed variance, respectively (Figure 3). The first principal component (PC1) was strongly influenced by negative values of variables related to body size of the specimens, such as length from snout to posterior end of anal-fin (LEA) and LAF. The second component (PC2) was positively influenced by head length (HL) and negatively by DPAF and DAAF. The third component was negatively influenced by HL and positively by LAF (Table 2). PCA ordination separated males and females of *G. rondoni* mainly along the second principal component (Figures 3a and 3b). Females were larger than males, had a shorter head and body heigth, and a wider distance between the urogenital papilla and the anal fin origin, whereas males were smaller, had a longer head and a higher body height, and a smaller space between the urogenital papilla and the anal fin origin.

We found differences in the shape and position of the urogenital papilla between males and females (Figure 4). Female papillae were more horizontally elongated and approximately 10 times larger than those of males, and were located on a vertical line below the eye, while male papillae were located on a vertical line below the operculum. In females, papillae may expand remarkably during oocyte passage (Figures 4g and 4h).

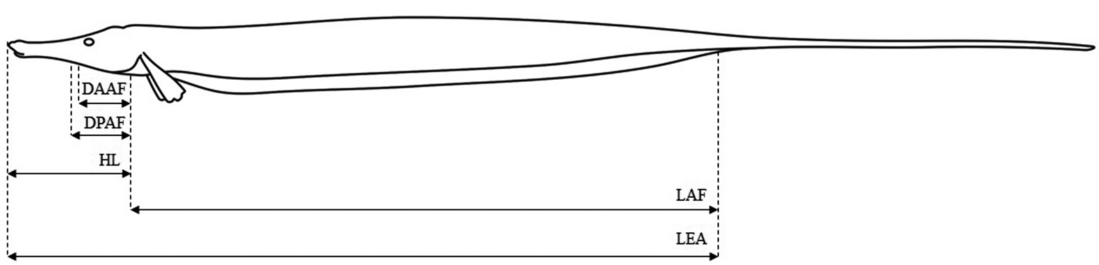

Figure 1. Schematic drawing of *Gymnorhamphichthys rondoni* in lateral view showing the morphological measurements used in this study: DAAF = distance from anus to anal-fin origin; DPAF = distance from urogenital papilla to anal-fin origin; HL = head length; LAF = length of anal-fin; LEA = length from snout to posterior end of anal-fin.

Figure 2. Images of a female and male *Gymnorhamphichthys rondoni* collected in a forest stream tributary of the Cuieiras River in the Negro River basin, central Brazilian Amazon. LEA female = 123.74 mm; LEA male = 117.3 mm. Scale bars = 10 mm

Table 1. Summary of morphometric measurements (median (minimum – maximum)) in mm, and statistics of the Kruskal-Wallis rank sum test for females (n=63) and males (n=63) of *Gymnorhamphichthys rondoni*. For all tests, df = 1. Values followed by * indicate significant differences between genders.

Measurements	Females	Males	H	p-value
Length from snout to posterior end of anal-fin (LEA)	129.99 (77.19 - 185.15)	126.3 (102.1 - 153.3)	0.9006	0.3426
Length of anal-fin (LAF)	103.54 (60.32 - 143.50)	94.56 (65.38 - 120.87)	54.736	0.01931*
Distance from the urogenital papilla to the anal-fin origin (DPAF)	13.65 (2.24 - 22.14)	4.32 (2.42 - 5.88)	82.678	2.20E-16*
Distance from the anus to the anal-fin origin (DAAF)	11.070 (0.94 - 19.310)	4.82 (2.67 - 6.64)	67.635	2.20E-16*
Body height (BH)	4.05 (2.05 - 6.65)	4.03 (3.07 - 5.09)	0.45012	0.5023
Head length (HL)	28.18 (12.13 - 40.53)	32.01 (26.17 - 38.79)	14.042	0.0001788*

