

Original article

## A new mouth brooder species of *Gymnogeophagus* with hypertrophied lips (Cichliformes: Cichlidae)

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A new mouth breeder species of *Gymnogeophagus* is described from a tributary of the rio Uruguay. It is distinguished from most species of the genus by the presence of hypertrophied lips, and from *G. labiatus* and *G. pseudolabiatus* by the color pattern. The presence of successive allopatric species of the *Gymnogeophagus gymnogenys* clade inhabiting the tributaries of the rio Uruguay is discussed.

**Keywords:** Distribution, Endemism, *Gymnogeophagus gymnogenys* clade, New species, Río Uruguay.

Una nueva especie incubadora bucal de *Gymnogeophagus* es descrita de un tributario del Río Uruguay. Se distingue de la mayoría de las especies del género por la presencia de labios hipertrofiados, y de *G. labiatus* y *G. pseudolabiatus* por su patrón de coloración. Se discute la presencia de sucesivas especies alopatricas del clado *Gymnogeophagus gymnogenys* habitando los tributarios del Río Uruguay.

**Palabras Clave:** Distribución, Endemismo, Clado *Gymnogeophagus gymnogenys*, Especie nueva, Río Uruguay.

### Introduction

Cichlidae constitutes one of the major vertebrate families, with more than 1,700 species (Fricke *et al.*, 2018). The genus *Gymnogeophagus* Ribeiro is included in the tribe Geophagini (López-Fernández *et al.*, 2005a, 2005b, 2010) along with approximately 14 other genera of the Neotropical subfamily Cichlinae. Species belonging to *Gymnogeophagus* are easily recognized by sharing two synapomorphies (Reis, Malabarba, 1988): the absence of supraneurals, and the presence of a forward-directed spine in the first pterygiophore of the dorsal fin (Fig. 1). *Gymnogeophagus* includes one extinct species, *G. eocenicus* Malabarba, Malabarba & Del Papa, 2010, known from fossil records of the Eocene Luján Formation in northwestern Argentina, and 18 extant species from Paraná, Paraguay and Uruguay basins and small coastal drainages of Uruguay and southern Brazil, with one species, *G. balzanii*, also occurring in the rio Guaporé, Amazon drainage (Malabarba *et al.*, 2015; Loureiro *et al.*, 2016; Casciotta *et al.*, 2017a).

A brief review of the taxonomic and phylogenetic works dealing with *Gymnogeophagus* was given by Malabarba *et al.* (2015) and is not repeated here. Two major clades of *Gymnogeophagus* are recognized: one containing substrate

breeder species, whose females deposit adhesive eggs on a surface and one or both parents guard and tend them, and another that includes mouth breeder species, where one or both parents brood orally the eggs and young (Reis, Malabarba, 1988; Wimberger *et al.*, 1998). The substrate breeder clade has been treated as the *G. rhabdotus* clade, *G. rhabdotus* species group or *G. rhabdotus* group (Malabarba *et al.*, 2010; Loureiro *et al.*, 2016; Řičan *et al.*, 2018, respectively) and includes *G. rhabdotus* (Hensel, 1870), *G. che* Casciotta, Casciotta, Gómez & Toresanni, 2000, *G. meridionalis* Reis & Malabarba, 1988, *G. setequedas* Reis, Malabarba & Pavanelli, 1992, *G. taroba* Casciotta, Almirón, Piálek & Řičan, 2017, and *G. terrapurpura* Loureiro, Zarucki, Malabarba & González-Bergonzoni, 2016. The mouth breeder clade has been treated as the *G. gymnogenys* clade and *G. gymnogenys* group (Malabarba *et al.*, 2010; Řičan *et al.*, 2018, respectively), and includes *G. gymnogenys* (Hensel, 1870), *G. australis* (Eigenmann, 1907), *G. balzanii* (Perugia 1891), *G. caaguazuensis* Staeck, 2006, *G. constellatus* Malabarba, Malabarba & Reis, 2015, *G. labiatus* (Hensel, 1870), *G. lacustris* Reis & Malabarba, 1988, *G. lipokarenos* Malabarba, Malabarba & Reis, 2015, *G. mekinos* Malabarba, Malabarba & Reis, 2015, *G. missioneiro* Malabarba, Malabarba & Reis, 2015, *G. pseudolabiatus* Malabarba, Malabarba & Reis,

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2015, and *G. tiraparae* González-Bergonzoni, Loureiro & Oviedo, 2009. In this paper we describe a new species of the *G. gymnogenys* clade from a tributary of the lower río Uruguay, the río Arapey Grande.

### Material and Methods

Examined material of *Gymnogeophagus* belong to the fish collections of the Museu de Ciências e Tecnologia, Pontifícia Universidade Católica do Rio Grande do Sul, Porto Alegre (MCP), Museo Nacional de Historia Natural, Montevideo (MHNM), Universidade Federal do Rio Grande do Sul, Porto Alegre (UFRGS), and Facultad de Ciencias de la Universidad de la República, Montevideo (ZVC-P). Additional comparisons were done using data or specimens listed by Reis, Malabarba (1988), González-Bergonzoni *et al.* (2009), Malabarba *et al.* (2015) and Loureiro *et al.* (2016). Counts and measurements were taken according to Malabarba *et al.* (2015) and asterisks represents counts from the holotype. Specimens listed as non-types are referred for geographical distribution record, and were not counted or measured for species description. The localities of collection of specimens listed under Comparative material session are also given for distributional purposes.

