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A NEW SPECIES OF *PARETROPLUS* (TELEOSTEI: CICHLIDAE: ETROPLINAE) FROM NORTHWESTERN MADAGASCAR, WITH A DISCUSSION OF ITS RELATIONSHIPS WITHIN THE *P. DAMII* CLADE

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ABSTRACT

Paretroplus risengi, new species, is described from the middle to lower reaches of the Anjingo-Ankofia drainage basin, including Lake Andrapongy, in northwestern Madagascar. *Paretroplus risengi* is recovered within the "*Paretroplus damii* clade" based on several apomorphic anatomical features shared with other members of that assemblage, including the presence of a rounded or triangular, black pectoral-axil patch, chest scales that are markedly reduced in size and highly embedded, and flank scales characterized by a thin and unossified posterior field. The new species is recovered as the sister taxon to a clade comprising *P. damii* and *P. loisellei*. *Paretroplus risengi* is distinguished from the two other members of this clade by pigmentation pattern in preservation comprising a dark head, followed by broad, much lighter anterolateral band, and dark posterior body (vs. uniform dark gray to dark grayish-brown in *P. damii* and *P. loisellei*), with adult specimens frequently appearing quite blotchy or mottled, and fewer gill rakers on the lower limb of the first arch (mode 11 vs. 12 [*P. damii*] or 13 [*P. loisellei*]). *Paretroplus risengi* and *P. damii* are distinguished from *P. loisellei* by a strongly rounded and convex profile extending from the anterior margin of the lower jaw to the ventroposterior margin of the suspensorium (vs. horizontal), oblique oral jaws with thin lips (vs. horizontally oriented with fleshy lips), a lighter non-breeding overall pigmentation pattern (vs. uniform dark brown or grayish-brown), and distinctive bright yellow, orange, or brick red breeding coloration (on head and anterior flank) over a blackish base (vs. uniform golden). *Paretroplus risengi* and *P. loisellei* are distinguished from *P. damii* by the presence of weakly tricuspid symphyseal teeth in the upper jaw (vs. lacking lateral cusps). *Paretroplus risengi* is further distinguished from *P. damii* by a smaller maximum adult size (not exceeding 170 mm SL, and usually much smaller vs. regularly exceeding 300 mm SL), and from *P. loisellei* by a lower lateral line scale count (mode 37 vs. 38), fewer vertebrae (mode 31 vs. 32), and a lower epibranchial raker count (9-10 vs. 11-12).

Keywords: Anjingo River, damba, gas bladder, Madagascar, *Paretroplus risengi* sp. nov., *Paretroplus damii* clade, phylogeny

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We are especially grateful to K. Riseng, T. Ravelomanana, C. Braun, and R. Schelly for considerable assistance with fieldwork. Thanks to P. Loiselle, M. Stiassny, P. de Rham, and the late J.-C. Nourissat for freely sharing their collections, field images, vast knowledge of Malagasy cichlids, and field data. Thanks to L. Frank and R. Berquist of the SIO/UCSD Digital Fish Library for permission to use MRI segmentation of new species. For the loan or gift of specimens in their care we are grateful to P. Loiselle, P. de Rham, J.-C. Nourissat, D. Nelson and Randy Singer (UMMZ), D. Siebert (BMNH), G. Duhamel, P. Pruvost, and R. Causse (MNHN), C. Weber and S. Fisch-Muller (MHNG), and M. van Oijen (RMNH). For curatorial assistance with materials at the AMNH and for help with radiographs we are grateful to R. Arindell. Fieldwork in Madagascar was facilitated by B. Andriamahaja and the MICET (Institute for the Conservation of Tropical Environments, Madagascar) staff, and we are grateful for their continued support of ichthyological field research in Madagascar. Collection permits were obtained from the Direction des Eaux et Forêts and the Association National pour la Gestion des Aires Protégées (ANGAP), Madagascar, in accordance with AMNH IACUC guidelines. This study was supported by an award from the National Science Foundation to JSS (IOS-0749943) and by the American Museum of Natural History.

INTRODUCTION

Paretroplus comprises 13 valid species and is endemic to Madagascar (Sparks, 2008, 2022), not including the new taxon formally described herein. Based on comprehensive surveys conducted throughout Madagascar over the past three decades by various research groups, several new species of *Paretroplus* have been discovered and formally described, including *P. menarambo* Allgayer, 1996, *P. nourissati* (Allgayer, 1998), *P. maromandia* Sparks and Reinthal, 1999, *P. tsimoly* Stiassny et al., 2001, *P. dambabe* Sparks, 2002a, *P. gymnopreopercularis* Sparks, 2008, *P. lamenabe* Sparks, 2008, and *P. loisellei* Sparks and Schelly, 2011. With continued survey efforts exploring remote regions of the island, it is likely that additional novel species of *Paretroplus* will be discovered, however, nearly all members of the genus have suffered significant population and range declines in recent years due to the combined pressures of deforestation, overfishing, and competition from exotic species (Sparks and Stiassny, 2022). Based on the most recent IUCN Red List assessment (IUCN, 2021; Ravelomanana et al., 2018; Sparks and Stiassny, 2022), several species of *Paretroplus* are now listed as Critically Endangered, including *P. dambabe*, *P. maculatus*, *P. menarambo,* and *P. gymnopreopercularis*. Despite repeated survey attempts within their former ranges, both *P. dambabe* and *P. maculatus* have not been collected in recent years and are very likely extinct in the wild (pers. obs.). *Paretroplus loisellei*, *P. lamenabe*, *P. nourissati*, *P. tsimoly*, and *P. maromandia* were assessed as Endangered, whereas the more widespread species, *P. kieneri* and *P. damii*, which inhabit both rivers and floodplain lakes and occur across multiple drainage basins, were assessed as Vulnerable. Only the widespread *P. polyactis*, occupying both fresh and brackish water habitats spanning nearly the entire eastern coast, was listed as Least Concern.

Paretroplus is recovered as the sister taxon to a clade comprising the genera *Etroplus* and *Pseudetroplus*, whose members are endemic to southern India and Sri Lanka, and this assemblage of three genera comprises the subfamily Etroplinae (Sparks, 2004; Sparks and Smith, 2004; Pethiyagoda et al., 2014; Fig. 1). Members of *Paretroplus* are restricted to westward draining freshwater basins in the northwestern and northern region of the island, except for *P. polyactis*, which is widespread in both freshwater and brackish-water habitats along most of the eastern coast, and *P. loisellei*, which occurs in the eastward draining Mahanara River, located to the north of Sambava near the town of Antsirabe-Nord, in northern Madagascar. All northwestern and northern species of *Paretroplus* are narrowly endemic and restricted to single drainage basins, or to only portions of a single drainage basin, except *P. damii* and *P. kieneri*, which comparatively exhibit widespread distributions and occur across multiple basins. Species of *Paretroplus* are absent from central highland, central western, and extreme southern and southwestern drainages.

Sparks (2008: fig. 1B) recovered two major clades within *Paretroplus* with strong support, one comprising more elongate and shallow-bodied, primarily lotic species, referred to as the "*P. damii* clade", and the other restricted primarily to deep-bodied lacustrine forms. Martinez and Sparks (2017: fig. 2) recovered this same pattern of relationships and demonstrated a strong covariation between body shape evolution and jaw shape in Etropline cichlids (Martinez and Sparks, 2017: fig. 7). The "*P. damii* clade" currently comprises five species: *P. damii* Bleeker, 1868, *P. nourissati* (Allgayer, 1998), *P. tsimoly* Stiassny et al., 2001, *P. lamenabe* Sparks, 2008, and *P. loisellei* Sparks and Schelly, 2011 (Fig. 1). *Paretroplus loisellei* is the only member of the clade to occur in an eastern drainage. Multiple phylogenetic analyses (Sparks, 2008; Sparks and Schelly, 2011; Martinez and Sparks, 2017) also revealed the existence of an additional novel taxon within this clade, endemic to the Anjingo and Ankofia river drainage basins, including Lac Andrapongy, in northwestern Madagascar, which is formally described herein. The new species is recovered as the sister taxon to

a clade comprising *P. damii* and *P. loisellei*, with which it shares the four apomorphic features that distinguish this group from the *Paretroplus nourissati* species group, including a characteristically uniform brown (grayish-, reddish-, or golden-brown) overall coloration as adults (unstressed and breeding individuals may exhibit a broad golden-yellow, vivid orange, or brick red band on the anterior flank, with similar coloration on the cheek, over a blackish base), the absence of a dark vertical barring pattern covering the flank, the absence of broad, converging black midlateral bars, and the presence of weak lateral cusps on the enlarged symphyseal teeth in the upper jaw, such that these teeth are weakly tricuspid (lateral cusps absent on upper symphyseal teeth in *P. damii*) (Sparks, 2008; Sparks and Schelly, 2011).

