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New species of the *Corumbataia cuestae* group (Siluriformes: Loricariidae) from the Rio Tocantins basin, with comments on its phylogenetic relationships

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A new species of *Corumbataia* is described from Rio Maranhão, Rio Tocantins basin, central Brazil. The new species is distinguished from all congeners by the presence of a small, naked area on snout tip; by having the abdomen covered with small platelets forming a shield which reaches the lateral mid-ventral plates; by the anterior profile of the head rounded in dorsal view; by the lower lip not reaching the transversal line of the pectoral girdle; and by the presence of 28 or 29 vertebrae. High genetic divergence in mitochondrial cytochrome c oxidase subunit I (COI) further supports the validity of this new species. Our phylogenetic analysis shows a derived subclade in *Corumbataia*, herein named as the *Corumbataia cuestae* group, composed of the new species plus *C. cuestae*, *C. tocantinensis*, *C. britskii*, *C. liliai*, and *C. lucianoi*. This group is defined by having a conspicuous crest of hypertrophied odontodes on head; absence of the adipose fin or a single series of platelets at adipose-fin position; and anastomosis of the infraorbital and otic sensory canals over the pterotic-supracleithrum. Here we also restrict the distribution of *C. tocantinensis* to the Rio Araguaia basin.

Keywords: Cytochrome C Oxidase, Diversity, Freshwater fishes, Hypoptopomatinae, Central Brazil.

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Uma nova espécie de *Corumbataia* é descrita para o Rio Maranhão, na bacia do Rio Tocantins na região central do Brasil. A nova espécie é diagnosticada dos demais congêneres pela presença de uma pequena área nua na ponta do focinho; por possuir o abdômen coberto por pequenas placas formando um escudo que alcança as placas laterais mid-ventrais; perfil anterior da cabeça arredondado em vista dorsal; lábio inferior não alcançando a linha transversal da cintura peitoral; e presença de 28 ou 29 vértebras. Altos valores de divergência genética também suportam a validade dessa nova espécie. Nossa análise filogenética encontrou um subclado derivado em *Corumbataia*, aqui denominado grupo *Corumbataia cuestae*, composto pela nova espécie mais *C. cuestae*, *C. tocantinensis*, *C. britskii*, *C. liliai* e *C. lucianoi*. Esse grupo é definido por possuir uma crista conspícua de odontódeos hipertrofiados na cabeça; ausência de nadadeira adiposa ou série única de placas na posição da nadadeira adiposa; anastomose dos canais sensoriais infraorbital e ótico sobre o pterótico-supracleitro. Aqui, nós também restringimos a distribuição de *C. tocantinensis* à bacia do Rio Araguaia.

Palavras-chave: Brasil Central, Citocromo C Oxidase, Diversidade, Peixes de água doce, Hypoptopomatinae.

INTRODUCTION

Loricariidae is the most diverse family of Siluriformes with almost 1000 valid species (Fricke *et al*., 2020) recognized mainly by having the body covered by bony plates, external tooth-like structures (odontodes), and a ventral mouth with lips forming an oral disk used to adhere to surfaces and to soft substrate for foraging (Greerinckx *et al*., 2007; Garg *et al*., 2010). Hypoptopomatinae is a subfamily of loricariids popularly known as cascudinhos, which contains 247 valid species (Fricke *et al*., 2020) arranged in six major clades: Hisonotini, Neoplecostomini, Otothyrini, *Corumbataia* clade, *Otocinclus* clade, and Hypoptopomatini (Roxo *et al*., 2019).

Corumbataia was proposed by Britski (1997) when describing *Corumbataia cuestae* from the Upper Paraná basin in the Rio Tietê and *Corumbataia tocantinensis*, from the Rio Araguaia and Rio Tocantins basins. This genus was delimited by an exposed portion in the middle of the scapular bridge formed only by the coracoid; compound hypurals 1 and 2 completely fused to the compound hypurals 3–5; atrophic maxillary barbel, and anastomosis of the infraorbital and otic sensory canals over the pterotic-supracleitrum (Britski, 1997). Four species were subsequently described: *C. britskii* Ferreira & Ribeiro, 2007, *C. veadeiros* Carvalho, 2008, *C. lucianoi* Silva, Roxo, Souza & Oliveira, 2018 and *C. liliai* Silva, Roxo, Souza & Oliveira, 2018. Additionally, two species formerly described in *Gymnotocinclus* were transferred to *Corumbataia* by Roxo *et al*. (2019): *C. anosteos* (Carvalho, Lehmann & Reis, 2008) and *C. canoeiro* (Roxo, Silva, Ochoa & Zawadzki, 2017).

Detailed examination of specimens of *Corumbataia* from the Rio Maranhão in the Rio Tocantins basin indicated that these represent a new species of this genus, which is formally described herein. We also provide and discuss a hypothesis for its phylogenetic position.

MATERIAL AND METHODS

Morphology. Measurements and counts were taken from the left side of 27 specimens and were made point to point to the nearest 0.1 mm with digital calipers. Nomenclature of body plates and osteology follow Schaefer (1997). Measurements and abbreviations follow Carvalho, Reis (2009), except for the measurement of body depth at dorsal-fin origin that were not included. We additionally included the following measurements: preanal length (from tip of snout until anal-fin insertion), base of dorsal-fin length (from anterior margin of dorsal-fin spinelet until insertion of last dorsal-fin ray), lower caudal-fin spine length (from posterior margin of last lateral plate of ventral plate series to the tip of the lower caudal-fin spine), body width at anal-fin insertion (from left side of the body until right side of the body at anal-fin insertion), snout-opercle length (from tip of snout until opercle opening), and head width (from opercle opening of the left side of the body until opercle opening of the right side of the body). Morphometrics are given as percentages of standard length (SL), except for subunits of head expressed as percentages of head length (HL). Four specimens were cleared and stained (c&s) according to Taylor, Van Dyke (1985). Vertebral counts include the five vertebrae of the Weberian apparatus and the compound caudal centrum (PU1+U1) that was counted as one element. Counts of dorsal-fin rays include the spinelet as the first unbranched ray. Institutional abbreviations follow Sabaj (2019). Specimens were deposited at the Laboratório de Biologia e Genética de Peixes, Universidade Estadual Paulista, Botucatu, Brazil (LBP); Museu de Zoologia, Universidade de São Paulo, São Paulo, Brazil (MZUSP). Zoological nomenclature follows the International Code of Zoological Nomenclature (ICZN, 1999).

