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## A new species of *Pseudobunocephalus* Friel, 2008 (Siluriformes: Aspredinidae) from the lower Tocantins and Mearim river drainages, North and Northeast of Brazil

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### Abstract

*Pseudobunocephalus timbira*, new species, is described from streams of the lower Tocantins and the Mearim river drainages, in North and Northeast of Brazil. *Pseudobunocephalus timbira* can be distinguished from all congeners by having the second hypobranchial and the third basibranchial cartilaginous (*vs.* ossified). Additionally, it can be distinguished from *P. lundbergi* by the following putative apomorphic features within *Pseudobunocephalus*: posterolateral process of premaxilla present (*vs.* absent); bony knobs in dorsal lamina of Weberian apparatus absent (*vs.* present); distal end of posterior margin of 5th parapophysis not enlarged (*vs.* enlarged); number of ribs three (*vs.* four or five) and infraorbital sensory canal entering neurocranium via frontal (*vs.* via sphenotic). It is distinguished from *P. bifidus* and *P. iheringii* by having a gracile body not surpassing 34 mm SL (*vs.* robust body, reaching up to 59 mm SL, respectively); by having the posterior margin of cranial fontanel concave (*vs.* posterior margin somewhat straight with parieto-supraoccipital extending anteriorly); by having a conspicuous knobby ornamentation on dorsal surface of skull (*vs.* skull knobs slightly pronounced); by having Weberian ventral blade of hemal canal opened (*vs.* closed) and by the absence of serrations on the proximal portion of the anterior margin of pectoral-fin spine (*vs.* serrations covering entire anterior margin of the pectoral spine). Additionally, it can be distinguished from *P. amazonicus*, *P. rugosus* and *P. quadriradiatus*, by having the posterolateral mental barbel with at least one fleshy lobe located proximally along the posterior margin (*vs.* posterolateral mental barbel simple, not having fleshy lobes). It also differs from *P. amazonicus* and *P. rugosus* by having five branchiostegal rays (*vs.* four). It also can be distinguished from *P. amazonicus* by having the contact of hyomandibula cartilage with neurocranium limited to the sphenotic (*vs.* extending to both sphenotic and pterotic); by having the ventral blade of Weberian apparatus open (*vs.* closed) and by anterior exit of hemal canal in abdominal vertebra (*vs.* in complex vertebra); from *P. rugosus* by coloration of proximal portion of caudal fin similar to rest of caudal fin (*vs.* clear patch) and from *P. quadriradiatus* by the total number of pectoral fin-rays six (*vs.* five). Variable characteristics within *Pseudobunocephalus* species are summarized and comments on the phylogenetic relationships and the disjunct distribution of the new species are made. [Species zoobank url: <urn:lsid:zoobank.org:act:392F95E0-86E1-4386-8779-C4F71098DBCC>]

**Key words:** Banjo catfish, Endemism, Neotropical region, Taxonomy

### Resumo

*Pseudobunocephalus timbira*, espécie nova, é descrita de córregos do baixo rio Tocantins e do rio Mearim, Norte e Nordeste do Brasil. *Pseudobunocephalus timbira* pode ser distinguida de todos os congêneres por possuir o segundo hipobrânquial e terceiro basibrânquial cartilaginosos (*vs.* ossificados). Adicionalmente, pode ser distinguida de *P. lundbergi* pelas seguintes características apomórficas dentro de *Pseudobunocephalus*: processo posterolateral da pré-maxila presente (*vs.* ausente); protuberâncias ósseas na lâmina dorsal do aparato de Weber ausente (*vs.* presente); extremidade distal

da margem posterior da parapófise da 5<sup>o</sup> vértebra não ampliada (vs. ampliada); número de costelas três (vs. quatro ou cinco) e canal sensorial infraorbital entrando no neurocrânio através do frontal (vs. através do esfenótico). Distingue-se de *P. bifidus* e *P. iheringii*, por possuir um corpo grácil não ultrapassando 34 mm CP (vs. corpo robusto, atingindo 59 mm CP, respectivamente); por possuir a margem posterior da fontanela côncava (vs. margem posterior um tanto reta com extensão anterior do parieto-supraoccipital); pelas ornamentações do crânio visivelmente nítidas em sua superfície dorsal (vs. ornamentações ligeiramente pronunciadas); por possuir a lâmina ventral weberiana do canal hemal aberta (vs. fechada) e pela ausência de serrilhas na porção proximal da margem anterior do espinho peitoral (vs. serrilhas cobrindo toda a margem anterior do espinho peitoral). Além disto, pode ser distinguida de *P. amazonicus*, *P. rugosus* e *P. quadriradiatus* por possuir barbilhões posterolaterais mentonianos com um ou mais lóbulos carnosos proximais ao longo da margem posterior (vs. barbilhões posterolaterais mentonianos simples, não formando lóbulos carnosos). Também se difere de *P. amazonicus* e *P. rugosus* por possuir cinco raios branquiostegais (vs. quatro). Difere de *P. amazonicus* pelo contato da cartilagem da hio-mandíbula com o neurocrânio limitado pelo esfenótico (vs. estendendo para ambos esfenótico e pterótico); por possuir a lâmina ventral weberiana do canal hemal aberta (vs. fechada) e pela saída anterior do canal hemal na vértebra abdominal (vs. no complexo vertebral); de *P. rugosus* pela coloração da porção proximal da nadadeira caudal similar ao resto do da nadadeira (vs. mancha clara) e de *P. quadriradiatus* pelo número total de raios da nadadeira peitoral seis (vs. cinco). As características variáveis dentro das espécies de *Pseudobunocephalus* são resumidas e comentários sobre as relações filogenéticas e a distribuição disjunta da nova espécie são apresentados.

**Palavras-chave:** Rabeca, Endemismo, Região Neotropical, Taxonomia

## Introduction

*Pseudobunocephalus* was described by Friel (2008) to allocate *P. lundbergi* Friel, 2008 from the Orinoco River drainage, plus five other previously described species that were placed in *Bunocephalus* (Friel, 2003): *P. amazonicus* (Mees, 1989), *P. bifidus* (Eigenmann, 1942) and *P. quadriradiatus* (Mees, 1989) from the Amazon River basin, *P. iheringii* (Boulenger, 1891) from the La Plata River basin and Laguna dos Patos System, and *P. rugosus* (Eigenmann & Kennedy, 1903) from the Paraná-Paraguay River basin. The species of *Pseudobunocephalus* are generally smaller than 8 cm in standard length and exclusively found in freshwaters (Friel, 2008; Eschmeyer *et al.*, 2018) with preference for small rivers shaded by marginal vegetation, living amidst aquatic vegetation and background debris composed of dead leaves and branch remains (Burgess, 1989). The monophyly of the genus is supported by a series of synapomorphic features (Friel, 2008): (1) dentary teeth restricted to a broad tooth patch near the symphysis of lower jaw, (2) metapterygoid lacking a bony connection with the quadrate, (3) posterior end of autopalatine distinctly forked, bearing two separate terminal cartilages, (4) absence of the fourth pharyngobranchial, (5) absence of gill rakers on all branchial arches, and (6) absence of bifid hemal spines on vertebrae that articulate with anal-fin pterygiophores, which are derived from an unpublished phylogeny of Aspredinidae (Friel, 1994; see also de Pinna, 1998: fig. 17). Within aspredinids, *Pseudobunocephalus* is reported as the sister-group of all remaining genera and retains a series of plesiomorphic characters (Friel, 1994; 2008). *Pseudobunocephalus* is also recognized by non-unique characters (shared with *Acanthobunocephalus*) of external anatomy and is readily recognizable: (1) terminal mouth, lower and upper jaws equal, (2) lateral line truncated at the level of the origin of the dorsal fin, (3) lower and uppermost principal caudal-fin rays distinctly smaller than the other main rays, and (4) last ray of the dorsal and anal fins not adnate by membrane to body (Friel, 2008). Recently, a study based in molecular data also supported *Pseudobunocephalus* as a monophyletic group sister to the remaining Aspredinidae, and a new subfamily, Pseudobunocephalinae (Carvalho *et al.*, 2018) was proposed.

In this paper a new species of *Pseudobunocephalus* is described from the lower Tocantins and the Mearim rivers, and we comment on its endemism, relationships and species limits within *Pseudobunocephalus*.

## Material and methods

Measurements were taken point to point with digital calipers. Measurements are expressed as percents of the standard length (SL), except subunits of head, which are expressed as percents of the head length (HL). The measurements follow Friel (1995) and Cardoso (2010); except for cleithral process length, which was taken from

the anterior margin of the cleithrum, on its lateral anteriorly projected process, to the posterior tip of the cleithral process (Carvalho *et al.*, 2015; Friel & Carvalho, 2016).

The Phylogenetic Species Concept was used; this species concept categorizes a species as an irreducible group whose members are descended from a common ancestor and who all possess a combination of certain defining, or derived, traits (Cracraft, 1983; Nixon & Wheeler, 1990). This concept is in accordance to other more pluralistic species concept such as the The Unified Species Concept (de Queiroz, 2007), in which species are equated with independently evolving metapopulation lineages. Although relationships within *Pseudobunocephalus* are not comprehensively known, current knowledge on phylogenetic relationships of the group (Friel, 1994; Carvalho *et al.*, 2018) permits us to evaluate putative plesiomorphic or apomorphic conditions of characters (see more on discussion). Cleared and stained (c&s) specimens were prepared according to the methods of Taylor & Van Dyke (1985). Vertebral counts were based on c&s specimens and include all preural vertebrae, including the five vertebrae modified into the Weberian apparatus (PU1+U1 centra on the caudal skeleton counted as a single element). In general, anatomical terminology follows the Teleost Anatomical Ontology (TAO; Dahdul *et al.*, 2010) an integral part of the Uberon Ontology covering anatomical structures in animals (Mungall *et al.*, 2012; <http://uberun.github.io/>). Nomenclature of elements associated with the caudal skeleton follow Lundberg & Baskin (1969) and de Pinna & Ng (2004), and the elements of pectoral-fin spine follow Vanscoy *et al.* (2015). The distribution maps were made using *Quantum Gis* (QGIS—Geographic Information System; <https://www.qgis.org/en/site/>). Museum acronyms follow Sabaj (2016).

