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Two New Goatfish Species of the *Upeneus sulphureus*-Species Group (Mullidae), with a Redescription of *U. sulphureus* Cuvier, 1829 and a Review of Barbel Length in the Genus

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For the goatfish genus *Upeneus*, the new *sulphureus*-species group is established, which includes five species, *U. doriae*, *U. nigromarginatus*, *U. sulphureus*, and the two new species, *U. alama* and *U. brevianalis*. This taxonomic group differs from the other seven species groups and four ungrouped species of this genus in the following combination of characters: 8 dorsal-fin spines, 14–17 pectoral-fin rays, 25–33 total gill rakers, 32–37 lateral-line scales, and lack of bars on caudal fin. *Upeneus sulphureus* is redescribed based on examination of a large set of morphometric, meristic, and color characters in 211 specimens, which revealed a bimodal distribution in barbel length prompting separation into short- and long-barbel morphs. This bimodality was neither sex-, size-, nor population-dependent, but found in co-occurring individuals of *U. sulphureus* in many areas of its distributional range from East Africa to Japan. The two new species differ from all other congeners primarily in *U. alama*, new species, having longer barbels (28–30% SL) and *U. brevianalis*, new species, having a shorter and shallower anal fin (8.1 and 12% SL, respectively) as well as a broad, dark-brown vertical band along the anterior third of the first dorsal fin. For *U. nigromarginatus*, new records from Papua New Guinea, Indonesia (West Papua), and three areas of the Philippines north of Mindanao are reported. For *U. doriae*, *U. sulphureus*, and *Mulloides pinnivittatus*, the latter a junior synonym of *U. sulphureus*, lectotypes are designated. An updated account for the genus *Upeneus* is provided. The barbel-length data of all 53 species of *Upeneus* are reviewed, and the finding of a wide range combined with a distinct dimorphism of this character in *U. sulphureus* is discussed.

THE goatfish genus *Upeneus* consists of 51 valid species of which 47 have been divided into eight taxonomic species groups to facilitate identification (Uiblein et al., 2024). The species in one of these groups, the so-called *moluccensis*-species group, share the following combination of characteristics: 8 dorsal-fin spines, 14–17 pectoral-fin rays, 25–33 total gill rakers, and lack of bars on lower caudal-fin lobe in fresh specimens (Uiblein and Heemstra, 2010). Uiblein and Heemstra (2010) included four species in this group: *Upeneus doriae*, *U. moluccensis*, *U. quadrilineatus*, and *U. sulphureus*. The most recently described species, *U. nigromarginatus*, was added to this group by Uiblein et al. (2024) based on data from Uiblein et al. (2016). No bars occur on the entire caudal fin in *U. doriae*, *U. nigromarginatus*, or *U. sulphureus*, whereas *U. moluccensis* and *U. quadrilineatus* do have dark oblique bars on the upper caudal-fin lobe (Randall and Kulbicki, 2006; Uiblein and Heemstra, 2010; Bos, 2014; Uiblein et al., 2016).

To emphasize the complete lack of caudal-fin bars as a diagnostic character, we establish here the new "*sulphureus*-species group," consisting of the three nominal species *U. doriae*, *U. nigromarginatus*, and *U. sulphureus*. This group can be distinguished from all other congeners by the following combination of characters: 8 dorsal-fin spines, 14–17 pectoral-fin rays, 25–33 total gill rakers, 32–37 lateral-line scales, and lack of bars on caudal fin. Lateral-line scales are added to allow reliable distinction from the ungrouped *Upeneus filifer*, which also lacks caudal-fin bars, but differs in having a lower scale count (28–29 lateral-line scales) and an extremely high first dorsal fin (Randall and Kulbicki, 2006; Uiblein et al., 2016). Accordingly, whereas *U. doriae*, *U. nigromarginatus*, and *U. sulphureus* are being transferred to the new *sulphureus* group, *U. moluccensis* and *U. quadrilineatus* remain in the *moluccensis* group based on the following characters shared by those two species: 8 dorsal-fin spines, 14–17 pectoral-fin rays, 26–30 total gill rakers, 33–36 lateral-line scales, and presence of oblique bars exclusively on

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upper caudal-fin lobe (Randall and Kulbicki, 2006; Uiblein and Heemstra, 2010; Uiblein et al., 2016).

Two of the three species in the *sulphureus* group, *U. doriae* and *U. nigromarginatus*, are currently known from relatively restricted areas, the Persian/Arabian Gulf and Gulf of Oman and the SE Philippines, respectively (Kim and Nakaya, 2003; Uiblein and Heemstra, 2010; Bos, 2014). The third species, *U. sulphureus*, is much more widely distributed from South Africa to the Red Sea, Japan, Fiji, and New Caledonia and is regarded as a senior synonym of five species, *Mulloides pinnivittatus*, *Upeneoides belaque*, *Upeneus bilineatus*, *U. bivittatus*, and *U. sanctaehelenae* (Lachner, 1954; Edwards and Glass, 1987; Randall and Kulbicki, 2006; Uiblein et al., 2024).

The taxonomy of *U. sulphureus* requires additional investigation. For instance, White et al. (2013) and Uiblein and Randall (2022) indicated the possible existence of one or two undescribed species referred to as *U.* cf. *sulphureus*, which were documented by fresh photographs of a specimen from Lombok, Indonesia (CSIRO H 7853-47), and one from Mozambique (SAIAB 82237), respectively.

In the current study, the two specimens of *U.* cf. *sulphureus* were compared in detail with types and non-type specimens of *U. doriae*, *U. nigromarginatus*, and *U. sulphureus* using a comprehensive alpha-taxonomy approach based on a large set of morphological characters (including color patterns), to evaluate inter- as well as intraspecific differentiation across their entire geographic distribution (see also Uiblein et al., 2024 and studies cited therein). We clarify the status of the two previously unidentified specimens and confirm the validity of the three *sulphureus*-group species including the junior synonymy of the above-listed five species.

Insufficiently reported variation in dorsal-fin color and barbel length, the latter character showing an exceptionally wide range, makes a redescription of *U. sulphureus* necessary. During this process, lectotypes were designated for both *U. sulphureus* and its junior synonym *M. pinnivittatus*. Three specimens from Philippines and Thailand were found to deviate in several characters including barbel length and anal-fin size, prompting the description of two new species in the *sulphureus* group, *U. alama* and *U. brevianalis*. Updated accounts of the genus *Upeneus* as well as *U. doriae* and *U. nigromarginatus* are provided and include a lectotype designation for the former and new records for the latter species. Barbel-length variation in the genus *Upeneus* is reviewed for all 53 species to better understand the extent of differentiation of this character in the *sulphureus*-species group. The discussion highlights the discovery of barbel-length dimorphism in *U. sulphureus*.

MATERIALS AND METHODS

We examined 41 morphometric and ten meristic characters for 251 specimens of the *sulphureus*-species group including types. Whereas the major focus of the study was on adults (≥ 65 mm SL), ten subadults of *U. sulphureus* and one *U. doriae* were also examined. Color patterns were studied using photos of fresh and preserved specimens considering both inter- and intraspecific variation. Methods of data collection, analysis, and presentation follow Uiblein and Heemstra (2010), Uiblein and McGrouther (2012), Uiblein and Causse (2013), Uiblein and Gouws (2014), Uiblein et al. (2016), Uiblein et al. (2020), and Uiblein and Motomura (2021).

Barbel-length data obtained from 1,388 specimens of all 53 species of *Upeneus* (including the two new species) were analyzed based on earlier published data and additional measurements collected from several species during the current study. For species comparisons of barbel length, only data of specimens considered to have reached adult status were used (≥ 120 mm SL in *U. taeniopterus*, ≥ 80 mm SL in *U. stenopsis*-group species, ≥ 70 mm SL in *U. tragula*-group species, and ≥ 65 mm SL in all other species; see respective publications above). In contrast to other species with a rather wide range in barbel length, like *Upeneus tragula* (see also Uiblein and Gouws, 2014), barbel length showed a bimodal distribution in *U. sulphureus* independent of size (Fig. 1). Two groups were established for analysis, a short-barbel morph ("SBM," maximum barbel length 18% SL) and a long-barbel morph ("LBM," barbel length >18% SL; Fig. 1). Subsequently, possible population-, sex-, or size-related distinctions between the two morphs were evaluated. Selected specimens from both morphs were sexed by visual inspection after careful opening of the gut region in front of anus. Subadults were studied separately.

All populations of *U. sulphureus* and populations split into barbel-length morphs ("subpopulations") were compared for three large geographic regions: the Western Indian Ocean, the CEITPAS region (coastal waters of the Eastern Indian Ocean and Tropical Pacific of Asia; see Uiblein and Motomura, 2021; Uiblein et al., 2024), and the area from Australia to Papua New Guinea (Oceania). Smaller-scale comparisons among subregions focused on the CEITPAS region, which was divided into Asian Eastern Indian Ocean, Japan, and the Asian West Pacific excluding Japan.

Comparisons among the *sulphureus*-group species involved the entire morphological dataset and both fresh and preserved color patterns, with focus on the most important diagnostic characters (i.e., differential diagnosis). Comparisons with other, morphologically similar species included published morphometric and meristic data from Uiblein and Gouws (2015) to circumvent challenges arising from preservation-related loss of diagnostically important color characters.

All morphometric and meristic data involved in the species comparisons are listed in Tables 1–7. Table 8 was prepared to facilitate the subsequent differential diagnosis. The figures support and illustrate comparisons and differential diagnosis. Ranges or single values of morphometric data from ten upward are rounded to full numbers, whereas data below ten are shown with one decimal digit. Means are provided with a decimal digit regardless of being above or below ten. An exception is the presentation of species comparisons of barbel length, with all values for this character provided with one decimal digit.

Lectotypes are designated for *Mulloides pinnivittatus*, *U. doriae*, and *U. sulphureus* based on preservation status, retained color patterns, completeness of morphometric and meristic data, and representative size of syntypes.

Institutional abbreviations follow Sabaj (2020). Other abbreviations are as follows: HT = holotype; LT = lectotype; PLT = paralectotype; PT = paratype; ST = syntype; SL = standard length; SBM = short-barbel morph (see above definition); LBM = long-barbel morph (see above definition); Min = minimum; Max = maximum; *n* = number (count); N = North; S = South; E = East; W = West; WCA = Western Central Atlantic (FAO Major Fishing Area 31); NWCA = WCA from

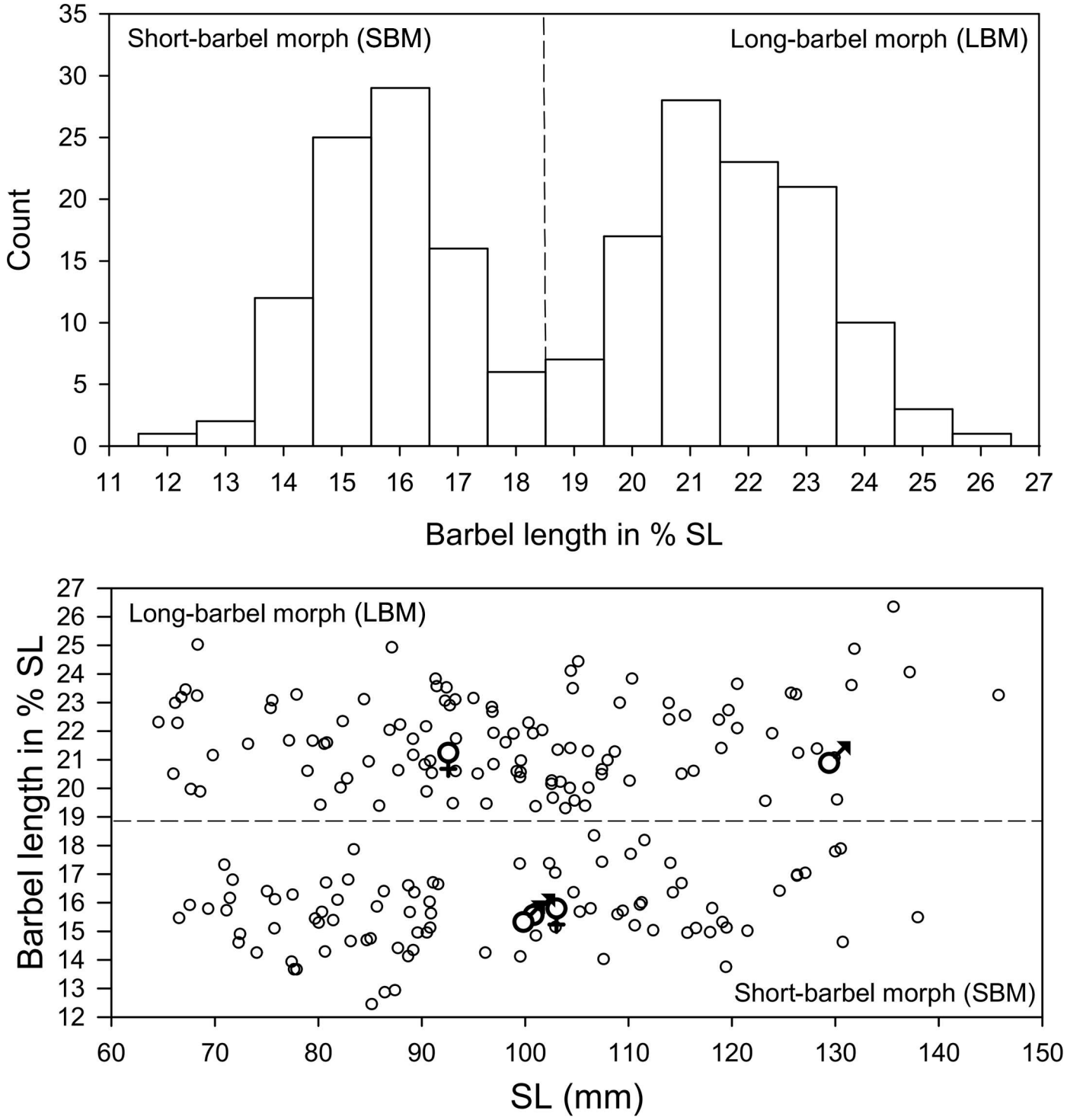

Fig. 1. Barbel length (expressed as % SL) in *Upeneus sulphureus* studied (n = 201). Top: Histogram with dashed vertical line for separation between short-barbel morph (SBM) and long-barbel morph (LBM). Bottom: Relationship with size (SL), showing separating line for the two morphs and symbols for five sexed specimens.

Mexico and Greater Antilles northward; SWCA = WCA from Belize and Lesser Antilles southward; SWA = Southwestern Atlantic; WIO = Western Indian Ocean (S Africa to Red Sea to W India and Sri Lanka); EIO = Eastern Indian Ocean (W Malaysia to S coast of Sunda Islands and waters of Timor Sea to SW Australia); WPAC = Western Pacific (Singapore to Japan and Oceania, south to New Zealand and Australia including Arafura Sea).

Mulliformes Rafinesque, 1815

Mullidae Rafinesque, 1815

Remarks.—For diagnostic information and rationale for establishing a monotypic order Mulliformes, see Uiblein et al. (2024). Six genera and 105 species in the single family Mullidae, including the two new species described herein.

Table 1. Measurements and counts for types of *Upeneus sulphureus*, its junior synonyms, and *U. doriae* and *U. nigromarginatus*.

	Upeneus sulphureus			*U. belaque*						*U. bilineatus*
					Paratypes					
	LT	PLT	PLT	HT	Min	Mean	Max	*n*	subadult	HT
SL (mm)	80	86	64	93	82	90.1	104	4	49	66
In % SL										
Body depth at first dorsal-fin origin	27	26	—	29	28	28.6	30	4	29	28
Body depth at anal-fin origin	25	24	23	25	24	24.8	26	4	25	24
Half body depth at first dorsal-fin origin	24	—	—	23	23	24	26	4	23	22
Half body depth at anal-fin origin	20	19	18	19	18	18.5	19	3	—	18
Caudal-peduncle depth	11	11	11	12	12	12	12	4	12	11
Caudal-peduncle width	3.7	3.8	3.8	5	4.1	4.2	4.7	4	4.2	3.4
Maximum head depth	22	22	21	23	24	24.8	26	4	25	23
Head depth through eye	18	17	18	18	19	19.6	21	4	19	17
Suborbital depth	9.9	10.7	9.8	10	10	11.3	12	4	10	9.3
Interorbital length	8	7.7	8	8.2	8.2	8.3	8.7	4	8.3	9
Head length	29	30	31	31	31	31.6	33	4	32	30
Snout length	11	—	11	11	11	11.9	13	4	12	10
Postorbital length	11	11	12	13	13	13.7	14	4	14	13
Orbit length	8.2	7.6	8.4	8.1	8.2	8.7	9.1	4	9.6	8.2
Orbit depth	7.3	6.8	7.4	7.1	7.3	7.8	8.1	4	8.7	7.5
Upper-jaw length	12	—	12	13	13	13.4	14	4	14	13
Lower-jaw length	11	11	11	13	13	13	14	4	13	12
Snout width	7.8	—	—	10	9	9.4	9.9	4	9.8	9
Barbel length	16	16	15	23	20	22	24	4	19	21
Maximum barbel width	1	0.8	0.8	1.2	0.9	1.1	1.2	4	1.1	0.8
First pre-dorsal length	38	—	37	40	39	41	43	4	39	39
Second pre-dorsal length	67	—	64	68	65	67.3	69	4	69	69
Interdorsal distance	18	17	18	15	13	14.1	15	4	13	15
Caudal-peduncle length	20	22	20	21	21	21.5	22	4	22	22
Pre-anal length	70	68	67	69	67	69	70	4	67	68
Pre-pelvic length	32	32	32	35	32	33.6	35	4	32	33
Pre-pectoral length	32	30	30	33	32	33.3	34	4	34	31
Second dorsal-fin depth	26	25	24	26	24	25.2	27	4	26	25
Pelvic-fin depth	26	26		28	27	28.2	30	4	29	27
Pectoral-fin depth	18	17	16	19	16	17.4	19	4	17	19
Length of first dorsal-fin base	15	14	15	17	17	17.8	19	4	18	16
Length of second dorsal-fin base	16	14	15	14	14	15	15	4	16	16
Caudal-fin length	—	—	—	31	31	31.6	33	4	32	28
Length of anal-fin base	12	10.9	9.9	13	13	12.7	13	4	13	11
Anal-fin height	17	17	—	19	16	18.1	19	4	19	17
Pelvic-fin length	19	18	18	21	21	22	22	4	22	17
Pectoral-fin length	24	23	23	24	25	26.1	27	4	26	22
Pectoral-fin width	4.9	4.4	4.5	4.9	4.7	5.1	5.4	4	5	4
First dorsal-fin height	—	—	—	25	24	24.9	26	4	26	—
Second dorsal-fin height	—	—	18	18	17	18	19	4	—	—
Meristic characters										
Pectoral-fin rays	15	15	15	15	15	15	15	4	15	15
Rudimentary gill rakers on upper limb	0	1	0	2	1	1.3	2	4	1	0
Developed gill rakers on upper limb	8	7	8	6	6	7.5	8	4	7	8
Developed gill rakers on lower limb	20	19	20	17	17	19.5	21	4	22	17
Rudimentary gill rakers on lower limb	0	1	0	4	0	1.8	4	4	0	3
Total gill rakers on upper limb	8	8	8	8	8	8.8	9	4	8	8
Total gill rakers on lower limb	20	20	20	21	21	21.3	22	4	22	20
Total gill rakers	28	28	28	29	29	30	31	4	30	28
Scales along lateral line	—	—	—	34	33	33.3	34	3	—	36

Table 1. Extended.

U. bivittatus	*U. pinnivittatus*		*U. sanctaehelenae*	*U. doriae*					*U. nigromarginatus*				
					Paralectotypes					Paratypes			
HT	LT	PLT	HT	LT	Min	Mean	Max	*n*	HT	Min	Mean	Max	*n*
116	110	99	92	82	65	76.2	94	13	201	140	153.2	162	6
26	28	26	28	30	27	27.5	29	13	33	30	31.3	34	6
25	24	24	23	26	23	24.1	26	13	27	24	25.9	28	6
21	23	21	23	23	20	21.0	23	13	26	23	24.1	26	6
18	19	19	17	19	17	17.7	19	13	18	17	18.2	20	6
11	11	11	10	11	10	11.0	12	13	12	12	12.1	12	6
4.9	4.2	4.2	5.2	3.9	3.2	3.8	4.1	13	4.1	3.8	4.1	4.5	6
23	22	21	23	23	22	22.5	24	13	27	25	26	28	6
18	17	16	17	18	17	17.4	19	13	20	20	20.3	21	6
11	10	9.9	10.4	9.8	9.0	9.7	11	13	13	12	12.1	12	6
9.1	8.6	8.4	7.7	8.1	7.4	7.8	8.4	13	8.2	8.1	8.4	8.8	6
30	29	28	30	31	29	30.2	31	13	32	32	32.8	34	6
10	10	9.7	11	12	9.4	10.1	11	13	13	12	12.4	13	6
12	13	12	13	13	11	12.2	14	13	13	12	12.9	13	6
7.4	7	7.5	8.2	8.1	7.8	8.6	9.5	13	7.5	8.1	8.2	8.4	6
6.7	6.4	6.7	7.2	7.5	6.8	7.7	8.4	13	6.8	7	7.1	7.2	6
13	12	12	13	12	11	12.1	13	13	13	13	13.3	14	6
13	11	12	12	11	11	11.5	12	13	13	12	12.9	13	6
8.9	9	8	9.8	9.5	7.9	8.5	9.2	13	11	9.5	10.5	11	6
15	18	17	23	19	15	16.8	19	13	19	19	20	20	6
0.9	0.9	0.7	1	1.0	0.8	0.9	1.0	13	1.4	1.2	1.3	1.4	6
41	37	37	40	39	38	39.6	41	13	42	42	43	43	6
68	67	68	69	67	64	66.4	68	13	68	66	67.6	69	6
14	17	17	16	16	14	15.4	17	13	14	14	14.8	16	6
20	20	21	20	23	20	21.9	23	13	20	19	19.9	21	6
65	67	67	68	67	65	67.3	70	13	68	69	70.2	71	6
35	33	32	33	35	32	34.4	35	13	34	34	34.7	35	6
32	30	30	32	33	31	32.6	33	13	32	33	33.4	34	6
26	24	25	24	26	24	25.2	27	13	28	26	27.2	30	6
27	28	26	29	29	26	26.8	28	13	33	30	31.6	35	6
18	16	16	20	17	16	17.2	18	13	20	18	19.7	20	6
14	15	16	17	15	14	15.1	17	13	14	14	14.9	16	6
13	14	14	14	14	13	14.6	16	13	14	15	15.6	17	6
29	28	28	28	29	27	28.6	30	11	31	30	31	32	6
10	11	12	12	12	11	11.5	12	13	9.5	9.1	9.6	10	6
17	15	—	16	16	14	15.1	16	11	17	17	17.2	18	6
19	18	18	19	20	17	19.0	21	12	20	19	20.4	21	6
25		22	25	25	22	23.6	25	10	28	27	27.7	29	6
4.1	4.7	5	5.1	5.3	4.5	4.9	5.2	13	5.7	4.8	5	5.4	6
22	22	23	24	24	21	22.4	23	12	25	25	26.2	27	6
16	17	—	16	15	14	14.6	15	10	18	18	19.1	20	6
16	15	17	16	16	15	15.6	16	13	16	16	16.2	17	6
1	2	1	1	0	0	0.5	2	13	3	1	2.8	5	6
7	6	7	7	8	7	7.9	9	13	5	3	4.8	6	6
17	18	19	17	21	17	20.6	23	13	13	12	12.7	13	6
5	3	3	2	1	0	1.8	4	13	5	5	5.3	6	6
8	8	8	8	8	8	8.5	9	13	8	7	7.7	8	6
22	21	22	19	22	21	22.5	24	13	18	17	18	19	6
30	29	30	27	30	30	30.9	33	13	26	25	25.7	27	6
35	35	35	34	33	32	33.3	34	6	34	33	34.3	35	6

Table 2. Measurements and counts for adults (≥65 mm SL) of the five *sulphureus*-group species including types of the two new species, with distinction of barbel-length morphs in *Upeneus sulphureus*.