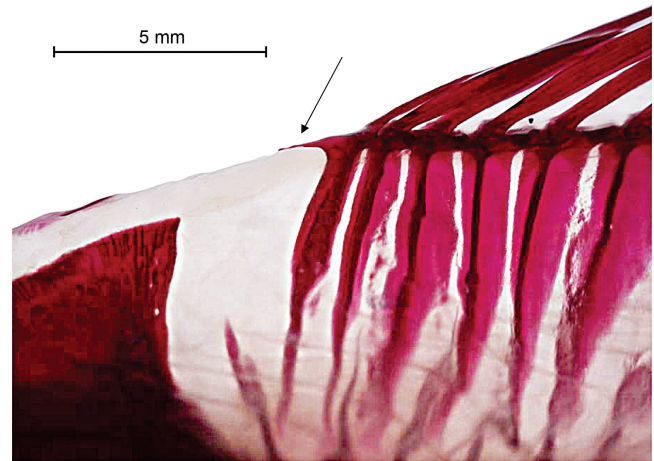
### *Gymnogeophagus peliochelynion*, new species

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### Figs. 1-5

**Holotype.** ZVC-P 12493, male, 101.9 mm SL, Uruguay, Salto, arroyo de las Tunas on Ruta 31, tributary to río Arapey Grande, 31°20'4.87"S 57°19'36.42"W, 8 Sep 2005, V. Bertaco, F. Cantera, J. Ferrer & L. R. Malabarba.

**Paratypes.** Uruguay, Departamento de Salto. Río Arapey drainage: MHNM 3711, 4, 1 male 79.9 mm SL, 3 females or juveniles 50.0-69.5 mm SL, río Arapey Chico on Ruta 4, 31°2'7.44"S 56°53'50.21"W, 22 Nov 2005, F. Teixeira, A. D'Anatro, I. González, S. Oviedo & M. Loureiro. UFRGS 8042, 7, 2 males 93.1-106.1 mm SL and 5 unsexed juveniles 19.7-64.1 mm SL, tributary stream to río Arapey Grande on Ruta 4, 31°07'44.0"S 56°59'57.0"W, 8 Sep 2005, V. Bertaco, F. Cantera, J. Ferrer & L. R. Malabarba. UFRGS 8076, 14, 3 males 99.7-100.1 mm SL (1 c&s 74.2 mm SL), 2 females 74.3-77.2 mm SL and 9 unsexed juveniles 51.2-67.1 mm SL (1 c&s 40.8 mm SL), collected with the holotype. UFRGS 8101, 1, female 70.3 mm SL, stream on Ruta 4, tributary of stream Valentin Grande, 31°16'32.0"S 57°09'22.0"W, 8 Sep 2005, L. R. Malabarba, V. Bertaco, J. Ferrer & F. Cantera. ZVC-P 13084, 4, 2 males, 76.4-79.7 mm SL, 2 females or juveniles 46.4-55.6 mm SL, Cañada de la Taperá, tributary of río Arapey, 31°09'02.15"S 56°13'25.18"W, 13 Dec 2014, M. Loureiro, A. Duarte, S. Serra, J. Bessonart & S. Paullier. ZVC-P



**Fig. 1.** Anterior portion of dorsal-fin skeleton of *Gymnogeophagus peliochelynion* (anterior towards left), UFRGS 8076, paratype, 74.2 mm SL. Arrow indicates the anterior spine in the first dorsal pterygiophore. Note the lack of supra-neurals between supraoccipital and first dorsal pterygiophore.

