



A new catfish of the genus *Trichomycterus* from the Rio Paraíba do Sul Basin, south-eastern Brazil, a supposedly migrating species (Siluriformes, Trichomycteridae)

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http://zoobank.org/42902D76-51B9-449A-8A41-8E548B13C2AD

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Academic editor: Nicolas Hubert ◆ Received 30 July 2021 ◆ Accepted 10 December 2021 ◆ Published 14 January 2022

Abstract

A new species of the catfish genus *Trichomycterus* is described from the Rio Paraíba do Sul, south-eastern Brazil. This species exhibits some morphological character states that are unique amongst congeners, including a robust opercle and a long interopercle with numerous odontodes (50–60 opercular and 90–100 interopercular), a black bar on the basal portion of the caudal fin and a dark brown flank with a well delimited dorsal yellow stripe. It also exhibits some morphological traits that are uncommon amongst congeners, such as the presence of nine pectoral-fin rays. The presence of a shallow hyomandibular outgrowth and a ventrally expanded pre-opercular ventral flap suggests that this species is closely related to *T. melanopygius*, *T. pradensis* and *T. tete*. The new species also differs from *T. melanopygius*, *T. pradensis* and *T. tete* by having an emarginate caudal fin and a single median supra-orbital pore S6. Anecdotal evidence suggests that *T. largoperculatus* and *T. pradensis* have migratory habits, a condition not previously reported for eastern South American trichomycterines.

Key Words

Biodiversity, Brazilian Atlantic Forest, comparative osteology, fish migration, Neotropical Region, systematics

Introduction

The Trichomycterinae, one of the eight subfamilies of the Neotropical catfish family Trichomycteridae, comprises a diversified group with most species inhabiting swift freshwater environments between southern Central America and southern South America (Katz et al. 2018). Taxonomy of the Trichomycterinae has, for long time, been considered particularly problematic due to the traditional non-monophyletic delimitation of the most diverse trichomycterine genus *Trichomycterus* Valenciennes, 1832 (Costa 1992; Costa and Bockmann 1993; de Pinna 1998). Recent studies, using molecular evidence, have consistently indicated that different lineages involving over 150 species, formally placed in *Trichomycterus*, are closer to distinct trichomycterine genera, corroborating the former

view about the paraphyletic nature of Trichomycterus (Ochoa et al. 2017; Katz et al. 2018; Costa et al. 2021a, 2021b). This problem was tentatively solved, by restricting Trichomycterus (hereafter Trichomycterus s.s. [sensu stricto]), to a clade including the type species of the genus, T. nigricans Valenciennes, 1832, sister to a clade containing Cambeva Katz, Barbosa, Mattos & Costa, 2018 and Scleronema Eigenmann, 1917 (Katz et al. 2018). Trichomycterus s.s. comprises 60 valid species distributed between the Rio de Contas, in north-eastern Brazil and rivers draining the Baía de Paranaguá in southern Brazil (Costa 2021). However, the greatest species diversity is concentrated in the area of the Atlantic Forest of south-eastern Brazil comprising the Rio Paraiba do Sul Basin and adjacent smaller coastal river basins, with a total of 25 valid species (e.g. Costa et al. 2020a, b; Vilardo et al. 2020).

Species of *Trichomycterus* from the Rio Paraíba do Sul and adjacent coastal basins have been studied and described since the nineteenth century (Valenciennes 1832; Boulenger 1896; Eigenmann and Eigenmann 1889) and sporadic studies in the first half of the twentieth century recorded some new species (Miranda-Ribeiro 1906; Eigenmann 1917, 1918; Miranda-Ribeiro 1943, 1949). However, the great species diversity of this region was revealed only after 1992, following intensive efforts to sample small, swift riverine habitats (Costa 1992; Barbosa and Costa 2003, 2008, 2010a, b, 2012a, b; Lima and Costa 2004; Lima et al. 2008; Costa et al. 2020b; Vilardo et al. 2020).

This study focuses on a new species collected over 10 years ago in the main channel of the Rio Paraiba do Sul, noteworthy by exhibiting a distinctive colour pattern and some unique osteological features amongst eastern South American trichomycterines. Equally remarkable is the report of upstream migration during the collection, which is new for eastern South American trichomycterines. Due to the peculiar combination of morphological character states exhibited by the new species, making its phylogenetic positioning uncertain amongst trichomycterines, a formal description was not made before the conclusion of deeper phylogenetic studies on trichomycterines from eastern South America (Katz et al. 2018; Costa 2021). Herein, we provide a formal description for the new species and discuss morphological variation considered relevant for its phylogenetic positioning, as well as migration in trichomycterines.

