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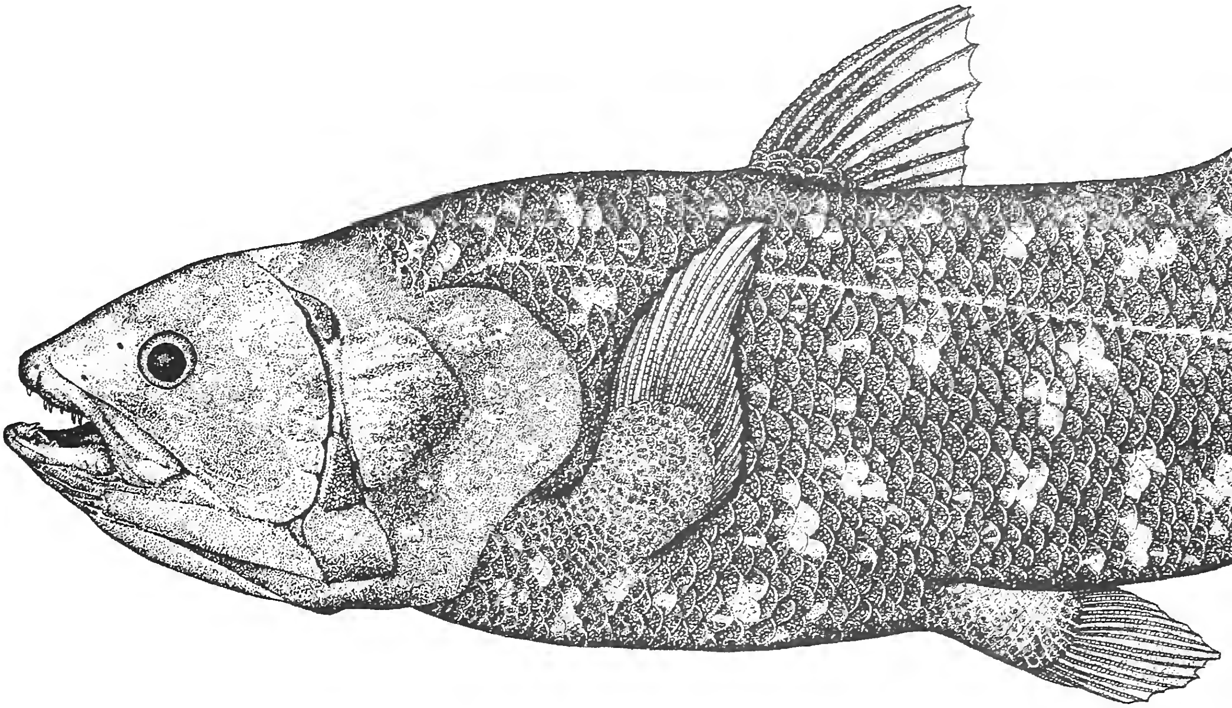

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Margaret Mary Smith (1916–1987),
James Leonard Brierley Smith (1897–1968)
with their dog Marlin

The publication series (Monographs, Bulletins & Special Publications) of SAIAB (formerly the JLB Smith Institute of Ichthyology), in its new format, honours James Leonard Brierley Smith and Margaret Mary Smith with the name Smithiana, in recognition of their many years of devoted service to African aquatic biology. Their life's work, a team effort, established modern ichthyology in southern Africa and laid the groundwork for the expansion of aquatic biology throughout the region.

CONTENTS

Smithiana Bulletins and Monographs are publications of the South African Institute for Aquatic Biodiversity, for original scientific articles in the fields of taxonomy, systematics, ethology, ecology, biogeography and conservation of the fishes of Africa and its surrounding waters. Priority will be given to papers by staff and associates of the Institute. Manuscripts from outside the Institute will be considered if they are pertinent to the work of the Institute or use the Institute's collections.

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The commercial fishery of the middle Nyong River, Cameroon: productivity and environmental threats

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Abstract. Fishing methods, catches, fish species diversity, water quality and diets were examined in the middle Nyong River basin of south-central Cameroon over five years. Out of 79 indigenous species from the upper and middle Nyong in museum collections, 17 indigenous species added in this study (total = 100) and two feral alien species, only 38 are regularly captured by commercial fishers, and only 18 of these are sufficiently abundant and large enough to be of importance as food fish. Two of the most important are the alien *Oreochromis niloticus* and *Heterotis niloticus*. In the 2004/2005 season, fishers fished an average of 181 days per year, with a CPUE = 3.4 kg/fisher/day. Extrapolated, an estimated 37,000 fishers catch 24,500 t of fish per annum (24.6 kg/ha of watershed). Despite intensive sampling, 17 species previously reported for the Nyong, were not recaptured during this study. Most commercially important species, are detritus and/or aquatic arthropods feeders, with a high level of dietary overlap, but observed overlap between the most common commercial species and the introduced aliens is low. Although quantitative data are lacking on the state of the ecosystem at the time of earlier fish collections, there is circumstantial evidence that indigenous species may have suffered from competition with introduced aliens and/or changes in the ecosystem resulting from poor land use management and the use of pesticides in fishing.

Keywords: Lower Guinea Rainforest, fish biodiversity, dietary overlap

INTRODUCTION

The Nyong River is in the Lower Guinea Equatorial Forest, one of the world's oldest and most biodiverse ecosystems, with about 500 species of fish (Brummett & Teugels 2004; Stiassney *et al.* 2007), 71% of which are endemic (Hugueny & Lévêque 1994). The Nyong flows 520 km west and south from its point of origin to the east of Abong-Mbang in the tropical rainforest of east-central Cameroon, discharging an annual average of 443 m^3/sec into the Gulf of Guinea at the small island fishing village of Behondo (Fig. 1). The headwaters lie very close to those of the Congo River Basin, and hence the two systems share a certain amount of biodiversity (Teugels & Guégan 1994). The major affluent streams to the Nyong are the rivers M'foumou (entering from the North) and So'o (entering from the South), both contributing to the river in its middle reaches. The basin covers approximately 27,800 km^2 between 2°48′ and 4°32′ N latitude and 9°54′ and 13°30′ E longitude (Hugueny 1989). The climate is transitional equatorial with one short (July-August) and one long (December-March) dry season alternating with rains (Fig. 2).

The Nyong is a typical "blackwater" river, with a mean pH of 6.2, hardness of <10 mg/l (as $CaCO_3$) and electrical conductivity between 20 and 30 μS/cm. Water temperature is always between 20 and 24° C. The water is naturally clear and tea-coloured as a result of the low dissolved nutrient concentration, low light (due to narrowness of valleys and canopy cover) and high tannin concentrations leaching from the large amount of allochthonous vegetative matter that falls or flushes into the water from the surrounding forest (Welcomme & de Merona 1988).

As for most of the Lower Guinea forest, there exists for the Nyong River little biological or ecological information, nor any sort of practical management plan that might track changes in the ecosystem. The Nyong Basin has already lost an estimated 46% of its primary forest to logging and conversion to agriculture and continues to lose forested watershed at an average rate of 7% per year (Revenga et al. 1998). Logging in Central Africa is undertaken in a largely irresponsible manner that alters stream courses and increases runoff and siltation. In addition, roads, sawmills and other infrastructure associated with logging attracts people into the forest, resulting in wholesale transformation of the ecosystem (Burns 1972; Garman & Moring 1993).

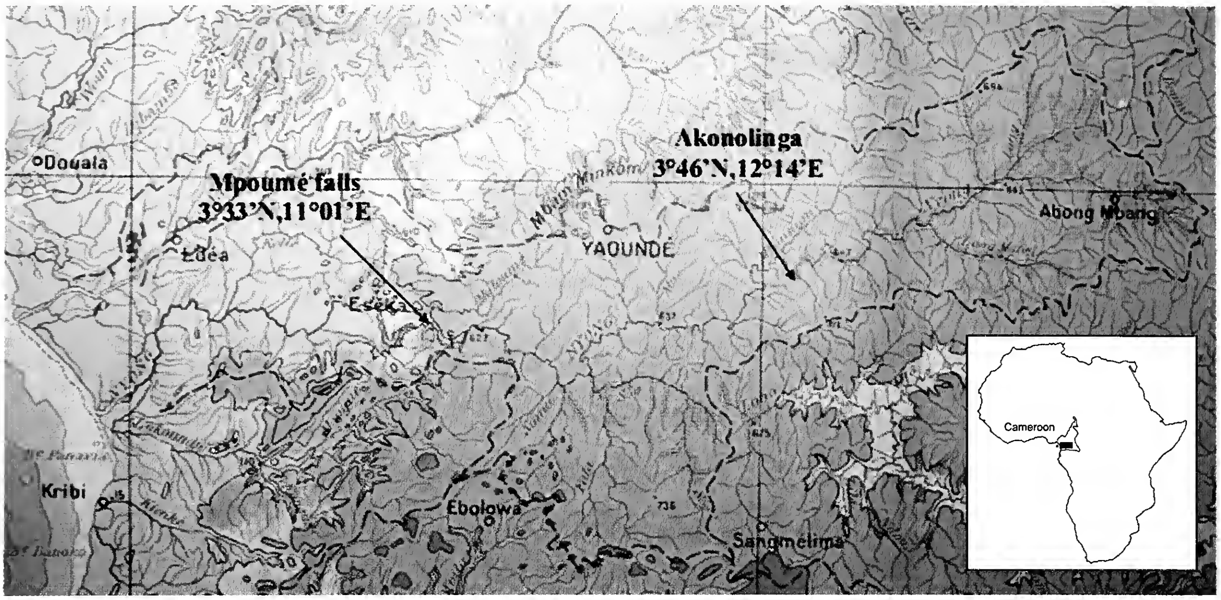

Fig. 1. Map of the Nyong River basin in Cameroon.

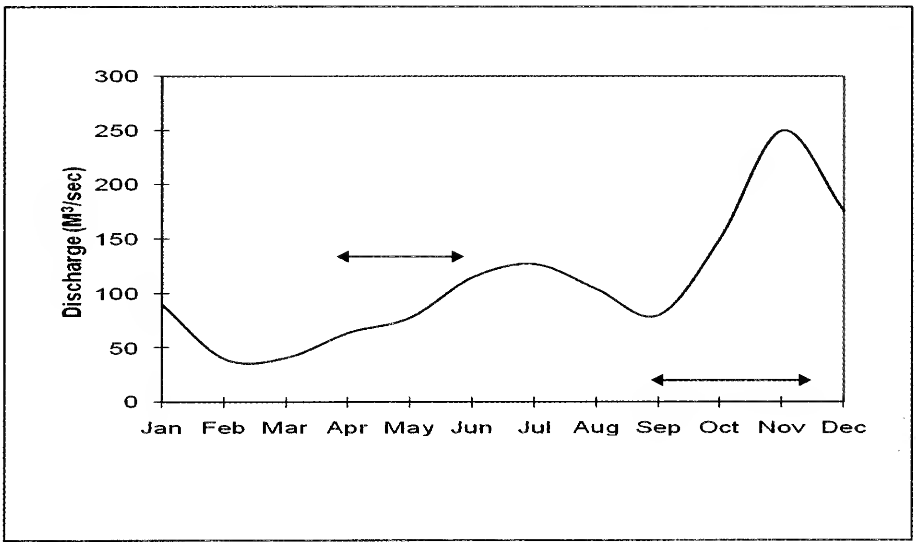

Fig. 2. Seasonal discharge of the middle Nyong River at Mbalmayo, indicating the reported timing of peak fishing (discharge data from SAGE 2003).

Improper use of agricultural pesticides has become widespread as a result of expanding small-scale oil palm cultivation, and is even used as a fishing method. Insecticides can be highly destructive of the entire food web and human deaths have been reported as a result of eating poisoned fish (du Feu 2001).

In addition, a number of alien species have been introduced, accidentally (by escape from aquaculture facilities) or on purpose to enhance capture fisheries, into the Nyong. These robust and aggressive species (*Oreochromis niloticus*, *Clarias gariepinus*, *Cyprinus carpio* and *Heterotis niloticus*) are highly invasive and could represent a serious threat to indigenous biodiversity.

To better understand the fishery and attempt to identify potential threats to this and other tropical rainforest rivers, a five-year study of fishing gears and techniques, fish diversity in commercial catches and the diets of both indigenous and introduced species was carried out on the middle Nyong River in southern Cameroon.

MATERIALS AND METHODS

The section of the river here designated as the middle Nyong (Fig. 3b) is that part that passes through rainforest between the altitudes of 500 and 1000 m above MSL from a point about 10 km downstream from Makak (3°33′ N, 11°01′ E) where the Mpoumé falls separate the middle from the lower reaches (Fig. 3c), up to Akonolinga (3°46′ N, 12°14′ E) above which the upper river occupies a large seasonal floodplain (Fig. 3a).

Monthly fish sampling was conducted between February 2001 and February 2006 at eight sites in the middle Nyong watershed: Akonolinga (3°46′ N, 12°14′ E), Anga'a (3°47′ N, 11°31′ E), Mbalmayo (3°30′ N, 11°30′ E), Pont So'o (3°19′ N, 11°29′ E), N'kol Ebae (3°19′ N, 11°26′E), N'tang (3°15′ N, 11°23′ E), Avèbe (03°20' N, 11°30' E) and Minlaba (3°11' N, 11°19' E). Samples consisting of at least five individuals each of all species available on each sampling date and at each sampling site were collected from commercial fishers, who employ a range of capture methods.

All samples were measured (TL) to the nearest mm, fixed in 95% ethanol and identified in the laboratory using Daget (1984), Vivien (1991), Mbega & Teugels (2003), Paugy *et al.* (2003), Geerinckx *et al.* (2004), Ng (2004) and Stiassny *et al.* (2007). Fishes that could not be identified from this literature were sent to the Belgian Royal Museum for Central Africa (MRAC) and/or the American Museum of Natural History (AMNH) for identification. Species regularly appearing in catches and marketed were deemed "commercial" while those occurring only infrequently and/or predominantly used for home consumption were considered by-catch.

To quantify the catch, a 13-month study (July 2004 – July 2005) was conducted among fishers in the villages of Pont So'o, N'kol Ebae, N'tang, Avèbe and Minlaba, which are representative of the majority of small fishing communities in the middle Nyong basin. Fishers in these villages exploit a number of rivers in the area, most importantly the Nyong, So'o, Fala, Bissi, Ossoe Koss, Soumou, Yenne, Nsono, N'tang Mebe Ossoe Beva'a, Akoumbegue, Ossoe Bissegué and Mimiteme. Of the 99 people reported by the local population to be fishing full-time in the area (Table 1), 27 agreed to participate in the creel survey and five (one from each village) volunteered as data collectors and were equipped with a spring balance and trained in completion of a basic survey form that captured data on weight and value of the catch by species.

During each sampling visit, visual observations were made of fishing activities, gears employed and the general condition of the river. Structured interviews were used to systematically collect information from fishers related to catch and environmental trends. In addition, measurements of temperature and dissolved oxygen were made with a Sentry III Oxygen/Temperature Monitor, and water samples were collected for later measurement of electrical conductivity with a benchtop TPS 900C EC meter.

To quantify the natural diet of commercially important species,

Fig. 3. The upper Nyong River at Ayos in June (A), middle at Mbalmayo in March (B), and lower at Song Abwé in October (C). Photos: R E Brummett.

Table1. Number of households, fishers, fish traders and canoe builders in five typical fishing communities engaged in the commercial fishery of the middle Nyong River basin.

Village	Households (avg. pers.)	Full-time fishers Male	Female	Fish traders	Canoe builders
Pont So'o	9 (16.1)	37	4	28	3
N'tang	5 (8.0)	17	2	12	1
Avebe	6 (11.7)	9	0	17	2
N'kol Ebae	7 (10)	18	7	10	0
Minlaba	8 (12.3)	9	3	0	0
Total	**35 (11.7)**	**83**	**16**	**67**	**6**

stomachs of 24 individuals (two fish of each species per month between February 2001 and February 2002) were dissected and fixed in 10% formalin. For species with no true stomach (e.g. *Labeo lukulae*) the upper 5 cm of the digestive tract was taken. Stomach contents were analysed according to the frequency of occurrence method described by Hyslop (1980) and Bowen (1983). Ingested items were classified as detritus, plant material, insects (both adult and larval forms), aquatic crustaceans (primarily *Macrobrachium* spp) or fish. Data were recorded as a percentage of full stomachs containing one or more item from each food category represented. Statistica 4.5 (1993) software was used to perform cluster analysis to identify major food groups. The Schoener index (SI) (Schoener 1974) was used as an indicator of dietary overlap among species.

RESULTS AND DISCUSSION

The middle Nyong river is special in Cameroon for two important reasons: 1) Unlike the big coastal and larger river fisheries on the Sanaga and Benue Rivers which are dominated by foreign commercial fishers, predominantly from Mali and Nigeria, the middle Nyong river fishery is a traditional subsistence fishery operated by the indigenous population; and, 2) much of the southern portion of the middle Nyong basin (where our sampling was concentrated) drains seasonal swampforest, a critical spawning habitat for many rainforest river fishes.

Table 2. List of known indigenous species in the Nyong River (excluding those with marine affinity). Fish captured in this study are shown in bold font. Fish species not captured, but reported in the reference collections of the Royal Museum for Central Africa (RMAC), Tervuren, Belgium and/or the Muséum National de l'Histoire Naturelle, Paris or FishBase (2004) are shown in normal font. Species one would expect to have collected, but which did not appear in our samples are indicated with a question mark (?).

Alestes macrophthalmus	***Mastacembelus cryptacanthus***
Amphilius longirostris	*Mastacembelus niger*
Anaspidoglanis macrostoma	***Microctenopoma nanum***
Aphyosemion ahli	*Micropanchax camerunensis*
Aphyosemion bivittatum	***Microsynodontis batesii***
Aphyosemion cameronense	*Mormyrops anguilloides* ?
Aphyosemion exiguum	*Mormyrops caballus* ?
Aphyosemion loennbergii	***Mormyrus tapirus***
Aphyosemion splendopleure	*Nannaethiops unitaeniatus*
Barbus aspilus	*Nannocharax intermedius*
Barbus brazzai	***Nannocharax cf. rubrolabiatus***
Barbus camptacanthus	***Neolebias trewavasae***
Barbus guirali	*Neolebias unifasciatus*
Barbus holotaenia ?	***Opsaridium ubangiense***
Barbus jae	***Parailia occidentalis***
Barbus martorelli	***Parachanna obscura***
Benitochromis batesii	***Paramormyrops kingsleyae***
Bostrychus africanus	**Paramormyrops curvifrons**
Brienomyrus brachyistius	***Paranochromis « N'tem »***
Brycinus kingsleyae	***Parauchenoglanis altipinnis***
Brycinus longipinnis	***Parauchenoglanis balayi***
Brycinus macrolepidotus	***Parauchenoglanis longiceps***
Brycinus nurse	*Pelvicachromis taeniatus*
Bryconaethiops microstoma ?	*Petrocephalus christyi* ?
Chiloglanis cameronensis	***Petrocephalus microphthalmus***
Chrysichthys auratus	***Petrocephalus simus***
Chrysichthys nigrodigitatus	*Phenacogrammus major*
Chrysichthys nyongensis ?	***Phractura longicauda***
Clariallabes longicauda	*Procatopus similis*
Clarias camerunensis	*Prolabeops nyongensis*
Clarias jaensis	***Raiamas batesii***
Clarias longior ?	***Raiamas buchholzi***
Clarias pachynema	*Sarotherodon galilaeus sanagaensis* ?
Ctenopoma maculatum	***Sarotherodon mvogoi***
Distichodus notospilus	*Schilbe brevianalis*
Doumea « Cameroon »	*Schilbe grenfelli* ?
Epiplatys sangmelinensis	***Schilbe intermedius***
Epiplatys sexfasciatus	***Schilbe multitaeniatus***
Hemichromis elongatus	*Schilbe nyongensis* ?
Hemigrammocharax ocellicauda	***Synodontis batesii***
Hepsetus odoe	***Synotontis marmoratus***
Kribia kribensis	***Synodontis rebelilobesus***
Kribia nana	***Synodontis steindachneri***
Labeo annectens ?	*Synodontis tessmanni* ?
Labeo lukulae	***Tilapia margaritacea***
Labeobarbus rocadasi	*Tilapia mariae* ?
Labeobarbus batesii ?	***Tilapia nyongana***
Labeobarbus micronema ?	***Varicorhinus sandersi***
Malapterurus electricus	*Varicorhinus tornieri* ?
Marcusenius moorii	*Varicorhinus werneri* ?

Table 3. Fishing techniques and the species they target in the middle Nyong River, Cameroon.

Technique	Description	Targeted Species
Filet Cablé	Comprised of three layers of gill net of differing mesh sizes; an active gear resembling a trammel net but fished like a seine by groups of 4-5 fishers.	*Heterotis niloticus*
Gill Nets	12 to several hundred meters in length, 4 m depth and mesh sizes of 30-60 mm. Installed more or less permanently parallel to river banks and checked periodically.	Mormyrids, Alestids
Nlop Mekwel Mekos	Two baited hooks attached on short lines to the center of a pole, which is wedged in the weeds across routes frequented by fish.	*Parachanna obscura*
Adsegneng	A cane pole with appx. 30 cm of line and a size 13/14 hook (usually baited with soap), jammed into a mud bank overnight.	*Clarias, Schilbe*
Élong	Size 14/15 baited hook on a weighted 6-10 m line thrown into the river and anchored to the bank or to overhanging branches	Large Cyprinids, Catfish
Ôngaè	Up to 50 m hook line with hooks every 2 m baited with crab claws and strung from bank to bank or from the bank to a large mid-water boulder.	Large *Barbus*
Méfog	A baited size 13/14 hook on 1-2m of line attached to a cane pole, fished by wading along the bank and flicking the baited hook under cut banks or into holes.	*Clarias*
Agara	A long (2.5m) version of Méfog used in rapids.	*Schilbe*
Nlop Bekara	Manioc attached to a cord, left overnight among boulders near rapids.	Crabs
Mbere	A weighted line attached to a wooden float with a worm-baited hook on 30 cm trailer.	All species, esp. *Parauchenoglanis*
Bap	Cane pole with a baited hook, mostly used by children.	*Opsaridium, Brycinus, Barbus, Petrocephalus, Schilbe*
Nsong	A large open-ended basket installed in fast water; facing upstream, fish are captured and held in place by water pressure.	Small individuals of all species
Aya	Basket trap made of reeds or bamboo with a conical entrance, anchored in low order tributaries by women to supplement household food supplies.	*Macrobrachium*, crabs, Misc. small fishes
Nkoé	A larger, longer version of Aya baited with manioc.	Crabs
N'dayirga	Pole with a baited hook on a trailer jammed into bottom in stagnant water.	*Clarias*
N'touk	A garden basket with worms or other bait attached to the interior and lowered into still water at night. When fish are felt bumping around, the basket is slowly raised.	*Clarias*
Ebam	Handline with multiple small hooks and weighted with a stone to facilitate casting.	Mormyrids
Alok	Small earthen dams across low order forest streams. Several dams are constructed in series, effectively blocking water flow. Women then bucket out any remaining water, catching the fish by hand or with the help of baskets.	Smaller individuals + small species, esp. *Barbus, Paramormyrops, Clarias*
Alam	Dam constructed of branches and boulders, with a chute in which fish are trapped as waters rise and recede in the rainy seasons (Figure 4). Used exclusively in the So'o watershed.	Most species, esp. *H. niloticus, mormyrids, Raimas*

Species Diversity

In total, 15 families, 38 genera and 56 indigenous species were recorded (Table 2). Of these, only 18 (including two alien species, *Heterotis niloticus* and *Orochromis niloticus*) are currently important in the commercial catch. *H. niloticus* and *O. niloticus* are indigenous to the Niger River and Lake Chad basins and were stocked and/or escaped from aquaculture facilities in the Nyong watershed in the late 1950s and early 1960s and have since become established (Depierre & Vivien 1977; Welcomme 1988).

Hugueny (1989) reported 79 exclusively freshwater species in the collections of the MRAC, the French Muséum National d'Histoire Naturelle (MNHN) and the Natural History Museum, London (BMNH). On the list of Nyong River species held at the MRAC alone there are 64 species (Jos Snoeks, MRAC, pers. comm., Jan. 2004). At the MNHN in Paris, there are an additional 15 species not on the MRAC list, making a total of 79 (D. Paugy, MNHN, personal communication, October 2005). In contrast, Teugels & Guégan (1994) recorded 107 species. Although Teugels and Guégan did not present a list of species, a large part of the difference in count is probably due to their inclusion of euryhaline fishes, which can make up as much as 20–50% of the fish fauna in the lower reaches of African coastal rivers (Djama 2001; Teugels, Reid & King 1992). In a brief visit made to the lower Nyong in May 2005, representatives of several typically marine families, i.e. Carangidae, Clupeidae, Cynoglossidae, Haemulidae, Lutjanidae, Polynemidae, Sciaenidae and Scombridae were collected from fishers' catches.

Of the 83 species on the MRAC and MNHN lists, 38 were recaptured in 2001–2006 (Table 2). In addition, 17 species captured in 2001–2006 were not previously on the list (*Alestes macrophthalmus, Bostrychus africanus, Brycinus longipinnis, Brycinus nurse, Chrysichthys auratus, Distichodus notospilus, Doumea* "Cameroon", *Mastacembelus cryptacanthus, Microsynodontis batesii, Nannocharax* cf *rubrolabiatus, Parailia occidentalis, Paramormyrops curvifrons, Parananochromis* "Ntem", *Phractura longicauda, Schilbe intermedius, Synodontis marmoratus & Varicorhinus sandersi*) bringing the total to 96. Including the two aliens, the current list includes 98 species.

Every effort, including visits to MNHN, MRAC and the AMNH and extensive consultations with other taxonomists, was made to update and correct taxonomic errors and changes on the list. Four errors (*Micralestes humilis, Paramormyrops sphekodes, Parananochromis caudifasciatus* and *Parauchenoglanis guttatus*) were found on the original lists (Stiassny et al. 2007), and considering the uncertainty surrounding the fish fauna of the region others undoubtedly persist. Nevertheless, there remains a substantial discrepancy between the species caught in the 2001–2006 survey and those reported to be in the river by earlier observers.

As the principal method of sampling was based on the gears used in the commercial fishery, it could be that gear selectivity accounts for some of this discrepancy. Fishers tend to concentrate their effort on the main river and do not target very small species. Although a number of smaller and rarer species were taken, of the

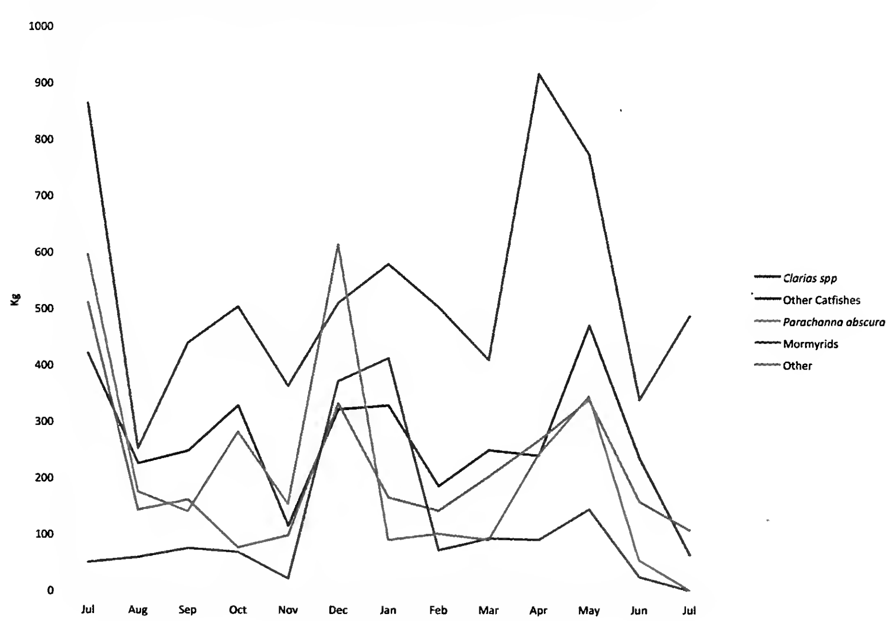

Fig. 4. Monthly catch by species group in five villages of the Middle Nyong River Basin in 2004/2005.

fish on the combined list (Table 2) that were not caught in 2001–2006, 25 species seldom exceed 10 cm in total length and were generally unknown to local fishers interviewed and shown photographs. In addition, reclusive or predominantly swamp species such as *Malapterurus electricus* and *Mastacembelus niger* might be expected to be infrequently captured in a fishery focused on the main river channels. However, sampling intensity or gears alone cannot explain why some species were not recaptured, as many of the missing species are very similar in size and shape to the species that were captured and 17 extra species were added to those on the earlier lists.

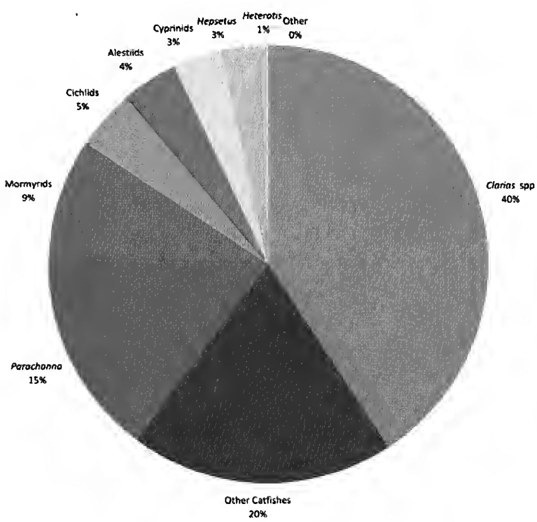

Fig. 5. Catch composition from a survey of five villages in the middle Nyong River basin in 2004/2005).

THE FISHERY

The main gears used in the middle Nyong basin are shown in Table 3. The large amount of allochthonous wood and boulders in the streambed constrains the use of active fishing gears. Traditional indigenous methods rely on dams, basket traps and various hook-lines. Gill-nets, introduced more recently, are the dominant gear used by full-time fishers.

Fishers can be differentiated as professional/full-time (most of whom are Malians based in the towns of Mbalmayo and Akonolinga and who target *Heterotis niloticus*) or seasonal fishers. The majority are seasonal, fishing as part of a diverse livelihood strategy that includes hunting, small livestock and both cash and food crops. Of the 27 fishers participating in the 2004/2005 catch survey, seven (26%) were full-time and the rest were seasonal. On average, fishers fish about 181 days per year (full-time fishers fish about 288 days each, while seasonal fishers fish about 144 days), capturing an average of 614 kg of fish (Fig. 4). Catch per unit of effort (CPUE) in the area sampled is thus 3.4 kg/fisher/fishing day. Average village selling price for fresh fish is fcfa 500 per kg (approximately US$ 2.00 in 2007); fishing households thus gross an average of something on the order of fcfa 1.37 million annually from fishing (including household consumption, not measured in this study), compared to the Cameroonian average gross income of fcfa 585,000 reported by the World Bank in 2006 (http://devdata.worldbank.org/AAG/cmr_aag.pdf).

Leaving out the large urban centers of Mbalmayo and Yaoundé, the population density in the middle Nyong Basin is estimated at 17 persons per km²

Fig. 6. A fish dam, or alam, constructed on the Fala River, a tributary of the So'o in the central Nyong watershed. Fish migrating upstream to spawn pass over the dam which is submerged at high water. As water levels drop, adult fish returning from the spawning grounds are trapped, while smaller individuals pass through. Inset shows a detail of the chute where fish are stranded. (Photo: R E Brummett.)

Fig. 7. Seasonal variation in water clarity in the Nyong River basin. During the dry season (A), water is clear. Following rains (B) exposure of soil in the watershed due to logging, farming and associated road construction results in increased silt loads. (Photo: R E Brummett.)

(Essama-Nssah & Gockowski 2000) spread over 10,300 km^2 (37% of the entire Nyong basin). If fishing practices in the five villages and catches in the 2004/2005 survey can be considered representative, about 40,000 full-time fishers catch an estimated 24,500 t of fish per annum from the middle Nyong River fishery (2.5 t/km^2 or 25 kg/ha of watershed), somewhat higher than catches of 16 kg/ha of watershed in the upper Cross River, a system similar to the Nyong, estimated from a frame survey conducted in October-December 2000 (Mdaihli *et al.* 2003).

The main fishing season is from September through December when river levels are increasing (Fig. 2) and many species are undertaking upstream migrations into flooded swampforest to spawn (Munro *et al.* 1990). A second peak occurs in April/May. A total of 25 species were recorded in the professional catch, the bulk of the catch is clariid catfishes and *Parachanna obscura* (Fig.

Table 4. Percentage occurrence of different food items in the stomachs of 18 species of fish most commonly captured in the Nyong River, Cameroon (TL = Total Length ± Standard Deviation).

	Brycinus macrolepidotus	*Brycinus kingsleyae*	*Hemichromis elongatus*	*Oreochromis niloticus*	*Clarias camerunensis*	*Chrysichthys nigrodigitatus*	*Anaspidoglanis macrostoma*	*Parauchenoglanis longiceps*	*Labeo lukulae*
Number Stomachs	10	140	14	10	10	33	10	10	112
Full stomachs	8	105	9	10	10	10	6	10	32
TL Range (mm)	240-330	111-155	123-145	180-326	199-370	162-305	210-300	224-315	235-340
TL Average ± SD	279.2 ± 45.8	138.1 ± 6.0	137.6 ± 8.4	224 ± 46.2	257 ± 21.4	237.1 ± 36.3	253.8 ± 36.8	285.6 ± 25.4	292.7 ± 24.6
Detritus	-	11	-	100	100	100	-	-	16
Plant Material	-	-	-	40	-	-	-	-	100*
Insects	75	56	67	12	100	90	75.0	86	-
Aquatic Crustacea	50	51	-	3	83	-	100	43	-
Fish	-	-	70	-	-	-	10	14	-

* *L. lukulae* stomachs contained mostly epiphytic algae grazed from submerged surfaces.

	Raimas batesii	*Hepsetus odoe*	*Brienomyrus brachyistius*	*Marcusenius moorii*	*Mormyrus tapirus*	*Parachanna obscura*	*Petrocephalus simus*	*Heterotis niloticus*	*Schilbe intermedius*
Number Stomachs	10	16	10	54	10	21	121	65	22
Full stomachs	8	4	10	35	10	13	73	15	10
TL Range (mm)	191-235	257-300	130-140	142-217	393-405	238-399	70-95	210-800	192-263
TL Average ± SD	213.6±24.9	274.4 ± 13.1	135.0 ± 7.1	154.5 ± 36.7	400.0 ± 6.2	296 ± 23.1	81.3 ± 4.3	578.2 ± 196.5	231.0 ± 21.5
Detritus	-	-	50	86	100	-	17.1	100	80
Plant Material	-	-	-	-	-	-	-	100	-
Insects	100	-	100	69	100	34	100	27	50
Aquatic Crustacea	-	-	27	14	80	-	12	7	-
Fish	47	100	-	-	-	100	-	-	-

5).

Fishers reported that catches have remained more or less steady over recent years, in some cases actually increasing with the availability of gill netting and fish hooks. Although not yet having a major impact on the fish catches of the villages sampled in the middle Nyong, fishers more generally report a gradual shift in emphasis from indigenous species to the introduced *O. niloticus* and *H. niloticus* since their introduction at Akonolinga in the early 1960s (Depierre & Vivien 1977; Abina 2005).

Missing Species

Despite gear selectivity, 17 species were not captured in 2001-2006 although they reach commercial sizes and are found in the same habitats as those species which were captured. These include species of *Clarias, Chrysichthys, Labeo, Labeobarbus, Mormyrops, Parauchenoglanis, Sarotherodon, Schilbe, Synodontis* and *Varicorhinus*, some of which reach sizes of >50 cm and weights >10 kg and which were previously reported as important components of the fishery by Depierre & Vivien (1977). When presented with a list and photos of the missing species, fishers reported that *Labeo annectens, Labeobarbus batesii, Labeobarbus micronema* and *Synodontis rebeli* in particular were much more common in the past. During August (one of the peak fishing seasons) of 2006, a two-week expedition of eight fishers and two of the authors fished the area between the confluence of the So'o River and the town of Mbalmayo specifically to capture the missing species. Using every traditional fishing method shown in Table 2, *Barbus guirali, Clariallabes longicauda* and *Paramormyrops curvifrons*, previously missing, were added to the list, but none of the other missing species were captured.

In recent years, substantial habitat modification associated with rural development in the Nyong Basin, could have affected species which were once abundant (Abina 2005). Observation of the Nyong

Table 5. Schoener index (SI) of dietary overlap for 18 commercially important fish species from the Nyong River, Cameroon. Values for the introduced alien species *Oreochromis niloticus* (4) and *Heterotis niloticus* (17) are in bold font. 1 = *Brycinus macrolepidotus*, 2 = *Brycinus kingsleyae*, 3 = *Hemichromis elongates*, 4 = *Oreochromis niloticus*, 5 = *Clarias camerunensis*, 6 = *Chrysichthys nigrodigitatus*, 7 = *Anaspidoglanis macrostoma*, 8 = *Parauchenoglanis longiceps*, 9 = *Labeo lukulae*, 10 = *Raimas batesii*, 11 = *Hepsetus odoe*, 12 = *Brienomyrus brachyistius*, 13 = *Marcusenius moorii*, 14 = *Mormyrus tapirus*, 15 = *Parachanna obscura*, 16 = *Petrocephalus simus*, 17 = *Heterotis niloticus*, 18 = *Schilbe intermedius*.

