



A new species of the catfish genus *Trichomycterus* from the La Plata River basin, southern Brazil, with comments on its putative phylogenetic position (Siluriformes: Trichomycteridae)

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Abstract

The genus *Trichomycterus* is a highly diverse group of Neotropical catfishes that encompass almost 60% of all the currently recognized species of the Trichomycteridae. A new species of this genus, *T. perkos*, is herein described from tributaries of the Paranapanema and Uruguai River basins, southern Brazil. The new species exhibits a remarkable ontogenetic change in its pigmentation, having a unique color pattern when adult. The adult pigmentation consists of three wide dark brown stripes, located in an inner skin layer of trunk and caudal peduncle, combined with a superficial light brown freckled pattern on the dorsum and caudal peduncle. Small, presumably juvenile specimens lack the superficial freckles but already have the dark stripes, thus resembling the color pattern of a few other congeners. Nevertheless, several unequivocal morphological features distinguish both juveniles and adults of *T. perkos* from these congeners. In spite of the difficulties in estimating phylogenetic relationships within *Trichomycterus*, the new species is tentatively proposed as being the sister-taxon of a small group of species composed by *T. crassicaudatus*, *T. igobi*, and *T. stawiarski*.

Key words: Loricarioidea, Ontogeny, Pigmentation, Paranapanema River, Uruguai River

Resumo

O gênero *Trichomycterus* é um grupo altamente diverso de bagres neotropicais que engloba quase 60% de todas as espécies atualmente reconhecidas de Trichomycteridae. Uma nova espécie deste gênero, *T. perkos*, é aqui descrita proveniente de tributários das bacias dos rios Paranapanema e Uruguai, no sul do Brasil. A nova espécie exibe uma notável modificação ontogenética em sua pigmentação, apresentando um padrão de colorido único quando adulto. A pigmentação dos adultos consiste de três listras marrom-escuras, localizadas em uma camada mais profunda da pele do tronco e pedúnculo caudal, combinados com um padrão que lembra sardas marrom-claras superficiais no dorso e pedúnculo caudal. Indivíduos pequenos, presumivelmente jovens, não possuem as sardas superficiais, mas já apresentam as listras escuras, lembrando, desta forma, o padrão de coloração de alguns poucos congêneres. Entretanto, várias características morfológicas inequívocas distinguem tanto jovens quanto adultos de *T. perkos* destes congêneres. Apesar das dificuldades em se aferir relações filogenéticas dentro de *Trichomycterus*, a nova espécie é tentativamente proposta como sendo o táxon-irmão de um pequeno grupo de espécies composto por *T. crassicaudatus*, *T. igobi* e *T. stawiarski*.

Introduction

The Trichomycteridae is highly diverse family of catfishes, with 251 currently valid species (Eschmeyer & Fong, 2011) that distributes through almost all major drainages of the Neotropics (de Pinna & Wosiacki, 2003). The

members of this family form a monophyletic group supported by a large number of unique synapomorphies, being the most conspicuous of them related to their highly modified opercular apparatus (*cf.* Baskin, 1973; Datovo & Bockmann, 2010; de Pinna, 1992a, 1998). The drastic modifications of this apparatus, which includes the presence of patches of odontodes on the opercle and interopercle in most members, forms a complex musculoskeletal system that allows trichomycterids to anchor themselves to the substrate or on their host's body (in the case of the semiparasitic "candirus").

In spite of constituting the second richest family of the Loricarioidea, the real diversity of the Trichomycteridae is still underestimated inasmuch several new trichomycterid taxa await description. Many of these undescribed taxa apparently belong to the genus *Trichomycterus*, a group of usually small rheophilic fishes popularly known in Brazil as *cambevas* (a name derived from indigenous Tupi composition *akánga péua*, meaning flat-heat; Weisz-flog, 2007). The genus encompasses almost 60% of all the currently recognized species of the family (Eschmeyer & Fricke, 2011; Eschmeyer & Fong, 2011). As presently conceived *Trichomycterus* lacks any diagnostic feature and apparently does not form a monophyletic unit (Datovo & Bockmann, 2010; de Pinna, 1989). The enormous amount of names currently recognized as supposedly valid species of *Trichomycterus* combined with the uncertainties about the phyletic status of the group make of the taxonomy of genus one of the most challenging problems in the systematics of the Neotropical catfishes (de Pinna, 1998).

The present study describes a new species of *Trichomycterus* from the drainages of the Paranapanema and Uruguai Rivers, both tributaries of the La Plata River basin. The phylogenetic position of the new species is also inferred on the basis of morphological characters.

Material and methods

Measurements were point to point, taken with digital calipers to the nearest 0.1 mm. Morphometrics followed Datovo and Landim (2005). Number of post-Weberian vertebrae includes the compound caudal centrum (de Pinna & Ng, 2004; Lundberg & Baskin, 1969) counted as one element. Number of odontodes, branchiostegal rays, unsegmented or procurrent fin rays, and all other osteological counts were taken from radiographed or cleared and stained specimens. In the text, lower case Roman numerals represent procurrent fin rays (*sensu* Arratia, 2008) of median fins; among principal fin rays (Arratia, 2008), anteriormost unbranched rays are represented by upper case Roman numerals and branched rays by Arabic numerals.

