

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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Received 17 June 2009; accepted 30 September 2009

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. mascarensis*, *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. mascarensis* 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* (Forsskal 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
HEAD1	head length - distance between snout tip to posteriormost margin of operculum
SNOUTL	snout length - distance between snout tip to anterior margin of orbit
FORBL	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
DD2	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
CAUL	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	
DT	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 (Forsskal 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* (Forsskal 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. mascarensis*, *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
<i>Upeneus asymmetricus</i> Lachner, 1954	W Pacific	<i>japonicus</i> group
<i>Upeneus australiae</i> Kim and Nakaya, 2002	E Indian Ocean, W Pacific	<i>japonicus</i> group
<i>Upeneus davidaromi</i> Golani, 2001	Red Sea	<i>vittatus</i> group
<i>Upeneus doriae</i> (Günther, 1869)	Persian Gulf, Gulf of Oman	<i>moluccensis</i> group
<i>Upeneus filifer</i> (Ogilby, 1910)	W Central and SW Pacific	-
<i>Upeneus francisi</i> Randall and Guézé, 1992	SW Pacific	<i>japonicus</i> group
<i>Upeneus guttatus</i> (Day, 1868)	Indian Ocean, W Pacific	<i>japonicus</i> group
<i>Upeneus indicus</i> sp. nov.	W Indian Ocean (SW India)	<i>vittatus</i> group
<i>Upeneus japonicus</i> (Houttuyn, 1782)	W Pacific	<i>japonicus</i> group
<i>Upeneus luzonius</i> Jordan and Seale, 1907	W Pacific	<i>tragula</i> group
<i>Upeneus margarethae</i> sp. nov.	Indian Ocean, SW Pacific (Arafura Sea)	<i>tragula</i> group
<i>Upeneus mascarensis</i> Fourmanoir and Guézé, 1967	Indian Ocean	<i>vittatus</i> group
<i>Upeneus moluccensis</i> (Bleeker, 1855)	Indian Ocean, W Pacific, E Mediterranean	<i>moluccensis</i> group
<i>Upeneus mouthami</i> Randall and Kulbicki, 2006	W Central Pacific	<i>tragula</i> group
<i>Upeneus oligospilus</i> Lachner, 1954	Persian Gulf	<i>tragula</i> group
<i>Upeneus parvus</i> Poey, 1852	W Atlantic	<i>japonicus</i> group
<i>Upeneus pori</i> Ben-Tuvia and Golani, 1989	W Indian Ocean, E Mediterranean	<i>japonicus</i> group
<i>Upeneus quadrilineatus</i> Cheng and Wang, 1963	E Indian Ocean, West Pacific	<i>moluccensis</i> group
<i>Upeneus subvittatus</i> (Temminck and Schlegel, 1843)	W Pacific	<i>vittatus</i> group
<i>Upeneus suahelicus</i> sp. nov.	W Indian Ocean, Red Sea	<i>vittatus</i> group
<i>Upeneus sulphureus</i> Cuvier, 1829	Indian Ocean, W Pacific	<i>moluccensis</i> group
<i>Upeneus sundaicus</i> (Bleeker, 1855)	Indian Ocean, W Pacific	<i>tragula</i> group
<i>Upeneus supravittatus</i> sp. nov.	Indian Ocean (S India, Sri Lanka)	<i>vittatus</i> group
<i>Upeneus taeniopterus</i> Cuvier in Cuvier and Valenciennes, 1829	Indian Ocean, Central Pacific	<i>tragula</i> group
<i>Upeneus tragula</i> Richardson, 1846	Indian Ocean, W Pacific	<i>tragula</i> group
<i>Upeneus vittatus</i> (Forsskal, 1775)	Indian Ocean, W and Central Pacific	<i>vittatus</i> 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. mascarensis*
- 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 vittatus [sic] (non Forsskal): 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	No. 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)
<i>davidaromi</i>	8	15-16	7	19-20	26-27	33-36	5-6	3-4	8-10	yes	0	no	+	yes [yes]
<i>doriae</i>	8	15-17	7-9	22-23	29-32	33-35	0	0	0	-	1	yellow	faintly/no	yes [faintly/no]
<i>guttatus</i>	7	13-14	6-8	16-18	23-25	28-31	5 *	5-8 *	10-13 *	no	0	no	+	no
<i>indicus</i> sp. nov.	8	15-16	9	20-22	29-31	36	4-6	4	8-10	faintly	3	pale brown	no	yes [yes]
<i>margaretthae</i> sp. nov.	8	13-14	4-7	16-18	21-24	28-30	4 *	5-6 *	9-10 *	no	1	yellow	no	no
<i>mascarensis</i>	8	15-16	7-8	19-22	26-29	35-38	3-6	3-4	7-10	yes	0	no	+	yes [yes]
<i>moluccensis</i>	8	14-16	7-8	18-20	26-27	33-35	6-8	0	6-8	faintly	1	yellow	no	no
<i>oligospilus</i>	8	13-14	4-7	16-18	20-24	24-31	3-5 ***	3-4 ***	6-9 ***	yes	1	brown to black	yes	yes [yes]
<i>pori</i>	7	14	7-8	19-20	26-27	29-30	4-6	5-9	11-15	yes	0	no	+	no
<i>subelatus</i> 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]
<i>sulphureus</i>	8	15-17	7-8	19-21	27-28	34-37	0	0	0	-	2	yellow	faintly/no	yes [yes]
<i>sumatrensis</i>	8	13-14	4-5	14-15	18-20	31-34	5-6 *	0	5-6 *	no	1	pale brown	no	no
<i>supravittatus</i> 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]
<i>taeniopernis</i>	8	13-14	5-6	16-17	21-23	35-39	4-8	3-6	7-13	yes	2	pale brown	no	no
<i>trigula</i>	8	13-14	3-8	14-17	19-24	28-30	5-6 ***	5-6 ***	10-12 ***	yes	1	brown to black	yes	yes [yes]
<i>vittatus</i>	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
<i>davidaromi</i>	24	20-21	9.2-9.4	24	21-22	32-33	9.1-9.8	14-15	20-21	26-29	16-17	20	23-24	20-21	16-17
<i>doriae</i>	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
<i>guttatus</i>	23-25	19-25	9.3-11	18-22	15-19	26-30	6.3-8.8	9.6-32	16-19	23-30	13-19	19-23	20-22	20-24	14-18
<i>indicus</i> 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
<i>margaretthae</i> 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
<i>mascarensis</i>	22-26	18-22	8.3-9.3	20-24	17-19	30-34	7.7-11	13-14	18-24	25-29	13-16	18-20	21-24	19-21	15-16
<i>moluccensis</i>	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
<i>oligospilus</i>	23-26	19-22	9.8-11	20-23	15-19	29-32	3.4-7.9	11-13	16-20	24-28	13-18	17-21	18-22	18-22	16-18
<i>pori</i>	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
<i>subelatus</i> sp. nov.	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
<i>sulphureus</i>	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
<i>sumatrensis</i>	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
<i>supravittatus</i> 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
<i>taeniopernis</i>	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
<i>trigula</i>	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
<i>vittatus</i>	23-29	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
<i>davidaromi</i>	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
<i>doriae</i>	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
<i>guttatus</i>	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
<i>indicus</i> sp. nov.	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
<i>margaretthae</i> 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
<i>mascarensis</i>	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	5.0-5.4	4.1-4.7	4.4-5.2	6.2-6.9
<i>moluccensis</i>	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
<i>oligospilus</i>	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
<i>pori</i>	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
<i>subelatus</i> 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
<i>sulphureus</i>	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
<i>sumatrensis</i>	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
<i>supravittatus</i> 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
<i>taeniopernis</i>	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
<i>trigula</i>	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
<i>vittatus</i>	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. mascarensis* 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. mascarensis* 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 Forsskal): 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 dorsally 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. mascarensis*, *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)

