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Taxonomy of *Triportheus* (Ostariophysi: Triportheidae) from the Paraná-Paraguai basin, South America

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A taxonomic review of *Triportheus* from the Paraná-Paraguai basin was conducted, with four valid species recognized: two natives, one introduced in the upper rio Paraná basin, and one new species described herein. Redescriptions, including osteological characters and detailed coloration patterns, are presented for all recognized species. An update on the distribution of *Triportheus* species in the Paraná-Paraguai basin is provided, along with discussions regarding introductions in the upper rio Paraná basin and hypothesis of occurrences. In this context, a key for the identification of *Triportheus* species from the rios Paraná-Paraguai basin is also provided.

Keywords: Characiformes, Freshwater sardines, Identification key, La Plata system, Taxonomic review.

Uma revisão taxonômica de *Triportheus* da bacia Paraná-Paraguai foi realizada, com quatro espécies válidas reconhecidas: duas nativas, uma introduzida na bacia do alto rio Paraná e uma espécie nova aqui descrita. Redescrições, incluindo caracteres osteológicos e padrões de coloração detalhados são apresentadas para todas as espécies reconhecidas. Uma atualização da distribuição das espécies de *Triportheus* da bacia Paraná-Paraguai é apresentada, com discussões sobre introduções no alto rio Paraná e hipótese de ocorrências. Neste contexto, uma chave de identificação das espécies de *Triportheus* das bacias dos rios Paraná-Paraguai também é fornecida.

Palavras-chave: Characiformes, Chave de identificação, Revisão taxonômica, Sardinhas de água doce, Sistema La Plata.

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INTRODUCTION

Triportheus Cope, 1872 is commonly known as freshwater sardines, and holds 16 valid species with distributions across most South American river basins (Malabarba, 2004). Almost all species are restricted to a specific river basin, except for *Triportheus albus* Cope, 1872 (from the rios Tocantins/Araguaia and Amazonas basins), *Triportheus brachipomus* (Valenciennes, 1850) (from the río Orinoco basin and coastal drainages between the Essequibo River in Guyana and drainage of the rio Araguari in Brazil) and *Triportheus auritus* (Valenciennes, 1850) (from the basins of the rios Amazonas, Tocantins/Araguaia, Orinoco and coastal drainages between the Essequibo River in Guyana and drainage of the rio Araguari in Brazil) (Malabarba, 2004; Mariguela *et al*., 2016). *Triportheus magdalenae* (Steindachner, 1878) is the only species which occurs in the Transandean region, found in the río Magdalena basin, in Colombia (Malabarba, 2004; Fricke *et al*., 2024).

Chalcinus nematurus Kner, 1858 (= *Triportheus nematurus*) was the first species described from the Paraná-Paraguai basin, based on syntypes from a locality not mentioned in the original description. Subsequently, Kner (1860) designated three localities in Mato Grosso State as type-localities to *C. nematurus*: "Cujaba, Suaguragua, Caiçara", currently defined as "Cuiabá", after the selection of a lectotype in Malabarba (2004). The second species described from the Paraná-Paraguai basin was *Chalcinus paranensis* Günther, 1874 (= *Triportheus nematurus*), described from the holotype with an inaccurate locality mentioned as "from the river Parana".

These two species remained valid until the catalog of Garman (1890), which not only examined specimens from the Paraná-Paraguai basin, but recognized, based on the original description, *Chalcinus nematurus* as a junior synonym of *C. angulatus* (Spix & Agassiz, 1829), described from the rio Amazonas basin, and *C. paranensis* as the only valid species from the Paraná-Paraguai basin. Posterior publications kept the proposition of Garman (1890), of *C. angulatus* (= *T. angulatus*) as a senior synonym of *C. nematurus* (= *T. nematurus*) (*e.g*., Eigenmann, Eigenmann, 1981; Miranda Ribeiro, 1941; Fowler, 1950; Géry, 1977).

Portugal (1990) was the first to consider *T. nematurus* as a valid species since Garman (1890), and to record *T. nematurus* and *T. paranensis* as species naturally distributed within the Paraná-Paraguai basin, besides mentioning the introduction of *Triportheus signatus* (Garman, 1890) within the rio Tietê, adding a third species of *Triportheus* to this river system. Lima *et al.* (2003) listed *T. nematurus* and *T. paranensis* from the rios Paraná-Paraguai basin. Still, they did not mention any inclusion of *T. signatus* for the rio Tietê basin or other rivers from the upper rio Paraná basin. Malabarba (2004) proposed *T. nematurus* as a senior synonym of *T. paranensis* and observed that the species named as '*Triportheus nematurus*' (non Kner, 1858) by Portugal (1990) and subsequent authors (Malabarba, 1998; Lima *et al*., 2003) was an undescribed taxon, described as *Triportheus pantanensis* Malabarba, 2004. Malabarba (2004) also did not mention any occurrence of *T. signatus* within the rios Paraná-Paraguai basin.

Triportheus angulatus and *T. signatus* remained cited as belonging to the rios Paraná-Paraguai basin after revision by Malabarba (2004), mainly within the upper rio Paraná basin, as species introduced for restocking reservoirs (Cetra, Petrere, 2006; Mariguela *et al*., 2016; Garcia *et al*., 2018; Pelicice *et al*., 2018). A possible new species was also registered in the rio Paraguai basin by Mariguela *et al*. (2016), named as *Triportheus* aff.

rotundatus due to its morphological similarity with *T. rotundatus* (Jardine, 1841), which occurs within the rio Amazonas basin.

Based on the complex taxonomic history described above, herein we review the taxonomy of the *Triportheus* species from the Paraná-Paraguai basin, thus providing diagnoses and an identification key for all the described species, proposing the recognition of a new species and reducing the Linnean shortfall (*sensu* Hortal *et al*., 2015) regarding the genus.

MATERIAL AND METHODS

Measurements and counts followed Fink, Weitzman (1974), with the modifications proposed by Malabarba (2004) and the addition of head depth (measured between the supraoccipital spine and the isthmus) and orbit to dorsal distance (measured between the posterior margin of the eye until the base of dorsal fin). All measurements were performed with a digital caliper, and were taken point-to-point, on the left side of the specimens whenever possible, approximating tenths of millimeters. Measurements are expressed in tables, as percents of standard length (SL) or head length (HL). In the description, the ranges of meristic data are followed by the frequency for each count in parenthesis, with an asterisk indicating the value of the holotype. Individuals of each species were cleared and stained (c&s) according to the method of Taylor, Van Dyke (1985). The nomenclature applied to the bones and cartilage follows Weitzman (1962), with some modifications adopted by Carvalho, Malabarba (2015). Only informative osteological characters were considered in the diagnosis and description of the species. The institutional abbreviations follow Sabaj (2020), with addition of CPUEMS, Coleção de Peixes da Universidade Estadual de Mato Grosso do Sul and CITL, Coleção Ictiológica de Três Lagoas, Três Lagoas, MS, Brazil.

Lots analyzed at CPUEMS that are not cataloged were added to the list of examined material, with the addition of "p" and "n". For this material, 'p' represents a sampling point along the rio Paraguai or rio Apa basin and the 'n' (numbering) represents the identification of the point of collection of the lot, according to the collection's curator, Professor Yzel Rondón Súarez.

RESULTS

We recognized four species of *Triportheus* in the Paraná-Paraguai basin: *T. nematurus*, *T. pantanensis*, *T. signatus*, and one new species from the rio Paraguai basin.

Triportheus claudiae, new species

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(Figs. 1–2; Tab. 1)

Triportheus aff. *rotundatus*. —Mariguela *et al*., 2016:132 [phylogenetic relationships and biogeography].

Holotype. CITL 400, 102.6 mm SL, bay on Pousada Arara Azul, Pantanal, Corumbá municipality, rio Paraguai basin, Mato Grosso do Sul State, Brazil, 19°19'0.01"S 57°03'14.00"W, 25 Mar 2019, H. Gimenes-Junior, T. T. M. Taveira, F. Severo-Neto & R. Rech.

Paratypes. Brazil, Mato Grosso do Sul State: CITL 401, 3, 94.3–99.7 mm SL, collected with the holotype. CITL 1135, 3 c&s, 45.3–52.7 mm. LBP 3720, 7, 45.2–69.3 mm SL, Aquidauana Municipality, rio Negro, 19°34'54"S 56°15'16.5"W, 3 Aug 2006, C. Oliveira & L. H. G. Pereira. LBP 3757, 16, 63.4–74.5 mm SL, rio Negro, rio Paraguai basin, Aquidauana Municipality, 19°34'33.7"S 56°14'49"W, 1 Aug 2006, C. Oliveira & L. H. G. Pereira. LBP 11917, 5, 37.9–49.4 mm SL, Corumbá municipality, rio Miranda, 19°34'58.3"S 57°01'18.9"W, 25 Nov 2009, C. Oliveira and team. **Mato Grosso State:** MNRJ 21681, 82.5 mm SL, Barão de Melgaço, rio Cuiabá, Baía Chacororé, 16 Jan 1978, E. P. Caramaschi & CEPIPAM.

Non-types. The following specimens were not included as type-material due to bad preservation of some morphological structures. **Rio Paraguai basin, Brazil, Mato Grosso State:** LBP 11916, 3, 55.2–70.7 mm SL. LBP 18627, 3, 68.0–96.1 mm. **Mato Grosso do Sul State:** SL. LBP 3557, 62.2 mm SL. LBP 3795, 4, 59.3–81.7 mm SL. LBP 5802, 4, 32.2–35.0 mm SL.

Diagnosis. *Triportheus claudiae* differs from its congeners by the following combination of characters: two non-elongated scales between the pectoral fin and the ventral keel (*vs*. one vertically elongated scale between the pectoral fin and the ventral keel in *T. albus*, *T. auritus*, *T. brachipomus*, *T. culter* (Cope, 1872), and *T. magdalenae*); gill rakers on the lower branch of the first branchial arch, 24–29 (mode = 25, n = 8) (*vs.* 40–47 in *T. trifurcatus* (Castelnau, 1855), 38–48 in *T. nematurus*, 52–57 in *T. guentheri* (Garman, 1890), 35–44 in *T. signatus*); predorsal scales regularly disposed, in series, or with maximum two scales out of series (*vs.* predorsal scales irregularly disposed, not in series, with more than three scales disorganized in *T. angulatus*, *T. rotundatus*, *T. nematurus*, *T. guentheri*, *T. curtus* (Garman, 1890), *T. pantanensis*, *T. orinocensis* Malabarba, 2004, and *T. venezuelensis* Malabarba, 2004); premaxilla teeth in three rows (*vs*. teeth of premaxilla in two rows in *T. curtus* and *T. pictus* (Garman, 1890); epipleural bones: 20–21 (*vs.* 16–17 in *T. pantanensis* and 22–23 *T. signatus*); ventral tubules in the laterossensory canal of the preopercule: 7 (*vs.* 4–5 in *T. nematurus* and 5 in *T. signatus*).

Description. Morphometric data in Tab. 1. Deep and short body, laterally compressed, with ventral keel by expansion of coracoids. Greatest body depth at vertical through origin of dorsal fin. Slightly convex dorsal profile. Ventral profile convex and expanded between insertion of head and origin of pelvic fin.