Osteological and myological terminologies follow Datovo and Bockmann (2010). The nomenclature for the cephalic laterosensory system follows Bockmann *et al.* (2004). For osteological observations, specimens were cleared and stained according to Taylor and Van Dyke (1985). The protocol of Datovo and Bockmann (2010) was used for preparing specimens for myological observations.

Institutional abbreviations: LIRP, Laboratório de Ictiologia de Ribeirão Preto, Universidade de São Paulo, Brazil; MCP, Museu de Ciências e Tecnologia da Pontifícia Universidade Católica do Rio Grande do Sul, Porto Alegre, Brazil; MZUSP, Museu de Zoologia da Universidade de São Paulo, Brazil; MNRJ, Museu Nacional do Rio de Janeiro, Brazil; UFRGS, Departamento de Zoologia, Universidade Federal do Rio Grande do Sul, Porto Alegre, Brazil. Specimen-preparation abbreviations: CS, cleared and stained; MS, dissected for musculature; XR, X-rayed. Morphometric abbreviations: SL, standard length; HL, head length.

Trichomycterus perkos, new species

(Figs. 1–2, Table 1)

Trichomycterus aff. *itaiyae*: Kantek *et al.* (2007: 797).

Trichomycterus sp. aff. *T. itaiyae*: Torres *et al.* (2004: 124).

Trichomycterus sp. aff. *T. itaiyae* [*sic*]: Sato *et al.* (2004: 45, 46, 47, Table 1, Table 2).

Holotype. MCP 46679 (93.5 mm SL), XR; Brazil, Rio Grande do Sul State, Passo Fundo Municipality; Uruguai River basin, Passo Fundo River, under the bridge on BR–285 road; approx. 28°14'07"S 52°24'53"W; W. Bruschi Jr. & J. F. P. Silva; 03 January 2003.

Paratypes. LIRP 8344, 4 (28.0–93.2 mm SL): 1 CS (28.0 mm SL), 1 MS (35.3 mm SL), 1 XR (28.3 mm SL); Brazil, Rio Grande do Sul State, Passo Fundo Municipality; Uruguai River basin, unnamed stream tributary of Passo Fundo River, about 1 km from BR–285 road; approx. 28°15'14"S 52°21'19"W; W. Bruschi Jr. & J. F. P. Silva; 03 January 2003. MCP 31763, 10 (16.2–99.8 mm SL): 1 CS (52.4 mm SL), 1 XR (99.81 mm SL); same data as LIRP 8344. MCP 31764, 2 (17.9–33.1 mm SL; XR); same data as holotype. MCP 31774, 1 (61.2 mm SL); same data as LIRP 8344. MCP 31776, 3 (27.0–43.3 mm SL); Brazil, Rio Grande do Sul State, Passo Fundo Municipality; Uruguai River basin, Passo Fundo River; 28°14'44"S 52°20'53"W; W. Bruschi Jr. & J. F. P. Silva; 04 January 2003. MCP 46701, 1 (48.9 mm SL); Brazil, Rio Grande do Sul State, São Valentim Municipality; Uruguai River basin, Passo Fundo River basin, unnamed stream tributary of Erechim River; 27°38'29"S 52°35'51"W; J. F. P. Silva; 20 October 2011. MCP 46711, 1 (69.1 mm SL); Brazil, Rio Grande do Sul State, Campinas do Sul Municipality; Uruguai River basin, unnamed stream tributary of Sepultura Stream, an affluent of reservoir of the Passo Fundo Hydroelectric Power Plant; 27°48'56"S 52°37'51"W; J. F. P. Silva; 20 October 2011. MCP 46715, 1 (32.9 mm SL); Brazil, Rio Grande do Sul State, Campinas do Sul Municipality; Uruguai River basin, unnamed stream affluent of reservoir of the Passo Fundo Hydroelectric Power Plant; 27°51'18"S 52°35'16"W; J. F. P. Silva; 20 October 2011. MCP 46718, 1 (71.4 mm SL); Brazil, Rio Grande do Sul State, Campinas do Sul Municipality; Uruguai River basin, unnamed stream tributary of Cipó Stream, an affluent of reservoir of the Passo Fundo Hydroelectric Power Plant; 27°52'24"S 52°33'35"W; J. F. P. Silva; 20 October 2011. MCP 46721, 1 (50.2 mm SL); Brazil, Rio Grande do Sul State, Campinas do Sul Municipality; Uruguai River basin, Cipó Stream, an affluent of reservoir of the Passo Fundo Hydroelectric Power Plant; 27°52'27"S 52°33'25"W; J. F. P. Silva; 20 October 2011. MZUSP 82372, 1 (72.2 mm SL); Brazil, Paraná State, Castrolanda Municipality; Paranapanema River basin; Tibaji River sub-basin, Iapó River sub-basin, unnamed stream tributary of da Onça River; approx. 24°49'30"S 49°54'28"W; A. L. A. Alves, R. Devid, A. Ferreira, & Y. R. Arvex; 20 March 2002; UFRGS 5922, 1 (41.1 mm SL), XR; Brazil, Rio Grande do Sul State, Condor Municipality; Uruguai River basin, Ijuí River sub-basin, Alegre River sub-basin, Palmeiras River; approx. 28°14'09"S 53°28'01"W; J. A. Anza & J. F. P. Silva; 02 November 2002.

