A titan among dwarfs:
Apistogramma kullanderi, new species
(Teleostei: Cichlidae)

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Apistogramma kullanderi, new species, is described from the upper rio Curuá (Iriri-Xingu drainage) on Serra do Cachimbo, Pará, Brazil, and diagnosed by its maximum size of 79.7 mm SL (vs. 65.3 mm SL among wild-caught congeners); mature females having the unique combination of intense dark pigmentation continuous along base of dorsal fin and on ventral surfaces from gular region to anal-fin base; and mature males having a coarse, irregular pattern of dark spots and vermiculations on cheek and opercular series, and sides with 10–12 dark stripes, each stripe occupying proximal limits of adjacent scale rows and separated by paler region central to each scale. *Apistogramma kullanderi* is tentatively allocated to the *A. regani* lineage, although some characteristics (e. g., large body size) are more consistent with members the *A. steindachneri* lineage. *Apistogramma kullanderi* is endemic to an upland watershed isolated by large waterfalls and depauperate of cichlid diversity. Under those conditions, we speculate that ecological opportunities, reduced competition and sexual selection contributed to the evolution of large body size in *A. kullanderi*.

Introduction

Apistogramma Regan 1913 is composed of 84 valid species including the one described herein (but not *Apistogrammoides pucallpaensis* Meinken, 1965), distributed in cis-Andean river systems throughout much of tropical and subtropical South America (Kullander, 2003; Römer, 2006; Eschmeyer, 2014). Only *Crenicichla*, with 86 valid species, is richer among cichlid genera (Kullander, 2003; Eschmeyer, 2014; HRV, unpubl. data).

The modern era of *Apistogramma* taxonomy began with Kullander's (1980) monographic revision, which reviewed the history of the genus and established many of the standards used to accurately compare and describe its morphological diversity. Kullander (1980) recognized 36 valid species in *Apistogramma*, 12 of which he newly described. Based in part on coloration, squamation, fin characteristics and body shape, Kullander (1980) distinguished nine species groups, two of them monotypic (*A. cacatuoides* and *A. steindachneri*). New species descriptions and regional revisions (e. g., Mesa & Lasso, 2011) aside, substantial contributions to our knowledge of the genus include popular literature (e. g., Linke & Staeck, 1995; Mayland & Bork, 1997; Stawikowski & Werner, 1998), and a compendium on *Apistogramma*

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Fig. 1. *Apistogramma kullanderi,* MZUSP 115057, holotype, 79.7 mm SL, adult, brooding male; Brazil: Pará: tributary of rio Curuá, rio Xingu basin; **a,** preserved; and **b,** alive, just after capture (photograph by José Birindelli).

and other dwarf cichlids by Römer (2006).

As developed by Kullander (1980, 1986, 1987) and Kullander & Nijssen (1989), characteristics of *Apistogramma* diagnostic in combination are: epibranchial lobe present and with marginal rakers; single supraneural bone; long, rod-like interarcual cartilage; reduced number of ossified external rakers on first ceratobranchial (commonly one, occasionally absent or as many as five); gill rakers laterally on lower pharyngeal tooth plate (fifth ceratobranchial); two infraorbital bones between lachrymal and sphenotic; and separate skin openings for the posterior anguloarticular canal foramen and anterior-most preopercular foramen (except anguloarticular canal absent in some species). Kullander (1987) considered the

last characteristic to be unique among cichlids to *Apistogramma* and monotypic *Apistogrammoides*, the latter distinguished most importantly by having 6–9 (vs. usually 3) anal-fin spines (Kullander, 1986).

Kullander (1998) provided phylogenetic evidence for placement of *Apistogramma* in the tribe Geophagini (i.e., lobed geophagines), sister to *Gymnogeophagus*, and considered monotypic genera *Apistogrammoides* and *Taeniacara* to be most similar to, if not congeneric with *Apistogramma*. In a total evidence approach combining morphological and molecular data, López-Fernández et al. (2005) supported a close relationship between *Apistogramma* (inclusive of *Apistogrammoides*) and *Taeniacara*, with those two genera consistently

Fig. 2. *Apistogramma kullanderi,* MZUSP 97597, paratype, 58.7 mm SL, adult, brooding female; Brazil: Pará: tributary of rio Curuá, rio Xingu basin; **a,** preserved; and **b,** alive, just after capture (photograph by Mark Sabaj Pérez).

sister to *Satanoperca* Günther. Kullander (1987) had previously noted a striking similarity between *Apistogramma*, *Apistogrammoides* and *Satanoperca* with respect to the rod-like shape and articulation of the interarcual cartilage. In a broader molecular study, López-Fernández et al. (2010) likewise supported the monophyly of a group (apistogrammines) composed of *Satanoperca* sister to *Taeniacara* + *Apistogramma* (inclusive of *Apistogrammoides*), and expanded Geophagini to include Kullander's Acarichthyini and Crenicaratini, as well as genera *Crenicichla* and *Teleocichla*.

A recent expedition to Serra do Cachimbo, Brazil, funded by the All Catfish Species Inventory (NSF DEB-0315963), discovered a striking new species of *Apistrogramma*. It was briefly noted and

figured under the informal name *Apistogramma* "gigas" by Birindelli et al. (2009) and as *Apistogramma* sp. by Sabaj Pérez (2009), both popular articles. The objective of this paper is to formally describe that species and comment on its placement in *Apistogramma*.

Material and methods

Measurements, counts and color pattern terminology follow Kullander (1980, 1986); counts for holotype are denoted by asterisks. Scale rows are numbered according to Kullander (1990). A half-scale row typically occurs adjacent to a fin base and is formed by scales approximately half

the size of a normal flank scale. The correspondence between coloration and breeding conditions of males and females was determined by examining, under stereomicroscope, the gonads of 20 specimens from 37.6 to 74.3 mm SL in an ontogenetic series. Vertebral counts include the last half-centrum and were taken from X-rays. Osteological notes were based on specimens prepared according to protocol of Datovo & Bockmann (2010), in which bone and cartilage are stained and muscle is not digested; those specimens are indicated in the material examined as "ms" (muscle). For illustration, sensory pores were traced from photographs using Adobe Illustrator CS6. Institutional abbreviations are as follows: ANSP, Academy of Natural Sciences, Philadelphia; MZUSP, Museu de Zoologia da Universidade de São Paulo, São Paulo; NRM, Naturhistoriska Riksmuseet, Stockholm.

Apistogramma kullanderi, new species
(Figs. 1–3, 6)

Apistogramma sp. Sabaj Pérez, 2009: 43–44 (photographs of live specimens and habitat).
Apistogramma sp. "gigas" Birindelli et al., 2009: 13–14 (photographs of live specimens and habitat).

Holotype. MZUSP 115057, 79.7 mm SL, adult male; Brazil: Pará: Altamira: unnamed tributary of rio Curuá (rio Iriri drainage, rio Xingu basin), at route BR163 bridge; 8°49'12"S 54°58'11"W; A. Netto-Ferreira, J. Birindelli, L. Sousa & P. Hollanda-Carvalho, 22 Jan 2009.

Paratypes. 88 specimens, 14.5–76.0 mm SL. All from Brazil: Pará: Altamira: rio Xingu basin: upper rio Curuá (Iriri drainage). ANSP 194896, 17: 4 males, 58.4–74.3 mm SL, 2 females, 55.1–56.1 mm SL, 9 unsexed or juveniles, 22.1–69.4 mm SL; 2 ms, 20.7–22.3 mm SL; MZUSP 97584, 16: 2 males, 65.2–76.0 mm SL, 4 females, 50.1–57.7 mm SL, 10 unsexed or juveniles, 21.2–47.0 mm SL; rio Escorpião, tributary of upper rio Curuá, at BR163 bridge; 8°53'54"S 54°59'20"W; J. Birindelli et al., 29 Oct 2007. – MZUSP 96874, 5: 4 males, 51.8–58.4 mm SL, 1 female 50.5 mm SL; main channel of rio Curuá immediately above ca. 10 m falls (sampled after dry down during construction of PCH Salto Buriti); 8°46'09"S 54°57'02"W; J. Birindelli et al., 21 Oct 2007. – MZUSP 97597, 14: 6 females, 48.0–58.7 mm SL, 8 unsexed or juveniles, 22.1–48.5 mm SL; NRM 66406, 11: 5 females, 32.3–53.9 mm SL, 6 unsexed or juveniles, 23.6–42.6 mm SL; same locality as holotype; J. Birindelli et al., 29 Oct 2007. – MZUSP 101380, 9: 4 males, 37.8–70.5 mm SL, 4 females, 42.3–47.5 mm SL, 1 juvenile, 20.5 mm SL; NRM 66407,

