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ORIGINAL ARTICLE

A new goatfish, *Upeneus seychellensis* sp. nov. (Mullidae), from the Seychelles Bank, with remarks on *Upeneus guttatus* and a key to Western Indian Ocean *Upeneus* species

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Abstract

The mullid genus *Upeneus* is highly diverse, with a considerable number of new species found only recently. Based on 16 specimens of *Upeneus* collected at the southeastern edge of the Seychelles Bank, a large oceanic platform in the Western Indian Ocean, a new species, *Upeneus seychellensis*, is described. Comparisons with and among populations of the closely related *U. guttatus* are made. By integration of an extensive, comparative data set consisting of 50 morphometric and meristic and several colour characters obtained from 25 additional *Upeneus* species, an updated key for the 18 Western Indian Ocean species is provided. The new species can be distinguished from all other congeners of the *japonicus*-species group, a complex of species with seven dorsal-fin spines, by a combination of number of pectoral fin rays and gill rakers, body depth at anal fin origin, caudal peduncle depth, anal fin size, first dorsal-fin height and colour of the lower caudal-fin lobe. Co-occurring specimens of *U. guttatus* are considerably differentiated in morphology and colour from other Indian Ocean populations and this was also found for a single specimen from the Gulf of Suez. These results indicate isolation and the formation of local adaptation in more remote areas of the Indian Ocean, but the influence of phenotypic plasticity also needs to be considered.

Key words: Goatfishes, Mullidae, new species, population differences, taxonomy, *Upeneus*

Introduction

The Seychelles Bank is a part of the Mascarene Plateau, Western Indian Ocean, that rises from depths between 1500 and 3000 m to a flat, nearly oval shelf platform of ca. 300 km maximum diameter and 50 m average depth (Gupta & Desa 2001). The fish fauna of the Seychelles Bank and associated islands has been studied during a number of surveys in the last 150 years and about 1000 fish species have been recorded, mostly from shallow reef habitats surrounding the islands (Jennings et al. 1999; Payet 2005).

In November 2008, during a cruise with the R/V *Dr. F. Nansen*, five bottom trawl hauls were made in the southern area of the Seychelles Bank at 60 m depth. Among the fishes collected were several goatfishes of the genus *Upeneus* (Mullidae) that could not be identified to species level on board

and hence representative specimens of each distinct form were selected, photographed, and later included in the fish collection of the South African Institute of Aquatic Biodiversity (SAIAB).

The genus *Upeneus* is highly diverse, with 27 species, five of which have been described only recently (Uiblein & Heemstra 2010; Uiblein & Heemstra 2011). All five occur in the Western Indian Ocean, in which 17 *Upeneus* species have been found so far. Because more new species can be expected, an integrative approach has been adopted for the study of additional material using a large set of taxonomic characters obtained from 26 *Upeneus* species (Uiblein & Heemstra 2010; Uiblein & Heemstra 2011). In this way important information on intraspecific variation and phenotypic divergence among populations becomes available (Uiblein et al. 1998; Uiblein & Heemstra 2010; Uiblein & Heemstra 2011).

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Among the *Upeneus* collected on the Seychelles Bank were 16 specimens belonging to the *japonicus*-species group with seven spines in the first dorsal fin (Uiblein & Heemstra 2010). We examined these specimens in detail based on body and fin colour patterns, 50 morphometric and meristic characters and comparative data from all valid species of the *japonicus* group. Based on three specimens, a new species is described. The other 13 specimens, identified as *Upeneus guttatus* (Day, 1868), are used for updating the species diagnosis and comparisons with specimens from other areas in the Indian Ocean in order to examine the extent of geographic variation and phenotypic differentiation among populations. In addition, an updated key for the now 18 valid *Upeneus* species from the Western Indian Ocean is provided.

Materials and methods

The data of specimens of *Upeneus* species published in Uiblein & Heemstra (2010, 2011) were used for species comparisons and the preparation of the key. Additional material of *U. australiae* Kim and Nakaya, 2002 and *U. guttatus* that was examined specifically for this study is listed below.

The measuring and counting methods follow Uiblein & Heemstra (2010). Examination of radiographs taken from the three specimens of *Upeneus parvus* Poey, 1852 used in our earlier account (Uiblein & Heemstra 2010) revealed the presence of a minute first dorsal spine hidden by skin (see also Kim & Nakaya 2002). In addition to the morphological studies, photographs of the freshly collected specimens were examined closely. Of the 13 *Upeneus guttatus* from the Seychelles Bank, 12 individuals were sexed to examine possible sexual differences in diagnostic characters using the aceto-carmine squash method (Guerrero & Shelton 1974).

In the comparisons, attention was paid to the most diagnostic characters, taking sample size into consideration. For the intraspecific comparison among *Upeneus guttatus*, Principal Component Analysis (PCA) based on 40 morphometric variables and 37 specimens, with size-adjustment based on the residuals gained from log–log regressions of the variables with standard length, was used to obtain information on optimal distinction (Uiblein & Winkler 1994).

Comparative material examined

Upeneus australiae: AMS 34384-012, 86 mm, holotype, Australia, Queensland, 2.5 km W of Island Head, FV Peggy, 22°19.73' S 150°38.03' E, depth 0–6 m, prawn trawl; AMS 34384-004, 2 (of 7): 86 mm, paratypes, same station data as holotype; AMS

34396-11, 89 mm, PT, Australia, Queensland, Port Clinton, FV Peggy, 22°34.24' S 150°44.62' E, depth 0–8 m, prawn trawl; *Upeneus guttatus*: AMS 22801-004, 1 (of 7): 93 mm, Australia, Eastern Indian Ocean, NW Shelf, off Port Hedland, RV *Soela*, 19°32' S, 118°09' E, depth 50–52 m, Engel trawl; HIFIRE (Institute of Marine Research, Bergen) F5898, 92 mm, Andaman Islands, Eastern Indian Ocean; SAIAB 88872, 98 mm, Egypt, Red Sea, Gulf of Suez; BPBM 31272, 108 mm, Mozambique, IIOE expedition, RV *Anton Bruun*, st. 403A, 19°09' S 26°20' E, depth 27–30 m, shrimp trawl; SAIAB 84255, 10 (6 females, 3 males, 1 not sexed): 93–117, Seychelles, Seychelles Bank, R.V. *Dr. F. Nansen*, ACEP 08-26, 5°41'52.8" S, 56°42'07.2" E, depth 59 m, bottom trawl; SAIAB 84281, 3 (1 female, 2 males): 106–117 mm, Seychelles, Seychelles Bank, R.V. *Dr. F. Nansen*, ACEP 08-27; 5°24'25.2" S, 56°25'43.8" E, depth 60 m, bottom trawl.

For institutional abbreviations, see Eschmeyer (2010).

