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ORIGINAL ARTICLE

## A new goatfish species of the genus *Upeneus* (Mullidae) based on molecular and morphological screening and subsequent taxonomic analysis

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### Abstract

A new goatfish, *Upeneus heemstra* sp. nov. (Mullidae), from the Western Indian Ocean and SE India is described from initial DNA barcoding and quantitative morphological screening, followed by a taxonomic analysis featuring the comparison of 56 meristic, morphometric and colour characters compiled from 340 specimens of 10 phenotypically similar species. The new species differs clearly from *U. oligospilus* (Persian Gulf), *U. tragula* (Eastern Indian Ocean and West Pacific) and *U. niebuhri* – resurrected here – from the Gulf of Suez (Red Sea) in the combination of the following characters: caudal peduncle, head, snout, postorbital, barbel and caudal-fin length, anal-fin and second dorsal-fin height, and the number of oblique bars on the caudal fin. These four species can be distinguished from the six other species of the so-called *tragula* group primarily by colour pattern and appear to represent a distinct ‘dark-freckled’ species complex. An updated identification key for the *tragula* species group is provided and remarks on size-related and population differences are made.

**Key words:** *Character displacement, DNA barcoding, population comparisons, size-related differences, species complex, Western Indian Ocean*

### Introduction

Ocean habitats are mostly connected and spacious, thus allowing highly mobile organisms such as fishes to distribute widely. Determining the spatial delimitations of fish populations or species is therefore often difficult, an additional obstacle being the still insufficiently known diversity. Detailed genetic and phenotypic studies, at best in combination, are a promising tool to uncover ‘cryptic’ diversity that is not immediately evident, thus providing new insights for both basic and applied marine biological science.

The family of the goatfishes (Mullidae), ecologically and commercially important inhabitants of sand-associated, shallow habitats (Uiblein 2007), is a clade that requires enhanced biodiversity-related research. For instance, in the Western Indian Ocean, 12 new species of the genera *Mulloidichthys*, *Upeneus* and *Parupeneus* have been described only recently (Randall & Heemstra 2009; Randall & King 2009;

Uiblein & Heemstra 2010, 2011a,b; Uiblein 2011; Uiblein & Lisher 2013) and preliminary evidence of population differentiation at various geographic scales has been documented for distinct species (e.g. Uiblein 2011; Uiblein & Heemstra 2011a,b).

In their regional revision of the *Upeneus* species from the Western Indian Ocean, Uiblein & Heemstra (2010) assembled phenotypically similar species into groups to simplify comparisons among the many species of this genus. This approach was followed in several recent taxonomic accounts (Uiblein & Heemstra 2011a,b; Yamashita et al. 2011; Motomura et al. 2012; Uiblein & McGrouther 2012; Uiblein & Causse 2013; Uiblein & Lisher 2013) with additional new species being added and species groups updated. Accordingly, one very distinct species, *U. filifer* (Ogilby, 1910), and five phenotypically separable species groups, each containing between four and nine species, have been

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distinguished (Uiblein & Heemstra 2010; Uiblein & Causse 2013; Uiblein & Lisher 2013): the *japonicus* group with *U. asymmetricus* Lachner, 1954, *U. australiae* Kim & Nakaya, 2002, *U. francisi* Randall & Guézé, 1992, *U. guttatus* (Day, 1868), *U. itoui* Yamashita et al., 2011, *U. japonicus* (Houttuyn, 1782), *U. pori* Ben-Tuvia & Golani, 1989, *U. saiab* Uiblein & Lisher, 2013, and *U. seychellensis* Uiblein & Heemstra, 2011; the *moluccensis* group with *U. doriae* (Günther, 1869), *U. moluccensis* (Bleeker, 1855), *U. quadrilineatus* Cheng & Wang in Chu et al., 1963, and *U. sulphureus* (Cuvier, 1829); the *stenopsis* group with *U. davidaromi* Golani, 2001, *U. mascarensis* Fourmanoir & Guézé, 1967, *U. stenopsis* Uiblein & McGrouther, 2012, *U. subvittatus* (Temminck & Schlegel, 1843), and *U. vanuatu* Uiblein & Causse, 2013; the *vittatus* group with *U. indicus* Uiblein & Heemstra, 2010, *U. parvus* Poey, 1852, *U. suahelicus* Uiblein & Heemstra, 2010, *U. supravittatus* Uiblein & Heemstra, 2010, and *U. vittatus* (Forsskål, 1775); and the *tragula* group with *U. luzonius* Jordan & Seale, 1907, *U. margarethae* Uiblein & Heemstra, 2010, *U. mouthami* Randall & Kulbicki, 2006, *U. oligospilus* Lachner, 1954, *U. randalli* Uiblein & Heemstra, 2011, *U. sundaicus* (Bleeker, 1855), *U. taeniopterus* Cuvier in Cuvier & Valenciennes, 1829, and *U. tragula* Richardson, 1846.

Species from the *tragula* group can be distinguished from all other congeners by the following combination of characteristics: VIII dorsal-fin spines, total gill rakers 18–26, pectoral-fin rays 12–15, pelvic-fin length 0.8–1.1 times in pectoral fins, bars on caudal fin in fresh fish of all species, and bars retained or not retained in preserved fish. The name-bearing species for this group, the freckled goatfish *Upeneus tragula*, has been documented to be particularly widely distributed in the Indo-Pacific from South Africa to Japan (e.g. Uiblein et al. 1998; Randall & Kulbicki 2006; Uiblein & Heemstra 2010) and one may be tempted to hypothesize the existence of a yet insufficiently explored diversity. In fact, Lachner (1954) described an additional species from the Persian Gulf, showing dark freckles on the body and fins like *U. tragula* and named it *U. oligospilus*. Assumptions were made that *U. tragula* may overlap with this second species in distribution (Thomas 1969). Another goatfish species, *U. niebuhri* Guézé, 1976, was described more recently from the Gulf of Suez. Both *U. niebuhri* and *U. oligospilus* were later synonymized with *U. tragula* by Bauchot et al. (1985) and Randall & Kulbicki (2006), respectively.

In their regional taxonomic review, Uiblein & Heemstra (2010) resurrected *U. oligospilus* based on its clear distinction from *U. tragula* in colour and morphometric characters. After this review was published, a large number of *Upeneus* specimens

from off Australia, Indonesia, Vietnam and several other areas were examined and compared with the Western Indian Ocean material. In parallel with this work, tissue samples mostly taken from collected or photographed voucher specimens from various localities in the Indo-West Pacific became available for molecular studies.

Here, we analyse a large number of genetic and phenotypic data gathered from specimens originally identified as *U. tragula* and from several other *Upeneus* species. Based on initial screening of three independent data sets, involving DNA sequencing and quantitative morphometric and meristic comparisons, we provide cumulative evidence for the existence of a still undescribed species that occurs in the Western Indian Ocean and SE India. Based on comparative studies of 56 meristic, morphometric and colour characters compiled from a total of 340 specimens representing all species of the *tragula* group, we describe *Upeneus heemstra* sp. nov., a species that was previously confused with *U. tragula*. We also confirm the validity of the species *U. oligospilus*, resurrect the species *U. niebuhri*, and present a key for the Indian Ocean species of the *tragula* group. Remarks on differences among size groups and populations are also made.

## Materials and methods

### Molecular approach

Representatives of four *Upeneus* species were included in the genetic analysis. These included *U. heemstra* sp. nov. and two representatives (*U. tragula* and *U. margarethae*) of the *tragula* species group (Uiblein & Heemstra 2010). Representatives of *U. tragula* were included from the West Pacific and Eastern Indian Ocean. These included specimens collected from Guangdong, China, near the type locality of the species (Richardson 1846). Representatives of *U. heemstra* sp. nov. were from the Western Indian Ocean and Sri Lanka. Three specimens of *U. suahelicus*, collected from Tanzania (Zanzibar) and Madagascar, served as more distantly related outgroups for the analysis. Representatives of the three other *Upeneus* species groups were not included in the present analysis, as the relationships among and constitution of these groups are the focus of ongoing research by the authors. Details of the specimens included and the data sources are provided in Table I.

Sequence data of the ‘DNA barcoding’ (*sensu* Hebert et al. 2003) fragment of the mitochondrial cytochrome oxidase *c* subunit I (*COI*) gene were downloaded from public repositories, including GenBank and BOLD (<http://www.boldsystems.org>)

Table I. Details of the representative specimens of the four *Upeneus* species (*U. heemstra* sp. nov., *U. margarethae*, *U. suahelicus* and *U. tragula*) included in the genetic study. These include the GenBank number (if available) or, alternatively, the BOLD Process ID, the collection locality, the accession details of the corresponding voucher specimen or unvouchered image, and details on the original reference for the data and other significant information. Voucher specimens included in the phenotypic studies are emphasized in bold.

Species	GenBank no.	BOLD Process ID	Locality	Voucher specimen (VS) or unvouchered image (UVI)	Source/ Comments
<i>Upeneus heemstra</i> sp. nov.	–	SAIAB741-08	Tanga, Tanzania	<b>VS: SAIAB 80384-1</b>	Paragenetype
	HQ972714	SAIAD166-10	Zanzibar, Tanzania	UVI: SAIAB 87071-1	
	HQ972715	SAIAD167-10	Zanzibar, Tanzania	UVI: SAIAB 87071-2	
	JF494768	DSFSE787-08	Pomene, Mozambique	<b>VS: SAIAB 88453</b>	Paragenetype
	JQ350408	SBF471-11	Nosy Bé, Madagascar	VS: ECOMAR:Ich: NBE1297 <sup>1</sup>	Hubert et al. (2012)
	JQ350409	SBF197-11	Nosy Bé, Madagascar	VS: ECOMAR:Ich: NBE0468 <sup>1</sup>	Hubert et al. (2012)
	KC147803	–	Shimoni, Kenya	UVI: SAIAB 96197-1	
	KC147804	–	Shimoni, Kenya	UVI: SAIAB 96167-1	
	KC147808	–	Shimoni, Kenya	VS: SAIAB 188307-1 <sup>3</sup>	Paragenetype
	KC147809	–	Shimoni, Kenya	VS: SAIAB 188307-2 <sup>3</sup>	Paragenetype
<i>Upeneus margarethae</i>	KC147810	–	Negombo, Sri Lanka	<b>VS: SAIAB 187361-1</b>	
<i>Upeneus suahelicus</i> (outgroup)	KC147802	–	Zanzibar, Tanzania	<b>VS: SAIAB 87108-1</b>	
	–	SAIAD329-11	Fort Dauphin, Madagascar	<b>VS: SAIAB 97929-1</b>	
<i>Upeneus tragula</i>	HM382775	SAIAB1251-10	Zanzibar, Tanzania	<b>VS: SAIAB 87011-4</b>	
	HM382777	SAIAB1253-10	Zanzibar, Tanzania	<b>VS: SAIAB 87011-6</b>	
	–	BW-A6552	Torres Strait, Australia	<b>VS: CSIRO H 6920-02</b>	
	–	BW-A11198	Lombok, Indonesia	<b>VS: CSIRO H 7217-02</b>	
	EF607611	FSCS209-06	Guangdong, China	VS: GD 9081057 <sup>2</sup>	Zhang (2011)
	EF607612	FSCS208-06	Guangdong, China	VS: GD 9081056 <sup>2</sup>	Zhang (2011)
	EF607613	FSCS207-06	Guangdong, China	VS: GD 9081055 <sup>2</sup>	Zhang (2011)
	EF607614	FSCS279-06	Guangdong, China	VS: GD 9082022 <sup>2</sup>	Zhang (2011)
	KC147799	–	Nha Trang, Vietnam	No voucher	
	KC147800	–	Nha Trang, Vietnam	UVI: SAIAB 188306-1	
KC147806	–	Ha Long, Vietnam	<b>VS: HIFIRE F 58 135</b>		

<sup>1</sup>Collection institutions code LEMUR according to Sabaj Pérez (2012); <sup>2</sup>Marine Biodiversity Collection of the South China Sea, Chinese Academy of Sciences; <sup>3</sup>voucher specimens became available after acceptance of this publication.

(accessed 21 October 2013)) (Table I) or generated specifically for this study. For the latter, DNA was extracted from ethanol-preserved tissues using the Wizard Genomic DNA Purification (Promega, Madison, Wisconsin) kit. The *COI* gene fragment was amplified for each sample by polymerase chain reaction (PCR) using the primers (dgLCO-1490 and dgHCO-2198) of Meyer (2003). Reactions contained 1 × buffer, 2.5 mM MgCl<sub>2</sub>, 0.2 μM of each primer, 0.2 mM of each dNTP, 0.5 U *Taq*-polymerase (Southern Cross Biotechnology, South Africa) and 3 μl of template DNA, and were made to the final 25 μl volume with ultrapure water. The thermocycling regime included an initial denaturing step of 95°C for 2 min, followed by 35 cycles of denaturing (94°C for 30 s), annealing (48°C for 30 s) and extension (72°C for 50 s). A final extension step (72°C) of 7 min followed. To determine whether amplification was successful, PCR products were visualized on a UV-transilluminator, following electrophoresis in 1% agarose gels stained with ethidium bromide. PCR products were purified using Millipore (Billerica, Massachusetts) Montage PCR filter units, sequenced using BigDye v3.1

(Applied Biosystems, Austin, Texas) terminator chemistry and analysed on an ABI 3730XL (Applied Biosystems) automated sequencer by a commercial sequencing facility (MacroGen, Seoul, South Korea).

The resulting sequences were checked against their chromatograms for misreads and sequencing errors using ChromasLITE (Technylesium). Sequences were aligned and edited further using Lasergene SeqMan Pro 9 (DNASTAR, Madison, Wisconsin). The final alignment of the data set was performed using ClustalX2 (Larkin et al. 2007). Data were analysed under maximum likelihood (ML) and unweighted parsimony (UP) phylogenetic frameworks in PAUP\*4b10 (Swofford 2002). In each case, heuristic searches were conducted to determine the most likely or parsimonious tree(s), using TBR-branch swapping of a starting tree obtained by a random addition of taxa. The likelihood and parsimony analyses employed 100 and 1000 such iterations, respectively. Prior to the ML analysis, ModelTest3.7 (Posada & Crandall 1998) was used to determine the optimal model of nucleotide evolution for the data set. The Akaike (1974) Information Criterion was used to select among competing

models and the parameters of the most likely model were then implemented in the analysis. Nodal support for clades and relationships was determined using non-parametric bootstrapping (Felsenstein 1985) of the data set under both approaches, with 1000 bootstrapping pseudo-replicates being used in each case. Relationships were also considered using a distance-based, minimum-evolution approach, through the construction of a neighbour-joining (NJ; Saitou & Nei 1987) tree. In this case, nodal support was determined through 10000 bootstrapping replicates.

Sequence divergences among individuals and taxa were calculated using PAUP. These included uncorrected and model-corrected divergences. A Kimura (1980) 2-parameter (K2P) model was employed here, rather than the ML-model selected above, to enable comparison to other DNA barcoding surveys.

#### *Phenotypic approach*

A total of 205 specimens from various museum collections were identified as *Upeneus tragula* using the available keys of Uiblein & Heemstra (2010, 2011b) and further examined based on a large set of characters including SL, 41 additional morphometric (all in mm, to the nearest second decimal) and 12 meristic characters following earlier published work (e.g. Uiblein & Heemstra 2010, 2011a,b; see Table II for descriptions, abbreviations, and use of these characters). In addition, three qualitative colour characters, the number and colour of lateral body stripes and the presence of a dark first dorsal-fin tip, were used for detailed comparisons. Methods for measuring and counting as well as descriptions of colour based on preserved specimens and photographs of fresh fish follow Uiblein & Heemstra (2010). The holotype of *U. niebuhri* and another more recently collected specimen from the Gulf of Suez (Red Sea), originally identified as *U. cf. tragula* by the senior author, were also studied. For interspecific comparisons, 124 specimens of 5 other phenotypically similar species from the Indian Ocean (*U. margarethae*, *U. oligospilus*, *U. randalli*, *U. sundaicus* and *U. taeniopterus*) and 9 specimens of 2 Pacific species (*U. luzonius*, *U. mouthami*) were studied. A complete list of the comparative material examined is provided at the end of the Material and Methods section.

#### *Quantitative morphological screening*

The morphological screening was performed in subsequent steps, starting with Principal Components Analysis (PCA; SYSTAT software) that allows

detection of possible groupings *a posteriori* using initially ungrouped data. The data were gathered from a subsample of 143 adult specimens (> 70 mm SL) originally identified as *Upeneus tragula* for which a complete matrix from measurements of 37 morphometric characters was available. The PCA was then followed by one-way ANOVA comparisons of groups previously identified by PCA for the characters with the highest loadings from those components that allowed the detection of the groupings. All morphometric data used in these analyses were size-adjusted using the residuals derived from log-log regressions against SL (Uiblein & Winkler 1994). All regressions were highly correlated and significant.

