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A new species of *Panaqolus* (Siluriformes: Loricariidae) from the rio Branco

Milton Tan[1], Lesley S. de Souza[2] and Jonathan W. Armbruster[1]

A new species of *Panaqolus* is described from material from the Takutu River and the mainstem rio Branco. The new species is diagnosed from congeners by its color pattern consisting of dark and light bars on the body, bands on the fins, and with dots and vermiculations absent (*vs.* no bars in *P. albomaculatus*, *P. nix*, *P. nocturnus*, and *P. koko*, *vs.* fins unbanded in *P. albomaculatus*, *P. dentex*, *P. koko*, and *P. nix*, and *vs.* dots and vermiculations present in *P. albivermis* and *P. maccus*). The new species is diagnosed from barred species of *Panaqolus* by its specific bar number and orientation and color pattern on its head, with bars oriented in a anteroventral-posterodorsal direction (*vs.* anterodorsal-posteroventral bars in *P. gnomus*), having consistently 5 bars (n = 4) on the trunk that do not increase with size (*vs.* number increasing with size in *P. purusiensis* and *vs.* 6-12 in *P. changae*), and the color pattern on the head of straight lines extending from posterior to the eye to the snout margin, splitting in the middle portion of the line in larger specimens (*vs.* small, dense reticulate lines in *P. changae*). Biogeographically, we infer that the new species ancestrally originated in the Amazon river, dispersing to the Takutu River after the Amazon captured part of the Proto-Berbice.

Uma espécie nova de *Panaqolus* é descrita do rio Branco e seu afluente, rio Tacutu. A nova espécie é diagnosticada de suas congêneres pelo padrão de colorido composto por barras escuras e claras alternadas no corpo e nadadeiras, não formando máculas ou vermiculações nas nadadeiras (*vs.* sem barras no corpo em *P. albomaculatus*, *P. nix*, *P. nocturnus*, e *P. koko*, e *vs.* sem barras nas nadadeiras em *P. albomaculatus*, *P. dentex*, *P. koko*, e *P. nix*, e *vs.* máculas e vermiculações presentes em *P. albivermis* e *P. maccus*). A nova espécie é diagnosticada das espécies de *Panaqolus* com barras pelo número e orientação das barras e pelo padrão de colorido cefálico, com as barras orientadas posterodorsalmente (*vs.* posteroventralmente em *P. gnomus*), pela presença de cinco barras (n = 4) no tronco que não aumentam com o tamanho (*vs.* número aumentando com o tamanho em *P. purusiensis* e *vs.* 6-12 barras em *P. changae*), e o padrão de colorido cefálico composto por linhas retas da margem posterior do olho à margem do focinho, dividida medianamente em indivíduos maiores (*vs.* linhas pequenas e vermiculadas em *P. changae*). Nos inferimos que a nova espécie originou-se ancestralmente no rio Amazonas, dispersando para o rio Tacutu após o Amazonas capturar parte do Proto-Berbice.

Keywords: Brazil, Guyana, Hypostominae, Takutu River.

Introduction

Panaqolus Isbrücker & Schraml 2001 is a genus of small-bodied, xylivorous loricariid catfishes. *Panaqolus* is widely distributed in the Amazon River, rio Orinoco, and coastal rivers of the Guianas (Lujan *et al.*, 2013). Although previously classified with the large-bodied, wood-eating *Panaque* (Schaefer & Stewart, 1993; Armbruster, 2004), molecular analyses have shown that these genera are distinct (Cramer *et al.*, 2011; Lujan *et al.*, 2015), and we follow previous taxonomic studies that also recognize *Panaqolus* (Lujan *et al.*, 2013; Cramer, 2014; Cramer & Rapp Py-Daniel, 2015). Currently, there are ten valid species of *Panaqolus*: *P. dentex* (Günther, 1868), *P. purusiensis* (LaMonte, 1935), *P. albomaculatus* (Kanazawa, 1958), *P. gnomus* (Schaefer & Stewart, 1993), *P. maccus* (Schaefer & Stewart, 1993), *P. nocturnus* (Schaefer & Stewart, 1993), *P. changae* (Chockley & Armbruster, 2002), *P. koko* Fisch-Muller & Covain, 2012, *P. albivermis* Lujan, Steele & Valesquez, 2013, and *P. nix* Cramer & Rapp Py-Daniel, 2015.