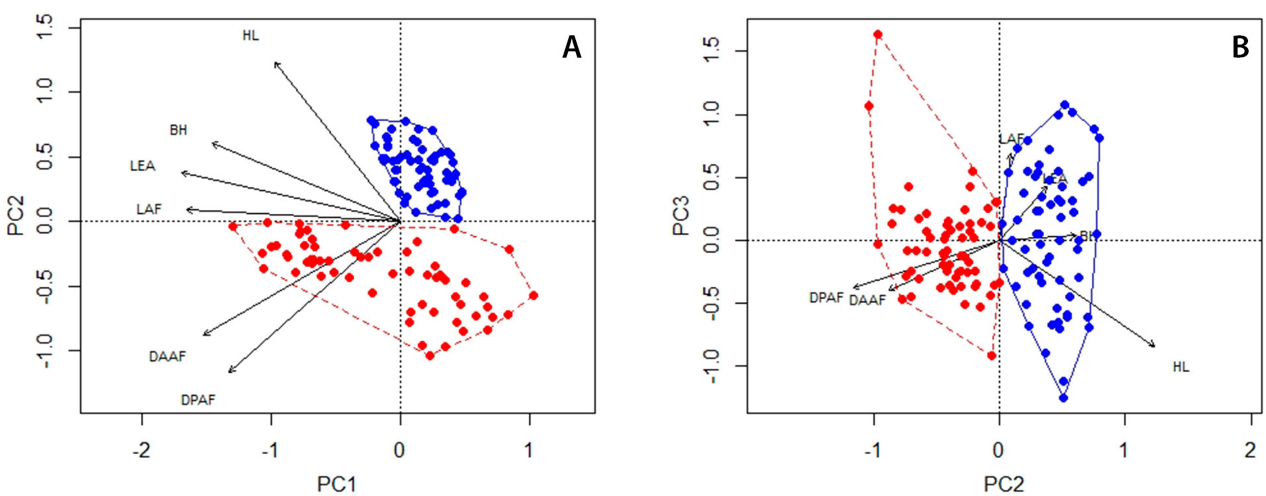

Figure 3. Principal Component Analysis of morphometric data of male and female specimens of *Gymnorhamphichthys rondoni* showing (a) the first and second components (PC1 x PC2), and (b) the second and third components (PC2 x PC3). Blue dots = males, red dots = females. HL = head length; BH = body height; LEA = length from snout to posterior end of anal-fin; LAF = length of anal-fin; DAAF = distance from anus to anal-fin origin; DPAF = distance from urogenital papilla to anal-fin origin. This figure is in color in the electronic version.

Table 2. Variable loadings on the first two principal components (PCs) for *Gymnorhamphichthys rondoni* (n= 126)

Measurements	PC1	PC2	PC3
Length from snout to posterior end of anal-fin (LEA)	-1.995	0.4436	0.5030
Length of anal-fin (LAF)	-1.944	0.1023	0.8152
Distance from the urogenital papilla to the anal-fin origin (DPAF)	-1.559	-1.3665	-0.4481
Distance from the anus to the anal-fin origin (DAAF)	-1.790	-1.0331	-0.4671
Body height (BH)	-1.718	0.7164	0.0462
Head length (HL)	-1.147	1.4522	-0.9878
Explained variance	64.5	21.0	8.4
Cumulative variance (%)	64.5	85.5	93.9

DISCUSSION

The observed sexual dimorphism in *G. rondoni* was related to body size, anal fin length, head length and to urogenital papilla shape and relative position on the body. Males had a proportionally larger head than females, whereas females had a longer anal fin, a larger distance between the urogenital papilla and the anal-fin origin, and a larger distance from the anus to the anal-fin origin. In females the papilla was elongated horizontally, longer than that of males and located on the vertical line below the eye. In males the papila was vertically elongated, smaller than that of females and located on a vertical line below the opercular opening. As far as we searched the scientific litterature, this is the first recorded case of sexual dimorphism in a species of Rhamphichthyidae.

