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A new species of *Hemigrammus* Gill, 1858 (Characiformes: Characidae) from the rio Madeira and rio Paraguai basins, with a redescription of *H. lunatus*

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A new *Hemigrammus* is described from the rio Paraguai and rio Madeira basins, Mato Grosso and Rondônia States, Brazil. The new species is characterized by possessing a wide dark horizontal stripe across the eye, a vertically elongated humeral blotch, and 4-5 gill-rakers on upper branch and 9-10 on lower. The new species can be easily diagnosed from *H. lunatus*, the sympatric and morphologically most similar congener, by the shape of humeral blotch and the number of gill rakers. Data of the type material of both *Hemigrammus lunatus* and *H. maxillaris*, as well as extensive examination of specimens, allowed us to conclude that *H. maxillaris* is a junior subjective synonym of *H. lunatus*. A redescription of *H. lunatus*, as well as a formal restriction of its type locality, is provided. A putative monophyletic group within *Hemigrammus*, composed by *H. barrigonae*, *Hemigrammus lunatus*, *H. machadoi* new species, and *H. ulreyi*, named *Hemigrammus lunatus* group, is proposed based on overall body morphology and color pattern. Additionally, a discussion on the biogeographical relationships between the rio Paraguai and rio Guaporé basins is provided.

Um *Hemigrammus* novo é descrito das bacias dos rios Paraguai e Madeira, estados de Mato Grosso e Rondônia, Brasil. A espécie nova é caracterizada por possuir uma ampla faixa escura horizontal atravessando o olho, mancha umeral verticalmente alongada, 4-5 rastros branquiais no ramo superior e 9-10 no inferior. A espécie nova pode ser facilmente diferenciada de *H. lunatus*, a congênere simpátrica e mais semelhante morfológicamente, pela forma da mancha umeral, e pelo número de rastros branquiais. Dados do material-tipo de *Hemigrammus lunatus* e *H. maxillaris*, bem como o exame de extenso material, levou à conclusão de que *H. maxillaris* é um sinônimo júnior de *H. lunatus*. É apresentada a redescrição de *H. lunatus* com a restrição formal de sua localidade-tipo. Um presumível grupo monofilético dentro de *Hemigrammus*, composto por *H. barrigonae*, *H. machadoi* espécie nova, *Hemigrammus lunatus*, and *H. ulreyi*, chamado grupo *Hemigrammus lunatus*, é proposto baseado na morfologia geral do corpo e padrão de colorido. Adicionalmente, uma discussão das relações biogeográficas entre as bacias dos rios Paraguai e Guaporé é apresentada.

Key words: Biogeography, Characidae *incertae sedis*, *Hemigrammus maxillaris*, *Hemigrammus ulreyi*, Type locality.

Introduction

Hemigrammus Gill is a speciose Characidae genus (54 species currently recognized as valid; Lima *et al.*, 2003; Lima & Sousa, 2009; Carvalho *et al.*, 2010; Mendonça & Wosiacki, 2011; Zarske, 2011) widespread in cis-Andean South America, including the Amazon, Orinoco, La Plata, and São Francisco

river basins, and rivers of Guyana, Suriname, French Guyana, and northeastern Brazil. The monophyly of *Hemigrammus* has been doubted for a long time, starting with Durbin, in Eigenmann, 1918: 135, who wrote: "(...) it seems quite certain that these genera [*Hemigrammus*, *Hyphessobrycon* Durbin] are of polyphyletic origin, that several sections have been and are arising independently from *Astyanax* Baird & Girard and

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Moenkhausia Eigenmann and probably other genera. These genera are conveniences rather than entities". *Hemigrammus* species remain being diagnosed by a set of homoplastic characters, i.e., the presence of two rows of premaxillary teeth, incomplete lateral line and basal third of caudal fin partially covered with small scales, the same ones used by Durbin (in Eigenmann, 1918) to define it. Not unexpectedly, a recent comprehensive phylogenetic analysis of the family Characidae (Mirande, 2010) did not recover a monophyletic *Hemigrammus*.

The alpha taxonomy of the genus also remains poorly understood. Durbin (in Eigenmann, 1918), remains the sole comprehensive taxonomic revision of *Hemigrammus*. However, since then, the number of valid species within the genus has more than doubled (from 25 to the present 54), demonstrating that much taxonomical work is still required on the group.

During the examination of extensive material of *Hemigrammus* from the rio Paraguai basin for a revision of the genus within this river basin, the subject of her master dissertation (Ota, 2010), the first author identified an undescribed species of the genus occurring in both the upper portion of the rio Paraguai and the rio Guaporé (a tributary of the upper rio Madeira). Among its congeners, the most similar-looking species is *H. lunatus*, known from several localities both in the Amazon and Paraguai river systems (e.g., Géry, 1964; Galacatos *et al.*, 1996; Lima *et al.*, 2013). We take this opportunity to propose that *Hemigrammus maxillaris* Fowler (1932), described from the rio Paraguai basin, only known from its type series, is a junior synonym of *H. lunatus*, a conclusion reached after the analysis of extensive material of the latter species, as well as data on the type series of both nominal taxa.

Therefore, the primary aim of the present paper is to describe a new species of *Hemigrammus* from the rio Madeira and rio Paraguai basins, and to discuss the biogeographical relationships between these two rivers basins. Additionally, we provide a redescription for *Hemigrammus lunatus*, based on the examination of extensive material from a broad geographical area (including type series) in order to provide the rationale for the synonymization of *H. maxillaris* herein proposed.

Material and Methods

Counts and measurements were taken on the left side of specimens using digital caliper to the nearest 0.1 mm. Methodology follows Fink & Weitzman (1974) and Menezes & Weitzman (1990), and the following measurements were added: distance between the tip of supraoccipital spine to dorsal-fin origin, distance between the end of dorsal-fin base to adipose-fin origin, distance from snout to the tip of the supraoccipital spine, distance from pelvic-fin origin to anal-

fin origin, and head depth, which was measured at vertical through the tip of supraoccipital spine. Measurements are expressed as percentages of standard length (SL), except for subunits of the head, which are expressed as percentages of head length (HL). Counts of horizontal scale rows between dorsal-fin origin and lateral-line do not include scales from median predorsal series situated immediately anterior to first dorsal-fin ray. Horizontal scale rows below lateral line were counted to the pelvic-fin insertion. In description, counts are followed by their frequency in parentheses, and an asterisk indicates the holotype. In the list of analyzed material, the total number of specimens of each lot is giving first, followed by the number of analyzed specimens in parentheses (when different from the total number of the lot), and by those cleared and stained (c&s), if any. Gonadal development was described following the scale of maturity proposed by Vazzoler (1996).

Vertebrae, supraneurals, branchiostegal rays, teeth cusps, and procurent caudal-fin rays counts were taken from five cleared and stained specimens (c&s) of the new species and from 11 specimens (c&s) of *H. lunatus*, prepared according to Taylor & Van Dyke (1985). Total vertebral count includes Weberian apparatus, counted as four elements; preural centrum 1 plus ural centrum 1 (PU1+U1) was counted as a single vertebral element. Patterns of scale *circuli* and *radii* were described according to Cockerell (1914), from scales sampled from the area between lateral line and dorsal-fin origin. Institutional abbreviations are: ANSP, Academy of Natural Sciences of Philadelphia of Drexel University, Philadelphia; CAS, California Academy of Sciences, San Francisco; INPA, Instituto Nacional de Pesquisas da Amazônia, Manaus; MCP, Museu de Ciências e Tecnologia da Pontifícia Universidade Católica do Rio Grande do Sul, Porto Alegre; MCZ, Museum of Comparative Zoology, Cambridge; MNHNP, Museo Nacional de Historia Natural del Paraguay, San Lorenzo; MZUEL, Museu de Zoologia da Universidade Estadual de Londrina, Londrina; MZUSP, Museu de Zoologia da Universidade de São Paulo, São Paulo; NUP, Coleção Ictiológica do Nupélia, Maringá; UF, University of Florida, Gainesville; UFRO-I, Universidade Federal de Rondônia, Porto Velho; and ZUEC, Museu de Zoologia da Universidade Estadual de Campinas, Campinas.

Results

Hemigrammus machadoi, new species

Figs. 1-3

Hemigrammus lunatus Durbin in Eigenmann, 1918: 165 [part; "rio Boa Ventura"].

Hemigrammus sp. "falso lunatus" Lima *et al.*, 2013: 272-273 [Brazil, rio Madeira basin: photo, short description, diagnosis, habitat preferences, distribution in the rio Madeira basin].



Fig. 1. *Hemigrammus machadoi*, INPA 39889, holotype, 30.4 mm SL, Brazil, Mato Grosso State, Pontes e Lacerda, igarapé Barreiro, tributary of rio Guaporé, rio Madeira basin.

Holotype. INPA 39889, 30.4 mm SL, Brazil, Mato Grosso State, Pontes e Lacerda, igarapé Barreiro, tributary of rio Guaporé, rio Madeira basin, road to Vila Bela da Santíssima Trindade, 15°11'34"S 59°25'26"W, 13 Dec 2011, W. M. Ohara.

