Rehabilitation of the Malagasy Endemic *Kuhlia sauvagii* Regan, 1913 (Teleostei: Perciformes), with the Designation of a Neotype for *Centropomus rupestris* Lacépéde, 1802

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ABSTRACT

Based on differences in adult coloration, behavior, and morphometric and meristic features, the endemic Malagasy kuhlid *Kuhlia sauvagii* Regan, 1913, is resurrected from synonymy with the Indo-Pacific *Kuhlia rupestris* (Lacépéde, 1802). Both species are redescribed, and a summary of their distribution, natural history, and conservation status on Madagascar is provided. No type specimens for *Centropomus rupestris* Lacépéde, 1802 (type locality, Réunion), are known, and considerable confusion persists in the literature regarding the taxonomic composition and limits of this purportedly widespread species. We designate as neotype for *Centropomus rupestris* a syntype of *Dules fuscus* Cuvier *in* Cuvier and Valenciennes, 1829, thereby unambiguously relating this taxon to material collected from the type locality of Lacépéde's *Centropomus rupestris*, the island of Réunion in the western Indian Ocean.

INTRODUCTION

The past decade and a half of fish collecting in the freshwaters of Madagascar has resulted in both the discovery of a large number of new taxa (Sparks and Stiassny, 2003) and the rehabilitation of a number of erroneously synonymized species (e.g., Watson, 1991; Sparks, 2003). A purported Malagasy endemic, *Kuhlia sauvagii*, was described in 1913 by Regan on the basis of material collected from "Imerina, Madagascar" (a designation used at

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the time to refer to a general region of the high plateau of Fianarantsoa and Tamatave provinces). Two years later, Boulenger (1915) synonymized the species with the widely distributed Indo-Pacific species *Kuhlia rupestris* (Lacépéde, 1802) but without providing any formal justification for this decision. Although subsequent authors have recognized the existence of two Malagasy "color forms" of *K. rupestris* (Pellegrin, 1933; Arnoult, 1959; Kiener, 1963), Boulenger's opinion on the status of *K. sauvagii* has gone unchallenged (e.g., Eschmeyer, 1998; Froese and Pauly, 2006). Field observations indicate that the two Malagasy phenotypes show differences in morphology, pigmentation pattern, and behavior and that they can often be found living syntopically. These data led us to critically reexamine existing holdings of Malagasy *Kuhlia* and to compare them with specimens collected both from Réunion, the type locality of *K. rupestris*, and from the surrounding region.

This paper presents evidence that Regan's initial diagnosis was correct and formally proposes the rehabilitation of *K. sauvagii* Regan, 1913, as a valid species endemic to Malagasy freshwaters. During the course of this study, we were frustrated by the insufficiency of Lacépéde's original description of *K. rupestris*, a problem rendered all the more vexing by the absence of type material of *Centropomus rupestris* Lacépéde, 1802 (Bauchot and Desoutter, 1986; Pruvost, personal commun.). However, two syntypes of *Dules fuscus* Cuvier *in* Cuvier and Valenciennes, 1829, a currently recognized synonym also from Réunion, are available for examination and we therefore take the opportunity to designate one of these as a neotype of *C. rupestris* and herein redescribe the taxon on the basis of that neotype, topotypical material from Réunion, and additional material from Madagasar. Finally, we summarize what is known of the natural history of both species on Madagascar and assess their conservation status.

A third species, *Kuhlia caudovittata* (Lacépéde, 1802), has been reported from Malagasy freshwaters (Arnoult, 1959; Kiener, 1963; Maugé, 1986; Froese and Pauly, 2006), but as noted by Sparks and Stiassny (2003) and Heemstra (in litt.), no museum records corroborating the presence of this species in Malagasy continental waters have been located, and its presence on the island is highly doubtful. Other *Kuhlia* species reported from Malagasy coastal waters (Kiener, 1963), *K. mugil* (Forster, 1801) and possibly also *K. splendens* Regan, 1913, are not known to enter freshwater systems in the Madagascar–Mascarene region.

MATERIALS AND METHODS

Counts and measurements follow Randall and Randall (2001), unless noted otherwise. Measurements were recorded to the nearest 0.1 mm using digital or dial calipers. Vertebral counts include the terminal, hypural-bearing vertebra, and vertebral and fin spine/ray counts and measurements were obtained from radiographs or cleared-and-stained skeletal preparations. The terminal dorsal and anal soft fin rays are counted as a single element, even if branched and split to the fin base, as this element is associated with a single supporting pterygiophore. Gill-raker counts correspond to the lower limb of the first arch and include the raker in the angle of the arch marking the transition from ceratobranchial to epibranchial.

Comparative material consisted of formalin-fixed specimens stored in 70–75% ethanol and specimens cleared and stained for bone and cartilage (C&S) using a modified protocol based on Taylor and Van Dyke (1985). Institutional abbreviations follow Leviton et al. (1985). The following comparative materials have been included in this study: *Kuhlia caudovittata*: MNHN 1988-436 (Réunion); *Kuhlia splendens*: BMNH 1861.11.7:49 (syntype, Mauritius), BMNH 1876.3.12:22-24 (syntypes, Rodriguez); *Kuhlia taeniura*: AMNH 17365 (Samoa), AMNH 220651 (Sumatra), AMNH 50619 (Marshall Islands).

Malagasy place names follow contemporary usage, as indicated by the Foiben-Taosarintanin'i Madagasikara. Equivalent colonial-era place names previously utilized in the literature are given within brackets following their initial appearance in the body of the text. Altitudes are given in meters above sea level, abbreviated as m a.s.l.

