Cryptocentrus steinhardti (Actinopterygii; Gobiidae): a new species of shrimp-goby, and a new invasive to the Mediterranean Sea (#56135)

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Cryptocentrus steinhardti (Actinopterygii; Gobiidae): a new species of shrimp-goby, and a new invasive to the Mediterranean Sea

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A new species of shrimp goby was collected at depths of 60-80 m, off the southern Israeli Mediterranean coast, revealed by a unique 'DNA barcoding' signature (mtDNA *COI* and *Cytb*) that differed from any other previously published goby species. Following a comprehensive morphological and anatomical examinations, this species is being described here as *Crypocentrus steinhardti* n. sp., clustered phylogenetically with the silt shrimp-gobies group, in which *Cryptocentrus* is the most speciose genus. This finding constitutes the third record of an invasive shrimp goby in the Mediterranean Sea, revealing an intriguing ecological consideration regarding possible formation of a fish-shrimp symbiosis in a newly invaded territory. Last, describing tropical species in the Mediterranean prior to their discovery in the native distribution is an unusual event, although not the first such case. Several similar examples are provided below.

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ABSTRACT

A new species of shrimp goby was collected at depths of 60-80 m, off the southern Israeli Mediterranean coast, revealed by a unique 'DNA barcoding' signature (mtDNA *COI* and *Cytb*) that differed from any other previously published goby species. Following comprehensive morphological and anatomical examinations this species is described here as *Cryptocentrus steinhardti* n. sp., clustered phylogenetically with the silt shrimp-gobies group, in which *Cryptocentrus* is the most speciose genus. This finding constitutes the third record of an invasive shrimp goby in the Mediterranean Sea, revealing an intriguing ecological consideration regarding possible formation of a fish-shrimp symbiosis in a newly invaded territory.

Describing tropical species from the Mediterranean prior to their discovery in their native distribution is an unusual event, although this is not the first such case. Several similar examples are provided.

INTRODUCTION

Since the opening of the Suez Canal in 1869, more than 400 multicellular nonnative species of Red Sea origin, including approx. 100 fish species, have been found along the Israeli Mediterranean coast (Galil et al., 2020). Out of this diverse invasive fauna, two species are the shrimp-gobies *Vanderhorstia mertensi* Klausewitz, 1974, (Goren, Stern and Galil, 2013) and *Cryptocentrus caeruleopunctatus* (Rüppell, 1830) (Rothman and Goren, 2015). These species are part of a group of near-reef fishes that inhabit sandy and silty habitats and display a remarkable mutualism with burrowing alpheid shrimps, exchanging burrow construction capabilities and sentinel services (Karplus and Thompson, 2011). Common throughout the tropics, this unique fish-shrimp association is documented from over 100 fish species that belong to eleven valid genera of gobies: *Amblyeleotris* Bleeker 1874; *Cryptocentrus* Valenciennes (ex Ehrenberg) in Cuvier & Valenciennes 1837; *Cryptocentroides* Popta 1922*, Ctenogobiops* Smith 1959, *Lotilia* Klausewitz 1960; *Mahidolia* Smith 1932; *Myersina* Herre 1934; *Psilogobius* Baldwin 1972; *Stonogobiops* Polunin & Lubbock 1977*; Tomiyamichthys* Smith 1956 and *Vanderhorstia* Smith 1949 (Karplus, 2014; Ray, Mohapatra and Larson, 2018). An additional genus, *Flabelligobius Smith* 1956 is considered a synonym of *Tomiyamichthys* (Hoese et al., 2016; Fricke and Eschmeyer, 2020).

During cruises to sample the benthic biota off Ashdod (southern Israel), three specimens of an unknown shrimp-goby were collected at depths of 60 to 80 m by a bottom trawl net. Integrative examinations of molecular taxonomy and traditional practices indicated that these fish belong to an undescribed species of *Cryptocentrus.*

MATERIALS & METHODS

Fish specimens were collected from the southern coast of the Israeli Mediterranean by the commercial 240 hp F/V bottom trawler, *Moty*, captained by L. Ornoy. The fish were preserved in 70% alcohol and stored at the fish collection of the Steinhardt Museum of Natural History, Tel-Aviv University (SMNHTAU). Muscle tissue samples were taken from fresh specimens for genetic analyses and preserved in 96% alcohol.

