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A new species of *Hamaticolax* (Copepoda: Bomolochidae) from *Helicolenus dactylopterus* (Delaroche, 1809) (Scorpaeniformes: Sebastidae) in NW Mediterranean deep waters and notes on patterns of host use and host-specificity of the genus

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Abstract

Hamaticolax juanji n. sp. is described from specimens collected from the blackbelly rosefish *Helicolenus dactylopterus* Delaroche 1809 (Scorpaeniformes: Sebastidae). It is the second *Hamaticolax* species described and reported from the Mediterranean Sea, after *Ha. resupinus* Pérez-i-García, Carrassón and Boxshall, 2017. It is distinguished from *Ha. resupinus* by the presence of only one dorsal naked seta on the third segment of the antennule (vs. four), two unequal short naked setae in distal part of the antenna (vs. four), and the absence of a minute spine on the third endopodal segment of leg 1, among others. It is differentiated from *Ha. prolixus* Cressey 1969 by a comparatively reduced fourth pedigerous somite, the presence of two naked setae on the third segment of the antennule (vs. three), two naked setae and three curved claws in the distal part of the apical segment of the antenna (vs. three and four), an outer naked seta on the basis of leg 2, and by larger length/width ratio of the third endopodal segment, among others. *Hamaticolax juanji* n. sp. also has relatively longer inner setae on the first and second endopodal segments of leg 4 than the two former species. Patterns of host-use and host-specificity of the genus *Hamaticolax* are also discussed. The frequently observed low host-specificity of its members may be better explained by host ecological similarity and host availability phenomena, rather than by host phylogenetic distance.

Introduction

Copepods are widely distributed and extremely abundant in marine ecosystems, which constitute the largest biome on the planet (Boxshall 2005). They are distributed into nine orders (Boxshall and Halsey 2004), four of which include at least some parasitic species that infect virtually all major animal phyla of the marine environment (Boxshall 2005). Among these, the *Cyclopoida* Burmeister, 1834 is of major relevance for including several important families of copepods parasitizing fishes (Boxshall 2005). In particular, the family *Bomolochidae* Claus, 1875 comprises about 141 species of

parasites which commonly infest the gills of their marine fish hosts (Boxshall and Halsey 2004). They are usually cyclopiform in shape and small in size (in contrast with other highly metamorphic parasitic copepods), and their antennules and first swimming legs are flattened and armed with swollen setae that form part of the rim of a cephalothoracic sucker that forms the seal against the mucous-covered skin of the host (Boxshall 2005). Within this family, the genus *Hamaticolax* Ho and Lin 2006 currently comprises 11 valid species parasitizing several orders of fishes mainly in the Pacific and Atlantic Oceans (Wilson 1913; Cressey 1969; Kabata 1971; Oldewage 1994; Ho and Lin 2006; Cardoso et al. 2017; among others). Only one species, *Hamaticolax resupinus* Pérez-i-García, Carrassón and Boxshall, 2017, has been reported to date in the Mediterranean Sea parasitizing *Coelorinchus mediterraneus* Iwamoto & Ungaro, 2002 and *Coryphaenoides mediterraneus* Giglioli, 1893 (Pérez-i-García et al. 2017).

The blackbelly rosefish *Helicolenus dactylopterus* (Delaroche 1809) (Scorpaeniformes: Sebastidae) is a deep-

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dwelling benthic fish widely distributed along the eastern Atlantic Ocean and the Mediterranean Sea (Froese and Pauly 2017), where it plays an important ecological role in deep-sea fish communities (Stefanescu et al. 1994). In the western Mediterranean, *He. dactylopterus* occurs over the continental shelf and the upper slope, reaching maximum abundance and biomass values between 100 and 500 m depth (Massutí et al. 2001).

Several parasitological records exist for this fish species in the Atlantic Ocean, North Sea, and Caribbean Sea: endoparasites such as myxozoans, acanthocephalans, nematodes, digeneans, and cestodes, and even some ectoparasites, such as isopods, affecting gills and the oral cavity (Manter 1934; Golvan and de Buron 1988; Fiala 2006; Deudero et al. 2002; Bray and Kuchta 2006; Sequeira et al. 2010; among others). In the Mediterranean Sea, existing records are limited to isopods in the oral cavity (Oktener et al. 2009) and monogeneans on the gills (Radujković and Euzet 1989).

During a preliminary parasitological examination of blackbelly rosefish specimens from deep waters of the northwestern Mediterranean Sea (unpublished data), some bomolochid copepods belonging to a new species of the genus *Hamaticolax* were collected from the gills of a few of the examined fishes.

The present paper presents the first description of this reported new species, *Hamaticolax juanji* n. sp. In addition, patterns of host use and host-specificity of the genus *Hamaticolax* are discussed.