Taxonomy

Family Mullidae

Genus *Upeneus* Cuvier, 1829

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

Diagnosis

Dorsal fins VII or VIII + 9; anal fin I, 6; pectoral-fin rays 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 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 colours, dark caudal-fin bars frequently retained on preserved fish.

Distribution

In all major oceans, tropical to subtropical, only a single species in the Atlantic and two in the Mediterranean, both immigrants from the Red Sea (Ben-Tuvia 1966).

Remarks

We recognize 28 species as valid. One single species, *Upeneus filifer*, and four species groups can be

distinguished based on number of dorsal spines and gill rakers, length of longest dorsal-fin spine, length of pelvic and pectoral fins, and presence or absence of caudal-fin bars and mid-lateral body stripes (Uiblein & Heemstra 2010). Here *Upeneus seychellensis* sp. nov. is added to the *japonicus* group, which includes also *U. asymmetricus* Lachner, 1954, *U. australiae* Kim & Nakaya, 2002, *U. francisi* Randall & Guézé, 1992, *U. guttatus* (Day, 1868), *U. japonicus* (Houttuyn, 1782), and *U. pori* Ben-Tuvia & Golani, 1989. The other three groups are the *moluccensis* group (*U. doriae* (Günther, 1869), *U. moluccensis* (Bleeker, 1855), *U. quadrilineatus* Cheng & Wang, 1963, *U. sulphureus* Cuvier, 1829), the *tragula* group (*U. luzonius* Jordan & Seale, 1907, *U. margarethae* Uiblein & Heemstra, 2010, *U. mouthami* Randall & Kulbicki, 2006, *U. oligospilus* Lachner, 1954, *Upeneus randalli* Uiblein & Heemstra, 2011, *U. sondaicus* (Bleeker, 1855), *U. taeniopterus* Cuvier in Cuvier & Valenciennes, 1829, *U. tragula* Richardson, 1846), and the *vittatus* group (*U. davidaromi* Golani, 2001, *U. indicus* Uiblein & Heemstra, 2010, *U. mascarensis* Fourmanoir & Guézé, 1967, *U. parvus* Poey, 1852, *U. suahelicus* Uiblein & Heemstra, 2010, *U. subvittatus* (Temminck & Schlegel, 1843), *U. supravittatus* Uiblein & Heemstra, 2010, *U. vittatus* (Forsskål, 1775)).

Key to species groups and Western Indian Ocean species of *Upeneus*

- 1a. Longest spine of first dorsal fin 2.5 times or less in SL, no caudal-fin bars or mid-lateral body stripes *U. filifer*
- 1b. Longest dorsal-fin spine more than 3 times in SL; caudal-fin bars and/or mid-lateral body stripes present in fresh fish [**four species groups**]..... 2
- 2a. Dorsal-fin spines 7, first 2 spines usually longest; total gill rakers 21–32; pectoral-fin rays 12–15; bars on upper caudal-fin lobe of fresh fish in all species (bars present or absent on lower lobe) [**japonicus group**] 3
- 2b. Dorsal-fin spines 8, first spine minute, recumbent, partly hidden by skin and scales at fin origin; total gill rakers 18–33; pectoral-fin rays 13–17; bars on caudal fin of fresh fish present or absent 5
- 3a. Pectoral-fin rays 12–14; total gill rakers 23–25; first dorsal-fin height 4.1–5.1 times in SL; body red dorsally, preserved fish pale brown, not darker dorsally (Indo-Pacific) *U. guttatus*
- 3b. Pectoral-fin rays 14–15; total gill rakers 25–27; first dorsal-fin height 4.8–5.3 times in SL;

- body grey, reddish-brown or red dorsally, preserved fish darker dorsally or pale brown..... 4
- 4a. Anal-fin base length 7.5–8.4 and anal-fin height 5.8–6.4 times in SL; orbit length 1.4–1.7 in snout; body depth at anal fin origin 4.6–5.1 times in SL; lower caudal-fin lobe with 5–9 grey or reddish brown bars ventrally; preserved fish darker dorsally (Red Sea to Oman, Madagascar, eastern Mediterranean) *U. pori*
- 4b. Anal-fin base length 9.7–10 and anal-fin height 6.5–7.0 times in SL; orbit length 1.8–1.9 in snout; body depth at anal fin origin 5.4–5.5 times in SL, lower caudal-fin lobe with a red stripe and no bars in fresh fish; preserved fish pale brown (Seychelles) *U. seychellensis* sp. nov.
- 5a. Total gill rakers 18–26; pectoral-fin rays 13–15; pelvic-fin length 0.8–1.1 times in pectoral fins; bars on caudal fin in fresh fish of all species; bars retained or not retained in preserved fish [**tragula group**] 6
- 5b. Total gill rakers 25–33; pectoral-fin rays 14–17; pelvic-fin length 1.1–1.5 times in pectoral fins; bars on caudal fin in fresh fish of several species; bars retained in preserved fish 11
- 6a. Dark dots or blotches on entire body and paired fins; first dorsal-fin tip dark; one brown to black mid-lateral body stripe in fresh and preserved fish; barbel yellow in fresh fish; upper-jaw length 7.1–9.2 times in SL 7
- 6b. No dark dots or blotches on body (except for area of lateral line in *U. randalli*) and paired fins; no dark dorsal-fin tip; 1–2 yellowish or pale brown lateral body stripes on fresh fish; barbel white or yellow in fresh fish; upper-jaw length 7.9–10 times in SL 8
- 7a. Total number of caudal-fin bars 6–9 (6 or fewer in juveniles < 7 cm SL), 3–4 bars on lower caudal-fin lobe; 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*
- 7b. Total number caudal-fin bars 10 or more (7–10 in juveniles < 7 cm SL), 4–7 bars on lower caudal-fin lobe; 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-Pacific)..... *U. tragula*
- 8a. Pectoral-fin length 5.0–5.8 times in SL; lateral-line scales 35–39; upper caudal-fin lobe with 4–8 dark bars, distinct on preserved fish; fresh fish with a pale brown