Multivariate analysis of 17 log-transformed morphometric variables was accomplished using a sheared principal component analysis (PCA) (Humphries et al., 1981; Bookstein et al., 1985). Principal components were factored from the covariance matrix of log-transformed variables. Sheared PCA is designed to eliminate size effects and is necessary to ensure size-free shape comparisons, particularly among groups of individuals of non-overlapping size classes. The PCA was conducted in *Sheared PCA*, a freeware program written for the Macintosh operating system by Norman Macleod and available for download at http://www.nhm.ac.uk/hosted_sites/paleonet/ftp/ftp.html.

Kuhlia rupestris (Lacépéde, 1802)

plates 1A–1B, table 1

Centropomus rupestris Lacépéde, 1802: 252, 273 (Type locality: Ravine du Gol, Île de Bourbon = Réunion).
Perca ciliata Cuvier *in* Cuvier and Valenciennes, 1828 (Type locality: Java).
Dules fuscus Cuvier *in* Cuvier and Valenciennes, 1829 (Type locality: Ravine du Gol, Île de Bourbon = Réunion).
Dules guamensis Valenciennes *in* Cuvier and Valenciennes, 1831 (Type locality: Guam).
Dules vanicolensis Valenciennes *in* Cuvier and Valenciennes, 1831 (Type locality: Vanicolo, Santa Cruz Islands).
Dules haswellii Macleay 1881 (Type locality: Rockingham Bay, Queensland).
*Kuhlia rupestris hedleyi* Ogilby 1897 (Type locality: New Caledonia).
Kuhlia caerulescens Regan 1913 (Type locality: Stirling Island, Solomon Islands).

NEOTYPE: MNHN 2006-0811 (ex. MNHN 000-0862), syntype of *Dules fuscus*, Ravine du Gol, Réunion (Île de Bourbon), 81.8 mm SL.

ADDITIONAL MATERIAL EXAMINED: MASCARENES: MNHN 000-0862, 1 ex., 81.5 mm SL, syntype of *Dules fuscus*, Ravine du Gol, Réunion. MNHN A-3013, 1 ex., 139.0 mm SL, Réunion. MNHN 1982-1009, 1 ex., 54.0 mm SL, St. Denis, Réunion. MNHN 1998-0513, 1 ex. 48.8 mm SL, St. Benoit, Réunion. MNHN 1998-0514, 3 ex., 138.6–170.1 mm SL, no locaty given. MNHN 1999-0551, 1 ex., 131.9 mm SL, Ravine du Gol, Réunion. MNHN 1982-1009, 1 ex., 54.0 mm SL, St. Denis, Réunion. MNHN 000-0832, 1 ex., 155.5 mm SL, Mauritius (Île de France). MNHN 2003-0105, 1 ex., 45.8 mm SL, Mauritius.

MADAGASCAR: MNHN 1935-4, 1 ex., 35.0 mm SL, no locality given. MNHN 1936-29, 161.8 mm SL, Farony River. MNHN A-4193, 3 ex., 59.0–61.5 mm SL, no locality given. AMNH 228094, 1 ex., 63.2 mm SL, Andranobe Creek near Ambodiatafana Village, Nosy Boraha [16°43′30 S, 50°00′78 E], < 1.0 m a.s.l., Toamasina [Tamatave] Province. AMNH 231261, 1 ex., 133.0 mm SL, main channel of the Mahanara River at Antsirabe-Nord [13°58′49 S; 49°57′81 E], 35 m a.s.l., Antsiranana [Diego Suarez] Province. AMNH 232408, 3 ex., 1 cleared and stained, 89.5–101.3 mm SL, lower reaches of Djabala Creek below and above Ampombilava Village, Nosy Be [13°23′11 S, 48°14′22 E]. c. 1.0 m a.s.l., Antsiranana Province. AMNH 233668, 1 ex., 29.5 mm SL, Ankoakoa Creek immediately S. of Antanambe on RN-5. [16°28′50 S, 49°51′00 E], c. 1.0 m a.s.l., Toamasina Province. AMNH 233676, 1 ex., 56.0 mm SL, Maloutrandro River upstream of bridge over RN-5 [16°36′33 S, 49°48′25 E], c. 2.0 m a.s.l., Toamasina Province. AMNH 228080, 2ex., 112.7–170.9 mm SL, Manandriana Creek near of Ankirihisy Village, Nosy Boraha [16°51′39 S, 49°54′99 E], c. 7.0 m a.s.l., Toamasina Province. AMNH 11688, 1 ex., 104.6 mm SL, no locality given. UMMZ 238289, 4 ex., 63.0–76.0 mm SL, Morondava River, Toliara [Tuléar] Province. UMMZ 234812, 3 ex., 67.6–118.4 mm SL, mouth of the Andranobe River, Masoala Peninsula, [15°40′54 S, 49°57′25 E], c. 1.0 m a.s.l., Antsiranana Province. UMMZ 234886, 1 ex., 91.0 mm SL, Manombo National Park, [23°01′10 S, 47°43′75 E], Fianarantsoa Province. UMMZ 239701, 3 ex., 186.3–216.7 mm SL, Ihazofotsy River c. 2 hour's walk from Sakalama Village [22°58′56 S, 46°22′07 E], Toliara Province.

