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Marine tardigrades of Princess Alice Bank (Azores, Northeast Atlantic) with a description of a new species of *Quisarctus* Fujimoto, 2015

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Abstract

A new marine tardigrade, *Quisarctus armatus* **sp. nov.**, found in samples from 151–306 m depths at the Princess Alice Bank (PAB), south of the Azores archipelago, is described in this study. It is the second species in the genus and differs from its putative sister species *Q. yasumurai* by the shape of leg IV sensory organ, the presence of lipoid eyes, a partially folded cuticle of the digits and an elongated mouth cone. *Quisarctus armatus* **sp. nov.** shows sexual dimorphism with the length of primary clavae, the shape of leg IV sensory organ, and with differently shaped cirri *E* in females and males. The associated marine tardigrade fauna of PAB consists of *Neostygarctus oceanopolis*, *Chrysoarctus briandi* and representatives of Halechiniscidae. The known marine tardigrade fauna from the Azores now covers six genera with four identified species plus records of Halechiniscidae.

Key words: *Chrysoarctus*, Halechiniscidae, Heterotardigrada, meiofauna biogeography, *Neostygarctus*, *Quisarctus*

Introduction

Marine tardigrades are part of the meiofauna—the community of microscopic-sized benthic metazoans and certain groups of protists. They are associated with the so-called "meiofauna paradox", which relates to the widespread distribution of many species in the absence of dispersal stages in their life cycle, such as planktonic larvae or floating eggs (Giere 2009). One approach for understanding such inexplicable distribution patterns is of course the study of potential dispersal vectors, either natural vehicles such as sea turtles (Ingels *et al*. 2020), or anthropogenic ones like sediments in ballast water tanks of commercial ships (Radziejewska *et al*. 2006), and even the unintended transportation with oyster cultures for commercial production (Herranz & Leander 2016). However, especially in the case of natural vectors, it is also worth considering the geographic distances that have to be bridged by meiofaunal organisms in order to maintain gene flow between populations. Seamounts with summits in shallow depths and with sandy sediments can provide biotopes suitable for many interstitial meiofaunal taxa amidst the vast world oceans. As such, these geographically isolated geological features could serve as "stepping stones" for long distance dispersal of meiobenthic organisms by splitting large distances into shorter fragments (Gad & Schminke 2004, George 2013). However, the fauna of marine tardigrades from seamounts still remains poorly studied and we only have some insights from the Faroe Bank, the Condor Seamount and the Great Meteor Seamount in the North Atlantic Ocean so far (Hansen *et al.* 2001, Jørgensen & Kristensen 2001, Kristensen *et al*. 2015, Tchesunov 2018). Regarding potential long distance dispersal and maintenance of gene flow via stepping stone habitats, not only seamounts, but also oceanic islands are of interest. A preliminary evaluation by Trokhymchuk & Kieneke (2025) has shown that 10 out of 15 marine tardigrade genera that are reported from Atlantic seamounts and archipelagos only have a shallow bathymetric distribution, while five genera occur along a great depth range down to the deep sea.

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Hence, a stepwise distribution from one habitat to another should occur in the former taxa, while the latter could, in principle, disperse just by population growth in combination with range expansion at the abyssal plains. Marine tardigrades from the Azores archipelago were studied in the course of two investigations so far, which yielded two species records: *Tholoarctus natans natans* Kristensen & Renaud-Mornant, 1983 from 340 m depth (Kristensen & Renaud-Mornant 1983), and *Neostygarctus oceanopolis* Kristensen *et al*., 2015 from 206 m depth, but also with reports of *Chrysoarctus, Coronarctus*, and *Tanarctus* occurring in the studied samples (Kristensen *et al*. 2015).

In the present paper the marine tardigrade fauna of the Princess Alice Bank, a seamount in the sea area of the Azores archipelago, is investigated in order to gain new distributional data of these microscopic animals for approaching a better understanding of the meiofauna paradox. In the course of our study, a new species of the rare heterotardigrade genus *Quisarctus* is described.

Material and methods

Samples were collected during R/V METEOR cruise M150 BIODIAZ (BIODIversity of the AZores) in 2018 from a multitude of stations in the sea area of the Azores (George *et al*. 2018, 2021), including the Princess Alice Bank (Fig. 1A, B). During this cruise a Henning grab (HG, Henning 2015) and a Shipek grab (SG) were used as sampling tools for depths of about 50 to 500 m for meiofauna. The substrate was mostly a mixture of bioclastic and volcanogenic sediments at shallower depth (*e.g*. Fig. 1C, D), or pure bioclastic sand at the deeper sites. Sediments taken with the HG were suspended with seawater and after sedimentation of grains filtered through a 40 µm mesh size sieve. The filtrate containing the meiofauna was fixed with Lugol's iodine, to 1% final concentration. The sediments retrieved from SG sampling were anesthetized with 7% (w/v) $MgCl_2$ solution for about 10 minutes before suspending, sedimentation and sieving. The filtrate containing the meiofauna was fixed with borax-buffered formaldehyde with an end concentration of 4–8%. Since the decanting with subsequent sieving resulted in retaining a certain amount of sediment grains in our samples, a further extraction of meiofauna was carried out with the gradient centrifugation technique (Pfannkuche & Thiel 1988) using colloidal silica Levasil®. During the M150 expedition, a multitude of sampling stations at different depths along a total of 17 transects at three islands and two seamounts of the Azores were completed (George *et al*. 2021). However, for technical reasons, we had to focus on the samples from the Princess Alice Bank from depths of about 150 to 300 m for the current study (Fig. 1A, B, Table 1). In total, four HG samples and one SG sample (Fig. 1C) were analysed (Table 1). Before identification and sorting of the meiofaunal higher-level taxa, each HG sample was split with a sample splitter (Jensen 1982) to eight parts; we analysed three 2/8 samples (M150-160, -161, -223; Table 1) and one whole sample, *i.e*. 2/8 + 6/8 fractions (M150-226; Table 1). In total, 75 tardigrade individuals were retrieved from the samples (Table 1). All specimens were mounted in glycerol surrounded with beeswax-paraffin 1:2 mixture (Trokhymchuk & Kieneke 2024, 2025, Trokhymchuk *et al*. 2024). Specimens were observed with an Olympus BX53 compound microscope equipped with differential interference contrast (DIC). Microphotographs were made with a digital microscope camera Euromex HD-Ultra VC.3036-HDS. After light microscopic documentation, two specimens were prepared for scanning electron microscopy (SEM) investigation following the methods explained in Trokhymchuk & Kieneke (2024, 2025) and Trokhymchuk *et al*. (2024). SEM was carried out with a TESCAN VEGA3 SEM operated with 10 kV acceleration tension and capturing mixed-channel-images using the SE- plus BSE-detectors. Image stacking with the software PICOLAY V2020-08-13 (www.picolay.de) was used to generate DIC images with a high focal depth. Holotype and allotype drawings were made using the Procreate app. The species identifications are based on morphological characters, the key of Fontoura *et al*. (2017), and primary taxonomic literature. All specimens (type and voucher specimens) are deposited in the Tardigrada collection of the Senckenberg Natural History Museum, Frankfurt am Main, Germany, under the inventory numbers SMF 1312–1385 (accessible via https://search.senckenberg.de/aquila-public-search/search). All the occurrences are additionally submitted to GBIF (Senckenberg Collection Tardigrada SMF. Occurrence dataset accessible via https://doi.org/10.15468/uvr84c).

TABLE 1. Analysed samples of Princess Alice Bank collected during expedition M150 and their tardigrade abundances (number of individuals). The breaks (2/8; 6/8) refer to sorted fractions of the sample splitter. SG—Shipek grab; HG—Henning grab.

