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Upeneus nigromarginatus, a new species of goatfish (Perciformes: Mullidae) from the Philippines

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Abstract. The goatfish, *Upeneus nigromarginatus*, new species, is described based on five specimens (151–196 mm) purchased at a fish market in Panabo City, Mindanao, Philippines. This species is diagnosed by the following counts and external morphology: dorsal fin rays (VIII, 9–10), pectoral fin rays (16), lateral line scales (36–37), total number of gill rakers (25–26), and anal fin rays (I–II, 6). When compared to congeners, *U. nigromarginatus*, new species has a relatively deeper body (31.1–34.8% in SL vs <30% in SL), shorter snout (7.1–9.0% in SL vs >9.6% in SL), and longer pectoral fin (27.7–29.1% in SL vs <25% in SL). *Upeneus nigromarginatus*, new species, has neither stripes on the body, nor bands on the caudal fin. However, a black band borders the distal edges of both the first and second dorsal fins, and at the posterior edge of the upper lobe of the caudal fin; hence the proposed common name 'black-margined goatfish'. The posterior edge of the ventral caudal lobe has a white margin. The comparisons of a fragment of the cytochrome C oxidase subunit I (COI; 28 specimens representing 10 *Upeneus* species) and 34 morphometric parameters (Principle Component Analysis; 56 specimens representing five genera and 12 mullid species) supported the description of *U. nigromarginatus*, new species.

Key words. COI, Coral Triangle, *Mulloidichthys*, *Mullus*, *Parupeneus*

INTRODUCTION

Representatives of the goatfish family Mullidae are recognised by an elongate body with two separate dorsal fins and two unbranched barbels on the chin. This family consists of six genera with 83 species worldwide. In the western Pacific Ocean, this family is represented by the genera *Mulloidichthys*, *Parupeneus* and *Upeneus* with 41 recognised species (Froese & Pauly, 2014). These genera can be differentiated based on the number of lateral line scales and the distance between the two dorsal fins: *Mulloidichthys* has 33–39 lateral line scales and 5 inter-dorsal fin scale rows, *Parupeneus* 26–31 lateral line scales and 3 inter-dorsal fin scale rows, and *Upeneus* 28–39 lateral line scales and 5–7 inter-dorsal fin scale rows (Randall, 2001; Uiblein & Heemstra, 2010). The presence and shape of teeth allow further generic discrimination (Randall, 2001). *Parupeneus* and *Mulloidichthys* lack teeth on the vomer and palatine. Teeth on oral jaws are conical in *Parupeneus* while villiform in the other two genera.

The genus *Upeneus* consists of 30 species worldwide, of which 11 species have been recorded in the Philippines (Froese & Pauly, 2014). Uiblein & Heemstra (2010) recognised four *Upeneus* species groups that include 25 of the 26 Indo-Pacific species. These groups are based on clustered combinations of the number of dorsal spines (VII or VIII), total number of gill rakers (18–33), the number of pectoral fin rays (13–17), and the presence/absence of bars on the caudal fin.

The present study is based on several goatfish specimens purchased at the Panabo City market near the northern coast of the Davao Gulf, a large bay in southeast Mindanao, the Philippines (Fig. 1). The species could not be identified using existing taxonomic keys and literature. External morphological characters, morphometric and genetic comparisons with other mullids supported the description of *Upeneus nigromarginatus*, new species, as presented in this manuscript.

MATERIAL AND METHODS

Morphological analysis. Five specimens were purchased at a market in Panabo City, the Philippines (see Fig. 1 in Bos et al., 2011a) on 26 June 2012. Specimens were measured after preservation in ethanol at the Naturalis Biodiversity Center in Leiden, the Netherlands in January 2014. Metric data, including counts of all fin rays and the scales along the lateral line were collected (Table 1). Gill rakers were counted on the first gill arch separating those from the upper and lower limbs (Table 1). Furthermore, gill rakers were categorised 'developed' (length-width ratio ≥1) or 'undeveloped' (length-width ratio <1). Morphological traits (Table 2) were adapted from Randall & Kulbicki (2006) and Uiblein & Heemstra (2010). Measurements were done with

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Table 1. Meristic data of the holotype, paratypes (n = 4), and mode of all specimens (n = 5) of *Upeneus nigromarginatus*, new species.

Meristic characteristic	Holotype	Paratypes	Mode
Rays in first dorsal fin	VIII	VIII	VIII
Rays in second dorsal fin	9	9–10	9
Rays in anal fin	I,6	I,6–II,6	II,6
Rays in pelvic fin	I,5	I,5	I,5
Rays in pectoral fin	16	16	16
Rays in caudal fin	15	15–16	15
Lateral line scales	36	36–37	36
Gill rakers (upper limb, undeveloped)	3	2–3	3
Gill rakers (upper limb, developed)	5	4–6	5
Gill rakers (lower limb, developed)	13	12–13	13
Gill rakers (lower limb, undeveloped)	4	5–6	5
Total gill rakers on upper limb	8	7–9	8
Total gill rakers on lower limb	17	17–18	18
Total gill rakers	25	25–26	25

a vernier caliper at 1 mm accuracy for measures >10 mm and at 0.1 mm accuracy for measures ≤10 mm.

All type specimens were deposited in the Naturalis Biodiversity Center (former Rijksmuseum voor Natuurlijke Historie; RMNH) in Leiden, the Netherlands. For comparison, representative species of the western Pacific genera of the Mullidae (*Mulloidichthys*, *Parupeneus*, *Upeneus*) were selected from the collections of RMNH and the Zoological Museum in Amsterdam (ZMA; presently stored at the RMNH). Some specimens of the genera *Mullus* and *Pseudupeneus* were included to increase the accuracy of the analysis. Similar-sized fishes were selected, if available, to avoid effects of ontogenetic changes on measured ratios (Standard Length [SL] between 140 and 230 mm).

