

<http://zoobank.org/urn:lsid:zoobank.org:pub:921B9BAE-6789-496A-BCDB-F0E0437F1C26>
Apistogramma megastoma: LSID urn:lsid:zoobank.org:act:3EC6039D-8F34-45A3-9728-F21B3387FCE2

Description of a new maternal larvophilic mouth-brooding cichlid species, *Apistogramma megastoma* sp. n. (Teleostei: Perciformes: Geophaginae), from Loreto, Peru *

UWE RÖMER^{1,2,3}, CLARA ISIS RÖMER^{1,4}, GUILLAIN ESTIVALS^{1,5}, ANTONIA VELA DÍAZ^{1,5}, FABRICE DUPONCHELLE^{1,6,7}, CARMEN ROSA GARCÍA DÁVILA^{1,5}, INGO HAHN⁸ & JEAN-FRANÇOIS RENNO^{1,6,7}

¹ Laboratoire Mixte International – Evolution et Domestication de l'Ichtyofaune Amazonienne [LMI–EDIA], Iquitos, Peru – ² University of Trier, Animal Research Group, Inst. Biogeography [UTIB], Dep. Geo-Sciences, Universitätsstraße 15, 54286 Trier, Germany – ³ Österwieher Straße 196, 33415 Verl; Germany; e-mail: eu.roemer@t-online.de (corresponding author) – ⁴ Bielefeld University, Faculty of Biology, Postfach 100131, 33501 Bielefeld – ⁵ Instituto de Investigaciones de la Amazonia Peruana [IIAP], km 2.5, Avenida Abelardo Quiñones, Iquitos, Perú – ⁶ Universidad Nacional Federico Villareal, Facultad de Oceanografía y Ciencias Alimentarias, 350 calle Roma, Miraflores, Lima, Perú – ⁷ Institut de Recherche pour le Développement [IRD], UMR ISE-M, 361 rue Jean-François Breton BP5095, 34196 Montpellier Cedex 5, France – ⁸ Munich University of Applied Sciences, Faculty of Geo-information, Karlstraße. 6, 80333 Munich, Germany; Germany

Accepted 5.v.2017.

Published online at www.senckenberg.de/vertebrate-zoology on 15.v.2017.

Abstract

Apistogramma megastoma sp. n. is described based on a total of 18 specimens from small forest streams in the Departamento Loreto, Peru, tributaries of the Río Jutai in the border area between Peru and Brazil south and west of the city of Leticia (Colombia) (near 04°12' S / 70°06' W). *Apistogramma megastoma* sp. n., which may be confused only with *A. barlowi*, is distinguished from all other *Apistogramma* species by the combination of: noticeably disproportionately large head; exceptionally massive jaws, lyrate densely vertically banded caudal fin, extended dorsal-fin membranes in males; in aggressive females sooty head pattern and up to 8 series of small black dashes on flanks; small round caudal spot; and, exceptional for *Apistogramma*, maternal mouth-brooding behaviour. Distinguished from *A. barlowi*, by differences in colour pattern and by higher number of scale rows on cheeks. *Apistogramma megastoma* sp. n. inhabits in small fast-flowing streams.

Resumen

Apistogramma megastoma sp. n. se describe sobre la base de un total de 18 especímenes que provienen de corrientes pequeños del bosque, tributarios del Río Jutai en la zona fronteriza entre Perú y Brasil al sur y al oeste de la ciudad de Leticia (Colombia) (cerca de 04°12' Sur y 70°06' Oeste). *Apistogramma megastoma* sp. n., que sólo puede confundirse con *A. barlowi*, se distingue de todas las otras especies de *Apistogramma* por la combinación de: notablemente cabeza desproporcionadamente grande; excepcionalmente enormes mandíbulas; aleta caudal (lira) densamente con bandas verticales; en machos la aleta dorsal con las membranas alargadas; en hembras agresivas el patrón de la cabeza hollín y hasta ocho series de pequeñas manchas de color negro en los flancos; pequeña mancha caudal redonda; y, excepcional para *Apistogramma*, con el comportamiento maternal de incubación oral. Se diferencia de *A. barlowi*, independientemente de las diferencias en el patrón de color, por un mayor número de hileras de escamas en las mejillas. *Apistogramma megastoma* sp. n. vive en pequeños arroyos de corriente rápida.

Kurzfassung

Apistogramma megastoma sp. n. wird auf Basis von 18 Exemplaren beschrieben, die aus kleinen Waldbächen im Bundesstaat Loreto, Peru, Zuflüssen des río Jutai in der Grenzregion zwischen Peru und Brasilien südlich und westlich der Stadt Leticia (Kolumbien) stammen (etwa

¹ This is publication number 7 from the *Apistogramma* Project within the Laboratoire Mixte International.

04°12' S / 70°06' W). Die nur mit *A. barlowi* verwechselbare Art unterscheidet sich von allen anderen *Apistogramma*-Arten durch die Kombination von deutlich überproportional großem Kopf und außergewöhnlich massigen Kiefern, leierförmiger dicht senkrecht gebänderter Schwanzflosse, verlängerten Membranen der Dorsale, bei drohenden Weibchen rußiger Kopfzeichnung und bis zu acht Reihen kleiner schwarzer Flecken auf den Körperseiten, kleinem runden Schwanzwurzelfleck und innerhalb der Gattung *Apistogramma* ungewöhnlichem maternalen Maulbrutverhalten. Von *A. barlowi* neben Unterschieden in Zeichnungsmuster und Färbung durch höhere Zahl von Schuppenreihen auf den Wangen unterschieden. *Apistogramma megastoma* sp. n. lebt in kleinen schnell fließenden Waldbächen.

Key words

Biodiversity, ichthyology, new taxa, systematics, Neotropics, freshwater, ecology, reproductive behaviour.

Prefatory Remarks

In recent decades numerous new species of the genus *Apistogramma* REGAN, 1913 have been discovered in Brazil, Venezuela, and especially Peru. Some of these forms have been scientifically studied and the vast majority of them described for the first time only in recent years (BRITZKE *et al.*, 2015; KULLANDER, 1980, 1986; KULLANDER & FERREIRA, 2005; MESA & LASSO 2011a-b; READY & KULLANDER, 2008; RÖMER, 1994, 1997; RÖMER & HAHN, 2008, 2013; RÖMER *et al.*, 2003, 2004a–b, 2006b–d, 2011, 2012, 2013; SCHINDLER & STAECK, 2013; STAECK, 1991, STAECK & SCHINDLER, 2008; VARELLA & BRITZKE, 2016; VARELLA & SABAJ PÉREZ, 2014), bringing the total number of valid species to significantly over 90 and making *Apistogramma* the largest genus among the Neotropical cichlids. However, there are still several forms awaiting formal description. Amongst the described species, *Apistogramma barlowi* RÖMER & HAHN, 2008 is extraordinary for being the only member of the genus to exhibit mouth-brooding behaviour. Based on observations by RÖMER (2006a–b), RÖMER & HAHN (*op.cit.*) mentioned the possibility that the taxon might in fact consist of two species, one of them cryptic, but after discussing the cryptic species concept for *Apistogramma* in general, the authors rejected the possibility in the case of *Apistogramma barlowi*. However, new evidence from field work carried out between 2010 and 2013 within the multinational project EVOLUTION ET DOMESTICATION DE L'ICHTYOFAUNE AMAZONIENNE (EDIA), run by the cooperative LABORATOIRE MIXTE INTERNATIONAL (LMI), has shed new light on the situation and led to a review of specimens hitherto identified as *Apistogramma barlowi*. Freshly preserved as well as live material that became available in 2011, 2012, and 2013 provided us with the opportunity for a more in-depth comparison of the different phenotypes of the taxon. On the basis of our research over the last four years, we have come to the conclusion that the original hypothesis that *Apistogramma barlowi* might consist of two distinguishable taxa is valid. Because recent research indicates that mate-choice behaviour may be responsible for speciation within rapidly radiating species clusters (ELMER *et al.*, 2010; ENGELKING *et al.* 2010; REICHARD & POLAČIK, 2010; RÖMER & BEISENHERZ, 2005; RÖMER *et al.*, 2014; SEEHAUSEN, 2000; SVENSSON *et al.*, 2009), and that different colour morphs may represent separate species (RÖMER & BEISENHERZ, 2005; READY *et al.*, 2006), and be-

cause we have diagnosed different brood-care strategies, we have decided to publish the formal description of a second mouth-brooding species of *Apistogramma*, based on our examination of preserved specimens and behavioural studies of numerous live specimens.

Methods

Except where otherwise stated, methods for counts and measurements are as detailed in RÖMER (2006), RÖMER & HAHN (2008), and RÖMER *et al.* (2003, 2004, 2006, 2011, 2012), with scale-row numbering following KULLANDER (1990). Gill rakers, pharyngeal elements, and details of dentition have not been included in this study (for reasons see RÖMER *et al.*, 2011). GPS locality data were not available. Preservation of all specimens collected followed the “low temperature preservation protocol” (LTPP), described in detail by RÖMER & HAHN (2008) and RÖMER *et al.* (2011), in the laboratory of the IAP in Iquitos, after observing the behaviour and colour patterns of the specimens (for reasons see RÖMER *et al.*, 2011). All specimens were initially preserved in 95 % ethanol to permit the taking of DNA samples, with most individuals being transferred into 75 % ethanol later. DNA samples were taken and preserved as described in RÖMER *et al.* (2011) and stored as detailed in RÖMER *et al.* (2012). The description is based on observations on all type specimens. Although we are fully aware of the overall difficulties of species recognition (reviewed in MENDELSON & SHAW, 2012), for practical reasons we basically follow the morphological/genetic cluster concept (M/GC) for species delimitation (*cf.* SITES & MARSHALL, 2004; also DAVIS & NIXON, 1992; WIENS & SERVEDIO, 2000). Comparative statistical analysis of all data was performed using the PC program STATISTICA for Windows [Dell Inc. (2015). Dell Statistica (software-system for data analysis), version 13. software. dell.com]. The description of live coloration of the species is based on observation and photographs of the type material taken under standardised conditions in aquaria as detailed in RÖMER *et al.* (2011), supplemented by observations of additional specimens (not preserved) kept long-term in aquaria. RÖMER (2000, 2006) and RÖMER *et*

al. (2003, 2004, 2006) have explained at length the reasons for giving precise descriptions of live coloration in *Apistogramma* species¹. Voucher specimens are stored in the fish collections of the IAP, MTD, and MUSM. For museum acronyms see LEVITON *et al.* (1985).

Comparative material. *Apistogramma allpahuayo* RÖMER *et al.*, 2012: type series; *Apistogramma barlowi*: type series, MUSM 53455, male, 59.2 mm SL; other material as listed in RÖMER (1994, 1997, 2006), RÖMER & WARZEL (1998), and RÖMER *et al.* (2003, 2004, 2006b-d, 2012, 2013, 2015).

Apistogramma megastoma sp. n.

(Figs. 1–5 & 7–19, Tables 1–4)

Apistogramma sp. “Jutai” RÖMER & RÖMER, 2015: 26–31 & title page (7 photographs of live specimens). *Apistogramma* sp. “Diamante” (trade name).

Holotype: (fig. 1) MUSM 52459, female, 61.9 mm SL, Peru, Departamento Loreto, small forest streams southwest of Leticia, probably draining to Rio Yavari, Amazonas system (approx. 04°12' S / 70°06' W); March 2012, leg. Albertino Maca Ausber.