Paratypes. All from Brazil. **Rondônia State, rio Madeira basin:** ANSP 194408, 2, 28.2-29.0 mm SL, Cerejeiras, igarapé Azul, about 10 km on road RO-399, 13°19'09"S 61°03'16"W, 2 Sep 2011, W. M. Ohara & G. Torrente Vilara; INPA 24098, 1, 26.2 mm SL, Guajará-Mirim, middle rio Cautário, 12°05'06"S 64°37'58"W, 12 Jul 2003, G. Torrente Vilara; INPA 39892, 1, 35.2 mm SL, Guajará-Mirim, rio Pacaás Novos, 10°56'15"S 65°14'11"W, 17 Jan 2012, W. M. Ohara; MCP 47946, 1, 28.0 mm SL, Jaci-Paraná, stream tributary of rio Madeira, road BR-364, 09°28'41"S 64°46'23"W, 19 Jul 2004, F. Langeani, F. C. T. Lima, E. H. L. Pereira & R. E. Reis; UFRO-I 11226, 2, 22.3-25.0 mm SL, Cerejeiras, igarapé do Trevo, tributary of rio Guaporé, 13°11'38"S 60°56'59"W, 2 Sep 2011, W. M. Ohara & G. Torrente Vilara; UFRO-I 11317, 3, 20.4-22.9 mm SL, Cerejeiras, igarapé tributary of rio Guaporé, road RO-399, 13°20'02"S 60°54'16"W, 2 Sep 2011, W. M. Ohara & G. Torrente Vilara; UFRO-I 11571, 2, 24.7-28.5 mm SL, Cerejeiras, igarapé Azul, about 10 km on road RO-399, 13°19'09"S 61°03'16"W, 2 Sep 2011, W. M. Ohara & G. Torrente Vilara; UFRO-I 11712, 6, 26.9-32.2 mm SL, Corumbiara, igarapé at Estrada dos Bois, tributary of rio Corumbiara, 12°59'54"S 61°08'52"W, 1 Sep 2011, W. M. Ohara; UFRO-I 14036, 2, 25.6-25.7 mm SL, Guajará-Mirim, rio Pacaás Novos, 10°56'15"S 65°14'11"W, 17 Jan 2012, W. M. Ohara; ZUEC 7637, 1, 32.6 mm SL, Ariquemes, stream tributary of rio Jamari, 09°38'33"S 63°02'05"W, 30 Apr 2013, D. T. B. Nielsen. **Mato Grosso State, rio Madeira basin:** MCP 46218, 2, 22.7-26.9 mm SL, Nova Lacerda, stream tributary of rio Guaporé, road BR-174, 14°46'15"S 59°20'22"W, 12 Jul 2004, V. A. Bertaco, F. C. T. Lima, J. F. Pezzi da

Silva & P. Lehmann; MZUSP 37611, 20, 24.6-35.8 mm SL; ZUEC 7770, 5, 26.7-34.9 mm SL, Nova Lacerda, stream on road Cuiabá-Porto Velho, 72 km from Pontes e Lacerda, ca. 14°46'S 59°20'W, 23 Sep-10 Oct 1984, MZ/Polonoroeste; MCP 45042, 5, 23.6-33.1 mm SL, Pontes e Lacerda, córrego Barreiro, road BR-174, 15°07'04"S 59°18'46"W, 12 Jul 2004, R. E. Reis, P. A. Buckup, F. Langeani & A. R. Cardoso; MCP 15730, 4, 22.6-29.2 mm SL, Pontes e Lacerda, rio Guaporé and floodplains, ca. 15°12'S 59°21'W, 13 Aug 1991, R. E. Reis, L. R. Malabarba, N. A. Menezes & M. J. Weitzman; MZUSP 95365, 54, 19.1-31.1 mm SL, 4 c&s, 24.9-27.2 mm SL, Vila Bela da Santíssima Trindade, rio Guaporé, 15°00'28"S 59°57'22"W, 13 Oct 2006, F. A. Machado, F. C. T. Lima, C. M. C. Leite & N. E. Silva; UFRO-I 12513, 3, 23.9-33.1 mm SL, Vila Bela da Santíssima Trindade, stream tributary of rio Guaporé, 15°08'24"S 59°59'21"W, 13 Dec 2011, W. M. Ohara; UFRO-I 12619, 8, 26.7-29.3 mm SL, 1 c&s, 28.4 mm SL; NUP 15053, 2, 27.1-28.4 mm SL; same data as holotype. **Rio Paraguai basin:** MCP 15718, 6, 24.8-26.6 mm SL; MZUSP 44390, 17.7-26.8 mm SL, Cáceres, rio Paraguai and surroundings, ca. 16°09'S 57°37'W, 11 Aug 1991, R. E. Reis, L. R. Malabarba, N. A. Menezes & M. J. Weitzman; MCP 15727, 18, 25.1-34.9 mm SL, stream crossing the road Cuiabá/Cáceres, 13 km east from Cáceres, tributary of rio Paraguai, 16°09'S 57°37'W, 14 Aug 1991, R. E. Reis, L. R. Malabarba, N. A. Menezes & M. J. Weitzman; MCP 44566, 30, 21.9-32.4 mm SL, Cuiabá, stream at road MT-060, 15°44'41"S 56°20'08"W, 10 Jul 2004, J. F. Pezzi da Silva, F. Langeani, E. H. L. Pereira & P. Lehmann.

Non-types. All from Brazil. Rondônia State, rio Madeira basin: INPA 21835, 18, 23.4-30.0 mm SL; INPA 21854, 25, 24.6-28.3 mm SL, Costa Marques, middle rio Cautário, tributary of rio Guaporé, 12°11'06"S 63°33'12"W; UFRO-I 7321, 1, 23.4 mm SL, São Francisco do Guaporé, igarapé tributary of rio Guaporé, 12°38'09"S

63°07'43"W; UFRO-I 8408, 1, 23.9 mm SL, Corumbiara, rio Guaporé, upstream mouth of rio Corumbiara, 13°19'02"S 62°01'37"W. Mato Grosso State, rio Madeira basin: MCP 44873, 6, 22.1-28.9 mm SL, Nova Lacerda, rio Galera (tributary of rio Guaporé), balneário Galera, 14°28'59"S 59°35'07"W; MZUSP 37648, 2, 18.6-24.9 mm SL, Vila Bela da Santíssima Trindade, rio Guaporé, ferryboat pier, 15°00'35"S 59°57'26"W; MCP 45070, 106, 19.2-32.6 mm SL, Vila Bela da Santíssima Trindade, stream at km 10 at the road between Pontes e Lacerda and Vila Bela da Santíssima Trindade, 15°12'02"S 59°24'30"W. Rio Paraguai basin: MZUSP 96658, 4, 23.4-24.6 mm SL, Barão de Melgaço, flooded areas 1 km from Mimoso, ca. 16°17'S 55°48'W; MZUSP 96714, 1, 20.5 mm SL, Barão de Melgaço, rio Mutum, between Mimoso and Joselândia, 16°19'30"S 55°49'59"W.

Diagnosis. *Hemigrammus machadoi* differs from most congeners by possessing a wide dark horizontal stripe across the eye (vs. eye stripe absent or, when present, vertical, except *H. barrigonae* Eigenmann & Henn, *H. lunatus*, and *H. ulreyi* (Boulenger)) and by the possession of a well defined narrow dark stripe at the basis of the anal fin (vs. dark stripe at the basis of anal fin absent, except *H. barrigonae*, *H. boesemani* Géry, *H. geisleri* Zarske & Géry, *H. lunatus*, *H. mimus* Böhlke, and *H. ulreyi*). *Hemigrammus machadoi* can be easily distinguished from *H. boesemani*, *H. geisleri*, and *H. mimus* by

Table 1. Morphometric data of *Hemigrammus machadoi*, new species, based on holotype and paratypes. N = Number of specimens, and SD = standard deviation.

	N	Holotype	Paratypes	Mean	SD
Standard length (mm)	72	30.4	20.2-34.9	26.8	-
Percentages of Standard length					
Depth at dorsal-fin origin	71	42.4	33.2-44.5	39.1	3.02
Snout to dorsal-fin origin	71	54.0	50.8-56.5	53.7	1.15
Snout to pectoral-fin origin	71	32.5	28.1-35.8	31.4	1.51
Snout to pelvic-fin origin	70	49.0	43.5-52.9	46.9	1.94
Snout to anal-fin origin	71	61.9	56.6-65.1	60.5	1.83
Caudal-peduncle depth	71	9.1	7.5-10.4	8.7	0.59
Caudal-peduncle length	71	8.4	7.0-9.8	8.5	0.44
Pectoral-fin length	71	21.6	19.8-25.1	22.8	1.24
Pelvic-fin length	70	19.8	19.3-23.0	20.8	0.80
Dorsal-fin base length	71	14.4	13.3-16.1	14.8	0.57
Dorsal-fin length	69	32.2	29.9-37.0	33.3	1.36
Anal-fin base length	71	37.0	33.7-38.2	36.2	1.09
Anal-fin lobe length	68	23.0	21.4-28.9	25.5	1.70
Eye to dorsal-fin origin	71	39.7	35.5-41.4	38.5	1.20
Dorsal-fin origin to caudal-fin base	71	54.1	48.9-56.0	53.1	1.52
Bony head depth	71	27.5	26.1-31.0	28.7	0.91
Bony head length	71	29.6	27.2-31.0	28.9	0.80
End of dorsal-fin base to adipose-fin origin	71	25.5	22.2-26.9	24.7	0.90
Pelvic-fin origin to anal-fin origin	71	17.8	14.6-18.7	17.3	0.82
Supraoccipital spine to dorsal-fin origin	71	25.3	21.8-27.6	25.0	1.29
Snout to supraoccipital spine tip	71	28.4	27.0-31.2	28.5	0.85
Percentages of Head length					
Horizontal eye diameter	71	45.3	39.4-49.1	44.5	1.76
Snout length	71	31.1	25.5-33.6	28.5	2.16
Least interorbital distance	71	36.6	29.6-36.6	33.1	1.09
Upper jaw length	71	45.3	38.4-45.5	41.2	2.31



Fig. 2. Scanning electronic micrograph of *Hemigrammus machadoi*, new species, MZUSP 95365, paratype, 27.2 mm SL, left internal lateral view of premaxilla, maxilla and dentary. Scale bar = 1 mm.

