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ARTICLE

Bisecting the type series of *Leporinus paranensis* Garavello & Britski, 1987 (Characiformes, Anostomidae)

Heraldo A. Britski[1]; Júlio C. Garavello[2]; Claudio Oliveira[3] & José L.O. Birindelli[4]

[1] Universidade de São Paulo (USP), Museu de Zoologia (MZUSP). São Paulo, SP, Brasil. ORCID: 0000-0002-5593-9651. E-mail: heraldo@usp.br
[2] Universidade Federal de São Carlos (UFSCAR), Centro de Ciências Biológicas e da Saúde (CCBS), Departamento de Ecologia e Biologia Evolutiva (DEBE). São Carlos, SP, Brasil. ORCID: 0000-0003-2985-6665. E-mail: jgaravello@ufscar.br
[3] Universidade Estadual Paulista "Júlio de Mesquita Filho" (UNESP), Instituto de Biociências, Departamento de Biologia Estrutural e Funcional. Botucatu, SP, Brasil. ORCID: 0000-0002-7010-8880. E-mail: claudio.oliveira@unesp.br
[4] Universidade Estadual de Londrina (UEL), Centro de Ciências Biológicas (CCB), Departamento de Biologia Animal e Vegetal (BAV). Londrina, PR, Brasil. ORCID: 0000-0001-9646-9636. E-mail: josebirindelli@uel.br

Abstract. The type series of *Leporinus paranensis* includes two distinct species, one of which is herein described as new. *Leporinus paranensis* is redescribed based on its holotype, two paratypes, and additional specimens recently sampled in tributaries of the Grande River, in the north portion of the upper Paraná basin in Brazil. A new species of *Leporinus* is described based on specimens collected in all major tributaries of the upper Paraná basin in Brazil, and tributaries of the Paraná River in Paraguay. Both species share the presence of three unicuspid teeth on the premaxillary and four on the dentary, a terminal mouth and three dark midlateral blotches on the body. The new species is distinguished from *L. paranensis* based on the number of scale series around the caudal peduncle (12 vs. 16). Despite the similar body shape, species delimitation analyses using *DNA barcodes,* applied to compare samples of the new species to congeners, corroborated the uniqueness of the new species. In addition, molecular data revealed that *L. bahiensis, L. octofasciatus,* and *L. taeniatus* are possibly closely related to the *L. paranensis* species group. Conservation statuses of *L. paranensis* and the new species are recommended based on the IUCN criteria.

Keywords. Taxonomy; Neotropics; COI; Systematics.

INTRODUCTION

Leporinus Agassiz, 1829 is one of the most diverse genera of Characiformes encompassing approximately 76 species that range throughout South America from Colombia to Argentina (Toledo-Piza *et al.,* 2024). Nevertheless, only a handful of species of *Leporinus* occur in the upper Paraná basin. Kner (1859) described *Leporinus striatus* from Orissanga, a locality in the Mogi-Guaçu River drainage within the upper Paraná. Amaral Campos (1945a) registered the occurrence of five species of *Leporinus* in the same river (Rio Mogi-Guaçu), and in the same year, Amaral Campos (1945b) diagnosed eleven species of *Leporinus* based on specimens from the La Plata basin deposited at the MZUSP, two of which were described as new: *Leporinus aguapeiensis* (a junior synonym of *Megaleporinus obtusidens,* Britski *et al.,* 2012) from the Aguapeí River (Tietê drainage) and *L. lacustris* from the Mogi-Guaçu River (Grande drainage). For comments on the identifications provided by Amaral Campos see Britski *et al.* (2012). In 1978, based on samples from the upper Paraná, Britski & Garavello redescribed *Leporinus octofasciatus,* which was originally described based on specimens from a coastal river in Santa Catarina state. A decade later, Garavello & Britski (1987) described *L. paranensis* based on samples from the upper Paraná basin, including the Tietê and Grande rivers. The main diagnostic features of their new species were the reduced number of premaxillary teeth (three) and the color pattern composed of three dark midlateral blotches. In the same year, and possibly unaware of the recently described *L. paranensis,* Géry *et al.* (1987) revised the species of *Leporinus* from the Paraguay basin, identifying some specimens as *"Leporinus* aff. *bahiensis."* *Leporinus bahiensis* was described by Steindachner (1875) and is apparently endemic to isolated coastal rivers in eastern Brazil (Camelier & Zanata, 2015; Toledo-Piza *et al.,* 2024). The color pattern composed of three dark midlateral blotches and the three unicuspid teeth on each

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side of the premaxillae of the Paraguayan specimens described by Géry *et al.* (1987) are two main diagnostic features shared by *L. bahiensis* and *L. paranensis*. In addition, Géry's Paraguayan specimens share the presence of 12 scale rows around the caudal peduncle with paratypes of *L. paranensis,* which led us to wonder if the specimens examined by Géry *et al.* (1987) from the Paraguay were conspecific with the ones described from the Paraná in the same year by two of us (HAB, JCG) as *L. paranensis*.

A few years later, one of us (HAB) visited the fish collection at Geneva, examined the specimens previously reported by Géry *et al.* (1987) and borrowed some for direct comparison with the type specimens of *L. paranensis*. The ensuing comparative study revealed that the type series of *L. paranensis* included specimens of two different species. The holotype (MZUSP 14453) and two paratypes (MZUSP 14454) from the Grande River represent the true *L. paranensis,* whereas the other paratypes, sampled in several tributaries of the Paraná River in Brazil, are conspecific with the Paraguayan specimens identified by Géry *et al.* (1987) as *Leporinus* aff. *bahiensis* (MHNG 2004.97, MHNG 2037.19-23, MHNG 2067.94, MHNG 2105.63-64, MHNG 2105.65-66, MHNG 2159.20, MHNG 2204.24, MHNG 2386.53, MHNG 2386.54, MHNG 2386.54, MHNG 2386.92, MHNG 2396.62). These represent an undescribed species.

The present contribution describes the new species, diagnoses it from congeners, and redescribes *L. paranensis,* re-examining its diagnostic features and geographical distribution. In addition, we recommend a conservation status for both species based on the IUCN criteria.

MATERIAL AND METHODS

Measurements and counts followed Britski & Garavello (1978) and Garavello (1979). Counts of unbranched fin rays were expressed in Roman symbols, and branched rays by Arabic symbols. The lateral-line scale count included the pored scales extending onto the base of the median caudal-fin rays; counts of the longitudinal scale rows above the lateral line exclude the lateral-line scale row and the middorsal scale row; counts of the longitudinal scale rows below the lateral line exclude the lateral-line scale row and include a half scale row when the pelvic-fin origin is immediately behind the middle of a scale. The pattern of radii was defined on scales immediately dorsal to the lateral line row at the vertical through the dorsal-fin origin. All examined specimens are alcohol preserved. Codes for scientific fish collections followed Sabaj (2020, 2022).

Morphometric and molecular comparisons were made between the two studied species. The body shape of the species was compared by examining the distribution individuals in a morphospace resulting from Principal Component Analysis (PCA). The analysis included the eight variables used in Garavello (1979) and Garavello & Britski (1988). Raw data were transferred to PAST v.4 (Hammer *et al.,* 2001), log transformed and analyzed as a variance-covariance matrix. *Leporinus lacustris* was used for comparisons in the analysis, as it is a closely related sympatric species that exhibits a distinct overall body shape.

