A New Species of the Neotropical Catfish Genus *Trichomycterus* (Siluriformes: Trichomycteridae) Representing a New Body Shape for the Family

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Trichomycterus crassicaudatus **is described as a new species from the Rio Iguaçu basin in southern Brazil. The new species has an exceptionally deep posterior region of the body (caudal peduncle depth 22.8–25.4% SL), resulting in an overall shape which distinguishes it at once from all other members of the Trichomycteridae. The caudal fin of the species is broad-based and forked, a shape also distinguishing it from all other species in the family. A number of autapomorphic modifications of *T. crassicaudatus* are associated with the deepening of the caudal region, including an elongation of the hemal and neural spines of the vertebrae at the middle of the caudal peduncle. Phylogenetic relationships of the new species are yet unresolved, but it shares a similar color pattern and a thickening of caudal-fin procurrent rays with *T. stawiarski*, a poorly-known species also from the Rio Iguaçu basin. Coloration and body shape also include similarities with *T. lewi* from Venezuela.**

THE genus *Trichomycterus* is the largest in the family Trichomycteridae, with approximately 100 nominal species and probably numerous others still undescribed. The genus is not demonstrably a monophyletic group (de Pinna, 1998), and its latest taxonomic revision is almost 90 years old (Eigenmann, 1918). Despite basic taxonomic problems, new species of *Trichomycterus* are often described (Bockmann et al., 2004; Wosiacki and Garavello, 2004; Fernández and Schaefer, 2005), a task which is often complicated by myriad nomenclatural problems related with already-named yet incompletely-diagnosed forms.

Some species assignable to *Trichomycterus*, however, are so distinctive that they can be easily diagnosed from all other species by one or more clearly defined characters, without the need for wide-ranging revisionary studies or fine-scale population analyses. Such is the case reported in the present paper.

Herein, we describe a new species from the Rio Iguaçu drainage in Brazil with a remarkable set of characteristics which set it apart from all other currently known species of *Trichomycterus*. In external aspect, this is perhaps the most distinct species of the genus yet found and represents a body shape previously unknown for trichomycterids. Such a unique condition is mostly a result of the pronounced expansion of the caudal peduncle and caudal fin, which are associated with a host of modifications in internal anatomy. Under traditional concepts of trichomycterid taxonomy, such major phenetic divergence might indicate a separate genus for our new species. However, as discussed below, inclusion of the new species in *Trichomycterus* seems to be the most sensible action at the moment. The striking aspect of the present new species is a result of autapomorphic modifications only, and does not reflect a special position in trichomycterid phylogeny.

The new species comes from the Rio Iguaçu Basin, which drains a large area of southern Brazil and Argentina. This is the ninth species of *Trichomycterus* recorded for the Rio Iguaçu Basin above the Iguaçu waterfalls (the others being *T. stawiarski*, *T. castroi*, *T. naipi*, *T. papilliferus*, *T. mboycy*, *T. taroba*, *T. plumbeus*, and *T. davisi*, the latter also occurring in the Rio Ribeira de Iguape Basin).

MATERIALS AND METHODS

All measurements were taken point-to-point with calipers on the left side of specimens. Caudal-peduncle length was measured from the last anal-fin ray base to the middle of the caudal-fin base; caudal-peduncle depth was taken at the vertical through the middle of its length; distance between pelvic-fin base and anus was measured from the base of the inner pelvic-fin ray and anterior margin of the anus; supraorbital pore distance was the distance between contralateral S6 pores; mouth width was measured between internal corners of mouth. Other measurements followed Tchernavin (1944). Dorsal and anal-fin ray counts included all branched rays plus all unbranched rays visible in transmitted light. The numbering of pores of the supra- and infraorbital sensory canals followed Arratia and Huaquin (1995).