Panaqolus has a widespread range throughout northern South America, but species are locally rare, and many

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[1] Department of Biological Sciences, 331 Funchess Hall, Auburn University, AL 36849, USA. (MT) miltontan@auburn.edu (corresponding author), (JWA) armbrjw@auburn.edu
[2] University of Illinois, Urbana-Champaign, Department of Natural Resources and Environmental Sciences, 1102 South Goodwin Ave, Urbana, IL 61801, USA. lesleydesouza4@gmail.com

species are disjunct; thus far, no *Panaqolus* species have been described from Guyana, and neither of the Brazilian species of *Panaqolus* inhabit drainages of the Guiana Shield (Schaefer & Stewart, 1993, Cramer & Rapp Py-Daniel, 2015). The only species known from the Guiana Shield are *P. maccus* from the rio Orinoco basin including the Caroni (Schaefer & Stewart, 1993), which drains the west and north sides of the Pakaraima Mountains and *P. koko* from the Maroni River of French Guiana (Fisch-Muller *et al.*, 2012).

The Takutu River is a medium-large (~25-50m across) river system draining the southwest portion of the Pakaraima mountains, the eastern Kanuku Mountains, and the Rupununi Savanna. It transitions from blackwater to whitewater and has a substrate of sandy bottoms, lateritic rocky stretches, and areas of moderate rapids with boulders. Recent work in the region has allowed for the discovery and description of several new loricariid species (*i.e.* Armbruster, 2003; Armbruster & Werneke, 2005; Tan & Armbruster, 2016). Lujan *et al.* (2015), in a phylogenetic analysis of Loricariidae focused on Hypostominae, include a specimen of *Panaqolus* from Guyana. This specimen, collected during LSD's and JWA's surveys of the Rupununi region of Guyana, represents a new species described herein, and it provides information on the enrichment of the fauna of the rio Takutu proposed by de Souza *et al.* (2012).

Material and Methods

Measurements and counts follow Armbruster (2003) with additional counts for mid-dorsal and mid-ventral plate series as in Armbruster *et al.* (2007). Anatomical nomenclature follows Schaefer (1987) and Geerinckx *et al.* (2007) for skeletal characteristics, Schaefer (1997) for names of plate rows, and Douglas *et al.* (2002) for the term *iris operculum*. Institutional abbreviations are as listed in Sabaj Pérez (2014). Paratypes below 20 mm SL were measured for SL, observed for morphology and coloration when specified, but were not observed for morphometrics and meristics. Morphometric data, jaw angles, and other characters for diagnosis from other *Panaqolus* species were derived from Lujan *et al.* (2013), Cramer (2014), and Cramer & Rapp Py-Daniel (2015). Bars are long vertical or oblique marks on the body and bands are lines on fins that run parallel with the fin margin per Jenkins & Burkhead (1994).

Results

Panaqolus claustellifer, new species

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Figs. 1-2

Holotype. CSBD F1702/AUM 44721 (dual-accessioned), 61.6 mm SL, Guyana, Amazon River - rio Branco drainage, Takutu River near Lethem, 3.47043°, -059.80993°, 27 Nov 2005, L. S. de Souza, N. K. Lujan, D. C. Taphorn, J. A. Hartsell, E. Liverpool, S. Lord.