Material and methods

Morphometric and meristic data were taken following Costa (1992), with modifications proposed by Costa et al. (2020a); measurements are presented as percentage of standard length (SL), except for those related to head morphology, which are expressed as percentage of head length. Fin-ray counts include all elements; following Bockmann and Sazima (2004), in descriptions, lower case roman numerals indicate unsegmented unbranched rays, upper case numerals indicate segmented unbranched rays and Arabic numerals indicate segmented branched rays. Vertebra counts do not include Weberian apparatus vertebrae and the compound caudal centrum was counted as a single element. Specimens were cleared and stained for bone and cartilage (C&S in lists of specimens) following Taylor and Van Dyke (1985); osteological characters included in the description are those belonging to structures that have informative variability amongst congeners (Costa et al. 2020a, b), including the mesethmoidal region, suspensorium, opercular apparatus and branchial arches. Terminology for bones is according to Costa (2021). Osteological illustrations were made using a stereomicroscope Zeiss Stemi SV 6 with camera lucida. Cephalic latero-sensory system terminology follows Arratia and Huaquin (1995), with modifications proposed by

Bockmann et al. (2004). Specimens are deposited in the ichthyological collection of the Institute of Biology of the Federal University of Rio de Janeiro, Rio de Janeiro City and in the Centre of Agrarian and Environmental Sciences, Federal University of Maranhão, Chapadinha (CICCAA). Comparative material is listed in Costa (2021). Geographical names follow Portuguese terms used in the region, thus avoiding common errors or generalisations when translating them to English, besides making it easier to find them in the field.

Results

Trichomycterus largoperculatus sp. nov.

http://zoobank.org/A5F16812-88EC-49FA-92CC-78E85C176A86 Figs 1-4, Table 1

Holotype. UFRJ 6987, 77.8 mm SL; Brazil: Estado do Rio de Janeiro: Município de Além Paraíba: Rio Paraíba do Sul just below Ilha dos Pombos Dam, 21°50'36"S, 42°34'46"W, about 105 m a.s.l.; L. P. Bastos, 10 March 2009.

Paratypes. UFRJ 6988, 7, 35.2–91.5 mm SL; UFRJ 6989, 3 (C&S), 55.7–46.2 mm SL; CICCAA 02695, 2, 50.7–51.3 mm SL; all collected with holotype.

Diagnosis. *Trichomycterus largoperculatus* is distinguished from all species of *Trichomycterus s.s.* by having more opercular odontodes (48–62 vs. 11–31), more interopercular odontodes (92–100 vs. 23–72) and a unique colour pattern consisting of a dark brown flank with a longitudinal pale yellow stripe on its dorsal portion (vs. never a similar colour pattern) and the presence of a black bar on the basal portion of the caudal fin (vs. absence).

Description. Morphometric data are in Table 1. Body moderately slender, subcylindrical and slightly depressed anteriorly, compressed posteriorly. Greatest body depth

Table 1. Morphometric data of *Trichomycterus largoperculatus* sp. nov.

	Holotype	Paratypes (n = 8)
Standard length (mm)	77.8	46.6-91.5
Percentage of standard length		
Body depth	16.4	14.3-17.5
Caudal peduncle depth	11.2	9.6-11.4
Body width	9.2	9.6-14.7
Caudal peduncle width	3.9	3.1-4.4
Pre-dorsal length	60.4	58.0-62.9
Pre-pelvic length	53.5	53.3-58.1
Dorsal-fin base length	13.6	11.9-13.4
Anal-fin base length	8.7	8.9-10.4
Caudal-fin length	16.7	15.0-16.8
Pectoral-fin length	15.5	13.8-17.0
Pelvic-fin length	11.5	10.7-12.9
Head length	21.9	21.9-25.1
Percentage of head length		
Head depth	45.2	42.4-48.5
Head width	81.8	73.9-83.6
Snout length	48.4	42.1-45.9
Interorbital length	24.3	21.6-28.3
Pre-orbital length	15.8	13.2-16.4
Eye diameter	11.7	12.2–16.1