The genetic data used herein included an approximately 570 bp fragment of the cytochrome c oxidase subunit I (COI) barcode region. All DNA barcoding sequences (COI) were obtained from GenBank (https://www.ncbi.nlm.nih.gov) or BOLD (https://www.boldsystems.org). The COI sequences matrix included 11 samples of *L. inexpectatus,* 1 of *L. paranensis,* 19 of *L. octofasciatus,* 2 of *L. bahiensis,* 20 of *L. taeniatus,* 11 of *L. lacustris* and 5 of *L. friderici*. The unique genetic sample of *L. paranensis* came from a larva collected in the Mogi Guaçu river. Due to the early developmental stage of this specimen, it was impossible to confirm its identification prior to the molecular analysis that consumed the entire voucher (Diogo Freitas Souza, personal communication). However, the identification of the latter sample is unequivocal based on its collection origin and the results obtained in the DNA analysis (see Results). The Mogi Guaçu river, where the larva came from, is also where most of the examined specimens of *L. paranensis* were collected (see Results). In fact, the fish fauna of the Mogi Guaçu is one of the most studied in South America (Godoy, 1954, 1975; Meschiatti & Arcifa, 2009). There are only five species of *Leporinus* occurring in that basin: *L. friderici, L. inexpectatus, L. lacustris, L. octofasciatus, L. paranensis,* and *L. striatus*. A complete list of specimens, GenBank and BOLD accession numbers used in the genetic analyses is available in Table 1. All sequences were aligned using Muscle v3.8.4 (Edgar, 2004) in MEGA XI (Kumar *et al.,* 2018; Stecher *et al.,* 2020) with default parameters. The best model for nucleotide evolution (in our case K2+G) was estimated in MEGA XI. The molecular matrix was used to estimate the genetic distance over sequences within samples/species, and between species pairs, with standard error calculated via 1,000 bootstrap pseudoreplicates. The matrix was also used in a species delimitation analysis through the method ASAP, available online at https://bioinfo.mnhn.fr/abi/public/asap/asapweb.html choosing Kimura K80 option as the substitution model to compute distances. A phylogenetic tree was generated using Maximum Likelihood in MEGA XI under the K2+G model. The tree was edited in FigTree v.1.4.4 (Rambaut, 2010) and used in a species delimitation analysis through the method PTP (Zhang *et al.,* 2013), available online at https://species.h-its.org/ptp.

RESULTS

Systematic Account

Leporinus paranensis Garavello & Britski, 1987 (Fig. 1)

Leporinus paranensis Garavello & Britski, 1987: 156, fig. 1B [Rio Grande at Marimbondo, 20°10'S 49°10'W] [in part, only MZUSP 14453, and MZUSP 14454]. – Oyakawa, 1996: 476-477 [type catalog, in part, only

Table 1. Sampling information for DNA Barcode molecular analyses, including voucher number, locality, accession number in GenBank or BoldSystem, and first publication using each COI sequence.

SPECIES	VOUCHER NUMBER	LOCALITY	ACCESSION NUMBER	SOURCE
Leporinus bahiensis	LBPV96851	Gongogi river	MT427929	Birindelli *et al.* (2020)
Leporinus bahiensis	LBPV96852	Gongogi river	MT427930	Birindelli *et al.* (2020)
Leporinus friderici	LBPV44953	Paraná river at Itaipu	FUPR1342-10	Pereira *et al.* (2013)
Leporinus friderici	LBPV44954	Paraná river at Itaipu	FUPR1343-10	Pereira *et al.* (2013)
Leporinus friderici	LBPV44955	Pardo river	FUPR1344-10	Pereira *et al.* (2013)
Leporinus friderici	LBPV9056	Paraná river at Itaipu	FUPR034-09	Pereira *et al.* (2013)
Leporinus friderici	LBPV9213	Paraná river at Itaipu	FUPR032-09	Pereira *et al.* (2013)
Leporinus friderici	LBPV9215	Paraná river at Itaipu	FUPR033-09	Pereira *et al.* (2013)
Leporinus inexpectatus	LBPV21936	Paranapanema river	EU185588	Avelino *et al.* (2015)
Leporinus inexpectatus	LBPV21937	Paranapanema river	EU185589	Avelino *et al.* (2015)
Leporinus inexpectatus	LBPV21938	Paraná river at Porto Rico	JN989015	Pereira *et al.* (2013)
Leporinus inexpectatus	LBPV21939	Paraná river at Marilena	JN989016	Pereira *et al.* (2013)
Leporinus inexpectatus	LBPV22443	Paraná river at Marilena	JN989017	Pereira *et al.* (2013)
Leporinus inexpectatus	Egg/Larva	Paranapanema river	PRP287-16	Lima *et al.* (2020)
Leporinus inexpectatus	Egg/Larva	Paranapanema river	PRP288-16	Lima *et al.* (2020)
Leporinus inexpectatus	Egg/Larva	Paranapanema river	PRP289-16	Lima *et al.* (2020)
Leporinus inexpectatus	Egg/Larva	Paranapanema river	PRP290-16	Lima *et al.* (2020)
Leporinus lacustris	LBPV15941	Tietê river	EU185566	Avelino *et al.* (2015)
Leporinus lacustris	LBPV17346	Pardo river	JN988992	Pereira *et al.* (2013)
Leporinus lacustris	LBPV17347	Mogi-Guaçu river	JN988993	Pereira *et al.* (2013)
Leporinus lacustris	LBPV20138	Mogi-Guaçu river	JN988994	Pereira *et al.* (2013)
Leporinus lacustris	LBPV20139	Mogi-Guaçu river	JN988995	Pereira *et al.* (2013)
Leporinus lacustris	LBPV20140	Mogi-Guaçu river	JN988996	Pereira *et al.* (2013)
Leporinus lacustris	LBPV20141	Paraná river at Itaipu	JN988997	Pereira *et al.* (2013)
Leporinus lacustris	LBPV21857	Paraná river at Itaipu	JN988998	Pereira *et al.* (2013)
Leporinus lacustris	LBPV8086	Paraguay river	EU185562	Avelino *et al.* (2015)
Leporinus lacustris	MZUSP113991	Paraguay river	KF568985	Ramirez *et al.* (2016)
Leporinus lacustris	MZUSP113994	Tietê river	KF568986	Ramirez *et al.* (2016)
Leporinus octofasciatus	LBPV19827	Paranapanema river	EU185586	Avelino *et al.* (2015)
Leporinus octofasciatus	LBPV19828	Paranapanema river	EU185587	Avelino *et al.* (2015)
Leporinus octofasciatus	LBPV22674	Paranapanema river	JN989009	Pereira *et al.* (2013)
Leporinus octofasciatus	LBPV44901	Paranaíba river	JN989012	
Leporinus octofasciatus	LBPV44902	Paranaíba river	JN989011	Avelino *et al.* (2015)
Leporinus octofasciatus	LBPV44903	Paranaíba river	JN989010	Avelino *et al.* (2015)
Leporinus octofasciatus	LBPV9231	Paranaíba river	JN989006	Pereira *et al.* (2013)
Leporinus octofasciatus	LBPV9239	Paranaíba river	JN989007	Pereira *et al.* (2013)
Leporinus octofasciatus	LBPV9244	Paranaíba river	JN989008	Pereira *et al.* (2013)
Leporinus octofasciatus	Egg/Larva	Paranapanema river	KM897638	Frantine-Silva *et al.* (2015)
Leporinus octofasciatus	Egg/Larva	Paranapanema river	KM897585	Frantine-Silva *et al.* (2015)
Leporinus octofasciatus	Egg/Larva	Paranapanema river	KM897578	Frantine-Silva *et al.* (2015)
Leporinus octofasciatus	Egg/Larva	Paranapanema river	KM897464	Frantine-Silva *et al.* (2015)
Leporinus octofasciatus	Egg/Larva	Paranapanema river	KM897450	Frantine-Silva *et al.* (2015)
Leporinus octofasciatus	Egg/Larva	Paranapanema river	KM897330	Frantine-Silva *et al.* (2015)
Leporinus octofasciatus	Egg/Larva	Paranapanema river	KM897311	Frantine-Silva *et al.* (2015)
Leporinus octofasciatus	Egg/Larva	Paranapanema river	KM897273	Frantine-Silva *et al.* (2015)
Leporinus octofasciatus	Egg/Larva	Paranapanema river	KM897207	Frantine-Silva *et al.* (2015)
Leporinus octofasciatus	Egg/Larva	Paranapanema river	KM897187	Frantine-Silva *et al.* (2015)
Leporinus paranensis	Egg/Larva	Mogi Guaçu river	PP335714	Souza *et al.* (in preparation)
Leporinus taeniatus	LBPV4174	São Francisco river	EU185597	Avelino *et al.* (2015)
Leporinus taeniatus	MCP44097	São Francisco river	BSB458-10	Carvalho *et al.* (2011)
Leporinus taeniatus	MCP44097	São Francisco river	KF568996	Ramirez *et al.* (2016)
Leporinus taeniatus	MCP44772	São Francisco river	BSB327-10	Carvalho *et al.* (2011)
Leporinus taeniatus	MCP45201	São Francisco river	BSB324-10	Carvalho *et al.* (2011)
Leporinus taeniatus	MCP45201	São Francisco river	BSB325-10	Carvalho *et al.* (2011)
Leporinus taeniatus	TIUFRN1179	Jaguaribe river	KY348889	Berbel-Filho *et al.* (2018)
Leporinus taeniatus	TIUFRN1815	Jaguaribe river	KY348888	Berbel-Filho *et al.* (2018)
Leporinus taeniatus	TIUFRN1853	Jaguaribe river	KY348892	Berbel-Filho *et al.* (2018)
Leporinus taeniatus	TIUFRN1869	Jaguaribe river	KY348891	Berbel-Filho *et al.* (2018)
Leporinus taeniatus	TIUFRN2005	Jaguaribe river	KY348890	Berbel-Filho *et al.* (2018)
Leporinus taeniatus	TIUFRN2024	Apodi-Mossoró river	KY348885	Berbel-Filho *et al.* (2018)
Leporinus taeniatus	TIUFRN2025	Apodi-Mossoró river	KY348886	Berbel-Filho *et al.* (2018)
Leporinus taeniatus	TIUFRN2026	Apodi-Mossoró river	KY348883	Berbel-Filho *et al.* (2018)
Leporinus taeniatus	TIUFRN2027	Apodi-Mossoró river	KY348887	Berbel-Filho *et al.* (2018)
Leporinus taeniatus	TIUFRN2028	Apodi-Mossoró river	KY348879	Berbel-Filho *et al.* (2018)
Leporinus taeniatus	TIUFRN2029	Apodi-Mossoró river	KY348880	Berbel-Filho *et al.* (2018)
Leporinus taeniatus	TIUFRN2030	Apodi-Mossoró river	KY348881	Berbel-Filho *et al.* (2018)
Leporinus taeniatus	TIUFRN2031	Apodi-Mossoró river	KY348882	Berbel-Filho *et al.* (2018)
Leporinus taeniatus	TIUFRN2033	Apodi-Mossoró river	KY348884	Berbel-Filho *et al.* (2018)

