

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

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**Keywords:** Integrative taxonomy, Lessepsian migration, Shrimp-goby, New species,  
Mediterranean Sea

**ABSTRACT**

A new species of shrimp-goby was collected at depths of 60-80 m, off the southern Israeli  
Mediterranean coast and described based on three specimens. A unique 'DNA barcoding'  
signature (mtDNA *COI* and *Cytb*) revealed that it differs from any other previously barcoded  
goby species clustered phylogenetically with the shrimp-gobies group, in which *Cryptocentrus* is  
the most speciose genus. A morphological study supported the assignment of the goby to  
*Cryptocentrus* and differentiated the new species from its congeners. The species is described  
here as *Cryptocentrus steinhardtii* n. sp. However, the present phylogenetic analysis demonstrates

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39 | a paraphyly of *Cryptocentrus* and emphasizes the need for revision of the genus based on  
40 | integrating morphological and genetic characteristics.  
41 | This finding constitutes the third record of an invasive shrimp-goby in the Mediterranean Sea,  
42 | raising an intriguing ecological issue regarding the possible formation of a fish-shrimp symbiosis  
43 | in a newly invaded territory. Describing an alien tropical species in the Mediterranean prior to  
44 | their discovery in the native distribution is an unusual event, although not the first such case.  
45 | Several similar examples are provided below.

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## 55 INTRODUCTION

56 Since the opening of the Suez Canal in 1869 more than 400 multicellular non-native species of  
57 Red Sea origin, including [ca. 100 fish species](#), have been found along the Israeli Mediterranean  
58 coast (Galil et al., 2020). [Among](#) this diverse invasive fauna [there are](#) two species [of](#) shrimp-  
59 gobies: *Vanderhorstia mertensi* Klausewitz, 1974 (Goren, [et al.](#), 2013) and *Cryptocentrus*  
60 *caeruleopunctatus* (Rüppell, 1830) (Rothman [&](#) Goren, 2015). These species are part of a group  
61 of near-reef fishes that inhabit sandy and silty habitats and display a remarkable mutualism with  
62 burrowing alpheid shrimps, exchanging tunnel construction capabilities and sentinel services  
63 (Karplus [&](#) Thompson, 2011). Common throughout the tropics, this unique fish-shrimp  
64 association is documented from over a 100 fish species that belong to eleven valid genera of  
65 gobies: *Amblyeleotris* Bleeker 1874; *Cryptocentrus* Valenciennes (ex Ehrenberg) in Cuvier &  
66 Valenciennes 1837; *Cryptocentroides* Popta 1922; *Ctenogobiops* Smith 1959; *Lotilia* Klausewitz  
67 1960; *Mahidolia* Smith 1932; *Myersina* Herre 1934; *Psilogobius* Baldwin 1972; *Stonogobiops*  
68 Polunin & Lubbock 1977; *Tomiyamichthys* Smith 1956 and *Vanderhorstia* Smith 1949 (Karplus,  
69 2014; Ray, [et al.](#), 2018). An additional genus, *Flabelligobius* Smith 1956 is considered a  
70 synonym of *Tomiyamichthys* (Hoese et al., 2016; Fricke [&](#) Eschmeyer, 2020).  
71 During cruises to sample the benthic biota off Ashdod (southern Israel, [Mediterranean coast](#)),  
72 three specimens of an unknown shrimp-goby were collected at depths of 60 to 80 m by a bottom  
73 trawl net. [An integrated study using both traditional practices and molecular taxonomy indicated](#)  
74 [that these fish belong to an undescribed species of \*Cryptocentrus\* genus.](#)

## 75 MATERIALS & METHODS

76 Fish specimens were collected from the southern coast of the Israeli Mediterranean by [a](#)  
77 commercial 240 hp [bottom trawler](#). The fish were preserved in 70% alcohol and stored at the fish

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100 collection of The Steinhardt Museum of Natural History, Tel-Aviv University (SMNHTAU).  
101 Muscle tissue samples were taken from fresh specimens for genetic analyses and preserved in  
102 96% alcohol.

103 [For counts and measurements of meristic characteristics we followed Allen et al. \(2018\).](#)

#### 104 Genetic analysis

105 Total genomic DNA was extracted from the three [specimens](#) using a micro tissue genomic DNA  
106 isolation kit following the manufacturer's protocol (AMBRD Laboratories, Turkey). Next, [ca. 50](#)  
107 ng of template DNA was used to amplify a 651 bp fragment of the mitochondrial cytochrome c  
108 oxidase subunit I gene (*COI*) and 467 bp of the mitochondrial Cytochrome b (*Cytb*). Primers and  
109 PCR reactions are detailed in supplementary table S1. The contiguous sequences of both genes,  
110 including measurements, photos and its trace files, were uploaded to BOLD system at  
111 [www.v4.boldsystems.org](#) under the BIM project (Biota of the Israeli Mediterranean) with BOLD  
112 Sample IDs: [BIM769-20](#) for the holotype and [BIM534-17](#) and [BIM770-20](#) for the two paratypes.