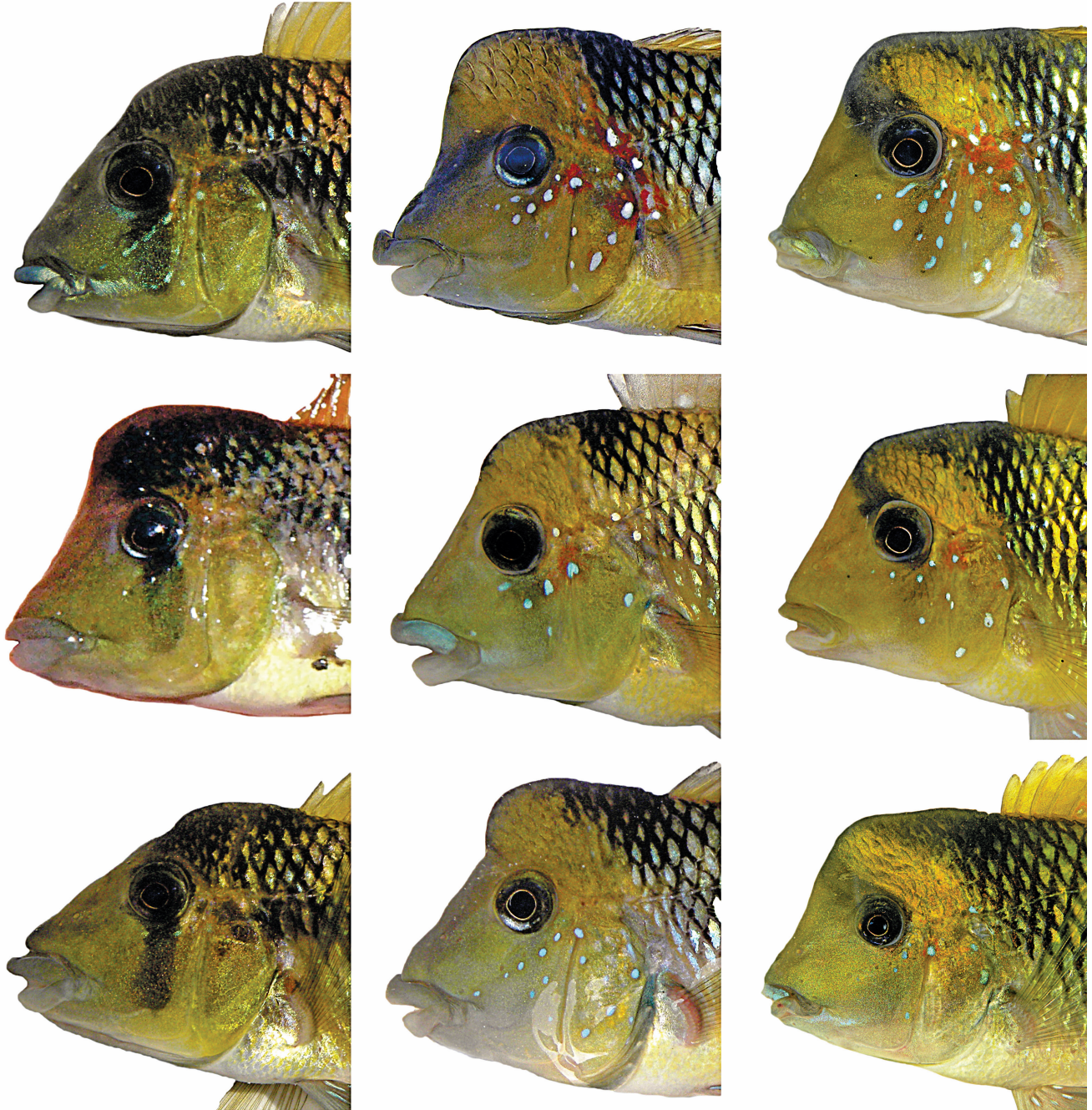
13210, 1 male 76.3 mm SL, río Arapey, Colonia Lavallega, Paso Elías, 31°02'50.94"S 57°00'46.04"W, 17 Dec 2014, M. Loureiro, A. Duarte, S. Serra, J. Bessonart, S. Paullier.

**Non-types:** Uruguay, Departamento de Salto. Río Arapey drainage: ZVC-P 7016, 16, 43.3-94.1 mm SL, Río Arapey Chico, Ruta 4, 31°02'07.44"S 56°53'50.21"W, 22 Nov 2005, F. Teixeira, A. D'Anatro, I. González, S. Oviedo & M. Loureiro. ZVC-P 12656, 3, 48.9-59.0 mm SL, Arroyo Sopas, Paso del Cementerio, 31°23'34.21"S 56°42'31.06"W, 13 Aug 2013, M. Loureiro, J. Bessonart, S. Serra & L. Montes de Oca. ZVC-P 12715, 4, 44.6-61.6 mm SL, Arroyo Sauce del Arapey, 31°19'27.25"S 56°37'24.55"W, 11 Aug 2013, M. Loureiro, J. Bessonart, S. Serra & L. Montes de Oca. ZVC-P 13013, 1, 51.7 mm SL, Arroyo Mataperros, 30°58'47.46"S 56°23'15.60"W, 15 Dec 2014, M. Loureiro, A. Duarte, S. Serra, J. Bessonart & S. Paullier. ZVC-P 13043, 4, 43.9-59.4 mm SL, Arroyo Arerunguá, Paso del Potrero, 31°27'07.02"S 56°50'37.01"W, 18 Dec 2014, M. Loureiro, A. Duarte & S. Serra. ZVC-P 13057, 2, 65.3-90.2 mm SL, Arroyo Sopas, Paso del Cementerio, 31°23'34.21"S 56°42'31.06"W, 18 Dec 2014, M. Loureiro, A. Duarte & S. Serra. ZVC-P 13079, 3, 57.6-77.1 mm SL, Arroyo Matajojo, Pueblo Fernandez, 31°10'37.01"S 56°21'56.54"W, 14 Dec 2014, M. Loureiro, A. Duarte, S. Serra, J. Bessonart & S. Paullier. ZVC-P 13118, 6, 56.3-77.2 mm SL, Río Arapey, Picada Sarandí, 31°03'52.47"S 56°22'44.84"W, 15 Dec 2014, M. Loureiro, A. Duarte, S. Serra, J. Bessonart & S. Paullier. ZVC-P 13139, 2, 52.7-57.7 mm SL, Arroyo Matajojo Grande, Paso de la Herreía, 31°11'45.40"S 56°36'11.65"W, 14 Dec 2014, M. Loureiro, A. Duarte, S. Serra, J. Bessonart & S. Paullier. ZVC-P 13178, 3, 51.2-55.9 mm SL, Río Arapey, Colonia Lavallega, Paso Elías, 31°02'50.94"S 57°00'46.04"W, 16 Dec 2014, M. Loureiro, A. Duarte, S. Serra, J. Bessonart & S. Paullier.



