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Original article

A new species of *Paralithoxus* (Siluriformes: Loricariidae: Ancistrini) from the highlands of Serra da Mocidade, Roraima State, Brazilian Amazon

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A new species of *Paralithoxus* is described from the Ajarani River, a small tributary of the Branco River basin, Roraima State, Brazilian Amazon. The genus *Paralithoxus* comprises species described from the Essequibo drainage in Guyana, Approuague and Maroni in French Guiana, Suriname River in Surinam, and more recently, from Jari and Amapá rivers, in Brazil. Despite occurring in a rock-bottomed fast-flowing stream as the other species of *Paralithoxus*, this is the first species of the genus collected at 900 m altitude, in the Serra da Mocidade highlands, an isolated and poorly accessible small mountain chain at the southern border of the Guiana Shield. The new species is distinguished from its congeners by having truncate teeth, color pattern with green spots on dark olive-brown background, alternating dark and light blotches on fins and by the pelvic fin being as long as or longer than the pectoral fin. Sex dimorphism of the species is described. Comments on morphology and osteology are provided and compared with congeners.

Keywords: Altitudinal fishes, Morphology, Osteology, Rio Branco basin, Taxonomy.

Uma nova espécie de *Paralithoxus* é descrita do rio Ajarani, um pequeno tributário da bacia do rio Branco, Estado de Roraima, Amazônia Brasileira. O gênero *Paralithoxus* é composto por espécies descritas para as drenagens do Essequibo na Guiana, Approuague e Maroni na Guiana Francesa, rio Suriname no Suriname, e mais recentemente, para os rios Jari e Amapá, no Brasil. Apesar de ocorrer em pequenos riachos com fundo rochoso e correnteza forte como o restante dos representantes de *Paralithoxus*, esta é a primeira espécie do gênero coletada a 900 m de altitude, na Serra da Mocidade, uma pequena cadeia de montanhas localizada em uma área isolada e de difícil acesso na porção sul do Escudo das Guianas. A nova espécie distingue-se de suas congêneres pela presença de dentes truncados, pelo padrão de coloração com manchas verde claras sobre fundo oliva-marrom escuro, alternando manchas claras e escuras nas nadadeiras e pelo comprimento relativo da nadadeira pélvica igual ou maior que o comprimento da nadadeira peitoral. O dimorfismo sexual da espécie é descrito. Comentários sobre a morfologia e osteologia da espécie são feitos e comparados com suas congêneres.

Palavras-chave: Bacia do rio Branco, Morfologia, Osteologia, Peixes de altitude, Taxonomia.

Introduction

Eigenmann (1910) proposed *Lithoxus lithoides* as a new loricariid genus and species, based on specimens from Guyana. The genus was diagnosed by its reduced adult size (up to 80.0 mm SL), body extremely depressed, presence of strong spines on cheek plates, large and almost perfectly round oral disc with short fringes at the border of the lips, premaxilla extremely reduced, small mouth opening and naked abdomen. Seventy years after the original description of *Ancistrus bovallii* Regan, 1906, Isbrücker (1980) assigned this species to *Lithoxus*.

Boeseman (1982) proposed the new subgenus *Paralithoxus* and described three new species, *L.* (*P.*) *planquettei*, *L.* (*P.*) *pallidimaculatus*, and *L.* (*P.*) *surinamensis*, and designated *L.* (*P.*) *bovallii* (Regan, 1906) as type species of *Paralithoxus*. *Lithoxus* (*Paralithoxus*) was distinguished from *Lithoxus* (*Lithoxus*) based on mandibular

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teeth numbering 8 (*vs.* 12), absence of an extension of the adipose fin (*vs.* presence) and pectoral fin shorter than head (*vs*. longer than head), rendering the subgenus *Lithoxus* with only one species, *Lithoxus* (*L*.) *lithoides*.

Nijssen, Isbrücker (1990) described *Lithoxus stocki* and proposed to allocate all *Paralithoxus* species in *Lithoxus*, due to the similarity between *Lithoxus bovalli* and *L. stocki*. The taxonomically simpler alternative of a single genus, *Lithoxus*, was judged preferable by the authors. After Nijssen, Isbrucker (1990) redefined the genus, two new species were described, *Lithoxus boujardi* Muller, Isbrücker, 1993 from the Approuague River basin, French Guiana, and *Lithoxus jantjae* Lujan, 2008 from the Ventuari River, Orinoco River basin, Venezuela.

Recently, phylogenetic studies using morphology (Armbruster *et al*., 2018; de Oliveira, 2018) and molecules (Lujan *et al*., 2018) recovered *Lithoxus lithoides* clearly separated from the remaining species of the genus, supporting the elevation of the subgenus *Paralithoxus* to genus and the placement of all non-*L. lithoides* species in it, except *Lithoxus jantjae*. In this same paper, Lujan *et al*. (2018) created a new genus, *Avalithoxus*, to accommodate *Lithoxus jantjae* and proposed the tribe Lithoxini to contain the genera *Lithoxus*, *Paralithoxus*, *Avalithoxus* and *Exastilithoxus*.

Both *Lithoxus* and *Paralithoxus* are mainly recorded from Guianese drainages with a few records from the Trombetas River (Pará, Brazil) (Ferreira, 1993; Lujan, 2008). Two new species were recently described, *Paralithoxus jariensis* from the Jari River and *Paralithoxus raso* from the Amapá River, both left-hand tributaries of the Amazon (Silva *et al*., 2017). *Avalithoxus jantjae* is the most westerly distributed species in the group, having been recorded only from the Ventuari River, upper Orinoco, Venezuela.

Currently, *Paralithoxus* comprises eigth species with a cratonic distribution restricted to basins of the Guiana Shield (Silva *et al*., 2017). Ferreira (1993) presented the first record of *Lithoxus lithoides* and *Paralithoxus bovalli* for the Trombetas River, in Northern Brazil. As the Ireng River (called Maú River in Roraima), type locality of *P. bovallii,* is a tributary of the Takutu River in the Brazil – Guyana border, the presence of *Paralithoxus* representatives in other Brazilian drainages was already expected.

In 2016, a multidisciplinary expedition to remote areas of the highlands of Parque Nacional da Serra da Mocidade in Roraima State, Brazil, produced a number of specimens of an undescribed species of *Paralithoxus*, collected from the Ajarani River, a high-altitude tributary of Branco River basin, which is described herein. Despite other extensive collections from Branco, Mucajaí (Ferreira *et al*., 1988) and Água Boa do Univini Rivers (Douglas A. Bastos, 2016, pers. obs.), *Lithoxus*, *Paralithoxus*, or *Avalithoxus* representatives have never been recorded from other tributaries of the Branco River basin, which strongly suggests that this new species may be restricted to high altitude streams and rivers of the southern portion of the Guiana Shield. This fieldwork resulted in the collection of several interesting new and possibly endemic species from high altitude aquatic habitats. Thus, the new *Paralithoxus* species from Serra da Mocidade is described herein, with comments on its morphological affinities with related species.

