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http://zoobank.org/urn:lsid:zoobank.org:pub:492A5DA4-73CD-45F0-8B9C-DC61F766174F

Apistogramma wolli: LSID urn:lsid:zoobank.org:act:566C3584-2A36-4463-8C88-DEA9B792E7C1

Apistogramma feconat: LSID urn:lsid:zoobank.org:act:4BA6F16C-C5C0-41C6-B478-ABAEAAEAC905

# Re-description of *Apistogramma payaminonis* KULLANDER, 1986, with descriptions of two new cichlid species of the genus *Apistogramma* (Teleostei, Perciformes, Geophaginae) from northern Peru<sup>1</sup>

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#### Abstract

Apistogramma payaminonis Kullander, 1986 is redescribed based on the only two type specimens available, and two new, closely-related Apistogramma species are described from Peru. Data from the original description of A. payaminonis are supplemented with information on phenotypic appearance, which is important for differentiating the taxon from several other species discovered in the last few years. Apistogramma feconat sp. n. is described from four specimens from the catchment of the Río Tigre, Loreto; information on its ecology, biology, and current conservation status is summarised. Apistogramma wolli sp. n. is described from six specimens from the catchment of the Napo river, Loreto, close to the Peru-Ecuador border; information on its ecology and biology is sparse. Both newly described species are representatives of the Apistogramma nijsseni complex that live in small forest streams influenced by blackwater. Information on differentiating females of some members of this group of related species is presented. At present no clear information based on voucher specimens is available regarding the possible distribution of the two species in Ecuador. Man-made environmental hazards potentially endangering the aquatic fauna in the western catchment of the Río Marañón and the Rio Amazonas, between their tributaries the Rio Pastaza and the Rio Napo, are discussed.

#### Resumen

En el presente trabajo, re-describimos *Apistogramma payaminonis* Kullander, 1986, en base a los únicos dos tipos existentes, y a dos nuevas especies de *Apistogramma* muy aparentadas de Perú. Los datos de la descripción original están complementados con información sobre la apariencia fenotípica, parámetro muy importante para diferenciar este taxón de varias nuevas especies descubiertas en los últimos años. *Apistogramma feconat* sp. n. esta descrita a partir de cuatro especímenes de la cuenca del Rio Tigre, Loreto; se resume información sobre su ecología, biología y presente estado de conservación. *Apistogramma wolli* sp. n. esta descrita a partir de seis especímenes de la cuenca del Rio Napo, Loreto, cerca de la frontera con Ecuador; Información sobre su ecología y biología es escasa. Las dos nuevas especies son representantes del complejo *Apistogramma nijsseni*, que vive en pequeñas quebradas y arroyos de bosque influenciados por agua negra. Se presenta información para diferenciar hembras de algunos miembros de este grupo. Todavía, no existe información o voucher para aclarar la posible distribución de las dos especies nuevas en Ecuador. Se discuten perturbaciones antropogénicas que podrían poner en peligro las faunas acuáticas al oeste de las cuencas del Rio Marañon y del Rio Amazonas, incluyendo algunos afluentes como el Rio Pastaza y el Rio Napo.

**CO** 

<sup>&</sup>lt;sup>1</sup> This is publication number 5 from the *Apistogramma* Project within the Laboratoire Mixte International.

## Kurzfassung

Apistogramma payaminonis wird auf Basis der zwei einzig verfügbaren Typus-Exemplare wiederbeschrieben. Zwei neue, nahe verwandte Taxa aus Peru werden beschrieben. Die Informationen aus der Originalbeschreibung werden um Angaben zum phänotypischen Erscheinungsbild der Art ergänzt, da diese für die Differenzierung von weiteren in den letzten Jahren entdeckten Arten erforderlich sind. Apistogramma feconat sp. n. wird auf Basis von vier Exemplaren aus dem Einzugsgebiet des Río Tigre, Loreto, beschrieben. Informationen zur ihrer Ökologie und Biologie zusammengefasst, sowie die aktuelle Gefährdungssituation werden für die Art dargestellt. Apistogramma wolli sp. n. wird anhand von sechs Exemplaren aus dem Rio Napo-Einzug, Loreto, in der peruanisch-equadorianischen Grenzregion beschrieben; verfügbare Informationen zur Ökologie und zur Biologie sind spärlich. Beide neu beschriebenen Apistogramma-Arten sind Vertreter des Apistogramma-nijsseni-Komplexes und leben in kleinen Waldbächen, die unter Schwarzwassereinfluss stehen. Informationen zur phänotypischen Unterscheidung von Weibchen verschiedener Arten dieser Verwandtschaftsgruppe werden dargestellt. Über die mögliche Verbreitung beider Arten in Ekuador liegen derzeit keine durch Belegmaterial gesicherten Erkenntnisse vor. Mögliche Ursachen einer potenziellen Gefährdung der aquatischen Fauna durch aktuell vom Menschen verursachte Umweltprobleme im westlichen Einzugsgebiet von Río Marañón und Rio Amazonas zwischen ihren Zuflüssen Rio Pastaza und Rio Napo werden diskutiert.

### Rey words

Apistogramma feconat sp. n., Apistogramma wolli sp. n., Apistogramma-nijsseni-complex, systematics, ichthyology, freshwater, ecology, new taxa, endangered species.

#### Introduction

In recent decades several new Apistogramma species have been discovered in Peru, including a number of taxa from the Apistogramma cacatuoides and Apistogramma nijsseni phylogenetic complexes (Kullander, 1980, 1986, Römer et al., 2003, 2004a-b, 2006b-d, Staeck, 1991). 19 of these forms have been scientifically studied and described; some of them, e.g. Apistogramma huascar Römer, Pretor & Hahn, 2006, A. pantalone Römer, RÖMER, SOARES & HAHN, 2006, A. rositae RÖMER, RÖMER & Hahn, 2006, A. allpahuayo Römer, Beninde, Dupon-CHELLE, VELA DÍAZ, ORTEGA, HAHN, SOARES, DÍAZ CATCHAY, GARCÍA DÁVILA, SIRVAS CORNEJO & RENNO, 2012, only in recent years. Usually the live colours of species from this area as well as several aspects of their biology are well known, as they are regularly collected for the ornamental fish trade (Tougard et al. submitted). But this group of related species also includes a few taxa that have been scientifically identified, but for which insufficient information on live coloration, ecology, behaviour, and other aspects of life history is currently available.

One of these still poorly known species is Apistogramma payaminonis Kullander, 1986, which was described from Peru and Ecuador on the basis of 17 preserved specimens. Information on live coloration was not available at that time. This situation appeared to change when what was thought to be the species was imported alive to Europe in the late 1990s. STAECK (in LINKE & STAECK, 1997; see also STAECK & LINKE, 2006) collected fish identified as Apistogramma payaminonis at a couple of locations in south-eastern Ecuador. Soon afterwards Römer (1998) published photographs of fish that had been imported to Germany by FISCHER some years earlier, and which were also identified as Apistogramma payaminonis. Fischer had collected these specimens in a tributary of the Río Payamino. Two years later Kästner (2000) published an article on Apistogramma payaminonis, but relating to fish he stated had been imported

from Manaus (Brazil). This was obviously intentional disinformation or an error on the part of the exporter, the importer, or the author. All the above-mentioned reports have one point in common: in one or more important respects the fish to which they refer do not really accord with the specimens depicted in the original description by KULLANDER.

In addition, the late Frank Martin Warzel took several photographs of some of the individuals kept by Kästner (here identified to represent *A. payaminonis*), but his sudden and far too early death meant he was never able to publish an article on the subject.

In spite of the fact that *A. payaminonis* was spawned (Kästner, 2000), as far as we know no specimens ever made it into the trade. Hence as the aquarium career of *A. payaminonis* turned out to be short and only episodic at best, the overall live appearance of this *Apistogramma* species remains more or less unknown to the present day.

In 2006 two of the authors (UR, DPS), together with Mike Wise (Denver, Colorado, USA), took the opportunity of re-examining the holotype and the female paratype of the species at the Field Museum in Chicago (FMNH); these specimens are shown in the plates in Kullander (1986). It was immediately apparent to the senior author of this paper that the fish presented by him in 1998, as well as those illustrated by all other authors, were not identical with the fish described by Kullander. After additionally comparing the pictorial material and associated text produced by Frank Martin WARZEL<sup>2</sup> in possession of the senior author, it was also obvious that a revision of Apistogramma payaminonis would be necessary sooner or later, as there were too many discrepancies between the scientific description and information available from the cited "grey" aquarium literature. But at that time no

<sup>&</sup>lt;sup>2</sup> Warzel Archiv [<sup>©</sup>Dr. Uwe Römer]

additional material was available for further closer examination.

The situation remained thus until 2010, when more individuals of Apistogramma payaminonis became available. Furthermore, specimens of at least three other closely-related species have subsequently been discovered during research activities by the LMI-EDIA in northern Peru close to the Ecuadorian border. We are thus now in a position to present details regarding the live identification of a) Apistogramma payaminonis and b) two of the other species, and accordingly have decided to prepare the redescription of Apistogramma payaminonis and the formal descriptions of two new species presented in this paper. On the one hand, in our view, regardless of the limitations of the preserved material, enough additional details regarding Apistogramma payaminonis are now available, while on the other hand the deteriorating environmental situation in the Peruvian Amazonia Occidental has reached a critical stage in the last few years, affecting the natural habitat of at least one of the three species since 2013.

#### Methods

The descriptions are based on examination of preserved specimens, as well as on observation and photographs of live type material taken in the aquarium, as detailed in RÖMER et al. (2011). Methods for counts and measurements are as described by RÖMER (2006) and RÖMER et al. (2003, 2004, 2006, 2011, 2012, 2013). Exceptions to this methodology are noted in the text. Preservation of specimens followed the "low temperature preservation protocol" (LTPP) described by RÖMER & HAHN (2008) and RÖMER et al. (2011), and took place either in the laboratory of the IIAP in Iquitos or at UTIB in Trier (in the latter case after anaesthetising the specimens with MS 222) after observation of behaviour and colour patterns (for reasons see RÖMER et al., 2011). All specimens except those of A. payaminonis were initially preserved in 96 % ethanol in preparation for DNA extraction. After DNA extraction and ethanol fixation for two weeks, all specimens were transferred into 80 % ethanol (as justified by RÖMER 2000a). No information is available on the initial preservation method for the A. payaminonis types. DNA samples of all specimens (except the A. payaminonis type material) were taken for analysis (still in progress) and registered under the same individual numbers as the source specimens. X-ray photographs of most of the type specimens and comparative material were taken using a Faxitron LX-60 (26 kV, auto-calibration) at MTD F, with the exception of the Apistogramma payaminonis types, which were x-rayed at FMNH. Vertebral counts were made as described in Varella & Sabaj Pérez (2014).

Because live coloration is a critical factor in the accurate determination of the species described herein, it is described in detail and illustrated by representative figures of live specimens of both sexes in different behavioural stages and moods. These notes on live coloration focus on essential diagnostic details in particular. 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* species.

For museum acronyms see Leviton et al. (1985).