Diagnosis. Large-sized specimens (more than 65.8 mm SL), presumably adults, of *Trichomycterus perkos* are distinguished from all their congeners in having a distinctive coloration with melanophores arranged in two distinct skin layers, forming (1) a freckled pattern, with minute light brown spots scattered on the superficial tegumentar layer of the dorsum and caudal peduncle, and (2) a striped pattern, with three – sagittal, midlateral, and ventrolateral – wide, irregularly bordered, and sometimes interrupted dark brown stripes running along an inner skin layer of the trunk and caudal peduncle (Fig. 1; vs. melanophores in only one skin layer in most other *Trichomycterus* or melanophores occurring in two layers, but with the inner layer forming blotches in *T. brasiliensis* Lütken, *T. castroi* de Pinna, *T. crassicaudatus* Wosiacki and de Pinna, *T. diabolus* Bockmann, Casatti, and de Pinna, *T. igobi* Wosiacki and de Pinna, *T. maracaya* Bockmann and Sazima, *T. mimonha* Costa, *T. stawiarski* (P. Miranda Ribeiro), and *T. tropeiro* Ferrer and Malabarba, or forming solely a midlateral stripe in *T. giganteus* Lima and Costa; pers. obs.; Bockmann *et al.*, 2004; Bockmann & Sazima, 2004; de Pinna, 1992b; Lima & Costa, 2004; Wosiacki & de Pinna, 2008a, 2008b).

Smaller individuals (less than 43.3 mm SL), presumably juveniles, of *Trichomycterus perkos* lack the superficial freckled pattern, but already exhibit the three wide dark stripes found in the adults (Fig. 2). This juvenile color pattern, although not identical, may resemble that of some *T. duellmani* Arratia and Menu-Marque, *T. itatiayae* A. Miranda Ribeiro, *T. nigroauratus* Barbosa and Costa, *T. pauciradiatus* Alencar and Costa, *T. reinhardti* (Eigmann), and *T. taenia* Kner. Nevertheless, both juveniles and adults of *T. perkos* unequivocally differ from these congeners in a number of morphological traits:

- (1) from *T. duellmani* in having modally seven pectoral-fin rays (vs. modally eight), two pores in the lateral line (vs. four), distal margin of the adpressed pelvic fin not reaching the anus (vs. distal margin extending posteriorly beyond the anus), modally ten branchiostegal rays (vs. six or seven), and modally 41 post-Weberian vertebrae (vs. 33–36) (Arratia & Menu-Marque, 1984);
- (2) from *T. itatiayae* by the first pectoral-fin ray not filamentous (vs. filamentous), distal margin of the adpressed pelvic fin not reaching the anus (vs. distal margin extending posteriorly beyond the anus), modally ten branchiostegal rays (vs. eight), and modally 41 post-Weberian vertebrae (vs. 35–37) (Barbosa & Costa, 2008; Caramaschi & Caramaschi, 1991; A. Miranda Ribeiro, 1906);
- (3) from *T. nigroauratus* by the first pectoral-fin ray not filamentous (vs. filamentous), modally seven pectoral-fin rays (vs. modally eight), modally ten branchiostegal rays (vs. seven or eight), and modally 41 post-Weberian vertebrae (vs. 35–36) (Barbosa & Costa, 2008);

- (4) from *T. pauciradiatus* in having the first pectoral-fin ray not filamentous (vs. filamentous), modally seven pectoral-fin rays (vs. modally six), five pelvic-fin rays (vs. four), distal margin of the addressed pelvic fin not reaching the anus (vs. distal margin extending posteriorly beyond the anus), pores i_1 and i_3 of the infraorbital laterosensory canal lacking (vs. i_1 and i_3 present), modally ten branchiostegal rays (vs. eight), and modally 41 post-Weberian vertebrae (vs. 36–38) (Alencar & Costa, 2006);
- (5) from *T. reinhardti* by the first pectoral-fin ray not prolonged as a filament (vs. ray filamentous), distal margin of the addressed pelvic fin not reaching the anus (vs. distal margin extending posteriorly beyond the anus), absence of the pores i_1 and i_3 of the infraorbital laterosensory canal (vs. i_1 and i_3 present), modally ten branchiostegal rays (vs. seven or eight), and modally 41 post-Weberian vertebrae (vs. 38) (Eigenmann, 1917, 1918; Morris *et al.*, 2006);
- (6) from *T. taenia* by the first pectoral-fin ray not filamentous (vs. filamentous), and distal margin of the addressed pelvic fin not reaching the anus (vs. distal margin reaching the anus) (Eigenmann, 1918).

Description. Morphometric data for type series given in Table 1. Refer to Figs. 1–2 for general external aspects.

TABLE 1. Morphometrics of *Trichomycterus perkoi*. n, number of specimens measured; SD, standard deviation.