METHODS

Specimens used in this study were fixed in 10% buffered formalin and stored in 75% ethanol. Cleared and double stained skeletal preparations (C&S) were produced using a modified protocol based on Taylor and Van Dyke (1985) and dry skeletal preparations were generated from specimens preserved in ethanol. Counts and morphometric measurements follow Barel *et al.* (1977) and Sparks (2008), unless noted otherwise. Measurements were verified at least twice and recorded to the nearest 0.1 mm using analog dial calipers. Vertebral and fin spine/ray counts were obtained from radiographs and C&S skeletal preparations. Vertebral counts exclude the terminal, hypural-bearing vertebra (= terminal

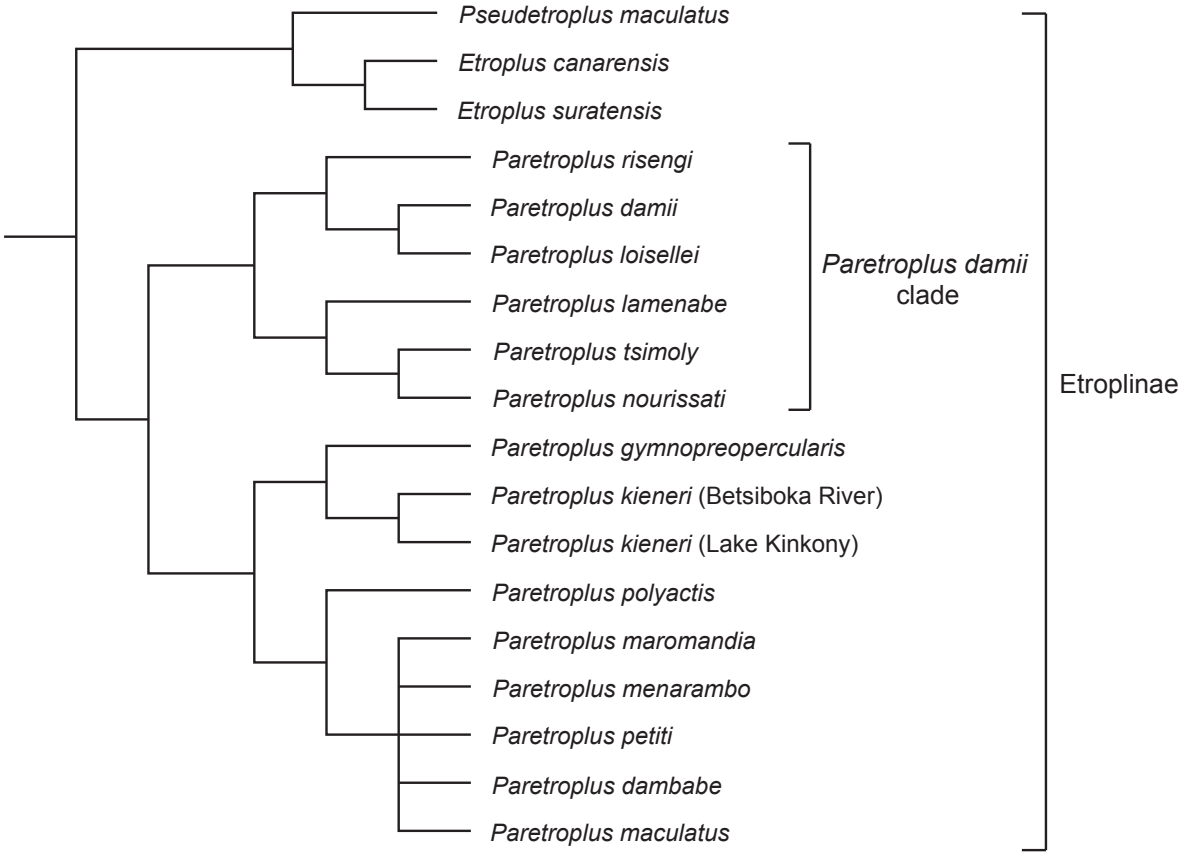


Figure 1. Phylogenetic relationships of Etroplinae, indicating placement of *Paretroplus risengi*, new species, within the "*P. damii* clade" after Sparks and Schelly (2011: fig. 1). See that study for phylogeny reconstruction methodology and additional details.

half centrum). The terminal dorsal- and anal-fin soft rays were counted as a single element, even if branched and split to the fin base, as this element is associated with a single supporting pterygiophore. Lateral line scales were counted following the method of Greenwood (1956) and include scales in the lower branch up to the hypural flexure (i.e., a vertical through the caudal border of the hypurals). Pored scales posterior of the hypural flexion were excluded from the count, regardless of size. Osteological features of the new species and related taxa were examined using alcohol preserved specimens, C&S and dry skeletal preparations (S), or obtained from radiographs. Gill raker counts (i.e., lower limb of the first gill arch, including rakers associated with both the ceratobranchial and hypobranchial) exclude the raker in the angle of the arch marking the transition from ceratobranchial to epibranchial. The MRI was generated at the UCSD Center for Scientific Computation in Imaging (CSCI), Digital Fish Library (DFL), using a 7T Bruker Biospec Avance II scanner with a 72 mm quadrature volume coil. The specimen was stored in 75% ethanol and rinsed well in water prior to imaging. The image contrast-enhancement agent ProHance(R) was used prior to scanning. Institutional abbreviations are as listed in Leviton *et al.* (1985) and are available online at http://www.asih.org/ (Sabaj Pérez, 2010).

RESULTS

Systematic Account

Paretroplus risengi, new species

Figures 2–6; Table 1

Paretroplus damii: Sparks and Stiassny, 2003: table 9.1 (in part).

Paretroplus damii: Rham and Nourissat, 2004 (in part).

Paretroplus damii: Sparks and Stiassny, 2008: table 1 (in part).

Paretroplus damii: Sparks, 2008 (in part).

Paretroplus n. sp. “anjingo”: Sparks and Schelly, 2011.

Paretroplus n. sp. “Anjingo”: Martinez and Sparks, 2017: fig. 2.

Paretroplus n. sp. “anjingo”: Sparks and Stiassny, 2022: tables 10-1 and 10-9.

Holotype: UMMZ 235022, 155.1 mm SL; northwestern Madagascar: Mahajanga (= Majunga) Province: northeast of Antsohihy: Lac Andrapongy, north basin: 14°41′49.0″S, 48°07′54.0″E; JSS94-21B; specimen 420; J. Sparks and K. Riseng, VIII-1994.

Paratypes: AMNH 236154, 2 ex., 52.4–110.8 mm SL; Madagascar: Mahajanga Province: Anjingo River: main channel below bridge on Antsohihy-Bealanala Road; P. V. Loiselle, 2004. AMNH 248081 (ex. UMMZ 239543), 1 ex., 76.0 mm SL; northwestern Madagascar: Mahajanga Province: northeast of Antsohihy: Anjingo River at RN31: 14°50′39.0″S, 48°1′39.0″E; JSS94-54; J. Sparks and K. Riseng, 15-XI-1994. AMNH 259875, 11 ex., 43.0–144.5 mm SL; northwestern Madagascar: Mahajanga Province: northeast of Antsohihy: Lac Andrapongy: 14°41′02.8″S, 48°09′29.9″E; JSS-MAD-11-38; J. Sparks et al., 14-VI-2011. AMNH 277098, 9 ex., 111.5–160.8 mm SL, northwestern Madagascar: Mahajanga Province: northeast of Antsohihy: Ambalihaberano River, near Lac Andrapongy: no GPS coordinates available; JSS-MAD-11-39; J. Sparks et al., 14-VI-2011. MHNG 2537.44, 7 ex., 91.4–162.2 mm SL; Madagascar: Mahajanga Province: Riviere Ankofia (= Anjingo) or Lac Andrapongy, environment Antsohihy; P. de Rham and J.-C. Nourissat, 17–19-X-1992. MHNG 2537.45, 6 ex., 98.6–154.3 mm SL; Madagascar: Mahajanga Province: Lac Andrapongy, environment Antsohihy; P. de Rham and J.-C. Nourissat, 17-X-1992. UMMZ 235021, 37 ex., 1 ex. C&S, 31–138 mm SL; northwestern Madagascar: Mahajanga Province: east of Antsohihy: Anjingo River (upstream and downstream of bridge

Table 1. Morphometric and meristic data for *Paretroplus risengi*. For meristics, numerals in parentheses indicate number of specimens examined with that count, and (H) indicates count corresponding to holotype.

Character	N	Holotype	Range	Mean	SD
Standard length (mm)	30	155.1	33.9-161.0	111.1	
Percentage of SL					
Head width (max.)	30	19.9	16.6-21.8	18.8	1.09
Head length	30	30.1	29.4-35.9	32.7	1.51
Body depth	30	54.5	46.4-57.5	52.5	2.36
Caudal peduncle length	30	3.5	3.5-7.0	4.9	0.88
Caudal peduncle width	30	5.1	2.1-6.5	4.6	0.90
Caudal peduncle depth	30	16.4	15.1-17.7	16.4	0.66
Pectoral-fin length	30	20.4	20.4-26.3	23.3	1.60
Pelvic-fin length	30	22.4	21.3-24.3	22.9	0.84
Pre-dorsal length	30	46.4	43.0-52.0	47.8	2.20
Pre-anal length	30	62.0	52.2-65.0	58.3	3.09
Pre-pelvic length	30	47.2	39.5-47.6	43.1	2.10
Percentage of HL					
Snout length	30	55.2	37.1-62.2	50.3	5.40
Orbit diameter	30	23.2	21.2-35.2	25.6	2.86
Upper jaw length	30	30.9	24.2-38.9	30.6	3.78
Lower jaw length	30	34.1	28.8-43.9	35.8	3.58
Interorbital width	30	41.2	28.5-52.3	39.3	6.57
Preorbital depth	30	33.9	16.8-49.1	32.9	6.67
Caudal peduncle length/width	30	0.7	0.7-2.7	1.1	0.42
Caudal peduncle length/depth	30	0.2	0.2-0.5	0.3	0.06
Scales in lateral line	30	35 (2), 36 (2), 37 (15) (H), 38 (11)			
Gill rakers (lower limb 1st arch)	30	10 (2), 11 (21) (H), 12 (7)			
Vertebrae (precaudal + caudal)	35	14 + 16 = 30 (1), 14 + 17 = 31 (8) (H), 15 + 16 = 31 (18) (H), 15 + 17 = 32 (8)			
Dorsal fin	35	XVIII 13 (4) (H), XVIII 14 (2), XIX 11 (1), XIX 12 (13), XIX 13 (6) (H), XX 11 (5), XX 12 (4)			
Anal fin	35	IX 10 (7) (H), IX 11 (4) (H), X 9 (12), X 10 (10), XI 8 (1), XI 9 (1)			

over RN31): 14°50′41.0″S, 48°14′38.0″E; JSS94-19; J. Sparks and K. Riseng, 28-VII-1994. UMMZ 235022, 34 ex., 1 ex. C&S, 82–170 mm SL; northwestern Madagascar: Mahajanga Province: northeast of Antsohihy: Lac Andrapongy, north basin: 14°41′49.0″S, 48°07′54.0″E; JSS94-21B; J. Sparks and K. Riseng, VIII-1994. UMMZ 239543, 4 ex., 1 ex. C&S, 56–72 mm SL; northwestern Madagascar: Mahajanga Province: northeast of Antsohihy: Anjingo River at RN31: 14°50′39.0″S, 48°1′39.0″E; JSS94-54; J. Sparks and K. Riseng, 15-XI-1994.