113 [Due to the absence of \*Cytb\* sequences for other shrimp-associated gobies, only the \*COI\* gene was](#)  
114 [used to explore the phylogeny of this group. For this purpose, 107](#) previously published  
115 sequences belonging to ten putative genera were mined from BOLD and NCBI [and aligned using](#)  
116 [ClustalW](#), with a single sequence of *Gobius niger* as an outgroup (Supplementary Table S2). The  
117 genetic vouchers were included in the dataset only if they indicated a precise information on the  
118 sampling localities and an unambiguous association with a Barcode Index Number (BIN) of their  
119 corresponding taxonomic identifications. [Sequences of \*Cryptocentrus yatsui\*, for example, were](#)  
120 excluded from the analyses since they shared a BIN with the gobies *Oligolepis formosanus* and  
121 *Redigobius bikolanus* ([BIN:BOLD:ADB4723](#)).

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129 | [The best model test for nucleotide substitution was verified for the aligned dataset using](#)  
130 | [jModelTest ver. 2.1.10](#) (Darriba et al., 2012) [under the Akaike Information Criterion \(AIC\).](#)  
131 | [Finally, Maximum Likelihood phylogenetic reconstruction was computed using the online](#)  
132 | [program NGPhylogeny.fr](#) (Lemoine et al., 2019) [and the model HKY85+G+I with 500](#)  
133 | [replicates.](#)

#### 134 | **Nomenclatural acts**

135 | The electronic version of this article in Portable Document Format (PDF) will represent a  
136 | published work according to the International Commission on Zoological Nomenclature (ICZN),  
137 | and hence the new name contained in the electronic version is effectively published under that  
138 | Code from the electronic edition alone. This published work and the nomenclatural acts it  
139 | contains have been registered in ZooBank, the online registration system for the ICZN. The  
140 | ZooBank LSIDs (Life Science Identifiers) can be resolved and the associated information viewed  
141 | through any standard web browser by appending the LSID to the prefix <http://zoobank.org/>. The  
142 | LSID for this publication is: [urn:lsid:zoobank.org:pub:B5279F4D-F5BC-454D-9ED8-](http://urn:lsid:zoobank.org:pub:B5279F4D-F5BC-454D-9ED8-3E2A13C69EAE)  
143 | [3E2A13C69EAE](http://urn:lsid:zoobank.org:pub:B5279F4D-F5BC-454D-9ED8-3E2A13C69EAE). The online version of this work is archived and available from the following  
144 | digital repositories: PeerJ, PubMed Central, and CLOCKSS.

#### 145 | **RESULTS**

146 | *Cryptocentrus steinhardti* n. sp.

147 | [Steinhardt's shrimp-goby](#)

148 | **Figures 1, 2**

149 | **Holotype:** SMNH P-16037 [\[BOLD voucher BIM769-20\]](#), 81.9 mm Total length (TL), Ashdod,  
150 | Israel (31°44.835 N, 34°24.787 E), depth 80 m, 8 [January](#), 2018, 19:45, coll. N. Stern.

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165 Paratypes: SMNH P-14556 [BOLD voucher BIM534-17], 71.5 mm TL, Ashdod, Israel  
 166 (31°45.202 N, 34°27.036 E), depth 60 m, 12 February 2012, night, coll. N. Stern; SMNH P-  
 167 16038 [BOLD voucher BIM770-20], 72.8 mm TL, Ashdod, Israel (31°45.589 N, 34°27.282 E),  
 168 depth 60 m, 11 December 2016, 19:45, coll. N. Stern.

# 169 **Diagnosis**

170 A *Cryptocentrus* species with 59-61 rows of cycloid scales along the body, 20-21 predorsal  
 171 scales, reaching ca. 3/4 of the distance to eye (Figure 2) and 19-21 transverse rows. Scales cover  
 172 abdomen and prepelvic region. No scales on pectoral-fin base. First dorsal fin with six spines;  
 173 second dorsal fin with a single spine and 10-11 segmented rays (last one branched). Anal fin  
 174 with one spine and 9-10 segmented rays (last one branched). Pectoral fins with 14-15 rays.  
 175 Pelvic fins completely united with a well-developed fraenum. Caudal fin with 17 segmented  
 176 rays, 13 of them branched.

177 Gill rakers: 10-11 on outer gill arch, two on upper limb, one at the angle, and 7-8 on lower limb.  
 178 Head sensory papillae in transverse pattern (*sensu* Miller, 1986).

