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Systematic assessment of the *Leporinus desmotes* species complex, with a description of two new species

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Members of the *Leporinus desmotes* species complex can be distinguished from other barred or banded congeners by the combination of nine distinct black bars across the head and trunk and long, pointed, laterally compressed and upward curving symphyseal dentary teeth. A taxonomic reassessment of this complex revealed two new species, one from the Orinoco and Negro rivers of Venezuela and Brazil, and the other from the Xingu and Tapajós rivers of Brazil. Both species are similar to *L. desmotes* and *L. jatuncochi*, but differ significantly in body shape morphology, coloration, and/or circumpeduncular scale counts. Genetic evidence also contributes to the recognition of both new species. This contribution also maps the geographic distribution of the four known species, and highlights the presence of an unusual meristic polymorphism within *Leporinus desmotes sensu stricto* that may suggest the presence of even more unrecognized diversity.

Keywords: Anostomidae, Characiformes, Morphology, South America, Taxonomy.

As espécies do complexo *Leporinus desmotes* diferem da maioria dos congêneres com base nas nove barras transversais escuras ao redor da cabeça e do corpo, e do dente sinfisiano do dentário alongado, comprimido lateralmente e ligeiramente curvado para cima. Uma revisão taxonômica desse complexo revelou a existência de duas espécies novas, uma dos rios Orinoco e Negro na Venezuela e Brasil, e outra das drenagens dos rios Xingu e Tapajós, no Brasil. As duas espécies novas são similares à *L. desmotes* e *L. jatuncochi*, das quais diferem significativamente por uma combinação de forma do corpo, coloração e número de séries de escamas ao redor do pedúnculo caudal. Dados genéticos também corroboram o reconhecimento das duas espécies novas. Esta contribuição ainda traz novos dados sobre a distribuição geográfica de cada uma das espécies do complexo, e discute a presença de um incomum polimorfismo no número de escamas ao redor do pedúnculo caudal em *Leporinus desmotes stricto sensu*, que sugere a presença de uma diversidade ainda maior de espécies não descritas.

Palavras-chave: América do Sul, Anostomidae, Characiformes, Morfologia, Taxonomia.

Introduction

Leporinus Agassiz, 1929 is the largest and most diverse genus in the characiform family Anostomidae, with roughly 90 species spread across most of South America (Britski, Garavello, 2005; Britski, Birindelli, 2008; Dos Santos, Zuanon, 2008; Feitosa *et al.*, 2011; Birindelli *et al.*, 2016). The genus reaches greatest diversity in the Amazon, Orinoco, and Guianas river drainages with 62 valid species described from those three regions (Sidlauskas, Birindelli, in press). New *Leporinus* species are described yearly, and the genus includes many poorly understood species complexes in need of taxonomic revision (Birindelli, Britski, 2013).

Members of *Leporinus* exhibit substantial morphological and ecological diversity, and vary in body size, trophic morphology, diet, habitat and color pattern. Mouth position varies from terminal to subinferior, and tooth shape ranges from rounded to multicuspidate to spatulate (Sidlauskas, Vari, 2008). Their diet is generally omnivorous, but the proportion of plant or animal material consumed can differ greatly between species (Knöeppel, 1972; Goulding *et al.*, 1988; de Mérona *et al.*, 2001). Most species exhibit one of three distinct color patterns: one to four midlateral blotches, one to six dark longitudinal stripes, or seven to 14 dark vertical dark bars (Sidlauskas, Vari, 2012; Sidlauskas, Birindelli, in press), and variation within these basic forms often helps to diagnose species.

The barred (also called banded) group of *Leporinus* as presently conceived (Britski, Birindelli, 2016), all possess dark vertical bars as adults and nine branched pelvic-fin rays (*versus* the eight typical of other *Leporinus*). The group currently includes nine species: *L. affinis* Gunther, 1864, *L. altipinnis* Borodin, 1929, *L. bleheri* Géry, 1999, *L. desmotes* Fowler, 1914, *L. fasciatus* (Bloch, 1794), *L. jatuncochi*

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Ovchynnyk, 1971, *L. pearsoni* Fowler, 1940, *L. tigrinus* Borodin, 1929, and *L. yophorus* Eigenmann, 1922. Within this group, *Leporinus desmotes* has long been recognized as among the most distinctive species. In its original description Fowler (1914) proposed *L. desmotes* as the type species of the subgenus *Myocharax* on the basis of its unusual tooth morphology. The upper teeth are directed forward obliquely, while the lower teeth project forward almost horizontally, with the symphyseal teeth forming an elongate laterally compressed "tusk" fitting medial and ventral to the superior pair (Fowler, 1914; Géry, 1977) (Fig. 1).

Fifty-seven years after Fowler (1914) described *Leporinus desmotes* from specimens collected in the Rupununi River of Guyana, Ovchynnyk (1971) named *Leporinus jatuncochi*, a similarly barred and tusked species, from a single specimen collected in Lake Jatun Cocha within the Napo province of Ecuador. Perplexingly, Ovchynnyk (1971) never compared the newly described *L. jatuncochi* from the upper Amazon river basin, with the morphologically similar *L. desmotes* from the Essequibo river drainage. Previous work has hypothesized that *L. jatuncochi* may be a synonym of *L. desmotes* (Garavello, 1979), while others have listed both species as provisionally valid (Garavello, Britski, 2003) but no formal morphological or molecular analysis has ever tested the validity of these two species. Neither has any study investigated the taxonomic status of populations of similar fishes that have been discovered in the Orinoco river basin in Venezuela as well as in several tributaries of the Amazon River in Brazil during the century that has elapsed since the original description. Taken together, these barred and tusked *Leporinus* with nine branched pelvic-fin rays form a complex of populations morphologically similar to *L. desmotes* and *L. jatuncochi*, but spanning most of the cis-Andean Neotropics and potentially including unrecognized species-level diversity. We refer to these fishes here in as the *Leporinus desmotes* species complex.

This study reexamined the *Leporinus desmotes* species complex by comparing morphometrics, meristics and coloration of specimens from at or near the type localities of the two nominal species, *L. desmotes* and *L. jatuncochi*, to samples collected widely in the Amazon, Orinoco and Essequibo basins. The study also compared the genetics of a more limited sample of specimens in a molecular phylogenetic context. In so doing, we aimed to formally test the validity of the upper Amazonian *L. jatuncochi* as a distinct species, to evaluate the possible presence of undescribed species within the complex, and describe and diagnose such unrecognized species.

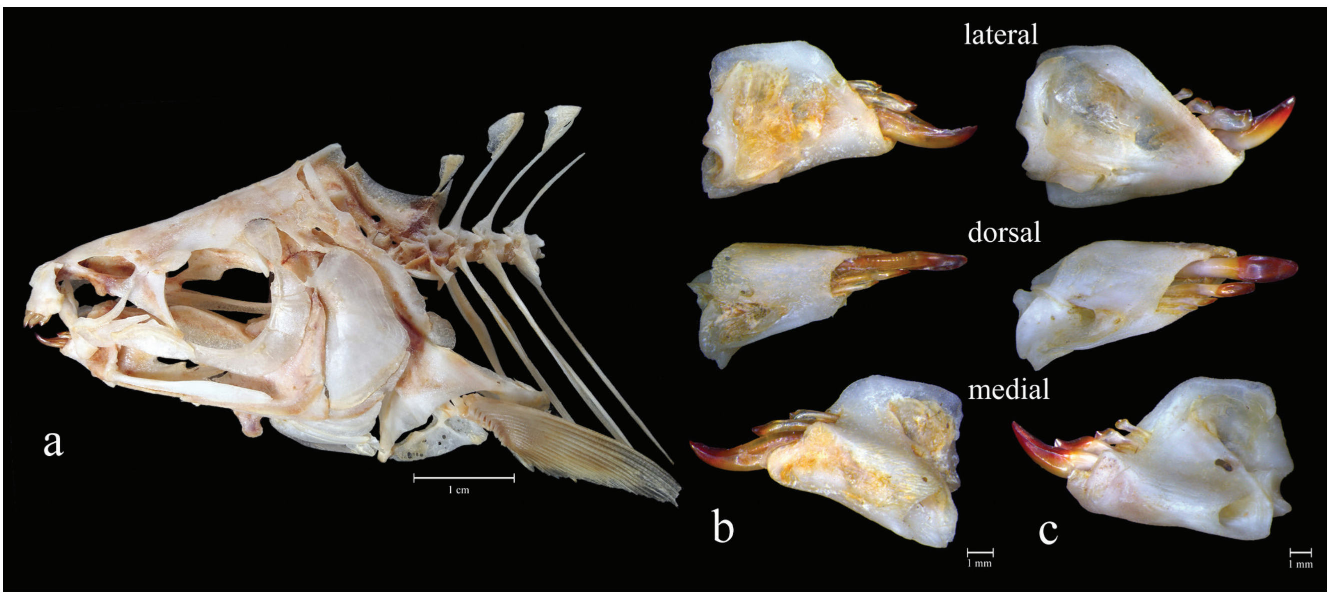

Fig. 1. (a) Head in lateral view and **(b)** lower jaw of *Leporinus enyae*, MZUEL 17001, 169.0 mm SL, río Caura, Orinoco basin in Venezuela, **(c)** lower jaw of *L. fasciatus*, MZUEL 14698, 221.5 mm SL, rio Negro in Brazil. All specimens dried skeletons.

Material and Methods

Sampling design. Overall, we examined the meristics, coloration and general morphology of hundreds of specimens (see materials examined), and collected detailed morphometric data from a smaller subset of 68 specimens. Genetic data for six individuals within the *Leporinus desmotes* complex and several examples of other banded *Leporinus* were extracted from an in-progress multilocus phylogenetic study of relationships within Anostomidea. Only specimens with meristic and morphometric measurements were included in the type series for each new species discovered. Due to the small genetic sample sizes, we did not require genetic data for specimens to be assigned to a type series.

Specimens listed under comparative material examined section are organized by species, type status, country, catalog acronym and catalog number. All are alcohol-preserved unless noted with CS for clear and stained or SK for dry skeletons. Information on number of specimens and standard length of smallest and largest specimen of the lot follow catalog number. Information on locality is organized by state, municipality, locality name, and geographical coordinates.

Specimens were examined from the following institutions: ANSP, Academy of Natural Sciences, Philadelphia; AUM, Auburn University Museum of Natural History, Auburn; BMNH, Natural History Museum, London; CAS, California Academy of Sciences, San Francisco; FMNH, Field Museum of Natural History, Chicago; INHS, Illinois Natural History Survey, Champaign; INPA, Instituto Nacional de Pesquisas da Amazônia, Manaus; MCP, Museu de Ciências e Tecnologia, Pontifícia Universidade Católica do Rio Grande do Sul, Porto Alegre; MCNG, Museo de Ciencias Naturales, Guanare; MCZ, Museum of Comparative Zoology, Harvard University, Cambridge; MNRJ, Museu Nacional do Rio de Janeiro, Universidade Federal de Rio de Janeiro, Rio de Janeiro; MPEG, Museu Paraense Emilio Goeldi, Belém; MSUM, The Museum, Michigan State University, East Lansing; MUSM, Museo de Historia Natural, Universidad Nacional Mayor de San Marcos, Lima; MZUEL, Museu de Zoologia da Universidade Estadual de Londrina, Londrina; MZUSP, Museu de Zoologia da Universidade de São Paulo; OS, Oregon State University Ichthyology Collection, Corvallis; ROM, Royal Ontario Museum, Toronto; UF, Florida Museum of Natural History, University of Florida, Gainesville; USNM, National Museum of Natural History, Smithsonian Institution, Washington D.C.; ZMB, Universität Humboldt, Zoologisches Museum, Berlin.

Morphology. Meristic counts follow the methodology of Sidlauskas *et al.* (2011). Meristic analyses and tabular data reflect a synthesis of observations of all authors. Morphometric analysis employed thirty-seven linear measurements following Burns *et al.* (2014), however we used the pelvic-fin and pectoral-fin origins rather than insertions for all morphometrics involving a landmark on those fins to reduce measurement variation as the insertion can be difficult to find on smaller specimens. Only specimens present at OS were used for morphometric analyses, thereby allowing a single observer (MC) to perform all measurements. Allometric differences among specimens were removed from the 37 log-transformed measurements by an allometric Burnaby technique implemented in PAST version 3.12 (Hammer, 2001). The size-standardized data were used in two different Principal Component Analyses (PCA). The first of these contained all specimens, while the second contained only the specimens from the Essequibo and upper Amazon drainages, from which the two nominal species were described. This second PCA was performed because the specimens from the Orinoco, Tapajós and Xingu populations proved to be the most morphologically distinct in the dataset, and their inclusion may have obscured more subtle differentiation between specimens from near the type localities of the described species. This more restricted PCA also helped to investigate possible morphological differentiation between specimens possessing alternative states of an intriguing scale polymorphism (see results). Because that second PCA did not reveal any greater differentiation between specimens from the Upper Amazon and Essequibo than did the global analysis, the first three eigenvectors from the global PCA, totaling 47% of the non-allometric shape variation, were employed in all further statistical analyses. The first three eigenvectors were found to account for most of the variability in the data through a scree plot investigation.

Specimens for morphometric analysis were assigned *a priori* to four geographically circumscribed groups, each representing a potentially distinct species or population due their separation into distinct drainage basins. These included specimens from the Essequibo drainage (including the Rupununi River, type locality of *Leporinus desmotes*), the upper Amazon (from which *L. jatuncochi* was described), the Xingu, and the Orinoco basins. A MANOVA implemented in PAST tested the overall statistical distinctiveness of each group using the first three principal components from the global PCA. Pairwise Tukey's *post-hoc* comparisons tested the significance of differences between the group means ($p < 0.05$) on each morphospace axis. The untransformed variables that explained the highest proportion of variance in the PCA were regressed against standard length (SL) for each species to determine if the ontogenetic trajectories for these variables differed among species. This standardized-major-axis (Type II) regression, as well as tests of equality of slope and intercept, were done in the smart package in R (Warton *et al.*, 2012).

Molecular data. Taxon sampling in the ingroup included seven individuals from the *Leporinus desmotes* species group, including three from the upper Amazon, one from the Orinoco, one from the Essequibo, and two from the Xingu drainages. These samples were subsetted from a more encompassing multilocus study of Anostomoidea, and represent all tissues available at the time of analysis. The voucher specimen for the tissue sample representing the Essequibo drainage has 15 circumpeduncular scales (see discussion for the relevance of this detail). The outgroup includes four other species of the banded species group (*L. affinis*, *L. altipinnis*, *L. fasciatus* and *L. pearsoni*), as well as the more distantly related *L. brunneus* and *L. ecuadorensis*.

DNA was extracted using a DNeasy Tissue Kit (Qiagen Inc). Three mitochondrial genes, 16S rRNA (16s); cytochrome oxidase C subunit 1 (COI) and cytochrome B (Cytb), were amplified through standard polymerase chain reaction (PCR) following the protocols of recent phylogenetic studies on characiforms (Oliveira *et al.*, 2011; Melo *et al.*, 2014; Melo *et al.*, 2016). Three nuclear genes, myosin heavy chain 6 gene (Myh6), recombination activating gene 1 (Rag1), and recombination activating gene 2 (Rag2) were amplified by nested-PCR following the protocol of Oliveira *et al.* (2011). See Tab. 1 for tissue voucher numbers and associated GenBank numbers.