Figure 1. *Trichomycterus largoperculatus* sp. nov., UFRJ 6987, holotype, 77.8 mm SL: **A.** Left lateral view; **B.** Dorsal view; **C.** Ventral view.

at vertical just anterior to pelvic fin base. Dorsal profile of head and trunk slightly convex, approximately straight on caudal peduncle; ventral profile straight to slightly convex between lower jaw and end of anal-fin base, straight on caudal peduncle. Anus and urogenital papilla at vertical through middle portion of dorsal-fin base. Head trapezoidal in dorsal view. Anterior profile of snout slightly convex in dorsal view. Eye relatively large, dorsally positioned in head. Minute skin papillae on ventral surface of head. Posterior nostril located nearer anterior nostril than orbital rim. Tip of maxillary and rictal barbels reaching anterior part of interopercular patch of odontodes; tip of nasal barbel reaching posterior part of orbit. Mouth subterminal. Jaw teeth pointed; premaxillary teeth 55–58, slightly curved, arranged in 5 irregular rows; dentary teeth 53-56, slightly curved backwards, irregularly arranged, more concentrated near symphysis. Branchial membrane attached to isthmus only at its anterior point. Branchiostegal rays 7.

Dorsal and anal fins subtriangular; total dorsal-fin rays 13 (iv + II + 7), total anal-fin rays 11 (iv + II + 5); anal-

fin origin posterior to dorsal-fin base. Dorsal-fin origin at vertical through centrum of 16th or 17th vertebra; anal-fin origin at vertical between centrum of 22nd or 23rd vertebra. Pectoral fin subtriangular in dorsal view, posterior margin slightly convex, first pectoral-fin ray terminating in filament, its length about 20% of pectoral-fin length without filament; total pectoral-fin rays 9 (I + 8). Pelvic fin truncate, its posterior extremity reaching urogenital papilla; pelvic-fin bases medially separated by interspace about half-length pelvic-fin base; total pelvic-fin rays 5 (I + 4). Caudal fin emarginated, upper and lower corners rounded to slightly pointed; total principal caudal-fin rays 13 (I + 11 + I), total dorsal procurrent rays 18–22 (xvii–xxi + I), total ventral procurrent rays 14-16 (xiii-xv + I). Vertebrae 35 or 36. Ribs 11 or 12. Two dorsal hypural plates, corresponding to hypurals 4 + 5 and 3, respectively; single ventral hypural plate corresponding to hypurals 1 and 2 and parhypural.

Laterosensory system (Fig. 2). Supraorbital sensory canal continuous, posteriorly connected to posterior section of infra-orbital canal. Supra-orbital sensory canal

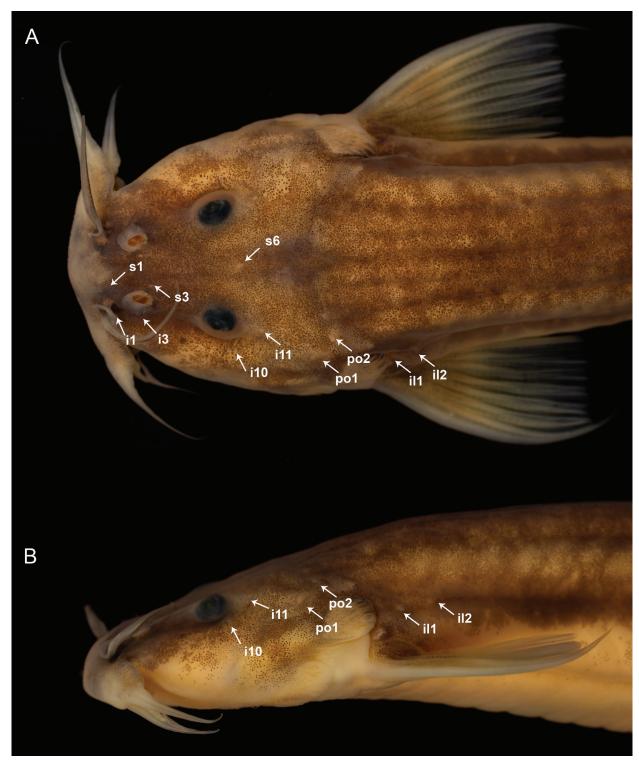


Figure 2. Head of Trichomycterus largoperculatus sp. nov., UFRJ 6987, holotype, 77.8 mm SL: A. Dorsal view; B. Left lateral view.