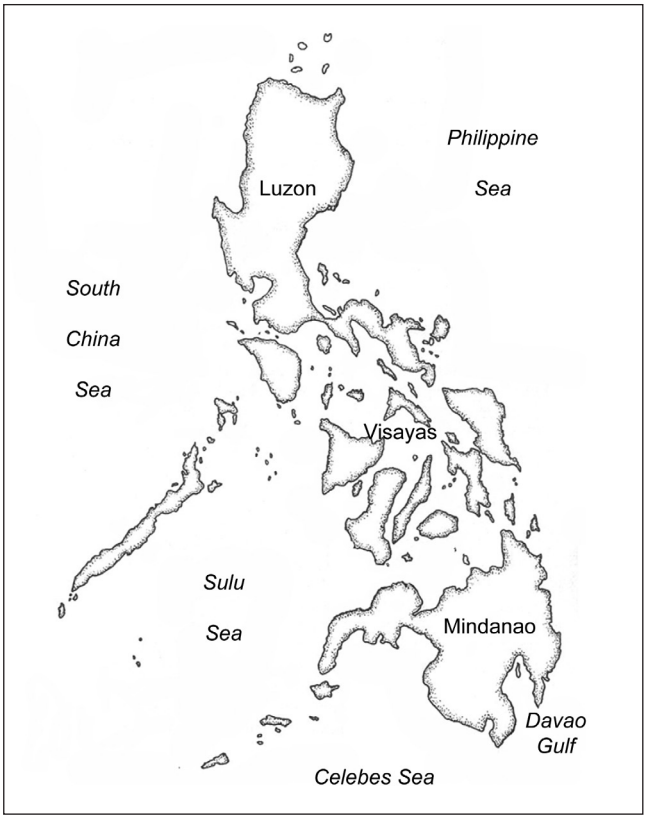

Fig. 1. Map of the Philippines archipelago with Davao Gulf in the South-East of Mindanao Island.

Molecular analysis. A gill arch was removed from all five type specimens, immediately preserved in 96% ethanol and stored in a freezer (at −80°C). For method verification, gill tissue of three other goatfishes was also collected in the Philippines in June 2012: one sample of *Parupeneus barberinus* (Lacepède, 1801), one sample of *Parupeneus indicus* (Shaw, 1803) and one sample of *Upeneus tragula* Richardson, 1846.

Genetic material was extracted from 25–50 mg of tissue with a proteinase K digestion using a QIA-amp DNA mini-kit protocol (QIAGEN). For DNA amplification and sequencing, a standard 25 µl Polymerase Chain Reaction (PCR) mix was used containing 5 µl of 5× PCR buffer, 0.75 µl dNTP, 0.25 µl Taq Polymerase, 1 µl of each primer (forward and reverse), 1.5 µl $MgCl_2$, 2 µl DNA template, and 13.5 µl H_2O. The following primers were used: FishF1- 5' TCAACCAACCACAAAGACATTGGCAC and FishR1-5' TAGACTTCTGGGTGGCCAAAGAATCA (Steinke & Hanner, 2010). A 655 base pair (bp) region of Cytochrome C Oxidase Subunit I (COI) was subsequently amplified under the following conditions: 5 min at 95°C; 35 cycles of 30 s at 95°C, 45 s at 45°C, and 60 s at 72°C; 7 min at 72°C; held at 4°C.

Data analysis. Principle Component Analysis (PCA) was conducted to visualise metric differences between the proportional morphologic measures (percentage of SL) with the highest variation of all studied specimens. Direct Oblimin Rotation with Kaiser Normalization (SPSS Statistics 20) was used to find the rotated components with the highest significance.

Nucleotide sequences (COI) of similar length (about 655 bp) were used to conduct the genetic comparison (GenBank, 2014). All *Upeneus* species, for which COI sequences were uploaded to GenBank, were included in the analysis (Table

Table 2. Proportional morphological measurements of the holotype, paratypes (n = 4), and mean for all specimens (n = 5) of *Upeneus nigromarginatus*, new species, as percentages of standard length (SL).

	Holotype	Paratypes	Mean
Standard Length (mm)	**196**	**151–156**	**162.6**
Measurement	**% SL**	**% SL**	**% SL**
Body depth at D1	34.7	31.1–34.8	32.9
Half body depth at D1	26.0	23.8–26.5	25.0
Body depth at A	28.6	27.1–30.3	28.4
Half body depth at A	20.4	19.2–20.6	20.0
Caudal peduncle depth	12.8	12.6–12.9	12.8
Jaw depth	12.8	11.9–12.3	12.3
Head depth through eye	21.9	21.3–23.2	22.4
Head length	29.1	29.1–30.3	29.8
Jaw length	11.2	11.3–12.3	11.7
Barbel length	19.9	20.5–20.6	20.4
Snout length	8.7	7.1–9.0	8.3
Orbit diameter	7.1	7.7–9.0	8.2
Pre dorsal length	36.2	35.5–37.2	36.2
D1 base length	15.3	14.7–15.9	15.1
D1 fin height	24.5	24.5–25.2	24.7
Inter dorsal length	15.3	14.6–16.1	15.4
D2 base length	13.8	14.6–17.4	15.2
D2 fin height	16.8	17.4–18.7	17.8
Pre pectoral length	30.6	31.6–34.0	32.2
Pectoral fin length	28.6	27.7–29.1	28.7
Pre pelvic length	33.2	32.9–35.1	33.7
Pelvic fin length	19.9	20.0–21.8	20.6
Pre anal length	70.9	68.4–71.8	70.3
Anal base length	10.2	10.3–11.0	10.6
Anal fin height	15.8	16.1–16.7	16.3
Caudal peduncle length	18.4	17.9–21.9	19.5
Caudal fin length	28.6	27.7–31.4	29.2
Caudal concavity	15.3	12.9–16.1	14.3
Body width	16.3	16.0–17.2	16.4
Inter orbit width	8.7	7.7–8.6	8.3
Nostril width	5.1	5.8–6.0	5.7

