

Apistogramma psammophila – a new geophagine dwarf cichlid (Teleostei: Cichlidae) from the Rio Atabapo drainage in Colombia and Venezuela

WOLFGANG STAECK¹ & INGO SCHINDLER²

¹ staeck@googlemail.com — ² ingoschindler@web.de

Submitted June 29, 2018.

Accepted January 10, 2019.

Published online at www.senckenberg.de/vertebrate-zoology on February 15, 2019.

Published in print on February 27, 2019.

Editor in charge: Uwe Fritz

Abstract

Apistogramma psammophila sp. n. is described from the lower Rio Atabapo drainage in Colombia (Departamento Guainía) and Venezuela (Estado Amazonas). It can be distinguished from all congeners by the following combination of characters: Two dark horizontal stripes on body side, two pectoral spots, suborbital stripe becoming much wider ventrally, and no caudal spot. In adult males soft dorsal and anal fins each with long filamentous prolongation almost reaching posterior margin of caudal fin, and pelvic fins with filamentous extension, nearly reaching middle of anal-fin base.

It is most similar to *Apistogramma diplotaenia* Kullander, 1987, but differs from this species by an irregular pattern of 6–8 short vertical dark bar-like markings below the lower lateral stripe, and adult males with reddish area on cheek and chest between eye and pectoral axilla and distinctly lanceolate caudal fin.

Resumen

Apistogramma psammophila sp. n. se describe a partir de la cuenca del río Atabapo bajo en Colombia (Departamento Guainía) y Venezuela (Estado Amazonas). La nueva especie se distingue de todas las demás especies descritas del género *Apistogramma* por la siguiente combinación de caracteres diagnósticos: dos bandas laterales oscuras horizontales en el lado del cuerpo, dos manchas pectorales, una banda suborbital que se vuelve ventralmente mucho más ancha, no hay una mancha caudal. En varones adultos aleta dorsal y anal blanda con prolongación filamentosa larga que llega hasta casi el borde posterior de la aleta caudal y una extensión filamentosa de las aletas pélvicas, que se extiende hasta casi la mitad de la base de la aleta anal.

La nueva especie es más similar a *Apistogramma diplotaenia* Kullander, 1987, pero se difiere de esta especie por un patrón irregular de 6–8 líneas oscuras verticales cortas debajo de la banda lateral inferior, un área rojiza en la mejilla y el tórax entre el ojo y la axila pectoral en machos adultos y su aleta caudal claramente lanceolada.

Kurzfassung

Apistogramma psammophila sp. n. wird aus dem Einzugsbereich des unteren Rio Atabapo in Kolumbien (Departamento Guainía) und Venezuela (Estado Amazonas) beschrieben. Die Art lässt sich von allen anderen beschriebenen *Apistogramma*-Arten durch die Kombination folgender diagnostischer Merkmale unterscheiden: Zwei horizontale dunkle Seitenbänder auf der Körperseite, zwei Brustflecken, ein suborbitaler Streifen, der ventral viel breiter wird, kein Schwanzwurzelfleck. Bei erwachsenen Männchen Rückenflosse und Afterflosse beinahe bis zum hinteren Ende der Schwanzflosse verlängert. Bauchflossen mit einer fadenförmigen Erweiterung, die bis fast zur Mitte der Afterflossenbasis reicht.

Die neue Art ist *Apistogramma diplotaenia* Kullander, 1987 am ähnlichsten, unterscheidet sich jedoch von dieser durch ein unregelmäßiges Muster von 6–8 kurzen vertikalen dunklen balkenähnlichen Markierungen unter dem unteren Längsband, einen rötlichen Bereich zwischen Auge und dem Ansatz der Brustflossen auf Wange und Brust erwachsener Männchen und deren deutlich lanzettförmige Schwanzflosse.

Key words

Apistogramma diplotaenia, Cichlinae, Departamento Guainía, Estado Amazonas, Geophagini, ichthyology, new species, Orinoco basin, taxonomy.

Introduction

In 1981 Schmettkamp, a German aquarist, found a single male specimen of an unknown *Apistogramma* species in a shipment of the Cardinal tetra (*Paracheirodon axelrodi*). He called it Doppelband Apistogramma (= Double Band Apistogramma) with reference to its unusual color pattern and informally described it as new in the aquarium literature (SCHMETTKAMP, 1981). One of us (WS) collected this species in 1981 and a second time 1986 in the Anavilhanas archipelago (lower Rio Negro, Brazil) and published the first details of its ecology (LINKE & STAECK, 1984, 1994). In 1987, KULLANDER described the species as *Apistogramma diplotaenia* from collecting sites in the upper and middle Rio Negro.