Upeneoides 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 hyaline 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. mascarensis* 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. 1/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

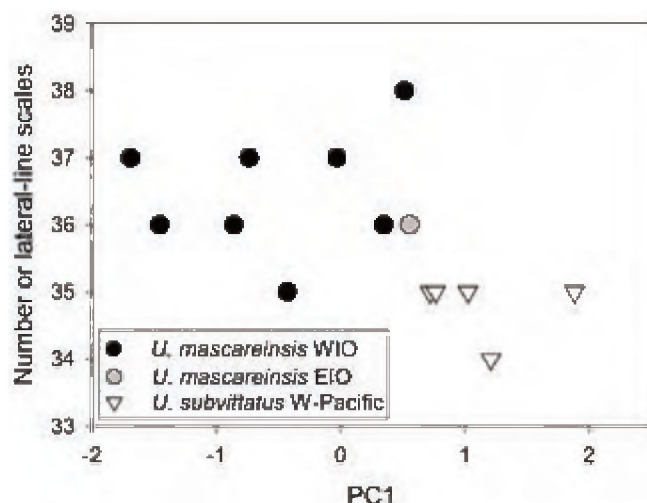


Fig. 1. First principal component (PC1) based on 37 morphometric characters against number of lateral-line scales for 9 *Upeneus mascareinsis* (Indian Ocean) and 5 *U. subvittatus* (West-Pacific) (WIO = Western Indian Ocean, EIO = Eastern Indian Ocean)

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; Kuroshima & 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.

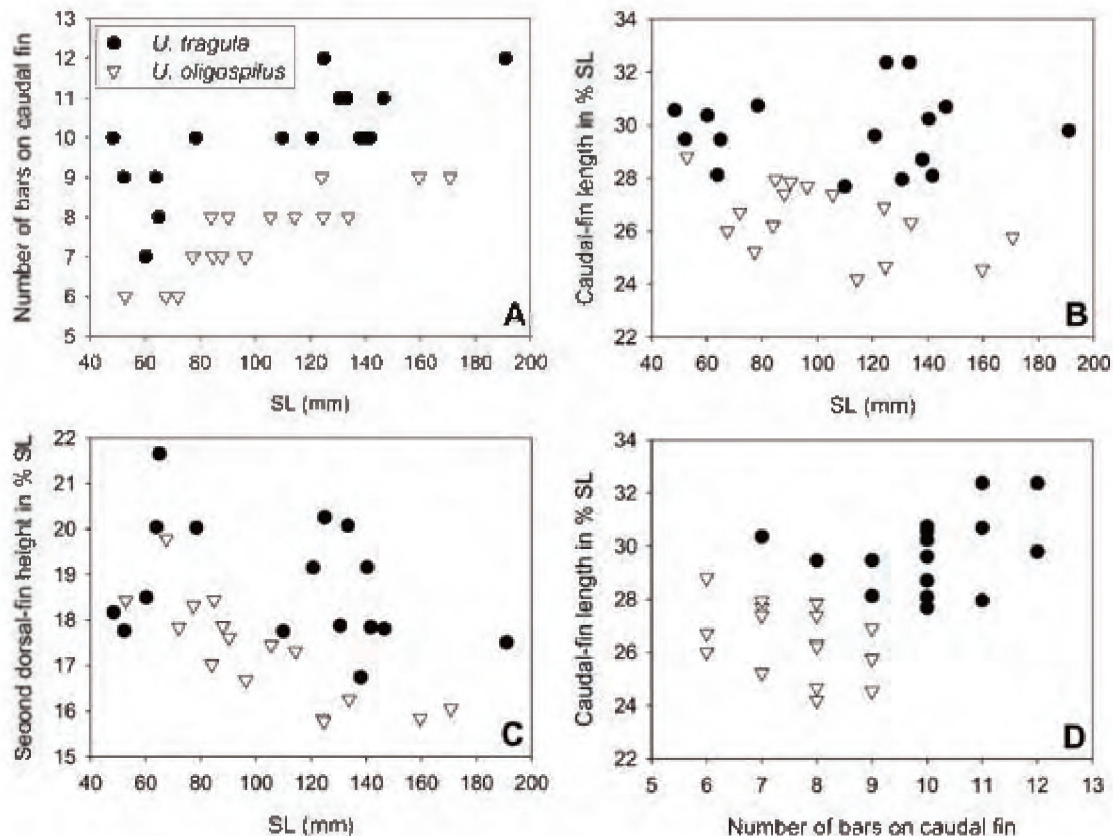


Fig. 3. Number of bars on caudal fin (A), caudal-fin length ratio (B), and second dorsal-fin height ratio (C) against SL in 16 *Upeneus oligospilus* and 16 *U. fragula*; the combination of caudal-fin length ratio and caudal-fin bar number (D) allows size-independent distinction between the two species.