Material and Methods

Measurements and counts follow Boeseman (1982), with the addition of dorsal-fin base length and interdorsal distance. Measurements were taken point-to-point with a digital caliper to the nearest 0.1 mm and expressed in percentages and ratios in the species description and Tab. 1. Standard length (SL) is expressed in millimeters; all other measurements are expressed as percentages of standard length (SL) or head length (HL). Specimens were cleared and stained (c&s) according to Taylor, Van Dyke (1985). Nomenclature of body plates follows Schaefer (1997). Ratios in Tab. 1 were included in order to compare with the original descriptions, as type material from all *Paralithoxus* species was not available for examination. For *P. pallidimaculatus*, *P. boujardi*, *P. jariensis* and *P. raso*, we used only the original descriptions to compare. Photographs of c&s parts were taken with a Leica M205A stereomicroscope coupled with a Leica DMC4500 and Leica Application Suite V4.10.0 Interactive Measurements Montage. Comparative material was provided by the following institutions: AMNH, American Museum of Natural History, New York; ANSP, Academy of Natural Sciences of Drexel University, Philadelphia; CAS, California Academy of Sciences, San Francisco; INPA, Instituto Nacional de Pesquisas da Amazônia, Manaus; MNRJ, Museu Nacional, Rio de Janeiro; MPEG, Museu Paraense Emilio Goeldi, Belém; MZUSP, Museu de Zoologia da Universidade de São Paulo, São Paulo; USNM, National Museum of Natural History, Smithsonian Institution, Washington DC.

Collecting site. The Serra da Mocidade National Park (PARNA Serra da Mocidade) was officially created in 1998, comprising more than 350,000 ha, distributed across two municipalities, Caracaraí (Roraima State) and Barcelos (Amazonas State). The Serra da Mocidade is an area of extensive mountain ranges that reach up to 1920 m above sea level, and our expedition was the first to explore areas between 600 m and 1350 m altitude. The park is a federal conservation unit with highly restricted access, being limited by a Yanomami Indigenous Reserve to the west and areas of the Brazilian Army to the east and northwest bounds. The park is part of the Branco River basin, containing headwater streams of the Branco River tributaries Ajarani, Água Boa do Univini and Pacu.

***Paralithoxus mocidade*, new species**

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(Figs. 1–4, 8–9; Tab. 1)

Fig. 1. *Paralithoxus mocidade*, holotype, INPA 54745, female, 50.5 mm SL, in lateral, dorsal and ventral views.

Fig. 2. Lateral view of *Paralithoxus mocidade*, paratype, INPA 52424, female, 49.5 mm SL. Photographed alive by Haroldo Palo Jr.

Holotype. INPA 54745, 50.5 mm SL, Brazil, Roraima State, Caracaraí Municipality, stream tributary to Ajarani River, Branco River basin, upstream of large waterfall, Serra da Mocidade, 01°42'52.70"N 61°48'17.64"W, 29 Jan 2016, D. A. Bastos, J. Zuanon, P. M. M. Ito and S. R. Briglia-Ferreira.

Paratypes. All from Brazil, Roraima State, Caracaraí Municipality. INPA 52422, 17, 20.6–47.2 mm SL (1 c&s, 47.2 mm SL), stream tributary to Ajarani River, Branco River basin, downstream of large waterfall, Serra da Mocidade, 01°42'50.26"N 61°48'18.65"W, 29 Jan 2016, D. A. Bastos, J. Zuanon, P. M. M. Ito and S. R. Briglia-Ferreira. INPA 52424, 17, 15.0–54.7 mm SL (1 c&s, 54.7 mm SL, 16 alc.), MNRJ 51531, 2, 23.0–26.0 mm SL, MPEG 38600, 2, 27.0–30.0 mm SL, MZUSP 125192, 2, 25.0–28.0 mm SL, ANSP 206987, 2, 26.0–33.0 mm SL, all collected with holotype.

Fig. 3. *Paralithoxus mocidade*, paratype, INPA 52424, male, 50.7 mm SL in lateral, dorsal, and ventral views.

Non-types. INPA 59028, 14, 13.8–19.0 mm SL, collected with the holotype.

Diagnosis. *Paralithoxus mocidade* differs from all congeners, except *P. bovallii,* by having truncate teeth (*vs.* pointed to acute teeth). It differs from *P. bovallii* by the truncate caudal fin (*vs*. caudal-fin forked). Adittionaly, *P. mocidade* differs from *P. pallidimaculatus* and *P. surinamensis* by the presence of adipose fin (*vs.* absence). It differs from *P. planquettei* and *P. stocki* by having a more depressed and elongate body: body depth 10–13.9% of SL (*vs*. 15.3–16.8% in *P. planquettei* and 15.7–16.9% in *P. stocki*), and body width at dorsal fin 19.3–23.0% of SL (*vs*. 23.3–26.5% in *P. planquettei* and 24.2–25.1% in *P. stocki*); from *P. raso* by the larger interorbital distance, 28.8–33 % of HL (*vs*. 27.1–28.6%) and larger dentaries 5.9–9.3% of HL (*vs*. 4.4–5.3%); from *P. stocki* and *P. boujardi* by the caudal fin conspicuously mottled, with alternating dark and light blotches (*vs*. caudal fin dark with clear distal band); and from *P. jariensis* by having seven to eight plates between dorsal and adipose fins (*vs*. four) and 24–26 lateral median plates (*vs*. 23–24).

Description. Morphometrics and counts in Tab. 1. Small species of Hypostominae, largest specimen examined 54.7 mm SL. Body very depressed and short. In lateral view, dorsal profile slightly convex from snout to dorsal-fin origin, descending almost straight to dorsal procurrent rays of caudal fin. Greatest body width at pectoral-fin origin; body of similar width between posterior base of pectoral fin and origin of pelvic fin, slightly narrowing from this point towards caudal-fin base. Caudal peduncle trapezoid in cross section. Ventral profile straight from snout to caudal-fin origin.

Head short, depressed and rounded in dorsal view. Snout tip hispid, completely covered by plates. Eye moderately small, dorsally positioned; interorbital region narrow and flat. Cheek plates with up to 20 hypertrophied odontodes. Parieto-supraoccipital large, hexagonal, with process posteriorly bordered by four plates. Predorsal area with three pairs of plates, misplaced in some specimens. Nuchal plate half-moon shaped; small but conspicuous. Seven to eight plates between dorsal and adipose fins. Body almost completely plated; abdomen naked. Body plates arranged in four longitudinal series anteriorly, five series between dorsal and anal fin, and five series on caudal peduncle. All plates covered by odontodes of similar size without carinae, except for two low keels on dorsal plates between dorsal and adipose fins. Ventral series of plates largely smooth, showing large median area without odontodes, except on nuptial male. Seven plates along dorsal-fin base; low pre-adipose plate. Median series with 24–26 plates not carinate; mid-ventral series not forming prominent keel. First anal-fin pterygiophore exposed, located anterior to anal-fin origin.

