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The first Arctic conspicuously coloured *Pleusymtes* (Crustacea: Amphipoda: Pleustidae) associated with sea anemones in the Barents Sea

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Abstract. The article presents a potentially obligate association of a pleustid amphipod of the genus *Pleusymtes* (Crustacea: Amphipoda: Pleustidae) with the large sea anemone *Urticina eques* (Gosse, 1858) (Anthozoa: Actiniaria: Actiniidae) from shallow waters of the Barents Sea. The new species shows a conspicuously striped (disruptive or aposematic) colouration, unlike other Arctic species of the genus, which shows a potential for its permanent connection with anemones. It is possible that this is the first known possibly obligatory anemone-associated species, within the genus and the family Pleustidae. The article discusses the taxonomy, morphological differences from congeners and ecological features of the new species, as well as the known symbiotic associations of sea anemones (as hosts) in Arctic and sub-Arctic waters.

Keywords. Biodiversity, Pleustidae, symbiosis, Anthozoa, Arctic.

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Introduction

The genus *Pleusymtes* Buchholz, 1874 (Crustacea: Amphipoda: Pleustidae) currently consists of 22 valid species known from the Northern Hemisphere (Horton *et al.* 2021), including 8 species from Russian coastal waters (e.g., Gurjanova 1951). Among the genus, several species are known to live in the cold waters of the Arctic Ocean, namely *Pleusymtes glaber* (Boeck, 1861), *Pleusymtes pulchella* (G.O. Sars, 1876) and *Pleusymtes karstensi* (J.L. Barnard, 1959) from the Barents and White seas, *Pleusymtes kariana* (Stappers, 1911) from the Kara Sea, and *Pleusymtes glabroides* (Dunbar, 1954), described from Ungava Bay in Canada (e.g., Gurjanova 1951; Dunbar 1954; Martin *et al*. 2007; Anisimova *et al*. 2010;

Solyanko *et al*. 2011; Zimina *et al*. 2019). These species, as well as some others from temperate water, for example, *Pleusymtes subglaber* (Barnard & Given, 1960) from southern California, are morphologically very similar and possibly related. The ecology of almost all species of the genus is poorly known, and there are only a few random data on their associations with other marine invertebrates (Barnard & Given 1960; Gamo & Shinpo 1992; Kumagai 2001; Myers & Hall-Spencer 2004; Marin *et al*. 2013; Marin & Sinelnikov 2016), while any ecological data on Arctic species of the genus is absent.

In the course of a biodiversity study in 2019, numerous small conspicuously coloured amphipods associated with large sea anemones *Urticina eques* (Gosse, 1858) (Anthozoa: Actiniaria: Actiniidae) were discovered and collected by SCUBA diving in the shallow Arctic waters of the Barents Sea. These amphipods were only found on sea anemones, where they live on the tentacles or the stalk (body) of the hosts (see below), which indirectly indicates their constant association (see Fig. 6). A thorough morphological study has shown that they belong to an undescribed species of the genus *Pleusymtes* (Pleustidae), described in detail here. The conspicuously striped colouration, characteristic for the new species is typical for symbiotic species (e.g., Knowlton & Keller 1985; Hurt *et al*. 2003; Bauer 2004) and is known in anemone-associated species as a warning (aposematic) pattern (Merilaita & Kelley 2018). Representatives of pleustid amphipods and even of the genus *Pleusymtes* have already been recorded in associations with Arctic and sub-Arctic sea anemones (Vader 1983; Bousfield & Hendrycks 1995; Vader & Tandberg 2020), but these species were not identified as permanent associates. We propose that our record represents the first potentially obligate association of pleustid amphipods with sea anemones from Arctic waters.

Material and methods

Arctic sea anemones and their macrosymbiotic assemblages were observed underwater with the help of SCUBA equipment in Dolgaya Bay (Guba Dolgaya) (69°11′07.5″ N, 34°58′02.8″ E) in the Barents Sea in August 2019. Sea anemones and associated amphipods were photographed in situ using a Canon G16 digital camera placed in a germetic underwater box. In total six specimens of *Pleusymtes* sp. were collected with a hand net from two specimens of the sea anemone *Urticina eques*. All collected amphipods were fixed in a 90% solution of ethanol. The drawings were accomplished with a camera lucida attached to an Olympus SZX10 light microscope. Underwater photos were taken on a Sony NEX 5n camera.

The type material is deposited in the collection of the Zoological Museum of the M.V. Lomonosov Moscow State University (ZMMU), Moscow; additional material is deposited at the first author's collection (IM) in A.N. Severtsov Institute of Ecology and Evolution (LEMMI), Moscow, Russia.

The total body length (tbl. in mm) is measured along the dorsal outline beginning at the anterior margin of the head to the distal margin of the telson.

Abbreviations

AI	=	antenna 1
AII	=	antenna 2
EpI–II	=	epimeral plates I–III
GnI	=	gnathopod 1
GnII	=	gnathopod 2
Md	=	mandible
MxI	=	maxilla 1
MxII	=	maxilla 2
Mxp	=	maxilliped
PIII–PVII	=	pereopods 3–7
UI–UIII	=	uropods 1–3

Results

Phylum Arthropoda von Siebold, 1848
Class Malacostraca Latreille, 1802
Order Amphipoda Latreille, 1816
Family Pleustidae Buchholz, 1874
Genus *Pleusymtes* J.L. Barnard, 1969

Pleusymtes actiniae sp. nov.
urn:lsid:zoobank.org:act:3053898B-8088-4AFD-84D7-4CCED1F81E97
Figs 1–5

Diagnosis

Eyes with distinct light rim; AI with peduncular article 1 relatively short, not produced distoventrally; Gn I–II weakly dimorphic, GI smaller than GII, propodus (palm) strongly beveled with a well-defined palmar margin, carpus of GnII with blunt distoventral process; EpI–III without strongly produced ventroproximal corners; PpIII–VII with long and simple dactyli, PVII with smooth posterior margin of basis; UI peduncle without distal ecdysial spine; telson entire, suboval; colouration distinctly yellow-brown-white banded.

Etymology

The species is named after its host – actinians, or sea anemones (Cnidaria: Anthozoa: Hexacorallia: Actiniaria), in the English-speaking version of the common name of these animals. However, in Russian-speaking version, the word '*актиния*' (Eng: '*actinia*') (gender feminine) has a more common meaning for these animals.

Type material

Holotype

NORTHEAST ATLANTIC – **Barents Sea** • ♀ (tbl. 8.5 mm); Russian (Murman) coast, Dolgaya Bay (Guba Dolgaya); 69°11′07.5″ N, 34°58′02.8″ E; 16–18 m depth; 21 Aug 2019; T. Antokhina leg.; SCUBA, on sea anemones *Urticina eques* growing on a rock wall; ZMMU Mb-1222.

Paratypes

NORTHEAST ATLANTIC – **Barents Sea** • 1 ♀ (tbl. 7.5 mm); same collection data as for holotype; ZMMU Mb-1224 • 1 ♂ (tbl. 7.0 mm) (dissected); same collection data as for holotype; ZMMU Mb-1223.