Molecular analysis. Three specimens were used for the molecular analysis: LBP 19095, 3, Rio Tocantins, tissues 77006–08. Total DNA extraction was performed using the Wizard Genomic DNA Purification Kit (Promega) from ethanol-preserved muscle, fin, or liver. Partial sequences of the cytochrome c oxidase subunit I (*COI*) gene were amplified in a total reaction volume of 12.5 uL. Each reaction included 1.25 uL of 10 X Buffer, 0.25 uL of MgCL2 (50 mM), 0.2 uL dNTPs (2mM), 0.5 uL of each primer (5 mM), 0.1 uL of PHT Taq DNA polymerase (Phoneutria, Belo Horizonte, Brazil), 1.0 uL of genomic DNA (20 ng) and 8.7 mL ddH2O. The conditions for the PCR reaction consisted of an initial denaturation (5 min at 94ºC), followed by 30 cycles of chain denaturation (40s at 94ºC), primer hybridization (30 s at 50–54º), nucleotide extension (1 min at 68ºC) and final extension (8 min at 68ºC). The amplified products were checked on 1% agarose gels and purified using ExoSap-IT (USB Corporation). DNA sequencing was conducted in an automatic sequencer ABI 3130 DNA Analyzer (Applied Biosystems).

All individual sequences for each species were initially assembled using the software Geneious 7.1.4 (Kearse *et al*., 2012), and aligned by Muscle (Edgar, 2004) under default parameters. Alignments include the newly-generated sequences and the sequences available from the phylogenetic study of Roxo *et al*. (2014, 2017). To evaluate the occurrence of substitution saturation in our molecular data, we estimated whether the Iss (index of substitution saturation) was significantly lower than Iss.cAsym (assuming asymmetrical topology) using the method described by Xia *et al*. (2003) and Xia, Lemey (2009) with the software DAMBE 5.3.38 (Xia, 2013). Nucleotide variation, substitution patterns, and genetic distances were examined using MEGA v.6.06 (Tamura *et al*., 2013).

The best-fit nucleotide substitution model for the entire data set was selected under the Akaike information criterion (AICc) and Maximum Likelihood (ML) analyses were performed using the software MEGA v.6.06 (Tamura *et al*., 2013). Bootstrap (BS) resampling (Felsenstein, 1985) was applied to assess support for individual nodes using 1,000 pseudoreplicates. Random starting trees were used for each independent ML tree search and all other parameters were set to default values. Bayesian inference (BI) (Huelsenbeck, Ronquist, 2001) was performed in MrBayes v.3.2 (Ronquist, Huelsenbeck, 2003), based on the model (GTR+I). Two independent runs of 10 million steps sampling tree every 1000th generation a tree was sampled. Genetic variation within and among species groups under the best fit nucleotide model was also calculated in the MEGA v.6.06 software (Tamura *et al*., 2013).

RESULTS

Genetic analysis. We used 18 specimens of *Corumbataia* representing a total of nine species and used *Curculionichthys paresi* (Roxo, Zawadzki & Troy, 2014), *C. oliveirai* (Roxo, Zawadzki & Troy, 2014), *Hisonotus nigricauda* (Boulenger, 1891), *Rhinolekos britskii* Martins, Langeani & Costa, 2011, *Rhinolekos longicollum* (Calegari & Reis, 2010), *Pareiorhina rosai* Silva, Roxo & Oyakawa, 2016, and *Neoplecostomus bandeirante* Roxo, Oliveira & Zawadzki, 2012 as related taxa and *Hypostomus strigaticeps* (Regan, 1908) to root the tree (Tab. 1). The combined sequence data resulted in a matrix with 580 bp. All sequences are deposited in GenBank (Tab. 1). The matrix does not contain any insertions, deletions or stop codons. The best nucleotide substitution model selected for the matrix was TN93+I+G (AICc = 6339.934). The nucleotide frequencies under TN93+I+G model were 0.23 (A), 0.27 (T), 0.30 (C), and 0.17 (G). Saturation was not observed, considering that the Iss < Iss.c for all NumOTU in the Xia *et al*. (2003) and Xia, Lemey (2009) tests. Genetic distances in *Corumbataia* species and among each nominal species are shown in Tab. 2.

The gene tree represents a 50% majority-rule consensus obtained by maximum likelihood analysis (LogL = – 3132.01, Fig. 1). Bayesian analysis resulted in 10001 trees of which the first 2500 were discarded and the remaining 7501 were used to perform the consensus tree. In our analysis the *C. canoeiro*, *C. veadeiros,* and *C. anosteos* are the first groups to diverge, respectively. *Corumbataia acanthodela*, *C. tocantinensis*, *C. cuestae*, *C. britskii*, *C. liliai*, and *C. lucianoi* grouped in a clade herein named *Corumbataia cuestae* group. *Corumbataia acanthodela* is sister of the remainder members of *Corumbataia*-cuestae group. The phylogenetic analysis using the COI marker did not resolve the relationships among *Corumbataia tocantinensis*, *C. cuestae*, *C. britskii*, *C. liliai*, and *C. lucianoi*, which appeared as a polytomy.

TABLE 1 | Specimens and species included in the molecular analysis. LBP = Laboratório de Biologia e Genética de Peixes, Universidade Estadual Paulista. The order of the species in the table follow the order of taxa in Fig. 1.

