

# A new genus and species of miniature tridentine catfish from the Amazon basin (Siluriformes: Trichomycteridae)

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A new miniature tridentine catfish is described from the rio Purus drainage, Amazon basin, Brazil. It differs from all other tridentines in having several unique autapomorphies: conspicuous anteromedial protuberance in the snout; set of symphyseal premaxillary and dentary teeth inclined posteromedially; distal process of the hyomandibula directed anteriorly; rod-like orbitosphenoid ossified only ventral to the optic nerve; mesethmoid cornua inclined ventrolaterally; opercular and interopercular odontophores separated by a large interspace; basipterygia fused sagittally; and conspicuous dark brown horizontal stripe in the middle of the caudal fin. The new taxon is hypothesized to be sister to the clade formed by *Tridensimilis* and *Tridens*. A detailed osteological description of the new taxon is provided based on X-ray microcomputed tomography ( $\mu$ CT-scans) data and on cleared and stained specimens. Our analysis also reveals that “*Tridens*” *brevis*, an enigmatic species that has been indecisively assigned to three different tridentine genera over the past 134 years, belongs to *Tridentopsis*. Consequently, *Tridensimilis* is a monotypic genus that currently includes only *T. venezuelae*.

**Keywords:** Freshwater, Loricarioidei, Ostariophysi, Systematics, Taxonomy.



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Um novo bagre tridentíneo miniatura é descrito para a drenagem do rio Purus, bacia Amazônica, Brasil. Ele difere de todos os outros tridentíneos por possuir diversas autapomorfias únicas: conspícua protuberância anteromedial no focinho; série de dentes sinfiseanos no pré-maxilar e dentário inclinados posteromedialmente; processo distal do hiomandibular direcionado anteriormente; órbito-esfenoide em forma de haste ossificado apenas ventralmente ao nervo óptico; cornua do mesetmoide inclinadas ventrolateralmente; odontodóforos operculares e interoperculares separados por um amplo espaço; basipterígio fundidos sagitalmente; e faixa escura horizontal conspícua ao longo da região mediana da nadadeira caudal. O novo táxon é proposto como grupo irmão do clado formado por *Tridensimilis* e *Tridens*. Uma descrição osteológica detalhada do novo táxon é fornecida baseada em dados de microtomografia computadorizada ( $\mu$ CT-scans) e em espécimes diafanizados e corados. Nossa análise também revela que “*Tridens*” *brevis*, uma espécie enigmática que tem sido indecisa alocada em três gêneros diferentes de tridentíneos nos últimos 134 anos, pertence a *Tridentopsis*. Consequentemente, *Tridensimilis* é um gênero monotípico que atualmente inclui apenas *T. venezuelae*.

**Palavras-chave:** Água doce, Loricarioidei, Ostariophysi, Sistemática, Taxonomia.

## INTRODUCTION

Tridentinae is a subfamily of Trichomycteridae originally created by Eigenmann (1918) to include three species: *Miuroglanis platycephalus* Eigenmann & Eigenmann, 1889, *Tridens melanops* Eigenmann & Eigenmann, 1889, and “*Tridens*” *brevis* (Eigenmann & Eigenmann, 1889) (= *Tridentopsis brevis*; Myers, 1925; Baskin, 1973; present study, see Discussion). Most classifications currently recognize four tridentine genera (*Miuroglanis* Eigenmann & Eigenmann, 1889, *Tridens* Eigenmann & Eigenmann, 1889, *Tridentopsis* Myers, 1925, and *Tridensimilis* Schultz, 1944) and nine species (Ochoa *et al.*, 2020; Henschel *et al.*, 2023). The monophyly of this group has been corroborated by both morphological and molecular evidence (Baskin, 1973; de Pinna, 1998; DoNascimento, 2013; Ochoa *et al.*, 2017, 2020). *Potamoglanis* Henschel, Mattos, Katz & Costa, 2017 (formerly “*Trichomycterus*” *hasemani* group) was included in Tridentinae by Henschel *et al.* (2017), but this hypothesis has not been corroborated by any subsequent study (see Discussion).

So far, Tridentinae includes only miniaturized species (*sensu* Weitzman, Vari, 1988) distributed in the Amazon, Orinoco, and Paraguay river basins. Members of the subfamily exhibit several typical paedomorphic features, such as a poorly ossified cranial roof, poorly developed lateral-line canals, and the presence in adults of fully cartilaginous skeletal elements that are typically found only in larval or juvenile stages.

Despite the increasing number of descriptions of new freshwater fishes in the Neotropical region, the diversity of miniature fishes is still poorly known. This is due to several factors, including the difficulty of sampling this type of fauna using standard collection methods and, sometimes, the misidentification of specimens as

juveniles of other taxa. Tridentine taxonomy has been characterized by long hiatuses of decades without the addition of new taxa (apart from the controversial allocation of *Potamoglanis*, see Discussion). A few years ago, de Pinna (2016) stated that “[w]ithout a doubt, the trichomycterid subfamily where the least progress was made [in terms of new taxa descriptions] in the last 40 years is the Tridentinae”. We present here the first description in almost 80 years of an undoubtedly new tridentine genus from a tributary of the rio Purus, Amazon drainage. Our study includes detailed osteological analyses and remarks on important aspects of the taxonomy and systematics of the subfamily.

## MATERIAL AND METHODS

Morphometric data were taken point-to-point with digital calipers on the left side of specimens to the nearest 0.1 mm under stereomicroscope. Measurements followed Tchernavin (1944), except for the following ones that were taken according to Dutra *et al.* (2012): caudal peduncle length (from the base of the last anal ray to the base of the median caudal rays); caudal peduncle depth (vertically through the middle of caudal peduncle length); body depth (vertically through the pectoral insertion); and eye diameter (horizontally from the anterior margin to the posterior margin of orbit). In the fin counts, soft (*i.e.*, non-spinous) unsegmented or procurrent (*sensu* Arratia, 2008) rays of median fins are represented by lowercase Roman numerals followed by a superscript ‘P’ (*e.g.*, iii<sup>P</sup>), unbranched segmented soft rays by simple lower case Roman numerals (*e.g.*, iii), and branched segmented rays by Arabic numerals (*e.g.*, 3). The two posteriormost closely-set rays in dorsal and anal fins were counted as separate elements. Counts were recorded for the holotype and paratypes, with absolute frequencies for each value given in square brackets throughout the description, and holotype counts indicated with an asterisk (\*). Numbers of branchiostegal rays, vertebrae, ribs, fin rays, number and position of dorsal- and anal-fin support elements, and other osteological features were obtained from paratypes CT-scanned and cleared and stained according to Taylor, Van Dyke (1985). Vertebral counts include only the post-Weberian vertebrae, with the urostyle (compound caudal centrum) counted as a single element. Anatomical terminology follows Datovo, Bockmann (2010) with the following modifications: angular complex (= angulo-articulo-retroarticular) instead of “angulo-articular” (Adriaens *et al.*, 2010) and odontophores instead of “patch of odontodes” (de Pinna, Dagosta, 2022). Only external morphology could be examined on specimens from some lots of the new taxon. These lots are therefore not designated as types, although their external characters allow their unequivocal taxonomic identification.

A paratype was scanned on Phoenix vltomelx m microfocus microcomputed tomography system (General Electric Company) with a 300 kV  $\mu$ -focus X-ray source. To improve image resolution a multiscan montage of the whole specimen was generated from three individual scans, totaling 1,440 images. X-ray projection images were recorded at 1,000 ms of time exposure per image, with 70 kV, 200 mA, and voxel resolution of 27  $\mu$ m. Three-dimensional visualization as well as the analysis of the reconstructed data was performed using VGStudio MAX2.2.3 64 bit (Volume Graphics GmbH, Heidelberg, Germany).

Institutional acronyms follow Fricke, Eschmeyer (2023). Abbreviations: eth, ethanol preserved specimens; c&s, cleared and stained specimens; HL, head length; SL, standard length; spec, specimen;  $\mu$ ct,  $\mu$ CT-scanned specimen (preserved in ethanol).