Sequences of each gene for each individual were aligned using default parameters in the Muscle (Edgar 2004) plugin for Geneious version 9.1 (Kearse *et al.*, 2012) A maximum likelihood (ML) topology was inferred with a partitioned RAxML analysis run through the CIPRES web server (Miller *et al.*, 2010) with *Leporinus brunneus* and *L. ecuadorensis* set as the outgroups. A random starting tree was used for the ML search with all other parameters set to default values. All ML analyses were performed under GTR + G since RAxML only applies this model (Stamatakis *et al.*, 2008). The robustness of the ML topology was tested with 1000 bootstrap replicates. Partitions were determined by Partitionfinder (Lanfear *et al.*, 2012) and parameters for each partition estimated using JModelTest2 (Darriba *et al.*, 2012). See Tab. 2 for partitions and individual models of evolution. A Bayesian topology was inferred using MrBayes 3.12 (Ronquist, Huelsenbeck, 2003) run through the CIPRES web server (Miller *et al.*, 2010). We performed 10 million generations, sampling a tree every 1000 generations. The distribution of log likelihood scores was examined in Tracer 1.5 (Rambaut, Drummond, 2007). We determined whether runs had reached convergence by checking to ensure that ESS scores exceeded 200 and that log likelihood scores had achieved stationarity. The first 10% of the posterior was disregarded as burnin after visualizing the posterior distribution in Tracer 1.5 (Rambaut, Drummond, 2007), with the remaining trees used to construct a maximum clade credibility tree.

Tab. 1. Voucher and GenBank numbers for tissues used in phylogenetic analysis.

	Tissue ID	Voucher ID	Basin	16s	Cytb	COX1	Rag1	Rag2	Myh6
Leporinus affinis	43695	LBP 12699	Araquaia	KY524562	KY524551	KY524537	KY524510	KY524523	KY524496
Leporinus altipinnis	24381	LBP 24381	Negro	MF285868	MF285876	-	MF285883	MF285887	MF285879
Leporinus brunneus	7575	AUM 53512	Oinoco	KY524560	KY524549	KY524535	KY524508	KY524521	KY524494
Leporinus brunneus	T09239	AUM 53512	Orinoco	MF285870	-	-	MF285884	MF285888	MF285881
Leporinus desmotes	2068	ANSP179650	Essequibo	KY524572	KY524548	KY524534	KY524507	KY524520	KY524493
Leporinus ecuadorensis	T13726	ECU12-10	Vinces	KY524569	KY524558	KY524544	KY524517	KY524530	KY524503
Leporinus ecuadorensis	T13727	ECU12-10	Vinces	MF285871	MF285875	MF285872	MF285885	MF285889	-
Leporinus enyae	V5274	AUM 43700	Oinoco	-	KY524559	KY524545	KY524518	KY524531	KY524504
Leporinus fasciatus	157_2	MHNG uncat	Nickerie	KY524490	KY524546	KY524532	KY524505	KY524519	KY524491
Leporinus fasciatus	NS61	ANSP 180321	Nanay	KY524565	KY524554	KY524540	KY524513	KY524526	KY524499
Leporinus fasciatus	22701	LBP 4248	Amazon	KY524561	KY524550	KY524536	KY524509	KY524522	KY524495
Leporinus fasciatus	157_8	MHNG uncat	Tapanahony	KY524571	KY524547	KY524533	KY524506	-	KY524492
Leporinus jatuncochi	PE10-164	OS 18325	Upper Amazon	KY524567	KY524556	KY524542	KY524515	KY524528	-
Leporinus jatuncochi	PE10-165	OS 18325	Upper Amazon	KY524568	KY524557	KY524543	-	KY524529	-
Leporinus jatuncochi	PE10-166	OS 18325	Upper Amazon	MF285869	-	MF285873	-	-	MF285880
Leporinus pearsoni	4124	ANSP 180841	Upper Amazon	MF285867	MF285877	MF285874	MF285882	MF285886	MF285878
Leporinus villasboasorum	T10752	ANSP 195954	Xingu	KY524564	KY524553	KY524539	KY524512	KY524525	KY524498
Leporinus villasboasorum	T8731	INPA 40521	Xingu	KY524563	KY524552	KY524538	KY524511	KY524524	KY524497

Tab. 2. Gene partitions and their models as selected by JModelTest2.

Gene and position	Partitions	Best-fit model
16s	1-592	GTR+G+I
COI 1st position	593-1415/3	TrN+G
COI 2nd position	594-1415/3	F8I
COI 3rd position	595-1415/3	GTR+G
Cytb 1st position	1416-2517/3	TrN+I
Cytb 2nd position	1417-2517/3	GTR+G
Cytb 3rd position	1418-2517/3	TrN+I
Myh6 1st position	2518-3286/3	GTR+G+I
Myh6 2nd position	2519-3286/3	GTR+I
Myh6 3rd position	2520-3286/3	HKY+G
Rag1 1st position	3287-4740/3	TVM+I+G
Rag1 2nd position	3288-4740/3	TVM+G
Rag1 3rd position	3289-4740/3	TVM+I+G
Rag2 1st position	4741-5770/3	TVM+G
Rag2 2nd position	4742-5770/3	TVM+G
Rag2 3rd position	4743-5770/3	TVM+G

Results

Meristic differentiation. With the important exception of circumpeduncular scale counts, the four geographically defined groups do not differ meristically (Tabs. 3-4). However, circumpeduncular scale counts vary from population to population, with some fixed at 14 or 16 scales, and others polymorphic. All specimens from the Orinoco, the Casiquiare canal, the upper Negro drainage, the middle and upper Xingu and upper Tapajós drainages (Fig. 2) have 16 circumpeduncular scales, while all specimens from the upper, middle and lower Amazon, including samples from the lower Xingu and the Jamanxim River (the latter of which is part of the Tapajós drainage) have 14. The specimens of *Leporinus desmotes* from the Essequibo drainage (including the paratype series at ANSP) are polymorphic for this character, with most specimens possessing either 14 (four specimens) or 16 scales (four specimens) around the caudal peduncle, and one specimen possessing 15. The holotype of

L. desmotes (ANSP 39324) possesses 16 circumpeduncular scales, and the holotype of *L. jatuncochi* (MSUM 5868) possesses 14. The same polymorphism occurs in specimens from the Araguaia and Tocantins rivers and tributaries, with 17 specimens possessing 14 and six possessing 16 scale rows around the caudal peduncle. Interestingly, sympatric specimens from the Essequibo and from the Araguaia-Tocantins have both distinct counts (*i.e.*, specimens from the same lot exhibit 14 and 16 scale rows around caudal peduncle), as in the paratype series of *L. desmotes* and in several lots from the Araguaia-Tocantins (*e.g.*, UNT 9095, INPA 1555). In this case, variation is not related to sex or size, as specimens of the same sex and size exhibit distinct scale counts.

Tab. 3. Meristic counts of *Leporinus enyae* and *L. villasboasorum* summarized as ranges followed by the mean ± 1 standard deviation in parentheses. Single values in a cell indicate invariant counts among the examined specimens for a given species.

	L. enyae (holotype)	*L. enyae*	*L. villasboasorum* (holotype)	*L. villasboasorum*
Number of specimens		27		7
Unbranched dorsal-fin rays	ii	ii	ii	ii
Branched dorsal-fin rays	10	10-11 (10 ± 1.9)	10	10
Unbranched anal-fin rays	ii	ii	ii	ii
Branched anal-fin rays	9	8-9 (8.6 ± 0.5)	8	8
Unbranched pectoral-fin rays	i	i	i	i
Branched pectoral-fin rays	16	16	16	15-16 (15.9 ± 0.4)
Unbranched pelvic-fin rays	i	i	i	i
Branched pelvic-fin rays	9	9	9	9
Upper principal caudal-fin rays	10	10	10	10
Lower principal caudal-fin rays	9	8-9 (8.9 ± 1.9)	9	9
Total lateral line scales	42	39-43 (40.9 ± 0.8)	41	38-45 (41 ± 2.2)
Upper transverse scales at dorsal-fin origin	6	6	6	6
Lower transverse scales at pelvic-fin origin	5	5	5	5
Lower transverse scales at anal-fin origin	5	5	5	5
Circumpeduncular scales	16	16	16	16
Predorsal scales	11	11-14 (12.9 ± 0.7)	13	12-15 (13 ± 0.9)
Dentary Teeth	3	3	3	3
Premaxilla Teeth	3	3	3	3
Vertebrae	38	38	38	38

Tab. 4. Meristic counts of *Leporinus desmotes* and *L. jatuncochi* summarized as ranges followed by the mean ± 1 standard deviation in parentheses. Single values in a cell indicate invariant counts among the examined specimens for a given species. *Represents data gathered from Ovchynnyk (1971).

	L. desmotes (holotype)	*L. desmotes*	*L. jatuncochi* (holotype)*	*L. jatuncochi*
Number of specimens		6		24
Unbranched dorsal-fin rays	ii	ii	Ii	ii
Branched dorsal-fin rays	10	10	10	10
Unbranched anal-fin rays	ii	ii	Ii	ii
Branched anal-fin rays	8	8	8	8-9 (8.3 ± 0.5)
Unbranched pectoral-fin rays	i	i	I	i
Branched pectoral-fin rays	16	16	16	15-16 (15.9 ± 0.3)
Unbranched pelvic-fin rays	i	i	-	i
Branched pelvic-fin rays	9	9	-	9
Upper principal caudal-fin rays	-	10	-	10
Lower principal caudal-fin rays	-	9	-	9
Lateral lines scales to anterior margin of hypural plate	-	34-37 (36 ± 1.1)	-	32-36 (34.3 ± 0.9)
Scales over hypural plate	-	6	-	5-6 (5.9 ± 0.3)
Total lateral line scales	41	40-42 (40.8 ± 0.8)	39	38-42 (40.2 ± 0.9)
Upper transverse scales at dorsal-fin origin	5	6	5	5-6 (5.6 ± 0.5)
Lower transverse scales at pelvic-fin origin	5	5	4.5	4-5 (4.6 ± 0.5)
Lower transverse scales at anal-fin origin	-	4-5 (4.7 ± 0.5)	-	4-5 (4.5 ± 0.5)
Circumpeduncular scales	16	14-16 (15.2 ± 1.0)	14	14
Predorsal scales	11	11-13 (12.7 ± 0.8)	11	12-14 (12.9 ± 0.64)
Dentary Teeth	3	3-4 (3.7 ± 0.04)	4*	3
Premaxilla Teeth	3	3-4 (3.7 ± 00.4)	4*	3
Vertebrae	-	38	-	38

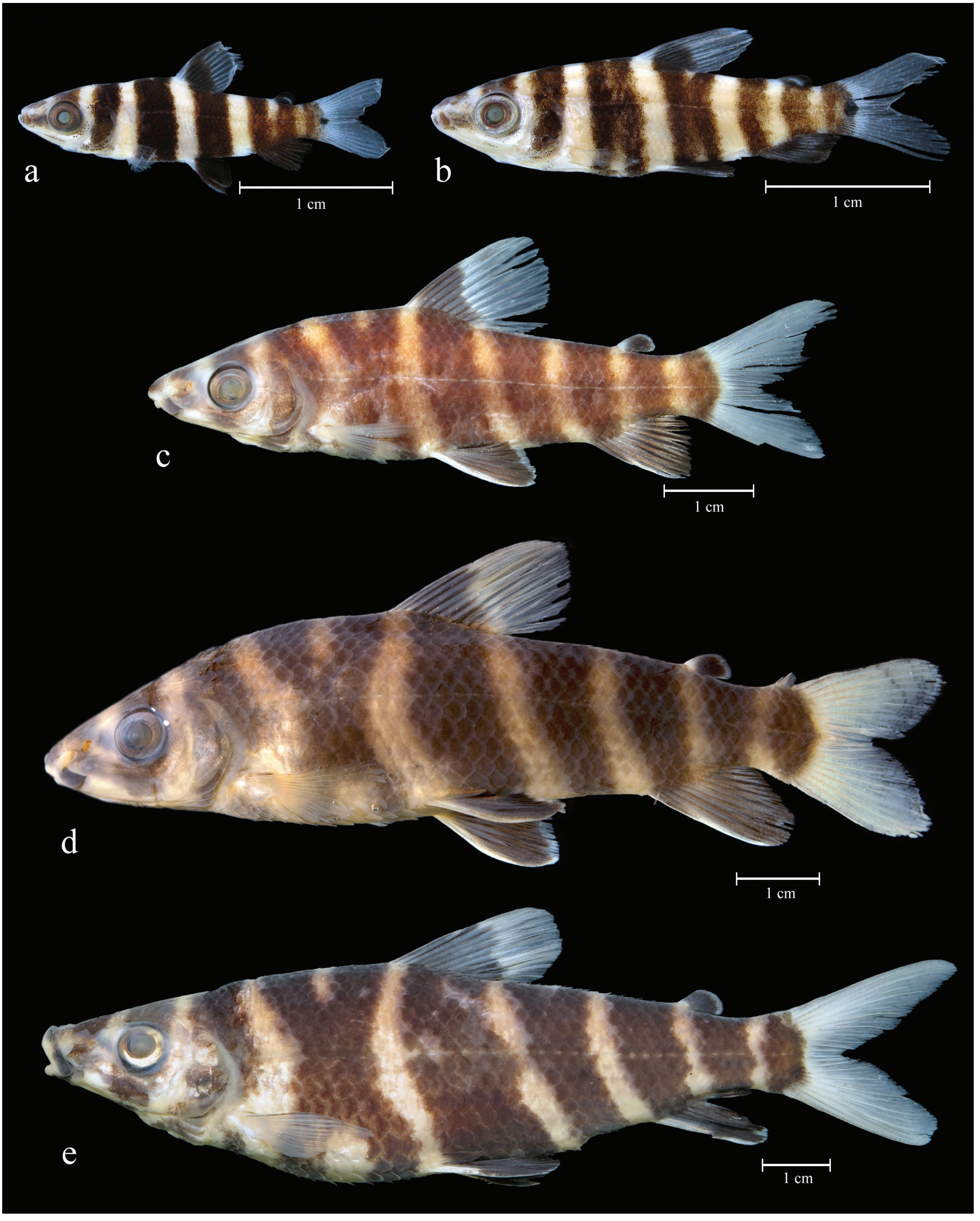

Fig. 2. Alcohol-preserved specimens of *Leporinus villasboasorum*: **(a)** paratype, MZUSP 100071, 19.5 mm SL, rio Teles Pires, Tapajós basin in Brazil, **(b)** paratype, MZUSP 100071, 24.9 mm SL, rio Teles Pires, Tapajós basin in Brazil, **(c)** paratype, MZUSP 91895, 62.0 mm SL, rio Culuene, Xingu basin in Brazil, **(d)** holotype, MZUSP 116530, 91.0 mm SL, rio Culuene, Xingu basin in Brazil, **(e)** MZUEL 7916, 109.5 mm SL, Juruena river, Tapajós basin in Brazil.

Morphometric differentiation. In the PCA of size-standardized variables, the first principal component primarily indexes the relative depth of the body, the length of the anal-fin base, the length of the caudal peduncle, and the elongation of the snout and anterior portion of the head (**S1** - Available only as online supplementary file accessed with the online version of the article at http://www.scielo.br/ni). Larger PC1 values relate to decreases in body depth and the length of the anal fin, with concomitant increase in the length of the caudal peduncle and the protrusion of the snout. The second component describes variation in the length of the dorsal- and anal-fin bases, as well as variation in body width. Larger PC2 values relate to longer fin bases, with corresponding decreases in separation of those fins from the adipose and pelvic-fin origins. Body width increases towards positive values of PC2. The third axis (not shown) is dominated by the length of the anal-fin base, with a substantial contribution of caudal peduncle depth and the distance between the dorsal-fin insertion and pelvic-fin origin.

In this morphospace, specimens from the Essequibo and upper Amazon drainages overlap substantially in body shape (Fig. 3), while those from the Xingu and Orinoco basins have obviously different centroids and overlap little with each other or with specimens from the Essequibo River (Fig. 3). The MANOVA for the first three Principal Components revealed statistically significant differences overall (Wilks' $\lambda = 0.9$, $p < 0.0001$). Statistically significant differences on at least one morphospace axis exist among all pairwise comparisons of groups, (Tab. 5) with the specimens from the Xingu basin particularly divergent from the other three groups along PC1, and those from the Orinoco basin and Essequibo basin diverging in opposite directions on PC2. The most similar groups are those from the upper Amazon and Essequibo, which are indistinguishable on PC1, and only slightly separated ($p = 0.025$) on PC2.