**Diagnosis.** The new species can be distinguished from the species of the *Gymnogeophagus rhabdotus* group and from *G. balzanii* by the shape of the caudal peduncle longer than deep (vs. deeper than long). It is distinguished from all congeners, except *G. labiatus* and *G. pseudolabiatus*, by the possession of thick lips. It differs from *G. labiatus* and *G.*

*lacustris* by the lack of an oblique bar from the eye to the dorsal-fin origin (vs. oblique bar present), and by the color pattern of the caudal, dorsal and anal fins with dots (vs. caudal fin and posterior portion of anal fin with longitudinal hyaline stripes). It differs from *G. pseudolabiatus* and *G. mekinos* by the hump entirely black in males (Fig. 2; vs.



**Fig. 2.** Head of *Gymnogeophagus peliochelynion* (first column), *G. pseudolabiatus* (second column) and *G. mekinos* (third column) showing the entirely black hump in males in *G. peliochelynion* (vs. yellow with black margin), and upper lip not folded dorsally over anterior margin of snout (vs. upper lip folded dorsally in *G. pseudolabiatus* and undeveloped in *G. mekinos*). *G. peliochelynion* from top to bottom, paratype, ZVC-P 13210, paratype, 76.3 mm SL; ZVC-P 7016, 89.9 mm SL; ZVC-P 13057, 90.2 mm SL. *G. pseudolabiatus* from top to bottom, paratype, UFRGS 7754, 102.0 mm SL; MHNM 4010, 88.8 mm SL; MHNM 4010, 95.3 mm SL. *G. mekinos* from top to bottom, MHNM 3511, 105.1 mm SL; MHNM 3511, 97.2 mm SL; MHNM 4009, 121.3 mm SL.

yellow with black margin), and upper lip not folded dorsally over anterior margin of snout (*vs.* upper lip folded dorsally, usually with a well-developed medial lobe dorsally projected in *G. pseudolabiatius*).

**Description.** Standard length of specimens examined 19.2 to 106.1 mm. Morphometric data summarized in Tab. 1. Body elongated, laterally compressed. Dorsal profile of head slightly convex between mouth and interorbital area in young and females, slightly straight in males; slightly convex from interorbital region to dorsal-fin origin. Reproductive males with adipose hump from interorbital region to dorsal-fin origin; dorsal-fin base gently convex. Caudal peduncle rectangular, longer than deep, with slightly concave dorsal and ventral profiles. Prepelvic contour straight to slightly convex; abdominal contour straight and base of anal fin straight to slightly convex.

**Tab. 1.** Morphometric data of *Gymnogeophagus peliochelynon*, new species. Standard length is expressed in mm. Range includes measurements of holotype and 22 paratypes, except individuals smaller than 45 mm SL.

|                            | Holotype | Min   | Max    | Mean  | SD   |
|----------------------------|----------|-------|--------|-------|------|
| Standard length (mm)       | 101.9    | 46.42 | 106.08 | 73.87 | -    |
| Percent of standard length |          |       |        |       |      |
| Head length                | 38.3     | 35.0  | 39.2   | 36.8  | 1.07 |
| Body depth                 | 38.5     | 33.8  | 39.9   | 37.7  | 1.44 |
| Dorsal-fin base length     | 48.2     | 45.4  | 54.1   | 50.3  | 2.05 |
| Pectoral-fin length        | 33.6     | 30.1  | 39.3   | 34.4  | 3.19 |
| Caudal peduncle depth      | 13.2     | 11.9  | 14.2   | 13.3  | 0.52 |
| Caudal peduncle length     | 15.1     | 14.0  | 18.1   | 15.3  | 1.10 |
| Percent of head length     |          |       |        |       |      |
| Eye diameter               | 21.3     | 20.2  | 32.3   | 25.1  | 3.27 |
| Interorbital width         | 28.5     | 24.6  | 32.4   | 28.0  | 1.97 |
| Upper jaw length           | 26.7     | 19.7  | 29.7   | 23.5  | 3.39 |
| Pre-orbital length         | 33.4     | 26.9  | 36.6   | 30.7  | 2.83 |
| Snout length               | 57.7     | 30.5  | 59.7   | 46.4  | 7.64 |

Head depth larger than head length. Snout triangular in lateral aspect; slightly rounded anteriorly, pointed in dorsal aspect. Eyes small, close to dorsal profile of head in juveniles and progressively farther from it in larger specimens (about eye diameter in specimens up to 80 mm); eyes near middle of head length. Interorbital area slightly convex in young and female, and deeply convex in large males; interorbital width larger than eye diameter, except in individuals smaller than 25 mm. Mouth terminal. Posterior tip of maxilla not reaching vertical line across anterior margin of eyes. Upper jaw slightly longer than lower jaw; lips developed, lower lip thicker than upper lip; margin of lower lip convex, deeper in middle length of each dentary, deeply notched medially at symphysis. Snout longer than postorbital length, except in individuals up to 48 mm SL.