Three-dimensional skeletal models of whole or anterior portion of body were generated to aid on osteological comparisons and illustrations. Computed microtomography of representatives of species of *Pseudobunocephalus* were used, except for *P. quadriradiatus*. Most scans were performed on a Bruker SkyScan 1173 micro-CT scanner at 3D resolution (i.e., voxel size) ranging from 25–50  $\mu\text{m}$ , 40–65 kV and 55–123  $\mu\text{A}$ . Scans of *P. lundbergi* were made using a Nano-CT - GE v|tome|x m 240 scanner with a resolution of 10.3  $\mu\text{m}$ , kV and 170  $\mu\text{A}$ . We reconstructed the scans using the software N-Recon (Bruker Inc.), and whenever more than a single specimen was scanned together, we digitally isolated each specimen from the scan using DataViewer (Bruker Inc.). Illustration of three-dimensional skeletal reconstructions were done using CT-vox (Bruker Inc.). CT image stacks for each specimen used in this study are available on Morphosource - Duke University (<https://www.morphosource.org/>) with their respective morphosource identifier and museum catalog numbers: *Pseudobunocephalus amazonicus* # M34562 (MCP 35751); *Pseudobunocephalus bifidus* # M34563 (MUSM 33855), *Pseudobunocephalus iheringii* # M34567 (ANSP 202244); # M34569 (UFRGS 7175), *Pseudobunocephalus lundbergi* # M29216 (ANSP 168813), *Pseudobunocephalus rugosus* # M34570 (ANSP 170401), # M34571 (MCP 15540) and the new species described herein # M33704 (MCN 19274).

## Results

### *Pseudobunocephalus timbira*, new species

(Figs. 1, 2; Tables, 1, 2)

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*Acanthobunocephalus* sp. nov. 3—Cardoso, 2008: 166 [unpublished phylogenetic study, listed as an undescribed species].

**Holotype.** MPEG 21057, 31.8 mm SL, Brazil, Maranhão, Alto Alegre do Pindaré, Jundiá Creek, Mearim River basin, 3°39'14"S 45°42'19"W, T. M. S. Freitas, 11 June 2011.

**Paratypes.** All from Brazil. INPA 6519, 1, 18.4 mm SL, Pará, Itupiranga, Jatobal Creek 1 km upstream its mouth, Tocantins River basin, 4°28'S 49°27'W, INPA staff, 15 Nov 1981. INPA 6520, 3, 23–26 mm SL, Pará, Itupiranga, Jatobal Creek, Tocantins River basin, 4°28'S 49°27'W, INPA staff, 8 Jul 1982. INPA 6532, 4, 22.7–23.1 mm SL, Pará, Itupiranga, Tocantins River, Tocantins River basin; INPA staff, 15 Jul 1980. MCN 19274, 2, 25.7–29.2 mm SL, Tocantins, São Sebastião do Tocantins, Lake at Fazenda Ozara, Tocantins River Basin, 05°16'04"S 48°10'20"W, A. Cardoso & staff, 20 Sep 2010. MCP 54089, 5, 19.2–25.5 mm SL, Pará, Marabá, Tapirapé River upstream Bacaba base, REBIO Tapirapé, Tocantins River basin, 5°40'7"S 50°18'49"W, I. Fichberg & J. Muriel-Cunha, 3 Aug 2008. MCP 54090, 5, 23.6–33 mm SL, Pará, Marabá, Grotão do Wilson Creek, Trilha Bacaba,

REBIO Tapirapé, Tocantins River basin, 5°40'28"S 50°19'21"W, I. Fichberg & J. Muriel-Cunha, 8 Aug 2008. MHNG 2551.010, 10, 1 c&s, 23.7–24.9 mm SL, Pará, São João do Araguaia, small tributary to Tocantins River 12 km from São João do Araguaia, Tocantins River basin, approx. 05°21'S 48°47'W, R. Stawikowski, 18 Sep 1990. MPEG 30384, 1, 22.7 mm SL, Pará, Bom Jesus do Tocantins, Flexeiras River, Tocantins River basin, 5°15'35"S 48°59'35"W, C. Costa, 20 May 2012. MPEG 37432, 1, 28.8 mm SL: collected with holotype. MPEG 38466, 5, 1 c&s, 21.6–26.9 mm SL, Pará, Marabá, Tapirapé River upstream Bacaba base, REBIO Tapirapé, Tocantins River basin, 5°40'7"S 50°18'49"W, I. Fichberg & J. Muriel-Cunha, 3 Aug 2008. MPEG 38467, 5, 1 c&s, 23.7–28 mm SL, Pará, Marabá, Grotão do Wilson Creek, Trilha Bacaba, REBIO Tapirapé, Tocantins River basin, 5°40'28"S 50°19'21"W, I. Fichberg & J. Muriel-Cunha, 8 Aug 2008. MZUSP 105309, 49, 17.9–32.5 mm SL, Pará, Marabá, Tapirapé River upstream Bacaba base, REBIO Tapirapé, Tocantins River basin, 5°40'7"S 50°18'49"W, I. Fichberg & J. Muriel-Cunha, 3 Aug 2008. MZUSP 105368, 51, 22.0–33.4 mm SL, Pará, Marabá, Grotão do Wilson Creek, Trilha Bacaba, REBIO Tapirapé, Tocantins River basin, 5°40'28"S 50°19'21"W, I. Fichberg & J. Muriel-Cunha, 8 Aug 2008.



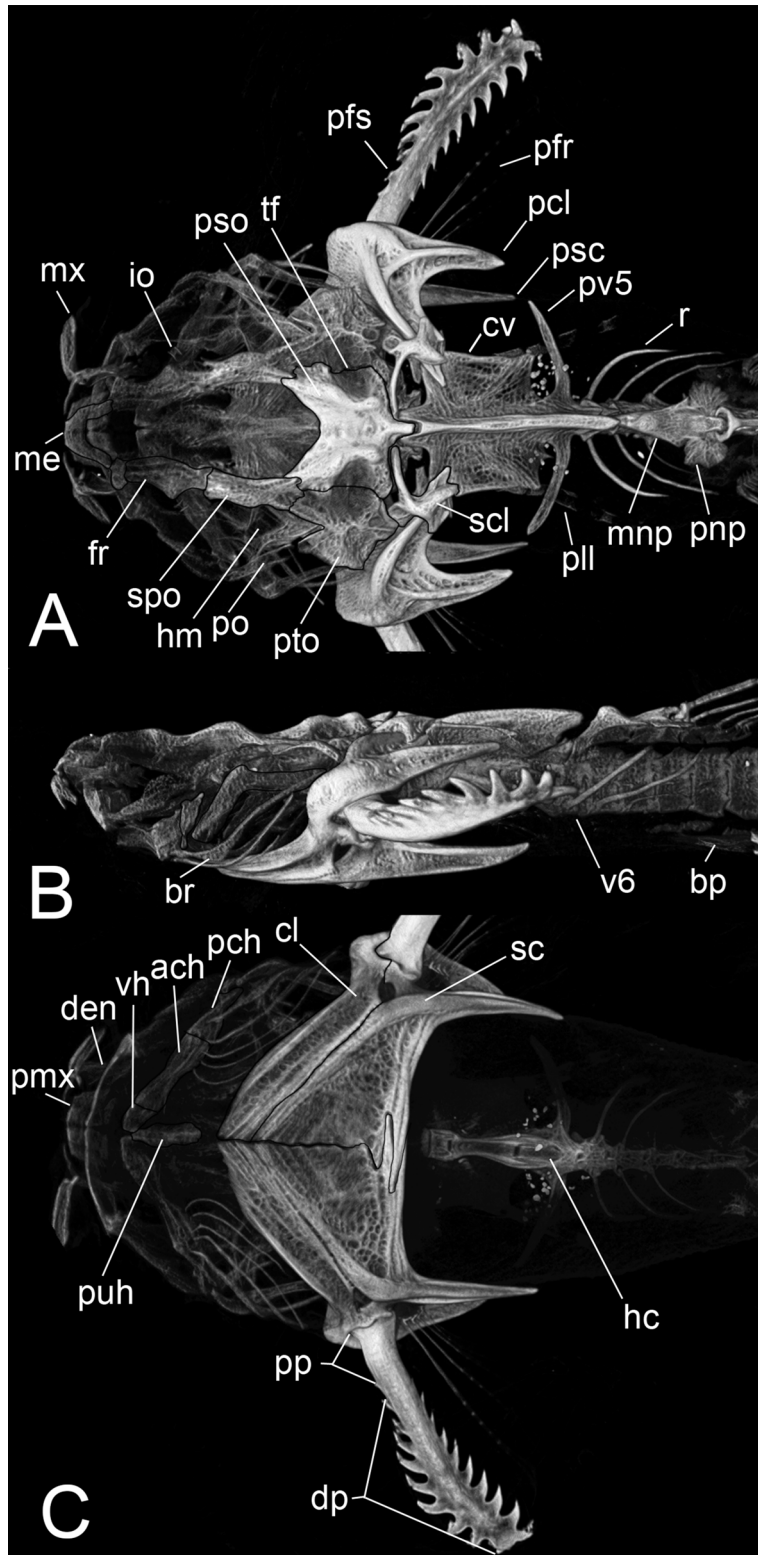
**FIGURE 1.** Dorsal, lateral and ventral views of *Pseudobonocephalus timbira*, holotype, MPEG 21057, 31.8 mm SL, Brazil, Maranhão, Alto Alegre do Pindaré, Jundiá Creek, Mearim River basin.

**Diagnosis.** *Pseudobunocephalus timbira* can be distinguished from all congeners by having the second hypobranchial and the third basibranchial cartilaginous (*vs.* ossified). Additionally, it can be distinguished from *P. lundbergi* by the following putative apomorphic features within *Pseudobunocephalus*: posterolateral process of premaxilla present (Fig. 2C *vs.* absent); bony knobs in dorsal lamina of Weberian apparatus absent (Fig. 2B *vs.* present, Fig. 3A, B); distal end of posterior margin of 5th parapophysis not enlarged (Fig. 2B *vs.* enlarged, Fig. 3A, C.); three pairs of ribs (Fig. 2B *vs.* four or five, Fig. 3A); infraorbital sensory canal entering neurocranium via frontal (Fig. 2A *vs.* via sphenotic, Fig. 3A).