	Station	Date	Device	Latitude	Longitude	Depth [m]
1	M150-123-1-SG	05.09.2018	SG	37° 59.968'N	029° 17.054'W	151
2	M150-160-1-2/8	06.09.2018	HG	38° 01.058'N	029° 19.690'W	304
3	M150-161-1-2/8	06.09.2018	HG	38° 01.061'N	029° 19.691'W	306
4	M150-223-1-2/8	09.09.2018	HG	37° 59.425'N	029° 18.577'W	294
5 (1)	M150-226-1-2/8	09.09.2018	HG	37° 59.427'N	029° 18.573'W	295
5 (2)	M150-226-1-6/8	"	"	"	"	"
TOTAL						

TABLE 1. (Continued)

	Quisarctus armatus sp. nov.	*Neostygarctus oceanopolis*	*Chrysoarctus briandi*	Halechiniscidae representatives
1	2	0	0	0
2	5	0	3	1
3	1	42	2	3
4	1	0	0	0
5 (1)	4	1	3	1
5 (2)	5	0	1	0
TOTAL	**18**	**43**	**9**	**5**

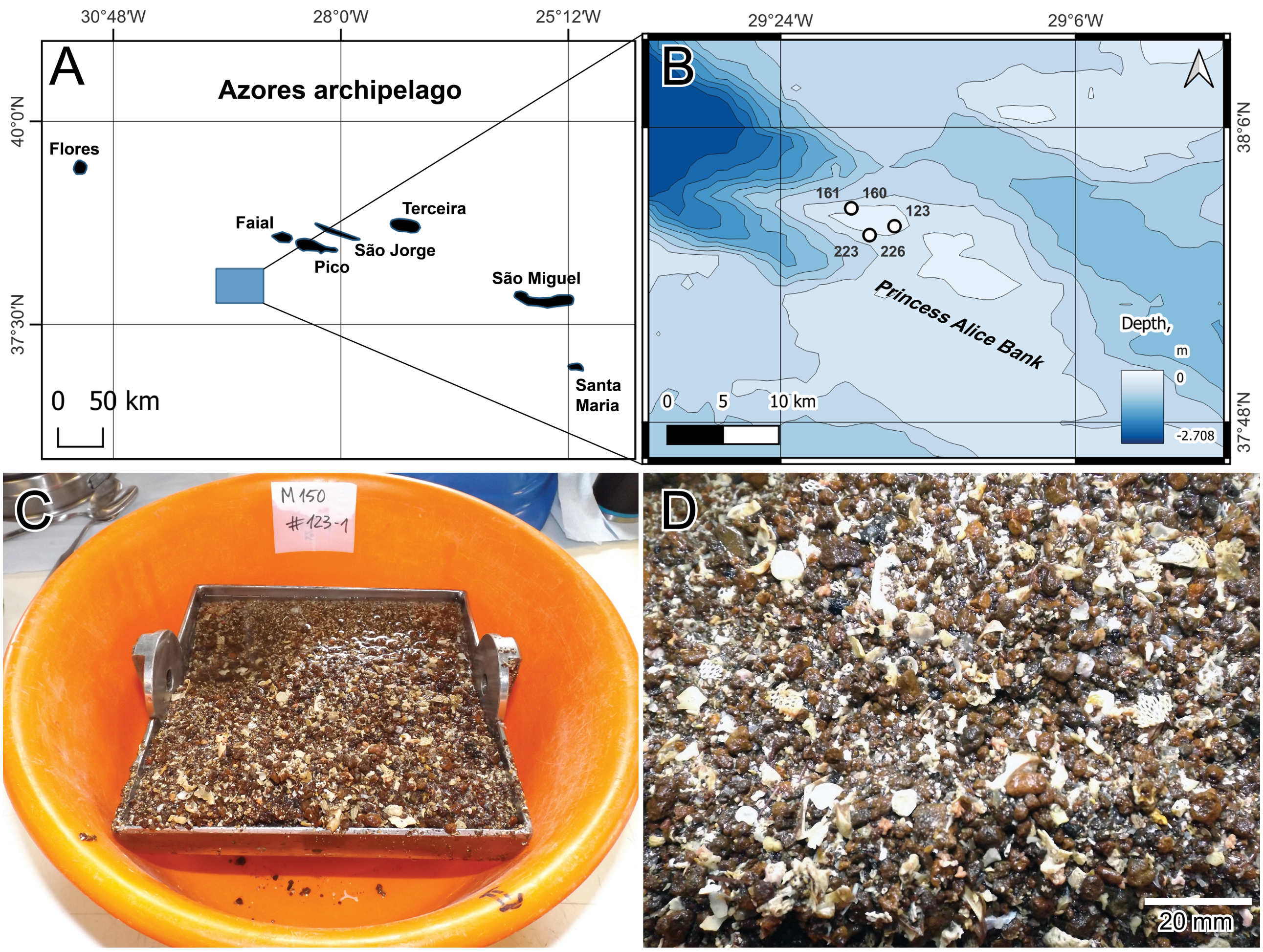

FIGURE 1. Study area (**A, B**) and sediment sample in the Shipek Grab (**C, D**). Blue rectangle (A) delineates sampling area. White dots (B) indicate sampling sites. Station code (B) shortened to the station number (*e.g.* "M150-123-1-SG" becomes "123"). Bathymetry data from GEBCO, map created in QGIS 3.34.12. Photos (C, D) by H. Arndt.

Results

A total of three tardigrade species and representatives identified to the family level are present in samples from the Princess Alice Bank, all belonging to the Heterotardigrada (Table 1). A comprehensive description of one species new to science and remarks on the other associated tardigrade fauna are given below.

Systematics

Phylum: Tardigrada Doyère, 1840

Class: Heterotardigrada Marcus, 1927

Family: Halechiniscidae Thulin, 1928

Subfamily: Quisarctinae Fujimoto, 2015

Amended diagnosis (following Fujimoto 2015 with additions in **bold**)

Halechiniscidae with cylindrical body; primary clava and lateral cirrus arise from common cirrophore; primary clava longer than lateral cirrus; secondary clava undeveloped; leg IV sense organ as papilla; legs terminate in digits without peduncles, proximal pads, pretarsi or wrinkles **but may have folds**; internal digits longer than external digits; each digit terminates in sheathed, small, crescent-shaped claw with minute calcar; pair of ventrally opening seminal receptacles each with slender, sinuous duct terminating in spherical vesicle.

Genus: *Quisarctus* Fujimoto, 2015

Amended diagnosis (following Fujimoto 2015 with additions in **bold**)

Quisarctinae with cylindrical body; primary clava and lateral cirrus arise from common cirrophore; primary clava longer than lateral cirrus; secondary clava undeveloped; **eyes may be present;** stylet supports **may be** present; leg IV sense organ as elongate papilla with distal spine; legs terminate in digits without peduncles, proximal pads, pretarsi or wrinkles **but may have folds**; internal digits longer than external digits; each digit terminates in sheathed, small, crescent-shaped claw with minute calcar; pair of ventrally opening seminal receptacles each with slender, sinuous duct terminating in spherical vesicle.

***Quisarctus armatus* sp. nov.**
(Figs 2–8A, B, Table 2)
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Diagnosis

Quisarctus with sexual dimorphism in the shape of cirri *E*: female has flagellum-shaped cirri, male has lance-shaped cirri. Body cuticle with punctation and dorsal transverse folds. Buccal apparatus consists of buccal tube, stylets and a pharyngeal bulb with three placoids. Legs I–III sensory organs as tripartite spines. Leg IV sensory organ developed as an elongated papilla with tubular tip. Digits may have proximal folds. Seminal receptacles open ventrally.

Type material

The holotype (Figs 2A, 3) is an adult female (specimen ID M150-123-1-SG_2v2, SMF 1313) with seminal receptacles, and rosette gonopore. The allotype (Figs 2B, 4) is an adult male (specimen ID M150-161-1-2_2v48, SMF 1323) with one seminal vesicle filled with spermatozoa and oval gonopore. Sixteen further specimens are paratypes (Figs 5–7). Two of them, M150-226-1-6_5v6, SMF 1384 (female, Fig. 6) and M150-226-1-6_3v6, SMF 1382 (adult male exuvium, Fig. 7) were prepared for the SEM investigation. The other 14 specimens are three males, four females, two juveniles and five specimens with undetermined sex. The whole type series is deposited at the Senckenberg Natural History Museum as part of the Tardigrada collection under inventory numbers as specified in Table 2.