## RESULTS

### *Rhinotridens*, new genus

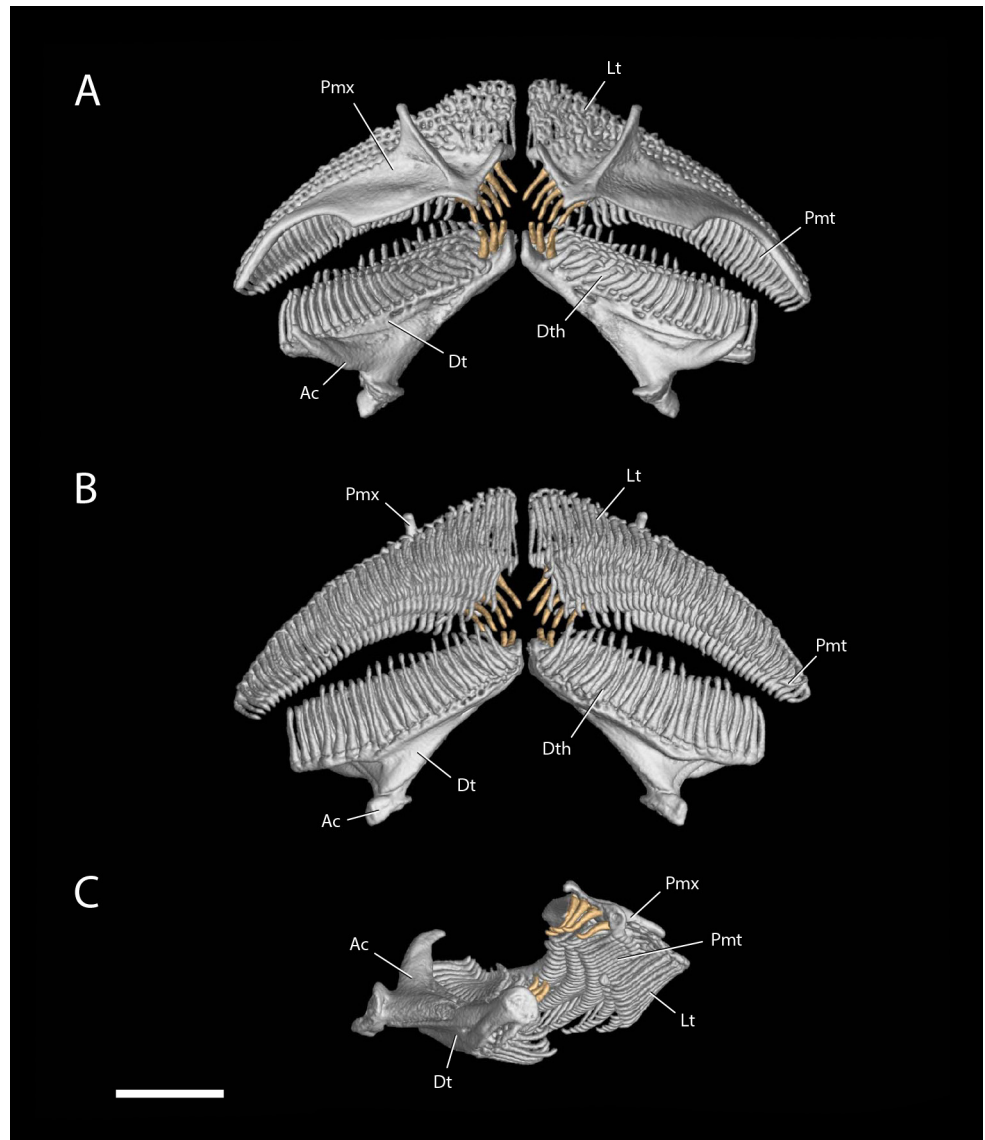
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**Type-species.** *Rhinotridens chromocaudatus*, new species.

**Diagnosis.** *Rhinotridens* is distinguished from all other tridentine genera by the following unique autapomorphies: presence of a conspicuous anteromedial protuberance on the snout, with a length greater than 35% of its width (Fig. 1; *vs.* protuberance absent or limited to a discreet convexity with a length less than 18% of its width; see Baskin, 1973: fig. 66; Henschel *et al.*, 2023: figs. 2, 8, 12, 13); set of symphyseal premaxillary and dentary teeth inclined posteromedially (Fig. 2; *vs.* not inclined, see Azpelicueta, 1990: figs. 2, 3; Henschel *et al.*, 2023: fig. 9); rod-like orbitosphenoid ossified only ventral to the optic nerve (Fig. 3; *vs.* laminar bone ossified around the optic nerve, with a foramen for its exit, see Baskin, 1973: figs. 28, 29; Henschel *et al.*, 2023: fig. 3); mesethmoid cornua inclined ventrolaterally (Fig. 4; *vs.* cornua horizontally straight); distal process of the hyomandibula directed anteriorly (Fig. 5; *vs.* posteriorly, see Baskin, 1973: fig. 51;



**FIGURE 1.** *Rhinotridens chromocaudatus*, new genus and species, holotype, MZUSP 128216, 17.57 mm SL. Brazil, Amazonas, rio Ipixuna, tributary of the rio Purus, rio Solimões basin. Scale bar = 2.0 mm.



**FIGURE 2** | Premaxilla and lower jaw of *Rhinotridens chromocaudatus*,  $\mu$ CT-scan images, paratype, MZUSP 128217, 16.37 mm SL; **A.** Dorsal view; **B.** Ventral view; **C.** medial view, left side. Symphyseal teeth highlighted in yellow. Ac, angular complex; Dt, dentary; Dth, dentary teeth; Lt, labial teeth; Pmt, premaxillary teeth; Pmx, premaxilla. Scale bar = 0.3 mm.

Henschel *et al.*, 2017: fig. 2g; Henschel *et al.*, 2023: fig. 4); opercular and interopercular odontodophores separated by a large interspace, greater than the depth of the opercular patch (Fig. 5; *vs.* patches nearly juxtaposed, separated by a distance less than the depth of the opercular patch, see Baskin, 1973: fig. 51; Azpelicueta, 1990: fig. 4; Henschel *et al.*, 2017: fig. 2g; Henschel *et al.*, 2023: fig. 4); and basipterygia fused sagittally (Fig. 6; *vs.* separated).

**Etymology.** From *rhino*, latinized form of the Greek word *rhinos* (ῥινόσ), meaning nose or snout, and *Tridens*, the type genus of the subfamily. In allusion to the rostral protuberance of the new genus. An adjective.

*Rhinotridens chromocaudatus*, new species

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(Figs. 1–9; Tab. 1)

**Holotype.** MZUSP 128216, 17.57 mm SL, Brazil, Amazonas State, Humaitá Municipality, rio Amazonas basin, rio Purus drainage, rio Ipixuna, mouth of Lago Comprido, 07°30'37"S 63°20'23"W, 21 Jul 2012, W. M. Ohara.

**Paratypes.** INPA 28592, 25 eth (14.65–16.87 mm SL), Brazil, Amazonas State, Beruri Municipality, rio Amazonas basin, rio Purus drainage, igarapé Itabocão, lago Aiapúa, Reserva de Desenvolvimento Sustentável Piagaçu Purus, approx. 04°25'41"S 62°08'05"W, 14 Nov 2007, L. R. Py-Daniel, E. Ferreira, F. Rossoni & A. Galluch; MCP 55013, 6 eth (15.39–16.48 mm SL); MNRJ 54171, 6 eth (15.99–16.33 mm SL); MPEG 39635, 6 eth (15.59–17.16 mm SL); MZUSP 128217, 19 eth (16.10–17.48 mm SL), 1  $\mu$ ct (16.37 mm SL), 1 c&s (16.72 mm SL); UFRO-ICT 15431, 20 eth (15.31–16.40 mm SL), same data as holotype.

**TABLE 1** | Morphometric data for *Rhinotridens chromocaudatus*; n = 10; range includes holotype. SD, standard deviation.

	Holotype	Range	Mean	SD
Standard length (mm)	17.57	16.10–17.57	–	–
<b>Percentage of standard length</b>				
Body depth	10.66	9.67–12.11	10.97	0.7
Caudal peduncle length	13.75	7.90–15.38	12.38	2.3
Caudal peduncle depth	6.26	5.63–7.49	6.51	0.4
Predorsal length	68.43	66.79–70.22	68.68	1.0
Preanal length	61.66	59.44–71.81	62.62	3.5
Dorsal-fin base length	8.46	7.67–11.15	9.04	1.0
Anal-fin base length	20.17	20.17–25.59	22.39	1.6
Distance between dorsal-fin origin and middle of caudal-fin base	32.48	29.33–35.96	33.08	1.7
Distance between anal-fin origin and middle caudal-fin base	38.55	34.31–40.95	38.84	1.9
Pectoral girdle width	10.87	9.71–11.80	10.88	0.6
Pectoral fin length	8.67	8.17–10.33	9.30	0.7
Prepelvic length	47.20	42.07–49.92	46.35	2.4
Head length	18.80	16.48–19.40	18.18	1.1
<b>Percentage of head length</b>				
Head width	60.04	55.91–72.72	63.19	5.1
Head depth	43.59	43.59–51.47	46.75	2.6
Interorbital distance	19.78	19.78–29.39	24.77	3.1
Snout length	38.85	34.11–47.96	41.60	4.2
Maxillary-barbel length	17.76	17.76–24.87	22.21	2.5
Rictal-barbel length	9.89	8.85–16.44	12.27	2.6
Mouth width	40.46	40.45–51.84	44.41	3.8
Eye diameter	23.51	20.02–30.91	26.77	3.2

