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Redescription of *Astyanax guianensis* Eigenmann 1909 (Characiformes: Characidae), a poorly known and widespread fish from the Amazon, Orinoco and Guiana Shield drainages

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Abstract

Astyanax guianensis is redescribed based on the holotype, paratypes, and additional specimens from the rio Essequibo in Guyana, rio Orinoco in Venezuela and from several localities in the Amazon river basin in Brazil, Colombia and Bolivia. *Astyanax guianensis* is diagnosed by having five to 10 maxillary teeth, 31 to 35 pored lateral-line scales, 21 to 25 branched anal-fin rays, and a dark vertical humeral blotch followed by a clear area and then by a dark longitudinal stripe, ending before the caudal-fin rays. In addition, comments on the importance of revisionary studies on the species of the Characidae are provided.

Key words: *Astyanax guaporensis*, *Astyanax multidens*, *Moenkhausia collettii*, Neotropical, taxonomy

Resumo

Astyanax guianensis é redescrita com base no holótipo, parátipos e exemplares adicionais coletados no rio Essequibo na Guiana, no rio Orinoco na Venezuela e em diversas localidades da bacia do rio Amazonas no Brasil, Colômbia e Bolívia. *Astyanax guianensis* é diagnosticada por apresentar de cinco a 10 dentes no maxilar, 31 a 35 escamas perfuradas na linha lateral, 21 a 25 raios ramificados na nadadeira anal e uma mancha umeral escura seguida de uma área clara e, posteriormente, de uma faixa longitudinal escura terminando antes dos raios medianos da nadadeira caudal. Além disso, comentários sobre a importância de revisões taxonômicas de espécies de Characidae são fornecidos.

Palavras-chave: *Astyanax guaporensis*, *Astyanax multidens*, *Moenkhausia collettii*, Neotropical, taxonomia

Introduction

The Neotropical genus *Astyanax* Baird & Girard is the most species-rich genus of the Characiformes, comprising almost 140 valid species (Eschmeyer & Fricke 2014). The species of the genus are distributed in American freshwater drainages from Texas (USA) to Argentina, living in environments such as, for example, caves (Wilkens & Streaker 2003), fast current streams (Bertaco & Malabarba 2001), and lakes (Meschiatti *et al.* 2000). *Astyanax* is one of the most taxonomically poorly known genus of the family Characidae. Some species were grouped into units defined mainly by color patterns, morphometric, and meristic data: the *Astyanax bimaculatus* (Linnaeus) species group (Garutti 1999), the *A. fasciatus* (Cuvier) species complex (Melo & Buckup 2006), and the *A. scabripinnis* (Jenyns) species group (Moreira-Filho & Bertolo 1991; Bertaco & Malabarba 2001; Bertaco & Lucena 2006). Most species belonging to these groups are difficult to diagnose. Recently, revisionary papers have been published to elucidate the identity of several species of *Astyanax* (e.g., Melo & Buckup 2006; Garutti & Langeani 2009; Pavanelli & Oliveira 2009; Bertaco *et al.* 2010), but there are still lots of poorly known forms that need an appropriate taxonomic characterization.

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During recent taxonomic studies of two Amazonian species, *Astyanax guaporensis* Eigenmann and *A. multidens* Eigenmann (Marinho & Ohara 2013 and Marinho & Birindelli 2013, respectively), a similar species was found, *Astyanax guianensis*. It is an interesting find since this poorly known species is currently only known to occur in the Guiana Shield drainages. After the examination of several collections and recently collected material, *A. guianensis* revealed to be also widespread throughout the Amazon and Orinoco basins**.** Most lots of *A. guianensis* examined were previously identified as *Astyanax* sp., *Moenkhausia* sp. or even *Moenkhausia collettii* Steindachner, indicating the taxonomic confusion regarding this species. In this paper, we redescribe *A. guianensis* based on the examination of the holotype, several paratypes, and additional material from several drainages of South America. We also update the geographical distribution of the species and comment on the importance of revisionary studies on species of the Characidae.

Material and methods

The description is based on the holotype, 60 of the 214 paratypes, and 1,369 non-type specimens. Counts and measurements were taken according to Fink & Weitzman (1974), with the exception of longitudinal scale rows below the lateral line, counted to the pelvic-fin origin instead of to the anal-fin origin. In addition, a single small scale between the dorsal-fin origin and the first longitudinal scale row present in some specimens was excluded from the count of the longitudinal scale rows above the lateral line. Measurements are given as percents of standard length (SL), except for subunits of the head given as percents of head length (HL). Counts of vertebrae, supraneurals, gill-rakers on first arch, tooth cusps, smaller dentary teeth, unbranched anal-fin rays, and procurrent caudal-fin rays were taken from six cleared and stained (cs) specimens, prepared following Taylor & van Dyke (1985). Vertebrae of the Weberian apparatus were counted as four elements and the compound ural centrum as a single element. Abdominal vertebrae are considered to be the vertebrae associated with ribs and bearing hemal arches without hemal spine. Caudal vertebrae are those bearing hemal spine. Counts are followed by their frequencies in parentheses. Counts of the holotype are marked with an asterisk. The pectoral-fin rays of the holotype were not counted as the fin is damaged; dentary teeth were not counted to avoid further damages. Osteological data cited for the holotype were taken from radiographs.

Meristic data from other species of *Astyanax* were taken by direct examination of specimens (see 'Comparative material') or from original descriptions and/or redescriptions (e.g., Eigenmann 1927; Garutti 2003; Melo & Buckup 2006; Pavanelli & Oliveira 2009). Except when mentioned, the information included in 'Habitat and ecological notes' section was obtained from recently collected data pertaining to lots MZUSP 111803, MZUSP 115554, and MZUSP 115555.

Institutional abbreviations are: ANSP (Academy of Natural Sciences, Philadelphia), BMNH (Natural History Museum, London), CAS (California Academy of Science, San Francisco), FMNH (Field Museum of Natural History, Chicago), MCP (Museu de Ciências e Tecnologia da Pontifícia Universidade Católica do Rio Grande do Sul, Porto Alegre), MZUSP (Museu de Zoologia da Universidade de São Paulo, São Paulo), NMW (Naturhistorisches Museum Wien, Vienna), SU (Stanford University, now in CAS), UFRO-ICT (Universidade Federal de Rondônia, Porto Velho), and ZMB (Zoologisches Museum, Humboldt-Universitat, Berlin).