Museum catalog	Voucher	GenBank	Species	Locality	Geographic coordinates
LBP 1673	11258	GU701954.1	*H. strigaticeps*	Rio Paranapanema, Andirá, PR, Brazil	22°56’35.4”S 50°15’13.8”W
LBP 2861	18616	JN089808.1	*N. bandeirante*	Rio Tietê, Salesópolis, SP, Brazil	23°31’37.2”S 45°45’43.8”W
LBP 17393	67147	KY711268.1	*P. rosai*	Rio Paraopeba, Cristiano Otoni, MG, Brazil	15°31’30.2”S 47°29’41.6”W
LBP 17060	68278	KY711265.1	*R. logicollum*	Rio Paranaíba, Planaltina, DF, Brazil	15°31’30.2”S 47°29’41.6”W
LBP 7245	34405	KM104459.1	*R. britskii*	Rio Paranaíba, Bela Vista de Goiás, GO, Brazil	17°07’10.4”S 48°44’23.7”W
LBP 6037	29056	JN998542.1	*H. nigricauda*	Rio Maquiné, Osório, RS, Brazil	23°38’30.1”S 51°51’32.3”W
LBP 1325	11237	KM365063.1	*C. oliveirai*	Rio Tibaji, Marialva, PR, Brazil	23°38’30.1”S 51°51’32.3”W
LBP 17532	68705	KM365042.1	*C. paresi*	Rio Paraguai, Tangará da Serra, MT, Brazil	14°22’40.7”S 57°35’11.7”W
LBP 19303	77929	KY711260.1	*C. canoeiro*	Rio Paranã, Cavalcante, GO, Brazil	13°43’13.0”S 47°27’20.0”W
LBP 19303	77930	KY711261.1	*C. canoeiro*	Rio Paranã, Cavalcante, GO, Brazil	13°43’13.0”S 47°27’20.0”W
LBP 19311	79119	MW206773	*C. veadeiros*	Rio Paranã, Teresinha de Goiás, GO, Brazil	13°47’39.6”S 47°17’29.1”W
LBP 19290	77898	MW206774	*C. veadeiros*	Rio Paranã, Cavalcante, GO, Brazil	13°44’34.0”S 47°26’33.0”W
LBP 17125	68274	KY711271.1	*C. anosteos*	Rio Piçarras, Alto Paraíso de Goiás. GO. Brazil	14°15’45.8”S 47°30’08.5”W
LBP 17125	68275	MW206775	*C. anosteos*	Rio Piçarras, Alto Paraíso de Goiás, GO, Brazil	14°15’45.8”S 47°30’08.5”W
LBP 19095	77008	MW206776	*C. acanthodela*	Rio Maranhão, Niquelândia, GO, Brazil	14°38’16.9” 48°45’59.1”W
LBP 19095	77006	MW206777	*C. acanthodela*	Rio Maranhão, Niquelândia, GO, Brazil	14°38’16.9”S 48°45’59.1”W
LBP 19095	77007	MW206778	*C. acanthodela*	Rio Maranhão, Niquelândia, GO, Brazil	14°38’16.9”S 48°45’59.1”W
LBP 1653	11827	FJ625822.1	*C. tocantinensis*	Rio Vermelho, Goiás, GO, Brazil	15°55'01.5"S 50°07'43.3"W
LBP 1653	11477	KM104484.1	*C. tocantinensis*	Rio Vermelho, Goiás, GO, Brazil	15°55'01.5"S 50°07'43.3"W
LBP 2896	18714	GU701820.1	*C. cuestae*	Rio Tietê, Bofete, SP, Brazil	23°09'S 48°16'W
LBP 2896	18716	GU701821.1	*C. cuestae*	Rio Tietê, Bofete, SP, Brazil	23°09'S 48°16'W
LBP 9598	44934	JN988808.1	*C. britskii*	Rio Sucuriú, Inocêncio, MS, Brazil	19°14’44.6”S 52°39’10.7”W
LBP 9590	44923	JN988807.1	*C. bristkii*	Rio Sucuriú, Inocêncio, MS, Brazil	19°14’44.6”S 52°39’10.7”W
LBP 25734	95559	MW206781	*C. lucianoi*	Rio Corrente, Aporé, GO, Brazil	18°30’50.7”S 52°05’48.4”W
LBP 25734	95560	MW206780	*C. lucianoi*	Rio Corrente, Aporé, GO, Brazil	18°30’50.7”S 52°05’48.4”W
LBP 26428	96777	MW206779	*C. liliai*	Córrego Cachoeira, Aporé, GO, Brazil	18°34’50.0”S 52°05’50.1”W

TABLE 2 | Genetic distance and standard deviation among *Corumbataia* species based on the TN93+G+I model. Intraspecific genetic divergences are highlighted in diagonal bold numbers. Below the main diagonal is the value of interspecific genetic divergence. The values are shown as percentages.

		1	2	3	4	5	6	7	8	9
1	*C. canoeiro*	**0.0±0.0**								
2	*C. veadeiro*	17.2±0.2	**1.2±0.0**							
3	*C. anosteos*	13.2±0.2	9.6±0.1	–						
4	*C. acanthodela*	16.5±0.2	12.5±0.2	7.4±0.1	**0.1±0.0**					
5	*C. tocantinensis*	18.7±0.2	15.7±0.2	9.4±0.1	6.0±0.0	**4.1±0.1**				
6	*C. cuestae*	17.1±0.2	13.8±0.2	7.8±0.1	4.8±0.1	3.5±0.1	–			
7	*C. britskii*	16.4±0.2	12.9±0.2	7.3±0.1	3.8±0.1	3.1±0.0	1.8±0.0	**0.2±0.0**		
8	*C. lucianoi*	16.3±0.2	13.2±0.2	7.3±0.1	3.7±0.0	2.8±0.0	1.4±0.0	0.8±0.0	**0.0±0.0**	
9	*C. liliai*	16.3±0.2	13.2±0.2	7.3±0.1	3.7±0.0	2.8±0.0	1.4±0.0	0.8±0.0	0.00	NA

