

<https://doi.org/10.11646/zootaxa.4938.3.2>

<http://zoobank.org/urn:lsid:zoobank.org:pub:DF5541CF-E4BE-43DF-BE55-615F4D4CEFBD>

Three new goatfishes of the genus *Upeneus* from the Eastern Indian Ocean and Western Pacific, with an updated taxonomic account for *U. itoui* (Mullidae: *japonicus*-species group)

FRANZ UIBLEIN^{1,2,3,4*} & HIROYUKI MOTOMURA⁵

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

²National Research Foundation - South African Institute for Aquatic Biodiversity, Makhanda, South Africa

³Natural History Museum, University of Oslo, Norway

⁴Vietnam National Museum of Nature, Vietnam Academy of Science and Technology, Ha Noi, Vietnam

⁵The Kagoshima University Museum, Korimoto, Kagoshima, Japan.

 motomura@kaum.kagoshima-u.ac.jp;  <http://orcid.org/0000-0002-7448-2482>

*Corresponding author:  franz@hi.no;  <http://orcid.org/0000-0002-5642-0384>

Abstract

Coastal marine fish diversity from E India and Indonesia to S Japan is still insufficiently investigated. Of the 42 species of goatfishes (Mullidae) recorded from this area, 12 were described only since 2010 and ten of those belong to the genus *Upeneus*. During a recent review of species of *Upeneus* of the so-called *japonicus*-species group (characterized by seven dorsal-fin spines), 13 specimens that had been previously identified as *U. guttatus* from Indonesia and Vietnam were found to be distinct, representing possibly two undescribed species. These specimens were studied together with 20 *U. itoui* from S Japan, a rather similar species, and a yet unidentified congeneric from S Japan. In total 41 morphometric, 10 meristic and several colour characters were examined and detailed comparisons with a large data set from all 14 *japonicus*-group species conducted. Three new species, *U. dimipavlov* n. sp. from Nha Trang, S-central Vietnam, *U. elongatus* n. sp. from Tanega-shima Island, Kagoshima, S Japan and *U. willwhite* n. sp. from Lombok, S Indonesia are described and an updated account for *U. itoui* is provided. Among these four featured species, *U. elongatus* is the most different, having more gill rakers, the shallowest head and body and distinct colour patterns on caudal and dorsal fins. *Upeneus dimipavlov* differs from the remaining two species in having a more rounded and less laterally compressed body with a wider caudal peduncle and no conspicuous mid-lateral body stripe in fresh fish. *Upeneus willwhite* differs from *U. itoui* in deeper head, larger eyes, longer upper jaw and barbels and oblique bars on the lower caudal-fin lobe which do not cross the entire lobe. Additional comparisons of each of the four featured species with all other *japonicus*-group species and *U. heterospinus* were conducted providing evidence for distinction and differential diagnosis. Unvouchered *in-situ* photographs of four goatfish specimens from the Central Philippines that resemble *U. elongatus* in caudal- and dorsal-fin colour patterns are presented. The need for further sampling and associated taxonomic investigations as prerequisites for appropriate assessment of ecological and conservation parameters such as diversity, distribution and rarity is emphasized in the discussion.

Key words: S Indonesia, S-central Vietnam, S Japan, caudal-fin oblique bars, species diversity and distribution

Introduction

Coastal waters of the Eastern Indian Ocean and tropical Western Pacific from India and Indonesia to S Japan are particularly rich in marine fish diversity (e.g., Carpenter & Springer 2005; Motomura *et al.* 2010; Allen & Erdmann 2012; Uiblein & White 2015; Motomura *et al.* 2017; Miller *et al.* 2018; Ho *et al.* 2019; Psomadakis *et al.* 2019). Still, a considerable portion of the biodiversity in this area (abbreviated in the following as “CEITPAS” for “coastal Eastern Indian Ocean and tropical Pacific waters of Asia”) remains to be discovered, requiring ongoing taxonomic efforts (e.g., Hoeksema 2007). This also applies to the goatfish family (Mullidae), of which 42 species belonging to the genera *Mulloidichthys* (n=4), *Parupeneus* (n=16) and *Upeneus* (n=22) are known from the CEITPAS area (Randall 2004; Uiblein 2011; Uiblein *et al.* 2018; Table 1). Twelve of these species have been described since 2010: *Mulloidichthys ayliffe* Uiblein, 2011, from E Sri Lanka, the Andaman Islands and, elsewhere, from South Africa to

Oman and the Seychelles, Western Indian Ocean, *Parupeneus inayatae* Uiblein & Fahmi, 2018 from Lombok, S Indonesia, and 10 species of *Upeneus* (Table 1).

Recently, along with the description of *Upeneus floros* Uiblein & Gouws, 2020 from South Africa and Mozambique, SW Indian Ocean, updated taxonomic accounts for the rather similar species *U. guttatus* Day, 1868 and *U. pori* Ben-Tuvia & Golani, 1989 were provided (Uiblein *et al.* 2020a). These three species belong to the *japonicus* group (Uiblein & Heemstra 2010) which is characterized by seven dorsal-fin spines and currently includes 14 of the 43 valid species of *Upeneus* (Uiblein *et al.* 2020a). During this earlier study 13 specimens from Lombok, S Indonesia and Nha Trang, S-central Vietnam which had been previously identified as *U. guttatus* (White *et al.* 2013; Uiblein *et al.* 2017a), turned out to deviate from all known *japonicus*-group species in the combination of several morphometric, meristic and colour characters. In addition, between the specimens from Lombok and Nha Trang differences in body structure and colour patterns were detected.

The present study examines the hypothesis that these 13 specimens represent two undescribed species. Comparisons with all *japonicus*-group species as well as other co-occurring congeners were conducted. Special attention was devoted to distinction from the most similar species including *U. itoui* Yamashita, Golani & Motomura, 2011 from S Japan and Taiwan. When examining a larger sample of *U. itoui* from the KAUM fish collection, we also studied a single specimen from Tanega-shima Island, S Japan which had previously been identified only to genus level (Tashiro *et al.* 2014) and turned out to represent a third undescribed species during the course of our study.

Three new species, *U. dimipavlov n. sp.*, *U. elongatus n. sp.* and *U. willwhite n. sp.* are described and an updated taxonomic account for *U. itoui* is provided. Detailed comparisons and differential diagnosis focus on the main differences between the four featured species and all *japonicus*-group species, considering in particular those which co-occur and/or are most similar. The co-occurring and rather similar *U. heterospinus* Uiblein & Pavlov, 2019 (Indonesia, Philippines and Singapore to Japan) of the so-called *margarethae* group (Uiblein *et al.* 2019) is also compared. The high diversity of the genus *Upeneus* and the need to further explore the CEITPAS area regarding distribution and abundance patterns of recently discovered species and the possible occurrence of yet undescribed species are discussed.

Material and methods

From 31 adult *Upeneus* specimens from Indonesia, Vietnam and Japan, 41 morphometric, 10 meristic and several colour characters were examined and analyzed with comparative data of 293 specimens (284 adults and 9 subadults < 65 mm SL) and fresh-colour photographs of the 14 *japonicus*-group species available from Uiblein *et al.* (2016, 2017a, 2020a). In addition, comparative data of 101 *Upeneus heterospinus* specimens with seven dorsal-fin spines available from Uiblein *et al.* (2019) were included. To avoid allometric effects, morphometric comparisons were restricted to data from adult specimens. Meristic counts did not show allometry and data of subadult fish were used in pectoral-fin and gill-raker counts (Uiblein *et al.* 2019, 2020a). For two species, *U. francisi* Randall & Guézé, 1992 and *U. pori*, published data from Randall & Guézé (1992) and Yamashita *et al.* (2011) were used to complete size and meristic-character information.

Methods of measuring, counting and colour pattern determination follow Uiblein *et al.* (2020a). As in this former study, important diagnostic characters were selected based on main differences among the most similar species. Because of considerable differences in the number of total gill rakers among *japonicus*-group species, this character was given high weight by grouping species with overlapping gill-raker counts in comparisons (see also Uiblein *et al.* 2017a). The terms “mostly” or “slightly” were used for differences in characters that show overlap and hence may require combination with other characters to achieve complete distinction (Uiblein *et al.* 2020a). In the account of *U. elongatus*, of which only a single specimen was available for study, meristic counts from left and right sides, respectively, were considered. To facilitate the comparisons, an overview table was compiled (Table 2), much improved from the former version published by Uiblein *et al.* (2020a) with additional characters and the three new species included. Additional tables showing all quantitative characters for all species were also prepared (Tables 3–5).

Institutional abbreviations follow Sabaj (2019). Other abbreviations are: CEITPAS = coastal Eastern Indian Ocean and tropical Pacific waters of Asia; EIO = Eastern Indian Ocean; HT = holotype; NRF-SAIAB = National Research Foundation - South African Institute for Aquatic Biodiversity, Makhanda, South Africa; PT = paratype; SL = standard length; WIO = Western Indian Ocean.

TABLE 1. Species of *Upeneus* known from the CEITPAS area before this study. Species of the *japonicus* group are emphasized in bold.

Species	Occurrence in the CEITPAS area	Occurrence elsewhere
<i>Upeneus asymmetricus</i> Lachner, 1954 ¹	Lombok, S Indonesia; Central Philippines	
<i>Upeneus farnis</i> Uiblein & Peristwady, 2017 ²	NE Sulawesi, N Indonesia	
<i>Upeneus guttatus</i> (Day, 1868) ³	E India to Japan	WIO; Australia to New Caledonia
<i>Upeneus heemstra</i> Uiblein & Gouws, 2014 ⁴	Chennai (Madras), SE India	WIO
<i>Upeneus heterospinus</i> Uiblein & Pavlov, 2019 ⁵	Lombok, S Indonesia; Central Philippines; South China Sea to S Japan	
<i>Upeneus itoui</i> Yamashita, Golani & Motomura, 2011 ^{6,7}	S Japan, Taiwan	
<i>Upeneus japonicus</i> (Houttuyn, 1782) ⁸	South China Sea to Japan and Peter the Great Bay, E Russia; Philippines	
<i>Upeneus lombok</i> Uiblein & White, 2015 ¹	Lombok, S Indonesia	
<i>Upeneus luzonius</i> Jordan & Seale, 1907 ⁹	Central and N Philippines	
<i>Upeneus margaretha</i> Uiblein & Heemstra, 2010 ⁵	E India to W Thailand	WIO; NW and N Australia to inner Gulf of Carpentaria
<i>Upeneus moluccensis</i> Bleeker, 1855 ⁹	E India to S Japan	WIO; Australia to New Caledonia; E Mediterranean ^a
<i>Upeneus nigromarginatus</i> Bos, 2014 ¹⁰	S and Central Philippines	
<i>Upeneus quadrilineatus</i> Cheng & Wang, 1963 ¹¹	Indonesia to S Japan	NE Australia
<i>Upeneus spottocaudalis</i> Uiblein & Gledhill, 2017 ²	S Indonesia	N to NE Australia
<i>Upeneus stenopsis</i> Uiblein & McGrouther, 2012 ¹²	Quezon, Central Philippines	
<i>Upeneus subrikttus</i> (Temminck & Schlegel, 1843) ¹²	W Indonesia to S Japan	WIO; Australia to New Caledonia and Fiji ^b
<i>Upeneus sulphureus</i> Cuvier, 1829 ⁹	E India to S Japan	Mauritius and Persian Gulf; WIO; Australia to Papua New Guinea
<i>Upeneus sundaeicus</i> (Bleeker, 1855) ^{9,13}	Myanmar to Hainan, S China; Indonesia; Philippines	S Iran to W Sri Lanka, WIO
<i>Upeneus supravittatus</i> Uiblein & Heemstra, 2010 ^{14,15}	E India to Myanmar	Pinda Bank, N Mozambique and Rodrigues to Laccadives, WIO; Cocos Islands, SE Indian Ocean; Biak ^c , E Indonesia; Samoa and Palau to Hawaii, French Polynesia and Cook Islands
<i>Upeneus taeniopterus</i> Cuvier, 1829 ¹⁶	E Sri Lanka; Macao, S China; Ryukyu Islands, S Japan	Australia to New Caledonia, Papua New Guinea and Palau
<i>Upeneus tragula</i> Richardson, 1846 ⁴	Andaman Islands, E India to Japan	WIO; Australia to Hawaii and Marquesas
<i>Upeneus vittatus</i> (Forsskål, 1775) ^{11,14}	E India to Japan	

¹ Uiblein & White 2015; ² Uiblein *et al.* 2017a; ³ Uiblein *et al.* 2020a; ⁴ Uiblein & Gouws 2014; ⁵ Uiblein & Koeda 2019; ⁶ Yamashita *et al.* 2011; ⁷ Tashiro & Koeda 2019; ⁸ Uiblein & Gledhill 2015; ⁹ Uiblein & Heemstra 2010; ¹⁰ Bos 2014; ¹¹ Randall 2001; ¹² Uiblein & McGrouther 2012; ¹³ Uiblein & Gouws 1998; ¹⁴ Uiblein *et al.* 1998; ¹⁵ Psomadakis *et al.* 2016; ¹⁶ Uiblein *et al.* 2019; ^a as Lessepsian migrant; ^b *U. sanctaehelena* is regarded as a junior synonym with doubtful type locality (Saint Helena Island, South Atlantic, see also Edwards & Glass 1987); ^c Papua province, Oceania

TABLE 2. (A) Number of specimens, SL, meristic and colour characters and (B) morphometric characters as ratios of SL for the four features species, all other *japonicus*-group species and *U. heterospinus* (*margarithae*-species group).

(A)	n adults (+ subadults)	Maximum known size (SL, mm)	Dorsal-fin spines	Pectoral- fin rays	Total gill rakers	Body stripe absent/weak/ distinctive *	Barbel colour *	Oblique bars on lower caudal-fin lobe *	Lower caudal-fin lobe bars position (form or size) *	Lower caudal-fin lobe bars in preserved fish			
<i>U. dimidipinnis</i> n. sp.	11	134	7	14–15	22–25	absent	rose whitish or white	present	at lobe margins (short)	well retained or some traces			
<i>U. elongatus</i> n. sp.	1	89	7	13	27–28	weak	white	present	partly crossing lobe (blotches)	well retained			
<i>U. itoui</i>	20	144 ^c	7	13–14	22–25	distinctive	white	present	partly crossing lobe	well retained or some traces			
<i>U. willwhitei</i> n. sp.	2	92	7	14	21–23	distinctive	reddish white	present	at lobe margins (short)	well retained			
<i>U. asymmericus</i>	8	100	7	12–14	26–28	absent or weak	white or pale reddish	present	crossing lobe	well retained			
<i>U. australiae</i>	45 (+4)	128	7	13–15	22–25 ^a	distinctive	white	present	crossing lobe	well retained			
<i>U. farnis</i>	14	141	7	15–16	28–31	weak	pale-grey	mostly absent	at ventral lobe margin (short)	absent or some traces			
<i>U. floros</i>	17	144	7	13–15	23–25	absent or weak	white	present	at lobe margins (short)	absent or some traces			
<i>U. francisi</i>	6 (+4)	88 ^b	7	13–15 ^{a,b}	29–33 ^b	absent	white	present	at lobe margins (short)	absent or some traces			
<i>U. guttatus</i>	74	159	7	12–14	22–26	absent or weak	mostly yellow (rarely white)	often present	at ventral lobe margin (variable)	mostly absent			
<i>U. japonicus</i>	37	123	7	13–15	24–28	absent	yellow	absent	-	absent			
<i>U. lombok</i>	2 (+1)	94	7	14–15	27–29	absent ^a	white ^a	absent ^a	-	absent			
<i>U. pori</i>	32	136 ^c	7	13–15	25–29	absent, weak or distinctive	white or creamy white	present	at lobe margins (short)	well retained or some traces			
<i>U. satiab</i>	6	102	7	14–15	29	weak	white	absent	-	absent			
<i>U. seychellensis</i>	3	115	7	14–15	25–26	absent	pale reddish	absent	-	absent			
<i>U. spottocaudalis</i>	17	103	7	12–13	21–23	absent	yellow	present	mostly at middle of lobe (spots)	well retained or some traces			
<i>U. torres</i>	20	103	7	13–15	22–25	absent	yellow	absent	-	absent			
<i>U. heterospinus</i>	101	152	7 or 8	13–15	21–24	distinctive	yellow	present	crossing lobe	well retained or some traces			
(B)	Body depth at dorsal-fin origin	Body depth at anal-fin origin	Caudal-pe- nuncle depth	Caudal-pe- nuncle width	Maximum head depth	Head through head depth	Head eye	Snout length	Orbit length	Pectoral- fin length	First dorsal-fin height	Second dorsal-fin height	
<i>U. dimidipinnis</i> n. sp.	23–25	20–22	9.7–10	4.8–5.4	19–20	16–17	28–30	11–13	5.7–6.8	11–12	19–21	27–29	16–18
<i>U. elongatus</i> n. sp.	21	18	8.3	3.3	18	14	27	10	6.7	11	17	29	16–20
<i>U. itoui</i>	21–24	19–22	9.0–10	3.9–4.6	17–19	13–15	27–29	10–12	5.4–6.4	9.8–11	17–18	27–30	15–17
<i>U. willwhitei</i> n. sp.	23–24	20–21	9.6–9.9	4.2–4.3	20–21	16	29	10–11	7.1–7.5	12	20	28–30	16–17
<i>U. asymmericus</i>	22–24	20–22	8.5–9.9	3.7–5.0	19–20	15–16	26–29	9.9–11	5.7–7.7	8.7–11	17–19	27–30	15–16
<i>U. australiae</i>	23–27	20–23	9.9–12	3.2–5.1	20–22	15–18	27–30	9.9–13	6.0–8.0	9.3–12	16–20	27–32	15–18
<i>U. farnis</i>	23–25	20–22	8.8–9.9	3.4–4.4	19–21	15–17	28–31	9.9–12	5.6–7.2	9.6–12	18–23	27–29	12–15
<i>U. floros</i>	22–25	19–22	8.7–9.8	3.7–4.8	19–21	15–17	29–32	11–13	5.9–7.7	11–13	18–20	26–29	15–18
<i>U. francisi</i>	23–25	20–22	9.9–10	3.2–4.1	20–22	15–16	28–30	10–11	6.9–7.9	9.9–11	17–19	28–30	15–17
<i>U. pori</i>	21–26	18–22	9.3–11	3.2–5.1	18–22	15–18	26–29	9.4–12	5.9–8.5	9.5–12	16–20	27–31	15–19
<i>U. guttatus</i>	21–25	18–22	8.0–11	3.1–4.8	18–21	15–17	27–31	10–12	6.1–8.2	9.7–12	18–23	25–29	15–19
<i>U. japonicus</i>	21–23	19	9.2–9.3	3.8–4.2	19–20	14–15	28–30	9.2–9.6	7.5–7.9	9.4–10	19–20	28–29	12–13
<i>U. lombok</i>	22–25	18–22	8.8–10	3.5–4.6	18–21	15–16	26–30	9.5–12	5.8–7.8	9.9–12	16–19	27–29	14–17
<i>U. pori</i>	21–24	17–19	8.7–9.2	3.0–3.9	18–20	15–17	29–30	10–11	6.8–7.5	9.5–12	19–22	27–29	14–16
<i>U. satiab</i>	20–22	18–19	9.2–10	3.6–4.1	18–20	15–17	27–30	11–12	6.0–6.5	11	17–22	28–30	14–15
<i>U. seychellensis</i>	22–25	19–22	8.6–10	2.9–4.3	19–22	15–18	30–32	9.7–12	6.9–8.2	10–13	19–22	28–32	16–19
<i>U. spottocaudalis</i>	23–27	18–22	8.6–11	3.5–4.5	19–23	15–19	28–31	9.8–12	7.1–8.9	10–12	23–27	27–30	16–20
<i>U. torres</i>	22–26	18–22	9.2–11	3.5–5.0	19–23	15–18	27–31	9.7–13	5.9–8.3	9.4–13	16–20	27–32	15–19
<i>U. heterospinus</i>													19–23