Genetic analysis

Total genomic DNA was extracted from the three individuals using a micro tissue genomic DNA isolation kit following the manufacturer's protocol (AMBRD Laboratories, Turkey). Next, approx. 50 ng of template DNA was used to amplify a 651 bp fragment of the mitochondrial cytochrome c oxidase subunit I gene (*COI*) and 467 bp of the mitochondrial Cytochrome b (*Cytb*). Primers and PCR reactions are detailed in supplementary table S1. The contiguous sequences of both genes, including measurements, photos and its trace files, were uploaded to BOLD system at www.v4.boldsystems.org under the BIM project (Biota of the Israeli Mediterranean) with BOLD Sample IDs: BIM769-20 for the holotype and BIM534-17 and BIM770-20 for the two paratypes. In order to investigate the total genetic divergence of shrimp-associated gobies complex, 101 previously published sequences belonging to ten putative genera were mined from BOLD and NCBI to comprise an aligned dataset, with a single sequence of *Gobius niger* as an outgroup (Supplementary Table S2). The genetic vouchers were included in the dataset only if they indicated a precise information on the sampling localities and an unambiguous association with a Barcode Index Number (BIN) of their corresponding taxonomic identifications. In this regard, sequences of *Cryptocentrus yatsui* for example, were excluded from the analyses since they shared a BIN with the gobies *Oligolepis formosanus* and *Redigobius bikolanus* (BIN:BOLD:ADB4723). The best model test for nucleotide substitution was checked for the aligned dataset using Mega X (Kumar et al., 2018) prior to further analyses. Last, phylogenetic reconstruction and genetic distances between species were computed for the dataset using the model HKY+G+I with 5,000 replicates.

Nomenclatural acts

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RESULTS

***Cryptocentrus steinhardti* n. sp**

Figures 1,2

Holotype: SMNH P-16037, Ashdod, Israel (31°44.835 N, 34°24.787 E), depth 80 m, January 8, 2018, 19:45. Col. N. Stern, Total length (TL) 81.9 mm, BOLD voucher BIM769-20.

Paratypes: SMNH P-14556 Ashdod, Israel (31°45.202 N, 34°27.036 E), depth 60 m, February 12, 2012, night. Col. N. Stern, TL 71.5, BOLD voucher BIM534-17; SMNH P-16038, Ashdod, Israel (31°45.589 N, 34°27.282 E), depth 60 m, December 11, 2016, 19:45. Col. N. Stern, TL 72.8 mm, BOLD voucher BIM770-20.

Diagnosis

A *Cryptocentrus* species with 58-61 rows of cycloid scales along the body, 20-21 pre-dorsal scales, reaching ca. 3/4 of the distance to eye (Figure 2) and 20-21 transverse rows. Scales cover abdomen and pre-pelvic region. First dorsal fin with six spines; second dorsal fin with a single spine and ten segmented rays (last one branched). Anal fin with one spine and nine segmented rays (last one branched). Pectoral fins with 14-15 rays. Pelvic fins completely united with a well-developed fraenum. Caudal fin with 17 segmented rays, 13 of them branched. Gill rakers: 7-8 on outer gill arch, two on upper arch, one at the angle, and 4-5 on lower arch. Head sensory papillae in transverse pattern.

Description

Body elongate and compressed. Upper profile of head convex. Mouth oblique. Maxilla to below a vertical from posterior margin of eye. Upper jaw with outer row of 16 caniniform teeth (eight on each side of the jaw) curved backward. Internal teeth in 1-2 rows small, pointed, curved backward. Lower jaw with outer 2-3 rows of small caniniform teeth, curved backward. Internal teeth in a single row of six large canines (three on each side of the jaw). No teeth on vomer. Tongue rounded. Gill opening moderate, to below rear edge [?? unclear] posterior preoperculum, restricted by a membrane at lower part. Any small spine at lower edge of opercle? Lower margins of opercula intersect at isthmus. Gill membrane connected to side of isthmus. Gill rakers short, 7-8 rakes on outer arch, two on upper arch, one at the angle, and 4-5 on lower arch. Anterior nostril, a tube, close above upper lip. Posterior nostril, a pore, in front of eye.

Scales: Body covered with cycloid scales, including abdomen and pre-pelvic region; 59-61 scales in longitudinal series; 20-21 mid-pre-dorsal scales reaching ca. 3/4 of the distance between dorsal fin and interorbital; 19-21 series of scales from origin of first dorsal fin to mid-abdomen. Pectoral base scalation?

Fins: First dorsal fin with six spines, third and fourth spines elongate reaching the third ray of second dorsal fin. Second dorsal fin with a single spine and ten segmented rays (last one branched).

Second dorsal fin rays long, the last three reach the caudal fin. Anal fin with one spine and nine segmented rays (last one branched). Pectoral fins with 14-15 rays. Pelvic fins completely united with a well-developed fraenum. Caudal fin with 17 segmented rays, 13 of them branched.

[description seems close to *C. fasciatus* which occurs in the Red Sea but has not been bar-coded. How do you know it is not this species? Your photo is not very clear but looks similar]

Selected meristic characteristics and proportions are given in Table 1.

Cephalic sensory system: The skin of the head of all three type specimens was severely damaged in the commercial trawl nets, hindering detection of the cephalic canal and papillae. Figure 2 presents the cephalic system of the best preserved specimen (holotype).