Additional material

NORTHEAST ATLANTIC – Barents Sea • 2 ♀♀, 1 ♂; same collection data as for holotype; LEMMI.

Description

Body (Fig. 1). Slightly inflated, pereonal and pleonal sternites smooth, without any sculpture or dorsal/middorsal carina.

Head (Fig. 1). Slightly longer than pereonites I and II combined, rostrum short, about 0.2 times length of basal peduncular segment of antenna I; eyes large, occupying most of the head, subreniform, with distinct light rim; anterior head lobe prominent, bluntly rounded.

Antenna I (Fig. 2a). Medium length, nearly 0.8 times body length (Fig. 1); peduncular article 1 about 1.5 times as long as wide; about twice as long as peduncular article 2, covered with simple setae, with small blunt anterodorsal process (Fig. 2a); article 2 about as long as wide, with small blunt anterodorsal process; article 3 about 1.3 times as long as wide, equal to article 2; with small blunt anterodorsal process; accessory flagellum reduced; flagellum bearing 30–35 articles, aesthetascs absent.

Antenna II (Fig. 2b). About 0.7 times as long as antenna I; peduncle with short article 5; article 4 as long as wide, equal to article 3 with blunt anteroventral protrusion (Fig. 2b); article 3 about as long as wide; about half the length of article 2; article 2 about 2.5 times as long as wide, slightly longer than article 1, about 2.5 times as long as wide; flagellum with about 25 articles.

Mandible (Fig. 2d–e). With strong molar process; incisor process 5-dentate, left lacinia mobilis 5–7-dentate, with 5 robust plumose accessory setae (Fig. 2e); palp 3-articulated, article 1 without setae, article 2 with 6 simple D-setae, article 3 equal to article 2, slightly curved, with posterior row of 6–7 simple D-setae, and 6–7 subdistal E-setae.

Labrum. Without specific features, apical lobes well marked.

Labium (Fig. 2c). With inner lobes feebly developed; outer lobes well marked, subdistally rounded.

Maxilla I (Fig. 3d). With suboval inner plate bearing 3 plumose setae apically; outer plate elongate, apically with 9 strong pectinate setae; palp 2-articulated, apical margin of article 2 with 5–6 stout spine-like setae and with a row of 6–7 subapical simple setae.

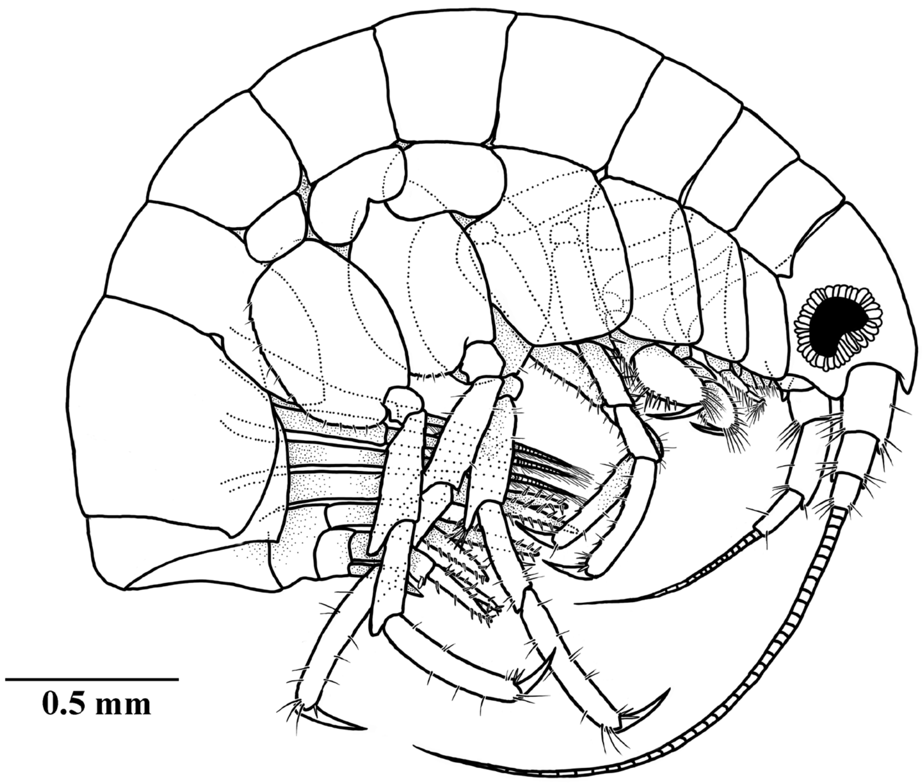

Fig. 1. General view (habitus) of *Pleusymtes actiniae* sp. nov., holotype, ♀, from Dolgay Bay, Barents Sea (ZMMU Mb-1222).

