Article

Upeneus floros, a new goatfish from South Africa and Mozambique, with updated taxonomic accounts for *U. guttatus* and *U. pori* and a key to Western Indian Ocean *Upeneus* species (Mullidae)

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Dedication: We dedicate this study to the memory of Dr. Phillip C. Heemstra (1941–2019)

Abstract

The highly diverse goatfish genus *Upeneus* (Mullidae) requires enhanced attention regarding the possible occurrence of undescribed species in insufficiently explored regions. This study focuses on the South-Western Indian Ocean region (SWIO), and on the so-called *japonicus*-group, a taxonomic species group of *Upeneus*. Based on *in-situ* observations and collections in Sodwana Bay, KwaZulu-Natal, South Africa, the Floros goatfish, *U. floros* **n. sp.**, is described. Detailed comparative studies of colour patterns and morphological characters of all other 13 *japonicus*-group species were undertaken as well as COI barcoding. The new species occurs in the coastal area between Angoche, N Mozambique and KwaZulu-Natal and partly overlaps in distribution with two similar species, *U. guttatus,* widely distributed in the Indo-W Pacific, and *U. saiab*, assumed to be endemic in a small area off Angoche. Two additional *japonicus*-group species occurring in the SWIO, *U. seychellensis* from the Seychelles Bank and *U. pori* from the Mediterranean Sea (as Lessepsian migrant), Northern Red Sea and Madagascar, were also compared. Because specimens as well as *in-situ* photographs of *U. floros* have been erroneously identified as either *U. guttatus* or *U. pori* during previous studies, updated taxonomic accounts and diagnoses are provided for these species taking size-related and population differences into account. For *U. pori*, of which a single preserved specimen from SW Madagascar was known so far, a new record from NE Madagascar is reported based on three specimens and a fresh-colour photo. *Upeneus floros* can be distinguished from *U. guttatus* and *U. pori* by a combination of three characters: head length, first dorsal-fin height and number of gill rakers. *Upeneus guttatus* can be distinguished from the other two species by disproportionally higher anterior dorsal-fin spines vs. a proportional decrease of dorsal-fin spines in height, barbels mostly yellow vs. white or creamy-white, and slightly fewer pectoral-fin rays. COI barcoding detected a clear distinction between *U. guttatus* and *U. floros* and *U. pori*, respectively, but no significant divergence between the two latter species. COI barcoding also failed to differentiate several other *Upeneus* species which are clearly distinguished morphologically. Possible interrelationships between species distribution patterns and physical oceanography are discussed. An identification key for the 22 WIO *Upeneus* species is provided.

Key words: Colour patterns; comprehensive and integrative taxonomy; COI barcoding; *in-situ* observation; physical oceanography; population differences

Introduction

The goatfish genus *Upeneus* (Mullidae) is highly diverse, with 42 valid species of which 13 have been included

in the so-called *japonicus*-group (Uiblein *et al.* 2017; 2019). The most distinguishing character of this taxonomic group is the number of dorsal-fin spines. While *japonicus*-group species all have seven dorsal-fin spines (Uiblein & Heemstra 2010; Uiblein & Gledhill 2015; Uiblein *et al.* 2016; 2019), 28 of the other 29 *Upeneus* species have eight spines and the recently described *U. heterospinus* Uiblein & Pavlov, 2019 has either seven or eight dorsal-fin spines (Uiblein *et al.* 2019). The latter species can be distinguished from the *japonicus*-group species in the combination of several morphometric, meristic and colour characters, as well as by geographic distribution (Uiblein *et al.* 2019). The number of species included in the *japonicus*-group has recently increased significantly. Since 2011, seven new species have been described: *U. farnis* Uiblein & Peristiwady, 2017 from Sulawesi, Indonesia, *U. itoui* Yamashita, Golani & Motomura, 2011 from S Japan, *U. lombok* Uiblein & White, 2015 from Lombok, Indonesia, *U. saiab* Uiblein & Lisher, 2013 from N Mozambique, *U. seychellensis* Uiblein & Heemstra, 2011 from the Seychelles Bank, *U. spottocaudalis* Uiblein & Gledhill, 2017 from NE Australia and *U. torres* Uiblein & Gledhill, 2014 from N Australia and Vanuatu. In recent descriptions of *japonicus*-group species the authors concluded that there is a high probability of more undescribed species or unrecorded species in insufficiently studied areas. Hence, exploration of these areas should continue, more specimens should be collected using various methods and from fish markets, colour of live or freshly-deceased fish should be documented, and the available museum material should be thoroughly screened (Uiblein & Lisher 2013; Uiblein & Gledhill 2015; Uiblein & White 2015; Uiblein *et al.* 2017).

In the South-Western Indian Ocean (SWIO), off continental SE Africa, Madagascar, the Mascarenes and the Seychelles, four *japonicus*-group species have been recorded so far, *U. guttatus* Day, 1868, *U. pori* Ben-Tuvia & Golani, 1989, *U. saiab* and *U. seychellensis*. *Upeneus saiab* and *U. seychellensis* are only known from a single locality NE off Angoche, N Mozambique, and the Seychelles Bank, respectively. *Upeneus pori* was originally described from the Northern Red Sea and the SE Mediterranean Sea (as Lessepsian migrant) (Ben-Tuvia & Golani 1989). A single specimen was reported by Uiblein & Heemstra (2010) from Madagascar. *Upeneus guttatus* has the widest distribution of all *japonicus*-group species, occurring from the Western Indian Ocean (WIO) including the Red Sea to Japan and New Caledonia, W Pacific (Randall & Kulbicki 2006). For the SWIO *U. guttatus* was verifiably reported from Madagascar as *U. crosnieri* Fourmanoir & Guézé, 1967, a junior synonym of *U. guttatus* (Bauchot *et al.* 1985, reconfirmed by Uiblein & Heemstra 2010). Uiblein & Heemstra (2010) reported records from Kenya, Mozambique, the Mascarene Islands and the Seychelles, confirming the distribution information provided by Randall & Kulbicki (2006). In addition, Uiblein & Heemstra (2010) reported *U. guttatus* from off KwaZulu-Natal, South Africa, based on a single preserved specimen.

More recently, there have been indications of unrecorded or even undescribed *japonicus*-group species occurring in the SWIO, particularly off KwaZulu-Natal. Uiblein & Lisher (2013) published two *in-situ* images from Sodwana Bay, N KwaZulu-Natal coast, showing shoaling goatfish over sandy bottom near Ribbon Reef. Because the overall colour pattern resembled *U. pori* and recent records of this species from the SWIO (Madagascar), the authors assumed this species was also distributed on the KwaZulu-Natal coast. However, no specimens of the Sodwana Bay population were collected.

Two years later, when comparing populations of *U. guttatus* across its entire range, Uiblein & Gledhill (2015) reported considerable deviations in body form, with longer heads and lower first dorsal fins, in the population from KwaZulu-Natal. Later, colour photographs of two of these specimens, taken shortly after being caught, became available. Goatfishes can change colour significantly when alive and after death (e.g., Uiblein *et al.* 2019), therefore *in-situ* colour documentation (Uiblein & Lisher 2013) and preserved specimens (Uiblein & Heemstra 2010; Uiblein & Gledhill 2015) are necessary to investigate colouration comprehensively.

In April 2017, three specimens were collected with spear-gun in Sodwana Bay. Additional photographs of specimens were made after the catch and tissue samples were taken before the specimens were preserved and incorporated in the SAIAB collection. These specimens and the associated photographs were then studied and compared with the published (see above) and newly generated data. Specific focus was on *japonicus*-group species from the SWIO and adjacent areas by means of a combined comprehensive and integrative taxonomy approach using a large comparative set of morphological data and molecular methods (Uiblein 2016).

Upeneus floros **n. sp.** Uiblein & Gouws is described based on 16 specimens from seven localities in KwaZulu-Natal, South Africa, and three localities in Mozambique. Three additional specimens of *U. pori* are reported from off Madagascar. Updated diagnoses are provided for *U. guttatus* and *U. pori*, which are both rather similar to and co-occur with the new species in the SWIO, and population differences among these species are considered in interspecific comparisons. Furthermore, detailed comparisons among the five SWIO *japonicus*-group species are

provided, along with an overview of the most important diagnostic characters for all species of the *japonicus*-group. The results are discussed with respect to the need to further explore the SWIO region regarding the distribution and local abundance of goatfish species and their biology and ecology with reference to the particular and complex oceanographic conditions in this region.

Finally, for practical use in species identification, an up-to-date identification key of all *Upeneus* species of the WIO is provided.

Material and methods

Morphological and colour studies
In total 276 adult fishes of the *Upeneus japonicus*-species group were studied based on a set of 41 morphometric characters (all in mm, to the nearest second decimal) and 10 meristic characters following Uiblein *et al.* (2016; 2017; 2019). Several colour characters including the presence of a mid-lateral body stripe, oblique bars on the caudal fin lobes, and barbel colour were studied based on photographic or video documentation of live or recently deceased fish (= "fresh-colour photos") and by examining the pigmentation retained in preserved specimens. To consider the widest-possible ranges of meristic characters in interspecific comparisons, data of 24 subadults of three species (four *U. australiae* Kim & Nakaya, 2002, four *U. francisi* Randall & Guézé, 1992 and 16 *U. torres*) were added, after confirming that the respective characters did not show allometry (see Uiblein *et al.* 2017).

The holotype and two paratypes of *U. floros* were collected by speargun in Sodwana Bay with approval of the iSimangaliso Wetland Park Authority from a known shoal of which *in-situ* photographs had been taken shortly before. Photographs of the collected specimens were taken shortly after catch and once again after freezing and defrosting.

Ranges and single values of morphometric characters were rounded to the nearest first decimal for values < 10 mm and larger values were rounded to the first digit. Means of both morphometric and meristic characters were rounded to the first decimal value. Data focused primarily on the three target species *U. floros*, *U. guttatus* and *U. pori*, as well as, *U. saiab* and *U. seychellensis*, which co-occur with *U. floros* in the SWIO, and the rather similar *U. itoui* from Japan. For these and all additional comparisons among *japonicus*-group species data from earlier publications (Uiblein & Heemstra 2011a; Yamashita *et al.* 2011; Uiblein & Lisher 2013; Uiblein *et al.* 2017) were used. In comparisons the terms "mostly" or "slightly" were used for differences in characters that show overlap and hence may require combination with other characters to achieve complete distinction.

An overview table of selected characters gathered from the entire study material was prepared (Table 1) that also allows direct comparisons with the other eight *japonicus*-group species *U. asymmetricus* Lachner, 1954 (Indonesia, Philippines), *U. australiae (*Australia, New Caledonia), *U. farnis, U. francisi* (Norfolk Island, New Zealand), *U. japonicus* (Houttuyn, 1782) (W Malaysia to South Korea, and Peter the Great Bay, Russia), *U. lombok, U. spottocaudalis* and *U. torres*.

For the preparation of the identification key the material and data used for the present work and the following publications by the senior author were considered: Uiblein & Heemstra (2010); Uiblein & Heemstra (2011 a,b); Uiblein & Causse (2013); Uiblein & Lisher (2013); Uiblein & Gouws (2014); Uiblein & Gouws (2015); Uiblein *et al.* (2016); Uiblein *et al.* (2019). Importance was given to provide a key of practical use under field conditions and in scientific collections, e.g. by referring to both fresh and preserved colour patterns important for species diagnostics.

Institutional abbreviations follow Sabaj (2019). Other abbreviations are: EIO = Eastern Indian Ocean; HT = holotype; NRF-SAIAB = National Research Foundation—South African Institute for Aquatic Biodiversity; PT = paratype; SL = standard length; SWIO = South-Western Indian Ocean; WIO = Western Indian Ocean.

Genetic studies
Data from specimens of *Upeneus floros*, some of which had previously been identified as *U. guttatus* from South Africa, and specimens of *U. guttatus* from elsewhere were generated or sourced for this study (Table 2). Data from representatives of seven of the other 12 *japonicus*-group species (*U. asymmetricus, U. australiae, U. japonicus, U. lombok, U. pori, U. spottocaudalis* and *U. torres*), three of the six species of the *margarethae*-group (*U. caudofasciatus* Uiblein & Gledhill, 2019, *U. heterospinus* Uiblein & Pavlov, 2019, and *U. margarethae* Uiblein & Heemstra,

2010; see Uiblein *et al.* 2019), *U. moluccensis* (Bleeker, 1855), *U. subvittatus* (Temminck & Schlegel, 1843) and *U. supravittatus* Uiblein & Heemstra, 2010 were included. For the two WIO japonicus-group species *U. saiab* and *U. seychellensis,* no tissue samples and COI barcoding data were available. Sourced data were downloaded from BOLD Data Systems v4 (Ratnasingham & Hebert 2007), from publicly-available, unpublished data sets and data held in private (NRF-SAIAB) projects (KZNMF, SAIAB and SAIAD) on BOLD, or from GenBank for already-published data (e.g., Bos 2014; Uiblein & Gouws 2014; 2015). Downloaded data were only included if the sequence lengths exceeded 570 nucleotides and if the specimen from which the data were derived had been studied taxonomically (previously or during the course of the present study) or their identifications confirmed by the senior author through the examination of photographs. The compiled data set included genetypes (Chakrabarty 2010), including the hologenetype of *U. floros* and paragenetypes of *U. caudofasciatus*, *U. floros*, *U. heterospinus*, *U. lombok*, *U. spottocaudalis* and *U. torres* (Table 2). As in earlier studies (Uiblein & Gouws 2015; Uiblein *et al.* 2016), sequences of *Mulloidichthys vanicolensis* (Valenciennes, 1831) and *Parupeneus barberinus* (Lacepède, 1801) were used as outgroups.

DNA was extracted using an Invitrogen (Carlsbad, California) PureLink Miniprep kit or a Wizard Genomic DNA Purification (Promega, Madison, Wisconsin) kit, following the manufacturers' protocols, or by Sunnucks & Hales's (1996) protocol. The 'barcoding' (*sensu* Hebert *et al.* 2003) fragment of the cytochrome *c* oxidase subunit I (COI) gene was amplified and sequenced as before (Uiblein & Gouws 2014), using the VF2-t1 (Ivanova *et al.* 2007) and FishR1 (Ward *et al.* 2005), or dgLCO-1490 and dgHCO-2198 (Meyer 2003) primer combinations.

Data were aligned using ClustalX2 (Larkin *et al.* 2007). Phylogenetic analyses were performed in PAUP*4.0a166 (Swofford 2003), using maximum likelihood (ML) and distance-based, neighbour-joining (Saitou & Nei 1987) approaches. Prior to the construction of the ML tree, the optimal model of nucleotide substitution for the data was determined, using jModeltest 2.1.4 (Darriba *et al.* 2011), with competing models evaluated using the Akaike (1974) Information Criterion. Support for nodes was determined using Bayesian Inference in MrBayes 3.2.5 (Ronquist *et al.* 2011). The analysis followed the procedure documented by Uiblein & Gouws (2015), but with sampling of trees and parameters from the posterior distribution every 5000 generations, and with MrBayes estimating the model parameters from an initial parameter-rich General Time Reversible (GTR: Tavaré *et al.* 1986) model. Sequence divergences among representatives, corrected according to the Kimura (1980) two-parameter (K2P) model were calculated in PAUP.

Taxonomy

Genus *Upeneus* Cuvier 1829

***Upeneus floros* n. sp. Uiblein & Gouws**
Floros goatfish
(Figures 1–5, 7; Tables 1–3, 6)
urn:lsid:zoobank.org:act:1543439A-5A2E-44D6-ABC1-DE477C0650F2

Upeneus guttatus Day, 1868, in part: Uiblein & Heemstra 2010; 2011a (Figure 3 B, fresh-colour photograph of *U. floros*); Uiblein & Lisher 2013; Uiblein & Gledhill 2015; 2017
U. pori Ben-Tuvia & Golani, 1989: Uiblein & Lisher 2013, in part (Figure 1 e, f: *in-situ* fresh-colour photographs of *U. floros*)

Material examined. *Holotype,* SAIAB 204583, adult, 105 mm SL, South Africa, SW Indian Ocean, Sodwana Bay, KwaZulu-Natal, Two-Mile Reef, Deep Receiver oceanographic station, 27° 30.735' S, 32° 41.224' E, speargun, 19 m depth, Jade Maggs, 6th April 2017.

Paratypes (n = 12, 90–144 mm SL). SWIO, South Africa, KwaZulu-Natal: SAIAB 51020, 144 mm SL, N of Durban, 29° 39' S, 31° 08' E; SAIAB 62725, 102 mm SL, St. Lucia River Mouth; SAIAB 186410, 2, 113–119 mm SL, off Thukela, 29° 21.82' S, 31° 48.76' E, 70 m depth; SAIAB 186445, 116 mm SL, N of Durban, 28° 40.660' S, 32° 17.470' E, 27 m depth, trawl; SAIAB 188756, 107 mm SL, Park Rynie, 30° 20' S, 30° 45' E; SAIAB 188765, 116 mm SL, St. Lucia, 28° 13.41' S, 32° 32.05' E, 18 m depth; SAIAB 188774, 3, 90–107 mm SL, same data as previous; SAIAB 209539, 2, 94–108 mm SL, same data as HT.

Non-types (n = 4, 92–97 mm SL). SWIO, Mozambique: BPBM 31272, 106 mm SL, NE off Beira, Sofala Bank,

19° 09' S, 36° 20' E, RV *Anton Bruun*, cruise 8, st. 403A, International Indian Ocean Expedition; SAIAB 82794, 93 mm SL, off Inhambane, RV *Dr. Fridtjof Nansen*, st. M07-36, 24° 56.6' S, 35° 03' E, 65 m depth, bottom trawl; SAIAB 188305, 92 mm SL, NE off Angoche, northernmost Sofala Bank, RV *Dr. Fridtjof Nansen*, st. 29, 16° 02.75' S, 40° 20.26' E, 29–40 m depth, bottom trawl; SAM MB-F034156, 1 (of 66), 97 mm SL, off Beira, 19° 49' S, 36° 05' E, bottom trawl.

