ZooKeys 791: 71–95 (2018)
doi: 10.3897/zookeys.791.28775
http://zookeys.pensoft.net

RESEARCH ARTICLE

A peer-reviewed open-access journal
ZooKeys
Launched to accelerate biodiversity research

Five new coexisting species of copepod crustaceans of the genus *Spaniomolgus* (Poecilostomatoida: Rhynchomolgidae), symbionts of the stony coral *Stylophora pistillata* (Scleractinia)

Mercedes Conradi[1], Eugenia Bandera[1], Sofya V. Mudrova[2], Viatcheslav N. Ivanenko[3]

1 *Laboratorio de Biología Marina, Departamento de Zoología, Facultad de Biología, Universidad de Sevilla, Reina Mercedes 6, 41012, Sevilla, Spain* **2** *Red Sea Research Center, King Abdullah University of Science and Technology (KAUST), Thuwal, 23955, Saudi Arabia* **3** *Department of Invertebrate Zoology, Faculty of Biology, Lomonosov Moscow State University, Moscow, 119992, Russia*

Corresponding author: *Viatcheslav Ivanenko* (ivanenko@mail.bio.msu.ru; ivanenko.slava@gmail.com)

Academic editor: *D. Defaye* | Received 3 August 2018 | Accepted 20 September 2018 | Published 22 October 2018

http://zoobank.org/5F5F1685-BCF9-41E2-B372-D65BFA005B2E

Citation: Conradi M, Bandera E, Mudrova SV, Ivanenko VN (2018) Five new coexisting species of copepod crustaceans of the genus *Spaniomolgus* (Poecilostomatoida: Rhynchomolgidae), symbionts of the stony coral *Stylophora pistillata* (Scleractinia). ZooKeys 791: 71–95. https://doi.org/10.3897/zookeys.791.28775

Abstract

Spaniomolgus is a symbiotic genus of copepods of the poecilostomatoid family Rhynchomolgidae and is known to be associated with shallow-water reef-building hermatypic corals. Three species of this genus were previously found only in washings of *Acropora* and *Stylophora* in northern Madagascar. Four coral morphotypes of *Stylophora pistillata* (Pocilloporidae) were collected by SCUBA at 1 to 28 m depth in five sites in the Saudi Arabian Red Sea in 2013. Copepods found on these colonies were studied using light, confocal and scanning electron microscopy. Five new, and one known, species of the genus *Spaniomolgus* were discovered in washings and inside the galls of the hermatypic coral *S. pistillata*. The description of these new species (*Spaniomolgus globus* **sp. n.**, *S. stylophorus* **sp. n.**, *S. dentatus* **sp. n.**, *S. maculatus* **sp. n.**, and *S. acutus* **sp. n.**) and a key for the identification of all of its congeners is provided herein.

Keywords

Copepoda, Crustacea, symbiosis, biodiversity, Pocilloporidae, coral reefs, Red Sea

Introduction

Rhynchomolgidae Humes and Stock, 1973 is one of the largest families of poecilostomatoid copepods comprising over 250 species living in association with various marine invertebrates (Ho and Kim 2001; Boxshall and Halsey 2004). There are 44 genera in the family Rhynchomolgidae with the genus *Doridicola* Leydig, 1853 being the largest in the family and comprising 52 species (Ho and Ivanenko 2013, Walter and Boxshall 2018). Thirty-eight genera of the family include only up to six species. One of these small genera, *Spaniomolgus* Humes & Stock, 1973, consists of three species: the type species *S. compositus* (Humes & Frost, 1964), *S. geminus* (Humes & Ho, 1968) and *S. crassus* (Humes & Ho, 1968), all previously attributed to the genus *Lichomolgus* Thorell, 1859. *Spaniomolgus* are found in association with scleractinians of the genera *Acropora* Oken, 1815, *Seriatopora* Lamarck, 1816, and *Stylophora* Schweigger, 1820 from Madagascar (Humes and Ho 1968, Humes and Stock 1972, 1973). There have been no records of *Spaniomolgus* since the revision of the lichomolgoid complex (Humes and Stock 1972, 1973) and until the discovery of an unidentified species of *Spaniomolgus* living in modified polyps (galls) of *Stylophora pistillata* Esper, 1797 in the Red Sea (Ivanenko et al. 2014, Shelyakin et al. 2018).

Branching corals of *Stylophora pistillata* are widely distributed around the Indo-Pacific and are phenotypically plastic, i.e., morphological variation across different habitats, depths, and geographic regions can be observed. The latest study based on seven DNA loci demonstrated that *Stylophora* corals from the Red Sea belong to a single molecular clade, and that morphospecies of *Stylophora pistillata*, *S. danae* Milne Edwards & Haime, 1850, *S. subseriata* (Ehrenberg, 1834), and *S. kuehlmanni* Scheer & Pillai, 1983 from the Red Sea are now considered as synonyms of *S. pistillata* (Arrigoni et al. 2016).

This paper describes five new species of *Spaniomolgus* living in symbiosis with four morphotypes of *Stylophora pistillata* from the Red Sea. Comments on the relationships with other congeners are given, and a key to the species of the genus *Spaniomolgus* is presented.

Materials and methods

The sampling was undertaken in accordance with the policies and procedures of the King Abdullah University of Science and Technology (KAUST). Permissions for KAUST to undertake the research were obtained from the appropriate governmental agencies of the Kingdom of Saudi Arabia.

Four colonies of *Stylophora pistillata* from the Thuwal reefs in the central Red Sea and one colony from the reef close to Al Lith in the southern Red Sea were sampled (distance between the sampling locations is about 280 km) (Fig. 1, Table 1). The map was created using Python scripts (Jones et al. 2001), labels were included using the software Adobe Photoshop CS4 (Adobe Systems, San Jose, CA, USA). The coral colonies were collected using a hammer and chisel, and encased in sealed plastic bags while snorkeling and SCUBA diving at depths ranging from 1 to 28 m. The coral samples

Table 1. Sampling localities in the Red Sea.

Specimen of the coral host	Species	Coordinates	Locality	Depth (m)	Date
SA13-12	*Stylophora pistillata*	22°12'4.30"N, 38°57'31.40"E	Thuwal	1	24.04.2013
SA13-25	*Stylophora pistillata* (morphotype *subseriata)*	22°19'9.26"N, 38°51'15.78"E	Thuwal	10.4	25.04.2013
SA13-31	*Stylophora pistillata* (morphotype *danae)*	22°20'23.45"N, 38°50'52.33"E	Thuwal	28	26.04.2013
SA13-61	*Stylophora pistillata*	22°03'48.5"N, 38°45'51.2"E	Thuwal	1	29.04.2013
SA13-72	*Stylophora pistillata* (morphotype *mordax)*	20°08'02.1"N, 40°05'58.86"E	Al Lith	2.5	03.05.2013

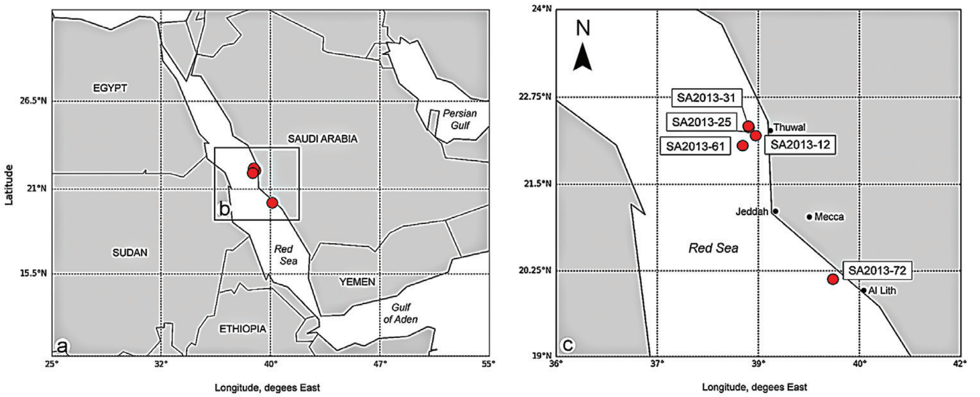

Figure 1. a–c Sampling localities and study area in the Red Sea (Saudi Arabia). The red circles indicate sampling localities of the indicated samples of *Stylophora pistillata* (see Table 1).

were rinsed on board as follows: 96% ethanol was added to each sample until the overall solution reached a concentration 10% to relax the animals attached to the coral. After 15 minutes, the samples were shaken, and the water with the detached symbionts was filtered through a 100 µm sieve. Copepods were sorted under a Carl Zeiss™ Stemi 2000-C stereomicroscope. Coral colonies were also examined for copepods in modified corallites and galls. Galls were dissected, and copepods were extracted from inhabited polyps using entomological needles and preserved in 96% ethanol.

In the lab, copepods were dissected in lactic acid and then stained with Chlorazol black E (Sigma C-1144) for contrast enhancement (Ivanenko and Defaye 2004). Specimens were then examined as temporary mounts in lactophenol and later sealed with Entellan as permanent mounts. The coral hosts (Fig. 2) were bleached in sodium hypochlorite for 48 h, rinsed with fresh water, dried and photographed. The copepods were kept in 2 mL vials in 96% ethanol with a small drop of glycerol.

For confocal microscopy, exoskeletons were individually transferred to distilled water and then stained with Fuchsin (Ivanenko et al. 2012; Corgosinho et al. 2018).