with 2 paired pores, s1, adjacent to medial margin of anterior nostril and s3, adjacent and just posterior to medial margin of posterior nostril; supra-orbital pore s6 single, on centre of head, at transverse line through posterior half of orbit. Infra-orbital sensory canal arranged in 2 segments, each with two pores; anterior segment with pore i1, at transverse line through anterior nostril and pore i3, at transverse line just anterior to posterior nostril; posterior segment with pore i10, adjacent to ventral margin

of orbit and pore i11, posterior to orbit. Postorbital canal with 2 pores: po1, at vertical line above posterior portion of interopercular patch of odontodes and po2, at vertical line above posterior portion of opercular patch of odontodes. Lateral line of body short, with 2 pores, posterior-most pore at vertical just posterior to pectoral-fin base.

Mesethmoidal region and adjacent structures (Fig. 4A). Anterior margin of mesethmoid nearly straight, mesethmoid cornu robust, subcylindrical, tip



Figure 3. *Trichomycterus largoperculatus* sp. nov., left lateral view: **A.** UFRJ 6988, paratype, 70.0 mm SL; **B.** UFRJ 6988, paratype, 49.0 mm SL.

rounded. Antorbital and sesamoid supra-orbital narrow, rod-like, sesamoid supra-orbital longer, its length about 2.5 times antorbital length. Premaxilla sub-rectangular in dorsal view. Maxilla boomerang-shaped, slender, about equal premaxilla in length, slightly curved, with minute posterior process. Autopalatine sub-rectangular in dorsal view when excluding posterolateral process, narrow, its shortest width about half autopalatine length, lateral and medial margins slightly concave; latero-posterior process of autopalatine subtriangular, long, its length about two thirds of autopalatine length.

Jaw suspensorium and opercular apparatus (Fig. 4B). Metapterygoid trapezoidal, slightly longer than deep. Quadrate robust, dorsoposterior outgrowth continuous to hyomandibular outgrowth. Hyomandibula long, anterior outgrow shallow, slightly concave; postero-dorsal process of hyomandibula pointed. Opercle robust; opercular odontodes 48–62; odontodes pointed, arranged in irregular transverse rows; odontode patch depth about half opercle length; dorsal process of opercle short and blunt, about 2.5 times interopercular odontode patch length. Interopercle long, about three fourths hyomandibula length, with 92–100 odontodes; odontodes pointed, arranged in irregular longitudinal rows; dorsal interopercular process with deep anterior concavity. Pre-opercle compact, with expanded ventral flap.

Branchial arches (Fig. 4C). Basibranchial 2 and 3 subcylindrical, approximately equal in length, basibranchial 2 wider anteriorly; basibranchial 4 cartilage sub-pentagonal, longer than wide. Hypobranchial 1 subcylindrical, slightly widening at its distal tip; hypobranchial 2 and 3 subtriangular, anterior portion well-ossified. Ceratobranchial 1 broad in its proximal portion, gradually narrowing

to its distal tip; ceratobranchials 2 and 3 widened in their middle portion, ceratobranchial 3 with deep concavity on posterior margin of basal portion; ceratobranchial 4 sub-rectangular, slightly narrowing proximally; accessory cartilage of ceratobranchial 4 minute; ceratobranchial 5 sub-rectangular, slightly curved, narrower than ceratobranchial 4; medial-proximal portion of ceratobranchial 5 bearing 24-26 small, slightly curved, conical teeth. Epibranchial 1 slender, with well-developed anterior uncinate process and minute posterior process; epibranchial 2 slender, with rudimentary anterior uncinate process; epibranchial 3 slender, with well developed, curved posterior uncinate process; epibranchial 4 broad, sub-rectangular. Pharyngobranchial 3 short, subcylindrical; pharyngobranchial 4 long, bearing broad dentigerous plate with 22–28 fang-shaped teeth.