Nasal pores (pair) in front of eye, close to second nostril pore. Anterior interorbital pore (single) is above anterior margin of eye. Posterior interorbital pore is above 1/6 posterior of eye. Post orbital pores (pair) are above posterior margin of eye. Three pores in anterior oculoscapular canal. Posterior canal could not be detected (or does not exist). Two pre-opercular pores. Papillae on head arranged in a transversal pattern (Fig. 2). [any papillae on chin or along lower edge of lower jaw or preopercle]

Color (preserved): Body yellow with dark brown pigmentation that becomes denser on back and head. Three irregular wide darker bars on each side of body: the first bar under 1st dorsal fin and second and third bars under anterior and posterior 2nd dorsal fin. [describe colour of fins. No spots on head or fins? I can see some dark spots on the body]

Genetic analysis

Comparing the genetic sequences of both *COI* and *Cytb* with previously published data have shown great differences with any known gobies, with minimum distances of 17.41% of nucleotide diversity between the new species and *Cryptocentrus albidorsus* and *C. nigrocellatus* (BOLD vouchers GBGCA2109-13 and GBGCA1963-13, respectively) in *COI* (Table 3), and 12.8% differences between *C. cinctus* in *Cytb* (NCBI voucher MT199211). Although clustered with relatively low bootstrap values, phylogenetic analysis of available *COI* sequences has shown monophyletic relationship for *Cryptocentrus* species, including the newly described species, as well as clustering with all species of silt shrimp gobies (Thacker and Roje, 2011) from the genera *Lotilia*, *Myersina* and *Stonogobiops*, and sister-grouping with *Mahidolia* spp. (Fig. 3). Other phylogenetic studies regarding these taxa, have also related *Stonogobiops* and *Mahidolia* spp. within the *Cryptocentrus* species complex, while *Lotila* and *Myersina* were absent from their dataset (Thacker and Roje, 2011; Thacker, 2015; McCraney, Thacker and Alfaro, 2020). In fact, to the best of our knowledge this present study is the first to incorporate these genera, as well as *Psilogobius* spp. in a phylogenetic evaluation of shrimp-associated gobies.

Moreover, the cluster of reef shrimp gobies has revealed two possible misidentifications: (1) *Tomiyamichthys lanceolatus*, which may be regarded as a *Vanderhorstia* species (see Fig. 1 in Thacker, Thompson and Roje 2011), (2) and *Vanderhorstia mertensi*, which is shown here based on a single sequence from its invasive population in the Mediterranean Sea. Both putative species in this case are suspected to be a result of a wrong assignment, considering the weak diagnostic characteristics of the genus (Shibukawa and Suzuki, 2004).

Etymology

The new species is named after Michael H. Steinhardt in recognition of his immensely important contribution to the establishment and construction of the Steinhardt Museum of Natural History at Tel Aviv University, Israel.

DISCUSSION

As evident from the genetic results of this study, as well as from the findings of Thacker and Roje (2011), Thacker (2015) and McCraney et al. (2020), the generic status and validity of some shrimp-associated gobies are yet to be settled, and required further revisional examinations with more species involved. In the present study, we followed the status of the genera and species as presented by Fricke et al. (2020).

[But you have not compared your species morphologically with *C. fasciatus* or any other *Cryptocentrus* that occurs in the Red Sea. This must be done.]

Thacker et al. (2011) recognized two different clades in this group: one clade includes the genera *Amblyeleotris, Ctenogobiops* and *Vanderhorstia* and the other includes *Cryptocentrus*, *Mahidolia, Tomiyamichthys* and *Stonogobiops*. Later studies by Thacker (2015) and McCraney et al. (2020) followed this approach and assigned the genera *Amblyeleotris*, *Ctenogobiops* and *Vanderhorstia* to the lineage *Asterropteryx* and the eight other genera to the lineage "*Cryptocentrus*". The shrimp-associated gobies belonging to the *Asterropteryx* lineage are all characterized by longitudinal suborbital papillae rows (*sensu* Miller, 1986), while the species of the lineage *Cryptocentrus* are characterized by transverse rows (with the exception of *Tomiyamichthys*). *C. steinnhardti* differs from species of *Cryptocentroides* spp. by its wide gill opening, reaching to below the pre-opercular margin, while *Cryptocentroides* species are characterized by a restricted gill opening, extending to below pectoral base. *Lotilia* spp. and *Mahidolia* spp. differ from the new species by their naked nape and lower scale count along the body (less than 53 in *Lotilia* spp. and less than 40 in *Mahidolia* spp.). *Myersina* spp. differ from *C. steinhardti* by their lack of scales on mid nape. *Psilogobius* spp. differ from the new species in possessing ctenoid scales on body, at least on its posterior part. *Stonogobiops* spp. differ from the new species by their large vomerine teeth.