Fish	1	2	3	**4**	5	6	7	8	9	10	11	12	13	14	15	16	**17**	18
1		0.85	0.36	**0.25**	0.21	0.68	0.70	0.84	0.21	0.40	0.13	0.51	0.36	0.17	0.06	0.33	**0.46**	0.98
2	0.85		0.64	**0.45**	0.59	0.77	0.78	0.84	0.47	0.62	0.46	0.73	0.69	0.56	0.55	0.64	**0.35**	0.91
3	0.36	0.64		**0.33**	0.29	0.52	0.58	0.71	0.37	0.86	0.76	0.55	0.57	0.47	0.68	0.54	**0.21**	0.67
4	0.25	0.45	0.33		0.48	0.21	0.23	0.33	0.60	0.31	0.36	0.50	0.70	0.67	0.30	0.59	**0.80**	0.36
5	0.21	0.59	0.29	**0.48**		0.68	0.62	0.58	0.08	0.43	0.04	0.74	0.72	0.81	0.14	0.75	**0.38**	0.62
6	0.68	0.77	0.52	**0.21**	0.68		0.94	0.81	0.24	0.61	0.28	0.67	0.52	0.50	0.37	0.58	**0.11**	0.85
7	0.70	0.78	0.58	**0.23**	0.62	0.94		0.82	0.25	0.60	0.34	0.61	0.53	0.43	0.43	0.52	**0.12**	0.84
8	0.84	0.84	0.71	**0.33**	0.58	0.81	0.82		0.35	0.78	0.46	0.77	0.64	0.59	0.56	0.68	**0.23**	0.93
9	0.21	0.47	0.37	**0.60**	0.08	0.24	0.25	0.35		0.34	0.46	0.35	0.37	0.27	0.37	0.33	**0.71**	0.39
10	0.40	0.62	0.86	**0.31**	0.43	0.61	0.60	0.78	0.34		0.62	0.69	0.56	0.62	0.54	0.68	**0.19**	0.71
11	0.13	0.46	0.76	**0.36**	0.04	0.28	0.34	0.46	0.46	0.62		0.31	0.33	0.23	0.91	0.29	**0.17**	0.43
12	0.51	0.73	0.55	**0.50**	0.74	0.67	0.61	0.77	0.35	0.69	0.31		0.80	0.83	0.37	0.91	**0.39**	0.77
13	0.36	0.69	0.57	**0.70**	0.72	0.52	0.53	0.64	0.37	0.56	0.33	0.80		0.87	0.32	0.88	**0.59**	0.67
14	0.17	0.56	0.47	**0.67**	0.81	0.50	0.43	0.59	0.27	0.62	0.23	0.83	0.87		0.19	0.92	**0.57**	0.60
15	0.06	0.55	0.68	**0.30**	0.14	0.37	0.43	0.56	0.37	0.54	0.91	0.37	0.32	0.19		0.28	**0.12**	0.52
16	0.33	0.64	0.54	**0.59**	0.75	0.58	0.52	0.68	0.33	0.68	0.29	0.91	0.88	0.92	0.28		**0.48**	0.68
17	0.46	0.35	0.21	**0.80**	0.38	0.11	0.12	0.23	0.71	0.19	0.17	0.39	0.59	0.57	0.12	0.48		0.26
18	0.98	0.91	0.67	**0.36**	0.62	0.85	0.84	0.93	0.39	0.71	0.43	0.77	0.67	0.60	0.52	0.68	**0.26**	
Avg.	0.44	0.64	0.54	**0.44**	0.48	0.55	0.55	0.64	0.36	0.56	0.39	0.62	0.60	0.55	0.39	0.59	**0.36**	0.66

River during sampling revealed periodic substantial declines in water quality, especially increasing sediment loads, as a result of human activities in the forest (Fig. 7). These declines are particularly severe when some of the most commercially important species are, according to the fishers, undertaking reproductive migrations: early in the rainy seasons of March-June (*Brycinus, Chrysichthys, Labeo, Labeobarbus, Marcusenius*) and September-November (*Brienomyrus, Petrocephalus*). According to Munro *et al.* (1990), *Schilbe, Synodontis, Clarias, Distichodus* and *Alestes* are other important species reported to spawn in the wet seasons and may thus be vulnerable to sedimentation during early life stages. In undisturbed sites, water was clear brown with a mean temperature of 23.5°, dissolved oxygen between 4.2 and 6.5 mg/L (measured at noon) and electrical conductivity between 20 and 30 µS/cm. In sites affected by logging, the water was cloudy to muddy with a mean temperature of 27°, dissolved oxygen of <2.0 mg/L and average electrical conductivity of 48 µS/cm.

The use of pesticides such as Lindane, Thiosulfan 359 and Gammalin 20 for agriculture and fishing is widespread in the middle Nyong basin. These chemicals kill virtually all aquatic fauna to a depth of several centimetres into the mud and have long-lasting negative effects on fish diversity (du Feu 2001). Fishers report that stream sections fished with poisons may remain devoid of fish for up to 20 years.

In 1958, 20 fingerling *Heterotis niloticus* were introduced by the Cameroonian Forestry Service to the Nyong at Akonolinga in an effort to establish a commercial fishery (Depierre & Vivien 1977). In 1976, Depierre & Vivien estimated 60 t of *H. niloticus* captured in the vicinity of Ayos in the upper Nyong. Mengang (1984) estimated the *H. niloticus* catch landed at Akonolinga at 616 t/year. Abina (2005) calculated that *Oreochromis niloticus* accidentally introduced into the river from flooded government fish ponds, also at Akonolinga, now represents 12.5% of the total catch in the upper Nyong basin. As their populations continue to expand downstream, the introduced *O. niloticus* and *H. niloticus* could be expected to displace indigenous species (Lever 1996). In addition, after the end of formal sampling, fishers in Pont So'o captured a species they had never seen before, which upon inspection was identified as *Claris gariepinus*, another introduced species. Kamdem-Toham & Teugels (1998, 1999) and Mdaihli *et al.* (2003) showed how the collective impact of introduced species, increased turbidity and the poisoning of streams have altered the ecological structure of the Cross and N'tem Rivers in Southern and SE Cameroon, and it seems likely such changes may likewise be negatively affecting the Nyong River.

Dietary Characterisation

Fish diets (Table 4) reflect the food resources of the rainforest river environment. Low light and alkalinity limit the growth of phytoplankton, upon which many tropical ecosystems rely as the basis of the food web (Delincé 1992). The main nutrient inputs to rainforest rivers such as the Nyong, are comprised mainly of leaves and other plant materials that fall or are flushed in during rain or flooding events (Welcomme & de Merona 1988). The nutritional value of these decaying plant materials derives primarily from the protozoa and bacteria that colonise them (Anderson 1987, Moriarty 1987) and insects (primarily larval forms) and crustacean (primarily *Macrobrachium* spp) shredders and grazers that are in turn consumed by fishes (Wolfgang Junk, Max Plank Institute of Limnology, pers. comm., February 2003).

Cluster analysis identified four groups, based on diet. Group A (*Brycinus macrolepidotus, Brycinus kingsleyae, Chrysichthys nigrodigitatus, Anaspidoglanis macrostoma, Parauchenoglanis longiceps* & *Schilbe intermedius*) eat mostly insects and/or aquatic crustacea. Group B (*Clarias, camerunensis, Brienomyrus brachyistius, Marcusenius moorii, Mormyrus tapirus* & *Petrocephalus simus*) target insects and crustaceans as well, but include a larger proportion of detritus in the diet. Group C (*Hemichromis elongatus, Raimas batesii, Hepsetus odoe & Parachanna obscura*) are largely piscivores. Group D (*Oreochromis niloticus, Labeo lukulae* & *Heterotis niloticus*) depend heavily on detritus and aquatic plants.

Dietary overlap (Table 5) among species was significant, with 10 of 18 species having an average SI of at least the 0.6 considered as biologically significant (Wallace & Ramsey 1983). Insects and aquatic crustacea were the most often targeted food items overall, and those species that depend heavily on these groups showed the highest degrees of dietary overlap.

The large degree of feeding niche overlap among species is consistent with the findings of Matthes (1964) who studied the middle Congo River and Hickley & Bailey (1987) working on the Nile in Sudan. Fish can use spatial and/or temporal partitioning to minimise competition both among species and age-classes (Matthes 1964; Kandem-Toham & Teugels 1997; Brummett 2000). Although detailed behavioural and ecological niche data are unavailable, the relatively high indigenous biodiversity of rainforest rivers (Teugels & Guégan 1994), their antiquity (Maley 1987; Schwartz 1991) and the high level of dietary overlap, imply a complex of behaviours regulating and balancing the ecosystem.

The relatively low degree of dietary overlap between the introduced *H. niloticus* and *O. niloticus* and indigenous species implies that these aliens are either taking advantage of an underutilised niche, or have already eliminated those species with which they compete. Without dietary data on the missing species, it is premature to assume that such wholesale reduction in species diversity as is being witnessed in the Nyong River could be attributed exclusively to dietary competition with the introduced *O. niloticus* and *H. niloticus*, but some effect cannot be ruled out. Indeed, the detritus/plant diet of the indigenous *L. lukulae* significantly overlaps with only these two species and *L. lukulae* is one of the species reported by fishers to be in decline. Of the other genera also specifically reported to be decreasing in abundance, *Clarias, Chrysichthys, Labeo, Labeobarbus, Mormyrops, Parauchenoglanis, Sarotherodon, Schilbe, Synodontis* and *Varicorhinus* have all been reported to rely heavily on detritus and/or plant material as major components of the diet (Matthes 1964; Seegers 1996). Cases of competition for food having negative impacts on indigenous species have been observed elsewhere (Declerck *et al.* 2002) and although little is known of the ecological impacts of *H. niloticus* introductions, cases of competition for food among indigenous fishes and *O. niloticus* resulting in declines in the former have been widely reported (Lever 1996).

Depierre & Vivien in 1977 estimated the annual catch of *H. niloticus* at 1 t/fisher, for an average productivity of 150 kg/ha of water surface area in the upper Nyong (a floodplain). Catches in the Cross River basin, a similar rainforest river ecosystem to the Nyong, are about 16 kg/ha watershed (Mdaihli et al. 2003) and it seems unlikely that the reported quantity of introduced fish could be growing in the river without affecting the food web and indigenous species in some way.

CONCLUSIONS

Significant changes in the Nyong River basin over the last 20 years include localised deforestation, expanding slash-and-burn agriculture, widespread use of illegal chemical fishing and the introduction of alien fish species. Without quantitative data on pre-existing conditions and fish abundance, it is impossible to say for certain that these changes have resulted in the declines in indigenous species reported by local fishers. Nevertheless, the inability of researchers to recapture many once-common species indicates that some negative changes have occurred. Similar ecological disturbances elsewhere have resulted in similar declines in indigenous species, thus it seems likely that recent changes in the Nyong River basin have had a significant negative impact on aquatic biodiversity.

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Halichoeres zulu, a new labrid fish from South Africa

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Abstract. *Halichoeres zulu* is described as a new species of labrid fish from inshore on rocky bottom or shallow reefs of KwaZulu-Natal, South Africa from four specimens, 79–135 mm standard length. Formerly misidentified as the similar *H. nebulosus*, a common sympatric species that ranges to the western Pacific (here extended to Palau), it differs in colour and in attaining a larger size. It is also a close relative of *H. margaritaceus*, a widely distributed Pacific and eastern Indian Ocean species. Although sharing a unique colour pattern on the cheek, it differs from *H. margaritaceus* in body colouration, a strongly modal count of 14 compared to 13 pectoral rays, and in reaching larger size.

Keywords: taxonomy, Labridae, *Halichoeres*, new species, South Africa

INTRODUCTION

The labrid fish genus *Halichoeres* Rüppell is the largest of the wrasse family, with 70 species (Parenti & Randall, 2000). It is well represented in all tropical and subtropical seas. Barber & Bellwood (2005) published a phylogenetic molecular study of the genus. From a genetic standpoint, *Halichoeres* should be divided into several genera, but morphological characters are lacking to make this practicable.

Randall & Smith (1982) reviewed the genus *Halichoeres* for the western Indian Ocean, recognizing 15 species, six of which were described as new. They reported that seven of the species range to the Pacific Ocean. One of the widely distributed species, *H. nebulosus* (Valenciennes), with a type locality of Bombay, has been confused with two other species in the western Pacific. Kuiter & Randall (1981) differentiated the three in a paper entitled, "Three look-alike Indo-Pacific labrid fishes, *Halichoeres margaritaceus*, *H. nebulosus* and *H. miniatus*."

In May of 2002, the second author collected a specimen of *Halichoeres* measuring 79 mm in standard length from shallow water at Umhlanga Rocks, near Durban, that seemed different from any of the species known for the western Indian Ocean. It is most similar to the female of *H. nebulosus*, as illustrated in Randall & Smith (1982: Plate 4 C) and Smith & Heemstra (1986: Plate 99, Fig. 220), sharing the large pink area on the abdomen, two black spots on the head behind the eye, and the same oblique banded pattern of the dorsal and anal fins, with two black spots in the dorsal. He sent the specimen to Phillip C. Heemstra at the South African Institute for Aquatic Biodiversity in Grahamstown. Although the life colour of the fish was somewhat faded, Heemstra photographed it (Fig. 1 A), and deposited the specimen in the SAIAB fish collection.

In 2008, the second author took an aquarium photograph (Plate 1 A) at the uShaka Marine World in Durban of what he believed to be a male-female pair of the same species. He sent the photo to the first author, who noticed the similarity of the colour pattern of the head to the Pacific species, *H. margaritaceus* (Valenciennes), in particular the elongate green horseshoe-shaped mark on the cheek. Plate 1 B and C are underwater photographs of a female and male of *H. margaritaceus* taken in Taiwan, which show this pattern on the cheek. In *H. nebulosus*, there is a boomerang-shaped pink mark on the cheek surrounded by pale green (Plate 1 D and E show a male and female of *H. nebulosus* from Mauritius, and Plate 1 F an aquarium photo of a male at uShaka Marine World).

Knowing that the unidentified *Halichoeres* is not rare in KwaZulu-Natal, we inquired if there are specimens in the large SAIAB fish collection identified only to genus or misidentified as *H. nebulosus*. Two adult male specimens were found. Neither had been photographed when fresh, so the second author waited for a calm day, enlisted the aid of three other divers, captured a large male with the use of a fence net, and took a specimen photograph (Plate I G). He also obtained aquarium photos of a female and a male (Plate 1 H and I) at uShaka Marine World in Durban, and an underwater photograph of a large male (Plate 1 J).

We conclude from the colour differences from both *H. nebulosus* and *H. margaritaceus* that the KwaZulu-Natal wrasse is a new species, which we describe here.

MATERIALS AND METHODS

Type specimens of the new species are deposited in the South African Institute for Aquatic Biodiversity, Grahamstown (SAIAB).

Lengths given for specimens are standard length (SL), the straight-line distance from the median anterior point of the upper lip to the base of the caudal fin (posterior end of hypural plate). Head length (HL) is measured from the same anterior point to the posterior end of the opercular membrane, and snout length from the same point to the fleshy edge of the orbit. Body depth is the greatest depth from the base of the dorsal spines; body width is the greatest width measured just posterior to the gill opening. Orbit diameter is the greatest fleshy diameter, and interorbital width the least bony width. Caudal-peduncle depth is the least depth; caudal-peduncle length is measured horizontally from the rear base of the anal fin to the caudal-fin base. Predorsal, preanal, and prepelvic lengths are from the front of the upper lip to the origin of the respective fins. Lengths of fin spines and soft rays are measured from where they emerge from the contour of the body to their tips. Pectoral-ray counts include the very short unbranched upper ray. Lateral-line scale counts do not include the single pored scale on the base of the caudal fin. Suborbital sensory pores are counted from behind the middle of the orbit to below the bony anterior edge of the orbit. When there is a pore at the base and at the tip of a radiating sensory canal, only one pore is counted. Gill-raker counts were made on the first gill arch. Only the total count is given (it is difficult to determine which raker is at the angle in many species of labrid fishes).

Table I gives the measurements of the new species as percentages of the standard length. Proportional measurements in the text are rounded to the nearest 0.05. Data in parentheses in the description refer to the paratypes.

Fig. 1. Male and female of *Halichoeres zulu*, uShaka Marine World, Durban (D. R. King).

Halichoeres zulu, sp. nov.

(Fig. 1, Plate 1 A, G–J; Tables 1-2)

Holotype. SAIAB 83176, male, 135 mm, South Africa, KwaZulu-Natal, off Umhlanga Rocks, 29°43′31.775′ S, 31°5′23.02″ E, rocky substratum, 1 m, fence net, D. R. King, T. Kay, J. Haxton and G. Leisgang, 27 March 2009.

Paratypes. SAIAB 43793, male, 116 mm, KwaZulu-Natal, Six-Mile Reef (now Adlam's Reef), 27°37′30″ S, 32°39′24″ E (10 km south Jesser Point, Sodwana Bay), top of inner reef with encrusting algae, bedrock, stones and sand, 2 m, rotenone, R. W. Winterbottom, M. S. Christensen, and G. S. Butler, 26 July 1976; SAIAB 28252, male, 121 mm, KwaZulu-Natal, off Scottburgh, 30°16′45″ S, 30°45′30″ E, R. W. Jones, 4 December 1988; SAIAB 82005, female, 79 mm, KwaZulu-Natal, Umhlanga Rocks, 29°43′32″ S, 31°5′23″ E, off rocky shore, 1 m, hand net, D. R. King, March 2002.

Diagnosis. Dorsal rays IX, 11; anal rays III, 11; pectoral rays 14 (rarely 13); lateral-line scales 26; head naked (no small scales on opercle or behind eye); narrow median dorsal zone of nape naked; median prepelvic scales 7, the anterior third of chest naked; tubule branches on lateral-line scales 3–5; suborbital pores 11–15; gill rakers 19-21; body depth 2.95–3.6 in SL; caudal fin slightly rounded, 1.4–1.45 in HL. Colour of female in alcohol pale tan, the scales on upper two-thirds of body, posterior to pectoral fins, with brown centres, those below soft portion of dorsal fin and in lowermost row dark brown; three broad dusky bars on chest and abdomen, fading ventrally; a black spot shaped like an inverted comma on opercular flap at upper end of gill opening; a dark brown spot of near-pupil size usually present behind upper part of orbit; an oblique dusky band on snout; an elongate, dark-edged, horseshoe-shaped band across cheek and opercle; dorsal fin with oblique brown bands, a small black spot on first membrane, and an ocellated black spot between second and fourth dorsal soft rays; rays of caudal fin with small dark spots; male with the same basic colour pattern, but most markings darker; black spot anteriorly on dorsal fin and oblique bands in spinous portion of fin lost; a wavy dark band basally on anal fin with a pale spot at base of each membrane. Females mainly pink or lavender-pink in life, with narrow pale green bands, a bright red stripe on nape, extending below base of spinous portion of dorsal fin, and a row of small dark brown spots on side of body above anal fin; males with deep pink and bright green bands on head, the body with alternating wavy stripes of bright green and purplish red.

Description. Dorsal rays IX, 11; anal rays III, 11; all dorsal and anal rays branched, the last to base; pectoral rays 14 (one paratype 13 on one side), uppermost rudimentary, second unbranched; pelvic rays I, 5; principal caudal rays 14, the upper and lower unbranched; upper and lower procurrent caudal rays 5; lateral-line scales 26, (plus 1 pored scale on caudal-fin base); scales above first lateral-line scale to base of first dorsal spine 3.5; scales above lateral line to base of ninth dorsal spine 2.5; scales below lateral line to base of first anal spine 9.5; circumpeduncular scales 20; gill rakers 21(21, except one paratype with 19); branchiostegal rays 5; vertebrae 25.

Body depth progressively greater with growth, 2.95 (3.0–3.6) in SL; body moderately compressed, the width 2.2 (2.3–2.5) in body depth; head length 3.1 (3.0–3.1) in SL; snout length 2.65 (2.75–2.8) in HL; orbit diameter 6.2 (5.45–6.0); interorbital space convex, the least width 5.9 (5.4–5.7) in HL; caudal-peduncle depth 1.9 (2.05–2.1) in HL; caudal-peduncle length 2.65 (2.7–2.8) in HL.

Mouth terminal to slightly inferior, a little oblique, and small, the upper-jaw length 3.25 (3.1–3.3) in HL; a pair of strong, jutting, canine teeth anteriorly in jaws, the lower pair fitting inside upper when mouth closed; upper canines more projecting and slightly flaring, about a pupil diameter in length; side of jaws with a row of eight or nine progressively smaller, stout, conical teeth, ending at corner of mouth with a larger, forward-projecting tooth; side of jaws anteriorly with one to two rows of small nodular teeth. Tongue slender, triangular, and sharply pointed, nearly reaching rear base of teeth anteriorly in jaws; lips large and fleshy, the curving labial flap on side of lower jaw a pupil width at its greatest depth. Gill rakers short, the longest at angle about two-fifths length of longest gill filaments.

Anterior nostril a very small, pointed tubule, two-thirds orbit diameter anterior to middle of eye; posterior nostril an oblique slit, two-thirds pupil diameter dorsoposterior to anterior nostril, well-protected by an anterior hemispherical flap. Suborbital pores 12 (11–15); cephalic sensory pores of smallest paratype 23 from front of snout, passing above nostrils, encircling orbit and ending above corner of mouth (pores counted after staining; double pores considered as one); pores of preopercular-mandibular series 16.

Scales cycloid; lateral line continuous, deflected downward below last two dorsal soft rays to straight peduncular part; lateral-line scales with 3 to 5 branching tubules that end in a pore; scales on nape small, progressively smaller and more embedded anteriorly, reaching forward to a vertical one-half orbit diameter behind eye; no scales in a narrow median dorsal zone on nape; scales of prepelvic area and on chest angular, the largest about one-half height of largest body scales, becoming progressively smaller and more embedded ventroanteriorly; a diamond-shaped naked patch on isthmus as large as eye; no scales on base of dorsal, anal, and paired fins, except for a pointed scale, one-half orbit diameter in length midventrally at base of pelvic fins (a small rounded scale at base of this scale on smallest paratype); basal third of caudal fin with four to five approximately vertical rows of scales, progressively smaller posteriorly.

Origin of dorsal fin above first lateral-line scale, the predorsal length 3.2 (3.15–3.35) in SL; dorsal spines progressively longer, the first 4.25 (4.05–5.15) in HL, and the ninth 3.15 (2.95–3.0) in HL; first dorsal soft ray longest, 2.4 (2.35–2.55) in HL; origin of anal fin below base of first dorsal soft ray, the preanal length 1.8 in SL; first anal spine very slender and short, 11.1 (9.9–10.1) in HL; third anal spine 3.5 (3.7–3.85) in HL; first and second anal soft rays longest, 2.55 (2.5–2.7) in HL; caudal fin slightly rounded, and short, 1.4 (1.4–1.45) in HL; third pectoral ray longest,1.6 (1.55–1.65) in HL; origin of pelvic fins below midbase of pectoral fins, the prepelvic length 3.15 (3.05–3.15) in Sl: pelvic fins short, not reaching anus, 1.6 (1.5–1.8) in HL (clearly shortest in female).

Table 1. Proportional measurements of type specimens of *Halichoeres zulu* as percentages of Standard Length.

	Holotype	Paratypes		
	SAIAB 83176	SAIAB 82005	SAIAB 43793	SAIAB 28252
Standard length (mm)	135	79	116	121
Sex	male	female	male	male
Body length	34.2	27.8	29.7	33.2
Body width	15.5	11.2	11.8	14.4
Head length	32.3	33.2	33.6	32.3
Snout length	12.2	11.8	12.2	11.6
Orbit diameter	5.2	6.1	5.6	5.5
Interorbital width	5.5	5.7	5.9	6.0
Upper-jaw length	9.9	10.0	10.9	9.8
Caudal-peduncle length	17.1	16.3	16.0	15.9
Caudal-peduncle depth	12.2	12.4	12.4	12.5
Predorsal length	31.1	31.6	31.7	29.8
Preanal length	55.2	55.5	55.9	56.1
Prepelvic length	31.8	32.9	31.5	31.7
Base of dorsal fin	63.2	58.3	58.0	61.7
First dorsal-fin spine	7.6	7.7	6.5	8.0
Ninth dorsal-fin spine	10.3	11.3	11.1	10.9
Longest dorsal-fin ray	13.4	14.2	13.2	13.8
Base of anal fin	34.4	32.3	32.7	34.2
First anal-fin spine	2.9	3.3	3.4	3.2
Third anal-fin spine	9.2	8.9	8.7	8.5
Longest anal-fin ray	12.7	13.4	12.5	12.7
Caudal-fin length	23.2	23.9	23.5	23.1
Pectoral-fin length	20.1	19.9	20.5	20.7
Pelvic-fin spine length	12.4	11.6	11.6	12.2
Pelvic-fin length	20.1	18.2	19.0	21.4

Table 2. Pectoral-fin ray counts[1] of four species of *Halichoeres*.

Species	12	13	14	15
H. margaritaceus		101	7	
H. miniatus	2	44	1	
H. nebulosus		2	104	2
H. zulu		1	7	

[1]Counts were made of fin rays on both sides, and include rudimentary upper ray.

Colour of male holotype in alcohol: centres of scales on upper half of body dark brown, except for row of scales above lateral line and below the spinous portion of the dorsal fin, with only the upper half dark brown (of these, the fourth and ninth scales, and the scales above, nearly free of dark pigment); a pale band of about one-half scale height above upper edge of pectoral fin, narrowing posteriorly to middle of body; three dark bars of two to four scales in width extending ventrally from this pale band, the first two below pectoral fin and broadening below on abdomen, the third also broader ventrally where centred on anus; remaining ventral half of body pale with a longitudinal series of six dark blotches from dark centres of two to five scales; prepectoral area and chest covered by a large triangular dark brown area that gradually fades ventrally; ventral part of head with an elongate, horseshoe-shaped pale band, the open end anterior (upper free end at corner of mouth and the lower on throat; a pale band from side of upper lip to eye; two pale bands extending posteriorly from eye, the upper curving around a large vertically elongate black spot behind and above upper half of eye, continuing as pale band anteriorly on body above lateral line; second pale band posterior to eye expanding as it reaches a large black spot, shaped like an inverted comma, posteriorly on opercular flap adjacent to upper end of gill opening; nape with a middorsal pale band; spinous portion of dorsal fin pale, the soft portion with a wavy horizontal brown band near middle of fin, with a dark band extending below on each membrane, and containing a large black spot between third and fourth soft rays; anal fin with a wavy dark band on basal two-fifths of fin, enclosing a small pale spot at base of each membrane; upper two and lower two principal rays of caudal fin pale; scaled basal central part of caudal fin dark brown, the remainder of rays with a series of 5 or 6 small dark spots, smaller posteriorly; paired fins pale. Colour of holotype when fresh as in Plate 1 G.

Colour of female paratype in alcohol pale tan, the scales on upper two-thirds of body, posterior to pectoral fin, with brown centres, those below soft portion of dorsal fin and in lowermost row dark brown; three broad dusky bars on chest and abdomen, fading ventrally; a black spot shaped like an inverted comma on opercular flap at upper end of gill opening; a dark brown spot of near-pupil size usually present behind upper part of orbit; an oblique dusky band on snout; an elongate, dark-edged, horseshoe-shaped band across cheek and opercle, the open end anterior; dorsal fin with oblique brown bands, a small black spot on first membrane, and an ocellated black spot between second and fourth dorsal soft rays; rays of caudal fin with small dark spots; paired fins pale. Colour of female paratype after several days on ice shown in Plate 1 A.

Etymology. We name this species for the indigenous people of the Province of KwaZulu-Natal, South Africa.

Remarks. This species is described from four specimens from KwaZulu-Natal, collected over a span of 31 years, suggesting that it is rare. The explanation for the paucity of specimens is partly due to its misidentification as *Halichoeres nebulosus*, but also to its usual shallow-water habitat off exposed rocky shores, where it is difficult to collect, as well as being very elusive.

We could find no meristic separation of *Halichoeres zulu* from *H. nebulosus*, and no difference in proportional measurements. Table 2 shows a strong modal separation of pectoral-ray counts of *H. nebulosus* and *H. zulu* from *H. margaritaceus* and *H. miniatus*.

There is a clear separation in the maximum size of *H. nebulosus* and *H. zulu*. The largest male of 50 specimens in 23 lots of *H. nebulosus* examined for the present study measures 86 mm SL, and Kuiter & Randall (1981: Fig. 5) illustrated one from Japan 96 mm SL. The three males of *H. zulu* range from 116 to 135 mm SL. In addition to the aforementioned cheek colour pattern, there is a difference in body colouration, that of *H. zulu* being primarily longitudinally banded, compared to a more barred pattern for *H. nebulosus*.

We also failed to find any difference in proportional measurements between *H. zulu* and *H. margaritaceus*. However, as in *H. nebulosus*, there is a difference in the maximum size attained. Kuiter & Randall reported the largest specimen of *H. margaritaceus* as 102 mm SL, collected from the Cocos-Keeling Islands, but one male from Lord Howe Island in a total of 94 specimens in 31 Bishop Museum lots from the Pacific measures 113 mm SL. The largest individuals of tropical marine fishes are usually found at locations of cooler sea temperature. Lord Howe Island lies at 32.5° S. Except for this lot and one from subtropical Pitcairn Island, the largest specimen is 86 mm SL (see Material examined below).

Although there is similarity in the cheek colouration of *H. zulu* and *H. margaritaceus*, the body colour pattern is clearly different, that of *H. zulu* more linear, as may be seen by comparing figures of the two species of Plate 1. Also, the dark pigmentation seen on the scales of the female of *H. margaritaceus* is on the edges of the scales (actually the edges of the scale pockets), whereas it is broadly on the scale centres in *H. zulu*. In addition, the ocellated black spot near mid-length of the dorsal fin is higher in the fin of *H. margaritaceus*.

The third of Kuiter & Randall's look-alike species of *Halichoeres, H. miniatus* (Valenciennes), is not easily confused with *H. zulu*. The upper two-thirds of the body of the female is dark grey or black with dull green scale centres; the male has dark red and green stripes following the scale rows, the green as series of spots posteriorly, overlaid by blackish bars on the posterior two-thirds of the body; both sexes have a large, irregular, circular pink mark on the cheek, and a black spot at the upper base of the pectoral fin. *H. miniatus* is distributed from Queensland, north through Indonesia and the Philippines to southern Japan.

Halichoeres zulu has been observed in the sea by the second author from northern Transkei to Banganek just south of the mouth of Kosi Bay near the northern end of KwaZulu-Natal, but it should range at least to southern Mozambique. It is generally found on rocky bottom or sand with scattered patches of reef at depths of 0.5 to 1.5 m. The pool where the male of Plate 1 I was photographed is almost closed to the sea at low tide. It is about 5 m long, 2 m wide, and 1.2 m deep.

MATERIAL EXAMINED

Halichoeres margaritaceus. **Indonesia:** Bali, BPBM 40579, 29 mm. **Taiwan:** BPBM 8659, 54 mm. **Palau:** Koror, BPBM 40964, 2: 64-66 mm. **Mariana Islands:** Guam: BPBM 139, 2: 76-78 mm; BPBM 140, 50 mm; BPBM 4578, 60 mm. **Coral Sea**, Chesterfield Islands: BPBM 33715, 4: 49-67 mm. **Lord Howe Island:** BPBM 14841, 2: 90-113 mm. **Kiribati:** BPBM 4581, 78 mm; Onotoa Atoll, BPBM 15338, 42 mm. **Marshall Islands:** Enewetak Atoll, BPBM 6284, 57 mm; BPBM 8062, 18: 45-81 mm; BPBM 8171, 86 mm; BPBM 8187, 64 mm; BPBM 12914, 2: 65 mm; BPBM 29033, 14: 39-85 mm. **Fiji:** Viti Levu, BPBM 5917, 2: 25-32 mm; Kadavu, BPBM 31150, 36 mm. **Tonga:** Tongatapu, BPBM 5674, 16: 28-71 mm; BPBM 5677, 5: 30-40 mm; BPBM 28923, 38 mm; BPBM 38030, 71 mm. **Samoa:** BPBM 5353, 2: 50-52 mm. **Line Islands:** Howland Island, BPBM 4579, 6: 20-30 mm; Kiritimati (Christmas Island), BPBM 4580, 68 mm; BPBM 4583, 78 mm; BPBM 37466, 83 mm. **Society Islands:** Tahiti, BPBM 8377, 53 mm; BPBM 13338, 80 mm; Moorea, BPBM 9348, 69 mm; BPBM 9352, 74 mm. **Pitcairn Island:** BPBM 16719, 103 mm.

Halichoeres nebulosus. **Red Sea:** BPBM 9301, 70 mm; Egypt, BPBM 19841, 2: 38-52 mm. **South Africa:** KwaZulu-Natal, BPBM 21694, 46 mm; SAIAB 43782, 3: 43-86 mm. **Bassas da India:** SAIAB 48984, 2: 70-82 mm. **Seychelles:** Cosmoledo Group, Assumption Island, SAIAB 43796, 2: 61-84 mm; Mahé, BPBM 22936, 3: 44-56 mm; Cocos Island, BPBM 21626, 3: 47-70 mm. **Mauritius:** BPBM 22929, 2: 54-80 mm; SAIAB 43781, 85 mm. **Maldive Islands:** North Malé Atoll, BPBM 32996, 2: 58-67 mm. **India:** Kerala, BPBM 27677, 51 mm. **Sri Lanka:** BPBM 18760, 83 mm. **Andaman Sea:** Thailand, Similan Islands, Ko Miang, BPBM 22811, 3: 45-62 mm. **Western Australia:** Dampier Archipelago, Kendrew Island, BPBM 17402, 8: 23-80 mm. **Indonesia:** Bali, BPBM 20911, 53 mm; BPBM 20925, 3: 45-54 mm; BPBM 20939, 4: 50-75 mm. **Philippines:** Cebu, BPBM 22083, 63 mm; BPBM 22120, 3: 50-68 mm. **Palau**: Koror, BPBM 40965, 2: 60-64 mm

RANGE EXTENSION FOR *Halichoeres nebulosus*. The two specimens of *H. nebulosus* listed above from Palau represent the first record for any island of Oceania. They were taken by spearing from the island of Koror by Luiz A. Rocha, Matthew T. Craig, and Brian W. Bowen on 24 October 2006.

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We thank Tim Kay, Jason Haxton, and Gareth Leisgang of uShaka Marine World for assistance in collecting specimens, Simon Chater, also of uShaka Marine World, for aid in photography, Kholiwe Dubula of the South African Institute for Aquatic Biodiversity for the loan of specimens of *Halichoeres nebulosus* and *H. zulu*, and Phillip C. Heemstra of the same institution for his photograph of our only female specimen of *H. zulu*. We are grateful also to Luiz A. Rocha, Matthew T. Craig, and Brian W. Bowen for allowing us to report the first record of *H. nebulosus* from Palau. The manuscript was reviewed by Helen A. Randall and Paolo Parenti.

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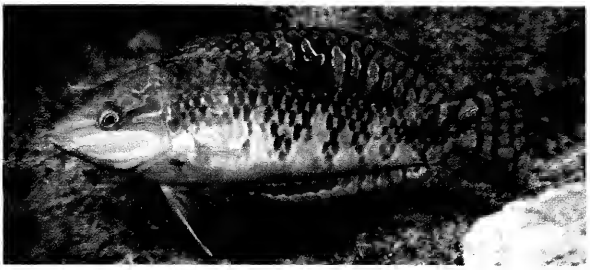
PLATE 1

A. Paratype of *Halichoeres zulu*, SAIAB 82005, female, 79 mm SL, KwaZulu-Natal (P. C. Heemstra).

B. Underwater photo of female of *Halichoeres margaritaceus*, Taiwan (J. E. Randall).

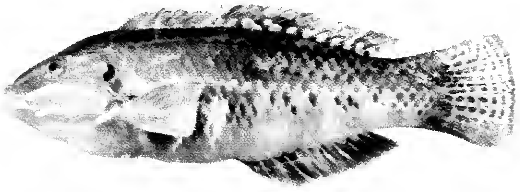


C. Underwater photo of male of *Halichoeres margaritaceus*, Taiwan (J. E. Randall).

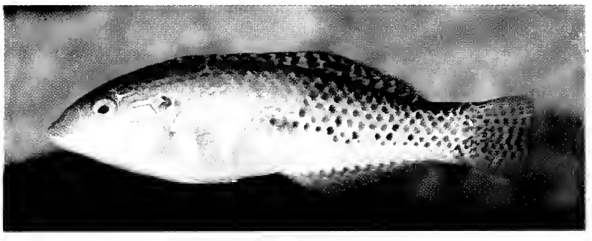
D. Underwater photo of female of *Halichoeres nebulosus*, Mauritius (J. E. Randall).

E. Underwater photo of male of *Halichoeres nebulosus*, Mauritius (J.E. Randall).

F. Photo of male of *Halichoeres nebulosus*, uShaka Marine World, Durban (D. R. King).

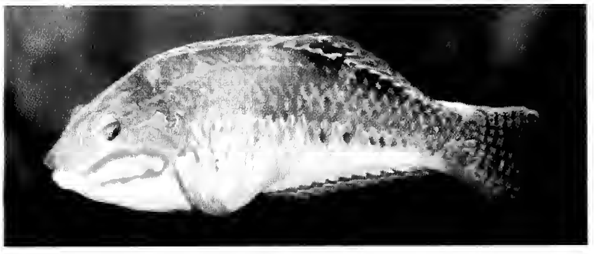


G. Holotype of *Halichoeres zulu*, SAIAB 83176, male, 135 mm SL, KwaZulu-Natal (D. R. King).



H. Photo of female of *Halichoeres zulu*, uShaka Marine World, Durban (D. R. King).

I. Underwater photo of female of *Halichoeres zulu*, in a rock pool with *Caulerpa* sp., KwaZulu-Natal (D. R. King).



J. Photo of large male of *Halichoeres zulu*, uShaka Marine World, Durban (D. R. King).

Range extension and a further female specimen of the grinning izak (*Holohalaelurus grennian* Human 2006; Scyliorhinidae; Chondrichthyes).

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Abstract. A specimen of *Holohalaelurus* shark (Scyliorhinidae; Chondrichthyes) recently collected off southern Mozambique, represents a southward range extension of 2200km for the recently described, *H. grennian* Human 2006. This specimen presents not only a significant extension of its known distribution, but is also only the second female specimen known for this species. Moreover, the specimen exhibits morphological characters, particularly colouration, which are more typically attributed to congeners occurring in the southern part of its range. This paper is an account of the range extension for *H. grennian*, and compares the morphological and colouration differences in this specimen compared to the original species description. A shape analysis is conducted on the specimen, and a revised zoogeography of the genus *Holohalaelurus* is presented.

Keywords: *Holohalaelurus*, Scyliorhinidae, Chondrichthyes, range extension, zoogeography, western Indian Ocean, conservation status.

INTRODUCTION

A recent review of the genus *Holohalaelurus* Fowler 1934 resolved the distribution of *Holohalaelurus* sharks in the western Indian Ocean (Human, 2006a). This resulted in the resurrection of *H. melanostigma* (Norman 1939), and the description of two new taxa, *H. favus* and *H. grennian*, from the western Indian Ocean.

Holohalaelurus sharks from the western Indian Ocean are poorly known and apparently rare, with the possible exception of *H. regani* in the southwest Indian Ocean (which is abundant in the southeast Atlantic), and their conservation status needs to be critically assessed. *Holohalaelurus favus* and *H. punctatus* from kwaZulu-Natal, South Africa, and southern Mozambique, were common by-catch species in trawl fisheries in the late 1960s and early 1970s (Human, 2006a). Since then both species have apparently suffered significant population declines and are possibly extinct there; no specimens of these species have been recorded since the 1970s, despite recent intensive biodiversity surveys as part of the African Coelacanth Ecosystem Programme.

Holohalaelurus punctatus has an apparently separate population distributed around Madagascar, although the current status of that population is unknown. The two species known from Kenya and Tanzania, *H. melanostigma* and *H. grennian*, are both known only from a handful of specimens, and females for *H. melanostigma* remain unknown.

Holohalaelurus grennian was described from four museum specimens consisting of three males and one female. The taxonomic history of this species was complicated by the placement of the female specimen in the *H. melanostigma* type series by Norman (1939), which he assumingly did on the grounds of supposed sexual dimorphism (Human, 2006a). The placement of the female in *H. melanostigma* was due to the lack of *bone fide* female specimens of *H. melanostigma* (which still holds true) and of male specimen conspecifics of the female specimen at the time. Male specimens readily identifiable as conspecific to Normans' female specimen have since been collected, validating the erection of the species *H. grennian*, and the assignment of the female specimen to that species (Human, 2006a). Additionally, shape variation analyses of the genus supported the validity of *H. grennian* and the specimens assigned to it (Human, 2007b).

