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New Species of *Astyanax* (Ostariophysi: Characiformes: Characidae) from the Upper Rio Paraná System, Brazil

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***Astyanax bockmanni*, a new species of characid, is widespread in streams in the upper Rio Paraná system of central, southeastern, and southern Brazil. Samples of the species were identified by previous authors as *A. eigenmanniorum*, a species originally described from far southern Brazil. *Astyanax bockmanni* differs from *A. eigenmanniorum* and all congeners in the combination of morphometric, meristic, and pigmentary features and details of oral dentition. Uncertainties concerning the generic placement of *Astyanax paranahybae* are discussed, and it is proposed that the species is a member of a clade within the Characidae that does not include *Astyanax*.**

***Astyanax bockmanni*, uma nova espécie de caracídeo, é amplamente distribuída em riachos do Alto Rio Paraná, nas regiões centro-oeste, sudeste e sul do Brasil. Amostras dessa espécie foram previamente identificadas por diversos autores como *A. eigenmanniorum*, uma espécie originalmente descrita do extremo sul do Brasil. *Astyanax bockmanni* difere de *A. eigenmanniorum* e demais congêneres por uma combinação de caracteres morfométricos e de pigmentação, além de detalhes da dentição oral. Incertezas quanto ao posicionamento genérico de *Astyanax paranahybae* são discutidas e propõe-se que a espécie seja membro de um clado de Characidae que não inclui *Astyanax*.**

THE nearly 100 species now recognized in the genus *Astyanax* in conjunction with the lack of a comprehensive treatment of the genus subsequent to Eigenmann (1921, 1927) greatly complicates the identification of population samples of *Astyanax* across the broad geographic range of the genus from Texas to Argentina. Our understanding of the diversity and limits of the genus is further encumbered by the fact that *Astyanax* as currently defined (i.e., members of the Characidae with two rows of multicuspid teeth on the premaxilla with the inner premaxillary tooth row consisting of five teeth, a complete lateral line, and the caudal fin not covered by scales) is likely non-monophyletic. The removal to other genera of various species which did, or would, fall within the traditional concept of *Astyanax* (e.g., Zanata, 1997; Mirande et al., 2004b) well exemplifies the problematic nature of the genus. In their comprehensive overview of the then-known species of *Astyanax* within the upper Rio Paraná basin, Garutti and Britski (2000) recognized seven species of the genus. Notwithstanding the fact that the upper Rio Paraná is one of the best sampled river systems in Brazil (Castro et al., 2005), recent collecting efforts in that drainage basin yielded at least two undescribed species of *Astyanax*. One of these was recently described from the Rio Paranapanema basin of the upper Rio Paraná system (Castro and Vari, 2004), and the second species, identified as *A. eigenmanniorum* by some previous authors, is described as new herein. We also reevaluate *Astyanax paranahybae* which was described by Eigenmann (1911) from the northern portions of the Rio Paraná basin and propose that it is a member of a clade within the Characidae that does not include *Astyanax*.

Materials and Methods

Measurements of subunits of the body and of head length are given as proportions of standard length (SL) except for subunits of the head that are presented as proportions of head length (HL). Lateral-line scale counts include all pored scales along that series, including pored scales situated posterior to the hypural joint. In fin-ray counts, lower-case Roman numerals indicate unbranched rays, and Arabic numerals indicate branched rays. The last two anal-fin rays that are joined at the base were counted as one element. Counts for the holotype are indicated in brackets and values in parentheses indicate the number of specimens with a particular count. Measurements were made following the methods outlined in Fink and Weitzman (1974:1–2) with the addition of gape width and head height, with the latter measured at the vertical running through the base of the supraoccipital spine. The descriptions of the dentition and of stomach contents were based on two cleared-and-counterstained specimens (CS) prepared following a modification of the method outlined by Taylor and Van Dyke

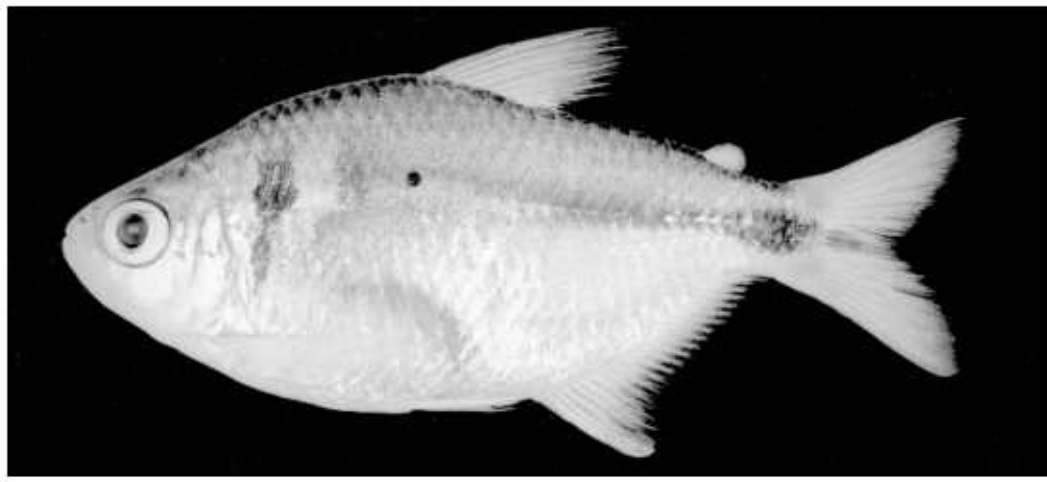

Fig. 1. *Astyanax bockmanni*, new species, holotype, LIRP 5638, 65.0 mm SL, Brazil, Goiás, Rio Paranaíba basin, Município de Catalão, Córrego Fundo, 18°07′29″S, 47°43′27″W.

(1985). Vertebral counts were taken from both radiographs and cleared-and-counterstained specimens and include the four vertebrae associated with the Weberian apparatus with the terminal element in the ural complex counted as one centrum. Nomenclature of the species of *Astyanax* in the upper Rio Paraná basin follows Lima et al. (2003) and Castro and Vari (2004). Institutional abbreviations are as listed in Leviton et al. (1985) with the addition of LIRP (Laboratório de Ictiologia de Ribeirão Preto, Universidade de São Paulo, Ribeirão Preto).

Astyanax bockmanni, new species
Figure 1

Astyanax cf. *eigenmanniorum* (not of Cope, 1894), Castro and Arcifa, 1987:495–496 [Brazil, state of São Paulo; occurrence in reservoir of upper Rio Tietê].–Shibatta et al., 2002:409, 414 [Brazil, Paraná, Rio Tibagi basin; distribution within river system].

