



Three new goatfishes of the genus *Upeneus* (Mullidae) from the Indo-Pacific, with a redescription of colour patterns in *U. margarethae*

FRANZ UIBLEIN^{1,2,3,8}, DANIEL C. GLEDHILL⁴, DIMITRI A. PAVLOV⁵,
TUAN ANH HOANG^{3,6} & SHAKER SHAHEEN⁷

¹Institute of Marine Research, P.O. Box 1870 Nordnes, N-5817 Bergen, Norway.

²South African Institute for Aquatic Biodiversity, Grahamstown, South Africa

³Vietnam National Museum of Nature, Vietnam Academy of Science and Technology (VAST), Ha Noi, Vietnam

⁴Division of Water and Marine Resources, Department of Primary Industries, Parks, Water and Environment, Hobart, Australia

⁵Biological Faculty, Moscow State University, Moscow, Russia

⁶Graduate University of Science and Technology, VAST, Ha Noi, Vietnam

⁷Faculty of Marine Sciences and Fisheries Red Sea University, Port Sudan, Sudan

⁸Corresponding author. E-mail: franz@hi.no

Abstract

For the goatfish genus *Upeneus* Cuvier 1829 (Mullidae), a new taxonomic species group called the “*margarethae* group” is established which can be distinguished from the six species of the most similar “*tragula* group” by a combination of the following characteristics: absence of dark pigmentation in the area of the first dorsal-fin tip, 21–25 total gill rakers and 28–30 lateral-line scales. Initially, three recently-described species have been included in the *margarethae* group: *Upeneus margarethae* Uiblein & Heemstra, 2010, known from the Indian Ocean including the Red Sea and from the Arafura Sea (W Pacific), *U. mouthami* Randall & Kulbicki, 2006, from New Caledonia and Vanuatu (W Pacific), and *U. randalli* Uiblein & Heemstra, 2011, from the Arabian/Persian Gulf and the inner Gulf of Oman (NW Indian Ocean). The present taxonomic review of the *margarethae* group analyses a large data set of 41 morphometric, 10 meristic and many colour characters obtained from 279 preserved goatfish specimens and 166 fresh-colour photos (plus a fresh-colour drawing). For the nominal species of the group, *U. margarethae*, a redescription of the colour patterns is provided and new records for Myanmar, Andaman Sea (NE Indian Ocean) and the Gulf of Carpentaria, N Australia (W Pacific), are reported. Three new species are described: *U. caudofasciatus* **n. sp.** from the area of the Great Barrier Reef to Torres Strait off NE Australia (Coral Sea, W Pacific), *U. gubal* **n. sp.** from the S Gulf of Suez (Northern Red Sea), and *U. heterospinus* **n. sp.** from S Indonesia to Singapore, the Gulf of Thailand, Vietnam, Philippines, China, Taiwan and Japan (W Pacific). A comprehensive alpha-taxonomic approach is adopted, considering population differences as well as intraspecific size-related variation in morphology and colour patterns by splitting the data set into two size classes, adults (≥ 65 mm SL) and smaller subadults. Inter- and intraspecific comparisons include statistical analyses for species and population with sufficiently large samples sizes ($n \geq 20$). Colour-pattern characterization and analysis are based on photos of recently collected and deceased fish (partly associated with voucher specimens), photos obtained from active or resting fishes *in situ* or in a tank, and inspection of pigmentation patterns retained in preserved specimens. Species differences are elaborated under consideration of distribution patterns and the characteristics found in the closest-most population of widely distributed species such as *U. margarethae*, resulting in clear and consistent distinction among the six species in single or in a combination of several characteristics. Comparisons among size classes revealed species-specific patterns in morphometric, meristic and colour changes with increasing size. One species, *U. heterospinus* **n. sp.**, has seven or eight spines in the dorsal fin which occur in balanced ratio across populations. This is a unique characteristic for *Upeneus* species which usually have either seven or eight dorsal-fin spines, respectively. The best distinction of *Upeneus heterospinus* **n. sp.** from all other congeners is reached by combined examination of dorsal-fin spines with several other characters such as barbel colour, presence of a mid-lateral body stripe, pigmentation patterns (partly retained also in preserved fish), gill-raker and pectoral-fin ray numbers, and body-shape variables. The high degree of overall morphological differentiation among the three most common species *U. caudofasciatus* **n. sp.**, *U. heterospinus* **n. sp.** and *U. margarethae*, as revealed by the statistical comparisons, strongly contrasts with a still significant, but much lower degree of differentiation among populations. The diagnostic characteristics of the *margarethae* group are updated and the importance to use the results of this taxonomic review in ongoing fisheries-related and ecological research is emphasized. Requirements for future taxonomic research featuring the stunning diversity of the goatfish genus *Upeneus* are also discussed.

Key words: *margarethae* species group, meristic characters, body shape, colour patterns, comprehensive alpha taxonomy

Introduction

Margaretha's goatfish, *Upeneus margarethae* Uiblein & Heemstra, 2010 (Mullidae), is a fairly widespread species that occurs in the Western Indian Ocean (WIO) between Mozambique, the Red Sea, S India and Sri Lanka, the Eastern Indian Ocean (EIO) off W Thailand and NW Australia, as well as in the Arafura Sea off N Australia, SW Pacific. It has been found to be rather common in bottom trawl catches at soft shallow bottoms to depths of 50 m (Uiblein & Heemstra 2010; 2011), but detailed ecological and biological data are still lacking.

Among the 39 valid *Upeneus* species (Uiblein *et al.* 2017), *U. margarethae* has been included in the so-called *tragula* group based on similarities in meristic, morphometric and colour characters (Uiblein *et al.* 2016), along with eight other species: *Upeneus heemstra* Uiblein & Gouws, 2014, *U. luzonius* Jordan & Seale, 1907, *U. mouthami* Randall & Kulbicki, 2006, *U. niebuhri* Gueze, 1976, *U. oligospilus* Lachner, 1954, *U. randalli* Uiblein & Heemstra, 2011, *U. sundaicus* (Bleeker, 1855) and the nominal species *U. tragula* Richardson, 1846. The main characteristics of the *tragula* group are eight dorsal-fin spines, low pectoral-fin ray and gill-raker counts (12–15 pectoral fin-rays; 19–25 total gill rakers) and the presence of oblique bars on both caudal-fin lobes and a mid-lateral body stripe, at least when fresh or in life.

Three species, *U. margarethae*, *U. mouthami* and *U. randalli*, can be distinguished from the other *tragula*-group species by a combination of the following characteristics: absence of dark pigmentation in the area of the first dorsal-fin tip, 21–25 total gill rakers and 28–30 lateral-line scales (Uiblein *et al.* 2016). *Upeneus heemstra*, *U. niebuhri*, *U. oligospilus* and *U. tragula* all have a dark first dorsal-fin tip, and *U. luzonius* and *U. sundaicus* have 18–22 gill rakers and 31–34 lateral-line scales (Uiblein *et al.* 2016). In contrast to *U. margarethae*, *U. randalli* and *U. mouthami* are more restricted in their distribution, occurring in the Arabian/Persian Gulf and Gulf of Oman (*U. randalli*), and in New Caledonia and Vanuatu (*U. mouthami*) (Uiblein *et al.* 2016). These three species are here included in a new taxonomic group, the so-called “*margarethae* group”.

Since the descriptions of *U. margarethae* and *U. randalli*, the first author examined a large number of specimens with similar characteristics of the *margarethae* group during fish collection visits. Many of the newly studied specimens are from formerly unknown occurrence areas in the Indian Ocean, such as the Gulf of Suez (Northern Red Sea) and Myanmar (NE Indian Ocean), and in the W Pacific, such as the Gulf of Carpentaria, Torres Strait, and the Great Barrier Reef (NE Australia, Queensland), SW Indonesia and Singapore, the Gulf of Thailand, the South China Sea off Vietnam, and the Philippines.

In addition to the fish collection visits, two of the authors (DAP, FU) collected a large number of fresh goatfishes from local markets or directly from fishermen in Vietnam during research stays at the coastal and main departments of the Joint Vietnamese-Russian Tropical Research and Technological Centre (VRTC), in Nha Trang and Ha Noi, respectively. Photos were taken and specimens of many of these fishes preserved, which - after preliminary inspection - belonged to the *margarethae* species group. Specimens were deposited in the fish reference collection of the Institute of Marine Research, Bergen, Norway (HIFIRE), for detailed studies. Furthermore, *in-situ* photos became available from various sources during the course of the above activities. When trying to identify this new material to species level, several problems were encountered including the following: (1) photos of fresh *U. margarethae* taken shortly after capture or encountered *in situ*, as well as detailed examination of preserved conspecifics revealed a more diverse colour pattern than hitherto documented; (2) specimens from NE Australia (Torres Strait to S Great Barrier Reef) deviated considerably in a combination of several meristic and morphometric characters; (3) specimens from the South China Sea and adjacent areas differed in barbel colour and showed a rather unique meristic dimorphism of seven or eight dorsal-fin spines; (4) a single preserved specimen from the Gulf of Suez (Northern Red Sea) clearly deviated in a combination of two meristic and one morphometric characters from the population of *U. margarethae* occurring in the South-central and Southern Red Sea. These findings require a taxonomic review of the *margarethae* species group with updated taxonomic accounts, a redescription of fresh colour pattern in *Upeneus margarethae*, and the description of three new species.

As in previous taxonomic studies of the genus *Upeneus*, we adopted a comprehensive alpha-taxonomic approach that considers intraspecific variation in size and associated body shape allometry and ontogenetic variation

in colour patterns as well as population differences (e.g., Uiblein & Gledhill 2015; Uiblein & Gouws 2015; Uiblein *et al.* 2016). Making use of a large number of preserved fish specimens, quantitative statistical comparisons were conducted to provide additional evidence for intra- and interspecific differentiation. Furthermore, many photos of freshly deceased or live fishes were used to describe and analyze colour patterns. The results are discussed with respect to the need for a more complete understanding of the diversity of *Upeneus* goatfishes and to take steps towards studying the ecology and biology of the various species and populations in a comparative context.

Material & methods

During the course of this study, the following institutions were visited: the Australian Museum, Sydney (AMS), the Australian National Fish Collection (CSIRO), the California Academy of Sciences, San Francisco, USA (CAS), the Museum of Natural Sciences, College of Fisheries and Ocean Sciences, University of the Philippines Visayas, Iloilo, Philippines (UPVMI), the National Museum of Natural History, Paris, France (MNHN), the Natural History Museum, University of Oslo, Norway (NHMO), the Queensland Museum, Brisbane, Australia (QM), the Senckenberg Research Institute and Natural History Museum, Frankfurt, Germany (SMF), the South African Institute of Aquatic Biodiversity, Grahamstown, South Africa (SAIAB), the Western Australian Museum, Perth (WAM), and the Zoological Museum, University of Copenhagen, Denmark (ZMUC).

In total 279 preserved specimens that were identified as belonging to the *margarethae* group were studied based on a large set of characters including standard length (SL), 40 additional morphometric characters (all in mm, to the nearest second decimal), and 10 meristic characters following Uiblein *et al.* (2016, 2017). The preserved specimens, and a total of 166 photos and one colour drawing of freshly deceased or live fish (= fresh-colour photos) were studied regarding the presence and number of oblique bars on the caudal fin, the presence of dark dots along the body stripe and/or lateral line, a dark saddle behind second dorsal fin, and a dark stripe or blotch on or close to the tip of the second dorsal fin (=distal dorsal-fin stripe). All photos and the drawing were also used to identify fresh barbel colour and the colour and shape of the mid-lateral body stripe.

Regarding colour patterns of preserved fish, the number of retained bars on each caudal-fin lobe were recorded for all specimens along with the absence or presence of the following pigmentation patterns: remains of bars on each single and both caudal-fin lobes, a dark distal dorsal-fin stripe, a dark saddle behind the second dorsal fin, and dark dots occurring mid-laterally on the body (= remains of dark dots on the mid-lateral body stripe). Based on these data, an index of pigmentation degree was calculated for each fish, ranging from 0 (= total absence of the four colour patterns) to 4 (= presence of all four colour patterns).

In the taxonomic analyses, particular attention was paid to elaborate the most important diagnostic characters for distinction among species in the subsequent comparisons, either singly or in combination, taking sample size and intraspecific variation into account. Intraspecific comparisons were made between two different size groups and among populations. In order to consider growth-related allometric variation, two size groups were identified, following previously published information from taxonomic studies of other, similar-sized *Upeneus* species (Uiblein & Gledhill 2015; Uiblein *et al.* 2017). Specimens of 65 mm SL or more were termed “adults” and specimens of less than 65 mm SL “subadults”. Types were chosen from the available material according to their condition, the availability of a fresh-colour photo, and their occurrence relatively close to the type locality.

Quantitative statistical analyses were conducted to provide detailed information from comparisons of populations and species with larger sample sizes. For this purpose, the morphometric data of adult fish of the three species and populations of two of these species, all with sample sizes of $n \geq 20$, were size-adjusted using the residuals derived from log-log regressions against SL (Uiblein & Winkler 1994) generated for the analyzed data set, respectively. All regressions were highly correlated and significant. Then, One-way ANOVA comparisons of populations and species were conducted. The main meristic characters that varied in each of the three quantitatively examined species (pectoral-fin rays, gill rakers on either limb and both limbs together, lateral-line scales) did not show size-dependency and were therefore analyzed after pooling the data of adults and subadults using Chi² test for trends (GraphPad Prism software). This analytical method was also applied to pigmentation degree, but only to adults, as subadults showed considerable deviations and their sample sizes were too low for separate statistical treatment. For presence/absence data of colour patterns 2x2 tables were prepared and analyzed using Fisher’s exact test. The significance level was globally set at $p \leq 0.01$.

In the material lists accompanying each species account, fresh-colour photos and the single fresh-colour drawing of studied voucher specimens are presented and all fresh-colour photos of specimens that were not retained for further examination are listed with locality details and photographer, publication, or institutional reference. Institutional abbreviations follow Sabaj (2019; <https://asih.org/standard-symbolic-codes/about-symbolic-codes>). Other abbreviations are: SL = standard length; TL = total length; HT = holotype; PT = paratype.

Taxonomy

Genus *Upeneus* Cuvier 1829

Upeneus margarethae Uiblein & Heemstra, 2010

Margaretha's goatfish

(Figures 1–6; Tables 1–7)

Upeneus margarethae Uiblein & Heemstra, 2010. Type locality off Beira, Mozambique, SW Indian Ocean.

Upeneus margarethae: Uiblein & Heemstra 2011 (fresh colour photo of holotype); Bogorodsky *et al.* 2014 (S Saudi Arabia, Red Sea).

Upeneus luzonius non Jordan & Seale, 1907: Ray *et al.* 2016 (fresh-colour photo from the N Bay of Bengal, E India, EIO).

Upeneus tragula Richardson, 1846: Sainsbury *et al.* 1985 (vouchered fresh-colour photo from NW Australia, EIO).

Upeneus tragula non Richardson, 1846: Ratmuangkhwang 2018 (fresh-colour photo from W Thailand, Andaman Sea, EIO).

Holotype. SAIAB 82217, male, 82 mm SL, WIO, Mozambique, off Beira, 19°56.17' S, 35°47.16' E, RV *Dr. F. Nansen*, bottom trawl, 47 m depth; collectors Phil & Elaine Heemstra, 21 Oct 2007 (fresh-colour photo).

Paratypes. (20 adults: 67–124 mm SL; 1 fresh-colour photo). WIO, Somalia: USNM 396092, PT, 124 mm SL, off Bargaal, 11°14' N, 51°08' E; Kenya: SAIAB 82817, 5: 89–110 mm SL, off Kipini, 02°38' S, 40°28' E, RV *Dr. F. Nansen*, bottom trawl, 11–12 m depth; Mozambique: SAIAB 82209, 89 mm SL, off Beira, 19°47.45' S, 35°30.73' E, RV *Dr. F. Nansen*, bottom trawl, 28 m depth; SAIAB 82814, 2: 89–97 mm SL, same collecting data as holotype (fresh-colour photo); Madagascar: SAIAB 82815, 11: 67–94 mm SL, Tsimipaika Bay, 8–12 m depth.

Non-types. (66 adults, 11 subadults: 40–129 mm SL, 14 fresh-colour photos): WIO proper: Kenya: SAIAB 82825, 12: 40–95 mm SL, same collection data as PT SAIAB 82817; Tanzania: BPBM33441, 100 mm SL, Mafia Island, Mafia Channel, 10–50 m depth; SAIAB 87108, 112 mm SL, Zanzibar, Mazizini, landing site adjacent to Zanzibar Beach Resort; Mtwara, Mikindani landing site (each with fresh-colour photo): HIFIRE F 58449, 79 mm SL; HIFIRE F 58450, 70 mm SL; SAIAB 104431, 77 mm SL; Zanzibar, Stone Town, landing site and fish market (each with fresh-colour photo): HIFIRE F 58451, 90 mm SL; HIFIRE F 58452, 87 mm SL; HIFIRE F 5453, 84 mm SL; HIFIRE F 58454, 85 mm SL, HIFIRE F 58455, 95 mm SL; SAIAB 104432, 3: 90–114 mm SL; Mozambique: SAIAB 81741, 128 mm SL, off Machangulo, 26°10' S, 32°59' E, 45 m depth; SAIAB 86466, 2: 75–84 mm SL, off Beira, 19°47.44' S, 35°30.72' E, RV *Dr. F. Nansen*, bottom trawl, 28–29 m depth; Madagascar: MNHN 1966–881, 90 mm SL, no locality information; SW-India, Kerala State: BPBM27694, 2, 71–82 mm SL, Vizhinjam fishing harbor; Sri Lanka: USNM 396094, 78–79 mm SL, Colombo fish market, landed at Eravur; WIO, Red Sea: Sudan: BMNH 1960.3.15.841, 63 mm SL, Ibn Abbas Island, 5 km S of island, FRV *Manihine*; Saudi Arabia, off Jizan, FV *Attiat Alrahman 2*, bottom trawl: KAUMM 27, 90 mm SL, 16° 44.32' N, 42° 26.941' E, 42 m depth; KAUMM 49, 5: 96–113 mm SL, 16° 53.621' N, 42° 23.633' E, 25.5–28 m depth; KAUMM 59, 1 of 5: 109 mm SL, 16° 44.508' N, 42° 29.497' E, 18.5–21.5 m depth; KAUMM 109, 2 of 11: 67–91 mm SL, 16° 54.869' N, 42° 26.044' E, 21 m depth; SMF 34972, 4: 93–111 mm SL, 16° 53.621' N, 42° 23.633' E, 25.5–28 m depth; SMF 35011, 3: 90–116 mm SL, 16° 44.508' N, 42° 29.497' E, 18.5–21.5 m depth; SMF 35030, 90 mm SL, 16° 57.873' N, 42° 25.523' E, 16–19 m depth (fresh-colour photo); SMF 35059, 91 mm SL, 16° 54.869' N, 42° 26.044' E, 21 m depth; SMF 35060, 91 mm SL, 16° 44.32' N, 42° 26.941' E, 42 m depth; Eritrea: MNHN1984–455, 2: 93–94 mm SL, RV *Dr. F. Nansen*, bottom trawl (possibly off Assab, 13°21' N, 42°25' E, 30 m depth); EIO: Andaman Sea: Myanmar (new record): SAIAB 203672, 110 mm SL, S of Buda Island, 10°19.43' N, 98°14.69' E, RV *Dr. F. Nansen*, bottom trawl, 104 m (fresh-colour photo); SAIAB 203480, 95 mm SL, NW of Bashuhino Island, 14°40.29' N, 97°15.93' E, RV *Dr. F. Nansen*, bottom trawl, 57 m depth; Thailand, Phuket: ZMUC P49560, 85 mm SL; NW Australian shelf: AMS 22831–021, 3 (of 6): 81–97 mm SL, 140 km W of Port Hedland, 20°00' S, 117°16' E, 50 m depth; BMNH 1983 5.5.28–30, 3:

108–117 mm SL, off Port Hedland, 20°10' S, 118°25' E; CSIRO CA 3052, 98 mm SL, off Port Hedland, 20°03.8' S, 117°57.2' E, 38–39 m depth (fresh-colour photo); WAM 25397.004, 3 (of 7): 94–102 mm SL, Rowley Shoals, 17°29' S, 121°52' E, 42 m depth; Exmouth Gulf: WAM 23785-6, 100 mm SL; WAM 32680-002, 93 mm SL, Exmouth Gulf, Bundegi Reef, 21°50.879' S, 114°15.530' E, 24 m depth; W Pacific: N Australia, Northern Territory, Arafura Sea: AMS I.21849-009, 6: 95–101 mm SL, off Arnhem Land, 11°29' S, 134°23' E, RV *Soela*, Engel trawl, 105 m depth; Queensland, Gulf of Carpentaria (new record): CSIRO A 2881, 95 mm SL, E of Mornington Island, 16°35.7' S, 140°41.6' E, FV *Rama*, prawn trawl, 18 m depth.

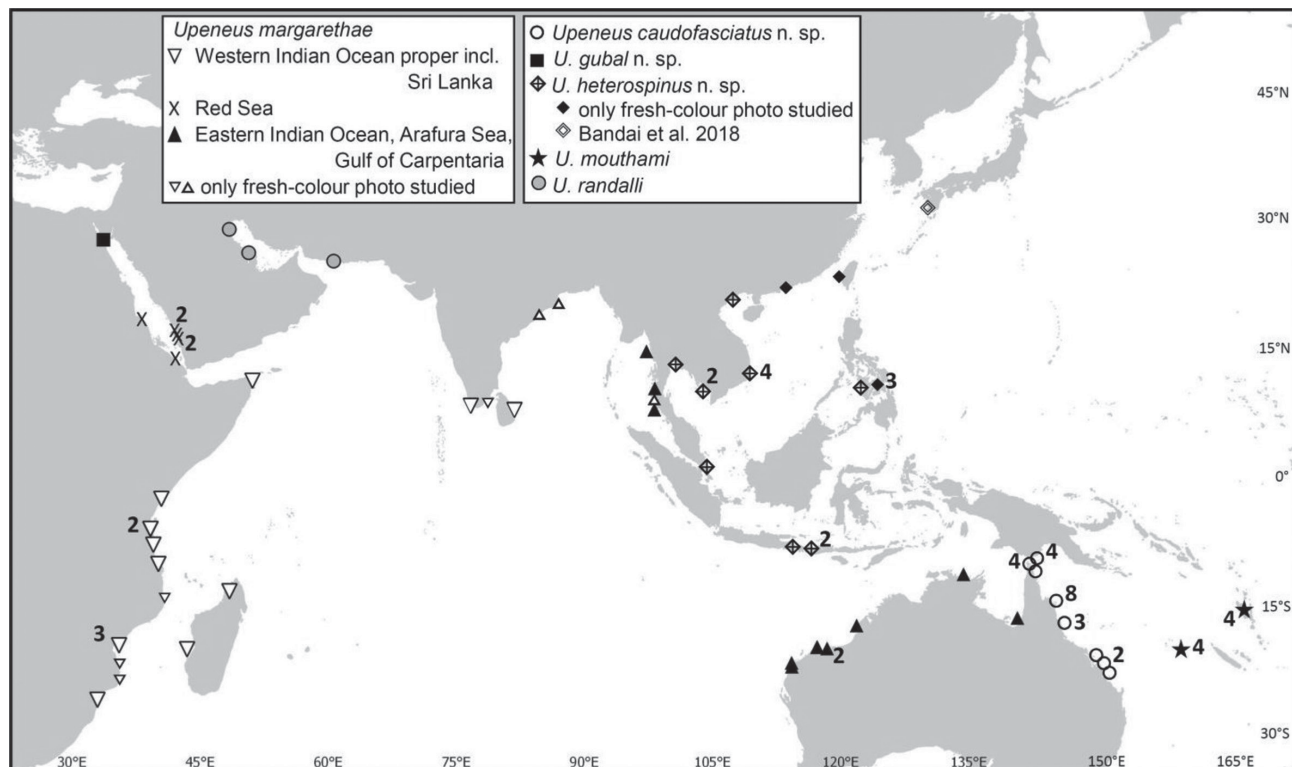


FIGURE 1. Map showing the distribution of the six species of the *margarethae* group. Three populations of *Upeneus margarethae* are indicated by different symbols. Numbers indicate multiple sampling localities.

Fresh-colour photos of specimens not retained ($n=16$): WIO proper: subadult or adult, Pemba Bay, near Pemba harbour, N Mozambique (R. Koch); subadult or adult, Pomene, South-central Mozambique (M. & V. Fraser); adult, Lunene Island, off Vilanculos, South-central Mozambique (A. Lund); adult and subadult, Tanzania, Mafia Channel (J.E. Randall); adult, Tuticorin, S India (K.K. Bineesh); Red Sea: 3 adults, Jizan, Saudi Arabia (S. Bogorodsky); EIO: adult, Digha Morona, West Bengal, E India (Ray *et al.* 2016); 4 adults, Puri, Odisha, E India (S. K. Roul); subadult, Kampuan mangrove forest, Amphoe Suksamran, Ranong, Thailand (S. Ratmuangkhwang); adult, off NW Australia, unknown locality, RV *Soelae* (CSIRO staff).

Diagnosis. Dorsal fins VIII + 9, the first spine minute; pectoral fins 13–15; gill rakers 5–7 + 15–18 = 21–24; lateral-line scales 28–30; measurements in % SL, adults: body depth at first dorsal-fin origin 22–27; body depth at anus 20–24; caudal-peduncle depth 9.3–12; caudal-peduncle width 3.5–5.7; maximum head depth 18–23; head depth through eye 15–18; suborbital depth 8.3–12; interorbital length 7.3–9.1; head length 27–31; snout length 9.7–12; postorbital length 10–13; orbit length 6.2–9.1; upper-jaw length 9.8–12; barbel length 15–20; interdorsal distance 12–16; caudal-peduncle length 22–26; caudal-fin length 27–31; anal-fin height 14–18; pelvic-fin length 20–24; pectoral-fin length 19–24; pectoral-fin width 4.1–5.3; first dorsal-fin height 18–23; second dorsal-fin height 15–20; subadults: body depth at first dorsal-fin origin 24–26; body depth at anus 21–23; caudal-peduncle depth 10–11; caudal-peduncle width 3.4–4.4; maximum head depth 19–22; head depth through eye 15–17; suborbital depth 7.6–9.4; interorbital length 7.6–8.1; head length 28–32; snout length 9.9–12; postorbital length 11–13; orbit length 7.5–9.0; upper-jaw length 11–12; barbel length 17–18; interdorsal distance 14–17; caudal-peduncle length 24–26; caudal-fin length 29–33; anal-fin height 17–19; pelvic-fin length 22–24; pectoral-fin length 21–23; pectoral-fin width 4.3–5.1; first dorsal-fin height 21–24; second dorsal-fin height 19–21; fresh colour: head and body dorsally red, brown or pale red-brown mottled, ventrally white, often with pale red brown dots or larger red blotches

(the latter together with dark vertical bands in inactive, live fish); caudal fin with maximally 15 red, brown or dark-grey oblique bars on both lobes; on upper caudal-fin lobe 4 or 5 (rarely 6) bars (3 or 4 bars in subadults), on lower lobe 6–9 bars (3–6 bars in subadults) which are often crossed or covered by a red, brown or dark-grey stripe that may cover the dorsal half of lobe or almost the entire lobe leaving only the ventral margin free; caudal-fin bars and hyaline interspaces of about pupil width in adults; lower caudal lobe tip sometimes black; barbels entirely white or mostly white, intermingled with pale rose; a single yellow, beige, or orange mid-lateral body stripe of pupil width from snout tip through eye to caudal-fin base; stripe sometimes covered by 1–4 sections with horizontal series of 2–4 dark brown or black dots, the posteriormost series of dots behind second dorsal-fin base, often connecting to a dark saddle placed behind second dorsal fin; first dorsal fin with often closely fused pale-red or pale-grey brown stripes; the tip region of first dorsal fin not darker than remainder of fin and often without any pigmentation; the tiny first dorsal-fin spine sometimes dark pigmented, also in preserved fish; second dorsal fin with 3 or 4 red or brown, well-separated stripes with hyaline interspaces; preserved fish entirely brown, pale brown or pale grey, the mid-lateral stripe completely lost, but often with remains of pigmentation deriving from caudal-fin bars, dark mid-lateral dots, a saddle and/or second dorsal-fin distal stripes.

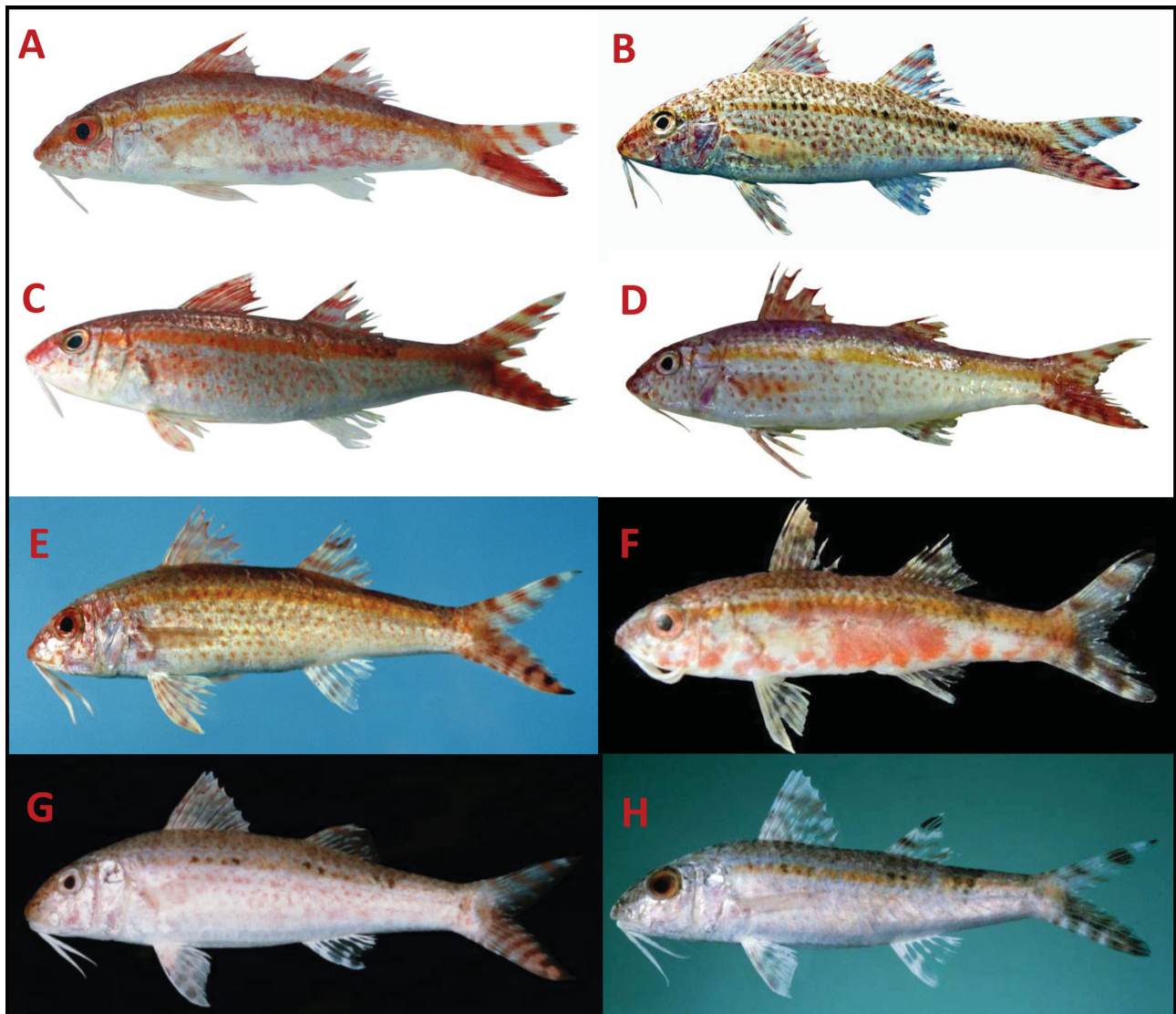


FIGURE 2. (A–F) *Upeneus margarethae*; (A) HT, SAIAB 82217, 82 mm SL, WIO, Mozambique, off Beira (O. Alvheim); (B) SMF 35030, 90 mm SL, Red Sea, Saudi Arabia, off Jizan, (S.V. Bogorodsky); (C) 86 mm SL, Tuticorin, S India (K.K. Bineesh); (D) SAIAB 203480, 95 mm SL, EIO, Myanmar, NW of Basuhino Island (P. Psomadakis; side-reversed image); (E) CSIRO CA 3052, 98 mm SL, EIO, NW Australia, off Port Hedland (CSIRO staff); (F) subadult, 47 mm SL, EIO, Thailand, Kampuan Mangrove forest, Suksamran, Ranong (S. Ratmuangkhwang); (G, H) *U. randalli*: (G) HT, BPBM 33180, 101 mm SL, Arabian/Persian Gulf, off S Kuwait, (J.E. Randall); (H) BPBM29498, 60 mm SL, Bahrain (J.E. Randall).