Table 1. Standard length in millimeters and proportional measurements of the holotype and 45 paratypes of *Apistogramma kullanderi.* Caudal-fin length was obtained from 42 specimens only. Holotype measurements included in sample range. SD, standard deviation.

	holotype	range	mean	SD
Standard length (mm)	79.7	20.5–79.7	47.1	
Percents of standard length				
Body depth	37.9	34.2–41.3	37.9	1.4
Head length	36.7	35.1–39.8	37.7	1.3
Caudal peduncle depth	17.1	15.1–17.7	16.7	0.6
Caudal peduncle length	12.7	9.9–14.9	11.3	1.0
Last dorsal-fin spine length	12.9	11.6–16.0	13.9	1.2
Pectoral-fin length	27.3	26.1–32.1	29.2	1.4
Pelvic-fin length	39.8	25.0–39.8	29.4	2.6
Caudal–fin length*	32.3	30.2–36.9	32.8	1.9
Head depth	28.9	25.2–32.0	28.6	1.3
Head width	15.0	14.5–17.1	15.7	0.7
Orbital diameter	9.0	9.0–13.9	11.1	1.4
Interorbital width	10.4	8.2–10.9	9.7	0.7
Snout length	14.0	8.3–14.3	11.5	1.7
Preorbital depth	5.3	2.3–6.4	4.8	1.2
Upper jaw length	11.5	9.0–13.0	11.0	0.8
Lower jaw length	14.6	13.5–16.8	15.3	0.8

4: 3 males, 39.9–70.7 mm SL, 1 juvenile, 31.8 mm SL; collected with holotype. – MZUSP 101388, 11, 14.5–35.2 mm SL, unsexed or juveniles; same locality as ANSP 194896; A. Netto-Ferreira et al., 22 Jan 2009. – MZUSP 115058, 1 mus, 68.5 mm SL, male; from one of the collecting sites listed above for 2009 expedition to rio Curuá (kept in aquarium prior to preservation).
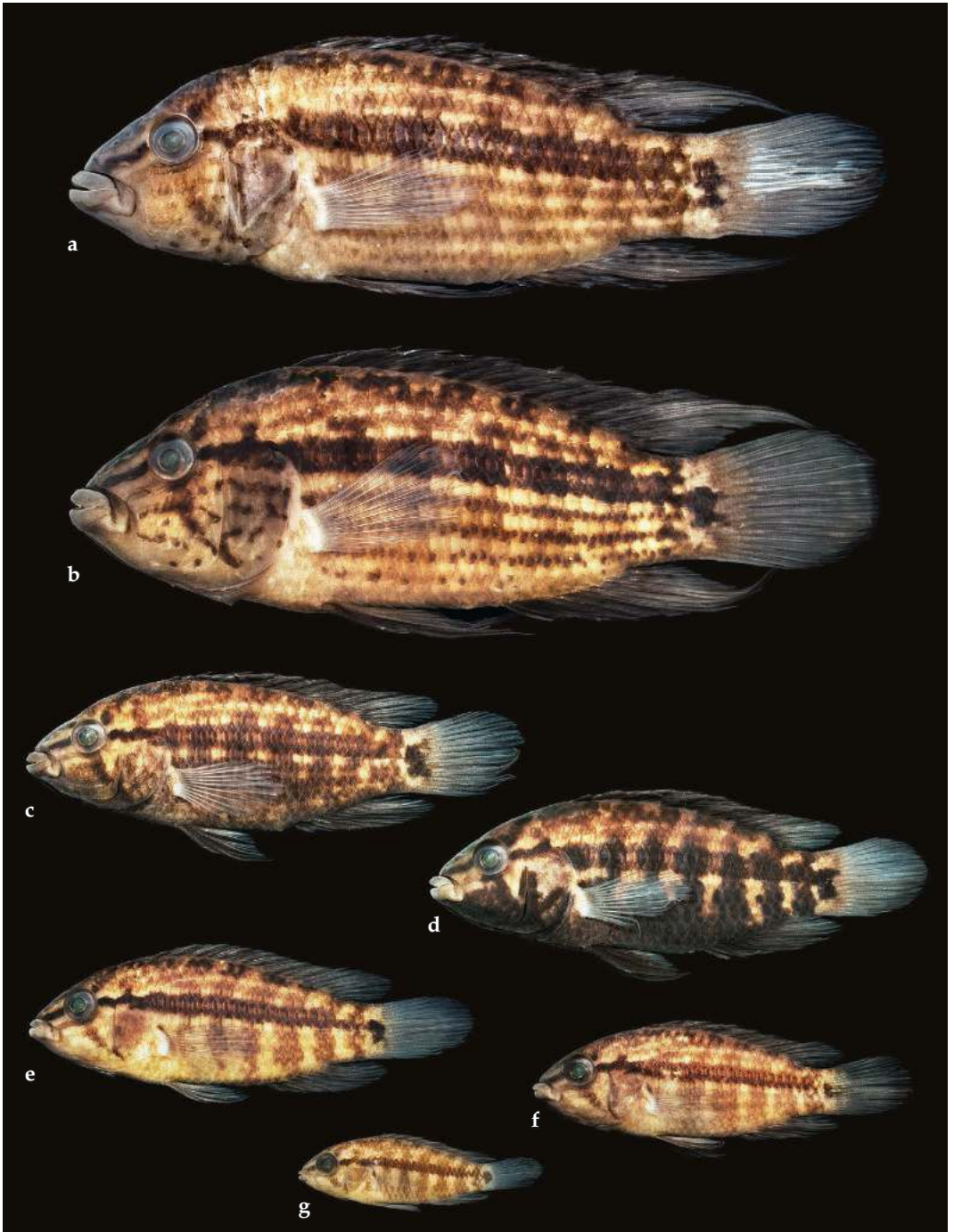
Diagnosis. *Apistogramma kullanderi* is diagnosed by different aspects of coloration found separately in mature females and males. Mature females are diagnosed from all congeners by the unique combination of intense dark pigmentation continuous along basal portion of dorsal fin and on ventral surfaces from gular region to anal-fin base (Figs. 2, 3c–d). Among nominal species of *Apistogramma*, that pattern is most closely approximated by mature females of *A. baenschi* Römer et al., 2004, distinguished from *A. kullanderi* by having dark pigmentation in dorsal fin discontinuous, alternating with pale regions (see Römer, 2006: 429, bottom figure). Mature males of *A. kullanderi* have a coarse, irregular pattern of dark spots and vermiculations on cheek and opercular series, and sides with 10–12 dark stripes, each stripe occupying junction between adjacent scale rows and separated by paler region central to each scale (Figs. 1, 3a–b). Among nominal species of *Apistogramma*, a similar pattern is found in mature males of *A. rubrolineata* Hein et al., 2002 and *A. tucurui* Staeck, 2003. Mature males of *A. kullanderi* are distinguished from those species by having enlarged jaws with large, fleshy lips (vs. jaws and lips not enlarged), five (vs. four) dentary pores, and head profile acutely angular with distinct concavity in interorbital region (vs. profile more broadly rounded, lacking concavity in interorbital region). *Apistogramma kullanderi* is also diagnosed from all congeners by its maximum size, 79.7 mm SL for a wild-caught adult male (vs. 65.3 mm SL among wild-caught congeners). Additional characteristics useful for identifying *A. kullanderi* include: deep body (depth 34.2–41.3 % SL), caudal fin broad and evenly rounded, first gill arch with 1–4 rakers, most scales in lateral line with distinct tube (vs. simple perforation), and immature individuals with dark midlateral band, lacking midlateral blotch (Figs. 3e–g).