possessing a distinct dark humeral blotch (vs. humeral blotch absent) and by lacking a blotch on caudal peduncle or any distinct patch of pigmentation on caudal fin (vs. dark blotch on caudal peduncle present in *H. boesemani* and *H. geisleri*, a dark marking present at the basis of each caudal-fin lobe basis in *H. mimus*). *Hemigrammus machadoi* can be distinguished from *H. barrigonae* and *H. ulreyi* by lacking a narrow, well-defined longitudinal midlateral dark stripe (vs. present) and by lacking a discrete blotch on caudal peduncle (vs. present in *H. barrigonae*) and a dark pigmentation patch on the basis of anteriormost dorsal-fin rays (vs. present in *H. ulreyi*). The new species can be diagnosed from *Hemigrammus lunatus*, the sympatric and morphologically most similar congener, by having a conspicuous vertically elongated dark humeral blotch, extending horizontally from second through sixth lateral-line scales, and vertically from third row above lateral line to first row below it (vs. a small roundish humeral blotch, extending horizontally from fourth through sixth lateral-line scales, and vertically from fourth through fifth scale rows above lateral line), and by having 4-5 gill-rakers on upper branch and 9-10 on lower (vs. 6-7, and 11-12, respectively). Additionally, the higher number of cusps on inner premaxillary, dentary, and maxillary largest tooth (5-7 cusps, mode 7, in premaxillary and dentary, vs. 5; 3-5 cusps, mode 5, in maxillary vs. 1-3), and total vertebrae (34-35 vs. 32-33) helps to distinguish the new species from *H. lunatus*.

Description. Morphometric data summarized in Table 1. Body compressed, moderately high; greatest body depth located anteriorly to dorsal-fin origin. Dorsal profile of head convex from tip of snout to anterior naris, straight to slightly concave

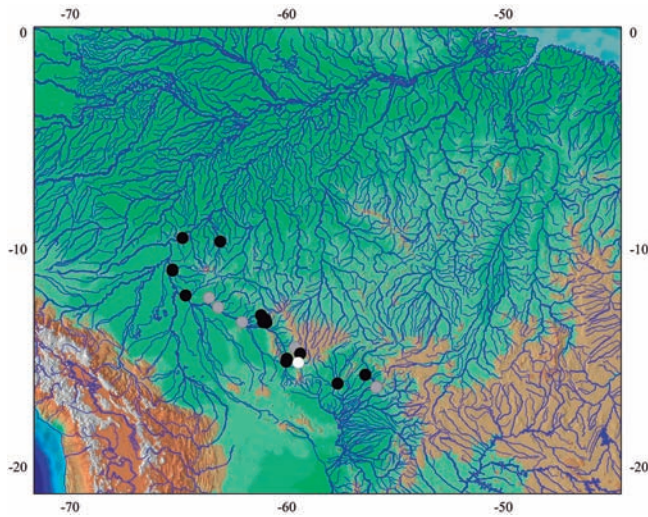


Fig. 3. Map of northern South America showing distribution of *Hemigrammus machadoi*. The white circle represents the type locality, black circles represent the paratypes localities, and the grey circles represent the non-types localities.

from latter point to tip of supraoccipital spine. Dorsal profile of trunk moderately convex from tip of supraoccipital spine to dorsal-fin origin; inclined from latter point to adipose-fin origin and slightly concave along caudal peduncle. Ventral profile of body convex from tip of lower jaw to anal-fin origin; inclined along anal-fin base. Ventral profile of caudal peduncle slightly concave.

Jaws equal, isognathous; mouth terminal. Maxillary slightly curved; posterior terminus surpassing vertical through anterior margin of eye. Premaxillary teeth in two rows, outer row composed by 2(4), 3(52), or 4*(15) tri- to pentacuspoid teeth, central cusp longer; inner row with 5*(72) penta- to heptacuspoid teeth, central cusp longer. Maxilla with 2(26), 3*(37), or 4(5) tri to pentacuspoid teeth along anteroventral margin, anteriormost tooth broader. Dentary with 9-15 teeth, anteriormost four teeth distinctly larger than remaining teeth, with 5-7 cusps, central cusp longer, then abruptly decreasing in size, 1-2 tri to pentacuspoid teeth, and remaining 4-9 tri- or unicuspid, small teeth (Fig. 2).

Scales cycloid, with *circuli* marked anteriorly, but absent distally; with two to six *radii* ("*Hemigrammus* type" of Cockerell, 1914). Lateral line incomplete, slightly curved ventrally, with 6(1), 7(2), 8(1), 9(9), 10*(14), 11(19), 12(9), 13(8), 14(5), or 15(1) pored scales; longitudinal series including perforated scales 30(1), 31(3), 32(5), 33(17), 34*(19), 35(19), or 36(4); 5(1) or 6*(66) scales rows between dorsal-fin origin and lateral line; 3(1) or 4*(66) scales rows between lateral line and pelvic-fin insertion. Predorsal scales 9*(19), 10(42), or 11(8). Anal sheath along anal-fin base composed by 5(3) or 6*(8) scales in a single row, covering base of first unbranched to fifth branched anal-fin rays. Circumpeduncular scales 11(4), 12(13), 13*(20), or 14(35).

Caudal-fin scales covering about basal third of upper and lower caudal-fin lobes, mainly arranged on upper and lower caudal lobes margins, gradually decreasing in size.

Dorsal-fin rays ii,9*(72), first unbranched ray approximately one-third of second unbranched ray; small ossification anterior to first unbranched ray present in all five c&s specimens examined. Distal margin of dorsal fin straight. Dorsal-fin origin at midbody or slightly behind this point; base of posterior most dorsal-fin ray slightly behind vertical through anal-fin origin. First dorsal-fin pterygiophore insertion posterior to neural spine of tenth vertebra. Adipose fin small. Pectoral-fin rays i,10*(46), 11(20), or 12(5). Pelvic-fin rays i,7*(72); its origin ahead of vertical through dorsal-fin origin; tip of longest ray surpassing anal-fin origin. Anal-fin rays iv, 22(2), 23(18), 24*(28), 25(19), or 26(5); anal fin falcate, last unbranched ray to fourth branched ray longest, with remaining rays decreasing gradually in size towards anal-fin end; last anal-fin pterygiophore insertion behind hemal spine of fifteenth caudal vertebrae (5). Caudal fin bifurcated; lobes slightly pointed, almost equal in size, inferior lobe slightly longer than superior. Principal caudal-fin rays i,17,i*(67); dorsal procurent caudal-fin rays 11(5); ventral procurent caudal-fin rays 8(3) or 9(2). Precaudal vertebrae 13(4) or 14(1); caudal vertebrae 21(5); total vertebrae 34(4) or 35(1). Supraneurals 4(3) or 5(2). Branchiostegal rays 4(5). Upper branch of gill-rakers 4(4) or 5(67), lower branch 9(43) or 10(28).

Color in alcohol. Overall ground coloration of body light tan. Anterior portion of lower jaw, snout and dorsal portion of head with dense concentration of small dark chromatophores, imparting an overall darker color. Gular area and infraorbitals clearer; third infraorbital and opercle silver in specimens retaining guanine pigmentation.

Opercle upper half and fourth and fifth infraorbital with scattered, relatively large dark chromatophores. Eye with broad dark longitudinal midlateral stripe (not discernible in specimens retained for long period in formalin). Longitudinal dark stripe along midline of body present, faint and very narrow, originating at end of second humeral spot, becoming wider and more conspicuous at vertical of insertion of dorsal fin. Scales from dorsal region of body posteriorly bordered with dark chromatophores, forming subtle reticulate pattern. Dark humeral blotch conspicuous, its contour slightly blurred, vertically elongated, extending horizontally from second through sixth lateral-line scales, and vertically from third row above lateral line to first row below it. Dark chromatophores below midlateral line arranged along margins of hypaxial muscles bundles from area above anal fin to caudal peduncle. Dorsal fin mostly hyaline, with few dark chromatophores concentrated along unbranched rays and third or fourth branched rays and its interradyal membranes. Adipose, pectoral and pelvic fins almost hyaline, with few dark chromatophores scattered mainly along their distal margins. Anal

fin hyaline, with few dark chromatophores usually concentrated on unbranched rays and its interradiar membranes, forming dark narrow margin. Anal fin with narrow, very conspicuous dark stripe along anal-fin base. Caudal fin hyaline, main outer rays with dark chromatophores along its margins. Dark caudal spot absent (Fig. 1).

Color in life. Based on the picture of two specimens collected during the Transcontinental Catfish Expedition, at the type locality, the Igarapé Barreiro, taken by the second author, that unfortunately could not be located during a recent search in MCP (field number TCE2004071101B). Opercle, infraorbital bones, and sides of body below midline light yellow to light orange, with a silvery hue. Tip of dentary, snout and top of head dark gray. Dorsum and posterior portion of body (area immediately behind vertical passing through anal-fin origin) translucent, with a light brown hue. Dorsal, pelvic, anterior portion of anal, caudal and adipose fins, and caudal peduncle light orange. Dark midlateral stripe faint, broad, plumbeous, extending into caudal peduncle.

Sexual dimorphism. Anal- and pelvic-fin hooks were observed in males of *Hemigrammus machadoi* collected during December and January (UFRO-I 12513 and 14036, respectively). The pelvic fin bears tiny hooks (usually one pair of hooks per ray segment), anterodorsally arranged almost all over the entire length of the unbranched ray and first two branched fin rays. The anal fin bears 7-11 tiny hooks, anterodorsally arranged along the last unbranched ray and first three branched fin rays, one pair per ray segment.