Astyanax guianensis Eigenmann 1909

Figs. 1–2, Table 1

Astyanax guianensis Eigenmann 1909: 16 [type locality: Warraputa (= rio Essequibo at Warraputa cataract, Guyana)].—Eigenmann 1910: 434 [citation].—Eigenmann, 1911: 177 [closely allied to *Astyanax guaporensis*].—Eigenmann 1912: 350 [identification key; literature compilation].—Eigenmann 1921: 274, plate 53, Fig. 4 [identification key; literature compilation].—Eigenmann 1927: 328 [literature compilation].—Henn 1928: 60 [type catalog].—Böhlke 1953: 22 [type catalog].—Géry 1977: 426 [identification key].—Nijssen *et al*. 1982: 14 [type catalog].—Böhlke 1984: 47 [type catalog].—Ibarra & Stewart 1987: 12 [type catalog].—Vari & Howe 1991: 6 [type catalog].—Nijssen *et al*. 1993: 216 [type catalog].—Garutti & Venere 2009 [literature compilation].—Lima 2009: 29 [Guiana Shield at Amazonas and Bolivar States, Venezuela].—Lima *et al*. 2003: 109 [questionably Venezuela].—Marinho & Birindelli 2013: 46 [similar to *Astyanax multidens* and *A. guaporensis*].—Marinho & Ohara 2013: 476 [tentative identification of material from rio Beni].

Moenkhausia sp. "*collettii* alta".—Lima *et al.* 2013: 322 [rio Madeira basin, brief description].

Diagnosis. *Astyanax guianensis* can be distinguished from all congeners, except *A. angustifrons* (Regan), *A. aurocaudatus* Eigenmann, *A. gisleni* Dahl, *A. goyanensis* (Miranda Ribeiro), *A. guaporensis*, *A. henseli* Melo & Buckup, *A. leopoldi* Géry, Planquette & Le Bail, *A. multidens*, *A. nasutus* Meek, *A. nicaraguensis* Eigenmann, *A. superbus* Myers, and *A. totae* Haluch & Abilhoa by having five to 10 maxillary teeth (vs. none to four). *Astyanax guianensis* is distinguished from the aforementioned species, except *A. angustifrons*, *A. goyanensis*, *A. guaporensis*, *A. leopoldi*, *A. multidens*, *A. nicaraguensis*, and *A. totae*, by having 31 to 35 pored lateral-line scales (vs. more than 35). It can be distinguished from *A. angustifrons*, *A. goyanensis*, *A. leopoldi*, *A. multidens*, and *A. nicaraguensis* by having the middle caudal-fin rays hyaline (vs. middle caudal-fin rays dark), from *A. guaporensis* by having five, rarely six (4 out of 59 examined specimens) horizontal scale row above lateral line (vs. six to seven) and the absence of a midlateral series of dark anteriorly-directed chevrons (vs. presence), and from *A. totae* by presenting 21 to 25 branched anal-fin rays (vs. 15 to 18).

Description. Morphometric data for *Astyanax guianensis* presented in Table 1. Small sized species (largest examined specimen 53.3 mm SL). Body compressed laterally, moderately elongate. Greatest body depth at dorsal-fin origin. Dorsal profile of head convex from tip of snout to vertical through anterior border of anterior nostril and straight from that point to tip of supraoccipital spine. Dorsal profile of body straight to slightly convex at predorsal region, straight at dorsal-fin base, straight from end of dorsal-fin base to adipose-fin origin, and concave along caudal peduncle. Ventral profile of head and body slightly convex from anterior tip of lower lip to anal-fin origin, straight along anal-fin base, and slightly concave along caudal peduncle.

TABLE 1. Morphometric data of *Astyanax guianensis*. SD for Standard Deviation. The mean and SD include the values of the holotype, paratypes, and non-type specimens.

	Holotype	Paratypes		Non-type specimens			
		n	Range	n	Range	Mean	SD
Standard length (mm)	41.0	22	30.8–43.6	43	29.1–51.4		
Percentages of SL							
Depth at dorsal-fin origin	38.1	22	33.4–39.4	43	28.2–39.9	35.3	2.3
Snout to dorsal-fin origin	49.8	22	46.1–51.6	43	46.8–51.3	48.5	1.1
Snout to pectoral-fin origin	27.3	21	25.1–29.3	43	25.5–31.0	27.6	1.1
Snout to pelvic-fin origin	48.1	22	45.9–49.7	43	44.2–49.7	47.1	1.1
Snout to anal-fin origin	63.3	22	61.3–64.7	43	59.8–67.0	62.8	1.6
Caudal-peduncle depth	10.4	22	8.6–10.5	43	8.3–10.9	9.6	0.6
Caudal-peduncle length	11.3	22	8.9–12.6	43	6.9–12.6	10.1	1.0
Pectoral-fin length	14.4	22	20.8–26.5	43	19.2–26.0	22.8	1.7
Pelvic-fin length	18.0	22	15.9–19.5	43	16.0–20.7	18.2	1.0
Dorsal-fin base length	13.5	22	13.6–16.1	43	13.4–16.2	14.9	0.7
Dorsal-fin length	–	22	30.4–34.1	43	29.0–35.3	32.3	1.3
Anal-fin base length	31.5	22	28.7–34.6	43	28.8–36.2	32.2	1.6
Anal-fin lobe length	20.0	17	18.7–25.2	43	15.8–25.1	22.1	1.8
Eye to dorsal-fin origin	35.3	22	31.1–35.3	43	30.4–35.3	33.2	1.1
Dorsal-fin origin to caudal-fin base	53.9	21	53.4–59.5	43	53.5–59.9	55.7	1.3
Head length	27.0	21	24.9–29.4	43	25.4–30.3	27.4	1.2
Percentages of HL							
Horizontal eye diameter	41.7	19	41.9–47.1	41	33.6–43.6	40.9	4.0
Snout length	24.8	21	22.0–29.7	43	20.2–31.3	26.1	2.1
Interorbital width	30.4	21	27.5–33.2	43	26.7–33.8	30.6	1.7
Upper jaw length	43.6	21	36.1–46.0	43	36.4–46.9	41.2	2.5