The only other specimens reported in the literature, additional to the type series, were a female specimen that was not catalogued and discarded by Norman (1939), and an illustration by Igor Sidorenko from the Southern Scientific Research Institute of Marine Fisheries and Oceanography (YugNIRO), USSR, of a presumed female specimen from an unknown locality (Human, 2006a). The type locality of *H. grennian* is off Ras Ngomeni, Kenya. Other specimens have been collected off Zanzibar Island and off Dar es Salaam, Tanzania, from depths ranging between 238–300m (Fig. 1; Human, 2006a). At the time *H. grennian* was described, it was thought to be sympatric with only one other species of *Holohalaelurus, H. melanostigma*.

Recently, a female specimen of *Holohalaelurus* (SAIAB 81902) was captured off Mozambique and was assigned to *H. punctatus*. However this specimen is identifiable as *H. grennian* and represents a significant range extension for the species, is the second female specimen of *H. grennian* in a collection, and exhibits minor, but noteworthy, morphometric and colouration differences from the original species description.

METHODS AND MATERIALS

Voyage Details

The specimen was collected by P.C. and E. Heemstra aboard the R/V Dr Fridtjof Nansen, and deposited in the ichthyological collection of the South African Institute for Aquatic Biodiversity as SAIAB 81902. The research cruise was a joint venture involving SAIAB, the Instituto Nacional de Investigacao Pesqueira of Mozambique, FAO, and the Institute for Marine Research, Bergen, Norway. The specimen was collected in a bottom trawl approximately 285km eastnortheast of Maputo, and about 140km south of Inhambe, Mozambique (Fig. 1). The start position of the trawl was 25° 05.5′ S, 35° 18.4′ E, and finished at 25° 07.2′ S, 35°17.6′ E, with a bottom depth of 347-353m.

Morphometrics and Meristics

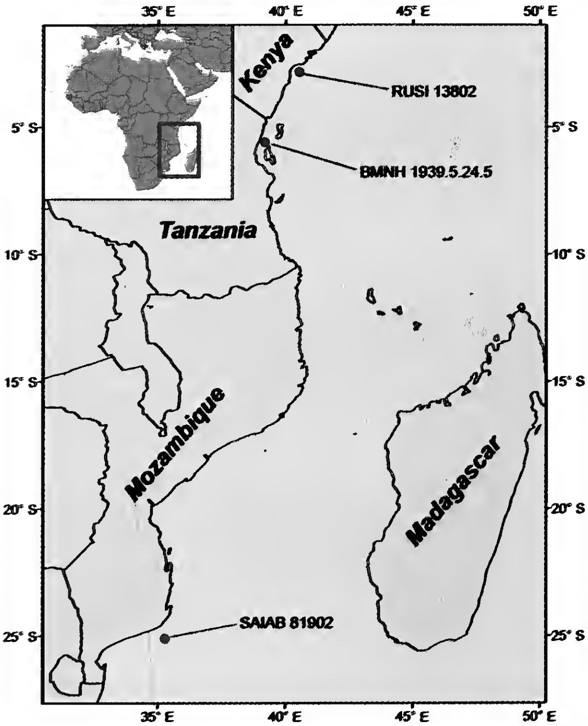

Fig. 1. The known distribution of *Holohalaelurus grennian*. The new female specimen (SAIAB 81902) represents a southward range extension of 2,200km. Other specimens (not shown on this chart) have been collected off Dar es Salaam, Tanzania, without further details.

Morphometric and meristic measures were taken according to Compagno (2001), with modifications (Human, 2006b) suited for scyliorhinid sharks. The new specimen was compared to *Holohalaelurus* specimens recorded in Human (2006a, 2007b; Appendix 1).

Shape Analyses

Human (2006b, 2007a, b) introduced a methodology for whole body shape analysis of congeneric species, using a wholly multivariate approach that is followed here. Briefly, a size corrected and classification analysis is made to examine whether specimens cluster into *a priori* assigned species groups. The morphometrics of the current specimen were combined with the *Holohalaelurus* dataset used by Human (2007b) to determine if the current specimen clustered with other *H. grennian* specimens, based on shape.

RESULTS

Morphometrics and Meristics

The morphometric and meristic measures of the female *H. grennian* specimen described here, are compared to the morphometric and meristic measures of other *H. grennian* specimens (from Human, 2006a) in Table 1; the abbreviations used are listed in Appendix 2.

Overall, the morphometric and meristic measures of the specimen were within the range of those recorded for previous *H. grennian* specimens (Table 1), but differed slightly from other specimens in having a proportionately smaller, less depressed head, i.e. a shorter PP1, HDL, PG1, PSP, and longer DPI. The head is proportionately narrower with a longer snout (longer PRN), narrower mouth width (shorter MOW), eyes positioned closer together and positioned more posteriorly to the mouth (shorter INO, and longer EMA), and narrower spacing between the nares (shorter INW and IOW). The speciman also has proportionately smaller 1^{st} and 3^{rd} gill slits (shorter GS1, GS3). In common with the head, the trunk is less depressed and the anterior body was generally stouter and longer than other *H. grennian* specimens (larger HDH2, HDW2, HDH, HDW, TRH, TRW, GIR, ABH, ABW, longer TRL and PPS). The caudal peduncle is more compressed (larger TAH, smaller CPW), seemingly to accommodate a proportionately longer caudal fin (shorter PCL, ACS, and longer CDM). The specimen also has a slightly higher vertebral count due to a larger number of caudal diplospondylous vertebrae.

This specimen of *H. grennian* also has enlarged denticles on the dorsal midline between the pectoral fin and the origin of the first dorsal fin, visible only under close inspection. It has no enlarged denticles on the dorsal surfaces of the pectoral fins. Human (2006a) noted slightly enlarged denticles on the dorsal midline for this species, but denticles were enlarged more so in those specimens compared to this specimen. The only *Holohalaelurus* species that lacks enlarged denticles on the dorsal midline is *H. punctatus* (Human, 2006a). The inconspicuous buccal papillae is in agreement with the original species description of *H. grennian*, in contrast to *H. punctatus*, which has obvious buccal papillae.

This specimen's pectoral fin radials (P1R) were undetectable through manual manipulation of the fin, as were those of the female paratype, whereas the pectoral fin radials of the male specimens could be detected and were measurable, despite male specimens being smaller than the female specimens. This apparent difference in the pectoral fin radial flexibility may represent a sexual dimorphic character state for this species.

Shape Analyses

Holohalaelurus specimens used in shape analysis are

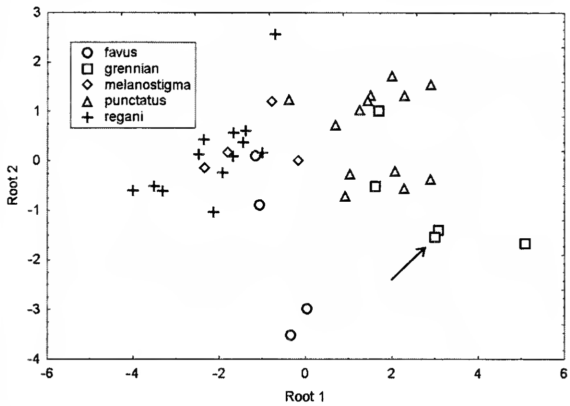

Fig. 2. Projection of the canonical scores for each *Holohalaelurus* specimen against the first and second discriminant roots. The arrow points to the *H. grennian* specimen collected from Mozambique.

given in Appendix 1. The results were very similar to those recorded by Human (2007b), the first nine eigenvectors accounting for 75% of the overall variance in the dataset, and the first seventeen eigenvectors accounting for 90% of the overall variance (Table 2). From the MPCA analysis, seven size corrected morphometric measures had 25% or more of their variance accounted for by the first and second eigenvectors, and six of these were incorporated into the DFA model, with only MOL, GS5, and D1P contributing significantly to the model (Table 3). Four roots resulted from the canonical analysis, although only the first and second roots contributed significantly to the discriminating power of the model (Table 4). The first root accounted for ~80%, and the second root ~13%, of the discriminatory power of the model.

There was little evidence of species separation in the canonical analysis (Fig. 2), although species clustering was evident, particularly for *H. regani;* and the recent *H. grennian* specimen clustered within that species group. The *H. punctatus, H. favus,* and *H. melanostigma* species groups are less resolved compared to previous analyses (Human, 2007b). Consequently, the classification analysis was not as successful in discriminating species (82.1% correct overall; Table 5), compared to the results previously achieved (89.7% correct overall; 2007b). Table 5 shows that all of the *H. regani* specimens were correctly identified and only one *H. melanostigma* specimen was incorrectly classified. However, two specimens of *H. grennian* and *H. punctatus* had been misidentified.

Colouration

The current specimen (Fig. 3) agrees in colouration with the description for *H. grennian* in most respects (Human, 2006a), with many small dark brown spots on a yellow-brown background dorsally, the spots becoming larger along the lateral midline and on the dorsal surface of the pectoral fins, but not developing into the small stripes observed on some other *H. grennian* specimens; there are few white spots on the dorsum, with a white spot at the second dorsal-fin origin, and a large white spot above the pectoral-fin insertion, about level with the gill slits; characteristic stripe present on both dorsal fins, stripe narrow and bordered by a pale margin; caudal fin with dusky patches on the hypaxial fin web and on the terminal lobe; ventrum uniformly off-white, with no markings or spots, although sensory pores are noticeably black, confirming that black ventral sensory pores appear to be a character common to all *Holohalaelurus* sharks when alive or freshly preserved.

The notable exception to the colouration and patterning given in the original description of the species is the presence of some dorsal fin markings that are superficially similar to those seen in congenerics. This female specimen has V-shaped markings on both dorsal fins, which are absent in other known *H. grennian* specimens (Fig. 4). Similar patterning has only been described for *H. punctatus*, although these markings had faded on the specimens by the time they were examined by Human (2006a), and were recorded accordingly, although the distinguishing black stripes surrounded by a pale margin are present on this specimen, they are situated much lower, closer to the inner margins, and not reaching to the posterior margins of the dorsal fins, compared to other *H. grennian* specimens in which the stripe is positioned midway along the posterior margin of the fin (Human, 2006a).

DISCUSSION

The known distribution of *H. grennian* spans more than 22 degrees of latitude (Fig. 1), and is apparently restricted to the African upper continental slope. The specimen described here represents a southward range extension of 2,200km, which significantly extends its distribution.

The species has previously been recorded from depths of 238–300 m, and at 234–353 m depth, this specimen represents the deepest record for the species. Despite this, the depth range for the species is restricted to just over 100m, possibly indicating a close affinity for a particular habitat. It is not known if the apparent depth range difference between the Mozambique specimen and the Kenyan/Tanzanian specimens represents regional differences in habitat preferences,

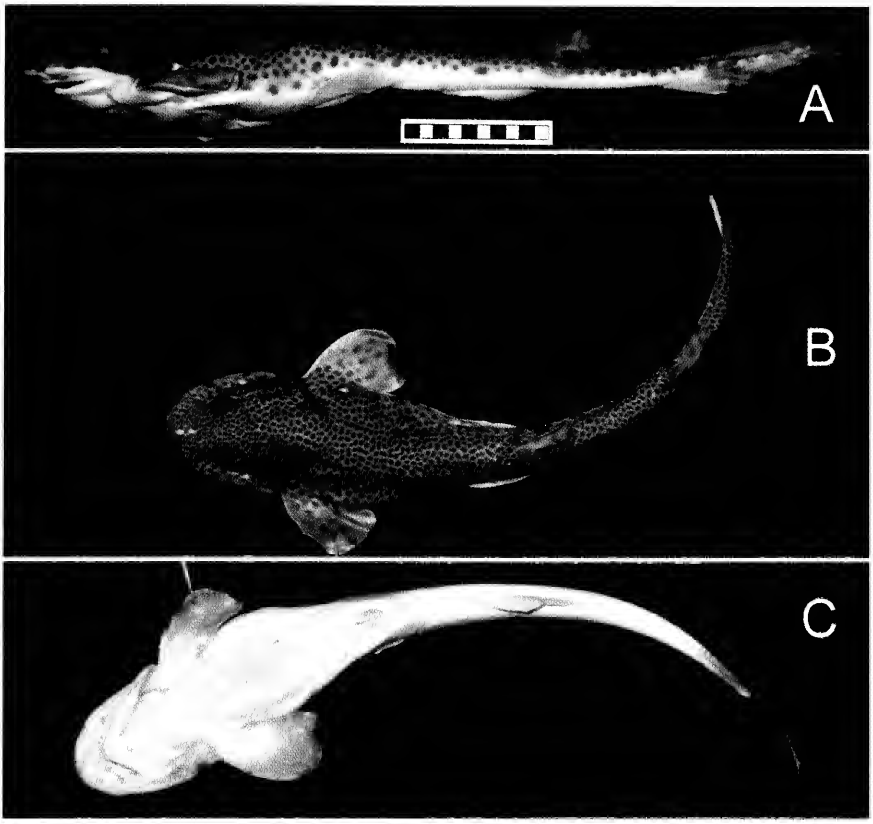

Fig. 3. Lateral (A), dorsal (B), and ventral (C) photographs of the female *H. grennian* specimen (SAIAB 81902) collected off Mozambique. Note the V-shaped markings present on both dorsal fins, and the black ventral sensory pores.

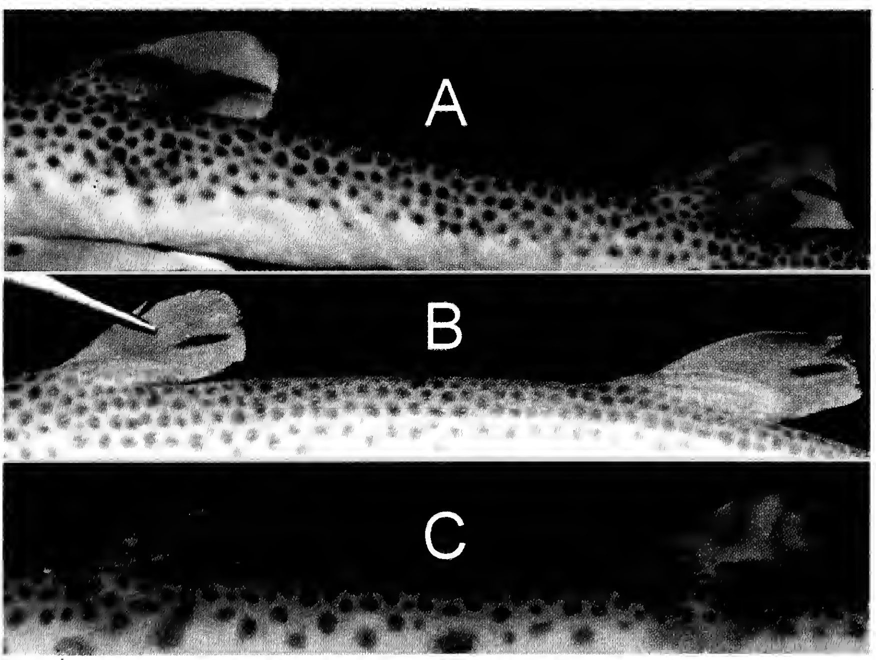

Fig. 4. Comparison of dorsal fin markings of *H. grennian* specimens illustrating the differences between those specimens collected off Tanzania and Kenya (A, B), compared to the specimen collected off Mozambique (C). Holotype RUSI 13802, male (A); Paratype BMNH 1939.5.24.5, female (B); and SAIAB 81902, female(C).

or an artefact of small sample size.

This specimen of *H. grennian* is interesting because it exhibits characters that are more typically associated with *H. punctatus*, which has a restricted southwestern Indian Ocean distribution. The reduced dorsal midline denticles and the presence of the V-shaped markings on this *H. grennian* specimen is more typical of *H. punctatus*, representing possible regional differences and potential population sub-structuring within *H. grennian*. Furthermore, these differences may also speculatively be attributed to hybridisation between *H. grennian* and *H. punctatus* in the southern Mozambique region at some time, or are remnants of a speciation event, and that these characters were lost as the species dispersed northwards.

Given the total length of the specimen, it is assumed that it is either adolescent or mature. The specimen was, however, not gravid and was not dissected to ascertain maturity. Egg cases and reproductive traits of *H. grennian* remain unknown.

Despite the differences in morphometric statistics, dorsal midline denticles (enlarged, but easily overlooked) and colouration described for this specimen, the key for *Holohalaelurus* of Human (2006a) remains effective for discriminating species in the genus, even though the morphometric differences were sufficient to reduce the resolution of the shape analyses of the genus compared to Human (2007b). It is hypothesised that the reduced performance of the DFA and classification analyses is a result of this female introducing stronger signals of sexual dimorphism into the analyses. Additional female specimens of all *Holohalaeurus* species are required in order to test this hypothesis.

ZOOGEOGRAPHY OF *HOLOHALAELURUS*

Holohalaelurus sharks are distributed on the African continental shelf and upper to mid-slopes from Namibia, in the southeast Atlantic Ocean, around South Africa and northwards to at least Kenya, and probably Somalia, in the western Indian Ocean. The exception to this distribution is a population, possibly disjunct from the African shelf population, of *H. punctatus*, that occurs around Madagascar. *Holohalaelurus punctatus* is also found from kwaZulu-Natal, South Africa, to southern Mozambique (although possibly extinct there now) and is sympatric with *H. favus* with a similar distribution, although also possibly extinct there now. *Holohalaelurus regani* is also sympatric in this region, although it is more commonly found south and west of kwaZulu-Natal, around South Africa and to southern Namibia, and is the only representative of *Holohalaelurus* south and west of kwaZulu-Natal.

Holohalaelurus grennian is (was) sympatric with *H. punctatus* and *H. favus* in the southern part of its range, but may be the only species occurring in northern Mozambique and southern Tanzania. In northern Tanzania and Kenya *H. grennian* is sympatric with *H. melanostigma*. However, while *H. grennian* inhabits the upper continental slope, there is apparent niche partitioning between the two species with *H. melanostigma* inhabiting the mid-slope at depths of 607–658m. It is possible that both *H. grennian* and *H. melanostigma* occur north of Kenya, as there are anecdotal reports of *Holohalaelurus* sharks occurring off Somalia which may be either or both of these species (Human, 2006a).

Although it is likely that *Holohalaelurus* sharks occur in Somalia, they probably do not occur north of there, as they have not been recorded from the Red Sea (a relatively well known ichthyofauna), and are unlikely to leave the African continental shelf to inhabit the Arabian shelf as the Somali upwelling represents a significant ecological barrier. The range extension described here suggests that further deep water trawling of the lower continental shelf, and upper and mid continental slopes in the western Indian Ocean will lead to further range extensions of the genus *Holohalaelurus*.

ACKNOWLEDGEMENTS

Elaine Heemstra (SAIAB) brought my attention to the Mozambique specimen and encouraged me to examine it. Thanks to Kholiwe Dubula, Phillip Heemstra, Roger Bills, and the South African Institute of Aquatic Biodiversity for allowing and organising the loan of the specimen. I am grateful to Susan Morrison for making available the X-ray facilities at the Western Australian Museum.

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5 February 2010

Table 1. Comparison of the morphometric and meristic measurements of the female *H. grennian* specimen (SAIAB 81902) compared to other *H. grennian* specimens (3 male, 1 female, from Human 2006a). WT is measured in grams, TL in millimeters, and all other measurements are expressed as percentage of TL. See Appendix 2 for abbreviations.

	SAIAB 81902	Average	Range
WT	51.8	34.8	10.5 - 61.9
TL	257	227.8	165 - 273
PCL	75.9	78.8	76.9 - 80.1
PD2	58.4	59.9	56.7 - 62.9
PD1	39.3	39.4	38.2 - 41.2
BDL	62.6	60.6	59.4 - 63.1
IDS	14.8	16.0	15.2 - 16.7
D2C	34.4	33.5	31.5 - 35.8
DCS	13.0	13.5	12.0 - 14.6
PAL	48.6	48.6	45.8 - 53.2
PP2	33.9	31.9	29.1 - 34.8
PP1	15.2	17.6	16.7 - 18.1
SVL	36.6	34.3	32.7 - 37.1
TRL	20.2	16.8	15.8 - 18.0
PPS	13.6	9.9	8.6 - 11.5
PAS	9.3	9.9	8.0 - 11.6
VCL	64.2	64.0	62.6 - 65.9
PCA	35.4	37.4	36.7 - 37.9
ACS	15.6	16.7	14.6 - 17.9
HDH2	7.8	5.7	5.3 - 6.4
HDW2	12.5	14.0	13.3 - 14.5
INO	5.8	6.7	6.4 - 7.0
HDH	8.8	6.9	6.3 - 8.1
HDW	13.2	13.4	12.6 - 14.3
TRH	9.1	7.7	7.0 -8.6
TRW	13.2	10.2	7.9 - 12.1
GIR	37.0	28.3	26.7 - 31.1
ABH	10.3	8.6	7.9 - 9.7
ABW	12.8	8.1	7.5 - 9.5
TAH	5.6	4.4	3.6 - 4.9
TAW	5.4	5.0	4.7 - 5.3
CPH	2.7	2.4	2.2 - 2.6
CPW	1.4	1.8	1.7 - 1.9
HDL	15.6	18.1	17.0 - 19.2
PG1	13.8	15.6	14.6 - 16.7
PSP	9.3	10.8	10.4 - 11
POB	6.2	6.8	6.2 - 7.3
EYL	3.5	3.5	2.9 - 4.1
EYH	1.4	1.6	1.2 - 2.2
SPL	0.8	0.8	0.6 - 1.0
ESL	0.6	0.6	0.5 - 0.7
EMA	1.9	0.6	0.4 - 0.9
ING	1.6	2.3	1.6 - 2.7
GS1	1.6	2.3	2.1 - 2.6
GS2	1.6	1.9	1.5 - 2.4
GS3	1.2	1.8	1.5 - 2.0
GS4	0.8	1.3	0.9 - 1.6
GS5	0.4	0.6	0.3 - 1.1

	SAIAB 81902	Average	Range
D1L	8.4	7.2	6.1 - 8.2
D1A	8.0	7.0	5.5 - 8.2
D1B	5.6	4.6	3.6 - 5.5
D1H	3.9	3.9	3.0 - 4.9
D1I	2.7	2.8	2.4 - 3.4
D1P	3.9	3.3	2.9 - 3.5
P2L	10.9	12.5	11.5 - 13.9
P2A	5.1	5.5	4.0 - 6.7
P2B	7.0	7.7	7.1 - 8.3
P2H	2.3	2.6	2.2 - 3.2
P2I	5.1	5.5	4.1 - 7.3
P2P	5.8	6.8	5.8 - 7.7
CLO	-	5.2	2.1 - 10.3
CLI	-	6.9	4.8 - 11.7
CLB	-	0.8	0.6 - 1.5
D2L	9.7	9.4	9.1 - 9.7
D2A	9.1	9.3	8.7 - 9.7
D2B	6.2	6.2	6.0 - 6.4
D2H	4.1	3.9	3.0 - 4.3
D2I	2.9	3.4	2.9 -3.9
D2P	3.9	3.8	3.4 - 4.2
ANL	13.6	13.5	12.1 - 15.2
ANA	6.8	6.9	5.9 - 7.3
ANB	11.3	11.0	10.0 - 12.0
ANH	2.9	2.6	2.4 - 3.0
ANI	2.7	2.7	2.1 - 3.1
ANP	7.2	7.4	5.5 - 8.8
CDM	21.8	21.0	19.9 - 21.5
CPV	7.0	7.4	5.8 - 8.4
CPU	9.9	10.3	9.5 - 10.9
CST	4.7	6.1	4.8 - 7.9
CSW	2.3	2.6	2.4 - 3.0
CTR	3.1	3.5	2.4 - 4.0
CTL	5.8	7.2	5.9 - 8.5
DPI	24.9	19.8	17.0 - 22.5
DPO	8.9	11.0	8.8 - 14.4
PDI	6.2	6.1	4.9 - 7.5
PDO	21.6	22.2	19.7 - 24.5
DAO	10.9	10.2	9.4 - 11.0
DAI	5.4	5.7	4.8 - 7.0
P2 fused	0.0	0.5	0.0 - 0.9
P2 free	5.4	4.2	3.6 - 5.1
VERT	112	102.0	90 - 108
mono	27	26.5	24 - 28
predip	52	50.3	49 - 52
caudaldip	33	25.3	17 - 30

Table 1 continued.

POR	3.7	3.7	2.8 - 4.4
PRN	3.9	2.7	1.9 - 3.3
MOL	2.7	3.8	2.7 - 5.3
MOW	7.4	9.5	8.7 - 10.1
NOW	2.7	2.4	2.1 - 2.7
INW	3.1	3.7	3.2 - 4.2
IOW	7.8	8.4	8.2 - 8.5
ANF	1.2	1.0	0.7 - 1.2
P1L	12.3	12.0	11.2 - 13.7
P1A	11.3	11.9	10.0 - 13.9
P1B	7.0	7.4	7.1 - 8.0
P1H	8.2	7.9	6.7 - 9.4
P1I	6.2	5.6	4.4 - 7.1
P1P	7.8	7.8	6.1 - 9.3
P1R	0.0	5.0	0.0 - 7.5

DENT			
UL	21	20.0	19 - 21
US	0	1.5	0 - 3
UR	22	20.0	19 - 21
U tot	43	41.5	40 - 43
LL	19	18.0	17 - 19
LS	0	2.5	0 - 4
LR	18	18.5	17 - 22
L tot	37	39.0	38 - 41

Table 2. The first nine eigenvectors from the multigroup principal component analysis that account for 75% of the variance in the dataset.

Eigenvector	Eigenvalue	%	Cumulative	Cumulative %
1	0.141319	29.3	0.141319	29.3
2	0.083411	17.3	0.224730	46.5
3	0.039191	8.1	0.263921	54.7
4	0.023374	4.8	0.287296	59.5
5	0.022920	4.7	0.310216	64.2
6	0.019582	4.1	0.329798	68.3
7	0.015453	3.2	0.345251	71.5
8	0.013648	2.8	0.358899	74.3
9	0.012924	2.7	0.371823	77.0

Table 3. Summary of the stepwise discriminant function analysis. Wilks' Lambda approx. 0.08264, F (24,102) 4.4515 p<0.0000. *denotes variables that contributed significantly to the model.

	Wilks' lambda	Partial lambda	F – remove (4, 29)	*p* level	Tolerance	1 – tolerance (r^2)
*MOL	0.182	0.455	8.687	0.000	0.503	0.497
*GS5	0.114	0.727	2.719	0.049	0.412	0.588
*D1P	0.114	0.724	2.760	0.047	0.409	0.591
P2H	0.104	0.792	1.909	0.136	0.250	0.750
GS4	0.106	0.779	2.057	0.112	0.487	0.513
P2I	0.097	0.851	1.273	0.303	0.321	0.679

Table 4. Chi squared test of significance from the successive removal of canonical roots to examine which roots contribute significantly to the discriminating power of the model.

Roots removed	Eigenvalue	Canonical *R*	Wilks' lambda	Chi-square	d.f.	*p* level
0	4.190	0.899	0.083	81.03005	24	0.000
1	0.660	0.630	0.429	27.50822	15	0.025
2	0.290	0.474	0.712	11.04145	8	0.199
3	0.089	0.285	0.919	2.75787	3	0.430

Table 5. Percentage and numbers of specimens correctly classified into their putative species of *Holohalaelurus*. The first column shows the observed species classification, and the following columns the species classification of specimens predicted from the discriminatory functions model.

	% correct	favus	grennian	melanostigma	punctatus	regani
favus	50	2	0	0	0	2
grennian	60	0	3	0	2	0
melanostigma	75	0	0	3	0	1
punctatus	85	0	1	0	11	1
regani	100	0	0	0	0	13
Total	82.1	2	4	3	13	17

APPENDICES

APPENDIX 1. *Holohalaelurus* comparative material. Those lots highlighted with an asterisk were used in the shape variation analyses and includes all specimens within the lot. Abbreviations: BAH - Brett Human field number; BMNH - British Museum Natural History; LJVC - Leonard Compagno field number; MNHN - Muséum National d'Histoire Naturelle; RUSI - SAIAB (previously Rhodes University/ J.L.B. Smith Institute of Ichthyology); SAIAB - South African Institute for Aquatic Biodiversity; and SAM - South African Museum.

Holohalaelurus favus Human 2006 - RUSI 6139*, holotype, mature male 515mm TL; RUSI 6138*, paratype, mature female 423mm TL; RUSI 6140*, adolescent female 291mm TL; and RUSI 6271*, immature male 193mmTL.

Holohalaelurus grennian Human 2006 - RUSI 13082*, holotype, mature male 267mm TL; BMNH 1939.5.24.5*, paratype, also paratype of *Scyliorhinus* (*Halaelurus*) *melanostigma* Norman 1939, juvenile female 206mm TL; SAM 36077*, mature male 273mm TL; SAM 36078*, juvenile male 165mm TL; and SAIAB 81902*, immature female 257mm TL.

Holohalaelurus melanostigma (Norman 1939) - BMNH 1939.5.24.2*, holotype, adolescent male 335mm TL; BMNH 1939.5.24.3*, paratype, adolescent male 330mm TL; BMNH 1939.5.24.4*, paratype, juvenile male 267mm TL; and RUSI 14114*, mature male 384mm TL.

Holohalaelurus punctatus (Gilchrist 1914) - RUSI 6128*, neotype, mature male 298mm TL; MNHN 1987-1291, male 348mm TL; MNHN 1987-1292, male 321mm TL; MNHN 1987-1293, female 277mm TL; MNHN 1987-1294, male 335mm TL; MNHN 1988-0356, male 355mm TL; MNHN 1991-0410, female 272mm TL; MNHN 1991-0411, female 220mm TL; MNHN 1991-0412, male, 330mm TL; RUSI 6129*, adolescent male 235mm TL; RUSI 6131*, immature female 181mm TL; RUSI 6132*, immature female 227mm TL; RUSI 6133*, immature female 196mm TL; RUSI 6134*, immature male 176mm TL; RUSI 6136*, adolescent female 236mm TL; RUSI 6137*, immature female 218mm TL; RUSI 40829*, 4 specimens, all mature males 303mm TL, 310mm TL, 323mm TL, and 326mm TL; and BMNH 1921.3.1.1*, holotype of *H. polystigma* (Regan 1921), mature male 316mm TL.

Holohalaelurus regani (Gilchrist 1922) - SAM 32448*, neotype, mature male 628mm TL; BAH 20020110.01*, mature male 630mm TL; BAH 20020414.06*, mature male 598mm TL; BAH 20020414.07*, mature female 460mm TL; BAH 20020414.08*, mature female 483mm TL; BAH 20020414.09*, gravid female 455mm TL; BAH 20020414.10*, mature female 428mm TL; BAH 20020414.11, gravid female 431mm TL; BAH 20020414.12*, mature male 598mm TL; BAH 20020419.02*, mature male 600mm TL; BAH 20020419.03, mature female 515mm TL; BAH 20020419.04*, gravid female 466mm TL; LJVC 860111, juvenile female 140mm TL; RUSI 952, 2 specimens, both juvenile females, 254mm TL and 205mm TL; RUSI 2800*, juvenile female 349mm TL; RUSI 25726*, mature male 598mm TL; RUSI 38280, adolescent female 351mm TL; RUSI 48813, immature female 224mm TL; RUSI 53725*, mature male 604mm TL; SAM 12986, adolescent male; SAM 12987, 3 specimens, juvenile males, 270mm TL and 420mm TL, immature male, 270mm TL; SAM 12988, gravid female 425mm TL; SAM 12989, juvenile male 270mm TL; SAM 12990, 5 specimens, 4 juvenile females, 176mm TL, 200mm TL, 230mm TL, and 254mm TL, and one juvenile male, 232mm TL; SAM 12991, adolescent female; SAM24408, 2 specimens, one adolescent female, one mature male; SAM 27027; SAM 31695; SAM 32619, mature female; SAM 32995; SAM 33287; SAM 34500; and SAM 34648.

APPENDIX 2. Morphometric and meristic abbreviations based on Compagno (2001) and Human (2006b).

WT, weight; TL, total length; PCL, precaudal length; PD2, pre-second dorsal fin length; PD1, prefirst dorsal fin length; BDL, body length; IDS, inter-dorsal space; D2C, second dorsal - caudal length; DCS, dorsal - caudal space; PAL, pre-anal length; PP2, pre-pelvic length; PP1, pre-pectoral length; SVL, snout - vent length; TRL, trunk length; PPS, pectoral - pelvic space; PAS, pelvic - anal space; VCL, vent - caudal length; PCA, pelvic - caudal space; ACS, anal - caudal space; HDH2, head height 2; HDW2, head width 2; INO, inter-orbital width; HDH, head height; HDW, head width; TRH, trunk height; TRW, trunk width; GIR, girth; ABH, abdomen height; ABW, abdomen width; TAH, tail height; TAW, tail width; CPH, caudal peduncle height; CPW, caudal peduncle width; HDL, head length; PG1, pre-first gillslit length; PSP, pre-spiracular length; POB, pre-orbital length; EYL, eye length; EYH, eye height; SOD, subocular pocket depth; SPL, spiracle length; ESL eye spiracle length; EMA, anterior eye mouth length; ING, inter-gill length; GS1-GS5, gill slit height; POR, pre-oral length; PRN, pre-narial length; MOL, mouth length; ULA, upper labial furrow length; ULH, upper labial furrow height; LLA, lower labial furrow length; NOW, nostril width; INW, internarial width; IOW, internarial outer width; ANF, anterior nasal flap length; P1L, pectoral fin length; P1A, pectoral fin anterior margin length; P1B, pectoral fin base length; P1H, pectoral fin height; P1I, pectoral fin inner margin length; P1P, pectoral fin posterior margin length; P1R, pectoral fin anterior most radial length; DIL, first dorsal fin length; D1A, first dorsal fin anterior margin length; D1B, first dorsal fin base length; D1H, first dorsal fin height; D1I, first dorsal fin inner margin length; D1P, first dorsal fin posterior margin length; P2L, pelvic fin length; P2A, pelvic fin anterior margin length; P2B, pelvic fin base length; P2H, pelvic fin height; P2I, pelvic fin inner margin length; P2P, pelvic fin posterior margin length; P2fused, pelvic fin fused inner margin length; P2free, pelvic fin free inner margin length; CLO, clasper outer length; CLI, clasper inner length; CLB, clasper base length; D2L, second dorsal fin length; D2A, second dorsal fin anterior margin length; D2B, second dorsal fin base length; D2H, second dorsal fin height; D2I, second dorsal fin inner margin length; D2P, second dorsal fin posterior margin length; ANL, anal fin length; ANA, anal fin anterior margin length; ANB, anal fin base length; ANH, anal fin height; ANI, anal fin inner margin length; ANP, anal fin posterior margin length; CDM, dorsal caudal margin length; CPV, pre-ventral caudal margin length; CPU, upper post-ventral caudal margin length; CST, subterminal caudal lobe length; CSW, subterminal caudal lobe width; CTR, terminal caudal fin margin height; CTL, terminal caudal fin lobe length; DPI, first dorsal fin midpoint to pectoral fin insertion length; DPO, first dorsal fin midpoint to pelvic fin origin length; PDI, pelvic fin midpoint to first dorsal fin insertion; PDO, pelvic fin midpoint to second dorsal fin origin; DAO, second dorsal fin origin to anal fin origin length; DAI, second dorsal fin insertion to anal fin insertion length; VERT, total vertebral count; mono, monospondylous vertebral count; predip, precaudal diplospondylous vertebral count; caudaldip, caudal diplospondylous vertebral count; DENT, dentition; UL, upper jaw left tooth count; US, upper jaw symphysial tooth count; UR, upper jaw right tooth count; U tot, upper jaw total tooth count; LL, lower jaw left tooth count; LS, lower jaw symphysial tooth count; LR, lower jaw right tooth count; L tot, lower jaw total tooth count.

A taxonomic review of the Western Indian Ocean goatfishes of the genus *Upeneus* (Family Mullidae), with descriptions of four new species

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Abstract. The taxonomy of the goatfish species of the genus *Upeneus* from the Western Indian Ocean is reviewed. Sixteen species are recognized: *U. davidaromi, U. doriae, U. guttatus, U. indicus* sp. nov., *U. margarethae* sp. nov., *U. mascareinsis, U. moluccensis, U. oligospilus, U. pori, U. suahelicus* sp. nov., *U. sulphureus, U. sundaicus, U. supravittatus* sp. nov., *U. taeniopterus, U. tragula,* and *U. vittatus. Upeneus oligospilus,* which had been synonymized with *U. tragula,* is resurrected as a valid species, and *U. taeniopterus* is shown to be a senior synonym of *U. arge.* A neotype is designated for *U. vittatus,* the type species of the genus, and described. Several new occurrences of species in distinct areas of the Western Indian Ocean are documented. Four species complexes are distinguished, based on numbers of dorsal-fin spines, gill rakers and pectoral-fin rays, and caudal-fin colour. These complexes include 25 of the total 26 valid *Upeneus* species. Based on examination of 24 species from the Indo-Pacific, the Atlantic and the Mediterranean, within-group comparisons are made using the best distinguishing characters. Fresh colouration of the head, body and fins is important for species diagnosis. The number and the configuration of bars on the caudal fin are also useful to distinguish several species. Dark bars often persist in preserved fish and can be used to identify both fresh and preserved *Upeneus* specimens of several species. Morphometric characters are shown to clearly distinguish many species and provide valuable information on differentiation in body shape among populations and life-history stages. Implications for further research priorities on the taxonomy of *Upeneus* are discussed.

Keywords: Morphology, colour patterns, new species, Mullidae, *Upeneus,* Western Indian Ocean

INTRODUCTION

The Western Indian Ocean region extends from South Africa to the Northern Red Sea, the Persian Gulf, Sri Lanka, and a line south from the tip of India. The fish fauna of this large area that comprises many different coastal, island, and deep-water habitats is not well known. Only a few parts of this area have been studied and a comprehensive inventory of the entire region is lacking. Preparation of a book on the coastal fishes of the Western Indian Ocean has motivated detailed taxonomic studies of the fishes of this area. One of the groups urgently requiring revision is the goatfish genus *Upeneus.*

The genus *Upeneus* Cuvier 1829 was revised by Lachner (1954), who recognized 10 species. Subsequently an additional seven species were described: *U. mascareinsis* Fourmanoir & Guézé 1967 from Réunion Island, *U. crosnieri* Fourmanoir & Guézé 1967 from Madagascar, *U. pori* Ben-Tuvia & Golani 1989 from the Red Sea, *U. francisi* Randall & Guézé 1992 from Norfolk Island, New Zealand, *U. davidaromi* Golani 2001 from the Red Sea, *U. australiae* Kim & Nakaya 2002 from Queensland, NE Australia, and *U. mouthami* Randall & Kulbicki 2006 from the Chesterfield Bank in the Coral Sea. One species, *Upeneus crosnieri,* was later synonymized with *U. guttatus* (Day 1868) (Bauchot et al. 1985). Another species, *U. oligospilus* Lachner 1954, described from the Persian Gulf, was assumed to have only subspecies status by Randall (1995) and was more recently synonymized with *U. tragula* by Randall & Kulbicki (2006).