Two pairs of nostrils, anterior and posterior opening of similar size; anterior opening circular and posterior opening oval. Terminal mouth, lower jaw largest than the upper jaw. Premaxillary teeth in three rows: outer row with 4(2), 5*(26), or 6(6) tricuspid small teeth; medial row with rarely 2(1) or 3*(33) tricuspid, large teeth and inner row with 5(6), 6(24), or 7*(4) pentacuspid teeth, largest from other teeth on premaxilla. Maxillary bone with 0(12), 1(6), 2*(12), or 3(4) tiny tricuspid teeth. Lower jaw teeth in two rows: outer

TABLE 1 | Morphometric data of *Triportheus claudiae*. N = Number of individuals; Min-Max = Minimum and maximum; SD = Standard deviation.

	Holotype	Paratypes				Non-types			
		N	Min-Max	Mean	SD	N	Min-Max	Mean	SD
Standard length (mm)	102.6	23	37.9–99.7	63.7	–	15	32.4–96.1	64.5	–
Percents of standard length									
Body depth	38.0	23	32.8–39.6	35.9	1.9	15	33.8–38.6	36.1	1.6
Head length	23.4	23	23.6–30.5	26.0	1.8	15	21.6–30.1	25.9	1.9
Head depth	21.3	23	20.3–26.9	23.7	1.7	15	20.6–27.6	23.9	1.7
Predorsal distance	63.1	23	59.6–64.3	61.8	1.4	15	58.0–66.0	62.4	1.8
Preventral distance	56.1	22	53.7–59.7	56.6	1.8	15	52.4–57.6	54.8	1.4
Preanal distance	74.1	23	69.7–77.0	73.5	2.0	15	70.8–74.5	72.1	1.1
Caudal peduncle height	10.9	23	7.8–10.7	9.3	0.8	15	6.5–10.3	8.7	1.1
Dorsal-fin base length	10.5	23	9.6–12.3	11.1	0.7	15	9.8–13.3	10.9	1.1
Anal-fin base length	27.5	23	25.7–31.6	29.0	1.2	15	24.3–30.1	27.7	1.9
Pectoral-fin length	37.0	23	36.8–43.2	39.8	1.7	15	37.1–41.7	39.4	1.4
Pelvic-fin length	14.7	22	11.3–17.6	13.9	1.6	15	11.8–14.1	12.9	0.9
Dorsal-fin length	18.1	23	17.5–22.9	20.3	1.4	15	16.0–21.8	18.9	1.8
Anal-fin length	11.1	23	8.5–14.1	11.7	1.6	15	8.6–12.7	10.7	1.4
Caudal peduncle length	9.9	23	7.8–10.7	9.0	0.8	15	8.2–10.1	9.0	0.6
Dorsal-fin to adipose-fin distance	27.1	23	25.2–28.1	26.4	1.0	15	26.0–30.0	27.6	1.3
Orbit to dorsal-fin distance	52.7	23	45.8–52.9	49.4	1.9	15	46.4–51.8	49.6	1.8
Dorsal-fin to caudal peduncle distance	41.2	23	36.0–41.5	39.2	1.4	15	37.5–43.9	39.7	2.0
Percents of head length									
Orbital diameter	28.6	23	29.2–34.6	31.5	1.7	15	27.9–31.8	29.6	1.5
Snout length	27.1	23	21.8–26.2	23.9	1.0	15	22.4–27.6	24.5	1.5
Interorbital distance	30.8	23	26.4–32.6	30.0	1.8	15	29.0–33.0	31.3	1.2
Upper jaw length	25.5	23	21–26.6	24.0	1.9	15	20.5–26.6	23.6	1.9

row with 4(2), 5(27), or 6*(5) large pentacuspid teeth, and inner row with one conical symphysial, large tooth. Gill rakers smaller and wider than branchial filaments; gill rakers on lower branch of first branchial arch: 24(4), 25(8), 26(4), 27*(7), 28(6), or 29(5).

Dorsal fin with ii,9 rays (33); anal fin with iii,26(1), 27*(6), 28(13), 29(9), 30(2) or 31(3) rays, its origin at vertical through last ray of dorsal fin. First branched ray of anal fin larger; pectoral fin with i,10(3), 11*(16) or 12(15) rays, extending more than half length of pelvic fin; pelvic fin with i,6 rays (32); caudal fin with i,9/8,i rays (31), bifurcated margin in juveniles and truncated margin in adults. Middle caudal rays with small extensions in large individuals.

Scales cycloid, large, with approximately same size of orbit. Lateral line complete, curved, its origin dorsally at flank, on supracleithrum and following to ventral region of body after pectoral fin, in third row of scales in vertical of pelvic fin, finishing at medial rays of caudal fin. Canals of lateral line scales with one to three branches; generally, small individuals (less than 50 mm SL) with one single branch and large individuals (more than 50 mm SL) with two or three branches. Perforated scales on lateral line: 31(7), 32(5), 33(7), or 34*(15); six scales above lateral line and two scales below lateral

line; two scales on vertical line between origin of pectoral fin and ventral keel; predorsal scales: 9(1), 10(2), 11(6), 12(7), or 13*(2), in regular series; 10(8) or 11(29) scales around caudal peduncle.

Total vertebrae: 35(2) or 36(1); precaudal vertebrae: 17(3); caudal vertebrae: 18(2) or 19(1); epineural bones: 35(2) or 37(1), with first three unbranched; epipleural bones: 20(1) or 21(2), with first epipleural unbranched; epipleural bones from second to 12th branched in dorsal portion; epipleural bones from 13th to 21st unbranched. Upper procurrent rays: eight (1) or nine (2); lower procurrent rays: seven (1) or eight (2).

Coloration in alcohol. Overall ground coloration yellowish silver, darker dorsally. Melanophores on proximal and distal fields of scales, forming five to eight fainted black stripes on flank. Stripes above lateral line generally with grouped melanophores, mainly on third to fifth stripes (from dorsal to ventral region). Remaining stripes with scattered melanophores. One inconspicuous stripe on scales from lateral line, by presence of few scattered melanophores; black stripes on flank converging with diffuse spot at hypural plate and base of caudal fin rays. Melanophores in anterodorsal region of head, from premaxilla to supraoccipital; anterior portion of lower jaw, posterior region of maxilla, antorbital, infraorbitals 4, 5, and 6, supraorbital and all the opercle with scattered melanophores (Fig. 1). Fins mostly hyaline: dorsal fin with distal tip and interradial membrane black; anal fin, occasionally, with black stripe on scales of base and rays generally hyaline, with scattered melanophores on interradial membrane and grouped melanophores on distal tip; adipose fin with scattered melanophores; caudal fin with melanophores grouped on rays, most evident on medial rays and scattered in interradial membrane. Distal tip of caudal fin black; pectoral fin hyaline, with scattered melanophores on interradial membrane and distal tip; pelvic fin with few scattered melanophores.

Coloration in life. Overall silvery coloration, darker dorsally. Greenish tones on posterior portion of head, in parietal, supraoccipital and opercle. Green metallic chromatophores scattered in scales on flank, between supracleithrum and caudal peduncle most conspicuous on anterior and posterior extremities. Scattered xanthophores on head, mainly in frontal, eyes, infraorbitals 5 and 6 and opercle; scattered xanthophores

FIGURE 1 | *Triportheus claudiae*, CITL 400, holotype, 102.6 mm SL, bay on Pousada Arara Azul, Pantanal, Corumbá municipality, rio Paraguai basin, Mato Grosso do Sul State, Brazil.

on scales above the lateral line, most conspicuous in medial portion of body. Scattered melanophores on proximal and distal field of scales, forming five to seven black stripes, inconspicuous, above lateral line. Scattered melanophores in head, conspicuous on lower jaw, maxilla, premaxilla, eyes, antorbital, infraorbitals series, supraorbital, opercle and infraopercle. Fins hyaline, with few scattered melanophores: Dorsal fin hyaline, with rays yellow ground and numerous scattered melanophores. Base of anal fin with diffuse black stripe; anal fin hyaline, with scattered melanophores. Caudal fin hyaline, with yellowish tones on base of interradial membranes and scattered melanophores; medial rays and interradial membrane with scattered melanophores. Adipose fin yellowish, with distal tip hyaline and scattered melanophores. Pectoral fin hyaline, with yellow tones anteriorly and scattered melanophores in all extension. Pelvic fin hyaline, with scattered melanophores (Fig. 2). Small individuals with high concentration of melanophores in dorsal and pectoral fins, and generally, with one black stripe on base of anal fin; in large individuals, fins hyaline, with scattered melanophores and black stripe on base of anal fin inconspicuous or absent.

Sexual dimorphism and ontogenetic variations. No secondary sexual dimorphism characters were found, including differences in size between females and males. *Triportheus claudiae* presents differences in caudal fin form and coloration pattern between adults and juveniles. In small individuals (smaller than 50 mm SL) caudal fin bifurcated, without elongated medial rays; in large individuals, caudal fin truncated, with elongated medial rays (Fig. 3).

Geographical distribution. *Triportheus claudiae* is known to inhabit the floodplain of the upper rio Paraguai basin (Fig. 4).

FIGURE 2 | *Triportheus claudiae*, uncataloged, 32.6 mm SL, collected at rio Miranda, near to the "Base de Estudos do Pantanal da Universidade Federal de Mato Grosso do Sul", Corumbá municipality, Mato Grosso do Sul State, Brazil. Photo: H. Gimenes-Junior.

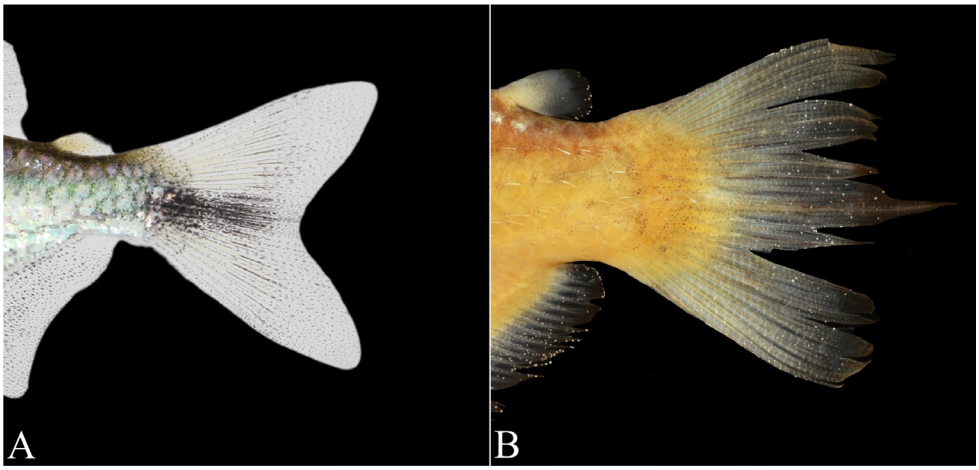

FIGURE 3 | Caudal fin form in *Triportheus claudiae*. **A.** Juvenile, uncataloged individual, 32.6mm SL; **B.** Adult, CITL 400, holotype, 102.6 mm SL.