Paratypes. Guyana, Amazon River - rio Branco drainage: AUM 47717, 1, 17.6 mm SL, Takutu River rock beach, 3.47058°, -059.80990°, 11 Nov 2007, L. S. de Souza, D. C. Taphorn, J. N. Baskin, T. Geerinckx, J. L. Hwan; AUM 65708, 1, 16.7 mm SL, same locality data as holotype. Brazil, Amazon River drainage: MZUSP 33704, 1, 52.7 mm SL, rio Branco, backwater of Bem Querer rapids (cachoeira do Bem Querer), Brazil, 1.933°, -061.000°, 1 Aug 1984, M. Goulding.

Diagnosis. *Panaqolus claustellifer* is diagnosed from most other described species of *Panaqolus* by its color pattern of dark and light bars on the body, bands on the fins, and with dots and vermiculations absent (*vs.* no bars in *P. albomaculatus*, *P. nix*, *P. nocturnus*, and *P. koko*, *vs.* fins unbanded in *P. albomaculatus*, *P. dentex*, *P. koko*, and *P. nix*, and *vs.* dots and vermiculations present in *P. albivermis* and *P. maccus*). Additionally, *Panaqolus claustellifer* is diagnosed from *P. albivermis*, *P. albomaculatus*, and *P. nix* by dentaries forming an acute angle ~70º *vs.* dentaries forming a very acute angle to dentaries parallel), and from *P. koko* by spoon-shaped teeth with small lateral cusps *vs.* quadrate teeth with strong lateral cusps. *Panaqolus claustellifer* is diagnosed from other barred species of *Panaqolus* by the specific bar number and orientation and color pattern on the head, with bars oriented in a anteroventral-posterodorsal direction (*vs.* anterodorsal-posteroventral bars in *P. gnomus*), having consistently 5 bars (n = 4) on the trunk that do not increase with size (*vs.* number increasing with size in *P. purusiensis* and fading at body sizes >85 mm SL, and *vs.* 6-12 in *P. changae*), and the color pattern on the head of straight lines extending from posterior to the eye to the snout margin, splitting in the middle portion of the line in larger specimens (*vs.* small, dense reticulate lines in *P. changae*).

Description. Morphometrics in Table 1. All counts n = 2 (holotype AUM 44721, paratype MZUSP 33704). Largest observed specimen 61.6 mm SL. Head depth increases at roughly 45º angle between snout tip and anterior margin of the orbit. Horizontal distance from snout tip to anterior margin of orbit greater than horizontal distance from anterior margin of orbit to posterior tip of supraoccipital. Body depth gradually increasing with body profile convex from anterior margin of orbit to greatest body depth at origin of dorsal fin. Body depth decreasing from origin of dorsal fin to posterior margin of adipose fin with a slight increase to the origin of the caudal fin. Ventral surface flat from snout to anus, slightly concave between anus and caudal fin. In dorsal view, head with straight lateral margins forming angle nearly 90º with rounded snout tip.

Fig. 1. *Panaqolus claustellifer*, new species, CSBD F1702/AUM 44721, Takutu River, holotype, adult male, 61.6 mm SL, lateral view is of right side and flipped horizontally. Photo by Milton Tan.

Table 1. Morphometric data for *Panaqolus claustellifer*. Morphometric data except standard length are given as percentages of standard length or head length. Dorsal-fin spine is broken in the holotype, so this measurement is excluded. L. = length, D. = distance, W. = width, Dp. = depth.