Measurement	Holotype	Range	Mean	SD	n
STANDARD LENGTH (mm)	93.5	16.2–99.8	-	-	19
PERCENTS OF STANDARD LENGTH					
Total length	113.4	111.9–117.3	114.9	1.7	19
Predorsal length	65.3	63.1–67.0	65.3	1.1	19
Preanal length	72.7	66.2–72.7	69.2	1.8	19
Prepelvic length	55.1	54.3–59.1	56.1	1.5	19
Caudal peduncle length	24.0	20.5–26.7	22.9	1.6	19
Body depth	14.1	12.4–15.7	14.3	0.8	19
Caudal peduncle depth	10.5	9.3–11.6	10.5	0.6	19
Dorsal-fin base length	9.9	8.3–12.2	11.1	1.1	19
Anal-fin base length	7.5	5.9–9.2	8.0	0.8	19
First pectoral-fin length	10.4	9.6–13.0	11.0	0.9	19
Pectoral width	14.3	13.5–18.0	15.9	1.3	19
Head length	18.0	18.0–23.6	21.1	1.5	19
PERCENTS OF HEAD LENGTH					
Head depth	53.0	44.1–59.1	50.2	3.8	19
Head width	93.0	70.1–94.3	85.9	6.0	19
Interorbital width	26.6	20.2–29.6	25.0	2.8	19
Eye diameter	9.1	8.9–13.3	10.7	1.6	19
Snout length	39.2	30.2–41.4	36.7	2.9	19
Maxillary barbel length	49.9	34.7–55.6	45.9	4.4	19
Rictal barbel length	35.0	34.1–51.6	43.9	5.6	19
Nasal barbel length	47.1	34.8–49.2	39.8	4.4	19
Breadth of mouth	37.2	33.4–42.3	38.1	2.6	19

Body elongate. Dorsal and ventral profiles of trunk ranging from straight to slightly convex; dorsal and ventral profiles of caudal peduncle from straight to slightly concave. Cross section of trunk nearly oval, becoming gradually more compressed posterior to pectoral girdle.



FIGURE 1. *Trichomycterus perkos*, holotype, MCP 46679, 93.5 mm SL; Brazil, Rio Grande do Sul State, Passo Fundo Municipality; Uruguai River basin, Passo Fundo River.



FIGURE 2. Lateral view of presumed juveniles of *Trichomycterus perkos*. (A) Medium-sized paratype, MCP 31776, 43.3 mm SL; (B) second smallest paratype, MCP 31764, 17.9 mm SL. Specimens represented in scale.

Head wide, depressed, trapezoidal in dorsal view. Larger specimens usually with region lateral to eyes swollen by hypertrophied *adductor mandibulae* A2A3 muscles. Dorsal profile of head straight; ventral profile ranging from straight to convex. Eyes on dorsolateral region of head, progressively migrating towards more dorsal position with

specimen growth. Orbital rim not free. Thin and translucent skin covering eye, not adhered to eyeball surface and forming anteroposteriorly elongated ocular capsule. Anterior nostril surrounded by tubular flap continuous with nasal barbel base; posterior nostril opening slightly smaller than anterior one and with crescent thin flap on anterior border.

Mouth subterminal and slightly curved. Lower lip with lateral fleshy lobes posteromedial to rictal-barbel base. Nasal barbel emerging from lateral region of anterior nostril and reaching center of neurocranium. Maxillary and rictal barbels about same size and usually reaching anterior portion of interopercular patch of odontodes. Branchial membranes thick, united to isthmus only anteriorly and forming small free fold across isthmus. Branchiostegal rays modally ten (one among five CS, MS, and XR specimens with nine); medial most rays hardly visualized through skin.

Opercular patch of odontodes rounded and dorsolaterally placed on head; 8–14 conical odontodes. Interopercular patch of odontodes narrow, posteriorly curved, and placed anterior to opercular patch; 11–17 conical odontodes. Odontodes progressively larger and more curved towards posterior region of both opercular and interopercular patches.

Pectoral-fin rays modally I+6 (four among 27 specimens with I+5); first ray not prolonged as a pectoral filament. Pectoral-fin posterior margin convex. Anterior portion of pectoral-fin base covered by branchial membrane. Axillary pore present.

Pelvic-fin rays I+4, thin pelvic splint parallel to first pelvic ray. Pelvic-fin origin anterior to origin of dorsal fin; posterior margin convex. Bases of pelvic fins contacting to each other. Distal margin of adpressed pelvic fin not reaching urogenital and anal openings.

Dorsal-fin rays i–ii+II+7; eight basal radials distributed between neural spines of 20th–21st and 25th–26th post-Weberian vertebrae. Dorsal fin located on posterior half of trunk; origin approximately at vertical through posterior margin of adpressed pelvic fin; posterior margin convex.

Anal-fin rays i–iii+II+5; six basal radials distributed between haemal spines of 22nd–23rd and 26th–27th post-Weberian vertebrae. Anal-fin origin slightly posterior to vertical through dorsal-fin origin; posterior margin convex.

Caudal-fin rays xiv–xvii+I+5 on dorsal lobe and xii–xiv+I+6 on ventral lobe. Caudal-fin posterior margin slightly convex with rounded dorsal and ventral corners. Two upper hypural plates, presumably hypural 3 (ventral) and compound hypural 4+5 (dorsal); single lower hypural plate (compound hypural 1+2) fused to parhypural (de Pinna & Ng, 2004; Lundberg & Baskin, 1969).