As a further step, 204 specimens from the same areas as the 2 groups identified by PCA were analysed regarding possible group differences in 5 selected meristic characters using frequency tables and Chi<sup>2</sup> test for trends (GraphPad Prism 5 software).

In both analysis steps geographical subgroups were identified to allow additional comparisons.

#### *Taxonomic analysis*

In the taxonomic study, particular attention was paid to elaborate the most important diagnostic characters for distinction among species in the subsequent comparisons, either singly or in combination, taking sample size and intraspecific variation into account. During the preparation of the identification key, special emphasis was given to the combined use of two or three different character types and to include also diagnostically important information on colour patterns of fresh and preserved fish. Types were chosen from the available material according to their condition and the collection area being relatively close to the type locality (E and SE African coast).

Attention was paid to detect possible geographical variation in the new species, *Upeneus heemstra* sp. nov. To account for allometric changes, the morphometric and caudal-fin bar data obtained from subadults of *U. heemstra* sp. nov., *U. oligospilus* and *U. tragula* were studied separately from adults (> 70 mm SL).

#### *Comparative material examined*

Institutional abbreviations follow Sabaj Pérez (2012). HIFIRE is the abbreviation for the scientific fish reference collection at the Institute of Marine Research, Bergen, Norway. Measurements of specimens examined refer to SL.

*Upeneus luzonius* ( $n = 5$ ): W Pacific, Philippines: SU 9244, 95 mm, holotype, Cavite, Luzon; SU 20101, 2: 68–70 mm, paratypes, same locality as

Table II. Abbreviations and descriptions of morphometric and meristic characters examined in the current study.

*Morphometric characters*

SL	standard length – distance between snout tip and caudal fin base at mid-body
BODYDD	body depth at first dorsal-fin origin
BODYDA	body depth at anal-fin origin
HALFDD	half body depth (from lateral line downwards) at first dorsal-fin origin
HALFDA	half body depth (from lateral line downwards) at anal-fin origin
CPDD	caudal-peduncle depth, minimum depth anterior to caudal dorsal origin
CPDW	caudal-peduncle width at position of CPD measurement
HEAD1	maximum head depth, vertical distance at ventral edge of operculum
HEAD2	head depth across a vertical midline through eye
SUBORB	suborbital depth – distance between lower edge of orbit to ventral midline of head
INTORB	interorbital length – least distance between upper bony edges of orbits
HEADL	head length - distance between snout tip to posteriormost margin of operculum
SNOUTL	snout length -distance between snout tip to anterior margin of orbit
PORB	postorbital length, distance between posterior edge of orbit and posterior margin of operculum
ORBITL	orbit length, horizontal fleshy orbit diameter
ORBITD	orbit depth, vertical fleshy orbit diameter
UJAWL	upper-jaw length – distance between symphysis and posterior end of upper jaw
LJAWL	lower-jaw length – distance between symphysis of lower jaw and posterior end of upper jaw
SNOUTW	snout width – least distance between hinder margins of upper jaw, with closed mouth
BARBL	barbel length
BARBW	maximum barbel width, horizontal width measured at base of soft part of barbel
SD1	first pre-dorsal length – distance between snout tip to origin of first dorsal fin
SD2	second pre-dorsal length – distance between snout tip to origin of second dorsal fin
D1D2	interdorsal distance - distance between last spine of first dorsal and first ray of second dorsal fin
CPDL	caudal-peduncle length – distance between last anal ray and ventral origin of caudal fin
SANL	pre-anal length – distance between snout tip to origin of anal fin
SPEL	pre-pelvic length – distance between snout tip to origin of pelvic fin
SPEC	pre-pectoral length – distance between snout tip to dorsal origin of pectoral fin
D2ANL	second dorsal-fin depth – distance between origin of second dorsal fin to origin of anal fin
D1PELV	pelvic-fin depth – distance between origin of first dorsal fin to origin of pelvic fin
D1PEC	pectoral-fin depth – distance between origin of first dorsal fin to dorsal origin of pectoral fin
D1B	length of first dorsal-fin base
D2B	length of second dorsal-fin base
CAUH	caudal-fin length – distance between dorsal caudal-fin origin and upper caudal-lobe tip
ANALB	length of anal-fin base
ANALH	anal-fin height – distance between anal-fin origin and anal-fin anterior tip (= to tip of first long anal ray)
PELVL	pelvic-fin length – distance between pelvic-fin origin and pelvic-fin tip
PECTL	pectoral-fin length – distance between pectoral-fin dorsal origin and pectoral-fin tip
PECTW	width of pectoral-fin base
D1H	first dorsal-fin height – distance between first dorsal-fin origin and first dorsal-fin anterior tip (= to tip of first long dorsal-fin spine)
D2H	second dorsal-fin height – distance between second dorsal-fin origin and second dorsal-fin anterior tip (= to tip of second dorsal-fin ray)
ANH/POL	postorbital length in anal-fin height (= as ratio of anal-fin height)

*Meristic characters*

P	pectoral-fin rays
GrUud	rudimentary (= width larger than its depth) gill rakers on upper limb
GrUd	developed gill rakers on upper limb
GrLd	developed gill rakers on lower limb (including gill raker in corner)
GrLud	rudimentary gill rakers on lower limb
GrU	total gill rakers on upper limb
GrL	total gill rakers on lower limb
Gr	total gill rakers
LLSCAL	lateral line scales – pored scales from operculum to caudal-fin base (excluding scales on caudal fin)

*Colour characters*

CBUL	upper caudal-fin lobe bars – number of dark, oblique bars on upper caudal-fin lobe
CBLL	lower caudal-fin lobe bars – number of dark, oblique bars on lower caudal-fin lobe
CBALL	caudal-fin bars – number of dark, oblique bars on both caudal-fin lobes

previous lot; USNM 53067, 2: 65–71 mm, paratypes, Manila.

*Upeneus margarethae* ( $n = 50$ ): W Indian Ocean: Kenya: SAIAB 82825, 2: 65–95 mm, off Kipini, 02° 38'S 40°28'E, 12 m; Tanzania: SAIAB 87108, 112 mm, Zanzibar, Mazizini, landing site adjacent to Zanzibar Beach Resort; Mozambique: SAIAB 81741, 128 mm, 26.16°S 32.98°E, 45 m; SAIAB 86466, 4: 75–84 mm, 19°47.44'S 35°30.72'E, 28–29 m; Red Sea, Sudan: BMNH 1960.3.15.841, 63 mm, Ibn Abbas Island, 5 km south of island; Madagascar: MNHN 1966–881, 90 mm, no locality; E Indian Ocean: Thailand: ZMUC P49560, 85 mm, Phuket; NW Australia: AMS 22831-021, 3 (of 6): 81–97 mm, Northwest Shelf, 140 km west of Port Hedland, 20°00'S 117°16'E, 50 m; CSIRO-CA 3052, 98 mm, off Port Hedland, 20°01'S 117°13'E, 46–49 m; WAM 23785-6, 100 mm, Exmouth Gulf; WAM 25397.004, 3 (of 7): 94–102 mm, Rowley Shoals, 17°29'S 121°52'E, 42 m; WAM 32680-002, 93 mm, Exmouth Gulf, Bundegi Reef, 21°50.879'S 114° 15.530'E, 24 m; and 30 specimens (including 21 types) from the Western Indian Ocean studied by Uiblein & Heemstra (2010, 2011b).

*Upeneus mouthami* ( $n = 4$ ): SW Pacific, E Australia: MNHN 2004-1571, 73 mm, Chesterfield Islands, Chesterfield Bank; and three specimens from same area studied by Uiblein & Heemstra (2010).

*Upeneus niebuhri* ( $n = 2$ ): Holotype: MNHN 1977-174, 105 mm, Red Sea, Egypt, Gulf of Suez. Non-type: SAIAB 88873, 74 mm, Gulf of Suez.

*Upeneus oligospilus* ( $n = 21$ ): Persian Gulf: BMNH 2000.4.19.1190, 73 mm, United Arab Emirates, Abu Dhabi, south side of Ras Ghurab, 24°35'48"N 54°31'11"E; BPBM 29499, 4: 72–118 mm, Bahrain; and 16 specimens from same area studied by Uiblein & Heemstra (2010).

*Upeneus randalli* ( $n = 8$ ): 8 types from the Persian Gulf studied by Uiblein & Heemstra (2011b).

*Upeneus sundaicus* ( $n = 28$ ): W Indian Ocean: Persian Gulf: Iran: SMF26056, 119 mm, 28°57'49" N 49°43'81"E; SMF 26057, 103 mm, 29°11'51"N 49°13'04"E; ZMUC P49121, 132 mm, Bushehr; ZMUC P49122, 110 mm, same locality as previous lot; ZMUC P49123, 105 mm; ZMUC P49124, 109 mm, off Kangan; Kuwait: BPBM 33212, 81 mm, Kuwait Bay, 8–10 m; E Indian Ocean: Myanmar: USNM 379299, 6: 118–141 mm, 15°32'00"N 94° 53'00"E, 16–29 m; Thailand: ZMUC P49402, 119 mm, East of Phuket, 07°53'N 98°50'E; ZMUC P49403, 115 mm, same locality as previous lot; ZMUC P49562, 127 mm, Phuket; W Indonesia: RMNH 5735, 6: 89–125 mm, Bleeker types, Java, Madoera, Nias; NW Australia: AMS 3006, 109 mm, Exmouth Gulf, 22°S 114°E; AMS 21638-001, 158

mm, Timor Sea, 13°41'S 129°15'E, 35 m; CSIRO-CA 2028, 130 mm, SE of Barrow Island; CSIRO-CA 2036, 137 mm, west of Bynoe Harbour, 12°30'S 130°05'E, 38–44 m; RMNH 24737, 119 mm, Exmouth Gulf; WAM 25095.049, 100 mm, Exmouth Gulf, 22°05'S 114°15'E, 12 m.

*Upeneus taeniopterus* ( $n = 17$ ): all specimens from the Indian Ocean studied by Uiblein & Heemstra (2010).

*Upeneus tragula* ( $n = 171$ ): E Indian Ocean: Myanmar to Northwestern Australia (Timor Sea): Myanmar: USNM 360813, 78 mm, Rakhine, Sandoway, Gwa, Sar Chet Chaung, 17°47'N 94°30'E; Thailand: FRLM 30610, 82 mm, Libong Island, Trang, 7°15'00"N, 99°15'00"E; FRLM 30611, 66 mm, same station data as previous lot; ZMUC 49406-07, 2: 160–174 mm, Thai-Danish Expedition st. 1079, 07°50'N 98°48'E; ZMUC P49589, 98 mm, Phuket; ZMUC P49611, 147 mm, Phuket; ZMUC P49613, 141 mm, Phuket; Singapore: SU 31233; 4: 98–122 mm, Sutton Shoal, AWH III-34; SU 33356, 124 mm, AWH 7-V-37; W Indonesia: RMNH 480, 2: 140–158 mm, Java; USNM 396085, 147 mm, Bali, Kedonganan; Lombok, Tanjung Luar: CSIRO LM383, 3: 81–115 mm; CSIRO LM607, 118 mm; CSIRO LM608, 81 mm; CSIRO LM609, 91 mm; CSIRO LM728, 103 mm; CSIRO LM770, 181 mm; CSIRO LM771, 144 mm; CSIRO LM772, 132 mm; CSIRO LM846, 120 mm; CSIRO LM847, 132 mm; CSIRO LM848, 133 mm; CSIRO LM960, 126 mm; CSIRO LM961, 122 mm; Lombok, Gerupuk: FRLM 16109, 83 mm; FRLM 16110, 58 mm; Northwestern Australia: BMNH 1983.5.5.23-26, 4: 131–51 mm, 20°10'0"S 118°25'00"E; CSIRO C2582, 142 mm, off Carnarvon, Shark Bay, Lancelin; CSIRO H1451-3, 165 mm, North West Shelf, FRV *Soela*, 20°03'S 118°14'E, 20–21 m; WAM 4402.001, 112 mm, Exmouth Gulf, 22°05'S 114° 15'E; WAM 5485.001, 115 mm, Exmouth Gulf, 22°05'S 113°44'E; WAM 25108.006, 2: 141–169 mm, Dampier Archipelago, Kendrew Island, 20°29' S 116°32'E, 6–10 m; WAM 25397.004, 4: 123–137 mm, Rowley Shoals, 17°29'S 121°52'E, 42 m; WAM 28883.002, 159 mm, Carnarvon, 24°55'S 113°30'E; WAM 30084.007, 114 mm, Shark Bay, Slope Island, 26°07'S 113°14'E, 1–4 m; WAM 30320.029, 4: 64–113 mm, Buccaneer Archipelago, Powerful Island, 16°05'00"S 123°27'00"E; WAM 30321.019, 82 mm, Sunday Island, 16°26'00"S 123°11'00"E, 1.5 m; WAM 31097.032, 2: 63–83 mm, Cape Londonderry, 13°45'S 126°58'E, 1–2 m; WAM 31240.017, 1 (of 4): 75 mm, Berthier Island, 14°30'S 125°00'E, 1–2 m; WAM 32277.001, 178 mm, Shark Bay, Cape Peron North, 25°22.958'S 113°37.141'E, 16 m; WAM 32667.008, 120 mm,

Exmouth Gulf, Bundegi Reef, 21°51.815'S 114°11.902'E, 22–23 m; W Pacific: E Indonesia: RMNH 459, 190 mm, Celebes, Macassar; Moluccas, Ambon: CSIRO KD898, 155 mm, Teluk Baguala, off Suli, 3°38'00"S 128°17'30"E, 0–1.5 m; FRLM 24034, 71 mm, Maluku, Baguala Bay; FRLM 24763, 63 mm, same locality; N Australia (Arafura Sea to Torres Strait, 142.5°E): CSIRO H 3349-01, 139 mm, Torres Strait, NW of Prince of Wales Island, FRV *Southern Surveyor*, 10°23'S 141°47'E, 8 m; CSIRO H 3637-09, 92 mm, W of Thursday Island, FRV *Southern Surveyor*, 10°34'S 141°59'E, 12 m; CSIRO H 6558-02, 152 mm, Torres Strait, Endeavour Strait, RV *Gwendoline May*, 10°49'S 142°09'E, 15 m; CSIRO H 6558-03, 139 mm, same station data as previous lot; CSIRO H 6795-02, 83 mm, Torres Strait, W of Prince of Wales Island, 10°41.65'S, 141°53.61'E, 14 m; CSIRO H 6895-03, 138 mm, same station data as CSIRO H 6558-02; CSIRO H 6920-02, 2: 152–182 mm, Torres Strait, N of Cape York Peninsula, RV *Gwendoline May*, 10°24'S 142°41'E, 20 m; CSIRO-H 7203-01, 126 mm, Torres Strait, W of Saibai Island, 9°27.90'S 142°26.74'E, 7m; WAM 28943.001, 141 mm, Gulf of Carpentaria, 14°00'S 140°00'E, 12 m; Eastern Australia (Torres Strait (142.5°E) to Moreton Bay): AMS 20753-003, 16: 54–128 mm, Lizard Island area, two miles off Nymph Island, 14°36'S 145°14'E, 15 m; AMS 34397-028, 2 (of 5): 130–160 mm, Port Clinton, adjacent to West Flat, South Arm channel, SWB 93-98, 22°34'08"S 150°44'34"E, 10–11 m; CSIRO-DGQ0414, 2: 95–112 mm, NE of Yeppoon, 22°39.88'S 151°16.40'E, 13 m; CSIRO H 6717-03 (DGQO-133), 146 mm, N of Rockingham Bay, site 896, 17°38.82'S 146°22.28'E, 26 m; WAM 28824.003, 79 mm, Moreton Bay, 27°05'S 153°09'E, 1–2 m; Western Thailand: CAS 206431, 10: 59–105 mm, Thailand Bay, Rayong, southeast Ban Phe Fisheries Training Center, 12°35'40"N 101°25'43"E, 0–1 m; CAS 206433, 10: 50–93 mm, Gulf of Thailand, west shore of Ko Samet; Cambodia: MNHN 1963-580, 2: 79–84 mm, 10°21' N 104°18' E; Vietnam: Ha Long: HIFIRE F58133, 119 mm, st. 5201; HIFIRE F58134, 137 mm, st. 5258; HIFIRE F58135, 130 mm, st. 5257; Nha Trang: FRLM 31773, 107 mm; HIFIRE F58100, 111 mm; HIFIRE F58101, 7: 116–174 mm; ZMUC 49481, 165 mm, Luong Son, north of Nha Trang; ZMUC 49489, 100 mm; Vung Tau: USNM 305043, 191 mm, Cap St. Jacques, Vung Tau fish market, 10°21'N 107°15'E; no locality information: MNHN 1905-223, 121 mm. Philippines: CAS 52572, 80 mm, Mindanao Island, Zamboanga, JD VI-48ZAM; SU 9686, 2: 74–98 mm, Luzon Island, Manila, GAL 1901; SU 20882, 108 mm, Luzon

Island, Sorsogon, Bacon, CJP; SU 38939, 114 mm, Palawan, Coron, Busuanga, AWH 29-VI-40; SU 38941, 87 mm, Panay Island, Iloilo, AWH 27-VII-40; Palau: CAS 206389, 2: 90–104 mm, Btilawel District, Koror Island, GVF 1378, 7°20'39"N 134°30'44"E, 0–2 ft; CAS 206435, 4: 82–107 mm, Madalai District, west end of Koror Island, GVF 0509, 7°20'22"N 134°28'5"E, 0–7 ft; CAS 206464, 118 mm, Kossol Reef, GVF 1968, 7°54'30"N 134°40'50"E, 1–3 fa; Papua New Guinea: CSIRO A4, 60 mm, New Britain, Matupi Island, Simpson Harbour, FRV *Fairwind*; CSIRO C1772, 71 mm, New Britain, Matupi Isl., Rabaul Hbr., FRV *Fairwind*; ZMUC 49479-80, 2: 112–122 mm, Bay of Port Moresby, Galathea Expedition st. 527, 3 m; New Caledonia: AMS 25756-001, 159 mm, St Vincent; S China: SU 61120, 2: 101–120 mm, Hong Kong Spec. Admin. Reg., Kau Sai Chau, GVF 1717, 22°22'35"N 114°18'42"E, 0–2 ft; Taiwan: SAIAB 35138, 135 mm, Penghu Islands, southern end of island, 23°30.6'N 119°34.3'E; SAIAB 35638, 3: 125–140 mm, Penghu Islands, Makung market; SU 21003, 3: 72–165 mm, Kaohsiung (Takao); Japan: FRLM 16819, 98 mm, Shima City, Mie Pref, Ago Bay; FRLM 22176, 105 mm, Iriomote Island, Kaira River; FRLM 22177, 118 mm, same locality as previous lot; FRLM 29923, 140 mm, same locality as FRLM 16819; SU 23506, 2: 87–92 mm, Honshu Island, Shizuoka Province, Shizuoka market.