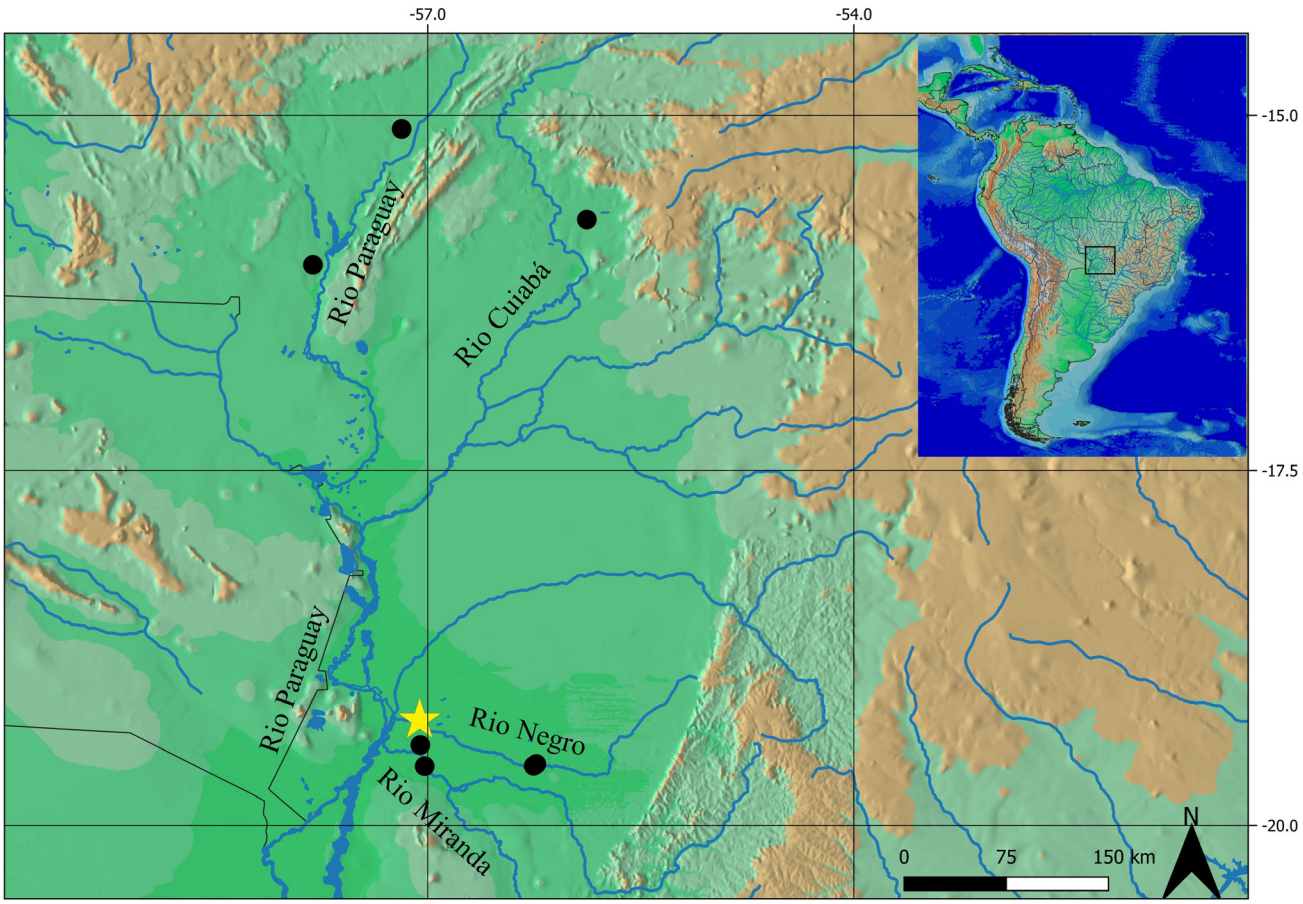

FIGURE 4 | Distribution of *Triportheus claudiae* in the Paraná-Paraguai basin. Black circles represent locations with analyzed lots and the yellow star represents the type-locality defined here.

Etymology. The specific name, a genitive form for Claudia, is an homage to Maria Claudia de Souza Lima Malabarba, for highly relevant contributions to the knowledge of the *Triportheus* species and Neotropical palaeoichthyology. A noun in a genitive case.

Conservation status. *Triportheus claudiae* is a species with wide distribution in the rio Paraguai and tributaries floodplain, with records in Mato Grosso and Mato Grosso do Sul States, Brazil. Despite the Pantanal wetland has suffered a series of impacts of anthropogenic origin in the last years, such as the conversion of native floodplain fields to exotic pasture, large-scale fires, introduction of allochthonous and exotic fish species and mining, we have no evidence that these activities are effectively affecting this species' population size, distribution, or biology. Additionally, the known distribution of *T. claudiae* includes preserved environments, as the Parque Estadual do Rio Negro, Parque Estadual do Encontro das Águas, Parque Nacional do Pantanal Mato-Grossense and several private natural heritage reserves (RPPNs). Using the criteria and categories of International Union for Conservation of Nature (IUCN, 2022), *Triportheus claudiae* can be classified as Least Concern (LC).

Remarks. *Triportheus claudiae* was mentioned as *T.* aff. *rotundatus* by Mariguela *et al*. (2016), based on the examination of specimens from the rio Miranda, an important tributary of left margin of the rio Paraguai. This species is morphologically similar to *T. rotundatus*, it is known to inhabit only the rio Amazonas basin, and is genetically closer to *T. nematurus*.

Triportheus nematurus (Kner, 1858)

(Figs. 5–7; Tab. 2)

Chalcinus nematurus Kner, 1858:163 [original description]. —Kner, 1860:13–15 [more detailed description and type-locality indicated as: "Cujaba, Suaguragua, Caiçara"]. —Garman, 1890:3 [synonym of *Chalcinus angulatus angulatus*]. —Eigenmann, Eigenmann, 1891:56 [synonym of *Chalcinus angulatus*]. —Ulrey, 1895:294 [synonym of *Chalcinus angulatus*]. —Miranda Ribeiro, 1941:162–69 [morphometric data, synonym of *Chalcinus angulatus*]. —Fowler, 1950:356 [synonym of *Triportheus angulatus angulatus*].

Chalcinus paranensis Günther, 1874:454 [description, type-locality: Rio Paraná]. —Garman, 1890:4 [listed]. —Eigenmann, Eigenmann, 1891:56 [listed: río de La Plata system]. —Travassos, 1940:720 [listed and notes about parasitism]. —Miranda Ribeiro, 1941:171 [diagnosis and comments about morphology].

Triportheus paranensis. —Fowler, 1950:358 [new combination, listed: rios Paraná-Paraguai basin]. —Géry, 1977:343 [listed and key to identification]. —Portugal, 1990:136 [revision and redescription]. —Fernández, Butí, 1996:252 [listed to Argentina]. —Gómez, Chebez, 1996:48 [listed from Misiones, Argentina]. —Malabarba, 1998:76 [phylogenetic relationships]. —Britski *et al*., 1999:29 [listing and key to identification]. —Lima *et al*., 2003:58 [listed]. —López *et al*., 2003:19 [listed from Argentina]. —Menni, 2004:74. —Malabarba, 2004:182 [synonym of *Triportheus nematurus*]. —Britski, 2007:44 [listed and key to identification].

Triportheus nematurus. —Cope, 1878:692 [listed]. —Fowler, 1906:448 [synonym of *Chalcinus angulatus*]. —Fowler, 1950:356 [synonym of *Triportheus angulatus angulatus*]. —Portugal, 1990:166–72 [revalidation and redescription, name erroneously attributed to an undescribed species]. —Malabarba, 1998:76 [phylogenetic relationships]. —Britski *et al*., 1999:29 [listing and key to identification]. —Lima *et al*., 2003:158 [listed]. —

Malabarba, 2004:182 [redescription, lectotype designation; locality of lectotype: "Cujaba"]. —Britski *et al.*, 2007:44 [listed and key to identification]. —Buckup *et al.*, 2007:44 [listed from Brazil]. —Langeani *et al.*, 2007:185 [listed as an allochthonous species in upper rio Paraná basin]. —Graça, Pavanelli, 2007:75 [listed from the upper rio Paraná floodplain]. —Mirande, 2010:485 [phylogenetic relationships]. —Nakagawa, 2011:44 [comments about distribution, identification and study of cephalic musculature]. —Oliveira *et al.*, 2011:13 [phylogenetic relationships and new propose to Triportheidae]. —Litz, Koerber, 2014:10–11 [listed from Uruguay]. —Mariguela *et al.*, 2016:132 [phylogenetic relationships]. —Ota *et al.*, 2018:54 [listed from upper rio Paraná floodplain]. —Reis *et al.*, 2020:463 [listed from Paraná State, Brazil]. —Lopes *et al.*, 2022:247 [illustrated guide and key to identification]. —Brandão *et al.*, 2022:57 [listed from the lower rio Taquari, Paraná State, Brazil]. —Toledo-Piza *et al.*, 2024:436–37 [list]. —Dagosta *et al.*, 2024:69–70, 81 [list and discussion about it is origin in the upper rio Paraná basin].

Diagnosis. *Triportheus nematurus* differs from its congeners by the following combination of characters: two non-elongated scales between the insertion of the pectoral fin and the ventral keel (*vs.* one elongate scale between the origin of the pectoral fin and the ventral keel in *T. albus*, *T. auritus*, *T. brachipomus*, *T. culter*, and *T. magdalenae*); 38–48 (mode = 43, n = 23) gill rakers on the lower branch of the first branchial arch (*vs.* 29–37 in *T. angulatus*, 24–32 in *T. rotundatus*, 52–57 in *T. guentheri*, 22–24 in *T. pictus*, 23–28 in *T. curtus*, 26–32 in *T. pantanensis*, 24–28 in *T. orinocensis*, 27–33 in *T. venezuelensis* and 24–29 in *T. claudiae*). It further differs by the number of perforated scales on the lateral line, 33–37 (mode = 34, n = 62) (*vs.* 30–33 [mean = 32.1] in *T. guentheri*, 30–32 in *T. pictus*, 28–32 in *T. pantanensis*); irregularly disposed scales on the predorsal line, never in one aligned series (*vs.* regularly disposed scales of the predorsal line, in one aligned series, in *T. signatus*, *T. trifurcatus*, *T. pictus*, and *T. claudiae*); number of scales on the transversal line between the origin of the dorsal fin and the lateral line, six (*vs.* five in *T. trifurcatus*, *T. guentheri*, and *T. curtus*); 36–37 epineurals (*vs.* 34–35 in *T. pantanensis*), 21 epipleurals (*vs.* 16–17 in *T. pantanensis*, and 22–23 in *T. signatus*); number of supraneurals, 9 (*vs.* 10 in *T. pantanensis* and 10–11 in *T. claudiae*); and 4–5 ventral tubules in the laterosensory canal of the preoperculum (*vs.* 7 in *T. pantanensis* and *T. claudiae*).

FIGURE 5 | *Chalcinus nematurus*, lectotype, NMW 69034, 148.2 mm SL, type-locality: "Cujaba" [= Cuiabá], Mato Grosso State, Brazil. Photo: B. Riedel (NWM).

Description. Morphometric and meristic data in Tab. 2. Other characters and color in alcohol in Malabarba (2004). Total vertebrae, 36; precaudal vertebrae, 17. Fifteenth precaudal vertebrae with a hemal arch and canal; caudal vertebrae, 18. Epineurals: 35(2), 36(3) or 37(2), first three unforked; epipleurals 21(5) or 22(2). First epipleural unforked, second to 12th forked proximally and 13th to 21st, unforked. Supraneurals: nine (7). Upper procurrent rays, eight (2) or nine (5); lower procurrent rays, seven (7).

TABLE 2 | Morphometric and meristic data of *Triportheus nematurus*. N = Number of individuals; Min-Max = Minimum and maximum; SD = Standard deviation.

