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Filling in a biogeographic gap: the first Trichomycteridae from the Parnaíba River basin (Siluriformes: Trichomycteridae)

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Trichomycterid catfishes have long been considered as absent in the Parnaíba River basin, Northeastern Brazil, in what constitutes their most conspicuous gap in geographic distribution. Herein we report on the first occurrence of the family in that basin. The new species is described from the riacho da Volta, right tributary to the upper rio Parnaíba, Piauí State. It is distinguished from its congeners by the combination of two or three pairs of ribs; 36–38 post Weberian vertebrae; a color pattern composed of round, similar-sized, non-coalescent spots; I,5 pectoral-fin rays; the first haemal arch on the 5th or 6th vertebrae; and the first completely fused (to the tip) haemal spine on the 15th vertebra. A putative autapomorphy is the partial (minimally 50% of their length) or total fusion between the anterior arms of the basipterygium. Preliminary evidence suggests that the new species can be related to northern South American forms, a pattern that fits the general Amazonian relationships of the fishes in the Parnaíba River drainage. Although the new species fills in an important qualitative gap in trichomycterid continental distribution, the taxon is apparently rare and extremely restricted in distribution, with the type series being its only record so far. The paucity of trichomycterids in the Parnaíba remains a puzzling biogeographical phenomenon.

Keywords: *Ituglanis*, New species, Taxonomy, Trichomycterinae.

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Os bagres tricomicterídeos têm estado surpreendentemente ausentes na bacia do rio Parnaíba, Nordeste do Brasil, no que constitui sua lacuna mais evidente na distribuição. Relatamos a primeira ocorrência da família na bacia. A espécie nova é descrita do riacho da Volta, tributário do lado direito do alto rio Parnaíba em Uruçuí, Piauí. Ela é distinguida de suas congêneres pela combinação de dois ou três pares de costelas; 36–38 vértebras pós weberianas; padrão de coloração composto de manchas arredondas, de tamanhos semelhantes e não coalescentes; I,5 raios nas nadadeiras peitorais; o primeiro arco haemal na 5° ou 6° vértebra, e o primeiro espinho haemal completamente fusionado (até a extremidade) na 15° vértebra. Uma possível autapomorfia é a fusão parcial (mínimo de 50% do seu comprimento) ou total entre os braços anteriores do basiopterígio. Evidências preliminares sugerem que a espécie nova pode estar relacionada com as formas do norte da América do Sul, padrão que se encaixa nas relações amazônicas dos peixes da drenagem do rio Parnaíba. Embora a espécie nova preencha uma importante lacuna na distribuição continental dos tricomicterídeos, o táxon é aparentemente raro e extremamente restrito em distribuição, sendo a série-tipo seu único registro até o momento.

Palavras-chave: *Ituglanis*, Nova espécie, Taxonomia, Trichomycterinae.

INTRODUCTION

The absence of any species of Trichomycteridae in the Parnaíba River basin, in Northeastern Brazil, is the most puzzling distributional gap of the family. Trichomycterids have one of the broadest and densest geographical distributions of any neotropical freshwater fish family, with representatives ranging from Costa Rica, in Central America, to Patagonia in southern South America, on both sides of the Andes (de Pinna, Wosiacki, 2003; Fernández, Schaefer, 2005; Fricke *et al.*, 2023). The southernmost record of any primary freshwater fish in South America is a trichomycterid, *Hatcheria macraei* (Girard, 1855) (*cf.*, Darlington, 1957; de Pinna, Wosiacki, 2003; Berra, 2007), with members of the family also inhabiting some offshore islands. They are ubiquitous in the Amazon, Orinoco, and Essequibo basins, the Maracaibo and Magdalena, the Guyana Shield, the Paraná-Paraguay, the Uruguay, the São Francisco, the Southeastern Brazilian drainages, and many other smaller basins, spanning an immense array of different ecological conditions (Wosiacki, 2004; Wosiacki, Garavello, 2004; Castellanos-Morales, 2018; Donin *et al.*, 2020; Ferrer, Malabarba, 2020; Dagosta, de Pinna, 2021; de Pinna, Dagosta, 2022). In view of that, their absence in the entire Parnaíba River basin, a major drainage in Northeastern Brazil, is indeed strange. The anomaly is compounded by the ichthyological affinities of the Parnaíba River basin with the Amazon drainage, a basin tremendously rich in trichomycterid species representing almost all of the currently recognized subfamilies.

Herein, we report on a new species of the genus *Ituglanis* Costa & Bockmann, 1993 which is the first Trichomycteridae from the Parnaíba River basin. Specimens of the taxon have been collected by one of us (WS) many years ago and their existence has been previously recorded in Ramos (2012) and Ramos *et al*. (2014), but they have not been the object of detailed taxonomic analysis. *Ituglanis* is a species-rich genus of the Trichomycteridae, with 30 valid species (11 of which described in the last ten years) (Fricke *et al*., 2023). Its taxonomy is increasingly complex and the majority of species are diagnosed by combinations of characters. The new species is noteworthy mostly because of its biogeographic significance. It shows that trichomycterids are actually present in the Parnaíba basin, although their diversity there remains oddly low for a basin of that size and with relationships with the trichomycterid-rich Amazonian ichthyofaunistic.

MATERIAL AND METHODS

Morphometric data were taken point to point with a digital calliper to the nearest 0.1 mm. Nomenclature of measurements followed Tchernavin (1944) for length of barbels; Wosiacki, de Pinna (2008) for length and depth of caudal peduncle and for supraorbital pore s6 distance; Ferrer, Malabarba (2011) for scapular girdle width; Ferrer *et al*. (2015) for length of interopercular odontodophore; and de Pinna (1992) for other measurements. Osteological data were obtained from four specimens (MZUSP 126756, one of which later also cleared and stained) radiographed with a Faxitron digital x-ray system, and other two (UFPB 12208) cleared and counterstained specimens prepared according to Taylor, Van Dyke (1985). Vertebral counts excluded those in the Weberian complex and the compound caudal centrum was counted as one. Terminology for external-anatomical structures of the opercular apparatus followed de Pinna, Dagosta (2022). Nomenclature of bones and cartilages followed Bockmann *et al.* (2004), except for the use of parurohyal instead of urohyal following Arratia, Schultze (1990) and of barbular, which followed de Pinna *et al*. (2020). Nomenclature of laterosensory canals and associated pores followed Rizzato, Bichuette (2016).

In meristics, number of specimens with each count is given in parentheses, and an asterisk indicates the count for the holotype. Meristics derived from subdivisions of the vertebral column have been regularly utilized in *Ituglanis* systematics. However, the landmarks adopted are still confusing throughout the literature and difficult to compare in different studies. Traditional regions of vertebral column in bony fishes do not adequately reflect the anatomy of sequential vertebral modifications in the genus (or the family Trichomycteridae). Herein we define three sectors based on clear-cut landmarks in the regionalization of the anterior post-Weberian vertebral column of the genus which may be useful as general reference for expressing taxonomically-informative variations: 1– Vertebrae lacking haemal spines and haemal canal (rib-bearing or not; the rib-bearing number is simply expressed in number of ribs); 2– vertebrae with a haemal canal (starting as a strut between the bases of parapophyses that moves distally gradually in more posterior vertebrae); 3– vertebrae with haemal spines fused to the very tip, with no trace of the median strut or split. Abbreviations used in the text are c&s (cleared and stained specimens), SL (standard length), and xr (radiographs). Institutional acronyms: LIRP, Laboratório de Ictiologia de Ribeirão Preto, Faculdade de Filosofia, Letras e Ciências Humanas, Universidade de São Paulo, Ribeirão Preto; MNHN, Muséum National d'Histoire naturelle, Systématique et Évolution, Laboratoire d'Ichthyologie

Générale et Appliquée, Paris; MNRJ, Museu Nacional, Rio de Janeiro; MZUSP, Museu de Zoologia da Universidade de São Paulo, São Paulo; UFPB, Universidade Federal da Paraíba, João Pessoa.

RESULTS

Ituglanis crispim, new species

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(Fig. 1; Tab. 1)

Ituglanis sp. —Ramos *et al*., 2014:04 [listed to Parnaíba River basin].

Holotype. MZUSP 126762, 28.8 mm SL, Brazil, Piauí, Uruçuí, riacho da Volta, right tributary to Parnaíba River, Parnaíba River basin, 07º24'18"S 44º50'21"W, 18 Jul 2005, W. Severi, B. Dourado & A. Antonello.

Paratypes. All collected with holotype. MZUSP 126756, 3 (1 c&s), 29.4–32.6 mm SL; UFPB 12208, 9 (2 c&s), 26.0–31.3 mm SL.