- mid-lateral body stripe and a weaker, more yellowish stripe below (Indo-Pacific) *U. taeniopterus*
- 8b. 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 or without a yellow or pale brown mid-lateral body stripe 9
- 9a. 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; barbel frequently yellow in fresh fish; 5–6 red or grey bars on upper caudal-fin lobe in fresh fish (Indo-Pacific) *U. sundaicus*
- 9b. Total gill rakers 21–25; lateral-line scales 28–30; first dorsal-fin height 4.3–5.3 times in SL; caudal-peduncle depth 9.0–10 times in SL; barbel white; 4 (rarely 5) red bars on upper caudal-fin lobe in fresh fish 10
- 10a. Total gill rakers 21–24; caudal-peduncle width 17–28 times in SL and 4.9–7.9 in head length; anal-fin base 7.2–9.9 times in SL; pectoral-fin width 17–23 times in SL and 4.9–6.5 in head length; 4 (rarely 5) red bars on upper caudal-fin lobe in fresh fish, 3 (rarely 4) distally from fork; broad red band on lower caudal-fin lobe, covering up to 5 or 6 red bars, the latter only partly visible along ventral fin margin in fresh fish; mid-lateral body stripe running through eye, red from snout tip to eye and yellow from eye to caudal-fin base; stripe absent in preserved fish (Indian Ocean and Arafura Sea)..... *U. margarethae*
- 10b. Total gill rakers 23–25; caudal-peduncle width 27–34 times in SL and 7.5–10 in head length; anal-fin base 8.9–11 times in SL; pectoral-fin width 22–26 times in SL and 6.3–7.6 in head length; 5 red bars on upper caudal-fin lobe in fresh fish, 4 distally from fork; lower caudal-fin lobe with up to 8 dark red bars, bars not covered by a band; beige mid-lateral body stripe only faintly visible in fresh fish; stripe absent in preserved fish (Persian Gulf) *U. randalli*
- 11a. No bars on lower caudal-fin lobe; bars on upper caudal-fin lobe in some species; bars retained in preserved fish [***moluccensis* group**] 12
- 11b. Bars on both caudal-fin lobes in fresh and preserved fish [***vittatus* group**] 14
- 12a. No bars on entire caudal fin, also not in live or fresh fish; first dorsal-fin tip black or pale brown to yellowish in fresh fish, can be absent in preserved fish; body depth at first dorsal-fin origin 3.0–3.7 times in SL in adult fish (> 7 cm SL); head length 3.2–3.5 times in SL 13
- 12b. Caudal fin with 6–8 red bars on upper lobe, no bars on lower lobe; bars conspicuous in live fish and mostly distinct in preserved fish; brown to black first dorsal-fin tip, retained in preserved fish; body depth at first dorsal-fin origin 3.9–4.2 times in SL in adult fish (> 7 cm SL); head length 3.5–3.7 times in SL (Indo-Pacific, eastern Mediterranean) *U. moluccensis*
- 13a. 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 in preserved fish; fresh fish with a narrow, yellow mid-lateral body stripe; anal-fin length 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, Gulf of Oman) *U. doriae*
- 13b. 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 2 conspicuous, yellow lateral body stripes; anal-fin length 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-Pacific) *U. sulphureus*
- 14a. Caudal-fin bars pale brown to brown, mostly uniformly coloured, pale spaces between bars of nearly equal width; bars on upper caudal-fin lobe curved; 2 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 gillrakers 26–32 15
- 14b. Caudal-fin bars at least partly black or dark brown, vary frequently in colour intensity, bars or the spaces between them vary often in width; upper caudal-fin lobe bars mostly straight and not curved; no or more than 2 yellow or pale-brown 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 gillrakers 26–29 17
- 15a. 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*
- 15b. 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 16

- 16a. Total number of gill rakers 26–28; rakers on lower limb 19–21; pectoral-fin length 3.8–4.1 times in SL and subequal to body depth at anal-fin origin; head length 3.2–3.6 times in SL; barbel length 4.9–6.6 times in SL (East Africa, southern Red Sea) *U. suahelicus*
- 16b. Total number of gill rakers 29 (rarely 28)–32; rakers on lower limb 21–23; pectoral-fin length 3.5–4.0 times in SL and longer than body depth at anal-fin origin; head length 3.0–3.4 times in SL; barbel length 4.3–5.4 times in SL (South India, Sri Lanka) *U. supravittatus*
- 17a. Head depth through eye 4.6–4.8 times in SL; anal-fin length 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*
- 17b. Head depth through eye 5.0–6.1 times in SL; anal-fin length 6.3–7.9; second dorsal-fin height 6.2–7.2 times in SL; no or more than 2 lateral body stripes on fresh fish 18
- 18a. 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 bars of lower caudal-fin lobe narrower than orbit length; no lateral body stripes on fresh fish (Indian Ocean) *U. mascareinsis*
- 18b. 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 bars of lower caudal-fin lobe subequal to or wider than orbit length; 3 or 4 lateral body stripes on fresh fish: 2 yellow or coppery stripes mid-laterally and below, and one or 2 brown or pale brown stripes dorsally (Indo-Pacific) *U. vittatus*

***Upeneus seychellensis* sp. nov.**

Tailstripe goatfish

(Table I; Figures 1 and 2)

Holotype

SAIAB 96980, 115 mm, Seychelles, Seychelles Bank, R.V. *Dr. F. Nansen*, ACEP08-27; 5°24'25.2" S, 56°25'43.8" E, depth 60 m, bottom trawl.

Paratypes

SAIAB 84280, 96–102 mm, same station data as holotype.

Diagnosis

Dorsal fins VII + 9; pectoral-fin rays 14–15; gill rakers 7 + 18–19 = 25–26; lateral-line scales 29–31; measurements in % SL: body depth at first dorsal-fin origin 20–22; body depth at anus 18–19; caudal-peduncle depth 9.2–9.6; maximum head depth 18–20; head length 27–30; caudal-fin length 28–30; anal-fin height 14–15; pelvic-fin length 20–21; pectoral-fin length 21; pectoral-fin width 3.9–4.2; first dorsal-fin height 19–20; total bars on caudal fin 5, all on upper caudal-fin lobe, with 4 red bars distally from fork and one red bar close to fin base; lower caudal-fin lobe with a broad carmine stripe bordered by a thin white margin dorsally and by a wider pale margin ventrally; lower caudal-lobe tip black; dorsal fins pale with reddish stripes; fin pigmentation not retained in preserved fish apart from remains of lower caudal-fin lobe tip and upper caudal-fin lobe bars; barbels pale reddish; body and head dorsally reddish, snout reddish, lateral and ventral side of body and head white in fresh fish; entire body uniformly pale beige in preserved fish, with a weak pale brown mid-body band.

Description

Measurements in % SL and counts are given in Table I; morphometric data as ratios of SL for holotype, with data for paratypes in brackets: body elongate, body depth at first dorsal-fin origin 4.5 (4.7–5.0), subequal to pectoral-fin length 4.8 (4.7), body depth at anal-fin origin 5.4 (5.5), caudal-peduncle depth 10 (11), much larger than orbit length 15 (16–17), snout length 8.2 (8.4–9.1), slightly more than twice as long as orbit, head depth across eye 5.1 (5.1–5.5), head length 3.3 (3.6–3.7), larger than maximum depth of body and subequal to caudal-fin length 3.4 (3.4–3.5), barbel length 4.5 (5.9–6.0), pelvic-fin length 4.8 (4.8–5.0), subequal to pectoral-fin length, pectoral-fin width 26 (24–25), first dorsal-fin length 5.3 (4.9–5.0), second dorsal-fin length 6.0 (6.4).