# 179 **Description**

180 Body elongate and compressed. Upper profile of head convex. Mouth oblique. Maxilla extending  
 181 to below a vertical from posterior margin of eye. Upper jaw with outer row of 16 caniniform  
 182 teeth (eight on each side of the jaw) curved backward. Teeth in inner 1-2 rows small, pointed,  
 183 curved backward. Lower jaw with outer 2-3 rows of small caniniform teeth, curved backward.  
 184 Internal teeth in a single row of six large canines (three on each side of the jaw). No teeth on  
 185 vomer. Tongue rounded.

186 Gill opening moderate, extending forward to below posterior margin of preopercle, restricted by  
 187 a membrane on lower part (Figure 2). The membranes of left and right sides are completely

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214 | separate. Lower margin of opercle intersect at isthmus. Gill membrane connected to side of  
215 | isthmus. Gill rakers short, 10-11 rakes on outer arch, two of them on upper jimb, one at the  
216 | angle, and 7-8 on lower jimb. Anterior nostril, a tube, close above upper lip. Posterior nostril, a  
217 | pore, in front of eye.

218 | Scales: Body covered with cycloid scales, including abdomen and prepelvic region; 59-61 scales  
219 | in longitudinal series; 20-21 mid-predorsal scales reaching ca. 3/4 of the distance between dorsal  
220 | fin and interorbital; 19-21 series of scales from origin of first dorsal fin to mid-abdomen.

221 | Fins: First dorsal fin with six spines, third and fourth spines elongate reaching the third ray of  
222 | second dorsal fin. Second dorsal fin with a single spine and 10-11 segmented rays (last one  
223 | branched). Rays long, the last three reach the caudal fin. Anal fin with one spine and 9-10  
224 | segmented rays (last one branched). Pectoral fins with 14-15 rays. Pelvic fins completely united  
225 | with a well-developed fraenum. Caudal fin with 17 segmented rays, 13 of them branched.

226 | Selected meristic characteristics and proportions are given in Table 1.

227 | Cephalic sensory system: The skin of the head of all three type specimens was severely  
228 | damaged in the commercial trawl net, hindering detection of the cephalic canal and papillae.

229 | Figure 2 presents the cephalic system of the best preserved specimen (holotype).

230 | Nasal pores (pair) in front of eye, close to second nostril pore. Anterior interorbital pore (single)  
231 | is above anterior margin of eye. Posterior interorbital pore is above 1/6 posterior of eye.

232 | Postorbital pores (pair) are above posterior margin of eye. Three pores in anterior oculoscapular  
233 | canal. Posterior canal could not be detected (or does not exist). Two preopercular pores. Papillae  
234 | on head arranged in a transverse pattern (Figure 2).

235 | Color (preserved): Body yellow with dark brown pigmentation that becomes denser on back and  
236 | head. Three irregular wide darker bars on each side of body: the first bar under 1<sup>st</sup> dorsal fin and

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251 second and third bars under anterior and posterior parts of 2<sup>nd</sup> dorsal fin. Chin with dark dense  
252 pigmentation. Distal half of first dorsal and anal fins' membranes are black.

### 253 Genetic analysis

254 Comparing the genetic sequences of both *COI* and *Cytb* with previously published data have  
255 shown great differences with any known gobies, with minimum distances in *COI* of 18.77% and  
256 18.54% of nucleotide diversity between the new species and *Cryptocentrus albidorsus* and  
257 *Stonogobiops xanthorhinica* (BOLD vouchers GBGCA2109-13 and GBGCA2095-13,  
258 respectively) (Table 2), and 12.85% in *Cytb* differences between *C. cinctus* (NCBI voucher  
259 MT199211).

260 Phylogenetic reconstruction of all available shrimp-associated gobies, incorporating for the first  
261 time representatives from the genera *Lotilia*, *Myersina* and *Psilogobius*, has revealed a basal  
262 separation between two groups of shrimp-gobies, in accordance with the suggestion by Thacker  
263 & Roje (2011): silt shrimp-gobies, which include our newly described species, and reef shrimp-  
264 gobies. Nevertheless, the poorly supported internal nodes within the tree emphasizes a systematic  
265 conundrum within this group (Figure 3). *Cryptocentrus steinhardtii* shares a branch with four  
266 other genera: *Mahidolia*, *Myersina*, *Psilogobius* and *Stonogobiops*, with no support for its genus  
267 assignment in terms of mtDNA phylogeny (Figure 3).

268 Finally, the cluster of reef shrimp-gobies reveals two possible misidentifications: (1)  
269 *Tomiamichthys lanceolatus*, which may be regarded as a *Vanderhorstia* species (see Figure 1 in  
270 Thacker et al., 2011), (2) and *Vanderhorstia mertensi*, which is shown here based on a single  
271 sequence from its invasive population in the Mediterranean Sea. Both putative species in this  
272 case are suspected to be the result of a wrong assignment, considering the weak diagnostic  
273 characteristics of the genus (Shibukawa & Suzuki, 2004).