The genus *Cryptocentrus* currently comprises 36 species (Froese and Pauly, 2020). Allen and Randall (2011) distinguished a group of four species characterized by possessing fewer than 70 [low scale counts don't always work as a tool in damaged specimens] series of scales along the body. They included four species in this group: *C. caeruleomaculatus* (Herre, 1933), *C. cyanospilotus* Allen & Randall, 2011, *C. insignitus* (Whitley, 1956) and *C. strigilliceps* (Jordan & Seale, 1906). The group was expanded with the descriptions of *C. epakros* Allen, 2015 (Allen, 2015) and *C. altipinna* Hoese, 2019 (Hoese, 2019). None of these species have been reported to date from the Red Sea (Golani and Fricke, 2018).[but 2 of them occur within the western Indian Ocean region]

C. steinhardti differs from all other members of this group, except *C. insignitus*, in possessing cycloid scales only. It differs from *C. insignitus* in possessing a higher number of scales along the body and the presence of mid-pre-dorsal scales (Table 2). [morphologically is very like *C. fasciatus* but for scale counts]

The finding of a new Indo-Pacific invasive species in the Mediterranean prior to its discovery in the Indo-Pacific Ocean or Red Sea is an unusual event, although other such events have been documented. The snapping shrimp *Alpheus migrans* Lewinsohn & Holthuis, 1978, which belongs to an Indo-Pacific species group, was first described from the Mediterranean (Lewinsohn and Holthuis, 1978); the jellyfish *Marivagia stellata* Galil and Gershwin, 2010 was described from the Mediterranean and later on also reported from India (Galil, Kumar and Riyas, 2013); The flounder *Arnoglossus nigrofilamentosus* Fricke, Golani and Appelbaum-Golani 2017 (Fricke, et al. 2017) that is probably a Red Sea species, and the jellyfish *Rhopilema nomadica* Galil, Spanier & Ferguson, 1990 (Galil et al., 1990) was described on the basis of types from the Mediterranean although it is an Indo- Pacific species.

Finding this shrimp-associated goby, however, which is also the third such goby to be documented [so what are they? Please tell the reader. Text above is about shrimp, jellyfish and a flatfish, not gobioids. And note that you have overlooked Engin et al 2018, yet another goby] as an invasive species in the Mediterranean, raises the question of its current association with an alpheid shrimp. Since this taxon of gobies possesses either an obligatory or facultative association with shrimps (Lyons, 2013), pairing with one of the approx. twenty candidate species of alpheids shrimp from the Mediterranean and the Red Sea (Karplus, 2014) is a key factor for its survival and population establishment success in the invaded territory. Unfortunately, the catch of *C. steinhardti* in this study was not associated with any shrimp species, thus the question of its possible symbiosis in the Mediterranean remains open and required further observations.

C. steinhardti was collected at depths of 60 to 80 m during night trawls. Finding this species during the period of dark and beyond the depth limits of recreational diving, despite this possibly having been accidental, could be an additional reason for overlooking this species and its possible shrimp associates to date in its native origin.

ACKNOWLEDGMENTS

We thank Mr. O. Rittner for the photographs of the fish and to Ms. N. Paz for editing the manuscript.

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Figure 1

Holotype of *Cryptocentrus steinhardti* n.sp.

(SMNHTAU P-16037, Total length 81.9 mm

Figure 2

Cephalic sensory system of *Cryptocentrus steinhardti*.

NP -nasal pore; AIO - anterior interorbital pore; AO- anterior oculoscapular canal; PIO - posterior interorbital pore; PO - post orbital pore; POP- preopercolar pores.

