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Gymnogeophagus taroba (Teleostei: Cichlidae), A NEW SPECIES FROM THE RÍO IGUAZÚ BASIN, MISIONES, ARGENTINA

*Gymnogeophagus taroba (Teleostei: Cichlidae),
una nueva especie de la cuenca del río Iguazú, Misiones, Argentina*

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Abstract. The *Gymnogeophagus setequetas* group is based on our results composed of three endemic species of which one, *G. taroba* sp. n., is described as a new species. The three species are diagnosable from each other and from other species of *Gymnogeophagus* by stable differences in several morphological characters among which the best are found in coloration patterns. Body and head shapes and meristic characters show lesser differentiation but several are also clearly diagnostic in the *G. setequetas* group. The *G. setequetas* group is strongly structured allopatrically. The prime candidates for this fragmentation and speciation are the origins of the waterfalls on the individual tributaries. The largest of the waterfalls, the famous Cataratas del Iguazú, with a height of 72 m, separate *G. taroba* sp. n. from its closest relatives *G. che* and *G. setequetas*. The original 28 m high Uruguaí falls separate *G. che* from *G. setequetas*. *Gymnogeophagus setequetas* is separated from *G. che* and *G. taroba* by large rapids (about 65m in total elevation above the río Paraná) and a former fall on the Acaray river and by the 45 m high Monday falls located a few km from the mouth of the Monday into the río Paraná just opposite the mouth of the Iguazú.

Key words. Cichlid fishes, endemism, morphology, La Plata River basin, Paraná river basin

Resumen. En base a nuestros resultados, el grupo *Gymnogeophagus setequetas* esta compuesto por tres especies endémicas, de las cuales, *G. taroba* sp. n., se describe como una nueva especie. Las tres especies son diagnosables entre sí y de otras especies de *Gymnogeophagus* por diferencias estables en varios caracteres morfológicos, entre los cuales los mejores son los patrones de coloración. La forma del cuerpo, la cabeza y los caracteres merísticos muestran una menor diferenciación, pero algunos también son claramente diagnósticos en el grupo *G. setequetas*. El grupo *G. setequetas* está fuertemente estructurado alopátricamente. La causa principal para esta fragmentación y especiación es la formación de cascadas en los afluentes. La más grande de las cascadas, la famosa Catarata del Iguazú, con una altura de 72 m, separa *G. taroba* sp. n. de sus parientes más cercanos *G. che* y *G. setequetas*. El salto original del Uruguaí de 28 m de altura, separa *G. che* de *G. setequetas*. *Gymnogeophagus setequetas* está separada de *G. che* y *G. taroba* por grandes rápidos (unos 65 m de elevación total sobre el río Paraná) y un primer salto en el río Acaray y por otro salto de 45 m de altura en el río Monday localizado a unos pocos kilómetros de la desembocadura del Monday en el río Paraná justo enfrente de la desembocadura del Iguazú.

Palabras clave. Cíclidos, endemismo, morfología, Cuenca del Plata, Cuenca del río Paraná

INTRODUCTION

The genus *Gymnogeophagus* inhabits the La Plata basin, Laguna Los Patos system, the Tramandaí basin and one record of *G. balzanii* is from the Guaporé basin (Malabarba *et al.*, 2015; Loureiro *et al.*, 2016). *Gymnogeophagus* is currently diagnosed by the presence of a forward directed spine on the top of the first dorsal pterygiophore and the loss of bony supraneurals (Reis and Malabarba, 1988). The species of the genus *Gymnogeophagus* are informally included in two species group, the *G. gymnothenys* species group, characterized by mouthbrooding reproductive strategy and the *G. rhabdotus* species group with substrate brooding (Loureiro *et al.*, 2015). The later group includes *G. rhabdotus* (Hensel, 1870) from río Uruguay and Laguna dos Patos basins; *G. meridionalis* Reis and Malabarba, 1988 with a wide geographical distribution including río Paraná, Uruguay and Río de la Plata basins; *G. setequedas* Reis, Malabarba and Pavanelli, 1992 from the middle río Paraná basin; *G. che* Casciotta, Gómez and Toresanni, 2000 restricted to the arroyo Uruguaí, río Paraná basin; and *G. terrapurpura* Loureiro, Zarucki, Malabarba and González Bergonzi, 2016 from lower río Uruguay, Río de la Plata coastal drainages and Atlantic Ocean coastal drainages in Uruguay. Casciotta *et al.* (2016) reported for the first time specimens of *Gymnogeophagus* from the río Iguazú basin above the Iguazú falls. The specimens were preliminarily identified as *G. aff. setequedas* due to their closest similarity to *G. setequedas*. Several diagnostic differences were however noted and the aim of this paper is thus to describe these specimens as a new endemic species of *Gymnogeophagus*.

MATERIAL AND METHODS

The Unified Species Concept (de Queiroz, 2007) was employed in the present study.

Consistent morphological differences between morphogroups were used as a proxy for lineage independence in the absence of a molecular phylogeny which is the focus of a parallel study.

Genetic sequences from type and non-type specimens are included in the present study and follow the GenSeq nomenclature of Chakrabarty *et al.* (2013). Genomic DNA was extracted from ethanol-preserved fin tissue using the JETQUICK Tissue DNA Spin Kit (Genomed, Germany) following standard protocol. The primers and reaction conditions of polymerase chain reaction (PCR) amplification for all loci are as in Říčan *et al.* (2008). Each PCR reaction volume of 25 µl contained 12.5 µl of Combi PPP Master Mix (Top-Bio, <http://www.top-bio.cz>), 1.5 µl of each primer (10 pmol/µl), and 1 µl of extracted DNA. PCR reactions were performed in a Bioer XP Thermal Cycler and PCR products were purified using the JETQUICK PCR Purification Spin Kit (Genomed). Sequencing reactions were performed following standard protocol with the use of the same primers as in Říčan *et al.* (2008), and the products were analysed in an ABI 3730XL automated sequencer (Applied Biosystems; both steps done by Macrogen Inc., Korea). Contiguous sequences of the gene segments were created by assembling DNA strands (forward and reverse) using GENEIOUS v. 11.0.2 (<http://geneious.com>, Kearse *et al.*, 2012) and were also translated into protein sequences to check for possible stop codons or other ambiguities.

Measurements and counts were taken as described by Reis and Malabarba (1988) and Malabarba *et al.* (2015), except body depth taken at dorsal fin origin. Measurements were taken as straight line distances with digital caliper to 0.1 mm on left side of specimen. Morphometric characters are expressed as percents of the standard length (SL) except for subunits of the head which are recorded as percents of the head length

(HL). Scale row nomenclature follows Kulander (1996). Specimens were cleared and counterstained (c&s) following Taylor and Van Dyke (1985). Vertebral counts include the last half centrum. In the descriptions, the number of specimens is indicated in parentheses and values of the holotype are indicated by an asterisk. All material came from Argentina except where noted. Non-type specimens are listed in geographical distribution, and mapped in distribution maps, but were not used in species descriptions. Institutional abbreviations are as listed in Ferraris (2007), except IBIGEO (Instituto de Bio y Geociencias del NOA-Ictiología, Salta, Argentina).