Fresh colour (Figure 1)

Head and body dorsally reddish; body becoming laterally paler and white from about mid body to ventral margin, partly overlain with weak red pigmentation; faint pale rose lateral band from

Table I. Measurements and counts for *Upeneus seychellensis* sp. nov. and the species of the *japonicus* group (morphometric characters in % SL; main differences with *U. seychellensis* are emphasized).

	<i>Upeneus seychellensis</i> sp. nov.			<i>U. guttatus</i>			<i>U. pori</i>			<i>U. australiae</i>			<i>U. asymmetricus</i>			<i>U. francisi</i>		<i>U. japonicus</i>		
	HT	PT1	PT2	Min	Max	<i>n</i>	Min	Max	<i>n</i>	Min	Max	<i>n</i>	Min	Max	<i>n</i>	<i>n</i> = 1	Min	Max	<i>n</i>	
SL (mm)	115	102	96	77	146	44	66	110	5	84	130	12	74	100	4	78	104	115	4	
Body depth at first dorsal-fin origin	22	21	20	22	26	37	21	24	5	23	26	7	22	24	4	24	23	25	4	
Body depth at anal-fin origin	19	18	18	19	23	37	20	22	5	20	23	7	20	22	4	19	19	22	4	
Half body depth (from lateral line downwards) at first dorsal fin origin	19	19	17	17	21	33	18	20	5	17	22	8	19	20	4	18	19	21	3	
Half body depth (from lateral line downwards) at anal fin origin	15	14	14	14	18	33	14	16	5	16	18	8	14	16	4	15	15	17	4	
Caudal-peduncle depth	9.6	9.3	9.2	9.3	11	37	9.1	10	5	10	11	8	8.8	9.9	4	9.9	8.7	10	4	
Caudal-peduncle width	3.6	3.8	4.1	3.2	5.1	37	3.5	3.9	5	3.6	5.0	8	3.7	4.8	4	2.3	3.1	5.7	4	
Maximum head depth	20	19	18	18	23	37	18	20	5	20	22	8	20	20	4	20	20	21	4	
Head depth across a vertical midline through eye	17	15	15	15	19	37	15	16	5	15	19	8	15	16	4	18	16	16	4	
Suborbital depth	10	10	9.2	8.7	12	37	8.9	9.7	5	9.5	13	8	9.4	10	4	8.4	9.1	10	4	
Interorbital length	7.7	6.8	6.7	7.2	9.0	37	7.4	7.9	5	7.3	9.5	8	8.0	9.0	4	7.6	7.2	8.5	4	
Head length	30	28	27	26	30	37	26	28	5	27	30	8	27	29	4	31	28	29	4	
Snout length	12	12	11	9.6	13	37	11	11	5	11	13	8	9.9	11	4	10	11	12	4	
Postorbital length	12	12	12	10	12	36	11	12	5	11	13	8	11	13	4	13	10	12	4	
Orbit length	6.5	6.4	6.0	6.3	8.8	37	6.3	7.8	5	6.1	7.9	8	7.0	7.7	4	8.2	6.8	8.0	4	
Orbit depth	6.2	5.6	5.5	5.2	7.6	37	5.7	7.7	5	5.0	6.6	8	5.6	6.5	4	6.7	5.2	7.2	4	
Upper-jaw length	11	11	11	9.6	12	37	10	11	5	10	12	8	9.6	11	4	12	10	11	4	
Lower-jaw length	11	11	10	9.0	12	37	9.7	10	5	9.2	11	8	9.1	10	4	11	9.6	9.9	4	
Snout width	9.2	8.0	7.3	7.7	11	35	8.0	10	5	8.6	10	6	8.1	9.3	4	7.0	7.7	9.2	4	
Barbel length	22	17	17	16	19	36	16	18	5	17	19	8	18	19	4	18	18	22	4	
Maximum barbel width	0.8	0.7	0.8	0.7	1.0	37	0.6	0.7	5	0.8	1.3	8	0.8	1.0	4	0.8	0.6	0.8	4	
First pre-dorsal length	39	37	38	33	38	37	34	37	5	34	37	8	37	38	4	38	34	37	4	
Second pre-dorsal length	63	64	65	60	67	37	63	65	5	62	64	8	64	66	4	66	63	64	4	
Interdorsal distance	12	14	16	13	17	37	13	16	4	13	16	8	14	16	4	15	15	18	4	
Caudal-peduncle length	24	24	24	22	26	37	22	23	5	22	26	8	22	24	4	23	23	25	4	
Pre-anal length	68	67	65	60	68	37	60	65	5	60	64	8	63	68	4	66	61	67	4	
Pre-pelvic length	33	32	30	28	34	37	28	32	5	30	36	8	32	34	4	33	30	33	4	
Pre-pectoral length	32	30	28	26	32	37	28	30	5	29	32	8	30	31	4	33	27	33	4	
Second dorsal-fin depth (second dorsal-fin origin to anal-fin origin)	19	19	18	19	23	37	20	22	5	20	24	8	19	22	4	20	19	22	4	
Pelvic-fin depth (first dorsal-fin origin to pelvic-fin origin)	23	22	21	22	26	37	22	23	5	23	27	8	22	24	4	24	22	25	4	
Pectoral-fin depth (first dorsal-fin origin to dorsal origin of pectoral fin)	17	16	17	15	18	37	16	17	5	16	18	8	15	17	4	16	14	18	4	
Length of first dorsal-fin base	14	14	14	12	18	37	14	16	4	14	17	8	13	15	4	14	14	17	4	
Length of second dorsal-fin base	13	12	12	11	16	37	13	15	5	13	15	8	13	14	4	11	13	15	4	
Caudal-fin length (dorsal caudal-fin origin to upper caudal-lobe tip)	30	29	28	25	30	37	27	29	4	26	30	7	27	27	4	28	25	27	4	

Table I (Continued)