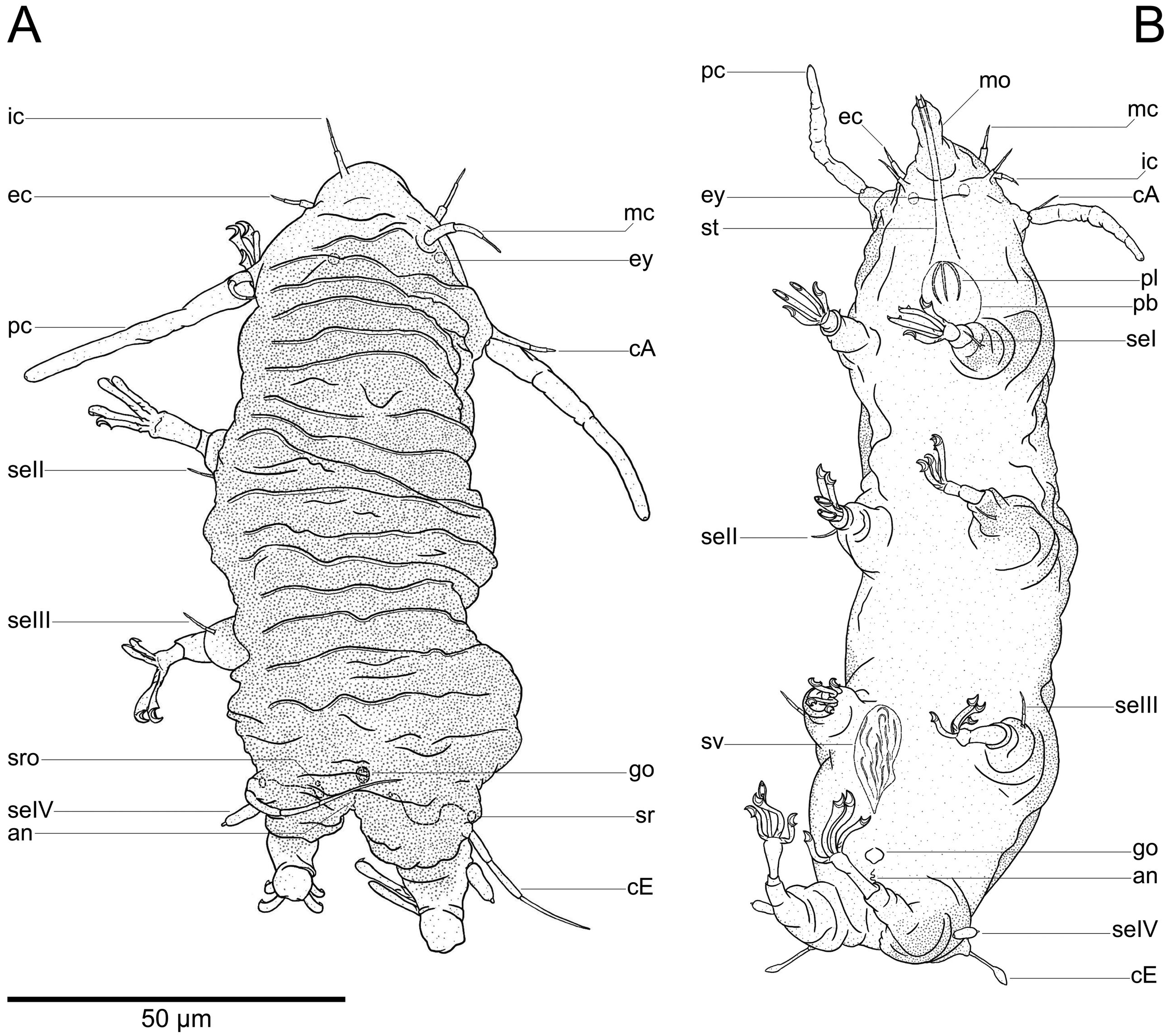

FIGURE 2. Drawing of the holotypic female, dorsal view (**A**) and allotypic male, ventral view (**B**) of *Quisarctus armatus* **sp. nov.** Abbreviations: an—anus, cA—cirrus *A*, cE—cirrus *E*, ec—external cirrus, ey—eye, go—gonopore (in **A** it is delineated in the ventral side), ic—internal cirrusmc—median cirrus, mo—mouth cone, pb—pharyngeal bulb, pc—primary clava, pl—placoid, seI–IV—leg I–IV sensory organ, sr—seminal receptacle, sro—seminal receptacle opening, st—stylet, sv—seminal vesicle.

Type locality

Princess Alice Bank, Azores; holotype: 37°59.968'N, 029°17.054'W; 151 m depth, bioclastic and volcanogenic sediment (Fig. 1C), collected on 5th September 2018; allotype: 38°01.061'N, 029°19.691'W; 306 m depth, bioclastic sediment; collected on 6th September 2018.

Etymology

The name *armatus* (from Latin; means *armed*) refers to lance-shaped cirrus *E* in males and dorsal transverse folds forming a pattern of dorsal armour plating in females.

Description of holotype (SMF 1313)

(Figs 2A, 3, Table 2)

Adult female tardigrade with cylindrical body (95 µm long × 30.8 µm wide) and loose, punctated cuticle. A number of transverse folds with less punctated margins on the dorsal side (Fig. 3A). The punctation of the dorsal side is more prominent; the ventral surface, distal portions of legs, head cuticle and the margins of dorsal transverse folds have less marked or no cuticle punctation. Long primary clavae have a mid-portion of folded cuticle (Fig. 3A) and an apical pore. Primary clava and the cirrus *A* arise from a common cirrophore. Cirri *A* situated antero-dorsally to primary clavae. Cephalic cirri present as paired internal and external cirri plus an unpaired median cirrus; all cirri, including cirri *A*, consist of three parts: scapus, tubular portion and short flagellum. The internal cirri are dorsolateral; the external cirri are ventrolateral. Secondary clavae are absent. Lipoid eyespots present about at the position of the median cirrus (Fig. 3C). Mouth cone is retracted (Fig. 3C). Pharyngeal bulb is macerated. Leg I–III sensory organs present as tripartite spines with scapus, tubular portion and short flagellum (Fig. 3D, E). Sensory organ of the leg IV as an elongated papilla with a short distal tubular tip (Figs 2A, 3E, 8A). Cirri *E* are flagellum-shaped with a proximal portion, distal portion and spine, arising from a cirrophore (Figs 2, 3A). All legs have two internal digits longer than two external digits. Each digit terminates in a simple crescent-shaped claw with calcar. Leg IV digits are larger than legs I–III digits. Proximal part of digits sometimes has folds (Fig. 2A). Rosette-shaped female gonopore present (Fig. 3G). A pair of seminal receptacle openings ventrally at the bases of legs IV is connected to slender, slightly S-shaped ducts and terminates as vesicles (Figs 2A, 3F). Anus is 4.7 µm posterior to gonopore and appears as a zigzag cuticle fold (Fig. 3G).

