Paretroplus dambabe, a new cichlid fish (Teleostei: Cichlidae) from northwestern Madagascar, with a discussion on the status of P. petiti

John S. Sparks

Division of Vertebrate Zoology, American Museum of Natural History, Central Park West at 79th Street, New York, NY 10024-5192, U.S.A., e-mail: jsparks@amnh.org

Abstract.—Paretroplus dambabe, n. sp., is described from Lake Kinkony, northwestern Madagascar. The new species is distinguished from congeners in life and preservation by light yellowish-olive body coloration in combination with a series of 6–7 vertical charcoal bars on the flanks, a blunt head profile, body depth not exceeding 57.1%SL, and uniform dark charcoal-gray or black fins. *Paretroplus dambabe* is further distinguished from *P. petiti*, a species to which it has been mistakenly referred for decades, by overall pigmentation pattern (light yellow-olive vs. dark brown), the presence of bright red pigmentation on the flanks in life, a prominent vertical barring pattern, and a shallower body.

Paretroplus Bleeker, 1868, the most speciose cichlid genus in Madagascar, comprises nine described species, excluding the new taxon (Table 1). Paretroplus is endemic to Madagascar, and members are distributed throughout the northwestern part of the island (8 species) and in eastern drainages (1 species), where the range of P. polyactis extends nearly the length of the island (Fig. 1). Monophyly of Paretroplus, and that of a more inclusive clade encompassing Paretroplus and Etroplus (endemic to southern India and Sri Lanka), is well established based on numerous morphological and nucleotide characters (Stiassny 1991, Sparks & Reinthal 1999, Sparks 2001, Stiassny et al. 2001). Sparks (2001) formally recognized the latter clade, Etroplinae, and assigned the taxon subfamilial rank. Major modifications of the anterior swimbladder, posterior neurocranium, palato-vomerine region, hyoid-mandibular and premaxillarymaxillary linkages, and oral and pharyngeal dentition characterize Paretroplus. Externally, members of Etroplinae are easily recognized by an elevated number of anal-fin spines (usually 7-10), a well-developed

pelvic axillary scale, and well-developed ridges of scales ("scale sheathing" of Cichocki, 1976) extending over, but not fused to, both the dorsal- and anal-fin bases. A number of additional features diagnostic of both Etroplinae and *Paretroplus*, as well as a species-level phylogenetic analysis, are presented by Sparks (2001). All *Paretroplus* but a single described taxon, *P. polyactis*, are restricted to northwestern Madagascar; a number of species from that region still await description (J. Sparks, pers. obs.).

Madagascar is generally considered to have a markedly depauperate freshwater ichthyofauna (Kiener & Richard-Vindard 1972). Results of a recent summary study of ichthyofaunal diversity, however, indicate that Madagascar is comparable in terms of the number of native and endemic freshwater species to other landmasses of similar size (Sparks & Stiassny 2002a, Sparks & Stiassny 2002b). Moreover, the number of extant freshwater species slightly exceeds that expected for a landmass with a surface area of just under 600,000 sq. km. (Riseng 1997, Sparks & Stiassny 2002b). Table 1.—List of Malagasy and South Asian cichlids according to current generic assignment, and subfamilial designation (discussed in text).

Taxon	
chochrominae:	
tychochromis oligacanthus (Bleeker)	
tychochromis grandidieri Sauvage	
tychochromis inornatus Sparks	
tychochromoides betsileanus (Boulenger)	
tychochromoides katria Reinthal & Stiass	ny
tychochromoides vondrozo Sparks & Reir	ithal
Dxylapia polli Kiener & Maugé	
oplinae:	
troplus suratensis (Bloch)	
troplus maculatus (Bloch)	
troplus canarensis Day	
aretroplus dami Bleeker	
aretroplus polyactis Bleeker	
aretroplus petiti Pellegrin	
aretroplus kieneri Arnoult	
aretroplus maculatus_Kiener & Maugé	
aretroplus menarambo Allgayer	
aretroplus nourissati (Allgayer)	
aretroplus maromandia Sparks & Reintha	ıl
Paretroplus tsimoly Stiassny et al.	
ratilapia:	
aratilapia polleni Bleeker	
aratilapia bleekeri Sauvage	

Many new cichlid species endemic to Madagascar have recently been, or are in the process of being, described (Allgayer 1996, 1998; Reinthal & Stiassny 1997; Sparks & Reinthal 1999, 2001; Stiassny et al. 2001, Sparks 2002). Most of these recently discovered species are restricted to relatively remote regions of the island where limnological analyses indicate limited ecosystem disturbance (Reinthal & Stiassny 1991, Riseng 1997). Where there is a great deal of ecosystem degradation, including a vast majority of Madagascar's freshwater systems, primarily exotic species survive (Benstead et al. 1999, Sparks & Stiassny 2002b). Increased sediment load and water turbidity, resulting from extensive deforestation and subsequent runoff, appear to be major factors leading to the rapid decline of endemic species.

Despite relatively low species diversity,

morphological variation among the endemic Malagasy and South Asian cichlids is substantial (Reinthal & Stiassny 1997, Sparks 2001, Sparks & Reinthal 2001, Sparks 2002). Within this monophyletic assemblage two major subfamilial lineages have been diagnosed based on both morphological and molecular characters; Ptychochrominae, comprising Ptychochromis, Ptychochromoides, and Oxylapia, and Etroplinae, comprising Paretroplus and Etroplus (Sparks 2001). Herein a new species of Paretroplus from Lake Kinkony, a large (oligotrophic) floodplain lake in northwestern Madagascar and part of the Mahavavy du Sud basin, is described. Further, the identity of P. petiti is clarified. For decades members of the new species have been mistakenly attributed to P. petiti, a taxon from which it is easily distinguished based on a number of morphological features.

Materials and Methods

Counts and morphometric measurements follow Barel et al. (1977), Kullander (1986) for upper-jaw length and pelvic-fin length, and Sparks & Reinthal (1999), unless noted otherwise. Measurements were recorded to the nearest 0.1 mm using Sylvac digital calipers. Vertebral counts exclude the last hypural-bearing vertebra (i.e., last half centrum) and were obtained from radiographs. Members of Paretroplus frequently possess abdominal ribs on the first caudal vertebra. The first caudal vertebra is here defined as the most anterior vertebra bearing a fully developed hemal spine, regardless of the presence or absence of abdominal ribs. The hemal spine of the first caudal vertebra terminates distally either between the first and second, or between the second and third anal-fin pterygiophores. All counts and measurements of fin elements were obtained from radiographs or cleared and stained preparations. Each of the terminal dorsal- and anal-fin soft rays is counted as two rays if this element is split completely to the fin base (Barel et al. 1977), which is