RESULTS

Taxonomy

Family Cichlidae Bonaparte, 1835

Genus *Gymnogeophagus* Miranda Ribeiro, 1918

Gymnogeophagus taroba, new species (Figures 1-7; Table 1)

Gymnogeophagus aff. *setequedas* Casciotta et al., 2016 (photo of live holotype, first mention of the species)

All type and non type material from Argentina, Misiones Province, río Iguazú basin, above falls.

Holotype. MLP 11258, 1 ex., 86.9 mm SL., Parque Nacional Iguazú (PNI), boca del arroyo Ñandú ($25^{\circ}42'10.9''S$, $54^{\circ}25'31.3''W$), Casciotta et al., December 2015, (Figure 1).

Paratypes. MLP 11259, 12 ex. (1 c&s), 18.8-80.9 mm SL, arroyo Lobo ($25^{\circ}42'57''S$ - $54^{\circ}05'59''W$), Casciotta et al., November 2001. MLP 11260, 19 ex., 48.8-84.7 mm SL, PNI, río Iguazú in Pasarela a Garganta del Diablo ($25^{\circ}41'47.5''S$, $54^{\circ}26'20.4''W$), Casciotta et al., October, 2015. MLP 11138,

6 exs., 59.1-90.7 mm SL., same data as holotype. MLP 11261, 2 ex., 80.9-83.8 mm SL., PNI, arroyo Yacuí in route 101 ($25^{\circ}40'50.2''S$, $54^{\circ}10'05.8''W$), Casciotta et al., October, 2015. IBIGEO-I 449, 7 ex., 64.0-93.5 mm SL., PNI, arroyo Yacuí in camping ($25^{\circ}35'41.50''S$, $54^{\circ}08'55.51''W$), Říčan et al., February 2012 (Figures 1-7).

Non type material. MLP 11262, 4 ex., 65.2-81.2 mm SL., arroyo Deseado in camping ($25^{\circ}40'16''S$ - $53^{\circ}55'59''W$), Říčan et al., November 2007. MLP 11263, 10 ex., 29.6-52.5 mm SL., PNI, bañado de Ope ($25^{\circ}41'26.4''S$, $54^{\circ}27'16.1''W$), Gómez, November 1985. MLP 11264, 3 ex., 75.7-93.0 mm SL., Parque Nacional Iguazú (PNI), boca del arroyo Ñandú ($25^{\circ}42'10.9''S$, $54^{\circ}25'31.3''W$), Říčan et al., November, 2016. MLP 11265, 7 ex. (2 c&s) 49.3-85.3 mm SL., same data as holotype. MLP 11266, 3 ex., 38.6-89.0 mm SL, arroyo Lobo ($25^{\circ}42'57''S$, $54^{\circ}05'59''W$), Říčan et al., November 2007.



Figure 1 - *Gymnogeophagus taroba*, male, holotype, MLP 11258, 86.9 mm SL., Parque Nacional Iguazú, boca del arroyo Ñandú ($25^{\circ}42'10.9''S$, $54^{\circ}25'31.3''W$).

Diagnosis. *Gymnogeophagus taroba* is distinguished from all species of *Gymnogeophagus* in the *G. gymnoenys* group by the possession of 23 to 25 E1 scales and the absence of a well developed adipose hump in adult males. *Gymnogeophagus taroba* is most easily distinguished from all species in the *G. rhabdotus* group (*G. terrapurpura*, *G. rhabdotus*, *G. meridionalis*, *G. setequedas* and *G. che*) by the pigmentation of the dorsal fin.

The spiny section of the dorsal fin lacks any markings vs. various types of markings. The soft section has long and thin whitish light blue lines parallel to rays vs. wide stripes in *G. rhabdotus* vs. a combination of roundish spots at the base and stripes of various length and width distally in *G. meridionalis*, *G. terrapurpura*, *G. setequetadas* and *G. che*. The anal fin also has long and thin whitish light blue lines parallel to rays vs. spotted in *G. terrapurpura* vs. a combination of roundish spots at the base and stripes of various length and width distally in *G. rhabdotus*, *G. meridionalis*, *G. setequetadas* and *G. che*. In *G. setequetadas* only the posterior half of the anal fin has markings, the anterior half is immaculate. Within the *G. setequetadas* group the following additional characters separate *G. taroba*: opalescent lines on posterior part of body and on caudal peduncle narrow, start behind the midlateral blotch and are not found on the dorsum above the upper lateral line vs. wide, start in front of the midlateral blotch and are found on the dorsum in *G. setequetadas* and *G. che*; midlateral blotch usually conspicuous and dominant (as in *G. che*) vs. inconspicuous in *G. setequetadas*; opalescent markings on head large and dominant, present on opercular series (as in *G. che*) vs. small and inconspicuous, usually absent from opercular series in *G. setequetadas*; body scales or their centers are grey (as in *G. setequetadas*) vs. scale centers on at least the posterior part of body and caudal peduncle distinctly reddish-brown in *G. che*; caudal fin with best developed white longitudinal lines and most pronounced difference between a yellow to orange central portion of the fin and red dorsal and ventral margins. Besides the color patterns, *G. taroba* can be distinguished from *G. setequetadas* by a longer snout (44.4-53.7 vs. 30.8-44.7 % of HL) and from *G. che* by deeper body (40.2-46.1 vs. 37.3-40.7 % of SL).

Description. Meristic and morphometric data are summarized in Table 1. Body com-

pressed, moderately elongated. Predorsal and dorsal profiles convex; decreasing in depth to caudal peduncle. Caudal peduncle rectangular, deeper than long, ventral profile slightly concave. Body contour slightly convex between lower lip and last anal-fin ray, with straight segment between pelvic and anal fins. Snout pointed, nearly straight dorsally and ventrally in lateral aspect; short and anteriorly rounded in dorsal aspect. Eyes close to dorsal profile of head; eye near middle of head length. Interorbital area slightly concave. Posterior tip of maxilla not reaching vertical through anterior margin of eye. Mouth terminal, jaws isognathous. Body scales ctenoid. Opercle scales ctenoid; scales on preopercle small and cycloid. Cheek scales cycloid in 4 rows. Other unpaired fins without scales. Scales in E1 row 23(4*), 24(15), 25(6). Scales in transverse row 4/8(11*), 4/9(3), 5/8(10), 5/9(1). Upper lateral line scales 15(3), 16(12*), 17(7), 18(2), 19(1). Lower lateral line scales 6 (1), 7(3), 7+1(1), 7+2(1), 8(6), 8+1(2), 8+2(1), 9(9*), 9+1(1). Dorsal fin XII,10(1); XII,11(3); XIII,9(2); XIII,10(10*); XIII,11(6); XIV,9(2); XIV,10(1). Anal fin III,7 (6); III,8(13*); III,9(5), III,10(1). Caudal-fin squamation not reaching middle of fin. Dorsal-fin origin anterior to vertical line through posterior bony margin of opercle, posterior end of depressed fin surpassing caudal-fin base. Pectoral-fin edge surpassing the anal-fin origin. Anal-fin edge surpassing caudal-fin base. Caudal fin truncate or slightly concave.