3). If available, three specimens per species were selected to increase genetic diversity among conspecifics. Specimens of the genus *Parupeneus* were selected as outgroup taxa. Sequence alignment (MUSCLE; 20 refinement iterations) and phylogeny reconstruction (Maximum Likelihood under the General Time Reversible substitution model; Gamma distributed with Invariant site; Nearest-Neighbor-Interchange; and maximum parsimony with 500 replicates bootstrap analysis) were conducted with the software package MEGA 5.10. Bootstrap values ≤50% at the nodes of the clades did not allow exact reconstruction of the phylogenetic history of the *Upeneus* species and are not shown.

RESULTS

Morphological comparison. The PCA resulted in four principle components respectively explaining 29.3, 16.2, 12.7 and 6.2% of the variance in the data matrix (Fig. 2). Component 1 explained variance of (listed by decreasing importance) jaw depth, head depth through eye, D2 base length, anal base length, pelvic fin length, body depth at A, half body depth at D1, half body depth at A, body depth at D1, number of scales, snout length, barbel length, inter dorsal length, pectoral fin length. Component 2 explained variance of pre-pelvic length, pre-anal length, D1 height, caudal peduncle length, pre-dorsal length, orbit diameter and pre-pectoral length. The five represented genera *Mulloidichthys*, *Mullus*, *Parupeneus*, *Pseudupeneus*, and *Upeneus* occupied unique regions within the rotated axes (Fig. 2). Species of *Parupeneus* and *Pseudupeneus*, and those of *Mullus* and *Upeneus* partly overlapped, whereas the specimens representing *Mulloidichthys* were relatively isolated. The five specimens of *Upeneus nigromarginatus*, new species, formed a completely isolated cluster (Fig. 2), positioned nearest to specimens of *Mullus* and *Upeneus*.

Table 3. GenBank Accession numbers of goatfish specimens (Mullidae) with taxonomic author used in the phylogenetic analysis.

Species	Author	Accession number
Parupeneus barberinus	(Lacepède, 1801)	JQ350179[1], JQ350180[1]
Parupeneus indicus	(Shaw, 1803)	DQ885037[2], FJ237883[2]
Upeneus japonicus	(Houttuyn, 1782)	EF607603[3], EF607604[3], JF952884[4]
Upeneus margarethae	Uiblein & Heemstra, 2010	KC147801[2], KC147805[2], KC147798[2]
Upeneus mascareinsis	Fourmanoir & Guézé, 1967	KC147807[2]
Upeneus moluccensis	(Bleeker, 1855)	KC501833[5], KC501851[5], KC501852[5]
Upeneus parvus	Poey, 1852	JQ365613[6], JQ365615[6], KF930519[2]
Upeneus pori	Ben-Tuvia & Golani, 1989	KF564319[2]
Upeneus sulphureus	Cuvier, 1829	EF607609[3], EF609635[7], EF609636[7]
Upeneus tragula	Richardson, 1846	EF607612[3], KC147799[2]
Upeneus vittatus	(Forskåll, 1775)	FJ237538[7], GU804972[2], JX676155[2]

[1](Hubert et al., 2012); [2] unpulished data; [3](Zhang, 2011); [4](Zhang & Hanner, 2011); [5](Keskin & Atar, 2013); [6](Oliveira Ribeiro et al., 2012); [7](Lakra et al., 2011)

TAXONOMY

Upeneus nigromarginatus, new species

Black-margined goatfish

(Figs. 3–5; Tables 1, 2)

Material examined. Holotype (Fig. 3): RMNH.PISC.37991, 1 ex., 196 mm SL; The Philippines, Panabo City, fish market, 7°18′23″N, 125°41′1″E, coll. A.R. Bos, 26 June 2012. Paratypes: RMNH.PISC.36422, 1 ex., 151 mm SL; RMNH.PISC.36423, 1 ex., 155 mm SL; RMNH.PISC.36424, 1 ex., 156 mm SL; RMNH.PISC.37992, 1 ex., 155 mm SL, same collection information as holotype.