PROCEEDINGS OF THE BIOLOGICAL SOCIETY OF WASHINGTON

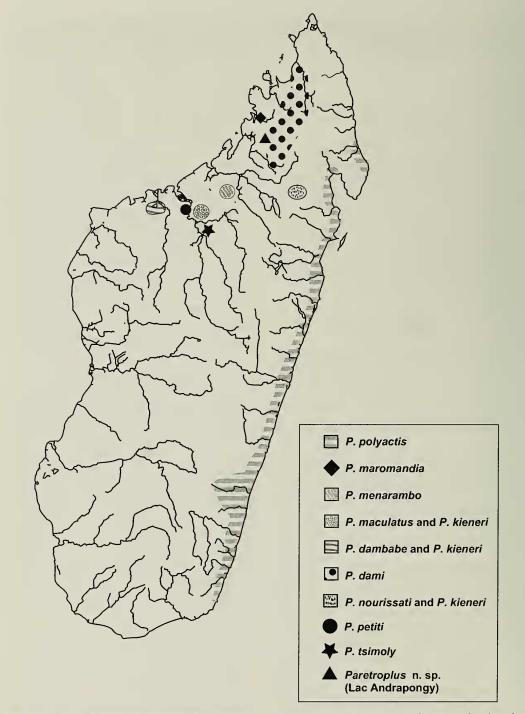


Fig. 1. Map of Madagascar illustrating current geographic ranges for members of *Paretroplus*, based on localities from which specimens have been collected in recent surveys (except *P. petiti*, which is only known from the holotype). These are only approximate distributions, as many remote areas of the island remain poorly surveyed.



Fig. 2. *Paretroplus dambabe*, holotype, UMMZ 238724, adult male, 169.4 mm SL, northwestern Madagascar, Province of Majunga, Lake Kinkony.

generally the case in *Paretroplus*. There is only one supporting (articulating) pterygiophore for this terminal split ray in *Paretroplus*. Without the use of radiographs this condition is difficult to detect, and it appears as though two distinct rays are present. Gill-raker counts exclude the raker (if present) in the angle of the arch.

Comparative anatomical analyses included specimens preserved in 70% ethanol, specimens cleared and double stained for bone and cartilage using a modified protocol based on Taylor & Van Dyke (1985), and dry skeletal preparations. A list of comparative material is presented at the end of this paper. Institutional abbreviations are as listed in Leviton et al. (1985).

Paretroplus dambabe, new species Figs. 2–3, Table 2

Paretroplus petiti.—Kiener 1963 (in part).—Kiener & Thérézien 1963.—Kiener & Maugé 1966 (in part).

Holotype.-UMMZ 238724, adult male,

169.4 mm SL, Madagascar, Majunga Province, south of Mitsinjo, Mahavavy (du sud) drainage basin, Lake Kinkony (16°05′ 37.7″S, 45°51′37.4″E), JSS 94-15, 14–16 July 1994, J. S. Sparks, K. J. Riseng, and local Malagasy guides.

Paratypes.—UMMZ 199406 (3, 67.0– 113.0 mm SL), ex. MNHN 60579, Madagascar; AMNH 232398 (10, 61.0–170.0 mm SL), data as for holotype; UMMZ 235024 (29, 40.2–225.0 mm SL, 3 ex. C&S), data as for holotype.

Non-type material examined.—All from Madagascar, Majunga Province, Mahavavy (du sud) drainage basin, Lake Kinkony: MNHN 1960-0579 (3, 125.5–179.9 mm SL), Kiener; MNHN 1962-0239 (2, 23.3– 24.6 mm SL), Kiener; MNHN 1965-0316 (2, 64.2–129.3 mm SL), Petit; MNHN 1996-123 (1, 105.2 mm SL), Nourissat and de Rham.

Differential diagnosis.—A deep-bodied Paretroplus distinguished from congeners, in life and preservative, by pale yellow to

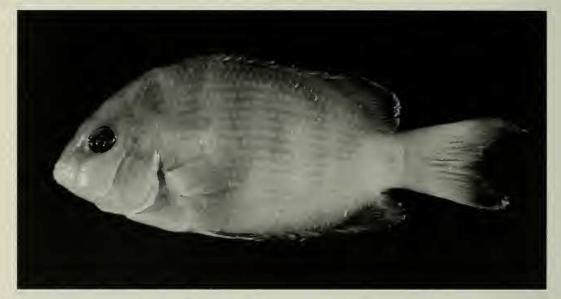


Fig. 3. Paretroplus dambabe, paratype, UMMZ 235024, juvenile, 93.5 mm SL.

Table 2.—Morphometric and meristic data for holotype and some paratypes of *Paretroplus dambabe* n. sp. Measurements (mm) in percent standard length (SL) or percent head length (HL), unless noted otherwise. (H) indicates count corresponding to holotype.

			P. dambabe n. sp.		
Character	N	Holotype	Range	Mean	SD
Standard length (mm)	20	169.4	40.7-186.8	115.9	
Head width (max.) % SL	20	17.4	16.0-17.5	16.7	0.49
Head length % SL	20	30.4	27.8-33.2	30.7	1.51
Body depth % SL	20	57.0	48.3-57.1	52.8	2.92
Caudal peduncle length % SL	20	6.2	5.1-8.6	6.4	0.66
Caudal peduncle width % SL	20	5.9	2.7-5.9	4.5	0.82
Caudal peduncle depth % SL	20	17.7	15.1-18.2	16.7	0.88
Pectoral fin length % SL	20	22.3	20.1-23.4	21.6	1.05
Pelvic fin length % SL	20	23.6	22.1-26.3	23.5	0.96
Last dorsal spine length % SL	19	14.5	13.3-16.9	15.4	0.97
Snout length % HL	20	48.5	31.9-48.9	43.7	4.64
Orbit diameter % HL	20	26.4	26.4-39.3	31.3	3.74
Upper jaw length % HL	20	30.1	25.7-31.3	28.3	1.59
Lower jaw length % HL	20	35.7	29.9-36.3	34.1	1.79
Interorbital width % HL	20	36.5	28.2-41.7	35.5	3.07
Preorbital depth % HL	20	34.4	22.2-37.6	31.4	4.10
Caudal peduncle length/width	20	1.1	1.1-2.0	1.5	0.26
Scales in lateral line	20	36 (10), 37 (7) (H), 38 (3)		
Scales: lateral line to dorsal fin	20	6 (3), 6.5 (1),	7 (16) (H)		
Gill rakers (lower limb)	20	9 (13), 10 (7)	(H)		
Vertebrae (pre-caudal + caudal)	30	14 + 18 = 32	(5), 14 + 19 = 33	(1), 15 + 16 =	= 31 (1), 15
		+ 17 = 32	(17) (H), $15 + 18 =$	33 (6)	
Dorsal fin	30	XVI 18 (3), X	VI 19 (1), XVII 17	(6), XVII 18 (15) (H),
), XVIII 17 (1)		
Anal fin	30	VIII 14 (3), V	111 15 (2), 1X 13 (9)	1X 14 (11) (H	H), 1X 15 (2)
		X 13 (2), X	14 (1)		

olive body coloration in combination with a series of 6–7 vertical, dark-olive bars on the flanks, a blunt and steep head profile, body depth not exceeding 57.1%SL, and the possession of dark, uniform black or charcoal-gray fins. *Paretroplus dambabe* is further distinguished from *P. petiti*, a species with which it has been erroneously associated, by overall pigmentation pattern and coloration (light yellow-olive vs. dark brown), the presence of a prominent vertical barring pattern on the flanks (vs. no barring), bright red pigmentation on the flanks in life, and a shallower body [mean 52.8% (ranges from 48.3–57.1) vs. 57.9% SL].