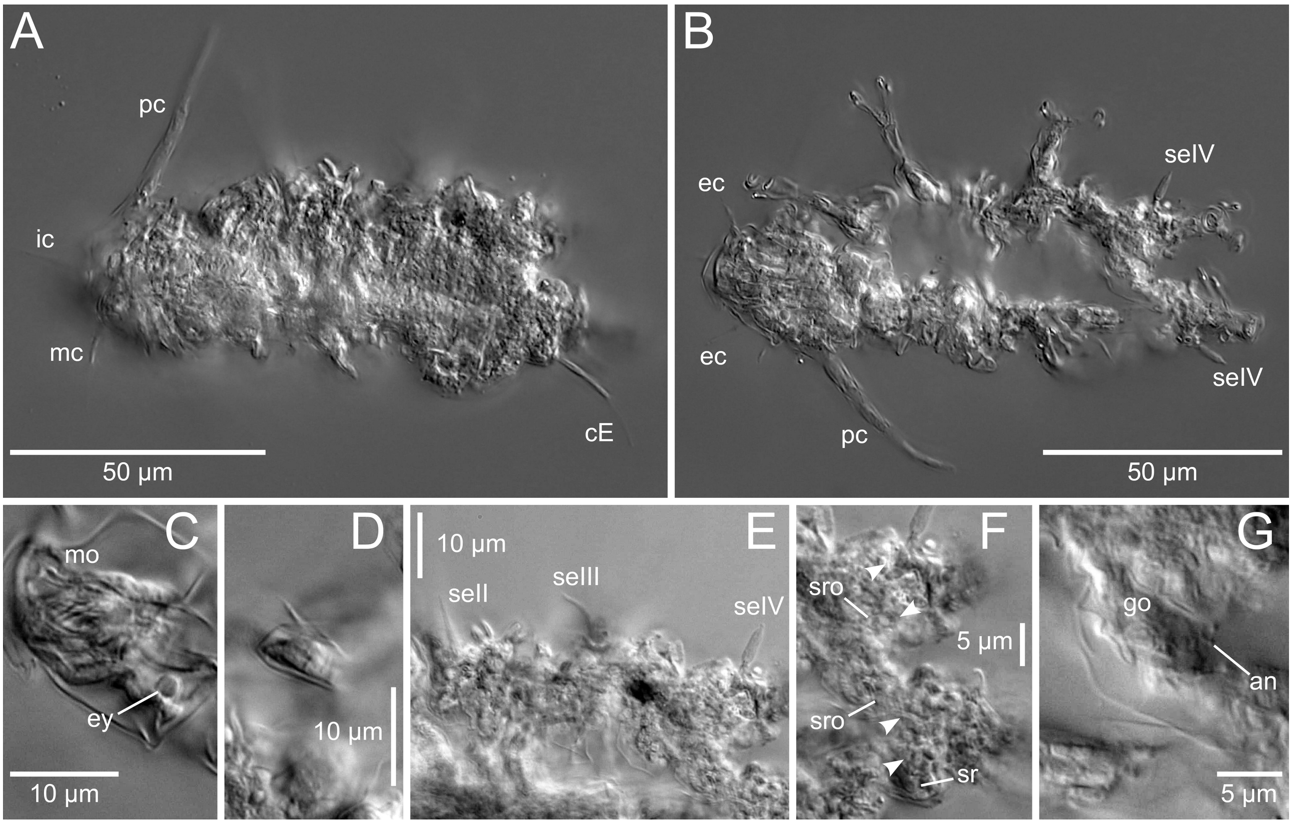

FIGURE 3. DIC microphotographs of *Quisarctus armatus* **sp. nov.** (holotypic female, SMF 1313). **A** habitus, dorsal view. **B** habitus, ventral view. **C**–**G** details in close-up. **C** cephalic region. **D** sensory organ I. **E** sensory organs II–IV. **F** caudal region, ventral view, note seminal duct (arrowheads). **G** caudal region, ventral view. Abbreviations: an—anus, cE—cirrus *E*, ec—external cirrus, ey—eye, go—gonopore, ic—internal cirrus, mc—median cirrus, mo—mouth cone, pc—primary clava, seI–IV—leg I–IV sensory organ, sro—seminal receptacle opening.

Remarks on the allotype (SMF 1323)

(Figs 2B, 4, Table 2)

Male with cylindrical body (118.4 µm long × 29.0 µm wide) and loose, thin, punctated cuticle, which forms transversal folds on the dorsal side. Long primary clavae with folded cuticle (Fig. 4A, D). Secondary clavae absent. Lipoid eyespots present (Fig. 4D). Mouth cone is rather narrow (diameter: 3.8 µm) and directed anteriorly (Fig. 4A). About 25 µm long stylets without supports are present in the head section and inside the mouth cone. Three placoids (Fig. 4E) are visible in the oval pharyngeal bulb (10 × 8.5 µm). The pharyngeal bulb is followed by a globular oesophagus (Fig. 4A). Leg I–III sensory organs present as tripartite spines with scapus, tubular portion and short flagellum (Fig. 4F–H). Sensory organ of leg IV is an elongated papilla with a short distal tubular tip (Figs 2B, 4I,

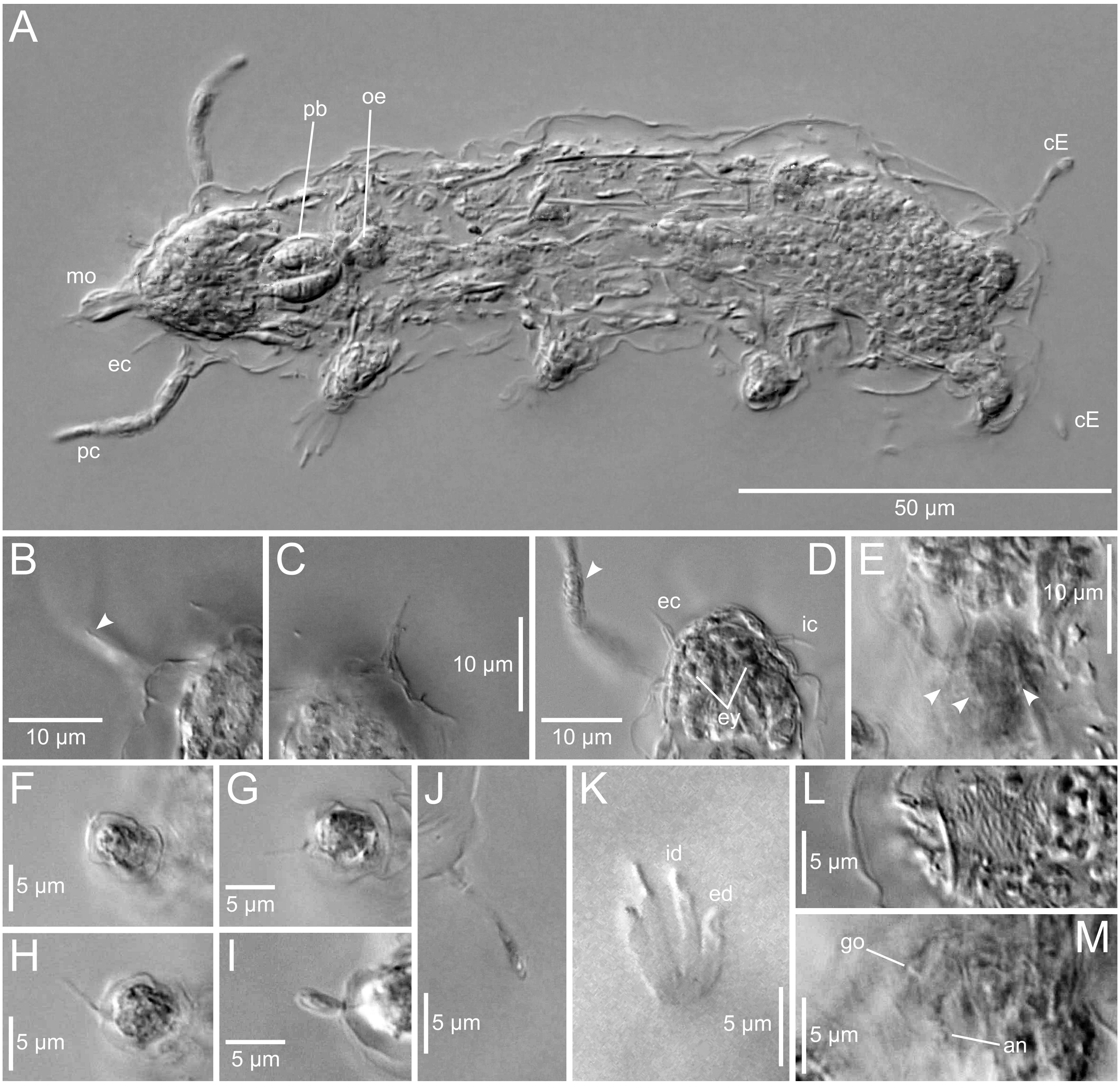

FIGURE 4. DIC microphotographs of *Quisarctus armatus* **sp. nov.** (allotypic male, SMF 1323). **A** habitus. **B**–**M** details in close-up. **B** cirrus *A* (arrowhead). **C** median cirrus. **D** cephalic region, note folded median portion of primary clava (arrowhead). **E** pharyngeal bulb, note three placoids (arrowheads). **F** sensory organ I. **G** sensory organ II. **H** sensory organ III. **I** sensory organ IV. **J** cirrus *E*. **K** leg I digits. **L** seminal vesicle with spermatozoa. **M** caudal region, ventral view. Abbreviations: an—anus, cE—cirrus *E*, ec—external cirrus, ed—external digit, ey—eye, go—gonopore, ic—internal cirrus, id—internal digit, mo—mouth cone, oe—eosophagus, pb—pharyngeal bulb, pc—primary clava.

