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An integrated approach clarifies the cryptic diversity in *Hypostomus* Lacépède 1803 from the Lower La Plata Basin

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Abstract: *Hypostomus commersoni* Valenciennes 1836, *Hypostomus cordovae* (Günther 1880) and *Hypostomus laplatae* (Eigenmann 1907) have been little studied since their original descriptions. This study shows a comprehensive review of these species from the Lower La Plata Basin, including their taxonomic history, distribution, color patterns, morphology, and ecological and molecular phylogenetic data. Morphological and phylogenetic analyses based on D-loop sequences suggested that *H. commersoni* can be separated into two subclades, or subgroups. Based on these results and on the non-overlapping distribution range of the two subclades, we conclude that they represent two distinct species, thereby revalidating *H. spiniger*. The results also suggest that *H. paranensis* should be considered as species inquirenda and *H. cordovae* as valid species. This integrated approach provides key information for assessing the conservation status and biogeographic aspects of the genus *Hypostomus* in the Lower La Plata Basin.

Key words: Argentina, Brazil, freshwater fishes, molecular phylogenetics, Paraná Basin.

INTRODUCTION

Within the family Loricariidae, *Hypostomus* Lacépède 1803 is the most diverse genus, with more than 146 valid species (Eschmeyer et al. 2017). The species are widely distributed in South America, from Costa Rica to the Salado River Basin in Argentina (Ringuelet 1975). Two recent studies show the phylogenetic relationships of several species of *Hypostomus* in the southern part of its distribution, which comprises the Lower Paraná and the Río de la Plata Basin (Cardoso et al. 2012, 2016).

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Cardoso et al. (2012) raised the question of the sources of diversity in *Hypostomus* in the La Plata Basin, showing that the richness of species has been shaped by both inter- and intra-basin pressures. However, no further information on the biology, validated distribution, ecology, taxonomic status, or abundance of most of the species inhabiting the basin is available. More than 20 species of *Hypostomus* are recorded in the Lower La Plata Basin (Koerber and Weber 2014, Litz and Koerber 2014, Mirande and Koerber 2015), but this is likely to be underestimated. This gap in basic biological data makes obtaining thorough knowledge of the evolutionary and biogeographical events shaping this group of catfish a challenge.

The present study contributes to a more complete assessment of species diversity and expands available biological data on *Hypostomus* species inhabiting the Lower La Plata Basin. This work focuses on *H. commersoni* Valenciennes 1836, *H. cordovae* (Günther 1880), and *H. laplatae* (Eigenmann 1907), species that have been little studied since their original description. The descriptions are outdated and imprecise, and subsequent taxonomic work has often been undertaken without examination of the type material or was based on a small number of specimens or a limited distribution range. Here, an integrated approach, based on taxonomic history, geographic distribution, morphology, morphometrics, live color pattern, and ecological and molecular phylogenetic data of the type-series, together with newly collected topotypes of these species, were used to re-evaluate their taxonomy.

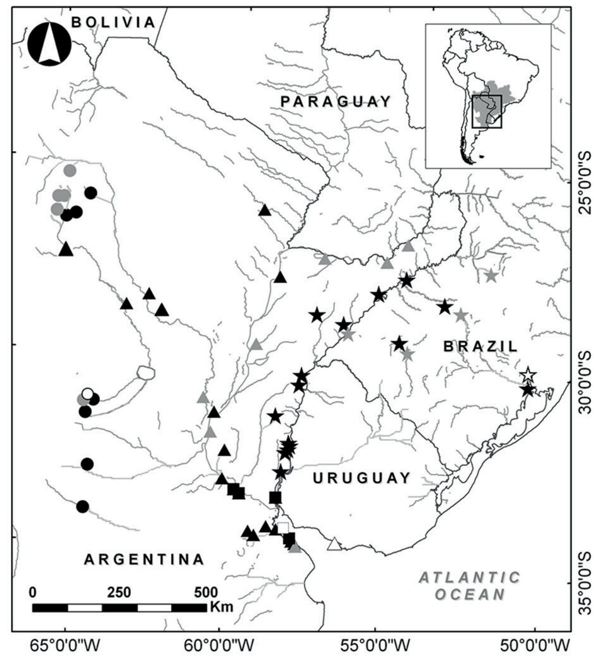

Figure 1 - Map of collection localities of *Hypostomus commersoni* (triangle), *H. spiniger* (star), *H. cordovae* (circles) and *H. laplatae* (squares). White symbols are type localities and grey symbols are specimens used only in molecular analyses.

MATERIALS AND METHODS

Fishes were collected with gillnets, trammel nets, hand nets, and cast nets. Locations sampled are presented in Fig. 1. A tissue sample was taken from each specimen for molecular analysis, preserved in 96% ethanol, and stored at -20°C. Voucher specimens were fixed in 4% formalin and deposited in the ichthyology collection of the Fundación de Historia Natural Félix de Azara, Buenos Aires, Argentina (CFA-IC). Specimens and photographs of type series were examined from the AMNH, American Museum of Natural History, New York; BMNH, British Natural History Museum, London; CAS, California Academy of Sciences, San Francisco; MACN, Museo Argentino de Ciencias Naturales "Bernardino Rivadavia," Buenos Aires; MCP, Museu de Ciências e Tecnologia da Pontifícia Universidade Católica do Rio Grande do Sul, Porto Alegre; MFA-ZV, Museo Provincial "Florentino Ameghino," Santa Fe; MHNG, Muséum d'Histoire Naturelle, Genève; MNHN, Museum National d'Histoire Naturelle, Paris; MLP, Museo de La Plata, Buenos Aires, and ZMB, Zoological Museum of Berlin, Berlin (see Appendix).

Total DNA was obtained using the salt-extraction protocol (Aljanabi and Martinez 1997). The PCR amplification of the control region (D-loop) of the mitochondrial DNA was performed as in Cardoso et al. (2011). The PCR products were purified and sequenced by Macrogen Inc. (Korea). New sequences were deposited in GenBank for: *H. commersoni* (JF290450 to JF290458, MG457220 to MG457223, MG457234 to MG457242), *H. cordovae* (KX852401 to KX852410), *H. laplatae* (KX852411 to KX852418), and *H. spiniger* (MG457224 to MG457233). Also, published data for *Hypostomus* (Montoya-Burgos 2003, Cardoso et al. 2012, 2016) were used, so some specimens were incorporated only in the molecular analyses (see Fig. 1). In total, 109 sequences were edited and manually aligned using BioEdit 7.0.1 (Hall 1999). Two phylogenetic analyses were conducted, regardless of species assignment. Appropriate substitution models were selected with the Akaike information criterion (AIC) and the phylogeny was inferred using maximum likelihood (ML) implemented in MEGA.7 (Kumar et al. 2016). Confidence values for the limits of the ML tree were computed with 1000 bootstrap replications (Felsenstein 1985). Subsequently, Bayesian inference (BI) analysis was conducted in MrBayes 3.2.2 (Huelsenbeck and Ronquist 2001, Ronquist et al. 2012) on CIPRES Science Gateway (Miller et al. 2010). Four chains were run simultaneously (three heated, one cold) for 30 million generations, with sampling every 500 generations. Following graphic analysis of the evolution of the likelihood scores, the first 25% of generations were discarded as burn-in. The remaining trees were used to calculate the consensus tree.

Measurements were made using an Essex digital electronic calipers with 0.1 mm accuracy following the methods of Boeseman (1968) and Weber (1985). Morphometric characteristics are expressed as percentage of standard length (SL) or head length (HL). Analysis included 21 continuous morphometric variables and 12 discrete meristic variables of 91 specimens (Tables I and II). Missing data were estimated using the least-squares method with SL as explanatory variable. All measurements were standardized according to SL and log-transformed to control for size. This transformation, equivalent to the additive log ratio of Aitchinson (1986), controls for size effect, preserves and linearizes allometric growth, and prevents spurious correlations of simple ratios (Atchley et al. 1976, Atchley and Anderson 1978, Hills 1978). The data were submitted to a between-class analysis (BCA), a particular case of principal component analysis (PCA) with respect to instrumental variables in which there is only a single factor as explanatory variable. In this case, *species* was used as the explanatory factor. To explore the more closely related species, a second analysis, based on 30 specimens of *H. commersoni,* 31 of *H. spiniger,* five *H. affinis* (Steindachner 1877), two *H. interruptus* (Miranda Ribeiro 1918) and three *H. ancistroides* (Ihering 1911) was submitted to further BCA. Both analyses were performed with the ade4 1.4-14 (Dray and Dufour 2007) package in R 3.4.1 (R Core team 2014).

Assessment of the conservation threat level of the analyzed species was primarily based on the application of the IUCN Red List Criterion B (IUCN 2001). This criterion focuses on two spatial measures related to the distribution of the species: area of occupancy (AOO) and extent of occurrence (EOO) (IUCN 2017). Both measures were performed with the ConR (Dauby 2017) package in R 3.4.1 (R Core team 2014) according to IUCN (2017).

RESULTS

PHYLOGENETIC ANALYSES

Mitochondrial D-loop sequences were obtained from several specimens recently collected in Argentina and Brazil, covering a wide distribution

TABLE I
Morphometric and meristic data of *Hypostomus commersoni* and *H. spiniger*. Range, mean (or mode for the meristic data), standard deviation (SD) and number of specimens (n). Morphometric and meristic variables used in the BCA analysis (Figs. 3 and 4) are showed with abbreviations in squared brackets.