Fresh-colour photographs of non-examined specimens. In-situ photographs and video footage of several adults and subadults, SWIO, South Africa, KwaZulu-Natal, Sodwana Bay, Two-Mile Reef, Deep Receiver oceanographic station (type locality; C. Floros, M. Mellet, F. Uiblein, C. van Jaarsveld)

Diagnosis. Dorsal fins VII + 9; pectoral fins 13–15; gill rakers 6–7 + 16–18 = 23–25; measurements as % SL: body depth at first dorsal-fin origin 22–25; body depth at anus 19–22; caudal-peduncle depth 8.7–9.8; maximum head depth 19–21; head depth through eye 15–17; head length 29–32; snout length 11–13; orbit length 5.9–7.7; upper jaw length 11–13; barbel length 18–20; caudal-fin length 26–29; anal-fin height 15–18; pelvic-fin length 19–21; pectoral-fin length 19–22; first dorsal-fin height 17–20, dorsal-fin spines proportionally decreasing in height; second dorsal-fin height 15–18; total oblique bars on caudal fin 8–14, upper caudal-fin lobe with 4–6 reddish bars, narrower than the pale interspaces between bars; lower caudal-fin lobe with 4–8 red bars ventrally, connecting dorsally to a broad red stripe, and with 3–4 short dark-grey bars along dorsal margin and a dark fin tip; caudal-fin lobe bars and stripe fade away post mortem, only traces retained when preserved; barbels white when fresh; body colour variable, often white or rose below lateral line, covered by red pigmentation above lateral line which may also reach down ventrally and to head, sometimes forming red patches or blotches; belly white; body pale brown and not dorsally darkened when preserved.

Description. Measurements in % SL and counts are given in Table 3; morphometric data as ratios of SL for holotype, data for paratypes in brackets: body elongate, body depth at first dorsal-fin origin 4.2 [4.0–4.6]; body depth at anal-fin origin 4.5 [4.7–5.1]; head length 3.2 [3.1–3.4], larger than maximum body depth and caudal-fin length (3.7 [3.5–3.9]); first dorsal-fin height 5.1 [5.0–6.1], subequal to barbel length (6.6 [5.1–5.7]) and subequal or only slightly larger than second dorsal-fin height (6.3 [5.5–6.8]; pelvic-fin length 4.9 [4.7–5.3], subequal to pectoral-fin length (4.9 [4.7–5.4]) and body depth at anal-fin origin; caudal-peduncle depth 10 [10–12] larger than orbit length (15 [13–17]); and caudal-peduncle width 25 [22–27], subequal to pectoral-fin width (21 [20–25]).

Colour. *Fresh HT and two PTs collected with HT* (Figure 1A). Head and body ventrally white or silvery white and ventro-laterally pale grey with small pale-brown spots on three horizontal scale rows; indication of a pale-reddish mid-lateral stripe from snout tip to caudal-fin base produced by a red band from snout tip to eye and by two horizontal rows of red spots on operculum behind eye and distally on scales following the lateral line until below second dorsal-fin base and then above lateral line to caudal-fin base; head and body dorsally pale reddish brown, dorsal fins with up to three red stripes, caudal fin with 5–6 oblique red bars on upper fin lobe, 4–5 bars on lobe itself or on lobe tip and one, only weakly visible, bar proximally at lobe base; bars straight or partly curved, their width about half of pupil diameter and half of pale, semitransparent interspaces; ventral third of lower lobe with 5–7 oblique red bars of similar width as bars on upper lobe, connecting to a broad red stripe covering much of the remaining two thirds of lobe; stripe ending in a black lobe tip connected proximally to the mid-lateral body stripe; lower lobe dorsal margin with three very short, dark-grey bars (HT), with a dark margin posteriorly or mostly unpigmented (PTs); paired fins and anal fin mostly pale transparent, apart from some red pigmentation proximally on pelvic fins; barbels white (only slightly visible in one PT).

Thawed HT after freezing (Figure 1B). Head and body ventrally pale whitish and laterally and dorsally carmine red, with four red-brown stripes on each dorsal fin, five oblique red bars on upper caudal-fin lobe and the lower caudal-fin lobe with at least five oblique bars on lower third of lobe, connecting to a carmine red stripe and at least three short dark-grey bars on dorsal lobe margin and a black lobe tip; barbels white; unpaired fins and anal fin pale semitransparent.

Preserved HT. Head and body entirely pale brown, some remnants of pigmentation on dorsal and caudal fins; 5 upper caudal-fin lobe bars partly retained as pale-grey pigmentation, some pale-grey pigmentation remains of lower-lobe ventral and dorsal bars and dark-grey fin tip retained; barbels, paired fins and anal fin pale.

Live fish in situ (Figure 2). Body and head ventrally and ventro-laterally silvery whitish, with a weak rose-marbled pattern laterally, bordered dorsally by a thin rose-orange mid-lateral stripe that reaches from snout through eye (iris dorsally of same colour) to caudal-fin base; head and body dorsally of stripe with dark-reddish pigmentation pattern produced by small red spots on head, dorsal operculum and 3–4 dorsal-most scale rows; sometimes a

nearly vertical red bar of pupil width from below eye to ventral head margin; dorsal fins with 2–3 red-brown stripes and white pigmentation on parts of fins in between stripes and on tips, remaining parts of fins transparent; caudal-fin upper lobe with 3–5 oblique red-brown bars of less than pupil width and interspaces between bars partly transparent or white pigmented; lobe tip also sometimes white pigmented; caudal-fin lower lobe with indications of up to seven brown bars and white interspaces ventrally and white pigmentation dorsally, with a broad dark-red stripe in between and a dark lobe tip visible in some of the photographed or filmed specimens; paired and anal fins whitish semitransparent; barbels white.

Etymology. The name "*floros*" is used as a noun in apposition and acknowledges Dr. Camilla Floros, marine biologist, South African Association for Marine Biological Research -Oceanographic Research Institute, Durban, South Africa (ORI), who organized the collection of the holotype and two paratype specimens and provided photographic documentation of the types as well as of specimens encountered *in situ* at the type locality.

Distribution and size. SWIO from Park Rynie (south of Durban), KwaZulu-Natal, South Africa to Angoche, N Mozambique; 18–70 m depth, mostly on sandy bottoms; attains 144 mm SL.

Remarks. The following lots of *Upeneus floros* had been identified as *U. guttatus* in earlier studies: SAIAB 51020, studied by Uiblein & Heemstra (2010); SAIAB 82794, studied by Uiblein & Heemstra (2010), referred to erroneously as SAIAB 82714 in this and subsequent papers, and documented by a fresh-colour photo in Uiblein & Heemstra (2011a) which is here reproduced (Figure 1C); SAIAB 188305, studied by Uiblein & Lisher (2013) and SAIAB 62725, SAIAB 186410 and SAIAB 188756, studied by Uiblein & Gledhill (2015).
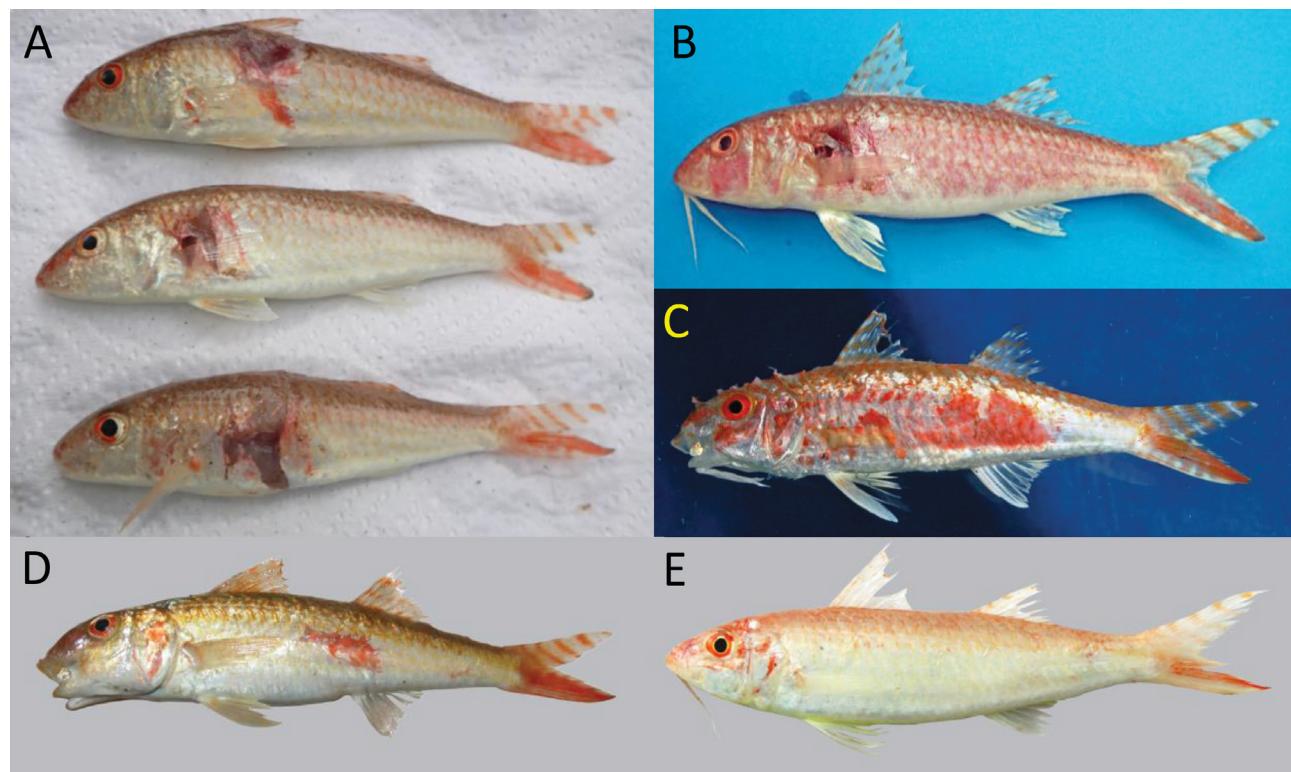
FIGURE 1. (A–C) *Upeneus floros* **n. sp.**, KwaZulu-Natal, South Africa: (A) HT, SAIAB 204583, 107 mm SL (centre) and two PTs, SAIAB 204583, 94 mm SL (top) and 108 mm SL (bottom), shortly after *in-situ* collection near Two Miles Reef, Sodwana Bay (C. Floros); (B) HT, after freezing and thawing (C. Floros); (C) PT, SAIAB 82794, 94 mm SL, Mozambique (P.C. Heemstra); (D) *Upeneus saiab*, HT, SAIAB 188298 , 102 mm SL, NE off Angoche, N Mozambique (M. Lisher); (E) *Upeneus seychellensis,* ca. 110 mm SL, Seychelles Bank (O. Alvheim, D. Tweddle).

In-situ photographs of *Upeneus floros* taken during dives near the type locality were initially identified as *U. pori* by Uiblein & Lisher (2013, Figure 1e, f). The in-*situ* photographs of *U. floros* presented in the current study provide further documentation of colour in life from the type locality (Figure 2). *In-situ* observations made by the senior author at the type locality revealed a large shoal of subadult and small adult *U. floros* associated with the acoustic telemetry receiver mooring (part of the shoal shown in Figure 2D). The shoal of more than 100 individuals moved close to the bottom around the mooring in a stop-and-go behavioural mode, probing the bottom with

the barbels during stops, then slightly lifting above the bottom, swimming a short distance and then probing again. Interestingly, this was the only shoal observed in the area and during the entire dive, which included also a coast-directed transect of at least 50 m into shallower water.

The four specimens from Mozambique are very similar with the types of *U. floros* in all characters and deviate only in having a slightly longer caudal fin and a slightly higher anal fin (Table 3).
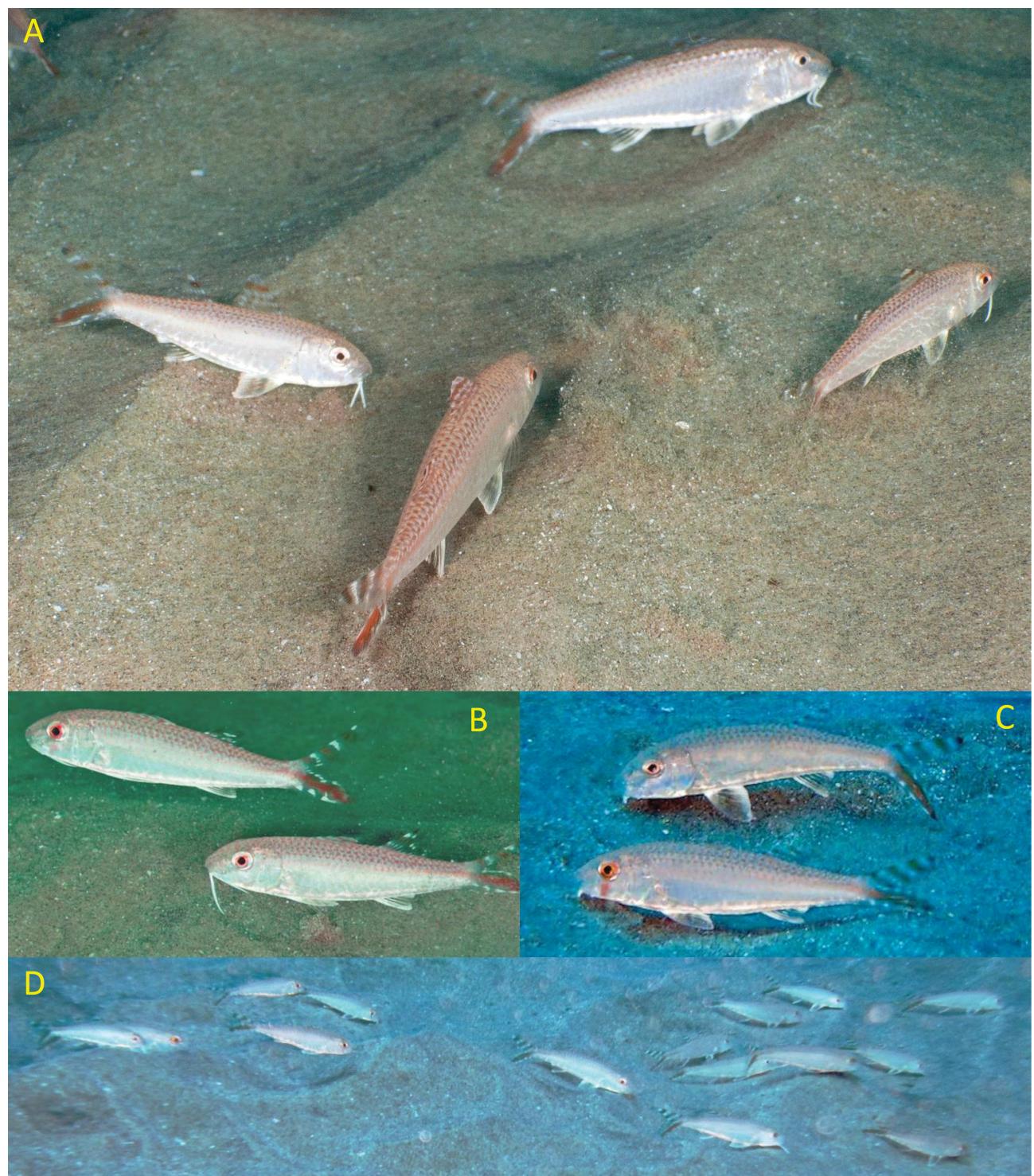
FIGURE 2. *Upeneus floros* **n. sp.**, *in-situ* photographs at Two Mile Reef, Sodwana Bay, KwaZulu-Natal, South Africa. (A, B) adults, ca. 90–100 mm SL (C. Floros); (C, D) small adults or subadults, ca. 60–70 mm SL (C: M. Mellet; D: F. Uiblein).

Upeneus guttatus (Day, 1868)
Two-tone goatfish
(Figures 3–7; Tables 1, 2, 4, 6)

Upeneus guttatus (Day, 1868): Uiblein & Heemstra 2010; 2011a; Motomura *et al*. 2012; Psomadakis *et al*. 2015; 2019; Uiblein
    & Gledhill 2015; Uiblein *et al*. 2016; 2017
U. pori non Ben-Tuvia & Golani, 1989: Khalaf & Disi 1997 (p. 120, fresh-colour photo of specimen from Gulf of Aqaba, Jordan,
    Northern Red Sea)
U. taeniopterus non Cuvier, 1829: Taquet & Diringer 2007 (p. 267, fresh-colour photo)

Diagnosis. Dorsal fins VII + 9; pectoral fins 12–14; gill rakers 5–8 + 16–19 = 22–26; measurements as % SL for adults: body depth at first dorsal-fin origin 21–26; body depth at anus 18–22; caudal-peduncle depth 9.3–11; maximum head depth 18–22; head depth through eye 15–18; head length 26–29; snout length 9.4–12; orbit length 5.9–8.5; upper jaw length 9.5–12; barbel length 16–20; caudal-fin length 27–31; anal-fin height 15–19; pelvic-fin length 19–22; pectoral-fin length 19–22; first dorsal-fin height 20–25, at least one of the first three spines disproportionally higher; second dorsal-fin height 14–18; total oblique bars on caudal fin 7–16 in adults, upper caudal-fin lobe with 5–6 (rarely 4) reddish bars with 4–5 (rarely 3) bars distally from fork and one bar close to lobe base, of similar width or narrower than the pale interspaces between bars; 2–10 often faint, rather short and/or irregularly arranged red bars on ventral margin of lower caudal-fin lobe, sometimes extending to dorsal half of lobe or 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, mostly faded completely when preserved; barbels when fresh usually yellow, rarely white; body colour variable, often white or rose below lateral line, covered by red pigmentation above lateral line which may also reach down ventrally and to head, sometimes forming red patches or blotches; body rarely with a faint red or red-orange mid-lateral stripe from behind eye to caudal-fin base; belly white; body pale brown and not dorsally darkened when preserved.
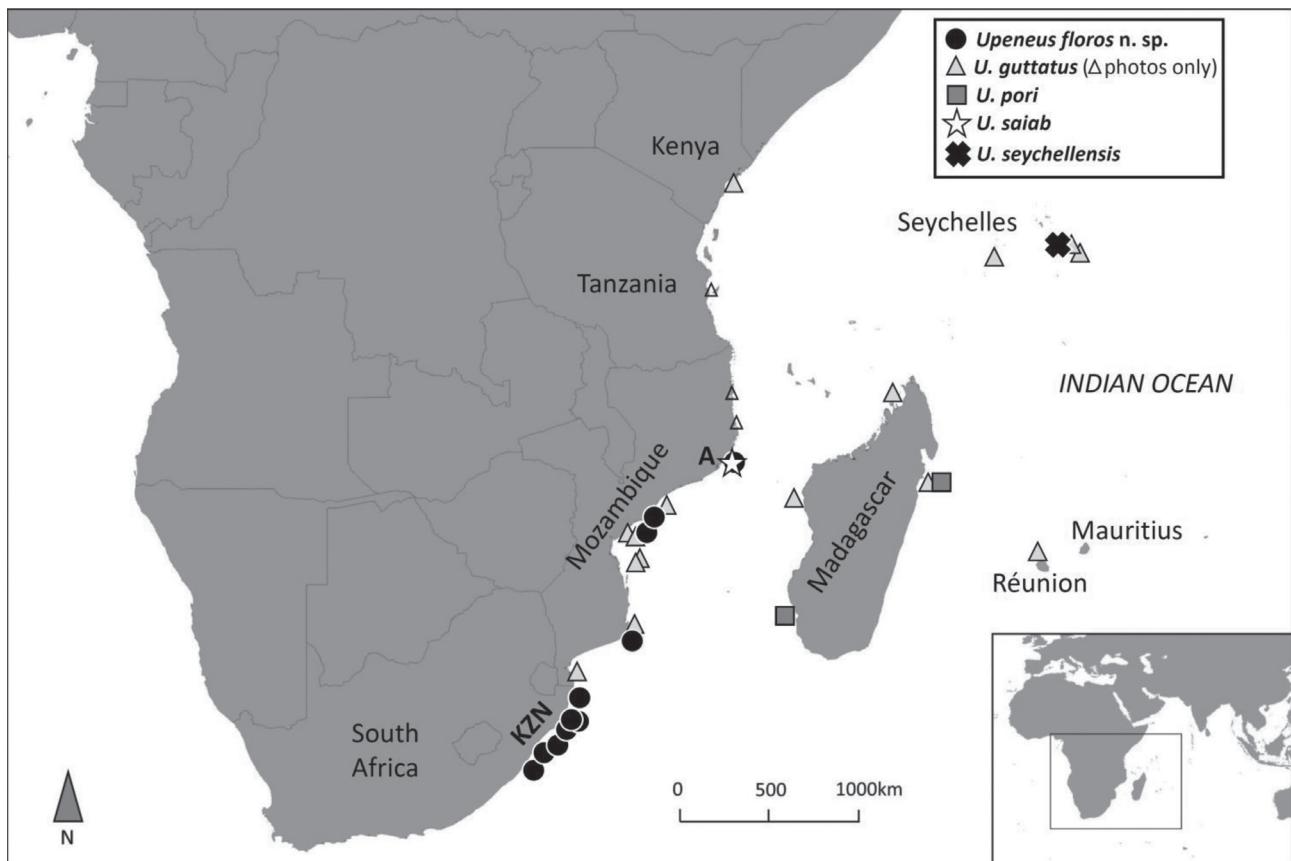
FIGURE 3. Map showing the distribution of the five SWIO *japonicus*-group species based on the studied material. For *Upeneus guttatus* three localities are added which are documented by unvouchered fresh-colour photographs taken *in situ* or shortly after collection (A = Angoche; KZN = KwaZulu-Natal).