Astyanax eigenmanniorum (not of Cope, 1894), Agostinho and Júlio, 1999:378 [Brazil, upper Rio Paraná basin].–Fauaz et al., 1994:157 [Brazil, Minas Gerais, Rio Grande; triploidy].–Garutti and Britski, 2000:84 [Brazil, upper Rio Paraná; taxonomic problems associated with species].–Bennemann et al., 2005:250 [Brazil, Paraná, Rio Tibagi; ecology and food habits in different habitats].–Hoffmann et al., 2005 [Brazil, Paraná and São Paulo, Rio Paranapanema; occurrence in reservoirs].

Astyanax sp., Castro and Casatti, 1997:337, 342–43, 346–47, pl. 1e [Brazil, São Paulo, Rio Pardo basin; ecology].–Castro et al., 2004:12, 20, 26, 32, fig. 4a–7 [Brazil, São Paulo, Rio Grande basin; identification key and ecology].–Castro et al., 2005:40, 43, 44, fig. 4e [Brazil, state of São Paulo, Rio do Peixe and Rio Aguapeí; ecology].

Astyanax sp. 1., Castro et al., 2003:13, 18–19, 21, 23–24, 28, fig. 6.5 [Brazil, Paraná, Rio Paranapanema basin; identification key and ecology].

Holotype.—LIRP 5638, 65.0 mm SL, Brazil, Goiás, Rio Paranaíba basin, Município de Catalão, Córrego Fundo, just above bridge along dirt road, right hand tributary of Rio São Marcos, 18°07′29″S, 47°43′27″W, 22 April 2002, C. A. A. Figueiredo and E. S. S. Rêgo.

Paratypes.—LIRP 3401, 4, 55.1–70.7 mm SL; LIRP 4020, 2, 55.0–70.8 mm SL (CS); MZUSP 88367, 3, 57.8–65.0 mm SL; USNM 373495, 10, 47.6–68.1 mm SL, Brazil, all collected with holotype. MNRJ 28723, 10, 55.8–68.3 mm SL; Goiás, Rio Paranaíba basin, Município de Catalão, Ribeirão Buracão, right hand tributary of Rio São Marcos, on Fazenda do Zé Martins, just upriver from site of dam of future UHE (hydroelectric reservoir) Serra do Facão, 17°45′46.0″S, 47°41′05.8″W, 17 Nov. 1999, F. A. Bockmann, C. A. A. Figueiredo, and A. P. R. Pires.

Non-type specimens.—All specimens from Brazil: LIRP 3244, 2, 59.5–78.7 mm SL, Goiás, Rio Paranaíba basin, Município de Catalão, Rio São Marcos at Fazenda Dorvinas, 18°04′04.8″S, 47°40′26.4″W; LIRP 3288, 3, 42.5–84.4 mm SL, Goiás, Rio Paranaíba basin, Município de Catalão, Rio São Marcos, Porto Carapina, under bridge along road GO-506, 17°54′36″S, 47°40′44.4″W; LIRP 3295, 12, 33.1–57.1 mm SL,

Goiás, Rio Paranaíba basin, Município de Catalão, Ribeirão Buracão (or Barracão), upriver from bridge, 17°55′44.4″S, 47°41′02.4″W; LIRP 3327, 2, 39.4–45.9 mm SL, Goiás, Rio Paranaíba basin, Município de Catalão, Ribeirão do Segredo, near corral of Fazenda Segredo, 17°51′46.8″S, 47°40′51.6″W; LIRP 1100, 3, 36.9–51.8 mm SL, Minas Gerais, Rio Grande basin, Município de Peixoto, right hand tributary of Rio Grande, just downriver from dam of UHE (hydroelectric reservoir) Mascarenhas de Moraes, approximately 20°19′27.84″S, 47°06′16.92″W; LIRP 3388, 1, 70.2 mm SL, Minas Gerais, Rio Paranaíba basin, Município de Paracatu, Rio São Marcos at Fazenda of José Bertholdo, 17°21′10.8″S, 47°31′19.2″W; LIRP 2736, 1, 57.1 mm SL, Paraná, Rio Paranapanema basin, Município de Rancho Alegre, Fazenda Fartura, Córrego Água da Laranjinha, 23°02′30″S, 50°3′26.3″W; LIRP 2743, 1, 48.9 mm SL, Paraná, Rio Paranapanema basin, Município de Paranavaí, Fazenda Rancho de Zinco e Cristo Rei, Córrego Santa Clara, 22°44′30.84″S, 46°54′05.04″W; LIRP 2747, 2, 39.8–46.5 mm SL, São Paulo, Rio Aguapeí basin, Município de Lins, Fazenda Santa Marina, Córrego Desfiladeiro, 21°43′57.2″S, 49°50′10.7″W; LIRP 2746, 15, 30.8–68.9 mm SL, São Paulo, Rio Aguapeí basin, Município de Araçatuba, stream tributary to Córrego Água Boa, 21°26′35.6″S, 50°34′42.4″W; LIRP 2745, 2, 33.7–45.5 mm SL, São Paulo, Rio Aguapeí basin, Município de Osvaldo Cruz, unnamed stream on Fazenda São Manoel, 21°43′53.2″S, 50°50′28.5″W; LIRP 2742, 1, 45.0 mm SL, São Paulo, Rio Capivari basin, Município de Mombuca, Fazenda Serra D'Água, Córrego São Matias, 22°55′44.4″S, 47°37′16.7″W; LIRP 2744, 10, 19.6–43.3 mm SL, São Paulo, Rio Capivari basin, Município de Indaiatuba, unnamed stream on Sítio Solidão, 23°08′36.1″S, 47°10′33.5″W; ZUEC 3630, 7, 34.9–61.0 mm SL, São Paulo, Rio Jaguari basin, Pedreira, 44°06′36″S, 17°25′12″W; LIRP 2748, 322, 26.1–64.7 mm SL, São Paulo, Rio Paranapanema basin, Município de Jacarezinho, Fazenda Sertãozinho, Riacho Água Seca, 23°10′41.2″S, 40°52′52.9″W; LIRP 2738, 5, 23.7–58.5 mm SL, São Paulo, Rio Paranapanema basin, Município de Cerqueira César, Córrego Virado, 23°05′45.2″S, 49°12′36.4″W; LIRP 2737, 18, 22.8–49.5 mm SL, São Paulo, Rio Paranapanema basin, Município de Pirajú, unnamed stream at Chácara Monte Alegre, 23°14′46.9″S, 49°20′20.4″W; LIRP 2739, 68, 24.0–61.5 mm SL, São Paulo, Rio Paranapanema basin, Município de Paranapanema, unnamed stream at Sítio Santa Luzia, 23°24′34.5″S, 48°53′55.2″W; MZUSP 51881, 10, 20.5–71.0 mm SL, São Paulo, Rio Paranapanema basin, Município de Ribeirão Grande, Ribeirão Grande, under bridge on road between towns of Ribeirão Grande and Intervales, 24°06′00″S, 48°21′00″W; LIRP 2740, 35, 18.1–76.9 mm SL, São Paulo, Rio Paranapanema basin, Município de Salto Grande, Sítio Santo Antonio, Ribeirão Santana, 22°49′03.1″S, 49°58′24.2″W; MZUSP 17117, 15, 34.9–62.7 mm SL, São Paulo, Rio Pardo basin, Município de São José do Rio Pardo, Usina do Limoeiro, Rio Pardo, 21°35′00″S, 46°54′00″W; LIRP 132, 1, 48.2 mm SL, São Paulo, Rio Pardo basin, Município de Cajuru, Córrego Barro Branco, Fazenda Santa Carlota, 21°16′01.2″S, 47°21′00″W; LIRP 2735, 1, 49.8 mm SL, São Paulo, Rio do Peixe basin, Município de Pompéia, Córrego da Guairuvira, 22°10′19.9″S, 50°14′04.6″W; LIRP 2741, 56, 21.3–55.4 mm SL, São Paulo, Rio Piracicaba basin, Município de Piracicaba, Distrito de Artemis, unnamed stream, 22°42′16.8″S, 47°46′43.4″W; LIRP 3521, 18, 36.7–84.9 mm SL, São Paulo, Rio Sapucaí basin, Município de Nuporanga, Fazenda Mangueira, Córrego do Arrozal, 20°40′57″S, 47°40′18.4″W; LIRP 3526, 3, 32.8–39.4 mm SL, São Paulo, Rio Sapucaí basin, Município de Altinópolis, Fazenda São José, Córrego Água do Pinheiro, 20°59′54.4″S, 47°11′16.2″W; LIRP 3538, 20, 35.8–70.8 mm SL, São Paulo, Rio Sapucaí basin, Município de Santo Antônio da Alegria, unnamed stream flowing into Rio Pinheiro or Sapucaí, 21°00′40.7″S, 47°13′11.5″W; MZUSP 84641, 7, 33.0–62.2 mm SL, São Paulo, Rio Tietê basin, Município de Cerquilho, Rio Sorocaba, about 5 km upriver from São João dam, 7 km from Cerquilho, approximately 23°09′54″S, 47°44′35.16″W.