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 head 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. mascarensis* 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

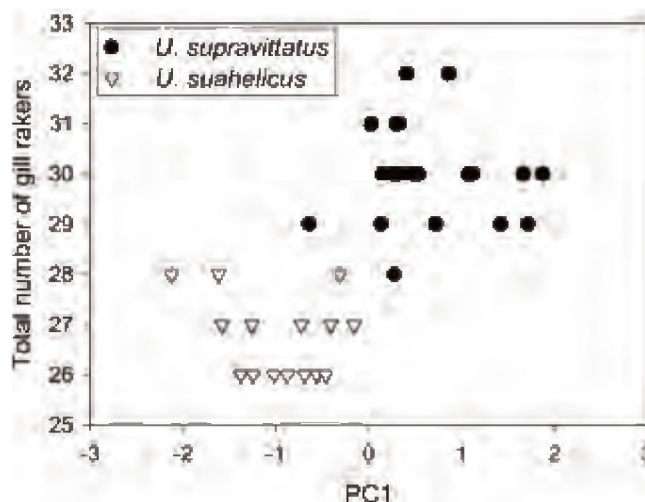


Fig. 4. First principal component based on 40 morphometric characters against total number of gill rakers for *Upeneus suahelicus* and *U. supravittatus*.

southern Red Sea (HJ 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

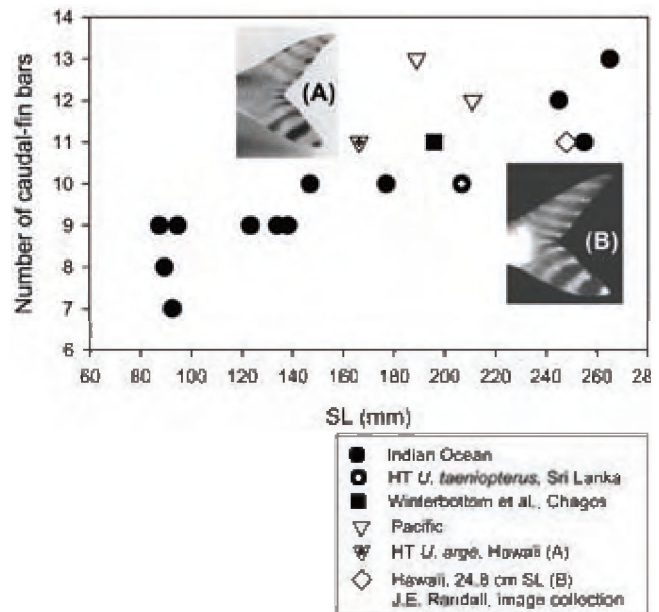


Fig. 5. Number of bars on caudal fin against SL in *Upeneus taeniopterus* from the Indian Ocean (filled symbols) and Pacific (hollow symbols); (A) caudal fin of holotype (HT) of *U. arge* based on an illustration accessible online from the USNM fish collection; (B) caudal fin from a photograph of a fresh 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.

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.

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 line 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 Forsskål 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. mascarensis* (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. mascarensis*, 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. mascarensis*, 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 ontogenetic changes in body colouration and shape were also found in *Upeneus doriae* of the “*moluccensis* group” and *U. mascarensis* of the “*vittatus* group”. In the latter case the differences were so marked that the species identity of the juvenile remained uncertain (= cf. *mascarensis*). 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.

ACKNOWLEDGMENTS

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 Zetsche (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 Zetsche, 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.

Thanks to scientific party and crew of the R.V. *Dr. Fridtjof Nansen* during the cruise in October/November 2007 off South Africa and Mozambique for assistance. The first author thanks the South African Institute for Aquatic Biodiversity, the SYNTHESYS Project DK-TAF 3990 (<http://www.synthesys.info/>) financed by European Community Research Infrastructure Action under the FP6 "Structuring the European Research Area" Programme and the Nansen Programme of the Center for Developmental Fisheries at the Institute of Marine Research (IMR), Bergen, for travel support.

PLATE 1



A. *U. davidaromi*, SL 165 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)



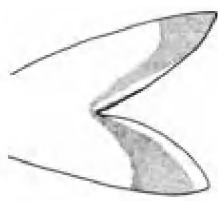
J. *U. vittatus*, SL 155 mm, Mauritius (J.E. Randall)

PLATE 3

Drawings of caudal-fin patterns in preserved fish



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



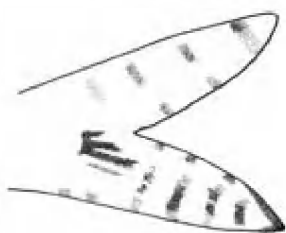
B. *U. doriae*
SMF 26055
71 mm SL



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



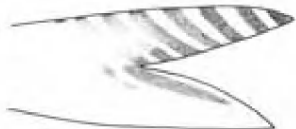
D. *U. indicus*
HT BPBM 27524
137 mm SL



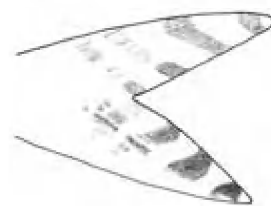
E. *U. margarethae*
SAIAB 82817
108 mm SL



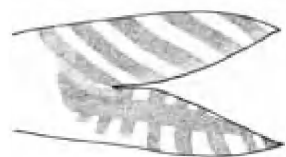
F. *U. mascarensis*
SAIAB 81951
162 mm SL



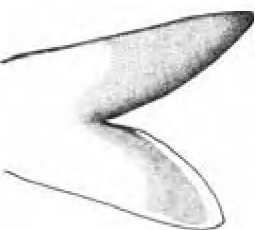
G. *U. moluccensis*
SAIAB 82509
103 mm SL



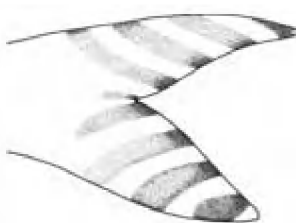
H. *U. oligospilus*
NRM 16480
171 mm SL



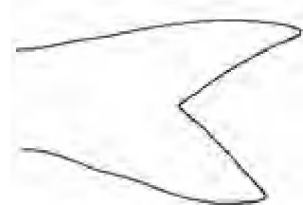
I. *U. pori*
MNHN 1992-977
97 mm SL



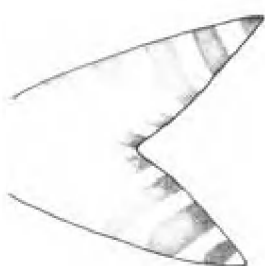
J. *U. sulphureus*
SAIAB 82237
99 mm SL



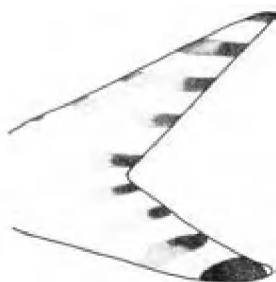
K. *U. suahelicus*
SAIAB 13948
101 mm SL



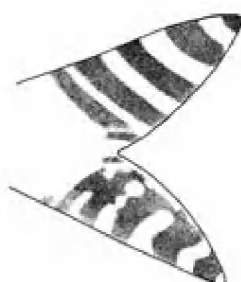
L. *U. sundaicus*
ZMUC P49124
109 mm SL



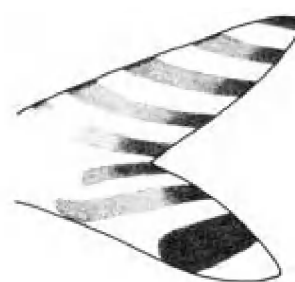
M. *U. supravittatus*
BPBM 20504
120 mm SL



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, 26°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, Thalaiaaddy, 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, 4.6418328° S, 55.380165° 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).