RÖMER (1992a, b) described reproduction under aquarium conditions and provided information on the ecological conditions in the field. Later he documented several mood-dependent variations in its live coloration, published further details of its ecology and characterized it as a sand-dwelling species with a habitat preference of beaches and sand banks (RÖMER, 1998). Sand-dwelling contrasts the majority of other members of the genus, which generally inhabit aggregations of dead leaves.

ANDERSON (1994) probably was the first to mention a population of *A. diplotaenia* in the Rio Atabapo (forming the border between Columbia and Venezuela). One year later GOTTWALD and KOSLOWSKI (in STAWIKOWSKI *et al.*, 1995: 62–63) published color photos of specimens collected in this river. They designated them as *Apistogramma cf. diplotaenia* „Orinoco“, based on hybridization experiments indicating that populations in the Rio Negro and the Rio Atabapo drainages were probably different species. In the following years, a few specimens of the Atabapo dwarf cichlid were exported as aquarium fish from both Colombia and Venezuela to Germany.

Until recently, exports and reports were rare, rendering available information about *Apistogramma cf. diplotaenia* “Orinoco” extremely patchy. Although the dwarf cichlid from the Rio Atabapo is relatively well known in the aquarium hobby, it has been neglected by the scientific literature published on the fish fauna of the Orinoco drainage (KULLANDER, 2003; MESA & LASSO, 2011; ORTEGA-LARA, 2016). The only exception is LASSO *et al.* (2004). Recent collections and observations at collecting sites in the Rio Atabapo revealed previously unknown details of the ecology of this species and confirmed the hypothesis that it is distinct from the Rio Negro population. The objective of this paper is to formally describe this dwarf cichlid, distinguish it from *A. diplotaenia*, and provide new information on its ecology.

Material and methods

The type specimens were fixed either in 75% ethanol or formalin, the latter specimens transferred to 75% etha-

nol. The types are deposited in the fish collections of the Instituto de Ciencias Naturales, Museo de Historia Natural, Universidad Nacional de Colombia in Bogotá (ICN-MHN) and in the Senckenberg Naturhistorische Sammlungen, Museum für Tierkunde, Dresden (MTD-F).

The techniques for taking measurements and meristic data follow those described in KULLANDER (1980, 1986). Measurements were made with electronic digital caliper to the nearest 0.1 mm. Specimen lengths are given as standard length (SL). Scale rows are numbered as described in KULLANDER (1990). Numbers in parentheses after counts indicate the number of specimens examined with that condition. Meristic data are given for eight type specimens with SL > 20 mm.

In the following, we use a pragmatic approach for species recognition (KOTTELAT, 1995). In accordance with current taxonomic publications on the genus *Apistogramma* (e.g., MESA & LASSO, 2011; VARELLA & SABA, 2014), the new species is diagnosed by external characters. This procedure is consistent with the diagnostic variant of the phylogenetic species concept (cf. NIXON & WHEELER, 1990).

Comparisons were made with three specimens of *Apistogramma diplotaenia* (SL 24.5–30.5 mm) in the collections of the authors and by consulting published sources (KULLANDER, 1987; RÖMER, 1992a, b, 1998).

Apistogramma psammophila n. sp.

urn:lsid:zoobank.org:act:AF18F667-5FFD-4B3E-A711-49C331082C8C

Figs. 1–8, Table 1

Holotype. ICN-MHN 24052, male 27.5 mm SL. Colombia (Departamento Guainía), lower Rio Atabapo, close to the mouth of Caño Chamuchina (approx. 3°47'22"N, 67°38'12"W), a left-bank tributary, import of aquarium-fish trade, *leg.* Javier León Barreto, *don.* R. Grossklaus 2018.

Paratypes. MTD-F 38845–38847, 3 ex., 38.4–41.5 mm SL. Venezuela (Estado Amazonas), lower Rio Atabapo, mouth of an unnamed right-bank tributary (approx. 3°57'34"N, 67°41'20"W) situated between Isla Zapó and Isla Guaimara (Isla Guanare), import of aquarium-fish trade, *leg.* and *don.* R. Rietsch 2012. MTD-F 38848–38856, 9 ex., 15.9–24.3 mm SL. Same data as in holotype.