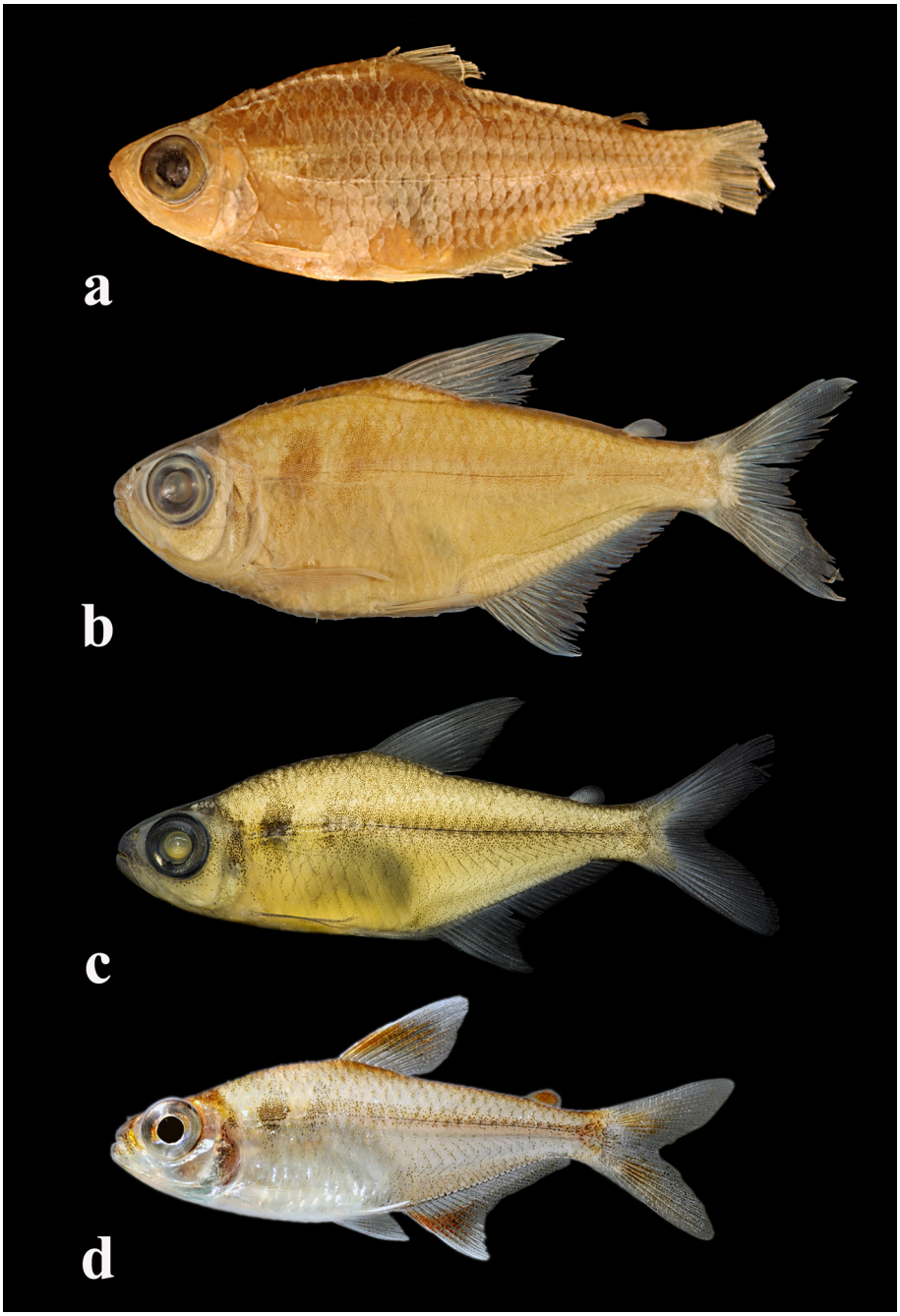

FIGURE 1. *Astyanax guianensis*: (a) holotype, FMNH 51518, 41.0 mm SL, Guyana, rio Essequibo basin; (b) MZUSP 25526, 53.3. mm SL, Brazil, Pará, rio Tapajós basin; (c) MZUSP 115554, 35.7 mm SL, Brazil, Mato Grosso, rio Guaporé basin; and (d) live specimen, Brazil, Amazonas, rio Negro at Santa Isabel do Rio Negro, not preserved.

Jaws aligned vertically, mouth terminal. Premaxillary teeth in two rows. Outer row with 2(4), 3(32), 4(30) or 5*(3) tricuspid teeth. Inner row with 5*(66) or 6(3) teeth, 4 of which pentacuspid, and lateralmost one tricuspid. Maxilla with 5(17), 6*(22), 7(22), 8(5), 9(3) or 10(1) uni- to tetracuspid teeth. Dentary with 4(26) large pentacuspid teeth, followed by one or two smaller tricuspid and one series of 5 to 12 small uni- to tricuspid teeth. Central median cusp in all teeth longer than lateral cusps (Fig. 2). Branchiostegal rays 4. First gill arch with 2(3) or 3(3) rakers on hypobranchial, none (3) or 1(3) raker on intermediate cartilage, 10(2) or 11(4) rakers on ceratobranchial, 1(6) raker on intermediate cartilage, and 7(3) or 8(3) rakers on epibranchial. Each gill raker bearing small denticles.

Supraneurals 3(3) or 4*(4), upper portion with bony lamellae. Dorsal-fin rays ii,9*(65), first unbranched ray about one-half length of second unbranched ray. First dorsal-fin pterygiophore inserted posterior to neural spine of

7th(1) or 8th*(6) vertebrae. Dorsal-fin origin slightly posterior to vertical through pelvic-fin origin. Adipose-fin origin at vertical through base of 18th or 19th branched anal-fin rays. Pectoral-fin rays i(64), 12(22), 13(37) or 14(4). Tip of adpressed pectoral fin extending beyond pelvic-fin origin. Pelvic-fin rays i*(65), 6(1) or 7*(64). Tip of adpressed pelvic fin extending beyond anal-fin origin. Anal-fin rays iv*(7), 21(8), 22(6), 23*(18), 24(27) or 25(5). First anal-fin pterygiophore inserted posterior of haemal spine of 15th*(7) vertebra. Anal-fin origin located at vertical through base of 5th or 6th branched dorsal-fin ray. Principal caudal-fin rays i,9*(57) at upper and i,8*(57) at lower lobe. Dorsal procurrent caudal-fin rays 11(1), 12(4) or 13(1) and ventral procurrent caudal-fin rays 9(2), 10(2) or 11(2). Caudal fin forked, lobes pointed.