	Upeneus sulphureus																							
	All				Short-barbel morph (SBM)				Long barbel morph (LBM)				*U. alama*, new species		*U. brevianalis*, new species	*U. doriae*				*U. nigromarginatus*			
	Min	Mean	Max	*n*	Min	Mean	Max	*n*	Min	Mean	Max	*n*	HT	PT	HT	Min	Mean	Max	*n*	Min	Mean	Max	*n*
SL (mm)	65	96.9	146	201	66	96.5	138	91	65	97.3	146	110	117	125	137	65	90.5	164	22	83	139.1	201	14
In % SL																							
Body depth at first dorsal-fin origin	25	29.1	33	201	26	29.4	33	91	25	28.8	33	110	31	30	32	27	28.0	31	22	30	31.3	34	14
Body depth at anal-fin origin	22	25.4	29	201	24	26.0	29	91	22	24.8	27	110	25	28	23	23	24.4	26	22	24	25.6	28	14
Half body depth at first dorsal-fin origin	20	23.1	26	194	21	23.5	26	85	20	22.9	26	109	25	24	25	20	21.6	24	22	23	24.4	27	13
Half body depth at anal-fin origin	17	19.1	23	198	18	19.7	23	90	17	18.5	21	108	19	19	17	17	18.2	20	22	17	18.4	21	14
Caudal-peduncle depth	10	11.3	12	201	10	11.3	12	91	10	11.3	12	110	12	12	11	10	11.1	12	22	10	11.8	12	14
Caudal-peduncle width	3.4	4.2	5.2	200	3.6	4.1	4.9	91	3.4	4.2	5.2	109	4.0	3.9	4.5	3.2	3.9	4.9	22	3.7	4.2	4.6	14
Maximum head depth	21	23.9	27	201	21	24.1	27	91	21	23.7	26	110	26	26	27	22	23.0	25	22	24	25.9	28	14
Head depth through eye	16	18.3	21	201	16	18.3	20	91	16	18.4	21	110	22	22	21	17	18.2	21	22	18	19.9	21	14
Suborbital depth	8.7	10.8	12	201	9.2	10.8	12	91	8.7	10.7	12	110	14	14	14	9.0	10.2	12	22	11	11.8	13	14
Interorbital length	7.1	8.1	9.1	201	7.5	8.3	9.1	91	7.1	8.1	9.0	110	9.3	8.4	8.7	7.4	8.0	8.7	22	7.8	8.4	8.8	14
Head length	28	30.1	33	201	28	29.9	32	91	28	30.4	33	110	34	34	33	29	30.3	31	22	30	32.1	34	14
Snout length	9.5	10.8	13	200	9.6	10.8	12	90	9.5	10.7	13	110	13	13	13	9.4	10.5	12	21	11	12.1	13	14
Postorbital length	11	12.6	14	201	11	12.2	13	91	11	12.9	14	110	14	14	14	11	12.2	14	22	12	12.8	13	14
Orbit length	7.0	8.0	9.5	201	7.0	8.0	9.2	91	7.2	8.1	9.5	110	8.2	7.7	8.0	6.6	8.2	9.5	22	7.2	8.2	9.2	14
Orbit depth	6.1	7.2	8.5	201	6.1	7.1	8.0	91	6.4	7.3	8.5	110	7.6	6.9	7.3	5.7	7.4	8.4	22	6.3	7.2	8.2	14
Upper-jaw length	11	12.5	14	200	11	12.3	14	90	11	12.7	14	110	15	15	14	10	11.8	13	22	13	13.3	14	14
Lower-jaw length	9.9	11.9	14	201	10	11.7	13	91	9.9	12.0	14	110	14	14	13	10	11.3	12	22	12	12.7	14	14
Snout width	7.8	9.5	12	195	7.8	9.3	12	88	8.2	9.8	12	107	11	10	11	7.9	8.7	9.5	20	8.9	10.2	11	14
Barbel length	12	19.0	26	201	12	15.7	18	91	19	21.7	26	110	30	28	20	15	16.9	20	22	18	20.7	24	14
Maximum barbel width	0.7	1.0	1.3	201	0.7	1.0	1.3	91	0.7	1.0	1.2	110	1.6	1.7	1.5	0.7	0.9	1.1	22	0.9	1.3	1.4	14
First pre-dorsal length	35	39.7	43	200	35	39.6	43	90	37	39.8	43	110	44	43	43	38	39.7	41	22	40	42.5	43	14
Second pre-dorsal length	64	67.5	70	200	64	67.7	70	90	64	67.4	70	110	69	70	72	64	66.6	69	22	66	67.9	70	14
Interdorsal distance	13	16.1	19	201	13	16.2	19	91	13	16.0	19	110	16	15	18	14	15.4	17	22	13	14.9	17	14
Caudal-peduncle length	18	20.8	23	201	18	20.8	23	91	18	20.7	23	110	22	21	19	20	21.5	23	22	17	19.6	21	14
Pre-anal length	63	67.9	71	201	64	67.8	70	91	63	68.0	71	110	70	72	71	65	67.8	72	22	67	69.7	71	14
Pre-pelvic length	30	33.4	38	201	31	33.4	37	91	30	33.4	38	110	36	36	35	32	34.5	36	22	34	34.8	37	14
Pre-pectoral length	30	31.6	35	201	30	31.4	34	91	30	31.7	35	110	36	34	34	31	32.5	34	22	32	33.2	34	14
Second dorsal-fin depth	22	26.1	30	201	24	26.7	30	91	22	25.6	27	110	27	28	24	24	25.5	27	22	25	26.8	30	14
Pelvic-fin depth	25	28.6	33	201	26	29.1	33	91	25	28.3	32	110	31	29	32	26	27.6	31	22	30	31.5	35	14
Pectoral-fin depth	16	19.1	22	201	16	19.1	22	91	16	19.0	21	110	20	19	21	16	17.7	20	22	18	19.7	22	14
Length of first dorsal-fin base	14	16.1	19	201	14	16.1	18	91	14	16.1	19	110	14	17	17	13	15.0	17	22	14	15.3	16	14
Length of second dorsal-fin base	13	14.8	17	201	13	14.9	17	91	13	14.8	16	110	14	14	15	13	14.8	16	22	14	15.0	17	14
Caudal-fin length	27	29.7	33	189	27	29.6	32	83	27	29.7	33	106	32	28	31	27	28.3	30	19	29	30.9	32	14
Length of anal-fin base	9.9	11.6	13	201	9.9	11.5	13	91	10	11.6	13	110	9.8	9.9	8.1	11	11.4	12	22	9.1	10.3	11	14
Anal-fin height	15	17.1	20	198	15	16.7	20	88	16	17.5	20	110	17	15	12	14	15.0	16	20	17	17.5	18	14
Pelvic-fin length	17	19.9	22	200	18	19.9	22	90	17	20.0	22	110	20	20	20	17	19.0	21	21	19	20.5	22	14
Pectoral-fin length	22	24.5	27	197	22	24.8	27	89	22	24.2	27	108	28	28	26	22	24.6	26	19	27	28.1	30	13
Pectoral-fin width	3.7	4.8	5.9	201	4.1	4.9	5.7	91	3.7	4.7	5.9	110	5.5	5.9	6.0	4.5	5.1	5.9	22	4.4	5.1	5.7	14
First dorsal-fin height	22	24.5	28	191	22	24.2	27	83	23	24.8	28	108	24	25	23	20	22.1	24	21	25	26.0	27	13
Second dorsal-fin height	16	17.5	20	190	16	17.1	20	81	16	17.8	20	109	17	17	17	14	14.6	16	19	18	18.8	20	14
Meristic characters																							
Pectoral-fin rays	14	15.7	17	201	15	15.6	17	91	14	15.7	17	110	16	16–16	16–16	15	15.8	17	22	14	15.9	17	14
Rudimentary gill rakers on upper limb	0	1.2	4	201	0	1.1	4	91	0	1.4	4	110	1–4	2–3	6–3	0	0.5	2	22	0	2.5	5	13
Developed gill rakers on upper limb	4	6.8	9	201	4	6.9	8	91	4	6.6	9	110	8–5	6–5	2–5	7	8.0	9	22	3	5.3	8	13
Developed gill rakers on lower limb	15	17.7	22	201	15	18.1	22	91	15	17.4	22	110	18–18	17–18	15–15	17	20.9	23	22	12	13.8	19	13
Rudimentary gill rakers on lower limb	0	2.7	6	201	0	2.3	6	91	0	3.1	6	110	4–3	3–3	5–5	0	1.7	4	22	1	4.8	6	13

Table 2. Continued.

	Upeneus sulphureus												*U. alama*, new species		*U. brevianalis*, new species		*U. doriae*			*U. nigromarginatus*			
	All				Short-barbel morph (SBM)				Long barbel morph (LBM)														
	Min	Mean	Max	*n*	Min	Mean	Max	*n*	Min	Mean	Max	*n*	HT	PT	HT	PT	Min	Mean	Max	*n*	Min	Mean	Max	*n*
Total gill rakers on upper limb	7	8.0	9	201	7	8.0	9	91	7	8.0	9	110	9–9	8–8	8–8		8	8.6	9	22	7	7.8	9	13
Total gill rakers on lower limb	18	20.4	22	201	19	20.3	22	91	18	20.5	22	110	22–21	20–21	20–20		21	22.6	24	22	17	18.6	20	13
Total gill rakers	26	28.4	31	201	26	28.3	30	91	27	28.5	31	110	31–30	28–29	28–28		30	31.2	33	22	25	26.5	28	13
Scales along lateral line	32	34.2	37	178	32	34.1	36	73	33	34.2	37	105	33–33	33–33	32–31		32	33.7	35	15	33	34.2	35	13

Upeneus Cuvier, 1829

Diagnosis.—Dorsal fins VII or VIII + 9; pectoral fins 12–17; anal fin (I),6–7; principal caudal-fin rays 7 + 8 (median 13 branched); gill rakers 4–9 upper + 13–24 lower = 18–33 total; lateral-line scales 28–39; lateral line complete; small scales present basally on second dorsal, anal, and/or caudal fins; teeth on jaws multiserial and villiform; body oblong, slightly compressed or nearly rounded; barbels 12–30% 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 live or freshly deceased fish; oblique bars often present on caudal-fin lobes, usually retained in preservative when darkly pigmented (their number, color, and form are of diagnostic importance); all species lacking caudal-fin bars with a dark or yellowish first dorsal-fin tip in life or when fresh (pigmentation often retained in preservation), or with an extremely high first dorsal fin.

Remarks.—The diagnosis has been updated to include the present findings on *sulphureus*-group species, in particular the new barbel-length data. The genus *Upeneus* consists of 53 valid species taking this study into account.

Upeneus sulphureus Cuvier, 1829

Sulphur Goatfish

Figures 1–6; Tables 1–6, 8

Upeneus sulphureus Cuvier in Cuvier and Valenciennes, 1829 (Java, Indonesia): Lachner, 1954; Edwards and Glass, 1987; Ben-Tuvia and Kissil, 1988; Kim and Nakaya, 2003; Randall and Kulbicki, 2006; Uiblein and Heemstra, 2010; Uiblein and McGrouther, 2012; White et al., 2013; Uiblein et al., 2016, 2024; Motomura et al., 2017; Uiblein and Maclaine, 2021; Gloerfelt-Tarp and Kailola, 2022; Uiblein and Randall, 2022.

Mulloides pinnivittatus Steindachner, 1870.

Upeneoides belaque Fowler, 1918.

Upeneus bilineatus Valenciennes in Cuvier and Valenciennes, 1831.

Upeneus bivittatus Valenciennes in Cuvier and Valenciennes, 1831.

Upeneus sanctaehelenae Bauchot, 1967.

Upeneus sulphureus: Fowler, 1933 (in part).

Upeneus cf. *sulphureus*: White et al., 2013; Uiblein and Randall, 2022.

Types.—*Upeneus sulphureus*: MNHN-IC-A-3458, LT, SBM, 80 mm SL, WPAC, Indonesia, Java, Sunda Strait, Pulau Ayer; MNHN-IC-2021-0446 (former MNHN-IC-A-3458), 2 PLTs, SBM, 64–86 mm SL, same locality as above; *U. belaque*: WPAC, Philippines: ANSP 47512, HT, LBM, 93 mm SL; ANSP 47513, 4 PT, 4 LBM, 49–91 mm SL; ANSP 47514, PT, LBM, 104 mm SL; *U. bilineatus*: MNHN-IC-0000-4064, HT, LBM, 66 cm SL, WPAC, Indonesia, Moluccas, Ambon; *U. bivittatus*: MNHN-IC-A-3816, HT, SBM, 116 mm SL, WIO, India, Maarashtra, Mumbai, 18°55′59″N, 72°51′E; *U. pinnivittatus*, NMW 71996, LT, SBM, 110 mm SL, Japan, Nagasaki; NMW 101581, PLT, SBM, 99 mm SL, same locality; *U. sanctaehelenae*, ZMUC P49301, HT, LBM, 92 mm SL, SE Atlantic, St. Helena Island (unverified area and locality).

Table 3. Measurements and counts for subadults (<65 mm SL) of *Upeneus sulphureus* and *U. doriae*, with distinction of barbel-length morphs in *U. sulphureus*.

	Upeneus sulphureus						
	SBM				LBM		*U. doriae*
	Min	Mean	Max	*n*	*n* = 2		*n* = 1
SL (mm)	53	58.2	64	8	49	64	58
In % SL							
Body depth at first dorsal-fin origin	25	27.4	30	7	29	28	25
Body depth at anal-fin origin	23	24.3	27	8	25	23	21
Half body depth at first dorsal-fin origin	21	22.0	24	6	23	22	20
Half body depth at anal-fin origin	17	18.7	21	8		19	16
Caudal-peduncle depth	11	11.4	12	8	12	11	9.9
Caudal-peduncle width	3.5	3.6	3.8	8	4.2	3.8	3.9
Maximum head depth	21	22.7	24	8	25	21	21
Head depth through eye	18	18.8	20	8	19	19	18
Suborbital depth	8.1	9.4	10	8	10	9.6	9.4
Interorbital length	8.0	8.3	8.6	8	8.3	8.3	8.5
Head length	30	30.8	31	8	32	30	28
Snout length	9.2	10.0	11	8	12	10	9.7
Postorbital length	12	13.3	14	8	14	14	10.5
Orbit length	8.1	8.4	8.8	8	9.6	7.5	9.3
Orbit depth	7.4	7.7	8.0	8	8.7	6.8	8.3
Upper-jaw length	12	12.2	13	8	14	13	11
Lower-jaw length	11	11.7	12	8	13	11.5	11
Snout width	7.8	8.3	8.9	7	9.8	9.2	9.0
Barbel length	14	15.1	18	8	19	22	20
Maximum barbel width	0.8	0.9	1.0	8	1.1	0.0	0.8
First pre-dorsal length	37	39.1	40	8	39	40	36
Second pre-dorsal length	64	66.9	69	8	69	67	68
Interdorsal distance	15	16.7	18	8	13	13	16
Caudal-peduncle length	20	22.2	23	8	22	21	21
Pre-anal length	65	67.0	69	8	67	66	68
Pre-pelvic length	32	33.2	35	8	32	30	32
Pre-pectoral length	30	32.2	33	8	34	33	29
Second dorsal-fin depth	22	24.7	28	8	26	23	23
Pelvic-fin depth	26	27.4	29	7	29	26	26
Pectoral-fin depth	16	17.2	19	8	17	18	18
Length of first dorsal-fin base	15	16.2	18	8	18	17	14
Length of second dorsal-fin base	13	15.4	17	8	16	14	13
Caudal-fin length	28	30.3	31	6	32	28	–
Length of anal-fin base	9.9	11.7	12	8	13	12	13
Anal-fin height	16	17.1	18	6	19	16	17
Pelvic-fin length	18	19.4	20	8	22	18	19
Pectoral-fin length	23	24.1	25	7	26	24	24
Pectoral-fin width	4.4	4.8	5.2	8	5.0	4.6	5.8
First dorsal-fin height	25	25.8	27	7	26	26	19
Second dorsal-fin height	16	17.7	19	8	–	16	15
Meristic characters							
Pectoral-fin rays	15	15.4	16	8	15	16	16
Rudimentary gill rakers on upper limb	0	0.3	1	8	1	1	1
Developed gill rakers on upper limb	7	7.9	9	8	7	8	6
Developed gill rakers on lower limb	17	19.9	22	8	22	20	18
Rudimentary gill rakers on lower limb	0	0.8	3	8	0	2	4
Total gill rakers on upper limb	8	8.1	9	8	8	9	7
Total gill rakers on lower limb	20	20.6	22	8	22	22	22
Total gill rakers	28	28.8	31	8	30	31	29
Scales along lateral line	33	34.0	35	5	–	35	35

Table 4. Measurements and counts for adult *Upeneus sulphureus* from three regions.

	WIO				CEITPAS				Australia and PNG			
	Min	Mean	Max	*n*	Min	Mean	Max	*n*	Min	Mean	Max	*n*
SL (mm)	66	93.7	130	54	65	97.9	146	141	82	108.1	138	9
In % SL												
Body depth at first dorsal-fin origin	26	29.1	33	54	25	29.1	33	141	26	29.9	33	9
Body depth at anal-fin origin	23	25.1	27	54	22	25.5	29	141	23	25.5	28	9
Half body depth at first dorsal-fin origin	20	23.2	25	54	20	23.1	26	134	22	23.8	26	9
Half body depth at anal-fin origin	17	18.8	21	54	17	19.2	23	138	18	19.0	21	9
Caudal-peduncle depth	10	11.2	12	54	10	11.3	12	141	11	11.5	12	9
Caudal-peduncle width	3.4	4.2	5.2	53	3.4	4.1	5.1	141	3.8	4.0	4.3	9
Maximum head depth	21	24.0	26	54	21	23.8	27	141	25	25.3	27	9
Head depth through eye	17	18.6	21	54	16	18.2	21	141	18	19.2	20	9
Suborbital depth	9.3	10.8	12	54	8.7	10.7	12	141	10	11.2	12	9
Interorbital length	7.3	8.1	9.1	54	7.4	8.2	9.1	141	7.1	8.0	8.6	9
Head length	29	30.4	33	54	28	30.0	33	141	29	30.4	32	9
Snout length	9.6	10.8	12	54	9.5	10.7	13	140	10	11.1	12	9
Postorbital length	11	13.0	14	54	11	12.4	14	141	12	12.7	14	9
Orbit length	7.4	8.2	9.5	54	7.0	8.0	9.1	141	7.2	7.9	9.2	9
Orbit depth	6.6	7.4	8.5	54	6.1	7.2	8.1	141	6.5	7.0	8.0	9
Upper-jaw length	12	12.7	14	54	11	12.5	14	140	12	12.6	13	9
Lower-jaw length	10	12.0	13	54	9.9	11.8	14	141	11	11.9	13	9
Snout width	8.2	9.8	12	52	7.8	9.4	12	137	9.9	10.8	12	7
Barbel length	15	20.4	25	54	12	18.4	26	141	14	18.2	24	9
Maximum barbel width	0.8	1.0	1.2	54	0.7	1.0	1.3	141	0.8	0.9	1.1	9
First pre-dorsal length	37	39.9	42	54	35	39.6	43	140	38	39.6	41	9
Second pre-dorsal length	65	67.4	70	54	64	67.6	70	140	66	67.4	69	9
Interdorsal distance	14	16.0	18	54	13	16.2	19	141	14	15.8	17	9
Caudal-peduncle length	18	20.6	23	54	18	20.8	23	141	18	19.8	21	9
Pre-anal length	65	67.8	71	54	63	68.0	70	141	64	68.1	70	9
Pre-pelvic length	30	33.4	36	54	31	33.3	38	141	33	35.3	37	9
Pre-pectoral length	30	31.9	34	54	30	31.5	35	141	31	32.4	34	9
Second dorsal-fin depth	24	25.8	28	54	22	26.2	30	141	24	26.2	29	9
Pelvic-fin depth	26	28.5	32	54	25	28.6	33	141	28	29.9	33	9
Pectoral-fin depth	17	19.2	21	54	16	19.0	22	141	19	19.9	22	9
Length of first dorsal-fin base	14	16.1	18	54	14	16.1	19	141	15	15.5	17	9
Length of second dorsal-fin base	13	15.0	16	54	13	14.8	17	141	13	14.0	16	9
Caudal-fin length	27	29.6	32	53	27	29.7	33	130	27	29.1	31	9
Length of anal-fin base	10	11.8	13	54	9.9	11.5	13	141	10	11.4	12	9
Anal-fin height	15	17.6	20	54	15	17.0	20	138	15	16.6	18	9
Pelvic-fin length	19	20.2	22	53	17	19.8	22	141	19	20.3	22	9
Pectoral-fin length	22	24.3	26	52	22	24.5	27	139	25	26.1	27	9
Pectoral-fin width	4.1	4.8	5.9	54	3.7	4.8	5.7	141	4.3	4.6	5.2	9
First dorsal-fin height	22	24.7	27	53	22	24.4	28	132	24	25.3	27	8
Second dorsal-fin height	16	17.8	20	52	16	17.4	20	132	16	17.5	18	8
Meristic characters												
Pectoral-fin rays	15	15.8	17	54	14	15.6	17	141	15	15.7	17	9
Rudimentary gill rakers on upper limb	0	1.2	4	54	0	1.2	4	141	0	1.3	3	9
Developed gill rakers on upper limb	4	6.6	8	54	4	6.8	9	141	5	6.8	8	9
Developed gill rakers on lower limb	15	17.1	20	54	15	17.9	22	141	16	17.7	19	9
Rudimentary gill rakers on lower limb	0	3.1	6	54	0	2.6	6	141	1	2.9	4	9
Total gill rakers on upper limb	7	7.8	9	54	7	8.1	9	141	7	8.1	9	9
Total gill rakers on lower limb	19	20.2	22	54	18	20.5	22	141	20	20.6	22	9
Total gill rakers	27	28.0	30	54	26	28.5	31	141	27	28.7	31	9
Scales along lateral line	33	34.3	37	51	32	34.1	37	121	34	34.6	37	9

Table 5. Measurements and counts for the two barbel-length morphs of adult *Upeneus sulphureus* from three regions.