Comparative material: Apistogramma allpahuayo Römer et al., 2012: Type series. Apistogramma atahualpa Röмer, 1997: type series, & additional 32 specimens: MTD F 32653 (3 Ex.), MTD F 32653 (3 Ex.), MTD F 32690 (4 Ex.), MTD F 32691 (2 Ex.), MTD F 32692 (5 Ex.), MUSM 41819 (3 Ex.), MUSM 41820 (3 Ex.), <u>MUSM 41822</u> (2 Ex.), <u>MUSM 41823</u> (3 Ex.), <u>MUSM</u> 42053 (1 Ex.), MUSM 42054 (2 Ex.), MUSM 42056 (4 Ex.), & MUSM 42056 (4 Ex.), all authorized specimens, all from locations west of the road Iquitos-Nauta at northern boundary of Reserva National Forestal Allpahuayo Missana, Loreto, Peru, collected August 2011 by R. Mori s., Roger Mori jr., J. Beninde, F. Kervarek & U. Römer (LMI-EDIA). Apistogramma baenschi RÖMER et al.: type series. Apistogramma barlowi RÖMER & HAHN, 2008: type series. Apistogramma luelingi Kullander, 1976: 18 specimens: MUSM 21393 (10 Ex.), Peru, Madre de Dios, Manu, Pozo Pedro, Aguajal CICRA, Cca. R. Los Amigos [12°33.61."S 70°06.59.3"], collected 05.12.2001 by M. Hidalgo; MUSM 22163 (8 Ex.), Peru, Madre de Dios, Tambopata, Aguajal trigoso, Cca. del Rio Madre de Dios, aguajal bajo del Rio Madre de Dios [05°14'97.6" S / 86°22'69.6" W], collected 29.02.2004 by M. Hidalgo et al. Apistogramma martini Römer et al., 2003: type series; Apistogramma panduro Römer, 1997: type series. Apistogramma pantalone RÖMER et al., 2006: type series & 35 specimens: CAS 225481 (5 males, 5 females; 25.2-34.2 mm SL), MTD F 33496 (13 Ex.), MUSM 43062 (2 females; 29.9-36.4 mm SL), MUSM 43063 (2 males, 2 females; 32.2-41.8 mm SL), MUSM 43061 (2 males, 4 females; 28.4-38.3 mm SL); all authorized specimens. Apistogramma rositae Römer et al., 2006: type series. Other species as listed in Römer (1994, 1997, 2006), Römer & Warzel (1998), and RÖMER et al. (2003a, 2004, 2006b-d, 2012).

# Apistogramma payaminonis Kullander, 1986

(figs. 1-6)

Holotype (fig.1). FMNH 96564; male, 39.6 mm SL; Ecuador, Provincia del Napo, Río Napo drainage system, Rio Payamino drainage, Quebrada Ahuano, above Ahuanopaccha (a 42 m vertical waterfall), headwaters of Rio Tutapishcu (Tutapischo), few kilometres south-west of San José de Payamino (the village at confluence of Río Tutapishcu and Río Payamino (approximately 00° 31.12′ S / 077° 20.42′ W, data corrected from FMNH catalogue)) (field station DJS 83-75); 15. November 1983, leg. D.J. Stewart, M. Ibarra, R. Barriga, A. Echeverria.

**Paratype** (fig. 1) (16 specimens): FMNH 105928 (formerly FMNH 96546*pt*) (topotype); female, 30.8 mm SL; same data as given for holotype; MCZ 40327 (15 specimens), not inspected.

[Remark 1. The available type material was in good condition when inspected in 2006; only minor damage, if any; colours moderately faded as might be expected; dark pigment pattern clearly visible, but already faded from black to dark brown.

**Remark 2.** Paratypes MCZ 40327 (15 specimens) were not available for the revision: 30 years after the description was published these specimens are still registered in the catalogue of the MCZ as



**Fig. 1.** *Apistogramma payaminonis*. **A**: FMNH 56564, holotype, male, 39.6 mm SL; **B**: FMNH 105928, paratype, female, 30.8 mm SL. August 2006. All photographs except where otherwise stated: U. Römer.

on loan, with the following annotations in the data base: "Remarks: specimens not seen at MCZ, since loaned as Cichlidae sp.", and: "Remarks: Empty bottle found on shelf with note 'on loan - - 74/2 J. P. Gosse ". But Staeck (2003) notes: "... 17 Typusexemplare werden im Fieldmuseum of Natural History in Chicago aufbewahrt3", giving the impression that all specimens had been transferred to FMNH by Kullander after finishing the description. From KULLANDER'S description it seems likely that the missing paratypes will be in comparatively bad condition, as he mentioned that they all were "strongly faded, the smaller specimens virtually without pigment". So, even if the specimens were to turn up in one of the collections, it is to be expected that their value as a source of information on coloration may be rather limited. An electronic request sent by UR to MCZ was answered by Karsten Edward HARTEL (in litt.), Curatorial Associate in Ichthyology, on 6.4.2015 as follows: "The original loan was to Gosse in 1974. Kullander apparently saw the material in Gosse's lab and borrowed part of it as a transfer from Belgium to Stockholm in the early 1980s. Some other types made it back to MCZ. ..." and on 9.4.2015 as follows: "I have spent the morning poring through old correspondence. I have just written to Sven Kullander since it appears that the MCZ paratypes were still in Stockholm at least in 2010." At the time of writing there has been no further update to this information.]

#### Description

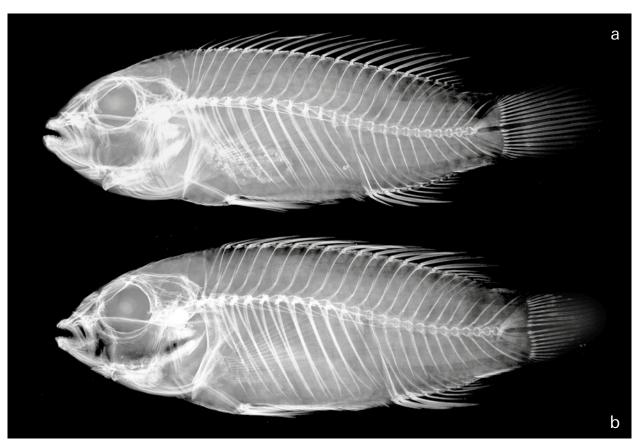
Morphological characters: (Partially extended, based on Kullander (1986), revision of the FMNH type material, and numerous photographs of live specimens taken by Frank Martin Warzel (†).) For biometric data see tables 1 & 2, for meristic data see table 3 (data partially taken from Kullander 1986).

Habitus [figs. 1–6, for more figures of habitus see Kullander (1986: plate XX 1 & 2, page 413)]: *Apistogramma payaminonis* is a medium-sized (males up to 40 mm, females to 31 mm SL), moderately high-backed, laterally compressed, and moderately elongate *Apistogramma* species, exhibiting pronounced sexual dimorphism and dichromatism. Body clearly compressed laterally, about twice as deep as wide, head fairly large (33.3–35.4 % SL, mean 34.3 % SL), but, unlike as noted in Kullander (1986), proportions normal for adults of species closely related to *Apistogramma nijsseni* Kullander, 1979: both individuals inspected seem to be fully adult specimens in optimal reproductive condition, and, again unlike as stated in Kullander (1986), not giving any impression of being starved.

Adult males 20–25% larger than females, with lyrate caudal fin, larger head, lips and lower jaw, wider interorbital, and longer pelvic fins. Upper head profile regularly convex in females; in males with clear indentation above

<sup>3 &</sup>quot;17 type specimens are stored at the Field Museum of Natural History in Chicago" [translation from German original by UR)

Kullander 1986, page 184: "holotype and topotype rather slender; ..., appearing starved." and page 187: "The two specimens from the type locality have a pronounced starved appearance."



**Fig. 2.** *Apistogramma payaminonis*, x-rays. **A**: FMNH 56564, holotype, male, 39.6 mm SL (top); **B**: FMNH 105928, paratype, female, 30.8 mm SL (bottom). Combined from digitalized x-ray photographs: February 2015; © Field Museum of National History, Chicago, USA; courtesy of the FMNH.

posterior third of eye, strongly expressed in large males; lower head profile only slightly curved in both sexes. Mouth wide, terminal, rounded, noticeably large; lips hypertrophied, folded, and fleshy, especially in males, jaws stout; maxillary extending to around vertical anterior margin of pupil or slightly beyond; cheeks and opercula completely scaled, scale pattern as shown in Kullander (1986); 5 dentary and 3 infraorbital pores (for pattern see Kullander 1986, fig. 64). Ventral fins [V I.5 (n=2)] clearly prolonged in adult males, extending to posterior edge of anal-fin base, in females only exceptionally extending to anus. Pectoral fins [11 (n=1), 12 (n=8), 13 (n=1)] rounded. Dorsal fin [D. XVI.6 (n=10), XVI.7 (n=6), XVII.5 (n=1)] with length of spines increasing from D1 to D6 or D7 in both sexes, thereafter remaining about equal, last dorsal spine slightly longer, first spine about 45% of length of last; in adult males fin margin serrate, dorsal membranes significantly prolonged past tips of spines, extensions about 1.5 times to twice length of spines, lappets 5 to 7 longest, extending back for about two thirds of dorsal-fin base, soft-rayed portion pointed, only slightly extended; in females rounded, dorsal fin neither prolonged nor serrate, lacking any prolonged membranes. Anal fin [A. III.6 (n=6), III.7 (n=11)] in adult males pointed, soft portion nearly extending to posterior edge of caudal fin; in females and smaller males rounded, when folded extending for first third of caudal fin. Caudal fin with 16 (n=2) principal soft rays; round in juveniles

and females, initially truncate in immature males, lyrate in mature males from about 30 mm SL, caudal rays V4 (-5) and D4 (-5) symmetrically prolonged relative to remainder, intervening rays around same length and thus forming straight edge, outer rays decreasing rapidly in length; caudal fin in both sexes scaled on first third to half. In adults caudal peduncle one third deeper than long. Squamation as given in Kullander 1986; scales in median longitudinal row 21 to 22 (21 (n=1), 22 (n=16). Vertebrae 11+13=24 (n=2), (including last half centrum) (fig.2).

Coloration of preserved specimens (23 years after preservation) (fig. 1): Apistogramma payaminonis is characterised by a combination of the following characters: in both sexes two distinct lateral spots on positions of vertical bars 3 and 4; black marking on pectoral base in both sexes, more strongly expressed in females; faint lateral band (hardly visible in male holotype, significantly clearer in female paratype examined) about half to one scale wide, more pronounced between head and first lateral spot; distinct caudal spot in both sexes, occupying half to two thirds of caudal peduncle height, round in females, squarish in males; caudal fin and dorsal-fin lappets milky white to faint yellowish, without markings.

Adult females with unique pattern of black markings on ventral surface, consisting of rectangular streak on lower lip, branchiostegal membrane from point im-

Table 1. Biometric data for Apistogramma payaminonis, A. wolli sp. n. and Apistogramma feconat sp. n., taken from the type specimens
and, for A. payaminonis calculated from Kullander (1986), expressed as % SL; SL given in mm.