**Non-types.** INPA 33819, 24 eth (14.74–16.95 mm SL), same data as INPA 28592. INPA 42139, 19 eth (15.28–17.81 mm SL), Brazil, Amazonas State, Tapauá Municipality, rio Amazonas basin, rio Purus drainage, rio Ipixuna drainage, igarapé dos Caetanos, Floresta Estadual Tapauá, 06°19'57" S 63°12'46"W, 17 Aug 2012, T. Couto & M. Carvalho. INPA 42148, 1 eth (16.57 mm SL), Brazil, Amazonas State, Tapauá Municipality, rio Amazonas basin, rio Purus drainage, rio Ipixuna drainage, igarapé dos Mutuns, Floresta Estadual Tapauá, 06°22'29"S 63°16'27"W, 18 Aug 2012, T. Couto & M. Carvalho. INPA 56815, 1 eth (16.21 mm SL), Brazil, Amazonas State, Beruri Municipality, rio Amazonas basin, rio Purus drainage, stream in lago Aiapuá, 04°26'16.84"S 62°07'24"W, 28 Sep 2008, E. Ferreira. INPA 56885, 3 eth (15.38–15.56 mm SL), INPA 56920, 76 eth (14.12–16.85 mm SL), same data as INPA 56815. UFRO-ICT 15405, 4 eth (15.0–16.3 mm SL), Brazil, Amazonas State, Humaitá Municipality, rio Amazonas basin, rio Purus drainage, unnamed tributary of rio Ipixuna, 07°32'3"S 63°21'8"W, 22 Jul 2012, W.M. Ohara. UFRO-ICT 15520, 2 eth (16.0–16.0 mm SL), Brazil, Amazonas State, Humaitá Municipality, rio Amazonas basin, rio Purus drainage, rio Ipixuna, 07°31'19"S 63°21'00" W, 21 Jul 2012, W.M. Ohara. UFRO-ICT 15538, 1 eth (15.5 mm SL), Brazil, Amazonas State, Humaitá Municipality, rio Amazonas basin, rio Purus drainage, rio Açuã, 08°11'47"S 63°51'45"W, 9 Aug 2012, W.M. Ohara.

**Diagnosis.** The new species differs from all other tridentines by having a conspicuous dark brown horizontal stripe in the middle of the caudal fin (Fig. 1). Ongoing studies indicate the existence of additional undescribed species of *Rhinotridens* that lack this caudal stripe (see Discussion). As a result, this character is preemptively proposed as autapomorphic for *R. chromocaudatus* rather than as a synapomorphy for the genus as a whole.

**Description. External morphology.** Morphometric data for holotype and paratypes given in Tab. 1. Body elongate, roughly cylindrical at pectoral girdle level, progressively more compressed towards caudal peduncle (Fig. 1). Dorsal profile slightly convex from tip of snout to dorsal fin, gently concave from that point to caudal peduncle. Ventral profile straight to gently convex from tip of snout to pectoral-fin origin, then slightly convex to pelvic-fin origin, straight from that point to anal-fin origin, concave from anal-fin origin to end of caudal peduncle. Anal opening shortly anterior to anal-fin origin. Greatest body depth shortly anterior to vertical through pelvic-fin origin.

Head depressed, longer than wide. Snout with round anteromedial protrusion particularly evident in dorsal and ventral views. Anterior nostril small and round, surrounded by short tube of integument, positioned closer to upper lip than to anterior margin of eye. Nasal barbel absent. Posterior nostril smaller than anterior one and located at midline between anterior nostril and eye. Mouth ventral, crescent-shaped, its corners slightly posterolaterally-oriented in ventral view. Anterior margin of upper lip gently rounded and continuous laterally with maxillary-barbel base. Lower lip thicker than upper one, with gently convex anterior margin and continuous laterally with rictal-barbel base. Bases of maxillary and rictal barbels continuous with lower lip. Maxillary barbel surpassing middle of eyeball, but not reaching its posterior margin. Rictal barbel slightly shorter than maxillary one. Eyes large and circular, covered by thick translucent skin not adhered to eyeball's surface. Eyes located laterally on head, at middle of HL. Interorbital space slightly convex and about same length as eyeball diameter. Greatest head width at level of interopercular odontodophores. Interopercle

with 6(4\*)–8(1) conical odontodes. Opercle with 4(1)–6(1) conical odontodes, their posterior margins reaching vertical through base of first pectoral-fin ray. Branchiostegal membrane forming free fold ventrally across isthmus.

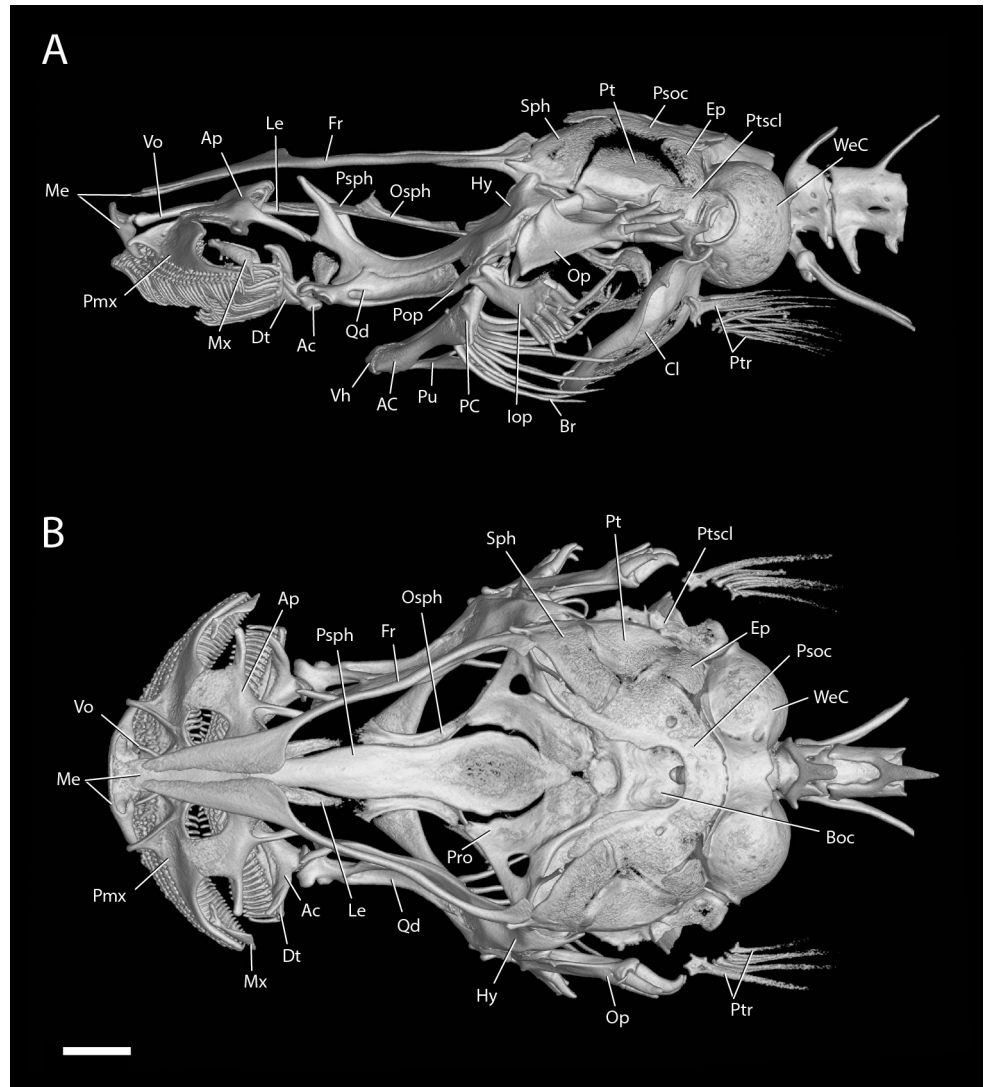
Pectoral-fin rays similar in length, resulting in slightly convex distal margin. Pectoral-fin rays i,4 (both sides of 6 spec, including holotype) or i,3,i (4 spec). Pelvic-fin rays i,4 (5 spec; holotype) or i,3,i (5 spec). Dorsal fin with distal margin gently convex, its origin slightly posterior to that of anal fin. Dorsal-fin rays i,7 (6 spec; holotype), i,6,i (3 spec) or rarely i,5,i (1 spec). Anal fin elongate, with distal margin straight to slight concave. Anal-fin rays i<sup>p</sup>,i,17 (4 spec, holotype) or i<sup>p</sup>,i,16 (2 spec), rarely i<sup>p</sup>,i,18 (2 spec), i<sup>p</sup>,i,19 (1 spec) or ii<sup>p</sup>,i,18 (1 spec). Caudal fin ranging from truncate to emarginate. Caudal-fin rays ix<sup>p</sup>,i,5 on dorsal lobe and x<sup>p</sup>,i,6 on ventral lobe. First procurrent rays of both caudal-fin lobes rudimentary.