Colouration in alcohol. Flank dark brown with longitudinal pale yellow stripe on dorsal portion, ventral portion yellowish white; in juveniles and most adult specimens (Fig. 3B), highly contrasting dark and lighter flank zones; in some specimens, including holotype (Fig. 1), dark zone paler and not expanding on venter and on pale yellow stripe, in some others, dark zone intensively pigmented, pale yellow stripe faint (Fig. 3A). Dorsal surface of head and trunk brown, ventral surface yellowish-white. Side of head brown, with unpigmented area on cheek at vertical line just anterior to orbit; dark chromatophores more concentrated between and around nostrils. Maxillary and rictal barbels pale yellow, nasal barbel pale yellow, posterior margin dark brown. Opercular and interopercular patches of odontodes pale yellow, posterior margin of opercle dark grey to black. Unpaired fins yellowish-white; dark brown chromatophores concentrated on basal portion of dorsal

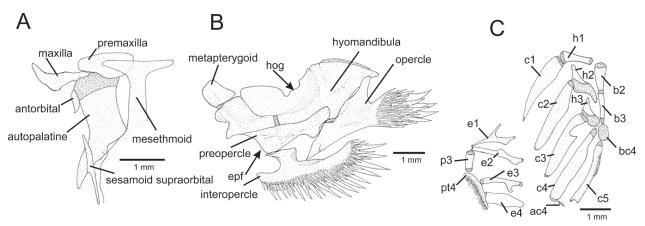


Figure 4. Osteological structures of *Trichomycterus largoperculatus*: **A.** Mesethmoidal region and adjacent structures, middle and left portion, dorsal view; **B.** Left jaw suspensorium and opercular apparatus, lateral view; **C.** Middle and left portion of brachial arches, ventral view of dorsal elements on left, dorsal view of ventral elements on right. Abbreviations: ac4, accessory cartilage basibranchial 4; b2–3, basibranchials 2–3; bc4, cartilaginous basibranchial 4; c1–5, ceratobranchials 1–5; e1–4, epibranchials 1–4; epf, expanded pre-opercular ventral flap; p3, pharyngobranchial 3; h1–3, hypobranchials 1–3; hog, hyomandibular outgrowth; pt4, pharyngobranchial 4 tooth-plate. Larger stippling represents cartilages.

fin, forming diffuse brown area; horizontally elongated brown spot on caudal fin base and black bar on basal portion, almost inconspicuous in some specimens. Paired fins pale yellow, basal portion of pectoral fin dark brown.

Colouration in life. Not recorded.

Distribution. *Trichomycterus largoperculatus* is known only from the type locality, in the middle Rio Paraíba do Sul, south-eastern Brazil (Fig. 5). Specimens of the type series were collected while they were migrating upstream, just below Ilha dos Pombos hydroelectric dam.

Etymology. From the Latin, the name *largoperculatus* (with large opercle) refers to the broad opercular odontode patch resulted from the high number of odontodes (48–62) (Fig. 4B), a unique condition amongst congeners.

Discussion

Comparative morphology

Two conspicuous apomorphic conditions of the external morphology of T. largoperculatus include the presence of an emarginate caudal fin and nine pectoral-fin rays. Although these conditions may be present in different trichomycterine lineages, the occurrence of these morphological character states is uncommon amongst eastern South American trichomycterines. In the over 40 species included in the clade comprising Cambeva and Scleronema, which is sister to Trichomycterus s.s., the caudal fin is always truncate or subtruncate and there are eight rays or less in the pectoral fin, never nine (Costa et al. 2020a). According to Costa et al. (2020a), an apomorphic concave posterior margin of the caudal fin yielding an emarginate shape, is synapomorphic for species of the T. nigricans group (subgenus Trichomycterus), but an emarginate caudal fin is also present in T. astromycterus Reis, de Pinna & Pessali, 2020, a species with uncertain phylogenetic

position (Reis et al. 2020; Costa 2021). The T. nigricans group is a clade highly supported by molecular data (Costa et al. 2020b), comprising T. caipora Lima, Lazzarotto & Costa, 2008, T. immaculatus (Eigenmann & Eigenmann, 1889), T. nigricans and T. santaeritae (Eigenmann, 1918) Interestingly, all of these four species also possess nine pectoral-fin rays, considered to be another synapomorphy for the *T. nigricans* group (Costa et al. 2020a), although independently occurring in T. giganteus Lima & Costa, 2004 of the subgenus Megacambeva Costa, 2021 and T. pradensis Sarmento-Soares, Martins-Pinheiro, Aranda & Chamon, 2005 of the subgenus Psammocambeva Costa, 2021 (Costa et al. 2020a, b; Costa 2021). Therefore, the combination of an emarginate caudal fin and nine pectoral-fin rays would suggest that T. largoperculatus is a member of the T. nigricans group, although these apomorphic conditions are not exclusive of the group, as well as two other congeners not closely related to the T. nigricans group. On the other hand, the T. nigricans group was also diagnosed by the apomorphic presence of a pronounced posterior process in the maxilla (Costa et al. 2020a: fig. 2A, D and G; Costa 2021), which is not present in T. largoperculatus (Fig. 4A). Therefore, considering these conflicting character states, it would not be possible to unambiguously assign T. largoperculatus to the T. nigricans group of the subgenus Trichomycterus.