Figure 1. *Leporinus paranensis,* holotype, MZUSP 14453, 170.9 mm SL, rio Grande at Marimbondo (above); MZUEL 22894, 125.1 mm SL, Ribeirão do Pântano, tributary of rio Mogi-Guaçu (below, a better color-preserved specimen).

MZUSP 14453, and MZUSP 14454]. – Pérez-Jr. & Garavello, 2007: 331 [Rio do Pântano, tributary of Rio Mogi-Guaçu, LISDEBE uncat., MZUEL 22894]. – Apone *et al.,* 2008: 102, fig. 7-36 [Rio Quilombo, Rio do Pântano, tributary of Rio Mogi-Guaçu, LISDEBE 1417]. – Oliveira *et al.,* 2009: 492 [tributaries of the Mogi Guaçu river, LISDEBE 1417].

Type specimens: MZUSP 14453, holotype, 1 alc, 170.9 mm SL, Marimbondo, Rio Grande, SP, 20 Nov 1975. MZUSP 14454, paratypes, 2 alc, 154.6-162.6 mm SL, collected with holotype.

Remarks: The type locality was likely flooded by the hydroelectric dam of U.H.E. Marimbondo, and it herein interpreted as São Paulo state, Guaraci municipality, Rio Grande at Marimbondo, c.20°15′S 49°05′W.

Non-type specimens: Brazil, São Paulo state, Rio Grande basin. LIRP 3828, 1 alc, 45.0 mm SL, Luís Antônio, Rio Mogi-Guaçu, near Estação Ecológica de Jataí, 21°36′44″S 47°49′09″W, 01 Oct 2002. LIRP 4919, 1 alc, 49.0 mm SL, Luís Antônio, Rio Mogi-Guaçu, near Estação Ecológica de Jataí, 21°36′44″S 47°49′09″W, 01 Oct 2002. LISDEBE 1417, 1 alc, 124.72 mm SL, São Carlos, Rio Quilombo, tributary of the Rio Mogi-Guaçu, 21°46′23″S 47°46′44″W, F. Apone, A.K. Olivera & J.L.O. Birindelli, 03 Jun 2004. LISDEBE uncat., 1 alc, 148.14 mm SL, São Carlos, Ribeirão do Pântano, tributary of the Rio Mogi-Guaçu, 21°51′46.5″S 47°40′25.5″W, O.R. Pérez-Jr. & L.H. Silva, 30 Mar 2001. MZUEL 22894, 1 alc, 125.13 mm SL, São Carlos, Ribeirão do Pântano, a tributary of Rio Mogi-Guaçu, 21°51′46.5″S 47°40′25.5″W, O.R. Pérez-Jr. & L.H. Silva, 01 Jun 2001. MZUSP 62409, 1, 64.2 mm SL, Pirassununga, Mogi-Guaçu river at Cachoeira de Emas, 21°55′S 47°23′W, 14 Oct 1950, W. Bockermann.

Remarks: Benedito-Cecilio *et al.* (2004: 375) identified specimens collected in tributaries of rio Paranaíba, at Parque Nacional de Emas (including NUP 792, NUP 793, NUP 799, NUP 800, NUP 810, NUP 1949, NUP 2310) as *Leporinus paranensis.* However, the examination of these specimens revealed that these do not belong to *L. paranensis,* but rather to *L. octofasciatus.* The coloration of these specimens is faded (*i.e.,* the dark transversal bars are not as conspicuous as most specimens of *L. octofasciatus*), which could have led to the misidentification. These specimens have more lateral-line scales (37 or 38) than specimens herein identified as *L. paranensis* (35 or 36). A similar case of misidentification occurred in Avelino *et al.* (2015) (see Discussion for further information).

Diagnosis: *Leporinus paranensis* is distinguished from congeners, except *L. amae, L. amblyrhynchus, L. bahiensis, L. bistriatus, L. bleheri, L. desmotes, L. enyae, L. guttatus, L. inexpectatus, L. marcgravii, L. melanopleura, L. microphthalmus, L. microphysus, L. moralesi,*

L. multimaculatus, L. octofasciatus, L. octomaculatus, L. reticulatus, L. sexstriatus, L. striatus, L. taeniatus, L. taeniofasciatus, L. torrenticola, and *L. tigrinus* by having three premaxillary teeth (vs. four). *Leporinus paranensis* is distinguished from *L. amae, L. amblyrhynchus, L. bistriatus, L. bleheri, L. desmotes, L. enyae, L. guttatus, L. marcgravii, L. melanopleura, L. microphthalmus, L. microphysus, L. moralesi, L. multimaculatus, L. octofasciatus, L. octomaculatus, L. reticulatus, L. sexstriatus, L. striatus, L. taeniatus, L. taeniofasciatus, L. torrenticola,* and *L. tigrinus* by having three dark midlateral blotches on the body (vs. body with dark transversal bars in *L. bleheri, L. desmotes, L. enyae, L. octofasciatus,* and *L. tigrinus,* or body with a dark midlateral stripe in *L. amae, L. amblyrhynchus, L. bistriatus, L. melanopleura, L. melanopleurodes, L. microphysus, L. moralesi, L. sexstriatus, L. sidlauskasi, L. striatus, L. taeniatus, L. taeniofasciatus,* or body with four to eight dark midlateral blotches in *L. guttatus, L. marcgravii, L. microphthalmus, L. multimaculatus, L. octomaculatus, L. reticulatus, L. torrenticola*). *Leporinus paranensis* is distinguished from *L. bahiensis* and *L. inexpectatus* by having 16 scale rows around caudal peduncle (vs. 12).

Description: Morphometric data in Table 2. Medium-sized species, largest known specimen 170 mm SL. Head and trunk elongate and moderately compressed. Dorsal profile strongly convex from tip of upper lip to anterior naris, straight from this point to tip of supraoccipital spine, somewhat straight from there to origin of dorsal fin; dorsal-fin base straight; slightly convex from terminus of dorsal-fin base to origin of adipose fin and distinctly concave on dorsal margin of caudal peduncle. Ventral profile convex from tip of lower lip to the vertical through anterior naris, straight from this point to vertical through pectoral-fin origin; straight or somewhat convex from latter point to origin of anal-fin; anal base straight and concave on ventral margin of caudal peduncle. Body depth greatest at origin of dorsal fin.