DIAGNOSIS: Differs from congeners, with the exception of *K. sauvagii*, in the possession in adults of an emarginate (vs. deeply forked) caudal fin. *Kuhlia rupestris* is distingushed from *K. sauvagii* in iris coloration (silvery white vs. light brown), the absence of a distinctive wide orange-red cresent-shaped mark covering the upper half of eye (present in *K. sauvagii*), the persistence into adulthood of a large black blotch on each lobe of the caudal fin, a higher gill-raker count (18–23 [mode 20] vs. 18–20 [mode
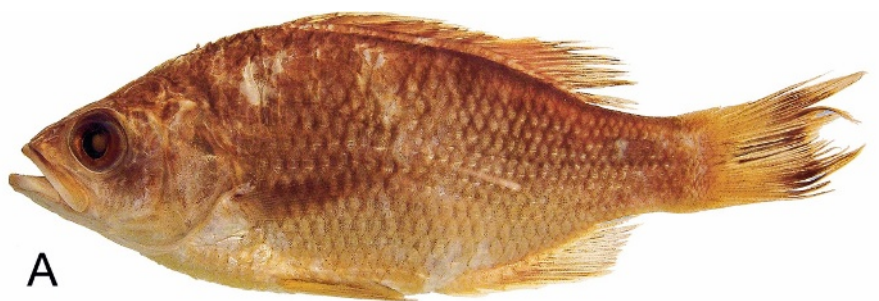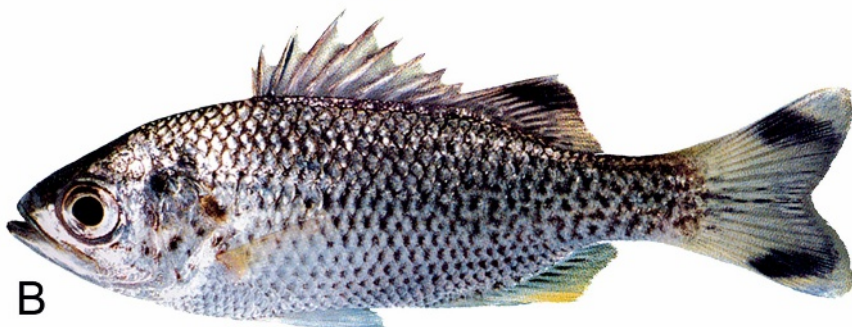
Plate 1. **A**. Neotype of *Kuhlia rupestris* MNHN 2006-0811, 81.8 mm SL (syntype of *Dules fuscus*), Ravine du Gol, Réunion. **B**. *Kuhlia rupestris*, in life, Réunion [photograph: E. Vigneux]. **C**. Holotype of *Kuhlia sauvagii*, BMNH 1895-10-29:91, 122.5 mm SL, Imerina, Madagascar. **D**. *Kuhlia sauvagii*, freshly captured and showing life coloration, Sahavana River, Rianila drainage, Toamasina Province, Madagascar, specimen not retained [photograph: Johann Rall, ECOSUN©].

TABLE 1
Morphometric and Meristic Data for the Neotype and 24 Additional Specimens
($N = 25$) of *Kuhlia rupestris* from Réunion and Madagascar
Values in parentheses indicate number of specimens examined with that count

	Neotype	Range	Mean	SD
Standard length (SL)	81.8	216.7–54.0		
Percentage of SL				
Head length (HL)	31.6	28.1–36.6	32.3	2.34
Body depth	35.7	34.9–40.9	37.5	1.55
Predorsal length	37.2	35.2–42.7	38.2	1.82
Prepelvic length	38.7	34.1–40.7	37.6	2.05
Preanal length	58.5	58.5–64.5	61.9	1.60
Dorsal base	48.1	33.7–46.9	43.8	3.20
Anal base	25.9	22.9–28.9	25.0	1.39
Percentage of HL				
Snout length	26.3	21.9–30.5	25.1	2.12
Upper jaw length	42.1	37.6–51.2	44.1	3.87
Orbit diameter	29.2	22.5–34.7	28.2	3.08
Interorbital width	33.3	26.4–35.6	31.5	3.11
Preorbital depth	41.5	34.7–53.8	46.8	4.23
Caudal peduncle length	57.3	39.3–61.2	49.3	5.49
Caudal peduncle depth	45.6	39.4–48.2	43.2	2.96
Dorsal spine length	47.4	39.9–57.5	47.7	4.83
Anal spine length	33.9	28.7–43.3	35.6	4.20
Scales in lateral line	38	38(2), 39(15), 40(7), 41(1)		
Dorsal-fin	X, 11	X, 11(24)		
Anal-fin		X, 10	X, 10(24)	

19]), and fewer pored lateral line scales (38–41 vs. 42–44).

DESCRIPTION: Morphometric and meristic data for neotype, topotypical, and Malagasy specimens are given in table 1. Largest specimen available is a male, 216.7 mm SL; however, adult lengths of 450 mm SL have been reported (Merrick and Schmida, 1984). Snout relatively short, 21.9–30.5% HL (mean 25.1% SL), dorsal head profile smoothly convex to dorsal fin origin. Jaws more or less isognathous, becoming slightly prognathous in large individuals. Posterior tip of maxilla usually attains, or extends beyond, vertical at mid-orbit, even in juveniles. Preorbital is weakly serrate; preopercle is more strongly so. Preorbital serrae tend to become obsolete in specimens >150.0 mm SL. Two short spines at the angle of the opercle, lower slightly longer than upper. Gill rakers on lower limb of first gill arch elongate and denticulate: 18 (1), 20 (14), 21 (5), or 23 (1).

Both jaws with a single outer row of minute, somewhat recurved unicuspid teeth. An inner band of villiform teeth, 3–4 rows in width, situated rostrally and tapering posteriorly to a single row. Teeth of outer row less than twice as long as those of inner band. Patches of fine conical teeth present on vomer, palatines, endopterygoid sand ectopterygoids.

Head and body covered from mid-orbit to caudal fin with regularly imbricate, ctenoid scales. Those on chest and venter only slightly smaller than those on flanks and dorsum. Cheek scale rows: 3 (5) or 4 (17). Pored scales in lateral line: 38 (2), 39 (15), 40 (7), 41 (1); often with 5–7 small pored scales extending onto base of caudal fin. Lateral line dips downwards to midlateral line at sixth or seventh scale from its origin. Scale rows from origin of anal fin to base of dorsal fin: 14 (1), 15 (1), 16 (18), or 17 (1). Four scale rows between origin of lateral line and mid-dorsal line. Five scale rows between pectoral in-

sertion and anal-fin origin. Circumpeduncular scales: 22 (1), 24 (21). Dorsal and anal scaly sheaths well developed, basal 25–30% of caudal fin heavily scaled.