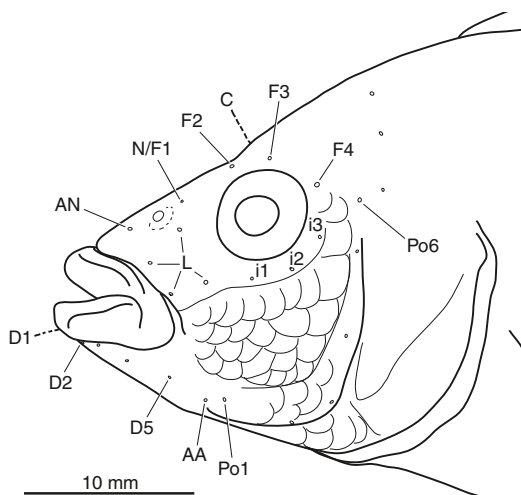**Description.** Largest male 79.7 mm SL (Fig. 1), largest female 58.7 mm SL (Fig. 2). Body deep (34.2–41.3 % SL, mean 37.9 %), greatest depth between verticals through second and fifth dorsal-fin spines. Dorsal and ventral head profiles convex in juveniles, approximately straight and with interorbital concavity in adults. Snout relatively long (8.3–14.3 % SL, mean 11.5 %); posterior border of maxilla reaching vertical through anterior margin of orbit in most specimens, falling short of orbital margin in largest specimens (>60 mm SL). Orbit dorsolateral, diameter negatively allometric, decreasing with increase of standard length; dorsal margin of orbit tangent with contour of head in specimens smaller than 26 mm SL, becoming more remote from head contour as standard length increases. Posterior margins of preopercle and supracleithrum entire; posttemporal serrations lacking.

Ctenoid scales on flank; cycloid scales on antero-ventral portion of cheek, preopercle, interopercle, subopercle, opercle (except for some ctenoid scales on dorsal border of opercular bone), area anterior of dorsal fin, interpelvic area and eventually around urogenital papilla. Scales in E1 row 22 (n = 14) or 23 (30). Cheek fully scaled, 4–5 horizontal scale rows (Fig. 4). Predorsal scales 8–10. Prepelvic area scaled; 3–4 scales anterior to tips of cleithra, 7–9 scales from tips of cleithra to pelvic fin. Transverse row with 1 ½ scales above and 7 scales below anterior ramus of lateral line. Circumpeduncular scale rows 16; 2 lateral line scales plus 7 dorsally and 7 ventrally. Lateral-line scales range from 13–16/6–9 with frequencies as follows: 13/6 (1), 13/7 (1), 14/8 (2), 14/9 (2), 15/5 (1), 15/7 (3), 15/8 (12), 15/9 (6), 16/7 (1), 16/8 (8), 16/9* (3). Tube-bearing scales range from 11–16/3–9. Scales between upper lateral line and first dorsal-fin spine 2 (2), 3* (31), or 4 (7). Scales between anterior ramus of lateral line and last dorsal-fin spine ½ (4), 1 (12), 1 ½ (11) or 2* (15). Fins naked except caudal fin, which is scaled basally for about one-third its length.

Infraorbital series composed of three bony elements: lachrymal, infraorbital one and infraorbital 2 + 3 (co-ossification interpreted by presence of median pore). Infraorbital canal (Fig. 4) with four pores on lachrymal, ventro-posterior one shared by anterior opening of canal through infraorbital one; postlachrymal infraorbital pores three: anteriormost pore shared between infraorbital one and infraorbital 2 + 3, second pore median, and posteriormost pore close to posterior end of infraorbital 2 + 3. Dentary with five pores; anguloarticular canal present with simple pore. Preopercular pores six; nasal with pores at each

Fig. 3. *Apistogramma kullanderi,* all MZUSP 101380, paratypes; Brazil: Pará: tributary of rio Curuá, rio Xingu basin; **a,** 70.7 mm SL, adult male, intermediate stage of maturation; **b,** 70.5 mm SL, adult brooding male; **c,** 42.4 mm SL, adult female, intermediate stage of maturation; **d,** 42.3 mm SL, brooding female; **e,** 37.8 mm SL, unsexed subadult; **f,** 31.8 mm SL, unsexed juvenile; and **g,** 20.4 mm SL, unsexed juvenile.
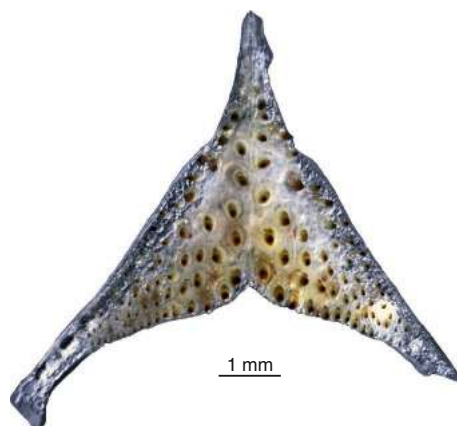
Fig. 4. *Apistogramma kullanderi*, MZUSP 115058, 68.5 mm SL; pattern of sensory *lateralis* pores on head. **AA**, anguloarticular pore; **AN**, anterior nasal pore; **C**, *coronalis* pore; **D1–D5**, dentary pores; **F2–F4**, frontal pores; **i1–i3**, post-lachrymal infraorbital pores; **L**, lachrymal pores; **N/F1**, pore shared by the nasal and first frontal *lateralis* canal; **Po1–Po6**, preopercular pores.

Fig. 5. *Apistogramma kullanderi*, MZUSP 97597, 55.6 mm SL, lower pharyngeal tooth plate, in dorsal view (posterior right horn broken during preparation).

end, posterior one shared with anterior opening of frontal canal. Frontal with four pores plus coronalis pore.

Dorsal fin XIII.7 (1), XV.6 (1), XV.7* (14), XV.8 (9), XVI.6 (7), XVI.7 (14). Dorsal-fin spines with lappets evident in mature males. In holotype (largest adult male examined), lappets longest on spines IV–IX, their length approximately one-third to one-half the length of corresponding spine (except lappet of spine VIII, which is slightly more than half length of spine); lappets on posteriormost dorsal-fin spines X–XVI much shorter, but extending well beyond tips of their respective spines. Smaller adult males with less developed lappets, their length approximately one-third length of corresponding spines IV–VIII or IX. In females and males <50 mm SL, lappets relatively inconspicuous, truncate or rounded. In four largest males examined, soft dorsal fin pointed with 4th ray longest and 3rd and 5th rays nearly as long; tip of 4th ray reaching one-half to three-quarters length of caudal fin. Soft dorsal fin also pointed in mature females, but tip extending only slightly beyond caudal fin base, to approximately one-fifth the length of caudal fin.

Pectoral fin rounded with 12* (31) or 13 (15) rays; 6th ray longest, tip almost reaching vertical

through genital papilla. Pelvic fin pointed, first ray elongated in males; tip of first pelvic-fin ray reaching base of 3rd soft ray of anal fin in holotype (79.7 mm SL), base of 3rd anal-fin spine or slightly beyond in other large males (70.4–76.0 mm SL), and base of 1st anal-fin spine in smaller males. In females and unsexed juveniles, pelvic fin pointed, tip reaching genital papilla or base of 1st anal-fin spine. Anal fin III.7 (10), III.8* (34), IV.7 (1), IV.8 (1). Soft anal fin pointed in males and females; 4th ray longest and 5th ray nearly as long; 4th ray extending beyond middle of caudal fin in males and only slightly beyond caudal-fin base in females. Caudal fin rounded with 3 procurrent and 8 principal rays per half.

Jaw teeth unicuspid, erect, cusp strongly retrorse; outer row teeth similar in size or slightly larger than inner row teeth; 26–28 teeth in upper right jaw outer hemi-series, 25–28 in upper left, 27–33 in lower right jaw outer hemi-series, 27–32 in lower left. Outer row of teeth occupying almost entire premaxilla and dentary margins; inner row of premaxilla expanded as far as outer row in large specimens but only to one-third of jaw margin in smaller ones; inner row of dentary expanded to one third of jaw margin; few teeth forming one additional, short, middle row near symphysis of upper and lower jaws in some specimens.

Gill rakers on first epibranchial lobe 5 (9), 6* (24), 7 (10), 8 (2); one gill raker in angle and 1 (6), 2 (30), 3* (9), 4 (1) gill raker(s) on ceratobranchial. Gill rakers laterally on lower pharyngeal toothplate 10 (3), 11* (2), 12 (17), 13 (16), 14 (7). No tooth

plates on ceratobrachial four. No microbranchiospines on gill arches.