Description.-Morphometric and meristic data presented in Table 2. Comparative data of other closely related Paretroplus species presented in Table 3. Morphological characteristics and general pigmentation pattern can be observed in Figs. 2-3. A deep-bodied, laterally compressed Paretroplus, belonging to 'deep-bodied' clade identified and discussed by Sparks & Reinthal (1999) and Sparks (2001). Comparatively a large Paretroplus, frequently exceeding 200 mm SL, and reportedly attaining 400 mm TL (Kiener 1963), although large specimens now rare. Head blunt and steeply sloping in lateral view. Predorsal profile rounded and convex, especially in larger individuals. Caudal peduncle short, deep, and laterally compressed. Females smaller than males, but no additional sexually dimorphic characters apparent.

Total vertebral count 31-33 (mode 32), with formulae of: 14 + 18, 14 + 19, 15 + 16, 15 + 17, and 15 + 18, precaudal and caudal vertebrae, respectively.

Jaws isognathous. A single row of spatulate, unicuspid teeth in both upper and lower jaws. Teeth laterally expanded, flattened at crown, and implanted procumbently. In upper jaw, tooth on either side of premaxillary symphysis greatly enlarged, other teeth graded in size laterally. Lower-jaw teeth at symphysis not enlarged (and frequently reduced to accommodate enlarged upper symphyseal teeth). Teeth in upper jaw usually number 6–8 on each side, rarely 5. Teeth in lower jaw number 3–5 on each side. Lower jaw teeth irregularly spaced and sized.

Upper and lower pharyngeal dentition robust, tooth plates well developed. Dentition on lower pharyngeal toothplates [= lower pharyngeal jaws (LPJ) or fifth ceratobranchials] hooked and bicuspid both laterally and anteriorly, becoming progressively enlarged medially; robust molariform teeth present postero-medially (Fig. 4). LPJ well sutured, with numerous interdigitating sutures on postero-ventral margin. Robust toothplates covering majority of dorsal surface of fourth ceratobranchials. Toothplates not confluent with outer-row gill rakers of these elements (Fig. 4). Dentition on fourth ceratobranchial toothplates unicuspid or weakly hooked and bicuspid laterally, hooked and bicuspid medially (similar to lateral LPJ dentition). Dentition on third upper pharyngobranchial toothplates molariform medially, hooked and bicuspid peripherally. Dentition on second pharyngobranchial toothplates hooked and bicuspid (Fig. 5).

Nine or 10 triangular, somewhat elongate, gill rakers arrayed along lower limb of first gill arch. Rakers edentate in small individuals (<100 mm SL) and weakly denticulate dorso-medially in larger specimens. All other lower-limb rakers (i.e., gill arches 2–4) short and strongly denticulate dorsally. Epibranchial rakers elongate, numbering 8–10. Robust toothplates present on dorsal surface of fourth ceratobranchials.

Body covered with large, regularly imbricate, cycloid scales. Well-developed scale ridges present along dorsal- and analfin bases (into which dorsal and anal fins may partially retract). Scale ridges free from spiny dorsal and anal fins but becoming weakly attached to both soft dorsal and anal. Pelvic axillary scale present and well developed. Lateral-line scales 36–38. Chest scales somewhat smaller than other body scales, but not greatly reduced in size, and

552

		P. menarambo			P. maculatus			P. maromandia			P. petiti
Character	N	Range	Mean	z	Range	Mean	z	Range	Mean	z	Holotype
Standard length (mm)	18	72.1-166.8	125.3	18	48.4-148.1	106.5	2	113.0-126.9	120.0	I	82.8
Head length % SL	18	28.0 - 30.1	29.1	18	28.4-32.4	29.6	0	28.9-29.3	29.1	-	30.7
Body depth % SL	18	54.8-60.3	57.8	18	51.2-60.5	56.8	0	57.7-60.1	58.9	-	57.9
Head width (max.) % SL	18	14.9-17.2	16.0	18	16.3-17.5	16.8	0	15.2-15.8	15.5	-	17.6
Caudal peduncle length % SL	18	5.7-8.8	7.1	18	5.2-7.1	6.3	0	6.2	6.2	-	6.8
Caudal peduncle width % SL	18	3.7-6.4	4.6	18	3.6-4.6	4.1	0	4.3	4.3	I	5.3
Caudal peduncle depth % SL	18	15.0-17.4	16.3	18	15.3-16.6	15.9	0	15.8-16.7	16.3	-	17.2
Pelvic fin length % SL	18	22.4-25.2	23.8	18	22.7–25.1	24.0	0	22.4-22.9	22.7	-	24.0
Pectoral fin length % SL	18	20.7-23.1	21.7	18	20.9-24.5	22.2	0	20.4-21.2	20.8	-	23.3
Last dorsal spine length % SL	18	14.2-17.6	15.9	18	12.9-18.2	16.6	0	15.5-17.0	16.3	-	16.8
Upper jaw length % HL	18	26.4-29.4	27.9	18	26.1-29.3	27.5	0	27.0-28.0	27.5	-	28.0
Lower jaw length % HL	18	32.7-36.4	34.4	18	32.1-36.6	34.6	0	33.6-35.6	34.6	1	36.2
Snout length % HL	18	38.5-47.9	44.2	18	36.9-47.0	43.0	0	44.2-46.2	45.2	-	41.3
Orbit diameter % HL	18	27.3-32.5	30.6	18	30.3-37.6	33.7	0	31.5-32.2	31.8	μ	34.3
Interorbital width % HL	18	33.3-40.9	36.6	18	33.1-40.0	37.3	0	33.1–33.3	33.2	-	36.6
Preorbital depth % HL	18	26.8-36.5	33.3	18	27.4–34.7	31.3	6	32.8	32.8	-	30.7
Caudal peduncle length/width	18	1.1 - 2.0	1.6	18	1.3-1.9	1.6	0	1.4	1.4	-	1.3
Scales in lateral line	18	37 (13), 38 (5)		18	34 (1), 35 (1), 36 (3),	5 (3),	0	40 (1), 41 (1)		-	39
					37 (4), 38 (7), 39 (2)	(2)					
Dorsal fin	24	XV 19 (1), XV 20 (4), XV	0 (4), XV	31	XV 19 (1), XV 20 (1)	0 (1),	0	XVI 21 (1), XVI 23 (1)	23 (1)	-	XVII 18
		21 (5), XVI 19 (3), XVI	(3), XVI		XVI 16 (1), XVI 18 (2),	VI 18 (2),					
		20 (8), XVI 21 (2), XVII	(2), XVII		XVI 19 (10), XVI 20	KVI 20					
		19 (1)			(4), XVII 17 (2), XVII	2), XVII					
					18 (0), AVII 19 (2), VVII 20 (1) VVIII 18 (1)	9 (2), VIII 10 (1)					
Anal fin	74	VII 17 (1) VIII 15 (5)	5 (5)	31	VII 15 (4) VIII 16 (1) 1X	16 (1) 1X	c	TX 15 (1) 1X 16 (1)	11.	,	IX 14
	1	VIII 16 (10), 1X 15 (8)	X 15 (8)	•	13 (2), IX 14 (5), IX 15	(5), IX 15	1		Ì	•	
			·		(14), IX 16 (3), X 15 (2)), X 15 (2)					
Gill rakers (lower limb)	18	9 (16), 10 (2)		18	10 (16), 11 (2)		0	10 (2)		-	6
Vertebrae (pre-caudal + caudal)	24	15 + 17 = 32 (1),),	31	14 + 18 = 32 (11),	1),	6	16 + 18 = 34 (2)		-	15 + 18
		15 + 18 = 33 (21),	1),		14 + 19 = 33 (14),	4),					= 33
		15 + 19 = 34 (1),),		15 + 18 = 33 (6)	(
		16 + 18 = 34 (1)	~								
Scales: lateral line to dorsal fin	18	6 (1), 6.5 (1), 7 (13)	13),	18	6.5 (1), 7 (17)		0	7 (1), 8 (1)		-	7
		7.5 (1), 8 (2)									