	Short-barbel morph (SBM)												Long-barbel morph (LBM)											
	WIO				CEITPAS				Australia				WIO				CEITPAS				Papua New Guinea			
	Min	Mean	Max	*n*	Min	Mean	Max	*n*	Min	Mean	Max	*n*	Min	Mean	Max	*n*	Min	Mean	Max	*n*	Min	Mean	Max	*n*
SL (mm)	66	94.2	130	12	68	96.3	131	73	82	103.6	138	6	67	93.5	120	42	65	98.9	146	64	93	116.9	131	3
In % SL																								
Body depth at first dorsal-fin origin	26	29.0	32	12	26	29.4	33	73	29	31.0	33	6	26	29.1	33	42	25	28.7	32	64	26	27.6	29	3
Body depth at anal-fin origin	25	25.7	27	12	24	26.0	29	73	25	26.4	28	6	23	24.9	27	42	22	24.9	27	64	23	23.6	25	3
Half body depth at first dorsal-fin origin	21	22.9	25	12	21	23.5	26	67	23	24.4	26	6	20	23.3	25	42	20	22.6	26	63	22	22.6	23	3
Half body depth at anal-fin origin	18	19.0	20	12	18	19.8	23	72	18	19.5	21	6	17	18.7	21	42	17	18.5	20	62	18	18.1	19	3
Caudal-peduncle depth	11	11.3	12	12	10	11.3	12	73	11	11.6	12	6	10	11.2	12	42	10	11.3	12	64	11	11.2	12	3
Caudal-peduncle width	3.7	4.2	4.9	12	3.6	4.1	4.9	73	3.8	4.0	4.3	6	3.4	4.2	5.2	41	3.4	4.1	5.1	64	3.9	3.9	4.0	3
Maximum head depth	23	24.2	26	12	21	23.9	27	73	25	25.6	27	6	21	24.0	26	42	21	23.5	26	64	25	24.6	25	3
Head depth through eye	18	18.4	20	12	16	18.3	20	73	18	19.2	20	6	17	18.7	21	42	16	18.1	21	64	19	19.2	20	3
Suborbital depth	9.4	10.5	12	12	9.2	10.8	12	73	11	11.5	12	6	9.3	10.9	12	42	8.7	10.5	12	64	10	10.4	10	3
Interorbital length	7.8	8.4	9.1	12	7.6	8.2	9.1	73	7.5	8.2	8.6	6	7.3	8.0	9.0	42	7.4	8.1	9.0	64	7.1	7.4	7.8	3
Head length	29	30.2	31	12	28	29.8	32	73	29	30.5	32	6	29	30.4	33	42	28	30.3	33	64	29	30.3	31	3
Snout length	9.7	10.7	12	12	9.6	10.8	12	72	10	11.1	12	6	9.6	10.9	12	42	9.5	10.6	13	64	11	11.1	11	3
Postorbital length	10.7	12.3	13	12	11	12.1	13	73	12	12.5	13	6	11.9	13.2	14	42	11	12.8	14	64	13	13.2	14	3
Orbit length	7.4	8.1	8.6	12	7.0	7.9	8.8	73	7.6	8.1	9.2	6	7.5	8.2	9.5	42	7.2	8.0	9.1	64	7.2	7.5	7.9	3
Orbit depth	6.7	7.3	7.8	12	6.1	7.1	8.0	73	7.0	7.3	8.0	6	6.6	7.5	8.5	42	6.4	7.2	8.1	64	6.5	6.6	6.8	3
Upper-jaw length	12	12.5	13	12	11	12.3	14	72	12	12.3	13	6	12	12.7	14	42	11	12.7	14	64	13	13.2	13	3
Lower-jaw length	11	12.0	13	12	10	11.7	13	73	11	11.7	13	6	10	12.0	13	42	9.9	12.0	14	64	12	12.2	13	3
Snout width	8.3	9.4	10	12	7.8	9.2	11	72	9.9	10.9	12	4	8.2	9.9	12	40	8.2	9.6	12	63	10	10.6	11	3
Barbel length	15	16.3	17	12	12	15.6	18	73	14	15.6	17	6	19	21.5	25	42	19	21.8	26	64	23	23.3	24	3
Maximum barbel width	0.8	0.9	1.0	12	0.7	1.0	1.3	73	0.8	0.9	1.0	6	0.8	1.0	1.2	42	0.7	1.0	1.2	64	0.9	1.0	1.1	3
First pre-dorsal length	38	40.3	42	12	35	39.5	43	72	38	39.3	40	6	37	39.8	42	42	37	39.8	43	64	39	40.0	41	3
Second pre-dorsal length	66	67.7	69	12	64	67.7	70	72	66	67.7	69	6	65	67.3	70	42	64	67.4	70	64	66	67.0	68	3
Interdorsal distance	14	16.0	18	12	13	16.3	19	73	14	15.9	17	6	14	16.0	18	42	13	16.0	19	64	14	15.5	17	3
Caudal-peduncle length	18	21.0	23	12	19	20.9	23	73	18	19.7	21	6	18	20.5	23	42	18	20.9	23	64	20	19.8	20	3
Pre-anal length	65	67.0	69	12	64	67.8	70	73	68	68.8	70	6	66	68.0	71	42	63	68.1	70	64	64	66.5	69	3
Pre-pelvic length	32	33.7	35	12	31	33.1	36	73	35	35.8	37	6	30	33.2	36	42	31	33.4	38	64	33	34.2	35	3
Pre-pectoral length	30	31.9	33	12	30	31.3	34	73	31	32.5	34	6	30	31.9	34	42	30	31.6	35	64	32	32.3	33	3
Second dorsal-fin depth	25	26.2	28	12	24	26.7	30	73	26	27.2	29	6	24	25.6	27	42	22	25.6	27	64	24	24.2	25	3
Pelvic-fin depth	27	28.6	30	12	26	29.0	33	73	28	30.7	33	6	26	28.5	32	42	25	28.1	31	64	28	28.5	29	3
Pectoral-fin depth	17	18.6	21	12	16	19.1	22	73	19	20.4	22	6	17	19.3	21	42	16	18.8	21	64	19	19.0	19	3
Length of first dorsal-fin base	14	15.7	17	12	14	16.2	18	73	15	15.4	16	6	15	16.2	18	42	14	16.1	19	64	15	15.7	17	3
Length of second dorsal-fin base	13	15.1	16	12	14	14.9	17	73	13	14.3	16	6	14	14.9	16	42	13	14.8	16	64	13	13.3	14	3

Table 5. Continued.

	Short-barbel morph (SBM)												Long-barbel morph (LBM)											
	WIO				CEITPAS				Australia				WIO				CEITPAS				Papua New Guinea			
	Min	Mean	Max	*n*	Min	Mean	Max	*n*	Min	Mean	Max	*n*	Min	Mean	Max	*n*	Min	Mean	Max	*n*	Min	Mean	Max	*n*
Caudal-fin length	28	29.4	32	11	27	29.6	32	66	28	29.5	31	6	27	29.7	32	42	28	29.9	33	60	27	28.3	30	3
Length of anal-fin base	10	11.7	13	12	9.9	11.5	13	73	10	11.2	12	6	11	11.8	13	42	10	11.5	13	64	11	11.7	12	3
Anal-fin height	15	17.1	19	12	15	16.6	20	70	15	16.1	17	6	16	17.7	20	42	16	17.4	19	64	17	17.6	18	3
Pelvic-fin length	19	19.9	21	11	18	19.9	22	73	19	20.5	22	6	19	20.2	22	42	17	19.8	22	64	19	19.8	21	3
Pectoral-fin length	22	24.0	26	11	22	24.8	27	72	25	26.0	27	6	22	24.4	26	41	22	24.0	27	63	26	26.1	27	3
Pectoral-fin width	4.1	4.8	5.3	12	4.2	4.9	5.7	73	4.4	4.8	5.2	6	4.1	4.8	5.9	42	3.7	4.6	5.4	64	4.3	4.4	4.8	3
First dorsal-fin height	22	24.5	26	11	22	24.1	27	67	24	25.3	27	5	23	24.7	27	42	23	24.8	28	62	25	25.3	26	3
Second dorsal-fin height	16	17.0	19	10	16	17.1	20	66	16	17.5	18	5	16	18.0	20	42	16	17.7	20	63	17	17.7	18	3
Meristic characters																								
Pectoral-fin rays	15	15.8	16	12	15	15.6	17	73	15	15.3	16	6	15	15.7	17	42	14	15.6	17	64	16	16.3	17	3
Rudimentary gill rakers on upper limb	0	1.0	4	12	0	1.1	3	73	0	1.2	3	6	0	1.3	4	42	0	1.4	4	64	1	1.7	3	3
Developed gill rakers on upper limb	4	6.8	8	12	4	7.0	8	73	5	6.5	8	6	4	6.5	8	42	4	6.7	9	64	6	7.3	8	3
Developed gill rakers on lower limb	15	17.3	20	12	15	18.2	22	73	16	17.7	19	6	15	17.0	20	42	15	17.5	22	64	17	17.7	19	3
Rudimentary gill rakers on lower limb	1	2.8	5	12	0	2.2	6	73	1	2.5	4	6	0	3.2	6	42	0	3.0	5	64	3	3.7	4	3
Total gill rakers on upper limb	7	7.8	9	12	7	8.0	9	73	7	7.7	8	6	7	7.8	9	42	7	8.1	9	64	9	9.0	9	3
Total gill rakers on lower limb	19	20.2	22	12	19	20.4	22	73	20	20.2	21	6	19	20.3	22	42	18	20.6	22	64	21	21.3	22	3
Total gill rakers	27	27.9	30	12	26	28.4	30	73	27	27.8	29	6	27	28.0	29	42	27	28.7	31	64	30	30.3	31	3
Scales along lateral line	33	34.2	35	10	32	34.1	36	57	34	34.2	35	6	33	34.3	37	41	33	34.2	37	60	34	35.3	37	3

Table 6. Measurements and counts for the two barbel-length morphs of adult *Upeneus sulphureus* from three subregions of CEITPAS.

	Short-barbel morph (SBM)												Long-barbel morph (LBM)								
	EIO				WPAC				Japan				EIO				WPAC				Japan
	Min	Mean	Max	*n*	Min	Mean	Max	*n*	Min	Mean	Max	*n*	Min	Mean	Max	*n*	Min	Mean	Max	*n*	*n* = 1
SL (mm)	71	108.1	131	14	68	91.4	126	50	99	105.6	110	5	66	109.5	137	21	65	95.1	146	45	99
In % SL																					
Body depth at first dorsal-fin origin	28	30.1	33	14	26	29.4	33	50	26	27.6	28	5	25	28.9	32	21	25	28.6	32	45	28
Body depth at anal-fin origin	25	26.3	28	14	24	26.1	29	50	24	24.7	26	5	23	25.1	27	21	22	24.7	27	45	25
Half body depth at first dorsal-fin origin	22	23.8	25	14	21	23.6	26	44	21	22.4	23	5	20	22.8	25	21	20	22.5	26	44	22
Half body depth at anal-fin origin	18	19.8	22	14	18	20.0	23	49	19	19.1	20	5	17	18.6	20	21	17	18.4	20	43	18
Caudal-peduncle depth	11	11.1	12	14	10	11.4	12	50	11	11.1	11	5	11	11.3	12	21	10	11.3	12	45	10
Caudal-peduncle width	3.8	4.1	4.5	14	3.6	4.2	4.9	50	3.9	4.2	4.5	5	3.7	4.3	5.1	21	3.4	4.1	5.1	45	4.2
Maximum head depth	24	25.1	27	14	22	23.7	26	50	21	22.5	23	5	21	23.7	25	21	21	23.5	26	45	22
Head depth through eye	18	19.2	20	14	17	18.1	20	50	16	17.0	18	5	17	18.1	20	21	16	18.2	21	45	18
Suborbital depth	10	11.4	12	14	9.5	10.8	12	50	9.2	10.0	11	5	8.8	10.6	12	21	8.7	10.5	12	45	9.8
Interorbital length	8.0	8.4	8.9	14	7.6	8.2	9.1	50	8.3	8.5	8.8	5	7.4	8.1	9.0	21	7.1	8.1	9.0	45	7.7
Head length	30	30.9	32	14	28	29.5	31	50	28	28.9	30	5	28	30.3	32	21	28	30.4	33	45	29
Snout length	11	11.3	12	14	9.9	10.8	12	49	9.6	9.9	10	5	9.7	10.5	11	21	9.5	10.7	13	45	9.5
Postorbital length	12	12.8	13	14	11	11.9	13	50	11	12.2	13	5	12	12.9	14	21	11	12.7	14	45	12
Orbit length	7.5	8.0	8.5	14	7.1	7.9	8.8	50	7.0	7.2	7.5	5	7.3	8.0	8.8	21	7.2	8.0	9.1	45	7.7
Orbit depth	6.7	7.2	7.6	14	6.4	7.1	8.0	50	6.1	6.4	6.7	5	6.6	7.2	7.8	21	6.4	7.2	8.1	45	6.7
Upper-jaw length	12	12.7	13	14	11	12.2	14	49	12	12.0	12	5	11	12.5	13	21	11	12.8	14	45	13
Lower-jaw length	12	12.1	13	14	10	11.6	13	50	11	11.3	12	5	9.9	11.7	13	21	10	12.1	14	45	12
Snout width	8.4	9.5	10	14	7.8	9.2	11	49	8.0	8.6	9.2	5	8.5	9.9	11	21	8.2	9.6	12	44	9.4
Barbel length	14	15.7	18	14	12	15.3	18	50	16	17.4	18	5	19	21.9	26	21	19	21.8	25	45	21
Maximum barbel width	0.9	1.0	1	14	0.8	1.0	1.3	50	0.7	0.8	0.9	5	0.8	1.0	1.1	21	0.7	1.0	1.2	45	1.0
First pre-dorsal length	40	41.1	43	14	35	39.2	42	49	37	38.1	39	5	38	40.2	42	21	37	39.7	43	45	39
Second pre-dorsal length	67	68.7	70	14	64	67.3	70	49	67	67.4	68	5	65	67.4	69	21	64	67.4	70	45	67
Interdorsal distance	14	16.4	18	14	14	16.3	19	50	14	16.2	17	5	14	15.9	18	21	13	16.0	19	45	16
Caudal-peduncle length	19	20.6	21	14	19	21.1	23	50	20	20.4	21	5	18	20.5	22	21	18	21.0	23	45	21
Pre-anal length	66	67.9	70	14	66	67.8	70	50	67	68.0	70	5	66	68.4	70	21	63	67.9	70	45	67
Pre-pelvic length	33	33.8	35	14	31	33.0	36	50	32	32.7	34	5	31	33.3	36	21	31	33.5	38	45	34
Pre-pectoral length	31	32.4	34	14	30	31.1	33	50	30	30.4	31	5	30	31.4	33	21	30	31.7	35	45	31
Second dorsal-fin depth	26	27.0	28	14	24	26.9	30	50	24	25.2	26	5	24	26.0	27	21	22	25.3	27	45	26
Pelvic-fin depth	28	29.9	32	14	26	28.9	33	50	26	27.8	29	5	25	28.3	31	21	25	28.1	30	45	27
Pectoral-fin depth	18	19.4	21	14	17	19.2	22	50	16	17.4	20	5	17	19.1	21	21	16	18.7	21	45	18
Length of first dorsal-fin base	14	16.3	18	14	14	16.2	18	50	15	15.1	16	5	15	16.0	17	21	14	16.1	19	45	16
Length of second dorsal-fin base	14	14.8	16	14	14	15.0	17	50	14	14.2	15	5	13	14.3	16	21	13	14.9	16	45	14
Caudal-fin length	29	29.6	32	13	27	29.6	32	46	28	28.4	29	3	28	29.8	33	21	27	29.8	33	41	29
Length of anal-fin base	11	11.4	12	14	9.9	11.5	13	50	10	11.3	12	5	10	11.2	13	21	10	11.6	13	45	12
Anal-fin height	15	16.3	18	14	15	16.8	20	48	15	16.1	17	4	16	17.0	18	21	16	17.6	19	45	17
Pelvic-fin length	19	19.6	22	14	18	20.1	22	50	18	18.1	19	5	18	19.5	21	21	17	19.9	22	45	19
Pectoral-fin length	23	25.1	27	14	22	24.9	27	50	22	22.1	22	4	22	23.9	26	20	22	24.2	27	45	23

Table 6. Continued.

	Short-barbel morph (SBM)										Long-barbel morph (LBM)									
	EIO				WPAC				Japan			EIO			WPAC				Japan	
	Min	Mean	Max	*n*	Min	Mean	Max	*n*	Min	Mean	Max	*n*	Min	Mean	Max	*n*	Min	Mean	Max	*n*	*n* = 1
Pectoral-fin width	4.2	5.0	5.6	14	4.3	4.9	5.7	50	4.7	4.9	5.0	5	3.7	4.6	5.3	21	4.0	4.6	5.4	45	4.6
First dorsal-fin height	22	23.1	26	14	22	24.4	26	44	22	22.6	23	5	23	24.2	26	21	23	25.1	28	43	25
Second dorsal-fin height	16	16.8	18	14	16	17.1	20	44	16	16.6	17	4	16	17.3	19	21	16	17.9	20	44	18
Meristic characters																					
Pectoral-fin rays	15	15.6	16	14	15	15.6	17	50	15	15.6	17	5	14	15.7	17	21	15	15.6	17	45	16
Rudimentary gill rakers on upper limb	0	1.7	3	14	0	0.9	2	50	0	0.8	2	5	0	1.8	4	21	0	1.2	4	45	2
Developed gill rakers on upper limb	4	6.2	8	14	6	7.2	8	50	6	7.2	8	5	4	6.2	8	21	4	7.0	9	45	6
Developed gill rakers on lower limb	16	17.2	19	14	15	18.5	22	50	17	18.4	20	5	16	17.6	22	21	15	17.6	21	45	17
Rudimentary gill rakers on lower limb	2	3.6	6	14	0	1.7	4	50	0	2.4	4	5	0	3.0	5	21	0	3.0	5	45	4
Total gill rakers on upper limb	7.0	7.9	9	14	7	8.1	9	50	7	8.0	9	5	7	8.0	9	21	7	8.2	9	45	8
Total gill rakers on lower limb	20	20.8	22	14	19	20.2	22	50	20	20.8	22	5	19	20.6	22	21	18	20.6	22	45	21
Total gill rakers	27	28.7	30	14	26	28.3	30	50	27	28.8	30	5	27	28.7	31	21	27	28.8	31	45	29
Scales along lateral line	33	34.0	35	14	32	33.9	35	35	34	35.0	36	5	33	34.3	37	21	33	34.2	37	42	—

Non-type material.—(*n* = 197, 53–146 mm SL) WIO: Red Sea: BMNH 1858.6.1.8, SBM, 109 mm SL; HUJ 11665, 3 SBM, 62–86 mm SL, Eritrea, Massawa, 20–40 m depth; Kenya: SAIAB 13935, 3 LBM, 106–120 mm SL, Malindi, R/V *Dr. F. Nansen*, 3°7′S, 40°11′E, 17 m depth, bottom trawl; SAIAB 82821, SBM, 115 mm SL, same locality and sampling data; Mozambique: ICM 7794, LBM, 99 mm SL, 19°26′S, 35°56′E, 15 m depth; ICM 7802, LBM, 97 mm SL, 19°26′S, 35°56′E; SAIAB 82237, 7 LBM, 99–108 mm SL, R/V *Dr. F. Nansen*, 19°35.3′S, 35°31.6′E, 22 m depth; SAM MB-F 034160, LBM, 101 mm SL (1 of 7), R/V *Algoa*, 17°32′S, 38°18′E, 50 m depth, bottom trawl; South Africa: SAM MB-F 025008, SBM, 130 mm SL, Tugela River, 29°13′S, 31°29′E; Seychelles: MNHN-IC-A-3815, SBM, 103 mm SL (1 of 14), Mahé; Madagascar: MNHN-IC-1966-0830, 7 LBM, 102–114 mm SL (7 of 8), Nossi Be; MNHN-IC-1966-0880, LBM, 104 mm SL, Nossi Be; MNHN-IC-1966-1099, LBM, 79 mm SL; MNHN-IC-1992-1030, SBM, 71 mm SL, Ile aux Nattes; MNHN-IC-1992-1031, 4 LBM, 68–80 mm SL, Toliara; NRM 10647, 5 LBM, 67–81 mm SL (5 of 12), Boeny, Mahajanga; SAIAB 97930, LBM and SBM, 102–116 mm SL, Libanona Beach, Fort Dauphin, Anosy, 25°2.347′S, 46°59.743′E, gill net; W India: ANSP 208633, LBM, 64 mm SL, Kerala, N of Trivandrum, 2–6 m depth, rotenone; BMNH 89.2.1.3015, SBM, 81 mm SL, Maharashtra, Mumbai; MNHN-IC-1981-1167, LBM, 75 mm SL (1 of 2), Kerala, Kochin; ZMO J 7188, LBM, 89 mm SL, Kerala, Ashtamudi, 22–37 m depth; Sri Lanka: NMW 87010, 3 LBM and 2 SBM, 66–88 mm SL, Kalkudah; SAIAB 187364, 5 LBM, 91–105 mm SL, Negombo fish market, 7°12′20″N, 79°49′42″E.