LITERATURE CITED

- BARANES, A. & D. GOLANI. 1993. An annotated list of deep-sea fishes collected in the northern Red Sea, Gulf of Aqaba. *Israel Journal of Zoology*, **39**: 299–336.
- BAUCHOT, M. -L. & G. BIANCHI. 1984. *Guide des Poissons Commerciaux de Madagascar*. FAO species identification sheets for fishery purposes. Food and Agriculture Organization of the United Nations, Rome. xx + 135 pp. (in French).
- BAUCHOT, M. L., DESOUTTER, M., GUÉZÉ, P. & J. E. RANDALL. 1985. Catalogue critique des types de poissons du Muséum national d'Histoire naturelle. *Bulletin du Muséum national d'histoire naturelle*, Paris 4 (7), sect. A 2, supplement 1–125.
- BEN-TUVIA A. 1966. Red Sea fishes recently found in the Mediterranean. *Copeia* **1966**: 254–275.
- BEN-TUVIA A. & D. GOLANI. 1989. A new species of goatfish (Mullidae) of the genus *Upeneus* from the Red Sea and the eastern Mediterranean. *Israel Journal of Zoology*, **36**: 103–112.

- BEN-TUVIA, A. & G. W. KISSIL. 1988. Fishes of the family Mullidae in the Red Sea, with a key to the species in the Red Sea and the eastern Mediterranean. *Ichthyological Bulletin of the J. L. B. Smith Institute of Ichthyology* **52**: 1–16.
- BLEEKER P. 1855. Zesde bijdrage tot de kennis der ichthyologische fauna van Amboina. *Natuurkunde Tijdschrift voor Nederlandsch Indië* **8**: 391–434.
- BLEGVAD, H. & B. LØPPENTHIN. 1944. *Fishes of the Iranian Gulf*, Danish Scientific Investigations in Iran, Einar Munksgaard, Copenhagen. 247 pp.
- CALDWELL, M. C. 1962. Development and distribution of larval and juvenile fishes of the family Mullidae of the Western North Atlantic. *Fishery Bulletin* **213**, 62: 103–457.
- CARPENTER, K. E., F. KRUPP, D. A. JONES AND U. ZAJONZ (EDS.). 1997. *Living marine resources of Kuwait, eastern Saudi Arabia, Bahrain, Qatar, and the United Arab Emirates*. FAO species identification field guide for fishery purposes. Food and Agriculture Organization of the United Nations, Rome. 293 pp.
- CUVIER G. 1829. *Le règne animal, distribué d'après son organisation, pour servir de base à l'histoire naturelle des animaux et d'introduction à l'anatomie comparée*, vol. 2. Paris: Chez Déterville, xv + 406 pp.
- CUVIER G. & A. VALENCIENNES. 1829. *Histoire Naturelle des Poissons*. vol. 3. Paris: Chez F.G. Levrault, xxviii + 500 pp.
- DAY, F. 1868. On some new or imperfectly known fishes of India. *Proceedings of the General Meetings for Scientific Business of the Zoological Society of London* 1867 (pt 3): 935–942.
- DE BRUIN, G. H. P., B. C. RUSSELL & A. BOGUSCH. 1994. *The marine fishery resources of Sri Lanka*. FAO species identification field guide for fishery purposes. Food and Agriculture Organization of the United Nations, Rome. 400 pp., 32 plates.
- DESMAREST E. 1856. Reptiles et poissons. In: J.G. Chenu *Encyclopédie d'histoire naturelle; ou, Traité complet de cette science d'après les travaux des naturalistes les plus éminents de toutes les époques*, **19**: 1–360 + 1–62.
- FISCHER, W., I. SOUSA, C. SILVA, A. DE FREITAS, J. M. PUTIERS, W. SCHNEIDER, T. C. BORGES, J. P. FERAL & A. MASSINGA. 1990. *Guia de Campo das Espécies Comerciais Marinhas e de águas Salobras de Moçambique*. FAO species identification sheets for fishery purposes. Food and Agriculture Organization of the United Nations, Rome. 124 pp. (in Portuguese).
- FOURMANOIR, P. & P. GUÉZÉ. 1967. Poissons nouveaux ou peu connus provenant de la Réunion et de Madagascar. *Cahiers O.R.S.T.O.M. Série Océanographie*, **5**: 47–58.
- FORSSKÅL P. 1775. Pisces in *Descriptiones animalium avium, amphibiorum, piscium, insectorum, vermium; quae in itinere orientali*. Copenhagen: Mölleri, pp. 22–75.
- FRICKE, R. MULOCHAU T., DURVILLE P., CHABANET P., TESSIER, E. & Y. LETOURNEUR. 2009. Annotated checklist of the fish species (Pisces) of La Réunion, including a Red List of threatened and declining species. *Stuttgarter Beiträge zur Naturkunde A, Neue Serie*, **2**: 1–168.
- GILCHRIST, J.D.F. & W.W. THOMPSON. 1908. Descriptions of fishes from the coast of Natal. *Annals of the South African Museum* **6**: 145–206.
- GOLANI, D. 2001. *Upeneus davidaromi*, a new deepwater goatfish (Osteichthyes, Mullidae) from the Red Sea. *Israel Journal of Zoology* **47**: 111–121.
- GÜNTHER, A. 1869. Descriptions of two new species of fishes discovered by the Marquis J. Doria. *Annals and Magazine of Natural History (Series 4)*, **3** (no. 18): 444–445.
- GUÉZÉ, P. 1976. *Upeneus niebuhri*, espèce nouvelle de Mullidae de la Mer Rouge (Pisces, Perciformes). *Revue des Travaux de l'Institut des Pêches Maritimes* **40**: 596.
- HOOUTUYN, M. 1782. Beschryving van eenige Japanese visschen, en andere zee-schepzelen. *Verhandelingen der Hollandsche Maatschappij der Wetenschappen, Haarlem* **20**(2): 311–350.
- JORDAN, D. S. & B. W. EVERMANN. 1903. Descriptions of new genera and species of fishes from the Hawaiian Islands. *Bulletin of the U. S. Fish Commission* **22**: 161–208.
- JORDAN, D. S. & A. SEALE. 1907. Fishes of the islands of Luzon and Panay. *Bulletin of the Bureau of Fisheries* **26**: 1–48.
- KHALAF, M. A. & A. M. DISI. 1997. *Fishes of the Gulf of Aqaba*. Marine Science Station, Aqaba, Jordan. 252 pp.
- KIM, B.-J. & K. NAKAYA. 2002. *Upeneus australiae*, a new goatfish (Mullidae: Perciformes) from Australia. *Ichthyological Research* **49**: 128–132.
- KIM, B.-J. & K. NAKAYA. 2003. Redescription of a poorly known goatfish, *Upeneus doriae* (Perciformes: Mullidae) from the Persian Gulf and comparison with *U. sulphureus*. *Korean Journal of Ichthyology*, **15**: 109–113.
- KLAUSEWITZ, W. 2002. Eduard Rüppell – Mensch und Wissenschaftler. *Natur & Museum* **132**: 157–169.
- KUMARAN, M. & J. E. RANDALL. 1984. Mullidae. In: Fischer, W. & G. Bianchi (eds.). 1984. FAO species identification sheets for fishery purposes. Western Indian Ocean. Fishing area 51, Vol. 3. Food and Agriculture Organization of the United Nations, Rome.
- KURONUMA, K. & Y. ABE. 1972. *Fishes of Kuwait*. Kuwait Institute for Scientific Research, Kuwait, xiv + 123 pp.
- LACHNER, E. A. 1954. A revision of the goatfish genus *Upeneus* with descriptions of two new species. *Proceedings of the United States National Museum* **103**: 497–532.