	N	Min-Max	Mean	SD
Standard length (mm)	160	31.8–220.0	99.6	–
Percents of standard length				
Body depth	160	28.3–37.9	34.2	1.8
Head length	160	22.0–29.0	24.9	1.8
Head depth	160	20.0–30.5	23.5	1.8
Predorsal distance	160	53.5–65.8	59.6	1.8
Prepelvic distance	159	45.7–56.9	52.9	1.7
Preanal distance	160	63.0–76.0	71.9	1.9
Caudal peduncle depth	160	6.4–12.4	8.6	0.5
Dorsal-fin base length	160	7.9–13.3	10.6	0.8
Anal-fin base length	160	21.5–32.0	27.1	1.6
Pectoral-fin length	153	32.9–41.8	37.8	1.8
Pelvic-fin length	156	8.3–17.0	14.0	1.4
Dorsal-fin length	151	13.9–24.0	19.7	1.7
Anal-fin length	157	7.1–16.7	12.8	1.9
Caudal peduncle length	160	6.4–12.9	9.1	1.0
Dorsal-fin to adipose-fin distance	160	23.9–39.1	29.2	1.8
Orbit to dorsal-fin distance	160	43.0–53.6	47.8	2.0
Dorsal-fin to caudal peduncle distance	160	38.2–48.7	43.2	1.8
Percents of the bony head length				
Orbit diameter	160	26.1–34.9	31.8	2.1
Snout length	160	19.8–28.0	24.1	1.6
Interorbital distance	160	27.6–41.0	33.2	3.1
Upper jaw length	160	19.2–28.6	23.1	2.2
Counts			**Mode**	
Dorsal-fin rays	152	ii,9	ii,9	–
Anal-fin rays	157	iii,25–31	iii,29	–
Caudal-fin rays	155	i,9/8,i	i,9/8,i	–
Pectoral-fin rays	153	i,10–12	i,12	–
Pelvic-fin rays	156	i,6	i,6	–
Scales on lateral line	152	33–37	34	–
Scales around caudal peduncle	156	12–14	12	–
Scales above lateral line	156	6	6	–
Scales below lateral line	156	2	2	–
Scales on the base of anal -fin	160	19–28	23	–
Scales on predorsal line	160	9–13	11	–
Premaxillary teeth – outer row	160	4–6	5	–
Premaxillary teeh – medial row	160	3	3	–
Premaxillary teeth – inner row	160	6–7	6	–
Maxillary teeth	160	0–2	0	–
Lower jaw teeth – outer row	160	4–5	5	–
Lower jaw teeth – inner row	160	1	1	–
Gill rakers on lower branch o first branchial arch	160	38–48	43	–

Coloration in life. Overall coloration silvery, darker dorsally than ventrally. Dorsolateral region of body greenish. Grouped melanophores on proximal field of scales, forming one to six black longitudinal fainted stripes on dorsolateral region of body, above lateral line, converging to one single stripe, which continues on medial caudal fin rays. Fins mostly hyaline, with few scattered melanophores; origin of pectoral fin, base of first five pectoral fin rays and distal tip of pectoral fin with scattered melanophores; grouped melanophores only on base of pectoral fin and first unbranched ray. Distal tip of dorsal and anal fin with scattered melanophores. Last rays of anal fin with scattered melanophores in all extension. Caudal fin with vertical inconspicuous bands of scattered melanophores, barely visible without stereomicroscope; medial caudal fin rays black in all extension, by presence of closely grouped melanophores (Fig. 7). Juveniles with large concentration of grouped melanophores in all fins; in adults, fins hyaline with few scattered melanophores.

FIGURE 6 | *Triportheus nematurus*, ZUFMS 4857, 119.1 mm SL, rio Miranda, in front of the Pantanal Study Base, Corumbá municipality, Mato Grosso do Sul State, Brazil. Photo: ZUFMS.

FIGURE 7 | *Triportheus nematurus*, 219 mm SL, Bioparque Pantanal, Campo Grande municipality, Mato Grosso do Sul State, Brazil. Photo: H. Gimenes-Junior and R. Rech.

Sexual dimorphism and ontogenetic variations. No characteristics of secondary sexual dimorphism were found, including variations of size. Variations in caudal fin form and coloration between large and small individuals. In small individuals, less than 50 mm SL, caudal fin bifurcated, without elongated medial rays; in large individuals, caudal fin truncated, and medial rays elongated, largest than upper and lower caudal fin rays.

Geographical distribution. *Triportheus nematurus* is widely distributed in lowlands of Paraná-Paraguai basin (Fig. 8). Its natural occurrence known is from the rio Paraguai and lower rio Paraná basins. In the upper rio Paraná basin, *T. nematurus* is recognized as a possible introduced species (Dagosta *et al*., 2024).

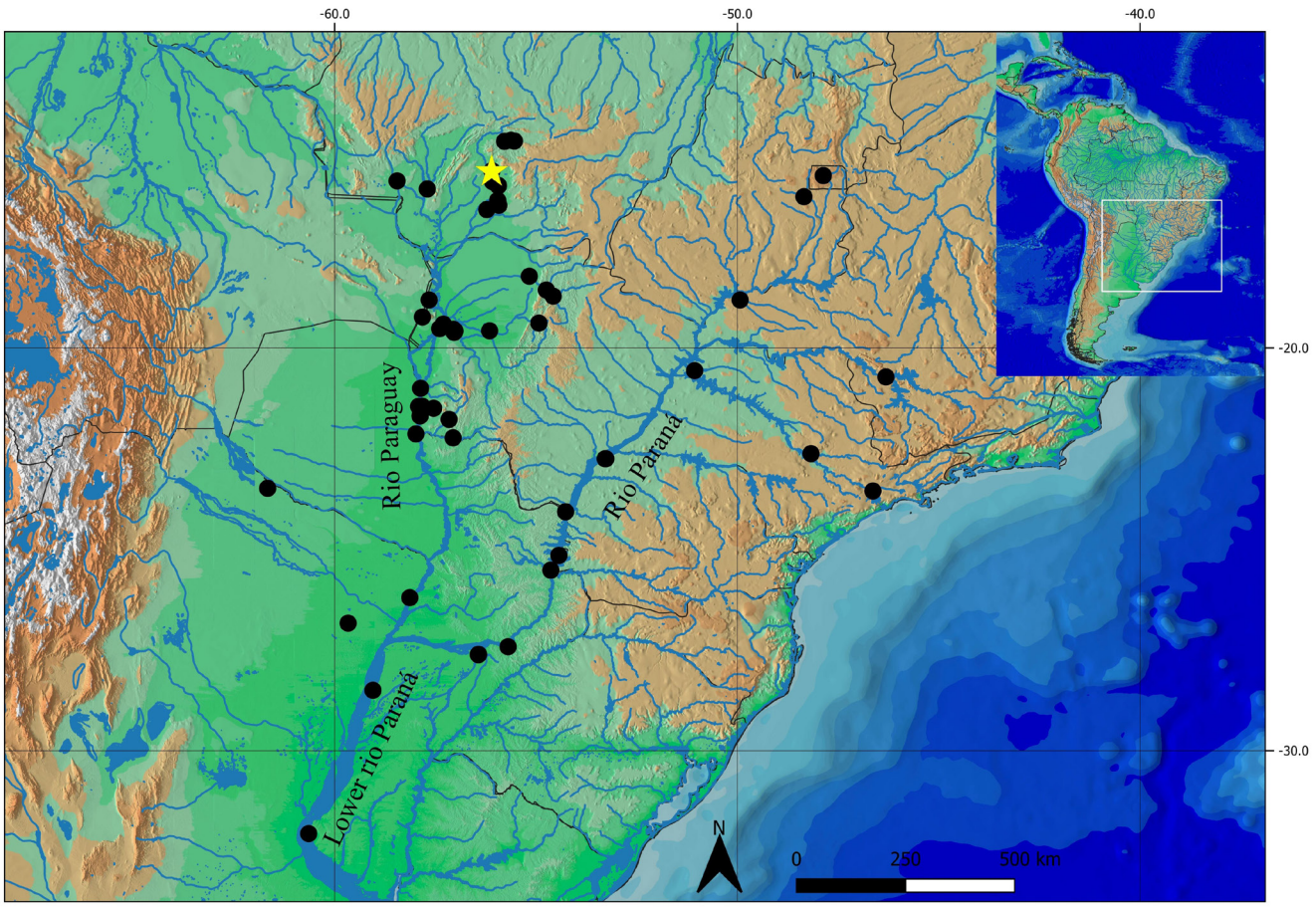

FIGURE 8 | Distribution of *Triportheus nematurus* in the Paraná-Paraguai basin. Black circles represent locations with analyzed lots and yellow star represents the type-locality of the species.

Ecological notes. *Triportheus nematurus* is a generalist species and occurs in lentic environments, such as ponds, lakes, bays, and impoundments (Polaz *et al*., 2014; Severo-Neto *et al*., 2015), and in lotic environments, such as rivers (Súarez *et al*., 2013; Polaz *et al*., 2014). When juveniles, they are associated with beds of aquatic macrophytes (Súarez *et al*., 2013). The species is omnivorous, its diet based mainly on terrestrial insects, algae, zooplankton, and terrestrial plant matter (including seeds and fruit). The species presents a high feeding plasticity, evidenced mainly by the temporal variations of its diet (Novakowski *et al*., 2008; Lopes *et al*., 2017). In the Pantanal wetlands, they can act as seed dispersers, due to their frugivorous interaction during the flood season (Yule *et al*., 2016). There is no information about the reproductive biology of this species.

Remarks. *Chalcinus nematurus* (= *Triportheus nematurus*) Kner, 1858 was described based on three lots (syntypes) with locality not mentioned in the original description. Posteriorly, Kner (1860) mentioned the localities as: "Cujaba, Suaguragua, Caicara", both in Mato Grosso State, collected by J. Natterer. *Chalcinus paranensis* (= *Triportheus nematurus*) Günther, 1874 was described based on a unique individual that corresponded to the holotype, collected in a locality defined simply as "from the river Parana" and probably refers to an exemplar sampled in the lower rio Paraná basin. Malabarba (2004) recognized *T. nematurus* as senior synonym of *T. paranensis* and designated a lectotype (NMW 69034) and the type-locality was fixed as Cuiabá. In the upper rio Paraná basin, the occurrence of this species was historically attributed to the construction of the Itaipu reservoir in the beginning of the 1980's, which flooded and consequently eliminated the Sete Quedas waterfalls, the biogeographic divisor between the upper rio Paraná basin and the lower rio Paraná basin (Langeani *et al*., 2007; Graça, Pavanelli, 2007; Petesse, Petrere, 2012; Ota *et al*., 2018; Garcia *et al*., 2018; Pelicice *et al*., 2018; Jarduli *et al*., 2019). Dagosta *et al*. (2024) consider *T. nematurus* as non-native species in the upper rio Paraná basin, however, recognize that a molecular approach is necessary to investigate its occurrence within both basins.