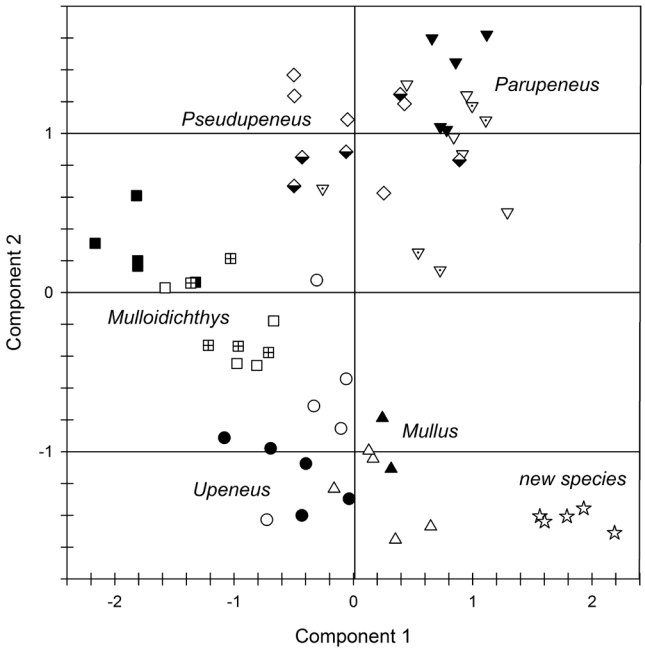

Fig. 2. Principle Component Analysis of 34 morphological parameters of 56 specimens representing the Mullidae. Species clusters are shown for five genera (*Mulloidichthys flavolineatus* [black square], *Mulloidichthys martinicus* [crossed square], *Mulloidichthys vanicolensis* [open square], *Mullus auratus* [black triangle], *Mullus surmuletus* [open triangle], *Parupeneus barberinus* [black inverted triangle], *Parupeneus heptacanthus* [open inverted triangle], *Parupeneus indicus* [open inverted triangle with dot], *Pseudupeneus maculatus* [open diamond], *Pseudupeneus prayensis* [half-filled diamond], *Upeneus nigromarginatus*, new species [star], *Upeneus tragula* [black circle], *Upeneus vittatus* [open circle]).

Diagnosis. Meristic data of the holotype and the range and/or median of all type specimens are provided in Table 1. Data in parentheses refer to the paratypes when different from the holotype. Dorsal fin VIII + 9, first dorsal spine small, second dorsal spine longest, last dorsal soft ray branched to base. Anal fin I, 6, three paratypes with unusual two spines instead of one, with first spine short and thin (Fig. 4), second spine up to two-third of first soft ray, first anal soft ray segmented and unbranched, last ray branched to base. Pectoral fin rays 16, upper 2 rays unbranched. Pelvic fin rays I, 5. Principal caudal fin rays 15 (15–16), uppermost and lowermost rays unbranched. Lateral line scales 36 (36–37), five scale rows between dorsal fins. Total gill rakers on first gill arch 25 (25–26). Gill rakers on upper and lower limb of first arch

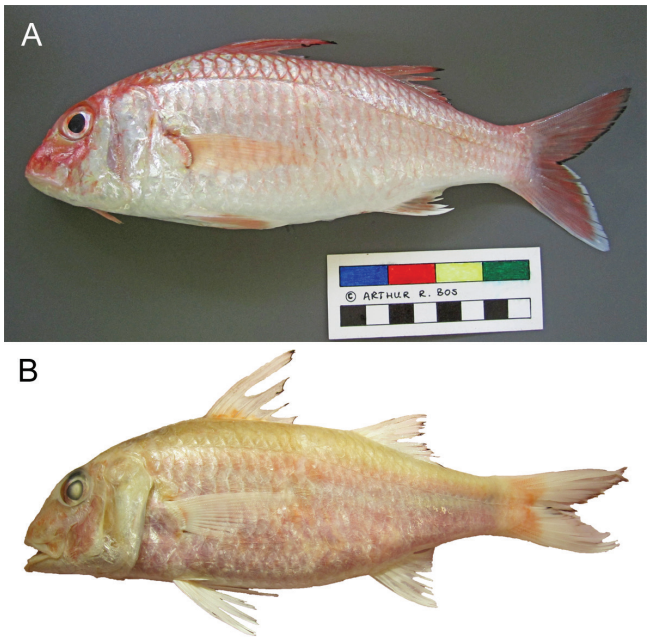

Fig. 3. A, *Upeneus nigromarginatus*, new species, holotype, RMNH.PISC.37991, fresh specimen; B, holotype after 4 months in ethanol, SL 196 mm.

8 + 17 (7–9 + 17–18), several anterior rakers undeveloped but visible on both limbs.

Proportional measurements of the holotype, paratypes, and the mean value of all specimens are presented in Table 2. Body relatively deep, its depth at first dorsal fin origin 2.9 (2.9–3.2) in SL. Body width 2.1 (1.8–2.2) in body depth. Anterior dorsal fin height 4.1 (4.0–4.1) in SL. Head length (HL) 3.4 (3.3–3.4) in SL. Snout relatively short, its length 3.4 (3.4–4.3) in HL. Orbit diameter 4.1 (3.6–3.9) in HL. Nostrils at horizontal axis of ventral edge of orbit. Mouth terminal and slightly oblique, the cleft forming an angle of about 10° to the horizontal axis of body. Both jaws with several rows of unevenly placed villiform teeth. Palatine and vomer with villiform teeth. Vomer with smaller teeth than those on palatine, forming rough surface covered by membrane tissue. Maxilla reaching vertical through anterior half of pupil, upper jaw length 2.3 (2.4–2.5) in HL. Barbels reaching vertical at two third of distance between orbit and posterior margin of pre-operculum, their length 1.5 (1.4–1.5) in HL.

Origin of dorsal fin over fifth lateral-line scale, pre-dorsal length 2.8 (2.7–2.8) in SL. Longest dorsal spine 1.2 in HL. First dorsal spine very short; pectoral fin relatively long, its length 1.0 (1.0–1.1) in HL. Pelvic fin length 1.5 (1.4–1.5) in HL. Caudal fin length relatively short, its length 1.0 (1.0–1.1) in HL. Caudal fin moderately forked, caudal concavity 1.9 (1.9–2.4) in HL. Caudal peduncle depth 2.3 (2.3–2.4) in HL. Caudal peduncle length 1.6 (1.4–1.7) in HL. Pre-anal length 1.4 (1.4–1.5) in SL. Anal fin height 1.8 (1.8–1.9) in HL.