Diagnosis.—*Astyanax bockmanni* is distinguishable from its congeners in the upper Rio Paraná basin (*A. biotae, A. altiparanae, A. fasciatus, A. paranae, A. schubarti,* and *A. trierythropterus*; see remarks under Comments on *Astyanax paranahybae* concerning that nominal form) by the presence of teeth on the maxilla and the possession of a distinctly vertically-elongate humeral mark (vs. an edentulous maxilla and a rotund, slightly horizontally-elongate humeral spot in *A. altiparanae*), in having the terminus of the base of the dorsal fin situated along the vertical through the vent and in the absence of a distinct overall reticulate pattern formed by dark pigmentation on the exposed portion of the scales (vs. the terminus of the base of the dorsal fin located along the vertical through the base of the first or second branched anal-fin ray and the presence of a reticulated pigmentation pattern on the scales in *A. biotae*), in the dark mark on the caudal peduncle that is three or four scales high and the anteriorly more diffuse and wider midlateral dark stripe that typically is more densely pigmented anteriorly in the form of a second, vertically-

TABLE 1. MORPHOMETRIC VALUES FOR HOLOTYPE AND 29 PARATYPES OF *Astyanax bockmanni*, NEW SPECIES. Standard length is expressed in millimeters; measurements 1–15 as percentages of standard length; 16–21 as percentages of head length.

	Holotype	Paratypes	Mean
Standard length	65.0	47.6–70.8	64.9
1. Greatest body depth	41.1	42.2–50.8	45.0
2. Snout to dorsal-fin origin	52.3	48.1–56.9	53.5
3. Length of base of dorsal fin	14.0	12.7–20.1	15.0
4. Posterior terminus of base of dorsal fin to adipose fin	24.2	21.4–27.5	23.8
5. Posterior terminus of dorsal fin to caudal-fin base	40.5	37.8–44.1	41.9
6. Snout to insertion of pelvic fin	49.7	48.4–52.3	50.5
7. Snout to anus	62.0	59.7–67.0	64.3
8. Snout to origin of anal fin	65.8	64.4–70.8	66.3
9. Length of base of anal fin	30.9	28.0–34.1	30.9
10. Length of caudal peduncle	11.7	11.7–17.6	14.0
11. Length of longest dorsal-fin ray	29.4	26.3–33.4	29.5
12. Length of first pectoral-fin ray	22.8	22.0–26.4	23.3
13. Length of first pelvic-fin ray	17.2	16.6–21.1	18.4
14. Least depth of caudal peduncle	12.5	12.0–14.1	13.3
15. Head length	25.5	25.3–29.8	26.9
16. Head height	109.6	96.7–121.6	108.7
17. Snout length	30.0	25.5–31.8	28.8
18. Gape width	32.5	28.8–35.4	30.6
19. Orbital diameter	36.7	34.8–39.3	37.1
20. Postorbital head length	34.9	37.6–46.1	42.1
21. Interorbital width	32.5	31.7–40.1	35.3

elongate humeral bar (vs. dark pigmentation on the caudal peduncle that is two scales high and the anteriorly narrower midlateral, dark stripe not forming a second humeral bar in *A. fasciatus* [see Castro and Casatti, 1997:fig. 1c]), in the possession of 33 or 34 vertebrae (vs. 35 to 37 in *A. fasciatus*, 35 or 36 in *A. paranae*, and 35 or 36 in *A. trierythropterus*), in the possession of 19 to 25 branched anal-fin rays (vs. 15 to 17 in *A. paranae*, 27 to 31 in *A. schubarti*, and 26 to 30 in *A. trierythropterus*), and in the red to rosy life coloration of portions of the dorsal, anal, and caudal fins (vs. the yellow coloration on those fins in *A. schubarti*). Differences between *Astyanax bockmanni* and congeners from outside the upper Rio Paraná basin are discussed under Remarks.