## Results

### *Molecular approach*

Once sequences were aligned and trimmed to equal length, the *COI* data set provided 626 nucleotides for analysis. The alignment included 107 variable characters, of which 86 were parsimony-informative. A transversional model with a gamma-distribution of rate variation (TvM +  $\Gamma$ : Posada & Crandall 1998) was selected as being the most appropriate among those models available in Modeltest for the data set. Implementing the parameters of this model in a heuristic search in the ML analysis provided a topology with a log-likelihood ( $\ln L$ ) of  $-1426.733$  (Figure 1).

The parsimony analysis yielded two equally parsimonious trees, each 102 steps in length (CI = 0.971, RI = 0.987, Rescaled CI = 0.958). Strict and majority-rule consensus trees of these equally parsimonious trees (not shown) were in agreement with both the ML-phylogram (above) and the NJ tree (not shown), with the retrieval of two reciprocally monophyletic clades corresponding to *Upeneus heemstra* sp. nov. and *U. tragula*, respectively (Figure 1). Both clades were well supported, with bootstraps  $\geq 80\%$ ,



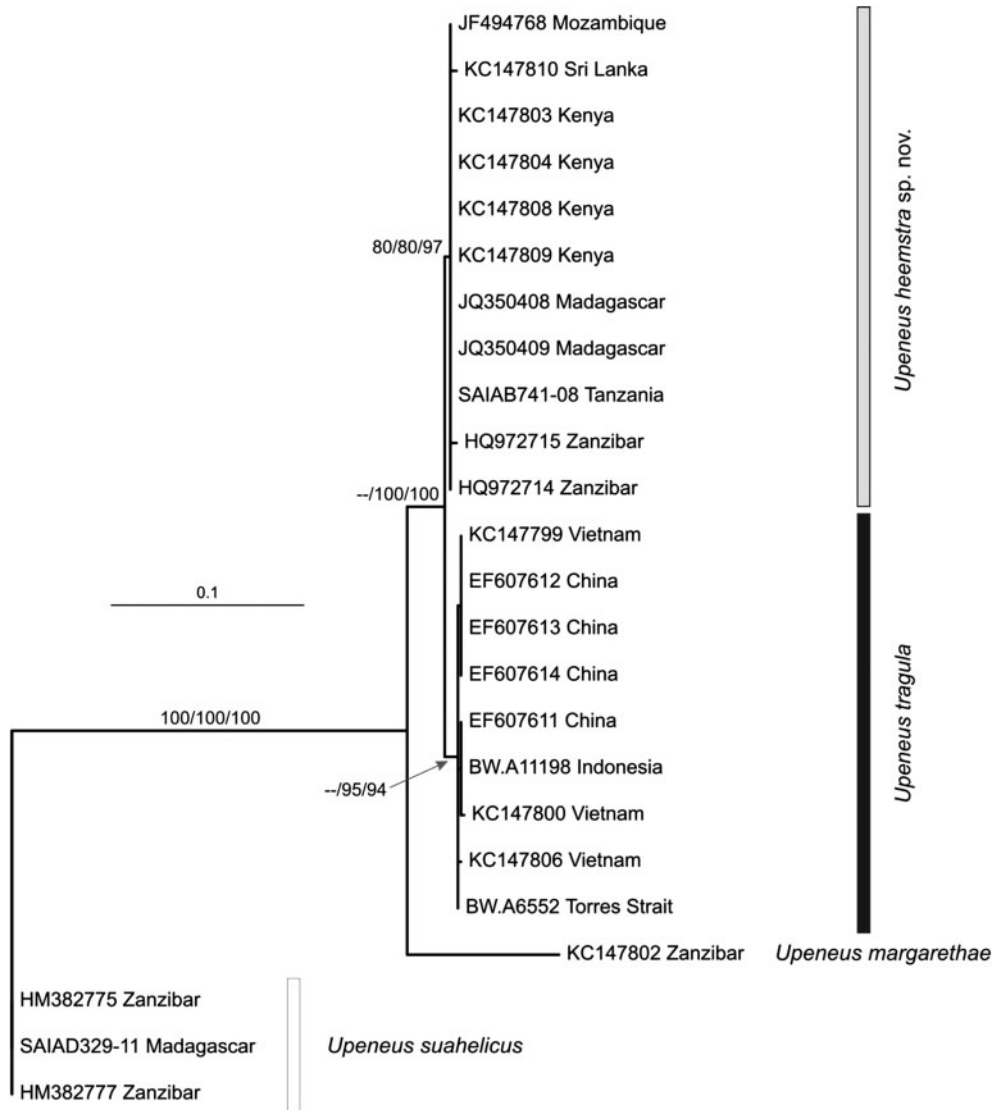


Figure 1. Maximum likelihood phylogram ( $-\ln L = 1426.733$ ) of evolutionary relationships among the included specimens from three *Upeneus* species of the *U. tragula* species group. The tree was rooted using specimens of *Upeneus suahelicus* as outgroups. Bootstrap supports for relationships from the likelihood, parsimony and neighbour-joining analyses are indicated on the respective branches (in the order ML/UP/NJ). Only bootstrap support values  $\geq 75\%$  are shown. Terminal names include GenBank accession numbers or BOLD Sequence/Process IDs, as well as regions of origin.

with the exception of the ML analysis, which provided only fair support (64%, not shown) for *U. tragula*. These two clades were well supported by UP and NJ (bootstraps of 100%) and weakly supported (55%, not shown) by ML as sister taxa. *Upeneus margarethae* was sister to both, and this larger *U. tragula* species group was well supported (100% bootstrap) as a monophyletic group with respect to the included outgroup (*U. suahelicus*).

Sequence divergences among representatives of the included taxa are presented in Table III. Sequence divergences among conspecific individuals ranged from zero to 0.6% (irrespective of whether distances were corrected according to the K2P model), with mean intraspecific values between

zero and 0.2% for the three taxa with multiple individuals included. Uncorrected sequence divergences among individuals belonging to different *Upeneus* species ranged from 0.8 to 14.1%, while the corresponding K2P model-corrected values ranged from 0.8 to 15.8%. The mean interspecific divergences obtained between *U. heemstra* sp. nov. and *U. tragula* (1.1% uncorrected, 1.2% corrected) were the lowest observed, with mean uncorrected and corrected divergences among the remaining species being greater than 7.4 and 7.9%, respectively. Regardless, distances obtained in comparisons among conspecific individuals were always lower and showed no overlap with the range of values obtained in interspecific comparisons.

Table III. Means and ranges (in parentheses) of *COI* sequence divergences among representatives of the four included *Upeneus* species. Values below the diagonal represent uncorrected sequence divergences (presented as percentages), while those above the diagonal represent divergences corrected according to the Kimura (1980) two-parameter model of nucleotide substitution. Values on the diagonal (in bold) represent the intraspecific sequence divergences for those species where multiple individuals were included. Uncorrected and corrected mean divergences and ranges were identical for intraspecific comparisons.

	<i>U. heemstra</i> sp. nov.	<i>U. margarethae</i>	<i>U. suahelicus</i>	<i>U. tragula</i>
<i>Upeneus heemstra</i> sp. nov.	<b>0.1 (0–0.6)</b>	7.9 (7.8–8.2)	14.9 (14.7–15.2)	1.2 (0.8–1.6)
<i>Upeneus margarethae</i>	7.4 (7.3–7.7)	–	15.8 (15.8–15.8)	8.2 (8.0–8.6)
<i>Upeneus suahelicus</i>	13.3 (13.1–13.6)	14.1 (14.1–14.1)	<b>0</b>	15.1 (14.8–15.3)
<i>Upeneus tragula</i>	1.1 (0.8–1.6)	7.7 (7.5–8.0)	13.4 (13.3–13.6)	<b>0.2 (0–0.5)</b>

#### Quantitative morphological screening

The results of the PCA are shown in Figure 2 and Table IV. The third and fourth principal components (PCs) in combination resulted in a clear separation of two geographical groups, one from the Western Indian Ocean (WIO), including Sri Lanka and SE India, and the other from the Eastern Indian Ocean (Myanmar southwards to eastern Indonesia and eastern Australia) and the Pacific. The latter group is here ascribed to *Upeneus tragula*. In the NE Indian Ocean, the specimens of *U. tragula* occurring from Myanmar to Singapore are particularly well separated from the WIO and SE Indian form, described as *Upeneus heemstra* sp. nov. in the following section. The characters showing the highest loadings for these two PCs are caudal-fin length, anal-fin height, first and second dorsal-fin height, caudal-peduncle length, length of first dorsal-fin base and pectoral-fin length (Table IV).

When compared using one-way ANOVA, the two groups differed significantly in seven characters: caudal-fin length, caudal-peduncle length, first and second dorsal-fin height, anal-fin height, barbel length and pectoral-fin length. Barbel length is the only character that was not among the most important contributing characters in the PCA, while first dorsal-fin base did not show significant differences.

*Upeneus heemstra* sp. nov. could also be distinguished from *U. tragula* in meristic characters (Figure 3). In addition, there were some differences between two geographic subgroups of the latter species, one from the NE Indian Ocean and the other from the SE Indian Ocean and Pacific. Regarding pectoral rays and number of lateral-line scales, the differences between the NEIO population and *U. heemstra* sp. nov. were stronger than with the other subgroup of *U. tragula*.

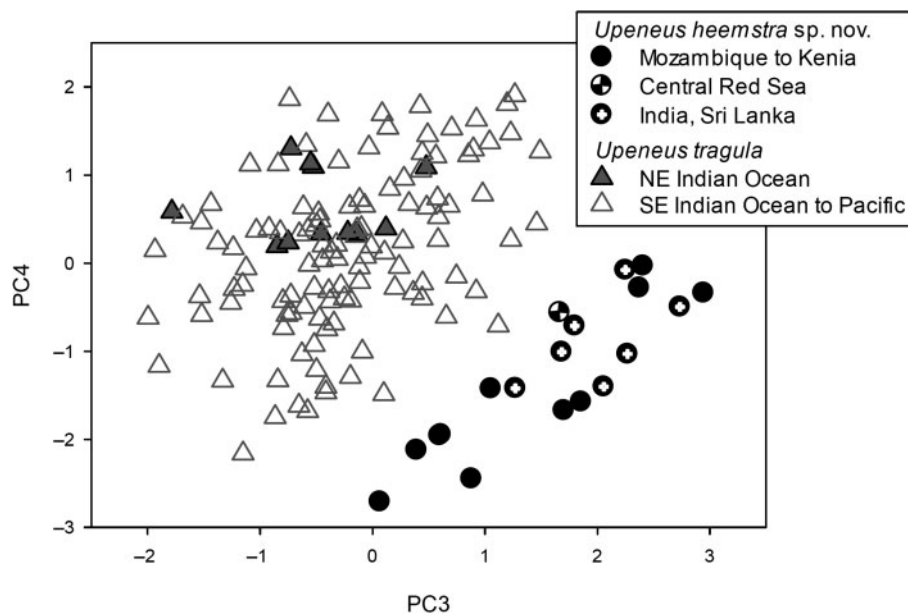


Figure 2. Third and fourth components derived from the PCA based on 37 morphometric characters from 143 specimens separated into two geographical groups corresponding to *Upeneus heemstra* sp. nov. ( $n = 19$ ) and *U. tragula* ( $n = 124$ ), with additional subdivision into populations.

Table IV. Results of multi- and univariate analysis of 37 morphometric characters from 19 *Upeneus heemstra* sp. nov. and 124 *U. tragula* individuals, with character loadings, Eigenvalues and variance explained (PCA; highest loadings for components 3 and 4 emphasized), means of residuals (log-log regressions with SL), and *F*-values (one-way ANOVA; values reflecting highly significant differences ( $P < 0.01$ ) are emphasized); see Table II for explanation of abbreviations.

Morphometric characters	Character loadings for the first four principal components				Means of residuals from log-log regressions with SL		One-way ANOVA results
	PC1	PC2	PC3	PC4	<i>U. heemstra</i>	<i>U. tragula</i>	<i>F</i> value
BODYDD	0.765	-0.464	0.142	0.044	0.42	-0.04	0.007
BODYDA	0.360	-0.762	0.054	0.185	-3.95	0.59	0.747
CPDD	0.473	-0.539	0.034	0.179	-4.32	0.64	1.353
CPDW	0.093	-0.167	0.074	0.063	-1.68	0.27	0.040
HEAD1	0.827	-0.209	0.089	-0.057	1.33	-0.25	0.073
HEAD2	0.834	0.024	-0.097	-0.033	-6.41	1.02	1.355
SUPORB	0.683	0.069	-0.039	0.030	-5.26	0.79	0.445
INTORB	0.530	-0.179	0.125	-0.128	3.89	-0.59	0.645
HEADL	0.732	0.428	0.161	0.116	5.26	-0.79	1.969
SNOUTL	0.724	0.187	0.072	0.198	-2.42	0.38	0.192
PORB	0.573	0.338	0.182	-0.001	5.95	-0.95	0.974
ORBITL	0.003	0.428	-0.259	-0.320	6.12	-0.97	0.886
ORBITD	0.021	0.467	-0.263	-0.231	0.42	-0.09	0.004
UJAWL	0.648	0.434	0.008	0.085	3.37	-0.53	0.318
LJAWL	0.568	0.471	0.052	0.034	5.47	-0.80	0.707
BARBL	0.638	0.309	-0.289	0.132	-28.21	4.33	<b>15.625</b>
BARBW	0.603	0.054	-0.011	0.050	-11.71	1.81	1.314
SD1	0.528	0.399	0.103	0.222	-2.11	0.36	0.423
SD2	0.405	0.228	0.361	0.126	2.40	-0.35	1.668
D1D2	-0.291	-0.015	0.489	0.121	16.37	-2.51	5.072
CPDL	-0.195	-0.092	<b>-0.525</b>	0.383	-33.16	5.10	<b>78.781</b>
SANL	0.335	0.369	0.166	0.126	5.02	-0.78	4.464
SPEL	0.518	0.099	0.030	0.229	-2.53	0.39	0.565
SPEC	0.669	0.394	0.097	0.144	0.90	-0.14	0.079
D2ANL	0.405	-0.762	-0.005	0.134	-4.84	0.82	1.246
D1PELV	0.774	-0.429	0.155	0.063	0.29	-0.05	0.004
D1PEC	0.634	-0.292	0.163	-0.021	-1.26	0.21	0.061
D1B	0.300	-0.132	-0.116	<b>-0.521</b>	4.68	-0.73	0.835
D2B	0.503	-0.240	-0.063	-0.466	5.47	-0.88	1.164
CAUH	0.093	-0.055	<b>-0.719</b>	0.387	-39.47	6.09	<b>179.613</b>
ANALB	0.083	-0.089	-0.357	-0.332	-4.16	0.60	0.402
ANALH	0.250	0.128	<b>-0.638</b>	0.128	-20.47	3.17	<b>20.089</b>
PELVL	0.434	0.058	-0.228	-0.265	-2.90	0.42	0.577
PECTL	0.356	0.089	-0.002	<b>-0.508</b>	12.46	-1.90	<b>9.272</b>
PECTW	0.593	-0.147	0.008	-0.346	17.91	-2.71	5.002
D1H	0.388	-0.171	<b>-0.542</b>	-0.247	-13.47	2.03	<b>7.684</b>
D2H	0.265	-0.115	<b>-0.697</b>	0.235	-33.47	5.12	<b>70.424</b>
Eigenvalues	9.842	3.987	2.995	1.999			
Variance explained	9.842	3.987	2.995	1.999			
% Variance explained	26.601	10.777	8.095	5.402			

## Taxonomy

### Family Mullidae

#### Genus *Upeneus* Cuvier, 1829

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

#### Diagnosis

Dorsal fins VII or VIII + 9; anal fin I, 6; pectoral fins 12–17; pelvic fins I, 5; principal caudal-fin

rays 7 + 8 (median 13 branched); gill rakers 4–9 + 13–24 = 18–33; lateral-line scales 28–39, lateral line complete; small scales present basally on second dorsal, anal and caudal fins; small teeth present on vomer, palatines and jaws, multiserial and villiform on jaws; body oblong, slightly compressed; barbel length in adults 4–7 times in SL; snout length 7–11 times in SL, subequal to postorbital length (6–10 times in SL); in fresh fish lateral body stripes and/or caudal-fin bars of differing colours, dark caudal-fin bars frequently retained on preserved fish.