TABLE 1. Morphometric, meristic and preserved colour characters in the three populations and all examined specimens of adult *Upeneus margarethae*, with data of the holotype of *U. gubal* n. sp. (with meristic counts for left and right body sides). Area abbreviations: WIOP ... Western Indian Ocean proper; EIO/NA ... Eastern Indian Ocean and N Australia (Arafura Sea and Gulf of Carpentaria).

| Morphometric characters | <i>Upeneus margarethae</i> | | | | | | | | | | | | HT | | | | |
|--|----------------------------|------|-----|----|-----|------|--------|----|-----|------|-----|----|-----|------|------|-----|-----|
| | WIOP including types | | | | | | EIO/NA | | | | | | | all | | | |
| | Min | Mean | Max | n | Min | Mean | Max | n | Min | Mean | Max | n | | Min | Mean | Max | n |
| Standard length (SL) in % SL | 65 | 89.3 | 129 | 44 | 67 | 98.2 | 116 | 21 | 81 | 99.0 | 117 | 22 | 65 | 93.9 | 129 | 87 | 86 |
| Body depth at first dorsal-fin origin | 22 | 24.7 | 26 | 44 | 23 | 25.0 | 26 | 21 | 24 | 25.2 | 27 | 22 | 22 | 24.9 | 27 | 87 | 24 |
| Body depth at anal-fin origin | 20 | 21.2 | 24 | 44 | 20 | 22.1 | 24 | 21 | 21 | 21.9 | 23 | 22 | 20 | 21.6 | 24 | 87 | 21 |
| Half body depth at first dorsal-fin origin | 18 | 20.2 | 22 | 44 | 19 | 20.7 | 22 | 21 | 19 | 20.8 | 22 | 21 | 18 | 20.5 | 22 | 86 | 20 |
| Half body depth at anal-fin origin | 15 | 16.3 | 18 | 43 | 15 | 16.6 | 19 | 21 | 15 | 16.6 | 17 | 20 | 15 | 16.4 | 19 | 84 | 17 |
| Caudal-peduncle depth | 9.3 | 10.5 | 11 | 44 | 10 | 10.8 | 11 | 21 | 10 | 10.8 | 12 | 22 | 9.3 | 10.6 | 12 | 87 | 11 |
| Caudal-peduncle width | 3.5 | 4.4 | 5.7 | 44 | 3.5 | 4.0 | 4.5 | 21 | 3.8 | 4.2 | 5.3 | 22 | 3.5 | 4.3 | 5.7 | 87 | 3.3 |
| Maximum head depth | 19 | 20.7 | 23 | 44 | 18 | 20.4 | 21 | 21 | 19 | 21.5 | 23 | 22 | 18 | 20.8 | 23 | 87 | 20 |
| Head depth through eye | 16 | 16.6 | 18 | 44 | 15 | 16.1 | 17 | 21 | 16 | 16.7 | 18 | 22 | 15 | 16.5 | 18 | 87 | 16 |
| Suborbital depth | 8.8 | 9.9 | 12 | 44 | 9.3 | 10.3 | 12 | 21 | 8.3 | 10.2 | 12 | 22 | 8.3 | 10.0 | 12 | 87 | 9.0 |
| Interorbital length | 7.3 | 8.1 | 9.1 | 44 | 7.5 | 8.0 | 8.9 | 21 | 7.6 | 8.2 | 8.8 | 22 | 7.3 | 8.1 | 9.1 | 87 | 8.2 |
| Head length | 27 | 28.5 | 31 | 44 | 27 | 28.0 | 29 | 21 | 27 | 28.4 | 30 | 22 | 27 | 28.4 | 31 | 87 | 29 |
| Snout length | 9.7 | 11.1 | 12 | 44 | 10 | 10.8 | 12 | 21 | 10 | 11.2 | 12 | 22 | 9.7 | 11.0 | 12 | 87 | 11 |
| Postorbital length | 10 | 11.3 | 12 | 44 | 11 | 11.6 | 12 | 21 | 11 | 11.4 | 13 | 22 | 10 | 11.4 | 13 | 87 | 11 |
| Orbit length | 6.6 | 7.7 | 9.1 | 44 | 6.2 | 6.9 | 8.1 | 21 | 6.7 | 7.4 | 8.0 | 22 | 6.2 | 7.4 | 9.1 | 87 | 7.4 |
| Orbit depth | 5.5 | 6.6 | 8.0 | 44 | 5.4 | 6.1 | 6.6 | 21 | 5.9 | 6.5 | 7.5 | 22 | 5.4 | 6.5 | 8.0 | 87 | 6.3 |
| Upper-jaw length | 9.8 | 10.9 | 12 | 44 | 9.8 | 10.8 | 12 | 21 | 10 | 11.0 | 12 | 22 | 9.8 | 10.9 | 12 | 87 | 11 |
| Lower-jaw length | 9.1 | 10.2 | 11 | 44 | 9.5 | 10.3 | 11 | 21 | 8.9 | 10.2 | 12 | 22 | 8.9 | 10.2 | 12 | 87 | 10 |
| Snout width | 7.8 | 9.3 | 11 | 44 | 7.7 | 8.4 | 9.3 | 21 | 8.1 | 9.0 | 10 | 18 | 7.7 | 9.0 | 11 | 83 | 8.6 |
| Barbel length | 15 | 17.2 | 19 | 44 | 15 | 16.3 | 18 | 21 | 16 | 17.9 | 20 | 22 | 15 | 17.2 | 20 | 87 | 19 |
| Maximum barbel width | 0.7 | 0.9 | 1.0 | 44 | 0.7 | 0.8 | 0.9 | 21 | 0.8 | 0.9 | 1.0 | 22 | 0.7 | 0.8 | 1.0 | 87 | 0.8 |
| First pre-dorsal length | 35 | 36.8 | 40 | 44 | 34 | 36.3 | 38 | 21 | 34 | 36.6 | 40 | 22 | 34 | 36.6 | 40 | 87 | 37 |
| Second pre-dorsal length | 60 | 63.5 | 67 | 44 | 60 | 63.5 | 67 | 21 | 61 | 63.5 | 67 | 22 | 60 | 63.5 | 67 | 87 | 66 |
| Interdorsal distance | 12 | 14.3 | 16 | 44 | 12 | 14.2 | 16 | 21 | 12 | 14.3 | 16 | 22 | 12 | 14.3 | 16 | 87 | 16 |
| Caudal-peduncle length | 22 | 24.1 | 26 | 44 | 22 | 24.0 | 25 | 21 | 22 | 23.6 | 25 | 22 | 22 | 23.9 | 26 | 87 | 24 |
| Pre-anal length | 61 | 63.8 | 68 | 44 | 61 | 63.4 | 69 | 21 | 61 | 64.1 | 68 | 22 | 61 | 63.8 | 69 | 87 | 64 |
| Pre-pelvic length | 28 | 30.5 | 34 | 44 | 29 | 30.7 | 33 | 21 | 30 | 32.7 | 35 | 22 | 28 | 31.1 | 35 | 87 | 31 |

.....continued on the next page

TABLE 1. (Continued)

| | <i>Upeneus margarethae</i> | | | | | | | | | | | <i>U. gubal</i> n. sp. | | | | | |
|---------------------------------------|----------------------------|------|-----|----|-----|------|---------|----|-----|------|-----|------------------------|-----|------|-----|----|-------|
| | WIOP including types | | | | | | Red Sea | | | | | EIO/NA | | | all | | |
| | Min | Mean | Max | n | Min | Mean | Max | n | Min | Mean | Max | n | Min | Mean | Max | n | HT |
| Pre-pectoral length | 28 | 29.8 | 33 | 44 | 28 | 29.3 | 31 | 21 | 28 | 30.5 | 32 | 22 | 28 | 29.8 | 33 | 87 | 30 |
| Second dorsal-fin depth | 20 | 21.8 | 24 | 44 | 21 | 22.8 | 24 | 21 | 21 | 22.7 | 24 | 22 | 20 | 22.3 | 24 | 87 | 22 |
| Pelvic-fin depth | 22 | 24.7 | 27 | 44 | 24 | 25.3 | 27 | 21 | 24 | 25.3 | 26 | 22 | 22 | 25.0 | 27 | 87 | 24 |
| Pectoral-fin depth | 15 | 16.9 | 18 | 44 | 15 | 16.9 | 18 | 21 | 16 | 17.2 | 18 | 22 | 15 | 17.0 | 18 | 87 | 16 |
| Length of first dorsal-fin base | 14 | 15.6 | 17 | 44 | 14 | 16.1 | 18 | 21 | 14 | 15.3 | 17 | 22 | 14 | 15.7 | 18 | 87 | 16 |
| Length of second dorsal-fin base | 12 | 14.1 | 16 | 44 | 13 | 14.2 | 16 | 21 | 12 | 13.4 | 15 | 22 | 12 | 13.9 | 16 | 87 | 15 |
| Caudal-fin length | 27 | 28.7 | 31 | 44 | 28 | 29.6 | 31 | 21 | 27 | 28.3 | 30 | 21 | 27 | 28.8 | 31 | 86 | 31 |
| Length of anal-fin base | 10 | 12.0 | 14 | 44 | 10 | 11.6 | 13 | 21 | 9.8 | 11.2 | 13 | 22 | 9.8 | 11.7 | 14 | 87 | 13 |
| Anal-fin height | 14 | 16.6 | 18 | 44 | 16 | 16.5 | 18 | 21 | 14 | 16.2 | 18 | 22 | 14 | 16.5 | 18 | 87 | 19 |
| Pelvic-fin length | 20 | 21.7 | 24 | 44 | 20 | 21.0 | 22 | 21 | 20 | 21.0 | 23 | 22 | 20 | 21.4 | 24 | 87 | 22 |
| Pectoral-fin length | 19.7 | 21.9 | 24 | 43 | 19 | 20.7 | 22 | 21 | 20 | 21.3 | 23 | 22 | 19 | 21.4 | 24 | 86 | 22 |
| Pectoral-fin width | 4.3 | 4.8 | 5.3 | 44 | 4.1 | 4.5 | 5.1 | 21 | 4.2 | 4.7 | 5.2 | 22 | 4.1 | 4.7 | 5.3 | 87 | 4.8 |
| First dorsal-fin height | 19 | 21.5 | 23 | 43 | 20 | 21.3 | 23 | 21 | 18 | 20.3 | 22 | 22 | 18 | 21.1 | 23 | 86 | 22 |
| Second dorsal-fin height | 16 | 17.7 | 20 | 44 | 16 | 17.7 | 19 | 21 | 15 | 16.6 | 18 | 22 | 15 | 17.4 | 20 | 87 | 19 |
| Meristic characters | | | | | | | | | | | | | | | | | |
| Dorsal-fin spines | 8 | 8.0 | 8 | 44 | 8 | 8.0 | 8 | 21 | 8 | 8.0 | 8 | 22 | 8 | 8.0 | 8 | 87 | 8 |
| Pectoral-fin rays | 13 | 13.8 | 14 | 44 | 13 | 13.8 | 14 | 21 | 13 | 14.0 | 15 | 22 | 13 | 13.9 | 15 | 87 | 15-15 |
| Rudimentary gill rakers on upper limb | 2 | 3.1 | 5 | 44 | 2 | 3.0 | 4 | 21 | 2 | 3.4 | 4 | 22 | 2 | 3.1 | 5 | 87 | 2-2 |
| Developed gill rakers on upper limb | 2 | 2.6 | 4 | 44 | 2 | 2.5 | 3 | 21 | 2 | 2.4 | 3 | 22 | 2 | 2.6 | 4 | 87 | 4-4 |
| Developed gill rakers on lower limb | 11 | 12.4 | 14 | 44 | 11 | 12.1 | 13 | 21 | 11 | 11.7 | 12 | 22 | 11 | 12.1 | 14 | 87 | 14-15 |
| Rudimentary gill rakers on lower limb | 3 | 4.4 | 6 | 44 | 3 | 4.6 | 6 | 21 | 4 | 5.1 | 6 | 22 | 3 | 4.6 | 6 | 87 | 5-4 |
| Total gill rakers on upper limb | 5 | 5.8 | 7 | 44 | 5 | 5.5 | 6 | 21 | 5 | 5.8 | 6 | 22 | 5 | 5.7 | 7 | 87 | 6-6 |
| Total gill rakers on lower limb | 16 | 16.8 | 18 | 44 | 16 | 16.7 | 17 | 21 | 15 | 16.8 | 18 | 22 | 15 | 16.8 | 18 | 87 | 19-19 |
| Total gill rakers | 21 | 22.5 | 24 | 44 | 21 | 22.2 | 23 | 21 | 21 | 22.6 | 24 | 22 | 21 | 22.5 | 24 | 87 | 25-25 |
| Scales along lateral line | 28 | 29.0 | 30 | 40 | 28 | 29.0 | 30 | 20 | 29 | 29.4 | 30 | 20 | 28 | 29.1 | 30 | 80 | 29-28 |
| Colour patterns | | | | | | | | | | | | | | | | | |
| Bars on upper caudal-fin lobe | 0 | 2.8 | 6 | 44 | 0 | 3.2 | 6 | 21 | 0 | 1.3 | 5 | 22 | 0 | 2.5 | 6 | 87 | 0 |
| Bars on lower caudal-fin lobe | 0 | 2.8 | 8 | 44 | 0 | 3.9 | 6 | 21 | 0 | 1.6 | 6 | 22 | 0 | 2.7 | 8 | 87 | 0 |
| Bars on both caudal-fin lobes | 0 | 4.7 | 14 | 44 | 2 | 7.1 | 11 | 21 | 0 | 2.9 | 11 | 22 | 0 | 4.8 | 14 | 87 | 0 |
| Pigmentation-degree index | 0 | 2.5 | 4 | 43 | 2 | 2.9 | 4 | 21 | 0 | 0.8 | 3 | 22 | 0 | 2.2 | 4 | 86 | 0 |

TABLE 2. Morphometric, meristic and preserved colour characters in all examined subadults of five *margarethae*-group species.

| Morphometric characters | <i>Upeneus margarethae</i> | | | | | <i>U. caudofasciatus</i> | | | | | <i>U. heterospinus</i> | | | | | <i>U. mouthami</i> | | | | | <i>U. randalli</i> | | | | | | | | |
|--|----------------------------|------|-----|----|-----|--------------------------|------|-----|-----|------|------------------------|------|-----|------|-----|--------------------|------|-----|---|----|--------------------|------|-----|---|----|-----|------|-----|---|
| | Min | Mean | Max | n | SL | Min | Mean | Max | n | SL | Min | Mean | Max | n | SL | Min | Mean | Max | n | SL | Min | Mean | Max | n | SL | Min | Mean | Max | n |
| Standard length (SL) | 40 | 54.7 | 64 | 11 | 50 | 58.9 | 64 | 13 | 43 | 56.1 | 64 | 7 | 46 | 50.3 | 55 | 4 | 60 | | | | | | | | | | | | |
| in % SL | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| Body depth at first dorsal-fin origin | 24 | 25.5 | 26 | 11 | 24 | 25.6 | 27 | 11 | 22 | 22.8 | 24 | 6 | 21 | 22.3 | 23 | 4 | 22 | | | | | | | | | | | | |
| Body depth at anal-fin origin | 21 | 22.2 | 23 | 11 | 19 | 20.4 | 22 | 11 | 18 | 19.2 | 21 | 6 | 18 | 19.0 | 20 | 4 | 19 | | | | | | | | | | | | |
| Half body depth at first dorsal-fin origin | 19 | 20.9 | 22 | 10 | 19 | 20.4 | 21 | 6 | 19 | 18.7 | 19 | 1 | 18 | 19.0 | 20 | 3 | 17 | | | | | | | | | | | | |
| Half body depth at anal-fin origin | 15 | 17.3 | 19 | 10 | 15 | 15.3 | 16 | 6 | 15 | 15.2 | 15 | 1 | 13 | 14.3 | 15 | 3 | 15 | | | | | | | | | | | | |
| Caudal-peduncle depth | 10 | 10.6 | 11 | 11 | 9.6 | 10.1 | 11 | 11 | 9.1 | 9.8 | 10 | 6 | 9.1 | 9.5 | 10 | 4 | 9.0 | | | | | | | | | | | | |
| Caudal-peduncle width | 3.4 | 3.8 | 4.4 | 11 | 2.7 | 3.3 | 3.8 | 9 | 3.6 | 3.7 | 3.8 | 3 | 3.0 | 3.3 | 3.5 | 4 | 3.5 | | | | | | | | | | | | |
| Maximum head depth | 19 | 20.5 | 22 | 11 | 20 | 21.8 | 23 | 9 | 19 | 19.9 | 21 | 3 | 19 | 19.4 | 21 | 4 | 18 | | | | | | | | | | | | |
| Head depth through eye | 15 | 16.2 | 17 | 11 | 17 | 18.2 | 20 | 9 | 15 | 16.2 | 18 | 3 | 15 | 15.5 | 16 | 4 | 16 | | | | | | | | | | | | |
| Suborbital depth | 7.6 | 8.7 | 9.4 | 11 | 9.4 | 10.4 | 11 | 9 | 9.0 | 9.4 | 10 | 3 | 7.5 | 8.3 | 9.2 | 4 | 7.0 | | | | | | | | | | | | |
| Interorbital length | 7.6 | 7.9 | 8.1 | 11 | 7.6 | 8.2 | 8.6 | 9 | 7.6 | 7.9 | 8.1 | 3 | 7.0 | 7.3 | 7.6 | 4 | 7.7 | | | | | | | | | | | | |
| Head length | 28 | 29.4 | 32 | 11 | 30 | 31.2 | 32 | 9 | 29 | 29.4 | 30 | 3 | 30 | 31.0 | 32 | 4 | 28 | | | | | | | | | | | | |
| Snout length | 9.9 | 10.6 | 12 | 11 | 11 | 11.3 | 12 | 9 | 11 | 11.1 | 12 | 3 | 10 | 11.0 | 12 | 4 | 12 | | | | | | | | | | | | |
| Postorbital length | 11 | 12.0 | 13 | 11 | 11 | 11.8 | 13 | 9 | 11 | 11.5 | 13 | 3 | 11 | 11.7 | 13 | 4 | 10 | | | | | | | | | | | | |
| Orbit length | 7.5 | 8.0 | 9.0 | 11 | 8.1 | 8.5 | 8.8 | 9 | 7.8 | 7.9 | 7.9 | 3 | 8.4 | 8.8 | 9.1 | 4 | 8.2 | | | | | | | | | | | | |
| Orbit depth | 6.6 | 7.1 | 8.0 | 11 | 6.5 | 7.5 | 8.0 | 9 | 7.0 | 7.1 | 7.1 | 3 | 7.4 | 7.8 | 8.1 | 4 | 7.1 | | | | | | | | | | | | |
| Upper-jaw length | 11 | 11.3 | 12 | 11 | 11 | 12.0 | 13 | 9 | 9.9 | 10.7 | 12 | 3 | 9.7 | 10.8 | 12 | 4 | 11 | | | | | | | | | | | | |
| Lower-jaw length | 9.6 | 10.7 | 12 | 11 | 9.7 | 11.1 | 12 | 9 | 9.4 | 10.4 | 12 | 3 | 9.5 | 10.4 | 11 | 4 | 10 | | | | | | | | | | | | |
| Snout width | 7.6 | 8.2 | 9.2 | 11 | 7.3 | 8.3 | 9.3 | 6 | 7.0 | 8.6 | 9.6 | 3 | 6.6 | 7.2 | 7.8 | 3 | 7.9 | | | | | | | | | | | | |
| Barbel length | 17 | 17.3 | 18 | 11 | 19 | 21.1 | 23 | 11 | 18 | 18.7 | 19 | 3 | 21 | 22.4 | 23 | 4 | 19 | | | | | | | | | | | | |
| Maximum barbel width | 0.8 | 0.8 | 1.0 | 11 | 0.8 | 1.0 | 1.1 | 9 | 1.0 | 1.0 | 1.0 | 3 | 0.8 | 0.9 | 1.0 | 4 | 0.9 | | | | | | | | | | | | |
| First pre-dorsal length | 36 | 37.1 | 40 | 11 | 36 | 38.4 | 41 | 9 | 37 | 37.2 | 37 | 3 | 36 | 36.7 | 38 | 4 | 36 | | | | | | | | | | | | |
| Second pre-dorsal length | 62 | 64.7 | 66 | 11 | 63 | 64.0 | 65 | 9 | 62 | 62.3 | 63 | 3 | 62 | 62.5 | 65 | 4 | 64 | | | | | | | | | | | | |
| Interdorsal distance | 14 | 14.9 | 17 | 11 | 12 | 13.5 | 15 | 9 | 12 | 13.6 | 14 | 3 | 13 | 13.4 | 14 | 4 | 14 | | | | | | | | | | | | |
| Caudal-peduncle length | 24 | 25.3 | 26 | 11 | 22 | 23.4 | 24 | 9 | 22 | 23.1 | 25 | 3 | 23 | 24.9 | 26 | 4 | 23 | | | | | | | | | | | | |
| Pre-anal length | 62 | 63.4 | 65 | 11 | 63 | 64.8 | 67 | 9 | 62 | 65.2 | 67 | 3 | 62 | 63.5 | 65 | 4 | 64 | | | | | | | | | | | | |
| Pre-pelvic length | 30 | 31.7 | 33 | 11 | 33 | 35.0 | 38 | 9 | 34 | 34.1 | 35 | 3 | 31 | 32.2 | 34 | 4 | 32 | | | | | | | | | | | | |
| Pre-pectoral length | 30 | 31.2 | 33 | 11 | 32 | 33.5 | 35 | 9 | 31 | 32.0 | 33 | 3 | 30 | 31.3 | 32 | 4 | 31 | | | | | | | | | | | | |
| Second dorsal-fin depth | 21 | 22.8 | 24 | 11 | 19 | 21.1 | 23 | 9 | 18 | 18.9 | 20 | 3 | 19 | 19.3 | 20 | 4 | 20 | | | | | | | | | | | | |

.....continued on the next page

TABLE 2. (Continued)

| | <i>Upeneus margarethae</i> | | | | | <i>U. caudofasciatus</i> | | | | | <i>U. heterospinus</i> | | | | | <i>U. mouthami</i> | | | | | <i>U. randalli</i> | | |
|---------------------------------------|----------------------------|------|-----|----|-----|--------------------------|------|-----|----|-----|------------------------|------|-----|---|-----|--------------------|------|-----|---|-----|--------------------|---|-----|
| | Min | Mean | Max | n | | Min | Mean | Max | n | | Min | Mean | Max | n | | Min | Mean | Max | n | | Max | n | n=1 |
| Pelvic-fin depth | 24 | 25.4 | 26 | 11 | 22 | 24.9 | 26 | 26 | 9 | 21 | 22.0 | 23 | 23 | 3 | 20 | 22.4 | 23 | 23 | 4 | 22 | | | |
| Pectoral-fin depth | 15 | 16.5 | 18 | 11 | 15 | 16.9 | 18 | 18 | 9 | 15 | 16.0 | 16 | 16 | 3 | 14 | 14.2 | 15 | 15 | 4 | 15 | | | |
| Length of first dorsal-fin base | 15 | 16.5 | 18 | 11 | 14 | 15.3 | 17 | 17 | 9 | 13 | 13.6 | 14 | 14 | 3 | 13 | 14.0 | 15 | 15 | 4 | 15 | | | |
| Length of second dorsal-fin base | 13 | 14.9 | 16 | 11 | 13 | 14.1 | 15 | 15 | 9 | 12 | 13.1 | 15 | 15 | 3 | 13 | 14.3 | 15 | 15 | 4 | 12 | | | |
| Caudal-fin length | 29 | 30.1 | 33 | 11 | 28 | 30.2 | 32 | 32 | 9 | 29 | 29.7 | 31 | 31 | 3 | 30 | 30.4 | 31 | 31 | 3 | 29 | | | |
| Length of anal-fin base | 11 | 12.4 | 13 | 11 | 10 | 11.9 | 13 | 13 | 9 | 10 | 10.4 | 11 | 11 | 3 | 11 | 11.9 | 13 | 13 | 4 | 12 | | | |
| Anal-fin height | 17 | 18.2 | 19 | 11 | 16 | 17.9 | 19 | 19 | 9 | 16 | 17.4 | 19 | 19 | 3 | 16 | 16.2 | 17 | 17 | 4 | 16 | | | |
| Pelvic-fin length | 22 | 22.8 | 24 | 11 | 22 | 23.5 | 25 | 25 | 11 | 21 | 21.5 | 22 | 22 | 3 | 22 | 22.3 | 23 | 23 | 4 | 21 | | | |
| Pectoral-fin length | 21 | 21.9 | 23 | 11 | 21 | 22.0 | 23 | 23 | 9 | 21 | 20.8 | 21 | 21 | 3 | 21 | 21.4 | 22 | 22 | 4 | 20 | | | |
| Pectoral-fin width | 4.3 | 4.7 | 5.1 | 11 | 3.8 | 4.2 | 4.6 | 4.6 | 9 | 3.8 | 3.9 | 4.2 | 4.2 | 3 | 3.5 | 3.7 | 3.8 | 3.8 | 4 | 3.7 | | | |
| First dorsal-fin height | 21 | 22.8 | 24 | 11 | 20 | 21.3 | 23 | 23 | 9 | 21 | 21.6 | 22 | 22 | 2 | 19 | 21.1 | 22 | 22 | 4 | 21 | | | |
| Second dorsal-fin height | 19 | 19.9 | 21 | 10 | 18 | 20.1 | 21 | 21 | 11 | 17 | 18.7 | 20 | 20 | 3 | 19 | 19.6 | 20 | 20 | 3 | 19 | | | |
| Meristic characters | | | | | | | | | | | | | | | | | | | | | | | |
| Dorsal-fin spines | 8 | 8.0 | 8 | 11 | 8 | 8.0 | 8 | 8 | 13 | 7 | 7.3 | 8 | 8 | 7 | 8 | 8.0 | 8 | 8 | 4 | 8 | | | |
| Pectoral-fin rays | 13 | 13.6 | 14 | 11 | 13 | 13.6 | 14 | 14 | 13 | 13 | 13.9 | 14 | 14 | 7 | 12 | 12.8 | 13 | 13 | 4 | 13 | | | |
| Rudimentary gill rakers on upper limb | 1 | 2.5 | 3 | 11 | 3 | 3.1 | 4 | 4 | 13 | 2 | 2.8 | 3 | 3 | 6 | 1 | 2.5 | 3 | 3 | 4 | 3 | | | |
| Developed gill rakers on upper limb | 3 | 3.2 | 5 | 11 | 2 | 2.9 | 3 | 3 | 13 | 2 | 3.0 | 4 | 4 | 6 | 3 | 3.5 | 5 | 5 | 4 | 3 | | | |
| Developed gill rakers on lower limb | 12 | 12.9 | 14 | 11 | 12 | 13.1 | 15 | 15 | 13 | 12 | 13.0 | 14 | 14 | 6 | 12 | 13.0 | 14 | 14 | 4 | 14 | | | |
| Rudimentary gill rakers on lower limb | 3 | 3.7 | 5 | 11 | 3 | 4.5 | 6 | 6 | 13 | 3 | 3.5 | 4 | 4 | 6 | 4 | 4.8 | 5 | 5 | 4 | 3 | | | |
| Total gill rakers on upper limb | 5 | 5.6 | 6 | 11 | 6 | 6.0 | 6 | 6 | 13 | 5 | 5.8 | 6 | 6 | 6 | 6 | 6.0 | 6 | 6 | 4 | 6 | | | |
| Total gill rakers on lower limb | 16 | 16.6 | 17 | 11 | 16 | 17.6 | 19 | 19 | 13 | 16 | 16.5 | 17 | 17 | 6 | 17 | 17.8 | 18 | 18 | 4 | 17 | | | |
| Total gill rakers | 21 | 22.3 | 23 | 11 | 22 | 23.6 | 25 | 25 | 13 | 21 | 22.3 | 23 | 23 | 6 | 23 | 23.8 | 24 | 24 | 4 | 23 | | | |
| Scales along lateral line | 28 | 28.6 | 29 | 9 | 28 | 28.3 | 29 | 29 | 3 | 29 | 29.0 | 29 | 29 | 1 | 30 | 30.0 | 30 | 30 | 1 | 29 | | | |
| Colour patterns | | | | | | | | | | | | | | | | | | | | | | | |
| Bars on upper caudal-fin lobe | 3 | 3.6 | 4 | 11 | 1 | 3.2 | 4 | 4 | 13 | 3 | 3.6 | 4 | 4 | 7 | 3 | 3.0 | 3 | 3 | 4 | 3 | | | |
| Bars on lower caudal-fin lobe | 0 | 3.6 | 5 | 11 | 3 | 3.8 | 4 | 4 | 13 | 3 | 4.4 | 5 | 5 | 7 | 3 | 3.0 | 3 | 3 | 4 | 3 | | | |
| Bars on both caudal-fin lobes | 3 | 7.3 | 9 | 11 | 4 | 7.1 | 8 | 8 | 13 | 6 | 8.0 | 9 | 9 | 7 | 6 | 6.0 | 6 | 6 | 4 | 6 | | | |
| Pigmentation degree | 1 | 3.4 | 4 | 10 | 3 | 3.6 | 4 | 4 | 10 | 2 | 3.0 | 4 | 4 | 6 | 2 | 2.3 | 3 | 3 | 4 | 2 | | | |

Colour Description. *Freshly collected fish.* (Figure 2 A-F). Head and body ventrally white or pale brassy, in adult fish (Figure 2 A-E) with numerous tiny red or red-brown dots placed on individual scales and covering up to five vertical scale rows at mid body; in some fish, as in holotype (Figure 2 A) and subadult (Figure 2 F) larger red blotches are formed on ventral side of head and body; head from above snout and eye and body above lateral line red or brown-greyish mottled, bordered below by a mid-lateral stripe of pupil width which runs rather straight or only slightly bent from caudal-fin base to eye in yellow, beige or orange colour, becoming more reddish when crossing pupil (iris entirely or partly red) and bending ventrally towards snout tip; on the mid-lateral body stripe in several adult or subadult specimens of the entire distribution area (Figure 2 B-F) 1-3 sections with horizontal series of 2-4 black, red or brown dots of about half-pupil diameter, the anterior-most section below first dorsal-fin base, the second section below second dorsal-fin base, and the third series of dots just behind second dorsal fin; the latter section is the most frequently encountered (also in preserved specimens) and often connected to a dark saddle of about half of second dorsal-fin base length which reaches from behind second dorsal fin to mid-lateral body stripe; from head behind eye until below base of second dorsal fin, a thin white stripe separates the dorsal body pigmentation from the mid-lateral body stripe; lateral line weakly visible as a series of red or brownish-grey dots placed well above mid-lateral stripe in anterior half of body starting to cross the stripe just anterior to second dorsal-fin base, continuing behind second dorsal fin just below stripe towards caudal-fin base; barbels entirely white or mostly white, partly intermingled with pale rose pigmentation proximally (Figure 2 E) or distally (Figure 2 C, D); caudal fin of adults entirely crossed by 10-15 red, red-brown or partly darker oblique bars; upper caudal-fin lobe covered by 4-5 (6 in a single large specimen) bars of pupil or slightly narrower width, the distal-most bar covering fin tip in some specimens (Figure 2 B, C-F); bars separated by hyaline interspaces of similar width or slightly wider; lower caudal-fin lobe covered by 6-9 bars of similar width as on upper fin lobe, with hyaline interspaces sometimes slightly narrower; in addition, the lower fin lobe is frequently covered by a red stripe that reaches from base of fin to fin tip, covering the dorsal half of lobe or almost the entire lobe, leaving at least the ventral lobe margin free where the bars and interspaces can be well recognized (Figure 2 A, C, D); in most fish with the stripe pigmentation on lower caudal-fin lobe, bars and interspaces can be still seen shining through the entire fin lobe (Figure 2 B, E); furthermore, dark markings of bars can be also sometimes found at dorsal margin of lower caudal-fin lobe, especially distally, where the bars may turn into black close to or on lobe tip (Figure 2 A-E); subadults with 3 brown bars of more irregular form and size on each caudal-fin lobe, the 2 proximal bars on lower lobe nearly fused; first dorsal fin with irregular red or pale red (adults, Figure 2 A-E) or pale brown (subadult, Figure 2 F) pigmentation which does not become darker (adults), or becomes lighter (subadult), towards tip; the tiny first dorsal-fin spine is often dark pigmented; second dorsal fin with 3-4 red stripes of less than orbit width in adults, one stripe at fin base, one at or close to fin tip, the latter being darker than the other stripes in some specimens (Figure 2 C, E); 2 brown second dorsal-fin stripes in subadult, the distal stripe darker (Figure 2 F); pelvic fins hyaline with up to four narrow red stripes; anal fin with or without stripes, pectoral fins hyaline.

Live fish in situ. Active fish. (Figure 3 A, B). Head and body ventrally white, with numerous tiny red or grey dots associated with scale rows; head from above snout and eye and body above lateral line pale-grey mottled, bordered ventrally by a mid-lateral body stripe of pupil width which runs rather straight from caudal-fin base to eye in yellow or orange colour, becoming red or brown when crossing pupil (iris pigmented in same colour and in shape of stripe) and bending ventrally towards snout tip; five dark, well separated, rectangular, brown or dark-grey rectangular sections on mid-body stripe, 2 shorter ones behind eye and gill cover, three longer ones each covered by a horizontal series of 2-4 black or dark brown dots of approximate pupil size (or slightly smaller); four dots on the section below first dorsal fin, two dots on the section below anterior part of second dorsal fin and three dots on posterior-most section behind second dorsal-fin base; of the latter three dots the last one is slightly elevated connecting closely to a grey saddle that reaches from dorsal body margin behind second dorsal fin to stripe; lateral line, as also observed in recently deceased fish (see further above), well visible, proceeding parallel above lateral mid-body stripe within first half of body, then crossing and continuing just below stripe to caudal-fin base; barbels white; caudal fin with 6-10 red-brown (Figure 3 B) or black (Figure 3 A) oblique bars; upper caudal-fin lobe covered by 3-4 bars of pupil or slightly narrower width, the distal-most bar covering fin tip; bars separated by hyaline interspaces of similar width or slightly wider, overlain with white pigmentation in middle parts; lower caudal-fin lobe covered by 3-6 bars of either variable (Figure 3 A) or similar (Figure 3 B) size and form; in both photographed specimens a stripe is formed along dorsal two thirds of lower caudal-fin lobe which ends with second bar in one specimen (Figure 3 A) and extends to black tip in the other fish (Figure 3 B); first dorsal fin only weakly pale grey or pale brown pigmented,

without dark-pigmented tip region (in contrast to *U. heemstra*; Figure 3 B); second dorsal fin with three pale grey or pale brown to brown or dark-brown stripes, the distal two stripes more intensely coloured than the rather weak stripe at or close to fin base; interspaces between stripes in part white pigmented; pelvic and anal fins partly hyaline with weak pale-grey or pale-brown stripes and whitish interspaces and margin, pectoral fins hyaline, only faintly visible.