Lower pharyngeal tooth-plate dissected from three specimens (MZUSP 115058, 68.5 mm SL; MZUSP 97584, 65.3 mm SL; and MZUSP 97597, 55.6 mm SL, Fig. 5): slightly wider than long (length 90–91 % of width), posterior contour deeply emarginated in dorsal view, with long horns; strongly depressed in lateral view but with deep, thin keel anteriorly; 15–17/16 teeth in left/right posterior row, 5–7/6–7 teeth in left/right median row. Medioposterior teeth largest and more robust, teeth gradually decreasing in height and more slender rostrally and laterally; posterior and median teeth bicuspid, lateral and rostral teeth unicuspid.

Vertebrae 11 + 12 = 23 (1), 11 + 13 = 24 (1), including last half-centrum. Hypurals 1–5 separate.

Color pattern in alcohol. Within species of *Apistogramma*, pigmentation patterns vary considerably among males, females and juveniles. Some of that variation stems from different social and behavioral contexts, such as aggressive vs. neutral males and brooding vs. non-brooding females (Römer, 2006; Rodrigues et al., 2009). The following descriptions are based on wild-caught individuals preserved at site of capture; sex, maturity and breeding condition are inferred from comparisons to other species of *Apistogramma*, particularly those described and figured by Römer (2006).

Juveniles and immature specimens (22–45 mm SL; Figs. 3e–g) with tan ground color, markings light to dark brown, dorsal half of head and body slightly darker than ventral half. Brown preorbital stripe from anterior margin of orbit to postlabial skin fold, aligned with postorbital stripe from posterior margin of orbit across dorsal margin of opercle, and continuing posteriorly as midlateral band to caudal peduncle. Dark supraorbital, interorbital, lachrymal and suborbital (cheek) stripes generally present, particularly in smallest specimens (< 25 mm SL). Supraorbital stripe runs obliquely from dorsoposterior margin of orbit onto nape; reduced to rounded blotch near orbit in some specimens. Interorbital stripe indistinct, broad and irregularly pigmented between dorsal margins of orbits, but usually with paired branches extending anteriorly, medial to nostrils and confluent across snout. Lachrymal stripe faint, from antero-ventral margin of orbit to posterior terminus of jaws. Suborbital stripe usually evident, oblique from just beneath ventral margin of orbit to articulation of sub- and interopercle, often with brief pale hiatus across posterior margin of preopercle. Pre-, post-, and supraorbital stripes dark brown and most distinct; interorbital, lachrymal and suborbital stripes light brown, more faint, particularly in larger juveniles.

Body with medium to dark brown midlateral band finishing just before caudal flexure and separate from darker caudal blotch. Midlateral band occupying entire depth of E1 scale row plus the adjacent thirds of scales in flanking rows E0 and E2; band darkest in smallest specimens (< 25 mm SL), uniformly pigmented or with middle portion scarcely lighter (i.e., dark pigment less crowded on central base vs. along margins of E1 scales); dorsal and ventral limits of band relatively entire, not jagged. Caudal blotch ovate to vertical rectangular, situated between V3–4 and D3–4 caudal-fin rays; posterior margin entire or with pale central notch.

About eight shallow, irregularly pigmented dark brown blotches from nape, along dorsal-fin base, to caudal peduncle. Dark brown dorsal blotches transition into about six wide, light to medium brown vertical bars ending on lower flank; additional anterior-most bar sometimes evident on nape to dorsal margin of opercle where it joins postorbital stripe. Vertical bars 1–4 anterior to anal-fin origin; bars 5 and 6 extending between soft portions of dorsal and anal fins; bar 7 on caudal peduncle. Vertical bars distinct in small juveniles (< 25 mm SL) and larger immature specimens (perhaps females), scarcely evident in other immature specimens (perhaps males). In lattermost case, vertical bars obscured by a faint horizontal pattern of narrow dusky stripes formed by a greater concentration of pigment in dorsal and ventral thirds of each scale; typically, one dusky stripe evident above midlateral band, and three such stripes below.

Spinous portion of dorsal fin dusky with melanophores scattered on spines and membranes; soft portion with dusky blotches loosely to regularly aligned to form 4–5 vertical bands separated by pale interspaces. Anal fin similarly patterned with spinous portion dusky and soft portion having 3–4 vertical bands. Pectoral fin hyaline except for dark hairlines outlining each ray and its branches. Pelvic fin with spine, first and sometimes second ray, and intervening membrane(s) dusky with scattered dark pigment; remaining portion relatively hyaline. Up to four dusky vertical bands scarcely evident in caudal

fin; widest band across fin base, darkest band occupies distal margin.

Coloration in adult females largely based on specimens presumed to exhibit pigmentation pattern of active brooders (Figs. 2, 3d). Ground color medium brown on dorsal head and flank, lighter on ventral flank; dark markings on head and body brownish-black, extensive, dominating overall pattern. Orbital stripes as described for juveniles, except lachrymal stripe lacking, other stripes more intensely pigmented, and suborbital stripe almost entirely incorporated into dark coloration masking lower head. Entire ventral surface darkly pigmented, brownish-black from gular region across breast and abdomen to posterior base of anal fin; dark pigmentation extending dorsally onto cheek and separately along distal margin of preopercle and anteroventral portion of opercle; dark ventral mask joining suborbital stripe on cheek to form broadly triangular blotch with apex truncated by orbit.

As in juveniles, brooding females have about eight shallow, irregular dark brown blotches from nape, along dorsal-fin base, to caudal peduncle, and six vertical bars on flanks, posterior to opercle. Unlike juveniles, bars much more intensely pigmented and confluent with dark pigmentation masking ventral surfaces. In large female (ANSP 194896, 58.4 mm SL), flank almost completely brownish-black except for narrow pale windows separating vertical bars above and below continuous midlateral band. In smaller brooding female (ANSP 194896, 56.1 mm SL), relatively pale brown region separating dark dorsal blotches from vertical bars (vs. dorsal blotches and vertical bars confluent in larger females). Also in smaller female, midlateral band lacking, broken into a series of seven dark blotches aligned with vertical bars. In larger females, continuous midlateral band persistent, but no more distinct than vertical bars. In smaller female, dark caudal blotch vertical rectangular with distinct outline; larger females with caudal blotch somewhat enlarged, expanded vertically and posteriorly onto caudal fin, outline irregular.

Dorsal and anal fins darkly pigmented except soft portions of fins becoming pale distally; bands in soft portion of dorsal fin scarcely evident, bands lacking from soft portion of anal fin. Pectoral fin hyaline except for small melanophores scattered on and along rays. Pelvic fin darkly pigmented, especially along base and anteriorly, becoming slightly less so towards distal medial portion.

Caudal fin uniformly dusky, without distinct markings.

Coloration in adult males variable, presumably dependent upon condition at time of capture (e.g., aggressive vs. neutral, dominant vs. subdominant); three patterns observed, the first one most closely resembling that of juveniles (Figs. 3a–b). Ground color tan to medium brown; orbital stripes distributed as in juveniles; pre-, supra-, post- and suborbital stripes conspicuous. Cheek with additional dark brown narrow stripe below lachrymal one, extending horizontally from terminus of jaw to suborbital stripe; small dark brown spots scattered on remaining portion of cheek and on opercular series. Dark brown midlateral stripe scarcely evident as such, pigmentation non-uniform with central portion of E1 scales relatively pale. Horizontal pattern more conspicuous, consisting of approximately ten narrow dark brown stripes formed by greater concentration of dark pigment in dorsal and ventral thirds of each scale (limits and course of each stripe thereby dependent on scale distribution). Two such stripes marking dorsal and ventral limits of midlateral band. Four stripes above midlateral band; two dorsalmost stripes short, oblique, finishing before middle of base of spinous dorsal fin; 3rd stripe involving dorsal third of scales in anterior ramus of lateral line and finishing below anterior base of soft dorsal fin; 4th involving ventral limits of scales in dorsal lateral line and finishing on caudal peduncle. Four stripes below midlateral band; three longest extending from pectoral-fin base to caudal peduncle; 4th ventral to pectoral-fin base, ending above base of soft anal fin. Scarcely evident in adult males is conspicuous juvenile pattern of shallow dark blotches along dorsal-fin base transitioning into seven wide vertical bars (one on nape plus six on flank). Caudal spot present, dark brown, vertical rectangular. Fin pigmentation similar to juveniles, except vertical banding pattern in caudal fin inconspicuous; caudal fin dusky except for rows of pale windows restricted to membranes, windows most evident along membranes between the seven central fin rays.