Lateral line straight to slightly curved ventrally, with 31(3), 32(7), 33(17), 34(17) or 35*(16) perforated scales from supracleithrum to caudal-fin base. Longitudinal scale rows between dorsal-fin origin and lateral line 5*(55) or 6(4). Longitudinal scale rows between lateral line and pelvic-fin origin 4*(44) or 5(10). Predorsal scales 8(14) or 9(51) in one aligned series. Single row of 4–8 scales overlying base of anteriormost anal-fin rays. Scale rows around caudal peduncle 14*(50). Scales usually at base of caudal fin, not extending over lobes; some specimens with scales along basal one-sixth of lower lobe. Abdominal vertebrae 14*(5) or 15(2), caudal vertebrae 18(3) or 19*(4). Total vertebrae 32(1) or 33*(6).

Color in alcohol. General body color pale yellow (Figs. 1a–c). Upper and lower lips, anterior portion of maxilla, snout, top of head, dorsal portion of opercle and pectoral girdle with scattered small dark chromatophores. Some specimens with dark chromatophores scattered on third infraorbital. Middorsal horizontal scale rows bordered by dark pigmentation, forming slightly reticulated pattern. More pigmented specimens with faint dark chromatophores bordering all scales, except on ventral portion of body. Scattered dark chromatophores above anal-fin base. More pigmented specimens with dark chromatophores concentrated along margins of myosepta of posterior half of lower portion of body, between lateral line and anal-fin base. Humeral blotch vertically oriented, extending over one scale row ventral to, and three scale rows dorsal to lateral line, and over three scales horizontally. Portion of humeral blotch located dorsal to lateral line often interrupted by clear horizontal stripe. Humeral blotch followed posteriorly by clear area and then by pigmented area progressively fading posteriorly as a longitudinal stripe, from vertical through 7th or 8th lateral-line scale to caudal peduncle. Some specimens retaining guanine over longitudinal stripe. Dark pigmentation along horizontal septum extending approximately from vertical through dorsal-fin origin to caudal peduncle, falling short of caudal-fin base. Faint pigmented area at caudal peduncle. First unbranched dorsal-fin ray with dark chromatophores, remaining dorsal-fin rays hyaline. Distal half of interadial membranes of all dorsal-fin rays with scattered dark chromatophores. Pectoral, pelvic, caudal and adipose fins with few scattered dark chromatophores. Distal portion of interadial membranes of branched anal-fin rays with concentration of dark chromatophores; proximal portion with few scattered dark chromatophores.

Color in life. General body coloration silver to pale (Fig. 1d). Dorsal portions of head and eye, middle portions of dorsal and anal fins (especially anteriorly), adipose fin, and base of upper and lower caudal-fin lobes yellow to orange. Humeral blotch and longitudinal stripe conspicuous in life. Tip of the three longest pelvic-fin rays white. Tip of first six dorsal- and anal-fin rays milky white.

Sexual dimorphism. No sexually dimorphic characters observed.

Geographic distribution. *Astyanax guianensis* is widespread throughout the Guiana Shield drainages and also in the Amazon and Orinoco river basins (Fig. 3).

Habitat and ecological notes. *Astyanax guianensis* was collected in clear water streams, running over sand and silt bottoms, at altitudes ranging from 204 to 240 m above sea level, in habitats characterized by slow to moderate water current, less than one meter deep. The riparian vegetation was mainly composed by grass, shrubs, and trees. The analysis of stomach contents of five specimens of *A. guianensis* (MZUSP 97149 and MZUSP 109674) revealed the presence of organic debris, aquatic insects (caddisflies larvae, chironomids pupae, and Odonota nymph), and fragments of other unidentified arthropods.

Remarks. Most features described by Eigenmann (1909) in the original description of *Astyanax guianensis* matches those observed by us. There are only two exceptions. Eigenmann (1909) mentioned four to seven maxillary teeth. In 70 examined specimens, five to 10 tiny teeth were counted in the maxilla, none had four. Eigenmann (1909) also mentioned the presence of 34 to 35 (rarely 36) scales on the lateral series. In 60 examined specimens, 31 to 35 scales were counted on the lateral series, none had 36.

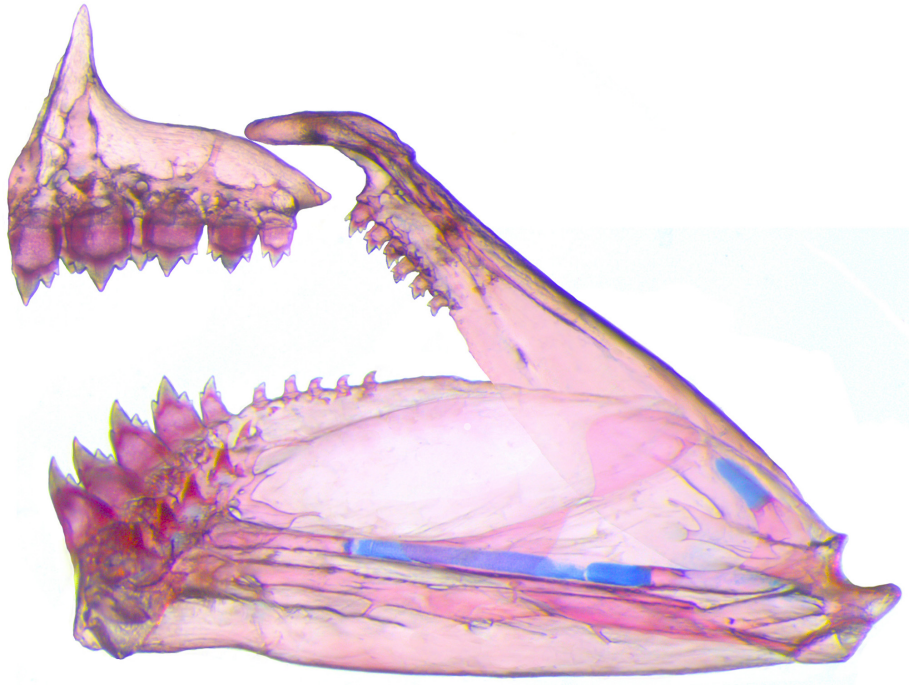

FIGURE 2. Upper and lower jaws of *Astyanax guianensis* (medial view, right side), MZUSP 109674, 46.7 mm SL. Coronomeckelian bone is missing.