EIO: India, Tamil Nadu: MNHN-IC-A-3459, LBM, 98 mm SL, Chennai; MNHN-IC-A-3501, 2 LBM, 120–126 mm SL, Puducherry; NMW 73658, LBM, 91 mm SL, Chennai; USNM 395432, LBM, 128 mm SL, Cuddalore; USNM 429429, LBM, 137 mm SL (1 of 3), Chinnur, Vellar Estuary; USNM 429431, LBM, 136 mm SL (1 of 9), Thirumullivasal; Bay of Bengal, Myanmar: SAIAB 203678, SBM, 130 mm SL, R/V *Dr. F. Nansen*, 18°52.27′N, 93°22.72′E, 48 m depth, bottom trawl; Andaman Sea, Myanmar: NMW 101619, LBM, 130 mm SL, male, R/V *Dr. F. Nansen*, 14°44.22′N, 96°55.06′E, 52–58 m depth, bottom trawl; SAIAB 208324, 2 LBM and SBM, 119–126 mm SL, R/V *Dr. F. Nansen*, 14°37.04′N, 97°34.82′E, 58 m depth, bottom trawl; SAIAB 208641, 2 LBM, 119–120 mm SL, R/V *Dr. F. Nansen*, 15°24.17′N, 94°53′E, 32 m depth, bottom trawl; Thailand, Phuket: KAUM-I.59652, SBM, 89 mm SL, Phuket Fishing Port; ZMUC P49372, SBM, 111 mm SL; ZMUC P49373, SBM, 85 mm SL; ZMUC P49374, SBM, 103 mm SL; ZMUC P49376, SBM, 126 mm SL; ZMUC P49377, SBM, 131 mm SL; ZMUC P49378, SBM, 127 mm SL; ZMUC P49559, SBM, 118 mm SL; Thailand, Thai-Danish Expedition, 6°57′N, 99°23′E: ZMUC P49405, SBM, 103 mm SL, female; ZMUC P49468, SBM, 101 mm SL, male; ZMUC P49469, SBM, 100 mm SL, female; Indonesia, W Sumatra, Padang: NMW 73653, 2 LBM and SBM, 71–93 mm SL; NMW 73654, 2 LBM, 84–107 mm SL; Central Java, Cilacap, 7°44′S, 109°1′E: CSIRO H 7469-13, SBM, 109 mm SL; CSIRO H 9285-10, SBM, 101 mm SL; CSIRO H 9285-24, SBM, 114 mm SL; Lombok, Tanjung Luar, 8°48′S, 116°29′E: CSIRO H 7217-46, LBM, 115 mm SL; CSIRO H 7305-09, 3 SBM, 53–56 mm SL; CSIRO H 7363-46, LBM, 66 mm SL; CSIRO H 7853-46, LBM, 104 mm SL; CSIRO H 7853-47, LBM, 110 mm SL; CSIRO H 8409-47, LBM, 99 mm SL; CSIRO H 9379-01, SBM, 89 mm SL; Western Australia: CSIRO CA 228, SBM, 111 mm SL, F/R/V *Courageous*; CSIRO CA 2120, SBM, 89 mm SL, N of

Table 7. Measurements and counts for *Upeneus nigromarginatus* from different areas.

	Philippines								
	Mindanao, Negros Oriental					Indonesia		Papua New Guinea	
	Min	Mean	Max	*n*	Luzon	W Papua		Madang	
SL (mm)	101	153.4	201	9	83	142	127	128	88
In % SL									
Body depth at first dorsal-fin origin	30	31.4	34	9	31	33	31	30	30
Body depth at anal-fin origin	24	25.7	28	9	25	27	27	24	25
Half body depth at first dorsal-fin origin	23	24.3	26	8	25	27	24	23	23
Half body depth at anal-fin origin	17	18.1	20	9	18	21	19	18	19
Caudal-peduncle depth	11	12.0	12	9	12	12	12	10	11
Caudal-peduncle width	3.7	4.1	4.5	9	4.1	4.6	4.6	4.1	4.0
Maximum head depth	24	25.9	28	9	25	27	26	25	26
Head depth through eye	20	20.1	21	9	19	20	19	18	20
Suborbital depth	11	11.9	13	9	11	13	11	11	12
Interorbital length	7.8	8.3	8.8	9	8.2	8.4	8.2	8.6	8.7
Head length	31	32.4	34	9	33	33	30	30	32
Snout length	12	12.3	13	9	11	13	12	11	12
Postorbital length	12	12.8	13	9	13	13	12	13	13
Orbit length	7.5	8.3	9.2	9	8.8	7.2	7.9	7.6	8.5
Orbit depth	6.8	7.2	8.2	9	8.0	6.5	6.8	6.3	7.6
Upper-jaw length	13	13.3	14	9	13	14	14	13	13
Lower-jaw length	12	12.8	13	9	12	14	12	12	12
Snout width	8.9	10.2	11	9	9.6	11	10	10	11
Barbel length	19	20.4	24	9	18	24	20	23	21
Maximum barbel width	1.2	1.3	1.4	9	0.9	1.3	1.1	1.0	1.4
First pre-dorsal length	42	42.9	43	9	42	43	41	40	41
Second pre-dorsal length	66	67.6	69	9	69	70	69	67	69
Interdorsal distance	13	14.7	16	9	17	15	15	16	14
Caudal-peduncle length	17	19.6	21	9	21	20	20	18	19
Pre-anal length	68	70.0	71	9	70	71	70	67	68
Pre-pelvic length	34	34.5	35	9	35	37	34	34	36
Pre-pectoral length	32	33.4	34	9	33	34	32	32	33
Second dorsal-fin depth	25	26.9	30	9	27	28	28	25	27
Pelvic-fin depth	30	31.6	35	9	31	34	31	31	30
Pectoral-fin depth	18	19.4	20	9	20	22	20	19	19
Length of first dorsal-fin base	14	15.0	16	9	16	16	15	16	16
Length of second dorsal-fin base	14	15.2	17	9	15	16	14	14	15
Caudal-fin length	30	31.1	32	9	32	30	31	29	30
Length of anal-fin base	9.1	9.9	11	9	11	10	11	11	11
Anal-fin height	17	17.5	18	9	18	17	17	18	18
Pelvic-fin length	19	20.6	22	9	21	19	21	21	21
Pectoral-fin length	27	28.0	29	9	28	—	28	28	30
Pectoral-fin width	4.8	5.2	5.7	9	5.1	5.3	4.9	4.4	5.2
First dorsal-fin height	25	26.1	27	9	27	25	—	26	26
Second dorsal-fin height	18	19.0	20	9	18	18	18	18	19
Meristic characters									
Pectoral-fin rays	16	16.1	17	9	16	16	15	14	16
Rudimentary gill rakers on upper limb	1	2.8	5	8	0	2	2	2	5
Developed gill rakers on upper limb	3	4.9	6	8	8	6	6	6	4
Developed gill rakers on lower limb	12	12.8	13	8	19	15	15	16	13
Rudimentary gill rakers on lower limb	5	5.3	6	8	1	5	5	4	5
Total gill rakers on upper limb	7	7.6	8	8	8	8	8	8	9
Total gill rakers on lower limb	17	18.0	19	8	20	20	20	20	18
Total gill rakers	25	25.6	27	8	28	28	28	28	27
Scales along lateral line	33	34.1	35	8	33	34	34	35	35

Table 8. Diagnostic characters for the five *sulphureus*-group species (including the two barbel morphs of *Upeneus sulphureus*), *U. suahelicus*, and *U. supravittatus* (body shape characters in % SL).

Species/morph	Maximum size SL (mm)	Total gill rakers (upper limb)	Total gill rakers (lower limb)	Total gill rakers	Scales (along lateral line)	Number of lateral body stripes[b]	First dorsal-fin tip pigmentation	First dorsal-fin vertical stripe	Posterior dorsal-fin margins	Caudal-fin bars
Upeneus sulphureus	146	7–9	18–22	26–31	32–37	2	black	no	no	no
SBM	138	7–9	19–22	26–30	32–36	2	black	no	no	no
LBM	146	7–9	18–22	27–31	33–37	2	black	no	no	no
U. alama	125[a]	8–9	20–22	28–31	33	not known	black	no	no	no
U. brevianalis	137[a]	8	20	28	31–32	not known	dark brown	yes	no	no
U. doriae	164	8–9	21–24	30–33	32–35	1	pale-brown to yellowish[c]	no	no	no
U. nigromarginatus	201	7–9	17–20	25–28	33–35	0	black	no	yes	no
U. suahelicus	153	6–8	18–21	26–28	33–35	2	black	no	no	yes[d]
U. supravittatus	144	7–9	19–23	27–32	34–36	2	black	no	no	yes[d]

Species/morph	Body depth at anal-fin origin	Maximum head depth	Head depth through eye	Suborbital depth	Head length	Snout length	Postorbital length	Upper-jaw length	Barbel length	Maximum barbel width
Upeneus sulphureus	22–29	21–27	16–21	8.7–12	28–33	9.5–13	11–14	11–14	12–26	0.7–1.3
SBM	24–29	21–27	16–20	9.2–12	28–32	9.6–12	11–13	11–14	12–18	0.7–1.3
LBM	22–27	21–26	16–21	8.7–12	28–33	9.5–13	11–14	11–14	19–26	0.7–1.2
U. alama	25–28	26	22	14	34	13	14	15	28–30	1.6–1.7
U. brevianalis	23	27	21	14	33	13	14	14	20	1.5
U. doriae	23–26	22–25	17–21	9.0–12	29–31	9.4–12	11–14	10–13	15–20	0.7–1.1
U. nigromarginatus	24–28	24–28	18–21	11–13	30–34	11–13	12–13	13–14	18–24	0.9–1.4
U. suahelicus	22–26	21–25	17–20	8.7–12	29–31	9.7–12	11–14	12–13	15–21	0.7–1.1
U. supravittatus	22–25	22–26	16–20	9.2–12	30–33	9.7–12	12–15	12–14	17–23	0.6–1.0

Species/morph	Caudal-peduncle length	Second dorsal-fin base length	Caudal-fin length	Length of anal-fin base	Anal-fin height	Pelvic-fin length	Pectoral-fin length	Pectoral-fin width	First dorsal-fin height	Second dorsal-fin height
Upeneus sulphureus	18–23	13–17	27–33	9.9–13	15–20	17–22	22–27	3.7–5.9	22–28	16–20
SBM	18–23	13–17	27–32	9.9–13	15–20	18–22	22–27	4.1–5.7	22–27	16–20
LBM	18–23	13–16	27–33	10–13	16–20	17–22	22–27	3.7–5.9	23–28	16–20
U. alama	21–22	14	28–32	9.8–9.9	15–17	20	28	5.5–5.9	24–25	17
U. brevianalis	19	15	31	8.1	12	20	26	6	23	17
U. doriae	20–23	13–16	27–30	11–12	14–16	17–21	22–26	4.5–5.9	20–24	14–16
U. nigromarginatus	17–21	14–17	29–32	9.1–11	17–18	19–22	27–30	4.4–5.7	25–27	18–20
U. suahelicus	18–22	12–15	26–30	10–13	15–17	18–21	23–25	4.2–5.6	21–26	14–18
U. supravittatus	18–22	12–15	27–31	9.8–12	15–17	18–21	23–28	4.1–5.9	22–26	15–17

[a] only known from types.
[b] in fresh specimens (rarely retained in preservative).
[c] pale gray in preserved specimens.
[d] usually retained in preservative, with very few exceptions.

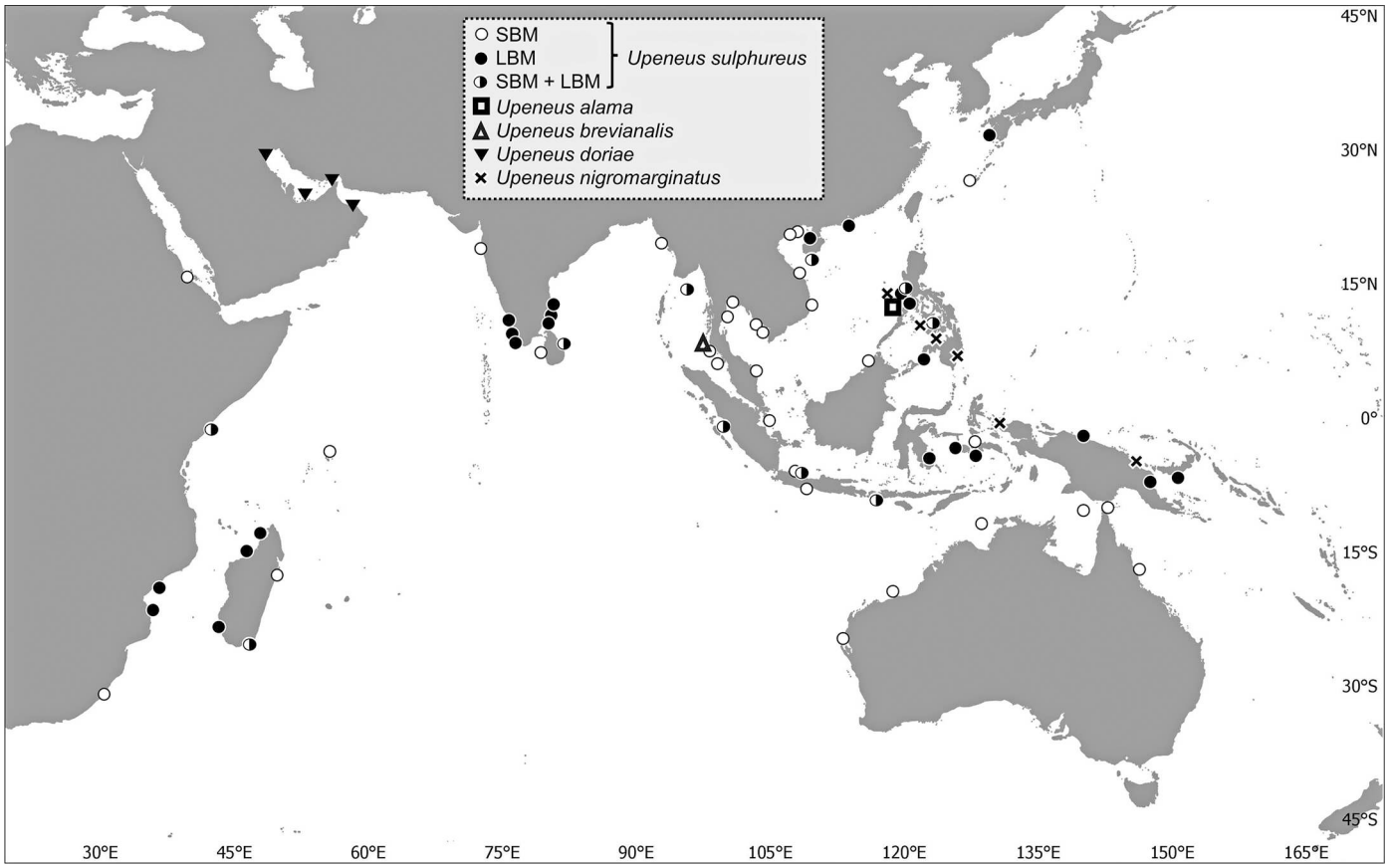

Fig. 2. Distribution of the five *sulphureus*-group species; short- and long-barbel morph occurrence in *Upeneus sulphureus* indicated by different symbols. For multiple occurrences at single locations, see also material list in species account.

Joseph Bonaparte Gulf, F/R/V *Soela*, 13°18′S, 128°21′E, 84–87 m depth, mesh wing trawl; CSIRO CA 3645, SBM, 119 mm SL, East of Bedout Island, F/R/V *Soela*, 19°23′S, 118°24′E, 66–68 m depth; WAM P.28941-001, SBM, 138 mm SL, Shark Bay, 25°20′S,113°30′E.

WPAC: Singapore: NMW 73651, 2 SBM, 75–78 mm SL (2 of 3); NMW 73652, SBM, 71 mm SL (1 of 5); Malaysia, Terengganu, Kuala Terengganu: KAUM-I.16965, SBM, 118 mm SL, Port Pelabuhan Cendring; KAUM-I.17097, SBM, 125 mm SL, Central Market; KAUM-I.105250, SBM, 74 mm SL, off Bidong Island; Malaysia, Sabah, Kota Kinabalu, Central Fish Market: KAUM-I.12155, SBM, 90 mm SL; KAUM-I.49169, SBM, 111 mm SL; Thailand, Gulf of Thailand: KAUM-I.22955, SBM, 116 mm SL, Chachoengsao Province, Bang Pakong fish market, mouth of Bang Pakong River; KAUM-I.22956, SBM, 99 mm SL, Chachoengsao Province, Bang Pakong fish market, mouth of Bang Pakong River; KAUM-I.33094, SBM, 119 mm SL, Prachuab Khiri Khan Province, fish landing bridge at Klong Wan, 11°44.33′N, 99°47.26′E, trawl; KAUM-I.23303, SBM, 86 mm SL, Samut Prakan Province, Mahachai fish market, trawl; Cambodia: MNHN-IC-1988-1829, SBM, 57 mm SL; Vietnam, Phu Quoc: HIFIRE F 58306, SBM, 81 mm SL; HIFIRE F 58307, SBM, 76 mm SL; HIFIRE F 58308, SBM, 78 mm SL; Indonesia, Java, Rawa Saban fish market: NCIP HN 688, 4 SBM, 68–91 mm SL; Java, Jakarta: MNHN-IC-0000-4020, 2 LBM, 96–109 mm SL; NCIP CA 782, SBM, 69 mm SL, Muara Karang; NMW 16213, SBM, 83 mm SL; NMW 16214, SBM, 72 mm SL; ZMUC P49475, LBM, 93 mm SL, female, fish market; Java: NMW 6332, LBM, 87 mm SL (1 of 3); NMW 73659, LBM, 130 mm SL (1 of 5), Novara expedition (1857–59); ZMUC P99, LBM, 93 mm SL; Indonesia, Muna Island: SMF 9971, LBM, 101 mm SL, Raha, 4°51′S, 122°43′E; Indonesia, Moluccas: MNHN-IC-0000-4021, LBM, 77 mm SL, Ambon; MNHN-IC-0000-4022, 2 LBM, 65–66 mm SL, Buru; NMW 73657, 2 SBM, 88–89 mm SL (2 of 3); Indonesia, West Papua: RMNH 25103, LBM, 90 mm SL, Humboldt Bay, near Holtekam; Indonesia: MNHN-IC-1989-0676, LBM, 90 mm SL; Philippines: MNCN 48183, LBM, 119 mm SL; MNCN 48184, LBM, 93 mm SL; MNHN-IC-1979-0086, LBM and SBM, 101–123 mm SL; Luzón: CAS 233387, 2 LBM, 82–97 mm SL, Batangas fish market; USNM 145214, LBM, 104 mm SL, Manila Bay, Corregidor Light, Philippines Expedition (1907–1910), R/V *Albatross*, 14°24′15″S, 120°41′30″E, 22 m depth, 25-foot Agassiz beam trawl; USNM 145226, 8 LBM, 86–115 mm SL (8 of 15), River at Pasacao, Ragay Gulf, Philippines Expedition (1907–10), R/V *Albatross*, seine; Metro Manila, Cubao, Farmer's Market: USNM 403093, SBM, 111 mm SL; USNM 403094, SBM, 105 mm SL; USNM 403095, SBM, 92 mm SL; Santa Cruz, Pasig River: NRM 1439, LBM, 75 mm SL; Panay Island: KAUM-I.95409, SBM, 72 mm SL, Tigbauan fish market; Iloilo City: KAUM-I.57209, LBM, 91 mm SL, Jaro Fish Market; KAUM-I.95381, LBM, 132 mm SL, Central Market; KAUM-I.95382, LBM, 146 mm SL, Central Market; KAUM-I.95612, LBM, 68 mm SL, Oton Fish Market; KAUM-I.98903, SBM, 64 mm SL, Oton Fish Market; Mindanao: USNM 89593, LBM, 114 mm SL, Zamboanga; Papua New Guinea: AMS I.16749-004, LBM,

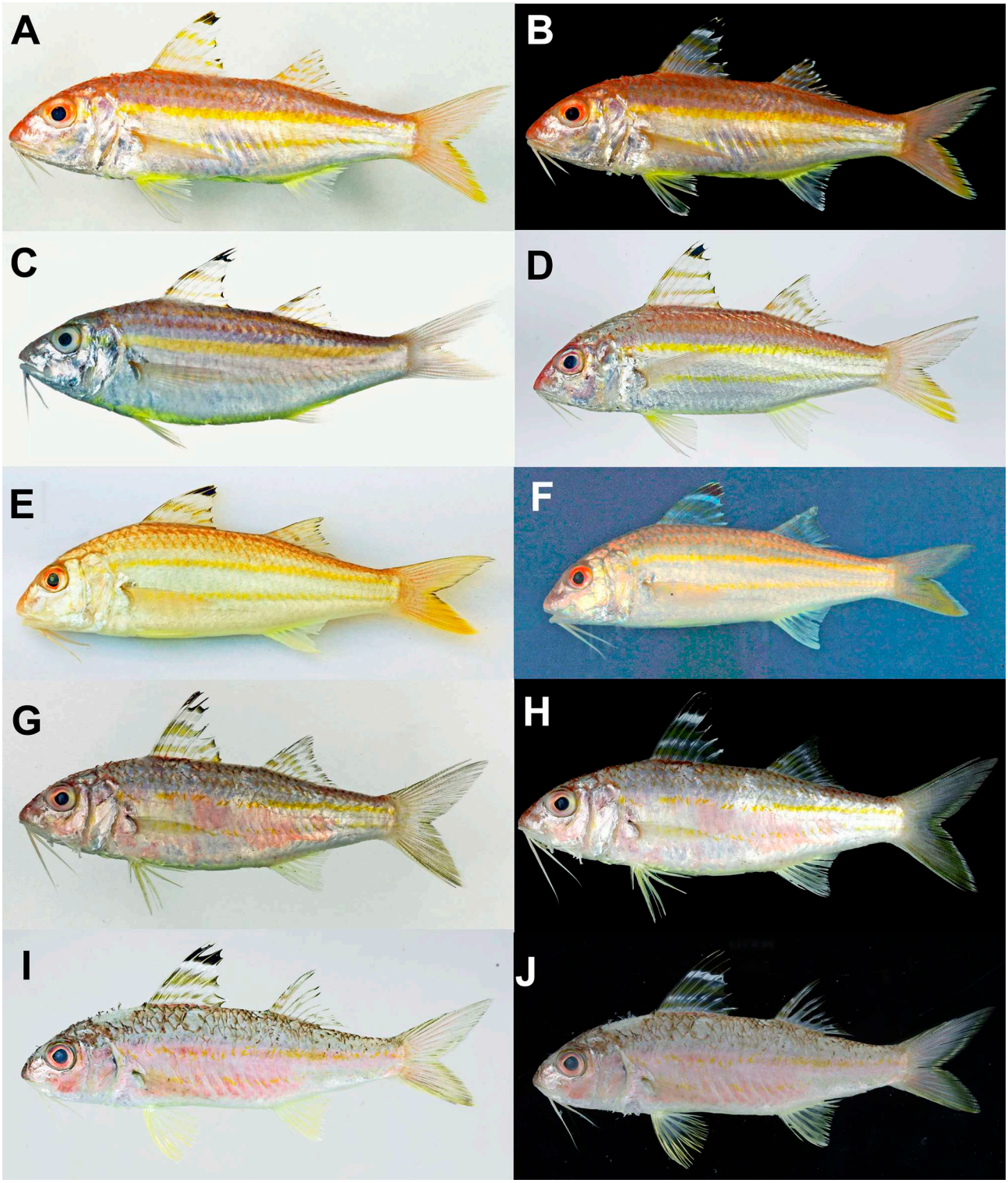

Fig. 3. *Upeneus sulphureus*. (A, B) KAUM-I.33094, SBM, 119 mm SL, Thailand, Gulf of Thailand, Prachuab Khiri Khan Province (H. Motomura); (C) USNM 403094, SBM, 105 mm SL, Philippines, Metro Manila (copyright J. T. Williams); (D) KAUM-I.67460, SBM, 90 mm SL, Vietnam, Ha Long Bay (H. Motomura); (E, F): SAIAB 82237, LBM, 106 mm SL, Mozambique (E: copyright O. Alvheim, F: copyright P. C. Heemstra); (G, H) KAUM-I.57209, LBM, 91 mm SL, Philippines, Panay Island, Iloilo City (H. Motomura); (I, J) KAUM-I.123161, LBM, 99 mm SL, Japan, Kagoshima, NE of Matsushima (H. Motomura).