First complete haemal arch on seventh–ninth post-Weberian vertebrae; first complete haemal spine on 15th–16th post-Weberian vertebrae. Post-Weberian vertebrae modally 41 (one specimen with 39 and another with 40 among eight CS and XR specimens). Ribs 12–14.

Laterosensory cephalic canals with simple (non-dendritic) tubes ending in single pores. Supraorbital canal mostly into frontal bone with pores s_1 , s_3 and s_6 . Infraorbital canal mostly into soft tissue ventroposterior to eyeball and with branches and pores i_{10} and i_{11} . Otic canal without pores and running through sphenotic-prootic-pterosphenoid. Postotic canal traversing pterotic and posttemporo-supracleithrum, with pores po_1 (= preoperculomandibular of Schaefer & Aquino, 2000) and po_2 (= pterotic of Schaefer & Aquino, 2000) located anterodorsal to opercular patch of odontodes. Short lateral line canal with pores ll_1 and ll_2 positioned dorsoposterior to pectoral-fin base.

Coloration in alcohol. Unpigmented body background pale yellow (Figs. 1, 2). Dark brown melanophores located on inner skin layer and forming three wide body stripes: sagittal, midlateral, and ventrolateral. Sagittal stripe unpaired; midlateral and ventrolateral stripes bilaterally paired. All stripes with notched borders and usually interrupted at some points, thereby occasionally forming few isolated irregular blotches. Stripes borders gradually more notched in larger specimens. Sagittal and midlateral stripes running along entire lengths of trunk and caudal peduncle; sagittal stripe about two times wider than midlateral one. Ventrolateral stripe thinnest and running along posterior part of trunk and caudal peduncle; ventrolateral stripe most often interrupted, sometimes taking form of row of irregular blotches. Dark brown pigmentation from inner tegumentar layer forming highly irregular marks on dorsolateral region of head and small spots on barbel bases. Smallest individuals lacking dark pigmentation on all fins. Median fins and dorsal surface of pectoral fin progressively acquiring increasing number of small spots with specimen growth. Spots on fins also dark brown and located on inner tegumentar layer. Larger individuals (more than 65.8 mm SL), presumably adults, with caudal peduncle and dorsum covered with tiny light brown spots forming a freckled pattern (Fig. 1). Freckled pattern of larger individuals located on outer skin layer and covering part of

dark stripes and blotches of inner tegumentar layer. Ventral surface of head and trunk devoid of dark pigmentation (Figs. 1, 2).

Etymology. From the Greek *perkos* (περκός), meaning “spotted or streaked with black marks (Valpy, 1826: 227), in allusion to the color pattern of the new species formed by either dark stripes (small-sized specimens) or dark stripes combined with small spots (larger individuals). An adjective.

Distribution. A single paratype (MZUSP 82372) is from the Tibaji River basin, a tributary of the Paranapanema River (Fig. 3; see Discussion below). All remaining type series is from two sub-basins of the Uruguai River system, the Ijuí and Passo Fundo drainages (Fig. 3). The Paranapanema is an affluent of the Paraná River, which joins the Uruguai to form the La Plata River/Estuary.

Habitat notes. Ecological data from all localities is unavailable. Most types were collected in clear water streams with 1 to 3 m wide, with bottoms composed of stone, gravel, and sand (Fig. 4). Streamlets were usually surrounded by modified riparian vegetation.