Table 1. (A) Number of specimens, SL, meristic and colour characters and (B) morphometric characters in % SL for the *japonicus*-group species.

(A)	n adults (+ subadults)	Maximum size (SL, mm)	Pectoral-fin rays	Gill rakers on lower caudal-fin lobe	Total gill rakers	Body stripe absent/weak/distinctive *	Barbel colour *	Oblique bars on lower caudal-fin lobe *	Caudal-fin bars in preserved fish
U. floros **n. sp.**	17	144	13–15	16–18	23–25	absent or weak	white	present	absent or some traces
U. asymmetricus	8	100	12–14	19–21	26–28	absent or weak	white or pale reddish	present	well retained
U. australiae	45 (+4)	128	13–15	16–18	22–25 [a]	distinctive	white	present	well retained
U. farnis	14	141	15–16	20–22	28–31	weak	pale-grey	mostly absent	absent or some traces
U. francisi	6 (+4)	88 [b]	13–15 [a][b]	21–24 [b]	29–33 [b]	absent	white	present	absent or some traces
U. guttatus	77	159	12–14	16–19	22–26	absent or weak	mostly yellow, rarely white	mostly present	absent or some traces
U. itoui	3	144 [b]	13–14	16–18 [b]	22–25 [b]	distinctive	white	absent	well retained or some traces
U. japonicus	37	123	13–15	18–21	24–28	absent	yellow	absent	absent
U. lombok	3	94	14–15	20–21	27–29	absent	white	absent	absent
U. pori	32	125 [b]	13–15	18–21	25–29	absent, weak or distinctive	white or white-creamy	present	well retained or some traces
U. saiab	6	102	14–15	20–21	29 [a]	absent or weak	white	absent	absent
U. seychellensis	3	115	14–15	18–19	25–26	weak	pale reddish	absent	absent
U. spottocaudalis	16	103	12–13	16–18	22–23	absent or weak	yellow	present	well retained or some traces
U. torres	11 (+16)	101	13–15	16–19 [a]	22–25	weak	yellow	absent	absent

(B)	Body depth at anal-fin origin	Caudal-peduncle depth	Head depth through eye	Head length	Snout 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
U. floros **n. sp.**	19–22	8.7–9.8	15–17	29–32	11–13	11–13	18–20	26–29	15–18	19–21	19–22	17–20	15–18
U. asymmetricus	20–22	8.5–9.9	15–16	26–29	9.9–11	8.7–11	17–19	27–30	15–16	19–22	18–21	19–21	15–17
U. australiae	20–23	9.9–12	15–18	27–30	9.9–13	9.3–12	16–20	27–32	15–18	20–23	19–23	18–23	14–18
U. farnis	20–22	8.8–9.9	15–17	28–31	9.9–12	9.6–12	18–23	27–29	12–15	19–21	18–20	16–20	12–15
U. francisi	20–22	9.9–10	15–16	28–30	10–11	9.9–11	17–19	28–30	15–17	19–22	21–22	20–21	16–18
U. guttatus	18–22	9.3–11	15–18	26–29	9.4–12	9.5–12	16–20	27–31	15–19	19–22	19–22	20–25	14–18
U. itoui	20–21	9.4–9.9	13–14	27–28	11–12	10–11	17–18	28–32 [b]	16–17	18–19	19–20	19–20	16–17
U. japonicus	18–22	8.0–11	15–17	27–31	10–12	9.7–12	18–23	25–29	15–19	19–23	21–25	20–24	15–19
U. lombok	18–19	9.2–9.5	14–16	28–30	9.0–9.6	9.4–9.8	17–20	28–29	12–15	20–22	20–21	19–20	14–16
U. pori	18–22	8.8–10	14–16	26–30	9.5–12	9.9–12	16–19	27–29	14–17	19–23	18–22	18–22	13–17
U. saiab	17–19	8.7–9.2	15–17	29–30	10–11	9.5–12	19–22	27–29	14–16	20–21	20–21	19–22	14–16
U. seychellensis	18–19	9.2–9.6	14–15	27–30	11–12	11	17–22	28–30	14–15	20–21	21	19–20	16–17
U. spottocaudalis	19–22	8.6–10	15–17	30–32	9.7–12	10–13	19–22	28–32	16–19	22–24	19–22	19–22	18–21
U. torres	19–22	8.9–11	15–19	28–31	9.8–12	10–12	24–26	28–30	16–20	20–23	24–26	21–24	16–19

* Fresh fish; [a] data of subadults considered; [b] data from Ben Tuvia & Golani (1989), Randall & Guézé (1992) and Yamashita *et al.* (2011) considered

TABLE 2. Sources and accession details (GenBank accession numbers and/or BOLD process IDs), details of voucher specimens and confirmations of identification for representatives of fourteen species of *Upeneus* and representatives of the outgroups *Mulloidichthys vanicolensis* and *Parupeneus barberinus* used in the cytochrome *c* oxidase subunit I (COI) mtDNA genetic study. The hologenetype (H) of *U. floros* **n. sp.** and the paragenetypes (P) of other species are indicated, where applicable.

Species	GenBank[1]	BOLD Process ID	Locality	Voucher	Sequence source	Vouchers examined
Upeneus asymmetricus	HQ564359	FOAK907-10	Tanjung Luar, Lombok, Indonesia	CSIRO H 7417-02	BOLD public data	Uiblein & White (2015)
	-	FOAK909-10	Tanjung Luar, Lombok, Indonesia	MZB 22711	BOLD public data	Uiblein & White (2015)
Upeneus australiae	-	FOAOI716-19	NE of Broad Sound, Queensland, Australia	CSIRO H 7690-02	BOLD public data	This study (preserved-colour photograph)
	-	FOAOI717-19	Torres Strait, NE of Cape York, Queensland, Australia	CSIRO H 6927-03	BOLD public data	This study (preserved-colour photograph)
Upeneus caudofasciatus	(P)	FOAI620-09	NE of Cooktown, Queensland, Australia	CSIRO H 6519-21	BOLD public data	Uiblein *et al.* (2019)
Upeneus floros **n. sp.**	MT348768 (H)	-	Two Mile Reef, Sodwana Bay, South Africa	SAIAB 204583	This study	This study
	KF489798 (P)	DSFSG461-11	Park Rynie, KwaZulu-Natal, South Africa	SAIAB 188756	BOLD public data	Uiblein & Gledhill (2015); This study
	KF489800 (P)	DSFSG510-11	St Lucia, KwaZulu-Natal, South Africa	SAIAB 188774-1	BOLD public data	Uiblein & Gledhill (2015); This study
	KF489799 (P)	DSFSG614-11	St Lucia, KwaZulu-Natal, South Africa	SAIAB 188774-3	BOLD public data	Uiblein & Gledhill (2015); This study
	KF489796 (P)	DSFSG634-11	St Lucia, KwaZulu-Natal, South Africa	SAIAB 188774-2	BOLD public data	Uiblein & Gledhill (2015): This study
	KF489797 (P)	DSFSG708-11	St Lucia, KwaZulu-Natal, South Africa	SAIAB 188765	BOLD public data	This study
	- (P)	KZNMF014-12	NE of Durban, KwaZulu-Natal, South Africa	SAIAB 186445	BOLD unpublished data	This study
Upeneus guttatus	HM422398	FOAI621-09	NE of Cooktown, Queensland, Australia	CSIRO H 6519-18	BOLD public data	Uiblein & Gledhill (2015); this study
	-	FOAOI252-18	N of Cape Lambert, Western Australia	CSIRO H 8223-05	BOLD public data	This study (fresh-colour photograph)
	-	FOAOI392-18	NE of Montebello Island, Western Australia	CSIRO H 8295-01	BOLD public data	This study (fresh-colour photograph)
	-	FOAOI718-19	Torres Strait, S of Dalrymple Island, Queensland, Australia	CSIRO H 7693-02	BOLD public data	This study (preserved-colour photograph)
	-	FOAOI719-19	Torres Strait, NE of Bramble Cay, Queensland, Australia	CSIRO H 6736-07	BOLD public data	This study (preserved-colour photograph)
	-	FOAOI720-19	NE of Hinchinbrool Island, Queensland, Australia	CSIRO H 6752-04	BOLD public data	This study (preserved-colour photograph)
	MT348769	-	Bay of Bengal, off Myanmar	SAIAB 203675	This study	Uiblein *et al.* (2017); this study

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TABLE 2. (Continued)

Species	GenBank[1]	BOLD Process ID	Locality	Voucher	Sequence source	Vouchers examined
	MT348770	-	Bay of Bengal, off Myanmar	SAIAB 203668	This study	Uiblein *et al.* (2017); this study
	MT348771	-	Nha Trang, Vietnam	HIFIRE 58 154	This study	Uiblein & Gledhill (2015); this study
Upeneus heterospinus	MT348772 (P)	-	Nha Trang, Vietnam	HIFIRE 58 110	This study	Uiblein *et al.* (2019)
Upeneus lombok	HM902439 (P)	FOAJ836-09	Tanjung Luar, Lombok, Indonesia	MZB 22710	BOLD unpublished data	Uiblein & White (2015)
Upeneus japonicus	HQ564529	FOAL207-10	Hong Kong, China	CSIRO H 7072-10	BOLD unpublished data	Uiblein & Gledhill (2015)
	HQ564530	FOAL208-10	Hong Kong, China	CSIRO H 7072-11	BOLD unpublished data	Uiblein & Gledhill (2015)
	MT348773	-	Nha Trang, Vietnam	HIFIRE 58 151	This study	Uiblein & Gledhill (2015)
Upeneus margarethae	KC147802	-	Mazizini, Zanzibar, Tanzania	SAIAB 87108-1	Uiblein & Gouws (2014)	Uiblein *et al.* (2019)
	MT348774	-	Andaman Sea, S of Buda Island, Myanmar	SAIAB 203672	This study	Uiblein *et al.* (2019)
	MT348775	-	Andaman Sea, off Myanmar	SAIAB 203480	This study	Uiblein *et al.* (2019)
Upeneus moluccensis	-	SAIAB810-08	Tanga, Tanzania	SAIAB 80433-1	Uiblein & Gouws 2015	Uiblein & Gouws 2015
	HQ972732	SAIAD185-10	Malindi landing site, Zanzibar, Tanzania	SAIAB 87080-3	Uiblein & Gouws 2015	Uiblein & Gouws 2015
Upeneus pori	-	BIM097-13	Mediterranean Sea, Haifa, Israel	SMNHTAU P. 14910	Unpublished (BOLD public)	This study (fresh photograph)
	-	BIM098-13	Mediterranean Sea, Nitzanim, Israel	SMNHTAU P. 14703	Unpublished (BOLD public)	This study (fresh-colour photograph)
	KF564319	-	Mediterranean Sea, Nitzanim, Israel	SMNHTAU P. 14829	Bos (2014) (BOLD public)	This study (fresh-colour photograph)
Upeneus spottocaudalis	(P)	FOAO1701-19 (GT)	E of Newcastle Bay, Queensland, Australia	CSIRO H 7642-02	Unpublished (BOLD public)	Uiblein *et al.* (2017)
	- (P)	FOAO1703-19 (GT)	E of Shelburne Bay, Queensland, Australia	CSIRO H 6799-02	Unpublished (BOLD)	Uiblein *et al.* (2017)
Upeneus supravittatus	KR057891	-	Karachi area, Pakistan	SAIAB 200573-1	Uiblein & Gouws (2015)	Uiblein & Gouws (2015)
	KP293724	-	Negombo, Sri Lanka	SAIAB 187367-20	Uiblein & Gouws (2015)	Uiblein & Gouws (2015)
Upeneus cf. *subvittatus*	MT348776	-	Andaman Sea, off Myanmar	SAIAB 208593	This study	F. Uiblein (unpublished data)
Upeneus torres	- (P)	FOAG1012-08 (GT)	W of Shark Bay, Western Australia	CSIRO H 6452-04	Unpublished (BOLD public)	Uiblein & Gledhill (2015)
	- (P)	FOAH627-08 (GT)	E of Saibai Island, Torres Strait, Queensland, Australia	CSIRO H 7202-01	Unpublished (BOLD public)	Uiblein & Gledhill (2015)
Outgroups						
Mulloidichthys vanicolensis	HQ972716	SAIAD168-10	Malindi, Zanzibar, Tanzania	SAIAB 87073-1	BOLD (SAIAB)	This study (fresh-colour photograph)
Parupeneus barberinus	HM382708	SAIAB1171-10	Chwaka Bay, Zanzibar, Tanzania	SAIAB 86951-1	BOLD (SAIAB)	F. Uiblein (unpublished data)

[1]In cases where BOLD has mined GenBank data and this is indicated as such on BOLD, the GenBank accession number is provided as the primary source or reference point, and the BOLD Process ID is not reported.

TABLE 3. Morphometric and meristic characters for *Upeneus floros* **n. sp.**, *U. saiab* and *U. seychellensis*.

| Morphometric characters | *Upeneus floros* **n. sp.** | | | | | | | | | | | | | *U. saiab* | | | | *U. seychellensis* | | | |
| | HT + 12 PTs, South Africa | | | | | Non-types, Mozambique | | | | All fish | | | | HT + PTs pooled | | | | HT + PTs pooled | | | |
	HT	Min	Mean	Max	n	Min	Mean	Max	n	Min	Mean	Max	n	Min	Mean	Max	n	Min	Mean	Max	n
SL	107	90	107.6	144	12	92	96.9	106	4	90	105.0	144	17	70	83.6	102	6	96	104.2	115	3
in % SL																					
Body depth at first dorsal-fin origin	24	22	23.5	25	12	23	23.9	25	4	22	23.6	25	17	21	22.0	24	6	20	21.2	22	3
Body depth at anal-fin origin	22	19	20.4	21	12	20	20.5	21	4	19	20.5	22	17	17	18.4	19	6	18	18.2	19	3
Half body depth at first dorsal-fin origin	19	18	19.4	21	12	19	19.0	20	4	18	19.3	21	17	16	17.6	19	5	17	18.1	19	3
Half body depth at anal-fin origin	16	15	16.1	17	11	15	16.0	18	3	15	16.1	18	15	13	14.2	15	6	14	14.2	15	3
Caudal-peduncle depth	9.5	8.7	9.4	9.8	12	9.3	9.6	9.7	4	8.7	9.4	9.8	17	8.7	8.9	9.2	6	9.2	9.4	9.6	3
Caudal-peduncle width	4.0	3.7	4.1	4.6	12	4.3	4.4	4.8	4	3.7	4.2	4.8	17	3.0	3.6	3.9	6	3.6	3.8	4.1	3
Maximum head depth	20	19	19.8	21	12	20	19.9	20	4	19	19.8	21	17	18	19.5	20	6	18	19.1	20	3
Head depth through eye	16	15	15.8	17	12	16	16.4	17	4	15	15.9	17	17	15	16.0	17	6	15	15.7	17	3
Suborbital depth	9.7	8.7	9.6	10	12	9.7	9.8	10	4	8.7	9.7	10	17	8.4	9.5	11	6	9.2	9.8	10	3
Interorbital length	7.9	7.1	7.6	8.2	12	7.0	7.4	7.8	4	7.0	7.5	8.2	17	7.0	7.6	8.2	6	6.7	7.1	7.7	3
Head length	31	29	30.3	32	12	29	29.7	30	4	29	30.2	32	17	29	29.6	30	6	27	28.3	30	3
Snout length	12	11	11.5	13	12	11	11.9	12	4	11	11.6	13	17	10	10.4	11	6	11	11.7	12	3
Postorbital length	13	11	12.2	13	12	11	12.0	12	4	11	12.2	13	17	12	12.7	13	6	12	11.8	12	3
Orbit length	6.6	5.9	7.0	7.7	12	6.6	7.1	7.3	4	5.9	7.0	7.7	17	6.8	7.1	7.5	6	6.0	6.3	6.5	3
Orbit depth	6.3	5.4	6.1	6.8	12	5.6	6.1	6.6	4	5.4	6.1	6.8	17	6.2	6.6	7.0	6	5.5	5.7	6.2	3
Upper-jaw length	12	11	11.6	13	12	11	11.6	12	4	11	11.6	13	17	9.5	10.5	12	6	11	11.0	11	3
Lower-jaw length	12	10	11.0	12	12	10	10.9	12	4	10	11.0	12	17	8.9	9.7	11	6	10	10.5	11	3
Snout width	9.1	7.9	8.7	9.6	12	8.7	8.9	9.3	4	7.9	8.8	9.6	17	7.5	8.0	8.5	6	7.3	8.2	9.2	3
Barbel length	18	18	18.6	20	12	18	18.5	20	4	18	18.5	20	17	19	19.9	22	6	17	18.7	22	3
Maximum barbel width	0.9	0.8	0.9	1.1	12	0.7	0.9	1.1	4	0.7	0.9	1.1	17	0.9	0.9	1.0	6	0.7	0.8	0.8	3
First pre-dorsal length	38	36	37.6	39	12	37	37.6	38	4	36	37.6	39	17	37	37.4	38	6	37	38.0	39	3
Second pre-dorsal length	65	64	64.9	67	12	65	66.4	67	4	64	65.3	67	17	64	65.4	68	6	63	64.0	65	3
Interdorsal distance	17	15	16.2	17	12	16	16.1	17	4	15	16.2	17	17	14	14.9	16	6	12	14.1	16	3
Caudal-peduncle length	22	22	23.2	25	12	23	23.2	24	4	22	23.1	25	17	22	23.0	24	6	24	23.9	24	3
Pre-anal length	65	64	65.4	68	12	65	65.8	68	4	64	65.4	68	17	65	66.1	67	6	65	66.6	68	3
Pre-pelvic length	31	30	31.8	33	12	30	32.1	34	4	30	31.8	34	17	32	33.3	35	6	30	31.7	33	3