In Gymnotiformes, it is relatively common to find sexual dimorphism in head shape and snout size (de Santana 2003; Albert and Crampton 2009). Tooth shape, size and

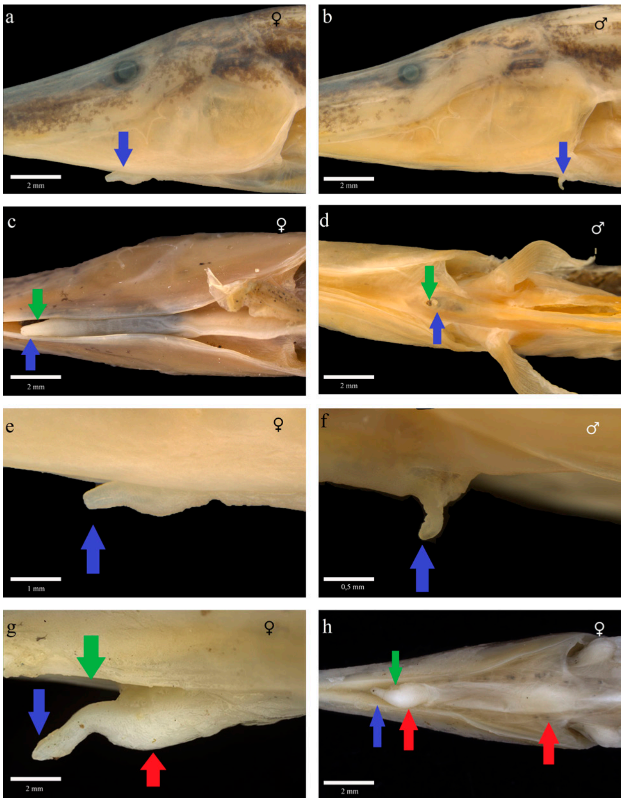

Figure 4. Urogenital papilla of female and male *Gymnorhamphichthys rondoni*. In all images, the anterior portion of the body is towards the left. (a) Side view of head of a female showing urogenital papilla (blue arrow). (b) Side view of head of a male showing urogenital papilla (blue arrow). (c) Ventral view of head of a female showing urogenital papilla (blue arrow) and anus (green arrow). (d) Ventral view of head of a male showing urogenital papilla (blue arrow) and anus (green arrow). (e) Side view of female urogenital papilla. (f) Side view of male urogenital papilla. (g) Side view of urogenital papilla of a female with an oocyte (red arrow) inside. (h) Ventral view of head of a female with oocyte at the end of urogenital papilla. Blue arrow = urogenital papilla, green arrow = anus, red arrow = oocyte position. LEA female = 145.83 mm; LEA male = 144.83 mm. This figure is in color in the electronic version.

position also differ between genders of several species of the apteronotid genus *Sternarchorhynchus* (de Santana and Vari 2010), and in "super-males" of *Sternarchogiton nattereri* (Cox Fernandes *et al.* 2010), in which males have hypertrophied and partially exteriorized teeth that seems to be related to male-male conflicts, or to their use when courting females (Cox Fernandes *et al.* 2010). However, the ecological or behavioral meaning of the larger head in male *G. rondoni* is not clear. Contrary to the obvious potential use of a hyperthophied mouth and teeth during aggressive encounters or agonistic displays by male apteronotid knifefishes, the small mouth and delicate tubular snout of male *G. rondoni* seems of little value during a male-male conflict. A possible alternative explanation for such a sexually dimorphic characteristic may be related to differences in foraging tactics or microhabitat use between genders, which remains to be verified.

Sexual dimorphism of the Gymnotiform urogenital papilla position was reported for 15 species of *Sternarchorhynchus* (Santana and Vari 2010). However, unlike *G. rondoni,* in *Sternarchorhynchus* species the urogenital papilla of males is located in a more anterior position on the body compared to females (de Santana and Vari 2010). In addition to this form of dimorphism, Cox Fernandes *et al.* (2014) also found a difference in the size of the urogenital papillae in *Procerusternarchus pixuna* (Hypopomidae), with male papillae smaller than those of females, as recorded here for *G. rondoni*.