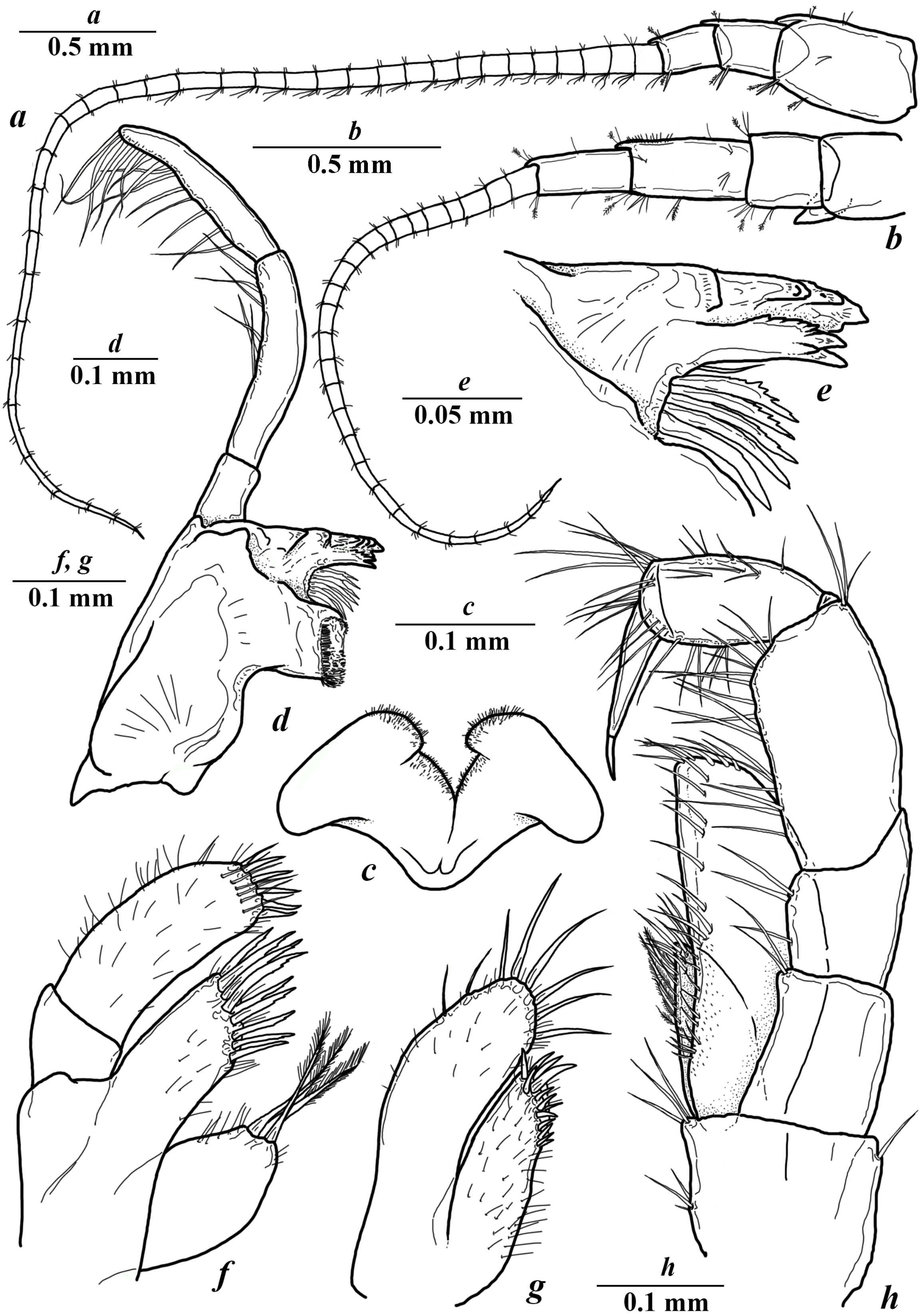

Fig. 2. *Pleusymtes actiniae* sp. nov., paratype, ♀ (ZMMU Mb-1224). **a**. Antenna I. **b**. Antenna II. **c**. Labium (lower lip). **d**. Left mandible. **e**. Left lacinia mobilis. **f**. Maxilla I. **g**. Maxilla II. **h**. Maxilliped.

Maxilla II (Fig. 3e). With almost subequal inner and outer plates; inner plate narrowing distally, with group of dense short spine-like setae on apex, fringed with plumose and simple setae; outer plate weakly narrowing distally, with 8 apical long and simple setae.

Maxilliped (Fig. 3f). With small inner plates, fringed with plumose setae distally; outer plate elongated, rounded apically, inner margin covered with numerous submarginal stiff simple setae of different length; palp 4-articulated; article 4 (dactylus) slender, curved.

Gnathopod I (Fig. 3a). Coxa deep, anterior margin distally expanded, with posteroventral blunt tooth and with 7–10 small distal setae; basis straight anteromarginally, distal half expanded posteromarginally, with a pair of posterodistal setae; ischium about as long as wide, with several posterodistal setae; merus about as long as ischium, about 1.3 times as long as wide, with a simple long seta in medial part of posterior margin, posterodistal margin with a dense row of numerous long simple setae; carpus about 1.5 times as long as maximal width, equal to propodus, posterior lobe shallow, with several groups of long, simple and plumose setae; propodus (Fig. 3b) suboval, about 2.2 times as long as wide, palmar margin smoothly oblique, 1.4 times as long as posterior margin, with several clusters of posterodistal robust setae associated with a few setae; dactylus shorter than palmar margin of propodus, curved, pointed distally, with 3 outer simple setae.

Gnathopod II (Fig. 3c). Coxa deep, subquadrate, larger than coxa of gnathopod I, with posteroventral blunt tooth and with 7–10 small distal setae; basis straight anteromarginally, distal half expanded posteromarginally, with several long simple posterodistal setae; ischium triangular, about as long as wide, with several posterodistal setae; merus slightly longer than ischium, about 1.5 times as long as wide, with subdistal produced lobe, armed with a dense row of numerous long simple setae; carpus about 1.4 times of maximal width, smaller than propodus, with well-marked posterodistal lobe, armed with several groups of long simple and plumose setae, with long simple and plumose setae in medial part; propodus (Fig. 3d) suboval, about 2.2 times as long as wide, palmar margin smoothly oblique, 1.5 times as long as posterior margin, with several clusters of posterodistal robust setae associated with a few setae; dactylus shorter than palmar margin of propodus, curved, pointed distally, with 3 outer simple setae.

Pereopod III (Fig. 4a). Coxa relatively shallow, rectangular, about 2.5 times as long as wide, anterior and posterior margins smooth, unarmed; basis linear, about 5 times as long as wide; ischium about as long as wide, unarmed; merus about 3 times as long as wide, slightly longer than carpus, with distally produced anterodistal angle; carpus about 2.5 times as long as wide, with several groups of spine-like setae along posterior margin; propodus linear, narrower and 1.8 times as long as carpus, about 5.5 times as long as wide, with several small spines along posterior margin, with a pair of small spines posterodistally, and a tuft of long simple setae anterodistally; dactylus (Fig. 4b) long, curved, about 6 times as long as wide, and 0.6–0.7 times as long as propodus, with sharp tip.

Pereopod IV (Fig. 4c). Generally similar to pereopod III; coxa about as long as wide, subquadrate, rounded distally and with deep excavation posteromarginally; basis linear, about 4 times as long as wide; ischium about as long as wide, unarmed; merus about 2.5 times as long as wide, slightly longer than carpus, with feebly produced anterodistal angle; carpus about 3 times as long as wide, with a group of spine-like setae posterodistally; propodus linear, narrower and 1.7 times as long as carpus, about 6 times as long as wide, with several small spines along posterior margin, with a pair of small spines posterodistally, and a tuft of long simple setae anterodistally; dactylus long, curved, about 6 times as long as wide, and 0.6–0.7 times as long as propodus, with sharp tip.

Pereopod V (Fig. 4d). Coxa posterolobate, with rounded anterior margin, posteriorly subquadrate, posterior lobe pulled back and down; basis wide, with straight parallel margins, without posterior