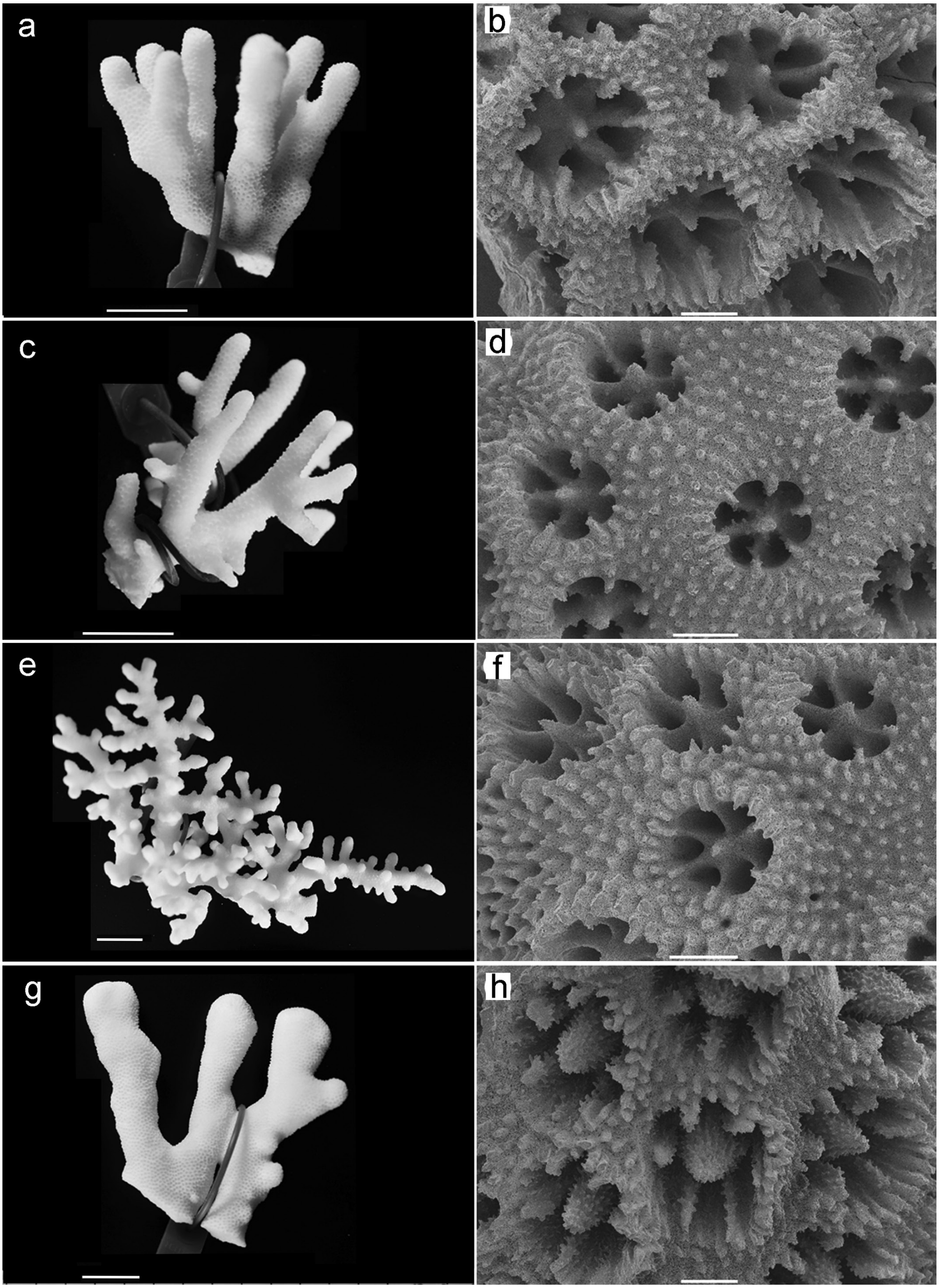

Figure 2. *Stylophora pistillata*, coral skeletons and corallite structures (SEM). **a, b** Specimen SA13-12 **c, d** Morphotype *subseriata*, specimen SA13-25 **e, f** Morphotype *danae* SA13-31 **g, h** Morphotype *mordax*, specimen SA13-61. Scale bars: 20 mm (**a, c, e, g**); 0.5 mm (**b, d, f, h**).

The copepods were inspected using an inverted Nikon A1 confocal laser scanning microscope (CLSM, Nikon Corporation, Tokyo, Japan) at Lomonosov Moscow State University, using a 40× oil immersion objective and lasers with wavelengths of 532 and 640 nm. The laser power was set to 60%. The amplitude offset and detector gain were manually adjusted. CLSM image stacks were obtained throughout the whole animal, and the scanning software was adjusted to perform the optimal number of scans. Image size was set for 2000×2000 dpi and the reconstruction of the external anatomy was obtained by maximum projection. The final images were adjusted for contrast and brightness using the software Adobe Photoshop CS4.

All figures were prepared using a Leica DM5500B differential interference microscope equipped with a camera lucida. The armature formula of swimming legs 1–4 follows Sewell (1949), spines are indicated by Roman numerals and setae by Arabic numerals. Mean body length (MBL) of copepods was measured from the anterior margin of the rostrum to the posterior margin of the caudal rami.

For scanning electron microscopy (SEM), copepods were dehydrated through increasing ethanol concentrations, critical point dried, mounted on aluminium stubs, coated with gold, and examined in a CamScan SEM (CamScan Electron Optics Ltd, London, UK) at the Faculty of Biology of Lomonosov Moscow State University. The bleached fragments of corals were mounted on metal stands using glue, coated with a conductive gold film and examined with the same SEM.

Type specimens of copepods are deposited in the collection of the Zoological Museum of Lomonosov Moscow State University (ZMMU). The coral hosts are deposited in the collection of King Abdullah University of Science and Technology (KAUST).

Results

Five new and one described species of the genus *Spaniomolgus* were found in washings and inside of polyps of four morphotypes of the hermatypic coral *Stylophora pistillata* collected from five sites (Table 1, Fig. 1) at depths ranging from 1 to 28 m. The description of the five new species (*Spaniomolgus globus* sp. n., *S. stylophorus* sp. n., *S. dentatus* sp. n., *S. maculatus* sp. n., and *S. acutus* sp. n.) is provided herein.

Taxonomy

Poecilostomatoida Thorell, 1859
Family Rhynchomolgidae Humes & Stock, 1973

Genus *Spaniomolgus* Humes & Stock, 1973

Type species. *Lichomolgus compositus* Humes & Frost, 1964 now regarded as a synonym of *Spaniomolgus compositus* (Humes & Frost, 1964), by original designation.

Other species. *Spaniomolgus geminus* (Humes & Ho, 1968), *S. crassus* (Humes & Ho, 1968), *S. globus* sp. n., *S. stylophorus* sp. n., *S. dentatus* sp. n., *S. maculatus* sp. n., *S. acutus* sp. n.

Remarks. The publication by Humes and Stock in 1972 of a list of new taxa, including *Spaniomolgus* and Rhynchomolgidae, without diagnoses of the new taxa is considering by us as interrupted and continued in 1973 (ICZN 1999: Art. 10.1.1); therefore the publication date of the genus becomes 1973.

Spaniomolgus globus sp. n.

http://zoobank.org/9EC98428-E87D-4854-B2C7-7BEAA59DF14A

Figs 3, 4

Type locality. Saudi Arabian Red Sea, reef near Thuwal, 22°03'48.5"N, 38°45'51.2"E.

Material examined. 1 ♀ holotype (ZMMU Me-1209) and 3 ♀♀ paratypes (ZMMU Me-1210) from tubular-shaped modification of corallites of *Stylophora pistillata* (KAUST SA2013-61) collected at 1 m depth.

Etymology. The specific Latin epithet *globus*, globe, refers to the body shape in life when the urosome forms an s-shaped flexure.

Description. Adult female.

Body cyclopiform, with oval cephalothorax and cylindrical urosome (Fig. 3a). Total body length ranging from 1.1 to 1.5 mm (mean = 1.3 mm, n = 4); width ranging from 580 to 600 μm (mean = 590 μm, n = 4). Prosome consists of cephalothorax (first pedigerous somite incompletely separated by an indistinct furrow) and three free pedigerous somites. Rostral area covered with hyaline setules (not figured). Second and third pedigerous somites with epimeral areas slightly angular. Fourth pedigerous somite smaller than preceding ones, its epimeral areas much less expanded.

Urosome s-shaped when alive, with the genital double-somite drawn forward under the metasome and the postgenital somites in line with the prosome (Fig. 3a); 5-segmented, comprising fifth pedigerous somite, genital double-somite, and three free abdominal somites (Fig. 3b). In dorsal view, only the postgenital somites are visible. Leg 5-bearing somite bell-shaped, slightly wider than long.

Genital double-somite (Fig. 3b) narrow, squarish (200 × 200 μm); its dorsal length (120 μm) much shorter than its ventral length (200 μm). Paired genital apertures bipartite, each comprising ventrolateral copulatory pore and dorsolateral gonopore (oviduct opening); lateral margins nearly parallel. Each genital area with two minute setae (Fig. 3b). Egg sac unknown. Width and length of three postgenital somites, 120 × 180, 85 × 130 and 105 × 120 μm from anterior to posterior.

Caudal rami (Fig. 3b) elongated, 180 × 45 μm, 4.0 times longer than wide. With six setae relatively short and naked. Outer lateral seta 52 μm, outermost terminal seta 41 μm, innermost terminal seta 47 μm. Two median terminal setae broadened, 58 μm (outer) and 52 μm (inner) in length. Dorsal seta 35 μm.

