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A new species of *Leporinus* (Characiformes: Anostomidae) from the Serra do Cachimbo, Pará State, Brazil

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A new small-sized species of *Leporinus* is described from rio Braço Norte, a tributary of rio Teles Pires, in the Tapajós drainage in the Brazilian Amazon, and its phylogenetic position is proposed based on molecular data. The new species is diagnosed among Anostomidae by having three unicuspid teeth on the premaxilla and four on the dentary, 12 scale rows around the caudal peduncle, dark blotches on the trunk, and large non-midlateral dark blotches over the body, with one or two large blotches in region ventral to the lateral line between the pectoral and pelvic fins. DNA Barcode sequences suggest that the new species is closely related to *Leporinus octomaculatus*. In addition, samples of intermediate forms in altered areas are herein identified as putative hybrids between the new species and *L. octomaculatus*. The new species is popular in the international aquarium market, and its area of occurrence has been affected by anthropogenic changes in the last years.

Keywords: Amazon basin, Anostomoidea, DNA Barcode, Systematics, Taxonomy.

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Uma nova espécie de pequeno porte de *Leporinus* é descrita do rio Braço Norte, um tributário do rio Teles Pires, bacia do rio Tapajós, na região Amazônica brasileira, e sua posição filogenética é proposta com base em dados moleculares. A espécie nova é diagnosticada entre os Anostomidae por possuir três dentes uniscuspidados no pré-maxilar e quatro no dentário, 12 fileiras de escamas ao redor do pedúnculo caudal, manchas escuras no tronco, e grandes manchas escuras não mediolaterias no corpo, possuindo uma ou duas grandes manchas entre as nadadeiras peitoral e pélvica, entre a região ventral e a linha lateral. Sequências de DNA Barcode sugerem que a nova espécie é próxima de *Leporinus octomaculatus*. Além disso, amostras de indivíduos intermediários, coletados em áreas alteradas, são aqui identificados como híbridos putativos entre a nova espécie e *L. octomaculatus*. A nova espécie é popular no mercado do aquarismo internacional, e a sua área de ocorrência foi afetada por alterações antrópicas nos últimos anos.

Palavras-chave: Anostomoidea, Bacia Amazônica, DNA Barcode, Sistemática, Taxonomia.

INTRODUCTION

Understanding systematics, how species are related, is essential for understanding biodiversity (Carvalho *et al*., 2005). Anthropogenic changes have accelerated the rate of species extinction (Abell *et al*., 2008), making it essential to increase knowledge about those species that remain. The South American fish fauna is megadiverse, with approximately 6,500 species currently recognized as valid and around 2,500 yet to be described (Reis *et al*., 2016; Sidlauskas, Birindelli, 2017), of which about 40% belong to Characiformes (Reis *et al*., 2003). Among the most diverse families of the order Characiformes is Anostomidae, which comprises about 150 valid species arranged in 16 genera (Fricke *et al*., 2021). The species of Anostomidae occupy a wide range of habitats in South America, from northern Colombia to central Argentina (Sidlauskas, Vari, 2008). Half of the species diversity of the family is concentrated in *Leporinus* Agassiz, 1829. Although many species of *Leporinus* have been described in recent years, surveys still discover new species, especially in unexplored areas of the Amazon.

The Serra do Cachimbo is in the southern portion of the Pará State and the northern portion of the Mato Grosso State and includes the highest mountain peaks of the southeastern portion of the Amazon. Many headwaters of tributaries of the Xingu and Tapajós are found in the area, and streams form small and large waterfalls along their course. The scenario has been recognized as housing a rich and endemic fish fauna (Goulding *et al*., 2003; Lima, Birindelli, 2006), and a variety of new species have been described from the region in recent years (*e.g*., Birindelli *et al*., 2009; Sousa *et al*., 2010; Varella, Sabaj, 2014).

In 1955, Lauro Pereira Travassos Filho sampled fishes in the Salto do Cachimbo, a waterfall at rio Braço Norte located inside the Brazilian Air Force (FAB) military base. The sample included a single specimen of *Leporinus* that represents a new species

described herein. Additional specimens were collected by Keve de Silimon in 2005 during studies regarding the licensing of small hydroelectric plants in the main channel of the rio Braço Norte. More recent scientific expeditions (Pipe Expedition in 2007 and AquaRios in 2010) yielded specimens with precise collection and habitat data and photographs of live individuals. Some specimens collected in flood zones have a slightly different color pattern from the other specimens collected in the rio Braço Norte, this coloration resembles that of another anostomid found in the Tapajós, *Leporinus octomaculatus* described by Britski, Garavello (1993), but also presents differences with the pattern exhibited by this species, therefore, it has an apparently intermediate coloration between the two species.

In 2016, the staff of the Piscicultura Tanganyika, an ornamental fish farm in the Ceará State, Brazil, successfully bred the new species of *Leporinus* in captivity through hormonal-induction techniques and introduced it to national and international markets (Lucanus, 2021). This study describes the new species of *Leporinus* from the Serra do Cachimbo using morphological and molecular data, investigates its phylogenetic position, and evaluates its geographic distribution and conservation status.

MATERIAL AND METHODS

Studied specimens belong to Museu de Zoologia da Universidade Estadual de Londrina, Londrina (MZUEL), Museu de Zoologia da Universidade de São Paulo, São Paulo (MZUSP), and Museu Nacional, Universidade Federal do Rio de Janeiro, Rio de Janeiro (MNRJ), and included 70% ethanol-preserved specimens (alc). Specimens provided by Piscicultura Tanganyika were deposited at MZUEL and included larvae and juveniles bred and raised in captivity. Reproduction was induced using Ovaprim in two doses for males (0.5 ml per kg of body weight) and one for females (0.4 ml per kg of body weight), with extrusion occurring within hours from first hormone injection. Egg incubation took place in trays at 27°C and hatching occurred approximately 55 h later. Fish larvae and juveniles were preserved in calcium-buffered formaldehyde.

Two specimens were cleared and counterstained (c&s) for cartilage and bone using the method outlined by Taylor, Van Dyke (1985) and dissected following the Ridewood method, described in Bemis *et al*. (2004). The stained specimens were photographed with a DFC295 digital camera attached to a Leica M205A stereomicroscope. The images were edited in image editing software for background standardization. One holotype was selected from the material provided by MNRJ. Meristic (*i.e*., counts of scales and fin rays) and morphometric data were taken according to Birindelli, Britski (2013). Counts and measurements were taken on the left side of the specimens using a digital caliper with a precision of 0.01 mm. Counts indicated by an asterisk belong to the holotype. The measurements were compared through minimum, maximum, mean, and standard deviation values.

A Principal Component Analysis (PCA) was performed with logarithmic measures in PAST v. 4.10 software (Hammer *et al*., 2001). For this analysis, *Leporinus octomaculatus* specimens were chosen as the comparative material due to its similarity with the new species and its nearby distribution. Individuals with intermediate coloration between the new species and *L. octomaculatus* also were included to investigate the possibility

of hybridization using morphological features, no tissue samples of the intermediate specimens were available for molecular analyses.

Genomic material (DNA) was isolated from muscle tissue using the Wizard Kit (Promega). GoTaq Master Mix Kit (Promega) was used to amplify the region of interest, following the manufacturer's recommendations. For this study, a ±640 bp segment of the mitochondrial gene cytochrome c oxidase subunit I (COI), called DNA Barcode (Herbert *et al*., 2003), was amplified and sequenced using Fish F1 and Fish R1 primers (Ward *et al*., 2005). The sequences were edited in the MEGA v. 11 program (Kumar *et al*., 2018) and aligned using the MUSCLE v. 3.8.4 algorithm (Edgar, 2004) implemented in MEGA. The best-fit models of nucleotide evolution were calculated in MEGA and used for Maximum-Likelihood and genetic distance analyses. The K2P model (Kimura, 1980) was used to calculate a genetic distance matrix between and within species. Sequences available in the GenBank (Clark *et al*., 2015) also were used (Tab. 1) and belong to Instituto Nacional de Pesquisas da Amazônia (INPA), MZUEL and Grupo de Estudos de Peixes do Médio Araguaia (GEPEMA), Universidade Federal de Mato Grosso. Phylogenetic relationships were investigated through an analysis of Maximum-Likelihood, also in MEGA, using HKY+G as the model for nucleotide evolution.

TABLE 1 | Information about the *Leporinus* species used in the DNA Barcode sequence analyses, including voucher data. *C. A. Nascimento and collaborators, work in progress.