	Holotype AUM 44721	Paratype MZUSP 33704
SL	61.6	52.7
	% SL	
Predorsal L.	44.9	45.2
Head L.	37.2	39.0
Head-dorsal L.	7.2	6.1
Cleithral W.	33.9	32.7
Head-pectoral L.	30.6	30.5
Thorax L.	22.8	23.7
Pectoral-spine L.	33.1	32.6
Abdominal L.	24.4	23.5
Pelvic-spine L.	28.9	27.6
Postanal L.	35.2	29.2
Anal-fin spine L.	15.7	11.0
Dorsal-pectoral D.	32.1	30.1
Dorsal spine L.	–	33.7
Dorsal-pelvic D.	25.4	21.4
Dorsal-fin base L.	29.4	27.4
Dorsal-adipose D.	15.9	13.1
Adipose-spine L.	9.1	8.3
Adipose-up. caudal D.	13.2	11.5
Caudal peduncle Dp.	12.7	10.3
Adipose-low. caudal D.	22.3	19.7
Adipose-anal D.	19.2	16.4
Dorsal-anal D.	17.0	13.7
Pelvic-dorsal D.	30.7	27.2
	% HL	
Head-eye L.	36.3	36.2
Orbit Dia.	20.1	21.1
Snout L.	59.8	56.8
Internares W.	15.8	13.6
Interorbital W.	51.6	45.3
Head Dp.	75.1	83.9
Mouth L.	48.2	48.5
Mouth W.	41.4	48.1
Barbel L.	14.7	11.7
Dentary tooth cup L.	14.2	15.3
Premax. tooth cup L.	10.8	11.3

Ossified dermal plates with odontodes on head and lateral surfaces of the body, and ventrally posterior to the anus. Area around dorsal-fin base and snout tip naked. Ventral surface from head to anus largely naked, with small platelets supporting odontodes distributed ventral to the pectoral girdle, extending posteriorly from the pectoral-fin origin almost to the pelvic-fin origin, and forming a *U*-shaped pattern posterior to the pelvic-fin insertion and with prongs of the 'U' extending posteriorly; ventral platelets absent in specimens <20 mm SL. Body widest at cleithrum; exposed posterior margin of cleithrum tapering to a point. Lateral median plates 23-24, middorsal plates 22-23, midventral plates 23; anteriormost midventral plates strongly bent forming slight lateral ridge continuous with exposed cleithrum extending posteriorly to vertical through pelvic-fin origin. Caudal peduncle plate rows five. One preadipose plate, two predorsal plate rows not including nuchal plate.

Supraorbital crest raised slightly. Orbit positioned dorsolaterally on head with orbital opening oriented slightly less than 45º from sagittal plane in anterior view. Interorbital isthmus between supraorbital crests slightly convex. Slight ridge extending from anterolateral corner of nares to dorsal margin of orbit continuous with supraorbital crest. Eye large with iris operculum present. Supraoccipital not raised, profile continuous with dorsal plates. Gill chamber opening ventrally and laterally.

Frontal, infraorbitals, nasal, preopercle, compound pterotic, and suprapreopercle supporting odontodes. Opercle not exposed, not supporting odontodes. Dermal plates on body supporting odontodes, odontodes hypertrophied on holotype. Cheek plates bearing hypertrophied, distally-hooked odontodes (mean 33; holotype 37, MZUSP 33704 paratype 29) evertible to greater than 90º from sagittal plane in dorsal view, longest odontodes reaching to posterior tip of exposed margin of the cleithrum.

Oral disk elliptical, length greater than width. Oral disk width roughly half of head width; posterior margin of lower lip not extending posteriorly past cheek plates. Premaxillae forming roughly 90º angle, dentaries forming roughly 30º angle. Premaxillary teeth 4 on left ramus, dentary teeth 4 on left ramus. All teeth with thick, strong shafts; cusps bifid, medial cusp large and spoon-shaped becoming adze-shaped when worn, lateral cusp small; teeth slightly larger on dentary, medial teeth generally larger than lateral teeth (though medial-most tooth on each ramus is smaller than the second-most medial tooth). Maxillary barbel short, not reaching to posterior margin of lower lip, attached to lower lip for roughly the first half of length. Lips papillose, with papillae decreasing in size toward lip margin.