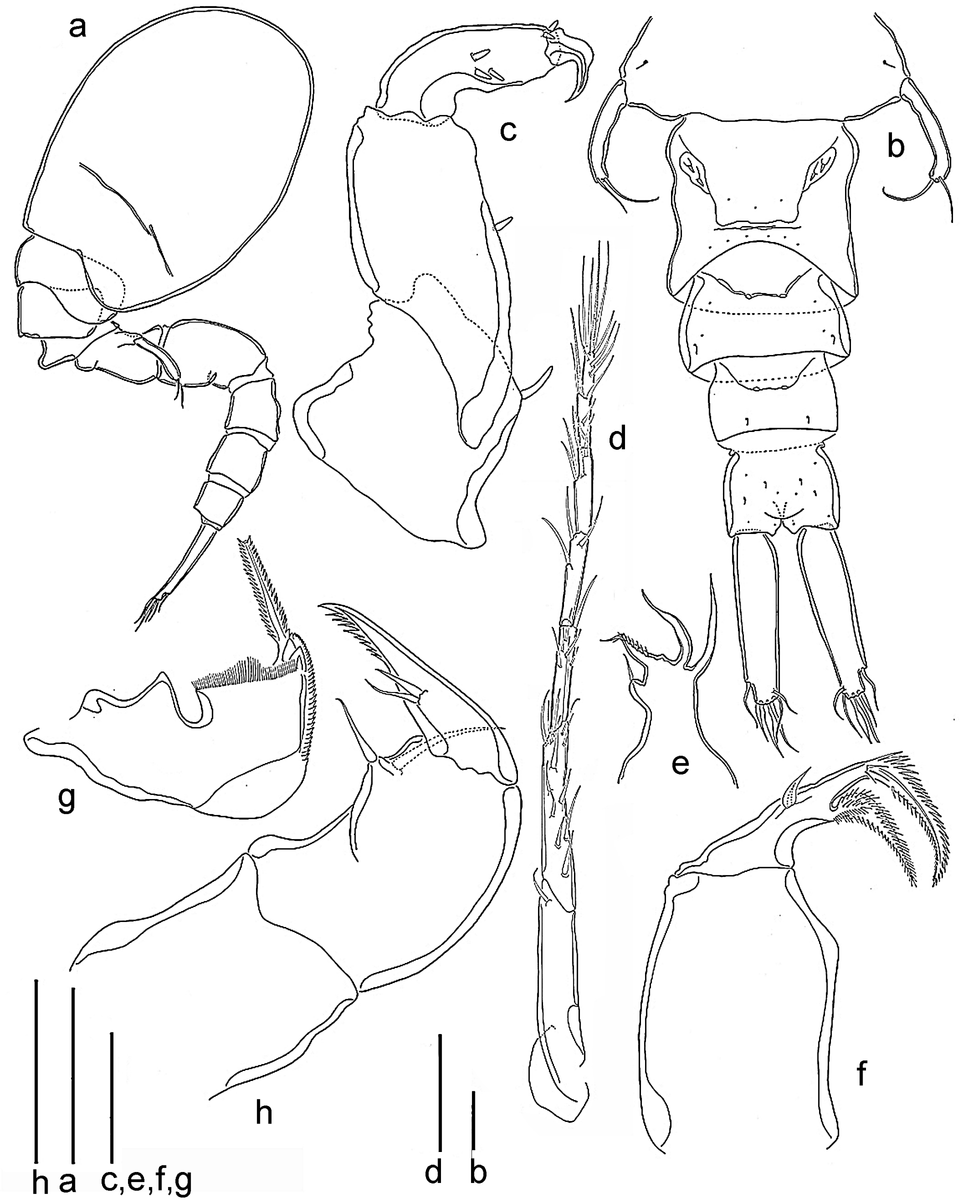

Figure 3. *Spaniomolgus globus* sp. n., female. **a** Habitus lateral **b** Urosome dorsal **c** Antenna **d** Antennule **e** Maxillule **f** Maxilla **g** Mandible **h** Maxilliped. Scale bars: 300 µm (**a**); 100 µm (**b**); 50 µm (**c–h**).

Antennule (Fig. 3d) 7-segmented, segments 67, 97, 41, 39, 35, 21 and 20 µm long respectively (measured along their posterior margin). Armature formula as follows: 1, 13, 6, 3, 4 and 1 aesthetasc, 3 and 1 aesthetasc and 7 (two of them joined at the base) and 1 aesthetasc. All setae relatively short and naked.

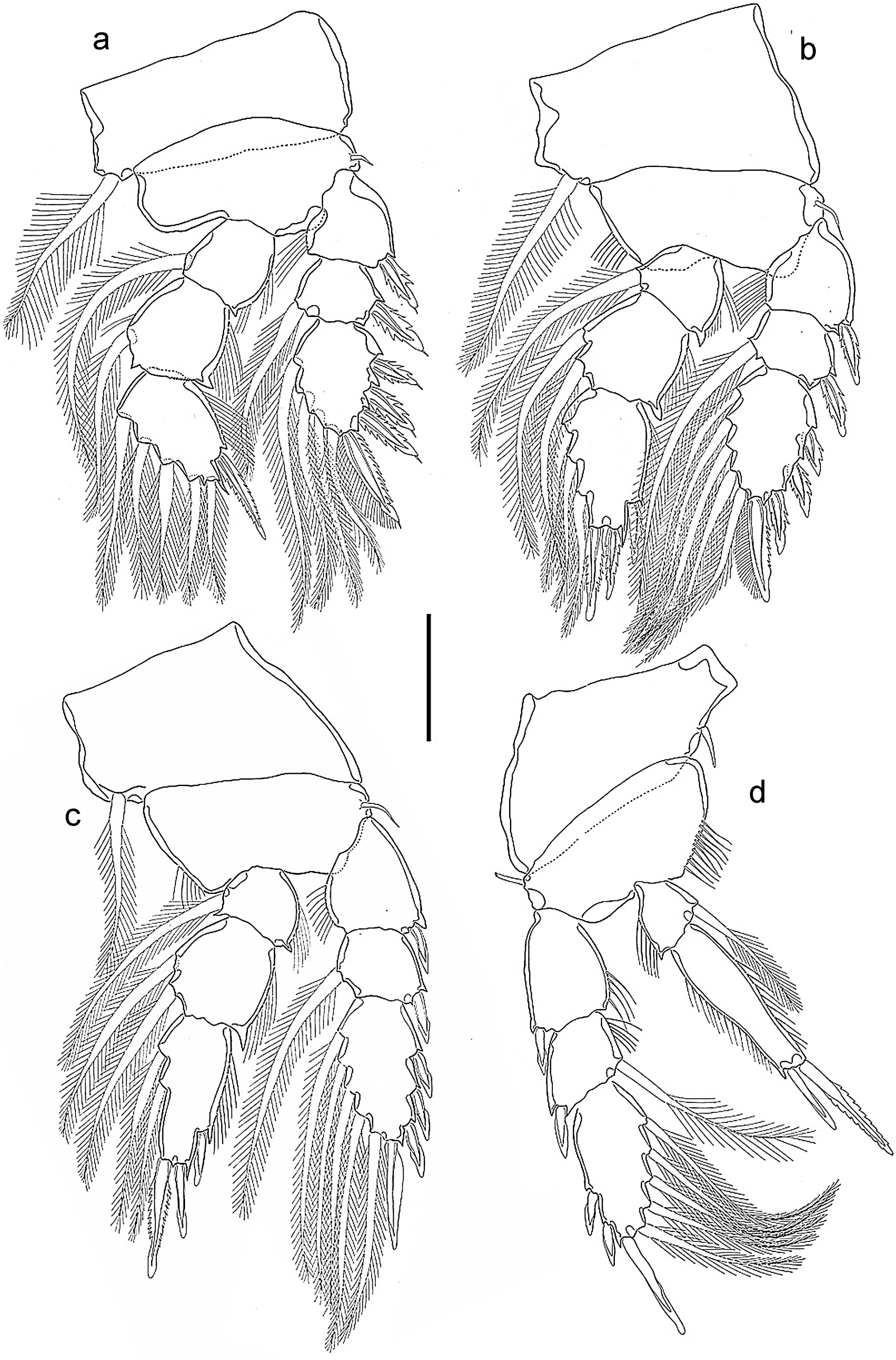

Figure 4. *Spaniomolgus globus* sp. n., female. **a** Leg 1 **b** Leg 2 **c** Leg 3 **d** Leg 4 Scale bar: 50 μm.

Antenna (Fig. 3c) 3-segmented; first segment 81µm long with small terminal hyaline seta; second segment 113 µm long with similar seta medially; third segment (formed by fusion of original segments 3 and 4 in *Lichomolgus*) 63 µm long with three hyaline setae medially (representing the usual three setae on penultimate segment in *Lichomolgus*) and two apical hyaline setae. Small recurved terminal claw 32 µm long. Length ratio of second to third segment (measured along inner margin) 2.1:1.

Mandible (Fig. 3g). Basal region with a rounded hyaline expansion and a distal row of small teeth on inner margin, and a fringe of setules on the outer margin. Terminal lash long, denticulated.

Maxillule (Fig. 3e) a single segment with a small seta and three hyaline prolongations (seemingly not articulated), one of them ornamented with setules.

Maxilla (Fig. 3f) 2-segmented; proximal segment unarmed; distal segment with a small seta medially, and two setiform processes apically, one barbed, the other with spinules.

Maxilliped (Fig. 3h) 3-segmented; first segment unarmed; second segment robust, with two naked inner setae; third segment claw-like denticulated distally, with two setae medially.

Legs 1–4 (Fig. 4a-d) with 3-segmented rami except for 2-segmented leg 4 endopod. Inner coxal seta long and plumose in legs 1–3, short and naked in leg 4. Outer basal seta short and naked in all legs. Endopod of leg 4 reaching beyond middle of third exopodal segment; with two terminal spines unequal in length, outer 32 µm long, inner 55 µm long, the latter spines with hyaline. Outer spines on leg 4 exopod with smooth lamellae. Armature formula as follows:

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

Fifth leg (Fig. 3b) with protopod incorporated into somite; outer basal smooth seta minute. Free exopodal segment long, slender and recurved, 6.7 times as long as wide, bearing two apical setae unequal in length, innermost more than twice the length of outer one.

Sixth leg (Fig. 3b) represented by two very small articulated spines near attachment of eggs sacs.

Male unknown.

Spaniomolgus dentatus **sp. n.**

http://zoobank.org/4A6D3CC9-2492-4092-82D8-38F95675696A

Fig. 5

Type locality. Saudi Arabian Red Sea, reef near Thuwal, 22°03'48.5"N, 38°45'51.2"E.

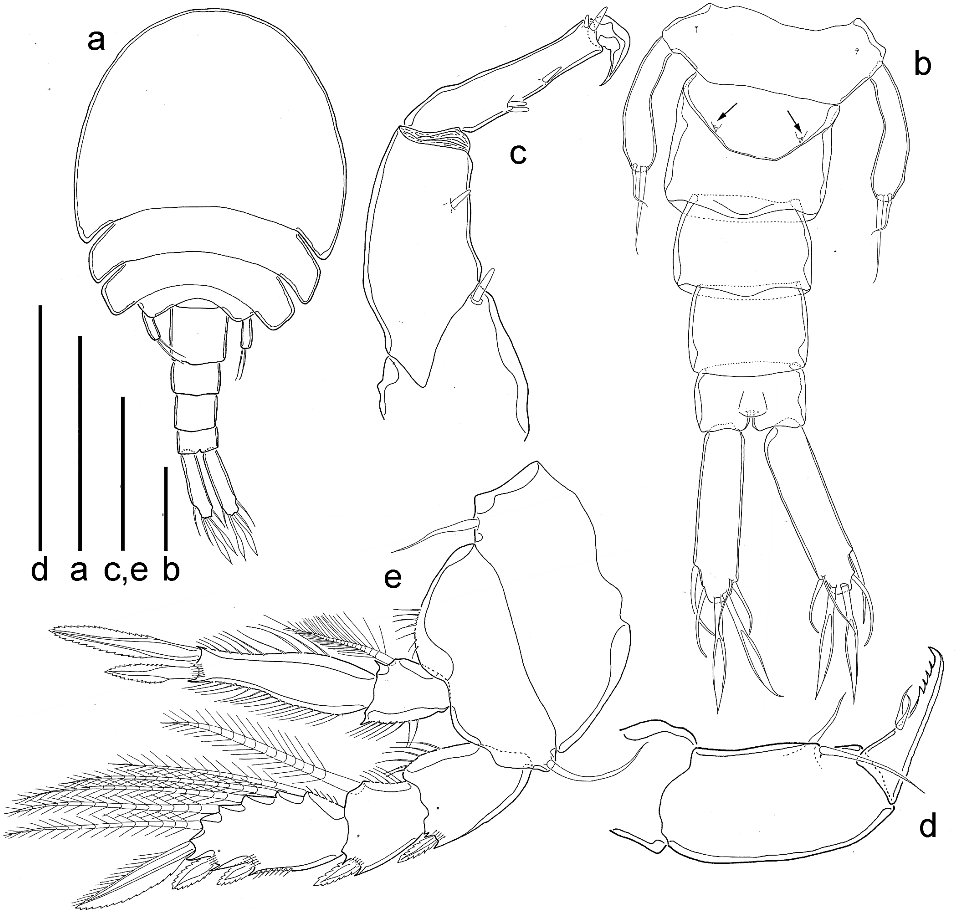

Figure 5. *Spaniomolgus dentatus* sp. n., female. **a** Habitus dorsal **b** Urosome dorsal (Leg 6 arrowed) **c** Antenna **d** Maxilliped **e** Leg 4. Scale bars: 300 µm (**a**); 100 µm (**b**); 50 µm (**c–e**).