Osteological observations were made on specimens cleared and counterstained (CS) for cartilage and bone according to a modified version of the method of Dingerkus and Uhler (1977). Radiographs of specimens were prepared with a Faxitron digital x-ray system, model MX-20. The Weberian complex and compound caudal centrum were not included in vertebral counts. Numbers of vertebrae and pleural ribs were taken from cleared and stained preparations and radiographs of alcoholic specimens.

Institutional abbreviations follow Leviton et al. (1985), with the addition of NUP, Núcleo de Pesquisa em Limnologia, Ictiologia e Aqüicultura, Maringá, Brazil; and MHNCI, Museu de História Natural "Capão da Imbuia," Curitiba, Brazil.

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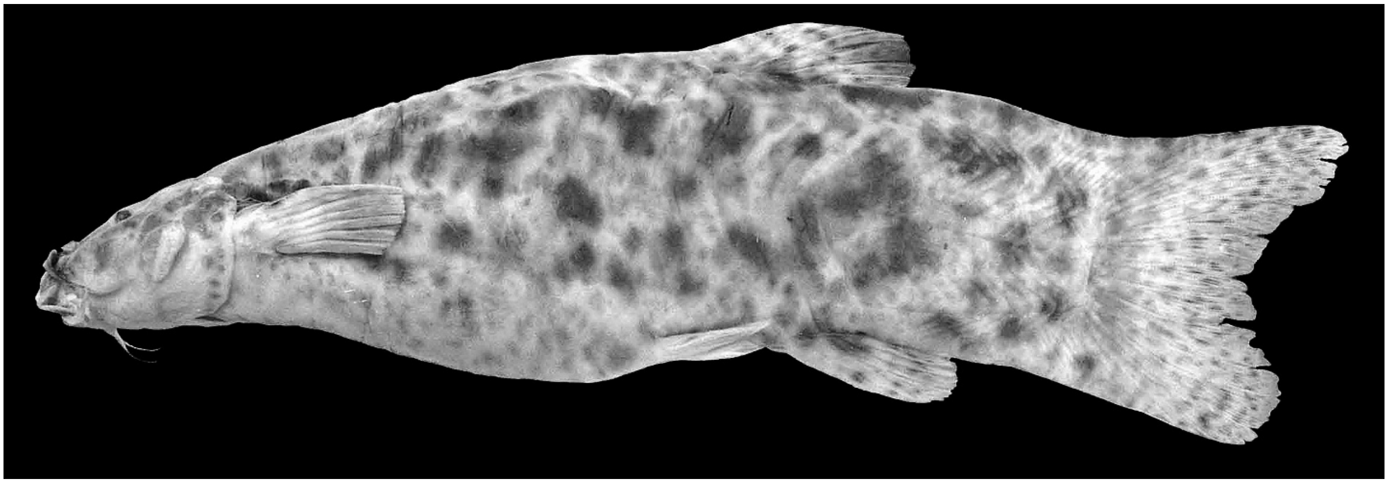

Fig. 1. *Trichomycterus crassicaudatus*, holotype, MZUSP 88518, 108.8 mm SL, left lateral view.

***Trichomycterus crassicaudatus*, new species**
Figures 1, 2; Table 1

Holotype.—MZUSP 88518, 108.8 mm SL, Brazil, Estado do Paraná, Rio Jordão at Município de Foz do Jordão, near border with Município de Reserva do Iguaçu, 28 May 1996, NUP team.

Paratypes.—MZUSP 88519, 105.6 mm SL, and MPEG 7931, 113 mm SL, same locality and collectors as holotype, 29 July 1996; MZUSP 88517, 2, 110.9–121.3 mm SL; MHNCI 7908, 105.2 mm SL, stained disarticulated skeleton, Brazil, Estado do Paraná, Município de Candoi, Rio Jordão, ca. 2 km upstream from mouth on Rio Iguaçu, 20 Oct. 1991, W. B. Wosiacki, E. S. Grando, and A. C. Carrillo; MPEG 13057, 34.1 mm SL, and MPEG 13058, 56.6 mm SL, Brazil, Estado do Paraná, município de Candói, Rio Jordão, Rio Iguaçu Basin, no date, NUP team.