Material examined. Brazil: Goiás State: upper rio Paraná basin: MCP 47744, 3, 133.5–168.7 mm SL. NUP 8705, 1, 175.8 mm SL. **Mato Grosso State: upper rio Paraguai basin:** MCP 15630, 1, 80.6 mm SL. MCP 44032, 2, 130.9–153.5 mm SL. MZUSP 19825, 1, 125.1 mm SL. MZUSP 20440, 1, 125.4 mm SL. MZUSP 28100, 1, 137.7 mm SL. MZUSP 79140, 1, 80.5 mm SL. NUP 1974, 1, 125.2 mm SL. NUP 2935, 1, 220.0 mm SL. NUP 6954, 2, 124.8–128.7 mm SL. NUP 6994, 1, 147.7 mm SL. NUP 7056, 2, 81.1–84.0 mm SL. NUP 7100, 2, 72.6–113.0 mm SL. NUP 7595, 2, 72.5–96.9 mm SL. NUP 11492, 1, 137.9 mm SL. UFRGS 13453, 2, 56.1–76.8 mm SL. ZUFMS 3274, 7, 39.1–68.9 mm SL. ZUFMS 3438, 1, 41.8 mm SL. **Mato Grosso do Sul State: upper rio Paraguai basin:** CPUEMS not catalogued p.18, 3, 31.9–38.2 mm SL. CPUEMS not catalogued p.42, 1, 80.1 mm SL. CPUEMS not catalogued p.47, 1, 102.5 mm SL. CPUEMS not catalogued p.89, 3, 61.1–74.6 mm SL. CPUEMS not catalogued p.90, 1, 81.0 mm SL. CPUEMS not catalogued p.92, 4, 75.8–99.6 mm SL. CPUEMS not catalogued p.99, 6, 60.6–70.1 mm SL. CPUEMS not catalogued p.102, 3, 65.5–80.9 mm SL. CPUEMS not catalogued p.110, 1, 98.5 mm SL. DZSJRP 20143, 2, 97.4 mm SL. MZUSP 19740, 1, 134.8 mm SL. NUP 12548, 1, 95.4 mm SL. NUP 12549, 1, 66.5 mm SL. NUP 14220, 2, 132.6–138.6 mm SL. NUP 14268, 1, 73.5 mm

SL. NUP 19898, 1, 140.7 mm SL. NUP 19978, 1, 149.4 mm SL. UFRGS 17443, 2, 56.1–76.8 mm SL. ZUFMS 814, 1, 89.8 mm SL. ZUFMS 856, 3, 74.0–135.3 mm SL. ZUFMS 3208, 1, 153.3 mm SL. ZUFMS 3209, 1, 126.6 mm SL. ZUFMS 3259, 4, 117.2–154.2 mm SL. ZUFMS 3268, 5, 108.3–146.3 mm SL. ZUFMS 3661, 1, 150.8 mm SL. ZUFMS 3704, 11, 74.6–130.2 mm SL. ZUFMS 4857, 3, 119.1–125.2 mm SL. ZUFMS, 5031, 1, 81.9 mm SL. ZUFMS 5056, 12, 90.0–194.3 mm SL. ZUFMS 5184, 1, 75.3 mm SL. ZUFMS 5263, 9 (4 c&s), 37.3–59.8 mm SL. ZUFMS 5447, 1, 50.1 mm SL. ZUFMS 5715, 5, 31.8–143.9 mm SL. ZUFMS 5744, 4, 67.9–82.3 mm SL. ZUFMS 5756, 2, 90.3–93.4 mm SL. ZUFMS 5770, 8, 77.0–102.6 mm SL. **Minas Gerais State: upper rio Paraná basin:** MCP 44034, 1, 153.7 mm SL. NUP 16876, 2, 48.24–75.4 mm SL. **Paraná State: upper and lower rio Paraná basin:** MCP 40735, 2, 142.8–153.6 mm SL. MCP 40765, 2, 189.36–192.1 mm SL. MZUSP 19854, 1, 171 mm SL. MZUSP 21086, 1, 187.1 mm SL. MZUSP 37181, 1, 134.3 mm SL. NUP 97, 1, 62.5 mm SL. NUP 516, 1, 180.8 mm SL. NUP 1961, 2, 61.2–62.8 mm SL. NUP 7058, 1, 183.6 mm SL. NUP 7146, 2, 185.6–211.1 mm SL. **São Paulo State: upper rio Paraná basin:** DZSJRP 621, 1, 83.4 mm SL. DZSJRP 624, 2, 92.7–97.1 mm SL. DZSJRP 4298, 2, 64.9–89.3 mm SL. DZSJRP 10591, 2, 76.9–95.3 mm SL. DZSJRP 13077, 2, 71.9–93.5 mm SL. DZSJRP 13112, 2, 63.9–100.4 mm SL. DZSJRP 13132, 2, 96.0–102.8 mm SL. ZUFMS 5362, 3, 145.0–163.6 mm SL. **Paraguay: Alto Paraguay Departament: Río Paraguay basin:** MZUSP 54148, 1, 74.4 mm SL; MZUSP 54149, 2, 74.3–87.7 mm SL.

Triportheus pantanensis Malabarba, 2004

(Figs. 9–10; Tab. 3)

Triportheus pantanensis Malabarba, 2004:197 [original description; type-locality: Transpantaneira road, pond below bridge, 70 km South of Poconé, Mato Grosso, Brazil]. —Buckup *et al*., 2007:44 [listed from Brazil]. —Mirande, 2010:485 [phylogenetic relationships]. —Nakagawa, 2011:49 [comments about distribution, taxonomy, and study of cephalic musculature]. —Mariguela *et al*., 2016:134 [phylogenetic relationships]. —Koerber *et al*., 2017:27 [list from Paraguay]. —Lopes *et al*., 2022:247 [illustrated guide and key to identification]. —Toledo-Piza *et al*., 2024:437 [list].

Triportheus nematurus (non Kner 1858). —Portugal, 1990:166 [misidentification, redescription]. —Malabarba, 1998:76 [phylogenetic relationships within *Triportheus* and *Lignobrycon*]. —Britski *et al*., 1999:29 [listed and key to identification]. —Lima *et al*., 2003:158 [listed]. —Britski *et al*., 2007:44 [listed and key to identification].

Diagnosis. *Triportheus pantanensis* differs from its congeners by the following combination of characters: two non-elongated scales between the insertion of the pectoral fin and ventral keel (*vs.* one elongated scale between the origin of the pectoral fin and ventral keel in *T. albus*, *T. auritus*, *T. brachipomus*, *T. culter*, and *T. magdalenae*); 26–33 (mode = 28, n = 19) gill rakers on the lower branch of first branchial arch (*vs.* 40–47 in *T. trifurcatus*, 38–48 in *T. nematurus*, 52–57 in *T. guentheri*, 22–24 in *T. pictus*, 35–44 in *T. signatus*); perforated scales on the lateral line: 28–32 (mode = 31, n = 29) (*vs.* 34–37 in *T. angulatus*, 33–37 in *T. nematurus*, 34–37 in *T. signatus*, 34–39 in *T. orinocensis*, and 33–36 in *T. venezuelensis*); three rows of cuspid teeth on the premaxilla (*vs.* two rows of cuspid teeth in *T. curtus* and *T. pictus*); scales of the predorsal series irregularly disposed

(*vs.* scales of the predorsal series regularly disposed in *T. trifurcatus*, *T. signatus*, *T. pictus*, and *T. claudiae*); six scale series on the lateral of caudal peduncle (*vs.* five in *T. angulatus*, *T. curtus*, and *T. orinocensis*, four or five in *T. guentheri*, *T. rotundatus*, *T. trifurcatus*, and *T. venezuelensis*); epineural bones, 34–35 (*vs.* 36–37 in *T. nematurus*); epipleural bones: 16–17 (*vs*. 21 in *T. nematurus*, 22–23 in *T. signatus*, and 20–21 in *T. claudiae*); number of supraneurals: 10 (*vs.* nine in *T. nematurus* and *T. signatus*); seven ventral tubules in the laterossensorial canal of the preopercule (*vs.* 4–5 in *T. nematurus* and 5 in *T. signatus*).

Description. Morphometric and meristic data in Tab. 3. Other characters and color in alcohol in Malabarba (2004). Total vertebrae: 36(1) or 37(3); precaudal vertebrae: 17(4). Caudal vertebrae: 18(1) or 19(3); 34(2) or 35(2) epineural bones; first to 25th or 26th epineural bones branched in ventral region; 27th to 34th or 35th epineural bone unbranched; epipleural bones 18(3) or 19(1); first epipleural unbranched; second to nineth epipleural branched in dorsal portion; 10th to 16th or 17th epipleural unbranched. Supraneurals: 10(4). Upper procurrent rays: 8(1) or 9(3); lower procurrent rays: six (4).

Coloration in life. Overall coloration silvery, darker dorsally. Dorsal-middle region of body with greenish or yellowish tones. Scattered or concentrated melanophores on proximal field of scales, forming five or six longitudinal black fainted stripes on dorsolateral portion of body, above lateral line. Fins mostly hyaline, with scattered melanophores. First five pectoral-fin rays darker, with concentrated melanophores. Medial rays of caudal fin, black in all extension. Some individuals with conspicuous melanophores in first dorsal and anal fin rays (Fig. 10). Small individuals with high concentration of melanophores in dorsal and pectoral fins and a black stripe on base of anal fin; in adults, fins hyaline, with scattered chromatophores and black stripe on base of anal-fin inconspicuous or absent.

FIGURE 9 | *Triportheus pantanensis*, holotype, MCP 35006, 97.1 mm SL, Transpantaneira road, pond below the bridge, 70 km to South of Poconé municipality, Mato Grosso State, Brazil. Photo: B. Calegari.

TABLE 3 | Morphometric and meristic data of types and non-types of *Triportheus pantanensis*. N = Number of individuals; Min-Max = Minimum and maximum; SD = Standard deviation.

	Holotype	Paratypes				Non-types			
		N	Min-Max	Mean	SD	N	Min-Max	Mean	SD
Standard length (mm)	97.1	11	65.9–88.7	79.9	–	89	18.9–125.5	72.8	–
Percents of standard length									
Body depth	38.0	11	36.5–43.0	40.3	1.7	89	34.4–43.0	38.1	2.1
Head length	24.0	11	24.4–26.1	25.3	0.6	89	22.1–29.4	25.0	1.2
Head depth	23.3	11	21.7–27.0	24.2	1.5	89	20.9–31.4	24.0	1.9
Predorsal distance	61.6	11	62.2–65.7	63.5	1.1	89	56.0–66.7	61.9	2.0
Preventral distance	53.8	10	53.3–58.9	55.9	1.7	89	50.1–61.9	55.1	2.0
Preanal distance	71.3	11	70.5–75.3	73.3	1.7	89	67.5–77.2	72.5	1.7
Caudal peduncle height	10.5	11	9.7–10.9	10.3	0.4	89	6.7–10.9	9.6	0.8
Dorsal-fin base length	12.4	11	11.3–13.2	12.0	0.5	89	7.9–10.9	11.2	1.1
Anal-fin base length	28.7	11	28.2–30.9	29.9	0.8	89	23.8–33.8	28.7	1.7
Pectoral-fin length	38.8	11	30.7–44.3	40.8	2.4	86	33.0–43.8	39.7	2.5
Pelvic-fin length	14.0	10	10.8–16.1	14.1	1.5	83	10.5–17.4	14.8	1.4
Dorsal-fin length	20.6	11	18.5–23.0	20.1	1.3	89	13.9–23.4	20.0	1.7
Anal-fin length	13.0	11	12.8–18.0	15.3	1.6	89	10.7–20.5	14.6	2.0
Caudal peduncle length	9.5	11	8.3–11.5	9.7	1.0	89	6.7–11.5	9.1	1.1
Dorsal-fin to adipose-fin distance	27.2	11	21.8–25.3	23.8	1.2	89	24.3–31.1	27.1	1.4
Orbit to dorsal-fin distance	50.8	11	50.5–53.1	52.1	0.8	89	44.6–54.8	50.6	1.8
Dorsal-fin to caudal peduncle distance	40.8	11	40.4–43.7	42.0	1.2	89	36.3–45.5	41.0	1.8
Percents of head length									
Orbital diameter	32.4	11	34.9–39.9	36.4	1.4	89	24.7–33.2	29.3	2.4
Snout length	25.9	11	23.8–28.7	26.4	1.4	89	18.5–28.1	23.9	1.8
Interorbital distance	38.0	11	32.8–40.0	36.4	2.2	89	31.4–39.3	35.0	1.9
Upper jaw length	24.6	11	21.8–25.3	23.8	1.2	89	19.5–27.4	23.3	1.7
Counts				**Mode**					
Dorsal-fin rays	ii,9	11	ii,9	ii,9	–	89	ii,8–9	ii,9	–
Anal-fin rays	iii,29	11	iii,27–29	iii,28	–	89	iii, 24–31	Iii,28	–
Caudal-fin rays	i,9/8,i	11	i,9/i,8	25.3	–	89	i,9/8,i	i,9/8,i	–
Pectoral-fin rays	i,11	11	i,11–12	i,11	–	89	i,10–12	i,11	–
Pelvic-fin rays	i,6	11	i,6	i,6	–	89	i,6	i,6	–
Scales on lateral line	28	11	29–32	29	–	89	28–32	31	–
Scales around caudal peduncle	14	11	14	14	–	89	13–14	14	–
Scales above lateral line	6	11	6	6	–	89	6	6	–
Scales below lateral line	2	11	2	2	–	89	2	2	–
Scales on the base of anal-fin	27	11	22–26	24	–	89	20–27	24	–
Scales on presorsal line	12	11	8–12	10	–	86	8–13	11	–
Premaxillary teeth - outer row	5	11	4–5	5	–	83	4–6	5	–
Premaxillary teeth – medial row	3	11	3	3	–	89	3	3	–
Premaxillary teeth – inner row	6	11	6	6	–	89	6–7	6	–
Maxillary teeth	1	11	0–2	0	–	89	0–3	0	–
Lower jaw teeth – outer row	4	11	4–5	4	–	89	4–5	4	–
Lower jaw teeth – inner row	1	11	1	1	–	89	1	1	–
Gill rakers on lower branch of first branchial arch	27	11	27–30	28	–	89	26–33	28	–