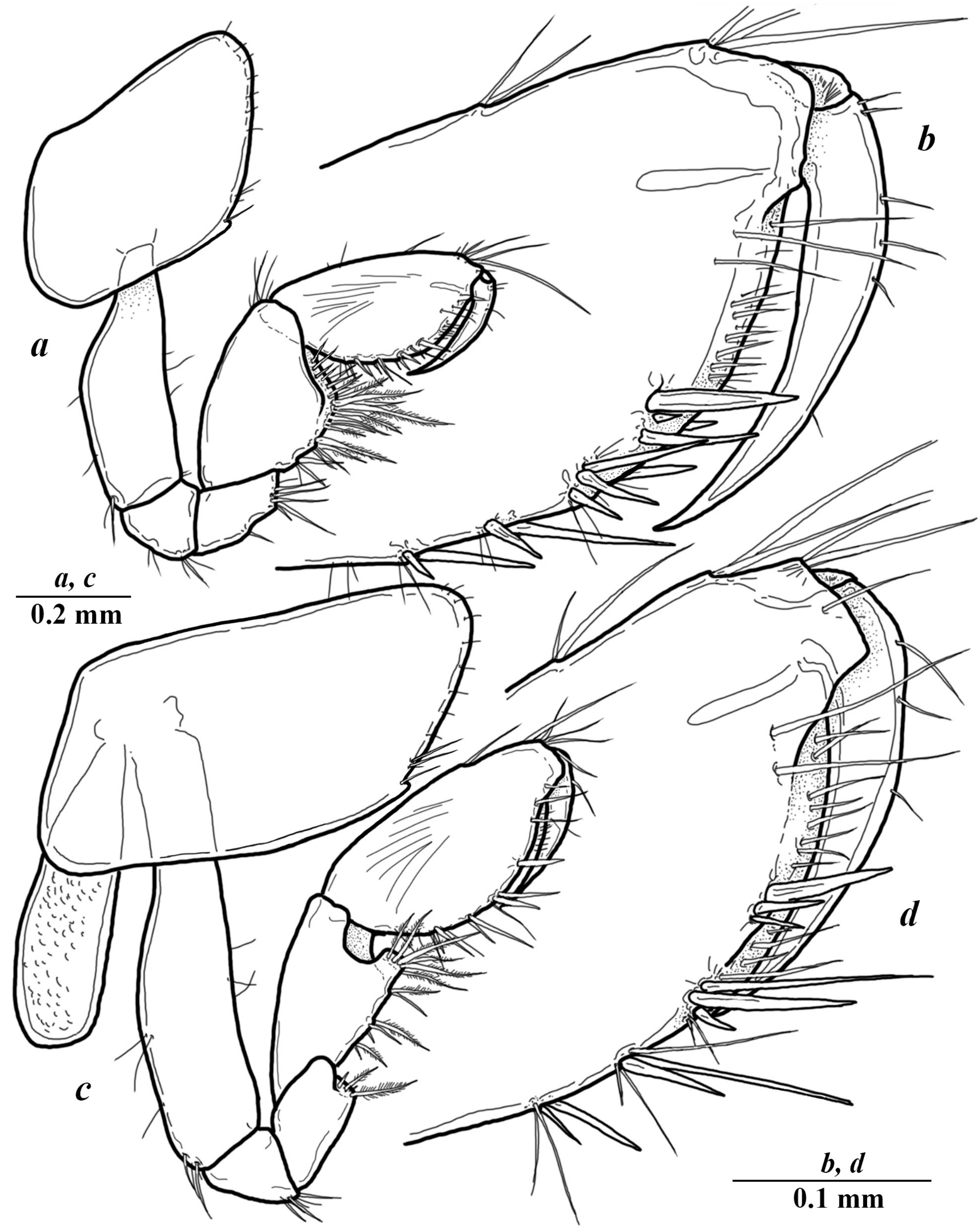

Fig. 3. *Pleusymtes actiniae* sp. nov., paratype, ♂ (ZMMU Mb-1223). **a**. Gnathopod I. **b**. Distoventral palmar margin of propodus (chela) of GnI. **c**. Gnathopod II. **d**. Distoventral palmar margin of propodus (chela) of GnII.

wing, anterior margin armed with 4 medial small and stout spines-like or robust setae and 1 small seta anterodistally, posterior margin smooth, unarmed; ischium small, about as long as wide, unarmed; merus about 2 times as long as wide, slightly longer than carpus, with posterodistal angle produced forward and armed with several small spine-like setae, anterior margin armed with several group of small spines accompanied with simple setae; carpus about 2.2 times as long as wide, with a group of spine-like setae along anterior margin and anterodistally; propodus linear, more narrow and 1.3 times as long as carpus, about 6 times as long as wide, with several small spine accompanied with small simple setae along posterior margin, with a pair of small spines posterodistally, and a tuft of long simple setae anterodistally; dactylus (Fig. 4e) long, curved, about 6 times as long as wide, and 0.6–0.7 times as long as propodus, with sharp tip.

Pereopod VI (Fig. 4f). Coxa posterolobate, with rounded anterior margin, posterior lobe pulled back and down, proximally with produced angulated posterior margin; basis with narrow posterior lobe, width 0.4–0.5 times as length, posterior margin convex, with numerous small notches, anterior margin armed with 5–8 small stout spine-like setae; ischium small, about as long as wide, unarmed; merus about 2.2 times as long as wide, slightly longer than carpus, with posterodistal angle produced forward and armed with several small spine-like setae, anterior margin armed with several groups of small spines accompanied with simple setae; carpus about 3.2 times as long as wide, with a group of spine-like setae along anterior and posterior margins; propodus linear, more narrow and 1.3 times as long as carpus, about 6 times as long as wide, with several small spines accompanied with small simple setae along posterior margin, with a pair of small spines posterodistally, and a tuft of long simple setae anterodistally; dactylus long, curved, about 6 times as long as wide, and 0.6–0.7 times as long as propodus, with sharp tip.

Pereopod VII (Fig. 4g). Coxa suboval; basis with narrow posterior lobe, width 0.4–0.5 times of length, posterior margin convex, with numerous small notches, anterior margin armed with 5–8 small stout spine-like setae; ischium small, about as long as wide, unarmed; merus about 2.2 times as long as wide, equal to carpus, with posterodistal angle produced forward and armed with several small spine-like setae, anterior margin armed with several group of small spines accompanied with simple setae; carpus about 3.2 times as long as wide, with a group of spine-like setae along anterior and posterior margins; propodus linear, narrower and 1.2 times as long as carpus, about 6 times as long as wide, with several small spine accompanied with small simple setae along posterior margin, with a pair of small spines posterodistally, and a tuft of long simple setae anterodistally; dactylus (Fig. 4h) long, curved, about 6 times as long as wide, and 0.6–0.7 times as long as propodus, with sharp tip.

Coxal gills II–VI. Without specific features.

Epimeral plates (Fig. 5a–c). With anterior, posterior and ventral margins unarmed; epimeral plate I (Fig. 5a) nearly triangular, with bluntly pointed ventral margin, unarmed; epimeral plate II (Fig. 5b) with slightly produced posteroventral corner; epimeral plate III (Fig. 5c) with slightly produced and pointed posteroventral corner.

Pleopods (Fig. 5f). Normal; peduncle with 2 small coupling hooks and 1 long simple seta in retinacula (Fig. 5g); inner ramus slightly shorter than outer ramus.

Uropod I (Fig. 5h–i). Peduncle about 5.5 times as long as wide, with dorsomedial row of 7–9 thin short spines, dorsolateral row of 4–5 thin short spines, and 1 subdistal short spine and 1 dorsolateral thin short spine, without distal ecdysial spine; outer ramus subequal to inner one in length; both outer and inner rami with 4 dorsolateral, 1 subapical spine; distal part of both outer and inner rami armed with specific structures including pointed distal protrusions with a movable thickened spine in the middle, accompanying subapical thickened spine-like setae (Fig. 5j).