Mouth terminal, opening longitudinally aligned with ventral margin of pupil in large specimens (100 mm SL or more). Lips smooth or slightly fringed. Premaxillary with three unicuspid teeth gradually decreasing in size away from symphyseal tooth. Dentary with four unicuspid teeth decreasing in size postero-laterally.

Scales large and cycloid with 5 or 6 radii. Lateral line extending from supracleithrum to base of caudal-fin median rays, with 35*(3) or 36(3) pored scales. 4*(3) or 5(3) longitudinal series of scales between dorsal-fin origin and lateral line, and 5*(6) series of scales between lateral line and pelvic-fin origin. 16*(6) longitudinal series of scales around caudal peduncle, with at least three specimens (LISDEBE uncat., MZUEL 22894, MZUSP 14454) having scale rows irregular and slightly fewer than 16 rows on part of caudal peduncle. Middorsal line with 10(1) or 11*(5) scales between supraoccipital tip and dorsal-fin origin.

Dorsal fin ii, 10*(6); its origin slightly anterior to midpoint of standard length and anterior to vertical through pelvic-fin origin. Distal margin of dorsal-fin convex. Adipose fin small, its origin posterior to origin of anal fin by diameter of one or two scales. Pectoral fin i,14(3) or i,15*(3); its margin slightly convex; its tip when adpressed extending to fourth or fifth scale anterior to pelvic-fin origin. Pelvic fin i,8*(6); its margin concave. Anal fin ii,8*(6), distal margin concave in most specimens; rays not reaching the caudal fin base when adpressed. Caudal fin i,8,9,i*(6); fin distinctly forked with approximately symmetrical lobes.

Coloration: Body ground coloration brown to yellow, distinctly countershaded. Three large rounded to oval dark-brown blotches on midlateral portion of trunk, each larger than orbit (blotches nearly rectangular in a couple of specimens). Anteriormost blotch ventral to dorsal-fin base; median one between dorsal-fin terminus and adipose fin; and posterior one on posterior half of caudal peduncle. Trunk with eight to 12 dark transversal bars on dorsum and extending ventrally below lateral line; bars much less conspicuous than midlateral blotches, being fragmented in larger specimens forming inconspicuous blotches. Inconspicuous dark lines between scale series present on median and posterior half of lateral portion of trunk in some specimens, including the holotype, but absent in recently collected specimens. Dark inconspicuous spot on base of trunk lateral scales in some of the recently collected specimens (absent on holotype). Head distinctly countershaded; upper lip dark. Fins hyaline or uniformly tan, except for adipose fin with dark distal margin.

Table 2. Morphometric data for *Leporinus paranensis* and *L. inexpectatus.* SD means Standard Deviation.

	Leporinus paranensis						*Leporinus inexpectatus*					
	Holotype	**n**	**Mean**	**Range**		**SD**	**Holotype**	**n**	**Mean**	**Range**		**SD**
Standard Length (mm)	170,0	6	147,5	124,7 —	170,0		155,6	22	107,5	56,5 —	155,6	
Percentages of standard length												
Predorsal distance	50,00	6	49,74	49,33 —	50,03	0,32	49,84	22	49,40	47,33 —	54,72	1,53
Body depth	33,82	6	32,42	30,84 —	34,09	1,43	31,21	22	29,55	27,50 —	32,83	1,45
Caudal peduncle depth	11,06	6	11,18	10,92 —	11,43	0,20	11,27	22	10,84	9,92 —	11,53	0,38
Head length	22,76	6	24,11	22,76 —	25,37	1,01	24,95	22	25,85	24,12 —	28,67	1,13
Percentages of head length												
Snout length	43,93	6	42,78	41,84 —	43,93	0,81	40,56	22	41,67	37,14 —	45,23	1,89
Eye diameter	18,60	6	21,34	17,40 —	24,73	3,06	26,02	22	21,18	24,80 —	32,28	5,10
Bony interorbital	50,39	6	45,37	39,39 —	50,39	4,41	44,29	22	42,66	37,86 —	46,95	2,06

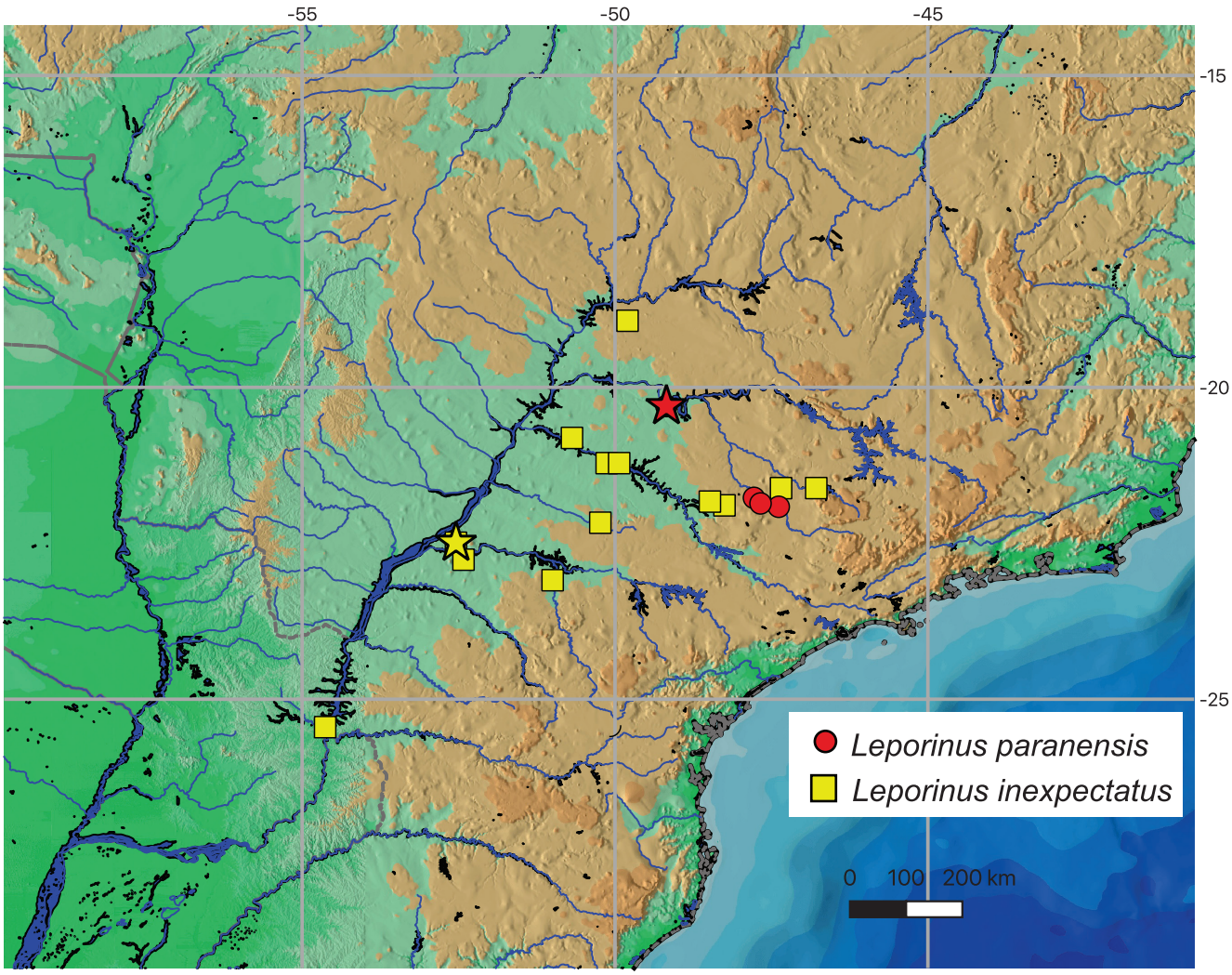

Figure 2. Geographical distribution of *Leporinus paranensis* (circles) and *L. inexpectatus* (squares) in southeast South America. Open symbols represent the type localities.

Distribution: *Leporinus paranensis* is known from the type specimens collected in the Grande river, in an area currently flooded by the hydropower dam UHE Marimbondo; and from specimens collected in tributaries of the Mogi-Guaçu river, itself a tributary of the Grande river (Fig. 2).