126 mm SL, Bostrem Bay, Madang harbor, R/V *Alpha Helix*, 5°5′S, 145°48′E, 3–10 m depth, otter trawl; CSIRO A 34, LBM, 93 mm SL, Salamaua, F/R/V *Fairwind*, 7°3′S, 147°4′E; CSIRO C 821, LBM, 131 mm SL, W New Britain, Ringring, F/R/V *Fairwind*; South China Sea, Vietnam, Ha Long Bay: HIFIRE F 58147, SBM, 89 mm SL; HIFIRE F 58148, SBM, 91 mm SL; Ha Long City Fish Market: KAUM-I.67460, SBM, 90 mm SL; KAUM-I.95333, SBM, 85 mm SL; KAUM-I.95686,

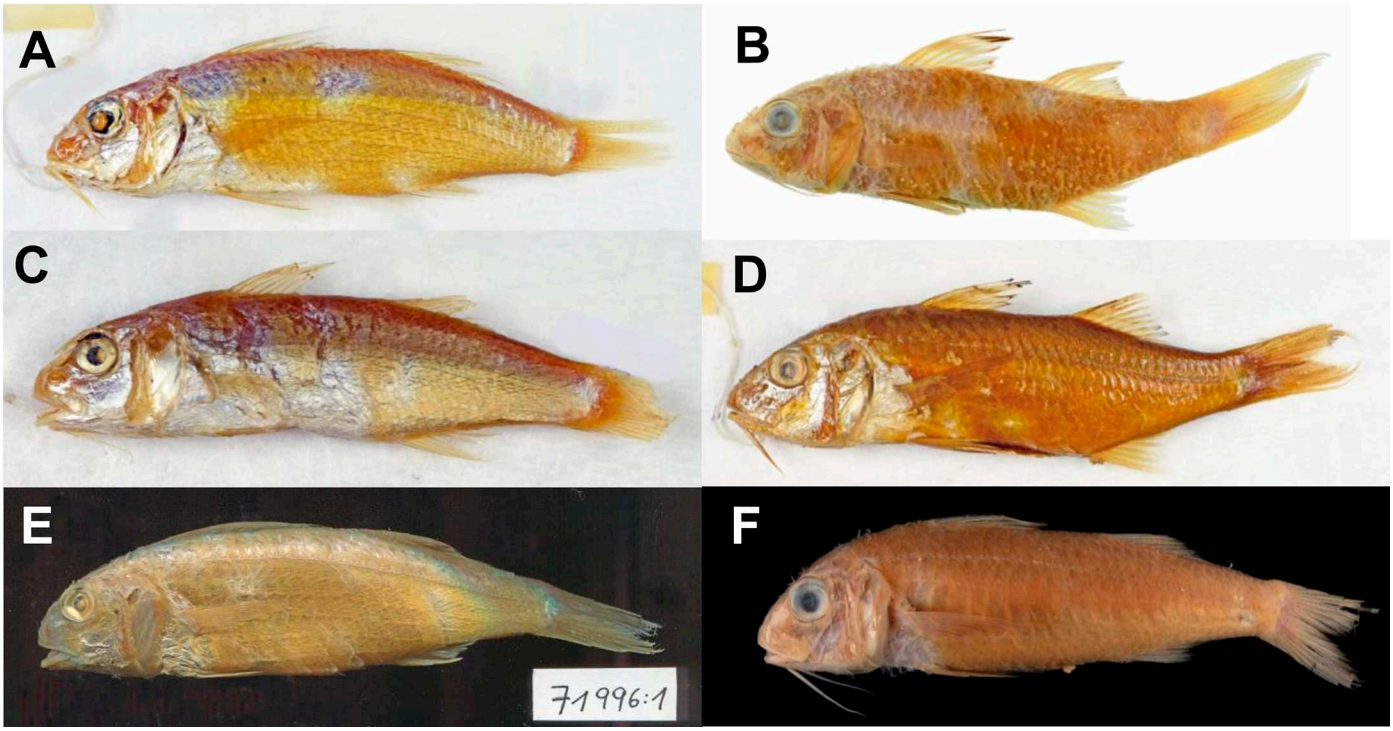

Fig. 4. (A) MNHN-IC-A-3458, LT of *Upeneus sulphureus*, 80 mm SL, Indonesia, Java, Sunda Strait (copyright J. Pfliger); (B) ANSP 47512, HT of *U. belaque*, 93 mm SL, Philippines (copyright L. Tuffy); (C): MNHN-IC-0000-4064, HT of *U. bilineatus*, 66 mm SL, Philippines, Ambon, Moluccas (copyright J. Pfliger); (D) MNHN-IC-A-3816, HT of *U. bivittatus*, 116 mm SL, India, Mararashtra, Mumbai (copyright J. Pfliger); (E) NMW 71996, LT of *U. pinnivittatus*, 110 mm SL, Japan, Nagasaki; (F) ZMUC P49301, HT of *U. sanctaehelenae*, 92 mm SL, locality not verified (copyright M. Krag).

SBM, 91 mm SL; KAUM-I.95729, SBM, 87 mm SL; KAUM-I.96500, SBM, 96 mm SL; Hai Phong, fish landing port at Ngoc Hai: KAUM-I.25125, SBM, 81 mm SL; KAUM-I.25126, SBM, 83 mm SL; Da Nang, My Khe Beach landing site close to Tho Quang Village: VNMN-I 07, SBM, 126 mm SL; VNMN-I 08, SBM, 112 mm SL; VNMN-I 09, SBM, 121 mm SL; Khánh hòa Province, Nha Trang, Cửa bé landing site: VNMN-I 10, SBM, 80 mm SL; VNMN-I 11, SBM, 77 mm SL; China, Guangdong: CAS 76428, LBM, 102 mm SL, off Kwangtung, southwest of Hong Kong; Hainan: SMF 25438, LBM, 78 mm SL, Boaozhen, 19°10′N, 110°36′E; Sanya Bay, 18°16′N, 109°27′E: SMF 25441, 2 SBM, 108–114 mm SL; SMF 25442, LBM and 2 SBM, 91–106 mm SL (3 of 16); SMF 25445, LBM and SBM, 81–85 mm SL (2 of 5); Japan: RMNH 4700, 2 SBM, 105–107 mm SL (wrongly assigned lecto- and paralectotype of *U. subvittatus* [Temminck and Schlegel, 1843], see Lachner [1954] and Uiblein and McGrouther [2012]); Kagoshima: KAUM-I.123161, LBM, 99 mm SL, NE of Matsu-shima island, Kasasa, Minami-satsuma, 31°25.06′N, 130°12.32′E, set net; Ryukyu Islands, Okinawa: USNM 71838, SBM, 107 mm SL, off Naha, Lu Chu Islands, North Pacific Expedition (1906), R/V *Albatross*; Australia, Northern Territory, Arafura Sea: AMS I-19294-004, SBM, 83 mm SL, 140 km offshore, R/V *Alpha Helix*, 10°29′S, 138°3′E, 49–50 m depth, 5 m otter trawl; Queensland: CSIRO H 7208-01, SBM, 82 mm SL, Coral Sea, E of Port Douglas, F/R/V *Gwendoline May*, 16°29.70′S, 145°33.71′E, 18 m depth; CSIRO H 7209-01, SBM, 58 mm SL, Torres Strait, SE of Saibai Island, F/R/V *Gwendoline May*, 9°29.49′S, 143°1.77′E, 9 m depth, bottom trawl.

Diagnosis.—Dorsal fins VIII + 9; pectoral fins 14–17; gill rakers 7–9 upper + 18–22 lower = 26–31 total; lateral-line scales 32–37; body moderately deep or rather deep; measurements as % SL: body depth at anal-fin origin 22–29; maximum head depth 21–27; head depth through eye 16–21; suborbital depth 8.7–12; head length 28–33; snout length 9.5–13; postorbital length 11–14; upper-jaw length 11–14; barbel length 12–26; barbel width 0.7–1.2; caudal-peduncle length 18–23; second dorsal-fin base length 13–17; caudal-fin length 27–33; length of anal-fin base 10–13; anal-fin height 15–20; pelvic-fin length 17–22; pectoral-fin length 22–27; pectoral-fin width 3.7–5.9; first dorsal-fin height 22–28; first three to four long dorsal-fin spines slightly protruding; second dorsal-fin height 16–20; caudal fin without bars; first dorsal fin with conspicuous black tip in fresh specimens that is usually well retained in preservative; both dorsal fins in fresh fish with dark, rather variable, horizontal or slightly oblique stripes, which are mostly lost in preservative; two yellow or pale-orange lateral body stripes in fresh fish, one more conspicuous mid-lateral stripe at eye level from behind operculum to caudal-fin base; second stripe of variable length originating behind pectoral-fin base, sometimes absent in subadults; stripes often lost in preservation; barbels white, pale beige, or pale rose, pale in preservation; head and body silvery-whitish ventrally and gray to red brown dorsally, belly, pelvic and anal-fins often yellowish in fresh fish; in preservative, head and body uniformly brown or dorsally darker and fins pale brown, except for dark first dorsal-fin tip.

Description.—Measurements as % SL and counts for types, adults, and subadults are provided in Tables 1–3.

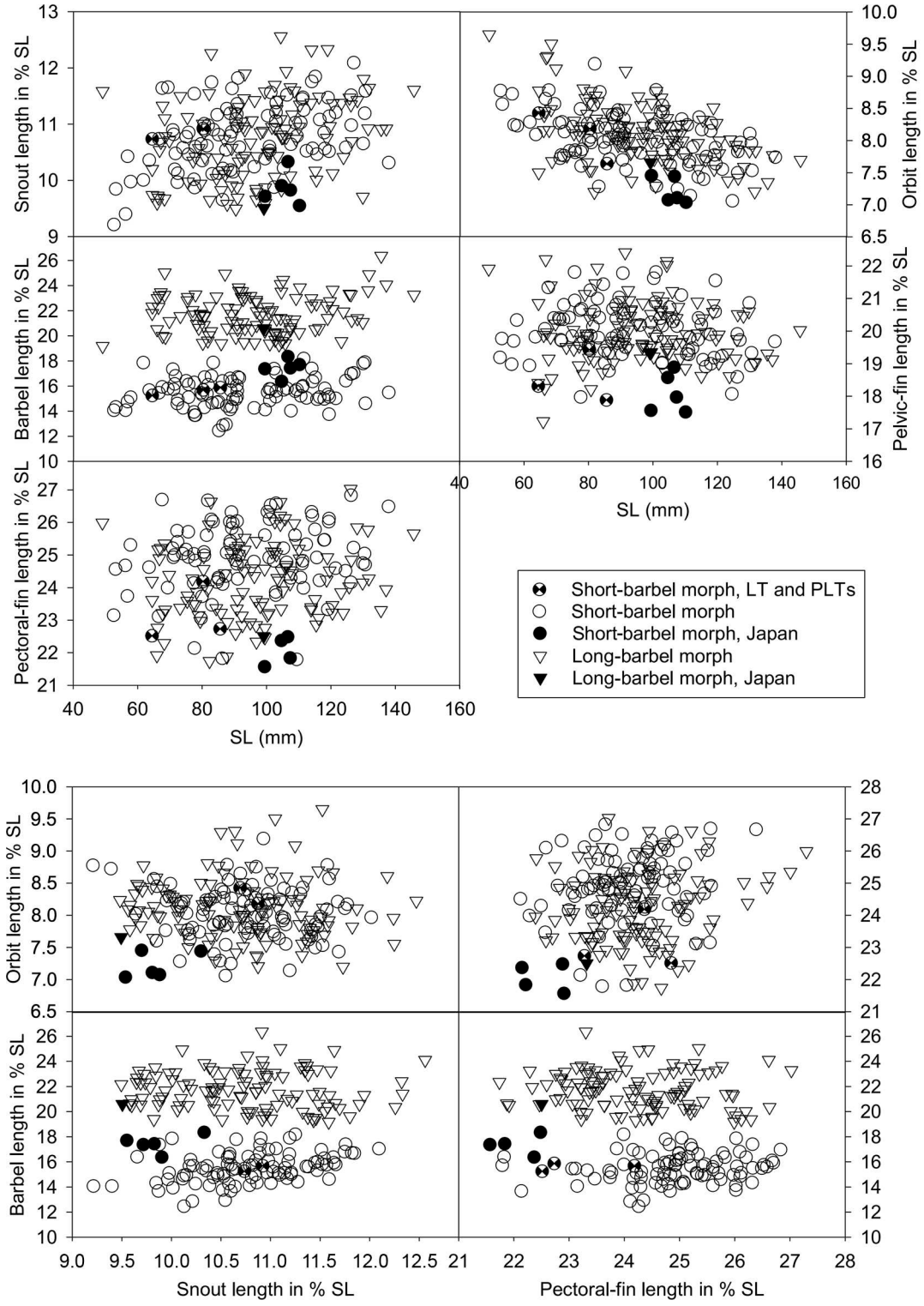

Fig. 5. Relationships among six morphometric characters including SL for the 211 studied adult and subadult specimens of *Upeneus sulphureus*, with different symbols for types and barbel morphs, the population from Japan shown separately.

Morphometric data expressed as quotient of SL/measurement (adults and subadults combined; LT data in squared brackets): body moderately deep or rather deep; body depth at first dorsal-fin origin 3.0–4.1 [3.8]; maximum head depth 3.7–4.7 [4.5], subequal to or slightly larger than pelvic-fin length (4.5–5.8 [5.1]) and subequal to pectoral-fin length (3.7–4.6 [4.1]); caudal-peduncle depth 8.0–9.7 [8.3], clearly larger than both orbit length (10–14 [12]) and interorbital length (11–14 [13]); caudal-peduncle width 19–29 [27], about half of orbit and interorbital length and subequal to or slightly narrower than pectoral-fin width (17–27 [21]); head depth through eye 4.8–6.3 [5.6]; head length 3.0–3.6 [3.4], mostly subequal to body depth at first dorsal-fin origin; snout length 8.0–11 [9.2], clearly shorter than first and

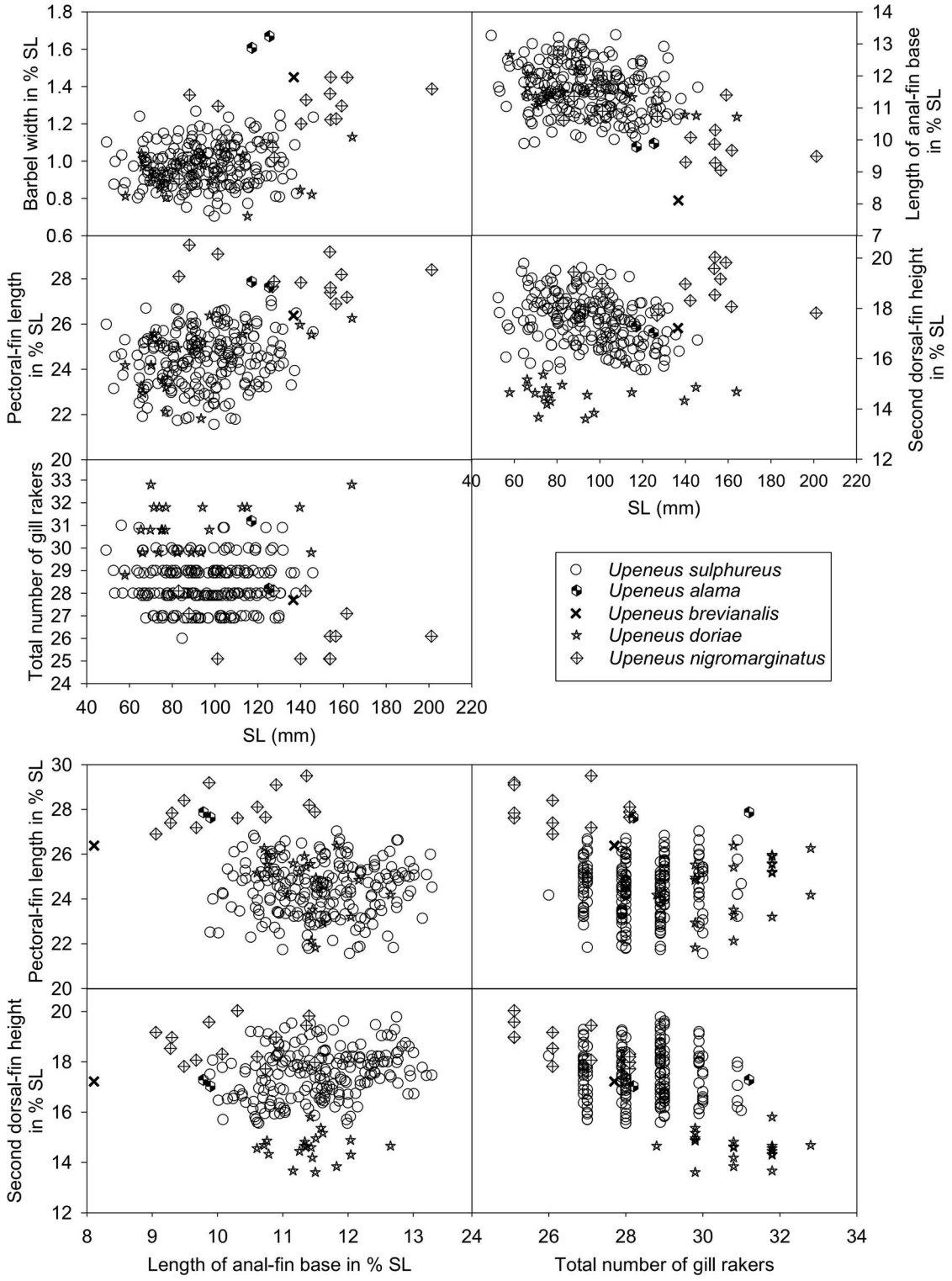

Fig. 6. Relationships among five morphometric characters including SL and total number of gill rakers for the 251 studied adult and subadult specimens of the five *sulphureus*-group species.

second dorsal-fin base (5.3–7.3 [6.7] and 5.9–7.7 [6.4], respectively) and anal-fin height (5.1–6.9 [5.7]); barbel length 3.8–8.0 [6.4], showing a particularly large range, shortest barbels just reaching eye level, longest barbels extending beyond preoperculum; upper-jaw length 7.1–9.3 [8.2], subequal to postorbital length (7.0–9.5 [8]) and about half of first dorsal-fin height (3.6–4.6); first three to four long dorsal-fin spines slightly protruding; caudal-fin length 3.1–3.7, larger than maximum head depth and subequal to head length; second dorsal-fin height 5.1–6.4, clearly shallower than first dorsal fin and subequal to head depth through eye.

Fresh color.—(Fig. 3) Head and body from snout tip dorsally gray, pale brown, or red brown, and white silvery below eye and lateral line; pelvic and anal fins and belly near fin bases

often yellowish; two yellow or pale-orange lateral body stripes, one more conspicuous mid-lateral stripe about as wide as pupil diameter at eye level from behind end of operculum to dorsal origin of caudal-fin base; further below, a mostly thinner, less conspicuous stripe from behind ventral edge of pectoral-fin base to level of second dorsal fin or to caudal-fin base; in some individuals and especially subadults, this stripe is poorly developed and may not be detectable or barely so; caudal fin partly hyaline with variable gray, pale brown, or yellowish pigmentation; the latter pigmentation, if present, covering the lower caudal-fin lobe distally to tip; sometimes traces of yellowish or pale gray pigmentation along inner margins of caudal-fin lobe; first dorsal fin with a black tip and two to three horizontal, yellowish, pale brown, or pale gray stripes (= well-pigmented stripes) bordered by white-hyaline stripes (= pale whitish stripes) or dorsal body margin at fin base; black tip of about orbit diameter covering the first four long spines; dark tip ventrally bordered by a similarly pale whitish stripe that is ventrally bordered by a well-pigmented stripe at half depth of fin of similar or narrower width as tip that may decrease in width distally; below this stripe follows another pale whitish stripe of similar or slightly narrower width as stripes above which ventrally is bordered by a narrow, well-pigmented stripe; the latter stripe either borders body margin at fin base or is separated from it by a third narrow pale whitish stripe and a mostly incomplete third well-pigmented stripe below; all first dorsal-fin stripes are horizontally directed and straight, but may occasionally be slightly bent upward posteriorly; second dorsal fin with two or three straight horizontal or oblique, posteriorly downward directing, yellowish, pale brown, or pale gray stripes (= well-pigmented stripes); these well-pigmented stripes being bordered by two to three white-hyaline stripes (= pale whitish stripes); the dorsal-most well-pigmented stripe as wide as pupil diameter or slightly thinner, covering fin tip and posterior fin margin partly or entirely, or completely lacking; the dorsal-most pale whitish stripe of variable width, either bordering two well-pigmented stripes on each side or reaching dorsally to fin tip; the latter ventrally bordered by a well-pigmented stripe with pupil- to orbit-diameter width crossing fin entirely or only the anterior half to two-thirds of fin, followed ventrally by a variably formed pale whitish stripe, depending also on formation of ventral-most well-pigmented stripe, the latter sometimes completely missing or only present in anterior part of fin; pelvic and anal fins hyaline expect for yellow proximal-most part and fin base, with belly in between fins also yellowish along ventral body margin; pectoral fins hyaline; barbels white, pale-beige yellowish, or pale rose.