* Fresh fish; ^a subadults considered; ^{b, c} data from Randall & Guézé (1992)^b and Yamashita *et al.* (2011)^c considered

Taxonomy

Genus *Upeneus* Cuvier 1829

Diagnosis. Dorsal fins VII or VIII + 9; pectoral fins 12–17; principal caudal-fin rays 7 + 8 (median 13 branched); gill rakers 4–9 + 13–24 = 18–33; lateral-line scales 28–39; lateral line complete; small scales present basally on second dorsal, anal and/or caudal fins; small teeth present on vomer and palatines; teeth on jaws multiserial and villiform; body oblong, slightly compressed or nearly rounded; barbels 15–27% SL; snout length 9.1–14% SL, subequal to or slightly shorter than postorbital length (9.7–15% SL); body frequently with one to several longitudinal stripes, varying from yellow to red, brown or black in life; oblique bars often present on caudal-fin lobes, usually retained in preservative when darkly pigmented, and their number, colour and form of diagnostic importance.

Remarks. Forty-six species, including the three new species, distributed in all major oceans. Two Indo-Pacific species in the Mediterranean as Lessepsian migrants. Many species targeted by fisheries or landed as bycatch and can be found in fish markets, having moderate to high local economic value. Many different fishing methods are used including angling, beach seine, gillnetting, trapping and trawling. Most species occur in coastal waters to less than 100 m depth, maximum depth reached is 600 m. Maximum size range among species is about 89 to 300 mm SL.

Upeneus dimipavlov n. sp.

Pavlov's Goatfish

(Figures 1A, 2–6; Tables 2, 3)

Upeneus guttatus Day, 1868, in part: Uiblein *et al.* 2017a

Material examined. Holotype. VNMN-I 2056 (formerly HIFIRE F 58334), 120 mm SL, South China Sea, S-central Vietnam, Khan Hoa Province, Nha Trang, Bai Tre Bay, N of Hon Tre Island, 12°13.35' N, 109°18.50' E, obtained from hookah divers, ca. 15 m depth, Dimitri A. Pavlov, 19-01-2012 (photo of fresh HT, Figure 1A).

Paratypes ($n = 10$, 111–134 mm SL). South China Sea, S-central Vietnam, Khan Hoa Province, Nha Trang, Xom Moi Market: HIFIRE F 58183, 129 mm SL; HIFIRE F 58184, 117 mm SL; NHMO J7223 (formerly HIFIRE F 58185), 124 mm SL; MNHN 2020-0474 (formerly HIFIRE F 58186), 122 mm SL; NMMBP 34705 (formerly HIFIRE F 58187), 111 mm SL; KAUM-I. 146834 (formerly HIFIRE F 58188), 123 mm SL; AMS I.49516-001 (formerly HIFIRE F 58189), 122 mm SL; CAS-ICH 247243 (formerly HIFIRE F 58190), 122 mm SL; Nha Trang fish market: VNMN-I 2057 (formerly HIFIRE F 58174), 134 mm SL; VNMN-I 2058 (formerly HIFIRE F 58177), 128 mm SL.

Diagnosis. Dorsal fins VII + 9; pectoral fins 14–15; gill rakers 6–7 + 16–18 = 22–25; body nearly rounded and moderately elongate; measurements as % SL: body depth at first dorsal-fin origin 23–25; body depth at anal-fin origin 20–22; caudal-peduncle depth 9.7–10; caudal-peduncle width 4.8–5.4; maximum head depth 19–20; head depth through eye 16–17; head length 28–30; snout length 11–13; orbit length 5.7–6.8; upper-jaw length 11–12; barbel length 19–21; caudal-fin length 27–29; anal-fin height 16–18; pelvic-fin length 20–22; pectoral-fin length 18–20; first dorsal-fin height 19–21; dorsal-fin spines proportionally decreasing in height; second dorsal-fin height 16–18; total oblique bars on caudal fin 12–14, upper caudal-fin lobe with 5–6 red mostly straight bars; lower caudal-fin lobe with 7–8 short red bars along ventral margin which connect dorsally to a red stripe, the latter slightly wider than orbit diameter, and with about 3 short red or reddish-grey bars along dorsal margin of fin lobe that do not correspond with bars on ventral-lobe margin; caudal-fin colour patterns partly or completely lost after preservation; dorsal fins in fresh fish with 3–4 thin red or brown stripes, may be weakly retained in preservative; barbels rose whitish or white when fresh; body colour in freshly deceased specimens dorsally pale reddish orange, ventral half creamy white, sometimes with red patches or blotches, ventral margin pale creamy white; no conspicuous mid-lateral body stripe; head dorsally pale red and silvery white ventrally, with red patches below and behind eyes; body and head dorsally pale brown or brown and ventrally white when preserved.

Description. Measurements in % SL and counts are given in Table 3; morphometric data as ratios of SL for holotype, data for paratypes in brackets: body nearly rounded, rather robust and moderately elongate, body depth

at first dorsal-fin origin 4.2 [4.1–4.4]; body depth at anal-fin origin 4.9 [4.6–5.0]; head depth through eye 6.3 [6.0–6.4]; head length 3.4 [3.4–3.5], larger than maximum body depth and subequal to caudal-fin length (3.6 [3.4–3.8]); first dorsal-fin height 5.0 [4.8–5.4], subequal to barbel length (5.0 [4.7–5.4]) and larger than second dorsal-fin height (6.2 [5.7–6.2]); pelvic-fin length 4.9 [4.5–5.0], larger than pectoral-fin length (5.1 [5.1–5.5]) and subequal to body depth at anal-fin origin; caudal-peduncle depth 10 [9.8–10], clearly larger than orbit length (15 [15–17]); and caudal-peduncle width 19 [19–21], mostly larger than pectoral-fin width (22 [21–23]).

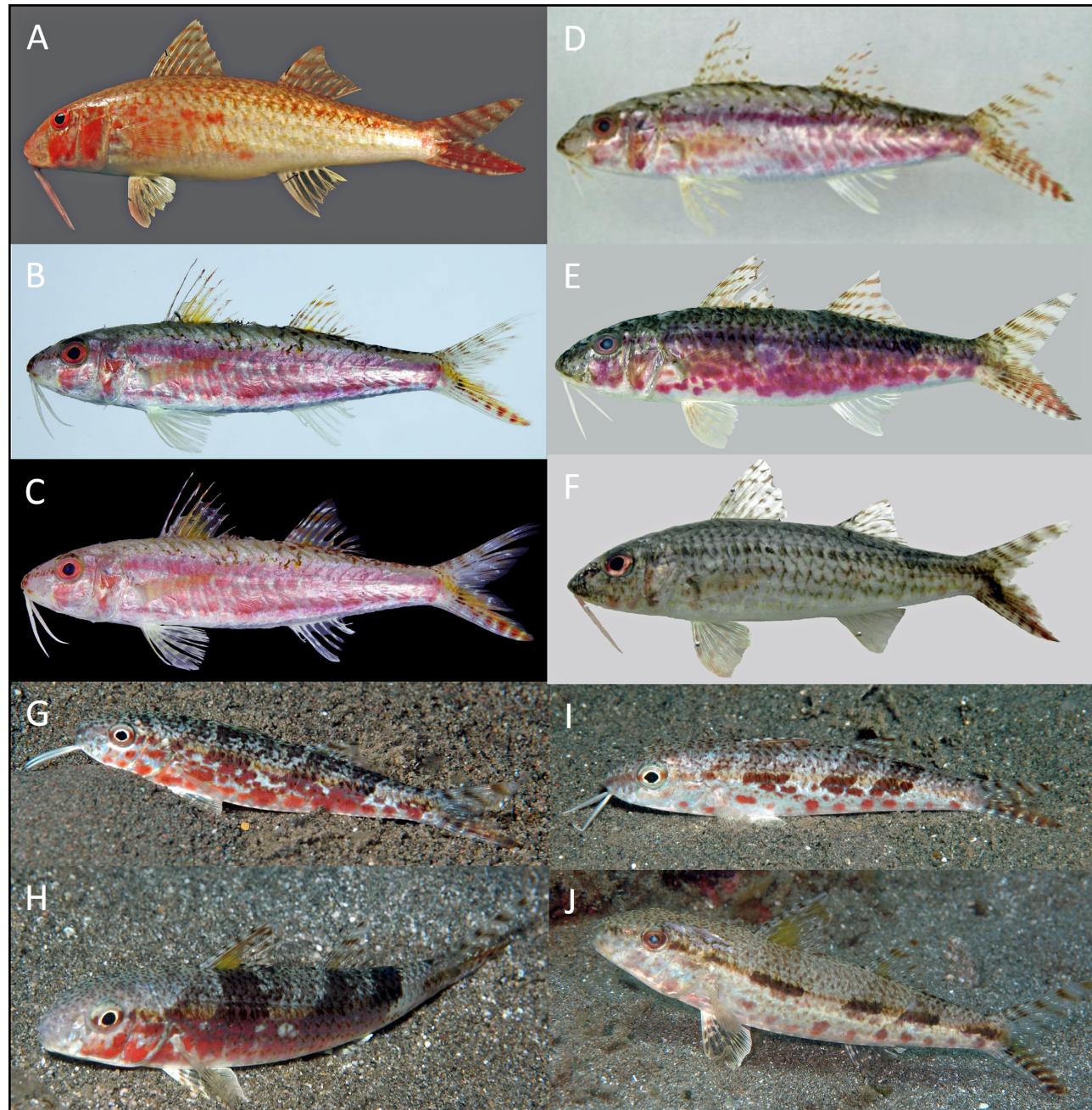


FIGURE 1. A: *Upeneus dimipavlov* n. sp., VNMN-I 2056, HT, 120 mm SL, N of Hon Tre Island, Nha Trang, S-central Vietnam (D.A. Pavlov); B, C: *Upeneus elongatus* n. sp., KAUM-I. 58746, HT, 89 mm SL, Tanega-shima Island, S Japan (H. Motomura); D, E: *Upeneus itoui*, Kagoshima Prefecture, S Japan; D: KAUM-I. 13591, PT, 104 mm SL; E: KAUM-I. 13595, PT, 118 mm SL; F: *U. willwhite* n. sp., CSIRO 7217-07, HT, 90 mm SL, Lombok, S Indonesia (W.T. White); G–J: *U. cf. elongatus*, Central Philippines, Visayas, adults, unvouchered; G: Panay; H: Leyte; I, J: Negros (P. & G. Poppe – <https://poppe-images.com>).

Colour. Fresh HT (Figure 1A). Body pale red orange above lateral line and creamy white below, ventral side pale creamy white; several red spots and blotches from pelvic-fin base and behind opercle at eye level to level of second dorsal-fin origin; lateral line indistinct, no mid-lateral body stripe; dorsal margin of head from snout tip to

above eye pale red; silvery-pale beige mouth region followed by a large bright-red patch below eye and another one posteriorly on bony opercle with three bright-red blotches just above; iris bright red; barbels whitish rose; caudal fin with five oblique, mostly straight red bars of approximately half pupil width on upper lobe, with white hyaline interspaces between bars increasing in width from being narrower than bar width proximally to double-bar width distally; tip of upper caudal-fin lobe white hyaline; lower caudal-fin lobe with seven very short red bars along ventral margin covering up to four ventral-most fin rays; creamy-hyaline interspaces between bars of less than bar width proximally with increasing width distally, continued as a pale creamy stripe behind distal-most seventh bar, not reaching lobe tip; broad red stripe along middle of lower caudal-fin lobe slightly wider than orbit diameter, stripe extending from caudal-fin base to lower lobe tip; four red bars with dark-grey tips dorsally on lower caudal-fin lobe along lobe margin being slightly wider than bars on ventral side of lobe and with white-hyaline interspaces of similar width as bars, the interspaces connecting to red stripe; first dorsal fin with hyaline-red spots on and around spines forming a dotted pattern of four horizontal stripes; first dorsal-fin tip weakly pale-whitish pigmented; second dorsal fin whitish hyaline with four red horizontal stripes, one at fin base and one at fin tip; pectoral, pelvic and anal fins hyaline creamy; pelvic fins with pale-red pigmentation on spine tip and anterior four rays.

Preserved HT. Dark brown dorsally from mouth and below eye to pectoral-fin origin and distal end of lateral line near caudal-fin base; creamy white ventrally from cheeks and below pelvic-fin origin to ventral half of caudal-fin base; caudal-fin bars and stripe and dorsal-fin pigmentation only faintly retained; other fins and barbels pale.

Etymology. The name “*dimipavlov*” is used as a composed noun in apposition. It honours the ichthyologist Dr. Dimitri Alexandrovich “Dimi” Pavlov, Lomonosov University, Moscow, Russia, for collecting, photographing and donating mullid specimens from Vietnam (including the holotype of *Upeneus dimipavlov*) for taxonomic research.

Distribution, habitat, size. Currently only known from Nha Trang, S-central Vietnam; possibly occurs on sandy bottoms near reefs; depth ca. 15 m; attains 134 mm SL.

Remarks. The nearly rounded, robust body is a typical characteristic of this species and rather unique among *japonicus*-group species. The photograph of the HT (Figure 1A) is the only high-quality colour documentation of fresh fish available so far. In photos of several PT’s made during or after collection at fish markets the body colour is less intense and in two specimens barbel colour is white instead of whitish rose. After specimens were kept in a refrigerator over several days or thawed, the body and head became almost entirely red which is most likely an artefact and does not reflect natural colouration. This species has been encountered at fish markets near the type locality, indicating local commercial value.

Upeneus elongatus n. sp.