Diagnosis. A slender geophagine dwarf cichlid with distinct sexual dimorphism, but only slight sexual dichromatism. Males grow larger than females and have prolonged rays in their soft dorsal and anal fin and a filamentous extension of the first pelvic-fin ray.

It can be distinguished from all the other described species of *Apistogramma* by the following combination of characters: (1) two dark horizontal bands on side of body; (2) two pectoral spots; (3) suborbital stripe becoming much wider ventrally; (4) no caudal spot; (5) adult males with shallow dorsal fin; (6) soft part of dorsal and anal fins each with long filamentous prolongation almost reaching posterior margin of caudal fin; (7) pelvic fin with filamentous extension nearly reaching middle of anal-fin base.

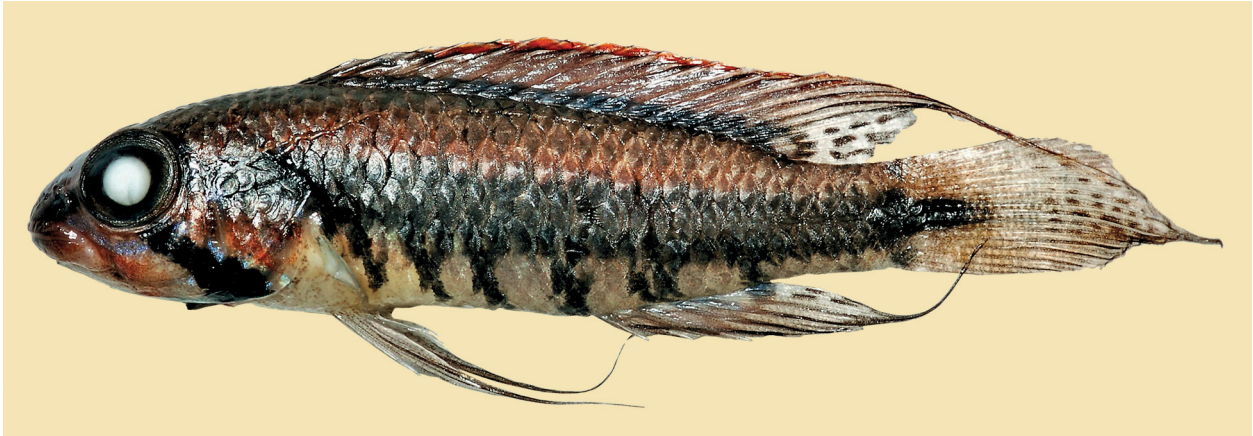


Fig. 1. *Apistogramma psammophila* (male, SL 27.5 mm), holotype (ICN-MHN 24052) from Rio Atabapo (Caño Chamuchina, Departamento Guainía, Colombia), one day after fixation.

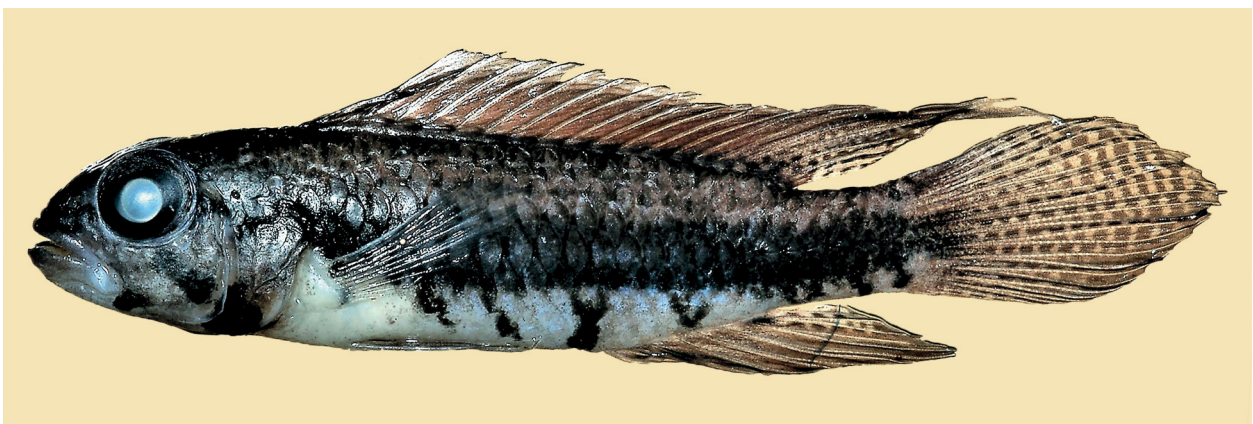


Fig. 2. Male of *Apistogramma psammophila* (38.4 mm SL), paratype (MTD-F 38857) from lower Rio Atabapo (mouth of an unnamed right-bank tributary, Estado Amazonas, Venezuela), three weeks after fixation.