Dorsal fin: X, 11 (25). Origin of dorsal fin usually anterior to pelvic insertion. Anal fin: III, 10 (25). Pectoral fin with 13 (4), 14 (19), or 15 (2) rays. Pectoral and pelvic fins short and rounded. Pelvic fins do not extend to urogenital papilla when adducted. Caudal somewhat forked in juveniles and young adults (e.g., plate 1B), becoming moderately emarginate in adults. Vertebral count 25 (10 + 15) in all specimens.

COLORATION IN LIFE (plate 1B): Snout, top of head, and dorsum light brown. Lips, cheek, opercle, and flanks silvery olive with bluish highlights; venter silvery white. Upper two-thirds of flanks densely speckled with irregular olive-brown spots. Similar spotting variably present on opercle and, more rarely, on cheek. Each scale in the five rows immediately below lateral line marked with a small olive-brown basal dot and a row of somewhat larger brown spots usually present on squamous anal fin sheath. Basal two-thirds of spiny dorsal greyish with a silvery-olive or bluish cast, distal third dusky. Soft dorsal, caudal, and anal fins clear yellow. Diffuse black blotch present distally between first to fifth or sixth dorsal fin soft rays. Specimens <100.0 mm TL typically with distinct pattern of dark inter-radial spots and streaks present medially in caudal fin membranes; reduced to an irregular pattern of darker spots in larger individuals. Large black spot invariably present on middle of each lobe of caudal fin of juveniles and characteristically retained in adults, distal tips of both caudal lobes white or hyaline. Single row of dark brown inter-radial spots variably present along anal fin base. Pelvic fins grayish with silvery-olive or bluish cast basally, hyaline distally. Pectorals hyaline. Iris of eye silvery, with narrow reddish-brown crescent dorsally.

COLORATION IN PRESERVATIVE: Snout, top of head, and dorsum light brown. Lips, cheek, opercle, and flank beige; venter dirty white. Pattern of dark spotting on head and body as described for living individuals, but spots are dark brown. Spiny portion of dorsal fin off-white; remaining unpaired fins clear yellow.

Dark markings of unpaired fins as described for living individuals. Pelvic fins off-white; pectorals hyaline. Iris of eye silvery-white, with narrow dark crescentic marking in upper quadrant.

DISTRIBUTION: As currently recognized, the range of Kuhlia rupestris extends from the east coast of Africa to Samoa and from Australia to the Ryukyu Islands (Randall and Randall, 2001). In the western Indian Ocean, its presence has been documented on the Comoros, both coasts of Madagascar (fig. 1), Réunion, and Mauritius, but confirmation of its presence in the Seychelles is lacking (Valade et al., 2004). In this study, we have concentrated on examination of specimens from localities on Madagascar and from islands in the western Indian Ocean, and we can neither confirm nor refute the identity of specimens currently identified as K. rupestris beyond this region.

NATURAL HISTORY: While juveniles are frequently found in estuarine habitats over the species' entire range, on Madagascar subadult and adult K. rupestris are essentially inhabitants of fresh waters. On the eastern versant of Madagascar, K. rupestris is restricted to the lower reaches of rivers. There are no records of this species from elevations much in excess of 30.0 m a.s.l., and upstream of the head of navigation, K. rupestris is typically replaced by K. sauvagii. However, in westward-flowing rivers such as the Onilahy, K. rupestris is routinely found as far as 250 km inland from the coast at altitudes of up to 900 m a.s.l.