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Comment [6]: Looking at the tree (Fig.3), I see that new species shares a branch with *Lotilia* and "Cryptocentrus" whereas these 4 genera share branch with true *Cryptocentrus*. However, with low bootstrap support, and as correctly noted below a relationship of the new species is provisional.

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## 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 & 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 and genetic markers. In the present study, we followed the status of the genera and species as presented by Fricke et al. (2020).

The Red Sea is the main origin for over 400 alien species reported from the Mediterranean coast of Israel, among them five goby species (Galil et al., 2020). In the Red Sea the number of shrimp-goby species is 23, as featuring in the latest checklist of the Red Sea fishes (Golani & Fricke, 2018). These species belong to eight genera: *Amblyeleotris* (Bleeker 1874, (6 spp.), *Cryptocentroides* (1 sp.), *Cryptocentrus* (4 spp.), *Ctenogobiops* (3 spp.), *Lotilia* (1 sp.), *Psilogobius* (1 sp.), *Tomiyamichthys* (3 spp.) and *Vanderhorstia* (4 spp.). *Cryptocentrus steinhardtii* differs from the species of the genera *Vanderhorstia*, *Ctenogobiops*, *Cryptocentroides* and *Tomiyamichthys* in possessing transvers sensory papillae on the head vs. longitudinal sensory papillae on the head (Larson & Murdy, 2001; Bogorodsky et al., 2011). The Red Sea species *Cryptocentroides arabicus* (Gmelin, 1789), which is superficially similar to *C. steinhardtii*, differs from the new species in possessing longitudinal sensory papillae on the head. In addition, *C. arabicus* differs in possessing a thin dermal crest on top of the head in front of the dorsal fin (Larson & Murdy, 2001) and a restricted gill opening, extending to below

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376 pectoral-fin base (Akihito et al., 1984) vs. no a dermal crest on top of the head and wide gill  
 377 opening, reaching to below the preopercular margin, in *C. steinhardtii* (Fig. 2).  
 378 *Psilogobius* spp. differ from the new species in possessing ctenoid scales on the posterior part of  
 379 the body, lacking preopercular pores (Watson & Lachner, 1985) and the presence of thin vertical  
 380 white lines on side of the body (Larson & Murdy, 2001).  
 381 *Cryptocentrus steinhardtii* differs from the species of *Amblyeleotris* in possessing pelvic fins  
 382 completely united with a well-developed fraenum vs. completely separated pelvic fins in  
 383 *Amblyeleotris* (Hoesel, 1986).  
 384 *Lotilia* spp. differ from the new species in possessing naked predorsal midline and lower scale  
 385 count along the body (fewer than 53 in *Lotilia* spp. (Shibukawa et al., 2012)).  
 386 Thacker et al. (2011) recognized two different clades in this group: one clade contains the genera  
 387 *Amblyeleotris*, *Ctenogobiops* and *Vanderhorstia* and the other contains *Cryptocentrus*,  
 388 *Mahidolia*, and *Stonogobiops*. McCraney et al. (2020) assigned the species of the genera  
 389 *Amblyeleotris*, *Ctenogobiops*, *Vanderhorstia* and *Tomiyamichthys latruncularius* (Klauewitz,  
 390 1974) to the clade *Asterropteryx* (together with non-shrimp associated genera *Asterropteryx* and  
 391 *Gladiogobius*) and the other shrimp-goby genera, including *Tomiyamichthys oni* (Tomiyama,  
 392 1936) to the clade “*Cryptocentrus*”. Hoesel & Larson (2004) suggested, after examining 28  
 393 species of *Cryptocentrus*, that this genus is not monophyletic. This approach was supported by  
 394 the generic dendrogram of McCraney et al. (2020, Fig. 6), although their “*Cryptocentrus*” clade  
 395 contains only ten species of *Cryptocentrus*. Our findings also show that the “*Cryptocentrus*” is a  
 396 polyphyletic group (Fig. 3) and includes species of the genera *Stonogobiops*, *Mahidolia*,  
 397 *Myersina*, *Psilogobius* and *Lotilia*. Based on present phylogenetic analysis (Fig. 3) in case of  
 398 splitting of the genus *Cryptocentrus* into two groups, species which closely related to the type

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**Comment [8]:** In their Fig.6 I see Vanderhorstia ornatissima and Tomiyamichthys lanceolatus. I cannot trust to Thacker's data because her ID always contained mistakes (another example wrong ID of cardinalfishes). I almost believe her ID of *Cryptocentrus caeruleomaculatus* is wrong.

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**Comment [9]:** In my knowledge, a lineage is related to species level and clade is group of lineages/species.