The only previous review of the Western Indian Ocean *Upeneus* species dates back ca. 25 years (Kumaran & Randall 1984) and lists nine species: *Upeneus asymmetricus* Lachner 1954, *Upeneus bensasi* (Temminck & Schlegel 1843), *Upeneus luzonius* Jordan & Seale 1907, *Upeneus moluccensis* (Bleeker 1855), *Upeneus sulphureus* Cuvier 1829, *Upeneus sundaicus* (Bleeker 1855), *Upeneus taeniopterus* Cuvier 1829, *Upeneus tragula* Richardson

1846, and *Upeneus vittatus* (Forsskål 1775). Of these, Randall et al. (1993) found that *U. bensasi* was a junior synonym of *U. japonicus* (Houttuyn 1782). In a review of the goatfishes of the western Central Pacific, Randall (2001) reported that *U. arge* Jordan & Evermann 1903 occurred at several Western Indian Ocean localities. The need for a review of the Western Indian Ocean species became evident when we participated in a cruise of the Dr. Fridtjof Nansen in the southWestern Indian Ocean from September to November 2007. *Upeneus* species that were collected could not be identified using the available literature on the coastal fishes of this area.

A particular problem in the taxonomy of the Mullidae is the dearth of diagnostic meristic characters. One of the few useful meristic characters is the number of dorsal-fin spines, which requires careful examination in order to detect the minute, recumbent first spine in the eight-spine species group that distinguishes it from the seven-spine group (Lachner 1954; Kim & Nakaya 2002). Another important character is the number of pectoral-fin rays which may differ among species by only one ray. A third useful character is the number of gill rakers. These can be separated into several sub-characters according to position on the lower or upper limb and whether they are rudimentary or well-developed. The number of lateral-line scales is often used, but this is a less reliable character, as scales are frequently lost during collecting, transport or preservation. Also, in many species the scales extend from the body onto the base of the caudal fin and hence

Table 1. Abbreviations and description of characters.

Morphometric characters	
SL	standard length, distance between snout tip and caudal fin base at mid-body
BODYDD	body depth at first dorsal-fin origin
BODYDA	body depth at anal-fin origin
HALFDD	half body depth (from lateral line downwards) at first dorsal fin origin
HALFDA	half body depth (from lateral line downwards) at anal fin origin
CPDD	caudal-peduncle depth, minimum depth anterior to caudal dorsal origin
CPDW	caudal-peduncle width at position of CPD measurement
HEAD1	maximum head depth, vertical distance at ventral edge of operculum
HEAD2	head depth across a vertical midline through eye
SUBORB	suborbital depth - distance between lower edge of orbit to ventral midline of head
INTORB	interorbital length - least distance between upper bony edges of orbits
HEADL	head length - distance between snout tip to posteriormost margin of operculum
SNOUTL	snout length - distance between snout tip to anterior margin of orbit
PORBL	postorbital length, distance between posterior edge of orbit and posterior margin of operculum
ORBITL	orbit length, horizontal fleshy orbit diameter
ORBITD	orbit depth, vertical fleshy orbit diameter
UJAWL	upper-jaw length - distance between symphysis and posterior end of upper jaw
LJAWL	lower-jaw length - distance between symphysis of lower jaw and posterior end of upper jaw
SNOUTW	snout width – least distance between rear margins of maxilla, with closed mouth
BARBL	barbel length
BARBW	maximum barbel width, horizontal width measured at base of soft part of barbel
SD1	first pre-dorsal length - distance between snout tip to origin of first dorsal fin
SD2	second pre-dorsal length - distance between snout tip to origin of second dorsal fin
D1D2	interdorsal distance - distance between last spine of first dorsal and first ray of second dorsal fin
CPDL	caudal-peduncle length - distance between last anal ray and ventral origin of caudal fin
SANL	pre-anal length - distance between snout tip to origin of anal fin
SPEL	pre-pelvic length - distance between snout tip to origin of pelvic fin
SPEC	pre-pectoral length - distance between snout tip to dorsal origin of pectoral fin
D2ANL	second dorsal-fin depth - distance between origin of second dorsal fin to origin of anal fin
D1PELV	pelvic-fin depth - distance between origin of first dorsal fin to origin of pelvic fin
D1PEC	pectoral-fin depth - distance between origin of first dorsal fin to dorsal origin of pectoral fin
D1B	length of first dorsal-fin base
D2B	length of second dorsal-fin base
CAUH	distance between dorsal caudal-fin origin and upper caudal-lobe tip
ANALB	length of anal-fin base
ANALH	distance between anal-fin origin and anal-fin anterior tip (= to tip of first anal ray)
PELVL	distance between pelvic-fin origin and pelvic-fin tip
PECTL	distance between pectoral-fin dorsal origin and pectoral-fin tip
PECTW	width of pectoral-fin base
D1H	first dorsal-fin height - distance between first dorsal-fin origin and first dorsal-fin anterior tip (= to tip of first long dorsal-fin spine)
D2H	second dorsal-fin height - distance between second dorsal-fin origin and second dorsal-fin anterior tip (= to tip of second dorsal-fin ray)
Meristic characters	
D1	first dorsal-fin spines
P	pectoral-fin rays
GrUud	rudimentary (= width larger than its depth) gill rakers on upper limb
GrUd	developed gill rakers on upper limb
GrLd	developed gill rakers on lower limb (including gill raker in corner)
GrLud	rudimentary gill rakers on lower limb
GrU	total gill rakers on upper limb
GrL	total gill rakers on lower limb
Gr	total gill rakers (including all rudiments)
LLscal	scales along lateral line to caudal-fin base (excluding scales on caudal fin)

it may be difficult to count the exact number of scales. There has consequently been considerable variation in scale counts (Thomas 1969).

In this account we examined 252 specimens of 24 species from the Western Indian Ocean from recent field collections and several museums, as well as comparative material from the Eastern Indian Ocean, the Pacific, the Mediterranean and the Atlantic. One of the goals was to prepare a key to the Western Indian Ocean species that could be used for both fresh and preserved fish. Special emphasis is placed on the use of relatively quickly identifiable meristic, morphometric and colour characters. Forty morphometric characters were recorded to compare body shape variation among individuals and species. A further goal of this study was to designate a neotype for *Upeneus vittatus*, as no original type material exists (Randall 1974 and pers. comm.).

MATERIALS AND METHODS

Abbreviations and descriptions of 51 characters are provided in Table 1. An overview of all *Upeneus* species currently recognized as valid is given in Table 2. Morphometric characters were measured with an electronic caliper and expressed as % SL. For comparison with earlier studies—and in order to facilitate the application in the field—the diagnostically most important morphometric characters are provided as ratios of the SL in the key and in Table 3c. Morphometric ratios less than 100 are given to two significant digits.

Only meristic characters that vary among species are referred to in the diagnoses and comparisons: the number of dorsal-fin spines, pectoral-fin rays, rudimentary and developed gill rakers on lower and upper limb, and lateral-line scales. Rare counts are given in parentheses. In order to see the first minute dorsal-fin spine in eight-spine species a stereomicroscope was used. Sometimes it was also necessary to move the scales at the base of the second spine to see the first spine. Gill rakers were identified as rudimentary if their length was less than their width. The gill raker in the angle between the upper and lower limbs of the first gill arch was included in the count for the lower limb. Lateral-line scale counts are difficult on specimens with missing scales and do not include scales on the caudal fin.

Measurements showing high overall intraspecific variation, e.g. fin distances from the snout, were not included in the diagnoses and only rarely in species comparisons. Body depth measurements were only considered when there was consistent co-variation with other closely correlated measurements.

Colour characters that fade in preserved fish, particularly yellowish, pale brown or reddish patterns, were only included as supplementary information along with comments on their restricted applicability. Bands on the dorsal fins are often difficult to detect on preserved fish and were not considered in the key with the exception of the black first dorsal-fin tip which is usually retained. Because the latter occurs independently of other markings, it was treated separately in all cases and was not included in counts of dorsal-fin bands. Counts of caudal-fin bars include all bars from the base of each lobe to the lobe tip. The count of bars on the upper caudal-fin lobe also includes the bar close above or behind the end of lateral line.

Colour photographs for each species were selected from the Western Indian Ocean material that we examined in the current study, or material from the area that was identifiable (Plates 1, 2). Caudal fin photographs of selected preserved specimens were used to prepare drawings of caudal fin colour patterns (Plate 3).

In cases where species showed no clear separation in any one character, but where a combination of several characters showed only minor overlap, Principal Component Analysis (PCA), with size-adjustment based on the residuals gained from log-log regressions of the morphometric variables with standard length, was used to obtain information on the optimal distinction (e.g., Uiblein & Winkler 1994; Nielsen 2002).

Complementary information on species distributions was obtained from Fischer et al. (1990), Randall (2001), Randall & Kulbicki (2006) and Fricke et al. (2009).

TAXONOMY

Genus *Upeneus* Cuvier 1829

Upeneus Cuvier 1829: 157. Type species *Mullus vittatus* (Forsskål 1775) by subsequent designation of Desmarest 1856.

Diagnosis. Dorsal fins VII or VIII + 9; anal fin I, 6; pelvic fins I, 5; pectoral-fin rays 13(12)–17; principal caudal-fin rays 7 + 8 (median 13 branched); gill rakers 4–9 + 14–24 = 18–33; lateral-line scales 28–39, lateral line complete; small scales present basally on second dorsal, anal and caudal fins; small teeth present on vomer, palatines and both jaws, multiserial and villiform on jaws; body oblong, slightly compressed; barbel length in adults 4–7 times in SL, snout length 7–11 times in SL, subequal to postorbital length (7–10 times in SL); in fresh fish lateral body stripes and/or caudal-fin bars of differing colour, dark caudal-fin bars frequently retained on preserved fish.

Distribution (Table 2). In all major oceans, tropical to subtropical, only a single species in the Atlantic and two in the Mediterranean, both so-called "Lessepsian" immigrants from the Red Sea after the opening of the Suez Canal (Ben-Tuvia 1966).

Remarks. We recognize 26 species as valid, 16 species from the Western Indian Ocean (Table 2). Smith (1965) considered *Upeneus queketti* Gilchrist & Thompson 1908, described from Durban, as a synonym of *Mulloidichthys auriflamma* (Forsskål 1775). Bauchot et al. (1985) considered *U. niebuhri* Guézé 1976, described from the Gulf of Suez, a synonym of *U. tragula*.

SPECIES ACCOUNTS

Based on a combination of the number of dorsal-fin spines, gill rakers, number of pectoral-fin rays, and bars on caudal fin (all used in earlier accounts, e.g. Lachner 1954, Thomas 1969, Sainsbury et al. 1985, Golani 2001, Randall 2001, Kim & Nakaya 2002), four major species complexes can be distinguished (Table 2).

Species complex 1, the "*japonicus* group": 7 dorsal-fin spines distinguish this group clearly from all others; in addition, these species have 21–32 total gill rakers and 13–15 pectoral-fin rays; fresh fish of this group all have bars on the upper caudal-fin lobe and several species also on the lower caudal-fin lobe. This complex includes *Upeneus guttatus* and *U. pori* and the non-Western Indian Ocean species, *U. asymmetricus*, *U. australiae*, *U. francisi*, *U. japonicus*, and *U. parvus*, the last being the only Atlantic representative of the genus.

Species complex 2, the "*tragula* group": 8 dorsal-fin spines, 18–25(rarely 26) total gill rakers, and 13–14 (rarely 15) pectoral-fin rays; all species with bars on the upper caudal-fin lobe and several with bars on the lower caudal-fin lobe. This complex includes *U. margarethae* sp. nov., *U. oligospilus*, *U. sundaicus*, *U. taeniopterus*, *U. tragula*, and the non-Western Indian Ocean species *U. luzonius*, and *U. mouthami*.

Species complex 3, the "*moluccensis* group": 8 dorsal-fin spines, 26(rarely 25)–33 total gill rakers, 15(rarely 14)–17 pectoral-fin rays, and no bars on the lower caudal-fin lobe, but some species have bars on the upper caudal-fin lobe. This complex includes *U. doriae*, *U. moluccensis*, *U. sulphureus*, and the non-Western Indian Ocean species *U. quadrilineatus*.

Species complex 4, the "*vittatus* group": 8 dorsal-fin spines, 26–32 total gill rakers, 15–17 pectoral-fin rays, and bars on both caudal-fin lobes in fresh and preserved fish. This complex includes *U. davidaromi*, *U. indicus* sp. nov., *U. mascareinsis*, *U. suahelicus* sp. nov., *U. supravittatus* sp. nov., *U. vittatus*, and the non-Western Indian Ocean species *U. subvittatus*.

The Pacific species *Upeneus filifer* has 8 dorsal-fin spines with a unique, extremely long second spine that extends beyond the base of the second dorsal fin. This species is not included in any of the four species complexes; it has 24–27 gill rakers, 13 or 14 pectoral-fin rays, and no bars on the caudal fin (Randall & Kulbicki 2006, Uiblein, unpublished data).

Table 2. Distribution and taxonomic grouping of all 26 currently recognized *Upeneus* species. The species occurring in the Western Indian Ocean are emphasized in bold.

Species	Distribution	Species group
Upeneus asymmetricus Lachner, 1954	W Pacific	*japonicus* group
Upeneus australiae Kim and Nakaya, 2002	E Indian Ocean, W Pacific	*japonicus* group
***Upeneus davidaromi* Golani, 2001**	Red Sea	*vittatus* group
***Upeneus doriae* (Günther, 1869)**	Persian Gulf, Gulf of Oman	*moluccensis* group
Upeneus filifer (Ogilby, 1910)	W Central and SW Pacific	-
Upeneus francisi Randall and Guézé, 1992	SW Pacific	*japonicus* group
***Upeneus guttatus* (Day, 1868)**	Indian Ocean, W Pacific	*japonicus* group
***Upeneus indicus* sp. nov.**	W Indian Ocean (SW India)	*vittatus* group
Upeneus japonicus (Houttuyn, 1782)	W Pacific	*japonicus* group
Upeneus luzonius Jordan and Seale, 1907	W Pacific	*tragula* group
***Upeneus margarethae* sp. nov.**	Indian Ocean, SW Pacific (Arafura Sea)	*tragula* group
***Upeneus mascareinsis* Fourmanoir and Guézé, 1967**	Indian Ocean	*vittatus* group
***Upeneus moluccensis* (Bleeker, 1855)**	Indian Ocean, W Pacific, E Mediterranean	*moluccensis* group
Upeneus mouthami Randall and Kulbicki, 2006	W Central Pacific	*tragula* group
***Upeneus oligospilus* Lachner, 1954**	Persian Gulf	*tragula* group
Upeneus parvus Poey, 1852	W Atlantic	*japonicus* group
***Upeneus pori* Ben-Tuvia and Golani, 1989**	W Indian Ocean, E Mediterranean	*japonicus* group
Upeneus quadrilineatus Cheng and Wang, 1963	E Indian Ocean, West Pacific	*moluccensis* group
Upeneus subvittatus (Temminck and Schlegel, 1843)	W Pacific	*vittatus* group
***Upeneus suahelicus* sp. nov.**	W Indian Ocean, Red Sea	*vittatus* group
***Upeneus sulphureus* Cuvier, 1829**	Indian Ocean, W Pacific	*moluccensis* group
***Upeneus sundaicus* (Bleeker, 1855)**	Indian Ocean, W Pacific	*tragula* group
***Upeneus supravittatus* sp. nov.**	Indian Ocean (S India, Sri Lanka)	*vittatus* group
***Upeneus taeniopterus* Cuvier in Cuvier and Valenciennes, 1829**	Indian Ocean, Central Pacific	*tragula* group
***Upeneus tragula* Richardson, 1846**	Indian Ocean, W Pacific	*tragula* group
***Upeneus vittatus* (Forsskål, 1775)**	Indian Ocean, W and Central Pacific	*vittatus* group

KEY TO THE WESTERN INDIAN OCEAN SPECIES OF *UPENEUS*
(see also Table 3, Plates 1–3)

1a. Dorsal-fin spines 7, first 2 spines usually the longest; pectoral-fin rays 13–14; total gill rakers 23–27; lateral-line scales 28–31; pectoral and pelvic fins subequal in length 2

1b. Dorsal-fin spines 8, first spine minute, recumbent, partly hidden by skin and scales at fin origin; pectoral-fin rays 13–17; total gill rakers 19–33; lateral-line scales 28–39; pectoral and pelvic fins subequal in length or pectoral fins longer than pelvic fins 3

2a. Pectoral-fin rays mostly 13 (rarely 14); total gill rakers 23–25; body red dorsally, preserved fish pale brown, not darker dorsally; with caudal-fin bars not retained (Indo-West Pacific) .... *U. guttatus*

2b. Pectoral-fin rays 14; total gill rakers 26–27; body grey to reddish-brown dorsally, preserved fish darker dorsally; with caudal-fin bars commonly retained (Red Sea to Oman, Madagascar, Mediterranean) .... *U. pori*

3a. Total gill rakers 18–24; rakers on lower limb 14–18; pectoral-fin rays 13–14; pectoral and pelvic fins subequal in length 4

3b. Total gill rakers 26–33; rakers on lower limb 18–24; pectoral-fin rays 14–17; pectoral fins longer than pelvic fins 8

4a. Dark dots or blotches on body and paired fins; first dorsal-fin tip dark; one brown to black mid-lateral body stripe in fresh and preserved fish; upper-jaw length 7.1–9.2 times in SL 5

4b. No dark dots or blotches on body and paired fins; no dark dorsal-fin tip; one or two yellowish or pale brown lateral body stripes on fresh fish; upper-jaw length 7.9–9.8 times in SL 6

5a. Total number of caudal-fin bars 6–9 (6 or fewer in juveniles < 7 cm SL); caudal-fin length 3.5–4.1 times in SL and 1.0–1.3 times in head length; pelvic-fin length 4.7–6.0 times in SL (Persian Gulf) .... *U. oligospilus*

5b. Total number caudal-fin bars 10 or more (7–10 in juveniles < 7 cm SL); caudal-fin length 3.1–3.6 times in SL and 0.9 - 1.1 times in head length; pelvic-fin length 4.2–5.0 times in SL (Indo- West Pacific) .... *U. tragula*

6a. Pectoral-fin length 5.0–5.8 times in SL; lateral-line scales 35–39; upper caudal-fin lobe with 4-8 dark bars, well retained on preserved fish; fresh fish with a pale brown mid-lateral body stripe and a weaker, more yellowish stripe below (Indo-Central Pacific) .... *U. taeniopterus*

6b. Pectoral-fin length 4.0–4.9 times in SL; lateral-line scales 28–34; upper caudal-fin lobe with 4-6 red or grey bars, not or only traces retained on preserved fish; fresh fish with a yellow or pale brown mid-lateral body stripe 7

7a. Total gill rakers 21–24; lateral-line scales 28–30; first dorsal-fin height 4.3–5.1 times in SL; caudal-peduncle depth 9.0–10 times in SL; barbels white; four red bars on upper caudal-fin lobe in fresh fish, three distally from fork (Indian Ocean and Arafura Sea) .... *U. margarethae* sp. nov.

7b. Total gill rakers 18–21; lateral-line scales 31–34; first dorsal-fin height 3.4–4.1 times in SL; caudal-peduncle depth 7.9–8.7 times in SL; barbels frequently yellow in fresh fish; 5–6 red or grey bars on upper caudal-fin lobe in fresh fish (Indo-Pacific) .... *U. sundaicus*

8a. No bars on caudal fin, also not in live or fresh fish; first dorsal-fin tip black or pale brown to yellowish, colour may disappear on preserved fish; body depth at first dorsal-fin origin 3.0–3.7 times in SL in adult fish (> 7 cm SL); pectoral-fin length 1.1–1.2 times in head length 9

8b. Caudal fin with either 6–8 red bars on upper lobe only or 7–13 pale brown to black bars on entire fin (3–6 bars on upper and 3–5 on lower lobe); bars conspicuous in live fish and mostly well retained on preserved fish; brown to black first dorsal-fin tip, retained on preserved fish; body depth at first dorsal-fin origin 3.2–4.5 times in SL in adult fish (> 7 cm SL); pectoral-fin length 1.0–1.6 times in head length 10

9a. Total gill rakers 29–33; rakers on lower limb 22–24; tip of first dorsal fin pale brown to yellowish in fresh fish, not or only faintly retained on preserved fish; fresh fish with a narrow, yellow mid-lateral body stripe; anal-fin height 6.7–7.0 times in SL; first dorsal-fin height 4.5–5.0 times in SL; second dorsal-fin height 6.6–7.3 times in SL (Persian Gulf and Gulf of Oman) .... *U. doriae*

9b. Total gill rakers 27–28; rakers on lower limb 19–21; tip of first dorsal fin black in fresh and preserved fish; fresh fish with two conspicuous, yellow lateral body stripes; anal-fin height 5.4–6.4 times in SL; first dorsal-fin height 3.9–4.4 times in SL; second dorsal-fin height 5.5–5.9 times in SL (Indo-West Pacific) .... *U. sulphureus*

10a. No bars on lower caudal-fin lobe; upper lobe with 6–8 red bars, faintly retained on preserved fish; one conspicuous yellow or gold mid-lateral body stripe in fresh fish; head length 3.5–3.7 times in SL; head depth through eye 5.8–6.3 times in SL (Indo-West Pacific, eastern Mediterranean) .... *U. moluccensis*
10b. Lower caudal-fin lobe with 3–4 brown or black bars; upper caudal-fin lobe with 3–6 brown or black bars; no or at least two lateral body stripes in fresh fish; head length 3.0–3.6 times in SL; head depth through eye 4.6–6.1 times in SL 11

11a. Caudal-fin bars pale brown to dark brown, uniformly coloured, pale spaces between bars of nearly equal width; bars on upper caudal-fin lobe curved; two yellow or pale brown lateral body stripes on fresh fish; body depth at anal-fin origin 3.7–4.6 times in SL; pectoral-fin length 3.5–4.4 times in SL and 1.1–1.3 in head length; total gill rakers 26–32 12
11b. Caudal-fin bars at least partly black or dark brown, vary in colour intensity, bars or the spaces between them vary often in width; caudal-fin bars on both lobes mostly straight and not curved; no or more than two lateral body stripes on fresh fish; body depth at anal-fin origin 4.1–5.6 times in SL; pectoral-fin length 4.1–4.7 times in SL and 1.3–1.6 in head length; total gill rakers 26–29 14

12a. Pectoral-fin length 4.2–4.4 times in SL and 1.3 times in head length, shorter than body depth at anal-fin origin, the latter 3.7–3.9 times in SL (SW India) .... *U. indicus* sp. nov.
12b. Pectoral-fin length 3.5–4.1 times in SL and 1.1–1.2 times in head length, subequal to or longer than body depth at anal-fin origin, the latter 3.8–4.6 times in SL 13

13a. Total number of gill rakers 26–28; rakers on lower limb 19–21; barbel length 4.9–6.6 times in SL; pectoral-fin length 3.8–4.1 times in SL and 0.9–1.0 times in (= subequal to) body depth at anal-fin origin; head length 3.2–3.6 times in SL (East Africa and southern Red Sea) .... *U. suahelicus* sp. nov.
13b. Total number of gill rakers 29(rarely 28)–32; rakers on lower limb 21–23; barbel length 4.3–5.4 times in SL; pectoral-fin length 3.5–4.0 times in SL and 0.8–0.9 times in (= greater than) body depth at anal-fin origin; head length 3.0–3.4 times in SL (South India and Sri Lanka) .... *U. supravittatus* sp. nov.

14a. Head depth through eye 4.6–4.8 times in SL; anal-fin height 5.8–6.3; second dorsal-fin height 5.8–6.1 times in SL; no lateral body stripe in fresh fish (Red Sea) .... *U. davidaromi*
14b. Head depth through eye 5.0–6.1 times in SL; anal-fin height 6.3–7.9; second dorsal-fin height 6.2–7.2 times in SL; no or more than two lateral body stripes on fresh fish 15

15a. Body depth at anal-fin origin 4.6–5.6 times in SL; caudal-peduncle depth 11–12 times in SL; first dorsal-fin height 4.4–5.2 times in SL; vertical length of black tip on first dorsal fin and width of largest bar and/or interspace between distal-most bars of lower caudal-fin lobe narrower than orbit; no lateral body stripes on fresh fish (Indian Ocean) .... *U. mascareinsis*
15b. Body depth at anal-fin origin 4.1–4.7 times in SL; caudal-peduncle depth 8.6–10 times in SL; first dorsal-fin height 4.0–4.5 times in SL; vertical length of black tip on first dorsal fin and width of largest bar and/or interspace between distal-most bars of lower caudal-fin lobe sub-equal to or wider than orbit; 3 or 4 lateral body stripes on fresh fish: two yellow or coppery stripes mid-laterally and below, and one or two brown or pale brown stripes dorsally (Indo-West Pacific) .... *U. vittatus*

Upeneus davidaromi Golani 2001
(Tables 3, 8; Plates 1, 3)

Upeneus subvittatus (non Temminck & Schlegel 1843): Ben-Tuvia & Kissil 1988: 12, Fig. 11 (type locality: Elat, Gulf of Aqaba, Red Sea); depth range 200–600 m; Baranes & Golani 1993: 310.
Upeneus vitatus [*sic*] *(non* Forsskål): Khalaf & Disi 1997: 120 (misspelling of name).
Upeneus davidaromi Golani 2001: 112, Fig. 1a (type locality Eilat, Gulf of Aqaba).

DIAGNOSIS. Dorsal fins VIII + 9; pectoral fins 15 or 16; gill rakers 7 + 19–20 = 26–27; lateral-line scales 33–36; body depth at first dorsal-fin origin 24% SL; body depth at anus 20–21; caudal-peduncle depth 9.2–9.4; maximum head depth 24; head depth through eye 21–22; head length 32–33; orbit length 9.1–9.8; upper jaw length 14–15; barbel length 20–21; caudal-fin length 28–29; anal-fin height 16–17; pelvic-fin length 20; pectoral-fin length 23–24; first dorsal-fin height 20–21; second dorsal-fin height 16–17% SL; total number of caudal-fin bars 8–10, 5–6 dark bars on upper caudal-fin lobe (including one bar close to rear end of lateral line), colour of bars changing from pale brown proximally to dark brown or black at rear caudal-fin margin and tip in fresh fish; 3–4 bars on lower caudal-fin lobe, slightly increasing in width distally, one usually at tip and smaller, the distal-most two or three bars almost entirely dark brown or black; first dorsal-fin tip black;

Table 3. Meristic and colour characters (a), morphometric characters as %SL (b), and morphometric characters as ratios of SL (c) for the Western Indian Ocean *Upeneus* species.

(a)	Dorsal spines	Pectoral-fin rays	Gill rakers on upper limb	Gill rakers on lower limb	Total gill rakers	Lateral-line scales	Bars on upper caudal-fin lobe *	Bars on lower caudal-fin lobe	Total bars on caudal fin	Caudal-fin bars retained in preserved fish	Nr. of lateral body stripes	Colour of lateral body stripes	Lateral body stripe(s) retained in preserved fish	Dark first dorsal-fin tip [retained in preserved fish]
davidaromi	8	15-16	7	19-20	26-27	33-36	5-6	3-4	8-10	yes	0	no	-	yes [yes]
doriae	8	15-17	7-9	22-23	29-32	33-35	0	0	0	-	1	yellow	faintly/no	yes [faintly/no]
guttatus	7	13-14	6-8	16-18	23-25	28-31	5 *	5-8 *	10-13 *	no	0	no	-	no
indicus sp. nov.	8	15-16	9	20-22	29-31	36	4-6	4	8-10	faintly	3	pale brown	no	yes [yes]
margarethae sp. nov.	8	13-14	4-7	16-18	21-24	28-30	4 *	5-6 *	9-10 *	no	1	yellow	no	no
mascareinsis	8	15-16	7-8	19-22	26-29	35-38	3-6	3-4	7-10	yes	0	no	-	yes [yes]
moluccensis	8	14-16	7-8	18-20	26-27	33-35	6-8	0	6-8	faintly	1	yellow	no	no **
oligospilus	8	13-14	4-7	16-18	20-24	28-31	3-5 ***	3-4 ***	6-9 ***	yes	1	brown to black	yes	yes [yes]
pori	7	14	7-8	18-20	26-27	29-30	4-6	5-9	11-15	yes	0	no	-	no
suahelicus sp. nov.	8	15-16	6-8	19-21	26-28	34-35	4-6	3-4	8-10	yes/faintly ****	2	pale brown	no	yes [yes]
sulphureus	8	15-17	7-8	19-21	27-28	34-37	0	0	0	-	2	yellow	faintly/no	yes [yes]
sundaicus	8	13-14	4-5	14-15	18-20	31-34	5-6 *	0	5-6 *	no	1	pale brown	no	no
supravittatus sp. nov.	8	16-17	7-9	21-23	28-32	34-36	4-6	3-5	8-10	yes	2	pale brown	no	yes [yes]
taeniopterus	8	13-14	5-6	16-17	21-23	35-39	4-8	3-6	7-13	yes	2	pale brown	no	no
tragula	8	13-14	5-8	14-17	19-24	28-30	5-6 ***	5-6 ***	10-12 ***	yes	1	brown to black	yes	yes [yes]
vittatus	8	15-16	7-8	19-21	27-29	36-38	4-5	3-4	7-9	yes	3 or 4	2 yellow, 1 or 2 light brown above	no	yes [yes]

*** not retained in preserved fish; ** sometimes a very tiny dark patch at or close to tip; *** less in juveniles < 70 mm; **** faintly retained in Red Sea specimen**

(b)	Body depth at first dorsal-fin origin	Body depth at anal-fin origin	Caudal-peduncle depth	Maximum head depth	Head depth through eye	Head length	Orbit length	Upper jaw length	Barbel length	Caudal-fin length	Anal-fin height	Pelvic-fin length	Pectoral-fin length	First dorsal-fin height	Second dorsal-fin height
davidarami	24	20-21	9.2-9.4	24	21-22	32-33	9.1-9.8	14-15	20-21	28-29	16-17	20	23-24	20-21	16-17
doriae	27-29	24	10-12	23-24	18-22	29-31	6.6-9.7	11	16-20	26-28	14-15	18-20	25-28	20-22	14-15
guttatus	22-25	19-23	9.3-11	18-22	15-19	26-30	6.3-8.8	9.6-12	16-19	25-30	15-19	19-23	20-22	20-24	14-18
indicus sp. nov.	29-31	26-27	11	25	18-19	30-31	7.0-7.1	12	19-20	27-28	13-14	19	23-24	23-24	15-16
margarethae sp. nov.	22-26	20-24	9.3-11	19-23	15-19	27-31	6.5-9.1	10-12	16-20	27-31	14-18	20-24	21-25	20-23	16-20
mascareinsis	22-26	18-22	8.3-9.3	20-24	17-19	30-34	7.7-11	12-14	18-24	25-29	13-16	18-20	21-24	19-23	15-16
moluccensis	24-26	21-23	9.0-10	20-22	16-17	27-29	7.3-8.9	11-12	15-17	27-30	13-15	17-22	25-27	20-23	14-16
aligospilus	23-26	19-22	9.8-11	20-23	15-19	29-32	5.4-7.9	11-13	16-20	24-28	15-18	17-21	18-22	18-22	16-18
pari	21-24	20-22	9.1-10	18-20	15-16	26-28	6.3-7.8	10-11	16-18	27-29	16-17	20-23	20-22	20-21	15-16
suahelicus sp. nav.	26-30	22-26	9.9-11	22-25	17-19	28-31	7.1-9.4	12-14	15-20	26-30	15-17	18-21	25-26	22-26	16-18
sulphureus	29-33	25-27	11-12	23-25	18-20	29-30	7.4-8.7	11-13	17-21	27-30	16-18	20-22	24-26	23-26	17-18
sundaicus	25-28	22-24	11-13	21-23	17-20	27-30	6.1-7.2	11-12	18-21	26-29	16-18	20-23	21-23	25-29	16-18
supravittatus sp. nov.	26-30	22-25	9.9-11	23-26	17-20	30-33	6.8-8.5	12-14	19-23	27-31	14-17	18-21	25-28	23-26	15-17
taeniopterus	22-25	20-23	9.7-11	17-21	14-17	25-29	4.4-6.3	11-13	17-21	28-32	15-17	18-20	17-20	20-23	14-16
tragula	22-26	20-23	9.9-11	19-23	15-17	27-31	6.1-8.3	11-14	15-19	28-32	16-19	20-24	19-21	21-24	17-20
vittatus	25-29	21-24	9.9-12	21-26	18-20	30-31	7.0-8.7	11-13	17-21	26-30	15-16	18-21	22-24	22-25	14-16

(c)	Body depth at first dorsal-fin origin	Body depth at anal-fin origin	Caudal-peduncle depth	Maximum head depth	Head depth through eye	Head length	Orbit length	Upper jaw length	Barbel length	Caudal-fin length	Anal-fin height	Pelvic-fin length	Pectoral-fin length	First dorsal-fin height	Second dorsal-fin height
davidaromi	4.1	4.7-5.0	11	4.1-4.2	4.6-4.8	3.0-3.1	10-11	6.7-7.2	4.8-5.0	3.5-3.6	5.8-6.3	5.0-5.1	4.3	4.7-4.9	5.8-6.1
dariae	3.4-3.7	4.1-4.2	8.6-9.6	4.1-4.4	4.6-5.5	3.2-3.5	10-15	8.8-9.2	5.0-6.4	3.5-3.8	6.7-7.0	5.1-5.7	3.6-4.0	4.5-5.0	6.6-7.3
guttatus	4.0-4.6	4.4-5.2	9.3-11	4.5-5.5	5.3-6.7	3.4-3.9	11-16	8.3-10	5.2-6.3	3.4-4.1	5.3-6.8	4.4-5.2	4.5-5.0	4.1-5.0	5.6-7.1
indicus sp. nav.	3.2-3.4	3.7-3.9	8.9-9.0	4.0-4.1	5.3-5.4	3.2-3.3	14	8.0-8.2	5.1-5.3	3.5-3.8	7.3-7.5	5.4	4.2-4.4	4.2-4.3	6.4-6.8
margarethae sp. nov.	3.8-4.6	4.2-5.1	9.0-11	4.3-5.2	5.2-6.6	3.2-3.7	11-15	8.5-9.8	5.1-6.4	3.3-3.7	5.6-7.1	4.2-5.1	4.0-4.9	4.3-5.1	4.9-6.3
mascareinsis	3.8-4.5	4.6-5.6	11-12	4.2-5.0	5.2-6.1	3.0-3.3	9.5-13	6.9-8.0	4.2-5.4	3.5-4.0	6.3-7.9	5.0-5.6	4.1-4.7	4.4-5.2	6.2-6.9
moluccensis	3.9-4.2	4.3-4.7	9.8-11	4.5-4.9	5.8-6.3	3.5-3.7	11-14	8.5-8.8	6.0-6.6	3.3-3.7	6.7-7.7	4.6-5.8	3.7-4.0	4.4-5.1	6.3-7.3
aligospilus	3.8-4.3	4.6-5.2	9.4-10	4.3-4.9	5.1-6.5	3.2-3.5	13-18	7.5-9.1	5.0-6.4	3.6-4.1	5.5-6.6	4.7-6.0	4.6-5.7	4.5-5.6	5.4-6.3
pari	4.2-4.7	4.6-5.1	10-11	5.0-5.6	6.4-6.8	3.5-3.9	13-16	9.1-9.8	5.6-6.2	3.5-3.7	5.8-6.4	4.4-5.0	4.5-5.1	4.8-5.1	6.1-6.6
suahelicus sp. nov.	3.3-3.9	3.8-4.5	8.7-10	4.0-4.6	5.2-6.0	3.2-3.6	11-14	7.3-8.7	4.9-6.6	3.4-3.8	5.8-6.6	4.8-5.6	3.8-4.1	3.9-4.5	5.5-6.4
sulphureus	3.0-3.4	3.8-4.1	8.6-9.5	4.0-4.3	5.1-5.6	3.3-3.5	12-13	7.5-9.4	4.7-6.0	3.3-3.7	5.4-6.4	4.6-5.1	3.8-4.1	3.9-4.4	5.5-5.9
sundaicus	3.5-4.0	4.1-4.5	7.9-8.7	4.3-4.8	5.0-5.9	3.3-3.7	14-17	8.1-8.9	4.8-5.7	3.5-3.9	5.6-6.4	4.4-5.0	4.4-4.9	3.4-4.1	5.6-6.5
supravittatus sp. nov.	3.3-3.8	4.1-4.6	9.0-10	3.8-4.4	4.9-5.9	3.0-3.4	12-15	7.1-8.7	4.3-5.4	3.2-3.7	5.9-6.9	4.7-5.6	3.5-4.0	3.9-4.4	5.8-6.9
taeniapterus	3.9-4.5	4.4-5.0	9.4-10	4.7-5.9	5.7-7.0	3.5-4.0	16-23	7.9-9.4	4.7-6.0	3.1-3.6	5.8-6.9	5.0-5.7	5.0-5.8	4.3-5.0	6.3-7.2
tragula	3.8-4.5	4.4-5.1	9.0-10	4.3-5.3	5.7-6.6	3.2-3.8	12-16	7.1-9.2	5.4-6.7	3.1-3.6	5.2-6.4	4.2-5.0	4.7-5.3	4.2-4.8	4.9-6.0
vittatus	3.4-4.0	4.1-4.7	8.6-10	3.9-4.7	5.0-5.5	3.2-3.3	12-14	7.7-8.7	4.7-5.8	3.3-3.8	6.4-6.9	4.8-5.5	4.2-4.6	4.0-4.5	6.3-7.2

caudal-fin bars and black dorsal-fin tip retained on preserved fish; barbels white; no lateral body stripes; head and body silvery laterally, the snout and dorsal part of head and body reddish, and belly white in fresh fish; white belly colouration partly retained and body dorsally darkened in preserved fish.

Distribution. Red Sea

Comparisons. A Western Indian Ocean species of the *vittatus* group (Tables 3, 8; Plates 1–3): *Upeneus davidaromi* differs from *U. indicus* in fewer gill rakers, body and caudal-peduncle less deep, deeper head through eye, larger suborbital depth, longer head, larger orbit, longer upper jaw, higher anal fin, lower first dorsal-fin, caudal-fin bars less uniformly coloured, and lateral body stripes absent; from *U. mascareinsis* it differs in deeper head through eye, greater suborbital depth, longer postorbital and head, and body colouration silvery instead of rose-red; it differs from *U. suahelicus* in body and caudal-peduncle less deep, deeper head through eye, larger suborbital depth, longer head and snout, shorter pectoral fins, lower first dorsal-fin, lateral body stripes absent, and caudal-fin bars less uniformly coloured; it differs from *U. supravittatus* in fewer gill rakers, body and caudal-peduncle less deep, deeper head through eye, larger suborbital depth, larger orbit, shorter pectoral fins, lower first dorsal-fin, lateral body stripes absent, and caudal-fin bars less uniformly coloured; and it differs from *U. vittatus* in body less deep at dorsal-fin origin and caudal-peduncle less deep, deeper head through eye, larger suborbital depth, longer head, larger orbit, longer upper jaw, shorter distance between dorsal fins, shorter anal-fin base, lower first dorsal fin, lateral body stripes absent and widest bar on lower caudal-fin lobe smaller.