**Neurocranium.** Skull roof poorly ossified, forming a single, large fontanel bordered by mesethmoid, frontal, sphenotic–prootic–pterosphenoid, and parieto-supraoccipital (Figs. 3, 4, 7). Mesethmoid T-shaped in dorsal view, with cornua strongly bent ventrolaterally. Mesethmoid axis extremely thin and covered posterodorsally by frontal. Frontal elongate and slender posteriorly, not contacting its antimere sagittally. Sphenotic, prootic, and pterosphenoid fused. Parieto-supraoccipital with curved anterolateral projections bordering posterolateral portion of cranial fontanel. Pterotic with small lateral process. Vomer constricted at middle portion and split posteriorly into three laminar processes. Middle posterior process longest, overlapping ventrally part of parasphenoid. Vomer with lateral tubercle for articulation with autopalatine. Lateral ethmoid tiny, laminar, restricted to neurocranial floor. Orbitosphenoid rod-like, gently curved dorsally, lacking any foramen, and restricted to neurocranial floor. Parasphenoid not overlapping basioccipital posteriorly. Basioccipital lacking anterior processes and not sutured to parasphenoid.

**Jaws.** Premaxilla large, tapering distally, with conspicuous anteromedial ascending process articulating with mesethmoid cornu (Figs. 2–4). Premaxillary teeth arranged in three arched rows. Three or four additional rows of labial teeth implanted in upper-lip connective tissue just anterior to premaxilla. Posteromedial margin of premaxilla with 4–6 large, posteromedially-oriented symphyseal teeth. Tiny maxilla paralleling concave posterior profile of premaxilla and providing support to maxillary and rictal barbels. Lower jaw much wider than long. Coronoid process formed mostly by angular complex (= angulo-articulo-retroarticular). Dentary with numerous teeth arranged in five rows. Anteromedial margin of dentary with three offset posteromedially-oriented symphyseal teeth. Meckel's cartilage small and located just ventral to the last row of dentary teeth. Coronomeckelian absent.

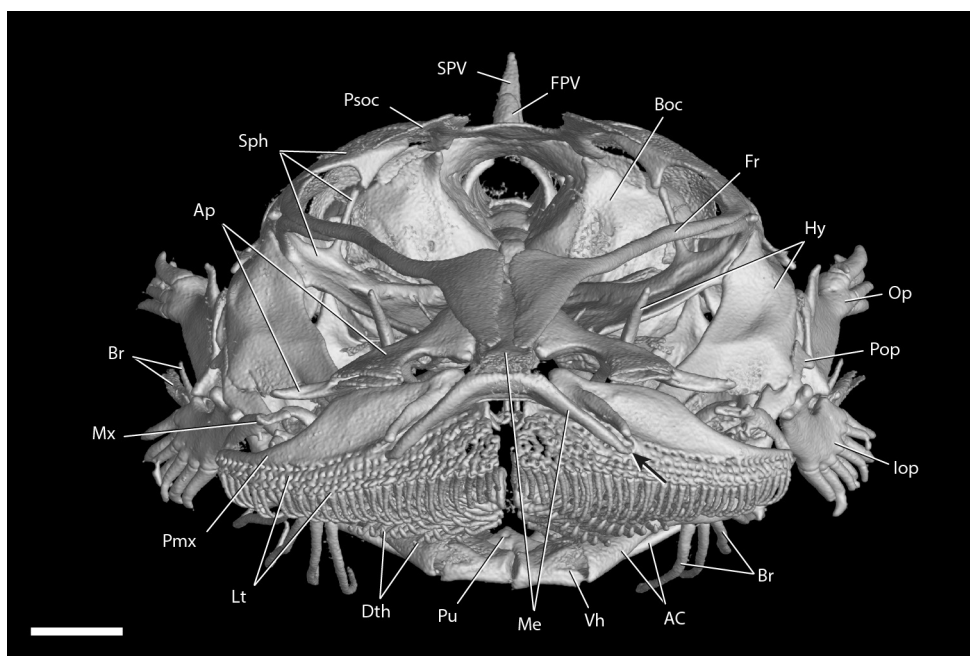
**Suspensorium and opercular series.** Autopalatine with broad, undivided anterior cartilage and two elongate processes: lateral and posterior (Figs. 3–5). Quadrate with anterior portion laminar and posterior portion elongate. Metapterygoid absent. Hyomandibula with broad distal process directed anterodorsally. Preopercle with lateral condyle for articulation with interopercle. Interopercle expanded posteriorly and with dorsal concavity for articulation with opercle. Opercle with conspicuous adductor crest and dilatator process. Anteroventral process of opercle short.





**FIGURE 3** | Cranium, pectoral skeleton, and anterior portion of axial skeleton of *Rhinotridens chromocaudatus*,  $\mu$ CT-scan images, paratype, MZUSP 128217, 16.37 mm SL; **A.** Left lateral view; **B.** Dorsal view. Ac, angular complex; AC, anterior ceratohyal; Ap, autopalatine; Boc, basioccipital; Br, branchiostegal rays; Cl, cleithrum; Dt, dentary; Ep, epioccipital; Fr, frontal; Hy, hyomandibula; Iop, interopercle; Le, lateral ethmoid; Me, mesethmoid; Mx, maxilla; Op, opercle; Osph, orbitosphenoid; Pop, preopercle; Psph, parasphenoid; Psoc, parieto-supraoccipital; Ptr, pectoral-fin rays; Ptscl, posttemporo-supracleithrum; PC, posterior ceratohyal; Pmx, premaxilla; Pop, preopercle; Pt, pterotic; Pu, parurohyal; Qd, quadrate; Sph, sphenotic-prootic-pterosphenoid; Vh, ventral hypohyal; Vo, vomer; WeC, Weberian capsule. Scale bar = 0.3 mm.

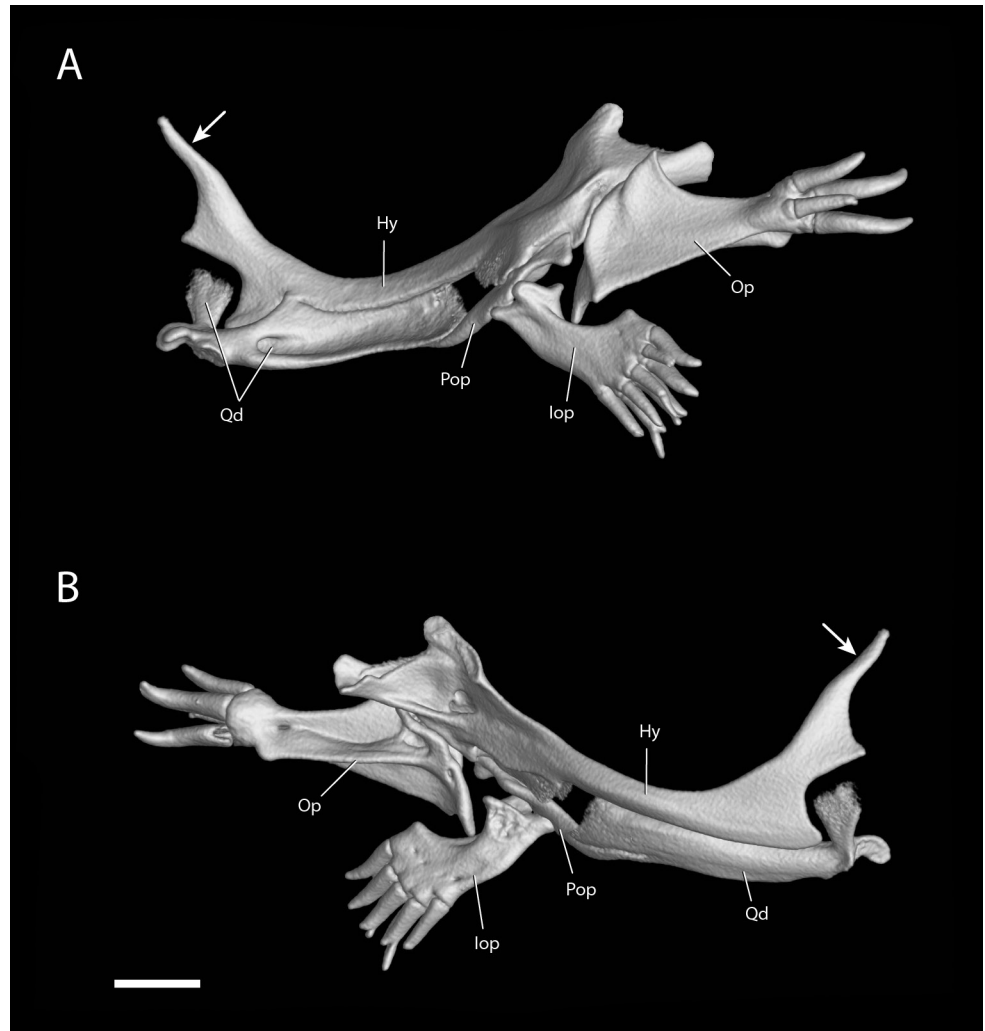
**Hyoid bar.** Parurohyal with thin, elongate lateral arms and short posterior process (Fig. 8). Ventral hypohyal with ventral fovea for articulation with parurohyal condyles. Dorsal hypohyal absent. Anterior ceratohyal constricted at midlength. Posterior ceratohyal short and compressed. Interhyal absent. Branchiostegal rays 6, approximately equal in length. Three branchiostegal rays articulating with anterior ceratohyal and three with posterior ceratohyal.