Distribution. *Hemigrammus machadoi* is known from the upper rio Paraguai basin, from the rio Guaporé and some other smaller tributaries of the rio Mamoré and rio Madeira, on the upper and middle portions of the rio Madeira basin in Brazil (Fig. 3). Comparisons between *Hemigrammus machadoi* specimens from rio Guaporé, rio Pacaás Novos and upper rio Paraguai basins revealed no differences in morphometric, meristics or color pattern, and the data of these distinct populations are pooled together in the description and Table 1.

Ecological notes. Specimens of *Hemigrammus machadoi* are typically found in slow flowing, low-gradient streams and small rivers, with clear, sometimes slightly dark-stained waters, as the upper rio Guaporé and the type locality, the igarapé Barreiro. River bottom at those sites was constituted mainly of sand and clay. Aquatic vegetation was abundant at the igarapé Barreiro and at some sites at the rio Guaporé and *H. machadoi* seemed to prefer its surroundings. The species was also captured in clear water wetlands, adjacent to the rio Guaporé. Analyses of dissected specimens (MZUSP 95365) collected in November revealed two mature females, 26.6-27.2

mm SL, possessing large yellowish oocytes and two mature males, 24.9-25.9 mm SL, with lobulated, whitish testicles.

Etymology. The specific name honors Francisco de Arruda Machado, ichthyologist from the Universidade Federal de Mato Grosso, Brazil, for his tireless dedication in surveying the fishes of his native State, as well as for his struggle for their conservation and the conservation of the rivers from the Mato Grosso State. A genitive noun.

Hemigrammus lunatus Durbin, 1918

Figs. 4-7

Hemigrammus lunatus Durbin in Eigenmann, 1918: 164 [type locality: "Amazon basin", restricted herein to "Brazil, Amazonas, Codajás, lago Badajós (ca. 03°21'S 62°41'W)"; see below; "Obidos", "Caceres", "Jauru"].

Hyphessobrycon maxillaris Fowler, 1932: 354 [type locality: "Descalvados", rio Paraguai basin, Mato Grosso, Brazil].

Hemigrammus maxillaris. Weitzman, 1985: 808 [new combination].

Diagnosis. *Hemigrammus lunatus* differs from most congeners, except from *H. barrigonae*, *H. machadoi*, and *H. ulreyi*, by possessing a wide dark horizontal stripe across the eye (vs.



Fig. 4. *Hemigrammus lunatus*: MCZ 20964, (a) holotype, 26.5 mm SL; (b) paratype, 21.7 mm SL, and (c) paratype, 23.9 mm SL; Brazil, Amazonas State, Codajás, lago Badajós, tributary of rio Solimões.

eye stripes absent or, when present, vertical in the remaining congeners). It can be distinguished from most congeners, with the exception of *H. barrigonae*, *H. boesemani*, *H. geisleri*, *H. machadoi*, *H. mimus*, and *H. ulreyi*, by the possession of a well defined narrow dark stripe at the basis of the anal fin (vs. dark stripe at the basis of anal fin absent). *Hemigrammus lunatus* can be easily distinguished from *H. boesemani*, *H. geisleri*, and *H. mimus*, by possessing a distinct roundish dark humeral blotch (vs. humeral blotch absent) and by lacking a blotch on caudal peduncle or any distinct patch of pigmentation on caudal fin (vs. blotch on caudal peduncle present in *H. boesemani* and *H. geisleri*, a dark marking present at the basis of each caudal-fin lobe basis in *H. mimus*). *Hemigrammus lunatus* can be distinguished from *H. barrigonae* and *H. ulreyi* by lacking a narrow, well-defined longitudinal dark stripe (vs. present), and by lacking a discrete blotch on caudal peduncle (vs. present in *H. barrigonae*) or a dark pigmentation patch on the basis of anteriormost dorsal-fin rays (vs. present in *H. ulreyi*). It can be diagnosed from *H. machadoi*, the most similar congener by having a small roundish dark humeral blotch, extending horizontally from fourth through sixth lateral-line scales, and vertically from fourth through fifth scale rows above lateral line (vs. conspicuous, vertically elongated humeral blotch, extending horizontally from second through sixth lateral-line scales, and vertically from third row above lateral line to first row below it), and by having 6-7 gill-rakers on upper branch and 11-12 on lower (vs. 4-5, and 9-10, respectively). Additionally, the lower number of cusps of inner premaxillary, dentary, and maxillary largest tooth (5 vs. 5-7 cusps, mode 7, in premaxillary and dentary; 1-3 vs. 3-5, mode 5, in maxillary), and total vertebrae (32-33 vs. 34-35) helps to distinguish *H. lunatus* from the new species.

Description. Morphometric and meristic data summarized in Table 2. Body compressed, moderately elongated; greatest body depth located anteriorly to dorsal-fin origin. Dorsal profile

of head convex from tip of snout to anterior naris, straight to slightly concave from latter point to tip of supraoccipital spine. Dorsal profile of trunk moderately convex from tip of supraoccipital spine to dorsal-fin origin; inclined from latter point to adipose-fin origin and slightly concave along caudal peduncle. Ventral profile of body convex from tip of lower jaw to anal-fin origin; inclined along anal-fin base. Ventral profile of caudal peduncle slightly concave.

Jaws equal, isognathous; mouth terminal. Maxillary slightly curved; posterior terminus surpassing vertical through anterior margin of eye. Small ossification anterior to first unbranched ray present in all 11 c&s specimens examined. Distal margin of dorsal fin straight. Dorsal-fin origin at midbody or slightly behind this point; base of posterior most dorsal-fin ray slightly behind vertical through anal-fin origin. First dorsal-fin pterygiophore insertion posterior to neural spine of tenth vertebra. Adipose fin small. Pelvic-fin origin ahead of vertical through dorsal-fin origin; tip of longest ray surpassing anal-fin origin. Anal fin falcate, last unbranched ray to fourth branched ray longest, with remaining rays decreasing gradually in size towards anal-fin end; last anal-fin pterygiophore insertion behind hemal spine of fifteenth caudal vertebrae (11). Caudal-fin scales covering about one-third of upper and lower caudal lobes, mainly arranged on upper and lower caudal lobes margins, gradually decreasing in size. Caudal fin bifurcated; lobes slightly pointed, almost equal in size, inferior lobe slightly longer than superior. Precaudal vertebrae 12-13; caudal vertebrae 20(11); total vertebrae 32(5) or 33(6). Supraneurals 3(3), 4(7), or 5(1). Branchiostegal rays 4(11).

Color in alcohol. Overall ground coloration of body light tan. Anterior portion of lower jaw, snout, and dorsal portion of head with dense concentration of small dark chromatophores, imparting an overall dark color. Gular area and infraorbitals



Fig. 5. *Hemigrammus lunatus*, NUP 2112, 35.9 mm SL, Brazil, Mato Grosso State, Rosário Oeste, córrego Imbaúba, tributary of rio Cuiabá, rio Paraguai basin.

clearer; third infraorbital and opercle silver in specimens retaining guanine pigmentation. Tip of maxillary, opercle and fourth and fifth infraorbital with scattered, relatively large dark chromatophores. Eye with broad dark longitudinal midlateral stripe (not discernible in specimens retained for a long period in formalin). Longitudinal dark stripe along midline of body present, very faint and narrow, originating after dark humeral blotch and extending up to approximately vertical through middle of caudal peduncle or slightly behind this point. Scales from dorsal region of body posteriorly bordered with dark chromatophores, conferring a moderately developed reticulate pattern. Dark humeral blotch conspicuous, small, roundish, with well-defined contour, extending from fourth through sixth lateral-line scales, and vertically from fourth through fifth scale rows above lateral line. Dark chromatophores arranged along margins of hypaxial muscles bundles from area above anal fin to caudal peduncle. Dorsal fin mostly hyaline, with few dark chromatophores concentrated along unbranched rays and third branched rays and its interradial membranes. Adipose, pectoral and pelvic fins almost hyaline, with few dark chromatophores scattered mainly along their distal margins. Anal fin hyaline, with few dark chromatophores usually concentrated on its unbranched rays and interradial membranes, forming a dark narrow margin. Anal fin with narrow, conspicuous dark stripe along anal-fin base. Caudal fin hyaline, its main external rays with few dark chromatophores along their margin. Caudal spot absent (Fig. 7).

Color in life. Based on a picture of a freshly collected specimen from Manso Reservoir, upper rio Paraguai basin, and freshly collected specimens from the rio Amazonas near Santarém, Pará (ZUEC 7995). Overall coloration pattern light

yellow or clear. Gular region, opercle, infraorbital bones, and abdominal with silver hue. Tip of dentary, snout and top of head light brown, with yellow tinge. Dorsal, pelvic, anterior portion of anal and caudal fins, and adipose fin yellow to light orange, translucent in the specimens from rio Amazonas. Dark midlateral stripe faint, plumbeous, extending into caudal peduncle (Fig. 5).

Sexual dimorphism. As previously mentioned by Lima & Sousa (2009: 162), mature males of *Hemigrammus lunatus* bear anal- and pelvic-fin hooks. Fin hooks were observed in males collected from November through April. Pelvic-fin hooks are anterodorsally arranged almost all over the entire length of all fin rays; usually one pair of hooks per ray segment. The anal fin bears 5-15 tiny hooks, anterodorsally arranged almost over the entire length of the last unbranched ray and first three or four branched fin rays, one pair per ray segment.

Habitat and ecological notes. Habitat preferences are somewhat similar to those presented by *Hemigrammus machadoi*. Thus *H. lunatus* is commonly found in slow flowing, low-gradient streams and small rivers. In fact, both species are found syntopically at some localities on the rio Guaporé basin. However, *H. lunatus* has a substantially broader distribution than *H. machadoi* and occurs in habitats where the latter species is unknown, as floodplain lakes associated with white-water rivers in central Amazon. At the río Napo basin in Amazonian Ecuador, *H. lunatus* was found to be an ubiquitous and abundant species found in lagoons and riverine habitats across a piedmont/lowland river stretch (Galacatos *et al.*, 1996, 2004).