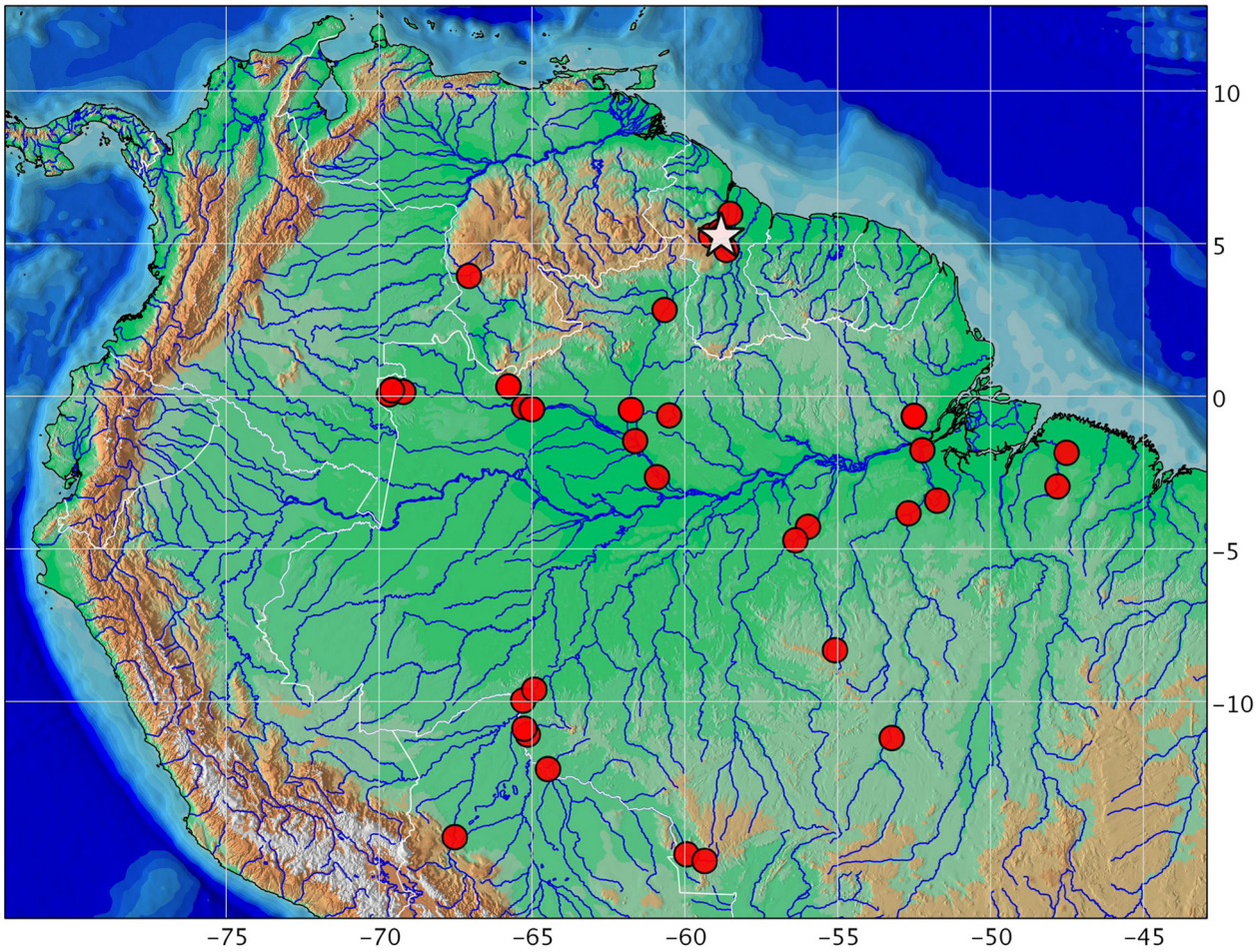

FIGURE 3. Distribution of *Astyanax guianensis* in the Guiana Shield drainages, Amazon, and Orinoco basins. Type locality is represented by the star.

In the label corresponding to lot CAS 68733 (ex IU 12078), the word cotype, is written in reference to one specimen of *Astyanax guianensis* collected by Eigenmann at Rupununi, near Rockstone. A second label was found inside the jar, stating that this specimen was not cited in the original description of *A. guianensis* and should not be considered as cotype. We agree with this remark and thus will not consider this specimen as paratype.

Pearson (1924) mentioned 12 specimens of *Astyanax guaporensis* from lagoons near Reyes [= pampa town 24 mi NE of Rurrenabaque], rio Beni, Bolivia, identified as *Astyanax* cf. *guianensis* by Marinho & Ohara (2013). Examination of this material (CAS 68730 [ex IU 17322]) confirmed the identification of the specimens as *Astyanax guianensis*.

Lowe-McConnell (1991) cited *Astyanax guianensis* from rio das Mortes, rio Araguaia basin. These specimens could not be analyzed herein. However, extensive material from that drainage was examined and did not yield any specimen of *A. guianensis*.

Discussion

Most species-rich genera of the Characidae are also the most taxonomically poorly known: *Astyanax*, *Bryconamericus* Eigenmann, *Hemigrammus* Gill, *Hyphessobrycon* Durbin, and *Moenkhausia* Eigenmann (Lima *et al.* 2003). Together, they encompass almost 420 valid species (Eschmeyer & Fricke 2014). Taxonomic problems related to these genera range from the presence of poorly known widespread species complexes, old and short descriptions, and type specimens poorly preserved to unknown type localities and geographical distributions. Many species of the aforementioned taxa were described in the beginning of the last century, and most of them were very poorly characterized. Studies conducted to better understand the boundaries and the complete geographic distribution of the available names are still very few. The limited knowledge of species-level taxonomy and the inadequate distributional information for most species are two important factors that preclude the progress of studies in biogeography of the Neotropical ichthyofauna (Vari & Weitzman 1990; Ribeiro 2006).