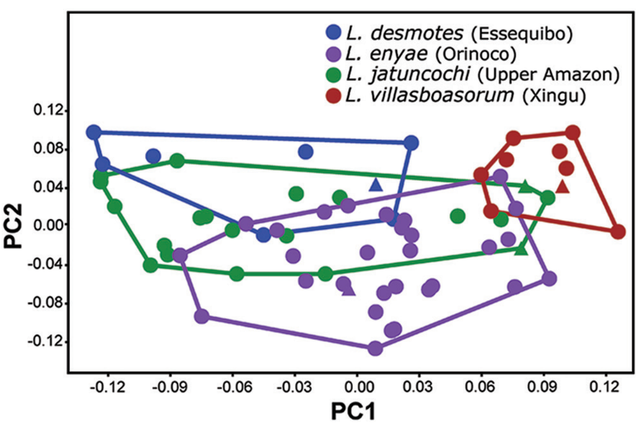

Fig. 3. Scatterplot of principal component 1 (PC1) *versus* principal component 2 (PC2) in the size corrected morphospace for *Leporinus villasboasorum* (brown), *L. enyae* (purple), *L. desmotes* (blue), and *L. jatuncochi* (green) showing separation of species centroids, but partial overlap of morphologies. Triangles represent individuals used in genetic analyses.

Tab. 5. P-values for post-hoc Tukey's pairwise comparisons on the principal component scores from the linear morphometrics for species of *Leporinus*. PC1 p-values are above the diagonal and PC2 p-values are below the diagonal. Statistically significant differences ($P < 0.05$) are marked with an asterisk.

	L. jatuncochi	*L. desmotes*	*L. enyae*	*L. villasboasorum*
	(Upper Amazon)	(Essequibo)	(Orinoco)	(Xingu)
L. jatuncochi	-	0.975	0.016*	0.000*
L. desmotes	0.025*	-	0.044*	0.000*
L. enyae	0.002*	0.000*	-	0.006*
L. villasboasorum	0.018*	0.999	0.000*	-

A morphospace constructed from just the upper Amazon and Essequibo specimens fails to reveal any major morphological differences between them, Wilks' λ =.76, $p = 0.08$ (Fig. 4). In this morphospace, the Essequibo specimens with 14 (two specimens) *versus* 16 (four specimens) circumpeduncular scales separate slightly along PC1, with the specimens with 14 circumpeduncular scales having a larger distance between the dorsal-fin origin and dorsal-fin insertion to the pelvic-fin origin than the specimens with 16 circumpeduncular scales. However, the small sample sizes make it unclear whether this separation reflects biological reality, or a sampling artifact (Fig. 4).

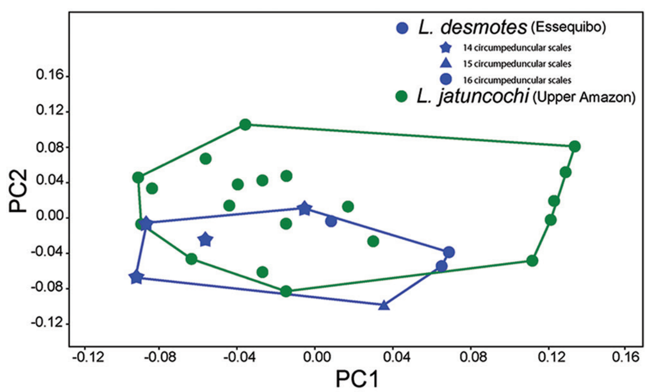

Fig. 4. Scatterplot of principal component 1 (PC1) *versus* principal component 2 (PC2) for the analysis containing only *Leporinus desmotes* (blue), and *L. jatuncochi* (green). *Leporinus desmotes* symbols exhibit variation in circumpeduncular scale counts. Stars are specimens with 14 circumpeduncular scales, circles are specimens with 16 circumpeduncular scales, and the triangle represents the specimen with 15 circumpeduncular scales.

Genetic differentiation. Results from a maximum likelihood and Bayesian phylogenetic analysis of six genes (16s, COI, Cytb, Myh6, Rag1, Rag2) appear in Fig. 5. That analysis recovers a monophyletic *Leporinus desmotes* complex (100 bootstrap, 1.0 posterior probability), and suggest that the Essequibo and Upper Amazon specimens are closely related (100 bootstrap, 1.0 posterior probability, 99.6% sequence similarity), with that clade sister to the specimen from the Orinoco (74 bootstrap, .99 posterior probability). The specimens from the Xingu separate from all others at the basal split within the complex. The relatively low support values for the placement of the Orinoco specimen suggest that additional sampling could easily alter that result, and that this phylogeny should not be considered canonical with respect to interspecific relationships within the complex.

That uncertainty notwithstanding, the sequenced individuals separate into three groups, each of which is genetically distinct and subtended by a long branch. The average pairwise distances between the specimens from the Xingu basin, that from the Orinoco basin, and the clade containing the specimens from the Essequibo and upper Amazon drainage is 5.3% for the mtDNA and 0.85% for the nDNA. Though the sample sizes are too low to be conclusive on their own, this level of differentiation suggests the presence of at least three distinct species under a phylogenetic species concept. Similar levels of differentiation have been found among other closely related species in *Leporinus* (Avelino *et al.*, 2015), as well as many other Neotropical fish groups (Gomes *et al.*, 2015; Pugedo *et al.*, 2016).

Overall, specimens from the Xingu and Orinoco drainages each proved statistically separable from all other populations on morphometric grounds, and easily diagnosable from all specimens from the upper Amazon River and most specimens from the Essequibo, Araguaia and Tocantins rivers via circumpeduncular counts. Furthermore, the Xingu and Orinoco samples sequenced proved genetically divergent from each other and from the available samples from the upper Amazon and Essequibo. Taken together, these data indicate that that Xingu and Orinoco populations represent novel species, which we describe formally below.

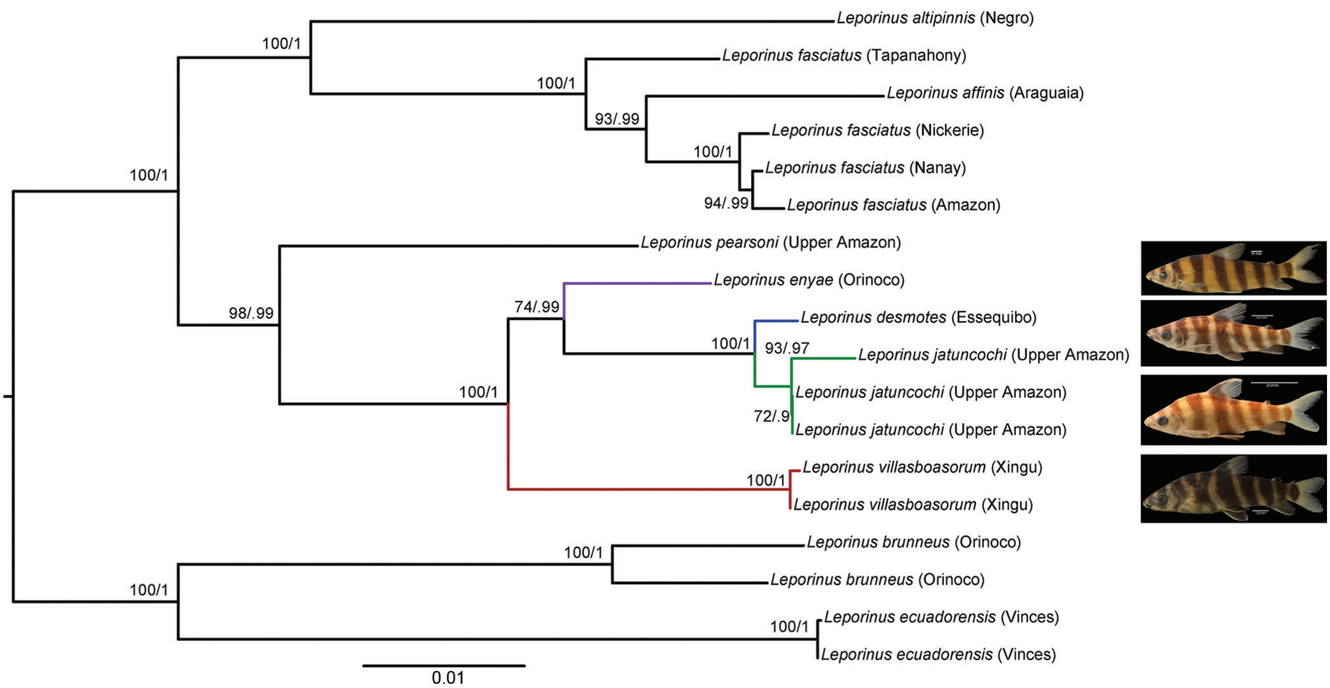

Fig. 5. Phylogenetic relationships within the *Leporinus desmotes* species complex showing the ML tree. Node values represent bootstrap support and posterior probabilities, respectively.

Leporinus villasboasorum, new species

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Figs. 2, 6-7; Tabs. 3 and 6

Leporinus desmotes - Camargo *et al.*, 2004:132 (in part; Iriri and middle Xingu, checklist). -Camargo *et al.*, 2005:12 (rio Parazinho, tributary of rio Curuá, checklist). -Camargo, Giarrizo, 2007:3 (in part; unspecific record for the Xingu basin, checklist). -Birindelli, Britski, 2009:8 (rio Culuene, Campinápolis, Mato Grosso State; comparative material). -Oliveira *et al.*, 2012:5 (rio Iriri, report of sympatry with *Leporinus tigrinus*, *Leporellus* cf. *vittatus*, among other non-anostomid fishes). -Birindelli, Britski, 2013:1159 (rio Culuene, Campinápolis, Mato Grosso State; comparative material).

Holotype. MZUSP 116530, 1, 91.0 mm SL, Brazil, Mato Grosso, Campinápolis, rio Culuene, tributary of rio Xingu, at cofferdam of PCH Paranatinga 2, 13°51’01”S 53°15’33”W, 2 Jul 2007, L. M. Sousa & A. Netto-Ferreira.

Tab. 6. Linear morphometrics for all examined species summarized as observed ranges, with mean ± standard deviation in parentheses. Measures 1 to 29 are percentages of SL, measures 30-37 are percentages of head length.

		L. enyae (holotype)	*L. enyae* (paratypes)	*L. villasboasorum* (holotype)	*L. villasboasorum* (paratypes)	*L. desmotes*	*L. jatuncochi*
	Standard length (mm)	145.6	37.7 - 181.4 (110.4 ± 39.9)	91.0	69.9 - 127.9 (97.7 ± 19.6)	56.4 - 170.8 (96.2 ± 46.5)	22.8 - 84.8 (58.5 ± 19.3)
1	Snout to dorsal-fin origin	43.4	41.9 - 47.2 (44.3 ± 1.3)	46.7	43.6 - 46.7 (45.3 ± 1.1)	42.6 - 46.0 (44.5 ± 1.1)	41.8 - 49.2 (44.8 ± 1.9)
2	Snout to adipose-fin origin	82.0	78.7 - 83.7 (81.4 ± 1.3)	80.9	80.1 - 82.8 (81.0 ± 0.9)	80.1 - 82.9 (81.5 ± 0.9)	78.6 - 83.0 (81.0 ± 1.1)
3	Snout to anal-fin origin	78.8	75.4 - 79.7 (77.9 ± 1.2)	76.9	74.6 - 78.0 (76.3 ± 1.2)	76.8 - 79.5 (77.9 ± 0.9)	75.1 - 80.5 (77.0 ± 1.4)
4	Snout to pelvic-fin origin	46.2	45.4 - 49.5 (47.1 ± 1.0)	47.8	45.9 - 50.0 (48.4 ± 1.4)	45.8 - 50.1 (48.4 ± 1.5)	44.8 - 52.1 (47.5 ± 2.4)
5	Snout to pectoral-fin origin	24.3.	22.3 - 28.2 (25.2 ± 1.2)	27.2	24.7 - 28.6 (27.3 ± 1.3)	24.0 - 27.3 (25.8 ± 1.4)	25.1 - 33.4 (27.6 ± 2.2)
6	Dorsal-fin origin to pectoral-fin origin	27.9	25.4 - 30.5 (27.8 ± 1.2)	28.2	26.1 - 28.8 (27.4 ± 0.9)	27.3 - 30.9 (29.0 ± 1.3)	21.8 - 30.3 (27.6 ± 1.9)
7	Dorsal-fin origin to pelvic-fin origin	26.4	22.1 - 28.3 (25.6 ± 1.4)	25.3	22.7 - 25.3 (24.4 ± 0.9)	23.1 - 29.7 (26.7 ± 2.1)	22.2 - 30.1 (27.1 ± 1.9)
8	Dorsal-fin origin to anal-fin origin	43.8	40.1 - 43.8 (42.1 ± 1.0)	40.6	39.1 - 41.3 (40.3 ± 0.9)	40.2 - 46.2 (43.1 ± 1.9)	38.3 - 44.1 (42.2 ± 1.5)
9	Dorsal-fin origin to anal-fin insertion	49.6	33.9 - 54.4 (47.6 ± 3.2)	46.9	44.5 - 48.7 (46.3 ± 1.3)	46.5 - 52.7 (49.7 ± 2.0)	43.9 - 51.0 (48.3 ± 2.1)
10	Dorsal-fin origin to posterior margins of the hypurals	61.1	56.0 - 62.4 (59.5 ± 1.4)	58.7	56.5 - 60.5 (59.0 ± 1.3)	58.0 - 62.8 (60.3 ± 1.5)	55.3 - 62.2 (59.7 ± 1.7)
11	Dorsal-fin origin to adipose-fin origin	41.4	36.2 - 42.6 (39.8 ± 1.5)	38.0	36.7 - 39.4 (38.4 ± 0.9)	36.6 - 43.1 (40.3 ± 1.9)	35.7 - 42.1 (39.7 ± 1.6)
12	Length of dorsal-fin base	13.7	11.7 - 15.5 (13.9 ± 0.8)	15.5	14.4 - 15.6 (15.0 ± 0.4)	15.4 - 16.9 (16.0 ± 0.5)	13.8 - 17.0 (15.6 ± 0.9)
13	Dorsal-fin insertion to pelvic-fin origin	24.0	20.9 - 26.7 (23.8 ± 1.3)	25.0	22.1 - 25.0 (23.1 ± 0.9)	22.3 - 28.2 (24.9 ± 1.7)	20.4 - 27.9 (24.8 ± 2.1)
14	Dorsal-fin insertion to adipose-fin origin	28.1	22.9 - 28.7 (26.1 ± 1.5)	20.8	20.8 - 26.5 (23.7 ± 1.6)	21.7 - 26.6 (24.1 ± 1.5)	20.2 - 26.9 (24.2 ± 1.7)
15	Dorsal-fin insertion to anal-fin origin	30.9	27.3 - 31.3 (29.3 ± 1.1)	27.7	25.9 - 29.3 (27.1 ± 1.1)	25.2 - 31.5 (28.4 ± 1.9)	24.5 - 30.1 (27.9 ± 1.8)
16	Dorsal-fin insertion to anal-fin insertion	35.7	31.7 - 36.4 (34.3 ± 1.2)	31.4	30.4 - 33.4 (31.6 ± 1.0)	30.0 - 35.5 (33.6 ± 1.8)	29.3 - 36.0 (33.2 ± 1.8)
17	Adipose-fin origin to anal-fin origin	17.3	15.1 - 19.1 (16.9 ± 1.0)	17.1	16.3 - 17.4 (17.0 ± 0.4)	17.9 - 19.8 (18.7 ± 0.7)	15.9 - 20.8 (18.3 ± 1.2)
18	Adipose-fin origin to anal-fin insertion	13.0	12.1 - 14.8 (13.1 ± 0.7)	12.5	12.5 - 13.6 (13.1 ± 0.4)	13.9 - 15.6 (14.7 ± 0.6)	11.6 - 15.6 (14.2 ± 1.1)
19	Adipose-fin origin to posterior margins of the hypurals	19.9	18.3 - 22.1 (19.7 ± 0.8)	20.8	19.7 - 21.8 (20.6 ± 0.6)	18.6 - 20.9 (20.2 ± 0.7)	18.3 - 21.8 (20.0 ± 1.0)
20	Length of anal-fin base	9.5	8.0 - 11.3 (9.4 ± 0.9)	9.3	9.0 - 10.0 (9.3 ± 0.4)	9.0 - 12.1 (10.5 ± 1.1)	10.0 - 13.2 (11.6 ± 1.0)
21	Anal-fin insertion to posterior margin of hypurals	16.3	13.9 - 17.2 (15.4 ± 0.8)	16.7	15.1 - 18.4 (16.7 ± 1.1)	13.9 - 16.1 (14.8 ± 0.6)	12.2 - 16.2 (14.8 ± 1.1)
22	Pelvic-fin origin to anal-fin origin	33.4	29.0 - 36.3 (32.2 ± 1.6)	29.5	27.5 - 31.4 (29.2 ± 1.2)	28.7 - 34.4 (30.7 ± 2.1)	24.8 - 34.5 (30.6 ± 2.5)
23	Pelvic-fin origin to adipose-fin origin	42.0	36.7 - 43.7 (40.4 ± 1.5)	38.4	36.3 - 38.6 (37.7 ± 0.9)	38.5 - 43.4 (40.2 ± 1.7)	34.8 - 43.2 (40.1 ± 1.9)
24	Pelvic origin to posterior margin of hypurals	58.5	53.2 - 58.5 (55.9 ± 1.2)	55.3	53.7 - 55.7 (54.6 ± 0.8)	52.9 - 57.1 (55.0 ± 1.6)	50.8 - 57.5 (55.3 ± 2.0)
25	Pelvic-fin origin to pectoral-fin origin	22.5	20.4 - 24.9 (22.4 ± 1.1)	22.7	20.9 - 23.4 (22.5 ± 0.9)	21.5 - 24.9 (23.1 ± 1.1)	18.4 - 26.7 (21.1 ± 1.8)
26	Greatest body depth	26.0	23.2 - 28.7 (25.4 ± 1.4)	24.4	23.0 - 24.9 (24.0 ± 0.6)	25.1 - 28.9 (26.7 ± 1.3)	24.2 - 29.7 (27.0 ± 1.6)
27	Greatest body width	12.2	10.3 - 13.9 (11.9 ± 1.0)	12.6	11.2 - 13.2 (12.6 ± 0.7)	11.3 - 15.5 (13.2 ± 1.5)	10.8 - 14.2 (12.4 ± 1.0)
28	Caudal-peduncle depth	9.4	8.1 - 10.9 (9.5 ± 0.6)	9.7	9.1 - 10.3 (10.0 ± 0.4)	10.1 - 11.2 (10.6 ± 3.7)	8.6 - 11.6 (10.4 ± 0.8)
29	Head length	21.6	21.6 - 26.3 (23.4 ± 1.0)	24.8	24.1 - 26.0 (25.1 ± 0.7)	22.5 - 26.3 (24.9 ± 1.5)	23.9 - 30.1 (26.4 ± 1.9)
30	Preopercle length	82.1	76.1 - 83.7 (80.8 +- 1.8)	79.7	78.8 - 82.6 (80.0 +- 1.2)	77.9 - 82.0 (79.8 ± 1.2)	72.1 - 82.9 (78.2 ± 2.7)
31	Snout to anterior margin of the eye	43.0	37.2 - 43.9 (41.4 +- 1.5)	38.7	38.7 - 43.6 (40.8 +- 1.9)	36.8 - 42.4 (40.8 ± 1.9)	32.6 - 45.7 (39.1 ± 3.4)
32	Head depth	78.8	69.9 - 78.9 (73.9 +- 2.7)	73.6	71.2 - 80.9 (75.1 +- 3.1)	67.8 - 78.7 (72.8 ± 3.6)	60.8 - 78.4 (70.9 ± 4.5)
33	Snout depth	53.2	44.5 - 53.2 (47.9 +- 2.2)	49.1	47.8 - 56.5 (50.0 +- 3.0)	42.9 - 51.7 (47.5 ± 3.1)	42.3 - 49.7 (45.5 ± 2.4)
34	Jaw length	24.1	20.1 - 26.8 (23.5 +- 1.9)	22.2	21.1 - 25.1 (23.0 +- 1.4)	20.7 - 27.2 (23.4 ± 2.7)	18.4 - 26.9 (21.5 ± 2.2)
35	Eye diameter	27.4	23.7 - 32.9 (28.1 +- 2.7)	28.8	22.7 - 29.7 (26.9 +- 2.1)	25.1 - 34.9 (29.5 ± 3.1)	27.1 - 37.0 (31.4 ± 3.1)
36	Interorbital width	43.3	35.2 - 44.7 (40.6 +- 2.2)	38.9	35.8 - 41.7 (38.7 +- 1.8)	40.9 - 47.8 (43.9 ± 2.5)	35.8 - 44.1 (39.7 ± 2.5)
37	Snout to supraoccipital crest	92.2	82.9 - 1.0 (87.6 +- 4.0)	93.1	80.9 - 93.1 (88.1 +- 4.0)	79.4 - 86.7 (83.5 ± 2.6)	76.3 - 89.4 (82.8 ± 3.5)