Gill rakers externally on first gill arch 9-11 (3). Premaxillary and dentary outer row teeth slightly movable, inner ones fully depressible. Premaxillary ascending process longer than dentigerous one. Premaxilla with 14-17 (3) unicuspids teeth on outer row, larger than inner ones. Four teeth rows near symphysis. Dentary with 17-18 (3) unicuspids teeth on outer row, 4 rows near symphysis. Lower pharyngeal tooth plate with unicuspids and bicuspid anteriorly curved teeth, those of posterior and medial one to three rows larg-

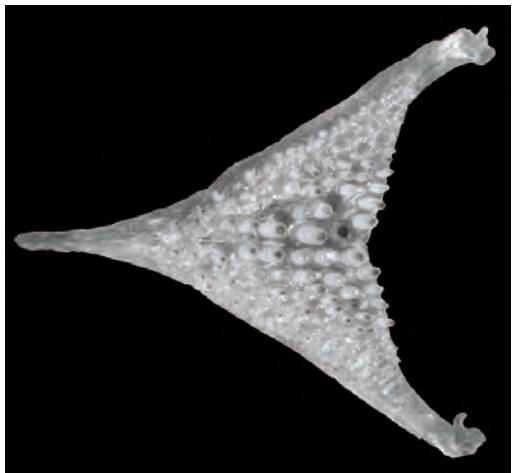


Figure 2 - *Gymnogeophagus taroba*, lower pharyngeal tooth plate in occlusal view, MLP11265, 83.4 mm SL.

er than remaining ones (Figure 2). Upper pharyngeal tooth plate with unicuspид and bicuspid teeth. Frashed zone bearing one concavity with small unicuspид teeth. Two to four patch of unicuspид teeth on fourth ceratobranchial. Vertebrae 26-27, 13+13 (1), 13+14 (1), 14+13 (1) (3 c&s).

Color in life. Background color of dorsal region of body light olivaceous with five indistinct diffuse vertical bars (Figure 3). Black quadrangular mid-lateral spot at third vertical bar, surrounded by bright, yellow-green area in some specimens. Mid-lateral blotch usually conspicuous and dominant, it can be extended dorsally to the base of dorsal fin. Five horizontal bright light blue narrow bands from behind the black mid-lateral blotch to caudal-fin base. Ventral portion of body and head whitish; isthmus and branchiostegal region black in adult males and females during reproductive season. Head with black bar traversing eye from nape to ventral edge of preopercle. Bright light blue elongated or rounded dots usually present on cheeks, usually forming one interrupted nearly straight line from tip of maxilla to upper portion of preopercle with additional dots ventrally. Most specimens with several bright light blue dots on the opercle and one on the upper part of first lateral line scale. Dorsal fin (Figures



Figure 3- *Gymnogeophagus taroba*, coloration of live specimens immediately after capture. (A-B) IBIGEO-I 449, paratype specimens, 87.8 mm, 79.8 mm. (C-D) MLP uncat., Ríčan et al., February 2014, data as holotype.

3-5) with background light ochre; spiny portion immaculate, soft portion with long and thin opalescent and whitish light blue lines parallel to rays. Dorsal-fin border black in reproductive adults. Anal-fin (Figures 3, 6) background yellow to ochre with mostly long whitish light blue narrow bands, parallel and diagonal to rays, surrounded by dark red. Caudal-fin (Fig-

ures 3, 7) background yellow, orange to light green with upper and lower margin light purple, centre of fin covered with numerous elongated hyaline spots, arranged in horizontal series between rays. Pectoral fin hyaline, light yellow. Pelvic fin green to ochre, with first rays black; several whitish light blue stripes surrounded by dark red between rays.

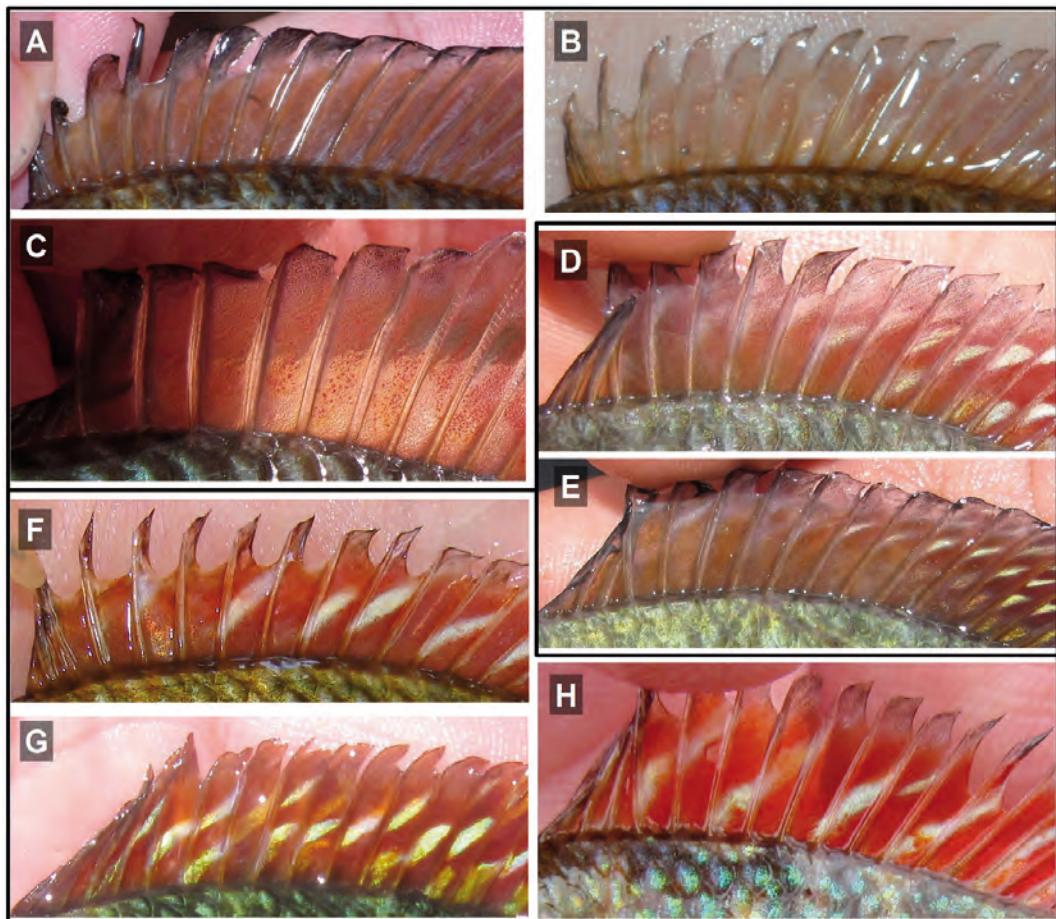


Figure 4 - Coloration of the spinous portion of the dorsal fin in the *G. setequedas* group: (A-C) *Gymnogeophagus taroba*, paratypes; (D-E) *G. setequedas*; (F-H) *G. che*.