**FIGURE 4** | Cranium of *Rhinotridens chromocaudatus*,  $\mu$ CT-scan images, paratype, MZUSP 128217, 16.37 mm SL; anterior view; arrow indicates right mesethmoid cornu. AC, anterior ceratohyal; Ap, autopalatine; Boc, basioccipital; Br, branchiostegal rays; Dth, dentary teeth; FPV, first post-Weberian vertebrae; Fr, frontal; Hy, hyomandibula; Iop, interopercle; Lt, labial teeth; Me, mesethmoid; Mx, maxilla; Op, opercle; Pop, preopercle; Psoc, parieto-supraoccipital; PC, posterior ceratohyal; Pmx, premaxilla; Pop, preopercle; Pu, parurohyal; Sph, sphenotic-prootic-pterosphenoid; SPV, second post-Weberian vertebrae; Vh, ventral hypohyal. Scale bar = 0.25 mm.

**Gill arches.** Basibranchials and hypobranchials completely cartilaginous (Fig. 9). Basibranchial 1 globose and autogenous; basibranchials 2 and 3 conjoined in elongate anterior copula; basibranchial 4 nearly hexagonal. Hypobranchials 1 and 2 thinner than hypobranchial 3. Ceratobranchials ossified at middle portion, cartilaginous distally to tips. Ceratobranchials 1–3 with posterior laminar projections; ceratobranchial 5 more densely ossified than others in series and bearing two short strong teeth. Ceratobranchial-hypobranchial articulations forming acute angle. Epibranchials 1–3 poorly ossified at middle portion, cartilaginous distally to tips. Epibranchial 1 with protruding uncinuate process; epibranchials 2 and 3 slender, rod-like; epibranchial 4 more robust and densely ossified than others. Only cartilaginous pharyngobranchial 4 present. Large arched upper pharyngeal tooth plate associated with pharyngobranchial 4 and bearing 8–9 elongate, conical teeth.

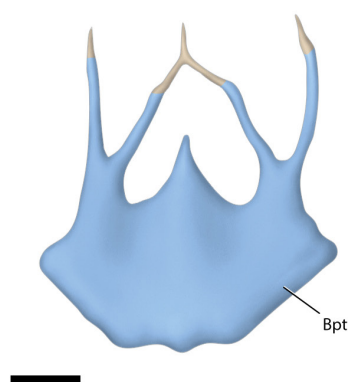
**Weberian apparatus and axial skeleton.** Weberian apparatus mostly encapsulated with narrow lateral opening (Figs. 3, 7). Neck-like lateral constriction of the Weberian capsule absent. Post-Weberian vertebrae 38. First post-Weberian vertebra nearly half length of subsequent one. First complete haemal arch and spine on third post-Weberian vertebrae. Pleural ribs two, second one not contacting parapophysis.



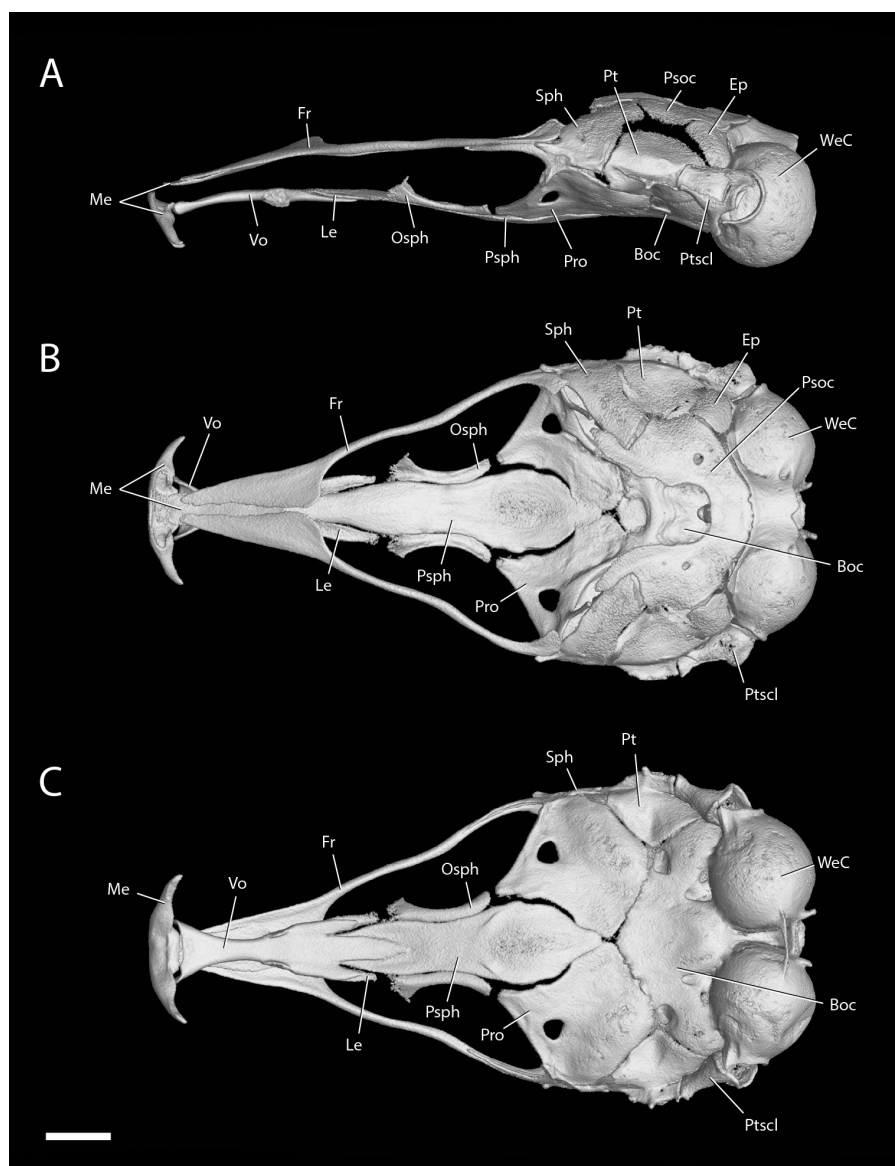
**FIGURE 5** | Suspensorium and opercular series of *Rhinotridens chromocaudatus*, left side,  $\mu$ CT-scan images, paratype, MZUSP 128217, 16.37 mm SL; **A**. Lateral view; **B**. Medial view; arrow indicates distal process of hyomandibula. Hy, hyomandibular; lop, interopercle; Op, opercle; Pop, preopercle; Qd, quadrate. Scale bar = 0.2 mm.

**Paired girdles.** Posttemporo-supracleithrum tightly articulated with neurocranium (Fig. 3). Cleithrum ossified only at its margins. Scapulo-coracoid mostly cartilaginous. Two pectoral radials fully cartilaginous. Basipterygia fused sagittally, mostly cartilaginous, with tiny ossifications restricted to distal tips of anterolateral and anteromedial spines. Pelvic splint absent (Fig. 6).

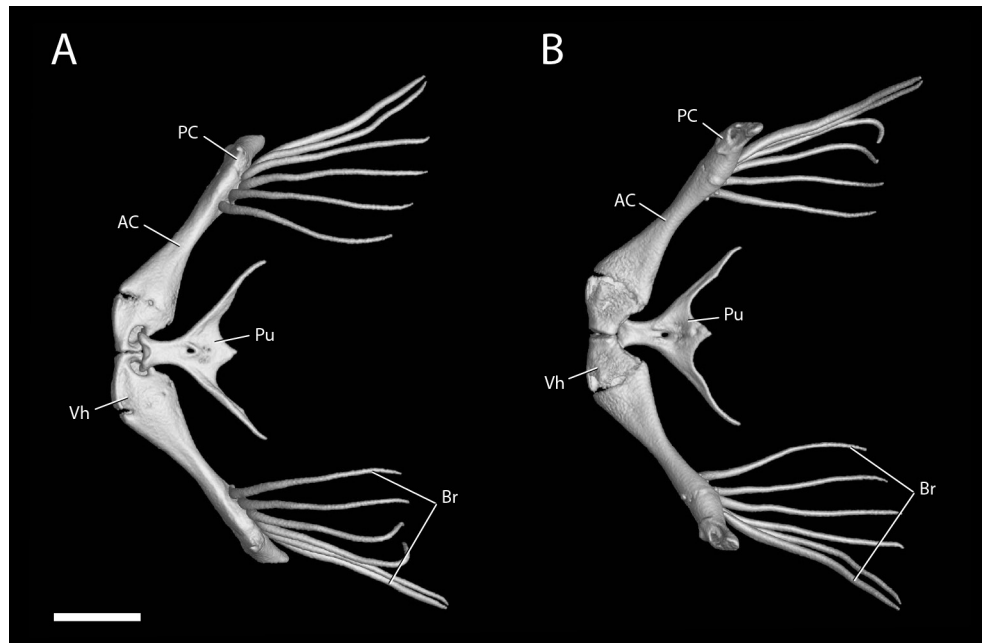
**Median-fins supports.** Dorsal-fin basal radials 8, distributed between neural spines of 21<sup>st</sup> and 26<sup>th</sup> post-Weberian vertebrae. Anal-fin basal radials 19, distributed between haemal spines of 19<sup>th</sup> and 30<sup>th</sup> post-Weberian vertebrae. Uroneural continuous with compound caudal centrum (PU1+U1). Parhypural and hypurals 1–2 fused, forming lower hypural plate. Single upper hypural plate, presumably formed by fused hypurals 3–5. Uroneural anterodorsal to upper hypural plate. Epurals absent.