Non-type material.—NUP 3783, 3, 78.6–134.5 mm SL, Brazil, Estado do Paraná, Rio Jordão above the hidroelectric dam of Santa Clara, Município de Candoi, Pinhão, April 2005, NUP team; NUP 4006, 3, 107.5–114.3 mm SL, same data as NUP 3783.

Diagnosis.—*Trichomycterus crassicaudatus*, new species, is distinguished from all other species in the Trichomycteridae by the deep posterior region of the body, including the caudal peduncle and caudal fin (caudal-peduncle depth 22.8–25.4% SL in adults). *Trichomycterus crassicaudatus* also differs from all congeners by the shape of the caudal fin in adults, in which the fin is prolonged into long, markedly diverging and somewhat irregular lobes forming a concave posterior margin. In other species of *Trichomycterus*, the caudal fin is either truncate, emarginate, or round. Another characteristic which sets *T. crassicaudatus* apart from all other congeners and possibly all other trichomycterids is the pronounced elongation of the neural and hemal spines of the caudal vertebrae along the mid-portion of the caudal peduncle (see Discussion). *Trichomycterus crassicaudatus* is further distinguished from all other trichomycterids, except *T. stawiarski*, by its thicky-ossified and rigid procurrent caudal-fin rays, markedly distinct from the flexible and splint-like procurrent rays in other trichomycterids. The coloration pattern of *T. crassicaudatus*, composed of closely-set large irregular blotches overlain by a more superficial layer of small round markings, distinguishes it from the majority of other species currently in *Trichomycterus*, but not *T. stawiarski*. Other characteristics which could not be checked in all species of Trichomycteridae but which may be useful to identify *T. crassicaudatus* include the urohyal foramen reduced to a slender canal and the presence of 5–7 lateral line pores (figures overlapping with those in *Bullockia maldonadoi* and *Hatcheria macraei*).

Description.—Morphometric data for the holotype and paratypes given in Table 1. Body elongate, cylindrical at pectoral girdle, gradually becoming compressed along trunk and caudal peduncle until caudal-fin base. Ventral and dorsal profiles of body slightly convex and straight along caudal peduncle. Dorsal-fin base situated in a depression of dorsal profile of body (Fig. 1).

Integument thick, especially over base of dorsal, anal, and pectoral fins. Small papillae present over body, visible only under stereomicroscope. Larger papillae over lips and mental region.

Head broad, slightly longer than wide, ellipsoid in transverse section at level of eyes (Fig. 2). Dorsal profile of head straight or slightly convex, ventral profile straight. Head triangular in dorsal view. Snout slightly rounded in dorsal view. Interorbital region flat. Lateral region of head swollen by well-developed jaw muscles in contact with margin of eye. Eye small, round, dorso-laterally oriented, anterior and posterior margin equidistant from those of contra lateral eye. Orbital rim not free. Skin covering eye thin and transparent, distinctly separate from surface of eyeball. Anterior nostril smaller than eye and larger than posterior nostril. Anterior nostril surrounded by fleshy flap of integument, posterolaterally continuous with nasal barbel. Posterior nostril partially surrounded anteriorly, laterally and medially by thin but long flap of skin. Branchial membranes thick, united to isthmus anteriorly. Gill opening wide. Eight or nine branchiostegal rays, covered with thick skin. Mouth subterminal, with corners posterolateraly oriented. Upper and lower lips thick, upper lip more so anteriorly; both lips covered with conspicuous papillae. Lower lip with large fleshy lobes, medial to origin of rictal barbels.