In general appearance this species is most similar to *Apistogramma diplotaenia* Kullander, 1987, but differs from this species by 6–8 short dark vertical bars of irregular shape in the abdominal region below the lower lateral band (versus no such pattern), and adult males with reddish area on cheek and chest between eye and pectoral axilla (versus no such coloration) and caudal fin distinctly lanceolate with middle rays longest (versus elongated, ovoid with rounded posterior margin; cf. Fig. 10, 11).

Description. Refer to the figures for general appearance. Morphometric data are summarized in Table 1. A relatively small species of *Apistogramma* (maximum SL approx. 42 mm). Body comparatively elongated (average body depth in the three largest specimens 27 % of SL).

Head with approximately equally steep predorsal and preventral contours; frontal contour tangential to orbit. Snout short, rounded in lateral and dorsal views. Orbit situated in anterior half of head, ventrally reaching into lower half of head. Mouth terminal, lower jaw slightly shorter. Maxilla extending to margin of orbit. Caudal peduncle longer than high.

Dorsal fin comparatively shallow, dorsal-fin lappets short, with edge rounded or subtruncate in females. In adult males, soft dorsal fin with long filamentous pro-

Table 1. Morphometric data of holotype (ICN-MHN 24052) and five paratypes (MTD-F 38845-38849) of *Apistogramma psammophila* in percent of SL (in mm); min = lowest value, max = highest value, mean = arithmetic mean, sd = standard deviation.

	min	max	mean	sd
Standard length (mm)	22.8	41.5	32.2	8.25
Total length	137.5	141.2	139.4	1.36
Head length	31.3	32.6	32.1	0.51
Body depth	24.3	27.6	25.5	1.22
Eye diameter	11.3	13.6	12.3	0.93
Interorbital distance	5.7	6.7	6.2	0.45
Preorbital length	3.3	3.9	3.6	0.22
Peduncle depth	12.4	13.7	13.1	0.47
Peduncle length	14.2	15.0	14.6	0.31
Pectoral-fin length	21.8	28.1	25.5	2.61
Pelvic-fin length	31.0	49.1	39.8	7.78
Length last D spine	16.2	17.1	16.8	0.33
Dorsal-fin base length	55.6	59.9	58.1	1.90
Anal-fin base length	18.9	21.8	20.1	1.08

longation nearly reaching posterior margin of caudal fin. Anal fin with distal tip pointed, extending slightly beyond middle of caudal fin. Caudal fin rounded in fe-



Fig. 3. Adult dominant male of *Apistogramma psammophila* (no type) from lower Rio Atabapo (right-bank tributary, Estado Amazonas, Venezuela) photographed in aquarium.

Fig. 4. Adult female of *Apistogramma psammophila* (no type) from lower Rio Atabapo (right-bank tributary, Estado Amazonas, Venezuela) photographed in aquarium.

Fig. 5. Aggressive male of *Apistogramma psammophila* (no type).

Fig. 6. Adult male of *Apistogramma psammophila* (no type) in neutral mood.

Fig. 7. Threatening male of *Apistogramma psammophila* (no type).

Fig. 8. Adult female of *Apistogramma psammophila* (no type) exhibiting brood care coloration.

males, lanceolate in adult males, with middle rays much longer. Pectoral fins rounded. Pelvic fins with filamentous prolongation, first ray nearly reaching middle of anal fin base.