Description.—Morphometrics of holotype and paratypes presented in Table 1. Body moderately compressed and deep, less so in individuals of less than 50 mm SL, greatest body depth located within region delimited anteriorly by vertical through insertion of pelvic fin and posteriorly by vertical through origin of dorsal fin. Average body depth variable among population samples, but with broad overlap in ranges among examined samples. Dorsal profile of head distinctly convex from margin of upper lip to vertical through posterior nostril, straight to very slightly convex from latter point to tip of supraoccipital spine. Dorsal profile of body moderately convex from tip of supraoccipital spine to origin of dorsal fin, straight and posteroventrally-slanted along base of dorsal fin, straight to slightly convex from posterior terminus of base of dorsal fin to adipose fin, and slightly concave along caudal peduncle. Broad middorsal ridge present along predorsal region of body, with ridge less obvious anteriorly. Dorsal region of body between posterior terminus of dorsal fin and adipose fin transversely rounded overall, but slightly flattened middorsally in some individuals. Ventral profile of head strongly convex anteriorly from margin of lower lip approximately to vertical through anterior nares, then straight or very slightly convex from that point to vertical through posterior margin of eye. Ventral profile of body convex to insertion of pelvic fin, nearly straight but slightly posteroventrally-aligned from that point to origin of anal fin, straight to slightly convex and posterodorsally-slanted along base of anal fin, and slightly concave along caudal peduncle. Prepelvic region of body somewhat flattened transversely.

Head obtusely rounded anteriorly in lateral profile. Mouth terminal. Upper jaw with maxilla distinctly posteroventrally-angled relative to ventral margin of premaxilla and extending ventral of orbit to point somewhat short of, or reaching,

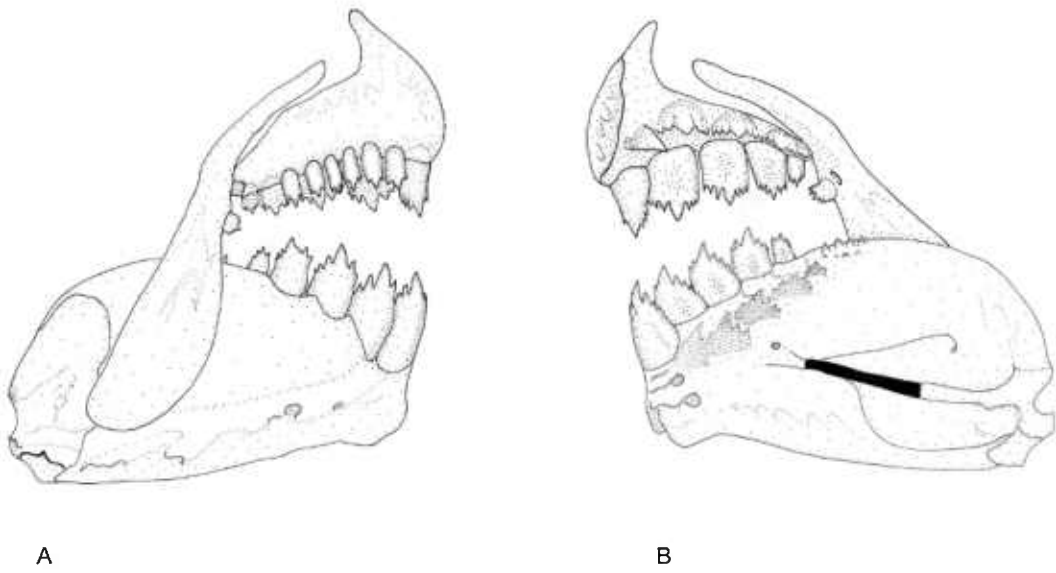

Fig. 2. *Astyanax bockmanni*, LIRP 4050, paratype, 55.0 mm SL, upper and lower jaws, right side: (A) lateral view; (B) medial view (cartilage indicated by black).

vertical through anterior margin of pupil. Nares of each side of head very close together; anterior opening circular, posterior crescent-shaped with distinct flap between nares. Eye relatively large and lacking distinct adipose eyelid. Median fronto-parietal fontanel extending from mesethmoid to supraoccipital spine. Width of fontanel approximately one-fifth distance across bony interorbit. Infraorbital series complete with third infraorbital by far largest. All infraorbitals carrying laterosensory canal segments proximate to margin of orbital rim. Supraorbital absent. Dorsal surface of head in some specimens with small, scattered papillae. Branchiostegal rays four. Gill-rakers long and setiform; 6–7+1+9–12 rakers present on first gill-arch (in five whole and two CS paratypes).

Teeth on premaxilla in two rows (Fig. 2). Inner tooth row with five teeth, with four anterior teeth larger than teeth of outer tooth row. Symphyseal tooth of inner tooth series more elongate than other teeth of row and with five cusps. Second tooth more massive than first tooth and with seven cusps. Third and fourth teeth smaller than second tooth, with seven cusps on third tooth and five to seven cusps on fourth tooth. Fifth tooth distinctly smaller than all other teeth in series and with five or six cusps. Outer row of teeth on premaxilla with five or six teeth, each of which has three to five cusps. Teeth of outer series arranged in regular pattern and gradually decreasing in size laterally. Maxilla bearing one or two teeth along dorsal limit of its anteroventral margin. Anterior tooth of maxilla with five cusps and second tooth, when present, with three cusps. Dentary with nine to 14 teeth arranged in two contiguous or slightly separated groups. Anterior group consisting of four or five massive teeth followed by much smaller tooth; each tooth with three to seven cusps. Anterior group of teeth followed by series of three to eight very small, thin, conical or tricuspid teeth.

Scales cycloid, relatively large, and firmly implanted. Lateral line decurved anteriorly approximately to vertical through origin of dorsal fin, then slightly posterodorsally-angled to onto caudal peduncle, and then running horizontally to terminus of scale series. Lateral line completely pored from supracleithrum to base of caudal fin and followed posteriorly by ossified tubular extension running along lateral margin of membrane joining middle rays of caudal fin. Lateral-line scales 33(3), 34(4), 35(13), 36(6), or 37(1) [35]; scales in transverse series from origin of dorsal fin to lateral line 6(18) or 7(9) [6]; scales in transverse series from insertion of pelvic fin to lateral line 5(6) or 6(21) [6]; scales in transverse series from origin of anal fin to lateral line 5(12) or 6(15) [6]; scales along middorsal line between tip of supraoccipital process and origin of dorsal fin 8(2), 9(4), 10(12), or 11(9) [10]; scales along middorsal line between posterior termination of base of dorsal fin and adipose fin 7(1), 8(2), 9(20), 10(3), or 11(1) [9]; horizontal scale rows around caudal peduncle 13(1), 14(18), or 15(12) [14]. Vertebrae 33(4) or 34(4) [34].