Characters	*H. commersoni*			*H. spiniger*		
	Range	Mean±SD	n	Range	Mean±SD	n
Standard length	60.2-408.5	210.09±124.19	24	52.5-325.0	143.77±95.88	27
Predorsal length [D]	33.9-44.1	40.33±2.57	24	35.4-53.1	42.34±3.78	27
Cleithral width [F]	23.5-30.9	28.60±2.17	24	21.2-30.2	27.79±2.00	27
Head length [E]	26.6-38.7	33.03±3.59	24	27.5-38.7	33.60±3.13	27
Body height	17.7-24.5	21.52±1.60	24	17.8-24.7	22.4±1.13	27
Dorsal fin spine length [K]	26.2-37.6	31.11±3.58	20	24.6-33.3	29.08±2.35	26
Dorsal fin base length [L]	25.3-32.1	28.94±1.86	24	23.8-32.2	27.05±2.03	27
Inter-dorsal distance [M]	14.4-19.5	17.08±1.34	24	14.7-21.4	18.43±1.69	27
Pectoral fin spine length [O]	24.4-33.6	30.17±2.36	24	26.3-36.1	29.64±2.02	27
Thoracic length [N]	18.0-26.3	22.16±2.15	24	20.3-28.5	25.08±1.83	27
Pelvic fin spine length [Q]	21.7-30.1	25.26±2.19	24	20.0-30.6	24.78±1.98	27
Abdominal length [P]	16.7-23.9	20.04±1.84	24	17.0-22.8	19.65±1.73	27
Caudal-peduncle length [R]	27.7-32.7	30.50±1.37	24	24.8-33.3	29.64±1.87	27
Caudal-peduncle depth [S]	7.5-10.3	8.96±0.61	24	7.9-10.4	9.47±0.52	27
Adipose fin spine length [T]	6.3-8.9	7.29±073	24	4.8-10.4	6.86±1.10	26
Upper caudal fin ray length [U]	22.1-40.3	30.61±5.54	17	16.6-43.5	31.74±5.50	20
Lower caudal fin ray length [V]	19.0-42.4	34.12±6.36	21	15.3-42.7	34.06±6.16	22
Head length						
Head depth [G]	49.0-71.6	60.84±5.93	24	48.5-76.4	60.78±5.97	27
Snout length [H]	54.6-63.9	60.39±2.52	24	50.4-68.3	58.46±3.57	27
Orbit diameter [I]	7.2-14.9	10.37±2.39	24	9.3-25.4	15.15±4.18	27
Inter-orbital width [J]	36.2-43.2	40.29±1.79	24	38.3-56.3	43.96±4.87	27
Maxillary barbel length [barb]	5.1-11.8	8.91±2.02	24	7.9-56.9	14.99±9.54	26
Mandibular ramus length [RM]	10.7-14.1	12.34±0.92	24	10.4-15.3	12.93±1.47	24
Other characters						
Orbit diameter:snout length	11.8-27.2	17.30±4.59	24	15.6-34.5	24.18±5.01	27
Orbit diameter:inter-orbital width	18.1-37.4	25.71±5.72	24	24.4-45.4	33.18±5.77	27
Mandibular width:inter-orbital width	26.9-35.5	30.66±2.34	24	25.0-37.6	30.64±3.62	24
First dorsal fin spine length:predorsal length	59.7-97.0	78.05±9.61	20	49.7-85.9	68.88±7.49	26
First pectoral fin spine length:predorsal length	63.5-83.0	74.90±5.02	24	51.0-85.6	70.47±7.12	27
Lower caudal fin unbranched ray length:predorsal length	44.0-105.0	85.31±16.44	21	28.8-101.2	81.21±15.29	22
Adipose fin spine length:caudal-peduncle depth	69.8-96.6	81.52±7.47	24	53.6-114.7	72.59±12.05	26

TABLE I (continuation)

Characters	*H. commersoni*			*H. spiniger*		
	Range	**Mean±SD**	**n**	**Range**	**Mean±SD**	**n**
Caudal-peduncle depth:caudal-peduncle length	23.5-33.9	29.47±2.90	24	24.4-37.7	32.09±2.83	27
Mandibular width:cleithral width	12.2-16.3	14.23±1.24	24	13.1-20.3	15.66±2.05	24
Interdorsal length:dorsal fin base length	49.6-68.3	59.19±5.12	24	52.7-83.0	68.58±8.63	27
Meristic data	Range	Mode±SD	n	Range	Mode±SD	n
Standard length (SL) mm	38.4-408.5	234±78.49	32	52.5-325.0	213.46±73.98	24
Lateral scutes series [Lateral]	26-29	28±0.59	32	27-28	27±0.48	24
Predorsal plates	3	3±0.00	32	3	3±0.00	24
Dorsal plates at dorsal fin base [baseD]	8-10	9±0.49	32	8-10	9±0.62	24
Plates between dorsal and adipose fin [baseD.Adi]	6-8	7±0.36	32	6-8	6±0.54	24
Plates at adipose fin base [baseAdi]	3-4	3±0.49	32	2-4	3±0.48	24
Plates between adipose-caudal fins [baseAdi.Cau]	3-6	5±0.62	32	3-5	3±082	24
Plates anal fin base [baseAnal]	2-3	3±0.18	32	2-3	3±0.38	24
Postanal plates [Postanal]	13-15	14±0.55	31	11-15	13±0.88	24
Left premaxillary teeth [PremaxIzq]	14-41	24±7.65	31	17-38	27±6.15	23
Right premaxillary teeth [PremaxDer]	14-41	33±8.02	32	17-40	27±5.95	23
Left dentary teeth [DentIzq]	18-43	20±7.68	32	18-36	26±5.63	23
Right dentary teeth [DentDer]	16-40	25±6.74	31	16-38	29±5.16	22
Dorsal fin branched rays	7	7±0.00	24	7	7±0.00	27
Pectoral fin branched rays	6	6±0.00	24	6	6±0.00	27
Pelvic fin branched rays	5	5±0.00	24	5	5±0.00	27
Anal fin branched rays	4	4±0.00	24	4	4±0.00	27
Caudal fin branched rays	14-14	14±0.00	24	14-14	14±0.00	27

range in the Lower La Plata Basin and Dos Patos Lagoon. The alignment of the mitochondrial D-loop region comprised 584 positions (from which 167 were variable) and 100 sequences of *Hypostomus*, plus nine outgroups. The best-fit substitution model found for the dataset was GTR+I+G. Evolutionary relationships within the genus (Fig. 2) were similar to those reported by Montoya-Burgos (2003) and Cardoso et al. (2012, 2016), with four main lineages: D1, D2, D3, and D4 (Fig. 2). However, in the analyses, the statistical support was generally low among species, generating polytomies in the BI tree due to the collapse of some branches supported by posterior probabilities < 0.5. Nevertheless, in both the ML and BI analyses, all specimens collected in the Lower Río de la Plata Basin appeared in four strongly supported and reciprocally monophyletic clades. These phylogenetic results indicated that the specimens identified as *H. commersoni* are organized into two non-sister subclades. One

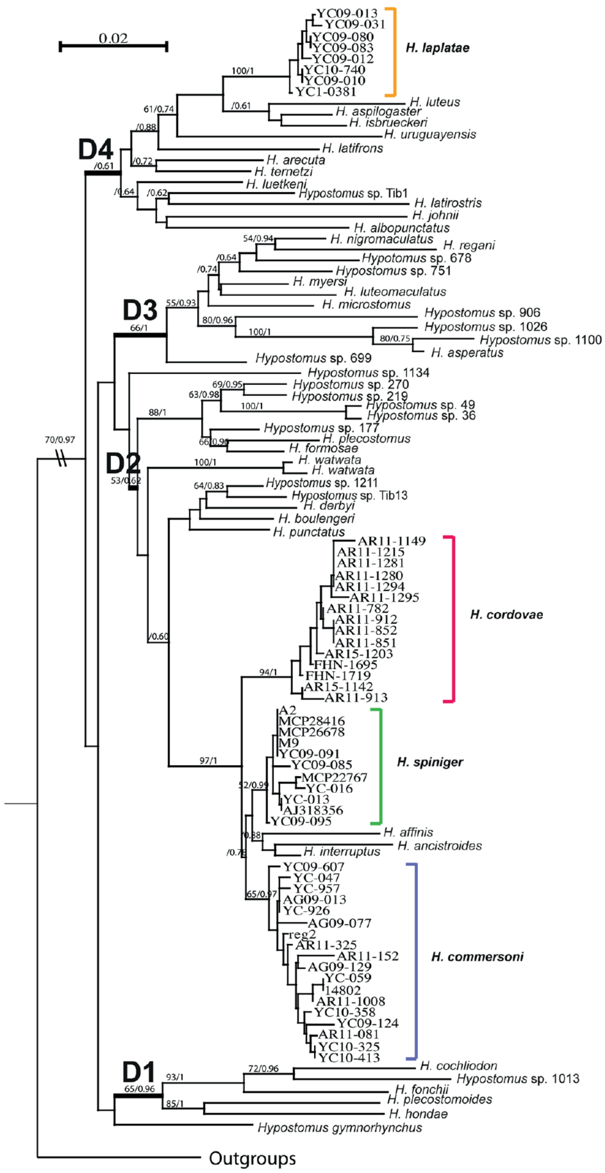

Figure 2 - Maximum likelihood tree based on the mitochondrial D-loop region. Numbers next to branches are bootstrap values (1000 pseudoreplicates) followed by Bayesian posterior probabilities when these are above 50% or 0.5. Specimens of *H. laplatae*, *H. cordovae*, *H. commersoni* and *H. spiniger* sequenced in this work are in bold and their field number are given.

subclade comprises the specimens collected in the Uruguay River and Dos Patos Lagoon, corresponding to the species previously recognized as *H. spiniger*, which is revalidated here and is the name that will be used henceforth (see Remarks section of Results and Discussion).

The phylogenetic tree shows *H. cordovae*, *H. commersoni*, and *H. spiniger* grouped in lineage D2 (Fig. 2). This lineage also contains other species from the La Plata Basin (*e.g. H. boulengeri*, *H. formosae*, *H. ancistroides*, and *H. derby*); *H. watwata* and *H. plecostomus* from the Guyana Shield; and *H. affinis*, *H. punctatus*, and *H. interruptus* from Eastern South America coastal rivers. According to the present analysis *H. spiniger* forms a clade with *H. affinis*, *H. ancistroides*, and *H. interruptus* instead of being the sister group of *H. commersoni*.

Specimens of *H. laplatae* were grouped within the D4 lineage, principally composed of species from La Plata Basin: *H. aspilogaster*, *H. luteus*, *H. isbrueckeri*, *H. uruguayensis*, *H. latifrons*, *H. arecuta*, *H. ternetzi*, *H. albopunctatus*, and *H. latirostris*.