Materials and methods

A total of 59 specimens of the blackbelly rosefish, *He. dactylopterus*, were sampled by means of a commercial fishing gear (BOU) and a semi-balloon otter trawl (OTSB) off Barcelona (41.24°N, 2.45°E) and Ibiza (39.19°N, 1.31°E), between 500 and 550 m depth, in the northwestern Mediterranean Sea. Fish were freshly frozen individually on board at − 20 °C for further parasitological examination. Once in the laboratory, fish were thawed and examined under stereomicroscope for the presence of parasites, according to a standardized protocol. Specific, the gills were dissected out and examined in saline solution under a stereomicroscope and parasitic copepods recovered were stored in 70% ethanol. For morphological examination, they were dissected and mounted in glycerine as temporary slide preparations. Drawings were made with the aid of a drawing tube attached to an Olympus BH light microscope with Nomarsky interference contrast. Measurements were obtained with a stage micrometer; all measurements are in micrometers and are presented as the range followed by the mean ± standard deviation and the number of measurements taken (*n*) both in parentheses.

Prevalence and mean intensity were calculated following Bush et al. (1997). The scientific and common names of fishes follow Froese & Pauly (2017) and the morphological terminology for the copepods follows Boxshall (1990) and Huys and Boxshall (1991).

Type material has been deposited in the Natural History Museum, London (UK) (NHMUK) and the Helminthological collection of the Universitat Autònoma de Barcelona, Barcelona (Spain) (UABhc).

Results

Family Bomolochidae Claus, 1875
Genus *Hamaticolax* Ho & Lin, 2006
Hamaticolax juanji n. sp.
Type host: *Helicolenus dactylopterus* (Delaroche 1809) (Scorpaeniformes: Sebastidae)
Type-locality: Off Ibiza, Northwestern Mediterranean Sea (39.19°N, 1.31°E); depth: 508 m; 17.x.2011
Other localities: Off Barcelona, Northwestern Mediterranean Sea (41.24°N, 2.45°E); depth: 550 m; 17.ix.2007
Site of infection: Gills
Prevalence (%) of infection: 6.78 (4 fishes infected out of 59)
*Mean intensity of infection*: 2.75
Specimens deposited: Holotype and paratypes in NHMUK (nos. 2017.464 (holotype) and 2017.465–466 (paratypes)). Paratypes in UABhc (nos. Co5–Co9)
Etymology: This species is dedicated to Juan José, the father of the first author (SD) [= Juanjo (abbreviated form of Juan José), *juanji*].
Description: (Figs. 1 and 2) (based on whole mounts of 11 adult female specimens observed with light microscope):
Adult female: Body cyclopiform (Fig. 1a), 1141–1417 (1234 ± 101; *n* = 8) long; prosome length 718–903 (799 ± 53; *n* = 9), maximum width 631–820 (712 ± 64; *n* = 7). Prosome comprising broad cephalothorax and free second to fourth pedigerous somites; third somite not overlapping fourth in dorsal view (Fig. 1a). Cephalothorax bearing pair of acutely pointed, tapering tines in rostral area (Fig. 1b). Urosome (Fig. 1c) 417–534 (471 ± 35; *n* = 8) long, comprising fifth pedigerous somite, genital double-somite, and three free abdominal somites. All urosomites wider than long; genital double-somite with convex lateral margins, 1.0–1.24 (1.09 ± 0.07; *n* = 10) times wider than first free abdominal somite; third to fifth urosomites progressively decreasing in size; anal somite weakly incised posteromedially. Surfaces of all urosomites smooth, lacking ornamentation. Caudal rami (Fig. 1c) lacking ornamentation, with width/length ratio 1.0:1.22–1.48 (1.34 ± 0.09; *n* = 10), bearing single terminal principal seta plus three shorter terminal setae, one short subterminal dorsal seta, and one short lateral seta.