Dorsal-fin rays ii,8(9) or 9(18) [ii,9]. Anal-fin rays iii,19(1), 20(4), 21(10), 22(5), 23(3), 24(3), or 25(1) [iii,21]. Pectoral-fin rays i,10(2), 11(7), 12(15), or 13(3) [i,13]. Pelvic-fin rays i,5(1), 6(1), 7(22), or 8(3) [i,7]. Principal caudal-fin rays 10/9(26) [10/9].

Dorsal-fin margin distally rounded to slightly truncate; first unbranched ray approximately 40–50% length of second unbranched ray. Dorsal-fin origin situated along vertical located approximately at middle of SL. Origin of adipose fin located slightly anterior of vertical through posterior terminus of base of anal fin. Profile of adpressed pectoral fin distinctly acute. Tip of pectoral fin extending distinctly beyond vertical through insertion of pelvic fin in smaller individuals but only approximately to that line in larger specimens. Profile of expanded pelvic fin pointed, with first branched ray either longest in fin or subequal to unbranched ray. Insertion of pelvic fin located distinctly anterior to vertical through origin of dorsal fin. Tip of adpressed pelvic fin extending to origin of anal fin in smaller specimens, but falling short of that point in larger individuals. Some larger, apparently male, specimens with posteriorly-directed hooks along posterior margins of second through sixth pelvic-fin rays; hooks rarely also present on first ray. Hooks limited to posterior branch of hook-bearing rays. Each hook-bearing segment typically with one hook, although two hooks occasionally present on some segments. Distal margin of anal fin slightly concave in smaller individuals and distinctly concave in larger individuals in which third unbranched and first and second branched rays longest and subequal or first through third branched rays longest with subsequent branched rays gradually decreasing in length. Some larger, apparently male, individuals with hooks present on various rays of anal fin. Hooks most often arise along posterior margin of posterior branch of second through seventh branched rays. Some individuals with hooks also present in different combinations on posterior-most unbranched and/or first unbranched rays and sometimes eighth to tenth branched anal-fin rays. Hooks extending onto unbranched segments of some rays. Caudal fin forked, with distal margins of lobes obtusely pointed.

Coloration in alcohol.—Overall ground color of body in specimens fixed in formalin yellowish-brown. Guanine remaining on lateral and ventral portions of head and on ventral and, to a degree, lateral surfaces of body. Snout and dorsal portion of head relatively dark. Middorsal and immediately adjoining portions of body dark. Distinct, wedge-shaped, ventrally-attenuated humeral mark with irregular margins extending from approximately three scales dorsal of lateral line to about two scales ventral of lateral line. Pigmentation of humeral mark typically most intense in region dorsal to lateral line, with pigmentation of remaining ventral portion of mark variably lighter, but still quite obvious. Humeral mark followed posteriorly first by largely unpigmented vertical area of irregular form about two scales wide and then by area of variably diffuse dark pigmentation. Chromatophores of anterior portion of this region of overall diffuse dark pigmentation concentrated into second, smaller, vertically-elongate, anteroventrally-angled or less often vertically-oriented humeral mark. Pigmentation of second humeral mark less intense than that of first mark, but still obvious in all specimens. Dark midlateral pigmentation more obvious on portion of body beginning at vertical through posterior terminus of dorsal fin, with stripe widening posteriorly on caudal peduncle into distinct, horizontally-elongate, ovoid spot. Pigmentation of spot more intense than that of remainder of stripe. Small dark spot on lateral surface of left side of body below dorsal-fin origin (Fig. 1), not present on other side of holotype or on other specimens.

Dorsal, anal, and caudal fins with interradial membranes covered by small dark chromatophores, with chromatophores often more concentrated proximate to margins of fin rays. Dark pigmentation on caudal fin more intense along middle fin rays in most specimens and forming stripe variably continuous anteriorly with midlateral dark spot on caudal peduncle. Anal fin with unbranched rays and sometimes first branched rays unpigmented. Distal half of remainder of fin with dark chromatophores in all individuals, with fields of chromatophores extending nearly to base of fin membranes in some larger specimens. Adipose fin lightly colored overall, but often freckled with small dark spots. Pectoral and pelvic fins with small, dark spots located both along fin-ray margins and on membranes. Dark pigmentation on pectoral fin more concentrated in transverse band located about two-thirds of distance from base of fin.

Coloration in life.—Observations based on photographs taken in the field of live, recently collected specimens in aquaria. Dark coloration as in preserved specimens, other than being masked to varying degrees by guanine covering on scales. Guanine covering particularly well developed on lateral and ventral surfaces of head, ventral, ventrolateral, and lateral surfaces of body, and ventral portion of caudal peduncle. Dorsal portions of head and body dark, with

slightly purplish tint. Dorsal fin with slight to distinctly rosy tint on distal portions of middle fin-rays and with clear to slightly whitish region on distal portions of anterior rays of fin. Caudal fin with rosy coloration often forming variably distinct band along distal one-quarter to one-third of fin. Rosy coloration in some individuals limited to dorsalmost and ventralmost lobes of fin and forming well separated patches of coloration. Basal portion of middle rays of each lobe of caudal fin with yellowish pigmentation in some specimens. Anal fin with small to moderate sized area of rosy to red coloration located at base of anterior fin-rays and with white band having form of narrow, distally-widening triangle covering distal two-thirds of anteriormost fin rays. Distal portions of remaining rays of anal fin with rosy to red tint. Basal portions of anal fin variably yellow in some specimens. Lateral rays of pelvic fin whitish, with white pigmentation also extending onto distal portions of all fin rays in some individuals. Band of yellowish pigmentation present on basal portions of pelvic fin of some specimens.

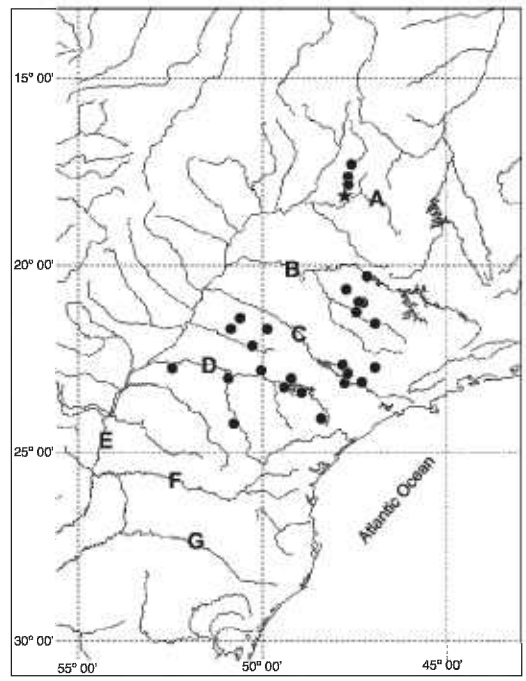

Fig. 3. Map of the upper Rio Paraná basin and adjoining regions showing distribution for *Astyanax bockmanni* (star indicates type locality). Major river systems in the basin: A = Rio Paranaíba; B = Rio Grande; C = Rio Tietê; D = Rio Paranapanema; E = Rio Paraná; F = Rio Iguaçu; G = Rio Uruguay.