MORPHOMETRIC ANALYSES

The first morphological dataset, comprising the four analyzed species, showed a clear structure on the first two axes of the BCA (Fig. 3c). The species were chiefly aligned along the first axis (Fig. 3a). On the negative side of axis 1, *H. cordovae* corresponded to high number of dentary and premaxillary teeth, inter-dorsal distance, and caudal-peduncle length (Fig. 3b). On the positive side of axis 1, *H. commersoni* and *H. spiniger* are characterized by high values of snout length, inter-orbital width, pelvic-fin spine length, orbit diameter. On the negative side of axis 2, *H. laplatae* corresponded to high values for dorsal plates below the dorsal-fin base, lateral scute series, plates bordering the supraoccipital, and postanal plates. The second morphological dataset was based on the five most closely related species of the D2 lineage defined in the phylogenetic tree. This BCA was mainly structured on the first two axes (Fig. 4c). The first axis separated the specimens of *H. commersoni* and *H. spiniger*, while the second separated *H. affinis*, *H. ancistroides*, and *H.*

TABLE II
Morphometric and meristic data of *Hypostomus cordovae* and *H. laplatae*. Range, mean (or mode for the meristic data), standard deviation (SD) and number of specimen (n). Morphometric and meristic variables used in the BCA analysis (Figs. 3) are showed with abbreviations in brackets.

Characters	*H. cordovae*			*H. laplatae*		
	Range	Mean±SD	n	Range	Mean±SD	n
Standard length	100.9- 247.5	184.39±50.99	17	151.5-466.0	360.61±96.69	15
Predorsal length [D]	32.7-40.4	36.38±2.62	17	37.4-40.3	38.81±0.76	15
Cleithral width [F]	23.9-30.0	25.99±1.71	17	25.5-31.4	27.68±1.52	15
Head length [E]	25.9-32.7	28.91±2.39	17	28.5-33.6	30.77±1.40	15
Body height	13.2-18.1	15.13±1.48	17	17.5-23.9	20.29±1.68	15
Dorsal fin spine length [K]	21.1-33.3	25.40±3.17	14	26.2-38.7	30.63±3.59	10
Dorsal fin base length [L]	23.2-28.7	25.55±1.52	17	25.0-30.3	28.24±1.35	15
Inter dorsal distance [M]	17.3-22.2	19.32±1.45	17	15.7-20.7	18.08±1.52	15
Pectoral fin spine length [O]	21.1-29.0	23.86±2.01	17	24.8-33.6	29.11±2.35	13
Thoracic length [N]	18.2-22.5	20.63±1.31	17	17.5-27.8	24.25±2.39	15
Pelvic fin spine length [Q]	18.6-28.4	23.21±2.37	17	20.6-28.0	22.77±1.92	15
Abdominal length [P]	16.5-20.2	18.84±1.06	17	17.6-20.4	18.83±0.94	15
Caudal peduncle length [R]	30.1-36.8	34.06±2.10	17	29.0-33.9	31.59±1.37	15
Caudal peduncle depth [S]	7.0-9.4	7.88±0.65	17	8.1-9.8	8.98±0.47	15
Adipose fin spine length [T]	3.6-8.1	7.19±1.17	15	5.2-7.4	6.22-0.62	15
Upper caudal fin ray length [U]	22.6-33.4	27.60±3.69	12	29.7-41.1	35.75±3.84	9
Lower caudal fin ray length [V]	25.8-34.8	28.84±2.76	14	31.1-41.8	37.02±3.09	10
Head length						
Head depth [G]	45.2-54.2	50.02±2.61	17	51.9-68.2	59.96.±4.86	15
Snout length [H]	60.7-66.1	63.42±1.67	17	54.4-60.9	58.10±1.70	15
Orbit diameter [I]	8.9-12.5	10.38±0.81	17	6.3-11.2	7.94±1.38	15
Inter-orbital width [J]	32.7-40.3	35.91±2.18	17	30.5-38.6	35.23±2.02	15
Maxillary barbel length [barb]	6.2-14.8	11.07±2.50	14	6.7-14.0	10.24±1.92	15
Mandibular ramus length [RM]	11.2-23.9	17.36±4.36	17	9.9-12.7	11.40±0.86	15
Others characters						
Orbit diameter:snout length	13.8-20.6	16.39±1.46	17	10.5-20.0	13.71±2.71	15
Orbit diameter:inter-orbital width	24.9-33.5	28.99±2.48	17	18.2-29.7	22.47±3.09	15
Mandibular width:inter-orbital width	29.6-69.5	49.06±14.60	17	27.5-36.3	32.45±2.81	15
First dorsal fin spine length:predorsal length	57.6-82.5	68.55±7.13	14	69.6-100.0	79.03±8.85	10
First pectoral fin spine length:predorsal length	62.0-71.8	65.59±2.70	17	66.0-86.8	75.02±5.77	13
Lower caudal fin unbranched ray length:predorsal length	70.6-88.5	77.63±4.82	14	79.7-107.9	95.69±8.21	10
Adipose fin spine length:caudal peduncle depth	47.7-106.2	90.29±13.57	15	53.5-83.9	69.47±8.02	15

TABLE II (continuation)

Characters	***H. cordovae***			***H. laplatae***		
	Range	**Mean±SD**	**n**	**Range**	**Mean±SD**	**n**
Caudal-peduncle depth in caudal-peduncle length	19.8-31.1	23.30±3.34	17	24.6-30.5	28.45±1.75	15
Mandibular width:cleithral width	12.0-26.5	19.36±5.10	17	10.4-14.7	12.70±1.21	15
Interdorsal length:dorsal fin base length	60.8-91.7	76.79±8.78	17	57.0-78.5	64.21±6.99	15
Meristic data	Range	Mode±SD	n	Range	Mode±SD	n
Standard length (SL) mm	37.6-247.5	123.00±69.80	47	151.5-466.0	360.61±96.69	15
Lateral scute series [Lateral]	28-30	29±0.57	47	31-32	31±0.33	15
Predorsal plates	3-4	3±.015	47	3	3±0.00	15
Dorsal plates at dorsal fin base [baseD]	8-9	8±0.47	47	9-12	10±0.64	15
Plates between dorsal and adipose fin [baseD.Adi]	6-8	8±0.76	47	7-9	8±0.46	15
Plates on adipose fin base [baseAdi]	3-5	4±0.62	47	3-4	3±0.52	15
Plates between adipose caudal fins [baseAdi.Cau]	4-6	4±0.67	47	4-5	5±0.49	15
Plates anal fin base [baseAnal]	3-4	3±0.44	47	3-4	3±0.35	15
Plates postanal [Postanal]	13-15	14±0.40	47	14-16	15±0.52	15
Left premaxillary teeth [PremaxIzq]	24-79	34±14.03	46	15-37	30±6.44	15
Right premaxillary teeth [PremaxDer]	21-75	31±13.88	44	17-36	29±5.39	15
Left dentary teeth [DentIzq]	27-75	61±12.41	45	13-31	26±5.24	15
Right dentary teeth [DentDer]	25-75	39±12.62	46	14-32	28±4.46	15
Dorsal fin branched rays	7	7±0.00	17	7	7±0.00	15
Pectoral fin branched rays	6	6±0.00	17	6	6±0.00	15
Pelvic fin branched rays	5	5±0.00	17	5	5±0.00	15
Anal fin branched rays	4	4±0.00	17	4	4±0.00	15
Caudal fin branched rays	14-14	14±0.00	17	14-14	14±0.00	15

interruptus (Fig. 4a). On the negative side of axis 1, *H. commersoni* corresponded to high number of dentary and premaxilla teeth, number of plates between adipose and caudal fins, number of plates between dorsal and adipose fins, thoracic length, mandibular ramus length, caudal-peduncle depth, and orbit diameter (Fig. 4b).

Hypostomus commersoni Valenciennes 1836

Hypostomus commersoni Valenciennes 1836: Pl. 7. Type locality: Río de La Plata, Montevideo, Uruguay.

Hypostomus commersoni Valenciennes 1836, in Valenciennes 1835-47: pl. 7 (Fig. 5). Type locality: not stated (considered to have come from La Plata River, Uruguay). Holotype or lectotype: MNHN a-9444 (Fig. 5). Name made available from caption to plate, with as illustrated specimen the holotype (if recognizable). Described in Cuvier and Valenciennes (1840b: 495, 366 of Strasbourg deluxe edition).

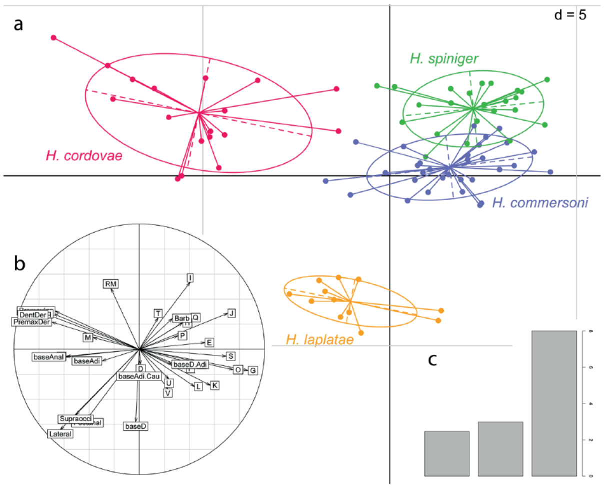

Figure 3 - Between-class Analysis (BCA) of morphological data of *H. laplatae*, *H. cordovae*, *H. commersoni* and *H. spiniger*. **a**. Projection of individuals's scores onto first factorial plane of BCA, axis 1 horizontal and axis 2 vertical; **b**, Correlation of the variables labelled as in Tables I and II; **c**, Eigenvalues.

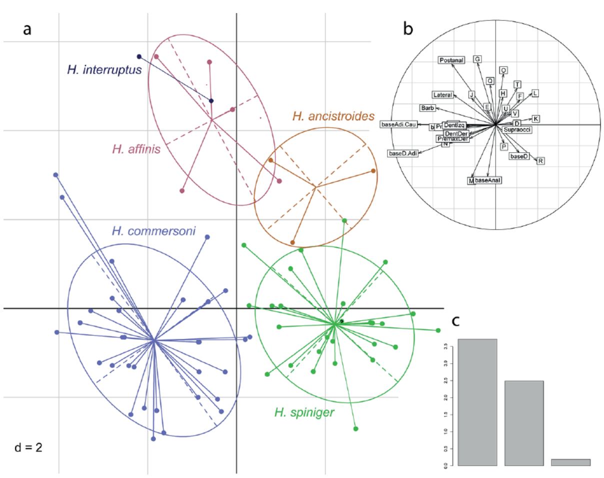

Figure 4 - Between-class Analysis (BCA) of morphological data of *H. commersoni*, *H. spiniger*, *H. affinis*, *H. punctatus* and *H. ancistroides*. **a**. Projection of individuals's scores onto first factorial plane of BCA, axis 1 horizontal and axis 2 vertical; **b**, Correlation of the variables labelled as in Tables I and II; **c**, Eigenvalues.