Oral disc large, nearly circular. Mouth opening U-shaped, wider than long. Oral internal papillae absent. Maxillary barbel very short, projected anteriorly from oral disc. Lips well developed. Whole border of oral disc covered with large round papillae. Surface of upper and lower lips covered by round papillae not densely packed. Lip surface with shallow notches mostly without papillae distributed at top of premaxillae, around dentaries and on midline on lower lip.

Tab. 1. Morphometrics, meristics and ratios of *Paralithoxus mocidade*.

	Holotype	Mean (N=7)	SD	Min	Max
Standard length	50.49			38.35	55.2
Percents in standard length					
Predorsal length	44.6	44.9	2.0	42.0	48.3
Head length	34.5	34.1	1.4	32.1	36.2
Head depth	14.1	12.1	1.0	10.8	14.1
Head width	30.7	30.0	1.6	27.3	32.6
Body depth at dorsal fin origin	13.9	11.6	1.2	10.0	13.9
Body width at dorsal origin	23.0	20.6	1.7	19.3	23.0
Body width at anal origin	15.3	12.4	1.6	10.2	15.3
Snout length	17.9	18.4	1.0	17.2	20.6
Orbit diameter	3.6	3.8	0.3	3.2	4.4
Interorbital width	10.4	10.7	0.5	10.2	11.7
Dorsal-fin base length	20.0	18.8	1.4	15.8	21.1
Interdorsal distance	23.6	22.2	2.2	18.2	24.8
Caudal peduncle length	25.9	25.7	1.1	24.5	27.9
Caudal peduncle depth	7.5	7.9	0.4	7.1	8.4
Dorsal-fin spine length	21.5	22.0	1.6	20.6	24.5
Pectoral-fin spine length	27.9	25.5	1.9	23.8	28.7
Pelvic-fin spine length	27.0	27.8	1.8	25.5	30.5
Anal-fin first ray length	11.5	9.8	1.8	7.6	13.6
Adipose-fin spine length	7.3	6.8	1.1	4.9	8.1
Lower lip width	25.2	25.3	1.3	23.5	27.4
Lower lip length	10.2	10.3	0.7	9.5	11.4
Dentary length	2.6	2.6	0.3	2.1	3.2
Premaxillary length	2.7	2.6	0.4	2.2	3.2
Percents in head length					
Head depth	40.8	35.6	3.1	30.1	40.8
Head width	89.1	88.0	4.2	80.4	96.1
Interorbital	30.3	31.4	1.4	28.8	33.1
Orbit diameter	10.3	11.1	1.0	9.2	12.2
Pectoral length	80.9	74.4	5.6	66.9	84.9
Pelvic length	78.4	81.4	5.6	74.8	93.6
Snout length	52.1	53.8	1.8	51.6	56.8
Premaxillary length	7.8	7.7	1.1	6.1	9.9

Tab. 1. (Continued)

	Holotype	Mean (N=7)	SD	Min	Max
Dentary length	7.5	7.6	1.0	5.9	9.3
Percents in interorbital					
Dentary length	24.7	24.1	2.4	20.4	28.2
Percents in caudal peduncle length					
Caudal peduncle depth	29.0	30.8	2.0	27.6	33.5
Meristics		Mode	Min	Max	
Mid-ventral plates	26	26	24	26	
Predorsal plates	3	3	3	5	
Plates limiting supraoccipital	4	4	2	4	
Plates between dorsal - adipose	7	7	6	8	
Plates between adipose - caudal	2	2	2	7	
Procurrent plates caudal-fin superior lobe	2	2	1	3	
Plates between anal - caudal	11	11	10	11	
Procurrent plates caudal-fin inferior lobe	2	2	1	2	
Plates at base of dorsal fin	7	7	7	7	
Plates at base of anal fin	2	2	2	3	
Hemiseries premaxilar teeth	6	6	4	6	
Hemiseries dentary teeth	6	6	5	7	
Ratios of standard length		Mean	SD	Min	Max
Head length	2.9	2.9	0.1	2.8	3.1
Head width	3.3	3.3	0.2	3.1	3.7
Predorsal	2.2	2.2	0.1	2.1	2.4
Dorsal-fin base length	5.0	5.3	0.4	4.7	6.3
Body depth	7.2	8.7	0.9	7.2	10.0
Caudal ped.depth	13.3	12.7	0.6	11.9	14.0
Caudal ped. length	3.9	3.9	0.2	3.6	4.1
Pectoral length	3.6	3.9	0.3	3.5	4.2
Pelvic length	3.7	3.6	0.2	3.3	3.9
Body width at dorsal	4.1	4.8	0.4	4.1	5.2
Body width at anal	6.6	8.2	1.0	6.6	9.8
Ratios of head length					
Head depth	2.5	2.8	0.2	2.5	3.3
Head width	3.3	3.2	0.1	3.0	3.5
Interorbital	3.3	3.2	0.1	3.0	3.5
Orbit diameter	9.7	9.0	0.8	8.2	10.9
Pectoral length	1.2	1.4	0.1	1.2	1.5
Pelvic length	1.3	1.2	0.1	1.1	1.3
Snout length	1.9	1.9	0.1	1.8	1.9
Interorbital/dentary length	4.1	4.2	0.4	3.6	4.9
Caudal ped. length/ Caudal ped depth	3.4	4.2	0.4	3.6	4.9
Pectoral-fin spine Length/pelvic length	1.0	0.9	0.1	0.8	1.1

Teeth bicuspid; crown yellow and shaft translucent (Fig. 4). Premaxillary teeth much larger than mandibular teeth, arranged in crescent from lateral to mesial. Cusps of premaxillary teeth asymmetrical; larger cusp with straight border, truncate; internal cusp slightly larger. Dentary teeth extremely delicate, bifurcate; cusps small, worn to similar size. Premaxilla with 5–6 and dentary with up to 8 teeth.

Dorsal fin II,7, branched rays decreasing in length posteriorly; last branched ray 1/3 shorter than dorsal-fin spine. Spinelet reduced, locking mechanism not functional and with small area exposed, covered by odontodes. Pectoral fin I,6; distal tip of branched rays not surpassing insertion of pelvic fin when adpressed. Pectoral-fin spine robust, flat and slightly curved inward; spine of equal size of first branched ray. Pectoral-fin spine distal region covered with hypertrophied odontodes, mainly in mature males. Adipose fin low but conspicuous, with small membranous extension posteriorly. Pelvic fin i,5, distal tip of branched rays surpassing insertion of anal fin when adpressed. First pelvic unbranched ray leaf-like, enlarged medially; whole ray flat and covered by odontodes (Fig. 9b). Pelvic fin larger than pectoral fin in majority of specimens; ratio between pectoral/pelvic length with mean of 0.9 and standard deviation of 0.1. Anal fin ii,4, i,4 or i,5, branched rays coequal in length. Caudal fin i,14,i; seven branched rays on each lobe. Caudal fin almost truncate; principal rays mostly coequal in length, with lower rays slightly longer than upper lobe; all rays with small odontodes.