Elongate Goatfish

Iwanaga-himeji (new standard Japanese name)

(Figures 1B, C, 2; Tables 2, 3)

Upeneus sp.: Tashiro *et al.* 2014

Material examined. Holotype. KAUM-I. 58746, 89 mm SL, Philippine Sea, S Japan, Kagoshima Prefecture, Osumi Islands, Tanega-shima Island, Kumage-gun, Nakatane, off Kumano, 30°28.13' N, 130°58.32' E, 25 m, set net, Mayumi Takayama, 20-01-2012 (photo of fresh holotype, Figure 1B, C)

Unvouchered *In situ* photos of *Upeneus* cf. *elongatus*, Central Philippines, Visayas (most probably all adults): Panay, Caridad, Culasi, Antique, 11°26.89' N, 122°03.55' E, 7 m depth (Figure 1G); Leyte, Albuera, 10°53.45' N, 124°42.36' E, 20 m depth (Figure 1H); Negros, Bonbonon, Siaton, 9°03.53' N, 123°05.97' E, 10 m depth (Figure 1I); same locality, 7 m depth (Figure 1J).

Diagnosis. Dorsal fins VII + 9; pectoral fins 13; gill rakers 8 + 19–20 = 27–28; body elongate and laterally compressed; measurements as % SL: depth at first dorsal-fin origin 21; body depth at anal-fin origin 18; caudal-peduncle depth 8.3; caudal-peduncle width 3.3; maximum head depth 18; head depth through eye 14; head length 27; snout length 10; orbit length 6.7; upper-jaw length 11; barbel length 17; caudal-fin length 29; anal-fin height 16; pelvic-fin length 23; pectoral-fin length 21; first dorsal-fin height 20, dorsal-fin spines proportionally decreasing in height; second dorsal-fin height 15; total oblique bars on caudal fin 12, upper caudal-fin lobe with 5 red bars; lower caudal-fin lobe with 7 red-brown blotch-like bars which are most conspicuous along middle of lobe and dorsally

with a faint yellowish-beige stripe of less than orbit diameter in width that connects to caudal-fin base; bars mostly retained after preservation; first dorsal fin with large yellowish-beige triangular patch close to fin base covering central part of ventral half of fin; a similarly coloured, but much smaller patch at middle of second dorsal-fin base; barbels white when fresh; body and head colour in freshly deceased fish pale greyish dorsally and mostly red below eye level except for pale-grey snout region; ventral margin of head and body silvery white; a vermillion mid-lateral body stripe from snout tip through eye to middle of caudal-fin base; body and head pale brown, mid-body darkened when preserved.

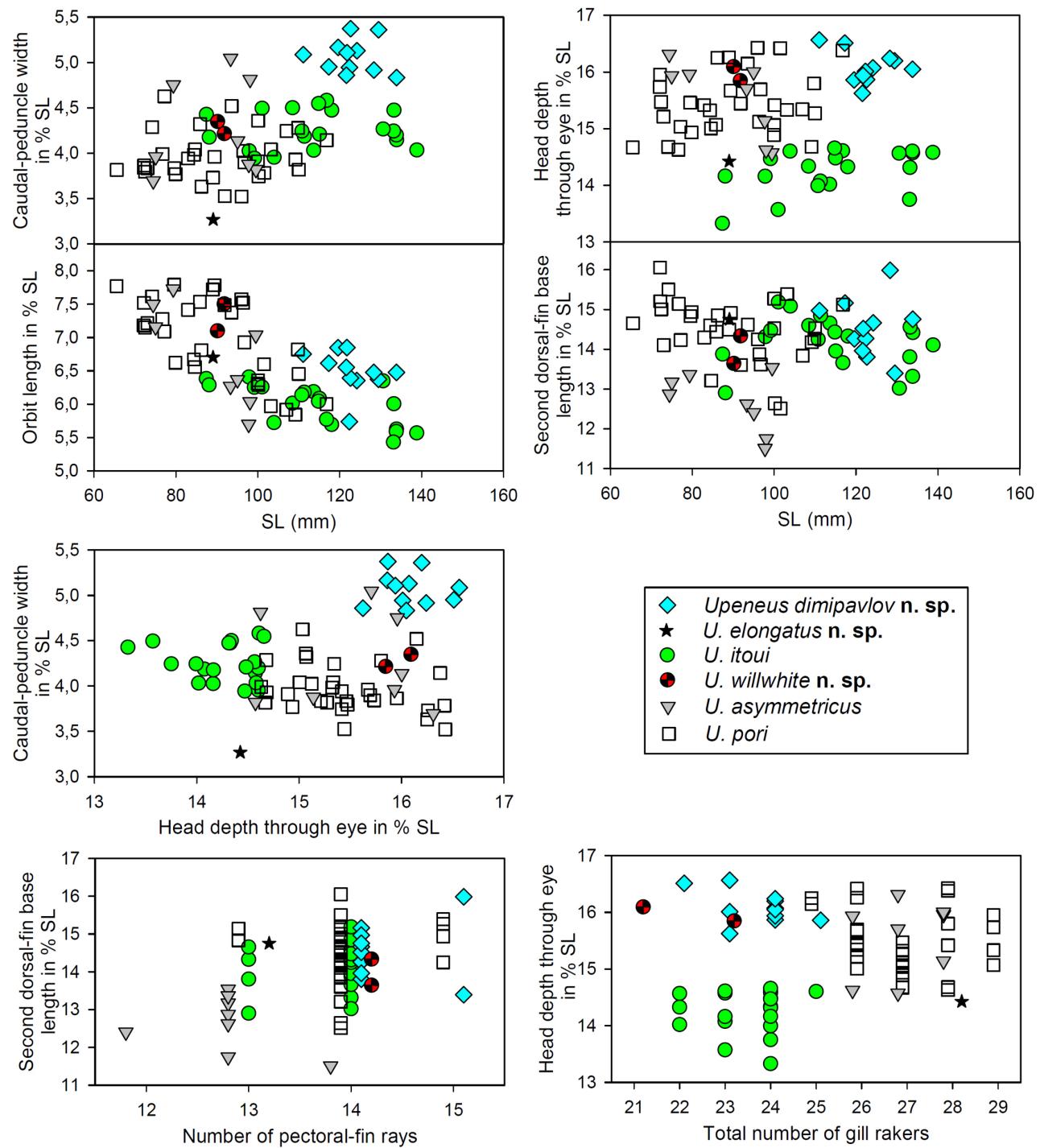


FIGURE 2. Relationship among two meristic and five morphometric characters in the four featured species of *Upeneus* and *U. asymmetricus* and *U. pori*.

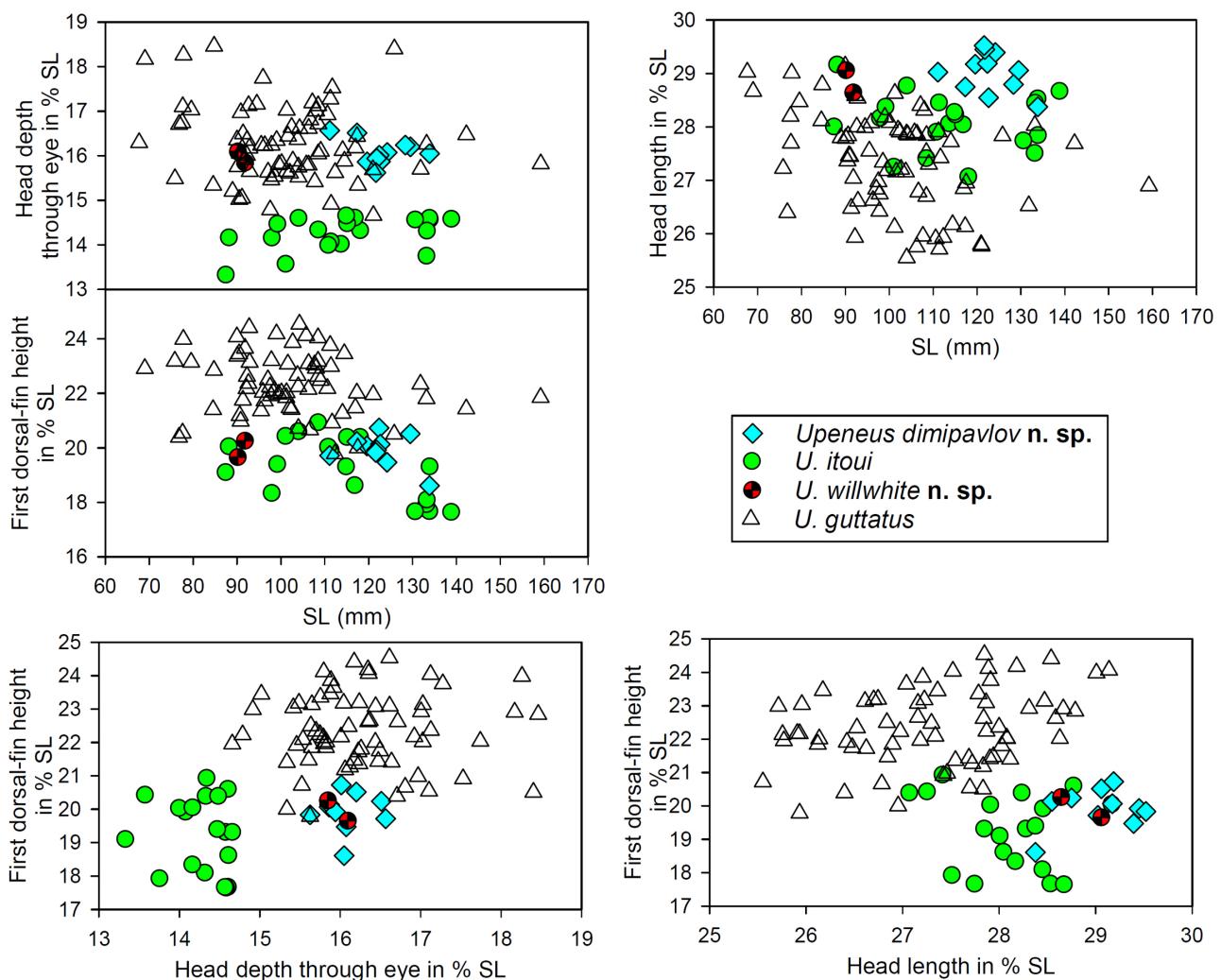


FIGURE 3. Relationship among four morphometric characters in three featured species of *Upeneus* and *U. guttatus*.

Description. Measurements in % SL and counts are given in Table 3; morphometric data as ratios of SL for holotype: body elongate and laterally compressed, body depth at first dorsal-fin origin 4.9; body depth at anal-fin origin 5.5; head depth through eye 6.9; head length 3.7, much larger than maximum body depth and subequal to caudal-fin length (3.5); first dorsal-fin height 4.9, larger than barbel length (6.0) and second dorsal-fin height (6.6); pelvic-fin length 4.4, larger than pectoral-fin length (4.8) and body depth at first dorsal-fin origin; caudal-peduncle depth 12, distinctly larger than orbit length (15); and caudal-peduncle width 31, much smaller than pectoral-fin width (23).

Colour. Fresh HT (Figure 1B, C). Body with all scales missing, pale greyish dorsally above eye level with tiny dark-brown dots scattered along dorsal margin from below second dorsal fin to caudal-fin base; also, with a few tiny, similar-coloured dots further ventrally between first dorsal-fin origin and middle of second dorsal fin base; broad vermillion stripe of pupil diameter from behind eye to middle of caudal-fin base a; series of about 20 oblique red bands separated by thin silvery lines ventrally of stripe behind pectoral-fin base; few red blotches along ventral margin of posterior half of body partly overlapping with the oblique bands and white-silvery ventral side of body; head pale grey anterior to eye, with a weak red stripe from snout to eye of about half pupil width, stripe continues behind eye as mid-lateral body stripe; cheek below eye red and opercle region silvery white with red blotches; iris red; barbels white; caudal fin with five oblique, mostly straight brown bars of about half pupil width on upper lobe, with white hyaline interspaces between bars increasing in width from being narrower than bars proximally to more than double-bar width distally; tip of upper caudal-fin lobe white hyaline; lower caudal-fin lobe with seven red-brown blotch-like bars which are most conspicuous along middle of lobe becoming mostly hyaline towards lobe margins, with narrow hyaline-white interspaces; the two proximal bars only very weakly indicated by fine streaks

on two ventral-most fin rays fusing dorsally into a single dark brown bar, followed distally by a weakly indicated red spot composed by three short streaks on two adjacent fin rays along middle of lobe; four more conspicuous red spots further distally, two as wide as pupil, positioned mainly along middle of fin lobe and tip; dorsal part of lobe with a yellowish-beige stripe of less than orbit diameter, extending from central caudal-fin base to tip of lower caudal-fin lobe, covering nearly entire lobe distally and surrounding the two distal-most red blotches; first dorsal fin with a triangle-shaped patch of yellowish-beige skin, of about snout length in its maximum extension, patch connecting fin base and second to sixth spine, covering central part of ventral half of fin, except for the first spine; first dorsal-fin spine with four or five weakly indicated brown dots, spine tip unpigmented; second to third spine with brown pigmentation close to tip (second spine however broken), spines otherwise pale; second dorsal fin with four weakly indicated pale brown stripes and a yellowish-beige patch, similarly coloured as patch on first dorsal fin but much smaller, at middle of fin base between fourth and fifth spine; pectoral, pelvic and anal fins hyaline whitish, pelvic fins pale yellowish white at base.

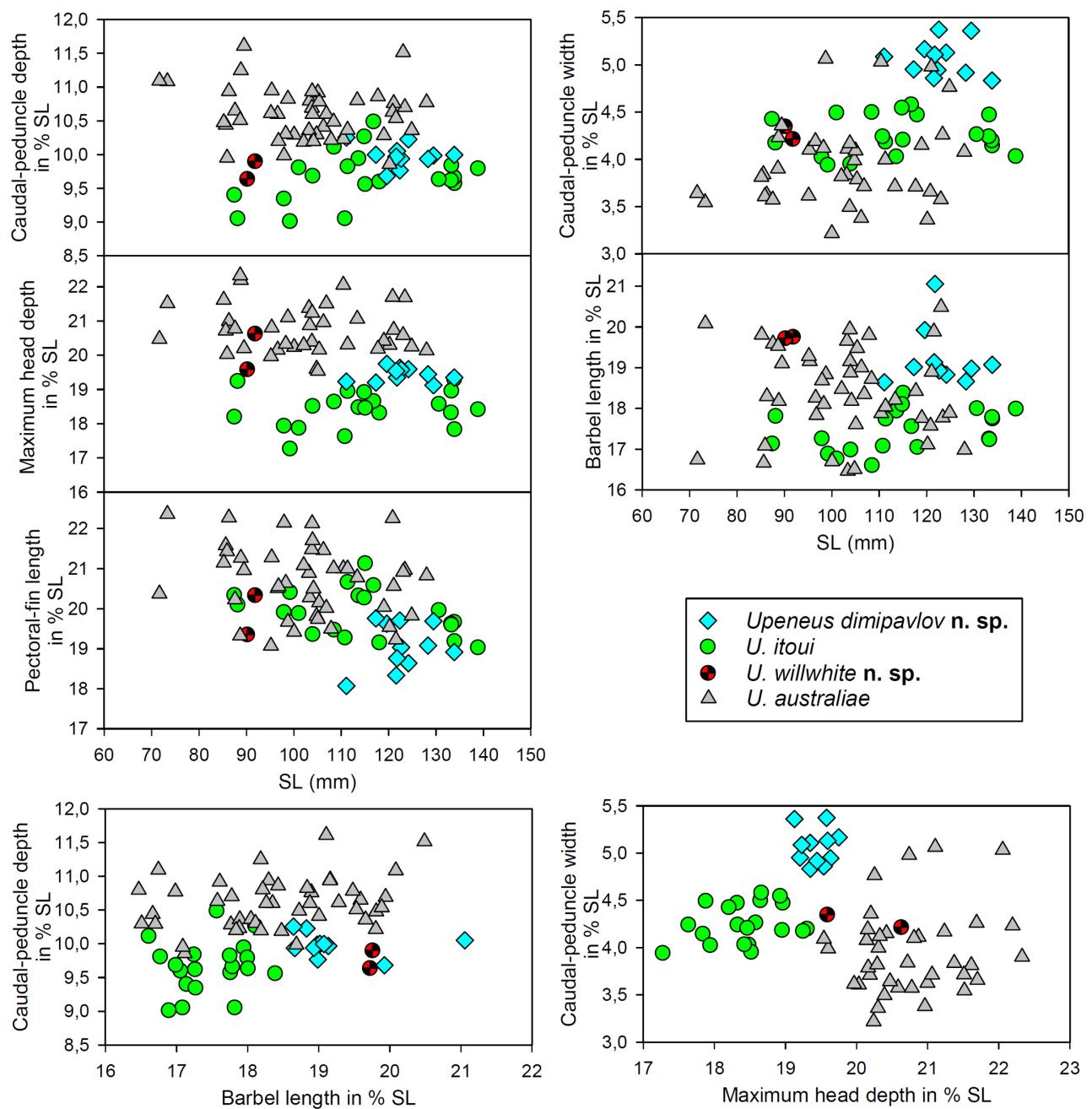


FIGURE 4. Relationship among six morphometric characters in three featured species of *Upeneus* and *U. australiae*.