Fin spines and rays supporting odontodes. Dorsal-fin origin slightly anterior to pelvic-fin origin, with pelvic-fin origin at vertical through origin of first branched dorsal-fin ray. Dorsal fin II,7; dorsal-fin spinelet small, *V*-shaped, dorsal-fin spine locking mechanism functional. Posterior dorsal-fin rays free from body, reaching to preadipose plate. Pectoral-fin origin slightly posterior to orbit. Pectoral fin I,6; adpressed pectoral-fin spine reaching past pelvic-fin spine origin, robust spine having hypertrophied odontodes increasing in length distally in holotype. Pelvic fin i,5; pelvic-fin spine reaching past insertion of anal fin when adpressed. Anal-fin origin posterior to vertical through origin of posterior-most dorsal-fin ray. Anal fin i,4 (holotype) or i,3 (MZUSP 33704). Adipose-fin spine slightly curved distally, attached to caudal peduncle with membrane with convex posterior margin. Caudal fin i,14,i; caudal fin emarginate with lower lobe longer than upper lobe.

Coloration. Freshly-caught specimens have an orange-red base coloration. Live coloration has been described as alternating of dark brown and cream-colored bands (Miller, 2002). In ethanol, body with light-brown base coloration with dark brown bars. Head with alternating dark lines and light interspaces. Dark lines on head medial to the orbits roughly parallel to sagittal plane, leading from snout margin posterior to the horizontal through posterior margin of orbit. Snout lines connect to each other near the anterior-most and posterior-most ends, leaving a central light-brown, keyhole-shaped opening. Dark line extending from posteroventral margin of eye to anterior of cheek plate. Five oblique dark bars on body oriented in anteroventral-posterodorsal direction, with anterior bars oblique and posterior bars nearly vertical. Dorsal portion of first three bars above horizontal through eye shift to anterodorsal-posteroventral angle; in dorsal view, the first bar roughly forms a *W*-shape. Dark bars may be bifurcated ventrally with light base color between separate portions of the bars. Extent of split is greatest in second-most anterior bar, reaching dorsal to horizontal through eye, while vertical extent of splits in second and third bars ventral to lateral line. Posterior bars also expanded dorsally (although not necessarily interspersed by light background color). Posteriormost bar on body extending onto posterior margin of adipose-fin spine and membrane. Fins with an alternating pattern of wide and narrow dark bands on a lighter ran color, bands closest to body wide. Dorsal fin with two wide bands, bands curved in parallel to dorsal-fin margin. Caudal fin with three wide bands, most posterior band only on lower lobe of caudal fin. Three dark wide bands on pectoral fins and pelvic fins, with most proximal dark band starting roughly at fin base.

In small specimens (<20 mm SL), color pattern is slightly different (Fig. 2). More intense reddish coloration present, with dark bars darker brown than in adult specimens. Five oblique dark bars on body oriented in anteroventral-posterodorsal direction; angle of anterior bars does not shift dorsally to anterodorsal-posteroventral direction, and bars not bifurcated. Posteriormost bar on body posterior to adipose fin, thus not extending onto adipose fin as in adult. Dorsal fin with two dark bands, caudal fin with two bands, pectoral fins with two dark bands (with most proximal band starting at base of fin), and pelvic fins with one band (roughly midway on fin length).

Size. Maximum size observed 61.6 mm SL. Known to reach at least 11 cm TL (Miller, 2002).

Sexual Dimorphism. Male holotype with hypertrophied odontodes well developed posterior to dorsal fin indicating it is in nuptial condition.

Distribution. *Panaqolus claustellifer* occurs in the Takutu river and the mainstem rio Branco of Brazil and Guyana (Fig. 3).

Ecological notes. Individuals of *Panaqolus claustellifer* were found in shallow cataracts along the Takutu river, a whitewater system. The substrate was sandy with lateritic rocks interspersed. Surrounding habitat consisted of a narrow strip of gallery forest, but mostly savanna. Small specimens <20 mm SL (AUM 47717, AUM 65708) likely represent young-of-year that have hatched less than a couple weeks prior to collection.

Etymology. From the Latin *claustellum*, meaning keyhole, and the Latin *fero*, meaning to bear. Refers to the dark brown lines on the snout surrounding a keyhole-like shape of light-brown base coloration. Treated as a masculine adjective.