Species	Voucher number	Locality	GenBank accession	Reference
Leporinus bistriatus	MZUEL 20489-28	Tocantins-Araguaia	OR497024	Present study
Leporinus bistriatus	MZUEL 20489-29	Tocantins-Araguaia	OR497025	Present study
Leporinus cylindriformis	MZUEL 10210-56	Uatumã	OR497014	Present study
Leporinus cylindriformis	MZUEL 10210-57	Uatumã	OR497015	Present study
Leporinus multimaculatus	MZUEL 20500-23	Tocantins-Araguaia	OR497019	Present study
Leporinus multimaculatus	MZUEL 20500-24	Tocantins-Araguaia	OR497020	Present study
Leporinus multimaculatus	MZUEL 20550-25	Tocantins-Araguaia	OR497021	Present study
Leporinus multimaculatus	MZUEL 20500-26	Tocantins-Araguaia	OR497022	Present study
Leporinus multimaculatus	MZUEL 20500-27	Tocantins-Araguaia	OR497023	Present study
Leporinus octomaculatus	MZUEL 69386	Upper Tapajós	OR497016	Present study
Leporinus octomaculatus	MZUEL 7917-38	Upper Tapajós	OR497017	Present study
Leporinus octomaculatus	MZUEL 7918-35	Upper Tapajós	OR497018	Present study
Leporinus octomaculatus	MZUSP 113992	Upper Tapajós	KF568989	Ramirez *et al*. (2016)
Leporinus sp. n.	MZUEL 20844-1	Upper Tapajós	OR497012	Present study
Leporinus sp. n.	MZUEL 20844-2	Upper Tapajós	OR497010	Present study
Leporinus sp. n.	MZUEL 20844-3	Upper Tapajós	OR497011	Present study
Leporinus reticulatus	MZUEL 7345-44	Upper Tapajós	OR497026	Present study
Leporinus sidlauskasi	MZUEL 21738-4186	Upper Tapajós	OR497013	Present study
Leporinus tristriatus	MZUEL 9134-45	Upper Tapajós	OR497027	Present study
Leporinus vanzoi	MZUEL 8006-47	Upper Tapajós	OR497028	Present study
Leporinus unitaeniatus	INPATO601	Tocantins-Araguaia	OP782399	*
Leporinus unitaeniatus	INPATO602	Tocantins-Araguaia	OP782400	*
Leporinus unitaeniatus	INPATO600	Tocantins-Araguaia	OP782398	*
Leporinus unitaeniatus	INPATO599	Tocantins-Araguaia	OP782397	*
Leporinus unitaeniatus	MZUEL 20674-80	Tocantins-Araguaia	OR497029	Present study
Leporinus unitaeniatus	MZUEL 20937-118	Tocantins-Araguaia	OR497032	Present study
Leporinus unitaeniatus	MZUEL 20674-81	Tocantins-Araguaia	OR497030	Present study
Leporinus unitaeniatus	MZUEL 20674-83	Tocantins-Araguaia	OR497031	Present study
Leporinus unitaeniatus	GEPEMA 5549	Tocantins-Araguaia	KF569000	Ramirez *et al*. (2016)

Two models were used for species delimitation analyses: The Poisson Tree Processes (PTP) model to infer putative species boundaries on a given phylogenetic input tree and Assemble Species by Automatic Partitioning - ASAP (Puillandre *et al*., 2021). For PTP, the maximum likelihood tree generated in MEGA was uploaded to the website (https://species.h-its.org/ptp/.) For ASAP, a file with aligned sequences was used on the online server (https://bioinfo.mnhn.fr/abi/public/asap/asapweb.html), with the K80 distance used as the model and other parameters used in default. A geographical distribution map was elaborated using the Quantum Giz program following procedures detailed by Calegari *et al*. (2016).

RESULTS

Leporinus oliveirai, new species

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(Figs. 1–7; Tab. 2)

Holotype. MNRJ 34085, 94.4 mm SL, Brazil, Pará, Novo Progresso, rio Braço Norte, a tributary of rio Peixoto de Azevedo, Teles Pires drainage, Amazon basin, below the CPBV-FAB power plant, 09°21'47.48"S 54°54'11.47"W, 1 Oct 2008, P. A. Buckup, J. L. O. Birindelli, F. C. Jerep, C. Chamon & J. A. Maldonado-Ocampo (AquaRios expedition).

Paratypes. All from Brazil, Pará, Novo Progresso. MNRJ 34085, 2 alc, 96.3–107.6 mm SL, collected with holotype. MZUEL 23321, 1 alc, 109.3 mm SL, collected with holotype. MZUSP 87068, 1 alc, 92.2 mm SL, rio Braço Norte, near FAB-NDB, 09°21'46.32"S 54°54'11.18"W, 17 May 1955, L. P. Travassos. MZUSP 96833, 1 alc, 23.5 mm SL, rio Braço Norte, BR-163 bridge, near FAB, 09°26'8.51"S 54°53'13.83"W, 18 Oct 2007, J. L. O. Birindelli, M. H. Sabaj, L. M. Sousa, A. L. Netto-Ferreira & N. K. Lujan (Pipe Expedition). MZUSP 96836, 14, 38.9–53.5 mm SL, rio Braço Norte, BR-163 bridge, near FAB, 09°28'32.94"S 54°52'34.94"W, 18 Oct 2007, Pipe expedition. MZUSP 119371, 18 alc, 2 c&s, 97.3–137.1 mm SL, rio Braço Norte, below the CPBV-FAB power plant, 09°21'46.13"S 54°54'11.07"W, 3 Aug 2015, W. M. Ohara & M. N. L. Pastana.

Non-types. MZUEL 20844, 2 alc (17.4–32.7 mm SL), specimens bred in captivity for ornamental purposes.

Diagnosis. *Leporinus oliveirai* can be distinguished from other anostomids, except *Hypomasticus megalepis* (Günther, 1863), *Leporinus amae* Godoy, 1980, *L. bahiensis* Steindachner, 1875, *L. bistriatus* Britski, 1997, *L. guttatus* Birindelli & Britski, 2009, *L. marcgravii* Lütken, 1875, *L. melanopleura* Günther, 1864, *L. microphthalmus* Garavello, 1989, *Leporinus moralesi* Fowler, 1942, *L. octofasciatus* Steindachner, 1915 , *L. octomaculatus*, *L. paranensis* Garavello & Britski, 1987, *L. reticulatus* Britski & Garavello, 1993, *L. sexstriatus* Britski & Garavello, 1980, *L. striatus* Kner, 1858, *L. taeniatus* Lütken, 1875, *L. taeniofasciatus* Britski, 1997, *L. tigrinus* Borodin, 1929, and *Megaleporinus garmani*

(Borodin, 1929), by having three unicuspid teeth on the premaxilla and four on the dentary (*vs*. four unicuspid teeth on the premaxilla and the dentary, or teeth multicuspid). *Leporinus oliveirai* is distinguished from *H. megalepis*, *L. bahiensis*, *L. melanopleura*, *L. moralesi*, *L. octofasciatus*, *L. paranensis*, *L. striatus*, *L. taeniatus*, *L. taeniofasciatus* and *L. tigrinus* by having 12 circumpeduncular scale series (*vs*. 16). *Leporinus oliveirai* differs from *L. amae*, *L. bistriatus*, *L. sexstriatus*, and *M. garmani* by having dark blotches on the trunk (*vs*. dark longitudinal stripes in *L. amae*, *L. bistriatus*, *L. sexstriatus*, and only one dark caudal blotch in *M. garmani*). *Leporinus oliveirai* differs from *L. reticulatus* by large round dark blotches over the body (*vs*. dark blotches formed by the reticulation of oblique dark bars). *Leporinus oliveirai* is distinguished from *L. guttatus*, *L. marcgravii*, *L. microphthalmus*, and *L. octomaculatus* by its pattern of dark blotches on the body in adults including one large midlateral blotch below posterior dorsal-fin base that is isolated from neighboring midlateral blotches by a wide gap (*vs*. midlateral blotches more regularly sized and spaced) and one or two large blotches in region ventral to the lateral line between the pectoral and pelvic fins (*vs*. 2 to 3 small blotches in same region).

Description. Morphometric data of the holotype and paratypes are presented in Tab. 2. Lateral view of holotype and lateral view of live specimen in Fig. 1. Small-sized species for genus *Leporinus*, largest examined specimen 137.1 mm SL. Body elongated and compressed. Dorsal profile gently convex from snout (posterior to upper lip) to dorsal-fin origin, straight to slightly convex in dorsal-fin base, generally straight from posterior insertion of dorsal fin to adipose-fin origin, and distinctly concave from adipose-fin origin to origin of upper lobe of caudal-fin. Ventral profile broadly convex from lower jaw to the posterior insertion of anal-fin rays and gently concave from this

FIGURE 1 | *Leporinus oliveirai*, **A.** MNRJ 34085, holotype, 94.4 mm SL. **B.** MZUSP 96836, paratype, Brazil, Pará, rio Braço Norte, a tributary of the Peixoto de Azevedo (photo by Mark H. Sabaj).

point to the origin of lower lobe of caudal fin. Greatest body depth at dorsal-fin origin. Head somewhat compressed; mouth subinferior, anterior opening of mouth positioned at longitudinal through lower border of orbit.