Body scales moderately large and ctenoid, smaller ctenoid scales in preventral area. Proximal third to half of cau-

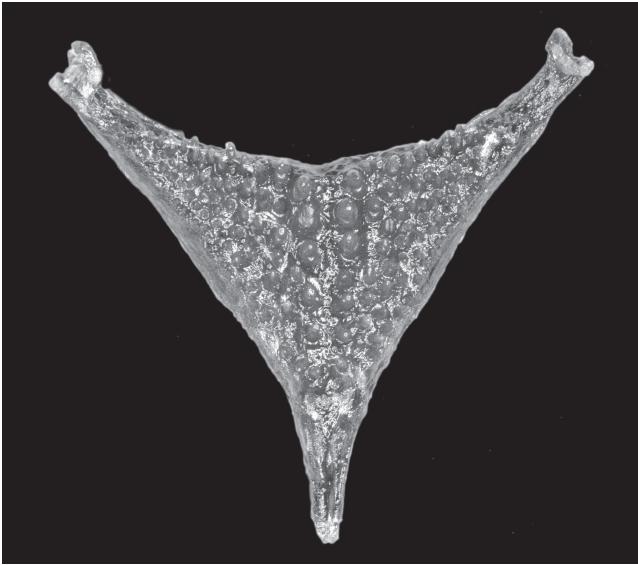
dal fin with small elongated cycloid scales in single series between contiguous rays. Dorsal fin without scales. Cheek naked. Small cycloid scales on opercle. Subopercular scales ctenoid in 1-2 irregular rows. Ctenoid scales on base of hump (in adult reproductive males only) to approximately vertical line passing on anterior margin of eye. Scales in longitudinal series 26\*(5), 27(6), 28(3). Anterior lateral line 15(1), 17\*(8), 18(5). Posterior lateral line 8\*(4), 9 (6), 10(1), 11(2), 12(1). Scales between anterior lateral line and dorsal fin 6\*(12), 7(2). Scales between anterior lateral line and anal fin 8\*(11), 9(3).

Dorsal-fin spines 12(1), 13(2), 14\*(11); dorsal-fin soft rays 9(1), 10\*(11), 11(2). First dorsal-fin spine inserted right above vertical line across posterior bony margin of opercle. Soft dorsal fin slightly pointed in young and adult females, reaching or almost reaching caudal-fin base. Fourth or fifth dorsal-fin soft ray longest in mature males, reaching proximal two third to half of caudal-fin length. Three anal-fin spines; anal-fin soft rays 8\*(11), 9(3); anal-fin profile rounded in young and females, reaching or almost reaching caudal-fin base; slightly pointed in reproductive males, surpassing caudal-fin base. Pectoral fin with pointed tip, reaching or almost reaching anal-fin origin in juveniles and females and surpassing anal-fin origin in reproductive males. Pelvic fin slightly pointed; second soft ray longest, reaching anal-fin base in mature males. Caudal-fin margin concave.

Jaw teeth small, conical, with recurved tips. Upper jaw with outer regular row of 16-26 teeth in each premaxilla (number increasing with specimen size) and two irregular internal rows of slightly smaller teeth. Lower jaw with 3-5 irregular rows of small conical teeth; outer hemiseries with 20-28 teeth. Lower limb of first gill arch with 6-10 gill rakers; upper limb lobed with 3-4 gill rakers in its margin. Lower pharyngeal tooth plate wide; teeth covering whole occlusion surface. Teeth on medial rows larger than remaining ones. Posterolateral teeth elongated; posteromedial teeth larger, cylindrical with medial, blunt cusps of molariform aspect (Fig. 3).

**Coloration after fixation in formalin.** (Fig. 4) Mature males: ground color of body dark brown above longitudinal series of scales of posterior lateral line and light yellowish brown below. Series of double vertical bars clearly discernible along midventral lateral surface of flanks, distributed between pectoral-fin base and end of caudal peduncle, anterior to caudal-fin base. Number of vertical double dark bars 5-6. Midlateral spot without defined borders. Hump entirely black in males making dark band in front of dorsal-fin origin hardly detectable. Head dark brown with some black spots on cheek and near posterior margin of opercle; dark band covering cheek hardly distinct. Isthmus and branchiostegal membranes dark brown. Pectoral fin hyaline. Pelvic fin dark gray. Spinous dorsal fin dark brown; soft dorsal fin light brown with circular dots. Distal one third of anal-fin rays and spines dark brown, without additional marks. Two proximal thirds of anal-fin rays covered with small circular dots. Caudal fin covered with white dots, except near upper and lower borders.





**Fig. 3.** Pharyngeal tooth plate of *Gymnogeophagus peliochelynion*, 74.2 mm SL, UFRGS 8076, paratype. Dorsal view; anterior to bottom.

Color in alcohol of preserved females and young not distinct from that described for males. Main differences are: isthmus and branchiostegal membrane yellow; clearly distinct dark band covering cheek, below eye; distinct dark band on dorsal-fin origin; and larger size of white spots on dorsal, anal, and caudal fins.