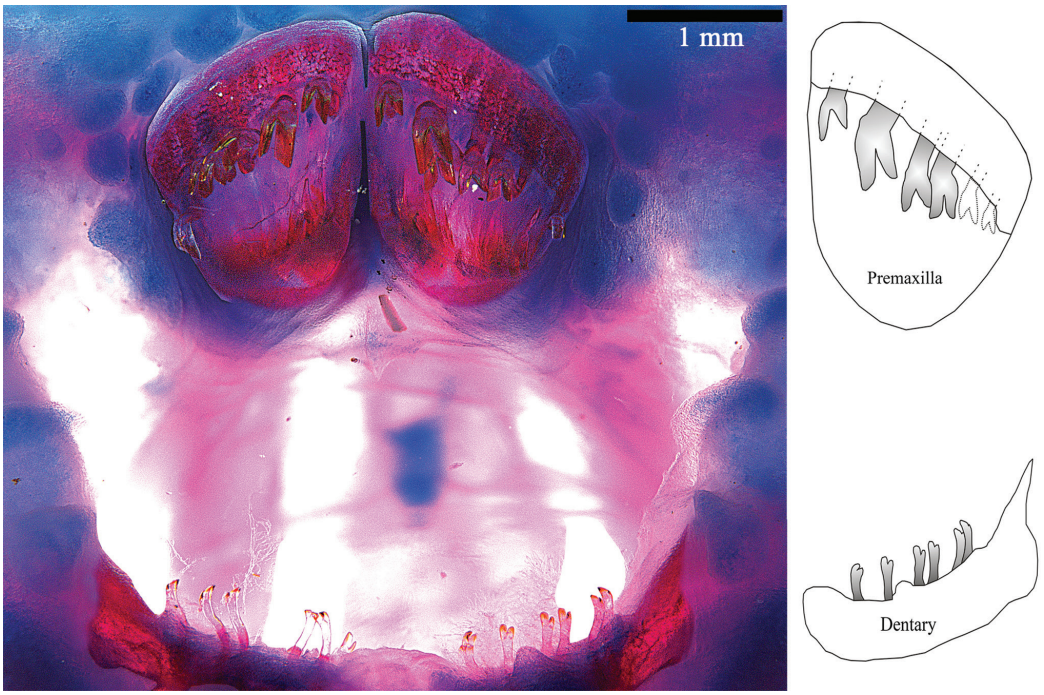

Fig. 4. Jaw teeth of *Paralithoxus mocidade*, INPA 52424, 55.2 mm SL. On the right, schematic representation of left mandibles.

Color in alcohol. Body with dark olive-brown background with irregular light blotches; blotches slightly smaller and more densely organized on head than on trunk and fins. Four inconspicuous large transverse light bars on body: first on dorsal-fin origin, second large bar on posterior dorsal-fin base, third anterior to adipose, and fourth on base of caudal fin. Ventral surface of body uniformly cream to beige colored. All fins with checkered pattern, alternating large dark blotches with clear ones.

Color in life. Very similar to preserved coloration, but with overall body color dark olive-brown on dorsum with light green spots on snout and cheek (Fig. 2); thin creamy to light green vermiculations over interorbital area and posterior portion of head; clear marks on anterior portion of dorsum becoming larger and more irregular towards caudal peduncle. Ventral side of body uniformly beige.

Sexual dimorphism. Urogenital papilla small, but conspicuous on all specimens. The only externally mature male specimen was dissected and had a more melanic coloration, darkened on body and lips, losing bars and blotches along body and fins; dorsal, pectoral and pelvic fins with branched rays darkened showing light bar close to tip; caudal fin uniformly dark (Fig. 3). Male with odontodes on cheek plates and pectoral fin more hypertrophied than on females. Mature male with fins more developed than females: pectoral spine large, strong, bearing more developed odontodes on distal half; first pelvic-fin unbranched ray strong, rounded for entire length and enlarged medially; branched rays on pelvic fin conspicuously longer than unbranched ray. Male has caudal peduncle covered with odontodes, except around anal fin, whereas females and juveniles present caudal peduncle ventrally smooth, without aligned odontodes.

Geographic distribution and habitat. *Paralithoxus mocidade* has only been recorded from an unnamed tributary of the Ajarani River, in the area of Serra da Mocidade, Branco River basin, Caracaraí Municipality, Roraima State, Brazil (Fig. 5). All specimens were collected up and downstream of a 20-m high waterfall located at approximately 900 m elevation. The Ajarani River at the collection site is a small fast-flowing river (up to 15 m width and 2 m depth, as measured in dry season) with clear water, low temperature (about 21.7 ºC), acidic (pH 5.5), dissolved oxygen (DO) 20.7%, and smooth rocks on the bottom (Fig. 6). During the day, juveniles were observed grazing in the open over smooth rocks, and adults were found in narrow cracks or under rock slabs during the night. Juveniles were captured with hand-nets and adults were collected by hand while snorkeling (Fig. 7).

Etymology. The specific epithet "mocidade" is in allusion to the type locality, in Serra da Mocidade National Park. A noum in apposition.

Conservation status. *Paralithoxus mocidade* is known only from the type locality in a geographically isolated river system, which could generate concerns about its conservation status. However, the inaccessibility of the area and the fact that nearly two-thirds of the area of Serra da Mocidade are formally protected by the Serra da Mocidade National Park and Yanomami Indigenous Territory indicate that there are no imminent threats to the species, which can be categorized as Least Concern (LC) (IUCN, 2017).