TABLE 3. (Continued)

	Upeneus floros n. sp.													U. saiab				U. seychellensis			
	HT + 12 PTs, South Africa					Non-types, Mozambique				All fish				HT + PTs pooled				HT + PTs pooled			
	HT	Min	Mean	Max	n	Min	Mean	Max	n	Min	Mean	Max	n	Min	Mean	Max	n	Min	Mean	Max	n
Pre-pectoral length	31	29	31.1	32	12	29	30.6	32	4	29	30.9	32	17	31	31.7	33	6	28	29.9	32	3
Second dorsal-fin depth	23	20	21.1	22	12	20	21.3	22	4	20	21.2	23	17	17	18.4	19	6	18	18.7	19	3
Pelvic-fin depth	24	22	23.3	25	12	23	23.9	25	4	22	23.5	25	17	20	21.4	23	6	21	21.7	23	3
Pectoral-fin depth	17	16	16.3	17	12	16	16.5	17	4	16	16.4	17	17	14	14.7	16	6	16	16.6	17	3
Length of first dorsal-fin base	14	14	14.9	16	12	15	15.3	17	4	14	14.9	17	17	14	15.2	16	6	14	13.8	14	3
Length of second dorsal-fin base	15	13	14.1	15	12	13	13.1	14	4	13	13.9	15	17	13	13.9	15	6	12	12.5	13	3
Caudal-fin length	27	26	27.1	28	7	28	28.6	29	4	26	27.6	29	12	27	27.9	29	6	28	29.1	30	3
Length of anal-fin base	11	11	11.5	12	12	12	11.8	12	4	11	11.6	12	17	11	11.7	13	6	9.6	10.0	10	3
Anal-fin height	17	15	15.8	17	10	16	16.8	18	4	15	16.1	18	15	14	15.2	16	6	14	14.8	15	3
Pelvic-fin length	20	19	19.8	21	12	20	20.4	21	4	19	20.0	21	17	20	20.9	21	6	20	20.6	21	3
Pectoral-fin length	20	19	19.9	21	11	20	20.5	22	4	19	20.1	22	16	20	20.7	21	6	21	21.1	21	3
Pectoral-fin width	4.7	4.0	4.4	5.1	12	4.4	4.7	5.0	4	4.0	4.5	5.1	17	4.4	4.6	5.0	6	3.9	4.0	4.2	3
First dorsal-fin height	20	17	17.9	20	12	19	19.0	19	4	17	18.3	20	17	19	20.6	22	6	19	19.8	20	3
Second dorsal-fin height	16	15	15.6	18	11	16	16.8	18	4	15	15.9	18	16	14	15.5	16	6	16	16.0	17	3
Meristic characters																					
Pectoral-fin rays	14	13	13.9	15	12	13	13.8	14	4	13	13.9	15	17	14	14.8	15	6	14	14.7	15	3
Rudimentary gill rakers on upper limb	1	1	3.2	4	12	1	2.3	3	4	1	2.8	4	17	1	2.2	3	6	4	4.3	5	3
Developed gill rakers on upper limb	6	2	3.8	6	12	4	4.5	5	4	2	4.1	6	17	5	6.0	7	6	2	2.7	3	3
Developed gill rakers on lower limb	14	12	13.1	14	12	13	13.5	14	4	12	13.2	14	17	15	16.5	17	6	13	13.0	13	3
Rudimentary gill rakers on lower limb	4	3	4.3	5	12	3	3.8	4	4	3	4.2	5	17	3	4.3	6	6	5	5.3	6	3
Total gill rakers on upper limb	7	6	6.9	7	12	6	6.8	7	4	6	6.9	7	17	8	8.2	9	6	7	7.0	7	3
Total gill rakers on lower limb	18	16	17.4	18	12	17	17.3	18	4	16	17.4	18	17	20	20.8	21	6	18	18.3	19	3
Total gill rakers	25	23	24.3	25	12	23	24.0	25	4	23	24.3	25	17	29	29.0	29	6	25	25.3	26	3
Scales along lateral line	30	28	29.4	30	7	28	28.0	28	2	28	29.2	30	10	29	29.3	30	4	29	29.7	31	3

Measurements as % SL for subadults (from Uiblein & Gledhill 2015): body depth at first dorsal-fin origin 22–26; body depth at anus 18–21; caudal-peduncle depth 8.4–9.6; maximum head depth 21–23; head depth through eye 18–19; head length 29–32; orbit length 7.8–9.0; upper jaw length 11–13; barbel length 19–21; caudal-fin length 31–33; anal-fin height 17–20; pelvic-fin length 21–23; pectoral-fin length 22–23; first dorsal-fin height 19–24; second dorsal-fin height 17–19.

Distribution and size. Indo-W Pacific, from S Mozambique and the Red Sea to Japan, N Australia and New Caledonia; 8–165 m depth; attains 160 mm SL.

Remarks. The WIO population of *Upeneus guttatus* does not show any marked differences in morphometric and meristic characters from the EIO and W Pacific Ocean populations (Table 4).
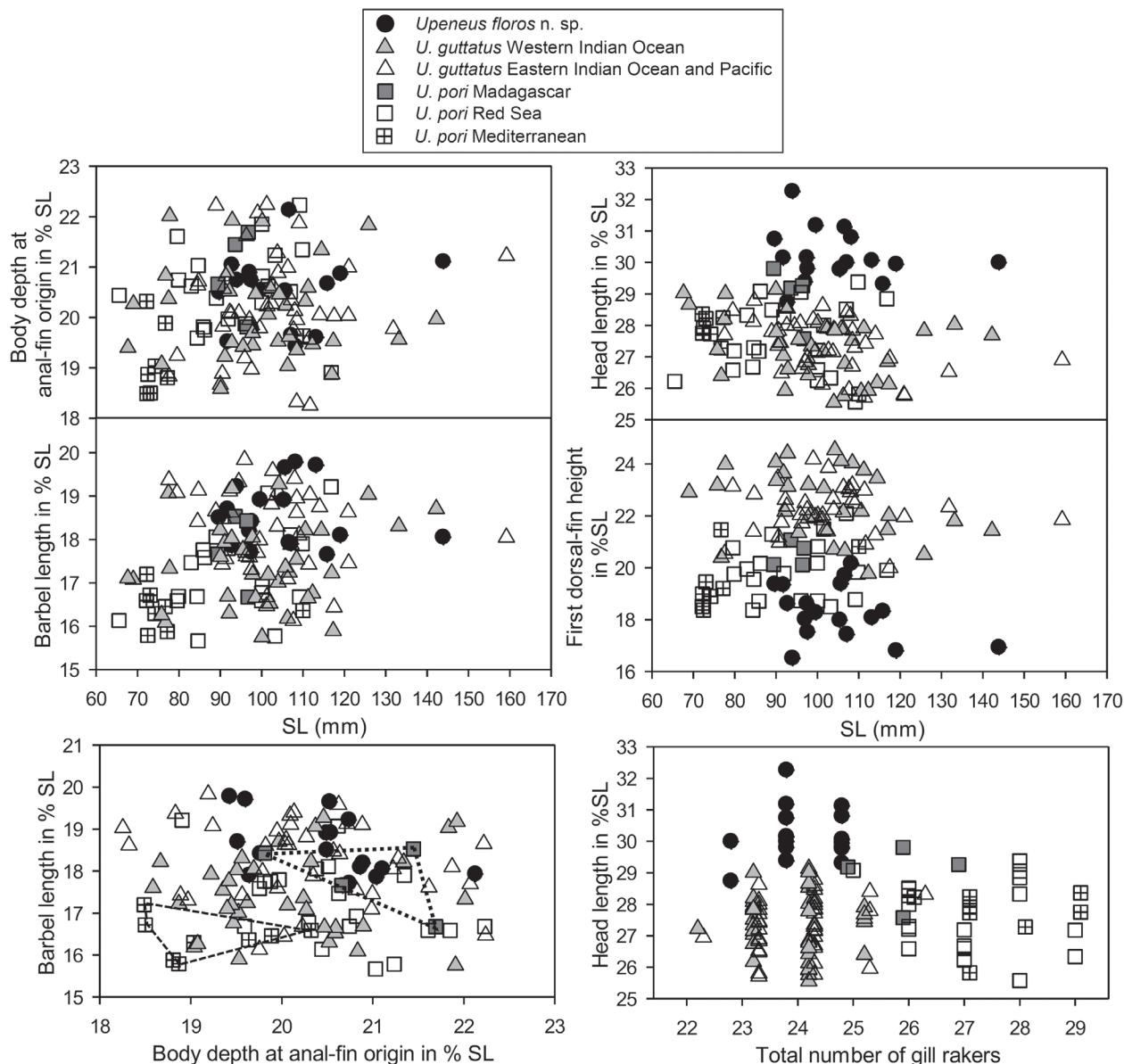
FIGURE 4. Relationships between SL, four morphometric characters, and total number of gill rakers in *Upeneus floros* **n. sp.** and *U. guttatus* and *U. pori* populations. The bottom left diagram includes dashed and dotted outlines for specimens of the Mediterranean Sea and Madagascar, respectively.

Motomura *et al.* (2012) examined one of the syntypes of *U. guttatus* (AMS I.25, Madras = Chennai, E India), and gave a head length of 28.8 % SL and a count of 22 total gill rakers. These data fall within the ranges given in our study (Table 4). As recorded by Day (1868) in his original description of *U. guttatus*, the second spine of the first dorsal fin was highest in the specimen he examined. Our inspection of photographs of the syntype revealed that this spine is rather high, but its tip is broken (Figure 6A). Hence, first dorsal-fin height, an important diagnostic charac-

ter for *U. guttatus*, cannot be accurately determined. One can however assume that – when still intact—the second spine of the dorsal fin was indeed highest in the syntype. Our own studies indicate that at least one of the first three spines is disproportionally higher in *U. guttatus*.

Barbel colour, an important diagnostic character for many *Upeneus* species, is mostly yellow in *U. guttatus*. White barbel colour is currently only documented in a fresh-colour photograph of a single specimen from the type locality (Madras) published by Randall & Kulbicki (2006). Day (1868) did not provide any information on barbels. In their description of *U. crosnieri*, a junior synonym of *U. guttatus*, Fourmanoir & Guézé (1967) recorded white barbels to occur. To our knowledge, no verifiable evidence of *U. guttatus* showing white barbels is currently available for the WIO and Red Sea.

The fresh-colour photograph of a 140 mm SL specimen from the Gulf of Aqaba, Jordan (Northern Red Sea) identified by Khalaf & Disi 1997 as *U. pori* is a misidentification of *U. guttatus*. The photograph included in the species account of *U. taeniopterus* by Taquet & Diringer (2007) also shows a *U. guttatus* specimen. Typical characteristics of *U. guttatus* shown in both photographs are a high dorsal fin, with two of the first three spines disproportionally higher, bars along the ventral margin of the lower-caudal-fin lobe and yellow barbels.

Upeneus pori Ben Tuvia and Golani, 1989
Por's goatfish
(Figures 3–7; Tables 1, 2, 5, 6)

Upeneus pori Ben Tuvia and Golani, 1989: Uiblein & Heemstra 2010; 2011a; Yamashita *et al.* 2011; Uiblein & Lisher 2013; Uiblein & Gledhill 2015; Uiblein *et al.* 2016; 2017

Diagnosis. Dorsal fins VII + 9; pectoral fins 13–15; gill rakers 7–8 + 18–21 = 25–29; measurements as % SL: body depth at first dorsal-fin origin 21–24; body depth at anus 18–22; caudal-peduncle depth 8.8–10; maximum head depth 18–21; head depth through eye 14–16; head length 26–30; snout length 9.5–12; orbit length 5.8–7.8; upper jaw length 9.9–12; barbel length 16–19; caudal-fin length 27–29; anal-fin height 14–17; pelvic-fin length 19–23; pectoral-fin length 18–22; first dorsal-fin height 18–22, dorsal-fin spines proportionally decreasing in height; second dorsal-fin height 13–17; total bars on caudal fin 11–16 in adults, upper caudal-fin lobe with 5–6 reddish or red-brown bars with 4–5 (rarely 3) bars distally from fork and one bar close to lobe base, mostly narrower than the pale interspaces between bars; 5–9 red, red-brown or grey bars on ventral half side of lower lobe, extending to a broad red, brown or dark-grey stripe along middle of lobe; 3–4 red, red-brown or grey bars on inner, dorsal third of lower caudal-fin lobe; caudal-fin bar pigmentation often retained when preserved; fresh fish sometimes with a faint or (in life) conspicuous red or red-brown mid-lateral stripe from snout through eye to caudal-fin base, not retained in preservative; barbels white or creamy white in fresh fish; head and body colour white, pale grey or pale yellow ventrally and red brown or grey dorsally; belly white; body pale brown ventrally and often dorsally darkened when preserved.

Distribution and size. Mediterranean Sea (as Lessepsian migrant), Northern Red Sea and Madagascar, WIO; shallow littoral to 52 m depth; attains 140 mm SL.

Remarks. The Mediterranean population shows a slightly shallower body at anal-fin origin than the Northern Red Sea population and the four specimens from Madagascar (Table 5). The latter differ from the other two populations in a slightly longer head, and from the Mediterranean population in slightly longer barbels and fewer gill rakers. All these morphological differences do however – singly and in combination—overlap in the three populations. Also, no marked colour differences have been observed in these populations.

Comparisons and differential diagnosis of WIO *japonicus*-group species
(Figures 1–6: Tables 1, 3–5)

Upeneus floros differs from the four co-occurring species of the *japonicus*-group in the SWIO as follows: from *U. guttatus* it differs in longer head, lower first dorsal fin with the first three spines highest, but none of them disproportionally higher and all seven spines proportionally decreasing in height, and in white vs. mostly yellow barbels when fresh; from *U. pori* it differs in slightly longer head and barbels, lower first dorsal fin and fewer gill rakers; from *U. saiab* it differs in mostly deeper body at anal-fin origin, longer snout and lower first dorsal fin, fewer gill rakers, and

presence of bars on lower caudal-fin lobe; from *U. seychellensis* it differs in mostly deeper body and longer second dorsal-fin base, shorter and mostly lower anal fin, slightly fewer gill rakers and presence of oblique bars on lower caudal-fin lobe. From *U. itoui*, the most similar *japonicus*-group species with disjunct distribution, *Upeneus floros* differs in deeper head through eye, longer head, slightly longer paired fins and wider pectoral fin, and absence of a conspicuous mid-lateral body stripe when fresh.

Upeneus guttatus differs from *U. pori* in a slightly higher first dorsal fin, with the first spine and sometimes also the second and third spines disproportionally higher vs. all spines rather proportionally decreasing in height, slightly fewer pectoral-fin rays and total gill rakers, and mostly yellow vs. white or white creamy barbels when fresh. Moreover, preserved *U. guttatus* frequently shows no remnants of caudal-fin bars, while *U. pori* usually does, and *U. guttatus* exhibits a uniform pale-brown body colour, while *U. pori* is often dorsally darker. Furthermore, *U. guttatus* differs from *U. saiab* in slightly deeper body at anal-fin origin, deeper caudal peduncle, mostly shorter head and shorter barbels, higher anal fin and first dorsal fin, fewer gill rakers, barbels mostly yellow vs white when fresh and oblique bars usually present on lower caudal-fin lobe; from *U. seychellensis* it differs in deeper body at dorsal-fin origin, slightly longer and higher anal fin, higher first dorsal fin and fewer pectoral-fin rays, fewer gill rakers, barbels mostly yellow vs pale reddish when fresh and oblique bars usually present on lower caudal-fin lobe; and from *U. itoui* it differs in deeper head through eye, mostly longer pelvic fins and higher first dorsal fin, absence of a distinctive body stripe and barbels mostly yellow vs white.
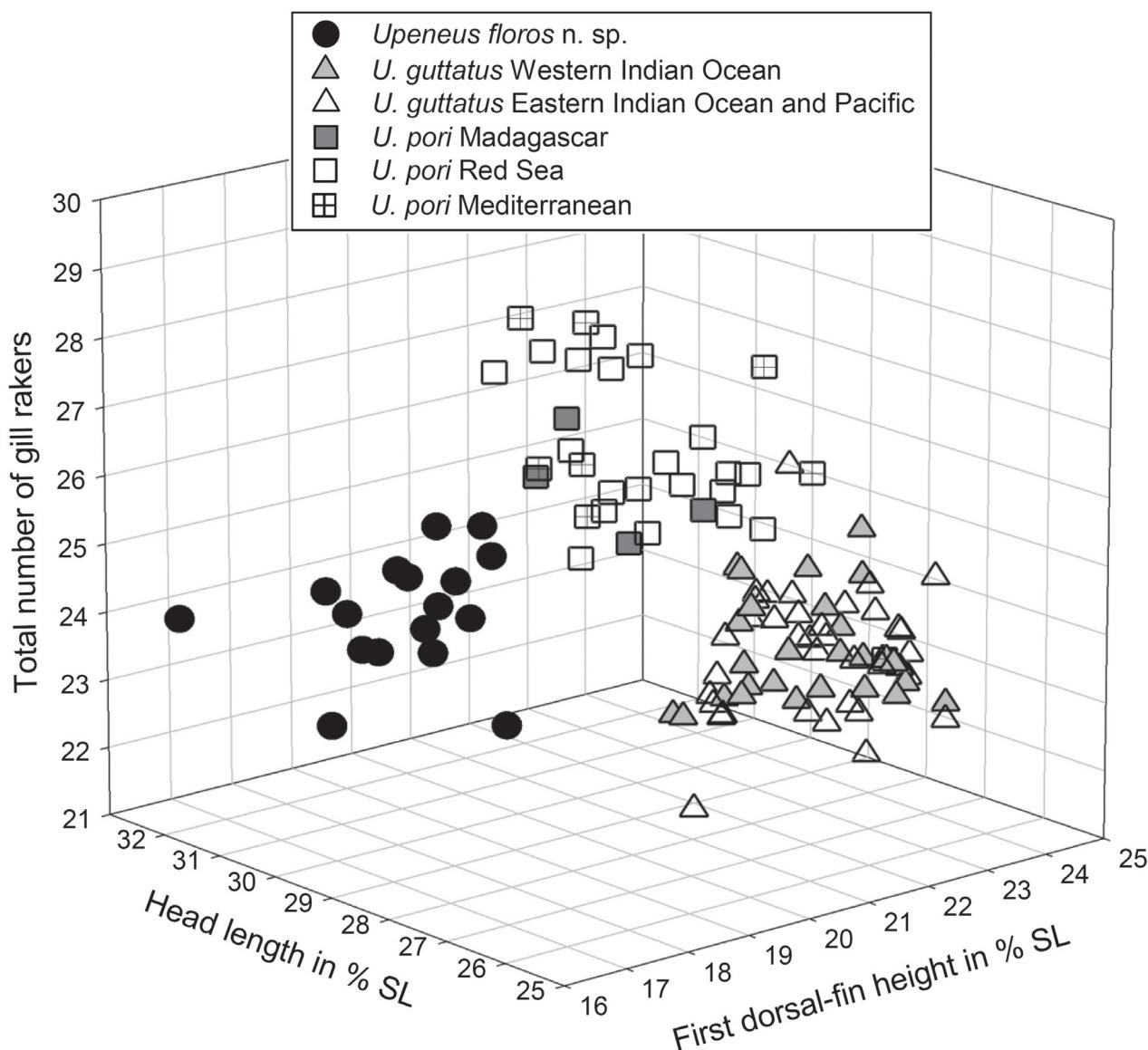
FIGURE 5. Relationship between head length, first dorsal-fin height and number of total gill rakers in *Upeneus floros* **n. sp.** and *U. guttatus* and *U. pori* populations.