%	Apistogramma payaminonis						Apistogramma wolli sp. n.					pistogra	amma fe	conat s	abbreviations	
	(n)	Mean	min.	max.	st.dev.	(n)	mean	min.	max.	st.dev.	(n)	mean	min.	max.	st.dev.	HT = Holotype / PT = Paratype
SL	10	32.5	28.5	39.6	4.45	5	37.3	26.9	51.2	9.17	5	36.6	24.6	44.2	7.46	standard length (in mm)
TL						5	132.3	131.7	133.0	0.51	5	134.3	130.9	138.1	2.71	total length
TLS						5	133.4	131.7	135.9	1.79	5	134.3	130.9	138.1	2.71	total length plus streamer
HL	10	34.3	33.3	35.4	0.61	5	33.0	32.1	33.6	0.56	5	35.0	33.8	36.4	1.03	head length
HD	10	29.3	27.6	31.1	0.88	5	28.4	26.7	30.2	1.24	5	30.6	29.1	32.4	1.50	head depth
BD	10	36.5	34.1	37.9	1.39	5	36.0	33.4	38.2	1.92	5	37.8	35.3	39.4	1.59	body depth
HW						5	18.6	18.0	19.6	0.60	5	19.5	17.9	20.8	1.13	head width
PDL	10	34.3.	33.3	35.4	0.61	5	35.3	33.7	36.8	1.43	5	37.7	36.2	38.8	1.20	pre-dorsal length
TDL						5	91.0	89.5	92.7	1.24	5	91.1	89.4	92.4	1.49	trans-dorsal length
PPL	10	41.6	40.6	42.7	0.79	5	40.1	37.8	41.5	1.50	5	41.2	40.7	41.9	0.61	pre-pelvic length
PAL						5	79.5	77.4	81.2	1.55	5	79.3	77.7	80.3	1.05	pre-anal length
TAL						5	89.4	88.88	90.2	0.72	5	90.0	88.4	91.6	1.24	trans-anal length
Eye	10	12.0	11.4	12.6	0.39	5	11.5	9.3	13.0	1.59	5	11.6	10.9	13.4	1.03	eye diameter
SNL	10	7.5	7.0	8.6	0.49	5	7.8	7.0	9.1	1.00	5	9.1	7.6	12.3	1.91	snout length
CHD	10	8.3	7.5	9.8	0.81	5	9.0	8.1	10.0	0.79	5	10.2	9.2	10.6	0.59	cheek depth
POD						5	3.6	2.5	4.6	0.78	5	3.7	3.3	4.0	0.32	pre-orbital depth
IOW	10	8.8	8.2	9.6	0.44	5	9.0	8.3	10.0	0.65	5	9.1	8.4	10.3	0.74	inter-orbital width
UJL	10	12.2	10.9	15.4	1.44	5	10.7	7.1	13.9	2.88	5	11.3	8.4	15.0	3.30	upper jaw length
LJL	10	15.2	13.6	18.4	1.41	5	13.7	12.5	15.0	1.14	5	13.6	10.8	17.1	2.88	lower jaw length
CPD	10	17.7	16.4	18.9	0.83	5	15.6	14.8	17.2	1.00	5	16.4	15.2	17.6	1.09	caudal peduncle depth
CPL	10	12.3	11.2	13.1	0.67	5	10.8	10.0	11.9	0.90	5	12.1	10.4	14.2	1.45	caudal peduncle length
DFB	10	59.7	58.1	61.1	0.82	5	61.3	59.5	64.0	1.83	5	59.3	57.4	61.7	1.71	dorsal fin base length
AFB	10	19.7	18.8	21.0	0.71	5	18.8	15.9	20.4	1.94	5	19.2	17.8	21.0	1.24	anal fin base length
PecL	10	31.5	28.9	33.3	1.52	5	28.6	25.2	32.8	2.99	5	29.1	26.7	32.7	2.53	pectoral fin length
PelL	10	38.3	33.1	50.3	5.13	5	29.3	24.9	34.9	3.77	5	30.5	22.3	36.5	5.52	pelvic fin length
PelSL	10	14.0	12.4	15.2	0.87	5	12.9	11.7	14.8	1.27	5	13.7	11.6	18.3	2.70	pelvic fin spine length
LDS	10	18.0	16.2	19.7	1.08	5	13.2	10.2	15.0	1.90	5	14.6	10.5	18.6	3.83	last dorsal spine length
LAS	10	17.6	16.2	18.9	0.79	5	12.9	11.3	13.7	0.93	5	13.9	13.0	15.1	0.81	last anal spine length

mediately below anterior margin of eye to distal end of the membrane, breast spot occupying about three rows of scales in front of and including ventral-fin insertion, continuing in narrow mid-ventral stripe framing anal opening and extending along anterior outer margin of anal fin along its hard rays (fig. 19a); areas between black markings yellowish white to porcelain. Lips brownish grey in males, yellowish white in females. In both sexes dark marking on posterior pectoral-fin base, in males faint irregular brownish, in females about as high as pectoral-fin base, half-moon-shaped, blackish. Other details as given in Kullander (1986).

## Coloration of live specimens and sexual dimorphism

(figs. 3–6): Apistogramma payaminonis is highly sexually dimorphic and dichromatic. Furthermore males (figs. 3–4) seem to be polychromatic, some having an overall yellowish to light green body, others a light bluish colour on the body combined with a slightly yellowish head. Markings as follows: two large lateral spots regularly visible in females (figs. 5–6), especially in breeding mood; males normally with one lateral spot, only exceptionally second (mostly when under stress). Caudal fin of males with orange to red upper and lower sub-marginal bands; outer margins black; centre of fin translucent yel-

lowish to (rarely) light greenish, without any markings; marginal bands usually absent in females, exceptionally rudimentarily visible in some individuals. Caudal spot black, comparable to preserved specimens, about half as high as caudal base in both sexes, squarish with rounded corners, sometimes upright near-oval.

**Distribution and ecology:** Specimens unequivocally identifiable as *Apistogramma payaminonis* are known only from the *terra typica* and a second location in the Río Payamino system in Ecuador (fig. 28). According to ecological information given by STEWART (cited as *in litt.* in KULLANDER, 1986), specimens were collected in a slow-flowing backwater of a swift river about 8 to 10 m in width, in slightly acid (pH 6.4) and relatively cool clear water (22.5 °C, visibility to over 0.5 m). Specimens were collected along a stretch of shore surrounded by undisturbed rainforest. Water depth was about 0.5 to 1 m, and the substrate consisted of bedrock, large rocks, dead wood, and silty sand in backwaters. Otherwise no reliable information on the ecology of this species has been added to our knowledge since the description in 1986.

The information on the ecology of *Apistogramma* payaminonis given by STAECK (2003) is comparable, but probably relates to fish not representing this taxon, col-

Table 2. Biometric data for Apistogramma wolli sp. n. and Apistogramma feconat sp. n., taken from the type specimens and, for A. pay-
aminonis taken from Kullander (1986), expressed in mm.

mm	Apistogramma payaminonis						Apistogi	ramma	wolli sp	). n.	Apistogramma feconat sp. n.					abbreviations
	(n)	mean	min.	max.	st.dev.	(n)	mean	min.	max.	st.dev.	(n)	mean	min.	max.	st.dev.	HT = Holotype / PT = Paratype
SL	10	32,5	28,5	39,6	4,45	5	37.3	26.9	51.2	9. 17	5	36.8	24.6	44.2	7.46	standard length (in mm)
TL						5	49.3	35.8	67.8	12.14	5	49.4	33.3	59.4	10.18	total length
TLS						5	49.8	35.8	69.5	12.84	5	49.4	33.3	59.4	10.18	total length plus streamer
HL	10	11.1	9.9	14.0	1.51	5	12.3	9.0	16.4	2.81	5	12.8	9.0	14.9	2.36	head length
HD	10	9.5	8.3	12.3	1.48	5	10.7	7.2	15.4	3.10	5	11.2	7.8	14.3	2.37	head depth
BD	10	11.9	10.5	15.0	1.59	5	13.4	10.1	19.6	3.66	5	13.9	9.7	17.1	2.83	body depth
HW						5	7.0	4.8	9.5	1.78	5	7.2	5.0	9.2	1.53	head width
PDL	10	11.1	9.9	14.0	1.51	5	13.2	9.9	18.7	3.44	5	13.8	9.6	16.0	2.52	pre-dorsal length
TDL						5	34.0	24.7	47.4	8.61	5	33.5	22.7	39.5	6.64	trans-dorsal length
PPL	10	13.5	11.6	16.9	2.01	5	14.9	11.1	20.2	3.48	5	15.1	10.3	18.5	3.07	pre-pelvic length
PAL						5	26.9	19.9	36.0	6.06	5	26.5	18.0	31.7	5.22	pre-anal length
TAL						5	33.3	23.9	45.6	8.13	5	33.1	22.6	39.8	6.61	trans-anal length
Eye	10	3.9	3.5	4.7	0.44	5	4.2	3.5	5.4	0.90	5	4.2	3.3	4.9	0.60	eye diameter
SNL	10	2.5	2.0	3.4	0.49	5	2.9	1.9	3.6	0.70	5	3.4	1.9	5.4	1.28	snout length
CHD	10	2.7	2.2	3.9	0.65	5	3.4	2.2	4.8	0.97	5	3.8	2.6	4.7	0.85	cheek depth
POD						5	1.4	1.0	2.4	0.60	5	1.4	1.0	1.6	0.23	pre-orbital depth
IOW	10	2.9	2.4	3.8	0.53	5	3.4	2.2	5.1	1.07	5	3.3	2.2	4.0	0.69	inter-orbital width
UJL	10	4.0	3.3	6.1	1.05	5	4.1	1.9	6.2	1.83	5	4.3	2.2	6.6	1.92	upper jaw length
LJL	10	5.0	4.0	7.3	1.12	5	5.2	3.6	7.7	1.61	5	5.1	2.7	7.1	1.91	lower jaw length
CPD	10	5.7	5.1	7.5	0.77	5	5.9	4.0	8.2	1.65	5	6.1	3.8	7.6	1.53	caudal peduncle depth
CPL	10	4.0	3.3	5.2	0.67	5	4.1	2.7	5.9	1.27	5	4.5	2.8	6.3	1.31	caudal peduncle length
DFB	10	19.4	17.3	23.8	2.62	5	22.9	16.4	32.7	6.12	5	21.8	14.6	25.6	4.49	dorsal fin base length
AFB	10	6.4	5.4	7.8	0.89	5	7.1	4.3	10.4	2.35	5	7.1	4.7	8.2	1.55	anal fin base length
PecL	10	10.2	8.9	12.9	1.51	5	10.7	7.6	13.6	2.72	5	10.7	6.9	13.3	2.40	pectoral fin length
PelL	10	12.6	9.6	19.9	3.42	5	10.9	7.8	14.1	2.86	5	11.4	6.9	14.7	3.69	pelvic fin length
PelSL	10	4.5	4.1	6.0	0.58	5	4.7	3.7	6.0	0.94	5	4.9	4.1	5.5	0.56	pelvic fin spine length
LDS	10	5.8	5.0	7.8	1.00	5	4.9	3.9	7.7	1.59	5	5.6	2.6	7.9	2.31	last dorsal spine length
LAS	10	5.7	5.0	7.2	0.77	5	4.7	3.6	5.8	0.84	5	5.1	3.2	6.1	1.16	last anal spine length

lected in the Rio Aguarico system, which lies more than 150 km further north north-west, and is a parallel river system with no direct connection to the Rio Payamino, only via more than 500 km of intervening waterways.

# Apistogramma wolli sp.n.

(figs. 7-18)

**Holotype** (fig. 7): MUSM 43068, male, 51.2 mm SL, Peru, Departamento Loreto, Province Maynas, District Napo, wider vicinity of Cabo Pontoja, small forest stream feeding into the Rio Napo close to the border with Ecuador (about 75°12′ W / 0°57′ S); August 2013, leg. Sergio Llanos, preserved November 2013.

**Paratypes** (5 specimens): MUSM 43069, 1 female, 38.4 mm SL (fig. 8); MTD F 33490, 1 male, 27.0 mm SL; MTD F 33491, 1 male, 31.4 mm SL; MTD F 33492, 1 male, 38.3 mm S mm SL; same data as given for holotype MUSM 43070, 1 male, same data as holotype, except: preserved August 2015 (not used for biometrics).

**Supplementary material** (non types): 125 live  $F_1$  individuals of both sexes kept in the aquarium for behavioural studies; these will later either be transferred to MUSM, MTD F, and FMNH as "*authorized specimens*" (*cf.* Römer *et al.* 2012; Zarske, 2011), or kept in the personal collection of UR after preservation.

**Diagnosis:** Apistogramma wolli sp. n. is a medium-sized (males to 62 mm, females to 40 mm SL), laterally compressed, moderately high-backed and elongate Apistogramma species of the Apistogramma nijsseni complex, exhibiting pronounced sexual dimorphism and dichromatism. It is distinguished from all other Apistogramma species known to date on the basis of a combination of the following characters: adult males with massive jaws and hypertrophied yellow lips; dorsal fin with serrated membranes, truncated in females; small (but in females large) squarish lateral spot on centre of vertical bar 3; large round, in females upright oval, caudal spot; caudal fin lyrate, in females rounded, with red marginal band to upper and lower lobes.

#### Description

**Morphological characters:** (taken from 5 specimens: holotype and 4 paratypes, 26.9 to 51.2 mm SL). For biometric data see tables 1 & 2, for meristic data see table 3.

**Habitus** (figs. 7–18): *Apistogramma wolli* sp. n. is a rather robust looking, sexually dimorphic species with a fairly deep body, as is typical for species of this group



Fig. 3. Apistogramma payaminonis, live dominant male, slightly aggressive. Photo: F. M. Warzel; Warzel Archive © U. Römer.