Fig. 1 *Hamaticolax juanji* n. sp. Paratype female. **a** Habitus, dorsal view. B Antennule and rostrum. **c** Urosome, ventral view. **d** Antenna. **e** Labrum and paragnaths in situ. **f** Mandible. **g** Maxillule. **h** Maxilla
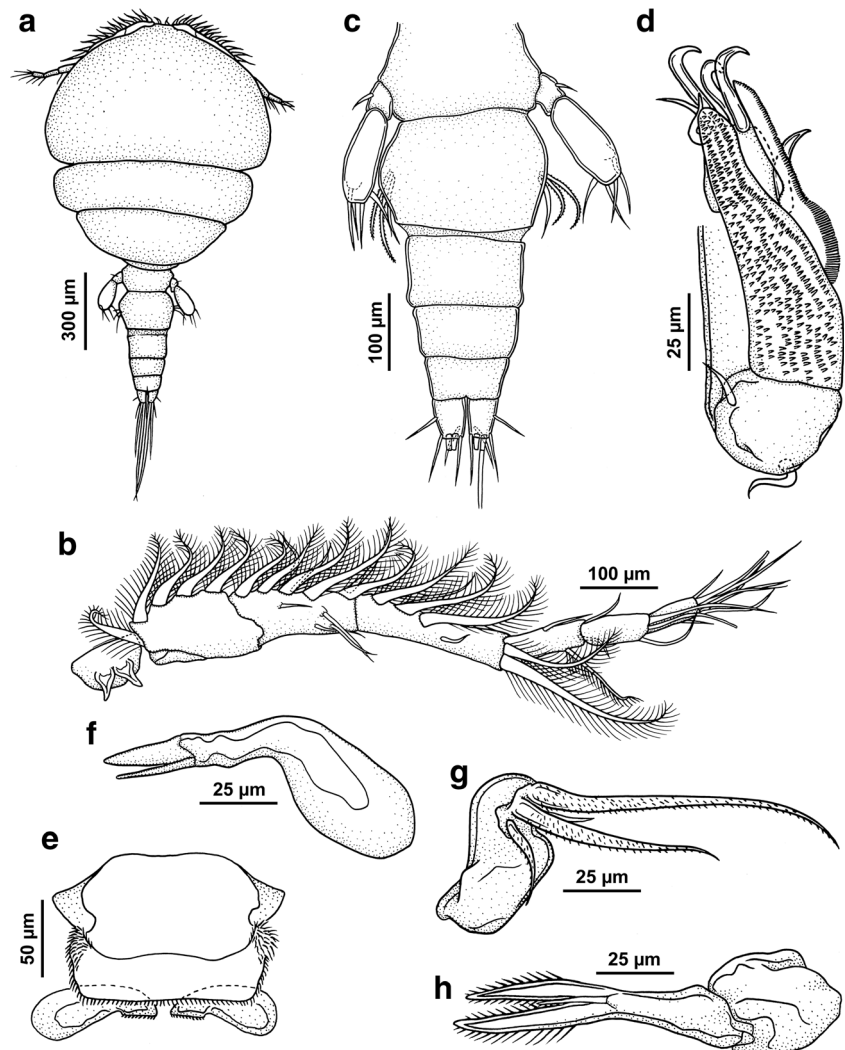
Antennule (Fig. 1b) comprising broader proximal part and slender distal part, both three-segmented; third segment of proximal part divided by partial suture. First segment bearing five pilose setae, none modified; second segment bearing five pilose setae, three dorsal naked setae, and four short naked setae on ventral surface; third segment bearing five pilose setae, distalmost long, reaching apex of antennule, one dorsal naked seta, and one short naked seta on ventral surface; fourth to sixth segments with setal formula: 4, 2 + 1ae, 7 + 1ae.

Antenna (Fig. 1d) uniramous, three-segmented; comprising long proximal segment (coxobasis) bearing one naked seta, short middle segment (first endopodal) with one short naked seta and highly ornamented apical segment. Apical segment comprising partly fused second and third endopodal segments: proximal part (representing second endopodal segment) transformed into blunt distal process ornamented with rows of spinules ventrally, continuous with multiple rows over ventral surface of segment, and armed with stout curved claw and pectinate process distally; distal part (third endopodal segment) bearing three curved claws and two unequal short naked setae.

Labrum (Fig. 1e) wider than long, ornamented with short setules laterally and along free posterior margin. Mandible (Fig. 1f) tipped with two blades, almost equal in length, anterior blade wider than posterior. Paragnath (Fig. 1e) forming long blunt process ornamented distally with small spinules on ventral surface. Maxillule (Fig. 1g) lobate, armed with three unequal large setae covered by very short setules and one small naked seta. Maxilla (Fig. 1h) two-segmented; proximal segment (syncoxa) unarmed; second segment (basis) narrowing distally and bearing two spinulate apical elements almost equal in length, plus small naked seta. Maxilliped (Fig. 2a) three-segmented; syncoxa ornamented with one short naked seta at mid-length; basis armed with one pilose and one naked short setae located on medial margin; terminal (endopodal) segment forming sigmoid claw provided with short accessory process and armed with proximal naked seta.

Legs 1 to 4 biramous, with armature as indicated in Table 1.