Dorsal fin XIV.8(1), XV.6(1), XV.7(6). Anal fin III.6(8). E1 row scales 22(6), 23(2). Tube bearing scales 11–13 in upper lateral line and 2–6 in lower lateral line. Pectoral fin rounded with usually 12 rays. Dental pores 4. First

ceratobranchial bearing 1 or usually 2 external gill rakers. Preopercular serrations variable in number (8–17), irregularly distributed along lower part of vertical limb and corner; inconspicuous in smaller specimens (< 20 mm SL). Margin of preopercle smooth in larger specimens (> 35 mm SL). Lower pharyngeal tooth-plate (dissected from one paratype of 41.5 mm SL) wider than long (length about 75% of width); with 13/14 teeth in



Fig. 9. Unnamed right-hand tributary of the lower Rio Atabapo (Departamento Guainía, Colombia), collecting site of paratypes of *Apistogramma psammophila*.

posterior row and 5/6 teeth in median row. Teeth bicuspid, two most medial-posterior with prominent major cusp; lateral and rostral teeth slender.

Coloration of live specimens (Figs. 3–8). Description based on observations immediately after capture, underwater observations in native habitats and observations of specimens kept in aquarium. Back, nape and forehead pale brown. Head pale grey, chest and abdomen whitish. Tips of dorsal-fin lappets red, forming a narrow red rim on the fin. In adult males reddish area on cheek and chest between eye and pectoral axilla.

Manifestation and intensity of black or dark brown markings is variable and mood-dependent as in other species of *Apistogramma* (see RÖMER, 1998; VARELLA & SABAJ, 2014). Suborbital stripe running obliquely from postero-ventral margin of orbit across cheek; stripe not uniform, antero-dorsal portion narrower than pupil, postero-ventral portion much wider, often enlarged as conspicuous black blotch. Postorbital stripe intense, continuous with dark stripe on flanks. Preorbital stripe less distinct. Pectoral axilla with two blackish pectoral spots, one dorsally, the other ventrally on adjacent side; also a blackish spot above upper base of pectoral fin. Two dark horizontal stripes on side of body side. The upper one above lower lateral line, straight, with approximately half the depth of a scale; lower stripe slightly wider, width nearly the depth of one scale; Lower stripe anteriorly curved, running ventrad from the postorbital stripe,

becoming horizontal behind pectoral axilla and converging with the upper stripe on caudal peduncle and anterior edge of caudal fin. Interspace between two stripes grey in males, orange or reddish brown in females. In the abdominal region below the lower lateral stripe, a pattern of 6–8 conspicuous dark vertical bars of different shapes, the first behind the pelvic-fin origin, the last on caudal peduncle; interspaces pale and highly contrasted. Fins pale greyish or bluish, more or less opaque. Soft portion of dorsal and anal with alternating pattern of brownish dots and hyaline windows on posterior membranes. Dorsal lobe of caudal fin with pattern of dark dots alternating with hyaline windows; ventral half hyaline.

Geographical distribution and ecology. *Apistogramma psammophila* is currently known only from localities in the lower Rio Atabapo, and is possibly endemic to this drainage. One of the documented collecting sites is situated close to the mouth of Caño Chamuchina (approx. 3°47'22"N, 67°38'12"W), a left-bank tributary. Another is in the mouth of an unnamed right-bank tributary (approx. 3°57'34"N, 67°41'20"W) situated between Isla Zapó and Isla Guaimara (Isla Guanare).

All specimens of the type material were collected in the low-water season between the second half of January and the first half of February. During this time the water level was about six meters below its maximum height in the high-water season, but still more than one



Fig. 10. Male *Apistogramma diplotaenia* from the Anavilhanas archipelago (lower Rio Negro, Brazil).

Fig. 11. Threatening male of *Apistogramma diplotaenia* (documentation of rounded caudal fin).

Fig. 12. Female of *Apistogramma diplotaenia* exhibiting brood care coloration.

meter above its minimum. Both collecting sites are sandy beaches (Fig. 9). The fish were exclusively found and collected at a distance of several meters from the exposed beach, where the water depth varied from approximately 1.5 to at least 2 meters. According to our underwater observations in the field, the dwarf cichlids lived singly and spread far apart over a wide sandy area where shelter was scarce.

Both collecting sites are typical blackwater habitats with clear, very acidic and extremely soft, tea-colored water. The following data were collected at both localities in different years: pH 4.1–4.5; maximum electrical conductivity 10 $\mu\text{S}/\text{cm}$; total and temporary hardness < 1 °dH (degrees of hardness); water temperature 27.3–29.4 °Celsius.

Reproductive biology. According to our aquarium observations, spawning takes place in concealed localities. Approximately 20 to 50 eggs are attached to the ceiling of the shelter. The female guards the eggs, larvae, and free-swimming young while the male defends the territory. When kept in an aquarium, the fish form pairs at least during the breeding season.