Paratypes: 17 specimens: IAP 302869, male, 38.2 mm SL; IAP 302870, male, 41.7 mm SL; IAP 302871, male, 36.1 mm SL; small forest streams draining to the Rio Jutai south of Leticia, Amazonas system, border area between Brazil and Peru, 29th August 2012, leg. Albertino Maca Ausber. MTD F 32642, male, 50.5 mm SL; MTD F 32700, female, 39.7 mm SL; MTD F 32701, female, 48.1 mm SL; MTD F 32702, male, 56.1 mm SL; MTD F 32704, male, 57.0 mm SL; MUSM 52449, male, 55.9 mm SL; MUSM 52450 (allotype), male, 76.3 mm SL (fig 2); MUSM 52451, female, 58.2 mm SL (fig. 3); MUSM 52452, 1 male, 48.6 mm SL; MUSM 52453, female, 48.3 mm SL; MUSM 52454, female, 36.7 mm SL; MUSM 52456, 1 female, 44.3 mm SL; MUSM 52457, male, 59.7 mm SL; MUSM 52458, male, 55.4 mm SL; collection data as given for holotype.

Supplementary material (non types): 15 male and 15 female wild-caught specimens, as well as about 150 individuals of their F₁ and F₂ offspring, kept in the aquarium for behavioural observation. These will eventually be preserved and deposited mainly in either the MUSM or the MTD F collections, with some possibly retained in the personal collection of UR.

Diagnosis. *Apistogramma megastoma* sp. n. is a large (males up to 76 mm, females to 62 mm SL), high-backed, laterally compressed, and little elongated maternal mouth-brooding species of the *Apistogramma caca-tuoides* complex, exhibiting pronounced sexual dimorphism and dichromatism, similar only to *Apistogramma barlowi*.

The species is readily differentiated and distinguished from all *Apistogramma* species known to date except *Apistogramma barlowi* on the basis of the combination of the following characters: Adult males with disproportionately large head, enormously enlarged mouth with wide massive jaws and hypertrophied lips; tooth rows and adjacent epidermal tissue yellow in males, in brood-caring females conspicuously deep red (*vs.* yellow in *A. barlowi*); in both sexes 3 to 4 infraorbital (*vs.* 3 in *A. barlowi*) and up to 8 preopercular pores. Caudal fin lyrate in adult specimens of both sexes, truncate and immaculate in juveniles and sub-adult individuals; caudal extensions in most males orange posterior to distal edge of caudal centre; males with 10 to 12 continuous vertical rows of light spots on translucent bluish caudal fin. Mature males with extended and pointed dorsal lappets for entire length of fin; old males with lappets of spines 2 to 6 (or 7) more than twice length of spines. Longitudinal band about 1.5 scales wide extending to base of caudal fin; caudal-peduncle spot (visible only in subordinated live specimens) small, rounded. In males longitudinal band fades during threat and display, while several red spots and/or lines appear on cheek, lower part of gill cover, and anterior third of body (absent in *A. barlowi*). Breeding females without any extended black band-like markings immediately behind pectoral-fin base (present in *A. barlowi*); instead some individuals with few blackish scales on base of pectoral; 5 to 7 rows of drop-shape spots or dashes on flanks, dashes positioned on lower and upper edge of scales on body. Females and juvenile or subordinated males with upright oval mid-lateral spot extending slightly above upper margin of longitudinal band. Cheek stripe extending from eye to lower posterior margin of operculum in both sexes, hardly ever visible in (live) males, about pupil width below eye on infraorbital, in most females widened to more or less cover whole cheek and lower part of operculum.

The species differs from *Apistogramma barlowi* by: higher number of rows of cheek scales (4 to 5 *vs.* 3 to 3.5); higher number of infraorbital (4 *vs.* 3) and preopercular pores (6–8 *vs.* 5–6); different caudal-fin colour pattern (uniformly barred in *A. megastoma* sp. n.); no black breast band in females (*vs.* present in *A. barlowi*); cheek stripe significantly narrower; rows of spots/dashes on flanks (*vs.* absent in *A. barlowi*); entire mouth region of females sooty from lips to interorbital and cheek stripe during direct intrasexual aggressive threat (*vs.* only lips sooty in *A. barlowi*).

Description

Morphological characters: (n=16; 36.1 to 76.3 mm SL). For biometric data see tables 1–2 & 4, for meristic data see table 3.

Habitus (figs. 1–5, 7–19): As given for *Apistogramma barlowi*, with few biometric differences detectable during comparison. The following differences were re-

¹ In a recent publication, STAECK (2015) critically reviewed the historical development of requirements for diagnostic differentiation in species descriptions. He also highlighted aspects and limitations of species diagnosis using descriptions of live coloration in some genera of cichlids (*Heros*, *Hemichromis*), but also explicitly confirmed the usefulness of information on colour and colour pattern for others including *Apistogramma*.



Fig. 1. *Apistogramma megastoma* sp. n., MUSM 52459, holotype, female, 61,9 mm SL; 6 months after preservation. December 2012. All photographs U. Römer except where otherwise stated.

corded between this sexually dimorphic species and other members of the genus: Body noticeably deep overall (34.7–43.8 % SL, mean 38.8 % SL), laterally compressed, about twice deeper than wide, head long (35.0–39.5 % SL, mean 37.0 % SL), appearance altogether strikingly robust. Meristic and morphometric differences between sexes not significant except maximum size (table 1). Adult males about fifth larger than females, with proportionally slightly smaller eye, greater preorbital depth, larger upper and lower jaws, wider interorbital bone, shorter anal-fin spines, longer snout, deeper cheek, and longer pelvic fin. Upper head profile regular apart from indentation above eye, convex from tip of mouth to interorbital and from interorbital to beginning of dorsal base, creating “humped” impression, clearly visible in specimens of about 30 mm SL upwards, but more pronounced in larger males; lower head profile slightly convex, in large males roughly straight from lip to posterior margin of lower jaw, then curving slightly upwards and continuing straight to lower posterior edge of unserrated operculum. Mouth terminal, noticeably large and wide (broadest within genus in relation to head width) (figs. 1–5, 17 & 19), jaws stout, lower jaw long (about 11.1–19.3 % SL, mean 15.5 % SL); allometry of snout and upper jaw positive, of lower jaw roughly linear, in relation to body size; lips extremely thick and hypertrophied, folded; maxillary extending approximately to vertical through anterior margin of pupil; eye relatively small (diameter 8.5–12.9 % SL, mean 10.8 % SL), negatively allometric in correlation with increasing SL; depth of cheek positively allometric with increasing SL; cheek fully scaled, 4 to 5 horizontal rows of cycloid scales (*vs.* 3 to 3 ½ in *A. barlowi*); scales on gill cover cycloid, for scale pattern see fig. 3; 5 dentary and unusual variable within the genus 3 to 4 infraorbital pores [2 specimens (MUSM 52454, MUSM 52456) with divi-

ating number of pores (3 *vs.* 4) on both sides of head], unusually high number (6 to 8) of preopercular pores for genus. Ventral fin [V. 1.5 (n=16)] slightly prolonged in males, extending to start of anal-fin base or up to third spine; in females short, only exceptionally extending to anus. Pectoral fin [P.12 (n=12)] rounded, without modifications. Dorsal fin [D. XV.6.i (n=2), XV.6.ii (n=1), XV.7 (n=8), XV.7.i (n=1), XV.8 (n=2), XVII.6 (n=1), XVI.7 (n=1)] with significantly pointed soft portion extending back to central posterior margin of caudal fin in adult males, even in females slightly pointed, but not extended; length of spines increasing from D1 to D5, thereafter remaining roughly constant to slightly decreasing; fifth and last spine normally about equal in length, occasionally last dorsal spine longest; in MUSM 52454 spine 16 doubled; pointed dorsal membranes significantly prolonged past tips of spines; in most adult males extensions of membranes D2 to D7 about double length of associated spines, remainder about 1.5 times longer than spines; lappets 2 to 5 longest, regularly extending back to vertical through anterior edge of anal-fin base. Anal fin [A. III.6 (n=12), III.7 (n=4)] pointed with soft portion extending to distal edge of first half of caudal fin in adult males, rounded to slightly pointed (but not extended) in females and small males and extending to base of caudal fin when folded. Caudal fin with 15 (n=1) or usually 16 (n=15) principal soft rays; in males and females of about 40 mm SL or larger slightly asymmetrically lyrate, more developed in males, in smaller females rounded or truncate; upper lobe longer than lower; caudal rays D4 to D5 and V4 to V5 significantly prolonged relative to remaining rays, D5 and V5 usually longest; intervening rays about same length, forming straight or (less frequently) slightly convex central edge, outer rays decreasing rapidly in length; caudal fin in both sexes scaled on first third to half. In adults

Table 1. Biometric data for *Apistogramma megastoma* sp. n., taken from the type specimens and expressed as % SL; SL given in mm.

	HT	AT	<i>Apistogramma megastoma</i> sp. n. (all)						males				females				abbreviations	
			(n)	mean	min.	max.	st.dev.	(n)	mean	min.	max.	st.dev.	(n)	mean	min.	max.	st.dev.	HT = Holotype / PT = Paratype
SL	61.9	76.3	15	49.0	36.1	76.3	10.66	9	51.1	36.1	76.3	12.26	6	45.9	36.7	61.9	7.59	standard length
TL	127.5	128.1	15	132.1	127.5	135.4	2.19	9	132.4	128.1	135.4	2.17	6	131.1	127.5	132.7	1.93	total length
TLS	133.0	135.7	15	138.3	127.8	158.5	8.19	9	142.2	132.9	158.5	8.28	6	132.6	127.8	137.5	3.48	total length plus streamer
HL	34.7	37.6	15	37.0	35.0	39.5	1.26	9	36.9	35.0	39.5	1.45	6	37.2	34.7	38.4	1.02	head length
HD	26.4	30.9	15	30.3	26.4	31.9	1.17	9	30.7	28.3	31.9	1.06	6	29.9	26.4	31.4	1.25	head depth
BD	36.5	37.6	15	38.8	34.7	43.8	2.32	9	39.4	36.4	43.8	2.30	6	37.9	34.7	41.3	2.23	body depth
HW	18.8	16.6	15	18.5	16.6	20.0	0.79	9	18.4	16.6	20.0	0.94	6	18.7	18.1	19.4	0.52	head width
PDL	37.6	34.0	15	38.1	34.0	41.4	1.95	9	38.1	34.0	40.9	2.21	6	38.1	36.6	41.4	1.70	pre-dorsal length
TDL	89.8	87.6	15	90.8	87.6	92.7	1.39	9	91.0	87.6	92.7	1.70	6	90.5	89.0	91.0	0.76	trans-dorsal length
PVL	44.0	40.9	15	40.8	39.3	42.7	0.92	9	40.9	39.3	42.0	0.86	6	40.7	39.8	42.7	1.08	pre-pelvic length
PAL	77.0	73.5	15	76.6	73.5	79.2	1.99	9	76.5	73.5	79.2	2.32	6	76.8	74.1	78.4	1.55	pre-anal length
TAL	88.4	87.1	15	88.9	86.2	100.2	3.26	9	89.5	86.2	100.2	4.13	6	88.0	86.6	89.4	0.94	trans-anal length
Eye	9.2	10.0	15	10.8	8.5	12.9	1.15	9	10.4	8.5	11.6	1.03	6	11.4	9.8	12.9	1.09	eye diameter
SNL	12.2	12.3	15	10.2	8.8	12.4	1.24	9	10.4	8.8	12.4	1.39	6	9.8	8.9	12.2	0.95	snout length
CHD	11.4	13.5	15	11.8	10.0	13.5	1.16	9	12.3	11.0	13.5	1.00	6	11.1	10.0	12.4	1.06	cheek depth
POD	5.7	4.6	15	4.9	3.1	6.2	0.91	9	5.1	3.5	6.2	0.93	6	4.6	3.1	5.7	0.88	pre-orbital depth
IOW	8.8	9.8	15	9.3	8.3	10.0	0.47	9	9.5	9.3	10.0	0.24	6	9.1	8.3	9.9	0.63	inter-orbital width
UJL	14.9	17.0	15	13.6	9.8	17.0	2.12	9	14.2	11.3	17.0	1.14	6	12.6	9.8	14.9	1.87	upper-jaw length
LJL	17.9	16.1	15	15.5	11.1	19.3	2.22	9	15.5	13.3	19.3	2.25	6	15.3	11.1	18.0	2.38	lower-jaw length
CPD	16.6	15.9	15	16.9	14.8	18.7	1.04	9	17.3	15.9	18.7	0.85	6	16.3	14.8	17.4	1.04	caudal-peduncle depth
CPL	11.9	12.4	15	13.0	10.3	16.3	1.71	9	13.8	11.9	16.3	1.73	6	11.9	10.3	12.6	0.84	caudal-peduncle length
DFB	54.1	59.4	15	59.9	54.1	62.6	1.77	9	60.3	58.8	62.6	1.32	6	59.3	54.1	62.0	2.30	dorsal-fin base length
AFB	19.9	20.5	15	19.4	17.9	21.3	1.06	9	19.6	17.9	20.6	0.98	6	19.1	18.1	21.3	1.16	anal-fin base length
PecL	24.8	30.6	15	27.6	22.0	31.3	2.56	9	27.7	24.0	30.6	2.12	6	27.5	22.0	31.1	3.33	pectoral-fin length
PelL	29.2	29.9	15	31.7	25.4	43.7	5.50	9	34.8	27.5	43.7	5.12	6	27.2	25.4	29.2	1.06	pelvic fin length
PeISL	9.9	10.3	15	12.9	9.9	18.5	2.02	9	12.5	10.3	14.0	1.26	6	13.4	9.9	18.5	2.87	pelvic-fin spine length
LDS	17.1	16.1	15	14.9	12.0	19.1	1.91	9	15.7	12.9	19.1	1.91	6	13.8	12.0	17.1	1.27	last dorsal spine length
LAS	13.9	12.6	15	14.2	12.6	16.9	1.21	9	14.5	12.6	16.9	1.40	6	13.8	12.7	15.0	0.83	last anal spine length