Remarks. Among the two known deep-water species of *Upeneus* from the Indian Ocean region, *U. davidaromi* occurs deepest, with a reported depth range of 150 to 600 m depth, while the maximum depth reported for *U. mascareinsis* is 400 m (Fourmanoir & Guézé 1967). The photographed specimen (Plate 1) differs from another individual of *Upeneus davidaromi* illustrated in the species description by Golani (2001) in a more regular bar and interspace width on the lower caudal-fin lobe.

Upeneus davidaromi attains 24 cm SL.

Upeneus doriae (Günther 1869)

(Tables 3, 7; Plates 1, 3)

Upeneoides doriae Günther 1869: 445 (type locality: Bender Abassi, Persian Gulf).

Mulloichthys auriflamma (*non* Forsskål): Blegvad & Løppenthin 1944: 133, Plate 7, Fig. 1 (Persian Gulf).

Upeneus doriae: Randall 1995: 243, Fig. 633 (photo of 20 cm fish from Oman); diagnosis and colour photograph; Carpenter et al. 1997: 193, Pl. 13, Fig. 88 (Persian Gulf); Kim & Nakaya 2003, 109 ff., Fig.1; re-description and photograph of preserved fish.

Diagnosis. Dorsal fins VIII + 9; pectoral fins 15–17; gill rakers 7–9 + 22–24 = 29–33; lateral-line scales 33–35; body depth at first dorsal-fin origin 27–29% SL; body depth at anus 24; caudal-peduncle depth 10–12; maximum head depth 23–24; head depth through eye 18–22; head length 29–31; orbit length 6.6–9.7; upper jaw length 11; barbel length 16–20; caudal-fin length 26–28; anal-fin height 14-15; pelvic-fin length 18–20; pectoral-fin length 25–28; first dorsal-fin height 20–22; second dorsal-fin height 14–15% SL; no bars on caudal fin; one narrow, yellow mid-lateral body stripe, usually not retained on preserved fish; first dorsal-fin tip pale brown to yellowish in fresh fish, pigmentation faintly retained or lost in preserved fish; barbels white; body silvery, dorsally darkened in fresh fish and pale to dark brown, sometimes dorally darker in preserved fish.

Distribution. Persian Gulf and Gulf of Oman

Comparisons. Western Indian Ocean species of the *moluccensis* group (Tables 3, 7, Plates 1–3): *Upeneus doriae* differs from *U. moluccensis* in more gill rakers, deeper body and head, no bars on caudal fin, and body colouration silvery vs red in fresh fish; and it differs from *U. sulphureus* in more total gill rakers and gill rakers on lower limb body less deep, shorter pelvic fins, and lower dorsal fins.

Remarks. In their redescription of *Upeneus doriae*, Kim and Nakaya (2003) emphasize the higher number of gill rakers on the lower limb as important for the distinction with *U. sulphureus*. Comparison of material from the two Gulf areas revealed geographic differences in orbit size and caudal-fin length in adult specimens (Table 7). However, because the Gulf of Oman specimens are clearly larger in size than those of the Persian Gulf, the possibility of allometric changes during ontogeny cannot be ruled out. One juvenile (< 58 mm SL) from the Persian Gulf, which was examined in detail, clearly deviated in several morphometric measurements from adult specimens and hence, similar to *U. mascareinsis*, *U. tragula*, and *U. oligospilus*, was treated separately, together with the second juvenile specimen (46 mm SL, Table 7).

Meristic and selected morphometric data, and photographs of fresh and preserved fish from the eastern Gulf of Oman (BPBM 31270, 31268, and 31269) were made available by Jack Randall, Arnold Suzumoto, Jerry Finan and Jeff Williams, indicating that in the Gulf of Oman the first dorsal-fin tip of fresh fish is pale yellowish rather than pale brown, and this pigmentation can be completely lost after preservation. The same is true for the yellow mid-lateral body stripe; the body color in preserved fish varies from pale brown to brown and is in some instances dorsally darker, or a broad darker stripe appears along the mid body. There is a tight overlap in counts, the BPBM material having 31–33 total gill rakers (22–24 on lower limb). If the morphometric measurements of adult fish (> 70 cm SL) examined in the current study are combined with data from the BPBM specimens, important diagnostic characters such as body depth at first dorsal-fin origin (27–30% SL), body depth at anal-fin origin (24–28% SL), and head length (29–35% SL) retain rather narrow ranges and overlap. The BPBM specimens are included as "additional material" in the material list.

Upeneus doriae attains 20 cm SL; it occurs in shallow water to 45 m depth.

Upeneus guttatus (Day 1868)

(Tables 3, 4; Plates 1, 3)

Upenoides guttatus Day 1868: 938 (type locality: Madras, India).

Upeneus crosnieri Fourmanoir & Guézé 1967: 52, Fig.

I/c (type locality Mitsio, Pracel Bank, Madagascar); Bauchot et al. 1985: 7 (synonym of *Upeneoides guttatus* Day 1868).

Upeneus guttatus: Randall & Kulbicki 2006, pp. 301, Figs. 3–4 (diagnosis and two colour photographs).

Upeneus bensasi (non Temminck & Schlegel): De Bruin et al. 1994: 270, Pl. 9, Fig. 136; (Sri Lanka).

Diagnosis. Dorsal fins VII + 9; pectoral fins 13–14 (mostly 13, in 24 of 27 specimens); gill rakers 6–8 + 16–18 = 23–25; lateral-line scales 28–31; body depth at first dorsal-fin origin 22–25% SL; body depth at anus 19–23; caudal-peduncle depth 9.3–11; maximum head depth 18–22; head depth through eye 15–19; head length 26–30; orbit length 6.3–8.8; upper jaw length 9.6–12; barbel length 16–19; caudal-fin length 25–30; anal-fin height 15-19; pelvic-fin length 19–23; pectoral-fin length 20–22; first dorsal-fin height 20–24; second dorsal-fin height 14–18% SL; total bars on caudal fin 10–13, upper caudal-fin lobe with 5 reddish bars, of similar width or narrower than the pale interspaces between the bars, not retained on preserved fish; 5–8 faint, irregular red bars on exterior margin of lower caudal-fin lobe, sometimes extending over entire lobe or absent, not or only traces retained on preserved fish; no lateral body stripes; first dorsal-fin tip pale; barbels yellow or white in fresh fish; body white below lateral line, covered by red pigmentation above lateral line which may also reach down ventrally, forming red patches or blotches; belly white; body pale brown and not dorsally darkened in preserved fish.

Distribution. Red Sea to Somalia, Kenya, Mozambique, South Africa (KwaZulu-Natal), Madagascar, Réunion, Seychelles, India, Sri Lanka, Bay of Bengal, Andaman Sea, Malaysia, Singapore, northern Australia and Philippines.

Comparisons. Western Indian Ocean species of the *japonicus* group (Tables 3, 4, Plates 1, 3): *Upeneus guttatus* differs from *U. pori* in mostly 13 vs 14 pectoral-fin rays, fewer gill rakers, no or only traces of bars vs conspicuous bar patterns on both caudal-fin lobes of preserved fish, and pale brown vs dorsally dark body on preserved fish.

Non-Western Indian Ocean species of the *japonicus* group (Table 4): *Upeneus guttatus* differs from *U. asymmetricus* in fewer gill rakers, half body at anal-fin origin less deep, bars not crossing entire lower caudal-fin lobe in fresh fish, no lateral body stripe in fresh fish, and bars in most cases not retained on preserved fish; from *U. australiae* it differs in mostly 13 vs 14 pectoral-fin rays, lateral body stripe absent in fresh fish, lower caudal-fin lobe not entirely crossed by bars in fresh fish, caudal-fin bars in most cases not retained on preserved fish, and body dorsally paler in preserved fish; from *U. francisi* it differs in mostly 13 vs 14 pectoral-fin rays, fewer gill rakers, shorter head, shorter postorbital length, shorter paired fins and body colour red vs silvery in fresh fish; from *U. japonicus* it differs in fewer gill rakers, shorter barbels, shorter pectoral fins, and bars present along ventral margin of lower caudal-fin lobe in fresh fish; and from the Atlantic *U. parvus* it differs mostly in 13 vs 15 pectoral-fin rays, fewer gill rakers and lateral-line scales, shorter barbels, longer and higher anal fin, shorter pectoral fin, and bars not crossing lower caudal-fin lobe entirely on fresh fish.

Remarks. Bauchot et al. (1985) synonymized *Upeneus crosnieri* Fourmanoir & Guézé 1967 with *U. guttatus* (Day 1868). We follow this conclusion based on examination of the holotype of *U. crosnieri* which overlaps *U. guttatus* in all important characters.

New record for the Red Sea. *Upeneus guttatus* attains 16 cm SL; depth range 8–80 m.

Upeneus indicus sp. nov.

(Tables 3, 8; Plates 1, 3)

Holotype: BPBM 27524, 137 mm, Cochin, western India, collected by J. E. Randall via local fishermen (31-01-1980).

Paratype: BPBM 40987, 132 mm, Cochin, collected together with holotype.

Diagnosis. Dorsal fin VIII + 9; pectoral fins 15–16; gill rakers 9 + 20–22 = 29–31; lateral-line scales 36; body depth at first dorsal-fin origin 29–31% SL; body depth at anal-fin origin 26–27; caudal-peduncle depth 11; maximum head depth 25; head depth through eye 18–19; head length 30–31; orbit length 7.0–7.1; upper jaw length 12; barbel length 19–20; caudal-fin length 27–28; anal-fin height 13-14; pelvic-fin length 19; pectoral-fin length 23–24; first dorsal-fin height 23–24; second dorsal-fin height 15–16% SL; total bars on caudal fin 8–10, 4–6 pale brown bars on upper caudal-fin lobe, 4 of same colour on lower caudal-fin lobe; the three proximal bars on upper caudal-fin lobe slightly curved; caudal-fin bars wider than pale interspaces between them; bars faintly retained on preserved fish; three pale brown lateral body stripes on fresh fish, one mid-lateral stripe reaching from behind head to caudal-fin base, one stripe well below starting behind pectoral-fin base, and a third, short stripe just above lateral line below dorsal fins; length of dark first dorsal-fin tip clearly smaller than orbit; head and body silvery-rose laterally, dorsally dark reddish, and belly silvery white in fresh fish; body in preserved fish uniformly brown.

Description. Measurements in % SL and counts are given in Table 8; morphometric data as ratios of SL for holotype, data for paratype, if different, in brackets: body deep, its depth at first dorsal-fin origin 3.2 [3.4], body depth at anal-fin origin 3.7 [3.8], head length 3.2 [3.3], similar to maximum depth of body and longer than caudal-fin length (3.6 [3.7]), height of second dorsal fin 6.7 [6.3] less than barbel length (5.0 [5.3]); pectoral-fin length 4.2 [4.3], clearly longer than pelvic-fin length (4.8); caudal-peduncle depth 9.1, clearly larger than orbit (14).

Fresh colour (Plate 1): Head and body silvery-rose, belly silvery-white, dorsal surface of body and head reddish; body with three narrow, pale brown lateral stripes, one mid-lateral from head to caudal-fin base, anteriorly well below lateral line, crossing line below second dorsal fin, and connecting to proximal-most bar of upper caudal-fin lobe, one stripe starting behind pectoral-fin base and connecting to proximal-most bar of lower caudal-fin lobe, and a third, short stripe just above lateral line, starting below first dorsal and ending below second dorsal fin; upper lobe of caudal fin white, rays pale rose-gray proximally and hyaline distally, with 5 or 6 pale brown bars, the fin lobe tip dark, the proximal 3 or 4 bars slightly curved; lower caudal-fin lobe white, rays mostly hyaline with 4 straight pale brown bars, the lobe tip pale; bars and white interspaces on both lobes uniform in width, the bars slightly wider than the interspaces; spinous dorsal fin white, with two pale brown horizontal stripes, the lower one thin and considerably separated by a pale white interspace from base, the upper one as wide as the black fin tip above, vertical length of black fin tip smaller than orbit and nearly equal to caudal-fin bar width; all three pale interspaces between stripes wider than stripes or fin tip; soft dorsal fin pale white, with four pale brown horizontal stripes, the uppermost stripe covering the fin tip almost completely except for a tiny pale spot at the very tip itself; the two lower stripes narrow, the lowest one only present on distal part of the fin; the two uppermost stripes of similar width as the middle stripe on the spinous dorsal fin; anal and pelvic fins hyalibane with white rays, rose at base; pectoral fins hyaline.

Preserved colour (Plate 3): Head and body uniformly brown; black, first dorsal-fin tip distinct; lateral body stripes absent; bars on caudal-fin lobes faint and rather indistinct (not retained on upper caudal-fin lobe of paratype); pectoral, pelvic and anal fins transparent.

Distribution. Only known from the type locality, Cochin, Western India

Etymology. The name "*indicus*" derives from the type locality and is treated as a noun in apposition.

Comparisons. Western Indian Ocean species of the *vittatus* group (Tables 3, 8, Plates 1–3): *Upeneus indicus* differs from *U. davidaromi* in more gill rakers, deeper body and caudal peduncle, head through eye less deep, smaller suborbital depth, shorter head, smaller orbit, shorter upper jaw, lower anal fin, higher first dorsal fin, caudal-fin bars more uniformly coloured, and lateral body stripes present in fresh fish; *U. indicus* differs from *U. mascareinsis* in more gill rakers on upper limb, deeper body and caudal peduncle, larger head depth, smaller orbit, caudal-fin bars more uniformly coloured and more regularly sized on lower lobe, and lateral body stripes present in fresh fish; it differs from *U. suahelicus* in more gill rakers and lateral-line scales, deeper half body at first dorsal-fin origin, orbit, lower anal fin, shorter pectoral fins, and lateral head and body colour reddish vs silvery-white; it differs from *U. supravittatus* in a deeper body, shorter pectoral fins, and lateral head and body colour reddish vs brassy in fresh fish; and it differs from *U. vittatus* in more gill rakers on upper limb, deeper body at anal-fin origin, smaller orbit, caudal-fin bars less intensely and more uniformly coloured, more regularly-sized on lower lobe, black first dorsal-fin tip smaller, and lateral body and head colour reddish vs silvery white.

Remarks. *Upeneus indicus* attains 14 cm SL; no depth information is available.

Upeneus margarethae sp. nov.

(Tables 3, 5; Plates 1, 3)

Upeneus bensasi (Temminck & Schlegel 1843): Bauchot & Bianchi. 1984, in part; Fischer et al. 1990, 155; in part.

Holotype: SAIAB 82217, male 82 mm, Mozambique, R.V. *Dr. F. Nansen*, M07-78, 35°78.60′ S, 19°93.61′ E, 47 m, bottom trawl.

Paratypes: **Somalia**: USNM 396092, 124 mm, 11°14′ N, 51°08′ E; **Kenya:** SAIAB 82817, 5: 89–110 mm, off Kipini, 02°38′ S, 40°28′ E, 25–50 m; **Mozambique:** SAIAB 82209, 89 mm, R.V. *Dr. F. Nansen*, M07-77, 35°51.21′ S, 19°79.08′ E, 28 m, bottom trawl; SAIAB 82814, 89–97 mm, Western Indian Ocean, Mozambique, R.V. *Dr. F. Nansen*, M07-78, 35°78.60′ S 19°93.61′ E, 47 m, bottom trawl; **Madagascar**: SAIAB 82815, 11: 67–94 mm, Tsimipaika Bay, MAD 95-10, 8–12 m.

Non-types: MNHN1984-455, 93–94 mm, 20°00′ N, 39°00′ E (Eritrea); ZMUC P49161, 105 mm (Persian Gulf); USNM 396094, 78–79 mm, Colombo fish market, landed at Eravur (Sri Lanka); BMNH 1983 5.5.28-30, 3: 108–117 mm, 20°10′ S, 118°25′ E (NW Australia); AMS I.21849-009 95 mm, 11°29′ S, 134°23′ E, Arafura Sea, R.V. *Soela*, 100-105 m, engel trawl (N Australia).

Diagnosis. Dorsal fins VIII + 9; pectoral fins 13–14, mostly 14 (in 26 of 29 individuals); gill rakers 4–7 + 16–18 = 21–24; lateral-line scales 28–30; body depth at first dorsal-fin origin 22–26% SL; body depth at anus 20–24; caudal-peduncle depth 9.3–11; maximum head depth

19–23; head depth through eye 15–19; head length 27–31; orbit length 6.5–9.1; upper jaw length 10–12; barbel length 16–20; caudal-fin length 27-31; anal-fin height 14-18; pelvic-fin length 20–24; pectoral-fin length 21–25; first dorsal-fin height 20–23; second dorsal-fin height 16–20% SL; total bars on caudal fin 8–10, 4 bars on upper caudal-fin lobe, 3 on lobe itself and one at lobe base; broad red band on lower caudal-fin lobe, covering up to 5 or 6 red bars which are only partly visible along the outer, ventral fin margin in fresh fish, bars may become more visible in preserved fish; but are usually not retained on preserved fish, apart from some traces of bars and dark pigmentation at the lower lobe fin tip; a single mid-lateral body stripe running through eye, red from snout tip to eye and yellow from behind eye to caudal-fin base, not retained on preserved fish; first dorsal-fin tip pale; barbels white; body red above lateral line, body and head white laterally, with red or rose dots or blotches, ventral side of head and belly white; body uniformly pale brown in preserved fish; first minute dorsal-fin spine frequently dark pigmented forming a small spot at fin origin that is often distinct from above in preserved fish.

Description. Measurements in % SL and counts are given in Table 5; morphometric data as ratios of SL for holotype, data for paratypes in brackets: body elongate, body depth at first dorsal-fin origin 3.9 [3.8–4.5], body depth at anal-fin origin 4.2 [4.3–5.0], head length 3.4 [3.2–3.7] larger than maximum depth of body and subequal to caudal-fin length (3.7 [3.2–3.7]), second dorsal-fin length 5.6 [5.0–6.3], similar to barbel length (5.9 [5.0–6.3]), pelvic-fin length 4.3 [4.2–5.0], similar to length of pectoral fins (4.3 [4.0–4.8]), caudal-peduncle depth 9.1 [9.1–11], larger than orbit length (11 [11–15]).

Fresh colour (Plate 1): Head and body white laterally, with some irregular faint red markings, red dorsally (above lateral line), belly white; a red mid-lateral stripe on snout through eye, yellow from eye to caudal-fin base, stripe anteriorly below lateral line, posteriorly along or slightly above lateral line; the stripe sometimes overlain with red. Iris completely red. Dorsal fins pale, with two sub-horizontal red stripes; pectoral fins hyaline, the rays pale reddish; pelvic fins pale, with 3 or 4 faint, dusky-red stripes; caudal-fin upper lobe hyaline, with three red bars on fin lobe itself and a fourth bar at the base of lobe; bar width equal to width of pale interspaces between bars; lower lobe with broad red band covering 5 or 6 red bars visible along ventral fin margin (89 mm paratype with inner margin of lower caudal-fin lobe dark, and a series of three small pale spots); anal fin hyaline, with white rays; barbels white.

Preserved colour (Plate 3): head and body pale beige to pale brown, some isolated dark patches on operculum on dorsal side of body; a few types show a dark saddle behind the second dorsal fin that reaches to lateral line; all fins transparent and without pigment, except for a dark interior margin on lower caudal-fin lobe towards tip of lobe and some small dark spots or stripes on both lobes; sometimes also remains of bars on caudal-fin lobes, on lower lobe up to six dark narrow bars reaching from close to ventral margin to about two-thirds of lobe width, becoming most conspicuous at mid of lobes. In holotype and several paratypes the minute spine in front of the first dorsal fin is indicated by a dark dot. In specimens with intact scales, the lateral line is distinct, extending to or slightly beyond caudal-fin base.

Distribution. Red Sea to Somalia, Kenya, Mozambique, Madagascar, Persian Gulf, Sri Lanka, NW Australia, N Australia (Arafura Sea).

Etymology. The name of this species "*margarethae*" is in honour of the mother of the first author, the late Margaretha Uiblein (née Feichtinger).

Comparisons. Western Indian Ocean species of the *tragula* group (Tables 3, 5, 6; Plates 1–3): *Upeneus margarethae* differs from *U. oligospilus* in shorter snout and postorbital length, longer caudal fin, longer pelvic and pectoral fins, 4 red vs 3–4 brown or black bars on upper caudal-fin lobe, no conspicuous dark bars on lower caudal-fin lobe, body and fins lacking dark blotches or dots, first and second dorsal-fin tips pale in both fresh and preserved fish, colour of mid-lateral body stripe yellow vs brown or dark brown, and mid-lateral body stripe not retained on preserved fish; it differs from *U. sundaicus* in more gill rakers, fewer lateral-line scales, caudal peduncle and suborbital less deep, lower first dorsal fin, 4 vs 5–6 bars on upper caudal-fin lobe, the mid-lateral body stripe starting at snout vs behind eye, and barbels white vs yellow (colour patterns apply to fresh fish only); from *U. taeniopterus* it differs in fewer lateral-line scales, larger orbit, longer pelvic and pectoral fins, higher second dorsal fin, one vs two lateral body stripes in fresh fish, and caudal-fin bars in most cases not retained on preserved fish; and from *U. tragula* it differs in mostly 14 (in 26 of 29 fish) vs mostly 13 (in 13 of 16 fish) pectoral-fin rays, shorter jaws, longer pectoral fins, 4 red vs 5–6 brown or black bars on upper caudal-fin lobe in adults (> 70 cm SL), dark bars on lower caudal-fin lobe absent, the body and fins lacking dark blotches or dots, the first and second dorsal-fin tips pale, mid-lateral body stripe yellow vs brown to black, and mid-lateral body stripe colour not retained on preserved fish.

Non-Western Indian Ocean species of the *tragula* group (Tables 5, 6): *Upeneus margarethae* differs from *U. luzonius* in more gill rakers, fewer lateral-line scales, half body at anal-fin origin and caudal peduncle less deep, head and body not darker dorsally in preserved fish, and pale interspaces between upper lobe bars wider; from *U. mouthami* it differs in mostly 14 vs 13 pectoral-fin rays, shorter barbels, shorter first dorsal-fin base, broad red band vs brown to red bars on lower caudal-fin lobe in fresh fish, no bar remains or only weak lines vs dark blotches as remains of bars on lower caudal-fin lobe in preserved fish, and white vs yellow barbels in fresh fish.

REMARKS. Since Lachner (1954) there has been speculation that there may be a different form of *Upeneus bensasi* (Houttyn, 1782) in the Western Indian Ocean, a name that he applied erroneously to *Upeneus guttatus*, which was described from off Madras, India. Since the synonymization of *U. bensasi* with the earlier described, seven dorsal-spine *U. japonicus* by Randall et al. (1993), it is clear that this eight-spine form cannot be ascribed to *U. bensasi*. Earlier workers such as Thomas (1969) may have already encountered this material, but probably missed the minute spine in front of the dorsal, as he did when examining the holotype of *U. taeniopterus* at MNHN in Paris (see also the species account of *U. taeniopterus* below).

No information on colouration of fresh fish from areas other than the southern East African coast is currently available. Also, the specimens from northern parts of the Western Indian Ocean region, Sri Lanka and NW Australia showed some deviation in a PCA based on morphometric characters (Uiblein, unpublished data) and hence were not given a type status.

Upeneus margarethae attains 11 cm SL; depth range 8 – 50 m.

Upeneus mascareinsis Fourmanoir & Guézé 1967

(Tables 3, 8; Plates 1, 3)

Upeneus mascareinsis Fourmanoir & Guézé 1967: 50-51, Fig.I/b; photograph of preserved fish (type locality: Réunion); Letourneur et al. 2004, 212; Fricke et al. 2009.

DIAGNOSIS. Dorsal fins VIII + 9; pectoral fins 15–16; gill rakers 7–8 + 19–22 = 26–29; lateral-line scales 35–38; body depth at first dorsal-fin origin 22–26 %SL; body depth at anus 18–22; caudal-peduncle depth 8.3–9.3; maximum head depth 20–24; head depth through eye 17–19; head length 30–34; orbit length 7.7–11; upper jaw length 12–14; barbel length 18–24; caudal-fin length 27–31; anal-fin height 13-16; pelvic-fin length 20–24; pectoral-fin length 21–24; first dorsal-fin height 19–23; second dorsal-fin height 15–16% SL; total bars on caudal fin 7–10, 3–6 bars on upper caudal-fin lobe, colour of bars changing from pale brown proximally to dark brown or black at distal margin of lobe; 3–4 brown bars on lower caudal-fin lobe, becoming darker distally, last two completely dark brown or black, bars slightly increasing in width distally, bar on tip small; width of largest lower caudal-fin lobe bar and/or space between distal-most bars less than orbit; no lateral body stripes; first dorsal-fin tip dark; barbels white; body white ventrally and rose-red laterally, becoming dorsally darker with some gold iridescence along dorsal flanks and a darkened saddle behind second dorsal fin; preserved fish body uniformly brown or a bit darker dorsally, bars and black first dorsal-fin tip retained.

DISTRIBUTION. Madagascar, Mozambique, Réunion, Western Indonesia

COMPARISONS. Western Indian Ocean species of the *vittatus* group (Tables 3, 8, Plates 1–3): *Upeneus mascareinsis* differs from *U. davidaromi* in head through eye less deep, smaller suborbital depth, shorter postorbital distance, and head and body colouration rose-red laterally instead of silvery; from *U. indicus* it differs in fewer gill rakers on upper limb, body and caudal peduncle less deep, smaller maximum head depth, larger orbit, caudal-fin bars less uniformly coloured and less regularly sized on lower lobe, lateral body stripes absent in fresh fish; from *U. suahelicus* it differs in body and caudal-peduncle less deep, shorter pectoral fin, caudal-fin bars less uniformly coloured and less regularly sized on lower lobe, lateral body stripes absent, and head and body colour reddish vs pale brown laterally; from *U. supravittatus* it differs in body and caudal peduncle less deep, shorter pectoral fin, lower first dorsal fin, caudal-fin bars less uniformly coloured and less regularly sized on lower lobe, bar interspace width on both lobes not generally narrower than bars; lateral body stripes absent, and head and body colour more reddish than brassy; and it differs from *U. vittatus* in caudal peduncle less deep, smaller suborbital depth, the largest bar and/or pale interspace between distal-most bars on lower caudal fin-lobe narrower, first dorsal-fin black tip smaller, lateral body stripes absent, and body and head colour laterally reddish instead of silvery-white.

Non-Indian Ocean species of *vittatus* group (Table 8, Fig. 1): *U. mascareinsis* differs from *U. subvittatus* in more lateral-line scales, body and caudal peduncle less deep, shorter snout and postorbital length, lower anal-fin and shorter pectoral fins; the two species largely resemble each other in colour, *U. subvittatus* laterally silvery-grey in contrast to reddish, the dark saddle behind the second dorsal fin longer, extending from immediately behind second dorsal-fin base to base of upper caudal-fin lobe. Because of considerable overlap of morphometric measurements, a PCA based on 37 variables gathered from 9 *U. mascareinsis* and 5 *U. subvittatus* was carried out (Fig. 1). A clear separation was found between the two species. Body depth at first dorsal-fin origin, caudal-peduncle depth, maximum head depth, snout length, and pectoral-fin length are among the variables contributing most to the 31% of total variance explained by the first principal component.

REMARKS. Our data agree well with several details given in the original species description of *U. mascareinsis* by Fourmanoir & Guézé 1967. Similar to *U. davidaromi*, considerable intraspecific variation in width of lower

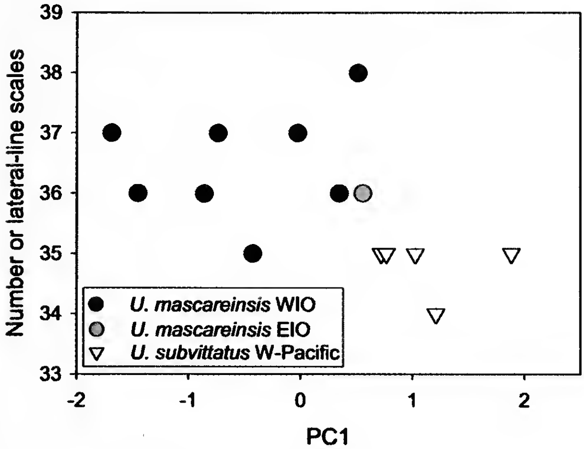

Fig. 1. First principal component (PC1) based on 37 morphometric characters against number of lateral-line scales for 9 *Upeneus mascareinsis* (Indian Ocean) and 5 *U. subvittatus* (West-Pacific) (WIO = Western Indian Ocean, EIO = Eastern Indian Ocean)

caudal-fin lobe bars and pale interspaces were found. These differences occur also among individuals of similar size and overlapping distribution and hence may indicate a colour polymorphism.

One silvery juvenile specimen with an elongated body and short pectoral fins collected off Mozambique was found to be closely related to *Upeneus mascareinsis* based on meristic characters, some measurements of body form, and collecting depth (100 m; Fig. 2). This fish differed however considerably from adults of the species in orbit length, pectoral-fin length, distance of pectoral-fin origin from snout tip, maximum head depth, and the body colour dorsally silvery-bluish instead of reddish (Table 8, Plate 1, Fig. 2). Some of these deviations may reflect an early ontogenetic transition in lifestyle, as similar differences have been reported for other goatfish species (e.g., Caldwell, 1962, Uiblein 2007). Due to these considerable differences and lack of additional comparative material this specimen is only referred to as cf. *mascareinsis*.

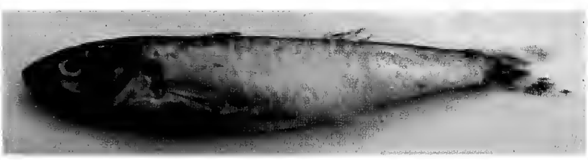

Fig. 2. Photograph of *Upeneus* cf. *mascareinsis*, SAIAB 82328, 6.9 cm SL, collected off Mozambique (O. Alvheim, IMR)

During the course of comparing *U. mascareinsis* with *U. subvittatus* we found indications for considerable variation in body colour among *U. subvittatus* specimens from different areas in the Pacific. Comparison of a specimen photographed by J. E. Randall from the Molucca Islands, Indonesia (BPBM 32266, 18 cm SL) with photographs of two specimens from Japan, one shown in Masuda et al. (1984) and another one in Okamura & Amaoka (1997), suggests the existence of additional colour variants with either a ventrally pale grey and dorsally brown body or an overall reddish body. Both specimens from Japan lack a dark saddle behind the second dorsal fin. Detailed taxonomic studies of these different forms are needed.

To date *Upeneus mascareinsis* had only been recorded from Réunion and was assumed to be endemic there (Letourneur et al. 2004, Fricke et al. 2009). Our records for Madagascar, Mozambique and Western Indonesia are new for this species. It has been collected between 100 and 400 m depth and thus inhabits the lower shelf and upper slope in the Indian Ocean proper, as does *U. davidaromi* in the Red Sea. *Upeneus mascareinsis* attains 18 cm SL.

Upeneus moluccensis (Bleeker 1855)

(Tables 3, 7; Plates 1, 3)

Upeneoides moluccensis Bleeker, 1855: 409 (type locality: Ambon, Moluccan Islands).

Upeneus moluccensis: Kumaran & Randall 1984, no page number, Plate III; colour photograph; Ben-Tuvia & Kissil 1988: 11, Fig. 10 (Red Sea: Eritrea and Elat, Gulf of Aqaba); De Bruin et al. 1994: 270, Pl. 20, Fig. 137 (colour photo, Sri Lanka); Randall & Kulbicki 2006, 301-302, Fig. 5 (diagnosis and colour photograph, New Caledonia).

Diagnosis. Dorsal fins VIII + 9; pectoral fins 14–16; gill rakers 7–8 + 18–20 = 26–27; lateral-line scales 33–35; body depth at first dorsal-fin origin 24–26% SL; body depth at anus 21–23; caudal-peduncle depth 9.0–10; maximum head depth 20–22; head depth through eye 16–17; head length 27–29; orbit length 7.3–8.9; upper jaw length 11–12; barbel length 15–17; caudal-fin length 27–30; anal-fin height 13-15; pelvic-fin length 17–22; pectoral-fin length 25–27; first dorsal-fin height 20–23; second dorsal-fin height 14–16% SL; 6–8 thin red bars on upper caudal-fin lobe, faintly retained on preserved fish; no bars on lower caudal-fin lobe, but a red broad band covering the entire lower lobe apart from distal, inner margin, the latter somewhat darker; most of lower caudal-fin lobe pigmentation lost in preserved fish; one conspicuous yellow or gold mid-lateral body stripe from eye to upper caudal-fin base, not (or only faintly) retained on preserved fish; first dorsal-fin tip dark, also in preserved fish; barbels white; body silvery-rose, darkened above lateral stripe; in preserved fish body pale brown, slightly darkened dorsally.

Distribution. Eastern Mediterranean, Red Sea to Mozambique, Arabian Sea, Madagascar, India, Andaman Sea, Indonesia, New Caledonia, Philippines, Taiwan and southern Japan.

Comparisons. Western Indian Ocean species of the *moluccensis* group (Tables 3, 7, Plates 1–3, Fig. 2): *Upeneus moluccensis* differs from *U. doriae* in fewer gill rakers, body and head less deep, bars on caudal fin present, and body colouration red vs silvery in fresh fish; and it differs from *U. sulphureus* in body, head and caudal peduncle less deep, shorter and lower anal and dorsal fins, bars on the upper caudal-fin lobe present, one vs two lateral stripes and red vs white to silvery body colouration in fresh fish.

Remarks. *Upeneus moluccensis* attains 18 cm SL; depth range: 1–99 m.

Upeneus oligospilus Lachner 1954
(Tables 3, 6; Plates 1, 3)

Upeneus oligospilus Lachner 1954 (type locality: Persian Gulf).
Upeneus tragula: Richardson 1846; Kuronuma & Abe 1972, p. 88, Fig. 29 (drawing of 13.8 cm specimen from Kuwait with typical features of *U. oligospilus*).
Synonym of *Upeneus tragula*: Randall & Kulbicki 2006, p. 305.

Diagnosis: Dorsal fins VIII + 9; pectoral fins 13–14; gill rakers 4–7 + 16–18 = 20–24; lateral-line scales 28–31; body depth at first dorsal-fin origin 23–26 %SL; body depth at anus 19–22; caudal-peduncle depth 9.8–11; maximum head depth 20–23; head depth through eye 15–19; head length 29–32; orbit length 5.4–7.9; upper jaw length 11–13; barbel length 16–20; caudal-fin length 24–28; anal-fin height 15–18; pelvic-fin length 17–22; pectoral-fin length 18–22; first dorsal-fin height 18–22; second dorsal-fin height 16–18% SL; total number of bars on caudal fin 6–9 in adults (6 or less in juveniles > 7 cm SL), upper caudal-fin lobe with 3–5 brown, dark brown or black bars; 3–4 brown, dark brown or black bars on lower lobe; a brown or dark-brown mid-lateral body stripe from tip of snout to caudal-fin base; body above stripe greenish grey, body below stripe white or beige, with irregular dark reddish brown spots and blotches, also on paired fins; dark marks on or very close to first and second dorsal-fin tips; barbels yellow in fresh fish; most of body and fin pigmentation retained on preserved fish.

Distribution. Persian Gulf

Comparisons. Western Indian Ocean species of the *tragula* group (Tables 3, 6, Plates 1–3, Fig. 3): *Upeneus oligospilus* differs from *U. margarethae* in longer snout and postorbital length, shorter caudal fin, shorter pelvic and pectoral fins, 3–4 brown or black vs 4 red bars on upper caudal-fin lobe, conspicuous dark bars on lower caudal-fin lobe present in fresh fish, body and fins showing dark blotches or dots, first and second dorsal-fin tips dark in both fresh and preserved fish, colour of mid-lateral body stripe brown or dark brown vs yellow, and mid-lateral body stripe retained on preserved fish; from *U. sundaicus* in more gill-rakers, fewer lateral-line scales, body at anal-fin origin and caudal peduncle less deep, paired fins mostly shorter, first dorsal fin considerably lower, lower caudal-fin lobe with 3 or 4 dark bars, dark blotches and dots on body and paired fins present, black dorsal-fin tips in both fresh and preserved fish present, and mid-lateral body stripe brown or dark brown vs pale brown, retained on preserved fish; from *U. taeniopterus* it differs in fewer lateral-line scales, greater maximum head depth, longer head and snout, shorter caudal fin, higher second dorsal fin, dark blotches and dots on body and paired fins present, black dorsal-fin tips in both fresh and preserved fish present, and mid-lateral body stripe brown or dark brown vs pale brown, only the former retained on preserved fish; and it differs from *U. tragula* in shorter caudal fin and fewer caudal-fin bars both in adults (6–9 vs 10–12) and juveniles (6 vs 7–10) (Figs. 3A, B, D) and in greater postorbital length, longer distance between tip of snout to pectoral-fin origin, shorter pelvic fin, and lower second dorsal fin in adult fish, if size is referred to (e.g. Fig. 3C). [FIG. 3]

Non-Western Indian Ocean species of the *tragula* group (Table 6): *Upeneus oligospilus* differs from *U. luzonius* in more gill rakers, caudal peduncle less deep, longer head and snout, shorter pelvic fin, lower first dorsal fin, dark dots and blotches on body and paired fins present, and dark dorsal-fin tips present; it differs from *U. mouthami* in longer snout and postorbital length, smaller orbit, longer upper jaw, shorter barbels, longer first dorsal-fin base, shorter caudal fin, shorter paired fins, brown or dark brown vs yellow lateral body stripe, the former retained on preserved fish, dark dots and blotches on body and paired fins present, and dark dorsal-fin tips present.

Remarks. *Upeneus oligospilus* is resurrected from synonymy with *U. tragula* (Randall & Kulbicki 2006), because these two species can be clearly distinguished by the combination of two characters, the total number of dark bars on the caudal fin and caudal-fin length (Fig. 3D). This distinction did not become apparent in the earlier taxonomic studies of Lachner (1954) and Thomas (1969) who provided caudal-fin bar counts, but no detailed comparisons of caudal-fin length.

A photograph of a freshly collected 9.7 cm fish from the Gulf of Suez with short unpaired fins and 8 bars on the caudal fin that became recently available to the first author (Sergey Bogorodsky, pers. comm.) may indicate that *U. oligospilus* is distributed more widely. Thomas (1969) attributed one specimen from northern Sri Lanka to this species. The two juvenile specimens from Sri Lanka examined in this study clearly fall within the caudal-fin length range of *Upeneus tragula*.

Upeneus oligospilus attains 17 cm SL; maximum reported depth is 13 m.