DIAGNOSIS

Hypostomus commersoni can be differentiated from all remaining species of the genus, except *H. affinis*, *H. punctatus*, *H. ancistroides*, and *H. spiniger*, by having the following features: bifid teeth (*vs.* spoon-shaped teeth), dark spots on a light background (*vs.* light spots on a dark background or not spotted), possession of four rough lateral ridges on flanks (*vs.* lacking strong ridges on flanks), 26-29 lateral series plates (*vs.* fewer than 28 in several species or 31-32 in *H. laplatae*), 1-2 plates bordering the posterior margin of the supraoccipital bone (*vs.* 3-4 in *H. laplatae*). *Hypostomus commersoni* can be distinguished from *H. affinis*, *H. punctatus*, and *H. ancistroides* by inter-dorsal distance (14.4-19.5% *vs.* 18.9-21.0% in SL in *H. affinis, H. punctatus*, and *H. ancistroides*) and head depth (49.0-71.6% *vs.* 48.2-49.9 in HL in *H. affinis, H. punctatus*, and *H. ancistroides*). It can be differentiated from *H. spiniger* by having fine lateral ridges with odontodes posteriorly inclined (*vs.* large lateral ridges with odontodes in all directions), weak lateral ridges in caudal peduncle (*vs.* strong lateral ridges in caudal peduncle), mid lateral ridge from first plate (*vs.* mid lateral ridge from 2nd or 3rd plates). Adult of *H. commersoni* (more than 120mm SL) can be also distinguished from adult of *H. spiniger* by having a

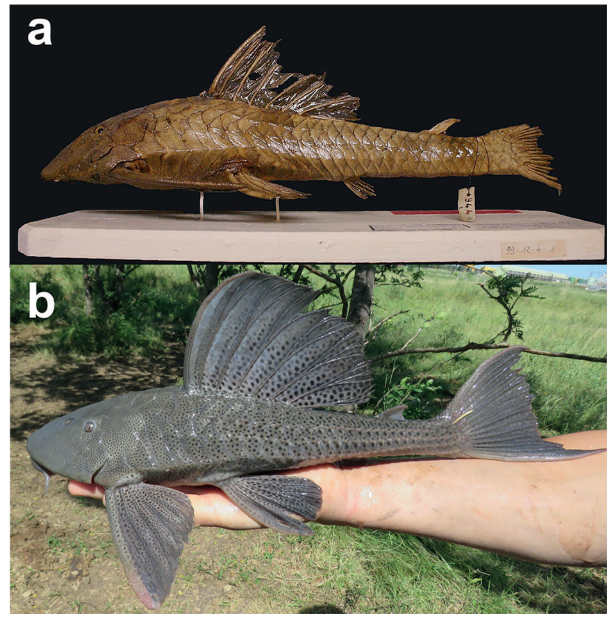

Figure 5 - *Hypostomus commersoni*: (**a**) holotype, MNHN A-9444, Dorsal view. (Photograph: Zawadzki, Claudio); (**b**) Live specimen from Arroyo El Morejón, Campana, Buenos Aires.

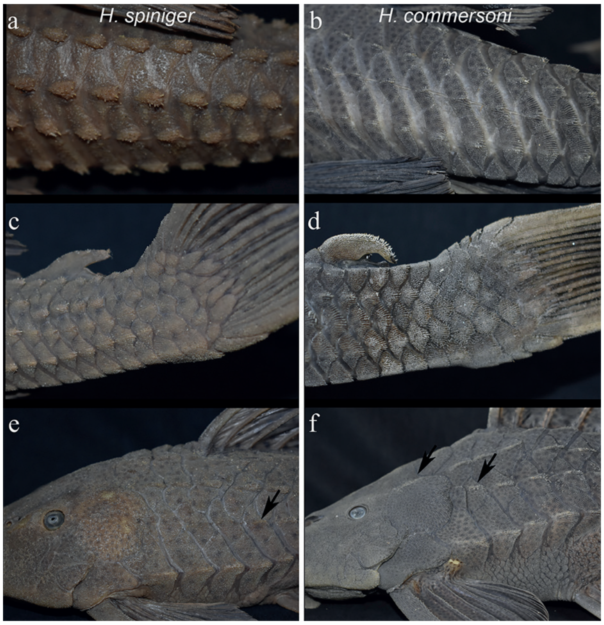

Figure 6 - Details of diagnostic characters between (**a, c, e**) *H. spiniger* and (**b, d, f**) *H. commersoni*. (**a, b**) lateral ridges; (**c, d**) lateral ridges in caudal peduncle; (**e, f**) mid lateral-rigde origin and rigde in temporal plate.

strong ridge on temporal plate (*vs*. very weak ridge on temporal plate) (Fig. 6).

According to the BPA (Fig. 4), other morphological characters might differentiate *H. commersoni* from *H. spiniger* but the range of these features partially overlaps: dentary and premaxillary teeth, plates between adipose and caudal fins, plates between dorsal and adipose fins, thoracic length, mandibular ramus length, caudal-peduncle depth, and orbit diameter, and by lower values of predorsal length and dorsal-fin spine length.

DESCRIPTION

Morphometric and meristic data in Table I. Overall view of body shape in Fig. 5. Dorsal profile rather straight from snout tip to interorbital area. Dorsal plates between end of dorsal-fin and adipose-fin spine flattened. Body width at cleithral region greater than head depth. Head covered dorsally with plates. Mouth rounded, lower lip not reaching transversal through gill openings, ventral surface covered with numerous small papillae. Dorsal-fin rays II,7; slightly convex. Adipose-fin spine curved inward. Pectoral-fin rays I,6; posterior border straight. Pectoral-fin spine slightly curved inward surpassing pelvic-fin origin when depressed. Pelvic-fin rays I,5; posterior border slightly curved. Pelvic-fin spine surpassing anal-fin origin when depressed. Anal-fin rays I,4; tip reaching seventh plate after its origin. Anal-fin rays progressively increasing in size, third branched ray usually longest. Caudal-fin rays I,14,I. Lower caudal-ray longer than upper.

COLORATION

Background color of head and trunk dark brown or gray with small, irregular-shaped black spots on head and larger and more widely-spaced spots on dorsum, some specimens with more prominent dots. All fins dark brown or gray with inter-radial membranes hyaline and irregularly-shaped small black spots. Abdominal region light brown or gray, usually with vermiculated spots but some specimens without. Coloration is more pronounced in live specimens.

GEOGRAPHIC DISTRIBUTION

Hypostomus commersoni inhabits the Lower Paraná, including the Iguazú (Garavello et al. 2012), Paraguay, Río de la Plata, and Dulce Rivers. In a thorough survey of *Hypostomus* species from the Paraíba do Sul River, Mazzoni et al. (1994) concluded that *H. commersoni* does not occur in this river basin, and that previous citations of this species in this river were misidentifications. Similarly, Oyakawa et al. (2005) confirmed its absence in the Ribeira de Iguape River system. The present analysis of *Hypostomus* specimens from the Uruguay River and the Dos Patos Lagoon system previously identified as *H. commersoni* revealed that these specimens exhibit several discriminating features when compared to those from the Río de la

Plata, Paraná, and Paraguay rivers. The examined specimens from the Uruguay River and the Dos Patos Lagoon system previously attributed to *H. commersoni* are herein identified as *H. spiniger* (Hensel 1870).

ECOLOGICAL NOTES

The substrate of the rivers from which specimens were obtained was composed chiefly of muddy sand. *Hypostomus commersoni* was found in moderately oxygenated waters (6.1-9.1 mg/l) with moderate current. Water turbidity was 23.7-442 NTU, conductivity 1.087-2.654 µS/cm, pH 7.2-9.2, and temperature 16.8-27.8°C.

CONSERVATION STATUS

Populations of *H. commersoni* studied here were from a broad region. The estimated values for IUCN criterion B were: EOO = 551.286 km² and AOO = 100 km², categorizing *H. commersoni* as a Species of Least Concern.

REMARKS

Valenciennes (1836) based the description of *H. commersoni* on two specimens from São Francisco Basin (Brazil) and two specimens from Río de la Plata (Uruguay). Weber (1986) after revision of type-series in the Museum National d'Histoire de Paris, designated MNHN a-9444 as lectotype and restricted the type-locality to Río de la Plata, Montevideo, Uruguay. *Hypostomus spiniger* from Cadeira River was described by Hensel (1870), but Steindachner (1877) considered this species a junior synonym of *H. commersoni*. *Hypostomus limosus* from Rio Grande do Sul was described by Eigenmann and Eigenmann (1888). Malabarba (1989) added *H. limosus* as another junior synonym of *H. commersoni.* Reis et al. (1990) re-described *H. commersoni*, but they reviewed only specimens from the Uruguay River and Dos Patos Lagoon system in Southern Brazil; and outside this region examined only the lectotype. Garavello et al. (2012) also re-described *H. commersoni*, but examined only specimens from the Iguazú Basin. Based on the morphological and molecular results, specimens previously identified as *H. commersoni* can be clearly separated into two species: *Hypostomus commersoni* inhabiting the Paraná, Paraguay, and Río de La Plata and a second species inhabiting the Uruguay River and Dos Patos Lagoon system which is considered here as *H. spiniger* described by Hensel (1870).