PROCEEDINGS OF THE BIOLOGICAL SOCIETY OF WASHINGTON

VOLUME 115, NUMBER 3

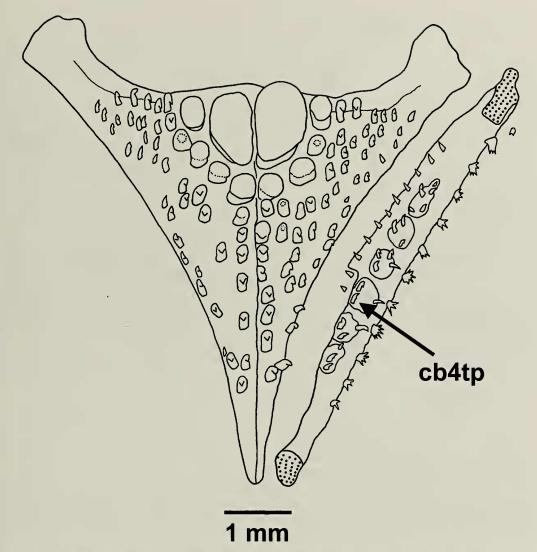
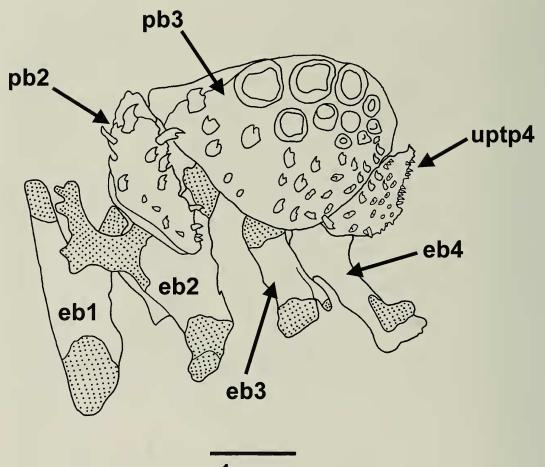


Fig. 4. Isolated 4th and 5th ceratobranchial elements, dorsal view, in *Paretroplus dambabe*, UMMZ 235024, paratype, juvenile, 64.0 mm SL. Abbreviation: cb4tp = 4th ceratobranchial toothplates. Scale bar = 1 mm.

embedded. Those along ventral midline smallest. Four to 6 rows of scales on cheek. Opercle and interopercle scaled. Snout, lacrimal, and anterior portion of interorbital region naked. Scales on caudal fin reduced in size and extending posteriorly ²/₃ to ³/₄ length of fin on dorsal and ventral lobes, and ¹/₄ to ¹/₃ length of fin medially.

Dorsal with XVI–XVIII spines, 17–19 soft rays. Anal with VIII–X spines, 13–15 soft rays. Origin of dorsal fin slightly anterior of vertical through pectoral-fin insertion. Caudal fin emarginate, trailing margins of upper and lower lobes produced (especially in larger individuals). Pectoral fin broad and rounded at distal margin. Distal margins of soft dorsal and anal fins produced and pointed in larger specimens. Pelvic fin extending just to anal-fin origin in smaller specimens, well beyond origin in larger individuals.

Miscellaneous osteology and anatomy.— Large, well-developed exoccipital excavations present. Anterior swimbladder cham-



1 mm

Fig. 5. Isolated right upper pharyngeal elements, ventral view, in *Paretroplus dambabe*, UMMZ 235024, paratype, juvenile, 64.0 mm SL. Abbreviations: eb 1-4 = epibranchials 1-4; pb 2-3 = pharyngobranchials 2-3; uptp4 = 4th upper toothplate. Scale bar = 1 mm.

bers thick-walled, anteriormost chambers lodged in exoccipital recesses. Well-developed concavity (= supraoccipital notch of Stiassny et al. 2001) present along posterior margin of supraoccipital. Supraoccipital extending anteriorly over neurocranial median frontal pores (NLF₀ of Barel et al. 1977). Two distinct and well-separated proximal premaxillary-maxillary ligaments present (rostral ligament unique to *Paretroplus* within Cichlidae). An extra, fully ossified, anal- and dorsal-fin pterygiophore, not associated with any fin rays, present terminally.

Coloration in life.-Base body colora-

tion pale yellow or pink to light olive. Body usually darker dorsally, but sometimes uniform. Six or seven broad dark olive bars extending from anterior region of trunk to caudal peduncle; bars very obvious in juveniles, becoming less conspicuous in large adults. Vivid reddish spots or patches present on flank; degree and intensity of spotting varying considerably. Some individuals with each flank scale outlined in red; in others, red pigmentation restricted to region below upper branch of lateral line. Nape and region below anterior spinous dorsal golden in juveniles. Black interorbital bar present in adults, dark gold in juveniles. Dorsal and anal fins uniform black proximally. Soft dorsal and anal fins with white distal margin. Caudal fin orangish anteriorly, becoming black distally, with white terminal band. Pelvic fin black with white leading edge. Pectoral fin reddish-orange proximally, white distally. Pigmentation pattern of young fish (<30 mm SL) blotchy and mottled [see juvenile *P. petiti* (now *P. dambabe*) illustrated by Kiener 1963: PL 16].

Coloration in preservative.—Ground coloration pale yellow-olive or light tan. Six or seven broad brownish to charcoal bars on flank. Barring more conspicuous in younger individuals (<150 mm SL) (Fig. 3), becoming somewhat obscure in larger specimens (Fig. 2). Reddish coloration on anterior flank lost in preservative. Unpaired fins and pelvic fin near uniform charcoal gray. Pectoral fin olive proximally and mostly hyaline distally. Anterior interorbital region and snout light gray.

Viscera and diet.—Gut contents comprised entirely of macerated gastropods in all individuals examined. *Paretroplus dambabe* appears to feed exclusively on gastropods.