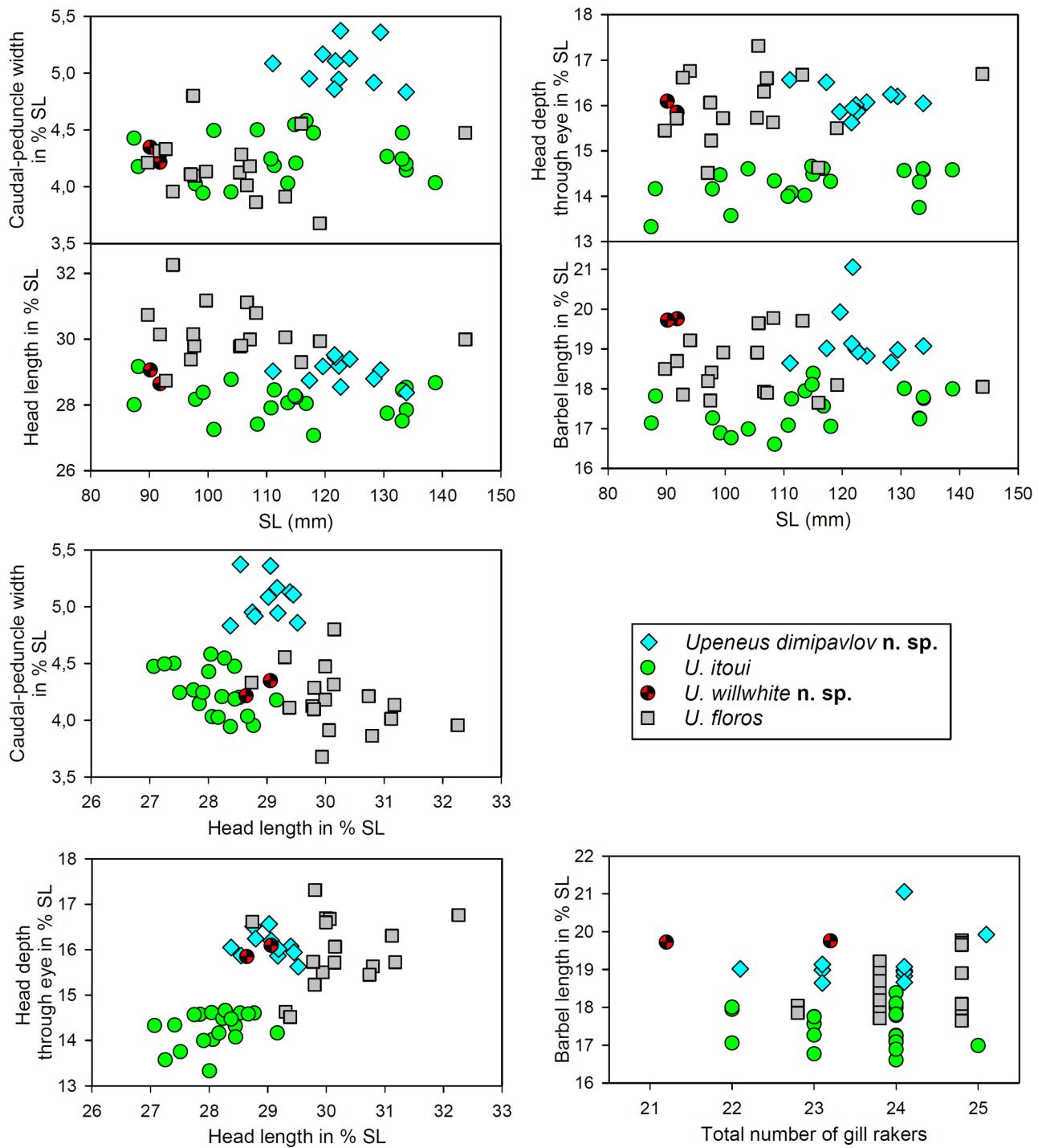


FIGURE 5. Relationship among one meristic and five morphometric characters in three featured species of *Upeneus* and *U. floros*.

Preserved HT. Head and body mostly pale brown, head in front of eyes, belly and underside of body pale beige; a brownish mid-lateral band wider than orbit diameter along body from behind opercle to caudal-fin base, becoming thinner behind second dorsal-fin base and then widening again close to caudal-fin base; tiny scattered dark-brown dots along dorsal body margin from below second dorsal fin to caudal-fin base and, just above dark mid-body band between dorsal fins; lower half of opercle silvery white; bar pigmentation on caudal fin mostly retained; stripe on lower caudal-fin lobe lost as well as most of dorsal-fin pigmentation except for a few traces distally on first dorsal fin and at mid and further distally on second dorsal fin; other fins and barbels pale.

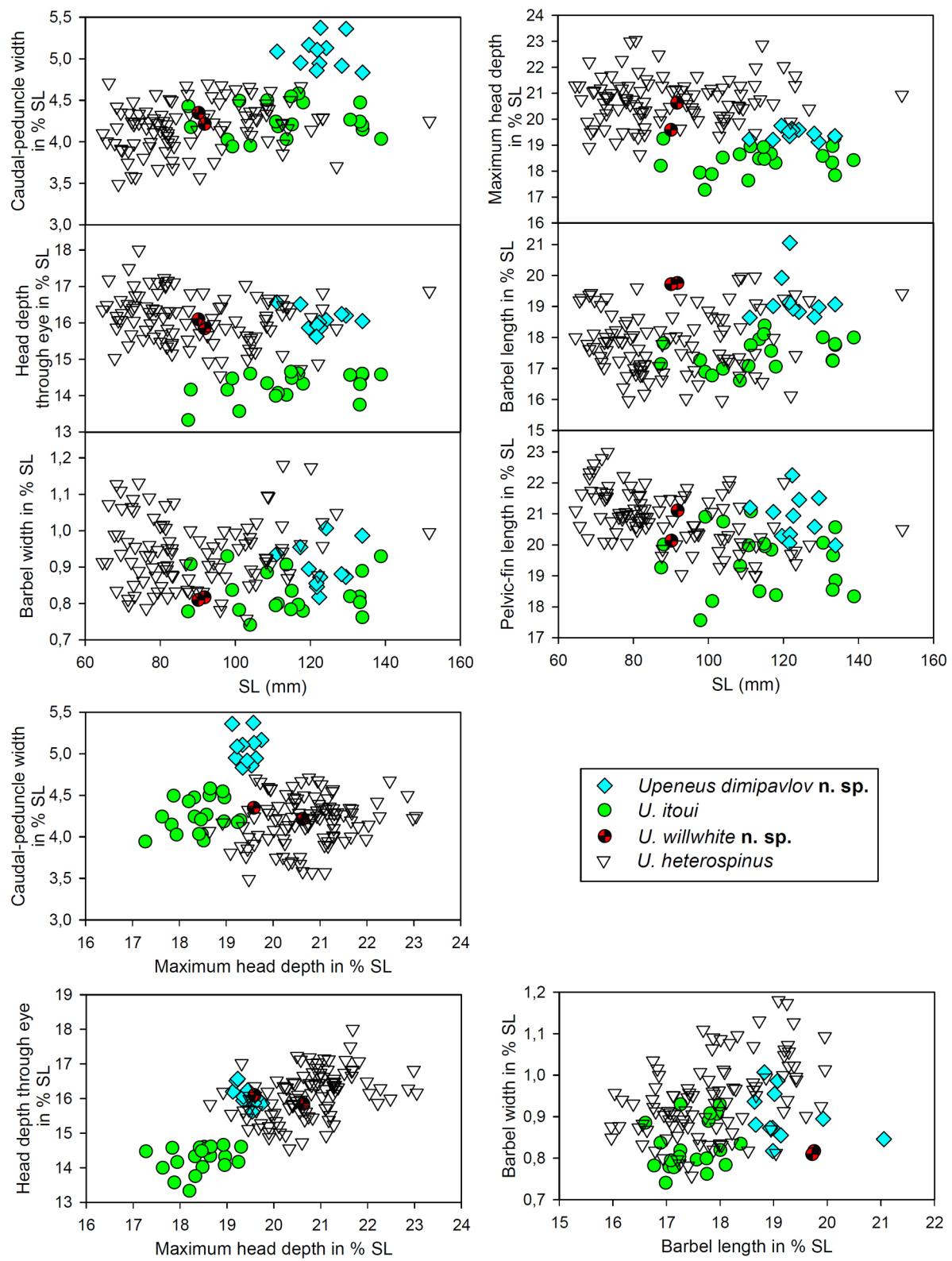


FIGURE 6. Relationship among seven morphometric characters in three featured species of *Upeneus* and *U. heterospinus*.

Etymology. The name “*elongatus*” refers to the elongate, very shallow body and head of this species. The standard Japanese name Iwanaga-himeji has two meanings: (1) “elongate goatfish”; (2) “goatfish of goddess Iwanaga”, sister of the myth goddess Sakuya, whose grandchild is considered to be the first Emperor of Japan. Accordingly, the standard Japanese name for the rather similar *U. itoui* is Sakuya-himeji.

Distribution, habitat, size. Known only from a single locality in S Japan, Tangea-shima Island, Kagoshima Prefecture; occurs on shallow sandy bottoms (25 m depth); attains at least 89 mm SL. This species may also occur in the central Philippines (see also Remarks below).

Remarks. *Upeneus elongatus* most likely also occurs in the Philippines as indicated by unvouchered *in situ* photos of shallow-bodied goatfish specimens with very similar colour patterns on caudal and dorsal fins (Figure 1G–H). However, the body colour in those specimens differs considerably from the fresh HT from S Japan, which may be due to the absence of scales in the HT. Until preserved specimens with scales intact associated with colour photographs of fish in fresh condition become available for comparative studies, we refer to this form as *U. cf. elongatus*.

***Upeneus itoui* Yamashita, Golani & Motomura, 2011**

Itou's Goatfish

Sakuya-himeji (standard Japanese name)

(Figures 1D, E, 2–6; Tables 1–3)

Upeneus itoui Yamashita, Golani & Motomura, 2011: Uiblein & Lisher 2013; Tashiro *et al.* 2014; Uiblein *et al.* 2017a, 2020a.

Material examined. *Paratypes* ($n = 6$, 87–134 mm SL). S Japan, Kagoshima Prefecture: KAUM-I. 10384, 87 mm SL, Minamisatsuma, Kasasa, Kataura, off E of Sakinoyama, $31^{\circ}25.44' N$, $130^{\circ}11.49' E$, 27 m depth, set net; KAUM-I. 13595, 118 mm SL, same sampling data (photo of fresh PT, Figure 1 E); KAUM-I. 13591, 104 mm SL, Minamisatsuma, Kasasa, NE of Matsu-shima Island, $31^{\circ}25.06' N$, $130^{\circ}12.32' E$, 20 m depth, set net (photo of fresh PT, Figure 1D); KAUM-I. 13594, 108 mm SL, Minamisatsuma, Kasasa, Kataura, off Kouzaki-yama, $31^{\circ}26.00' N$, $130^{\circ}10.05' E$, 36 m depth, set net; KAUM-I. 13715, 134 mm SL, Ibusuki, Kaimonkawajiri, 1 km SW of Kawajiri Fishing Port, $31^{\circ}10' N$ $130^{\circ}32' E$, 40 m depth, set net; MNHN 2010-1050, 114 mm SL, Minamisatsuma, Kasasa, Kataura, off E of Sakinoyama, $31^{\circ}25.44' N$, $130^{\circ}11.49' E$, 27 m depth, set net.

Non-types ($n = 14$, 88–139 mm SL). KAUM-I. 14661, 111 mm SL, Ibusuki, Kaimonkawajiri, 1 km SW of Kawajiri Fishing Port, $31^{\circ}10' N$ $130^{\circ}32' E$, 40 m depth, set net; KAUM-I. 27549, 111 mm SL, same sampling data; KAUM-I. 35617, 139 mm SL, Minamisatsuma, Kasasa, Kataura, off E of Sakinoyama, $31^{\circ}25.44' N$, $130^{\circ}11.49' E$, 27 m depth, set net; KAUM-I. 56303, 115 mm SL, same sampling data; KAUM-I. 97832, 98 mm SL, same locality and catch data; KAUM-I. 131500, 133 mm SL, same sampling data; KAUM-I. 35944, 133 mm SL, Kimotsuki, Uchinoura Bay, $31^{\circ}17' N$, $131^{\circ}05' E$, set net; KAUM-I. 123984, 117 mm SL, same sampling data; KAUM-I. 54077, 99 mm SL, Osumi Islands, Tanega-shima Island, Kumage-gun, Nakatane, off Kumano, $30^{\circ}28.13' N$, $130^{\circ}58.32' E$, 25 m depth, set net; KAUM-I. 59466, 101 mm SL, same sampling data; KAUM-I. 56749, 115 mm SL, Kimotsuki, Uchinoura Bay, $31^{\circ}24.28' N$ $131^{\circ}02.55' E$, 40–45 m depth, set net; KAUM-I. 73580, 88 mm SL, Minamisatsuma, Kasasa, NE of Matsu-shima Island, $31^{\circ}25.06' N$, $130^{\circ}12.32' E$, 20 m depth, set net; KAUM-I. 110071, 131 mm SL, same sampling data; KAUM-I. 86533, 134 mm SL, Kimotsuki, Kishira, off Funama Fishing Port, $31^{\circ}10' N$, $130^{\circ}59' E$, set net.

Diagnosis. Dorsal fins VII + 9; pectoral fins 13–14(15); gill rakers 6–7 + 16–18 = 22–25; body elongate and laterally slightly compressed; measurements as % SL: depth at first dorsal-fin origin 21–24; body depth at anal-fin origin 19–22; caudal-peduncle depth 9.0–10; caudal-peduncle width 3.9–4.6; maximum head depth 17–19; head depth through eye 13–15; head length 27–29; snout length 10–12; orbit length 5.4–6.4; upper-jaw length 9.8–11; barbel length 17–18; caudal-fin length 27–30; anal-fin height 15–17; pelvic-fin length 18–21; pectoral-fin length 19–21; first dorsal-fin height 18–21, dorsal-fin spines proportionally decreasing in height; second dorsal-fin height 15–17; total oblique bars on caudal fin 11–18, upper caudal-fin lobe with 5–7 mostly straight red or red-brown bars; lower caudal-fin lobe with 6–11 red or red-brown bars that are only faintly visible along ventral-lobe margin, becoming more conspicuous along central lobe; several of these bars and especially three of the most proximal ones reach dorsal-lobe margin, becoming pale reddish grey; lower caudal-fin lobe in life with a red or red-brown stripe of about orbit diameter in maximum width, covering bars only partly, that fades away post mortem; bars are mostly retained in the first years after preservation, but may be lost later; dorsal fins in fresh fish with 3–4 thin red or brown stripes, may be retained in preservative; barbels white or creamy white when fresh; body colour in freshly deceased fish dark red or dark brown dorsally and pale red or rose with red blotches or spots on lower half, ventral margin

TABLE 3. Morphometric and meristic characters for three new species of *Upeneus* and *Upeneus itou*.