**Coloration in life.** (Fig. 5) Ground color of dorsal profile golden or dark olivaceous with longitudinal series of light blue spots. Well defined black, circular midlateral spot, covering scales 9-11 of the anterior lateral line, scales 10-12 of the scale row just below anterior lateral line and scales 8-10 of the next scale row below. Large dark bar below eye, usually not reaching midline of mouth in larger individuals. Numerous small bright blue spots usually present on cheeks. Red marks on cheeks usually present in mature males, concentrated on upper portion of opercle and preopercle, region behind eye and above pectoral fin. Usually grayish blue lips in reproductive males and gray in females and young. Adipose hump, when present, black. Ventral portion of body light olivaceous to yellow pale in mature males with longitudinal series of



**Fig. 4.** *Gymnogeophagus peliochelynion*: top, holotype, male, ZVC-P 12493, 101.9 SL; bottom, paratype, female, UFRGS 8076, 77.2 SL. Both from arroyo de las Tunas on road 31, tributary of río Arapey Grande, Salto, Uruguay. Photographs taken just after collection and fixation in formalin.



**Fig. 5.** *Gymnogeophagus peliochelynion*: above, paratype, male, ZVC-P 13210, paratype, 76.3 mm SL, río Arapey, Colonia Lavalleja, Paso Elías, Salto, Uruguay; below, female, ZVC-P 13057, 65.3 mm SL, Arroyo Sopas, Paso del Cementerio, Salto, Uruguay. Photographs of live specimens.

light blue spots. Spinous dorsal fin and base of soft dorsal fin yellowish brown; most soft dorsal fin red with relatively large and numerous hyaline dots. Distal tip of dorsal fin hyaline. Pectoral fin hyaline and pelvic fin dark orange to dark gray with light blue spots at base. Anal fin yellowish orange proximally with numerous clear spots and hyaline on half distal portion with dark gray margin. Caudal fin yellowish brown with numerous light spots, extending along middle of caudal fin; dorsal and ventral portions of fin hyaline.

**Geographic distribution.** This species is known from the río Arapey Grande drainage, a tributary of the lower río Uruguay basin, Uruguay (Fig. 6).

**Ecological notes.** The new species was collected in rivers with clear water, usually with rocky or muddy bottom and little vegetation.

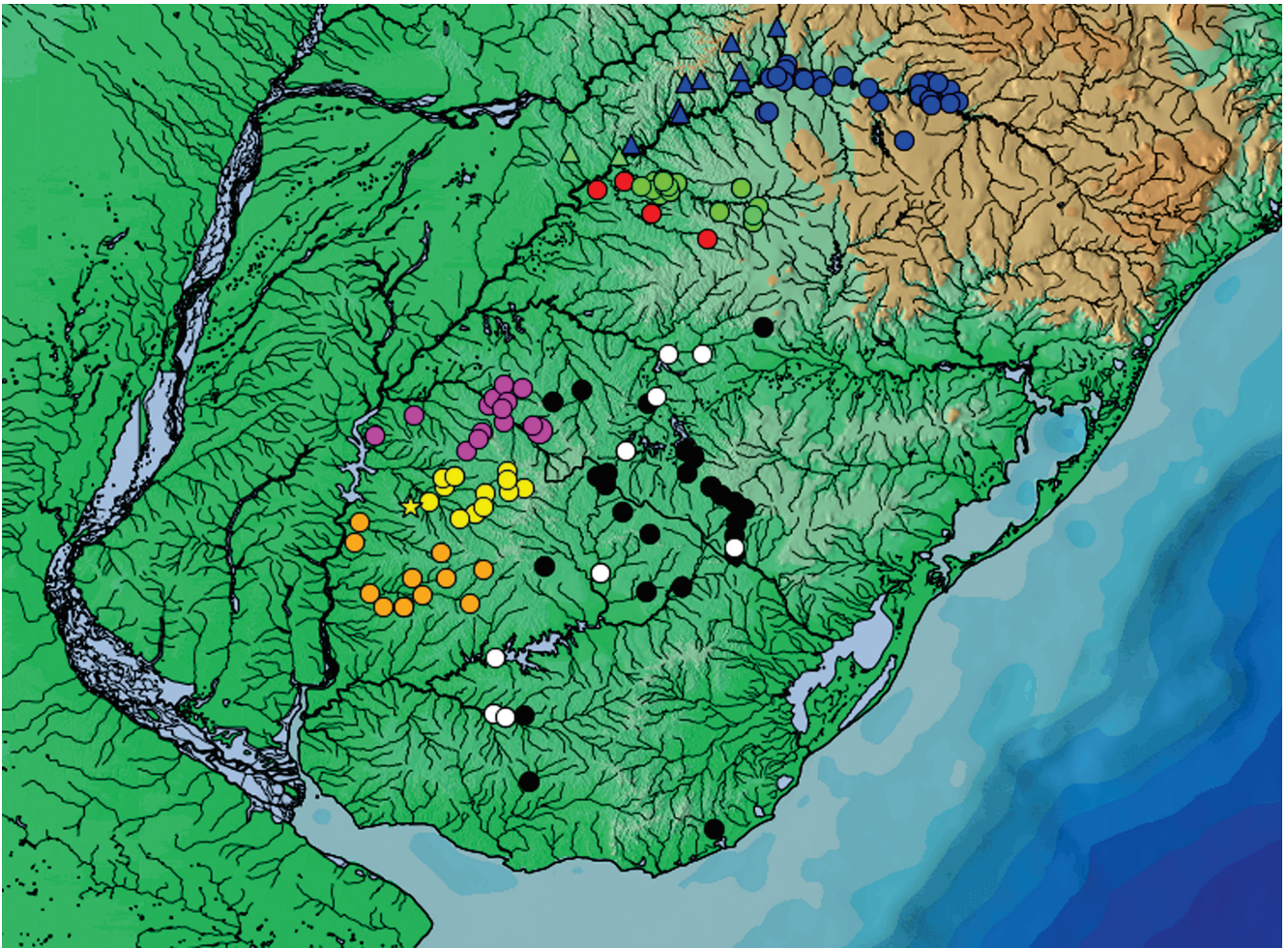
**Etymology.** The name *peliochelynion* is from the Greek *pelios*, meaning black and blue, and *chelyne*, meaning lip, in reference to the color of the lips of the new species. A name in apposition.