During brood care, females in many species in *Apistogramma* species exhibit special color patterns consisting of species-specific intense black markings on a contrasting bright yellow background. However, *A. psammophila* lacks such specialized brood care coloration (Fig. 8). Only the color of the anterior interspace between the two lateral stripes is intensified and turns orange or reddish brown during brood care.

Etymology. The species epithet (Greek ψάμμος = sand; φιλία = friendship) is an adjective (cf. psammophilous). It refers to the habitat preference of the species.

Discussion

Apistogramma diplotaenia and *A. psammophila* have a vicariant distribution in the Rio Negro and Rio Atabapo, respectively. Several other pairs of closely related cichlid species have a similar complementary distribution pattern in those two drainages (KULLANDER & FERREIRA, 1988; STAWIKOWSKI, 1989).

Allopatric sister species may pose problems because morphology and osteological differences are often small and hence discrimination and classification is difficult (MAYR, 1969). Closely related species in South American cichlids are usually most easily distinguished by differences in live color patterns (KULLANDER, 1980, 1989; KULLANDER & FERREIRA, 1988).

Even minor deviations in coloration or patterns of dark markings may be of biological significance as these differences are important in mate choice. Cichlid species are separated mostly by pre-zygotic and pre-mating, behavioral isolating mechanisms, more specifically by female choice preferences (KOCHER, 2004). In cichlids, mating preferences and mate choice are based on visual factors (COULDRIDGE & ALEXANDER, 2002; BLAIS *et al.*, 2009), and the females of *Apistogramma* species can discriminate between conspecific and heterospecific court-

ing males even if they are closely related and look similar (BEISENHERZ *et al.*, 2006; READY *et al.*, 2006; ENGELKING *et al.*, 2010). There are indications that such pre-mating behavioral mechanisms isolate *Apistogramma diplotaenia* and *A. psammophila* (see GOTTWALD and KOSLOWSKI in STAWIKOWSKI *et al.*, 1995: 62–63).

Among congeneric species, *Apistogramma psammophila* resembles only *A. diplotaenia*. On their flanks the two species have the same unique color pattern of two dark horizontal bands that fuse both anteriorly in front of the pectoral fin and posteriorly on the caudal peduncle. Females lack the yellow breeding coloration typical of other *Apistogramma* species (cf. Figs. 8 and 12). In addition, both are sand-dwelling species, an ecological specialization that is unique within the genus.

KULLANDER (1987) regarded *A. diplotaenia* as a highly distinctive species in the genus. Despite the thorough comparative osteological study, placement of *A. diplotaenia* within the genus remained obscure, and therefore, KULLANDER did not hypothesize close relatives. A preliminary phylogenetic analysis based on molecular data (MILLER & SCHLIEWEN, 2005) produced similar results. This study confirmed *A. diplotaenia* as a distinct lineage, but its relationship to congeners remained unsolved. On the basis of the results of a cluster analysis based on phenotypical and behavioral characters, RÖMER (2006) placed *Apistogramma diplotaenia* in a complex of its own within his *Apistogramma agassizii* supercomplex.

Apistogramma species live under different environmental conditions in a variety of water bodies such as rivers, lakes, lagoons, brooks, creeks, ponds, and even seasonal pools, which may dry up during the low-water season. In spite of this, their habitat preferences are surprisingly uniform and homogeneous. They prefer lentic waters and live close to the margins in extremely shallow zones where the water depth generally varies from approximately ten to forty centimeters. The typical biotope of the vast majority of *Apistogramma* species is the leaf litter found at the edge of small forest streams or lagoons. Only a few species prefer shelters in aquatic plants or floating meadows of macrophytes (e.g., *Eichhornia* spp., *Cabomba* spp. or *Paspalum repens*) near the water's surface (STAECK & SCHINDLER, 2008).

Unlike their conspecifics, *Apistogramma psammophila* and *A. diplotaenia* live in completely different habitats. They occupy an ecological niche that is unique within the genus (cf. RÖMER, 1998), for we did not find *A. psammophila* in shallow waters or leaf litter close to the riverbank. In contrast to its conspecifics, *A. psammophila* lives over sandy bottoms at a distance of several meters from the exposed beach, where the water is more than one meter deep (Fig. 9).

Systematics and interspecific phylogenetic relationships in *Apistogramma*, the second largest genus of neotropical cichlids, need further analysis.

