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Isopods on isopods: integrative taxonomy of Cabiropidae (Isopoda: Epicaridea: Cryptoniscoidea) parasitic on anthuroid isopods, with descriptions of a new genus and three new species from Japan

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Running title: Three new *Anthuroniscus* gen. nov. species

ABSTRACT

Species in the parasitic isopod family Cabiropidae are known to utilize various isopods as hosts but there are no records of its members parasitizing anthuroid hosts to date. We describe *Anthuroniscus* **gen. nov.** for three new cabiropid species, *Anthuroniscus shimomurai* **sp. nov.**, *Anthuroniscus dentatus* **sp. nov.**, and *Anthuroniscus latus* **sp. nov.**, all of which are parasitic on anthuroid isopods. *Anthuroniscus* **gen. nov.** differs from the other 14 cabiropid genera and 10 genera treated as family *incertae sedis* in females having an elongate, dorsally compressed, posteriorly tapering body with six pairs of lateral bulges; and in cryptoniscus

larvae by the following combination of characters: (1) eyes lacking, (2) antennular article 1 with eight teeth on the posterior margin, (3) uropodal exopod and endopod rectangular rather than tapering, and endopod longer than exopod, and (4) pleotelson trapezoidal, with the width twice the length. *Anthuroniscus shimomurai* **sp. nov.** was parasitic on *Mesanthura* sp. from Kaichu Doro, Uruma, Okinawa, southwestern Japan; *A. dentatus* **sp. nov.** on *Accalathura* sp. from Irabu Island, Miyako Islands, Okinawa; and *A. latus* **sp. nov.** on *Colanthura nigra* from Kanagawa, central Japan. In pairwise comparisons, the three new species showed p-distances of 0.6–1.3% for the *18S* rRNA gene (1440 positions); *A. shimomurai* **sp. nov.** and *A. latus* **sp. nov.** showed a p-distance of 36.2% for the *16S* rRNA gene (412 positions). In an *18S*-based maximum-likelihood tree, an *Anthuroniscus* **gen. nov.** clade was the sister group to *Cryptoniscoidea* sp., parasitic on an ostracod species. This is the first study reporting Cabiropidae from Japan and anthuroids as hosts for *Cryptoniscoidea*.

ZooBank: urn:lsid:zoobank.org:pub:2EE042E2-AE48-4B87-B495-8436462146B9

Keywords: Anthuroidea, biodiversity, Bopyroidea, Crustacea, Cymothoida, new host, phylogeny, systematics.

Short Summary

Species in the parasitic isopod family Cabiropidae are known to utilize various isopods as hosts but there are no records of its members parasitizing anthuroid hosts to date. We describe *Anthuroniscus* gen. nov. for three new cabiropid species, *Anthuroniscus shimomurai* sp. nov., *Anthuroniscus dentatus* sp. nov., and *Anthuroniscus latus* sp. nov., all of which are parasitic on anthuroid isopods. In a phylogenetic analysis, the new genus was the sister group to *Cryptoniscoidea* sp., parasitic on an ostracod species. This is the first study reporting

51 Cabiropidae from Japan and anthuroids as hosts for not only cabiropids but also cryptoniscoids.

52

Introduction

The parasitic isopod group Epicaridea Latreille, 1825 (containing Bopyroidea Rafinesque, 1815 and Cryptoniscoidea Kossmann, 1880) utilizes crustaceans as both intermediate and definitive hosts (Williams and Boyko 2012; An *et al.* 2023). As far as is currently known, epicarideans use only planktonic copepods as intermediate hosts, but members of various groups as definitive hosts, including decapods, ostracods, peracarids, and cirripedes (Williams and Boyko 2012). The life cycle contains three larval stages (Williams and An 2009): epicaridium (first stage; pelagic), microniscus (second stage; parasitic on intermediate host), and cryptoniscus (third stage; pelagic or parasitic on definitive host) larvae.

Cryptoniscoidea currently contains twelve valid families (Asconiscidae Bonnier, 1900; Cabiropidae Giard & Bonnier, 1887; Capitoniscidae Boyko & Williams, 2023; Crinoniscidae Bonnier, 1900; Cryptoniscidae Kossmann, 1880; Cumoechidae Boyko & Williams, 2023; Cyproniscidae Giard & Bonnier, 1887; Dajidae G. O. Sars, 1883; Entophilidae Richardson, 1903; Hemioniscidae Bonnier, 1900; Podasconidae Giard & Bonnier, 1895; and Stellatoniscidae Oanh & Boyko, 2020; Boyko *et al.* 2024a). These families are defined mainly by the host taxa rather than by synapomorphies, and the relationships among them remain unresolved (Boyko 2013; Boyko *et al.* 2013). Cryptoniscoidea also contains ten monotypic genera treated as family *incertae sedis* (Buhl-Mortensen *et al.* 2020; Boyko *et al.* 2024b), nine of which were described only from cryptoniscus larvae; the remaining one, *Apocumoechus* Nierstrasz & Brender à Brandis, 1931, was based only on females. Cryptoniscoid females have a highly reduced, sac-like, unsegmented body, whereas males retain the segmented body. Morphologically, immature females and males are indistinguishable at the segmented cryptoniscus larval stage (Hosie 2008; Boyko 2013).

Cabiropidae, with 14 genera (Boyko 2013; Buhl-Mortensen *et al.* 2020; Williams *et*

al. 2024), is one of two cryptoniscoid families parasitic on isopods (Oanh and Boyko 2020). Both males and mature females are known for six genera (*Ancyroniscus* Caullery & Mesnil, 1919; *Arcturocheres* Hansen, 1916; *Bourdonia* Rybakov, 1990; *Cabirops* Kossmann, 1884; *Cirolanoniscus* Pillai, 1966; and *Clypeoniscus* Giard & Bonnier, 1895), whereas only mature females are known for four genera (*Aegoniscus* Barnard, 1925; *Gnomoniscus* Giard & Bonnier, 1895; *Munnoniscus* Giard & Bonnier, 1895; and *Perezina* Nierstrasz & Brender à Brandis, 1930). These genera are classified into four groups based on female morphology (Boyko 2013). The other four genera (*Cironiscus* Nielsen, 1967; *Podoniscus* Bourdon, 1981; *Pleuroniscus* Williams & Boyko in Williams *et al.*, 2024; and *Rolandoniscus* Boyko, 2013) lack information on mature females. Various isopod groups serve as hosts for cabiropids, including asellotes, cymothoid cymothoidans, epicarideans, sphaeromatideans, and valviferans (Table 1). To date, there are no verified records of cabiropids parasitizing anthuroid isopods, although an epicaridean reported by Wägele (1979) on *Eisothisistos macrurus* Wägele, 1979 may be such a case.

During a shallow-water faunal survey in Japan, we collected cabiropids parasitic on anthuroids. This represents the first report of cryptoniscoids parasitizing anthuroid and the first report of cabiropids from Japan. Through morphological observations and a phylogenetic analysis, we detected three different, undescribed species and concluded that a new genus should be established for them. Here we erect the new genus, describe the three new species and analyze their partial *18S* rRNA (*18S*) gene sequences to infer their phylogenetic position in Epicaridea, and present partial *16S* rRNA (*16S*) gene sequences for future DNA barcoding.

Material and methods

Sampling, observation, and host identification

Three host anthuroid isopods were collected from three localities in Japan (Fig. 1). The first

host individual, identified as *Mesanthura* sp. and probably parasitized by a cabiropid cryptoniscus larva (the parasite was not recognized when collected, but a female cabiropid appeared later through rearing; see Results), was collected from seaweed at 0.5 m depth at Kaichu Doro, Uruma, Okinawa, southwestern Japan (26°19'57.1"N 127°55'22.6"E), on 21 April 2023. The living host with parasite was maintained for 11 days in a small aquarium filled with seawater from the sampling locality, at room temperature and under ambient light. The host and a female cabiropid were fixed and preserved in 99% ethanol on 2 May 2023 when the host died. The second host individual, identified as *Accalathura* sp. and parasitized by a cabiropid cryptoniscus larva, was collected from coral rubble at 10–15 m depth at Irabu Island, Miyako Islands, Okinawa, southwestern Japan (24°51'54.0"N 125°09'22.2"E), on 23 April 2022, and fixed in 70% ethanol and preserved in 99% ethanol. The third host individual, identified as *Colanthura nigra* Nunomura, 1975 and parasitized by a cabiropid cryptoniscus larva, was collected from seaweed at 1 m depth at Jogashima, Kanagawa, central Japan (35°08'11.4"N, 139°36'39.3"E), on 14 July 2022, and fixed and preserved in 70% ethanol.

The habitus of the female parasite was observed and photographed by using a Nikon SMZ1500 stereomicroscope and an Olympus BX51 digital camera. After removal of the posterior portion for DNA extraction (see below), the remaining part was mounted on glass slides in glycerin. Exoskeletons of cryptoniscus parasites that were recovered after DNA extraction (see below) were mounted on glass slides in glycerin. Slides were observed with an Olympus BX53 microscope and then sealed with Canada balsam. Illustrations were prepared with Adobe Illustrator CC from draft line drawings made from sequential photographs (female) or with a camera lucida (cryptoniscus larvae). In the cryptoniscus parasites, body length was measured from tip of cephalon to tip of telson, and body width at the widest portion of pereonite 5; the body length of the female was measured from the

anterior to posterior ends of the body. We treated segmented cabiropid specimens as cryptoniscus larvae; males in previous studies are treated as cryptoniscus larvae in terms of their morphology in this study, since this larval stage is indistinguishable from males and immature females.

Host isopods were partly dissected with sharpened tungsten needles under a Nikon SMZ1500 microscope, and their appendages were observed with an Olympus BX53 microscope. Identifications of the host anthuroid species were based on Poore (2001) for *Mesanthura* sp., Poore (2001) and Jarquín-Martínez and García-Madrigal (2021) for *Accalathura* sp., and Nunomura (1975) and Poore (1984) for *C. nigra*. We treated host specimens with slender antennulae as females and those with swollen antennulae as males.