Second pigmentation pattern observed in mature males (Fig. 1) similar to above with following exceptions: dark spots on cheek and opercular series larger, some irregularly joining each other and/or suborbital stripe to form coarse vermiculations (thereby obscuring suborbital stripe, sometimes rendering it inconspicuous), horizontal pattern more conspicuous due to

Fig. 6. *Apistogramma kullanderi*, MZUSP 97584, 76.0 mm SL; Brazil: Pará: tributary of rio Curuá, rio Xingu basin; mature male, live specimen photographed just after capture; dark coloration perhaps induced by stress during capture and/or subsequent photography (photograph by Mark Sabaj Pérez).
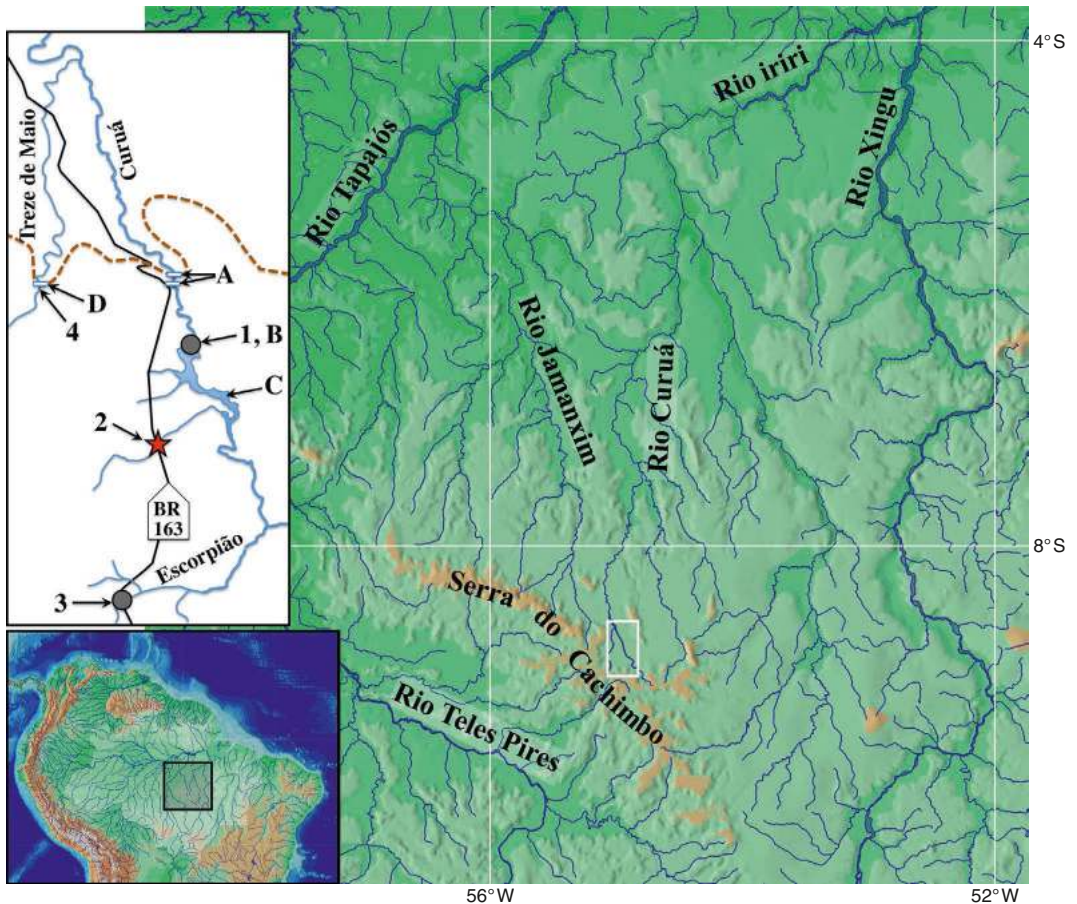

Fig. 7. Distributions of *Apistogramma kullanderi* and other cichlids in upper rio Curuá on Serra do Cachimbo, Brazil. *Apistogramma kullanderi* collected at sites 1, 2 (type locality) and 3; *Apistogramma* "upper Curuá" collected at site 2; *Apistogramma* "Treze de Maio" collected at site 4; *Aequidens* aff. *rondoni* collected at sites 1, 2, 3 and 4. **A,** 60 m (downstream) and 40 m (upstream) waterfalls; **B,** site of 10 m falls and weir for PCH Salto Buriti; **C,** reservoir; **D,** major waterfalls on rio Treze de Maio. Brown dashed line approximates escarpment of Serra do Cachimbo.

Fig. 8. Type locality of *Apistogramma kullanderi*, unnamed tributary of rio Curuá (Iriri drainage), at BR163, bridge, 29 October 2007. (Photographs by Mark Sabaj Pérez).

greater contrast between darker stripes and paler ground color, and with two additional stripes evident (i.e., twelve overall), one from gill cover to anal-fin origin and second shorter stripe from gill cover to pelvic-fin origin.

Third pigmentation pattern most extreme and perhaps induced by stress during capture and/or subsequent photography (Fig. 6). Sides entirely black except for pale central portions of a few scales scattered on flank and those in scale row above dorsal lateral line. Head also darkly pigmented, but with some contrast between black markings (orbital stripes, vermiculations on cheek and opercular series) and dark brown ground color. All fins black except pectoral.

Color in life. Descriptions based on adults presumably in breeding coloration and photographed live in the field immediately after capture (Figs. 1b, 2b, 6). Males (Figs. 1b, 6) with ground color yellow green on head, nape, breast, and uppermost flank (above pectoral-fin base and along dorsal fin base), transitioning to shades of aqua-blue ventrally and posteriorly to caudal peduncle; bluish hues most evident in regions occupied by

dark vertical bars described for preserved specimens. Dark markings on head and body black, strongly contrasted with lighter ground color. In holotype (Fig. 1b), magenta wash completely covers snout and dark pre- and interorbital stripes. Magenta coloration also on portions of jaws and skin between jaws and snout, irregularly on nape and scales along dorsal fin base, on distal portions of dorsal and anal fins (particularly on prolonged soft portions of those fins), and throughout caudal fin (similar magenta coloration occurs in caudal fin of wild caught males of *A. cacatuoides*; see figure in Mayland & Bork, 1997: 51). Pectoral fin yellow green. Small dark blotches evident in basal portions of soft dorsal and anal fins, and on central basal portion of caudal fin.

A female (Fig. 2b), presumably in brooding coloration, with ground color gold to yellow orange, lightest in region below midlateral band and between four posteriormost vertical bars; dark markings black, four posteriormost vertical bars prominent, more or less uniformly pigmented from dorsal to ventral contour of body. Dorsal fin black except for yellow orange in distal quarter to half of spinous portion, and distal three-quarters

of soft portion. Anal fin black anteriorly, yellow orange in posterior half of soft portion. Pectoral fin hyaline; pelvic fin black. Caudal fin uniformly yellow orange, appearing slightly darker than similarly colored portions of dorsal and anal fins. Similar pattern involving yellow orange ground color and intense black markings reported for brooding females of *A. baenschi* (see figures in Römer, 2006: 446, 447).

Distribution and habitat. *Apistogramma kullanderi* is known only from the upper rio Curuá and two of its larger tributaries on Serra do Cachimbo (Fig. 7), an isolated plateau of the Brazilian (Guaporé) Shield. *Apistogramma kullanderi* has not been recorded below the uppermost of three waterfalls marking the Curuá's departure from the plateau. Below the falls, the rio Curuá flows north into the rio Iriri, a major tributary to the lower rio Xingu (Amazonas Basin). Tributaries to the upper Curuá are clear to mild blackwaters; specimens were captured in shallow, sluggish backwaters shaded by bank vegetation (Fig. 8).

Etymology. The species is named in honor of Swedish ichthyologist Sven Oscar Kullander whose four decades of careful and comprehensive work have transformed the taxonomy of Neotropical Cichlidae and continue to inspire all those fascinated with its diversity.