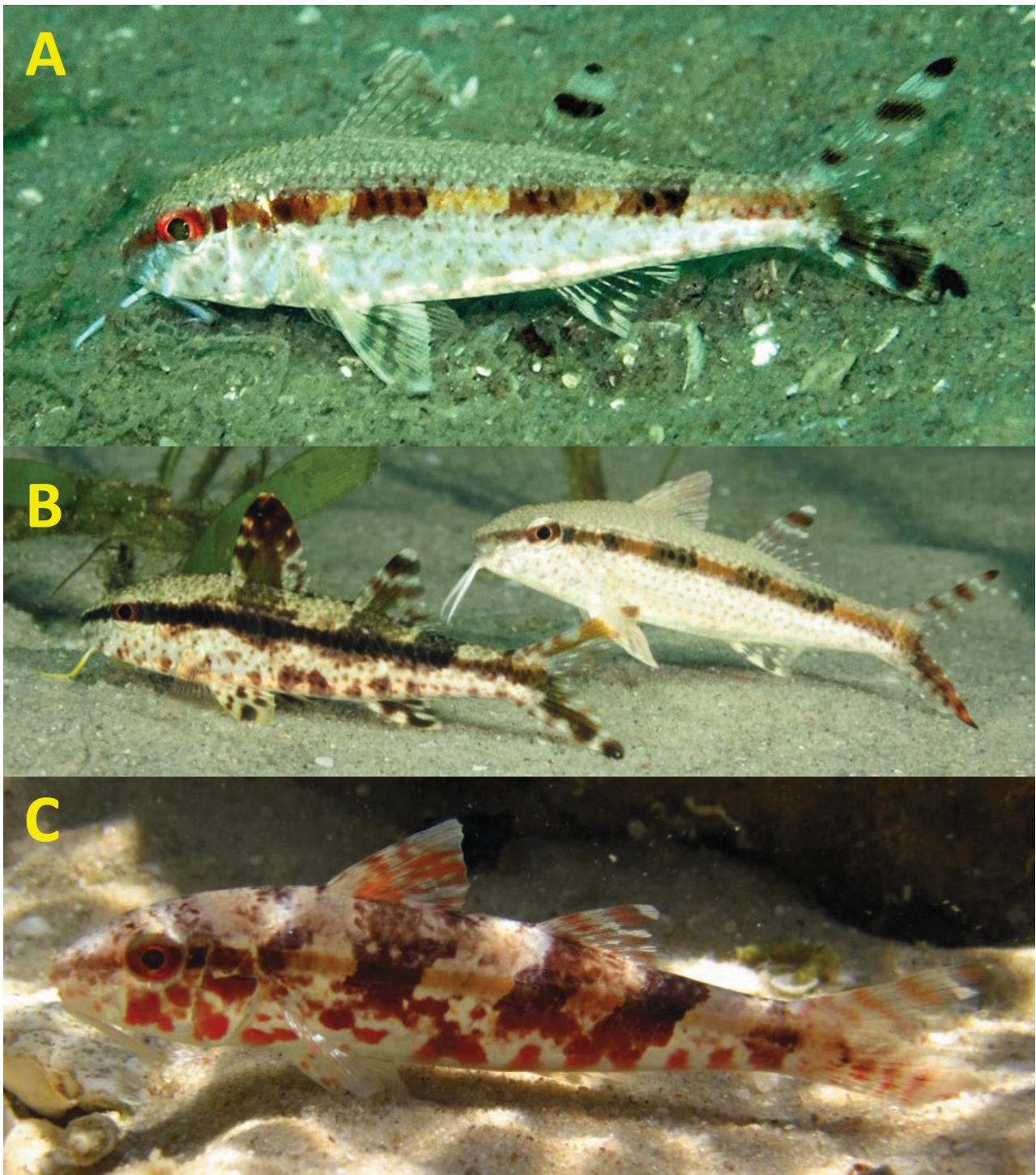


FIGURE 3. *Upeneus margarethae* photographed *in situ* in Mozambique, WIO; (A) subadult or small adult, Pemba Bay, N Mozambique, near Pemba harbour (R. Koch); (B) at right: subadult or small adult, with subadult *U. heemstra* (at left), Pomene, South-central Mozambique (M. & V. Fraser); (C) adult, resting on bottom, Lunene Island, off Vilanculos, South-central Mozambique (A. Lund).

Inactive, “resting” fish (Figure 3C; only differences from the above colour description are indicated). Head and body ventrally with at least 25 irregularly formed and distributed, mostly rounded red to dark-red blotches of

about orbit size or smaller, extending from below eye to caudal peduncle; head from above snout and eye and body above lateral line pale brown, the latter with 5 oblique brown or dark-brown bands overlapping with the dark-brown rectangular sections on orange mid-lateral body stripe (see also above); the second to fourth band connect in part to dark-red blotches on ventral body side; behind, one weaker coloured and more isolated brown band is placed at posterior end of mid-lateral body stripe, connecting to the posterior-most red blotch ventrally; caudal fin with 5 pale red to pale brown oblique bars on dorsal lobe and at least 5 red bars on ventral lobe (lobe tip appears to be broken); no stripe apparent on lower caudal-fin lobe; dark pigmentation of first minute spine on first dorsal fin well visible.

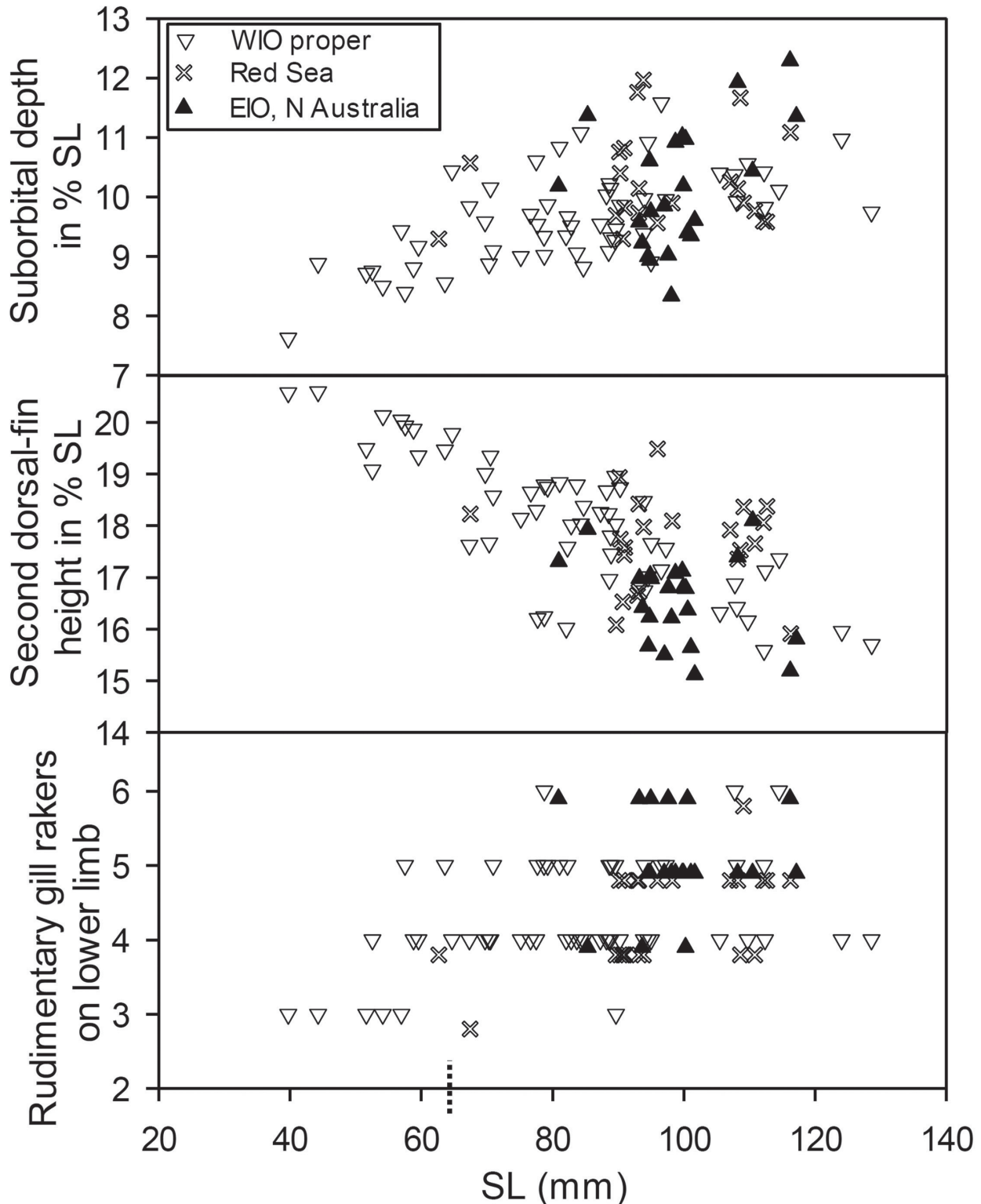


FIGURE 4. Three selected morphological characters against SL in *Upeneus margarethae*. The 65 mm demarcation between subadults and adults is indicated by a dotted black dash. The three populations are indicated by different symbols.

Preserved fish. Head and body mostly uniformly pale brown greyish brown or brown, sometimes slightly darker dorsally, gill cover silvery or pale and partly transparent, lateral line, when intact, well visible in entire range from behind head to caudal-fin base; barbels pale brown or pale creamy; mid-lateral body stripe completely lacking, but often remains of dark dots in the area of stripe below and posterior to dorsal fins (in 24 % of 87 adults vs. 73 % of 11 subadults); dark pigmentation remains occur also in other areas: saddle behind second dorsal fin (60 % adults vs. 82 % subadults), caudal fin (66 % vs. 100 %), and second dorsal-fin distal stripe (55 % vs. 90 %); on caudal fin with retained pigmentation remains of up to 6 oblique bars visible on upper and up to 8 bars on lower lobe visible; in adults 55 % (of 87 fish) show remains of bars on both caudal-fin lobes, in subadults 82 % (of 11 fish); of all adults 19 % (= 16 of 86 fish) show no pigmentation remains (pigmentation degree 0), while a pigmentation degree of 4 (remains of all four colour characters retained) is found in 21 % (= 18 of 86 fish). All subadults do show dark pigmentation, with pigmentation degree 4 occurring in 70 % (7 of 10 individuals). Unpigmented areas of caudal and second dorsal fins and other fins entirely pale and partly hyaline.

Distribution, habitat and size. WIO: East African coast from S Mozambique and Madagascar to Central Red Sea (northernmost record from off Ibn Abas Island, S Sudan), W and S coast of India from Kerala and Tamil Nadu to Sri Lanka; EIO: E coast of India, Odisha and West Bengal, Andaman Sea off S Myanmar (new record) and W Thailand; NW Australian coast and shelf from Exmouth Gulf to Rowley Shoals; Arafura Sea, Northern Territory, and inner Gulf of Carpentaria, Queensland (new record) (Figure 1); depth from 8 m (or possibly shallower) to 105 m, commonly trawled above soft bottoms at between 20 and 30 m depth, encountered during diving on shallow sandy bottoms (Figure 3); maximum size 13 cm SL.

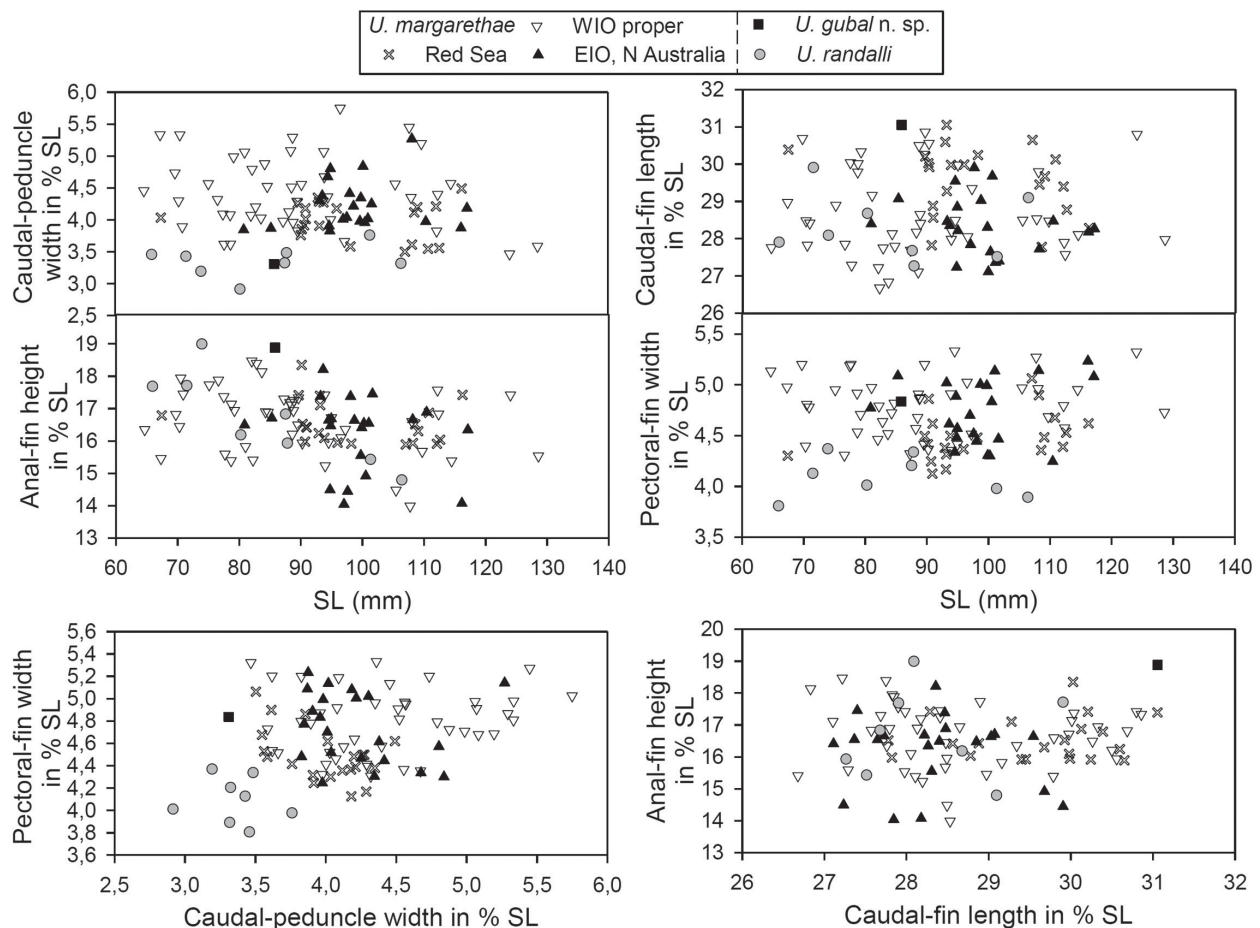


FIGURE 5. Four morphometric characters in adults of three *Upeneus* species of the *margarethae* group against SL and each other. For *Upeneus margarethae*, the three populations are indicated by different symbols.

Intraspecific Comparisons. Among the two size classes, main differences occur in both morphology and colour patterns. Subadults differ from adults in having slightly fewer rudimentary gill rakers on lower limb (Figure 4), while total gill-raker numbers on both limbs do not change, a slightly shallower suborbital depth, longer caudal fin, higher anal fin and higher second dorsal fin (Tables 1, 2; Figure 4); they differ in colour in having fewer bars

on the caudal fins and the bars especially on the lower caudal-fin lobe are more varied in form and size (Tables 1, 2; Figures 2,3); in preserved subadults dark pigmentation patterns are more often retained than in adults (Tables 1, 2; see also preserved-colour description above).

TABLE 3. Means, F-values of ANOVA, p-values for significant ($p \leq 0.01$) differences and results from multiple comparisons with Scheffé test for residuals of morphometric characters (values transformed by multiplication with 1000) in the three populations of *Upeneus margarethae*. Letters in parentheses refer to pairs of populations showing no significant differences. Area abbreviations are explained in legend of Table 1.

| | WIOP | Red Sea | EIO/NA | F-value | p | Scheffe test |
|--|-------|---------|--------|---------|---------|--------------|
| | (A) | (B) | (C) | | | |
| Body depth at first dorsal-fin origin | -1.78 | 0.81 | 2.86 | 0.55 | ns | |
| Body depth at anal-fin origin | -6.84 | 8.79 | 5.20 | 5.67 | <0.01 | (A,C)(B,C) |
| Half body depth at first dorsal-fin origin | -3.88 | 3.57 | 4.69 | 1.39 | ns | |
| Half body depth at anal-fin origin | -1.07 | 1.10 | 1.10 | 1.10 | ns | |
| Caudal-peduncle depth | -5.77 | 7.05 | 4.73 | 5.38 | <0.01 | (A,C)(B,C) |
| Caudal-peduncle width | 11.89 | -24.90 | 0.14 | 4.46 | 0.01 | (A,C)(B,C) |
| Maximum head depth | -0.50 | -10.35 | 10.91 | 7.84 | <0.001 | (A,B)(A,C) |
| Head depth through eye | 3.26 | -11.49 | 4.27 | 5.95 | <0.01 | B(A,C) |
| Suborbital depth | -4.21 | 8.62 | 0.18 | 1.05 | ns | |
| Interorbital length | 3.30 | -9.24 | 2.17 | 3.40 | ns | |
| Head length | 1.55 | -5.33 | 1.87 | 2.25 | ns | |
| Snout length | 4.41 | -12.12 | 2.82 | 4.85 | 0.01 | (A,C)(B,C) |
| Postorbital length | -1.25 | 4.43 | -1.85 | 0.70 | ns | |
| Orbit length | 6.27 | -21.43 | 8.00 | 8.03 | <0.001 | B(A,C) |
| Orbit depth | 3.23 | -17.48 | 10.41 | 5.03 | <0.01 | B(A,C) |
| Upper-jaw length | 0.87 | -4.64 | 2.64 | 0.82 | ns | |
| Lower-jaw length | 1.25 | 0.43 | -2.91 | 0.23 | ns | |
| Snout width | 13.26 | -27.75 | -0.11 | 10.30 | 0.0001 | (A,B)(A,C) |
| Barbel length | 3.35 | -24.81 | 17.14 | 14.74 | <0.0001 | (A,B)(A,C) |
| Maximum barbel width | 4.98 | -19.76 | 8.88 | 2.94 | ns | |
| First pre-dorsal length | 1.24 | -3.26 | 0.44 | 0.85 | ns | |
| Second pre-dorsal length | -0.09 | -0.08 | 0.32 | 0.09 | ns | |
| Interdorsal distance | 2.73 | -3.67 | -2.00 | 0.23 | ns | |
| Caudal-peduncle length | 0.01 | 4.34 | -4.14 | 0.87 | ns | |
| Pre-anal length | 1.10 | -3.29 | 0.95 | 1.12 | ns | |
| Pre-pelvic length | -6.20 | -6.95 | 19.18 | 15.95 | <0.0001 | (A,B)C |
| Pre-pectoral length | -0.77 | -7.90 | 9.18 | 6.65 | <0.01 | (A,B)(A,C) |
| Second dorsal-fin depth | -7.93 | 9.70 | 6.68 | 7.66 | <0.001 | A(B,C) |
| Pelvic-fin depth | -3.48 | 3.62 | 3.71 | 1.94 | ns | |
| Pectoral-fin depth | -0.04 | -3.86 | 3.68 | 0.63 | ns | |
| Length of first dorsal-fin base | 0.20 | 11.29 | -11.14 | 4.06 | ns | |
| Length of second dorsal-fin base | 4.95 | 7.81 | -17.56 | 5.20 | <0.01 | C(A,B) |
| Caudal-fin length | -2.16 | 11.58 | -6.90 | 8.50 | <0.001 | B(A,C) |
| Length of anal-fin base | 7.05 | 1.15 | -15.18 | 3.29 | ns | |
| Anal-fin height | 0.50 | 3.90 | -4.77 | 0.64 | ns | |
| Pelvic-fin length | 2.73 | -3.62 | -1.94 | 1.08 | ns | |
| Pectoral-fin length | 6.63 | -12.95 | -0.58 | 8.44 | <0.001 | (A,C)(B,C) |
| Pectoral-fin width | 8.30 | -20.19 | 2.56 | 8.46 | <0.001 | B(A,C) |
| First dorsal-fin height | 3.45 | 6.79 | -13.45 | 6.76 | <0.01 | C(A,B) |
| Second dorsal-fin height | 2.07 | 11.56 | -15.05 | 8.61 | <0.001 | C(A,B) |

TABLE 4. Means, F-values of ANOVA, p-values for significant ($p \leq 0.01$) differences and results from multiple comparisons with Scheffe test for residuals of morphometric characters (values transformed by multiplication with 1000) in the three species of the *margarethae* group. Letters in parentheses refer to pairs of species showing no significant differences.

| | <i>U. margarethae</i> | <i>U. caudofasciatus</i> | <i>U. heterospinus</i> | F value | p | Scheffe test |
|--|-----------------------|--------------------------|------------------------|---------|---------|--------------|
| | (A) | (B) | (C) | | | |
| Body depth at first dorsal-fin origin | 2.34 | 25.02 | -12.71 | 66.73 | <0.0001 | A,B,C |
| Body depth at anal-fin origin | 7.46 | 9.55 | -10.53 | 24.98 | <0.0001 | C(A,B) |
| Half body depth at first dorsal-fin origin | 0.92 | 20.05 | -9.75 | 25.23 | <0.0001 | A,B,C |
| Half body depth at anal-fin origin | 3.83 | 3.61 | -5.67 | 5.10 | <0.01 | C(A,B) |
| Caudal-peduncle depth | 8.63 | 3.43 | -8.83 | 23.20 | <0.0001 | C(A,B) |
| Caudal-peduncle width | 13.40 | -50.76 | 9.75 | 38.36 | <0.0001 | B(A,C) |
| Maximum head depth | -4.36 | 23.55 | -6.06 | 39.30 | <0.0001 | B(A,C) |
| Head depth through eye | -0.52 | 31.17 | -12.61 | 77.89 | <0.0001 | A,B,C |
| Suborbital depth | 1.67 | 32.36 | -14.85 | 30.56 | <0.0001 | A,B,C |
| Interorbital length | 2.34 | 1.52 | -2.68 | 1.27 | ns | |
| Head length | -4.51 | 11.00 | -0.70 | 19.59 | <0.0001 | B(A,C) |
| Snout length | -3.37 | 9.52 | -1.12 | 4.74 | <0.01 | B(A,C) |
| Postorbital length | 1.06 | 12.12 | -5.92 | 10.06 | <0.0001 | B(A,C) |
| Orbit length | 3.51 | 7.10 | -6.01 | 5.59 | <0.01 | C(A,B) |
| Orbit depth | -0.18 | 6.50 | -2.55 | 1.73 | ns | |
| Upper-jaw length | -3.21 | 16.60 | -4.11 | 15.20 | <0.0001 | B(A,C) |
| Lower-jaw length | -3.10 | 13.03 | -2.69 | 5.93 | <0.01 | (A,B)(B,C) |
| Snout width | 8.48 | 6.75 | -9.59 | 7.26 | <0.001 | (A,B)(B,C) |
| Barbel length | -19.08 | 44.48 | -2.13 | 73.97 | <0.0001 | A,B,C |
| Maximum barbel width | -27.14 | 15.62 | 16.87 | 27.01 | <0.0001 | A(B,C) |
| First pre-dorsal length | 1.26 | 4.24 | -2.86 | 4.66 | 0.01 | (A,B)(A,C) |
| Second pre-dorsal length | -0.65 | 4.81 | -1.49 | 6.14 | <0.01 | B(A,C) |
| Interdorsal distance | -10.57 | -1.33 | 9.71 | 7.83 | <0.001 | (A,B)(B,C) |
| Caudal-peduncle length | 3.09 | -12.64 | 2.54 | 12.00 | <0.0001 | B(A,C) |
| Pre-anal length | -1.57 | 4.74 | -0.65 | 4.79 | <0.01 | B(A,C) |
| Pre-pelvic length | -10.07 | 24.55 | -1.50 | 44.83 | <0.0001 | A,B,C |
| Pre-pectoral length | -4.99 | 19.60 | -3.88 | 35.74 | <0.0001 | B(A,C) |
| Second dorsal-fin depth | 7.08 | 11.38 | -10.94 | 26.92 | <0.0001 | C(A,B) |
| Pelvic-fin depth | 4.26 | 22.21 | -13.18 | 58.60 | <0.0001 | A,B,C |
| Pectoral-fin depth | 0.60 | 15.19 | -6.98 | 14.80 | <0.0001 | B(A,C) |
| Length of first dorsal-fin base | 2.69 | 10.64 | -6.89 | 8.32 | <0.001 | C(A,B) |
| Length of second dorsal-fin base | -1.16 | 10.79 | -3.46 | 3.69 | ns | |
| Caudal-fin length | -5.84 | 9.84 | 0.89 | 14.06 | <0.0001 | A,B,C |
| Length of anal-fin base | 6.98 | 2.93 | -7.49 | 5.06 | <0.01 | (A,B)(B,C) |
| Anal-fin height | -4.61 | 12.67 | -1.32 | 6.96 | <0.01 | B(A,C) |
| Pelvic-fin length | 3.43 | 18.54 | -10.81 | 47.73 | <0.0001 | A,B,C |
| Pectoral-fin length | 11.29 | 5.43 | -12.35 | 47.66 | <0.0001 | C(A,B) |
| Pectoral-fin width | 29.04 | -2.19 | -24.18 | 75.08 | <0.0001 | A,B,C |
| First dorsal-fin height | 7.30 | 8.05 | -9.76 | 17.78 | <0.0001 | C(A,B) |
| Second dorsal-fin height | -7.95 | 27.45 | -3.61 | 35.84 | <0.0001 | B(A,C) |

TABLE 5. Occurrence frequency of meristic-character counts for the six *margarethae* species and three population of two species, with results of statistical comparisons by Chi² test. Letters in parentheses refer to pairs of species or populations showing no significant differences. Area abbreviations are explained in legend of Table 1.

| Species | Dorsal-fin spines | | Pectoral-fin rays | | | Total gill rakers | | | | | Lateral-line scales | | | | |
|-------------------------------------|-------------------|----|-------------------|----|----|-------------------|----|----|----|----|---------------------|----|----|----|---|
| | 7 | 8 | 12 | 13 | 14 | 15 | 21 | 22 | 23 | 24 | 25 | 28 | 29 | 30 | |
| <i>Upeneus margarethae</i> (A) | | 98 | | 18 | 79 | 1 | 14 | 34 | 42 | 8 | | 17 | 52 | 20 | |
| <i>U. caudofasciatus</i> n. sp. (B) | | 55 | 1 | 25 | 29 | | | 3 | 20 | 26 | 6 | 7 | 18 | 7 | |
| <i>U. gubal</i> n. sp. | | 1 | | | | 1 | | | | | 1 | | 1 | | |
| <i>U. heterospinus</i> n. sp. (C) | 53 | 55 | | 20 | 84 | 4 | 24 | 42 | 38 | 3 | | 8 | 41 | 18 | |
| <i>U. mouthami</i> | | 8 | 1 | 7 | | | | | | 3 | 4 | 1 | 1 | 1 | |
| <i>U. randalli</i> | | 9 | | 1 | 8 | | | | | 3 | 2 | 4 | 1 | 6 | 2 |
| Chi ² test: | C(A,B)** | | B(A,C)** | | | B(A,C)** | | | | | ns | | | | |
| Populations | | | | | | | | | | | | | | | |
| <i>U. margarethae</i> | | | | | | | | | | | | | | | |
| WIOP (A) | | 50 | | 12 | 38 | | 8 | 14 | 23 | 5 | | 13 | 25 | 6 | |
| Red Sea (B) | | 22 | | 4 | 18 | | 3 | 13 | 6 | | | 4 | 13 | 4 | |
| EIO/NA (C) | | 22 | | 2 | 19 | 1 | 3 | 5 | 12 | 2 | | | 12 | 8 | |
| Chi ² test: | ns | | ns | | | ns | | | | | (A,B)(B,C)* | | | | |
| <i>U. heterospinus</i> | | | | | | | | | | | | | | | |
| Gulf of Thailand (A) | 22 | 23 | | 9 | 36 | | 19 | 20 | 6 | | | 2 | 16 | 4 | |
| South-central Vietnam (B) | 16 | 15 | | 6 | 24 | 1 | 1 | 13 | 14 | 3 | | 2 | 18 | 7 | |
| N Vietnam (C) | 10 | 11 | | 3 | 15 | 3 | 3 | 7 | 11 | | | | 5 | 6 | |
| Chi ² test: | ns | | ns | | | A(B,C)* | | | | | ns | | | | |

* p<0.01; ** p<0.0001

Among the three populations of *Upeneus margarethae* from the WIO proper (WIOP), the Red Sea, and the EIO, Arafura Sea and Gulf of Carpentaria (N Australia, E Pacific) (EIO/NA), there is no clear distinction in any single or combination of morphological or colour characters that would support separation into different taxa (Table 1, Figures 2–6). However, each population can be distinguished statistically (Table 3). For instance, the EIO/NA population has significantly longer snout-pelvic-fin distance, shorter second dorsal-fin base and shallower dorsal fins than the other two populations; the Red Sea population has a significantly shallower head, smaller eyes, longer caudal fin, and narrower pectoral fins than the other two populations; the main distinction of the WIOP population is a significantly shallower body at anal-fin origin. Furthermore, several additional significant differences in morphometric characters occur among pairs of the three populations (Table 3). The considerable number of significant differences among populations contrasts however with a much higher degree of differentiation among species, as revealed by the statistical comparisons of *U. margarethae* with two of the other four species (Table 4, see also section on Interspecific comparisons at end of taxonomic account)

Regarding meristic and colour characters, the EIO/NA population has a significantly higher number of lateral-line scales than the WIOP population (Table 5) and significantly less dark pigmentation in preserved condition than the other two populations (Table 6), with significantly fewer remains of bars on upper caudal-fin lobe and second dorsal-fin distal stripe and no occurrence of mid-lateral dots (Table 7). Additional significant differences in preserved pigmentation pattern concern the WIOP and the Red-Sea populations which differ in two and three color characters from the other two populations, respectively (Table 7). Regarding fresh colour patterns, no obvious population differences could be found based on the available photo documentation.

Remarks. The tiny first dorsal-fin spine is an important diagnostic character for this species (Uiblein & Heemstra 2010) that can be best identified by using a binocular microscope and a needle, sometimes after removing scales attached to the anterior dorsal-fin base. In four of 98 studied specimens the spine was found to be reduced to a flap or little knob, making detection more difficult.

TABLE 6. Occurrence frequency of fresh barbel colour (adults and subadults) and pigmentation degree for the six *margarethae*-group species, three populations of two species, and all studied subadults, with results of statistical comparisons by Chi² test for the three dominant species and the populations. Letters in parentheses refer to pairs of species or populations showing no significant differences. Area abbreviations are explained in legend of Table 1.

| Species | Fresh barbel colour | | Pigmentation degree | | | | | | | | | |
|-------------------------------------|-----------------------|-----------------|---------------------|----|----|----|-----------|---|---|---|---|---|
| | white or mostly white | entirely yellow | adults | | | | subadults | | | | | |
| | | | 0 | 1 | 2 | 3 | 4 | 0 | 1 | 2 | 3 | 4 |
| <i>Upeneus margarethae</i> (A) | 32 | | 16 | 10 | 23 | 19 | 18 | | 1 | 1 | 1 | 7 |
| <i>U. caudofasciatus</i> n. sp. (B) | 3 | | 3 | 5 | 8 | 11 | 14 | | | | 4 | 6 |
| <i>U. gubal</i> n. sp. ¹ | | | 1 | | | | | | | | | |
| <i>U. heterospinus</i> n. sp. (C) | | 125 | 2 | 3 | 34 | 31 | 36 | | | 2 | 2 | 2 |
| <i>U. mouthami</i> | | 3 | 1 | 1 | 2 | | | | | 3 | 1 | |
| <i>U. randalli</i> | 3+1 ² | | 1 | 2 | 3 | 2 | | | | 1 | | |
| Chi ² test: | | | (A,B)(B,C)** | | | | | | | | | |
| Populations | | | | | | | | | | | | |
| <i>U. margarethae</i> | | | | | | | | | | | | |
| WIOP (A) | 19 | | 4 | 6 | 9 | 13 | 11 | | | | | |
| Red Sea (B) | 4 | | | | 9 | 5 | 7 | | | | | |
| EIO/NA (C) | 9 | | 12 | 4 | 5 | 1 | | | | | | |
| Chi ² test: | | | C(A,B)** | | | | | | | | | |
| <i>U. heterospinus</i> | | | | | | | | | | | | |
| Gulf of Thailand (A) | | 42 | | | 26 | 17 | | | | | | |
| South-central Vietnam (B) | | 27 | | 1 | | 4 | 25 | | | | | |
| N Vietnam (C) | | 41 | | 1 | 5 | 6 | 8 | | | | | |
| Chi ² test: | | | A,B,C* | | | | | | | | | |

¹ fresh colour unknown; ² fresh-colour drawing added; * p<0.01 (Chi² Test); ** p<0.0001 (Chi² Test).