Material examined. 1 ♀ holotype (ZMMU Me-1213) and 1 ♀ paratype (ZMMU Me-1214) from *Stylophora pistillata* (morphotype *S. danae*) (KAUST SA2013-31) collected at 28 m depth.

Etymology. The specific name from the Latin *dentatus*, refers to the denticulated margin of the maxillipedal claw.

Description. Adult female.

Body cyclopiform, with oval cephalothorax and cylindrical urosome (Fig. 5a). Body length 750 µm and maximum width 390 µm. Prosome comprising cephalothorax and three free pedigerous somites. Second and third pedigerous somites with slightly rectangular epimeral areas. Fourth pedigerous somite smaller than preceding ones, its epimeral areas much less expanded.

Urosome 5-segmented, comprising fifth pedigerous somite, genital double-somite and three free abdominal somites (Fig. 6b). Leg 5-bearing somite wider than long.

Genital double-somite (Fig. 5b) slightly longer than wide (95 × 83 µm); lateral margins nearly parallel. Paired genital apertures bipartite, each comprising ventrolateral copulatory pore and dorsolateral gonopore (oviduct opening). Each genital area with two minute spiniform elements (Fig. 5b). Egg sac unknown. Three postgenital somites 55 × 83, 53 × 72 and 39 × 67 µm from anterior to posterior.

Caudal rami (Fig. 5b) elongated, 108 × 25 µm, 4.3 times as long as wide. With six setae; all setae relatively short and naked. Outer lateral seta 44 µm, outermost terminal seta 41 µm, innermost terminal seta 33 µm. Two median terminal setae broadened, 72 µm (outer) and 66 µm (inner) in length. Dorsal seta 39 µm.

Antennule, mandible, maxillule, maxilla and armature formula for legs 1–4 as for *Spaniomolgus globus* sp. n.

Antenna (Fig. 5c) 3-segmented; first segment 53 µm long with small terminal hyaline seta; second segment 68 µm long with seta medially; third segment 60 µm long with three hyaline setae medially and two apical hyaline setae, small recurved terminal claw 24 µm long. Second and third segments measured along inner margin subequal in length.

Maxilliped (Fig. 5d) 3-segmented. First segment unarmed; second segment slightly elongated, with two naked inner setae; third segment claw-like, denticulate distally, with two setae medially.

Leg 4 (Fig. 5e) with 3-segmented exopod and 2-segmented endopod. Inner coxal seta and outer basal seta naked. Endopod reaching beyond middle of third exopodal segment; second segment with two apical spines unequal in length, outer 30 µm long, inner 50 µm long, the latter spines with hyaline and weakly serrated margins. Outer spines of exopod with barbed lamellae.

Fifth leg (Fig. 5b) with protopod incorporated into somite; outer basal seta not observed. Free segment long, slender and recurved, 4.2 times as long as wide, bearing two apical setae unequal in length, inner most about twice as long as outer one.

Sixth leg (arrowed in Fig. 5b) represented by two very small articulated projections near attachment of eggs sacs.

Male unknown.

***Spaniomolgus maculatus* sp. n.**

http://zoobank.org/3269010E-C96D-4F9B-8FBB-4189C01F6455

Fig. 6

Type locality. Saudi Arabian Red Sea, reef near Thuwal, 22°19'09.26"N, 38°51'15.78"E.

Material examined. 1 ♀ holotype (ZMMU Me-1215) and 1 ♀ paratype (ZMMU Me-1216) from *Stylophora pistillata* (morphotype *S. subseriata*) (KAUST SA2013-25) collected at 10.4 m depth; 1 additional ♀ from *Stylophora pistillata* (morphotype *S. danae*) (KAUST SA2013-31) (22°03'48.5"N, 38°45'51.2"E) collected at 28 m depth.

Etymology. The specific Latin epithet *maculatus* refers to the maculate body surface, light brown when alive.

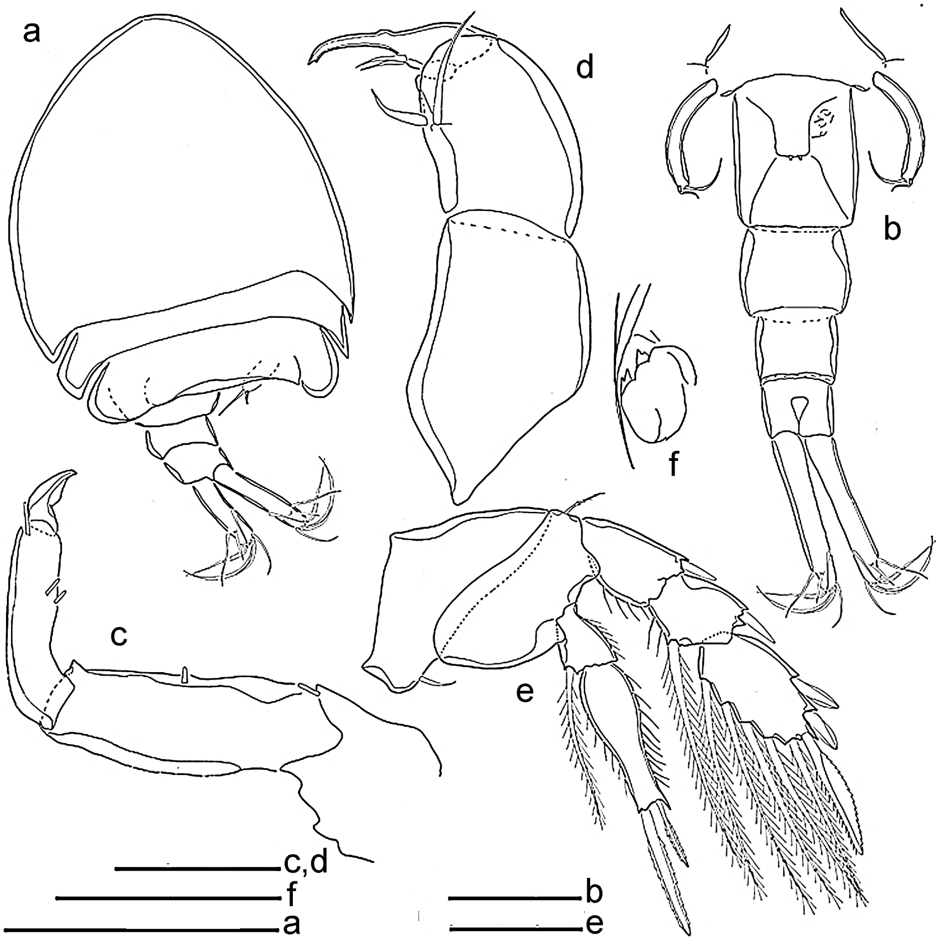

Figure 6. *Spaniomolgus maculatus* sp. n., female. **a** Habitus dorsal **b** Urosome dorsal **c** Antenna **d** Maxilliped **e** Leg 4 **f** Genital area. Scale bars: 300 µm (**a**); 100 µm (**b**); 50 µm (**c–f**).

Description. Adult female.

Body cyclopiform; oval cephalothorax slightly pointed on top and cylindrical urosome (Fig. 6a). Mean body length 710 µm (with range of 700 – 720 µm) and mean maximum width 315 µm (with range of 270 – 360 µm), based on two specimens. Prosome comprising cephalothorax and three free pedigerous somites. Second pedigerous somite with epimeral area slightly angular and third pedigerous somite with epimeral area rounded. Fourth pedigerous somite smaller than preceding ones, almost invisible in dorsal view.

Urosome s-shaped when alive, with the genital double-somite drawn forward under the metasome and the postgenital somites retained in line with the prosome. Urosome 5-segmented, comprising fifth pedigerous somite, genital double-somite and three free abdominal somites (Fig. 6b). In dorsal view, only the postgenital somites visible. Leg

5-bearing somite slightly wider than long. Genital double-somite (Fig. 6b) narrow, slightly longer than wide (108 × 92 µm); lateral margins nearly parallel. Paired genital apertures bipartite, each comprising ventrolateral copulatory pore and dorsolateral gonopore (oviduct opening). Each genital area with two very small articulated projections (Fig. 6f). Egg sac unknown. Three postgenital somites 67 × 83, 50 × 63 and 42 × 54 µm from anterior to posterior.

Caudal rami (Fig. 6b) elongated, 125 × 21 µm, 5.0 times longer than wide. With six setae, all short and naked. Outer lateral seta 42 µm, outermost terminal seta 54 µm, inner lateral seta 33 µm, innermost terminal seta 37 µm, median terminal setae 71 µm in length. Dorsal seta 20 µm.

Antennule, mandible, maxillule, maxilla and armature formula for legs 1–4 as for *Spaniomolgus globus* sp. n.

Antenna (Fig. 6c) 3-segmented; first segment 45 µm long with small hyaline apical seta; second segment 87 µm long with one hyaline seta medially; third segment 55 µm long with two hyaline setae medially, and one apical hyaline seta, with small recurved terminal claw 22 µm long. Length ratio of second to third segments (measured along inner margin) 1.7:1.