Scales finely ctenoid. Sensory canals on lateral-line scales with four to six branches. A row of about 17 sensory canals on posterior edge of pre-operculum. Opercular membrane forms pointed lobe at horizontal axis of mid-eye position, but lacks a spine. Cheek and pre-operculum covered with scales. Small scales present basally on posterior dorsal and anal fin. Slender pelvic axillary scale about half the length of the pelvic fin.

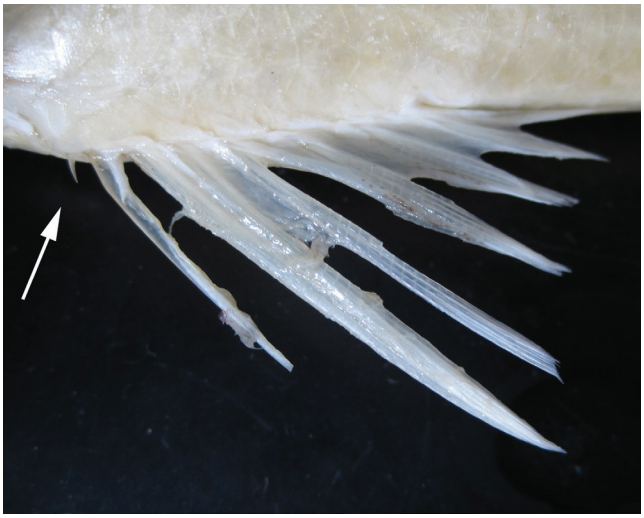

Fig. 4. *Upeneus nigromarginatus*, new species, paratype, RMNH. PISC.36423, anal fin with two spines and six soft rays. White arrow points at short, thin first spine.

Coloration in life. Coloration based on the freshly dead specimen of the holotype (Fig. 3A). Body and abdomen pearly white without conspicuous stripes or bands. Snout red, color continuing until pre-operculum. Nape reddish. Silver white line at an angle of about 20° to the horizontal axis of body from nostril to eye, line continues along margin of the orbit decreasing in width posteriorly. Scales above lateral line on body with red margins, but less conspicuous on caudal peduncle. Barbels white with rosy tips. Inter-radial tissue of D1 red between 2nd and 3rd rays, translucent between other rays (Fig. 5A). Second dorsal fin translucent with scattered reddish blotches (Fig. 5B). Distal endings of D1 and D2 with a thin black margin, some specimens with a thin white line or few white blotches proximal to the black margin in the anterior dorsal fin. Caudal fin reddish with increasing intensity towards fin tips (Fig. 5C). Posterior end of dorsal lobe of caudal fin with a black margin, terminating slightly ventral to the caudal fork. Ventral lobe of caudal fin has a bright white margin at its proximal end, which increases in width towards the tip of the lobe. A brownish blotch or line anterior to the white margin on the ventral lobe of caudal fin (Fig. 5C). Anal fin white with a translucent sphere in its center. Pectoral fins translucent. Small red blotches just dorsal of pectoral fin bases. Pelvic fins translucent with white tips.

Coloration in preserved specimens. Coloration of the holotype after preservation in ethanol is shown in Figure 3B. Area dorsal to lateral line pale white; ventral to lateral line red-purplish. All fins pale white, with black margins along anterior dorsal fin, posterior dorsal fin, and upper lobe of caudal fin. Silver-white line from nostril to eye.

Distribution. This species is only known from the northern region of the Davao Gulf in the Philippines (Fig. 1).

Etymology. The name of this species derives from the black margins along both dorsal fins and the dorsal lobe of the caudal fin.

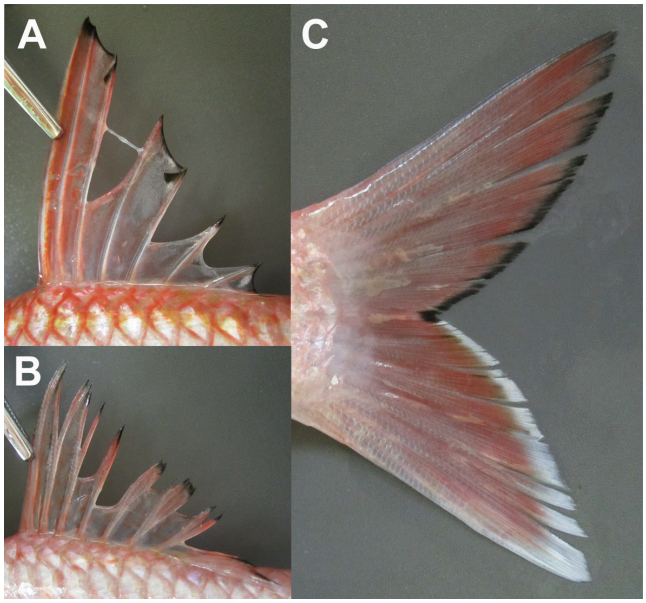

Fig. 5. Selected fins of fresh specimen of *Upeneus nigromarginatus*, new species, holotype, RMNH PISC.37991 (not to scale); A, anterior dorsal fin; B, posterior dorsal fin; C, caudal fin.