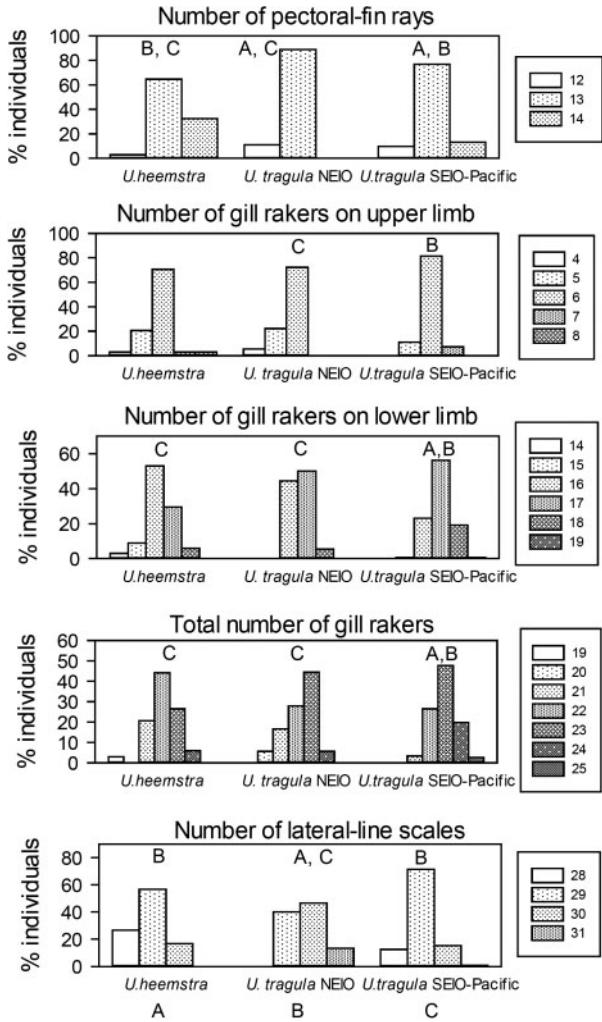


Figure 3. Meristic characters in *Upeneus heemstra* sp. nov. and two populations of *U. tragula*, with results of pairwise comparisons indicating significant differences based on Chi<sup>2</sup> test for trends (significance level 0.05; the letter symbols appearing as the lowermost x-axis labels refer to the respective species/species groups above and in the graphs they indicate significant differences with those species/species groups; NEIO: Northeast Indian Ocean; SEIO: Southeast Indian Ocean).

**Distribution**

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

**Remarks**

We recognize 34 species as valid, *Upeneus heemstra* sp. nov. and *U. niebuhri* included. The Eastern Pacific *Upeneus xanthogrammus* Gilbert, 1892 is probably a synonym of *Mulloidichthys dentatus* (Gill, 1862) (FU, unpublished data including type material from CAS).

**Key to Indian Ocean species of the *tragula* group**

- 1a. No dark dots, spots or blotches on body and paired fins in adult fish (except for area of lateral line in fresh *U. randalli*); no dark blotch around or on first dorsal-fin tip; 0–2 yellowish or pale brown lateral body stripes on fresh fish, mostly not retained in preserved fish; barbels white or yellow in fresh fish ..... 2
- 1b. Dark dots, spots or blotches on body and paired fins; dark blotch close to or on first dorsal-fin tip; one dark (red, brown or black) mid-lateral body stripe in fresh and preserved fish; barbels yellow or pale brown in fresh fish ..... 3
- 2a. Lateral-line scales 35–39; pectoral-fin length 5.0–5.8 in SL; second-dorsal fin height 6.3–7.2 times in SL; at least two lateral body stripes in fresh fish, one pale brown mid-lateral body stripe and a weaker, more yellowish stripe below; caudal-fin with 7–13 dark bars in adult fish, well retained in preserved fish (Indo-Pacific) ..... *U. taeniopterus*
- 2b. Lateral-line scales 28–34; pectoral-fin length 4.2–5.3 in SL; second-dorsal fin height 5.1–6.7 times in SL; no or only one yellow or pale brown mid-lateral body stripe in fresh fish; caudal-fin lobe with 4–13 red or grey bars in adult fish, not or only weakly retained on preserved fish ..... 6
- 3a. Bars on lower caudal-fin lobe 3–5 (3 in subadults ≤ 7 cm SL); postorbital length in anal-fin height 1.2–1.4 times; caudal-fin length 3.5–4.1 times in SL and 1.0–1.3 times in head length; pelvic-fin length 4.6–6.0 times in SL (Persian Gulf) ..... *U. oligospilus*
- 3b. Bars on lower caudal-fin lobe 4–10 (4–5 in subadults ≤ 7 cm SL); postorbital length in anal-fin height 1.4–2.0 times; caudal-fin length 2.9–3.7 times in SL and 0.8–1.1 times in head length; pelvic-fin length 4.2–5.4 times in SL ..... 4
- 4a. Bars on lower caudal-fin lobe 4–5; barbel length 4.5–4.7 in SL; upper-jaw length 9.6–10 in SL; first-dorsal fin height 5.3 in SL (Gulf of Suez) ..... *U. niebuhri*
- 4b. Bars on lower caudal-fin lobe 4–10; barbel length 4.8–7.5 in SL; upper-jaw length 7.2–10 in SL; first-dorsal fin height 3.9–5.3 in SL ..... 5
- 5a. Caudal-fin length 3.5–3.7 in SL, caudal-peduncle length 4.3–4.7; first dorsal-fin height 4.4–5.3; second-dorsal fin height 5.4–6.0 in

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Table V. Comparative data for the Indian Ocean *Upeneus* species of the *tragula* group; (a) meristic and colour characters, (b) morphometric characters as %SL and (c) morphometric characters as ratios of SL and postorbital length in anal-fin height (last column); morphometric and caudal-fin bar data taken from adult fishes only (nd = no data).

(a)	Dorsal spines	Pectoral-fin rays	Gill rakers on upper arch	Gill rakers on lower arch	Total gill rakers	Lateral-line scales	Oblique bars on upper caudal-fin lobe	Oblique bars on lower caudal-fin lobe	Total oblique bars on caudal fin	Oblique caudal-fin bars retained in preserved fish	Nr. of lateral body stripes	Colour of lateral body stripes	Lateral body stripe(s) retained in preserved fish	Dark first dorsal-fin tip (retained in preserved fish)
<i>heemstra</i> sp. nov.	8	12–14	4–8	14–18	19–24	28–30	4–6	5–6	9–12	Yes	1	Brown to black	Yes	Yes [yes]
<i>margarethae</i>	8	13–15	5–7	15–18	21–24	28–30	4–5	(5–7 <sup>1</sup> )	4(8 <sup>1</sup> )–5(11 <sup>1</sup> )	Occasionally	1	Yellow	No	No
<i>niebuhri</i>	8	13–14	5–6	16–17	22–23	29–30	3–4	4–5	8	Yes <sup>2</sup>	1	Brown to black	Yes <sup>3</sup>	Yes [yes] <sup>3</sup>
<i>oligospilus</i>	8	13–14	4–7	15–18	20–24	29–31	3–5	3–5	6–10	Yes	1	Brown to black	Yes	Yes [yes]
<i>randalli</i>	8	13–14	6–7	17–19	23–25	28–30	5	6–8	11–13	Occasionally	1	Beige	No	No
<i>sundaicus</i>	8	13–15	4–6	13–17	18–22	31–34	5–6 <sup>4</sup>	0	5–6 <sup>4</sup>	No	1	Pale brown	Faintly/no	No
<i>taeniopterus</i>	8	13–14	5–6	16–17	21–23	35–39	4–7	3–6	7–13	Yes	2	Pale brown	No	No
<i>tragula</i>	8	12–14	4–7	15–19	20–25	28–31	3–9	4–10	7–19	Yes	1	Brown to black	Yes	Yes [yes]

<sup>1</sup>Bars on lower caudal-fin lobe sometimes visible in fresh specimens; <sup>2</sup>only faintly retained in holotype; <sup>3</sup>not retained in holotype; <sup>4</sup>faintly visible only in fresh specimens.

(b)	Body depth at first dorsal-fin origin	Body depth at anal-fin origin	Caudal-peduncle depth	Caudal-peduncle width	Maximum head depth	Head depth through eye	Head length	Postorbital length	Orbit length	Upper jaw length	Barbel length	Caudal-peduncle length	Caudal-fin length	Anal-fin height	Pelvic-fin length	Pectoral-fin length	Pectoral-fin width	First dorsal-fin height	Second dorsal-fin height
<i>heemstra</i> sp. nov.	22–26	19–23	9.5–11	2.9–4.6	19–22	14–17	27–31	10–13	6.3–8.3	9.8–13	15–20	21–23	27–30	16–19	20–22	19–21	3.7–4.9	19–23	17–18
<i>margarethae</i>	22–26	20–24	9.3–12	3.6–5.7	19–23	16–18	27–31	11–12	6.6–9.1	10–12	16–20	22–26	27–31	14–18	20–24	20–24	4.1–5.3	19–23	15–20
<i>niebuhri</i>	23–26	19–22	9.7–9.9	3.2–3.7	19–20	16–17	29–31	11–12	6.9–7.3	10	21–22	21–23	29	nd	21	21	4.1–4.7	19	17
<i>oligospilus</i>	22–26	19–22	9.6–11	2.2–4.1	19–23	15–19	29–33	12–13	5.5–8.1	11–14	16–22	20–25	24–28	15–17	17–22	18–22	3.6–5.4	18–22	16–18
<i>randalli</i>	22–24	19–22	9.0–11	2.9–3.8	18–21	15–16	27–30	10–12	6.2–8.2	10–11	16–20	23–25	27–30	15–19	20–22	20–22	3.7–4.4	19–22	16–20
<i>sundaicus</i>	22–28	21–24	11–13	3.1–4.9	19–24	15–20	26–30	9.9–13	5.7–7.4	10–12	16–21	22–27	26–31	15–18	19–23	19–22	3.7–5.7	22–27	15–18
<i>taeniopterus</i>	22–25	20–23	9.7–11	3.4–4.3	17–21	14–17	25–29	9.9–13	5.2–6.3	11–13	17–21	22–24	28–32	15–17	18–20	17–20	3.8–4.7	20–23	14–16
<i>tragula</i>	21–28	18–24	9.5–12	3.1–4.9	18–24	14–20	26–32	9.9–13	5.3–8.9	9.8–14	13–21	22–27	29–34	16–20	19–24	17–22	3.5–5.3	20–25	17–21

(c)	Body depth at first dorsal-fin origin	Body depth at anal-fin origin	Caudal-peduncle depth	Caudal-peduncle width	Maximum head depth	Head depth through eye	Head length	Postorbital length	Orbit length	Upper jaw length	Barbel length	Caudal-peduncle length	Caudal-fin length	Anal-fin height	Pelvic-fin length	Pectoral-fin length	Pectoral-fin width	First dorsal-fin height	Second dorsal-fin height	Postorbital length in anal-fin height
<i>heemstra</i> sp. nov.	3.8–4.6	4.3–5.2	8.9–10	22–34	4.5–5.4	5.7–7.3	3.2–3.7	7.8–10	12–16	7.5–10	5.0–6.7	4.3–4.7	3.5–3.7	5.4–6.2	4.5–5.0	4.7–5.2	21–27	4.4–5.3	5.4–6.0	1.4–1.8
<i>margarethae</i>	3.8–4.6	4.2–5.1	8.7–11	17–28	4.3–5.2	5.4–6.4	3.2–3.7	8.0–9.4	11–15	8.1–9.8	5.0–6.4	3.8–4.6	3.2–3.7	5.4–7.1	4.2–5.1	4.2–5.0	19–24	4.3–5.3	5.1–6.6	1.2–1.7
<i>niebuhri</i>	3.9–4.4	4.5–5.3	10	27–31	4.9–5.1	5.9–6.1	3.3–3.5	8.6–9.2	14–15	9.6–10	4.5–4.7	4.3–4.7	3.4	nd	4.7	4.8–4.9	21–25	5.3	6.0	nd
<i>oligospilus</i>	3.8–4.6	4.6–5.4	9.4–10	24–46	4.3–5.3	5.1–6.5	3.0–3.5	7.4–8.5	12–18	7.2–9.1	4.5–6.4	4.0–5.0	3.5–4.1	5.8–6.8	4.6–6.0	4.6–5.7	19–28	4.5–5.6	5.4–6.3	1.2–1.4
<i>randalli</i>	4.1–4.4	4.6–5.4	9.4–10	27–34	4.7–5.3	6.1–6.6	3.3–3.7	8.4–9.7	13–16	8.9–10	4.9–6.1	4.0–4.4	3.3–3.7	5.3–6.8	4.5–5.0	4.6–4.9	23–26	4.5–5.3	5.1–6.3	1.3–1.7
<i>sundaicus</i>	3.5–4.5	4.1–4.8	7.9–8.9	20–32	4.2–5.3	5.0–6.5	3.3–3.8	7.6–10	13–18	8.1–9.9	4.8–6.2	3.7–4.5	3.2–3.9	5.6–6.6	4.4–5.3	4.5–5.3	18–27	3.7–4.6	5.6–6.5	1.3–1.7
<i>taeniopterus</i>	4.0–4.5	4.4–5.0	9.4–10	23–30	4.7–5.9	5.7–7.0	3.5–4.0	7.9–10	16–19	7.9–9.4	4.7–6.0	4.1–4.6	3.1–3.5	5.8–6.9	5.0–5.7	5.0–5.8	21–27	4.3–5.0	6.3–7.2	1.3–1.6
<i>tragula</i>	3.6–4.7	4.2–5.4	8.6–11	20–33	4.2–5.5	5.0–7.0	3.1–3.9	7.4–10	11–19	7.2–10	4.8–7.5	3.7–4.6	2.9–3.5	4.9–6.4	4.2–5.4	4.5–5.8	19–31	3.9–5.1	4.7–6.0	1.4–2.0

- SL (Western Indian Ocean, incl. SE India)  
 ..... *U. heemstra* sp. nov.
- 5b. Caudal-fin length 2.9–3.5 in SL, caudal-peduncle length 3.7–4.6; first dorsal-fin height 3.9–5.1; second dorsal-fin height 4.7–6.0 in SL (Eastern Indian Ocean, W Pacific)  
 ..... *U. tragula*
- 6a. Total gill rakers 18–22; lateral-line scales 31–34; first dorsal-fin height 3.7–4.6 times in SL; caudal-peduncle depth 7.7–9.1 times in SL; barbels frequently yellow in fresh fish (Indo-Pacific) ..... *U. sundaicus*
- 6b. Total gill rakers 21–25; lateral-line scales 28–30; first dorsal-fin height 4.3–5.3 times in SL; caudal-peduncle depth 8.7–11 times in SL; barbels white ..... 7
- 7a. Total gill rakers 21–24; caudal-peduncle width 17–28 times in SL and 4.9–7.9 in head length; anal-fin base 7.2–10 times in SL; pectoral-fin width 19–24 times in SL and 5.2–7.1 in head length; lower caudal-fin lobe with broad red band, covering up to 5 or 6 red bars, the latter only partly visible along ventral fin margin in fresh fish (Western Indian Ocean); mid-lateral body stripe running through eye, red from snout tip to eye and yellow from behind eye to caudal-fin base, stripe absent in preserved fish (Indian Ocean and Arafura Sea)  
 ..... *U. margarethae*
- 7b. Total gill rakers 23–25; caudal-peduncle width 27–34 times in SL and 7.5–10 in head length; anal-fin base 8.9–11 times in SL; pectoral-fin width 23–26 times in SL and 6.5–7.6 in head length; lower caudal-fin lobe with 6–8 dark red bars, bars not covered by a band; mid-lateral body stripe only vaguely visible in fresh fish, stripe absent in preserved fish (Persian Gulf)  
 ..... *U. randalli*

***Upeneus heemstra* sp. nov.**

Heemstra goatfish

(Tables V, VI; Figures 4–8)

*Upeneus tragula* Richardson, 1846: Ben-Tuvia 1986: 613, plate 70; Uiblein & Heemstra 2010: 55–56, plates 2–3 (in part); Uiblein & Heemstra 2011a: 639; Uiblein & Heemstra 2011b: 588.