Conservation status: The apparently rarity of *Leporinus paranensis* is puzzling. The distribution of the species is at best speculative and its abundance and biology in the wild are completely unknown. The fact that the type series was collected almost 50 years ago in an area that has been largely altered by the construction of a hydroelectric dam is a concern. However, the putative distribution of the species (in at least the Grande River basin) is relatively broad, encompassing parts of the states of São Paulo, and Minas Gerais. The species has been recently recorded (2003-2007) from tributaries of the Mogi-Guaçu river in areas where no potential impacts are expected in the near future. Furthermore, the species is not commercially relevant and does not suffer under any direct anthropological impact (such as overfishing, for example). Therefore, given the IUCN criteria, the species is herein recommended to be considered as Least Concern (LC).

Leporinus inexpectatus, new species (Fig. 3)

Leporinus aff. *bahiensis*. – Géry *et al.,* 1987: 387, fig. 16 [in part; Paraguay; Río Acaray (and Arroyo Yuquyri, a stream of the latter), tributary of the Rio Paraná, a few kilometers below Itaipu dam, and Río Itapo-Guazu and Arroyo Pyrapyta, tributaries of the Itaipu reservoir].

Leporinus paranensis. – Garavello & Britski, 1987: 156, [in part, MZUSP 14455, MZUSP 37406, MZUSP 37407, MZUSP 37408, MZUSP 37409, MZUSP 37411]. – Oyakawa, 1996: 476-477 [type catalog, in part, MZUSP 14455, MZUSP 37406, MZUSP 37407, MZUSP 37408, MZUSP 37409, MZUSP 37411]. – Durães *et al.,* 2001: 184 [Rio Araguari, Minas Gerais]. – Castro *et al.,* 2003: 13, figs. 6-18 [tributaries of the Rio Paranapanema, LIRP 2254]. – Britto & Carvalho, 2006: 382 [Rio Paranapanema at Taquaruçu reservoir]. – Langeani *et al.,* 2007: 184 [upper Paraná, considered autochthonous and native; DZSJRP 22]. – Brandão *et al.,* 2009: 454 [Rio Novo, tributary of Rio Paranapanema, LBP 4845]. – Reis *et al.,* 2020: 457 [list of species from Paraná state].

Leporinus aff. *paranensis.* – Langeani *et al.,* 2007: 196 [species mentioned as being described by Heraldo Britski]. – Avelino *et al.,* 2015: 101 [molecular data, COI sequence, LBP 3808].

Type specimens

Holotype: MZUEL 14311, 155.6 mm SL, São Paulo state, Euclides da Cunha Paulista municipality, Córrego Água Branca, tributary of Rio Paranapanema, 22°29′34.1″S 52°32′32.8″W, M. Rocha, J.L.O. Birindelli, F.C. Jerep & E. Santana, 14 Jan 2016.

Paratypes: Brazil, Paraná state. LIRP 2254, 1 alc, 97.9 mm SL, Paranavaí, Córrego Santa Clara at Fazenda Rancho Zinco e Cristo Rei, Paranapanema drainage, 22°45′54″S 52°25′19″W, R.M.C. Castro *et al.,* 08 Aug 2000. MZUEL 6517, 2 alc, 46.9-56.7 mm SL, Sertanópolis, Ribeirão Couro do Boi, tributary of Rio Tibagi, 23°05′39.2″S 50°59′49.6″W, L.C. Silva, E. Santana, A. Souza, 21 Oct 2010. MZUEL 8807, 1 alc, 57.1 mm SL, Sertanópolis, Ribeirão Couro do Boi, tributary of Rio Tibagi, 23°05′39.2″S 50°59′49.6″W, L.C. Silva, E. Santana, A. Souza, 29 Mar 2010. MZUEL 8902, 1 alc, 43.6 mm SL, Sertanópolis, Ribeirão Couro do Boi, tributary of Rio Tibagi, 23°05′39.2″S 50°59′49.6″W, L.C. Silva, E. Santana, A. Souza, 20 May 2009. **Brazil, São Paulo state.** DZSJRP 10948, 3 alc, 47.1-65.5 mm SL, Brejo Alegre, F.B. Teresa and J.L. Veronezi, 29 Sep 2007. LBP 3808, 5 alc, 14.0-19.8 mm SL, Avaré, Rio Novo, tributary of Rio Paranapanema, 23°01′26.2′W 48°49′32.6″. LBP 4845, 2 alc, 16.7-19.1 mm SL, Salto Grande, Rio Paranapanema, at Salto Grande reservoir, 22°50′23″S 49°50′50″W. LIRP 2252, 11 alc, 50.3-155.0 mm SL, Santo Antônio do Aracangua, Córrego das Cruzes, Tietê drainage, 20°48′44″S 50°41′16″W, R.M.C. Castro *et al.,* 06 Sep 1999. LIRP 7626, 1 alc, 96,6 mm SL, Gavião Peixoto, Rio Jacaré-Guaçu, Tietê drainage, 21°50′46″S 48°31′28″W, A. Esguícero, 04 Jan 2010. MZUSP 48852, 5 alc, 84.3-123.0 mm SL, Córrego Fundo, Murutinga do Sul, Atílio Storti, 28 Mar 1975. MZUSP 71790, 2 alc, 90.6-95.2 mm SL, Rio do Peixe, approximately 1.5 km below UHE Rio do Peixe, São José do Rio Pardo, Pedro Gehard, 10 Jan 2001.

Non-type specimens: Brazil, Minas Gerais state. MZUSP 36777, 2 alc, Ituiutaba, Rio Tejuco at Salto do Morais, 18°56′S 49°48′W, A.L. Godinho, Oct 1985 to Feb 1986. **Brazil, São Paulo state.** FMNH 71240, 1, 39.4 mm SL, Barbosa, Rio Tietê at Salto do Avanhadava, c.21°13′S 49°56′W, J.D. Haseman, 14 Sep 1908. MZUSP 14455, 4 alc [paratypes of *L. paranensis*], 92.0-102.0 mm SL, Murutinga do Sul, Córrego Fundo, c.21°37′S 47°20′W, A. Storti, 24 Dec 1974. MZUSP 37406, 1 alc [paratype of *L. paranensis*], 97.0 mm SL, Araraquara, Rio Jacaré Guaçu, at road between Araraquara and Guarapiranga, 21°53′38″S 48°15′01″W, J.R. Moreira, 15 Feb 1985. MZUSP 37407, 1 alc [paratype of *L. paranensis*], 119.0 mm SL, Rio Paranapanema, J.C. Garavello, 14-20 May 1979. MZUSP 37408, 1 alc [paratype of *L. paranensis*], 123.0 mm SL, Araraquara, Rio Jacaré Guaçu at small waterfall upstream of PCH Gavião Peixoto dam, c.21°50′S 48°29′W, J.R. Moreira, 13 Mar 1984. MZUSP 37409, 1 alc [paratype of

Figure 3. *Leporinus inexpectatus,* holotype, MZUEL 14311, 156.1 mm SL, Córrego Água Branca, tributary of rio Paranapanema, photographed preserved in alcohol (large above) and live (left corner), paratype, MZUEL 6517, 46.9 mm SL, Ribeirão Couro do Boi, tributary of rio Tibagi (right corner).