Fig. 6. Live specimens of *Leporinus villasboasorum*: **(a)** MZUSP 91895, 70.2 mm SL, paratype, rio Culuene, Xingu basin in Brazil, photographed by Leandro Sousa, **(b)** INPA 40080 , 56.0 mm SL, rio Xingu at Altamira, Brazil, photographed by Mark Sabaj.

Fig. 7. Rio Culuene, tributary of Xingu river in Brazil, at the type locality of *Leporinus villasboasorum*. The river stretch herein illustrated is currently dried by the diversion of the river channel due to the construction of the Paranatinga 2 hydroelectric dam.

Paratypes. All from Brazil (Xingu basin). ANSP 195954, 1, 124.1 mm SL, Pará, Altamira, rio Xingu at middle of Volta Grande, 03°33’41”S 51°51’29”W, 10 Mar 2014, M. H. Sabaj-Pérez *et al.* INPA 30985, 1, 80.7 mm SL, Pará, Altamira, rio Iriri, tributary of rio Xingu, 03°50’30”S 52°52’20”W, H. López-Fernández *et al.* MZUEL 17000, 3, 98.1-115.5 mm SL, 1 sk, 96 mm SL, 1 CS, 90.6 mm SL, Mato Grosso, Campinápolis, rio Culuene, at future area of PCH Paranatinga 2, 13°51’01”S 53°15’33”W, 21 Aug 2006, J. L. Birindelli *et al.* MZUSP 88045, 1, 117.9 mm SL, Mato Grosso, Gaúcha do Norte, rio Culuene, 13°30'52"S 53°5'34"W, J. L. Birindelli *et al.* MZUSP 88046, 1, 99.3 mm SL, Mato Grosso, Canarana, ribeirão Água Limpa, tributary of rio Sete de Setembro, 13°28'7"S 52°14'54"W, J. L. Birindelli *et al.* MZUSP 88047, 1, 95.6 mm SL, Mato Grosso, Gaúcha do Norte, rio Curisevo, tributary of rio Culuene, 13°2'5"S 53°25'19"W, C. R. Moreira *et al.* MZUSP 88048, 1, 75.4 mm SL, Mato Grosso, Gaúcha do Norte, rio Batovi, 13°14'46"S 54°01'30"W, J. L. Birindelli *et al.* MZUSP 88050, 7, 133.7-147.2 mm SL, Mato Grosso, Paranatinga, rio Jabotá, tributary of rio Ronuro, 12°49'19"S 54°09'24"W, J. L. Birindelli *et al.* MZUSP 89730, 9, 100.0-119.0 mm SL, Mato Grosso, Campinápolis, rio Culuene, 13°51'01"S 53°15'33"W, A. Akama & J. L. Birindelli. MZUSP 89803, 1, 93.1 mm SL, Mato Grosso, Paranatinga, rio Sucuri, tributary of rio Culuene, 13°55'40"S 53°17'10"W, A. Akama & J. L. Birindelli. MZUSP 91895, 15, 62.2-130.4 mm SL, 1 sk, 83.0 mm SL, 1 CS, 102.0 mm SL, Mato Grosso, Campinápolis, rio Culuene, at future area of PCH Paranatinga 2, 13°51'01"S 53°15'33"W, 21 Aug 2006, J. L. Birindelli *et al.* MZUSP 94099, 2, 96.1 mm SL, Mato Grosso, Paranatinga, rio Culuene, 13°30'53"S 53°05'40"W, J. L. Birindelli *et al.* MZUSP 94868, 7, 69.9-127.9 mm SL, collected with holotype. MZUSP 98149, 3, 116.4-117.5 mm SL, Mato Grosso, Campinápolis, rio Culuene at Cachoeira do Adelino, 13°47'50"S 53°14'46"W, F. C. T. Lima *et al.* MZUSP 98111, 2, 130.5-133.3 mm SL, Mato Grosso, Campinápolis, rio Culuene, 13°51'01"S 53°15'33"W, F. C. T. Lima *et al.* MZUSP 105865, 1, 113.6 mm SL, Pará, Altamira, rio Iriri, tributary of rio Xingu, 03°48'49"S 52°38'6"W, UFPA. MZUSP 107527, 1, 132.5 mm SL, Pará, Altamira, rio Xingu at Caitucá, 03°33'48"S 51°51'49"W, UFPA. OS 20074, 2, 98.4-109.8 mm SL, Brazil, Mato Grosso, Campinápolis, rio Culuene, tributary of rio Xingu, at cofferdam of PCH Paranatinga 2, 13°51'01"S 53°15'33"W, 2 Jul 2007, L. M. Sousa & A. Netto-Ferreira. OS 20075, 2, 75.1-124.2 mm SL, collected with holotype.

Non-type specimens. All from Brazil (Tapajós basin). MZUEL 7916, 1, 109.5 mm SL, Mato Grosso, Brasnorte, tributary of rio Norato, tributary of rio do Sangue, a tributary of rio Juruena, 12°11'13"S 57°59'33"W, 31 Aug 2013, J. L. O. Birindelli *et al.* MZUSP 63050, 1, 117.6 mm SL, Mato Grosso, Paranatinga, rio Teles Pires, 14°27'34"S 54°37'15"W, F. Machado & R. Calegari. MZUSP 95857, 81.7-101.5 mm SL, Mato Grosso, Itaúba, rio Teles Pires, 10°58'30"S 55°44'3"W, 1 Oct 2007, J. L. Birindelli & P. Hollanda Carvalho. MZUSP 96609, 1, 88.4 mm SL, Mato Grosso, Peixoto de Azevedo, rio Peixoto de Azevedo, tributary of rio Teles Pires, 10°13'14"S 54°58'02"W, J. L. Birindelli *et al.* MZUSP 98671, 1, 79.7 mm SL, Mato Grosso, Paranaíta, rio Teles Pires, 09°19'28"S 56°46'42"S, M. V. Loeb & A. de Castro. MZUSP 100071, 5, 19.5-28.7mm SL, Mato Grosso, Paranaíta, Rio Teles Pires, 9°24'5"S 56°33'49"W, 16 Jun 2008, L.M. Sousa & A.L. Netto-Ferreira.

Diagnosis. *Leporinus villasboasorum* can be separated from all other members of *Leporinus* except *L. desmotes*, *L. jatuncochi*, and *L. enyae* by possession of laterally compressed, elongate (more than twice as long as the second dentary tooth) tusk-like symphyseal dentary teeth (Fig. 1b), *versus* the more truncate conical or incisiform teeth (less than twice as long as the second dentary tooth) typical of other members of *Leporinus* (Fig. 1c), and from all other members of *Leporinus* except *Leporinus bleheri*, *L. desmotes*, *L. enyae*, *L. jatuncochi*, and *L. yophorus* by a color pattern on the head and trunk consisting of nine dark bars, some of which fork dorsally or ventrally, the fifth of which continues onto the dorsal and pelvic fins, *versus* various other color patterns in the approximately 90 other described species of *Leporinus*. It separates most easily from *Leporinus jatuncochi* and some specimens of *L. desmotes* by the possession of 16, *versus* 14 circumpeduncular scales. It separates from *Leporinus enyae* by having the dark bar anterior to the dorsal fin well-divided dorsally, *versus* having that bar undivided or barely divided dorsally. It is most similar in meristics and coloration to specimens of *Leporinus desmotes* with 16 circumpeduncular scales, but can be separated from those specimens morphometrically. Of the numerous morphometrics that differ in mean values between *Leporinus villaboasorum* and *Leporinus desmotes*, the most diagnostic are the shallower body depth in the former (23.0-24.9% SL *versus* 25.1-28.9% SL) and the shorter distance from the pelvic-fin origin to adipose-fin origin (36.3-38.6% SL *versus* 38.5-43.4% SL) with the regression lines differing greatly between the species (Fig. 8).

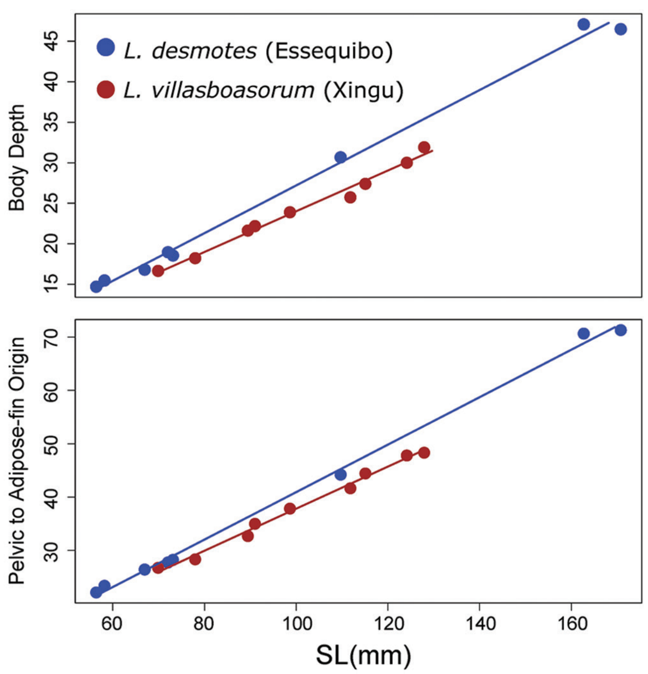

Fig. 8. Regressions of body depth and the distance between the pelvic-fin and adipose-fin origins against SL for *Leporinus desmotes* (blue) and *L. villasboasorum* (brown) showing different slopes.

Description. Holotype and paratype meristic values in Tab. 3, and morphometric values in Tab. 6. Body fusiform, elongate, slender, slightly compressed, deepest and widest at dorsal origin. Slight keel anterior of dorsal insertion and posterior to supraoccipital crest, all other margins of body gently rounded. Caudal peduncle compressed and equally long as deep. Head conical, compressed slightly dorsally and more so ventrally. Dorsal surface of head straight and inclined in lateral profile. Anterior profile of head forms a rounded point. Head widest at back of opercle. Eye rounded and laterally placed. Anterior nostril tubular, flared at distal end, positioned just anterior of second black transverse bar on head and overhanging the upper lip. Posterior nostril in form of sharply upturned slit positioned slightly posterior to anterior nostril at angle paralleling angle of lateral profile of head. Mouth small and subterminal. Lips fleshy, thick with fleshy, deeply-cleft lamellae. Upper lip with two series of lamellae, outer series longer than inner. Bottom lip with three or more series of lamellae much shorter than those of top lip and irregular in pattern, with outer series terminating on either side with a deep-cleft narrow fleshy lobe. Upper teeth three on each premaxilla, broader than the lower teeth and slightly spoon shaped, vaguely tricuspid and curving faintly posteriorly, with lateral teeth on smaller than those more medial. Lower teeth three on each dentary in number with lateral teeth much smaller than symphyseal. Symphyseal teeth long, pointed, laterally compressed and upward curving. Gill openings restricted. Opercle and preopercle smooth, with opercular flap pronounced and extending posteriorly from operculum. Four branchiostegal rays on each side.