8B). Cirri *E* arise from a cirrophore and have a lance-shaped distal portion (Fig. 4J). All legs have two internal digits longer than two external digits (Fig. 4K). Each digit terminates in a simple crescent-shaped claw with calcar. The claw sheath completely covers the claw. Leg IV digits are larger than legs I–III digits. Proximal part of digits sometimes has folds. One seminal vesicle with spermatozoa present (Fig. 4L). Oval male gonopore present a short distance anterior to leg IV insertions (Fig. 4M). Anus slightly posterior to gonopore and appears as a zigzag cuticle fold (Fig. 4M).

Remarks on paratypes
(Figs 5–7, Table 2)

A number of 16 paratype specimens were either investigated with light microscopy, or with SEM in order to study further structural details and character variability. All paratypes exhibit morphology coherent with that of the holotype and the allotype (Fig. 5). Males are 96–123 µm in body length (n=2) and the primary clavae are 27–30 µm (n=2) long. Females are 92–118 µm in body length (n=3) and the primary clavae are 32–35 µm (n=3) long. Juvenile specimens are 75–93 µm in body length (n=2) and the primary clavae are 24 µm (n=1) long. The primary clavae of the investigated females appeared significantly longer than that of the males (Mann-Whitney test, z = 2.653, p = 0.002). The juveniles have cirri *E* in the shape of a flagellum, which may indicate either the potential late development of the lance-shaped cirri *E* specific to males, or that the juvenile specimens are immature females. During SEM investigation, we were able to better examine and confirm the cuticular structures, especially dorsal transverse folds forming a pattern of segmentation or dorsal armour plating (Fig. 6B) and the epicuticular pillars (Fig. 7). Furthermore, SEM imaging helped to investigate the differences in cirri *E* between sexes (Figs 6G, 7D, E), and the fine structure of the sensory organs and digits folds (Figs 6F, 7C).

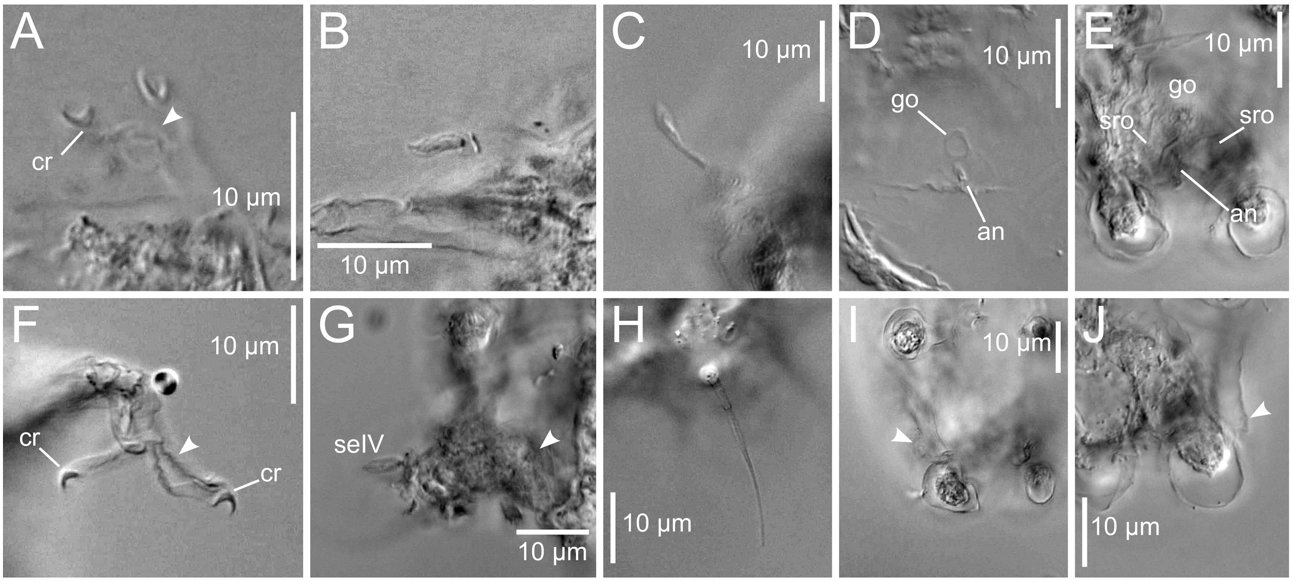

FIGURE 5. DIC microphotographs of *Quisarctus armatus* **sp. nov.** (paratypes). **A**–**D** males; **E**–**J** females. **A** leg I digits, note folds (arrowhead). **B** sensory organ IV. **C** cirrus *E*. **D** caudal region, ventral view. **E** caudal region, ventral view. **F** leg IV digits, note folds (arrowhead). **G** caudal region, ventral view, note gonopore (arrowhead). **H** cirrus *E*. **I** caudal region, ventral view, note seminal receptacle vesicle (arrowhead). **J** caudal region, ventral view, note seminal receptacle vesicle (arrowhead). Abbreviations: an—anus, cr—calcar, go—gonopore, seI–IV—leg I–IV sensory organ, sro—seminal receptacle opening.

The sexual dimorphism in *Quisarctus armatus* **sp. nov.** is observable in the difference between the length of primary clavae; the shape of leg IV sensory organ, and the shape of cirri *E*: males have spine-like cirri with a lance-shaped distal end, while females have flagellum-shaped tripartite cirri. Males have oval gonopores situated close to the anus, and females have rosette-shaped gonopores opened further from the anus.

TABLE 2. *Quisarctus armatus* **sp. nov.** measurements of important taxonomic characters of the holotype, allotype, and all paratypes (in µm). Abbreviations (in column order): BL—body length, BW—body width, pc—primary clava length, cA—cirrus *A* length, mo—mouth cone length, pb—pharyngeal bulb size, ic—internal cirrus length, ec—external cirrus length, mc—median cirrus length, seI–IV—sensory organ I–IV length, cE—cirrus *E* length, go/an—distance between gonopore and anus, n/a—data not available.