Dorsal fin ii,10*(40), origin slightly in front of vertical through pelvic-fin origin; base extending through six scales, distal margin rounded. Pectoral fin i,13(4), 14(19), 15*(9), or 16(8), base located posterior to gill opening, lobe extending through five to six scales from fin base, distal margin rounded. Pelvic fin i,8*(40), lobe extending through two or three scales, distal margin rounded. Anal fin ii,8*(40), anal-fin origin at vertical through the fifth scale anterior to adipose-fin origin, when adpressed, anal fin not reaching base of lower caudal-fin rays, distal margin straight or slightly rounded. Caudal-fin rays i,8,9,i*(40), caudal fin forked, upper lobe slightly more elongated than lower lobe.

Scales with few radii (6–8)*. Lateral line complete with 36*(20), 37(19) or 38(1) perforated scales; transversal series with 4*(40) scales from dorsal-fin origin to lateral line and 3.5(14) or 4*(26) scales from lateral line to pelvic-fin base, 3.5*(40) scales from lateral line to anal-fin base, 10(19) to 11*(21) predorsal scales, 12*(40) horizontal scale rows around caudal peduncle.

Osteology. Infraorbital series composed of six plate-like infraorbitals, nasal, antorbital, and supraorbital (Fig. 2) Antorbital not bearing canal, sickle-shaped, longer than infraorbital 1. Nasal large, with ventral lamina much larger than dorsal one. Supraorbital relatively small, rhomboid, not bearing canal. First infraorbital with straight three-pored canal and posteroventral portion overlapped by infraorbital 2 with dorsal and ventral lamina well-developed, dorsal margins form a rounded 90° angle. Third infraorbital largest, comprising most of ventral margin of orbit, with ventral lamina much larger than dorsal one. Fourth infraorbital with tripartite canal, posterior pore close to fifth infraorbital and extended to posterior margin. Sixth infraorbital relatively small and bearing a tripartite canal with two pores opened dorsally and one ventral directed toward fifth infraorbital.

TABLE 2 | Morphometric data of *Leporinus oliveirai* from rio Braço Norte, Pará, Brazil. H = holotype, N = number of specimens, SD = Standard deviation.

	H	N	Mean	Range	SD
Standard length (mm)	94.4	41	–	23.5–137.1	–
Percentages in standard length					
Predorsal distance	46.5	41	48.6	45.9–54.1	1.4
Dorsal-fin origin to adipose-fin origin	36.0	41	36.7	31.9–41.4	1.7
Prepelvic distance	48.0	41	50.2	47.3–52.5	1.3
Body depth	23.6	41	24.8	22.6–28.3	1.1
Caudal peduncle depth	9.5	41	9.4	7.2–10.8	0.6
Caudal peduncle length	9.8	41	10.5	8.4–14.0	1.7
Anal-fin lobe length	17.5	41	16.9	15.4–18.8	0.8
Head length	23.3	41	24.6	20.8–27.0	1.5
Percentages in head length					
Preopercle length	73.9	39	76.7	68.6–86.3	2.9
Snout length	42.3	39	40.4	34.2–50.6	3.5
Head depth	74.1	39	74.3	69.2–86.7	3.5
Eye diameter	23.3	39	23.8	18.3–31.5	4.2
Bony interorbital	33.8	39	34.8	30.1–41.5	2.3

Premaxilla bone trapezoidal, with dorsal process bent posteroventrally, and dorsoanterior margin with distinct protuberance (Fig. 2). Three unicuspid incisiform teeth on premaxilla, teeth broad (not compressed), with concave scoop-like lingual fossa boarded by ridge along lateral and median margins, teeth decreasing gradually in size laterally. Maxillary bone arranged vertically and curved with distal tips posterior to median portion, dumbbell-shaped with median portion constricted and dorsal portion wider than ventral: and bearing four unicuspid teeth gently decreasing in size laterally Lower jaw trapezoidal, composed of dentary, anguloarticular, and retroarticular. Mesethmoid triangular, forming anteriormost border of anterior cranium fontanel and bearing a relatively large anteroventral process where contralateral premaxillae articulate (Fig. 3). Lateral ethmoid longer than wide, with distinct lateral process directed posterolaterally. Frontal large, square-shaped, united to contralateral bone via epiphyseal bar crossing large anterior cranium fontanel. Parietals wide (width twice length), contralateral parietals separated by large posterior cranium fontanel. Sphenoitc somewhat triangular with distinct lateral process directed posterolaterally. Pterotic on posterolateral border of neurocranium, with distinct posterolateral process. Supraoccipital small triangular forming posterior border of posterior cranium fontanel. Epiotic forming a three-

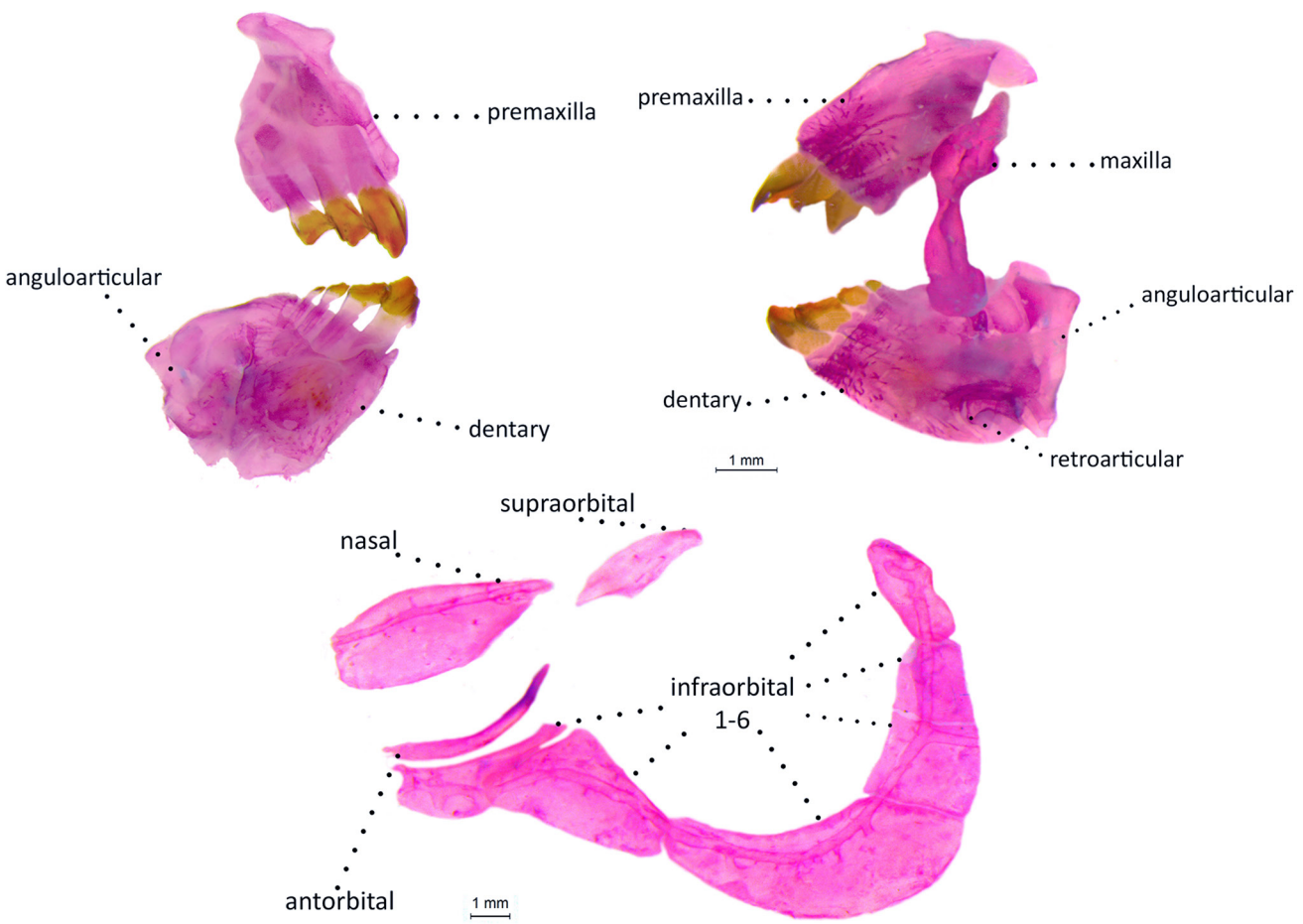

FIGURE 2 | Infraorbital series, medial (left) and lateral (right) views of left jaws *Leporinus oliveirai*, MZUSP 119371, paratype, 103.6 mm SL.