Maxilliped (Fig. 6d) 3-segmented; first segment unarmed; second segment robust, with two naked inner setae; third segment claw-like, with two setae medially equal in length; apex with pore.

Leg 4 (Fig. 6e) with 3-segmented exopod and 2-segmented endopod. Inner coxal seta short and naked, outer basal seta short and plumose. Endopod reaching beyond middle of third exopodal segment; with two distal spines unequal in length, outer 30 µm long, inner 50 µm long, the latter spines with hyaline and weakly serrated margins. Outer spines of exopod with smooth lamellae.

Fifth leg (Fig. 6b) with protopod incorporated into somite; outer basal smooth seta short. Free segment long, slender and recurved, 7.6 times as long as wide, bearing two apical setae unequal in length, inner most about twice as long as outer one.

Male unknown.

***Spaniomolgus acutus* sp. n.**

http://zoobank.org/10C25D5C-ED4B-4234-B6BA-F0B3988225B7

Fig. 7

Type locality. Saudi Arabian Red Sea, reef near Thuwal, 22°19'9.26"N, 38°51'15.78"E.

Material examined. 1 ♀ holotype (ZMMU Me-1217) and 1 ♀ paratype (ZMMU Me-1218) from *Stylophora pistillata* (morphotype *S. subseriata*) (KAUST SA2013-25) collected at 10.4 m depth; 1 additional ♀ from *Stylophora pistillata* (morphotype *S. danae*) (KAUST SA2013-31) (22°03'48.5"N, 38°45'51.2"E) collected at 28 m depth.

Etymology. The specific Latin epithet *acutus*, pointed, refers to the pointed epimeral areas of the second and third pedigerous somites.

Description. Adult female.

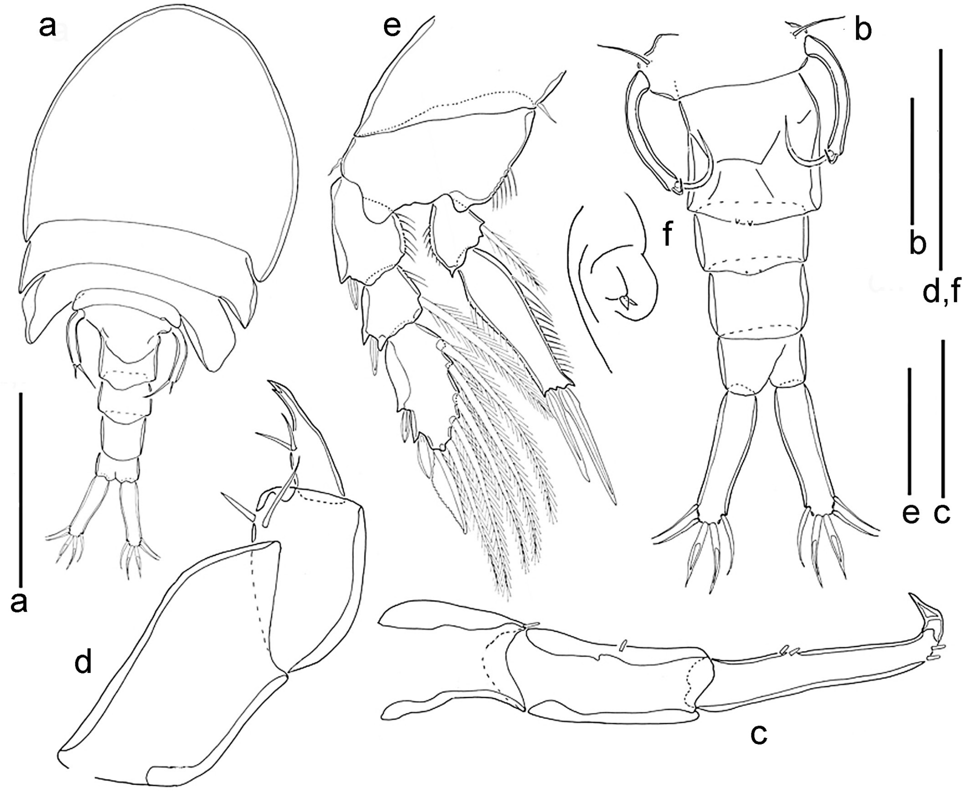

Figure 7. *Spaniomolgus acutus* sp. n., female. **a** Habitus dorsal **b** Urosome dorsal **c** Antenna **d** Maxilliped **e** Leg 4 **f** Genital area. Scale bars: 300 µm (**a**); 100 µm (**b**); 50 µm (**c–f**).

Body cyclopiform, with oval cephalothorax and cylindrical urosome (Fig. 7a). Mean body length 855 µm (with range of 850 – 860 µm) and mean maximum width 365 µm (with range of 320 – 410 µm), based on two specimens. Prosome comprising cephalothorax and three free pedigerous somites. Second and third pedigerous somites with epimeral areas pointed. Fourth pedigerous somite smaller than preceding ones, its epimeral areas much less expanded.

Urosome 5-segmented, comprising fifth pedigerous somite, genital double-somite and three free abdominal somites (Fig. 7b). Leg 5-bearing somite slightly wider than long. Genital double-somite (Fig. 7b) narrow, slightly longer than wide (107 × 100 µm); lateral margins nearly parallel. Paired genital apertures bipartite, each comprising ventrolateral copulatory pore and dorsolateral gonopore (oviduct opening). Each genital area with two minute spiniform elements (Fig. 7f). Egg sac unknown. Three postgenital somites 48 × 89, 52 × 78 and 40 × 70 µm from anterior to posterior.

Caudal rami (Fig. 7b) elongated, 111 × 30 µm, 3.7 times longer than wide. With five setae, all relatively short and naked. Outer lateral seta 44 µm, outermost terminal seta 41 µm, innermost terminal seta 48 µm. Two median terminal setae broadened, 52 µm (outer) and 59 µm (inner) in length. Dorsal seta not observed.

Antennule, mandible, maxillule, maxilla and armature formula for legs 1–4 as for *Spaniomolgus globus* sp. n.

Antenna (Fig. c) 3-segmented; first segment 48µm long with small terminal hyaline seta; second segment 60 µm long, with similar seta medially; third segment 76 µm long, with two hyaline setae medially, and two apical hyaline setae, with small recurved terminal claw 20 µm long. Length ratio of second to third segments (measured along inner margin) 1:1.2.

Maxilliped (Fig. 7d) 3-segmented; first segment unarmed; second segment robust, with two naked inner setae; third claw-like segment with two setae medially, and a tooth subapically.

Leg 4 (Fig. 7e) with 3-segmented exopod and 2-segmented endopod. Inner coxal seta and outer basal seta short and naked. Endopod reaching tip of third exopodal segment, with two apical spines unequal in length, outer 39 µm long, inner 52 µm long, the latter spines with hyaline and smooth margins. Outer spines on leg 4 exopod with smooth lamellae.

Fifth leg (Fig. 7b) with protopod incorporated into somite; outer basal seta smooth. Free segment long, slender and recurved, 9.3 times as long as wide, bearing two apical setae unequal in length, inner most 3.6 times the length of outer one.

Sixth leg (Fig. 7f) represented by two very small articulated projections near attachment of eggs sacs.

Male unknown.

***Spaniomolgus stylophorus* sp. n.**

http://zoobank.org/56C93061-E2C5-47E5-8A3C-977D264B169E

Figs 8, 9 b–d

Type locality. Saudi Arabian Red Sea, reef near Thuwal, 22°12'04.30"N, 38°57'31.40"E.

Material examined. 1 ♀ holotype (ZMMU Me-1211) and 1 ♀ paratype (ZMMU Me-1212) from *Stylophora pistillata* (KAUST SA2013-12) collected at 1 m depth in the inner part of the reef; 1 additional ♀ from *Stylophora pistillata* (morphotype *S. danae*) (KAUST SA2013-31) collected at 28 m depth in the outer part of reef (22°20'23.45"N, 38°50'52.33"E).

Etymology. The specific epithet *stylophorus* refers to the host name *Stylophora.*

Description. Adult female.

Body cyclopiform, with oval cephalothorax and cylindrical urosome (Figs 8a, 9b). Mean body length 1.15 mm (with range of 1.1 – 1.2 mm) and mean maximum width 365 µm (with range of 320 – 410 µm), based on two specimens. Somite bearing leg 1 completely separated from cephalosome. Epimeral areas of metasomal somites slightly angular. Fourth pedigerous somite smaller than preceding ones, its epimeral areas not visible in dorsal view.

Urosome 5-segmented, comprising fifth pedigerous somite, genital double-somite and three free abdominal somites (Fig. 8b). In dorsal view, only the postgenital somites visible. Leg 5-bearing somite slightly wider than long. Genital double-somite (Fig. 8b) bell-