Trichomycterus largoperculatus has a long maxilla that is conspicuously longer than the premaxilla (Fig. 4A). This character state was considered the only apomorphic condition diagnosing the subgenus *Psammocambeva*, but independently occurring in *T. santaeritae* of the *T. nigricans* group (Costa et al. 2020a; Costa 2021); therefore, not useful to place *T. largoperculatus* in this subgenus. On the other hand, *T. largoperculatus* shares two apomorphic character states, first described by Costa (2021: fig. 3C), with three species of *Psammocambeva* from eastern Brazil (Fig. 5), *T. melanopygius* Reis, dos Santos, Britto, Volpi & de Pinna,

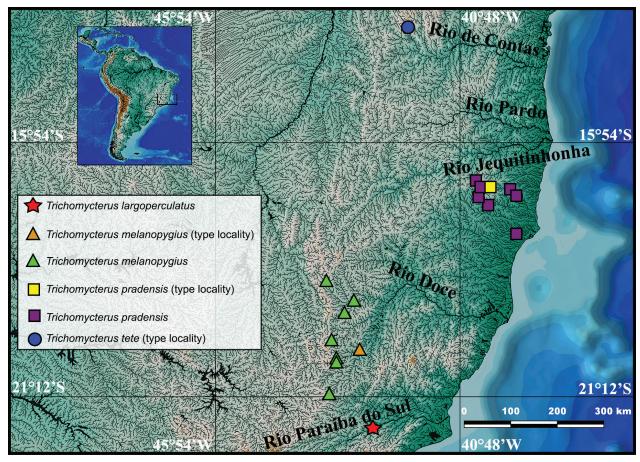


Figure 5. Map of geographical distribution of Trichomycterus largoperculatus sp. nov. and closely related species.

2020, T. pradensis Sarmento-Soares, Martins-Pinheiro, Aranda & Chamon, 2005 and *T. tete* Barbosa & Costa, 2011, that do not occur in other species of *Trichomycterus s.s.*: the presence of a shallow anterior outgrowth of the hyomandibula and an expanded ventral pre-opercular flap (Fig. 4B). Besides the unique morphological character states listed in the diagnosis (see also discussion below), T. largoperculatus also differs from T. melanopygius, T. pradensis and T. tete by having an emarginate caudal fin (vs. subtruncate) and a single median supra-orbital pore S6 (vs. paired). Interestingly, some anecdotal evidence suggests that T. largoperculatus and T. pradensis have migratory habits (see discussion below), a condition not previously reported to occur in other species of Trichomycterus s.s. and the closely related genera Cambeva and Scleronema, suggesting its being a derived biological condition shared by these species.

Some morphological character states, here recorded as diagnostic for *T. largoperculatus*, are interpreted as autapomorphies. Firstly, in this species, the opercular and interopercular patches of odontodes are broad, with numerous odontodes. There are about 50–60 opercular and 90–100 interopercular odontodes, thus greatly surpassing the maximum of about 30 opercular and 70 interopercular odontodes in all other species of *Trichomycterus s.s.*, as well as in all species of its sister group, the clade containing *Cambeva* and *Scleronema*. Secondly, no other trichomycterid has a flank colour pattern consisting of a dark brown flank crossed by

a dorsal yellow stripe like that present in T. largoperculatus (Figs 1 and 3). Species of the subgenus *Paracambeva* Costa, 2021 may have a colour pattern superficially similar to that in T. largoperculatus. They have a yellow flank with a dark brown to black stripe on the flank mid-line in juveniles that is substituted by a diffuse dark brown zone on the flank midline and another on dorsum, resting a yellow unpigmented longitudinal zone on the dorsal part of the flank (Costa and Katz 2021). This pattern differs from the colour pattern of T. largoperculatus, in which both juveniles and adults have a dark brown ground colouration with a well-delimited dorsal yellow stripe on the body side (Fig. 3B), indicating that these colour patterns are not homologous. Finally, T. largoperculatus has a black bar on the basal portion of the caudal fin, which is not present in any species of the genus. In T. caudofasciatus Alencar & Costa, 2004, for example, there are four vertical zones of chromatophores on the caudal fin, producing a colour pattern of faint grey bars (Alencar and Costa 2004: fig. 2), greatly differing from the black bar on the basal portion of the fin occurring in T. largoperculatus that is conspicuous in most specimens (Fig. 3).