The three parasite specimens and their host anthuroids have been deposited in the Invertebrate Collection of the Hokkaido University Museum (ICHUM), Sapporo, Japan. Species in the systematics section are treated in alphabetical order after the type species.

Molecular analysis

Total DNA was extracted from the posterior part (female parasite) or whole body (cryptoniscus parasites) by using a NucleoSpin Tissue XS Kit (Macherey-Nagel, Germany); cryptoniscus exoskeletons were recovered and mounted after extraction. For the *16S* gene, primers Copepod16S_F and Copepod16S_R (Kakui *et al.* 2023) were used for PCR amplification and cycle sequencing; for *18S*, primers 18S-a1F and 18S-a9R (Kakui *et al.* 2011) were used for PCR amplification and 18S-b3F, 18S-b4F, 18S-b4R, 18S-b5F, 18S-b6F, 18S-a6R, 18S-b8R, and 18S-b8F (Kakui *et al.* 2011; Kakui and Shimada 2017) for cycle sequencing. Amplification conditions for *16S* with KOD One (Toyobo Life Science, Japan) were as described by Kakui *et al.* (2023); those for *18S* with KOD One (a female and a cryptoniscus larvae from Jogashima) were 45 cycles of 98°C for 10 s, 53°C for 5 s, and 68°C for 10 s. Those for *18S* with KOD FX Neo (Toyobo Life Science; the cryptoniscus larva from

Irabu) were 94°C for 2 min; 45 cycles of 98°C for 10 s, 52°C for 30 s, and 68°C for 75 s; and 68°C for 3 min. All nucleotide sequences were determined by direct sequencing with a BigDye Terminator Kit ver. 3.1 and 3730 DNA Analyzer (Life Technologies, USA). Sequences were deposited in the International Nucleotide Sequence Database (INSD) through the DNA DATA Bank of Japan (DDBJ).

The *18S* dataset for phylogenetic analysis included three sequences we determined, and 14 bopyroid, four cryptoniscoid, and one outgroup sequences (1915–2607 bp; Table 2) taken from DNA databases. The dataset was aligned by using MAFFT ver. 7 (Katoh and Standley 2013) with the “Q-INS-I” strategy (Katoh and Toh 2008), and then trimmed with MEGA7 (Kumar *et al.* 2016) to match the shortest length among sequences. Alignment-ambiguous sites were then removed with Gblocks ver. 0.91b (Castresana 2000) in NGPhylogeny.fr (Lemoine *et al.* 2019) under the “relaxed” parameters described in Talavera and Castresana (2007), for a final length of 1578 positions. Methods for selecting the optimal substitution model (GTR+F+R4), the maximum likelihood (ML) analysis, estimating nodal support (1000 pseudoreplicates for both SH-like approximate likelihood ratio tests [SH-aLRT] and ultrafast bootstraps [UFBoot]), and drawing the tree were as described by Shimada *et al.* (2023). We considered nodes having SH-aLRT $\geq$ 80% and UFBoot $\geq$ 95% to be well supported.

Taxonomy

Family **Cabiropidae** Giard & Bonnier, 1887

[New Japanese name: Waraji-yadori-mushi-ka]

Genus *Anthuroniscus* Shiraki & Kakui, gen. nov.

[New Japanese name: Uminanafushi-yadori-zoku]

(Fig. 2–10.)

178 ZooBank: urn:lsid:zoobank.org:act:DD042896-564C-488C-873C-202B764F461D

179 **Type species**

180 *Anthuroniscus shimomurai* Shiraki & Kakui, sp. nov., by original designation.

181

182 **Etymology**

183 The generic name is a combination of *anthura*- (the stem of Anthuroidea, the host group) and
184 *-oniscus* (a common suffix for cryptoniscoid genera). The gender is masculine.

185

186 **Diagnosis**

187 Female: body dorsally compressed, elongate, tapering posteriorly; segments fused, with six
188 pairs of lateral bulges. Cryptoniscus larva: eyes lacking; antennular article 1 with eight teeth
189 on posterior margin; uropodal exopod and endopod rectangular, not tapering, endopod longer
190 than exopod; pleotelson trapezoidal, width twice the length.

191

192 *Anthuroniscus shimomurai* Shiraki & Kakui, sp. nov.

193 [New Japanese name: Soramame-uminanafushi-yadori]

194 (Fig. 2–4.)

195 ZooBank: urn:lsid:zoobank.org:act:4082716F-FE71-4702-90CD-6E812AA721BA

196

197 **Etymology**

198 The specific name is a noun in the genitive case honoring Dr. Michitaka Shimomura, who has
199 greatly contributed to the taxonomy of isopods and related groups in Japan.

200

201 **Type material**

202 **Holotype.** Female (ICHUM8643; 3.10 mm; 1 vial), 26°19'57.1"N 127°55'22.6"E, 0.5 m

depth, Kaichu Doro, Uruma, Okinawa, Japan, 21 April 2023, from marsupium of female
Mesanthura sp. (ICHUM8644, 2 slides and 1 vial; Anthuridae Leach, 1814).

Attachment site

Inside the marsupium of female *Mesanthura* sp.

Diagnosis

Female: same as for the genus. Male/cryptoniscus larva unknown.

GenBank accession numbers

Holotype ICHUM8643: LC794718 (*18S*) and LC794716 (*16S*).

Description of holotype female

Body elongate, dorsally compressed, tapering posteriorly, length 3.10 mm, segments fused, with six pairs of lateral bulges (Fig. 3*a, b, 4*). Head with one pair of eyes, and one ventral hook posteriorly (Fig. 3*c, e*). Putative pereopod 1 located between head and first pair of bulges (Fig. 3*c, d*).

Remarks

The female *Mesanthura* sp. from which we collected the holotype individual was ovigerous on 21 April 2023 (Fig. 2*b, d*), and we did not detect the mature female parasite at that time. On 29 April, however, eggs were observed not in the marsupium but on the bottom of the aquarium, and the mature female parasite was in the marsupium instead (Fig. 2*c, e*). No observations were made between 21 and 29 April. This suggests that, during 8-day period with no observations, the larval parasite molted, pushed out the host's eggs, and grew to

occupy >50% of the space of the host marsupium. It should be noted that, as we failed to count the number of eggs on the bottom of the aquarium, the parasite may have eaten some eggs as expected in other cryptoniscoids (Williams *et al.* 2022) No increase in the size of the parasite was observed between 29 April and 1 May (Fig. 2*e,f*). The host died on 2 May 2023.

Anthuroniscus dentatus Shiraki & Kakui, sp. nov.

[New Japanese name: Gizagiza-uminanafushi-yadori]

(Fig. 5–7.)

ZooBank: urn:lsid:zoobank.org:act:65FA893E-7D84-4A53-8D04-63465138C6D0

Etymology

The specific epithet *dentatus* (Latin: toothed) is a singular adjective in the nominative case, referring to the toothed pygidium of the pleotelson.

Type material

Holotype. Cryptoniscus larva (ICHUM8645; 0.45 mm; 1 slide), 24°51'54.0"N 125°09'22.2"E, 10–15 m depth, Irabu Island, Miyako Islands, Okinawa, Japan, 23 April 2022, from right pereopod 3 of male *Accalathura* sp. (ICHUM8646, 1 slide and 1 vial; Leptanthuridae Poore, 2001)

Attachment site

Right pereopod 3 of male *Accalathura* sp.

Diagnosis

Cryptoniscus larva: body teardrop shaped, length 2.89 times body width; pereomeres 1–7

with coxal plate tooth formula of 4, 5, 5, 4, 4, 4, 4; pygidium with eight teeth; propodi of pereopods 6 and 7 with two stout setae. Female/male unknown.

GenBank accession number

Holotype ICHUM8645: LC794719 (*18S*).

Description of holotype cryptoniscus larva

Body (Fig. 6*a, c*) teardrop shaped, length 0.45 mm, 2.89 times body width, widest at pereonite 5 (0.15 mm). Cephalon anterior margin rounded, with several knobs on anterior part. Eyes absent.

Antennule (Fig. 6*a, c, 7a*) article 1 without demarcated area and with two distal simple setae and eight teeth on posterior margin; fifth tooth from inner margin with dorsal cylindrical structure bearing simple seta. Article 2 tridentate on distal margin, with two middle and two distal simple setae. Article 3 rounded, covered ventrally by article 2, with mid-ventral setal area and two conical extensions each bearing two and four simple setae. Antenna (Fig. 6*a, c*) with four peduncular articles and five flagellar articles. Peduncular article 1 broadest; articles 2–4 each with distal simple seta. Flagellar articles 1–4 naked; article 5 with several simple setae. Oral cone (Fig. 6*a*) triangular, directed ventrally.

Pereomeres 1–7 with coxal plate tooth formula of 4, 5, 5, 4, 4, 4, 4 (Fig. 6*b*). Pereopods 1 (Fig. 7*b*; P1) and 2 (Fig. 7*c*; P2) similar, subchelate, short. Dactylus curved, simple, not bifid, with three outer spiniform projections. Propodus oval, with bifurcate stout seta, simple stout seta, and three (P1) or one (P2) simple setae. Carpus triangular, with distal lamellar projection and two (P1) or one (P2) simple setae. Merus rounded, with outer stout seta bearing seta, and distal simple seta. Ischium with outer lamellar projection. Basis cylindrical, naked. Pereopod 3 (Fig. 7*d*) subchelate, narrower than pereopods 1 and 2.

Dactylus slender, elongate. Propodus with three stout setae. Carpus trapezoidal, with stout seta and simple seta. Merus with outer stout seta and two simple setae. Ischium with outer ventral and outer dorsal bifurcate lamellar projections. Pereopods 4 (Fig. 7e) and 5 similar to pereopod 3 but propodi narrower and carpi triangular. Pereopods 6 (Fig. 7f) and 7 similar, narrower than pereopods 1–5. Dactylus slender, elongate. Propodus elongate, tapering, with two stout setae. Carpus triangular, with stout seta and simple seta. Merus with outer stout seta and two simple setae. Ischium with outer dorsal bifurcate lamellar projection.