*Material examined*

*Holotype*: SAIAB 119042, 124 mm, Kenya, off Kipini, 02°38'S, 40°28'E, RV *Dr. F. Nansen*, station

889, shrimp trawl, 12 m, 15 Dec. 1980, collector Phil C. Heemstra.

*Paratypes* ( $n = 19$ ): W Indian Ocean: Kenya: SAIAB 13763, 7: 52–121 mm, same data as holotype; Tanzania: SAIAB 13894, 3: 94–150 mm, Dar es Salaam; SAIAB 13898, 79 mm, Zanzibar, Zanzibar market; SAIAB 80384, 142 mm, Nyama reef (paragenotype: BOLD sequence SAIAB741-08); SAIAB 188307, 2: 173–177 mm, Shimoni (paragenotypes: GenBank KC147808 and KC147809); Mozambique: SAIAB 3955, 98 mm, Ibo Island; SAIAB 88453, 2: 118–128 mm, Pomene (paragenotype: GenBank JF494768); SAIAB 186009, 2: 117–147 mm, Pemba.

*Non-types* ( $n = 16$ ): W Indian Ocean: Mozambique: SAIAB 13899, 3: 90–101 mm, Delagoa Bay; SAIAB 13911, 104 mm, same locality; Seychelles: SAIAB 13896, 113 mm, Mahé; SAIAB 13908, 100 mm, Aldabra; SW India: BPBM 27721, 2: 92–99 mm, Vizhinjam, Kerala; Sri Lanka: SAIAB 187361, 133 mm, Negombo; USNM 396086, 3: 48–131, Jaffna area, Kakaithivu, about 3 miles south of Vaddukkodai, 2–3 m; USNM 396087, 110 mm, Trincomalee, south side of second bay north of harbour, 0–8 m; ZMUC P4946, 138 mm, Sri Lanka or India; Red Sea: Saudi Arabia: BMNH 1982.7.27.8, 113 mm, coast of Jeddah; E Indian Ocean: SW India: BPBM 20656, 128 mm, Chennai (Madras).

*Diagnosis*

Dorsal fins VIII + 9; pectoral-fin rays 12–14; gill rakers 4–8 + 14–18 = 19–24; lateral-line scales 28–30; measurements in %SL: body depth at first dorsal-fin origin 22–26; body depth at anal-fin origin 19–23; caudal-peduncle depth 9.5–11; caudal-peduncle width 2.9–4.6; maximum head depth 19–22; head depth through eye 14–17; head length 27–31; postorbital length 10–13; orbit length 6.3–8.3; upper jaw length 9.8–13; barbel length 15–20; caudal-peduncle length 21–23; caudal-fin length 27–30; anal-fin height 16–19; pelvic-fin length 20–22; pectoral-fin length 19–21; pectoral-fin width 3.7–4.9; first dorsal-fin height 19–23; second dorsal-fin height 17–18; postorbital length 1.4–1.8 times in anal-fin height; all fins with red, brown or black stripes, bars or blotches; caudal fin with 9–12 oblique bars, 4–6 bars on upper caudal-fin lobe and 5–6 bars on lower caudal-fin lobe; first dorsal fin with a large blotch around tip; one pale- or dark-brown mid-lateral body stripe from tip of snout through eye to caudal base; body and head ground colour white or beige, slightly darker above lateral line, with irregular red, brown or black spots and/or blotches; barbels yellow or pale brown in fresh fish;

fin and body pigmentation mostly retained in preserved fish.

#### *Description*

For measurements in %SL, a single ratio, and counts of meristic and colour characters see [Table VI](#); morphometric data as ratios of SL for holotype (with ranges for the 17 paratypes in brackets): body elongate, body depth at first dorsal-fin origin 4.3 [3.8–4.4] exceeding length of pectoral fin (5.0 [4.4–5.1]), body depth at anal-fin origin 4.8 [4.3–5.1], caudal-peduncle depth 9.5 [8.9–10], much larger than orbit length (13 [12–16]), maximum head depth 4.8 [4.5–5.2], head depth across eye 6.6 [5.8–6.4], head length 3.4 [3.1–3.6], larger than maximum depth of body and subequal to caudal-fin length (3.6 [3.1–3.7]), pelvic-fin length 4.6 [4.2–4.9], pectoral-fin width 23 [21–27], first dorsal-fin height 4.6 [4.2–5.0], second dorsal-fin height 5.4 [4.8–5.8], greater than barbel length (6.2 [5.5–6.5]).

*Fresh colour* (based on types and field photographs of specimens from Mozambique; [Figure 4](#)): head and body ground colouration white below and beige or brown above lateral line, with red or brown spots associated with individual scales creating a speckled pattern and with large red or brown blotches differing in size occurring in various body regions; one brown mid-lateral body stripe from tip of snout through eye to caudal-fin base, positioned slightly below lateral line on anterior half of body and closely associated with it posteriorly; up to five vertical rows of brown bands of differing width and colour intensity extending from dorsal edge of body to or beyond mid-lateral body stripe, the most prominent band forming a dark-brown ‘saddle’ behind second dorsal fin; first dorsal fin showing a large red, pale-brown or dark-brown blotch that covers or surrounds the fin tip, indistinctly separated from or closely connected to a second smaller and paler blotch that covers mostly the central part of the fin base; second dorsal fin with one or two weaker stripes closer to fin base and one dark stripe covering fin tip or close to white fin tip; pectoral fins hyaline with mostly indistinct pigmentation, pelvic and anal fins hyaline with red or brown stripes or blotches; caudal fin hyaline or whitish pigmented, overlain with up to 12 oblique red, brown or dark-brown bars which mostly traverse entire fin lobes, being usually wider than unpigmented or white interspaces and in some instances interconnected with each other by a perpendicular dark stripe at mid of lobes; 4–6 bars on upper and 5–6 bars on lower lobe, distal-most bars close to or covering lobe tips; barbels pale-yellow, yellow, or pale brown.

*Preserved colour*: head and body pale or dark brown or grey, dark blotches sometimes visible; body of

holotype rather uniformly brown, becoming darker dorsally, with broad dark-brown mid-lateral body stripe from snout to caudal-fin base; holotype and several paratypes show dark saddle behind second dorsal fin that reaches to lateral line; all fins hyaline with pigment mostly retained, especially on first dorsal and anal fins, and on lower caudal-fin lobe in holotype; first dorsal-fin blotch around tip and caudal fin bars mostly fully retained.

#### *Distribution and size*

Western Indian Ocean proper, Mozambique to Central Red Sea, Seychelles, W India and Sri Lanka, and SE India ([Figure 7](#)); 0–12 m depth; *Upeneus heemstra* sp. nov. attains 15 cm SL.

#### *Etymology*

The name of this species ‘*heemstra*’ is in honour of the esteemed ichthyologist Phil C. Heemstra, who collected and photographed the holotype on a cruise of the RV *Dr. F. Nansen* and his wife Elaine Heemstra, who provided the head drawings and assistance throughout this study.

#### *Upeneus niebuhri* Guézé, 1976

Niebuhr’s goatfish

([Tables V, VI](#); [Figures 4–8](#))

*Upeneus niebuhri* Guézé, 1976: 596 (type locality: Gulf of Suez)

*Upeneus tragula* Richardson, 1846; Bauchot et al. 1985: 8; Ben-Tuvia & Golani 1989: 110.

#### *Diagnosis*

Dorsal fins VIII + 9; pectoral-fin rays 13–14; gill rakers 5–6 + 16–17 = 22–23; lateral-line scales 29–30; measurements in %SL: body depth at first dorsal-fin origin 23–26; body depth at anal-fin origin 19–22; caudal-peduncle depth 9.7–9.9; caudal-peduncle width 3.2–3.7; maximum head depth 19–20; head depth through eye 16–17; head length 29–31; postorbital length 11–12; orbit length 6.9–7.3; upper jaw length 10; barbel length 21–22; caudal-peduncle length 21–23; caudal-fin length 29; pelvic-fin length 21; pectoral-fin length 21; pectoral-fin width 4.1–4.7; first dorsal-fin height 19; second dorsal-fin height 17; all fins with brown or black stripes, bars or blotches; caudal fin with 8 oblique bars, 3–4 bars on upper caudal-fin lobe and 4–5 bars on lower caudal-fin lobe; first and second dorsal fin tips with dark-brown blotches; one brown mid-lateral body stripe from behind opercle to caudal base; body and head ground colour beige, darker above lateral line, with irregular red, brown or black spots and





Table VI. (Continued)

HT	<i>Upeneus heemstrae</i> sp. nov.												<i>U. niebuhri</i>			<i>U. oligospilus</i>			<i>U. tragula</i>										
	Paratypes			East Africa			Red Sea			Seychelles (Aldabra)			South India, Sri Lanka			Indian Ocean			Gulf of Suez			Persian Gulf (incl. types)			Indo-Pacific				
	Min	Mean	Max	Min	Mean	Max	n	Min	Mean	Max	n	Min	Mean	Max	n	Min	Mean	Max	n	Min	Mean	Max	n	Min	Mean	Max	n	Min	Mean
18.4	17	17.9	18	9	17	17.9	18	13	17.3	17.3	18	7	17	17.7	18	22	18	22	16.6	16	17.0	18	19	17	19.3	21	140		
1.6	1.4	1.5	1.8	11	1.4	1.5	1.8	16	1.4	1.5	1.5	2	1.4	1.5	1.8	26	1.6	1.8	1.2	1.3	1.4	19	1.4	1.6	2.0	148			
13	3	3.8	5	11	2	3.6	5	16	2	4	4.5	5	2	3	4.0	5	7	2	3.7	5	26	4	1	2	3.5	5	150		
2	1	1.9	3	11	1	2.1	3	16	3	1	1.5	2	2	2	2.1	3	7	1	2.1	3	26	2	5	2	2.5	4	150		
11	9	10.3	12	11	9	10.8	13	16	11	10	11.0	12	2	10	10.6	11	7	9	10.7	13	26	11	13	9	11.1	12	150		
6	4	5.7	7	11	4	5.5	7	16	6	4	5.0	6	2	5	5.7	7	7	4	5.5	7	26	5	4	3	5.3	7	150		
6	5	5.7	6	11	4	5.6	6	16	5	6	6.0	6	2	5	6.1	8	7	4	5.8	8	26	6	4	6.0	7	150			
17	14	16.0	18	11	14	16.3	18	16	17	16	16.0	16	2	16	16.3	17	7	14	16.3	18	26	16	17	15	16.4	18	150		
23	19	21.7	24	11	19	21.9	24	16	22	22	22.0	22	2	21	22.4	24	7	19	22.0	24	26	22	23	20	22.4	24	150		
29	28	28.8	30	10	28	28.8	30	15	-	28	28.5	29	2	29	29.6	30	7	28	29.0	30	24	30	29	29	29.6	31	120		
6	4	5.0	6	10	4	5.1	6	12	5	-	-	0	4	4.7	5	7	4	5.0	6	20	4	3	3	3.9	5	127			
6	5	5.3	6	10	5	5.3	6	14	5	-	-	0	5	5.3	6	7	5	5.3	6	22	4	5	3	3.8	5	138			
12	9	10.3	12	10	9	10.4	12	12	10	-	-	0	9	10.0	11	7	9	10.3	12	20	8	8	6	7.7	10	127			

## Morphometric characters

DZH

Ratio

ANH/POL

Mensuric characters

P

GrUud

GrUd

GrLd

GrLud

GrU

GrL

Gr

LLSCAL

Colour characters

CBUL

CBLL

CBALL

blotches; barbels pale brown in fresh fish; fin and body pigmentation retained in preserved fish.

## Distribution and size

Gulf of Suez (Figure 7); depth: shallow; *Upeneus niebuhri* attains at least 11 cm SL.

*Upeneus oligospilus* Lachner, 1954

Short-fin goatfish

(Tables V, VI; Figures 4, 6–8)

*Upeneus oligospilus* Lachner, 1954: 525, plate 14 (type locality: Persian Gulf); Uiblein & Heemstra 2010: 48, plate 1; Uiblein & Heemstra 2011a: 639; Uiblein & Heemstra 2011b: 588.

## Diagnosis

Dorsal fins VIII + 9; pectoral-fin rays 13–14; gill rakers 4–7 + 15–18 = 20–24; lateral-line scales 29–31; measurements in %SL: body depth at first dorsal-fin origin 22–26; body depth at anal-fin origin 19–22; caudal-peduncle depth 9.6–11; caudal-peduncle width 2.2–4.1; maximum head depth 19–23; head depth through eye 15–19; head length 29–33; post-orbital length 12–13; orbit length 5.5–8.1; upper-jaw length 11–14; barbel length 16–22; caudal-peduncle length 20–25; caudal-fin length 24–28; anal-fin height 15–17; pelvic-fin length 17–22; pectoral-fin length 18–22; pectoral-fin width 3.6–5.4; first dorsal-fin height 18–22; second dorsal-fin height 16–18; postorbital length 1.2–1.4 times in anal-fin height; all fins with dark brown or black stripes, bars or blotches; caudal fin with 6–10 oblique bars, 3–5 bars on upper caudal-fin lobe and 3–5 bars on lower caudal-fin lobe; first dorsal fin with a large blotch around tip; one dark-brown or black mid-lateral body stripe from tip of snout through eye to caudal base; body and head ground colour white or beige, slightly darker above lateral line, with irregular dark brown or black spots, dots and blotches; barbels yellow or pale brown; fin and body pigmentation mostly retained in preserved fish.

## Distribution and size

Persian Gulf (Figure 7); depth: 0–13 m; *Upeneus oligospilus* attains 13 cm SL.