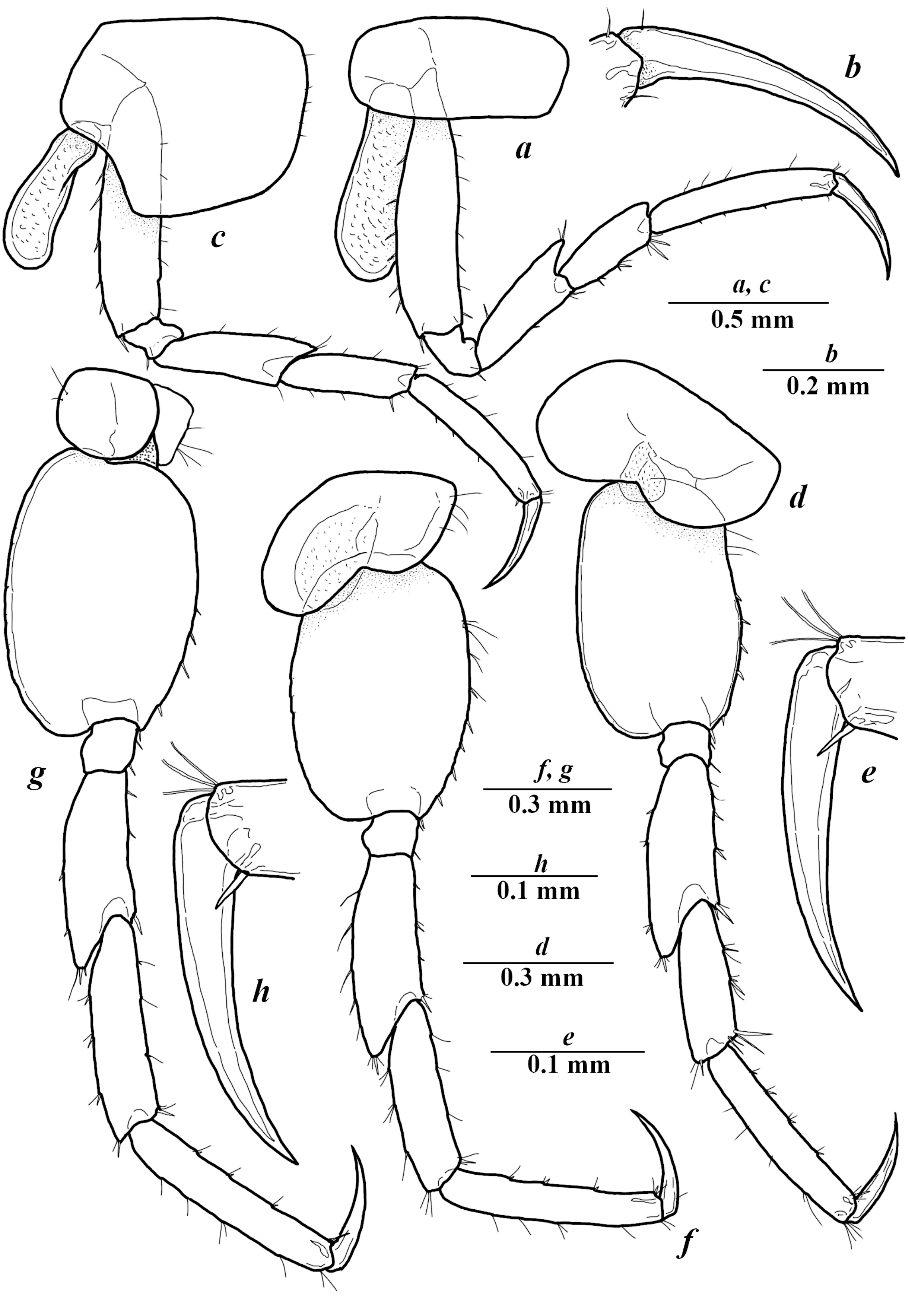

Fig. 4. *Pleusymtes actiniae* sp. nov., paratype, ♀ (ZMMU Mb-1224). **a**. Pereopod III. **b**. Dactylus of PIII. **c**. Pereopod IV. **d**. Pereopod V. **e**. Dactylus of PV. **f**. Pereopod VI. **g**. Pereopod VII. **h**. Dactylus of PVII.

Uropod II (Fig. 5k). Peduncle about 3 times as long as wide, subequal to outer ramus in length and slightly shorter than inner ramus, with 1 strong basal, 3 medial smaller and 1 short subdistal outer spine; outer ramus about 0.8 times length of endopodite, with 3 outer spines; inner ramus with 3 outer spines; distal part of both outer and inner rami armed with specific structures including pointed distal protrusions with a movable thickened spine in the middle, accompanying subapical thickened spine-like setae.

Uropod III (Fig. 5l). Peduncle about 1.5 times as long as wide, about twice shorter than inner ramus in length, with 1 leaf-shaped subdistal outer spine (Fig. 5m); outer ramus about 0.8 times length of inner ramus, with 3 outer spines, including leaf-like most distal spine, and pointed apex; inner ramus with 3 outer simple spines and pointed apex.

Telson (Fig. 5d–e). Suboval, elongate, tapering distally and apically rounded, about 1.5 times as long as wide, with well-developed ventral keel, with a pair of plumose medial marginal setae and a small simple subapical seta on each side.

Taxonomic remarks

Among congeners, the new species is morphologically similar to *P. glaber*, *P. pulchella*, *P. kariana* and *P. karstensi*, which are probably closely related. These species are rather distinct from other species of the genus by the weakly dimorphic gnathopods, not strongly produced ventroproximal corners of epimeral plates, long and simple dactyli of pereopods III–VII, entire telson and the geographic distribution in cold western Arctic seas. Although these species, especially the last two, are described rather poorly, nevertheless, the new species has enough features to differ from them by the features of antennae, gnathopods, epimeral plates, uropod III and conspicuous colouration.

From *P. glaber*, a relatively common Arctic-Boreal shallow benthic species (see G.O. Sars 1893: pl. 126; Gurjanova 1951: fig. 450; Bousfield 1973; Berge 2003), the new species can be easily separated by 1) not distinctly produced distoventral margin of peduncular article 1 of antenna I (vs distinctly produced in *P. glaber*); 2) not distinctly produced distoventral margin of epimeral plate III (vs distinctly produced pointed posteroventral corner in *P. glaber*); 3) smooth posterior margin of basis of pereopod VII (vs serrated in *P. glaber*); and 4) distinctly banded yellow-brown-white colouration (vs whitish with reddish brown patches in *P. glaber*).

From *P. pulchella*, known from Greenland and Iceland to the North and East Siberian seas, usually at a depth of 30–40 m, but can be at depths of more than 700–1300 m in the Norwegian Sea (see G.O. Sars 1893: pl. 126; Gurjanova 1951: fig. 451), the new species can be clearly separated by 1) shorter peduncular articles of both antenna I and II; 2) carpus of gnathopod II directed forward, about 1.5 times as long as wide, with blunt distoventral process (vs triangular carpus without distoventral process in *P. pulchella*); 3) propodus (palm) of gnathopod I and II strongly beveled with a well-defined palmar margin (vs short sinuous palmar margin in *P. pulchella*); and 4) distinctly banded yellow-brown-white colouration (whereas the colouration of *P. pulchella* is described as “color albidus” (after G.O. Sars 1876) and whitish with small pinky spots (after G.O. Sars 1893).