The most comprehensive taxonomic survey of *Astyanax* is that of Eigenmann (1921). Later on, little attention was given to understanding the true diversity hidden behind old species names within the genus. During the last 10 years, only nine species of *Astyanax* described in the beginning of the last century were formally revised and redescribed: *A. correntinus* (Holmberg) (Mirande *et al.* 2006), *A. erythropterus* (Holmberg) (Soneira *et al.* 2010), *A. goyacensis* Eigenmann (Garutti & Langeani 2009), *A. gymnodontus* (Eigenmann) (Pavanelli & Oliveira 2009), *A. guaporensis* (Marinho & Ohara 2013), *A. laticeps* (Cope) (Bertaco & Lucena 2010), *A. multidens* (Marinho & Birindelli 2013), *A. obscurus* (Hensel) (Bertaco & Lucena 2010), and *A. stenohalinus* Messner (Almirón *et al.* 2010). Although these studies represent considerable progress, the taxonomic knowledge of the genus remains very limited and more studies should be encouraged.

As stated by Wheeler (2004: 575), "the confidence one has in a species hypothesis is directly proportionate to the extent to which that hypothesis has been tested". Taxonomic revisionary studies are tests of previously proposed hypotheses; they may be either corroborated or refuted, as samples are increased and/or previously unexamined populations are studied (Wheeler 2004). Therefore, to best test previous species hypotheses, as many populations as possible should be examined and compared to distinct populations of morphologically similar taxa. Only then will the limits and geographical distribution of the taxa be comprehensively understood. Such revisionary studies are important to the knowledge of biological diversity and should not be neglected. Accessible information on the occurrence and complete morphological characterization of species avoid further problems such as description of synonyms and proliferation of non-identified taxa in inventory studies. In addition, revisionary studies are sources of information for studies on the conservation of biodiversity.

Material examined. Type specimens. Holotype of *Astyanax guianensis*: FMNH 51518, 41.0 mm SL, Guyana, Warraputa, cataract, rio Essequibo, C.H. Eigenmann. Paratypes of *Astyanax guianensis*: BMNH 1911.10.31.319–20, 2, 41.8–43.3 mm SL, Guyana [specific locality not mentioned], C.H. Eigenmann. BMNH 1911.10.31.314–18, 5, 32.1–36.5 mm SL; CAS 39208 (ex IU 11717), 26, 28.7–43.6 mm SL; MHNG 2185.089, 2, 31.5–32.6 mm SL; NMW 58824, 4, 30.8–36.6 mm SL; SU 21945, 6, 31.1–34.6 mm SL, Guyana, Rockstone, rio Essequibo basin, C.H. Eigenmann, 29 Sep–5 Oct 1908. CAS 39211 (ex IU 11720), 10, 32.8–45.2 mm SL; NMW 62783, 1, 40.2 mm SL; SU 21957, 2, 37.0–41.4 mm SL, Guyana, rio Potaro at Tumatumari cataract, rio Essequibo basin, C.H. Eigenmann, 7–14 Oct 1908. CAS 39209 (ex IU 11718), 1, 34.1 mm SL, Guyana, Crab falls, rio