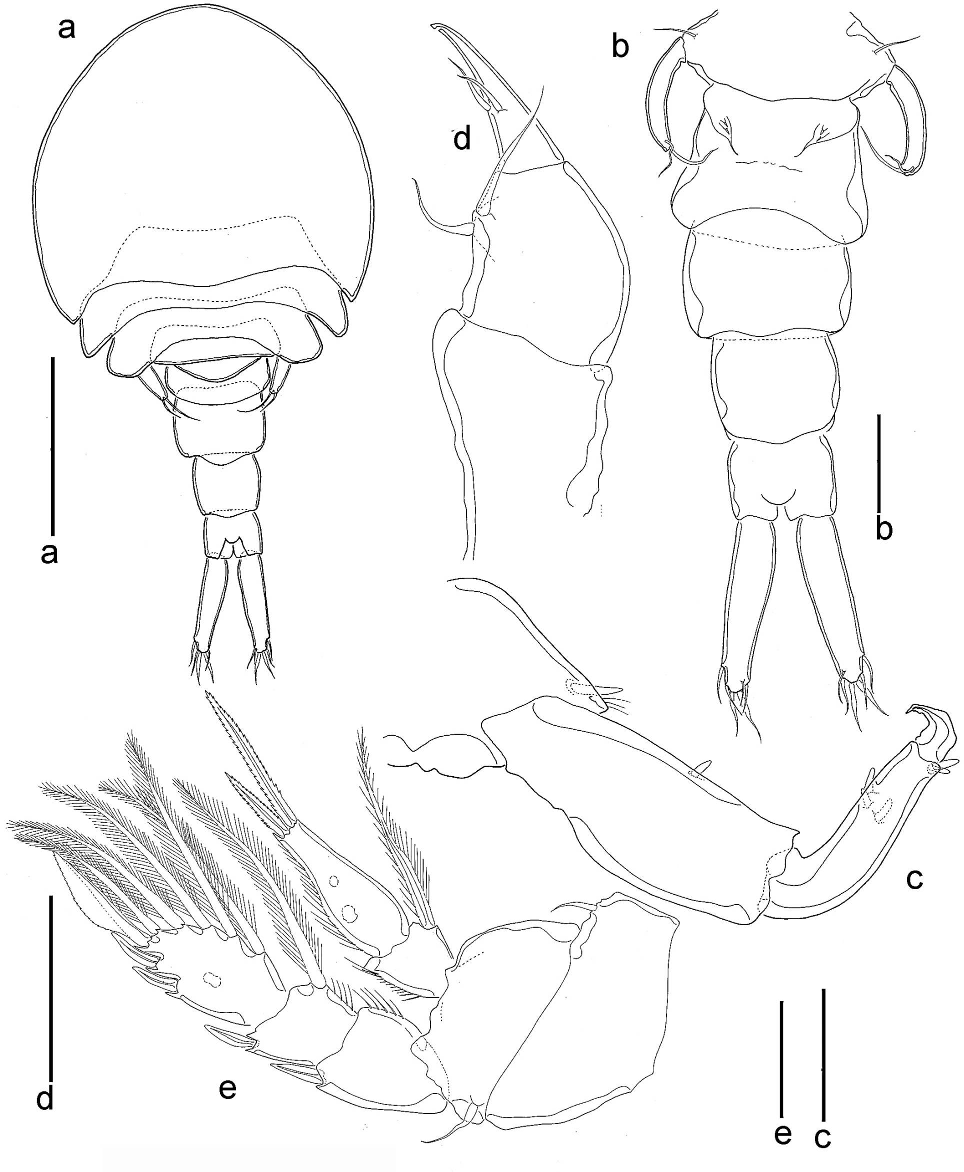

Figure 8. *Spaniomolgus stylophorus* sp. n., female. **a** Habitus dorsal **b** Urosome dorsal **c** Antenna **d** Maxilliped **e** Leg 4. Scale bars: 300 µm (**a**); 100 µm (**b**); 50 µm(**c–e**).

shaped; 170 µm minimum width (anterior half), 220 µm maximum width (posterior half) and 155 µm long; shorter dorsally than ventrally. Paired genital apertures bipartite, each comprising ventrolateral copulatory pore and dorsolateral gonopore (oviduct opening). Each genital area with two minute spiniform setae (Fig. 8b). Egg sac unknown. Three postgenital somites 120 × 180, 120 × 130 and 94 × 110 µm from anterior to posterior.

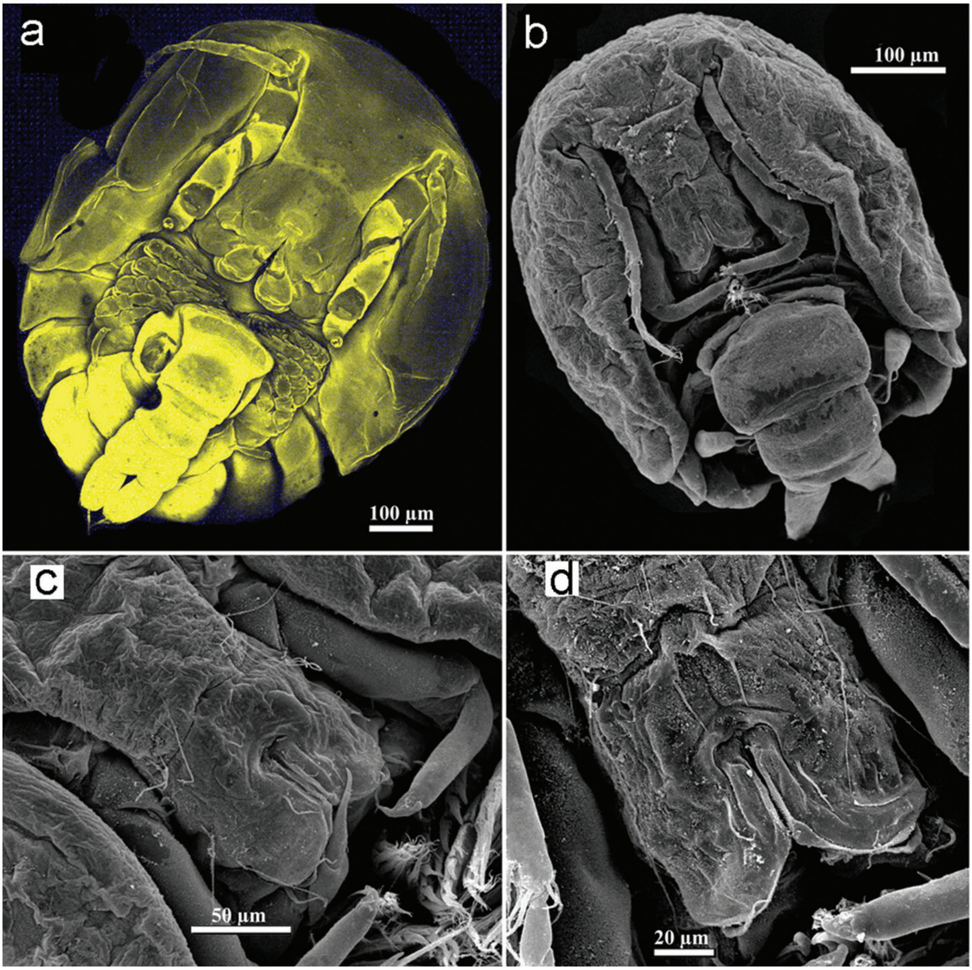

Figure 9. *Spaniomolgus,* females. **a** *S. crassus* (Humes & Ho, 1968), confocal photo. *S. stylophorus* sp. n., SEM **b** Habitus ventral **c** Rostral area **d** Labrum.

Caudal rami (Fig. 8b) elongated, 200 × 45 µm, 4.4 times as long as wide. With six setae, all relatively short and naked. Outer lateral seta 40 µm, outermost terminal seta 40 µm, innermost terminal seta 30 µm. Two median terminal setae broadened, 50 µm (outer) and 60 µm (inner) in length. Dorsal seta 25 µm.

Rostral area with hyaline setules (Fig. 9c, d).

Antennule, mandible, maxillule, maxilla and armature formula for legs 1–4 as for *Spaniomolgus globus* sp. n.

Antenna (Fig. 8c) 3-segmented; first segment 80µm long with small terminal hyaline seta; second segment 115 µm long with a seta medially; third segment 78 µm long with three hyaline setae medially, and two apical hyaline setae, with small recurved terminal claw 30 µm long. Length ratio of second to third segments (measured along inner margin) 1.5:1.

Maxilliped (Fig. 8d) 3-segmented; first segment unarmed; second segment robust, with two naked inner setae; third segment claw-like, with two setae medially equal in length; apex with pore.

Leg 4 (Fig. 8e) with 3-segmented exopod and 2-segmented endopod. Inner coxal seta and outer basal seta short and naked. Endopod reaching beyond middle of third exopodal segment, with two apical spines unequal in length, outer 38 µm and inner 70 µm, the latter spines with hyaline and serrated margins. Outer spines of exopod with smooth lamellae.

Leg 5 (Fig. 8b) with protopod incorporated into somite; outer basal seta naked. Free segment long, slender and recurved, 5.0 times as long as wide, bearing two apical setae unequal in length, inner most more than twice the length of outer one.

Male unknown.

***Spaniomolgus crassus* (Humes & Ho, 1968)**
Fig. 9a

Material examined. 2 ♀♀ found in tubular-shaped modification of corallites of *Stylophora pistillata* (morphotype *S. mordax*) (KAUST SA2013-72) collected on a reef near Al Lith at 2.5 m depth (20°08'02"N, 40°05'59"E).

Discussion

Taxonomy

Designation of the genus *Spaniomolgus* Humes & Stock, 1973 was based on three previously known species of *Lichomolgus* copepods associated with scleractinian corals: the type species *S. compositus*, *S. geminus*, and *S. crassus* from northern Madagascar (Humes and Frost 1964, Humes and Ho 1968). The finding of five new species and *S. crassus* in the Red Sea is the first record since 1968. Although *Spaniomolgus* is a rather homogenous genus, there are differences among its eight species.

The body has a broadened and thickened prosome in *S. crassus* and *S. globus,* but it is moderately widened, and the epimeral areas of the second and third pedigerous somites are slightly rectangular or angular in *S. stylophorus*, *S. geminus*, *S. compositus*, *S. dentatus*, *S. maculatus,* and *S. acutus*. Another key character to separate the species of *Spaniomolgus* is the body organization. For example, the first pedigerous somite is clearly set off from the cephalosome in *S. crassus* and *S. stylophorus,* incompletely separated from the cephalosome by an indistinct furrow in *S. geminus*, *S. compositus,* and *S. globus*, and completely fused to the cephalosome in *S. dentatus, S. maculatus*, and *S. acutus*.

The antennules are very similar in all eight species, with the only difference being the presence of an extra seta in the sixth segment in *S. globus*, *S. stylophorus*, *S. dentatus*, *S. maculatus*, and *S. acutus*.

The antenna of all species, except for *S. maculatus* and *S. acutus*, have the same armature formula (1,1,3+2+claw). *Spaniomolgus maculatus* and *S. acutus* have a reduced armature of 1,1,2+1+claw and 1,1,2+2+claw, respectively. The length ratio of the second and the third segments of the antenna can be also used for species delimitation. For example, the length ratio of the two distal antennary segments is 1.1:1 in *S. crassus*, *S. geminus*, *S. compositus,* and *S. dentatus*, but 1.5:1 in *S. stylophorus*, 1.7:1 in *S. maculatus*, 2.1:1 in *S. globus* (2.1: 1), and 1:1.2 in *S. acutus.*

The maxillules of *S. globus*, *S. stylophorus*, *S. dentatus*, *S. maculatus,* and *S. acutus* are represented by a single segment bearing a small seta and three hyaline prolongations without evident articulation. However, according to Humes and Frost (1964) and Humes and Ho (1968), the maxillule shows four hyaline prolongations without articulation in *S. geminus*, *S. compositus,* and *S. crassus*. The condition of the maxillulary projections of the latter three species needs to be reassessed because the articulation of one of these elements was probably overlooked.