TABLE 4. Morphometric and meristic characters for *Upeneus guttatus* from three populations

<table>
<thead>
<tr><th rowspan="2">Morphometric characters</th><th colspan="4">WIO</th><th colspan="4">EIO</th><th colspan="4" style="text-align:center">Upeneus guttatus
Pacific</th><th colspan="4">All fish</th></tr>
<tr><th>Min</th><th>Mean</th><th>Max</th><th>n</th><th>Min</th><th>Mean</th><th>Max</th><th>n</th><th>Min</th><th>Mean</th><th>Max</th><th>n</th><th>Min</th><th>Mean</th><th>Max</th><th>n</th></tr>
</thead>
<tbody>
<tr><td>SL</td><td>68</td><td>99.7</td><td>142</td><td>36</td><td>78</td><td>95.7</td><td>112</td><td>16</td><td>85</td><td>107.4</td><td>159</td><td>23</td><td>68</td><td>101.3</td><td>159</td><td>74</td></tr>
<tr><td>in % SL</td><td></td><td></td><td></td><td></td><td></td><td></td><td></td><td></td><td></td><td></td><td></td><td></td><td></td><td></td><td></td><td></td></tr>
<tr><td>Body depth at first dorsal-fin origin</td><td>22</td><td>23.5</td><td>25</td><td>35</td><td>22</td><td>24.0</td><td>26</td><td>16</td><td>21</td><td>23.4</td><td>26</td><td>23</td><td>21</td><td>23.6</td><td>26</td><td>74</td></tr>
<tr><td>Body depth at anal-fin origin</td><td>19</td><td>20.1</td><td>22</td><td>35</td><td>18</td><td>20.3</td><td>22</td><td>16</td><td>18</td><td>20.3</td><td>22</td><td>23</td><td>18</td><td>20.2</td><td>22</td><td>74</td></tr>
<tr><td>Half body depth at first dorsal-fin origin</td><td>18</td><td>19.3</td><td>21</td><td>31</td><td>17</td><td>19.7</td><td>21</td><td>13</td><td>18</td><td>19.3</td><td>21</td><td>19</td><td>17</td><td>19.4</td><td>21</td><td>63</td></tr>
<tr><td>Half body depth at anal-fin origin</td><td>15</td><td>15.8</td><td>18</td><td>30</td><td>14</td><td>15.9</td><td>17</td><td>14</td><td>15</td><td>15.8</td><td>18</td><td>16</td><td>14</td><td>15.8</td><td>18</td><td>60</td></tr>
<tr><td>Caudal-peduncle depth</td><td>9.3</td><td>9.9</td><td>11</td><td>35</td><td>9.6</td><td>10.2</td><td>11</td><td>16</td><td>9.4</td><td>10.1</td><td>11</td><td>23</td><td>9.3</td><td>10.0</td><td>11</td><td>74</td></tr>
<tr><td>Caudal-peduncle width</td><td>3.2</td><td>3.8</td><td>5.1</td><td>35</td><td>3.3</td><td>3.8</td><td>4.6</td><td>16</td><td>3.3</td><td>4.0</td><td>5.0</td><td>23</td><td>3.2</td><td>3.9</td><td>5.1</td><td>74</td></tr>
<tr><td>Maximum head depth</td><td>18</td><td>20.2</td><td>22</td><td>35</td><td>19</td><td>20.9</td><td>22</td><td>16</td><td>18</td><td>19.9</td><td>21</td><td>23</td><td>18</td><td>20.3</td><td>22</td><td>74</td></tr>
<tr><td>Head depth through eye</td><td>15</td><td>16.3</td><td>18</td><td>35</td><td>16</td><td>16.9</td><td>18</td><td>16</td><td>15</td><td>15.7</td><td>17</td><td>23</td><td>15</td><td>16.3</td><td>18</td><td>74</td></tr>
<tr><td>Suborbital depth</td><td>8.6</td><td>9.7</td><td>12</td><td>35</td><td>8.7</td><td>9.9</td><td>11.1</td><td>16</td><td>8.6</td><td>9.4</td><td>11</td><td>23</td><td>8.6</td><td>9.7</td><td>12</td><td>74</td></tr>
<tr><td>Interorbital length</td><td>7.0</td><td>7.7</td><td>8.4</td><td>35</td><td>7.1</td><td>7.9</td><td>8.7</td><td>16</td><td>7.1</td><td>7.8</td><td>8.9</td><td>23</td><td>7.0</td><td>7.8</td><td>8.9</td><td>74</td></tr>
<tr><td>Head length</td><td>26</td><td>27.3</td><td>29</td><td>35</td><td>26</td><td>27.8</td><td>29</td><td>16</td><td>26</td><td>27.1</td><td>29</td><td>23</td><td>26</td><td>27.4</td><td>29</td><td>74</td></tr>
<tr><td>Snout length</td><td>9.8</td><td>10.6</td><td>12</td><td>35</td><td>9.4</td><td>10.7</td><td>12</td><td>16</td><td>9.6</td><td>10.4</td><td>11</td><td>23</td><td>9.4</td><td>10.5</td><td>12</td><td>74</td></tr>
<tr><td>Postorbital length</td><td>9.7</td><td>11.0</td><td>13</td><td>35</td><td>10</td><td>11.0</td><td>12</td><td>16</td><td>9.8</td><td>10.6</td><td>12</td><td>23</td><td>9.7</td><td>10.8</td><td>13</td><td>74</td></tr>
<tr><td>Orbit length</td><td>6.3</td><td>7.2</td><td>8.5</td><td>35</td><td>6.4</td><td>7.1</td><td>7.9</td><td>16</td><td>5.9</td><td>7.0</td><td>7.8</td><td>23</td><td>5.9</td><td>7.1</td><td>8.5</td><td>74</td></tr>
<tr><td>Orbit depth</td><td>5.2</td><td>6.2</td><td>7.6</td><td>35</td><td>5.3</td><td>6.2</td><td>7.3</td><td>16</td><td>5.0</td><td>6.1</td><td>6.8</td><td>23</td><td>5.0</td><td>6.2</td><td>7.6</td><td>74</td></tr>
<tr><td>Upper-jaw length</td><td>9.6</td><td>10.9</td><td>12.1</td><td>35</td><td>10</td><td>11.2</td><td>12</td><td>16</td><td>9.5</td><td>10.6</td><td>11</td><td>23</td><td>9.5</td><td>10.9</td><td>12</td><td>74</td></tr>
<tr><td>Lower-jaw length</td><td>8.7</td><td>10.2</td><td>11.2</td><td>35</td><td>9.4</td><td>10.7</td><td>11</td><td>16</td><td>8.9</td><td>10.0</td><td>11</td><td>23</td><td>8.7</td><td>10.2</td><td>11</td><td>74</td></tr>
<tr><td>Snout width</td><td>7.7</td><td>8.8</td><td>11.0</td><td>32</td><td>7.7</td><td>8.5</td><td>10</td><td>16</td><td>7.6</td><td>8.2</td><td>9.7</td><td>23</td><td>7.6</td><td>8.5</td><td>11</td><td>71</td></tr>
<tr><td>Barbel length</td><td>16</td><td>17.4</td><td>19</td><td>35</td><td>17</td><td>18.5</td><td>20</td><td>16</td><td>16</td><td>18.0</td><td>20</td><td>22</td><td>16</td><td>17.8</td><td>20</td><td>73</td></tr>
<tr><td>Maximum barbel width</td><td>0.7</td><td>0.8</td><td>1.0</td><td>35</td><td>0.7</td><td>0.7</td><td>0.9</td><td>16</td><td>0.7</td><td>0.8</td><td>0.9</td><td>23</td><td>0.7</td><td>0.8</td><td>1.0</td><td>74</td></tr>
<tr><td>First pre-dorsal length</td><td>33</td><td>35.6</td><td>38</td><td>35</td><td>35</td><td>35.9</td><td>37</td><td>16</td><td>33</td><td>35.3</td><td>37</td><td>23</td><td>33</td><td>35.6</td><td>38</td><td>74</td></tr>
<tr><td>Second pre-dorsal length</td><td>60</td><td>63.3</td><td>66</td><td>35</td><td>62</td><td>63.5</td><td>66</td><td>16</td><td>61</td><td>63.3</td><td>66</td><td>23</td><td>60</td><td>63.3</td><td>66</td><td>74</td></tr>
<tr><td>Interdorsal distance</td><td>14</td><td>15.9</td><td>18</td><td>35</td><td>15</td><td>16.5</td><td>18</td><td>16</td><td>14</td><td>15.9</td><td>18</td><td>23</td><td>14</td><td>16.0</td><td>18</td><td>74</td></tr>
<tr><td>Caudal-peduncle length</td><td>22</td><td>23.6</td><td>26</td><td>35</td><td>22</td><td>23.7</td><td>25</td><td>16</td><td>22</td><td>23.8</td><td>26</td><td>23</td><td>22</td><td>23.7</td><td>26</td><td>74</td></tr>
</tbody>
</table>

TABLE 4. (Continued)

Upeneus guttatus

	WIO				EIO				Pacific				All fish			
	Min	Mean	Max	n	Min	Mean	Max	n	Min	Mean	Max	n	Min	Mean	Max	n
Pre-anal length	61	64.9	68	35	61	63.8	67	16	63	65.2	69	23	61	64.7	69	74
Pre-pelvic length	29	31.4	34	35	30	31.5	34	16	29	31.4	34	23	29	31.4	34	74
Pre-pectoral length	28	29.2	32	35	28	29.9	32	16	28	29.1	32	23	28	29.3	32	74
Second dorsal-fin depth	19	20.7	24	35	19	20.9	23	16	19	21.0	23	23	19	20.8	24	74
Pelvic-fin depth	22	23.3	25	35	22	24.0	26	16	22	23.2	25	23	22	23.4	26	74
Pectoral-fin depth	15	16.3	18	35	16	16.5	19	16	14	15.8	18	23	14	16.2	19	74
Length of first dorsal-fin base	13	14.9	17	35	13	14.9	16	16	13	14.3	16	23	13	14.7	17	74
Length of second dorsal-fin base	12	13.5	16	35	12	13.7	15	15	12	13.7	15	23	12	13.6	16	73
Caudal-fin length	27	29.2	31	34	27	28.9	30	13	27	29.6	31	20	27	29.2	31	67
Length of anal-fin base	9.5	11.3	13	35	9.8	11.2	13	16	11	11.5	13	23	9.5	11.4	13	74
Anal-fin height	14.8	16.4	19	35	16	16.7	18	16	15	16.5	19	23	15	16.5	19	74
Pelvic-fin length	18.8	20.9	22	35	20	20.9	22	16	19	20.6	22	23	19	20.8	22	74
Pectoral-fin length	18.9	20.5	22	35	19	20.2	22	16	19	19.8	21	23	19	20.2	22	74
Pectoral-fin width	3.5	4.1	4.9	35	3.7	4.0	4.5	16	3.7	3.9	4.5	23	3.5	4.0	4.9	74
First dorsal-fin height	20	22.5	25	32	21	22.1	24	15	20	22.2	24	20	20	22.3	25	67
Second dorsal-fin height	14	16.1	18	34	14	16.2	18	16	15	16.2	18	19	14	16.1	18	69
Meristic characters																
Pectoral-fin rays	12	13.1	14	36	13	13.1	14	16	12	13.0	14	23	12	13.1	14	75
Rudimentary gill rakers on upper limb	2	3.7	5	36	2	3.9	5	15	2	3.7	5	23	2	3.7	5	74
Developed gill rakers on upper limb	2	2.8	4	36	2	2.3	4	15	2	2.7	4	23	2	2.7	4	74
Developed gill rakers on lower limb	11	12.5	14	36	11	11.9	12	15	11	12.4	14	23	11	12.4	14	74
Rudimentary gill rakers on lower limb	3	4.7	6	36	5	5.5	7	15	4	5.0	6	23	3	4.9	7	74
Total gill rakers on upper limb	6	6.5	8	36	5	6.2	7	15	6	6.4	7	23	5	6.4	8	74
Total gill rakers on lower limb	16	17.2	18	36	17	17.3	18	15	16	17.4	19	23	16	17.3	19	74
Total gill rakers	22	23.7	25	36	23	23.5	24	15	22	23.8	26	23	22	23.7	26	74
Scales along lateral line	28	29.5	31	22	28	29.2	30	13	29	29.4	30	10	28	29.4	31	45

TABLE 5. Morphometric and meristic characters for *Upeneus pori* from three populations and for *U. itoui*

| Morphometric characters | *Upeneus pori* | | | | | | | | | | | | | | | | | | *U. itoui* | | | |
| | Red Sea | | | | Mediterranean Sea | | | | SW Madagascar | NE Madagascar | | | | All fish | | | | S Japan | | | |
	Min	Mean	Max	n	Min	Mean	Max	n		Min	Mean	Max	n	Min	Mean	Max	n	Min	Mean	Max	n
SL	66	93.7	117	20	72	78.5	110	8	97	89	93.1	96	3	66	89.9	117	32	87	106.4	118	3
in % SL																					
Body depth at first dorsal-fin origin	21	23.2	24	20	22	22.9	24	8	24	22	23.1	24	3	21	23.1	24	32	22	21.8	22	3
Body depth at anal-fin origin	19	20.6	22	20	18	19.2	20	8	22	20	20.6	21	3	18	20.3	22	32	20	20.6	21	3
Half body depth at first dorsal-fin origin	18	19.0	21	20	18	18.3	20	8	20	19	19.4	20	3	18	18.9	21	32	18	18.0	18	3
Half body depth at anal-fin origin	14	15.7	17	20	13	14.3	15	8	16	15	16.3	17	3	13	15.4	17	32	16	15.7	16	3
Caudal-peduncle depth	9.0	9.6	10	20	8.8	9.6	10	8	9.6	9.0	9.3	9.6	3	8.8	9.6	10	32	9.4	9.6	9.9	3
Caudal-peduncle width	3.5	3.9	4.4	20	3.8	4.0	4.6	8	3.9	4.0	4.2	4.5	3	3.5	4.0	4.6	32	4.0	4.3	4.5	3
Maximum head depth	18	19.4	21	20	18	18.9	19	8	19	19	19.3	20	3	18	19.2	21	32	18	18.3	18	3
Head depth through eye	14	15.4	16	20	15	15.2	16	8	16	15	15.6	16	3	14	15.4	16	32	13	13.9	14	3
Suborbital depth	8.2	9.4	10	20	8.3	9.2	10	8	9.3	9.0	9.5	9.9	3	8.2	9.4	10	32	8.9	9.0	9.2	3
Interorbital length	7.1	7.9	8.8	20	7.1	8.1	9.2	8	7.5	7.1	7.2	7.4	3	7.1	7.9	9.2	32	6.7	7.5	8.1	3
Head length	26	27.6	29	20	26	27.7	28	8	28	29	29.4	30	3	26	27.8	30	32	27	27.7	28	3
Snout length	9.9	10.9	12	20	9.5	10.3	11	8	11	11	11.0	11	3	9.5	10.8	12	32	11	11.3	12	3
Postorbital length	11	11.7	13	20	11	11.5	12	8	11	11	11.9	12	3	11	11.6	13	32	11	11.4	12	3
Orbit length	5.8	6.8	7.8	20	6.5	7.2	7.6	8	6.9	7.4	7.6	7.8	3	5.8	7.0	7.8	32	5.7	6.1	6.4	3
Orbit depth	4.8	6.0	7.7	20	5.8	6.5	6.8	8	6.0	6.1	6.2	6.4	3	4.8	6.2	7.7	32	5.0	5.4	5.8	3
Upper-jaw length	9.9	10.7	11.5	20	10	10.9	12	8	10	11	10.9	11	3	9.9	10.8	12	32	10	10.4	11	3
Lower-jaw length	9.1	10.1	11.2	20	9.7	10.5	11	8	10	10	10.4	11	3	9.1	10.2	11	32	9.8	9.9	10	3
Snout width	7.4	8.2	9.2	20	8.0	8.3	8.4	8	10	8.2	9.0	9.5	3	7.4	8.3	10.3	32	7.6	7.9	8.4	3
Barbel length	16	17.3	19	20	16	16.4	17	8	17	18	18.2	19	3	16	17.1	19	32	17	17.4	18	3
Maximum barbel width	0.6	0.8	1.0	20	0.6	0.9	1.0	8	0.7	0.9	1.0	1.0	3	0.6	0.8	1.0	32	0.8	0.8	0.9	3
First pre-dorsal length	34	36.7	38	20	35	36.8	38	8	37	37	36.8	37	3	34	36.8	38	32	35	35.2	36	3
Second pre-dorsal length	63	64.8	67	20	64	65.1	67	8	64	64	65.0	66	3	63	64.9	67	32	61	62.0	63	3
Interdorsal distance	14	16.4	18	19	15	16.3	17	8	14	15	15.2	16	3	14	16.2	18	31	14	15.1	16	3
Caudal-peduncle length	22	23.5	25	20	23	25.4	26	8	23	22	22.6	23	3	22	23.9	26	32	24	24.7	25	3
Pre-anal length	60	64.6	67	20	63	64.6	67	8	64	65	65.5	66	3	60	64.7	67	32	63	63.2	63	3
Pre-pelvic length	28	31.4	32	20	30	30.5	32	8	29	32	31.9	32	3	28	31.1	32	32	31	31.1	32	3