Pleon with five pairs of pleopods. All pleopods similar in shape; sympod rounded, endopod rectangular, exopod pyriform and narrow proximally (Fig. 6a). Pleopod 1 (Fig. 7g) sympod with two inner simple setae. Endopod with three distal simple setae and exopod with four distal simple setae. Uropod (Fig. 7h) biramous, sympod with three outer simple setae. Endopod rectangular, not tapering, with three distal simple setae and two distal triangular lamellar projections. Exopod rectangular, not tapering, 0.56 times as long as endopod, with four distal simple setae, distal seta (tip broken), and two distal triangular lamellar projections. Pleotelson (Fig. 6c) trapezoidal; pygidium (Fig. 6d) with eight teeth.

Remarks

The cryptoniscus larva of *Anthuroniscus dentatus* sp. nov. was found on a male anthuroid host (Fig. 5a). As with *A. shimomurai* sp. nov. and other cabiropids (Boyko 2013), mature females of *A. dentatus* sp. nov. likely inhabit the marsupium of host females. Although little information is available on anthuroid reproduction, Horikoshi (2012) reported, for the anthurid *Cyathura muromiensis* Nunomura, 1974, the temporary cohabitation of a male and a female in a single tube, until female oviposition. During this period of cohabitation, a cabiropid on the male host might move to inside the marsupium of the female.

303 *Anthuroniscus latus* Shiraki & Kakui, sp. nov.

304 [New Japanese name: Futo-maru-uminanafushi-yadori]

305 (Fig. 8–10.)

306 ZooBank: urn:lsid:zoobank.org:act:3D601783-7FAB-433C-B79F-27E9FB044432

307

308 **Etymology**

309 The specific epithet *latus* (Latin: broad) is a singular adjective in the nominative case,
310 referring to the broad body.

311

312 **Type material**

313 **Holotype.** Cryptoniscus larva (ICHUM8647; 0.478 mm; 1 slide), 35°08'11.4"N,
314 139°36'39.3"E, 1 m depth, Jogashima, Kanagawa, Japan, 14 July 2022, from pereonite-3
315 sternite of female *Colanthura nigra* (ICHUM8648; 1 vial; Paranthuridae Menzies & Glynn,
316 1968).

317

318 **Attachment site**

319 Pereonite-3 sternite of female *Colanthura nigra*.

320

321 **Diagnosis**

322 Cryptoniscus larva: body teardrop shaped, length 2.58 times body width; pereomeres 1–7
323 with coxal plate tooth formula of 3, 4, 4, 4, 4, 4, 4; pygidium roundly projecting distally;
324 propodi of pereopods 6 and 7 without stout seta. Female/male unknown.

325

326 **GenBank accession numbers**

327 Holotype ICHUM8647: LC794720 (18S) and LC794717 (16S).

328

329 **Description of holotype cryptoniscus larva**

330 Body (Fig. 9*a, c*) teardrop shaped, length 0.48 mm, 2.58 times body width, widest at
331 pereonite 5 (0.19 mm). Cephalon anterior margin rounded, with several knobs on anterior
332 part. Eyes lacking.

333 Antennule (Fig. 9*a*) article 1 without demarcated area and with two distal simple setae
334 and eight teeth on posterior margin; fifth tooth from inner margin broadest, with dorsal
335 cylindrical structure bearing simple seta. Article 2 tridentate on distal margin, with two distal
336 simple setae. Article 3 rounded, covered by article 2 ventrally, with mid-ventral setal area and
337 two conical extensions each bearing one and two simple setae. Antenna (Fig. 10*a*) with four
338 peduncular articles and five flagellar articles. Peduncular article 1 longest and broadest;
339 articles 2–4 with one, two, and one distal simple setae, respectively. Flagellar article 1 with
340 distal simple seta; articles 2–4 naked; article 5 with two distal simple setae. Oral cone (Fig.
341 9*a*) triangular, ventrally directed.

342 Pereomeres 1–7 with coxal plate tooth formula of 3, 4, 4, 4, 4, 4, 4 (Fig. 9*b*).

343 Pereopods 1 and 2 (Fig. 10*b*) similar, subchelate, short. Dactylus curved, simple, not bifid.

344 Propodus oval, with bifurcate stout seta and simple stout seta. Carpus triangular, with three
345 stout setae and two simple setae. Merus rounded, with distal simple seta. Ischium and basis
346 naked. Pereopod 3 (Fig. 10*c*) subchelate, narrower than pereopods 1 and 2. Dactylus slender,
347 elongate. Propodus with three stout setae. Carpus trapezoidal, with distal stout seta. Merus
348 with outer stout seta bearing simple seta. Ischium with distal simple seta and outer ventral
349 and dorsal lamellar projections. Pereopods 4 (Fig. 10*d*) and 5 similar to pereopod 3 but
350 propodi narrower and carpi triangular. Pereopods 6 (Fig. 10*e*) and 7 similar, narrower than
351 pereopods 1–5. Dactylus slender, elongate. Propodus elongate, naked. Carpus triangular, with
352 distal stout seta. Merus with outer stout seta and simple seta. Ischium with outer ventral

lamellar and dorsal bifurcate lamellar projections.

Pleon with five pairs of pleopods. All pleopods similar in shape; sympod rounded, endopod rectangular, exopod pyriform and narrow proximally (Fig. 9a). Pleopod 1 (Fig. 10f) sympod naked. Endopod and exopod each with five distal simple setae. Uropod (Fig. 10g) biramous, sympod with two outer simple setae. Endopod rectangular, not tapering, with two outer simple setae, three distal simple setae, and two distal triangular lamellar projections. Exopod rectangular, not tapering, 0.55 times as long as endopod, with two distal simple setae and two distal triangular lamellar projections. Pleotelson (Fig. 9c) trapezoidal; pygidium (Fig. 9c) smooth and roundly projecting posteriorly.

Molecular phylogeny

The *18S* tree shows two clades in Epicaridea (Fig. 11), one with full nodal support containing all bopyroid taxa, the other with moderate support (SH-aLRT = 71.4% and UFBoot = 66%) containing all cryptoniscoid taxa. The three new *Anthuroniscus* gen. nov. species form a highly supported clade (SH-aLRT = 96.6% and UFBoot = 97%) that is the sister group with full support to *Cryptoniscoidea* sp., parasitic on the ostracod *Metavargula* sp. (Boyko *et al.* 2013).

The p-distances for *18S* sequences among confamilial genera (1440 positions after the elimination of all positions containing gaps and missing data) were 4.0–11.0%. Pairwise *18S* p-distances among the three new *Anthuroniscus* gen. nov. species were 0.6% (*shimomurai*–*dentatus*), 0.8% (*shimomurai*–*latus*), and 1.3% (*dentatus*–*latus*). The p-distance for *16S* between *A. shimomurai* sp. nov. and *A. latus* sp. nov. (412 positions) was 36.2%.

Discussion

Based on (1) their host group being Anthuroidea Leach, 1814, (2) *18S* p-distances among our

three species (0.6–1.3%) lower than the minimum value (4.0%) observed among confamilial genera in our analysis, and (3) morphological similarity between cryptoniscus larvae, we deemed our three species to be congeneric. *Anthuroniscus* gen. nov. is placed in Cryptoniscoidea because the cryptoniscus larvae have antenna consisting of four peduncular and five flagellar articles, and females have a highly reduced, sac-like body (Boyko 2013; Boyko and Williams 2015). Our phylogenetic analysis (Fig. 11) supports this conclusion from morphology, showing the clade of *Anthuroniscus* gen. nov. within the Cryptoniscoidea clade, and comprising the sister group to the ostracod-parasitic Cryptoniscoidea sp.

Only Cabiropidae and Stellatoniscidae are cryptoniscoid families currently known to be parasitic on isopods (Boyko 2013; Oanh and Boyko 2020). In females, these families can be distinguished by body shape, which is sac-like in Cabiropidae but star-like in Stellatoniscidae. Cryptoniscus larvae in Cabiropidae have the antennular plate without a demarcated area and pereopod 1 similar to pereopod 2, while those in Stellatoniscidae have the antennular plate with a demarcated area and pereopod 1 dissimilar to pereopod 2. *Anthuroniscus* gen. nov. shows the character states characteristic of Cabiropidae, and we concluded the genus belongs in this family.

Anthuroniscus gen. nov. can be distinguished morphologically from the other 14 cabiropid genera and ten genera treated as family *incertae sedis*. Females have an elongate, dorsally compressed body, and thus *Anthuroniscus* gen. nov. belongs in Boyko's (2013) "group 2" in Cabiropidae, containing *Aegoniscus*, *Cirolanoniscus*, and *Clypeoniscus*. *Anthuroniscus* gen. nov. differs from these three genera and *Apocumoechus* (family *incertae sedis*) in having a more-elongate, posteriorly tapering body (Fig. 3a, b, 4). Cryptoniscus larvae of *Anthuroniscus* gen. nov. differ from the ten cabiropid genera in which cryptoniscus larvae are known in lacking eyes, having eight teeth on antennular article 1, and having a rectangular uropodal endopod.

Cryptoniscus larvae of *Anthuroniscus* gen. nov. differ from those of the nine cryptoniscoid genera described from cryptoniscus larvae and treated as "family *incertae sedis*" in having eight teeth on antennular article 1 (two in *Elocryptus* Schultz, 1977; eight in *Chimaeroniscus* Williams, Boyko & Moritaki, 2022; nine in *Osicryptus* Schultz, 1977; none in the other six genera) and the trapezoidal pleotelson twice as wide as long (eight of the nine genera have a different pleotelson; information on the pleotelson is lacking for *Trisopodoniscus* Bourdon, 1981) (Schultz 1977; Bourdon 1981, 1983; Williams *et al.* 2022). There are also differences in body size and recorded depths. Cryptoniscus larvae of *Anthuroniscus* gen. nov. are small (length 0.45–0.48 mm) and were collected from depths of 0.5–15 m, whereas cryptoniscus larvae of the nine genera are larger (length 1.11–3.10 mm) and were collected from depths of 183–5340 m.