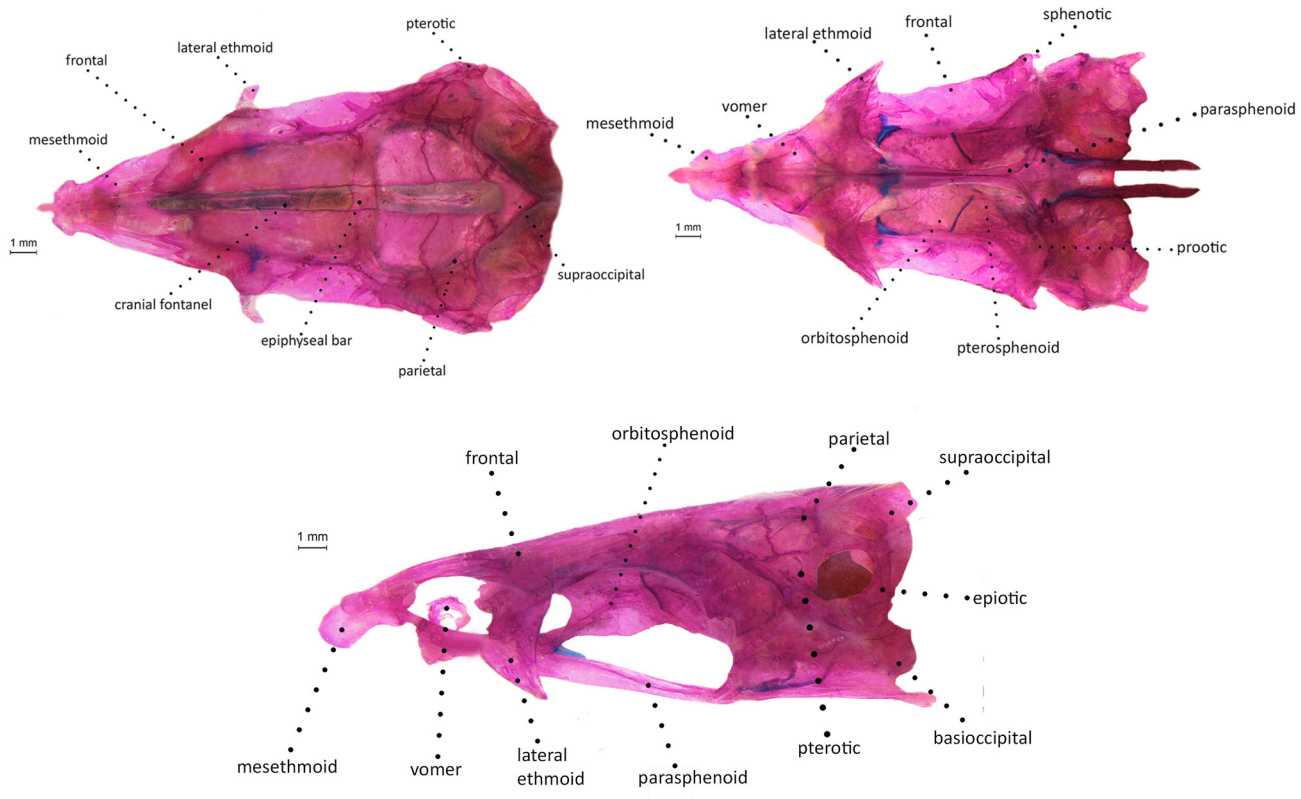

FIGURE 3 | Neurocranium in dorsal, ventral and lateral view, respectively, from top to bottom left to right of *Leporinus oliveirai*, MZUSP 119371, paratype, 103.6 mm SL.

armed bridge on posterior border of neurocranium. Vomer pentagonal in ventral view, with prominent rounded dorsal projection and paired anterior projections articulated to autopalatine. Parasphenoid long and thin, forming ventral margin of neurocranium, with dorsolateral projection forming border of carotid foramen, and paired posteroventral projections extended ventrally to basioccipital and running close to carotid artery. Orbitosphenoid, pterosphenoid, and prootic dorsal to parasphenoid, ventral to frontal, and forming ventral wall of braincase. Exoccipital forming part of the posteroventral face of neurocranium. Basioccipital ventral to exoccipitals and forming ventral process of lagenar capsule. Baudelot´s ligament located on ventromedial surface of basioccipital. Weberian apparatus includes centra and associated elements of four anteriormost vertebrae. Neutral complex laminar and triangular. Claustrum small and rod-like; scaphium small and shell-shaped; intercalarium also small, articulated to tripus via strong ligament. Tripus roughly triangular at base with long hook-shaped posterior process passing ventral to os suspensorium; latter composed of lateral and medial processes.

Hyoid arch composed of dorsal and ventral hypohyals (Fig. 4), anterior and posterior ceratohyals, urohyal, and four branchiostegals. Branchiostegals spatula-shaped, first three articulated to anterior ceratohyal, and last articulated to posterior ceratohyal. Basihyal elongate rod-like and connected to basibranchial 1 via cartilage. Basibranchials 1, 2, and 3 ossified and rod-like. Posterior copula elongate, cartilaginous. Three pairs of ossified, somewhat square basibranchials bordered posteriorly, laterally, and medially by

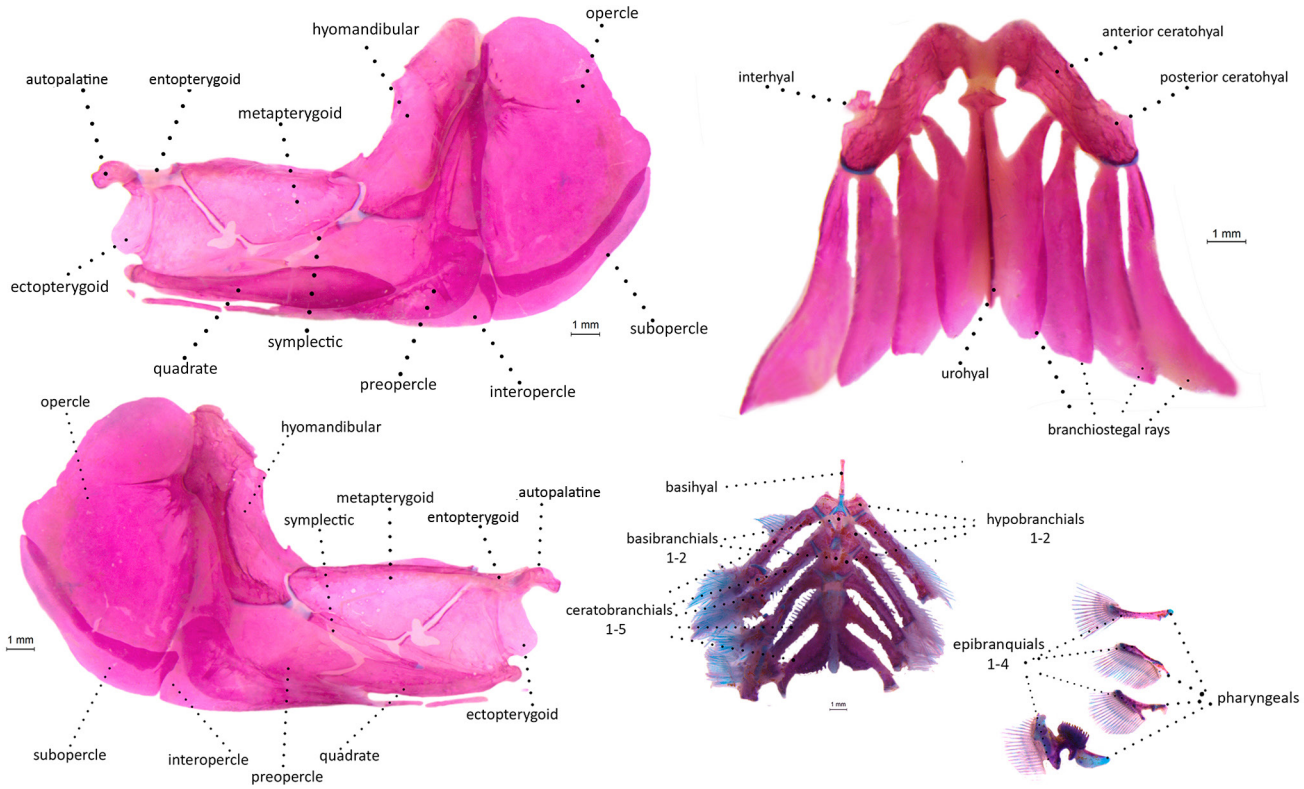

FIGURE 4 | Suspensory and opercular series in medial view (below) and lateral view (above); hyoid arch in ventral view, and branchial arches in dorsal view (except for the dorsal elements on the left side, in ventral view) of *Leporinus oliveirai*, MZUSP 119371, paratype, 103.6 mm SL.

cartilage. First four ceratobranchials elongate, rod-like, with minute rakers along both anterior and posterior margins. Fifth ceratobranchial with rakers restricted to anterior margin, and bony expansion on posterior margin bearing small conical teeth. Four epibranchials, third and fourth, with uncinate process. Four pharingobrachials, fourth associated with uncinate process of third epibranchial. Pharyngeal tooth plate bearing small conical teeth associated with fourth epibranchial.