Fig. 4. Apistogramma payaminonis, live dominant male, neutral mode. Photo: F. M. Warzel; Warzel Archive © U. Römer.

of related species within the genus. Differences in morphometrics between the sexes are evident, but statistical evaluation has to be postponed until larger series of this new species are available for analysis. Information on biometric proportions taken from non-preserved specimens has been included.

Body fairly deep (33.3-38.2 % SL), distinctly compressed laterally (width only about 18 to 19% of SL), about 1.5 times to twice as deep as wide, head relatively short (32.1-33.3 % SL).

Adult males usually about 20–25% larger than females, with slightly larger eye, larger head depth, cheek depth, preorbital depth, lower jaw, caudal-peduncle depth, noticeably longer dorsal-fin base and last dorsal spine. Upper head profile regularly convex; lower head profile only slightly convex, in large males approximately 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, large, jaws massive, lower jaw comparatively short



Fig. 5. Apistogramma payaminonis, live female, subdominant, stress coloration. Photo: F. M. Warzel; Warzel Archive © U. Römer.



Fig. 6. Apistogramma payaminonis, live female, neutral breeding coloration. Photo: F.M. Warzel; Warzel Archive © U. Römer.

(12.5–15.0 % SL), allometry of jaws roughly linear (material limited); lips thick, hypertrophied, and folded; maxillary extending to vertical before anterior margin of pupil; eye size average for the genus, diameter 10.6–13.4 % SL; cheek and operculum completely scaled, scales fairly large, pattern as shown for *Apistogramma payaminonis* in Kullander (1986); 5 dentary and 3 infraorbital pores, pattern as for *Apistogramma payaminonis* in Kullander (1986). Ventral fin (V I.5 (n=5)) only slightly prolonged, in both males and females only exceptionally extend-

ing to anus, in no specimen examined extending beyond anal-fin base. Pectoral fin (12 (n=5)) rounded. Dorsal fin (D. XVI.5 (n=1), XVII.3 (n=1), XVII.4.i (n=1), XVII.5.i (n=2)) with length of spines increasing from D1 to D6 in both sexes, thereafter remaining roughly constant, last dorsal spine normally slightly longer; in adult males serrate dorsal membranes significantly prolonged past tips of spines, extensions of all membranes about third of length of spines, lappets 4 to 6, rarely 7, longest; soft-rayed portion of fin pointed, extending back to about



Fig. 7. Apistogramma wolli sp. n., holotype, MUSM 43068, male, 51.2 mm SL, habitus; a) 1 week and b) 1 year after preservation.

centre of caudal fin; in females dorsal membranes short and truncated, lacking any extensions; soft-rayed portion of fin usually rounded, exceptionally slightly pointed, only reaching to first third of caudal fin. Anal fin (A. III.5 (n=1), III.6 (n=1), III.6.i (n=2), III.7 (n=1)) in adult males pointed with soft portion extending to centre of caudal fin; in females and smaller males rounded, when folded extending to first third of caudal fin. Caudal fin with 15 (n=1) to 16 (n=4) principal soft rays; in mature males of about 30 mm SL or larger initially truncate, later clearly lyrate, symmetrical, caudal rays V2 (-3) and D2 (-2) prolonged relative to remainder (approx. up to 2 % of SL), intervening rays around same length and thus forming straight edge, outer rays decreasing continuously in length; in females and juvenile males regularly rounded; caudal fin in both sexes scaled on first third to half. In adults caudal peduncle about third deeper than

long. Scales in median longitudinal row 20 to 22 (20 (n=1), 21 (n=3), 22 (n=1)); 16 scales around caudal peduncle (n=6). Vertebrae 11+12=23 (n=1) 11+13=24 (n=1), (including last half centrum) (fig. 9). Dentition, gill rakers, and pharyngeal elements have been excluded from this study, as these form part of further research still in progress (Mühle *et al.* in prep.).

Coloration of preserved specimens (described after preservation for eight months to two and a half years in 90% ethanol; only slight differences in intensity of coloration between specimens after different times of conservation, fresh material from 2014 overall slightly darker) (figs. 7-8): Basic colour of body predominantly light greyish to brownish, somewhat darker on dorsum in some specimens, especially males. Upper body above lateral band significant darker than lower, more brown-

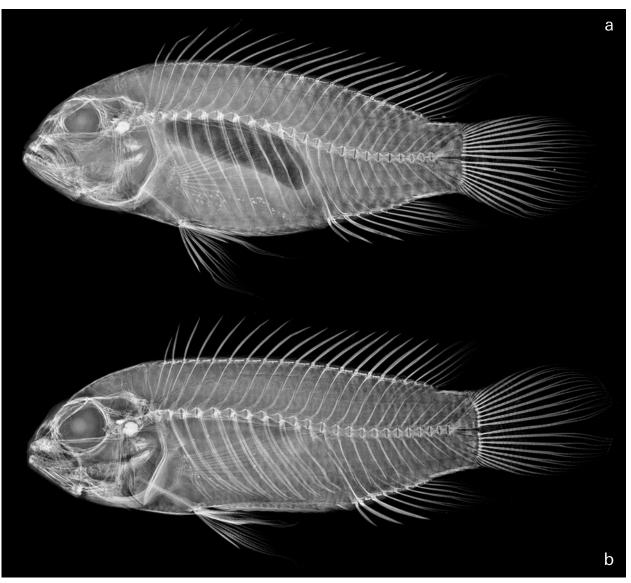




**Fig. 8.** Apistogramma wolli sp. n., paratype, MUSM 43069; female, 38.4 mm SL, habitus, showing typical colour pattern; **a**) 1 week and **b**) 1 year after preservation.

ish in males, greyish in females. Margins of body scales with somewhat darker edgings created by dense rows of blue (males) or black (females) spots. Pre-orbital, unscaled lower part of cheek, pre-operculum, infraorbital, lower jaw, and pectoral-fin base whitish in males; in females pre-orbital, pre-operculum, unscaled lower part of cheek, and posterior half of lower jaw brownish with milky overlay, pectoral-fin base greyish with black pigment and large black spot framing it along upper edge. In males lips basically blue (fresh material) or brownish with whitish overlay (after several months of preservation), in females milky greyish blue. Interorbital stripe absent in most specimens, in few small individuals slight counter-shading present, hardly visible. In both sexes scaled parts of cheek and operculum light brownish; operculum with black cheek stripe; cheek stripe in males initially as wide as pupil, beginning between foramina 1

and 2 of posterior orbital of suborbital series (for terminology see Kullander 1987), running back- and downwards in straight line between lateral canal foramina (LCF) 10 and 11 across posterior half of cheek to lower posterior margin of operculum, tapering to only half its initial width; stripe in same position in females, but around twice to three times as wide as in males. Blackish grey nasal stripe measuring about 10 % of orbit diameter, visible in all specimens. Chin and branchiostegal membrane light grey to whitish in males, lacking any black pattern, likewise entire ventral surface; females completely different: basic colour of ventral surface whitish grey, typical pattern of black markings comprising a) black line on branchiostegal membrane from point immediately below anterior edge of orbit to posterior lower margin of operculum, b) black spot on chest before ventral-fin base, c) black mid-ventral stripe running



**Fig. 9.** *Apistogramma wolli* sp. n., x-rays of: MUSM 43068, holotype, male, 51.2 mm SL (top); MUSM 43069, paratype, female, 38.4 mm SL (bottom). Digital x-rays: L. Fels, N. Leiwes, & C. Mühle.

backwards from about 2 to 3 scales behind ventral-fin insertion to outer margin of anal fin, ending approximately at tip of fourth soft ray (see fig. 19b). Small brownish anal spot present in most specimens studied. Lateral band straight, extending from posterior edge of orbital to last scale on body just above middle of caudal-fin base, clearly separated from caudal-fin spot; about one scale wide in males for most of its length, slightly narrower next to head; about 20 to 25 % wider in females. Two (males) to three (females) regular rows of squarish to upright rectangular or oval abdominal dots visible in most specimens, parallel to and below lateral band, all spots equal in size, one positioned on distal edge of every body scale below lateral band; pattern reminiscent of spot patterns in e. g. Apistogramma atahualpa Römer, 1997, Apistogramma huascar, and above all Apistogramma payaminonis. Forehead and predorsal area from interorbital to dorsum below first dorsal spine dark grey to blackish. Iris dark bluish grey or black, pupil white. In females distinct squarish to upright oval lateral spot at position of vertical bar 3, about 2 to 3 times wider than lateral band and occupying 3 scales longitudinally and 3 to 4 vertically; significantly smaller and hardly visible in males. Seven vertical bars on body visible only in sub-adult to semi-adult individuals, narrow below lateral band, as wide as interspaces; wider on dorsal part of body, interspaces about half as wide as bars. Six to seven dorsal spots visible in both sexes, about one scale high, as wide as dorsal vertical bars. Caudal spot squarish in males, occupying about half or more of caudal-peduncle height, roughly upright oval to half-moon-shaped in females, occupying about 90% of caudal-peduncle height. Under microscope caudal fin with small light greyish to brownish spots (melanophores), producing more or less uniform cloudy milky to greyish white impression, in males upper and lower distal fifth slightly darker with translucent edges to membranes; in both sexes entire fin without any band or spot pattern. Basic colour of all



**Fig. 10.** *Apistogramma wolli* sp. n., holotype, MUSM 43068: live coloration, male, neutral mood shortly before preservation.



**Fig. 11.** *Apistogramma wolli* sp. n., holotype, MUSM 43068: live coloration, male, dominant, slightly aggressive.



**Fig. 12.** *Apistogramma wolli* sp. n., holotype, MUSM 43068: live coloration, male, dominant; breeding coloration, aggressive.



**Fig. 13.** *Apistogramma wolli* sp. n., paratype, MUSM 43069: live coloration, female, dominant; breeding coloration, aggressive.



**Fig. 14.** *Apistogramma wolli* sp. n., paratype, MUSM 43069: live coloration, female, dominant; breeding coloration, aggressive while caring for fry.

other fins likewise cloudy milky to pale grey. Pectorals finely pigmented blackish or bluish along rays, intervening membranes milky. Ventral fins in males lacking dark markings, in females anterior part along spine and adjacent two (rarely three) soft rays densely speckled with black, leaving about one quarter of fin blackish grey. Anal fin with faint greyish (males) or blackish (females)



**Fig. 15.** *Apistogramma wolli* sp. n., paratype, MUSM 43069: live coloration, female, ventral view, dominant; breeding coloration while caring for larvae, typical black ventral pattern.



**Fig. 16.** *Apistogramma wolli* sp. n., paratype, MUSM 43069: live coloration, female, frontal view, dominant; breeding coloration while caring for larvae, typical black throat and breast pattern.



**Fig. 17.** *Apistogramma wolli* sp. n., holotype, MUSM 43068: live coloration, male, frontal view, dominant; in breeding coloration, showing typical massive jaws and thick lips.



**Fig. 18.** *Apistogramma wolli* sp. n., live coloration: female paratype, MUSM 43069, dominant; breeding coloration while caring for fry about 1 month of age; male in background.

edging. Coloration of dorsal greyish on spines, whitish along membranes, lacking bands or other distinct markings except darker first membranes: in males first, in females first two membranes and spines black, in some subadult males dark greyish.

**Coloration of live specimens and sexual dichromatism** (figs. 10–18): *Apistogramma wolli* sp. n. is highly sexually dimorphic and dichromatic.