When describing *Gymnorhamphichthys rosamariae*, Schwassmann (1989) reported mature males and females with elongated urogenital papillae and located at the vertical line passing through the eye, and that papilla growth and position are related to gonad development. In this way, papillae larger and closer to the eye line would indicate reproductively mature individuals, regardless of sex. There are records in Gymnotiformes species of the anus and urogenital papilla changing position on the body during ontogeny, moving gradually from the posterior region of the abdominal cavity to the cephalic region (e.g. *Apteronotus caudimaculosus*: de Santana 2003; *Archolaemus blax*: Vari *et al.* 2012; *Distocyclus conirostris:* Dutra *et al.* 2014; *Eigenmannia besouro*: Peixoto and Wosiacki 2016; *E. meeki*: Dutra *et al.* 2017; and *E. sayona:* Peixoto and Waltz 2017). This change in the relative position of the anus and urogenital papila was not detected in other examined apteronotids (*Apteronotus eschmeyeri*: de Santana *et al.* 2004; *Sternarchogiton labiatus*: de Santana and Crampton 2007; *S. nattereri*: de Santana and Crampton 2007, and Crampton 2007; *Apteronotus anu*: de Santana and Vari 2013; *A. baniwa*: de Santana and Vari 2013). We did not find evidence of an ontogenetic change in the position of the urogenital papilla of *G. rondoni*, as our study was limited to the analysis of adult specimens, which prevented the detection of ontogenetic variations.

The presence of larger urogenital papillae in females than in males may be related to the size of the gametes to be released, so that this characteristic should be more apparent in those species whith proportionately larger oocytes, such as *G. rondoni* (Garcia and Zuanon, unpublished data). On the other hand, the elongated urogenital papilla of Gymnotiform females may be related to some tactic of oocyte deposition. *Gymnorhamphichthys rondoni* lives only in places where the substrate is composed largely of sand, in which individuals remain buried during the day, emerging only at night to forage and perform reproductive activities (Zuanon *et al.* 2006). It is therefore possible that the horizontally elongated papilla aid in selection of oviposition sites, which remains to be studied. At the moment, we lack a functional explanation for the difference in the position of the urogenital papilla and anus observed in male and female *G. rondoni*. An anatomical study involving a complete ontogenetic series from the larval phase to sexually mature adults, would likely help to better understand the process and the biological significance of the differences reported here.

In a review of the Rhamphichthyoidea, Carvalho (2013) did not mention the occurrence of sexual dimorphism in species of *Rhamphichthys, Gymnorhamphichthys* or in *Iracema caiana* (Rhamphichthyinae *sensu* Carvalho 2013). However, our study found sexual dimorphism in relation to head length and the shape, size and position of urogenital papila for *G. rondoni*. Accordingly, it is possible that this species might also show sexual dimorphism in other characteristics, such as electric organ discharge patterns or in behavioral aspects, which deserve to be investigated.

CONCLUSIONS

The description and quantification of secondary sexual differences in a rhamphichthyid species may help providing important new information for the understanding of the evolution of sexual dimorphism among Gymnotiformes. Moreover, the known occurrence of external morphological differences could allow sex identification of living individuals in ecological or behavioral studies, avoiding the unnecessary sacrifice of fish and reducing impacts in natural populations, which may be specially important in protected areas.

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SUPPLEMENTARY MATERIAL (only available in the electronic version)

GARCIA & ZUANON. Sexual dimorphism in the electric knifefish, *Gymnorhamphichthys rondoni* (Rhamphichthyidae: Gymnotiformes)

Table S1. Measurements (mm) used in the study of sexual dimorphism of females (F) and males (M) of *Gymnorhamphichthys rondoni*. LEA – length from snout to posterior end of anal fin, LAF – length of anal fin, DPAF – distance from urogenital papilla to anal fin, DAAF – distance from anus to anal fin, BH – body height, HL – length of head. DIMONA = study area at the BDFF Project; INPA-ICT = specimens from INPA's ichthyological collection. * = Uncatalogued specimen.