Fig. 2. *Apistogramma megastoma* sp. n., MUSM 52450, paratype, male, 76.3 mm SL; *top*: 2 days after preservation, *bottom*: 6 months after preservation. December 2013.

caudal peduncle 21.6 to 51.6 % (mean 31.3 %) deeper than long, correlation of allometry strongly negative with increasing size (SL). Scales in median E1 row 21 to 23 [21 (n=9), 22 (n=6), 23 (n=1)]; 16 circumpeduncular scales (n=16). Lateral-line scales in series E4, E2, and E1, exceptionally some in E3, counts ranging from 13 to 16/ 0 to 3 / 4 to 8, with frequencies as follows: 13/1/7 (1), 13/2/6 (1), 13/2/8 (1), 14/0/6 (1), 14/0/7 (1), 15/1/5 (1), 15/1/8 (1), 15/2/4 (1), 15/2/6 (1), 15/2/7 (1), 15/3/8 (1), 16/1/6 (1) (3 IIAP- and 3 MUSM-specimens not included). Vertebrae 11 + 11 = 24 (7), 11 + 12 = 23 (3), 12 + 12 = 24 (1), 12 + 13 = 25 (1)² (fig. 5). Jaw teeth unicuspid, erect, cusp strongly recurved; teeth of outer row significantly larger than inner row in males, in females only slightly larger or similar in size.

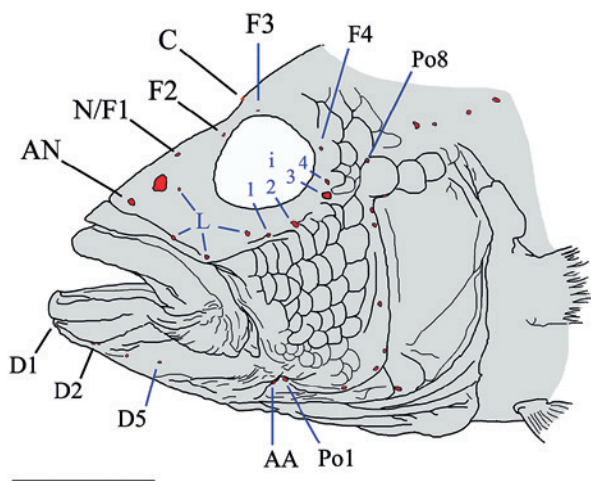
Other details of dentition, gill rakers, and pharyngeal elements have been excluded from this study, as forming part of further studies still in progress.

Coloration of preserved specimens: (described after preservation for six months and three to five years in 75% ethanol; only slight differences in intensity of coloration

² In the sister species *A. barlowi* lateral line scale frequencies (taken from the type material and one authorized specimen) are as follows: 11/0/5 (1), 12/0/5 (1), 12/1/6 (1), 13/0/5 (1), 13/0/6 (1), 13/0/7 (2), 13/1/3 (1), 13/1/5 (1), 13/1/6 (1), 13/1/7 (1), 13/2/6 (1), 13/3/6 (1), 14/0/3 (2), 14/0/6 (1), 14/0/7 (4), 14/0/8 (1), 14/1/7 (1), 14/1/8 (1), 15/0/4 (1), 15/0/6 (2), 15/0/7 (3), 16/0/8 (1), 17/0/6.



Fig. 3. *Apistogramma megastoma* sp. n., MUSM 52451, paratype, female, 58.2 mm SL; *top*: 2 days after preservation, *bottom*: 6 months after preservation. December 2013.



visible after different times of conservation, although fresh material from 2013 slightly darker overall) (figs. 1–3)

Basic colour of body predominantly fairly uniform light brownish, in all specimens darker on dorsum, in small specimens more greyish. Scales on body darker on base and centre, with light, comparatively broad margin

← **Fig. 4.** *Apistogramma megastoma* sp. n., MUSM 52450, 76.3 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–i4**: post-lachrymal infraorbital pores; **L**: lachrymal pores; **N/F1**: pore shared by the nasal and first frontal *lateralis* canal; **Po1–Po8**: preopercular pores.

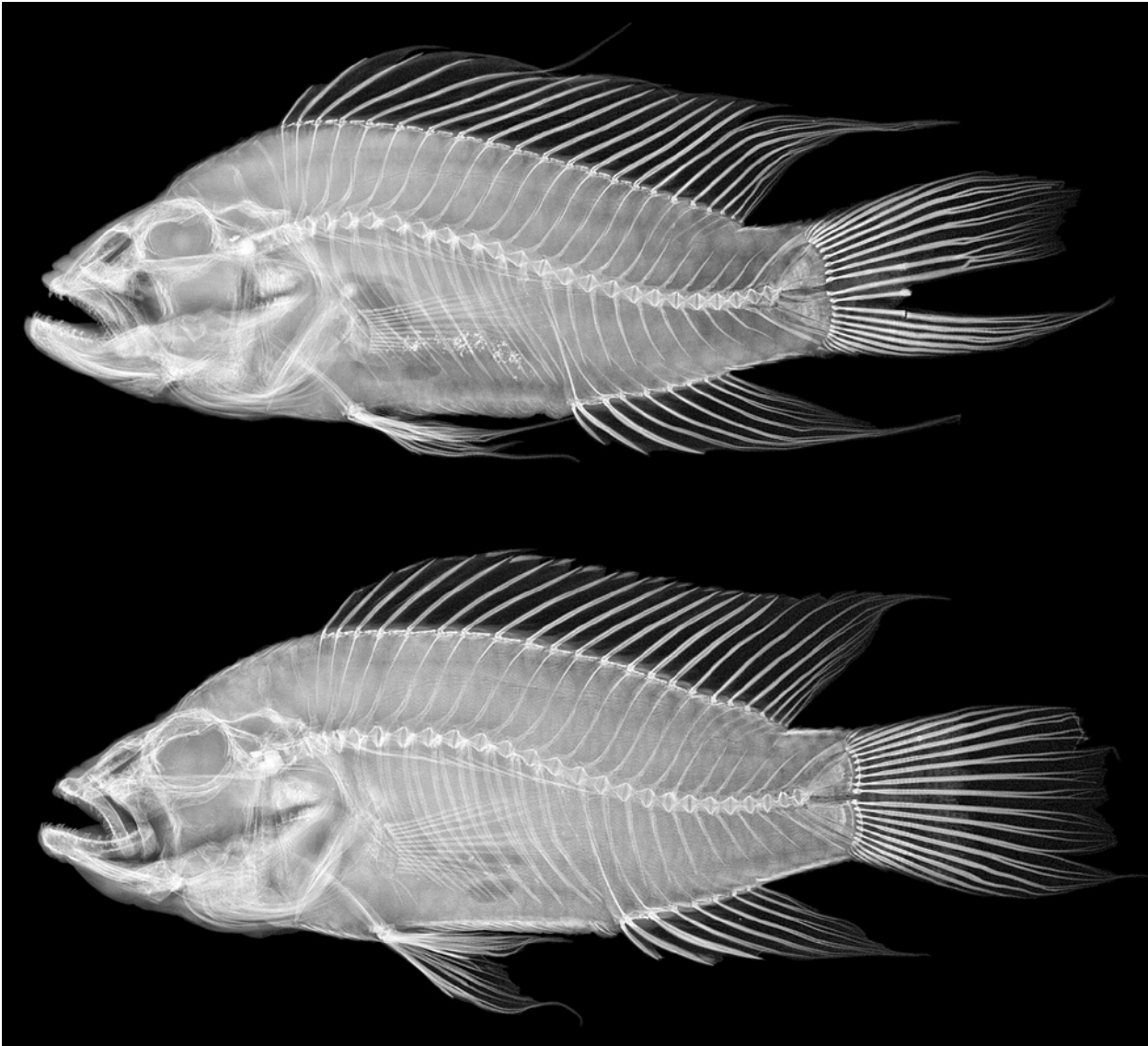


Fig. 5. *Apistogramma megastoma* sp. n., MUSM 52450, male, 76.3 mm SL (*top*); MUSM 52451, female, 58.2 mm SL (*bottom*). Digital x-rays: Mario Richter.

on exposed edge; margin about fifth to third width of visible part of scale along median horizontal line, broadest in mid-lateral scale rows, narrowest on anterior part of dorsum; in some specimens preserved for longer time light margin counter-shaded by dark brown submarginal line. Basic colour of lips, unscaled lower parts of cheeks, preoperculum, infraorbital, lower jaw, pectoral-fin base, and breast bluish white with numerous small grey, brown, or black chromatophores; significantly darker in largest specimens, giving dusky to dirty grey impression; anterior parts of lips generally darker than posterior. In some specimens distinct blackish interorbital stripe with widened oval to squarish centre and widened edges close to orbitals. Preorbital, scaled parts of cheeks, and operculum light greyish to brownish; operculum with more greyish area directly above black cheek stripe. Cheek (lachrymal) stripe in both sexes about pupil width at origin between foramina 1 and 2 of posterior orbital of suborbital series (for terminology see KULLANDER, 1987),

remaining similar width for entire extent in all males, in several females becoming much wider (frequently up to orbit diameter) running backwards across posterior lower half of cheek, covering most to all of area to lower posterior margin of operculum. Blackish or dark grey snout stripe from orbit to upper lip, about half width of cheek stripe at orbit, significantly wider (1.5 times) at anterior end close to upper-lip fold, visible in few specimens only. Chin and central parts of branchiostegal membrane grey in normal mood, blackish in aggression. No distinct supraorbital stripe, but completely black or dark grey (fresh material) or chestnut brownish (preserved), area from interorbital to dorsum below first dorsal spine, in all cases significantly darker than rest of upper body. Iris dark, blackish or bluish grey in dorsal half, remainder light greyish brown or beige; in some (fresh) specimens pupil with golden, in remainder light brown margin. Abdominal stripes and small anal spot present in most female specimens studied. Lateral band, if present, black-



Fig. 6. For comparison: *Apistogramma barlowi*, MUSM 52455, male, 59.2 mm SL. Digital x-ray: L. Fels, N. Leiwes & C. Mühle.