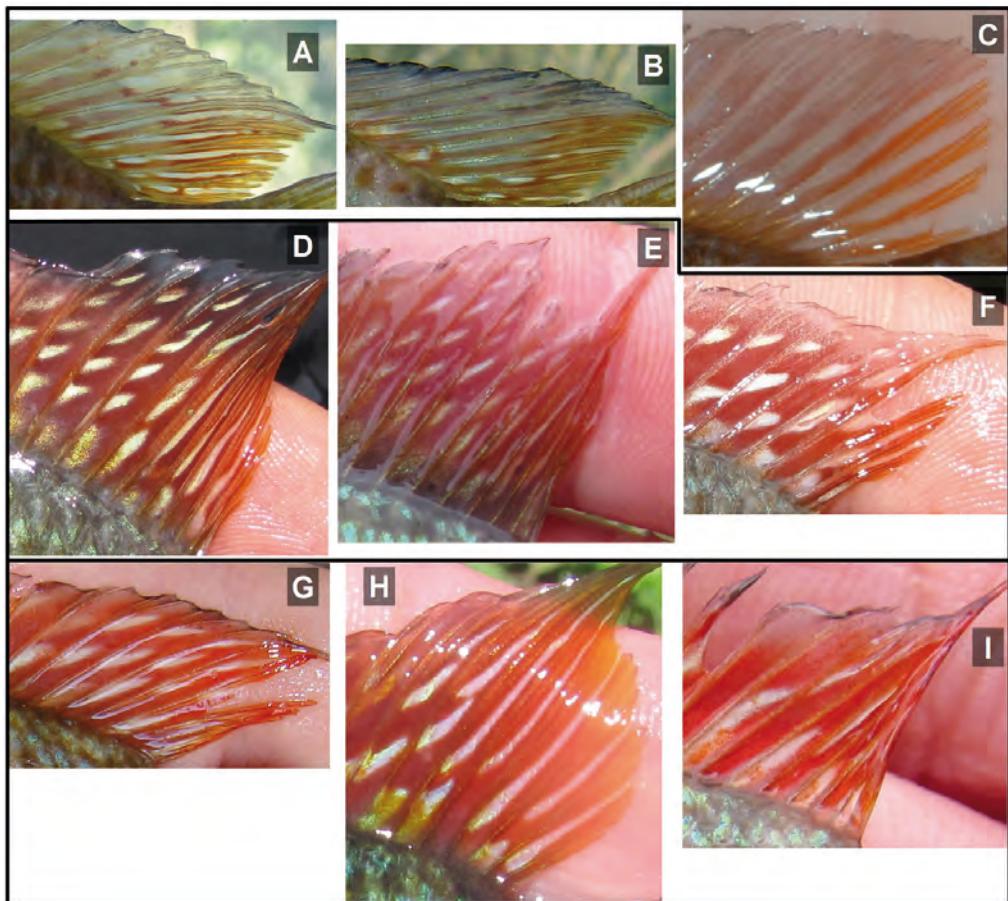


Figure 5- Coloration of the soft-rayed portion of the dorsal fin in the *G. setequedas* group: (A-C) *Gymnogeophagus taroba*, holotype (A) and paratypes; (D-F) *G. setequedas*; (G-I) *G. che*.

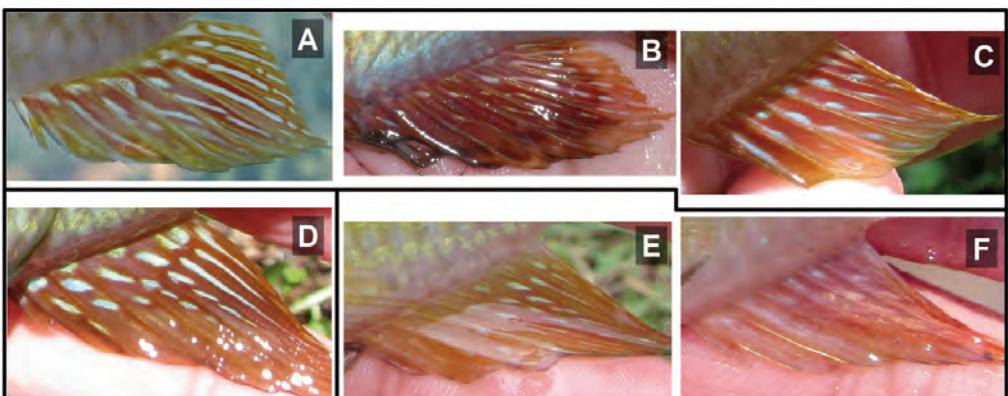


Figure 6 - Coloration of the anal fin in the *G. setequedas* group: (A-C) *Gymnogeophagus taroba*, holotype (A) and paratypes; (D) *G. che*; (E-F) *G. setequedas*.

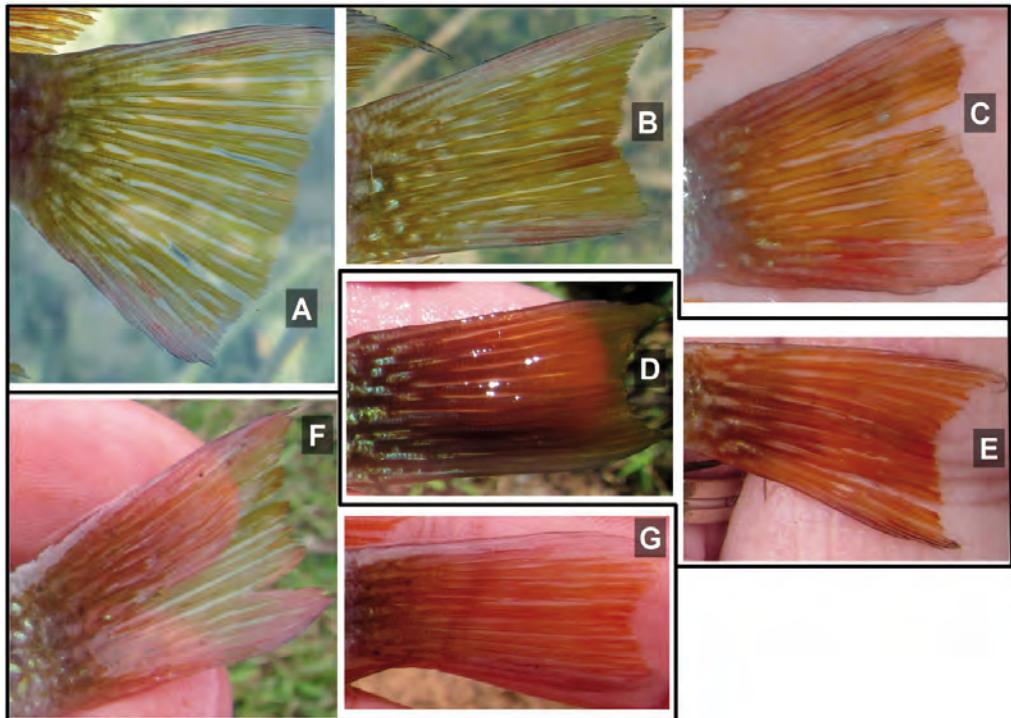


Figure 7 - Coloration of the caudal fin in the *G. setequedas* group: (A-C) *Gymnoeophagus taroba*, holotype (A) and paratypes; (D-E) *G. che*; (F-G) *G. setequedas*.