All barbels with wide flat bases; gradually narrowing distally. Nasal barbel thick and moderately long, reaching

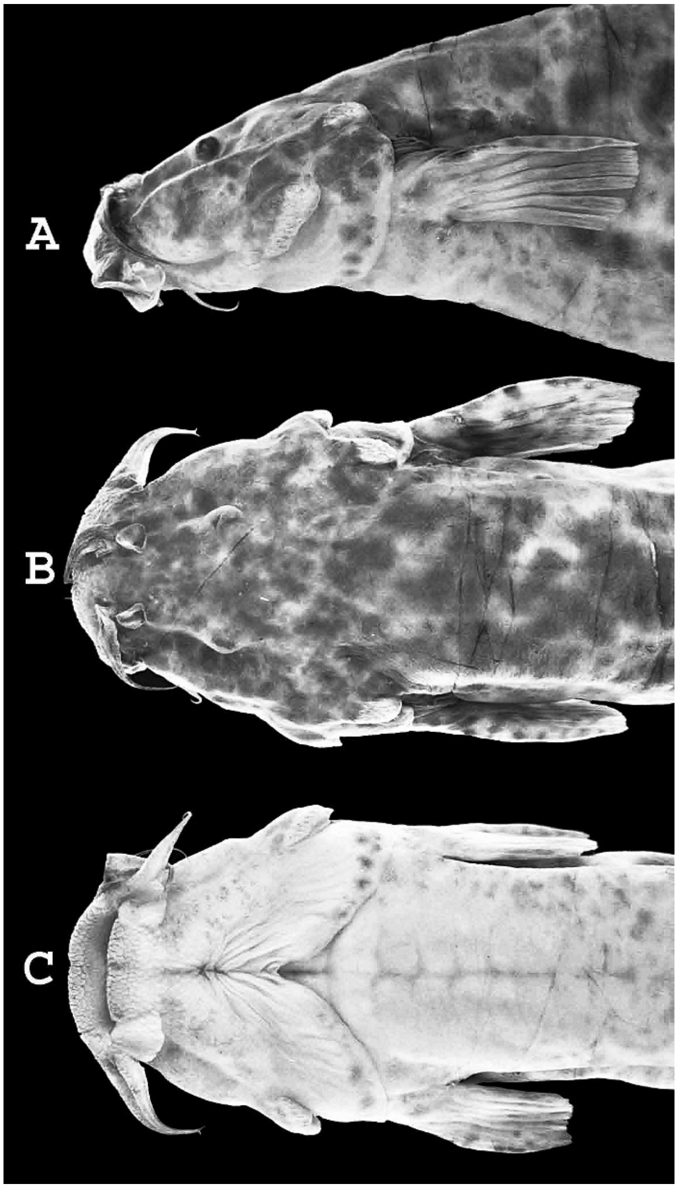

Fig. 2. Head of *Trichomycterus crassicaudatus*, holotype, MZUSP 88518, 108.8 mm SL: (A) Lateral view; (B) dorsal view; (C) ventral view.

beyond posterior margin of eye. Origin of nasal barbel on posterolateral portion of integument flap around anterior nostril. Maxillary and rictal barbels thick and short, both reaching to or slightly beyond vertical through posterior margin of eye. Pectoral fin wide, with i+7 rays and gently convex distal margin; first and second rays longest; first one (unbranched) thick, not prolonged as filament. Dorsal fin with iv+8 rays (three anterior ones vestigial, and visible only in radiographs), second and third branched rays longest. Anal fin with iv+6 rays (three anterior ones vestigial, and visible only in radiographs) as long as dorsal fin; base of first anal-fin ray at vertical through base of seventh dorsal-fin ray, second and third longest. Pelvic fin with i+4 rays, first and second rays longest; its base anterior to vertical through dorsal-fin origin; tip of fin reaching urogenital opening. In adult specimens, caudal fin forked with dorsal lobe longer, both lobes with round tips; juvenile specimens (56.6 mm SL and under) with truncate or emarginate caudal fin; 6/7 principal caudal-fin rays. Procurrent caudal-fin rays 24–26 dorsally (holotype 25) and 17 or 18 ventrally (holotype 17).