Diagnosis: *Paretroplus risengi* is recovered within the "*Paretroplus damii* clade" based on the following apomorphic features shared with other members of that assemblage, including the presence of a dark gray to black pectoral-axil patch, highly embedded chest scales that are greatly reduced in size, and flank scales with a thin, unossified posterior field. *Paretroplus risengi* is recovered as the sister taxon to a clade comprising *P. damii* and *P. loisellei*, and is distinguished from these two species by pigmentation pattern in preservation comprising a dark head, followed by broad, light colored anterolateral band, and dark posterior body (vs. mostly uniform dark gray to dark grayish-brown in non-breeding individuals of *P. damii* and *P. loisellei*), with even large adult specimens frequently appearing quite blotchy and mottled, and fewer gill rakers on the lower limb of the first arch (mode 11 vs. 12 [*P. damii*] or 13 [*P. loisellei*]). *Paretroplus risengi* and *P. damii* are further distinguished from *P. loisellei* by a strongly rounded and convex profile extending from the anterior margin of the lower jaw to the ventroposterior margin of the suspensorium (vs. horizontal), obliquely oriented, thin lips (vs. horizontal with fleshy lips), a lighter non-breeding overall pigmentation pattern (vs. uniformly dark brown or grayish-brown flank), and striking yellow, vivid orange, or brick red breeding coloration on head and anterior flank, over a blackish base (vs. uniform bright golden). *Paretroplus risengi* and *P. loisellei* are distinguished from *P. damii* by the presence of weakly tricuspid symphyseal teeth in the upper jaw (vs. lacking lateral cusps). *Paretroplus risengi* is further distinguished from *P. loisellei* by a lower lateral line scale count (mode 37 vs. 38), fewer vertebrae (mode 31 vs. 32), and a lower epibranchial raker count (9-10 vs 11-12), and from *P. damii* by a considerably more blotchy and mottled pigmentation pattern (in both preservation and non-breeding individuals), and by a smaller maximum adult size (max. size ~170 mm SL vs. regularly exceeding well over 300 mm SL).

Description: Morphometric and meristic data presented in Table 1. Pigmentation pattern in life and preservation, as well as external morphological features, shown in Figures 2 and 3. A relatively shallow bodied member of *Paretroplus* recovered within the "*Paretroplus damii* clade" of Sparks (2008), which also includes *P. damii*, *P. loisellei*, *P. nourissati*, *P. tsimoly*, and *P. lamenabe*, all shallow-bodied species (Fig. 1).

Head moderately pointed and snout mostly straight. Predorsal profile moderately to strongly curved, with an indentation anterior to the orbit. Dorsal and ventral body outlines moderately to strongly curved, and about equal in degree of curvature. Degree of curvature in both dorsal and ventral profiles more pronounced posteriorly. Degree of curvature/convexity in ventral profile becoming more pronounced with increasing size. Ventrally, profile mostly straight to weakly rounded, extending from the anterior margin of the lower jaw to the ventroposterior margin of the suspensorium. Caudal peduncle short, deep, and strongly laterally compressed. Of the material examined, no sexually dimorphic features were apparent.

Total vertebral count 30 to 32, with formulae of: 14 + 16, 14 + 17, 15 + 16 (mode), 15 + 17, precaudal and caudal vertebrae, respectively.

Jaws isognathous. Oral jaws with moderately oblique orientation and lips thin. Single row of spatulate unicuspid (except as noted below) teeth



Figure 2. *Paretroplus risengi*, holotype, UMMZ 235022, 155.1 mm SL; northwestern Madagascar: Mahajanga Province: northeast of Antsohihy: north basin Lac Andrapongy.

in both upper and lower jaws. Teeth in both upper and lower jaws laterally expanded, flattened at crown, and procumbently implanted. Premaxillary symphyseal teeth greatly enlarged and weakly tricuspid, with small, yet distinct and sharp lateral cusps (Fig. 4A). Remaining upper jaw teeth graded in size and becoming progressively much smaller posteriorly. Lower-jaw teeth at symphysis reduced in size compared to adjacent lateral teeth to accommodate enlarged upper symphyseal teeth when jaws closed. In upper jaw teeth number six or seven on each side (occasionally eight on one side), and total 12 to 14. Teeth in lower jaw number six or seven on each side, and total 12 to 13. In both upper and lower jaws, in general teeth widely and irregularly spaced, particularly posteriorly.

Upper and lower pharyngeal tooth plates robust and well developed. Lower pharyngeal jaws [= lower pharyngeal jaws (LPJ) or fifth ceratobranchial tooth plates] strongly fused and well sutured, with numerous interdigitating sutures along both ventral and posteroventral margins. Dentition on lower pharyngeal tooth plates hooked and bicuspid both laterally and anteriorly, becoming progressively enlarged and robust medially. Molariform teeth present only posteromedially on LPJ (Fig. 4B). Smallest teeth present posterolaterally on both fifth ceratobranchial toothplates. Five to eight robust tooth plates cover majority of dorsal surface of fourth ceratobranchial bones (Fig. 4B). Fourth ceratobranchial tooth plates not confluent with, but separated from, outer-row gill rakers of these paired elements. Bases of individual tooth plates on fourth ceratobranchials exhibit varying degree of fusion depending on individual examined, but all are closely set. Teeth on fourth ceratobranchial tooth plates unicuspid or weakly hooked and bicuspid laterally, becoming more strongly hooked and bicuspid medially (similar in morphology to lateral LPJ dentition).



Figure 3. A, *Paretroplus risengi*, paratype, AMNH 277098, 142.5 mm SL, northwestern Madagascar: Mahajanga Province: northeast of Antsohihy: Ambalihaberano River, near Lac Andrapongy. In preservation.
B, *Paretroplus risengi*, paratype, AMNH 259875, approx. 140 mm SL; northwestern Madagascar: Mahajanga Province: northeast of Antsohihy: Lac Andrapongy. Photographed immediately after capture.

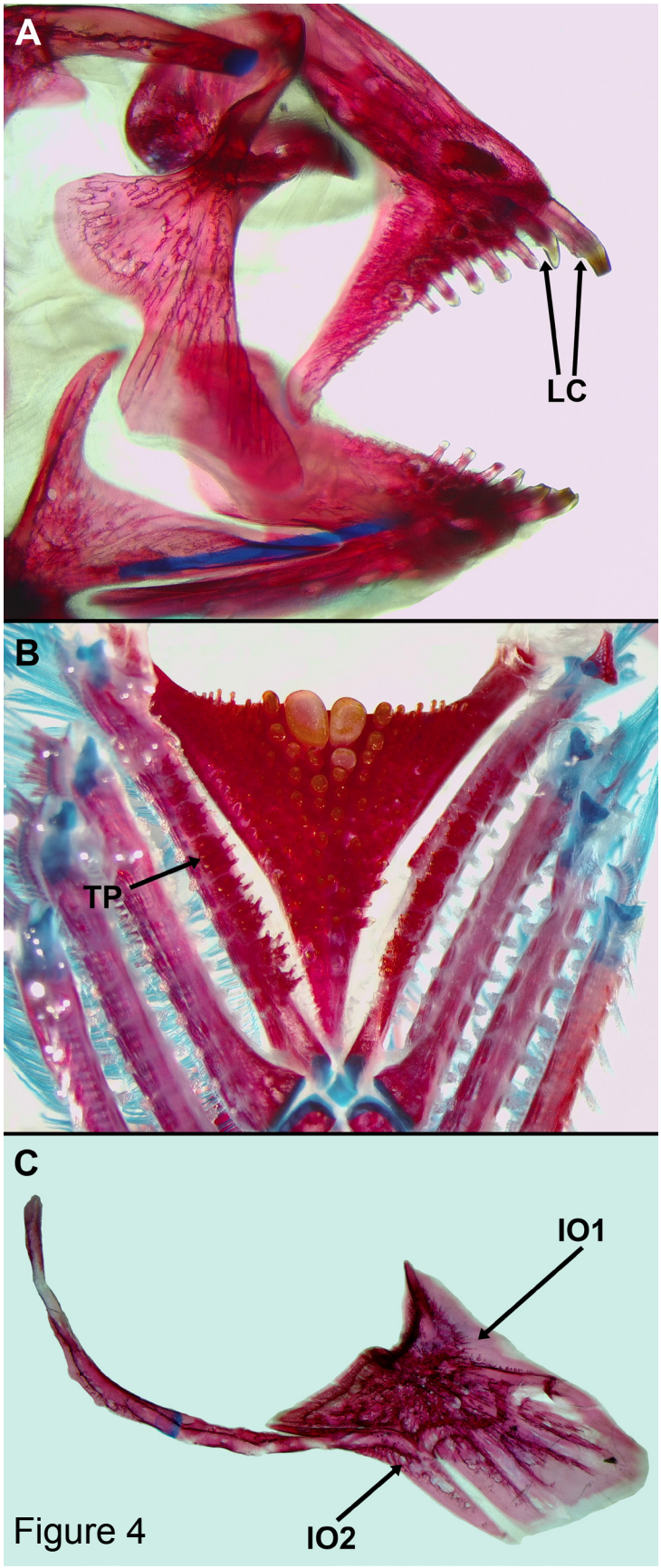


Figure 4. *Paretroplus risengi*:
A, UMMZ 235022, 88.4 mm SL, C&S, isolated right premaxilla in lateral view showing weakly tricuspid symphyseal teeth in the upper jaw (LC = lateral cusps).