Morphometric characters	Upeneus dimipavlov n. sp.						U. elongatus n. sp.						U. itou					
	Paratypes						all						Types and non-types					
	HT	Min	Mean	Max	n	Min	Mean	Max	n	HT	Min	Mean	Max	n	HT	PT		
Standard length (in mm) in % SL	120	111	123.3	134	10	111	122.9	134	11	89	87	114.5	139	20	90	92		
Body depth at first dorsal-fin origin	24	23	23.6	25	10	23	23.6	25	11	21	21	22.1	24	20	24	23		
Body depth at anal-fin origin	20	20	20.8	22	10	20	20.7	22	11	18	19	21.0	22	20	21	20		
Half body depth at first dorsal-fin origin	20	19	19.6	21	9	19	19.7	21	10		17	18.4	20	14	20	20		
Half body depth at anal-fin origin	17	16	16.5	17	9	16	16.5	17	10		15	16.1	18	15	16	16		
Caudal-peduncle depth	9.7	9.8	10.0	10	10	9.7	10.0	10	11	8.3	9.0	9.7	10	20	9.6	9.9		
Caudal-peduncle width	5.2	4.8	5.1	5.4	10	4.8	5.1	5.4	11	3.3	3.9	4.3	4.6	20	4.3	4.2		
Maximum head depth	20	19	19.4	20	10	19	19.4	20	11	18	17	18.4	19	20	20	21		
Head depth through eye	16	16	16.1	17	10	16	16.1	17	11	14	13	14.3	15	20	16	16		
Suborbital depth	9.8	9.9	10.2	11	10	9.8	10.1	11	11	8.3	8.3	9.1	9.8	20	9.8	9.6		
Interorbital length	7.8	7.4	7.8	8.1	10	7.4	7.8	8.1	11	7.4	6.7	7.8	8.4	20	7.5	8.0		
Head length	29	28	29.0	30	10	28	29.0	30	11	27	27	28.1	29	20	29	29		
Snout length	12	11	11.9	13	10	11	11.9	13	11	10	10	11.2	12	20	10	11		
Postorbital length	12	11	11.7	12	10	11	11.7	12	11	11	11	11.6	12	20	12	12		
Orbit length	6.8	5.7	6.5	6.8	10	5.7	6.5	6.8	11	6.7	5.4	6.0	6.4	20	7.1	7.5		
Orbit depth	5.8	4.9	5.5	5.8	10	4.9	5.5	5.8	11	5.7	4.7	5.2	5.8	20	6.2	6.6		
Upper-jaw length	11	11	11.0	12	10	11	11.0	12	11	11	9.8	10.7	11	20	12	12		
Lower-jaw length	10	9.7	10.3	11	10	9.7	10.3	11	11	9.6	9.4	10.1	11	20	11	11		
Snout width	8.7	8.5	8.9	10	10	8.5	8.9	10	11	7.7	7.6	8.4	9.3	20	9.4	10		
Barbel length	20	19	19.1	21	10	19	19.2	21	11	17	17	17.5	18	20	20	20		
Maximum barbel width	0.9	0.8	0.9	1.0	10	0.8	0.9	1.0	11	0.9	0.7	0.8	0.9	20	0.8	0.8		
First pre-dorsal length	37	36	36.6	37	10	36	36.6	37	11	35	34	35.6	37	20	37	37		
Second pre-dorsal length	64	62	64.3	66	10	62	64.3	66	11	62	61	63.4	65	20	64	65		
Interdorsal distance	14	14	15.2	17	10	14	15.1	17	11	14	14	15.3	17	20	15	16		
Caudal-peduncle length	23	23	23.6	24	10	23	23.6	24	11	24	23	24.1	25	20	23	24		

.....continued on the next page

TABLE 3. (Continued)

	<i>Upeneus dimipiniov</i> n. sp.						<i>U. elongatus</i> n. sp.						<i>U. itou</i>						<i>U. willwhitei</i> n. sp.							
	Paratypes						all						Types and non-types													
	HT	Min	Mean	Max	n	Min	Mean	Max	n	HT	Min	Mean	Max	n	HT	PT	Min	Mean	Max	n	HT	PT				
Morphometric characters																										
Pre-anal length	64	63	64.3	66	10	63	64.3	66	11	63	63	63.9	65	20	66	20	66	20	66	20	66	20	66	20	66	20
Pre-pelvic length	31	31	31.1	32	10	31	31.0	32	11	32	31	31.3	33	20	33	20	33	20	33	20	33	20	33	20	33	20
Pre-pectoral length	30	29	29.4	30	10	29	29.5	30	11	30	28	29.4	31	20	30	20	30	20	30	20	30	20	30	20	30	20
Second dorsal-fin depth	21	20	21.2	22	10	20	21.2	22	11	19	20	21.4	23	20	21	20	21	21	20	21	21	21	21	21	21	21
Pelvic-fin depth	24	23	23.5	25	10	23	23.5	25	11	21	21	22.2	24	20	24	20	24	20	24	20	24	20	24	20	24	20
Pectoral-fin depth	17	15	16.2	17	10	15	16.2	17	11	14	14	15.3	17	20	17	20	17	20	17	20	17	20	17	20	17	20
Length of first dorsal-fin base	15	14	15.0	16	10	14	15.0	16	11	14	14	14.5	15	20	15	20	15	20	15	20	15	20	15	20	15	20
Length of second dorsal-fin base	14	13	14.5	16	10	13	14.5	16	11	15	13	14.2	15	20	14	20	14	20	14	20	14	20	14	20	14	20
Caudal-fin length	27	27	28.1	29	10	27	28.0	29	11	29	27	28.9	30	20	28	20	28	20	28	20	28	20	28	20	28	20
Length of anal-fin base	11	11	11.5	12	10	11	11.5	12	11	12	11	11.6	12	20	11	20	11	20	11	20	11	20	11	20	11	20
Anal-fin height	17	16	17.0	18	10	16	16.9	18	11	16	15	16.3	17	20	16	20	16	20	16	20	16	20	16	20	16	20
Pelvic-fin length	20	20	20.9	22	10	20	20.9	22	11	23	18	19.5	21	20	20	20	20	20	20	20	20	20	20	20	20	20
Pectoral-fin length	20	18	19.0	20	10	18	19.1	20	11	21	19	19.9	21	20	20	20	20	20	20	20	20	20	20	20	20	20
Pectoral-fin width	4.6	4.3	4.6	4.8	10	4.3	4.6	4.8	11	4.4	3.8	4.2	4.5	20	4.3	20	4.3	20	4.3	20	4.3	20	4.3	20	4.3	20
First dorsal-fin height	20	19	19.9	21	9	19	19.9	21	10	20	18	19.3	21	20	20	20	20	20	20	20	20	20	20	20	20	20
Second dorsal-fin height	16	16	16.8	18	10	16	16.8	18	11	15	15	16.3	17	19	17	19	17	19	17	19	17	19	17	19	17	19
Meristic characters																										
Pectoral-fin rays	14	14	14.2	15	10	14	14.2	15	11	13	13	13.8	14	20	14	20	14	20	14	20	14	20	14	20	14	20
Rudimentary gill rakers on upper limb	2	0	3.0	4	10	0	2.9	4	11	2-3 *	0	2.5	4	20	3	20	3	20	3	20	3	20	3	20	3	20
Developed gill rakers on upper limb	5	3	3.6	6	10	3	3.7	6	11	6-5 *	3	4.1	6	20	3	20	3	20	3	20	3	20	3	20	3	20
Developed gill rakers on lower limb	14	12	13.0	14	10	12	13.1	14	11	16-15 *	12	13.1	14	20	12	20	12	20	12	20	12	20	12	20	12	20
Rudimentary gill rakers on lower limb	4	3	3.9	5	10	3	3.9	5	11	4-4 *	3	3.9	6	20	3	20	3	20	3	20	3	20	3	20	3	20
Total gill rakers on upper limb	7	6	6.6	7	10	6	6.6	7	11	8-8 *	6	6.6	7	20	6	20	6	20	6	20	6	20	6	20	6	20
Total gill rakers on lower limb	18	16	16.9	18	10	16	17.0	18	11	20-19 *	16	17.0	18	20	15	20	15	20	15	20	15	20	15	20	15	20
Total gill rakers	25	22	23.5	24	10	22	23.6	25	11	28-27 *	22	23.5	25	20	21	21	21	21	21	21	21	21	21	21	21	21
Scales along lateral line	29	29	29.1	30	7	29	29.1	30	8	no data	28	29.1	30	10	30	29	30	29	30	29	30	29	30	29	30	

* counts at left and right body side, respectively.

silvery white; a rather conspicuous dark brown, dark red or red mid-lateral body stripe of about pupil diameter in width at eye level from behind eye to caudal-fin base and in front of eye to nose tip, not retained in preservative; head below and behind eye silvery white, often covered with red patches or blotches; body and head dorsally grey or grey brown and ventrally often silvery white when preserved.

Distribution and size. Known from S Japan, including Kagoshima, Miyazaki, Kochi and Ehime Prefectures and Okinawa-jima Island, Ryukyu Islands, and Taiwan; occurs on sandy bottoms; depth 4–40 m; attains 144 mm SL.

Remarks. *Upeneus ituoi* is a rather common species which is often caught by set net in S Japan and has local commercial value. It co-occurs frequently with *U. tragula* Richardson, 1846 (Yamashita *et al.* 2011). Two specimens have been collected off Tanega-shima Island, Osumi Islands in the same area as the HT of *U. elongatus* (Tashiro *et al.* 2014).

Upeneus willwhite n. sp.

White's Goatfish

(Figures 1F, 2–6; Tables 2, 3)

Upeneus guttatus Day, 1868: White *et al.* 2013; Uiblein *et al.* 2017a (in part)

Material examined. Holotype. CSIRO 7217-07, 90 mm SL, EIO, S Indonesia, Lombok, Tanjung Luar, fish market, William White (photo of fresh HT, Figure 1F)

Paratype. MZB 23014, 92 mm SL, same sampling data as holotype.

Diagnosis. Dorsal fins VII + 9; pectoral fins 14; gill rakers $6 + 15\text{--}17 = 21\text{--}23$; body moderately elongate and laterally slightly compressed; measurements as % SL: body depth at first dorsal-fin origin 23–24; body depth at anal-fin origin 20–21; caudal-peduncle depth 9.6–9.9, caudal-peduncle width 4.2–4.3; maximum head depth 20–21; head depth through eye 16; head length 29; snout length 10–11; orbit length 7.1–7.5; upper-jaw length 12; barbel length 20; caudal-fin length 28–30; anal-fin height 16–17; pelvic-fin length 20–21; pectoral-fin length 19–20; first dorsal-fin height 20, dorsal-fin spines proportionally decreasing in height; second dorsal-fin height 17; total oblique bars on caudal fin 11–14, upper caudal-fin lobe with 5–6 brown mostly straight bars; lower caudal-fin lobe with 6–8 short brown bars ventrally, connecting dorsally to a brown stripe of about orbit diameter in its maximum width, and with about 3 short red, brownish-ochre bars along dorsal margin that do not correspond with bars on ventral-lobe margin; caudal-fin stripe and bars retained after preservation; dorsal fins in fresh fish with 3–4 thin brown stripes, retained in preservative; barbels reddish white when fresh; body colour in freshly deceased fish dark brown dorsally and pale brown ventrally, ventral margin white; mid-lateral body stripe dark brown, rather inconspicuous on snout and posterior half of body; head entirely grey brown; body and head dark brown dorsally and pale brown ventrally when preserved.

Description. Measurements in % SL and counts are given in Table 3; morphometric data as ratios of SL for holotype, data for paratype in brackets: body moderately elongate and laterally slightly compressed, body depth at first dorsal-fin origin 4.3 [4.3]; body depth at anal-fin origin 4.9 [4.9]; head depth through eye 5.1 [4.8]; head length 3.4 [3.5], larger than maximum body depth and subequal to caudal-fin length (3.6 [3.4]); first dorsal-fin height 5.1 [4.9], subequal to barbel length (5.1 [5.1]) and larger than second dorsal-fin height (6.0 [5.8]); pelvic-fin length 5.0 [4.7], slightly larger than pectoral-fin length (5.2 [4.9]) and subequal to body depth at anal-fin origin; caudal-peduncle depth 10 [10], distinctly larger than orbit length (14 [13]); and caudal-peduncle width 23 [24], subequal to pectoral-fin width (22 [23]).

Colour. Fresh HT. Dorsal part of head and body grey brown from snout to above eye and above lateral line; dorsal body colour appearing marbled due to grey scales with dark grey-brown edges; dark grey-brown band of about pupil diameter in width along entire dorsal body margin, becoming more conspicuous behind first dorsal fin and narrows behind second dorsal fin to a dark grey, partly blackish stripe; a similarly coloured dark grey, partly blackish mid-lateral body stripe of pupil diameter in width from behind eye to caudal-fin base crossing the faint white-greyish lateral line below second dorsal fin; below of mid-lateral body stripe scales pale grey or white with brown-greenish edges forming four oblique bands that become weaker and more ochre-coloured distally, before ending on lower part of caudal-fin base or above posterioventral half of body; a fifth faint-yellowish band from

below pectoral-fin base to above anal-fin origin; head below eye from behind snout pale grey with grey-brown dots or streaks and two faint-reddish blotches on ventral margin below and behind eye; iris red to rose whitish; ventral part of head and body white creamy; caudal fin with five oblique brown-ochre bars of about half pupil width on upper lobe, the most anterior bar at lobe base bent, the remaining bars more straight; white-hyaline interspaces between bars increasing in width from being narrower than bars proximally to double-bar width distally; tip of upper caudal-fin lobe white hyaline; lower caudal-fin lobe with eight short brown bars, along ventral margin of lobe brown streaks on ventral-most fin rays; white-hyaline interspaces between bars increasing distally to more than double-bar width; dark brown stripe along middle of lower caudal-fin lobe of about orbit diameter in its maximum width, stripe originating from a large, vertically extended dark-brown patch on caudal-fin base, connecting there with mid-lateral body stripe; lower caudal-fin lobe stripe changes from dark brown to brown red distally, ending as a dark-brown lobe tip; dorsal part of lower caudal-fin lobe with three brownish-ochre bars of about twice the width of bars on ventral side of lobe and with white-hyaline interspaces as wide as these bars; first dorsal fin hyaline with rather irregularly arranged pale-brown pigmentation spots, streaks or small blotches on or between individual spines giving a weak indication of a horizontal stripe close to fin base and three more oblique stripes further above; first dorsal-fin tip unpigmented; second dorsal fin hyaline with pale-brown spots arranged into three horizontal stripes, fin tip pale-brown; pectoral, pelvic and anal fins hyaline, weakly pale reddish-brown along several fin rays; barbels rose whitish, pale red on base.

Preserved HT. Dark brown dorsally at level of snout to termination of lateral line at caudal-fin base; pale brown to beige ventrally below eyes and level of pectoral-fin base; behind pectoral-fin base to second dorsal-fin base two weakly indicated brown bands intermingled with beige; caudal-fin bars and stripe and dorsal-fin pigmentation well retained; other fins pale hyaline; barbels pale.

Etymology. The name “*willwhite*” is used as a composed noun in apposition. It honours the ichthyologist Dr. William T. White, Australian National Fish Collection, CSIRO National Research Collections Australia, Hobart, Australia, for collecting and photographing mullid specimens from S Indonesia and making them available for taxonomic research (including the types of *Upeneus willwhite*).

Distribution, habitat, size. Only known from Lombok, S Indonesia; occurs most probably on shallow sandy bottoms; attains at least 92 mm SL.

Remarks. This species was obtained at a fish market and hence may have local commercial value.

Comparisons and differential diagnosis

Featured species (Figures 1–6; Tables 2, 3). *Upeneus elongatus* is the most distinct among the four featured species. It differs from *U. dimipavlov*, *U. itoui* and *U. willwhite* in higher number of gill rakers, shallower body at anal-fin origin, shallower and narrower caudal peduncle, longer pelvic fins and yellowish-beige colour patches close to base of both dorsal fins in fresh fish vs. no such colour patterns; in addition, it differs from *U. dimipavlov* and *U. willwhite* in fewer pectoral-fin rays, shallower and shorter head and shorter barbels.

Upeneus dimipavlov differs from *U. itoui* and *U. willwhite* in wider caudal peduncle, mostly deeper suborbital and absence of a conspicuous mid-lateral body stripe in fresh fish; in addition, it differs from *U. itoui* in mostly deeper body, deeper head and suborbital, longer barbels, pelvic fins mostly longer than pectoral fins vs. both fins of subequal length, and short bars on dorsal margin of lower caudal-fin lobe not corresponding to short bars on ventral lobe margin vs. bars often crossing entire lobe; and, it differs from *U. willwhite* in slightly more gill rakers and mostly longer snout.

Upeneus itoui differs from *U. willwhite* in shallower head, smaller eyes (excluding allometric influences due to size overlap), shorter upper jaw, narrower snout, shorter barbels, subequal length of paired fins vs. pelvic fins longer than pectoral fins, mostly higher number of gill rakers and bars on lower caudal-fin often crossing entire lobe vs. short bars on dorsal margin of lower caudal-fin lobe that do not correspond to short bars on ventral lobe margin.