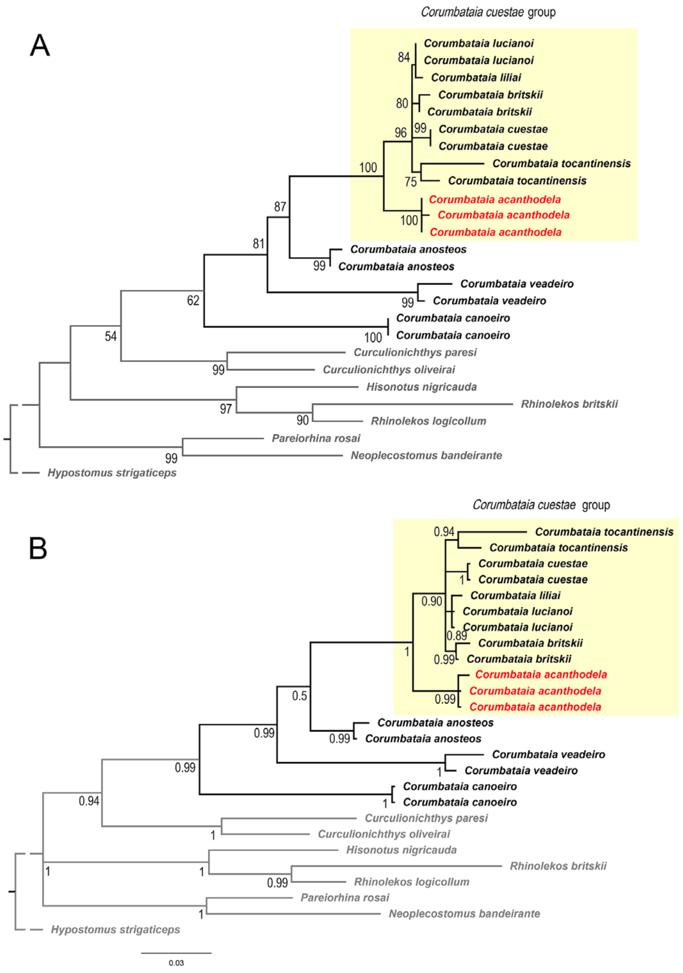

FIGURE 1 | **A**. Maximum likelihood – ML (LogL = -3132.01) tree of *Corumbataia* species using TN93+G+I nucleotide substitution model and based on the analysis of partial sequence of cytochrome oxidase C subunit I (COI). Numbers at nodes are bootstrap values based on 1000 pseudoreplicates. Values below 50% are not shown. **B**. Majority rule consensus tree obtained in Bayesian analysis using GTR+I. Numbers below branches are posterior probabilities obtained from 10000 trees.

Corumbataia acanthodela, new species

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(Fig. 2, Tab. 3)

Corumbataia tocantinensis Bristki, 1997:237 (original description; in part, paratypes MZUSP 51224, 51225, 50158; UFRJ 3000, 3001, 2999; Rio Maranhão, Rio Tocantins). —Carvalho, 2008:554 (diagnosis, fig. 2A, MCN 13462).

Holotype. MZUSP 125794, 27.9 mm SL, male, Goiás, Niquelândia, Rio do Peixe, Rio Maranhão, Rio Tocantins basin, 14°30'39.3"S 48°41'10.0"W, 23 Nov 2012, B. F. Melo, J. H. Martinez, G. S. C. Silva & R. Devidé.

Paratypes. All from Brazil, Goiás: LBP 17153, 10, 28.9–16.8 mm SL, 2 c&s, 26.1–26.4 mm SL, collected with holotype. LBP 19095, 10, 27.3–16.1 mm SL, 2 c&s, 29.4–26.5 mm SL (tissues 77006–10), Goiás, Niquelândia, Rio Maranhão, Rio Tocantins basin, 14°38'16.9"S 48°45'59.1" W, 5 Aug 2014, B. F. Melo, C. Oliveira, G. S. C. Silva & M. Taylor. LBP 25634, 1, 28.4 mm SL, Goiás, Mara Rosa, Rio Vaivém, Rio Maranhão, Rio Tocantins basin, 14º03'45.10"S 49º05'34.25"W, 25 Nov 2017, R. Devidé, B. F. Melo, C. Araya, G. S. C. Silva. NUP 22694, 3, 17.1–24.9 mm SL, Goiás, Niquelândia, Rio Maranhão, Rio Tocantins basin, 14°38'16.9"S 48°45'59.1"W, 5 Aug 2014, B. F. Melo, C. Oliveira, G. S. C. Silva & M. Taylor.

FIGURE 2 | *Corumbataia acanthodela*, holotype, MZUSP 125794, male 27.9 mm SL, from Rio Maranhão, Rio Tocantins basin, Niquelândia, Goiás, Brazil.