From *P. kariana*, known from the Kara Sea at the depth of 165 m (see Stappers 1911: pl. II, 10–20; Gurjanova 1951: fig. 453), the new species can be clearly separated by 1) eyes with distinct light rim (vs without light rim in *P. kariana*); 2) carpus of gnathopod II with blunt distoventral process (vs without distoventral process in *P. kariana*); and 3) anterior margin of coxal plate I distally expanded (vs coxal plate I with parallel margins in *P. kariana*).

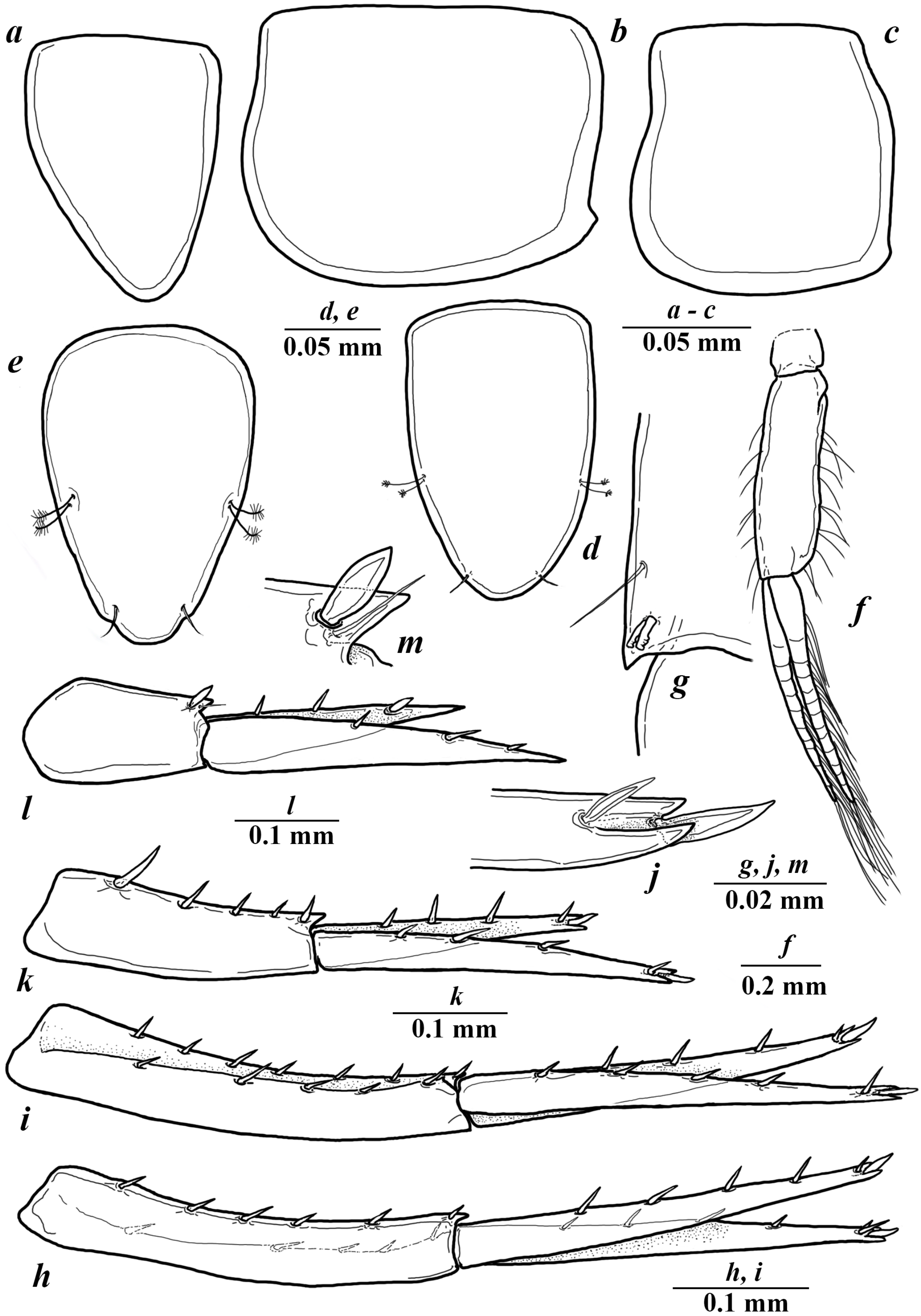

Fig. 5. *Pleusymtes actiniae* sp. nov. **a–d, f–m**. Paratype, ♀ (ZMMU Mb-1224). **e**. Paratype, ♂ (ZMMU Mb-1223). **a**. Epimeral plate I. **b**. Epimeral plate II. **c**. Epimeral plate III. **d–e**. Telson. **f**. Pleopod II. **g**. Retinacula of pleopod I. **h–i**. Uropod I. **j**. Same, distal part of outer ramus. **k**. Uropod II. **l**. Uropod III. **m**. Distodorsal angular spine of peduncle of uropod III.

From *P. karstensi*, known from the coastal waters of Spitzbergen (Svalbard) (see Barnard, 1959; Macnaughton *et al*. 2007: figs 7–10), the new species can be clearly separated by 1) larger eyes with distinct light rim (vs without light rim in *P. karstensi*); 2) more elongated suboval telson; and 3) distinctly banded yellow-brown-white colouration (vs translucent reddish in *P. karstensi*).

Morphologically similar species from other areas, such as *Pleusymtes glabroides* (Dunbar, 1954), another subarctic species described from Ungava Bay in Canada (Dunbar 1954), and *Pleusymtes subglaber* (Barnard & Given, 1960), known from southern California (Barnard & Given 1960; Blake *et al*. 1995), can be separated from the new species by the sinuous posterior margins and well-developed posteroventral teeth of epimeral plates II–III and the presence of a distinctly produced distoventral margin of peduncular article 1 of antenna I in *P. glabroides* (that is rather similar to *P. glaber*) (see Dunbar 1954; Barnard & Given 1960).

Measurements

The largest collected ♀ has tbl. 8.5 mm; the largest collected ♂ has tbl. 8.5 mm.

Living colouration

Conspicuously striped species; antennas I–II, dorsal part of body and telson are yellow or light green; lateral median margin of coxal plates and entire epimeral plates are brown; ventral margin of coxal plates and appendages are white; eyes are a gold colour (Fig. 6).

Ecology

Amphipods were collected from both the stalk and from the tentacles of the sea anemone *Urticina eques* (Gosse, 1858) (Anthozoa: Actiniaria: Actiniidae), which were found growing on a steep underwater rock wall at a depth of about 16–18 meters, where, apparently, there is a weak but constant flow of water. Clusters of amphipods, up to two dozen individuals, were observed on some of the studied sea anemones. It is worth noting that amphipods were observed only on sea anemones living on this rock wall, whereas they were not found on other sea anemone specimens within this bay, although quite a diversity of sea anemones (including *Metridium* spp.) were examined during the survey. Previously, this species was not observed from benthic samples taken in this bay and other places along Murman coast of the Barents Sea.