B, UMMZ 235022, 88.4 mm SL, C&S, lower pharyngeal jaw in dorsal view showing fused fifth ceratobranchial bones and both right and left fourth ceratobranchial bones to highlight series of robust tooth plates on dorsal surface (TP = 4th ceratobranchial toothplates).

C, UMMZ 235022, 88.4 mm SL, C&S, isolated right lacrimal bones and infraorbital series in lateral view (IO1 = anterior lacrimal plate; IO2 = primitive, plate-like, second infraorbital).

Dentition on third upper pharyngobranchial tooth plates hooked and bicuspid laterally and anteromedially, molariform only posteromedially. Dentition on second pharyngobranchial tooth plates strongly hooked and bicuspid, and arrayed in three rows.

Ten to 12 (mode 11) triangular and moderately elongate outer gill rakers arrayed along lower limb of first gill arch (= hypobranchial and ceratobranchial), excluding raker in angle of arch. Outer (= lateral) rakers of first arch weakly denticulate dorsomedially. All other lateral and medial lower-limb rakers (i.e., those on gill arches 2 through 4) well developed, short, triangular or arched in shape (not spherical), and strongly denticulate dorsally, except for weakly developed rakers on medial margin of fourth ceratobranchials. A single, dorsally-denticulate hypobranchial raker present on arches 1 through 3. Epibranchial rakers feeble and elongate, not denticulate, and numbering 9 or 10.

Body covered with large, regularly imbricate, cycloid scales. Posterior field (= caudal margin) of flank scales thin, mostly unossified and lacking circuli, creating a thin, flexible posterior "flap" (Fig. 5). Dorsal- and anal-fin bases characterized by well-developed ridges of scales extending along their length (= scale sheathing of Sparks, 2008). Ridges of scales free from spiny dorsal and anal fins. Scales becoming weakly attached to both soft dorsal and anal fins. One to four (rarely up to 5 or 6) rows of smaller ovoid scales extending onto both soft dorsal and anal fins between rays. Numerous rows of smaller scales extend well onto caudal fin between rays, posterior of hypural flexure, for approximately 3/4 of its length (particularly dorsally and ventrally on fin). Pelvic axillary scale well developed and elongate. Lateral-line scales number 35 to 38 (mode 37). Chest scales reduced in size and highly embedded, with scales along ventrum

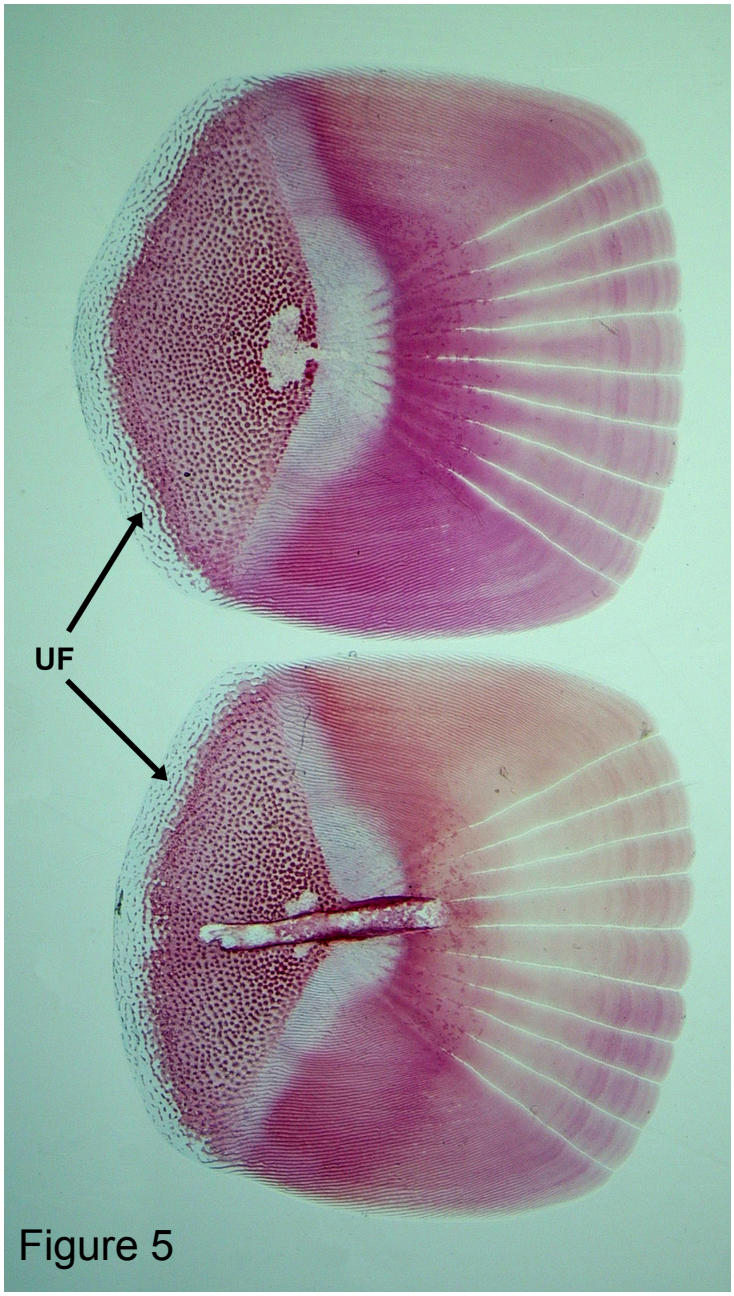


Figure 5. UMMZ 235021, 110.6 mm SL, alizarin stained flank scales showing unique posterior field morphology described in text [midflank (upper) and pored upper lateral line (lower) scales shown]. UF = unossified posterior "flap."

extremely reduced in size. Four to five rows of relatively embedded scales present on cheek. Opercle, subopercle, and interopercle fully scaled, and scales embedded. Preopercle asquamate ventrally, scaled only on anterodorsal portion of shaft where posteriormost cheek scales overlap. Snout, lacrimal, and anterior portion of interorbital region, to about mid-orbit, asquamate.

Dorsal fin with XVIII–XX spines and 11–14 soft rays (mode XIX 12). Anal fin with IX–XI spines and 8–11 soft rays (mode X 9). Origin of dorsal fin at level of, or just posterior to, vertical through pectoral-fin insertion at its dorsal insertion point. Pectoral fin large, broad, and rounded at distal margin, extending to about origin of anal fin when adducted. Distal margins of soft dorsal and anal fins becoming increasingly well developed and pointed in larger specimens (rounded in smaller individuals), with both fins extending well past caudal origin. Pelvic fin extending to about level of anal-fin origin when adducted. Caudal fin weakly emarginate, with broad upper and lower lobes. Upper and lower lobes of caudal fin weakly produced and pointed, particularly in larger specimens.

OTOPHYSIC CONNECTION AND MISCELLANEOUS OSTEOLOGY: As noted by Sparks (2008) and Sparks and Schelly (2011), members of *Paretroplus damii* clade (Sparks, 2008: fig. 20C) exhibit most anatomically complex anterior gas bladder diverticula and associated intercranial bullae within subfamily Etroplinae. Paired anterior gas bladder bullae characterized by tough and thickened tunica externa. Anterior chambers of bullae firmly lodged in expansive exoccipital recesses that comprise multiple internal chambers (Sparks, 2008: figs. 8A and 9B) and closely apposed to otoliths of inner ear. Segmentation of anterior gas bladder diverticula from micro-CT scan of new species shows these structures (highlighted in green) extending anteriorly from main gas bladder chamber and approaching labyrinth of inner ear (highlighted in magenta) (Fig. 6; Berquist et al., 2012; Digital Fish Library, 2009), creating direct otophysic connection between main gas bladder chamber and inner ear. As a result, members of Etroplinae, especially species of *Paretroplus*, exhibit enhanced hearing relative to cichlid species lacking otophysic connection (Braun et al., 2012). Supraoccipital extends anteriorly and covers median frontal pores of neurocranium (NLF_0 of Barel *et al.*, 1977), which are coalesced in the midline forming continuous tube with single dorsal pore, features unique to members of Etroplinae (Sparks, 2008: fig. 6C). Excavation (= supraoccipital notch of Stiassny *et al.*, 2001) along posterior margin of supraoccipital, a feature also unique to Etroplinae, almost always poorly developed and ranging from shallow or narrow, to small and rounded, to lacking entirely. Similar to other members of Etroplinae, lacrimal comprised of two distinct plates, including anteroventrally expanded and paddle-shaped lacrimal proper (= anterior plate; IO1), bearing elongate lateral line canals with constricted foramina, and expanded plate-like "primitive second infraorbital" (= IO2) (Cichocki, 1976) (Fig. 4C). Marginal canal shared between IO1 and IO2 either greatly reduced or lacking entirely.