Diagnosis. *Ituglanis crispim* is distinguished from all congeners by the combination of the following characters: two or three pairs of ribs; 36–38 post Weberian vertebrae; a color pattern composed of round, uniformly-sized, evenly-spaced, non-coalescent spots; I,5 pectoral-fin rays; the first haemal arch on the 5th or 6th vertebra; the first completely fused (to the tip) haemal spine on 15° vertebrae. The presence of two or three pairs of ribs (*vs*. four pairs or more) distinguish the species from all congeners with the exception of *I. amazonicus* (Steindachner, 1882), *I. apteryx* Datovo, 2014, *I. compactus* Castro & Wosiacki, 2017, *I. eichhorniarum* (Miranda Ribeiro, 1912), *I. gracilior* (Eigenmann, 1912), *I. herberti* (Miranda Ribeiro, 1940), *I. ina* Wosiacki, Dutra & Mendonça, 2012, *I. inusitatus* Ferrer & Donin, 2017, *I. macunaima* Datovo & Landim, 2005, *I. metae* (Eigenmann, 1917), *I. nebulosus* de Pinna & Keith, 2003, and *I. parkoi* (Miranda Ribeiro, 1944). The count of 36–38 post Weberian vertebrae distinguish *I. crispim* from *I. amazonicus*, *I. apteryx*, *I. gracilior*, *I. herberti*, *I. inusitatus*, *I. metae*, and *I. parkoi*, all with 39 or more vertebrae. The pigmentation pattern composed by round, similar-sized, non-coalescent dark spots, slightly larger than eye (*vs*. color patterns either uniform, or mottled with irregular-sized spots or partly coalescent markings, or blotched, sometimes forming longitudinal strips) separates *I. crispim* from congeners, except for *I. amazonicus*, *I. gracilior*, *I. guayaberensis*, *I. macunaima*, and *I. metae*. The presence of I,5 pectoral-fin rays distinguishes *I. crispim* from *I. agreste* Lima, Neves & Campos-Paiva, 2013, *I. apteryx*, *I. bambui* Bichuette & Trajano, 2004, *I. boticario* Rizzato & Bichuette, 2015, *I. cahyensis* Sarmento-Soares, Martins-Pinheiro, Aranda & Chamon, 2006, *I. goya*, *I. epikarsticus* Bichuette & Trajano, 2004, *I. guayaberensis* (Dahl, 1960), *I. herberti*, *I. inusitatus*, *I. laticeps* (Kner, 1863), *I. gracilior*, *I. macunaima*, *I. mambai* Bichuette & Trajano, 2008, *I. paraguassuensis* Campos-Paiva & Costa, 2007, *I. parahybae* (Eigenmann, 1918), *I. parkoi*, *I. passensis* Fernández & Bichuette, 2002, *I. payaya* (Sarmento-Soares, Zanata & Martins-Pinheiro 2011), *I. proops* (Miranda Ribeiro, 1908), and *I. ramiroi* Bichuette & Trajano, 2004, all with I,4; I,6 or more. The first haemal arch on 5th or 6th vertebrae distinguishes *I. crispim* from *I. bambui* (10th,12th), *I. boticario* (8th), *I. compactus* (4th), *I. epikarsticus* (7th, 9th), *I. goya* (9–10th), *I. nebulosus* (4th), and *I. ramiroi* (7th, 8th, 10th); the first complete haemal spine on 15th vertebra distinguishes *I. crispim* from *I. amazonicus* (17th), *I. australis* Datovo & de Pinna, 2014 (12–13th), *I. eichhorniarum* (16th, 18th), *I. epikarsticus* (13–14th), *I. goya*, (16th, 18th), *I. gracilior* (16th, 17th, 20th), *I. nebulosus* (16th), *I. payaya* (14th), *I. paraguassuensis* (12th), *I. passensis* (14th), I. proops (14th), and *I. ramiroi* (12–14th), (the latter two characteristics have been verified in limited samples of some species, intraspecific variation may be larger than recorded). A putatively autapomorphic character for the new species is the partial or total fusion between the anterior arms of the basipterygium (united minimally for 50% of their length) (Fig. 2).

FIGURE 1 | *Ituglanis crispim*, MZUSP 126762, holotype, 28.8 mm SL, riacho da Volta, right tributary to Parnaíba River, Parnaíba River basin. Left lateral, dorsal, and ventral views.

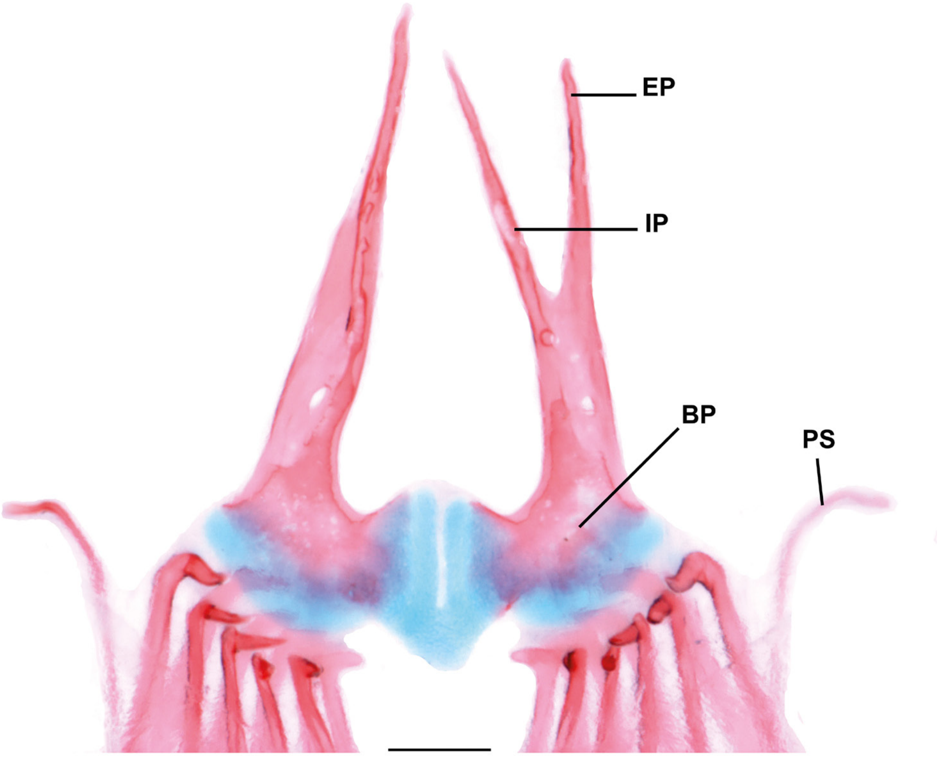

FIGURE 2 | Pelvic girdle of *Ituglanis crispim*, paratype, MZUSP 126756, 29.7 mm SL (c&s), dorsal view. Abbreviations: basipterygium (BP); external process (EP); internal process (IP); pelvic splint (PS). Scale bar = 0.2 mm.

Description. External morphology. Morphometric data in Tab. 1. Body elongate, roughly cylindrical in cross-section at trunk, gradually compressed towards caudal peduncle. Dorsal and ventral profiles of trunk slightly convex and slightly concave at caudal peduncle

Head depressed, trapezoid in dorsal view, slightly longer than wide. Dorsal profile straight and ventral profile straight to slightly convex. Snout round in dorsal view. Eyes on anterior half of head, close to posterior nostril. Orbital rim not free. Elliptical ocular capsule formed by thin and transparent skin. Nostrils smaller than eye diameter. Anterior nostril surrounded by fleshy flap of integument posterolaterally continuous with nasal barbel. Posterior nostril surrounded anterolaterally by thin flap of integument. Gill openings narrowly united to isthmus anteriorly, forming free fold. Mouth subterminal and slightly convex in ventral view. Lower lip with lateral fleshy folds continuous with rictal barbel base. Lips covered with small papillae.

Barbels with wide bases, tapering gradually towards tips. Nasal barbel emerging from posterolateral region of anterior nostril, its tip reaching to posterior portion of opercular odontodophore. Maxillary barbel reaching to pectoral-fin base. Rictal barbel reaching to posterior portion of interopercular odontodophore.

Pectoral fin with distal margin convex, first ray unbranched and prolonged as short filament, followed with five branched rays (13*). Pelvic-fin origin anterior to vertical

TABLE 1 | Morphometric data for *Ituglanis crispim*. Ranges include holotype and paratypes. N = 13; SD = Standard deviation.