Upeneus caudofasciatus n. sp. Uiblein & Gledhill

Tailbar goatfish

(Figures 1, 6–8; Tables 2, 4–9)

Holotype. CSIRO H 6717-02, adult, 116 mm SL, W Pacific, NE Australia, Queensland, Great Barrier Reef, N of Rockingham Bay, 17° 38.57' S, 146° 22.79' E, FRV *Gwendoline May*, otter trawl, 26 m depth; collector Daniel Gledhill, 25 Nov 2003 (fresh-colour photo)

Paratypes. (30 adults, 4 subadults: 53–124 mm SL, 1 fresh-colour photo). W Pacific, NE Australia, Queensland: Torres Strait: CSIRO H 6441-03, 90 mm SL, Torres Strait, S of Bristow Island, 09° 15.65' S, 143° 20.72' E, FRV *Gwendoline May*, otter trawl, 28 m depth; QM I.15833, 83 mm SL, W of Adolphus Passage, 10° 38' S, 142° 28' E, 16–18 m depth, trawl; QM I.16503, 124 mm SL, Aureed Island area, 9° 57' S, 143° 17' E, trawl; Great Barrier Reef: AMS I.20753-004, 14: 53–99 mm SL, Lizard Island area, 2 nm NW of Nymph Island, 14° 36' S, 145° 14' E, prawn trawl, 15 m depth; AMS I.34398-034, 89 mm SL, South Arm Channel, Port Clinton, adjacent to West Flat, 22° 33' 29" S, 150° 45' 19" E, 11 m depth; CSIRO H 5957-22, 2: 83-86 mm SL, near Cape Flattery, 14°46.8'S, 145°15.7'E, FRV *Gwendoline May*, otter trawl, 17 m depth; CSIRO H 6519-21, 2: 78-98 mm SL, NE of Cooktown, 15° 01.91' S, 145° 29.40' E, FRV *Gwendoline May*, trawl, 39 m depth; CSIRO H 7212-01, 95 mm SL, SE of Cairns, 17° 08.90' S, 146° 12.11' E, FRV *Gwendoline May*, trawl, 35 m depth (fresh-colour photo); CSIRO H 7660-01, 2: 110-112 mm SL, E of Northumberland Islands, 21° 37.38' S, 150° 07.79' E, FRV *Gwendoline May*, 34 m depth, trawl; CSIRO H 7664-01, 105 mm SL, NE of Gladstone, 23° 37.47' S, 151° 41.48' E, FRV *Gwendoline May*, otter trawl, 38 m depth; QM I.15628, 89 mm SL (largest of 11), 2 nm off NW of Nymph Island, 14° 36' S, 145° 14' E, trawl, 15 m depth; QM I.15677, 83 mm SL, 5 nm WNW of Lizard Island, 15° 30' S, 145° 22' E, trawl, 20 m depth; QM I.16213, 83 mm SL, (1 of 6 (marked)), 3 ml NW of Lizard Island, 14° 38' S, 145° 24' E, trawl, 26 m depth; QM I.17982, 93 mm SL,

SE of Cooktown, 15° 46' S, 145° 35' E, 27 m depth; QM I.18044, 86 mm SL, Lizard Island, W of, 14° 36' S, 145° 3' E, 13 m depth; QM I.39294, 105 mm SL, NE of Yeppoon, 22° 44.16' S, 151° 26.56' E, FRV *Gwendoline May*, trawl, 60 m depth; QM I.39316, 2, 94-111 mm SL, Flora Passage, 17° 3' S, 146° 14' E, trawl, 37-42 m depth.

TABLE 7. Presence (with percentage) and absence of remains of six colour characters in three species and three populations of two species of the *margarethae* group, with results of statistical comparisons by Fisher's exact test. Letters in parentheses refer to pairs of species or populations showing no significant differences. Area abbreviations are explained in legend of Table 1.

| Species | Present (%) | Absent | Present (%) | Absent | Present (%) | Absent | Fisher's exact test |
|---------------------------------|---------------------------|--------|------------------------------|--------|----------------------------|--------|---------------------|
| | <i>U. margarethae</i> (A) | | <i>U. caudofasciatus</i> (B) | | <i>U. heterospinus</i> (C) | | |
| Upper caudal-fin lobe bars | 57 (66) | 30 | 30 (71) | 12 | 97 (96) | 4 | C(A,B)** |
| Lower caudal-fin lobe bars | 56 (64) | 31 | 37 (88) | 5 | 99 (98) | 2 | A(B,C)* |
| Caudal-fin bars on both lobes | 48 (55) | 39 | 30 (71) | 12 | 97 (96) | 4 | C(A,B)** |
| Second dorsal-fin distal stripe | 47 (55) | 39 | 32 (76) | 10 | 93 (92) | 8 | C(A,B)* |
| Saddle behind 2nd dorsal fin | 52 (60) | 35 | 21 (50) | 21 | 65 (65) | 35 | ns |
| Mid-lateral dots | 21 (24) | 66 | 21 (51) | 20 | 35 (35) | 65 | (A,C)(B,C)* |
| Populations | | | | | | | |
| <i>U. margarethae</i> | WIOP (A) | | Red Sea (B) | | EIO/NA (C) | | |
| Upper caudal-fin lobe bars | 30 (68) | 14 | 20 (95) | 1 | 7 (32) | 15 | C(A,B)* |
| Lower caudal-fin lobe bars | 27 (61) | 17 | 20 (95) | 1 | 9 (41) | 13 | B(A,C)* |
| Caudal-fin bars | 22 (50) | 22 | 19 (90) | 2 | 7 (32) | 15 | B(A,C)* |
| Second dorsal-fin distal stripe | 23 (53) | 20 | 20 (95) | 1 | 4 (18) | 18 | A,B,C* |
| Saddle behind 2nd dorsal fin | 37 (84) | 7 | 11 (52) | 10 | 4 (18) | 18 | A(B,C)* |
| Mid-lateral dots | 12 (27) | 32 | 9 (43) | 12 | 0 (0) | 22 | C(A,B)* |
| <i>U. heterospinus</i> | Gulf of Thailand (A) | | South-central Vietnam (B) | | N Vietnam (C) | | |
| Upper caudal-fin lobe bars | 43 (98) | 1 | 29 (97) | 1 | 20 (100) | 0 | ns |
| Lower caudal-fin lobe bars | 44 (100) | 0 | 30 (100) | 0 | 20 (100) | 0 | ns |
| Caudal-fin bars | 43 (98) | 1 | 29 (97) | 1 | 20 (100) | 0 | ns |
| Second dorsal-fin distal stripe | 44 (100) | 0 | 30 (100) | 0 | 20 (100) | 0 | ns |
| Saddle behind 2nd dorsal fin | 18 (42) | 25 | 29 (97) | 1 | 14 (70) | 6 | B(A,C)* |
| Mid-lateral dots | 0 (0) | 43 | 25 (83) | 5 | 9 (45) | 11 | A,B,C* |

* $p \leq 0.01$; ** $p < 0.000$

Non-types. (11 adults, 9 subadults: 50–107 mm SL, 1 fresh-colour photo). W Pacific, NE Australia, Queensland: Torres Strait: AMS I.20827-027, 3: 80–107 mm SL, Cape York, 2 nm NE of Hannibal Island, 11° 33' S, 142° 57' E, prawn trawl, 23 m depth; AMS I.20923-001, 5: 63–97 mm SL, Cape York, 10° 39' S, 142° 30' E, prawn trawl; CSIRO H 3637-10, 69 mm SL, W of Thursday Island, 10° 34' S, 141° 59' E, FRV *Southern Surveyor*, trawl, 12 m depth (fresh-colour photo); CSIRO H 3637-11, 50 mm SL, W of Thursday Island, 10° 34' S, 141° 59' E, FRV *Southern Surveyor*, trawl, 12 m depth; CSIRO H 7661-01, 2: 60 mm SL (both), S of Banks Island, 10° 25.20' S, 142° 18.60' E, FRV *Gwendoline May*, trawl, 14 m depth; CSIRO H 7689-02 3: 56–62 mm SL, NE of Dungeness Island, 9° 39.49' S, 142° 47.61' E, FRV *Gwendoline May*, trawl, 10 m depth; QM I.16482, 104 mm SL, sand cay SE of Coconut Island, 10° 11' S, 143° 14' E, trawl; QM I.16483, 97 mm SL, Aureed Island area, 9° 57' S, 143° 17' E, Trawl; Great Barrier Reef: AMS I.20752-013, 3 (of 5): 54–92 mm SL, 5 nm WNW of Lizard Island, 14° 30' S, 145° 22' E, prawn trawl, 20 m depth.

Diagnosis. Dorsal fins VIII + 9, the first spine minute; pectoral fins 12–14; gill rakers 5–7 + 16–19 = 22–25; lateral-line scales 28–30; measurements in % SL, adults: body depth at first dorsal-fin origin 24–28; body depth at anus 19–24; caudal-peduncle depth 9.9–11; caudal-peduncle width 2.6–4.3; maximum head depth 20–24; head depth through eye 16–20; suborbital depth 9.2–13; interorbital length 7.5–8.8; head length 28–31; snout length 9.9–12; postorbital length 10–13; orbit length 6.7–8.7; upper-jaw length 9.9–13; barbel length 18–23; interdorsal distance 12–17; caudal-peduncle length 21–25; caudal-fin length 27–32; anal-fin height 16–20; pelvic-fin length

20–24; pectoral-fin length 19–23; pectoral-fin width 3.6–4.8; first dorsal-fin height 19–23; second dorsal-fin height 18–21; measurements in % SL, subadults: body depth at first dorsal-fin origin 24–27; body depth at anus 19–22; caudal-peduncle depth 9.6–11; caudal-peduncle width 2.7–3.8; maximum head depth 20–23; head depth through eye 17–20; suborbital depth 9.4–11; interorbital length 7.6–8.6; head length 30–32; snout length 11–12; postorbital length 11–13; orbit length 8.1–8.8; upper-jaw length 11–13; barbel length 19–23; interdorsal distance 12–15; caudal-peduncle length 22–24; caudal-fin length 28–32; anal-fin height 16–19; pelvic-fin length 22–25; pectoral-fin length 21–23; pectoral-fin width 3.8–4.6; first dorsal-fin height 20–23; second dorsal-fin height 18–21; fresh colour: head and body dorsally red-brown or dark grey mottled, ventrally white, often with pale beige dots; upper lobe of caudal fin with 4 or 5 red or brown bars (3 or 4 bars in subadults), lower caudal-fin lobe with 4 to 9 red, brown or dark-brown bars, sometimes dorsally covered by a red, brown or dark-brown stripe; bars on both lobes of pupil width or less, interrupted by pale, partly hyaline interspaces of less or similar width; lower caudal-lobe tip sometimes black; barbels white, pale rose whitish, or white with beige tip region; a single yellow, beige or pale brown mid-lateral body stripe of pupil width from snout tip through eye to caudal-fin base, following lateral line in anterior two thirds of body; stripe covered by 1–4 sections with horizontal series of 2–4 dark dots, the posteriormost dots behind second dorsal-fin base; first dorsal fin with 3 or 4 red or brown, often fused stripes and the tip region pale or not darker than rest of fin; second dorsal fin with 3 or 4 red or brown well-separated stripes with hyaline interspaces; pectoral fins hyaline, pelvic and anal fins weakly pigmented and partly hyaline; preserved fish pale, often with remains of dark pigmentation deriving from caudal-fin bars, mid-lateral dots, saddle and/or second dorsal-fin distal stripe.

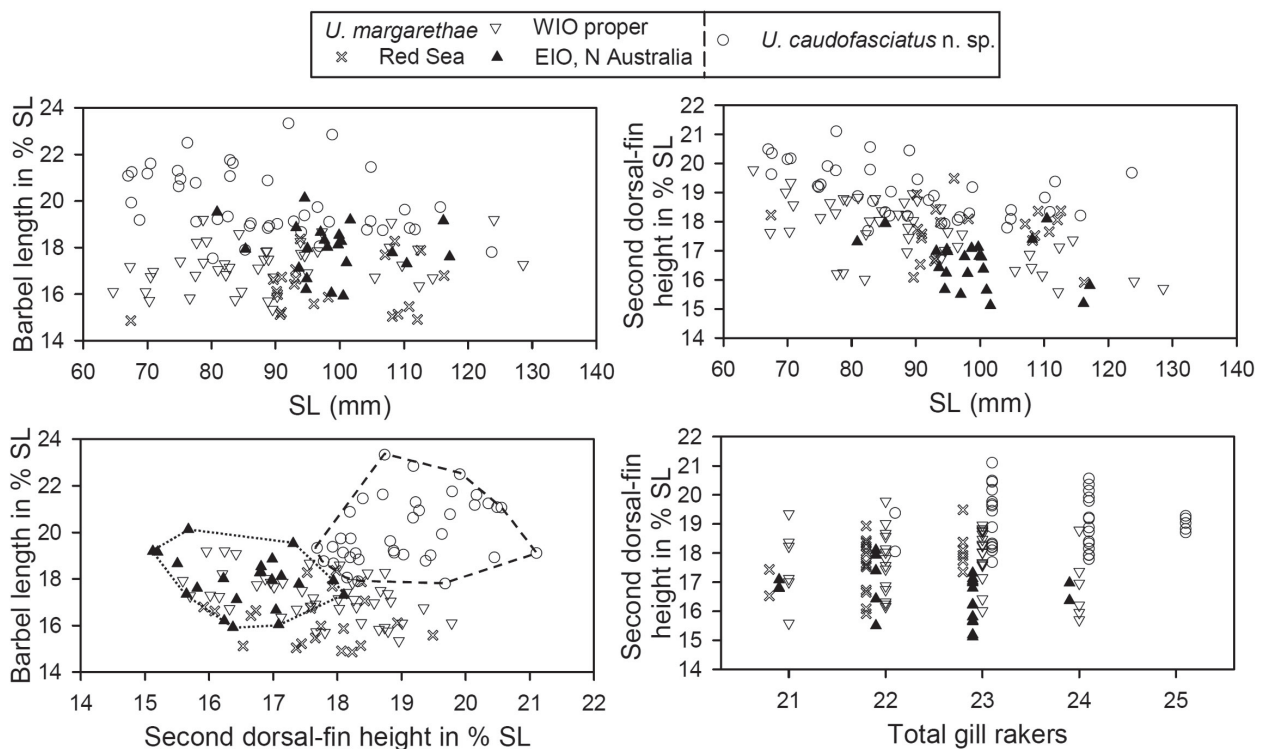


FIGURE 6. Two morphometric characters against SL and each other and second dorsal-fin height against total number of gill rakers in adults of two *margarethae*-group species. For *Upeneus margarethae*, the three populations are indicated by different symbols. The distinction between *U. caudofasciatus* n. sp. and the EIO/N Australian population of *U. margarethae* is indicated by dashed and dotted outlines, respectively.

Description. Measurements in % SL and counts for types are given in Table 8; morphometric data as ratios of SL for holotype, data for paratypes in brackets: body elongate, body depth at first dorsal-fin origin 3.9 [3.5–4.2], body depth at anal-fin origin 4.7 [4.2–5.2], head length 3.4 [3.2–3.6] subequal to caudal-fin length (3.6 [3.1–3.7]), second dorsal-fin height 5.5 [4.7–5.7], only slightly shallower than first dorsal fin (5.1 [4.3–5.1]) and similar to barbel length (5.1 [4.4–5.6]), pelvic-fin length 4.7 [4.0–5.0], similar to length of pectoral fins (5.0 [4.3–5.2]) and body depth at first dorsal-fin origin; caudal-peduncle depth 9.8 [8.9–10], larger than orbit length (15 [12–15]); and caudal-peduncle width 30 [24–38], narrower than pectoral-fin width (22 [21–27]).

Colour. *Freshly collected fish.* (Figure 7 A–C). All three specimens and especially holotype and paratype (Figure 7 A, B) show obvious signs of lesions (most probably due to trawling damage) with large red, skin-lacking patches on head below eye, gill cover or mid of body. Otherwise head and body are ventrally white, overlain by small beige to beige-rose dots associated with individual scales in paratype (Figure 7 B) and non-type (Figure 7 C); belly and ventral part of caudal peduncle white; head from above snout and eye and body above lateral line pale brown-red to dark-grey mottled, bordered below by a mid-lateral stripe of pupil width which runs rather straight or only slightly bent from caudal-fin base to eye in yellow or greenish beige colour, becoming reddish on head and bending ventrally towards snout tip (stripe on head not visible in holotype); on the mid-lateral body stripe from behind head to behind second-dorsal fin up to 4 well-separated sections just behind head, below each dorsal, and behind second dorsal fin, each with 1–3 red, brown or black dots of less than pupil width; from behind head until below base of second dorsal fin, a thin white stripe separates the dorsal body pigmentation from the mid-lateral body stripe; lateral line weakly visible as a series of mostly red dots placed well above mid-lateral stripe in anterior half of body starting to cross the stripe just in front of anterior second dorsal-fin base, continuing behind dorsal fin just below stripe towards caudal-fin base; barbels entirely white (paratype), white, intermingled with pale rose (holotype) or white with a beige tip region (non-type) (Figure 7 A–C); caudal fin with 9–14 oblique red bars crossing both lobes entirely, or placed on fin tips; upper caudal-fin lobe with 4–5 bars of pupil width or slightly narrower, the distal-most bar covering fin tip in holotype and non-type; bars separated by hyaline interspaces of similar width or slightly wider; in holotype and non-type blotches of dark red or black pigmentation on some of the bars; lower caudal-fin lobe covered by 5–9 red bars of similar width or slightly narrower (holotype) than bars on dorsal fin lobe, with hyaline interspaces being of similar width or slightly narrower; in all three specimens the ventral lobe ends in a black tip and some of the other bars contain dark-red or black blotches; the lower fin lobe is in addition crossed longitudinally by a pale-red stripe that reaches from base of fin to fin tip, crossing nearly the entire fin lobe apart from ventral margin (types) or the dorsal half of lobe (non-type); first dorsal fin almost entirely covered with pale red or pale orange pigmentation intermingled with hyaline areas; second dorsal fin with 3 red stripes of orbit width or less, one stripe at fin base, one intermediate and one at or close to fin tip, the latter being darker than the other stripes; pelvic fins hyaline with up to five narrow red stripes; anal fin with or without stripes, pectoral fins hyaline.

Preserved fish. Head and body mostly uniformly pale brown, greyish brown or brown, sometimes slightly darker dorsally, gill cover silvery or pale and partly transparent, lateral line, when intact, well visible in entire range from behind head to caudal-fin base; barbels pale brown or pale creamy; mid-lateral body stripe completely lost, but often remains of dark dots mid-laterally in the area of stripe below and posterior to dorsal fins (51 % of 41 adults, 60 % of 10 subadults); dark pigmentation remains occur also in other areas: saddle behind second dorsal fin (50 % in adults vs. 100 % in juveniles), caudal fin (88 % vs. 100 %), and second dorsal-fin distal stripe (76 % vs. 100 %); on caudal fin with retained pigmentation remains of up to 6 oblique bars visible on each lobe; in adults 71 % (of 42 fish) show remains of bars on both lobes, in subadults 100 % (= all 13 fish); of all adults only 7 % show no dark pigmentation remains (pigmentation degree 0) and 34 % have dark pigmentation in all body and fin regions (pigmentation degree 4) vs. 60 % in adults. Unpigmented areas of caudal and second dorsal fins and other fins pale hyaline.

Etymology. The name refers to the occurrence of oblique conspicuous bars which cross both caudal-fin lobes entirely.

Distribution, habitat and size. SW Pacific, NE Australia, Queensland, from W of Thursday Island and S of Daru Island, Torres Strait to NE of Gladstone, Great Barrier Reef; maximum depth 60 m, commonly trawled above soft bottoms at between 15 and 40 m; maximum size 12.5 cm SL.

Intraspecific comparisons. Subadults differ from adults in having a slightly longer head, shallower pelvic-fin depth and longer pelvic fins (Tables 2, 9; Figure 8); they differ in having fewer bars on the caudal fin (only preserved fish could be compared; Tables 2, 9); dark pigmentation is more often found in preserved subadults than in preserved adults (Tables 2, 9; see also preserved colour description above).

Remarks. Because of the relatively small distribution area of the species and low numbers of specimens available from the most distant localities, no quantitative population comparisons could be conducted. In two of the 55 studied specimens the tiny first-dorsal fin spine is overgrown with skin or very small and hence difficult to detect. Though this species appears to be rather common on shallow soft bottoms near coral reefs, we could not find any *in-situ* fresh-colour photo documentation.

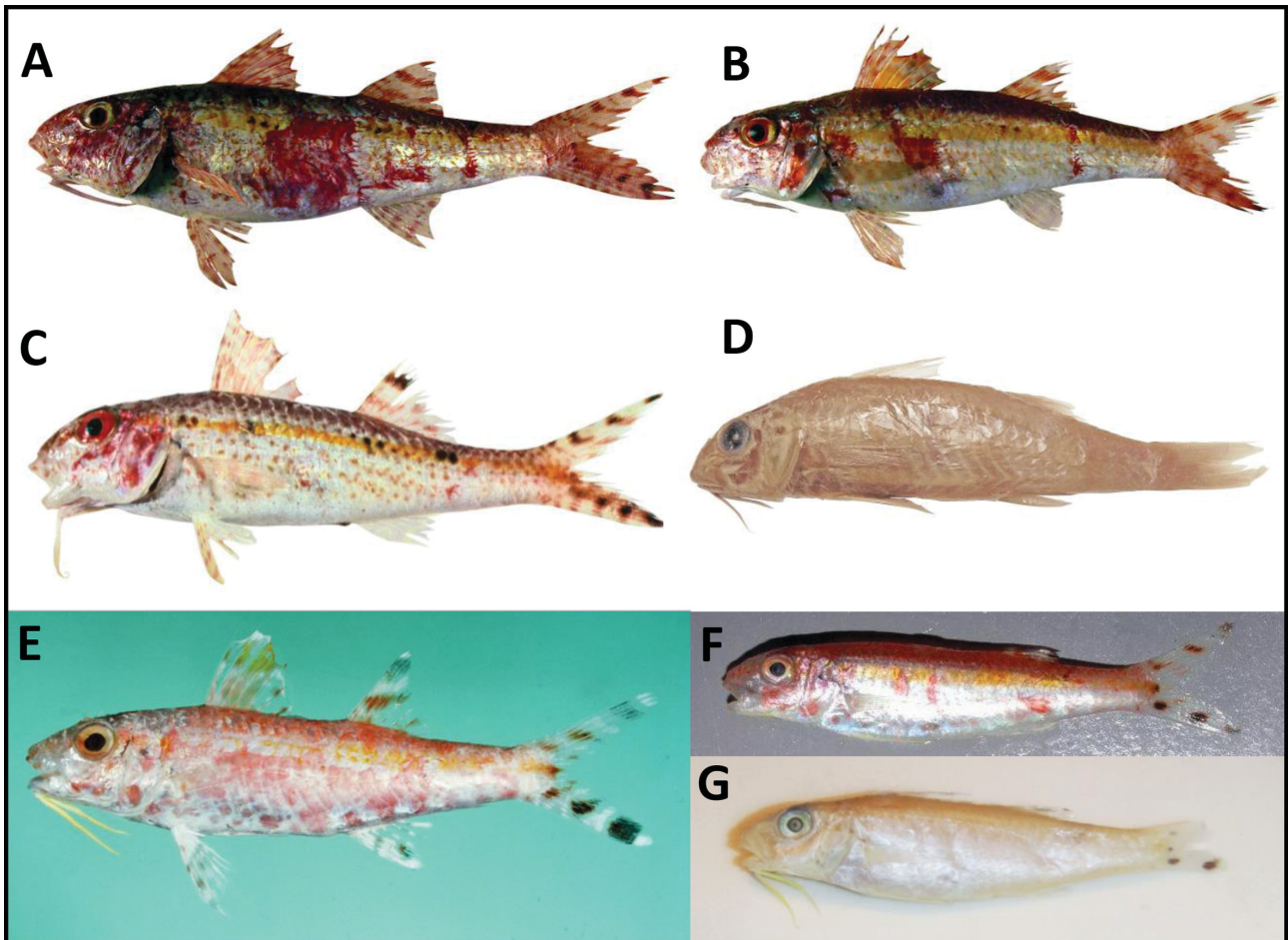


FIGURE 7. (A–C) *Upeneus caudofasciatus* n. sp. : (A) HT, CSIRO H 6717-02, 116 mm SL, NE Australia, Great Barrier Reef, N of Rockingham Bay (D.C. Gledhill); (B) PT, CSIRO H 7212-01, 95 mm SL, same region, SE of Cairns (D.C. Gledhill); (C) CSIRO H 3637-10, 69 mm SL, Torres Strait W of Thursday Island, (G. Yearsley); (D) *U. gubal* n. sp., 87 mm SL, Red Sea, S Gulf Of Suez (F. Uiblein); (E–G) *U. mouthami*; (E) HT, BPBM 33858, 70 mm SL, Chesterfield Bank, Coral Sea (J.E. Randall); (F) MNHN 2008-1433, 49 mm SL, Vanuatu, off Malo Island, Bruat Channel (C. Ferrara); (G) same specimen preserved (F. Uiblein).

Upeneus gubal n. sp. Uiblein

Gubal goatfish

(Figures 1, 5, 7; Tables 1, 5, 6)

Holotype. MNHN 2011-1515, adult, 86 mm SL, WIO, Red Sea, Gulf of Suez, Strait of Gubal, N of Gubal Island, 27° 49' 59" N, 33° 43' 1" E, 70 m depth, 28 Dec. 1928, collector Robert P. Dollfus.

Diagnosis. Dorsal fins VIII + 9, the first spine minute; pectoral fins 15; gill rakers 6 + 19 = 25; lateral-line scales 28–29; measurements in % SL: body depth at first dorsal-fin origin 24; body depth at anus 21; caudal-peduncle depth 11; caudal-peduncle width 3.3; maximum head depth 20; head depth through eye 16; suborbital depth 9.0; interorbital length 8.2; head length 29; snout length 11; postorbital length 11; orbit length 7.4; upper-jaw length 11; barbel length 19; interdorsal distance 16; caudal-peduncle length 24; caudal-fin length 31; anal-fin height 19; pelvic-fin length 22; pectoral-fin length 22; pectoral-fin width 4.8; first dorsal-fin height 22; second dorsal-fin height 19; preserved colour pale brown.

Description. Measurements in % SL and counts are given in Table 1; morphometric data as ratios of SL for holotype: body elongate, body depth at first dorsal-fin origin 4.2, body depth at anal-fin origin 4.8, head length 3.4, larger than maximum body depth and subequal to caudal-fin length (3.2); second dorsal-fin height 5.2, shallower than first dorsal fin (4.4) and similar to barbel length (5.4); pelvic-fin length 4.5, equal to length of pectoral fins (4.5)

and similar to body depth at first dorsal-fin origin; caudal-peduncle depth 9.2, much larger than orbit length (14); and caudal-peduncle width 30, much narrower than pectoral-fin width (21).

Colour. *Preserved fish.* (Figure 7 D). Body and head entirely pale brown, with brown patches or blotches on head below and behind eyes and on anterior ventral side of body; barbels pale creamy; no remains of dark pigmentation deriving from caudal-fin bars, dark mid-lateral dots, saddle behind second dorsal fin, or second dorsal-fin distal stripe; fins pale brown, partly hyaline.

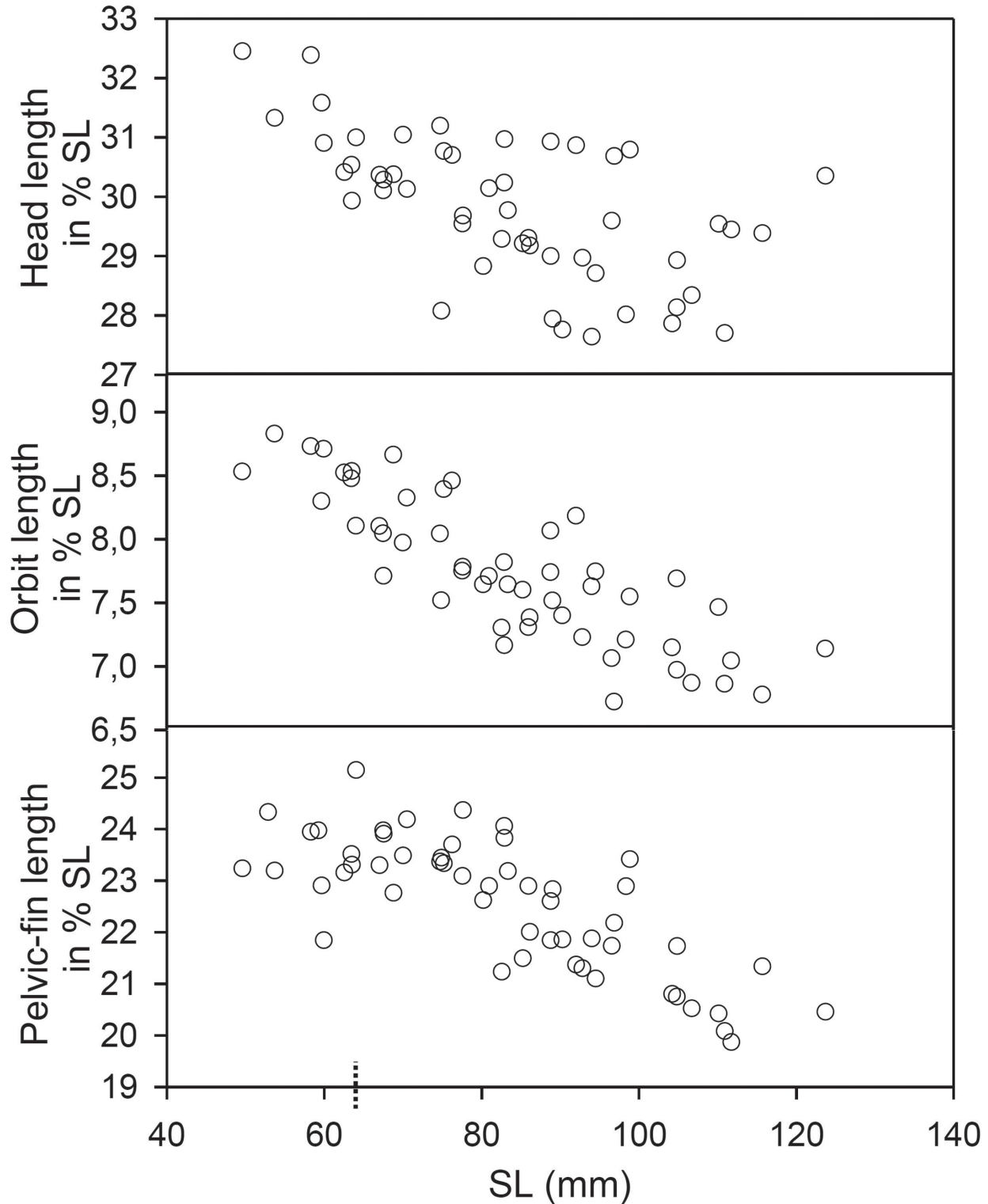


FIGURE 8. Three selected morphological characters against SL in *Upeneus caudofasciatus* n. sp. The 65 mm demarcation for subadults and adults is indicated by a dotted black dash.