Scales almost uniformly large with only slightly smaller scales in predorsal and ventral regions. Lateral line well defined, complete and straight with simple well-defined tubes. Pointed sheath scale twice as long as fin base on pelvic, starting at pelvic origin and pointing posteriorly.

Dorsal-fin origin located about halfway between snout tip and adipose origin. Pelvic-fin insertion located at vertical through origin of seventh branched dorsal-fin ray. Adipose-fin origin located at vertical through origin of third branched anal fin ray. Distal end of posterior branched anal-fin ray located at vertical through shallowest point of caudal peduncle. Dorsal- and pectoral-fins sharply falcate, all other fins come to slightly rounded points. First unbranched fin ray about half as long as first branched fin ray, with first branched fin ray being the longest, on both dorsal- and anal-fins. Caudal-fin deeply forked. Vent located anterior of anal origin about one-third the distance between anal origin and pelvic insertion.

Coloration in alcohol. Ground color white to brownish tan, weakly countershaded. Nine well-defined dark black transverse bars encircling head and trunk in specimens larger than 30 mm SL, eight such bars in small juveniles. Head with one dark bar on top of snout, one dark stripe running from tip of lower jaw, through end of maxillary bone, to anterior margin of orbit, conspicuously present in specimens of 30 mm SL or less, and slightly less conspicuous and distinctly arranged in larger specimens (with faint connections to the second dark bar). Head with one dark bar extending from dorsalmost portion of head (between frontals and parietals) to dorsal margin of eye; bar extended below ventral margin of eye only in specimens of 50 mm SL or more. Bars on main body slope slightly toward posterior from dorsal to ventral. Trunk with six dark bars in specimens of 30 mm SL or less and with seven in larger specimens. Variation in bar number stems from division of bar dorsal to pelvic fin over ontogeny. First dark bar of trunk encompasses opercle and much of the isthmus with a slight ventral division in line with gill opening and black resuming in space between pectoral-fins ventrally. Second dark bar of body between head and dorsal-fin; bar wide and undivided in specimens of approximately 20 mm SL, bar wide and only slightly divided into two parallel bars in specimens of around 25 mm SL, bar completely dorsally and ventrally shaped as an "X" in specimens of 60 mm SL or larger. Third and fourth dark bar united into a single bar in specimens of 20 mm SL, divided dorsally and ventrally in specimens of 25 mm SL, and completely divided into two bars in specimens larger than 60 mm SL. Third dark bar extended on base on dorsal-fin rays, forming a dark triangle, with anteriormost rays darker than posteriormost; and extended on pelvic-fin. Pelvic-fin completely dark, except anteriormost tip, in specimens of 25 mm SL or less; pelvic-fin dark except for anteriormost tip, first two unbranched rays and posterior margin in larger specimens. Fifth dark bar in front of adipose fin and extended to base of four to six anteriormost rays of anal-fin. Sixth dark bar running from posterior portion of adipose to posterior portion of anal-fin. Adipose-fin dark except for middle portion in specimens of 25 mm SL or less, and dark except for insertion and distal margin in larger specimens. Seventh dark bar covering posterior third of caudal peduncle. Specimens with 25 mm SL or less with a dark semicircular bar extended on base of caudal-fin rays, and a conspicuous dark spot on base of middle caudal-fin rays. Caudal-fin generally dusk with a clear semicircular bar anteriorly in specimens of 25 mm SL or less; and hyaline in larger specimens.

Coloration in life. Body yellow to brownish. Patterns of dark bars otherwise as described for preserved specimens. Dorsal margin of maxilla dark, with coloration extending posteriorly to vertical through posterior margin of outer fleshy lamellae of lower lip. Coloration faintly connecting dorsally to the dark bar through nares with only slight lightening in color of space between. Lips generally yellow with darkening of dorsal edge of upper lip and dark black on both sides of upper lip.

Geographical distribution. *Leporinus villasboasorum* occurs throughout the middle and upper Xingu drainage, from Volta Grande rapids near Belo Monte, downstream of the city of Altamira in Pará State to the headwaters of the Xingu River in Mato Grosso State. It also occurs in the Teles Pires and Juruena rivers, which are tributaries of the upper Tapajós River, in Mato Grosso State, Brazil (Fig. 9).

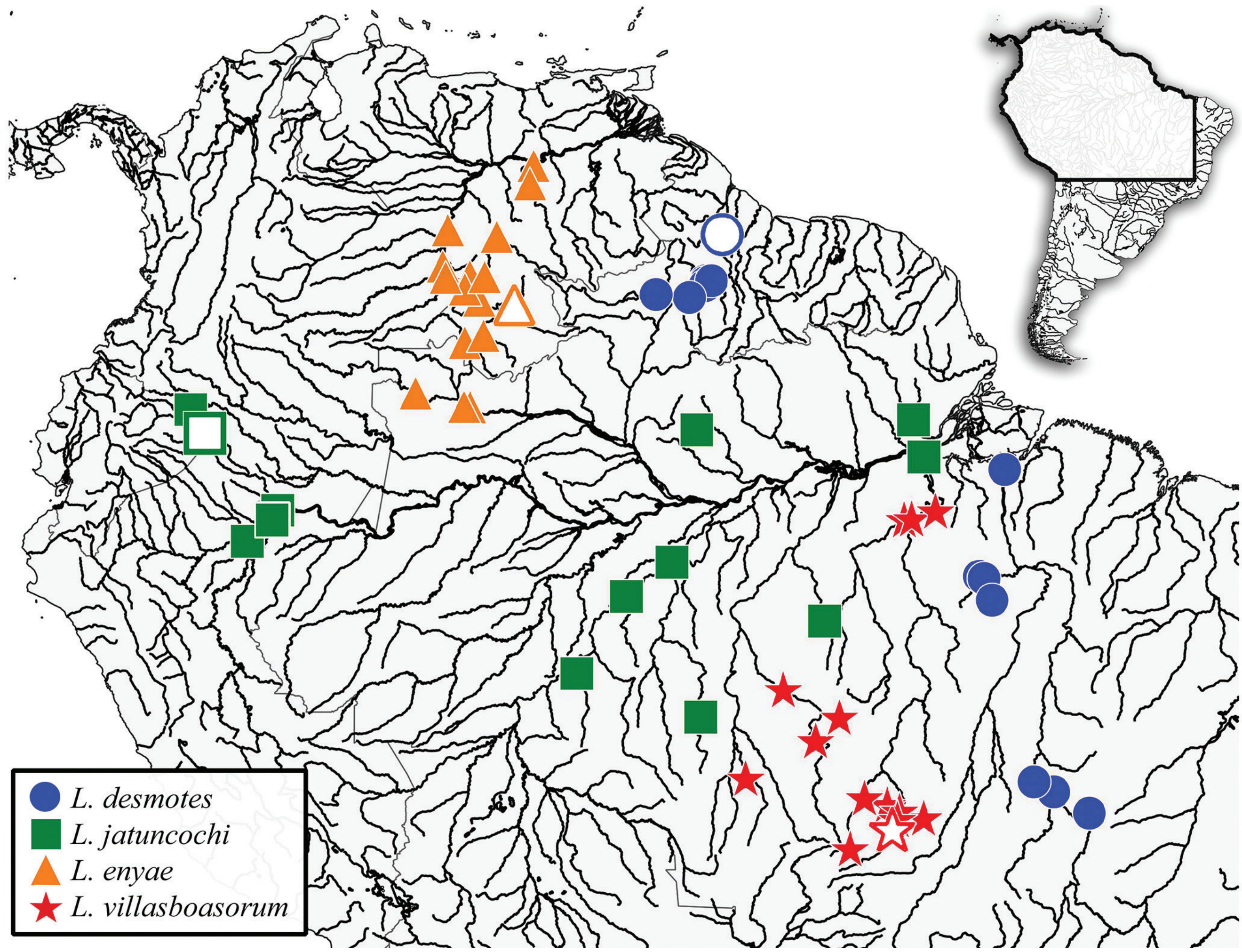

Fig. 9. Map of South America showing the distribution of *Leporinus desmotes* (blue circles), *L. enyae* (orange triangles), *L. jatuncochi* (green squares), *L. villasboasorum* (red stars). Type localities indicated by open symbols.

Etymology. Named in honor of Orlando, Cláudio and Leonardo Villas-Bôas, in recognition of their pioneering efforts to conserve and protect the rio Xingu's marvelous biodiversity, of which *Leporinus villasboasorum* forms part. A noun in the genitive case.

Conservation status. *Leporinus villasboasorum* is relatively frequent and abundant in the Xingu (520,300 km^2) and Tapajós (489, 628 km^2) river basins. It is widespread throughout the both basins and the species can be categorized as Least Concern (LC) according to the International Union for Conservation of Nature (IUCN) categories and criteria (IUCN Standards and Petitions Subcommittee, 2016), as the species occurs in several areas of preservation priority, such as indigenous parks.

Remarks. *Leporinus villasboasorum* occurs in the middle and upper Xingu and in the upper Tapajós basins. Since the Xingu and Tapajós basins are nowadays not connected it is possible that future more detailed studies will recognize the populations of those two basins as not conspecific as considered here. To prevent a polytypic type series in the advent of such a split, only specimens from the Xingu basin were included as paratypes of *L. villasboasorum*.

***Leporinus enyae*, new species**

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Fig. 10; Tabs. 3 and 6

Leporinus desmotes. -Mago-Leccia 1970:76 (Venezuela). -Mojica, 1999: (Orinoco in Colombia). -Lasso *et al.*, 2004:1 (Orinoco, Río Negro). -Bogotá-Gregory, Maldonado-Ocampo, 2006:63 (Orinoco basin in Colombia). -Maldonado-Ocampo *et al.*, 2006:6 (río Tomo, Orinoco basin, Colombia). -Maldonado-Ocampo *et al.*, 2008:156 (Orinoco basin in Colombia). -Lasso *et al.*, 2009: río Atabapo, in Venezuela; usage as ornamental and food resource).

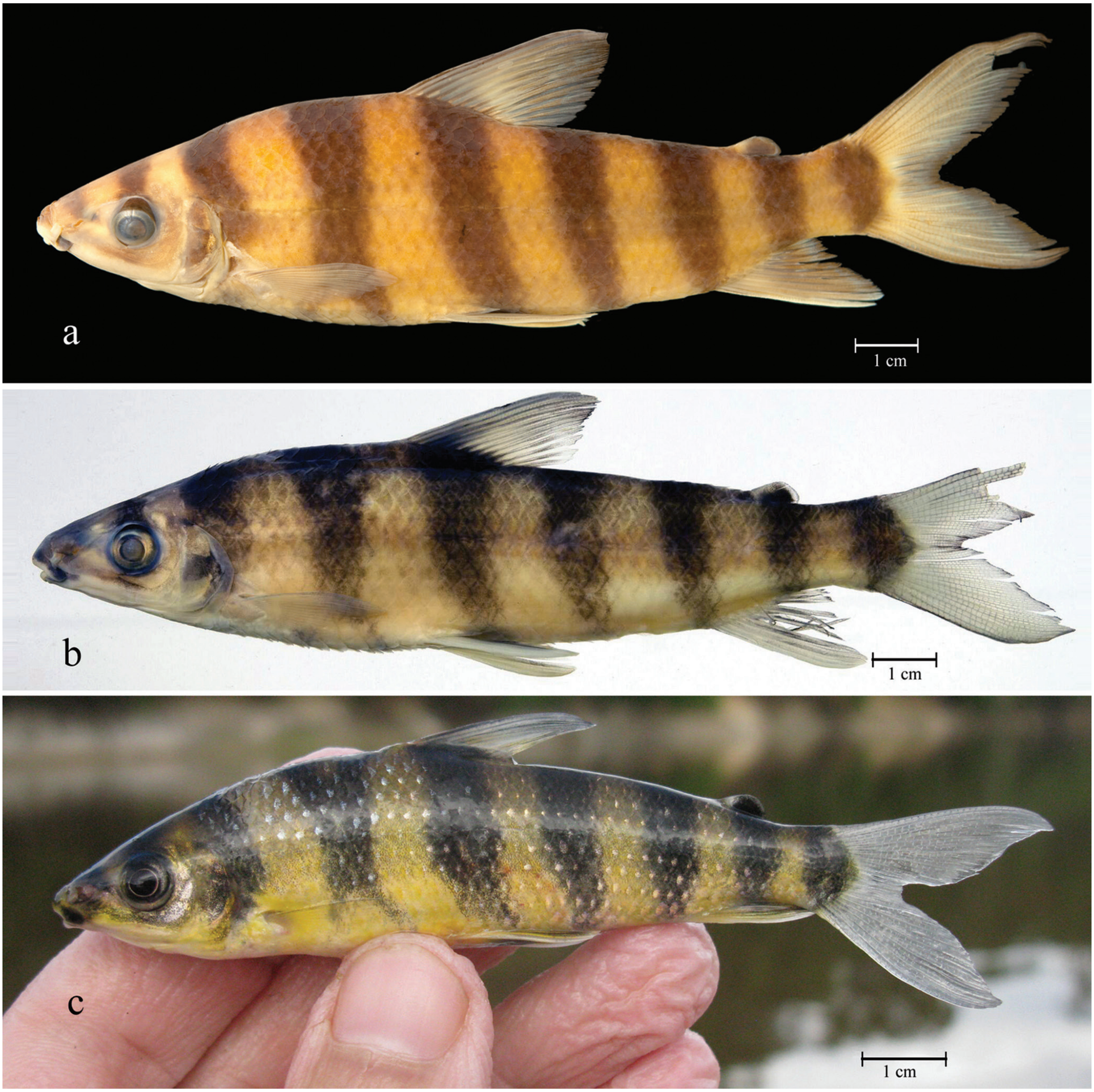

Fig. 10. *Leporinus enyae*: **(a)** holotype, MCNG 56681, 1, 145.5 mm SL, río Iquapo, Orinoco basin in Venezuela, alcohol-preserved, **(b)** INPA 43068, 137.6 mm SL, rio Negro at Cachoeira Bububri, São Gabriel, alcohol-preserved, photographed by Douglas Bastos, **(c)** paratype, AUM 53793, 80.3 mm SL, río Caura, Orinoco basin in Venezuela, photographed live by José Birindelli.

Holotype. MCNG 56681 (ex ANSP 200287), 1, 145.5 mm SL, Venezuela, Amazonas, río Iguapo, *ca*. 1 hour above the mouth, 03°08'59"N 65°28'00"W, 13 Mar 1987, H. López *et al.*

Paratypes. Brazil. INPA 3180, 67.7 mm SL, Amazonas, São Gabriel da Cachoeira, rio Uaupés, tributary of rio Negro, below Cachoeira Ipanoré, 00°17'28"N 68°39'30"W, 9 Dec 1989, L. Rapp Py-Daniel & M. Jégu. INPA 4930, 2, 161.8-163.8 mm SL, Amazonas, São Gabriel da Cachoeira, rio Negro at Ilha do Acará, 00°9'16"S 66°53'43"W, 12 Feb 1991, M. Jégu. INPA 43068, 1, 137.6 mm SL, Amazonas, São Gabriel da Cachoeira, rio Negro at Cachoeira Buburi, 00°08'38"S 67°05'19"S, 9 Dec 2013, D. Bastos *et al.* **Venezuela.** ANSP 158265, 3, 56.2-65.8 mm SL, Bolivar, Caño feeding río Caura near confluence of río Orinoco, 07°37'48"N 64°50'42"W, 22 Nov 1985, B. Chernoff *et al.* ANSP 161712, 10, 102.2-175.15 mm SL, collected with holotype. ANSP 190754, Amazonas, río Ventuari, tributary of río Orinoco, at Raudales Chipirito, 04°04'06"N 66°54'13"W, 1 Apr 2010, M. H.