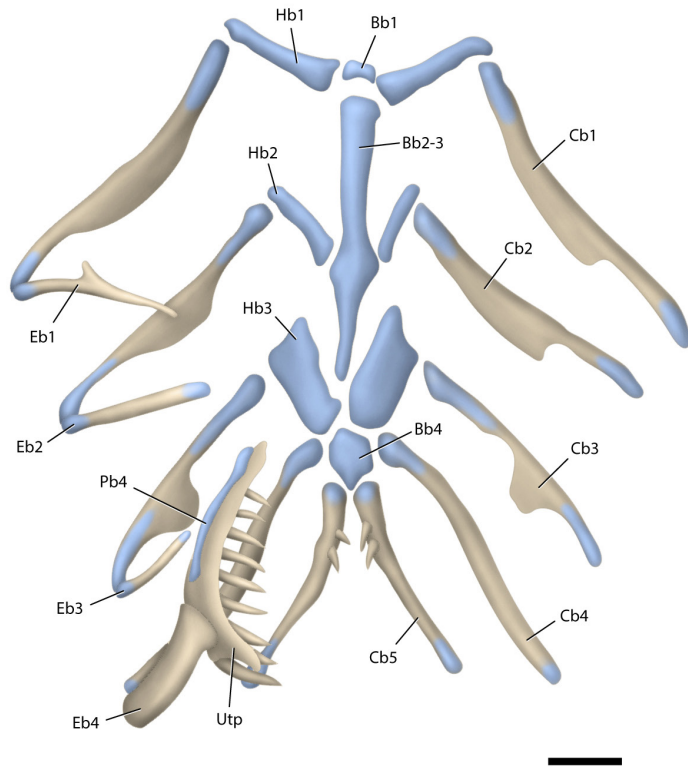
**FIGURE 6** | Pelvic girdle of *Rhinotridens chromocaudatus*, digital illustration of c&s specimen, ventral view, paratype, MZUSP 128217, 16.72 mm SL. Bpt, basipterygium. Scale bar = 0.15 mm.



**FIGURE 7** | Neurocranium and associated structures of *Rhinotridens chromocaudatus*,  $\mu$ CT-scan images, paratype, MZUSP 128217, 16.37 mm SL; **A.** Left lateral view; **B.** Dorsal view; **C.** Ventral view. Boc, basioccipital; Ep, epioccipital; Fr, frontal; Le, lateral ethmoid; Me, mesethmoid; Osph, orbitosphenoid; Psph, parasphenoid; Psoc, parieto-supraoccipital; Ptscl, posttemporo-supracleithrum; Pro, prootic; Pt, pterotic; Sph, sphenotic-prootic-pterosphenoid; Vo, vomer; WeC, Weberian capsule. Scale bar = 0.3 mm.



**FIGURE 8 |** Hyoid arch of *Rhinotridens chromocaudatus*,  $\mu$ CT-scan images, paratype, MZUSP 128217, 16.37 mm SL; **A.** Ventral view; **B.** Dorsal view; anterior to left. AC, anterior ceratohyal; Br, branchiostegal rays; PC, posterior ceratohyal; Pu, parurohyal; Vh, ventral hypohyal. Scale bar = 0.3 mm.

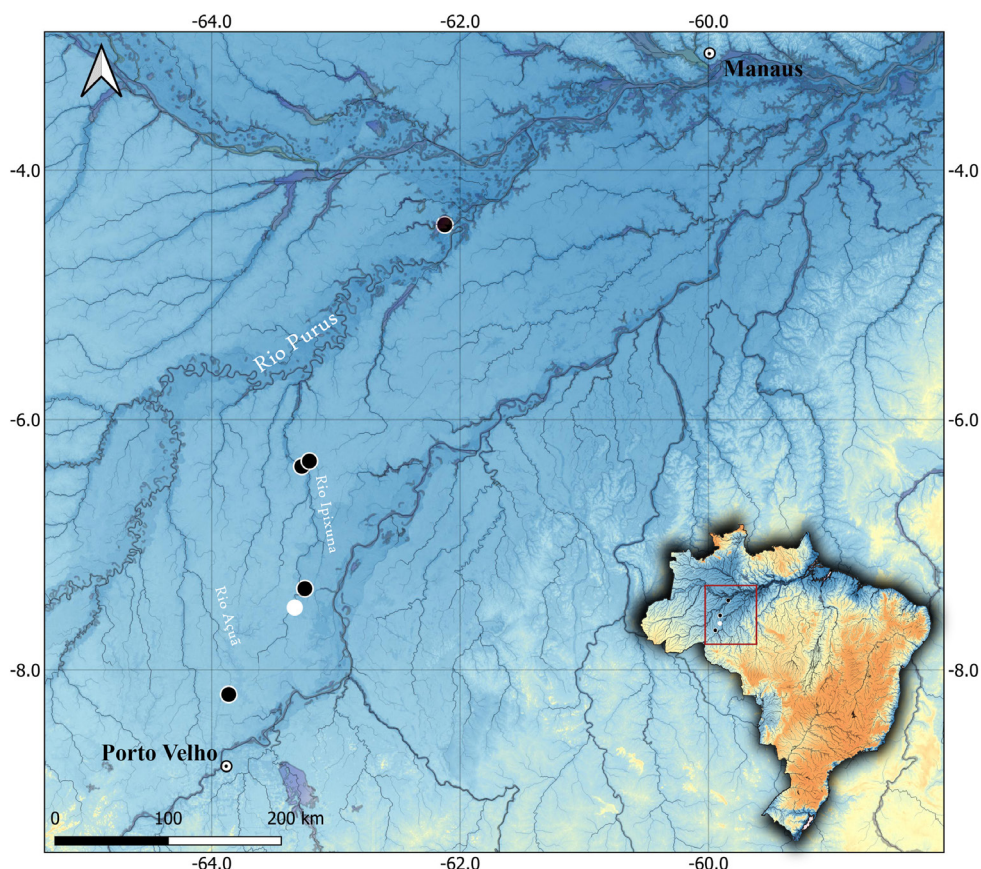


**FIGURE 9 |** Gill arches of *Rhinotridens chromocaudatus*, digital illustration of c&s specimen, dorsal view, paratype, MZUSP 128217, 16.72 mm SL; right dorsal elements not shown. Bb1-4, basibranchials 1 to 4; Cb1-5, ceratobranchials 1 to 5; Eb1-4, epibranchials 1 to 4; Hb1-3, hypobranchials 1 to 3; Pb4, pharyngobranchial 4; Utp, upper pharyngeal tooth plate. Scale bar = 0.1 mm.

**Coloration in alcohol.** Unpigmented body background uniformly white to pale yellow (Fig. 1). Dark brown melanophores distributed in specific regions of head, trunk, and fins. Melanophores on skin of head clustered around cranial fontanel, along sagittal region and lateral borders of snout, and on opercular region. Pigments on connective membrane covering brain visible externally through cranial fontanel and translucent skin. Melanophores scattered along skin of dorsosagittal region of trunk, more densely between occiput and dorsal fin. Midlateral line of trunk with thin line of melanophores on skin, gradually expanding toward caudal-fin base. Caudal fin with broad midlateral horizontal dark brown stripe. Other fins with scattered melanophores concentrated at their bases and others irregularly scattered amid interradial membranes. Melanophores at dorsal region of peritoneum externally visible through thin abdominal wall, forming ventrolateral stripe between pectoral region and anus.

**Coloration in life.** Body background mostly translucent with a faint superficial iridescent blue tint. Dark pigmentation as described in “Coloration in alcohol”.

**Geographical distribution.** *Rhinotridens chromocaudatus* is known from three tributaries (rio Ipixuna, rio Açuã, and lago Aiapuá) of the rio Purus, Amazon basin, Brazil (Fig. 10).