Suspensorium L-shaped, with longitudinal axis longer than vertical one. Autopalatine elongate with prominent curved anterior tip. Ectopcterygoid vertically elongated, with convex anterior margin. Entopterygoid relatively small, associated with cartilage on dorsum of quadrate. Quadrate relatively large, with dorsal triangular bony projection and lateral bony projection on lateral plane relative to most suspensorium bones. Metapterygoid large, triangular. Metapterygoid-quadrate window relatively small, especially when compared to most anostomids (see, *e.g.*, Sidlauskas *et al.*, 2020: fig. 9; Sidlauskas, Vari, 2008: figs. 40–42). Symplectic on medial face of suspensorium, rod-like. Hyomandibular relatively large, with two dorsal condyles articulated to sphenotic and pterotic. Preopercle large, overlapped by hyomandibular and overlapping interopercular. Opercular large, somewhat triangular, rounded dorsally, and overlapping subopercle. Pectoral girdle connected to neurocranium via extrascapular and posttemporal, and pterotic (Fig. 5). Supracleithrum large, vertically elongated. Cleithrum large with short triangular posterior process. Coracoid with short acute posterior process. Mesocoracoid

columnar, forming strut on posterior face of girdle between scapula and cleithrum. Scapula columnar and located on ventromedial face of girdle. Three postcleithra present, ventralmost one including a long ventral process. Pelvic bone elongated, parallel to its counterpart, with fanned anterior portion and prominent ischiatic process, supporting one unbranched plus eight branched rays. Dorsal fin with 11 pterygiophores, first with enlarged anterior bony expansion and partially cartilaginous stay, supporting two unbranched and ten branched rays. Anal fin with nine pterygiophores united by sutured ventral bony expansions and partially cartilaginous stay, supporting three unbranched and eight or nine-branched rays. Caudal-fin skeleton composed of parahypural and two hypural plates on lower lobe (parahypural and second hypural fused to terminal compound centra), and four hypurals on upper lobe, with hypurals decreasing in size dorsally, third hypural contacting terminal compound centra, last hypurals separate. Uroneural one larger than two and associated with pleurostyle. Three separate epurals dorsal to modified neural process of pleurostyle. Neural and haemal spines adjacent to caudal-fin skeleton with anterior bony projections.

Coloration in alcohol. Overall, ground color tan (Fig. 1). Head and body gently counter-shaded, becoming gradually darker above longitudinal line from mouth, through lower border of orbit to midline of opercle, and body above lateral line. Smaller specimens with eight transversal bars, of which the one below posterior insertion of dorsal fin and

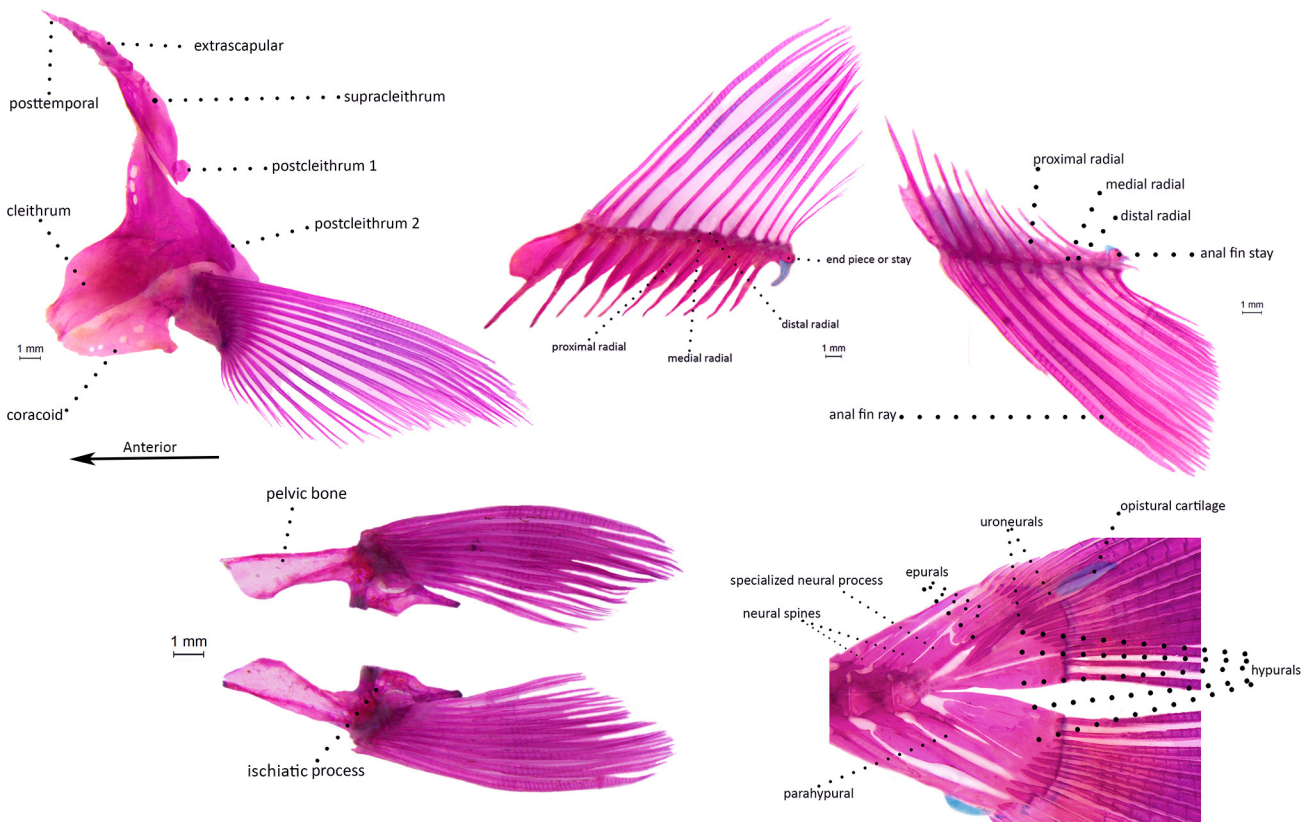

FIGURE 5 | Left pectoral girdle in lateral view, pelvic girdle in dorsal view, and caudal skeleton, dorsal fin, and anal fin in lateral view of *Leporinus oliveirai*, MZUSP 119371, paratype, 103.6 mm SL.

the subsequent one are slightly enlarged (Fig. 6A). In gradually larger specimens, the bars become interrupted midlaterally (bars 3 and 5, sometimes 7), or enlarged midlaterally, forming tall blotches corresponding to the second, fourth, sixth and eighth bars (Fig. 6B). In larger specimens (holotype, 94.4 mm SL), the second midlateral blotch becomes two, one dorsolateral and rounded, the second larger, vertically elongated from midlateral region to area posterior to pectoral-fin base; the third and fifth bars are broken into dorsolateral and ventrolateral blotches, respectively; the fourth bar becomes a large midlateral blotch; the sixth bar is dominated by a midlateral blotch; the seventh bar remains continuous (or nearly so); and the eighth bar is enlarged as a caudal blotch. Ventral surfaces of head and body pale to cream, without chromophores. Adipose fin with dark distal margin. The remaining fins nearly hyaline with few chromophores along margins of rays.

Sexual dimorphism. In one of the two c&s specimens, a mature male, the first and second ribs are hypertrophied and posteriorly concave in a "shovel-like" shape (Fig. 7). Observations during induced breeding failed to verify any occurrence of sound production in breeding males.

Geographical distribution. *Leporinus oliveirai* is only known from the upper rio Braço Norte (also known as rio Cachimbo, see comments in Birindelli *et al*., 2009), at Serra do Cachimbo, in Pará State. Rio Braço Norte is a tributary of rio Teles Pires, a large tributary of upper rio Tapajós (Fig. 8). The absence of *L. oliveirai* from inventories in the lower portion of rio Braço Norte indicates that the new species likely is restricted to the upper portion of the river. The series of waterfalls along the course of the river may be responsible for the geographic isolation of *L. oliveirai* in the upper portion of the river.

FIGURE 6 | *Leporinus oliveirai*, MZUEL 20844. **A.** Larva, 17.4 mm SL, and **B.** Juvenile, 32.7 mm SL.