Discussion

Sexual dimorphism. *Apistogramma kullanderi* is sexually dimorphic for fin development, a condition common among congeners. In mature males, the pelvic fin is distinctly elongated, its tip reaching the base of the 3rd soft anal-fin ray in the largest male examined (vs. reaching anal-fin origin in mature females), and soft portions of the dorsal and anal fins are prolonged, reaching more or less midlength of caudal fin. Other sexually dimorphic fin features generally found in *Apistogramma* are membranes between anterior dorsal-fin spines prolonged as lappets, and caudal fin with prolonged rays affecting lanceolate or lyreate shapes. In *A. kullanderi*, the caudal fin remains shallowly rounded to truncate, and is not sexually dimorphic. Less clear is the condition of sexual dimorphism in the anterior dorsal fin. In the largest males examined, the anterior membranes are somewhat prolonged relative to

the remaining portion of the spinous dorsal fin, whereas in mature females such prolongation is not distinguishable from smaller mature males. In all mature males of *A. kullanderi*, the spinous dorsal fin certainly lacks the extreme lappets found in species such as *A. bitaeniata* Pellegrin, 1936, *A. cacatuoides* Hoedeman, 1951, and *A. macmasteri* Kullander, 1979.

Relationships. *Apistogramma kullanderi* is not clearly assignable to any of the species groups proposed by Kullander (1980, 1986) and Kullander & Nijssen (1989). Exclusive to members of Kullander's *A. macmasteri* group is the presence of a dark blotch on the chest in females, a condition shared with *A. kullanderi*; however, males of the *A. macmasteri* group typically have a taller dorsal fin with longer lappets. *Apistogramma kullanderi* shares the characteristics used to distinguish the *A. regani* group (sensu Kullander, 1986: 168), such as four infraorbital and five dentary pores, mid-lateral band relatively narrow and not reaching caudal fin, caudal spot distinct, lateral spot absent, dorsal-fin lappets short, caudal fin rounded, pre-pelvic region fully scaled, and anterior dorsal-fin membranes black; however, the dark chest blotch is absent from females of the *A. regani* group (vs. present in *A. kullanderi*).

On the basis of a cluster analysis of 116 species-level taxa of *Apistogramma* (63 nominal and 53 undescribed), Römer (2006) recognized three major lineages: *A. agassizii*, *A. regani* and *A. steindachneri*. Kullander's *A. macmasteri* and *A. regani* species groups are both placed in the *A. regani* lineage of Römer, and the composition of the former species group corresponds well with Römer's *A. macmasteri* complex. Members of Kullander's *A. regani* group are distributed among multiple complexes within Römer's expanded *A. regani* lineage. As noted earlier, mature males of *A. kullanderi* have 10–12 dark longitudinal stripes, a condition approximated by *A. rubrolineata* and *A. tucurui*, both members of Römer's *A. regani* lineage (*A. commbrae* and *A. linkei* complexes, respectively).

Two characteristics of *A. kullanderi* are at odds with its placement in the *A. regani* lineage of Römer (2006). As previously noted, mature females of *A. kullanderi* share striking similarities in coloration (i. e., ventral surfaces intensely black) with females of *A. baenschi*, a member Römer's *A. steindachneri* lineage placed in either the *A. cacatuoides* complex (sensu Römer, 2004) or

A. nijsseni complex (sensu Römer, 2006). Secondly, the large size of mature male *A. kullanderi* (up to 79.7 mm SL) is most closely approached by that of *A. steindachneri* (65.3–75.8 mm SL). Despite those characteristics, and in the absence of a comprehensive cladistic analysis of *Apistogramma*, we tentatively consider *A. kullanderi* to be a member of the *A. regani* lineage of Römer (2006), and the *A. regani* species group of Kullander (1986).

Biogeography. The rio Curuá departs Serra do Cachimbo via two major waterfalls approximately 40 meters (upstream) and 60 meters (downstream) in height and separated by about 50 meters of river channel (Birindelli & Britski, 2009). Above the 40 m waterfall is a smaller falls (ca. 10 m) and site of the weir (i.e. dam) for PCH Salto Buriti, a run-of-the-river hydroelectric complex constructed in 2007. The weir impounds the rio Curuá upstream of the 10 m falls, creating a reservoir from which water is diverted through a penstock to power turbines before returning to the river just downstream of the 60 m waterfall. The waterfalls, collectively referred to as Salto do Curuá, apparently isolate the upper Curuá from the remaining portion of the watershed, which drains into the rio Iriri, a major tributary to the lower rio Xingu. Five characiforms were recently described as endemic to the upper Curuá: *Leporinus guttatus* Birindelli & Britski, 2009 (Anostomidae); *Jupiaba kurua* Birindelli et al., 2009, *Moenkhausia petymbuaba* Lima & Birindelli, 2006 (Characidae), and *Lebiasina marilynae* Netto-Ferreira, 2012 and *L. melanoguttata* Netto-Ferreira, 2012 (Lebiasinidae). *Apistogramma kullanderi* appears to represent a sixth endemic species.

In 2007 and 2009, fishes were sampled in the rio Curúa basin at three sites above the 10 m waterfalls, one site just upstream of the 40 m falls, and sites downstream of the 60 m falls. One 2007 collection was made during an artificial dry down of the stretch of the main channel immediately above the 10 m falls (all water temporarily re-routed for dam construction). *Apistogramma kullanderi* was only recorded from the three sites above the 10 m waterfalls, one in the upper Curuá mainstem and two others in separate tributaries (rio Escorpião and another unnamed). Only two other species of cichlid have been recorded from the upper Curuá, and both occur syntopically with *A. kullanderi*.

One is tentatively identified as *Aequidens* aff. *rondoni* and occurs in both the upper Curuá (same three sites as *A. kullanderi*) and upper rio Treze de Maio, a tributary of the Curuá. Headwaters of the rio Treze de Maio similarly arise on Serra do Cachimbo and are isolated by large waterfalls from the lower Treze de Maio, which joins the Curuá downstream of Salto do Curuá. *Aequidens rondoni* was described by Miranda-Ribeiro (1918) from rio do Sangue above Salto Bello and is distributed in the upper Tapajós basin.

The second species also belongs to the genus *Apistogramma* and appears to be an undescribed member of the *A. regani* group (sensu Kullander, 1980). *Apistogramma* "upper Curuá" was found only in one of the two tributaries occupied by *A. kullanderi* (i. e., type locality). Based on seven specimens (mature male 46.7 mm SL, immature male and five unsexed, immature specimens, 26.8–35.0 mm SL), *Apistogramma* "upper Curuá" is easily recognized by having four anal-fin spines vs. three (n = 44) or rarely four (n = 2) in *A. kullanderi*, and by differences in coloration. The mature male of *Apistogramma* "upper Curuá" lacks the coarse pattern of dark markings on head and the dark pigmentation in dorsal and anal fins described for males of *A. kullanderi,* and has a conspicuous pattern of dark bars on caudal fin that are absent in mature *A. kullanderi*. *Apistogramma kullanderi* also has a conspicuous pattern of stripes on flanks, whereas the undescribed species has only two or three longitudinal series of faint markings in the abdominal region formed by a greater concentration of dark pigment on central posterior border of each scale.

A second undescribed species of the *Apistogramma regani* group (sensu Kullander, 1980) occurs in the upper rio Treze de Maio, and is not sympatric with *A. kullanderi*. It matures at a much smaller size (ca. 40 mm SL), similar to other species of *Apistogramma*. In mature females of *Apistogramma* "upper Treze de Maio", the dorsal-fin base presents dark blotches alternating with pale interspaces (vs. dorsal-fin base entirely dark in *A. kullanderi*), and the dark pigmentation on ventral part of body is restricted to gular region (vs. covering almost entire ventral surface of body in *A. kullanderi*). Males and juveniles of the upper Treze de Maio species are distinguished by having three to five longitudinal series of abdominal markings formed by greater concentration of dark pigment on central posterior border of each scale, a pattern similar to *Apistogramma* "upper Curuá", but absent from *A. kullanderi*.

Body size. *Apistogramma kullanderi* is the largest known member of the genus with wild-caught males reaching at least 79.7 mm SL (holotype). *Apistogramma steindachneri* (Regan, 1908) is the next largest congener with males reaching 65.3 mm SL in the wild, and at least 75.8 mm SL under aquarium conditions (Kullander & Nijssen, 1989: 82). Records of *Apistogramma erythrura* Staeck & Schindler, 2008 reaching 140 mm SL (e. g., Steele & López-Fernández, 2014: table S1) are in error; that value pertains correctly to TL (60.7 mm) as a percentage of SL (43.4 mm), reported as 139.8 by Staeck & Schindler (2008: 200, tab. 1).