Code	LEA	LAF	DPAF	DAAF	BH	HL	Sex	Source	Catalog Number	Drainage
F1	149.94	115.8	17.67	15.61	5.8	33.37	F	DIMONA	*	Negro River
F2	155.06	124.27	15.52	14.92	4.92	32.44	F	DIMONA	*	Negro River
F3	152.18	118.87	17.39	15.52	4.32	34.48	F	DIMONA	*	Negro River
F4	140.84	112.48	13.61	9.92	4.05	28.61	F	DIMONA	*	Negro River
F5	128.77	102.64	13.04	9.26	3.86	26.53	F	DIMONA	*	Negro River
F6	117.98	94.4	11.11	9.79	3.94	12.26	F	DIMONA	*	Negro River
F7	159.11	124.93	19.65	17.72	4.95	36.5	F	DIMONA	*	Negro River
F8	151.48	121.22	17.65	14.92	5.05	32.19	F	DIMONA	*	Negro River
F9	148.26	116.12	16.38	14.73	4.47	32.76	F	DIMONA	*	Negro River
F10	145.52	118.54	12.8	11.07	4.48	28.06	F	DIMONA	*	Negro River
F11	167.47	131.73	20.68	18.08	6.06	34.53	F	DIMONA	*	Negro River
F12	171.96	134.28	21.61	19.31	4.85	37.02	F	DIMONA	*	Negro River
F13	171.88	135.5	20.13	17.22	4.91	37.2	F	DIMONA	*	Negro River
F14	159.1	124.65	19.26	16.69	5.56	34.05	F	DIMONA	*	Negro River
F15	161.94	125.71	19.62	17.37	5.73	35.59	F	DIMONA	*	Negro River
F16	157.52	125.81	17.78	14.81	5.12	31.13	F	DIMONA	*	Negro River
F17	160.86	125.74	19.4	16.43	6.65	35.96	F	DIMONA	*	Negro River
F18	159.12	127.17	19.33	17.05	4.84	33.47	F	DIMONA	*	Negro River
F19	131.72	103.54	14.9	12.43	4.29	26.19	F	DIMONA	*	Negro River
F20	119.28	93.47	10.33	9.78	4.12	25.07	F	DIMONA	*	Negro River
F21	77.19	60.32	3.29	2.55	2.44	17.11	F	DIMONA	*	Negro River
F22	185.15	143.5	22.14	18.9	5.63	40.53	F	DIMONA	*	Negro River
F23	158.9	121.08	17.68	15.23	5.01	36.89	F	DIMONA	*	Negro River
F24	154.37	123.02	17.18	14.95	5.14	31.42	F	DIMONA	*	Negro River
F25	162.68	128.36	16.06	13.62	4.62	33.33	F	DIMONA	*	Negro River
F26	164.05	132.24	16.24	13.84	5.18	32.86	F	DIMONA	*	Negro River
F27	164.85	130.47	16.01	13.51	4.61	34.5	F	DIMONA	*	Negro River
F28	167.98	134.25	16.3	12.73	5	33.73	F	DIMONA	*	Negro River
F29	140.56	112.06	14.98	13.82	4.45	28.69	F	DIMONA	*	Negro River
F30	137.41	107.57	13.88	12.24	4.32	30.41	F	DIMONA	*	Negro River
F31	152.8	119.8	17.8	15.89	4.84	33.1	F	DIMONA	*	Negro River
F32	95.14	75.54	2.24	0.94	2.67	20.11	F	DIMONA	*	Negro River
F33	152.23	123.83	16.8	16.01	4.25	32.01	F	DIMONA	*	Negro River
F34	151.27	120.43	11.79	11.33	4.53	31.09	F	DIMONA	*	Negro River
F35	133.93	107.32	11.69	10.82	4.09	29.07	F	DIMONA	*	Negro River
F36	141.96	111.79	16.52	15.5	4.6	31.86	F	DIMONA	*	Negro River
F37	123.74	111.61	9.42	6.16	2.68	12.13	F	INPA-ICT	INPA-ICT 014995	Negro River
F38	126.35	92.65	13.54	6.15	2.59	33.7	F	INPA-ICT	INPA-ICT 015876	Negro River
F39	104.07	77.29	9.89	6.28	2.24	26.78	F	INPA-ICT	INPA-ICT 020101	Negro River
F40	108.33	74.29	9.91	5.4	2.41	34.04	F	INPA-ICT	INPA-ICT 020101	Negro River
F41	114.19	87.54	10.81	6.79	2.65	26.65	F	INPA-ICT	INPA-ICT 022461	Negro River
F42	120.52	94.68	11.74	6.65	3.08	25.84	F	INPA-ICT	INPA-ICT 023164	Negro River
F43	111.52	84.55	11.37	6.92	2.99	26.97	F	INPA-ICT	INPA-ICT 023223	Negro River
F44	111.03	84.61	11.1	6.72	2.78	26.42	F	INPA-ICT	INPA-ICT 024657	Negro River
F45	121.85	97.41	14.64	6.99	2.88	24.44	F	INPA-ICT	INPA-ICT 024657	Negro River
F46	115.9	90.41	10.25	7.41	3	25.49	F	INPA-ICT	INPA-ICT 024657	Negro River