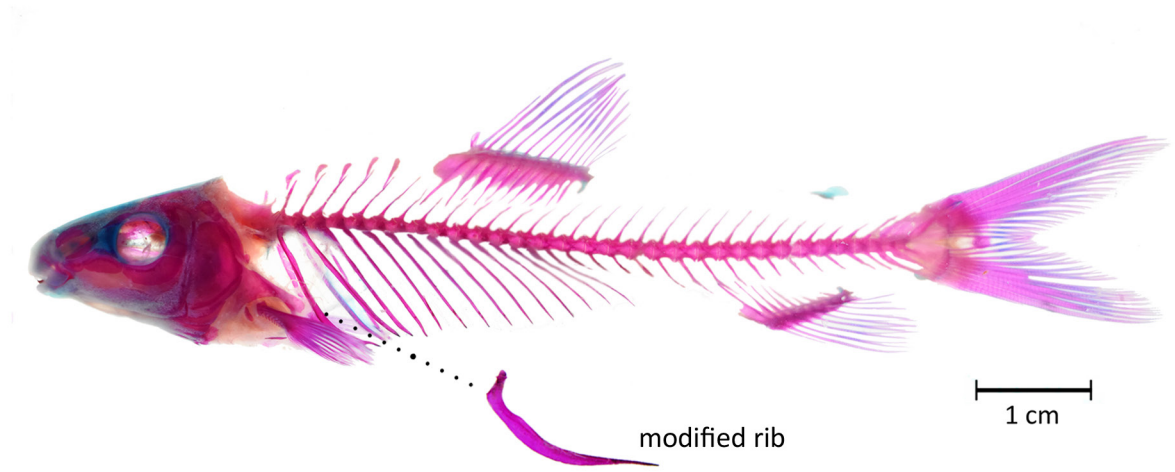

FIGURE 7 | *Leporinus oliveirai* in lateral view of the body skeleton, with the first modified rib highlighted, MZUSP 119371, paratype, 103.6 mm SL.

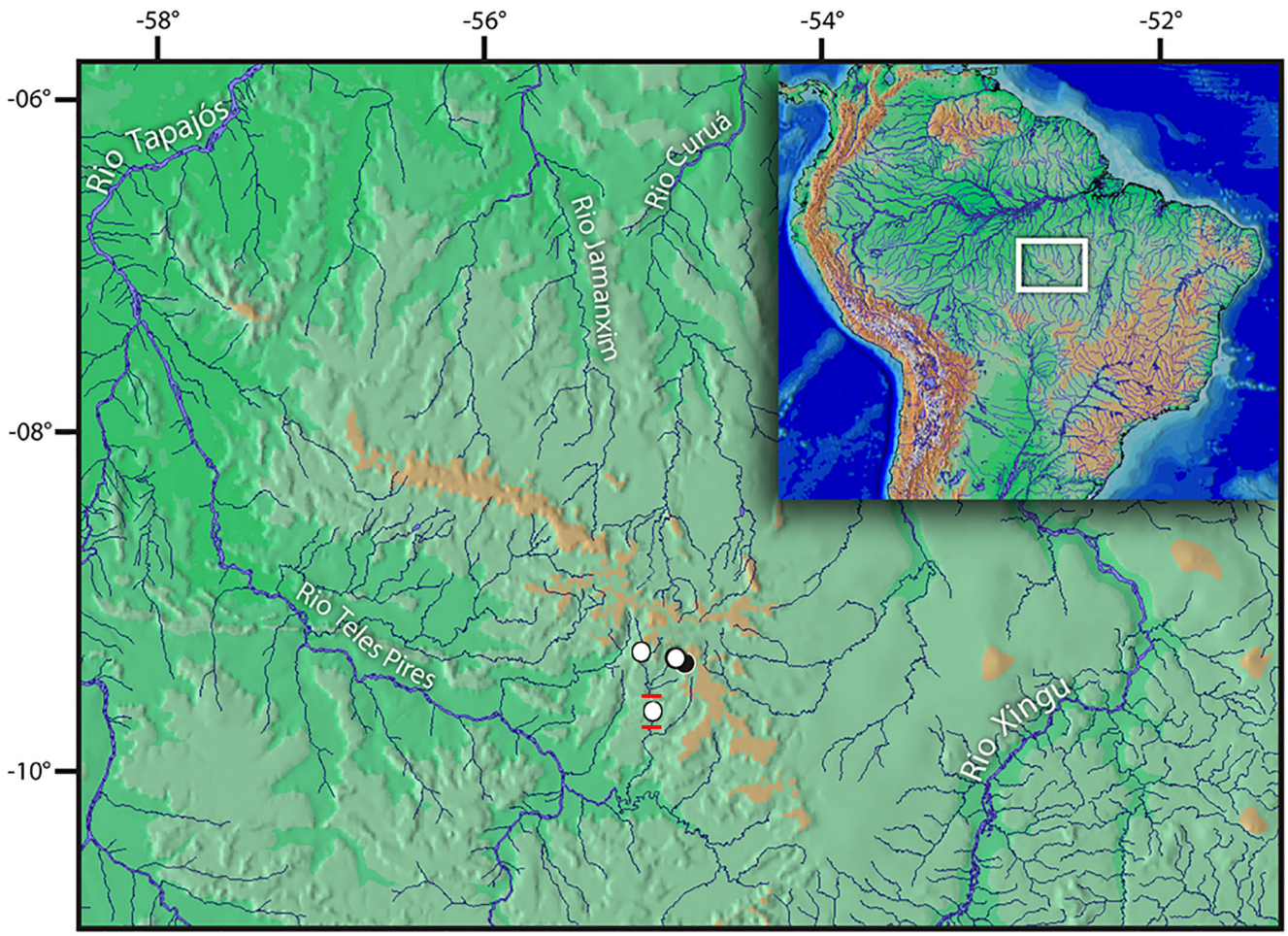

FIGURE 8 | Geographic distribution of *Leporinus oliveirai*. The black dot represents the type-locality, and the red bars indicate the dams.

Ecological notes. Most specimens were caught in fast flowing clear and black water streams in high altitude tributaries (460 m asl) of rio Braço Norte on Serra do Cachimbo (Fig. 9).

Etymology. Named in honor of Ivan Oliveira Nogueira da Silva, for his intensive work on introducing fishes bred and raised in captivity into the International Aquarium trade. Ivan is a fishing engineer who has been working since 2005 on the creation and reproduction of ornamental fish, as part of the Psicultura Tanganyika team. He was primarily responsible for introducing the new species to the International Aquarium trade. A patronym.

Conservation status. Due to anthropogenic alterations along the rio Braço Norte basin in recent years, especially the construction of a series of dams for small hydroelectric power plants (see Discussion), it is probable that the species' abundance and distribution have recently experienced a significant reduction. However, there is no data to support this hypothesis, and the species' population size, distribution, and habitat preferences remain unknown. On the other hand, the species distribution encompasses the Nascentes da Serra do Cachimbo Biological Reserve and the Brazilian Air-Force military base (FAB), which are protected areas. Therefore, according to the International Union for Conservation of Nature (IUCN) categories and criteria (IUCN Standards and Petitions Committee, 2022) *Leporinus oliveirai* can be classified as Least Concern (LC). Given its restricted geographical distribution and recent impacts to rivers within its range, additional collection effort is needed to better understand the species' population size and ecology for future conservation status assessment.

FIGURE 9 | Salto do Cachimbo, at the Brazilian Air Force base, rio Braço Norte, a tributary of rio Teles Pires, upper rio Tapajós basin, Pará State.

Comparative analyses. *Morphometric analysis*. The principal component analysis showed no overlap between specimens confidently identified as either *L. octomaculatus* and *L. oliveirai* (Fig. 10). Specimens exhibiting coloration intermediate between the two species (*i.e.*, putative hybrids) plotted between *L. octomaculatus* and *L. oliveirai* and overlapped with both. The morphometric variables that showed the most differences when comparing the two species were caudal peduncle length, preadipose distance, eye diameter, caudal peduncle depth, interorbital bone distance, and body depth at the origin of the dorsal fin.

Genetic distance. The genetic distance (Tab. 3) between *Leporinus oliveirai* and the closest described congener *L. octomaculatus* was 3.9% for the DNA Barcode (COI gene). The distance is greater than the limit used for delimitation of many species, which is 2% (Pereira *et al*., 2013). *Leporinus oliveirai* also has a relatively high distance from its other congeners (*L. cylindriformis* Borodin, 1929, *L. multimaculatus* Birindelli, Teixeira & Britski, 2016, *L. reticulatus*, *L. tristriatus* Birindelli & Britski, 2013, *L. bistriatus*, *L. unitaenitatus* Garavello & Santos, 2009, *L. vanzoi* Britski & Garavello, 2005, and *L. sidlauskasi* Britski & Birindelli, 2019), with all values being higher than 7%. These values are relatively high for congeners, compared to species in other genera (Ramirez, Galetti, 2015; Burns *et al*., 2017; Ramirez *et al*., 2020). On the other hand, intraspecific distances were low in all species samples, ranging from 0 to 0.60%.