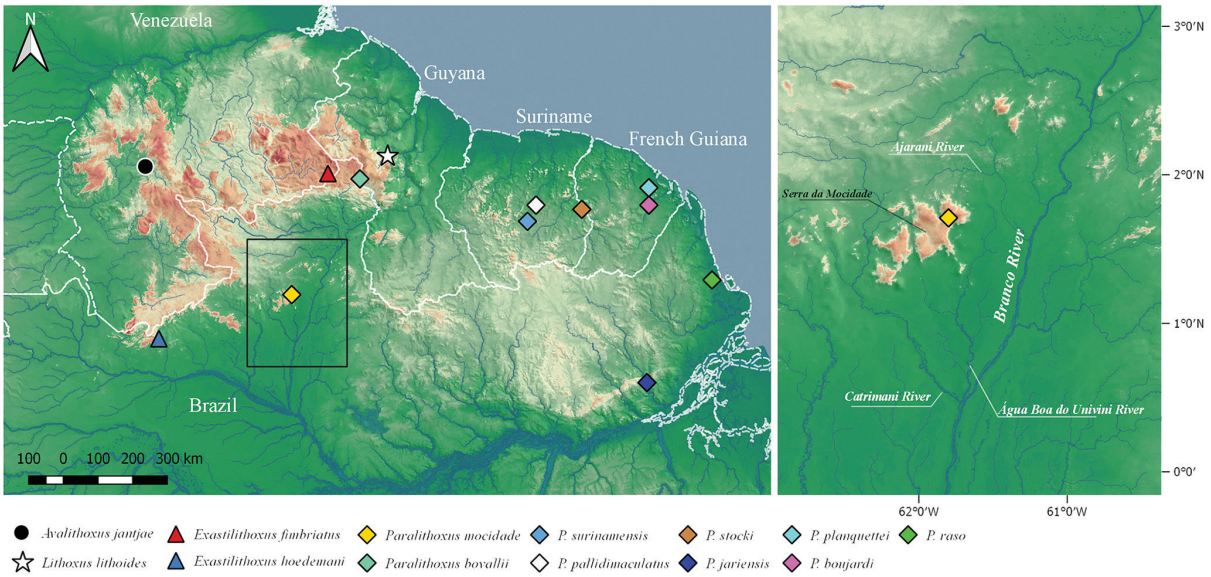

Fig. 5. Distribution of all type-material of Lithoxini in northern South America (ranges not included) and detail of Serra da Mocidade, Roraima, Brazil.

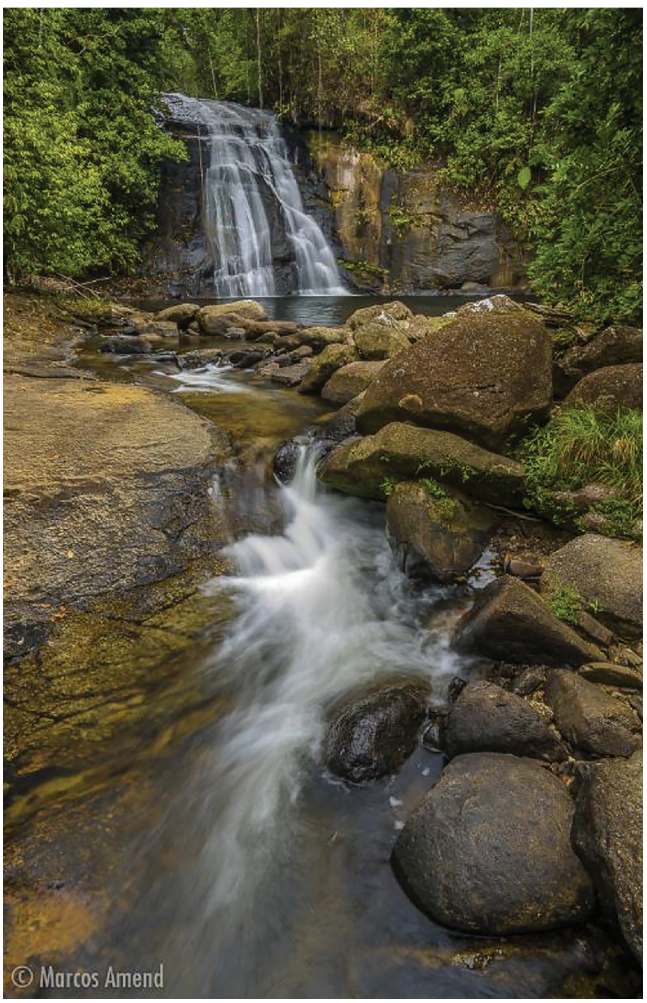

Fig. 6. Type-locality of *Paralithoxus mocidade* in Ajarani River, tributary of the Branco River basin, located immediately downstream of a large waterfall. Photo by Marcos Amend.

Fig. 7. Hand collecting (a) specimens of *Paralithoxus mocidade* from a (b) narrow crevice in a rock slab during snorkelling.

Taxonomic remarks. *Paralithoxus mocidade* and *P. bovallii* were recorded from the Branco River basin: *P. bovallii* from the Takutu (Branco)-Essequibo drainages and *P. mocidade* from the Ajarani River. Recent collections in the upper Ireng River by N. K. Lujan and J. W. Armbruster produced new specimens of *P. bovallii* from the type-locality, as listed in the redescription of the species by Lujan *et al.* (2018). Based on this and the original description (Regan, 1906), we

conducted a morphological comparison. Both *P. bovallii* and *P. mocidade* share a mottled color pattern on body and fins, a similar number of teeth on the jaws (6 to 8), same tooth shape (truncate) (Fig. 4), and similar number of plates between dorsal and adipose fins. However, these species differ in eye size, with *P. mocidade* having a usually smaller eye, with orbit representing 9–12% (average 11%) *vs*. 11–19% (average 14.6%) in *P. bovallii* (Lujan *et al.*, 2018). Based on Regan's original ratios, the orbital diameter in *P. bovallii* was contained 6–7.5 times and interorbital distance 3 times in head length, whereas in *P. mocidade*, the orbit is contained 8–10 times and the interorbital 3–3.5 times in head length. Besides, *P. bovallii* has the pectoral fin larger than the pelvic whereas in *P. mocidade* pectoral and pelvic are equal or the pelvic is slightly larger: pectoral length 23.8–28.7% (mean of 25.5%) in SL in *P. mocidade vs*. 6.9–33.0% (26.2%) in *P. bovallii*; pelvic fin 25.5–30.5% (27%) in SL in *P. mocidade vs*. 4.9–29% (22.8%) in *P. bovallii* (Lujan *et al.*, 2018).

The other species described from the Essequibo River drainage is *Lithoxus lithoides* (also distributed in other drainages such as the Trombetas River, following Ferreira, 1993). *Lithoxus lithoides* is extremely different from *Paralithoxus mocidade* having larger eyes, larger pectoral fins (more developed in nuptial males), larger posterior membranous extension of the adipose fin, dorsal fin almost touching the adipose-fin plate, and three series of plates in the caudal peduncle. However, *L. lithoides* shares with *P. mocidade* the truncate teeth and membranous extension of the adipose (reduced in *P. mocidade* when compared to *L. lithoides*). Some paratypes of *L. lithoides* were examined and measured, and differences in orbit and caudal peduncle were highly evident between the two species: orbit diameter ranged from 19–21% of head length in *L. lithoides vs*. 9.2–12.2% in *P. mocidade*; caudal peduncle depth ranged from 18.8–23% of caudal peduncle length in *L. lithoides vs*. 27.6–33.5% in *P. mocidade*. Besides, *L. lithoides* has the premaxilla much smaller than the dentary, whereas in *P. mocidade* the toothed area in both jaws is of similar size, despite difference in the size of the teeth, reinforcing the general dissimilarity between both species.