Cryptoniscus larva of *Anthuroniscus dentatus* sp. nov. differs from that of *A. latus* sp. nov. in the following characters (character state of *A. latus* sp. nov. in parentheses): body narrower, length 2.89 times body width (2.58 times); pygidium with eight teeth, not roundly projecting distally (without teeth, roundly projecting distally); pereomeres 1–7 with coxal plate tooth formula of 4, 5, 5, 4, 4, 4, 4 (3, 4, 4, 4, 4, 4, 4); and propodi of pereopods 6 and 7 with two stout setae (without stout setae). Their host species also differ: *A. dentatus* sp. nov. is parasitic on *Accalathura* sp. (Leptanthuridae), whereas *A. latus* sp. nov. is parasitic on *Colanthura nigra* (Paranthuridae).

We could not morphologically compare female *A. shimomurai* sp. nov. (AS) with cryptoniscus larvae of *A. dentatus* sp. nov. (AD) and *A. latus* sp. nov. (AL) due to the large morphological difference, but the host of *A. shimomurai* sp. nov. (*Mesanthura* sp.; Anthuridae) differed from those of latter two species. The *16S* sequences for *A. shimomurai* sp. nov. and *A. latus* sp. nov. showed a p-distance of 36.2%, much larger than expected for intraspecific *16S* sequence variation (up to 10%; Riehl *et al.* 2018). Given that the *18S* p-

distances for the pairwise comparisons AS–AD and AS–AL were similar (0.6% and 0.8%, respectively), we concluded that *A. shimomurai* sp. nov. was likewise not conspecific with *A. dentatus* sp. nov. The elongate, dorsally compressed body in *A. shimomurai* sp. nov. may be a synapomorphy for cabiropids parasitic on anthuroids; anthuroid females have a narrow marsupium, which might require the parasites to be elongate.

Prior to our study, Wägele (1979) was the only previous work to report an epicaridean parasitizing an anthuroid isopod (an epicaridean cryptoniscus larvae parasitic on *Eisothistos macrurus*). Based on its host, the epicaridean was likely a species of *Anthuroniscus* gen. nov. Even so, it was likely a different species from the three *Anthuroniscus* species described herein. Its locality (Gulf of Naples, Italy) was far from Japan, and its host anthuroid family (Expanathuridae Poore, 2001) was different from those of our species (Anthuridae, Leptanthuridae, and Paranthuridae); cryptoniscoid species tend to have high host specificity (Nielsen and Strömberg, 1973).

This study added Anthuroidea to the list of cabiropid host groups (Table 1). Cabiropid parasites remain unknown for various isopod groups, such as Limnoriidea Brandt & Poore, 2002 and Microcerberidea Lang, 1961.

Data availability. The data that support this study are available in the article and on INSD.

Conflicts of interest. The authors declare that there is no known conflict of interest in the work reported in this paper.

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Figure legends

Fig. 1. Map showing sampling sites in Japan, indicating the *Anthuroniscus* gen. nov. species detected at each site. Circle: Kaichu Doro, Uruma, Okinawa, southwestern Japan. Triangle: Irabu Island, Miyako Islands, Okinawa, southwestern Japan. Square: Jogashima, Kanagawa, central Japan.

Fig. 2. *Mesanthura* sp. (ICHUM8644) parasitized by female *Anthuroniscus shimomurai* sp. nov. (ICHUM8643) during rearing; living specimen. (a) Dorsal view. (b, c) Lateral views. (d–f) Ventral views. (a, c, e, f) Holotype female of *A. shimomurai* sp. nov. in the marsupium on 29 April 2023 (a, c, e) and 1 May 2023 (f); (b, d) marsupium filled with eggs on 21 April 2023. Scale bar, 2 mm.

Fig. 3. *Anthuroniscus shimomurai* sp. nov. (ICHUM8643), holotype female. (a) Ventral view. (b) Dorsal view. (c) Anterior end, ventral view. (d, e) Anterior end, left lateral view. White arrowheads, putative pereopod 1; open arrowheads, ventral hook. Scale bars, 2 mm (a, b), 200 μ m (c–e).

Fig. 4. *Anthuroniscus shimomurai* sp. nov. (ICHUM8643), holotype female. (a) Dorsal view. (b) Right lateral view. (c) Ventral view. Scale bar, 1 mm.

Fig. 5. *Anthuroniscus dentatus* sp. nov. (ICHUM8645), holotype cryptoniscus larva, attached to *Accalathura* sp. (ICHUM8646). (a) Dorsal view of host; living specimen. (b–d) Dorsal, right lateral, and ventral views of *Anthuroniscus dentatus* sp. nov.; photomicrographs of fixed specimens. Arrowheads, parasite attached to right pereopod 3. Scale bars, 1 mm.

648

649 **Fig. 6.** *Anthuroniscus dentatus* sp. nov. (ICHUM8645), holotype cryptoniscus larva. (a)
650 Ventral view. (b) Left lateral view (cephalon and most appendages omitted). (c) Dorsal view;
651 pygidium not illustrated. (d) Pygidium. Scale bars, 100 μ m.

652

653 **Fig. 7.** *Anthuroniscus dentatus* sp. nov. (ICHUM8645), holotype cryptoniscus larva. (a)
654 Ventral view of right antennule. (b–f) Ventral views of right pereopods 1, 2, 3, 4, 6. (g)
655 Ventral view of left pleopod 1. (h) Ventral view of right uropod. Scale bar, 50 μ m.

656

657 **Fig. 8.** *Anthuroniscus latus* sp. nov. (ICHUM8647), holotype cryptoniscus larva, attached to
658 *Colanthura nigra* (ICHUM8648); living specimen. (a) Lateral view of host. (b) Ventral view
659 of host. Arrowheads, parasite attached to pereonite-3 sternite. Scale bar, 1 mm.

660

661 **Fig. 9.** *Anthuroniscus latus* sp. nov. (ICHUM8647), holotype cryptoniscus larva. (a) Ventral
662 view. (b) Lateral view of left side (cephalon, appendages, and pleon omitted). (c) Dorsal
663 view. Scale bar, 100 μ m.

664

665 **Fig. 10.** *Anthuroniscus latus* sp. nov. (ICHUM8647), holotype cryptoniscus larva. (a)
666 Dorsal view of left antenna. (b–e) Ventral view of right pereopods 2, 3, 4, 6. (f) Ventral view
667 of right pleopod 1 (setae omitted). (g) Ventral view of right uropod. Scale bar, 50 μ m.

668

669 **Fig. 11.** Maximum likelihood (ML) tree based on 1578 positions of the *18S* rRNA gene.
670 Values near nodes are SH-aLRT/UFBoot (clades having SH-aLRT $\geq$ 80% and UFBoot $\geq$ 95%
671 were considered to be well supported). Dark orange shading, Bopyroidea; blue shading,
672 Cryptoniscoidea; light orange shading, *Anthuroniscus* gen. nov. Taxa for which sequences

673 were obtained in this study are in bold font. The scale bar indicates branch length in number
674 of substitutions per site.

Table 1. Host isopods for each genus in Cabiropidae. ^a, Barnard (1920) reported, but did not name, two larval specimens attached on *Lanocira capensis* Barnard, 1914 (Corallanidae Hansen, 1890; junior synonym of *Lanocira gardineri* Stebbing, 1904; cf. Bruce and Sidabalok 2011), which may belong in *Clypeoniscus*, but Nielsen (1967) was doubtful about their affiliation. nd, no host information.