	Holotype	Range	Mean	SD
Standard length (mm)	28.8	26.0-32.6	28.7	-
Percent of standard length				
Head length	19.7	18.4-20.2	19.4	0.64
Predorsal length	74.6	70.7-76.7	73.8	1.81
Prepelvic length	62.1	59.0-63.8	62.0	1.68
Preanal length	71.9	69.4-75.5	73.2	1.91
Scapular girdle width	16.9	16.0-18.8	17.4	0.77
Trunk length	47.4	45.1-49.9	47.6	1.82
Pectoral-fin length	12.8	11.8-14.3	13.1	0.83
Pelvic-fin length	8.9	8.3-9.6	8.9	0.38
Distance between pelvic-fin base and anus	6.1	5.0-6.9	5.7	0.54
Caudal peduncule length	20.1	15.0-20.1	17.3	1.60
Caudal peduncule depth	14.7	11.6-15.1	13.4	1.03
Body depth	17.5	14.7-17.7	16.6	0.97
Length of dorsal-fin base	11.5	9.8-13.0	11.5	0.90
Length of anal-fin base	9.2	7.5-9.5	8.5	0.63
Percent of head length				
Head width	88.5	87.3-98.1	91.0	3.20
Nasal barbel length	72.1	52.7-85.3	75.6	9.44
Maxillary barbel length	86.1	80.8-98.4	88.2	5.27
Rictal barbel length	60.7	60.7-81.0	74.4	6.17
Snout length	26.3	26.3-32.5	28.9	2.29
Interorbital	15.7	15.3-21.0	18.4	1.88
Mouth width	32.6	32.6-38.4	35.5	1.69
Eye diameter	12.9	9.4-16.5	12.7	1.64
Supra-orbital pore distance	14.2	10.1-16.1	14.2	1.66
Interopercular length	30.8	27.1-32.6	29.8	1.74

through origin of dorsal fin, with distal margin convex, covering urogenital papilla and almost reaching origin of anal fin. Pelvic fin with one (13*) unbranched ray and four branched rays (13*; 1 specimen with three on one side). Bases of contralateral pelvic fins contacting each other medially (one specimen with bases tightly adpressed to each other).

Dorsal fin with distal margin convex, with two (2 xr*, 1xr–c&s) or three (1xr, 2c&s) procurrent rays, two (11*) or three (2) unbranched rays and six (6) or seven (7*) branched rays. Dorsal fin located on posterior one-third of trunk with fin origin approximately at vertical through posterior margin of adpressed pelvic fin.

Anal fin elongated with distal margin convex, approximately same size of dorsal fin, with two (3 xr*, 1 xr–c&s, 2 c&s) procurrent rays, two unbranched rays (13*) and five branched rays (13*). Origin of anal fin located slightly posterior to vertical through dorsal-fin origin. Caudal fin with distal margin round. Upper plate with one (12*) or two (1) unbranched ray and five (12*) or four (1) branched rays; lower caudal plate with one (10) or two (3*) unbranched rays and six (10) or five (3*) branched rays. Procurrent caudal-fin rays 15 (first of them vestigial) (2 xr*, 1 xr–c&s, 1 c&s) or 14 (1xr) dorsally and ten (1xr, 1xr–c&s,1 c&s), 11 (1xr) or 12 (1xr*, 2 c&s) ventrally.

Osteology. Mesethmoid shaft expanded laterally along anterior half, with convex margins, narrowing at base of cornua. Mesethmoid cornua directed straight laterally, with tips slightly curved posteriorly, gradually narrower toward tip, reaching laterally two-thirds of premaxilla (Fig. 3A). Anterior cranial fontanel small, teardrop-shaped, its posterior margin slightly posterior to transverse line through exit for infraorbital branch of latero-sensory canal (Fig. 3A). One specimen with vestigial anterior fontanel, reduced to slight spacing along median frontal suture at corresponding position. Posterior cranial fontanel teardrop-shaped, smaller than anterior one, situated posteriorly in supraoccipital, its center approximately at tranverse line through midlength of pterotic (Fig. 3A).

Lacrimal-antorbital short, longer than broad, positioned dorsal to anterior portion of autopalatine (Fig. 4). Barbular long, inserted at lateral-ethmoid-orbitosphenoid limit, gently curved laterally anteriorly; Widest portion of barbular at its anterior third,

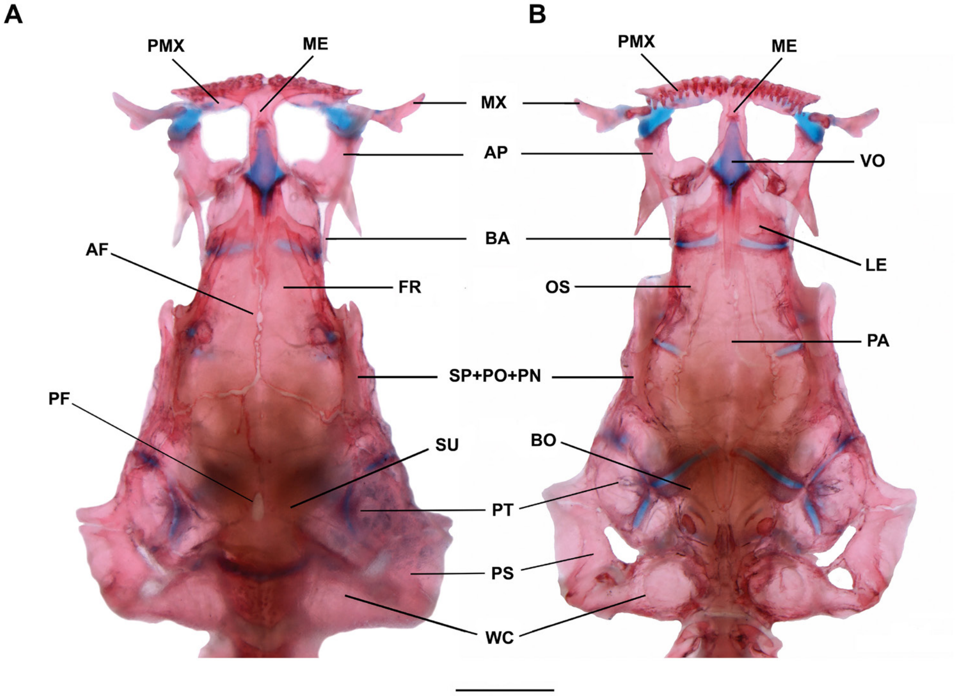

FIGURE 3 | Neurocranium and related structures of *Ituglanis crispim*, paratype, MZUSP 126756, 29.7 mm SL (c&s). **A.** Dorsal and **B.** Ventral views. Abbreviations: mesethmoid (ME); premaxilla maxilla (PMX); maxilla (MX); anterior fontanel (AF); autopalatine (AP); frontal (FR); barbular (BA); parieto-supraoccipital (SU); orbitosphenoid (OS); posterior fontanel (PF); lateral ethmoid (LE); parasphenoid (PA); sphenotic-prootic-pterosphenoid complex bone (SP+PO+PN); vomer (VO); basioccipital (BO); Weberian capsule (WC). Some elements are not shown. Scale bar = 1 mm.

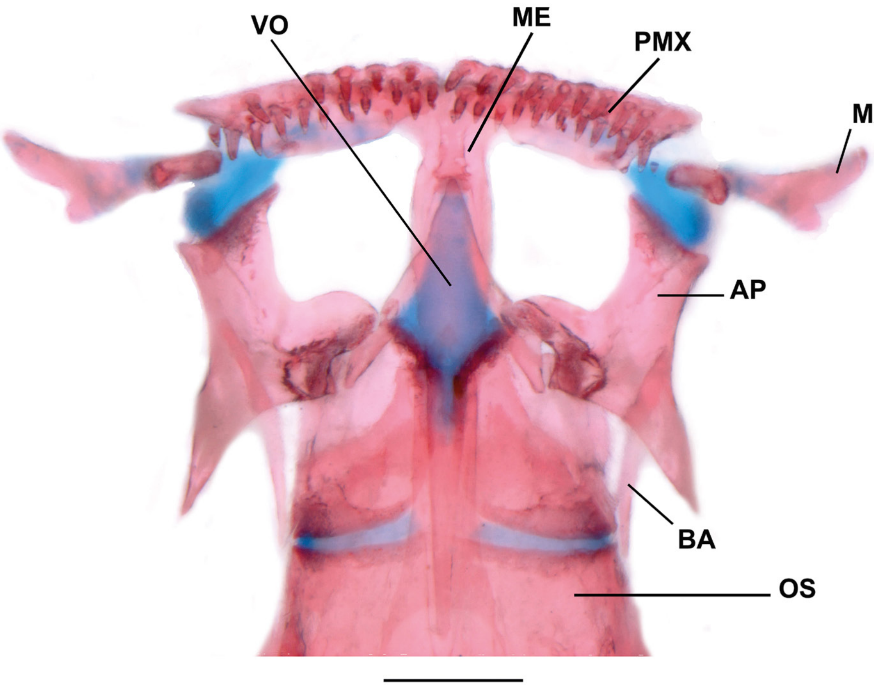

FIGURE 4 | Anterior part of skull and related structures of *Ituglanis crispim*, paratype, MZUSP 126756, 29.7 mm SL (c&s). Ventral view. Abbreviations: mesethmoid (ME); premaxilla (PMX); maxilla (MX); barbular (BA); orbitoshpenoid (OS); autopalatine (AP); and vomer (VO). Some elements are not shown. Scale bar = 0.5 mm.

forming attenuated processes dorsally and ventrally (Figs. 3–4). Sphenotic with anterior margin protruding anteriorly, clearly diverging from lateral margin of frontal (Fig. 3A). Sphenotic, prootic, and pterosphenoid fused (Fig. 3). Trigeminofascialis foramen oval, formed at limit between anterior margin of former bone and posterior margin of orbitosphenoid. Proximal portion of emerged trigeminofascialis nerve following protruded portion of sphenotic dorsal to it. Vomer arrow-shaped, its anterior narrow tip not reaching base of mesethmoid cornua. Lateral arms of vomer large and well-defined, directed posterolaterally (Figs. 3, 4B). Posterior shaft of vomer long, spike-like, overlapping anterior portion of parasphenoid, nearly to transverse line through midlength of orbitosphenoids. Parasphenoid extending posteriorly as long narrow process reaching anterior third of basioccipital (Fig. 3B). Weberian capsule small and oval, with anterior margin fused to basioccipital, capsule produced laterally into long tube with small distal openings (Fig. 3B).