**Conservation status.** *Gymnogeophagus peliochelynion* is relatively frequent and abundant in the río Arapey Grande drainage. No specific threats were detected, and the species can be categorized as Least Concern (LC) according to IUCN criteria (IUCN, 2016).

### Discussion

*Gymnogeophagus peliochelynion* shares the two synapomorphies that diagnoses the genus (Reis, Malabarba, 1988): the lack of supraneurals and the presence of a forward-directed spine on anterodorsal margin of the first





**Fig. 6.** Geographic distribution of *Gymnogeophagus peliochelynion* (yellow; star refers to type-locality), *G. cf. peliochelynion* (orange) and other species of the *Gymnogeophagus gymnogenys* clade: *G. lipokarenos* (blue), *G. constellatus* (green), *G. missioneiro* (red), *G. tiraparae* (white), *G. mekinos* (black), *G. pseudolabiatus* (pink) in the río Uruguay basin. Records of *Gymnogeophagus lipokarenos* and *Gymnogeophagus constellatus* from Argentina (triangles) are based on Casciotta *et al.* (2017b) and Řičan *et al.* (2017), respectively.

dorsal-fin pterygiophore (Fig. 1). The new species also belong to a clade that includes *G. gymnogenys*. Species in this clade are easily recognized by sharing two synapomorphies (more easily observed in females and juveniles; Fig. 5): the absence of an oblique bar between the dorsal border of the eye and the nape, and the possession of a black bar originating in the dorsal contour near the dorsal-fin origin and directed downward and backward on the dorsum (Reis, Malabarba, 1988; Malabarba *et al.*, 2015). The conspicuous secondary sexual dimorphism (including development of a nuchal hump in reproductive males), mouthbrooding reproductive strategy, and elongated caudal peduncle, longer than deep (Wimberger *et al.*, 1998), which are not observed in the *G. rhabdotus* group, further support the inclusion of *G. peliochelynion* in the *G. gymnogenys* clade.

Species of the *Gymnogeophagus gymnogenys* clade have an allopatric distribution (Fig. 6) along several tributaries of the río Uruguay (Malabarba *et al.*, 2015; Casciotta *et al.*, 2017b; Řičan *et al.*, 2017). *Gymnogeophagus lipok-*

*arenos* is endemic to the upper portion of the río Uruguay, upstream to San Javier (Argentina)/Porto Xavier (Brazil). *Gymnogeophagus constellatus* and *G. missioneiro* occur in tributaries immediately downstream of San Javier and Porto Xavier, the first occurring mainly in the río Ijuí (Brazil), arroyo Itacaruaré and arroyo Chimiray-Mini (Misiones) drainages, and the second occurring in río Piratini (Brazil) drainage, all draining a basaltic rock bed of the Serra Geral Formation (Batezelli *et al.*, 2005). The next main tributary of the Río Uruguay, in a downstream direction, is the río Ibicuí, with a fine grain sedimentary substrate, corresponding to the unique tributary of the middle Río Uruguay where *G. tiraparae* and *G. mekinos* are found. These two species are present too in lower tributaries of Uruguay and La Plata river basins in Uruguay and Brazil. In the next downstream drainage, the río Quaraí, with basaltic rock bed, we find *G. pseudolabiatus*. The next downstream tributary, the río Arapey, is occupied by the new species described herein, *G. peliochelynion*. This successive substitution of allopatric

species of the *Gymnogeophagus gymnogenys* clade along río Uruguay tributaries suggests the main channel act as a physical or ecological barrier to dispersal of these species, all of which are adapted to small affluents. Similar patterns have been observed in the tributaries of the río Amazonas for other groups of fish (Junk *et al.*, 2001; Hubert, Renno 2006) and for Atlantic coastal rivers connected through freshwater lakes (Hirschmann *et al.*, 2015).