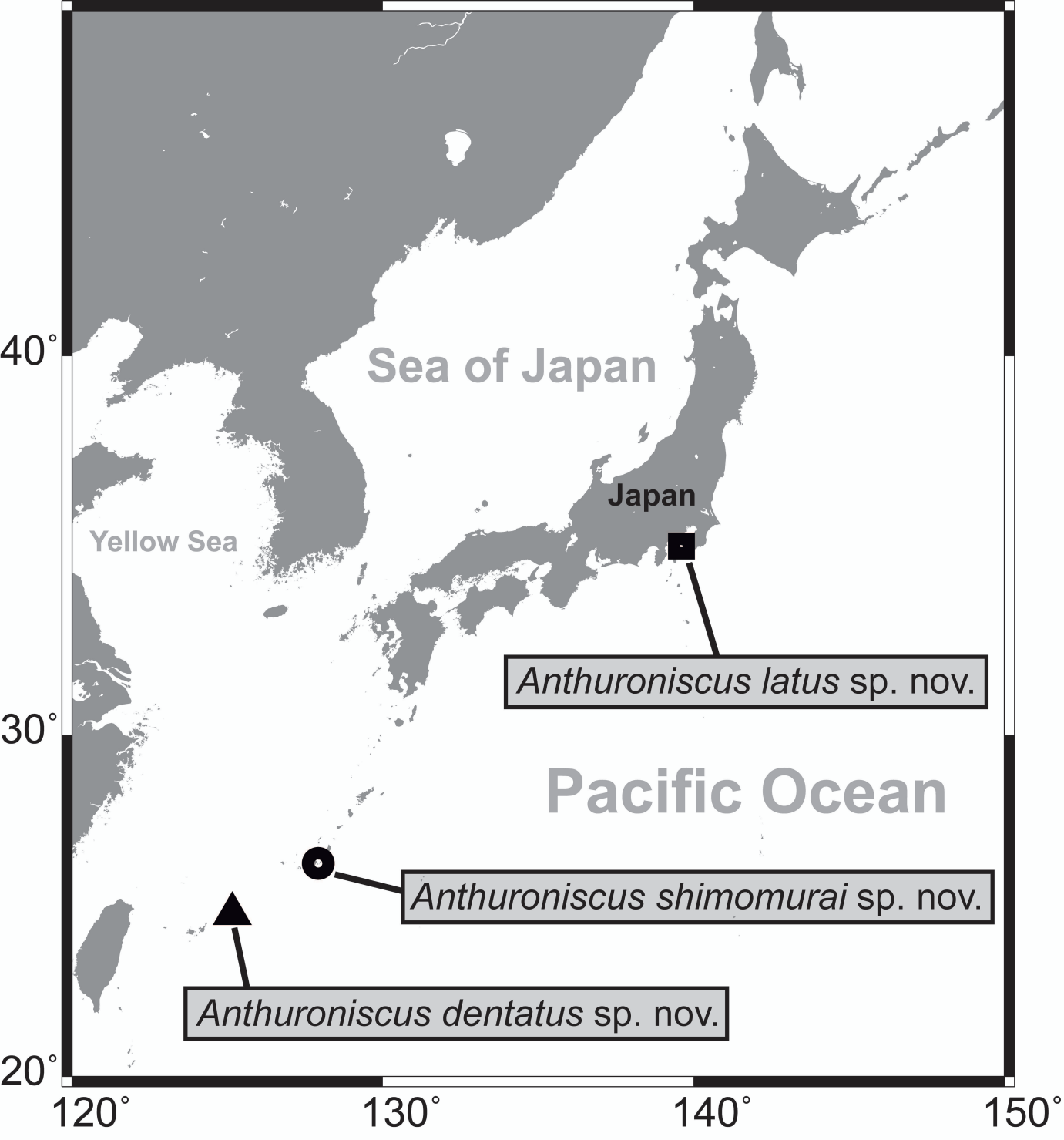
Cabiropid genus	Host isopods			References
	Suborder	Superfamily	Family	
<i>Aegoniscus</i>	Cymothoida	Cymothooidea	Aegidae	Barnard (1925)
<i>Ancyroniscus</i>	Cymothoida	Cymothooidea	Aegidae	Bourdon and Bruce (1980)
	Sphaeromatidea	Sphaeromatoidea	Sphaeromatidae	Caullery and Mesnil (1919)
<i>Arcturocheres</i>	Valvifera	(no superfamily rank)	Arcturidae	Schultz (1980)
			Austrarcturellidae	Schultz (1980)
			Holidoteidae	Schultz (1980)
<i>Bourdonia</i>	Epicaridea	Bopyroidea	Bopyridae	Rybakov (1990)
<i>Cabirops</i>	Epicaridea	Bopyroidea	Bopyridae	Boyko (2013)
<i>Cirolanoniscus</i>	Cymothoida	Cymothooidea	Cirolanidae	Pillai (1966)
<i>Cironiscus</i>	Cymothoida	Cymothooidea	Cirolanidae	Nielsen (1967)
<i>Clypeoniscus</i>	Asellota	Stenetrioidea	Stenetriidae	Barnard (1920)
	Cymothoida ^a	Cymothooidea ^a	Corallanidae ^a	Barnard (1920)
	Valvifera	(no superfamily rank)	Idoteidae	Bourdon (1967)
<i>Gnomoniscus</i>	Epicaridea	Cryptoniscoidea	Podasconidae	Giard and Bonnier (1895)
<i>Munnoniscus</i>	Asellota	Janiroidea	Munnopsidae	Giard and Bonnier (1895)

<i>Perezina</i>	Non-isopod (Rhizocephala)			Nierstrasz and Brender à Brandis (1929)
<i>Pleuroniscus</i>	Epicaridea	Bopyroidea	Bopyridae	Williams <i>et al.</i> (2024)
<i>Podoniscus</i>	nd	nd	nd	Bourdon (1981)
<i>Rolandoniscus</i>	Epicaridea	Bopyroidea	Bopyridae	Boyko (2013)
<i>Anthuroniscus</i> gen. nov.	Cymothoida	Anthuroidea	Anthuridae	This study
			Leptanthuridae	This study
			Paranthuridae	This study

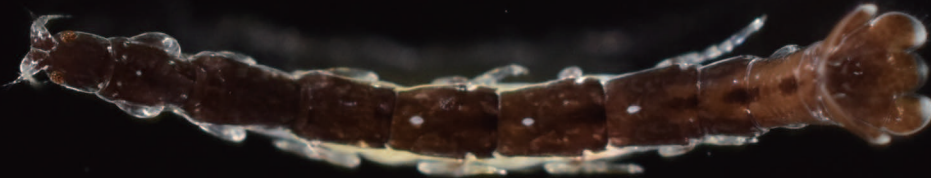
Table 2. Taxa included in the phylogenetic analysis of *18S* rRNA gene sequences. Information for species sequenced in this study is in bold font.

Family	Species	Locality	Accession No.	Reference
Bopyroidea				
Bopyridae	<i>Allokepon sinensis</i>	Bohol, Philippines	KF765766	Boyko <i>et al.</i> (2013)
	<i>Argeia pugettensis</i>	Coos Bay, Oregon, USA	KF765770	Boyko <i>et al.</i> (2013)
	<i>Athelges takanoshimensis</i>	Discovery Bay, Hong Kong	KF765762	Boyko <i>et al.</i> (2013)
	<i>Athelges takanoshimensis</i>	Discovery Bay, Hong Kong	KF765769	Boyko <i>et al.</i> (2013)
	<i>Athelges takanoshimensis</i>	Discovery Bay, Hong Kong	KF765773	Boyko <i>et al.</i> (2013)
	<i>Hemiarthrus abdominalis</i>	Baltic Sea	AF255684	Dreyer and Wägele (2001)
	<i>Probopyrus buitendijki</i>	Sungai Timun, Negeri Sembilan, Malaysia	KF765767	Boyko <i>et al.</i> (2013)
	<i>Probopyrus pacificiensis</i>	Guerrero, Mexico	AF255683	Dreyer and Wägele (2001)
	<i>Probopyrus pandalicola</i>	Georgia, USA	EU848422	Cho (2012)
	<i>Pseudione longicauda</i>	32°47'N, 130°36'E, Japan	KF765760	Boyko <i>et al.</i> (2013)
	<i>Pseudione longicauda</i>	32°47'N, 130°36'E, Japan	KF765774	Boyko <i>et al.</i> (2013)
Entoniscidae	<i>Portunion conformis</i>	Limfjord Inlet, Denmark	KF765764	Boyko <i>et al.</i> (2013)
Ionidae	<i>Ione cornuta</i>	Pigeon Point, Oregon, USA	KF765761	Boyko <i>et al.</i> (2013)
	<i>Ione cornuta</i>	Charleston mud flat, Oregon, USA	KF765771	Boyko <i>et al.</i> (2013)
Cryptoniscoidea				
Cabiropidae	<i>Anthuroniscus shimomurai</i> sp. nov.	Kaichu Doro, Uruma, Okinawa, Japan	LC794718	This study
	<i>Anthuroniscus dentatus</i> sp. nov.	Irabu Is., Miyako Islands, Okinawa, Japan	LC794719	This study

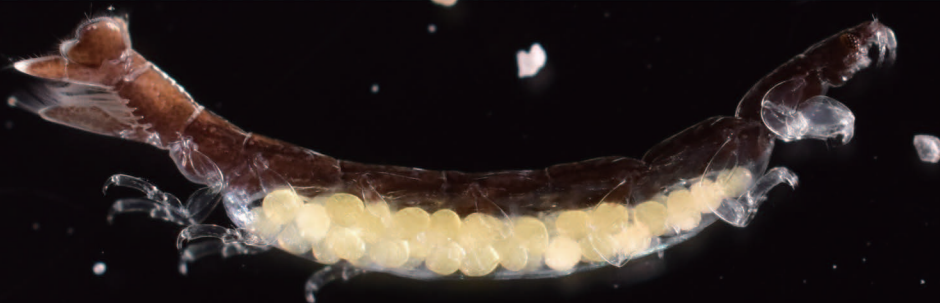
	<i>Anthuroniscus latus</i> sp. nov.	Jogashima, Kanagawa, Japan	LC794720	This study
Dajidae	<i>Zonophryxus dodecapus</i>	Candelaria, Tenerife, Canary Islands	KF765768	Boyko <i>et al.</i> (2013)
	<i>Zonophryxus quinquedens</i>	Weddell Sea, Antarctica	DQ008451	Raupach and Thatje (2006)
Entophilidae	<i>Entophilus mirabiledictu</i>	Royal Diving Club, Aqaba, Red Sea	KF765763	Boyko <i>et al.</i> (2013)
Unidentified	Cryptoniscoidea sp.	No data	KF765772	Boyko <i>et al.</i> (2013)
Cymothooidea				
Cymothoidae	<i>Excorallana quadricornis</i>	Venezuela	AF255688	Dreyer and Wägele (2001)



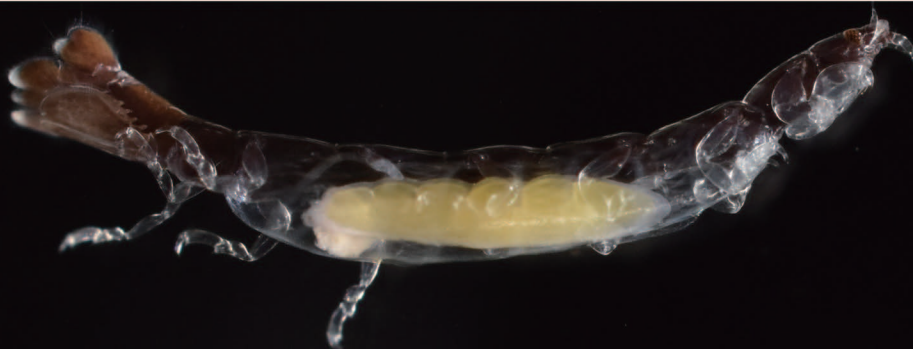
(a)



(b)



(c)