Premaxilla long, with lateral portion narrowing to pointed process flush with anterior margin, with 16–20 conical similar-sized teeth, distributed in two regular rows (Figs. 3–4). Dentary with 15–22 conical teeth, variable in size distributed in two regular rows not reaching coronoid process. Autopalatine with sinusoid anterior margin, capped with large cartilage articulating anteriorly with premaxilla and maxilla (Figs. 3–4). Medial margin of autopalatine produced mesially at right angle into broad articular region (= with deep concavity in previous works). Articular surface of palatine bipartite, with anterior portion articulating with vomer and posterior one with lateral ethmoid. Posterior process of autopalatine overlapping anterior portion of metapterygoid. Metapterygoid longer than broad, tapering posteriorly and ventrally curved, connected to quadrate through narrow cartilage-mediated articulation located at its anterior region, forming roundish fenestra with corresponding recesses in anterodorsal portion of metapterygoid and posterodorsal region of dorsal process of quadrate (Fig. 5). Quadrate with large anterodorsal process, expanded anteriorly and posteriorly, former expansion triangular (Fig. 5). Hyomandibula strongly expanded anterodorsally, with well-developed notch (sometimes two, closely positioned) at midlength on dorsal margin (Fig. 5). Opercular odontodophore oval or round, with 13–19 conical odontodes in circular arrangement (counted in three c&s specimens). Opercle with double articulation, dorsal one with hyomandibula and ventral, smaller one, with preopercle. Opercle with large pointed ascending process. Interopercular odontodophore elongate with 14–19 conical odontodes (counted in three c&s specimens), arranged in two rows and not extending anteriorly beyond articulation with the suspensorium. Opercular and interopercular odontodes increasing in size posteriorly (Fig. 5).

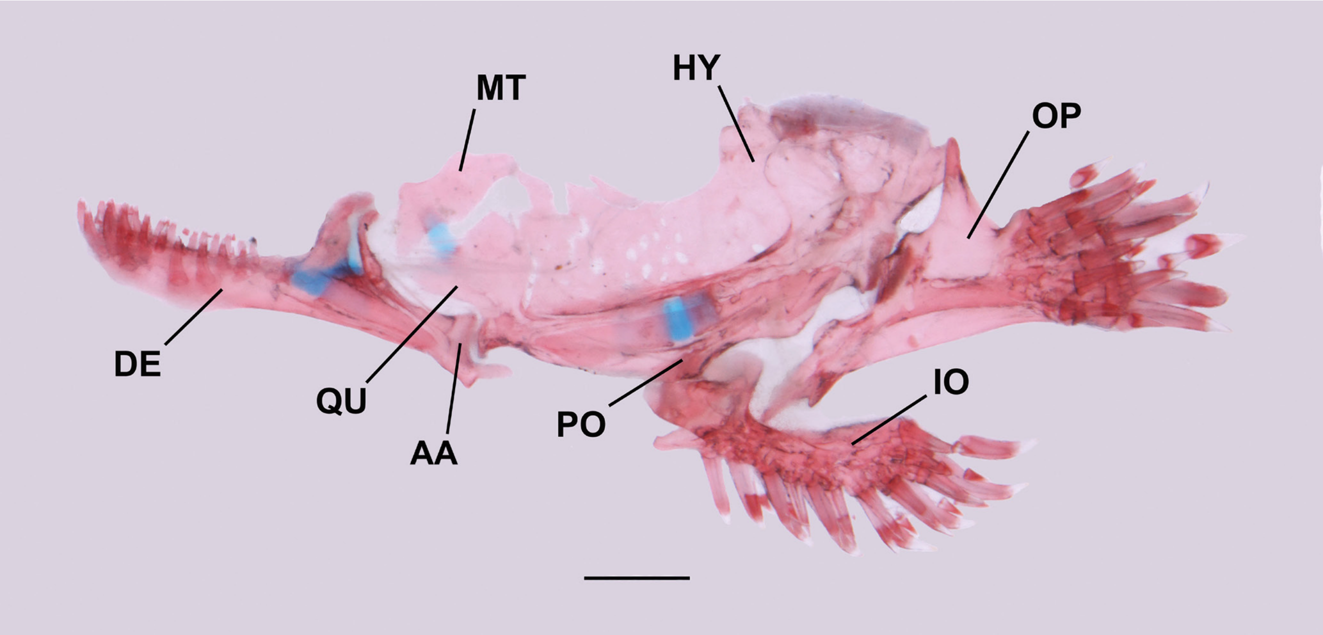

FIGURE 5 | Suspensorium and opercular apparatus of *Ituglanis crispim*, paratype, MZUSP 126756, 29.7 mm SL (c&s). Lateral view. Abbreviations: metapterygoid (MT); quadrate (QU); preopercle (PO); interopercle (IO); opercle (OP); hyomandibula (HY); dentary (DE), and anguloarticular (AA). Image from right side, inverted to conform to standard position. Scale bar = 0.5 mm.

Ventral (and only) hypohyal triangular. Anterior ceratohyal elongate, expanded at both anterior and posterior ends, with plane of expansions orthogonal to each other. Posterior ceratohyal short and roughly triangular, narrowing markedly from base to tip. Eight branchiostegal rays: three in contact with anterior ceratohyal, four closely-set on interceratohyal cartilage, and posterior one distantly connected with rest of series. Four posterior branchiostegal rays expanding distally (Fig. 6). Interhyal absent. Parurohyal with well-defined anterior arms diverging anterolaterally and wide posterolateral wings narrowing distally, with round tips. Parurohyal with fine posterior process and wide round hyoid foramen (Fig. 7).

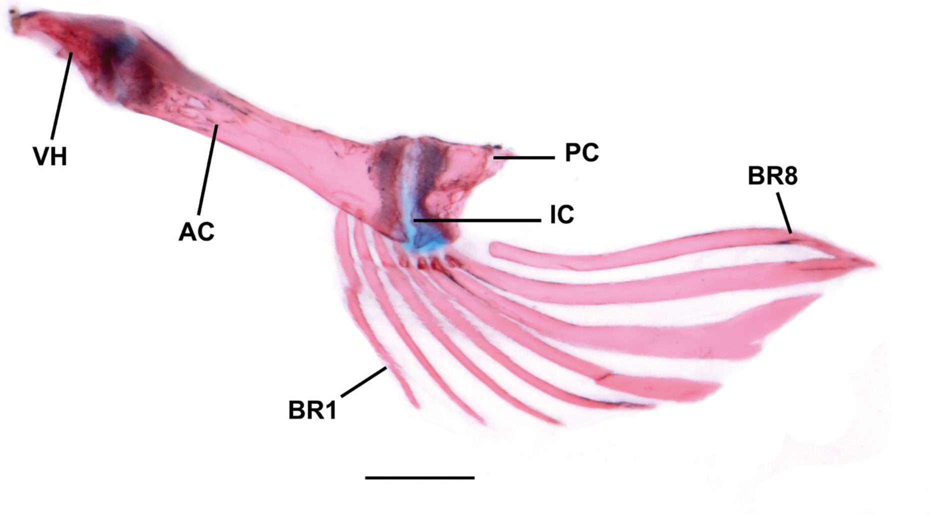

FIGURE 6 | Hyoid arch of *Ituglanis crispim*, paratype, MZUSP 126756, 29.7 mm SL (c&s). Lateral view. Abbreviations: anterior ceratohyal (AC); BR1–8, branchiostegal rays 1 to 8; inter-ceratohyal cartilage (IC); posterior ceratohyal (PC); ventral hypohyal (VH). Image from right side, inverted to conform to standard position. Scale bar = 0.5 mm.

FIGURE 7 | Parurohyal of *Ituglanis crispim*, paratype, MZUSP 12208, 26.7 mm SL. Dorsal view. Scale bar = 0.2 mm.