Fig. 2 *Hamaticolax juanji* n. sp.
Paratype female. **a** Maxilliped. **b**
Leg 1, arrowhead shows inner
basal element modified into short
knob-like structure. **c** Leg 2. **d** leg
3. **e** Leg 4. **f** Leg 5
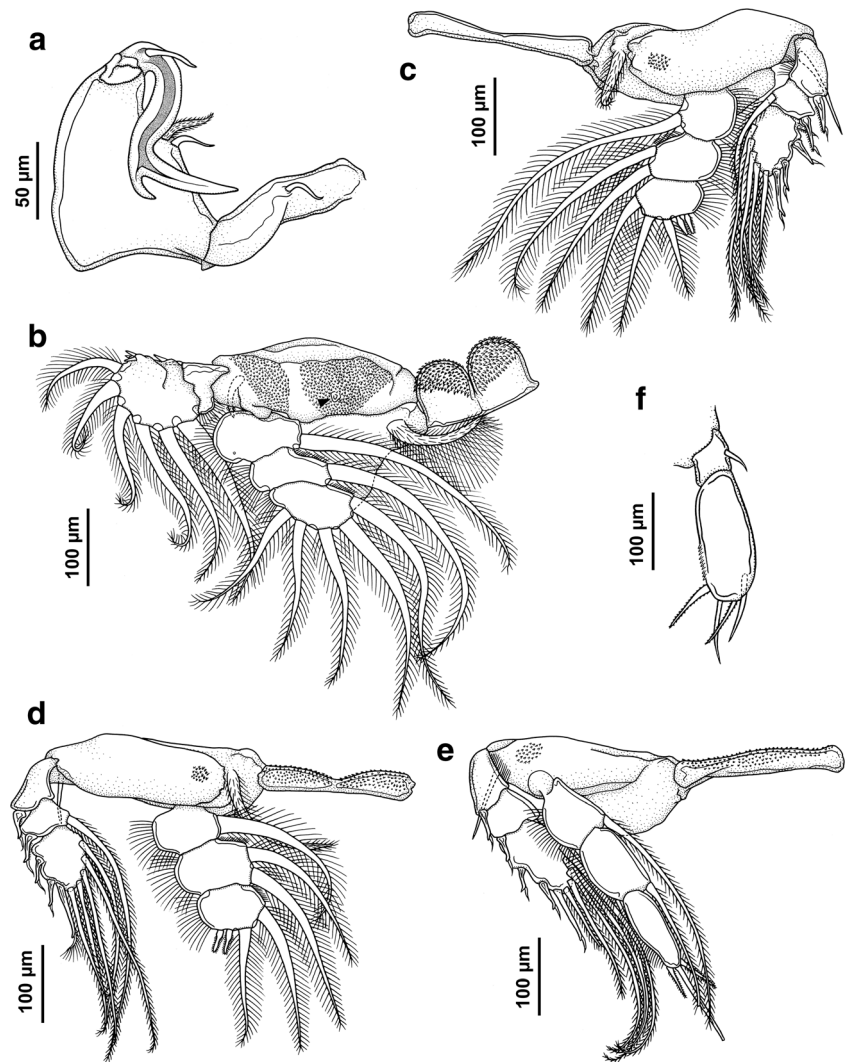
Leg 1 (Fig. 2b) modified, with flattened rami. Interpodal
sclerite ornamented with patches of surface spinules. Protopod
with hirsute outer basal seta; inner coxal seta transformed into
flattened broad, hirsute element with blunt tip and inner basal
element modified into short knob-like structure; basis
ornamented with patches of fine surface spinules. Exopod
indistinctly two-segmented, retaining almost complete suture
between first and second segments but only partial suture
between second and third. First exopodal segment with spine

in distal part of outer margin and inner row of long setules;
compound distal segment bearing four outer spines and six
plumose setae. Endopod three-segmented, all endopodal seg-
ments with outer margins bearing long setules; second and
third segments with inner row of short setules.

Leg 2 (Fig. 2c) with three-segmented rami; interpodal
sclerite unornamented. Coxa bearing hirsute inner seta
with blunt tip and basis with outer naked seta and inner
patch of spinules. Outer spines on exopodal segments each
provided with subterminal flagellum; outer spines on first
and second segments and first spine on third segment uni-
laterally denticulate. First exopodal segment with inner
row of setules. Endopodal segments broad and flattened,
with outer margins bearing long setules; second segment
with inner row of setules.

Leg 3 (Fig. 2d) with three-segmented rami; anterior surface
of interpodal sclerite ornamented with spinules. Coxa with
hirsute inner seta and basis with outer naked seta and inner
patch of spinules. Outer spines on exopodal segments

Table 1 Armature of legs 1–4 of adult female of *Hamaticolax juanji* n. sp.

	Coxa	Basis	Exopod	Endopod
Leg 1	0–1	1-I	I-0; IV, 6	0–1; 0–1; 5
Leg 2	0–1	1–0	I-0; I-1; III, I, 5	0–1; 0–2; II, 3
Leg 3	0–1	1–0	I-0; I-1; II, I, 5	0–1; 0–2; II, 2
Leg 4	0–0	1–0	I-0; I-1; II, I, 5	0–1; 0–1; I, 1, I

provided with subterminal flagellum; outer spines on first and second segments unilaterally denticulate; flagellum and terminal part of third spine of third segment ornamented with long setules. Endopodal segments broad and flattened, with outer margins ornamented with long setules; second and third segments with inner row of setules.