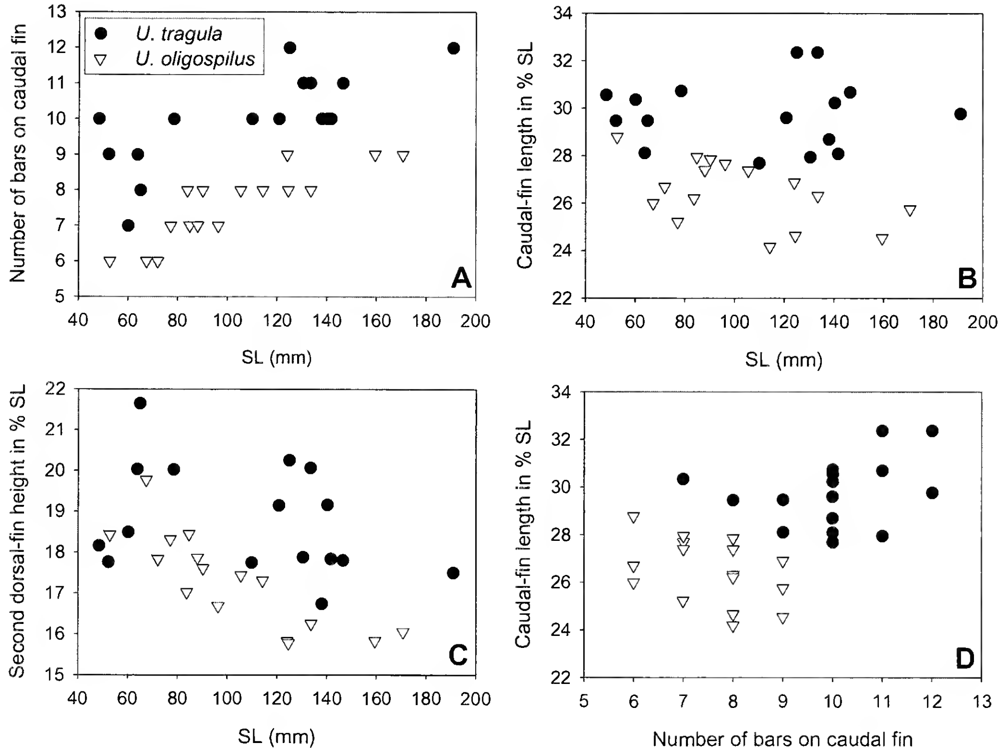

Fig. 3. Number of bars on caudal fin (A), caudal-fin length ratio (B), and second dorsal-fin height ratio (C) against SL in 16 *Upeneus oligospilus* and 16 *U. tragula;* the combination of caudal-fin length ratio and caudal-fin bar number (D) allows size-independent distinction between the two species.

Upeneus pori Ben-Tuvia & Golani 1989
(Tables 3, 4; Plates 1, 3)

Upeneus pori Ben-Tuvia & Golani 1989: 13 ff., Figs. 1–2; photographs of fresh fish (*ex-situ* and *in-situ*) (type locality: Elat, Gulf of Aqaba, Red Sea); Kim & Nakaya 2002, 131, Fig. 3; diagnostic characters and photograph showing caudal-fin pattern.

Diagnosis. Dorsal fins VII + 9; pectoral fins 14; gill rakers 7–8 + 18–20 = 26–27; lateral-line scales 29–30; body depth at first dorsal-fin origin 21–24% SL; body depth at anus 20–22; caudal-peduncle depth 9.1–10; maximum dead depth 18–20; head depth through eye 15–16; head length 26–28; orbit length 6.3–7.8; upper jaw length 10–11; barbel length 16–18; caudal-fin length 27–29; anal-fin height 16-17; pelvic-fin length 20–23; pectoral-fin length 20–22; first dorsal-fin height 20–21; second dorsal-fin height 15–16% SL; total bars on caudal fin 11–15, upper caudal-fin lobe with 4–6 red-brown bars; 5–9 red-brown or grey bars on ventral half side of lower lobe, extending to a broad brown or dark grey stripe along middle of lobe; 3 or 4 brownish-red or grey bars on inner, dorsal half of lower caudal-fin lobe; in preserved fish bar patterns often retained, showing dark brown colouration; no or only faint indication of a mid-lateral body stripe in fresh fish; first dorsal fin not pigmented; barbels white or yellow; body greyish or red-brown, dorsally darkened and covered with grey to reddish-brown spots extending to lateral side; live fish may show a dark-brown or red bar from eye vertically downwards; body dorsally darkened in preserved fish.

Distribution. Mediterranean, Red Sea to south coast of Oman, Madagascar.

Comparisons. Western Indian Ocean species of the *japonicus* group (Tables 3, 4, Plates 1, 3): *Upeneus pori* differs from *U. guttatus* in 14 vs mostly 13 pectoral-fin rays, more gill rakers, 5–9 brown or grey bars on ventral half side of lower caudal-fin lobe vs 5–8 red, partly hidden bars along ventral margin of lower caudal-fin lobe of fresh fish, in conspicuous bar patterns vs no or only traces of bars on both caudal-fin lobes of preserved fish, and dorsally darkened vs pale brown body in preserved fish.

Non-Western Indian Ocean species of the *japonicus* group (Table 4): *Upeneus pori* differs from *U. asymmetricus* in 14 vs 13 pectoral-fin rays, smaller interorbital distance, shorter and thinner barbels, longer and higher anal fin, and dark bars on ventral margin of lower caudal-fin lobe vs bars only on inner, dorsal side of lower lobe; from *U. australiae* it differs in more gill rakers, body at first dorsal origin smaller, smaller half body depth at anal-fin origin, caudal peduncle more compressed and less deep, smaller head (both vertically and horizontally, with smaller interorbital distance), shorter and thinner barbels, and dark bars on ventral margin of lower caudal-fin lobe vs bars crossing entire lower lobe; it differs from *U. francisi* in fewer gill rakers, deeper body at anal-fin origin, head through eye less deep, shorter head and postorbital length, larger orbit, shorter jaws, longer second dorsal-fin base, shorter paired fins, and caudal bars in most cases well retained on preserved material; it differs from *U. japonicus* in shorter head length, shorter barbels and shorter caudal peduncle, longer caudal fin, shorter pectoral fin, lower dorsal fins, and bars on lower caudal-fin lobe present; and it differs from *U. parvus* in 14 vs 15 pectoral-fin rays, fewer lateral-line scales, body at anal-fin origin and head less deep, shorter jaws, shorter barbels and shorter interdorsal distance, longer caudal peduncle, longer and higher anal fin, shorter pectoral fins, and bars restricted to ventral margin of lower caudal-fin lobe vs bars crossing entire lobe.

Remarks. Comparison of colour patterns with the Red Sea population is restricted to preserved fish due to the absence of photographs of live or fresh fish from the Western Indian Ocean proper.

This is the first record of *Upeneus pori* in the southWestern Indian Ocean. The species attains 19 cm SL; maximum reported depth is 45 m.

Upeneus suahelicus sp. nov.
(Tables 3, 8; Plates 2, 3)

Holotype: SAIAB 13948, male, 101 mm, Kenya, off Malindi, R.V. *Dr. F. Nansen*, PCH 80-32, 03°07′ S, 40°11′ E, collected by P.C. Heemstra, December 1980.

Paratypes: **Kenya:** SAIAB 82816, 102 mm, off Malindi, R.V. *Dr. F. Nansen*, PCH 80-32, 03°07′ S 40°11′ E; **Mozambique**: SAIAB 82805, 135 mm, Lipobane estuary, 19°00′14″ S 39°04′44″ E; SAIAB 55589, 100 mm, Lipobane estuary, 19°00′14″ S 39°04′44″ E; SAIAB 74521, 3: 100–114 mm, off Quelimane, 20m; SAIAB 81957, 88 mm, R.V. *Dr. F. Nansen*, M07-43, 34°22.15′ S 25°00.03′ E, 46 m depth, bottom trawl; SAIAB 82820, 89 mm, R.V. *Dr. F. Nansen*, M07-86, 36°31.38 ′S 19°22.85′ E, 29 m, bottom trawl; USNM 396113, 93 mm, Ponta Mahone-Inhaca; **South Africa**: SAIAB 11478, 101 mm, Durban, 29° S 31° E; SAIAB 76122, 107–121 mm, KwaZulu-Natal, Richards Bay, 28°49′54″ S 32°10′04″ E, 45 m depth.

Non-types: HUJ 8555, 124 mm, Massawa, Eritrea (Red Sea); SAIAB 81952, 95 mm, R.V. *Dr. F. Nansen* M07-42, 34°46.57′ S 25°07.31′ E, bottom trawl, depth 99 m (Mozambique); SAIAB 82824, 79 mm, KwaZulu-Natal, Richards Bay, 28°49′54″ S 32°10′04″ E; 45 m depth (South Africa).

Diagnosis. Dorsal fins VIII + 9; pectoral fins 15–16; gill rakers 6–8 + 19–21 = 26–28; lateral-line scales 34–35; body depth at first dorsal-fin origin 26–30% SL; body depth at anal-fin origin 22–26; caudal-peduncle depth 9.9–11; maximum head depth 22–25; head depth through eye 17–19; head length 28–31; orbit length 7.1–9.4; upper jaw length 12–14; barbel length 15–20; caudal-fin length 26–30; anal-fin height 15-17; pelvic-fin length 18–21; pectoral-fin length 25–26; first dorsal-fin height 22–26; second dorsal-fin height 16–18% SL; total number of bars on caudal fin 8–10, 4–6 pale brown bars on upper caudal-fin lobe, and 3–4 of same colour on lower caudal-fin lobe; the three proximal bars on upper caudal-fin lobe slightly curved; caudal-fin bars and white interspaces nearly equal in width; all bars entirely retained on preserved fish; two yellow or pale brown lateral body stripes on fresh fish, one close to lateral line, reaching from behind head to caudal-fin base; the other stripe below, starting behind pectoral-fin base; first dorsal-fin tip dark, also in preserved fish; barbels white; head and body silvery white laterally and reddish-brown darker dorsally in fresh fish; belly white; in preserved fish body pale brown, sometimes darker dorsally.

Description. Measurements as % SL and counts are given in Table 8; morphometric data as ratios of SL for holotype, data for paratypes in brackets: body moderately deep, body depth at first dorsal-fin origin 3.6 [3.3–3.8] and at anal-fin origin 4.1 [3.8–4.5]; head length 3.2 [3.2–3.6], similar to maximum depth of body and caudal-fin length (3.6 [3.4–3.8]); height of second dorsal fin 6.0 [5.6–6.3], similar to barbel length (6.5 [5.0–6.7]); pectoral-fin length 3.8 [3.8–4.0], clearly longer than pelvic-fin length (4.9 [4.8–5.4]); caudal-peduncle depth 9.4 [9.1–10], larger than orbit length (11 [11–13]).

Fresh colour (Plate 2): Head and body silvery white laterally, dorsal surface dark reddish or reddish grey, belly white; with two pale brown or yellow lateral body stripes; the upper stripe from head to caudal-fin base, anteriorly well below lateral line, crossing line below second dorsal fin and connecting to proximal-most bar of upper caudal-fin lobe; the lower stripe narrower, starting behind pectoral-fin base and connecting to proximal-most bar of lower caudal-fin lobe; in one of the two photographed specimens a third, indistinct, reddish-brown stripe, separated dorsally by a series of pale spots can be seen, extending dorsolaterally from head to behind second dorsal-fin base; upper lobe of caudal fin white or pale grey with 5 or 6 pale brown bars, the fin-lobe tip dark, the proximal 3 to 4 bars slightly curved; lower caudal-fin lobe white or pale grey, with four pale brown bars, the first two proximal ones slightly curved, mostly uniform in width, and the lobe tip pale or dark; pale interspace between bars of similar width or wider than bars on upper lobe, and often narrower on lower lobe; spinous dorsal fin white to pale grey, with two pale brown horizontal stripes, the lower separated from fin base by a narrow pale interspace, the upper stripe separated from the lower one and the black fin tip by a pale interspace of similar width to the stripe and the tip, width about or less than half orbit diameter; soft dorsal fin similar but with three pale brown horizontal stripes, the lower one connected to the fin base and the uppermost one covering the tip; anal and pelvic fins hyaline with rays pale yellow or white at the fin base; pectoral fins hyaline.

Preserved colour (Plate 3): Head and body uniformly pale brown, with white silvery or pale yellow pigmentation on ventral side and on head, with large white colour patches on opercular margin and below eyes. Black first dorsal-fin tip distinct, bars on both caudal-fin lobes pale or dark brown; pectoral, pelvic and anal fins transparent.

Distribution. Kenya to South Africa, Eritrea (Red Sea)

Etymology: The name *suahelicus* is derived from the Arabic 'sawahil' meaning 'coast', and refers to the occurrence of this species off the East African coast. In a large part of this area the lingua franca is Swahili, which has the same derivation.

Comparisons. Western Indian Ocean species of the *vittatus* group (Tables 3, 8, Plates 1-3, Fig. 4): *Upeneus suahelicus* differs from *U. davidaromi* in deeper body and caudal peduncle, head through eye less deep and smaller suborbital depth, shorter head and snout, longer pectoral fins, taller first dorsal fin, lateral body stripes present and caudal-fin bars more uniformly coloured; it differs from *U. indicus* in fewer gill rakers and lateral-line scales, half body depth at first dorsal-fin origin less deep, larger orbit, longer anal and pectoral fins, and lateral head and body colour silvery white vs reddish; from *U. mascareinsis* it differs in deeper body and caudal peduncle, longer pectoral fins, caudal-fin bars more uniformly coloured and more regularly sized on lower lobe, lateral body stripes present, and head and body colour pale brown vs reddish laterally; from *U. supravittatus* it differs in fewer gill rakers, shorter barbels and head, shorter distances from tip of snout to paired fin origins, shorter pectoral fins, higher second dorsal fin, and body colour silvery white vs brassy (for further results of comparisons, see also next paragraph); and from *U. vittatus* it differs in fewer lateral-line scales, longer pectoral fins, higher second dorsal fin, caudal-fin bars more uniformly coloured, and black first dorsal-fin tip smaller.

Because *Upeneus suahelicus* and *U. supravittatus* are rather similar in body shape and overlap slightly in all characters, a PCA of 40 morphometric variables from all specimens studied (n=37) was conducted, which showed a clear distinction when the first principal component was plotted against total number of gill rakers (Fig. 4). Maximum head depth, head length, distances from snout to paired fin and both dorsal-fin origins, barbel length, orbit depth, postorbital length, lower jaw length, and pectoral-fin length were among the variables contributing most to the 22 % of total variance explained by the first principal component.

Non-Western Indian Ocean species of the *vittatus* group (Table 8): *Upeneus suahelicus* differs from *U. subvittatus* in less deep caudal peduncle, shorter head, snout, lower jaw and barbels, higher first dorsal fin, lateral body stripes present in fresh fish, and more uniform caudal-fin bar pattern.

Remarks. The specimen of *U. suahelicus* from the

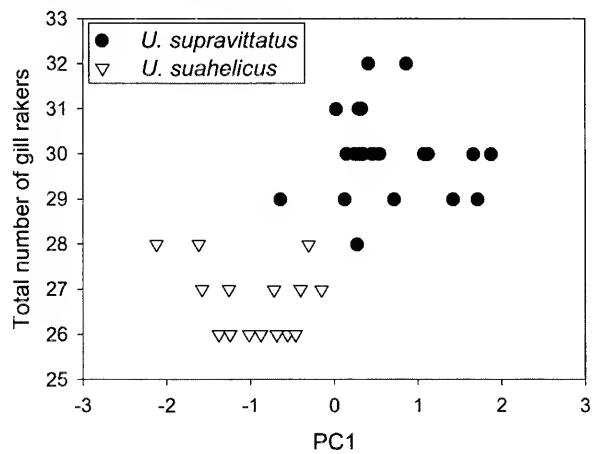

Fig. 4. First principal component based on 40 morphometric characters against total number of gill rakers for *Upeneus suahelicus* and *U. supravittatus.*

southern Red Sea (HUJ 8555) has smaller eyes (see Table 8) and the caudal-fin bar colouration is more faint compared to the other specimens examined, which all originate from further south along the east African coast. This specimen was listed among the material examined in an earlier account of *Upeneus vittatus* by Ben-Tuvia and Kissil (1988). These authors also provided a live colour description based on a photograph of a specimen collected in the Red Sea which, however, was not published (see also the remarks section of the account of *U. vittatus* further below).

Upeneus suahelicus attains 13.5 cm; depth range is 20–99 m.

Upeneus sulphureus Cuvier 1829

(Tables 3, 7; Plates 2–3)

Upeneus sulphureus Cuvier in Cuvier & Valenciennes 1829: 450 (type locality: Antjer, western Java); Kumaran & Randall 1984: no page number, Plate III (colour photograph); Ben-Tuvia & Kissil 1988: 12, Fig. 12 (black and white photograph; Red Sea, Gulf of Aden); De Bruin et al. 1994: 271, Pl. 20, Fig. 138 (Sri Lanka); Randall & Kulbicki 2006: 304, Fig. 7 (diagnosis and colour photograph of Lombok specimen).

Diagnosis. Dorsal fins VIII + 9; pectoral fins 15–16; gill rakers 7–8 + 19–21 = 27–28; lateral-line scales 34–37; body depth at first dorsal-fin origin 29–33% SL; body depth at anus 25–27; caudal-peduncle depth 11–12; maximum head depth 23–25; head depth through eye 18–20; head length 29–30; orbit length 7.4–8.7; upper jaw length 11–13; barbel length 17–21; caudal-fin length 27–30; anal-fin height 16-18; pelvic-fin length 20–22; pectoral-fin length 24–26; first dorsal-fin height 23–26; second dorsal-fin height 17–18% SL; no bars on caudal-fin lobes; lower lobe base yellowish, upper lobe base grey, some of the caudal-fin lobe pigmentation retained on preserved fish, including a dark inner margin of fin lobes; two conspicuous yellow body stripes, one mid-lateral from operculum to caudal-fin base, the other starting behind pectoral-fin base and reaching back to caudal-fin base; both stripes not or only faintly retained on preserved fish; first dorsal-fin tip black, also in preserved fish; barbels white; body ventrally white and dorsally pale brown; in preserved fish body pale brown with some reddish or darker brown area at mid-body in preserved fish.

Distribution. Red Sea, Persian Gulf, Madagascar, Seychelles, Réunion, Pakistan, India, Sri Lanka, Andaman Sea, Indonesia, New Guinea, Fiji, New Caledonia, Philippines and southern Japan

Comparisons. Western Indian Ocean species of the *moluccensis* group (Tables 3, 7, Plates 1–3, Fig. 2): *Upeneus sulphureus* differs from *U. doriae* in fewer gill rakers, deeper body, longer pelvic fins, and higher dorsal fins; and it differs from *U. moluccensis* in deeper body, head and caudal peduncle, higher dorsal fins, longer dorsal-fin bases, higher anal fin with longer base, bars on the upper caudal-fin lobe absent, two vs one lateral body stripes in fresh fish, and white to silvery vs red body colouration in fresh fish.

Remarks. First fully documented record (cf. Randall 1995) from the Persian Gulf (ZMUC P49156). *Upeneus sulphureus* attains 20 cm; depth range 20 to 60 m.

Upeneus sundaicus (Bleeker, 1855)

(Tables 3, 6; Plates 2, 3)

Upeneoides sundaicus Bleeker, 1855 (type locality: Ambon, Indonesia).

Upeneus sundaicus (Bleeker, 1855): Kumaran & Randall 1984, no page number, Plate III; colour photograph; De Bruin et al. 1994: 271 (Pl. 20, Fig. 139 (Sri Lanka); Randall 1995, 242, Fig. 632; diagnosis and colour photograph (Oman and Persian Gulf).

Diagnosis. Dorsal fins VIII + 9; pectoral fins 13–14; gill rakers 4–5 + 14–15 = 18–20; lateral-line scales 31–34; body depth at first dorsal-fin origin 25–28% SL; body depth at anal-fin origin 22–24; caudal-peduncle depth 11–13; maximum head depth 21–23; head depth through eye 17–20; head length 27–30; orbit length 6.1–7.2; upper jaw length 11–12, barbel length 18–21; caudal-fin length 26–29; anal-fin height 16–18; pelvic-fin length 20–23; pectoral-fin length 21–23; first dorsal-fin height 25–29; second dorsal-fin height 16–18 %SL; 5–6 weak, red or grey bars on upper caudal-fin lobe, not retained on preserved fish; lower lobe without bars, fully or partly covered with a reddish or greyish band, lost in preserved fish; a single pale brown mid-lateral body stripe from behind eye to caudal-fin base, sometimes retained on preserved fish; no dark dorsal-fin tip; barbels yellow in fresh fish; body whitish-rose ventrally, dorsally reddish or dark grey, head with red or grey pigmentation at snout and above eyes; body in preserved fish may darken dorsally.

Distribution. Mauritius, Persian Gulf to Thailand, Indonesia, NW Australia, N Australia, Queensland, Papua New Guinea, Philippines and Vietnam.

Comparisons. Western Indian Ocean species of the *tragula* group (Tables 3, 5, 6, Plates 2–3): *Upeneus sundaicus* differs from *U. margarethae* in fewer gill rakers, more lateral-line scales, deeper caudal peduncle, larger suborbital depth, higher first dorsal fin, 5–6 vs 4 bars on upper caudal-fin lobe, the mid-lateral body stripe starting behind eye vs at snout, and barbels yellow vs white (all colour patterns apply to fresh fish only); from *U. oligospilus* it differs in fewer gill rakers, more lateral-line scales, deeper body at anal-fin origin and deeper caudal peduncle, paired fins mostly longer, first dorsal fin considerably higher, lower caudal-fin lobe bars absent, no dark blotches and dots on body or paired fins, no black dorsal-fin tips, and mid-lateral body stripe pale brown vs brown or dark brown, the former not retained after preservation; from *U. taeniopterus* it differs in fewer gill rakers, fewer lateral-line scales, deeper body at dorsal origin, deeper caudal peduncle and head through eye, shorter interdorsal distance, longer paired fins, both dorsal fins taller and longer, bars at lower caudal-fin lobe absent, and one lateral body stripe vs two in fresh fish; and from *U. tragula* it differs in more lateral-line scales, deeper caudal peduncle, deeper head through eye, greater suborbital depth, longer and wider barbels, shorter caudal fin, longer pectoral fin, higher first dorsal fin, lower caudal-fin lobe bars absent, no dark blotches or dots on body or paired fins, no black dorsal-fin tips, and mid-lateral body stripe pale brown vs brown to black, not retained on preserved *U. sundaicus*.

Non-Western Indian Ocean species of the *tragula* group (Table 6): *Upeneus sundaicus* differs from *U. luzonius* in deeper half body at anal origin, wider barbels, higher first dorsal fin, no bars on lower caudal-fin lobe, and bars on caudal fin disappearing on preserved fish; and from *U. mouthami* it differs in fewer gill rakers, fewer lateral-line scales, deeper body and caudal peduncle, greater suborbital depth, much higher and longer first dorsal fin, and no lower caudal-fin lobe bars.

Remarks. In the-Western Indian Ocean, *U. sundaicus* may be restricted to the northern area. It has been reported to co-occur with *U. luzonius* in Sri Lanka by Thomas (1969), but no material of the latter species was preserved from that study and no other material has become available since. The diagnosis given by Thomas for *U. luzonius* indicates that the caudal-fin length is longer than head length which disagrees with our findings of a similar length of both characters (head length 27–30% SL, caudal-fin length 26 – 29% SL; Table 6). Also, the lateral-line scale count is higher. The description of a dark brown mid-lateral body stripe from tip of snout to caudal-fin base deviates from descriptions of body colour for this species given by other authors (e.g., Sainsbury et al. 1985). Lachner (1954) placed *U. sundaicus* in a doubtful status and suggested that it might represent either *U. luzonius* or *U. tragula* and emphasized the necessity of further comparative studies with inclusion of material from the Pacific. Our study indicates that both species are valid, but closely related.

Upeneus sundaicus attains 20 cm SL; depth range 3–20 m.

Upeneus supravittatus sp. nov.
(Tables 3, 8; Plates 2, 3)

U. taeniopterus Cuvier 1829: Kumaran & Randall 1984, Plate III; colour photograph (Madras).

Holotype: NRM 51635, 96 mm, Sri Lanka, Colombo, Slave Island Market, Kelani river drainage, 6°55′55″ N, 79°50′52″ E; collected by H. Sundberg (November 1934).

Paratypes: **India**: USNM 267679, 5: 104–108 mm, Kerala State, Vizhingam, 8°22′ N, 76°58′ E; USNM 396114, 6: 127–144 mm, Madras State; Pondicherry; BPBM 20504, 3: 112–133 mm, Madras, 40 m depth, trawl; **Sri Lanka**: NRM 18877, 118 mm, off Negombo, Western province; NRM 24606, 6: 85–99 mm, Colombo, Slave Island Market, Kelani river drainage, 6°55′ 55″ N, 79°50′52″ E.

Diagnosis. Dorsal fins VIII + 9; pectoral fins 16–17; gill rakers 7–9 + 21–23 = 28–32; lateral-line scales 34–36; body depth at first dorsal-fin origin 26–30% SL; body depth at anal-fin origin 22–25; caudal-peduncle depth 9.9–11; maximum head depth 23–26; head depth through eye 17–20; head length 30–33; orbit length 6.8–8.5; upper jaw length 12–14; barbel length 19–23; caudal-fin length 27–31; anal-fin height 14-17; pelvic-fin length 18–21; pectoral-fin length 25–28; first dorsal-fin height 23–26; second dorsal-fin height 15–17% SL; total bars on caudal fin 8–10, 4–6 brown bars on upper caudal-fin lobe, 3–5 of same colour on lower caudal-fin lobe; the three proximal bars on upper lobe strongly curved, the two proximal bars on lower lobe slightly curved; pale interspaces between bars are of nearly equal width on both lobes, and narrower than bars; lower lobe in adult specimens often considerably shortened, with only three bars, and the distal-most one increased in size; bars retained on preserved fish; two lateral body stripes on fresh fish, one pale-brown mid-lateral stripe reaching from behind head to caudal-fin base, and one below of same colour, from pectoral-fin base to caudal-fin base; first dorsal-fin tip dark, also in preserved fish; head and body brassy or silvery grey, light rose laterally and slightly darker dorsally, and belly pale in fresh fish; body and head uniformly brown or dorsally darkened in preserved fish.

Description. Measurements in % SL and counts are given in Table 8; morphometric data as ratios of SL for holotype, data for paratypes in brackets): body moderately deep, body depth at first dorsal-fin origin 3.6 [3.3–3.8] and body depth at anal-fin origin 4.3 [4.0–4.5]; head length 3.3 [3.0–3.3], subequal to or larger than body depth at first dorsal-fin origin, and caudal-fin length (3.3 [3.2–3.7]); height of second dorsal fin 6.2 [5.9–6.7], clearly less than barbel length (4.8 [4.3–5.3]); pectoral-fin length 3.7 [3.6–4.0], clearly longer than pelvic-fin length (5 [4.8–5.6]), and nearly subequal to body depth at first dorsal-fin origin; caudal-peduncle depth (9.5 [9.1–10]) larger than orbit length (12 [12–15]).

Fresh colour (Plate 2): Head and body brassy to silvery-grey and dorsally grey to red brown, body with two narrow, pale brown lateral stripes, one from head to caudal-fin base, anteriorly well below lateral line, crossing lateral line below second dorsal fin and extending to caudal-fin base where it connects to proximal-most bar of upper caudal-fin lobe; the second stripe from behind pectoral-fin base and extending to caudal-fin base where it connects to proximal-most bar of lower caudal-fin lobe; upper lobe of caudal fin white with six red-brown bars on the photographed paratype (Plate 2), the three proximal bars on upper caudal-fin lobe strongly curved, the third distal bar connecting to the fourth bar; tip of upper caudal-fin lobe covered by bar; four red-brown bars on lower caudal-fin lobe, the two proximal bars slightly curved, overlain with reddish colour derived from several red fin rays on ventral half of caudal fin; the distal-most bar darkest, tip of lower caudal-fin lobe pale; pale interspaces between bars of nearly equal width on both lobes and slightly narrower than bars; spinous dorsal fin white to grey, with two red brown horizontal stripes of equal width, one near base, separated from it by a pale interspace of equal width, the other one at middle of fin separated by pale interspaces of equal width from lower stripe and black fin tip; vertical length of black first dorsal-fin tip about half of orbit diameter; soft dorsal fin whitish-grey with three red-brown horizontal stripes of nearly equal width, separated by three interspaces starting from the fin base, the lower one narrow proximally and wider distally, the other two interspaces of similar width as colour stripes; the uppermost stripe covering the fin tip, smaller and less distinct than first dorsal-fin tip; anal and pelvic fins hyaline, rays white at base; pectoral fins hyaline.

Preserved colour (Plate 3): Body of holotype yellowish white laterally and ventrally and pale brown dorsally; head yellowish white ventrally, becoming darker laterally and dorsally, with large white patches below eye and on gill cover; spinous dorsal fin pale with two horizontal pale brown bands, one near base, the other at middle, fin tip dark brown; fin tip of second dorsal fin dark brown; lateral body stripes absent; caudal fin with nine bars, five on upper and four on lower lobe, all bars pale brown, darker at inner margins of lower lobe and at lower lobe tip; proximal-most bars on both lobes curved, more strongly on upper lobe; bars width equal on both lobes, larger than pale interspaces; pectoral, pelvic and anal fins pale brown to transparent. Body and head of photographed paratype dark brown and fins pale brown, lateral stripes not visible; all 10 caudal-fin bars well visible, mostly light grey, darker towards inner margins of both lobes, and distal-most lower lobe bar darker; other fin colour as on holotype; lower caudal-fin lobe in 13 of the 20 types shorter than upper fin lobe with only three bars retained, the distal-most bar increased in width, mostly rounded, and followed by a tiny pale tip.

Distribution. Sri Lanka, southern India

Etymology. The name "*supravittatus*" derives from the high gill-raker count and the long pectoral-fin length, which in combination place this species "above" all other species of the *vittatus* group (Table 8, Fig. 4).

Comparisons. Western Indian Ocean species of the *vittatus* group (Tables 3, 8, Plates 1–3, Fig. 4): *Upeneus supravittatus* differs from *U. davidaromi* in more gill rakers, deeper body and caudal peduncle, head through eye less deep, smaller suborbital depth, smaller orbit, longer pectoral fins, higher first dorsal fin, lateral body stripes present, and caudal-fin bars more uniformly coloured and more regularly sized on lower lobe; it differs from *U. indicus* in body less deep, longer pectoral fins, and lateral head and body colour brassy vs reddish in fresh fish; from *U. mascareinsis* it differs in deeper body and caudal peduncle, longer pectoral fin, higher first dorsal fin, caudal-fin bars more uniformly coloured and more regularly sized on lower lobes, lateral body stripes present, and the head and body colour more brassy than reddish; from *U. suahelicus* it differs in more gill rakers, longer barbels, longer head, longer distances between tip of snout to paired fin origins, longer pectoral fins, lower second dorsal fin, and body colour brassy vs silvery white (for further comparisons, see the account of *U. suahelicus*); and from *U. vittatus* it differs in more gill rakers on lower limb, fewer lateral-line scales, longer pectoral fin, caudal-fin bars more uniformly coloured and more regularly sized on lower lobe, head and body colour brassy vs of silvery white laterally, and the black first dorsal-fin tip smaller.

Non-Western Indian Ocean species of the *vittatus* group (Table 8): *Upeneus supravittatus* differs from *U. subvittatus* in more gill rakers, deeper caudal peduncle, shorter snout, higher first dorsal fin, more uniform caudal-fin bar colour, two lateral body stripes present, and head and body colour more brassy than reddish.

Remarks. *Upeneus supravittatus* attains 14 cm SL; maximum reported depth is 40 m.

Upeneus taeniopterus Cuvier 1829

(Tables 3, 6; Plates 2, 3)

Upeneus taeniopterus Cuvier in Cuvier & Valenciennes 1829: 451 (type locality: Sri Lanka, Trincomalee); Winterbottom et al. 1989, p. 41, Fig. 222.

Upeneus arge Jordan & Evermann 1903 (type locality: Hawaii); Randall 2001, p. 3195.

Diagnosis. Dorsal fins VIII + 9; pectoral fins 13–14; gill rakers 5–6 + 16–17 = 21–23; lateral-line scales 35–39; body depth at first dorsal-fin origin 22–25% SL; body depth at anus 20–23; caudal-peduncle depth 9.7–11; maximum head depth 17–21; head depth through eye 14–17; head length 25–29; orbit length 4.4–6.3; upper jaw length 11–13; barbel length 17–21; caudal-fin length 28–32; anal-fin height 15-17; pelvic-fin length 18–20; pectoral-fin length 17–20; first dorsal-fin height 20–23; second dorsal-fin height 14–16% SL; total bars on caudal fin 9–13 (7–9 in fish < 10 cm), upper caudal-fin lobe with 4–8 black bars, the proximal bars slightly curved; 3–6 bars on lower lobe; bars on both lobe tips black, other bars mostly red or brown becoming black at distal inner margin of lobes; at least the black parts of bars retained on preserved fish; mostly two lateral body stripes, one pale brown at mid-body from snout or eye to caudal-fin base, the other shorter, fainter, and more yellowish below, starting at operculum or behind pectoral-fin base; sometimes a weak third yellow stripe below; stripes not retained on preserved fish; first dorsal-fin tip pale; barbels yellow in fresh fish; body pale grey, dorsally somewhat darker, with faint red patches laterally and red scale markings above upper stripe; body uniformly pale brown in preserved fish.

Distribution. Mozambique, Sri Lanka, Seychelles, Rodrigues, Cocos Islands, Chagos, Solomons, Hawaii, Japan

Comparisons. Western Indian Ocean species of the *tragula* group (Tables 3, 5, 6, Plates 1–3): *Upeneus taeniopterus* differs from *U. margarethae* in more lateral-line scales, smaller orbit, shorter pelvic and pectoral fins, lower second dorsal fin, two vs one lateral body stripe in fresh fish, and caudal-fin bars always retained after preservation; from *U. oligospilus* it differs in considerably more lateral-line scales, smaller maximum head depth, shorter head and snout, longer caudal fin, lower second dorsal fin, no dark blotches and dots on body and paired fins, no black dorsal-fin tips in both fresh and preserved fish, and mid-lateral body stripe pale brown vs brown or dark brown, only the latter retained after preservation; from *U. sundaicus* it differs in more gill rakers, more lateral-line scales, body at dorsal-fin origin and caudal peduncle less deep, head through eye less deep, larger interdorsal distance, shorter paired fins, both dorsal fins smaller, bars at lower caudal-fin lobe present, and two lateral body stripes vs one in fresh fish; and from *U. tragula* in having many more lateral-line scales, smaller orbit length, shorter pelvic fins,lower second dorsal fin, two pale brown vs one brown to black lateral body stripes, the former not retained after preservation, no dark dorsal-fin tips and no dark dots and/or blotches on body and paired fins.

Non-Western Indian Ocean species of the *tragula* group (Table 6): *Upeneus taeniopterus* differs from *U. luzonius* in more gill rakers and lateral-line scales, deeper half body at anal origin, caudal peduncle less deep, smaller head depth, greater interdorsal distance, longer caudal fin, shorter paired fins, lower second dorsal fin; and from *U. mouthami* it differs in fewer gill rakers, more lateral-line scales, head through eye less deep, smaller orbit, longer caudal fin, lower anal fin, shorter paired fins, less elevated second dorsal fin, two vs one lateral body stripes on fresh fish, and more bars on upper caudal-fin lobe.

Remarks. Species identification was based on thorough examination and comparison of the holotypes of *Upeneus taeniopterus* and *U. arge* with inclusion of additional material from the Indian Ocean and Pacific (Table 6, Plates 2–3, Fig. 5). Thomas (1969) checked the holotype of *U. taeniopterus* at MNHN, but obviously missed the minute dorsal-fin spine and did not go any further in comparing it with other material. Lachner (1954) treated *U. taeniopterus* as a doubtful species. More recently the species has been recorded in the Western Indian Ocean by Kumaran and Randall (1984) and later by Randall (Randall 2001). Their identification, based on 8 dorsal-fin spines, a black fin tip, and a relatively low lateral-line scale count, points to a misidentification of the now newly described *U. suahelicus* and *U. supravittatus*, (see also the species accounts). From those two species it differs in many characters that also justify its inclusion in the *tragula* species group. The holotype of *Upeneus arge* falls together with the other specimens from the Pacific in the range of the measurements and counts for the *U. taeniopterus* type and Indian Ocean specimens and hence *U. arge* is to be treated as a junior synonym of the former.

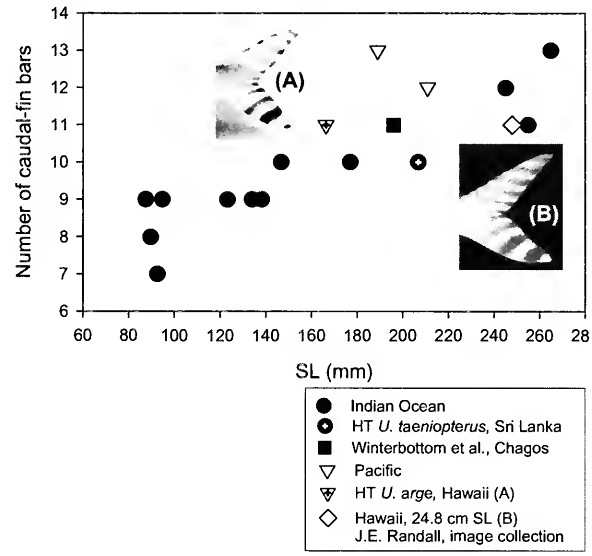

Fig. 5. Number of bars on caudal fin against SL in *Upeneus taeniopterus* from the Indian Ocean (filled symbols) and Pacific (hollow symbols); (A) caudal fin of holotype (HT) of *U. arge* based on an illustration accessible online from the USNM fish collection; (B) caudal fin from a photograph of a fresh fish from the online image collection of J.E. Randall; The caudal-fin bar number based on a photograph of *U. taeniopterus* from Chagos published by Winterbottom *et al.* (1989) is also included.

Upeneus taeniopterus attains 27 cm SL; maximum reported depth is 50 m.

Upeneus tragula Richardson, 1846

(Tables 3, 6; Plates 2, 3)

Upeneus tragula Richardson 1846: 220 (type locality: Guangzhou, China); Blegvad & Løppenthin 1944: 135, Pl. 7, Fig. 3 (inaccurate colour painting) Smith 1965: 228, Pl. 27, Fig. 560 (diagnosis, uncommon south of Delagoa Bay, Mozambique); Kumaran & Randall 1984, no page number, Plate III; (photograph); Ben-Tuvia & Kissil 1988: 13, Fig. 13 (diagnosis, black and white photograph) Gulf of Suez, Massawa, Eritrea); De Bruin et al. 1994: 271, Plate 20, Fig. 141 (colour photograph); Randall 1995: 243, Fig.635 (diagnosis, Oman, colour photograph); Randall & Kulbicki 2006, 305–306, Fig. 8; diagnosis and colour photograph.

DIAGNOSIS. Dorsal-fin rays VIII + 9; pectoral-fin rays 13–14, mostly 13 (in 11 of 14 specimens); gill rakers 5–6 + 14–17 = 19–23; lateral-line scales 28–30; body depth at first dorsal-fin origin 22–26% SL; body depth at anus 20–22; caudal-peduncle depth 9.9–11; maximum head depth 19–23; head depth through eye 15–17; head length 27–31; orbit length 6.1–8.3; upper jaw length 11–14; barbel length 15–18; caudal-fin length 28–32; anal-fin height 16-19; pelvic-fin length 20–24; pectoral-fin length 19–21; first dorsal-fin height 21–24; second dorsal-fin height 18–22% SL; total bars on caudal fin 10–12 (or more) (7–10 in juveniles < 7 cm SL), upper caudal-fin lobe with 4–6 brown, dark brown or black bars; 4–7 brown, dark brown or black bars on lower lobe; one brown to black mid-lateral body stripe from tip of snout to caudal-fin base; body above stripe greenish grey, body below stripe white or beige, with irregular dark reddish brown spots and blotches, also on paired fins; dark marks on or very close to first and second dorsal-fin tips; barbels yellow in fresh fish; most of body and fin pigmentation retained on preserved fish.