SMF	type	locality/specimen	sex	BL	BW	pc	cA	mo	pb	ic	ec	mc	seI	seII	seIII	seIV	cE	go/an
1313	holotype	M150-123-1-SG_2v2	female	95.0	30.8	37.0	7.8	n/a	n/a	11.0	10.0	16.3	4.3	7.2	7.2	7.0	24.0	4.7
1323	allotype	M150-161-1-2_2v48	male	118.4	29.0	23.0	6.5	11.3	10×8.5	6.3	9.5	7.9	4.0	4.9	6.5	4.5	12.5	2.3
1314	paratype	M150-160-1-2_1v9	undetermined	103.0	33.5	n/a	5.5	9.3	11×8.5	6.0	7.0	7.0	n/a	4.5	5.0	5.0	n/a	n/a
1315	paratype	M150-160-1-2_2v9	male	123.0	38.0	27.0	5.3	11.5	11×8	5.5	7.5	n/a	4.0	5.0	5.0	4.5	13.0	2.0
1317	paratype	M150-160-1-2_4v9	undetermined	107.0	n/a	n/a	n/a	11.0	11×8	n/a	n/a	n/a	n/a	3.0	3.5	3.7	n/a	n/a
lost	paratype	M150-160-1-2_6v9	male	118.0	n/a	22.5	n/a	11.3	11×8	n/a	n/a	5.0	n/a	n/a	n/a	4.0	12.3	n/a
1319	paratype	M150-160-1-2_7v9	juvenile	75.0	n/a	24.0	n/a	10.5	10×7.3	n/a	n/a	n/a	n/a	n/a	n/a	3.0	n/a	n/a
1370	paratype	M150-223-1-2_1v1	undetermined	88.0	n/a	19.0	n/a	9.0	n/a	n/a	n/a	n/a	n/a	n/a	n/a	4.3	n/a	n/a
1373	paratype	M150-226-1-2_3v9	male	96.0	32.0	30.0	n/a	12.0	10×8.5	6.0	7.3	6.0	3.0	4.3	5.5	4.0	11.3	2.0
1375	paratype	M150-226-1-2_5v9	juvenile	93.0	n/a	n/a	n/a	n/a	11×7.5	5.5	6.5	12.3	n/a	5.0	n/a	4.5	n/a	n/a
1377	paratype	M150-226-1-2_7v9	undetermined	110.0	n/a	22.0	6.5	7.0	11×9.5	n/a	n/a	n/a	4.5	n/a	5.3	5.0	n/a	n/a
1379	paratype	M150-226-1-2_9v9	female	110.0	n/a	32.0	5.5	12.0	11.7×9	7.3	n/a	15.5	5.0	6.0	7.0	6.0	17.5	n/a
1380	paratype	M150-226-1-6_1v6	female	118.0	34.0	32.0	7.7	11.5	11.3×9	9.5	6.7	11.0	n/a	7.0	7.0	5.3	n/a	6.3
1382	paratype	M150-226-1-6_3v6	male exuvium	139.0	40.0	28.3	6.8	12.0	12.5×11	6.7	8.3	6.7	n/a	5.0	5.0	5.0	12.5	2.3
1383	paratype	M150-226-1-6_4v6	female	86.0	26.0	33.0	6.5	n/a	10×8	11.0	8.5	13.0	n/a	n/a	6.0	6.3	23.0	n/a
1384	paratype	M150-226-1-6_5v6	female	100.0	36.5	34.0	5.7	12.0	10.5×9	7.0	9.3	12.5	4.5	6.5	4.5	5.3	19.5	n/a
1385	paratype	M150-226-1-6_6v6	undetermined	90.0	n/a	31.0	n/a	n/a	11×8	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a
1312	paratype	M150-123-1-SG_1v2	female	92	30.0	35.0	8.0	n/a	n/a	11.0	9.0	n/a	3.7	n/a	5.7	6.5	n/a	n/a

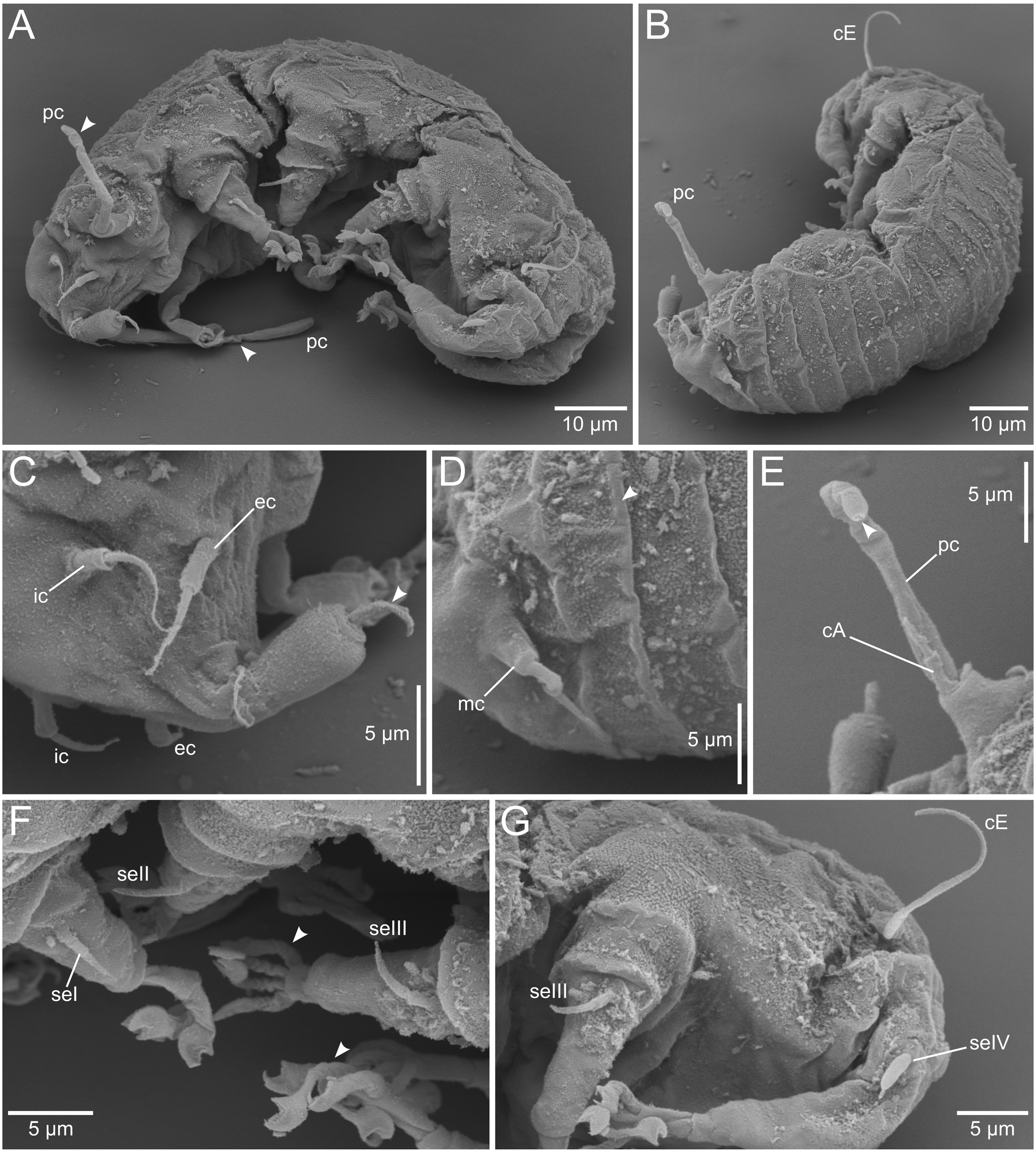

FIGURE 6. SEM micrographs of *Quisarctus armatus* **sp. nov.** (paratypic female). **A** habitus, ventrolateral view, note folded portion of primary clava (arrowheads). **B** habitus, dorsolateral view. **C** cephalic region, note protruded stylets (arrowhead). **D** cephalic region, dorsal view, note less punctated zone (arrowhead). **E** cephalic region, note primary clava pore (arrowhead). **F** leg sensory organs, note digit folds (arrowheads). **G** caudal region, ventrolateral view. Abbreviations: cA—cirrus *A*, cE—cirrus *E*, ec—external cirrus, ic—internal cirrus, mc—median cirrus, pc—primary clava, seI–IV—leg I–IV sensory organ.

Differential diagnosis

Quisarctus armatus **sp. nov.** (both sexes) differs from the only other congeneric species *Quisarctus yasumurai* Fujimoto, 2015 most significantly in the shape of leg IV sensory organ (Fig 8): in *Quisarctus armatus* **sp. nov.** it is an elongated papilla with a short distal spine-like tip (Fig. 8A, B), while in *Q. yasumurai* it has a distal tapering and is rather leaflet-shaped (Fig. 8C). Further differences between both species are the presence of lipoid eyes (Kristensen 1978, Greven 2007), absent in *Q. yasumurai*, and proximal folds on the digits that are only reported for *Quisarctus armatus* **sp. nov.** The mouth cone is more elongated and narrow in *Quisarctus armatus* **sp. nov.** compared to *Q. yasumurai*. Also the seminal receptacle ducts appear longer in *Quisarctus armatus* **sp. nov.**, however, the small sample size of mature females for both species limits the confidence in this putative character difference.