With respect to body size among Neotropical cichlids (subfamily Cichlinae), *Apistogramma* rules the small extreme. In a recent study of body size diversity in 498 species of Cichlinae by Steele & López-Fernández (2014), *Apistogramma* included both the smallest species (i. e., *A. staecki*, 21 mm SL) and the most species below 36 mm SL (n = 22) and 50 mm SL (n = 53). Only ten species from other genera (e. g., *Dicrossus*, *Teleocichla*) shared the small-bodied morphospace occupied by *Apistogramma*.

Athough body size appeared to be phylogenetically constrained within *Apistogramma*, it was divergent at a more inclusive level, the *Crenicichla*–*Apistogramma*–*Satanoperca* (CAS) clade of Geophagini (Steele & López-Fernández, 2014). Body size frequency distributions of the CAS clade were consistent with three possible optima around 35, 100 and 250 mm SL, with *Apistogramma* and *Satanoperca* corresponding to the first two optima, respectively. Those two genera are closely related and form a well-supported clade with *Taeniacara* (López-Fernández et al., 2010), yet occupy distinct areas of body size space (Steele & López-Fernández, 2014). Body size divergence, under an ecological opportunity model, may help co-existing, closely related taxa to minimize competition for limited resources such as food and habitat (Mahler et al. 2010; Steele & López-Fernández, 2014). Furthermore, ecological opportunity predicts that speciation rates and morphological evolution, such as changes in body size, will be elevated in a taxon after its colonization of insular areas unoccupied by competitors (Harmon et al., 2008).

Ecological opportunity may play a role in the extreme body size of *A. kullanderi*, known only from the rio Curuá above Salto do Curuá. Only two other species of cichlid, *Aequidens* aff. *rondoni* and *Apistogramma* "upper Curuá" are known to co-exist with *A. kullanderi* in the upper Curuá.

The maximum sizes observed for the species of *Aequidens* and *Apistogramma* "upper Curuá" are 126.7 and 47.3 mm SL, respectively. The insular nature of the upper Curuá, coupled with its apparently depauperate cichlid fauna, may provide ecological opportunities for body size diversification in an otherwise small-bodied taxon such as *Apistogramma*. Concordantly, large body size may have evolved in *A. kullanderi* to minimize competition with the smaller *Apistogramma* "upper Curuá", and is presumably constrained to some degree by the larger species of *Aequidens*.

In addition to its extremely large body size relative to congeners, *A. kullanderi* exhibits male-biased sexual size dimorphism wherein mature males are larger than mature females. Within a taxon, the evolution of larger body size in males vs. females is generally attributed to sexual selection mediated by male-male competition and/or female choice (Woolbright, 1983). Larger males tend to be more reproductively successful when mating involves behaviors (e. g., courtship displays and nest defense) that are both energetically costly and incur a greater risk of predation (Emery, 1968; Knapp, 1995; Johnson & Hixon, 2011). Within *Apistogramma*, male-biased sexual size dimorphism is particularly strong in polygynous species (Römer, 2006), wherein males defend spawning territories. We speculate that in the context of an insular watershed depauperate of cichlids, ecological opportunities and reduced competition relax phylogenetic constraints on body size in *Apistogramma*, allowing sexual selection to drive male body size to a larger optimum.

Comparative material. *Apistogramma* sp. "upper Curuá": MZUSP 95794, 7, 26.8–47.3 mm SL, 2 males and five immature unsexed specimens, examined by photos; Brazil: Pará: Altamira: rio Xingu basin: unnamed tributary of rio Curuá (Iriri drainage), at route BR163 bridge; 8°49'12"S 54°58'11"W.

Apistogramma sp. "upper Treze de Maio": MZUSP 97095, 2, 25.0–39.1 mm SL, 1 female, 1 juvenile; MZUSP 101422, 5, 23.8–39.5 mm SL, 1 male, 1 female, 3 unsexed or juveniles; Brazil: Pará: Altamira: rio Xingu basin: rio Treze de Maio, a tributary of rio Curuá (Iriri drainage), upstream of PCH Salto Treze de Maio dam; 8°45'06"S 55°02'05"W.

Aequidens aff. *rondoni*: all from Brazil: Pará: Altamira: rio Xingu basin. MZUSP 96872, 4, main channel of rio Curuá immediately above ca. 10 m falls (sampled after dry down during construction of PCH Salto Buriti); 8°46'09"S 54°57'02"W; J. Birindelli et al., 21 Oct 2007. – MZUSP 97094, 2, 34.4–60.2 mm SL; rio Treze de Maio, tributary of rio Curuá (rio Iriri drainage), up-

stream of PCH Salto Treze de Maio dam; 8°45'06"S 55°02'05"W. – MZUSP 97580, 17 of 22, 58.5–126.0 mm SL; Brazil: Pará: rio Escorpião, tributary of upper rio Curuá, at BR163 bridge; 8°53'54"S 54°59'20"W. – MZUSP 97582, 48 of 54, 40.5–126.7 mm SL; unnamed tributay of upper rio Curuá (rio Iriri drainage), at route BR163 bridge; 8°49'12"S 54°58'11"W.

Other comparative material. *Apistogramma agassizi*: MZUSP 7916, 4, 12.4–30.6 mm SL. *Apistogramma bitaeniata*: MZUSP 15321, 2, 22.2–33.3 mm SL; MZUSP 46714, 2, 27.2–28.8 mm SL. *Apistogramma borelli*: MZUSP 25269, 2, 25.4–26.2 mm SL. *Apistogramma cacatuoides*: MZUSP 46714, 53, 11.8–33.6 mm SL. *Apistogramma diplotaenia*: MZUSP 28214, 23, paratypes, 15.2–29.2 mm SL. *Apistogramma gossei*: MZUSP 38982, 1, paratype, 25.5 mm SL; MZUSP 38991, 1, paratype, 24.3 mm SL. *Apistogramma hippolytae*: MZUSP 6657, holotype, 30.8 mm SL; MZUSP 19396–19428, 33, paratypes, 21.8–34.4 mm SL. *Apistogramma inconspicua*: MZUSP 38944, 1, paratype, 23.3 mm SL. *Apistogramma iniridae*: MZUSP 14888, 1, paratype, 28.1 mm SL. *Apistogramma linkei*: MZUSP 28726, 8, paratypes, 17.4–25.9 mm SL. *Apistogramma macmasteri*: ANSP 127328, 9, 20.7–38.8 mm SL; ANSP 127330, 1, 50.8 mm SL; ANSP 127389, 13, 20.4–45.1 mm SL. *Apistogramma paucisquamis*: MZUSP 36952, holotype, 29.2 mm SL; MZUSP 42322, 4, paratypes, 17.5–27.9 mm SL. *Apistogramma pulchra*: MZUSP 38989, 2, paratypes, 20.0–26.7 mm SL. *Apistogramma regani*: MZUSP 38992, 2, paratypes, 29.4–27.4 mm SL; MZUSP 38967, 6, paratypes, 24.0–27.3 mm SL. *Apistogramma wapisana*: MZUSP 100673, holotype, 27.9 mm SL; MZUSP 100674, 1, paratype, 24.8 mm SL.

Acknowledgments

Literature cited

Birindelli, J. L. O., A. M. Zanata, L. M. Sousa & A. L. Netto-Ferreira. 2009. New species of *Jupiaba* Zanata (Characiformes: Characidae) from Serra do Cachimbo, with comments on the endemism of upper rio Curuá, rio Xingu basin, Brazil. Neotropical Ichthyology, 7: 11–18.

Birindelli, J. L. O. & H. A. Britski. 2009. New species of the genus *Leporinus* Agassiz (Characiformes: Anostomidae) from the rio Curuá, rio Xingu basin, Serra do Cachimbo, Brazil, with comments on *Leporinus reticulatus*. Neotropical Ichthyology, 7: 1–10.

Birindelli, J. L. O., L. M. Sousa, A. Netto-Ferreira, N. Lujan & M. H. Sabaj Pérez. 2009. The Pipe Expedition: relatos da expedição à Serra do Cachimbo. Boletim da Sociedade Brasileira de Ictiologia, 95: 10–15.

Bork, D. 2005. Die neuesten/the latest *Apistogramma*. Aqualog Extra. Verlag A. C. S., Rodgau, 48 pp.