Species of *Paralithoxus* recorded from French Guiana (*P. planquettei*, *P. boujardi* and *P. stocki*) share some features distinct from *P. mocidade*: teeth with acute cusps and caudal fin with distinct distal light bar *vs*. teeth truncate and caudal fin with alternating clear and dark blotches in *P. mocidade*. Besides, both *P. boujardi* and *P. stocki* have a larger pectoral fin (pectoral length 3.3–3.7 and 2.8–3.6 times in SL in *P. boujardi* and *P. stocki* respectively *vs*. 3.5–4.2 in *P. mocidade*) and shorter caudal peduncle (caudal peduncle length 3–3.25 and 3.5 times in SL in *P. boujardi* and *P. stocki* respectively *vs*. 3.6–4.1 in *P. mocidade*). *Paralithoxus planquettei* also has a shorter pectoral fin and a deeper caudal peduncle (caudal peduncle depth 9.8–11.75% in SL *vs*. 7.1–8.4% in *P. mocidade*) and larger mandible (dentary length 2.5–2.8 times in interorbital distance *vs*. 3.6–4.9 in *P. mocidade*).

Paralithoxus jariensis and *P. raso* were originally distinguished from other *Paralithoxus* species by a set of morphological features. *Paralithoxus raso* has a peculiar color pattern with light large blotches similar to *P. pallidimaculatus* (Silva *et al.*, 2017). Both recently described species were recorded for the eastern part of the Amazon, in Pará and Amapá States. *Paralithoxus jariensis* is morphometrically very similar to *P. mocidade* but shows a reduction in number of plates: four plates between dorsal and adipose fin (*vs*. 7–8 in *P. mocidade*) and 23–24 lateral median plates (*vs*. 24–26 in *P. mocidade*). *Paralithoxus raso* differs from *P. mocidade* mainly by having a larger pectoral-fin spine (27–29% *vs*. 23–28% in SL in *P. mocidade*), and smaller mandibles (premaxilla 3.3–4% and dentary 4.4–5.3% in head length in *P. raso vs*. 6.1–9.9% and 5.9–9.3% in head length in *P. mocidade*). In their original description, the authors also conducted a molecular analysis using sequences of the COI mitochondrial gene for most available species of *Paralithoxus* (*P. planquettei*, *P. bovallii*, *P. pallidimaculatus*, *P. boujardi* and *P. stocki*). *Paralithoxus jariensis* and *P. raso* came out as sister group of *P. planquettei*, also from Eastern Guiana (Oyapock River).

Osteological remarks. Armbruster *et al.* (2018) presented a morphology-based phylogeny for Lithoxini in which synapomorphies were proposed for the genera *Lithoxus*, *Paralithoxus* and *Avalithoxus* as a way to compare their results with the molecular phylogeny presented in Lujan *et al.* (2018). Most of the synapomorphies listed for *Paralithoxus* were confirmed in this study with slight variation in *P. mocidade*, such as: first hypobranchial angled at 45° relative to the sagittal plane, maxilla distal end enlarged, and metapterygoid weakly sutured to lateral ethmoid.

Although cited as a synapomorphy for the tribe Lithoxini (Armbruster *et al.*, 2018), in *P. mocidade* the difference in size between the teeth on both mandibles and the distinct shape of the cusps are remarkable (Fig. 4): cusps truncate and subequal in size on the premaxilla, and pointed and equally forked on the dentary. As cited above, truncate teeth were also observed in *L. lithoides* and *P. bovallii*. *Lithoxus lithoides*, however, has the mesial cusp of premaxillary teeth almost three times the size of the lateral cusp. Also, the size and enlargement of the distal end of the maxilla deserves attention. In *P. mocidade*, the maxilla is well developed, its length more than 50% the length of the palatine, and its distal enlargement is rather pronounced.

The suspensorium in *P. mocidade* is similar to that of other Lithoxini and comparable to *P. bovallii*, the closest species to *P. mocidade*. However, the metapterygoid anterior processes, both the digitiform and the "spoon-shaped" (Armbruster, 2004), are much more enlarged in *P. mocidade* than in *P. bovallii* and other Lithoxini. The anterior opercular process is also highly enlarged, similar to *Avalithoxus jantjae* (Armbruster *et al.*, 2018, fig. 4-A).

The branchial apparatus in *P. mocidade* has a strong hyoid arch, and strongly pointed, villiform teeth on both pharyngeal plates (upper and lower), a condition already registered by Armbruster (2004) for *L. lithoides* and *P. bovallii*. *Paralithoxus mocidade* has only one basibranchial (BB) (Fig. 8), ossified and very elongate, almost filling the whole mesial extension of the branchial apparatus; the other basibranchial is a cartilaginous mass connected to the fourth and fifth ceratobranchials. The ordinary siluriform condition is the absence of the first basibranchial (Arratia, 2003), second (BB2) ossified, and third (BB3) reduced, ossified or not (Schaefer, 2003). Most loricariids show the generalized siluriform condition. In *Paralithoxus mocidade*, the long ossified BB can be explained by the fusion of BB2 and BB3 (very elongate BB) or BB2 lost (Armbruster, 2004 – for *L. lithoides* and *P. bovallii*). This condition was also observed in *Exastilithoxus fimbriatus* and other members of Lithoxini (Armbruster *et al*., 2018).

Paralithoxus mocidade has a highly reduced accessory flange of the first ceratobranchial (CB1) (Fig. 8) (approximately 1/5 of the ceratobranchial properly). Most Hypostominae have a well-developed CB1 accessory flange (Schaefer, 1987; Armbruster, 2004), an extra sheet of thin bone originating on the same point of the ceratobranchial, of similar size and, usually, bearing a row of branchial filaments. *Lithogenes* and astroblepids lack this accessory flange. The condition in *P. mocidade* has been already cited for *P. bovalli*, *L. lithoides*, and some other non-hypostomines (Armbruster, 2004) and it was also observed in *Exastilithoxus fimbriatus*.

Finally, the pectoral girdle in *P. mocidade* has a conspicuous small hornlike process (Fig. 9a) on the anterior surface of the cleithrum. *Lithoxus lithoides* and *P. bovallii* have a short and dense bony crest at the same point, but in *P. mocidade* this crest comes forward as a small, blunt, cylindrical process, inclined towards the lateral sides of the body, with an extra blue-stained tissue coming off its extremity that could be a tendon or a thin cartilage. This condition is quite unusual, and it was not observed in *E. fimbriatus*, but it has been observed in one specimen of *Hypostomus gymnorhynchus*.