DISTRIBUTION. Red Sea to Mozambique, Oman, Persian Gulf, India, Sri Lanka, Myanmar, Indonesia, Cambodia, Thailand, Singapore, Sabah, Vietnam, Philippines, Papua New Guinea, New Caledonia, Palau and southern Japan.

COMPARISONS. Western Indian Ocean species of the *tragula* group (Tables 3, 6, Plates 1–3, Fig. 3): *Upeneus tragula* differs from *U. margarethae* in mostly 13 (in 13 of 16 fish) vs mostly 14 (in 26 of 29 fish) pectoral-fin rays, longer jaws, shorter pectoral fins, 5–6 brown or black vs 4 red bars on upper caudal-fin lobe in adults (> 7 cm SL), dark bars on lower caudal-fin lobe present, the body and fins with dark blotches or dots, the first and second dorsal-fin tips dark, the colour of mid-lateral body stripe brown to black vs yellow, and mid-lateral body stripe retained on preserved fish; it differs from *U. oligospilus* in longer caudal fin and more total caudal-fin bars both in adults (10–12 vs 6–9) and juveniles (7–10 vs 6–7) (Fig. 3A, B, D), shorter postorbital length, shorter distance between tip of snout to pectoral-fin origin, longer pelvic fin, and higher second dorsal fin in adult fish, if size is referred to (e.g. Fig. 3C); from *U. sundaicus* it differs in fewer lateral-line scales, caudal peduncle less deep, head through eye less deep, smaller suborbital depth, shorter and thinner barbels, longer caudal fin, shorter pectoral fin, lower first dorsal fin, lower number of caudal-fin lobe bars, dark blotches or dots on body and paired fins, black dorsal-fin tips in both fresh and preserved fish, and mid-lateral body stripe brown to black vs pale brown, retained on preserved *U. tragula*; from *U. taeniopterus* it differs in fewer lateral-line scales, greater orbit length, longer pelvic fins, higher second dorsal fin, one brown to black vs two pale brown lateral body stripes, stripes retained on preserved fish, dark dorsal-fin tips, and dark dots and/or blotches on body and paired fins.

Non-Western Indian Ocean species of the *tragula* group (Table 6): *Upeneus tragula* differs from *U. luzonius* in fewer pectoral-fin rays (mostly 13, in 13 of 16 individuals, vs 14 or 15), fewer lateral lines scales, deeper half body at anal-fin origin, caudal-peduncle less deep, longer lower jaws, and fresh and preserved fish having dark dorsal-fin tips and dark dots and/or blotches on body and paired fins; from *U. mouthami* it differs in slightly fewer gill rakers, head through eye less deep, longer jaws, shorter and thinner barbels, shorter pectoral fin, higher first dorsal fin with a longer base, more bars on upper caudal-fin lobe, brown to black vs yellow lateral body stripe, the former retained on preserved fish, presence of dark tips on both dorsal fins, and presence of dark dots and/or blotches on body and paired fins.

REMARKS. *Upeneus tragula* shows an increase in number of caudal-fin bars during ontogeny, similar to its close relative *U. oligospilus* (Fig. 3). Both species co-occur in the Persian Gulf, as indicated by photographs provided by J. E. Randall, one of a 11.6 cm *U. tragula* specimen (shown in De Bruin et al. 1994 and Carpenter et al. 1997) and another one of a 6.1 cm juvenile (BPBM 29498), both collected in Bahrain.

Upeneus tragula attains 33 cm SL; maximum reported depth is 50 m.

Upeneus vittatus (Forsskål 1775)

(Tables 3, 8; Plates 2, 3)

Mullus vittatus Forrskål 1775: 31; (type locality: Jeddah, Red Sea, type material lost).

Upeneus vittatus: Blegvad & Løppenthin 1944: 134, Pl. 7, Fig. 2, (Persian Gulf, inaccurate colour painting); Smith 1965: 228, Pl. 27, Fig. 561 (reported from South Africa south to East London); Kumaran & Randall 1984: no page number, Plate III; colour photograph; Ben-Tuvia & Kissil 1988: 14, Fig. 14 (black and white photograph of fish from Society Islands). Randall & Kulbicki 2006, 306, Fig. 9, (diagnosis and colour photograph)

Neotype: SMF 1185, 163 mm, Red Sea, collected by Eduard Rüppell, 1834, most probably off Eritrea (see Remarks).

DIAGNOSIS. Dorsal fins VIII + 9; pectoral fins 15–16; gill rakers 7–8 + 19–21 = 27–29; lateral-line scales 36–38; body depth at first dorsal-fin origin 25–29% SL; body depth at anal-fin origin 21–24; caudal-peduncle depth 9.9–12; maximum head depth 21–26; head depth through eye

18–20; head length 30–31; orbit length 7.0–8.7; upper jaw length 11–13; barbel length 17–21; caudal-fin length 26–30; anal-fin height 15-16; pelvic-fin length 18–21; pectoral-fin length 22–24; first dorsal-fin height 22–25; second dorsal-fin height 14–16% SL; total number of bars on caudal fin 7–9, upper caudal-fin lobe with 4–5 brown or dark brown bars; 3 (rarely 4) bars on lower caudal-fin lobe, increasing distally in width, the widest, distal-most bar black or dark brown, the other bars pale brown or brown; width of largest lower caudal-fin lobe bar and/or pale interspace between distal-most bars equal to or larger than orbit; tip of lower fin lobe pale; bars on both caudal-fin lobes retained on preserved fish; first dorsal-fin tip dark, the vertical length of the pigmented area similar in size to width of widest lower caudal-fin lobe bar; two yellow or pale brown mid-lateral body stripes, one from eye to caudal-fin base, where it joins the proximal upper caudal-fin lobe bar, and the other stripe below, from pectoral-fin base to caudal peduncle, continued by proximal-most lower caudal-fin lobe bar; two dorsolateral brown or pale brown stripes, the lower one distinct and well-separated from pale body surface, extending from operculum to behind second dorsal fin, the upper one indistinct or hidden and much shorter, beginning immediately below first dorsal-fin origin and bordered dorsally by a horizontal series of pale spots; lateral body stripes not retained on preserved fish; barbels white; body white to silvery, dorsally dark reddish-brown, belly white, faint yellowish patches along pelvic and anal-fin bases; body pale brown in preserved fish, slightly darker above lateral line.

Description of Neotype. Measurements as % SL and counts of neotype are given in Table 8; morphometric data as ratios of SL) of neotype: body moderately deep, body depth at first dorsal-fin origin 3.9, body depth at anal-fin origin 4.6, head length 3.2; caudal-fin length 3.5, greater than body depth at first dorsal-fin origin and shorter than head length; height of second dorsal fin 6.7, clearly smaller than barbel length (5.6); pectoral-fin length 4.4, clearly longer than pelvic-fin length (5.5) and shorter than body depth at first dorsal-fin origin; caudal-peduncle depth 8.7, much larger than orbit length (14).

Fresh colour: No description of fresh colour of the neotype is available. Our species diagnosis is based on a photograph of a fresh fish collected off Mozambique (Plate 2), which was also included in the comparison with the neotype (Table 8), and a photograph of a fresh fish from off Mauritius by J. E. Randall.

Preserved colour (Plate 2): Body pale brown, slightly darker above lateral line, a few scales missing on either side; large white patch on belly from just anterior to pelvic fins to base of pectoral fins; head yellowish-white ventrally and laterally and pale brown anteriorly on snout and dorsally; spinous dorsal fin pale, with two horizontal pale brown bands, one near fin base, the other at middle, fin tip dark brown, vertical length equals orbit depth; two faint horizontal bands on second dorsal fin, fin tip pale brown; lateral body stripes absent; seven caudal-fin bars, four bars on upper and three on lower lobe, all bars pale brown on pale background with exception of the distal-most bar on the lower lobe which is darker and wider, its maximum horizontal extension reaching about three quarters of the orbit length; the pale interspace between the second and third lower caudal-fin lobe bar enlarged and nearly equal to orbit length; pale area on tip of lower caudal-fin lobe as wide as distal-most bar; pectoral, pelvic and anal fins pale brown to transparent.

Distribution. Red Sea to South Africa, Madagascar, Réunion, Mauritius, Indonesia, Thailand, New Guinea, New Caledonia, southern Japan, Palau, Mariana Islands, Fiji, Samoa Islands, Society Islands, Marquesas Islands and Hawaii.

Comparisons. Western Indian Ocean species of the *vittatus* group (Tables 3, 8, Plates 1–3, Fig. 1): *Upeneus vittatus* differs from *U. davidaromi* in deeper body at dorsal-fin origin and deeper caudal peduncle, head through eye less deep, smaller suborbital depth, shorter head, smaller orbit, shorter upper jaw, larger distance between dorsal fins, longer anal-fin base, higher first dorsal fin, lateral body stripes present and widest bar on lower caudal-fin lobe larger; it differs from *U. indicus* in fewer gill rakers on upper limb, body at anal-fin origin less deep, larger orbit, colour of caudal-fin bars more intense and more variable, lower caudal-lobe bar and interspace width less uniform, black first dorsal-fin tip larger, and lateral body and head colour silvery-white vs reddish; it differs from *U. mascareinsis* in deeper caudal peduncle, greater suborbital depth, the largest bar and/or pale interspace between distal-most bars on lower caudal-fin lobe wider, the first dorsal-fin black tip larger, lateral body stripes present, and body and head colour laterally silvery-white vs reddish; it differs from *U. suahelicus* in more lateral-line scales, shorter pectoral fins, lower second dorsal fin, more variable caudal-fin bar colour, bars on lower lobe less regular in size, and the black first dorsal-fin tip larger; and from *U. supravittatus* it differs in fewer gill rakers on lower limb, more lateral-line scales, shorter pectoral fins, more variable caudal-fin bar colour, bars on lower lobe less regular in size, head and body colour laterally silvery-white vs brassy, and black first dorsal-fin tip larger.

Non-Western Indian Ocean species of the *vittatus* group (Table 8): *Upeneus vittatus* differs from *U. subvittatus* in more lateral-line scales, shorter head, shorter jaws, shorter pectoral fins, lateral body stripes present, largest bar and/or pale interspace between distal-most bars on lower caudal-fin lobe wider, and first dorsal-fin black tip.

REMARKS. For the purpose of neotype selection and designation an inquiry was made at five collections (BMNH, BPBM, HUJ, MNHN, SMF) to find an appropriate specimen of *Upeneus vittatus* from the Red Sea as close as possible to the original type locality (Jeddah, Saudi Arabia). The SMF specimen proved to be in excellent condition compared to all others, apart from a few missing scales and the caudal-fin bars showing some indication of fading, most probably due to long-term preservation. The neotype overlaps in all important characters with *Upeneus vittatus* from the Indian Ocean proper (Table 8). The Senckenberg collection in Frankfurt recorded receipt of the specimen from Eduard Rüppell in 1834, after his return from the second Red Sea expedition to Ethiopia/Eritrea (1830–33, see also Klausewitz 2002). Therefore we assume that this fish was collected at the central or southern Red Sea coast across from Jeddah.

According to Ben-Tuvia and Kissil (1988) and Daniel Golani (personal communication) *Upeneus vittatus* may be absent from the Northern Red Sea. Ben-Tuvia and Kissil (1988) provided a colour description based on a slide of a fresh specimen identified as *U. vittatus* collected in Eritrea. The colouration of the caudal-fin bars is described as yellow with dusky black edges. No information on the variation in colour intensity and width of bars and the pale interspaces between the bars is given. This description contrasts with the photograph provided in their account which shows a *U. vittatus* specimen from off French Polynesia made by J. E. Randall with dark caudal-fin bars. It contrasts also with our diagnosis based on photographs of *U. vittatus* specimens collected off Mozambique and Mauritius. One specimen cited in the paper of Ben-Tuvia and Kissil (1988) has been examined by us (HUJ 8555) and identified as *U. suahelicus* (see the description of this species above).

Upeneus vittatus attains 28 cm SL; it reaches depths of at least 100 m.

DISCUSSION AND CONCLUSIONS

The present account is the first comprehensive review of the goatfish genus *Upeneus* in the Western Indian Ocean since that of Kumaran and Randall (1984). A total of 16 valid species have been identified, with four species, *U. indicus, U. margarethae, U. suahelicus,* and *U. supravittatus,* being described as new. One species, *U. oligospilus,* has been resurrected from synonymy with *Upeneus tragula,* and another species, *U. arge,* reported earlier from the area was found to be a junior synonym of *U. taeniopterus.* New records of the following four species have been documented for larger areas of the Indian Ocean: *U. guttatus* (Red Sea), *U. mascareinsis* (Madagascar, Mozambique, Eastern Indian Ocean), *U. pori* (southwestern Indian Ocean), and *U. sulphureus* (Persian Gulf).

The Western Indian Ocean *Upeneus* species differ considerably in their distributions, with some species restricted to distinct sub-regions, like *U. davidaromi* which is confined to the Red Sea, and some occurring in the Western and Eastern Indian Ocean proper, like *U. mascareinsis,* or occurring widely in the Indo-West Pacific, like *U. tragula.* Most species can be characterized as typically coastal shallow-water inhabitants, but there are two species, *U. davidaromi* and *U. mascareinsis,* that have invaded the upper slope. *U. taeniopterus,* which has been described from Sri Lanka, appears to be primarily insular, occurring in coastal waters of remote islands and lagoons of atolls, and is widely distributed from Pinda Island off Mozambique to Hawaii.

The most conspicuous characters in the genus *Upeneus* are the colour patterns and in particular the occurrence of lateral body stripes, caudal-fin bars, and dark dorsal-fin tips. Using these patterns alone greatly enhances species identification when live or freshly caught fishes are available. Because much of the colour patterns fade in preservative (apart from dark caudal-fin bars and dorsal-fin tip pigmentation), the inclusion of other characters both in identification keys and species diagnoses is essential. Some of the colour characters seem also to vary considerably during catch or handling of collected material, diurnal variation in nature, differences among individuals, or differences among populations. These differences need to be accounted for and hence it appears to be of primary importance to have both fresh and preserved colouration and overall morphology documented in a consistent and representative manner.

Six meristic, 15 morphometric, and 8 colour characters were given high diagnostic significance (Table 3), but many additional characters including overall colouration of live or fresh fish and body-shape variables allow distinction among species. Inclusion of several body-shape characters showing covariance such as distinct body depth, head depth, or head length measurements has greatly facilitated species diagnoses. Distinction among different life history stages has been important in the current study, as considerable ontogenetic variation in body colour and morphometrics was detected. For instance, in three species of the "*tragula* group", the number of caudal-fin bars and the body shape changes during the transition from juveniles to adults. Marked ontogentic changes in body colouration and shape were also found in *Upeneus doriae* of the "*moluccensis* group" and *U. mascareinsis* of the "*vittatus* group". In the latter case the differences were so marked that the species identity of the juvenile remained uncertain (= cf. *mascareinsis*). In such doubtful cases genetic studies may be of particular value as a tool to evaluate taxonomic hypotheses based on phenotypic characters (e.g. Randall et al. 2007). Also, the ecological significance of life history changes in body colour, morphology, and associated behaviour should be considered (e.g. Uiblein 1991, 1996), as well as the effects of phenotypic plasticity on differences among populations and species (Uiblein et al. 1998).

In this study we have tried to cover all the *Upeneus* species of the entire Western Indian Ocean area as completely as possible. For some areas, however, like the Gulf of Suez, no material could be studied. For a full coverage, more sampling is required, especially in the Red Sea and along the entire coast from the Gulf of Aden to India. More new species and/or new records of known species of the genus *Upeneus* can be expected from other under-studied areas outside the Western Indian Ocean.

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We thank Elaine Heemstra for assistance in field collections, handling of collected material, acquisition of literature and photographs, and providing the drawings of caudal bar patterns. Monica Mwale and Gavin Gouws provided assistance in material preservation. For the loan of specimens and/or making collection visits by the first author possible we thank Mark McGrouther, John Paxton and Amanda Hay (AMS), James Maclaine (BMNH), Jack Randall, Lori O'Hara, and Arnold Suzumoto (BPBM), Daniel Golani (HUJ), Romaine Causse and Patrice Pruvost (MNHN), Martin Gomon (NMV), Sven Kullander and Erik Åhlander (NRM), Alan Whitfield and Wouter Holleman (SAIAB), Friedhelm Krupp and Horst Zetzsche (SMF), Jeff Williams and Jerry Finan (USNM), Peter R. Møller, Jørgen G. Nielsen, and Tammes Menne (ZMUC). For photographs of fresh or preserved material and/or additional information we thank Jack Randall, Oddgeir Alvheim, Friedhelm Krupp, Monica Mwale, Sergey Bogorodsky, Romaine Causse, Daniel Golani, Jerry Finan, Alastair Graham, Les Knapp, James Maclaine, Sandra Raredon, Jeff Williams, Horst Zetzsche, Diane Bray, Martin Gomon, Mark McGrouther, Dimitri Pavlov, Clive Roberts, G. David Smith, Arnold Suzumoto, Rajan P. Thomas, Denis Tweddle and William White. Jack Randall, Wouter Holleman, and Jeff Williams are thanked for commenting on earlier versions of the manuscript.

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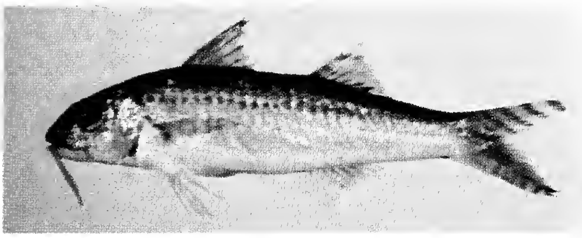
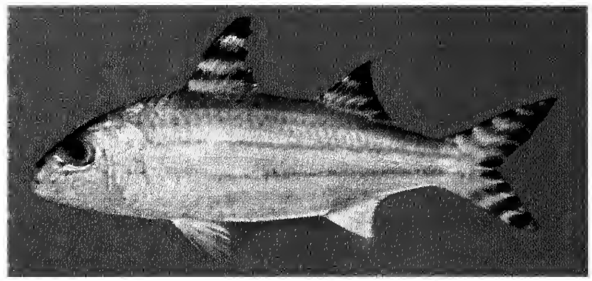
PLATE 1

A. *U. davidaromi*, SL165 mm, Gulf of Aqaba (J.E. Randall)

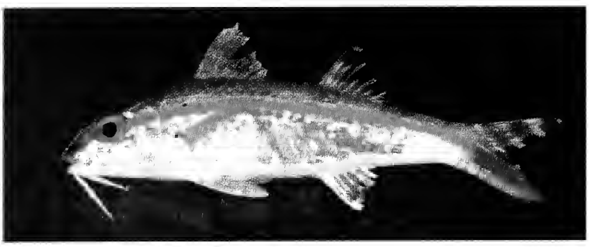
B. *U. doriae*, SL 106 mm, Bahrain (J.E. Randall)



C. *U. guttatus*, SAIAB 13947, SL 100 mm, Kenya (P.C. Heemstra)

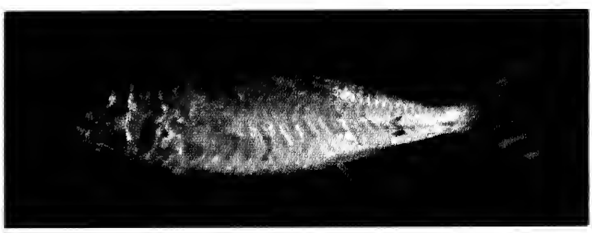


D. *U. indicus* sp. nov., holotype, BPBM 27524, SL 137 mm, West India (J.E. Randall)

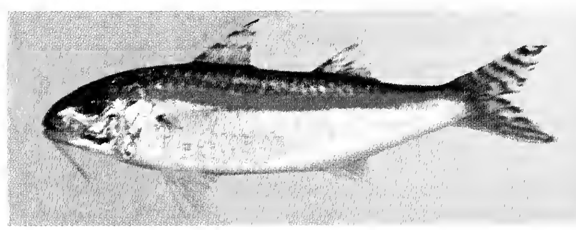


E. *U. margarethae* sp. nov., holotype , SAIAB 82217, SL 82 mm, Mozambique (P.C. Heemstra)

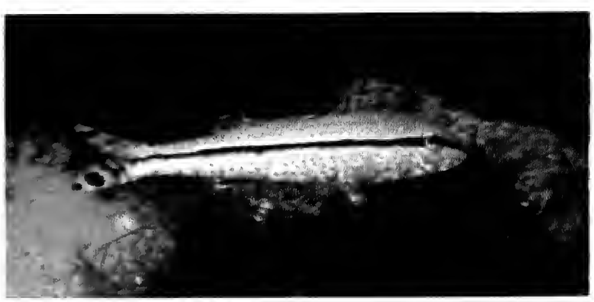
F. *U. margarethae* sp. nov., paratype, SAIAB 82814, SL 89 mm, Mozambique (P.C. Heemstra)



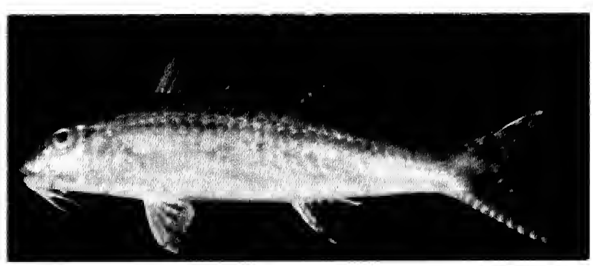
G. *U. mascareinsis*, SAIAB 81951, SL 162 mm, Mozambique (P.C. Heemstra)



H. *U. moluccensis*, SAIAB 13948, SL 112 mm, Kenya (P.C. Heemstra)



I. *U. oligospilus*, Persian Gulf, N of Abu Ali, Saudi Arabia (F. Krupp)



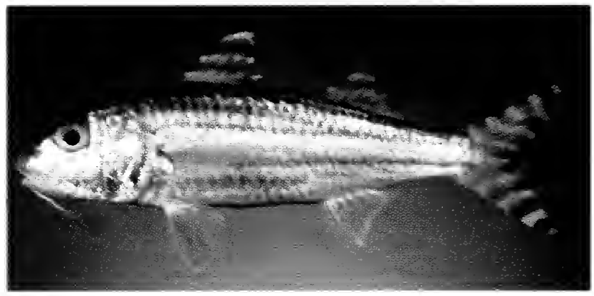
J. *U. pori*, SL 114 mm, Red Sea, Egypt (J.E. Randall)

PLATE 2

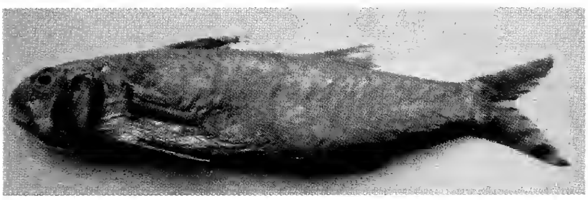
A. *U. suahelicus* sp. nov., holotype, SAIAB 13948, SL 101 mm, Kenya (P.C. Heemstra)

B. *U. sulphureus*, SAIAB 82237, SL 106 mm, Mozambique (P.C. Heemstra)

C. *U. sundaicus*, SL 81 mm, Kuwait (J.E. Randall)



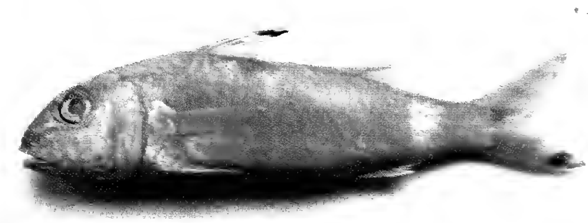
D. *U. supravittatus*, BPBM 20504, SL 120 mm, Madras (J.E. Randall)



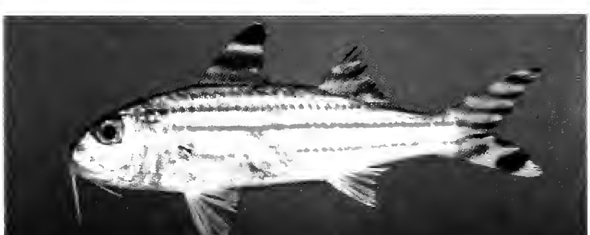
E. *U. taeniopterus*, holotype, MNHN 0000-9568, SL 207 mm, Sri Lanka (F. Uiblein)

F. *U. taeniopterus*, SAIAB 69803, SL 134 mm, Rodrigues (P.C. Heemstra)

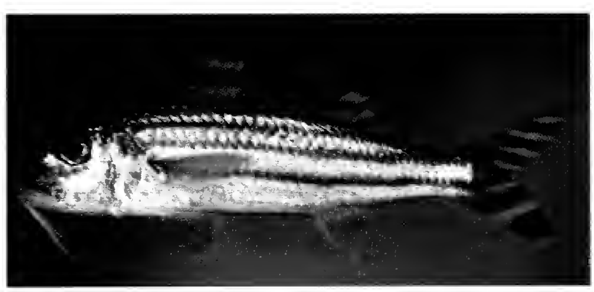
G. *U. tragula*, SAIAB 80384, SL 142 mm, Tanzania (M. Mwale)



H. *U. vittatus*, neotype, SMF 1185, SL 163 mm, Red Sea (F. Uiblein)



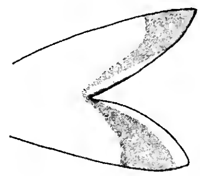
I. *U. vittatus*, SAIAB 82327, SL 146 mm, Mozambique (P.C. Heemstra)



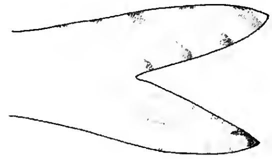
J. *U. vittatus*, SL 155 mm, Mauritius (J.E. Randall)

PLATE 3

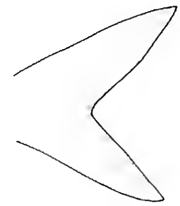
A. *U. davidaromi*
SAIAB 42630
110 mm SL



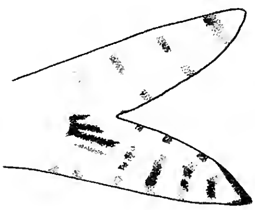
B. *U. doriae*
SMF 26055
71 mm SL



C. *U. guttatus*
SAIAB 82714
94 mm SL

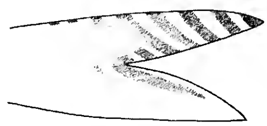


D. *U. indicus*
HT BPBM 27524
137 mm SL

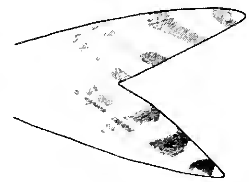


E. *U. margarethae*
SAIAB 82817
108 mm SL

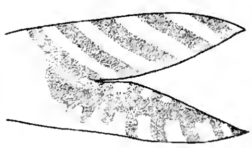
F. *U. mascareinsis*
SAIAB 81951
162 mm SL



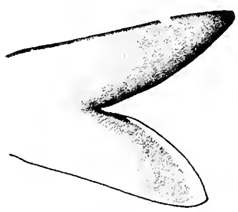
G. *U. moluccensis*
SAIAB 82509
103 mm SL



H. *U. oligospilus*
NRM 16480
171 mm SL

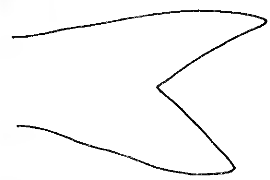


I. *U. pori*
MNHN 1992-977
97 mm SL

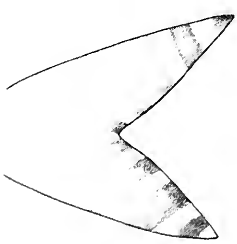


J. *U. sulphureus*
SAIAB 82237
99 mm SL

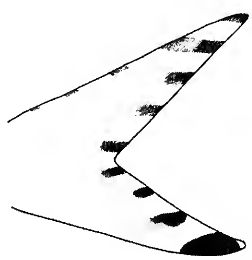
K. *U. suahelicus*
SAIAB 13948
101 mm SL



L. *U. sundaicus*
ZMUC P49124
109 mm SL



M. *U. supravittatus*
BPBM 20504
120 mm SL



N. *U. taeniopterus*
SAIAB 69803
134 mm SL

O. *U. tragula*
SAIAB 80384
142 mm SL

P. *U. vittatus*
SAIAB 82327
146 mm SL

MATERIAL EXAMINED

Upeneus asymmetricus: ***Holotype***: USNM 154659, 75 mm, Philippines, Pandanon Island, between Cebu and Bohol; **Philippines:** USNM 154660, 74–79 mm, paratypes, Pandanon I., between Cebu and Bohol; USNM 154661, 100 mm, paratype, off Western Samar, Catbalogan.

Upeneus australiae: **Western Australia**: BMNH 1983 5.5.17-22, 6: 117-130 mm, 20°15′0″ S, 117°50′00″ E; BMNH 1983 5.5.27-30, 112 mm, 20°10′0″ S, 118°25′00″ E; **Vietnam**: ZMUC P49483, 84 mm, Nha Trang Bay.

Upeneus davidaromi: **Israel, Red Sea**: SAIAB 42630, 105–110 mm, off Eilat; MNHN 1987-1195, 160 mm, Gulf of Aqaba, 20°00′ N, 39°00′ E, depth 550 m.

Upeneus doriae: **Iran, Persian Gulf:** SAIAB 58782, 46–58 mm; SMF 26055, 3: 71–97 mm, 29°01′293″ N, 50°05′136″ E, depth 45 m; **Oman, Gulf of Oman**: NRM 41325, 3: 116–145 mm, Masqat fish market.

Additional material (see Remarks section in species account): **Iran, Gulf of Oman**: BPBM 31268, 2(of 4):124-143 mm, "R.V. *Anton Bruun*", IIOE cruise 4B, st. 253A, 25°25′ N, 58°20′ E, depth 45 fms; BPBM 31269, 1 (of 9), 126 mm, "R.V. *Anton Bruun*", IIOE cruise 4B, st. 258A, 26°58′ N, 56°43′ E, depth 18 fms; BPBM 31270, 92-98 mm, "R.V. *Anton Bruun*", IIOE cruise 4B, st. 259A, 25°35′ N, 56°25′ E, depth 39.5 fms.

Upeneus francisi: **Norfolk Island:** USNM 317286, 49 mm, paratype, Duncombe Bay, 29°05′ S, 167°59′ E, 18 m, collected with dip net.

Upeneus guttatus: **Sudan**: BMNH 1960-315.8.42-1, 77 mm, 5 miles south of Ibn Abbas Island; **Somalia, Indian Ocean:** USNM 396093, 114 mm, 11°14′ N, 51°08′ E; **Kenya**: SAIAB 13947, 100 mm, R.V. *Dr. F. Nansen* 80, PCH 80-32, 03°07′ S, 40°11′ E; **Mozambique**: SAIAB 82216, 91 mm, Western Indian Ocean, R.V. *Dr. F. Nansen*, M07-78, 35°78.60′ S, 19°93.61′ E, 47 m, bottom trawl; SAIAB 82714, 94 mm, R.V. *Dr. F. Nansen*, M07-36, 35°04.98′ S, 24°94.41′ E, 65 m, bottom trawl; SAIAB 81746, 91 mm, R.V. *Dr. F. Nansen*, M07-07, 32°97.25′ S, 26°50.63′ E, 82 m, bottom trawl; SAIAB 82007, 93–108 mm, R.V. *Dr. F. Nansen*, M07-46, 35°25.92′ S, 24°56.19′ E, 51 m, bottom trawl; SAIAB 82819, 93 mm, R.V. *Dr. F. Nansen*, M07-130, 40°51.41′ S, 12°93.71′ E, 73 m, bottom trawl; SAIAB 82813, 102 mm, R.V. *Dr. F. Nansen*, M07-77, 35°51.21′ S, 19°79.08′ E, 28 m, bottom trawl; **South Africa, Indian Ocean**: SAIAB 51020, 146 mm, Natal, 29°39′00 S, 31°08′00 E; **Madagascar**: MNHN 1967-555, 104–114 mm, Banc de Pracel / Canal du Mozambique, 20°00′ S, 42°30′ E; MNHN 1965-0017, 126 mm, holotype of *U. crosnieri*, Banc de Pracel, 20°00′ S, 42°30′ E, depth 45 m; SAIAB 52827, 92 mm, Tsimipaika Bay, MAD 95-10, 8–12 m; SAIAB 52836, 4: 87–96 mm, Tsimipaika Bay, MAD 95-10, 8–12 m; **Réunion:** MNHN 1967-554, 92 mm, 20°53′, S, 55°21′ E, 80 m; **Seychelles:** MNHN1982-44, 3: 111–126 mm. Seychelles, R.V. *Coriolis* /Reves2, st. 3, 5°13′ S, 56°40′ E, depth 50 m; **India**: BPBM 40986, 113 mm, Madras, depth 73 m, trawl; **Sri Lanka:** USNM 395449, 84 mm, Thalaiaddy, Jaffna area; **Malaysia, Indian Ocean**: ZMUC P4947, 97 mm, Malakka; ZMUC P49432, 108 mm.

Upeneus japonicus: **China, South China Sea**: SMF 25449, 107 mm, Hainan, Qinglan; **Japan**: NRM 55484, 3: 104–115 mm, Seto Inland Sea, Honsho, Shimonoseki Fish market, 33.95° N, 130.95° E.

Upeneus luzonius: **Philippines:** USNM 53067, 65 mm, paratype, Manila; USNM 53067; 71 mm, paratype, Manila; USNM 102649, 91 mm, Iloilo, Panay Island; USNM 106829, 81 mm, Panay Island, Garo River; USNM 138658, 49 mm, Manila Bay; Manila Bay and Vicinity, 6 m.

Upeneus mascareinsis: **Holotype:** MNHN 65-0072, 152 mm, Réunion, 21°07′0″ S, 55°35′00″ E; **Mozambique**: SAIAB 74603, 135–160 mm, 18°02′06″ S, 37°37′12″ E, 162–200 m; SAIAB 81951, 138 -162 mm, R.V. *Dr. F. Nansen*, M07-42 34°46.57′ S, 25°07.31 E, depth 99 m, bottom trawl; **Réunion**: BMNH 1968.11.5.79, 99 mm; depth 140 m; MNHN 1965-73, 90–97 mm, 21°07′0″ S, 55°35′00″ E; MNHN 1965-79, 3: 84–111 mm; 21°07′0″ S, 55°35′00″ E; MNHN 1989-0090, 141 mm; 21°00′ S, 55°15′ E; USNM 204033, 155 mm, 366 m; **Madagascar**: MNHN 1989-0202, 145 mm, FAO 60, st.73/059, 21°47′ S, 43°10′ E, 250 m; **Indonesia, Indian Ocean**: BMNH 1986.10.1.38 88, 88 mm.

Upeneus cf. *mascareinsis*: **Mozambique**: SAIAB 82328, juvenile, 69 mm, R.V. *Dr. F. Nansen*, M07-110, 38°89.43′ S, 17°27.83′ E 114 m, bottom trawl.

Upeneus moluccensis: **Kenya**: SAIAB 82822, 112 mm, R.V. *Dr. F. Nansen* 80, PCH 80-32, 03°07′ S, 40°11′ E; **Mozambique**: SAIAB 81954, 127–133 mm, R.V. *Dr. F. Nansen*, M07-42, 34°46.57′ S, 25°07.31′ E, depth 99 m, bottom trawl; SAIAB 82509, 103–115 mm, R.V. *Dr. F. Nansen*, M07-130, 40°51.41′ S, 12°93.71′ E, depth 73 m, bottom trawl; **China, South China Sea**: SMF 31671, 103 mm, Hainan, Qinglan, H-90-763T.

Upeneus mouthami: **Papua New Guinea**: BPBM 33855, paratype, 94 mm, Coral Sea, Chesterfield Bank, 20°51′0″ S, 158°45′00″ E, 71 m; BPBM 39467, paratype, 88 mm, Bellona Reefs, 21°24′54″ S, 159°09′18″ E, 60 m. **Eastern Australia**: USNM 378143, paratype, 81 mm, Coral Sea, Chesterfield Bank, 19°12′23″ S, 158°42′02″ E.

Upeneus oligospilus: ***Holotype***: USNM 153988, 111 mm, Persian Gulf, Saudi Arabia, Tarut B. Zaal, Ras Tanura; **Kuwait**: SMF 10285, 53 mm, Shuiba, 60 km S of Kuwait City; NRM 16480, 171 mm, UAE, Ras al Kahaimah, Bin Majid Beach Hotel, 300 m south of hotel; **Saudi Arabia,**

Persian Gulf: USNM 147995, paratypes, 11: 67–152 mm, Tarut B. Zaal, Ras Tanura; USNM 196238, 77–84 mm, south point of Half Moon Bay, 7 fms.

Upeneus parvus: **USA, Gulf of Mexico**: USNM 394942, 110–119 mm, Texas, 27°15′59″ N, 96°27′58″ W, 100 m; USNM 395433, 148 mm, Bahamas, ORE 10859, 23°04′ N, 78°46′ W.

Upeneus pori: **Egypt, Mediterranean**: BMNH 1979.3.20.24, 110 mm, off Alexandria. **Israel, Red Sea**: USNM 303539, 100 mm, paratype, Elat; SAIAB 28958, paratype, 92 mm; SAIAB 65781, 66 mm, Elat, N beach; **Madagascar**: MNHN 1992-977, 97 mm, Vontira.

Upeneus subvittatus: **Indonesia, Pacific**: BPBM 32266, 166–180 mm, Molucca Islands, Ambon, depth 120 m; **Philippines**: BPBM 32724, 3: 105–109 mm, Samar Sea, Carigara Bay, U.P. College Fisheries Trawler Cruise, depth 83–88 m.

Upeneus sulphureus: **Kenya**: SAIAB 82821, 115 mm, off Malindi, R.V. *Dr. F. Nansen*, PCH80-32, 03°07′ S, 40°11′ E; **Mozambique**: SAIAB 82237, 8: 95–108 mm, R.V. *Dr. F. Nansen*, M07-81, 35°52.71′ S, 19°58.83′ E, 22 m, bottom trawl; **United Arabian Emirates, Persian Gulf**: ZMUC P49156, 116 mm, Chahbar; **India:** USNM 395432, 128 mm, Madras State; Porto Novo; Pondicherry.

Upeneus sundaicus: **Iran, Persian Gulf**: ZMUC P49121, 132 mm, Bushire; ZMUC P49122, 110 mm, Bushire; ZMUC P49123, 105 mm; ZMUC P49124, 109 mm, off Kangan; **Thailand, Indian Ocean:** ZMUC P49562, 127 mm; **Thailand, Pacific**: ZMUC P49402, 119 mm, Thai Bay, 07°53′ N, 98°50′ E; ZMUC P49403, 115 mm, Thai Bay, 07˚53′N 98˚50′E; **Philippines**: USNM 106793, 110–123 mm, Iloilo.