Basibranchials 2 and 3 elongate, connected to each other by cartilage; basibranchial 2 with gentle expansions at anterior and posterior ends, longer than rod-like basibranchial 3. Basibranchial 4 catilaginous, pentagonal with concave edges. Hypobranchial 1 rod-like, slightly broader laterally than mesially, with cartilaginous tips. Hypobranchial 2 mostly cartilaginous, oriented obliquely to anteroposterior axis, with small conical ossification at anterolateral corner. Hypobranchial 3 mostly cartilaginous, twice as broad as hypobranchial 2 and with anterolateral bony cap similar in shape to that of hypobranchial 2 but twice as large. Five elongate ceratobranchials with cartilaginous tips. Ceratobranchials 1 to 4 abruptly and variably narrowing towards proximal ends. Ceratobranchial 5 shorter than preceding elements, with 10–12 conical teeth irregularly concentrated on dorsal surface near mesial margin of anterior half of bone. Gill rakers present on ceratobranchials 3–5, weakly ossified, spaced out and loosely attached. Vestigial ossified raker elements occasionally also present in ceratobranchial 2. Epibranchial 1 with large pointed uncinate process at midlength of anterior margin; epibranchial 2 with small process in anterior margin; epibranchial 3 with rounded process on posterior margin. Epibranchial 4 rectangular, with wide articular surface with upper pharyngeal plate and narrow one with ceratobranchial 4. Pharyngobranchials 1 and 2 absent. Pharyngobranchial 3 small, rod-like, similar in shape to hypobranchial 1, but smaller in size. Pharyngobranchial 4 cartilaginous and attached to dorsolateral surface of very large, curved, upper pharyngeal plate, the latter with conical teeth, arranged in two irregular rows, increasing in size posteriorly (Fig. 8).

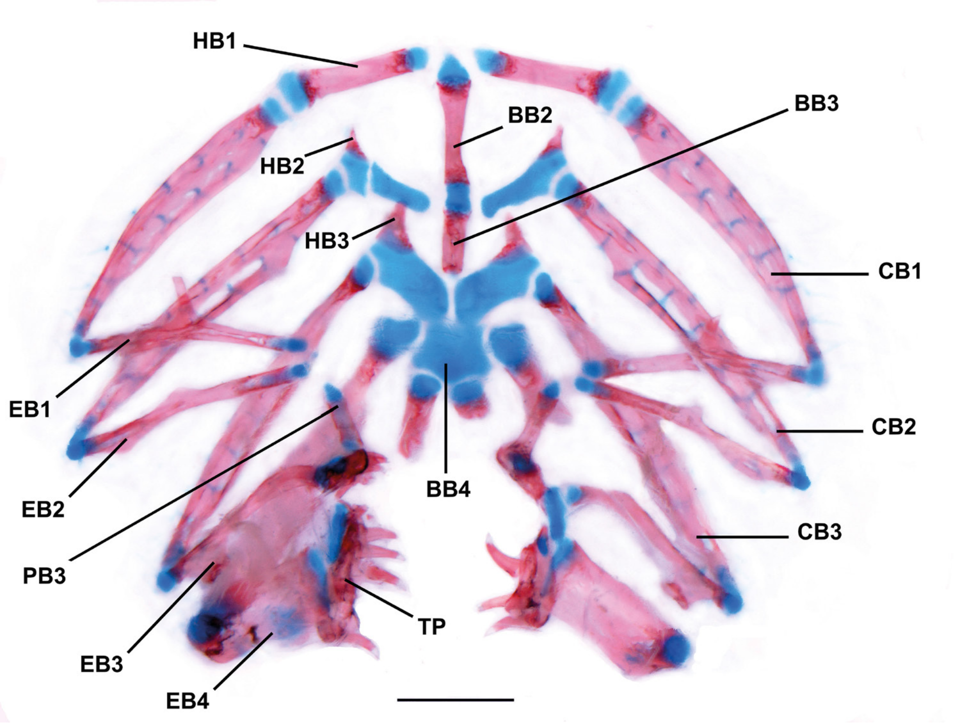

FIGURE 8 | Gill arches of *Ituglanis crispim*, paratype, MZUSP 126756, 29.7 mm SL (c&s). Dorsal view. Abbreviations: basibranchials 2 to 4 (BB2–4); ceratobranchials 1 to 3 (CB1–3); epibranchials 1 to 4 (EB1–4); hypobranchials 1 to 3 (HB1–3); pharyngobranchial 3 (PB3). Ceratobranchials 4 and 5 (CB4–5), and upper pharyngeal tooth plate (TP) damaged and partly missing. Scale bar = 0.5 mm.

Pelvic bone small in overall size, with small basal plate produced mesially into flared articular surface for its counterpart. Cartilages for fin rays and interbasipterygial articulation thick and well developed, with two cartilaginous regions continuous or nearly so. Anterior arms of basipterygium variable. One specimen with one side deformed, the other with two separate arms united by medial lamina of bone for at least 50% of their length. Another specimen with one side partly separate as in previous specimen and the other side entirely fused, forming single basally broad anterior arm, tapering to fine tip (Fig. 2). Third specimen with one side with arms partly separate as in previous specimens and the other side with arms almost entirely fused but retaining separate tips, fused region broad for entire length, not tapering. Fused morphology of basipterygial arms apparently extreme condition of partial fusion observed in specimens with separate arms.

Dorsal fin with eight (2 xr, 1xr–c&s, 2c&s) or (1xr*) nine pterygiophores, first one inserted anterior to neural spine of 24th (1xr), 23rd (2 xr*, 1 xr–c&s) or 22nd (1c&s) vertebrae. Anal fin with six pterygiophores (3 xr*, 1xr–c&s, 2c&s), first one inserted anterior to haemal spine of 25th (xr), 24th (2xr*, 1xr–c&s) or 23rd (1c&s) vertebrae. Epural variable, present as a comma-shaped bone in two specimens (1xr, 1xr–c&s), as a small round distal element in two (1xr, 1c&s) and absent in two (1 xr*, 1c&s). Uroneural independent of hypural elements. Upper hypural plate as single element (presumably including fused hypurals 3, 4 and 5) or with two elements, a slightly smaller upper one (presumably independent hypural 5) and a slightly larger lower one (presumably fused hypurals 3 and 4) (relative sizes of each element not matching usual proportions of such components in other trichomycterid taxa) (Figs. 9–10). Lower hypural plate (presumably co-ossified parhypural and hypurals 1 and 2) fused to compound caudal centrum (Figs. 9–10). Branched caudal fin splitting once. Post-Weberian vertebrae 36 (1c&s), 37 (1 1xr–c&s) or 38 (3 xr*); ribs two (1 xr, 1c&s) or three (2 xr*, 1xr–c&s) (Fig. 3); first haemal arch on vertebrae 5th (2 c&s) or 6th (1 c&s); first fully fused haemal spine on vertebrae 15th (3 c&s).

Laterosensory system. Laterosensory canals with simple (non-dendritic) branches ending in single pores. Nasal and frontal canals of supraorbital branch continuous, with three pores (s1, s3, and s6). Supraorbital pores s1 and s3 located at posterior portion of anterior and posterior nostrils, respectively; supraorbital pore s6 aligned with posterior margin of eyes.

Antorbital segment of infraorbital canal absent. Sphenotic canal present with two pores, i10 and i11 (one specimen with three pores on right side). Otic, postotic, and scapular canals present, with preoperculomandibular branch and pterotic branch short and with one associated pore each. Postotic canal with preoperculomandibular and pterotic branches located anterodorsal to opercular odontodophore; po1 pore located at horizontal line through i11; pterotic pore po2 (located at posterior margin of opercular odontodophore, medial to preoperculo-mandibular pore. Trunk canal short with two pores (one specimen with three pores on left side; one with three pores on right side and one with one pore on left side) anteriorly located between pectoral-fin base and opercular odontodophore.