	<i>Upeneus seychellensis</i> sp. nov.			<i>U. guttatus</i>			<i>U. pori</i>			<i>U. australiae</i>			<i>U. asymmetricus</i>			<i>U. francisi</i>		<i>U. japonicus</i>		<i>n</i>
	HT	PT1	PT2	Min	Max	<i>n</i>	Min	Max	<i>n</i>	Min	Max	<i>n</i>	Min	Max	<i>n</i>	<i>n</i> = 1	Min	Max		
Length of anal-fin base	10	10	9.6	9.3	14	37	12	13	5	11	13	8	10	12	4	12	11	12	4	
Anal-fin height	14	15	15	15	19	36	16	17	5	14	17	7	15	16	2	16	15	18	4	
Pelvic-fin length	21	20	21	19	22	37	20	23	5	20	22	8	20	21	4	24	21	22	4	
Pectoral-fin length	21	21	21	19	22	36	20	22	5	21	24	8	19	21	3	25	24	24	4	
Pectoral-fin width (width of pectoral-fin base)	3.9	3.9	4.2	3.7	5.0	37	4.4	5.7	5	4.2	5.9	8	4.1	5.9	4	4.2	3.7	5.8	4	
First dorsal-fin height	19	20	20	20	24	33	20	21	4	18	21	8	20	20	3	21	21	22	4	
Second dorsal-fin height	17	16	16	14	18	36	15	16	4	14	17	12	15	16	2	16	16	18	4	
Pectoral-fin rays	14	15	15	12	14	44	14	14	5	13	15	12	13	13	4	14	13	15	4	
Rudimentary gill rakers on upper limb	5	4	4	2	5	44	0	2	5	1	4	12	1	4	4	1	2	3	4	
Developed gill rakers on upper limb	2	3	3	2	5	44	6	7	5	2	5	12	3	6	4	8	4	4	4	
Developed gill rakers on lower limb	13	13	13	11	14	44	14	18	5	11	14	12	15	17	4	23	12	16	4	
Rudimentary gill rakers on lower limb	6	5	5	4	6	44	2	5	5	3	5	12	2	5	4	0	4	7	4	
Total gill rakers on upper limb	7	7	7	6	8	44	7	8	5	5	7	12	7	7	4	9	6	7	4	
Total gill rakers on lower limb	19	18	18	16	18	44	18	20	5	16	17	12	19	21	4	23	18	20	4	
Total gill rakers	26	25	25	23	25	44	26	27	5	21	24	12	26	28	4	32	24	27	4	
Scales along lateral line to caudal-fin base	31	29	29	28	31	44	29	30	5	28	31	9	28	29	4	28	28	29	2	



Figure 1. A: *Upeneus seychellensis* sp. nov., holotype, SAIAB 96980, SL 115 mm, and (above) paratype, SAIAB 84280, SL 102 mm, Seychelles Bank (O. Alvheim); B: *Upeneus guttatus*, SAIAB 84281, female, SL 117 mm, and (below) male, SL 111 mm, Seychelles Bank (O. Alvheim).

caudal-fin base to operculum in the region between the dorsally red and ventro-laterally white body areas; paratypes with a few small red patches laterally on body, probably deriving from injuries; head white below a line through orbit parallel to head contour, snout reddish; a few small red patches on white area of head of types; first dorsal fin pale whitish with some tiny patches of red pigmentation, possibly the remains of two to three red stripes, fin tip pale; second dorsal fin pale white with four narrow red stripes; pectoral fins hyaline, rose at base; caudal-fin upper lobe pale whitish, with 4 red bars on lobe itself (lobe tip white in larger fish) and a fifth weaker bar at lobe base; bar width less than width of pale interspaces between bars; lower caudal-fin lobe with three different stripes: a thin white stripe along dorsal margin from fork to close to lobe tip, followed by a broad carmine stripe (> two-thirds of lobe width) from fin base to lobe tip and bordered ventrally by a pale to white ventral margin, wider than the dorsal margin (= about one-fourth of lobe width), running from base to close to lobe tip; lower-caudal-fin lobe tip black; barbels pale reddish.

Preserved colour

Head and body pale beige, belly somewhat darker anteriorly, a pale brown band at mid body from behind operculum to caudal-fin base; operculum

transparent, gill cavity shining through; dorsal, ventral, and pectoral fins hyaline without any pigmentation; caudal fin mostly lacking pigmentation, only fin tip of lower lobe weakly pigmented and some remains of pigmentation deriving from 4 to 5 bars on upper caudal-fin lobes of all three types.

Distribution

Seychelles Bank, Western Indian Ocean.

Etymology

The name of this species '*seychellensis*' derives from the tiny distributional range currently known for this species, which is limited to a single trawling station close to the southeastern edge of the Seychelles Bank.

Comparisons (Table I, Figures 1 and 2)

Upeneus seychellensis differs from *U. guttatus* in more pectoral-fin rays, more gill rakers, more slender body, longer postorbital, lower anal and first dorsal fin, no bars on lower caudal fin lobe and red stripe on lower lobe more conspicuous in fresh fish; from *U. pori* it differs in more total gill rakers, more slender body at anal-fin origin, shorter jaws, longer caudal peduncle, shorter second dorsal-fin base, smaller anal fin, narrower pectoral-fin width, no bars

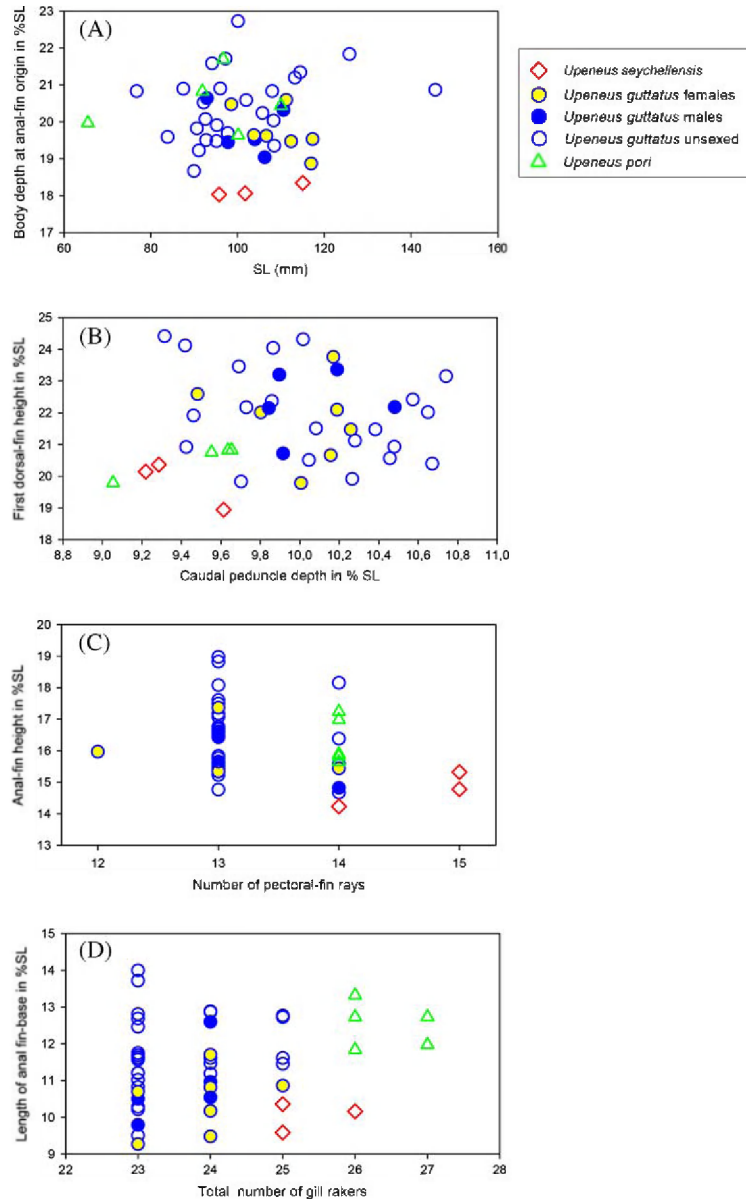


Figure 2. Body depth at anal-fin origin against SL (A), first dorsal-fin height against caudal-peduncle depth (B), anal-fin height against number of pectoral-fin rays (C), and length of anal-fin base against total number of gill rakers (D), in the three Western Indian Ocean species of the *japonicus* group (morphometric variables expressed in % SL).