Males (figs. 10-12, 17-18) polychromatic, with overall light bluish colour on body when mature, but

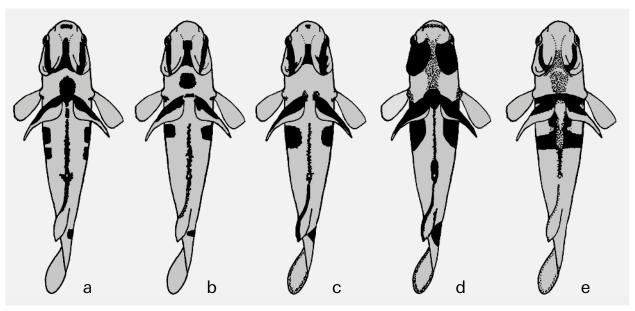


Fig. 19. Black ventral pattern of typical adult brooding females of five *Apistogramma* species: a) *A. payaminonis*, b) *A. wolli* sp. n., c) *A. feconat* sp. n., d) *A. nijsseni*, and e) *A. panduro*.

may also appear yellowish or green. Some large individuals with light pinkish hue overlaying light blue on side below lateral band. Lips, cheek, and lateral parts of chin may appear yellow or orange. In old males lips may become more brownish, cheek and lateral part of chin bluish white or rarely light pinkish. Most males with light blue line following upper margin of cheek along infraorbital; frequently joined by irregular faint light blue spotting on cheek, occasionally extending onto gillcover. In females (figs. 13-16, & 18) cheek stripe pupil width at origin close to eye, running backwards to lower distal edge of gill cover, tapering to only about third of initial width; in males cheek stripe more regular, only about half pupil width, running from central lower eye to point on gill cover immediately below distal margin of cheek. Triangular nape spot well expressed in most moods in both sexes, broader in females than males, extending about halfway to base of first dorsal spine in females, about third of way in males. Nasal stripe in front of eye rarely visible, narrow, width about quarter pupil width, mostly reduced to oval spot in males, invisible in territorial or brooding females. Adult females with pattern of black markings on ventral surface comprising a) black branchiostegal membrane from point immediately below distal margin of lip fold to distal end of membrane, b) breast spot occupying about 2 rows of scales in front of ventral fin and leaving 2 to 3 rows unpigmented at fin insertion, in rare cases faint black line between ventral-fin bases (fig. 16), c) narrow midventral stripe running from quarter- to halfway between ventral insertion and anal opening, framing latter, then continuing for half outer margin of anal fin (fig. 15); areas between black markings white to porcelain; males without ventral markings. Adults of both sexes with broad somewhat irregular lateral band extending from behind orbit onto base of caudal fin, width about two

thirds scale height above pectoral-fin insertion and widening to 1.5 times scale height posteriorly. In some specimens scale edges significantly darker than rest of lateral band, creating impression of partially zig-zag band. In both sexes distinct lateral spot on position of vertical bar 3; in females about third body height, in males less strongly expressed, smaller, only about fifth body height (fig. 11-14). In adult males two rows of irregular small spots running parallel to lateral band from pectoral-fin insertion to caudal peduncle, each row following lower edge of first or second scale series below lateral band. Black marking on pectoral-fin base in both sexes, in males faint narrow black streak on upper edge of orange fin base, in females black half-moon-shaped spot on centre of fin base, at least half height of latter. Distinct caudal spot in both sexes; in males round to squarish, occupying half to two thirds caudal-peduncle height; in females upright oval, occupying about two thirds to three quarters caudal-peduncle height. Caudal fin without distinct markings except bright orange or red on upper and lower margins, significantly more strongly expressed and intensely coloured in males (figs. 10–13) than females (figs. 13-14, & 18); central part of caudal translucent hyaline in males, exceptionally in very large males with impression of slightly irregular bluish spot pattern, translucent to faint yellowish in females. In females first two dorsal-fin membranes sooty, basal third of remaining fin yellowish, central half yellowish overlain with blue metallic sheen, remaining distal part translucent; in males first membrane black, second greyish with blue sheen, central three quarters of remaining fin light metallic blue, less intense in soft caudal-most portion of fin, distal part translucent to yellowish, rarely orange, base of membranes along spines 5 to 6, (8) 9 to 10, 13, 16 to 18, and final soft rays with brownish marking deriving from dark spots on dorsum.

**Distribution and ecology:** The species is known only from around the terra typica in the wider vicinity of Cabo Pontoja in northwestern Peru (fig. 28); S. LLANOS (personal communication to UR and DPS) has reported collecting this fish in a few small, shallow blackwater rainforest streams (quebradas) along both sides of the border between Ecuador and Peru. The fish usually hide among the leaf litter, which (apart from scarce driftwood) is the main substrate covering the sandy bottom. He has also reported that population density at collection sites is usually comparatively low and rarely exceeds one specimen per square metre, which makes commercial collection uneconomic and may be one of the reasons why the species is so rarely collected for commercial purposes. CHRISTOFFERSEN, WISE and others (personal communication with UR) have also visited the border area between Peru and Ecuador, in October 2012, together with local professional fishermen, and were able to collect a few specimens of the species described here. Water conditions on 5th October 2012 were as follows: temperature 24.7 °C, pH 6.3, conductivity about 40 to 60 µS/cm. So far none of the expedition members has reported breeding the species or published any article on its ecology. The fish presented by STAECK (2003) as Apistogramma payaminonis, which resemble the type specimens of the species described here only at first sight, were collected in the Río Aguarico system, which is part of the Rio Napo system further upstream. Nevertheless, the ecological information given by STAECK may also be relevant for Apistogramma wolli sp. n.. Generally speaking, information on the distribution and ecology of the new species is at best fragmentary and incomplete, and further field research is required.

**Biology:** At present no detailed reports on the behaviour of this species in the field or the aquarium are available. Only very few specimens have been imported in recent decades, most of them more or less accidentally. General behavioural features resemble those of close relatives such as Apistogramma baenschi, A. nijsseni, and A. panduro. The behaviour of the species listed above has been extensively described by Römer (1998, 2000a, 2006). Based on observations by DPS and UR, males of Apistogramma wolli sp. n. usually occupy large territories in which they allow a few females to settle. As soon as the dominant female is ready to spawn, she selects a spawning cave with a small entrance and hence inaccessible to the much larger male. Clutches can be quite productive, with about 200 fry or even more per brood being nothing unusual. Depending on water temperature, the eggs hatch after about 48 to 72 hours, and the larvae become free-swimming after another seven or eight days. Normally only the female practises brood care, but in rare cases accepts help from the male in guarding the offspring (fig. 18), as well as in retrieving them and carrying them to the centre of the territory. If conditions are optimal, the pair may care for the offspring for up to two months before they are chased away from the territory by the female, usually about one or two days before producing a new spawn.

Apistogramma wolli sp. n. prefers very soft (< 50  $\mu S$ ) and acid water (pH < 6) with a relatively low temperature of around 20 to 24 °C. When kept at higher temperatures the species has proved to be susceptible to several diseases such as skin fungus or bacterial infections of the fins. More detailed information will be available in a future publication by Römer & Soares (2015). But all in all our knowledge of the species' biology is still rudimentary, and its field biology in particular requires intensive research

**Etymology:** The species is named wolli, a noun in apposition, in honour of Wolfgang "Wolli" Friedrich. Wolfgang Friedrich was one of the most notable and skilled professional German fish breeders of recent decades until he finally closed down his facility in early 2014. Apart from different characids and catfishes, he was the first to breed several cichlids such as Dicrossus maculatus Steindachner, 1875 and various species of the African cichlid genus Schwetzochromis Poll, 1948. His long-term work in breeding cichlid fishes has substantially contributed to our present knowledge of this family of the Teleostei. Known to his friends by his nickname Wolli, Wolfgang Friedrich gave helpful and always constructive and mostly humorous comments on fish maintenance and breeding whenever required, positively influencing the work of several ichthyologists including the senior author of this paper.

# Apistogramma feconat sp. n.

(figs. 20-27)

Apistogramma sp. "Zwilling" Römer & Pretor, 2003b: 22–23 (photographs of live specimens).

Apistogramma sp. "Zwilling/Twin" Römer, 2006: 1126–1147 (photographs of live specimens including fry and juveniles, sketch of typical male and female).

Apistogramma sp. (Zwilling) STAECK & LINKE, 2006: 185 (photographs of live specimens)

**Holotype** (fig. 20, see also Römer, 2006: 1128, top): MUSM 43066, male, 39.0 mm SL, Peru, Departamento Loreto, District Instituto, just outside Zona Reservada Pucacuro, "headwaters" of small right-hand forest stream feeding the Rio Pucacuro, about 10 km from the confluence of the Rio Pucacuro with the Rio Tigre (about 75°02′ W / 03°14′ S); August 2012, leg.: Albertino MacAuber.

**Paratypes**: 3 specimens: <u>MTD F 33489</u>, female, 24.6 mm; <u>MUSM 43067</u>, female, 35.6 mm SL (fig. 21, see also Römer, 2006: 1128, second from top); <u>MTDF 32703</u>, male, 40.5 mm SL; all same data as given for holotype.

**Supplementary material** (non types): 18 males and 13 females, tank-raised  $F_1$  generation, which will be kept in the personal collection of UR after preservation.

**Diagnosis.** Apistogramma feconat sp. n. is a small to medium-sized (males up to 40 mm, females to 36 mm SL),



Fig. 20. Apistogramma feconat sp. n., holotype, MUSM 43066, male, 39.0 mm SL, about one year after preservation.



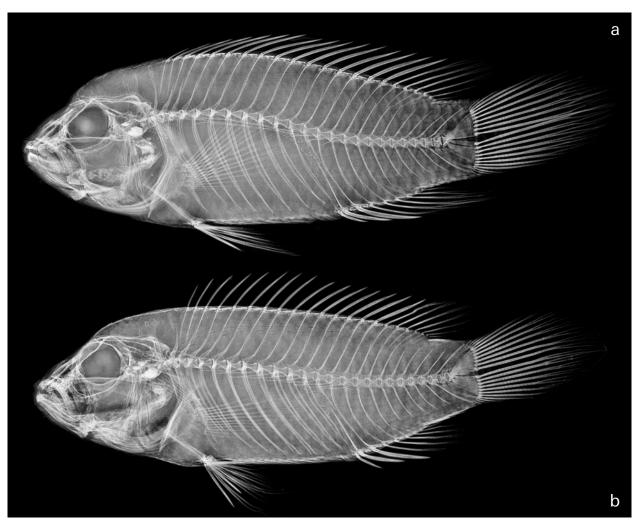
Fig. 21. Apistogramma feconat sp. n., paratype, MUSM 43067; female, 31.4 mm SL, about 1 year after preservation.

moderately high-backed, laterally compressed, and moderately elongate Apistogramma species of the Apistogramma nijsseni complex, exhibiting distinct sexual dimorphism and dichromatism. It is distinguished from all other Apistogramma species known to date on the basis of a combination of the following characters: Adult males with fairly large yellow to orange head and metallic blue or pinkish body; overall grey slightly hypertrophied lips; bluish or pinkish dorsal fin with slightly prolonged serrated membranes, tips yellowish; large rhombic caudal spot, rounded caudal fin with bright orange to red submarginal and black marginal band. Females with large lateral spot about half body height; broad cheek stripe, nape spot, and pectoral spot; small chin spot; squarish throat spot, clearly separated from broad mid-ventral stripe extending onto anal-fin margin.

#### Description

**Morphological characters:** (taken from 4 specimens: holotype and 3 paratypes, 24.6–40.5 mm SL) For biometric data see tables 1 & 2, for meristic data see table 3.