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species *C. cryptocentrus* (Valenciennes, 1837) can apply to the true *Cryptocentrus* whereas another generic name will require for the remaining group of “*Cryptocentrus*” species, with unclear position of *Lotilia* in between *C. steinhardti* and rest of “*Cryptocentrus*”. Thus, the relationship of the new species among its congeners and closely-related genera should be further studied. The differences between the new species and the species of *Psilogobius* and *Lotilia* are described above. *Mahidolia* spp. differ from *C. steinhardti* in having fewer than 45 scales along the body (vs. more than 55) and in the absence of an anterior interorbital pore vs. the presence of an interorbital pore (Hoese, 1986). *Myersina* spp. differ from *C. steinhardti* in lacking scales on mid nape (Winterbottom, 2002). *Stonogobiops* spp. differ from the new species in having large vomerine teeth (Winterbottom, 2002) vs. none in the new species.

In light of the all mentioned above morphological characteristics, we allocate the new species in the genus *Cryptocentrus*, despite the phylogenetic tree that has allegedly positioned it within a different clade of genera (Fig. 3). This genus currently comprises 36 species (Froese & Pauly, 2020). Allen & Randall (2011) distinguished a group of four species characterized by possessing fewer than 70 scales in longitudinal series along the body. They included the following four species in this group: *C. caeruleomaculatus* (Herre, 1933), *C. cyanospilotus* Allen & Randall, 2011, *C. insignitus* (Whitley, 1956) and *C. strigiliceps* (Jordan & Seale, 1906). The group was then expanded with the descriptions of *C. epakros* Allen, 2015 (Allen, 2015) and *C. altipinna* Hoese, 2019 (Hoese, 2019). Two of these species, *C. caeruleomaculatus* and *C. strigiliceps* are known from the western Indian Ocean (Froese & Pauly, 2020), but none of these have been reported to date from the Red Sea (Golani & Fricke, 2018).

*Cryptocentrus steinhardti* differs from all other members of this group, except *C. insignitus* and *C. epakros* in possessing cycloid scales only. It differs from *C. insignitus* in possessing a higher

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**Comment [10]:** I already raised this moment. Authors answered that they “does not attempt to revise the *Cryptocentrus* complex”. Definitely purpose of article to show that *C.reinhardtii* is a separate genetic lineage related to a distinct (new) species. I meant another hence added two sentences in form of proposal. Because, as noted also in previous studies, *Cryptocentrus* seems is paraphyletic and one group is true genus and another becomes is another unnamed genus (in this case the name *Cryptocentrus* for new species is preliminary/provisional). Moreover, the group of “*Cryptocentrus*” from *C.leptocephalus* to *C.reinhardtii* is paraphyletic with inclusion of *Lotilia*. Bootstrap support for *Lotilia* is low so impossible to say about its position, and inclusion of *Cryptocentroides* (e.g. *C. arabicus*) can help to answer. I.e. I interpreted Fig.3 as can see any reader. Authors can delete my sentences or to correct them, but I suggest to comment what was done in analysis.

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**Comment [12]:** I recommend to cite here Catalog of fishes instead Fishbase.

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**Comment [13]:** Best to provide original data of records than compiled data in Fishbase

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number of scales along the body (50-55 vs. 59-61), the presence of mid predorsal scale (Table 3) and no ocellus on first dorsal fin. *Cryptocentrus epakros* differs from *C. steinhardti* by possessing lower number of scales along the body (47 vs. 59-61) and fewer transverse scale series (12 vs. 19-21, Table 3).

According to Golani & Fricke (2018) four species of *Cryptocentrus* have been reported from the Red Sea: *Cryptocentrus caeruleopunctatus* (Rüppell, 1830, *Cryptocentrus cryptocentrus* (Valenciennes, 1837), *Cryptocentrus fasciatus* (Playfair, 1867) and *Cryptocentrus lutheri* (Klausewitz, 1960. *Cryptocentrus steinhardti* differs from these four species in lower scale count along the body (59-61 vs. 77-108), lower transverse scale series (19-21 vs. 29-43) and lower number of gill rakers on the lower limb of first arch (8-9 vs. 11-13, including angle's raker; Table 4).

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 & Holthuis, 1978); the jellyfish *Marivagia stellata* Galil & Gershwin, 2010 was described from the Mediterranean and later on also reported from India (Galil et al., 2013); the flounder *Arnoglossus nigrofilamentosus* Fricke, Golani & Appelbaum-Golani, 2017 (Fricke et al., 2017) that is probably a Red Sea species; the goby *Hazeus ingressus* Engin, Larson & Irmak, 2018, which belongs to an Indo-Pacific genus, was discovered in the Mediterranean (Engin et al., 2018) and later was found in Abu Dabab, Egypt, Red Sea (Bogorodsky, pers. comm.); 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.