Preserved color.—(Fig. 4) In LT of *Upeneus sulphureus* and HT of *U. bilineatus*, head and body dark gray or dark brown dorsally to about mid-eye level, ventrally pale brown or silvery—especially head and anterior body section; head and body uniformly pale brown to brown in HT of *U. belaque*, LT of *U. pinnivittatus*, and HT of *U. sanctaehelenae*; body dark brown in HT of *U. bivittatus* except for pale anterior-most ventral section where scales are missing, head pale-brown silvery, at snout and above eye level brown; fins pale brown, partly hyaline in all types; barbels pale or pale brown. Preserved nontypes showing similar variation in color as types, in subadults the anterior belly area may be darkened due to the peritoneum visible through the skin.

Distribution and size.—Indo-W Pacific: Eastern South Africa to Red Sea, S Japan, Fiji, and New Caledonia. No verified record in the Atlantic. Absent from the Persian Gulf and Gulf of Oman, where it is replaced by *Upeneus doriae*. Found at 2–90 m depth. Maximum size 146 mm SL.

Remarks.—In contrast to earlier findings by Lachner (1954), no increase in barbel length was found in *Upeneus sulphureus* with increasing size/age (Fig. 1). In Lachner's study, barbel-length data were only presented and analyzed in the form of frequency tables and corrected for length-dependency using percentage of head length instead of SL (as in the current study). Because head length itself may show allometry during ontogeny in species of *Upeneus*, caution must be given to account for this possibility, especially when comparing larger numbers of subadult specimens with adults (e.g., Uiblein and Gledhill, 2015; Uiblein et al., 2019). Lachner's methodological difference may explain why he did not discover a clear-cut bimodality in barbel-length distribution in *U. sulphureus* (Fig. 1), while noting the particularly wide range of this character.

Both specimens referred to as *Upeneus* cf. *sulphureus* by White et al. (2013: plate 78, image 78.20) and Uiblein and Randall (2022) appear to be the LBM of *U. sulphureus*, being distinct from the types of this species and all other specimens of the SBM by having longer barbels.

The differentiation recognized in the two barbel-length morphs was not mirrored by any other character (morphometric, meristic, color), singly or in combination (Fig. 5; Tables 3, 5, 6). Multivariate analyses using both principal components (PCA) and discriminant function analysis confirmed this conclusion (Uiblein, unpubl. data). Both morphs occur sympatrically, or in rather close vicinity of each other (Fig. 2). Only in the area between E Malaysia to Vietnam and off Australia is the SBM rather isolated from LBM populations. However, the LBM occurs in adjacent areas such as S China and Papua New Guinea (Fig. 2). A notable, but still incomplete distinction was encountered for the specimens from Japan in the combination of morphometric characters, indicating a slightly differentiated population consisting of both barbel morphs (Fig. 5; see also Comparisons and Differential Diagnosis section below).

Regarding the type locality of *Upeneus sanctaehelenae*, junior synonym of *U. sulphureus*, we agree with the earlier assumption by Edwards and Glass (1987) that Saint Helena in the SE Atlantic must have been in error. The specimen was most certainly collected during the far-ranging expedition of the Danish zoologist Ole Theodor Jensen Mortensen from Java, Indonesia, to South Africa in 1929–1930. The last two legs of this expedition to Mauritius (SW Indian Ocean) and St. Helena (SE Atlantic) were only about five weeks apart, and it may well have happened that material from both legs was not properly separated during transport and/or at the ZMUC fish collection. Accordingly, Edwards and Glass (1987) stated that "from examination of other specimens with the same labelling, it is clear that this collection was of tropical Indo-Pacific origin and not from St. Helena. Possibly these specimens were collected by Mortensen at Mauritius, which he visited not long before going to St. Helena. In the light of this new evidence we conclude that

the holotype of *U. sanctaehelenae* is probably a specimen of *U. sulphureus* of Indo-Pacific origin."

In areas of co-occurrence of *U. sulphureus* with species of the *suahelicus* group (*U. indicus*, *U. suahelicus*, and *U. supravittatus*), long-term preserved specimens require particular attention during identification, because confusion may arise from partial or almost complete fading of the caudal-fin color pattern in *suahelicus*-group species (Uiblein and Gouws, 2015). For instance, a specimen of *U. supravittatus* (ZMUC P49156) from off Chabahar, S Iran (Gulf of Oman, NWIO), collected and preserved nearly 100 years ago, was misidentified as *U. sulphureus* by Uiblein and Heemstra (2010), as revealed by Uiblein and Gouws (2015). On the other hand, three specimens collected off Eritrea, S Red Sea, in the 1950s (HUJ 11664), which had been tentatively referred to *U. suahelicus* by Uiblein and Gouws (2015), were reidentified as *U. sulphureus* in the current study after a much larger comparative dataset and the associated comprehensive diagnostic information became available. These specimens and the single specimen of BMNH 1858.6.1.8 (no detailed locality information) are to our knowledge the only currently known records of *U. sulphureus* in the Red Sea.

Upeneus alama Uiblein and Motomura, new species

urn:lsid:zoobank.org:act:7EAD12C4-B2B7-4C75-85AC-3BC26D51D3F0
Cavite Goatfish
Figures 2, 6, 7A, B; Tables 2, 8

Upeneus sulphureus: Fowler, 1933 (in part).

Holotype.—USNM 466258 (formerly USNM 145214), 117 mm SL, WPAC, Philippines, Luzon, Cavite, off Corregidor Island Lighthouse, Philippines Expedition (1907–10), R/V *Albatross*, 14°24.25′N, 120°41.52′E, 22 m depth, 25-foot Agassiz beam trawl, 8–9 February 1909.

Paratype.—USNM 466257 (formerly USNM 145214), 125 mm SL, same collecting and locality data as HT.

Diagnosis.—Dorsal fins VIII + 9; pectoral fins 16; gill rakers 8–9 upper + 20–22 lower = 28–31 total; lateral-line scales 33; body moderately deep; measurements as % SL: body depth at anal-fin origin 25–28; maximum head depth 26; head depth through eye 22; suborbital depth 14; head length 34; snout length 13; postorbital length 14; upper-jaw length 15; barbel length 28–30; barbel width 1.6–1.7; caudal-peduncle length 21–22; second dorsal-fin base length 14; caudal-fin length 28–32; length of anal-fin base 9.8–9.9; anal-fin height 15–17; pelvic-fin length 20; pectoral-fin length 28; pectoral-fin width 5.5–5.9; first dorsal-fin height 24–25; first two or three long dorsal-fin spines protruding; second dorsal-fin height 17; caudal fin without bars; first dorsal fin with black tip, retained in preservative; preserved fish with silvery-whitish head, pale brown body ventrally and dark brown dorsally; fins except for first dorsal-fin tip pale brown, partly hyaline; barbels very long, pale.

Description.—Measurements as % SL and counts for the two types are provided in Table 2. Morphometric data below expressed as quotient of SL/measurement: body moderately deep; body depth at first dorsal-fin origin 3.2–3.4; maximum head depth 3.8, larger than pelvic-fin length (5.1) and only slightly smaller than pectoral-fin length (3.6); caudal-peduncle depth 8.2–8.7, clearly larger than orbit and interorbital length (12–13 and 11–12, respectively); caudal-peduncle width 25–26, half of orbit length and clearly narrower than pectoral-fin width (17–18); head depth through eye 4.6; head length 2.9–3.0, slightly larger than body depth at first dorsal-fin origin; snout length 7.4–7.6, shorter than first dorsal-fin base (5.9–7.0) and smaller than anal-fin height (6.0–6.6); barbels very long (3.3–3.6), subequal to body depth at dorsal-fin origin, reaching beyond opercular level; upper-jaw length 6.6–6.8, slightly longer than postorbital length (7.0–7.2) and clearly longer than half of first dorsal-fin height (3.9–4.3); first two to three long dorsal-fin spines protruding; caudal-fin length 3.1–3.5, slightly larger than maximum head depth and slightly shorter than head length; second dorsal-fin height 5.8–5.9, noticeably shallower than first dorsal fin and head depth through eye.

Preserved color.—First dorsal fin of both types with black tip, subequal or less than orbit diameter in its maximum extension, covering the distal-most part of the first two to three long spines; body pale brown ventrally to about mid-line and dark brown dorsally; silvery-whitish head with pale brown snout region; body behind operculum immediately above and in front of pectoral-fin base with silvery-whitish patches that connect to belly at pelvic-fin base; fins, apart from first dorsal-fin tip, pale brown or pale, partly hyaline; barbels pale.

Etymology.—The new species name "*alama*" is used as a noun in apposition and honors the late Mr. Ulysses Banga Alama (1959–2023), who was employed at the College of Fisheries and Ocean Sciences, University of the Philippines Visayas, Miagao, Iloilo, Philippines, and manager of the UPVM fish collection, to commemorate his contributions to marine ichthyology.

Distribution and size.—Currently only known from the type locality, Luzon, Philippines. Known maximum size is 125 mm SL.

Remarks.—HT and PT collected with one *U. sulphureus* (USNM 145214) and one *U. nigromarginatus* (USNM 477289) at the same trawl station, indicating the sympatric occurrence of these three *sulphureus*-group species.

Upeneus brevianalis Uiblein and Boonphienphol, new species

urn:lsid:zoobank.org:act:B0708E15-4E74-4FC9-A007-97CEB32A5250
Phuket Goatfish
Figures 2, 6, 7C; Tables 2, 8

Holotype.—ZMUC P49375, 137 mm SL, NEIO, Thailand, Andaman Sea, Phuket, Phuket Trawler Harbor, Dan Carlsson, donation of the Phuket Marine Biological Center in connection with a FAO/DANIDA seminar, 14 August 1972.

Diagnosis.—Dorsal fins VIII + 9; pectoral fins 16; gill rakers 8 upper + 20 lower = 28 total; lateral-line scales 31–32; body moderately deep; measurements as % SL: body depth at anal-fin origin 23; maximum head depth 27; head depth

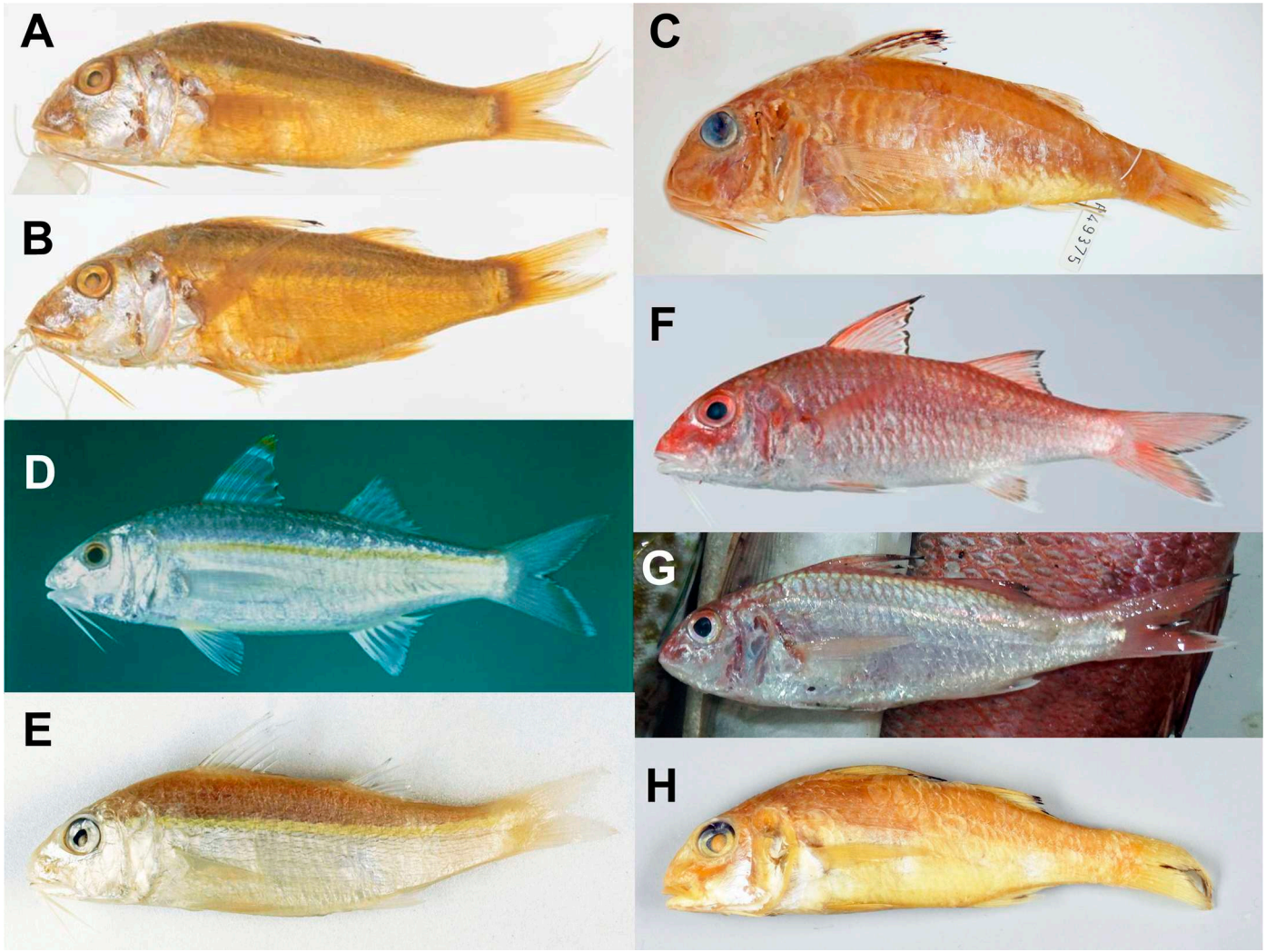

Fig. 7. (A, B) *Upeneus alama*: (A) USNM 466258, HT, 117 mm SL, Philippines, Manila Bay, Cavite (copyright D. Pitassy); (B) USNM 466258, PT, 125 mm SL, same locality (copyright D. Pitassy); (C) *U. brevianalis*, ZMUC P49375, HT, 137 mm SL, Thailand, Andaman Sea, Phuket (F. Uiblein); (D, E) *U. doriae*: (D): USNM FIN 31104 (unvouchered photograph), 106 mm SL, Persian/Arabian Gulf, Bahrain (copyright J. E. Randall); (E) ZMB 7056, LT, 104 mm SL, Iran, Persian/Arabian Gulf, Bandar Abbas (copyright E. Aßel); (F, G, H) *U. nigromarginatus*: (F) USNM 403319, 159 mm SL, Philippines, Negros Oriental, Dumaguete Citz (copyright J. T. Williams); (G) VNMN-I 1986 (unvouchered image), ca. 70 mm SL, Philippines, Panay Island, Tigbauan market near Iloilo City (F. Uiblein); (H) AMS I.18495-001, 88 mm SL, Papua New Guinea, Madang Province, Broken Water Bay (K. Parkinson).

through eye 21; suborbital depth 14; head length 33; snout length 13; postorbital length 14; upper-jaw length 14; barbel length 20; barbel width 1.5; caudal-peduncle length 19; second dorsal-fin base length 15; caudal-fin length 31; length of anal-fin base 8.1; anal-fin height 12; pelvic-fin length 20; pectoral-fin length 26; pectoral-fin width 6.0; first dorsal-fin height 23, first five long dorsal-fin spines slightly protruding; second dorsal-fin height 17; caudal fin without bars; anterior third of first dorsal fin forming a broad, dark-brown vertically oriented band, becoming slightly wider dorsally; head and body pale brown to brown, belly lighter; paired and anal fins pale hyaline; barbels pale to pale brown.

Description.—Measurements as % SL and counts for the single type are provided in Table 2. Morphometric data below expressed as quotient of SL/measurement: body moderately deep; body depth at first dorsal-fin origin 3.1; maximum head depth 3.6, larger than pelvic-fin length (5.1) and only slightly larger than pectoral-fin length (3.8); caudal-peduncle depth 9.0, clearly larger than orbit, interorbital, and anal-fin base length (all 12); caudal-peduncle width 22, slightly larger than half of orbit, interorbital, and anal-fin base length and clearly narrower than pectoral-fin width (17); head depth through eye 4.7; head length 3.0, subequal to body depth at first dorsal-fin origin; snout length 7.5, clearly shorter than first dorsal-fin base (5.9) and larger than anal-fin height (8.6); barbels moderately long (5.1), shorter than body depth at anal-fin origin, reaching about preopercular level; upper-jaw length 7.1, subequal to postorbital length (7.1) and larger than half of first dorsal-fin height (4.4); in the latter, the first four long dorsal-fin spines protruding; caudal-fin length 3.3, slightly larger than maximum head depth and slightly shorter than head length; second dorsal-fin height 5.8, clearly shallower than first dorsal fin and head depth through eye.

Preserved color.—Preserved HT with anterior third of first dorsal fin forming a broad, vertically oriented dark brown

band that widens toward fin tip; stripe formed by variably intense brown to dark brown pigmentation starting from tip of tiny first spine, continuing along posterior margin of first long spine to close to its tip, becoming darker dorsally, but not reaching fin tip; dark-brown interspine skin connecting to second long spine close to tip and then to third and to fourth long spine anteriorly; second long spine with brown vertical pigmentation line from fin base, third long spine only brown pigmented along its dorsal half and fourth long spine only brown pigmented anteriorly below tip; tips of first four long spines only weakly pale brown pigmented and partly unpigmented; fifth and sixth long spines attached to pigmented skin close to tips, last spine unpigmented; no signs of horizontally oriented pigmentation (e.g., indicating presence of horizontal stripes) on first dorsal fin; second dorsal fin only very weakly, irregularly pale brown pigmented with scattered, tiny streaks or spots, no formation of any distinct color pattern; head and body pale brown to brown, lighter along ventral head margin, belly, and ventral tail region to well behind anal fin; fins apart from first dorsal fin pale, partly hyaline; caudal fin pale brown posteriorly at lobe insertion; barbels pale to pale brown.

Etymology.—The new species name "*brevianalis*" refers to the short anal fin, an important diagnostic character of this species.

Distribution and size.—Currently only known from the type locality. Only known specimen measures 137 mm SL.

Remarks.—The dark vertical band formed on the anterior third of the first dorsal fin of this species is unique among goatfishes. The first dorsal fin in several species of *Upeneus* shows dark pigmentation on or close to fin tip and/or horizontal stripes or is entirely darkly pigmented. Formation of a vertical band on the first dorsal fin has not been reported in any of the six goatfish genera.

The short and rather shallow anal fin is also of diagnostic importance. Only in one congener, *U. parvus*, is the anal fin of similar height and almost as short, with a minimum base length of 8.5% SL in adult specimens (Franz Uiblein, pers. obs.).

Examination of *sulphureus*-group specimens from or near the type locality in several fish collections including PMBC (fish collection of the Phuket Marine Biological Center) and catches at fisheries-landing sites in the Phuket area were not successful in discovering more specimens of this species.

Upeneus doriae **(Günther, 1869)**

Gilded Goatfish

Figures 2, 6, 7D, E; Tables 2, 3, 8

Upeneoides doriae Günther, 1869 (Bandar Abbas, Iran, Persian Gulf).

Upeneus doriae: Kim and Nakaya, 2003; Uiblein and Heemstra, 2010; Uiblein et al., 2016, 2024; Uiblein and Maclaine, 2021; Uiblein and Randall, 2022.

Type material.—ZMB 7056, LT, 104 mm SL, NWIO, Iran, Arabian Gulf, Bandar Abbas, Marquis G. Doria; ZMB 39526, PLT, 90 mm SL, same collecting information as LT; BMNH 1869.3.4.36, 2 of 5 PLTs, 77–93 mm SL, NWIO, Arabian Gulf, Kuwait; MSNG 13056, 10 of 11 PLTs, 65–94 mm SL, same collecting information as LT.

Non-type material.—(*n* = 8, 58–164 mm SL) NRM 41325, 3, 115–145 mm SL, NWIO, Oman, Gulf of Oman, Muscat fish market; SAIAB 58782, subadult, 58 mm SL (1 of 7), NWIO, United Arab Emirates, Arabian Gulf, 24°44.4′N, 53°27.03′E, midwater trawl; SMF 26055, 3, 71–97 mm SL, NWIO, Iran, Arabian Gulf, R/V *Akademik*, 29°1.293′N, 50°5.136′E, 45 m depth; SMF 29079, 2, 113–164 mm SL, NWIO, Kuwait, Arabian Gulf, 29°10.113′N, 48°8.54′E.

Unvouchered image.—USNM FIN 31104, 106 mm SL, Persian/Arabian Gulf, Bahrain (J. E. Randall).

Diagnosis.—Dorsal fins VIII + 9; pectoral fins 14–16; gill rakers 7–9 upper + 21–24 lower = 29–33 total; lateral-line scales 32–35; body slightly elongated; measurements as % SL: body depth at anal-fin origin 23–26; maximum head depth 22–25; head depth through eye 17–21; suborbital depth 9.0–12; head length 29–31; snout length 9.4–12; postorbital length 11–14; upper-jaw length 10–13; barbel length 15–20; barbel width 0.7–1.1; caudal-peduncle length 20–23; second dorsal-fin base length 13–16; caudal-fin length 27–30; length of anal-fin base 11–12; anal-fin height 14–16; pelvic-fin length 17–21; pectoral-fin length 22–26; pectoral-fin width 4.5–5.9; first dorsal-fin height 20–24; dorsal-fin spines decreasing in height starting with second long spine; second dorsal-fin height 14–16; caudal fin without bars; first dorsal fin with pale brown to yellowish tip in fresh specimens that may fade away in preservative; a yellow lateral body stripe in fresh fish at level of upper edge of eye, sometimes retained in preservative; barbels white when fresh, pale in preservative; head and body silvery-whitish ventrally and laterally and dark gray dorsally, pelvic fins yellowish at origin; in preservative, head and body rather uniformly pale to dark brown or dorsally darker and fins pale, except for weakly pigmented first dorsal-fin tip sometimes still retained.

Distribution and size.—Only known from Persian/Arabian Gulf and Gulf of Oman (NWIO). In shallow water to 45 m depth. Attains ca. 200 mm SL.

Upeneus nigromarginatus **Bos, 2014**

Black-margined Goatfish

Figures 2, 6, 7F, G, H; Tables 2, 7, 8

Upeneus sulphureus: Fowler, 1933 (in part).