PIGMENTATION IN LIFE: Non-breeding individuals (Fig. 3B): Base body coloration grayish to dark grayish-black, and darker dorsally. Overall pigmentation pattern blotchy and mottled, much more so than two other closely-related species, *P. damii* and *P. loisellei*, which exhibit more or less uniform coloration. Interorbital region with dark grayish-black bar extending between eyes. Triangular or rounded black patch present in pectoral-fin axil and extending dorsal to pectoral-fin base. Unpaired fins gray to dark grayish-black. Pectoral fins grayish-orange. Pelvic fin gray, grayish-black, or black. Lips range from dark bluish-gray to charcoal. Head pigmentation darker ventrally. Operculum light bluish-gray. Chest and anterior portion of belly darker than surrounding body regions. Breeding coloration (not shown): Base body coloration greenish-gray to jet black. Pale yellow,

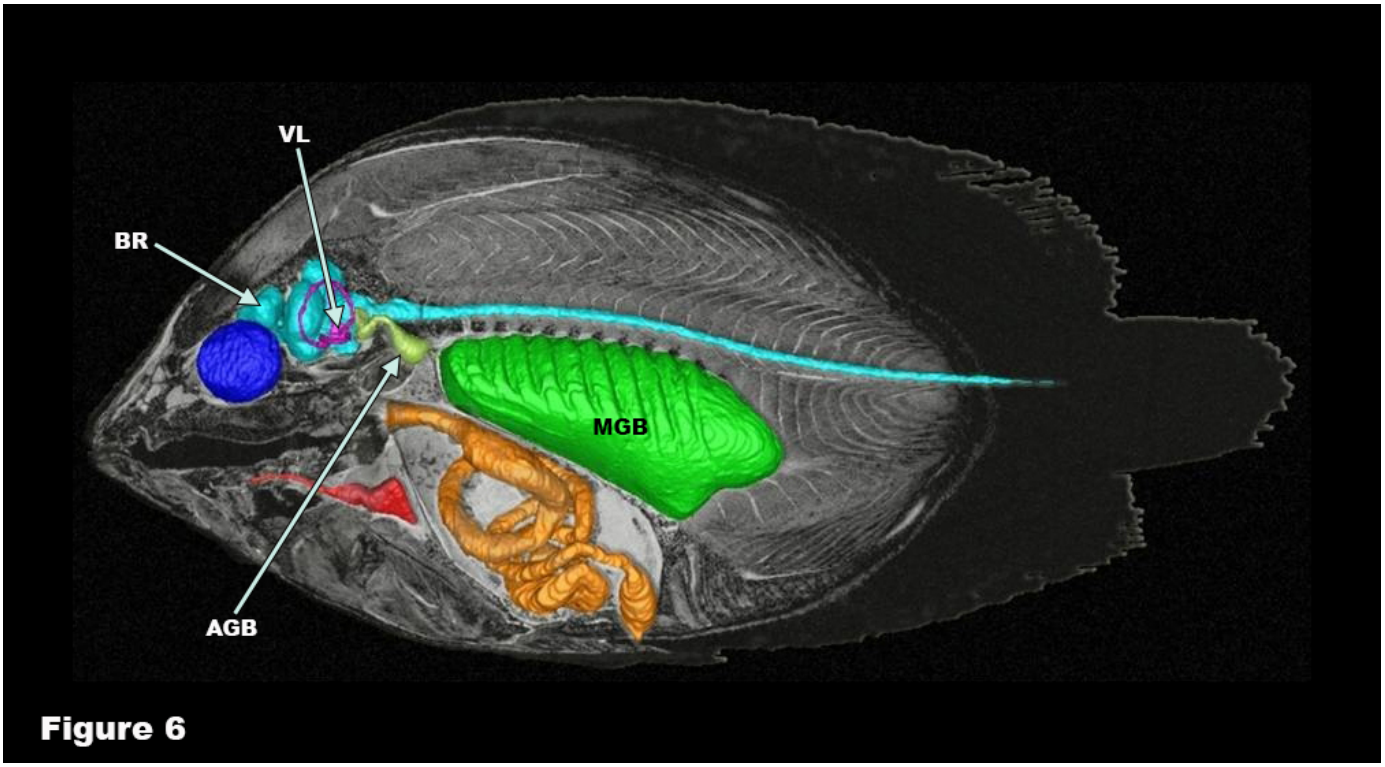


Figure 6. MRI segmentation of *Paretroplus damii*, paratype, AMNH 248081, 76.0 mm SL. Specimen imaged at 7*T*, slice thickness = 100 µm, resolution = 90 µm^3. MRI slice data overlain with color-coded segmented soft tissue structures: light blue = brain and spinal cord (BR); dark blue = eyes; magenta = vestibular labyrinth (VL); green = gas bladder (MGB = main gas bladder chamber; AGB = paired anterior gas bladder bullae); light brown = alimentary tract; red = heart and dorsal aorta. Image used with permission of UCSD CSCI, Digital Fish Library (DFL); http://www.digitalfishlibrary.org/library/ViewSpecies.php?id=274.

vivid orange, or brick red mid-lateral band present that can extend onto the spinous portion of the dorsal fin. Cheek region ranges from bright orange to vivid red. Interorbital band ranges from weakly developed and gray to prominent dark grayish-black. Unpaired fins range from grayish-black to black. Pectoral fins grayish-orange to dark grayish-black. Lips pale pink to grayish-blue.

For comparison, given that both *P. damii* and *P. risengi* appear relatively similar in breeding coloration, with the exception of *P. risengi* being somewhat more mottled and blotchy overall, an image of an adult *P. damii*, presumably from the Sambirano River population, is included to highlight the bright, vivid yellow, orange, or brick red and contrasting jet-black pigmentation pattern that these two species exhibit when breeding (Fig. 7). Rham and Nourissat (2004: 114) report observing a male specimen of the new species from the Anjingo River that very briefly exhibited brick red coloration on the head and a large vertical band of the same color on the anterior portion of the flank. As Rham and Nourissat (2004: 114) also report, when removed from the water and stressed, individuals of *P. damii* and *P. risengi* very quickly lose their bright coloration and instead exhibit an overall drab, mostly uniform greyish to greyish-black body coloration. In contrast, *P. loisellei* exhibits a uniform bright golden-yellow breeding coloration and lacks the strongly contrasting lighter midlateral band present in both *P. damii* and *P. risengi* (compare Fig. 7 with image of breeding coloration of *P. loisellei* shown in Rham and Nourissat 2004: 117).

PIGMENTATION IN PRESERVATIVE (Figures 2 & 3A): Overall body base coloration light rusty brown to dark grayish-brown; body somewhat darker dorsally, particularly along base of dorsal fin and on dorsal portion of head. Triangular or rounded black patch characteristic of clade present in pectoral-fin axil and extending dorsal to pectoral-fin base (Figs. 2 and 3). Wide, lightly pigmented mid-lateral band extending from just posterior to darkly pigmented pectoral axil patch to about mid-flank and ranging from light gray to yellowish-tan. Mid-lateral band prominent and easy to visualize in majority of preserved adults (e.g., Fig. 3A). Snout and interorbital region dark tan to grayish-black. Dark interorbital stripe extending slightly posterior to orbit ranging from dark rusty brown to dark grayish-black. Lighter rounded region on cheek ranging from yellowish-tan to grayish-orange. Lower lips pale tannish-yellow to light bluish-gray. Upper lip olive-brown to grayish-black. Unpaired fins brownish-gray to grayish-black. Pectoral fin pale yellowish-tan to olive. Pelvic fin brownish-gray to grayish-black. Body exhibits more blotchy and mottled overall pigmentation pattern in preservation than other two closely-related species, *P. damii* and *P. loisellei*.

DISTRIBUTION AND HABITAT: The new species is known only from the middle to lower reaches of the Anjingo and Ankofia river drainage basins and their smaller tributaries, including Lac Andrapongy, in northwestern Madagascar (Fig. 8). This species is found in clear, rather swift flowing rivers over sandy to muddy substrate, generally among submerged tree branches and root systems, and also throughout Lac Andrapongy, type locality, which is a large, shallow, turbid floodplain lake within the Anjingo-Ankofia drainage basin (Fig. 9).

LOCAL NAME: *Damba, damba mena, lamena*.

ETYMOLOGY: Named in honor of limnologist Karen J. Riseng, who collected the new species with the first author on their initial trip to Madagascar in 1994 as graduate students, in appreciation of her immense help and support in the field on that and subsequent expeditions to document the poorly known freshwater ecosystems and ichthyofauna of Madagascar.