Distribution.—The samples of *Astyanax bockmanni* examined in this study originated in a series of tributaries of the upper Rio Paraná basin (Fig. 3). It is likely that the species is broadly distributed throughout that river system. Various authors (e.g., Severi and Cordeiro, 1994; Garavello et al., 1997) have cited *Astyanax eigenmanniorum* as a component of the ichthyofauna of the Rio Iguaçu, a tributary of the Rio Paraná, and these records may refer to *A. bockmanni*. In light of the high degree of endemicity in the fish fauna of the Rio Iguaçu and given that we did not examine the specimens that served as the basis for those records, we defer from formally equating those citations with *A. bockmanni*.

Ecology.—In their analysis of the fish fauna of the Rio Pardo, Castro and Casatti (1997:347) considered *Astyanax bockmanni* to be an omnivore with a tendency to insectivory. The species exploited both autochthonous insects and algae and also allochthonous insects, arachnids, detritus, nematodes, and thecamoebas. Stomach contents from the two specimens of the species examined during this study were consistent with that diet, with the addition of sand and small bits of gravel that were presumably ingested incidental to feeding on other items. Bennemann et al. (2005) found that the populations of the species in the Rio Tibagi, Paraná State (identified by those authors as *A. eigenmanniorum*) had similar feeding habits. Further information on the collecting localities and the habitat of *A. bockmanni* in various portions of the upper Rio Paraná basin can be found in Castro et al. (2003, 2004, 2005).

Remarks.—*Astyanax bockmanni* has been previously cited as *A. eigenmanniorum* by various authors who have studied the species in the upper Rio Paraná basin (see synonymy). These identifications were based on the treatment of *Astyanax* by Eigenmann (1921, 1927), under which these populations keyed out to *A. eigenmanniorum*. Garutti and Britski (2000) noted that *Astyanax eigenmanniorum* was originally described by Cope (1894) from Rio Grande do Sul, Brazil (specifically the Laguna dos Patos basin, see Malabarba, 1989:121, 129), a considerable distance from the upper Rio Paraná. Those authors consequently proposed that *A. eigenmanniorum* might be part of a species complex, but noted that a resolution of that issue lay beyond the aims of their analysis. More recently, the range of *A. eigenmanniorum* has been considered to be less extensive than proposed by some previous authors, being reportedly limited to the lower Rio Paraná, the Rio Uruguay, and the Laguna dos Patos drainage basin of the state of Rio Grande do Sul, Brazil

(Lima et al., 2003:108). This restriction of the reported range of the species was not derived from a comprehensive treatment of *A. eigenmanniorum*. In lieu of a critical analysis and redescription *A. eigenmanniorum*, an effort which lies beyond the scope of this study, we examined the holotype of the species. The present dark brown coloration of the specimen, which is presumably a consequence of changes in preservative, made it impossible to critically analyze its pigmentation pattern. Nonetheless, a number of meristic and morphometric differences are apparent between *A. eigenmanniorum* and *A. bockmanni*. The most trenchant of these involved the number of teeth in the outer row of the premaxilla (four in the holotype of *A. eigenmanniorum* vs. five or six in *A. bockmanni*), the number of scales in the transverse series from the insertion of the pelvic fin to the lateral line (four vs. five or six, respectively), and the number of scales in the transverse series from the origin of the anal fin to the lateral line (four vs. five or six, respectively). Morphometric differences between the holotype of *A. eigenmanniorum* and the examined material of *A. bockmanni* include the length of the snout (16.2% of HL vs. 25.5–31.8% of HL, respectively) and to a lesser degree the width of the gape (26.4% of HL vs. 28.9–35.4% of HL, respectively).

The nearly 100 species now recognized in *Astyanax* (see Lima et al., 2003:106; Miquelarena and Menni, 2005), the broad distribution of the members of the genus from Texas to Argentina, and in particular the lack of a comprehensive treatment of the species of *Astyanax* greatly complicate the diagnosis of *A. bockmanni* from all congeners. Information from the literature (Eigenmann, 1921, 1927; Géry, 1977) indicates that *A. bockmanni* can be differentiated from its congeners by the combination of the possession of a body with the greatest body depth at the origin of the dorsal fin (vs. deepest and most robust in the area proximate to middle of pectoral fin in the species of the *A. scabripinnis* complex [see Bertaco and Lucena, 2006:54]), the presence of two humeral marks, with the first of these pigmentation patches being vertically elongate, the presence of a series of scales along the midline of the predorsal region of the body, the rounded, somewhat pointed snout (vs. the blunt, abruptly tapering snout of the species of the *A. scabripinnis* complex [see Bertaco and Lucena, 2006:fig. 2]), the possession of 33 to 37 scales along the lateral line, 22 to 28 total anal-fin rays, one or two premaxillary teeth, and various morphometric features (see comparisons in following sections). Literature information on many species of *Astyanax* is limited or in some cases questionable. This situation makes it appropriate to provide more detailed comparisons to the nominal species of *Astyanax* in regions adjoining the upper Rio Paraná basin.

The differential characters noted in the Diagnosis serve to unequivocally separate *Astyanax bockmanni* from its congeners within the upper Rio Paraná. A very different overall ichthyofauna at the species level characterized the lower portions of the Rio Paraná system below the now-drowned Sete Quedas falls (Vari, 1988:358; Reis et al., 1992:271) and includes a number of nominal species of *Astyanax*. Although a key to the species of *Astyanax* occurring in Argentina including the lower Rio Paraná and its tributaries in that country was recently published by Miquelarena and Menni (2005), no comprehensive analysis of the species of *Astyanax* in the lower portions of the Rio Paraná system has been attempted. Among the species of *Astyanax* that have been reported to occur in the lower Rio Paraná basin including the tributary Rio Iguaçu and Rio Uruguay, *A. bockmanni* is similar in overall pigmentation (specifically the presence of the vertically-elongate humeral mark and the presence on the caudal peduncle of a dark, rounded, mid-lateral spot wider than the preceding midlateral stripe) to *A. hermosus*, *A. ita*, *A. leonidas*, *A. ojiara*, *A. pampa*, *A. paris*, *A. pynandi*, *A. saguazu*, *A. totae*, *A. troya*, and *A. tupi*.