ish or dark brown with centres of scales on caudalmost half slightly lighter than edges, straight, extending from posterior edge of orbital to just above centre of caudal-fin base, about one scale high in anterior third, covering complete height of row E1 scales, overlapping lower quarter of row E2 scales and upper third of row 0 scales, widening to about 1.5 times scale height posterior to anal opening and covering full height of row E1 and upper half of row 0 scales; absent in most larger males. Seven vertical bars on body visible only in few individuals; bars 3 to 7 equally wide below and above lateral band; bar 2 narrower below lateral band, merging above it with bar 1 to form conspicuous subdorsal patch; all bars more conspicuous on dorsal part of body; intervals about third width of bars; upper part of bars 2 and 3 merging roughly at lateral band producing Y- or V-shaped pattern below dorsal-fin base. All female specimens without vertical band on lower half of body at position of vertical bar 2 (*vs.* present in *Apistogramma barlowi*), few with small black area between and around bases of ventral fins. Few specimens with faint upright oval lateral spot at position of vertical bar 3, exceptionally area below lateral band at position of vertical bar 3 slightly darker than rest of ventral body between pectoral- and anal-fin bases; both markings always missing in large males. Dorsal spots visible in some specimens at positions of vertical bars 1 to 5, small, restricted to scale rows (E4 to E5) next to dorsal-fin base. No caudal-peduncle spot visible in any type specimens (but see coloration of live specimens), but in some entire caudal peduncle slightly darker greyish compared to rest of body³. Under microscope caudal fin in males with 9 to 12 vertical-band-like rows of

small hyaline rectangular light grey melanophores on membranes between rays; pattern absent in females, but anterior third to half of fin (*vs.* quarter to third in *A. barlowi*) yellowish to orange (fresh material only) or milky white, (unlike in *A. barlowi*) extending at least two thirds length of rays (to about where principal rays branch) or frequently to end of rays, colour sharply separated from rest of transparent hyaline fin (*vs.* washed-out transition zone in *A. barlowi*). Base colour of all other fins likewise cloudy milky to pale grey or, in some larger males, light brownish. Pectoral transparent, slightly milky whitish, with few finely greyish chromatophores on fin rays. Ventral fin in males without clear dark markings, but duskier along spine with whitish (in fresh material) to orange tip; in females anterior part along spine and adjacent soft rays densely speckled with dark black chromatophores, leaving only narrow strip of fin, usually less than 20% fin width, yellow or whitish posteriorly. Anal fin light milky grey, in larger males with faint greyish to blackish edging and 4 to 6 light vertical bars on soft portion (missing in smaller males), in females outer two thirds translucent hyaline. Coloration of dorsal fin uniform greyish, without marginal or other bands, or other distinct markings except first membrane in males significantly darker blackish and soft portion with up to 8 light hyaline vertical bars; in females first 2 to 3 membranes blackish. Basal part of teeth milky or glassy translucent, distal third reddish brown with dark brown tip.

Coloration of live specimens and sexual dimorphism: (figs. 7–19) Information and illustrations restricted to diagnostic elements, for supplementary photographs of live specimens see RÖMER & RÖMER (2015).

Overall coloration strongly resembles that of *Apistogramma barlowi*, but with some diagnostic differences: *Apistogramma megastoma* sp. n. is highly sexually di-

³ But caudal spot regularly visible in several significantly smaller F₁ specimens.

Table 2. Biometric data for *Apistogramma megastoma* sp. n., taken from the type specimens and expressed in mm.

Coll. No.	Status	Sex	SL	TL	TLS	HL	HD	BD	HW	PDL	TDL	PPL	PAL	TAL	Eye	SNL	CHD	POD	IOW	UJL	LJL	CPD	CPL	DFB	AFB	Peel	Peil	PeiSL	LDS	LAS
MUSM 52450	PT	m	76.3	97.6	103.5	28.7	23.6	28.7	12.7	25.9	66.8	31.2	51.0	66.4	7.6	9.4	10.3	3.5	7.5	13.0	12.3	12.1	9.5	45.3	15.7	23.4	22.8	7.8	12.3	9.6
MUSM 52459	HT	f	61.9	78.9	82.3	21.5	16.3	22.6	11.6	23.3	55.6	27.3	43.3	54.7	5.7	7.5	7.1	3.5	5.4	9.2	11.1	10.3	7.4	36.6	12.3	15.3	18.1	5.2	10.6	8.7
MUSM 52451	PT	f	58.2	77.0	78.0	21.4	17.9	22.3	10.9	21.3	52.6	24.9	41.5	52.1	6.2	6.7	7.2	3.2	5.7	8.6	8.9	9.4	7.2	34.6	10.7	18.2	16.0	6.1	8.6	7.4
MTD F 32704	PT	m	57.0	76.6	79.1	20.5	17.7	21.7	10.8	21.5	51.6	22.8	38.8	49.7	4.8	5.0	7.2	3.5	5.3	9.3	11.0	10.1	7.2	35.1	11.5	15.1	18.7	7.7	7.4	9.6
MTD F 32702	PT	m	56.1	73.6	81.9	19.7	17.3	23.1	10.5	21.5	51.0	22.7	37.9	48.3	5.3	5.4	7.4	3.0	5.2	7.2	9.9	9.7	7.2	33.2	10.8	16.0	24.5	6.4	9.0	8.1
MUSM 52449	PT	m	55.9	74.8	82.5	20.7	17.8	24.5	11.2	21.8	51.6	23.5	39.6	49.8	6.3	6.9	6.9	2.3	5.4	7.1	7.8	10.5	8.0	35.0	11.5	15.0	21.1	7.0	9.6	7.56
MTD F 32642	PT	m	50.5	67.0	80.0	17.7	14.3	18.4	9.3	18.0	45.0	20.6	35.3	44.6	5.9	5.0	5.6	1.8	4.7	7.1	7.0	8.4	6.3	29.7	10.2	12.1	16.5	6.6	6.6	7.2
MUSM 52452	PT	m	48.6	65.3	71.7	19.2	15.0	18.7	8.9	19.7	45.1	20.1	32.7	42.7	5.1	5.7	6.5	3.0	4.6	8.2	8.7	8.4	5.8	29.9	10.0	14.8	19.7	5.9	9.23	7.5
MUSM 52453	PT	f	48.3	61.8	61.8	18.5	14.5	18.7	8.7	18.1	43.8	19.3	33.8	42.4	5.6	4.5	5.2	2.2	4.3	5.6	8.7	8.3	5.9	29.7	8.9	13.9	12.9	8.9	7.4	6.9
MTD F 32701	PT	f	48.1	63.2	63.9	17.1	14.5	18.2	9.0	18.3	43.8	19.1	34.0	42.5	4.7	4.9	6.0	2.3	4.8	7.0	7.3	8.1	5.8	28.7	9.1	13.5	13.4	7.2	6.78	6.34
MUSM 52456	PT	f	44.3	58.8	59.8	16.5	13.9	18.3	8.1	16.4	40.3	18.2	29.8	38.4	5.1	4.4	4.8	2.4	4.0	5.8	7.5	7.7	5.1	27.5	9.4	13.1	11.3	5.4	6.2	6.3
IIAP 302870	PT	m	41.7	55.2	57.2	15.3	12.4	16.0	7.6	15.8	38.3	17.3	29.8	36.9	4.1	3.8	4.8	2.3	4.0	6.0	5.6	7.3	6.4	24.8	8.0	12.0	11.5	4.8	6.2	5.2
MTD F 32700	PT	f	39.7	52.6	52.6	14.6	11.1	13.8	7.7	15.1	35.4	16.0	28.0	35.0	5.1	3.5	4.0	1.7	3.4	4.8	4.4	5.9	4.1	22.7	7.2	8.8	10.8	4.9	4.78	5.4
IIAP 302869	PT	m	38.2	50.8	50.8	14.6	11.8	15.8	6.8	15.6	35.3	15.0	27.5	34.0	4.1	4.0	4.4	2.1	3.8	4.6	5.2	6.5	6.1	22.9	7.1	10.2	12.8	5.4	6.2	5.7
MUSM 52454	PT	f	36.7	47.6	47.6	14.1	10.6	13.4	7.1	15.2	33.3	14.8	25.3	32.2	4.4	3.3	3.7	1.2	3.1	3.6	5.7	5.6	4.6	20.6	7.1	9.3	10.4	4.5	4.6	5.5
IIAP 302871	PT	m	36.1	48.9	48.9	13.4	11.4	14.3	6.8	14.1	33.0	15.11	26.0	32.0	4.1	3.4	4.0	1.6	3.4	4.1	5.1	6.5	5.9	21.7	6.5	9.6	12.4	5.0	5.8	5.5

morphic and dichromatic. Mature males (figs. 7–11) are about one and a half to two times larger than females (figs. 12–17) and initially have a truncate, later a clearly lyrate caudal fin (figs. 7–10), while in juvenile males and females the latter is rounded truncate (fig. 13), in older female individuals with asymmetric extensions (absent in *A. barlowi*), that on the upper lobe significantly longer than that on the lower lobe of the fin (fig. 14). In males the hyaline caudal fin typically exhibits a fine barring pattern of ten bluish vertical lines (absent in *A. barlowi*) extending on to the central part of the fin and varying from about 80 % to the full height of it, depending on the individual (figs. 7–10). The translucent yellowish caudal fin of females (figs. 12–16) never exhibits such a pattern.

The dorsal fin in males is serrate, with noticeably extended membranes for the entire length of the fin and the soft-rayed portion prolonged to a point (fig. 7). In some adult males the tips of the fin membranes may exhibit an orange colour, likewise the tip of the soft portion of the dorsal fin (fig. 8). The first five, occasionally six, dorsal-fin membranes in females are pointed but not serrate (*vs.* truncated in *A. barlowi*), with no extended membranes (figs. 14–16). The membranes of the first to second and the lower half of the second or third spine to the soft portion of the fin, are usually sooty. The remaining membranes from the first to the sixth are hyaline pinkish to violet (*vs.* uncoloured in *A. barlowi*); there is a yellowish margin and bluish sub-marginal band along the spinous part of the fin, while the remainder is yellowish with small light bluish spots along the spines. The ventral fins in males are transparent blue at their base to yellowish distally, with orange tips; by contrast those of the female are nearly entirely black with a narrow posterior yellow margin. Adult males have a pattern of light blue and red stripes and spots on the head and gill covers (fig. 7), in some individuals with an irregular red dotted pattern extending on to the anterior third of the body (always absent in *A. barlowi*). Sexually mature females usually have a yellowish coloured body, and typically exhibit a broad black cheek band, black ventral fins and anterior dorsal spines, and exceptionally lateral band (subordinated individuals), but no other black markings (figs. 12–15); by contrast dominant mature males suppress most of these black markings (fig. 7), but may express the broad lateral band and a narrow interorbital stripe and cheek band (figs. 8–9). On becoming territorial, females engage in intense intrasexual fights during which the anterior part of the head develops blackish coloration from the tip of the snout to a vertical behind the orbit. The extent of this blackish head coloration varies individually and could be observed repeatedly only during this early stage of breeding behaviour. Females at any stage of brood care may exhibit seven light brownish to greyish vertical bars (fig. 15), more prominent in subordinated individuals and when potential predators are present; these bars are visible only exceptionally in males when subordinated by dominant non-brooding females (fig. 8). During the

Table 3. Morphometric counts for *Apistogramma megastoma* sp. n., taken from the type specimens; SL given in mm.