Diagnosis. The new species differs from all congeners, except for the members of *Corumbataia cuestae* group by having a conspicuous pair of tufts with enlarged odontodes on the tip of the supraoccipital (*vs*. absence of crest of enlarged odontodes in *C. anosteos*, *C. canoeiro*, and *C. veadeiros*); by the absence of an adipose fin or single series of platelets at adipose fin position (*vs*. presence of an adipose fin in *C. canoeiro*, or single series of platelets in *C. anosteos* and *C. veadeiros*); by anastomosis of the infraorbital and otic sensory canals over the pterotic-supracleithrum (Fig. 3A) (*vs*. anastomosis of infraorbital and otic sensory canals over the sphenotic in *C. anosteos*, *C. canoeiro*, and *C. veadeiros*) (Fig. 3B). Additionally, the new species differs from all species of *Corumbataia cuestae* group by having a small naked area on snout tip (*vs*. large naked area on snout tip, Fig. 4). Moreover, *Corumbataia acanthodela* differs from *C. cuestae*, *C. liliai*, *C. lucianoi,* and *C. britskii* by having abdominal platelets reaching the mid-ventral lateral plates (*vs*. abdominal platelets far from reaching mid-ventral lateral plates); from *C. cuestae*, *C. liliai*, and *C. tocantinensis* by having two rounded and more anteriorly positioned hyaline areas on the caudal-fin (Fig. 2) (*vs*. absence of two smaller rounded hyaline areas, see fig. 3 in Silva *et al*., 2018). It differs from *C. tocantinensis* by having the anterior profile of the head rounded in dorsal view (*vs*. elliptical) and from *C. lucianoi* and *C. liliai* by the presence of plates on dorsal portion of snout (*vs*. presence of a broad naked area without plates or odontodes on dorsal portion of snout). It differs from *C. britskii*, *C. lucianoi,* and *C. liliai* by the presence of 28–29 vertebrae (*vs*. 27) and from *C. britskii* by having lower lip far from reaching pectoral girdle line (*vs*. reaching pectoral girdle transversal line).

Description. Morphometric and meristic data are summarized in Tab. 3. Small-sized loricariid (maximum 27.3 mm SL). Snout rounded in dorsal view. Dorsal profile of head ascending convexly approximately 45° to parieto-supraoccipital. Eyes relatively small (15.3–21.8% of HL), dorsolaterally positioned, just posterior to midpoint of head. Iris

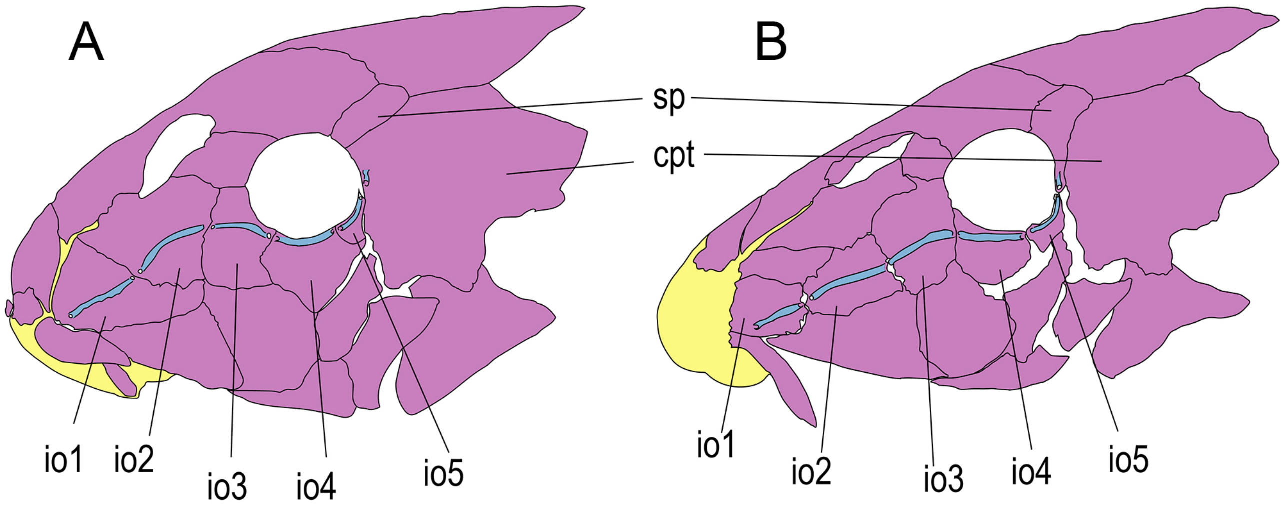

FIGURE 3 | Infraorbital series of *Corumbataia acanthodela*, LBP 19095, paratype (**A**), and *C. anosteos*, LBP 17125 (**B**). io1-io5 (Infraorbitals); sp (sphenotic); cpt (pterotic-supracleithrum). Scale bars = 1 mm.

operculum present and poorly developed. Mouth moderate in size; oral disk ellipsoid with papillae randomly distributed. Lower lip larger than upper lip, not reaching cleithrum; its border fringed; lower lip inner surface covered with small papillae, similar in size. Maxillary barbel adnate to lower lip. Teeth slender with two cusps; central cusp larger than lateral cusp. Premaxillary teeth 29–42 (mode 37). Dentary teeth 22–37 (mode 32).

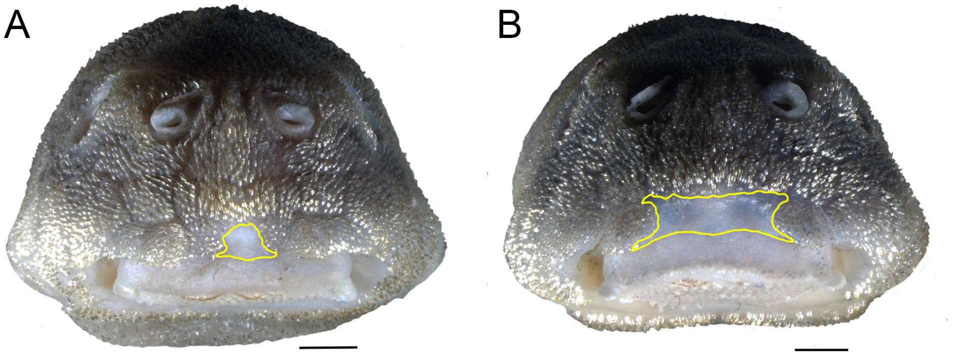

FIGURE 4 | Frontal view of snout tip showing a naked area without odontodes. **A**. *Corumbataia acanthodela*, LBP 19095, paratype; **B**. *Corumbataia cuestae*, LBP 1309. Scale bars = 1 mm.

TABLE 3 | Morphometrics of the holotype and 27 paratypes of *Corumbataia acanthodela*. SD = standard deviation.