Sexual dimorphism and ontogenetic variations. No characteristics of secondary sexual dimorphism were found in *Triportheus pantanensis*, including variations in size. This species presents differences in caudal fin form and coloration pattern between large and small individuals. In small individuals (smaller than 50 mm SL) the caudal fin is bifurcated, without elongated medial rays; in adults' caudal fin is emarginated, with elongated medial rays.

Geographical distribution. *Triportheus pantanensis* presents a wide distribution within the floodplain of the rio Paraguai basin (Fig. 11) and in the lower rio Paraná basin, including rivers from Argentina (Mirande, Koerber, 2015) and Paraguay (Koerber *et al*., 2017).

Ecological notes. *Triportheus pantanensis* occurs in lentic and lotic environments (Súarez *et al*., 2013; Polaz *et al*., 2014; Severo-Neto *et al*., 2015), including reservoirs (Corrêa *et al*., 2009). Omnivorous, with tendencies to insectivory or herbivory, depending on the dynamics of the hydrological periods (Corrêa *et al*., 2009). Despite the issue that its effectiveness as a seed disperser has not been tested, it is a known fact that this species consumes small fruits (Costa-Pereira *et al*., 2011), therefore we can assume that it possibly plays an interactive biological role in the dispersion of seeds. There is no information on the reproductive biology to this species.

Material examined. Brazil: Mato Grosso State: rio Paraguai basin: MCP 35006, 1, 97.1 mm SL, holotype. MCP 10733, 3, 88.3–88.7 mm SL, paratypes. MCP 10751, 3, 77.5–78.3 mm SL, paratypes. MCP 15741, 1, 88.5 mm SL, paratype. MCP 35824, 4, 65.9–78.5 mm SL, paratypes. MCP 11119, 1, 99.1 mm SL. MCP 38829, 1, 58.8 mm SL.

FIGURE 10 | *Triportheus pantanensis*, 160 mm SL, Bioparque Pantanal, Campo Grande municipality, Mato Grosso do Sul State, Brazil. Photo: H. Gimenes-Junior and R. Rech.

MZUSP 38106, 2, 40.4–59.1 mm SL. NUP 888, 2, 112.4–116.7 mm SL. NUP 3136, 3, 87.8–105.1 mm SL. NUP 6945, 1, 84.7 mm SL. NUP 7053, 1, 76.3 mm SL. **Mato Grosso do Sul State: rio Paraguai basin:** CITL 1136, 4 (c&s) of 17, 52.5–69.1 mm SL. CPUEMS not catalogued p.24, 1, 41.8 mm SL. CPUEMS not catalogued p.84, 2, 42.5–44.0 mm SL. CPUEMS not catalogued p.89, 1, 64.1 mm SL. CPUEMS not catalogued p.90, 2, 63.1–70.2 mm SL. MZUEL 12268, 2, 68.3–74.7 mm SL. MZUSP 49968, 1, 50.2 mm SL. MZUSP 59827, 2, 46.7–56.6 mm SL. NUP 12552, 2, 18.9–31.0 mm SL. ZUFMS 857, 1, 51.2 mm SL. ZUFMS 858, 1, 58.9 mm SL. ZUFMS 859, 1, 75.2 mm SL. ZUFMS 880, 2, 45.1–51.0 mm SL. ZUFMS 1055, 8, 68.2–94.3 mm SL. ZUFMS 1525, 3, 65.5–65.8 mm SL. ZUFMS 3723, 3, 84.9–95.5 mm SL. ZUFMS 3886, 7, 67.7–86.9 mm SL. ZUFMS 5716, 5, 65.6–103.4 mm SL. ZUFMS 5729, 2, 62.3–64.2 mm SL. **Paraguay: Alto Paraguay Department: Río Paraguay basin:** MZUSP 54144, 1, 58.6 mm SL. MZUSP 54146, 2, 52.9–55.0 mm SL. MZUSP 54147, 2, 60.4–66.9 mm SL. MZUSP 54148, 2, 64.2–70.8 mm SL.

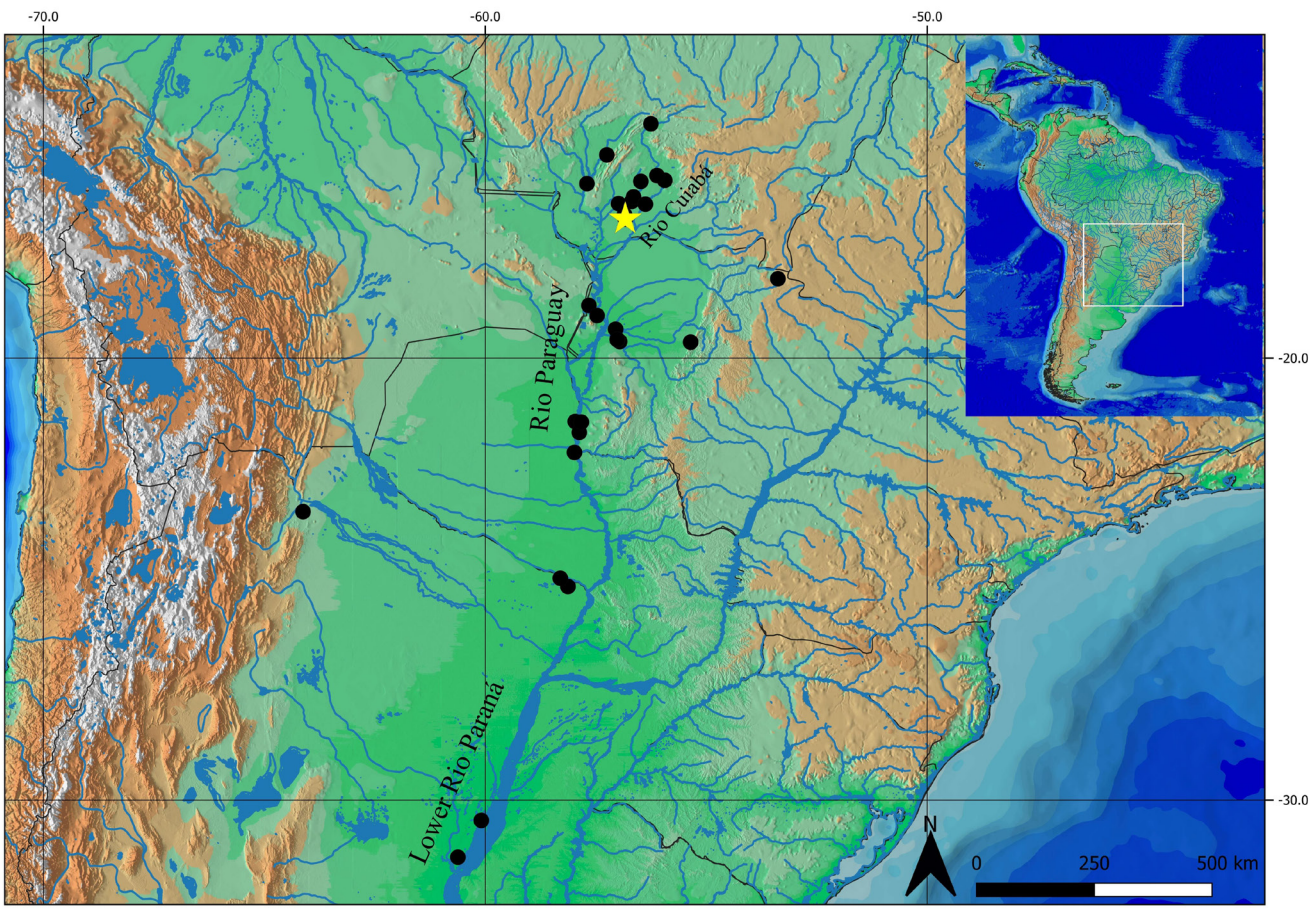

FIGURE 11 | Distribution of *Triportheus pantanensis* in the Paraná-Paraguai basin. Black circles represent locations with analyzed lots and yellow star represents the type-locality of the species.

Triportheus signatus (Garman, 1890)

(Fig. 12-13; Tab. 4)

Chalcinus angulatus signatus Garman, 1890:4 [original description; type-locality: rio Puty, Therezina, Brazil (rio Potí, tributary of the rio Parnaíba, Terezina municipality, Piauí State, Brazil)]. —Eigenmann, Eigenmann, 1891:58 [listed]. —Miranda Ribeiro, 1941:171 [keys to identification and comments regarding subspecies of *C. angulatus*].

Triportheus angulatus signatus. —Fowler, 1941:194 [listed as synonym of *Triportheus angulatus*]. —Fowler, 1950:357 [redescription, type-locality: "Brazil, rio Itapicura"].

Triportheus signatus. —Portugal, 1990:159–65 [redescription, illustration, and distribution]. —Lima *et al*., 2003:158 [list]. —Malabarba, 2004:193–94 [redescription and distribution]. —Buckup *et al*., 2007:44 [listed from Brazil]. —Nakagawa, 2011:57–61 [comments regarding distribution and morphology]. —Ramos *et al*., 2014:4 [list from rio Parnaíba basin, Brazil]. —Mariguela *et al*., 2016:132 [phylogenetic relationships]. —Melo *et al*., 2016:376 [list from lower rio Parnaíba basin, with discussions regarding occurrence of the species in Northeastern Brazil]. —Reis *et al*., 2020:463 [list from Paraná State, Brazil, invasive within upper rio Paraná basin]. —Silva *et al*., 2020:9 [list from Bahia State, Brazil]. —Koerber *et al*., 2022:32 [list from Maranhão State, Brazil]. —Toledo-Piza *et al*., 2024:437 [list]. —Dagosta *et al*., 2024:81 [listed as introduced in the upper rio Paraná basin].