Differences from other co-occurring *japonicus*-group species (Figures 1–3, 7; Tables 1–4). Of the six other species occurring in the CEITPAS area (Table 1), *U. guttatus*, *U. japonicus* (Houttuyn, 1782) and *U. spottocaudalis* Uiblein & Gledhill, 2017 overlap in gill-raker counts with three of the four featured species, respectively. They differ from all four species in yellow vs. whitish barbels when fresh. In addition, *U. guttatus* differs from the four species as well as from most other species of the *japonicus* group (see also Uiblein *et al.* 2020a) in the first three

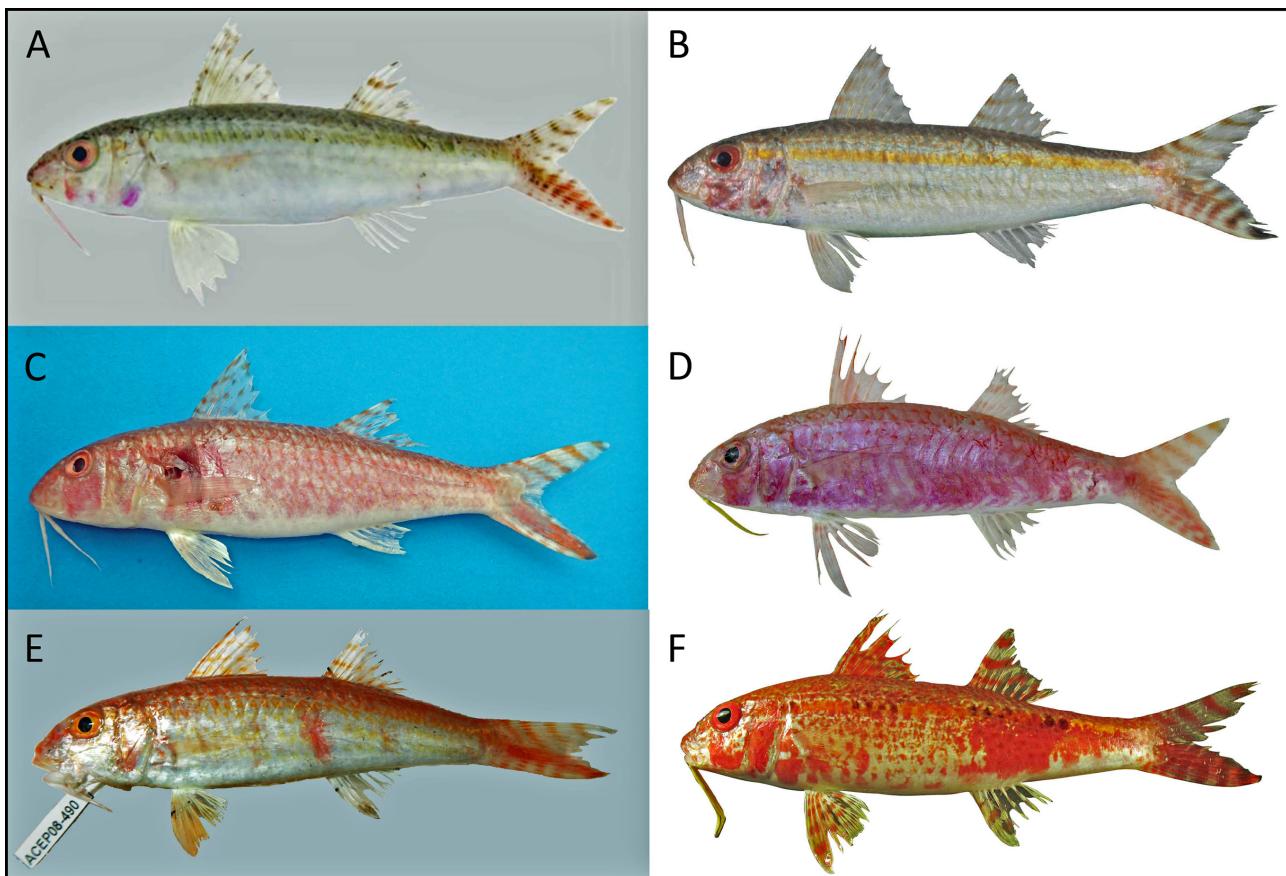


FIGURE 7. A: *Upeneus asymmetricus*, CSIRO H 7517-02, 93 mm SL, Lombok, S Indonesia (W.T. White); B: *U. australiae*, CSIRO H 4056-01, 105 mm SL, NW of Port Hedland, NW Australia (A. Graham); C: *U. floros*, SAIAB 204583, HT, 107 mm SL, Sodwana Bay, KwaZulu Natal, South Africa (C. Floros); D: *U. guttatus*, CSIRO H 7212-02, 121 mm SL, S of Cairns, NE Australia (D.C. Gledhill); E: *U. pori*, SAIAB 192775, 94 mm SL, off NE Madagascar (J. Escobar-Porras); F: F 58336 *U. heterospinosus*, VNMN-I 2026, PT, N off Hon Tre Island, Nha Trang, S-central Vietnam (D. A. Pavlov).

dorsal-fin spines being disproportionately elongated vs. proportionally decreasing in height; *U. japonicus* differs in bars on lower caudal-fin lobe absent vs. present; and *U. spottocaudalis* differs in having three or four large rounded or triangular spots on the lower caudal-fin lobe vs. 6–11 bars or spots in the four featured species.

In addition, *U. guttatus* differs from *U. dimipavlov* in slightly fewer pectoral-fin rays, slightly shorter head, slightly shorter barbels, slightly longer pectoral fins, paired fins of subequal length vs. pelvic fins mostly longer than pectoral fins and mostly higher first dorsal fin; it differs from *U. elongatus* in fewer gill rakers, deeper caudal peduncle, deeper head through eye suborbital, shorter pelvic fins, and yellowish-beige patches basally on dorsal fins absent vs. present in fresh fish; it differs from *U. itoui* in mostly deeper head through eye and slightly higher first dorsal fin; and it differs from *U. willwhite* in slightly more gill rakers, slightly shorter head, upper jaw and barbels and slightly higher first dorsal fin.

Upeneus japonicus differs from *U. dimipavlov* in slightly higher number of gill rakers, mostly narrower caudal peduncle, longer pectoral fins, pelvic fins slightly shorter than pectoral fins vs. pelvic fins mostly longer than pectoral fins and slightly higher first dorsal fin; it differs from *U. elongatus* in deeper head through eye, longer barbels, pelvic fins slightly shorter than pectoral fins vs. pelvic fins longer than pectoral fins and yellowish-beige patches basally on dorsal fins absent vs. present in fresh fish; it differs from *U. itoui* in slightly more gill rakers, mostly deeper head through eye, mostly longer barbels, mostly longer pectoral fins and slightly higher first dorsal fin; and it differs from *U. willwhite* in more gill rakers, longer pectoral fins and pectoral fins slightly longer than pelvic fins vs. pelvic fins mostly longer than pectoral fins.

Upeneus spottocaudalis differs from *U. dimipavlov* in fewer pectoral-fin rays, slightly fewer total gill rakers, narrower caudal peduncle, mostly longer head, slightly longer caudal-fin, slightly longer paired fins, mostly nar-

TABLE 4. Morphometric and meristic characters for six *japonicus*-group species and *U. heterospinus* of the CEITPAS area.

	<i>Upeneus asymmetricus</i>	<i>U. farnii</i>	<i>U. guttatus</i>	<i>U. japonicus</i>	<i>U. lombok</i>	<i>U. spottocaudalis</i>	<i>U. heterospinus</i>																			
	Min	Mean	Max	n	Min	Mean	Max	n	Min	Mean	Max	n	Min	Mean	Max	n										
Morphometric characters																										
Standard length (in mm) in % SL	74	89.1	100	8	70	111.0	141	14	68	101.3	159	74	66	99.4	123	37	94	86	67	77.9	103	17	65	90.0	152	101
Body depth at first dorsal-fin origin	22	23.1	24	8	23	24.1	25	14	21	23.6	26	74	21	23.5	25	37	21	23	22	24.2	25	17	22	24.1	26	99
Body depth at anal-fin origin	20	20.4	22	8	20	21.4	22	14	18	20.2	22	74	18	19.7	22	37	19	19	19	20.5	22	17	18	20.7	22	100
Half body depth at first dorsal-fin origin	19	19.3	20	8	19	20.4	22	14	17	19.4	21	63	18	19.7	21	27	18	20	19	20.7	22	6	18	19.9	22	86
Half body depth at anal-fin origin	14	15.6	17	8	15	16.4	17	14	14	15.8	18	60	14	16.0	18	26	14	14	15	15.8	16	9	15	16.0	17	82
Caudal-peduncle depth	8.5	9.2	9.9	8	8.8	9.2	9.9	14	9.3	10.0	11	74	8.0	9.6	11	37	9.2	9.3	8.6	9.4	10	17	9.2	10.2	11	101
Caudal-peduncle width	3.7	4.3	5.0	8	3.4	3.9	4.4	14	3.2	3.9	5.1	74	3.1	3.9	4.8	37	3.8	4.2	2.9	3.7	4.3	17	3.5	4.2	4.7	99
Maximum head depth	19	19.7	20	8	19	20.0	21	14	18	20.3	22	74	18	19.8	21	37	19	20	19	20.7	22	17	19	20.7	23	101
Head depth through eye	15	15.5	16	8	15	16.1	17	14	15	16.3	18	74	15	15.9	17	37	14	15	15	16.6	18	17	15	16.1	18	101
Suborbital depth	8.8	9.4	10	8	8.7	9.4	10	14	8.6	9.7	12	74	8.2	9.4	10	37	8.5	9.7	8.3	9.5	11	17	8.3	9.6	11	101
Interorbital length	8.0	8.6	9.0	8	7.2	8.1	8.6	14	7.0	7.8	8.9	74	6.9	7.7	8.7	37	7.2	8.3	7.3	7.9	8.9	17	7.2	8.0	9.2	99
Head length	26	27.1	29	8	28	29.2	31	14	26	27.4	29	74	27	28.6	31	37	28	30	30	30.4	32	17	27	28.7	31	101
Snout length	9.9	10.2	11	8	9.9	10.8	12	14	9.4	10.5	12	74	10	11.0	12	37	9.2	9.6	9.7	11.1	12	17	9.7	11.1	13	101
Postorbital length	11	11.4	13	8	11	12.2	14	14	9.7	10.8	13	74	9.8	11.1	13	37	12	12	11	11.8	13	17	10	11.3	13	101
Orbit length	5.7	6.7	7.7	8	5.6	6.5	7.2	14	5.9	7.1	8.5	74	6.1	7.4	8.2	37	7.5	7.9	6.9	7.7	8.2	17	5.9	7.3	8.3	101
Orbit depth	4.8	5.5	6.5	8	5.0	5.6	6.1	14	5.0	6.2	7.6	74	5.2	6.4	7.2	37	6.5	6.9	5.9	6.7	7.7	17	4.9	6.5	7.4	101
Upper-jaw length	8.7	9.6	11	8	9.6	10.4	12	14	9.5	10.9	12	74	9.7	10.6	12	37	9.4	9.7	10	11.5	13	17	9.4	10.9	13	101
Lower-jaw length	8.4	9.1	10	8	9.1	9.8	11	14	8.7	10.2	11	74	9.2	10.1	11	37	8.6	9.3	9.4	10.9	12	17	8.9	10.3	12	101
Snout width	7.6	8.2	9.3	8	7.5	8.4	9.8	14	7.6	8.5	11	71	7.1	8.4	9.8	37	8.0	7.8	7.1	8.4	10	16	7.1	8.6	11	98
Barbel length	17	17.9	19	8	18	20.0	23	14	16	17.8	20	73	18	21.1	23	36	19	20	19	20.3	22	17	16	17.9	20	101
Maximum barbel width	0.7	0.8	1.0	8	0.7	0.9	1.1	14	0.7	0.8	1.0	74	0.6	0.8	1.0	36	0.7	0.8	0.8	0.9	1.0	17	0.8	0.9	1.2	101
First pre-dorsal length	35	36.5	38	8	35	37.1	40	14	33	35.6	38	74	34	36.1	39	37	38	35	36.3	39	17	34	36.3	39	101	
Second pre-dorsal length	62	64.3	66	8	64	65.5	67	14	60	63.3	66	74	61	63.7	67	37	64	66	61	63.9	66	17	60	63.3	67	100
Interdorsal distance	14	15.5	16	8	15	15.9	17	14	14	16.0	18	74	14	15.6	18	37	15	16	14	15.9	17	17	13	14.9	17	100
Caudal-peduncle length	22	23.2	24	8	21	22.7	25	14	22	23.7	26	74	21	23.2	25	37	23	21	21	23.1	24	17	22	23.9	26	100
Pre-anal length	62	64.2	68	8	64	66.1	69	14	61	64.7	69	74	61	65.1	69	37	65	67	63	65.5	68	17	61	63.9	68	100
Pre-pelvic length	31	32.3	34	8	30	32.9	35	14	29	31.4	34	74	30	32.5	35	37	30	32	33	34.3	37	17	30	31.8	35	100

.....continued on the next page

TABLE 4. (Continued)

	<i>Upeneus asymmetricus</i>			<i>U.farini</i>			<i>U.guttatus</i>			<i>U.japonicus</i>			<i>U.lombok</i>			<i>U.spottocaudalis</i>			<i>U.heterospinus</i>							
	Min	Mean	Max	n	Min	Mean	Max	n	Min	Mean	Max	n	Min	Mean	Max	n	Min	Mean	Max	n						
Morphometric characters																										
Pre-pectoral length	29	29.7	31	8	29	30.7	33	14	28	29.3	32	74	29	31.0	33	37	29	31	30	31.8	34	17	28	30.0	33	100
Second dorsal-fin depth	19	20.7	22	8	21	21.9	23	14	19	20.8	24	74	18	20.4	22	37	20	20	19	20.7	22	17	19	21.3	23	99
Pelvic-fin depth	22	23.0	24	8	23	24.3	26	14	22	23.4	26	74	21	23.4	25	37	23	24	22	23.6	25	17	22	24.0	26	99
Pectoral-fin depth	14	15.5	17	8	16	16.8	18	14	14	16.2	19	74	14	16.2	18	37	16	16	14	15.5	17	17	15	16.6	18	99
Length of first dorsal-fin base	13	14.4	15	8	13	14.6	15	14	13	14.7	17	74	14	14.7	17	37	14	15	14	14.9	16	17	13	15.3	17	99
Length of second dorsal-fin base	12	12.7	14	8	12	13.6	15	14	12	13.6	16	73	12	13.4	15	37	13	14	12	13.4	15	17	12	13.8	16	100
Caudal-fin length	27	28.3	30	8	27	27.9	29	14	27	29.2	31	67	25	26.9	29	34	28	29	28	29.9	32	16	27	29.3	32	93
Length of anal-fin base	9.9	10.9	12	8	11	11.9	13	14	9.5	11.4	13	74	9.9	11.5	13	37	11	10	11	11.6	13	17	10	11.4	13	99
Anal-fin height	15	15.9	16	6	12	13.8	15	14	15	16.5	19	74	15	17.3	19	34	12	13	16	17.6	19	16	15	16.8	19	98
Pelvic-fin length	19	20.3	22	8	19	19.8	21	14	19	20.8	22	74	19	20.7	23	36	21	22	22	23.2	24	17	19	20.8	23	100
Pectoral-fin length	18	19.5	21	7	18	19.1	20	14	19	20.2	22	74	21	22.9	25	36	20	21	19	20.6	22	17	19	20.4	22	97
Pectoral-fin width	4.0	4.5	5.1	8	3.9	4.5	5.2	14	3.5	4.0	4.9	74	3.7	4.3	5	37	4.1	4.3	3.5	3.9	4.3	17	3.4	4.1	4.7	101
First dorsal-fin height	19	20.4	21	7	16	18.4	20	14	20	22.3	25	67	20	22.0	24	36	-	19	19	20.7	22	15	18	20.4	23	98
Second dorsal-fin height	15	15.8	17	6	12	13.9	15	14	14	16.1	18	69	15	17.4	19	34	14	14	18	19.1	21	17	16	17.8	20	97
Meristic characters																										
Pectoral-fin rays	12	13.0	14	8	15	15.2	16	12	12	13.1	14	75	13	13.9	15	37	14	15	12	12.9	13	17	13	13.9	15	101
Rudimentary gill rakers on upper limb	1	2.6	4	8	1	2.9	5	10	2	3.7	5	74	2	3.2	5	37	3	3	1	2.7	4	17	2	3.0	4	101
Developed gill rakers on upper limb	3	4.6	7	8	4	5.0	6	10	2	2.7	4	74	2	3.6	5	37	4	5	2	2.9	4	17	2	2.7	4	101
Developed gill rakers on lower limb	15	16.3	17	8	14	15.6	17	10	11	12.4	14	74	11	13.7	17	37	15	15	10	12.4	14	17	11	12.1	14	101
Rudimentary gill rakers on lower limb	2	3.6	5	8	4	5.1	7	10	3	4.9	7	74	3	5.3	7	37	5	6	3	4.6	6	17	3	4.5	6	101
Total gill rakers on upper limb	7	7.3	8	8	7	7.9	9	10	5	6.4	8	74	6	6.8	8	37	7	8	5	5.6	6	17	4	5.7	6	101
Total gill rakers on lower limb	19	19.9	21	8	20	20.7	22	10	16	17.3	19	74	18	19.1	21	37	20	21	16	16.9	18	17	15	16.5	18	101
Total gill rakers	26	27.1	28	8	28	28.6	31	10	22	23.7	26	74	24	25.9	28	37	27	29	21	22.5	23	17	21	22.2	24	101
Scales along lateral line	28	29.1	31	8	29	29.2	30	9	28	29.4	31	45	29	29.3	30	17	31	30	29	29.7	31	3	28	29.2	30	66

TABLE 5. Morphometric and meristic characters for seven *japonicus*-group species from outside the CEITPAS area.