Leg 4 (Fig. 2e) with three-segmented rami; anterior surface of interpodal sclerite ornamented with spinules. Coxa lacking inner seta; basis with outer naked seta and inner patch of spinules. Exopodal segments bearing non-denticulate outer spines each provided with subterminal flagellum. First exopodal segment with inner row of setules. Outer margins of endopodal segments bearing long setules. Inner setae of first and second endopodal segments long, both extending well beyond distal margin of third endopodal segment. Third segment bearing inner and outer apical spines ornamented with short setules on margins; apical seta about as long as segment.

Leg 5 (Fig. 2f) two-segmented; protopodal segment small, armed with small outer seta; free exopodal segment armed with outer naked subterminal spine and outer spinulate, inner naked and inner spinulate terminal spines. Exopodal segment ornamented with spinules extending along distal part of inner margin.

Leg 6 (Fig. 1c) represented by one naked and two spinulated setae in egg sac attachment area on genital double-somite.

Remarks

The placement of *Ha. juanji* in the genus *Hamaticolax* is justified by the presence of a pair of ventral hooks in the rostral region, by the linear margin of the first two segments of the antennule and by the presence of an accessory process on the claw of the maxilliped in the female.

Hamaticolax juanji n. sp. resembles the only other *Hamaticolax* species described in the Mediterranean Sea, *Ha. resupinus*. However, these two species can be readily distinguished by the following features: the lack of spinules on the ventral surface of the anal somite and caudal rami in *Ha. juanji* (vs. presence of rows of spinules in these locations in *Ha. resupinus*), the presence of only one dorsal naked seta on the third segment (vs. four dorsal naked setae) of the antennule, the presence of two unequal short naked setae in the distal part of the antenna (vs. four unequal naked setae), different ornamentation of the labrum, mandibular blades almost equal in length and with smooth margins (vs. mandibular blades markedly unequal in length and with spinulate margins), non-bipartite paragnath (vs. bipartite), the setae of the maxillule ornamented with short setules (vs. with pilose setae), the basis of the maxilliped armed with one pilose and one naked short setae (vs. one pilose and one vestigial setae), and

the terminal segment of the maxilliped armed with a naked seta (vs. a spinulate seta). With regard to the swimming legs, important features allowing the differentiation of *Ha. juanji* from *Ha. resupinus* are the presence of an outer naked seta on the basis of legs 2, 3, and 4 (vs. a plumose seta), the row of long setules along the inner margin of the first segment of the exopod of legs 1 and 2 (vs. the lack of such rows of setules), and the smooth surface of the first exopodal segment of legs 3 and 4 (vs. ornamented with a patch of spinules). Additional differences include leg 1: absence of rows of spinules on first segment and lack of a minute spine on third endopodal segment in *Ha. juanji* (vs. presence of such structures in *Ha. resupinus*); leg 2: only first spine of third exopodal segment unilaterally denticulate (vs. all spines on segment unilaterally denticulate) and presence of an inner row of setules on the second endopodal segment only (vs. inner row of setules on second and third endopodal segments); leg 3: third spine of third exopodal segment bearing long setules (vs. lacking setules) and spines on third exopodal segment non-denticulate (vs. unilaterally denticulate); leg 4: outer spines on exopodal segments non-denticulate (vs. unilaterally denticulate), apical part of the third exopodal segment smooth (vs. ornamented with a patch of spinules), inner seta on first and second endopodal segments long (vs. short) and inner and outer apical spines on third endopodal segment are both ornamented with short setules along both margins (vs. naked).

The *Hamaticolax* species that most resembles *Ha. resupinus* is *Ha. maleus*. Although some observational errors and/or apparent misinterpretations were pointed by Pérez-i-García et al. (2017) in the description of *Ha. maleus*, some clear differences were found with *Ha. juanji*. Some of them are shared with *Ha. resupinus*: body length apparently larger (1.6 mm (*Ha. maleus*) vs maximum length 1.4 mm of *Ha. juanji*) and genital double-somite with parallel lateral margins and of equal diameter to three abdominal segments (vs. genital double-somite with convex lateral margins and wider than abdominal segments). Other differences are different setation in all segments of the antennule and antenna or unequal blades of the mandibule (vs. equal in *Ha. juanji*).