Coll.No.	Status	DNA-No.	Sex	SL	DF (h)	DF (s)	DF (n)	AF (h)	AF (s)	PF (h)	PF (s)	PecF	CF	LRS	abbreviations
MUSM 52450	PT	UR.101.2318	m	76.3	15	7	0	3	7	1	5	12	16	22	
MUSM 52459	HT	UR.101.2406	f	61.9	15	7	1	3	7	1	5	12	16	22	HT = Holotype
MUSM 52451	PT	UR.101.2319	f	58.2	15	8	0	3	6	1	5	12	16	21	
MTD F 32704	PT	UR.101.2286	m	57.0	15	7	2	3	6	1	5	12	16	21	PT = Paratype
MTD F 32702	PT	UR.101.2085	m	56.1	15	7	0	3	7	1	5	12	16	21	
MUSM 52449	PT	UR.101.2038	m	55.9	15	7	0	3	6	1	5	12	16	21	AT = Allotype
MTD F 32642	PT	UR.101.2296	m	50.5	15	7	0	3	7	1	5	12	15	22	
MUSM 52452	PT	UR.101.2290	m	48.6	15	7	0	3	7	1	5	12	16	21	AF = anal fin
MUSM 52453	PT	UR.101.2292	f	48.3	16	7	0	3	6	1	5	12	16	23	
MUSM 52456	PT	UR.101.2291	f	44.3	15	8	0	3	6	1	5	12	16	22	CF = caudal fin
MTD F 32701	PT	UR.101.2084	f	48.1	15	6	1	3	6	1	5	12	16	21	
IIAP 302870	PT	IIAP 302870	m	41.7	15	7	0	3	6	1	5	12	16	21	DF = dorsal fin
MTD F 32700	PT	MTD F 32700	f	39.7	15	6	1	3	6	1	5	12	16	22	
IIAP 302869	PT	IIAP 302869	m	38.1	15	7	0	3	6	1	5	12	16	21	PecF = pectoral fin
MUSM 52454	PT	UR.101.2289	f	36.7	17	6	0	3	6	1	5	12	16	22	
IIAP 302871	PT	IIAP 302871	m	36.1	15	7	0	3	6	1	5	12	16	21	PF = pelvic fin

Table 4. Biometric data for *Apistogramma megastoma* sp. n. and *A. barlowi* for comparison; taken from the type specimens and expressed as % SL; SL given in mm.

	<i>Apistogramma megastoma</i> sp. n.						<i>Apistogramma barlowi</i>						abbreviations
	HT	(n)	mean	min.	max.	st.dev.	HT	(n)	mean	min.	max.	st.dev.	
SL	61.9	15	49.0	36.1	76.3	10.66	60.0	32	43.0	28.8	63.7	9.15	standard length
TL	127.5	15	132.1	127.5	135.4	2.19	129.4	32	131.6	118.7	147.0	4.70	total length
TLS	133.0	15	138.3	127.8	158.5	8.19	137.6	32	133.9	121.7	147.0	5.26	total length plus streamer
HL	34.7	15	37.0	35.0	39.5	1.26	34.4	32	36.8	32.8	42.7	2.03	head length
HD	26.4	15	30.3	26.4	31.9	1.17	28.3	32	29.5	26.7	35.5	1.74	head depth
BD	36.5	15	38.8	34.7	43.8	2.32	36.8	32	36.2	32.0	41.7	2.25	body depth
HW	18.8	15	18.5	16.6	20.0	0.79	19.5	32	19.6	17.5	23.7	1.44	head width
PDL	37.6	15	38.1	34.0	41.4	1.95	37.8	32	39.3	36.5	43.1	1.67	pre-dorsal length
TDL	89.8	15	90.8	87.6	92.7	1.39	88.9	32	89.4	87.0	92.5	1.43	trans-dorsal length
PVL	44.0	15	40.8	39.3	42.7	0.92	41.1	32	41.6	38.5	47.3	1.72	pre-pelvic length
PAL	77.0	15	76.6	73.5	79.2	1.99	75.7	32	77.1	72.6	82.6	2.45	pre-anal length
TAL	88.4	15	88.9	86.2	100.2	3.26	86.7	32	87.6	82.1	96.4	2.76	trans-anal length
Eye	9.2	15	10.8	8.5	12.9	1.15	9.0	32	10.5	8.8	12.9	0.93	eye diameter
SNL	12.2	15	10.2	8.8	12.4	1.24	12.5	32	11.3	8.7	14.1	1.34	snout length
CHD	11.4	15	11.8	10.0	13.5	1.16	11.0	32	10.6	8.7	12.6	0.97	cheek depth
POD	5.7	15	4.9	3.1	6.2	0.91	6.4	32	5.2	4.0	6.4	0.75	pre-orbital depth
IOW	8.8	15	9.3	8.3	10.0	0.47	10.9	32	9.3	7.7	12.0	1.00	inter-orbital width
UJL	14.9	15	13.6	9.8	17.0	2.12	15.3	32	13.9	8.8	17.7	1.75	upper-jaw length
LJL	17.9	15	15.5	11.1	19.3	2.22	17.3	32	16.8	12.5	19.8	1.59	lower-jaw length
CPD	16.6	15	16.9	14.8	18.7	1.04	16.0	32	16.1	11.6	18.1	1.17	caudal-peduncle depth
CPL	11.9	15	13.0	10.3	16.3	1.71	14.5	32	13.5	10.6	18.4	1.65	caudal-peduncle length
DFB	54.1	15	59.9	54.1	62.6	1.77	58.6	32	57.3	54.0	69.9	2.93	dorsal-fin base length
AFB	19.9	15	19.4	17.9	21.3	1.06	19.2	32	18.9	14.9	22.1	1.43	anal-fin base length
PecL	24.8	15	27.6	22.0	31.3	2.56	25.5	32	27.4	21.3	30.7	2.57	pectoral-fin length
PelL	29.2	15	31.7	25.4	43.7	5.50	28.1	32	27.1	21.4	39.3	3.68	pelvic-fin length
PelSL	9.9	15	12.9	9.9	18.5	2.02	9.3	32	11.7	9.3	13.4	1.03	pelvic fin spine length
LDS	17.1	15	14.9	12.0	19.1	1.91	15.4	32	13.6	9.5	18.0	1.96	last dorsal spine length
LAS	13.9	15	14.2	12.6	16.9	1.21	13.6	32	13.9	11.6	16.1	0.97	last anal spine length

early stages of brood care (i. e. the larval stage) some females exhibit greyish brown dorsal spots (fig. 14), in some cases merging with a mid-lateral spot on vertical bar 3, creating a band-like pattern on the body above the lateral band, slightly resembling a similar pattern known from *Apistogramma hippolytae* KULLANDER, 1982 (figs. 12 & 16).

Females caring for free-swimming fry may exceptionally exhibit a few blackish scales on the base of the pectorals (fig. 14), always combined with five to seven, rarely eight, rows of (depending on the degree of aggression) round to drop-shape spots or dashes on the flanks, irregularly following lower and upper edges of scales (cf. figs. in RÖMER & RÖMER, 2015, pp. 29 & 30). Analyses of



Fig. 7. *Apistogramma megastoma* sp. n., adult male; not preserved; coloration while aggressively displaying to mouth-brooding female (behind).



Fig. 8. *Apistogramma megastoma* sp. n., adult male; not preserved; vertical bars are visible only in subdominant males subordinated by aggressive dominant females.

large series of photographs of several females showing this colour pattern have revealed that these line-forming spots or dashes are positioned on the outer radius of the scales a short distance from their upper or lower edges. Female *A. barlowi* may also sometimes exhibit black spots generally reminiscent of those described here, but they never follow the scale edges as in *Apistogramma megastoma* sp. n., but are randomly distributed over the abdomen, never forming such regular lines. In females in a high state of aggression the ground colour changes from bright yellow to whitish yellow, with a pronounced

narrow straight black interorbital stripe, a roughly triangular blackish area between the upper margins of the orbits and extending halfway to the start of the dorsal-fin base, a broad black cheek stripe, black first two to three dorsal membranes, and black ventral fins. Males also exhibit an interorbital stripe, as well as greyish lips and branchiostegal stripes, and bluish cheeks and gill covers (fig. 11). In subdominant mature males the lateral band may occasionally be expressed in combination with a faint round greyish caudal spot, which covers about a third of the height of the caudal base (figs. 8–9).



Fig. 9. *Apistogramma megastoma* sp. n., adult male; not preserved; coloration of non-territorial subdominant male in neutral mood.



Fig. 10. *Apistogramma megastoma* sp. n., adult male; not preserved; coloration of dominant territorial male in neutral mood.

Less obviously, the colour of the teeth and adjacent epidermal tissue may be used as an additional character (taken from live photographs) to differentiate *Apistogramma megastoma* sp. n. from its congener *A. barlowi*: in most *Apistogramma* species this internal skin tissue is more or less uniformly whitish to light grey leaving the brownish (in most species) tips of the teeth visible. In species related to *Apistogramma cacatuoides* HOEDEMAN, 1951 or *A. nijsseni* KULLANDER, 1979, which develop fleshy hypertrophied lips, the tooth rows are deeply embedded in fleshy skin tissue, which is, however, pushed aside dur-

ing feeding activities such as picking larger insects from the bottom. The teeth of *Apistogramma barlowi* conform to this pattern. But adult specimens of *Apistogramma megastoma* differ significantly from this norm, as they usually exhibit yellowish (males) (fig. 17) or reddish (females) teeth with reddish brown tips. In addition, unique within the genus, the inner mouth tissue embedding the teeth of brood-caring females turns deep red (fig. 18).

Systematic relationships: The systematic positioning suggested here has to be seen as provisional pending



Fig. 11. *Apistogramma megastoma* sp. n., adult male; not preserved; typical head pattern of slightly aggressive dominant male, with pronounced interorbital stripe and grey lips.

Fig. 12. *Apistogramma megastoma* sp. n., adult female; not preserved; typical coloration (including broad cheek stripe, dorsal spots, and lateral spot) while guarding fry immediately after free-swimming.

Fig. 13. *Apistogramma megastoma* sp. n., adult female; not preserved; aggressive coloration while guarding about 2-week-old fry.

Fig. 14. *Apistogramma megastoma* sp. n., adult female; not preserved; highly aggressive coloration (expressing broad cheek stripe, nearly completely black ventral fin, dorsal spots, and spot line pattern) while guarding fry in presence of *Crenicichla regani*, about 1 week after release from mouth.

Fig. 15. *Apistogramma megastoma* sp. n., adult female; not preserved; picking up fry as juvenile *Crenicichla regani* approaches; typical coloration when predators are present, including broad cheek stripe, vertical bars, and spot line pattern.

Fig. 16. *Apistogramma megastoma* sp. n., adult female; not preserved; typical brownish coloration after losing fry, including broad cheek stripe, black dorsal spots, and lateral spot.



17



18



19

Fig. 17. *Apistogramma megastoma* sp. n., adult male; not preserved; portrait of male in frontal threat showing coloration of teeth and inner mouth tissue.

Fig. 18. *Apistogramma megastoma* sp. n., adult female; not preserved; frontal portrait of brood-caring female showing coloration of teeth and adjacent tissue.

Fig. 19. *Apistogramma megastoma* sp. n., adult male; not preserved; portrait showing extreme size of mouth when protruded.

more precise analysis on completion of further ongoing morphological, behavioural, and genetic⁴ studies (QUÉROUIL *et al.*, 2016). But it is currently known that *Apistogramma megastoma* sp. n. shares typical morphological features of the members of the *Apistogramma cacatuoides* complex within the *Apistogramma steindachneri* lineage (nomenclature following RÖMER, 2006c), with *Apistogramma barlowi* seemingly its closest relative. On

⁴ Results of initial, as yet unpublished, genetic analysis also clearly separate *Apistogramma megastoma* sp. n. from *A. barlowi*.

the basis of cluster analysis studies of the phylogenetic relationships within the genus (RÖMER, 2006c), these two species, along with a further, as yet undescribed, form, constitute the *Apistogramma barlowi* subcomplex within this species-rich phylogenetic group. This subcomplex represents the basal sister group to the remaining subcomplexes and species of the *Apistogramma cacatuoides* complex. In opsite to this, resulting on molecular analysis (TOUGARD *et al.*, submitted), *A. barlowi* and *A. megastoma* sp. n. (referred to as *Apistogramma* sp. 7 in that paper) represent the basal sister group to species lumped in the *Apistogramma nijsseni* complex excluding *A. ca-*

catuoides to another clade, leaving the relationships in between this major branches partially unresolved and the necessity for further close inspection.

Etymology: The specific name *megastoma*, a composite noun in apposition, is derived from the Greek μέγα (mega) meaning large and στόμα (stoma) meaning mouth. The name refers to the exceptionally large mouth of the species, which enables it to perform mouth-brooding behaviour and swallow relatively large prey.