As for the maxilliped, small interspecific differences in the third claw-like segment were detected. The margin of the claw has three very small subterminal spinules in *S. geminus*, *S. compositus,* and *S. crassus,* but it is smooth and with an apical pore in *S. stylophorus* and *S. maculatus*. The distal half of the claw's margin is denticulated in *S. globus* and *S. dentatus;* but with as single subapical tooth in *S. acutus*.

The armature of the legs is the same for the eight species; only the ornamentation of the fourth leg varies among the species. The exopodal spines have barbed lamellae in *S. geminus*, *S. compositus*, *S. dentatus*, *S. maculatus*, and *S. acutus*, but they are smooth in *S. crassus*, *S. globus*, and *S. stylophorus*. With respect to the terminal spines of the second endopodal segment, they are hyaline and smooth in *S. acutus* and *S. crassus*, but serrated in *S. stylophorus*, *S. dentatus*, *S. maculatus*, *S. compositus,* and *S. geminus*. In *S. globus* the outer terminal spine is serrated and the inner one is smooth.

The genital double-somite, generally rather narrow, can be present in three different shapes. In *S. crassus, S. compositus,* and *S. geminus* it is wider in its anterior third than in its posterior two-thirds; it is longer than wide with almost parallel margins in *S. dentatus, S. maculatus* and *S. acutus*, and completely square and bell-shaped in *S. globus* and *S. stylophorus* (wider in its posterior part).

The fifth leg in all species shows a long, slender and recurved segment of exopod with two apical setae. The length:width ratio of the free segment varies among the species, it is 10.5 times as long as wide in *S. geminus*, 9.3 times in *S. acutus,* 7.9 times in *S. compositus*, 7.6 times in *S. maculatus*, 6.7 times in *S. globus*, 6.3 times in *S. crassus*, 5.0 times in *S. stylophorus*, and 4.2 times in *S. dentatus*. Noteworthy, the outer basal seta of is minute in *S. globus* and has not been observed in *S. dentatus*.

The length:width ratio of the caudal rami, characteristically elongated in all the species, is also variable. The caudal rami are 9.1 times as long as wide in *S. geminus*, 5.0 times in *S. compositus* and *S. maculatus*, between 4.0 and 4.5 times in *S. globus*, *S. stylophorus* and *S. dentatus*, 3.7 times in *S. acutus*, and 2.8 times in *S. crassus*. The eight species present six terminal setae that are characteristically short and naked, except for *S. acutus* in which the dorsal seta has not been observed.

Key to species of the genus *Spaniomolgus* Humes & Stock, 1973 (females)

1 First pedigerous somite completely separated from cephalothorax **2**
– First pedigerous somite not completely separated from the cephalothorax **3**
2 Prosome unusually broadened and thickened; caudal rami 2.8 times as long as wide; length ratio of second to third segments of the antenna 1.1:1; terminal claw of maxilliped with subterminal spinules ....***S. crassus*** **(Humes & Ho, 1968)**
– Prosome broad; caudal rami 4.4 times as long as wide; length ratio of second to third segments of the antenna 1.5:1; terminal claw of maxilliped with apical pore ....***S. stylophorus*** **sp. n.**
3 First pedigerous somite incompletely separated from cephalosome by an indistinct furrow **4**
– Cephalosome fully incorporating first pedigerous somite **6**
4 Caudal rami greatly elongated, 9.1 times as long as wide; outer exopodal spines of fourth leg with barbed lamellae; free segment of fifth leg 10.5 times as long as wide... ***S. geminus*** **(Humes & Ho, 1968)**
– Caudal rami 5.0 times as long as wide or less **5**
5 Caudal rami 5.0 times as long as wide; length ratio of second to third segment of the antenna 1.1:1; outer exopodal spines of fourth leg with barbed lamellae; free segment of fifth leg 7.9 times as long as wide............ ***S. compositus*** **(Humes & Frost, 1964)**
– Caudal rami 4.0 times as long as wide; length ratio of second to third segment of the antenna 2.1:1; outer exopodal spines of fourth leg with smooth lamellae; free segment of fifth leg 6.7 times as long as wide ....***S. globus*** **sp. n.**
6 Outer exopodal spines of fourth leg with barbed lamellae; caudal rami 4.3 times as long as wide; length ratio of second to third segment of the antenna 1:1; free segment of fifth leg 4.2 times as long as wide................................ ***S. dentatus*** **sp. n.**
– Outer exopodal spines of fourth leg with smooth lamellae **7**
7 Caudal rami 5.0 times as long as wide; length ratio of second to third segment of the antenna 1.7:1; free segment of fifth leg 7.6 times as long as wide; terminal claw of maxilliped with apical pore .... ***S. maculatus*** **sp. n.**
– Caudal rami 3.7 times as long as wide; length ratio of second to third segment of the antenna 1:1.2; free segment of fifth leg 9.3 times as long as wide; terminal claw of maxilliped with a tooth subapically ....***S. acutus*** **sp. n.**

Hosts

Spaniomolgus compositus found by Humes and Frost (1964) in washings of *Stylophora subseriata,* and *Spaniomolgus crassus* and S. *geminus* reported by Humes and Ho (1968) from washings of *Stylophora mordax* (Dana, 1846) should be now considered as co-occurring symbionts of one coral host, *Stylophora pistillata.* We assume that the coral indicated by Humes and Frost (1964) as *Seriatopora subseriata* is actually *Stylophora subseriata* (Ehrenberg, 1834) as the name *Seriatopora subseriata* is not valid. Thus, all eight species of *Spaniomolgus* reported in the present paper are now considered as associates of a single host species, *Stylophora pistillata*.

Ecological comments

The scleractinian coral *Stylophora* is considered to be one of the main Indo-Pacific reef-framework builders and is one of the dominant species in shallow-water reef environments exposed to strong wave action (Veron 2000). *Stylophora pistillata* hosts a great variety of copepods, including highly transformed xarifiids, which live in the gastrovascular cavities of the polyps. These symbiotic copepods were first noticed by Dr. Sebastian A. Gerlach during the Xarifa Expedition to the Red Sea and the Maldives Archipelago in 1957–1958 (Humes 1985a). Since then, copepods of three different orders have been found in association with this scleractinian coral: one species of Harpacticoida, *Alteuthellopsis corallina* Humes, 1981 (Peltidiidae, ectosymbiotic), three species of Siphonostomatoida, *Asteropontius corallophilus* Stock, 1966, *A. magnisetiger* Kim, 2010, *Gascardama longisiphonata* Kim, 2010, and seven species of Poecilostomatoida (Stock 1966, Humes 1981, Kim 2010). Among these poecilostomatoid copepods, five endosymbiotic species belong to the family Xarifiidae, *Xarifia decorata* Humes & Ho, 1968, *X. dissona* Humes, 1985, *X. lissa* Humes & Ho, 1968, *X. obesa* Humes & Ho, 1968, and *X. lissa* Humes & Ho, 1968, and three ectosymbiotic species belong to the family Rhynchomolgidae, *S. crassus*, *S. compositus*, and *S. geminus* (Humes and Frost 1964, Humes and Ho 1968, Humes 1985b).

Though coral-associated copepods have been studied for a considerable period of time, there remains a scarcity of data on their biology and ecology (Humes 1994, Ho 2001, Cheng et al. 2016, Ivanenko et al. 2018). Relationships between copepods and their hosts remain poorly studied due to the microscopic size of these crustaceans making *in situ* observations difficult. There are only few studies that include information about the interactions between copepods and corals (e.g. Ivanenko et al. 2014, Shelyakin et al. 2018).

Recent experiments by Cheng and Dai (2009) showed the ability of xarifiid copepods to get inside of the polyp of *S. pistillata* and to stay there as a symbiont. These copepods can make a polyp open its mouth either by releasing specific chemicals which induce feeding behaviour or act as muscle relaxants. However, it is still unclear which mechanism is actually utilized. It is also unknown if other coral species may be infected in a similar manner. Gall-inducing copepods are another example of coral hosts being affected by copepods. These copepods appear to attach to the soft tissues of the coral, and by disturbing it with their swimming legs, elicit the defence mechanism of a coral to grow a calcareous barrier (Dojiri 1988, Ivanenko et al. 2014). The multifocal purple spots syndrome of sea fans, which was thought to be caused by a fungous pathogen, appears to be induced by endoparasitic copepods sitting in the tissue outgrowths (Ivanenko et al. 2017).

It is often unclear whether copepods should be classified as parasites, because of the absence of rigorous experimental documentation. If we want to study copepod-coral relationships, it is crucial to know which copepod species are involved in symbiosis and what is their effect on the host. Therefore, it is important to provide detailed descriptions as well as identification keys for all copepod species associated with corals, so species composition and abundance of copepod communities can be tracked and used as a bioindicator for environmental changes and coral health (Ho 2001, Zeppilli et al. 2015, 2018).

Moreover, most of the symbiotic copepods depend entirely on the well-being of their hosts, and with the loss of corals during the recent bleaching events, many species of copepods associated with these corals could disappear, some even before being described. For instance, reefs close to Al Lith in the central Red Sea, where some of our samples were collected, were severely affected by the major bleaching event of 2015–2016 (Monroe et al. 2018, Osman et al. 2018). Most of the colonies of *S. pistillata* at the Al Lith reefs and about 20% of colonies at the Thuwal reefs were bleached and died (Monroe et al. 2018, Osman et al. 2018, personal observations of V.N. Ivanenko and S.V. Mudrova in May 2017). Therefore, abundance and diversity of copepods could have also been strongly affected, and some of the species collected from the reefs near Al Lith may already be gone from this region.

Acknowledgments

We thank Michael Berumen (KAUST) for organizing the expedition and the crew of the M/Y Dream Island and the KAUST Coastal and Marine Resources Core Lab for assistance during field work. The authors acknowledge Jessica Bouwmeester (KAUST) for taking photos of the coral skeletons, Alexandra Petrunina (Moscow State University) for helping with using of confocal laser scanning microscope, and Matthew Tietbohl (KAUST) for proofreading, Samuel Gomez (Universidad Nacional Autónoma de México) and Geoff Boxshall (Natural History Museum, London) for reviewing manuscript and valuable comments.

The sampling and research of S.V. Mudrova were supported by award No.1389-CRG1 and baseline funding from the King Abdullah University of Science and Technology (KAUST) to M.L. Berumen. Scanning electronic microscopy was conducted with support from the Russian Foundation for Basic Research (grant 18-04-01192). Confocal microscopy and paper preparation were supported by the Russian Foundation for Basic Research (grant 18-54-45016). Field work of V.N. Ivanenko was conducted with support of the Russian Science Foundation (grant 14-50-00029).