The key to species of *Hamaticolax* provided by Pérez-i-García et al. (2017) led us to *Ha. prolixus* (Cressey 1969). However, a number of morphological differences are apparent between this species and *Ha. juanji* n. sp., including a comparatively reduced fourth pedigerous somite, the lack of rows of spinules on the anal somite and caudal rami (vs. presence of such rows, similar to *Ha. resupinus*), the presence of two naked setae on the third segment of the antennule (vs. three naked setae), the presence of two naked setae and three curved claws in the distal part of the apical segment of the antenna (vs. three setae and four claws), differences in the mandible (similar to those with *Ha. resupinus*), the maxillule bearing one naked seta and three setae covered with short setules (vs. two naked and three plumose setae), the maxilla bearing two

spinulate apical elements and one naked seta (vs. two pectinate processes and two naked setae), the basis of the maxilliped lacking a corrugated adhesion pad (vs. with such structure), and terminal segment of the maxilliped ornamented with a naked proximal seta (vs. spinulate seta, similar to *Ha. resupinus*). Regarding the swimming legs, *Ha. juanji* can be distinguished from *Ha. prolixus* by the presence of a row of setules along the inner margin of the second and third endopodal segments of leg 1 (vs. lack of such ornamentation). Additional differences include leg 1: the spines on outer margin of the exopod are smaller, especially on first segment; leg 2: basis bearing outer naked seta (vs. seta absent), inner margin of second endopodal segment bearing row of setules (vs. lacking setular ornamentation); leg 3: first exopodal segment without inner row of setules (vs. bearing such elements); leg 4: setae on first and second endopodal segments longer relative to length of the ramus, and with a larger length:width ratio of the third endopodal segment; leg 5: protopodal segment with smooth surface (vs. ornamented with large patch of spinules on outer distal corner) and different patterns of ornamentation regarding patches of spinules on the exopodal segment.

Hamaticolax prolixus was described as *Bomolochus prolixus* by Cressey (1969) and was later redescribed by Ho (1972) (as *Holobomolochus prolixus*) more accurately and in more detail (our comparisons are thus mainly based on this latter work). However, Ho (1972) did not address the morphology of legs 2–5 in females, which contain important diagnostic features. The drawings and description of the swimming legs in Cressey (1969) are also incomplete, which has prevented us from making detailed comparisons with *Ha. prolixus*. Therefore, we consider that a complete redescription of *Ha. prolixus* is necessary before differences between this and other species can be comprehensively determined.

Discussion

Several parasites belonging to a wide range of zoological groups have been described from *He. dactylopterus* (e.g., Manter 1934; Golvan and de Buron 1988; Radujkovic and Euzet 1989; Køie 1993; Bray and Kuchta 2006; Fiala 2006; Sequeira et al. 2010). Surprisingly, copepods were not counted among them, and the present description is the first report of a species of parasitic copepod from *He. dactylopterus*. At the family level, this represents the second *Hamaticolax* species reported from a sebastid host, the first being *Ha. spinulus* (Cressey 1969), which was recovered from *Sebastodes mystinus* (Jordan and Gilbert) and *S. serranoides* (Eigenmann and Eigenmann), off the Californian coast (Cressey 1969).

Hamaticolax juanji is the second *Hamaticolax* species described and reported from the Mediterranean Sea, after *Ha. resupinus*. Both species were collected in deep waters from the Balearic Sea off the same localities (Barcelona and Ibiza), although *Ha. resupinus* was recovered from deeper waters (1236–1626 vs. 508–550 m depth) and from macrourid hosts (Pérez-i-García et al. 2017).

Hamaticolax juanji could potentially be found over the entire bathymetric range and geographical distribution of its type-host. In the western Mediterranean, *He. dactylopterus* occurs between 50 and 800 m depth (100–800 in the Balearic Sea), although it is most abundant below 200 m (Massutí et al. 2001). This species is also distributed in the Atlantic and Indian oceans (Froese and Pauly 2017), where it can extend into deeper grounds (Allain and Lorance 2000).

To date, the 12 valid species included within the genus *Hamaticolax* have been reported from at least 16 different families and 27 different species of teleost fishes (each species utilizing a mean of 1.3 host families and 2.25 host species) representing 6 different orders (Table 2). This genus seems to show, therefore, a high degree of euryxeny, which extends to the species level. The best example of this trend is *Ha. prolixus*, which has been recovered from as many as eight different fish families from four distinct orders. Four more species, though having been reported from fewer host families and orders, still show highly generalist infection patterns: *Ha. occultus* (Kabata, 1971) and *Ha. attenuatus* (Wilson, 1913) have been recovered from three different families belonging to three different orders, *Ha. spinulus* from three scorpaeniform families, and *Ha. resupinus* from two gadiform families. The remaining seven species (i.e., *Ha. embiotocae* (Hanan, 1976), *Ha. galeichthyos* (Luque and Bruno, 1990), *Ha. maleus* (Oldewage, 1994), *Ha. paralabracis* (Luque and Bruno, 1990), *Ha. scutigerulus* (Wilson, 1935), *Ha. unisagittatus* (Tavares and Luque, 2003), and *Ha. juanji*) show the highest degree of host specificity, each having been recovered from only a single fish family to date (Table 2).