L. paranensis], 146.0 mm SL, Araraquara, Rio Jacaré Guaçu at Fazenda Alabama, upstream of PCH Gavião Peixoto dam, c.21°50′S 48°29′W, J.R. Moreira, 13 Mar 1984. MZUSP 37411, 1 alc [paratypes of *L. paranensis*], 129.0 mm SL, Araraquara, Rio Jacaré Guaçu, at Fazenda Alabama, upstream of Gavião Peixoto dam, c.21°50′S 48°29′W, J.R. Moreira, 30 Apr 1985. **Paraguay.** All from Dept. Alto Parana, c.25°27′S 54°38′W. MHNG 2004.97, 1 alc, 142.0 mm SL, río Acaray, C. Dlouhy, 21 Oct 1978. MHNG 2037.19-23, 5 alc, 79.0-105.2 mm SL, Porto Ponte Stroessner, C. Dlouhy, 11 Apr 1980. MHNG 2067.94, 1 alc, 112 mm SL, Río Itabo-Guazu, C. Dlouhy, 06 May 1980. MHNG 2105.63-64, 2 alc, 109.0-134.6 mm SL, Ao. Acaray, C. Dlouhy, 15 Sep 1981. MHNG 2105.65-66, 2 alc, 113.0-127.5 mm SL, Lac Represso, C. Dlouhy, 07 Sep 1982. MHNG 2159.20, 1 alc, 110.0 mm SL, Ao. Pyrapyta, C. Dlouhy, 03 Oct 1981. MHNG 2204.24, 5 alc, 89.0-98.3 mm SL, Alto Paraná, Lac Acaray, C. Dlouhy, 03 May 1984. MHNG 2386.53, 5 alc, 101.2-133.5 mm SL, Lac Acaray, Expct. Zool. Mus. Genève, 1986? MHNG 2386.54, 1 alc, 100.6 mm SL, Ao. Itaquyry, Expdt. Zool. Mus. Genève, 16 Oct 1986. MHNG 2386.54, 1 alc, 152.5 mm SL, Río Acaray, Expdt. Zool. Mus. Genève, 31 Oct 1986. MHNG 2386.92, 2 alc, 131.0-139.0 mm SL, Lac Acaray superior, Exped. Zool. Mus. Genève, 1986. MHNG 2396.62, 1 alc, 142.5 mm SL, Lagune Ao. Iguassu à Juan E.O. Leary, Expdt. Zool. Mus. Genève, 18 Oct 1987.

Remarks: The paratypes of *Leporinus paranensis* MZUSP 14456 (16 alc), and MZUSP 37410 (1 alc), that likely belonged to *Leporinus inexpectatus,* were not found at MZUSP (Oyakawa, 1996: 477). Géry *et al.* (1987: 387) mention a juvenile (c.55 mm SL) from Río Negro, 6 km north of Chaco-I, Paraguay basin, Paraguay, as belonging to *Leporinus* aff. *bahiensis* (= *L. inexpectatus*). This specimen was examined by one of us (HAB) and likely belongs to *Leporinus lacustris* because it has four teeth on each premaxillary and dentary, in addition to the three dark midlateral blotches, 34 lateral-line scales and 16 scale series around the caudal peduncle. Interestingly, the first specimen of *Leporinus inexpectatus* deposited in fish collections was sampled in 1908 (FMNH 71240), more than a hundred years ago, by J.D. Haseman in the Salto do Avanhadava, a waterfall that was flooded by a hydroelectric plant during the 1970's.

Diagnosis: *Leporinus inexpectatus* is distinguished from congeners, except *L. amae, L. amblyrhynchus, L. bahiensis, L. bistriatus, L. bleheri, L. desmotes, L. enyae, L. guttatus, L. marcgravii, L. melanopleura, L. microphthalmus, L. microphysus, L. moralesi, L. multimaculatus, L. octofasciatus, L. octomaculatus, L. paranensis, L. reticulatus, L. sexstriatus, L. striatus, L. taeniatus, L. taeniofasciatus, L. torrenticola,* and *L. tigrinus* by having three premaxillary teeth (vs. four). *Leporinus inexpectatus* is distinguished from *L. amae, L. amblyrhynchus, L. bistriatus, L. bleheri, L. desmotes, L. enyae, L. guttatus, L. marcgravii, L. melanopleura, L. microphthalmus, L. microphysus, L. moralesi, L. multimaculatus, L. octofasciatus, L. octomaculatus, L. reticulatus, L. sexstriatus, L. striatus, L. taeniatus, L. taeniofasciatus, L. torrenticola,* and *L. tigrinus* by having three dark midlateral blotches on the body (vs. body with dark transversal bars in *L. bleheri, L. desmotes, L. enyae, L. octofasciatus, L. tigrinus,* or body with a dark midlateral stripe in *L. amae, L. amblyrhynchus, L. bistriatus, L. melanopleura, L. melanoplerodes, L. microphysus, L. moralesi, L. sexstriatus, L. sidlauskasi, L. striatus, L. taeniatus, L. taeniofasciatus,* or body with four to eight dark midlateral blotches in *L. guttatus, L. marcgravii, L. microphthalmus, L. multimaculatus, L. octomaculatus, L. reticulatus, L. torrenticola*). *Leporinus inexpectatus* is distinguished from *L. paranensis* by having 12 scale rows around caudal peduncle (vs. 16); and from *L. bahiensis* by having a terminal mouth (mouth cleft longitudinally aligned with ventral border of eye) in specimens larger than 100 mm SL (vs. subterminal, mouth cleft longitudinally aligned with ventral border of infraorbital series), body pale brown to silver and slightly yellow to hyaline fins in life (vs. body dark brown and bright orange fins in life).

Description: Morphometric data in Table 2. Medium-sized species, largest known specimen 155.6 mm SL. Head and trunk elongate and moderately compressed. Dorsal profile slightly arched from anterior margin of snout to dorsal-fin insertion; declining in an almost straight line from dorsal-fin origin to adipose fin; and concave at caudal peduncle. Ventral profile in a slight convex line from lower jaw to anal-fin insertion; straight on anal-fin base, and concave on caudal peduncle. Body depth greatest at origin of dorsal fin.

Mouth terminal, opening horizontally aligned with ventral margin of eye in larger specimens (100 mm SL or more). Lips smooth or slightly fringed. Premaxillary with three unicuspid teeth gradually decreasing in size from symphyseal tooth. Dentary with four unicuspid teeth decreasing in size postero-laterally.

Scales large and cycloid, with 5 or 6 radii; lateral line extending from supracleithrum to base of caudal-fin median rays, with 34(1), 35(14) or 36*(6) perforated scales. 3(19) or 4*(2) longitudinal series of scales between dorsal-fin origin and lateral line, and 4(21) series of scales between lateral line and pelvic-fin origin. 12*(21) longitudinal series of scales around caudal peduncle. Middorsal line with 11*(21) scales between supraoccipital tip and dorsal-fin origin.

Dorsal fin ii,10*(21); its origin slightly anterior to half of standard length and anterior to pelvic-fin origin. Distal margin of dorsal-fin convex. Adipose fin small, its origin posterior to vertical through origin of anal fin by diameter of one or two scales. Pectoral fin i,14*(15), or i,15(6); its margin slightly convex; its tip when adpressed extending to fourth or fifth scale anterior to pelvic fin. Pelvic fin i,8*(21); its margin concave. Anal fin ii,8*(21), distal margin concave in most specimens; rays not reaching the caudal fin base when adpressed. Caudal fin i,8,9,i*(21); fin distinctly forked with approximately symmetrical lobes.

Coloration: In alcohol-preserved specimens, body ground coloration brown to yellow, distinctly counter-

shaded. Three large rounded to oval dark-brown blotches midlateral on trunk, larger than orbit. Anteriormost blotch below dorsal-fin base; median one dorsal to anal-fin origin; and posterior one on posterior half of caudal peduncle (posterior one always less conspicuous than anterior two, and sometimes completely confluent with last dark transversal bar). Trunk with eight to 14 dark transversal bars on dorsum extending ventrally below lateral line; bars much less conspicuous than midlateral blotches; bars fragmented in some specimens (especially on specimens larger than 80 mm SL) forming inconspicuous blotches. Small specimens (up to 60 mm SL) with eight dark transversal bars on trunk, first one not extending past lateral line scale series. Head distinctly countershaded; upper lip dark. Fins hyaline or uniformly tan except for adipose fin with dark distal margin.

Distribution: *Leporinus inexpectatus* is known from the entire upper Paraná river basin (Fig. 2), occurring in the main channel of large rivers such as the Paranapanema and the Tietê rivers, and also in smaller tributaries, in the São Paulo, Paraná, and Minas Gerais states of Brazil. The species was also sampled in the Acaray river, a Paraná-river tributary, a few kilometers below the Itaipu dam, and from tributaries of the Itaipu reservoir in Paraguay (Géry *et al.,* 1987).

Conservation status: Given the large distribution of the species encompassing almost the entire upper Paraná basin, its relatively common occurrence in fish collections and inventories, and its presence on smaller tributaries of large rivers, the species is herein recommended to be considered as Least Concern, following the IUCN Criteria.

Etymology: The specific name *inexpectatus* is a Latinized adjective in allusion to the surprising previous inclusion of this species in the type series of *Leporinus paranensis,* and the fact that it was undescribed, even though it occurs in one of the most sampled area in South America, the upper Paraná basin.