Remarks. *Panaqolus claustellifer* is included in Lujan *et al.*'s (2015) phylogenetic study. Genetic sequences have been accessioned for the holotype for partial mitochondrial 16S (GenBank number KP959780), and Cyt b (KP960156) genes, and nuclear RAG1 (KP959978), RAG2 (KP960254), and Myh6 (KP960402). These are genseq-1 sequences according to the GenSeq Nomenclature (Chakrabarty *et al.* 2013).

Panaqolus claustellifer is identified as a *Panaqolus*, L306, in the aquarium pet trade (Miller, 2002; Schraml & Schaffer, 2002). *Panaqolus claustellifer* is listed as *Panaque* sp. by de Souza *et al.* (2012) and *Panaqolus* n. sp. Tacutu L306 by Lujan *et al.* (2015).

The holotype of the species was dual accessioned at AUM and CSBD because the specimen will be kept at AUM for the near term, but will eventually be repatriated to Guyana. We feel that the specimen will be more readily available to other researchers at AUM, but recognize that the specimen must eventually return to Guyana, and this is the simplest way to ensure that the location of the holotype is known.

Conservation status. Considering that additional samples were carried out in the region without capturing the species, resulting in a reduced known geographic distribution, besides a low number of paratypes, and its potential to the pet trade, *Panaqolus claustellifer* could be classified as Data Deficient (DD), according to the International Union for Conservation of Nature (IUCN) categories and criteria (IUCN Standards and Petitions Subcommittee, 2016). Further studies on biology, ecology and distribution of the species should be strongly encouraged.