TABLE 8. Morphometric, meristic and preserved colour characters in types of *Upeneus caudofasciatus* n. sp. and *U. heterospinus* n. sp., with data for the latter split into two morphs with seven and eight dorsal-fin spines based on all examined adult specimens.

| Morphometric characters | <i>U. caudofasciatus</i> n. sp. | | | | | <i>U. heterospinus</i> n. sp. | | | | | | | | | | | | |
|--|---------------------------------|-----------|------|-----|-----------|-------------------------------|---------------------|-------|-----|---------------------|-----|------|-----|------|-----|------|-----|----|
| | HT | Paratypes | | HT | Paratypes | | 7 dorsal-fin spines | | | 8 dorsal-fin spines | | | | | | | | |
| | Min | Mean | Max | n | Min | Mean | Max | n | Min | Mean | Max | n | Min | Mean | Max | n | | |
| Standard length (SL) in % SL | 116 | 53 | 84.7 | 124 | 34 | 91 | 56 | 101.4 | 152 | 29 | 66 | 89.4 | 122 | 48 | 65 | 90.5 | 152 | 53 |
| Body depth at first dorsal-fin origin | 26 | 24 | 26.3 | 28 | 34 | 24 | 22 | 23.8 | 26 | 29 | 23 | 24.1 | 26 | 47 | 22 | 24.0 | 26 | 52 |
| Body depth at anal-fin origin | 21 | 19 | 21.6 | 24 | 34 | 20 | 18 | 20.9 | 22 | 29 | 19 | 20.7 | 22 | 48 | 18 | 20.6 | 22 | 52 |
| Half body depth at first dorsal-fin origin | 21 | 19 | 21.3 | 24 | 28 | 20 | 18 | 19.9 | 22 | 28 | 18 | 20.1 | 22 | 43 | 18 | 19.8 | 22 | 43 |
| Half body depth at anal-fin origin | 16 | 15 | 16.2 | 18 | 27 | 16 | 15 | 16.3 | 17 | 25 | 15 | 16.1 | 17 | 40 | 15 | 16.0 | 17 | 42 |
| Caudal-peduncle depth | 10 | 9.7 | 10.4 | 11 | 34 | 10 | 9.8 | 10.3 | 11 | 29 | 9.2 | 10.3 | 11 | 48 | 9.2 | 10.2 | 11 | 53 |
| Caudal-peduncle width | 3.4 | 2.6 | 3.7 | 4.3 | 32 | 4.8 | 3.6 | 4.2 | 5.0 | 29 | 3.5 | 4.2 | 5.0 | 47 | 3.6 | 4.2 | 4.8 | 52 |
| Maximum head depth | 22 | 20 | 22.2 | 24 | 32 | 21 | 19 | 20.9 | 22 | 29 | 19 | 20.8 | 23 | 48 | 19 | 20.6 | 23 | 53 |
| Head depth through eye | 18 | 16 | 17.9 | 20 | 32 | 17 | 15 | 16.2 | 17 | 29 | 15 | 16.2 | 18 | 48 | 15 | 16.0 | 17 | 53 |
| Suborbital depth | 11 | 9.6 | 10.7 | 13 | 32 | 9.9 | 8.8 | 9.8 | 11 | 29 | 8.5 | 9.6 | 11 | 48 | 8.3 | 9.7 | 11 | 53 |
| Interorbital length | 8.0 | 7.5 | 8.1 | 8.8 | 32 | 8.2 | 7.3 | 8.0 | 9.2 | 29 | 7.2 | 8.1 | 9.2 | 48 | 7.3 | 8.0 | 9.0 | 51 |
| Head length | 29 | 28 | 29.6 | 31 | 32 | 29 | 27 | 28.5 | 30 | 29 | 27 | 28.7 | 31 | 48 | 27 | 28.7 | 31 | 53 |
| Snout length | 12 | 9.9 | 11.4 | 12 | 32 | 11 | 9.9 | 11.0 | 12 | 29 | 9.9 | 11.1 | 13 | 48 | 9.7 | 11.1 | 12 | 53 |
| Postorbital length | 11 | 10 | 11.6 | 13 | 32 | 11 | 10 | 11.1 | 12 | 29 | 10 | 11.2 | 13 | 48 | 10 | 11.3 | 13 | 53 |
| Orbit length | 6.8 | 6.9 | 7.6 | 8.5 | 32 | 7.2 | 5.9 | 7.2 | 8.2 | 29 | 6.3 | 7.4 | 8.2 | 48 | 5.9 | 7.3 | 8.3 | 53 |
| Orbit depth | 5.9 | 6.0 | 6.7 | 7.9 | 32 | 6.7 | 4.9 | 6.3 | 7.1 | 29 | 5.5 | 6.5 | 7.4 | 48 | 4.9 | 6.5 | 7.3 | 53 |
| Upper-jaw length | 11 | 9.9 | 11.5 | 13 | 32 | 10 | 9.6 | 10.7 | 11 | 29 | 9.4 | 10.9 | 12 | 48 | 9.7 | 11.0 | 13 | 53 |
| Lower-jaw length | 11 | 8.6 | 10.7 | 12 | 32 | 9.5 | 9.0 | 10.0 | 11 | 29 | 8.9 | 10.3 | 12 | 48 | 9.0 | 10.3 | 12 | 53 |
| Snout width | 9.1 | 8.0 | 8.9 | 9.7 | 27 | 9.2 | 8.1 | 9.2 | 11 | 28 | 7.3 | 8.7 | 11 | 46 | 7.1 | 8.5 | 10 | 52 |
| Barbel length | 20 | 18 | 20.4 | 23 | 34 | 18 | 17 | 18.5 | 20 | 29 | 16 | 17.9 | 20 | 48 | 16 | 17.8 | 20 | 53 |
| Maximum barbel width | 1.0 | 0.8 | 0.9 | 1.1 | 32 | 0.8 | 0.8 | 1.0 | 1.2 | 29 | 0.8 | 1.0 | 1.2 | 48 | 0.8 | 0.9 | 1.1 | 53 |
| First pre-dorsal length | 36 | 34 | 37.2 | 41 | 32 | 37 | 35 | 36.0 | 38 | 29 | 34 | 36.5 | 38 | 48 | 35 | 36.2 | 39 | 53 |
| Second pre-dorsal length | 64 | 61 | 64.1 | 66 | 32 | 63 | 61 | 63.1 | 65 | 29 | 60 | 63.3 | 66 | 48 | 61 | 63.3 | 67 | 52 |
| Interdorsal distance | 15 | 12 | 14.2 | 17 | 32 | 15 | 12 | 14.6 | 16 | 29 | 13 | 14.9 | 17 | 48 | 13 | 14.9 | 17 | 52 |
| Caudal-peduncle length | 23 | 21 | 23.1 | 25 | 32 | 25 | 22 | 23.5 | 25 | 29 | 22 | 23.8 | 26 | 48 | 22 | 24.1 | 26 | 52 |
| Pre-anal length | 65 | 60 | 64.9 | 68 | 32 | 64 | 62 | 63.7 | 68 | 29 | 61 | 64.1 | 68 | 48 | 61 | 63.7 | 68 | 52 |
| Pre-pelvic length | 34 | 30 | 33.9 | 37 | 32 | 31 | 30 | 31.7 | 35 | 29 | 30 | 32.0 | 34 | 48 | 30 | 31.6 | 35 | 52 |

.....continued on the next page

TABLE 8. (Continued)

| | <i>U. caudofaciatus</i> n. sp. | | | | | | <i>U. heterospinus</i> n. sp. | | | | | | | | | | | | | |
|---------------------------------------|--------------------------------|------|------|-----------|-----|------|-------------------------------|-----|------|-----------|-----|----|---------------------|------|-----|---------------------|-----|------|-----|----|
| | HT | | | Paratypes | | | HT | | | Paratypes | | | 7 dorsal-fin spines | | | 8 dorsal-fin spines | | | | |
| | Min | Mean | Max | n | Min | Mean | Max | n | Min | Mean | Max | n | Min | Mean | Max | n | Min | Mean | Max | n |
| Pre-pectoral length | 32 | 29 | 31.9 | 35 | 32 | 30 | 30 | 29 | 29.6 | 32 | 29 | 29 | 28 | 30.1 | 33 | 48 | 28 | 30.0 | 33 | 52 |
| Second dorsal-fin depth | 21 | 20 | 22.5 | 24 | 32 | 21 | 21 | 19 | 21.4 | 23 | 29 | 29 | 19 | 21.4 | 23 | 47 | 19 | 21.2 | 23 | 52 |
| Pelvic-fin depth | 25 | 24 | 26.1 | 28 | 32 | 24 | 24 | 22 | 24.0 | 26 | 29 | 29 | 22 | 24.1 | 26 | 47 | 22 | 23.9 | 26 | 52 |
| Pectoral-fin depth | 17 | 15 | 17.5 | 19 | 32 | 17 | 17 | 15 | 16.8 | 18 | 29 | 29 | 15 | 16.6 | 18 | 47 | 15 | 16.6 | 18 | 52 |
| Length of first dorsal-fin base | 15 | 14 | 15.8 | 18 | 32 | 15 | 15 | 13 | 15.3 | 17 | 29 | 29 | 14 | 15.3 | 17 | 48 | 13 | 15.3 | 17 | 51 |
| Length of second dorsal-fin base | 14 | 12 | 14.1 | 16 | 32 | 13 | 13 | 12 | 14.1 | 15 | 29 | 29 | 12 | 13.8 | 15 | 48 | 12 | 13.8 | 16 | 52 |
| Caudal-fin length | 27 | 27 | 30.0 | 32 | 32 | 30 | 30 | 27 | 29.3 | 32 | 23 | 23 | 27 | 29.1 | 31 | 43 | 27 | 29.5 | 32 | 50 |
| Length of anal-fin base | 11 | 9.7 | 11.6 | 13 | 32 | 11 | 11 | 10 | 11.4 | 13 | 29 | 29 | 9.7 | 11.3 | 13 | 47 | 9.9 | 11.4 | 13 | 52 |
| Anal-fin height | 17 | 16 | 17.5 | 20 | 32 | 16 | 16 | 15 | 16.4 | 18 | 29 | 29 | 15 | 16.7 | 19 | 47 | 15 | 16.8 | 19 | 51 |
| Pelvic-fin length | 21 | 20 | 22.7 | 25 | 34 | 20 | 20 | 19 | 20.5 | 22 | 29 | 29 | 19 | 20.9 | 23 | 48 | 19 | 20.8 | 23 | 52 |
| Pectoral-fin length | 20 | 19 | 21.5 | 23 | 32 | 19 | 19 | 19 | 20.0 | 21 | 25 | 25 | 19 | 20.5 | 22 | 44 | 19 | 20.3 | 22 | 53 |
| Pectoral-fin width | 4.5 | 3.6 | 4.3 | 4.8 | 32 | 4.3 | 4.3 | 3.8 | 4.2 | 4.6 | 29 | 29 | 3.4 | 4.1 | 4.7 | 48 | 3.4 | 4.1 | 4.7 | 53 |
| First dorsal-fin height | 20 | 20 | 21.6 | 23 | 30 | 21 | 21 | 18 | 20.0 | 22 | 27 | 27 | 19 | 20.5 | 22 | 45 | 18 | 20.3 | 23 | 53 |
| Second dorsal-fin height | 18 | 18 | 19.4 | 21 | 34 | 16 | 16 | 16 | 17.2 | 19 | 27 | 27 | 16 | 17.8 | 20 | 45 | 16 | 17.7 | 20 | 52 |
| Meristic characters | | | | | | | | | | | | | | | | | | | | |
| Dorsal-fin spines | 8 | 8 | 8.0 | 8 | 34 | 7 | 7 | 7 | 7.5 | 8 | 29 | 29 | 7 | 7.0 | 7 | 48 | 8 | 8.0 | 8 | 53 |
| Pectoral-fin rays | 14 | 12 | 13.4 | 14 | 34 | 14 | 14 | 13 | 13.8 | 15 | 29 | 29 | 13 | 13.8 | 14 | 48 | 13 | 13.9 | 15 | 53 |
| Rudimentary gill rakers on upper limb | 3 | 3 | 3.2 | 5 | 34 | 3 | 3 | 2 | 2.8 | 4 | 29 | 29 | 2 | 3.1 | 4 | 48 | 2 | 2.9 | 4 | 53 |
| Developed gill rakers on upper limb | 3 | 2 | 2.9 | 4 | 34 | 3 | 3 | 2 | 3.0 | 4 | 29 | 29 | 2 | 2.6 | 3 | 48 | 2 | 2.7 | 4 | 53 |
| Developed gill rakers on lower limb | 11 | 11 | 12.7 | 15 | 34 | 13 | 13 | 11 | 12.3 | 14 | 29 | 29 | 11 | 11.9 | 13 | 48 | 11 | 12.2 | 14 | 53 |
| Rudimentary gill rakers on lower limb | 6 | 3 | 4.9 | 6 | 34 | 3 | 3 | 3 | 4.4 | 6 | 29 | 29 | 3 | 4.4 | 6 | 48 | 3 | 4.5 | 6 | 53 |
| Total gill rakers on upper limb | 6 | 6 | 6.1 | 7 | 34 | 6 | 6 | 5 | 5.8 | 6 | 29 | 29 | 5 | 5.7 | 6 | 48 | 4 | 5.6 | 6 | 53 |
| Total gill rakers on lower limb | 17 | 16 | 17.6 | 19 | 34 | 16 | 16 | 16 | 16.8 | 18 | 29 | 29 | 15 | 16.3 | 17 | 48 | 15 | 16.7 | 18 | 53 |
| Total gill rakers | 23 | 22 | 23.6 | 25 | 34 | 22 | 22 | 21 | 22.6 | 24 | 29 | 29 | 21 | 22.0 | 23 | 48 | 21 | 22.3 | 24 | 53 |
| Scales along lateral line | 29 | 28 | 29.0 | 30 | 21 | 29 | 29 | 28 | 29.2 | 30 | 25 | 25 | 28 | 29.1 | 30 | 32 | 28 | 29.2 | 30 | 34 |
| Colour patterns | | | | | | | | | | | | | | | | | | | | |
| Bars on upper caudal-fin lobe | 4 | 0 | 2.6 | 6 | 34 | 3 | 3 | 0 | 4.2 | 6 | 29 | 29 | 0 | 3.4 | 6 | 48 | 0 | 3.6 | 6 | 53 |
| Bars on lower caudal-fin lobe | 5 | 0 | 4.3 | 6 | 34 | 5 | 5 | 1 | 4.8 | 6 | 29 | 29 | 0 | 4.5 | 6 | 48 | 0 | 4.3 | 6 | 53 |
| Bars on both caudal-fin lobes | 9 | 0 | 6.9 | 11 | 34 | 8 | 8 | 1 | 9.0 | 12 | 29 | 29 | 0 | 7.9 | 12 | 48 | 0 | 7.9 | 12 | 53 |
| Pigmentation degree | 4 | 1 | 3.0 | 4 | 33 | 4 | 4 | 1 | 3.8 | 4 | 29 | 29 | 0 | 2.9 | 4 | 48 | 0 | 2.9 | 4 | 53 |

TABLE 9. Morphometric, meristic and preserved colour characters in all examined adults of four *margarethae*-group species.

| Morphometric characters | <i>U. caudofasciatus</i> n. sp. | | | | | <i>U. heterospinus</i> n. sp. | | | | | <i>U. mouthami</i> | | | | | <i>U. randalli</i> | | | | |
|--|---------------------------------|------|-----|----|-----|-------------------------------|------|-----|-----|------|--------------------|------|------|------|-----|--------------------|------|-----|---|----|
| | Min | Mean | Max | n | SL | Min | Mean | Max | n | SL | Min | Mean | Max | n | SL | Min | Mean | Max | n | SL |
| Standard length (SL) in % SL | 67 | 88.8 | 124 | 42 | 42 | 65 | 90.0 | 152 | 101 | 73 | 84.1 | 94 | 66 | 84.3 | 106 | 8 | 8 | 8 | 8 | 8 |
| Body depth at first dorsal-fin origin | 24 | 26.2 | 28 | 42 | 22 | 24.1 | 26 | 99 | 21 | 22.7 | 24 | 23 | 23.5 | 24 | 8 | 8 | 8 | 8 | 8 | 8 |
| Body depth at anal-fin origin | 19 | 21.6 | 24 | 42 | 18 | 20.7 | 22 | 100 | 19 | 19.9 | 21 | 19 | 20.2 | 22 | 8 | 8 | 8 | 8 | 8 | 8 |
| Half body depth at first dorsal-fin origin | 19 | 21.3 | 24 | 38 | 18 | 19.9 | 22 | 86 | 19 | 19.7 | 20 | 19 | 19.6 | 20 | 8 | 8 | 8 | 8 | 8 | 8 |
| Half body depth at anal-fin origin | 15 | 16.3 | 18 | 37 | 15 | 16.0 | 17 | 82 | 15 | 15.3 | 15 | 15 | 15.7 | 17 | 8 | 8 | 8 | 8 | 8 | 8 |
| Caudal-peduncle depth | 9.9 | 10.5 | 11 | 42 | 9.2 | 10.2 | 11 | 101 | 9.1 | 9.6 | 10 | 9.9 | 10.3 | 11 | 8 | 8 | 8 | 8 | 8 | 8 |
| Caudal-peduncle width | 2.6 | 3.7 | 4.3 | 42 | 3.5 | 4.2 | 5.0 | 99 | 3.2 | 3.6 | 3.9 | 2.9 | 3.4 | 3.8 | 8 | 8 | 8 | 8 | 8 | 8 |
| Maximum head depth | 20 | 22.2 | 24 | 42 | 19 | 20.7 | 23 | 101 | 20 | 20.1 | 21 | 19 | 20.3 | 21 | 8 | 8 | 8 | 8 | 8 | 8 |
| Head depth through eye | 16 | 17.8 | 20 | 42 | 15 | 16.1 | 18 | 101 | 17 | 17.6 | 18 | 15 | 15.6 | 16 | 8 | 8 | 8 | 8 | 8 | 8 |
| Suborbital depth | 9.2 | 10.8 | 13 | 42 | 8.3 | 9.6 | 11 | 101 | 9.0 | 10.2 | 11 | 8.0 | 9.1 | 10 | 8 | 8 | 8 | 8 | 8 | 8 |
| Interorbital length | 7.5 | 8.1 | 8.8 | 42 | 7.2 | 8.0 | 9.2 | 99 | 7.6 | 7.8 | 8.1 | 7.2 | 8.0 | 8.8 | 8 | 8 | 8 | 8 | 8 | 8 |
| Head length | 28 | 29.5 | 31 | 42 | 27 | 28.7 | 31 | 101 | 29 | 29.4 | 30 | 27 | 28.8 | 30 | 8 | 8 | 8 | 8 | 8 | 8 |
| Snout length | 9.9 | 11.4 | 12 | 42 | 9.7 | 11.1 | 13 | 101 | 11 | 11.4 | 12 | 11 | 11.3 | 12 | 8 | 8 | 8 | 8 | 8 | 8 |
| Postorbital length | 10 | 11.7 | 13 | 42 | 10 | 11.3 | 13 | 101 | 11 | 11.4 | 12 | 10 | 11.1 | 12 | 8 | 8 | 8 | 8 | 8 | 8 |
| Orbit length | 6.7 | 7.6 | 8.7 | 42 | 5.9 | 7.3 | 8.3 | 101 | 7.8 | 8.2 | 8.8 | 6.2 | 6.9 | 7.4 | 8 | 8 | 8 | 8 | 8 | 8 |
| Orbit depth | 5.8 | 6.7 | 7.7 | 42 | 4.9 | 6.5 | 7.4 | 101 | 6.6 | 7.0 | 7.7 | 5.1 | 5.9 | 6.4 | 8 | 8 | 8 | 8 | 8 | 8 |
| Upper-jaw length | 9.9 | 11.5 | 13 | 42 | 9.4 | 10.9 | 13 | 101 | 9.3 | 10.5 | 11 | 10 | 10.9 | 11 | 8 | 8 | 8 | 8 | 8 | 8 |
| Lower-jaw length | 8.6 | 10.7 | 12 | 42 | 8.9 | 10.3 | 12 | 101 | 8.8 | 10.3 | 11 | 9.1 | 10.0 | 10 | 8 | 8 | 8 | 8 | 8 | 8 |
| Snout width | 8.0 | 8.9 | 9.7 | 35 | 7.1 | 8.6 | 11 | 98 | 8.9 | 9.8 | 11 | 7.8 | 8.4 | 9.0 | 8 | 8 | 8 | 8 | 8 | 8 |
| Barbel length | 18 | 19.9 | 23 | 42 | 16 | 17.9 | 20 | 101 | 20 | 20.8 | 22 | 16 | 18.2 | 20 | 8 | 8 | 8 | 8 | 8 | 8 |
| Maximum barbel width | 0.8 | 0.9 | 1.1 | 42 | 0.8 | 0.9 | 1.2 | 101 | 0.9 | 1.1 | 1.4 | 0.6 | 0.7 | 0.7 | 8 | 8 | 8 | 8 | 8 | 8 |
| First pre-dorsal length | 34 | 37.0 | 40 | 42 | 34 | 36.3 | 39 | 101 | 37 | 37.7 | 39 | 34 | 36.6 | 38 | 8 | 8 | 8 | 8 | 8 | 8 |
| Second pre-dorsal length | 61 | 64.3 | 67 | 42 | 60 | 63.3 | 67 | 100 | 62 | 63.7 | 65 | 61 | 64.2 | 66 | 8 | 8 | 8 | 8 | 8 | 8 |
| Interdorsal distance | 12 | 14.5 | 17 | 42 | 13 | 14.9 | 17 | 100 | 12 | 13.8 | 16 | 13 | 14.4 | 15 | 8 | 8 | 8 | 8 | 8 | 8 |
| Caudal-peduncle length | 21 | 23.1 | 25 | 42 | 22 | 23.9 | 26 | 100 | 21 | 22.2 | 24 | 23 | 23.6 | 25 | 8 | 8 | 8 | 8 | 8 | 8 |
| Pre-anal length | 60 | 64.7 | 68 | 42 | 61 | 63.9 | 68 | 100 | 64 | 64.7 | 65 | 63 | 64.6 | 67 | 8 | 8 | 8 | 8 | 8 | 8 |
| Pre-pelvic length | 30 | 33.8 | 37 | 42 | 30 | 31.8 | 35 | 100 | 28 | 29.8 | 33 | 31 | 32.0 | 34 | 8 | 8 | 8 | 8 | 8 | 8 |
| Pre-pectoral length | 29 | 31.7 | 34 | 42 | 28 | 30.0 | 33 | 100 | 29 | 31.7 | 34 | 29 | 30.5 | 32 | 8 | 8 | 8 | 8 | 8 | 8 |
| Second dorsal-fin depth | 20 | 22.5 | 24 | 42 | 19 | 21.3 | 23 | 99 | 19 | 20.3 | 21 | 19 | 20.7 | 22 | 8 | 8 | 8 | 8 | 8 | 8 |

.....continued on the next page

TABLE 9. (Continued)

| | <i>U. caudofasciatus</i> n. sp. | | | | <i>U. heterospinus</i> n. sp. | | | | <i>U. mouthami</i> | | | | <i>U. randalli</i> | | | |
|---------------------------------------|---------------------------------|------|-----|----|-------------------------------|------|-----|-----|--------------------|------|-----|---|--------------------|------|-----|---|
| | Min | Mean | Max | n | Min | Mean | Max | n | Min | Mean | Max | n | Min | Mean | Max | n |
| Pelvic-fin depth | 24 | 26.0 | 29 | 42 | 22 | 24.0 | 26 | 99 | 21 | 23.1 | 24 | 4 | 23 | 23.4 | 24 | 8 |
| Pectoral-fin depth | 15 | 17.5 | 19 | 42 | 15 | 16.6 | 18 | 99 | 16 | 16.7 | 17 | 4 | 15 | 16.0 | 17 | 8 |
| Length of first dorsal-fin base | 14 | 15.9 | 18 | 42 | 13 | 15.3 | 17 | 99 | 11 | 12.2 | 13 | 4 | 15 | 15.2 | 16 | 8 |
| Length of second dorsal-fin base | 12 | 14.3 | 16 | 42 | 12 | 13.8 | 16 | 100 | 13 | 13.5 | 14 | 4 | 12 | 13.6 | 15 | 8 |
| Caudal-fin length | 27 | 29.9 | 32 | 42 | 27 | 29.3 | 32 | 93 | 27 | 27.8 | 29 | 4 | 27 | 28.3 | 30 | 8 |
| Length of anal-fin base | 9.7 | 11.6 | 13 | 42 | 10 | 11.4 | 13 | 99 | 11 | 12.2 | 13 | 4 | 9.4 | 10.2 | 11 | 8 |
| Anal-fin height | 16 | 17.3 | 20 | 42 | 15 | 16.8 | 19 | 98 | 17 | 17.9 | 19 | 4 | 15 | 16.7 | 19 | 8 |
| Pelvic-fin length | 20 | 22.3 | 24 | 42 | 19 | 20.8 | 23 | 100 | 22 | 22.3 | 23 | 4 | 20 | 21.2 | 22 | 8 |
| Pectoral-fin length | 19 | 21.3 | 23 | 42 | 19 | 20.4 | 22 | 97 | 22 | 22.7 | 23 | 4 | 20 | 21.1 | 22 | 8 |
| Pectoral-fin width | 3.6 | 4.3 | 4.8 | 42 | 3.4 | 4.1 | 4.7 | 101 | 4.0 | 4.2 | 4.3 | 4 | 3.8 | 4.1 | 4.4 | 8 |
| First dorsal-fin height | 19 | 21.3 | 23 | 39 | 18 | 20.4 | 23 | 98 | 20 | 20.2 | 21 | 3 | 19 | 20.7 | 22 | 8 |
| Second dorsal-fin height | 18 | 19.1 | 21 | 38 | 16 | 17.8 | 20 | 97 | 17 | 18.1 | 19 | 3 | 16 | 17.6 | 20 | 8 |
| Meristic characters | | | | | | | | | | | | | | | | |
| Dorsal-fin spines | 8 | 8.0 | 8 | 42 | 7 | 7.5 | 8 | 101 | 8 | 8.0 | 8 | 4 | 8 | 8.0 | 8 | 8 |
| Pectoral-fin rays | 12 | 13.5 | 14 | 42 | 13 | 13.9 | 15 | 101 | 13 | 13.0 | 13 | 4 | 14 | 14.0 | 14 | 8 |
| Rudimentary gill rakers on upper limb | 2 | 3.1 | 5 | 42 | 2 | 3.0 | 4 | 101 | 1 | 2.3 | 3 | 4 | 2 | 2.9 | 3 | 8 |
| Developed gill rakers on upper limb | 2 | 2.9 | 4 | 42 | 2 | 2.7 | 4 | 101 | 3 | 4.0 | 5 | 4 | 3 | 3.3 | 4 | 8 |
| Developed gill rakers on lower limb | 10 | 12.4 | 15 | 42 | 11 | 12.1 | 14 | 101 | 13 | 13.0 | 13 | 4 | 12 | 13.5 | 15 | 8 |
| Rudimentary gill rakers on lower limb | 4 | 5.1 | 7 | 42 | 3 | 4.5 | 6 | 101 | 4 | 4.5 | 5 | 4 | 4 | 4.6 | 6 | 8 |
| Total gill rakers on upper limb | 5 | 6.0 | 7 | 42 | 4 | 5.7 | 6 | 101 | 6 | 6.3 | 7 | 4 | 6 | 6.1 | 7 | 8 |
| Total gill rakers on lower limb | 16 | 17.5 | 19 | 42 | 15 | 16.5 | 18 | 101 | 17 | 17.5 | 18 | 4 | 17 | 18.1 | 19 | 8 |
| Total gill rakers | 22 | 23.6 | 25 | 42 | 21 | 22.2 | 24 | 101 | 23 | 23.8 | 25 | 4 | 23 | 24.3 | 25 | 8 |
| Scales along lateral line | 28 | 29.1 | 30 | 29 | 28 | 29.2 | 30 | 66 | 29 | 29.0 | 29 | 1 | 28 | 29.1 | 30 | 8 |
| Colour patterns | | | | | | | | | | | | | | | | |
| Bars on upper caudal-fin lobe | 0 | 2.5 | 6 | 42 | 0 | 3.5 | 6 | 101 | 0 | 0.8 | 2 | 4 | 0 | 0.5 | 2 | 8 |
| Bars on lower caudal-fin lobe | 0 | 3.9 | 6 | 42 | 0 | 4.4 | 6 | 101 | 0 | 2.3 | 3 | 4 | 0 | 1.1 | 4 | 8 |
| Bars on both caudal-fin lobes | 0 | 6.4 | 11 | 42 | 0 | 7.9 | 12 | 101 | 0 | 3.0 | 5 | 4 | 0 | 1.6 | 5 | 8 |
| Pigmentation degree | 0 | 2.7 | 4 | 41 | 0 | 2.9 | 4 | 100 | 0 | 1.3 | 2 | 4 | 0 | 1.8 | 3 | 8 |

TABLE 10. Morphometric, meristic and preserved colour characters in adult *U. heterospinus n. sp.*, from different areas, with published data from Bandai *et al.* (2018) for a single specimen from Japan added.

| Morphometric characters | Gulf of Thailand | | | South central Vietnam | | | N Vietnam | | | Indonesia | | | Singapore | Philippines | Japan | | | | | | |
|--|------------------|------|------|-----------------------|-----|-------|-----------|----|-----|-----------|-----|----|-----------|-------------|-------|---|-----|-----|-----|-----|--|
| | Min | Mean | Max | n | Min | Mean | Max | n | Min | Mean | Max | n | Min | Mean | Max | n | | | | | |
| Standard length (SL) | 66 | 78.6 | 123 | 44 | 70 | 103.3 | 152 | 30 | 72 | 96.2 | 122 | 20 | 65 | 88.4 | 127 | 4 | 78 | 81 | 96 | 96 | |
| in % SL | | | | | | | | | | | | | | | | | | | | | |
| Body depth at first dorsal-fin origin | 23 | 24.4 | 26 | 44 | 22 | 23.9 | 26 | 30 | 22 | 23.5 | 25 | 20 | 23 | 24.0 | 25 | 4 | - | - | 24 | 24 | |
| Body depth at anal-fin origin | 19 | 20.7 | 22 | 44 | 19 | 21.0 | 22 | 30 | 18 | 20.1 | 22 | 20 | 20 | 20.7 | 21 | 4 | 22 | - | 22 | 21 | |
| Half body depth at first dorsal-fin origin | 18 | 20.2 | 22 | 37 | 18 | 19.9 | 22 | 29 | 19 | 19.6 | 21 | 16 | 18 | 19.8 | 22 | 3 | - | - | 20 | 21 | |
| Half body depth at anal-fin origin | 15 | 15.9 | 17 | 38 | 15 | 16.3 | 17 | 26 | 15 | 15.8 | 17 | 14 | 15 | 15.3 | 16 | 3 | - | - | 17 | 16 | |
| Caudal-peduncle depth | 9.4 | 10.3 | 11 | 44 | 9.8 | 10.3 | 11 | 30 | 9.2 | 9.8 | 11 | 20 | 10 | 10.2 | 11 | 4 | 11 | 11 | 11 | 9.8 | |
| Caudal-peduncle width | 3.5 | 4.2 | 4.7 | 44 | 3.6 | 4.3 | 5.0 | 30 | 3.8 | 4.3 | 4.7 | 20 | 3.7 | 3.9 | 4.1 | 4 | - | - | 4.1 | 3.6 | |
| Maximum head depth | 19 | 20.9 | 23 | 44 | 19 | 20.9 | 22 | 30 | 19 | 19.9 | 21 | 20 | 20 | 20.8 | 21 | 4 | 21 | 20 | 20 | 20 | |
| Head depth through eye | 15 | 16.2 | 18 | 44 | 15 | 16.3 | 17 | 30 | 15 | 15.7 | 17 | 20 | 15 | 15.9 | 16 | 4 | 16 | 17 | 15 | 17 | |
| Suborbital depth | 8.7 | 9.7 | 11.1 | 44 | 8.8 | 9.8 | 11 | 30 | 8.5 | 9.3 | 10 | 20 | 8.8 | 9.8 | 11 | 4 | 8.7 | 8.5 | 8.3 | 9.4 | |
| Interorbital length | 7.5 | 8.2 | 9.2 | 42 | 7.3 | 8.0 | 9.2 | 30 | 7.2 | 7.7 | 8.2 | 20 | 7.3 | 7.8 | 8.3 | 4 | 8.7 | 9.0 | 8.0 | 7.8 | |
| Head length | 27 | 29.0 | 31 | 44 | 27 | 28.5 | 30 | 30 | 27 | 28.7 | 30 | 20 | 27 | 27.8 | 29 | 4 | 28 | 29 | 27 | 30 | |
| Snout length | 10 | 11.2 | 13 | 44 | 9.9 | 11.0 | 12 | 30 | 10 | 11.0 | 12 | 20 | 10 | 11.3 | 12 | 4 | 9.9 | 12 | 9.7 | 11 | |
| Postorbital length | 10 | 11.4 | 13 | 44 | 10 | 11.1 | 12 | 30 | 10 | 11.1 | 12 | 20 | 10 | 11.5 | 12 | 4 | 11 | 12 | 11 | 12 | |
| Orbit length | 6.4 | 7.5 | 8.3 | 44 | 5.9 | 7.2 | 8.2 | 30 | 6.3 | 7.3 | 8.0 | 20 | 6.8 | 7.4 | 8.0 | 4 | 7.3 | 7.4 | 7.4 | 7.3 | |
| Orbit depth | 5.8 | 6.7 | 7.4 | 44 | 4.9 | 6.3 | 7.0 | 30 | 5.5 | 6.5 | 7.1 | 20 | 6.0 | 6.5 | 7.1 | 4 | 6.4 | 5.9 | 6.6 | 6.2 | |
| Upper-jaw length | 10 | 11.3 | 13 | 44 | 9.6 | 10.7 | 11 | 30 | 9.4 | 10.6 | 11 | 20 | 9.8 | 10.9 | 12 | 4 | 11 | 12 | 11 | 11 | |
| Lower-jaw length | 9.5 | 10.6 | 12 | 44 | 9.0 | 10.0 | 11 | 30 | 8.9 | 10.0 | 11 | 20 | 9.5 | 10.2 | 11 | 4 | 10 | 11 | 10 | 10 | |
| Snout width | 7.1 | 8.2 | 11 | 44 | 8.1 | 9.2 | 11 | 29 | 7.9 | 8.6 | 9.5 | 20 | 7.5 | 8.1 | 8.8 | 4 | - | - | 9.1 | 8.8 | |
| Barbel length | 16 | 17.6 | 20 | 44 | 17 | 18.4 | 20 | 30 | 16 | 17.3 | 20 | 20 | 17 | 18.3 | 19 | 4 | 18 | 20 | 17 | 17 | |
| Maximum barbel width | 0.8 | 0.9 | 1.2 | 44 | 0.8 | 1.0 | 1.2 | 30 | 0.8 | 0.9 | 1.1 | 20 | 0.8 | 0.9 | 1.0 | 4 | 0.9 | 0.9 | 0.8 | 1.2 | |
| First pre-dorsal length | 35 | 36.7 | 39 | 44 | 35 | 36.0 | 38 | 30 | 34 | 36.0 | 38 | 20 | 35 | 36.3 | 39 | 4 | 36 | 36 | 36 | 37 | |
| Second pre-dorsal length | 60 | 63.7 | 67 | 44 | 61 | 63.2 | 65 | 30 | 61 | 62.9 | 64 | 20 | 61 | 62.9 | 64 | 4 | 63 | - | 64 | 64 | |
| Interdorsal distance | 13 | 15.1 | 17 | 44 | 13 | 14.6 | 16 | 30 | 13 | 14.7 | 16 | 20 | 14 | 14.9 | 16 | 4 | 15 | - | 16 | 16 | |
| Caudal-peduncle length | 22 | 24.0 | 26 | 44 | 22 | 23.6 | 25 | 30 | 22 | 24.1 | 25 | 20 | 24 | 24.2 | 25 | 4 | 25 | - | 24 | 24 | |
| Pre-anal length | 61 | 64.3 | 67 | 44 | 62 | 63.8 | 68 | 30 | 61 | 63.2 | 65 | 20 | 61 | 63.2 | 65 | 4 | 68 | - | 63 | 64 | |
| Pre-pe/vic length | 30 | 32.0 | 35 | 44 | 30 | 31.6 | 33 | 30 | 30 | 31.5 | 33 | 20 | 31 | 32.5 | 33 | 4 | 33 | - | 31 | 31 | |