Comparative analyses

The body shape analysis of samples of *L. paranensis, L. inexpectatus* and *L. lacustris* showed at least two different morphometric patterns (Fig. 4), one of *L. lacustris* and another of *L. inexpectatus* and *L. paranensis.* Data of latter two species was largely overlapping, showing that their general body shape is very similar, and quite distinct when compared to that of *L. lacustris.* 92.623% of data variation was included in Principal Component 1 (PC1), whereas 4.0701% was in PC2 and 1.4637% in PC3 (each remaining component includes less than 1% of the variance). The most important variables on PC2 were bony interorbital (0.51884), followed by standard length (–0.46083), predorsal distance (–0.43925), and eye diameter (0.41572) (Table 3). On PC3, the most important variables were eye diameter (0.83778) followed by bony interorbital (–0.46973), and body depth (–0.19824) (Table 3).

Table 3. Principal Component Analysis of *Leporinus inexpectatus* (n = 20), *L. paranensis* (n = 6) and *L. lacustris* (n = 8). Variable loadings for components 2 and 3. Variance included on each Principal Component was as follows: 92.623% in PC1, 4.0701% in PC2 and 1.4637% in PC3, each remaining components include less than 1% of data variance.

	PC 2	PC 3
Standard length	–0.46083	0.010754
Predorsal distance	–0.43925	0.08029
Body depth	0.0013259	–0.19824
Caudal peduncle depth	0.30639	–0.089551
Head length	–0.083233	0.077696
Snout length	–0.22776	0.1325
Eye diameter	0.41572	0.83778
Bony interorbital	0.51884	–0.46973

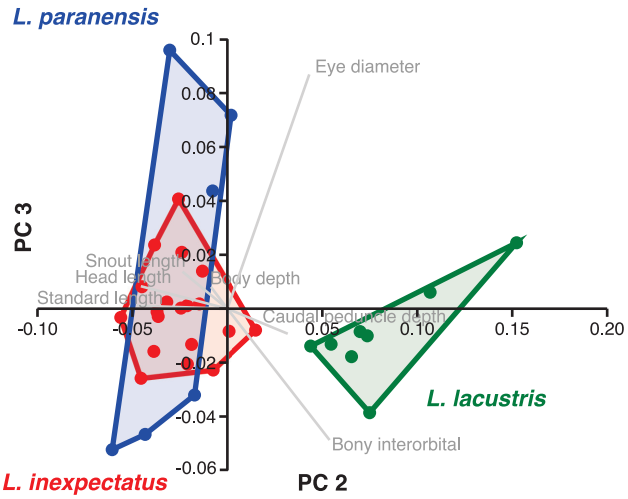

Figure 4. Principal Components Analysis showing the body shape variation in *L. paranensis, L. inexpectatus,* and *L. lacustris.*

Molecular data included 570 base pairs of cytochrome c oxidase subunit I (COI) from 69 samples. The molecular analyses clearly distinguished the new species from closely related congeners, including *L. bahiensis, L. paranensis L. octofasciatus* and *L. taeniatus,* as well as all these nominal species (Fig. 5). The genetic distance, based on Kimura-2-parameter model, ranges from 0.023 ± 0.006 between *L. paranensis* and *L. inexpectatus* to 0.094 ± 0.014 between *L. taeniatus* and *L. lacustris* (Table 4). The COI gene tree recovered *L. inexpectatus* and *L. paranensis* as closely related species forming a clade sister to the clade including *L. bahiensis* and *L. taeniatus,* and this larger clade sister to *L. octofasciatus.* On the other hand, *L. friderici* and *L. lacustris* were recovered at the base of the tree. Both species delimitation analyses (ASAP, PTP) confirmed the identifications based on external morphology, and supported the validity of *L. inexpectatus* and *L. paranensis.* These results also confirm the identification of the larva (accession number PP335714) as *L. paranensis.* Indeed, the identification of the latter sample is unequivocal based on its collection origin and the results obtained in the DNA analysis,

Table 4. Estimate of Genetic Distance (in percentage) over sequence within samples/species (diagonal in red), and between pairs (below diagonal in black); deviation of estimate between samples/species (above diagonal in blue).

	L. inexpectatus	*L. paranensis*	*L. octofasciatus*	*L. bahiensis*	*L. taeniatus*	*L. lacustris*	*L. friderici*
L. inexpectatus (n = 11)	**0,23**	0,67	0,80	1,01	1,08	1,30	1,20
L. paranensis (n = 1)	2,30	**n/c**	0,92	1,03	1,20	1,44	1,27
L. octofasciatus (n = 19)	3,43	3,90	**0,42**	1,09	1,29	1,21	1,17
L. bahiensis (n = 2)	4,64	4,53	5,37	**0,37**	0,74	1,44	1,35
L. taeniatus (n = 20)	4,80	5,50	6,70	2,74	**0,13**	1,61	1,50
L. lacustris (n = 10)	7,89	9,01	7,25	9,25	10,22	**0,75**	1,27
L. friderici (n = 5)	6,84	6,92	6,73	8,07	8,92	7,96	**0,18**

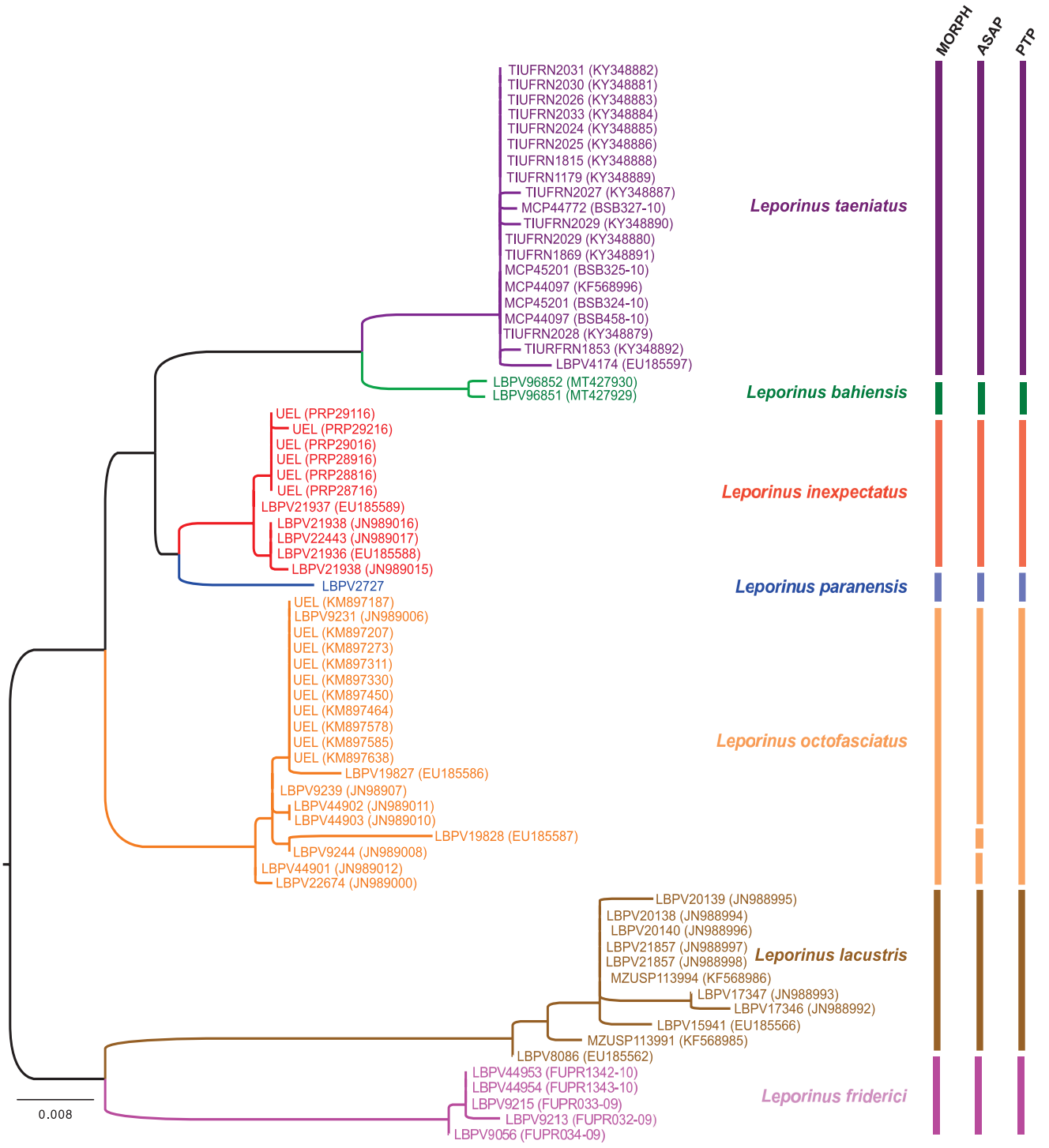

Figure 5. Phylogenetic analysis based on COI sequences and Maximum Likelihood of *L. inexpectatus* and closely related species, showing results of species delimitation analyses based on morphological (MORPH), and molecular (ASAP, bPTP) methods (bars on right).