Distribution

The new species is currently known only from the type locality, Dolgaya Bay in the Barents Sea (69°11′07.5″ N, 34°58′02.8″ E), but we are confident that this species is widespread along the coast of the Barents Sea and the surrounding area, at least in the cold-water Arctic.

Discussion

Marine symbiotic associations in the Arctic Ocean have been studied rather poorly, as sampling in high latitudes is very complex. In particular, the difficulty is the rarity of a high-quality collection of animals. For example, with the help of SCUBA diving equipment the connections between different animals can be detected. Unfortunately, trawl sampling does not reveal such associations. However, the species that are symbiotic or potentially could be symbionts of other larger invertebrates are recorded in the Arctic (e.g., Averincev 1990; Ho & Ivanenko 2003; Kutz *et al*. 2005; Yamaguchi 2006; Tarakhovskaya & Garbary 2009; Tandberg *et al*. 2010; Marin & Sinelnikov 2017; Vader & Tandberg 2020; Marin & Antokhina 2020). Quite a few obligately (permanent) anemone-associated species are known in Arctic and sub-Arctic waters (see Table 1), while all known representatives of the amphipod family Pleustidae are identified only at the generic level. Bousfield & Hendrycks (1995) showed the presence of *Chromopleustes lineatus* Bousfield & Hendrycks, 1995 on the sea

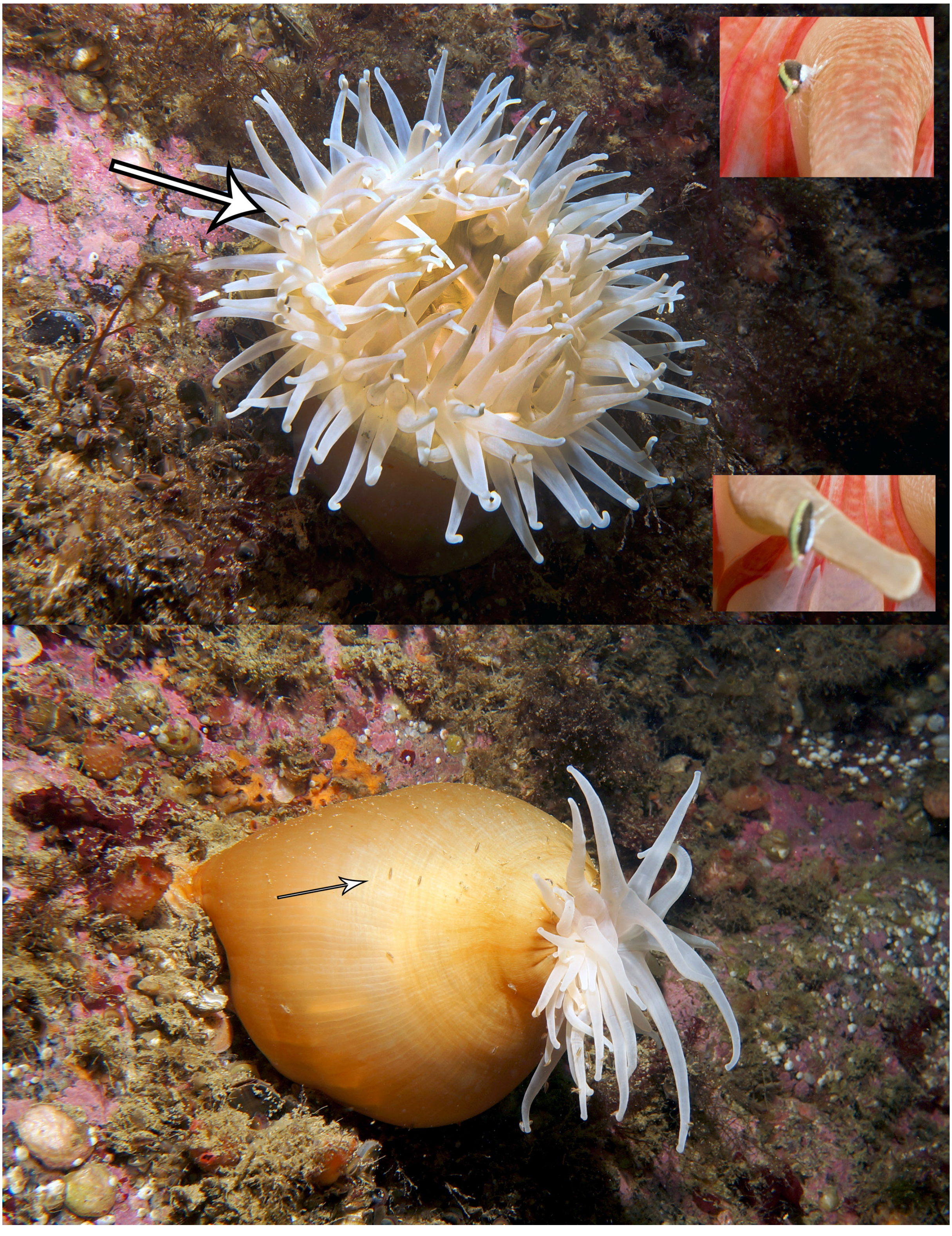

Fig. 6. Photo in situ of the sea anemone *Urticina eques* (Gosse, 1858) with associated amphipods *Pleusymtes actiniae* sp. nov. from Dolgaya Bay, Barents Sea.

Table 1 (continued on next two pages). The diversity of symbiotic species associated with sea anemones (actinians) from Arctic/sub-Arctic and adjacent temperate waters. Abbreviations: F = facultative (temporary) relationships; O = obligatory (permanent) relationships.

Symbiotic species	Host species (sea anemone)	Location	Type of relationship	Reference
		Polychaeta		
Alentiana aurantiaca (Verrill, 1885)	*Bolocera tuediae* (Johnston, 1832)	New England, USA	F	Pettibone 1963
Arctonoe vittata (Grube, 1855)	*Metridium senile* (Linnaeus, 1761)	Sea of Japan, Russia	O	Britayev 1991
		Nemertea		
Cryptonemertes actinophila (Bürger, 1904)	*Stomphia coccinea* (Müller, 1776) and *S. didemon* Siebert, 1973	Canada: Friday Harbor, San Juan Island, Puget Sound; Satellite Channel, off Vancouver Island	O	Gibson 1986
Galathenemertes giribeti Chernyshev & Polyakova, 2019	*Galatheanthemum* sp.	Kuril-Kamchatka Trench	O	Chernyshev & Polyakova 2019
		Copepoda		
Antheacheres duebenii M. Sars, 1857	*Bolocera tuediae* (Johnston, 1832)	Bergen and Drobak, Korsfjorden, Western Norway; Gull-marfjiorden, west coast of Sweden	O	M. Sars 1857, 1870; Bresciani & Liitzen 1962; Theel 1907; Vader 1970b, 1975
Doridicola antheae Ridley, 1879 (perhaps = *Paranthessius anemoniae* Claus, 1889 (see Humes & Stock 1973: 81))	*Anemonia sulcata* (Pennant, 1777)	Ilfracombe, North Devon, England		Ridley 1879
Doridicola confinis (Humes, 1982)	*Urticina piscivora* (Sebens & Laakso, 1978), *Anthopleura elegantissima* (Brandt, 1835) and *A. xanthogrammica* (Brandt, 1835)	California	O	Humes 1982
Doridicola pertinax (Humes, 1982)	*Urticina coriacea* (Cuvier, 1798) and *U. crassicornis* (Müller, 1776)	California	O	Humes 1982
Doridicola sunnivae (Humes, 1982)	*Epiactis prolifera* Verrill, 1869	California	O	Humes 1982
Doridicola turmalis (Humes, 1982)	*Anthopleura artemisia* (Pickering in Dana, 1846)	California	O	Humes 1982
Gastroecus arcticus Hansen, 1886	*Actinia equina* (Linnaeus, 1758) and *Anthea* sp. [Vader (1970b) suggested that the host may actually have been *Glandulactis spetsbergensis* (Carlgren, 1893)]	Kara Sea and Northwestern Pacific Ocean	O	Avdeev & Avdeev 1975
Gastroecus caulleryi (Okada, 1927)	*Nemanthus nitidus* (Wassilieff, 1908)	Misaki, Japan	O	Okada 1927
Gastroecus chukotensis (Avdeev & Avdeev, 1975)	*Aulactinia stella* (Verrill, 1864)	Sea of Okhotsk	O	Avdeev & Avdeev 1975
Gastroecus okadai (Avdeev & Avdeev, 1975)	*Urticina felina* (Linnaeus, 1761)	Pacific coast of Japan	O	Avdeev & Avdeev 1975