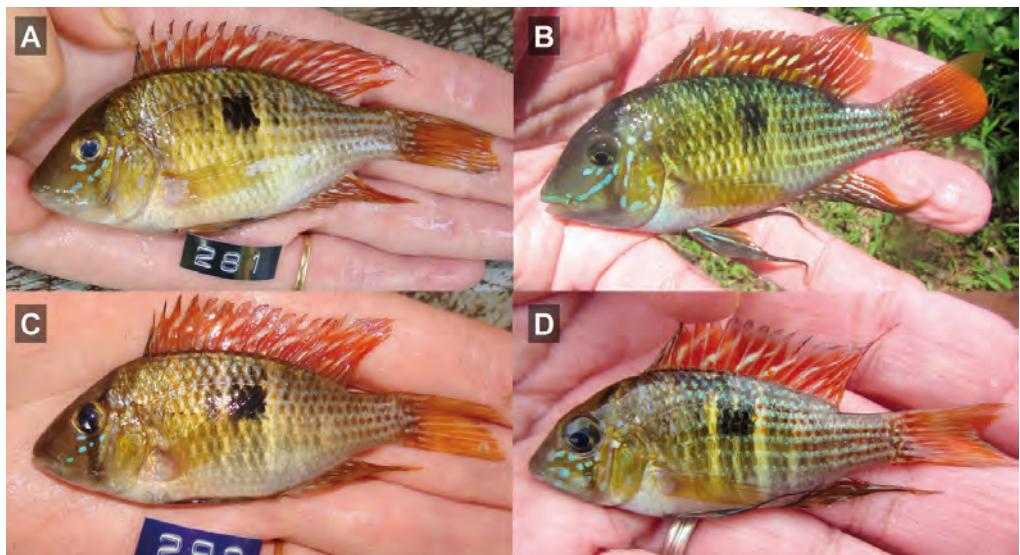


Figure 8 - *Gymnoeophagus che*, coloration of live specimens immediately after capture, non-type specimens: (A) MLP 11296, 83.0 mm, Casciotta et al., 2010; (B) MLP 11297, 98.5 mm, Říčan et al., 2016; (C) MLP 11296, 68.1 mm, Casciotta et al., 2010; (D) MLP 11297, 89.4 mm, Říčan et al., 2016.

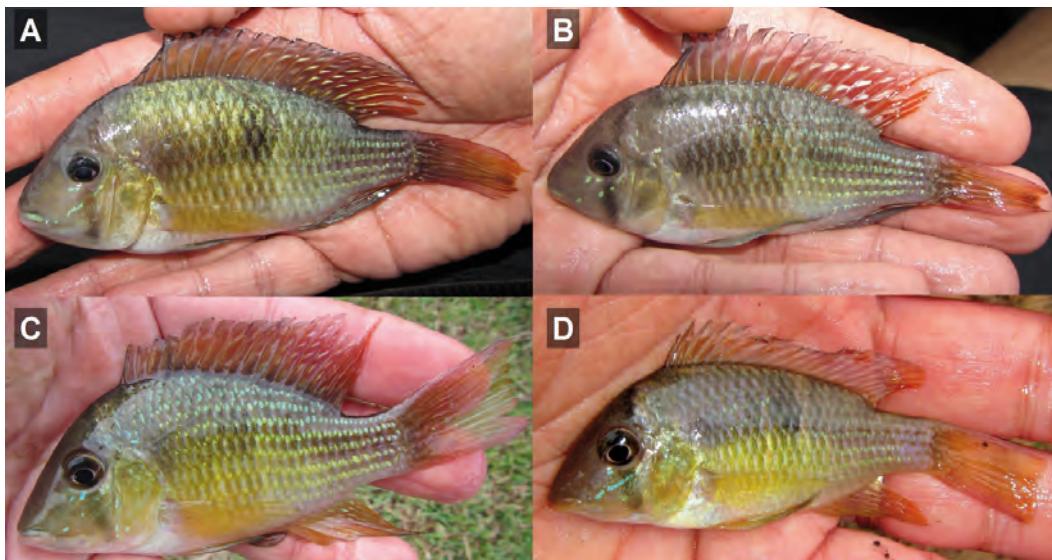


Figure 9- *Gymnogeophagus setequedas*, coloration of live specimens immediately after capture, non-type specimens: (A-B) Paraguay, tributary of Rio Monday above Salto Monday, 14.11.2009, 25°41'44.5"S, 55°05'09.7"W; (C) Paraguay, tributary of Rio Acaray, 31.8.2016, 25°23'31.6"S, 55°25'26.2"W; (D) Paraguay, tributary of Rio Acaray, 30.8.2016, 25°07'53.3"S, 55°57'51.4"W.

Color in alcohol. Background color of dorsal region of body light brown to gray with five to six diffuse and darker bars (Figure 1). Black quadrangular mid-lateral spot at third vertical band, surrounded by narrow light areas in some specimens. Ventral portion of body and head whitish to light brown; isthmus and branchiostegal region black in most adult males and females during reproductive season. Head with black bar traversing eye from nape to ventral edge of preopercle. Dorsal fin background light gray; elongated hyaline spots in soft portion. Dorsal fin border black in reproductive adults. Anal-fin background light gray with elongated hyalines spots. Caudal-fin background light gray entirely covered with numerous elongated hyaline spots, arranged in horizontal series between rays. Pectoral fin hyaline; pelvic fin dusky, with the first three rays and membranes black.

Sexual dimorphism. Genital papilla in

males slender and longer than those of female. Some males with filaments in dorsal, anal and pelvic-fins. Pelvic fins of males usually longer than those of females (2.3-2.8 vs. 2.7-3.1 in SL).

Geographic distribution. *Gymnogeophagus taroba* is endemic to the lower río Iguazú basin above the Iguazú falls (Figure 10).

Habitat. *Gymnogeophagus taroba* is found predominantly in pools and lentic stretches of smaller streams with predominantly muddy or sandy bottoms (Figures 11-12). The type locality, boca del arroyo Ñandú has a stone substrate covered with mud (Figure 11). Some specimens (e.g. MLP 11260, 19 ex.) have also been collected in pools between rock-gardens in the Iguazú main channel (Pasarela a Garganta del Diablo, Figure 13; pasarela a salto San Martín). These pools are ecologically very similar to the small tributary streams with similar stony substrates and muddy bottoms.