	Holotype	Min	Max	Mean	SD
Standard length	27.9	16.6	30.8	23.0	4.3
Percentages of standard length					
Predorsal length	44.2	40.4	50.3	44.2	2.0
Preanal length	61.5	55.9	63.2	59.7	1.9
Head length	31.7	28.8	35.1	31.7	1.6
Cleithral width	27.5	22.7	30.0	27.6	1.6
Dorsal-fin spine length	24.9	18.6	25.9	22.6	1.9
Base of dorsal-fin length	14.2	11.9	15.4	13.7	0.8
Thorax length	19.5	12.5	18.4	16.5	1.5
Pectoral-fin length	25.7	18.1	25.7	20.5	1.6
Abdomen length	26.1	20.4	26.8	23.5	1.5
Pelvic-fin spine length	19.9	17.3	23.4	21.0	1.6
Anal-fin spine length	19.2	16.1	21.1	18.8	1.3
Lower cd spine	24.7	22.8	34.8	28.7	3.7
Caudal peduncle depth	11.1	10.2	12.8	11.3	0.6
Caudal peduncle length	32.2	29.3	36.6	33.7	2.1
Anal width	14.2	10.6	14.9	13.4	1.1
Snout-opercle length	24.3	20.4	25.8	22.6	1.2
Percentages of head length					
Head width	86.7	76.1	90.3	83.3	3.8
Head depth	71.2	66.5	76.3	70.3	2.8
Snout length	56.9	51.2	59.8	55.5	1.9
Interorbital width	46.1	41.8	48.5	44.3	1.5
Orbital diameter	19.5	15.3	21.8	18.5	1.6
Suborbital depth	29.5	22.9	34.1	27.2	2.3
Mandibular ramus	11.3	10.6	15.4	13.1	1.5

Lower surface of head naked. Head lacking ridges. Parieto-supraoccipital process elevated and with conspicuous pair of tufts of hypertrophied odontodes in specimens of all examined sizes. Predorsal region without ridges. Body elongate and compressed at caudal peduncle. Greatest body width at cleithral region, progressively narrowing anteriorly towards snout tip and posteriorly towards caudal-fin. Head and trunk covered by dermal plates, except for naked area around dorsal-fin insertion. Body dorsoventrally compressed. Dorsal profile convex from snout tip to posterior margin of parieto-supraoccipital and slightly concave from that point to dorsal-fin origin. Dorsal profile slightly concave and descending from dorsal-fin origin to first upper procurrent caudal-fin ray, rising posteriorly to insertion of caudal fin. Greatest body depth at unbranched dorsal-fin ray insertion. Cleithrum and coracoid exposed in ventral view, covered by odontodes. *Arrector fossae* completely enclosed by ventral lamina of coracoid.

Ventral profile straight and descending from snout tip to opercular region, slightly convex from opercular region to anal-fin origin and slightly concave from that point to lower procurrent caudal-fin ray origin. Lateral surface of body entirely covered by plates; dorsal series with 23–24 plates. Mid-dorsal plate series truncated with 18–19 plates not reaching end of caudal peduncle. Lateral plate series with 22–23 plates. Lateral line incomplete, with gaps in line of pores along mid-length of body. Mid-ventral series of lateral plates well-developed, reaching middle of caudal peduncle (17–19 plates). Ventral plates series with 20–21 plates. Body plates covered with minute odontodes.

Dorsal fin ii,7; its origin slightly posterior to vertical with pelvic-fin origin. Unbranched rays of dorsal fin slightly convex. Tip of adpressed dorsal-fin rays surpassing anal-fin origin. Dorsal-fin spinelet small and rounded (4 c&s). Pectoral-fin rays i,6; tip of adpressed pectoral fin surpassing pelvic-fin origin. Pectoral-fin axillary slit small. Pelvic-fin rays i,5. Distal margin of pelvic fin straight to slightly convex; tip of adpressed pelvic-fin ray reaching anal-fin origin in mature males, but not in females. Adipose fin absent. Anal-fin rays i,5; distal margin slightly convex. Caudal-fin rays i,7–i,7. Slightly emarginated; unbranched rays of same size. Rays of all fins covered with pointed odontodes. Lowest body depth at caudal peduncle. Caudal peduncle ellipsoid in cross section, rounded dorsally and ventrally. Hypurals elements fused in a unique hypural plate. Total vertebrae 28 or 29 (4 c&s).

Color in alcohol. Background color of dorsal region of head and trunk brown. Four dark brown saddles along dorsal portion of body: first at dorsal-fin origin, second at end of dorsal-fin base, third at middle of caudal peduncle, and fourth reaching anteriormost caudal procurrent ray. Unpigmented portion of snout appears as two parallel hyaline stripes from rostral plate to nares. Mid-lateral dark brown stripe extending from tip of snout to caudal peduncle. Ventral portion of body almost entirely yellowish, except for dark, randomly-distributed chromatophores and for a concentration of chromatophores at anal-fin origin. Dorsal, pectoral, and pelvic fins with dark, irregularly distributed chromatophores. Caudal-fin brown, with two smaller rounded hyaline areas anteriorly, and two large rounded hyaline areas posteriorly (Fig.1).

Sexual dimorphism. Adult males possess a papilla located posterior to the urogenital opening; an unbranched pelvic-fin ray that supports dermal flap along its dorsal surface;

and a wider head (84.5–88.6% *vs*. 80.6–85.3 of HL in female) with hypertrophied odontodes on its lateral margin (Fig. 5).

Geographical distribution. *Corumbataia acanthodela* is known from Rio dos Patos, Rio do Peixe, and Rio Vaivém, all tributaries of the Rio Maranhão, in the headwaters of the Rio Tocantins basin, Goiás, Central Brazil (Fig. 6). The new species was found in clear water of fast-flowing stream with rocks and marginal vegetation.