Upeneus nigromarginatus Bos, 2014 (Panabo City, Mindanao, Philippines): Uiblein et al., 2016, 2024; Uiblein and Maclaine, 2021.

Holotype.—RMNH 37991, 201 mm SL, WPAC, Philippines, Mindanao, Panabo City Market, 7°18′23″N, 125°41′1″E.

Paratypes.—All from same locality as HT: BPBM 41113, 2, 140–154 mm SL; RMNH 36422, 154 mm SL; RMNH 36423, 156 mm SL; RMNH 37992, 154 mm SL.

Non-type material.—(*n* = 7, 83–159 mm SL) WPAC, Indonesia: RMNH 25084, 2, 127–142 mm SL, West Papua, Kabuy Bay; Philippines: USNM 403319, 159 mm SL, Negros Oriental, Dumaguete City market, USNM 408874, 101 mm SL,

Mindanao, General Santos Public Market (from off Glan); USNM 477289 (formerly 145214), 83 mm SL, Luzon, Cavite, off Corregidor Island Lighthouse, Philippines Expedition (1907–10), R/V *Albatross*, 14°24.25′N, 120°41.52′E, 22 m depth, 25-foot Agassiz beam trawl; Papua New Guinea, Madang Province: AMS I.16753-033, 128 mm SL (1 of 7 spms), off Ramu river mouth, R/V *Tagula*, 4°0′S, 144°40′E, demersal trawl; AMS I.18495-001, 88 mm SL, Broken Water Bay, R/V *Hokoku Maru* Nr. 2, 3°58′S, 144°40′E, 14–24 m depth, trawl.

Unvouchered image.—VNMN-I 1986, ca. 70 mm SL, WPAC, Philippines, Western Visayas, Panay Island, Tigbauan market near Iloilo City (F. Uiblein).

Diagnosis.—Dorsal fins VIII + 9; pectoral fins 14–17; gill rakers 7–9 + 17–20 = 25–28; lateral-line scales 33–35; body moderately deep to deep; measurements as % SL: body depth at anal-fin origin 24–28; maximum head depth 24–28; head depth through eye 18–21; suborbital depth 11–13; head length 30–34; snout length 11–13; postorbital length 12–13; upper-jaw length 13–14; barbel length 18–24; barbel width 0.9–1.4; caudal-peduncle length 17–21; second dorsal-fin base length 14–17; caudal-fin length 29–32; length of anal-fin base 9.1–11; anal-fin height 17–18; pelvic-fin length 19–22; pectoral-fin length 27–30; pectoral-fin width 4.4–5.7; first dorsal-fin height 25–27; first two dorsal-fin spines protruding; second dorsal-fin height 18–20; caudal fin pale red, without bars, with dark margin on upper lobe forming a dark lobe tip and a white margin on lower lobe forming a white lobe tip; white margin on lower lobe bordered inside by dark contrasting margin; dorsal fin red with black distal margins formed by dark-pigmented spine and ray tips; first two elongated long spines on dorsal fin forming a dark tip; head and body pale rose to reddish, darker dorsally, especially on head; paired and anal fins pale rose-whitish hyaline, anal fin sometimes with pale gray area centrally; barbels white, pale in preservative; dark pigmentation on dorsal, caudal, and anal fins at least partially retained in preservative, body and head uniformly brown or pale brown, becoming darker dorsally in preservative.

Distribution and size.—Philippines, SE Indonesia, E Papua New Guinea, shallow bottoms to at least 24 m depth. Attains 201 mm SL.

Remarks.—New records for Indonesia (West Papua), Papua New Guinea, and three areas in the Philippines N of Mindanao. No notable differences between areas in any morphometric, meristic, or color characters were found (Table 7).

Comparisons and Differential Diagnoses

***Intraspecific differences in* Upeneus sulphureus**.—(Figs. 1, 3, 4, 5; Tables 2–6) The distinction between two barbel-length morphs in *Upeneus sulphureus* is not mirrored by pronounced differences in any other character, hence splitting into well-separable taxa or even populations is unsupported. Rather, large overall overlap in body structure and only very few and minimal differences between populations can be found at various scales of regions or subregions independent of treating the two morphs as combined, single population units or as separate subpopulations.

When both barbel-length morphs are combined and populations compared at the larger regional scales of WIO, CEITPAS, and Australia/Papua New Guinea, a single notable difference occurs in the latter regional population, which has a slightly larger maximum head depth than the WIO population (25–27 vs. 21–26% SL; Table 4). No other differences between the three compared regions can be found in body structure (Table 4) or color patterns (Fig. 3).

When populations of the three large regions are compared after separation into barbel-length morphs, the Australian population (consisting only of the SBM) deviates from LBM of WIO and CEITPAS in having a slightly deeper body at the anal-fin origin (25–28 vs. 22–27% SL) and slightly deeper head (maximum head depth 25–27 vs. 21–26% SL; Table 5). At the subregional level between Australia (exclusively SBM) and Papua New Guinea (exclusively LBM), the latter population has a slightly shallower body (body depth at dorsal-fin origin 26–29 vs. 29–33 and body depth at anal-fin origin 23–25 vs. 25–28% SL; Table 5). For both subregions, sample size is low.

Regarding the smaller geographic scale of subregions within the CEITPAS area, the specimens of the two barbel-length morphs from Japan differ from each other and from other areas, but such differences also are based on very low sample sizes (Fig. 5; Table 6). The dorsal fins in the single LBM are higher compared to the SBM from Japan, but not the two other areas. Both morphs from Japan have a slightly shallower body than the SBM in EIO (e.g., body depth at dorsal-fin origin 26–28 vs. 28–33% SL), a slightly shallower head than the SBM of both other areas (e.g., maximum head depth 21–23 vs. 22–27% SL), and slightly shorter pectoral fins than both morphs in the other areas (22–23 vs. 22–27% SL). Other minor differences concern a slightly shallower body at the anal-fin origin in LBM from EIO and WPAC compared to SBM from those areas (22–27 vs. 24–29% SL) and a slightly shallower head in LBM compared to SBM from the EIO (21–25 vs. 24–27% SL).

In subadult *U. sulphureus*, the two barbel-length morphs closely overlap in all characters (Table 3). Subadults differ from adults only in a slightly shallower suborbital (suborbital depth 8.1–10 vs. 8.7–12% SL) and occasionally in fresh coloration, with only a single lateral body stripe at mid body vs. two stripes in other subadults as well as in all adults (Franz Uiblein and Tuan Anh Hoang, pers. obs.).

Interspecific differences among* sulphureus*-group species.—(Figs. 2, 3, 6, 7; Tables 2, 8) Each of the five *sulphureus*-group species can be distinguished as follows (Fig. 6; Table 2): *Upeneus alama* by longer barbels that are also clearly thicker when measured at base; *U. brevianalis* by shorter and shallower anal fin and dark vertical band vs. no such band on anterior first dorsal fin; *U. doriae* by the presence of a single mid-lateral body stripe in fresh adult fish and the combination of slightly more total gill rakers with slightly shallower second dorsal fin, and *U. nigromarginatus* by slightly fewer total gill rakers in combination with slightly longer pectoral fins.

Upeneus sulphureus can be distinguished in addition as follows: from *U. alama* by shallower head depth through eye, shorter head, upper jaw, and pectoral fins, and slightly longer anal-fin base; from *U. brevianalis* in shallower maximum

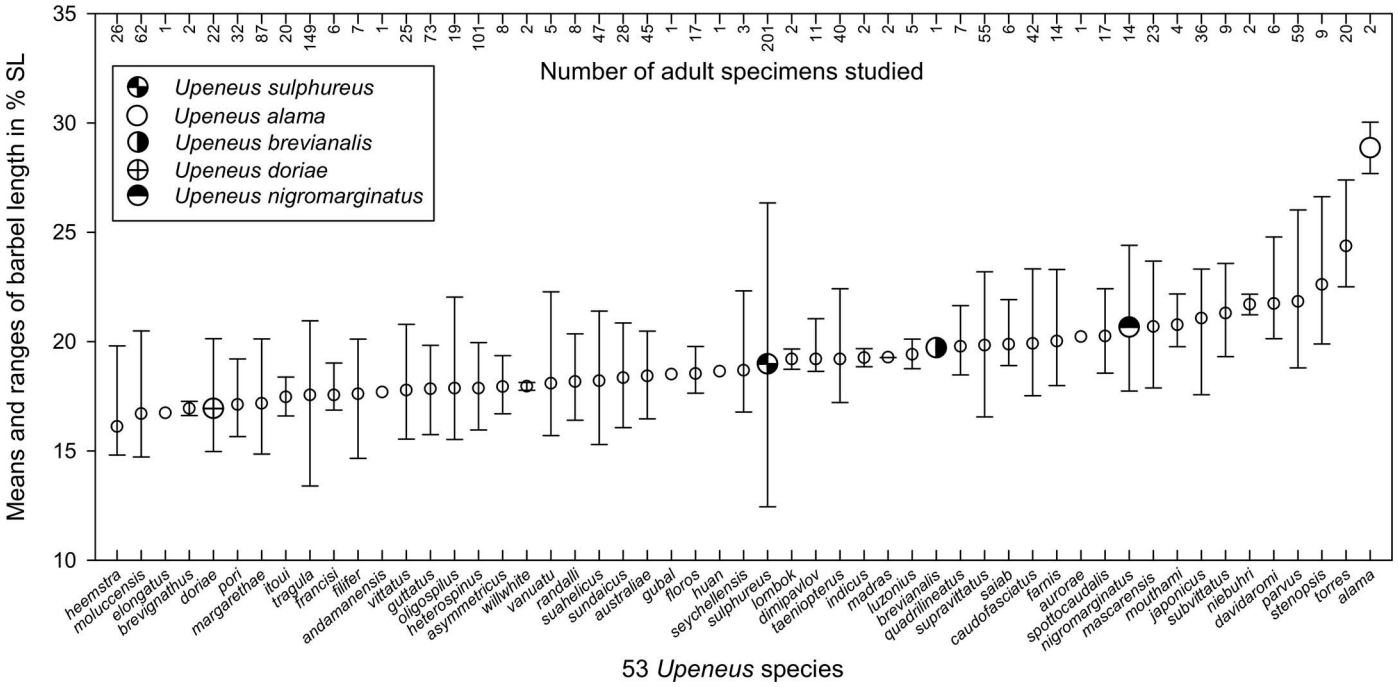

Fig. 8. Means and ranges of barbel length in the 53 species of *Upeneus*, in ascending order of mean barbel length.

head and suborbital depth, thinner barbels, and slightly narrower pectoral fin; from *U. doriae* by slightly higher anal and first dorsal fin, smaller maximum size (146 vs. ca. 200 mm SL), and non-overlapping distribution; and from *U. nigromarginatus* by presence (vs. absence) of lateral body stripes in fresh fish, absence (vs. presence) of dark posterior dorsal-fin margins, slightly shallower suborbital, slightly longer anal-fin base, and smaller maximum size (146 vs. 201 mm SL).

Both *U. alama* and *U. brevianalis* can be distinguished from *U. doriae* in greater maximum head depth, longer head and snout, shorter anal-fin base, smaller currently known maximum size (125–137 vs. ca. 200 mm SL), and non-overlapping distributions; and from *U. nigromarginatus* in deeper suborbital, longer postorbital, shallower second dorsal fin, and smaller currently known maximum size (125–137 vs. 201 mm SL); moreover, *U. brevianalis* and *U. nigromarginatus* have non-overlapping distributions.

Upeneus doriae can be distinguished from *U. nigromarginatus* by presence (vs. absence) of mid-lateral body stripe in fresh fish and absence (vs. presence) of dark posterior dorsal-fin margins, slightly shorter head, upper jaw, barbels, caudal and pectoral fins, longer and shallower anal fin, shallower first dorsal fin, and non-overlapping distributions. The single subadult of *U. doriae* can be clearly distinguished in several characters from subadult *U. sulphureus* (independent of barbel length), including shallower body at anal-fin origin and caudal peduncle, shorter head, and much shallower dorsal fins (Table 3).

Interspecific differences after color loss.—(Tables 2, 8; Uiblein and Gouws, 2015) In long-term preserved specimens of the *suahelicus* group (Uiblein and Gouws, 2015), the caudal-fin bars may have faded and in rare cases even be completely absent. In such cases, the distinction from co-occurring species of the *sulphureus* group may be difficult. Only a combination of several morphometric and meristic characters can then be used for identification. In the WIO area from South Africa to the Red Sea, *U. sulphureus* co-occurs with *U. suahelicus*, from which it differs in body structure by slightly longer second dorsal fin (length of base 13–17 vs. 12–15% SL), slightly longer caudal fin (length 27–33 vs. 26–30% SL), slightly higher second dorsal fin (height 16–20 vs. 14–18% SL), and slightly more gill rakers (number on upper limb 7–9 vs. 6–8; total number of gill rakers 26–31 vs. 26–28). Regarding *U. supravittatus* co-occurring with *U. sulphureus* in the area from Pakistan to Myanmar, the latter can be distinguished by shorter postorbital (length 11–14 vs. 12–15% SL), slightly longer second dorsal fin (length of base 13–17 vs. 12–15% SL), slightly higher second dorsal fin (height 16–20 vs. 15–17% SL), and slightly fewer gill rakers (total number of gill rakers 26–31 vs. 27–32).

Regarding overlap of occurrence with *U. supravittatus* in the Gulf of Oman, *U. doriae* can be distinguished from the former by slightly shorter head (length 29–31 vs. 30–33% SL), slightly longer caudal peduncle (length 20–23 vs. 18–22% SL), slightly shallower dorsal fins (first dorsal-fin height 20–24 vs. 22–26% SL; second dorsal-fin height 14–16 vs. 15–17% SL), and slightly more total gill rakers (number of total gill rakers 30–33 vs. 27–32).

Barbel Length in Species of *Upeneus*

(Figs. 1, 5, 8–10; Tables 2, 8, 9) Barbel length varies considerably among the 53 species of *Upeneus*, with the *sulphureus*-species group exhibiting the shortest and longest barbels as well as the widest range by far in barbel length for a single species (Table 9, Fig. 8). Whereas *U. sulphureus* shows an extremely wide range in barbel length, *U. alama* shows the longest barbels among all congeners (Fig. 8).

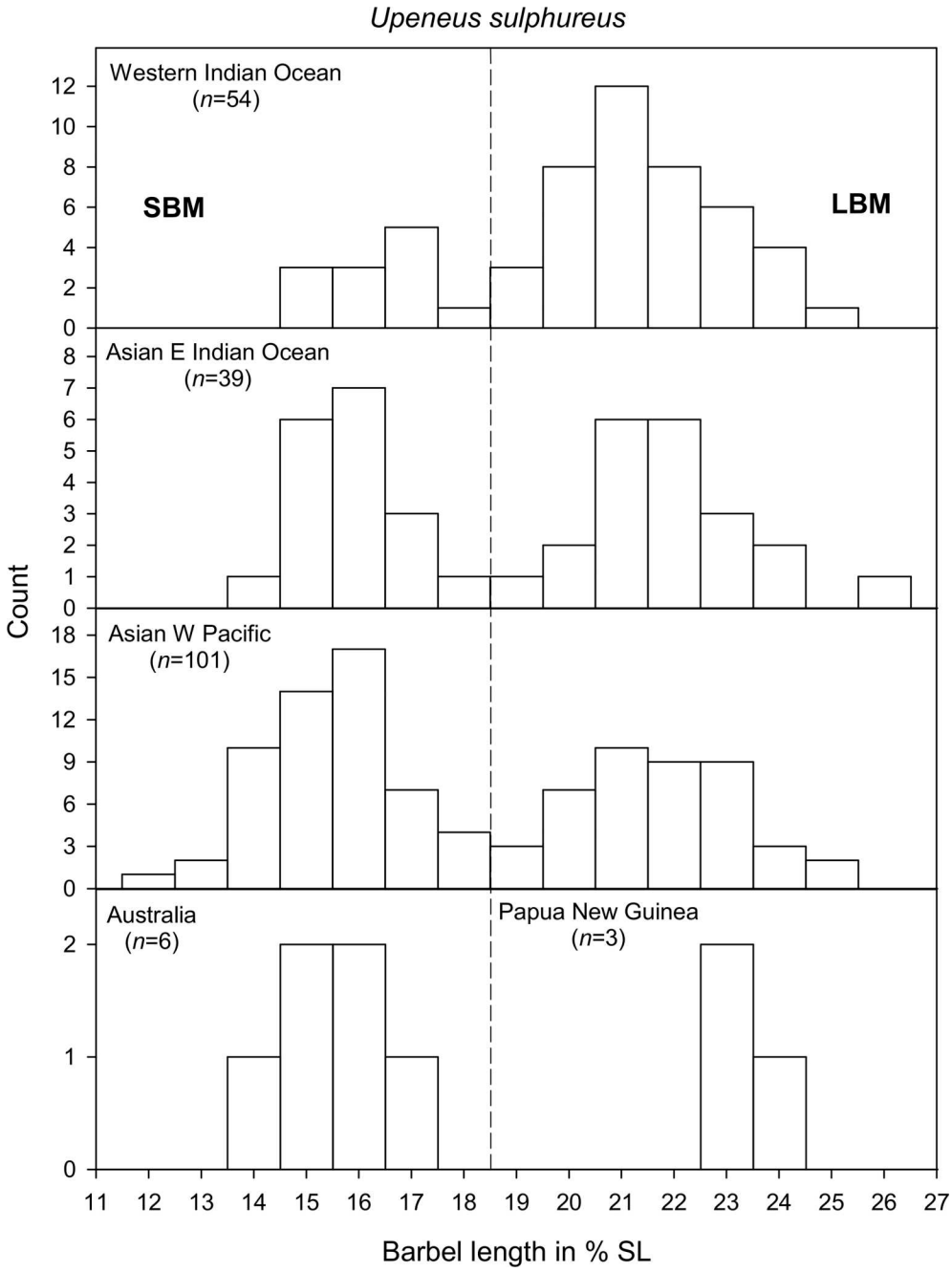

Fig. 9. Barbel-length distribution in populations of *Upeneus sulphureus* with separation line for the two barbel-length morphs. The adjacent areas of Australia and Papua New Guinea are shown in a single graph.

The bimodal distribution in barbel length found in *U. sulphureus* remains rather constant among different geographic areas, whereas abundance of either morph can change, or a morph can be completely absent from an area (Fig. 9). This pattern contrasts to the unimodal barbel-length distribution with rather narrow ranges in barbel length in other species of *Upeneus* (Fig. 10), which, regarded per se and in isolation from the comprehensive alpha-taxonomic approach adopted in this study, would suggest that there are two distinct species.

Many species of *Upeneus* have narrow barbel-length ranges that widen only slightly with increasing sample size (Table 9; Figs. 1, 8, 10), allowing the use of barbel length as a diagnostic character. This applies for instance to *U. japonicus* (NWPAC from Malaysia to Japan), which has mostly shorter barbels than its probable southern sister species *U. torres* (SWPAC, Australia to Vanuatu; Table 9, Fig. 10; Uiblein and Gledhill, 2015). *Upeneus australiae* shows even shorter barbels. Similarly, *U. tragula* (EIO and WPAC) has short barbels that are still slightly longer than those of its sister species, *U. heemstra*, which occurs in the WIO to SE India (NWEIO; Uiblein and Gouws, 2014; Table 9, Fig. 10). A single individual of the latter species deviates in having longer barbels (barbel length 20 vs. 15–17% SL; Fig. 10).

DISCUSSION

Two species of the *sulphureus*-species group differ from all other congeners in three barbel-length traits. *Upeneus alama*

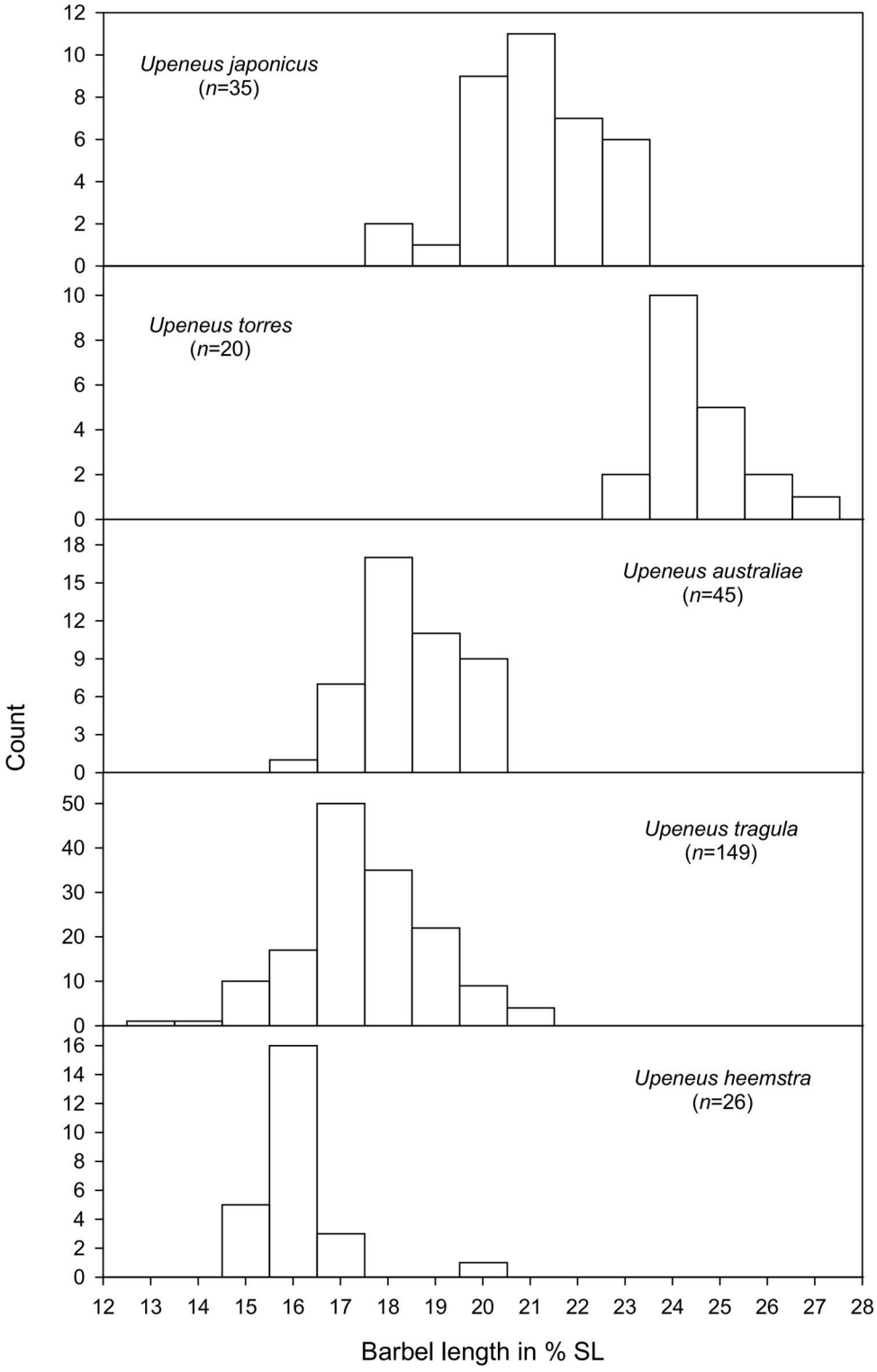

Fig. 10. Barbel-length distribution in five species of *Upeneus*.

has the longest barbels among all 53 congeners, and *U. sulphureus* shows the widest range and a unique bimodal distribution in barbel length. Particularly long barbels can be found in other mullid genera, too. For instance, in the genus *Parupeneus*, the four species of the *posteli*-species group exceed *U. alama* in barbel length with ranges of 31–37% SL in *P. posteli* and a length of 37% SL in the single type of *P. louise* (Uiblein, 2021).