Table S1. Continued.

Code	LEA	LAF	DPAF	DAAF	BH	HL	Sex	Source	Catalog Number	Drainage
F47	95.03	76.86	8.65	6.34	2.3	18.17	F	INPA-ICT	INPA-ICT 024657	Negro River
F48	107.67	81.15	10.93	7.39	3.74	26.52	F	INPA-ICT	INPA-ICT 024657	Negro River
F49	107.24	86.56	11.9	6.47	2.58	20.68	F	INPA-ICT	INPA-ICT 029952	Negro River
F50	113.27	87	11.52	6.1	2.73	26.27	F	INPA-ICT	INPA-ICT 029952	Negro River
F51	88.12	66.64	9.22	6.19	2.33	21.48	F	INPA-ICT	INPA-ICT 029963	Negro River
F52	104.86	82.52	9.28	7.44	3.05	22.34	F	INPA-ICT	INPA-ICT 029963	Negro River
F53	97.65	74.7	8.3	5.52	2.19	22.95	F	INPA-ICT	INPA-ICT 029963	Negro River
F54	101.08	81.35	10.79	7.93	2.67	19.73	F	INPA-ICT	INPA-ICT 029963	Negro River
F55	129.29	101.21	10.25	8.33	3.41	28.08	F	INPA-ICT	INPA-ICT 030026	Preto da Eva River
F56	99.58	75.77	10	8.48	2.8	23.81	F	INPA-ICT	INPA-ICT 030026	Preto da Eva River
F57	114.63	88.32	14.54	12.87	3.18	26.31	F	INPA-ICT	INPA-ICT 030026	Preto da Eva River
F58	101.95	77.68	12.87	10.33	3.6	24.27	F	INPA-ICT	INPA-ICT 030026	Preto da Eva River
F59	118.64	92.57	13.33	11.93	3.05	26.07	F	INPA-ICT	INPA-ICT 030360	Negro River
F60	111.34	89.81	14.73	11.37	3.15	21.53	F	INPA-ICT	INPA-ICT 030360	Negro River
F61	96.39	74.21	8.08	6.15	2.05	22.18	F	INPA-ICT	INPA-ICT 030360	Negro River
F62	96.79	75.4	8.82	7.68	2.42	21.39	F	INPA-ICT	INPA-ICT 030360	Negro River
F63	89.36	72.6	5.79	4.07	2.33	16.76	F	INPA-ICT	INPA-ICT 030360	Negro River
M1	145.15	110.6	3.15	3.98	4.57	33.47	M	DIMONA	*	Negro River
M2	127.48	98.95	3.59	3.83	3.85	28.24	M	DIMONA	*	Negro River
M3	145.14	116	2.42	2.67	4.17	28.42	M	DIMONA	*	Negro River
M4	135.59	106.2	3.66	3.84	4.14	30.48	M	DIMONA	*	Negro River
M5	145.49	114.85	3.67	4.02	4.76	28.08	M	DIMONA	*	Negro River
M6	117.3	84.03	3.4	3.78	3.49	32.07	M	DIMONA	*	Negro River
M7	142.09	114.25	5.23	5.6	3.9	28.32	M	DIMONA	*	Negro River
M8	152.86	120.14	3.05	4.11	5.08	32.01	M	DIMONA	*	Negro River
M9	153.28	120.87	3.52	3.93	5.09	32.99	M	DIMONA	*	Negro River
M10	109.9	78.24	3.38	4.24	3.72	31.66	M	INPA-ICT	INPA-ICT 014209	Negro River
M11	126.21	90.52	4.29	4.7	4.42	35.69	M	INPA-ICT	INPA-ICT 014209	Negro River