which demonstrated that the sample belong to a species distinct from all other included congeners (Fig. 5); and placed it as sister to *L. inexpectatus.*

DISCUSSION

The main feature that helps to distinguish the new species from *L. paranensis* is the number of scale rows around the caudal peduncle. Most species of *Leporinus* have either 12 or 16 scale rows around the caudal peduncle, with exception of *L. jatuncochi* and some specimens of *L. desmotes* with 14. Similar patterns of closely related species differing in the number of scale rows around the caudal peduncle is observed in *Hypomasticus pachycheilus* and *H. julii* (Santos *et al.,* 1996), *Leporinus granti* and *L. nijsseni* (Garavello, 1990), *L. arcus* and *L. tepui* (Birindelli *et al.,* 2019), *Sartor respectus* and congeners (Santos & Jégu, 1987), among others. Furthermore, there is no intra-specific variation in the number of scale rows in the caudal peduncle in any of the known species of Anostomidae, except for the minor variation from 14 to 16 scale rows in *L. desmotes* (Burns *et al.,* 2017), and from 18 to 20 in *Schizodon kneri* (Sidlauskas *et al.,* 2007). Nevertheless, some of the studied specimens of *L. paranensis* (LISDEBE uncat, MZUEL 22894) possesses irregular scale rows on parts of the body and have 14 or 15 scale rows in some parts of the caudal peduncle. That irregularity could have contributed to the inclusion of two species within the type series of *L. paranensis.*

Géry *et al.* (1987) correctly recognized the morphological similarity between *Leporinus bahiensis* (Fig. 6) and *L. inexpectatus,* identified therein as *"L.* aff. *bahiensis".* In fact, both species are extremely similar, especially when specimens have lost their live coloration (*i.e.,* are alcohol preserved). The COI sequence data further indicate a close relationship between these species, though not as sister taxa (*L. bahiensis* is even closer to *L. taeniatus* on the gene tree). *Leporinus taeniatus* is easily distinguished from *L. bahiensis* by the presence of a dark midlateral stripe (vs. three dark midlateral blotches on body).

Avelino *et al.* (2015) provided COI sequence data for specimens recognized herein as *Leporinus inexpectatus,* evidencing the genetic similarity of the species with *L. octofasciatus, L. bahiensis* and *L. taeniatus.* In that study, authors misidentified specimens of *L. octofasciatus* as *L. paranensis.* The molecular analysis herein performed (Fig. 4) included additional samples of *L. octofasciatus,* as well as of other closely-related congeners, and suggested that the specimens examined by Avelino *et al.* (2015) were *L. octofasciatus.* We confirmed that identification by re-examining the vouchers. The three specimens (LBP 9573) have their body coloration partially faded with dark transversal bars fragmented forming three vertically elongated blotches between the verticals through the dorsal- and anal-fin bases. Additionally, the number of premaxillary teeth and scale rows around caudal peduncle of *L. octofasciatus* and *L. paranensis* is exactly the same, which contributed to the previous misidentification. Nevertheless, the vouchers are relatively large (over 200 mm SL), have 37 or 38 lateral line scales, and the dark blotches on the body match the transversal bars present in most specimens of *L. octofasciatus.*

Comparative material: *Leporinus bahiensis:* MZUEL 9640 (1), MZUEL 15424 (2), MZUEL 17833 (15), MZUEL 18633 (7), MZUSP 112716. *Leporinus lacustris:* MZUSP 14464 (1), MZUSP 14465 (2), MZUSP 14466 (5). *L. octofasciatus*: MZUEL 415 (3), MZUEL 1741 (7), MZUEL 16375 (10), MZUEL 16960 (1), MZUEL 19496 (12). *L. taeniatus:* MZUSP 14522 (2), MZUSP 14523 (1), MZUSP 14524 (7), MZUSP 14525 (3).

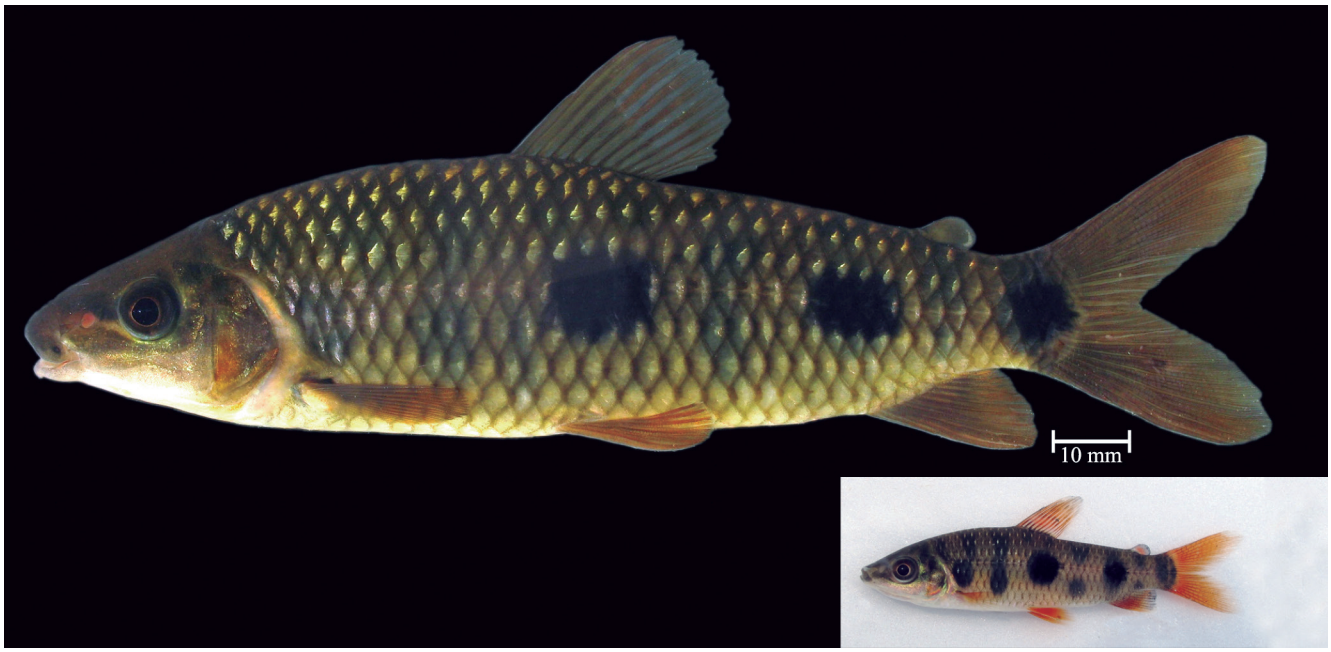

Figure 6. *Leporinus bahiensis,* MZUSP 112716, c. 90 mm SL (larger specimen) and c.40 mm SL (smaller specimen at right corner), rio Sarapuí, tributary of rio Vermelho, Bahia state.

CONCLUSIONS

Leporinus paranensis is redescribed based on its holotype, two paratypes and a few recently collected specimens, all from the Grande River and its tributaries in the upper Paraná basin. A few of its paratypes, and new recently sampled specimens are herein recognized and described as a new species: *Leporinus inexpectatus*. The latter is widespread in the upper Paraná basin, occurring in tributaries of all major rivers including the Paranaíba, Grande, Tietê and Paranapanema. Both species are distinguished from congeners based on the presence of three premaxillary teeth, four dentary teeth, terminal mouth and body with dark rounded midlateral blotches. The two species differ in the number of caudal-peduncle scale rows.

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