	<i>Upeneus australiae</i>	<i>U. floros</i>	<i>U. pori</i>	<i>U. francisi</i>	<i>U. seychellensis</i>	<i>U. saiba</i>	<i>U. torres</i>										
	Min	Mean	Max	n	Min	Mean	Max	n	Min	Mean	Max	n	Min	Mean	Max	n	
Morphometric characters																	
Standard length (in mm) in % SL	72	103.2	128	45	90	105.0	144	17	66	69.6	74	6	66	89.9	117	32	83.6
Body depth at first dorsal-fin origin	23	23.8	27	38	22	23.6	25	17	23	24.3	25	6	21	23.1	24	32	21
Body depth at anal-fin origin	20	21.1	23	38	19	20.5	22	17	20	21.0	22	6	18	20.3	22	32	17
Half body depth at first dorsal-fin origin	18	19.6	22	35	18	19.3	21	17	18	19.6	21	6	18	18.9	21	32	16
Half body depth at anal-fin origin	15	16.3	18	33	15	16.1	18	15	16	16.5	17	5	13	15.4	17	32	13
Caudal-peduncle depth	9.9	10.6	12	45	8.8	9.4	9.8	17	9.9	10.2	10	6	8.8	9.6	10	32	8.7
Caudal-peduncle width	3.2	4.0	5.1	38	3.7	4.2	4.8	17	3.2	3.5	4.1	6	3.5	4.0	4.6	32	3.0
Maximum head depth	20	20.8	22	38	19	19.8	21	17	20	20.3	21	6	18	19.2	21	32	18
Head depth through eye	15	16.4	18	38	15	15.9	17	17	15	15.8	16	6	15	15.4	16	32	15
Suborbital depth	9.0	10.2	12	38	8.7	9.7	10	17	8.3	8.8	9.6	6	8.2	9.4	10	32	8.4
Interorbital length	7.1	8.0	9.6	38	7.0	7.5	8.2	17	7.4	7.5	7.8	6	7.1	7.9	9.2	32	7.0
Head length	27	28.9	30	38	29	30.2	32	17	28	29.2	30	6	26	27.8	30	32	29
Snout length	9.9	11.6	13	38	11	11.6	13	17	10	10.5	11	6	9.5	10.8	12	32	10
Postorbital length	11	11.5	13	38	11	12.2	13	17	11	11.8	13	6	11	11.6	13	32	12
Orbit length	6.0	6.9	8.0	38	5.9	7.0	7.7	17	6.9	7.6	7.9	6	5.8	7.0	7.8	32	6.8
Orbit depth	5.0	6.0	6.8	38	5.4	6.1	6.8	17	6.1	6.8	7.1	6	4.8	6.2	7.7	32	6.2
Upper-jaw length	9.3	10.9	12	38	11	11.6	13	17	9.9	10.4	11	6	9.9	10.8	12	32	9.5
Lower-jaw length	9.0	10.3	11	37	10	11.0	12	17	9.4	9.8	10	6	9.1	10.2	11	32	8.9
Snout width	7.9	8.7	10	35	7.9	8.8	9.6	17	7.1	7.9	8.5	6	7.4	8.3	10	32	7.5
Barbel length	16	18.4	20	45	18	18.5	20	17	17	17.6	19	6	16	17.1	19	32	19
Maximum barbel width	0.8	0.9	1.1	38	0.7	0.9	1.1	17	0.8	0.9	1.0	6	0.6	0.8	1.0	32	0.9
First pre-dorsal length	33	36.3	39	38	36	37.6	39	17	36	37.5	40	6	34	36.8	38	32	37
Second pre-dorsal length	61	63.6	66	38	64	65.3	67	17	63	64.2	66	6	63	64.9	67	32	64
Interdorsal distance	13	14.5	16	38	15	16.2	17	17	14	14.7	16	6	14	16.2	18	31	14
Caudal-peduncle length	22	24.1	26	38	22	23.1	25	17	23	23.8	25	6	22	23.9	26	32	22

.....continued on the next page

TABLE 5. (Continued)

	<i>Upeneus australiae</i>				<i>U.floros</i>				<i>U.francisi</i>				<i>U.pori</i>				<i>U.saiab</i>				<i>U.seychellensis</i>				<i>U.torres</i>			
	Min	Mean	Max	n	Min	Mean	Max	n	Min	Mean	Max	n	Min	Mean	Max	n	Min	Mean	Max	n	Min	Mean	Max	n	Min	Mean	Max	n
Morphometric characters																												
Pre-anal length	60	63.4	67	38	64	65.4	68	17	63	65.0	66	6	60	64.7	67	32	65	66.1	67	6	65	66.6	68	3	60	64.2	67	20
Pre-pelvic length	30	32.4	35	38	30	31.8	34	17	32	33.0	34	6	28	31.1	32	32	32	33.3	35	6	30	31.7	33	3	31	33.3	37	20
Pre-pectoral length	29	30.2	32	38	29	30.9	32	17	29	30.7	32	6	28	29.4	31	32	31	31.7	33	6	28	29.9	32	3	30	31.8	34	20
Second dorsal-fin depth	20	21.5	24	38	20	21.2	23	17	21	22.1	23	6	19	20.8	23	32	17	18.4	19	6	18	18.7	19	3	18	20.6	22	20
Pelvic-fin depth	22	23.8	27	38	22	23.5	25	17	23	24.5	25	6	22	23.4	25	32	20	21.4	23	6	21	21.7	23	3	23	24.6	27	20
Pectoral-fin depth	15	16.7	19	38	16	16.4	17	17	15	16.3	17	6	16	16.3	18	32	14	14.7	16	6	16	16.6	17	3	15	16.3	18	20
Length of first dorsal-fin base	13	15.2	17	38	14	14.9	17	17	14	15.3	17	6	14	15.3	17	31	14	15.2	16	6	14	13.8	14	3	13	14.3	15	20
Length of second dorsal-fin base	12	13.6	15	38	13	13.9	15	17	13	14.7	16	6	13	14.5	16	32	13	13.9	15	6	12	12.5	13	3	12	13.6	15	20
Caudal-fin length	27	29.7	32	35	26	27.6	29	12	28	28.7	30	6	27	28.1	29	31	27	27.9	29	6	28	29.1	30	3	27	28.3	30	19
Length of anal-fin base	10	11.7	13	38	11	11.6	12	17	11	11.4	12	6	10	11.7	13	32	11	11.7	13	6	9.6	10.0	10	3	9.5	11.1	12	20
Anal-fin height	15	16.3	18	35	15	16.1	18	15	15	15.8	17	6	14	15.9	17	32	14	15.2	16	6	14	14.8	15	3	16	17.8	20	20
Pelvic-fin length	20	21.1	23	38	19	20.0	21	17	21	21.5	22	6	19	20.2	23	32	20	20.9	21	6	20	20.6	21	3	20	21.6	23	20
Pectoral-fin length	19	20.7	22	44	19	20.1	22	16	21	21.3	22	6	18	19.5	22	32	20	20.7	21	6	21	21.1	21	3	24	24.9	26	20
Pectoral-fin width	4.3	4.6	5.5	45	4.0	4.5	5.1	17	4.1	4.3	4.5	6	3.8	4.3	4.9	32	4.4	4.6	5.0	6	3.9	4.0	4.2	3	3.6	4.0	4.7	20
First dorsal-fin height	18	20.8	23	36	17	18.0	20	17	20	20.3	21	5	18	19.8	22	31	19	20.6	22	6	19	19.8	20	3	21	22.8	25	18
Second dorsal-fin height	14	15.9	18	36	15	15.9	18	16	16	16.9	18	6	15	15.9	17	30	14	15.5	16	6	16	16.0	17	3	16	17.0	19	19
Meristic characters																												
Pectoral-fin rays	13	14.2	15	45	13	13.9	15	17	14	14.0	14	6	13	14.1	15	32	14	14.8	15	6	14	14.7	15	3	13	14.0	15	20
Rudimentary gill rakers on upper limb	1	2.8	4	45	1	2.8	4	17	0	1.0	2	6	0	1.7	4	32	1	2.2	3	6	4	4.3	5	3	3	3.5	5	20
Developed gill rakers on upper limb	2	3.5	6	45	2	4.1	6	17	6	7.8	9	6	4	5.9	8	32	5	6.0	7	6	2	2.7	3	3	2	2.7	3	20
Developed gill rakers on lower limb	11	12.6	14	45	12	13.2	14	17	19	19.5	21	6	14	16.1	18	32	15	16.5	17	6	13	13.0	13	3	11	12.4	13	20
Rudimentary gill rakers on lower limb	3	4.2	6	45	3.0	4.2	5.0	17	1	2.7	4	6	1	3.3	5	32	3.0	4.3	6.0	6	5.0	5.3	6.0	3	4	4.8	7	20
Total gill rakers on upper limb	5	6.2	7	45	6.0	6.9	7.0	17	8	8.8	10	6	7	7.6	8	32	8.0	8.2	9.0	6	7.0	7.0	3	5	6.2	7	20	
Total gill rakers on lower limb	16	16.8	18	45	16	17.4	18	17	21	22.2	23	6	18	19.4	21	32	20	20.8	21	6	18	18.3	19	3	16	17.2	18	20
Total gill rakers	22	23.1	24	45	23	24.3	25	17	29	31.0	32	6	25	27.0	29	32	29	29.0	29	6	25	25.3	26	3	22	23.4	25	20
Scales along lateral line	27	28.9	30	26	28	29.2	30	10	29	29.3	30	3	28	29.1	30	27	29	29.3	30	4	29	29.7	31	3	28	29.1	30	8

rower pectoral fins and mostly higher second dorsal fin; it differs from *U. elongatus* in fewer gill rakers, deeper body, caudal peduncle and head, mostly longer head, longer barbels, narrower pectoral fins, higher second dorsal fin and yellowish-beige patches basally on dorsal fins absent vs. present in fresh fish; it differs from *U. itoui* in mostly deeper head, longer head, larger eyes, longer barbels and pelvic fins, pelvic fins mostly longer than pectoral fins vs. paired fins of subequal length and higher second dorsal fin; and it differs from *U. willwhite* in longer head and pelvic fins, mostly narrower pectoral fins and higher dorsal fins.

The three other *japonicus*-group species occurring in the CEITPAS area *Upeneus asymmetricus*, *U. farnis* Uiblein & Peristiwady, 2017 and *U. lombok* Uiblein & White, 2015 differ from *U. dimipavlov*, *U. itoui* and *U. willwhite* in higher gill-raker numbers. Two of them, *U. farnis* and *U. lombok*, differ from all four featured species in lower caudal-fin bars being mostly absent vs. present. *Upeneus farnis* differs also in mostly higher number of pectoral-fin rays and *U. lombok* differs in shorter snout and lower anal and second dorsal fin from the four featured species. In addition, *U. asymmetricus* Lachner, 1954 differs from *U. dimipavlov* in mostly fewer pectoral-fin rays, slightly shorter head, snout, jaws, barbels and anal fin and bars on lower caudal-fin lobe crossing entire lobe vs. positioned at lobe margins; it differs from *U. itoui* in mostly deeper head through eye, slightly wider interorbital and slightly shorter second dorsal-fin base; and it differs from *U. willwhite* in shorter jaws and barbels, slightly shorter first dorsal-fin base and bars on lower caudal-fin lobe crossing entire lobe vs. positioned at lobe margins.

Upeneus elongatus overlaps in gill-raker counts with *Upeneus asymmetricus*, *U. farnis* and *U. lombok*, however differs from those species in shallower body, caudal peduncle, head and suborbital, in narrower caudal peduncle, mostly shorter barbels, longer pelvic fins and yellowish-beige patches basally on dorsal fins present vs. absent in fresh fish; moreover, it differs from *U. farnis* and *U. lombok* in fewer pectoral-fin rays, shorter head and higher anal fin; and from *U. asymmetricus* it differs in narrower interorbital and longer second dorsal-fin base and pelvic fins.

Differences from *japonicus*-group species occurring in other areas (Figures 1, 2, 4, 5, 7; Tables 1–3, 5).

Among the seven *japonicus*-group species occurring outside the CEITPAS area, *U. australiae* Kim & Nakaya, 2002 (Australia, New Caledonia) and *U. floros* are most similar to *U. dimipavlov*, *U. itoui* and *U. willwhite*, while *U. elongatus* is very distinct. The latter differs from both *U. australiae* and *U. floros* in a higher gill-raker count, shallower body, caudal peduncle, head and suborbital, narrower snout, slightly shorter barbels, mostly longer pelvic fins and yellowish-beige patches basally on dorsal fins present vs. absent in fresh fish.

Upeneus australiae differs from *U. dimipavlov*, *U. itoui* and *U. willwhite* in slightly deeper caudal peduncle and stripe on lower caudal-fin lobe absent vs. frequently present in fresh fish. In addition, it differs from *U. dimipavlov* in slightly narrower caudal peduncle, mostly larger maximum head depth, slightly longer pectoral fins, a conspicuous mid-lateral body stripe in fresh fish present vs. absent and bars on lower caudal-fin lobe crossing entire lobe vs. bars positioned along lobe margins; it differs from *U. itoui* in deeper head, slightly longer pelvic fins and yellowish vs. red-brown mid-lateral body stripe in fresh fish; and from *U. willwhite* it differs in slightly shorter jaws and barbels, yellowish vs. dark brown mid-lateral body stripe in fresh fish and bars on lower caudal-fin lobe crossing entire lobe vs. bars positioned along lobe margins.

Upeneus floros differs from *U. dimipavlov*, *U. itoui* and *U. willwhite* in slightly longer head; in addition, it differs from *U. dimipavlov* in slightly shallower and narrower caudal peduncle, slightly longer pectoral fins, paired fins subequal in length vs. pelvic fins mostly longer than pectoral fins and slightly lower first dorsal fin; it differs from *U. itoui* in mostly deeper head, mostly longer upper jaw and barbels and absence vs. presence of a conspicuous mid-lateral body stripe in fresh fish; and it differs from *U. willwhite* in slightly longer snout, slightly shorter barbels, slightly lower first dorsal fin and absence vs. presence of a mid-lateral body stripe in fresh fish.

Upeneus pori (Mediterranean, Northern Red Sea, Madagascar), a species rather similar to *U. floros* (Uiblein *et al.* 2020a), overlaps with *U. dimipavlov*, *U. itoui* and *U. elongatus* in number of gill rakers, while having more gill rakers than *U. willwhite*. From the latter it differs also in slightly shorter jaws, shorter barbels and slightly lower second dorsal fin; of *U. dimipavlov* it differs in a mostly higher number of gill rakers, narrower caudal peduncle, slightly shallower suborbital, mostly shorter barbels and slightly lower anal fin and second dorsal fin; from *U. elongatus* it differs in slightly deeper body, deeper caudal peduncle and head, wider caudal peduncle, yellowish-beige patches basally on dorsal fins absent vs. present in fresh fish and bars on lower caudal-fin lobe positioned mainly at lobe margins versus crossing lobe; and from *U. itoui* it differs in mostly higher number of gill rakers, slightly deeper head, slightly larger pectoral-fin depth and bars on margins of lower caudal-fin lobe that do not correspond vs. several bars crossing lobe.

The four remaining *japonicus*-group species from outside the CEITPAS area *U. francisi* (Norfolk Island, Australia, North Island and Kermadec Islands, New Zealand), *U. saib* Uiblein & Lisher, 2013 (Angoche, N Mozambique), *U. seychellensis* Uiblein & Heemstra, 2011 (Seychelles Bank) and *U. torres* Uiblein & Gledhill 2014 (Australia, Vanuatu) are considerably distinct. *Upeneus francisi* has a higher gill-raker number than all four featured species. In addition, it differs from *U. dimipavlov* in narrower caudal peduncle, shallower suborbital, mostly shorter barbels and longer pectoral fins, among other characters; it differs from *U. elongatus* in deeper body, caudal peduncle and head, longer head, shorter pelvic fins and bars on lower caudal-fin at lobe margins vs. crossing lobe; it differs from *U. itoui* in deeper head, mostly longer paired fins and absence vs. presence of mid-lateral body stripe in fresh fish; and it differs from *U. willwhite* in narrower caudal peduncle, shorter jaws and barbels and absence vs. presence of mid-lateral body stripe in fresh fish.

Upeneus saib differs from the four featured species in more gill rakers and lack of bars on lower caudal-fin lobe; in addition it differs from *U. dimipavlov* in shallower body at anal-fin origin, shallower and narrower caudal peduncle, mostly lower anal fin, mostly longer pectoral fins and mostly lower second dorsal fin; it differs from *U. elongatus* in more pectoral-fin rays, deeper caudal peduncle, head through eye and suborbital, longer head and barbels and shorter pelvic fins; from *U. itoui* it differs in mostly shallower body at anal-fin origin and caudal peduncle, mostly narrower caudal peduncle, mostly deeper head through eye, larger eyes, longer barbels and mid-lateral body stripe in fresh fish absent vs. present; and from *U. willwhite* it differs in shallower and narrower caudal peduncle, thicker barbels, lower second dorsal fin and mid-lateral body stripe in fresh fish absent vs. present.

Upeneus seychellensis differs from the four featured species in bars on lower caudal-fin lobe lacking vs. being present. While having a mostly higher gill-raker count and a mostly narrower caudal peduncle than *U. dimipavlov*, *U. itoui* and *U. willwhite*, it has fewer gill rakers and a wider caudal peduncle than *U. elongatus*; in addition it differs from *U. dimipavlov* in shallower body, lower and shorter anal fin and longer and narrower pectoral fins; it differs from *U. elongatus* in more pectoral-fin rays, deeper caudal peduncle, head through eye and suborbital, shorter second dorsal-fin base, lower and shorter anal fin, shorter pelvic fins, narrower pectoral fins and lower second dorsal fin.