Hamaticolax parasitizes marine teleosts mostly inhabiting shallow coastal waters of the Atlantic and Pacific oceans and the Mediterranean Sea. Overall, its members show a marked preference for the closely related fish orders Perciformes and Scorpaeniformes (Froese and Pauly 2017). At the family level, embiotocids (Perciformes) and cottids (Scorpaeniformes) are the most commonly parasitized hosts (Table 2).

Only four *Hamaticolax* species have been reported in bathydemersal or bathypelagic fish hosts (i.e., *Ha. maleus* in the macrourid *Malacocephalus laevis* (Lowe) (Oldewage 1994), *Ha. occultus* in the pleuronectid *Lyopsetta exilis* (Jordan and Gilbert) (Kabata 1971), *Ha. resupinus* in the macrourids *Coelorinchus mediterraneus* Iwamoto and Ungaro and *Coryphaenoides mediterraneus* (Giglioli), and the bythitid *Cataetyx alleni* (Byrne) (Pérez-i-García et al. 2017; unpublished data of the ANTROMARE project) and *Ha. juanji* in the sebastid *He. dactylopterus* (present results)); the other eight *Hamaticolax* species seem restricted to shallow-water demersal hosts.

Table 2 Species of the genus *Hamaticolax* Ho & Lin, 2006 reported from different fish orders, families, and species

Parasite	Host orders	Host families	Host species	References
Hamaticolax attenuatus (Wilson, 1913)	Scorpaeniformes	Scorpaenidae	*Scorpaena guttata* Girard, 1854, *S. plumieri* Bloch, 1789	Wilson (1913), Love and Moser (1983)
	Perciformes	Sciaenidae	*Genyonemus lineatus* (Ayres, 1855), *Roncador stearnsii* (Steindachner, 1876)	Love and Moser (1983)
Hamaticolax embiotocae (Hanan, 1976)	Tetraodontiformes	Tetraodontidae	*Sphoeroides annulatus* (Jenyns, 1842)	Love and Moser (1983)
	Perciformes	Embiotocidae	*Cymatogaster aggregata* Gibbons, 1854, *Damalichthys vacca* (Girard, 1855), *Embiotoca jacksoni* Agassiz, 1853, *Phanerodon furcatus* Girard 1854, *Rhacochilus vacca* (Girard, 1855), *Zalembius rosaceus* (Jordan & Gilbert, 1880)	Hanan (1976), Ho and Lin (2006)
Hamaticolax galeichthyos (Luque & Bruno, 1990)	Siluriformes	Ariidae	*Galeichthys peruvianus* Lütken, 1874	Luque and Bruno (1990)
Hamaticolax juanji n. sp.	Scorpaeniformes	Sebastidae	*Helicolenus dactylopterus* (Delaroche, 1809)	Present study
Hamaticolax maleus (Oldewage, 1994)	Gadiformes	Macrouridae	*Malacocephalus laevis* (Lowe, 1843)	Oldewage (1994)
Hamaticolax occultus (Kabata, 1971)	Pleuronectiformes	Pleuronectidae	*Hippoglossoides elassodon* Jordan & Gilbert, 1880, *Lyopsetta exilis* (Jordan & Gilbert, 1880)	Kabata (1971)
Hamaticolax paralabracis (Luque & Bruno, 1990)	Perciformes	Embiotocidae	*R. vacca*	McDonald and Margolis (1995)
	Scorpaeniformes	Cottidae	*Hemilepidotus spinosus* Ayres, 1854	McDonald and Margolis (1995)
	Perciformes	Serranidae	*Paralabrax humeralis* (Valenciennes, 1828)	Luque and Bruno (1990)
	Perciformes	Embiotocidae	*Zal. rosaceus*	Ho and Lin (2006)
		Sciaenidae	*G. lineatus*	Ho and Lin (2006)
Hamaticolax prolixus (Cressey, 1969)	Pleuronectiformes	Cynoglossidae	*Symphurus atricaudus* (Jordan & Gilbert, 1880)	Ho and Lin (2006)
		Pleuronectidae	*Microstomus pacificus* (Lockington, 1879), *Parophrys vetulus* Girard, 1854, *Pleuronichthys coenosus* Girard, 1854, *P. verticalis* Jordan & Gilbert, 1880	Cressey (1969), Ho and Lin (2006)
		Paralichthyidae	*Citharichthys sordidus* (Girard, 1854), *C. stigmaeus* Jordan & Gilbert, 1882, *Hippoglossina stomata* Eigenmann & Eigenmann, 1890, *Paralichthys californicus* (Ayres, 1859)	Ho (1972), Ho and Lin (2006)
	Scorpaeniformes	Hexagrammidae	*Zaniolepis frenata* Eigenmann & Eigenmann, 1889, *Zan. latipinnis* Girard, 1858	Ho and Lin (2006)
		Cottidae	*Chitonotus pugetensis* (Steindachner, 1876), *Icelinus quadriseriatus* (Lockington, 1880), *Leptocottus armatus* Girard, 1854	Ho and Lin (2006)
	Batrachoidiformes	Batrachoididae	*Porichthys notatus* Girard, 1854	Ho and Lin (2006)
Hamaticolax resupinus Pérez-i-García, Carrasón & Boxshall (2017)	Gadiformes	Macrouridae	*Coelorinchus mediterraneus* Iwamoto & Ungaro, 2002, *Coryphaenoides mediterraneus* (Giglioli, 1893)	Pérez-i-García et al. (2017)
		Bythitidae	*Cataetyx alleni* (Byrne, 1906)	Unpublished data
Hamaticolax scutigerulus (Wilson, 1935)	Perciformes	Mullidae	*Pseudupeneus maculatus* (Bloch, 1793)	Wilson (1935)
Hamaticolax spinulus (Cressey, 1969)	Scorpaeniformes	Hexagrammidae	*Oxylebius pictus* Gill, 1862, *Zan. latipinnis*	Cressey (1969)
		Cottidae	*L. armatus, Oligocottus maculosus* Girard, 1856	Kabata (1971)
		Sebastidae	*Sebastodes mystinus* (Jordan & Gilbert, 1881), *S. serranoides* (Eigenmann & Eigenmann, 1890)	Cressey (1969)
		Scorpaenidae	*S. guttata*	Cressey (1969)
Hamaticolax unisagittatus (Tavares and Luque 2003)	Perciformes	Centropomidae	*Centropomus undecimalis* (Bloch, 1792)	Tavares and Luque (2003)