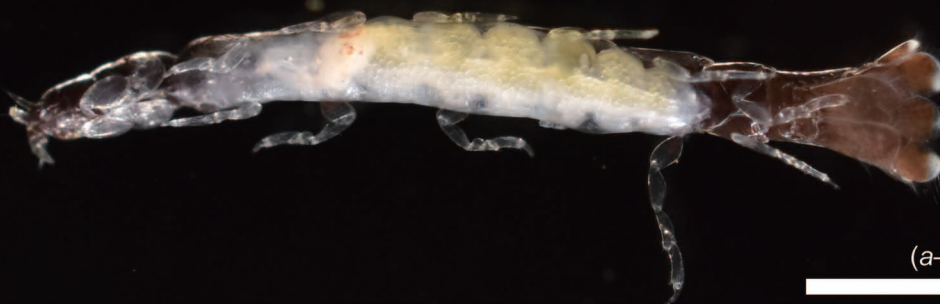
(d)



(e)

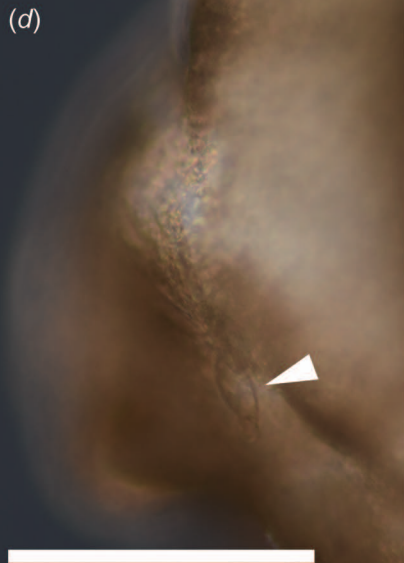
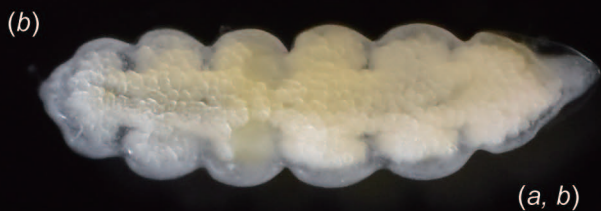
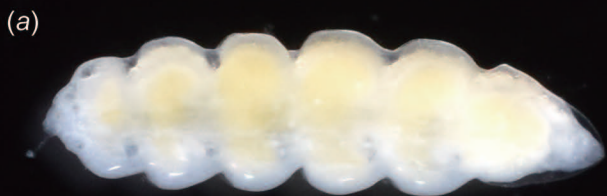


(f)

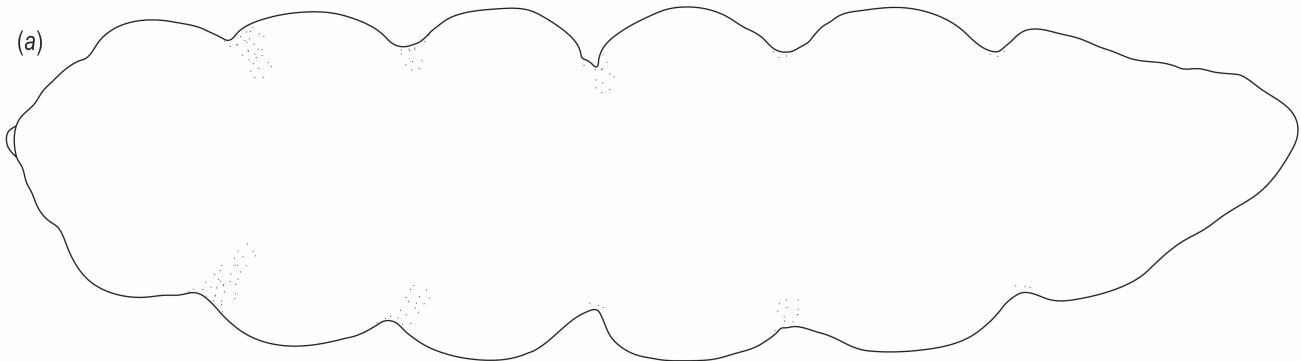


(a-f)

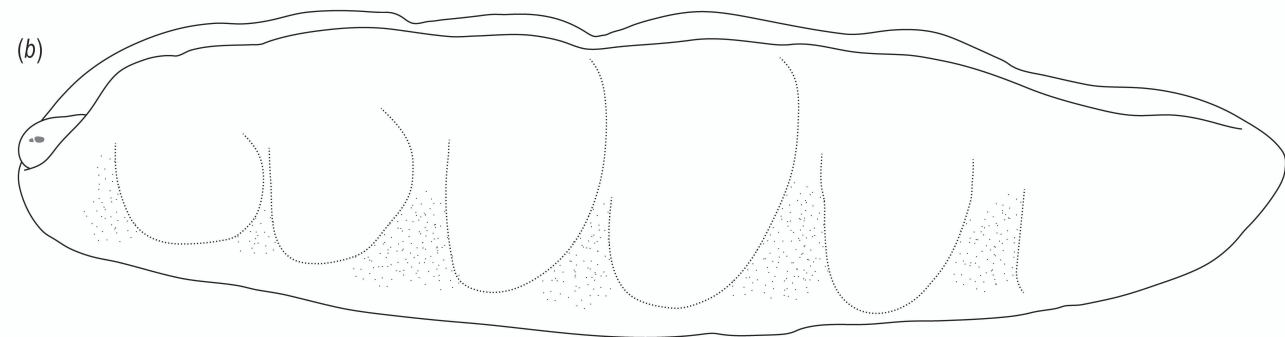




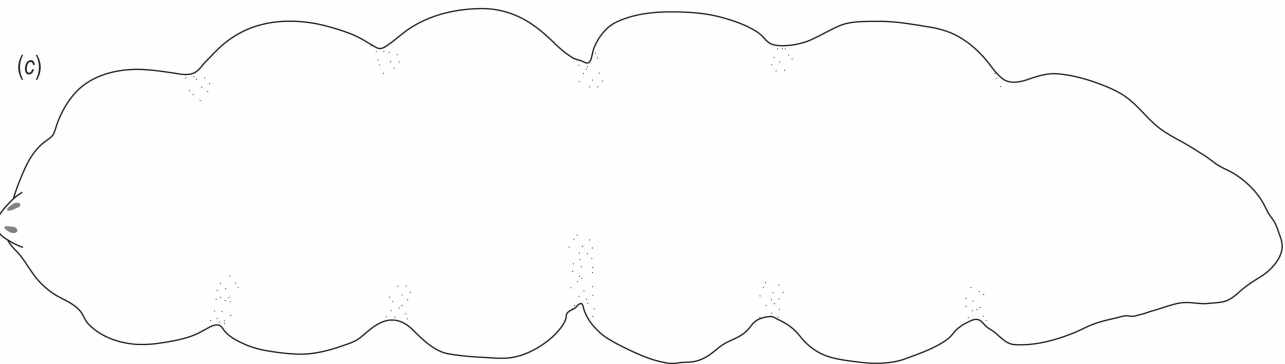
(a)



(b)



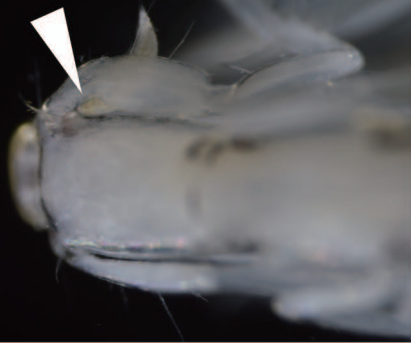
(c)



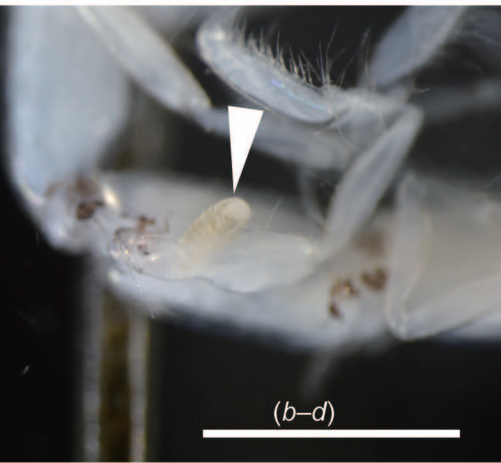
(a)



(b)