Upeneus torres differs from the four featured species in longer barbels, longer pelvic fins, mostly higher first dorsal fin and bars on lower-caudal fin lobe absent vs. present. Furthermore, it differs from *U. dimipavlov* in narrower caudal peduncle; it differs from *U. elongatus* in fewer gill rakers, deeper body, caudal peduncle and head, wider caudal peduncle, longer head and higher second dorsal fin; it differs from *U. itoui* in slightly deeper body at dorsal-fin origin, mostly deeper and longer head, larger eyes, slightly higher anal and longer pelvic fins, slightly higher second dorsal fin and absence vs. presence of mid-lateral body stripe in fresh fish; and it differs from *U. willwhite* in slightly more gill rakers and mid-lateral body stripe in fresh fish absent vs. present.

Differences from *Upeneus heterospinus* (Figures 1, 6, 7; Tables 1–4). The *margarethae*-group species *Upeneus heterospinus* overlaps with the *japonicus*-group species in having 7 or 8 dorsal-fin spines, while all other species that are not included in the *japonicus* group have exclusively 8 spines (Uiblein & Heemstra 2010; Uiblein *et al.* 2019, 2020a). It differs from all four featured species in about half of its population having eight dorsal-fin spines vs. exclusively seven spines, yellow vs. whitish barbels and slightly fewer bars on lower caudal-fin lobe (5–7 vs. 6–11 bars). Moreover, it differs from *U. dimipavlov* in slightly fewer gill rakers, narrower caudal peduncle, slightly larger maximum head depth, slightly shorter barbels, slightly longer pectoral fins, paired fins of subequal length vs. pelvic fins mostly longer than pectoral fins, a conspicuous mid-lateral body stripe in fresh fish present vs. absent and bars crossing lower caudal-fin lobe vs. bars positioned on margins of lobe; it differs from *U. elongatus* in fewer gill rakers, deeper body, caudal peduncle and head, wider caudal peduncle, higher second dorsal fin and yellowish-beige patches basally on dorsal fins absent vs. present in fresh fish; it differs from *U. itoui* in slightly fewer gill rakers, mostly deeper head, slightly longer pelvic fins, slightly higher second dorsal fin and mid-lateral body stripe yellow to pale brown vs. red brown in fresh fish; and it differs from *U. willwhite* in slightly shorter jaws, slightly shorter and thicker barbels, length of paired fins subequal vs. pelvic fins longer than pectoral fins, mid-lateral body stripe yellow to pale brown vs. dark brown in fresh fish and bars crossing lower caudal-fin lobe vs. bars positioned on margins of lobe.

Discussion

With the present study, the number of species of *Upeneus* has increased to 46 and the number of *japonicus*-group species to 17. This genus contributes almost half (47%) of all valid mullid species ($n = 98$; see also Froese & Pauly 2020; Uiblein 2021). In the CEITPAS area, there are now 25 species of *Upeneus* of which 13 (52%) have been described since 2010. Of the latter, seven (54%) are from the *japonicus* group. Possible reasons why so many species of this group have remained undiscovered are manifold. They show high similarity with other species leading to confusion and misidentification. This has been the case for both *U. dimipavlov* and *U. willwhite* which were previously identified as *U. guttatus*. Also, some of these species may be naturally rare and/or occur rather isolated and are possibly even under threat of extinction.

However, caution is needed to infer small-scale endemicity, rarity or even risk of extinction, before sufficient sampling and associated taxonomic screening has taken place. Each of the three new species is currently known from only a few specimens and narrow range, far apart from the other two species, respectively. However, as indicated by unvouchered *in-situ* photographs from the Philippines, *U. elongatus* may be more widely distributed. Clearly, more exploratory work including field sampling or fish-market surveys in association with the provision of scientific samples for taxonomic studies, detailed screening of relevant fish collections, as well as more *in-situ* monitoring should be carried out. This reasoning applies also to other *japonicus*-group species such as *U. lombok* and *U. farnis* which are currently known from three localities off Lombok (Uiblein & White 2015) and one locality of Bitung, NE Sulawesi, N Indonesia (Uiblein *et al.* 2017a), respectively.

Only in very specific cases, when a large area is relatively well sampled and screened, covered by detailed taxonomic studies of a distinct group of fishes and threat factors can be identified, a species may be assessed as being rare and possibly at risk according to IUCN Red List criteria (<https://www.iucnredlist.org/>). This has been the case for *U. saiab*, a *japonicus*-group species and the only species of the genus *Upeneus* assessed as endangered (Uiblein *et al.* 2020b). This species is only known from a small area off Angoche, N Mozambique, where there is an intense fishery and local threat of pollution by mining activities. The entire coast of Mozambique has been relatively well explored during recent years by research cruises with RV *Dr. Fridtjof Nansen* during which scientific samples were collected for subsequent fish-taxonomic studies (e.g., Uiblein & Heemstra 2010; Uiblein & Lisher 2013; Uiblein & Nielsen 2019; Uiblein *et al.* 2020a)

Of the four featured species, *Upeneus ituoi* is the only one of which many representative samples from a relatively large area in S Japan including the Ryukyu Islands have been collected and studied (Yamashita *et al.* 2011). Three years after the original description, a new record of this species from Tanega-shima Island, Osumi Islands (Kagoshima Prefecture) was reported based on two specimens collected at the same locality and with the same fishing gear (set net) as the HT of *U. elongatus* (Tashiro *et al.* 2014; this study). Because these two species co-occur, one may assume that *U. elongatus* is indeed a rare species in S Japan, but certainly it would be worthwhile to enhance sampling efforts on the islands further south as well as, e.g., off Taiwan and in the Philippines and screen scientific fish collections containing goatfish samples from these areas. This should allow to achieve a more complete picture of goatfish diversity, abundance and distribution. The same applies to Indonesia, Vietnam and many other still insufficiently explored parts of the CEITPAS area (see also, for instance, Motomura *et al.* 2012; Uiblein & White 2015; Uiblein *et al.* 2017a, b, 2018, 2019).

Acknowledgments

We thank the following colleagues for hospitality and assistance during collection visits or for providing other collection-related favors: Mark McGrouther, Amanda Hay & Kerryn Parkinson (AMS), James MacLaine (BMNH); Dave Catania and Jon Fong (CAS); Alastair Graham, Daniel C. Gledhill and William T. White (CSIRO); Rupert Wienerroither (HIFIRE); M. Takayama, Y. Haraguchi and other volunteers and students of KAUM; Zora Gabsi, Jonathan Pfliger, Patrice Pruvost, Romain Causse, Guy Duhamel and Philippe Béarez (MNHN); Dimitri A. Pavlov (Moscow); Åge Brabrand and Ann-Helen Rønning (NHMO); Hans Ho and Malena Yang (NMMBP); Roger Bills, Willem Coetzer, Mzwandile Dwani, Gavin Gouws, Bafo Konqobe, Nkosinathi Mazungula, Nonkoliso Mgibantaka and the NRF-SAIAB collection staff; Fareed Krupp and Sven Tränkner (SMF); Menachem Goren and Nir Stern (TAU); Tuan Anh Hoang (VNMN); and Peter Rask Møller, Jørgen G. Nielsen, Markus Krag, and Tammes Menne

(ZMUC). For providing or assistance in editing photos we thank Narissa Bax, Carlie Devine, Jessica Escobar-Porras, Camilla Floros, Daniel C. Gledhill, Alastair Graham, Dimitri A. Pavlov, Philippe and Guido Poppe and William T. White. The helpful comments and correction suggestions by the editor Ben Frable and the referees Jeff Johnson and Mark Lisher are gratefully acknowledged. The first author thanks the Center for Development Cooperation in Fisheries, Institute of Marine Research, Norway, CSIRO Hobart, Australia, NRF-SAIAB, South Africa, and the Russian-Vietnamese Tropical Research and Technological Center, Nha Trang, Vietnam, for travel and/or logistic support. This study was supported in part by JSPS KAKENHI Grant Numbers JP26450265, and 20H03311; the JSPS Core-to-Core Program: B Asia-Africa Science Platforms; and the “Establishment of Glocal Research and Education Network in the Amami Islands” project of Kagoshima University adopted by the Ministry of Education, Culture, Sports, Science and Technology, Japan.

References

- Allen, G.R. & Erdmann, M.V. (2012) *Reef Fishes of the East Indies. Vols. I–III*. Tropical Reef Research, Perth, 1292 pp.
- Bos, A.R. (2014) *Upeneus nigromarginatus*, a new species of goatfish (Perciformes: Mullidae) from the Philippines. *Raffles Bulletin of Zoology*, 62, 745–753.
- Carpenter, K.E &, Springer, V.G. (2005) The center of the center of marine shore fish biodiversity: the Philippine Islands. *Environmental Biology of Fishes*, 72, 467–480.
<https://doi.org/10.1007/s10641-004-3154-4>
- Edwards, A.J. & Glass, C.W. (1987) The fishes of Saint Helena Island, South Atlantic Ocean. I. The shore fishes. *Journal of Natural History*, 21, 617–686.
<https://doi.org/10.1080/00222938700770381>
- Froese, R. & Pauly, D. (Eds.) (2020) FishBase. World Wide Web electronic publication. www.fishbase.org, version (12/2020) (accessed February 2021)
- Ho, H.-C., Koeda, K. & Hilton, E.J. (2019) Study on the fish taxonomy and diversity of Taiwan. *Zootaxa*, 4702 (1), 1–229.
<https://doi.org/10.11646/zootaxa.4702.1.1>
- Hoeksema, B.W. (2007) Delineation of the Indo-Malayan centre of maximum marine biodiversity: the coral triangle. In: Renema, W. (Ed.), *Biogeography, Time and Place: Distributions, Barriers and Islands*. Springer, Dordrecht, pp. 117–178.
https://doi.org/10.1007/978-1-4020-6374-9_5
- Miller, E.C., Hayashi, K.T., Song, D. & Wiens, J.J. (2018) Explaining the ocean’s richest biodiversity hotspot and global patterns of fish diversity. *Proceeding of the Royal Society, B* 285, 20181314
<https://doi.org/10.1098/rspb.2018.1314>
- 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.
- Motomura, H., Kuriwa, K., Katayama, E., Senou, H., Ogihara, G., Meguro, M., Matsunuma, M., Takata, Y., Yoshida, T., Yamashita, M., Kimura, S., Endo, H., Murase, A., Iwatsuki, Y., Sakurai, Y., Harazaki, S., Hidaka, K., Izumi, H. & Matsuura, K. (2010) Annotated checklist of marine and estuarine fishes of Yaku-shima Island, Kagoshima, southern Japan. In: Motomura, H. & Matsuura, K. (Eds.), *Fishes of Yaku-shima Island—A World Heritage Island in the Osumi Group, Kagoshima Prefecture, Southern Japan*. National Museum of Nature and Science, Tokyo, pp. 65–261.
- Motomura, H., Yamashita, M., Itou, M., Haraguchi, Y. & Iwatsuki, Y. (2012) First records of the Two-tone Goatfish, *Upeneus guttatus*, from Japan, and comparisons with *U. japonicus* (Perciformes: Mullidae). *Species Diversity*, 17, 7–14.
<https://doi.org/10.12782/sd.17.1.007>
- Psomadakis, P.N., Htun Thein, Russell, B.C. & Mya Than Tun (2019) *Field identification guide to the living marine resources of Myanmar: FAO Species Identification Guide for Fishery Purposes*. FAO and MOALI, Rome, 694 pp., 63 colour pls.
- Randall, J.E. & Guézé, P. (1992) *Upeneus francisi*, a new goatfish (Perciformes: Mullidae) from Norfolk Island and New Zealand. *Cybium*, 16, 21–29.
- Randall, J.E. (2004) Revision of the goatfish genus *Parupeneus* (Perciformes: Mullidae), with descriptions of two new species. *Indo-Pacific Fishes*, 36, 1–64.
- Randall, J.E. (2001) Mullidae. In: Carpenter, K.E. & Niem, V.E. (Eds.), *FAO species identification guide for fishery purposes. The living marine resources of the Western Central Pacific. Vol. 5. Bony fishes part 3 (Menidae to Pomacentridae)*. Rome, FAO, 3175–3200.
- 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 1 October 2020)
- Tashiro, S. & Koeda, K. (2019) Family Mullidae. In: Koeda, K. & Ho, H.-C. (Eds.), *Fishes of Southern Taiwan*. National Museum of Marine Biology & Aquarium, Pingtung, pp. 902–924.
- Tashiro, S., Takayama, M. & Motomura, H. (2014) Distributional range extension of *Upeneus itoui* (Perciformes; Mullidae)

- in East Asia, with the first records from Tanega-shima Island in the Osumi Islands, Kagoshima, Japan, and notes on an unidentified specimen of *Upeneus* from Tanega-shima Island. *Nature of Kagoshima*, 40, 69–74.
- Uiblein, F. (2011) Taxonomic review of Western Indian Ocean goatfishes of the genus *Mulloidichthys* (Family Mullidae), with description of a new species and remarks on colour and body form variation in Indo-West Pacific species. *Smithiana Bulletin*, 13, 51–73.
- Uiblein, F. (2021) Taxonomic review of the “posteli-species group” of goatfishes (genus *Parupeneus*, Mullidae), with description of a new species from the northern Red Sea. *Cybium*, 45, 63–77.
- Uiblein, F., Everett, B., Maunde, C., Lisher, M., Matiku, P. & Sithole, Y. (2020b) *Upeneus saiba*. The IUCN Red List of Threatened Species, 2020, e.T159145328A159145590. <https://doi.org/10.2305/IUCN.UK.2020-2.RLTS.T159145328A159145590.en>
- 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. [first published online in 2014] <https://doi.org/10.1080/17451000.2014.958088>
- Uiblein, F., Gledhill, D.C. & Peristiwady T. (2017a) 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., Gledhill, D.C., Pavlov, D.A., Hoang, T.A. & Shaheen, S. (2019) Three new goatfishes of the genus *Upeneus* (Mullidae) from the Indo-Pacific, with a redescription of colour patterns in *U. margaretha*. *Zootaxa*, 4683 (2), 151–196. <https://doi.org/10.11646/zootaxa.4683.2.1>
- 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. & Stone, K. (2016) Just off the beach: intrageneric distinctiveness of the bandtail goatfish *Upeneus taeniopterus* (Mullidae) based on a comprehensive taxonomy and barcoding approach. *Marine Biology Research*, 12, 675–694. <https://doi.org/10.1080/17451000.2016.1190458>
- Uiblein, F., Gouws, G., Lisher, M. & Malauene, B.S. (2020a) *Upeneus floros*, a new goatfish from South Africa and Mozambique, with updated taxonomic accounts for *U. guttatus* and *U. pori* and a key to Western Indian Ocean *Upeneus* species (Mullidae). *Zootaxa*, 4834 (4), 523–555. <https://doi.org/10.11646/zootaxa.4834.4.3>
- 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., Hoang, T.A. & Gledhill, D. (2017b) Redescription and new records of Jansen’s goatfish, *P. jansenii* (Mullidae), from the Western Pacific and Eastern Indian Ocean. *Zootaxa*, 4344 (3), 541–559. <https://doi.org/10.11646/zootaxa.4344.3.6>
- Uiblein, F., Hoang, T.A., Alama, U., Causse, R., Chacate, O.E., Fahmi, Garibay, S. & Matiku, P. (2018) A new species and new records of goatfishes of the genus *Parupeneus* (Mullidae) from the Indian Ocean, with updated occurrence information for *P. jansenii* in the Western Pacific. *Cybium*, 42, 229–256.
- Uiblein, F., Köhler, C. & Tian, M.C. (1998) Quantitative examination of morphological variability among three goatfish species from the Malayan subprovince (Pisces: Perciformes: Mullidae: *Upeneus* spp.). *Senckenbergiana maritima*, 28, 123–132. <https://doi.org/10.1007/BF03043143>
- 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. & McGrouther, M. (2012) A new deep-water goatfish of the genus *Upeneus* (Mullidae) from northern Australia and the Philippines, with a taxonomic account of *U. subvittatus* and remarks on *U. mascareensis*. *Zootaxa*, 3550 (1), 61–70. <https://doi.org/10.11646/zootaxa.3550.1.4>
- Uiblein, F. & Nielsen, J.G. (2019) Redescription of the ocellus-bearing cuskeel *Neobythites kenyensis* (Ophidiidae), with new Southeast African records and remarks on intraspecific morphological and colour variation. *Cybium*, 43, 109–116
- 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>
- Yamashita Y., Golani, D. & Motomura, H. (2011) A new species of *Upeneus* (Perciformes: Mullidae) from southern Japan. *Zootaxa*, 3107 (1), 47–58. <https://doi.org/10.11646/zootaxa.3107.1.3>
- 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.