Diagnosis. *Triportheus signatus* differs from its congeners by the following combination of characters: two normal scales between the insertion of the pectoral fin and the ventral keel (*vs.* one elongated scale between the origin of the pectoral fin and the ventral keel in *T. albus*, *T. auritus*, *T. brachipomus*, *T. culter*, and *T. magdalenae*); 35–44 gill rakers (mode = 39, n = 9) on the lower branch of the first branchial arch (*vs*. 24–32 gill rakers in *T. rotundatus*, 52–57 in *T. guentheri*, 22–24 in *T. pictus*, 23–28 in *T. curtus*, 26–33 in *T. pantanensis*, 24–28 in *T. orinocensis*, 27–33 in *T. venezuelensis*, and 24–29 in *T. claudiae*); perforated scales on the lateral line: 34–38 (mode = 36, n = 12) (*vs.* 30–33 in *T. guentheri*, 30–32 in *T. pictus* and 28–32 in *T. pantanensis*); scales distributed in a regular series on predorsal line (*vs*. predorsal scales disposed irregularly, not in series, in

FIGURE 12 | *Triportheus signatus*, CITL 423, 62.2 mm SL, collected at the Canal de Pereira Barreto, Oscar's Ranch, between the rios Tietê and São José dos Dourados, Pereira Barreto municipality, São Paulo State, Brazil.

T. angulatus, *T. rotundatus*, *T. nematurus*, *T. guentheri*, *T. curtus*, *T. pantanensis*, *T. orinocensis*, and *T. venezuelensis*); six scales above the lateral line (*vs.* 5 scales above the lateral line in *T. trifurcatus*); 22–23 epipleural bones (*vs*. 21 in *T. nematurus*, 16–17 in *T. pantanensis*, and 20–21 in *T. claudiae*), 5 ventral tubules in laterossensorial canal of the preopercule (*vs.* 7 in *T. pantanensis* and *T. claudiae*).

Description. Morphometric and meristic data in Tab. 4. Other characters and color in alcohol in Malabarba (2004). Total vertebrae: 36(3) or 37(1); precaudal vertebrae: 17(4). Hemal arch and canal in the 15th or 16th caudal vertebrae. Caudal vertebrae, 19(3) or 20(1); 37(1) or 38(3) epineural bones; first to 22nd epineural bones branched in ventral region; epipleural bones 22(3) or 23(1); first epipleural unbranched; second to nineth epipleural branched in dorsal portion; 10th to 16th, or 17th epipleural unbranched. Number of supraneurals: nine (4). Upper procurrent rays: 9(1) or 10(3); lower procurrent rays: eight (4).

Coloration in life. Overall silvery coloration, darker dorsally. Dorsal-middle region of body with greenish or yellowish tones. Scattered melanophores on dorsal portion of head, as in premaxilla, frontal, supraorbital, infraorbitals 4, 5 and 6, parietal and opercle. Melanophores concentrated in proximal and central field of scales, forming four to seven longitudinal fainted black longitudinal stripes on dorsolateral portion of body, above lateral line. Lateral stripes converge on caudal peduncle as a single large stripe, which follow medial rays of caudal fin, black in all extension.

Sexual dimorphism and ontogenetic variations. No secondary sexual dimorphism characters were found in *Triportheus signatus*, including variation in size of females and males. Species present differences in caudal fin form in small and large specimens, similar to identified to all the other *Triportheus* species of rios Paraná-Paraguai basin. In small individuals (smaller than 50 mm), caudal fin bifurcated, without elongated medial rays; in large individuals, caudal fin truncated, with elongated medial rays.

Geographical distribution. *Chalcinus angulatus signatus* (= *Triportheus signatus*) was described by Garman (1890) with the type-locality in "rio Puty, Therezina", refering to the rio Potí, a tributary from the rio Parnaíba, in Teresina city, Piauí State, Brazil. The species occurs naturally within the rio Parnaíba basin and other coastal river basins from the Northeast region of Brazil. *Triportheus signatus* has also been identified within the upper rio Paraná basin tributaries, mainly in the rio Tietê basin (Fig. 13) since 1990 and it is an invasive species in this river basin.

Ecological notes. Data about the natural history of *Triportheus signatus* are scarce. According to Höfling *et al*. (2000), the species is generalist, mainly found in environments associated to aquatic macrophytes, with high heterogeneity of habitats. In situations of hypoxia on their natural distribution, they develop lip extensions, called as barbels, which aid surface respiration (Barros-Neto *et al*., 2019). However, none of the examined specimens in the rio Paraná basin presented barbels. In the upper rio Paraná basin, it occurs mainly in reservoirs with the rios Tietê and Paranapanema basins (Höfling *et al*., 2000; Nakagawa, 2011; Mariguela *et al*., 2016). It has an omnivorous or insectivorous diet and feeds on larvae and pupae of aquatic insects, fragments of

TABLE 4 | Morphometric and meristic data of *Triportheus signatus*. N = Number of individuals; Min-Max = Minimum and maximum; SD = Standard deviation.

	N	Min-Max	Mean	SD
Standard length (mm)	46	49.2–195.3	98.3	–
Percents of standard length				
Body depth	46	27.9–35.1	31.2	1.4
Head length	46	20.3–26.7	23.8	1.9
Head depth	46	17.9–22.3	20.3	1.2
Predorsal distance	46	56.0–64.7	60.2	1.5
Preventral distance	46	47.2–56.8	52.2	2.2
Preanal distance	46	65.6–74.1	68.4	2.3
Caudal peduncle height	46	7.7–9.3	8.5	0.4
Dorsal-fin base length	46	7.9–11.2	9.9	0.9
Anal-fin base length	46	23.9–29.7	27.1	1.2
Pectoral-fin length	40	30.1–36.9	33.4	2.0
Pelvic-fin length	45	10.6–14.6	12.5	1.1
Dorsal-fin length	36	15.2–21.7	18.0	1.7
Anal-fin length	46	11.1–16.9	14.2	2.0
Caudal peduncle length	46	7.5–11.5	9.4	0.9
Dorsal-fin to adipose-fin distance	46	25.3–33.8	29.5	1.5
Orbit dorsal-fin distance	46	46.2–52.7	48.7	1.4
Dorsal-fin to caudal peduncle distance	46	39.4–46.5	43.1	1.4
Percents of head length				
Orbital diameter	46	26.2–32.0	29.2	1.8
Snout length	46	21.1–29.7	25.0	1.6
Interorbital distance	46	26.3–33.8	30.2	1.9
Upper jaw length	46	20.9–27.9	25.2	2.0
Counts			**Mode**	
Dorsal-fin rays	36	ii,9	ii,9	–
Anal-fin rays	46	iii, 27–31	iii,29	–
Caudal-fin rays	46	i,9/8,i	i,9/8,i	–
Pectoral-fin rays	45	i,10–12	i,11	–
Pelvic-fin rays	45	i,6	i,6	–
Scales on lateral line	46	34–38	36	–
Scales around caudal peduncle	46	12	12	–
Scales above lateral line	46	6–7	6	–
Scales below lateral line	46	2	2	–
Scales on the base of anal-fin	46	21–27	24	–
Scales on predorsal line	46	10–15	13	–
Premaxillary teeth – outer row	46	5–6	5	–
Premaxillary teeh – medial row	46	2–3	3	–
Premaxillary teeth – inner row	46	5–7	6	–
Maxillary teeth	46	0–3	1	–
Lower jaw teeth – outer row	46	4–6	5	–
Lower jaw teeth – inner row	46	1	1	–
Gill rakers on lower branch of first branchial arch	46	35–44	39	–

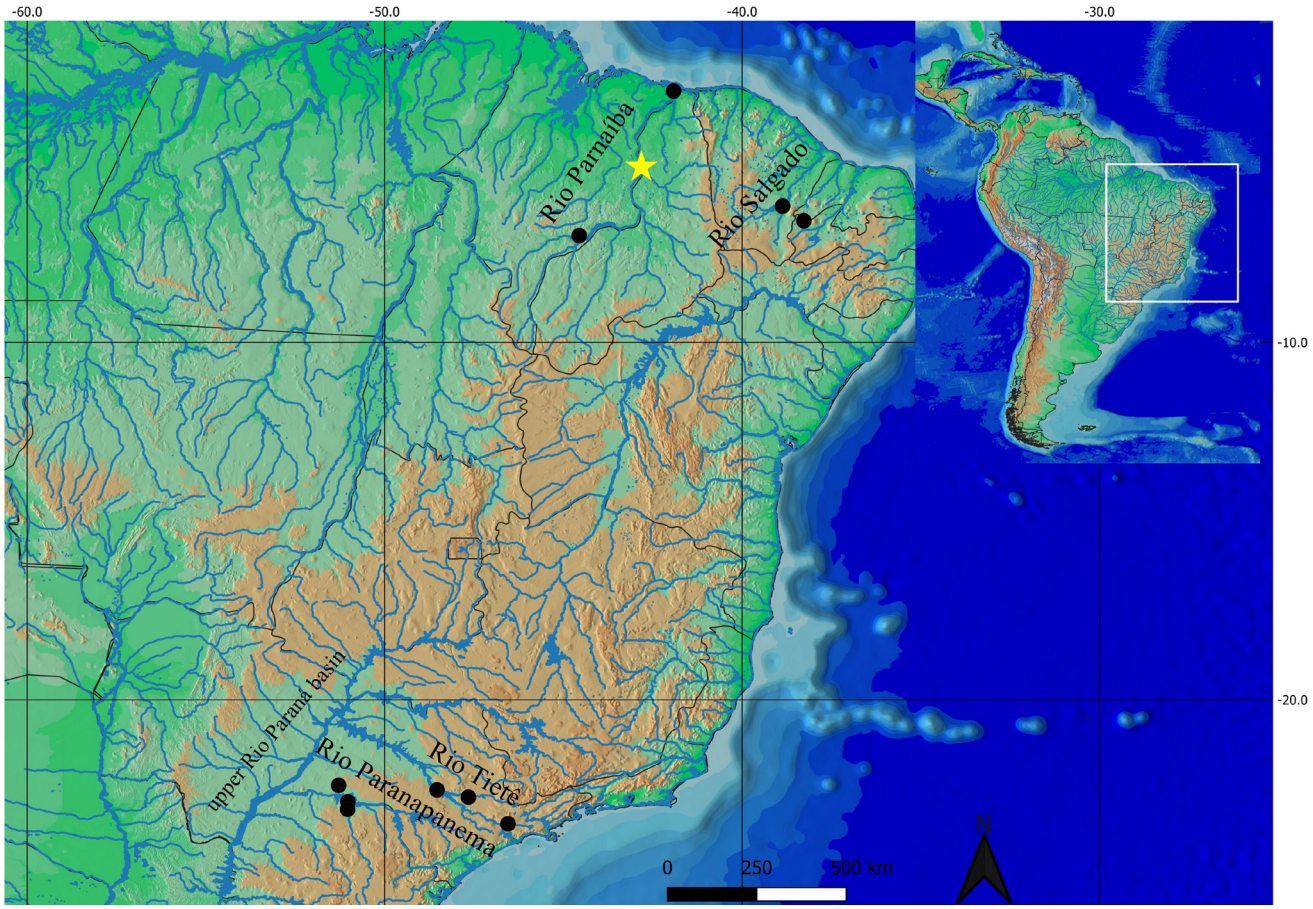

FIGURE 13 | Distribution of *Triportheus signatus* on the Paraná-Paraguai basin and in areas of their natural occurrence. Black circles represent locations with analyzed lots and the yellow star represents the type-locality of the species.

terrestrial insects, crustaceans, seeds, and fragments of superior terrestrial plants (Höfling *et al*., 2000; Mendes *et al*., 2011; Oliveira *et al*., 2019). According to Höfling *et al*. (2000), this species is most abundant in the hot and rainy season, between October and April, when they reproduce.