M12	117.9	89.44	4.01	4.64	3.4	28.46	M	INPA-ICT	INPA-ICT 014209	Negro River
M13	108.09	72.05	4.28	5.19	3.07	36.04	M	INPA-ICT	INPA-ICT 015881	Negro River
M14	116.25	80.23	3.7	4.2	3.58	36.02	M	INPA-ICT	INPA-ICT 015881	Negro River
M15	125.52	94.28	4.54	5.48	3.76	31.24	M	INPA-ICT	INPA-ICT 015904	Negro River
M16	133.18	101.23	4.32	4.65	3.13	31.95	M	INPA-ICT	INPA-ICT 015985	Negro River
M17	130.09	100.67	3.58	3.81	4.19	29.42	M	INPA-ICT	INPA-ICT 015763	Negro River
M18	147.24	115.82	4.92	6.16	3.43	31.42	M	INPA-ICT	INPA-ICT 020101	Negro River
M19	142.94	106.32	4.7	6.19	4.11	36.62	M	INPA-ICT	INPA-ICT 023223	Negro River
M20	109	82.83	4.23	4.52	3.58	26.17	M	INPA-ICT	INPA-ICT 023223	Negro River
M21	146	107.5	3.24	3.55	3.2	38.5	M	INPA-ICT	INPA-ICT 024657	Negro River
M22	133.58	97.75	3.5	4.21	3.61	35.83	M	INPA-ICT	INPA-ICT 024657	Negro River
M23	144.83	111.45	4.06	4.57	4.63	33.38	M	INPA-ICT	INPA-ICT 029847	Negro River
M24	126.27	98.7	5.8	6.3	4.8	27.57	M	INPA-ICT	INPA-ICT 029847	Negro River
M25	142.55	108.1	4.93	5.63	4.42	34.45	M	INPA-ICT	INPA-ICT 029952	Negro River
M26	133.54	105.66	5.5	6.17	3.47	27.88	M	INPA-ICT	INPA-ICT 029952	Negro River
M27	119.46	84.41	4.34	4.96	4.4	35.05	M	INPA-ICT	INPA-ICT 029963	Negro River
M28	102.28	65.38	4.47	4.95	4.03	36.9	M	INPA-ICT	INPA-ICT 029963	Negro River
M29	106.81	78.74	3.23	3.92	4.75	28.07	M	INPA-ICT	INPA-ICT 029963	Negro River
M30	116.46	79.72	3.24	3.84	4.3	36.74	M	INPA-ICT	INPA-ICT 029997	Preto da Eva River
M31	146.56	117.55	3.25	3.68	4.94	29.01	M	INPA-ICT	INPA-ICT 029997	Preto da Eva River
M32	131.6	100.7	3.62	4.13	3.28	30.9	M	INPA-ICT	INPA-ICT 029997	Preto da Eva River
M33	141.38	108.83	4.22	4.82	3.95	32.55	M	INPA-ICT	INPA-ICT 030360	Negro River
M34	121.3	84.13	4.75	5.18	3.15	37.17	M	INPA-ICT	INPA-ICT 030360	Negro River
M35	123.54	84.75	4.49	4.77	4.12	38.79	M	INPA-ICT	INPA-ICT 030360	Negro River
M36	102.06	70.13	3.28	3.72	4.56	31.93	M	INPA-ICT	INPA-ICT 030360	Negro River
M37	102.2	71.47	3.92	4.77	3.72	30.73	M	INPA-ICT	INPA-ICT 030360	Negro River
M38	102.98	65.54	5.6	6.52	4.59	37.44	M	INPA-ICT	INPA-ICT 030360	Negro River

Table S1. Continued.