Table 1. Morphometric Data from *Trichomycterus crassicaudatus*, New Species. 1. SL is in mm. Measurements 2 to 15 expressed as proportion of SL and 16 to 24 as proportions of HL. $n = 6$.

		Holotype	Min.	Max.	Mean
1.	Standard length (SL; mm)	108.8			
2.	Head length (HL)	23.7	21.4	23.8	23.0
3.	Predorsal length	66.7	61.7	68.8	66.8
4.	Prepelvic length	60.4	56.4	62.3	60.0
5.	Preanal length	70.3	70.3	75.4	73.0
6.	Scapular girdle width	19.7	16.9	19.7	18.6
7.	Trunk length	39.1	36.3	43.9	39.2
8.	Pectoral-fin length	15.4	10.8	15.4	13.8
9.	Pelvic-fin length	10.3	9.0	10.3	9.6
10.	Distance between pelvic-fin base and anus	6.6	5.8	9.3	7.1
11.	Caudal peduncle length	22.6	17.4	22.6	19.4
12.	Caudal peduncle depth	24.2	22.8	25.4	24.2
13.	Body depth	29.8	24.8	29.8	26.8
14.	Dorsal-fin length	13.6	10.0	13.6	11.9
15.	Anal-fin length	8.1	6.7	10.0	8.2
16.	Head width	95.3	84.7	95.3	90.5
17.	Nasal barbel length	36.4	33.1	42.5	36.8
18.	Maxillary barbel length	40.7	27.7	40.7	33.3
19.	Rictal barbel length	40.7	25.4	40.7	34.5
20.	Snout length	55.0	43.9	55.0	48.4
21.	Interorbital	31.4	22.1	31.4	26.1
22.	Mouth width	32.9	30.3	37.5	33.6
23.	Eye diameter	8.5	8.0	9.7	8.9
24.	Supra-orbital pore distance	6.2	5.7	8.5	7.2

Opercular patch of odontodes small, with 15 or 16 short, thin, straight odontodes with thickened tips. Interopercular patch with 19–22 short, thin, conic, and straight odontodes arranged in two irregular series (12+10).

Cephalic sensory canals including complete supraorbital canal and incomplete infraorbital canal. Infraorbital restricted to posterior region corresponding to pores i10 and i11. Supraorbital pores S1, S3, and S6. Two paired pores S6. Laterosensory canal reduced on trunk, comprising four to seven lateral-line pores, fourth pore at vertical through middle of pectoral fin.

Free vertebra 35 or 36 (holotype 35). Ribs 11 pairs, first thickest, ninth and tenth longest, in some specimens an extra rudimentary rib posteriorly. Dorsal-fin pterygiophores eight, first one inserting anterior to neural spine of 15th to 17th free vertebra (holotype 16th). Anal pterygiophores six, first one anterior to hemal spine of 19th to 21st free vertebra (holotype 20th). Two separate hypurals on upper hypural plate; parahypural and hypurals one and two fused on lower plate.

Color pattern in ethanol.—Dark pigmentation on body clearly disposed in distinct and overlapping layers of integument. Deep layer composed of several large dark spots of variable size and irregular shapes, more concentrated on dorsum of trunk; spots gradually becoming more scattered and smaller on sides and absent on ventral part of abdomen and head. Superficial layer with small rounded spots forming a uniform freckle over sides and dorsum of body, more concentrated on dorsum of trunk. Deep-layer spots, smaller than those on body, entering dorsal head region, more concentrated on occipital and interorbital region. Lateral surface of head with small spots irregularly distributed, slightly lighter than dorsal region. Odontode areas in both opercle and interopercle white, in stark contrast to remainder of head. Upper lip with uniform gray covering. Lower lip without dark pigment. Dorsal fin with spots over fin rays, most dense at base and along anterior edge of fin and fading gradually to margin. In some specimens, spots on dorsal fin arranged as faint stripe across middle of fin. Pigmentation of anal fin similar to that of dorsal fin, but lighter. Pectoral fin with irregular dark covering over basal portion of dorsal surface, fading gradually distally. Pelvic fin with sparse spots, mainly along anterior edge. Caudal fin uniformly covered with small dark spots, in some specimens roughly arranged in one or more irregular vertical lines. Nasal barbel with both surfaces darkly-pigmented. Maxillary and rictal barbels dark dorsally, more markedly so in former, and white ventrally.