Remarks. The black-margined goatfish *Upeneus nigromarginatus*, new species, differs from other *Upeneus* species (Table 2) in having a deeper body (31.1–34.8% in SL at origin of first dorsal fin), longer pectoral fins (27.7–29.1% in SL), and a shorter snout (7.1–9.0% in SL). Uiblein & Heemstra (2011) compared seven *Upeneus* species and found body depth at the first dorsal fin never to exceed 30% in SL. The longest pectoral fin (25% in SL) was found in *Upeneus francisi* and the shortest snout (9.6% in SL) was recorded for *Upeneus guttatus* (Uiblein & Heemstra, 2011). Several of the type specimens of *U. nigromarginatus*, new species, have two spines in the anal fin (Fig. 4), although one anal spine is diagnostic for *Upeneus* (Uiblein & Heemstra, 2011). All other characteristics justified the classification of the new species to the genus of *Upeneus*. The presence of palatine and vomerine teeth is diagnostic for *Upeneus* (Uiblein & Heemstra, 2011). *Upeneus nigromarginatus*, new species, has villiform teeth on the palate and the vomer, but teeth are smaller in size on the latter. Some individuals of *Upeneus filifer*, completely lack vomerine teeth (Kim, 2002) and therefore the smaller size of vomerine teeth was not considered a feature supporting separation from the *Upeneus* genus.

Ecological information. Specimens of *Upeneus nigromarginatus*, new species, were sold in a market in Panabo City by a vendor, who introduced me to the fisherman who caught the fish. An interview with the fisherman revealed that these fishes were caught with a gill net (mesh size 2 inches) at a depth of 40–80 m approximately at the coordinates 7°14′32″N, 125°40′17″E. The net was set at 0400 h of 26 June 2012 and then retrieved an hour later. *Upeneus nigromarginatus*, new species, was caught together with *Upeneus vittatus* (Forsskål, 1775), *Polydactylus longipes* Motomura, Okamoto, Iwatsuki, 2001, and *Rexea bengalensis* Alcock, 1894. *Upeneus nigromarginatus*, new species, is a relatively uncommon species, evidenced by the few individuals which have been caught by fishermen living along the shores of the Lasang River estuary. Anecdotal evidence suggested that fishermen from the northern villages in Samal Island (Davao Gulf) may have caught specimens of this species (pers. comm. N. Gallarda), but a 2-year survey conducted at local fish markets in Samal Island did not reveal other specimens of *U. nigromarginatus*, new species (Bos & Gumanao, 2012).

Genetic comparison. The COI fragments of 34 goatfishes provided, after alignment and trimming to equal length, 581 nucleotides for analysis with 208 variable characters. The phylogenetic tree resulting from the Maximum Likelihood construction is shown in Fig. 6. All specimens formed monophyletic sub-clades with their conspecifics with bootstrap values of ≥74% with only *Parupeneus barberinus* showing a lower bootstrap value. The five specimens of *U. nigromarginatus*, new species, were positioned within the monophyletic clade of *Upeneus* and formed a sub-clade with a bootstrap value of 97%.

A second sub-clade consisted of 10 specimens representing *U. japonicus*, *U. margarethae*, *U. pori*, and *U. tragula* was well supported with a bootstrap value of 77%. A third sub-clade included 10 specimens representing *U. mascareinsis*, *U. moluccensis*, *U. sulphureus*, and *U. vittatus* was supported with a bootstrap value of 57%. Three specimens representing *U. parvus* formed a fourth sub-clade with a bootstrap value of 99%.

DISCUSSION

Four taxa groups are recognised for 25 species of the genus *Upeneus* in the Indo-Pacific based on a combination of morphological characters: the number of dorsal fin spines (D1), pectoral fin rays (PFR), gill rakers (GR), and bars on the caudal fin (Uiblein & Heemstra, 2010). These four groups are; "*japonicus* group" (seven species: D1 VII, PFR 13–15, GR 21–32, bars present), "*tragula* group" (seven species: D1 VIII, PFR 13–14, GR 18–25, bars present), "*moluccensis* group" (four species: D1 VIII, PFR 15–17, GR 26–33, bars mostly absent), and "*vittatus* group" (seven species: D1 VIII, PFR 15–17, GR 26–32, bars present). Only one species occurring in the area, *Upeneus filifer* Ogilby, 1910, does not fit into these categories based on a unique combination of the above meristic data (D1 VIII, PFR 13–14, GR 24–27) and absence of bars on the caudal fin (Uiblein & Heemstra, 2010).

Based on its eight dorsal fin rays and the relatively low total number of gill rakers (25–26), *Upeneus nigromarginatus*, new species, could be added to the "*tragula* group". However, representatives of the "*tragula* group" are further recognised in having 13–14 pectoral fin rays and bars on the caudal fin. In contrast, *U. nigromarginatus*, new species, has 16 pectoral fin rays and does not have bars on the caudal fin. The caudal fin coloration of *U. nigromarginatus*, new species, is comparable to that of two representatives of the "*moluccensis* group"; *Upeneus doriae* Günther, 1869 and *Upeneus sulphureus* Cuvier, 1829 (Uiblein & Heemstra, 2010), but these respectively have 29–33 and 27–28 gill rakers. Therefore, *U. nigromarginatus*, new species, shares characteristics with representatives of more than one of the species groups and cannot be clearly categorised, as is the case with *Upeneus filifer*. However, the present COI analysis provided support for the species groups (Fig. 6). The two monophyletic sub-clades representing multiple *Upeneus* species exactly differentiated between "*moluccensis*" and "*vittatus*" representatives and "*japonicus*" and "*tragula*" representatives (Uiblein & Heemstra, 2010).

Phylogenetic relationships of the goatfishes have been studied, but were usually limited to relatively few species. Mamuris et al. (1999) found the genus *Pseudupeneus* being most genetically distinct from those of *Mullus* and *Upeneus*, which is congruent to the present morphological comparison (Fig. 2). Lakra et al. (2011) recovered three separate clades for the genera *Parupeneus*, *Mulloidichthys*, and *Upeneus*. As these earlier studies included only three species (*Upeneus moluccensis*, *U. sulphureus*, and *U. vittatus*), the present study with 10 representative species, comprises the most comprehensive COI comparison for the *Upeneus* genus.