Essequibo, rio Essequibo basin, C.H. Eigenmann, 4–5 Nov 1908. CAS 39210 (ex IU11719), 1, 36.9 mm SL, Guyana, Warraputa cataract, rio Essequibo, rio Essequibo basin, C.H. Eigenmann, 6 Nov 1908. **Non-type specimens.** *Astyanax guianensis*, Amazon basin: ANSP 194518, 30 of 64, 24.4–46.8 mm SL, Brazil, Pará, rio Xingu, vinicity of campsite 11 on downstream end of public beach along right bank, ca. 3 km downstream of Porto de Moz, 1º43'54.3"S 52º15'16"W. CAS 68730 (ex IU 17322), 9, 23.1–37.0 mm SL, Bolivia, El Beni, lagoons near Reyes, a pampa town 24 miles NE of Rurrenabaque, N. Pearson. MCP 23391, 48, not measured; MCP 32535, 9, 21.2–37.7 mm SL, Brazil, Pará, Paragominas, rio Capim and marginal lagoon, at ferry between Paragominas and Tomé Açú, about 56 km West of Paragominas, 2º56'49"S 47º48'48"W, R. Reis, J.P. Silva, E. Pereira & J. Montoya, 17 Jul 1998. MCP 27226, 10 of 11, 14.9–29.3 mm SL, Brazil, Pará, stream tributary of rio Guamá, at road Belém–Brasília (BR-10), between Mãe do Rio and Irituia, 1º50'56"S 47º31'14"W, R. Reis, J.P. Silva, E. Pereira & J. Montoya, 19 Jul 1998. MCP 45080, 185, 25.9–40.3 mm SL, Brazil, Rondônia, Porto Velho, Igarapé Taquarás at BR-425, between BR-364 and Guajará-Mirim, about 27 km of BR-364, rio Madeira basin, 9º57'43"S 65º17'45"W, A. Cardoso, V. Bertaco, F. Lima & J. Pezzi, 25 Jul 2004. MCP 45096, 5, 20.7–42.6 mm SL, Brazil, Mato Grosso, Pontes Lacerda, rio Guaporé, near road between Pontes e Lacerda and Vila Bela da Santíssima Trindade, rio Madeira basin, 15º12'58"S 59º21'18"W, R. Reis *et al.*, 11 Jul 2004. MCP 48292, 2, 24.0–28.0 mm SL, Brazil, Roraima, rio Negro, 0º37'15"N 60º31'5"W, T. Carvalho *et al.*, 27 Jan 2011. MZUSP 17706, 1, 33.2 mm SL, Brazil, Roraima, Boa Vista, rio Branco drainage, 2º50'N 60º40'W, T. Roberts, 9 Feb 1969. MZUSP 17697, 1, 21.6 mm SL, Brazil, Roraima, Rio Branco below Boiaçu, 0º40'S 60º51'W, T. Roberts, 2 Feb 1969. MZUSP 25526, 1, 53.3 mm SL, Brazil, Pará, Acará, left margin of rio Tapajós, upstream mouth of rio Jamanxim, near PARNA borders, 4°52'S 56°44'W, J.C. Oliveira, 19 Jan 1979. MZUSP 27775, 1, 37.6 mm SL, Brazil, Amazonas, Moura, Pedra do Gavião, rio Negro drainage, 1°28'S 61°38'W, L.P.S. Portugal, 13 Nov 1982. MZUSP 29417, 335, 23.9–44.9 mm SL, Brazil, Amazonas, rio Maraiuá, rio Negro drainage, 0º24'S 65º12'W, M. Goulding, 13 Oct 1979. MZUSP 29421, 117, 32.8–40 mm SL, Brazil, Amazonas, rio Marauiá near mouth, rio Negro drainage, 0º24'S 65º12'W, M. Goulding, 13 Oct 1979. MZUSP 29424, 17, 24.2–40.7 mm SL, Brazil, Amazonas, rio Negro below Daraá, 0°28'S 64°46'W, M. Goulding, 16 Feb 1980. MZUSP 31226, 1, 31.3 mm SL, Brazil, Amazonas, Lago do Prato, rio Negro at Anavilhanas, 2°42'S 60°45'W, M. Goulding, Oct 1980. MZUSP 37654, 46, 21.2–32.3 mm SL, Brazil, Mato Grosso, Vila Bela da Santíssima, Trindade rio Guaporé, Cais da Balsa, 23 Sep–10 Oct 1984. MZUSP 75244, 1, 38.6 mm SL, Brazil, Pará, rio Xingu, Posto Diauarum, Parque Indígena do Xingu, G.R. Kloss, 21 Nov 1973. MZUSP 92171, 14, 37.1–471 mm SL, Brazil, Amazonas, Igarapé Castanha, affluent of rio Tiquié, beaches at Santa Rosa community, 0º4'41"N 69º41'26"W, F.C.T. Lima *et al.*, 3–4 Sep 2006. MZUSP 92216, 98, 23.8–50.2 mm SL, Brazil, Amazonas, rio Tiquié near Pirarara Poço community, rio Negro drainage, 0º8'40"N 69º12'48"W, F.C.T. Lima *et al.*, 6–9 Sep 2006. MZUSP 92536, 10, 37.2–47.0 mm SL, Brazil, Amazonas, Igarapé Castanha, affluent of rio Tiquié, near mouth, rio Negro drainage, 0º12'N 69º35'W. F.C.T. Lima, M.C. Lopes *et al.*, Aug 2006. MZUSP 93026, 1, 45.3 mm SL, Igarapé Castanha, affluent of rio Tiquié, rio Negro drainage, Santa Rosa community, 0º4'N 69º41'W, F.C.T. Lima *et al.*, Nov 2006. MZUSP 93162, 64, 26.4–41.3 mm SL, rio Tiquié, beach of meander, near Serra do Mucura community, 0º9'49"N 69º9'7"W, F.C.T. Lima *et al.*, 9 Nov 2006. MZUSP 93174, 27, 28.5–38.0 mm SL, Brazil, Pará, Itaituba, left margin rio Tapajós at Itaituba, 4º16'14"S 55º58'34"W, L.M. Sousa & J.L.O. Birindelli, 7 Nov 2006. MZUSP 93366, 128, 27.6–42.2 mm SL, Brazil, Amazonas, port of Pirarara-Poço community, rio Tiquié, rio Negro drainage, 0º8'40"N 69º12'41"W, F.C.T. Lima *et al.*, 19–20 Nov 2006. MZUSP 93392, 1, 36.2 mm SL, Brazil, Amazonas, rio Tiquié between ports of Fronteira and São Luís community, 0º13'N 69º35'W, F.C.T. Lima *et al.*, 20 Nov 2006. MZUSP 97149, 76, 31.0–44.5 mm SL, Brazil, Pará, Altamira, rio Curuá at Castelo dos Sonhos village, rio Iriri drainage, rio Xingu basin, 8º19'7"S 55º5'23"W, J.L.O. Birindelli, L.M. Sousa, A.L. Netto-Ferreira, M. Sabaj-Perez & N. Lujan, 22 Oct 2007. MZUSP 101475, 28, 29.8–36.8 mm SL, Brazil, Amapá, Laranjal do Jari, left margin of rio Jari, beach at Santo Antônio village, downstream Cachoeira Santo Antônio, 0º39'42"S 52º30'54"W, J.L.O. Birindelli & P. Hollanda-Carvalho, 11 Sep 2008. MZUSP 102290, 5, 31.8–39.2 mm SL, Brazil, Amapá, Laranjal do Jari, rio Jari, right upstream and downstream of Cachoeira Santo Antônio, 0º38'35"S 52º30'31"W, J.L.O. Birindelli & P. Hollanda-Carvalho, 12 Sep 2008. MZUSP 104823, 16, 36.6–45.0 mm SL, 2 cs, 36.6–38.3 mm SL, Brazil, Amapá, left margin of rio Jari, at pier of Santo Antônio community, 0º38'22"S 52º30'33"W, J.L.O. Birindelli & M.C. Soares, 30 Apr 2009. MZUSP 109598, 10, 27.3–34.9 mm SL, Brazil, Amazonas, Santa Isabel do Rio Negro, rocky platform at left margin of rio Neuixi, near confluence with rio Negro, 0º21'45"S 65º4'13"W, O.T. Oyakawa, M. Toledo-Piza, M.M.F. Marinho, G. Mattox & J. Santana, 8 Feb 2011. MZUSP 109674, 130, 27.4–46.7 mm SL, 4 cs, 32.5–33.6 mm SL, Brazil, Amazonas, Santa