Sabaj Perez *et al.* ANSP 159363, 1, 96.1 mm SL, Amazonas, Puerto Ayacucho, Raudales de Atures, at Culebra, 05°35'N 67°31'W, 11 Nov 1985, W. G. Saul *et al.* AUM 40992, 1, 136.71 mm SL, Amazonas, San Juan de Manapiare, río Parcucito, at Raudales Salomon, 05°20'46"N 66°02'00"W, 16 Apr 2004, D. C. Werneke *et al.* AUM 43123, 2, 72.8-80.9 mm SL, Amazonas, San Fernando de Atabapo, río Orinoco, at Pasaganado, 03°17'23"N 66°36'00"W, 29 Mar 2005, N. K. Lujan *et al.* AUM 43657, 1, 100.6 mm SL, Amazonas, San Carlos de Rio Negro, rio Negro, 01°55'14"N 67°03'48"W, 19 Mar 2005, D. C. Werneke *et al.* AUM 43700, 1, 100.6 mm SL, Amazonas, río Casiquiare, left bank upstream from mouth of Siapa, 02°09'20"N 66°27'49"W, 19-22 Mar 2005, N. K. Lujan *et al.* AUM 44008, 1, 66.6 mm SL, Amazonas, La Esmeralda, río Orinoco, 03°17'23"N 66°36'00"W, 29 Mar 2005, N. K. Lujan *et al.* AUM 53542, 1, 103.16 mm SL, Amazonas, San Fernando de Atabapo, río Orinoco, at Paso Ganado, 04°23'03"N 67°46'29"W, 27 Mar 2010, N. K. Lujan *et al.* AUM 53793, 1, 80.3 mm SL, Bolivar, río Caura, at Raudales la Union, 07°02'37"N 64°57'40"W, 25 Apr 2010, N. K. Lujan *et al.* AUM 53954, 1, 181.41 mm SL, Amazonas, Puerto Ayacucho, Caño Yurebita, 04°03'07"N 66°25'25"W, 15 Apr 2010, N. K. Lujan *et al.* AUM 54405, 1, 74.3 mm SL, Amazonas, San Fernando de Atabapo, río Ventuari confluence with río Orinoco, 03°58'42"N 67°03'37"W, 29 Mar 2010, N. K. Lujan *et al.* CAS 20170, 1, 84.1 mm SL, Amazonas, San Fernando de Atabapo, río Atabapo, tributary of río Orinoco, 7 Apr 1925, C. Ternetz. MZUEL 17001, 1 sk, 169.0 mm SL, Amazonas, Caño Yurukita, tributary of río Ventuari, 04°13'07'N 66°25'26"W, J. L. Birindelli *et al.*, 15 Apr 2010. MZUSP 105826, 1 sk, 185.0 mm SL, Amazonas, Caño Yurukita, tributary of río Ventuari, 04°13'07'N 66°25'26"W, J. L. Birindelli *et al.*, 15 Apr 2010. OS 20076 (ex ANSP 161712), 2, 102.1-126.2 mm SL, collected with holotype. ROM 95359 (ex ANSP 161712), 125.1 mm SL, collected with holotype.

Diagnosis. *Leporinus enyae* can be separated from all other members of *Leporinus* except *Leporinus desmotes*, *L. jatuncochi*, and *L. villasboasorum* by possession of long, pointed, laterally compressed and upward curving symphyseal dentary teeth, *versus* the more truncate conical or incisiform teeth typical of other members of *Leporinus*, and from *Leporinus bleheri, L. desmotes*, *L. jatuncochi*, *L. villasboasorum*, and *L. yophorus* by a color pattern consisting of nine dark bars on the head and body, some of which fork dorsally or ventrally, the fifth of which continues onto the dorsal and pelvic fins, *versus* various other color patterns in the approximately 90 other described species of *Leporinus*. It separates most easily from *Leporinus jatuncochi* and some specimens of *L. desmotes* by the possession of 16, *versus* 14 circumpeduncular scales. It separates from *Leporinus villasboasorum* and specimens of *Leporinus desmotes* with 16 circumpeduncular scales by having the dark bar immediately anterior of the dorsal fin undivided or barely divided dorsally, *versus* well-divided dorsally.

Description. Holotype and paratype meristic values in Tab. 3, morphometric values in Tab. 6. Body fusiform, elongate, slightly compressed, deepest and widest at dorsal origin. Very slight keel between dorsal insertion and supraoccipital crest, all other margins of body gently rounded. Caudal peduncle compressed and slightly longer than its depth. Head conical, compressed slightly dorsally and more so ventrally. Lateral profile of head straight and inclined. Anterior profile of head forming rounded point. Head broadest at posterior margin of opercle part of head. Eye round and laterally placed. Anterior nostril tubular, flared at distal end, positioned just anterior of first black transverse bar and overhanging upper lip slightly. Posterior nostril a sharply upturned slit positioned slightly posterior of anterior nostril at angle paralleling lateral profile of the head. Mouth small and subterminal. Lips fleshy and thick with deeply-cleft lamellae. Upper lip with two series of lamellae of which outer longer than inner. Bottom lip with two or more series of lamellae, outermost terminating on either side with deep-cleft narrow fleshy lobe. Inner series irregular in pattern and much shorter than series on upper lip or of outer series of bottom lip. Teeth three on each premaxilla, all broader than dentary teeth and slightly spoon shaped, pointed and jutting slightly anteriorly, with lateral teeth on each side smaller than medial teeth. Teeth three on each dentary with lateral teeth much smaller than symphyseal. Symphyseal dentary teeth long, pointed, laterally compressed and upward curving. Gill openings restricted. Opercle and preopercle smooth, with opercular flap pronounced and extending posteriorly from operculum. Four branchiostegal rays on each side.

Scales almost uniformly large with only slightly smaller scales in predorsal and ventral regions. Lateral line well defined, complete and straight with simple well-defined tubes. Pointed sheath scale twice as long as fin base on pelvic, starting at pelvic-fin origin and pointing posteriorly. Dorsal-fin origin located about halfway between snout tip and adipose-fin origin. Pelvic-fin insertion located at vertical through origin of third branched dorsal-fin ray. Adipose-fin origin located at vertical through origin of third branched anal-fin ray. Distal end of posterior branched anal-fin ray located at vertical through caudal peduncle. All fins sharply falcate. First unbranched fin ray about half as long as first branched fin ray, with first branched fin ray being the longest, on both dorsal- and anal-fins. Caudal-fin deeply forked. Vent located anteriorly of anal-fin origin about one-third the distance between anal-fin origin and pelvic-fin insertion.

Coloration in alcohol. Pale white to brownish with nine well-defined dark black transverse bars which, on bars posterior to the dorsal-fin origin, meet dorsally and ventrally to form bands encircling head and trunk. First bar at snout, second at eye, third at opercle, and remaining six on trunk. Bars on main body sloping slightly toward posterior from dorsal to ventral. Head with one dark bar on snout, starting just posterior of origin of anterior tubular nostril and extending to just anterior of eye, with faint connections to the second dark bar extending at a slight posterior slope above and below posterior nostril. Head with second dark bar on dorsal and lateral surfaces of head, located on interorbital and infraorbital region, about two-thirds width of eye and centered on eye, with no connections to third dark bar. Trunk with seven dark bars. First dark bar on trunk encompasses operculum but does not extend onto branchiostegals or isthmus, with black only occurring in space between the pectoral-fins ventrally. Second dark bar is located anterior of dorsal-fin origin and is often distinctly forked below the midway point between lateral line and ventral surface of body. Occasionally second dark bar slightly forked above lateral line at midway point between lateral line and dorsal surface of the body. Third dark bar includes entire dorsal base, anterior dorsal-fin rays and entire pelvic-fin except first unbranched fin ray. Fourth dark bar begins just posterior to dorsal-fin insertion and lies midway between pelvic insertion and anal origin and does not include vent. Fifth dark bar lies anterior of adipose-fin and extends ventrally to include first three rays of anal-fin. Sixth dark band begins at adipose insertion and extends to include caudal peduncle and posterior half of anal-fin as well as the distal two-thirds of adipose. Seventh dark bar includes caudal base with no intrusion of color onto caudal-fin rays.

Lips generally whitish with faint darkening of dorsal margin of upper lip and dark black on both sides of upper lip. Fleshy lobes on both sides of lower lip dark black. Dark pigmentation on snout tip and dorsal margin of maxilla, extending posteriorly to vertical through posterior margin of outer fleshy lamellae of lower lip. Pigmentation on upper lip connects faintly to dark bar through nares with only slight lightening in color of space between. Iris grey-black. Fins whitish except where noted. Ventral portion of head whitish.

Coloration in life. Pale yellow to brownish dorsally. Coloration and pattern of bars otherwise similar to that described in preservative. Lips dark black with ventral portion of lower lip appearing lighter in color. Fins generally light in color with dark pigmentation occurring near bars on the body.

Geographical distribution. *Leporinus enyae* occurs throughout the southern tributaries of the Orinoco river drainage in Venezuela, including the Ventuari, Parcucito, Atabapo, and Caura rivers, and in the upper Negro River in Brazil and Venezuela, and in the Casiquiare canal, which connects the Negro and Orinoco rivers (Fig. 9).

Etymology. Named in honor of the singer Enya, whose beautiful song "Orinoco Flow" celebrates the flow of the mighty Orinoco River, which the new species inhabits. A noun in the genitive case.

Conservation status. *Leporinus enyae* is relatively frequent and abundant in the Orinoco River basin. It is widespread throughout the 880,000 km^2 of the Orinoco River basin and the species can be categorized as Least Concern (LC) according to the International Union for Conservation of Nature (IUCN) categories and criteria (IUCN Standards and Petitions Subcommittee, 2016).

Discussion

Taxonomic implications of circumpeduncular scale counts. Circumpeduncular scale counts are among the most frequently used diagnostic characteristics separating anostomid species. That ubiquity stems from the large-scale size of most anostomids, which in turn fixes the circumpeduncular scale counts in most species. Almost all known species of *Leporinus* possess a fixed count of either 12 or 16 circumpeduncular scale rows, excluding aberrant or deformed individuals. The only exceptions are *L. jatuncochi*, with 14 as discussed herein, and some specimens of *L. taeniatus* that also have 14 (Birindelli *et al.*, 2016). Therefore, the circumpeduncular polymorphism within the Essequibo, Tocantins and Araguaia populations of *Leporinus desmotes* (in which counts of 14 and 16 circumpeduncular scales are both frequent), is highly unusual for a *Leporinus* species.

Given the rarity of such polymorphism, one must consider whether the presence of 14- and 16-scaled individuals in the Essequibo and lower Amazon tributaries indicates that these regions harbor not one, but two distinct species in the *Leporinus desmotes* group, with the paratype series of *L. desmotes* including individuals of both. If two species do exist in the Essequibo, the name *Leporinus desmotes* would apply to the 16-scaled species, because the holotype possesses that count. The 14-scaled species would then either receive a new name, or fall into the synonymy of *Leporinus jatuncochi* from the upper Amazon, specimens of which universally possess 14 circumpeduncular scales. The morphometric separation between 14 and 16 scaled individuals (Fig. 4) also hints at the presence of two species in the Essequibo, though increased sample sizes may blur that distinction. The Tocantins specimens are remarkably similar to the Essequibo specimens in body coloration (Fig. 11), and possess the same circumpeduncular polymorphism. Thus, it may also be that only a single species in this complex (*Leporinus desmotes sensu stricto*) occupies the Essequibo and Tocantins. If so, the circumpenducular polymorphism would be an emergent characteristic helping to characterize the distinctiveness of that species, as no other species in the barred *Leporinus* group possesses such a polymorphism. With only one genetic sample of *L. desmotes* currently sequenced (and with that specimen, somewhat frustratingly, being the only known specimen with 15 circumpeduncular scales) it is impossible to test the conspecificity of the two meristic morphotypes, nor can we assess the distinctiveness of the population in the Essequibo versus that in the lower Amazon tributaries.

Fig. 11. (a) *Leporinus desmotes*, holotype, ANSP 39324, 146.4 mm SL, Rupununi river, Guyana, **(b)** *Leporinus desmotes*, MZUSP 105585, 152.0 mm SL, rio Itacaiúnas, Tocantins basin in Brazil, **(c)** *Leporinus jatuncochi*, holotype, MSUM 5868, 122.0 mm SL, Laguna Jatuncochi, Orellana in Ecuador, **(d)** *Leporinus jatuncochi*, MUSM 34192, 149.3 mm SL, Peru. All specimens alcohol-preserved.

On the status of *Leporinus jatuncochi*. Despite recognizing two new species in the *Leporinus desmotes* species complex our analysis was not fully able to resolve the taxonomic status of the upper Amazonian specimens assignable to *L. jatuncochi*. The mean body shape of these specimens differs only slightly from the Essequibo specimens assignable to *L. desmotes* (Figs. 3-4, Tab. 5), and the genetic separation between the three sequenced upper Amazonian specimens and the single sequenced Essequibo specimens is much less pronounced than the difference between either of these groups and the sequenced specimens of *L. enyae* or *L. villasboasorum*. Furthermore, specimens of *L. jatuncochi* are meristically identical to the portion of *L. desmotes* with 14 circumpeduncular scales. Ultimately, the taxonomic status of *L. jatuncochi* depends upon the resolution of the circumpeduncular conundrum described above. If all Essequibo and lower Amazonian specimens of *L. desmotes* are conspecific, then *L. jatuncochi* might be best considered a junior synonym (and geographically distinct population) of *L. desmotes*. However, if the circumpeduncular polymorphism with *L. desmotes* indicates the presence of two species in that drainage, *L. jatuncochi* might be a valid name, and potentially (but not necessarily) applicable to the 14-scaled species that occurs in the Essequibo. Given the overall low genetic sample sizes currently available, we prefer to place the question of the validity of *L. jatuncochi* into abeyance until increased genetic sampling allows a rigorous test of the possible presence of two species within the present concept of *L. desmotes* in the Essequibo, Araguaia and Tocantins, and until the levels of genetic divergence between the upper and lower Amazonian populations can be more fully characterized.

Geographic limits to species distributions. As herein delimited, *Leporinus desmotes* possesses two distinct populations, one from the Essequibo and another from the Tocantins, apparently separated by the main channel of the Amazon River and its left-margin's tributaries. The distribution of *L. villasboasorum* and *L. jatuncochi* provides another likely example of a species boundary formed by the Volta Grande rapids, as also shown by *Doras higuchii* (Sabaj Pérez, Birindelli, 2008). In the Xingu, *L. villasboasorum* is apparently restricted to the stretch above the great rapids of Volta Grande, near the city of Altamira, where Belo Monte dam was recently constructed. Specimens collected below the Volta Grande rapids belong to *L. jatuncochi*. That said, no obvious biogeographic barrier separates the distribution of these species in the Tapajós basin. *L. villasboasorum* occurs in the upper Tapajós River basin, including the Teles Pires and Juruena rivers, but is absent in the middle and lower Tapajós basin, including the Jamaxim River, where *L. jatuncochi* occurs.

New species of *Leporinus* continue to be described yearly (Birindelli, Britski, 2013; Birindelli *et al.*, 2016), but as our analysis has shown, many more undescribed species still exist across South America. The uncertain delimitation of even well-known species, such as *L. desmotes* and *L. jatuncochi*, stresses the importance of combining morphological and genetic approaches in the description and revision of species. An in-depth phylogenetic and biogeographic analysis of barred *Leporinus* species is still needed to fully understand the species diversity in this highly diverse genus.