It is distinguished from *P. bifidus* and *P. iheringii* by having a gracile body not surpassing 34 mm SL (*vs.* robust body, reaching 52 and 59 mm SL, respectively); by having the posterior margin of cranial fontanel concave (Fig. 2A *vs.* posterior margin somewhat straight with parieto-supraoccipital extending anteriorly, Fig. 3D); by conspicuously knobby skull ornamentation on its dorsal surface (Fig. 2A, B *vs.* skull knobs slightly pronounced, Fig. 3D, E); by having Weberian ventral blade of hemal canal opened (Fig. 2C *vs.* closed, Fig. 3F) and by the absence of serrations on the proximal portion of the anterior margin of pectoral-fin spine (Fig. 2A, C *vs.* serrations covering entire anterior margin of the pectoral spine, Fig. 3D–I).

**TABLE 1.** Morphometric data of holotype (H) and 14 paratypes of *Pseudobunocephalus timbira*. SD= Standard Deviation.

	H	Min	Max	Mean	SD
Standard length (mm)	31.8	21.6	31.8	25.5	-
Percent of Standard Length					
Head length	19.8	18.2	21.0	19.6	0.93
Prepectoral length	22.0	19.5	24.0	21.6	1.15
Cleithral width	26.9	26.3	28.6	27.2	0.71
Maximum head depth	12.0	10.9	12.3	11.5	0.48
Pectoral-spine length	20.5	16.3	20.5	18.0	1.07
Distance between coracoid processes	20.6	17.0	20.6	18.7	0.97
Coracoid process length	12.5	11.0	12.5	11.9	0.58
Distance between cleithral processes	22.2	18.9	22.5	20.3	1.10
Cleithral process length	10.8	10.3	12.6	11.5	0.73
Predorsal length	38.4	36.7	40.5	38.5	0.99
Depth at dorsal-spine insertion	10.9	9.5	12.0	10.7	0.79
Dorsal-spine length	11.8	9.4	13.4	11.4	1.16
Prepelvic length	43.0	39.4	44.7	42.2	1.55
Length of unb. pelvic fin ray	12.9	11.0	13.3	12.3	0.62
Preanal length	60.5	56.8	65.2	60.9	2.08
Anal-fin base length	16.4	14.8	20.0	17.2	1.33
Distance anal-fin origin to end of caudal peduncle	37.0	31.5	38.0	35.7	1.79
Caudal-peduncle length	21.5	16.5	24.0	20.4	1.87
Caudal-peduncle depth	5.4	5.4	7.7	6.8	0.80
Caudal-fin length	24.9	19.6	25.8	22.4	1.75
Percent of Head Length					
Snout length	31.0	27.5	35.2	31.0	2.30
Eye diameter	12.5	12.5	18.7	15.2	1.66
Interorbital width	35.1	25.9	39.7	35.9	3.91
Maxillary-barbel length	119.5	69.6	119.5	86.4	12.84
Distance between anterior nostrils	14.4	11.9	19.6	15.6	2.45
Distance between posterior nostrils	26.9	26.9	38.0	32.2	3.13
Mouth width	35.1	30.4	45.3	37.4	4.35



**FIGURE 2.** HRXCT model of skull and anterior body of *Pseudobunocephalus timbira*, MCN 19274, paratype, 29.2 mm SL. (A) dorsal view, (B) lateral view, and (C) ventral view. ach = anterior ceratohyal; bp = basipterygium; br = branchiostegal rays; cl = cleithrum; cv = complex vertebrae; den = dentary; dp = proximal portion of pectoral-fin spine; fr = frontal; hc = hemal canal; hm = hyomandibula; io = infraorbital; me = mesethmoid; mnp = middle nuchal plate; mx = maxilla; tf = temporal fontanel; pcl = posterior process of cleithrum; pnp = posterior nuchal plate; pfr = pectoral-fin rays; pfs = pectoral-fin spine; pll = posterior lateral line tubules; pmx = premaxilla; po = preopercle; pp = proximal portion of pectoral-fin spine; psc = posterior process of scapulocoracoid; pso = parietosupraoccipital; pto = pterotic; pv5 = parapophysis of fifth vertebra; puh = urohyal; r = ribs; sc = scapulocoracoid; scl = supracleithrum; spo = sphenotic; v6 = sixth vertebra; vh = ventral hypohyal. Limits between selected bones are highlighted in black.

Additionally, it can be distinguished from *P. amazonicus*, *P. rugosus* and *P. quadriradiatus*, by having the posterolateral mental barbels with at least one fleshy lobe located proximally along the posterior margin (*vs.* posterolateral mental barbel simple, not having fleshy lobes).

It also differs from *P. amazonicus* and *P. rugosus* by having five branchiostegal rays (Fig. 2C *vs.* four, Fig. 4D–I). It also can be distinguished from *P. amazonicus* by having the contact of hyomandibula cartilage with neurocranium limited to the sphenotic (*vs.* extending to both sphenotic and pterotic); by having the ventral blade of Weberian apparatus open (Fig. 2C *vs.* closed, Fig. 3I) and by anterior exit of hemal canal in abdominal vertebra (*vs.* in complex vertebra); from *P. rugosus* by coloration of proximal portion of caudal fin similar to rest of caudal fin (*vs.* clear patch) and from *P. quadriradiatus* by the total number of pectoral fin-rays six (*vs.* five).

**Description.** Dorsal, lateral and ventral views of holotype shown in Figure 1. Maximum body length observed 33.4 mm SL. Morphometric data for holotype and 14 paratypes summarized in Table 1. Head and anterior body depressed. Anterodorsal profile of body ascending from tip of snout to dorsal-fin origin. Posterodorsal profile of body descending from dorsal-fin to base of caudal fin. Ventral body profile convex from mouth to insertion of pelvic fin and concave from this point to anal-fin origin. Caudal peduncle rounded, long and slender.

Knobs on dorsal surface of skull approximately equal in size. Eye small and positioned dorsolaterally. Skin covering eye dense and pale. Anterior nostril tubular located at tip of snout. Posterior nostril without flap or barbel, located anteromedially to eye. Mouth terminal, upper and lower jaws equal. Maxillary barbel simple, beginning on mouth corner and its posterior end surpassing pectoral-fin spine insertion. Anteromedial mental barbel simple and posterolateral mental barbel bifid with one or more fleshy lobe proximally along posterior margin. Skin of trunk covered with small unculiferous tubercles in longitudinal rows; mid-dorsal row well defined and three or four well-defined rows on each side of caudal peduncle. Several poorly-defined rows ventrally.

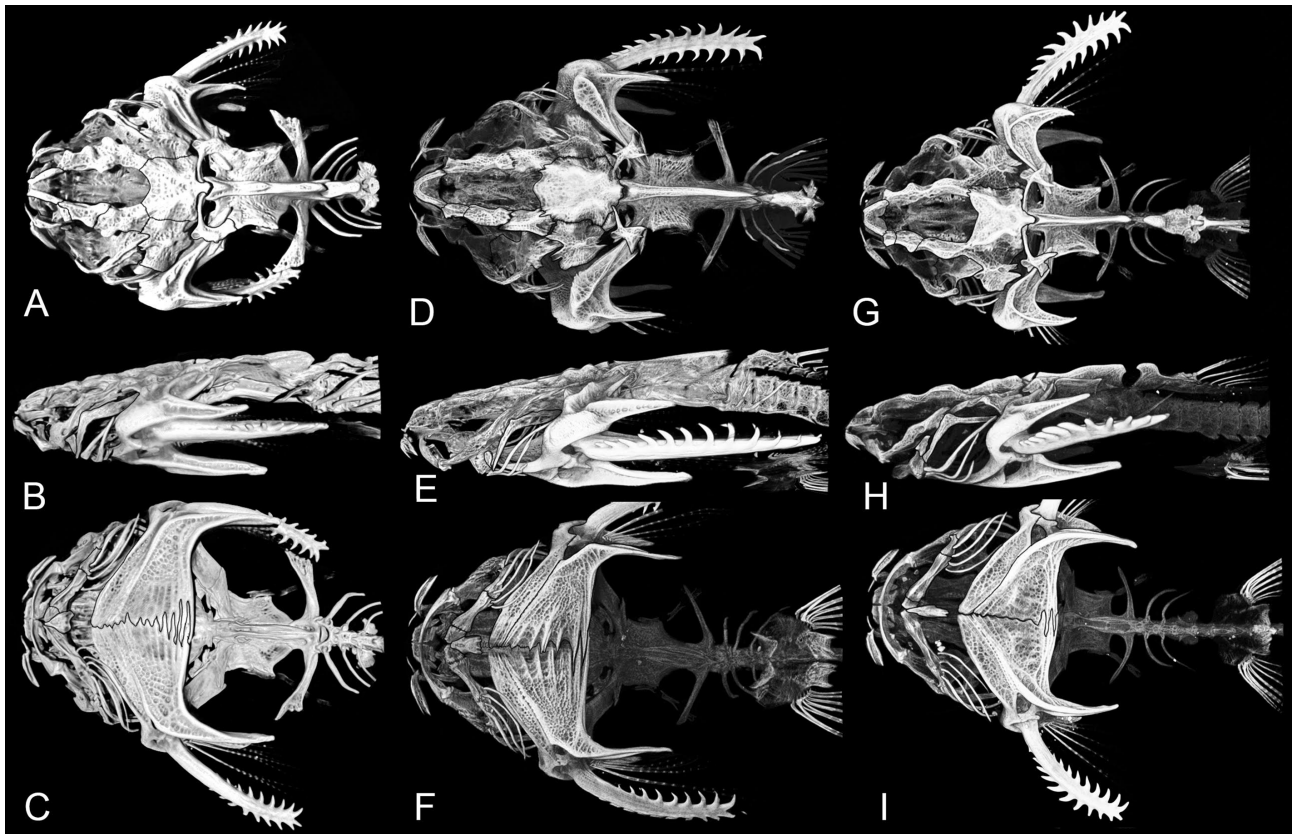
Anterior margin of mesethmoid straight, not anterolaterally projected (Fig. 2A), its anterior surface smooth. Posterior dorsal margin of mesethmoid contiguous with frontal. Ethmoid cartilage separated from articular facet of palatine. Lateral margin of frontal concave forming eye orbit and posterior margin not contacting the parieto-supraoccipital. Epyphiseal bar absent (Fig. 2A). Posterior portion of cranial fontanel opened between frontals and its parieto-supraoccipital margin concave. Laminar process in lateral margin of pterotic present. Pterotic with lateral margin rounded. Supratemporal fossa present. Posterior process of parieto-supraoccipital truncated. Premaxilla with posterolateral process and ventral surface smooth. Teeth on premaxilla through entire surface. Dentary teeth restricted to broad tooth patch near symphysis of lower jaw. Ascending process of Meckel's cartilage contacting main portion of this cartilage. Coronomeckelian bone present. Hyomandibula fused to preopercle. Posterodorsal portion of hiomandibula not associated to preopercular-mandibular laterosensory canal. Supraopercle absent. Cartilaginous articulation or joint of hyomandibula with neurocranium restricted to sphenotic. Opercular condyle of hyomandibula, directed posteroventrally. Metapterygoid present, not contacting hyomandibula or quadrate. Entopterygoid present. Posterior margin of autopalatine bifurcated, bearing two separate terminal cartilages. Opercle *L* shaped, posterior arm longer than ventral arm. Interopercle present, not attached to opercle. Dorsal hypohyal absent. Anterior and posterior ceratohyal contact with equal size. Anterior ceratohyal contacting posterior ceratohyal by serrated suture. Posterior ceratohyal with foramen, its posterior margin tapered. Interhyal absent. Five branchiostegal rays. Urohyal present, with medial foramen. Fourth pharyngobranchial absent. First hypobranchial ossified and second cartilaginous. Second basibranchial ossified and third basibranchial cartilaginous. Third epibranchial not bearing uncinat process. Fourth ceratobranchial elongated. Gill rakers absent on all arches. Pharyngeal teeth on upper tooth plate; two or three rows of teeth on fifth ceratobranchial.