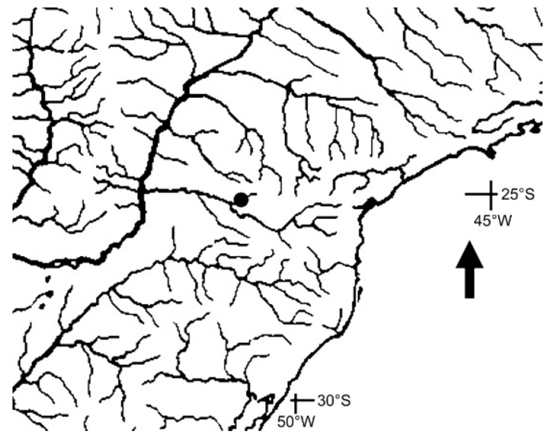

Fig. 3. Map of southern Brazil showing the type locality of *Trichomycterus crassicaudatus*, new species. Black circle represents type locality and more sites.

Habitat.—The Rio Iguaçu Basin (Fig. 3) drains an area of 72,000 km^2 in Brazil and Argentina (Maack, 1981) with an extensive waterfall section starting 22 km upstream from its mouth, composing a complex of over 200 cataracts, the largest being 72 m high, but with several others in the 30 and 40 m range (Maack, 1981). The waterfalls constitute an efficient geographic barrier for all species of fishes inhabiting the basin, and are associated with a high degree of endemism above the falls (F. A. Sampaio, pers. comm.).

Some of the paratypes of *T. crassicaudatus* were collected by WBW from a tributary of the Rio Iguaçu, Rio Jordão, around two kilometers upstream from its mouth. The river at that point is 100 m wide and maximally 2 m deep. The substrate is composed of angular basaltic rocks and pebble. The site is now submerged by an artificial dam. Those three specimens were trapped at the upper part of a gill net in a sector of the river with strong current and 1.2 m depth. The presence of *Trichomycterus* species in fast-running water is common (Arratia, 1983; pers. obs.), but the specimens are usually found near the substrate, between boulders and pebbles, protected from the strong current. None of the collections so far allow a definite determination of water depth and microhabitat preference of *T. crassicaudatus*. The peculiar caudal morphology of the species may be associated with some form of pelagic habit, but that still requires further information.

Etymology.—The specific epithet is from the Latin *crassus*, meaning thick, *cauda*, for tail, and *atus*, to posses. In allusion to the deep caudal peduncle.

DISCUSSION

Within the subfamily Trichomycterinae, the only other taxon which compares with *Trichomycterus crassicaudatus* in phenotypic divergence of external aspect is *Rhizosomichthys totae*, from Colombia. Under traditional concepts of trichomycterid taxonomy, such major phenetic divergence might indicate a separate genus for our new species, as was the case with the monotypic *Rhizosomichthys*. However, preliminary phylogenetic considerations discussed below indicate that such a move would be unjustified. The peculiar aspect of *T. crassicaudatus* is a result of autapomorphic divergence only, and the species seems to be phylogenetically nested within a group of species currently in the genus *Trichomycterus*.