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Comparative material examined. *Leporinus affinis*. Types. Brazil. BMNH 1849.11.8.52-53, 2 syntypes, 148.8-175.4 mm SL, Pará, rio Capim. **Non-types. Brazil.** MCP 18214, 3, 100.0-109.0 mm SL, Goiás, Luís Alves, lakes of rio Araguaia. MNRJ 25724, 1, 150.6 mm SL, Mato Grosso, rio das Mortes, tributary of rio Araguaia. MZUSP 47828, 3, 185.0-262.0 mm SL, Goiás, Cocalinho, rio Araguaia at Lago Rico. MZUSP 48038, 1 CS, 85.0 mm SL, Pará, Jatobal, rio Tocantins, 04°34'S 09°39'W. ***Leporinus altipinnis*. Types. Brazil.** MCZ 20487, 2 syntypes, 80.0-92.0 mm

SL, Amazonas, Jatuarana [probably a creek or small lake near Barreirinha, Parintins, Amazonas, approximately 02°38'S 56°43'W]. MZUSP 51827, 1 (holotype of *L. falcipinnis*), 223.0 mm SL, Pará, rio Arapiuns, tributary of the lower rio Tapajós. **Non-types. Brazil.** CAS 20169, 1, 185.9 mm SL, Amazonas, rio Negro, at Castanheiro. CAS 70567, 1, 180.4 mm SL, Amazonas, Boa Futura, rio Xeruiuni. FMNH 78805, 1, 168.4 mm SL, Amazonas, Manaus. MPEG 305, 2, 58.7-62.1 mm SL, Amazonas, rio Negro at Ilha de Tamaquaré. MPEG 312, 2, 35.9-141.5 mm SL, Amazonas, Barcelos, rio Negro at Lago da Ilha. MPEG 691, 2, 138.5-302.0 mm SL, Amazonas, rio Negro at Anavilhanas. MPEG 16120, 1, 153.8 mm SL, Amazonas, Maués, rio Paraconi, at FLONA do Pau Rosa, 03°48'58"S 08°17'09" W. MPEG 16147, 1, 134.5 mm SL, Amazonas, Maués, rio Paraconi, at FLONA do Pau Rosa, 03°49'50"S 58°17'27"W. MZUEL 7052, 1, 131.1 mm SL, purchased in a aquarium store in São Paulo city. MZUSP 6821, 3, 53.6-65.1 mm SL, Amazonas, Manaus, creek tributary of rio Tarumãzinho, 03°10'S 60°00'W. MZUSP 29134, 11, 65.9-83.0 mm SL, Amazonas, rio Arirará, rio Negro basin, 00°31'S 63°33'W. MZUSP 29135, 4, 69.5-11.4 mm SL, Amazonas, Barcelos, rio Negro, 00°58'S 62°57'W. MZUSP 29136, 15, 54.6-84.5 mm SL, Amazonas, rio Negro at Ilha de Cumuru. MZUSP 29138, 46, 53.0-87.5 mm SL, Amazonas, rio Negro at Ilha de Tamaquaré, 00°30'S 64°55'W. MZUSP 29139, 41, 64.0-95.7 mm SL, 1 CS, 81.3 mm SL, Amazonas, rio Negro at Ilha de Buiu-Açu. MZUSP 29140, 1, 92.3 mm SL, Amazonas, rio Negro, below rio Daraá, 00°28'S 64°46'W. MZUSP 29146, 3, 51.5-74.5 mm SL, Amazonas, Santa Isabel do Rio Negro, rio Negro at mouth of rio Urubaxi, 00°31'S 64°50'W. MZUSP 31067, 1, 61.6 mm SL, Amazonas, rio Negro at Ilha de Tamaquaré, 00°30'S 64°55'W. MZUSP 51011, 9, 36.0-51.0 mm SL, Amazonas, Manaus, rio Negro, 03°5'S 60°13'W. MZUSP 63461, 6, 48.1-65.4 mm SL, Amazonas, Paricatuba, rio Negro marginal lagoon. MZUSP 91437, 1, 315.7 mm SL, Amazonas, Lago do rio Aiuanã, rio Negro basin, 00°38'S 64°56'W. MZUSP 91583, 2, 224.4-229.8 mm SL, Amazonas, rio Uaupés, tributary of rio Negro, 02°55'S 69°38'W. MZUSP 110814, 2 SK, 220.0-228.0 mm SL, Roraima, Caracaraí, rio Jufari, 1°1'46"S 62°6'6"W. MZUSP 112215, 1, 248.2 mm SL, Amazonas, Manaus, rio Negro, 03°10'S 60°00'W. MZUSP 112216, 1, 240.6 mm SL, Amazonas, Manaus, tributary of igarapé Tarumãzinho, rio Negro basin. **Venezuela.** FMNH 104000, 1, 182.5 mm SL, Amazonas, San Fernando de Atabapo, río Atabapo. FMNH 104017, 1, 289.0 mm SL, Amazonas, río Autana, 04°43'42"N 67°38'07"W. MCNG 21378, 2, 160,9-161,2 mm SL, Laguna Larga, río Cinaruco. MCNG 3297, 8, 197,9-199 mm SL, Amazonas, río Marapiare, in front of Yutaje. MCNG 41968, 3, 50,4-67,4 mm SL, Dpto. Río Negro, Laguna Anapacoa at Piedra Anapacoa, río Pasimoni, 01º50'81"N 66º35'11"W. ***Leporinus bleheri*. Types. Bolivia.** MZUSP 58375, 1, paratype, 114.5 mm SL, Itenéz, río Verde, tributary of río Guapore, 14°08'S 60°30'W. **Non-types. Brazil.** MPEG 10791, 4, 128.1-154.3 mm SL, Amazonas, Coari. MPEG 16764, 2, 169.0-180.6 mm SL, Amazonas, Coari. MZUSP 66676, 1, 130.0 mm SL, Amazonas, Santa Isabel do Rio Negro, rio Tiquié, 00°16'27"N 69°54'56"W. MZUSP 85374, 1, 168.3 mm SL, Amazonas, Santa Isabel do Rio Negro, rio Tiquié, 00°15'22"S 69°50'23"W. MZUSP 93445, 1, 168.0 mm SL, Amazonas, Santa Isabel do Rio Negro, rio Tiquié, 00°10'N 69°07'W. ***Leporinus desmotes*. Types. Guyana.** ANSP 39324, holotype, 146.4 mm SL, Rupununi River (not available for morphometric analysis). ANSP 39324, 3 paratypes, 84.4-121.3 mm SL, Rupununi River (not available for morphometric analysis). **Non-types. Brazil.** INPA 2666, 1, 98.6 mm SL, Roraima, rio Tacutu. INPA 4611, 5, 117.7-171.4 mm SL; Amazonas, Uraricoera, rio Branco basin. INPA 15431, 4, 82.4-140.3 mm SL, Amazonas, Uraricoera, rio Branco basin. MZUSP 40734, 2, 119.0-127.6 mm SL, Goiás, Monte Alegre de Goiás, rio Paranã, tributary of rio Tocantins, 13°15'S 46°53'W. MZUSP 47906, 1, 125.3 mm SL, Pará, rio Cupijó, tributary of rio Tocantins, 02°10'S 49°37'W. MZUSP 105499, 1, 126.8 mm SL, Pará, Marabá, rio Tapirapé, 05°36'47"S 50°26'42"W. MZUSP 105585, 3, 136.5-162.2 mm SL, Pará, Marabá, rio Itacaiúnas, tributary of rio Tocantins, 05°41'18"S 50°17'51"W. MZUSP 107802, 1, 106.2 mm SL, Pará, Canaã dos Carajás, rio Paranapanema, at Poço do Jaú, 06°23'15"S 50°02'03"W. UNT 7679, 9, 88.9-120.3 mm SL, Tocantins, Paranã, rio Paranã, 12°34'36"S 48°02'27"W. UNT 9095, 3, 68.9-115.2 mm SL, Tocantins, Sucupira, rio Santa Teresa, 12°15'00"S 48°41'01"W. **Guyana.** ANSP 179650, 1, 56.4 mm SL, Upper Takutu-Upper Essequibo, Rupununi River, 03°51'44"N 59°17'04"W. ANSP 179656, 1, 162.7 mm SL, Upper Takutu-Upper Essequibo, Takutu River, 03°21'18"N 59°49'51"W. ANSP 179669, 1, 58.2 mm SL, Upper Takutu-Upper Essequibo, Rupununi River, 03°55'34"N 59°17'04"W. AUM 37636, 1, 67.0 mm SL, Upper Takutu-Upper Essequibo, Rupununi River, 03°51'44"N 59°17'03"W. AUM 37637, 1, 72.0 mm SL, Upper Takutu-Upper Essequibo, Rupununi River, 03°45'00"N 59°18'30"W. AUM 4404, 1, 73.1 mm SL, Upper Takutu-Upper Essequibo, Rupununi River, 03°55'03"N 59°06'00"W. AUM 35675, 2, 109.7-170.8 mm SL, Upper Takutu-Upper Essequibo, Takutu River, 03°21'18"N 59°49'51"W. BMNH 1972.7.27.124, 1, 69.5 mm SL, Arakwai creek, Rupununi basin. ***Leporinus fasciatus*. Types. Suriname.** ZMB 3543, holotype, 140.5 mm SL (only examined by photograph). **Peru.** ANSP 21467, 1 (holotype of *L. holostictus*), 101.1 mm SL, Peruvian Amazon. **Non-types. Brazil.** CAS 20167, 3, 104.3-200.0 mm SL, Amazonas, rio Negro at Castanheiro. CAS 139291, 1, 243.0 mm SL, Amazonas rio Amazonas at Villa Bella. MCP 21033, 1, 81.9 mm SL, Pará, Santarém, rio Tapajós at Lago Verde, 02°31'S 54°57'W. MCP 30008, 2, 90.9-96.3 mm SL, Amazonas, Alvarães, Lago Amanã, at mouth of rio Baré, 02°27'S 64°43'W. MCP 46072, 1, 119.7 mm SL; Roraima, Rorainópolis, rio Jauaperi, 00°13'55"S 61°03'52"W. MZUEL 10187, 1, 205.8 mm SL, Amazonas, Presidente Figueiredo, Igarapé do Boto, tributary of rio Uatumã, 02°07'00"S 59°18'24"W. MZUEL 10194, 2, 228.0-242.2 mm SL, Amazonas, Presidente Figueiredo, rio Uatumã at Cachoeira Morena, 02°07'21"S 59°34'43"W. MZUEL 10196, 13, 150.4-204.5 mm SL, Amazonas, Presidente Figueiredo, rio Pitinga, tributary of rio Uatumã, at Corredeira Quarenta Ilhas, 00°53'16"S 59°34'28"W. MZUEL 11547, 2, 114.5-117.6 mm SL, Amazonas, Presidente Figueiredo, rio Pitinga, tributary of rio Uatumã, 01°06'46"S 59°36'26"W. MZUEL 14698, 1 SK, 221.5 mm SL, Amazonas, Novo Airão, rio Negro, 02°43'02"S 60°44'41"W. MZUSP 3581, 3, 132.5-173.4 mm SL, Pará, Santarém, rio Tapajós. MZUSP 3816, 2, 217.2-221.5 mm SL, 'Pará and Amazonas'. MZUSP 5428, 10, 178.0-225.0 mm SL, Pará, Oriximiná, rio Trombetas. MZUSP 5808, 1, 288.0 mm