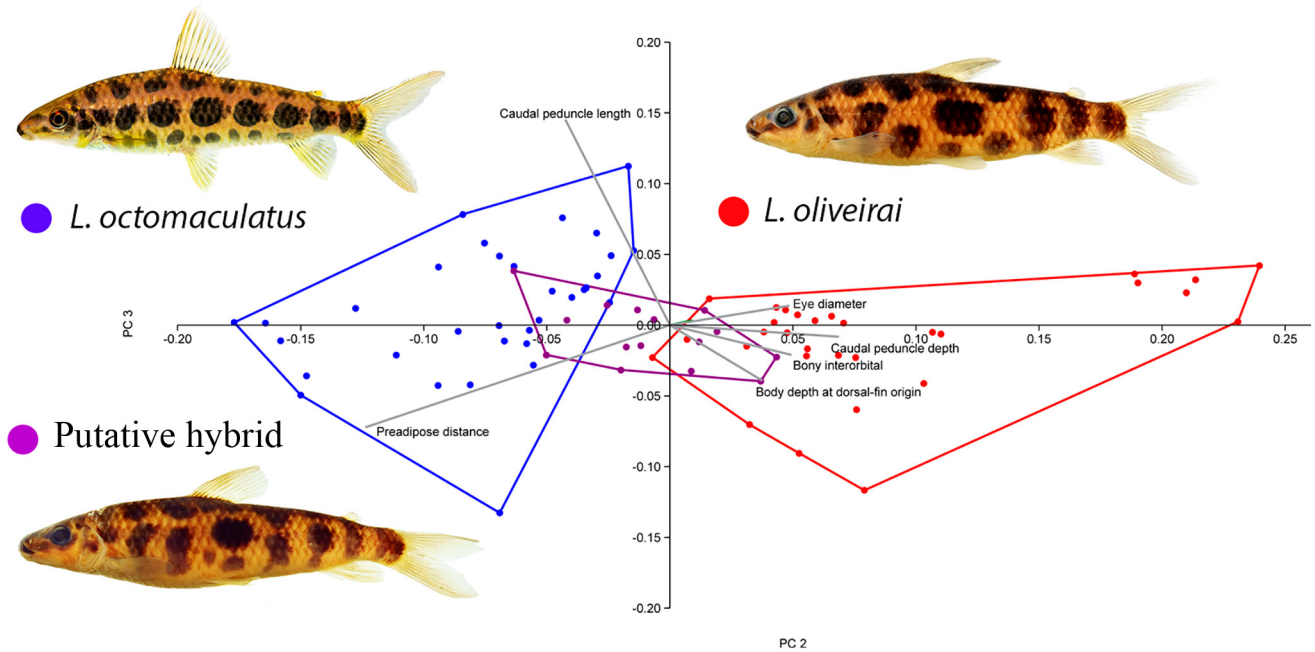

FIGURE 10 | Projection of individual scores of the second and third principal components of the samples of *Leporinus octomaculatus*, *L. oliveirai* and the putative hybrid specimens. In dark blue, *L. octomaculatus*; in red, *L. oliveirai*; in purple, individuals collected that show an intermediate pigmentation between *L. octomaculatus* and *L. oliveirai*.

Species delimitation analyses. Methods for species delimitation based on COI gene sequences generated different results (Fig. 11). The PTP analysis recovered 10 MOTUs (Molecular Operational Taxonomic Units) and ASAP found ten partitions, with the partition with the lowest asap-score (2.0) recovering 9 MOTUs. In both analyses, *Leporinus oliveirai* and *L. octomaculatus* were delimited as different species. A difference between the analyses was that, according to ASAP, *L. vanzoi and L. sidlauskasi* were considered in the same MOTU.

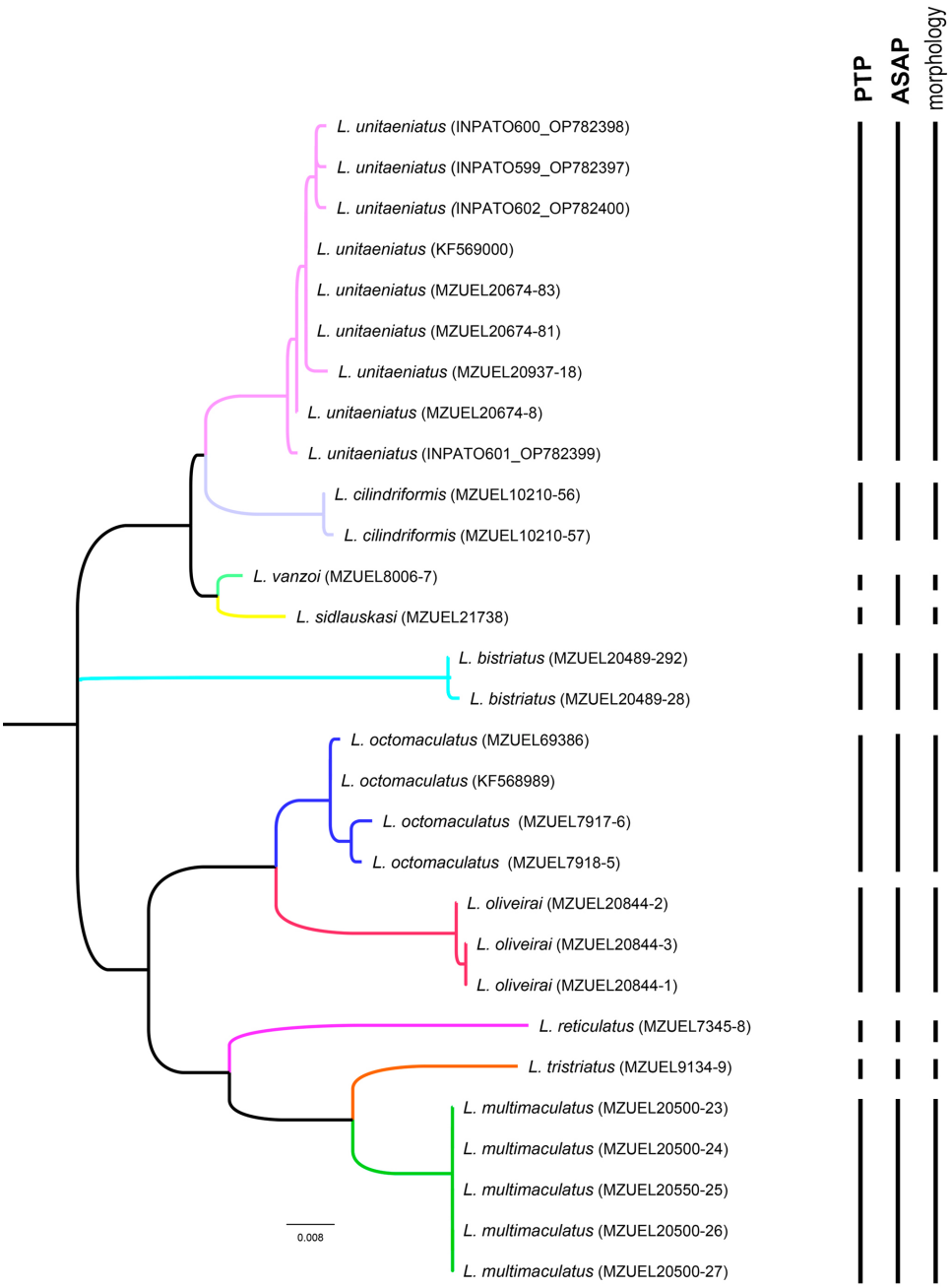

FIGURE 11 | Cladogram of phylogenetic relationships among *Leporinus oliveirai* and congeners based on DNA Barcode sequence and a Maximum-likelihood analysis.

TABLE 3 | Genetic distance between *Leporinus oliveirai* and congeners, based on DNA Barcode and Kimura-2-parameters. The numbers in bold on the diagonal represent the intra-sample distance, the numbers below the diagonal line represent the distances between samples, and the numbers above the diagonal line represent the standard deviation. Values expressed in percentage.