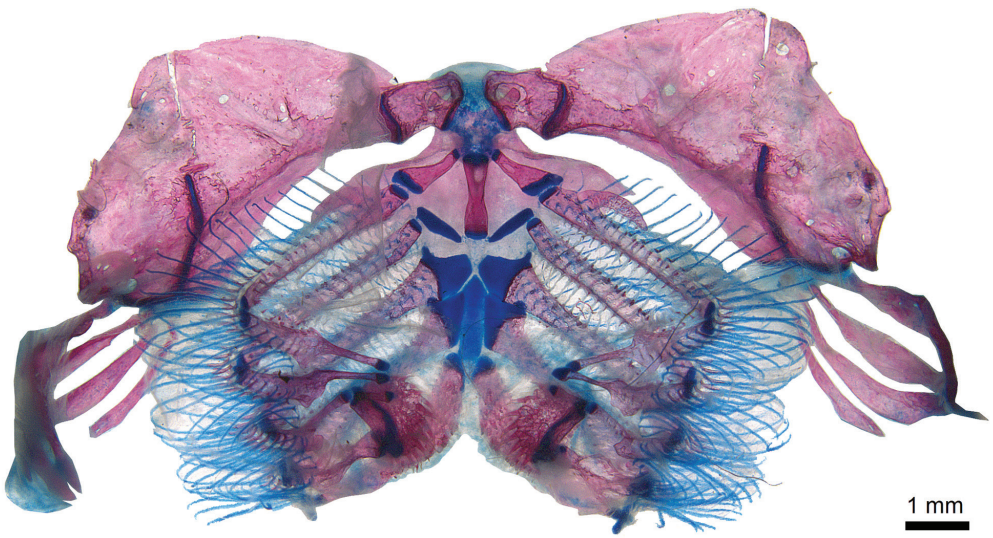

Fig. 8. Branchial apparatus of *Paralithoxus mocidade,* INPA 52424, 55.2 mm SL.

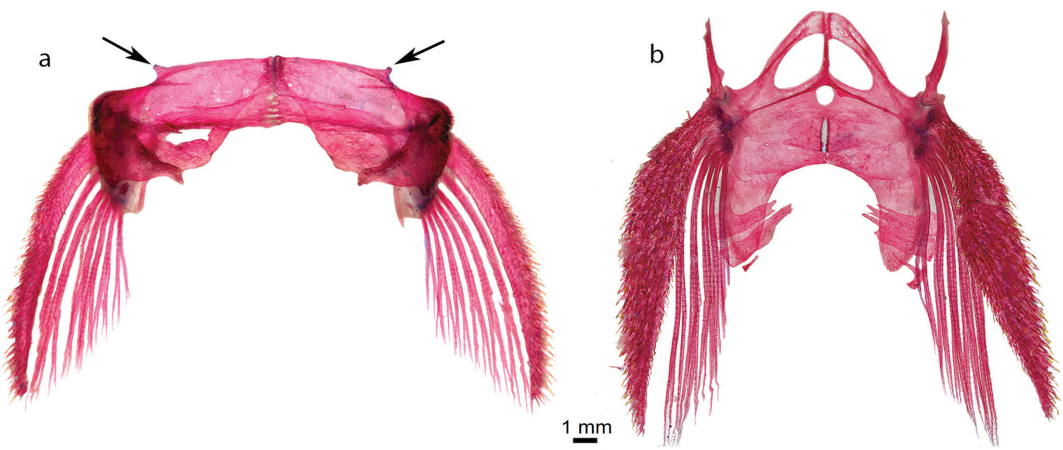

Fig. 9. a. Pectoral (dorsal view), with arrows for the cleithra processes, and b. pelvic (ventral view) of *Paralithoxus mocidade*, INPA 52424, 55.2 mm SL.

Discussion

Paralithoxus, *Lithoxus* and *Avalithoxus* are very close to *Exastilithoxus* Isbrücker, Nijssen, 1979. *Exastilithoxus* comprises only two valid species, *E. fimbriatus* (Steindachner, 1915), described from the Coquenan River, Caroni basin in Venezuela, and *E. hoedemani* Isbrücker, Nijssen, 1985, from waterfalls in the Marauiá River, Negro River basin, Brazil. *Exastilithoxus* shares with *Lithoxus* and *Paralithoxus* synapomorphies related to morphology and osteology (Armbruster, 2004; Armbruster *et al.*, 2018) such as: overall reduction of the branchial apparatus, loss of lateral walls of the metapterygoid channel, basipterygium with anterolateral and anteromesial processes fused, reduction in the number of plate rows on thinnest part of the caudal peduncle from five-four to three (as in *Lithoxus*), abdomen naked, and teeth large but not spoon-shaped.

In Lujan *et al*. (2018), the Lithoxini genera *Lithoxus*, *Paralithoxus*, *Exastilithoxus*, and *Avalithoxus* were recognized by sharing a small adult size, body strongly depressed, a large oral disc with papillate lips, and small oral opening. *Avalithoxus* was diagnosed mainly by a reduction in the number of branched caudal-fin rays (12 *vs*. 14 or 13 in all other Lithoxini representatives), reduction on the number of inter dorsal plates (five *vs*. six to nine), and absence of digitate papillae on the lips (*vs*. digitate papillae present in *Exastilithoxus*).

The two multilocus phylogenetic analyses with Hypostominae available (Lujan *et al.*, 2015; 2018) recovered two contrasting results. The first analysis, without representatives of *P. bovallii*, showed *Lithoxus lithoides* as the sister group of a large clade of undescribed species of *Exastilithoxus*; the second recovered *L. lithoides* as the sister group of the *Paralithoxus* species, and *Avalithoxus jantjae* as the sister group of a large clade comprising (*Exastilithoxus* (*Lithoxus*-*Paralithoxus*)).

Both Armbruster (2004) and de Oliveira (2018), in a morphology-based phylogeny, recovered *Lithoxus*, *Paralithoxus* and *Exastilithoxus* nested within Ancistrini clades comprising *Chaetostoma* and *Dekeyseria* among other genera. Some of the synapomorphies shared by these taxa are corroborated here, such as the peculiar shape of the opercle in *Paralithoxus*, which is very similar to that of *Dekeyseria*.

Armbruster *et al*. (2018) recovered a different ingroup arrangement from the morphological analyses cited above, with *Avalithoxus jantjae* as the sister-group of (*Exastilithoxus* (*Paralithoxus*, *Lithoxus*)), similar to the Lujan *et al.* (2018) molecular analysis results. Both the 2018 morphology and molecular-based analysis were quite reductionists, dealing mainly with the ingroup terminal taxa and very few outgroups. However, those analyses comprised more ingroup taxa than the other ones, which increases confidence level in the results as well.