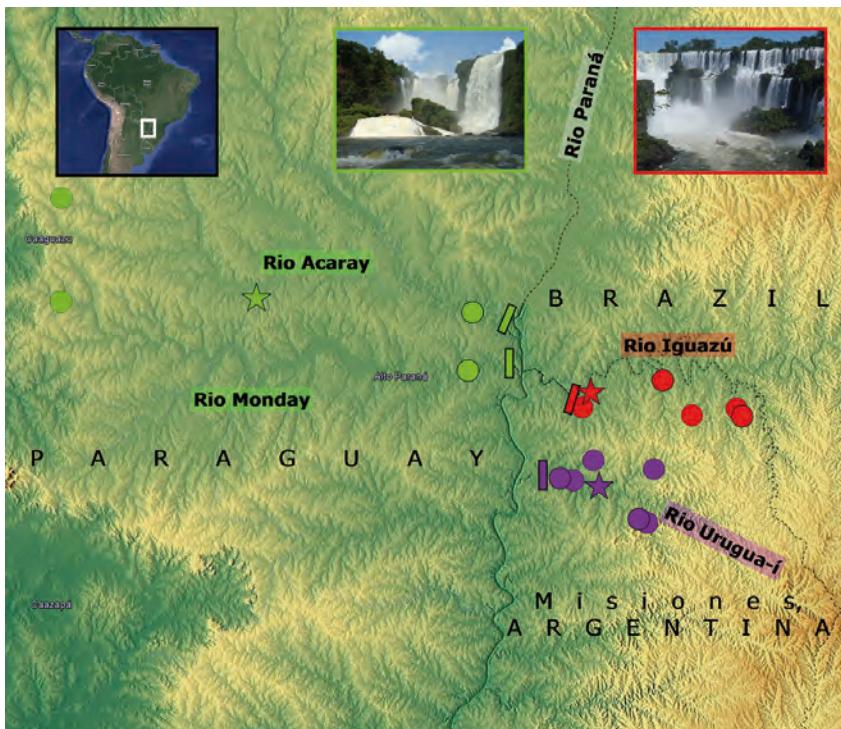


Figure 10 - Distribution of the *G. setequedas* group in Middle Paraná river basin. Colored localities show distribution of the *G. setequedas* group and material examined in the present study. Stars show type localities. Red: *G. taroba*, green: *G. setequedas* and violet: *G. che*. Inset photos show two of the major waterfalls in the area (Cataratas del Iguazú, Salto Monday) and location of the study area within South America.



Figure 11 - Type locality of *G. taroba*, mouth of the arroyo Ñandu into the Iguazú river, Parque Nacional Iguazú, Iguazú river basin ($25^{\circ}42'10.9''S$, $54^{\circ}25'31.3''W$), December 2014.



Figure 12- Paratype locality of *G. taroba*, pool in the arroyo Yacuí, Parque Nacional Iguazú, Iguazú river basin ($25^{\circ}35'41.50''S$, $54^{\circ}08'55.51''W$), February 2012.



Figure 13- Paratype locality of *G. taroba*, pools below Pasarela a Garganta del Diablo, Parque Nacional Iguazú, Iguazú river basin ($25^{\circ}41'47.5''S$, $54^{\circ}26'20.4''W$), December 2014.

Etymology. The specific epithet taroba refers to Tarobá, a warrior, and refers to a legend of the Kaingang people; a noun in apposition. The Kaingang were the original first inhabitants of the present province of Misiones in Argentina and the southern Brazilian states of Paraná, Santa Catarina and Rio Grande do Sul and also the southeastern state of São Paulo. Their language and culture is quite distinct from the neighboring Guarani. The Kaingang language is classified as a member of the Gê language family. The legend tells that at the beginning of time, the río Iguazú was inhabited by a huge and monstrous serpent called Mboi, a guardian god. The Kaingang sacrificed a beautiful young maiden every year to Mboi. When Tarobá meets Naipí, chosen for the sacrifice, he rebels against the elders of the tribe who refuse to release her. Tarobá and Naipí try to escape in a canoe by the river. Mboi becomes furious and brakes the course of the river forming the Iguazú falls, catching the lovers. Naipí is transformed into one of the rocks of the falls, perpetually punished by the turbulent waters, and Tarobá is turned into a palm tree on the bank of the waterfall. Mboi lives submerged in the Garganta del Diablo, from where he watches over the lovers, preventing them from joining again. However, on sunny days and as a bridge of love, the rainbow overcomes the power of Mboi by rejoining Naipí and Tarobá.

Genseq-2 CYTB. IBIGEO-I 449; GenBank accession number MG681194.

Genseq-3 CYTB. MLP 11262; GenBank accession number MG681195.

Genseq-3 CYTB. MLP 11264; GenBank accession number MG681196.

Morphological variation in the *G. setequeadas* group

The *G. setequeadas* group can be divided into three morphospecies that are diagnosable by stable differences in several morphological characters (Figures 1, 3-7). The best diagnostic characters in the *G. setequeadas* group are found in coloration patterns. The spinous portion of the dorsal fin (Figure 4) ranges from completely unpatterned (*G. taroba*), through only lightly patterned and limited to the posterior part with short triangular white spots (*G. setequeadas*), to heavily patterned throughout with long, wide and dominant white bands (*G. che*).

The soft-rayed portion of the dorsal fin (Figure 5) is patterned in all species but also diagnostic ranging from very light patterning made of long thin lines following the rays (*G. taroba*), through more distinct and wider lines distally and more pronounced spots proximally on the fin (*G. che*), to much more dominant blotches dispersed all the way to the distal margin of the fin in more than the anterior half of the soft portion with a much more reduced number of lines in the posterior part (*G. setequeadas*).

The anal fin pigmentation (Figure 6) is also diagnostic. All species have a patterned anal fin with the least patterning found in *G. setequeadas*, where it is limited to only the posterior portion of the fin, while *G. che* and *G. taroba* have the whole fin patterned. In *G. che* the anterior portion is covered by dots and the posterior part by dots at the base and thick lines distally (the posterior part is thus patterned as in *G. setequeadas*), while in *G. taroba* the whole anal fin is patterned by long white lines (that follow the fin rays) distally margined by red coloration in the largest specimens. The red coloration in the anal fin is also found in the other species but never to such extent as in *G. taroba* and never arranged in clearly defined lines.

The caudal fin coloration (Figure 7) is least diagnostic among the fins but *G.*

taroba has the caudal fin most heavily patterned by white longitudinal lines and has the most pronounced difference between a yellow to orange central portion of the fin and red dorsal and ventral margins (the red coloration covers about four rays in both the dorsal and ventral margins).

Noticeable differences are also found in the coloration of the body and the head (Figures 1, 8-9). *Gymnocephagus setequeadas* is different from the other species in that its midlateral blotch is always very diffuse and by far not so much well developed. The blue opalescent pigmentation on the head (face) is variable in its development but is invariably least developed again in *G. setequeadas*, made of usually small and inconspicuous dots which are absent from the opercular series. The opalescent lines on posterior part of body and on caudal peduncle are wide in *G. setequeadas* and *G. che* but are narrow in *G. taroba*. These opalescent lines start behind the midlateral blotch and are absent on the dorsum above the upper lateral line in *G. taroba* while in *G. setequeadas* and *G. che* they start in front of midlateral blotch and are conspicuous on the dorsum above the upper lateral line. Body scales or their centers are grey in *G. taroba* and in *G. setequeadas* while in *G. che* scale centers on at least the posterior part of body and caudal peduncle are distinctly reddish-brown.