Patterns of host use may be explained by different factors that are difficult to isolate and define clearly (Lootvoet et al. 2013). In the case of generalist parasites with direct life cycles, as is the case for many parasitic copepods, explanations of alternative host use have been mainly attributed to the ecological or phylogenetic distance among the different hosts parasitized (i.e., hosts that share ecological features or that are phylogenetically closer, will share more parasites (Timms and Read 1999; Cooper et al. 2012; Khokhlova et al. 2012)), or to host availability (i.e., more abundant and thus more available hosts will have greater encounter probability for a given parasite and support its populations (Poulin and Mouillot 2004; Loot et al. 2006)).

As described above, some *Hamaticolax* species parasitize a wide spectrum of hosts belonging to different phylogenetic groups. Though phylogenetically distant, they generally dominate local fish communities and show similar trends in habitat use. In these cases, host ecological similarity and host availability phenomena could be the main factors determining the low host-specificity observed.

For example, the species with the widest host spectrum, *Ha. prolixus*, has been reported from shallow waters off California from eight different fish families included in four distinct orders (Cressey 1969; Ho 1972; Ho and Lin 2006). These fishes are dominant in the soft-bottom-associated demersal fish communities of the area (Allen et al. 2006). The situation is similar for *Ha. occultus*, recovered off the British Columbia from three of these same fish families (Kabata 1971; McDonald and Margolis 1995), and for *Ha. spinulus*, reported off California and British Columbia from three scorpaeniforms (Cressey 1969; Kabata 1971; Love et al. 2002) which are an important component of the coastal groundfish communities off the USA west coast (Williams and Ralston 2002; Allen et al. 2006). Finally, *Ha. attenuatus* has been reported from three demersal fish families along the eastern Pacific Ocean and in the central-western Atlantic Ocean (Wilson 1913; Love and Moser 1983). Overall, these four *Hamaticolax* species infest host families of local abundance and coastal distribution that participate in abundant and species-rich ichthyic communities where host-switching phenomena are more likely to take place (Allen et al. 2006; Ojeda-Ruiz et al. 2016).

The remaining *Hamaticolax* species seem to be restricted to fewer host species (in the case of *H. resupinus*, although reported from two different families, its recovery from a member of the Bythitidae (i.e., *C. alleni*) in Mediterranean deep waters off Barcelona seems an accidental record, since only a single specimen was recovered in more than 50 dissected fishes (unpublished data of the ANTROMARE project)). Indeed, high variability in host-specificity has been reported for copepods infecting shallow to deep-water demersal fishes (Boxshall 1974, 1998). However, and as explained by Costello (2016), parasite host-specificity tends to be

overestimated for various reasons, including under sampling of hosts, selective sampling of more widespread or abundant hosts, and overlooking of parasites on hosts infected at low frequencies, among others. Considering such sampling biases, and taking into account the low host-specificity shown by various *Hamaticolax* species, we foresee that more hosts will emerge in the future for the least-known or recently described species, as is the case of *Ha. juanji*.

Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

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