Astyanax bockmanni differs from these 11 species in diverse attributes including the distance from the snout to the insertion of the pelvic fin (48.4–52.3% of SL vs. 41.5–47.0 in *A. hermosus*, 43.7–48.5% of SL in *A. ita*, 41.2–46.4% of SL in *A. saguazu*, and 44.0–49.6% of SL in *A. tupi*), the distance from the snout to the origin of the anal fin (64.4–70.8% of SL vs. 56.0–61.2% of SL in *A. saguazu*), the depth of the caudal peduncle (11.7–17.6% of SL vs. 6.8–10.4 in *A. hermosus* and 10.5–12.3% of SL in *A. pynandi*), the length of the pelvic fin (16.6–21.1% of SL vs. 12.8–16.9% of SL in *A. paris*), the length of the snout (25.5–31.8% of HL vs. 21.4–24.0% of HL in *A. ita*, 20.3–25.0% of HL in *A. leonidas*, 21.9–26.5% of SL in *A. pampa*, 18.5–24.6% of HL in *A. paris*, 22.7–26.4% of SL in *A. pynandi*, 18.6–22.9% of HL in *A. saguazu*, and 14.6–24.1 in *A. totae*), the diameter of the orbit (34.8–39.3% of HL vs. 29.1–36.2 in *A. ojiara*, and 41.4–45.4% of HL in *A. saguazu*), the width of the interorbital region of the head (31.7–40.1% of HL vs. 26.9–30.4% of HL in *A. leonidas*), the greatest body depth (42.2–50.8% of SL vs. 33.9–38.7% of SL in *A. hermosus*, 34.2–39.8% of SL in *A. ita*, 30.2–35.1% of SL in *A. leonidas*, 34.0–40.0% of SL in *A. ojiara*, 36.9–42.2% of SL in *A. pampa*, 34.9–39.4% of SL in *A. paris*, 35.4–42.9% of SL in *A. pynandi*, 34.9–39.4%

of SL in *A. saguazu*, 30.0–35.0 in *A. totae*, 33.0–40.9% of SL in *A. troya*, and 36.9–42.6% of SL in *A. tupi*), the number of circumpeduncular scales (13 to 15 vs. 16 or 17 in *A. pampa* and 15 to 19 in *A. totae*), the number of scales in the transverse series between the lateral line and the origin of the dorsal fin (six or seven vs. five in *A. ojiara*), the number of teeth on the maxilla (one or two vs. three or four in *A. paris*), the number of teeth on the outer row of the premaxilla (five or six vs. two to four in *A. ojiara*), to varying degrees in the number of vertebrae (33 or 34 vs. 34 to 36 in *A. hermosus*, 32, less often 33, in *A. leonidas*, 35 in *A. pynandi*, 30 or 31 in *A. troya*, 35 or 36 in *A. totae*, and 35 in *A. tupi*), the number of branched anal-fin rays (19 to 25 vs. 15 to 18 in *A. totae*, 25 to 29 in *A. saguazu*, and 24 to 27 in *A. tupi*), in the degree of development of cusps on the first tooth of the maxilla (five vs. seven cusps in *A. ojiara*), to a degree in the length of the base of the dorsal fin (12.7–20.1% of SL vs. 11.4–13.3% of SL in *A. leonidas*) and the length of the base of the anal fin (28.0–34.1% of SL vs. 16.3–23.8% of SL in *A. totae*, and 22.9–28.8% of SL in *A. troya*), in the form of the first humeral mark (ventrally-attenuating triangle vs. dorsally rounded to subcircular with ventral extension in *A. troya*), and to varying degrees in the overall form of the head and body and in the intensity and extent of development of the dark midlateral stripe on the body (data for *A. hermosus* from Miquelarena et al., 2005; for *A. ita* from Almirón et al., 2002; for *A. leonidas* from Azpelicueta et al., 2002a; for *A. ojiara* from Azpelicueta and Garcia, 2000; for *A. pampa* from Casciotta et al., 2005; for *A. paris* from Azpelicueta et al., 2002b; for *A. pynandi* from Casciotta, Almirón, Bechara, et al., 2003; for *A. saguazu* from Casciotta, Almirón, and Azpelicueta, 2003; for *A. totae* from Haluch and Abilhoa, 2005; for *A. troya* from Azpelicueta et al., 2002a; and for *A. tupi* from Azpelicueta et al., 2003).

In the Río Paraguay basin, *Astyanax chico* and *A. latens* are similar to *A. bockmanni* in both pigmentation patterns (specifically the presence of the vertically-elongate humeral mark and the presence on the caudal peduncle of a dark, rounded, mid-lateral spot wider than the preceding midlateral stripe) and overall head and body forms. *Astyanax bockmanni* differs from those species in the number of teeth in the outer row of the premaxilla (five or six vs. three or four teeth in *A. chico*), the predorsal distance (42.2–50.8 vs. 50.0–55.4 in *A. chico*), the number of branched anal-fin rays (19 to 25 vs. 24 to 29 in *A. latens*), the form of the teeth on the outer row of the premaxilla (with three to five cusps vs. consistently three cusps in *A. latens*) and in the form of the midlateral spot on the caudal peduncle (rounded vs. triangular in *A. latens*; information for *A. chico* from Casciotta and Almirón, 2004; for *A. latens* from Mirande et al., 2004a). *Nans indefessus*, a new genus and species of characid characiform described by Mirande et al. (2004b) from the Río Bermejo, in the Argentinian portions of the Río Paraguay basin, fits the traditional definition of *Astyanax*. Mirande et al. (2006) noted that *Nans* was preoccupied and proposed *Nantis* as a substitute. The new species was presumably assigned to a new genus by Mirande et al. (2004b) in light of its possession of various unusual autapomorphies, particularly those associated with the pelvic fin. Although *Nantis indefessus* shares a vertically-elongate humeral mark with *Astyanax bockmanni*, the two species differ strikingly in the number of branched anal-fin rays (10 to 15 vs. 19 to 25, respectively) along with alternative conditions of the characters of the pelvic fin that are autapomorphic for *Nantis*.

The type locality and various other locations in the northern reaches of the Rio Paranaíba basin at which *Astyanax bockmanni* was collected lie proximate to the southern headwaters of the north-flowing Rio Tocantins system. Only four species of *Astyanax* have been described from the Rio Tocantins basin, these being *A. argyrimarginatus*, *A. elachylepis*, *A. goyacensis*, and *A. unitaeniatus*. As noted by Bertaco and Lucinda (2005:393), all of these species except *A. elachylepis* are members of the *A. bimaculatus* group, the species of which are characterized by the possession of a horizontally-ovoid rather than vertically-elongate dark humeral mark. Although *A. bockmanni* and *A. elachylepis* share the possession of vertically-elongate humeral marks and overall body and head forms, they differ distinctly in the number of scales along the lateral line (33 to 37 vs. 48 to 52, respectively) and scales in the transverse series between the lateral line and the origin of the dorsal fin (6 or 7 vs. 8 to 10, respectively; data for *A. elachylepis* from Bertaco and Lucinda, 2005).