*Upeneus tragula* Richardson, 1846

Freckled goatfish

(Tables V, VI; Figures 4, 6–8)

*Upeneus tragula* Richardson, 1846: 220 (type locality: Guangzhou, China); Okamura & Amaoka 1997:

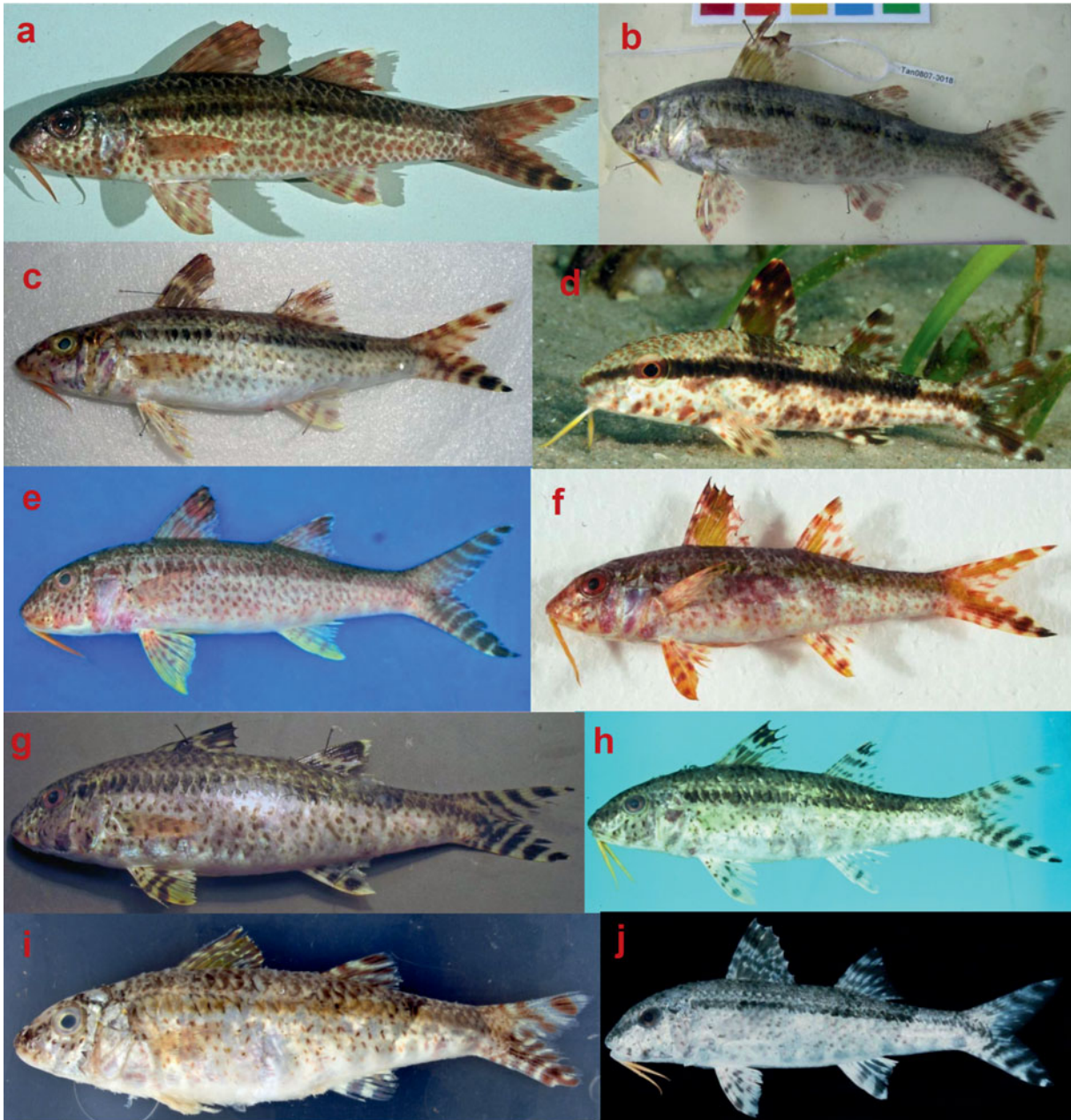


Figure 4. Photographs of four dark-freckled *Upeneus* species: *Upeneus heemstra* sp. nov.: (a) holotype, SAIAB 119042, 124 mm SL, off Kipini, Kenya (Phil C. Heemstra); (b) paratype, SAIAB 80384, 142 mm SL, Nyama reef, Tanzania (Monica Mwale); (c) SAIAB 187361, 133 mm SL, Negombo, Sri Lanka (Franz Uiblein); and (d) subadult specimen, Pomene, Mozambique (Mike & Valda Fraser). *Upeneus tragula*: (e) 260 mm SL, Andaman Islands (Rajan Thomas); (f) CSIRO H 3637-09, 92 mm SL, W of Thursday Island, Arafura Sea, Australia (Gordon Yearsley); (g) HIFIRE F58135, 130 mm SL, Vietnam, Ha Long (Dimitri A. Pavlov); and (h) SAIAB 35138, 135 mm SL, Taiwan (Phil C. Heemstra). *U. niebuhri*: (i) SAIAB 88873, 74 mm SL, Gulf of Suez, Egypt (Sergey Bogorodsky). *U. oligospilus*: (j) BPBM 29499, 118 mm SL, Persian Gulf, Bahrain (Jack E. Randall).

372; Randall et al. 1997: 212; Uiblein et al. 1998: 124–130, figure 1; Randall & Kulbicki 2006: 305–306, figure 8; Imamura et al. 2009: 176; Uiblein & Heemstra 2010: 55–56, plates 2–3 (in part); Allen & Erdmann 2012: 510.

*Upeneus luzonius* non Jordan & Seale, 1907; Gloerfelt-Tarp & Kailola 1984: 214–215; Sainsbury et al. 1985: 238–239.

#### Diagnosis

Dorsal fins VIII + 9; pectoral-fin rays 12–14; gill rakers 4–7 + 15–19 = 20–25; lateral-line scales 28–31; measurements in %SL: body depth at first dorsal-fin origin 21–28; body depth at anal-fin origin 18–24; caudal-peduncle depth 9.5–12; caudal-peduncle width 3.1–4.9; maximum head depth 18–24; head depth through eye 14–20; head length 26–32;

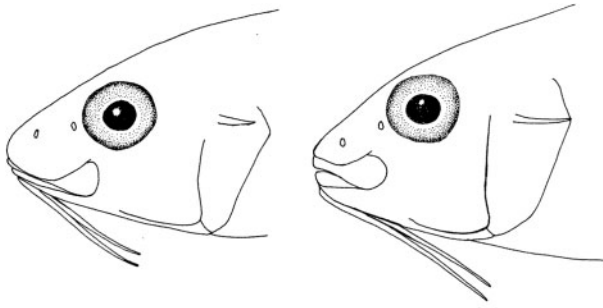


Figure 5. Schematic drawings of heads of the holotype of *U. heemstra* sp. nov. (left, SAIAB 119042) and of *U. niebuhri* (right, SAIAB 88873). Note the differences in barbel and jaw length.

postorbital length 9.9–13; orbit length 5.3–8.9; upper jaw length 9.8–14; barbel length 13–21; caudal-peduncle length 22–27; caudal-fin length 29–34; anal-fin height 16–20; pelvic-fin length 19–24; pectoral-fin length 17–22; pectoral-fin width 3.5–5.3; first dorsal-fin height 20–25; second dorsal-fin height 17–21; postorbital length 1.4–2.0 times in anal-fin height; all fins with red, brown or black stripes, bars or blotches; caudal fin with 7–19 oblique bars, 3–9 bars on upper caudal-fin lobe

and 4–10 bars on lower caudal-fin lobe; first dorsal fin with a large blotch around tip; one red, brown or black mid-lateral body stripe from tip of snout through eye to caudal base; body and head ground colour white or beige, slightly darker above lateral line, with irregular red, brown or black spots and/or blotches; barbels yellow, pale brown or orange in fresh fish; fin and body pigmentation mostly retained in preserved fish.

#### Distribution and size

Indo-Pacific from Andaman Islands to E Australia and to Japan and New Caledonia; depth: 0–42 m; *Upeneus tragula* attains 19 cm SL.

#### Comparisons among species of the *tragula* group

The four dark-freckled species *Upeneus heemstra* sp. nov., *U. niebuhri*, *U. oligospilus* and *U. tragula* differ from each other as follows (morphometric values in %SL, if not otherwise indicated; Tables V, VI, Figures 4–6, 8): *Upeneus heemstra* sp. nov. differs from *U. niebuhri* in deeper caudal peduncle (9.5–11 vs. 9.7–9.9), shorter barbels (15–20 vs. 21–22) and

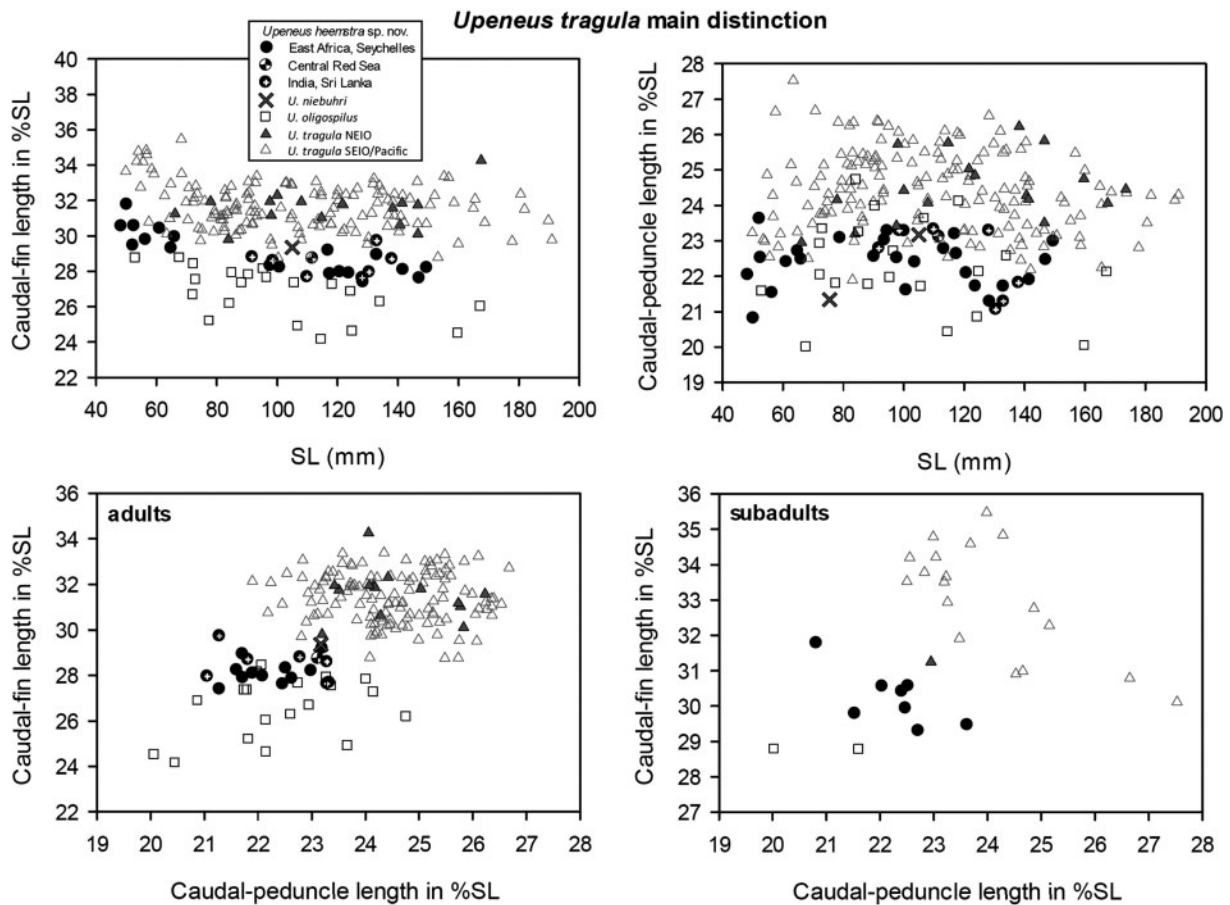


Figure 6. Distinction between *Upeneus heemstra* sp. nov. and *U. tragula* (both further subdivided into populations) based on two morphometric characters, caudal-fin length and caudal-peduncle length, plotted against SL (upper graphs) and against each other for adults and subadults (lower graphs). A few measurements for *U. niebuhri* and *U. oligospilus* are also included.

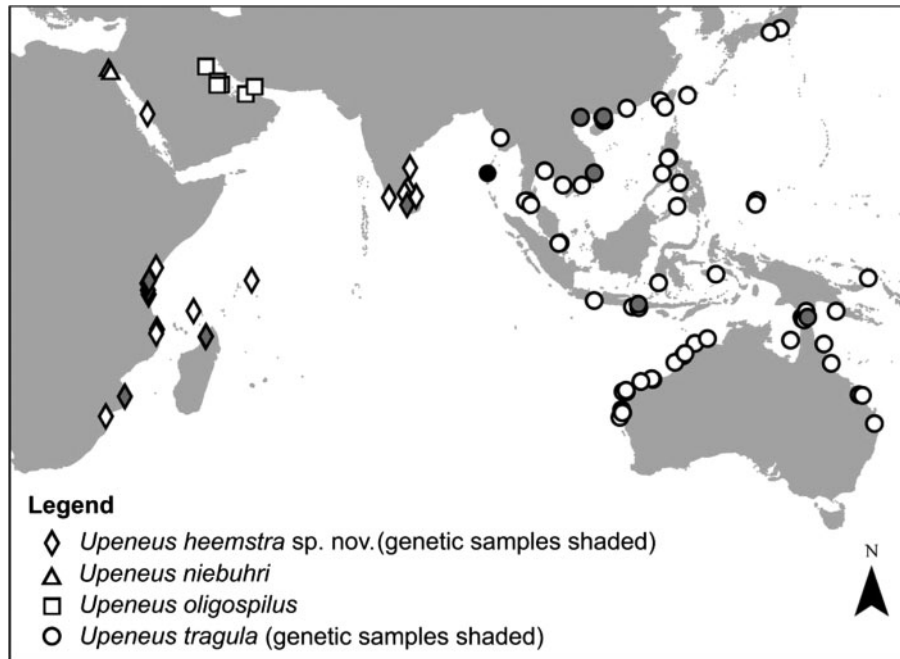


Figure 7. The distribution of the 'dark-freckled' *Upeneus* species complex (*Upeneus heemstra* sp. nov., *U. niebuhri*, *U. oligospilus* and *U. tragula*) through the Indo-West Pacific, as determined from the collection localities of the specimens included in the present study. Grey-filled symbols indicate those localities from which samples were included in the genetic study. The single solid symbol represents the unvouchered photograph of *U. tragula* from the Andaman Islands shown in Figure 4e.

more bars on caudal fin in total (9–12 vs. 8); from *U. oligospilus* it differs in shorter head (27–31 vs. 29–33), shorter snout (10–13 vs. 12–14), shorter post-orbital (10–13 vs. 12–13), shorter distance from snout to first dorsal-fin origin (33–38 vs. 36–41), longer caudal-fin length (27–30 vs. 24–28), larger anal-fin height (16–19 vs. 15–17), larger postorbital length in anal-fin height ratio (1.4–1.8 vs. 1.2–1.4 times) and more caudal-fin bars in total (9–12 vs. 6–10); and from *U. tragula* it differs in shorter caudal peduncle (21–23 vs. 22–27), shorter caudal fin (27–30 vs. 29–34) and shallower second dorsal fin (17–18 vs. 17–21). *Upeneus niebuhri* differs from *U. oligospilus* in shorter jaws (upper-jaw length 10 vs. 11–14; lower-jaw length 9.7 vs. 10–13), longer barbels (21–22 vs. 16–22) and longer caudal fin (29 vs. 24–28); and from *U. tragula* it differs in longer barbels (21–22 vs. 13–21), shorter caudal peduncle (21–23 vs. 22–27), shorter caudal-fin length (29 vs. 29–34) and shallower first dorsal fin (19 vs. 20–25). *Upeneus oligospilus* differs from *U. tragula* in shorter caudal fin (24–28 vs. 29–34), shallower anal fin (15–17 vs. 16–20), shallower dorsal fins (first dorsal-fin height 18–22 vs. 20–25; second dorsal-fin height 16–18 vs. 17–21), smaller postorbital length in anal-fin height ratio (1.2–1.4 vs. 1.4–2.0 times) and fewer bars in total on caudal fin (6–10 vs. 7–19).

The four dark-freckled species differ from other congeners as follows (Tables V–VII, Figure 4; Uiblein & Heemstra 2010, 2011a,b; Yamashita et al.

2011; Uiblein & McGrouther 2012): from all others by presence of dark-freckled colour patterns consisting of dark blotches or spots on the body, anal and paired fins, and the retention of those colour patterns in preserved fish. They differ from all other species of the *tragula* group by a dark blotch close to the tip of the first dorsal fin and by the presence of a single, dark mid-lateral body stripe that is retained in preserved fish. In addition, the four dark-freckled species differ from *U. margarethae* and *U. randalli* in yellow to pale brown vs. white barbels in fresh fish and caudal-fin bars fully retained in preserved fish, from *U. sundaicus* in shallower first dorsal fin (18–25 vs. 22–27 %SL) and presence of dark bars on lower caudal-fin lobe both in fresh and preserved fish, and from *U. taeniopterus* in fewer lateral line scales (18–31 vs. 35–39), higher second dorsal fin (16–21 vs. 14–16 %SL), one dark mid-lateral body stripe vs. two (or three) yellow to pale brown lateral body stripes in fresh fish, and the stripes not retained in preserved fish of the latter species. The main morphometric differences between the four dark-freckled species and the two Pacific species of the *tragula* group are the shallower first dorsal fin compared to *U. luzonius* (18–25 vs. 24–29 %SL) and the longer first dorsal-fin base compared to *U. mouthami* (14–17 vs. 11–13 %SL).