Migration in trichomycterine catfishes

The type series of *T. largoperculatus* was collected while fish were migrating upstream along the Rio Paraíba do

Sul main channel (V. Abilhoa, pers. com.). Although migration for feeding, reproduction and spawning is a common feature amongst large species of Neotropical pimelodid catfishes (e.g. Barthem et al. 2017), literature reports on migration of trichomycterids are restricted to a detailed record of massive juvenile upstream migration of a species of Trichomycterus sensu lato, T. barbouri (Eigenmann, 1911), in the Río Beni, Bolivian Amazon, by Miranda-Chumacero et al. (2015). In eastern South America, both juvenile and adults of all class sizes of Trichomycterus s.s. are commonly found at the same place, thus excluding occurrence of long range migrations for most species. For example, in the upper Rio Preto drainage, Rio Paraiba do Sul Basin, where one of us (WJEMC) has conducted regular field studies for about four decades, both adults in all reproductive stages of T. albinotatus Costa, 1992, T. auroguttatus Costa, 1992 and T. mirissumba have been collected at the same place and time as small juveniles about 20 mm of total length.

The only exception amongst trichomycterines from eastern South America river basins was observed during field studies on February 2014, when hundreds of specimens of *T. pradensis*, about 20 mm of total length, were seen forming a continuous upstream flow in the lower Rio Jucuruçu (16°23'34"S, 39°17'09"W), eastern Brazil, just about 25 km from the sea (WJEMC, pers. obs.), thus contrasting with larger specimens, between about 40 and 110 mm SL that were only found in the upper section of the basin (Sarmento-Soares et al. 2005). This upstream flow was recorded during a collecting stop of about one and a half hours and it was continuous and intense during all the time, characterising a migratory movement. However, whereas it is not possible to understand the whole migration cycle based only on this record, the existence of numerous juvenile specimens migrating upstream in a region where large adults are absent, highly suggests a migratory flow. The occurrence of juveniles actively and continuously swimming upstream in a lower altitude region where adults are not present and were not recorded in previous studies (Sarmento-Soares et al. 2005) is similar to that described for *T. barbouri* in the Bolivian Amazon and consistent with the hypothesis by Miranda-Chumacero et al. (2015) that reproduction occurs in upper areas and eggs are released into the flood, thus reaching lower areas. Further field research is needed to determine if migration is a widespread phenomenon amongst trichomycterines of eastern and south-eastern Brazil or if it is limited to some lineages including at least T. largoperculatus and T. pradensis.

Acknowledgements

Special thanks are due to Vinicius Abilhoa for donating specimens of the new species for study. Thanks are also due to Donald Taphorn, Heok Hee Ng and Paulo Andreas Buckup for suggestions and criticisms. This work was supported by Conselho Nacional de Desenvolvimento

Científico e Tecnológico (CNPq; grant 304755/2020-6 to WJEMC) and Fundação Carlos Chagas Filho de Amparo à Pesquisa do Estado do Rio de Janeiro (FAPERJ; grant E-26/202.005/2020 to AMK and E-26/201.213/2021 to WJEMC). This study was also supported by CAPES (Coordenação de Aperfeiçoamento de Pessoal de Nível Superior, Finance Code 001) through Programa de Pós-Graduação em: Biodiversidade e Biologia Evolutiva /UFRJ; Genética/UFRJ; and Zoologia, Museu Nacional/UFRJ.

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Zeitschrift/Journal: Zoosystematics and Evolution

Jahr/Year: 2022

Band/Volume: 98

Autor(en)/Author(s): Costa Wilson J. E. M., Katz Axel M.

Artikel/Article: A new catfish of the genus Trichomycterus from the Rio Paraíba do Sul Basin, south-eastern Brazil, a supposedly migrating species (Siluriformes,

Trichomycteridae) 13-21