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491 Finding this shrimp-associated goby, however, which is also the third such goby to be  
 492 documented as an invasive species in the Mediterranean ([after \*Vanderhorstia mertensi\* and](#)  
 493 [Cryptocentrus caeruleopunctatus](#)), raises the question of its [possible symbiosis](#) with an alpheid  
 494 shrimp. Since this taxon of gobies possesses either an obligatory or facultative association with  
 495 shrimps (Lyons, 2013), [its](#) pairing with one of the [ca.](#) twenty candidate species of alpheids  
 496 shrimps from the Mediterranean and the Red Sea (Karplus, 2014) [can be](#) a key factor for its  
 497 survival and population establishment success in the invaded territory. Unfortunately, [as](#) the  
 498 catch of *C. steinhardti* in this study was not associated with any shrimp species, [the](#) question of  
 499 its possible symbiosis in the Mediterranean remains open and [in need for](#) further observations.

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500 [Last](#), [Cryptocentrus](#), [steinhardti](#) was collected [during the night and at depths of 60 to 80 m](#),  
 501 Finding this species during the period of dark and [below](#) the depth limits of recreational diving,  
 502 [could](#) be an additional reason for overlooking this species and its possible shrimp associates [in](#) its  
 503 native origin.

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## 504 ACKNOWLEDGMENTS

505 We thank Mr. O. Rittner for the photographs of the fish and to Ms. N. Paz for editing the  
 506 manuscript. [We also thank B. Rinkevich \(IOLR\) and his dedicated staff for long-time assistance](#)  
 507 [in the molecular analyses.](#)

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**Comment [15]:** I will be grateful if authors can add my name to acknowledgments. I spent several days for review.

## 508 REFERENCES

509 [Allen GR. 2015. Descriptions of two new species of shrimpgobies \(Gobiidae: \*Cryptocentrus\* and](#)  
 510 [Tomiyamichthys\) from Papua New Guinea. \*Journal of the Ocean Sciences Foundation\*, 16:67–](#)  
 511 [81.](#)

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512 [Allen GR, Randall JE. 2011. Two new species of shrimp-associated gobies \(Gobiidae:](#)  
 513 [Cryptocentrus\) from the Western Pacific. \*Marine Biology Research\*, 7\(6\):554–564. doi:](#)

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10.1080/17451000.2010.530545.

Allen GR, Erdmann MV, Brooks WM. 2018. A new species of *Tomiyamichthys shrimpgoby* (Pisces: Gobiidae) from Papua New Guinea. *Journal of the Ocean Science Foundation* 31:38-46.

Akihito Prince, Hasayoshi M, Yoshino T. 1984. Suborder Gobioidae. *The fishes of the Japanese Archipelago*. In: Masuda H, Amaoka K, Muzik K, Uyeno TT, Yoshimo T (eds), 236-289, Pls. 235-355.

Bogorodsky SV, Kovačić M, Randall JE. 2011. A new species and three new records of gobiid fishes from the Red Sea. *Cybium* 35(3):213-222.

Bogorodsky SV, Suzuki T, Mal AO. 2016. Description of a new species of *Priolepis* (Perciformes: Gobiidae) from the Red Sea, a new record of *Priolepis compita*, and a distributional range extension of *Trimma fishelsoni*. *Zootaxa* 4150(2):168-184. doi: 10.11646/zootaxa.4150.2.5.

Darriba D, Taboada GL, Doallo R, Posada D. 2012. iModelTest 2: more models, new heuristics and parallel computing. *Nature Methods* 9(8):772. doi: 10.1038/nmeth.2109.

Engin S, Larson H, Irmak E. 2018. *Hazeus ingressus* sp. nov. a new goby species (Perciformes: Gobiidae) and a new invasion in the Mediterranean Sea. *Mediterranean Marine Science* 19(2):316-325. doi: 10.12681/mms.14336.

Fricke R, Eschmeyer WN, van der Laan LR. 2020. *Eschmeyer's Catalog of Fishes: Genera, Species, References*.

Fricke R, Golani D, Appelbaum-Golani B. 2017. *Arnoglossus nigrofilamentosus* n. sp., a new species of flounder (Teleostei: Bothidae) from off the Mediterranean coast of Israel, probably a new case of Lessepsian migration. *Scientia Marina* 81(4):257-265. doi:

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10.3989/scimar.04684.07a.

Froese R, Pauly D. 2020. *Fishbase. World Wide Web electronic publication., FishBase.*

Galil BS, Spanier E, Ferguson WW. 1990. The Scyphomedusae of the Mediterranean coast of Israel, including two Lessepsian migrants new to the Mediterranean. *Zoologische mededelingen* 64(7):95–105.

Galil BS., Mienis HK., Hoffman R, Goren M. 2020. Non-indigenous species along the Israeli Mediterranean coast: tally, policy, outlook. *Hydrobiologia* doi: 10.1007/s10750-020-04420-w.