The two specific barbel-length traits found in *U. sulphureus* are unique in the entire family Mullidae. The bimodal barbel-length distribution in *U. sulphureus* strongly suggests the existence of a consistent, species-encompassing dimorphism in this character that does not coincide with size/age-, sex-, or population-related differences and differentiation in other characters, be it body shape, meristics, or color. Instead of encountering distinct species with different barbel lengths,

Table 9. Barbel length in 53 species of *Upeneus* (1,388 adult specimens in total), with number of studied specimens, mean SL (or single value; in mm), mean (or single value) and range of barbel length (in % SL), and data source.

			Barbel length in % SL				
Species	*n*	SL	Min	Mean	Max	Range	Data source
Upeneus alama	2	121	27.7	28.9	30.0	2.3	This study
U. andamanensis Uiblein and Rajan, 2024	1	91		17.7		0.0	Uiblein et al., 2024
U. asymmetricus Lachner, 1954	8	89	16.7	17.9	19.4	2.7	Uiblein and Motomura, 2021
U. aurorae Uiblein and Williams, 2024	1	113		20.2		0.0	Uiblein et al., 2024
U. australiae Kim and Nakaya, 2002	45	103	16.5	18.4	20.5	4.0	Uiblein and Gledhill, 2015
U. brevianalis	1	137		19.7		0.0	This study
U. brevignathus Uiblein and Bailly, 2024	2	95	16.6	16.9	17.3	0.6	Uiblein et al., 2024
U. caudofasciatus Uiblein and Gledhill, 2019	42	89	17.5	19.9	23.3	5.8	Uiblein et al., 2019
U. davidaromi Golani, 2001	6	113	20.1	21.7	24.8	4.7	Uiblein and McGrouther, 2012
U. dimipavlov Uiblein and Motomura, 2021	11	123	18.6	19.2	21.1	2.4	Uiblein and Motomura, 2021
U. doriae (Günther, 1869)	22	91	15.0	16.9	20.1	5.2	This study
U. elongatus Uiblein and Motomura, 2021	1	89		16.7		0.0	Uiblein and Motomura, 2021
U. farnis Uiblein and Peristiwady, 2017	14	111	18.0	20.0	23.3	5.3	Uiblein et al., 2017
U. filifer (Ogilby, 1910)	7	79	14.7	17.6	20.1	5.5	Uiblein et al., 2016
U. floros Uiblein and Gouws, 2020	17	105	17.7	18.5	19.8	2.1	Uiblein and Motomura, 2021
U. francisi Randall and Guézé, 1992	6	70	16.9	17.6	19.0	2.2	Uiblein and Motomura, 2021
U. gubal Uiblein, 2019	1	86		18.5		0.0	Uiblein et al., 2019
U. guttatus (Day, 1868)	73	101	15.8	17.8	19.8	4.1	Uiblein and Mclaine, 2021
U. heemstra Uiblein and Gouws, 2014	26	115	14.8	16.1	19.8	5.0	Uiblein and Gouws, 2014
U. heterospinus Uiblein and Pavlov, 2019	101	90	16.0	17.9	20.0	4.0	Uiblein et al., 2019
U. huan Uiblein and Hoang, 2024	1	87		18.6		0.0	Uiblein et al., 2024
U. indicus Uiblein and Heemstra, 2010	2	133	18.9	19.3	19.7	0.8	Uiblein and Gouws, 2015
U. itoui Yamashita, Golani and Motomura, 2011	20	114	16.6	17.5	18.4	1.8	Uiblein and Motomura, 2021
U. japonicus (Houttuyn, 1782)	36	99	17.6	21.1	23.3	5.7	Uiblein and Gledhill, 2015
U. lombok Uiblein and White, 2015	2	168	18.7	19.2	19.7	0.9	Uiblein and White, 2015
U. luzonius Jordan and Seale, 1907	5	74	18.8	19.4	20.1	1.4	Uiblein and Gouws, 2014
U. madras Uiblein and Maclaine, 2021	2	111	19.3	19.3	19.3	0.0	Uiblein and Maclaine, 2021
U. margarethae Uiblein and Heemstra, 2010	87	94	14.9	17.2	20.1	5.3	Uiblein et al., 2019
U. mascareinsis Fourmanoir and Guézé, 1967	23	125	17.9	20.7	23.7	5.8	Uiblein and McGrouther, 2012
U. moluccensis (Bleeker, 1855)	62	111	14.7	16.7	20.5	5.8	Uiblein and Heemstra, 2010; this study
U. mouthami Randall and Kulbicki, 2006	4	84	19.8	20.8	22.2	2.4	Uiblein et al., 2019
U. niebuhri Guézé, 1976	2	90	21.2	21.7	22.2	0.9	Uiblein and Gouws, 2014
U. nigromarginatus Bos, 2014	14	139	17.7	20.7	24.4	6.7	This study
U. oligospilus Lachner, 1954	19	105	15.5	17.9	22.0	6.5	Uiblein and Gouws, 2014
U. parvus Poey, 1852	59	120	18.8	21.8	26.0	7.2	Uiblein and Heemstra, 2010; this study
U. pori Ben-Tuvia and Golani, 1989	32	90	15.7	17.1	19.2	3.5	Uiblein and Motomura, 2021
U. quadrilineatus Cheng and Wang, 1963	7	108	18.5	19.8	21.7	3.2	Uiblein et al., 2016; this study
U. randalli Uiblein and Heemstra, 2011	8	84	16.4	18.2	20.4	3.9	Uiblein et al., 2019
U. saiab Uiblein and Lisher, 2013	6	84	18.9	19.9	21.9	3.0	Uiblein and Lisher, 2013
U. seychellensis Uiblein and Heemstra, 2011	3	104	16.8	18.7	22.3	5.5	Uiblein and Motomura, 2021
U. spottocaudalis Uiblein and Gledhill, 2017	17	78	18.6	20.3	22.4	3.9	Uiblein et al., 2017
U. stenopsis Uiblein and McGrouther, 2012	9	126	19.9	22.6	26.6	6.7	Uiblein and McGrouther, 2012; this study
U. suahelicus Uiblein and Heemstra, 2010	47	111	15.3	18.2	21.4	6.1	Uiblein and Gouws, 2015
U. subvittatus (Temminck and Schlegel, 1843)	9	138	19.3	21.3	23.6	4.3	Uiblein and Causse, 2013
U. sulphureus Cuvier, 1829	201	97	12.5	19.0	26.4	13.9	Uiblein and Heemstra, 2010; this study
U. sundaicus (Bleeker, 1855)	28	117	16.1	18.3	20.9	4.8	Uiblein and Gouws, 2014
U. supravittatus Uiblein and Heemstra, 2010	55	107	16.6	19.8	23.2	6.6	Uiblein and Gouws, 2015
U. taeniopterus Cuvier, 1829	40	208	17.2	19.2	22.4	5.2	Uiblein et al., 2016
U. torres Uiblein and Gledhill, 2014	20	85	22.5	24.4	27.4	4.9	Uiblein and Motomura, 2021
U. tragula Richardson, 1846	149	117	13.4	17.6	21.0	7.6	Uiblein and Gouws, 2014
U. vanuatu Uiblein and Causse, 2013	5	86	15.7	18.1	22.3	6.6	Uiblein and Causse, 2013
U. vittatus (Forsskål, 1775)	25	141	15.5	17.8	20.8	5.3	Uiblein and Gouws, 2015
U. willwhite Uiblein and Motomura, 2021	2	91	17.8	18.0	18.1	0.4	Uiblein and Motomura, 2021

a divergent, single-character differentiation pattern among often co-occurring and otherwise very similar conspecifics has been documented. Clearly, both a wide range and bimodality in barbel length are closely interconnected traits in *U. sulphureus* producing two well-separated barbel-length peaks with minor overlap. One possible functional explanation for the establishment of such a distinct barbel-length dimorphism is the adoption of a trophic or resource polymorphism, i.e., intraspecific niche-based differentiation in feeding structures (e.g., Blackie et al., 2003; Swanson et al., 2003; Whiteley, 2007; Komiya et al., 2011).

Goatfish barbels are unique, actively moveable, versatile organs with adaptive significance in various foraging contexts, including search, location, and manipulation of food resources on or below the surface of soft sediments or uneven hard bottoms (Gosline, 1985; Uiblein, 1991, 2007; Kim et al., 2001; Uiblein and Randall, 2022; Uiblein et al., 2024). According to their frequent appearance in shallow bottom-trawl catches and artisanal net fisheries, the most typical habitats of *U. sulphureus* are sandy or muddy coastal bottoms including estuaries and the lowermost reaches of rivers (Guanco et al., 2009; Rainboth et al., 2012; Guzman and Capaque, 2014; Motomura et al., 2017; Clarito and Suerte, 2021). A good strategy to forage on soft sediments would be to not only skim the surface, but also to probe the interstitial spaces below the surface. With two different barbel-length morphs present in the same habitat, both foraging methods may proceed efficiently, available resources being exploited more fully, and possible intraspecific competition would be minimized.

Alternative functional explanations for the establishment of the two barbel-length morphs in *U. sulphureus* are less plausible. For instance, in *Pseudupeneus maculatus*, barbels are used in intraspecific social interactions by wriggling each other's barbels during pairwise encounters of conspecifics (Filkovsky and Springer, 2010). However, only long barbels may efficiently reach out to other individuals, whereas short barbels of the SBM of *U. sulphureus* would not be able to efficiently support such interactive behavior. Social interactions among goatfishes may also happen without support of barbels such as dragging each other after hooking the opponent's mouth as observed in *Parupeneus forsskali* (Franz Uiblein, pers. obs. from unpublished video footage). Similar social interactions have not been observed in the genus *Upeneus*.

Clearly, our findings of barbel-length dimorphism in *U. sulphureus* require further research to uncover its adaptive significance as well as its evolutionary background. This species is very common in many areas of its wide distributional range, and it is often found at fish markets in many countries or used for producing feed for aquaculture (e.g., Yean, 1998; Motomura et al., 2017; Sivadas et al., 2019; Irnawati et al., 2022). However, very few and mostly isolated, local studies of the ecology of *Upeneus sulphureus* have been carried out (e.g., Mittelheiser et al., 2025). No detailed investigations focusing on genetic differentiation among or within populations of *U. sulphureus* exist. In particular, detailed studies of habitat use and associated foraging patterns in the two barbel-length morphs of *Upeneus sulphureus* would be required to gain further insights into the adaptive significance of this dimorphism.

This work is part of the ongoing taxonomic revision of the genus *Upeneus* by the first author, which shall be continued in the near future to encompass the two currently known species of the *moluccensis* group, *U. moluccensis* and *U. quadrilineatus*, as well as two species of the *tragula* group, *U. luzonius* and *U. sundaicus*, and the ungrouped *U. parvus* (Uiblein et al., 2024).

MATERIAL EXAMINED

Below we list the material of four additional species, of which new, previously unpublished barbel-length data were gathered, as indicated in Table 8.

Upeneus moluccensis

Syntype.—RMNH 5722, 1 of 3 STs (2 subadults), 80 mm SL, WPAC, Indonesia, Moluccas, Ambon.

Non-type material.—(*n* = 61; 72–166 mm SL) Mediterranean: MNHN-IC-2002-1117, 2, 81–99 mm SL, no locality information.

WIO, Red Sea: MNHN-IC-1984-0454, 2, 99–103 mm SL, Eritrea; MNHN-IC-2011-0093, 86 mm SL, Egypt, Gulf of Suez, 2750′N, 3343′E, 70 m depth; SMF 33644, 124 mm SL, Saudi Arabia, Jeddah fish market; USNM 429496, 2 of 9, 95–119 mm SL, Eritrea, Bay of Massawa, F/V *Menelik*, 79 m depth; Kenya: SAIAB 82822, 112 mm SL, Malindi, R/V *Dr. F. Nansen*, 3°7′S, 40°11′E, 17 m depth, bottom trawl; Mozambique: SAIAB 81954, 3, 125–141 mm SL, R/V *Dr. F. Nansen*, 25°4.4′S, 34°27.9′E, 99–102 m depth, bottom trawl; SAIAB 82509, 2, 103–115 mm SL, N Mozambique, R/V *Dr. F. Nansen*, 12°58′S, 40°30′E, 60–73 m depth, bottom trawl; SAM MB-F034166, 1 of 3, 142 mm SL, R/V *Algoa*, 17°32′S, 38°18′E, 50 m depth, bottom trawl; South Africa: SAIAB 186411, 113 mm SL, KwaZulu-Natal, Bight between Thukela River and Richards Bay; SAIAB 186441, 4 of 5, 93–124 mm SL, South Africa, 29°21.815′S, 31°47.718′E, 69–71 m depth, bottom trawl; Seychelles: SAIAB 84279, 2, 121–127 mm SL, Seychelles Bank, R/V *Dr. F. Nansen*, 5°24.42′S, 56°25.73′E, bottom trawl; Madagascar: MNHN-IC-1965-0074, 123 mm SL, Nosy Mitsio; MNHN-IC-1989-201, 2, 125–150 mm SL; SAIAB 188283, 2, 128–129 mm SL, R/V *Dr. F. Nansen*, 25°3.16′S, 47°4.41′E, 64–69 m depth; SAIAB 192153, 1 of 3, 143 mm SL, R/V *Dr. F. Nansen*, 23°40.22′S, 47°41.63′E, 61–62 mm SL, pelagic trawl.

EIO, Indonesia, Sumatra: ZMA.PISC.136.260, 1 of 5, 72 mm SL, N Sumatra, Nias, Goenoeng Sitoli; Java: CSIRO H 7305-34, 90 mm SL, Lombok, Tanjung Luar, 8°48′S, 116°29′E; CSIRO H 7305-35, 4, 79–87 mm SL; CSIRO H 7360-51, 72 mm SL, East Java, Banyuwangi, 8°9′S, 114°23′E; CSIRO H 8042-37, 126 mm SL, West Java, Pelabuhanratu, 7°2′S, 106°32′E, Lombok, Tanjung Luar, 8°48′S, 116°29′E; W Australia: AMS I.22830-001, 3 of 6, 124–136 mm SL, 175 km NW Port Hedland, F/R/V *Soela*, 19°19′S, 117°13′E, 100–105 m depth, Engel trawl; CSIRO CA 391, 134 mm SL, W of Barrow Island, F/R/V *Courageous*; CSIRO H 4005-03, 146 mm SL, W of Barrow Island, F/R/V *Southern Surveyor*, 20°53.6′S, 114°59.4′E, 88–90 m depth; NMV A 24270, 2, 102–104 mm SL, NW Shelf, NW of Cape Thouin, 91–92 m depth, otter trawl; WAM P.26185-003, 149 mm SL, Barrow Island,

20°52′S, 115°10′E, 65–78 m depth; WAM P.32647-002, 3, 72–76 mm SL, Exmouth Gulf, 21°42.567′S, 114°46.969′E, 9 m depth; WAM P.5688, 6, 123–166 mm SL, Shark Bay, 25°21′S, 113°44′E; WPAC, Indonesia, Moluccas: RMNH 13171, 99 mm SL, Ambon, Bay of Ambon; ZMA.PISC.136.261, 92 mm SL, N Moluccas; Celebes: RMNH 25053, 111 mm SL, Sumbawa; China: SMF 25449, 102 mm SL, Hainan, Qing Lan Da Qiao, 19°41′N, 110°49′E; ZMUC 63, 3, 77–88 mm SL, Hongkong, *Galathea* Expedition; Australia, Coral Sea: CSIRO H 7204-01, 136 mm SL, Queensland, SE of Weary Bay, F/R/V *Gwendoline May*, 15°55.36′S, 145°39.60′E, 40 m depth, demersal trawl.

Upeneus parvus Poey, 1852

Type.—HT of *Pseudomulloides carmineus* Miranda Ribeiro, 1915: MNRJ 1656, 105 mm SL, SWA, Brazil, Rio de Janeiro, outside Guanabara Bay ("fora da barra"), ca. 22°57′30″S, 43°8′2″W (Franz Uiblein, unpubl. data).

Non-type material.—(*n* = 58; 68–182 mm SL) NWCA, USA, South Carolina: USNM 196980, 169 mm SL, R/V *Silver Bay*, 32°20′N, 79°23′W, 60 m depth, shrimp trawl; USNM 429398, 2, 137–145 mm SL, off South Carolina coast, R/V *Silver Bay*, 32°2′N, 79°23′W, 64 m depth; Gulf of Mexico, Mexico: USNM 158460, 8, 98–127 mm SL, off Tabasco, R/V *Oregon*, 18°45′N, 93°15′W; USA, Texas: USNM 394942, 4, 109–119 mm SL, 27°16′N, 96°28′W, 100 m depth, trawl; USNM 429400, 91 mm SL, R/V *Silver Bay*, 28°20′N, 94°W, 35 m depth, 76 ft trawl with rollers; Alabama: USNM 358221, 2, 111–129 mm SL, R/V *Suncoaster*, 29°21′N, 87°46.4′W; USNM 358247, 142 mm SL, Reef south of Double-Top, US Geological Survey, R/V *Suncoaster*, 29°23.38′N, 87°58.48′W; USNM 358248, 140 mm SL, US Geological Survey, R/V *Suncoaster*, 29°21.3′N, 87°46.59′W, 98 m depth; Greater Antilles, Cuba, channel between Cuba and Great Bahama Bank: USNM 395433, 2, 148–149 mm SL, R/V *Oregon*, 23°4.2′N, 78°46.2′W, 362 m depth, 40 ft shrimp trawl; USNM 429151, 2, 131–143 mm SL, R/V *Oregon II*, 22°59′N, 78°43′W, 0–278 m depth; USNM 466057, 107 mm SL, R/V *H.B. Bigelow*, 23°4′N, 78°46′W, 0–362 m depth; Puerto Rico: USNM 144555, 107 mm SL, Añasco, Añasco Bay.

SWCA, Guyana: BMNH 1961.9.1.152-157, 6, 108–163 mm SL, British Guiana Trawl Survey, 7°53′N, 57°25′W, 20–27 m depth, trawl; Cape St Mary, British Guiana Trawl Survey, trawl: BMNH 1982.5.13.6, 169 mm SL, 7°53′N, 57°25′W, 45–49 m depth; BMNH 1982.5.13.7, 147 mm SL, 8°17′N, 58°13′W; BMNH 1982.5.13.8, 143 mm SL, 7°18′N, 56°32′W, 42–49 m depth; BMNH 1982.5.13.9, 110 mm SL, 7°42′N, 57°36′W; BMNH 1982.5.13.10, 104 mm SL; BMNH 1982.5.13.11; 120 mm SL; BMNH 1982.5.13.12, 105 mm SL, 8°15′N, 58°47′W, 20 m depth; French Guiana: MNHN-IC-2002-0957, 4, 96–116 mm SL, 5°22′1″N, 52°31′1″W; MNHN-IC-2003-1636, 95 mm SL, 5°36′32″N, 52°27′11″W, shrimp trawl; MNHN-IC-2003-1664, 136 mm SL, 5°36′32″N, 52°27′11″W, shrimp trawl.

SWA, Brazil: BMNH 1923.7.30.239, 94 mm SL, Rio de Janeiro, fish market; MNHN-IC-1975-0207, 2, 68–98 mm SL, Bahia, Salvador, Sapoca Bay; MZUSP 42014, 112 mm SL, São Paulo, Ilhabela, fish market; MZUSP 42016, 151 mm SL, Rio de Janeiro, 22°21′S, 40°26′W, 111–112 m depth; MZUSP 42019, 2 of 10, 173–182 mm SL, 24°52′S, 47°0′W, 41–42 m; MZUSP 46288, 2, 78–85 mm SL, São Paulo, São Sebastião; MZUSP 121447, 110 mm SL, São Paulo, Santos, 24°24.03′S, 46°39.55′W; NPM 5787, 2, 92–104 mm SL, Brazil, Rio de Janeiro, Macaé, central fish market.

Upeneus quadrilineatus Cheng and Wang, 1963

Non-type material.—(*n* = 7; 81–133 mm SL) WPAC, Indonesia: NCIP 3495, 90 mm SL, West Java, Tanjung Pasir.

EIO, Indonesia, Java: CSIRO H 7696-01, 81 mm SL, East Java, Pacitan, 8°13′S, 111°4′E; Central Java, Cilacap fish market, 7°44′S, 109°1′E: CSIRO H 7469-02, 133 mm SL; CSIRO H 7469-03, 123 mm SL; CSIRO H 7697-01, 102 mm SL; CSIRO H 7697-02, 2, 112–117 mm SL.

Upeneus stenopsis Uiblein and McGrouther, 2012

Holotype.—AMS I.20918-017, 131 mm SL, WPAC, NE Australia, Queensland, Coral Sea, off Raine Island, 11°35′S, 144°2′E, 270–275 m depth, prawn trawl.

Paratypes.—WPAC: AMS I.21628-001, 108 mm SL, Australia, Northern Territory, Timor Sea, 9°46′S, 128°57′E, 165–190 m depth, bottom trawl; MNHN-IC-1984-0802, 101 mm SL, Philippines, off Quezon Island, 13°58′59″N, 120°18′0″E, 186–187 m depth, beam trawl; MNHN-IC-2012-0212, 112 mm SL, same station data.

Non-type material.—WPAC, Philippines: CAS 235576, 5, 123–147 mm SL, between Luzon and Mindoro Islands, 13°53′8″N, 120°7′47″E, 115–144 m depth, otter trawl.

DATA ACCESSIBILITY

AI STATEMENT

The authors declare that no AI-assisted technologies were used in the design and generation of this article and its figures.

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