MATERIAL EXAMINED

Argentina: CFA-IC-5543, 3, 40.8-60.2 mm SL, Pozo Añatuya, Santiago del Estero.CFA-IC-5539, 7, 61.3-214.0 mm SL, Tacañitas, Santiago del Estero. CFA-IC-5730, 1, 286.8 mm SL, Tacañitas, Santiago del Estero. CFA-IC-5517, 18, 45.5-85.2 mm SL, Saladillo River and Ruta 92 between Colonia Dora and Los Telares, Santiago del Estero. CFA-IC-3150, 4, 42.3-75.9 mm SL, Corrientes. CFA-IC-3161, 4, 38.4-2.5 mm SL, Entre Ríos. CFA-IC-3381, 3, 338.4-349.1 mm SL, San Nicolás de los Arroyos, Delta of the Paraná River, Buenos Aires. CFA-IC-3380, 9, 290.3-327.1 mm SL, Vuelta of Obligado, Delta of the Paraná, Buenos Aires. CFA-IC-3379, 15, 256.3-329.8 mm SL, San Pedro, Delta of the Paraná River, Buenos Aires. CFA-IC-3005, 1, 285.6 mm SL, Villa Paranacito, Entre Ríos. MLP 9400, 5, 55.6-197.7 mm SL, Reconquista River, Buenos Aires. MLP 7687, 9, 43.5–71.6 mm SL, Golf Club Lakes of Palermo, Buenos Aires. MLP 10003, 1, 70.9 mm SL, Stream Balta, approximately 100 of the bridge RN5, Mercedes, Buenos Aires. MLP 10025, 1, 71.2 mm SL, Stream La Choza, General Rodríguez, Buenos Aires. MLP 10026, 1, 71.5 mm SL, idem previous location.CFA-IC-3372,16, 332.3-366.7 mm SL, Club de Regatas, Ensenada, Rio Santiago, Buenos Aires. CFA-IC-3373, 1, 408.5 mm SL, Los Talas, Berisso, Buenos Aires.

Hypostomus spiniger (Hensel 1870)

Plecostomus spiniger Hensel, 1870: 73. Type locality: Rio Cadea (=Cadeia River), Rio Grande do Sul, Brazil. Holotype: ZMB 7444 (Fig. 7).

Plecostomus limosus Eigenmann and Eigenmann, 1888: 167. Type locality: Rio Grande do Sul, Brazil. Lectotype: MCZ 7869, designated by Reis et al. (1990: 737). Name made available by diagnostic features in key: 168.

DIAGNOSIS

Hypostomus spiniger can be differentiated from all remaining species of the genus, except *H. affinis*, *H. punctatus*, *H. ancistroides*, and *H. commersoni*, by having the following features: bifid teeth (*vs*. spoon-shaped teeth), dark spots on a light background (*vs*. light spots on a dark background or not spotted), the presence of four rough lateral ridges on flanks (*vs*. lacking strong ridges on flanks), 26-29 lateral series plates (*vs*. fewer than 28 in several species or 31-32 in *H. laplatae*), 1-2 plates bordering the posterior margin of the supraoccipital bone (*vs*. 3-4 in *H. laplatae*). *Hypostomus spiniger* can be distinguished from *H. affinis*, *H. punctatus*, and *H. ancistroides* by inter-dorsal distance (14.7-20.4% *vs*. in SL 18.9-21.0% in *H. affinis, H. punctatus*, and *H. ancistroides*) and head depth (48.8-76.4% *vs*. 48.2-49.9% in HL in *H. affinis, H. punctatus*, and *H. ancistroides*). It can be differentiated from *H. commersoni* by having large lateral ridges with odontodes posteriorly inclined (*vs*. fine lateral ridges with odontodes in all directions), strong lateral ridges in caudal peduncle (*vs*. weak lateral ridges in caudal peduncle), mid lateral ridge from 2nd or 3rd plate (*vs*. mid lateral ridge from first plate). Adult of *H. spiniger* (more than 120mm SL) can be also distinguished from adult of *H. commersoni* by having a very weak ridge on temporal plate (*vs*. strong ridge on temporal plate) (Figs. 6-8).

According to the BPA (Fig. 4), other morphological characters might differentiate *H. spiniger* from *H. commersoni* but the range of these features partially overlaps: dentary and premaxillary teeth, plates between adipose and caudal fins, plates between dorsal and adipose fins, thoracic length, mandibular ramus length, caudal-peduncle depth, and orbit diameter, and by lower predorsal length and dorsal-fin spine length.

Figure 7 - *Hypostomus spiniger*: (**a**) holotype, ZMB 7444 (Photographs: Allen, Mark); (**b**) Live specimen from Uruguay River Chajarí, Entre Ríos.

DESCRIPTION

Morphometric and meristic data in Table I. Overall view of body shape in Figs. 7 and 8. Dorsal profile nearly straight from snout tip to inter orbital area. Dorsal plates between the insertion of the dorsal fin and adipose fin. Body width at cleithral region greater than head depth. Head covered dorsally with plates. Mouth rounded, lower lip not reaching transversal line through gill openings, ventral surface covered with numerous small papillae. Dorsal-fin rays II,7; margin straight. Adipose-fin spine curved toward the body. Pectoral-fin rays I,6; posterior border straight. Pectoral-fin spine curved slightly inward. Pelvic-fin rays I,5; posterior border slightly curved. Pelvic-fin spine extends past anal-fin origin when depressed. Anal-fin rays I,4; tip reaching seventh plate posterior to the origin. Anal-fin rays progressively increasing in length, third branched ray usually longest. Caudal-fin rays I,14,I.

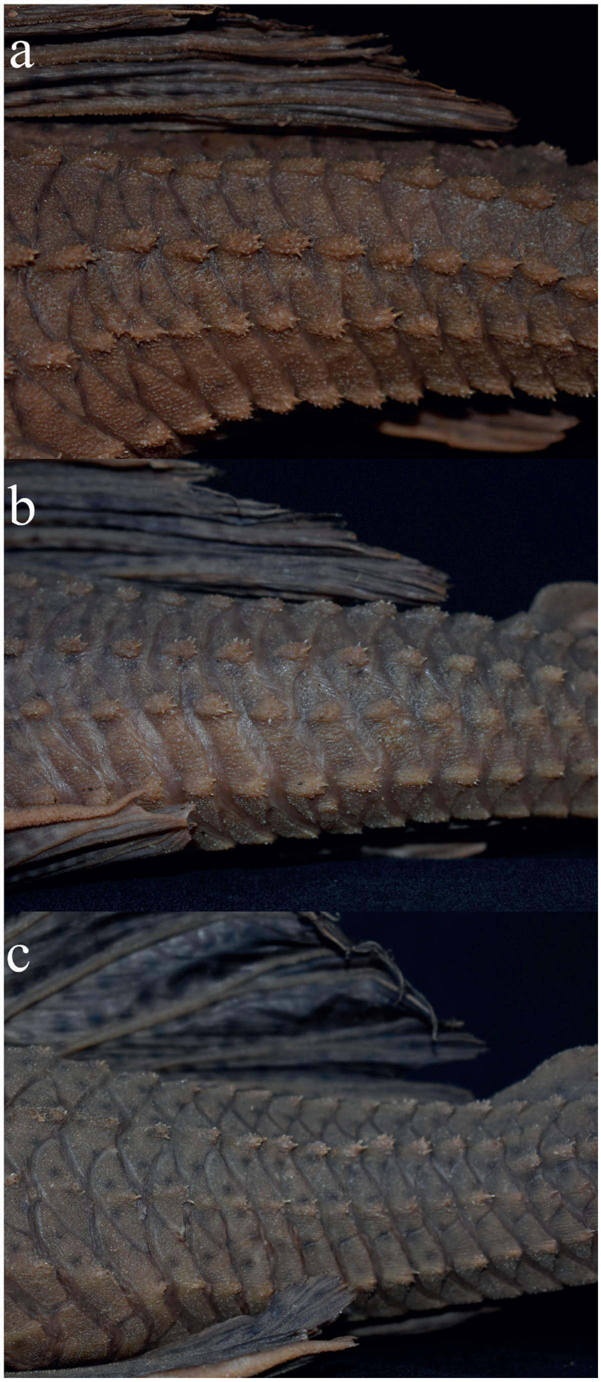

Figure 8 - Details of the lateral ridges in *H. spiniger*.

COLORATION

Background color of head and trunk dark brown or gray, small, irregular black spots on head and larger and more widely spaced spots on dorsum, some specimens with more prominent spots. All fins dark brown or gray, inter radial membranes hyaline with irregular small black spots. Abdominal region pale brown or gray, usually with circular or vermiculated spots. Coloration was more pronounced in live specimens.

GEOGRAPHIC DISTRIBUTION

Hypostomus spiniger inhabits the Uruguay River and Dos Patos system. The southernmost sampled locality was Gualeguaychú, Entre Ríos, Argentina.

ECOLOGICAL NOTES

Based on the locality of sample CFA-IC-3370 and CFA-IC-3371. The substrate is mainly composed of sand. *Hypostomus spiniger* was found in oxygenated waters (8.4-9.0 mg/l) with moderate current. Water turbidity was 22.4-74.2 NTU., conductivity 567-1909 µS/cm, pH 7.6-8.3, and temperature 19.8-25.3°C.

CONSERVATION STATUS

Hypostomus spiniger is reported from a wide region in Argentina and Brazil, and also occurs in Uruguay. The estimated values for criterion B were: EOO = 251.934 km^2 and AOO = 72 km^2. According to IUCN criteria *H. spiniger* can be categorized as a Species of Least Concern.

REMARKS

Hensel (1870) described *H. spiniger* as a new species, based on dry specimens from the Cadea (Cadeira, Cadeia) River, in Rio Grande do Sul State. Steindachner (1877) proposed *H. spiniger* as a junior synonym of *H. commersoni*. Later, Eigenmann and Eigenmann (1888:168) described *H. limosus* based on four specimens from the Rio Grande do Sul, name made available by diagnostic features in a key. Malabarba (1989) restricted the type locality of *H. limosus* to the Dos Patos Lagoon and considered this species a junior synonym of *H. commersoni*. Reis et al. (1990) described the lectotype of *H. limosus* and reviewed several specimens of *H. commersoni* from the Uruguay River and Dos Patos Lagoon system from Southern Brazil, as well as the type-series of *H. spiniger*. However, their examination was limited to the dry lectotype of *H. commersoni* from Río de La Plata; no other specimens from this basin or from the Paraná or Paraguay basins were analyzed. The morphological and molecular results show clear differences between the specimens from Uruguay/ Dos Patos Lagoon and Paraná/Paraguay/Río de La Plata. Of the species described from the Dos Patos system, *H. spiniger* has priority by date, thus it is considered a valid species, with *H. limosus* being its junior synonym.