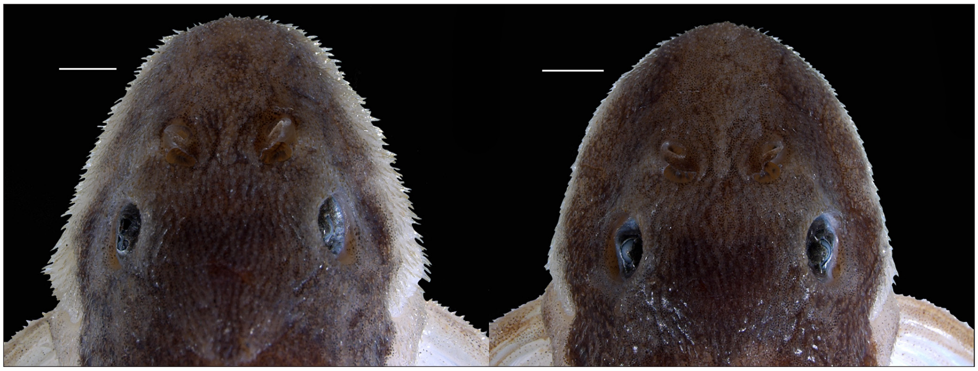

FIGURE 5 | Hypertrophied odontodes on the lateral margins of head in *Corumbataia acanthodela*, paratypes, male (left), NUP 22694 and female (right), LBP 19095. Scale bars = 1 mm.

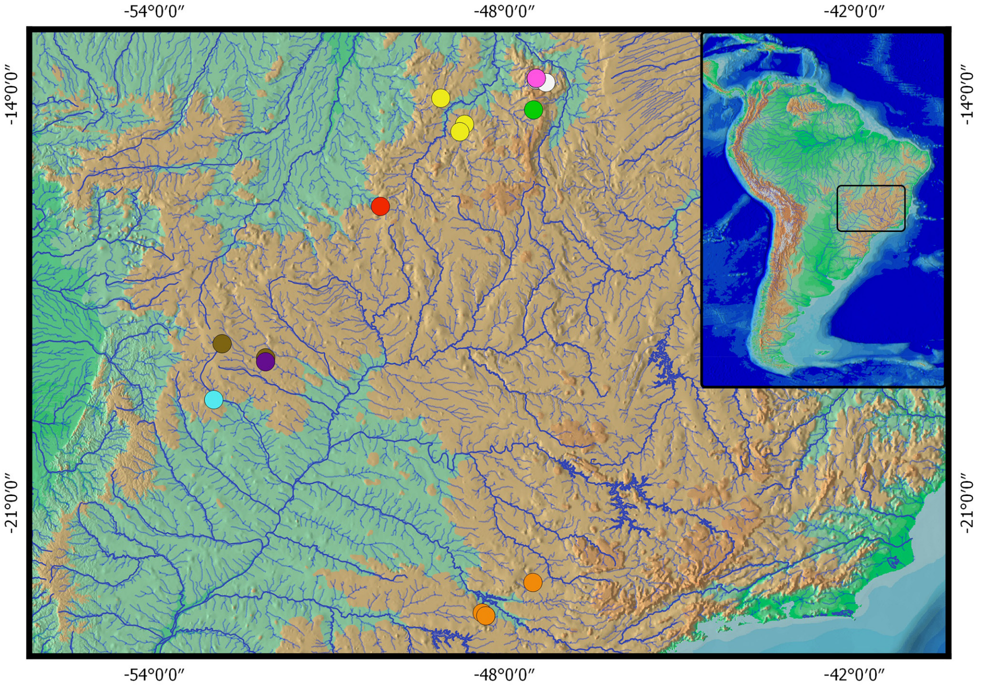

FIGURE 6 | Distribution of *Corumbataia* species. Yellow circles: *C. acanthodela*, Rio Maranhão; Green circle: *C. anosteos*, Rio Piçarras; Blue circle: *C. britskii*, Rio Sucuriu; White circle: *C. canoeiro*, Rio Paranã; Orange circles: *C. cuestae*, Rio Tietê; Purple circle: *C. liliai*, Rio Correntes; Brown circles: *C. lucianoi*, Rio Correntes; Red circle: *C. tocantinensis*, Rio Vermelho; Pink circle: *C. veadeiros*, Rio Paranã.

Etymology. The specific epithet *acanthodela* is from Greek *akantha* meaning thorn, and *delos* meaning conspicuous, in reference to the hypertrophied odontodes in the head of mature males. An adjective.

Conservation status. *Corumbataia acanthodela* is known from three localities in the Rio Maranhão basin. The areas where the specimens were collected are mountainous and relatively well preserved, which do not qualify it for threatened status. Therefore, *C. acanthodela* is here recommended to be categorized as Least Concern (LC) under the categories and criteria of the International Union for Conservation Nature (IUCN Standards and Petitions Subcommittee, 2019).

DISCUSSION

Britski (1997) described *Corumbataia tocantinensis* based on material from Rio Vermelho, tributary of the Rio Araguaia (locality of holotype), and from the Rio Maranhão, a tributary of the Rio Tocantins. Here, we found molecular and morphological evidence that the samples from Rio Maranhão (described here as *C. acanthodela*) form a distinct lineage from *C. tocantinensis*. Our mitochondrial data analysis showed a high value of genetic divergence between these two lineages (6.0%, Tab 2). Recent DNA barcode studies in loricariids have shown lower values than 6.0%, for valid and morphologically-distinct species [*i.e*., 2.0% between *Neoplecostomus microps* (Steindachner, 1877) and *N. paraty* Cherobim, Lazzarotto, Langeani & 2017; 1.0% between *N. botucatu* Roxo, Oliveira & Zawadzki, 2012, and *N. selenae* Zawadzki, Pavanelli & Langeani, 2008; 1.8% between *Paralithoxus jariensis* (Silva, Covain, Oliveira & Roxo, 2017) and *P. raso* (Silva, Covain, Oliveira & Roxo, 2017) (Silva *et al*., 2017); 3.0% between *Curculionichthys oliveirai* and *C. insperatus* (Britski, Garavello, 2003) (Silva *et al*., 2014)].