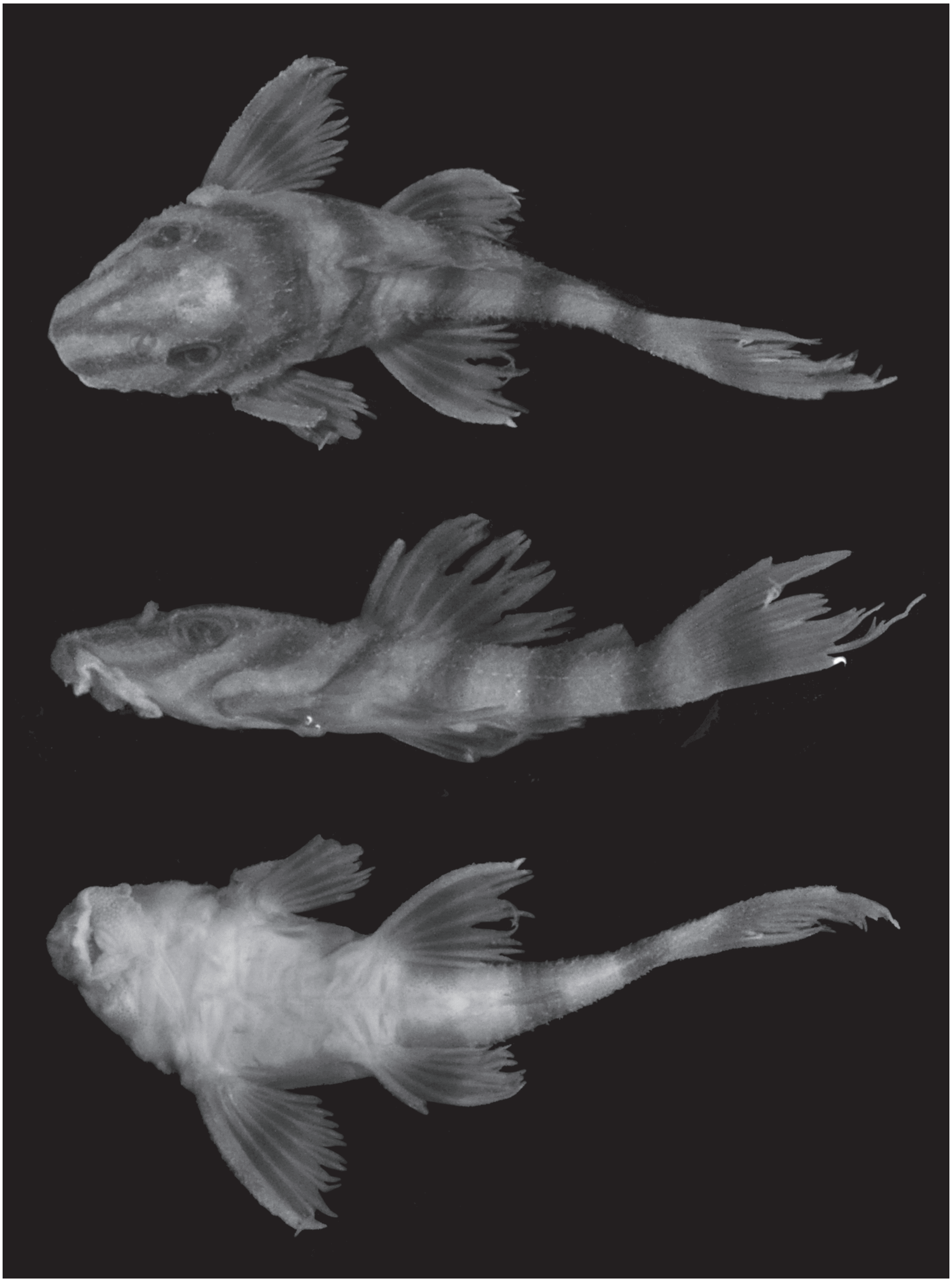

Fig. 2. *Panaqolus claustellifer*, AUM 65708, Takutu River, paratype, juvenile, 16.7 mm SL. Photo by Milton Tan.

Discussion

Because of the relative rarity of specimens of *Panaqolus*, the exact distribution of the genus is unknown, but continues to expand through the discovery of undescribed species (Cramer & Rapp Py-Daniel, 2015). Currently, the range of *Panaqolus claustellifer* is disjunct from other described species of *Panaqolus*, but there are other undescribed species from the central Amazon. The most geographically close described species of *Panaqolus* is *P. maccus* of Venezuela, which is found in the rio Orinoco basin, including the Caroni River, which drains the north-central portion of the western Guiana Shield (Schaefer & Stewart, 1993). The only other species of *Panaqolus* described from the Guiana Shield is *P. koko* from the Maroni River along the French Guiana/Suriname border (Fisch-Muller *et al.*, 2012).