Body and head shapes are quite variable within the *G. setequeadas* group with much of the variation being intraspecific. However, several of these shape characters are clearly diagnostic and distinguish some of the species. These characters include body depth (*G. taroba* vs. *G. che*) and snout length (*G. taroba* vs. *G. setequeadas*) (Table 1 and Reis *et al.*, 1992 and Casciotta *et al.*, 2000). The lower pharyngeal jaws are on the contrary not diagnostic showing most variation intraspecifically (see Description) and varying in degree of robustness and numbers of enlarged teeth (in one to three medial rows) (Figure 2).

Variation in meristic characters is also mostly intraspecific but *G. che* (Table 1 and Reis *et al.*, 1992 and Casciotta *et al.*, 2000) can be distinguished from *G. setequeadas* and *G. taroba* by a modally higher count of scales along lateral line (26 vs. 24), of lower lateral line scales (10 vs. 8), and marginally of dorsal fin spines modal count (14 vs. 13).

DISCUSSION

The *G. setequeadas* group is based on our results composed of three species that are diagnosable by stable differences in several morphological characters among which the best are found in coloration patterns, namely in the coloration of the dorsal fin, anal fin, and to some extent also in body and head coloration. Such differentiation in live coloration patterns is typical for this colourfull genus (Reis & Malabarba, 1988). The detailed differentiation in the coloration of unpaired fins has recently been noted also in several other *Gymnocephagus* species where it was also used to support the diagnoses of several newly described species (Malabarba *et al.*, 2015; Loureiro *et al.*, 2016). Body and head shapes and meristic characters show lesser differentiation with a much larger proportion of the variation being intraspecific as in most other *Gymnocephagus* species (see above refs.). However, several of the shape and meristic characters are clearly diagnostic in the *G. setequeadas* group.

Species of the *G. setequeadas* group appear to have a wide ecological valence since they are found in a wide variety of habitats and are common species of cichlids. *Gymnocephagus setequeadas* is a relatively common species found throughout eastern Paraguay in the Paraná tributaries except for the drainages emptying into the Itaipú reservoir and the reservoir itself both in Paraguay (OŘ, pers. obs.) and in Brazil (Paiz *et al.*, 2017) where the species has declined and is now

rare. Paiz et al. (2017) listed *G. setequeadas* as a threatened species (in Brazil) with a rheophilic ecology but that is a misunderstanding derived from too much focus on the Itaipú area in Brazil. In Paraguay *Gymnogeophagus setequeadas* is a relatively common species outside the Itaipú area, is predominantly found in lentic habitats (hence is definitely not rheophilic as also its body morphology reveals) and is even common in and around Paraguayan reservoirs (e.g. Embalse de Yguazu). The marked decline of populations of *G. setequeadas* in the Itaipú area is more likely the result of the unprecedented pressure from introduced non-native fish species and the changed ecology of the reservoir and of the tributaries (Agostinho *et al.*, 2004, 2005, 2016; Baumgartner *et al.*, 2012) in the Itaipú area. *Gymnogeophagus che* is common throughout the Uruguaí basin in all types of habitats including in the artificial Uruguaí reservoir. *Gymnogeophagus taroba* is based on our knowledge most common in small affluents of the Iguazú river with habitats and localities that are slow flowing to standing (i.e. pools in small tributaries and mouths of streams) with soft types of bottoms (mud and sand). Some of our specimens (e.g. MLP 11260, 19 ex.) have also been collected in pools between rock-gardens in the Iguazú main channel (see Habitat above). Paiz et al. (2017) listed *G. taroba* (as *G. setequeadas*) only from two localities apparently within the Iguazú river proper (one above and one below the Iguazú falls). No habitat information or precise description of the localities was however given; nor does the NUP catalogue (<http://www.splink.org.br/form?lang=pt&collectioncode=NUP>) for these specimens. Based on our records the localities of Paiz et al. (2017) are also most likely pools or slow-flowing sections of the river.

The *G. setequeadas* group is strongly structured allopatrically and made of three endemic species. The prime candidates for this

fragmentation and speciation are the origins of the waterfalls on the individual tributaries (Figure 10). The largest of the waterfalls are the famous Cataratas del Iguazú, one of the largest waterfalls in the world with a 2.7-kilometres-long ledge and a height of 72 to 78 m, located 25 km before the Iguazú enters the río Paraná. The Cataratas del Iguazú separate *G. taroba* from its closest relatives *G. che* and *G. setequeadas*. The 28 m high Uruguaí falls located eight km from the confluence with the Paraná river (in 1989 replaced by a hydroelectric dam) just south of the Iguazú separate *G. che*. *Gymnogeophagus setequeadas* is separated from *G. che* and *G. taroba* by a former fall (of unknown height, that is now also replaced by a hydroelectric dam) and by large rapids (about 65m in total elevation above the río Paraná) on the Acaray river and by the 45 m high Monday falls (Saltos del Monday) on the Monday river located seven km from its mouth into the río Paraná just opposite the mouth of the Iguazú (and hence the Cataratas del Iguazú).

Comparative Material

Gymnogeophagus balzanii: Misiones Province: MLP 8617, 1 ex., 106.9 mm, arroyo Don Lorenzo, Departamento Capital. Formosa Province: IML 452, 1 ex, 57.6 mm, río Paraguay. IML 304, 3 exs., 50.3-61.5 mm. Salta Province: IML 440, 1 ex., 91.5 mm, San Martín. Chaco Province: MLP 7925, 1 ex., 96.4 mm, Resistencia. Corrientes Province: MLP 8616, 7 exs., 48.9-134.2 mm, riacho Carrizal, Bella Vista. MLP 8615, 6 exs., 81.7-169.0 mm, laguna cerca de la escuela N° 12, camino Bella Vista-San Roque. MACN 7038, 1 ex., 54.8 mm, río Santa Lucía. MACN 7036, 2 exs., 57.4-63.6 mm, riacho Carrizal, Bella Vista. MACN 6401, 1 ex., 91.4 mm, Esteros del Iberá. Entre Ríos Province: MLP 8631, 1 ex., 66.7 mm, Salto Gran-