On the other hand, some well-diagnosed species (*Corumbataia britskii*, *C. cuestae*, *C. liliai*, and *C. lucianoi*) showed low inter-specific pairwise divergence with their closest relatives (Tab. 1), suggesting recent divergence among these species. Curiously, *C. tocantinensis* showed a high intraspecific divergence (4.1%), although no morphological differences have been found between these two specimens represented in the tree (vouchers: 11827 and 11477; Tab. 1). This unexpected value of intraspecific divergence may be explained by the high number of mutations (autapomorphies) found in the sequence 11477 (Genbank: KM104484.1), probably caused by error in sequencing or manual editing.

Roxo *et al*. (2019) recovered a monophyletic *Corumbataia* including *Gymnotocinclus* (now a junior synonym of *Corumbataia*). In their phylogeny, the first lineage to diverge was *C. canoeiro*, followed by *C. veadeiros* and the clade formed by *C. anosteos* plus *C. cuestae*. Complementary to Roxo *et al*.'s study, we found a well supported clade (see Fig. 1, BS = 100 and PP = 1), named here as the "*Corumbataia cuestae* group", and composed by *C. acanthodela*, *C. britskii*, *C. cuestae*, *C. liliai*, *C. lucianoi*, and *C. tocantinensis*. These six species share three putative morphological apomorphies:

(1) Conspicuous crest of hypertrophied odontodes on head (see fig. 2 in Carvalho, 2008). The conspicuous crest on head is absent in the majority of members of Hypoptopomatinae, such as in Neoplecostomini, *Otocinclus* clade, Hypoptopomatini, *Rhinolekos* subclade, *Microlepidogaster* subclade and in all others species of *Corumbataia* clade (*Microplecostomus forestii* Silva, Roxo, Ochoa & Oliveira, 2016, *Nannoplecostomus eleonorae* Ribeiro, Lima & Pereira, 2012, *Curculionichthys* Roxo, Silva, Ochoa & Oliveira, 2015, species, and *C. canoeiro*, *C. veadeiros,* and *C. anosteos*). In contrast, we found the derived condition, a conspicuous crest of hypertrophied odontodes in the members of *Corumbataia cuestae* group and in some members of the Hisonotini and Otothyrini (Carvalho, Reis, 2009; Sarmento-Soares *et al*., 2009; Roxo *et al*., 2012).

(2) Absence of an adipose fin or platelets at the adipose-fin region. The plesiomorphic species *Corumbataia canoeiro* possesses a developed adipose fin, whereas in *C. veadeiros* and *C. anosteos*, the next lineages to diverge in *Corumbataia*, there is a single series of platelets at the adipose-fin position. This suggests that the adipose fin, present in *C. canoeiro*, was reduced in *C. veadeiros* and *C. anosteos* and totally lost in the species of the *Corumbataia-cuestae* group. The primitive condition in *Corumbataia* clade is the presence of adipose fin or platelets at adipose-fin region, present in the first lineages to diverge in the *Corumbataia* clade: *Nannoplecostomus eleonorae* and *Microplecostomus foresti* (Roxo *et al*., 2019). *Curculionichthys*, the sister to *Corumbataia,* exhibits the derived condition (absence of platelets or adipose fin), suggesting that this derived condition occurs homoplastically in *Curculionichthys* and in the species of *Corumbataia cuestae* group.

(3) Anastomosis of the Infraorbital and otic canals over the pterotic-supracleithrum (Fig. 3a). This derived condition was proposed by Britski (1997) to *Corumbataia cuestae* and *C. tocantinensis*, and here was also observed in all members of *Corumbatia cuestae* group. The plesiomorphic condition is the anostomoids of the infraorbital and otic canals over the sphenotic (See fig. 3A in Ribeiro *et al*., 2012), and is found in *C. canoeiro*, *C. veadeiros,* and *C. anosteos,* and in the other members of *Corumbataia* clade.

Comparative material examined. Brazil: *Corumbataia anosteos*: LBP 17125, 3,18.8–33.0 mm SL, 1 c&s. *Corumbataia britskii*: LBP 9590, 48, 28.4–15.7 mm SL; 2 c&s, 24.5–26.8 mm SL. *Corumbataia canoeiro*: LBP 19469, 46, 28.0–54.3 mm SL. *Corumbataia cuestae*: LBP 8114, 19, 32.7–23.8 mm SL, 3 c&s, 22.7–29.4 mm SL; LBP 1309 (60, 28.9–19.4 mm SL). *Corumbataia liliai*: MZUSP 123826, holotype, 24.7 mm SL; LBP 9577, paratypes, 2, 18.4–23.2 mm SL; LBP 25544, paratypes, 2, 18.2–24.7 mm SL. *Corumbataia lucianoi*: MZUSP 123824, 24.0 mm SL; LBP 9570, paratypes 15, 12.8–25.5 mm SL. *Corumbataia tocantinensis*: LBP 1653, 27, 31.9–17.8 mm SL; LBP 1972, 10, 28.9-21.5, 1 c&s, 26.2 mm SL; MZUSP 50158, paratypes 2, 29.8–28.1 mm SL. *Corumbataia veadeiros*: LBP 19311, 2, 29.4–27.4 mm SL; LBP 19302, 3, 28.5–33.9 mm SL.

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Mateus Giovanni Rocha Thimotheo: Formal analysis, Investigation, Methodology, Writing-original draft.

Ricardo Cardoso Benine: Supervision, Writing-review and editing.

Claudio Oliveira: Data curation, Writing-review and editing.

Gabriel de Souza da Costa e Silva: Conceptualization, Formal analysis, Investigation, Methodology, Writing-original draft.

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The authors declare no competing interests.

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