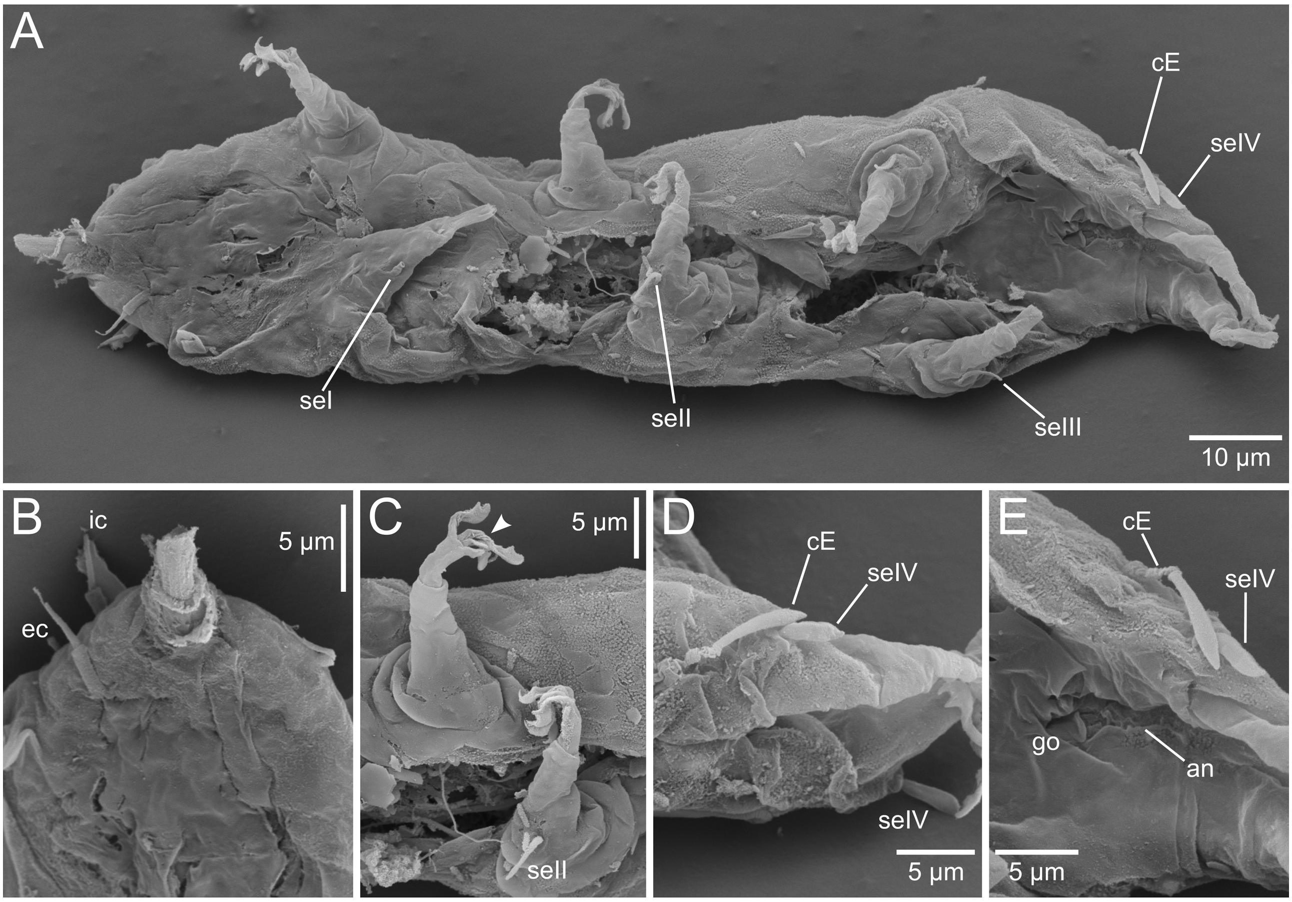

FIGURE 7. SEM micrographs of *Quisarctus armatus* **sp. nov.** (paratypic male exuvium). **A** habitus, ventral view. **B** cephalic region, ventral view. **C** legs II in close-up, note digit folds (arrowhead). **D** caudal region, dorsal view. **E** caudal region, ventral view. Abbreviations: an—anus, cE—cirrus *E*, ec—external cirrus, go—gonopore, ic—internal cirrus, seI–IV—leg I–IV sensory organ.

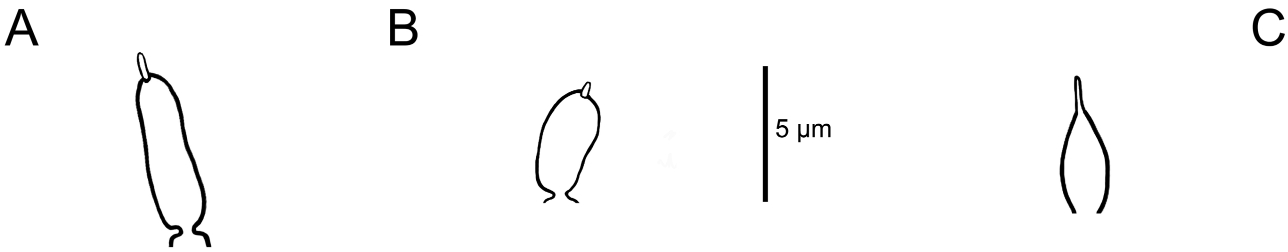

FIGURE 8. Comparison of leg IV sensory organs of *Quisarctus armatus* **sp. nov.** (**A** holotypic female, **B** allotypic male) and *Q. yasumurai* (**C** holotypic female, redrawn from Fujimoto 2015).

Associated tardigrade fauna

(Table 1, Figs 9, 10)

Family: Neostygarctidae Grimaldi de Zio, d'Addabbo Gallo & Morone de Lucia, 1987

Genus: *Neostygarctus* Grimaldi de Zio, d'Addabbo Gallo & Morone de Lucia, 1982

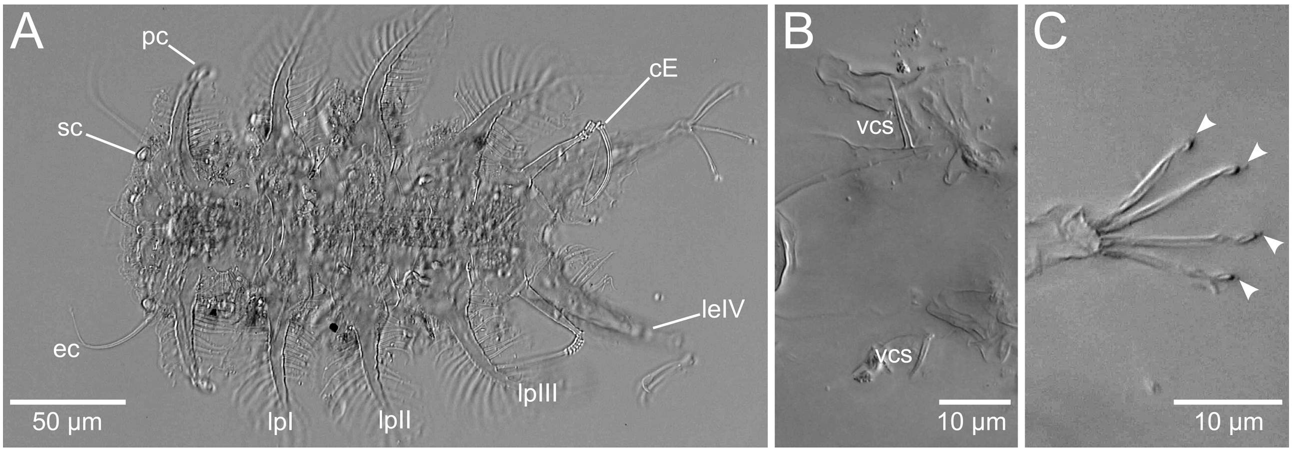

FIGURE 9. DIC microphotographs of *Neostygarctus oceanopolis*. **A** habitus. **B** cephalic region, ventral view. **C** leg I digits, note accessory spines (arrowheads). Abbreviations: cE—cirrus *E*, ec—external cirrus, leIV—leg IV, lpI–III—lateral process I–III, pc—primary clava, sc—secondary clava, vcs—ventral cephalic seta.