The Davao Gulf, located in the South East of the Philippines, is geographically isolated and has faunal elements differing from other parts of the archipelago as it is dominated by the Mindanao current entering the Celebes Sea (Hoeksema, 2007). Researchers have long neglected the biota in the southern islands of the archipelago due to continued political unrest (e.g., Russ & Alcala, 1996; Carpenter & Springer, 2005; Bos, 2011). In recent years however, new records of fishes have been observed in the Davao Gulf (Bos & Gumanao, 2013; Bos & Smits, 2013) and a new fish species *Polydactylus longipes* (Motomura et al., 2001) was described. Furthermore, unique ecological discoveries, such as a previously unknown corallimorph predator of the crown-of-thorns sea star *Acanthaster planci* (Bos et al., 2008; 2011b) and a commensal relationship between fishes and the mushroom coral *Heliofungia actiniformis* (Bos, 2012)—so

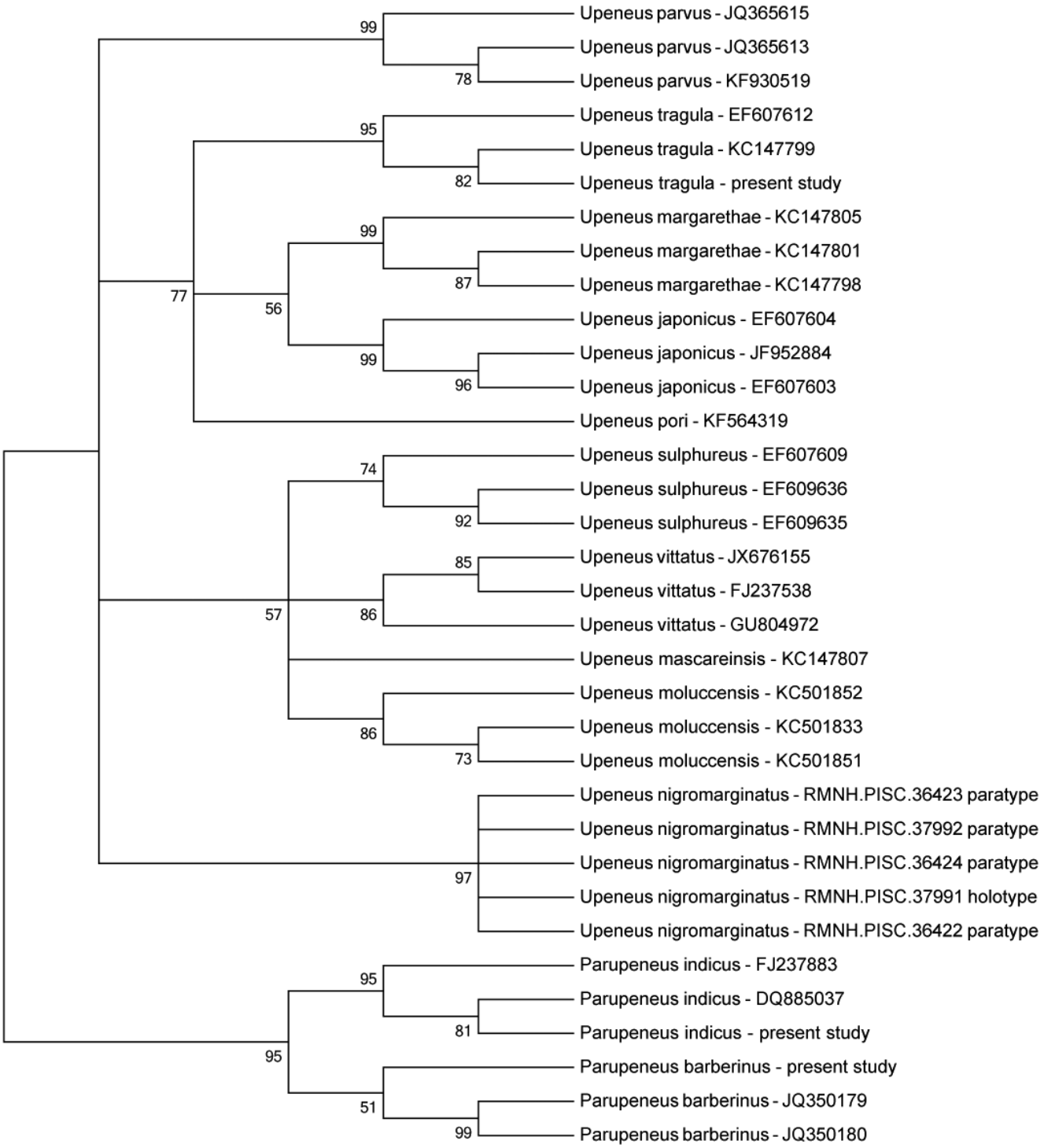

Fig. 6. Maximum likelihood phylogeny of representatives of the genus *Upeneus* (Mullidae). Species names are accompanied by GenBank association numbers, except for those specimens analysed during the 'present study' (method validation) and specimens of *Upeneus nigromarginatus*, new species (RMNH collection numbers). Representatives of the genus *Parupeneus* were used as an outgroup. Numbers at nodes represent maximum parsimony bootstrap proportions.

far unique to the Davao Gulf—were reported. The present description of *U. nigromarginatus*, new species, further emphasises the biological and ecological distinctiveness of the Davao Gulf.