Datovo, A. & F. A. Bockmann. 2010. Dorsolateral head muscles of the catfish families Nematogenyidae and Trichomycteridae (Siluriformes: Loricarioidei): comparative anatomy and phylogenetic analysis. Neotropical Ichthyology, 8: 193–246.

Emery, A. R. 1968. Comparative ecology of damselfishes (Pisces, Pomacentridae) from Alligator Reef, Florida Keys. Ph.D. University of Miami, Miami.

Eschmeyer, W. N. (ed.). 2014. Catalog of fishes: genera, species, references. Electronic version accessed 23 July 2014.

Harmon, L. J., J. Melville, A. Larson & J. B. Losos. 2008. The role of geography and ecological opportunity in the diversification of day geckos *(Phelsuma)*. Systematic Biology, 57: 562–573.

Hein, G., A. Zarske & J. Zapata. 2002. *Apistogramma rubrolineata* sp. n., ein neuer Buntbarsch (Teleostei: Perciformes: Cichlidae) aus dem Rio Manuripi, Departamento Pando, in Bolivien. Das Aquarium, 402: 15–19.

Hoedeman, J. J. 1951. Notes on the fishes of the cichlid family I. *Apistogramma cacatuoides* sp. n. Beaufortia, 4: 1–4.

Johnson, D. W. & M. A. Hixon. 2011. Sexual and lifetime selection on body size in a marine fish: the importance of life-history trade-offs. Journal of Evolutionary Biology, 24: 1653–1663.

Knapp, R. A. 1995. Influence of energy reserves on the expression of a secondary sexual trait in male bicolor damselfish, *Stegastes partitus*. Bulletin of Marine Science, 57: 672–681.

Kullander, S. O. 1979. Species of *Apistogramma* (Teleostei, Cichlidae) from the Orinoco drainage basin, South America, with descriptions of four new species. Zoologica Scripta, 8: 69–79.

— 1980. A taxonomical study of the genus *Apistogramma* Regan, with a revision of Brazilian and Peruvian species (Teleostei: Percoidei: Cichlidae). Bonner Zoologische Monographien, 14: 1–152.

— 1986. Cichlid fishes of the Amazon river drainage of Peru. Swedish Museum of Natural History, Stockholm, 431 pp.

— 1987. A new *Apistogramma* species (Teleostei, Cichlidae) from the Rio Negro in Brazil and Venezuela. Zoologica Scripta, 16: 259–270.

— 1990. *Mazarunia mazarunii* (Teleostei: Cichlidae), a new genus and species from Guyana, South America. Ichthyological Exploration of Freshwaters, 1: 3–14.

— 1998. A phylogeny and classification of the South American Cichlidae (Teleostei: Perciformes). Pp. 461–498 in: L. R. Malabarba, R. E. Reis, R. P. Vari, Z. M. S. Lucena & C. A. S. Lucena (eds.), Phylogeny and classification of neotropical fishes. Edipucrs, Porto Alegre, 603 pp.

— 2003. Family Cichlidae. Pp. 605–654 in: R. E. Reis, S. O. Kullander & C. J. Ferraris (eds.), Check list of the freshwater fishes of South and Central America. Edipucrs, Porto Alegre, 729 pp.

Kullander, S. O. & H. Nijssen. 1989. The cichlids of Surinam. Teleostei: Labroidei. Brill, Leiden, xxxii + 256 pp.

Lima, F. C. T. & J. L. O. Birindelli. 2006. *Moenkhausia petymbuaba*, a new species of characid from the Serra do Cachimbo, Rio Xingu basin, Brazil (Characiformes: Characidae). Ichthyological Exploration of Freshwaters, 17: 53–58.

Linke, H. & W. Staeck. 1995. American cichlids I: Dwarf cichlids: a handbook for their identification, care and breeding. Tetra Press, Melle, 232 pp.

López-Fernández, H., R. L. Honeycutt, M. L. J. Stiassny & K. O. Winemiller. 2005. Morphology, molecules, and character congruence in the phylogeny of South American geophagine cichlids (Perciformes, Labroidei). Zoologica Scripta, 34: 627–651.

López-Fernández, H., K. O. Winemiller & R. L. Honeycutt. 2010. Multilocus phylogeny and rapid radiations in Neotropical cichlid fishes (Perciformes: Cichlidae: Cichlinae). Molecular Phylogenetics and Evolution, 55: 1070–1086.

Mahler, D. L., L. J. Revell, R. E. Glor & J. B. Losos. 2010. Ecological opportunity and the rate of morphological evolution in the diversification of Greater Antillean anoles. Evolution, 64: 2731–2745.

Mayland, H. J. & D. Bork. 1997. South American dwarf cichlids. *Apistogramma*, *Crenicara*, *Microgeophagus*. Landbuch-Verlag, Hannover, 187 pp.

Meinken, H. 1965. Über eine neue Gattung und Art der Familie Cichlidae aus Peru (Pisces, Percoidea, Cichlidae). Senckenbergiana Biologica, 46: 47–53.

Mesa S., L. M. & C. A. Lasso. 2011. III. Revisión del género *Apistogramma* Regan, 1913 (Perciformes, Cichlidae) en la cuenca del río Orinoco. Serie Editorial Recursos Hidrobiológicas y Pesqueros Continentales de Colombia. Instituto de Investigación de Recursos Biológicos Alexander von Humboldt, Bogotá, 192 pp.

Miranda-Ribeiro, A. 1918. Historia Natural. Zoologia. Cichlidae. Commissão de Linhas Telegraphicas Estrategicas de Matto-Grosso ao Amazonas, 46: 1–18.

Netto-Ferreira, A. L. 2012. Three new species of *Lebiasina* (Characiformes: Lebiasinidae) from the Brazilian shield border at Serra do Cachimbo, Pará, Brazil. Neotropical Ichthyology, 10: 487–498.

Pellegrin, J. 1936. Un poisson d'aquarium nouveau du genre *Apistogramma*. Bulletin de la Société Nationale d'Acclimatation de France, 1936: 56–58.

Regan, C. T. 1908b. Description of a new cichlid fish of the genus *Heterogramma* from Demerara. Annals and Magazine of Natural History, Series 8, 1: 370–371.

— 1913c. Fishes from the River Ucayali, Peru, collected by Mr. Mounsey. Annals and Magazine of Natural History, Series 8, 12: 281–283.

Rodrigues, R. R., L. N. Carvalho, J. Zuanon & K. Del-Claro. 2009. Color changing and behavioral context in the Amazonian dwarf cichlid *Apistogramma hippolytae* (Perciformes). Neotropical Ichthyology, 7: 641–646.

Römer, U. 2006. Cichlid atlas, Volume 2. Natural history of South American dwarf cichlids, Part 2. Mergus Verlag, Melle, 1319 pp.

Römer, U., I. Hahn, E. Römer, D. P. Soares & M. Wöhler. 2004. *Apistogramma baenschi* sp. n. Beschreibung eines weiteren geophaginen Zwergcichliden (Teleostei: Perciformes) aus Peru. Das Aquarium, 422: 15–30.

Sabaj Pérez, M. H. 2009. PIPE-Expedition in die Serra do Cachimbo. Amazonas, 25: 36–43.

Staeck, W. 2003. Cichliden-Lexikon, Teil 3: Südamerikanische Zwergbuntbarsche. Dähne, Ettlingen, 219 pp.

Staeck, W. & I. Schindler. 2008. *Apistogramma erythrura* sp. n. – a new geophagine dwarf cichlid (Teleostei: Perciformes: Cichlidae) from the río Mamoré drainage in Bolivia. Vertebrate Zoology, 58: 197–206.

Stawikowski, R. & U. Werner. 1998. Die Buntbarsche Amerikas, Band 3. Erdfresser, Hecht- und Kammbuntbarsche. DATZ-Aquarienbücher. Ulmer, Stuttgart, 540 pp.

Steele, S. E. & H. López-Fernández. 2014. Body Size Diversity and Frequency Distributions of Neotropical Cichlid Fishes (Cichliformes: Cichlidae: Cichlinae). PLoS ONE, 9: e106336. doi:10.1371/journal.pone.0106336.

Woolbright, L. L. 1983. Sexual selection and size dimorphism in anuran Amphibia. The American Naturalist, 121: 110–119.