Analyses of dissected specimens, captured from November through April, from both rio Madeira and rio Paraguai basins, revealed mature females (INPA 21621, 2 ex.; NUP 2114, 1 ex.; NUP 7531, 2 ex.; NUP 7533, 4 ex.; NUP 8024, 15 ex.), possessing large yellowish oocytes, and mature males (INPA 21621, 1 ex.; NUP 2113, 1 ex.; NUP 2114, 2 ex.; NUP 7531, 6 ex.; NUP 7533, 4 ex.; NUP 8024, 5 ex.) with lobulated, whitish testicles.

Distribution. *Hemigrammus lunatus* is known from the central and western portions of the rio Amazonas basin, in Brazil, Bolivia (*e.g.*, Géry, 1964; Chernoff *et al.*, 2000), Peru (*e.g.*, Géry, 1964; Barthem *et al.*, 2003), Ecuador (*e.g.*, Galacatos *et al.*, 1996), and Colombia (*e.g.*, Mojica *et al.*, 2005), and along rio Paraguai basin in Brazil and Paraguay. The species is also recorded from the upper Corantijn River in Suriname, near the boundary with Brazil (Géry, 1965; Mol, 2012) and from the upper río Orinoco and río Caura in Venezuela (Lasso *et al.*, 2004). The map shows the localities of the material examined in the present study (Fig. 6). For comments on the identity of the remaining populations, see "Remarks".

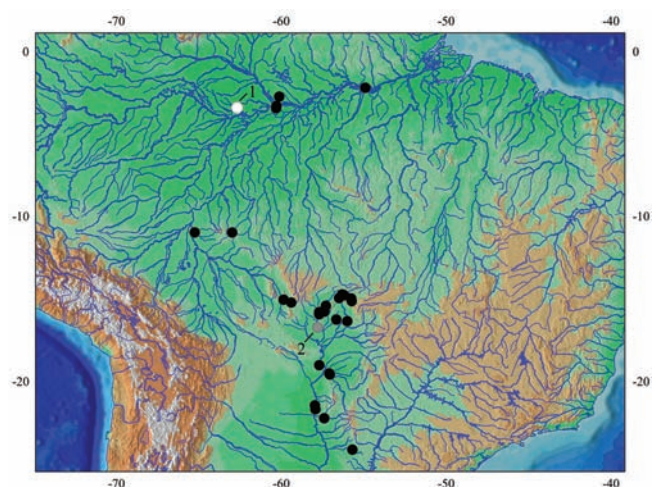


Fig. 6. Map of northern South America showing distribution of *Hemigrammus lunatus*: (1) the white circle represents the type locality of *Hemigrammus lunatus*, (2) the gray circle represents the type locality of *Hyphessobrycon maxillaris*, and black circles represent remaining localities of analysed material in the present study.

Table 2. Morphometric and meristic data of *Hemigrammus lunatus* (CAS 42679, paratype; *Hyphessobrycon maxillaris*, ANSP 53660, holotype and ANSP 53661, paratypes) and from non-type specimens. N = number of specimens; SD = standard deviation.

Measurements	<i>H. lunatus</i>	<i>H. maxillaris</i>		Range				
	Paratype	Holotype	Paratypes (n=3)	N	Min.	Max.	Mean	SD
Standard length (mm)	23.9	28.3	24.8-24.9	255	17.7	36.8	-	-
Percents of standard length								
Depth at dorsal-fin origin	39.7	35.2	33.4-36.6	255	30.2	44.6	36.5	2.23
Snout to dorsal-fin origin	51.4	52.7	51.6-53.9	249	49.1	54.7	51.9	0.94
Snout to pectoral-fin origin	30.9	30.9	30.5-32.5	249	28.2	34.4	30.6	1.15
Snout to pelvic-fin origin	47.1	48.5	46.1-49.0	249	43.9	49.2	46.3	1.06
Snout to anal-fin origin	64.3	61.5	58.8-62.0	249	54.8	64.4	61.5	1.32
Caudal-peduncle depth	10.8	8.5	8.5-9.2	255	8.1	10.9	9.3	0.49
Caudal-peduncle length	10.7	10.1	10.1-10.8	255	6.6	10.9	8.9	0.63
Pectoral-fin length	24.8	21.9	20.5-21.9	255	20.5	29.0	24.5	1.23
Pelvic-fin length		18.2	17.4-18.3	253	17.3	26.1	21.8	1.14
Dorsal-fin base length	14.0	14.4	13.3-14.7	255	12.6	16.6	14.7	0.66
Dorsal-fin length		32.2	31.9-34.0	251	30.7	42.2	35.2	1.44
Anal-fin base length	33.7	31.6	31.2-33.7	255	31.0	36.6	33.7	0.97
Anal-fin lobe length		26.3	24.2-26.3	245	21.1	32.5	27.8	1.48
Eye to dorsal-fin origin	35.8	35.2	34.5-36.3	251	33.7	40.8	36.7	1.10
Dorsal-fin origin to caudal-fin base		51.5	51.4-51.6	250	49.3	59.8	53.3	1.23
Bony head depth	29.5	27.2	26.7-28.4	255	25.7	34.7	28.2	0.95
Bony head length	30.8	26.5	26.3-28.3	255	26.1	32.9	28.8	1.32
Dorsal-fin end to adipose-fin origin	24.8	21.9	21.8-22.8	253	21.9	27.7	24.7	0.99
Pelvic-fin origin to anal-fin origin	18.8	16.5	15.9-16.9	250	14.6	19.8	17.5	0.79
Supra-occipital spine to dorsal-fin origin	24.3	23.6	23.5-23.6	254	19.7	27.2	23.4	1.26
Snout to supra-occipital spine end	27.5	28.3	28.2-28.6	255	25.7	31.0	27.8	0.86
Percents of head length								
Horizontal eye diameter	43.6	41.0	41.0-42.9	255	40.6	49.0	44.5	1.74
Snout length	25.6	25.8	25.7-27.2	255	22.8	31.4	27.3	1.28
Least interorbital distance	33.0	33.4	33.1-35.7	255	27.4	36.4	32.1	1.57
Upper jaw length	42.5	45.8	45.2-48.3	255	40.2	48.3	42.6	1.57
Counts				Range				
Number of inner premaxillary teeth	5	5	5	5(255)				
Cusp of inner premaxillary largest tooth	5	5	5	3(11), 5(244)				
Number of outer premaxillary teeth	4	3	4(3)	2(2), 3(72), 4(169), 5(12)				
Cusp of outer premaxillary teeth	3	3	3	3(255)				
Number of dentary largest teeth	4	4	4	4(255)				
Cusp of dentary largest tooth	5	5	5	3(21), 5(232)				
Number of maxillary teeth	3	-	-	1(10), 2(56), 3(108), 4(56), 5(16)				
Cusp of maxillary largest tooth	3	-	-	3(246)				
Predorsal scales	10	9	9(3)	9(84), 10(166), 11(5)				
Circumpeduncular scales	14	13	13(3)	12(73), 13(92), 14(90)				
Lateral-line perforated scales	7	8	9(1), 10(1)	6(1), 7(3), 8(31), 9(50), 10(43), 11(58), 12(21), 13(13), 14(7), 15(1)				
Longitudinal series (including perforated scales)	31	32	32(1), 33(2)	30(7), 31(29), 32(72), 33(79), 34(48), 35(10)				
Scales rows between dorsal-fin origin and lateral line	5	5	5(2), 6(1)	5(226), 6(19)				
Scales rows between lateral line and pelvic-fin insertion	3	4	3(2), 4(1)	3(215), 4(31)				
Dorsal-fin rays	ii,9	ii,9	ii,9	ii,9(255)				
Pectoral-fin rays	i,11	-	-	i,10(37), 11(115), 12(103)				
Pelvic-fin rays	i,7	i,7	i,7	i,7(255)				
Anal-fin rays	iv,22	iv,22	iv,22(1), 23(1)	iv,22(58), 23(94), 24(81), 25(20), 26(1)				
Gill rakers on lower limb	10	10	9(2), 10(1)	9(2), 10(143), 11(100), 12(6)				
Gill rakers on angle	1	1	1	1(251)				
Gill rakers on upper limb	6	7	6(3)	6(108), 7(141)				

Remarks. *Hemigrammus lunatus* was described by Durbin (in Eigenmann, 1918: 164-165), though the name had previously appeared without a description or diagnosis in Eigenmann (1910: 436) and Ellis (1911: 162). Although paratypes of *Hemigrammus lunatus* were collected both from the rio Paraguai (Jauru and Cáceres) and Amazon basins (Óbidos), no information on the locality of the holotype was provided at the description, and the type locality is indicated simply to

be “Amazon basin” by Durbin (in Eigenmann, 1918: 165). However, the holotype and the two paratypes (one paratype is missing), that belong to the same lot (MCZ 20964) actually have not lost their locality data (Figs. 4 and 6). The holotype and these two paratypes were collected at the lago Badajós, a large blocked-valley lake tributary of the rio Solimões/ Amazonas near Codajás, Amazonas (ca. 03°21’S 62°41’W). We therefore restrict the type locality of *Hemigrammus*

lunatus to “Brazil, Amazonas, Codajás, lago Badajós (ca. 03°21’S 62°41’W)”. Although the holotype is mixed with two paratypes in the same lot, the largest specimen was designated by Durbin (in Eigenmann, 1918) as the “type” of the species. Notwithstanding we have not examined material collected at the type locality, lago Badajós lies about 260 km in a straight line upstream from the lago Janauacá, a very similar blocked-valley lake from where much material of the species is available in collections (see Material examined). Géry (1964: 9-10) provided a short redescription of the species based on specimens from the Amazon basin in Peru and Bolivia considered that the population of *H. lunatus* occurring in the rio Paraguai basin might be distinct at the subspecific level, since the comparison of the specimens from the Amazon basin with a single specimen from the rio Paraguai basin in Paraguay showed the latter to be more elongated, and displaying a narrower infraorbital 3 and a longer maxillary. Géry (1964: 10) even suggested that *Hyphessobrycon maxillaris* might be an available name for that purported subspecies. The examination of extensive material from the Central Amazon, rio Madeira, and rio Paraguai basins during the present study did not reveal any features that might distinguish these different populations, and thus they are herein considered to represent a single species (Fig. 7). We have examined very few specimens of *H. lunatus* from western Amazon other than from the rio Madeira basin and for the moment we refrain from discussing their presumable conspecificity with the populations from Central Amazon, rio Madeira, and rio Paraguai basins. Records of *H. lunatus* from the upper Corantjin River in Suriname (Géry, 1965; Mol, 2012) and rio Orinoco basin in Venezuela (Lasso *et al.*, 2004) need to be reexamined. For a discussion on the synonym of *Hyphessobrycon maxillaris*, see the Discussion.