de. Santa Fé Province: MLP 8380 1 ex., 9 mm, laguna Vargas, Departamento San Javier. MLP 7292, 2 exs., 53.8-124.0 mm, río Colastiné. MLP 8375, 1 ex., 62.0 mm, río Santa Fé. MLP 7268, 1 ex., 83.1mm, madrejón Flores. MLP 6693, 1 ex., 74.7 mm, Parque Belgrano. Brasil: MSNG 7683 (holotype), 79.5 mm, Villa María, río Paraguay, Mato Grosso. Paraguay: ZMB17109, 1 ex., 77.5 mm, Asunción. ZMB 17108, 2 exs. 52.0-76.4 mm, Asunción. *Gymnogeophagus che*: Misiones Province, río Paraná basin: MLP 8747, (holotype), 91.9 mm, arroyo Urugua-í y ruta provincial 19 frente a la pasarela en parque provincial Islas Malvinas. MLP 8748, (paratypes), 5 exs., 67.1-96.3 mm, arroyo Urugua-í en Isla Palacios. MLP 8749, (paratype) 1 ex., 71.3 mm, arroyo Uruzú y ruta provincial 19, Parque provincial Islas Malvinas. MACN 8220, (paratype) 3 exs., 89.0-101.0 mm, arroyo Urugua-í y ruta provincial 19. MLP 8750, (paratype) 1 ex. 60.9 mm, arroyo Urugua-í, en el establecimiento «Alto Paraná». MLP 8751, (paratypes) 3 exs., 40.0-86.7 mm, arroyo Uruzú y ruta provincial 19, Parque provincial Islas Malvinas. MLP 8752, (paratypes) 2 exs., 68.5-88.6 mm, arroyo Grapia, afluente del arroyo Urugua-í, 10 km al NE de la ruta provincial 18. MLP 8758, (paratypes) 17 exs., 15.6-21.0 mm arroyo Urugua-í y ruta 12. MLP11296, 7 exs., 62.7-83.0 mm, Embalse Urugua-í at Policia lacustre. MLP 11297, 2 exs., 84.9-98.5 mm, arroyo Falso Urugua-í. *Gymnogeophagus gymnoensis*: Brasil: MLP11248 1 ex., (c&s), 68.8 mm, Brasil, RS, São Sebastião do Caí, río Caí. *Gymnogeophagus labiatus*: Brasil: MLP11246, 1 ex., 98.6 mm SL., Brasil, RS, Sto. Antonio da Patrulla, Vila N. S. Monte Serrat, río Dos Sinos. *Gymnogeophagus meridionalis*: MLP 8633, (paratypes) 12 exs., 42.5-68.5 mm, Corrientes Province, pond in road Bella Vista to San Roque, near

school Nº12. MLP 8404, 29 exs., 22.0-71.0 mm, Buenos Aires Province, río Salado basin, laguna Chascomús. MLP 4748, 3 exs., 58.0-67.2 mm, Buenos Aires Province, Río de La Plata basin, arroyo Pereyra. *Gymnogeophagus sp.* (since *G. terrapurpura* was diagnosed by colour pattern in specimens alive (Loureiro *et al.*, 2016) it is impossible to decide if all these samples are *G. terrapurpura*, *G. meridionalis* or both species). Misiones Province: MLP 6853, 1 ex., 37.6 mm, arroyo Piray Mini. Corrientes Province: MLP 8634, 1 ex., 40.6 mm, riacho Carrizal, Bella Vista. Entre Ríos Province: MLP 3346, 5 exs., 22.3-51.2 mm, laguna Mazaraca. MLP 3309, 2 exs., 57.7-73.9 mm, Concordia. MLP 6082, 2 exs., 68.4-78.8 mm, Entre Ríos, no other data. MLP 7684, 2 exs., 28.0-33.0 mm, río Nogoyá, cerca de Tres Bocas, Departamento de Gualeguaychú. Santa Fé Province: MLP 8382, 2 exs. 55.6-63.2 mm, laguna Setubal. Buenos Aires Province: MLP 7684, 21 exs., 26.3-39.0 mm, Delta del Paraná.. MLP 8636, 6 exs., 30.5- 45.8 mm, cantera de Los Talas, Berisso. MLP 5633, 2 exs., 43.1-67.9 mm, Magdalena. MLP 4748, 3 exs., 57.9-68.7 mm, arroyo Pereyra. MLP 6306, 7 exs., 51.0-91.1 mm, cantera de Los Talas, Berisso. MLP 8637, 2 exs., 19.5-26.2 mm, arroyo Villoldo, Punta Indio. MLP 8638, 2 exs., 18.5-24.7 mm, arroyo Castelli, Punta Indio. *Gymnogeophagus rhabdotus*: Brasil: MLP11247, 1 ex., 61.9 mm, RS, Brasil, Passo de Taquara, Gravataí, col: Reis *et al.*, 5/7/82. Uruguay: MLP11249, 2 exs., (c&s) 58.6-66.7 mm, río Uruguay, basin, arroyo Catalán Grande. *Gymnogeophagus setequedas*: Paraguay: MHNG 2518.19 (holotype), 1 ex., 80.3 mm, reservorio río Iguazú en Juan E. O'Leary, Provincia el Alto Paraná. MHNG 2269.49 (paratypes) 6 exs. (1 ex. c&s) 12.1-72.4 mm, reservorio río Iguazú en Juan E. O'Leary; Provincia el Alto Paraná. MHNG 2027 92-95 (paratypes) 4 exs., 44.7-64.7 mm, Alto Paraná: Itabo-Guazu. MHNG 2027.68-69 (para-

Table 1- Proportional measurements in percents of standard length of holotype and 24 paratypes of *Gymnogeophagus taroba* sp. n. SD=standard deviation. Measurements expressed as percentages of standard length, except those marked with *, which are percentages of head length.

	Holotype	Range	Mean	SD
Standard length (mm))	86.9	59.1-90.7		
Body depth	43.4	40.2-46.1	43.3	1.55
Head length	35.9	32.6-37.4	34.8	1.15
Dorsal-fin base	58.6	53.3-59.0	56.1	1.54
Pectoral-fin length	38.9	33.4-40.5	37.1	1.59
Caudal peduncle length	13.3	13.3-16.6	15.1	0.84
Caudal peduncle depth	16.1	13.3-16.1	14.8	0.73
Eye diameter*	29.8	26.4-31.4	28.6	1.37
Interorbital width*	32.7	26.6-34.1	30.5	2.22
Pre-orbital length*	27.9	23.2-30.7	27.2	1.99
Snout length*	49.4	44.4-53.7	49.7	2.07
Upper jaw length*	34.6	30.2-37.7	34.0	2.30

types) 2 exs., 57.4-67.8 mm, Provincia de Alto Paraná, río Acaray, near del Ciudad del Este. MCP 14636 (paratype), 1 ex., 68.8 mm, Alto Paraná, Juan E. O'Leary, área de inundación del río Iguazú. MCP 1437 (paratype) 1 ex., 96.8 mm, Alto Paraná, Juan E. O'Leary, arroyo Iguazú, sistema do río Paraná. *Gymnogeophagus cf. setequeadas*: MLP11250, 2 exs., 93.1-99.8 mm, Entre Ríos Province, río Paraná basin, Parque Nacional Pre-Delta, Tapera de Chano. *Gymnogeophagus terrapurpura*: MLP 11227, 1 ex., 62.0 mm, Entre Ríos Province, Municipio Villa Elisa, balneario municipal, arroyo Perucho Verna.

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