on lower caudal-fin lobe, and caudal-fin colour patterns not or only very weakly retained in preserved fish; from *U. australiae* it differs in more gill rakers, more slender body and head, thinner barbels, shorter dorsal-fin and anal-fin bases, smaller pectoral fins, and no bars on lower caudal lobe, and bars on upper caudal lobe not or only weakly retained; from *U. asymmetricus* it differs in more pectoral-fin rays, more gill rakers, more slender body, narrower interorbital, longer orbit, longer jaws, smaller anal fin, narrower pectoral fins, no bars on lower caudal-fin lobe, and caudal-fin colour

mostly not retained in preserved fish; from *U. francisi* it differs in fewer gill rakers, shallower body depth at first dorsal-fin origin, shallower head depth through eye, shorter head, longer snout, shorter postorbital, smaller eyes, shorter anal-fin base, and shorter paired fins; and from *U. japonicus* it differs in more slender body and head, shorter second dorsal-fin base, smaller anal fin, lower first dorsal fin, the lower caudal-fin lobe more pointed, usually four vs. three red bars on the upper lobe distally from fork, and the red stripe on the lower caudal-fin lobe not rounded in fresh fish.

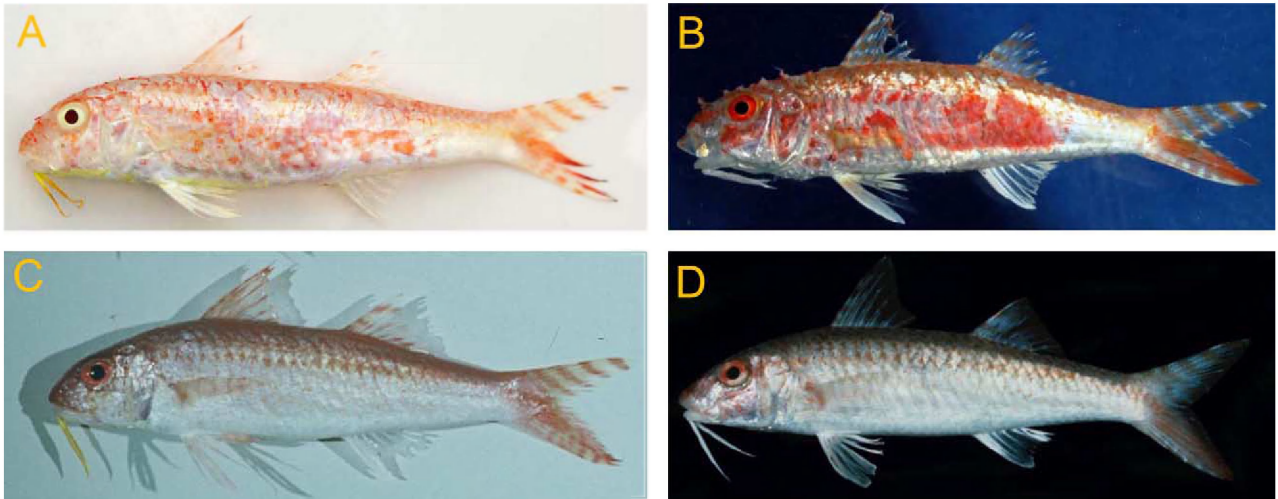


Figure 3. *Upeneus guttatus*: A: SAIAB 84255, female, SL 112 mm, Seychelles Bank (O. Alvheim); B: SAIAB 82714, SL 94 mm, Mozambique (P.C. Heemstra); C: SAIAB 13947, SL 100 mm, Kenya (P.C. Heemstra); D: BPBM 20658, SL 113 mm, Madras, India (J.E. Randall).

Remarks

Upeneus seychellensis sp. nov. is the only species of the *japonicus* group from the Western Indian Ocean which has no bars on the lower caudal-fin lobe, like *U. japonicus*. Its close relationship with *U.*

japonicus is also documented by considerable overlap in morphological characters (Table I). Another closely related species, *U. guttatus*, co-occurs with *U. seychellensis* (see also below).

Upeneus seychellensis attains 12 cm SL; depth 60 m.

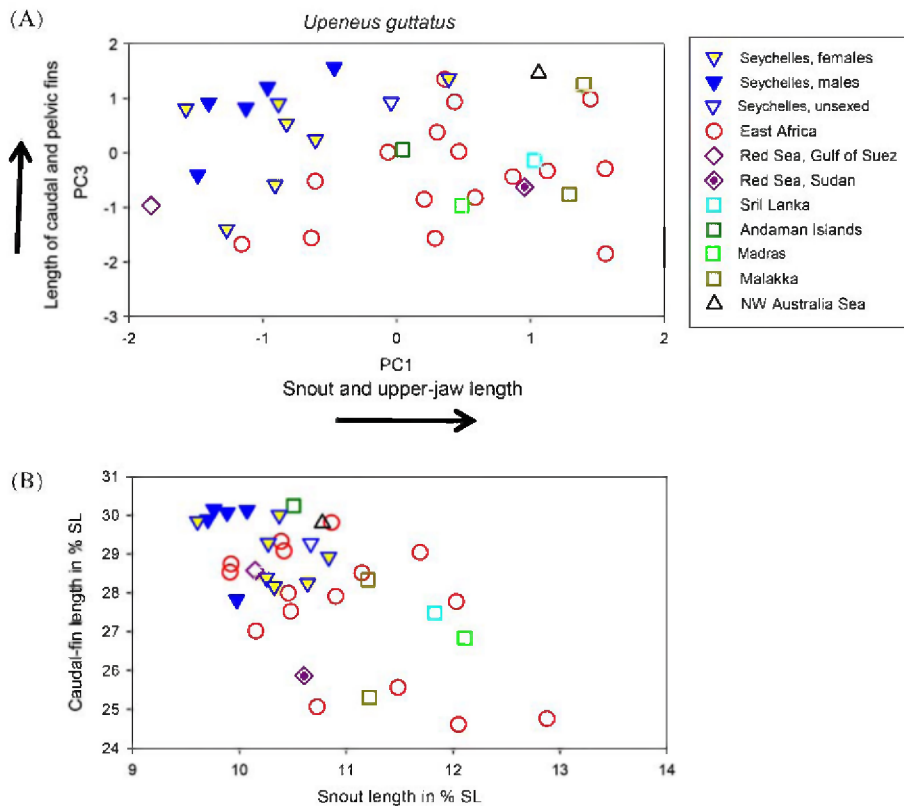


Figure 4. A: Scores of the first and third axis of Principal Component Analysis based on 40 morphometric characters in 37 *Upeneus guttatus* from different areas in the Indian Ocean, with trends for the highest-contributing characters indicated by arrows; B: caudal-fin length against snout length (both variables expressed in % SL).