Incomplete lateral line with simple tubules. Lateral line canal truncated just posterior to parapophyses of fifth vertebra and anterior to dorsal-fin origin, some specimens with isolated pores scattered more posteriorly, but never connected to main lateral-line canal. Nasal not ossified. Infraorbital canal limited to a single ossified tubule or none. Preopercle canal on preopercle with three pores. Mandibular canal interrupted anteriorly. Anterolateral branch of pterotic canal absent.

Dorsal lamina of Weberian apparatus extending to dorsal surface of body with anterior portion of lamina with dorsal concavity on its anterior margin (Fig. 2B). Reduced contact of parapophysis of fourth vertebra with parapophysis of fifth vertebra. Parapophysis of fifth vertebra larger than parapophysis of fourth vertebra and anteriorly oriented. Distal portion of fifth parapophysis not expanded. Free vertebrae without horizontal transverse process. Hemal and neural spine anteroposteriorly expanded. Hemal spines contacting anal-fin pterygiophores simple. Total vertebrae 35. Three pairs of ribs.



Dorsal fin i,4; spinelet absent; posterior margin of last dorsal-fin ray not adnate to body. Anterior nuchal plate and supraneural absent. Middle nuchal plate ornamented with single bony knob. Pectoral fin I,5. Pectoral-fin spine curved along its main axis. Serrations of pectoral-fin only middle portions to distal margin. Posterior margin of pectoral-fin spine with entirely serrated. Posterior scapulo-coracoid process of pectoral girdle extends slightly past posterior cleithral process in lateral view. Pelvic fin i,5 or i,4,i; first and second branched rays longest not reaching anal-fin origin; pelvic splint absent. Anal fin with seven or eight soft rays, anal-fin membrane not adnate to body. Caudal fin i,8,i; rounded plus one upper and one lower procurrent rays. Five rays associated with upper and five rays associated with lower lobe of caudal skeleton. Lowermost and uppermost caudal-fin rays unbranched, those slightly shorter than following branched rays. Adipose fin absent.



**FIGURE 3.** HRXCT model of skull and anterior body of selected *Pseudobunocephalus* species. (A) dorsal view, (B) lateral view, and (C) ventral view of *P. lundbergi* ANSP 168813, 30.3 mm SL. (D) dorsal view, (E) lateral view, and (F) ventral view of *P. iheringii* UFRGS 7175, 36.9 mm SL. (G) dorsal view, (H) lateral view, and (I) ventral view of *P. amazonicus* MCP 35751, 30 mm SL. Limits between selected bones are highlighted in black.

**Color in alcohol.** Dorsal and lateral surface of head and body mostly light to dark brown contrasting with scattered lighter areas. Dermal tubercles lighter than remaining areas. Ventral surface of head and trunk light yellow, with darker pigmentation on caudal peduncle. All fins hyaline with patterns of scattered dark brown chromatophores. Caudal-fin base with dark brown spot.

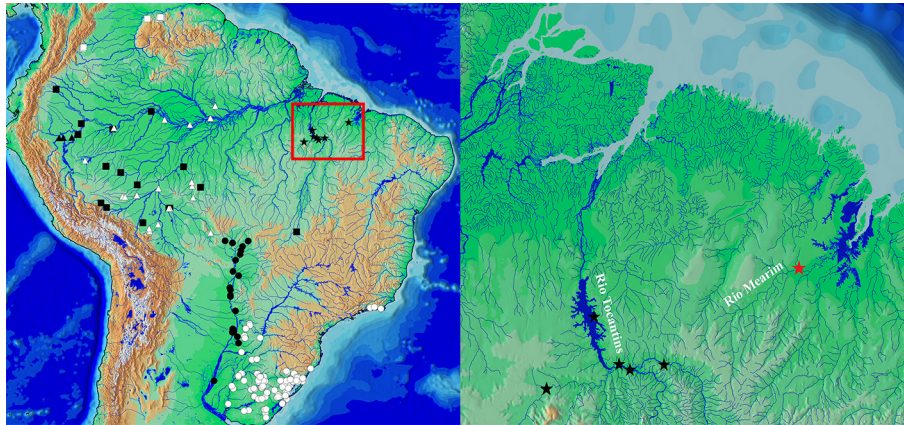
**Distribution.** *Pseudobunocephalus timbira* is known from small tributaries of the lower Tocantins and Mearim river basins in Maranhão, Pará and Tocantins states, Brazil (Fig. 4).

**Ecological notes.** The new species was collected in small and slow flowing streams running over sand or muddy bottom. The type locality in the Mearim River basin (Fig. 5) is a sediment rich tributary with moderate marginal and submersed vegetation.

**Etymology.** The specific epithet refers to the Timbira people who are the indigenous groups that live in the south of Maranhão, east of Pará and north of Tocantins, area of occurrence of the new species.

**Conservation status.** *Pseudobunocephalus timbira* is currently known from an Extention of Occurrence (EOO) larger than 48,000 square kilometers and no significative threats to the species were detected. In addition, part of the known population occurs inside a protected biological reserve (Reserva Biológica do Tapirapé). For

these reasons, *Pseudobunocephalus timbira* can be categorized as Least Concern (LC) according to the International Union for Conservation of Nature (IUCN) categories and criteria (IUCN Standards and Petitions Subcommittee, 2017).



**FIGURE 4.** Localities of species of *Pseudobunocephalus*. Black triangles: *P. quadriradiatus*, white triangles: *P. amazonicus*, black circles: *P. rugosus*, white circles: *P. iheringii*, black squares: *P. bifidus*, white squares: *P. lundbergi*, Star: *P. timbira*, Red Star: Holotype of *P. timbira*.



**FIGURE 5.** Jundiá Creek at the type locality for *Pseudobunocephalus timbira*, tributary of Mearim River drainage, Alto Alegre do Pindaré, Maranhão State, Brazil.

## Discussion

*Pseudobunocephalus* is defined as a monophyletic group by Friel (1994; 2008) by its shared exclusive derived characters: (1) dentary teeth restricted to a broad tooth patch near the symphysis of lower jaw, (2) metapterygoid lacking a bony connection with the quadrate, (3) posterior end of the autopalatine distinctly forked, bearing two separate terminal cartilages, (4) absence of the fourth pharyngobranchial, (5) absence of gill rakers on all branchial arches, and (6) absence of bifid hemal spines on vertebrae that articulate with anal-fin pterygiophores. All these derived character states are observed in *P. timbira* supporting its inclusion in this genus.

**TABLE 2.** Summary of variable characteristics within valid species of *Pseudobunocephalus*. Character states observed in *P. timbira* and shared by other species of *Pseudobunocephalus* are shaded in gray.

Character/species	<i>P. amazonicus</i>	<i>P. bifidus</i>	<i>P. iheringii</i>	<i>P. lundbergi</i>	<i>P. quadriradiatus</i>	<i>P. rugosus</i>	<i>P. timbira, new species</i>
Frontal epiphyseal bar	absent	absent straight or convex	absent convex	present/absent	absent	absent	absent
Posterior margin of cranial fontanel	concave	convex	convex	concave	concave	concave	concave
Knobby skull ornamentation	conspicuous	feeble	feeble	very conspicuous	conspicuous	conspicuous	conspicuous
Posterolateral process of premaxilla	present	present	present	absent	present	present	present
Extension of contact of hyomandibular cartilage with neurocranium	sphenotic and pterotic	sphenotic	sphenotic	sphenotic	sphenotic	sphenotic	sphenotic
Association of posterodorsal portion of hyomandibula and sensory canal	free	free	associated with sensory canal	free	free	free	free
Number of branchiostegal rays	four	five	four	five	five	four	five
Constitution of second hypobranchial	ossified	ossified	ossified	ossified	ossified	ossified	cartilagenous
Constitution of third basibranchial	ossified	ossified	ossified	ossified	ossified	ossified	cartilagenous
Bony knobs in dorsal lamina of Weberian apparatus	absent	absent	absent	present	-	absent	absent
Distal end of posterior margin of 5th parapophysis	not enlarged	not enlarged	not enlarged	enlarged	not enlarged	not enlarged	not enlarged
Total number of vertebrae	34 or 35	34 or 35	32	33 or 34	-	33-35	35
Weberian ventral blade of hemal canal	closed	closed	closed	open	-	open	open
Anterior exit of hemal canal	in complex vertebra	in abdominal vertebra	in abdominal vertebra	in abdominal vertebra	-	in abdominal vertebra	in abdominal vertebra
Number of ribs	2 or 3	3	3	4 or 5	-	2	3
Number of dorsal-fin rays	5	5	4	5	5	5	5
Origin of serrations on anterior margin of pectoral-fin spine	slightly posteriorly	anteriorly	anteriorly	posteriorly	-	slightly posteriorly	slightly posteriorly
Total number of pectoral-fin rays	6	6	5	6	5	6	6
Shape of posterior margin of basipterygium	straight	straight	jagged	straight	straight	straight	straight
Infraorbital canal tubules	none or one	one	none	three	none	none	none or one
Contact between the first dorsal-fin pterygiophore and Weberian apparatus	absent	absent	absent	present	absent	absent	absent
Infraorbital canal entering neurocranium	via frontal	via frontal	via frontal	via sphenotic	via sphenotic	via frontal	via frontal
Posterolateral mental barbel	simple	bifid	bifid	simple	simple	simple	bifid