**Habitus** [figs. 20–27, for additional sketches of habitus see Römer (2006a)]: The body of this sexually dimorphic species is fairly deep (35.3–39.4 % SL, mean 38.0 % SL), distinctly compressed laterally, about twice as deep as wide, with a moderately long head (33.8–36 % SL, mean 35.2 % SL), producing an overall fairly robust appearance. There are a number of significant morphological differences between the sexes. Adult males usually about fifth to quarter larger than females, with signifi-



**Fig. 22**. *Apistogramma feconat* sp. n., x-rays; **a**) MUSM 43066, holotype, male, 39.0 mm SL; **B**) MUSM 43067, paratype, female, 31.4 mm SL. Digital x-rays: L. Fels, N. Leiwes & C. Mühle.

cantly larger lower jaws, but no other relevant differences in proportions detectable from limited material. Upper head profile almost regularly convex, slightly flattened above eye in medium-sized individuals, in large individuals with indentation above anterior third of eye, more strongly expressed with increasing size of specimen, producing humped appearance; lower head profile regularly convex to lower posterior edge of unserrated operculum. Mouth terminal, large, jaws stout, lower jaw comparatively short (about 10.8–16.0 % SL, mean 12.7 % SL); lips thick, slightly hypertrophied, folded; maxillary extending to around vertical below anterior margin of pupil; eye relatively large (diameter 11.0-13.4 % SL); cheek and operculum completely scaled in adult males over 28 mm SL, partially naked ventrally and anteriorly in smaller specimens; 5 dentary and 3 infraorbital pores. Ventral fin (V I.5 (n=4)) pointed in males, rounded in females; normally only slightly prolonged, in males exceptionally extending to anus (information taken from additional material), not extending to anal-fin base. Pectoral fin (11 (n=1), 12 (n=3)) rounded. Dorsal fin (D. XV.7 (n=1), XVI.5.i (n=1), XVI.6.i (n=1), XVII.6 (n=1)) with length of spines increasing from D1 to D6 in

both sexes, thereafter remaining slightly shorter than D6 until third last, last three dorsal spines about as long as D6, with last spine longest; in adult males upper margin of fin serrate, dorsal membranes significantly prolonged past tips of spines, extensions of all membranes except D1 about 10 to 20 % longer than spines, lappets 2 to 7 usually longest; in females dorsal-fin membranes not prolonged, truncated at tips of spines; soft-rayed portion rounded in both sexes (n=4), exceptionally slightly pointed in larger males (n=1), extending back to centre of caudal fin (information supplemented from additional material). Anal fin (A. III.6 (n=2), III.7 (n=2)) rounded in all specimens, soft portion extending only to first third of caudal fin (n=2), in females and smaller individuals extending onto first fifth of caudal fin when folded (n=2)(same in additional material examined: n=25). Caudal fin with 16 (n=4) principal soft rays; in all specimens rounded, independent of size; in both sexes scaled on first third to half. Caudal peduncle about 30 % deeper than long in all specimens. Scales in median longitudinal row 21 (n=4); 16 scales around caudal peduncle (n=4). Vertebrae (including last half centrum): 11+13=24 (n= 2) (fig. 22). Dentition, gill rakers, and pharyngeal ele-

ments have been excluded from this study, as these form part of further research still in progress (Mühle *et al.* in prep.).

Coloration of preserved specimens (described after preservation for six months (n=2) and two years (n=2)in 75% ethanol; only marginal differences in intensity of coloration visible between specimens after different periods of conservation, fresh material slightly darker) (figs. 20-21): Basic colour of body predominantly yellowish to light brownish, darker on dorsum in most specimens, body scales with darker margins, more intense in females than males. Lips, unscaled lower parts of cheek, preoperculum, lower jaw, and pectoral-fin base cream to whitish; in few specimens lips with fine greyish pigmentation on anterior parts. Interorbital stripe visible only in few specimens, about wide as pupil. Preorbital, scaled parts of cheek, and operculum light brownish; operculum with lighter area directly above dark grey to blackish cheek stripe; cheek stripe in males barely wide as pupil, beginning between foramina 1 and 2 of posterior orbital of suborbital series, running backwards in roughly straight line between LCF 10 and 11 across posterior half of cheek to lower posterior margin of operculum; in females significantly wider, pupil width at infraorbital, about orbit width on lower cheek and gill cover. Preorbital stripe light grey, about half width of pupil, barely visible in most specimens. Chin and central parts of branchiostegal membrane porcelain or creamy whitish in males; in females only faint black pigmentation below lip and branchiostegal membrane, greyish in posterior third. Forehead and predorsal region from interorbital to below first dorsal spine greyish. Iris bluish grey, darker in females. Faint midventral stripe and anal spot in all females studied. Lateral band straight, about one scale high, extending from posterior edge of orbital to just above middle of caudal-fin base just before caudal spot, occasionally absent in large females. Conspicuous round to oval lateral spot at position of vertical bar 3, about as wide as lateral band in larger males, about 3 scales wide and twice as high as lateral band in most juveniles and females. Only vertical bars 3 to 7 expressed, if visible at all, on upper half of body in large individuals, bar 3 about as wide as interspace to bar 4, all others about twice as wide as interspaces. Dorsal spots visible in males, absent in females. Caudal spot rhombic, visible in all type specimens; in additional material irregular squarish or upright oval in some males, round in juveniles and smaller females; occupying about 90% to complete height of caudal-fin base. In large males three irregular rows of blackish spots on caudal peduncle, reminiscent of spots above anal-fin base in types of Apistogramma atahualpa, Apistogramma huascar, Apistogramma payaminonis, and Apistogramma wolli sp. n.; under microscope caudal fin with small melanophores on membranes between rays, producing cloudy milky to greyish white appearance, no pattern of spots or lines on centre of fin, but, as known from Apistogramma nijsseni and other congeners, distinct light submarginal and black marginal

band framing distal edge; pattern in females less intense, but still visible. Pectoral fin finely pigmented with small melanophores along rays. Ventral fin in males without any dark markings, in females overall slightly greyish, anterior part along spine and adjacent three (rarely four) soft rays uniformly speckled with melanophores. Basal parts of anal fin yellowish white, hard rays and distal third of soft rays with greyish edging. No stripe pattern on soft portions of dorsal and anal fins. Coloration of dorsal fin overall whitish, with irregular pattern of melanophores along rays, rays and distal 10 % of membranes between third and last hard rays hyaline translucent, but no distinct marginal banding, stripes, or other markings except first two membranes significantly darker, in males brownish, in females blackish.

**Coloration of live specimens and sexual dichromatism:** (figs. 23–27) *Apistogramma feconat* sp. n. is highly sexually dimorphic and dichromatic.

Males (figs. 23-25) polychromatic, with overall firstquarter body yellowish or brownish orange, rest of body light bluish when mature. Exceptionally large individuals sometimes with light pinkish hue overlaying light blue on posteriormost side of body. Lips either greenish, or upper lip yellowish brown and lower bluish in males, greyish yellow or greenish yellow in females. Cheek and lateral parts of chin in most males bluish white or grey, rarely yellowish green; gill cover yellow with some metallic blue spotting; rest of head greenish or loam yellow in males, yellowish brown in females, in both cases except for black markings. Usually no conspicuous blue markings on cheeks. Cheek band in females at least twice pupil width, occupying about half cheek and lower part of gill cover; in males less conspicuous, only about twice pupil width; in both sexes running straight from below eye to lower distal margin of gill cover. Nape spot well expressed in both sexes, roughly triangular in females, squarish to oval in males, extending about halfway to base of first dorsal spine. Nasal stripe in front of eye distinct but rarely visible, narrow, width about half that of pupil, mostly reduced to oval spot, hardly visible in brooding females. Adult females (figs. 26-27) with pattern of black markings on ventral surface (fig. 19c), comprising a) small black chin spot immediately below lower lip, b) black branchiostegal membrane from point immediately below posterior margin of eye to shortly before distal end of the membrane, c) small breast spot occupying about two rows of scales at base of ventral fin, d) broad mid-ventral stripe running from slightly posterior ventral-fin base along centre of body, framing anal opening, then continuing along outer margin of anal fin to tip of soft portion; areas between black markings yellow to whitish yellow; no ventral markings in any male examined. Lateral band in adults about one scale wide, extending onto base of caudal fin and merging with caudal spot, somewhat irregular in shape as often faded in central part; sometimes scale edges darker than rest of lateral band, creating zig-zag appearance, and if so darker zone on caudal peduncle formed by black dashes below



**Fig. 23.** Apistogramma feconat sp. n., live coloration: adult male (not preserved), territorial dominant; violet coloration in dorsal fin and slight indication of second lateral spot on vertical bar 4.



**Fig. 24.** Apistogramma feconat sp. n., live coloration: adult male (not preserved), territorial, highly aggressive, pronounced black zone on lower half of caudal peduncle.

lateral band also pronounced (see below) (figs. 24–25). In both sexes distinct lateral spot on position of vertical bar 3, large, roughly oval, in females about half body height, occupying three or more scale rows and four to six adjacent scales in each row (fig. 26); in males nearly same size, if visible (fig. 23). In adult males two to three rows of irregular dashes running parallel to lateral band from caudal peduncle to origin of pectoral fin, each row of dashes coinciding with anterior edges of scales of first to third series below lateral band, forming almost com-

pletely black area on caudal peduncle in some individuals (figs. 24–25), reminiscent of *Apistogramma panduro* (fig. 32) or male *Apistogramma eremnopyge* Ready & Kullander, 2004. Black marking on pectoral-fin base in both sexes: in males narrow black streak on upper edge of whitish grey fin base; in females black half-moonshaped spot about half to two thirds height of fin base. Distinct caudal spot in both sexes, rhombic, occupying full height of caudal peduncle in females (fig. 26), upright oval or rarely squarish in males, occupying about



Fig. 25. Apistogramma feconat sp. n., live coloration: adult male, display in front of juvenile female; both specimens not preserved.



**Fig. 26.** Apistogramma feconat sp. n., live coloration: adult female (not preserved), breeding coloration, typical black pattern when guarding fry.

75 to 80 % of caudal-peduncle height. Caudal fin with conspicuous markings in both sexes, with red, orange, or yellow sub-marginal band (fig. 23–26), in males black outer margin, absent in females, comparable to tail pattern in *Apistogramma nijsseni* (fig. 29), significantly more intense and conspicuous in males than females; central parts of caudal hyaline blue or greenish in males, translucent to faint yellowish in females. In females first two and lower half of third dorsal-fin membranes sooty, rest of fin translucent yellowish, in some cases with nar-

row dusky outer margin, dark grey or blackish; in males first dorsal-fin membrane black, second greyish with blue, violet, or green sheen, central three quarters of remaining fin along hard rays sky blue or violet, soft portion of fin either metallic greenish or yellowish, distal quarter of fin yellowish, rarely orange; no other black markings on fin.

**Distribution and ecology:** The species is known only from around the *terra typica*, the lower part of the Río



**Fig. 27.** Apistogramma feconat sp. n., live coloration: adult female (not preserved), highly aggressive, typical pattern when defending larvae.

Pucacuro northwest of Intuto in northern Peru (fig. 28). So far collections of the species have been made only on the left-hand side of the Rio Tigre. Even though at least five other species of the genus are known from the Rio Tigre system, there is no indication of any distributional overlap between *Apistogramma feconat* sp. n. and other, closely-related, species of the *Apistogramma nijsseni* complex.

The team of Tom Christoffersen (pers. com.) collected the species in 2010, but in spite of this there are to date no detailed reports on the field biology of this new species of Apistogramma. According to Christoffersen, Apistogramma feconat sp. n. appears to be limited to small clear- or blackwater forest streams. Water chemistry often changed considerably following heavy rainfall, and visibility within the water was very low. Water conditions measured: pH 5.78, conductivity 11 µS/cm, and temperature close to 27 °C. Leaf litter and dead wood were the only shelter available for small fish such as Apistogramma. The typical bottom substrate in this area is usually red or yellow latosol. The whole area is protected as a national forest reserve (Zona Reservada Pucacuro), and is still covered by dense primary forest. As well as Apistogramma feconat sp. n., several specimens of another as yet undescribed Apistogramma species and several Nannostomus morthenthaleri PAEPKE & Arendt, 2001 have been collected here. Further intensive field study is required to rectify our currently inadequate knowledge of the distribution and ecology of Apistogramma feconat sp. n.

**Biology:** The only substantial information on biology available is that published by RÖMER & PRETOR (2003) and RÖMER (2006). These papers are based exclusively on aquarium-based study and include detailed information on the species under its aquarium-hobby name of Zwillings or Twin *Apistogramma*. The species originates from an area in Peru that has recently been declared a national disaster area by the government (see below), hence any information on field ecology, behaviour, and species assemblages, including all data on actual collecting sites, is needed in order to evaluate whether the species is be under threat from changes in the local environment.