Additional differences between the four dark-freckled species and the other species of the *tragula* group are (Tables V–VII): *Upeneus heemstra* differs

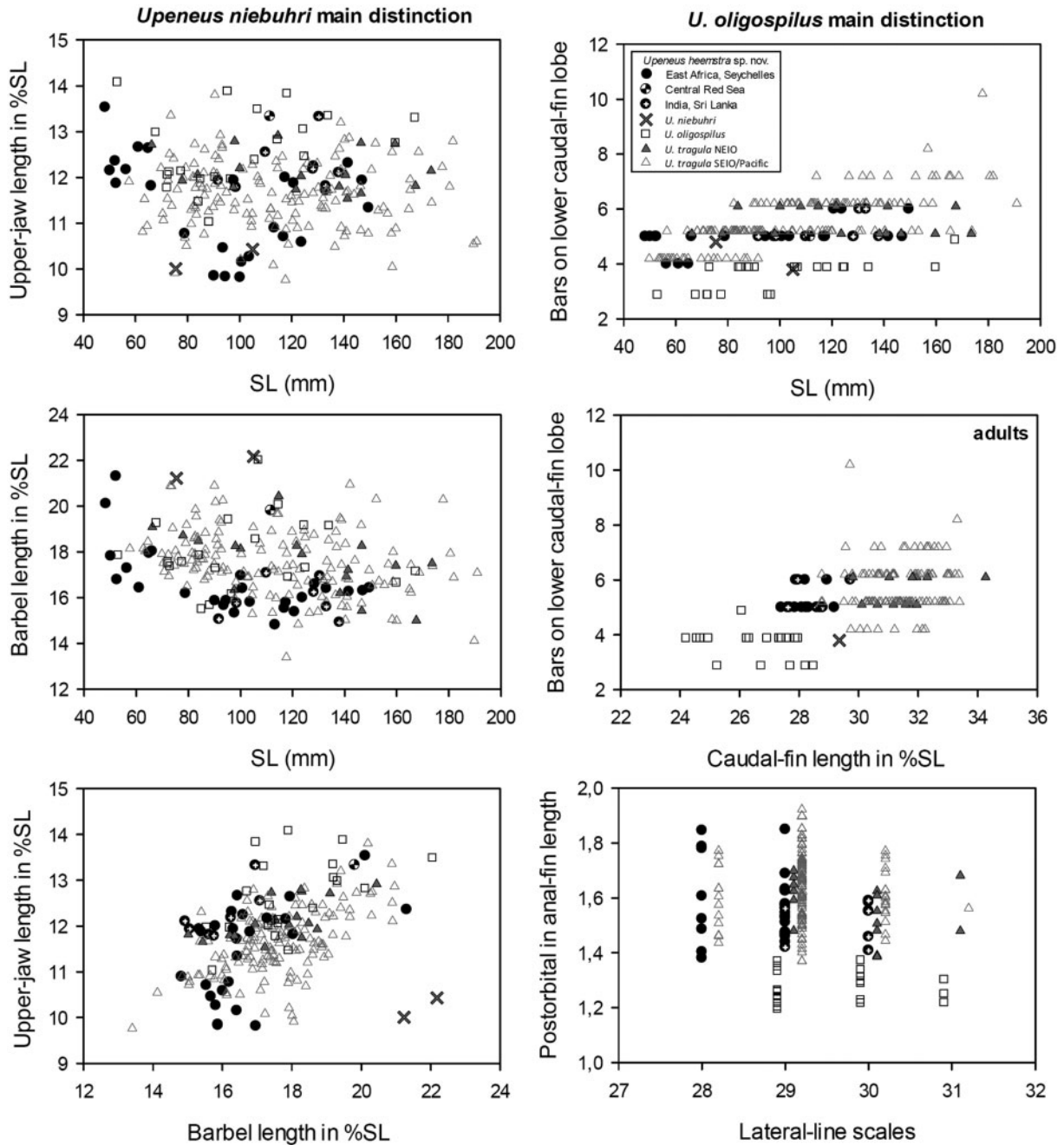


Figure 8. Most important morphometric and colour characters for the distinction of *Upeneus niebuhri* and *U. oligospilus*, respectively, from the three other dark-freckled species of the *tragula* group, with *U. heemstra* sp. nov. and *U. tragula* subdivided into populations.

from *U. margarethae* in shallower head through eye, shorter caudal peduncle and shorter pectoral length; from *U. randalli* in fewer total gill rakers, shorter caudal peduncle, and fewer bars on lower caudal-fin lobe; from *U. sundaicus* in fewer lateral-line scales, shallower and shorter caudal peduncle, shallower head through eye and suborbital distance, and shallower first dorsal fin; and from *U. taeniopterus* in longer head, larger eyes, and longer paired fins; from the Pacific *U. luzonius* in fewer lateral-line scales, shorter barbels, shorter caudal peduncle, shallower first dorsal fin, and more caudal-fin bars;

and from the Pacific *U. mouthami* it differs in fewer total gill rakers, greater maximum body depth, deeper head through eye, longer first dorsal-fin base, and shorter pectoral fins.

*Upeneus niebuhri* differs from *U. margarethae* in narrower and shorter caudal peduncle and longer barbels; from *U. randalli* in fewer gill rakers, longer barbels, shorter caudal peduncle and shorter first dorsal-fin base; from *U. sundaicus* in more total gill rakers, fewer lateral-line scales, shallower caudal peduncle, longer barbels and shallower first dorsal fin; it differs from *U. taeniopterus* in longer head,

Table VII. Morphometric, meristic and caudal-fin colour (preserved specimens only) characters in adults of *Upeneus margarethae*, *U. randalli*, *U. sundaicus*, and *U. taeniopterus* from the Indian Ocean, and *U. luzonius* and *U. mouthami* from the W Pacific; see Table II for explanation of abbreviations.

	<i>Upeneus margarethae</i>				<i>U. randalli</i>				<i>U. sundaicus</i>				<i>U. taeniopterus</i>				<i>U. luzonius</i>				<i>U. mouthami</i>			
	Indian Ocean				Persian Gulf				Indian Ocean				Indian Ocean				W Pacific (types)				SW Pacific			
	Min	Mean	Max	n	Min	Mean	Max	n	Min	Mean	Max	n	Min	Mean	Max	n	Min	Mean	Max	n	Min	Mean	Max	n
<i>Morphometric characters</i>																								
SL (mm)	65	91.6	129	50	66	84.3	106	8	81	117.5	158	28	88	155.6	265	17	65	74.0	95	5	73	84.1	94	4
<i>In % SL</i>																								
BODYDD	22	24.7	26	50	23	23.5	24	8	22	26.1	28	28	22	23.9	25	13	22	23.2	25	5	21	22.7	24	4
BODYDA	20	21.4	24	50	19	20.2	22	8	21	22.7	24	26	20	21.3	23	14	19	20.4	22	5	19	19.9	21	4
HALFDD	18	20.1	22	49	19	19.6	20	8	18	21.0	23	25	18	20.0	21	7	17	18.6	20	4	19	19.7	20	2
HALFDA	15	16.2	18	47	15	15.7	17	8	15	16.1	17	26	15	16.0	17	7	13	15.0	16	5	15	15.3	15	2
CPDD	9.3	10.5	12	50	9.9	10.3	11	8	11	11.8	13	28	9.7	10.1	11	9	10	10.9	12	5	9.1	9.6	10	4
CPDW	3.6	4.4	5.7	49	2.9	3.4	3.8	8	3.1	4.2	4.9	26	3.4	3.8	4.3	7	3.3	4.0	4.5	5	3.2	3.6	3.9	4
HEAD1	19	20.9	23	50	19	20.3	21	8	19	21.8	24	28	17	19.6	21	8	20	20.5	21	5	20	20.1	21	4
HEAD2	16	16.8	18	50	15	15.6	16	8	15	17.5	20	26	14	16.1	17	8	16	16.5	17	5	17	17.6	18	4
SUPORB	8.3	10.1	12	50	8.0	9.1	10	8	9.6	11.6	14	26	9.6	10.4	12	8	10	10.7	11	5	9.0	10.2	11	4
INTORB	7.3	8.1	9.1	50	7.2	8.0	8.8	8	7.5	8.3	9.2	28	7.5	8.3	9.2	8	7.3	7.9	8.3	5	7.6	7.8	8.1	4
HEADL	27	28.7	31	50	27	28.8	30	8	26	27.9	30	28	25	27.6	29	12	27	28.5	30	5	29	29.4	30	4
SNOUTL	10	11.2	12	50	11	11.3	12	8	11	12.3	14	28	10	11.2	12	8	11	11.8	12	5	11	11.4	12	4
PORBL	11	11.14	12	50	10	11.1	12	8	9.9	11.4	13	28	9.9	11.4	13	8	10	11.2	12	5	11	11.4	12	4
ORBITL	6.6	7.8	9.1	50	6.2	6.9	7.4	8	5.7	6.6	7.4	28	5.2	5.7	6.3	15	5.9	6.6	7.1	5	7.8	8.2	8.8	4
ORBITD	5.5	6.7	8	49	5.1	5.9	6.4	8	4.8	5.7	6.4	26	4.2	4.7	5.6	15	5.1	5.7	5.9	5	6.6	7.0	7.7	4
UJAWL	10	11.1	12	50	10	10.9	11	8	10	11.3	12	26	11	11.6	13	15	11	11.3	12	5	9.3	10.5	11	4
LJAWL	9.1	10.3	12	50	9.1	10.0	10	8	9.3	10.7	12	26	9.9	10.9	12	8	9.4	10.5	11	5	8.8	10.3	11	4
SNOUTW	7.9	9.3	11	46	7.8	8.4	9.0	8	8.0	9.9	12	23	9.3	10.3	11	6	7.9	8.9	9.8	5	8.9	10.5	12	3
BARBL	16	17.8	20	50	16	18.2	20	8	16	18.3	21	28	17	18.7	21	15	19	19.4	20	5	20	20.8	22	4
BARBW	0.7	0.8	1	50	0.6	0.7	0.7	8	0.7	1.0	1.2	28	0.7	0.8	1.0	8	0.8	0.9	1.1	5	0.9	1.1	1.4	4
SD1	34	36.8	40	50	34	36.6	38	8	32	36.4	39	28	35	37.1	38	8	35	36.7	38	5	37	37.7	39	4
SD2	60	63.3	67	50	61	64.2	66	8	61	63.1	66	28	61	64.9	66	8	61	62.1	64	5	62	63.7	65	4
D1D2	12	14.0	16	50	13	14.4	15	8	12	14.4	17	26	15	17.0	19	7	12	13.8	16	5	12	13.8	16	4
CPDL	22	23.8	26	50	23	23.6	25	8	22	24.2	27	26	22	22.9	24	8	24	25.3	27	5	21	22.2	24	4
SANL	61	64.0	69	50	63	64.6	67	8	62	63.8	67	28	64	65.8	70	8	61	62.8	64	5	64	64.7	65	4
SPEL	28	31.5	35	50	31	32.0	34	8	30	31.9	34	28	29	31.4	33	8	30	32.1	34	5	28	29.8	33	4
SPEC	28	30.3	33	50	29	30.5	32	8	27	29.5	31	28	27	29.1	30	8	29	30.2	32	5	29	31.7	34	4
D2ANL	20	21.9	24	50	19	20.7	22	8	22	23.7	25	28	21	21.7	23	8	19	20.2	21	5	19	20.3	21	4
D1PELV	22	24.7	27	50	23	23.4	24	8	22	26.1	29	26	20	23.5	26	8	22	23.4	26	5	21	23.1	24	4
D1PEC	15	16.9	18	50	15	16.0	17	8	16	18.4	20	28	14	15.9	18	8	16	16.9	17	5	16	16.7	17	4
D1B	13	15.4	17	50	15	15.2	16	8	13	15.1	17	28	12	13.5	15	8	15	15.9	17	5	11	12.2	13	4
D2B	12	13.7	16	50	12	13.6	15	8	13	14.3	15	28	12	12.2	14	8	13	14.1	15	5	13	13.5	14	4
CAUH	27	28.7	31	49	27	28.3	30	8	26	27.9	31	19	28	30.1	32	6	27	28.5	29	4	27	27.8	29	4
ANALB	9.8	11.7	14	50	9.4	10.2	11	8	9.9	11.3	14	28	9.3	10.7	13	8	11	11.8	13	5	11	12.2	13	4
ANALH	14	16.5	18	50	15	16.7	19	8	15	16.2	18	25	15	15.8	17	8	15	16.6	17	5	17	17.9	19	4
PELVL	20	21.6	24	50	20	21.2	22	8	19	20.6	23	25	18	18.5	20	8	21	21.8	22	5	22	22.3	23	4
PECTL	20	22.0	24	50	20	21.1	22	8	19	20.6	22	26	17	18.4	20	14	19	20.3	22	5	22	22.7	23	4
PECTW	4.1	4.8	5.3	50	3.8	4.1	4.4	8	3.7	4.6	5.7	26	3.8	4.1	4.7	8	3.9	4.2	4.6	5	4.0	4.2	4.3	4
D1H	19	21.2	23	48	19	20.7	22	8	22	24.9	27	23	20	21.3	23	13	24	25.7	29	5	20	20.2	21	3
D2H	15	17.3	20	48	16	17.6	20	8	15	16.6	18	26	14	15.2	16	13	16	16.9	19	5	17	18.1	19	3

Table VII. (Continued)

	<i>Upeneus margarethae</i>				<i>U. randalli</i>				<i>U. sundaicus</i>				<i>U. taeniopterus</i>				<i>U. luzonius</i>				<i>U. mouthami</i>							
	Indian Ocean				Persian Gulf				Indian Ocean				Indian Ocean				W Pacific (types)				SW Pacific							
	Min	Mean	Max	<i>n</i>	Min	Mean	Max	<i>n</i>	Min	Mean	Max	<i>n</i>	Min	Mean	Max	<i>n</i>	Min	Mean	Max	<i>n</i>	Min	Mean	Max	<i>n</i>				
<i>Ratio</i>																												
ANH/POL	1.2	1.4	1.7	50	1.3	1.5	1.7	8	1.3	1.4	1.7	25	1.3	1.4	1.6	8	1.4	1.4	1.5	3	1.5	1.6	1.7	4				
<i>Meristic characters</i>																												
P	13	13.9	15	50	14	14.0	14	8	13	14.0	15	28	13	13.8	14	15	14	14.0	14	5	13	13.0	13	4				
GrUud	2	3.2	5	50	2	2.9	3	8	1	2.7	4	26	2	3.1	4	15	1	1.6	2	5	1	2.3	3	4				
GrUd	2	2.6	4	50	3	3.3	4	8	1	2.3	4	26	2	2.7	3	15	3	3.4	4	5	3	4.0	5	4				
GrLd	11	12.2	14	50	12	13.5	15	8	10	10.8	13	26	10	12.0	13	15	11	11.8	13	5	13	13.0	13	4				
GrLud	3	4.6	6	50	4	4.6	6	8	2	4.3	6	26	3	4.3	6	15	2	3.0	4	5	4	4.5	5	4				
GrU	5	5.7	7	50	6	6.1	7	8	4	5.0	6	26	5	5.8	6	15	5	5.0	5	5	6	6.3	7	4				
GrL	15	16.7	18	50	17	18.1	19	8	13	15.0	17	28	16	16.3	17	15	14	14.8	16	5	17	17.5	18	4				
Gr	21	22.5	24	50	23	24.3	25	8	18	20.1	22	26	21	22.1	23	15	19	19.8	21	5	23	23.8	25	4				
LLSCAL	28	29.2	30	44	28	29.1	30	8	31	32.3	34	23	35	37.3	39	12	31	31.5	32	2	29	29.0	29	1				
<i>Colour characters</i>																												
CBUL	0	1.7	5	50	0	0.6	5	8	0	0.0	0	27	4	5.4	7	15	2	3.6	5	5	0	1.0	2	3				
CBLL	0	1.9	6	50	0	0.6	5	8	0	0.0	0	27	3	4.3	6	16	4	4.4	5	5	3	3.0	3	3				
CBALL	0	3.5	9	50	0	1.3	10	8	0	0.0	0	27	7	9.8	13	15	6	8.0	10	5	3	4.0	5	3				

Table VIII. Morphometric, meristic and caudal-fin colour (preserved specimens only) characters of subadults of *Upeneus heemstra* sp. nov., *U. oligospilus*, and *U. tragula* (no subadult specimen for *U. niebuhri* was available for study).