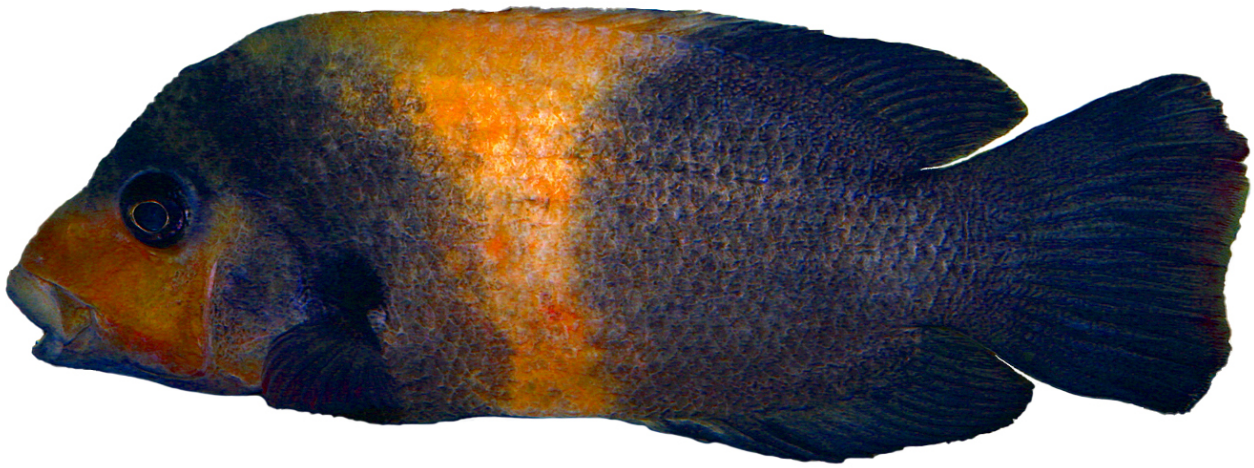


Figure 7. Aquarium specimen of *Paretroplus damii* photographed in breeding coloration, presumably collected in the Sambirano River (exact collection locality unknown). *Paretroplus damii* exhibits similar breeding coloration and pigmentation pattern as *Paretroplus risengi*, for which a breeding coloration image is lacking, except with a less mottled overall pigmentation pattern. Fish image removed from background and flipped horizontally for ease of comparison to other images. Image by Paul Loiselle.

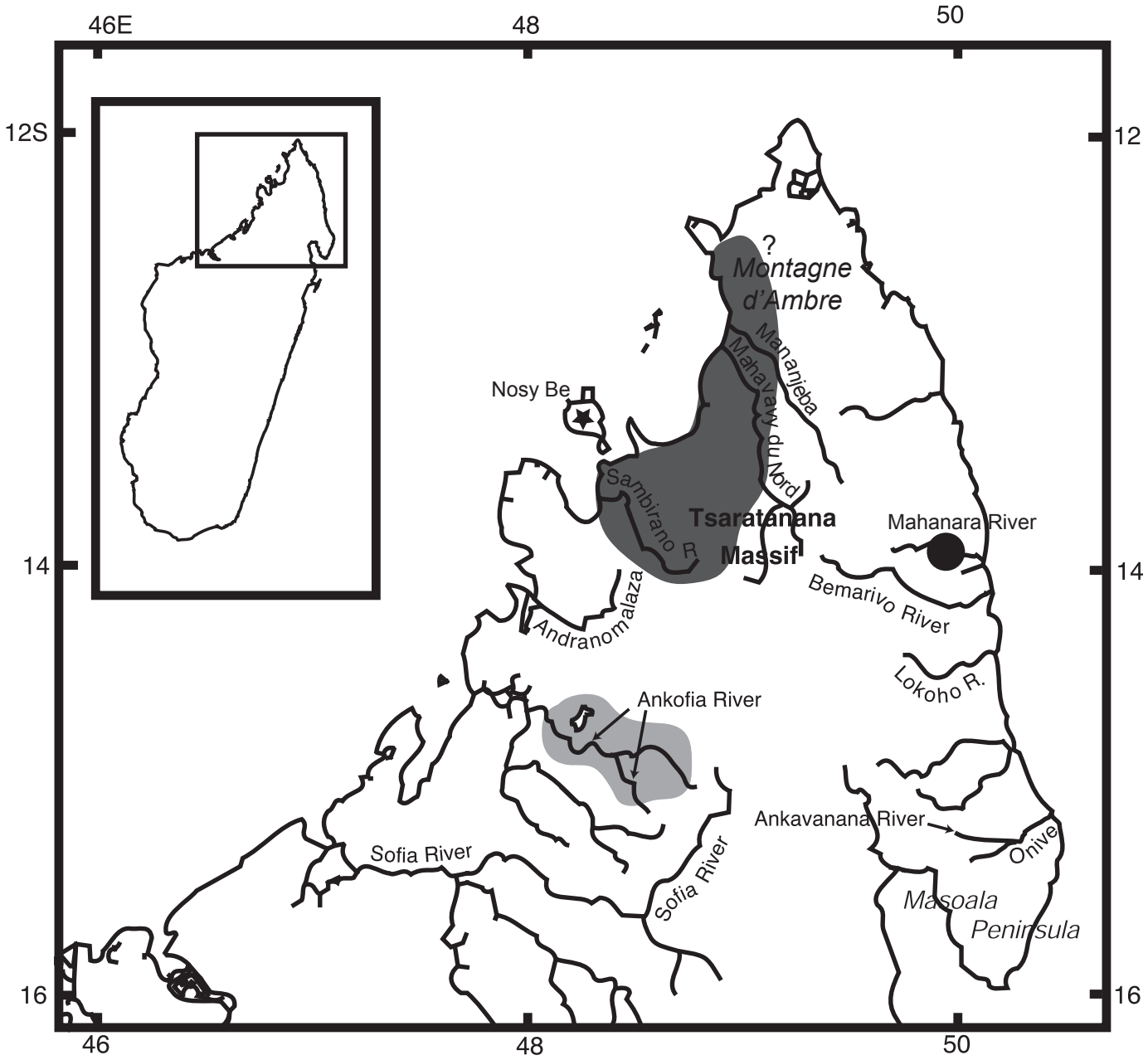


Figure 8. Map of northern Madagascar, illustrating the approximate geographic ranges for *P. damii* (dark gray shading), *Paretroplus loisellei* (black shading), and *P. risengi*, new species (light gray shading). Note that a black star is placed on the satellite island of Nosy Be, type locality for *P. damii*, to indicate that no specimens of *P. damii* have been collected from the type locality in several decades and that population is presumed to be extinct. A "?" near Montagne d'Ambre National Park indicates that extreme northern populations of *P. damii* exhibit unique coloration and distinct morphological features and may represent an undescribed species.



Figure 9. Type locality of *Paretroplus risengi*, Lac Andrapongy, a large floodplain lake in northwestern Madagascar, Mahajanga Province, northeast of Antsohihy.

DISCUSSION AND COMPARISONS

As reported by Sparks (2008) and Sparks and Schelly (2011), specimens historically assigned to *P. damii* (Fig. 10A), as well as populations of morphologically similar fishes discovered in northwestern (to the south of the range of *P. damii*) and far northeastern Madagascar (Figs. 8 and 10B), were hypothesized to represent possibly as many as three distinct species, a result corroborated by our prior phylogenetic analyses (Sparks, 2008; Sparks and Schelly, 2011; Sparks and Martinez, 2017) and current morphological comparisons (Fig. 1). As a result, we now recognize three distinct species within this assemblage, *P. damii*, *P. loisellei*, and *P. risengi*, new species. As early as the 1990s, Rham and Nourissat (2004: 114) noted significant color differences among the different geographical populations of putative *P. damii* and suggested that these populations may represent a species complex, including the Anjingo-Ankofia River population. Rham and Nourissat (2004: 114) further discussed unique coloration and morphological features of putative populations of *P. damii* to the far north (i.e., draining the western slopes of Montagne d'Ambre), and suggested that these populations might also represent another distinct species (Fig. 8).

Paretroplus risengi is endemic to the middle to lower reaches of the Anjingo and Ankofia river drainage basins and their tributaries, including Lac Andrapongy, in northwestern Madagascar (Figs. 8 and 9). Interestingly, the new species is absent from other

major basins within the region (e.g., the large Sofia River system to the south and the Andranomalaza River to the north). The westward flowing Anjingo-Ankofia drainage basin harbors a diverse and highly endemic fish fauna, with both a new aplocheiloid killifish, *Pachypanchax sparksorum* Loiselle, 2006, and new cichlid, *Ptychochromis inornatus* Sparks, 2002b, described from the basin since the year 2000. *Paretroplus damii* exhibits the widest geographic range of these three closely related species and occurs to the north of the range of *P. risengi*, with a distribution ranging from the Sambirano River northward to the Mananjeba River basin and tributaries, ranging as far north as the Sahinana and Sampiana rivers along the western slopes of Montagne d'Ambre (Rham and Nourissat, 2004), and also including the satellite island of Nosy Be, type locality for the species. It is important to note, however, that no specimens of *P. damii* have been collected from the type locality in several decades and that population is presumed to be extinct. *Paretroplus loisellei* is endemic to the middle reaches of the eastward draining Mahanara River, located to the north of Sambava near the town of Antsirabe-Nord, northeastern, Antsiranana Province, in far northeastern Madagascar (Fig. 8), although local villagers report that the species is more widespread in the region.

Paretroplus risengi is recovered within the "*Paretroplus damii* clade" (Sparks, 2008; Fig. 1) based on several apomorphic anatomical features shared with other members of that assemblage, including the presence of a triangular or rounded, dark gray to black pectoral-axil patch, chest scales that are markedly reduced in size and highly embedded, and flank scales characterized by a thin and unossified posterior field (see Sparks, 2008, and Sparks and Schelly, 2011; Figs. 2–3, 5 and 10). The new species is recovered as the sister taxon to a clade comprising *P. damii* and *P. loisellei*. Several morphometric and anatomical features that are described in detail above (e.g., in the Diagnosis and Description) serve to easily distinguish the new species from *P. damii* and *P. loisellei*.

The clade comprising *P. risengi*, *P. damii* and *P. loisellei*, is in turn recovered as the sister taxon to a clade comprising *P. nourissati*, *P. tsimoly*, and *P. lamenabe*. Members of the *P. risengi* + *P. damii* + *P. loisellei* clade are distinguished from members of its sister clade, *P. nourissati* + *P. tsimoly* + *P. lamenabe*, by the absence of a darkly pigmented vertical barring pattern on the flank, featuring prominent broad, converging black mid-lateral bands that are diagnostic of that clade (Fig. 11A), as well as lacking notably elongate nasal bones. All other species of *Paretroplus* are characterized by the presence of a prominent vertical barring pattern as adults (Fig. 11B), however, only in members of the clade comprising *P. nourissati* + *P. tsimoly* + *P. lamenabe* are the mid-lateral bands the most well developed and converging (Fig. 11A).