Isabel do Rio Negro, right margin of rio Negro downstream rio Urubaxi, 0º30'6"S 64º49'11"W, O.T. Oyakawa, M. Toledo-Piza, M.M.F. Marinho, G. Mattox & J. Santana, 9 Feb 2011. MZUSP 109885, 73, 23.2–32.8 mm SL, Brazil, Amazonas, Santa Isabel do Rio Negro, beach at rio Marauiá, confluence with rio Jaradi, rio Negro drainage, 0º23'33"S 65º12'18"W, O.T. Oyakawa, M. Toledo-Piza, M.M.F. Marinho, G. Mattox & J. Santana, 5 Feb 2011. MZUSP 111292, 43, 30.2–37.8 mm SL, Brazil, Pará, Altamira, beach at Cachoeira da Mucura, Jericoá, rio Xingu drainage, 3º24'39"S 51º44'50"W, O.T. Oyakawa, J.L.O. Birindelli, C. Moreira, A. Akama, L.M. Sousa & H.R. Varella, 9 Nov 2011. MZUSP 111483, 1, 35.8 mm SL, Brazil, Pará, rio Xingu at beach at Porto de Moz, 1º45'48"S 52º14'21"W. O.T. Oyakawa, J.L.O. Birindelli, C. Moreira, A. Akama, L.M. Sousa & H.R. Varella, 12 Nov 2011. MZUSP 111803, 1, 31.2 mm SL, Brazil, Pará, rio Iriri near mouth of rio Xingu, near camping, Altamira, 3º49'40"S 52º41'31"W. O.T. Oyakawa, J.L.O. Birindelli, C. Moreira, A. Akama, L.M. Sousa & H.R. Varella, 15 Nov 2011. MZUSP 115554, 15, 23.7–35.7 mm SL, Brazil, Mato Grosso, rio Barrero, affluent of rio Guaporé at road between Pontes e Lacerda and Vila Bela da Santíssima Trindade, 15º11'35.3"S 59º25'26.5"W, O.T. Oyakawa, F. Dagosta, M.M.F. Marinho & P. Camelier, 28 Aug 2013. MZUSP 115555, 19, 19.6–28.3 mm SL, Brazil, Mato Grosso, Vila Bela de Santíssima Trindade, rio Guaporé at Vila Bela da Santíssima Trindade, 15º0'18.7"S 59º57'19"W, O.T. Oyakawa, F. Dagosta, M.M.F. Marinho & P. Camelier, 28 Aug 2013. UFRO-ICT 430, 10 of 28, 26.3–32.9 mm SL, Brazil, Rondônia, Porto Velho, mouth of rio Mutumparaná, tributary of rio Madeira, 9º36'39.5"S 64º55'38.9"W, A.R. Santos, 7 Sep 2009. UFRO-ICT 13548, 3 of 6, 31.5–36.0 mm SL, Brazil, Rondônia, Guajará-Mirim, beach at rio Pacaás Novos mouth, 10º52'58"S 65º15'23.5"W, C. Ribeiro, 17 Jan 2012. UFRO-ICT 16857, 2 of 5, 32.9–35.3 mm SL, Brazil, Rondônia, Costa Marques, rio Cautário, 12º12'30"S 64º29'9.9"W, LIP/Unir team, 9 Jan 2012. UFROI-ICT 18964, 34 of 130, 25.3–39.2 mm SL, Brazil, Rondônia, Guajará-Mirim, rio Pacaás Novos, 11º4'47.7"S 65º8'49.9"W, D. Hungria, 7 Sep 2012. Guiana Shield drainages: ANSP 175698, 10 of 27, 30.0–33.6 mm SL, Guyana, Siparuni, rio Essequibo at Essequibo campsite, 4º45'41"N 58º45'53"W. CAS 68733, 1, not measured, Guyana, rio Rupununi, tributary of the rio Essequibo near Rockstone, C. Eigenmann, 30 Sep 1908. ZMB 18006, 2, 35.3–37.1 mm SL, Guyana, rio Potaro, C. Eigenmann. Orinoco basin: ANSP 191131, 1, 29.4 mm SL, Venezuela, Manapiare, rio Paru, left bank tributary of rio Ventuari, 164 km east-northeast of San Fernando de Atabapo, 4º23'33.2"N 66º15'42"W. ANSP 191238, 28, 27.5–37.5 mm SL, Venezuela, rio Orinoco near mouth of rio Ventuari, Macuruco Landing, 75 km E of San Fernando de Atabapo, 3º57'29"N 67º1'56"W. ANSP 191372, 1, 29.1 mm SL, Venezuela, Manapiare, Canõ Marujeta, left bank tributary of rio Ventuari, 159 km east-northeast of San Fernando de Atabapo, 4º17'41.3"N 66º17'20"W. CAS 235598 (ex SU 56904), 2, 27.0–37.5 mm SL, Venezuela, rio Orinoco, Santa Barbara, Amazonas, C. Ternetz, 4 Apr 1925.

Comparative material examined. *Astyanax ajuricaba*: MZUSP 96045, 10, 54.4–66.5 mm SL, Brazil, Amazonas, rio Negro. *Astyanax goyanensis*: MZUSP 113938, 39, 18.8–69.6 mm SL, Brazil, Goiás, rio Tocantins. *Astyanax guaporensis*: FMNH 54709, holotype, 38.6 mm SL; FMNH 54710, paratype, 1, 32.0 mm SL, Brazil, Rondônia, rio Guaporé at Maciel, rio Madeira basin. UFRO-ICT 3666, 541, 26.1–43.3 mm SL; UFRO-ICT 3696, 11, 39.9–47.4 mm SL, Brazil, rio Guaporé, rio Madeira basin. *Astyanax hamatilis*: MZUSP 111500, holotype, 30.3 mm SL, Brazil, Bahia, rio Paraguaçu basin. *Astyanax intermedius*: MZUSP 79409, 7, 28.7–72.7 mm SL, Brazil, São Paulo, rio Paraíba do Sul basin. *Astyanax multidens*: MCZ 89559, syntypes, 29, 26.0–30.0 mm SL, Brazil, rio Amazonas at Óbidos. MZUSP 96606, 75, 27.3–45.3 mm SL, Brazil, Mato Grosso, tributary of rio Teles Pires, rio Tapajós basin. *Astyanax ojiara*: MZUSP 40255, paratypes, 5, 39.6–44.5 mm SL, Argentina, province of Misiones, rio Uruguay. *Astyanax rivularis*: MZUSP 50734, 6, 76.7–99.1 mm SL, Brazil, Minas Gerais, rio São Francisco basin. *Astyanax vermilion*: MZUSP 101243, holotype, 39.4 mm SL; MZUSP 101244, paratypes, 10, 37.4–38.7mm SL, Brazil, Bahia, rio Cachoeira. *Astyanax xavante*. MZUSP 113886, 11, 66.4–71.0 mm SL, Brazil, Goiás, tributary of rio Tocantins. *Moenkhausia collettii*: MZUSP 73951, 4, 37.7–43.4 mm SL, Brazil, Amapá, rio Araguari. MZUSP 105535, 15, 28.6–36.8 mm SL, Brazil, Pará, rio Tocantins; NMW 57379, 3, syntypes, 39.3–50.1 mm SL; NMW 57380, 3, syntypes, 33.5–48.0 mm SL; NMW 57381, 2, syntypes, 47.0–47.9 mm SL, Brazil, Amazonas, Hyavari (= rio Javari, tributary of rio Solimões).

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