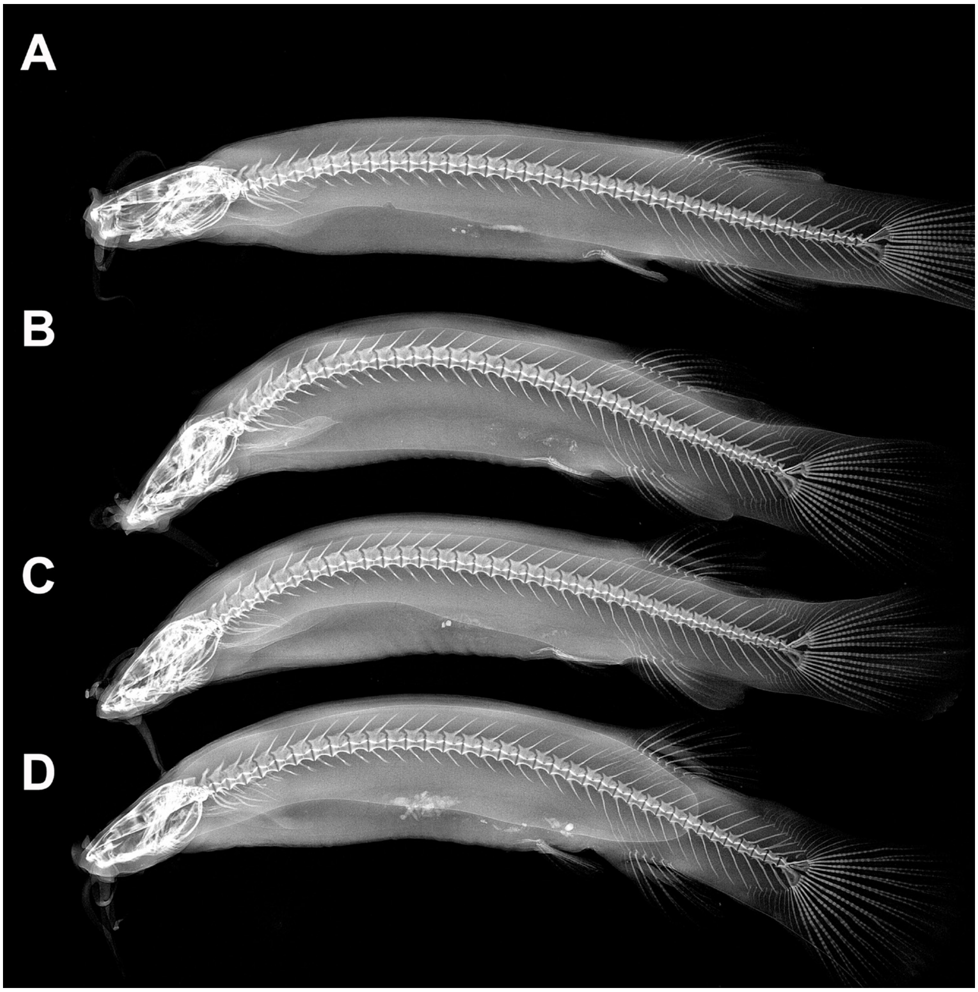

FIGURE 9 | Radiographs of types specimens of *Ituglanis crispim*. Lateral views. MZUSP 126756, paratypes, 32.6, 29.4, 29.7 mm SL, respectively (**A, C**, **D,** latter now c&s); **B.** MZUSP 126762, holotype, 28.8 mm SL.

Coloration in alcohol. Dorsal and lateral surface of body and head with uniform covering of round, similar-sized, non-coalescent dark spots, most of which slightly larger than eye (Fig. 1). Spots uniformly spaced, entirely individualized, separated from each other by thin frames of white. Markings not forming rows, stripes or concentrations anywhere on body, including middorsal and midlateral areas. Dark covering fading abruptly below limit of abdominal cavity along abdomen, but extending to ventral limit of body posterior to posterior margin of pelvic fins. Abdomen white, with some specimens (including holotype) with few faint spots anterior to pelvic-fin insertion. Dorsal and lateral surface of head with covering of spots similar to those on body, but slightly smaller in size. Ventral side of lower lip with few dark spots. Opercular odontodophore white in central portion but with dark streaks on surrounding periodontodal fold. Interopercular odontodophore darkly pigmented in central area, and predominantly white around margin in most specimens, in some others dark coloration irregular and not segregated between peripheral and central areas. Maxillary barbel with irregular dark markings on dorsal surface, most concentrated on proximal half. Nasal barbel pigmentation similar to that of maxillary one, but on both surfaces. Rictal barbel white, except for few dark spots on dorsal surface near base. Pectoral fin with elongate dark fields over rays until about two-thirds of their lengths, darkest along edge of first ray. Dorsal fin with concentration of spots along base, fading in middle of fin and then concentrated again at distal third, not reaching edge of fin. Anal-fin with dark covering similar to that of dorsal one, but fainter. Caudal fin with covering of elongate dark fields along entire length, forming faint jagged vertical rows. Distal margin of caudal fin white. Pelvic fin white.

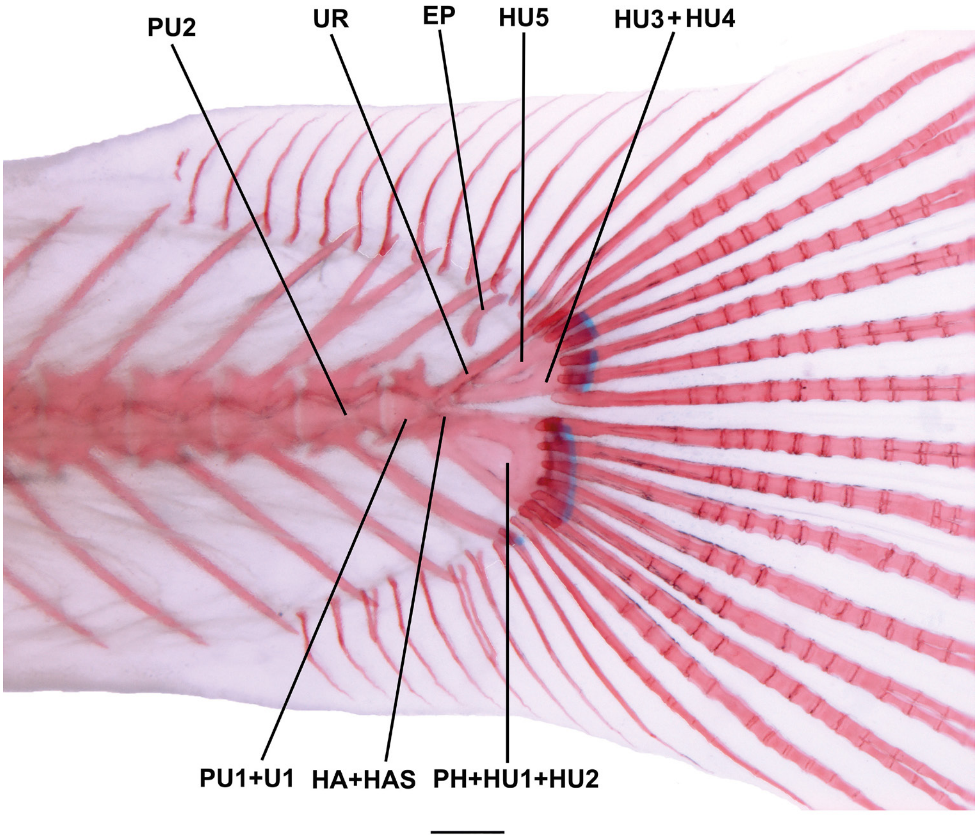

FIGURE 10 | Caudal-fin skeleton of *Ituglanis crispim*, paratype, MZUSP 126756, 29.7 mm SL (c&s). Lateral view. Abbreviations: epural (EP); hypurapophysis (ha) plus secondary hypurapophysis (has) (HA+HAS); hypural 5 (HU5); presumed hypurals 3 plus 4 (HU3+HU4); hypurals 1 plus 2 plus parhypural (PH+HU1+HU2); preural centrum 1 plus ural centrum 1 (PU1+U1); preural centrum 2 (PU2); uroneural (UR). Scale bar = 0.5 mm.

Geographical distribution. *Itugalnis crispim* is known so far from a single site in the riacho da Volta, right tributary to Parnaíba River, Parnaíba River basin (Fig. 11).

Ecological notes. *Ituglanis crispim* is so far known from a small clear water perennial creek, with moderate current, hard clay bottom, submerged filamentous algae, and riparian vegetation typical of the Cerrado biome, at *ca*. 200 m a.s.l. (Fig. 12). No other fish species were found at that spot. Stomach contents of two c&s specimens show larvae of Diptera (Simuliidae), Nematoda, and unidentified remains of insects. No evidence was found of mature gonads in external examination. Dissection of alcoholic specimens was not attempted because of rarity of specimens.