SL, Amazonas, Silves, Lago Saracá. MZUSP 5883, 1, 228.7 mm SL, Amazonas, Manacapuru, Lago Manacapuru. MZUSP 6071, 2, 178.1-198.5 mm SL, Amazonas, Manaus, rio Preto da Eva. MZUSP 6095, 1, 154.5 mm SL, Amazonas, rio Puraquequara, 02°56'S 59°49'W. MZUSP 6146, 1, 266.5 mm SL, Amazonas, Manaus, rio Negro, 03°10'S 60°00'W. MZUSP 6186, 1, 250.0 mm SL, Amazonas, Manaus, Igarapé Jaraqui, tributary of rio Negro. MZUSP 6770, 3, 93.9-253.0 mm SL, Amazonas, Manaus, tributary of Igarapé Tarumãzinho, rio Negro basin. MZUSP 7055, 1, 160.7 mm SL, Amazonas, rio Canumã, rio Madeira basin, 04°58'S 58°56'W. MZUSP 7641, 1, 114.4 mm SL, Amazonas, Parintins, Lago José-Açu. MZUSP 13209, 1, 104.9 mm SL, Amazonas, Rio Preto da Eva, 02°42'S 59°42'W. MZUSP 13211, 11, 72.5-293.0 mm SL, Pará, rio Trombetas at Lago Jacaré. MZUSP 13456, 1, 202.8 mm SL, Amazonas, Itacoatiara, rio Amazonas. MZUSP 13902-4, 3, 247.0-267.5 mm SL, Rondônia, rio Machado at Lago do Paraíso. MZUSP 15680, 2, 222.7-244.3 mm SL, Pará, Oriximiná, rio Trombetas, 01°25'S 56°37'W. MZUSP 15725, 1, 290.5 mm SL, Pará, rio Trombetas. MZUSP 15819, 3, 172.2-238.0 mm SL, Pará, rio Trombetas at Reserva Biológica do Rio Trombetas. MZUSP 27387, 1, 214.0 mm SL, Amazonas, rio Negro at Anavilhanas. MZUSP 27901, 2, 60.4-88.7 mm SL, Amazonas, Iranduba, Lago Janauacá, 03°13'S 60°04'W. MZUSP 29125, 30, 30.8-111.5 mm SL, 2 CS, 97.1-105.5 mm SL, Amazonas, rio Negro, below rio Daraá, 00°28'S 64°46'W. MZUSP 29126, 1, 123.8 mm SL, Amazonas, rio Negro at Anavilhanas, 02°42'S 60°45'W. MZUSP 29127, 3, 52.8-112.0 mm SL, Amazonas, rio Negro at Anavilhanas, 02°42'S 60°45'W. MZUSP 29128, 1, 103.2 mm SL, Amazonas, rio Negro at Anavilhanas, 02°42'S 60°45'W. MZUSP 29129, 1, 112.4 mm SL, Amazonas, rio Negro at Anavilhanas, 02°42'S 60°45'W. MZUSP 29130, 2, 24.1-56.2 mm SL, Roraima, Marará, rio Branco, 01°30'N 61°16'W. MZUSP 29132, 1, 54.2 mm SL, Amazonas, rio Negro at Anavilhanas, 02°42'S 60°45'W. MZUSP 29144, 7, 39.6-57.2 mm SL, Amazonas, Tefé, rio Tefé at Jauari-Atuuba, 03°22'S 64°43'W. MZUSP 29150, 18, 13.8-50.8 mm SL, Amazonas, Jurupari, rio Tefé. MZUSP 29151, 5, 42.8-64.8 mm SL, Amazonas, Araná-Tuba, rio Tefé. MZUSP 36068, 3, 162.7-216.0 mm SL, Amazonas, rio Japurá, at Lago Amanã, 02°29'S 64°37'W. MZUSP 36073, 1, 212.7 mm SL, Amazonas, rio Japurá, 02°45'S 64°30'W. MZUSP 36075, 3, 141.4-220.6 mm SL, Amazonas, rio Japurá, at Lago Amanã. MZUSP 36079, 4, 182.0-236.2 mm SL, Amazonas, rio Japurá at Lago Amanã. MZUSP 36930, 1, 221.0 mm SL, Mato Grosso, Vila Bela da Santíssima Trindade, rio Guaporé. MZUSP 37439, 2, 220.0-230.5 mm SL, Mato Grosso, Vila Bela da Santíssima Trindade, rio Guaporé. MZUSP 37469, 1, 394.3 mm SL, Mato Grosso, Vila Bela da Santíssima Trindade, rio Guaporé. MZUSP 48378, 150.6-152.0 mm SL, Pará, Oriximiná, rio Trombetas. MZUSP 48381, 4, 170.4-196.0 mm SL, Amazonas, rio Solimões at Lago Janauacá. MZUSP 48384, 3, 69.6-74.2 mm SL, Amazonas, Lago Janauacá. MZUSP 43444, 3, 65.2-88.4 mm SL, Amazonas, Tapera, rio Negro, 00°12'S 64°04'W. MZUSP 48386, 1, 112.7 mm SL, Amazonas, Manaus, rio Preto da Eva. MZUSP 48387, 1, 139.9 mm SL, Amazonas, Santo Antônio do Içá, rio Içá. MZUSP 48698, 1, 140.5 mm SL, Amazonas, Fonte Boa, Igarapé Tomé, tributary of rio Solimões, 02°31'S 66°06'W. MZUSP 59059, 11, 166.2-220.6 mm SL, Amazonas, Tapera, rio Negro. MZUSP 63209, 1, 47.0 mm SL, Amazonas, Tefé, rio Tefé, at Lago Amanã. MZUSP 63408, 2, 255.4-267.0 mm SL, Mato Grosso, Aripuanã, rio Aripuanã, 09°34'45"S 59°25'19"W. MZUSP 83552, 14, 182.0-299.0 mm SL, Amazonas, rio Marauiá, rio Negro basin, 00°24'S 65°12'W. MZUSP 84260, 1, 158.4 mm SL, Rondônia, Montenegro, tributary of rio Jamari, rio Madeira basin. MZUSP 91438, 2, 237.3-280.4 mm SL, Amazonas, Tapera, rio Negro. MZUSP 92358, 1, 172.2 mm SL, Amazonas, rio Tiquié, rio Negro basin, 00°10'N 69°7'W. MZUSP 101529, 1, 173.4 mm SL, Pará, Monte Dourado, rio Jari, 00°37'52"S 52°31'35"W. MZUSP 101537, 1, not measured, Amapá, Laranjal do Jari, rio Iratapuru, tributary of rio Jari. MZUSP 101543, 3, 101.8-108.9 mm SL, Amapá, Laranjal do Jari, rio Jari, 00°34'16"S 52°34'44"W. MZUSP 101696, 1, 226.4 mm SL, Pará, Monte Dourado, rio Jari, 00°35'38"S 52°38'55"W. MZUSP 101763, 1, 227.9 mm SL, Pará, Monte Dourado, rio Jari, 00°39'45"S 52°31'40"W. MZUSP 101740, 1, 153.8 mm SL, Pará, Monte Dourado, rio Jari, 00°37'01"S 52°31'33"W. MZUSP 101766, 3, 85.6-116.0 mm SL, Amapá, Laranjal do Jari, rio Jari, 00°33'59"S 52°34'40"W. MZUSP 101902, 99.5-105.8 mm SL, Amapá, Laranjal do Jari, rio Jari, 00°46'54"S 52°31'48"W. MZUSP 101903, 207.9 mm SL, Pará, Monte Dourado, rio Pacanari, tributary of rio Jari, 00°39'43"S 52°31'45"W. MZUSP 101904, 1, 97.1 mm SL, Pará, Monte Dourado, rio Iratapuru, tributary of rio Jari, 00°34'03"S 52°34'41"W. MZUSP 101905, 1, 212.9 mm SL, Pará, Monte Dourado, rio Jari, 00°39'15"S 52°31'13"W. MZUSP 102417, 1, 195.7 mm SL, Amapá, Laranjal do Jari, rio Jari. MZUSP 103178, 1, 207.0 mm SL, Amazonas, rio Japurá, 01°53'S 67°00'W. MZUSP 103228, 1, 251.9 mm SL, Amazonas, Canta Galo, rio Negro. MZUSP 103242, 4, 77.0-225.0 mm SL, Amapá, Laranjal do Jari, rio Iratapuru, tributary of rio Jari, 00°33'59"S 52°34'43"W. MZUSP 103453, 1, 232.9 mm SL, Pará, Monte Dourado, rio Jari, 00°33'59"S 52°34'43"W. MZUSP 104725, 1, 344.0 mm SL, Pará, Monte Dourado, rio Jari. MZUSP 104744, 1, 252.3 mm SL, Pará, Monte Dourado, rio Jari, 00°36'09"S 52°31'35"W. MZUSP 104835, 1, 170.2 mm SL, Amapá, Laranjal do Jari, Igarapé Arapiranga, tributary of rio Jari, 00°48'05"S 52°27'20"W. MZUSP 104857, 1, 213.2 mm SL, Pará, Monte Dourado, rio Jari, 00°36'09"S 52°31'35"W. MZUSP 104888, 1, 147.7 mm SL, Amapá, Laranjal do Jari, rio Iratapuru, tributary of rio Jari, 00°33'59"S 52°34'43"W. MZUSP 112000, 3, 84.2-103.1 mm SL, Pará, Porto de Moz, rio Xingu. MZUSP 112211, 1, 57.5 mm SL, Amazonas, rio Negro at Ilha do Buiu-Açu. MZUSP 112212, 1, 55.5 mm SL, Amazonas, rio Negro below rio Daraá, 00°28'S 64°46'W. MZUSP 112213, 4, 35.7-52.2 mm SL, Amazonas, Barcelos, rio Negro, 00°58'S 62°57'W. MZUSP 112214, 1, 136.6 mm SL, Amazonas, rio Uaupés. MZUSP 112210, 4, 19.2-24.9 mm SL, Amazonas, Santa Isabel do Rio Negro, rio Negro, 00°31'S 64°50'W. UF 100622, 1, 180.0 mm SL, Rondônia, rio Jamari, tributary of rio Madeira. USNM 305106, 3, not measured, Amazonas, Manaus, Lago Janauaca and Lago Murumuru. USNM 305163, 1, not measured, Amazonas, Lago Murumuru and Lago Janauaca. USNM 310735, 1, not measured, Amazonas, rio Solimões near Tefé. **French Guiana.** BMNH 1909.9.4.1, 1, 158.5 mm SL, San Lorenzo, Maroni River. **Guyana.** ANSP 176829, 2, 147.5-157.4 mm SL, Essequibo River at Paddle Rock Campsite. ANSP 176830, 1, 144.8 mm SL, Burro Burro River at Water Dog

Falls Campsite. BMNH 1911.10.3.1.475, 3, 68.9-230.0 mm SL, Essequibo River at Bartica. BMNH 1934.9.12.317-318, 1, 146.4 mm SL, Essequibo River at Bartica. BMNH 1972.7.27.148-150, 3, 116.0-246.0 mm SL, Essequibo River at Demerara. CAS 116628, 10, 55.3-171.5 mm SL, Essequibo River at Bartica Rock. MZUSP 108841, 1, 208.7 mm SL, Potaro-Siparuni, Kuribrong River, 05°23'48"N 59°32'00"W. MZUSP 108874, 1, 175.7 mm SL, Potaro-Siparuni, Kuribrong River, 05°32'46"N 59°17'3"W. MZUSP 108860, 1, 169.3 mm SL, Potaro-Siparuni, Kuribrong River, 05°32'4"N 59°18'37"W. USNM 402907, 1, not measured, Cuyuni-Mazaruni, Cuyuni River downstream from Kanaima Falls, 06°53'01"N 60°14'52"W. **Peru.** ANSP 21468, 1, 72.5 mm SL, 'Peruvian Amazon' (possibly collected with holotype of *L. holostictus*). ANSP 137831, 8, 153.0-182.0 mm SL, Loreto, Iquitos, río Nanay. CAS 117234, 1, 91.6 mm SL, Loreto, río Ampiyacu near Pebas. MZUSP 26723, 1, 38.6 mm SL, Ucayali, Colonel Portillo, río Ucayali. **Suriname.** MZUSP 13210, 4, 137.9-179.2 mm SL, Brokopondo, Sara creek. MZUSP 99416, 2, 81.5-102.2 mm SL, Maroni, Marowijne River. UF 16266, 1, 110.4 mm SL, Marowijne, Marowijne River. USNM 225990, 4, not measured, Nickerie, Corantijn river, 05°07'48"N 57°17'60"W. USNM 225991, 10, not measured, Nickerie, Corantijn River, 05°00'00"N 57°16'48"W. USNM 409883, 1, not measured, Middle Paloemeu River at Kasikasima basecamp, 02°57'53"N 55°23'11"W. **Venezuela.** AUM 43300, 1, not measured, Amazonas, San Antonio, río Orinoco, 03°06'01"N 66°27'45"W. CAS 20164, 3, 59.2-65.8 mm SL, Amazonas, río Orinoco, between Atabapo and Atures Rapids. CAS 20165, 1, 98.0 mm SL, Amazonas, río Atabapo, tributary of río Orinoco. CAS 20166, 1, 80.7 mm SL, río Orinoco at Chono Salata Rapids. CAS 20168, 1, 143.1 mm SL, Bolivar, río Orinoco at Caicara. CAS 70751, 1, 245.0 mm SL, Amazonas, río Orinoco at Laja Suspiro. FMNH 93087, 1, 157.5 mm SL, río Caroní, tributary of río Orinoco. MCNG 21340, 2, 120.0-161.5 mm SL, Bolivar, Sucre, río Caura at Jubillat, 06°38'00"N 64°37'00"W. MCNG 51526, 3, 75.1-91.6 mm SL, Apure, río Cunavichito at Puente San Felipe. MCNG 40686, 1, 177.4 mm SL, Apure, Pedro Camejo, río Cinaruco, 06°32'20"N 67°24'08.5"W. MCNG 53536, 1, 137.7 mm SL, Apure, Pedro Camejo, Caño La Guardia at Puerto La Laguna Morocoto. MCNG 52441, 2, 170.1-171.0 mm SL, Apure, Pedro Camejo, Caño La Guardia, downstream of Laguna Morocoto. USNM 233386, 5, not measured, Delta Amacuro, río Orinoco, tributary at mouth of Caño Fiscal, 08°31'48"N 61°01'48"W. USNM 233818, 1, not measured, Monagas, Laguna Guatero near Barrancas, 08°43'12"N 62°10'48"W. USNM 270315, 5, not measured, Bolivar, small tributary of río Orinoco immediately south of El Burro, 06°10'48"N 67°25'12"W. USNM 270317, 1, not measured, Amazonas, Ature, río Orinoco at Raudales de Ature, 05°35'60"N 67°37'12"W. ***Leporinus jatuncochi*. Types. Ecuador.** MSUM 5868, holotype, 122.0 mm SL, Orellana, Laguna Jatuncocha, 01°00'00"S 75°27'00"W (only examined by photograph). **Non-types. Brazil.** INPA 10607, 1, 145.2 mm SL, Rondônia, rio Jamari, tributary of rio Madeira, 08°44'S 63°37'W. INPA 10609, 1, 177.3 mm SL, Rondônia, rio Jamari, tributary of rio Madeira, 8°44'S 63°37'W. INPA 11012, 2, 196.1-202.1 mm SL, Amazonas, rio Aripuanã, 05°09'S 60°22'W. INPA 12239, 16, 22.8-78.7 mm SL, Amazonas, rio Madeira. MZUEL 10207, 8, 132.2-155.6 mm SL, Amazonas, Presidente Figueiredo, rio Pitinga, tributary of rio Uatumã, 00°53'16"S 59°34'28"W. MZUSP 97515, 10, 100.3-149.2 mm SL, Pará, Novo Progresso, rio Jamanxim, tributary of rio Tapajós, 07°03'52"S 55°26'28"W. MZUSP 100574, 2, 87.0-87.3 mm SL, Mato Grosso, Aripuanã, rio Aripuanã, tributary of rio Madeira, 10°09'S 59°26'W. MZUSP 101034, 1, 182.6 mm SL, Mato Grosso, Aripuanã, rio Aripuanã, 10°10'06"S 59°26'50"W. MZUSP 103526, 1, 93.2 mm SL, Amapá, Laranjal do Jari, rio Jari, 00°34'18"S 52°34'40"W. MZUSP 111492, 1, 161.4 mm SL, Pará, Porto de Moz, rio Xingu, 01°45'48"S 52°14'21"W. UF 100625, 1, 140.0 mm SL, Rondônia, rio Jamari, tributary of rio Madeira, 08°44'S 63°37'W. **Ecuador.** FMNH 102142, 2, 22.8-65.89 mm SL, Sucumbios, río Cuyabeno, 00°14'00"S 75°55'00"W. **Peru.** ANSP 178127, 34.5 mm SL, Loreto, Mazán, río Napo, 03°29'10"S 73°06'24"W. ANSP 178632, 1, 84.5 mm SL, Loreto, Iquitos, río Nanay at Pampa Chica, 03°45'09"S 73°17'00"W. ANSP 182680, 1, 59.5 mm SL, Loreto, Iquitos, río Itaya, near Puerto Belen, 03°49'59"S 73°18'07"W. INHS 38940, 7, 70.1-84.8 mm SL, Loreto, Santa Clara, 04°26'S 74°04'W. INHS 39926, 1, 37.2 mm SL, Loreto, Iquitos, río Itaya 03°47'51"S 73°17'29"W. INHS 40129, 1, 31.8 mm SL, Loreto, Iquitos, río Orosa, at mouth of Caño Tonche, 03°47'26"S 73°14'50"W. MUSM 34192, 1, 149.3 mm SL. OS 18325, 5, 42.6-64.4 mm SL, Loreto, purchased at Stingray Aquarium in Iquitos. ***Leporinus pearsoni*. Types. Peru.** ANSP 69069, holotype, 97.2 mm SL, río Chimore at Boca Chapare. **Non-types. Ecuador.** FMNH 102144, 1, 157.5 mm SL, Napo, río Arajuno, 01°04'30"S 77°32'00"W. FMNH 102145, 2, 150.0-184.0 mm SL, Napo, río Arajuno, 01°05'24"S 77°34'18"W. **Peru.** ANSP 143800, 1, 160.0 mm SL, Amazonas, Madre de Dios, río Manú. ANSP 180841, 1, 80.7 mm SL, Amazonas, Madre de Dios, río Tahuamano. CAS 60592, 1, not measured, Loreto, Caño del Chancho, near Pebas, 03°19'24"S 71°51'34"W. FMNH 84279, 1, 122.0 mm SL, río San Alejandro. ***Leporinus tigrinus*. Types. Brazil.** MCZ 20446, 2 syntypes, 138.3-143.9 mm SL, Goiás. **Non-types. Brazil.** CAS 70447, 3, 91.3-146.0 mm SL, Goiás, Santo Antônio, rio Tocantins. INPA uncatalogued, 8, 89.0-122.5 mm SL, Pará, Altamira, rio Xingu at Cachoeira do Espelho, 03°39'05"S 52°22'43"W. MCP 19738, 1, 111.5 mm SL, Goiás, Minaçu, rio Tocantins. MCP 33962, 3, 100.0-118.0 mm SL, Goiás, Santa Rosa Meia Ponte, rio Meia Ponte, tributary of rio Paranaíba. MZUSP 99495, 2 CS, 82.5-112.8 mm SL, Pará, Jacareacanga, rio Teles Pires, tributary of rio Tapajós, 09°20'24"S 56°46'33"W. ***Leporinus yophorus*. Types. Colombia.** CAS 61680, holotype, 163.9 mm SL, Barrigón, río Meta, Orinoco basin. **Non-types. Colombia.** ANSP 135435, 1, 222.0 mm SL, Meta, río Negrito. ANSP 191701, 1, not measured, Meta, Puerto Gaitán, río Manacacias. ANSP 191704, 1, not measured, Meta, río Yucao at río Meta. **Venezuela.** ANSP 160347, 1, 99.3 mm SL, Bolivar, confluence of río Caura and río Orinoco. FMNH 3765, 1, 123.3 mm SL, Bolivar, Ciudad Bolivar. FMNH 85504, 7, 50.0-61.8 mm SL, Apure, río Aruaca. FMNH 104001, 1, 54.8 mm SL, Barinas, río Anaro, close to mouth of río Suripa. FMNH 104004, 1, 59.0 mm SL, Barinas, Caño La Indiacita, tributary of río Suripa. FMNH 104006, 2, 75.9-76.5 mm SL, Barinas, Caõ Sucopo, tributary of río Suripa. MCZ 59632, 1, 128.3 mm SL, Lagoon close to río Orinoco, 08°41'N 62°00'W. UF 36167, 4, 45.5-72.6 mm SL, Apure, río Orinoco basin.

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