MATERIAL EXAMINED

Brazil: ZMB 7444, holotype of *Plecostomus spiniger*, examined by photograph, Cadeia River, Rio Grande do Sul. MCZ 7869 lectotype of *Plecostomus limosus*, examined by photograph, Rio Grande do Sul. BMNH 1904.1.28.1 paralectotype of *Plecostomus limosus* examined by photograph. MHNG 2517.62, 1, 127.5 mm SL, Ibicuí da Foxina. MCP10530, 1, 118.4 mm SL, Guaiba Lagoon Guiaba in Ponta do Jacare, Rio Grande do Sul. MCP10496, 1, 118.9 mm SL, Uruguay Basin, Conceição River, Rio Grande do Sul. MCP27618, 1, 84.6 mm SL, Uruguay Basin, Stream Carai-Passo, in São Francisco de Assis/ Manoel Viana, Rio Grande do Sul.

Argentina: MLP5132, 1, 52.5 mm SL, San Javier, Misiones. CFA-IC-, 1, 56.7 mm SL, Ayui River, Corrientes. CFA-IC-3745, 1, 92.1 mm SL, Tres Cerros in route 114, Corrientes. CFA-IC-3369, 1, 273 mm SL, route 14 to 15 km of Mocoretá, Corrientes. CFA-IC-3370, 1, 283 mm SL, Santo Tomé in route 94, Corrientes. CFA-IC-3371, 4, 295-325 mm SL, route 14 to 11 km of Chajari, Entre Ríos. CFA-IC-5829, 3, 65-157 mm SL, Stream El Doctor, Entre Ríos. CFA-IC-5305, 1, 198 mm SL, Stream El Pelado, Entre Ríos. CFA-IC-5854, 3, 103-242 mm SL, Stream Urquiza, Entre Ríos. CFA-IC-5960, 1, 86.7 mm SL, Concepción del Uruguay, Entre Ríos. MLP10067, 1, 126 mm SL, Stream without name to 10 km of Concepcion del Uruguay, Entre Ríos. MLP10068, 1, 76.4 mm SL, Stream without name to 10 km of Concepcion del Uruguay, Entre Ríos. MLP10069, 1, 63 mm SL, Stream without name to 10 km of Concepcion del Uruguay, Entre Ríos. CFA-IC-3324, 1, 82.7 mm SL, Stream Urquiza, Entre Ríos. CFA-IC-6904, 3, 66.7-79.2 mm SL, Stream La Capilla, Gualeguaychú, Entre Ríos.

Hypostomus cordovae (Günther 1880)

Plecostomus cordovae Günther 1880: 11-12.Type locality: Córdoba, Argentina. Holotype: BMNH 1878.4.4.1 (Fig. 9)

DIAGNOSIS

Hypostomus cordovae can be differentiated from all remaining species of the genus by having the following features: bifid teeth (*vs.* spoon-shaped teeth), dark spots on a light background (*vs.* light spots on a dark background or not spotted), absence of four rough lateral ridges on flanks (*vs.* presence strong ridges on flanks in *H. commersoni*, *H. spiniger* and *H. laplatae*), 28-30 lateral series plates (*vs.* fewer than 28 in several species or 31-32 in *H. laplatae*), height body (13.3-18.1% *vs.* 17.7-24.7% in SL in *H. commersoni*, *H. spiniger* and *H. laplatae*), and head length (25.9-30.7 *vs.* 27.5-38.7 in SL in *H. commersoni*, *H. spiniger* and *H. laplatae*).

DESCRIPTION

Morphometric and meristic data in Table II. Overall view of body shape in Fig. 9. Dorsal profile of body rises smoothly from snout to supraoccipital process, continuing to dorsal fin and descending to distal end of caudal peduncle. Height of body less than cleithral width. Body in cleithral region wider

Figure 9 - *Hypostomus cordovae*: (**a**) holotype, BMNH 1878.4.4.1. Dorsal view. (Photograph: Natural History Museum, London); (**b**) Live specimen from Quinto River, Córdoba.

than depth of head. Body width constant to base of pelvic fins and narrows toward base of caudal fin. Head roughly triangular in dorsal view, with flattened area between orbits. Head covered with plates dorsally, except for area on snout tip. Slightly rounded snout with crest. Labial disc rounded, upper lip with small papillae and lower lip covered by more than two rows of papillae, of which size decreases toward lip margin. Ventral surface of head and body completely covered by small plates. Lateral line on median series of plates complete. Caudal peduncle compressed, especially posterior to adipose-fin spine. Dorsal and ventral surfaces of caudal peduncle slightly flattened. Dorsal fin I,7; dorsal-fin spine usually shorter than head length, posterior edge slightly convex or nearly straight. Dorsal-fin base without dermal ossifications, extended dorsal fin not reaching origin of adipose fin. Pectoral fins I,6; distal edge nearly straight, when extended reaching past origin of pelvic fins. In adult males, pectoral fins with well-developed odontodes. Pelvic fin I,5; extend past anal-fin origin when extended, distal edge rounded. Anal fin, I,4; external edge almost straight. Caudal fin, I,14,I; posterior margin concave. Ventral-most caudal-fin ray usually longer than dorsal-most.

COLORATION

Background color of dorsal and lateral regions of body dark gray with roughly circular black spots. Spots small and closely spaced on head, larger and more widely spaced posterior. Ventral region with light gray background color and circular, irregular, and kidney-shaped spots. In small specimens, spots forming series of crosswise bands on body: first on head, second at origin of dorsal-fin spine, third at sixth dorsal-fin branched ray, fourth anterior to adipose-fin spine, and final on 3rd or 4th plate of caudal peduncle. Fins with black dots on inter radial membrane. In some specimens, dorsal fin with variable number of zigzagging black bands (Fig. 9). Dots on pectoral fin smaller than those on other fins. Black dots more prominent in live specimens. Background color of body yellowish brown in specimens from Segundo River Basin (Argentina).

GEOGRAPHIC DISTRIBUTION

Hypostomus cordovae occurs in the Primero, Segundo, Cuarto, and Quinto Rivers in the Córdoba Province; in the Horcones River in Santiago del Estero; the Juramento River in Salta; and in Del Cajón, Calera, and Salí Rivers in Tucumán Province. This species is also reported in Catamarca, Jujuy, Santa Fe (in the Carcarañá River), and San Luis (Liotta 2017). Ringuelet et al. (1967) cited *H. cordovae* from Ituzaingó, Corrientes (Paraná River), but the examination of this material allowed us to confirm that the specimens were misidentified.

ECOLOGICAL NOTES

Specimens were recently obtained from seven rivers. The substrate of those rivers was mainly composed of sandstone boulders with patches of coarse sand and pebbles. *Hypostomus cordovae* was found in well-oxygenated waters (6.9-11.2 mg/l) with strong current. Water turbidity was 1.29-

75.1 NTU, conductivity 77-4.530 μS/cm, pH 7.8-8.8, and temperature 20.7-31.4°C.

CONSERVATION STATUS

Populations of *H. cordovae* are known from a wide region in Argentina. They are endemic to this country, and not considered under imminent threat. The estimated values for criterion B were: EOO = 58.445 km^2 and AOO = 48 km^2, thus, according to IUCN criteria, *H. cordovae* can be categorized as a species of Least Concern (LC).

REMARKS

The name *H. paranensis* was used by Weyenbergh (1877) for a single specimen of *Hypostomus* from the marshes around Santa Fe. This author did not designate type material and only mentioned that "*La especie del Paraná me parece distinta por la forma y el menor número y tamaño de las manchitas negras, los que produce en general otro color*" (The Paraná species seems different because of the shape and the smaller number and size of the black spots, which usually produces a different pattern). According to Eschmeyer et al. (2017) there are (several) syntypes in the MNAC (supposedly referring to the MACN), however, no specimens of *Hypostomus paranensis* are included in the collection or in the database of this museum.

Later, Günther (1880) described *Plecostomus cordovae* on the basis of a specimen originating from Córdoba. Berg (1895) proposed that *P. cordovae* is synonymous with *Plecostomus commersonii affinis* (Eigenmann and Eigenmann 1888) and mentioned that this species "*se halla en los mismos ríos y arroyos que la especie típica* Plecostomus commersoni *(C. V.) Gunth*" (…is found in the same rivers and streams as the type species *Plecostomus commersoni (C. V.) Gunth*). Several decades later, Ringuelet et al. (1967) and López and Miquelarena (1991) recognized *H. cordovae* as valid, considering *H. paranensis* as a junior synonym. Weber (2003) considered the name *H. paranensis* as "*nomen oblitum*" and *H. cordovae* as a "*nomen protectum*", however this was suggested without providing justification. More recently, Ferraris (2007), based on the priority principle, established that *H. paranensis* is a valid species, and that *H. cordovae* is a junior synonym of *H. paranensis*. Recently, *H. paranensis* was included as a valid species on the list of species of *Hypostomus* from Argentina (Koerber and Weber 2014). Based on the analysis of the literature and according to the International Code of Zoological Nomenclature (1999), the name *H. paranensis* is considered available. However, the exhaustive examination of specimens from the region surrounding the cities of Santa Fe and Córdoba strongly suggests that *H. paranensis* must be considered as *species inquirenda*. The morphological and molecular results show that all specimens from the Paraná River near Santa Fe City can be identified as *H. commersoni*. The examination of the holotype of *H. cordovae* and the new material from Córdoba indicates that this species can be clearly differentiated and is valid.

MATERIAL EXAMINED

BMNH 1878.4.4.1, holotype of *Plecostomus cordovae*, examined by photograph (Fig. 9), Córdoba. CFA-IC-3140, 16, 40-171.7 mm SL (10, 42.1-171.7 mm SL), Horcones River, Santiago del Estero. CFA-IC-3131, 17, 37.5-70.9 mm SL (9, 37.5-70.9 mm SL), del Cajón River, Tucumán. CFA-IC-3041-3053, 13, 40-216.8 mm SL (8, 48.1-216.8 mm SL), Salí River, Calera River, Tucumán. CFA-IC-11914, 2, 56-68 mm SL, Primero River, in front of Isla Los Patos, Córdoba. CFA-IC-3368, 10, 114.2-231.4 mm SL, Mar Chiquita Basin, Anisacate River, Segundo River, Córdoba. CFA-IC-3734, 2, 65-87 mm SL, Cuarto River, Córdoba. CFA-IC-3367, 10, 73.6-247.5 mm SL, Quinto River, near to Villa Sarmiento, Córdoba.