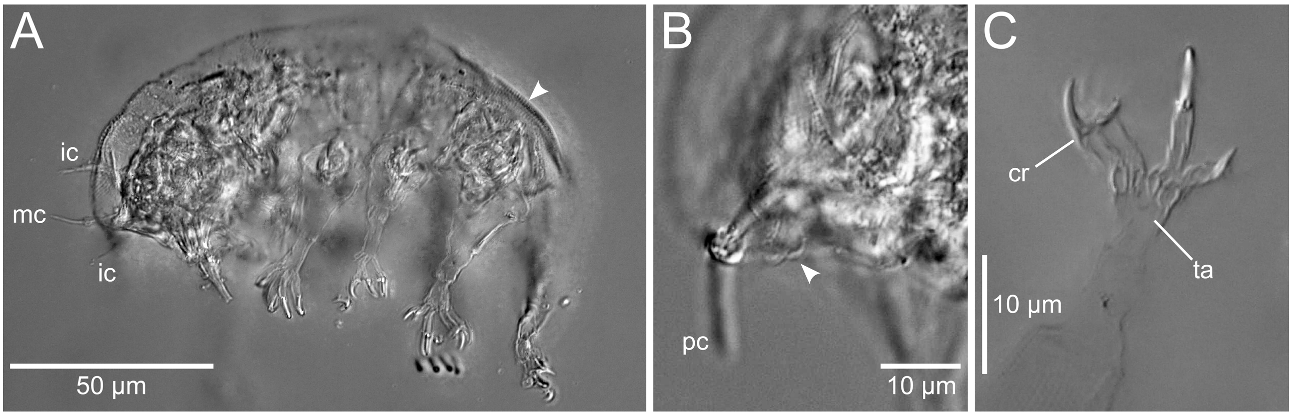

FIGURE 10. DIC microphotographs of *Chrysoarctus briandi*. **A** habitus, note cuticular punctation (arrowhead). **B** cephalic region, note unpunctated zone (arrowhead). **C** leg III digits. Abbreviations: cr—calcar, ic—internal cirrus, mc—median cirrus, pc—primary clava, ta—tarsus.

Neostygarctus oceanopolis **Kristensen, Sørensen, Hansen & Zeppilli, 2015**
Fig. 9; N=43; 295–306 m bsl

Remarks

Phenotypically remarkable tardigrades (115–188.5 µm in body length, n=12) with segmented body and three pairs of lateral body processes (Fig. 9A). All the specimens matched the original description (Kristensen *et al.* 2015). Mid-dorsal spines sometimes were broken, but we confirmed the presence of ventral body plates, always one pair of ventral cervical spines (Fig. 9B), the presence of accessory spine on each claw (Fig. 9C), and the absence of eyes. Measurements of selected specimens presented in Table 3.

As we mentioned earlier, this species has been described from the Condor seamount, Azores (Kristensen *et al*. 2015), and has not been reported yet outside of its type locality until this current record from the PAB.

TABLE 3. *Neostygarctus oceanopolis* measurements of characters of eleven selected specimens (in µm). Abbreviations (in column order): BL—body length, pc—primary clava length, sc—secondary clava size, pb—pharyngeal bulb size, ic—internal cirrus length, ec—external cirrus length, seIV—sensory organ IV length, cE—cirrus *E* length, n/a—data not available.

SMF	locality	sex	BL	pc	sc	pb	ic	ec	seIV	cE
1328	M150-161-1-2_7v48	male	170.0	6.0	5.5×5	15×14	35.5	58.0	9.0	87.0
1329	M150-161-1-2_8v48	male	134.7	5.0	5×4	17×14	28.0	48.0	6.5	64.5
1331	M150-161-1-2_10v48	male	157.0	6.0	5×3.7	n/a	n/a	33.0	6.0	57.0
1333	M150-161-1-2_12v48	female	132.5	5.0	5.5×3.7	11×13	22.5	38.0	6.7	97.3
1335	M150-161-1-2_14v48	female	188.5	6.3	6×5.5	12×12	33.7	48.0	6.0	n/a
1337	M150-161-1-2_16v48	male	153.5	4.5	5.5×4	11×11.5	19.0	33.7	5.0	65.0
1343	M150-161-1-2_22v48	female	139.5	5.0	5×4	12×12.3	24.0	49.0	5.0	85.0
1346	M150-161-1-2_25v48	male	150.0	5.3	5×3.5	n/a	19.0	35.7	5.3	74.5
1347	M150-161-1-2_26v48	female	184.0	5.0	5×3.5	n/a	2.0	53.0	6.0	98.3
1348	M150-161-1-2_27v48	male	116.0	5.0	4.5×3	10×11	15.0	34.0	n/a	61.0
1350	M150-161-1-2_29v48	female	123.0	4.7	5×4	11×9.5	17.7	43.0	n/a	n/a

Family: Halechiniscidae Thulin, 1928

Genus: *Chrysoarctus* Renaud-Mornant, 1984

***Chrysoarctus briandi* Renaud-Mornant, 1984**
Fig. 10; N=9; 295–306 m bsl

Remarks

Robust tardigrades (78–120 µm in body length, n=6) with distinct epicuticular pillars (Fig. 10A). Primary clavae are 12–16 µm long (n=6). The main trait for this species is the so-called fan-shaped tarsus, with all the digits attached and aligned in one line (Fig. 10C). Claws with calcar (Fig. 10C). Following the original description (Renaud-Mornant 1984), we searched and observed the unpunctated zone close to the mouth cone—presumably secondary clavae or their rudiments (Fig. 10B).

This species has a cosmopolitan distribution in the Mediterranean sea, Atlantic Ocean and Indian Ocean (Kaczmarek *et al*. 2015).

Halechiniscidae representatives
N=5; 295–306 m bsl

Remarks

We investigated five deteriorated tardigrades, probably juveniles (63–99 µm in body length, n=4), which could be assigned to the family Halechiniscidae. However, further determination to genus or species level is not possible because of the lack of morphological resolution.

Discussion

The known marine tardigrade fauna of the Azores was so far represented by five genera and two identified species: *Neostygarctus oceanopolis*, *Tholoarctus natans*, and undetermined specimens of the genera *Chrysoarctus*, *Coronarctus* and *Tanarctus* (Kristensen & Renaud-Mornant 1983, Kristensen *et al.* 2015). With the present study, we could add *Quisarctus armatus* **sp. nov.** and *Chrysoarctus briandi* to this list and in addition we found a few undetermined representatives of the family Halechiniscidae. Hence, the marine tardigrade fauna of the Azores now covers six genera with four identified species.

The new species described herein, *Quisarctus armatus* **sp. nov.**, is the second species known for the genus. The only known location for *Quisarctus* so far is the submarine cave Daidokutsu off the eastern coast of Iejima Island, Okinawa Islands, Japan, Pacific Ocean (Fujimoto 2015), the type locality of *Q. yasumurai*. The discovery of a new *Quisarctus* species at the Princess Alice Bank, Azores, Atlantic Ocean (this study) enlarges the potential distribution area of this rare genus. Furthermore, it raises questions about dispersal and evolutionary connectivity of the tentative sister species pair *Quisarctus armatus* **sp. nov.**/*Quisarctus yasumurai*, which have to be addressed by future studies. As generally desirable for all meiofauna taxa (e.g., Cerca *et al.* 2018), studies including phylogenetic and phylogeographic analyses based on DNA sequencing are mandatory for understanding the evolutionary relationships, time of divergence and potential dispersal routes for these rare tardigrade taxa. Likewise, also an increased sampling of meiofauna on seamounts, oceanic islands and adjacent coastal areas is necessary to gain a better resolved picture of the biogeographic patterns (see George 2013).

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