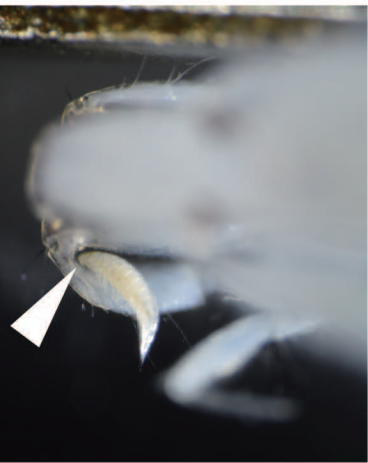


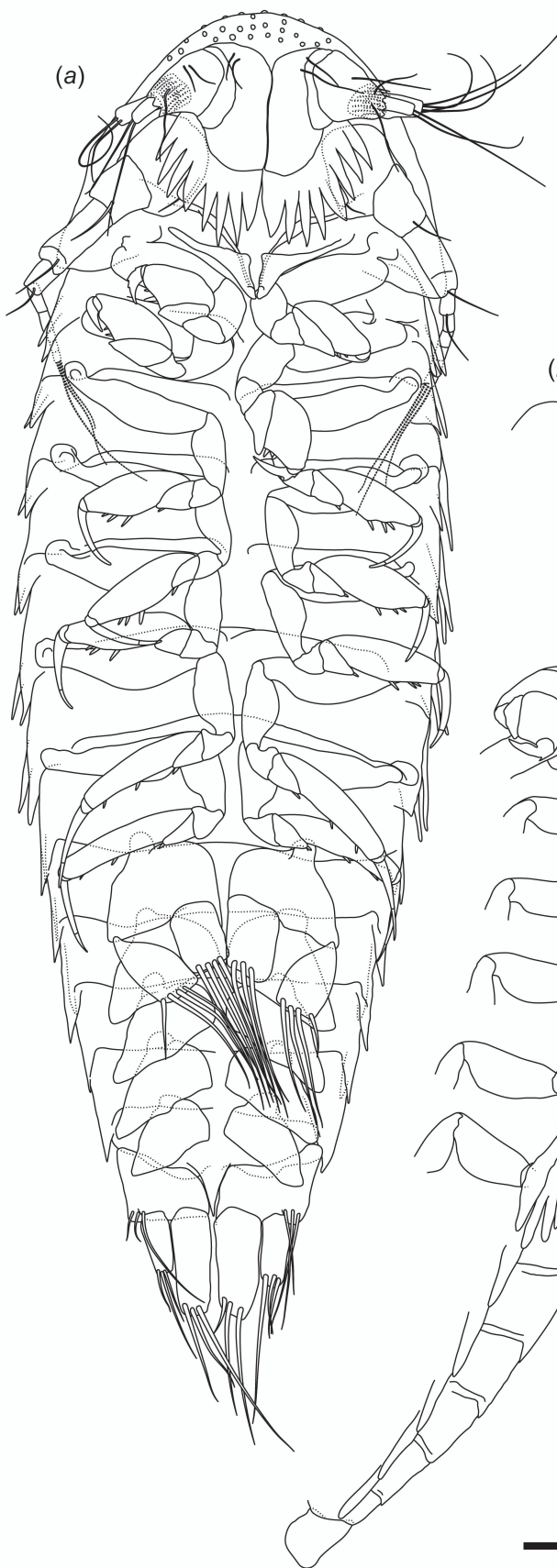
(c)



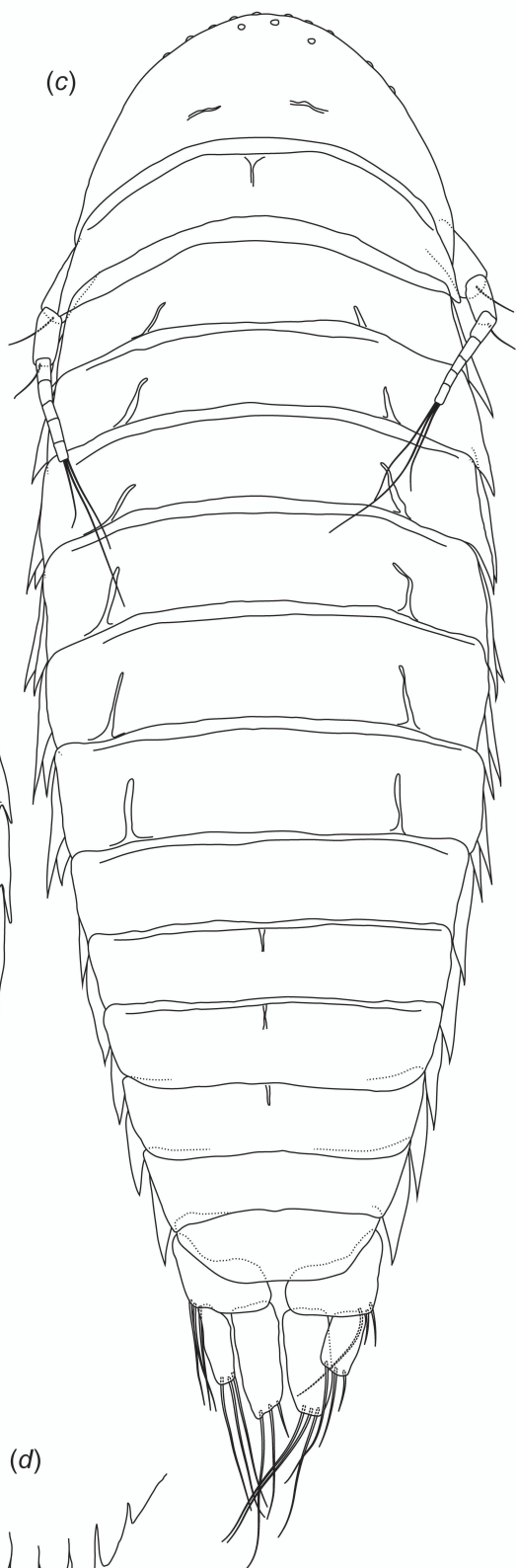
(b-d)

(d)

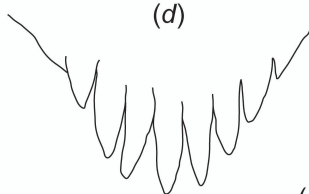




(a-c)

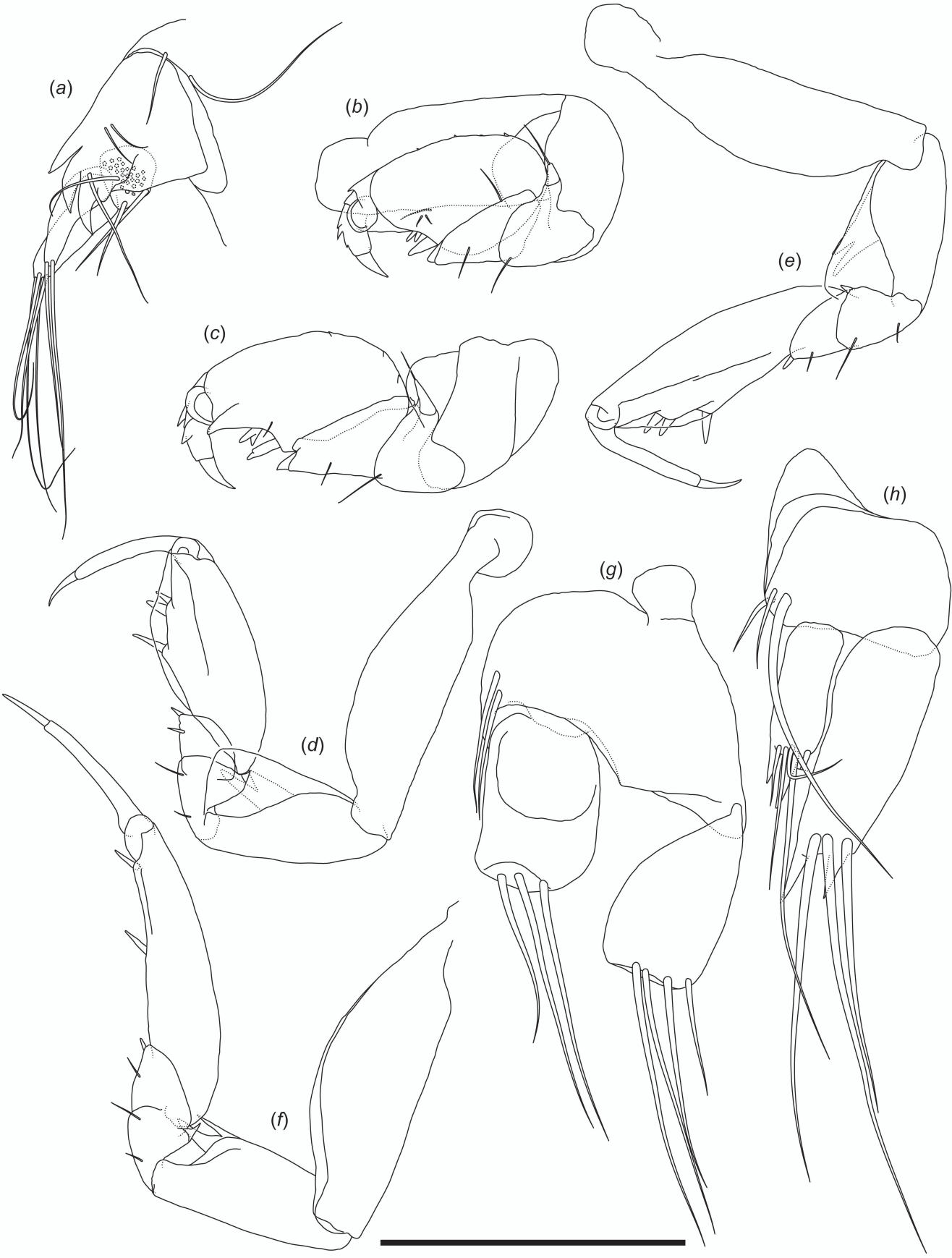


(d)



(d)





(a)



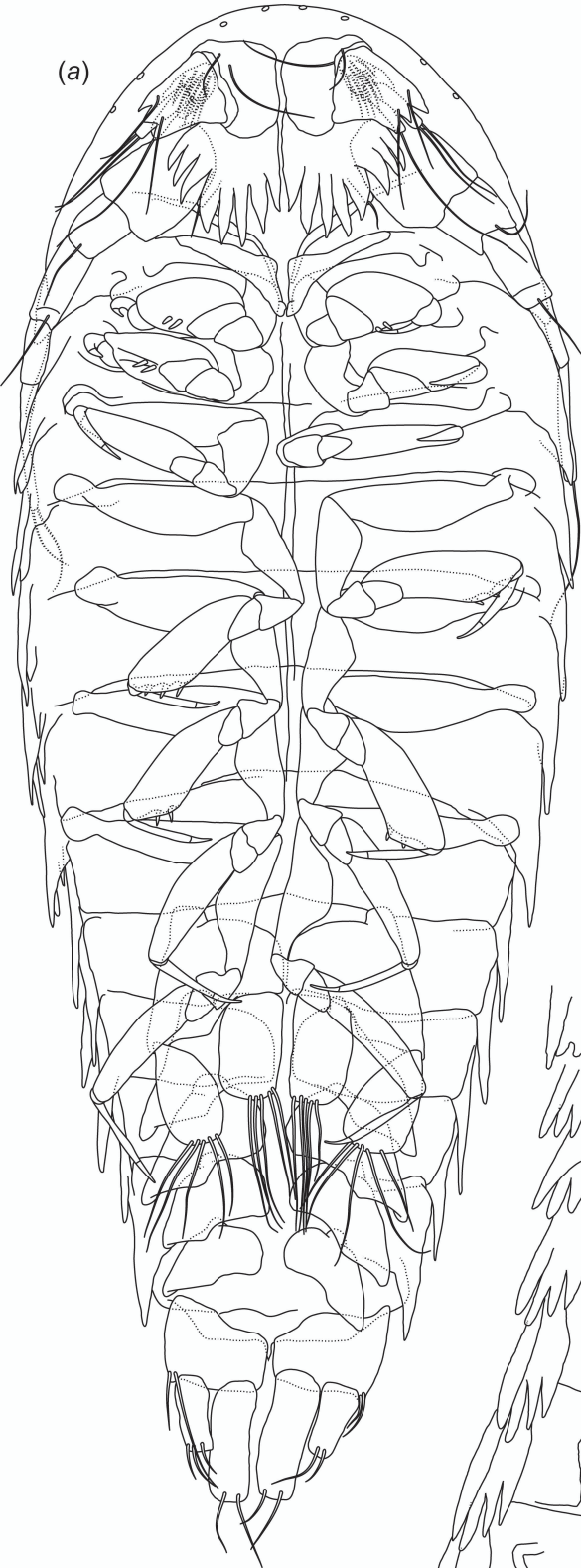
(b)