TABLE 5. (Continued)

| | Upeneus pori | | | | | | | | | | | | | | | | | | | U. ituoi | | | |
| | Red Sea | | | | Mediterranean Sea | | | | SW Madagascar | NE Madagasacar | | | | All fish | | | | S Japan | | | |
	Min	Mean	Max	n	Min	Mean	Max	n		Min	Mean	Max	n	Min	Mean	Max	n	Min	Mean	Max	n
Pre-pectoral length	28	29.3	30	20	28	29.1	30	8	30	29	30.2	31	3	28	29.4	31	32	29	29.4	30	3
Second dorsal-fin depth	20	21.1	23	20	19	19.8	21	8	22	20	21.0	22	3	19	20.8	23	32	20	21.0	22	3
Pelvic-fin depth	22	23.6	25	20	22	22.9	24	8	23	22	23.1	24	3	22	23.4	25	32	21	21.7	22	3
Pectoral-fin depth	16	16.4	18	20	16	16.1	17	8	16	16	16.1	17	3	16	16.3	18	32	15	14.9	15	3
Length of first dorsal-fin base	14	15.0	16	19	15	15.9	17	8	16	15	15.2	16	3	14	15.3	17	31	14	14.5	15	3
Length of second dorsal-fin base	13	14.3	15	20	14	15.0	16	8	14	14	14.5	15	3	13	14.5	16	32	14	14.3	15	3
Caudal-fin length	27	28.1	29	19	27	28.0	29	8	29	28	28.8	29	3	27	28.1	29	31	28	28.2	28	3
Length of anal-fin base	10	11.9	13	20	11	11.6	13	8	12	10	11.0	12	3	10	11.7	13	32	11	11.0	11	3
Anal-fin height	15	15.8	17	20	14	15.9	17	8	17	15	15.9	16	3	14	15.9	17	32	16	16.3	17	3
Pelvic-fin length	19	20.2	23	20	19	19.8	21	8	23	20	20.5	21	3	19	20.2	23	32	18	18.7	19	3
Pectoral-fin length	18	19.4	21	20	18	19.1	22	8	22	20	20.4	21	3	18	19.5	22	32	19	19.9	20	3
Pectoral-fin width	3.9	4.3	4.8	20	3.8	4.2	4.9	8	4.7	4.1	4.4	4.5	3	3.8	4.3	4.9	32	3.8	4.0	4.1	3
First dorsal-fin height	18	19.9	22	19	18	19.5	21	8	21	20	20.4	21	3	18	19.8	22	31	19	19.7	20	2
Second dorsal-fin height	13	15.9	17	19	15	15.7	16	8	16	16	16.1	17	3	13	15.8	17	31	16	16.8	17	2
Meristic characters																					
Pectoral-fin rays	13	14.2	15	20	13	13.9	14	8	14	14	14.0	14	3	13	14.1	15	32	13	13.3	14	3
Rudimentary gill rakers on upper limb	0	1.8	4	20	0	1.5	3	8	1	1	1.7	2	3	0	1.7	4	32	1	2.0	3	3
Developed gill rakers on upper limb	4	5.8	8	20	4	6.0	7	8	7	5	6.0	7	3	4	5.9	8	32	4	4.3	5	3
Developed gill rakers on lower limb	15	16.6	18	20	14	15.8	17	8	15	14	14.3	15	3	14	16.1	18	32	13	13.0	13	3
Rudimentary gill rakers on lower limb	1	2.9	5	20	3	4.3	5	8	3	4	4.0	4	3	1	3.3	5	32	3	3.3	4	3
Total gill rakers on upper limb	7	7.6	8	20	7	7.5	8	8	8	7	7.7	8	3	7	7.6	8	32	6	6.3	7	3
Total gill rakers on lower limb	18	19.5	21	20	18	20.0	21	8	18	18	18.3	19	3	18	19.4	21	32	16	16.3	17	3
Total gill rakers	25	27.0	29	20	26	27.5	29	8	26	25	26.0	27	3	25	27.0	29	32	22	22.7	24	3
Scales along lateral line	29	29.1	30	16	29	29.3	30	7	29	28	28.3	29	3	28	29.1	30	27	29	29.5	30	2

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Table 6: Inter- and intraspecific sequence divergences, corrected using the Kimura (1980) two-parameter (K2P) model, for the fifteen *Upeneus* species included in the present study, based on cytochrome *c* oxidase subunit I (COI) sequences. Mean sequence divergences (along with their standard deviations) among representatives of the species are presented, with ranges from individual comparisons in parentheses. Intraspecific values are on the diagonal, in italics.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
(1) *U. asymmetricus*	*0*														
(2) *U. australiae*	6.9 ±0.0 (6.9 – 6.9)	*0.7*													
(3) *U. caudofasciatus*	10.4 ±0.0 (10.4 – 10.4)	9.5 ±0.2 (9.4 – 9.6)	---												
(4) *U. floros* n. sp.	9.7 ±0.2 (9.4 – 10.0)	7.9 ±0.2 (7.5 – 8.3)	11.2 ±0.1 (11.0 – 11.3)	*0.5 ±0.2 (0 – 0.9)*											
(5) *U. guttatus*	11.3 ±0.1 (11.1 – 11.6)	8.9 ±0.5 (8.3 – 9.6)	10.6 ±0.1 (10.4 – 10.8)	11.3 ±0.2 (10.9 – 11.8)	*0.2 ±0.2 (0 – 0.5)*										
(6) *U. heterospinus*	10.9 ±0.0	9.9 ±0.2	0.4	11.6 ±0.1	11.0 ±0.1	---									
(7) *U. japonicus*	12.6 ±0.4 (12.2 – 13.1)	10.3 ±0.3 (10.0 – 10.7)	11.3 ±0.1 (11.3 – 11.5)	12.8 ±0.3 (12.2 – 13.1)	11.4 ±0.2 (11.1 – 11.8)	11.3 ±0.1 (11.3 – 11.5)	*0.6 ±0.1 (0.5 – 0.7)*								
(8) *U. lombok*	8.1 ±0.0 (8.1 – 8.1)	6.9 ±0.3 (6.7 – 7.1)	12.4	6.8 ±0.3 (6.3 – 7.1)	10.4 ±0.1 (10.3 – 10.7)	12.8	10.2 ±0.2 (10.0 – 10.4)	---							
(9) *U. margarethae*	10.2 ±0.2 (10.0 – 10.4)	9.3 ±0.2 (8.9 – 9.6)	0.3 ±0.4 (0 – 0.7)	10.9 ±0.4 (10.2 – 11.3)	10.2 ±0.4 (9.6 – 10.8)	0.7 ±0.4 (0.4 – 1.1)	11.1 ±0.3 (0.6 – 11.5)	12.0 ±0.5 (11.5 – 12.4)	*0.6 ±0.4 (0.2 – 0.9)*						
(10) *U. moluccensis*	16.4 ±0.1 (16.3 – 16.5)	15.3 ±0.1 (15.2 – 15.4)	16.4 ±0.5 (16.0 – 16.7)	15.6 ±0.3 (15.1 – 16.1)	17.2 ±0.3 (16.7 – 17.7)	16.4 ±0.5 (16.0 – 16.7)	17.7 ±0.3 (17.2 – 18.2)	16.1 ±0.2 (16.0 – 16.2)	16.5 ±0.2 (16.0 – 17.0)	*0.5*					
(11) *U. pori*	9.6 ±0.0 (9.6 – 9.6)	7.9 ±0.2 (7.7 – 8.1)	11.1 ±0.1 (11.0 – 11.3)	0.4 ±0.2 (0.2 – 0.9)	11.0 ±0.2 (10.7 – 11.4)	11.6 ±0.1 (11.5 – 11.7)	12.8 ±0.2 (12.6 – 13.1)	6.6 ±0.2 (6.5 – 6.9)	10.8 ±0.4 (10.2 – 11.3)	15.4 ±0.2 (15.1 – 15.6)	*0.2 ±0.2 (0 – 0.4)*				
(12) *U. spottocaudalis*	10.3 ±0.4 (10.0 – 10.6)	9.6 ±0.2 (9.4 – 9.8)	0.5 ±0.4 (0.2 – 0.7)	11.1 ±0.2 (10.8 – 11.3)	10.7 ±0.2 (10.4 – 11.1)	0.8 ±0.4 (0.5 – 1.1)	11.5 ±0.2 (11.3 – 11.7)	12.5 ±0.2 (12.4 – 12.6)	0.7 ±0.4 (0.2 – 1.1)	16.5 ±0.6 (15.8 – 17.2)	11.0 ±0.2 (10.8 – 11.3)	*0.9*			
(13) *U. subvittatus*	16.7 ±0.0 (16.7 – 16.7)	17.2 ±0.0 (17.2 – 17.2)	18.2	16.9 ±0.1 (16.7 – 17.0)	17.5 ±0.2 (17.2 – 17.9)	18.2	17.9 ±0.2 (17.6 – 18.1)	18.1	18.1 ±0.1 (17.9 – 18.2)	8.2 ±0.1 (8.1 – 8.3)	16.7 ±0.1 (16.5 – 16.7)	18.0 ±0.2 (17.9 – 18.2)	---		
(14) *U. supravittatus*	15.5 ±0.1 (15.4 – 15.6)	16.8 ±0.3 (16.6 – 17.0)	16.1 ±0.3 (15.9 – 16.3)	17.0 ±0.2 (16.6 – 17.4)	15.8 ±0.3 (15.2 – 16.3)	16.1 ±0.3 (15.9 – 16.3)	16.1 ±0.3 (15.8 – 16.5)	16.7 ±0.3 (16.5 – 17.0)	16.0 ±0.3 (15.6 – 16.3)	10.9 ±0.3 (10.6 – 11.3)	16.7 ±0.1 (16.5 – 16.9)	16.0 ±0.3 (15.6 – 16.3)	11.2 ±0.2 (11.1 – 11.3)	*0.5*	
(15) *U. torres*	12.7 ±0.5 (12.2 – 13.1)	10.7 ±0.6 (10.0 – 11.3)	12.2 ±0.6 (11.7 – 12.6)	12.9 ±0.8 (11.7 – 13.8)	11.5 ±0.3 (11.1 – 12.0)	12.2 ±0.6 (11.7 – 12.6)	1.3 ±0.2 (0.9 – 1.5)	10.7 ±0.9 (10.0 – 11.3)	11.9 ±0.6 (11.1 – 12.6)	17.9 ±0.6 (17.2 – 18.7)	12.9 ±0.8 (12.2 – 13.8)	12.1 ±0.6 (11.3 – 12.8)	17.6 ±0.7 (17.2 – 18.1)	16.5 ±0.9 (15.6 – 17.5)	*1.3*

Upeneus pori differs from *U. saiab* in slightly deeper body at anal-fin origin and greater pectoral-fin depth, mostly shorter barbels and presence of oblique bars on ventral margin of lower-caudal fin lobe. The four *U. pori* specimens from Madagascar differ from *U. saiab* in higher body at anal-fin origin, slightly shorter barbels and fewer gill rakers. Interestingly all six currently available specimens of *U. saiab* have 29 total gill rakers on each side, while *U. pori* from Madagascar has 25–27 total gill rakers. Furthermore, *U. pori* differs from *U. seychellensis* in slightly higher body and first dorsal-fin origin, shorter barbels, longer interdorsal distance, longer dorsal-fin bases and longer and higher anal fin, and presence of lower caudal-fin lobe bars. *Upeneus pori* differs from *U. itoui* in distribution, mostly deeper head through eye, longer pelvic fins and greater pectoral-fin depth and slightly more gill rakers.

Of the remaining eight species of the *japonicus*-group, *U. floros* and *U. pori* differ in distribution as well as in the following morphological and/or colour characteristics: *U. floros* differs from *U. asymmetricus* it in mostly longer head, snout and upper jaw and in fewer gill rakers, from *U. australiae* in shallower caudal peduncle, slightly longer head, longer interdorsal distance (15–17 vs. 13–16% SL), shorter caudal and pelvic fins and in frequent absence of conspicuous mid-lateral body stripe when fresh; from *U. farnis* in mostly higher anal and second dorsal fin and fewer pectoral-fin rays, and in fewer gill rakers and presence of oblique bars on lower caudal-fin lobe; from *U. francisi* in shallower caudal peduncle, longer snout and upper jaws, slightly longer head, shorter paired fins, lower first dorsal fin and in fewer gill rakers; from *U. japonicus* in mostly shorter pectoral fins and lower first dorsal fin, slightly fewer gill rakers, in presence of bars on lower caudal-fin lobe and white vs yellow barbels when fresh; from *U. lombok* it differs in a large number of characters including longer snout and upper jaw, fewer gill rakers and presence of bars on lower caudal-fin lobe; from *U. spottocaudalis* it differs in slightly shorter barbels and caudal fin, shorter pelvic fin, lower second dorsal fin and more pectoral-fin rays and total gill rakers, in bars vs. spots on lower caudal-fin lobe and white vs. yellow barbels when fresh; and from *U. torres* it differs in much shorter barbels and pectoral fins, lower first dorsal fin and presence of oblique bars on lower caudal-fin lobe.

Upeneus pori differs from *U. asymmetricus* in slightly longer dorsal fins (first dorsal-fin base 14–17 vs. 13–15% SL; second dorsal-fin base 13–16 vs. 12–14% SL) and more pectoral-fin rays; from *U. australiae* it differs in mostly deeper caudal peduncle and shallower head (maximum head depth 18–21 vs. 20–22% SL) and in more gill rakers; from *U. farnis* in slightly higher anal fin, fewer pectoral-fin rays and gill rakers, and presence of conspicuous oblique bars on lower caudal-fin lobe, which are frequently retained in preservative; from *U. francisi* in slightly shorter caudal fin and lower second dorsal fin, fewer gill rakers and oblique lower caudal-fin bars mostly absent in preservative; *from U. japonicus* in slightly shorter pectoral fins, presence of a body stripe and white vs. yellow barbels when fresh and presence of oblique lower caudal-fin lobe bars in fresh and preserved fish; from *U. lombok* in slightly longer snout, longer upper jaw and higher anal fin and presence of oblique bars on lower caudal-fin lobe; from *U. spottocaudalis* in mostly shorter head, shorter caudal fin and lower anal fin and second dorsal fin, more pectoral-fin rays and gill rakers, white vs. yellow barbels and oblique bars vs. rounded spots on lower caudal-fin lobe; and from *U. torres* in slightly shallower head through eye, shorter barbels, slightly lower anal fin and dorsal fins, shorter pectoral fins, more gill rakers, presence of a body stripe and white vs. yellow barbels when fresh and presence of oblique lower caudal-fin lobe bars.

Upeneus guttatus overlaps in distribution with most of the eight remaining *japonicus*-group species. Regarding morphology and colour pattern it differs from *U. asymmetricus* in slightly higher first dorsal fin, fewer gill rakers, mostly yellow versus white barbels and lower caudal-fin lobe bars usually not retained when preserved; from *U. australiae* in slightly longer interdorsal distance (14–18 vs. 13–16% SL), more pectoral-fin rays, absence of mid-lateral body stripe and mostly yellow vs white barbels when fresh and bars on lower caudal-fin lobe usually not retained when preserved; from *U. farnis* in slightly shorter head, higher anal and dorsal fins, fewer gill rakers, mostly yellow vs. pale-grey barbels and presence of oblique bars on lower caudal-fin lobe when fresh; from *U. francisi* in slightly fewer pectoral-fin rays, in fewer gill rakers and mostly yellow vs. white barbels when fresh; from *U. japonicus* in slightly shorter barbels, shorter pectoral fins, fewer pectoral-fin rays and gill rakers and presence of oblique bars on lower caudal-fin lobe; from *U. lombok* in slightly deeper head through eye, longer snout, higher anal fin and first dorsal fin, slightly fewer pectoral-fin rays, fewer gill rakers, mostly yellow vs. white barbels when fresh and presence of oblique bars on lower caudal-fin lobe when fresh; from *U. spottocaudalis* in shorter head, slightly shorter barbels, shorter pelvic fins and lower second dorsal fin, in slightly more pectoral-fin rays and oblique bars vs. rounded spots on lower caudal-fin lobe; and from *U. torres* in slightly shorter head, shorter barbels and pectoral fins and presence of oblique lower caudal-fin lobe bars.

FIGURE 6. (A–D) *Upeneus guttatus*: (A) Syntype, AMS I.25, 104 mm SL, Madras, with close-up of erected first dorsal fin at right top (K. Parkinson); (B) SAIAB 13947, 100 mm SL, off Kenya (P.C. Heemstra); (C) adult fish, *in situ*, Pemba, Cabo Delgado, N Mozambique (R. Koch); (D) adult fish, *in situ*, Nacala, Nampula, N Mozambique (R. Koch); (E–F) *U. pori*; (E) 114 mm SL, Red Sea, Egypt, Gulf of Aqaba, Nuweiba (J.E. Randall); (F) SAIAB 192775, 94 mm SL, off NE Madagascar (J. Escobar-Porras).

Genetic studies
(Figure 7; Tables 2, 6)

Once trimmed to equal length, the COI alignment included 533 nucleotide fragments for 43 representatives (including the two outgroup specimens). jModeltest determined the optimal model for the data set to be a Hasegawa *et al.* (1985) model with a proportion of invariant sites and among-site rate variation (HKY + I + G). The resulting ML topology (-lnL = 2732.613) obtained is presented in Figure 7. In the Bayesian inference to determine support for the nodes, stationarity was achieved early, but a liberal burn-in (of 50%) was implemented, and Bayesian Posterior Probabilities (i.e., support for nodes) calculated from the majority rule consensus of the 1 000 remaining trees. These are indicated on the nodes in Figure 7.