Material examined. Type specimens: *Hemigrammus lunatus*: CAS 42679, paratype, 1, 23.8 mm CP; MCZ 20964, holotype, 1, 26.5 mm SL, paratypes, 2, 21.7-23.9 mm SL, Codajás, lago Badajós, ca. 3°21’S, 52°41’W. **Non-type specimens:** Brazil: Amazonas State, rio Negro basin: INPA 15339, 1, 36.8 mm SL, Manaus, igarapé Tarumãzinho, road BR-174, km 28 rio Tarumã-Açu, 02°43’51”S 60°04’46”W. Rio Solimões basin: MZUSP 100860, 1, 23.4 mm SL, Manaus, rio Amazonas, lago Puraquequara, ca. 03°02’S 59°49’W; INPA 24765, 2, 24.5-26.4 mm SL; NUP 8023, 8, 23.2-27.0 mm SL, Careiro da Várzea, ilha Marchantaria, ca. 03°14’S 59°56’W; MZUSP 101287, 1, 24.4 mm SL, Careiro da Várzea, ilha Marchantaria, lago Camaleão, ca. 03°14’S 59°56’W; MZUSP 100794, 1, 24.5 mm SL, Careiro da Várzea, ilha Marchantaria, ca. 03°14’S 59°56’W; NUP 8024, 21 (16, 25.5-29.9 mm SL); NUP 9573, 4 c&s, 25.8-29.3 mm SL, Manaquiri, lago Murumuru, lago Janauacá system, 03°25’43”S 60°16’00”W; MCP 37131, 2, 23.0-23.4 mm SL, Manaquiri, lago Murumuru, lago Janauacá system, 03°25’43”S 60°16’00”W; MCP 37151, 3, 19.0-23.2 mm SL, Manaquiri, lago Murumuru, lago Janauacá system, 03°25’43”S 60°16’00”W; MCP 43956, 19, 22.8-

26.1 mm SL, Manaquiri, lago Murumuru, lago Janauacá system, 03°25’43”S 60°16’00”W; MCP 37149, 2, 26.6-27.5 mm SL, Manaquiri, paraná de Janauacá, mouth of lago Castanho, 03°24’S 60°16’W; MZUSP 102965, 1, 23.8 mm SL, Manaquiri, lago do Castanho, São José, lago Janauacá system, 03°24’S 60°16’W; MZUSP 102737, 1, 26.0 mm SL, Manaquiri, paraná de Janauacá, mouth of lago Castanho, 03°24’S 60°16’W; MZUSP 102722, 2, 24.0-26.9 mm SL, Manaquiri, lago Murumuru, lago Janauacá system, ca. 03°24’S 60°16’W; MZUSP 102980, 7, 22.2-29.8 mm SL, Manaquiri, channel between lago Murumuru and paraná de Janauacá, 03°24’S 60°16’W; MZUSP 102730, 16, 23.8-33.1 mm SL, Manaquiri, lago Murumuru, lago Janauacá system, ca. 03°24’S 60°16’W; MZUSP 102754, 9, 19.5-31.4 mm SL, Manaquiri, channel between lago Murumuru and paraná de Janauacá, ca. 03°24’S 60°16’W; MZUSP 100463, 1, 30.1 mm SL, Manaquiri, lago do Castanho, São José, lago Janauacá system, 03°24’S 60°16’W. Pará State: ZUEC 7995 (103, 19.7-28.0 mm SL), Santarém, lago do Pajau (or Tamoatá), rio Amazonas, 2°11’29”S, 54°51’28”W. Rondônia State: INPA 21621, 17, 25.9-33.2 mm SL; INPA 22571, 7, 27.5-30.2 mm SL, Guajará-Mirim, rio Pacaás-Novos, 10°52’S 65°16’W; INPA 39569, 5, 23.3-27.5 mm SL, Guajará-Mirim, middle rio Cautário, tributary of rio Guaporé, 10°59’05”S 62°56’12”W. Rio Madeira basin, Mato Grosso State: MCP 45041, 36, 20.5-31.1 mm SL, Comodoro, stream tributary of rio Novo (rio Guaporé basin), road BR-174, 14°13’26”S 59°41’27”W; MCP 45022, 18, 24.0-32.3 mm SL, Pontes e Lacerda, rio Pindaituba (tributary of rio Guaporé), BR-174, 15°00’41”S 59°17’18”W; MCP 45030, 6, 28.6-31.4 mm SL, Pontes e Lacerda, stream tributary of rio Guaporé, road BR-174, 14°55’15”S 59°17’29”W; MCP 15724, 6, 20.8-26.2 mm SL; MZUSP 44457, 5, 20.8-22.9 mm SL, Pontes e Lacerda, rio Guaporé and flooded areas, 15°12’S 59°21’W; MCP 45036, 24, 24.7-36.8 mm SL, Pontes e Lacerda, rio Bugre (tributary of rio Guaporé), BR-174, 14°51’35”S 59°17’57”W; MCP 45993, 1, 29.5 mm SL, Pontes e Lacerda, stream tributary of rio Pindaituba, road BR-174, 14°59’53”S 59°17’10”W; MCP 45994, 23, 21.5-28.8 mm SL, Nova Lacerda, rio Galera (tributary of rio Guaporé), balneário Galera, 14°28’59”S 59°35’07”W; MZUSP 95364, 33, 21.9-30.5 mm SL, Vila Bela da Santíssima Trindade, rio Guaporé, 15°00’28”S 59°57’22”W. Rio Paraguai basin: Mato Grosso State: MCP 15726, 24, 23.2-32.5 mm SL, stream at road Barra do Bugres/Cáceres, 99 km south of Barra do Bugres, tributary of rio Paraguai, ca. 15°45’S 57°20’W; MCP 15731, 7, 27.1-31.2 mm SL; MZUSP 44338, 7, 27.1-28.5 mm SL, stream at Porto Estrela, road Barra do Bugres/Cáceres, 35 km south of Barra do Bugres, tributary of rio Paraguai, 15°24’S 57°15’W; MCP 15733, 11, 24.5-31.8 mm SL, Barra dos Bugres, rio Jauquara (tributary of rio dos Pássaros) at Jauquara, ca. 15°10’S 57°05’W; MZUSP 44358, 24, 25.4-33.0 mm SL, stream crossing the road Barra do Bugres/Cáceres, about 90 km from Barra do Bugres, tributary of rio Paraguai, ca. 15°43’S 57°22’W; MZUSP 44481, 3, 27.0-30.9 mm SL, rio Sangradouro, at road Cáceres/Cuiabá about 90 km east from Cáceres, ca. 16°14’S 56°37’W; MZUSP 44473, 1, 31.8 mm SL, Cáceres, ribeirão das Flexas, road Cáceres/Cuiabá, 69 km E Cáceres, ca. 16°09’S 57°21’W; MZUSP 44285, 2,