Distribution and Ecology: The species is known only from a number of Peruvian waters in an area southwest of Leticia, close to the northern border area between Peru and Brazil (fig. 20). At present confirmed finds and reliable ecological information relate solely to observations from a few small forest streams nearby made by VAN GENNE (2010a-b). MACA AUSBER (pers. comm.) claims to have collected *A. megastoma* sp. n. in various small streams in the Río Jutai drainage close to the Brazilian border, but this information still needs to be independently confirmed (RÖMER & RÖMER, 2015). Just as with *Apistogramma barlowi*, collecting sites for *A. megastoma* sp. n. are only sporadically productive. The fact that this species has not been caught by other collectors is an obvious result of the remoteness of the collecting sites, which can be reached only by boat or long distances on foot through the rain forest. On the basis of information provided by the collector (pers. comm.), the distribution of *Apistogramma megastoma* sp. n. is limited to small fast-flowing forest streams (*igarapés*) with crystal-clear water. VAN GENNE (2010a-b) provides information more indicative of blackwater habitat species. On the basis of information given in RÖMER & HAHN (2008) for *A. barlowi*, this may be indicative of comparable ecological conditions in the habitat of *Apistogramma megastoma* sp. n. Given this limited data on the distribution and ecology of *Apistogramma megastoma* sp. n., further field studies are required.

Biology: A detailed overview of the behaviour of this species in captivity has been given elsewhere (RÖMER & RÖMER, 2015). The most important behavioural features are the highly ritualised threat behaviour and larvophilic mouth-brooding. The ritualised frontal threat behaviour seen in *Apistogramma barlowi* males, such as digging and building little sand piles, has not been observed in *Apistogramma megastoma* sp. n.. Instead *Apistogramma megastoma* sp. n. threatens its opponents frontally as well as laterally with its mouth wide open (*vs.* closed in *A. barlowi*) (fig. 17, cf. also figs. in RÖMER & RÖMER, 2015: p.28). During aggressive interactions male *Apistogramma megastoma* sp. n. often dispense with frontal threat behaviour and immediately proceed to lateral threat (fig. 7), while *Apistogramma barlowi* may perform highly ritualised frontal threat for long periods (up to several hours) before starting lateral threat. Females take their larvae into their mouths immediately after they hatch (from typical *Apistogramma* p-type eggs; for terminology see WICKLER, 1956) (fig. 15). Unlike in *Apistogramma barlowi*,

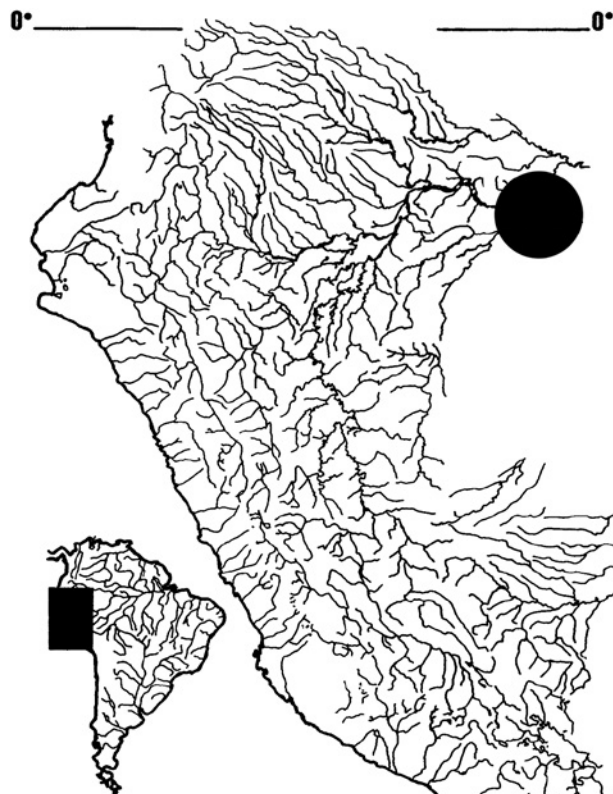


Fig. 20. Map of Peru showing known distribution of *Apistogramma megastoma* sp. n., type locality indicated by dot.

the eggs of *Apistogramma megastoma* sp. n. are neither enlarged nor reduced in number. As otherwise observed within the genus only in *Apistogramma barlowi*, female *Apistogramma megastoma* sp. n. keep their larvae inside the mouth almost constantly during their further development to the free-swimming stage. The larvae are put down regularly only to permit feeding. Unlike in *Apistogramma barlowi*, in *Apistogramma megastoma* sp. n. no facultative mouth-brooding by males or any type of attempt at it has been registered during our ongoing behavioural studies to date, even under highly variable maintenance conditions (cf. also RÖMER & HAHN, 2008; RÖMER & RÖMER, 2015): unlike what has been observed in *A. barlowi*, strong current apparently has no effect as regards inducing males to participate in direct brood care. In our opinion *Apistogramma megastoma* sp. n. has proved to be an exclusively maternal mouth-brooding species, further distinguishing the species from its congener *Apistogramma barlowi*, in which both parents may be involved in larval mouth-brooding behaviour. To date mouth-brooding in the genus is known only from these two species.

Discussion

Amongst the described species of *Apistogramma* there is only one that may morphologically be mistaken for the new species described here: *Apistogramma barlowi* (cf.

figs. in RÖMER & HAHN, 2008; RÖMER & RÖMER, 2015). Females of that species may be easily distinguished from *Apistogramma megastoma* sp. n. by the broad black band visible on the breast immediately posterior to the pectoral fins at the position of vertical bar 2; this black breast band is always absent in female *Apistogramma megastoma* sp. n.. None of the specimens investigated, and none of the nearly 80 female F₁ and F₂ offspring of several wild-caught specimens of *Apistogramma megastoma* sp. n. known to us, has exhibited such a breast band, while this marking is present in almost all female *A. barlowi*. Female *A. barlowi* exceptionally lacking this band usually exhibit an irregular pattern of black patches instead, as well as a significantly narrower cheek band, distinguishing them from the species described here. In addition, females of *Apistogramma megastoma* sp. n., unlike those of *A. barlowi*, exhibit a typical pattern of regular black dashes at the upper and lower edges of nearly every single body scale, creating a pattern of seven to nine dotted longitudinal lines extending for the complete height of the body (RÖMER & RÖMER, 2015, l. c.).

Along with *Apistogramma barlowi*, *A. megastoma* sp. n. can be differentiated from all other *Apistogramma* species (for specific details of the prior taxon see RÖMER & HAHN, 2008, for figures of other related taxa see RÖMER *et al.*, 2015) by its unique shape, proportionally much larger head and jaws, lack of regular rows of conspicuous black abdominal markings, overall coloration, and behaviour. The two species may be adequately differentiated from one other by their typical colour patterns, brooding behaviour, and a number of morphometric data (table 4). Compared to their congener *A. barlowi*, both sexes in *Apistogramma megastoma* sp. n. exhibit a clear tendency to have a narrower head, shorter snout, smaller preorbital distance, narrower interorbital width, slightly longer dorsal- and anal-fin bases, larger eyes, and overall deeper body, all relative to head length, plus a deeper body and longer dorsal- and anal-fin bases relative to interorbital width (in % SL). Compared to *A. barlowi*, male *Apistogramma megastoma* sp. n. have higher counts for preopercular pores (up to 8), an overall deeper cheek with at least one (or two) more rows of cycloid scales, and a shorter caudal peduncle. But given the still limited material available, biometric correlations could not be sufficiently tested for significance.

However, according to KULLANDER (1980), biometric differences are of limited diagnostic value within the genus *Apistogramma*. We share this opinion, as it is obvious that miniaturisation within the genus has resulted in a reduction in scope for differentiation in overall morphology. HANKEN & WAKE (1993) have discussed physiological and evolutionary consequences of miniaturisation. Unlike insects, which may be able to modify several parts of their exoskeleton, miniaturised vertebrates such as fishes have a greatly reduced capacity for changing their basic morphology. Biometric differentiation in small or dwarf fishes may thus be the result solely of environmental impact and highly variable, as the miniaturisation process may itself be linked to adaptation to specific

ecological conditions rather than to major evolutionary fundamentals. This could perhaps trigger the direction of morphometric development randomly, making the resulting characters more or less useless for taxonomists. In fact, measuring larger series of specimens has shown significant variation in some proportions even within a particular *Apistogramma* species, sometimes clearly exceeding value ranges such as those recently used as diagnostic for species delimitation by MESA & LASSO (2011), for example. Hence the pattern of black in *Apistogramma* (KULLANDER, 1980) and – even more importantly – live coloration, where evolutionary development is most probably driven by sexual selection rather than other factors, remain decisive for species determination. Despite our arguments and those of KULLANDER, MESA & LASSO (2011) do not use live coloration as a standard diagnostic feature, but instead place excessive value on statistical differences derived from inadequate data, and worse, regard collecting sites as diagnostic features.

Nevertheless, the most striking synapomorphic characters of *Apistogramma megastoma* sp. n. and *A. barlowi* are undoubtedly the extraordinary reproductive behaviour (described at length by BREEZE, 2007; KOSLOWSKI, 2002; RÖMER, 2006a-c; RÖMER & RÖMER, 2015) and the disproportionately large head and mouth (cf. RÖMER & HAHN, 2008, this work) (figs. 1–3, 5, 7–11, 18 & 19). This is especially noteworthy, as LÓPEZ-FERNÁNDEZ *et al.*, (2012), using compound analysis methods in a complex study on the radiation of South American geophagines, found a clear association between morphology and substrate sifting: among geophagines, substrate sifting is associated with short, deep heads. All *Apistogramma* species are small-bodied taxa that sift substrate for detritus to a moderate extent (RÖMER, 2006), and thus theoretically should conform with the associated head morphology. But on the contrary, at least half of the species of *Apistogramma* have long heads with a massively enlarged mouth structure. As *Apistogramma* species are also highly adept at picking individual benthic invertebrates from the substrate, the evolutionary pressure exerted on their morphology by their sifting behaviour would appear to be less significant than might be expected from the above-mentioned study, and simply cancelled out by the effects of other factors.

STEEL & LÓPEZ-FERNÁNDEZ (2014) have argued that miniaturisation in cichlid species, including *Apistogramma*, may be the result of niche-forming processes triggered by predation by larger species in general. Particularly under high pressure from predatory species such as *Crenicichla* or *Hoplias*, the ability to employ a mouth-brooding strategy ought to be of significantly higher efficiency compared to the fry-guarding behaviour known from other *Apistogramma* species. Not only because the larvae, and later the growing fry, can be protected within the mouth, but also because the brood may rapidly be moved from the actual danger zone to a safer area in the guarding parent's (in this case the female's) territory. Hence mouth-brooding behaviour might be seen as an adaptive result of niche forming under (extreme) predation.

Several other species of the genus *Apistogramma* have developed extraordinary modifications of morphological characters. They include some that have evolved extreme sexual size polymorphism and enlarged mouth and jaws, probably as a result of mate choice systems (cf. ENGELKING *et al.*, 2010; RÖMER, 2006; RÖMER *et al.*, 2014). But none of these species has been identified as mouth-brooding (LINKE & STAECK, 2006; MAYLAND & BORK, 1997; RÖMER, 2000, 2006; RÖMER & RÖMER, 2015; STAECK, 2003). RÖMER & HAHN (2008) discussed environmental conditions that might be expected to trigger mouth-brooding behaviour in the genus *Apistogramma*, including predation. We have subsequently obtained convincing evidence from field and laboratory observations (BENINDE *et al.*, in prep.; RÖMER, unpubl. data), that most species of *Apistogramma* are highly adapted to survive at very low levels of dissolved oxygen. BENINDE *et al.* (in prep.) have found breeding females of various *Apistogramma* species in water with extreme oxygen levels significantly lower than 1 mg /l. *Apistogramma* females were regularly observed in extremely shallow, warm (up to 35 °C), nearly anoxic, and acid water. Here numbers of large predators were low to zero, and, as usually only one *Apistogramma* species was observed in such physiologically extreme environments, it is possible that even interspecific competition is lacking, creating conditions that constitute safe territory for brooding dwarf cichlid females (RÖMER *et al.*, 2012). Nevertheless, in addition to continuous predation, interspecific competition may be a key factor in developing mouth-brooding behaviour against a given environmental background. In fact we have repeatedly found up to four, occasionally up to six, species of *Apistogramma* living sympatric in a variety of Peruvian and Brazilian locations (see also RÖMER 2000, 2006).