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Upeneus guttatus (Day 1868)

Two-tone goatfish

(Table I and II, Figures 1 to 4)

Upeneoides guttatus Day, 1868: 938 (type locality: Madras, India).*Upeneus crosnieri* Fourmanoir & Guézé, 1967: 52, figure 1/c (type locality Mitsio, Pracel Bank, Madagascar); Bauchot et al. 1985: 7 (synonym of *Upeneoides guttatus* Day 1868).*Upeneus guttatus*: Randall & Kulbicki 2006: 301, Figures 3 and 4 (diagnosis and two colour photographs).*Upeneus bensasi* (non Temminck & Schlegel, 1843): De Bruin et al. 1994: 270, pl. 9, figure 136 (Sri Lanka).*Upeneus guttatus*: Uiblein & Heemstra 2010: 42–43, tables 3, 4; pl. 1, 3.*Diagnosis*

Dorsal fins VII + 9; pectoral-fin rays 12–14, mostly 13 (in 37 of 44 specimens); gill rakers 6 – 8 + 16 – 18 = 23 – 25; lateral-line scales 28–31; measurements in % SL: body depth at first dorsal-fin origin 22–26; body depth at anus 19–23; caudal-peduncle depth 9.3–11; maximum head depth 18–23; head length 26–30; caudal-fin length 25–30; anal-fin height 15–19; pelvic-fin length 19–22; pectoral-fin length 19–22; pectoral-fin width 3.7–5.0; first dorsal-fin height 20–24; total bars on caudal fin 7–13, upper caudal-fin lobe with 5 (rarely 4) reddish bars with 4 (rarely 3) bars distally from fork and one bar close to fin base, of similar width or narrower than the pale interspaces between bars; 2–8 faint, irregular red bars on exterior margin of lower caudal-fin lobe, sometimes extending to dorsal half of lobe, connecting to a red stripe which covers the lobe dorsally to two-thirds of its width at maximum; caudal-fin lobe bars and stripe fade away post mortem, only traces retained in preserved fish; 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, Madagascar, Réunion, Seychelles, India, Sri Lanka, Andaman Sea, Malaysia, Singapore, Northern Australia, New Caledonia, Philippines.

Comparison

See account of *Upeneus seychellensis* sp. nov. above and Uiblein & Heemstra (2010) for comparisons with all other species of the *japonicus* group.

Remarks

Upeneus guttatus shows considerable geographic variation within the Indian Ocean, both in morphology and colour patterns. The Seychelles Bank individuals can be distinguished from all other areas using Principal Components Analysis (Figure 4A). The first and third principal components show the distinction, explaining 22 and 9% of the total variance, respectively. The characters showing the highest correlations with these two PCA axes reflect a trend towards longer caudal and pelvic fins in combination with shorter snout and upper jaw in the Seychelles Bank population. There is overlap with the single specimen from the Gulf of Suez, northern Red Sea, and one specimen from the East African population. If characters important for the multivariate separation are directly compared (Table II) or plotted singly against each other (Figure 4B), considerably more overlap occurs. No indication for sexual dimorphism was found.

Comparisons of photographs of eight fresh fish from the two Seychelles Bank stations with those of six fish from the East African coast and one from each the Gulf of Suez (Red Sea) and Madras (NE Indian Ocean) revealed that the Seychelles population has fewer lower caudal-fin lobe bars (2–5 vs. 5–8). Because the lower caudal-fin lobe bars are not completely developed and less conspicuous in this species, counting can sometimes be difficult. However, the general presence or absence of these bars can be used to distinguish freshly collected *U. guttatus* from *U. seychellensis*.

The number of upper caudal-fin lobe bars is equal in *U. guttatus* in all areas (four red bars distally of fork, one bar on fin base), except for the single Gulf of Suez specimen which has only four bars on the upper caudal-fin lobe with three bars placed distally of the fork. This specimen has yellow barbels, like seven of the eight photographed Seychelles Bank specimens (barbels not visible in one specimen). Among the seven photographs of freshly collected specimens from other areas (East Africa, Madras) are two with white and five with yellow barbels (Figure 3).

Upeneus guttatus attains 16 cm SL; depth 8–80 m.

Table II. Measurements and counts for the Indian Ocean *Upeneus guttatus* populations (morphometric characters in % SL).