**FIGURE 10** | Geographic distribution of *Rhinotridens chromocaudatus*. White dot indicates the type-locality, each symbol may represent than one lot or locality.

**Ecological notes.** The rio Ipixuna at the type-locality is a medium sized blackwater river (6.5 m wide) with slow water flow (Fig. 11). Sampling took place during ebb season when some beaches were already appearing. Specimens of *Rhinotridens chromocaudatus* were collected during the evening (18:00–20:00) in the middle-upper water column in moderate abundance near the margin. The bottom was muddy with patches of leaf litter. *Rhinotridens chromocaudatus* was captured with the catfishes *Bunocephalus coracoides* (Cope, 1874), *Corydoras robustus* Nijssen & Isbrücker, 1980, *Farlowella amazona* (Günther, 1864), *Mastiglanis asopos* Bockmann, 1994, *Microglanis poecilus* Eigenmann, 1912, *Ochmacanthus reinhardtii* (Steindachner, 1882), *Physopyxis ananas* Sousa & Rapp Py-Daniel, 2005, *P. lyra* Cope, 1872, *Rineloricaria lanceolata* (Günther, 1868), and *Scoloplax baskini* Rocha, de Oliveira & Rapp Py-Daniel, 2008.

**Etymology.** From *chroma*, latinized form of the Greek word *chrôma* (χρῶμα), meaning color, and *cauda*, a Latin word meaning tail. In reference to the presence of the dark brown pigmentation in the middle of the caudal fin. An adjective.

**Conservation status.** *Rhinotridens chromocaudatus* was captured in localities of the lower rio Purus, including within the Floresta Estadual Tapauá and Reserva Sustentável Piagaçu-Purus. No significant threats to the species have been identified in the area of occurrence. Consequently, *R. chromocaudatus* can be provisionally classified as Least Concern (LC) according to the categories and criteria of the International Union for Conservation of Nature (IUCN Standards and Petitions Committee, 2022).



**FIGURE 11** | Type-locality of *Rhinotridens chromocaudatus*; 07°30'37"S 63°20'23"W, rio Ipixuna, rio Purus drainage, rio Amazonas basin, Humaitá Municipality, Amazonas State, Brazil.

## DISCUSSION

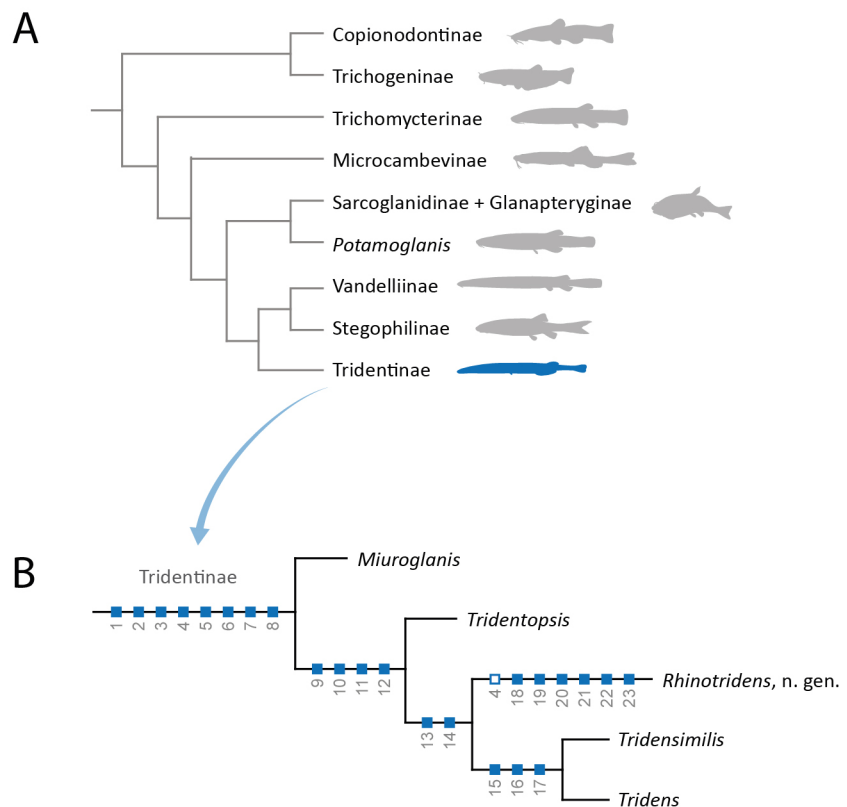
**Tridentine systematics.** Tridentinae has been a well-established subfamily of Trichomycteridae (Eigenmann, 1918; Baskin, 1973; de Pinna, 1998; Datovo, Bockmann, 2010; Ochoa *et al.*, 2017, 2020). The first phylogenetic definition of the subfamily was presented by Baskin (1973), who demonstrated that its four traditional genera form a monophyletic group: *Miuroglanis*, *Tridentopsis*, *Tridensimilis*, and *Tridens*. Later, Henschel *et al.* (2017) erected *Potamoglanis* (formerly “*Trichomyterus*” *hasemani* group) as a new tridentine genus. However, Ochoa *et al.* (2017, 2020) did not recover *Potamoglanis* as a tridentine, a fact recently recognized by authors of the original description of the genus (Henschel *et al.*, 2023; Fig. 12A). Therefore, the synapomorphies for Tridentinae are those proposed by Baskin (1973), which to date remains as the only phylogenetic study to include all tridentine genera. Our analysis confirms the material basis of all eight synapomorphies for the subfamily originally proposed by Baskin (1973), but the phylogenetic implications of some of them need qualifications because of discoveries in the intervening years (Fig. 12B): (1) cranial roof mostly unossified, forming a single greatly enlarged fontanel (Figs. 3B, 7B; *vs.* ossified cranial roof with none, one, or two small fontanels) — this condition occurs also in *Potamoglanis* and in the vandelliines *Paravandellia* Miranda Ribeiro, 1912 and *Paracanthopoma* Giltay, 1935 and may not be decisively synapomorphic for Tridentinae (de Pinna, 1989; DoNascimento, 2013; Henschel *et al.*, 2023); (2) maxilla extremely small, proportionally the smallest in the family (Figs. 3B, 4; *vs.* larger maxilla) — the large cartilaginous maxilla reported in Henschel *et al.* (2023) for *Tridens vitreus* Henschel, Ohara & Costa, 2023 appears to be mistaken for the lateral palatine cartilage, since the maxilla in bony fishes is dermal and never preformed in cartilage; (3) eyes exposed ventrally (Fig. 1; *vs.* not exposed ventrally) — paralleled to a lesser extent in the stegophiline *Haemomaster* Myers, 1927; (4) opercular and interopercular odontophores juxtaposed, being separated by a distance less than the depth of the opercular patch (*vs.* patches separated by a distance greater than the depth of the opercular patch) — this condition is not present in *Rhinotridens* (see below); (5) opercle with an anteroventral process shorter than the depth of its articular condyle with the hyomandibula (Figs. 3A, 5; *vs.* process longer than the articular condyle); (6) origin of dorsal fin at same level or posterior to that of anal-fin in external view (Fig. 1; *vs.* dorsal-fin origin anterior to anal-fin origin) — this condition is paralleled in all species of *Trichogenes* Britski & Ortega, 1983, several species of *Paracanthopoma*, and some species of *Potamoglanis* (Henschel *et al.*, 2017; de Pinna *et al.*, 2020; de Pinna, Dagosta, 2022); (7) anterior portion of hyomandibula with a dorsal distal process (Figs. 3A, 5; *vs.* process absent); and (8) anal fin with 15 or more rays (*vs.* 12 or less rays) — convergent in Trichogeninae (de Pinna *et al.*, 2020). These conditions are found in all previously known tridentine genera. *Rhinotridens chromocaudatus* shares all but the fourth character. Given its inferred phylogenetic position, this absence is most parsimoniously interpreted as a reversal (Fig. 12B; see below).

Baskin (1973) also proposed a hypothesis about the interrelationships among tridentine genera, with *Miuroglanis*, *Tridentopsis*, *Tridensimilis*, and *Tridens* in that order as successive sister groups. The clade formed by the three latter genera was supported by the following characters (Fig. 12B): (9) anal fin with 17 or more rays (corrected from 18 by DoNascimento, 2013:449; *vs.* 15 or less); (10) anteriormost anal-fin pterygiophore



inserting two or more vertebrae anterior to the insertion of the anteriormost dorsal-fin pterygiophore (*vs.* one or more vertebrae posterior); (11) ventral exposure of eye equal or greater than dorsal exposure (Fig. 1; *vs.* smaller); and (12) eye distinctly larger than in *Miuroglanis*. We confirm the presence of these character states in the examined specimens of *Tridentopsis*, *Tridensimilis*, *Rhinotridens*, and *Tridens*.