Hypostomus laplatae (Eigenmann 1907)

Plecostomus laplatae Eigenmann, 1907: 450-451, pl. 21 (Figs. 1-3). Type locality: Buenos Aires, Argentina. Paratype: CAS 77342 (Fig. 10).

Plecostomus taeniatus Regan, 1908: 358. Type locality: Río La Plata, Argentina.

Plecostomus commersonoides Marini, Nichols and La Monte, 1933: 3-4. Type locality: Dársena Norte, Buenos Aires, Argentina.

DIAGNOSIS

Hypostomus laplatae can be differentiated from all remaining species of the genus by having the following features: bifid teeth (*vs.* spoon-shaped teeth), dark spots on a light background (*vs*. light spots on a dark background or not spotted), possession of four rough lateral ridges on flanks (*vs*. lacking strong ridges on flanks), 31-32 lateral series plates (*vs*. fewer than 30 in several species), 3-4 plates bordering the posterior margin of the supraoccipital bone (*vs.* 1-2 in *H. commersoni* and *H. spiniger*) and inter-orbital width (30.5-38.6% *vs*. 36.2-56.3% in HL in *H. commersoni* and *H. spiniger*).

DESCRIPTION

Morphometric and meristic data in Table II. Overall view of body shape in Fig. 10. Dorsal profile of body convex from snout to supraoccipital bone, then continuing straight to origin of dorsal fin. Body height less than cleithral width. Cleithral region wider than head height. Body width constant to base of pelvic fin, then narrowing toward base of caudal fin. Head with flattened area between orbits. Slightly rounded snout, more than half length of head. Snout completely covered by small plates. Rounded labial disc, upper lip with small papillae and lower lip covered by more than two rows of papillae that became smaller toward labial margin. Bifid teeth. Relatively small eye; weak crest anterior to eye. Supraoccipital bone bordered by medial plate and 2-4 lateral plates. Smaller irregularly-

Figure 10 - *Hypostomus laplatae*: (**a**) paratype, CAS 77342. Dorsal view. (Photograph: California Academy of Sciences, San Francisco); (**b**) Live specimen from Lower Paraná River, San Pedro, Buenos Aires.

shaped plates on head. Ventral surface covered by small plates including between pectoral fins and anterior to anus. Compressed caudal peduncle, mainly anterior to adipose-fin spine, length greater than depth. Dorsal and ventral surfaces of caudal peduncle slightly flattened. Dorsal fin I,7; posterior border slightly convex or almost straight. Pectoral fins I,6; border almost straight, extending past origin of pelvic fins. In adult males, pectoral-fin spines has well developed odontodes. Pelvic fins I,5, extending past origin of anal fin, rounded distal border. Anal fin, I,4; external border nearly straight. Caudal fin I,14,I; with concave margin. Lower caudal-ray longer than upper.

COLORATION

Body and head dark grayish or brown background, with roughly circular spots of various sizes. Smaller and more numerous spots on head, more irregular spots in dorsal body. Ventral surface grayish-white, with irregular-shaped black spots. Fins with black spots on inter radial membrane, rays, and base, with exception of anal and caudal fins, uniformly colored; some specimens with a darker distal portion. Body and head more grayish background in live specimens.

DISTRIBUTION

Hypostomus laplatae occurs in the Río de la Plata (type locality) and the Lower Paraná River. The species has been reported in the provinces of Salta and Corrientes (Liotta 2017), but no collected specimens are available to corroborate the identification in these localities.

ECOLOGICAL NOTES

Specimens were recently obtained from two rivers, the substrates of which are primarily sand. *Hypostomus laplatae* was found in oxygenated waters (5.4-7.4 mg/l) with moderate current. Water turbidity was 260-392 NTU, conductivity 543-2,435 µS/cm, pH 7.8-8.1, and temperature 15.3-20.4°C.

CONSERVATION STATUS

Hypostomus laplatae is recorded in a limited region of the Lower Paraná River and Río de la Plata. The estimated values for criterion B were EOO = 15.827 km² and AOO = 20 km². Following the IUCN criteria (IUCN 2017), a given species can be categorized as "Endangered" if, in addition to small EOO (B1) and AOO (B2), two out of three sub criteria were found: (i) to be severely fragmented or occupy a limited number of locations (ii) present continuing generation decline; and (iii) present extreme fluctuations. Thus, *H. laplatae* can be classified as Near Threatened.

REMARKS

Plecostomus laplatae was described based on specimens from Buenos Aires (Eigenmann 1907). Forty years later, Gosline (1947) considered *H. taeniatus* and *H. commersonoides* as junior synonyms of *H. laplatae*, both also described from Buenos Aires. The holotype and paratypes of *Plecostomus commersonoides* (AMNH 12243 and AMNH 12244) were not found in the collection (checked recently). Gosline (1947) also suggested that *H. rachovii* (Regan 1913) could be related to the mentioned species, without having seen material of those species. López and Miquelarena (1991) presented a revised description of *H. laplatae* based on four specimens (not found in the collection of Museo de La Plata) from the Río de la Plata. Weber (2003) analyzed the syntypes of *H. taeniatus* and the holotype of *H. rachovii* and considered them synonyms, adding *H. rachovii* to the list of junior synonyms of *H. laplatae*. Ferraris (2007) stated that the synonymy of *H. taeniatus* and *H. rachovii* is probably an error.

MATERIAL EXAMINED

Argentina: *Plecostomus laplatae*: CAS 77342, paratype, examined by photograph (Fig. 10), Buenos Aires. *Plecostomus taeniatus*: BMNH 1908.8.29.17, syntype, examined by photograph, Río de la Plata. *Hypostomus laplatae*: CFA-IC-3011, 1, 343 mm SL, Villa Paranacito, Entre Ríos. CFA-IC-3020, 1, 345 mm SL, Vuelta de Obligado, Buenos Aires. CFA-IC-3007, 1, 371 mm SL, San Pedro, Buenos Aires. CFA-IC-3008, 1, 257 mm SL, San Pedro, Buenos Aires. CFA-IC-3010, 3, 385-466 mm SL, Río de la Plata, Punta Lara, Buenos Aires. CFA-IC-3018, 1, 370 mm SL, Río de la Plata, Punta Lara, Buenos Aires. CFA-IC-3013, 3, 385-461 mm SL, Río de la Plata, Punta Lara, Buenos Aires. CFA-IC-3012, 1, 385 mm SL and CFA-IC-3015, 2, 423-441 mm SL, Río de la Plata, Punta Lara, Buenos Aires.

DISCUSSION

The identification of *Hypostomus* species is a challenge, given the complex taxonomy of the group and the sparse morphological information available for many species. Thus application of multisource approaches (ecology, distribution, morphology, molecular phylogeny) takes advantage of complementarity among disciplines and is crucial to detecting cryptic diversity within the genus (Dayrat 2005). Valid taxonomic identification is critical to estimate the diversity of freshwater environments, including the Neotropical Region. Discoveries of new fish species contribute not only to evaluate regional faunal diversity but to reconstruct the geohistory of South American river basins.

SPECIES DIVERSITY AND TAXONOMIC IMPLICATIONS

Several of the many *Hypostomus* species identified and described in recent years were previously grouped under a single species name. In the present study, an exhaustive examination of *H. commersoni* specimens revealed the existence of a cryptic form which was resurrected and re-described as *H. spiniger*. Significant differences were documented between *H. commersoni* and *H. spiniger*: In the molecular analyses they formed separate monophyletic groups instead of being sister species. They show high levels of genetic and morphological differentiation and occur in different river basins without overlap of their distributional ranges. Comparison with other species inhabiting the Lower La Plata Basin and other watersheds, confirm that *H. spiniger,* although considered for several years a junior synonym of *H. commersoni,* is a valid species. Revalidation of formerly described species is being made possible by the examination of large numbers of specimens and robust analyzes. Similar results were found by Bertaco and Lucena (2010) when they analyzed two species of *Astyanax* from the Dos Patos system: *Astyanax obscurus* and *A. laticeps* were once considered junior synonyms of other species and recently re-validated. Interestingly, *Astyanax obscurus* was described by Hensel (1870) from the same type locality as *H. spiniger* (Cadeia River).

Hypostomus cordovae and *H. paranensis* are little-known species described more than a century ago and only cited in fish catalogues. The species were considered synonyms by several authors (López and Miquelarena 1991, Weber 2003, Ferraris 2007) without clear explanations. Based on morphological and molecular data of specimens from near Santa Fe (type locality), and on the original description of *H. paranensis* (without assigned type material), this name should be considered as *species inquirenda*. Thus, the name *H. paranensis* remains available in the event that further taxonomic studies reveal diagnostic characters to differentiate it from other species.

The examination of the holotype of *H. cordovae* and the new material from its type locality allows us to consider this species as valid. The molecular data showed that *H. cordovae* is closely related to *H. commersoni*; nevertheless, they are readily distinguished morphologically. The differentiation of these species is crucial, since they have the widest distribution of any fish species in the La Plata Basin. Haro and Bistoni (2007) stated that both species would be present in the Dulce and Cuarto Rivers. Both species were sampled in the Dulce and Salado Rivers but no evidence of sympatric distribution were found. *Hypostomus cordovae* was found exclusively in the headwaters of the rivers, on stony substrates and well-oxygenated, fast-flowing water, while *H. commersoni* is found primarily in lentic environments with muddy substrates. The ecological characteristics of *H. cordovae* support the premise that *H. paranensis* described from the marshes around Santa Fe cannot be considered the same species.

In this study freshly collected specimens of *H. laplatae* were compared with the species considered synonyms. The material concurs with the original description by Eigenmann (1907), and allows to conclude that *H. taeniatus* and *H. commersonoides* are the same species. However, the holotype of *H. rachovii* from Rio de Janeiro shows significant morphological differences: a narrower snout, wider interorbital distance, larger dorsal-fin base and a caudal fin with dark bars. These morphological features and the thousand kilometers separating the type locality of *H. rachovii* from the type locality of *H. laplatae*, suggest that *H. rachovii* is not a conspecific of *H. laplatae.* Similarly, Mazzoni et al. (1994) suggested *H. rachovii* as a junior synonym of *H. punctatus* Valenciennes 1840, also described from Rio de Janeiro. *Hypostomus laplatae* appears confined to the Lower Paraná River and the Río de la Plata. These data show that it is sympatric with *H. aspilogaster*, *H. uruguayensis*, and *H. commersoni*, and is one of the species with a southern distribution.