Comparative material. *Mulloidichthys flavolineatus* (Lacepède, 1801): ZMA.PISC.101.529, 3 ex., 154–200 mm SL; Indonesia, West Sumatra, Pulu Babi, coll. E. Jacobsen, April 1913; ZMA.PISC.132.456, 1 ex., 214 mm SL; Indonesia, East Nusa Tenggara, coll. G.A.J. van de Sande, 6 December 1908; ZMA.PISC.101.528, 1 ex., 222 mm SL; Indonesia, Siboga Expedition, 1899–1900.

Mulloidichthys martinicus (Cuvier, 1829): ZMA. PISC.119.332, 2 ex., 159–168 mm SL; Dutch Antilles, Curaçao, Caracas Bay, coll. C.J. van der Horst, 24 April 1920; ZMA.PISC.108.086, 3 ex., 153–186 mm SL; Dutch Antilles, Curaçao, Piscadera Bay, coll. H. Nijssen, 28 December 1966.

Mulloidichthys vanicolensis (Valenciennes, 1831): RMNH. PISC.25449, 2 ex., 151–202 mm SL; East Indian Archipelago, Sabang Bay, Pulu Weh, coll. P. Buitendijk, 1924; RMNH. PISC.11245, 1 ex., 186 mm SL; Samoa, Savaii, coll. M. Godeffroy, no date; ZMA.PISC.132.461, 1 ex., 213 mm SL; Indonesia, Sumatra, coll. E. Jacobsen, no date.

Mullus auratus Jordan & Gilbert, 1882: RMNH.PISC.23345, 2 ex., 175–179 mm SL; Margarita Island, coll. S. Zaneveld, 6 February 1955.

Mullus surmuletus Linneaus, 1758: RMNH.PISC.26809, 2 ex., 162–182 mm SL; North Sea, Lightship Haaks, 1 July 1932; RMNH.PISC.35909, 1 ex., 172 mm SL; The Netherlands, Oosterschelde, coll. V. Bakker, August 1983; ZMA.PISC.132.466, 2 ex., 213–256 mm SL; The Netherlands, Den Helder, 21 May 1946.

Parapeneus barberinus (Lacepède, 1801): ZMA. PISC.101.491, 2 ex., 139–151 mm SL; Indonesia, Makassar, coll. M. Weber, 1888; ZMA.PISC.101.485, 1 ex., 153 mm SL; Indonesia, South Sulawesi, Siboga Expedition, 1899–1900; ZMA.PISC.101.494, 1 ex., 206 mm SL; Indonesia, coll. P. Bleeker, 1842–1860; ZMA.PISC.101.497, 1 ex., 165 mm SL; Indonesia, South Sulawesi, Siboga Expedition, 1899–1900.

Parapeneus heptacanthus (Lacepède, 1802): RMNH. PISC.5737, 3 ex., 163–197 mm SL, East Indies, coll. P. Bleeker, 1879; RMNH.PISC.467, 1 ex., 166 mm SL; Indonesia, Macassar, coll. Piller, 1848; ZMA.PISC.101.422, 1 ex., 172 mm SL; Indonesia, Sulawesi, Ujung Pandang, coll. M. Weber, 1888.

Parapeneus indicus (Shaw, 1803): RMNH.PISC.13333, 2 ex., 177–195 mm SL; Indonesia, Java Sea, coll. P. Buitendijk, 1904–1907; ZMA.PISC.101.493, 2 ex., 159–192 mm SL; Indonesia, coll. P. Bleeker, 1842–1860; ZMA.PISC.101.489, 1 ex., 181 mm SL; Indonesia, Sulawesi, Ujung Pandang, coll. M. Weber, 1889.

Pseudupeneus maculatus (Bloch, 1793): ZMA.PISC.108.087, 2 ex., 164–164 mm SL; Dutch Antilles, Curaçao, Piscadera Bay, coll. H. Nijssen, 28 July 1966; ZMA.PISC.136.256, 2 ex., 147–165 mm SL; Dutch Antilles, Curaçao, Caracas Bay, coll. van der Horst, 1920; ZMA.PISC.136.257, 1 ex., 219 mm SL; Caribbean, coll. Weger & Broeke, no date.

Pseudupeneus prayensis (Cuvier, 1829): ZMA.PISC.136.262, 3 ex., 171–180 mm SL; Senegal, coll. Vermeulen, 1906; RMNH.PISC.486, 2 ex., 139–152 mm SL; Ghana, Ashanti, coll. Pel, 1840–1855.

Upeneus tragula Richardson, 1846: RMNH.PISC.480, 2 ex., 142–156 mm SL; Indonesia, Java, coll. Kuhl & van Hasselt, 1820; RMNH.PISC.13371, 2 ex., 131–135 mm SL; Indonesia, Java Sea, coll. P. Buitendijk, 1906–1929; RMNH.PISC.459, 1 ex., 191 mm SL; Indonesia, Makassar, coll. Piller, no date.

Upeneus vittatus (Forskåll, 1775): RMNH.PISC.11479, 1 ex., 205 mm SL; Samoa, coll. Godeffroy, June 1887; RMNH. PISC.13355, 1 ex., 173 mm SL; Indonesia, Halmaheira, coll. H.A. Bernstein, 1860–1865; ZMA.PISC.136.291, 2 ex., 176–192 mm SL; Indonesia, East Java, coll. Kromanly, no date; ZMA.PISC.136.302, 1 ex., 237 mm SL; Indonesia, Maluku, Buru Island, coll. Buitenzorg, 23 July 1913.

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