Finally, Baskin (1973) proposed five synapomorphies supporting the sister-group relationship between *Tridensimilis* and *Tridens*: (13) three to six opercular odontodes (Fig. 5A; *vs.* 10–15); (15) eyes facing more ventrally than dorsally (*vs.* equal or more dorsally; Fig. 1); (16) Weberian capsule with elongate, neck-like lateral constriction (*vs.* elongate constriction absent; Figs. 3B, 7B, C; paralleled in several stegophilines); (17) anal-fin origin three or more vertebrae anterior to dorsal-fin origin (*vs.* two or less); and rictal barbel not externally visible. The recent description of two species of *Tridens* with small but externally distinguishable rictal barbels refutes the validity of the last character (Henschel *et al.*, 2023). We confirm the presence of characters 13, 15, 16, and 17 in the specimens of *Tridensimilis* and *Tridens* that we examined. Of these characters, only character 13 is present in *Rhinotridens chromocaudatus*. We additionally found that *Rhinotridens*, *Tridensimilis*, and *Tridens* share (14) the basipterygium mostly



**FIGURE 12** | Phylogenetic relationships of **A.** Trichomycteridae (Ochoa *et al.*, 2020) and **B.** Tridentinae (Baskin, 1973; present study). See Discussion for character numbering and explanation.

or completely cartilaginous in adults (Fig. 6; *vs.* mostly ossified in juveniles and adults). Therefore, character evidence supports the hypothesis that the new species is the sister group to *Tridens* plus *Tridensimilis*. This being so, the most economical nomenclatural solution is to recognize it as representative of a new genus, *Rhinotridens* (Fig. 12B).

Several morphological features of *Rhinotridens chromocaudatus* are unique among tridentines (Fig. 12B): (4) opercular and interopercular odontophores separated by a large interspace (Fig. 5; reversal of the condition that evolved at the base of the Tridentinae; see above); (18) snout with a conspicuous anteromedial protuberance (Fig. 1; *vs.* protuberance absent or limited to a gentle convexity); (19) mesethmoid cornua directed ventrolaterally (Fig. 4; *vs.* cornua horizontally straight); (20) symphyseal series of premaxillary and dentary teeth inclined posteromedially (Fig. 2; *vs.* not inclined); (21) distal process of hyomandibula directed anteriorly (Figs. 3A, 5; *vs.* posteriorly); (22) rod-like orbitosphenoid ossified only ventral to the optic nerve (Figs. 3, 7; *vs.* laminar and ossified around the nerve, with a foramen for the nerve exit); (23) basipterygia fused sagittally (Fig. 6; *vs.* separated); and a (24) dark brown stripe in the middle of the caudal fin (Fig. 1; *vs.* stripe absent). The five former characters are also present in one, probably more, additional undescribed tridentine species from the Amazon basin. Consequently, we interpreted characters 4, 18–23 as synapomorphic for *Rhinotridens* (Fig. 12B), and character 24 as an autapomorphy for *R. chromocaudatus*. The description of the other purportedly new *Rhinotridens* species requires sampling of additional specimens and should therefore be presented in a future study. The caudal fin stripe of *R. chromocaudatus* (Fig. 1) is unique among tridentines and relatively uncommon in Trichomycteridae. A similar caudal stripe occurs in the trichomycterines *Trichomycterus barboursi* (Eigenmann, 1911), *T. melanopygius* Reis, Santos, Britto, Volpi & de Pinna, 2020, variably in *T. immaculatus* (Eigenmann & Eigenmann, 1889) (cf. Reis, de Pinna, 2022), in juveniles of *T. itatiayae* Miranda Ribeiro, 1906 and *T. ipatinga* Reis & de Pinna, 2022, in the stegophilines *Stegophilus septentrionalis* Myers, 1927, *Stegophilus panzeri* (Ahl, 1931), and *Haemomaster venezuelae* Myers, 1927, and in the vandelliine *Vandellia cirrhosa* Valenciennes, 1846.

**Remarks on tridentine taxonomy.** Uncertainties in the assignment of species to genera have historically characterized the description of new species in Tridentinae. Eigenmann, Eigenmann (1889) described the genus *Miuroglanis* to allocate *M. platycephalus* and *Tridens* to allocate *T. melanops* and *T. brevis*. The authors highlighted that the two later species were morphologically so disparate that they could belong to distinct genera. *Tridens brevis* was never illustrated, and its single type was lost shortly after its original description (see Eigenmann, 1918:370). Subsequent studies then transferred *T. brevis* to two other genera based solely on the textual descriptions of its external morphology provided by Eigenmann, Eigenmann (1889) and Eigenmann (1918).

Myers (1925) created the genus *Tridentopsis* to include *Tridentopsis pearsoni* Myers, 1925 and transferred *T. brevis* into that genus as well, thus restricting *Tridens* to *T. melanops*. *Tridentopsis tocantinsi* LaMonte, 1939 was described more than a decade later (LaMonte, 1939). Schultz (1944) then described the genus *Tridensimilis* to allocate a new species, *T. venezuelae* Schultz, 1944, and transferred *T. brevis* to that genus. Baskin (1973) disagreed with this transfer, arguing that *T. brevis* had morphological characters not found in *Tridensimilis venezuelae* but common to *Tridentopsis* species, such as the elongate

first pectoral-fin ray (= pectoral filament), a greater number of opercular odontodes, and an anal-fin origin only slightly anterior to the dorsal-fin origin. We agree with Baskin's (1973) interpretation and found additional corroborative evidence: the elongate maxillary and rictal barbels of *T. brevis*. These barbels were originally reported to extend "to the base of the pectoral" fin and the "gill opening", respectively (Eigenmann, Eigenmann, 1889, and Eigenmann, 1918). Among tridentines, such elongated maxillary and rictal barbels are found only in species of *Tridentopsis* (*vs.* barbels considerably shorter, with the maxillary barbel falling short of the branchiostegal opening and the rictal barbel not reaching the posterior margin of the eyeball). The elongate maxillary and rictal barbels are possibly reversals of reductions in these structures that could be optimized as having evolved at the base of the clade Tridentinae + Stegophilinae + Vandelliinae (Baskin, 1973). Moreover, we examined specimens collected near the type-locality of *T. brevis* (ZUEC 15118) that fit the diagnostic characters originally reported for the species. These specimens clearly belong to *Tridentopsis*. Therefore, all evidence indicate that *T. brevis* is a *Tridentopsis* and, consequently, *Tridensimilis* is a monotypic genus containing only *T. venezuelae*.

After the description of *Tridensimilis*, forty-six years passed before a new species of *Tridentopsis*, *T. cahuali* Azpelicueta, 1990, was described from the rio Paraguay drainage (Azpelicueta 1990). More recently, two new species of *Tridens* have been described from the Amazon basin, *T. chicomendesi* Henschel & Costa, 2023, and *T. vitreus* (Henschel *et al.*, 2023). With the description of *Rhinotridens chromocaudatus*, Tridentinae now contains ten valid species, being the third least diverse subfamily of Trichomycteridae.

**Comparative material examined. Argentina, Paraguay basin:** *Tridentopsis cahuali*, MZUSP 63092 (12 eth). **Bolivia, Amazon basin:** *Tridens melanops*, USNM 301661 (1 c&s). *Tridentopsis pearsoni*, CAS 28259 (3 of 17 eth paratypes). *Tridentopsis* sp. 3, UF 82214 (27 eth). **Brazil, Amazon basin:** *Miuroglanis platycephalus*, MCP 41080 (7 eth); MCZ 54363 (1 eth); MZUSP 106970 (5 eth). *Miuroglanis* sp. 1, MZUSP 7449 (2 eth, 1 c&s). *Rhinotridens* sp. 2, MZUSP 36302 (23 eth, 2 c&s); MZUSP 23449 (1 eth); MZUSP 72977 (1 eth). *Tridentopsis brevis*, ZUEC 15118 (31 eth). *Tridentopsis pearsoni*, MZUSP 109849 (29 eth, 1 c&s); MZUSP 126359 (68 eth). *Tridentopsis* sp. 1, MZUSP 116486 (7 eth, 2 c&s). **Paraguay basin:** *Tridentopsis cahuali*, MZUSP 123512 (18 eth). **Ecuador, Amazon basin:** *Tridentopsis* sp. 2, FMNH 99711 (273 eth, 10 c&s). **Paraguay, Paraguay basin:** *Tridentopsis cahuali*, MNHNP 1448 (12 eth). **Peru, Amazon basin:** *Tridens melanops*, INHS 40467 (1 c&s); MZUSP 121254 (2 eth). **Venezuela, Maracaibo basin:** *Tridensimilis venezuelae*, USNM 121290 (holotype); USNM 121291 (paratypes, 21 eth, 1 c&s).

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**Neotropical Ichthyology**

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**ETHICAL STATEMENT**

This study was carried out under approval of the Animal Care and Use Committee (ACUC) of the Instituto de Biociências, Universidade de São Paulo, to A. Datovo (Project #226/2015; CIAEP #01.0165.2014).

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The author declares no competing interests.

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