The head and mouth morphology of *A. megastoma* sp. n. is obviously related to mouth-brooding behaviour, and must be seen as the result of (sexual) selection and a general tendency to maximise reproductive success and optimise biological fitness. Small fishes have few opportunities to maximise direct reproductive success. They may, if they produce numerous small eggs, spawn repeatedly with high frequency and carry out some form of brood care on eggs, larvae, and even fry in order to positively influence the survival probability of their offspring. SHINE & GREER (1991) have discussed what triggers variation in species clutch size. And in fact many miniaturised species have a significantly increased relative egg size, compensated by a reduction in egg numbers and intensified brood-care behaviour. *Apistogramma* species are among the smallest Neotropical fishes and have significantly enlarged eggs compared to smaller non-cichlid species like characids. In addition, it is also well known that mouth-brooding species regularly produce significantly larger eggs compared to their non-mouth-brooding congeners. Furthermore, large body size in mouth-brooding species appears to be positively correlated with either egg number or egg size, with larger head size resulting in increased carrying capacity during incubation of the brood. The combination of these factors may directly result in higher reproductive

success *per se*, and, in the long term, in individual biological fitness. Hardly surprisingly, the two larvophilic mouth-brooding *Apistogramma* species are among the largest species known from the genus (cf. RÖMER & HAHN, 2008). Only wild-caught males of the recently described *Apistogramma kullanderi* VARELLA & SABAJ PÉREZ, 2014 grow to a larger size (reproductive details are still unknown), while wild-caught females of *Apistogramma megastoma* sp. n. are the largest known in the genus.

All species of *Apistogramma* lay p-type eggs of fairly uniform size (RÖMER, 2001, 2006). The eggs of *Apistogramma barlowi* are significantly larger than those of all congeners (KOSLOWSKI, 2000, 2002, 2003; RÖMER, 2006; STAECK, 2004). Females of most *Apistogramma* species, e.g. *A. cactuoides*, may produce about 100 to more than 250 eggs in a single clutch (RÖMER, 2001), but even females of the smallest species within the genus, e.g. *A. wapisana* RÖMER *et al.*, 2006, may regularly produce up to 150 eggs in a single clutch (RÖMER, 2001 & unpubl. data). In *A. barlowi* the size difference results in a significantly smaller clutch size and lower number of offspring compared to non-mouth-brooding species: *A. barlowi* clutches rarely contain more than about 30 eggs. It might thus be expected that *Apistogramma megastoma* sp. n. would share larger egg size and low egg numbers with *A. barlowi*, but this is not the case. Egg size in *Apistogramma megastoma* sp. n. is intermediate between that of *A. barlowi* and non-mouth-brooding species such as *A. cactuoides*. Comparably sized females of *Apistogramma megastoma* sp. n. (~ 25-30 mm SL) may lay about twice as many or even more eggs than those of *A. barlowi*, with clutch size in large females (>40 mm SL) regularly exceeding 100 or more eggs (CIR & UR, unpubl. data). The fact that clutches of *A. megastoma* sp. n. are much larger and the eggs smaller is another diagnostic but far less obvious feature of the reproduction of the two mouth-brooding species. In aquarium experiments, independent of the size of eggs or clutch the reproductive success of *Apistogramma megastoma* sp. n. proved to be significantly dependant on the mouth-carrying capacity of the guarding female when fry needed to be picked up in the event that the potential predator *Crenicichla regani* PLOEG, 1989 approached the offspring (RÖMER, 2000, 2001). Based on our observations it may be speculated that bi-parental mouth-brooding behaviour, as observed in *Apistogramma barlowi*, has developed from shelter-brooding ancestors (with female brood care) via maternal mouth-brooding relatives such as *Apistogramma megastoma* sp. n., as a response to high predation pressure.

The case of *Apistogramma barlowi* and *Apistogramma megastoma* sp. n. suggests the desirability of increased systematic focus on species or species groups within the genus with large distributions (e.g. *A. agassizii*, *A. bitaeniata*, and *A. cactuoides*), as these may in fact represent species clusters with several cryptic species included. The phenomenon is not restricted to *Apistogramma*: recently genetic microsatellite marker inspection of the hatchetfish *Carnegiella marthae* (MYERS, 1927) in the Brazilian Rio Negro system has brought

to light two cryptic species within that taxon (PIGGOTT *et al.*, 2011). And the tools for closer inspection of *Apistogramma* species and populations are now available following the development of specific microsatellite markers (QUÉROUIL *et al.*, 2016).

Acknowledgements

We are grateful to Albertino Maca Ausber (Iquitos, Peru) for collecting part of the study material including type specimens, for providing field observations, and indicating locality data. The Gobierno Regional de Loreto, Dirección Regional de la Producción (DIREPRO) kindly gave permission for the export of preserved as well as live specimens to the IRD-IIAP within the LMI-EDIA project *Caracterización y Valorización de la diversidad ictiológica amazónica para el desarrollo de una piscicultura razonable*. We thank David Panduro, Carlos Reyes, Tulio C. Correa Girón, and Debbie Regategui Ocampo (DIREPRO) for constructive discussions, unreserved cooperation, and friendly support. Hernan Ortega, Ana Maria Cortijo, Giannina Isabel Trevejo, and Silvia Soledad Valenzuela (MUSM) kindly supported UR during inspection of the MUSM collection. We also thank Hernan Ortega (MUSM) and Axel Zarske (MTD F) for their cooperation in the depositing of voucher specimens and / or the opportunity for examination of comparative material in their collections. Laura Fels, Nina Leiwes, and Charlotte Mühle produced x-rays for the BiA of which some were analysed for this study. We are especially grateful to Roger Mori sr. and Sergio Llanos for their skilled help in collecting comparative specimens for the project *Biodiversity in Apistogramma* within the LMI, even under the most bizarre and uncomfortable conditions. We also thank Fred Chu Co (IIAP) for his kind help in solving organisational problems. David P. SOARES (Sisters, Oregon, US), Edgard Panduro Noronha [Ornamental Amazon Fish Aquarium (O.A.F.A.)], as well as Ina and Andreas Fröhlich (Deister Aquaristik), provided technical assistance in exportation of live voucher specimens. We also especially thank Mary Bailey (Credition, Devon, UK) and two anonymous reviewers for reading and helpfully commenting on this manuscript.

References

- DAVIS, J.I. & NIXON, K.C. (1992): Populations, genetic variation, and the delimitation of phylogenetic species. – *Systematic Biology*, **48**: 502–511.
- BREEZE, M. (2007): *Apistogramma* sp. “Maulbrüter”, the one and only. – *Cichlidae: The Journal of the British Cichlid Association*, **28** (5): 5–15.
- ELMER, K.R., LETHONEN, T., KAUTT, A.F., HARROD, C. & MEYER, A. (2010): Rapid sympatric ecological differentiation of crater lake cichlid fishes within historical times. – *BMC Biology* **8** (60): 2–15. [doi: 10.1186/1741-7007-8-60]
- ENGELKING, B., RÖMER, U. & BEISENHERZ, W. (2010): Intraspecific colour preference in mate choice by female *Apistogramma cacatuoides* Hoedeman, 1951 (Teleostei: Perciformes: Cichlidae). – *Vertebrate Zoology*, **60**(2): 123–138.
- HANKEN, J. & WAKE, D.B. (1993): Miniaturization of body size: Organismal consequences and evolutionary significance. – *Annu. Rev. Ecol. Syst.*, **24**: 501–19.
- KOSLOWSKI, I. (2000): Putzverhalten und Maulbrutpflege. – *DATZ* **53** (11): 18–21
- KOSLOWSKI, I. (2002): Maulbrutpflege bei einer Art der Gattung *Apistogramma*. – *DCG-Informationen, Sonderheft 1*: 27–29.
- KOSLOWSKI, I. (2003): Die Buntbarsche Amerikas. Volume 2. *Apistogramma & Co.* – Eugen Ulmer, Stuttgart: 320 pp.
- KULLANDER, S.O. (1980): A Taxonomical Study of the Genus *Apistogramma* REGAN, with a Revision of Brazilian and Peruvian Species (Teleostei: Percoidae: Cichlidae). – *Bonner zoologische Monographien* **14**. Zoologisches Forschungsinstitut und Museum Alexander König, Bonn: 152 pp.
- KULLANDER, S.O. (1980): Description of a new species of *Apistogramma* from the Rio Madeira system in Brazil (Teleostei: Cichlidae). – *Bulletin Zoologisch Museum, Universiteit van Amsterdam* **7** (16): 157–164.
- KULLANDER, S.O. (1981): Description of a new species of *Apistogramma* (Teleostei: Cichlidae) from the upper Amazon basin. – *Bonner zoologische Beiträge* **32** (1/2): 183–194.
- KULLANDER, S.O. (1986): Cichlid Fishes from the Amazon River Drainage of Peru. – *Swedish Museum of Natural History, Stockholm*: 431 pp.
- KULLANDER, S.O. (1990): *Mazarunia mazarunii* (Teleostei: Cichlidae), a new genus and species from Guyana, South America. – *Ichthyological Exploration of Freshwaters* **1** (1): 3–14.
- LEVITON, A.E., GIBBS, R.H., HEAL, JR. E. & DAWSON, C.E. (1985): Standards in herpetology and ichthyology: Part I. Standard symbolic codes for institutional resource collections in herpetology and ichthyology. – *Copeia* **1985** (3): 808–832.
- LINKE, H. & STAECK, W. (2006): Amerikanische Cichliden I. Kleine Buntbarsche. 8th compl. rev. edition. – *Tetra Verlag, Berlin-Velten*: 296 pp.
- LÓPEZ-FERNÁNDEZ, H., WINEMILLER, K.O., MONTAÑA, C. & HONEYCUTT, R.L. (2012): Diet-Morphology Correlations in the Radiation of South American Geophagine Cichlids (Perciformes: Cichlidae: Cichlinae). – *PlosOne* **7** (4): e33997: 14 pp.
- MAYLAND, H.J. & D. BORK (1997): Zwergbuntbarsche: Südamerikanische Geophagen und Crenicarinen. – *Landbuch Verlag, Hannover*: 187 pp.
- MENDELSON, T.C. & SHAW, K.L. (2012): The (mis)concept of species recognition. – *TREE* **27** (8): 421–427.
- MESA SALAZAR, L.M. & LASSO, C.A. (2011a): *Apistogramma megaptera* (Perciformes: Cichlidae), una nueva especie para la cuenca del Orinoco. – *Biota Colombiana* **12** (1) 2011: 19–29.
- MESA SALAZAR, L.M. & LASSO, C.A. (2011a): Revisión del Género *Apistogramma* Regan, 1913 (Perciformes, Cichlidae) en la cuenca del río Orinoco. – *Serie Editorial Recursos Hidrobiológicos y Pesqueros Continentales de Colombia*. Instituto de Investigación de Recursos Biológicos Alexander von Humboldt; Bogotá, D. C., Colombia: 192 pp.
- PIGGOTT, M.P., CHAO, N.L. & BEHEREGARAY, L.B. (2011): Three fishes in one: cryptic species in an Amazonian floodplain forest species. – *Biological Journal of the Linnean Society* **102**: 391–403. [DOI: 10.1111/j.1095-8312.2010.01571.x]
- QUÉROUIL, S., A. VELA DIAZ, C. GARÍA-DÁVILA, U. RÖMER & J.-F. RENNO (2016): Development and characterization of polymorphic microsatellite markers in neotropical fishes of the genus