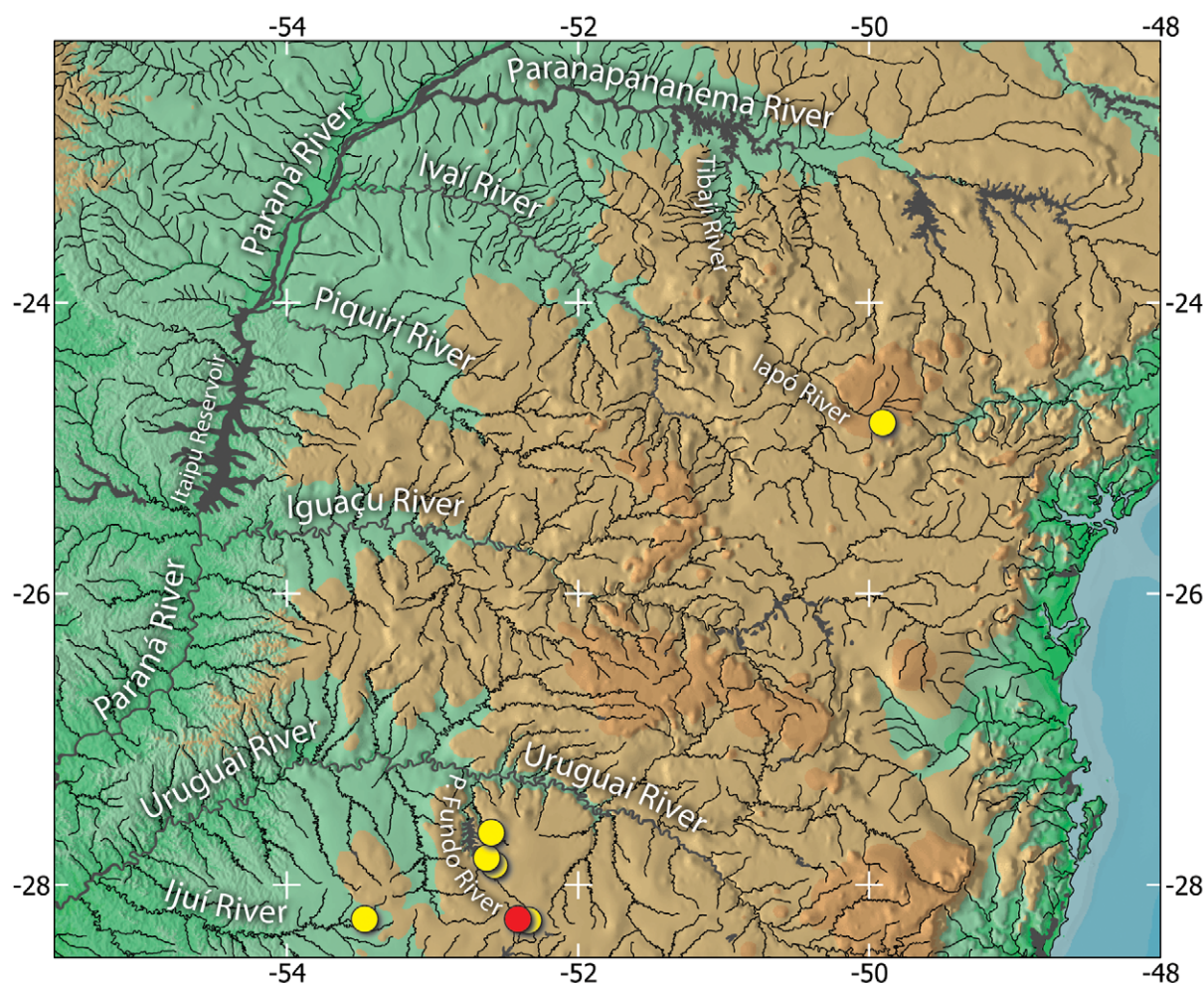


FIGURE 3. Geographic distribution of the *Trichomycterus perkos*. Red circle, holotype; yellow circles, paratypes. Each symbol may represent more than one lot.

Discussion

Taxonomic placement of *Trichomycterus perkos*. The new species is unequivocally placed within the Trichomycteridae since it has all the 11 synapomorphies for the family (Baskin, 1973; Datovo & Bockmann, 2010; de Pinna, 1992a, 1998). The new species also exhibits the 12 synapomorphies for the clade formed by all the trichomycterids except Copionodontinae and Trichogeninae (Bockmann *et al.*, 2004; Datovo & Bockmann, 2010; de Pinna, 1992a, 1998).



FIGURE 4. Type localities of *Trichomycterus perkos*. (A) Unnamed stream tributary of Erechim River, Passo Fundo River basin, São Valentim Municipality, Rio Grande do Sul State (MCP 46701); (B) unnamed stream tributary of Sepultura Streamlet, affluent of reservoir of the Passo Fundo Hydroelectric Power Plant, Campinas do Sul Municipality, Rio Grande do Sul State (MCP 46711).

The placement of *Trichomycterus perkos* within the Trichomycterinae is less obvious, given the current uncertainties about the phyletic status of the subfamily. All the supposed synapomorphies for the Trichomycterinae proposed by Arratia (1990, 1998) are demonstrably invalid (Datovo & Bockmann, 2010), even with the exclusion of “*Trichomycterus*” *hasemani* (Eigenmann) and “*T.*” *johnsoni* (Fowler), which are more closely related to other trichomycterid subfamilies (de Pinna, 1989). Consequently, the Trichomycterinae has been diagnosed by the absence of the synapomorphies for the lineage formed by the more derived trichomycterid subfamilies, the so-called TSVSG clade (composed by the Tridentinae, Stegophilinae, Vandelliinae, Sarcoglanidinae, and Glanapteryginae; Costa & Bockmann, 1993, 1994; Datovo & Bockmann, 2010). Recently, Datovo and Bockmann (2010) discovered a single derived condition shared by all the trichomycterine taxa they examined (their Clade D): the *levator internus 4* muscle (*sensu* Springer & Johnson, 2004) attached to the dorsal surface of the posttemporo-supracleithrum. Nevertheless, Datovo and Bockmann (2010) advertised that, given the enormous diversity of the group, only a more encompassing analysis across the Trichomycterinae could confirm this character as a valid synapomorphy for the entire subfamily. In any event, *T. perkos* lacks the four synapomorphies for the TSVSG clade (Costa & Bockmann, 1993, 1994; Datovo & Bockmann, 2010; de Pinna, 1998) and, at the same time, has the single myological derived condition shared by all trichomycterines examined in Datovo and Bockmann (2010). Consequently, the new species is assigned to the Trichomycterinae.

The Trichomycterinae is currently composed of eight genera: *Bullockia*, *Eremophilus*, *Hatcheria*, *Ituglanis*, *Rhizosomichthys*, *Scleronema*, *Silvinichthys*, and *Trichomycterus*. Among these, only *Trichomycterus* lacks any synapomorphy. The genus is a non-monophyletic assemblage that includes all those species lacking the characters diagnostic for the other trichomycterine genera (Baskin, 1973; Datovo & Bockmann, 2010; de Pinna, 1989, 1998). That is the very situation of the new species herein described, which is accordingly included within *Trichomycterus*.