Distribution and habitats.—Paretroplus dambabe has been collected only in Lake Kinkony, but is also reported to occur in surrounding 'satellite' lakes and the Mahavavy du Sud River (P. V. Loiselle, pers. comm.). I have only collected and examined material from Lake Kinkony proper, and cannot verify these additional localities. Lake Kinkony is a large (second largest lake in Madagascar, ca. 14,000 hectares), extremely shallow and turbid, oligotrophic floodplain lake characteristic of northwestern Madagascar (Kiener 1963). Similar lakes in northwestern Madagascar include lakes Andrapongy and Sarodrano. Several euryhaline and marine species, including anguillids, carangids, Scatophagus, and Chanos, also inhabit the lake. The Kinkony basin is moderately to highly disturbed and degraded. Seasonally, fishing pressure is very high. Much of the basin has been converted for rice cultivation and grazing of livestock. Little original riparian vegetation remains in the basin.

Relationships.-The new species is a member of the 'deep-bodied' clade of Paretroplus recognized by Sparks & Reinthal (1999) and Sparks (2001) on the basis of both morphological and molecular evidence. This clade also includes P. maculatus, P. maromandia, P. menarambo, P. petiti, and P. polyactis (Sparks 2001). All members of this clade are morphologically very similar except for pigmentation pattern and coloration (Figs. 2-3, 6-7). Morphologically, members of this clade are diagnosed by the presence of deep, disk-shaped bodies (body depth 48-60.5 %SL, regardless of standard length) in which body depth exceeds 57 %SL in adults, and is not less than 48 %SL in young. Body depth in all other Paretroplus ranges from 38-55 %SL, with body depth in young measuring less than 45 %SL.

Paretroplus polyactis is in turn the sister taxon to a clade comprising *P. dambabe, P. maculatus, P. maromandia, P. menarambo,* and *P. petiti.* Morphologically, members of this clade are diagnosed by the presence of conspicuous alternating, light and dark horizontal stripes on the flank (Sparks 2001, Figs. 2–3, 6–7). Based on the combined analysis of nucleotide characters from two mitochondrial genes, a 548 bp region of the large ribosomal subunit (16S) and a 649 bp region of cytochrome *c* oxidase subunit 1 (COI), *P. maculatus* is the hypothesized sister taxon to the new species (Sparks 2001, fig. 1.2).

Conservation status.—According to local fishermen the new species has suffered a severe decline in abundance in recent years. Lake Kinkony is subjected to severe fishing pressure, especially from migrant fishermen (catch is shipped to the capital, Antananarivo). The shores of the lake are home to a number of villages that subsist on fishing alone. Another member of *Paretroplus*, *P. kieneri*, is also found in the lake. This species has become increasingly rare in recent



Fig. 6. Paretroplus petiti Pellegrin, holotype, MNHN 1928-282, juvenile, 82.8 mm SL, northwestern Madagascar, Province of Majunga, Maintimaso River.



Fig. 7. Paretroplus menarambo, paratype, MNHN 1996-122, juvenile, 92.9 mm SL, northwestern Madagascar, Potamasina, Lake Sarodrano.

years according to local fishermen. All specimens of *P. kieneri* that were collected by our group, which were few, were in very poor condition and heavily infested with both external and internal parasites.

Local name.—Kotso.

Etymology.—Dambabe (pronounced dambah bay), a Malagasy word that translates as large or big damba, in reference to the comparatively large size attained by this species relative to other members of the genus. *Damba* is the Malagasy name that is used to refer to a number of species of *Paretroplus* in northwestern Madagascar, and *be* translates as big or large in Malagasy. Specific epithet used as a noun in apposition.

Discussion and Comparisons

Since at least the early 1960's individuals of the new species collected from Lac Kinkony have mistakenly been referred to *P. petiti* [Kiener 1963 (in part); Kiener & Thérézien 1963; Kiener & Maugé 1966 (in part)] (Fig. 6). Based on the results of this investigation, all specimens previously assigned to *P. petiti* that were collected in Lac Kinkony are determined to be members of the new species, and *P. petiti* is only known from the holotype described by Pellegrin (1929).

There is some confusion regarding the type locality of P. petiti, Pellegrin 1929, which is listed in the original description as the Maintimaso River in the province of Mahajunga (northwestern Madagascar). As far as I have been able to determine, the type specimen of P. petiti (MNHN 1928-282) was collected from a tributary (Maintimaso River) of the westward flowing Betsiboka River near the town of Maintimaso (16°10'60"S, 46°43'00"E), located approximately 37 km southeast of Majunga (= Mahajunga). In the MNHN database, however, the collection locality for P. petiti is listed as "Ambila." No town of this exact spelling appears to be in the vicinity of Majunga, although the town of Ambilo is located

near the Betsiboka River, 35 km south of Majunga (NW of Maintimaso). Further, while examining the type specimen at the MNHN in Paris, I noticed an old tag in the jar listing the species name and also including the word "Ambanja," a town located several hundred km to the north of Maintimaso and Mahajunga. I have been unable to obtain any additional information regarding either the Ambila or the Ambanja locality references, and believe that the most prudent course of action is to accept the locality information presented by Pellegrin (1929). As with many other fish species described from Madagascar in the latter part of the 19th century through the first half of the 20th century, collection localities are frequently ambiguous and questionable (Sparks 2002). Whether this is the case for P. petiti remains to be determined, as the region of the putative type locality has been poorly surveyed to date.

According to locality data presented in Pellegrin's original description, it appears likely that the type specimen of *P. petiti* was collected from within the Betsiboka basin, one of Madagascar's largest drainage systems. Regardless of the exact original collection locality, it is clear from the information that is available that the type specimen of *P. petiti* was not collected from the Mahavavy (du Sud) drainage basin, to which the new species is endemic (Fig. 1).

The holotype and only specimen of P. petiti is very similar in overall body shape and pigmentation pattern (in preservation) to P. menarambo, Allgayer 1996, a species restricted to floodplain lakes of the Sofia basin, northwestern Madagascar (Figs. 1, 6-7). Despite being collected in the 1920's, this specimen is remarkably well preserved, especially in terms of coloration and pigmentation pattern. Both P. petiti and P. menarambo are dark brown in overall coloration, with a lateral pattern of numerous, thin, alternating light and dark horizontal stripes (Figs. 6-7). In preservation, no other distinctive lateral markings are present in either of these species. In life, P. menar-

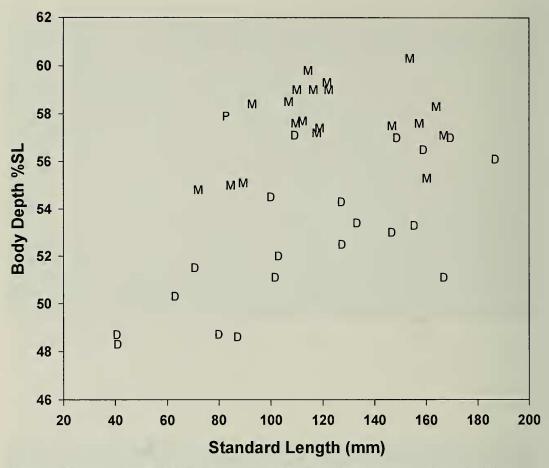


Fig. 8. Plot of body depth (BD) as a percentage of standard length (SL) verses SL for *P. dambabe* (D), *P. menarambo* (M), and holotype of *P. petiti* (P). Letters following specific name correspond to symbols shown on plot.

ambo is characterized by red terminal bands in the unpaired fins. Unfortunately, coloration in life for *P. petiti* is not known, and comparisons to *P. menarambo* cannot be made at this time.