Kuhlia rupestris up to 13.0 cm SL are typical inhabitants of clear, well-oxygenated, swiftly flowing waters. Larger individuals are usually found in deep pools where the current is less pronounced. Its Réunionais vernacular designation "doule des rochers" reflects its preference for rocky substrates. Juveniles feed predominantly on aquatic insect larvae and small freshwater shrimp but will take terrestrial insects from the water's surface. Adults are predators of macrocrustaceans and small fishes. Juveniles are at risk from larger predatory fishes, fish-eating birds, and small Nile crocodiles. While its flesh is highly esteemed by the Malagasy, K. rupestris is nowhere sufficiently abundant to support
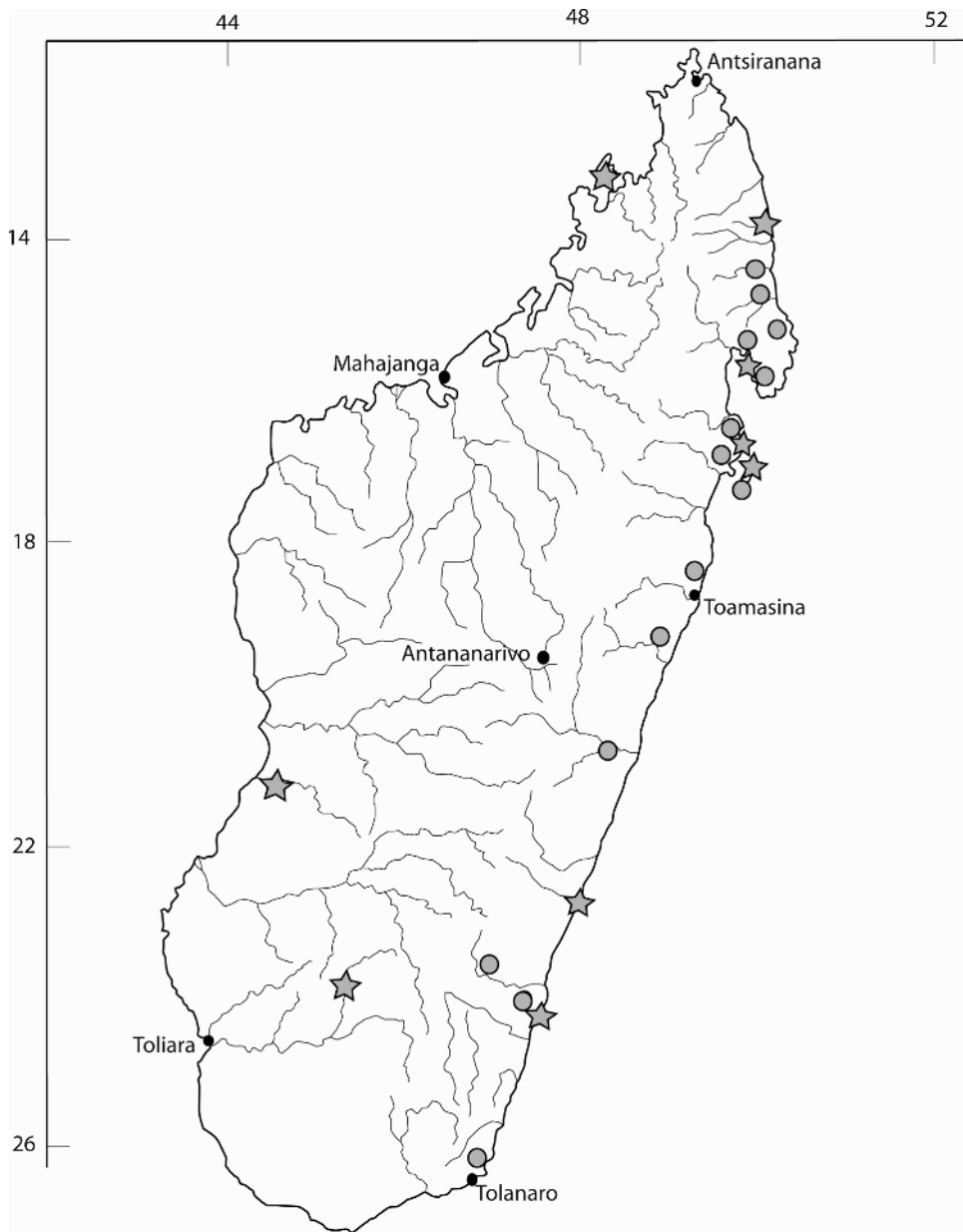
Fig. 1. Verified ranges of *Kuhlia rupestris* (shaded stars) and *Kuhlia sauvagii* (shaded circles) on Madagascar.

a significant commercial fishery (Kiener, 1963; Kiener and Therezien, 1963).

For a species whose value to recreational fisheries is recognized throughout its extensive range (Keith et al., 1999; Merrick and Schmida,1984), very little is known about the reproductive biology of *K. rupestris*. Its wide distribution implies the existence of a diadromous life-history pattern and a pelagic larval stage. Its mode of reproduction, however, is unknown, and it remains to be determined whether *K. rupestris* is a catadromous or an

TABLE 2
Morphometric and Meristic Data for the Holotype and 16 Additional Specimens
(*N* = 17) of *Kuhlia sauvagii* from Madagascar
Values in parentheses indicate number of specimens examined with that count

	Holotype	Range	Mean	SD
Standard length (SL)	122.5	207.2–55.4		
Percentage of SL				
Head length (HL)	28.2	27.8–32.1	30.1	1.53
Body depth	36.2	32.1–39.1	35.8	2.01
Predorsal length	36.0	35.1–42.4	38.1	2.42
Prepelvic length	35.9	31.4–39.4	36.5	2.01
Preanal length	61.4	55.2–62.1	59.8	1.81
Dorsal base	46.8	33.7–46.9	43.8	3.20
Anal base	28.9	21.9–28.9	25.6	1.88
Percentage of HL				
Snout length	23.9	20.5–27.3	24.5	1.74
Upper jaw length	41.7	33.9–43.4	39.1	3.01
Orbit diameter	32.7	28.2–36.8	32.0	2.18
Interorbital width	30.1	27.8–35.0	31.5	2.27
Preorbital depth	40.8	35.8–47.9	41.8	3.63
Caudal peduncle length	59.7	52.1–66.7	58.2	4.26
Caudal peduncle depth	44.9	38.8–48.3	43.8	3.04
Dorsal spine length	64.3	50.7–67.5	58.7	5.69
Anal spine length	53.6	35.8–53.8	45.7	5.45
Scales in lateral line	43	42(8), 43(5), 44(4)		
Dorsal-fin	X, 11	X, 11(16)		
Anal-fin	X, 10	X, 10(16)		

amphidromous spawner as well as to what degree, if any, its reproductive activity is characterized by seasonality.

CONSERVATION STATUS: Although it has been suggested that its numbers on Réunion have declined due to fishing pressure (Keith et al., 1999), there is no evidence to suggest that this is the case for the Malagasy populations. Following the criteria established by the World Conservation Union, *K. rupestris* is considered to be a low-risk species (Raminosoa et al., 2002).

DISCUSSION: Lacépéde's *Centropomus rupestris* is based entirely on Commerson's manuscript description, and no type material was designated at the time of description (Bauchot and Desoutter, 1986; Pruvost personal commun.). Considerable confusion exists in the literature regarding this purportedly widespread taxon and, as an aid for nomenclatural stabilization, the designation of a neotype is herein considered appropriate. Regan (1913) synonymized *Dules fuscus* Cuvier in

Cuvier and Valenciennes,1829, with *K. rupestris*. The type locality of both *Dules fuscus* and *Centropomus rupestris* are the island of Réunion. We have examined the syntypes of *D. fuscus*, two specimens measuring 81.8 mm and 81.5 mm SL. Following comparison with more recently collected material from Réunion, we can confirm the validity of Regan's decision to synonymize the two species. We thus formally propose the larger of the two specimens of *Dules fuscus* as the neotype of *C. rupestris*, a course of action that unambiguously relates this nomen to material collected from the designated type locality of Lacépéde's species, the island of Réunion in the western Indian Ocean.