Populations from río Queguay and río Dayman located downstream from the río Arapey are tentatively identified herein as *G. cf. peliochelynion*. Although they do not show hypertrophied lips, they show similar color pattern to that described for *G. peliochelynion*. Further investigation is needed in order to determine whether these populations constitute a separate species.

**Comparative material examined** (In addition to those listed by Malabarba *et al.*, 2015). *Gymnogeophagus cf. peliochelynion*. **Uruguay, Departamento de Salto. Río Dayman drainage:** ZVC-P 6686, 1, 57.7 mm SL, río Dayman, Ruta 4, 31°47'15.45"S 57°02'12.24"W, 21 Nov 2005, M. Loureiro, F. Teixeira, S. Oviedo, A. D'Anatro & I. González. ZVC-P 13242, 1, 54.2 mm SL, Río Dayman, Paso Morales, 31°28'40.92"S 57°49'40.14"W, 17 Dec 2014, M. Loureiro, S. Serra & A. Duarte. **Departamento de Paysandú. Río Queguay drainage:** ZVC-P 13299, 1, 53.7 mm SL, Río Queguay, Paso del Sauce, 32°16'55.46"S 56°45'17.24"W, 19 Dec 2014, A. Duarte, S. Serra & M. Loureiro. ZVC-P 13306, 1, 70.5 mm SL, Arroyo Corrales, Paso Castillo, 31°56'29.54"S 56°37'12.40"W, 19 Dec 2014, A. Duarte, S. Serra & M. Loureiro. ZVC-P 13348, 1, 48.5 mm SL, Río Queguay, Cerro del Inglés, 32°10'31.73"S 57°44'00.01"W, 19 Apr 2015, S. Paullier, J. Cabrera, M. Trillo, M. Loureiro & J. Bessonart. ZVC-P 13367, 1, 108.3 mm SL, Arroyo Ñacurutú Grande, 32°18'39.78"S 57°24'20.88"W, 21 Apr 2015, S. Paullier, J. Cabrera, M. Trillo, M. Loureiro & J. Bessonart. ZVC-P 13387, 1, 65.8 mm SL, Río Queguay Chico, Paso del Parque, 32°02'27.76"S 56°59'26.24"W, Apr 2015, S. Paullier, J. Cabrera, M. Trillo, M. Loureiro & J. Bessonart. ZVC-P 13439, 1, 67.7 mm SL, Arroyo Bacacua Grande, 32°19'12.30"S 57°36'16.66"W, 21 Apr 2015, S. Paullier, J. Cabrera, M. Trillo, M. Loureiro & J. Bessonart. *Gymnogeophagus gymnogenys*. **Brazil, Rio Grande do Sul State** (all from laguna dos Patos drainage): UFRGS 4242, 10, 47.3-65.4 mm SL, arroio Velhaco; UFRGS 13697, 1, 106.3 mm SL, arroio Forquetinha; UFRGS 14213, 8, 39.9-94.8 mm SL, arroio Forquetinha; UFRGS 16135, 1, 88.1 mm SL, lago Guaíba; UFRGS 16136, 1, 92.4 mm SL, lago Guaíba. *Gymnogeophagus mekinos*. **Uruguay, Departamento de Florida.** MHNM 3511, 2, 97.2-105.1 mm SL, Paso de la Arena, Río Santa Lucía Chico, 34°01'51.24"S 56°09'45.75"W, 11 Jan 2014, W.S. Serra & M. Pérez. **Departamento de Rocha.** MHNM 4009, 4, 49.9-121.3 mm SL, Arroyo Rocha, Parque La Estiva, Ciudad de Rocha, 34°29'38.43"S 54°20'43.58"W, 22 Jan 2018, W.S. Serra. *Gymnogeophagus pseudolabiatu*. **Uruguay, Departamento de Artigas.** MHNM 4010, 7, 55.3-95.3 mm SL, Arroyo Pintado y Ruta 30, 30°26'16.70"S 56°26'59.23"W, 2 Dec 2017, W.S. Serra & N. Ríos; ZVC-P 9893, 5, 34.9-88.2 mm SL, Cañada Mataojo, 30°47'46.93"S 56°56'52.66"W, Aug 2006, M. Loureiro, F. Teixei-

ra, I. González & F. Quintans; ZVC-P 10011, 11, 24.8-87.4 mm SL, Cañada Honda, 30°27'46.98"S 56°51'24.82"W, Aug 2006, M. Loureiro, F. Teixeira, I. González & F. Quintans; ZVC-P 10057, 27, 28.1-80.9 mm SL, Cañada Honda, 30°27'33.47"S 56°49'51.29"W, Aug 2006, M. Loureiro, F. Teixeira, I. González & F. Quintans; ZVC-P 12616, 7, 46.6-93.2 mm SL, Cuareim River, Laguna Salamanca, 30°46'36.21"S 56°02'16.71"W, Dec 2012, A. Duarte, W.S. Serra, M. Loureiro & L. Ziegler; ZVC-P 12684, 2, 98.2-101.6 mm SL, Cuaró Grande stream, Ruta 4, 30°46'57.96"S 56°47'05.08"W, Aug 2013, M. Loureiro, J. Bessonart, W.S. Serra & L. Montes de Oca.

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