Galil BS, Kumar BA, Riyas AJ. 2013. *Marivagia stellata* Galil and Gershwin, 2010 (Scyphozoa: Rhizostomeae: Cepheidae), found off the coast of Kerala, India. *BioInvasions Records* 2(4):317–318 doi: 10.3391/bir.2013.2.4.09.

Golani D, Fricke R. 2018. Checklist of the Red Sea Fishes with delineation of the Gulf of Suez, Gulf of Aqaba, endemism and Lessepsian migrants. *Zootaxa* 4509(1):1-215 doi: 10.11646/zootaxa.4509.1.1.

Goren M. 1979. The Gobiinae of the Red Sea (Pisces:Gobiidae). *Senckenbergiana biologica* 60:13-64.

Goren M, Stern N, Galil BS. 2013. Bridging the gap: First record of Mertens' prawn-goby *Vanderhorstia mertensi* in Israel. *Marine Biodiversity Records* 6 doi: 10.1017/S1755267213000419.

Herre AWCT. 1933. Twelve new Philippine fishes. *Copeia* (1):17-25.

Hoese DF. 1986. Family No. 240 Gobiidae. In: Smith MM, Heemstra PE (Eds.), *Smith's Sea Fishes*. Macmillan South Africa, Johannesburg, South Africa, pp. 774–807.

Hoese DF. 2019. A review of the *Cryptocentrus strigilliceus* complex (Teleostei: Gobiidae), with

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816 description of a new species. *Journal of the Ocean Science Foundation* 32:23–38 doi:  
817 10.5281/zenodo.2539733.

818 Hoese DF, Shibukawa K, Johnson JW. 2016. Description of a new species of *Tomiyamichthys*  
819 from Australia with a discussion of the generic name. *Zootaxa* 4079(5):582–594 doi:  
820 10.11646/zootaxa.4079.5.5.

821 Karplus I. 2014. *Symbiosis in fishes: the biology of interspecific partnerships*. John Wiley &  
822 Sons doi: 10.1002/9781118759769.

823 Karplus I, Thompson AR. 2011. The partnership between gobiid fishes and burrowing alpheid  
824 shrimps. In: *The Biology of Gobies*, pp. 559–607 doi: 10.1201/b11397-29.

825 Kumar S. et al. 2018. MEGA X: molecular evolutionary genetics analysis across computing  
826 platforms. *Molecular biology and evolution* 35(6):1547–1549.

827 Larson HK, Hoese DF. 2004. Description of a new species of *Cryptocentrus* (Teleostei:  
828 Gobiidae) from northern Australia, with comments on the genus. *Beagle: Records of the*  
829 *Museums and Art Galleries of the Northern Territory* 20:167–174.

830 Larson HK, Murdy EO. 2001. Suborder Gobioidae. In: Carpenter KE, Niem V.H. (Eds.), *Species*  
831 *identification guide for fishery purposes. The living marine resources of the western central*  
832 *Pacific. Bony fishes part 4 (Labridae to Latimeriidae), estuarine crocodiles, sea turtles, sea*  
833 *snakes and marine mammals*. FAO, Rome. v. 6: iii–v; 3381–4218, Pls. I–XIX.

834 Lemoine F, Correia D, Lefort V, Doppelt-Azeroual O, Mareuil F, Cohen-Boulakia S, Gascuel O.  
835 2019. NGPhylogeny.fr: New generation phylogenetic services for non-specialists. *Nucleic*  
836 *Acids Research* 47(W1):W260–W265. Doi: 10.1093/nar/gkz303.

837 Lewinsohn C, Holthuis LB. 1978. On a new species of *Alpheus* (Crustacea Decapoda, Natantia)  
838 from the eastern Mediterranean. *Zoologische Mededelingen* 53:75–82.

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Lyons PJ. 2013. The benefit of obligate versus facultative strategies in a shrimp-goby mutualism. *Behavioral Ecology and Sociobiology* 67(5):737-745. doi: 10.1007/s00265-013-1497-6.

McCraney WT, Thacker CE, Alfaro ME. 2020. Supermatrix phylogeny resolves goby lineages and reveals unstable root of Gobiaria. *Molecular Phylogenetics and Evolution* 151:106862. doi: 10.1016/j.ympev.2020.106862.

Miller PJ. 1986. Gobiidae. In: Whitehead PJP, Bauchot M-L, Hureau J-C, Nielsen JG, Tortonese E (Eds.) *Fishes of the North-eastern Atlantic and the Mediterranean*.

Polunin NV, Lubbock R. 1977. Prawn-associated gobies (Teleostei: Gobiidae) from the Seychelles, Western Indian Ocean: systematics and ecology. *Journal of Zoology* 183(1):63-101.