The character combination displayed by *T. crassicaudatus* indicates clearly that the species is neither a basal (Trichogeninae, Copionodontinae) nor a distal (Glanapteryginae, Sarcoglanidinae, Tridentinae, Stegophilinae and Vandelliinae) trichomycterid, and such components of relationships can be confidently excluded from consideration on the basis of a straight reading of character evidence available in the literature (de Pinna, 1998). *Trichomycterus crassicaudatus*, therefore, fits the Trichomycterinae, a large phylogenetically-intermediate assemblage of doubtful monophyly. Therein, *T. crassicaudatus* also lacks the known synapomorphies for each of *Bullockia*, *Eremophilus*, *Hatcheria*, *Ituglanis*, *Scleronema*, and *Silvinichthys* proposed by Arratia (1990, 1998), Costa and Bockmann (1993), and Fernández and de Pinna (2005). With those possibilities excluded, the new species is therefore assigned to the large waste-basket genus *Trichomycterus*, again an assemblage of questionable monophyly. Such positioning is not entirely satisfactory and is an unavoidable result of current lack of resolution in the relevant portion of the trichomycterid tree. However, inclusion of the new species in *Trichomycterus* is presently the best possible one, and any alternative generic placement will require further knowledge on trichomycterine phylogeny. Within *Trichomycterus*, the position of *T. crassicaudatus* can at present only be speculated on the basis of a few potentially informative characters. Its color pattern, composed of large dark blotches with a markedly irregular shape, is very similar if not identical, to that of another endemic to the Rio Iguaçu, *T. stawiarski*. The two species also share a thickening of the procurrent rays of the caudal fin, where those structures are rigid and spine-like. This contrasts with the putatively plesiomorphic condition in trichomycterids which is to have thin, splint-like flexible procurrent rays, present in the majority of species in the family, as well as in Nematogenyidae. The color pattern in *T. crassicaudatus* also superficially resembles the condition seen in *T. lewi*, described a few years ago from the Rio Kukenán, Orinoco drainage, Guyana shield in Venezuela (Lasso and Provenzano, 2002). However, in *T. lewi* the large dark blotches on the body are round and with well-defined borders, different from the irregular-shaped and poorly-defined ones in *T. crassicaudatus* and *T. stawiarski*. *Trichomycterus lewi* also seems to have the deepest caudal peduncle in *Trichomycterus* other than for *T. crassicaudatus* (see fig. 7 in Lasso and Provenzano, 2002). The precise meaning of such observations, however, is still uncertain and a resolution of the phylogenetic position of *T. crassicaudatus* will have to await an extensive phylogenetic analysis including most other species currently included in *Trichomycterus*. Likewise, we cannot at this time be conclusive as to the possible inclusion of the species in the so called *Trichomycterus brasiliensis* species-complex originally proposed by Costa (1992) and later discussed by Barbosa and Costa (2003) and Bockmann and Sazima (2004). While the character variation recorded in association with the recognition of the *Trichomycterus brasiliensis* species-complex is certainly real, much work remains to be done on determining states of the relevant characters among the several poorly-known species in the genus from throughout South America. In any event, *Trichomycterus crassicaudatus* has two of the four characters considered as valid evidence for the monophyly of the *Trichomycterus brasiliensis* species-complex by Bockmann and Sazima (2004), the close proximity of the pelvic-fin bases, and an integumentary color pattern formed by dark pigmentation distinctly arranged in two different layers of integument, a condition previously observed by de Pinna (1992) in *T. castroi*.

The peculiar body shape of *Trichomycterus crassicaudatus* includes evident autapomorphic modifications of the species. The depth of its caudal peduncle is the most extreme in trichomycterids and the anatomical modifications associated with it include an elongation of the neural and hemal spines of the caudal vertebrae at the mid-portion of the caudal peduncle. The length of hemal and neural spines markedly increases posterior to the last anal and dorsal pterygiophores, respectively, and then shorten again gradually towards the caudal fin. The longest hemal spines are those associated with preural vertebrae 9 to 11 and the longest neural ones are on preural vertebrae 10 to 13. In both series, the longest spines are approximately 33% longer than those immediately posterior to the last pterygiophore. Also related to the deepening of the caudal peduncle region is the marked posterior increase in length of the procurrent caudal-fin rays (Fig. 4). Both traits, at least to such a degree, are unique in Trichomycteridae. The shape of the caudal fin in *T. crassicaudatus* provides another autapomorphy for the species. A forked caudal fin is not present in any other species of *Trichomycterus* and is derived within trichomycterids, since most basal members of the family, Trichogeninae and Copionodontinae, as well as in the Nematogenyidae, have truncate, round or emarginate caudal fins. Although forked caudal fins also occur in a few species of other, distantly-related, trichomycterid subfamilies such as Stegophilinae (*Pareiodon microps*, *Parastegophilus maculatus*, *Henonemus taxistigmus*, *H. punctatus*, *H. macrops* and *Pseudostegophilus* spp.) and Vandelliinae (*Vandellia wieneri*), in none of those the morphological similarity to *T. crassicaudatus* goes beyond the mere bifurcation. The forked caudal fin in *T. crassicaudatus* is unique in the broad marginal concavity that separates the upper and lower lobes. Juveniles of the species have a truncate or emarginate caudal fin, which further corroborates the apomorphic condition of the fin morphology in adults.