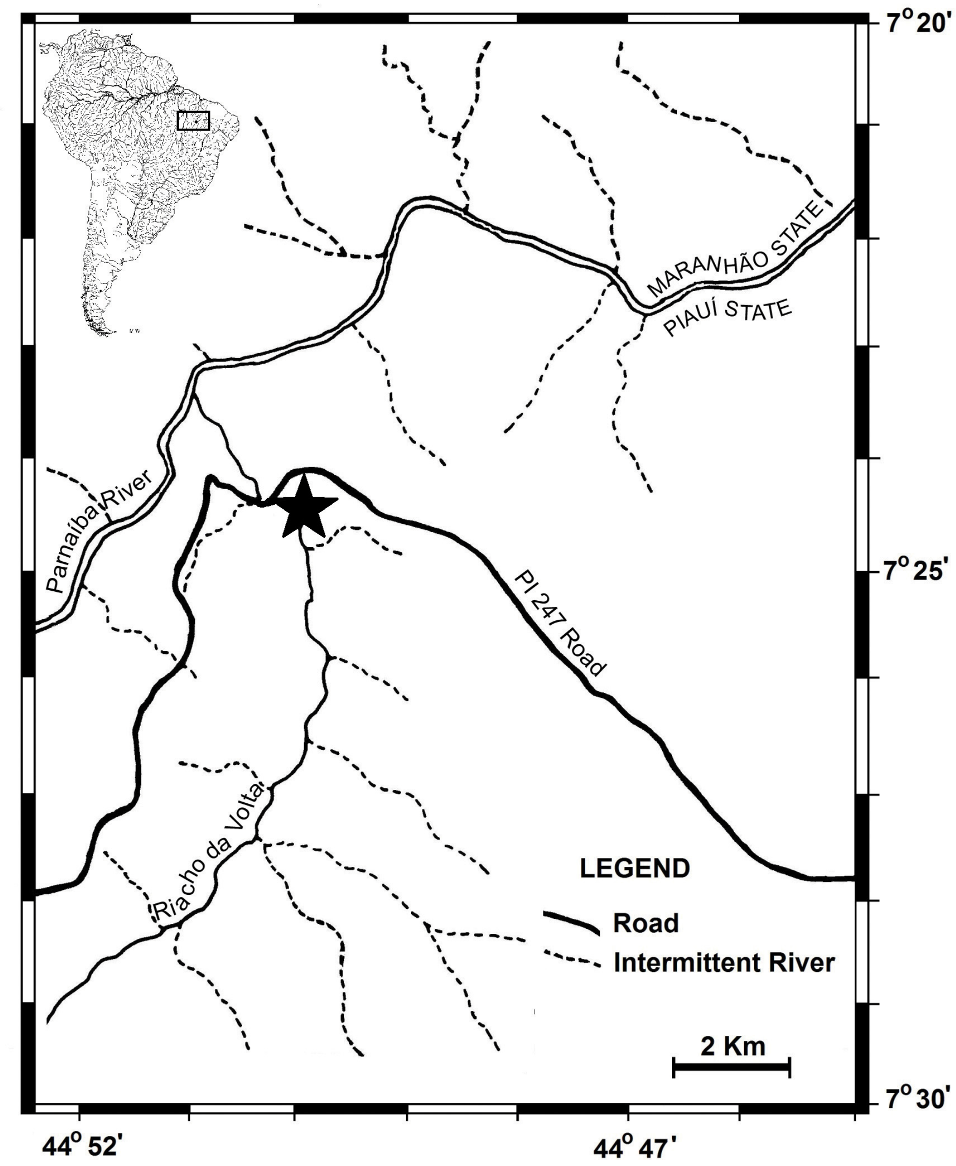

FIGURE 11 | Geographical distribution of *Ituglanis crispim* (black star).

Etymology. The specific epithet was given in reference to the Crispim, known for the local tragedy-legend "Cabeça de Cuia". Having murdered his own mother, Crispin was cursed and turned into a horrific aquatic creature with a gigantic "cuia" (bowl-shaped) head, condemned to perpetually wander the Parnaíba River and only to be redeemed after devouring seven virgins named Maria. A noun in apposittion.

Conservation status. *Ituglanis crispim* is endemic to Parnaíba River basin and known so far from a single locality in a small tributary within the Parnaíba River drainage. The lack of any additional records of the species, either in the type locality and elsewhere since 2005, despite at least one additional sampling attempt, suggests that the species is narrowly endemic and perhaps locally rare also. Despite the extremely restricted geographic range, no specific threats have been detected, therefore *I. crispim* can be categorized as Least Concern (LC) according to IUCN categories and criteria (IUCN Standards and Petitions Subcommittee, 2022). However, the apparently narrow distribution, lack of environmental monitoring of the type locality and the absence of any additional specimens since the type series, indicate that survival of the species is highly dependent on the preservation of its watercourse and of the Cerrado biome around its known range.

FIGURE 12 | **A.** Type locality of *Ituglanis crispim*, riacho da Volta, right tributary to Parnaíba River, Uruçuí, Parnaíba River basin, Piauí, Brazil. **B.** In detail the submerged filamentous algae. Photo taken on July 18, 2005.

DISCUSSION

Taxonomic status. The monophyly of *Ituglanis* has been recovered and supported by morphology (Costa, Bockmann, 1993; de Pinna, 1998; Datovo, Bockmann, 2010; Wosiacki *et al*., 2012), and by molecular analyses (Ochoa *et al*., 2017, 2020; Henschel *et al*., 2018; Katz *et al*., 2018; Fernández *et al*., 2021). The placement of *I. crispim* in *Ituglanis* is unequivocally supported by all the three synapomorphies originally proposed by Costa, Bockmann (1993): *i.* posterior cranial fontanel present as a small circular opening on the posterior region of the parietosupraoccipital (except in *Ituglanis payaya*); *ii*. a deep concavity in the mesial margin of the autopalatine (the result of an articular-bearing mesial projection of the bone); and *iii*. anterior portion of the sphenotic portion of the compound sphenotic-prootic-pterosphenoid directed anteriorly. Wosiacki (2002), Wosiacki *et al*. (2012) proposed additional synapomorphies for *Ituglanis*: *i*. presence of five or more abdominal vertebrae (*i.e*., post-Weberian vertebrae lacking both a complete haemal spine and an associated rib); *ii*. parapophyses of the first four post-Weberian vertebrae medially directed (or at least one of the first four parapophyses of the post-Weberian vertebrae medially directed; *cf*. discussion in Mendonça *et al*., 2018); *iii*. presence of two or fewer vertebrae between the first dorsal-fin pterygiophore and the first anal-fin pterygiophore; *iv*. presence of 23 or more post-Weberian vertebrae anterior to the first dorsal-fin pterygiophore. From that list, Datovo, de Pinna (2014) considered the presence of five or more abdominal vertebrae as the only unambiguous additional synapomorphy for *Ituglanis*, all others having exceptions or occurrences outside of the genus. In any event, for whatever comparative significance they may have, *I. crispim* shares all those condition except the last (the species has 22 vertebrae anterior to the first dorsal-fin pterygiophore).

Costa *et al*. (2021) proposed additional putative synapomorphies for *Ituglanis*: *i*. metapterygoid semi-circular with an antero-dorsal convex margin (*vs*. shape subtriangular to subtrapezoidal); *ii.* a narrow and elongated lateral process of the parurohyal (except in *I. goya*); and *iii*. eight or fewer pairs of ribs (previously proposed in Datovo, de Pinna, 2014). *Ituglanis crispim* shares all those conditions, with the metapterygoid showing a particularly extreme condition of the apomorphic condition, with the bone being more elongated, tapering posteriorly and surpassing the quadrate expansion posteriorly (Fig. 5). A similar condition was verified in *I. compactus* (*cf*. fig. 4 in Castro, Wosiacki, 2017), but a more extensive survey is necessary to assess the phylogenetic significance of such variations.

Morphological differentiation among species of *Ituglanis* is mostly subtle, falling along repetitive lines of combinations of meristic and qualitative characters, and integumentary pigmentation, rarely with unique characteristics. *Ituglanis crispim* is no exception. A single putative autapomorphy has been identified for the species, namely a fusion between the anterior arms of the basipterygium. This fusion is represented by a thin sheet of bone between the two arms. The degree of fusion is variable (even in different sides of the same specimen), but always beyond 50% of the length of the arms, with total fusion in one side of one specimen (Fig. 12). In all other examined specimens of *Ituglanis*, the basipterygium arms are entirely separate or united only basally (for no more than 25% of their length). This potential autapomorphy still needs further corroboration because it has been verified in only three c&s specimens available of *I. crispim*, and the pelvic skeleton is known to display large intraspecific variation in trichomycterines (Arratia *et al*., 1978). Still, a similar condition has not been observed in any of the numerous specimens of several different species examined of the genus, strongly suggesting that the condition in *I. crispim* lies outside of the range of intraspecific variation observed in the genus and is thus unique to the species. A situation similar to that in *I. crispim* is documented for some specimens of *Bullockia maldonadoi* (Eigenmann, 1920) (Arratia *et al*., 1978:166–67, figs. 5, 16), but most likely convergently, due to the phylogenetic distance between the two taxa.

Relationships within *Ituglanis* remain mostly uncharted. De Pinna, Keith (2003) proposed preliminary subgroups in *Ituglanis* as a first attempt of organization of the diversity and the relationships within the genus, suggesting the existence of a northern and a southern clade. The former is diagnosed by the presence of three or fewer ribs (*vs.* five or more); the southern clade would be diagnosed by the presence of a posterolateral process on the anterior third of the barbular bone (*vs*. bone rod-like, lacking such process). *Ituglanis crispim* has the first condition (2–3 pairs of ribs), shared with *I. amazonicus*, *I. apteryx*, *I. compactus*, *I. eichhorniarum*, *I. gracilior*, *I. herberti*, *I. ina*, *I. inusitatus*, *I. macunaima*, *I. metae*, *I. nebulosus*, and *I. parkoi*. The barbular process has been shown to vary markedly in *Ituglanis*, in a fashion that defies its potential phylogenetic meaning (Datovo, de Pinna, 2014; Rizzato, Bichuette, 2016; Mendonça *et al*., 2018). In any case, *I. crispim* has a thickening of bone in the expected position, not forming an actual process but possibly part of a homologous series of modifications.