The northeastern portions the Rio Paraná system approximate the headwaters of the Rio São Francisco basin. The latter basin is known to have three species of *Astyanax* within its ichthyofauna; *A. fasciatus*, *A. lacustris*, and *A. rivularis*. Characters differentiating *A. bockmanni* from *A. fasciatus* were noted in the Diagnosis. *Astyanax lacustris* (*sensu* Lima et al., 2003) is a member of the *A. bimaculatus* species complex, the members of which are characterized by an horizontally-ovoid humeral spot (see Britski et al., 1986:fig. 38; species cited by those authors as *A. bimaculatus lacustris*) rather than the vertically-elongate

humeral mark of *A. bockmanni*. *Astyanax rivularis* has a much shallower body than does *A. bockmanni* (see Casatti and Castro, 1998:fig. 3a) and, furthermore, differs in the lack of the second humeral mark that is present in the latter species and in having dark pigmentation on the dorsal portion of the opercle that is lacking in *A. bockmanni*.

The final drainage system proximate to the upper Rio Paraná basin is the Rio Paraíba do Sul, which according to Melo (2001) and Lima et al. (2003) has seven species of *Astyanax* in its ichthyofauna, five of which, *A. giton, A. intermedius, A. janeiroensis, A. parahybae*, and *A. taeniatus*, have been formally described. Among these five species, the humeral marks in *A. intermedius, A. janeiroensis*, and *A. parahybae*, albeit vertically-elongate, are distinctly more rotund overall than that present in *A. bockmanni* (see Melo, 2001:figs. 18, 27, 29). *Astyanax bockmanni* differs from the two remaining species, *A. giton* and *A. taeniatus*, in the number of distinct, vertical humeral marks (two in *A. bockmanni*, with second vertically-elongate mark situated posterior to the more lightly pigmented region behind the primary humeral mark vs. second humeral mark absent in *A. giton* [see Melo, 2001:fig. 3]) and dark pigmentation behind lightly pigmented region horizontally broad in *A. taeniatus* [see Melo, 2001:fig. 32], in the number of teeth in the outer row of the premaxilla (five or six in *A. bockmanni* vs. two to four in *A. giton* and one to four in *A. taeniatus*), and the number of vertebrae (33 or 34 in *A. bockmanni* vs. 31 in *A. giton* and 31 or 32 in *A. taeniatus*; information for *A. giton* and *A. taeniatus* from Melo, 2001).

Etymology.—The species name, *bockmanni*, is in honor of Flávio A. Bockmann of LIRP, the collector of many of the specimens that served as the basis of this paper, in appreciation of his contributions to our knowledge of the fishes of the upper Rio Paraná basin and Neotropical siluriforms.

Comments on Astyanax paranahybae.—*Astyanax paranahybae* was described by Eigenmann (1911:177) based on a single specimen that originated in Rio Paranaíba in the northern portions of the Rio Paraná system. *Astyanax bockmanni* is easily distinguished from *A. paranahybae* in the number of scales below the lateral line to the origin of the anal fin (six vs. four, respectively) and number of branched dorsal-fin rays (eight or nine vs. seven, respectively). The overall elongate head and body form of *A. paranahybae* are strikingly different from those features in purported congeners (see Eigenmann, 1911:pl. 8, fig. 1; and Eigenmann, 1921:pl. 55, fig. 3), which raises questions about the generic assignment. Eigenmann (1911) presumably assigned the species to *Astyanax* as a consequence of the reported presence of five teeth in the inner tooth row on the premaxilla (Eigenmann, 1911:177), a feature that jointly with the presence of two rows of multicuspid teeth on the premaxilla, the complete lateral line on the body, and the naked caudal fin served as the traditional definition of the genus within the Characidae.

Garutti and Britski (2000:81) noted that the holotype of *Astyanax paranahybae*, the only known specimen, was asymmetrical in the dentition of the inner row of the premaxilla, having five teeth on the right side of the inner row and four on the left side. *Astyanax paranahybae* is also unusual among putative species of *Astyanax* in having seven branched dorsal-fin rays (Garutti and Britski, 2000:7) contrary to the typical presence of nine branched dorsal-fin rays in other species assigned to that genus. If the presence of four, rather than five, teeth in the inner tooth row of the premaxilla represents the typical condition for *A. paranahybae*, then the species would not be a member of *Astyanax* as that genus is now delimited. The possession of four teeth in the inner tooth row on the premaxilla and a reduction to fewer than nine branched dorsal-fin rays is characteristic of the species of the Clade A assemblage within the Characidae defined by Malabarba and Weitzman (2003:fig. 2). In light of the details of its dentition and the number of dorsal-fin rays, it is likely that *A. paranahybae* may be a member of one of the genera within Clade A, perhaps *Bryconamericus* or *Piabina*, both of which share similar overall forms of the head and body with the holotype of *Astyanax paranahybae*. A resolution of that issue lies beyond the scope of this paper.

Material Examined

Astyanax altiparanae, LIRP 35, 126, 43.0–80.1 mm SL; USNM 373491, 10, 41.1–79.9 mm SL. *Astyanax biotae*, LIRP 4009, holotype, 49.8 mm SL; LIRP 2734, 15 paratypes, 27.5–52.3 mm SL; USNM 373492, 15 paratypes, 21.2–52.2 mm SL. *Astyanax chico*, USNM 306347, 7, 36.1–65.9 mm SL. *Astyanax eigenmanniorum*, ANSP 21598, holotype, 53.8 mm SL. *Astyanax fasciatus*, LIRP 32, 28, 42.0–93.5 mm SL; USNM 373493, 10, 45.7–83.8 mm SL. *Astyanax paranae*, LIRP 124, 562, 19.1–75.0 mm SL; USNM 373494, 10, 36.5–74.8 mm SL. *Astyanax schubarti*, MZUSP 4263, holotype, 82.9 mm SL; MZUSP 4264, 1

paratype, 90.4 mm SL. *Astyanax trierythriopterus*, LIRP 2017, 138, 26.3–41.2 mm SL; MZUSP 16502, 6, 17.0–25.1 mm SL; MZUSP 16646, 4, 25.8–35.6 mm SL; USNM 373496, 10, 27.8–41.1 mm SL.

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