The topology recovered from the ML and Bayesian analyses, which was congruent to the NJ topology with respect to the major retrieved clades, showed the clear separation of *Upeneus floros* from *U. guttatus* and most other included *Upeneus* species. K2P sequence divergences (Table 6) between *U. floros* and *U. guttatus* ranged between 10.9 and 11.8%, with a mean of 11.37 [± 0.2 standard deviation (SD)]. However, *U. floros* was recovered as paraphyletic with respect to the included representatives of *U. pori*. The sequence divergences between these two species (K2P: 0.2–0.9%; mean 0.5% ± 0.2) overlapped with the range of sequence divergences (0–0.9%) recorded among individuals within each species. A similar situation was observed with respect to the lack of monophyly for *U. japonicus*, *U. margarethae* and *U. spottocaudalis*. Overlapping inter- and intraspecific sequence divergences were also observed (Table 6) for these taxa and those included in their respective clades (i.e., *U. torres* for *U. japonicus*,
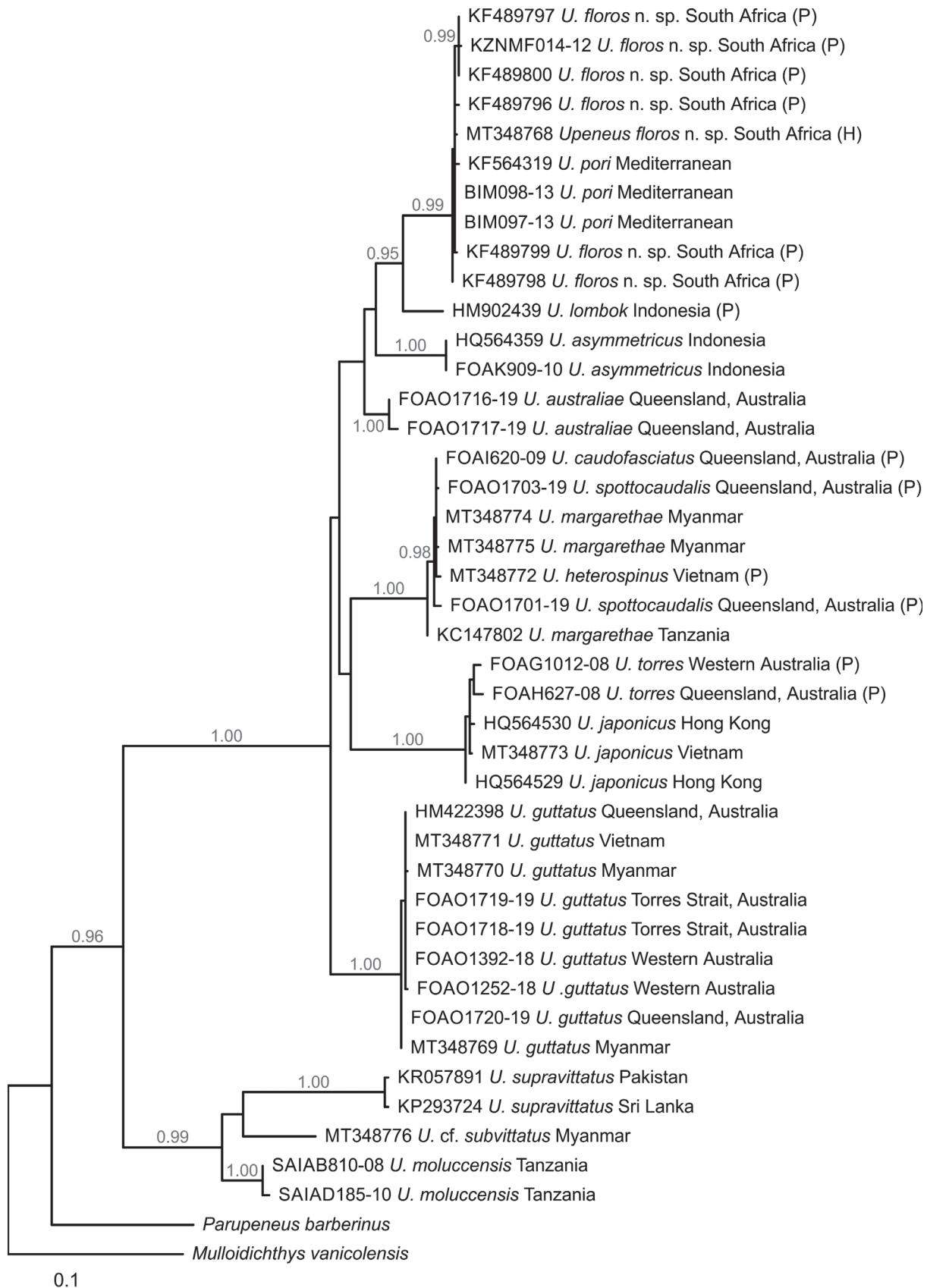
FIGURE 7. Maximum likelihood phylogram based on a 533 nucleotide cytochrome *c* oxidase subunit I (COI) mtDNA sequence alignment, depicting relationships among three *japonicus*-group species and additional representatives of the genus. Bayesian Posterior Probabilities ≥ 0.95 from Bayesian analysis are shown at the nodes. The hologenetype (H) and paragenetypes (P) of the relevant species are indicated.

and *U. caudofasciatus* and *U. heterospinus* for *U. margarethae* and *U. spottocaudalis*). Besides these examples, themselves included well-supported (BPP > 0.99) clades, other species for which multiple specimens were included were monophyletic and well-supported (BPPs of 1.00).

Discussion

Upeneus floros is a relatively common species off the coast of KwaZulu-Natal, occurring over sandy bottoms at moderate depths where it has been encountered by divers and caught by bottom trawls in fishing areas. It was likely not discovered earlier due to its similarity with other species of the *japonicus*-group and the lack of appropriate study material. Our discovery is based on closely combining studies of colour patterns in life with the collection of specimens and genetic tissues samples, detailed studies of morphology and fresh colour after death, and a large comparative dataset obtained from the most similar species occurring in the same, adjacent and more distant areas of the Indo-Pacific and the Mediterranean Sea.

While replacing *U. guttatus* off E South Africa, *U. floros* co-occurs with *U. guttatus* along the Mozambican coast, where only four specimens of *U. floros* have been identified so far. Additional numerous yet insufficiently examined *Upeneus* specimens from bottom trawl operations carried out mostly off S and central Mozambique are known in the SAM collection. Detailed examination of this material may reveal more information about the distribution and abundance of *U. floros* in that area. Fewer samples from N Mozambique and Tanzania are available, due to less scientific exploration in those areas and/or fewer fish collecting activities for taxonomic studies. However, just a small subsample from a single trawl catch during a cruise NE off Angoche, N Mozambique in 2009 included *U. saiab*, *U. floros* and *U. guttatus*; however, specimens of the latter species were not retained. Off Angoche during the 2009 cruise with RV *Dr. Fridtjof Nansen* (Olsen *et al.* 2009), *U. guttatus* were the most common *japonicus*-group species while *U. saiab* and *U. floros* were less abundant (Mark Lisher, pers. obs.). While *U. saiab* appears to be locally restricted to that area, this clearly does not apply for *U. floros* and *U. guttatus*.

Upeneus floros is closely related to *U. pori* as evident from the morphological, colour and genetic analyses. Distinction is best reached by combined examination of a few morphometric and meristic characters, while barcoding suggests strong overlap and hence very close relatedness (see below). These two species appear to be separated by the Mozambique Channel, as it applies also to *U. saiab* and *U. pori*. Furthermore, the SWIO population of *U. pori*, now known to occur off both the east and west coasts of Madagascar, is rather widely separated from the Northern Red Sea and Mediterranean Sea, where the two other populations of this species occur. It is unclear whether any connectivity between these populations exists that may, for example, be supported by a yet unknown occurrence of conspecifics between Madagascar and the Northern Red Sea. On the other hand, five other species of the *japonicus*-group occur in rather restricted areas contributing to high endemism, such as *U. farnis* (N Sulawesi, Indonesia), *U. itoui* (S Japan), *U. lombok* (Lombok, Indonesia), *U. saiab* (N Mozambique) and *U. seychellensis* (Seychelles Bank). The *U. pori* population from Madagascar differs slightly from the two northern populations and this population could represent a distinct taxon pending collection and critical examination of additional material (e.g. Uiblein & Gouws 2014).

In contrast to earlier studies (Uiblein & Heemstra 2011a; Uiblein & Gledhill 2015), no remarkable population differences in *U. guttatus* were found. This is most certainly due to two causes: (1) when populations from rather large regions such as entire oceans are compared, intraspecific diversity within those populations may be obscured, and (2) formerly recognized differences are teased out through refined levels of taxonomic distinction. Regarding (1), Uiblein & Heemstra (2011a) found indications of population differences in *U. guttatus* at much smaller scale, among the Seychelles, the Gulf of Suez and other areas of the Indian Ocean. For the scope of the present study, it was important to compare the entire WIO population with both *U. floros* and *U. pori*. Regarding (2), *U. floros* specimens were no longer identified as *U. guttatus*, as was the case in previous studies in which *U. guttatus* populations were compared (Uiblein & Heemstra 2011a; Uiblein & Gledhill 2015). Inter- and intraregional comparisons among populations can provide important insights into intra- and interspecific differentiation and, thus, assist in resolving taxonomic hypotheses (e.g., Uiblein *et al.* 2019). One challenge is, however, to assemble representative population data across the entire range of a widely distributed species (Uiblein *et al.* 2016).

The genetic analyses, using the barcoding region (*sensu* Herbert *et al.* 2003) of the COI gene, clearly demonstrated the separation and distinction of *U. floros* and *U guttatus*, as these formed the two most divergent lineages

within the *japonicus*-group (which itself was paraphyletic with the three included *margarethae*-group species nested within). However, DNA barcoding failed to delineate *U. floros* from *U. pori*, contradicting the clear morphological separation. *Upeneus floros* was paraphyletic with respect to the latter and sequence divergences between individuals of these taxa were no more extensive than divergences between individuals. As our results suggest, DNA barcoding performs poorly for delineating several species within this genus. Uiblein & Gouws (2015) demonstrated low sequence divergences, inconsistent separation and the sharing of COI haplotypes among *U. suahelicus* and *U. supravittatus*. Besides being allopatric, these species are readily distinguished by diagnostic characters and other characters in combination (Uiblein & Gouws 2015). The present study also demonstrated the failure of DNA barcoding to delineate well-established species, as is evident from the paraphyly of *U. japonicus* with respect to *U. torres*, and of species in the *margarethae*-group.

Uiblein & Gouws (2015) provided an overview of the factors leading to the failure of DNA barcoding to successfully or accurately delineate species (e.g., misidentifications, pseudogenes, hybridization and introgression, or recent radiation and the retention of ancestral polymorphism). As in Uiblein & Gouws (2015), the intensive and rigorous nature of an integrated, comprehensive taxonomic approach (Uiblein 2016), coupled with the clear morphological distinction of the species concerned, argues against misidentifications, while the retained functionality of the COI gene region suggests that pseudogenes are not a pervasive concern. This leaves hybridization and introgression or a recent radiation and speciation as alternatives. Additional studies, combining mtDNA, nuclear markers and detailed population- or individual-level morphometrics, are required to investigate the former suitably. A comprehensive, multiple marker, phylogenetic or genome-wide phylogenomic study, with comprehensive taxonomic representation, is needed to accurately depict evolutionary relationships among taxa, define species groups and to carefully interrogate the biogeographic history of the genus. This would enable a more nuanced understanding of the evolutionary and spatial relationships among those taxa that are poorly delineated by a single mtDNA (i.e., barcoding) marker, possibly indicating the underlying dynamics and causes, and potentially identifying more suitable markers for species delineation in this group.

To further refine the present comprehensive and integrative taxonomic approach towards a better understanding of the inter- and intraspecific diversity among *japonicus*-group goatfishes, a consideration of the possible effects of oceanographic conditions on species distribution patterns, speciation processes and population connectivity is needed. The SWIO region is a particularly active area in terms of dynamic, locally-distinct and diverse oceanographic conditions. Ocean circulation is characterized by the westward South Equatorial Current (SEC) flow towards the African mainland, where it bifurcates into the northwards directed East Africa Coastal Current and the southward N Mozambique flow that produces local eddies in the narrowest section of the Mozambique Channel (Shenoi *et al* 1999; Schott and McCreary 2001). This large-scale warm-water circulation pattern corroborates the wide distribution of *U. guttatus*. While nearly omnipresent elsewhere in the SWIO, *U. guttatus* has not been recorded from the South African coast, where decreasing water temperatures from north to south, possibly reinforced by cooling effects caused by cyclonic-eddy upwelling activities off KwaZulu-Natal (Morris *et al.* 2013; Roberts *et al.* 2016) may limit its occurrence.

Upeneus floros appears to be restricted to the coast from Angoche, N Mozambique, to KwaZulu-Natal, E South Africa, an area of frequent eddy formation and upwelling events with productive cold-water cells being established on the uppermost shelf and often close to the shore. Off Angoche and further south, a train of mesoscale eddies propagating southward on the western side of the Mozambique Channel (Sætre and da Silva 1984; de Ruijter *et al.* 2002; Halo *et al.* 2014) as well as productive upwelling cells and smaller-scale eddies prevail (Lutjeharms 2006, Lamont *et al.* 2010, Malauene *et al.* 2014, Cossa *et al* 2016). Further south, in Delagoa Bight off Maputo (S Mozambique), eddies from the Mozambique Channel and from the Southeast Madagascar Current form the south-westward flowing Agulhas Current along the South African coast (Lutjeharms 2006). In the KwaZulu-Natal Bight, the Agulhas Current is associated with a quasi-permanent upwelling cell and cyclone eddy at the inshore side of the current (Lutjeharms and Roberts 1988; Roberts *et al.* 2016). Off N Mozambique, the divergence of the SEC may impose a barrier for this species' dispersal (Obura *et al.* 2019).

The limited distribution of *U. saiab* may be viewed as a species-specific response to localized forcing by a trapped, quasi-permanent lee eddy in association with a local upwelling cell off Angoche (Nehring *et al.* 1987; Malauene *et al.* 2014). More sampling and research in this area is needed to better understand this assumed interrelationship and to find out to which extend *U. saiab* has adapted to locally prevailing hydrological constraints. Similarly, the distribution, abundance, phenotypic and genetic differentiation, and possible influences by oceanography

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and/or topography in *U. pori*, only known from Madagascar in the SWIO, and *U. seychellensis*, possibly endemic to the Seychelles Bank, requires more sampling and biologically, ecologically and evolutionary oriented research.

Given the importance of goatfishes as ecological indicators in sand-associated coastal habitats (Uiblein 2007), this study contributes to a more complete picture of the diversity, abundance and species-specific distribution patterns of the genus *Upeneus* in the SWIO region. While having only minor commercial value in this region, the relatively small-sized species of the *japonicus*-group generally occur as a bycatch in larger-scale fisheries such as bottom trawling, allowing more detailed biological and ecological studies, especially when larger samples are retained as reference material for scientific investigations. Monitoring taxonomically well-established species of goatfishes, together with other coastal bottom-associated species, may contribute to a better understanding of the environmental characteristics and variations occurring in the SWIO and their direct or indirect effects on coastal fish populations and communities at different spatial and temporal scales.

Identification key for the WIO *Upeneus* species

In total 22 species of the genus *Upeneus* including the five *japonicus*-group species are presently known to occur in the WIO (Uiblein *et al*. 2018; Uiblein *et al*. 2019; current study). The key below includes detailed geographic information for the distribution of each species in the WIO and, if appropriate, general occurrence information for other regions. Furthermore, the currently established taxonomic species groups and species complexes (with ungrouped species added) are indicated at respective nodes of the key together with the relevant literature sources.

1a First dorsal fin 7 spines, first 3 spines usually longest; pectoral fins 12–15 rays; total gill rakers 22–29; oblique bars on caudal fin present in life (but present or absent on lower lobe). . . . . 2 (*japonicus*-species group: this study; Uiblein & Heemstra 2011a; Uiblein & Lisher 2013)

1b First dorsal fin 8 spines, first spine minute, partly hidden by skin and scales; pectoral fins 13–17 rays; total gill rakers 18–33; oblique bars on caudal fin present or absent 6

2a Pectoral fins 12–14 rays; head depth through eye 1.5–1.8 in head length; first dorsal-fin height 4.1–5.1 in SL; at least one of the first three dorsal-fin spines disproportionally higher; barbels mostly yellow when fresh. . . . . *U. guttatus* (Day, 1868) (entire WIO including Red Sea, except for South Africa; EIO, W Pacific)

2b Pectoral fins 13–15 rays; head depth through eye 1.7–2.0 in head length; first dorsal-fin height 4.5–6.1 in SL; dorsal-fin spine height decreasing proportionally; barbels white, yellow or pale reddish when fresh 3

3a Total gill rakers 23–25; head and snout rather long, head length 3.1–3.5 in SL, snout length 7.8–9.4 n SL; oblique bars present on lower caudal-fin lobe in life (not or only some traces retained in preservative). . . . . .*U. floros* (South Africa, Mozambique)

3b Total gill rakers 25–29; head and snout short or moderately long, head length 3.3–3.9 in SL, snout length 8.2–11 in SL; oblique bars present or absent on lower caudal-fin lobe 4

4a Body depth at anal-fin origin 4.5–5.4 in SL and 1.2–1.5 in head length; oblique bars on lower caudal-fin lobe present. . . . . *U. pori* Ben-Tuvia & Golani, 1989 (WIO: Northern Red Sea, Madagascar; Mediterranean Sea as Lessepsian migrant)

4b Body depth at anal-fin origin 5.2–6.1 in SL and 1.5–1.8 in head length; oblique bars on lower caudal-fin lobe absent 5

5a Total gill rakers 29; snout length 9.0–10 in SL; postorbital length 7.6–8.0 in SL; barbels white when fresh. . . . . *U. saiab* Uiblein & Lisher, 2013 (N Mozambique, off Angoche)

5b Total gill rakers 25–26; snout length 8.2–9.1 in SL; postorbital length 8.3–9.6 in SL; barbels pale reddish when fresh . . . . *U. seychellensis* Uiblein & Heemstra, 2011 (Seychelles Bank)

6a Pelvic-fin length 0.8–1.1 in pectoral fins; total gill rakers 18–25; pectoral fins 13–15 rays; oblique bars on caudal fin present in life, present or absent in preservative. . . . . 7 (*tragula*-species group and *U. taeniopterus*: Uiblein *et al*. 2017)

6b Pelvic-fin length 1.1–1.5 in pectoral-fin length; total gill rakers 25–33; pectoral fins 14–17 rays; oblique bars on caudal fin present or absent. 13

7a Lateral-line scales 36–38 (rarely 39); pectoral fins 5.1–6.0 in SL; at least two lateral body stripes when fresh: pale-brown mid-lateral body stripe and weaker, more yellowish, stripe below; maximum size 300 mm SL . . . .*U. taeniopterus* Cuvier, 1829 (WIO: Pinda Bank, Mozambique, Seychelles, Mauritius, Chagos, Maldives, Laccadives, Sri Lanks; EIO, W and Central Pacific)

7b Lateral-line scales 28–34; pectoral fins 4.2–5.5 in SL; one yellow, pale-brown, or brown mid-lateral body stripe when fresh, or stripe absent; maximum size 170 mm SL. 8