Friel (2008) recovered *P. lundbergi* as the sister species of a larger group composed of all remaining congeners (*P. amazonicus*, *P. bifidus*, *P. quadriradiatus*, *P. iheringii*, and *P. rugosus*), defined by several derived features: (1) infraorbital canal exiting from frontal and not extending anteriorly passing anterior margin of the eye, (2) absence of frontal epiphyseal bar, (3) presence of posterolateral limb of the premaxilla; and (4) absence of contact between the first dorsal-fin pterygiophore and the Weberian apparatus. These derived character states were all observed in *P. timbira*, supporting this species as part of this monophyletic group within *Pseudobunocephalus* including all species except *P. lundbergi*. A variation on the presence of an epiphyseal bar between the frontals was observed in *P. lundbergi* (Fig. 3A, Table 2). Scanned specimen ANSP 168813 lacks the frontal epiphyseal bar, and intraspecific variation was also observed in other genera of Aspredinidae that typically possess an epiphyseal bar (e.g., *Bunocephalus* and *Xyliphius*; Carvalho *et al.*, 2015).

At the moment, morphological characters are ambiguous suggesting relationships within this less inclusive group of *Pseudobunocephalus*. In a recent study based on molecular data (Carvalho *et al.*, 2018), *Pseudobunocephalus* was allocated to the monogeneric Pseudobunocephalinae, where *P. iheringii* was sister to the remaining species and *P. rugosus* was sister to *P. amazonicus* (*P. lundbergi* and *P. quadriradiatus* were not included). The new species *P. timbira* has some putative apomorphic characters shared with *P. amazonicus*, *P. quadriradiatus*, and *P. rugosus* such as the conspicuous tuberculation of bones on head (Figs. 2 & 3) and origin of serrations distally on the anterior surface of the pectoral-fin spine (not examined in *P. quadriradiatus*), and similar body sizes. Contrastingly, the new species shares with *P. bifidus* and *P. iheringii* the presence of fleshy lobed posterior mental barbel. Despite recent studies and potential phylogenetic informative characters (Table 2), the phylogenetic relationships of *Pseudobunocephalus* species and the delimitation of some species (e.g., *P. amazonicus* and *P. rugosus* in Carvalho *et al.*, 2018) still need review.

*Pseudobunocephalus timbira* is endemic to the eastern Amazon River basin and its neighboring Mearim River drainage, with an apparently disjunct distribution to congeners. The eastern Amazon have been recently subject of large aquatic fauna inventories (e.g. Lower Xingu: iXingu and Lower Tapajós: Aquatic Faunal Survey of the Lower Amazon), which returned no additional records of *Pseudobunocephalus* between the lower Tocantins its current eastern known distributional limit in the Amazon basin around the mouth of the Negro River (Fig. 4). This distributional gap of some lineages between western and eastern portions of the Amazon basin are observed in other groups of Aspredinidae, for example: *Xyliphius* (Carvalho *et al.*, 2017), *Ernstichthys* (Jarduli *et al.*, 2014), and *Pterobunocephalus* (UFRGS 12939; Friel & Carvalho, 2017) and also by the disjunct distribution of *P. bifidus* in western Amazon and the upper Araguaia River (Fig. 4). However, for the above-mentioned genera the eastern portion of their distribution is restricted to upper portion of the Tocantins River contrasting with the distribution of *P. timbira* in the lower Tocantins River basin.

The ichthyofauna of the Mearim River is poorly known, and it shares a large amount of its diversity with the eastern Amazon basin (Soares, 2005), as exemplified by the newly described species. This region is an extremely relevant area in the conservation point of view because it comprises the transition zone of three Brazilian Biomes: Amazon, Cerrado and Caatinga (Guimarães *et al.*, 2018).

**Comparative material examined.** *Pseudobunocephalus amazonicus*: **Bolivia:** FMNH 106882, 2, 18–25 mm SL: Pando, backwater at right margin Río Nareuda, 3 km upstream mouth of Río Tahuamanu; FMNH 106683, 6, 20.7–31.8 mm SL, Pando, lake 12 km from Pto. Rico in Manuripi River, Mamoré River drainage; FMNH 106684, 2, 20.3–23.3 mm SL, Pando, Nareuda River at camp, alt 250 m; FMNH 106685, 1, 27.1 mm SL: Pando, lake at campsite c. 10 km upstream Pto. Rico, Mamoré River drainage. MNRJ 14068, 1, 35.6 mm SL: San Pedro, Road Brasil-Bolivia. UMMZ 204347, 2, 18.2–19.5 mm SL, Beni, Baures River at mouth in Itenez River, 6 km SW of Costa Marques, Guaporé-Itenez drainage; UMMZ 205164, 4, 18.9–26.5 mm SL: Beni, Backwater slough of Itenez River 10 km SE of Costa Marques, Guaporé-Itenez drainage; USNM 305574, 1, 22.5 mm SL: Beni, Ballivia, Matos River below road x-ing 48 km E of San Borja; USNM 305624, 2, 27.9–31.4 mm SL: Ballivia, stream Aguas Negras (tributary of Curibaba River) 3 km above mouth at 12 km N of El Porvenir; USNM 305861, 42: Beni, Trapiche La Pascana Maniqui River; USNM 305878, 2, 31.5–31.6 mm SL: Beni, Trapiche La Pascana Maniqui River; USNM 338697, 11, 18.9–20.3 mm SL: Beni, Balliva, Matos River below road x-ing 48 km E of San Borja. **Brazil:** FMNH 105328, 1, 21.9 mm SL: Rondônia, Maciel, Guaporé River; INPA 6530, 2, 24–30.4 mm SL; INPA 15478, 2, 17–18.2 mm SL: Amazonas, Uatumã River lake Caititu, Negro River basin; INPA 22655, 1, 28.9 mm SL: Amazonas, Solimões River at Ilha da Marchantaria, Solimões River basin; INPA 32485, 2, 19.6–22.8 mm SL: Rondônia, lake of Torre, Madeira River basin; LBP 4067, 23.7–25.1 mm SL: Acre, Japiim River, Juruá River