Identity of *Trichomycterus perkos*. Two specimens of *T. perkos* from the Paranapanema River basin were previously cited in the literature as *Trichomycterus* aff. *itatiayae* (Kantek *et al.*, 2007; Sato *et al.*, 2004; Torres *et al.*, 2004). One of these specimens was catalogued as MZUSP 82372 (Oliveira, pers. comm.) and is herein designated as a paratype of *T. perkos*. All the remaining known specimens of *T. perkos* were collected in tributaries of the Uruguai drainage (Fig. 3). Nevertheless, based on the available data, the lot from the Paranapanema is unequivocally identified as *T. perkos*, since it exhibits the distinctive adult color pattern and all the remaining external morphological characters presented by the specimens from the Uruguai.

Color pattern. As detailed above, the dark marks on the skin of *Trichomycterus perkos* are distributed into two distinct tegumentary layers: a striped pattern in an inner layer and a freckled pattern in an outer layer (Fig. 1). The two pigmentation patterns undergo remarkable ontogenetic changes in *T. perkos*. In smaller individuals, the

stripes of the inner skin layer are well defined, seldom discontinuous, and with less irregular borders (Fig. 2B). As specimens grow, these stripes gradually develop deeper notches at their borders (Fig. 2A). This process ultimately produces a few isolated blotches that, combined with the irregularly bordered stripes, makes the basic striped pattern to be less conspicuous in adults than in juveniles (Fig. 1). A similar process occurs in other *Trichomycterus* which also exhibit conspicuous widened dark stripes, such as *T. itatiayae*, *T. reinhardti*, and *T. pauciradiatus*. In all these species, the larger individuals exhibit highly notched stripes with associated blotches of various sizes, whereas smaller specimens present stripes with straight edges (pers. obs.; Barbosa & Costa, 2008; A. Miranda Ribeiro, 1906). Juveniles of other trichomycterids, such as *Copionodon lianae* Campanario and de Pinna, *C. pecten* de Pinna, *Eremophilus mutisii* Humboldt, *T. chapmani* (Eigenmann), *T. brasiliensis*, *T. mimonha* Costa, *T. potschi* Barbosa and Costa, and *T. rivulatus* Valenciennes, have a narrow midlateral stripe which is completely absent or replaced by a row of blotches in adults (pers. obs.; Barbosa & Costa, 2003; Campanario & de Pinna, 2000; Costa, 1992; de Pinna, 1992a; Eigenmann, 1918). Wosiacki and Oyakawa (2005) also mentioned that the slender midlateral stripe of *T. tupinamba* Wosiacki and Oyakawa is progressively lighter in larger specimens. The conspicuous longitudinal body stripes are considered a disruptive color pattern that breaks up the fish outline (Gottfried, 1989) and, for some reason, this pattern seems to be particularly important for the juveniles of many trichomycterids, such as those referred above.

In *Trichomycterus perkos*, only the presumable adults exhibit the freckled pattern on their outer skin layer (Fig. 1). A superficial freckled pigmentation is also present, at least, in *T. brasiliensis*, *T. castroi*, *T. crassicaudatus*, *T. diabolus*, *T. giganteus*, *T. igobi*, *T. maracaya*, *T. mimonha*, *T. stawiarski*, and *T. tropeiro* (pers. obs.; Bockmann *et al.*, 2004; Bockmann & Sazima, 2004; de Pinna, 1992b; Lima & Costa, 2004; Wosiacki & de Pinna, 2008a, 2008b). However, the precise distribution of the freckled pattern across *Trichomycterus* is unknown, once most species descriptions do not inform whether the dark pigments are distributed into one or two skin layers. Furthermore, the recognition of the two levels of pigmentation is extremely difficult in specimens that have been preserved for a long period of time (we could securely distinguish the two pigmentation layers in *T. mimonha* and *T. tropeiro* only in more recently preserved specimens). In any event, the striped pattern of the inner skin layer of *T. perkos* is relatively rare within the genus, and all the congeners exhibiting a comparable color pattern (*e.g.*, *T. reinhardti*) are readily distinguished from the new species by several other morphological traits (see Diagnosis). Among the *Trichomycterus* with known double-layered pigmentation, only *T. giganteus* also exhibits stripes in the inner skin layer. However, in this species, the sagittal and ventrolateral stripes are absent and the midlateral stripe has straight borders (Lima & Costa, 2004). *Trichomycterus perkos* is further distinguished from *T. giganteus* in having the first pectoral-fin ray not prolonged as a filament (*vs.* ray filamentous), modally seven pectoral-fin rays (*vs.* nine), a pair of epiphyseal pores (s_6) of the supraorbital laterosensory canal (*vs.* a single sagittal s_6 pore), absence of the pores i_1 and i_3 of the infraorbital laterosensory canal (*vs.* i_1 and i_3 present), modally ten branchiostegal rays (*vs.* seven or eight), and modally 41 post-Weberian vertebrae (*vs.* 36-37) (Lima & Costa, 2004).