.....continued on the next page

TABLE 10. (Continued)

| | Gulf of Thailand | | | South central Vietnam | | | N Vietnam | | | Indonesia | | | Singapore | Philippines | Japan | | | | | |
|---------------------------------------|------------------|------|-----|-----------------------|-----|------|-----------|----|-----|-----------|-----|----|-----------|-------------|-------|---|-----|-----|-----|-----|
| | Min | Mean | Max | n | Min | Mean | Max | n | Min | Mean | Max | n | Min | Mean | Max | n | | | | |
| Pre-pectoral length | 29 | 30.6 | 33 | 44 | 29 | 29.6 | 31 | 30 | 28 | 29.4 | 31 | 20 | 28 | 30.3 | 32 | 4 | 30 | - | 29 | 29 |
| Second dorsal-fin depth | 20 | 21.5 | 23 | 44 | 20 | 21.5 | 23 | 30 | 19 | 20.6 | 23 | 20 | 20 | 21.7 | 23 | 4 | - | - | 23 | 22 |
| Pelvic-fin depth | 22 | 24.4 | 26 | 44 | 22 | 24.1 | 26 | 30 | 22 | 23.0 | 25 | 20 | 23 | 23.9 | 25 | 4 | - | - | 24 | 25 |
| Pectoral-fin depth | 15 | 16.7 | 18 | 44 | 15 | 16.8 | 18 | 30 | 15 | 16.3 | 18 | 20 | 16 | 16.5 | 17 | 4 | - | - | 16 | 17 |
| Length of first dorsal-fin base | 14 | 15.2 | 17 | 43 | 13 | 15.4 | 17 | 30 | 14 | 15.1 | 17 | 20 | 14 | 15.2 | 16 | 4 | 16 | - | 15 | 15 |
| Length of second dorsal-fin base | 12 | 13.4 | 15 | 44 | 12 | 14.1 | 15 | 30 | 12 | 14.2 | 16 | 20 | 14 | 14.1 | 15 | 4 | 13 | - | 14 | 14 |
| Caudal-fin length | 27 | 29.1 | 30 | 43 | 27 | 29.3 | 32 | 24 | 28 | 29.7 | 31 | 20 | 29 | 29.2 | 30 | 4 | 29 | - | 30 | - |
| Length of anal-fin base | 9.7 | 11.4 | 13 | 44 | 10 | 11.4 | 13 | 30 | 10 | 11.2 | 12 | 20 | 10 | 11.0 | 12 | 4 | - | - | 12 | 11 |
| Anal-fin height | 15 | 17.1 | 19 | 43 | 15 | 16.3 | 18 | 30 | 15 | 16.7 | 18 | 20 | 15 | 17.2 | 19 | 4 | - | - | 15 | - |
| Pelvic-fin length | 19 | 21.1 | 23 | 43 | 19 | 20.4 | 22 | 30 | 19 | 20.9 | 22 | 20 | 20 | 20.5 | 21 | 4 | 21 | 20 | 21 | 22 |
| Pectoral-fin length | 19 | 20.6 | 22 | 44 | 19 | 19.9 | 21 | 26 | 19 | 20.8 | 22 | 20 | 20 | 19.8 | 20 | 4 | 20 | 20 | 19 | 21 |
| Pectoral-fin width | 3.4 | 4.0 | 4.7 | 44 | 3.9 | 4.2 | 4.6 | 30 | 3.7 | 4.2 | 4.6 | 20 | 3.9 | 4.3 | 4.6 | 4 | 4.6 | 4.3 | 4.0 | 4.8 |
| First dorsal-fin height | 19 | 20.6 | 23 | 43 | 18 | 20.0 | 22 | 29 | 19 | 20.6 | 23 | 19 | 19 | 19.9 | 21 | 4 | 22 | 20 | 21 | 21 |
| Second dorsal-fin height | 16 | 18.0 | 20 | 44 | 16 | 17.2 | 19 | 28 | 16 | 18.1 | 19 | 19 | 16 | 17.7 | 19 | 4 | 16 | - | 17 | 18 |
| Meristic characters | | | | | | | | | | | | | | | | | | | | |
| Dorsal-fin spines | 7 | 7.5 | 8 | 44 | 7 | 7.5 | 8 | 30 | 7 | 7.6 | 8 | 20 | 7 | 7.8 | 8 | 4 | 7 | 8 | 8 | 7 |
| Pectoral-fin rays | 13 | 13.8 | 14 | 44 | 13 | 13.9 | 15 | 30 | 13 | 14.0 | 15 | 20 | 13 | 13.8 | 14 | 4 | 13 | 14 | 14 | 13 |
| Rudimentary gill rakers on upper limb | 2 | 3.1 | 4 | 44 | 2 | 2.8 | 4 | 30 | 2 | 3.1 | 4 | 20 | 3 | 3.0 | 3 | 4 | 2 | 2 | 2 | 3 |
| Developed gill rakers on upper limb | 2 | 2.4 | 3 | 44 | 2 | 3.0 | 4 | 30 | 2 | 2.7 | 3 | 20 | 3 | 3.0 | 3 | 4 | 3 | 3 | 4 | 2 |
| Developed gill rakers on lower limb | 11 | 11.8 | 13 | 44 | 11 | 12.4 | 14 | 30 | 11 | 12.1 | 13 | 20 | 12 | 12.3 | 13 | 4 | 12 | 12 | 12 | 13 |
| Rudimentary gill rakers on lower limb | 4 | 4.4 | 6 | 44 | 3 | 4.4 | 6 | 30 | 3 | 4.6 | 6 | 20 | 4 | 4.8 | 5 | 4 | 4 | 5 | 5 | 5 |
| Total gill rakers on upper limb | 4 | 5.5 | 6 | 44 | 5 | 5.8 | 6 | 30 | 5 | 5.8 | 6 | 20 | 6 | 6.0 | 6 | 4 | 5 | 5 | 6 | 5 |
| Total gill rakers on lower limb | 15 | 16.2 | 18 | 44 | 16 | 16.8 | 18 | 30 | 15 | 16.6 | 18 | 20 | 17 | 17.0 | 17 | 4 | 16 | 17 | 17 | 18 |
| Total gill rakers | 21 | 21.7 | 24 | 44 | 21 | 22.6 | 24 | 30 | 21 | 22.4 | 23 | 20 | 23 | 23.0 | 23 | 4 | 21 | 22 | 23 | 23 |
| Scales along lateral line | 28 | 29.0 | 30 | 25 | 28 | 29.2 | 30 | 26 | 29 | 29.5 | 30 | 11 | 29 | 29.3 | 30 | 3 | 0 | 0 | 28 | - |
| Colour patterns | | | | | | | | | | | | | | | | | | | | |
| Bars on upper caudal-fin lobe | 0 | 2.7 | 6 | 44 | 0 | 4.1 | 6 | 30 | 1 | 4.2 | 6 | 20 | 3 | 4.5 | 6 | 4 | 0 | 0 | 6 | - |
| Bars on lower caudal-fin lobe | 3 | 4.1 | 6 | 44 | 1 | 4.8 | 6 | 30 | 3 | 4.7 | 6 | 20 | 5 | 5.5 | 6 | 4 | 0 | 0 | 3 | - |
| Bars on both caudal-fin lobes | 4 | 6.9 | 11 | 44 | 1 | 8.9 | 12 | 30 | 5 | 8.9 | 11 | 20 | 8 | 10.0 | 12 | 4 | 0 | 0 | 9 | - |
| Pigmentation degree | 2 | 2.4 | 3 | 43 | 1 | 3.8 | 4 | 30 | 1 | 3.1 | 4 | 20 | 2 | 3.0 | 4 | 4 | 0 | 0 | 1 | - |

Etymology. Named after the type locality which is situated close to Gubal Island and in the Strait of Gubal at the southern entrance to the Gulf of Suez, Northern Red Sea. The name “*gubal*” is used as a noun in apposition.

Distribution, habitat and size. Single locality off Gubal Island, S Gulf of Suez, Northern Red Sea; fish caught by trawling at 70 m depth, most probably on sandy or muddy bottom; size of the specimen is 8.7 cm SL.

Remarks. Fresh colour of *Upeneus gubal* n. sp. is yet unknown, but the available morphological evidence strongly suggests its inclusion in the *margarethae* group (see also the Interspecific comparisons section further below). The single type specimen was collected together with a specimen of *Upeneus moluccensis* (Bleeker, 1855) (registered as MNHN 2011-0093). The latter did not show any remains of dark pigmentation e.g. of first dorsal-fin tip and oblique bars on upper caudal-fin lobe as indicated to be diagnostic for preserved conspecifics (Uiblein & Heemstra 2010). The single known locality of *U. gubal* n. sp. in the S Gulf of Suez is about 1100 km north of the northernmost currently known occurrence of *U. margarethae* off Ibn Abbas Island, S coast of Sudan.

***Upeneus heterospinus* n. sp. Uiblein & Pavlov**

Varied-spine goatfish

(Figures 1, 9–12; Tables 2, 4–11)

Upeneus australiae Kim & Nakaya, 2002: Uiblein & Heemstra 2010 (Nha Trang, South-central Vietnam, South China Sea).

U. bensasi (Temminck & Schlegel, 1843): Provincial Keelung Girls' High School, Keelung, Taiwan 1985 (fresh-colour photo, no locality, but size information (92 mm SL) and collecting date (03/12/1979)).

U. guttatus (Day, 1868): Motomura *et al.* 2017 (vouchered fresh-colour photo, central Philippines, W Pacific).

U. margarethae: Pavlov & Emel'yanova 2016 (fresh-colour photos, South-central Vietnam, South China Sea).

U. cf. margarethae: Emel'yanova & Pavlov 2014; White *et al.* 2013 (vouchered fresh-colour photo, S Indonesia).

U. spottocaudalis Uiblein & Gledhill, 2017: Bandai *et al.* 2018 (vouchered fresh-colour photo and comparative data, S Japan, W Pacific).

U. tragula: Froese & Pauly 2019 (fresh colour photo by A. Cornell from off Hong Kong, South China; <https://www.fishbase.de/photos/PicturesSummary.php?StartRow=5&ID=5443&what=species&TotRec=14>).

Upeneus sp.: Kimura *et al.* 2018 (vouchered fresh colour photo, N Vietnam, Ha Long Bay).

Upeneus sp.1: Uiblein & Lisher 2013 (Nha Trang, South-central Vietnam, South China Sea).

Holotype. VNMN-I 2015, adult, 91 mm SL, W Pacific, South China Sea, South-central Vietnam, Khanh Hoa province, Nha Trang, N of Hon Tre, 12° 13'21" N, 109° 18'30" E, obtained from hookah divers, 23 Feb. 2010, collector: Dimitri Pavlov (fresh-colour photo)

Paratypes. (28 adults, 1 subadult: 56–152 mm SL, 15 fresh-colour photos). W Pacific, South China Sea, South-central Vietnam: Phu Yen province, Vung Ro Bay, 12° 52.11' N, 109° 24.66' E, obtained from hookah divers: VNMN-I 2016, 70 mm SL (fresh-colour photo); VNMN-I 2017, 101 mm SL (fresh-colour photo); VNMN-I 2018, 96 mm SL (fresh-colour photo); VNMN-I 2019, 56 mm SL (fresh-colour photo); Khanh Hoa province, Nha Trang Bay: N of Hon Tre, 12° 13'21" N, 109° 18'30" E, obtained from hookah divers: VNMN-I 2020, 97 mm SL (fresh-colour photo); VNMN-I 2021, 112 mm SL; VNMN-I 2022, 106 mm SL (fresh-colour photo); VNMN-I 2023, 113 mm SL (fresh-colour photo); VNMN-I 2024, 105 mm SL (fresh-colour photo); VNMN-I 2025, 109 mm SL; VNMN-I 2026, 100 mm SL (fresh-colour photo); VNMN-I 2027, 112 mm SL; VNMN-I 2028, 104 mm SL; VNMN-I 2029, 104 mm SL; VNMN-I 2030, 103 mm SL; VNMN-I 2031, 96 mm SL; VNMN-I 2032, 103 mm SL; S of Hon Tre, obtained from hookah divers: HIFIRE F 58110, 120 mm SL; HIFIRE F 58115, 109 mm SL; VNMN-I 2033, 123 mm SL; Cua Be: CSIRO H 8427-01, 90 mm SL (fresh-colour photo), landing site, 12° 12.09' N, 109° 12.12' E; HIFIRE F 58203, 105 mm SL (fresh-colour photo), fish market, 12° 12.10' N, 109° 12.05' E; Nha Trang city, fish market: CSIRO H 8428-01, 82 mm SL (fresh-colour photo); CSIRO H 8428-02, 82 mm SL (fresh-colour photo); HIFIRE F 58178, 152 mm SL; NHMO J 7217, 114 mm SL (fresh-colour photo); NHMO J 7218, 103 mm SL (fresh-colour photo); Nha Trang, no further locality details: MNHN 1965-272, 90 mm SL; ZMUC P49483, 84 mm SL.

Non-types. (72 adults, 6 subadults: 43–127 mm SL, 30 fresh colour photos). W Pacific, South China Sea, N Vietnam, Quảng Ninh province, Ha Long Bay, Van Don landing site, 21° 03.61' N, 107° 25.81' E: HIFIRE F 58382, 97 mm SL (fresh-colour photo); NHMO J 7219, 104 mm SL (fresh-colour photo); VNMN-I 2034, 109 mm SL (fresh-colour photo); VNMN-I 2035, 113 mm SL (fresh-colour photo); VNMN-I 2036, 104 mm SL (fresh-colour photo); VNMN-I 2037, 108 mm SL; VNMN-I 2038, 108 mm SL (fresh-colour photo); Ha Long: VNMN-I 2039, 83 mm SL (fresh-colour photo); VNMN-I 2040, 83 mm SL (fresh-colour photo); VNMN-I 2041, 122 mm SL (fresh-

colour photo); VNMN-I 2042, 93 mm SL (fresh-colour photo); VNMN-I 2043, 108 mm SL (fresh-colour photo); VNMN-I 2044, 94 mm SL (fresh-colour photo); VNMN-I 2045, 117 mm SL (fresh-colour photo); VNMN-I 2046, 87 mm SL (fresh-colour photo); VNMN-I 2047, 72 mm SL (fresh-colour photo); VNMN-I 2048, 82 mm SL (fresh-colour photo); VNMN-I 2049, 80 mm SL (fresh-colour photo); VNMN-I 2050, 77 mm SL (fresh-colour photo); VNMN-I 2051, 81 mm SL (fresh-colour photo); VNMN-I 2052, 64 mm SL (fresh-colour photo); VNMN-I 2053, 60 mm SL (fresh-colour photo); South-central Vietnam, Khanh Hoa province, Nha Trang Bay: HIFIRE F 58231, 123 mm SL, N of Hon Tre Island, 12°14'18"N 109°15'54"E, obtained from hookah divers (fresh-colour photo); Gulf of Thailand, S Vietnam, Phu Quoc, An Thoi market, 10° 0.90' N, 104° 0.86' E: HIFIRE F 58287, 93 mm SL (fresh-colour photo); NHMO J 7220, 88 mm SL (fresh-colour photo); VNMN-I 2054, 83 mm SL (fresh-colour photo); VNMN-I 2055, 114 mm SL (fresh-colour photo); Gulf of Thailand, Thailand, Ko-Sichang Island: CAS 17679, 41 (of 141): 56–94 mm SL, 13°8' N, 100°51' E, trawl, 18–24 m depth; Singapore: NHMO J 2134, 2, 78–81 mm SL; Philippine Sea, Central Philippines, Panay Island: UPVMI 155, 96 mm SL (fresh-colour photo); Indonesia, Bali Sea, E Java: CSIRO H 7360-04, 3: 43–66 mm SL, Banguwangi, 08°09' S 114°23' E; Lombok (border of W Pacific to Indian Ocean): MZB, unregistered (field code LM308 (large)), 54 mm SL; CSIRO H 8409-02, 65 mm SL, and CSIRO H 7364-02, 127 mm SL, Tanjung Luar, 8°45' S, 116°35' E (both with fresh-colour photo); BPBM 29896, 96 mm SL, no locality information (fresh-colour photo).

Fresh-colour photos of specimens not retained ($n=79$): W Pacific, Vietnam (D.A. Pavlov & F. Uiblein), South China Sea: 20 adults, Ha Long Bay, N Vietnam; 10 adults, Nha Trang Bay, South-central Vietnam; Gulf of Thailand, S Vietnam, Phu Quoc : 37 adults and 1 subadult or adult (*in-situ* photo); South China Sea, other areas: 1 adult, Hong Kong, China (A. Cornell); 1 adult, Taiwan (Provincial Keelung Girls' High School, Keelung, Taiwan, 1985); Philippine Sea, Philippines: 7 adults, 1 subadult, Central Philippines (various localities, *in-situ* photos; Philippe & Guido Poppe—www.poppe-images.com); Japan: adult, 96 mm SL, Satsuma Peninsula, Kagoshima, S Japan (Bandai *et al.* 2018).

Diagnosis. Dorsal fins VII or VIII + 9, the first spine minute in 8-spined fish; pectoral fins 13–15; gill rakers 4–6 + 15–18 = 21–24; lateral-line scales 28–30; measurements in % SL, adults: body depth at first dorsal-fin origin 22–26; body depth at anus 18–22; caudal-peduncle depth 9.2–11; caudal-peduncle width 3.5–5.0; maximum head depth 19–23; head depth through eye 15–18; suborbital depth 8.3–11; interorbital length 7.2–9.2; head length 27–31; snout length 9.7–13; postorbital length 10–13; orbit length 5.9–8.3; upper-jaw length 9.4–13; barbel length 16–20; interdorsal distance 13–17; caudal-peduncle length 22–26; caudal-fin length 27–32; anal-fin height 15–19; pelvic-fin length 19–23; pectoral-fin length 19–22; pectoral-fin width 3.4–4.7; first dorsal-fin height 18–23; second dorsal-fin height 16–20; measurements in % SL, subadults: body depth at first dorsal-fin origin 22–24; body depth at anus 18–21; caudal-peduncle depth 9.1–10; caudal-peduncle width 3.6–3.8; maximum head depth 19–21; head depth through eye 15–18; suborbital depth 9.0–10; interorbital length 7.6–8.1; head length 29–30; snout length 11–12; postorbital length 11–13; orbit length 7.8–7.9; upper-jaw length 9.9–12; barbel length 18–19; interdorsal distance 12–14; caudal-peduncle length 22–25; caudal-fin length 29–31; anal-fin height 16–19; pelvic-fin length 21–22; pectoral-fin length 21; pectoral-fin width 3.8–4.2; first dorsal-fin height 21–22; second dorsal-fin height 17–20; fresh colour: head and body dorsally red, brown or dark-grey mottled, ventrally white, often with pale beige or grey dots or red blotches (inactive, live fish with large red patches and broad vertical or oblique red bands on body); upper lobe of caudal fin with 4–6 red or brown bars (3 or 4 bars in subadults), lower caudal-fin lobe with 5–7 (3–5) red, brown or dark-brown bars, often crossed, entirely or only dorsally, by a yellow, beige, pale red or pale brown stripe; bars on both lobes of pupil width or less in adults, interrupted by pale, partly hyaline interspaces of similar width or slightly narrower; lower caudal-lobe tip sometimes black; barbels entirely yellow; a single yellow, beige, or pale brown mid-lateral body stripe of pupil width from snout tip through eye to caudal-fin base; stripe sometimes covered by 1–4 sections with 1–4 dark dots, the posteriormost group of dots behind second dorsal-fin base, often connecting to a dark saddle behind second dorsal fin; first dorsal fin with 3 or 4 often fused, pale-red, pale-brown or beige stripes, the fin-tip area not darker pigmented; second dorsal fin with 3 or 4 red or brown well-separated stripes with hyaline interspaces; pectoral fins hyaline, pelvic and anal fins weakly pigmented and partly hyaline; preserved fish pale brown, often with remains of dark pigmentation deriving from caudal-fin bars, mid-lateral dots, saddle and/or second dorsal-fin distal stripe.

Description. Measurements in % SL and counts for types are given in Table 8; morphometric data as ratios of SL for holotype, data for paratypes in brackets: body elongate, body depth at first dorsal-fin origin 4.2 [3.8–4.6], body depth at anal-fin origin 5.0 [4.5–5.4], head length 3.5 [3.3–3.7], larger than maximum body depth and subequal

to caudal-fin length (3.3 [3.2–3.7]), second dorsal-fin height 6.1 [5.3–6.4], slightly shallower than first dorsal-fin height (4.7 [4.5–5.6]), barbel length (5.5 [5.0–5.9]), pelvic-fin length 5.0 [4.5–5.3], similar to length of pectoral fins (5.2 [4.7–5.3]) and body depth at first dorsal-fin origin; caudal-peduncle depth 10 [8.9–10], clearly larger than orbit length (14 [12–17]); and caudal-peduncle width 21 [20–28], subequal to pectoral-fin width (23 [22–27]).

Colour. *Freshly collected fish.* (Figure 9). Head and body ventrally white and ventro-laterally white or pale-grey whitish with numerous red, brown or dark-grey dots of half pupil size or less, placed mostly on individual scales (Figure 9 A, B, E, F); in all six specimens shown in Figure 9 (least in holotype, Figure 9 A), red blotches of different form and size or larger red pigmentation patches below or behind eye on gill cover and/or on body ventrally or ventro-laterally either covering larger areas (Figure 9 B, C) or more restricted to smaller areas on or behind belly (Figure 9 E, F); some of these blotches and patches may have catch/treatment-related context; head from above snout and eye and body above lateral line red-brown or dark-grey mottled, bordered below by a mid-lateral stripe of pupil width which runs rather straight or only slightly bent from caudal-fin base to eye in yellow, beige, pale red or pale brown colour and continues from eyes (with red or pale-red iris) to snout either in similar colour and intensity (Figure 9 B–D), or slightly darker, but weaker (Figure 9 E, F), or rather faint and indistinct (Figure 9 A); on the mid-lateral body stripe from behind head to behind second-dorsal fin up to 4 sections with 1–3 red, brown or black dots of less than pupil width; behind head until below base of second dorsal fin in adults, a thin white or pale creamy stripe separates the dorsal body pigmentation from the mid-lateral body stripe (Figure 9 A, B, E); lateral line visible especially in subadult (Figure 9 C) and small adult (Figure 9 F) as a series of mostly red, dark-grey or black dots placed well above mid-lateral stripe in anterior half of body, then starting to cross the stripe just anterior of second dorsal-fin base, continuing behind dorsal fin just below stripe towards caudal-fin base; barbels entirely yellow; caudal fin with 9–13 red, dark brown or black oblique bars crossing mostly both lobes entirely, if not placed on fin base or fin tips; upper lobe covered by 4–6 (3–4 in subadults) red, red brown, or dark brown bars of pupil or slightly narrower width, the distal-most bar sometimes covering fin tip (Figure 9 A, F); bars separated by hyaline interspaces of similar width or slightly wider; in large adult (Figure 9 E) dark-brown blotches on three intermediate bars; lower caudal-fin lobe covered by 5–7 (3–5 in subadults) red, red brown or dark brown bars and hyaline interspaces of similar width or slightly narrower than on upper fin lobe in adults, whereas more variable in subadults; in four specimens (Figure 9 A–D), the lower caudal-fin lobe ends in a black tip; a red or brown stripe stretches entirely or only dorsally along the lower caudal-fin lobe covering partly the bars in both adults and subadults; first dorsal fin almost entirely covered with pale-red, beige or pale-brown pigmentation; second dorsal fin with 3 red stripes of orbit width or less, one stripe at or close to fin base, one at or close to fin tip, the latter and in some fish also the middle stripe slightly darker; pelvic fins hyaline with up to 5 narrow red or brown stripes; anal fin with 1–3 red or brown stripes and hyaline or whitish interspaces; pectoral fins hyaline.

Live fish in situ. Active fish. (Figure 10 A–D). Head and body ventrally white, with numerous tiny red or beige dots associated with 4 scale rows and, in three of four fish, with additional, larger rounded and partly connected red blotches, ca. 25 of the latter visible in fish from the type locality which was kept in a tank (Figure 10 A); fewer and more ventrally positioned blotches in two fish photographed *in situ* in Central Philippines (Figure 10 C, D); head from above snout and eye and body above lateral line pale-grey or rose mottled, bordered below by a mid-lateral stripe in red colour (that appears brown when photographed without flash, see Figure 10 B) of pupil width which runs rather straight from caudal-fin base to eye, continuing through eyes (with iris red-coloured in stripe shape) and then bending ventrally towards snout tip, becoming slightly narrower and weaker; 5 well separated, rectangular dark-red sections on mid-lateral body stripe (not well visible in Figure 10 B), one shorter behind gill cover, two longer ones below dorsal fins, one shorter behind second dorsal fin, and one less conspicuous, rather short section close to caudal-fin base; each section except for the posterior-most with a horizontal series of 2–4 black dots of a little less than pupil diameter; the dotted section behind the second dorsal fin connecting closely to red saddle in tank fish (Figure 10 A), the latter reaching from dorsal body margin behind second dorsal fin to stripe in V-form; lateral line, as also observed in freshly collected fish, proceeds parallel above mid-lateral body stripe during first half of body, then crossing and continuing just below stripe to caudal-fin base; lateral line marked by several small red, beige or grey dots that become more conspicuous in positions of dots on mid-lateral body stripe below; barbels entirely yellow; caudal fin with 8–12 red-brown oblique bars which appear dark-brown in the small possibly adult specimen photographed at distance without flash (Figure 10 B); dorsal fin lobe crossed by 3–5 bars of pupil width, the distal-most bar covering fin tip in two specimens (Figure 10 A, D); in three specimens the bars are reduced to dark red or dark brown blotches (Figure 10 B, C, D) leaving the remaining parts of bars as pale, mostly hyaline

traces (Figure 10 C, D); bars on upper lobe separated by hyaline interspaces of similar width; lower caudal-fin lobe crossed in adults by 5–7 dark red (dark brown in Figure 10 B) bars which are similarly shaped and sized as bars on upper lobe; while in the tank specimen the bars are of varying intensity but typically shaped, the bars in the other three active fish show a blotch-like concentration of intense colour in the middle of the lower lobe, leaving the ventral and dorsal areas of each bar rather inconspicuous (however still visible, e.g. Figure 10 C, D); in addition, a red stripe is formed on the lower lobe of the tank specimen that covers the lobe almost entirely (apart from ventral margin) and a pale red stripe is also weakly visible along the dorsal half of lobe in two of the three other specimens (Figure 10 C, D); the first dorsal fin (only well visible in Figure 10 A) is mostly weakly pale red, leaving the tip almost completely unpigmented hyaline; the second dorsal fin with 3–4 red to brown stripes of about pupil width or less, at least one of the distal two stripes more intensely coloured than the stripes (or single stripe) closer to fin base which appear rather pale red and partly hyaline; interspaces between stripes in part with white pigmented fin rays; pelvic and anal fins partly hyaline with weak pale grey pigmentation indicating stripes; pectoral fins hyaline, only very faintly visible.

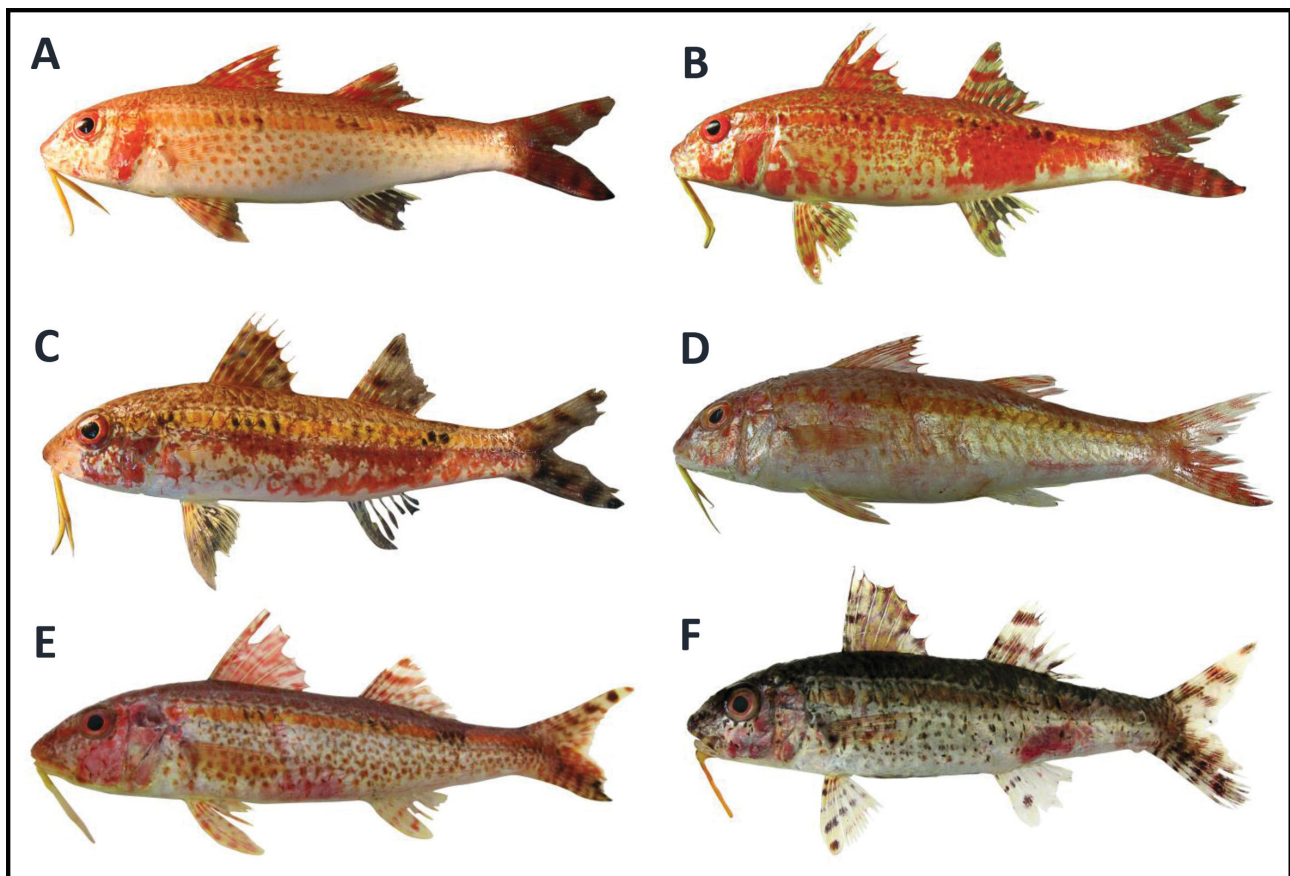


FIGURE 9. *Upeneus heterospinus* n sp.; (A) HT, VNMN-I 2015, 91 mm SL, N of Hon Tre Island, Nha Trang, South-central Vietnam (D.A. Pavlov); (B) PT, VNMN-I 2026, 100 mm SL, same locality; (C) VNMN-I 2019, 56 mm SL, subadult (D.A. Pavlov) (D) VNMN-I 2038, 108 mm SL, Van Don, Ha Long Bay, N Vietnam (D.A. Pavlov & F. Uiblein); (E) CSIRO H 7364-02, 127 mm SL, Tanjung Luar, Lombok, Indonesia (W.T. White), (F) CSIRO H 8409-02, 65 mm SL, same locality (W.T. White)

Resting fish. (Figure 10 E, only differences from the above colour description indicated). Large areas on head and body covered with red, in particular below eye, on gill cover, above pectoral-fin base, two large red bands running from dorsal fins down to ventral margin, the anterior band rather straight from first dorsal fin, the posterior band oblique and wider, covering also the area of and below saddle; the two bands connecting on ventral body margin with each other and covering most of ventral underside except for an inverted V-shaped pale area behind pelvic-fin base and caudal peduncle; caudal peduncle mostly white with three round orbit-sized red blotches on ventral margin and one more elongated red blotch just above the last ventral-margin blotch; mid-lateral body stripe only visible in areas without red band markings and almost indistinct whitish on caudal peduncle, then orange anterior to second dorsal fin between the large red bands and behind head, turning into red on gill cover, then crossing eye (with iris red-colour in stripe shape) and bending towards snout tip, still in red colour; caudal fin with 9 oblique dark

grey bars, on dorsal lobe 4 bars (including one on tip) which are dark pigmented only on dorsal margin of fin, while becoming ventrally pale grey and rather indistinct; the 5 bars on lower fin lobe entirely dark grey, slightly wider than whitish interspaces, with faint appearance of a grey stripe only close to caudal-fin base; area of red pigmentation on first dorsal fin concentrated centrally and in part of fin, leaving the tip entirely pale hyaline.