Upeneus taeniopterus: ***Holotype***: MNHN 0000-9568, 207 mm, Sri Lanka, Trincomalee, 8°34′0″ S, 81°13′00″ E; **Mozambique**: SAIAB 13915, 101 mm, Pinda Island, 14°13′ S, 40°46′ E; **Seychelles**: USNM 267590, 255–265 mm, Aldabra Islands, Aldabra Atoll, lagoon inside SE portion of West Island (Ile Picard), 9°22′40″ S, 46°14′40″ E, 1 m; SAIAB 76409, 93 mm, Mahé, Baie Ternay, PCH 2005-15, 4.6418328fiS, 55,380165fi E; SAIAB 69803, 134 mm, Rodrigues, Antonio's Finger, 19°39′41″S, 63°28′1″,E, depth 25–50 m; **Chagos (British Indian Ocean Territory)**: USNM 396089, 8: 88–177 mm, Diego Garcia Atoll, 7°25′56″ S, 72°25′43″ E, 1 m; USNM 39690, 211-245 mm, Diego Garcia Atoll, 7°15′33″ S, 72°22′40″ E, 3 m; **Cocos (Keeling) Islands**: BMNH 1949.11.29.220, 153 mm, Pulo Luar; **Kiribati**: USNM 115685, 265 mm, Canton Island Lagoon; **Solomons**: USNM 389116, 178 mm, Fenualoa Island on SW side across from Nuwea Village, 10°15′ S, 166°17′ E, 15 m; **Hawaii:** USNM 50667, holotype of *Upeneus arge*, 156 mm.

Upeneus tragula: **Kenya**: SAIAB 13763, 4: 60-121 mm, Western Indian Ocean, Kenya, off Kipini, 02°38′ S, 40°28′ E, 25-50 m; **Tanzania**: SAIAB 80384, 142 mm, Western Indian Ocean, Tanzania, Nyama reef; **Sri Lanka**: USNM 396086, 3: 48–131 mm, Jaffna area, Kakaithivu, Vaddukkodai, 2–3 m; USNM 396087, 110 mm, Trincomalee, 8 m; ZMUC P4946, 138 mm, Sri Lanka or India; **Myanmar**: USNM 360813, 78 mm, Rakhine, Sandoway, Gwa, Sar Chet Chaung, 17°47′ N, 94°30′ E; **Indonesia, Pacific**: USNM 396085, 147 mm, Teluk Baguala, Off Suli, Ambon, Moluccas, 3°38′ S, 128°17′30″ E, 1,5 m; **Taiwan**: SAIAB 35638, 3: 125–140 mm, Penghu Islands, Makung market; **Vietnam:** USNM 305043, 191 mm, Vung Tau fish market, Cap St. Jacques 10°21′ N, 107°15′ E.

Upeneus vittatus: **Mozambique**: SAIAB 82327, 146 mm, R.V. *Dr. F. Nansen*, M07-108, 38°21.44′ S, 17°42.77′ E, 25 m, bottom trawl; **South Africa, Indian Ocean**: SAIAB 40593, 161 mm, Natal, Sodwana; **Réunion**: MNHN 1965-76, 168 mm, 21°07′0″ S, 55°35′00″ E; MNHN 1965-77, 149 mm, 21°07′0″ S, 55°35′00″ E; **Mauritius**: SAIAB 31413, 144 mm; **Indonesia, Indian Ocean**: BMNH 1986.10.1.39, 156 mm.

Scientific institutions with abbreviations of fish collections: Australian Museum, Sydney (AMS), Bishop Museum, Honolulu (BPBM), British Museum of Natural History, London (BMNH), Hebrew University Jerusalem (HUJ), Institute of Marine Research (HIFIRE), Muséum national d'Histoire naturelle, Paris (MNHN), Museum Victoria, Melbourne (NMV), National Museum of Natural History, Washington (USNM), South African Institute of Aquatic Biodiversity, Grahamstown (SAIAB), Senckenberg Natural History Museum, Frankfurt (SMF), Swedish National Museum, Stockholm (NRM), Zoological Museum, University of Copenhagen (ZMUC).

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APPENDIX

Table 4. Measurements and counts for the seven species of the "*japonicus* group".

	U. guttatus Indian Ocean	n	*U. pori* Red Sea, Mediterranean	Madagascar	all	n	*U. asymmetricus* Pacific	n	*U. australiae* Indo-Pacific	n	*U. francisi* Pacific	*U. japonicus* Pacific	n	*U. parvus* Atlantic	n
SL (mm)	77-146	27	66-110	97	66-110	5	74-100	4	84-130	8	78	104-115	4	110-148	3
BODYDD	22-25	20	21-23	24	21-24	5	22-24	4	24-25	4	24	23-25	4	25-26	3
BODYDA	19-23	20	20-21	22	20-22	5	20-22	4	21-23	4	19	19-22	4	20-21	3
HALFDD	17-21	17	18-19	20	18-20	5	19-20	4	19-21	4	18	19-21	3	20-21	3
HALFDA	15-18	17	14-16	16	14-16	5	14-16	4	16-18	4	15	15-17	4	15-16	3
CPDD	9.3-11	20	9.1-9.7	9.6	9.1-10	5	8.8-9.9	4	10-11	4	9.9	8.7-10	4	8.4-9.4	3
CPDW	3.3-5.1	20	3.5-3.8	3.9	3.5-3.9	5	3.7-4.8	4	3.9-5.0	4	2.3	3.1-5.7	4	2.7-3.7	3
HEAD1	18-22	20	18-20	19	18-20	5	20	4	21-22	4	20	20-21	4	22-23	3
HEAD2	15-19	20	15	16	15-16	5	15-16	4	17-19	4	18	16	4	17-19	3
SUBORB	8.7-12	20	8.9-9.7	9.3	8.9-9.7	5	9.4-10	4	10-13	4	8.4	9.1-10	4	9.8-11	3
INTORB	7.2-9.0	20	7.4-7.9	7.5	7.4-7.9	5	8.0-9.0	4	8.4-9.5	4	7.6	7.2-8.5	4	7.8-8.2	3
HEADL	26-30	20	26-28	28	26-28	5	27-29	4	28-30	4	31	28-29	4	30-31	3
SNOUTL	9.9-13	20	11	11	11	5	9.9-11	4	11-12	4	10	11-12	4	11-12	3
PORBL	8.9-12	20	11-12	11	11-12	5	11-13	4	11-12	4	13	10-12	4	12	3
ORBITL	6.3-8.8	20	6.3-7.8	6.9	6.3-7.8	5	7.0-7.7	4	7.2-7.9	4	8.2	6.8-8.0	4	7.6-7.9	3
ORBITD	5.2-7.6	20	5.7-7.7	6.0	5.7-7.7	5	5.6-6.5	4	5.8-6.6	4	6.7	5.2-7.2	4	6.5-6.9	3
UJAWL	9.6-12	20	10-11	10	10-11	5	9.6-11	4	11	4	12	10-11	4	12-13	3
LJAWL	9.1-12	20	9.7-10	10	9.7-10	5	9.1-10	4	9.2-11	4	11	9.6-9.9	4	12	3
SNOUTW	7.8-11	18	8.0-8.4	10	8.0-10	5	8.1-9.3	4	9.7-9.9	3	7.0	7.7-9.2	4	8.4-11	3
BARBL	16-19	19	16-18	17	16-18	5	18-19	4	18-19	4	18	18-22	4	24-25	3
BARBW	0.7-1.1	20	0.6-0.7	0.7	0.6-0.7	5	0.8-1.0	4	0.8-1.3	4	0.8	0.6-0.8	4	0.6-0.9	3
SD1	34-38	20	34-36	37	34-37	5	37-38	4	34-36	4	38	34-37	4	39-40	3
SD2	61-67	20	63-65	64	63-65	5	64-66	4	62-64	4	66	63-64	4	67-68	3
D1D2	13-17	19	14-16	13	13-16	4	14-16	4	13-16	4	15	15-18	4	17-20	3
CPDL	22-26	20	22-23	23	22-23	5	22-24	4	22-26	4	23	23-25	4	21	3
SANL	60-68	20	60-65	64	60-65	5	63-68	4	61-64	4	66	61-67	4	68-70	3
SPEL	28-34	19	28-32	29	28-32	5	32-34	4	30-34	4	33	30-33	4	33-36	3
SPEC	26-32	19	28-30	30	28-30	5	30-31	4	29-31	4	33	27-33	4	33-34	3
D2ANL	19-23	20	20-21	22	20-22	5	19-22	4	22-24	4	20	19-22	4	20-22	3
D1PELV	22-26	20	22-23	23	22-23	5	22-24	4	23-25	4	24	22-25	4	25-26	3
D1PEC	15-18	20	16-17	16	16-17	5	15-17	4	16-17	4	16	14-18	4	16-17	3
D1B	12-18	20	14-16	16	14-16	4	13-15	4	15-17	4	14	14-17	4	13-15	3
D2B	12-16	20	13-15	14	13-15	5	13-14	4	14-15	4	11	13-15	4	12-13	3
CAUH	25-30	20	27-29	29	27-29	4	27	4	26-29	4	28	25-27	4	28-29	2
ANALB	10-14	20	12-13	12	12-13	5	10-12	4	11-13	4	12	11-12	4	8.7-9.3	3
ANALH	15-19	19	16-17	17	16-17	5	15-16	2	14-17	4	16	15-18	4	13-14	3
PELVL	19-23	20	20-23	23	20-23	5	20-21	4	20-22	4	24	21-22	4	17-21	3
PECTL	20-22	19	20-22	21	20-22	5	19-21	3	21-22	4	25	24	4	22-24	3
PECTW	3.8-5.0	20	4.4-5.7	4.7	4.4-5.7	5	4.1-5.9	4	4.2-5.0	4	4.2	3.7-5.8	4	4.4	3
D1H	20-24	16	20-21	21	20-21	4	20	3	20-21	4	21	21-22	4	21	2
D2H	14-18	19	15-16	16	15-16	4	15-16	2	14-17	4	16	16-18	4	16-17	2
D1	7	27	7	7	7	5	7	4	7	8	7	7	4	7	3
P	13-14	27	14	14	14	5	13	4	14	8	14	13-15	4	15	3
GrUud	2-5	27	0-2	1	0-2	5	1-4	4	2-4	8	1	2-3	4	3-4	3
GrUd	2-5	27	6-7	7	6-7	5	3-6	4	2-4	8	8	4	4	3-4	3
GrLd	11-14	27	14-18	15	14-18	5	15-17	4	11-13	8	23	12-16	4	14-17	3
GrLud	4-5	27	2-5	3	2-5	5	2-5	4	3-5	8	0	4-7	4	3-5	3
GrU	6-8	27	7-8	8	7-8	5	7	4	5-7	8	9	6-7	4	7	3
GrL	16-18	27	18-20	18	18-20	5	19-21	4	16-17	8	23	18-20	4	19-20	3
Gr	23-25	27	26-27	26	26-27	5	26-28	4	21-24	8	32	24-27	4	26-27	3
LLscal	28-31	20	29-30	29	29-30	5	28-29	4	29-31	5	28	28-29	2	36-37	2

Table 5. Measurements and counts for *Upeneus margarethae* sp.nov., a species of the "*tragula* group" (see also Table 6).

				U. margarethae sp. nov.					
	Holotype	Paratypes (n=20)	Red Sea (n=2)	Persian Gulf	Sri Lanka (n=2)	NW Australia (n=3)	N Australia	Indo-Pacific	n
SL (mm)	82	67-110	78-94	105	78-80	108-117	95	67-124	30
BODYDD	26	22-26	25	25	23-25	25-26	25	22-26	29
BODYDA	24	20-23	23	20	20	22	21	20-24	29
HALFDD	20	18-22	21	21	18-21	19-21	21	18-22	29
HALFDA	19	15-18	16	17	16-17	16-17	17	15-19	29
CPDD	11	9.3-11	11	10	10-11	11	11	9.3-11	29
CPDW	4.8	4.0-5.7	4.3-4.3	4.3	3.6-4.1	3.9-5.3	3,7	3.6-5.7	29
HEAD1	21	19-22	21-22	20	20-21	21-23	21	19-23	29
HEAD2	17	15-18	17-18	18	17	18-19	17	15-19	29
SUBORB	10	9.1-12	12	11	9.3-10	11-12	11	9.1-12	29
INTORB	8.2	7.3-9.1	8.4-8.9	7.7	7.6-8.4	8.1-8.8	8,7	7.3-9.1	29
HEADL	30	27-31	28-30	27	28-31	28-29	27	27-31	29
SNOUTL	12	11-12	11	11	11-12	11-12	11	11-12	29
PORBL	12	11-12	12	12	11-12	11-12	11	11-12	29
ORBITL	8.7	7.0-9.1	7.7-8.1	6.5	7.3-7.4	6.7-7.4	6,9	6.5-9.1	29
ORBITD	7.1	5.8-8.0	6.4-6.4	5.0	5.7-6.6	5.9-6.6	5,9	5.2-8.0	29
UJAWL	11	10-12	10-11	10	11	10-11	11	10-12	29
LJAWL	10	9.1-11	9.5-10	9.2	10	8.3-10	8,4	8.3-11	29
SNOUTW	11	9.0-11	-	-	8.5-9	10 **		8.5-11	24
BARBL	17	16-20	16-18	16	18-19	18-19	16	16-20	29
BARBW	0.9	0.7-1.2	0.9-0.9	0.9	0.7-0.9	0.9-1.0	0,9	0.7-1.2	29
SD1	40	35-39	35-37	33	37-38	35-36	37	35-40	29
SD2	67	60-66	62-63	62	62-65	61-63	62	60-67	29
D1D2	15	11-16	12-14	12	13-15	12-13	14	11-16	29
CPDL	23	22-26	22-25	22	24	22-24	25	22-26	29
SANL	66	59-68	67-70	66	64-66	62-67	65	59-70	29
SPEL	29	28-32	34	35	33-34	33-37	33	28-37	29
SPEC	31	28-31	31-33	29	30-33	32	30	28-33	29
D2ANL	24	20-23	23-24	22	21-22	22-23	23	20-24	29
D1PELV	25	22-26	25	24	23-24	25-26	26	22-26	29
D1PEC	18	15-18	16-17	16	16-17	16-17	18	15-18	29
D1B	15	15-18	14-16	15	14-15	15	15	14-18	29
D2B	15	12-16	14	14	13	13-15	13	12-16	29
CAUH	27	27-31	28-31	27	27-30	28	27	27-31	29
ANALB	12	10-14	11-12	11	11	11	11	10-14	29
ANALH	15	14-18	14-16	15	15-16	14-17	14	14-18	29
PELVL	23	20-24	23	20	21-22	20-22	20	20-24	29
PECTL	23	21-25	21-23	21	21-22	21-22	21	21-25	29
PECTW	4.8	4.4-5.8	4.8-5.6	4.5	4.9-5.2	5.1-5.2	4,4	4.4-5.8	29
D1H	21	20-23	20-22	20	20-22	20-21	20	20-23	29
D2H	18	16-20	17-18	16	16	16-19	16	16-20	29
D1	8	8	8	8	8	8	8	8	30
P	14	13-14	14	14	14	14	14	13-14	30
GrUud	3	2-4	2	3	3	2-3	3	2-4	30
GrUd	3	2-3	2-3	3	3	2-3	3	2-3	30
GrLd	12	11-13	13	12	11-13	12	12	11-13	30
GrLud	5	4-6	4	4	5	5-6	5	4-6	30
GrU	6	5-6	4-5	6	6	5-6	6	4-7	30
GrL	17	16-18	17	16	16-18	17-18	17	16-18	30
Gr	23	21-24	21-22	22	22-24	22-23	23	21-24	30
LLscal	28	28-30 *	29-30	29	30	29-30	29	28-30	27

*n=17; **n=1

Table 6. Measurements and counts for six species of the "*tragula* group".

	U. oligospilus				*U. sundaicus*		*U. taeniopterus*				*U. tragula*			*U. luzonius*		*U. mouthami*	
	HT	Persian Gulf	n	juveniles (n=2)	Indo-Pacific	n	HT	HT *U. arge*	Indo-Pacific	n	Indo-Pacific	n	juveniles (n=5)	Pacific	n	Pacific	n
SL (mm)	114	72-171	14	53-67	105-132	9	207	153	88-265	20	78-191	11	48-65	49-91	5	81-94	3
BODYDD	25	23-26	14	23-24	25-28	9	22	23	22-25	15	22-26	11	24-26	22-26	5	21-24	3
BODYDA	20	19-22	14	20-22	22-24	9	23	21	20-23	16	20-23	8	21-22	19-23	5	19-21	3
HALFDD	20	19-22	14	18-20	20-22	9	-	21	18-21	9	19-22	9	20-22	20-21	4	19-20	2
HALFDA	15	14-17	14	15	15-18	9	-	16	15-17	9	15-17	11	16-18	13-15	5	15	2
CPDD	10	9.8-11	14	10-11	11-13	9	10	10	9.7-11	11	9.9-11	11	10-12	11-13	5	9.1-10	3
CPDW	2.9	2.2-4.1	14	3.6-5.1	3.0-4.9	9	3.6	-	3.4-4.3	9	2.9-4.6	11	3.3-4.7	3.3-4.3	5	3.5-3.9	3
HEAD1	21	20-23	14	19-21	21-23	9	17	20	17-21	10	19-23	10	21-23	20-23	5	20-21	3
HEAD2	16	15-19	14	17	17-20	9	14	17	14-17	10	15-17	10	16-19	16-18	5	17-18	3
SUBORB	11	9.6-12	14	9.9	11-14	9	10	11	9.6-12	10	8.7-11	11	9.1-11	10-12	5	10-11	3
INTORB	8.6	7.9-9.9	14	8.7-9.1	7.9-9.2	9	7.9	9.0	7.5-9.2	10	7.5-9.0	11	7.9-9.2	7.3-8.7	5	7.6-7.9	3
HEADL	32	29-32	14	33	27-30	9	25	27	25-29	14	27-31	11	27-34	27-30	5	29-30	3
SNOUTL	13	12-14	14	12-13	12-14	9	10	11	10-12	10	11-13	11	11-13	11-12	5	11-12	3
PORBL	13	12-13	14	13	11-13	9	10	12	9.9-13	10	10-12	11	11-14	10-13	5	11-12	3
ORBITL	6.3	5.4-7.9	14	7.5-9.8	6.1-7.2	9	5.6	5.9	4.4-6.3	18	6.1-8.3	11	7.7-9.1	6.0-7.1	5	7.8-8.3	3
ORBITD	5.5	4.8-6.3	14	6.8-8.3	4.8-5.9	9	4.3	5.6	3.7-5.6	18	5.0-6.7	11	6.8-7.8	5.4-6.1	5	6.6-7.0	3
UJAWL	13	11-13	14	13-14	11-12	9	11	12	11-13	18	11-14	11	11-14	11-12	5	9.3-11	3
LJAWL	12	10-13	14	12	10-12	9	10	12	9.9-12	10	11-13	10	10-12	9.1-11	5	8.8-11	3
SNOUTW	10	9.8-12	13	12	11-12	8	-	11	9.3-11	8	8.4-12	11	8.2-11	9.3-9.8	4	11-12	2
BARBL	20	16-20	14	18-19	18-21	9	18	18	17-21	18	15-19	11	16-21	17-20	5	20-21	3
BARBW	0.8	0.6-1.0	14	0.8-0.9	1.0-1.7	9	0.8	0.9	0.6-1.0	10	0.7-0.9	11	0.6-0.8	0.6-0.9	5	0.9-1.4	3
SD1	38	37-40	14	40-41	36-38	9	35	37	35-38	10	35-39	11	35-40	35-37	5	37-39	3
SD2	65	62-66	14	65-68	63-64	9	65	61	61-66	10	62-66	11	63-70	60-64	5	62-65	3
D1D2	14	12-15	14	12-16	12-15	9	18	15	15-19	9	12-15	11	13-16	12-15	5	13-16	3
CPDL	20	20-25	14	20-22	22-26	9	24	22	22-24	10	21-24	11	21-25	23-25	5	21-23	3
SANL	66	61-68	14	65-67	62-67	9	70	64	64-70	10	62-67	11	64-66	61-63	5	64-65	3
SPEL	33	30-37	14	34-34	30-34	9	31	29	29-33	10	31-34	11	32-37	31-34	5	29-33	3
SPEC	34	30-35	14	33-36	28-31	9	28	27	27-30	10	29-31	11	31-37	29-32	5	29-32	3
D2ANL	21	20-23	14	20-22	23-25	9	21	21	21-23	10	20-23	11	20-23	19-24	5	19-21	3
D1PELV	24	23-26	14	24	25-29	9	20	24	20-26	10	23-26	11	23-26	24-26	5	21-24	3
D1PEC	17	16-19	14	17-19	17-20	9	14	17	14-18	10	15-18	11	17-18	16-18	5	17	3
D1B	15	14-17	14	15	15-17	9	13	15	12-15	10	14-16	11	14-16	14-16	5	11-13	3
D2B	15	13-16	14	13-14	13-17	9	12	13	12-14	10	13-15	11	13-15	13-15	5	13-14	3
CAUH	24	24-28	14	26-29	26-29	9	28	-	28-32	8	28-32	11	28-31	26-29	4	27-29	3
ANALB	12	10-12	14	13	11-14	9	9.3	11	9.3-13	10	10-13	11	12-14	9.7-13	5	11-13	3
ANALH	17	15-18	14	16-20	16-18	9	15	16	15-17	10	16-19	11	17-21	15-17	5	17-18	3
PELVL	19	17-21	14	22-23	20-23	9	18	18	18-20	10	20-24	11	21-24	21-22	5	22-23	3
PECTL	20	18-22	14	22-23	21-23	9	-	17	17-20	16	19-21	11	21-23	19-23	5	22-23	3
PECTW	4.8	3.9-5.4	14	4.2-5.6	3.9-5.7	9	3.9	4.0	3.8-4.7	10	3.9-4.8	11	3.8-5.2	3.9-4.6	5	4.0-4.2	3
D1H	19	18-22	14	21-23	25-29	8	-	21	20-23	16	21-24	11	21-24	21-24	5	20-21	3
D2H	17	16-18	14	18-20	16-18	9	-	16	14-16	16	17-20	11	18-22	16-19	5	17-19	3
D1	8	8	14	8	8	9	8	8	8	17	8	11	8	8	5	8	3
P	14	13-14	14	13	13-14	9	14	14	13-14	17	13-14	11	13-14	14-15	5	13	3
GrUud	3	2-5	14	2-5	2-3	9	4	3	2-4	17	2-5	11	2-4	0-2	5	2-3	3
GrUd	3	2-3	14	2-4	2	9	2	3	2-3	17	2-3	11	2-4	3-4	5	3-5	3
GrLd	12	9-12	14	11-12	10-12	9	12	12	10-13	17	10-12	11	10-12	11-12	5	13	3
GrLud	6	4-7	14	4-5	3-5	9	5	5	3-6	17	4-7	11	4-5	3	5	4-5	3
GrU	6	4-7	14	6-7	4-5	9	6	6	5-6	17	5-8	11	6-7	4-5	5	6-7	3
GrL	18	16-18	14	16	14-15	9	17	17	16-17	17	14-17	11	15-17	14-15	5	17-18	3
Gr	24	20-24	14	22-23	18-20	9	23	23	21-23	17	19-24	8	22-23	18-20	5	23-25	3
LLscal	29	28-31	14	29-31	31-34	8	-	36	35-39	14	28-30	11	28-30	31-32	4	29	1

Table 7. Measurements and counts for three species of the "*moluccensis* group".

	U. doriae				*U. moluccensis*		*U. sulphureus*				
	Persian Gulf (n=3)	Gulf of Oman (n=3)	All adults	Juveniles (n=2 **)	Indo-Pacific	n	Western Indian O.	n	Persian Gulf	Eastern Indian O.	Indian Ocean
SL (mm)	71-97	116-145	71-145	46-58	103-133	6	95-115	9	116	128	95-128
BODYDD	27-29	27-29	27-29	25	24-26	6	29-33	9	29	30	29-33
BODYDA	24	24	24	21	21-23	6	25-27	9	25	25	25-27
HALFDD	21-24	20-23	20-24	20	20-22	5	22-25	9	23	23	22-25
HALFDA	17-19	18	17-19	16	17-19	6	18-20	9	20	19	18-20
CPDD	10-11	11-12	10-12	9,9	9.0-10	6	11-12	9	11	11	11-12
CPDW	3.7-4.5	3.5-4.2	3.5-4.5	3,9	3.7-4.9	6	4.6-6.0	9	4.0	4.3	4.0-6.0
HEAD1	23-24	23-24	23-24	21	20-22	6	24-25	9	23	25	23-25
HEAD2	18-22	18-19	18-22	18	16-17	6	18-20	9	20	20	18-20
SUBORB	10-13	10-12	9.5-13	9,4	9.1-11	6	9.9-11	9	-	11	9.9-11
INTORB	8.0-8.3	7.9-8.4	7.9-8.4	8,5	7.5-8.3	6	7.6-8.4	9	9.1	9.0	7.6-9.1
HEADL	30-31	29-30	29-31	28	27-29	6	29-30	9	29	30	29-30
SNOUTL	10-11	9.8-11	9.8-11	9,7	10-11	6	10-12	9	11	11	10-12
PORBL	11-12	12-13	11-13	11	11-12	6	12-13	9	12	13	12-13
ORBITL	8.9-9.7	6.6-7.2	6.6-9.7	9,3	7.3-8.9	6	7.7-8.7	9	7.4	7.6	7.4-8.7
ORBITD	7.8-8.2	6.0-6.3	6.0-8.2	8,3	6.5-7.9	6	6.9-7.8	9	6.4	6.6	6.4-7.8
UJAWL	11	11	11	11	11-12	6	12-13	9	11	13	11-13
LJAWL	10-11	11	10-11	11	11	6	10-12	9	11	12	10-12
SNOUTW	10-12 *	8.3-9.1	8.3-12	9,0	7.6-11	6	9.7-12	9	-	11	9.7-12
BARBL	16-20	16-17	16-20	20	15-17	6	17-21	8	17	21	17-21
BARBW	0.9	0.7-0.8	0.7-0.9	0,8	0.8-1.2	6	0.5-0.8	9	-	0.8	0.5-0.8
SD1	39-41	39-40	39-41	36	37-40	6	37-41	9	38	42	37-42
SD2	65-67	65-67	65-67	68	65-67	6	66-68	9	67	69	66-69
D1D2	15-16	14-16	14-16	16	16-17	6	15-18	9	14	18	14-18
CPDL	19-23	21-23	19-23	21	19-22	6	18-21	9	21	19	18-21
SANL	68-68	68-71	68-71	68	66-70	6	66-69	9	69	69	66-69
SPEL	33-37	33-35	33-37	32	31-33	6	30-34	9	36	35	30-36
SPEC	32-35	30-32	30-35	29	29-31	6	30-32	9	34	32	30-34
D2ANL	25-26	25-26	25-26	21	21-24	6	25-26	9	25	26	25-26
D1PELV	28-30	27-29	27-30	26	23-27	6	29-31	9	30	30	29-31
D1PEC	18-19	17-19	17-19	18	16-17	6	20-21	9	18	21	18-21
D1B	13-15	14-16	13-16	14	12-15	6	15-18	9	17	17	15-18
D2B	16	14	14-16	11	13-15	6	14-16	9	13	14	13-16
CAUH	26 *	28	26-28	24	27-30	6	27-30	9	27	29	27-30
ANALB	11-12	9.7-11	10-12	13	10-11	6	11-13	9	12	11	11-13
ANALH	14-15	14-15	14-15	17	13-15	6	16-18	9	16	16	16-18
PELVL	18-20	18-19	18-20	19	17-22	6	20-22	9	20	20	20-22
PECTL	25-28	25-26	25-28	24	25-27	6	24-26	9	26	26	24-26
PECTW	5.2-5.9	4.5-5.0	4.5-5.9	6,2	4.0-5.9	6	4.3-5.9	9	4.4	4.9	4.3-5.9
D1H	20-22	20-22	20-22	19	20-23	6	23-26	9	25	26	23-26
D2H	14	14-15	14-15	16	14-16	6	17-18	9	17	18	17-18
D1	8	8	8	8	8	6	8	9	8	8	8
P	16-17	15-16	15-17	16	14-16	6	15-16	9	16	17	15-17
GrUud	0	0-1	0-1	0-1	0-4	6	0-3	9	2	3	0-3
GrUd	8-9	6-9	6-9	6-8	3-7	6	5-8	9	5	4	4-8
GrLd	19-23	21-23	19-23	18-22	14-20	6	16-20	9	18	16	16-20
GrLud	0-3	0-1	0-3	0-4	0-5	6	0-4	9	2	4	0-4
GrU	8-9	7-9	7-9	7-8	7-8	6	7-8	9	7	7	7-8
GrL	22-23	22-23	22-23	22	18-20	6	19-21	9	20	20	19-21
Gr	30-32	29-32	29-32	29-30	26-27	6	27-28	9	27	27	27-28
LLscal	33-34	35	33-35	35	33-35	6	34-37	9	35	34	34-37

* n=2; ** n=1 for all morphometric ratios

Table 8. Measurements and counts for the seven species of the "*vittatus* group".

	U. davidaroni		*U. indicus*		*U. mascareinsis*				*U. suahelicus* sp.nov.				*U. supravittatus* sp.nov.		*U. vittatus*				*U. subvittatus*
	Red Sea	n	HT	PT	HT	Indian O.	n	juv.	HT	12 PT's	Red Sea	all (n=16)	HT	HT and 21 PT's	Neotype	Indian O. proper	all	n	Pacific (n=5)
SL (mm)	105-160	3	137	132	152	84-162	15	69	101	88-135	124	79-135	96	85-144	163	144-168	144-168	7	105-180
BODYDD	24	2	31	29	26	22-26	14	19	28	26-30	28	26-30	28	26-30	26	25-29	25-29	7	26-28
BODYDA	20-21	2	27	26	20	18-22	14	18	25	22-26	25	22-26	23	22-25	22	21-24	21-24	7	21-23 **
HALFDD	20	2	25	24	21	18-22	12	-	23	21-23	22	21-23	23	21-25	21	19-24	19-24	7	21-23 **
HALFDA	15-16	2	20	19	15	14-17	12	-	18	17-20	19	17-20	17	17-18	16	16-18	16-18	7	16-19
CPDD	9.2-9.4	2	11	11	8.9	8.3-9.3	14	8.0	11	9.9-11	11	9.9-11	11	9.9-11	11	9.9-12	9.9-12	7	9.2-9.8
CPDW	3.4-4.2	2	3.8	4.2	3.1	3.1-4.3	13	3.3	4.0	3.7-4.9	3.9	3.7-4.9	4.3	3.4-4.6	3.9	3.8-4.8	3.8-4.8	7	3.5-4.4
HEAD1	24	2	25	25	22	20-24	14	17	24	22-25	24	22-25	24	23-26	24	21-26	21-26	7	22-25
HEAD2	21-22	2	19	18	-	17-19	13	14	17	17-19	18	17-19	18	17-20	19	18-20	18-20	7	18-20
SUBORB	14	2	12	11	-	8.7-11	13	6.8	11	9.3-11.6	10	9.3-12	11	10-12	12	11-12	11-12	7	10-11
INTORB	8.2-8.5	2	8.8	8.4	7.1	7.1-8.9	14	7.6	9.3	7.6-9.2	8.1	7.6-9.3	8.0	7.9-9.6	8.0	7.9-9.0	7.9-9.0	7	7.9-8.9
HEADL	32-33	2	31	30	32	30-34	14	29	31	28-31	28	28-31	31	30-33	31	30-31	30-31	7	32-33
SNOUTL	12	2	12	11	11	10-12	14	8.5	10	9.1-11	10	9.1-11	11	10-12	11	11-13	11-13	7	12-13
PORBL	14	2	13	13	12	12-13	14	14	12	10-14	12	10-14	12	12-14	12	12-14	12-14	7	13-14
ORBITL	9.1-9.8	2	7.1	7.0	9.2	7.7-11	15	6.6	9.4	7.6-8.9	7.1	7.1-9.4	8.4	6.8-8.5	7.3	7.0-8.7	7.0-8.7	7	7.8-9.1
ORBITD	7.9-8.5	2	6.2	6.0	7.2	6.6-9.0	15	5.7	8.0	6.7-8.1	6.4	6.4-8.1	7.0	6.1-7.5	6.7	6.4-7.7	6.4-7.7	7	6.4-7.1
UJAWL	14-15	2	12	12	14	12-14	14	10	12	12-14	12	12-14	12	12-14	12	11-13	11-13	7	14
LJAWL	12-13	2	12	12	13	11-14	14	9.3	11	10-12	11	10-12	11	11-13	11	11-12	11-12	7	13-14
SNOUTW	11	1	10	10	-	8.6-11	12	6.6	9.8	8.2-11	9.7	8.2-11	9.3	8.1-12	9.6	8.6-12	8.6-12	6	8.8-11
BARBL	20-21	2	20	19	22	18-24	13	12	15	16-20	15	15-20	21	19-23	18	17-21	17-21	7	20-22
BARBW	0.6-0.7	2	0.8	0.8	0.6	0.5-0.9	14	0.5	0.9	0.8-1.2	0.7	0.7-1.2	0.8	0.6-1.0	0.8	0.6-1.0	0.6-1.0	7	0.7-1.0
SD1	42	2	43	40	38	38-43	14	34	41	38-41	39	38-41	41	39-43	41	39-42	39-42	7	40-43
SD2	68	2	69	69	66	65-71	14	64	68	65-69	66	64-69	69	66-72	70	66-70	66-70	7	66-70
D1D2	13-14	2	16	16	13	13-18	12	17	16	13-17	13	12-17	17	14-18	18	15-20	15-20	7	14-18
CPDL	18-19	2	17	19	21	18-23	14	22	20	18-22	20	18-22	21	17-22	20	18-24	18-24	7	19-21
SANL	67-69	2	69	68	67	66-72	14	65	67	64-71	66	64-71	69	64-74	70	65-70	65-70	7	66-71
SPEL	33-36	2	34	34	34	33-37	14	30	31	32-34	32	31-34	36	33-37	35	33-34	33-35	7	33-35
SPEC	34-35	2	33	31	31	31-35	14	29	31	30-33	30	30-33	34	32-35	33	31-32	31-33	7	32-34
D2ANL	20-21	2	28	26	20	18-22	14	17	25	23-26	25	22-26	24	23-25	22	21-25	21-25	7	22-23
D1PELV	25-26	2	31	29	26	21-26	14	20	27	25-29	27	25-29	27	26-30	25	25-28	25-28	7	25-28
D1PEC	17	2	20	19	17	14-18	14	15	19	17-20	19	16-20	18	17-21	18	16-19	16-19	7	16-18
D1B	13-14	2	14	16	15	14-17	14	12	15	14-16	15	14-16	14	13-17	14	14-17	14-17	7	13-15
D2B	12-13	2	12	14	11	10-14	14	12	15	12-15	13	12-15	12	12-15	13	12-14	12-14	7	12-13
CAUH	28-29	2	28	27	-	25-29	12	26	28	26-30	27	26-30	30	27-31	29	26-30	26-30	7	26-29
ANALB	12	2	12	12	9.4	9.4-13	13	11	13	10-13	11	10-13	10	10-12	10	9.3-11	9.3-11	7	10-11
ANALH	16-17	2	13	14	14	13-16	14	13	16	15-17	16	15-17	16	14-17	16	15	15-16	7	15-18 **
PELVL	20	2	19	19	18	18-20	15	15	21	18-21	19	18-21	20	18-21	18	18-21	18-21	7	18-19
PECTL	23-24	2	24	23	22	21-24	15	18	26	25-26	25	25-26	27	25-28	23	22-24	22-24	7	24-26
PECTW	4.3-5.3	2	4.8	4.5	4.2	3.1-5.0	15	3.7	5.9	4.2-6.0	4.6	4.2-6.0	5.6	4.4-5.7	4.3	3.9-5.2	3.9-5.2	7	4.1-5.0
D1H	20-21	2	23	24	20	19-23	11	-	24	23-26	22	22-26	25	23-26	24	22-25	22-25	7	20-23
D2H	16-17	2	15	16	15	15-16	15	-	17	16-18	16	16-18	16	15-17	15	14-16	14-16	7	14-17
D1	8	3	8	8	8	8	15	8	8	8	8	8	8	8	8	8	8	7	8
P	15-16	3	16	15	16	15-16	15	15	16	15-16	15	15-16	16	16-17	16	15-16	15-16	7	16-17
GrUud	1-3	3	1	3	1	0-3	15	0	0	0-2	2	0-2	2	0-5	4	1-4	1-4	7	1-4
GrUd	4-6	3	8	6	6	4-7	15	8	7	5-7	5	5-7	6	3-8	4	4-7	4-7	7	4-7
GrLd	14-15	3	17	16	17	14-18	15	21	16	15-19	16	15-19	16	16-21	13	13-17	13-17	7	14-16
GrLud	4-6	3	5	4	3	2-5	15	0	4	1-5	4	1-5	6	2-5	6	4-6	4-6	7	4-6
GrU	7	3	9	9	7	7-8	15	8	7	6-8	7	6-8	8	7-9	8	7-8	7-8	7	7-9
GrL	19-20	3	22	20	20	19-22	15	21	20	19-21	20	19-21	22	21-23	19	19-21	19-21	7	19-20
Gr	26-27	3	31	29	27	26-29	15	29	27	26-28	27	26-28	30	28-32	27	27-29	27-29	7	26-28
LLscal	33-36	3	36	36	36	35-38	12	-	35	34-35	35	34-35 *	34	34-36	36	36-38	36-38	7	34-35

* n=15; ** n=4

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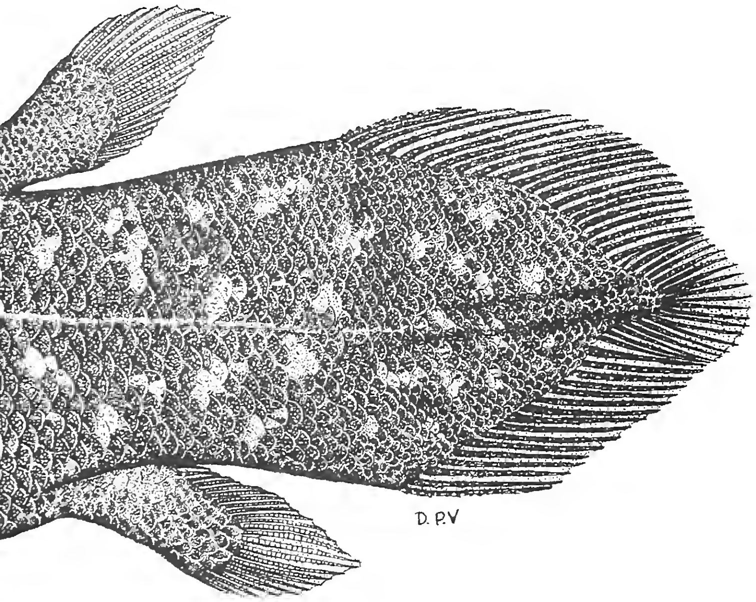

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