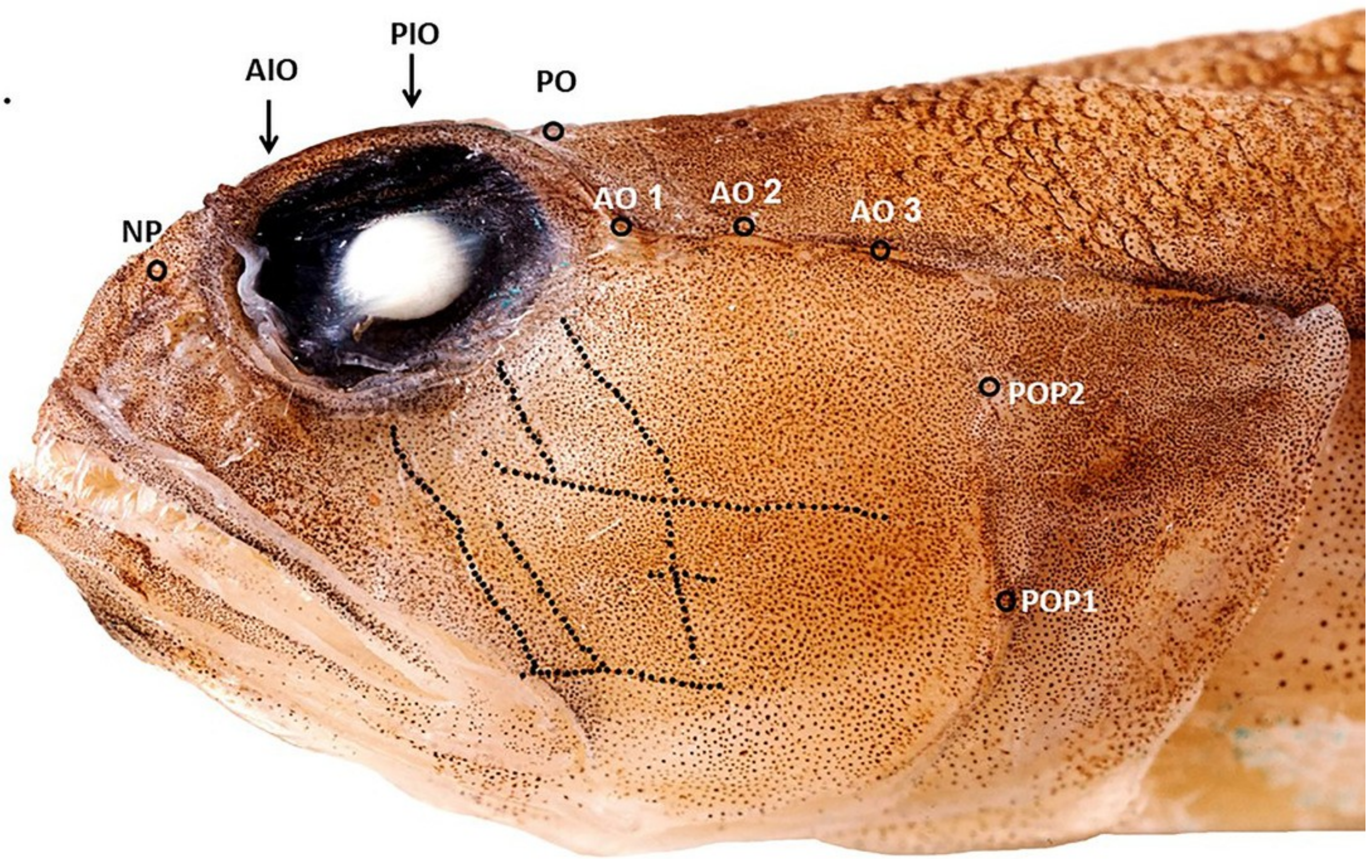

Figure 3

ML phylogenetic analysis for all available *COI* sequences of 10 genera of shrimp-gobies

Numbers above nodes are >50 bootstrap values; In red – the new species described in this study; In parentheses – number of sequences for each species. Information for this dataset is provided in Table S2.