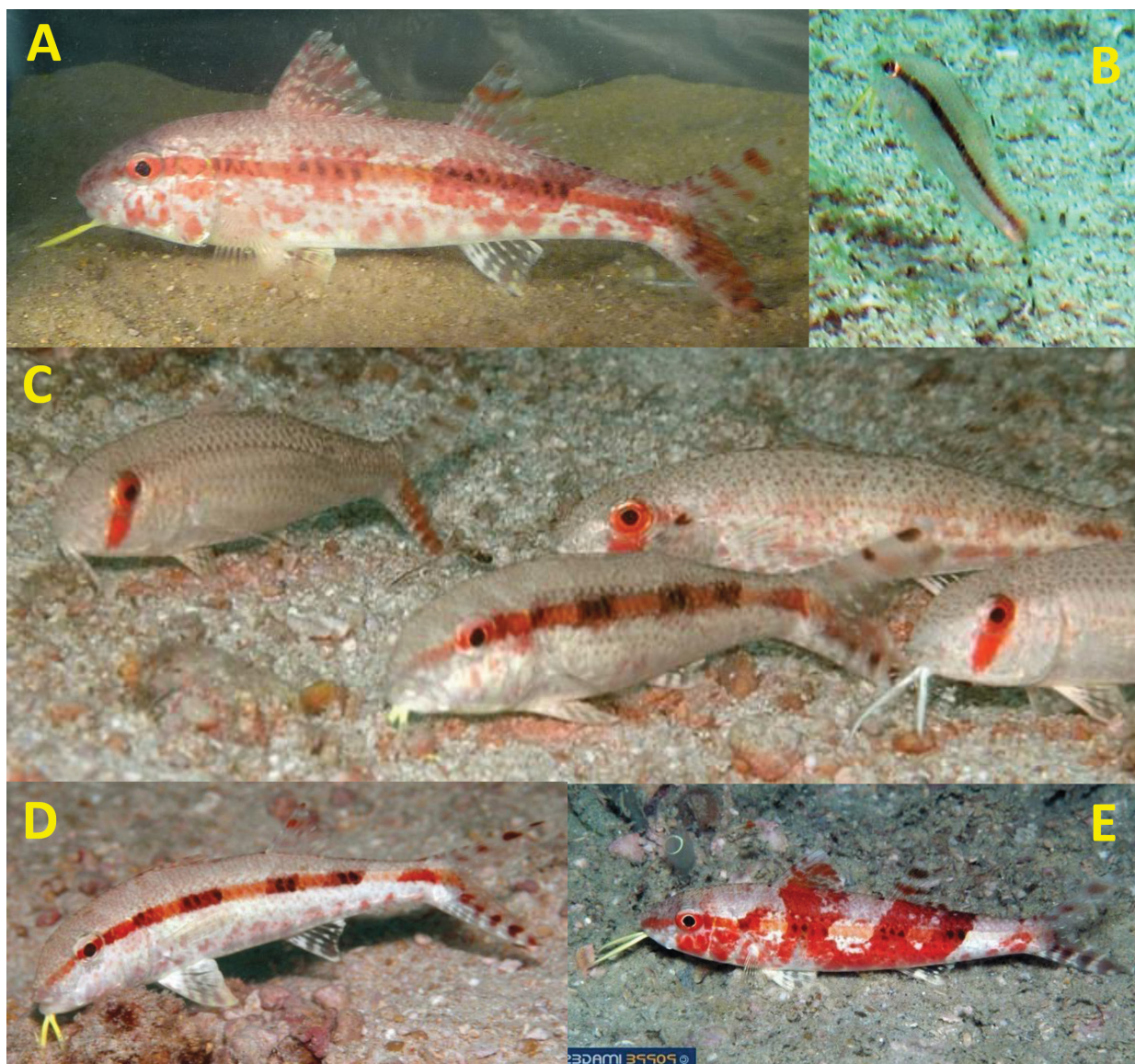


FIGURE 10. *Upeneus heterospinus* n. sp.; (A) HIFIRE 58231, 123 mm SL, N of Hon Tre Island, Nha Trang, South-central Vietnam, live tank photo (F. Uiblein); (B) subadult or small adult specimen (ca. 6–7 cm SL) encountered during dive off Phu Quoc, S Vietnam (F. Uiblein); (C) adult amongst three *U. asymmetricus* (with red oblique head bars), Chocolate Point, Malapascua Island, Chocolate Island, Philippines, 12 m depth; (D) adult, Yao Island, Bantayan Islands, Philippines; (E) adult, resting, Nocnocan Island, Bohol, Philippines (C-E: P. & G. Poppe - www.poppe-images.com)

Preserved fish. Head and body mostly uniformly pale brown, pale greyish, greyish brown or brown, sometimes slightly darker dorsally, gill cover silvery or pale and partly transparent, lateral line, when intact, well visible in entire range from behind head to caudal-fin base; barbels pale brown or pale creamy; mid-lateral body stripe completely lost, but often remains of dark mid-lateral dots in the area of stripe below and posterior to dorsal fins (in 35 % of 100 adults vs. 33 % of 6 subadults); dark pigmentation remains also in other areas: saddle behind second dorsal fin (65 % vs. 67 %), caudal fin (98 % vs. 100 %) and second dorsal-fin distal stripe (92 % vs. 100 %); on caudal fin with retained pigmentation remains of up to 6 oblique bars visible on each lobe; in adults 96 % (of 101 fish) and all subadults show remains of bars on both lobes; of all adults only 2 % show no pigmentation remains (pigmentation degree 0) and 36 % have pigmentation in all body and fin regions (pigmentation degree 4); all studied subadults

show pigmentation remains with pigmentation degree 4 occurring in 33 %. Unpigmented areas of caudal, second dorsal fins and other fins entirely pale and partly hyaline.

Etymology. The name refers to the variable number of 7 or 8 dorsal-fin spines in this species, which is in contrast to most other goatfish species and all other Indo-Pacific congeners which have either 7 or 8 dorsal-fin spines.

Distribution, habitat and size. W Pacific, from border to EIO in S Indonesia to Singapore, Gulf of Thailand, Vietnam, Central Philippines, South China, Taiwan, and S Japan; 6–24 m depth, sandy or muddy bottoms; maximum size 16 cm SL.

Intraspecific comparisons. To ensure that the dimorphic expression of seven and eight dorsal-fin spines in *U. heterospinus* **n. sp.** is indeed a single-species characteristic, as is unusual in goatfishes, the two morphs were compared using the entire set of studied characters. As was expected, no differences could be discovered in any single character (Table 8), nor in any combinations of characters or in statistical comparisons of morphometric, meristic and colour characters.

Subadults of *U. heterospinus* **n. sp.** differ from adults in slightly shallower body at anal-fin origin (especially when analyzing populations separately; Figure 11), fewer rudimentary gill rakers on lower limb (Figure 11; while total gill rakers do not differ among size classes), fewer oblique bars on caudal fin (Tables 2, 9), and the bars slightly wider, almost interconnected in fresh subadults (Figure 9 C) vs. narrower and more clearly separated in adults (Figure 9 A, B, D–F; Figure 10).

Among the three populations of *Upeneus heterospinus* **n. sp.** from N Vietnam, South-central Vietnam and the Gulf of Thailand no clear distinction was found in any single or combination of morphological or colour characters occurs that would support separation into different taxa. However, each population can be distinguished statistically (Table 11). For instance, the Gulf of Thailand population has a significantly higher maximum body depth than the other two populations. The N Vietnam population differs significantly from the two other populations in having a shallower body at anal-fin origin, shallower caudal peduncle, shallower maximum head and suborbital depth, shorter interorbital length, longer pectoral fins and higher second dorsal fin. The South-central Vietnam population has a significantly wider snout and longer barbels than the other two populations and differs in addition in pairwise comparisons with the northern population. As stated for *U. margarethae*, the considerable amount of significant differences among populations contrasts however with much greater differentiation among species, as revealed by the statistical comparisons among three of the five species (Table 4, see also section on Interspecific comparisons further below).

Regarding meristic characters, the Gulf of Thailand population has a significantly lower gill-raker count than the other two populations (Table 5). With respect to preserved colour patterns, the three populations differ significantly from each other with the South-central population showing the highest degree of dark pigmentation, followed by the N Vietnam and the Gulf of Thailand populations (Table 6). In none of the three populations, individuals that completely lack dark pigmentation remains (pigmentation degree 0) occur. When comparing the four examined pigmentation patterns individually, the only significant differences exist in the presence/absence of a saddle and mid-lateral dots (Table 7). The latter are completely lacking in the Gulf of Thailand population. Regarding fresh colour patterns, no clear population differences can be observed when comparing the available images (see also Figures 9, 10).

Remarks. *Upeneus heterospinus* **n. sp.** has been reported from many areas using various names and most recently as *U. spottocaudalis* from Japan (Bandai *et al.* 2018). From Vietnam, where it is a common species that is frequently encountered in fish markets, biological data have been recently collected and published using preliminary identification information (Emel'yanova & Pavlov 2014; Pavlov & Emel'yanova 2016).

Upeneus mouthami Randall & Kulbicki, 2006

Mou Tham's goatfish

(Figures 1, 7, 12; Tables 2, 5, 6, 9)

Upeneus mouthami Randall & Kulbicki, 2006. Type locality Chesterfield Bank, Coral Sea, New Caledonia, Chesterfield Islands.

Holotype. (only fresh-colour photo examined). BPBM 33858, adult, 70 mm SL, Coral Sea, New Caledonia, Chesterfield Islands, Chesterfield Bank, 20°59'48" S, 158°47'18" E, RV *Alis*, beam trawl, 71 m depth.

Paratypes. (4 adults: 73–94 mm SL). Coral Sea, New Caledonia, Chesterfield Islands: BPBM 33855, 94 mm

SL, Chesterfield Bank, 20°51'0" S, 158°45'00" E, RV *Alis*, shrimp trawl, 71 m depth; BPBM 39467, 88 mm SL, Chesterfield Bank, Bellona Reefs, 21°24'54" S, 159°09'18" E, RV *Coriolis*, beam trawl, 60 m depth; MNHN 2004-1571, 73 mm SL, and USNM 378143, 81 mm SL, Chesterfield Bank, north side, 19°12'23" S, 158°42'02" E, RV *Coriolis*, beam trawl, 68 m depth.

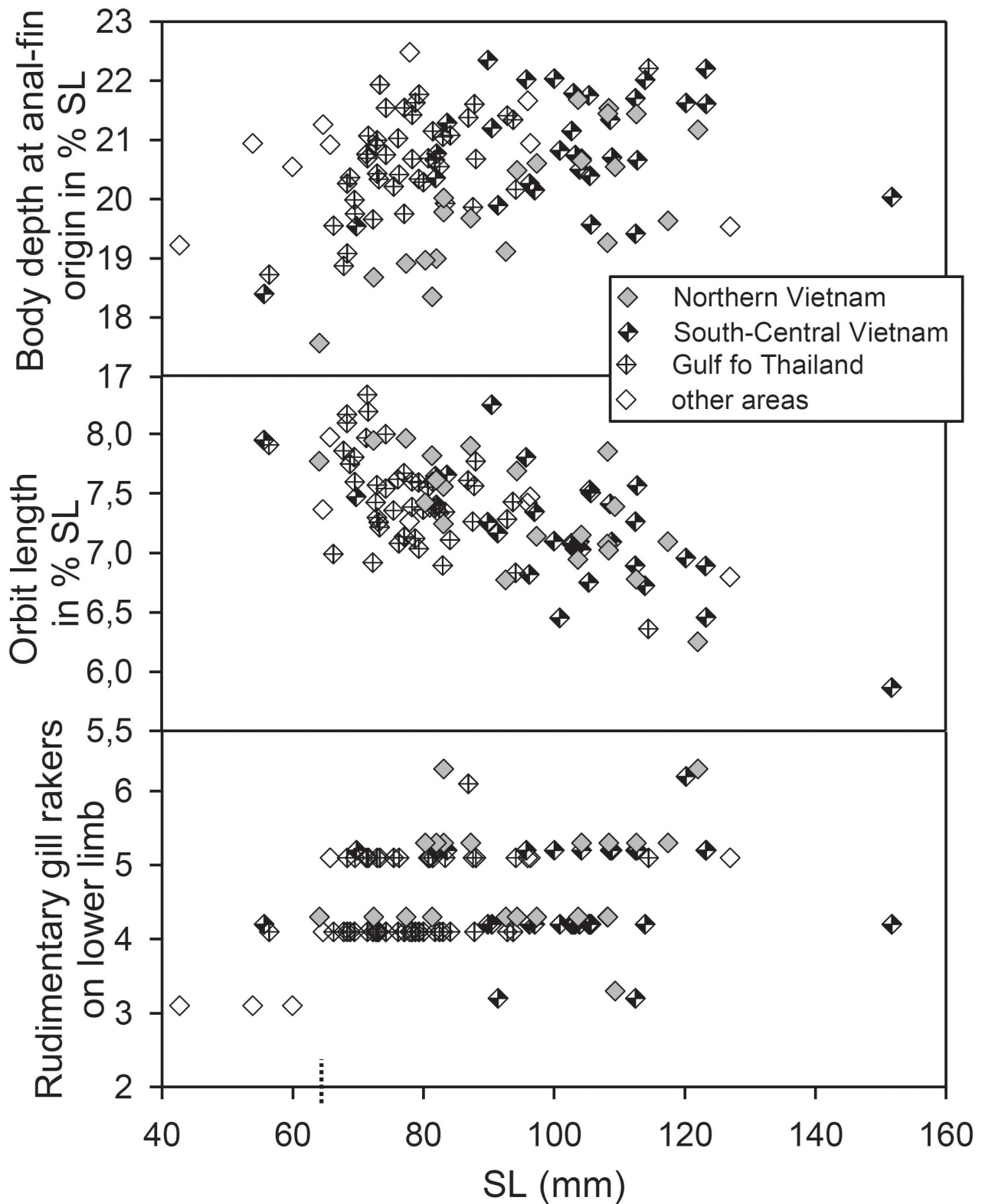


FIGURE 11. Three selected morphological characters against SL in *Upeneus heterospinus* n. sp. The 65 mm demarcation for subadults and adults is indicated by a dotted black dash. The three populations and specimens from other areas are indicated by different symbols.

TABLE 11. Means, F-values of ANOVA, p-values for significant ($p \leq 0.01$) differences and results from multiple comparisons with Scheffe test for residuals of morphometric characters (values transformed by multiplication with 1000) in three populations of *Upeneus heterospinus* n. sp. Letters in parentheses refer to pairs of populations showing no significant differences.

| | Gulf of Thailand (A) | South-central Vietnam (B) | N Vietnam (C) | F-values | p | Scheffe test |
|--|----------------------------|---------------------------------|------------------|----------|---------|--------------|
| Body depth at first dorsal-fin origin | 7.11 | -3.68 | -10.02 | 7.667 | <0.001 | A(B,C) |
| Body depth at anal-fin origin | 5.57 | 1.93 | -15.05 | 10.945 | <0.0001 | C(A,B) |
| Half body depth at first dorsal-fin origin | 5.88 | -2.93 | -7.94 | 3.359 | ns | |
| Half body depth at anal-fin origin | 2.45 | 2.20 | -10.71 | 3.488 | ns | |
| Caudal-peduncle depth | 5.48 | 4.46 | -18.80 | 18.820 | <0.0001 | C(A,B) |
| Caudal-peduncle width | 1.84 | -4.47 | 2.59 | 0.481 | ns | |
| Maximum head depth | 6.27 | 2.53 | -17.60 | 15.624 | <0.0001 | C(A,B) |
| Head depth through eye | 0.36 | 6.13 | -10.15 | 5.966 | <0.01 | (A,B)(A,C) |
| Suborbital depth | 4.66 | 4.13 | -16.20 | 5.252 | <0.01 | C(A,B) |
| Interorbital length | 6.50 | 1.56 | -16.20 | 6.300 | <0.01 | C(A,B) |
| Head length | -0.38 | 0.26 | 0.40 | 0.039 | ns | |
| Snout length | 1.50 | -0.17 | -3.10 | 0.318 | ns | |
| Postorbital length | 3.57 | -1.93 | -4.65 | 1.392 | ns | |
| Orbit length | -4.48 | 2.37 | 6.40 | 2.189 | ns | |
| Orbit depth | -5.11 | 1.13 | 9.40 | 3.238 | ns | |
| Upper-jaw length | 5.11 | -1.37 | -9.40 | 3.843 | ns | |
| Lower-jaw length | 5.45 | -1.77 | -9.30 | 3.027 | ns | |
| Snout width | -6.82 | 16.66 | -8.95 | 6.624 | <0.01 | B(A,C) |
| Barbel length | -3.03 | 13.07 | -12.85 | 9.108 | <0.001 | B(A,C) |
| Maximum barbel width | -3.19 | 12.27 | -11.55 | 2.218 | ns | |
| First pre-dorsal length | 1.82 | -0.85 | -2.71 | 0.931 | ns | |
| Second pre-dorsal length | 1.63 | -0.29 | -3.02 | 1.915 | ns | |
| Interdorsal distance | 5.86 | -5.14 | -5.30 | 1.722 | ns | |
| Caudal-peduncle length | -0.45 | -2.47 | 4.55 | 1.245 | ns | |
| Pre-anal length | 2.19 | -0.27 | -4.40 | 3.145 | ns | |
| Pre-pelvic length | 0.41 | 0.40 | -1.60 | 0.169 | ns | |
| Pre-pectoral length | 2.84 | -0.09 | -6.21 | 2.588 | ns | |
| Second dorsal-fin depth | 6.45 | 1.12 | -15.75 | 12.113 | <0.0001 | C(A,B) |
| Pelvic-fin depth | 8.27 | 0.56 | -19.10 | 18.974 | <0.0001 | C(A,B) |
| Pectoral-fin depth | 6.05 | -0.76 | -12.14 | 4.624 | 0.01 | (A,B)(B,C) |
| Length of first dorsal-fin base | 1.21 | 1.58 | -4.89 | 0.619 | ns | |
| Length of second dorsal-fin base | -3.39 | 0.10 | 7.21 | 1.304 | ns | |
| Caudal-fin length | -3.26 | 0.04 | 6.90 | 3.335 | ns | |
| Length of anal-fin base | 2.30 | 0.83 | -6.40 | 0.736 | ns | |
| Anal-fin height | 0.23 | -3.13 | 4.20 | 0.486 | ns | |
| Pelvic-fin length | -2.25 | -0.36 | 5.50 | 1.618 | ns | |
| Pectoral-fin length | -2.86 | -4.59 | 12.05 | 11.650 | <0.0001 | C(A,B) |
| Pectoral-fin width | -3.25 | 0.47 | 6.55 | 0.800 | ns | |
| First dorsal-fin height | 0.43 | -4.77 | 6.36 | 1.527 | ns | |
| Second dorsal-fin height | -2.87 | -4.89 | 13.95 | 5.005 | <0.01 | C(A,B) |

Non-types. (4 subadults: 46–55 mm SL, 2 fresh-colour photos): Vanuatu, NO *Alis*, chalut à perche: MNHN 2008-1459, 46 mm SL, Espirito Santo Island, 15°31.68'S, 167°10.80'E, 36–43 m depth (fresh-colour photo); MNHN

2010-0616, 51 mm SL, NW Malo Island, 15°39.90'S, 167°03.78'E, 114–132 m depth; MNHN 2019-0026, 1 of 3, 55 mm SL, 15°37.98'S, 167°03'E, 140–175 m depth (wrongly referred to as MNHN 2002-0070 in Uiblein *et al.* 2016); MNHN 2019-0027, 1 of 4, 49 mm SL, Malo Island, Bruat Channel, 15°37.32'S, 167°09.60'E, 52–66 m depth (fresh-colour photo).

Diagnosis. Dorsal fins VIII + 9, the first spine minute; pectoral fins 12–13; gill rakers 6–7 + 17–18 = 23–25; lateral-line scales 29–30; measurements in % SL, adults: body depth at first dorsal-fin origin 21–24; body depth at anus 19–21; caudal-peduncle depth 9.1–10; caudal-peduncle width 3.2–3.9; maximum head depth 20–21; head depth through eye 17–18; suborbital depth 9.0–11; interorbital length 7.6–8.1; head length 29–30; snout length 11–12; postorbital length 11–12; orbit length 7.8–8.8; upper-jaw length 9.3–11; barbel length 20–22; interdorsal distance 12–16; caudal-peduncle length 21–24; caudal-fin length 27–29; anal-fin height 17–19; pelvic-fin length 22–23; pectoral-fin length 22–23; pectoral-fin width 4.0–4.3; first dorsal-fin height 20–21; second dorsal-fin height 17–19; measurements in % SL, subadults: body depth at first dorsal-fin origin 21–23; body depth at anus 18–20; caudal-peduncle depth 9.1–10; caudal-peduncle width 3.0–3.5; maximum head depth 19–21; head depth through eye 15–16; suborbital depth 7.5–9.2; interorbital length 7.0–7.6; head length 30–32; snout length 10–12; postorbital length 11–13; orbit length 8.4–9.1; upper-jaw length 9.7–12; barbel length 21–23; interdorsal distance 13–14; caudal-peduncle length 23–26; caudal-fin length 30–31; anal-fin height 16–17; pelvic-fin length 22–23; pectoral-fin length 21–22; pectoral-fin width 3.5–3.8; first dorsal-fin height 19–22; second dorsal-fin height 19–20; fresh colour: head and body dorsally orange red or grey mottled, ventrally white rose or silvery, in adults covered with red blotches along ventral margin; caudal fin with 6 dark brown or black oblique bars on both lobes; on upper caudal-fin lobe 3 dark brown bars, on lower lobe 3 black bars, in adults the distal-most bar twice as wide as other bars; on both lobes hyaline interspaces mostly larger than bars; mid-laterally on caudal-fin base a brown spot both in adults and subadults; barbels yellow; a single yellow mid-lateral body stripe of pupil width from behind head to caudal peduncle; no dark dots on stripe, dark saddle behind second dorsal fin lacking or only weakly expressed; first dorsal fin with pale green pigmentation, tip pale white, often with closely fused pale-red or pale-grey brown stripes; second dorsal fin with up to 3 brown-red or grey stripes with whitish hyaline interspaces; preserved fish pale, mid-lateral stripe completely lost, yellow barbel colour sometimes retained (Figure 7 G), with remains of dark pigmentation deriving from caudal-fin bars and second dorsal-fin distal stripe or, more rarely, from saddle.

Distribution, habitat and size. Coral Sea, New Caledonia, Chesterfield Islands and Vanuatu off Malo and Spiritu Santo Islands; 36–175 m depth, muddy bottoms, adults occur shallower than juveniles; maximum size 9.5 cm SL.

Intraspecific comparisons. Subadults differ from adults in shallower head, narrower snout, slightly longer caudal peduncle and first dorsal-fin base, longer caudal fin and narrower pectoral fins (Tables 2, 9).

***Upeneus randalli* Uiblein & Heemstra, 2011**

Randall's goatfish

(Figures 1, 2, 5; Tables 2, 5, 6, 9)

Upeneus randalli Uiblein & Heemstra, 2011. Type locality off S Kuwait, Arabian/Persian Gulf, Kuwait.

Holotype. Arabian/Persian Gulf: BPBM 33180, HT, adult, 101 mm SL, Arabian/Persian Gulf, Kuwait, off S Kuwait, 29°00' N, 48°25' E, RV *Bahith*, trawl, 15–20 m depth (fresh-colour photo)

Paratypes (7 adults: 66–106 mm SL; 1 fresh colour photo, 1 fresh-colour drawing): Arabian/Persian Gulf: BPBM 21201, 6: 66–88 mm SL, Bahrain, fish market (fresh-colour photo of 80 mm SL fish); Gulf of Oman: ZMUC P49161, 106 mm SL, S Iran, Chahabar (fresh-colour drawing in Blegvad & Løppenthin (1944))

Non-type: Arabian/Persian Gulf: BPBM 29498, subadult, 60 mm SL, Bahrain (fresh-colour photo)

Diagnosis. Dorsal fins VIII + 9, the first spine minute; pectoral fins 13–14; gill rakers 6–7 + 17–19 = 23–25; lateral-line scales 28–30; measurements in % SL, adults: body depth at first dorsal-fin origin 23–24; body depth at anus 19–22; caudal-peduncle depth 9.9–11; caudal-peduncle width 2.9–3.8; maximum head depth 19–21; head depth through eye 15–16; suborbital depth 8.0–10; interorbital length 7.2–8.8; head length 27–30; snout length 11–12; postorbital length 10–12; orbit length 6.2–7.4; upper-jaw length 10–11; barbel length 16–20; interdorsal distance 13–15; caudal-peduncle length 23–25; caudal-fin length 27–30; anal-fin height 15–19; pelvic-fin length

20–22; pectoral-fin length 20–22; pectoral-fin width 3.8–4.4; first dorsal-fin height 19–22; second dorsal-fin height 16–20; measurements in % SL, subadults (based on single specimen): body depth at first dorsal-fin origin 22; body depth at anus 19; caudal-peduncle depth 9.0; caudal-peduncle width 3.5; maximum head depth 18; head depth through eye 16; suborbital depth 7.0; interorbital length 7.7; head length 28; snout length 12; postorbital length 10; orbit length 8.2; upper-jaw length 11; barbel length 19; interdorsal distance 14; caudal-peduncle length 23; caudal-fin length 29; anal-fin height 16; pelvic-fin length 21; pectoral-fin length 20; pectoral-fin width 3.7; first dorsal-fin height 21; second dorsal-fin height 19; fresh colour: head and body dorsally red-brown red or grey mottled, ventrally white or rose, in some fish with tiny red or brown dots; caudal fin with 11–13 (9 in subadult) brown or dark-grey oblique bars crossing both lobes; on upper caudal-fin lobe 4 or 5 bars, on lower lobe 5–8 bars; lower caudal lobe may be longitudinally crossed by a dark grey stripe (only observed in single subadult); caudal-fin bars and hyaline interspaces of about pupil width in adults; in subadult hyaline interspaces on upper lobe and bars on lower lobe wider (based on single subadults); lower caudal-fin lobe tip sometimes black; barbels white; a single yellow, pale beige or pale red mid-lateral body stripe of less than pupil width from behind head to caudal peduncle, the stripe covered by 3 sections with horizontal series of 2–4 dark brown or black dots, the posteriormost series of 2 dots behind second dorsal-fin base connecting to a dark saddle placed behind second dorsal fin; first dorsal fin with closely fused pale-red brown or pale-grey stripes; the tip region of first dorsal fin without dark pigmentation; second dorsal fin with 2–3 well-separated, brown or black stripes with hyaline interspaces, the dorsal-most stripe the largest and darkest; preserved fish brown or pale brown, mid-lateral body stripe completely lost, often with remains of dark saddle and—more rarely—other dark pigmentation patterns.

Distribution, habitat and size. Arabian/Persian Gulf and inner Gulf of Oman: depth 15–20 m; maximum size 11 cm SL.

TABLE 12. Overview of all valid *Upeneus* species and species groups

| Species | Species group | Species | Species group |
|--|--------------------------|---|----------------------------|
| <i>U. caudofasciatus</i> n. sp. | margarethae ⁶ | <i>U. quadrilineatus</i> Cheng & Wang, 1963 | moluccensis ¹ |
| <i>U. gubal</i> n. sp. | margarethae ⁶ | <i>U. sulphureus</i> Cuvier, 1829 | moluccensis ^{1,7} |
| <i>U. heterospinus</i> n. sp. | margarethae ⁶ | <i>U. davidaromi</i> Golani, 2001 | stenopsis ² |
| <i>U. margarethae</i> Uiblein & Heemstra, 2010 | margarethae ⁶ | <i>U. mascarensis</i> Fourmanoir & Guézé, 1967 | stenopsis ² |
| <i>U. mouthami</i> Randall & Kulbicki, 2006 | margarethae ⁶ | <i>U. stenopsis</i> Uiblein & McGrouther, 2012 | stenopsis ² |
| <i>U. randalli</i> Uiblein & Heemstra, 2011 | margarethae ⁶ | <i>U. subvittatus</i> (Temminck & Schlegel, 1843) | stenopsis ² |
| <i>U. asymmetricus</i> Lachner, 1954 | japonicus ⁵ | <i>U. vanuatu</i> Uiblein & Causse, 2013 | stenopsis ² |
| <i>U. australiae</i> Kim & Nakaya, 2002 | japonicus ⁵ | <i>U. indicus</i> Uiblein & Heemstra, 2010 | suahelicus ³ |
| <i>U. farnis</i> Uiblein & Peristiwady, 2017 | japonicus ⁵ | <i>U. suahelicus</i> Uiblein & Heemstra, 2010 | suahelicus ³ |
| <i>U. francisi</i> Randall & Guézé, 1992 | japonicus ⁵ | <i>U. supravittatus</i> Uiblein & Heemstra, 2010 | suahelicus ³ |
| <i>U. guttatus</i> (Day, 1868) | japonicus ⁵ | <i>U. heemstra</i> Uiblein & Gouws, 2014 | tragula ⁶ |
| <i>U. itoui</i> Yamashita, Golani & Motomura, 2011 | japonicus ⁵ | <i>U. luzonius</i> Jordan & Seale, 1907 | tragula ⁶ |
| <i>U. japonicus</i> (Houttuyn, 1782) | japonicus ⁵ | <i>U. niebuhri</i> Gueze, 1976 | tragula ⁶ |
| <i>U. lombok</i> Uiblein & White, 2015 | japonicus ⁵ | <i>U. oligospilus</i> Lachner, 1954 | tragula ⁶ |
| <i>U. pori</i> Ben-Tuvia & Golani, 1989 | japonicus ⁵ | <i>U. sundaicus</i> (Bleeker, 1855) | tragula ⁶ |
| <i>U. saiab</i> Uiblein & Lisher, 2013 | japonicus ⁵ | <i>U. tragula</i> Richardson, 1846 | tragula ⁶ |
| <i>U. seychellensis</i> Uiblein & Heemstra, 2011 | japonicus ⁵ | <i>U. filifer</i> (Ogilby, 1910) | ungrouped ⁴ |
| <i>U. spottocaudalis</i> Uiblein & Gledhill 2017 | japonicus ⁵ | <i>U. nigromarginatus</i> Bos, 2012 | ungrouped ⁴ |
| <i>U. torres</i> Uiblein & Gledhill 2015 | japonicus ⁵ | <i>U. parvus</i> Poey, 1852 | ungrouped ³ |
| <i>U. doriae</i> (Günther, 1869) | moluccensis ¹ | <i>U. taeniopterus</i> Cuvier, 1829 | ungrouped ⁴ |
| <i>U. moluccensis</i> (Bleeker, 1855) | moluccensis ¹ | <i>U. vittatus</i> (Forsskål, 1775) | ungrouped ³ |

Sources: ¹Uiblein & Heemstra (2010); ²Uiblein & Causse (2013); ³Uiblein & Gouws (2015); ⁴Uiblein *et al.* (2016); ⁵Uiblein *et al.* (2017); ⁶current study; ⁷*Upeneus sanctaehelenae* Bauchot, 1966 is here treated tentatively as a junior synonym of *U. sulphureus*.

Intraspecific comparison. The single subadult differs from adults in shallower maximum body and head depth, shallower caudal peduncle, shallower suborbital depth, larger eyes, longer anal-fin base, slightly narrower pectoral fins and wider bars on caudal fin, especially on lower fin lobe which is crossed by a dark stripe at mid of lobe (Tables 2, 9; Figure 2 G, H).

Interspecific comparisons and differential diagnosis of *margarethae*-group species

Similarities among margarethae group. The three new *Upeneus* species share common characteristics with the newly established *margarethae* group. *Upeneus caudofasciatus* **n. sp.** matches *U. margarethae*, *U. mouthami* and *U. randalli* in having 8 dorsal-fin spines, 12–15 pectoral-fin rays, 21–25 total gill rakers, 28–30 lateral-line scales, absence of dark pigmentation in the area of first dorsal-fin tip, and, at least when fresh or in life, oblique bars on both caudal-fin lobes and a mid-lateral body stripe. *Upeneus gubal* **n. sp.** also fits well into the ranges of meristic characters of the *margarethae* group. The complete lack of dark pigmentation in the long-preserved type specimen does not disagree with preserved colour in any of the other five species, although pigmentation degree 0 occurs rather infrequently except for the EIO/NA population of *U. margarethae*. *Upeneus heterospinus* **n. sp.** matches the group in fresh and preserved colour characteristics as well as in pectoral-fin ray, gill-raker and lateral-line scale counts. It differs however in the alternating occurrence of 7 or 8, instead of exclusively 8 dorsal-fin spines. Therefore, in order to well distinguish the *margarethae* group, comparisons of *Upeneus heterospinus* **n. sp.** with the *japonicus* group, in which all 13 *Upeneus* species with 7 dorsal-fin spines have been included (Uiblein *et al.* 2017), have to be carried out.