Kuhlia sauvagii Regan, 1913

plates 1C, D, table 2

Kuhlia sauvagii Regan, 1913 (Type locality: Imerina, Madagascar).

Kuhlia rupestris: Boulenger, 1915; Arnoult, 1959; Maugé, 1986; Sparks and Stiassny, 2003.
Kuhlia rupestris sauvagii: Pellegrin, 1933, fig. 48.
Kuhlia rupestris var.: Kiener, 1963.

HOLOTYPE: BMNH 1895-10-29:91, 122.5 mm SL, Imerina, Madagascar.

ADDITIONAL MATERIAL EXAMINED: MADAGASCAR: MNHN 1998-1512, 1 ex., 181.0 mm SL, Tolanaro (Fort Dauphin). AMNH 237599, 2 ex., 46.3–47.1 mm SL, head of navigation of the Mahavoua River at Antanambe, 2 km upstream of first bridge on RN-5 northbound. AMNH 233671, 1 ex., 51.8 mm SL, Maloko stream at Mavoutano Village, Toamasina Province. AMNH 097085, 5 ex., 90.6–207.2 mm SL, Nosivolo River near Ambatomasina Village, c. 16 km E-NE of Marolambo [19°59′25 S, 48°12′70 E], Tosmasina Province. AMNH 215492, 2 ex., 55.7–102.7 mm SL, Lokoho River downstream of Belaoke [14°33′90 S, 49°45′00 E], Antsiranana Province, Madagascar. AMNH 237598, 1 ex., 60.1 mm SL, Andranobe Creek near the village of Ambodiatafana, Nosy Boraha [16°43′30 S, 50°00′78 E], <1.0 m a.s.l., Toamasina Province. AMNH 228097, 1 ex., 80.9 mm SL, Ambanitsivory Creek near the village of the same name, Nosy Boraha [16°55′57 S, 49°54′74 E], 79 m a.s.l., Toamasina Province. AMNH 231239, 1ex., 40.3 mm SL, Ankavia River at Antsahanandriana Village, on the Antalaha–Maromandia road [14°59′45 S, 50°11′25 E], 9 m a.s.l., Antsiranana Province. AMNH 233664, 1 ex., 78.4 mm SL, Mahavoua River, c. 2 m upstream of the bridge on RN-5 north of Antanambe. [16°26′05 S, 49°49′24 E], c. 2.0 m a.s.l., Toamasina Province. UMMZ 234812, 7ex., 44.3–106.1 mm SL, mouth of the Andranobe River [15°40′54 S, 49°57′25 E], c. 1.0 m a.s.l., Antsiranana Province. UMMZ 234815, 7 ex., 33.7–72.0 mm SL, Lahantozona Creek, c. one hour south of Andranobe camp [15°42′70 S, 49°58′00 E], Antsiranana Province. UMMZ 234821, 11 ex., 27.0–68.0 mm SL, Ambanizana River [15°35′35 S, 49°28′40 E], Antsiranana Province. UMMZ 234860, 5 ex., 56.0–83.0 mm SL, Onive River, Masoala Peninsula [15°17′02 S, 50°17′05 E], Antsiranana Province. UMMZ 235285, 2 ex., 82.0–102.0 mm SL, Andrianbondro Creek at Mahavelo Village [22°21′47 S, 47°22′05 E], Fianarantsoa Province. UMMZ 239921, 5 ex., 27.0–51.0 mm SL, Manombo National Park [23°01′15 S, 47°43′75 E], Fianarantsoa Province.

DIAGNOSIS: Differs from congeners, with the exception of *K. rupestris,* in the possession of an emarginate (vs. deeply forked) caudal fin. *Kuhlia sauvagii* is distingushed from *K. rupestris* in the coloration of the iris (light brown vs. silvery white), the presence of a distinctive wide orange-red cresent-shaped marking covering the upper half of the eye (absent in *K. rupestris*), the absence of a black blotch on the upper and lower lobe of the caudal fin in specimens >50.0 mm SL, a lower gill-raker count (18–20 [mode 19] vs. 18–23 [mode 20]), and by more pored lateral line scales (42–44 vs. 38–41).

DESCRIPTION: Morphometric and meristic data for holotype and more recently collected specimens given in table 2. Largest specimen is female, 207.2 mm SL, however, this species can grow to 250 mm SL (Loiselle, unpublished data). Snout short, 20.5–27.3% HL (mean 24.5% HL), dorsal head profile straight to dorsal fin origin. Jaws more or less isognathous, becoming slightly prognathous in medium to large individuals. Posterior tip of maxilla barely extending beyond anterior orbital margin. Preorbital weakly serrate; preopercle more strongly so. Two short spines at the angle of the opercle, lower slightly longer than upper. Gill rakers on lower limb of first gill arch: 18 (5), 19 (11), or 20 (3).

Both jaws with a single outer row of minute, somewhat recurved unicuspid teeth. An inner band of villiform teeth, 3–4 rows in width, situated rostrally and tapering posteriorly to a single row. Teeth of outer row only a little longer than those of inner band. Small patches of fine conical teeth present on vomer and palatines. Endopterygoid and ectopterygoid tooth patches lacking or weakly developed.