- LETOURNEUR Y, CHABANET P, DURVILLE P, TAQUET M, TEISSEIR E, PARMENTIER M, ET AL. 2004. An updated checklist of the marine fish fauna of Réunion Island, south-Western Indian Ocean. *Cybiurn* **28**: 199–216.
- MASUDA, H., AMAOKA, K., ARAGA C., UYENO, T. & T. YOSHINO. 1984. *The fishes of the Japanese Archipelago*. Tokai Univ. Press. 437 pp., 370 pls.
- NIELSEN, J. G. 2002. Revision of the Indo-Pacific species of *Neobythites* (Teleostei, Ophidiidae), with 15 new species. *Galathea Report* **19**: 5–105.
- OKAMURA, O. & K. AMAOKA. 1997. *Sea Fishes of Japan*. Yama-Kei, Tokyo, 784 pp.
- RANDALL, J. E. 1974. The status of the goatfishes (Mullidae) described by Forsskål. *Copeia* **1974**: 275–277.
- RANDALL, J. E. 1995. *Coastal fishes of Oman*. University of Hawaii Press, Honolulu, Hawaii.
- RANDALL, J. E. 2001. Mullidae. In: K. E. Carpenter & V. E. Niem (eds.), *The living marine resources of the Western Central Pacific*. FAO species identification guide for fishery purposes. Volume 5. Bony fishes, part 3 (Menidae to Pomacentridae). Rome, FAO: 3175–3200.
- RANDALL, J. E. & P. GUÉZÉ. 1992. *Upeneus francisi*, a new goatfish (Perciformes: Mullidae) from Norfolk Island and New Zealand. *Cybiurn* **16**: 21–29.
- RANDALL, J. E., M. L. BAUCHOT & P. GUÉZÉ. 1993. *Upeneus japonicus* (Houttyn), a senior synonym of the Japanese goatfish *U. bensasi* (Temminck et Schlegel). *Japanese Journal of Ichthyology*, **40**: 301–305.
- RANDALL, J. E. & M. KULBICKI. 2006. A review of the goatfishes of the genus *Upeneus* (Perciformes: Mullidae) from New Caledonia and the Chesterfield Bank, with a new species, and four new records. *Zoological Studies*, **45**: 298–307.
- RANDALL, J. E., J. T. WILLIAMS & L. A. ROCHA. 2007. The Indo-Pacific tetraodontid fish *Canthigaster coronata*, a complex of three species. *Smithiana Bulletin* **9**, 3–13.
- RICHARDSON, J. 1846. Report on the ichthyology of the seas of China and Japan. *Report of the British Association for the Advancement of Science*, 15th Meeting: 187–320.
- SAINSBURY, K. J., P. J. KAILOLA & G. G. LEYLAND. 1985. *Continental shelf fishes of Northern and Northwestern Australia. An illustrated Guide*. CSIRO, Canberra, Australia; Clouston and Hall and Peter Pownall Fisheries Information Service, viii + 375 pp.
- SMITH, J.L.B. 1965. *The Sea Fishes of Southern Africa*. Central News Agency, Ltd., Cape Town. 580 pp., 111 pls.
- SMITH, M. M. & P. C. HEEMSTRA (eds). 1986. *Smiths' Sea Fishes*. Macmillan South Africa, Johannesburg. xx + 1047 pp.
- TEMMINCK, C. J. & H. SCHLEGEL. 1843. Pisces. In: Fauna Japonica, sive descriptio animalium quae in itinere per Japoniam suscepto annis 1823–30 collegit, notis observationibus et adumbrationibus illustravit P. F. de Siebold. Fauna Japonica, sive descriptio animalium quae in itinere per Japoniam, Parts 2–4: 21–72.
- THOMAS, P. A. 1969. Goatfishes (Mullidae) of the Indian seas. *Marine Biological Association of India Memoires* **3**: 1–174.
- UIBLEIN, F. 1991. Ontogenetic shifts in resource use and shoaling tendency related to body size in Red Sea goatfish (*Parupeneus forsskali*, Mullidae). *Marine Ecology* **12**: 153–161.
- UIBLEIN, F. 1996. Constraints and exploratory windows in light-reduced marine habitats. In: Uiblein, F., Ott, J. & M. Stachowitsch (Eds.): Deep-sea and extreme shallow-water habitats: affinities and adaptations. *Biosystematics and Ecology Series* **11**: 165–182.
- UIBLEIN, F. 2007. Goatfishes (Mullidae) as indicators in tropical and temperate coastal habitat monitoring and management. *Marine Biology Research* **3**: 265–288.
- UIBLEIN, F., C. KÖHLER & M. C. TIAN. 1998. Quantitative examination of morphological variability among goatfishes of the genus *Upeneus* from the Malayan Province (Pisces: Perciformes: Mullidae). *Senckenbergiana Maritima* **28**: 123–132.
- UIBLEIN, F. & H. WINKLER. 1994. Morphological variability among *Vimba* in Austrian waters: quantitative examination of a taxonomic and a functional hypothesis (Pisces: Cyprinidae). *Senckenbergiana Biologica*, **73**: 57–65.
- WINTERBOTTOM, R., A. R. EMERY & E. HOLM. 1989. An annotated checklist of Fishes of the Chagos Archipelago, Central Indian Ocean. *Royal Ontario Museum Life Sciences Contributions*, No. 145, 226 pp.