The absence of the antorbital segment of the infraorbital laterosensory canal (*i.e*., pores i1 and i3 absent) is considered as a putative apomorphic condition in *Ituglanis* (Rizzato, Bichuette, 2016) shared by species of the northwestern clade of Rizzato, Bichuette (2016), plus *I. cahyensis*, *I. parahybae*, and *I. goya* from the southeastern clade Rizzato, Bichuette (2016), and more recently in *I. inusitatus* (Ferrer, Donin, 2017) and *I. amphipotamus* Mendonça, Oyakawa & Wosiacki, 2018 (Mendonça *et al*., 2018). This condition also is shared among troglomorphic species, *I. bambui*, *I. ramiroi*, *I. passensis*, and *I. epikarsticus* (Rizzato, Bichuette, 2016) and is variable in *I. australis* (Datovo, de Pinna, 2014). The antorbital segment of the infraorbital laterosensory canal is absent in *I. crispim*.

Despite a well-documented wide range of intraspecific variation in integumentary pigmentation in most trichomycterines (Arratia, 1978; Silva *et al*., 2010; Nascimento *et al*., 2017; Donin *et al*., 2020; 2022), coloration may still be suggestive of the phylogenetic relationships of *I. crispim*. Its pattern of round, closely-set yet fully independent, similar-sized spots, uniformly-spaced, not coalescing or forming stripes or complex markings, is seen only in species in northern South America (greater Amazon and satellite basins). Those species are *I. amazonicus*, *I. compactus* (although known from mostly faded specimens, vestiges of dark pigment in some specimens in MZUSP 127009 reveal the pattern), *I. gracilior*, *I. guayaberensis*, *I. macunaima*, and *I. metae*. That list also includes the taxon described as *Pygidium gabrieli* Myers, 1926, currently included in *Trichomycterus* but actually related to *Ituglanis* and proposed by Mendonça (2017) as a synonym of *I. amazonicus*. The northern *Ituglanis* assemblage includes other species with different patterns, such as *I. apteryx*, *I. goya*, *I. ina*, *I. nebulosus*, and *I. parkoi* (an illustration of the holotype of *I. nebulosus* is herein included as Fig. 13 for current and future reference, because the original publication suffered a print defect). However, the regular-spotted pattern described above is not seen in any species outside of the northern range. This coloration pattern is thus further preliminary evidence that *I. crispim* may be to Amazonian congeners, an alignment also supported by the reduced number of ribs discussed above. Resolution of this issue certainly require additional data, most notably from DNA sequences.

FIGURE 13 | *Ituglanis nebulosus*, holotype, MNHN 2001–1128, 36.6 mm SL, Arataye River, tributary to Approuague River, near the natural preserve "Reserve naturelle des Nouragues", French Guiana.

Biogeographical implications. Despite the record of *I. crispim*, the paucity of trichomycterids in the Parnaíba River drainage remains a mystery. The fish fauna of the basin has long been recognized as having a strong Amazonian component (Agassiz, Agassiz, 1868; Roberts, 1968; Ramos, 2012; Ramos *et al*., 2014), although such affinity has not been unambiguously demonstrated by quantitative biogeographic analysis (Dagosta, de Pinna, 2017). The taxonomic composition of the Parnaíba is somewhat diminished compared to Amazonian tributaries of similar size. Morphological data indicate that *Ituglanis crispim* is related to the Amazonian subset of the genus (see Discussion), which fits the generally perceived general faunistic affinities of the Parnaíba River drainage. Virtually all Amazonian sub-drainages are inhabited by a rich diversity of trichomycterids, of both parasitic and non-parasitic taxa and including representatives of all subfamilies, with the exception of the Copionodontinae, Microcambevinae and Trichogeninae, both of which are relictual forms from eastern basins. They occupy all water types and habitats, from fast flowing "Terra Firme" streams to muddy lagoons, from deep water river channels to shallow margins of rivers. The ecological conditions in the Parnaíba River and its tributaries certainly cover favourably a wide array of environmental requirements of trichomycterids. Also, potential prey species for the parasitic taxa are abundant, including large pimelodids such as species of *Brachyplatystoma* Bleeker, 1862 and *Pseudoplatystoma* Bleeker, 1862, in addition to an assortment of large characiforms (*e.g*., *Prochilodus lacustris* Steindachner, 1907, *Serrasalmus rhombeus* (Linnaeus, 1766)). The headwaters and smaller tributaries include lotic environments which would be suitable for a number of the generalist non-parasitic species. Thus, current ecological constraints cannot be a determining factor in trichomycterid scarcity in the Parnaíba River basin. Despite recent advances (*e.g*., Ramos *et al*., 2014, 2017; Melo *et al*., 2016; Abreu *et al*., 2019; Dutra *et al*., 2022), it is true that the ichthyofauna of the basin remains poorly-known, especially in its upper reaches where some portions are yet entirely unexplored (de Pinna, Wosiacki, 2003). Still, if trichomycerids were as ubiquitous there as in other Amazonian rivers, they would certainly have been reported at current levels of knowledge. The absence of any parasitic forms from the lower reaches of the river is particularly revealing, because that sector has been sampled for many years. Besides, parasitic taxa are highly conspicuous and never go unnoticed by riverine folk. Therefore, the phenomenon of trichomycterid scarcity in the Parnaíba River stands out and it must have a historical explanation. Although a quantitative analysis is yet to be done, general circumstances suggest that this phenomenon is a result of large-scale local extinction. Whichever factors resulted in decreased fish diversity in the Parnaíba River basin when compared to the Amazon, their effect on trichomycterids has been particularly severe. There are other notable taxonomic absences in the Parnaíba, such as genera *Brycon* Müller & Troschel, 1844 (Characidae), *Semaprochilodus* Fowler, 1941 (Prochilodontidae), *Megalechis* Reis, 1997 (Callichthyidae), and the entire family Ctenoluciidae. Perhaps a fruitful approach to resolve the question might be to compile other taxa which are similarly depauperate or absent in the Parnaíba and then survey for intersecting factors or particularities which might suggest a specific common causative factor.

Comparative material examined. *Ituglanis amazonicus*: MZUSP 30449, 1 (c&s); MZUSP 86820, 1, 44.3 mm SL; MZUSP 86821, 1 (c&s); *Ituglanis amphipotamus*: MZUSP 65750, 2 (c&s); *Ituglanis apteryx*: MZUSP 115048, holotype, 62.4 mm SL; *Ituglanis australis*: MZUSP 112505, holotype, 55.9 mm SL; MCP 10420, 1 (c&s), paratype; *Ituglanis bambui*: MZUSP 79862, 1 (c&s), paratype; (MZUSP 79863, 1 (c&s), paratype; MZUSP 79864, 2 (c&s), paratypes; *Ituglanis boticario*: LIRP 11010, 1 (c&s); *Ituglanis compactus*: MZUSP 127009, 1 (c&s), 23.1 mm SL; *Ituglanis epikarsticus*: MZUSP 79871, 2 (c&s), paratypes; MZUSP 79872, 1 (c&s), paratype; *Ituglanis goya*: MNRJ 11489, 5 paratypes (c&s); MZUSP 40792, 2 (c&s); *Ituglanis herberti*: MNRJ 1428, holotype, 57.6 mm SL; MNRJ 1429, 2 paralectotypes, 51.9–54.3 mm SL; MNRJ 28466, 1 paralectotype; *Ituglanis macunaima*: MZUSP 86237, 1 (c&s), paratype; MZUSP 86251, 1 (c&s); MZUSP 103799, 2 (c&s); *Ituglanis mambai*: MZUSP 94719, 4 paratypes, 26.4–66.1 mm SL; *Ituglanis nebulosus*: MZUSP 69574, 1 (c&s), paratype; *Ituglanis paraguassuensis*: LIRP 5780, holotype, 38.2 mm SL; LIRP 5834, 5 paratypes, 33.1–41.3 mm SL; MZUSP 102535, 6, 37.8–41.9 mm SL; *Ituglanis parahybae*: MZUSP 79810, 2 (1 c&s); *Ituglanis passensis*: MZUSP 80098, 1 (c&s); *Ituglanis proops*: MZUSP 60255, 1 (c&s), 45.3 mm SL; *Ituglanis ramiroi*: MZUSP 79865, holotype, 27.5 mm SL; MZUSP 79866, 2 (c&s), paratypes; MZUSP 79867, 2 (c&s), paratypes.

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