Head and body covered from mid-orbit to caudal fin with regularly imbricate, ctenoid scales. Scales on chest and venter slightly smaller than those on flanks and dorsum. Scale rows present on cheek: 2 (1), 3 (9) , or 4 (8). Pored scales in lateral line: 42 (8), 43 (5), 44 (4); often with 5–7 small pored scales extending onto base of caudal fin. Lateral line dips downward to midlateral line at tenth scale caudad of origin. Scale rows from origin of anal fin to base of dorsal fin: 15 (9), 16 (2), 17
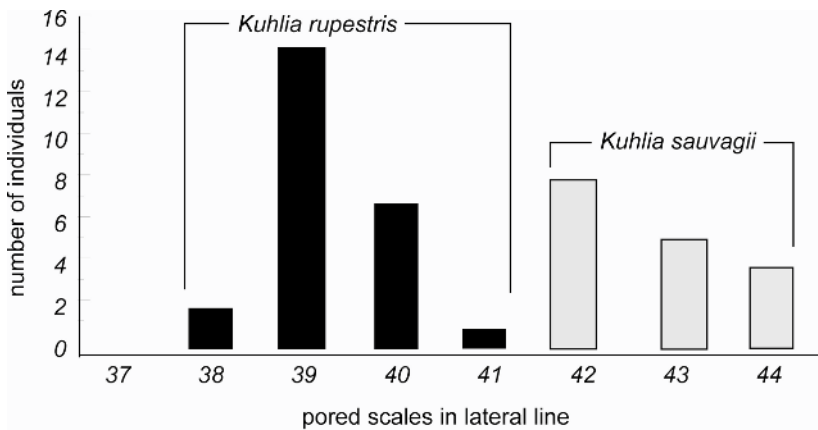
Fig. 2. Numbers of pored scales along the lateral line in individuals of *K. sauvagii* and *K. rupestris.*

(3). Five scale rows between origin of lateral line and mid-dorsal line. Five scale rows between pectoral insertion and anal fin origin. Circumpeduncular scales: 22 (2) or 24 (16). Dorsal and anal scaly sheaths well-developed, basal 25–30% of caudal fin heavily scaled.

Dorsal: X, 11 (17). Dorsal-fin origin at, or slightly posterior to, pelvic insertion. Anal: III, 10 (17). Pectoral fin with 14 (11), 15 (4) or 16 (2) rays. Pectoral and pelvic fins short and rounded. Pelvic fins do not extend to urogenital papilla when adducted. Caudal weakly emarginate, and fan-shaped; never strongly forked. Vertebrae. Vertebral count of 25 (10 + 15) in all specimens.

COLORATION IN LIFE (plate 1D): Snout, top of head, and dorsum pale beige. Lips, cheek, opercle, and flanks silvery beige with golden highlights; venter silvery white. Flanks sparsely speckled with irregular chestnut to maroon spots. Opercle and cheek usually devoid of spotting. A row of somewhat larger reddish-brown spots variably present on squamous sheath of anal fin. Spines and soft rays of dorsal fin grayish olive, with inter-radial membrane golden beige. Spinous dorsal marked with an extensive pattern of chestnut to maroon inter-radial spots and streaks. A less extensive patterning of smaller reddish-brown inter-radial spots present basally in soft dorsal fin. In individuals less than 70.0 mm SL, caudal fin silvery yellow with diffuse black blotch on each lobe and pattern of dark reddish-black inter-radial streaks medially. In larger individuals, black blotches in caudal lobes become diffuse and replaced by series of dusky-brown to black inter-radial streaks. Overall caudal fin coloration of adults is a pattern of alternating silvery-yellow and reddish-brown inter-radial streaks against a grayish background. Anal fin yellow basally, clear gray distally, and marked with a variable pattern of dark reddish-brown inter-radial spots. Pelvic fins clear yellow basally, dusky distally. Pectoral fins hyaline. Iris of eye light brown with wide orange-red crescent-shaped marking covering upper half of eye.

COLORATION IN PRESERVATIVE: Snout, top of head, and dorsum brownish beige. Lips, cheek, opercle, and flanks beige; venter dirty white. Pattern of dark spotting on head and body as described for living individuals, but spots light chestnut. Dorsal fin spines pale gray; membrane and all remaining unpaired fins clear yellow. Dark markings of unpaired fins as described for living individuals. Pelvic fins off-white; pectoral fins hyaline. Iris of eye silvery beige, with reddish-brown crescent-shaped marking in upper half.

DISTRIBUTION: *Kuhlia sauvagii* is endemic to Madagascar, where it is restricted to rivers draining the eastern coast of the island (fig. 1).