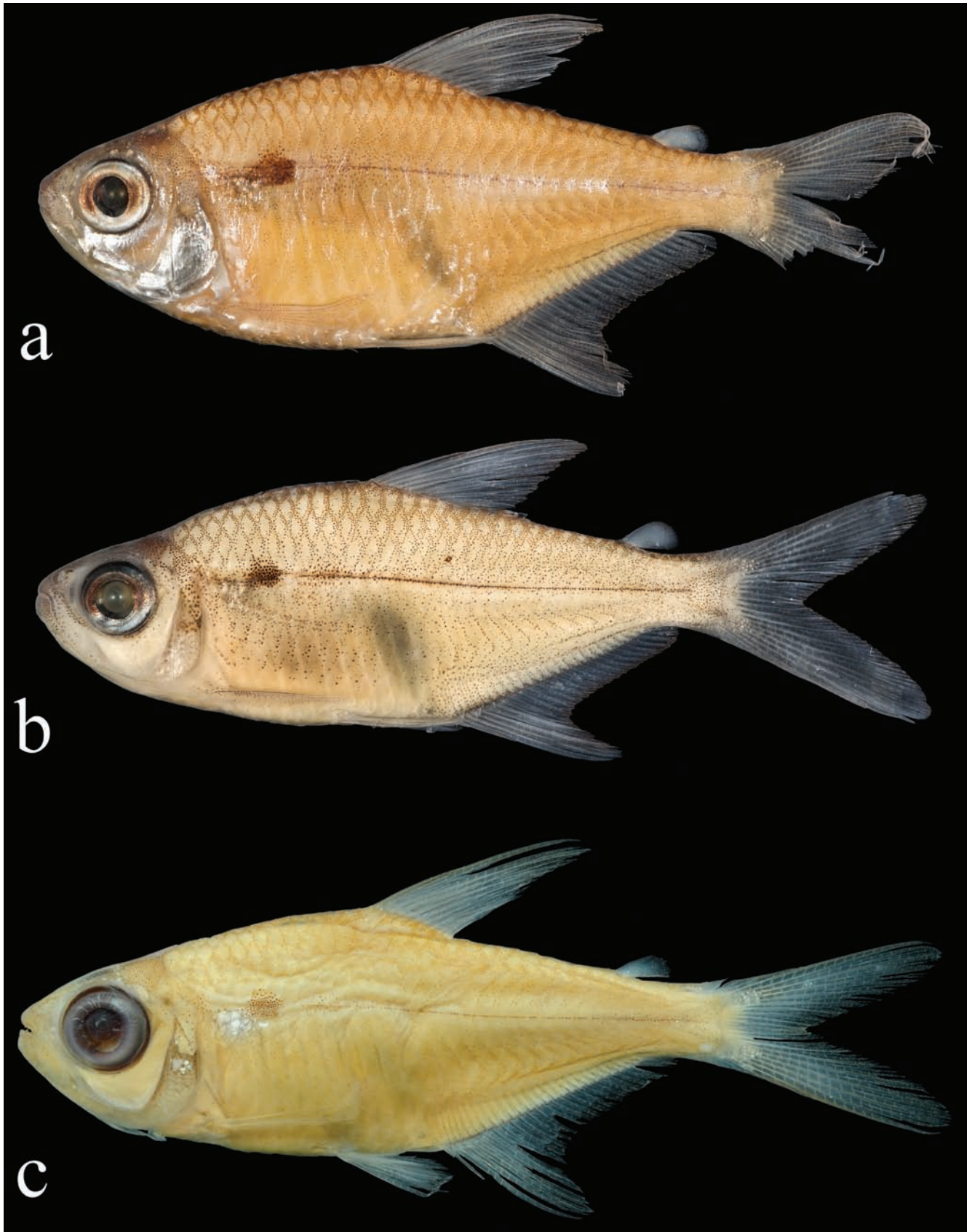


Fig. 7. *Hemigrammus lunatus*: both from Brazil, (a) MZUSP 102730, 33.1 mm SL, female, Amazonas State, Manaquiri, lago Janauacá system; (b) MZUSP 90475, 30.2 mm SL, male, Mato Grosso State, Cáceres, rio Sepotuba, rio Paraguai basin; *Hyphessobrycon maxillaris* (c) ANSP 53660, holotype, 28.3 mm SL, Brazil, Mato Grosso State, Descalvados, rio Paraguai basin.

27.7-30.0 mm SL, Jangada, ribeirão Chiqueirão, 21 km W Jangada, tributary of rio Jangada, ca. 15°07'S 56°39'W; MZUSP 90076, 12, 22.2-31.0 mm SL, Cáceres, rio Sepotuba, near its mouth, 15°53'34"S 57°38'44"W; MZUSP 90142, 11, 19.8-28.3 mm SL, Cáceres, mouth of rio Sepotuba, 15°54'53"S 57°39'24"W; MZUSP 90196, 11, 17.7-29.4 mm SL, Cáceres, lower rio Sepotuba, 15°47'33"S 57°39'20"W; MZUSP 90274, 41, 26.1-31.6 mm SL, Cáceres, lower rio Sepotuba, 15°46'07"S 57°38'54"W; MZUSP 90475, 7, 25.7-32.2 mm SL, Cáceres, lower rio Sepotuba, 15°43'53"S 57°39'53"W; MZUSP 90498, 6, 26.9-30.1 mm SL, Cáceres, rio Sepotuba (middle portion), 15°28'44"S 57°41'59"W; MZUSP 90481, 2, 26.6-32.3 mm SL, Cáceres, rio Sepotuba (middle portion), 15°31'01"S 57°42'26"W; MZUSP 4443, 3, 21.9-22.3 mm SL, Santo Antônio do Leverger, rio Cuiabá system; NUP 969, 2, 27.1-28.5 mm SL, Barão de Melgaço, rio Cuiabá, 16°20'02"S 55°57'10"W; NUP 2112, 1, 35.9 mm SL, Rosário Oeste, córrego Imbaúba, tributary of rio Cuiabá, 14°55'06"S 56°27'02"W; NUP 2113, 2, 21.2-22.7 mm SL, Rosário Oeste, córrego São Joaquim, tributary of rio Cuiabá, 14°44'58"S 56°07'39"W; NUP 2114, 3, 28.5-34.2 mm SL; NUP 7528, 5, 22.7-26.1 mm SL, Barão de Melgaço, córrego Cancela, tributary of rio Cuiabá, 14°42'30"S 56°15'51"W; NUP 9574, 4 c&s, 27.3-32.4 mm SL, Rosário Oeste, córrego Cancela, tributary of rio Cuiabá, 14°42'30"S 56°15'51"W; NUP 2115, 7, 25.8-28.6 mm SL, Chapada dos Guimarães, rio Quilombo, tributary of Manso Reservoir, 15°06'50"S 55°40'38"W; NUP 9548, 3 c&s, 19.3-27.2 mm SL, Chapada dos Guimarães, rio Quilombo, tributary of Manso Reservoir, 15°06'50"S 55°40'38"W; NUP 7527, 1, 30.7 mm SL, Chapada dos Guimarães, rio Casca, tributary of Manso Reservoir, 14°57'07"S 55°42'59"W. Mato Grosso do Sul State: MZUEL 5414, 5, 23.2-33.2 mm SL, Corumbá, bridge

on corixo Sará, Estrada Parque, 19°00'29"S 57°39'08"W; MZUEL 5415, 1, 25.5 mm SL, Corumbá, Base de Estudos do Pantanal (BEP), right margin of rio Miranda, 19°34'37"S 57°00'42"W; MZUEL 5416, 1, 24.8 mm SL, Corumbá, Estrada Parque, 9 km from Base de Estudos do Pantanal (BEP), 19°30'45"S 57°02'27"W; MZUSP 59467, 10, 25.8-30.8 mm SL, Corguinho, stream at Chacara da Portela, tributary of rio Aquidauana, 19°48'40"S 54°50'39"W; NUP 9881, 1, 28.7 mm SL, Porto Murtinho, riacho Amonguijá, tributary of rio Paraguai, 21°41'16"S 57°52'55"W. Paraguay. Concepción: MZUSP 54028, 55, 26.2-39.9 mm SL, riacho Blandengue, near mouth with río Apa, 22°14'00"S 57°21'00"W; MZUSP 54027, 21, 29.9-38.9 mm SL, Arroyo La Paz, below bifurcation of the mouth of Riacho Primavera, 22°24'S 57°43'W; MZUSP 54354, 3, 32.6-33.3 mm SL, Alto Paraguay, río Paraguay, marginal lagoon, estancia Cerrito, 21°27'00"S 57°55'00"W. Canindeyú: MNHNP 3246, 14 (13, 19.5-36.8 mm SL), oxbow lake of río Jejuí-Mí, 1 km from headquarters of Reserva Natural del Bosque Mbaracajú, 24°08'27"S 55°38'25"W; MNHNP 3619, 4, 29.9-36.5 mm SL, río Jejuí-Mí, Reserva Natural Del Bosque Mbaracajú, Puesto Jejuí-Mí, 24°08'27"S 55°38'25"W.

Discussion

Specimens belonging to *Hemigrammus machadoi* were previously identified by Durbin in Eigenmann (1918: 165) as atypical specimens of *H. lunatus*. She reported two specimens (45.0-48.0 mm SL), collected at "rio Boa Ventura" (not found, but mentioned by Haseman & Eigenmann, 1911: 310, as a tributary of the rio Guaporé "south of Villa de Mato Grosso", i.e., upstream from the Vila Bela da Santíssima Trindade), possessing two or three maxillary teeth with three, five or seven cusps, a diffuse humeral blotch and a longitudinal stripe not "overlaid with silvery", whereas *H. lunatus* was characterized by the presence of two or three uni- or tricuspid maxillary teeth, a roundish and well defined humeral blotch, and a longitudinal midlateral stripe with silvery pigmentation. Although we were unable to examine those specimens, we tentatively identified them as *Hemigrammus machadoi*.

Hyphessobrycon maxillaris was described by Fowler (1932) from Descalvados, a ranch situated at the left bank of the rio Paraguai, in the central area of the Pantanal, Mato Grosso State (ca. 16°44'S 57°45'W). Géry (1964) was the first to notice the similarity between *Hemigrammus lunatus* and *Hyphessobrycon maxillaris*, remarking that the latter might constitute a "geographical form" of the earlier in the rio Paraguai basin, even though both nominal species were not considered to be congeneric at the time. Weitzman (1985) remarked the presence of scales covering approximately the basal one third of the caudal fin of the type series (ANSP 53660-53663) and additional specimens from USNM and UMMZ, identified by her as conspecific to the type series, consequently transferred *Hyphessobrycon maxillaris* to the genus *Hemigrammus*.

Based exclusively on the original description of both

Table 3. Fish species known to be exclusively shared between the rio Paraguai/La Plata and rio Guaporé basins. Voucher lots documenting the occurrence of two species previously unrecorded for the rio Guaporé basin are cited.