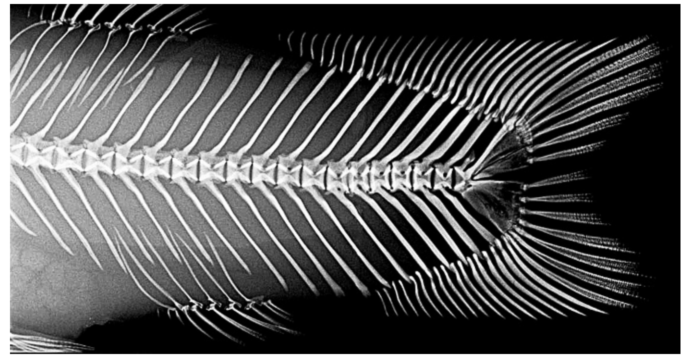

Fig. 4. Radiograph of the left lateral view of the caudal peduncle of *Trichomycterus crassicaudatus*, holotype, MZUSP 88518, 108.8 mm SL.

MATERIAL EXAMINED

Nematogenyidae. *Nematogenys inermis*, UFRGS 3955, 1 CS. Trichomycteridae. Copionodontinae: *Copionodon pecten*, MZUSP 42462, 10, 3 CS; *Glaphyropoma rodriguesi*, MZUSP 42466, 3, 1 CS. Trichogeninae: *Trichogenes longipinnis*, MZUSP 63478, 3 CS. Trichomycterinae: *Bullockia maldonadoi*, MZUSP 36958, 1 CS; *Eremophilus mutisii*, MZUSP 35409, 1 CS, AMNH 56092, 1 CS; *E. candidus* (paratypes), MZUSP 11762, 5, 2 CS; *Hatcheria macraei*, MZUSP 35687, 2 CS; *Ituglanis proops*, MZUSP 36502, 7, MZUSP 46902, 2, MZUSP 39027, 2; *Ituglanis* sp., MNRJ 11489, 13, 5 CS; *Scleronema minutum*, MCP 11169, 13 CS; *S. operculatum*, MCP 9315, 1 CS; *T. brasiliensis*, MPEG 13153, 12, 2 CS; *T. castroi*, MHNCI 7881, 1 CS, MHNCI 7643, 1; *T. davisi*, MCP 10646, 2 CS, MZUSP 38783, 34; *T. iheringi*, MHNCI 7916, 8, 1 CS; *T. mboycy*, MPEG 6695, holotype; *T. mimonha*, MZUSP 34344, 4, MCP 18021, 5; *T. naipi*, MPEG 6699, holotype, MZUSP 38788, paratypes, 2; *T. nigricans*, MCP 10649, 1 CS; *T. papilliferus*, MPEG 6692, holotype; *T. plumbeus*, MPEG 6686, holotype; *T. rivulatus*, ROM 403409, 6, 1 CS; *T. stawiarski*, MZUSP 94835, 2, MZUSP 94836, 2, MZUSP 94837, 2; *T. taroba*, MPEG 6689, holotype.

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