**Etymology:** The species name *feconat* is a noun in apposition. Because the new species originates from tributaries of the upper and middle Rio Tigre, the name has been chosen to honour the Federation of the Native COMMUNITIES OF THE TIGRE (FECONAT) for its struggle to protect the environment of the tribal lands of the local native people from the impact of modern society. FECONAT's priorities reflect the modern concept of sustainable environmental usage: the exploitation of natural resources, both current and fossil, should be nondestructive, with the emphasis on renewability and fair trade (i.e. fostering the economic and ecological interests of local people). The ongoing battle for Indian civil rights by FECONAT against powerful industrial opponents has repeatedly brought severe environmental problems to public awareness.

**Discussion:** When Kullander (1986) published the description of *Apistogramma payaminonis*, the problem of the systematic position of *Apistogramma nijsseni* seemed to be solved. In the years that followed, however, the Peruvian Loreto turned out to be home to several additional species closely related to those two taxa. First of all *Apistogramma norberti* Staeck, 1991 was discovered in right-bank tributaries of the Amazon River; then a whole series of species in the left-hand tributaries: *Apistogramma panduro* Römer, 1997, *Apistogramma martini* Römer, Hahn, Römer, Soares & Wöhler, 2003, *Apistogramma pantalone*, *Apistogramma rositae*, *Apistogramma wolli* sp. n., and *Apistogramma feconat* sp. n., as well as at least four further undescribed species that have been collected to date.

Based on cluster analysis performed on 116 species-level taxa, the genus *Apistogramma* has been split into three major lineages, the *A. agassizii*, *A. regani*, and *A. steindachneri* lineages (Römer, 2006). The species of the *Apistogramma agassizii* lineage can be distinguished comparatively easily from all other members of the genus by having a long, slender body. Species of the *Apistogramma regani* lineage are characterised by complete set of four infraorbital and five dentary pores, usually intense pattern of vertical bars, lacking distinct lateral spot and large dark chest blotches in females of all known species. They can additionally be distinguished from species of the *Apistogramma steindachneri* lineage by the latter having massive jaws and reduced infraor-

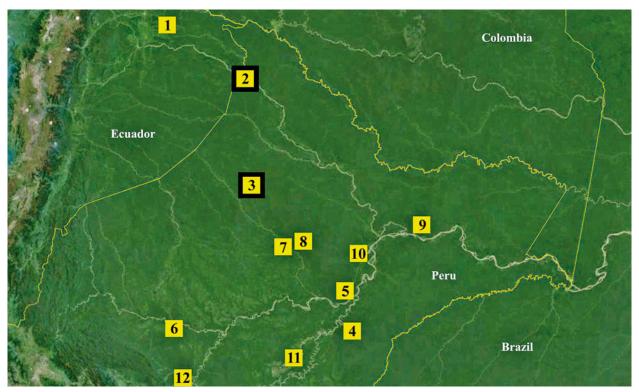


Fig. 28. Known collecting sites (squares) for species closely related to *Apistogramma nijsseni* in Northern Peru and adjacent countries. 1: *Apistogramma payaminonis.*, 2: *A. wolli* sp. n. (type area), 3: *A. feconat* sp. n. (type area), 4: *A. nijsseni*, 5: *A. panduro*, 6: *A. rositae*, 7: *A. pantalone*, 8: *A. martini*, 9: *A. barlowi*, 10: *A. atahualpa*, 11: *A. huascar*, 12: *A. baenschi*. Yellow lines denote country boundaries, black frames indicate type locations of species described in this paper.

bital pores (three vs. four). *Apistogramma payaminonis*, as well as the two species described here, belongs to the *Apistogramma steindachneri* lineage.

The Apistogramma steindachneri lineage further contains three species complexes comprising taxa most closely related to Apistogramma steindachneri REGAN, 1908, Apistogramma cacatuoides Hoedeman, 1951, or Apistogramma nijsseni. The three taxa dealt with in this paper can be distinguished from species of the Apistogramma steindachneri complex by completely different colour pattern, reduced number of infraorbital pores (vs. complete set), and in males massive jaws with hypertrophied lips (vs. normal proportions); from most of the species assigned to the Apistogramma cacatuoides complex by either: rounded caudal fin (versus forked), coloration of caudal fin (continuous red submarginal band), different dorsal-fin shape; or black pattern on underside in females (fig. 19). Thus the species described in this paper need only to be differentiated from their closest relatives, the members of the Apistogramma nijsseni complex.

In addition to overall different live coloration, males of both *Apistogramma feconat* sp. n. and *Apistogramma wolli* sp. n. differ from those of *A. martini* (fig. 30), *A. nijsseni*, and *A. pantalone* (fig. 31) by serrated dorsal-fin margin with extended fin lappets (*vs.* unserrated and short dorsal-fin membranes); from *A. panduro* (fig. 32) and *A. rositae* (fig. 33) by lacking sooty spot on caudal peduncle extending to centre of caudal fin; from *A. payaminonis* (figs. 1, 3–6) by generally relatively shorter

last anal-fin spine and only one lateral spot (vs. two); from *A. baenschi* (fig. 34) by lacking vertical bars; from *A. norberti* (fig. 35) by lacking black chin spot.

Even at first sight males of *Apistogramma wolli* sp. n. cannot be mistaken for any of the related species except *A. payaminonis*. They clearly differ from the latter taxon by relatively shorter head and greater pre-dorsal length relative to head length, form of lateral band, shape of caudal spot, and overall coloration. In addition to overall coloration, they differ from males of *A. baenschi* and *A. huascar* (fig. 36) by shorter dorsal-fin lappets 2 to 7; from *A. barlowi*, *A. huascar* and *A. nijsseni* by significantly larger caudal spot; from the latter species and *A. atahualpa* (fig. 37), *A. feconat* sp. n., *A. norberti*, *A. panduro*, and *A. rositae* by lyrate caudal fin (vs. rounded).

Males of Apistogramma feconat sp. n. cannot be mistaken for any of the related species except the very similar A. nijsseni and A. panduro. They clearly differ from A. nijsseni by shape of dorsal fin; from A. panduro by completely different live coloration; from A. payaminonis and A. wolli sp. n. by relatively longer head (also in correlation to shorter anal fin spine) (fig. 38); from A. atahualpa, A. norberti, and A. rositae by having red submarginal caudal-fin band; from A. norberti by lacking black spot on base of soft portion of dorsal fin; from A. atahualpa, A. barlowi Römer & Hahn, 2008, A. martini, A. pantalone, A. payaminonis, and A. rositae by having red submarginal and black marginal caudal-fin bands; from A. martini, A. pantalone, A. payaminonis,



Fig. 29. Apistogramma nijsseni, dominant adult male.



Fig. 30. Apistogramma martini, dominant adult male.



Fig. 31. Apistogramma pantalone, dominant adult male.



Fig. 32. Apistogramma panduro, dominant adult male.



Fig. 33. Apistogramma rositae, dominant adult male.



Fig. 34. Apistogramma baenschi, dominant adult male.



Fig. 35. Apistogramma norberti, dominant adult male.



Fig. 36. Apistogramma huascar, dominant adult male.

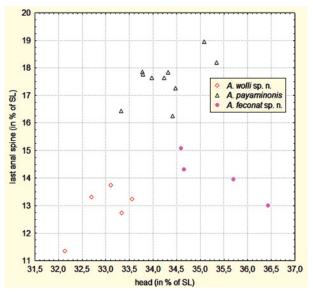


Fig. 37. Apistogramma atahualpa, dominant adult male.

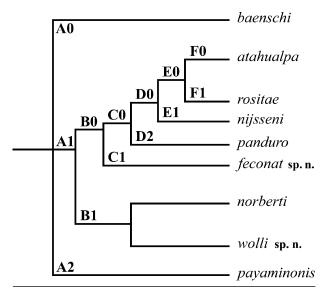
and *A. wolli* sp. n. by different caudal-fin shape (rounded vs. lyrate).

Females of both species described here as well as those of Apistogramma nijsseni, A. panduro, and A. payaminonis are easily distinguished by their unique ventralsurface patterns (fig. 19), consisting of species-typical combinations of various black elements, such as are also seen in some species of the Apistogramma macmasteri complex in the Apistogramma regani lineage. These black patterns are usually visible in mature females in breeding condition, exceptionally also in some subadult females when stressed. The most important diagnostic elements (clustered in fig. 39) are number and shape of lateral spots (state A2, present only in A. payaminonis); chin spot (present in A. feconat sp. n.); lower-lip stripe (or chin spot) (absent in A. wolli sp. n. and A. panduro); branchiostegal membrane spot (absent in A. nijsseni and A. panduro); breast spot separate to spot on ventral-fin base (state D1, present only in A. feconat sp. n.); caudal spots (absent in A. panduro); and extent of mid-ventral stripe (from ventral-fin base to along outer margin of anal fin in A. nijsseni and A. payaminonis; from behind base of ventral fin to along outer margin of anal fin in A. feconat sp. n.; from behind base of ventral fin to anal opening in A. panduro). Because these black patterns are unique to the individual species, females of A. payaminonis, A. wolli sp. n., and A. feconat sp. n. cannot be mistaken for any of the other related species or confused with one another.

During our field and laboratory studies it has become clear that the species richness within this group of small cichlids may still be significantly underestimated. This has also been confirmed by recent research on the molecular phylogeny of *Apistogramma* by members of our working group (Tougard *et al.*, submitted), which has identified at least six more new forms or species based on genetic studies. The study has also basically confirmed the status of the *Apistogramma* lineages mentioned above, which were originally identified using cluster analysis performed on a data set of morphological and behavioural characters from more than a hundred morphotypes or species (Römer, 2006 b, c), including *Apistogramma wolli* sp. n. and *A. feconat* sp. n. Using phylogenetic information from these studies [Römer, 2006 and Tougard

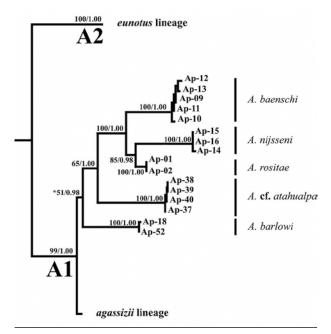


**Fig. 38.** Differentiating biometric proportions of three *Apistogramma* species. Relative length of last anal-fin spine plotted against relative length of head.

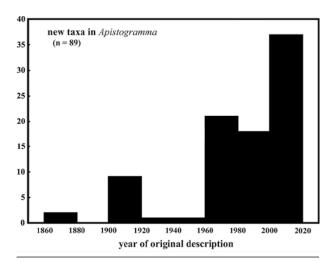


**Fig. 39.** Differentiation tree for females derived from dichotomous determination key based on black ventral-surface pattern: number of lateral spots (A0=absent, A1=1, A2=2 visible); lower lip stripe (B0=absent, B1=visible in most adults); branchiostegal membrane spot (C0=absent, C1=present), distinct breast spot (D0=absent, D1=separate from spot at ventral-fin base, D2=merging into spot at ventral-fin base); spot on ventral-fin base (E0=absent, E1=present), ventral stripe (F0=absent, F1=present). For more information see text. Note: This tree does not denote any phylogenetic relationships between the species included.

et al., submitted (fig. 40)], we predict that the two species described here will probably cluster between A. rositae and A. barlowi in future molecular studies. On the other hand, however, the systematic position of Apistogramma payaminonis still remains somewhat unclear in spite of the fact that the taxon is obviously a close relative of the Apistogramma nijsseni complex species.



**Fig. 40.** Tree of phylogenetic relations of selected species of the *Apistogramma nijsseni* complex, close related to *Apistogramma payaminonis* based on DNA-analysis. Extracted from Tougard *et al.* (subm.).



**Fig. 41.** The advance in species descriptions within the genus *Apistogramma* Regan since 1862: number of newly described species per 20 years. Note that the last column may yet increase further in number.