Acknowledgements

We are indebted to Javier León Barreto, José Leonel Calderón, Alonso Rodrigo Sotomayor (Puerto Inírida, Colombia), the staff of Fauna Acuática Amazonas (Puerto Ayacucho, Venezuela) and the friendly people of the Comunidad Santa Rosa (Departamento Guainía, Colombia) for valuable information or administrative assistance during fieldwork in Colombia and Venezuela. We are obliged to Roland Rietsch (Berlin, Germany) and René Grossklaus (Merenschwand, Switzerland) for providing the type material.

We thank Uwe Fritz (MTD) and the Instituto de Ciencias Naturales, Museo de Historia Natural (ICN-MHN) in Bogotá for depositing the type material in their institutes. We are grateful to Mark Sabaj for his valuable suggestions to improve an earlier version of the text and also thank three anonymous reviewers for their critical comments.

References

- ANDERSON, T. B. (1994). Ecuador und Kolumbien 1993. *DCG-Informationen*, **25**, 203–216.
- BEISENHERZ, W., RÖMER, U., MÜLLER, M. & ENGELKING, B. (2006). Wie wählen *Apistogramma* Weibchen ihre Partner? Intra- und interspezifische Partnerwahl durch Weibchen von *Apistogramma cacatuoides* Hoedeman, 1951 (Teleostei, Perciformes, Cichlidae), pp. 7–8 in: GREVEN, H. & RIEHL, R. (eds): *Biologie der Aquarienfische*. Velten, Tetra Verlag.
- BLAIS, J., PLENDERLEITH, M., RICO, C., TAYLOR, M. I., SEEHAUSEN, O., VAN OOSTERHOUT, C. & TURNER, G. F. (2009). Assortative mating among Lake Malawi cichlid fish populations is not simply predictable from male nuptial colour. *BMC Evolutionary Biology*, **9**, 53.
- COULDRIDGE, V. C. K. & ALEXANDER, G. J. (2002). Color patterns and species recognition in four closely related species of Lake Malawi cichlids. *Behavior Ecology*, **13**, 59–64.
- ENGELKING, B., RÖMER, U. & BEISENHERZ, W. (2010). Intraspecific colour preference in mate choice by female *Apistogramma cacatuoides* Hoedeman, 1951 (Teleostei, Perciformes, Cichlidae). *Vertebrate Zoology*, **60**, 123–138.
- KOCHER, T. D. (2004). Adaptive evolution and explosive speciation. The cichlid fish model. *Nature Reviews Genetics*, **5**, 288–298.
- KOTTELAT, M. (1995). Systematic studies and biodiversity: The need for a pragmatic approach. *Journal of Natural History*, **29**, 565–569.
- 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**, 1–152.
- KULLANDER, S. O. (1986). *Cichlid fishes of the Amazon River drainage of Peru*. Stockholm, Swedish Museum of Natural History.
- KULLANDER, S. O. (1987). A new *Apistogramma* species (Teleostei, Cichlidae) from the Rio Negro in Brazil and Venezuela. *Zoologica Scripta*, **16**, 259–270.
- KULLANDER, S. O. (1989). Description of a new *Acaronia* species (Teleostei, Cichlidae) from the Rio Orinoco and Rio Negro drainages. *Zoologica Scripta*, **18**, 447–452.
- KULLANDER, S. O. (1990). *Mazarunia mazarunii* (Teleostei: Cichlidae), a new genus and species from Guyana, South America. *Ichthyological Exploration of Freshwaters*, **1**, 3–14.
- KULLANDER, S. O. (2003). Cichlidae, pp. 605–654 in: REIS, R. E., KULLANDER, S. O. & FERRARIS, C. J. (eds) *Check List of the Freshwater Fishes of South and Central America*. Porto Alegre, Edipucers.