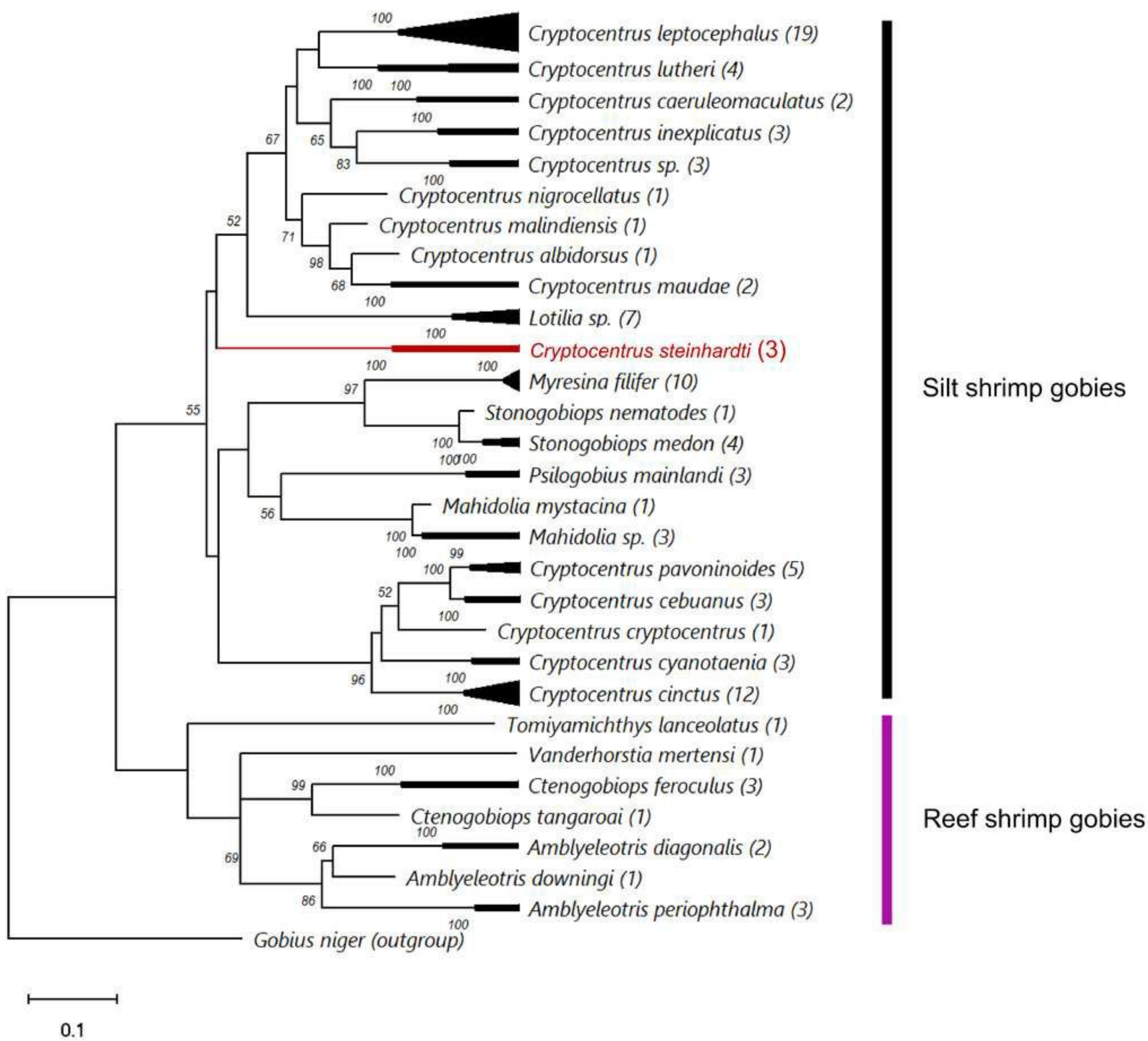

Table 1 (on next page)

Selected meristic characteristics and proportions (Measurements in mm; proportion in %)

Table 1 Selected meristic characteristics and proportions (Measurements in mm; proportion in %)

Measurements and counts	**Fish catalogue number (SMHTAU)**		
	16037	**16038**	**14556**
Total length	81.9	72.8	71.46
Standard length	58.5	51.1	49.95
Head length	14.8	14.2	12.9
Body depth	8.9	7.8	7.6
Head width	5.8	5.4	5.1
Eye diameter	3.44	4	3.6
Interorbital	1.1	1.1	1
Distance snout to origin of first dorsal fin	18	16.9	14.8
Distance snout to origin of second dorsal fin	30.2	29.2	25.8
Distance snout to origin of anal fin	33.4	30.5	28
No. of scale series along the body	61	59	60
No. of scale in transversal series	20	21	19
No. pre-dorsal scales	21	20	20
No. of spines in first dorsal fin	6	6	6
No. of spines/ segmented rays in second dorsal fin	I+10	I+10	I+10
No. of spines/ segmented rays in anal fin	I+9	I+9	I+9
No. of rays in pectoral fin (left side)	15	15	15
No. of caudal rays	17	17	17
Count of gill rakers on upper arch	2	2	2
Count of gill rakers on upper arch	5	4	4
Count of gill rakers at arch angle	1	1	1
Total count of gill rakers	8	7	7
Proportions (in %)			
Standard length of total length	71.4	70.2	69.9
Head length of standard length	25.3	27.8	25.8
Body depth of standard length	15.2	15.3	15.2
Eye diameter of head length	23.2	28.2	27.9
Interorbital space of head length	7.4	7.7	7.8
Distance snout to origin of first dorsal fin	30.8	33.1	29.6
Distance snout to origin of second dorsal fin	51.6	57.1	51.7
Distance snout to origin of anal fin	57.1	59.7	56.1

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Table 2(on next page)

Selected meristic counts of "*Cryptocentrus* low scale count" group.

[1] - cycloid scales only; [2] - anterior cycloid, posterior ctenoid. Abbreviations: LL - No. of scale series along the body; 2nd D – No. of spine and segmented rays in second dorsal fin; A - No. of spine and segmented rays in anal fin; PreD - No. pre-dorsal scales.

Table 2 Selected meristic counts of "*Cryptocentrus* low scale count" group.

Species	LL	2nd D	A	PreD-Mid line
Cryptocentrus steinhardti n.sp.	59-61[1]	I+10	I+9	20-21
Cryptocentrus cyanospilotus	49-59[2]	I+10	I+9	10-13
Cryptocentrus caeruleomaculatus	60[2]	I+10	I+9	none
Cryptocentrus strigilliceps	50-71[2]	I+10	I+9	"Predorsal midline and sides scaled to a point just before to just behind posterior preopercular margin" (Hoese, 2019)
Cryptocentrus insignitus	52-55[1]	I+12	I+11	Nape and shoulders incompletely scaled (Whitley, 1956).
Cryptocentrus altipinna	56-65[2]	I+10	I+9	none
Cryptocentrus epakros	47[2]	I+10	I+9	19

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Table 3(on next page)

Genetic relationships, in %, across all available *COI* sequences of shrimp-associated gobies

In parentheses, no. of sequences for each species; Below diagonal, pairwise genetic distances; above diagonal its standard errors. In red, values for the new species described in this study

Table 3. Genetic relationships, in %, across all available *COI* sequences of shrimp-associated gobies. In parentheses, no. of sequences for each species; Below diagonal, pairwise genetic distances; above diagonal its standard errors. In red, values for the new species described in this study