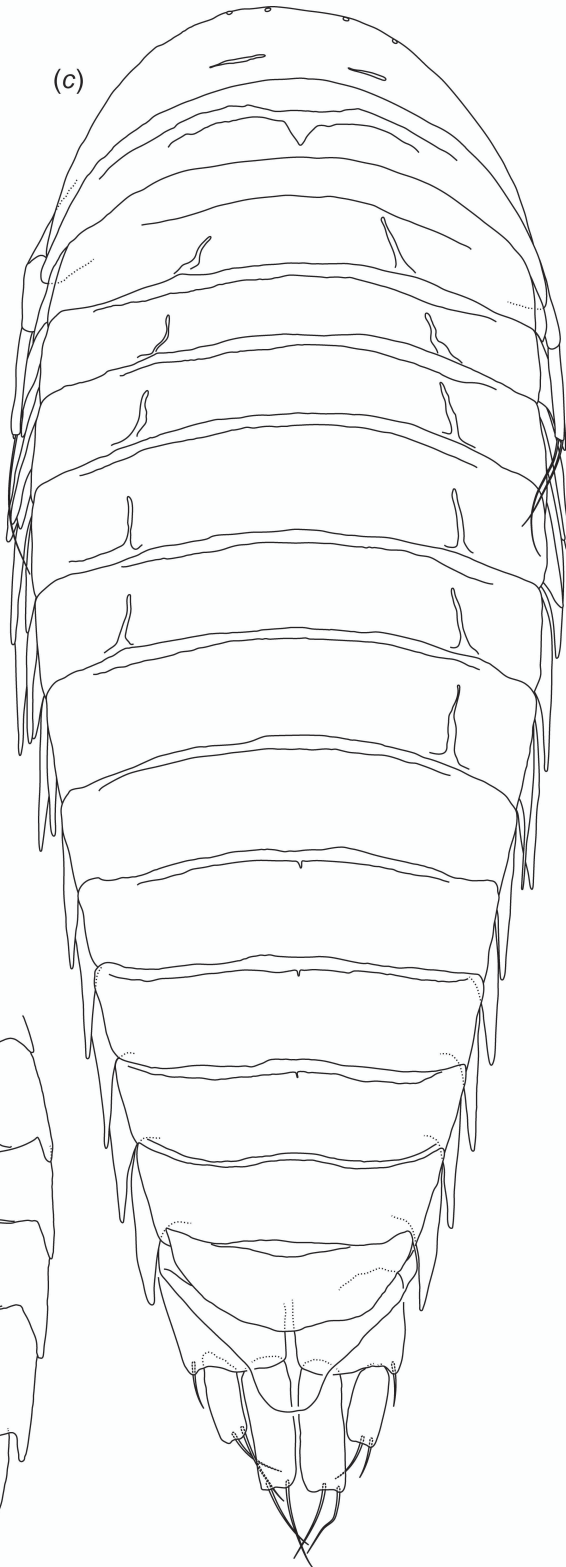
(a, b)



(a)

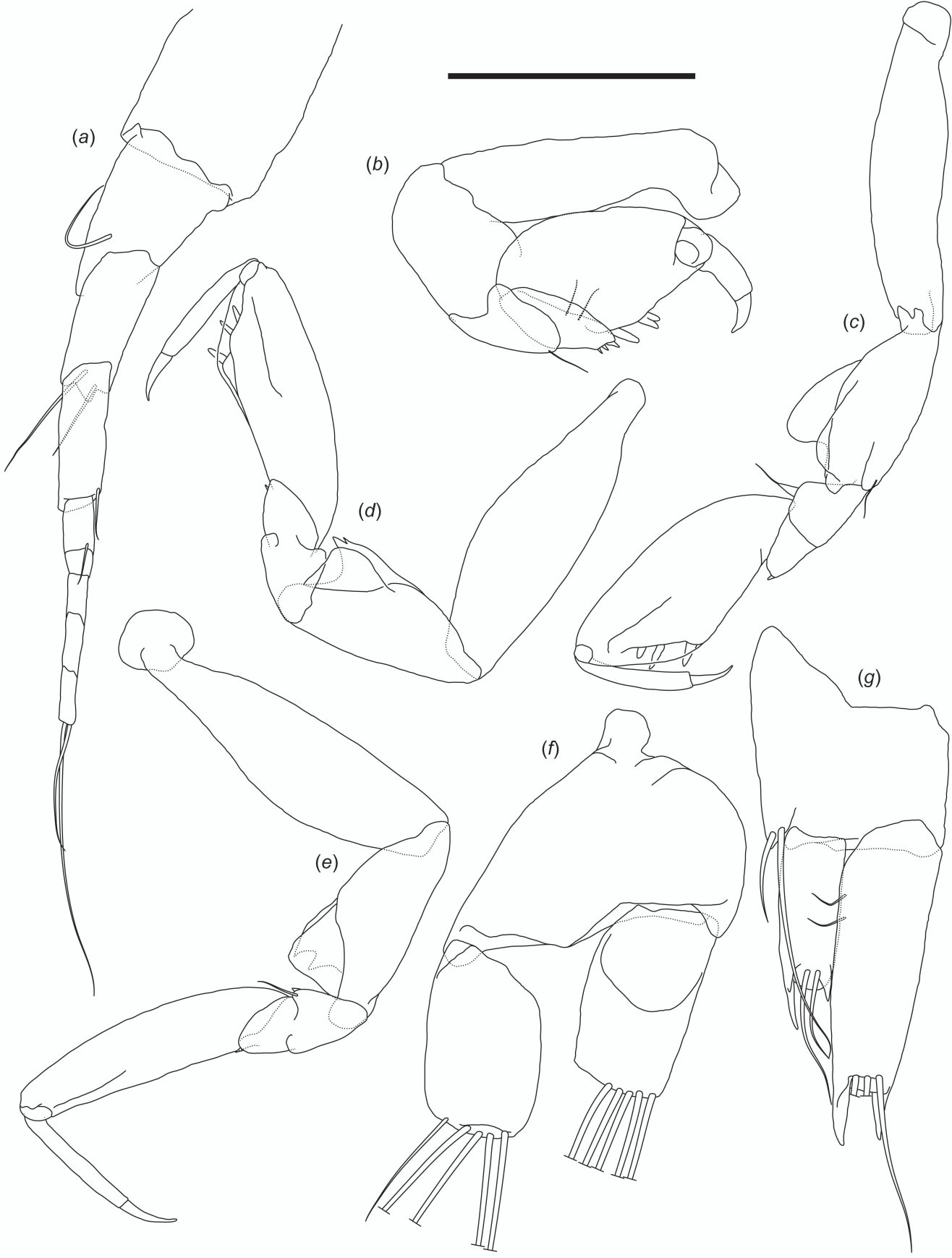


(c)

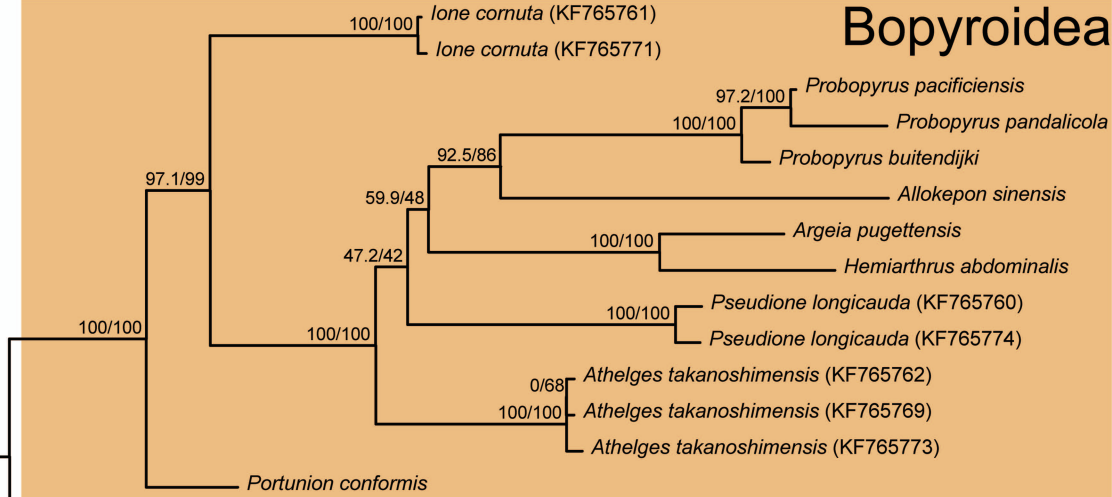


(b)





Bopyroidea



Cryptoniscoidea

***Anthuroniscus* gen. nov.**

***Anthuroniscus shimomurai* sp. nov.**

***Anthuroniscus dentatus* sp. nov.**

***Anthuroniscus latus* sp. nov.**

0.03