Code	LEA	LAF	DPAF	DAAF	BH	HL	Sex	Source	Catalog Number	Drainage
M39	102.49	75.29	3.18	3.95	4.32	27.2	M	INPA-ICT	INPA-ICT 030531	Negro River
M40	108.91	74.33	3.33	3.72	4.07	34.58	M	INPA-ICT	INPA-ICT 030531	Negro River
M41	119.18	89.47	4.57	5.33	4.56	29.71	M	INPA-ICT	INPA-ICT 027841	Negro River
M42	127.88	94.14	5.88	6.49	3.34	33.74	M	INPA-ICT	INPA-ICT 027841	Negro River
M43	123.9	97.03	3.24	4.14	3.98	26.87	M	INPA-ICT	INPA-ICT 030383	Negro River
M44	136.98	109.86	5.33	6.05	4.04	27.12	M	INPA-ICT	INPA-ICT 030562	Negro River
M45	122.14	87.53	3.84	4.81	3.63	34.61	M	INPA-ICT	INPA-ICT 027923	Amazonas River
M46	109.23	78.32	3.81	4.12	3.89	30.91	M	INPA-ICT	INPA-ICT 027235	Solimões River
M47	142.91	112.17	5.54	6.12	3.95	30.74	M	INPA-ICT	INPA-ICT 027235	Solimões River
M48	136.27	101.79	5.61	5.87	4.1	34.48	M	INPA-ICT	INPA-ICT 027279	Solimões River
M49	146.79	112.86	5.71	6.35	4.04	33.93	M	INPA-ICT	INPA-ICT 027279	Solimões River
M50	123.96	90.93	4.19	5.01	3.73	33.03	M	INPA-ICT	INPA-ICT 027279	Solimões River
M51	144.99	114.67	4.49	4.98	4	30.32	M	INPA-ICT	INPA-ICT 027302	Solimões River
M52	143.31	109.09	5.81	6.64	4.31	34.22	M	INPA-ICT	INPA-ICT 027302	Solimões River
M53	140.61	107.97	5.45	6.17	4.7	32.64	M	INPA-ICT	INPA-ICT 034182	Tapajós River
M54	112.21	82.81	5.61	6.23	3.4	29.4	M	INPA-ICT	INPA-ICT 034182	Tapajós River
M55	112.69	81.78	5.72	6.52	3.77	30.91	M	INPA-ICT	INPA-ICT 034182	Tapajós River
M56	103.75	71.08	4.49	4.82	3.33	32.67	M	INPA-ICT	INPA-ICT 034182	Tapajós River
M57	127.22	88.71	5.81	6.4	3.24	38.51	M	INPA-ICT	INPA-ICT 034182	Tapajós River
M58	119.18	87.21	5.45	6.06	3.62	31.97	M	INPA-ICT	INPA-ICT 034182	Tapajós River
M59	108.91	82.28	5.61	6.06	4.95	26.63	M	INPA-ICT	INPA-ICT 034182	Tapajós River
M60	148.02	113.4	5.71	6.04	4.51	34.62	M	INPA-ICT	INPA-ICT 034182	Tapajós River
M61	123.91	94.56	4.49	4.81	4.25	29.35	M	INPA-ICT	INPA-ICT 034182	Tapajós River
M62	114.06	79.41	5.81	6.33	4.5	34.65	M	INPA-ICT	INPA-ICT 034182	Tapajós River
M63	143.55	110	5.2	6.06	3.55	33.55	M	INPA-ICT	INPA-ICT 034182	Tapajós River