Remarks. *Triportheus signatus* occurs naturally in the rio Parnaíba basin and other coastal river basins of the Northeast region of Brazil. The occurrence of this species in the upper rio Paraná basin is probably a consequence of an introduction, which is supported by the sampling locations, which are always near to hydroelectric reservoirs, and by the restocking program conducted by energy company of São Paulo State, which begin in 1974 and includes the silver croaker *Plagioscion squamosissimus* (Heckel, 1840) as well other species considered as prey for the establishment of this predator (*e.g*., *Triportheus signatus* and two species of freshwater shrimp) (Queiroz-Sousa *et al*., 2018). The first citations of this species in the Tietê and Paranapanema basins were made by Portugal (1990) in their unpublished master's thesis. Published records of *T. signatus* in the upper rio Paraná basin date from the early 2000's (Silvano, Begossi, 2001; Buckup *et al*., 2007). However, specimens deposited at the DZSJRP and MZUSP indicate that the introduction of this species is even older and corroborates that this species was introduced in the region in 1970's–1980's (*e.g*., MZUSP 37221, collected in 1987;

DZSJRP 625, collected in 1988, both in rio Tietê). Currently, *T. signatus* is known to inhabit the upper rio Paraná basin within the rios Tietê, Paranapanema and the "Canal de Pereira Barreto", which connects the rios Tietê and São José dos Dourados. The lots of *T. signatus* which were collected in the 1980's and 1990's in the upper rio Paraná basin (*e.g.*, DZSJRP 625, DZSJRP 3248, and MZUSP 37221) were mistakenly identified as *T. angulatus*, *T. paranensis* (= *T. nematurus*), *T. nematurus*, or just *Triportheus* sp.

Material examined. Brazil: Ceará State: rio Salgado: MNRJ 44325, 2, 73.7–90.7 mm SL. **Paraíba State:** UFRGS 20345, 2, 138.5–144.0 mm SL. **Paraná State: rio Paranapanema basin:** MZUEL 2485, 2, 144.1–174.2 mm SL. MZUEL 2864, 1, 88.0 mm SL. **Piauí State: rio Parnaíba basin:** MNRJ 29130, 2, 58.2–60.8 mm SL. MNRJ 43204, 2, 61.6–66.4 mm SL. **São Paulo State: rio Tietê basin:** CITL 423, 13 (4 c&s), 49.2–57.8 mm SL. DZSJRP 625, 1, 122.7 mm SL. DZSJRP 3248, 1, 103.0 mm SL. DZSJRP 17731, 2, 100.8–117.3 mm SL. MZUEL 5667, 1, 133.1 mm SL. MZUSP 37221, 9, 135.3–157.8 mm SL. MZUSP 53890, 3, 84.4–148.5 mm SL. NUP 2678, 1, 195.3 mm SL. NUP 16530, 2, 175.0–186.8 mm SL.

Key to identification of *Triportheus* from the Paraná-Paraguai basin

1a. Scales along predorsal line, between tip of supraoccipital and dorsal fin origin, irregularly disposed (not forming a single, continuous line) (Fig. 14A) 2

1b. Scales along predorsal line, between tip of supraoccipital and dorsal-fin origin, in a single series (a maximum of two scales slightly offset from the main series) (Fig. 14B) 3

2a. Perforated lateral-line scales, 33–37 (mode = 34); 38–48 (mode = 43) gill rakers on the lower branch of the first branchial arch..... *T. nematurus*

2b. Perforated lateral-line scales, 28–32 (mode = 31); 26–32 (mode = 28) gill rakers on the lower branch of the first branchial arch..... *T. pantanensis*

3a. Gill rakers on the lower branch of the first branchial arch, 37–44 (mode = 44)..... *T. signatus*

3b. Gill rakers on the lower branch of the first branchial arch, 33 or fewer .... *T. claudiae*

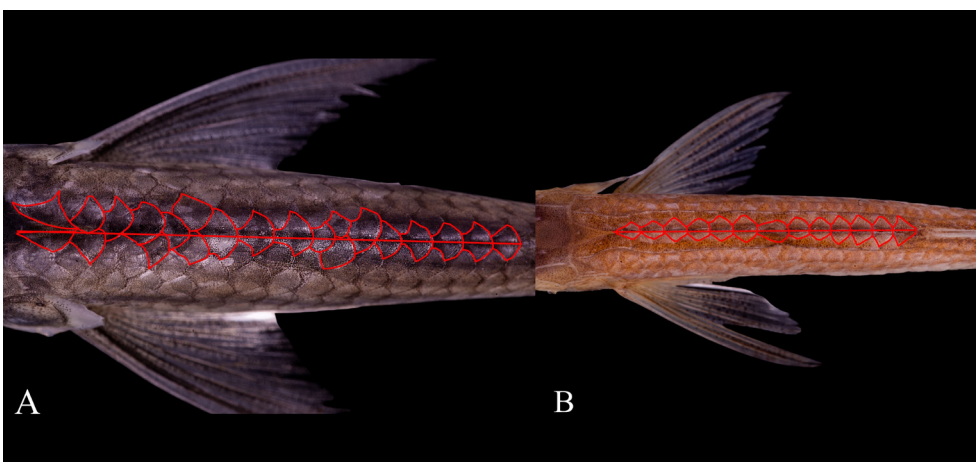

FIGURE 14 | Scales of predorsal line of *Triportheus pantanensis* (**A**), irregularly disposed, and *T. signatus* (**B**) regularly disposed in a single series.

DISCUSSION

The diversity of *Triportheus*, with the new species herein proposed, is updated to 17 valid species. The Paraná-Paraguai basin is second in richness, with four recognized species, with the rio Amazonas basin being the first with seven described species of *Triportheus* (Malabarba, 2004). Within the Paraná-Paraguai basin, the four recognized species, belong to the "deep-bodied group" (*sensu* Malabarba, 2004), which includes species with two scales between the pectoral fin and the ventral keel. Malabarba (2004) also mentioned differences on the presence of lateral stripes in deep bodied species (*vs*. absence of lateral stripes in species of elongated body). However, our data do not corroborate this characteristic and the coloration pattern can be variable within species of the deep-bodied group, mainly between small and large individuals. Mariguela *et al*. (2016) recovered at least four groups within *Triportheus*. Most of the deep-bodied species (*sensu* Malabarba, 2004), including *T. nematurus*, *T. pantanensis*, *T. signatus*, and *T. claudiae* (called as *T.* aff. *rotundatus*) are placed into a single group, that corroborates the separation of these species based on characters erected by Malabarba (2004) of the "elongate-bodied species" (*sensu* Malabarba, 2004).

The occurrence of *Triportheus angulatus* within the Paraná-Paraguai basin, as suggested by Garman (1890), Gomes, Miranda (2001), Cetra, Petrere (2006), Garcia *et al*. (2018), Pelicice *et al*. (2018), Jarduli *et al*. (2019), is in fact a misidentification of *T. signatus* or *T. nematurus*. *Triportheus angulatus* differs from the species of the Paraná-Paraguai basin in possessing 29–37 gill rakers on the first branchial arch (*vs*. 38–48 in *T. nematurus* and 37–44 in *T. signatus*); 34–37 perforated scales on the lateral line (*vs.* 28–32 in *T. pantanensis*), irregularly disposed scales on the predorsal line, between the supraoccipital and the origin of the dorsal fin (*vs*. regularly disposed predorsal line scales in aligned series, in *T. signatus* and *T. claudiae*). The combination of these mentioned characters is present only in specimens of the rio Amazonas basin and, therefore, the hypothesis of the occurrence of *T. angulatus* within the Paraná-Paraguai basin is not corroborated.

Specimens of *Triportheus* from the upper rio Paraná basin were identified as *T. nematurus* or *T. signatus* (Nakagawa, 2011; Mariguela *et al*., 2016; Reis *et al*., 2020). Our data corroborates the occurrence of both species within the upper rio Paraná basin. In both cases, they are recognized as species introduced into this aquatic ecoregion, associated with reservoirs and via the destruction of a biogeographical barrier to *T. nematurus*, or restocking programs using allochthonous species to *T. signatus* (Garcia *et al*., 2018; Queiroz-Sousa *et al*., 2018). Reservoirs are known as enabling regions for the introduction and establishment of allochthonous and exotic species (Leprieur, 2008). This fact is corroborated in the upper rio Paraná basin, where causes including aquaculture and sport-fishing are mentioned as dependent on non-native species and which can be directly related to introductions of invaders into reservoir zones (Garcia *et al*., 2018). Garcia *et al*. (2018) mentioned the occurrence of *T. angulatus* (but probably *T. signatus*) as an invasive within the rio Paranapanema reservoirs, a consequence of deliberate introduction. Regarding *Triportheus nematurus*, the available data is not conclusive about the origin of the species in the upper rio Paraná basin and a comparative population genetic analysis would help to elucidate this question.

Triportheus nematurus, *T. pantanensis*, and *T. claudiae* are recognized from the rio Paraguai basin. These species are morphologically similar and some of the external characters used to differentiate them present overlap (*e.g.*, number of perforated scales on the lateral line, branched rays at anal fin, and predorsal distance to *T. nematurus* and *T. pantanensis*) *sensu* Malabarba (2004). The number of epineural bones (35 or 36 in *T. nematurus* and 32 or 33 in *T. pantanensis*), and epipleural bones (22 in *T. nematurus* and 19 in *T. pantanensis*) have demonstrated to be good meristic traits to separate these taxa. The number of ventral tubules in the laterosensorial canal of the preopercle were also found to serve as distinguishable characters between the species analyzed here, with two patterns: 4–5 in *T. nematurus* and *T. signatus vs.* 7 in *T. pantanensis* and *T. claudiae*. The analysis of *Triportheus* osteological features, mainly from the laterosensorial system, is still poor explored, even though these types of characters can be very informative to the taxonomy and systematics of Characiformes (Pastana *et al*., 2020) as partially corroborated by our data. Future studies, exploring in greater detail the osteology and laterossensorial system of *Triportheus* can help to form a more robust diagnosis of the species of this genus, which presents conservative external morphology.

Triportheus claudiae, is herein recognized from the rio Paraguai basin. Phylogenetic analysis, based on molecular data from Mariguela *et al*. (2016), suggested that *T.* aff. *rotundatus* (= *T. claudiae*) as a different lineage, a sister group of *T. nematurus*, within a clade of "deep-bodied species" (*sensu* Malabarba, 2004). The individual analyzed by Mariguela *et al*. (2016) in their molecular phylogeny (LBP 11917) was analyzed in this work, and this taxon presents genetic (*sensu* Mariguela *et al*., 2016), morphometric, meristic and osteological differences from *T. nematurus* and the other species of *Triportheus.*

We did not find any sexual dimorphism character to the recognized species of *Triportheus* from the Paraná-Paraguai basin. However, all the analyzed species presented ontogenetic variations on caudal fin form and coloration patterns. These characters, although poor explored, can help on future to elucidated taxonomic confusions among *Triportheus* species, through understanding the development of morphological structures throughout life.

The new taxon from the Paraná-Paraguai basin show that the diversity of the genus remains underestimated and that taxonomic revisions are fundamental to the knowledge, classification and distribution of groups of species. A revision of Triportheidae is ongoing by the first author.

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AUTHORS' CONTRIBUTION

Douglas Alves Lopes: Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Project administration, Validation, Visualization, Writing-original draft, Writing-review and editing.

Fernando Rogério Carvalho: Conceptualization, Data curation, Funding acquisition, Investigation, Methodology, Resources, Validation, Visualization, Writing-review and editing.

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The author declares no competing interests.

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