basin; LBP 10826, 1, 22.1 mm SL: Mato Grosso, Guaporé River, Guaporé River basin; LBP 109888, 8, 23.2–28 mm SL: Rondônia, Lajeado River, Madeira River basin; MCP 35748, 1, 24.7 mm SL: Rondônia, small stream tributary to lake Grande on highway BR-364, between Cacoal and Ji-Paraná, Madeira River basin; MCP 35751, 18, 22.8–29.5 mm SL, Rondônia, Nova Mamoré, Madeira River basin; MPEG 21933, 1, 25.9 mm SL: Rondônia, REBIO Jaru, Amazonas River basin; MZUSP 9678, 2, 1 c&s, 24.98 mm SL: Amazonas, Codajás, lake Supiá. MZUSP 27628, 1, 26.4 mm SL, Pará, Tefé, Japurá River. USNM 301687, 1, 26.8 mm SL, Amazonas, lake near Manaus. **Colombia:** USNM 220851, 3, 37–45 mm SL, Amazonas, Leticia. *Pseudobunocephalus bifidus*: **Bolivia:** UMMZ 66329, 1, 32 mm SL, paratype: lake Rogoagua and lagoons near Lake; UMMZ 204301, 5, 19.6–36 mm SL: Beni, Itenez River at mouth of dry run 2 km above (SE) of Costa Marques, Guaporé-Itenez drainage; UMMZ 204374, 3, 19.7–22.7 mm SL: Beni, Río Baures at mouth of Río Itenez 6 km SW of Costa Marques, Guaporé-Itenez drainage. **Brazil:** INPA 6522, 3, 26.8–41.6 mm SL: Amazonas, Javari River; MCP 32722, 1 c&s: Acre, Branco River, Purus River; MCP 35751, 11, 22.79–29.44 mm SL: Rondônia, Nova Mamoré, Madeira River basin; MPEG 3293, 1, 43.9 mm SL: Acre, Tarauacá, Amazonas River basin; MPEG 21932, 1, 1 c&s, 26.97–38.96 mm SL: Rondônia, lake Iracema, Amazonas River basin; MZUSP 23398, 1, 42.2 mm SL: Amazonas, Fonte Boa; MZUSP 30707, 5, 29–46.7 mm SL: Acre, lake of Entendência, Juruá River basin; MZUSP 30708, 11, 23.1–48.4 mm SL: Acre, Tarauacá, Juruá River basin; MZUSP 30709, 1, 24.9 mm SL: Rondônia, Lake Jamarizinho, Madeira River basin; MZUSP 30710, 1, 25.0 mm SL: Rondônia, Machado River, Madeira River basin; MZUSP 50107, 40, 2 c&s, 49.8–53.2 mm SL: Acre, Manoel Urbano, Purus River; USNM 191561, 1, 54 mm SL: Goiás, Araguaia River near Aruanã. **Ecuador:** FMNH 99484, 1, 30.2 mm SL: Napo, tributary to lower Cuyabeno River. **Peru:** ANSP 174931, 1, 40.6 mm SL: Loreto, small stream ca 70 km S of Iquitos near Genaro Herrera (Ucayali River), Amazonas River basin; MZUSP 15293, 1, 49.5 mm SL: Loreto, Iquitos, Nanay River; USNM 300984, 1, 25.2 mm SL: Madre de Dios, Aguajal, Manu River, inundated forest; USNM 302707, 1, 51 mm SL: Madre de Dios, Parque Nacional Manu, Pakitza and Vicinity. *Pseudobunocephalus iheringii*: **Argentina:** MCP 13377, 7, 1 c&s, 23.5–48.0 mm SL; MCP 13328, 4, 28.9–38.31 mm SL: all from Azara, Misiones, Uruguay River; **Brazil:** FMNH 70628, 23, 22.1–46.1 mm SL: Rio Grande do Sul, Ibicuí River, Cacequi; FMNH 88242, 6, 33.6–44.3 mm SL: Rio Grande do Sul, Negro River or Paso de Los Toros, Uruguay River; LBP 595, 1, 49.1 mm SL: Rio Grande do Sul, stream tributary to lake Guaíba, Laguna dos Patos; LBP 3337, 3, 18.7–52.5 mm SL: Rio Grande do Sul, stream tributary to Laguna dos Patos; LBP 3368, 1, 42.2 mm SL: Rio Grande do Sul, Corrientes stream, Laguna dos Patos; LBP 4779, 2: Rio Grande do Sul, lake Guaíba, Laguna dos Patos; LBP 13152, 3, larger 24.8 mm SL: Rio Grande do Sul, Putiá Stream, Uruguay River basin; LBP 13228, 2, 37–39 mm SL: Rio Grande do Sul, unnamed stream, Laguna dos Patos; LBP 14492, 1: Rio Grande do Sul, unammed stream Laguna dos Patos; MCN 3335, 1, 23 mm SL: Rio Grande do Sul, Passo Raso stream, Laguna dos Patos; MCN 5146, 1, 46 mm SL: Rio Grande do Sul, Cai River north of mouth of Bom Jardim Stream, Laguna dos Patos; MCN 6101, 1, 26.9 mm SL: Rio Grande do Sul, Banhado Grande, Fazenda 4 irmãos, Laguna dos Patos; MCN 7812, 1, 20.3 mm SL: Rio Grande do Sul, Taim Stream, Laguna dos Patos; MCN 7820, 1, 21.8 mm SL: Rio Grande do Sul, Taim Stream confluence, Laguna dos Patos; MCN 11904, 1, 48.6 mm SL: Rio Grande do Sul, Gateados Lagoon, Laguna dos Patos; MCN 12661, 2, 16.7–20.4 mm SL: Rio Grande do Sul, Evaristo Stream, Laguna dos Patos; MCN 16930, 1, 16.2 mm SL: Rio Grande do Sul, Reserva Biológica Estadual de São Donato, Uruguay River basin; MCN 16962, 2, 18.1–40 mm SL: Rio Grande do Sul, Banhado na Reserva Ecológica Estação de São Donato, Uruguay River basin; MCN 17028, 2, 31.4–32.1 mm SL: Rio Grande do Sul, bridge between Itaquí and São Borja, Uruguay River basin; MCN 17521, 1, 47.1 mm SL: Rio Grande do Sul, Salso Stream, Laguna dos Patos; MCN 17545, 1, 45.2 mm SL: Rio Grande do Sul, Gateados Lagoon, Laguna dos Patos; MCN 17564, 1, 29.6 mm SL: Rio Grande do Sul, Lami Stream, Laguna dos Patos; MCN 17601, 1, 23.3 mm SL: Rio Grande do Sul, Gateados Lagoon, Laguna dos Patos; MCN 18037, 2, 22.8–41.3 mm SL: Rio Grande do Sul, Guará Stream, Laguna dos Patos; MCN 19009, 1, 29.5 mm SL: Rio Grande do Sul, Fazenda Volkmann, Laguna dos Patos; MCN 19601, 1, 25.2 mm SL: Rio Grande do Sul, lateral pools of Ibirapuitã River at Fazenda Sá de Brito, Uruguay River basin; MCP 9300, 3, 29.1–29.3 mm SL: Rio Grande do Sul, Dom Marcos Stream, Laguna dos Patos; MCP 9360, 4, 25–27 mm SL: Rio Grande do Sul, Saicã Stream, Uruguay River basin; MCP 9378, 1, 28.8 mm SL: Rio Grande do Sul, Ibicuí River on the bridge between São Rafael and Cacequi, Uruguay River basin; MCP 9401, 1, 34.5 mm SL: Rio Grande do Sul, floodplain of Rio dos Sinos on the road Tabai-Canoas, Laguna dos Patos; MCP 9415, 2, 27.2–28.6 mm SL: Rio Grande do Sul, Cacequi River between Cacequi and Vila São Simão, Uruguay River basin; MCP 9527, 1, 27.5 mm SL: Rio Grande do Sul, Santa Maria River, Uruguay River basin; MCP 9631, 3, 23.7–24.1 mm SL: Rio Grande do Sul, Santa Maria River on

highway BR-293 between km 245–246 Dom Pedrito/Livramento, Uruguay River basin; MCP 9646, 2, 27–30.9 mm SL: Rio Grande do Sul, Santa Maria River on highway BR-293 between km 245–246 Dom Pedrito/Livramento, Uruguay River basin; MCP 9767, 1, 37.7 mm SL: Rio Grande do Sul, Ilha da Pintada, Laguna dos Patos; MCP 10640, 1, 30.8 mm SL: Santa Catarina, Araranguá, Araranguá River basin; MCP 11310, 2, 29.2–34.8 mm SL: Rio Grande do Sul, Ladrões Stream, Laguna dos Patos; MCP 11385, 1, 40.7 mm SL: Rio Grande do Sul, Quarai-Mirim Stream on the road between Quarai and Alegrete, Uruguay River basin; MCP 12726, 3, 39–40 mm SL: Rio Grande do Sul, Mouth of Ijuí-Mirim River tributary to Ijuí River, Uruguay River basin; MCP 13316, 2, 24.8–40.2 mm SL: Rio Grande do Sul, Barreiro Stream at Barreiro, Uruguay River basin; MCP 13436, 4, 16.6–37.9 mm SL: Rio Grande do Sul, Barreiro Stream at Barreiro, Uruguay River basin; MCP 13467, 1, 21.4 mm SL: Rio Grande do Sul, Ijuí-Mirim River tributary to Ijuí River, Uruguay River basin; MCP 15043, 1, 40.6 mm SL: Rio Grande do Sul, Floodplain of Gravataí River at highway RS-118 about 500 meters from BR-290, Laguna dos Patos; MCP 15489, 5, 30.9–34.2 mm SL: Rio Grande do Sul, stream in the Varzinha at Itapuã, Laguna dos Patos; MCP 15768, 14, 24.3–38.6 mm SL, Rio Grande do Sul, Eldorado do Sul, Guaíba; MCP 16184, 4, 24.9–29.1 mm SL: Rio Grande do Sul, Marginal lagoon of Uruguay River at Praia da Formosa, Uruguay River basin; MCP 17687, 1, 26.4 mm SL: Rio Grande do Sul, Old drainage channel at Passo do Tabajara on the marsh of Pontal da Barra, Laguna dos Patos; MCP 17689, 3, 40.9–42.6 mm SL: Rio Grande do Sul, Banhado do Pontal da Barra, at Laranjal, Laguna dos Patos; MCP 18308, 1, 34.2 mm SL: Rio Grande do Sul, Ilha das Flores, Jacuí River basin; MCP 18354, 3, 29.4–31.1 mm SL: Rio Grande do Sul, Marginal lagoon of Uruguay River at Praia da Formosa, Uruguay River basin; MCP 19113, 1, 36.5 mm SL: Rio Grande do Sul, Ribeiro Stream on the highway BR-116, Laguna dos Patos; MCP 19231, 1, 31.7 mm SL: Rio Grande do Sul, Sapucaia Stream at Morro Agudo, Laguna dos Patos; MCP 19569, 15, 1 c&s, 23.1–39.8 mm SL: Rio Grande do Sul, Marginal lagoon of Uruguay River at Praia da Formosa, Uruguay River basin; MCP 19581, 5, 29.9–44.9 mm SL: Rio Grande do Sul, bridge on the road between São Gabriel and Tiaraju, Laguna dos Patos; MCP 19585, 20, 23.4–42.8 mm SL: Rio Grande do Sul, Inhatium, Uruguay River; MCP 19637, 1, 38.6 mm SL: Rio Grande do Sul, Abranjo Stream on the road between Encruzilhada do Sul and Canguçu, Laguna dos Patos; MCP 21656, 44, 21.7–29.8 mm SL: Rio Grande do Sul, Uruguay River and lateral pool in the Praia da Formosa at São Marcos, Uruguay River basin; MCP 23009, 2, 25.8–30.1 mm SL: Rio Grande do Sul, Bom Jardim Stream on the access road to III Polo Petroquímico, Laguna dos Patos; MCP 23129, 2, 28.6–34.2 mm SL: Rio Grande do Sul, Inhacunda River at São Francisco de Assis on the road exit to Manoel Viana, Uruguay River basin; MCP 23852, 15, 28.7–33.8 mm SL: Rio Grande do Sul, Arroio Velhaco on the road between Cerro Grande do Sul and Camaquã, Laguna dos Patos; MCP 25079, 1, 45.2 mm SL: Rio Grande do Sul, Arroio Piratinzinho in vicinal road to BR-293, Laguna dos Patos; MCP 25095, 2, 45.9–46.7 mm SL: Rio Grande do Sul, Pedro Osório, São Gonçalo, Pedro Osório; MCP 25127, 8, 33.9–50.4 mm SL: Rio Grande do Sul, Arambaré tributary of Piratini River on the road between Pedro Osório and Basílio, Laguna dos Patos; MCP 25190, 4, 1 c&s, 29.7–37.3 mm SL: Rio Grande do Sul, Inhacunda River at São Francisco de Assis on the road exit to Manoel Viana, Uruguay River basin; MCP 25226, 1, 38 mm SL: Rio Grande do Sul, Inhacunda River at São Francisco de Assis about 500 meters above brick factory, Uruguay River basin; MCP 26826, 3, 36.8–41.5 mm SL: Rio Grande do Sul, Salso Stream on highway BR-158 tributary to Ibicuí River of Armada, Uruguay River basin; MCP 27663, 1, 31.8 mm SL: Rio Grande do Sul, São Francisco de Assis, Uruguay River; MCP 34731, 33.3–44.6 mm SL: Rio Grande do Sul, Arambaré stream the road between Pedro Osório and Basílio, Laguna dos Patos; MCP 34787, 9, 38.7–46.4 mm SL: Rio Grande do Sul, Arambaré Stream on the road between Pedro Osório and Herval, Laguna dos Patos; MCP 37578, 1, 42 mm SL: Rio Grande do Sul, Lagoa do Nicola, Laguna dos Patos; MCP 38289, 10, 38–48 mm SL: Rio Grande do Sul, Arambaré Stream about 5 km S of vila Basílio on the road to Pedro Osório, Laguna dos Patos; MCP 39422, 1, 28 mm SL: Rio Grande do Sul, Camaquã River at fazenda Corticeira, Laguna dos Patos; MCP 41940, 1, 29 mm SL: Rio Grande do Sul, Stream tributary to Ibicuzinho River at fazenda Estância Nova and Invernada do Atalho, between road of Cacequi and Estação São Lucas, Uruguay River basin; MCP 43386, 6, 23.9–31.3 mm SL: Rio Grande do Sul, Negro River at road between Bagé and Aceguá, Uruguay River basin; MCP 44502, 4, 41.4–43 mm SL: Rio Grande do Sul, Stream at Fazenda Chimarrão, tributary to Boici Stream, Laguna dos Patos; MCP 45799, 2, 32.5–36 mm SL: Rio Grande do Sul, Corrientes Stream, Laguna dos Patos; MCP 46457, 1, 29.3 mm SL: Rio Grande do Sul, headwaters of Felizardo Stream, Uruguay River basin; MZUSP 23151, 1, 42.9 mm SL; MZUSP 23159, 1, 36.5 mm SL; MZUP 23165, 1, 26.7 mm SL; MZUP 23187, 1, 27.6 mm SL; MZUSP 23191, 2, 40.9–42.9 mm SL; Rio Grande do Sul, São Leopoldo, Sinos River; MZUSP 40966, 2, 21.4–23.6 mm SL; MZUSP 43327, 1, 43.3 mm SL: Rio Grande do Sul, Itaquí; UFRGS 694, 2, 40.1–42.5