In his original description of *P. petiti*, Pellegrin (1929) likewise made no mention regarding any additional distinctive markings. Although Pellegrin (1929) commented on the horizontal striping pattern mentioned above, he did not note the presence of bars on the flanks of *P. petiti*. Other members of the 'deep-bodied' clade of *Paretroplus* (except *P. polyactis*) possess this conspicuous horizontal striping pattern; however, none other than *P. petiti* and *P. menarambo* are dark brown with no additional lateral markings. Although the type specimen of *P. petiti*, a juvenile, is much deeper bodied than any individual of *P. dambabe* of similar standard length, and in fact is deeper bodied than any individual of *P. dambabe* examined, it is quite similar in body depth to specimens of *P. menarambo* of similar standard length (Fig. 8). The possibility exists that *P. petiti* and *P. menarambo* are conspecific; however, further studies are warranted and depend on the availability of additional specimens from the region of the type locality of *P. petiti*.

It is clear that *P. petiti* is not conspecific with *P. dambabe* from Lac Kinkony, al-

though members of the latter species have been assigned to P. petiti for decades (Kiener 1963, Kiener & Thérézien 1963, Kiener & Maugé 1966). Paretroplus petiti is currently known only from the holotype. As discussed, the new species is readily distinguished from P. petiti by overall pigmentation pattern and coloration (light yellowish-olive vs. dark brown), the presence of prominent broad vertical bars on the flanks (except very large individuals in which the bars are less conspicuous), and a shallower body (mean 52.8% vs. 57.9% SL). Paretroplus petiti is further distinguished from the new species by a much deeper supraoccipital crest that is markedly pointed (vs. rounded) at its dorso-caudal margin.

Comparative Material

Materials are arranged alphabetically by genus and species, with type specimens listed first followed alphabetically by museum acronym (C&S = cleared and stained preparation, S = dry skeletal preparation; values in parentheses indicate number of specimens examined, and do not necessarily correspond to the total number of specimens in the lot):

Etroplus canarensis: MCZ 4316 (1), possible syntype, Canara, Cannanore on Malabar Coast, Kerala, India; AMNH 217754 (1), River Kumaradhara at Kalikai, southern Canara, India; RMNH 1103 (1), Canara, India.

Etroplus maculatus: FMNH 58986 (2), Colombo, Sri Lanka; FMNH 76016 (37, 2 ex. C&S), India; MCZ 4311 (1), Kerala, Laccadive Sea, Canara, Cannanore on Malabar Coast, India; USNM 301168 (6, 2 ex. C&S), near Negombo Point, Sri Lanka.

Etroplus suratensis: FMNH 58987 (8), Colombo, Sri Lanka; MCZ 4306 (2), Kerala, Laccadive Sea, Canara, Cannanore on Malabar Coast, India; USNM 301178 (6, 2 ex. C&S), near Negombo Point, Sri Lanka.

Oxylapia polli: MNHN 1965-317 (1), syntype; AMNH 97098 (1); AMNH 97111 (10, 1 ex. C&S); MNHN 1966-1034 (2, 1 ex. C&S); UMMZ 235046 (2, 1 ex. C&S). All from Madagascar, Tamatave Province, Mangoro drainage, village of Marolambo, Nosivolo River.

Paratilapia polleni: RMNH 3.934 (2), syntypes, island of Nosy be, Madagascar; RMNH 4.483 (1), syntype, Madagascar; RMNH 6.690 (2), syntypes, "Ambassuana, Madagascar septentrionalis, in fluvis"; MNHN A.4195 (3), "marais et rizieres de l'Imerina, pres d'Antananarivo"; RMNH 6.692 (1), "Madagascar orientalis, in fluvis"; UMMZ 235043 (2 ex. C&S), Lac Anjavibe, island of Nosy be, Madagascar; UMMZ uncat., Lac de Deux Soures, island of Nosy be, Madagascar; UMMZ 235044, Vahifito River, near Vevembe, southeastern Madagascar; UMMZ 235045 (2 ex. C&S), Sahapindra River, near Vevembe, southeastern Madagascar; UMMZ uncat. (2 ex. C&S), rivers near Vevembe, southeastern Madagascar; UMMZ uncat., Manombo Special Reserve, south of Farafangana, southeastern Madagascar; UMMZ uncat. (1), Ampijoroa, Lake Ravelobe, northwestern Madagascar.

Paretroplus dami: RMNH 3.939 (1), syntype, "Nossibe (Lacus Pambilao)"; RMNH 4.478 (1), syntype, "Nossibe (Lacus Pambilao)"; UMMZ 233523 (S), northwestern Madagascar; UMMZ 235021 (3 ex. C&S), Anjingo River, east of Antsohihy, northwestern Madagascar; UMMZ 235022 (C&S), Lac Andrapongy, north basin, northeast of Antsohihy, northwestern Madagascar; UMMZ 235023 (1 ex. C&S), Andranomaloto River (tributary of Mananjeba River), north of Ambanja, northwestern Madagascar; UMMZ uncat. (C&S, S), northwestern Madagascar.

Paretroplus kieneri: MNHN 1960-580, holotype, Lac Kinkony, northwestern Madagascar; MNHN 1960-581, paratype, Lac Kinkony, northwestern Madagascar; MNHN 1966-1043 (13), Riviere Ankalamilotra, province of Majunga, northwestern Madagascar; UMMZ 235018 (5, 1 ex. C&S), Lac Ravelobe, near Ampijoroa Forestry station, northwestern Madagascar; UMMZ 236592 (4, 1 ex. CS), Lac Kinkony, near Majunga, northwestern Madagascar; UMMZ uncat. (2 ex. C&S, S), Amboaboa and Mangarahara Rivers, near Mandritsara, northern Madagascar.

Paretroplus maculatus: MNHN 1965-315 (2), syntypes, Ambato-boeny, province of Majunga, northwestern Madagascar; UMMZ 235019 (2 ex. C&S), Lac Ravelobe, near Ampijoroa Forestry Station, northwestern Madagascar; UMMZ 235020 (2 ex. C&S), Lac Ravelobe, near Ampijoroa Forestry Station, northwestern Madagascar; UMMZ uncat. (2 ex. S), Lac Ravelobe and vicinity, northwestern Madagascar.

Paretroplus maromandia: UMMZ 234790, holotype; AMNH 227336, paratype. Specimens from Antalaha province, region of Maromandia, Maintsomalaza River, immediately south of Maromandia, northwestern Madagascar.