	Seychelles				East-Africa				Red Sea		Sri Lanka	Madras	Andamans	Malacca (n = 2)		NW Australia
	Min	Mean	Max	n	Min	Mean	Max	n	Suez	Sudan	n = 1	n = 1	n = 1	Min	Max	n = 1
SL (mm)	92	107	126	17	87	103	146	19	98	77	84	113	91	97	108	93
Body depth at first dorsal-fin origin	22	23	24	13	22	24	25	16	23	23	24	23	22	24	25	26
Body depth at anal-fin origin	19	20	21	13	19	20	23	16	20	21	20	21	20	21	22	20
Half body depth (from lateral line downwards) at first dorsal fin origin	18	19	21	13	17	19	21	13	18	19	21	21	-	20	20	20
Half body depth (from lateral line downwards) at anal fin origin	15	15	16	13	15	16	18	13	15	16	15	17	-	17	18	17
Caudal-peduncle depth	9.4	10	10	13	9.3	10	11	16	9.5	11	10	10	9.4	10	11	10
Caudal-peduncle width	3.2	3.6	4.2	13	3.5	4.4	5.1	16	3.4	5.1	3.5	3.3	3.4	3.8	4	4
Maximum head depth	19	20	22	13	18	20	21	16	20	19	22	20	20	21	22	23
Head depth across a vertical midline through eye	16	16	19	13	15	16	19	16	15	17	16	16	16	16	16	17
Suborbital depth	9.0	9.6	12	13	8.7	9.8	12	16	8.7	9.9	9.7	11	9.1	9.7	11	10
Interorbital length	7.3	7.6	8.0	13	7.2	7.8	8.4	16	7.3	7.9	8.3	7.8	8.2	8.7	9.0	7.7
Head length	26	27	28	13	26	28	29	16	26	26	29	30	28	28	28	28
Snout length	9.6	10	11	13	9.9	11	13	16	10	11	12	12	11	11	11	11
Postorbital length	10	11	11	13	10	11	12	15	11	11	12	12	11	10	11	11
Orbit length	6.3	6.9	7.8	13	6.4	7.5	8.8	16	7.0	8.2	6.3	6.5	6.3	7.3	7.4	7.2
Orbit depth	5.4	6.0	6.6	13	5.2	6.4	7.6	16	6.1	5.9	6.0	5.8	5.7	6.3	6.9	5.7
Upper-jaw length	9.7	10	12	13	9.6	11	12	16	10	12	11	12	12	11	11	12
Lower-jaw length	9.0	9.7	10	13	9.5	10	12	16	9.6	11	10	11	11	10	11	11
Snout width	7.7	8.5	10	13	7.8	9.0	10	14	8.3	11	10	8.7	10	8.8	10	8.3
Barbel length	16	17	18	13	16	17	19	15	18	16	19	18	18	17	18	19
Maximum barbel width	0.7	0.7	0.9	13	0.7	0.8	1.0	16	0.7	0.8	0.8	0.9	0.8	0.8	0.9	0.9
First pre-dorsal length	33	35	37	13	34	36	38	16	35	38	36	37	37	35	36	35
Second pre-dorsal length	60	63	65	13	61	63	67	16	60	65	63	65	63	62	66	64
Interdorsal distance	15	16	16	13	14	16	17	16	13	17	15	16	16	13	17	17
Caudal-peduncle length	22	24	26	13	22	24	26	16	23	26	24	23	22	22	23	25
Pre-anal length	61	65	67	13	60	63	68	16	64	65	63	64	63	63	65	62
Pre-pelvic length	28	31	34	13	28	31	34	16	31	31	33	33	32	30	32	30
Pre-pectoral length	26	28	30	13	26	29	32	16	28	28	30	32	30	28	30	28
Second dorsal-fin depth (second dorsal-fin origin to anal-fin origin)	20	21	22	13	19	21	23	16	19	21	21	22	20	22	22	21
Pelvic-fin depth (first dorsal-fin origin to pelvic-fin origin)	22	23	25	13	22	24	26	16	22	23	23	24	22	24	24	26
Pectoral-fin depth (first dorsal-fin origin to dorsal origin of pectoral fin)	15	17	18	13	15	16	18	16	15	18	16	17	16	17	18	18
Length of first dorsal-fin base	12	15	16	13	12	15	17	15	14	17	15	13	13	15	17	15
Length of second dorsal-fin base	11	13	14	13	12	14	16	16	12	16	14	13	14	13	14	12
Caudal-fin length (dorsal caudal-fin origin to upper caudal-lobe tip)	28	29	30	13	25	28	30	16	29	26	27	27	30	25	28	30
Length of anal-fin base	9.3	11	13	13	11	12	14	16	11	13	12	10	12	10	11	11
Anal-fin height	15	16	17	13	15	17	19	15	16	17	17	15	17	15	16	16
Pelvic-fin length	19	21	22	13	19	21	22	16	20	21	20	21	22	20	22	21
Pectoral-fin length	19	20	21	13	20	21	22	15	20	21	20	21	22	21	22	20
Pectoral-fin width (width of pectoral-fin base)	3.7	3.9	4.2	13	3.8	4.4	5.0	16	3.9	4.3	4.3	4.6	3.9	4.0	4.7	4.2

Table II (Continued)

	Seychelles			East-Africa			Red Sea		Sri Lanka	Madras	Andamans	Malacca (n = 2)		NW Australia n = 1	
	Min	Mean	Max	Min	Mean	Max	n	Suez	Sudan	n = 1	n = 1	n = 1	Min	Max	n = 1
First dorsal-fin height	20	22	24	13	20	22	24	12	22	20	21	22	22	23	22
Second dorsal-fin height	14	16	17	13	14	16	18	15	16	16	17	16	16	16	15
Pectoral-fin rays	12	13	14	17	13	13	14	19	13	13	14	13	13	13	13
Rudimentary gill rakers on upper limb	2	3.7	5	17	2	3.3	5	19	4	4	3.0	3	3	3	4
Developed gill rakers on upper limb	2	2.7	4	17	2	3.3	5	19	2	3	3.0	2	3	3	2
Developed gill rakers on lower limb	11	12	14	17	11	13	14	19	12	12	12	12	13	13	12
Rudimentary gill rakers on lower limb	4	4.8	6	17	4	4.3	5	19	6	4	5	4	4	4	5
Total gill rakers on upper limb	6	6.4	7	17	6	6.6	8	19	6	7	6	6	6	6	6
Total gill rakers on lower limb	17	17	18	17	16	17	18	19	18	16	17	17	17	17	17
Total gill rakers	23	24	25	17	23	24	25	19	24	23	23	23	23	23	23
Scales along lateral line to caudal-fin base	29	30	31	11	28	29	31	13	29	29	31	30	30	30	30

Discussion

The Seychelles Bank is a large isolated shelf platform in the Indian Ocean surrounded by deep water, only the topographically similar Amirante Plateau and Saya de Malha Bank being relatively close. This biogeographical setting should enhance the potential for high endemism among the shallow-water fish fauna (Allen 2008). However, no clear estimates for the degree of endemism exist for this area due to the lack of a complete species inventory as it has been compiled for instance, for small oceanic islands like La Reunion (Fricke et al. 2009).

The encounter of a new *Upeneus* species on the Seychelles Bank in one of only five bottom trawl hauls may indicate that there are more undescribed fish species on the platform, as it can be also expected for the surrounding slopes and deep-water habitats (Bijoux et al. 2003). Only small subsamples from the trawl hauls were taken, but the inspection of additional photographs and on-board data recordings from the cruise suggest that *U. seychellensis* may be quite abundant close to the southern edge of the bank.

The geographic differentiation of *Upeneus guttatus* between the Seychelles Bank population, the single Gulf of Suez specimen, and the other areas of the Indian Ocean points to micro-evolutionary processes and local adaptation in body form and colour, but phenotypic plasticity needs to be considered, too (e.g. Uiblein 1995, 1996; Uiblein & Nielsen 2005). Earlier comparative morphological studies of the species *Upeneus sundaicus*, *U. sulphureus*, and *U. tragula* and two populations of *U. sulphureus* from Hainan Island, South China Sea, suggested phenotypic plasticity to be an important agent promoting rapid niche expansion and colonization of new habitats (Uiblein et al. 1998). Genetic studies of goatfishes have so far mainly dealt with species differences (see Uiblein 2007 for a review) and detailed investigations of gene flow and phylogeographic relationships among populations are still required.

With this and the two associated studies (Uiblein & Heemstra 2010; Uiblein & Heemstra 2011), we have now completed the taxonomic review of the genus *Upeneus* of the Western Indian Ocean. In total, six new species have been described and evidence for differentiation among populations and ontogenetic stages has been found. An identification key has been developed and comparisons with congeneric species from other ocean regions have been made, focusing on the practical need to base distinctions on a relatively small set of easily identifiable characters and to integrate both fresh and preserved fish. This approach shall now be extended towards other

regional reviews and, ultimately, a revision of the genus.

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