In contrast, *P. risengi*, *P. damii* and *P. loisellei* lack this vertical barring pattern at all stages of development (Figs. 2–3, 7 and 10), with the former two species possessing a single, broad lighter mid-lateral band of varying prominence on the anterior flank over a uniform gray, grayish-brown, golden-brown, or dark brown base coloration in unstressed, non-breeding individuals (Fig. 3A) (when removed from the water and stressed, both *P. risengi* and *P. damii* exhibit mostly uniform coloration; Fig. 3B). During breeding the mid-lateral band becomes bright golden-yellow, vivid orange, or brick red over a striking blackish-gray to jet black base coloration, with similar coloration on the cheek, in both *P. risengi* and *P. damii* (Fig. 7). *Paretroplus risengi*, in general, exhibits a more blotchy and mottled overall pigmentation pattern in life and preservation than either *P. damii* or *P. loisellei* (Figs. 3 and 10).

In addition to the features listed in the Diagnosis, *P. risengi*, can also be distinguished from *P. loisellei* by generally having fewer fourth ceratobranchial toothplates (5–8 vs. 7–9) (Fig. 4B). In members of *Paretroplus* characteristically robust tooth plates cover a majority of the dorsal surface of the fourth ceratobranchial bones. *Paretroplus risengi* can further be distinguished from *P. damii* (especially Sambirano River populations) by a much smaller maximum



Figure 10. A, *Paretroplus damii,* syntype, RMNH 3939, 69.2 mm SL, northwestern Madagascar, satellite island of Nosy Be, Lake Ampombilava (= Lacus Pambilao).
B, *Paretroplus loisellei,* holotype, AMNH 251631, 142.8 mm SL, northeastern Madagascar, Mahanara River.

adult size (reaching ~170 mm SL vs. regularly exceeding 300 mm SL and reaching nearly 400 mm TL) (Rham and Nourissat, 2004: 115), with large adults of *P. damii* becoming very deep bodied (particularly anteriorly), robust, and exhibiting a pronounced predorsal (= nuchal) hump, a feature absent in even the largest individuals of the new species.

Based on the most recent IUCN Red List assessment (IUCN, 2021; Ravelomanana et al., 2018; Sparks and Stiassny, 2022), of these three closely related species only *Paretroplus loisellei*, was assessed as Endangered, whereas the more widespread *P. damii*, which occurs in both rivers and floodplain lakes across multiple drainage basins, was assessed as Vulnerable. The new species was not assessed given that only formally described taxa are currently assessed by IUCN, however, as of our last visit to the region in 2011, populations in Lac Andrapongy and the surrounding tributary rivers were still quite healthy (we did not sample the Anjingo River in 2011). Nevertheless, our observations on recent surveys support the notion that almost all species of *Paretroplus* have experienced considerable declines in both abundance and geographic range over the course of our nearly three decades of work in Madagascar.

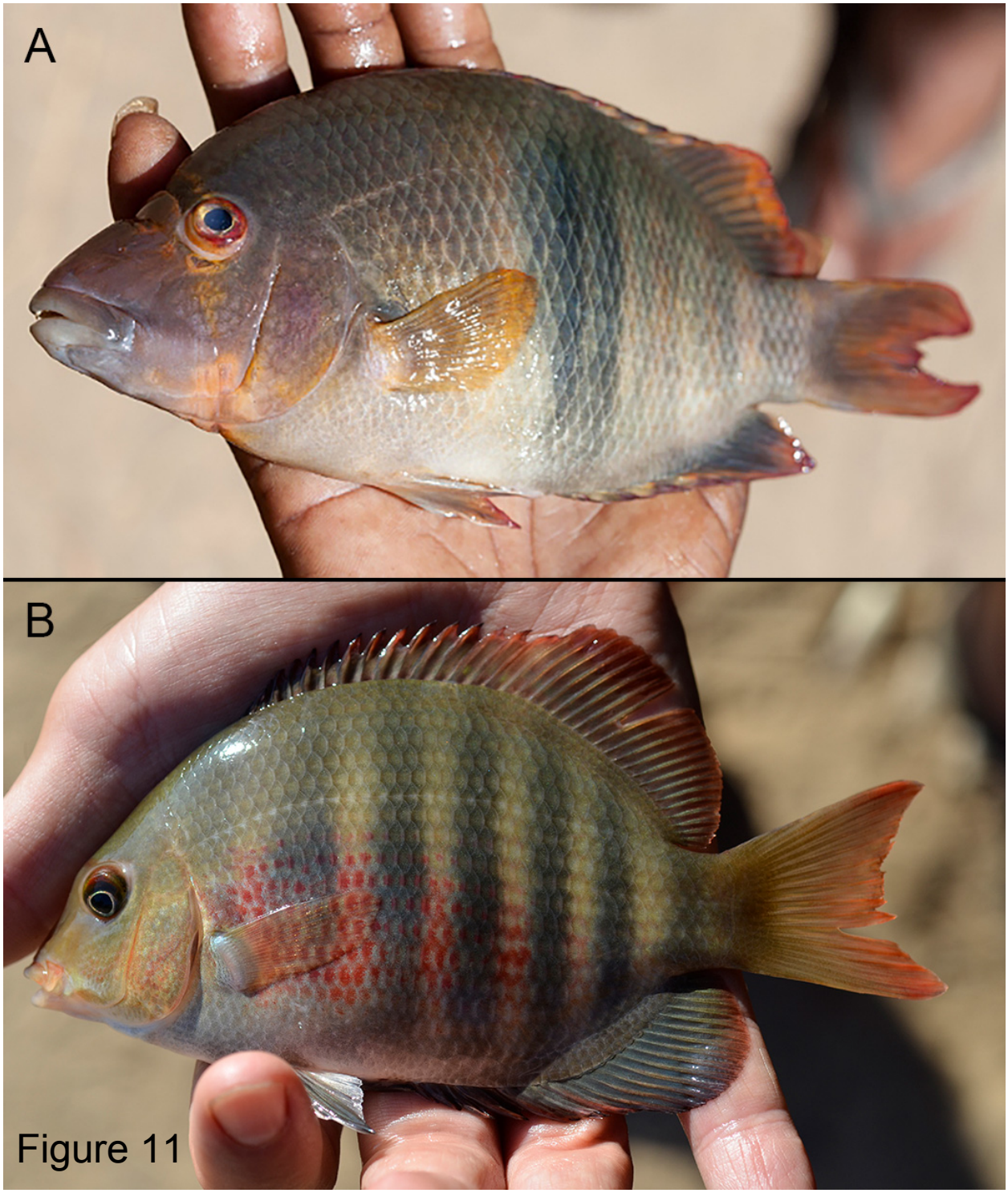


Figure 11. A, *Paretroplus lamenabe*, AMNH 266656, 118.7 mm SL, adult imaged immediately following collection in Lac Tseny, northwestern Madagascar, illustrating converging black midlateral bands.
B, *Paretroplus maromandia*, AMNH 263722, 112.8 mm SL, adult imaged immediately following capture in Maintsomalaza River near town of Maromandia, northwestern Madagascar, illustrating prominent lateral barring pattern present in all species of *Paretroplus*, less members of *P. damii* clade.

COMPARATIVE MATERIALS

Number of specimens following catalog numbers indicate count of individuals examined in this study and do not necessarily correspond to the total number of specimens in any particular lot.

Paretroplus damii: Syntypes: RMNH 3939, 1 ex., 69.2 mm SL; northwestern Madagascar: island of Nosy Be: Lake Pambilao ["Nossibe (Lacus Pambilao)"]; Van Dam and F. Pollen. RMNH 4478, 1 ex., 58.2 mm SL; northwestern Madagascar: island of Nosy Be: Lake Pambilao; Van Dam and F. Pollen. Additional Non-Type Material Examined: AMNH 232428, 2 ex., 48.0–49.0 mm SL; Madagascar: Antsiranana Province: Ifasy River at Ambodipont, Andraniaomby: adjacent oxbow lake: 13°22′7.8″S, 48°52′22.8″E; P. V. Loiselle, 25-X-2001. AMNH 232438, 3 ex., 77–108 mm SL; Madagascar: Antsiranana Province: Sambirano River at Ambodidimaka village: 13°45′18.0″S, 48°29′30.0″E; P. V. Loiselle and villagers, 26-X-2001. AMNH 232445, 3 ex., 20.0–25.0 mm SL; Madagascar: Antsiranana Province: Ramena River below bridge of Ambanja-Bemanevika road: 13°45′16.2″S, 48°31′9.6″E; P. V. Loiselle, J. Miandriaza, and local fishermen, 26-X-2001. AMNH 232473, 2 ex., 41.5–84.0 mm SL; Madagascar: Antsiranana Province: Ramena River at Antseva village: 13°42′42.4″S, 48°34′9.4″E; local fisherman and C. J. Raxworthy, 1-IV-2001. MHNG 2640.040, 1 ex., 141.0 mm SL; northern Madagascar: Ansiranana Province (Diego Suarez): Ramena River, near mouth of Sambirano River; P. de Rham and J.-C. Nourissat, X-1999. MNHN 1931-0225, 1 ex., 69.0 mm SL; Antsiranana Province: Sambirano: Coll. by Waterlot. UMMZ 235023, 51 ex., 3 ex. C&S, 9–182 mm SL; northwestern Madagascar: Antsiranana Province: north of Ambanja: Andranomaloto River (tributary of Mananjeba River): 13°12′46.0″S, 49°10′34.0″E; JSS96-22; J. Sparks and K. Riseng, 15-VII-1996. UMMZ 239544, 5 ex., 73–158 mm SL; northwestern Madagascar: Antsiranana Province: market purchase near Ambanja: J. Sparks and K. Riseng, VII-1996.