Randall JE, Goren M. 1993. A review of the gobioid fishes of the Maldives. *Ichthyological Bulletin of J.L.B. Smith Institute of Ichthyology* 58:1-39.

Ray D, Mohapatra A, Larson HK. 2018. First record of the shrimp-associate gobiid fish *Cryptocentrus filifer* (Valenciennes) from the Indian coast. *Indian Journal of Geo-Marine Sciences* 47(4):798-801.

Rothman SBS, Goren M. 2015. First record of the Red Sea shrimp-goby *Cryptocentrus caeruleopunctatus* in the Mediterranean Sea. *Marine Biodiversity Records* 8. doi: 10.1017/S1755267215001323.

Shibukawa K, Suzuki T. 2004. *Vanderhorstia papilio*, a new shrimp-associated goby from the Ryukyu Islands, Japan (Perciformes: Gobiidae: Gobiinae), with comments on the limits of the genus. *Ichthyological Research* 51(2):113-119. doi: 10.1007/s10228-004-0206-x.

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1063 Shibukawa K, Suzuki T, Senou H. 2012. Review of the shrimp-associated goby genus *Lotilia*  
1064 (*Actinopterygii*: *Perciformes*: *Gobiidae*), with description of a new species from the West  
1065 Pacific. *Zootaxa* 3362:54-64.

1066 Thacker CE. 2015. Biogeography of goby lineages (*Gobiiformes*: *Gobioidei*): Origin, invasions  
1067 and extinction throughout the Cenozoic. *Journal of Biogeography* 42(9):1615–1625. doi:  
1068 10.1111/jbi.12545.

1069 Thacker CE, Roje DM. 2011. Phylogeny of Gobiidae and identification of gobiid lineages.  
1070 *Systematics and Biodiversity* 9(4):329–347. doi: 10.1080/14772000.2011.629011.

1071 Thacker CE, Thompson AR, Roje DM. 2011. Phylogeny and evolution of Indo-Pacific shrimp-  
1072 associated gobies (*Gobiiformes*: *Gobiidae*). *Molecular Phylogenetics and Evolution*  
1073 59(1):168–176. doi: 10.1016/j.ympev.2011.02.007.

1074 Watson RE, Lachner EA. 1985. A new species of *Psilogobius* from the Indo-Pacific with a  
1075 redescription of *Psilogobius mainlandi* (Pisces: *Gobiidae*). *Proceedings of the Biological*  
1076 *Society of Washington* 98(3):644-654.

1077 Whitley GP. 1956. New fishes from Australia and New Zealand. *Proceedings of the Royal*  
1078 *Zoological Society of New South Wales* v. for 1954-55:34-38.

1079 Winterbottom R. 2002. A redescription of *Cryptocentrus crocatus* Wongratana, a redefinition of  
1080 *Myersina* Herre (*Acanthopterygii*: *Gobiidae*), a key to the species, and comments on  
1081 relationships. *Ichthyological Research* 49(1):69-75.

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1083 Captions for figures and tables

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1170 **Figure 1.** Holotype of *Cryptocentrus steinhardtii* n. sp., SMNHTAU P-16037, 81.9 mm total  
 1171 length.

1172 **Figure 2.** Cephalic sensory system *Cryptocentrus steinhardtii*. NP - nasal pore; AIO - anterior  
 1173 interorbital pore; AO - anterior oculoscapular canal; PIO - posterior interorbital pore; PO  
 1174 - post orbital pore; POP- preopercular pores. GO - lower margin of gill opening.

1175 **Figure 3.** ML phylogenetic analysis of all available *COI* sequences of shrimp-gobies. Numbers  
 1176 above nodes are >50 bootstrap values; In red – the new species described in this study; In  
 1177 parentheses – number of sequences for each species. Further information for this dataset  
 1178 is provided in Table S2.

1179 **Table 1:** Selected meristic characteristics and proportions (measurements in mm; proportion in  
 1180 %).

1181 **Table 2.** Genetic relationships, in %, across all available *COI* sequences of shrimp-associated  
 1182 gobies. In parentheses, no. of sequences for each species; Below diagonal, pairwise  
 1183 genetic distances; above diagonal its standard errors. In red, values for *Cryptocentrus*  
 1184 *steinhardtii*.

1185 **Table 3:** Selected meristic counts of “low scale count group” *Cryptocentrus* (*sensu* Allen and  
 1186 Randall, 2011).

1187 **Table 4:** Compression of selected counts of Red Sea species of *Cryptocentrus*.

1188 **Table S1.** Information for the primers used for PCR and sequencing in this study.

1189 **Table S2 –** BOLD information for *COI* sequences of all available shrimp-associated gobies used  
 1190 for the phylogenetic analysis in this study (n=111)  
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Deleted: Table 34. 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 Cryptocentrus steinhardtii. the species described in this study

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