Species	References/voucher lots
Characiformes	
Characidae	
<i>Aphyocharax rathbuni</i>	MZUSP 80050
<i>Gymnocorymbus ternetzi</i>	Lima <i>et al.</i> , 2003
<i>Hemigrammus machadoi</i>	Present paper
<i>Hyphessobrycon elachys</i>	MCP 46281
Siluriformes	
Scoloplacidae	
<i>Scoloplax empousa</i>	Schaefer <i>et al.</i> , 1989
Perciformes	
Cichlidae	
<i>Aequidens plagiazonatus</i>	Kullander, 2003
<i>Apistogramma inconspicua</i>	Kullander, 1982
<i>Apistogramma trifasciata</i>	Kullander, 1982
<i>Crenicichla lepidota</i>	Kullander, 2003
<i>Gymnogeophagus balzanii</i>	Reis & Malabarba, 1988
<i>Laetacara dorsigera</i>	Kullander, 2003
<i>Satanoperca pappterra</i>	Kullander, 2003

species, Bristki *et al.* (2007) diagnosed *H. lunatus* from *H. maxillaris* by the presence of five scales rows above lateral line, and three below (vs. seven and four, respectively). However, the examination of the type series of *H. maxillaris* (ANSP 53660, holotype; ANSP 53661, paratypes) revealed the presence of only five or six scales rows above and three scales rows below the lateral line in *H. maxillaris* (Fig. 7). This difference in counts of scales rows could be attributed by the methodology used by Fowler (1932), which included predorsal series in the count of scales rows above lateral line.

Analysis of pictures, morphometric, and meristic data of the type series of *H. maxillaris*, when compared to pictures, morphometric, and meristic data of the type series of *H. lunatus* (MCZ 20964, holotype and two paratypes; CAS 42679, paratype), as well as data on an extensive series of *H. lunatus* analyzed in this study, including material collected near the type locality of *H. maxillaris*, did not reveal differences between them (Table 2). The holotype of *Hyphessobrycon maxillaris* is now very faded (Fig. 7), but the little that is left of its pigmentation, as well as the description of coloration pattern provided by Fowler (1932: 355) is more similar to the coloration pattern found in *H. lunatus* than any other sympatric congener (or sympatric *Hyphessobrycon* species). Thus, we consider *Hemigrammus maxillaris* as a junior subjective synonym of *Hemigrammus lunatus*.

Among congeners, *Hemigrammus machadoi* is more similar in overall body shape and color pattern to *H. barrigonae*, *H. lunatus*, and *H. ulreyi*. These species share a similar color pattern that includes a broad longitudinal dark stripe on the eye and a conspicuous dark stripe at the anal-fin basis. *Hemigrammus barrigonae* and *H. ulreyi* share a conspicuous narrow dark midlateral stripe, which is absent from both *H. machadoi* and *H. lunatus*. *Hemigrammus lunatus* possess an overall paler color pattern when compared with *H. barrigonae*, *H. machadoi*, and *H. ulreyi*. Although a dark stripe along the anal-fin basis is known from some other congeners (see Diagnosis), the broad longitudinal dark stripe over the eye is unique, among *Hemigrammus* species, for *H. barrigonae*, *H. lunatus*, *H. machadoi*, and *H. ulreyi*. These derived traits suggest that these species might form a putative monophyletic group, hereafter named the *Hemigrammus lunatus* species-group. Among another small characids, the widespread *Moenkhausia collettii* shares a similar color pattern to the species of the *Hemigrammus lunatus* species-group. *Moenkhausia collettii* possess a complete lateral line (vs. incomplete in the species of the *Hemigrammus lunatus* species-group with the exception of some specimens of *H. barrigonae*) and has an overall body shape more elongate than the species belonging to the *Hemigrammus lunatus* species-group. Detailed phylogenetic hypotheses are needed for both testing the purported monophyly of the *Hemigrammus lunatus* species-group and whether *Moenkhausia collettii* may be closely related, or not, to the species belonging to this group.

Hemigrammus machadoi is known from the upper rio Paraguai and the upper and middle rio Madeira basins. At the rio Madeira basin, most known localities are within the rio Guaporé basin, except for records from the rio Pacáas Novos (UFRO-I 14036), rio Jaci-Paraná (MCP 47946), and rio Jamari (ZUEC 7637), all tributaries situated downstream the confluence of rio Guaporé and rio Mamoré. Carvalho & Albert (2011) recently discussed the relationships between the ichthyofauna of the La Plata and Amazon basins, and summarized in a table the distribution of several fish species shared between both basins. They listed eight fish species as shared exclusively between the La Plata and the rio Guaporé basins, i.e., *Aphyocharax nattereri* (Characidae), *Pyrrhulina australis* (Lebiasinidae), *Scoloplax empousa* (Scoloplacidae), *Apistogramma inconspicua*, *A. trifasciata*, *Crenicichla lepidota*, *Laetacara dorsigera*, and *Satanoperca pappaterra* (Cichlidae), but some species occurring primarily in the Paraguai/La Plata basin apparently were accidentally omitted for this basin (e.g., *Gymnocorymbus ternetzi*, *Aequidens plagiozonatus*, and *Gymnogeophagus balzanii*) (their table 11.1). Table 3 provides an updated, corrected list of fish species only known as occurring in the Paraguai/La Plata and the rio Guaporé basins. We excluded *Aphyocharax nattereri* and *Pyrrhulina australis* because neither of these species occurs exclusively, among the tributaries of the Amazon basin, in the rio Guaporé (for *A. nattereri*, see Lima, 2003: 198; for *Pyrrhulina australis*, A. L. Netto-Ferreira and M. M. F. Marinho, pers. comm.). We have not included species that are also known to occur in the rio Mamoré basin (e.g., *Psectrogaster curviventris*; see Carvalho & Albert, 2011, for other examples). We have included *Hemigrammus machadoi* in the list, even though the species is known from outside the rio Guaporé basin, because all remaining localities for the species are clear or dark water tributaries of the middle rio Madeira basin draining the Brazilian shield. Our suggestion is that exchanges between the rio Madeira and rio Paraguai basins have occurred in two different divides between these river basins caused by distinct events, both spatially and (presumably) temporally as well. The first is the divide between tributaries to the upper rio Mamoré and tributaries to the upper rio Paraguay in Bolivia that might have been driven recently by river avulsion in megafans (Wilkinson *et al.*, 2006, 2010). However, an independent river capture and consequent faunal exchange very likely have happened between the rio Guaporé and the upper rio Paraguai basins.

The rio Guaporé basin runs at the border between the Mamoré-Beni foreland basin and the Brazilian shield and has experienced neotectonic activities (Souza-Filho *et al.*, 1999; Bartorelli, 2013). The upper rio Guaporé is adjacent to the Pantanal basin, which originated in the late Tertiary/Quaternary (Irion *et al.*, 2011; Assine, 2004). Considering the recent active tectonic history of the Pantanal basin, it seems likely that a fauna exchange through river capture between these adjacent

basins might have happened in the recent past. This purported exchange probably was a capture of river from the upper rio Paraguai into the upper rio Guaporé, considering that, as earlier remarked by Carvalho & Albert (2011: 198), *Gymnogeophagus balzanii*, a derived species belonging to a genus otherwise only known from the La Plata basin and coastal river systems of southern Brazil and Uruguay, is shared between the rio Guaporé and the La Plata basin (Reis & Malabarba, 1988).

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Comparative material. All from Brazil, except if otherwise noted. *Hemigrammus barrigonae*: MZUSP 65681, 2, 31.9-38.0 mm SL, Amazonas, rio Tiquié; MZUSP 81312, 5, 23.1-27.0 mm SL, Amazonas, rio Tiquié; MZUSP 85018, 25, 13.4-40.9 mm SL, Colombia, Vaupés, rio Tiquié. *Hyphessobrycon maxillaris*: ANSP 53660, holotype, 1, 28.3 mm SL, Mato Grosso, Descalvados, rio Paraguai basin; ANSP 53661, paratypes, 3, 24.8-24.9 mm SL, same data as holotype. *Hemigrammus mimus*: MZUSP 17696, 15, 16.6-25.6 mm SL, Roraima, rio Branco basin; MZUSP 17707, 3, 21.8-21.9 mm SL, Roraima, Boa Vista, rio Branco basin. *Hemigrammus geisleri*: INPA 30024, 8, 14.5-19.0 mm SL, Amazonas, Rio Preto da Eva, rio Negro basin; INPA 32374, 717, 12.0-17.2 mm SL, Pará, Oriximiná, rio trombetas basin; INPA 36934, 98, 14.0-17.2 mm SL, Roraima, rio Branco basin. *Hemigrammus ulreyi*: MZUEL 5420, 12, 21.7-28.7 mm SL, Mato Grosso, Poconé, rio Paraguai basin; MZUSP 19100, 11 (6, 25.2-29.3 mm SL), Mato Grosso, Descalvados,

rio Paraguai basin; MZUSP 44389, 12, 24.7-32.7 mm SL, Mato Grosso, Cáceres, rio Paraguai basin; NUP 4143, 2, 24.9-25.7 mm SL, Mato Grosso, Barão de Melgaço, rio Cuiabá; MZUEL 5420, 3, 26.1-26.2 mm SL, Mato Grosso do Sul, Corumbá, rio Paraguai basin; MZUSP 59813, 112 (40, 8 c&s, 23.0-29.4 mm SL), Mato Grosso do Sul, Rio Verde de Mato Grosso; MNHNP 2564, 5, 25.5-32.2 mm SL, Paraguay, San Pedro, San Pedro de Ycuamandiyú, rio Jejuí, rio Paraguay basin; MNHNP 2948, 9, 29.2-34.2 mm SL, Paraguay, Misiones, Santa Rosa, rio Paraná basin. *Moenkhausia collettii*: INPA 28083, 19, 26.4-30.3 mm SL, Amazonas, rio Solimões basin; INPA 37302, 5, 25.4-35.6 mm, Amazonas, rio Uatumã basin; INPA 21623, 6, 25.5-32.9 mm SL, Rondônia, rio Madeira basin; NUP 8104, 10, 25.0-30.0 mm SL, Brazil, Tocantins, rio Tocantins-Araguaia basin. *Hemigrammus cf. lunatus*: UF 126240, 4, 32.9-38.2 mm SL, Peru, Loreto, rio Pacaya.

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