Paralithoxus mocidade differs from most species of *Paralithoxus* by the presence of a large pelvic fin, whereas in other species the pectoral is clearly larger than the pelvic fin. The new species lives in a fast-flowing river with rapids and waterfalls, similar to its congeners, and apparently represents the first record of a *Paralithoxus* species occurring in high-altitude water bodies. All species of *Paralithoxus* are adapted to high-energy waters, occupying cracks or crevices on rocks in clear water rivers with rapids and rocky/sandy substrates (Ferreira, 1993). Other species collected with *P. mocidade* in the same habitat included undescribed species of *Ancistrus* (Loricariidae) and *Trichomycterus sensu lato* (Trichomycteridae).

Species of *Lithoxus* and *Paralithoxus* occur in the drainages of the Guiana Shield, as other loricariid genera such as, *Corymbophanes*, *Exastilithoxus*, *Lithogenes*, *Metaloricaria* and *Neblinichthys*. Distributions of loricariid taxa suggest that connections to these other areas have been important, but that within the Guiana Shield there has been little mixing of upland faunas via the Western Atlantic Coastal and Caroni-Cuyuni/Mazaruni corridors (Lujan, Armbruster, 2011). Most distributions within the Guiana Shield can be explained via current watershed boundaries, stream-capture events in the uplands of larger systems, and/or ancient river systems such as the proto-Berbice (Lujan, 2008; Lujan, Armbruster, 2011). All species of *Paralithoxus* occur from an eastern limit in Amapá River, Brazil (Melo *et al*., 2016; Silva *et al*., 2017), to the west up to Cuyuni-Mazaruni River in Guyana to the North, and to the South up to Trombetas River basin, Brazil (Ferreira, 1993). Additional unpublished records of *Paralithoxus* spp. from other drainages in Brazil such as Uatumã (Amazonas State), Jari, Oriximiná, Maicuru (Lúcia Rapp Py-Daniel, pers. obs.) (Pará State) and Amapá Grande (Amapá State) confirm that the current geographic distribution observed for *Paralithoxus* ranges from the Guiana Shield tributaries to the left hand cratonic tributaries of the Amazonas River. The recent descriptions of *Paralithoxus jariensis* and *P. raso* corroborate the putatively larger area of occurrence of the genus. Interestingly, *Paralithoxus* has never been recorded from the Negro River basin, where *Exastilithoxus* occurs, or the Orinoco River, where *Avalithoxus* can also be found. The Serra da Mocidade range is completely disconnected from other mountain ranges in Roraima State, Brazil. The similarity of *P. mocidade* with the Potaro and Takutu taxa hints at ancient and unknown connections between these areas.

Comparative material examined. *Exastilithoxus fimbriatus*: **Guyana**, AMNH 220459, 1, 48.5 mm SL, Essequibo River basin. **Venezuela**, ANSP 160626, 1, 43.6 mm SL, Cataniapo River, Orinoco River basin. **Brazil**, INPA 38957 (1 c&s 37.3 mm SL), Auaris River, shore between Sanoma and Yekuana Indigenous villages. *Exastilithoxus hoedemani*: **Brazil**, INPA 506, holotype, 50.9 mm SL, Marauiá River, Negro River basin. *Exastilithoxus* sp.: **Brazil**, INPA 049716, 1, 30 mm SL, Negro River, bedrocks close

to São Sebastião village, São Gabriel da Cachoeira Municipality. *Paralithoxus bovallii*: **Suriname**, AMNH 54961, 9, 35.4–45.4 mm SL, Corintijn River basin. *Lithoxus jantjae*: **Venezuela**, ANSP 182809, 4 paratypes, 22.8–34.4 mm SL; Ventuari River, Orinoco River basin, above Salto Tencua, 58 km east-southeast of San Juan de Manapiare. *Lithoxus lithoides*: **Guyana**, AMNH 7119, 5 paratypes, 29.6–43.6 mm SL; Warraputa Falls and in rocks above falls, Essequibo River basin. ANSP 39121, 1 paratype, 38.6 mm SL, Warruputa Falls, Essequibo River basin. ANSP 185295, 1, 35.4 mm SL, Essequibo River (Atlantic Dr.) at Yukanopito Falls, 44.5 km SW of mouth of Kuyuwini River. CAS 77332, paratypes, 10, 43.1–46.8 mm SL, Amatuk cataract, Potaro River, Essequibo River basin. USNM 66223, 3 paratypes, 39.7–44.3 mm SL; Amatuk. **Brazil**, Amazonas State, INPA 845, 50 mm SL, 46147, 3, 24.5–41.2 mm SL, Presidente Figueiredo Municipality, Pitinga River, Uatumã River basin. *Paralithoxus planquettei*: **Suriname**, ANSP 189131, 17, 17.5–71.5 mm SL, Sipaliwini District, Litanie River at mouth and confluence with Marowini River. ANSP 189135, 1, 55.6 mm SL, Sipaliwini District, Lawa River, Marowijne River basin, Gransoela. **French Guiana**, INPA 3243, 2, 27.9–57.4 mm SL, Sinnamary River, igarapé Takari. **Brazil**, INPA 4910, 3, 27,5–30,1 mm Sl, Amapá State, Araguari River basin. INPA 7824, 2, 22.0–28.3 mm SL, Pará State, Oriximiná Municipality, Trombetas River basin. INPA 37610, 24, 32.4–58.8 mm SL, Amapá State, Macapá Municipality. MZUSP 103396, 26, 31.3–50.9 mm SL, Monte Dourado Municipality. MZUSP 101528, 17, 32.9–51.1 mm SL, Laranjal do Jari Municipality. MZUSP 101539, 6, 22.7–29.8 mm SL, Amapá State, Laranjal do Jari Municipality. *Paralithoxus stocki*: **Suriname**, ANSP 189130, 2, 67.7–68.4 mm SL, Sipaliwini District, Lawa River, Marowijne River basin. ANSP 189137, 1, 61.0 mm SL, Sipaliwini District, Lawa River, Marowijne River basin. **Brazil**, Pará State, Oriximiná Municipality, INPA 5537, 1 (c&s), 60 mm SL, INPA 5538, 5, 36.3–40.6 mm SL, INPA 33815, 20, 31.3–66.4 mm SL, Trombetas-Mapuera River. *Paralithoxus surinamensis*: **Brazil**, Pará State, INPA 7807, 1, 23.8 mm SL, Oriximiná Municipality, Poana River, Cachoeira Seca Superior. *Pseudolithoxus* sp.: **Brazil**, Amazonas State, INPA 16270, 7 (5 alc, 97.5-153.1 mm SL, 1 skl, 146.8 mm SL, 1 c&s, 73.6 mm SL), Presidente Figueiredo, Uatumã River, Cachoeira do Miriti. *Dekeyseria picta*: **Brazil**, Amazonas State, INPA 400, 3 (3, 42.7-74.8 mm SL, 1 c&s), Urubaxi River, near its mouth in Negro River, Barcelos Municipality.

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