8a Total gill rakers 18–22; lateral line scales 31–34; first dorsal-fin height 3.7–4.5 in SL; caudal-peduncle-depth 7.7–9.1 in SL; barbels frequently yellow when fresh. . . . . *U. sundaicus* (Bleeker, 1855) (WIO: Persian Gulf, India; EIO, W Pacific)

8b Total gill rakers 19–25; lateral line scales 28–31; first dorsal-fin height 4.2–5.6 in SL; caudal-peduncle depth 8.7–11 in SL; barbels white, yellow or pale brown when fresh 9

9a Pectoral-fin rays 12–14; total gill rakers 19–24; dark blotch on or close to first dorsal-fin tip; one dark (red, brown or black) mid-lateral stripe on body when fresh, retained when preserved; dark dots, spots or blotches present on body and paired fins; barbels yellow or pale brown when fresh. 10 (dark-freckled species complex: Uiblein & Gouws 2014)

9b Pectoral-fin rays 13–15; total gill rakers 21–25; no dark blotch on or around first dorsal-fin tip; one yellowish or pale-brown

mid-lateral stripe on body when fresh, mostly not retained in preservative; often with a few red, brown or black dots in a row along lateral line, remains of dots may be retained in preservative; barbels white when fresh . . . . 12 (*margarethae*-species group: Uiblein *et al*. 2019)

10a   Caudal-fin lower lobe with 3–5 bars (3 bars in subadults <70 mm SL); postorbital length 1.2–1.4 in anal-fin height; caudal-fin length 3.5–4.1 in SL, 1.0–1.3 in head length; pelvic-fin length 4.6–6.0 in SL . . . . *U. oligospilus* Lachner, 1954 (Persian Gulf)

10b   Caudal-fin lower lobe with 4–10 bars (4 or 5 bars in subadults <70 mm SL); postorbital length 1.4–2.0 in anal-fin height; cau-dal-fin length 2.9–3.7 in SL, 0.8–1.1 in head length; pelvic-fin length 4.2–5.4 in SL. 11

11a   Caudal fin with 8 bars (3 or 4 on upper lobe); barbel length 4.5–4.7 in SL; upper jaw 9.6–10 in SL. . . . . *U. niebuhri* Guézé, 1976 (Gulf of Suez)

11b   Caudal fin with 9–12 bars (4–6 bars on upper lobe); barbel length 5.0–6.7 in SL; upper jaw 7.5–10 in SL. . . . .*U. heemstra* Uiblein & Gouws, 2014
       (WIO: Central Red Sea to Mozambique, Seychelles, Chagos, Pakistan, India, Sri Lanka; EIO)

12a   Pectoral-fin rays 13–15; total gill rakers 21–24; caudal-peduncle width 17–29 in SL, 4.9–8.6 in head length; pectoral-fin width 19–24 in SL, 5.3–6.8 in head length; caudal-fin lower lobe with broad red, brown or grey band, covering up to 5 or 6 red or brown bars, the latter best visible along ventral margin when fresh (WIO); mid-lateral body stripe running through eye: red or orange from snout tip to eye, yellow or beige from behind eye to caudal-fin base (stripe absent when preserved) . . . . *U. margarethae* Uiblein & Heemstra, 2010
       (WIO: Red Sea, Somalia to Mozambique, Madagascar, SW India, Sri Lanka; EIO, W Pacific)

12b   Pectoral-fin rays 13–14; total gill rakers 23–25; caudal-peduncle width 27–34 in SL, 7.5–10 in head length; pectoral-fin width 23–27 in SL, 6.5–7.6 in head length; caudal-fin lower lobe with 6–8 dark-red bars, bars not covered by a band; mid-lateral body stripe only vaguely visible when fresh, absent when preserved. . . . .*U. randalli* Uiblein & Heemstra, 2011 (Persian Gulf, N Gulf of Oman)

12c   Pectoral-fin rays 15; total gill rakers 25; caudal-peduncle width 30 in SL, 8.8 in head length; pectoral-fin width 21 in SL, 6.0 in head length; colour of fresh fish not known; preserved fish pale brown, no remains of body stripe or caudal-fin bars . . . . *U. gubal* Uiblein 2019 (Gulf of Suez)

13a   No oblique bars on caudal-fin lower lobe, oblique bars present or absent on upper lobe and, when present when fresh, retained in preservative) . . . . 14 (*moluccensis*-species group: Uiblein & Heemstra 2010)

13b   Oblique bars on both caudal-fin lobes, usually well retained in preservative 16

14a   Caudal-fin upper lobe with 6–8 red oblique bars (usually retained in preservative), no bars on lower lobe; tip of first dorsal fin brown to black; body depth at anus 3.6–4.5 in SL (fish >70 mm SL); caudal-peduncle depth 9.8–12 in SL; head depth 3.5–3.7 in SL. . . . . . . *U. moluccensis* (Bleeker, 1855) (WIO: Red Sea to South Africa, Madagascar, Réunion, Pakistan, India; EIO, W Pacific, Mediterranean Sea as Lessepsian migrant)

14b   No oblique bars on caudal-fin lobes; tip of first dorsal fin black or pale brown to yellowish in life (may be lost in preservative); body depth at anus 4.0–5.3 in SL (fish >70 mm SL); caudal-peduncle depth 8.6–9.8 in SL; head depth 3.2–3.5 in SL 15

15a   Total gill rakers 29–33, 22–24 on lower limb; tip of first dorsal fin pale brown to yellowish in life (colour faint or not retained in preservative); narrow, eye-level, yellow stripe on body in life; anal-fin height 6.7–7.0 in SL; first dorsal-fin height 4.5–5.0 in SL . . . . *U. doriae* (Günther, 1869) (Persian Gulf, Gulf of Oman)

15b   Total gill rakers 27–28, 19–21 on lower limb; tip of first dorsal fin black; 2 narrow yellow stripes on mid-side of body; anal-fin height 5.4–6.4 in SL; first dorsal-fin height 3.7–4.5 in SL. . . . . *U. sulphureus* Cuvier, 1829 (WIO: Red Sea, Kenya to South Africa, Madagascar, Mascarenes, Persian Gulf, Pakistan, India, Sri Lanka; EIO, W Pacific)

16a   Oblique bars on caudal fin pale brown to brown, mostly uniformly coloured, pale spaces between bars nearly equal in width, bars on upper lobe curved; 2 narrow yellow or pale-brown lateral body stripes in life; body depth at anus 3.7–4.6 in SL; pectoral fins 3.5–4.5 in SL, 1.1–1.4 in head length; total gill rakers 26–32 . . . . 17 (*suahelicus*-species group: Uiblein & Gouws 2015)

16b   Oblique bars on caudal fin at least partly black or dark brown, frequently varying in colour intensity, bars or spaces between them often unequal in width, bars on upper lobe not curved; 0 or >2 yellow or pale-brown stripes on body in life; body depth at anus 4.1–5.5 in SL; pectoral fins 3.8–4.9 in SL, 1.3–1.6 in head length; total gill rakers 25–29 . . . . .19 (*stenopsis*-species group and *U. vittatus*: Uiblein & Causse 2013; Uiblein & Gouws 2015)

17a   Lateral-line scales 36; body depth at anus 3.7–3.9 in SL; pectoral-fin length 4.2–4.5 in SL, ~1.3 in maximum body depth; stripes on midbody not connecting to oblique bars on caudal fin . . . .*U. indicus* Uiblein & Heemstra, 2010 (SW India)

17b   Lateral-line scales 34–35 (rarely 36); body depth at anus 3.8–4.6 in SL; pectoral-fin length 3.5–4.4 in SL, and 1.0–1.2 in maxi-mum body depth; stripes on midbody connect to oblique bars on caudal fin 18

18a   Total gill rakers 26–28; head length 3.2–3.5 in SL; barbel length 4.7–6.5 in SL; pectoral-fin length 3.9–4.4 in SL . . . . *U. suahelicus* Uiblein & Heemstra, 2010 (Southern Red Sea, Kenya to South Africa)

18b   Total gill rakers 27–32 (mostly 29–31); head length 3.0–3.3 in SL; barbel length 4.3–6.0 in SL; pectoral-fin length 3.5–4.3 in SL . . . .*U. supravittatus* Uiblein & Heemstra, 2010 (WIO: N Gulf of Oman to India, Sri Lanka; EIO)

19a   Head depth through eyes 4.1–5.0 in SL; postorbital length 6.7–7.4 in SL; pectoral-fin length 3.8–4.3 in SL; no stripes on body . . . . *U. davidaromi* Golani, 2001 (Gulf of Aqaba)

19b   Head depth through eyes 4.9–6.3 in SL; postorbital length 7.3–9.3 in SL; pectoral-fin length 4.1–4.9 in SL; no or 3–4 stripes on body in life 20

20a   Body depth at anus 4.7–5.5 in SL; caudal-peduncle depth 11–12 in SL; first dorsal-fin height 4.4–5.4 in SL; height of black tip of first dorsal fin and width of largest oblique bar and/or interspace between distal oblique bars of caudal-fin lower lobe less than eye diameter; no stripes on body in life . . . . *U. mascareinsis* Fourmanoir & Guézé, 1967 (Mozambique, Madagascar, Réunion)

20b   Body depth at anus 4.1–4.9 in SL; caudal-peduncle depth 8.6–10 in SL; first dorsal-fin height 3.6–4.6 in SL; height of black

tip of first dorsal fin and width of largest oblique bar and/or interspace between distal oblique bars of caudal-fin lower lobe subequal to or greater than eye diameter; 3 or 4 narrow yellow or bronzy stripes on body in life . . . . *U. vittatus* (Forsskål, 1775)

(WIO: Red Sea, Tanzania to South Africa, Madagascar, Mascarenes, Pakistan, India; EIO, W and Central Pacific)

Material examined

The material examined for the species accounts of *Upeneus guttatus* and *U. pori* is listed below. For any additional material used to prepare the identification key, see the literature sources cited in the key.

Upeneus guttatus: WIO (*n* = 36, 68–142 mm SL). Red Sea, Egypt, Gulf of Suez: MNHN-IC-1967-0553, 77 mm SL; SAIAB 88872, 98 mm SL, local fishermen (Suez fish market ?); Sudan: BMNH 1960-315.8.42-1, 77 mm SL, 5 miles S of Ibn Abbas Island; Saudi Arabia: SMF 35012, 78 mm SL, 16° 54.869' N, 42° 26.044' E, 21 m depth; WIO proper, Somalia: USNM 396093, 114 mm SL, 11° 14' N, 51° 08' E; Kenya: SAIAB 13947, 100 mm SL, RV *Dr. Fridtjof Nansen* cruise 1980, 03° 07' S, 40° 11' E, 17 m depth, bottom trawl; Mozambique: SAIAB 82166, 95 mm SL, SW of Beira, RV *Dr. Fridtjof Nansen*, M73, 20° 53.80' S, 35° 39.60' E, 61 m depth; SAIAB 82216, 91 mm SL, 19° 56.2' S, 35° 47.2' E, RV *Dr. Fridtjof Nansen*, M07-78, 47 m depth, bottom trawl; SAIAB 81746, 91 mm SL, RV *Dr. Fridtjof Nansen*, M07-07, 26° 30.4' S, 32° 58.4' E, 82 m depth, bottom trawl; SAIAB 82007, 2, 93–108 mm SL, RV *Dr. Fridtjof Nansen*, M07-46, 24° 33.7' S, 35° 15.6' E, 51 m depth, bottom trawl; SAIAB 82813, 102 mm SL, RV *Dr. Fridtjof Nansen*, M07-77, 19° 47.4' S, 35° 30.7' E, 28 m depth, bottom trawl; SAM MB-F034164, 142 mm SL, 18° 30' S, 37° 15' E; VIMS 7487, 93 mm SL, 20° 30' S, 35° 49' E, 32 m depth; Madagascar: MNHN 1965-0017, HT of *U. crosnieri*, 126 mm SL, off SW Madagascar, Pracel Bank, 45 m depth; SAIAB 52827, 92 mm SL, NW Madagascar, Tsimipaika Bay, MAD 95-10, 8–12 m depth; SAIAB 192775, 2, 90–104 mm SL, off NE Madagascar, 17° 32.29' S, 49° 37.13' E, RV *Dr. Fridtjof Nansen*, st. 2008405-24, 51–52 m depth, bottom trawl; SAIAB 209011, 133 mm SL, same data; Réunion: MNHN-IC-1967-0554, 92 mm SL, Bay of La Possession, 20° 53' S, 55° 21' E, 80 m depth; Seychelles: BPBM 35580, 3 (of 6), 68–76 mm SL, Poivre Atoll, 5° 46' S, 53° 11' E, 57 m depth, Agassiz trawl; SAIAB 84255, 10, 93-117 mm SL, Seychelles, Seychelles Bank, RV *Dr. Fridtjof Nansen*, ACEP 08-26, 5° 41' 52.8'' S, 56° 42' 07.2'' E, 59 m depth, bottom trawl; SAIAB 84281, 3, 106-117 mm SL, Seychelles, Seychelles bank, RV *Dr. Fridtjof Nansen*, ACEP 08-27; 5° 24' 25.2'' S, 56° 25' 43.8'' E, 60 m depth, bottom trawl.

EIO (*n* = 16, 78–112 mm SL). India: Andaman Islands, HIFIRE F5898, 91 mm SL, South Andaman district; Myanmar, Bay of Bengal: SAIAB 203668, 109 mm SL, RV *Dr. Fridtjof Nansen*, 18° 37.61' N, 93° 39.53' E, St. 2015404-17, 36–38 m depth; SAIAB 203675, 104 mm SL, 19° 40.84' N, 92° 54,13' E, RV *Dr. Fridtjof Nansen*, St. 2015404-4, 45 m depth; SAIAB 203676, 99 mm SL, 19° 06.31' N, 93° 07.89' E, St. 2015404-10, RV *Dr. Fridtjof Nansen*, 78 m depth; Andaman Sea: VIMS 7521, 96 mm SL, 09° 54' N, 97° 42' E, 73 m depth; VIMS 7584, 102 mm SL, same locality as before; Malaysia, Malacca: ZMUC P49432, 108 mm SL; W Australia: AMS I.22801-004, 3, 78–94 mm SL, off Port Hedland, 19° 32' S, 118° 09' E, RV *Soela*, 50–52 m depth; AMS I.22831-012, 4, 80–91 mm SL, NW Shelf, 140km W of Port Hedland, 20° 00' S, 117° 16' E, FRV *Soela*, 50 m depth; CSIRO CA 283, 112 mm SL, N of Nickol Bay, 20° 06' S, 117° 06' E, FRV *Courageous*, 42-44 m depth; CSIRO CA 3044, 101 mm SL, NW of Port Hedland, 20° 06' S, 118° 00' E, FRV *Soela*, 29–30 m depth;

Pacific (*n* = 23, 85–159 mm SL). Malaysia, NE Pacific: KAUM 41717, 96 mm SL, Terengganu, 48 km off Cendering, Kuala Terengganu, 5° 16' N, 103° 11' E, 70–90 m depth; KAUM 41718, 101 mm SL, same collection data; Philippines: CAS 232885, 118 mm SL, Negros, N of Cadiz town, 11° 05' N, 123° 20' E, 18-36 m depth; Vietnam, Nha Trang: MNHN-IC-1965-0273, 159 mm SL, 12° 03' N, 112° 03' E; Nha Trang, fish market: HIFIRE F58153, 108 mm SL; HIFIRE F58154, 111 mm SL; HIFIRE F58172, 132 mm SL; NE Australia, Queensland: CSIRO H 6519-18, 2, 103–108 mm SL, NE of Cooktown, 15° 02.24' S, 145° 28.91' E, FRV *Gwendoline May*, 39 m depth; CSIRO H 7024-02, 114 mm SL, N of Cairns, 16° 33.20' S, 145° 52.69' E, FRV *Gwendoline May*, 37 m depth; CSIRO H 7206-01, 107 mm SL, Torres Strait, NE of Darnley Island, 9° 28.85' S, 143° 58.12' E, FRV *Gwendoline May*, 54 m depth; CSIRO H 7207-01, 108 mm SL, and CSIRO H 7207-02, 4, 92–108 mm SL, E of Cooktown, 15° 29.88' S, 145° 23.03' E, FRV *Gwendoline May*, 25 m depth; CSIRO H 7212-02, 121 mm SL, SE of Cairns, 17° 08.47' S, 146° 12.51' E, FRV *Gwendoline May*, 35 m depth; QM I.20325, 2: 89-104 mm SL, Flora Passage, 17° 03' S, 146° 14' E, 37–42 m depth; New Caledonia, Chesterfield Islands: BPBM 39472, 3: 90–102mm SL; Japan, Kagoshima: KAUM 13067, 121 mm SL, E of Sakinoyama, Kataura, Kasasa, Minamisatsuma, 31° 25.44' N, 130° 11.49' E, 27 m depth; KAUM 24423, 85 mm SL, same collection information.

Fresh-colour photographs of non-examined specimens. In-situ photographs of two specimens, SWIO, N Mozambique, Cabo Delgado, Pemba, boatyard (R. Koch); and N Mozambique, Nampula, Nacala (R. Koch); photograph of recently deceased specimen, **S**WIO, Tanzania, Mafia Channel, (J.E. Randall).

Upeneus pori: *Meditrereanean Sea* (n = 8, 72–110 mm SL). Egypt**:** BMNH 1979.3.20.24, 110 mm SL, off Alexandria; Lebanon: BPBM 31277, 7, 72–77 mm SL, off St. George's Bay.

WIO, Red Sea (*n* = 20, 66–117 mm SL). Egypt, Gulf of Suez, MNHN-IC-1980-1517, 96 mm SL, 28° 40' S, 32° 53' E; Gulf of Aqaba, Nuweiba: BPBM 19823, 6, 80–109 mm SL, El Muzeini; Israel, Gulf of Aqaba, Eilat: BPBM 30904, 6 (of 7), 80–117 mm SL, N beach, seine; BPBM 33505, PT, 110 mm SL; CAS 66225, PT, 107 mm SL, MNHN-IC-1977-1046, 89 mm SL, beach; MNHN-IC-1989-0537, PT, 102 mm SL; SAIAB 28958, PT, 92 mm SL; SAIAB 65781, 66 mm SL, N beach; USNM 303539, PT, 100 m SL.

WIO proper (*n* = 4, 89–97 mm SL). Madagascar: MNHN-IC-1992-977, 97 mm SL, off SW Madagascar, Toliara ("Vontira"); SAIAB 209540, 3, 89–96 mm SL, off NE Madagascar, 17° 32.29' S, 49° 37.13' E, RV *Dr. Fridtjof Nansen*, st. 2008405-24, 51–52 m depth, bottom trawl.

Acknowledgments

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