mm SL: Rio Grande do Sul, Estação Ecológica do Taim, Laguna dos Patos; UFRGS 1190, 12, 12.6–32.8 mm SL: Rio Grande do Sul, Sans Souci, Conde Stream at bridge Laguna dos Patos; UFRGS 1191, 3, 29.4–38 mm SL: Rio Grande do Sul, creek at BR-290, 2 km from BR-116, Laguna dos Patos; UFRGS 1192, 1, 38.6 mm SL: Rio Grande do Sul, Passo dos Carros Stream, Laguna dos Patos; UFRGS 1218, 2, 24.1–25.6 mm SL: Rio Grande do Sul, Arroio dos Ratos, Laguna dos Patos; UFRGS 1219, 1, 48.6 mm SL: Rio Grande do Sul, Três Mares Stream, Laguna dos Patos; UFRGS 1220, 1, 32.9 mm SL: Rio Grande do Sul, Stream at Branco River, Laguna dos Patos; UFRGS 1221, 1, 25.1 mm SL: Rio Grande do Sul, Arroio dos Ratos at bathing spot., Laguna dos Patos; UFRGS 1222, 1, 34.9 mm SL: Rio Grande do Sul lateral canal at Banhado do Taim, Laguna dos Patos; UFRGS 1223, 1, 35.3 mm SL: Rio Grande do Sul, Entrada do Arroio Taim right margin of BR-471 at Estação Ecológica do Taim, Laguna dos Patos; UFRGS 1224, 5, 39–44 mm SL: Rio Grande do Sul, Arroio da Estiva east of Lagoa da Nicola parallel to road of Albardão at Estação Ecológica do Taim, Laguna dos Patos; UFRGS 1225, 1, 22 mm SL: Rio Grande do Sul, pool at exit of pump station in the Estação Ecológica do Taim, Laguna dos Patos; UFRGS 1226, 2, 19.5–20.3 mm SL: Rio Grande do Sul, Bridge at Estrada do Albardão (Arroio da Estiva) at Estação Ecológica do Taim, Laguna dos Patos; UFRGS 1227, 10, 18.3–38.9 mm SL: Rio Grande do Sul, canal south of pump station DNOS at Estação Ecológica do Taim, Laguna dos Patos; UFRGS 1228, 1, 34.4 mm SL: Rio Grande do Sul, canal at right side of BR-471 parallel to Taim Stream, Laguna dos Patos; UFRGS 1232, 1, 34.4 mm SL: Rio Grande do Sul, first bridge at Estrada do Albardão, Laguna dos Patos; UFRGS 2023, 19.4–21 mm SL: Rio Grande do Sul, Bridge over Arroio Ribeirinho, Laguna dos Patos; UFRGS 2030, 5, 20–29.9 mm SL: Rio Grande do Sul, Arroio Passo dos Carros, Laguna dos Patos; UFRGS 4970, 1, 22.1 mm SL: Rio Grande do Sul, Floodplain of Rio Gravataí, Alvorada industrial district near BR-290, Laguna dos Patos; UFRGS 6708, 5, 21.0–42.4 mm SL: Rio Grande do Sul, Viamão, Lagoa Negra; UFRGS 6920, 4, 18.5–19.6 mm SL: Rio Grande do Sul, Rio Gravataí near the bridge os RS-118, Laguna dos Patos; UFRGS 7092, 1, 36.6 mm SL: Rio Grande do Sul, Negro River at BR-153 between Bagé and Aceguá, Uruguay River basin; UFRGS 7657, 2, 20.7–21.5 mm SL: Rio Grande do Sul, Gravataí River at Passo das Canoas, Laguna dos Patos; UFRGS 8244, 35.3–42.4 mm SL: Rio Grande do Sul, Stream tributary to Camaquã River at Bridge of detour of RS-471, Laguna dos Patos; UFRGS 8714, 1, 48.1 mm SL: Rio Grande do Sul, Arroio e várzea na propriedade Cerro Vermelho, Laguna dos Patos; UFRGS 9430, 1, 32.5 mm SL: Rio Grande do Sul, Arroio Tacuarembó, Uruguay River basin; UFRGS 12385, 1, 49.9 mm SL: Rio Grande do Sul, Piquiri River near bridge of highway BR-290, Laguna dos Patos; UFRGS 12392, 1, 41.8 mm SL: Rio Grande do Sul, Francisquinho River at BR-290 near bridge, Laguna dos Patos; UFRGS 13097, 27, 16.5–46.0 mm SL: Rio Grande do Sul, Estação agrônômica da UFRGS, Eldorado do Sul; UFRGS 13287, 11, 23.5–32.7 mm SL: Rio Grande do Sul, Arroio do Lami and floodplain at Estação Ecológica do Lami, Laguna dos Patos; UFRGS 13321, 2, 38.2–40.2 mm SL: Rio Grande do Sul, Irrigation channels within the aeolic park, Laguna dos Patos; UFRGS 13780, 3, 29.7–33.9 mm SL: Rio Grande do Sul, stream at margin of BR-290 10 km from Rosario do Sul, Uruguay River basin; UFRGS 14164, 2, 39.1–53.6 mm SL: Rio Grande do Sul, Arroio Travesseiro, Laguna dos Patos; UFRGS 14210, 1, 31.8 mm SL: Rio Grande do Sul, Arroio Forquetinha, Laguna dos Patos; UFRGS 14339, 1, 42.3 mm SL: Rio Grande do Sul, Arroio Tamanduá at linha Tamanduá, Laguna dos Patos; UFRGS 14340, 2, 50.6–52.6 mm SL: Rio Grande do Sul, Arroio Travesseiro, Laguna dos Patos; UFRGS 15294, 8, 25.7–33.7 mm SL: Rio Grande do Sul, Arroio Calombos near pump station at Estação Agrônômica da UFRGS, Laguna dos Patos; USNM 92975, 2, 23.9–25 mm SL, paratypes of *Bunocephalus salatheii*: Rio de Janeiro, 100 km from Rio de Janeiro, Morro Agudo, Fluminense drainage; USNM 301690, 8, 41.1–47.5 mm SL: Rio de Janeiro, Rio Regamê, Araruama; **Paraguay:** ANSP 171635, 28.5–33.7 mm SL: Misiones, Culvert pool plus marsh on road from Ayolas to main Asuncion/Encarnacion highway Ruta1, Paraná River basin; ANSP 174740, 1, 26.6 mm SL: Guaira, Backwater of Tebicuary-Mi River near where it crosses Coronel Oviedo-Villarica road, Parana River basin; ANSP 174741, 2, 30.5–32.5 mm SL: Guaira, Perulero Stream where it crosses road from Villarica, Paraná River basin; UMMZ 206226, 2, 40.6–44.6 mm SL: Monday River along SW side of dirt road 17.8 km S of ruta 2; UMMZ 206289, 4, 35–39.8 mm SL: Arroyo Curimbatay ca. 15.6 km WSW of Curuguay; UMMZ 206574, 1, 38.9 mm SL: Canendiyu, Corrientes River and adjacent flood pool, 32.4 km W of turnoff to Curuguay (60 km NE of Mbutuy intersection), Paraná River basin; UMMZ 206850, 1, 31.8 mm SL: Arroyo Pendo at bridge ca 9.2 km N of Mbutuy; USNM 181480, 1, 24 mm SL: Tebicuary River near Florida; **Uruguay:** ANSP 202244. FMNH 70629, 8, 28.3–47.3 mm SL: Treinta Y Tres, Estancia Jeffries 8 miles E of Treinta Y Tres, Uruguay River basin; MCP 9996, 9, 24.5–30 mm SL: Cerro Lago, Negro River at Fazenda Arreria, Uruguay River basin; MCP 43496, 1, 37 mm SL: Tranqueras, Swamp north of Ruta 30, Uruguay River basin; MCP 43497, 3, 1 c&s, 38–39.8 mm SL: Treinta y Tres,