Phylogenetic inferences. The enormous diversity of *Trichomycterus*, its highly problematic taxonomy, and the non-monophyly of the genus hamper most attempts to unambiguously delimit monophyletic lineages within the group. Despite these difficulties, Wosiacki and de Pinna (2008a, 2008b) were able to posit some tenable phylogenetic inferences involving a small group of species from the Iguazu River drainage (Fig. 3). According to these authors, *T. crassicaudatus*, *T. igobi*, and *T. stawiarski* would form a monophyletic group on the basis of the sharing of three derived character states: (1) possession of ten or 11 branchiostegal rays (*vs.* nine or less); (2) procurrent caudal rays thickly ossified, forming a rigid spinous structure (*vs.* procurrent rays thin and flexible); and (3) dorsal procurrent caudal rays extending anteriorly over the tips of the ten last neural spines (*vs.* procurrent rays extending over nine or less neural spines). We confirmed the validity of the characters of Wosiacki and de Pinna (2008a, 2008b) among the comparative material we examined and found that *T. perkos* presents the first character—modally ten branchiostegal rays—but lacks the two latter. Consequently, *T. perkos* is herein proposed as the sister-taxon of the clade formed by *T. crassicaudatus*, *T. igobi*, and *T. stawiarski* (Fig. 5). Since the pertinent osteological data from all other species of *Trichomycterus* is currently unavailable, this phylogenetic hypothesis is evidently tentative.

Trichomycterus davisi is a species that inhabits both Paranapanema and Iguazu River basins and lacks all the three characters of Wosiacki and de Pinna (2008a, 2008b) commented above (pers. obs.). In Datovo and Bockmann (2010), this species was grouped with *T. stawiarski* on the basis of an *extensor tentaculi* muscle originating on both suspensorium and neurocranium (*vs.* suspensorium only). This myological character is absent in *T. perkos* and

could not be verified in *T. crassicaudatus* and *T. igobi* (unavailable specimens for muscle dissection). Consequently, the origin of the *extensor tentaculi* on the suspensorium is ambiguously optimized across these species. Regardless of the possible distribution of this myological character in these taxa, the osteological derived features of Wosiacki and de Pinna (2008a, 2008b) more parsimoniously support *T. stawiarski* as closer to *T. crassicaudatus* and *T. igobi* than to *T. davisi*.

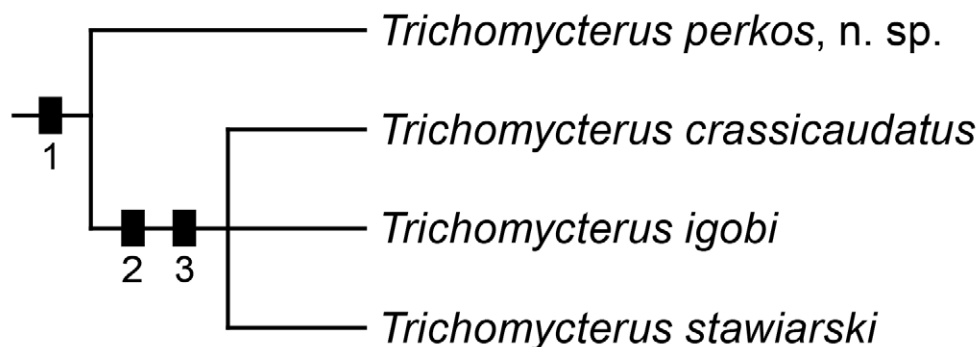


FIGURE 5. Inferred phylogenetic relationships of *Trichomycterus perkos* and related congeners. Characters (from Wosiacki & de Pinna, 2008a, 2008b) numbered as in Discussion.

Comparative material. *Trichomycterus brasiliensis*: LIRP 1968, 15 (2 CS); MZUSP 37145, 105; MZUSP 109365, 1; MZUSP 109433, 2. *T. castroi*: MZUSP 94954, 2 (2 XR). *T. crassicaudatus*: MZUSP 88518, holotype; MZUSP 94958, 1 (XR); MZUSP 94959, 1. *T. davisi*: LIRP 2799, 34 (3 CS); MZUSP 81039, 1 (XR); MZUSP 81041, 1 (XR); MZUSP 81045, 3. *T. diabolus*: MZUSP 78860, holotype; LIRP 1128, 21 paratypes; LIRP 3456, 9 paratypes (2 CS). *T. giganteus*: MCP 35028, 3 paratypes. *T. igobi*: MZUSP 94842, 2 paratypes (2 XR); MZUSP 94843, 3 paratypes; MZUSP 94960, 1 (XR). *T. maracaya*: MCP 34575, 2 paratypes. *T. mimonha*: MZUSP 43343, holotype; MZUSP 43344, 7 paratypes; MZUSP 107372, 1. *T. pauciradiatus*: MNRJ 17057, 17 (3 CS). *T. potschi*: MCP 29061, holotype. *T. reinhardti*: MZUSP 90850, 2; MZUSP 107365, 4; MZUSP 109371, 3; MZUSP 109431, 5. *T. stawiarski*: LIRP 5088, 10 (1CS); MZUSP 94835, 2; MZUSP 94836, 2; MZUSP 94837, 2; MZUSP 94838, 1. *T. tupinamba*: MZUSP 61686, 2. Additional trichomycterid comparative material listed in Datovo and Bockmann (2010) and Ferrer and Malabarba (2011).

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