SPECIES CONSERVATION STATUS

The IUCN Red List provides information on which species are most threatened and provides a basis for conservation priority. It is also a powerful tool for persuading governments to protect threatened species and their habitats (IUCN 2017). The Red List is a valuable compendium of information on threats to species, but coverage of little-studied freshwater taxa in the list is limited (Barletta et al. 2010). This is probably due to lack of knowledge of their taxonomic identity, distribution, evolution, and population dynamics (Baigún et al. 2012). These gaps in the knowledge of freshwater taxa need to be recognized, as biased and under-represented information compromises our capacity to describe existing biodiversity and to make accurate predictions of potential change (Hortal et al. 2015). For these reasons, works about species distribution and check-lists of different regions are still very important (Cabrera et al. 2017, Cardoso and Bogan 2015, Bogan and Cardoso 2017).

Based on criterion B, *H. laplatae* has small values of EOO and AOO and can consider into the Near Threatened category (IUCN 2017). The distribution range of this species is the greater urban area of La Plata Basin, impacting the quality of its water (Peluso et al. 2013). The Lower Paraná and Río de la Plata basins present high concentrations of solid waste, heavy metals, hydrocarbons, and persistent organic compounds, especially concentrated in sediments (FREPLATA 2005, Galindo et al. 2007, Peluso et al. 2013). The conservation status of *H. laplatae,* with benthic habits, may be dramatically affected by the environmental conditions of its limited distribution range. Indeed, *Hypostomus laplatae* suffers continuing decline in habitat quality, this partial meeting of the criteria will make this species Near Threatened. Currently there are not data to evaluate the criteria i and iii for this species which is essential and should be analyzed in subsequent studies.

BIOGEOGRAPHY OF *HYPOSTOMUS* IN THE LOWER LA PLATA BASIN

To the known species from the Lower La Plata Basin may potentially be added *H. itacua* Valenciennes 1836, which can be considered an "*incertae sedis species*" (Koerber and Weber 2014), along with several reported unidentified *Hypostomus* sp (unpublished data). The phylogenetic tree (Fig. 2) concurred with those presented previously (Montoya-Burgos 2003, Cardoso et al. 2012, 2016) and shows that *H. laplatae* belongs to a different lineage from *H. commersoni*, *H. spiniger*, and *H. cordovae*. This indicates that the diversity of *Hypostomus* in the Lower La Plata Basin is significant, not only in number of species, but also in number of phylo-groups. Elucidating phylogenetic relationships among *Hypostomus* of La Plata Basin is important for a better understanding of the biogeography of this basin.

Non-overlapping distribution ranges were found among the closely related species *H. cordovae*, *H. commersoni*, and *H. spiniger* belonging to the D2 lineage, with a distribution organized in a west-east geographic manner (Fig. 1). In the western site of the Lower La Plata Basin, *H. cordovae* inhabits the headwater streams in the piedmont, with strong flows and highly-oxygenated water rich in dissolved minerals. The substrate comprises rocks and stones (Miquelarena et al. 1990, Isasmendi et al. 2007). The species displays a morphology adapted to these environmental conditions, including a long, deep body and large mouth. *Hypostomus commersoni* and *H. spiniger* inhabit wide river channels: the Paraná River in the central area of the La Plata Basin, and the Uruguay River in the eastern La Plata Basin, respectively, rivers that are dissimilar in physical and chemical characteristics. The mean values of conductivity and suspended nutrients and solids are higher in the Paraná River than in the Uruguay River (Di Persia and Neiff 1986, Quirós and Cuch 1989). The load of suspended solids contributed by the Paraguay and Bermejo rivers is the source of the high turbidity in the Paraná River (Bonetto 1986). In contrast, the Uruguay River presents high clarity associated with slower current and low suspended solids (INCYTH, 1978). The substrate of the Paraná River consists of medium and fine sand and a large silt-clay fraction (Di Persia and Neiff 1986), while the Uruguay River has a rocky bed (Quirós and Cuch 1989). These characteristics persist until the Río de la Plata interior, where the north coast is sandy, while sediments on the south coast are principally silt-clays (Quirós and Cuch 1989).

Since there are no physical barriers to dispersion in the distribution areas of *H. commersoni*, *H. spiniger*, and *H. cordovae*, with the exception of some endorheic rivers for *H. cordovae*, the distribution of these species may be related to the contrasting environmental conditions of the tributaries of the Lower La Plata Basin. This raises the question of the processes responsible for the diversification in this clade. Given that the basins occupied by these species had a complex connection-disconnection history (Lundberg et al. 1998), two possible speciation events for these three species may be suggested: (i) an ancient allopatric speciation when the basins were separated, according to the hydrogeological hypothesis proposed by Montoya-Burgos (2003) or (ii) recent ecological speciation via dispersion after the connection among basins, as suggested by Silva et al. (2016). To help resolve this question, a robust time-calibrated phylogenetic tree of the genus should be constructed to compare time of the separation events with the geological events reported. Understanding the role of hydrogeology and ecology in species divergence is central to the study of fish evolutionary diversification and historical biogeography. In this regard, the present work is an important source of geographic, ecological, and diversity data of the genus *Hypostomus* from the Lower La Plata Basin that will contribute to a better understanding of the evolution and biogeography of *Hypostomus*.

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AUTHOR CONTRIBUTIONS

YPC, LP, SB conceived the ideas; YPC, FB, LP, AP, SB and JIMB conducted the fieldwork and collected the data with additional material from collaborators; YPC, FB, LP, SB and AP analysed the data; YPC drafted the manuscript; all prepared the final version of the manuscript.

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APPENDIX: COMPARATIVE MATERIAL EXAMINED

Hypostomus arecuta: **Argentina**: MACN-Ict 9677, holotype, 185.5 mm SL, Corrientes, Ituzaingó, Paraná River. MACN-ict 9678, 2, 174-243.3 mm SL, paratypes, Corrientes, Yahapé, Paraná River. *Hypostomus aspilogaster*: **Argentina**: CFA-IC-12154, 1, 395.0 mm SL, Buenos Aires, Punta Lara. CFA-IC- 12155,1, 372.9 mm SL, Buenos Aires, Punta Lara. CFA-IC- 12156, 2, 281.2-285.2 mm SL, Entre Ríos, Arroyo Mandisoví Grande, Departamento Federación. **Brasil**: MCP 11265, 1, 136.4 mm SL, Rio Grande do Sul, Mirim Oeste, rio Jaguarão no Passo do Centurião. MCP 21319, 1, 178.3 mm SL, Rio Grande do Sul, Jacuí, Lageado do Gringo ca 2 km da UHE Dona Francisca. *Hypostomus commersoni*: **Argentina**: CFA-IC-11910, 1, 134 mm SL, Buenos Aires, San Fernando. MFA- ZV-I-1765, 1, 420 mm SL, Santa Fe Capital: Manucho, Salado River. MFA-ZV-I-102, 1, 200 mm SL, Santa Fe Capital, Colastiné River. MFA-ZV-I-2854, 1, 252 mm SL; Santa Fe Capital, Parque del Sur. MFA-ZV-I-797, 1, 252 mm SL; Santa Fe Capital, Colastiné River. MACN-Ict 9724, 1, 176 mm SL; Formosa Province, El Colorado, Bermejo River. MHNG 2517.62, 1, 127.5 mm SL; Buenos Aires, Reconquista River, Río de la Plata. CFA-IC-3014, 1, 348 mm SL, Buenos Aires, Ramallo. CFA-IC-3379, 12, 345–453 mm SL, Buenos Aires, San Pedro. CFA-IC-3016, 1, 234 mm SL, Buenos Aires, Punta Lara. CFA-IC-3380,7, 342-389 mm SL, Buenos Aires, Vuelta de Obligado. CFA-IC-3382, CFA-IC-3381, 2, 234-236 mm SL, Buenos Aires, San Nicolás de los Arroyos. CFA-IC-5517, 18, 56-212 mm SL, Santiago del Estero, Saladillo River on Rute 92. CFA-IC-5543, 3, 87-98 mm SL, Santiago del Estero, Añatuya. **Brasil**: MCP 10496, 1, 118.9 mm SL, Rio Grande do Sul, Uruguay, rio Conceição, linha 8, Esquina Dutra, sistema do Uruguai. MCP 10530, 1, 118.5 mm SL, Rio Grande do Sul, Guaíba, Lago Guaíba na Ponta do Jacaré. MCP 27618, 1, 84.6 mm SL, Rio Grande do Sul, Uruguay, Arroio Caraí-Passo, na estrada São Fco. de Assis/Manuel Viana, Alf rio Ibicuí. MHNG 2680.32, 5, 120.5-153.0 mm SL, Ibicui da Foxina. *Hypostomus formosae*: **Argentina**: MACN-Ict 9720, 1, 177.0 mm SL, holotype, Formosa, Saladillo Stream tributary of Paraguay River. MACN-Ict 9721, 1, 170 mm SL, paratype, same data of holotype. MACN-Ict 9722, 4, 74.2-141 mm SL, Formosa, Bañado La Estrella, Pilcomayo River. CFA-IC 11972, 2, 64.1-74 mm SL, paratypes, Formosa, Pilcomayo River Basin: Porteño Stream, close to Veraí Lagoon. *Hypostomus luteus* (Godoy 1980): **Brasil**: MCP 19991, 1, Santa Catalina, Uruguay river basin, Uruguai river, proximo a pedra da Fortaleza. MCP 20751, 1, Santa Catalina, Uruguay river basin, Uruguai river, proximo a pedra da Fortaleza. *Hypostomus ternetzi*: **Argentina**: MACN-ict 9645, 1, 150 mm, Corrientes Province, rio Paraná, Yahapé. *Hypostomus uruguayensis:* **Argentina**: CFA-IC-3019, 11, 250-297.0 mm SL, Santa Fe, Puerto Gaboto, Paraná River. *Plecostomus rachovii*: **Brazil:** BMNH 1913.10.30.15, holotype, examined by photograph, near Rio Janeiro.