- Apistogramma* (Perciformes: Labroidei: Cichlidae). – Journal of Applied Ichthyology **31** (Supplement 4): 52 – 56 [doi: 10.1111/jai.12975].
- READY, J.S. & KULLANDER, S. (2004): *Apistogramma eremnopysge*, a new species of cichlid fish (Teleostei: Cichlidae) from Peru. – Zootaxa **564**: 1–10.
- READY, J.S., SAMPAIO, I., SCHNEIDER, H., VINSON, C., DOS SANTOS, T. & TURNER, G.F. (2006): Colour forms of Amazonian cichlid fish represent reproductive isolated species. – Journal of Evolutionary Biology **564**: 1–10.
- REICHARD, M. & POLAČIK, M. (2010): Reproductive isolating barriers between colour-differentiated populations of an African killifish, *Nothobranchius korthausae* (Cyprinodontiformes). – Biological Journal of the Linnean Society **100**: 62–72.
- RÖMER, C.I. & RÖMER, U. (2015): Anmerkungen zur Identifizierung von *Apistogramma* sp. „Jutai“, einem weiteren maulbrütenden Zwergbuntbarsch aus dem oberen Amazonas-Einzug. – DCG-Informationen **46** (2): 26–31.
- RÖMER, U. (1994): *Apistogramma mendezi* nov. spec. (Teleostei: Perciformes; Cichlidae): Description of a New Dwarf Cichlid from the Rio Negro System, Amazonas State, Brazil. – aqua Journal of Ichthyology and Aquatic Biology **1** (1): 1–12.
- RÖMER, U. (1997): Diagnoses of two new dwarf cichlids (Teleostei; Perciformes) from Peru, *Apistogramma atahualpa* and *Apistogramma panduro* n. spp. – Buntbarsche Bulletin – The Journal of the American Cichlid Association **182** (October 1997): 9–14.
- RÖMER, U. (2000): Cichlid Atlas 1: Natural history of South American dwarf cichlids. Volume **1**. – Mergus Publishers, Melle: 1311 pp.
- RÖMER, U. (2001): Influence of temperature on fertility, growth rates, and reproductive success on selected species of *Apistogramma* (Teleostei, Cichlidae). – Verhandlungen der Gesellschaft für Ichthyologie **2**: 87–106.
- RÖMER, U. (2006): Cichlid Atlas 2: Natural History of South American Dwarf Cichlids. Volume **2**. – Mergus Publishers, Melle: 1319 pp.
- RÖMER, U. & BEISENHERZ, W. (2005): Intra- and interspecific mate choice of female *Apistogramma cacatuoides* Hoedemann, 1951 (Teleostei, Perciformes, Cichlidae). – Ichthyological Exploration of Freshwaters **16** (4): 339–345.
- RÖMER, U., BENINDE, J. & HAHN, I. (2011): *Apistogramma playayacu* sp. n.: Description of a new cichlid species (Teleostei: Perciformes: Geophaginae) from the Rio Napo system, Ecuador. – Vertebrate Zoology **61** (3): 321–333.
- RÖMER, U., BENINDE, J., DUPONCHELLE, F., VELA DÍAZ, A., ORTEGA, H., HAHN, I., SOARES, D.P., DÍAZ CACHAY, C., GARCÍA DÁVILA, C.R., SIRVAS CORNEJO, S., RENNO, J.-F. (2012): Description of *Apistogramma allpahuayo* sp. n., a new dwarf cichlid species (Teleostei: Perciformes: Geophaginae) from in and around the Reserva Nacional Allpahuayo Mishana, Loreto, Peru. – Vertebrate Zoology **62** (2): 189–212.
- RÖMER, U., DUPONCHELLE, D., VELA DÍAZ, A., GARCÍA DÁVILA, C., SIRVAS, S., DÍAZ CACHAY, C. & RENNO, J.-F. (2011): *Apistogramma cinilabra* sp. n.: Description of a potentially endangered endemic cichlid species (Teleostei: Perciformes: Geophaginae) from the Departamento Loreto, Peru. – Vertebrate Zoology **61** (1): 3–23.
- RÖMER, U., ENGELKING, B. & BEISENHERZ, W. (2014): Genetically determined mate choice can be influenced by learning in *Apistogramma cacatuoides* Hoedemann, 1951 (Teleostei, Cichlidae). – Vertebrate Zoology **64** (2): 199–206.
- RÖMER, U. & HAHN, I. (2008): *Apistogramma barlowi* sp. n.: Description of a new facultative mouth-breeding cichlid species (Teleostei: Perciformes: Geophaginae) from Northern Peru. – Vertebrate Zoology **58** (1): 49–66.
- RÖMER, U., HAHN, I., MELGAR, J., SOARES, D.P. & WÖHLER, M. (2004): Redescription of *Apistogramma eremnopysge* Ready & Kullander, 2004. – Das Aquarium, **38**(12) (426): 17–34.
- RÖMER, U., HAHN, I., RÖMER, E., SOARES, D.P. & WÖHLER, M. (2003): *Apistogramma martini* sp. n. - Beschreibung eines geophaginen Zwergcichliden (Teleostei: Perciformes) aus dem nördlichen Peru. – Das Aquarium, **37**(4) (406): 14–29.
- RÖMER, U., HAHN, I., RÖMER, E., SOARES, D.P. & WÖHLER, M. (2004): *Apistogramma baenschi* sp. n.: Description of another geophagine Dwarf-Cichlid (Teleostei: Perciformes) from Peru. – Das Aquarium, **38**(8) (422): 15–30.
- RÖMER, U., HAHN, I. & VERGARA, P.M. (2010): Description of *Dicrossus foirni* sp. n. and *Dicrossus warzeli* sp. n. (Teleostei: Perciformes: Cichlidae), two new cichlid species from the Rio Negro and the Rio Tapajos, Amazon drainage, Brazil. – Vertebrate Zoology **60** (2): 123–138.
- RÖMER, U., PRETOR, P. & HAHN, I. (2006): *Apistogramma huascar* sp. n. – Description of a Dwarf Cichlid from Peru. – pp. 530–573 in: Römer, U. (ed.): Cichlid Atlas 2: Natural History of South American Dwarf Cichlids. Volume 2. Mergus Publishers, Melle.
- RÖMER, U., RÖMER, E. & HAHN, I. (2006): *Apistogramma rositae* sp. n. - Description of a new Dwarf Cichlid from Peru. – pp. 668–693 in: Römer, U. (ed.): Cichlid Atlas 2: Natural History of South American Dwarf Cichlids. Volume 2. Mergus Publishers, Melle.
- RÖMER, U., RÖMER, E., SOARES, D.P. & HAHN, I. (2006): *Apistogramma pantalone* sp. n. - Description of a geophagine Dwarf Cichlid (Teleostei: Perciformes) from northern Peru. – pp. 642–667 in: Römer, U. (ed.): Cichlid Atlas 2: Natural History of South American Dwarf Cichlids. Volume 2. Mergus Publishers, Melle.
- RÖMER, U., SOARES, D.P., GARCÍA DÁVILA, C.R., DUPONCHELLE, F., RENNO, J.-F. & HAHN, I. (2015): Re-description of *Apistogramma payaminonis* KULLANDER, 1986, with descriptions of two new cichlid species of the genus *Apistogramma* (Teleostei, Perciformes, Geophaginae) from northern Peru. – Vertebrate Zoology **65** (3): 287–314.
- RÖMER, U. & WARZEL, F. (1998): *Apistogramma arua* sp. n. (Teleostei: Perciformes: Cichlidae), a new species of dwarf cichlid from the Rio Arapiuns system, Pará State, Brazil. – aqua Journal of Ichthyology and Aquatic Biology **3** (2): 45–54.
- SCHINDLER, I. & STAECK, W. (2013): Description of *Apistogramma helkeri* sp. n., a new geophagine dwarf cichlid (Teleostei: Cichlidae): from the lower río Cuaó (Orinoco drainage) in Venezuela. – Vertebrate Zoology **63** (3): 311–306.
- SEEHAUSEN, O. (2000): Explosive speciation rates and unusual species richness in haplochromine cichlid fishes: Effects of sexual selection. – Advances in Ecological Research **31**: 237–274.

- SHINE, R. & GREER, A.E. (1991): Why are clutch sizes more variable in some species than in others. – *Evolution* **45**: 1696–1706.
- SITES, J.W. JR. & MARSHALL, J.C. (2004): Operational criteria for delimiting species. – *Annual Reviews in Ecology, Evolution, and Systematics* **35**: 199–277.
- STAECK, W. (2003): Cichliden Lexikon, Teil **3**: Südamerikanische Zwergbuntbarsche. – Dähne Verlag, Ettlingen, Germany: 219 pp.
- STAECK, W. (2004): *Apistogramma* sp. “Maulbrüter”: Zusammenfassung bisheriger Erkenntnisse. – *DCG-Informationen* **35** (6): 121–129.
- STAECK, W. (2012): Die *Apistogramma*-Arten des Orinoko-Beckens (1). – *DATZ* **65** (12): 20–27.
- STAECK, W. (2015): Färbung und Zeichnungsmuster als Mittel zur Bestimmung und Unterscheidung von Buntbarschen: Möglichkeiten und Grenzen. – *DCG-Informationen* **46** (10): 250–255.
- STAECK, W. & SCHINDLER, I. (2008): *Apistogramma erythrura* sp. n. – a new geophagine dwarf cichlid (Teleostei: Perciformes: Cichlidae) from the río Mamoré drainage in Bolivia. – *Vertebrate Zoology* **58** (2): 197–206.
- STEELE, S.E. & LÓPEZ-FERNÁNDEZ, H. (2014): Body Size Diversity and Frequency Distributions of Neotropical Cichlid Fishes (Cichliformes: Cichlidae: Cichlinae). – *PlosOne* **9** (9): e106336: 11pp.
- SVENSSON, E.I., ABBOTT, J.K., GOSDEN, T.P. & COREAU, A. (2009): Female polymorphism and limits to speciation processes in animals. – *Evolutionary Ecology* **23** (1): 93–108 [doi.org/10.1007/s10682-007-9208-2]
- TOUGARD, C., GARCÍA DAVILA, C. R., RÖMER, U., DUPONCHELLE, F., CERQUEIRA, F., GUINAND, B., CHAVEZ, C. A., SALAS, V., SIRVAS, S. & RENNO, J.-F. (submitted): Tempo and Rates of Diversification in the South American Cichlid Genus *Apistogramma* (Teleostei: Perciformes: Cichlidae). – *PlosOne*
- VAN GENNE, E. (2010a): *Leticia 2010*. – *Cichlidae (NVC)* **36** (2): 5–21.
- VAN GENNE, E. (2010b): *Leticia 2010*. – *Cichlidae (NVC)* **36** (3): 14–18.
- VARELLA, H.R. & BRITZKE, R. (2014): *Apistogramma eleutheria* and *A. flavipedunculata*, two new species of dwarf cichlids from the rio Curuá on Serra do Cachimbo, Brazil (Teleostei: Cichlidae). – *Ichthyol. Explor. Freshwaters* **27** (1): 81–95.
- VARELLA, H.R. & SABAJ PÉREZ (2014): A titan among dwarfs: *Apistogramma kullanderi*, new species (Teleostei: Cichlidae). – *Ichthyol. Explor. Freshwaters* **25** (3): 243–258.
- WERNER, U. (2015): Arten oder Farbformen? *Apistogramma* aus dem Orinoko-Einzug. – *DCG-Informationen* **49** (9): 214–220.
- WICKLER, W. (1956): Der Haftapparat einiger Cichliden-Eier. – *Zeitschrift für Zellforschung und Mikroskopische Anatomie* **45** (3): 304–327.
- Wiens, J.J. & Servedio, M.R. (2000): Species delimitation in systematics: inferring diagnostic differences between species. – *Proceedings of the Royal Society London, Series B* **267**: 631–636.