NATURAL HISTORY: *Kuhlia sauvagei* is found from sea level to 500 m a.s.l. Juveniles are typically found in estuarine habitats and in the lower reaches of rivers, where they often occur syntopically with *K. rupestris*. When the two species are found together, juveniles of *K. sauvagii* appear to be less social and associate with the substrate more closely than do those
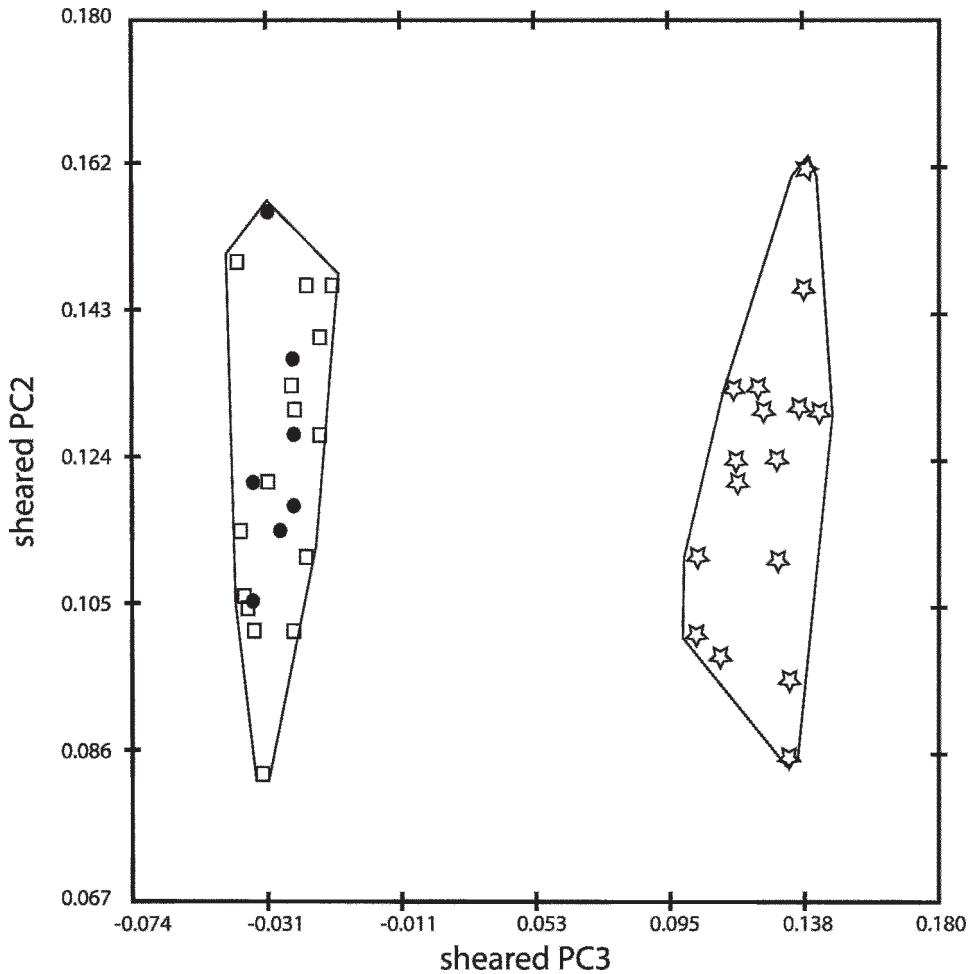
Fig. 3.   Scatterplot of sheared second and third PC scores of 17 log-transformed morphometric variables for *Kuhlia sauvagii* (open stars) and *Kuhlia rupestris* samples from Réunion (black circles) and Madagascar (open squares).

of *K. rupestris*, rarely rising more than a third of the way up into the water column. Subadult and adult *K. sauvagii* are most often found above the first significant set of rapids. It is unclear what factors operate to limit the upstream penetration of *K. sauvagii* in basins such as the Rianila, which lack major physiographic barriers to fish movement. It is worth noting in this context that west of the town of Beforona, the highest point on the Rianila from which *K. sauvagii* has been reported (Kiener, 1963), the stream gradient increases noticeably, and water temperatures are markedly cooler. This species has essentially the same habitat preferences as does its more

widely distributed congener, but large individuals of *K. sauvagii* appear to frequent areas of strong current to a greater extent than do *K. rupestris* of the same size. There are no significant differences in diet in the two species, and they are vulnerable to the same suite of predators.

Nothing is known of the reproductive biology of *K. sauvagii*. Its endemic character and the fact that all specimens <50.0 mm SL were collected from the lowermost reaches of rivers suggests an amphidromous life-history pattern coupled with a very brief planktonic larval stage. Existing holdings of the species are too limited to permit any conclusions to

Variable	Sheared PC2	Sheared PC3
Standard length	0.044	0.069
Head length	−0.019	−0.148
Snout length	−0.055	−0.427
Upper jaw length	−0.144	−0.330
Orbit diameter (horizontal)	0.067	−0.422
Interorbital width	−0.008	0.290
Preorbital depth	−0.090	−0.176
Body depth (maximum)	0.609	0.053
Predorsal length	0.063	0.050
Prepelvic length	0.021	0.078
Preanal length	0.394	−0.072
Dorsal fin base	−0.198	0.052
Anal fin base	−0.421	0.159
Caudal peduncle length	−0.289	0.004
Caudal peduncle depth	−0.136	0.331
Dorsal spine length	0.307	0.254
Anal spine length	−0.061	0.412

be drawn with regard to reproductive seasonality.

CONSERVATION STATUS: Unlike many of Madagascar's endemic fishes, *Kuhlia sauvagii* is widely distributed throughout the eastern versant of the island, and according to local peoples, its numbers do not appear to have diminished significantly over the past few decades. Following the criteria employed by the World Conservation Union, these observations would ordinarily result in its classification as a low-risk species (Raminosoa et al., 2002). However, in view of its habitat preferences, the known impact of deforestation on the water quality of the island's rivers, and the ongoing loss of forest cover east of the hydrographic divide, it would appear more prudent to classify *K. sauvagii* as a vulnerable species whose status should be monitored on a regular basis.

DISCUSSION

Kuhlia sauvagii and *K. rupestris* differ in a series of features of adult pigmentation patterning and coloration, and the two can readily be distinguished on the basis of a non-overlapping difference in the number of pored scales in the lateral line (42–44 in *K. sauvagii* vs. 38–41 in *K. rupestris*; fig. 2). To investigate species distinction further, a sheared principal components analysis of 17 log-transformed morphometric variables was undertaken. The scatterplot of sheared second and third PC scores indicates a clear separation of *K. sauvagii* and *K. rupestris* (fig. 3). No separation between the *K. rupestris* samples from Réunion and those from Madagascar indicated that—for these regions, at least—*K. rupestris* is a morphologically homogeneous entity. In the analysis, sheared PC2 loaded heavily for body depth while the variables that loaded most heavily on sheared PC3 were snout length, orbit diameter, and anal spine length (table 3).

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