Endemic species belonging to an *Apistogramma* lineage or complex (as in the case of the species related to *A. nijsseni*) appear to be gradually distributed along the Amazon River and its tributaries (Römer, 2006), although at present it appears that genetically close species are not necessarily geographically close as well (fig. 28). This may be an artefact and actually reflect the current state of research rather than the real situation, as so far only comparatively few species have been adequately investigated. The discovery of *A. feconat* sp. n. and *Apistogramma wolli* sp. n. has in fact closed the geographical gap between collecting sites for *Apistogramma* 

*payaminonis* in northern Ecuador and its relatives in the Peruvian Amazon of Loreto.

We predict that the number of *Apistogramma* species known will rise significantly within the next few years. The taxonomic history of the genus underlines this statement: more than 25% of the known taxa have been described within the last decade (fig. 41). This reflects the situation in other systematic groups of small Neotropical fishes such as characids, rivulids, and catfish, where numerous species have likewise been discovered in the last few decades. Our own recent field research in the Peruvian Loreto has brought to light not only the species of Apistogramma described here, but also several other species of Neotropical dwarf cichlids, all within comparatively limited geographical areas such as the Peruvian Loreto. This should encourage other researchers such as ecologists and taxonomists to focus especially on the hyperdiversity of small Neotropical fishes.

#### **Conservation Status**

In spite of the lack of information about their ecology and population numbers, Apistogramma payaminonis, A. wolli sp. n., and A. feconat sp. n. must be considered potentially endangered as a result of their relatively restricted distribution area in the Peruvian Loreto. Any type of environmental change can pose a risk to fish with very limited ranges. Clear-felling of the forest adjacent to the type and only known locality for Apistogramma cinilabra Römer et al., 2011 has already put that species under threat. But this type of human impact is comparatively limited and may be compensated by surviving individuals and/or populations. Different and far more problematic effects can be expected from industrial exploitation of the Amazonian lowlands, e.g. by gold mining and oil drilling. The oil-drilling industry in particular has severe effects. Large parts of the region are under intensive industrial use. Parts of it have already been polluted by repeated oil spills from the oil-drilling area "Block A" in the area of the border with Ecuador. Investigations by the ALIANZA ARKANA (2014) have shown that contamination with heavy-metal and (poly)cyclic hydrocarbons are beyond legal limits in several areas in the Rio Tigre and Rio Corrientes drainages. The Peruvian government has recently declared large parts of the Amazonian lowlands of Loreto, including the Rio Tigre area, a "NATIONAL DISASTER AREA" and announced the development of a restoration plan and provision of financial help for local indigenous people (ALIANZA ARKANA, 2014; COLLYNS, 2013, 2015; Hill, 2010, 2014; OCAC-OEFA, 2015). The long-term impact of such large scale pollution cannot be estimated at the present time, but must be expected to last for years or eventually even decades. It is known from the laboratory that all Apistogramma species are extremely sensitive to a wide variety of chemicals such as heavy metals and polycyclic aromates (RÖMER, 2000, and UR & DPS unpublished data). In consequence all fish species with a restricted distribution within Loreto and adjacent

areas should be monitored on a regular basis and placed on the red data lists of Peru, Ecuador, and ultimately the IUCN, as potentially endangered.

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## References

- ALIANZA ARKANA (2014): Pastaza. film-documentation (url: http://vimeo.com/98252871).
- Collyns, D. (2013): Peru declares environmental state of emergency in its rainforest. The Guardian 26.3.2013.
- Collyns, D. (2015): Indigenous Peruvians win Amazon pollution payout from US oil giant. The Guardian 5.3.2015.
- Hill, D. (2010): Oil Spill Devastates Amazon Region in Peru. Upside Down World (Online Magazine): 7.7.2010) [http://

- upsidedownworld.org/main/peru-archives-76/2582-oil-spill-devastates-amazon-region-in-peru].
- Hill, D. (2014): Brazil's Javari valley threatened by Peruvian oil, warn tribes. – The Guardian 28.11.2014.
- Hoedeman, J.J. (1961): Notes on the Cichlid Family I: *Apistogram-ma cacatuoides* sp. n. Beaufortia, 4: 1–4.
- Kästner, N. (2000): *Apistogramma payaminonis*. Das Aquarium, **34** (12): 15–17.
- KULLANDER, S.O. (1979): Description of a new species of the genus *Apistogramma* from Peru. Revue Suisse Zoology, 86 (4): 937–945.
- Kullander, S.O. (1980): A Taxonomical Study of the Genus *Apistogramma* REGAN, with a Revision of Brazilian and Peruvian Species (Teleostei: Percoidei: Cichlidae). Bonner zoologische Monographien, **14**: 152 pp.
- KULLANDER, S.O. (1986): Cichlid Fishes from the Amazon River Drainage of Peru. – Swedish Museum of Natural History, Stockholm: 431 pp.
- Kullander, S.O. (1987): A new *Apistogramma* species (Teleostei, Cichlidae) from the Rio Negro in Brazil and Venezuela. Zoologica Scripta, **16** (3): 259–270.
- 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. (1997): Amerikanische Cichliden I: Kleine Buntbarsche. Tetra Verlag GmbH, Bissendorf, Stockholm: 109–110.
- MEINKEN, H. (1962): Eine neue *Apistogramma*-Art aus dem mittleren Amazonas-Gebiet, zugleich mit dem Versuch einer Übersicht über die Gattung. Senckenbergiana Biologica, **43**: 137–143
- OFICINA DE COMUNICACIONES Y ATENCIÓN AL CIUDADANO (OCAC-OEFA) (2015): El OEFA capacita a las federaciones indígenas de Loreto en fiscalización ambiental. – State official anouncement: 18, 3, 2015.
- PAEPKE, H.-J. & ARENDT, K. (2001): *Nannostomus marginatus mortenthaleri* new subspec. from Peru (Teleostei: Lebiasinidae). Verhandlungen der Gesellschaft für Ichthyologie: 143–154.
- Ready, J.S. & Kullander, S.O. (2004): *Apistogramma eremnopyge* a new species of cichlid fish (Teleostei: Cichlidae) from Peru. Zootaxa, **564**: 1–10.
- 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. (1991a): Eine geeignete Methode zur Geschlechterbestimmung einiger *Apistogramma*-Arten. DCG-Informationen, **22**(3): 70–72.
- RÖMER, U. (1991b): Ein weiterer Beitrag zur Geschlechterbestimmung einiger *Apistogramma*-Arten. DCG-Informationen, **22**(11): 228–230.
- RÖMER, U. (1992): Dritter Beitrag zur Geschlechterbestimmung einiger *Apistogramma*-Arten. DCG-Informationen, **23**(4): 86–88.
- 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. (1998): Cichlid Atlas 1: Natural history of neotropical dwarf cichlids. – Mergus Publishers, Melle, Germany: 666– 677
- RÖMER, U. (2000a): Cichlid Atlas 1: Natural history of neotropical dwarf cichlids. Mergus Publishers, Melle, Germany: 1311 pp.
- RÖMER, U. (ed.) (2006a): Cichlid Atlas **2**: Natural History of South American Dwarf Cichlids. Volume 2. – Mergus Publishers, Melle, Germany: 1319 pp.
- Römer, U. (2006b): Annotated list of characters for cluster analysis of the phylogenetic relationships within the genus *Apistogramma* (Regan, 1913). In: Römer, U. (ed.): Cichlid Atlas 2: Natural History of South American Dwarf Cichlids. Volume 2. Mergus Publishers, Melle, Germany: 142–165.
- RÖMER, U. (2006c): Evolution and Biogeography of Neotropical Cichlids of the Genus *Apistogramma* (Regan, 1913) (Teleostei: Perciformes. In: RÖMER, U. (ed.): Cichlid Atlas 2: Natural History of South American Dwarf Cichlids. Volume 2. Mergus Publishers, Melle, Germany: 166–337.
- Römer, U., Beninde, J., Duponchelle, F., Garcia Dávila, C.R., Vela Díaz, A. & Renno, J.-F. (2013): Description of *Apistogramma paulmuelleri* sp. n., a new geophagine cichlid species (Teleostei: Perciformes) from the Amazonas river basin in Loreto, Peru. Vertebrate Zoology, **63**(1): 15–34.
- 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 DIAZ, A., GARCIA DAVILLA, C., SIRVAS, S., DIAZ CATCHAY, 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., Hahn, I., Melgar, J., Soares, D.P. & Wöhler, M. (2004a): Redescription of *Apistogramma eremnopyge* Ready & Kullander, 2004. Das Aquarium, **38**(12) (426): 17–34.
- 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., RÖMER, E., SOARES, D.P. & WÖHLER, M. (2003a): 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. (2004b): *Apistogramma baenschi* sp. n.: Description of an other geophagine Dwarf-Cichlid (Teleostei: Perciformes) from Peru. Das Aquarium, **38**(8) (422): 15–30.
- Römer, U. & Pretor, P. (2003b): "Inka"- und "Zwillings"-*Apisto-gramma* wieder zwei neue Zwergcichliden (Teleostei: Perciformes) aus Peru. Das Aquarium, **37**(6) (408): 22 23.
- RÖMER, U, PRETOR, P. & HAHN, I. (2006b): Apistogramma huascar sp. n. - Description of a Dwarf Cichlid from Peru. – In: RÖMER, U. (ed.): Cichlid Atlas 2: Natural History of South American Dwarf Cichlids. Volume 2. Mergus Verlag, Melle, Germany: 530–573.

- RÖMER, U, RÖMER, E. & HAHN, I. (2006c): Apistogramma rositae sp. n. – Description of a new Dwarf Cichlid from Peru. – In: RÖMER, U. (ed.): Cichlid Atlas 2: Natural History of South American Dwarf Cichlids. Volume 2. Mergus Verlag, Melle, Germany: 668–693.
- RÖMER, U., RÖMER, E., SOARES, D.P. & HAHN, I. (2006d): Apistogramma pantalone sp. n. Description of a geophagine Dwarf Cichlid (Teleostei: Perciformes) from northern Peru. In: RÖMER, U. (ed.): Cichlid Atlas 2: Natural History of South American Dwarf Cichlids. Volume 2. Mergus Verlag, Melle, Germany: 642–667.
- RÖMER, U. & SOARES, D.P. (2015): Anmerkungen zu Identifizierung von *Apistogramma payaminonis* und eines weiteren Zwergbuntbarsches aus dem peruanisch-ekuadorianischen Amazonas-Einzug mit Anmerkungen zur Biologie im Aquarium. DCG-Informationen, **46**(9): 222–229.
- 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.
- STAECK, W. (1991): Eine neue *Apistogramma*-Art (Teleostei: Cichlidae) aus dem peruanischen Amazonasgebiet. Ichthyological Exploration of Freshwaters, **2**(2): 139–149.
- STAECK, W. (2003): Südamerikanische Zwergbuntbarsche. Cichliden-Lexikon 3, Dähne Verlag, Ettlingen, Germany: 63–64.
- STAECK, W. & LINKE, H. (2006): Amerikanische Cichliden I: Kleine Buntbarsche. Tetra Verlag GmbH, Bissendorf: 121–122.
- Tougard, C., García Dávila, C.R., Römer, U., Duponchelle, F., Chávez, C.A., Salas, S. & Renno, J.-F. (submitted): Evolutionary history of the cichlid genus *Apistogramma* (Perciformes: Labroidei: Cichlidae) in northeastern Peruvian Amazonia. Molecular Phylogenetics and Evolution.
- Varella, H.R. & Sabaj Pérez, M.H. (2014): A titan among dwarfs: *Apistogramma kullanderi*, new species (Teleostei: Cichlidae). – Ichthyological Exploration of Freshwaters, **25** (3): 243–258.
- ZARSKE, A. (2011): Das Typusmaterial der Characiformes des Museums für Naturkunde zu Berlin. Teil 1 (3). Einleitung und afrikanische Taxa. Vertebrate Zoolgy, **61**(1): 47–89.