Paretroplus menarambo: MNHN 1996-121 and 1996-122 (2), paratypes, Lac Sarodrano, Sofia basin, Potomasina, Madagascar; UMMZ 233522 (6, 1 ex. S), Lac Sarodrano, approx. 30 km north of Mampikony, northwestern Madagascar; UMMZ 235013 (1), Lac Sarodrano, approximately 30 km north of Mampikony, northwestern Madagascar; UMMZ 235014 (2 ex. C&S), Lac Sarodrano, near village of Sarodrano, approx. 30 km north of Mampikony, northwestern Madagascar; UMMZ uncat., Lac Sarodrano, northwestern Madagascar.

Paretroplus nourissati: MNHN 1997-4172, holotype, Amboaboa River, Sofia basin, Madagascar; MNHN 1997-4173 (4), paratypes, Amboaboa River, Sofia basin, Madagascar; UMMZ 235205 (2 ex. C&S, S), Amboaboa River, near Mandritsara, northern Madagascar; UMMZ 235206 (3 ex. C&S, S), Amboaboa River near confluence with Mangarahara River, near Mandritsara, northern Madagascar.

Paretroplus petiti: MNHN 1928-282, holotype, Maintimaso River, Province of Majunga, Ambila, northwestern Madagascar.

Paretroplus polyactis: UMMZ 199407 (3), Madagascar, formerly MNHN 60-222;

UMMZ 235015 (10), Mananjary market and port, southeastern Madagascar; UMMZ 235016 (15, 3 ex. C&S, S), Farafangana market, southeastern Madagascar; UMMZ 235017 (C&S), Manombo Special Reserve, southeastern Madagascar; UMMZ 236593 (1), mangrove swamp near Lalona river, west coast of Masoala Peninsula, northeastern Madagascar; UMMZ uncat. (4), Maroansetra market, northeastern Madagascar.

Paretroplus tsimoly: AMNH 229558, holotype, AMNH 229559 (1 ex. C&S), paratype, UMMZ 236893 (1), paratype. Specimens from Akalimilotrabe River, Betsiboka Basin, northwestern Madagascar.

Paretroplus cf. maromandia: MHNG 2537.60 (2), Lac Andrapongy, near Antsohihy, northwestern Madagascar.

Ptychochromis oligacanthus: RMNH 3.936 (2), syntypes, "Madagascar, in flumine Samberano; (var. nossibeensis) Nossibé; in lacu Pambilao"; AMNH 215522 (4), Lac Bemapaza, island of Nosy be, northwestern Madagascar; AMNH 215523 (15), Lacs Djabala and Ampombilava, island of Nosy be, northwestern Madagascar; MNHN 1962-322 (1), Sambirano River, northwestern Madagascar; UMMZ 236591 (26, 4 ex. C&S), Lake Ampombilava, island of Nosy be, northwestern Madagascar; UMMZ 237498 (22, 2 ex. C&S), Lake Djabala, island of Nosy be, northwestern Madagascar; UMMZ 237493 (3), Lac de Deux Soures, island of Nosy be, northwestern Madagascar; UMMZ 237494 (1), Lac Amparihibe, island of Nosy be, northwestern Madagascar; UMMZ 237496 (6), Lac Bempazava, island of Nosy be, northwestern Madagascar; UMMZ 237497 (8), Lac Anjavibe, island of Nosy be, northwestern Madagascar; UMMZ 237499 (11, 1 ex. C&S), Mananjeba drainage, Andranomaloto River, northeast of Ambanja, northwestern Madagascar.

Ptychochromis grandidieri: MNHN A.310 and A.4147 (2), syntypes, Madagascar, region of high forests.

Ptychochromis cf. grandidieri: MNHN

A.7896 (2), originally designated as syntypes of P. madagascariensis, Lac Itasy, central Madagascar to the east of Antananarivo; MNHN 1901-0020 (1), Tamatave, eastern Madagascar; MNHN 1901-0021 (1), Tamatave, eastern Madagascar; MNHN 1901-0486 (3), Ankobo, Manambolo River, Madagascar; MNHN 1901-0487 (3), Ankobo, Manambolo River, Madagascar; MNHN 1932-0014 (1), Taraouy River, Madagascar; MNHN 1932-0082 (1), Manompana, eastern Madagascar; MNHN 1932-0083 (13), Manompana, eastcoast, Madagascar; MNHN 1935-0007 (1), Mananara, eastern Madagascar; UMMZ 233524 (17, S), eastcoast, Madagascar; UMMZ 237311 (9), Mananjary, southeastern Madagascar; UMMZ 237312 (3, 3 ex. C&S), Manombo Special Reserve, southeastern Madagascar; UMMZ uncat. (C&S), southeastern Madagascar; UMMZ 237495 (1), Karianga, Rianila drainage, Andriambondro River, southeastern Madagascar.

Ptychochromis sp.: MNHN 1962-0201 (6), Onilahy River, southwestern Madagascar.

Ptychochromis sp.: UMMZ 237066 (1), Amboaboa River, Sofia drainage, northeastern Madagascar.

Ptychochromoides betsileanus: BMNH 1882.2.25:69, lectotype, Betsileo, Madagascar; BMNH 1882.2.25:70 (1), paralectotype, Betsileo, Madagascar; BMNH 1909.7.27:53 (1), ex. Paris Museum, no locality information; AMNH 217753 (1), Ilanana River, near Ranohira, Onilahy drainage, Madagascar; AMNH 217763 (1), Manantanana River, headwaters near Iaritsena, Ambalavao Region, Mangoky drainage, Madagascar; MNHN 1907-0104 (2), Madagascar; MNHN 1919-11 (1 ex. C&S), Lac Itasy, central Madagascar; MNHN 1960-255 (1), Madagascar; MNHN 1965-314 (1), Ambalavao, southcentral Madagascar; UMMZ 199409 (3), Madagascar; UMMZ 238114 (3), Ilanana River, south of Isalo National Park, southcentral Madagascar; UMMZ 238115 (5 ex. S), Ilanana River, south of Isalo National Park, south-central Madagascar.

Ptychochromoides katria: AMNH 217739, holotype; AMNH 217740 (8), paratypes; AMNH 93701 (10, 2 ex. C&S); UMMZ uncat (5, 1 ex. C&S). All from Tamatave Province, Mangoro drainage, Nosivolo River, Marolambo, Madagascar.

Ptychochromoides vondrozo: UMMZ 235297, holotype, Fianarantsoa Province, Region of Vondrozo, near village of Vevembe, Mananara drainage basin, Ramanara River, tributary of Sahampindra River, southeastern Madagascar; AMNH 228488 (2), data as for holotype; UAZ 2000-1-1 (1), data as for holotype; UMMZ 235293 (1), Sahampindra River, southeastern Madagascar; UMMZ 235294 (3, 1 ex. C&S), Sahampindra River, approx. 10 km upstream from Vevembe Camp, southeastern Madagascar; UMMZ 235295 (1), Voatavobe River, tributary of Vahafito River; UMMZ 235296 (3, 1 ex. C&S), data as for holotype.