Paretroplus lamenabe: Holotype: MHNG 2676.30 (ex. MHNG 2640.039), 168.5 mm SL; northwestern Madagascar: Majunga (= Mahajanga) Province: Mahajamba River at Androka (ex. MHNG 2640.039, spec. 4); J.-C. Nourissat, 23-X-2001 to 06-XI-2001. Paratypes: AMNH 238557, 2 ex., 165.4–167.6 mm SL; data as for holotype (ex. MHNG 2640.039, spec. 2 and 3). AMNH 238565, 2 ex., 1 ex. C&S, tissue voucher specimens, 161.2–170.5 mm SL; northwestern Madagascar: Mahajanga Province: Mahajamba River, behind Ankarafantsika National Park; JSS 39-2003; J.-C. Nourissat, XI-2003. AMNH 238562, 2 ex., 178.3–181.3 mm SL; northwestern Madagascar: Majunga Province: Mahajamba River; JSS 36-2003; J.-C. Nourissat. AMNH 238566, 1 ex., 184.3 mm SL; northwestern Madagascar: Majunga Province: Mahajamba River; JSS 41-2003; J.-C. Nourissat. MHNG 2640.039, 10 ex., 161.4–183.9 mm SL; northwestern Madagascar: Majunga Province: Mahajamba River at Androka; J.-C. Nourissat, 23-X-2001 to 06-XI-2001. Additional Non-Type Material Examined: AMNH 266656, 2 ex., 87.7–118.7 mm SL, northwestern Madagascar, Majunga Province, Lac Tseny near Ambario village, 15°39′44.9″S, 47°50′35.5″E; JSS-MAD-11-41, Z. H. Baldwin et al., 18-XI-2011.

Paretroplus loisellei: Holotype: AMNH 251631, 142.8 mm SL; Madagascar: Antsiranana Province: Mahanara River: main channel of Mahanara River at Antsirabe-Nord, at bridge on Route N-5: 13°38′29.4″S, 49°57′48.6″E; P. V. Loiselle, 9-X-2000. Paratypes: AMNH 231248, 3 ex., 1 ex. C&S, 71.6–139.0 mm SL; Madagascar: Antsiranana Province: Mahanara River: main channel of Mahanara River at Antsirabe-Nord, at bridge on Route N-5: 13°38′29.4″S, 49°57′48.6″E; P. V. Loiselle, 9-X-2000. AMNH 231257, 4 ex., 1 ex. C&S, 74.9–88.5 mm SL; Madagascar: Antsiranana Province: Mahanara River: main channel at Antsirabe-Nord, at bridge on route N-5: 13°58′29.4″S, 49°57′48.6″E; P. V. Loiselle, 13-X-2000. AMNH 232457, 3 ex., 129.5–149.0 mm SL; Madagascar: Antsiranana Province: Mahanara River: ca. 4 km northwest of

Antsirabe-Nord: 13°57′18.0″S, 49°56′12.0″E; P. V. Loiselle and local fishermen, 31-X-2001. AMNH 232461, 3 ex., 96.0–134.1 mm SL; Madagascar: Antsiranana Province: Mahanara River: at Antsirabe-Nord just upstream of bridge over route N-5: 13°58′29.4″S, 49°57′48.6″E; P. V. Loiselle and local fishermen, 1-XI-2001. AMNH 236145, 1 ex., 112.5 mm SL; Madagascar: Antsiranana Province: Mahanara River, main channel at Antsirabe-Nord; P. V. Loiselle. AMNH 251632, 128.5 mm SL; Madagascar: Antsiranana Province: Mahanara River, main channel at Antsirabe-Nord: 13°58′51″S, 49°57′18″E; P. V. Loiselle, 18-X-2007.

Paretroplus maromandia: Non-Type Material Examined: AMNH 263722, 2 ex., 84.1-112.8 mm SL; northwestern Madagascar: Majunga Province: region of Ambanja: Maintsomalaza River, downstream of Manongarivo River near Maromandia: near village of Antanamandririna: 14°12′30.3″S, 48°03′56.0″E; JSS-MAD-11-37; J. S. Sparks et al., 13-XI-2011.

Paretroplus nourissati: Holotype: MNHN 1997-4172, 98.2 mm SL; northwestern Madagascar: Sofia River drainage basin: near town of Mandritsara: Mangarahara River; J.-C. Nourissat, X-1996. Paratypes: MNHN 1997-4173, 4 ex., 84.1–96.6 mm SL; data as for holotype. Additional Non-Type Material Examined: AMNH 229554, 2 ex., 1 ex. C&S, 87.0–106.0 mm SL; northwestern Madagascar: Mahajanga Province: Sofia River drainage basin: near town of Mandritsara: Amboaboa River near confluence with Mangarahara River: 15°50′1.0″S, 48°42′52.0″E; JSS 94-18; J. S. Sparks, K. J. Riseng, and local Malagasy guides, 24-VII-1994. AMNH 229555, 3 ex., 1 ex. C&S, 72.0–78.0 mm SL; northwestern Madagascar: Mahajanga Province: Sofia River drainage basin: near town of Mandritsara: Amboaboa River: 15°50′1.0″S, 48°42′51.0″E; JSS 96-25: altitude 210.3 m a.s.l.; J. S. Sparks, K. J. Riseng, and local Malagasy guides, 10 and 11-VII-1996. AMNH 229562, 1 ex., 64.0 mm SL; northwestern Madagascar: Mahajanga Province: Sofia River drainage basin: west of Mandritsara: Amboaboa River; PVL-93-VI-22; P. V. Loiselle, R. Morris, B. Vesta, and local villagers, 22-VI-1993. AMNH 236158, 4 ex., 40.8–107.0 mm SL; northwestern Madagascar: Mahajanga Province: Sofia River drainage basin: Amboaboa River at Andrahamamy village; PVL-04-09; P. V. Loiselle. UMMZ 235205, 76 ex., 4 ex. C&S, 1 ex. S; 49.0–124.0 mm SL; data as for AMNH 229555. UMMZ 235206, 40 ex., 3 ex. C&S, 7.0–160.0 mm SL; data as for AMNH 229554. UMMZ 239530, 6 ex., 76.0–127.0 mm SL; northwestern Madagascar: Mahajanga Province: Sofia River drainage basin: Mangarahara River just downstream from confluence with Amboaboa River, 15°50′ 1.0″S, 48°42′51.0″E: altitude 210.3 m a.s.l.; JSS 96-26; J. S. Sparks, K. J. Riseng, and local Malagasy guides, 11-VIII-1996. UMMZ 239545, 3 ex., 76.0–90.0 m SL; northwestern Madagascar: Mahajanga Province: Sofia River drainage basin: near town of Mandritsara: Amboaboa River near confluence with Mangarahara River: 15°50′2.0″S, 48°42′52.0″E; JSS 94-53; J. S. Sparks, K. J. Riseng, and local Malagasy guides, 14-XI-1994. UMMZ 240363, 1 ex. S, 62.5 mm SL; northwestern Madagascar: Mahajanga Province: Sofia River drainage basin: near town of Mandritsara: Amboaboa River near confluence with Mangarahara River; J. S. Sparks, K. J. Riseng, and local Malagasy guides, 10 and 11-VII-1996. UMMZ 243679, 1 ex. S, 70.7 mm SL; data as for UMMZ 240363.

Paretroplus tsimoly: Holotype: AMNH 229558, 140.3 mm SL, adult female; northwestern Madagascar: Majunga (= Mahajanga) Province: Betsiboka River drainage basin: Akalimilotrabe River (= Kalamilotra or Kamilotra River) at village of same name, ca. 43 km northwest of Maevatanana: 16°48′ 8.0″S, 47°00′57.0″E: alt. 318 m a.s.l.; P. V. Loiselle, 7-VI-1997. Paratypes: AMNH 229559, 2 ex., 1 ex. C&S, 99.3–138.1 mm SL, larger specimen adult female, smaller indeterminate sex; data as for holotype. MNHG 2609.44, 1 ex. 127.2 mm SL, adult female; data as for holotype; not examined. UMMZ 236893, 1 ex., 123.6 mm SL, adult female; data as for holotype. Additional Non-type Material Examined:

AMNH 229556, 2 ex., 110.1–129.5 mm SL, adult males; northwestern Madagascar: Mahajanga Province: region of Maevatanana: Betsiboka drainage (but with no more specific locality data). AMNH 229557, 1 ex. C&S, 52.0 mm SL, juvenile; data as for holotype. MHNG 2640.038, 2 ex., 133.6–137.0 mm SL; northwestern Madagascar: Mahajanga Province: Kamoro River at Antsalahina; P. de Rham and J.-C. Nourissat, 20-X-2001. AMNH 238563, 1 ex., 120.6 mm SL; northwestern Madagascar: Mahajanga Province: Betsiboka River drainage basin: Kanero/Kamoro River; JSS 37-2003; J.-C. Nourissat, C. Toumy, and J. Andriamianamihaja, X-2003. AMNH 238564, 1 ex., tissue voucher specimen, 89.7 mm SL; northwestern Madagascar: Mahajanga Province: Betsiboka River drainage basin: Kamoro River; JSS 38-2003, EE-1-2003; J.-C. Nourissat, C. Toumy, and J. Andriamianamihaja, X-2003.

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