APPENDIX

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

	<i>U. guttatus</i>		<i>U. pori</i>		<i>U. asymmetricus</i>		<i>U. australis</i>		<i>U. francisi</i>		<i>U. japonicus</i>		<i>U. porus</i>	
	Indian Ocean	n	Red Sea, Mediterranean	Madagascar	all	Pacific	n	Indo-Pacific	n	Pacific	n	Pacific	n	Atlantic
SL (mm)	77-146	27	66-110	97	66-110	74-100	4	84-130	8	78	104-115	4	110-148	3
BODYDD	22-25	20	21-23	24	21-24	22-24	4	24-25	4	24	23-25	4	25-26	3
BODYDA	19-23	20	20-21	22	20-21	20-22	4	21-23	4	19	19-22	4	20-21	3
HALFDD	17-21	17	18-19	20	18-20	19-20	4	19-21	4	18	19-21	3	20-21	3
HALFDA	15-18	17	14-16	16	14-16	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	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	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	20	4	21-22	4	20	20-21	4	22-23	3
HEAD2	15-19	20	15	16	15-16	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	9.4-10	5	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	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	27-29	4	28-30	4	31	28-29	4	30-31	3
SNOUTL	9.9-13	20	11	11	11	9.9-11	4	11-12	4	10	11-12	4	11-12	3
FORBL	8.9-12	20	11-12	11	11-12	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	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	5.6-6.5	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	9.6-11	4	11	4	12	10-11	4	12-13	3
IJAWL	9.1-12	20	9.7-10	10	9.7-10	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	8.1-9.3	4	9.7-9.9	4	7.0	7.7-9.2	4	8.4-11	3
BARBL	16-19	19	16-18	17	16-18	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	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	37-38	4	34-36	4	38	34-37	4	39-40	3
SD2	61-67	20	63-65	64	63-65	64-66	4	62-64	4	66	63-64	4	67-68	3
DID2	13-17	19	14-16	13	13-16	14-16	4	13-16	4	15	15-18	4	17-20	3
CPDL	22-26	20	22-23	23	22-23	22-24	4	22-26	4	23	23-25	4	21	3
SANL	60-68	20	60-65	64	60-65	63-68	4	61-64	4	66	61-67	4	68-70	3
SPEL	28-34	19	28-32	29	28-32	32-34	4	30-34	4	33	30-33	4	33-36	3
SPEC	26-32	19	28-30	30	28-30	30-31	4	29-31	4	33	27-33	4	33-34	3
DZANL	19-23	20	20-21	22	20-21	19-22	4	22-24	4	20	19-22	4	20-22	3
DIPELV	22-26	20	22-23	23	22-23	22-24	4	23-25	4	24	22-25	4	25-26	3
DIPEC	15-18	20	16-17	16	16-17	15-17	4	16-17	4	16	14-18	4	16-17	3
DIB	12-18	20	14-16	16	14-16	13-15	4	15-17	4	14	14-17	4	13-15	3
D2B	12-16	20	13-15	14	13-15	13-14	4	14-15	4	11	13-15	4	12-13	3
CAUH	25-30	20	27-29	29	27-29	27	4	26-29	4	28	25-27	4	28-29	2
ANALB	10-14	20	12-13	12	12-13	10-12	4	11-13	4	12	11-12	4	8.7-9.3	3
ANALH	15-19	19	16-17	17	16-17	15-16	2	14-17	4	16	15-18	4	13-14	3
PELVL	19-23	20	20-23	23	20-23	20-21	4	20-21	4	24	21-22	4	17-21	3
PECTL	20-22	19	20-22	21	20-22	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	4.1-5.9	4	4.2-5.0	4	4.2	3.7-5.8	4	4.4	3
DIH	20-24	16	20-21	21	20-21	20	3	20-21	4	21	21-22	4	21	2
D2H	14-18	19	15-16	16	15-16	15-16	2	14-17	4	16	16-18	4	16-17	2
DI	7	27	7	7	7	7	4	7	8	7	7	4	7	3
P	13-14	27	14	14	14	13	4	14	8	14	13-15	4	15	3
GrUd	2-5	27	0-2	1	0-2	1-4	4	2-4	8	1	2-3	4	3-4	3
GrUd	2-5	27	6-7	7	6-7	3-6	4	2-4	8	8	4	4	3-4	3
GrLd	11-14	27	14-18	15	14-18	15-17	4	11-13	8	23	12-16	4	14-17	3
GrUd	4-5	27	2-5	3	2-5	2-5	4	3-5	8	0	4-7	4	3-5	3
GrU	6-8	27	7-8	8	7-8	7	4	5-7	8	9	6-7	4	7	3
GrL	16-18	27	18-20	18	16-18	19-21	4	16-17	8	23	18-20	4	19-20	3
Gr	23-25	27	26-27	26	26-27	26-28	4	21-24	8	32	24-27	4	26-27	3
LLscal	28-31	20	29-30	29	29-30	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).

	Holotype		Paratypes (n=20)		Red Sea (n=2)		Persian Gulf		Sri Lanka (n=2)		NW Australia (n=3)		N Australia		Indo-Pacific	
	SL (mm)		67-110	78-94	105	78-80	108-117	95	67-124	n						
BODYDD	26	22-26	25	23	25	23-25	25-26	25	22-26	29						
BODYDA	24	20-23	23	21	20	18-21	22	21	20-24	29						
HALFDD	20	18-22	21	17	17	16-17	19-21	21	18-22	29						
HALFDA	19	15-18	16	11	10	10-11	16-17	17	15-19	29						
CPDD	11	9.3-11	11	4.3-4.3	4.3	3.6-4.1	11	11	9.3-11	29						
CPDW	4.8	4.0-5.7	21-22	17-18	20	20-21	3.9-5.3	3.7	3.6-5.7	29						
HEAD1	21	19-22	12	12	11	9.3-10	21-23	21	19-23	29						
HEAD2	17	15-18	18	11	18	17	18-19	17	15-19	29						
SUBORB	10	9.1-12	7.7	8.4-8.9	7.7	7.6-8.4	11-12	11	9.1-12	29						
INTORB	8.2	7.3-9.1	27	28-30	27	28-31	8.1-8.8	8.7	7.3-9.1	29						
HEADL	30	27-31	11	11	12	11-12	28-29	27	27-31	29						
SNOU1L	12	11-12	12	12	12	11-12	11-12	11	11-12	29						
PORBL	12	11-12	6.5	7.7-8.1	6.5	7.3-7.4	11-12	11	11-12	29						
ORBITL	8.7	7.0-9.1	5.0	6.4-6.4	5.0	5.7-6.6	6.7-7.4	6.9	6.5-9.1	29						
ORBITD	7.1	5.8-8.0	10-11	10-11	10	11	5.9-6.6	5.9	5.2-8.0	29						
UJAWL	11	10-12	9.2	9.5-10	9.2	10	10-11	11	10-12	29						
LJAWL	10	9.1-11	-	-	-	8.5-9	8.3-10	8.4	8.3-11	29						
SNOU1W	11	9.0-11	16	16-18	16	18-19	10 **	16	8.5-11	24						
BARBL	17	16-20	0.9	0.9-0.9	0.9	0.7-0.9	18-19	16	16-20	29						
BARBW	0.9	0.7-1.2	33	35-37	33	37-38	35-36	37	0.7-1.2	29						
SD1	40	35-39	62	62-68	62	62-65	61-63	62	35-40	29						
SD2	67	60-66	22	22-25	22	24	22-24	25	60-67	29						
D1D2	15	11-16	12	12-14	12	13-15	12-13	14	11-16	29						
CPDL	23	22-26	66	67-70	66	64-66	22-24	25	22-26	29						
SANL	66	59-68	35	34	35	33-34	33-37	33	59-70	29						
SPEL	29	28-32	29	31-33	29	30-33	32	30	28-37	29						
SPEC	31	28-31	22	23-24	22	21-22	22-23	23	28-33	29						
D2ANL	24	20-23	25	25	24	23-24	25-26	26	20-24	29						
D1PELV	25	22-26	16	16-17	16	16-17	16-17	18	22-26	29						
D1PEC	18	15-18	15	14-16	15	14-15	15	15	15-18	29						
D1B	15	15-18	14	14	14	13	13-15	13	14-18	29						
D2B	15	12-16	27	21-31	27	27-30	28	27	12-16	29						
CAUH	27	27-31	11	11-12	11	11	11	11	27-31	29						
ANALB	12	10-14	15	14-16	15	13-16	14-17	14	10-14	29						
ANALH	15	14-18	20	23	20	21-22	20-22	20	14-18	29						
PELVL	23	20-24	21	21-23	21	21-22	21-22	21	20-24	29						
PECTL	23	21-25	4.5	4.8-5.6	4.5	4.9-5.2	5.1-5.2	4.4	21-25	29						
PECTW	4.8	4.4-5.8	20-22	20-22	20	20-22	20-21	20-23	4.4-5.8	29						
D1H	21	20-23	16	17-18	16	16	16-19	16	20-23	29						
D2H	18	16-20	8	8	8	8	8	8	16-20	29						
D1	8	8	14	14	14	14	14	14	8	30						
P	14	13-14	3	2	3	3	2-3	3	13-14	30						
GrUud	3	2-4	12	13	12	11-13	12	12	2-4	30						
GrUd	3	2-3	4	4	4	5	5-6	5	2-3	30						
GrLd	12	11-13	6	4-5	6	6	5-6	6	11-13	30						
GrLud	5	4-6	17	16-18	16	16-18	17-18	17	4-6	30						
GrU	6	5-6	23	21-22	22	22-24	22-23	23	4-7	30						
Gr	17	16-18	28	29-30	29	30	29-30	29	16-18	30						
Gr	23	21-24							21-24	30						
Llscal	28	28-30 *							28-30	27						