	<i>Upeneus heemstra</i> sp. nov.												<i>U. oligospilus</i>				<i>U. tragula</i>											
	Paratypes (E Africa)				Sri Lanka				Indian Ocean				Persian Gulf				Indo-Pacific											
	Min	Mean	Max	<i>n</i>	Min	Mean	Max	<i>n</i>	Min	Mean	Max	<i>n</i>	Min	Mean	Max	<i>n</i>	Min	Mean	Max	<i>n</i>	Min	Mean	Max	<i>n</i>				
<i>Morphometric characters</i>																												
SL (mm)	50	58.5	66	6	48	50.3	52	2	48	56.5	66	8	53	60.1	67	2	50	60.7	70	20								
<i>In %SL</i>																												
BODYDD	23	24.4	26	6	24	25.1	26	2	23	24.6	26	8	23	23.5	24	2	21	23.9	27	9								
BODYDA	20	21.5	23	6	21	21.3	21	2	20	21.4	23	8	20	20.9	22	2	19	21.0	23	7								
HALFDD	19	20.5	22	6	20	20.6	21	2	19	20.5	22	8	18	19.0	20	2	19	20.1	21	7								
HALFDA	16	17.0	18	6	16	17.0	18	2	16	17.0	18	8	15	15.1	15	2	15	15.9	16	6								
CPDD	10	10.5	11	6	9.8	10.1	10	2	9.8	10.4	11	8	10	10.7	11	2	10	10.6	11	7								
CPDW	3.5	3.7	4.0	6	3.3	3.6	3.9	2	3.3	3.7	4.0	8	3.6	4.3	5.1	2	3.2	3.7	4.0	7								
HEAD1	19	20.5	22	6	22	22.6	23	2	19	21.0	23	8	19	20.1	21	2	18	20.7	23	7								
HEAD2	16	16.2	17	6	18	18.6	19	2	16	16.8	19	8	17	17.0	17	2	15	16.3	17	7								
SUPORB	7.9	9.3	10	6	10	10.3	10	2	7.9	9.6	10	8	9.9	9.9	9.9	2	7.8	9.0	9.8	7								
INTORB	7.6	8.1	8.6	6	8.1	8.4	8.7	2	7.6	8.2	8.7	8	8.7	8.9	9.1	2	7.3	8.1	8.7	7								
HEADL	30	30.7	33	6	33	33.6	34	2	30	31.5	34	8	33	33.0	33	2	28	29.9	31	8								
SNOUTL	11	11.3	11	6	12	12.4	13	2	11	11.6	13	8	12	13.0	13	2	11	11.4	12	7								
PORBL	11	12.1	13	6	13	13.2	14	2	11	12.4	14	8	13	13.4	13	2	11	11.9	13	11								

Table VIII. (Continued)

	<i>Upeneus heemstra</i> sp. nov.												<i>U. oligospilus</i>				<i>U. tragula</i>			
	Paratypes (E Africa)				Sri Lanka				Indian Ocean				Persian Gulf				Indo-Pacific			
	Min	Mean	Max	<i>n</i>	Min	Mean	Max	<i>n</i>	Min	Mean	Max	<i>n</i>	Min	Mean	Max	<i>n</i>	Min	Mean	Max	<i>n</i>
ORBITL	7.8	8.2	8.6	6	7.7	8.0	8.4	2	7.7	8.1	8.6	8	7.5	7.9	8.3	2	6.9	7.4	8.3	7
ORBITD	6.9	7.1	7.5	6	6.8	7.2	7.6	2	6.8	7.1	7.6	8	6.8	7.1	7.4	2	6.2	6.6	7.2	7
UJAWL	12	12.2	13	6	12	12.9	14	2	12	12.4	14	8	13	13.5	14	2	11	11.6	13	7
LJAWL	11	11.1	12	6	11	11.7	12	2	11	11.2	12	8	12	12.1	12	2	9.8	10.7	12	7
SNOUTW	8.3	8.9	9.5	6	10	10.4	11	2	8.3	9.3	11	8	12	11.6	12	2	7.1	8.6	9.3	6
BARBL	16	17.4	18	6	20	20.7	21	2	16	18.2	21	8	18	18.6	19	2	18	18.2	19	7
BARBW	0.8	0.9	1.0	6	0.6	0.7	0.8	2	0.6	0.9	1.0	8	0.8	0.8	0.9	2	0.8	0.9	1.0	7
SD1	37	38.0	39	6	39	39.5	40	2	37	38.4	40	8	40	40.6	41	2	35	37.6	39	7
SD2	63	65.4	67	6	69	69.6	70	2	63	66.4	70	8	65	66.6	68	2	60	63.5	65	7
D1D2	12	13.7	15	6	13	13.8	14	2	12	13.7	15	8	12	14.0	16	2	12	14.4	15	7
CPDL	21	22.1	23	6	22	22.8	24	2	21	22.3	24	8	20	20.8	22	2	23	24.0	28	19
SANL	64	66.7	69	6	66	66.1	66	2	64	66.5	69	8	65	65.9	67	2	62	64.7	66	11
SPEL	32	33.3	35	6	36	36.8	37	2	32	34.2	37	8	34	34.1	34	2	31	33.6	36	7
SPEC	31	32.4	34	6	35	35.6	37	2	31	33.2	37	8	33	34.2	36	2	31	31.7	33	7
D2ANL	20	22.3	23	6	20	21.3	22	2	20	22.1	23	8	20	21.0	22	2	19	21.6	24	7
D1PELV	23	24.4	26	6	23	24.1	25	2	23	24.3	26	8	24	24.0	24	2	22	24.8	27	7
D1PEC	16	16.9	18	6	17	17.3	18	2	16	17.0	18	8	17	17.9	19	2	15	16.4	17	7
D1B	15	16.2	17	6	14	14.4	15	2	14	15.7	17	8	15	14.8	15	2	12	14.0	15	7
D2B	14	15.0	16	6	13	14.3	15	2	13	14.8	16	8	13	13.6	14	2	12	13.5	15	7
CAUH	29	30.3	32	6	29	30.0	31	2	29	30.2	32	8	29	28.8	29	2	30	33.0	35	19
ANALB	12	13.2	14	6	12	11.9	12	2	12	12.9	14	8	13	13.1	13	2	11	12.0	13	7
ANALH	19	20.1	21	6	19	19.7	20	2	19	20	21	8	16	17.3	18	2	17	18.9	21	11
PELVL	22	23.2	24	6	22	23.1	24	2	22	23.2	24	8	22	22.9	23	2	21	22.2	24	7
PECTL	22	22.3	23	6	21	22.2	23	2	21	22.3	23	8	22	22.6	23	2	19	20.1	21	7
PECTW	4.1	4.4	4.8	6	4.4	4.8	5.2	2	4.1	4.5	5.2	8	4.2	4.9	5.6	2	3.6	4.2	4.6	7
D1H	23	23.2	24	6	21	21.1	21	2	21	22.7	24	8	22	22.4	23	2	21	22.5	25	6
D2H	20	20.5	21	6	18	18.0	18	2	18	19.9	21	8	18	19.1	20	2	18	20.1	23	18
<i>Ratio</i>																				
ANH/POL	1.5	1.7	1.8	6	1.5	1.5	1.5	2	1.5	1.6	1.8	8	1.2	1.3	1.4	2	1.5	1.6	1.7	11
<i>Meristic characters</i>																				
P	12	12.8	13	6	13	13.0	13	2	12	12.9	13	8	13	13.0	13	2	12	12.9	14	19
GrUud	3	3.8	4	6	3	3.5	4	2	3	3.8	4	8	2	3.5	5	2	2	3.3	4	19
GrUd	2	2.2	3	6	2	2.5	3	2	2	2.3	3	8	2	3.0	4	2	2	2.6	3	19
GrLd	10	11.0	12	6	11	11.5	12	2	10	11.1	12	8	11	11.5	12	2	11	12.6	14	19
GrLud	5	5.2	6	6	5	5.0	5	2	5	5.1	6	8	4	4.5	5	2	3	4.2	5	19
GrU	5	6.0	7	6	6	6.0	6	2	5	6.0	7	8	6	6.5	7	2	5	5.9	7	19
GrL	15	16.2	17	6	16	16.5	17	2	15	16.3	17	8	16	16.0	16	2	16	16.8	18	19
Gr	21	22.2	23	6	22	22.5	23	2	21	22.3	23	8	22	22.5	23	2	21	22.7	24	19
LLSCAL	28	28.4	29	5	29	29.0	29	1	28	28.5	29	6	29	30.0	31	2	28	29.3	30	7
<i>Colour characters</i>																				
CBUL	4	4.0	4	6	4	4.5	5	2	4	4.1	5	8	3	3.0	3	2	3	3.8	5	20
CBLL	4	4.5	5	6	5	5.0	5	2	4	4.6	5	8	3	3.0	3	2	4	4.3	5	20
CBALL	8	8.5	9	6	9	9.5	10	2	8	8.8	10	8	6	6.0	6	2	7	8.1	10	20



larger eyes, shorter jaws, longer barbels, longer paired fins and shallower first dorsal fin; from *U. luzonius* in more total gill rakers, fewer lateral-line scales, shorter barbels, shorter caudal peduncle, and shallower first dorsal fin; and from *U. mouthami* it differs in more pectoral rays and shorter paired fins.

*Upeneus oligospilus* differs from *U. margarethae* in narrower caudal peduncle, longer postorbital distance, longer jaws, and shorter caudal and paired fins; from *U. randalli* in fewer gill rakers, longer head and postorbital distance, shorter caudal fin, smaller postorbital length in anal-fin height ratio and fewer bars on caudal fin; from *U. sundaicus* more total gill rakers, fewer lateral-line scales, shallower body at anal-fin origin and caudal peduncle, longer head and postorbital distance, and smaller postorbital length in anal-fin height ratio; from *U. taeniopterus* in longer head and postorbital distance, shorter caudal fin, smaller postorbital length in anal-fin height ratio and fewer bars on upper caudal-fin lobe; from *U. luzonius* it differs in more total gill rakers, fewer lateral-line scales, in longer head and postorbital distance, shorter caudal peduncle, shorter caudal fin and smaller postorbital length in anal-fin height ratio; and from *U. mouthami* it differs in fewer total gill rakers, longer snout and postorbital distance, longer jaws and in shorter paired fins.

*Upeneus tragula* differs from *U. margarethae* in fewer pectoral-fin rays, longer caudal fin, higher anal fin, shorter pectoral fins and higher second dorsal fin; from *U. randalli* in fewer pectoral-fin rays, longer caudal fin and higher second dorsal fin; from *U. sundaicus* in fewer pectoral rays, more gill rakers, fewer lateral-line scales, shallower caudal peduncle, longer caudal fin, higher anal fin and longer second dorsal fin; from *U. taeniopterus* in larger eyes, longer pelvic fin, higher second dorsal fin and larger postorbital length in anal-fin height ratio; from *U. luzonius* it differs in fewer pectoral-fin rays, fewer lateral-line scales, longer caudal fin, higher anal fin and higher second dorsal fin; and from *U. mouthami* it differs in shorter barbels, longer caudal peduncle, longer caudal fin and higher first dorsal fin.

#### Remarks

For three of the four dark-freckled species, subadults were available for studies of allometric changes (Table VIII). When compared with the adults (> 70 mm SL; Table VI), subadult *Upeneus heemstra* sp. nov. and *U. oligospilus* showed longer heads, longer and higher fins, and fewer caudal-fin bars, while subadult *U. tragula* differ from adults in slightly longer caudal fins and fewer caudal-fin bars. Species differences in morphometric characters among the subadults mostly follow those of adults. Subadult *U. heemstra* sp. nov. differ from *U. oligospilus* in

smaller mouth width, longer caudal peduncle, longer caudal fin, longer anal fin and more caudal-fin bars and they differ from *U. tragula* in longer heads, shorter caudal peduncle, shorter caudal fin and longer pectoral fins. Subadult *Upeneus oligospilus* differ from *U. tragula* in longer head, snout and postorbital, longer jaws and wider mouth, shorter caudal peduncle, shorter caudal fin, longer anal-fin base, shallower anal fin, longer pectoral fins and fewer caudal-fin bars.

There are only minor differences among geographic groups of adult *U. heemstra* sp. nov. (Table VI), with the two specimens from Aldabra (Seychelles) having shorter heads, snouts and jaws and the central Red Sea specimen having a shallower half body depth at anal-fin origin, longer postorbital and longer barbels than all other conspecifics, respectively. Among subadults, the two specimens from Sri Lanka differ from those of the East African coast population in having a deeper and longer head, a wider snout, longer barbels and shallower dorsal fins (Table VIII).

*Upeneus heemstra* sp. nov. and *U. tragula* show considerable variation in colour patterns, based on direct observations in the field and freshly collected fish (Figure 4), and distinction among the four dark-freckled species based on colour characters alone is difficult. In fact, the only reliable diagnostic colour characters are the oblique bars on the caudal fin, which seem to undergo less variation and are also mostly retained in preserved fish. However, because also the number of bars overlaps among species and shows size-dependency (Figure 8), caudal-fin bars can only be used in combination with morphometric characters for a reliable diagnosis.

#### Discussion

Based on the cumulative evidence from molecular and quantitative morphological screening, a new goatfish species has been discovered and subsequently described.

The genetic approach, using DNA sequence data from the 'barcoding' fragment of the mitochondrial *COI* gene, provides important supporting evidence for the recognition of *Upeneus heemstra* sp. nov. as an independent taxon, distinct from *U. tragula*. The extent of sequence divergence observed between these two taxa was relatively low (0.8–1.6%), but exceeded the range of divergences observed among individuals within each of these species ( $\leq 0.6\%$ ). This lower range of intraspecific values and the disjuncture between these and the higher interspecific values among the two species – which occur adjacently and are separated by distances (i.e. the *U. heemstra* sp. nov. specimens from Sri Lanka

(WIO) and the Vietnamese or Indonesian *U. tragula* specimens) comparable to the geographic extent of sampling within each species – suggests taxonomic differentiation rather than geographic genetic structure or population differentiation within a wide-spread species.

Several DNA barcoding surveys of sequence variation at the *COI* fragment of both known and cryptic marine fish species have attempted to typify divergence values characteristic of conspecific and congeneric comparisons. Intraspecific divergence values in the current study were broadly comparable to those obtained in these studies (Ward et al. 2005; Mabragaña et al. 2011; Zhang 2011; Zhang & Hanner 2012) and were typical of those characterizing widespread species (Hubert et al. 2012). Similarly, divergences among the species included in the present study (with the exception of the comparison among *U. heemstra* sp. nov. and *U. tragula*) were comparable to documented mean interspecific values (Ward et al. 2005; Zhang 2011; Hubert et al. 2012; Weigt et al. 2012; Zhang & Hanner 2012). These intra- and interspecific divergences were also comparable to those calculated for the Mullidae specifically (Zhang 2011; Zhang & Hanner 2012). Against these, the divergence between *U. heemstra* sp. nov. and *U. tragula* appears slight. However, the extent of interspecific divergence varies widely by taxon (e.g. Ward et al. 2005; Zhang 2011) and mean values calculated for various groups (used comparatively here) are dependent on taxonomic coverage. Importantly, DNA barcoding has revealed low levels of divergence among valid species in certain genera (e.g. Ward et al. 2005). Species have also been recognized and designated on the basis of cumulative evidence despite low levels of sequence divergence in even more variable gene regions (e.g. Randall et al. 2008). More importantly, individuals of each species clustered together and formed tight units; *Upeneus heemstra* sp. nov. and *U. tragula* both formed well-supported, reciprocally monophyletic clades. Such patterns of cohesive units are typically retrieved for individual species through the barcoding approach (e.g. Mabragaña et al. 2011; Zhang & Hanner 2012).

Given the criticisms and limitations of single (mtDNA) marker sets and of the use of mtDNA and DNA barcoding in species delineation, it is important that results and conclusions are subjected to thorough examination through additional or extended sampling and the examination and rigorous, appropriate analyses of additional data sets or additional molecular – particularly nuclear – markers (Brower 2006, 2010; Elias et al. 2007; Ilves et al. 2010).

The multivariate morphometric comparisons support the barcoding results concerning the occurrence of a distinct new species. Detailed comparisons in the subsequent alpha-taxonomic approach further

revealed that *U. heemstra* sp. nov. can be clearly distinguished from the most similar species *U. niebuhri*, *U. oligospilus* and *U. tragula* by the combination of a relatively small set of mostly morphometric characters: caudal peduncle, head, snout, postorbital, barbel and caudal-fin length, anal-fin and second dorsal-fin height, and the number of oblique bars on the caudal fin. These four species represent a ‘dark-freckled’ species complex that can be primarily distinguished from all other species of the *tragula* group by a typical colour pattern consisting of dark dots, spots or blotches on the body and paired fins in both fresh and preserved fish. The occurrence of species complexes rooted within phenotypically similar species groups of *Upeneus* may not be uncommon, requiring an integration of alpha taxonomy with phylogenetic analyses (Uiblein & Causse 2013).

Preliminary evidence for intraspecific geographic differentiation has been found in the Red Sea and Seychelles populations of *U. heemstra* sp. nov. in morphometric characters. Also, the NE Indian Ocean *U. tragula* deviate from those of other areas in meristic characters and there are some indications of character displacement (in two meristic and a combination of several morphometric characters) with *U. heemstra* sp. nov. in areas of possible overlap. However, for the NEIO, where both species occur (Figure 7), only small sample sizes (12 *U. tragula* from Myanmar to Singapore and a single *U. heemstra* sp. nov. from SE India) were available for detailed examination, apart from an unvouchered photograph of *Upeneus tragula* from the Andaman Islands (Figures 4, 7). To further examine our preliminary evidence of population differentiation, large samples from geographically separated areas need be studied, genetically and phenotypically. Such an approach is currently underway towards thoroughly exploring the phenotypic and phylogeographic diversity among W Pacific and SE Indian Ocean *U. tragula* populations.

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