	1	2	3	4	5	6	7	8	9	10
1. *L. oliveirai*	**0.1**	0.83	1.39	2.22	1.8	1.66	1.51	1.54	1.52	1.57
2. *L. octomaculatus*	3.9	**0.6**	1.44	2.23	1.68	1.61	1.38	1.48	1.36	1.39
3. *L. multimaculatus*	7.5	7.5	**0**	2.1	1.6	1.03	1.58	1.71	1.65	1.91
4. *L. bistriatus*	11.8	11.6	11	**0.2**	2.22	2.36	1.73	1.81	1.88	1.92
5. *L. reticulatus*	9.6	9.2	8.6	11.7	**n/c**	1.66	1.71	1.88	1.89	1.92
6. *L. tristriatus*	9.3	8.8	4.4	12.2	9.4	**n/c**	1.66	1.96	1.79	1.99
7. *L. vanzoi*	7.9	7.1	8.4	9	9.4	9	**n/c**	0.56	0.85	0.77
8. *L. sidlauskasi*	8	7.3	8.7	9.2	10	10.5	1.5	**n/c**	0.99	0.85
9. *L. cylindriformis*	8.3	7.5	8.7	9.9	10.4	10	3.3	4	**0.2**	0.91
10. *L. unitaeniatus*	9.2	7.8	10.3	10.1	10.8	11.2	3	3.3	3.9	**0.4**

DISCUSSION

Leporinus oliveirai has a coloration composed of round blotches distributed throughout the body. This characteristic is shared by some congeners, such as *L. granti* Eigenmann, 1912, *L. gomesi* Garavello & Santos, 1981, *L. lebaili* Géry & Planquette, 1983, *L. marcgravii*, *L. microphthalmus*, *L. nijsseni* Garavello, 1990, *L. ortomaculatus* Garavello, 2000, *L. santosi* Britski & Birindelli, 2013, *L. torrenticola* Birindelli, Teixeira & Britski, 2016 and *L. octomaculatus*, as well as other anostomids, as *Hypomasticus megalepis* and *H. julii* (Santos, Jégu & Lima, 1996). However, the pattern of blotches in *L. oliveirai* is unique among all anostomids, both in terms of the quantity and irregularity of their distribution and their size. This characteristic is a useful tool for easily differentiating *L. oliveirai* from other anostomids. *Leporinus oliveirai* has three teeth in the premaxilla and four in the dentary, a characteristic shared with *Hypomasticus megalepis*, *Leporinus amae*, *L. bahiensis*, *L. bistriatus*, *L. marcgravii*, *L. melanopleura*, *L. microphthalmus*, *L. moralesi,* *L. octofasciatus*, *L. octomaculatus*, *L. paranensis*, *L. reticulatus*, *L. sexstriatus*, *L. striatus*, *L. taeniatus*, *L. taeniofasciatus*, *L. tigrinus* and *Megaleporinus garmani*. Dental formula is a useful characteristic for the diagnosis of anostomids. Most anostomids have four teeth in both the premaxilla and dentary, but this characteristic is variable in some species, with a reduction in the number of teeth in the premaxilla, dentary, or both, allowing for classification based on this feature.

The molecular analyses revealed a significant distance between *L. oliveirai* and *L. octomaculatus* (3.9%), indicating that the two species, despite being distinct, are likely closely related. These species present a close distribution in the Tapajós and a set of common meristic characteristics, but are distinguishable based on coloration and morphometrics.

The ribs of mature males of some *Megaleporinus* species are hypertrophied a condition possibly related to sexual courtship behavior during the reproductive period, according to Ramirez *et al*. (2017). This is the second report of hypertrophied ribs in Anostomidae and the first for *Leporinus*, suggesting that this feature might be much more widespread in the family than currently known.

Putative hybrids. The rio Braço Norte has the potential for energy generation due to its many waterfalls. It is currently being exploited by four small hydroelectric power plants, some of which might have already impacted the species' population. Satellite photographs taken in recent years (Fig. 12) show the impact of these dams on the river, with the appearance of large inundated areas and the disappearance of several waterfalls. In addition, some lots collected by Keve de Silimon in the lower stretches of the rio Braço Norte (MZUSP 108018) revealed specimens displaying intermediate coloration between *Leporinus oliveirai* and *L. octomaculatus* (Fig. 13). Herein, we interpret these specimens as putative hybrids resulting from the inundation of waterfalls that previously separated the two species and kept them from interbreeding. The principal component analyses reinforced this hypothesis with the intermediate individuals plotted between and overlapping with *L. octomaculatus* and *L. oliveirai*, however, all evidence supporting this possibility is morphological. Unfortunately, tissue sample of the intermediate specimens are not currently available for additional investigation using molecular markers.

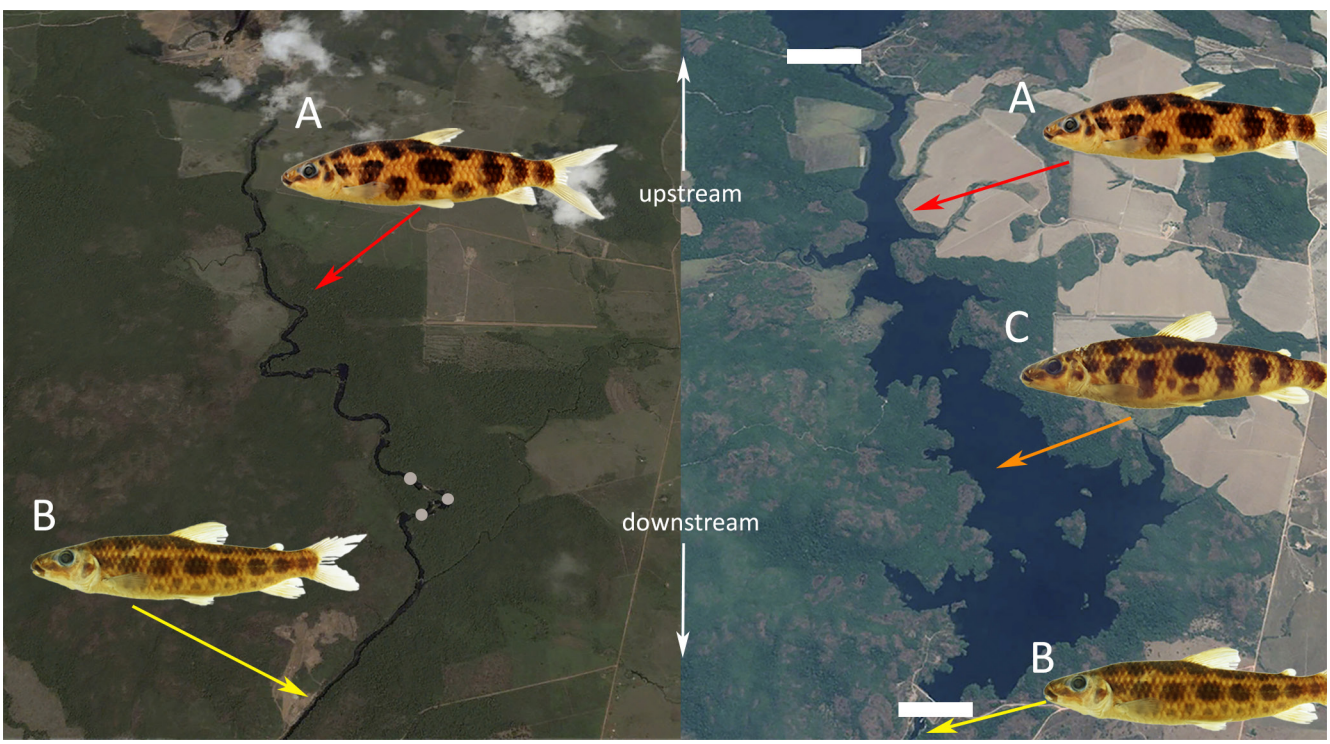

FIGURE 12 | Rio Braço Norte: on the left, a satellite photograph, taken in 2002, illustrates the geographical distribution limit between **A.** *Leporinus oliveirai* and **B.** *L. octomaculatus* separated by waterfalls. On the right, a photograph was taken in 2019 representing the location where an individual with intermediate coloration between the two species (**C**) was collected. The circles indicate waterfalls and the white bars indicate the dams. Images taken from Google Earth.

FIGURE 13 | Specimen (MZUSP 108018, 109.43 mm SL) with intermediate coloration between *Leporinus oliveirai* and *L. octomaculatus*, herein identified as a putative hybrid.

Comparative material examined. All from Brazil, rio Tapajós basin. *Leporinus octomaculatus*. MZUEL 7917, 5, 67.2–88.8 mm SL. MZUEL 7918, 5, 93.7–105.1 mm SL. MZUEL 7919,12, 52.3–78.5 mm SL. Putative hybrid between *L. octomaculatus* and *L. oliveirai*. MZUSP 108018, 15, 80.4–105.1 mm SL.

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AUTHORS' CONTRIBUTION

Ian Solon Bortoloci Ito: Conceptualization, Data curation, Formal analysis, Validation, Visualization, Writing-original draft, Writing-review and editing.

Lenice Souza-Shibatta: Data curation, Investigation, Methodology, Writing-review and editing.

Marcos Venturieri: Data curation, Methodology, Writing-review and editing.

José L. O. Birindelli: Conceptualization, Data curation, Funding acquisition, Methodology, Project administration, Resources, Software, Validation, Visualization, Writing-original draft, Writing-review and editing.

ETHICAL STATEMENT

Not applicable.

COMPETING INTERESTS

The author declares no competing interests.

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