Arroyo Yermal, Laguna dos Patos; MCP 43498, 1, 33.9 mm SL: Tacuarembó, creek near Ansina, Uruguay River basin; MCP 43499, 28, 17.2–30.3 mm SL: Salto, Palomas Stream, Uruguay River basin; MCP 43501, 3, 23–24.6 mm SL: Negro River, Uruguay River at Puerto Vieja, Uruguay River basin; MCP 43503, 2, 27.8–28.2 mm SL: Treinta y Tres, Yermal Stream tributary to Olimar Grande River, Uruguay River basin; MCP 43505, 1, 34.6 mm SL: Salto, Arroio Palomas tributary to Arapey Grande, Uruguay River basin; MCP 43506, 2, 1 c&s, 36.7–39.9 mm SL: Salto, Arroio Palomas tributary to Arapey Grande, Uruguay River basin; MCP 43507, 1, 36 mm SL: Rocha, India Muerta Stream on Ruta 13 km 231, Laguna dos Patos; MCP 43508, 2, 32.9–44.1 mm SL: Rocha, Ruta 14 km 270 near Cebollatí River north of Lascano, Laguna dos Patos; UFRGS 7173, 1, 37.9 mm SL: Durazno, Yí River at camping municipal, Uruguay River basin; UFRGS 7174, 1, 32.2 mm SL: Durazno, Arroyo Maestre de Campo on road to Polanco de Yí tributary to Yí River, Uruguay River basin; UFRGS 7175, 10, 25.1–40.9 mm SL: Rivera, Batovi Stream on ruta 27 km 24 tributary to Tacuarembó River, Uruguay River basin; UFRGS 7176, 2, 33.2–33.3 mm SL: Rivera, Negro River at el Diente in the highway ruta 44 at paso of Mazangano, Uruguay River basin; UFRGS 7177, 2, 31.7–34.8 mm SL: Tacuarembó, Tacuarembó River on ruta 26 at Vila Ansina, Uruguay River basin; UFRGS 7178, 2, 33.4–34 mm SL: Rivera, Lateral pools of Corrales Stream on ruta 27 tributary to Río Tacuarembó, Uruguay River basin; UFRGS 7179, 9, 33.9–47.7 mm SL: Rivera, Cunapiru Stream at km 12.3 of ruta 27, Uruguay River basin; UFRGS 7361, 1, 32.6 mm SL: Tacuarembó, Caraguatá River tributary to Tacuarembó River on road 36 at Las Toscas, Uruguay River basin; UFRGS 7744, 1, 38.8 mm SL: Salto, Uruguay River at lake of Salto dam at Belen, Uruguay River basin; UFRGS 13799, 1, 34.1 mm SL: Rivera, Batovi Stream on ruta 27 at km 24 tributary to Tacuarembó River, Uruguay River basin; UFRGS 13808, 3, 33.4–37.5 mm SL: Rivera, Cuñapiru Stream at km 12.3 of ruta 27, Uruguay River basin. *Pseudobunocephalus lundbergi*: **Colombia**: ANSP 131574, 4, 18.9–22.3 mm SL: Meta, Caño Rico at La Defensa, NW of Laguna Mozambique, becomes Caño Buenaventura before entering Río Negro, Orinoco River basin; ANSP 134530, 1, 23.4 mm SL: Meta, Tributary of Caño El Chocho ca 5 km N of La Siberia, Orinoco River basin; ANSP 168815, 4, 21.1–21.6 mm SL: Meta, Tributary of Caño La Raya, 1st stream N of La Siberia, Orinoco River basin; **Venezuela**: ANSP 160557, 1, 20.5 mm SL: Bolívar, Caño crossin road to Las Trincheras 37 km S of intersection with Ciudad Bolívar - Caicara hwy, Orinoco River basin; ANSP 160828, 1, 21.6 mm SL: Bolívar, Small stream crossing Caicara-Puerto Ayacucho hwy 18 km N of Maniapure, Orinoco River basin; ANSP 168809, 1, 21.1 mm SL: Bolívar, Sandbar along Río Caura some 400 yd upstream from Caño Barranca-Río Caura junction, Orinoco River basin; ANSP 168810, 37, 19.5–22.2 mm SL: Bolívar, Small stream tributary of Río Mato (left bank), Orinoco River basin; ANSP 168811, 5, 20–21.3 mm SL: Bolívar, Quebrada Cuchivero (Cuchiverito) tributary of Mato River (right bank), Orinoco River basin; ANSP 168812, 16, 16.2–21.8 mm SL: Bolívar, Mouth of Caño Chuapo ca. 20 min downstream from Jabillal on Caura River, Orinoco River basin; ANSP 168813, 11, 20.1–30.3 mm SL: Bolívar, Caño Puerto Cabello at Puerto Cabello, Orinoco River basin; ANSP 168814, 4, 19.2–25.8 mm SL: Bolívar, Caño Chuapo ca 20 min downstream from Jabillal (opposite bank) on Río Caura, Orinoco River basin; ANSP 174741, 1, 19.3 mm SL: Bolívar, Sandbar along Río Caura at junction of Caño Chuapo and Río Caura, Orinoco River basin; CU 94217, 8, 25.1–27.2 mm SL: Bolívar, Cano Barranca ca. 1.25 hours downstream from Jabillal (opposite bank), Orinoco River basin; FMNH 110017, 7, 21.4–23.2 mm SL: Bolívar, cano of Cano Mato a couple of kilometers upstream from mouth, Orinoco River basin; MCP 42737, 6, 22.7–25.5 mm SL, paratypes: Bolívar, caño narranca, río Caura. *Pseudobunocephalus quadriradiatus*: **Peru**: AMNH 96958, 4, 15.6–21.7 mm SL: Loreto, left bank of little brook (quebradita) half way between Hamburgo and Santa Elena, Amazonas River basin. UF 126260, 1, 26.1 mm SL: Loreto, caño cocha Zapote, Pacaya River. *Pseudobunocephalus rugosus*: **Argentina**: 185102, 11, 19.2–25.6 mm SL: Corrientes, arious sites including main and braided side of channel and backwaters of Río Paraná and Lower Guayquiraró ca. 25 km S of Esquina, Paraná River basin; **Brazil**: FMNH 52615, 1, 21.4 mm SL: Mato Grosso do Sul, Corumba, Paraguay River basin; LBP 2865, 40, 21.3–24 mm SL: Mato Grosso, Bento Gomes River, Transpantaneira km 2, Paraguay River basin; LBP 12156, 3, 23.3 mm SL: Mato Grosso, Paraguay River, Paraguay River basin; MCP 10746, 2, 19–21 mm SL: Mato Grosso, pool at brigde in the Transpantaneira road, 70 km South of Poconé, Paraguay River basin; MCP 15540, 3, 2 c&s, 19.6 mm SL: Mato Grosso, Paraguay River at Cáceres, Paraguay River basin; MNRJ 20897, 1, 28.3 mm SL: Mato Grosso, Lagoa marginal a rodovia transpantaneira km 110; MNRJ 27847, 1, 25.7 mm SL: Mato Grosso, arm of Paraguay River, Porto Esperidião, Paraguay River basin; MZUSP 4461, 2, 18.8–22.5 mm SL: Mato Grosso, Lagoa do Santo Antônio do Leverger, Paraguay River basin; MZUSP 28431, 1, 16.3 mm SL: Mato Grosso, Pixaim River, Paraguay River basin; MZUSP 44384, 2, 21–22 mm SL: Mato Grosso, Paraguay River at Cáceres and surroudings, Paraguay River basin; MZUSP 59365, 7, 22.9–24.9



mm SL: Mato Grosso do Sul, Corumbá, Paraguay River basin; USNM 366502, 2, 18.7–20.7 mm SL: Mato Grosso, Paraguay River at Cáceres and surroundings, Paraguay River basin; **Paraguay:** ANSP 170401, 1, 26.4 mm SL: Presidente Hayes, Pools at west end of Puente Remanso, Paraguay River basin; ANSP 174742, 5, 19.2–24.3 mm SL: Paraguari, Mud beach on Parador Las Mercedes side of inlet (Tebicuary River), Paraguay River basin; ANSP 174743, 1, 27 mm SL: Paraguari, mud beach on Parador Las Mercedes side of inlet (Tebicuary River), Paraguay River basin; FMNH 108093, 4, 23.2–25.1 mm SL: Alto Paraguay, Tributary of Paraguay River at Estancia Miranda, Paraguay River basin; FMNH 108094, 1, 21.3 mm SL: Alto Paraguay, Paraguay River ca. 1.5 km above Estancia Cerrito, Paraguay River basin; MZUSP 54243, 1, 18 mm SL: Alto Paraguay, Paraguay River and adjacent flood pools, Paraguay River basin; MZUSP 54244, 1, 24.7 mm SL: Alto Paraguay, Río Paraguay and adjacent flood pools, Paraguay River basin; UMMZ 205514, 1, 30.9 mm SL: Central, Flooded rd. and road side pools ca. 147 km E of Lugue, Paraguay River basin; UMMZ 205592, 1, 28.1 mm SL: Central, Overflow inlet along eastern shore of Paraguay River, Paraguay River basin; UMMZ 205875, 2, 17–20.5 mm SL: Flooded pastures and banks of E shore of Paraguay River, Paraguay River basin; UMMZ 206039, 1, 21 mm SL: Paraguari, Mbaey Stream at km 77 on Ruta 1, 13 km S of Paraguari, Paraguay River basin; UMMZ 206973, 5, 16.4–29.6 mm SL: Presidente Hayes, large lagoon above Dam and adjacent small pools below dam; about 34.8 km NW toll booth at Puente Remanso bridge, Paraguay River basin; UMMZ 207100, 9, 17.1–28.3 mm SL: Small stream ca 33.7 km NW of toll booth on Puente Remanso bridge, Paraguay River basin; UMMZ 207567, 3, 27.4–29.8 mm SL: Pilcomayo River and adjacent area flow pools at bridge to Argentina, Paraguay River basin; UMMZ 207820, 8, 22.8–31.6 mm SL: Concepción, Aquidaban River at Paso Horqueta ca. 24 km NNW of Loreto, Paraguay River basin; UMMZ 207945, 2, 22.9–24.2 mm SL: Paraguay River and adjacent flood pools at municipal airport, Paraguay River basin; UMMZ 267894, 3, 14.6–24.6 mm SL: Swamp pond and adj to Aquidaban River at Paso Horqueta, Paraguay River basin; USNM 232383, 3, 19.7–27 mm SL: Presidente Hayes, Paraguay River basin.

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