*n=17; **n=1

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

	U. oligocentrus			U. sandatiscus		U. lucinopterus			U. tragula		U. bezoniensis		U. nivosus		
	HT	Persian Gulf	n	juveniles (n=2)	Indo-Pacific	n	HT	HT	U. arge	Indo-Pacific	n	Indo-Pacific	n	Pacific	n
SL (mm)	114	72-171	14	53-67	105-132	9	207	153		88-265	20	78-191	11	49-91	5
BODYDD	25	23-26	14	23-24	25-28	9	22	23		22-25	15	22-26	11	22-26	5
BODYDA	20	19-22	14	20-22	22-24	9	23	21		20-23	16	20-23	3	19-23	5
HALEFDD	20	19-22	14	18-20	20-22	9	-	21		18-21	9	19-22	9	20-21	4
HALEFDA	15	14-17	14	15	15-18	9	-	16		15-17	9	15-17	11	13-15	5
CPDD	10	9.8-11	14	10-11	11-13	9	10	10		9.7-11	11	9.9-11	11	11-13	5
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	3.3-4.3	5
HEAD1	21	20-23	14	19-21	21-23	9	17	20		17-21	10	19-23	10	20-23	5
HEAD2	16	15-19	14	17	17-20	9	14	17		14-17	10	15-17	10	16-18	5
SUBORB	11	9.6-12	14	9.9	11-14	9	10	11		9.6-12	10	8.7-11	11	10-12	5
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	7.3-8.7	5
HEADL	32	29-32	14	33	27-30	9	25	27		25-29	14	27-31	11	27-30	5
SNOUTL	13	12-14	14	12-13	12-14	9	10	11		10-12	10	11-13	11	11-12	5
NORBL	13	12-13	14	13	11-13	9	10	12		9.9-13	10	10-12	11	10-13	5
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	5
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	5.4-6.1	5
UJAWL	13	11-13	14	13-14	11-12	9	11	12		11-13	18	11-14	11	11-12	5
UJAWL	12	10-13	14	12	10-12	9	10	12		9.9-12	10	11-13	10	9.1-11	5
SNOUTW	10	9.8-12	13	12	11-12	8	-	11		9.3-11	8	8.4-12	11	8.2-11	4
RARBL	20	16-20	14	18-19	18-21	9	18	18		17-21	18	15-19	11	16-21	5
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	5
SD1	38	37-40	14	40-41	36-38	9	35	37		36-38	10	35-39	11	35-40	5
SD2	65	62-66	14	65-68	63-64	9	65	61		61-66	10	62-66	11	63-70	5
DID2	14	12-15	14	12-16	12-15	9	18	15		15-19	9	12-15	11	13-16	5
CPDL	20	20-25	14	20-22	22-26	9	24	22		22-24	10	21-24	11	21-25	5
SANL	66	61-68	14	65-67	62-67	9	70	64		64-70	10	62-67	11	64-66	5
SPEL	33	30-37	14	34-34	30-34	9	31	29		29-33	10	31-34	11	32-37	5
SPEC	34	30-35	14	33-36	28-31	9	28	27		27-30	10	29-31	11	31-37	5
D2ANL	21	20-23	14	20-22	23-25	9	21	21		21-23	10	20-23	11	20-23	5
D1ELV	24	23-26	14	24	25-29	9	20	24		20-26	10	23-26	11	23-26	5
D1PEC	17	16-19	14	17-19	17-20	9	14	17		14-18	10	15-18	11	17-18	5
D1R	15	14-17	14	15	15-17	9	13	15		12-15	10	14-16	11	14-16	5
D2R	15	13-16	14	13-14	13-17	9	12	13		12-14	10	13-15	11	13-15	5
CAUH	24	24-28	14	26-29	26-29	9	28	-		28-32	8	28-32	11	28-31	4
ANALR	12	10-12	14	13	11-14	9	9.3	11		9.3-13	10	10-13	11	9.7-13	5
ANALH	17	15-18	14	16-20	16-18	9	15	16		15-17	10	16-19	11	15-17	5
PELVL	19	17-21	14	22-23	20-23	9	18	17		18-20	10	20-24	11	21-24	5
PECTL	20	18-22	14	22-23	21-23	9	-	17		17-20	16	19-21	11	19-23	5
PECTW	4.8	3.5-5.4	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	5
D1H	19	18-22	14	21-23	25-29	8	-	21		20-23	16	21-24	11	21-24	5
D2H	17	16-18	14	18-20	16-18	9	-	16		14-16	16	17-20	11	16-19	5
D1	8	8	14	8	8	9	8	8		8	17	8	11	8	5
P	14	13-14	14	13	13-14	9	14	14		13-14	17	13-14	11	14-15	5
GrtDud	3	2-5	14	2-5	2-3	9	4	3		2-4	17	2-5	11	0-2	5
GrtDd	3	2-3	14	2-4	2	9	2	3		2-3	17	2-3	11	3-4	5
GrtAd	12	9-12	14	11-12	10-12	9	12	12		10-13	17	10-12	11	11-12	5
GrtLud	6	4-7	14	4-5	3-5	9	5	5		3-6	17	4-7	11	3	5
GrtU	6	4-7	14	6-7	4-5	9	6	6		5-6	17	5-8	11	4-5	5
GrtL	18	16-18	14	16	14-15	9	17	17		16-17	17	14-17	11	14-15	5
Gr	24	20-24	14	22-23	18-20	9	23	23		21-23	17	19-24	8	18-20	5
ULscal	29	28-31	14	29-31	31-34	8	-	36		35-39	14	28-30	11	31-32	4