- KULLANDER, S. O. & FERREIRA, E. J. G. (1988). A new *Satanoperca* species (Teleostei, Cichlidae) from the Amazon River basin in Brazil. *Cybium*, **12**, 343–355.
- LASSO, C. A., MOJICA, J. I., USMA, J. S., MALDONADO-OCAMPO, J. A., DONASCIMIENTO, C., TAPHORN, D. C., PROVENZANO, F., LASSO-ALCALÁ, O. M., GALVIS, G., VÁSQUEZ, L., LUGO, M., MACHADO-ALLISON, A., ROYERO, R., SUÁREZ, C. & ORTEGA-LARA, A. (2004). Peces de la cuenca del río Orinoco. Parte 1: Lista de especies y distribución por subcuencas. *Biota Colombiana*, **5**, 95–158.
- LINKE, H. & STAECK, W. (1984). *Amerikanische Cichliden I. Kleine Buntbarsche*. Melle, Tetra Verlag.
- LINKE, H. & STAECK, W. (1994). *American Cichlids I. Dwarf Cichlids*. Melle, Tetra-Press.
- MAYR, E. (1969). *Principles of Systematic Zoology*. New York, McGraw-Hill.
- MESA, S. L. M. & LASSO, C. A. (2011). *Revisión del género Apistogramma Regan, 1913 (Perciformes, Cichlidae) en la cuenca del río Orinoco*. Serie Editorial Recursos Hidrobiológicos y Pesqueros Continentales de Colombia III. Bogotá, Instituto Humboldt.
- MILLER, M. & SCHLIEWEN, U. (2005). The molecular phylogeny of the genus *Apistogramma* – a working hypothesis, pp. 22–25 in: STAWIKOWSKI, R., KOSLOWSKI, I. & BOHNET, V. (eds) *Südamerikanische Zwergcichliden/South American Dwarf Cichlids*. Stuttgart, DATZ Sonderheft, Eugen Ulmer.
- NIXON, K. C. & WHEELER, Q. D. (1990). An amplification of the phylogenetic species concept. *Cladistics*, **6**, 211–223.
- ORTEGA-LARA, A. (2016). *Guía visual de los principales peces ornamentales continentales de Colombia*. Santiago de Cali, AUNAP.
- READY, J. S., SAMPAIO, I., SCHNEIDER, H., VINSON, C., DOS SANTOS, T. & TURNER, G. F. (2006). Colour forms of Amazonian cichlid fish represent reproductively isolated species. *Journal of Evolutionary Biology*, **19**, 1139–1148.
- RÖMER, U. (1992a). Beobachtungen zur Aquarienbiologie von *Apistogramma diplotaenia* Kullander, 1987. *DCG-Informationen*, **23**, 166–170.
- RÖMER, U. (1992b). Freilandbeobachtungen an *Apistogramma diplotaenia* Kullander, 1987. *Buntbarsch-Jahrbuch*, **1**, 58–71.
- RÖMER, U. (1998). *Cichlid Atlas, volume 1*. Melle, Mergus Verlag.
- RÖMER, U. (2006). *Cichlid Atlas, volume 2*. Melle, Mergus Verlag.
- SCHMETTKAMP, W. (1981). Neues aus der *Apistogramma*-Szene: 4. *Apistogramma* spec. nov. – Doppelband-*Apistogramma*. *DCG-Informationen*, **12**, 148–149.
- STAECK, W. & SCHINDLER, I. (2008). *Apistogramma erythrura* sp. n. – a new geophagine dwarf cichlid (Teleostei: Cichlidae) from the río Mamoré drainage in Bolivia. *Vertebrate Zoology*, **58**, 197–206.
- STAWIKOWSKI, R. (1989). Ein neuer Cichlide aus dem oberen Orinoco-Einzug: *Uaru fernandezyepezi* n. sp. (Pisces: Perciformes: Cichlidae). *Bonner zoologische Beiträge*, **40**, 19–26.
- STAWIKOWSKI, R., KOSLOWSKI, I. & BOHNET, V. (eds, 2005). *Südamerikanische Zwergcichliden/South American Dwarf Cichlids*. Stuttgart (DATZ Sonderheft), Eugen Ulmer Verlag, 129 pp.
- VARELLA, H. R. & SABAJ PÉREZ, M. H. (2014). A titan among dwarfs – *Apistogramma kullanderi*, new species (Teleostei: Cichlidae). *Ichthyological Exploration Freshwaters*, **25**, 243–258.

ZooBank registration

This published work and the nomenclatural acts it contains have been registered in ZooBank, the online registration system for the International Commission on Zoological Nomenclature (ICZN). The ZooBank LSIDs (Life Science Identifiers) can be resolved and the associated information can be viewed through any standard web browser by appending the LSID to the prefix <http://zoobank.org>. The LSID for this publication is as follows: urn:lsid:zoobank.org:pub:C30DB754-32A7-4F88-A4EB-400DAF20A16F