All necessary permits for sampling and observational field studies have been obtained by the authors from the competent authorities and are mentioned in the acknowledgements, if applicable.

References

Arrigoni R, Benzoni F, Terraneo TI, Caragnano A, Berumen ML (2016) Recent origin and semi-permeable species boundaries in the scleractinian coral genus *Stylophora* from the Red Sea. Scientific Reports 6: 34612. https://doi.org/10.1038/srep34612

Boxshall GA, Halsey SH (2004) An introduction to Copepod Diversity. The Ray Society, London.

Cheng YG, Dai C-F (2009) The infection process of the reef coral *Stylophora pistillata* by the parasitic copepod, *Xarifia obesa*. Coral Reefs 28: 681–681. https://doi.org/10.1007/s00338-009-0493-9

Cheng YG, Dai C-F (2010) Endosymbiotic copepods may feed on zooxanthellae from their coral host, *Pocillopora damicornis*. Coral Reefs 29: 13–18. https://doi.org/10.1007/s00338-009-0559-8

Cheng YG, Mayfield AB, Meng PJ, Dai CF, Huys R (2016) Copepods associated with scleractinian corals: a worldwide checklist and a case study of their impact on the reef-building coral *Pocillopora damicornis* (Linnaeus, 1758) (Pocilloporidae). Zootaxa 4174: 291–345. https://doi.org/10.11646/zootaxa.4174.1.20

Corgosinho PH, Kihara TC, Schizas NV, Ostmann A, Arbizu PM, Ivanenko VN (2018) Traditional and confocal descriptions of a new genus and two new species of deep water Cerviniinae Sars, 1903 (Copepoda, Harpacticoida, Aegisthidae) from the Southern Atlantic and the Norwegian Sea: with a discussion on the use of digital media in taxonomy. ZooKeys 766: 1–38. https://doi.org/10.3897/zookeys.766.23899

Dojiri M (1988) *Isomolgus desmotes*, new genus, new species (Lichomolgidae), a gallicolous poecilostome copepod from the scleractinian coral *Seriatopora hystrix* Dana in Indonesia, with a review of gall-inhabiting crustaceans of anthozoans. Journal of Crustacean Biology 8(1): 99–109. https://doi.org/10.2307/1548435

Ho J-S (2001) Why do symbiotic copepods matter? Copepoda: Developments in Ecology, Biology and Systematics. Hydrobiologia 453/454: 1–7. https://doi.org/10.1023/A:1013139212227

Ho J-S, Ivanenko VN (2013) *Doridicola indistinctus* n. sp. (Copepoda: Poecilostomatoida: Rhynchomolgidae) associated with the soft coral *Gersemia fruticosa* Sars (Octocorallia: Alcyonacea: Nephtheidae) from the White Sea. Systematic Parasitology 85: 235–241. https://doi.org/10.1007/s11230-013-9419-6

Ho J-S, Kim I-H (2001) New Species of *Doridicola* (Copepoda, Rhynchomolgidae) from Thailand, with a Cladistic Analysis of the Genus. Journal of Crustacean Biology 21: 78–89. https://doi.org/10.1163/20021975-99990110

Humes AG (1981) Harpacticoid copepods associated with Cnidaria in the Indo-West Pacific. Journal of crustacean Biology 1(2): 227–240. https://doi.org/10.2307/1548161

Humes AG (1985a) A review of the Xarifiidae (Copepoda, Poecilostomatoida), parasites of scleractinian corals in the Indo-Pacific. Bulletin of Marine Science 36: 467–632.

Humes AG (1985b) Cnidarians and copepods. A success story. Transactions of the American Microscopical Society 104: 313–320. https://doi.org/10.2307/3226484

Humes AG (1994) How many copepods? Hydrobiologia 292/293: 1–7. https://doi.org/10.1007/BF00229916

Humes AG, Frost BW (1964) New lichomolgid copepods (Cyclopoida) associated with alcyonarians and madreporarians in Madagascar. Cahiers ORSTOM Océanographie 6: 131–212.

Humes AG, Ho J-S (1968) Lichomolgid copepods (Cyclopoida) associated with corals in Madagascar. Bulletin of the Museum of Comparative Zoology, Harvard University 136: 353–503.

Humes AG, Stock JH (1972) Preliminary notes on a revision of the Lichomolgidae, Cyclopoid Copepods mainly associated with marine invertebrates. Bulletin Zoologisch Museum. Universiteit van Amsterdam 2: 121–133.

Humes AG, Stock JH (1973) A revision of the Lichomolgidae, cyclopoid copepods mainly associated with marine invertebrates. Smithsonian Contributions to Zoology 127: 1–368. https://doi.org/10.5479/si.00810282.127

ICZN, International Commission on Zoological Nomenclature (1999) International Code of Zoological Nomenclature (4th edn). The International Trust for Zoological Nomenclature, Natural History Museum, London.

Ivanenko VN, Corgosinho PH, Ferrari F, Sarradin PM, Sarrazin J (2012) Microhabitat distribution of *Smacigastes micheli* (Copepoda: Harpacticoida: Tegastidae) from deep-sea hydrothermal vents at the Mid-Atlantic Ridge, 37°N (Lucky Strike), with a morphological description of its nauplius. Marine Ecology 33: 246–25. https://doi.org/10.1111/j.1439-0485.2011.00484.x

Ivanenko VN, Defaye D (2004) A new genus and species of deep-sea cyclopoids (Copepoda, Cyclopinidae) from the Mid-Atlantic Ridge (Azores Triple Junction, Lucky Strike). Zoosystema 26(1): 49–64.

Ivanenko VN, Moudrova SV, Bouwmeester J, Berumen ML (2014) First report of tubular corallites on *Stylophora* caused by a symbiotic copepod crustacean. Coral Reefs 33: 637–637. https://doi.org/10.1007/s00338-014-1186-6

Ivanenko VN, Nikitin MA, Hoeksema BW (2017) Multiple purple spots in the Caribbean sea fan *Gorgonia ventalina* caused by parasitic copepods at St. Eustatius, Dutch Caribbean. Marine Biodiversity 47: 79–80. https://doi.org/10.1007/s12526-015-0428-3

Ivanenko VN, Hoeksema BW, Mudrova SV, Nikitin MA, Martínez A, Rimskaya-Korsakova NN, Berumen ML, Fontaneto D (2018) Lack of host specificity of copepod crustaceans associated with mushroom corals in the Red Sea. Molecular Phylogenetics and Evolution 127: 770–780. https://doi.org/10.1016/j.ympev.2018.06.024

Jones E, Oliphant TE, Peterson P (2001) SciPy: open source scientific tools for Python. http://scipy.org [accessed 15 May 2018]

Kim IH (2010) Siphonostomatoid Copepoda (Crustacea) associated with invertebrates from tropical waters. Animal Systematics, Evolution and Diversity 8: 1–176.

Monroe AA, Ziegler M, Roik A, Röthig T, Hardenstine RS, Emms MA, Jensen T, Voolstra CR, Berumen ML (2018) In situ observations of coral bleaching in the central Saudi Arabian Red Sea during the 2015/2016 global coral bleaching event. PloS One 13: e0195814 https://doi.org/10.1371/journal.pone.0195814

Osman EO, Smith DJ, Ziegler M, Kürten B, Conrad, C, El-Haddad KM, Voolstra CR, Suggett DJ, Suggett DJ (2018) Thermal refugia against coral bleaching throughout the northern Red Sea. Global change biology 24: e474–e484 . https://doi.org/10.1111/gcb.13895

Sewell RBS (1949) The littoral and semi-parasitic Cyclopoida, the Monstrilloida and Notodelphyoida. John Murray Expedition 1933–34. Scientific Reports 9(2): 17–199.

Shelyakin PV, Garushyants SK, Nikitin MA, Mudrova SV, Berumen M, Speksnijder AGCL, Hoeksema BW, Fontaneto D, Gelfand MS, Ivanenko VN (2018) Microbiomes of gall-inducing copepod crustaceans from the corals *Stylophora pistillata* (Scleractinia) and *Gorgonia ventalina* (Alcyonacea). Scientific Reports 8: 11563. https://doi.org/10.1038/s41598-018-29953-y

Stella JS, Pratchett MS, Hutchings PA, Jones GP (2011) Coral-associated invertebrates: diversity, ecological importance and vulnerability to disturbance. Oceanography and Marine Biology. An Annual Review 49: 43–104.

Stock JH (1966) Cyclopoida siphonostoma from Mauritius (Crustacea, Copepoda). Beaufortia 13(159): 145–194.

Veron JEN (2000) Corals of the World. Australian Institute of Marine Science, Townsville.

Walter TC, Boxshall G (2018) World of Copepods database. Rhynchomolgidae Humes and Stock, 1972. World Register of Marine Species. http://www.marinespecies.org/aphia.php?p=taxdetailsandid=128592 [accessed 21 February 2018]

Zeppilli D, Sarrazin J, Leduc D, Arbizu PM, Fontaneto D, Fontanier C, Gooday AJ, Kristensen RM, Ivanenko VN, Sørensen MV, Vanreusel A, Thébault J, Mea M, Allio N, Andro T, Arvigo A, Castrec J, Danielo M, Foulon V, Fumeron R, Hermabessiere L, Hulot V, James T, Langonne-Augen R, Le Bot T, Long M, Mahabror D, Morel Q, Pantalos M, Pouplard E, Raimondeau L, Rio-Cabello A, Seite S, Traisnel G, Urvoy K, Van Der Stegen T, Weyand M, Fernandes D (2015) Is the meiofauna a good indicator for climate change and anthropogenic impacts? Marine Biodiversity 45: 505–53. https://doi.org/10.1007/s12526-015-0359-z

Zeppilli D, Leduc D, Fontanier C, Fontaneto D, Fuchs S, Gooday AJ, Goineau A, Ingels J, Ivanenko VN, Kristensen RM, Neves RC, Sanchez N, Sandulli R, Sarrazin J, Sørensen MV, Tasiemski A, Vanreusel A, Autret M, Bourdonnay L, Claireaux M, Coquillé V, De Wever L, Rachel D, Marchant J, Toomey L, Fernandes D (2018) Characteristics of meiofauna in extreme marine ecosystems: a review. Marine Biodiversity 48: 35–71. https://doi.org/10.1007/s12526-017-0815-z