Differences from similar, non-margarethae group species. Among the 13 species of the *japonicus* group, *U. australiae* is most similar with *U. heterospinus* **n. sp.** in having 13–15 pectoral-fin rays, 22–25 gill rakers, 27–30 lateral-line scales, absence of dark pigmentation in the area of first dorsal-fin tip, and, at least when fresh or in life, oblique bars on both caudal-fin lobes and a mid-lateral body stripe (Uiblein & Gledhill 2015). *Upeneus heterospinus* **n. sp.** differs from *U. australiae* in yellow vs. white barbels, a slightly higher second dorsal fin (second dorsal-fin height 16–20 % SL vs. 14–18 % SL; see also Uiblein & Gledhill 2015), frequent presence of a dark saddle behind second dorsal fin and/or dark dots in the area of mid-lateral stripe both in fresh and in preserved condition vs. no such colour patterns, and/or frequent occurrence of a red or brown stripe on lower caudal-fin lobe vs. no such stripe in fresh fish; furthermore, the interspaces between bars being mostly of similar width on both caudal-fin lobes in adult *U. heterospinus* **n. sp.** vs. being clearly narrower on lower lobe in *U. australiae*. In addition, the two species differ in distribution, *U. australiae* being restricted to the Australian Shelf and the Coral Sea (Uiblein & Gledhill 2015), while *U. heterospinus* **n. sp.** occurs further north (Figure 1).

All other 12 species of the *japonicus* group lack bars that cross the entire lower caudal-fin lobe and either have higher gill-raker counts than *U. heterospinus* **n. sp.** (*U. asymmetricus* Lachner, 1954, *U. farnis* Uiblein & Peristiwady, 2017, *U. francisi* Randall & Guézé, 1992, *U. lombok* Uiblein & White, 2015, *U. pori* Ben-Tuvia & Golani, 1989, *U. saiab* Uiblein & Lisher, 2013, *U. seychellensis* Uiblein & Heemstra, 2011), lack a mid-lateral body stripe (*U. asymmetricus*, *U. farnis*, *U. francisi*, *U. guttatus*, *U. japonicus* (Houttuyn, 1782), *U. lombok*, *U. pori*, *U. saiab*, *U. seychellensis*, *U. spottocaudalis*), and/or have white or pale reddish instead of yellow barbels (*U. farnis*, *U. francisi*, *U. guttatus* (in part), *U. itoui* Yamashita, Golani & Motomura, 2011, *U. lombok*, *U. saiab*, *U. seychellensis*) (Uiblein & Heemstra 2011; Uiblein & Lisher 2013; Uiblein & White 2015; Uiblein & Gledhill 2015; Uiblein *et al.* 2017). Furthermore, *U. heterospinus* **n. sp.** can be clearly distinguished from *U. spottocaudalis* in the combination of barbel length and pelvic-fin length (Figure 12).

Differences among margarethae-group species. Distinction among the six *margarethae*-group species can be best achieved by pairwise comparisons using the entire phenotypic variation comprehensively, i.e. all morphometric, meristic and colour characters studied, singly or in combination, under consideration of intraspecific size- and population-related variation and results from additional statistical analyses. Distributional information can be also used comparatively. The results of these comparisons are presented unidirectionally for each species pair.

Differences from U. margarethae (Tables 1, 2, 4–7, 9; Figures 1–3, 5–7, 9, 10). *Upeneus caudofasciatus* **n. sp.** differs in slightly narrower caudal peduncle, longer barbels, more gill rakers (both adults and subadults), higher second dorsal fin (adults), deeper head through eye and suborbital depth, and shorter caudal peduncle (subadults); when compared with the EIO/NA population of *U. margarethae*, *U. caudofasciatus* **n. sp.** can be clearly distinguished by

the combination of barbel length, second dorsal-fin height, and gill-raker count (Figure 6). Furthermore, the two species differ statistically from each other in fewer pectoral-fin rays (Table 5), and—in preserved specimens—more caudal-fin bars on lower lobe and more mid-lateral dots in *U. caudofasciatus* **n. sp.** (Table 7), as well as in 24 of 40 morphometric characters (Table 4). *Upeneus gubal* **n. sp.** differs mainly in more gill rakers, narrower caudal peduncle, and in the combination of caudal-fin length and anal-fin height (Figure 5); moreover, it differs from the Red Sea population of *U. margarethae* in more pectoral-fin rays, shallower suborbital depth, longer barbels and higher anal fin. *Upeneus heterospinus* **n. sp.** differs in entirely yellow vs. white or mostly white barbels, 7 or 8 vs. exclusively 8 dorsal-fin spines, slightly narrower pectoral fins (both adults and subadults), and shallower body at anal-fin base; when preserved, *Upeneus heterospinus* **n. sp.** differs also in a significantly higher pigmentation degree (Table 6) and significantly greater occurrence of pigmentation remains from caudal-fin bars and second dorsal-fin distal stripe (Table 7); furthermore, the two species differ significantly from each other in 24 of 40 morphometric characters (Table 4). *Upeneus mouthami* differs in entirely yellow vs. white or mostly white barbels, slightly more gill rakers, shallower body at anal-fin origin, narrower caudal peduncle, longer barbels, shorter first dorsal-fin base (both adults and subadults), presence of a brown spot mid-laterally on caudal-fin base in both adults and subadults vs. absence of spot, fewer caudal-fin bars in adults, and the mid-lateral body stripe extending from behind head vs. starting at snout tip. *Upeneus randalli* differs in the combination of slightly more gill rakers, narrower caudal-peduncle, and narrower pectoral fins (adults and subadults; see also Figure 5); furthermore, the mid-lateral body stripe is much less conspicuous than in *U. margarethae*, starting from behind head vs. from snout tip in *U. margarethae*.

Differences from Upeneus caudofasciatus **n. sp.** (Tables 1, 2, 4–7, 9; Figures 1, 7, 9, 10). *Upeneus gubal* **n. sp.** differs in more pectoral-fin rays and in distribution by occurring widely separated from NE Australia in the S Gulf of Suez, Northern Red Sea. *Upeneus heterospinus* **n. sp.** differs in entirely yellow vs. white or at least partly white barbels, 7 or 8 vs. 8 dorsal-fin spines, fewer gill rakers, slightly shallower body at dorsal-fin origin and shorter barbels (adults and subadults); furthermore subadults differ in having shallower and shorter head, shorter first dorsal-fin base, and shorter pectoral and pelvic fins; *Upeneus heterospinus* **n. sp.** has significantly more pectoral-fin rays (apart from fewer gill rakers, see also above; Table 5) and preserved specimens have a significantly higher frequency of pigmentation remains deriving from caudal-fin bars and second dorsal-fin distal stripe (Table 7); furthermore, it differs significantly in as much as 32 of 40 morphometric characters (Table 4). *Upeneus mouthami* differs in deeper body at dorsal-fin origin (adults and subadults), shallower maximum head depth and shorter first dorsal-fin base (adults), and shallower head through eye and suborbital depth (subadults); furthermore, it differs by entirely yellow vs. white or mostly white barbels, wider and wider-spaced caudal-fin bars, and presence of a brown spot mid-laterally on caudal-fin base in both adults and subadults vs. absence of spot. *Upeneus randalli* differs in shallower body at first dorsal origin, shallower head and slightly shorter barbels (adults and subadults); the mid-lateral body stripe is much less conspicuous than in *U. caudofasciatus* **n. sp.**, starting from behind head vs. from snout tip in *U. caudofasciatus* **n. sp.**; furthermore, the two species differ in distribution occurring widely separated of each other off NE Australia vs. the Arabian/Persian Gulf (Figure 1).

Differences from Upeneus gubal **n. sp.** (Tables 1, 5, 6, 9; Figures 1, 5, 7, 9, 10). *Upeneus heterospinus* **n. sp.** differs in fewer gill rakers, wider caudal peduncle, narrower pectoral fins and in distribution with its occurrence in the area of S Indonesia to Japan widely separated from the S Gulf of Suez (Figure 1). *Upeneus mouthami* differs in a large number of morphometric characters such as shallower caudal peduncle, deeper head through eye, smaller eyes, longer barbels, shorter dorsal-fin bases and caudal fin, and shallower first dorsal fin, as well as in distribution (Figure 1); *Upeneus randalli* differs in fewer pectoral-fin rays, shorter interdorsal distance, shorter anal-fin base and caudal fin, and narrower pectoral fins (see also Figure 5). It occurs more closely to *U. gubal* **n. sp.** than the other two above-mentioned species in the Arabian/Persian Gulf and inner Gulf of Oman, but is still separated by the Gulf of Aden and Red Sea proper (where only *U. margarethae* occurs; Figure 1).

Differences from Upeneus heterospinus **n. sp.** (Tables 2, 5, 6, 9; Figures 1, 2, 7, 12). *Upeneus mouthami* differs in 8 vs 7 or 8 dorsal-fin spines, more gill rakers, longer barbels (subadults and adults), shorter first dorsal-fin base (adults), slightly shallower body at dorsal-fin origin, narrower caudal peduncle and longer anal-fin base (all subadults); furthermore, it differs by wider-spaced caudal-fin bars, and presence of a brown spot mid-laterally on caudal-fin base in both adults and subadults vs. absence of spot. *Upeneus randalli* differs in 8 vs 7 or 8 dorsal-fin spines, slightly more gill rakers, white vs. yellow barbels, narrower caudal peduncle (subadults and adults) and shorter head, longer first dorsal-fin base and anal-fin base in subadults; also, it differs in distribution, occurring widely separated from *U. heterospinus* (Figure 1).

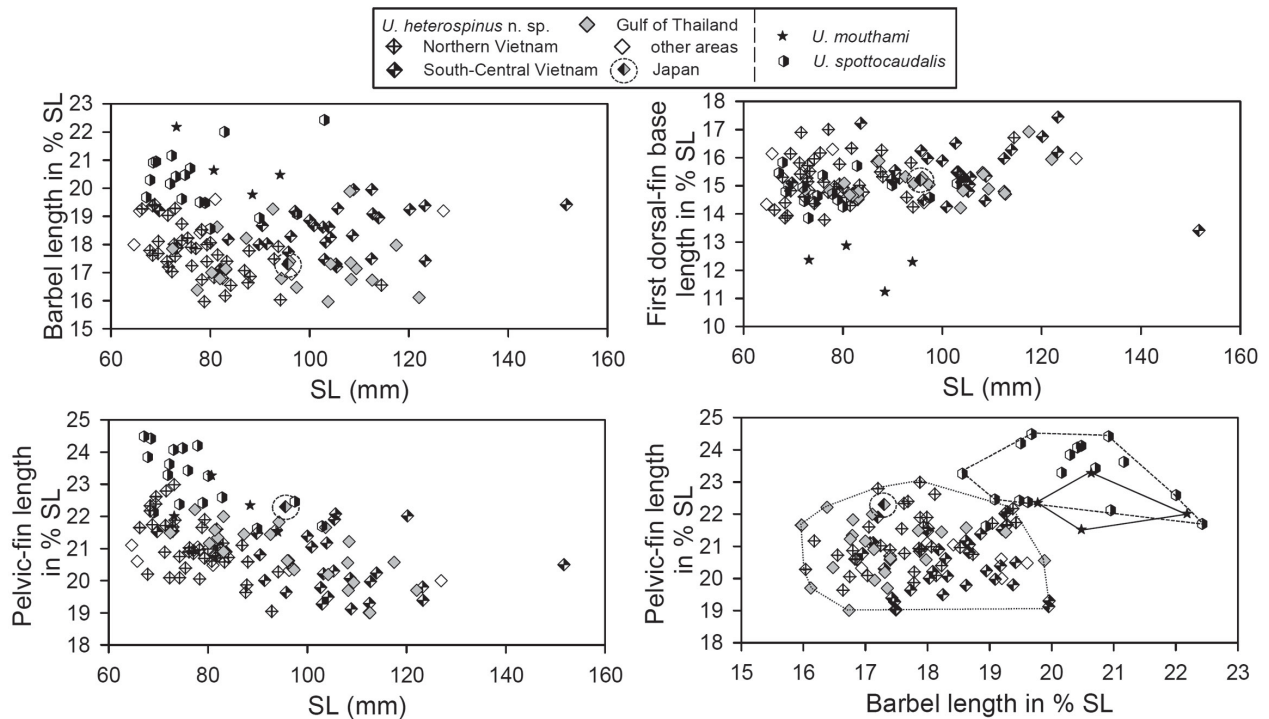


FIGURE 12. Three morphometric characters against SL and pelvic-fin length against barbel length in adults of *Upeneus heterospinus n. sp.*, *U. mouthami* and *U. spottocaudalis*. For *Upeneus heterospinus n. sp.*, the three populations and additional specimens from other areas are indicated by different symbols. The distinction among *U. heterospinus n. sp.* and the two other species is indicated by dotted, continuous, and dashed outlines, respectively. The data for the specimen from S Japan identified here as *U. heterospinus n. sp.* were taken from Bandai *et al.* (2018). The data for *U. spottocaudalis* are from Uiblein *et al.* (2017).

Finally, *U. mouthami* differs from *U. randalli* (Tables 2, 5, 6, 9; Figures 1, 2, 7) in deeper head (head through eye in adults and maximum head depth in subadults), longer head (subadults), larger eyes (adults and subadults), longer barbels (adults and subadults), shorter first dorsal-fin base (adults), longer caudal fin (subadults), and longer anal-fin base (adults); furthermore, it differs by entirely yellow vs. white barbels, wider-spaced caudal-fin bars, and presence of a brown spot mid-laterally on caudal-fin base in both adults and subadults vs. absence of spot; in addition, the two species occur widely separated of each other (Figure 1).

Discussion

With the three new species being added, the genus *Upeneus* consists now of 42 valid species, of which 37 species belong to six taxonomic species groups and five species are ungrouped (Table 12). The six species of the *margarethae* group can be distinguished from all other congeneric species based on the following common characteristics: 8 or 7–8 dorsal-fin spines, 12–15 pectoral-fin rays, 21–25 total gill rakers, 28–30 lateral-line scales, no dark pigmentation in the area of first dorsal-fin tip, oblique bars crossing both caudal-fin lobes entirely, the lower lobe sometimes longitudinally crossed or covered by a red, brown or dark-grey stripe, a mid-lateral body stripe with or without one or several dark dots, and often a dark saddle behind second dorsal fin; in preserved fish, dark pigmentation remains deriving from caudal-fin bars, mid-lateral dots, saddle and/or the distal-most stripe of the second dorsal fin are often retained.

All six *margarethae*-group species have been described only recently due to the absence of dedicated taxonomic research, confusion with superficially similar species earlier described, such as *U. australiae*, *U. guttatus*, *U. luzonius* or *U. tragula*, and/or insufficient availability of comparative material for detailed taxonomic studies.

All three limitations may apply, as the most recent revision of the genus is over 60 years old (Lachner 1954), species of the genus may have been confused with each other quite often, because many have lateral body stripes and oblique caudal-fin bars, and the identification of important meristic characters such as gill-raker number and the first dorsal-fin spine in eight-spined species requires closer inspection by use of a microscope. Only recently have research efforts such as a research cruise with RV *Dr. F. Nansen* off Mozambique in 2007 (Johnsen *et al.* 2008), the FRV *Gwendoline May* cruises off NE Australia (Pitcher *et al.* 2007a, b) and collections of market fishes and from fishermen in Vietnam conducted by two of the authors (DAP, FU; 2009–2013) resulted in the collection of sufficient scientific material including fresh-colour photos with associated voucher specimens required for detailed taxonomic analyses.

The high inter- and intraspecific phenotypic diversity among the genus *Upeneus* requires a careful taxonomic approach regarding both species diagnoses and descriptions, redescriptions, resurrections, or synonymizations. While several comprehensive alpha-taxonomic studies of *Upeneus* have incorporated genetic data with advantage (e.g., Uiblein & Gouws 2014; 2015; Uiblein *et al.* 2016), no genetic information currently exists for three of the six *margarethae*-group species (*U. gubal* n. sp., *U. mouthami*, *U. randalli*). Genetic analysis of material from specimens of the three other species utilising the COI barcoding method, which was successfully used in earlier studies, did not complement our findings of consistent distinction among these species in morphology and/or colour patterns (Gavin Gouws & Franz Uiblein, unpublished data). Our results of high overall inter- and intraspecific phenotypic differentiation deserve a more refined molecular approach with consideration of diversification across all six species with particular attention to possibly ongoing microevolutionary processes at the scale of ocean regions or subregions.

More information on intraspecific variation in colour patterns should be also collected for each of the six species. In particular, more *in-situ* observations and documentation should be gathered for the five rather shallow-occurring species and especially more fresh-colour photos should be collected together with voucher specimens. Of particular interest would be the documentation of colour changes that may go hand in hand with different behaviours adopted and/or habitat shifts. For instance, the stripe that partly or almost entirely covers the oblique bars on the lower caudal-fin lobe in *U. caudofasciatus* n. sp., *U. heterospinus* n. sp., and *U. margarethae* may appear or disappear or become lighter or darker under distinct, yet unknown conditions. The large vertical bands across the body displayed by *U. margarethae* and *U. heterospinus* n. sp. when encountered resting on the bottom may be reduced to rectangular dark sections that cover parts of the mid-lateral body stripe in more active fishes. The presence of dark dots on the mid-lateral body stripes appears to vary geographically. For instance, in *U. margarethae* these dots are rather inconspicuous in the EIO, while being darker in other areas. Also, considerable species differences appear to exist in the presence of mid-lateral dots.

Also, the documented size-related variation in colour patterns deserves to be further studied comparatively among species and populations, as do potential differences relating to lifestyle changes during ontogeny. In preserved specimens remains of dark pigmentation patterns can be found and used for identification in addition to morphological characters. For this purpose, however, it is also important to understand the effects of fixation and preservation methods on the perseverance of colour patterns, as well as to investigate more closely which type of fresh colour patterns are preserved and which not. For instance, two of the authors (DCG, FU) observed that in long-term (> 10 years) frozen specimens of *U. caudofasciatus* n. sp. from NE Australia that had been collected during the same research cruise as the specimens examined in this study, the pigmentation patterns were almost completely lost. Similar effects of long-term freezing on pigmentation loss have been observed in the ophidiid *Neobythites unicolor* Nielsen & Retzer, 1994 (Uiblein *et al.* 2019). The single type of *U. gubal* n. sp.—as well as the *U. moluccensis* specimen which had been collected with it—do not show any remains of dark pigmentation which may be due to unknown post-collection and/or fixation treatments or possibly (also) the result of the long preservation period since their collection in 1928. To better understand the various effects of catching, handling, storage, fixation and preservation on pigmentation loss in fishes, the conditions of collection and post-collection treatment would need to be known in detail for each preserved scientific specimen (Uiblein *et al.* 2019).

At least two species of the *margarethae* group, *U. heterospinus* n. sp. and *U. margarethae*, appear to be locally very common and may have considerable ecological and fisheries-related importance that has remained hitherto insufficiently recognized. *Upeneus heterospinus* n. sp., for instance, has been frequently encountered at small-scale fisheries landing sites and fish markets in the bays of Ha Long and Nha Trang (N and South-central Vietnam) and in Phu Quoc (S Vietnam, Gulf of Thailand) during sampling efforts for this and previous studies (e.g., Emel'yanova &

Pavlov 2014; Pavlov & Emel'yanova 2016). This species has been listed under various names for several areas of its entire distributional range (see list of synonymies) and may have been encountered and reported even more frequently without verification options, for example, photographic documentation. This assumption may also apply to the trawl-based shrimp fisheries off Vietnam and adjacent areas, which frequently listed *Upeneus* species as bycatch used for the production of surimi (Ha 2009; Park 2013). The present taxonomic account opens new avenues for conducting appropriate species- and population-oriented research, also related to the still incompletely investigated ecologically important roles of goatfishes as keystone or indicator species (Uiblein 2007).

Comprehensive alpha-taxonomic research has recently uncovered a previously unknown, stunning diversity at both inter- and intraspecific levels for the goatfish genus *Upeneus*. Scientific discoveries in this genus do not appear to have yet reached a satiation point. Too many important diagnostic details, when it comes to correct species identification irrespective of size, region, habitat, behaviour, etc. appear to be still insufficiently explored. Some of the less known species, or species from less investigated areas, deserve more attention and adoption of a similar fine-resolution taxonomy approach, ideally accompanied by integrative genetic studies, to more completely understand the overall diversity and the evolutionary pathways involved in a specious fish genus.

Acknowledgments

We thank the following colleagues for hospitality and assistance during collection visits or for providing other collection-related favors: Mark McGruther, Amanda Hay and Sally Reader (AMS); James Maclaine (BMNH); Jack Randall, Lori O'Hara, and Arnold Suzumoto (BPBM); Dave Catania, Jon Fong and Mysi Hoang (CAS); Alastair Graham, Narissa Bax, William T. White, Carlie Devine, Peter Last, and John Pogonoski (CSIRO); Peter Psomadakis (FAO); Rupert Wienerroither (HIFIRE); Romain Causse, Zouhaira Gabsi, Jonathan Pfliger, Philippe Béarez, Guy Duhamel, and Patrice Pruvost (MNHN); the staff of MZB; Jeffrey W. Johnson (QM); Elaine and Phil C. Heemstra, Willem Coetzer, Gavin Gouws, Wouter Holleman, Roger Bills, Mzwandile Dwani, Bafo Konqobe, Nkosinathi Mazungula, and the SAIAB National Fish Collection staff (SAIAB); Tilman Alpermann, Fareed Krupp, and Jennifer Stepler (SMF); Ulysses Alama and Soledad Garibay (UPVMI); Jeff Williams, David Smith, and Rick Feeney (USNM); Luong Thi Bich Thuan and Vo Thi Ha (Coastal Department, VRTC), Doan Doc Vinh, and the staff of the VRTC (Ha Noi and Nha Trang); Sue Morrison and Glenn Moore (WAM); Peter Rask Møller, Jørgen G. Nielsen, Markus Krag, and Tammes Menne (ZMUC); and Ann-Helen Rønning and Åge Brabrand (NHMO). For providing photos or assisting in editing photos we thank Oddgeir Alvheim, K.K. Bineesh, Sergey V. Bogorodsky; Claude Ferrara (MNHN); Mike & Valda Fraser, Phil C. Heemstra; Robert Koch, Angela Lund, Philippe & Guido Poppe, Peter Psomadakis, John E. Randall, Sahat Ratmuangkhwang (Kasetsart University, Ranong, Thailand), Subal K. Roul (Central Marine Fisheries Research Institute, Odisha, India), Sven Tränkner (SMF), and Gordon Yearsley (CSIRO). Furthermore, we thank the crews of the RV *Dr. Fridtjof Nansen* and FRV *Gwendoline May* for assistance and support. The comments by Gavin Gouws, Eric Hilton, and an anonymous reviewer on a former version of the manuscript are gratefully acknowledged. The first author thanks SAIAB, the Nansen Programme of the Center for Developmental Fisheries at the Institute of Marine Research, Bergen, the UNIDO Project nr. 130130, and CSIRO Hobart for travel support.

References

- Bandai, A., Itou, M. & Motomura, H. (2018) First Northern Hemisphere record of the tailspot Goatfish *Upeneus spottocaudalis* (Perciformes: Mullidae) from Kagoshima, Japan. *Japan. Journal of Ichthyology*, 65, 35–39.
<https://doi.org/10.11369/jji.17-056>
- Blegvard, H. & Løppenthin, B. (1944) *Fishes of the Iranian Gulf*. Einar Munksgaard, Copenhagen, 247 pp.
- Bogorodsky, S.V., Alpermann, T.J., Mal, A.O. & Gabr, M.H. (2014) Survey of demersal fishes from southern Saudi Arabia, with five new records for the Red Sea. *Zootaxa*, 3852 (4), 401–437.
<https://doi.org/10.11646/zootaxa.3852.4.1>
- Emel'yanova, N.G. & Pavlov, D.A. (2014) Gamete ultrastructure in two species of the genus *Upeneus* (Mullidae) from the South China Sea. *Journal of Ichthyology*, 54 (4), 286–292.
<https://doi.org/10.1134/S0032945214030023>
- Froese, R. & Pauly, D. (Eds.) (2019) FishBase. World Wide Web electronic publication. Available from: <https://www.fishbase.org>.

in/search.php (accessed 2 February 2019)

- Johnsen, E., Krakstad, J.O., Ostrowski, M., Serigstad, B., Strømme, T., Alvheim, O., Olsen, M., Zaera, D., André, E.R., Dias, N., Sousa, L., Sousa, B., Malauene, B. & Abdula, S. (2008) *Surveys of the Living Marine Resources of Mozambique. Ecosystem Survey and Special Studies, 27 September–21 December 2007. Cruise reports “Dr. Fridtjof Nansen”*. Institute of Marine Research, Bergen, 111 pp.
- Ha, V.V. (2009) A review on the marine fisheries resources as used for Surimi raw materials in Vietnam. In: SEAFDEC (Ed.), *Report of End-of-Project Meeting of the Working Party on Information Collection for Economically Important Species as Surimi Raw Materials in the Southeast Asian Region*, Southeast Asian Fisheries Development Center, Training Department, Samut Prakan, pp. 32–38.
- Kim, B.J. & Nakaya, K. (2002) *Upeneus australiae*, a new goatfish (Mullidae: Perciformes) from Australia. *Ichthyological Research*, 49, 128–32.
<https://doi.org/10.1007/s102280200016>
- Kimura, S., Imamura, H., Nguyen, V.Q. & Pham, T.D. (2018) *Fishes of Ha Long Bay, the Natural World Heritage Site in Northern Vietnam*. Fisheries Research Laboratory, Mie University, Shima, 314 pp.
- Krakstad, J., Michalsen, K., Krafft, B., Bagøien, E., Alvheim, O., Strømme, T., Mya Than, T. & San Thar, T. (2014) *Myanmar Ecosystem Survey, 13 November–17 December 2013. Cruise Report “Dr. Fridtjof Nansen”*. Institute of Marine Research, Bergen, 99 pp.
- Lachner, E.A. (1954) A revision of the goatfish genus *Upeneus* with descriptions of two new species. *Proceedings of the United States National Museum*, 103, 497–532.
<https://doi.org/10.5479/si.00963801.103-3330.497>
- Motomura, H., Alama, U.B., Muto, N., Babaran, R.P. & Ishikawa, S. (2017) *Commercial and Bycatch Market Fishes of Panay Island, Republic of the Philippines*. The Kagoshima University Museum, Kagoshima, University of the Philippines Visayas, Iloilo, and Research Institute for Humanity and Nature, Kyoto, 246 pp.
- Park, J.W. (2013) *Surimi and Surimi Seafood. 3rd Edition*. CRC Press, Boca Raton, 666 pp.
<https://doi.org/10.1201/b16009>
- Pavlov, D.A. & Emel’yanova, N.G. (2016) Reproductive features of *Upeneus margarethae* (Mullidae), a species recorded in the coastal zone of Vietnam for the first time. *Journal of Ichthyology*, 56 (4), 600–612.
<https://doi.org/10.1134/S0032945216040093>
- Pitcher, C.R., Doherty, P., Arnold, P., Hooper, J., Gribble, N., Bartlett, C., Browne, M., Campbell, N., Cannard, T., Cappo, M., Carini, G., Chalmers, S., Cheers, S., Chetwynd, D., Colefax, A., Coles, R., Cook, S., Davie, P., De’ath, G., Devereux, D., Done, B., Donovan, T., Ehrke, B., Ellis, N., Ericson, G., Fellegara, I., Forcey, K., Furey, M., Gledhill, D., Good, N., Gordon, S., Haywood, M., Jacobsen, I., Johnson, J., Jones, M., Kinninmoth, S., Kistle, S., Last, P., Leite, A., Marks, S., McLeod, I., Oczkovicz, S., Rose, C., Seabright, D., Sheils, J., Sherlock, M., Skelton, P., Smith, D., Smith, G., Speare, P., Stowar, M., Strickland, C., Sutcliffe, P., Van der Geest, C., Venables, W., Walsh, C., Wassenberg, T., Welna, A. & Yearsley, G. (2007a) *Seabed Biodiversity on the Continental Shelf of the Great Barrier Reef World Heritage Area. AIMS/CSIRO/QM/QDPI CRC Reef Research Task Final Report*. CSIRO Marine & Atmospheric Research, Hobart, 315 pp.
- Pitcher, C.R., Haywood, M., Hooper, J., Coles, R., Bartlett, C., Browne, M., Cannard, T.M., Carini, G., Carter, A., Cheers, S.J., Chetwynd, A.D., Cook, S., Davie, P., Ellis, A.N., Fellegara, I., Forcey, K., Furey, M., Gledhill, D.C., Hendriks, P. & Jacobsen, I. (2007b) *Mapping and Characterization of Key Biotic & Physical Attributes of the Torres Strait Ecosystem. CSIRO/QM/QDPI CRC Torres Strait Task Final Report*. CSIRO Marine & Atmospheric Research, Brisbane, 145 pp.
- Provincial Keelung Girls’ High School, Keelung, Taiwan (Ed.) (1985) *The Interesting Marine Fishes of Taiwan*. Taiwan Provincial Department of Education, Taipei, 221 pp.
- Randall, J.E. & Kulbicki, M. (2006) A review of the goatfishes of the genus *Upeneus* (Perciformes: Mullidae) from New Caledonia and the Chesterfield Bank, with a new species, and four new records. *Zoological Studies*, 45, 298–307.
- Ratmuangkhwang, S. (2018) *The Common Aquatic Fauna of Kampuan Mangrove Forest, Ranong Province*. Andaman Coastal Research Station for Development, Academic Supporting Division, Faculty of Fisheries, Kasetsart University, Bangkok, 199 pp. [in Thai language]
- Ray, D., Mohapatra, A. & Yennawar, P. (2016) Occurrences of seven new records of goatfishes (family: Mullidae) from the coastal waters of West Bengal, India. *International Journal of Experimental Research and Review*, 5, 1–7.
- Sabaj, M.H. (2019) Standard symbolic codes for institutional resource collections in herpetology and ichthyology: An online reference. Version 7.1. American Society of Ichthyologists and Herpetologists, Washington, D.C. Available from: <http://www.asih.org> (accessed 21 March 2019)
- Sainsbury, K.J., Kailola, P.J. & Leyland, G.G. (1985) *Continental Shelf Fishes of Northern and Northwestern Australia*. CSIRO Division of Fisheries Research, Clouston & Hall and Peter Pownall Fisheries Information Service, Canberra, 375 pp.
- Uiblein, F. (2007) Goatfishes (Mullidae) as indicators in tropical and temperate coastal habitat monitoring and management. *Marine Biology Research*, 3, 275–288.
<https://doi.org/10.1080/17451000701687129>
- Uiblein, F. & Gledhill, D.C. (2015) A new goatfish of the genus *Upeneus* (Mullidae) from Australia and Vanuatu, with inter- and intraspecific comparisons. *Marine Biology Research*, 11, 475–491.
<https://doi.org/10.1080/17451000.2014.958088>
- Uiblein, F., Gledhill, D.C. & Peristiwady, T. (2017) Two new goatfishes of the genus *Upeneus* (Mullidae) from Australia and

- Indonesia. *Zootaxa*, 4318 (2), 295–311.
<https://doi.org/10.11646/zootaxa.4318.2.4>
- Uiblein, F. & Gouws, G. (2014) A new goatfish species of the genus *Upeneus* (Mullidae) based on molecular and morphological screening and subsequent taxonomic analysis. *Marine Biology Research*, 10, 655–681.
<https://doi.org/10.1080/17451000.2013.850515>
- Uiblein, F. & Gouws, G. (2015) Distinction and relatedness – taxonomic and genetic studies reveal a new species group of goatfishes (*Upeneus*; Mullidae). *Marine Biology Research*, 11, 1021–1042.
<https://doi.org/10.1080/17451000.2015.1064963>
- Uiblein, F., Gouws G., Gledhill, D.C. & Stone, K. (2016). Just off the beach: intrageneric distinctiveness of the bandtail goatfish *Upeneus taeniopterus* (Mullidae) based on a comprehensive alpha taxonomy and barcoding approach. *Marine Biology Research*, 12, 675–694.
<https://doi.org/10.1080/17451000.2016.1190458>
- Uiblein, F. & Heemstra, P.C. (2010) A taxonomic review of the Western Indian Ocean goatfishes of the genus *Upeneus* (family Mullidae) with descriptions of four new species. *Smithiana Bulletin*, 11, 35–71.
- Uiblein, F. & Heemstra, P.C. 2011. Description of a new goatfish species, *Upeneus randalli* sp. nov (Mullidae), from the Persian Gulf, with remarks on and keys for Western Indian Ocean *Upeneus* species. *Scientia Marina*, 75, 585–94.
<https://doi.org/10.3989/scimar.2011.75n3585>
- Uiblein, F. & Lisher, M. (2013) A new goatfish of the genus *Upeneus* (Mullidae) from Angoche, northern Mozambique. *Zootaxa*, 3717 (1), 85–95.
<https://doi.org/10.11646/zootaxa.3717.1.7>
- Uiblein, F., Nielsen, J.G., Baldwin C.C., Quattrini, A.M. & Robertson, R. (2019) Discovery of a distinctive spotted color pattern in the cuskeel *Neobythites unicolor* (Teleostei, Ophidiidae) based on underwater-vehicle dives, with new records from the southern and eastern Caribbean. *Copeia*, 107, 277–286.
<https://doi.org/10.1643/CI-18-148>
- Uiblein, F. & White, W.T. (2015) A new goatfish of the genus *Upeneus* (Mullidae) from Lombok, Indonesia and first verified record of *U. asymmetricus* for the Indian Ocean. *Zootaxa*, 3980 (1), 51–66.
<https://doi.org/10.11646/zootaxa.3980.1.3>
- Uiblein, F. & Winkler, H. (1994) Morphological variability among *Vimba* in Austrian waters: quantitative examination of a taxonomic and a functional hypothesis (Pisces: Cyprinidae). *Senckenbergiana biologica*, 73, 57–65.
- White, W.T., Last, P.R., Dharmadi, Faizah, R., Chodrijah, U., Prisantoso, B.I., Pogonoski, J.J., Puckridge, M. & Blaber, S.J.M. (2013) *Market Fishes of Indonesia*. *ACIAR Monograph No. 155*. Australian Centre for International Agricultural Research, Canberra, 438 pp.