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30
1. *Cryptocentrus steinhardti* (3)		2.08	2.32	2.61	2.24	2.53	2.57	2.39	2.08	2.19	2.29	2.28	2.08	2.28	2.32	2.93	2.75	2.92	2.79	2.71	2.48	2.49	2.86	2.42	2.41	2.37	2.20	2.65	2.51	2.77
2. *Cryptocentrus albidorsus* (1)	17.41		2.03	2.66	2.41	2.45	2.45	1.92	1.88	1.69	1.43	1.32	1.65	2.55	1.94	2.73	2.29	2.80	2.64	2.78	2.28	2.37	2.54	2.43	2.43	2.49	2.39	2.60	2.74	2.66
3. *Cryptocentrus caeruleomaculatus* (2)	20.39	16.93		2.65	2.56	2.38	2.58	1.82	1.82	1.90	1.90	2.27	1.95	2.44	1.89	2.58	2.57	3.04	2.68	2.57	2.33	2.25	2.39	2.73	2.60	2.56	2.54	2.89	2.50	2.80
4. *Cryptocentrus cebuanus* (3)	22.43	22.81	22.57		2.12	1.71	1.90	2.71	2.31	2.65	2.52	2.80	2.66	0.86	2.66	3.15	2.97	3.12	2.84	2.99	2.74	2.79	2.79	2.57	2.94	2.57	2.71	3.42	3.31	3.03
5. *Cryptocentrus cinctus* (12)	19.90	22.40	23.74	17.96		1.84	2.19	2.53	2.27	2.52	2.32	2.51	2.33	1.94	2.45	2.69	2.88	2.64	2.77	2.80	2.56	2.48	2.90	2.30	2.62	2.39	2.35	2.84	2.92	3.01
6. *Cryptocentrus cryptocentrus* (1)	23.58	21.96	20.26	12.73	15.06		2.02	2.68	2.29	2.46	2.42	2.96	2.54	1.74	2.35	2.79	2.86	2.74	2.81	2.89	2.64	2.66	3.03	2.39	2.66	2.30	2.39	3.07	3.23	2.62
7. *Cryptocentrus cyanotaenia* (3)	21.70	20.93	21.01	14.13	18.15	15.55		2.44	2.22	2.63	2.28	2.67	2.50	1.72	2.64	3.28	2.58	2.93	3.17	3.06	2.63	2.47	2.51	2.44	2.70	2.93	2.95	3.27	3.19	3.06
8. *Cryptocentrus inexplicatus* (3)	21.17	15.67	14.52	24.27	22.56	24.03	20.64		1.92	1.88	2.02	1.97	2.01	2.58	1.70	2.60	2.76	2.79	2.66	2.66	2.39	2.48	2.68	2.53	2.44	2.77	2.69	2.63	2.56	2.95
9. *Cryptocentrus leptocephalus* (19)	18.06	15.49	14.12	19.96	21.07	20.31	19.26	16.44		1.60	1.85	1.88	1.74	2.11	1.94	2.70	2.72	2.81	2.79	2.56	2.21	2.22	2.49	2.48	2.55	2.50	2.36	2.66	2.58	2.75
10. *Cryptocentrus lutheri* (4)	19.19	13.26	14.37	23.30	23.24	22.76	22.73	15.28	12.59		1.75	1.78	1.80	2.46	1.90	2.75	2.70	2.80	2.73	2.91	2.29	2.49	2.77	2.40	2.39	2.47	2.39	2.72	2.68	2.53
11. *Cryptocentrus malindiensis* (1)	19.88	9.47	15.05	22.42	21.62	21.42	19.52	17.08	15.10	13.81		1.38	1.67	2.45	2.22	2.85	2.55	3.01	2.76	2.72	2.13	2.33	2.51	2.56	2.34	2.58	2.33	2.80	2.65	2.63
12. *Cryptocentrus maudae* (2)	19.63	8.22	19.12	25.53	23.88	27.21	23.54	16.29	15.11	13.67	9.03		1.88	2.58	2.25	2.94	2.61	3.12	3.05	3.02	2.48	2.61	2.74	2.67	2.48	2.89	2.72	2.94	2.84	2.85
13. *Cryptocentrus nigrocellatus* (1)	17.41	11.75	15.52	23.30	22.25	23.58	21.50	16.45	13.75	13.81	12.17	14.71		2.56	2.17	2.69	2.52	2.77	2.63	2.78	2.20	2.30	2.48	2.41	2.36	2.48	2.31	2.82	2.57	2.63
14. *Cryptocentrus pavoninoides* (5)	19.72	22.76	21.03	4.02	16.38	13.38	12.51	23.39	19.45	22.49	21.79	23.30	23.03		2.54	3.00	2.97	2.93	2.95	2.92	2.65	2.53	2.84	2.44	2.77	2.47	2.59	3.38	3.19	2.86
15. *Cryptocentrus* sp. (3)	21.18	15.59	14.83	23.99	22.68	22.05	22.74	13.48	16.60	15.85	18.71	18.53	17.81	23.43		2.75	2.75	2.79	2.76	2.63	2.71	2.49	2.58	2.51	2.58	2.23	2.32	2.63	2.61	3.14