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

	U. dorrine			Juveniles (n=2 **)	U. moluccensis Indo-Pacific	U. sulphureus				
	Persian Gulf (n=3)	Gulf of Oman (n=3)	All adults			Western Indian O.	n	Persian Gulf	Eastern Indian O.	Indian Ocean
SL (mm)	71-97	116-145	71-148	46-58	103-133	95-115	9	116	128	95-128
BODYDD	27-29	27-29	27-29	25	24-26	29-33	9	29	30	29-33
BODYDA	24	24	24	21	21-23	25-27	9	25	25	25-27
HALFDD	21-24	20-23	20-24	20	20-22	22-25	9	23	23	22-25
HALFDA	17-19	18	17-19	16	17-19	18-20	9	20	19	18-20
CPDD	10-11	11-12	10-12	9-9	9-10	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	4.6-6.0	9	4.0	4.3	4.0-6.0
HEAD1	23-24	23-24	23-24	21	20-22	24-25	9	23	25	23-25
HEAD2	18-22	18-19	18-22	18	16-17	18-20	9	20	20	18-20
SUBORB	10-13	10-12	9.5-13	9-4	9-11	9-11	9	-	11	9-11
INTORB	8.0-8.3	7.9-8.4	7.9-8.4	8.5	7.5-8.3	7.6-8.4	9	9.1	9.0	7.6-9.1
HEADL	30-31	29-30	29-31	28	27-29	28-30	9	29	30	29-30
SNOUTL	10-11	9.8-11	9.8-11	9.7	10-11	10-12	9	11	11	10-12
PORBL	11-12	12-13	11-13	11	11-12	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	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	6.9-7.8	9	6.4	6.6	6.4-7.8
UJAWL	11	11	11	11	11-12	12-13	9	11	13	11-13
LJAWL	10-11	11	10-11	11	11	10-12	9	11	12	10-12
SNOUTW	10-12 *	8.3-9.1	8.3-12	9.0	7.6-11	9.7-12	9	-	11	9.7-12
BARBL	16-20	16-17	16-20	20	15-17	17-21	8	17	21	17-21
BARBW	0.9	0.7-0.8	0.7-0.9	0.8	0.8-1.2	0.5-0.8	9	-	0.8	0.5-0.8
SD1	39-41	39-40	39-41	36	37-40	37-41	9	38	42	37-42
SD2	65-67	65-67	65-67	68	65-67	66-68	9	67	69	66-69
D1D2	15-16	14-16	14-16	16	16-17	15-18	9	14	18	14-18
CPDL	19-23	21-23	19-23	21	19-22	18-21	9	21	19	18-21
SANL	68-68	68-71	68-71	68	66-70	66-69	9	69	69	66-69
SPEL	33-37	33-35	33-37	32	31-33	30-34	9	36	35	30-36
SPEC	32-35	30-32	30-35	29	29-31	30-32	9	34	32	30-34
DZANL	25-26	25-26	25-26	21	21-24	25-26	9	25	26	25-26
D1PELV	28-30	27-29	27-30	26	23-27	28-31	9	30	30	29-31
D1PEC	18-19	17-19	17-19	18	16-17	20-21	9	18	21	18-21
D1B	13-15	14-16	13-16	14	12-15	15-18	9	17	17	13-18
D2B	16	14	14-16	11	13-15	14-16	9	13	14	13-16
CAUHI	26 *	28	26-28	24	27-30	27-30	9	27	29	27-30
ANALB	11-12	9.7-11	10-12	13	10-11	11-13	9	12	11	11-13
ANALH	14-15	14-15	14-15	17	13-15	16-18	9	16	16	16-18
PELVL	18-20	18-19	18-20	19	17-22	20-22	9	20	20	20-22
PECTL	25-28	25-26	25-28	24	25-27	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	4.3-5.9	9	4.4	4.9	4.3-5.9
D4H	20-22	20-22	20-22	19	20-23	23-26	9	25	26	23-26
D2H	14	14-15	14-15	16	14-16	17-18	9	17	18	17-18
D1	8	8	8	8	8	8	9	8	8	8
P	16-17	15-16	15-17	16	14-16	15-16	9	16	17	15-17
GrUud	0	0-1	0-1	0-1	0-4	0-3	9	2	3	0-3
GrUd	8-9	6-9	6-9	6-8	3-7	5-8	9	5	4	4-8
GrLd	19-23	21-23	19-23	18-22	14-20	16-20	9	18	16	16-20
GrLud	0-3	0-1	0-3	0-4	0-5	0-4	9	2	4	0-4
GrU	8-9	7-9	7-9	7-8	7-8	7-8	9	7	7	7-8
GrL	22-23	22-23	22-23	22	18-20	19-21	9	20	20	19-21
Gr	30-32	29-32	29-32	29-30	26-27	27-28	9	27	27	27-28
L1scal	33-34	35	33-35	35	33-35	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".

	<i>U. doerrii</i>		<i>U. indicus</i>		<i>U. muscurensis</i>		<i>U. suahelicus</i> sp. nov.			<i>U. supravittatus</i> sp. nov.		<i>U. vittatus</i>		<i>U. subvittatus</i> Pacific (n=5)					
	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
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	23-26	25	22-26	23	22-25	22	21-24	21-24	7	21-23 **
HALEDD	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 **
HALEDA	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
SUBORR	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	7.1-8.4	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	1	10	10	-	8.6-11	12	6.6	9.8	8.2-11	11	10-12	11	11-12	11	11-12	11-12	7	13-14
SNOUTW	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
BARBL	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
BARBW	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
SD1	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
DD2	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	23	20	18-23	20	18-23	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
SPFL	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
DZANL	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
DPELV	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
DPEFC	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 **
PELV	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	24	23-26	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	3	3	8	8	8	8	8	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
LLsal	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