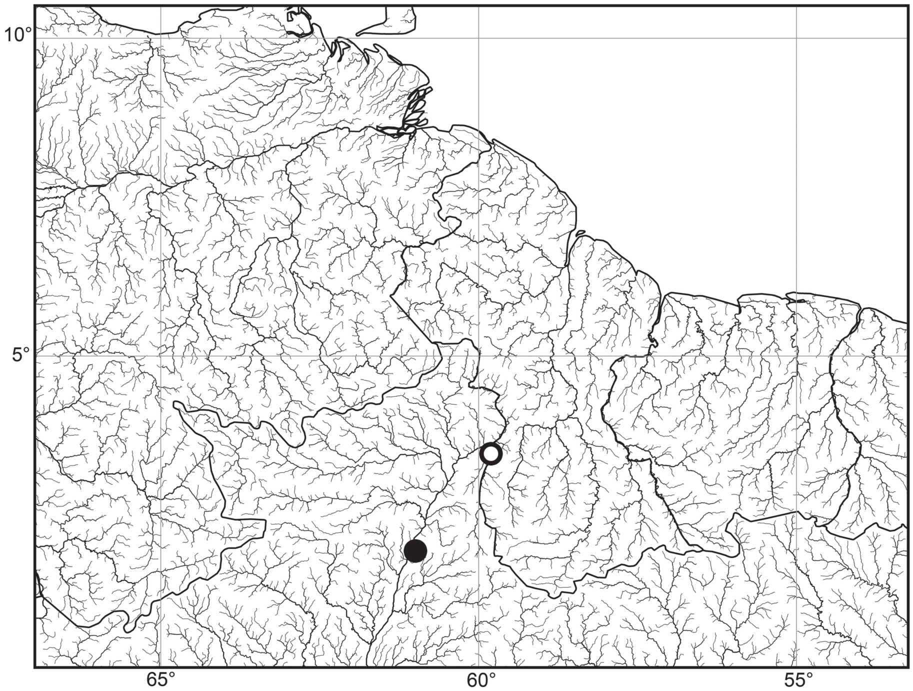

Fig. 3. Map of northern South America showing localities of *Panaqolus claustellifer*. Holotype and paratype specimens from Takutu river indicated by open circle (CSBD F1702/AUM 44721, AUM 47717, AUM 65708), paratype from mainstem rio Branco indicated by closed circle (MZUSP 33704).

In a recent molecular phylogeny of Loricariidae with focus on Hypostominae (Lujan *et al.*, 2015), *Panaqolus claustellifer* (as *Panaqolus* n. sp. Tacutu L306) was found to be sister to *P. gnomus*, a species endemic to the Pastaza and upper Maranõn basins, with *P. nocturnus* from the Santiago and Pastaza basins of the upper Napo sister to them. *Panaqolus koko* was not recovered within *Panaqolus* in this study. Differences in the body shape and dentition of *P. koko* suggest it may not belong to *Panaqolus* (Fisch-Muller *et al*., 2012; Cramer & Rapp Py-Daniel, 2015).

The relationships of the species of *Panaqolus* suggest that there is an Amazonian radiation of saddled or barred *Panaqolus*. The Takutu river was formerly part of the Proto-Berbice river system, which was composed of rivers that are now a part of the upper Branco, upper and middle Essequibo, and Berbice rivers, and that drained into the Caribbean Sea near the mouth of the current Berbice River (Lujan & Armbruster, 2011). The Takutu River flows off the edge of the Rupununi wetlands draining northwards along the Brazil/Guyana border before making an abrupt loop southward starting around Lethem, Guyana. The junction of the Takutu and the rio Uraricoera just northeast of Boa Vista, Brazil, forms the rio Branco. The distribution of *Panaqolus claustellifer* is from the rio Branco mainstem in a portion that likely always drained into the Amazon to parts of the Takutu River that were part of the Proto-Berbice.

Given its distribution and the lack of any other *Panaqolus* in the Western Guiana Shield other than the distantly related *P. maccus*, we suggest that the origin of *P. claustellifer* is in the Amazon, and it moved into former Proto-Berbice drainages like the Takutu sometime around the capture of the Uraricoera and Cotinga by the Branco in the Pliocene and the Takutu in the Pleistocene (Lujan & Armbruster, 2011). de Souza *et al.* (2012) suggested that the Takutu was enriched with Amazonian endemics when compared to the Rupununi because of the earlier capture of the Takutu. Currently, seasonal flooding of the Rupununi savannas allows for a hydrological connection known as the Rupununi Portal between the Essequibo river and the Amazon river (de Souza *et al*., 2012), and this may indicate that the Rupununi may be captured by the Amazon in the future (Lujan & Armbruster, 2011). The flooded savannas of the Rupununi Portal serve as a barrier to many fishes that cannot survive in lentic conditions. Given that *Panaqolus* can be found in high and low current (Cramer, 2014), and that known localities are close to the Rupununi Portal, we think it is possible that *P. claustellifer* could be present in the Essequibo system, but despite many collections in the region of the Rupununi Portal, it has not been collected there (de Souza *et al.,* 2012).

Panaqolus claustellifer appears to be an uncommon species. *Panaqolus* species tend to be locally rare, and thus are also uncommon in collections (Lujan *et al*., 2013). We have made multiple collections in the region and have collected only the specimens reported here (de Souza *et al*., 2012). This species also appears to be uncommonly sold in the pet trade (MT pers. obs.), in which it has been designated as L306 by DATZ (Miller, 2002). The rarity of this species should be more rigorously studied for future management, especially given its economic potential.

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