16. *Amblyeleotris diagonalis* (2)	26.56	24.70	22.63	27.87	25.95	25.11	29.37	22.81	23.60	25.05	25.11	26.32	23.18	27.16	24.14		1.82	2.07	2.32	2.51	2.84	2.90	2.97	2.93	2.65	3.06	3.06	2.43	2.42	2.79
17. *Amblyeleotris downingi* (1)	24.11	19.72	22.00	25.38	25.54	25.56	22.12	23.35	23.09	24.11	21.58	23.12	21.05	25.73	23.93	13.69		2.07	2.34	2.35	3.00	2.99	2.87	2.88	2.73	3.44	3.33	2.99	2.58	2.77
18. *Amblyeleotris periophthalma* (3)	27.29	26.12	27.43	27.76	24.11	24.96	26.07	24.69	25.35	25.83	27.57	28.44	25.55	26.92	24.88	17.77	16.17		2.34	2.32	3.00	2.92	2.98	2.86	2.91	3.04	2.92	2.72	2.63	3.03
19. *Ctenogobiops feroculus* (3)	24.98	23.86	23.86	25.07	25.25	24.40	27.37	23.31	25.33	24.90	24.97	27.83	23.31	26.34	24.70	20.01	18.67	20.91		1.74	2.86	2.67	2.87	2.63	3.11	3.06	3.01	2.56	2.96	2.88
20. *Ctenogobiops tangaroai* (1)	24.14	25.84	22.23	26.30	27.00	25.82	27.34	23.40	22.69	26.63	24.69	26.91	24.42	26.17	23.77	21.57	19.19	19.88	13.26		2.59	2.68	2.93	2.90	2.94	2.96	3.02	2.54	2.54	2.73
21. *Lotilia* sp. (7)	22.34	20.58	19.63	24.01	24.22	24.41	23.34	20.66	19.01	20.45	18.55	21.95	19.63	24.47	23.69	26.47	27.51	28.09	26.24	23.98		2.53	2.82	2.48	2.52	2.94	2.78	2.65	2.98	2.90
22. *Mahidolia mystacina* (1)	22.23	21.44	19.12	24.47	22.84	23.03	20.03	22.32	19.76	22.36	20.39	23.42	19.89	22.44	23.04	27.00	26.77	27.58	23.86	23.58	22.96		0.74	2.50	2.31	2.44	2.41	2.72	2.89	2.74
23. *Mahidolia* sp. (3)	24.13	21.75	20.11	23.07	25.56	24.98	19.29	22.87	20.83	23.71	20.06	23.35	20.16	23.30	22.37	26.03	24.14	25.64	24.24	24.45	23.74	3.22		2.78	2.41	2.61	2.51	2.90	3.12	3.13
24. *Myresina filifer* (10)	20.47	21.99	24.89	21.79	22.04	22.36	20.46	22.29	22.36	20.53	23.42	23.82	21.23	21.34	21.91	27.56	26.25	28.03	23.39	25.91	23.53	22.02	23.05		2.65	2.00	1.99	2.92	2.88	3.06
25. *Psilogobius mainlandi* (3)	20.39	21.97	23.17	26.40	24.76	24.31	23.26	22.41	23.14	21.55	20.31	21.86	19.80	25.71	23.59	23.22	23.92	26.50	27.98	26.12	22.59	19.71	19.39	24.62		2.75	2.69	2.97	2.62	2.80
26. *Stonogobiops medon* (4)	21.46	22.81	22.40	22.30	22.33	21.86	26.43	24.36	23.27	21.73	22.74	27.04	21.46	22.33	19.86	28.38	31.05	29.38	28.77	27.24	27.90	21.07	21.95	16.64	24.55		0.86	3.14	2.74	3.14
27. *Stonogobiops nematodes* (1)	19.63	21.97	22.77	23.79	22.03	23.04	26.84	23.96	21.61	21.05	20.40	25.45	19.89	23.64	20.57	28.49	29.90	27.59	28.19	28.19	26.83	20.66	20.76	16.27	23.78	3.97		2.98	2.63	3.26
28. *Tomiyamichthys lanceolatus* (1)	23.32	23.60	25.56	31.18	26.83	29.71	29.32	22.33	24.06	25.05	25.55	26.33	25.00	31.87	23.05	20.27	25.59	24.70	23.04	22.24	24.06	24.71	25.33	26.86	26.03	29.94	28.20		2.79	2.91
29. *Vanderhorstia mertensi* (2)	21.70	23.86	21.83	28.51	28.18	30.01	28.65	22.86	24.28	24.28	23.85	25.73	22.50	28.11	22.86	21.04	22.41	23.03	26.12	21.43	27.50	26.70	26.76	25.60	23.31	24.62	23.59	24.99		3.04
30. *Gobius niger* (Outgroup)	25.33	23.35	23.76	25.77	28.94	23.62	25.99	25.62	24.28	22.10	23.06	25.21	23.35	26.20	29.47	24.47	24.75	27.40	26.21	24.47	26.22	24.76	26.65	28.98	25.14	29.05	30.22	26.22	27.11	

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