Acknowledgments

Thanks to Karen Riseng and Roger Randriamampionina for considerable assistance in the field. Thanks to Peter Reinthal for his generous support, which allowed me to conduct fieldwork in Madagascar. I am grateful to Melanie Stiassny (AMNH) for the loan of specimens, for support to visit AMNH, and for generously sharing her knowledge of cichlid fishes. For the loan of material I am also thankful to Darrel Siebert (BMNH), and Susan Jewett (USNM). Collecting efforts and visits to Madagascar were facilitated by Benjamin Andriamahaja and the MICET (Institute for the Conservation of Tropical Environments, Madagascar) staff, to whom I am indebted. For helpful comments on this manuscript I thank M. Stiassny and P. Reinthal. This work was funded by grants from the National Science Foundation (DEB-9300996), and the United States Agency for International Development (University Development Linkage Program, US AID Cooperative Agreement, PCE-5063-A-00-3035-00) to P. Reinthal, and by the Carl L. and Laura C. Hubbs Research Fellowship and support from the Rackham School of Graduate Studies of the University of Michigan to the author.

Literature Cited

- Allgayer, R. 1996. Description d'une espèce nouvelle du genre *Paretroplus* Bleeker (Teleostei: Cichlidae) de Madagascar.—Revue Française des Cichlidophiles 159:6–20.
 - —. 1998. Descriptions de Lamena nourissati sp.
 n. genre et espèce nouveaux, endemiques de Madagascar (Teleostei: Etroplinae).—Revue Française des Cichlidophiles 179:7–17.
- Barel, C. D. N., M. J. P. Van Oijen, F. Witte, & E. Witte-Maas. 1977. An introduction to the taxonomy and morphology of the haplochromine Cichlidae from Lake Victoria.—Netherlands Journal of Zoology 27:333–389.
- Benstead, J. P., M. L. J. Stiassny, P. V. Loiselle, K. J. Riseng, & N. Raminosoa. 2000. River conservation in Madagascar. Pp. 205–231 in P. J. Boon, B. R. Davies, & G. E. Petts, eds., Global perspectives on river conservation: science, policy, and practice. John Wiley and Sons, New York, 548 pp.
- Bleeker, P. 1868. Description de trois espèces inédites de Chromidoides de Madagascar.—Verslagen en Medeedelingen der Koninklijke Akademie van Wetenschappen Amsterdam, Afdeeling Naturnkunde 2:307–314.
- Cichocki, F. P. 1976. Cladistic history of cichlid fishes and reproductive strategies of the American genera Acarichthys, Biotodoma, and Geophagus. Vol. 1, Unpublished Ph.D. dissertation, University of Michigan, Ann Arbor, 356 pp.
- Kiener, A. 1963. Poissons, pêche et pisciculture à Madagascar.—Publication du Centre Technique Forestier Tropical 24:1–244.
- —, & M. Maugé. 1966. Contribution à l'étude systématique et écologique des poissons Cichlidae endémiques de Madagascar.—Mémoires du Musée National d'Histoire Naturelle (Serie A), Zoologique, Paris 40:51–99.
 - , & G. Richard-Vindard. 1972. Fishes of the continental waters of Madagascar. Pp. 477–499 *in* R. Battistini & G. Richard-Vindard, eds., Biogeography and ecology in Madagascar. Dr. W. Junk, The Hague, 765 pp.
- —, & Y. Thérézien. 1963. Principaux poissons du lac Kinkony.—Bulletin de Madagascar 204: 395–415.
- Kullander, S. O. 1986. Cichlid fishes of the Amazon River drainage of Peru. Swedish Museum of Natural History, Stockholm, 431 pp.
- Leviton, A. E., R. H. Gibbs Jr., E. Heal, & C. E. Dawson. 1985. Standards in herpetology and ichthy-

ology: Part I. Standard symbolic codes for institutional resource collections in herpetology and ichthyology.—Copeia 1985:802–832.

- Pellegrin, J. 1929. Cichlidés de Madagascar recuellis par M. Georges Petit. Description d'une espèce nouvelle.—Bulletin de la Société Zoologique de France 54:252–255.
- Reinthal, P. N., & M. L. J. Stiassny. 1991. The freshwater fishes of Madagascar: a study of an endangered fauna with recommendations for a conservation strategy.—Conservation Biology 5:231–243.
 - —, & M. L. J. Stiassny. 1997. Revision of the Madagascan genus *Ptychochromoides* (Teleostei: Cichlidae), with description of a new species.—Ichthyological Exploration of Freshwaters 7:353–368.
- Riseng, K. J. 1997. The distribution of fishes and the conservation of aquatic resources in Madagascar. Unpublished M.S. thesis, University of Michigan, Ann Arbor, 149 pp.
- Sparks, J. S. 2001. Phylogeny and biogeography of the Malagasy and South Asian cichlid fishes (Teleostei: Perciformes: Cichlidae), including a survey of the freshwater fishes of Madagascar. Unpublished Ph.D. dissertation, University of Michigan, Ann Arbor, 518 pp.
 - 2002. Ptychochromis inornatus, a new cichlid (Teleostei: Cichlidae) from northwestern Madagascar, with a discussion of intrageneric variation in Ptychochromis.—Copeia 2002:120– 130.
 - —, & P. N. Reinthal. 1999. Paretroplus maromandia, a new cichlid fish from the northwest of Madagascar.—Occasional Papers of the Museum of Zoology, The University of Michigan 727:1–18.
 - —, & P. N. Reinthal. 2001. A new species of *Ptychochromoides* from southeastern Madagascar (Teleostei: Cichlidae), with comments on monophyly and relationships of the ptychochromine cichlids.—Ichthyological Exploration of Freshwaters 12:115–132.
 - —, & M. L. J. Stiassny. 2002a. Madagascar's freshwater fishes: an imperiled treasure. In M. Thieme, R. Abell, M. L. J. Stiassny, D. Olsen, E. Dinerstein, J. D'Amico, and E. Underwood, eds., Freshwater ecoregions of Africa. A conservation assessment. Island Press, Washington, D.C. (in press).
 - —, & M. L. J. Stiassny. 2002b. Introduction to Madagascar's freshwater fishes. *In S. M. Good*man and J. P. Benstead, eds., The natural history of Madagascar. The University of Chicago Press, Chicago (in press).
- Stiassny, M. L. J. 1991. Phylogenetic intrarelationships of the family Cichlidae: an overview. Pp. 1–35 *in* M. H. A. Keenleyside, ed., Cichlid fishes:

behaviour, ecology, and evolution. Chapman and Hall, London, 378 pp.

-, P. Chakrabarty, & P. V. Loiselle. 2001. Relationships of the Madagascan cichlid genus *Paretroplus* Bleeker 1868, with description of a new species from the Betsiboka River drainage of northwestern Madagascar.—Ichthyological Exploration of Freshwaters 12:29-40.

Taylor, W. R., & G. C. Van Dyke. 1985. Revised procedures for staining and clearing small fishes and other vertebrates for bone and cartilage study.—Cybium 9:107–119.