Table 1 (continued). The diversity of symbiotic species associated with sea anemones (actinians) from Arctic/sub-Arctic and adjacent temperate waters.

Symbiotic species	Host species (sea anemone)	Location	Type of relationship	Reference
Mesoglicola delagei Quidor, 1906	*Corynactis viridis* Allman, 1846	Roscoff, northern France	O	Taton 1934
		Amphipoda		
Abludomelita obtusata (Montagu, 1813)	*Anemonia sulcata* (Pennant, 1777)	Irish Sea	F	Hartnoll 1970
	Urticina felina (Linnaeus, 1761)	Scilly Islands, England	F	Sanderson 1973
Acidostoma obesum (Spence Bate, 1862)	*Actinostola callosa* (Verrill, 1882)	western Norway	F	Vader 1967
Aristias neglectus Hansen, 1888	*Bolocera tuediae* (Johnston, 1832)	Raunefjorden, western Norway	F	Vader 1970a
Hyperia medusarum (Müller, 1776)	*Bolocera tuediae* (Johnston, 1832)	Korsfjorden, Raunefjorden, western Norway	F	Vader 1970a
Leucothoe spinicarpa (Abildgaard, 1789)	*Bolocera tuediae* (Johnston, 1832)	northern North Sea	O	Vader 1983
Lysianopsis sp.	*Anthopleura elegantissima* (Brandt, 1835)	Alaska and California		Vader 1983
Onisimus normani G.O. Sars, 1891	*Bolocera tuediae* (Johnston, 1832), *Actinostola callosa* (Verrill, 1882), *Hormathia nodosa* (Fabricius, 1780) and *Liponema multicorne* (Verrill, 1880)	Korsfjorden, western Norway and northern Norway	O	Vader 1970a, 1983
Onisimus turgidus (G.O. Sars, 1879)	unidentified sea anemone	Barents Sea	O	G.O. Sars 1885; Vader 1967, 1983
Orchomene (s.l.) sp.	*Metridium senile* (Linnaeus, 1761)	Alaska and California	O	Vader 1983
Chromopleustes lineatus Bousfield & Hendrycks, 1995	*Tealia* Gosse, 1858	California	F	Vader & Tandberg 2020
Parapleustes sp.	*Anthopleura xanthogrammica* (Brandt, 1835), *Urticina coriacea* (Cuvier, 1798)	California	F	Vader 1983
Pleusymtes sp.	*Anthopleura xanthogrammica* (Brandt, 1835) and *Urticina coriacea* (Cuvier, 1798)	California	F	Vader 1983
Stenothoe brevicornis G.O. Sars, 1883	Unidentified sea anemone (Alaska) and *Actinostola callosa* (Verrill, 1882) (Norway)	Alaska and northern Norway	F–O	McGinitie 1955 Vader 1983
Stenula pugilla Krapp-Schickel & Vader, 2015	*Haliactis arctica* Carlgren, 1921	Chukchi Sea	O	Krapp-Schickel & Vader 2015
Stenula solsbergi (Schneider, 1884)	*Metridium senile* (Linnaeus, 1761)	Great Britain, Scotland, Newfoundland, Canada; Scotland	O	Elmhirst 1925; Lincoln 1979; Fenwick & Steele 1983; Vader 1983

Table 1 (continued). The diversity of symbiotic species associated with sea anemones (actinians) from Arctic/sub-Arctic and adjacent temperate waters.

Symbiotic species	Host species (sea anemone)	Location	Type of relationship	Reference
		Decapoda		
Atlantopandalus propinqvus (G.O. Sars, 1870)	*Bolocera tuediae* (Johnston, 1832)	Kosterfjord, west coast of Sweden	F	Jonsson *et al*. 2001
Pandalus borealis Krøyer, 1838	*Bolocera tuediae* (Johnston, 1832)	Kosterfjord, west coast of Sweden	F	Howard 1982; Jonsson *et al*. 2001
Pandalus montagui Leach, 1814	*Bolocera tuediae* (Johnston, 1832)	Kosterfjord, west coast of Sweden	F	Jonsson *et al*. 2001
Spirontocaris liljeborgii (Danielssen, 1859)	*Bolocera tuediae* (Johnston, 1832)	Kosterfjord, west coast of Sweden	F	Jonsson *et al*. 2001
Lebbeus polaris (Sabine, 1824)	*Bolocera tuediae* (Johnston, 1832)	Kosterfjord, west coast of Sweden	F	Jonsson *et al*. 2001
Lithodes maja (Linnaeus, 1758)	*Bolocera tuediae* (Johnston, 1832)	Kosterfjord, west coast of Sweden	F	Jonsson *et al*. 2001
Eualus suckleyi (Stimpson, 1864)	*Cribrinopsis fernaldi* Siebert & Spaulding, 1976	Kodiak, Alaska	F	Stevens & Anderson 1999
Spirontocaris sp.	*Cribrinopsis fernaldi* Siebert & Spaulding, 1976	Kodiak, Alaska	F	Stevens & Anderson 1999
Lebbeus grandimanus (Bražnikov, 1907)	*Cribrinopsis fernaldi* Siebert & Spaulding, 1976, *Urticina columbiana* Verrill, 1922 and *Utricina* sp.	Pacific coast of Canada; Kodiak, Alaska; Sea of Japan; Sea of Okhotsk	O	Butler 1980; Stevens & Anderson 1999; Marin 2013
Lebbeus groenlandicus (J.C. Fabricius, 1775)	*Cribrinopsis fernaldi* Siebert & Spaulding, 1976	Kodiak, Alaska	F	Stevens & Anderson 1999
Pandalus tridens Rathbun, 1902	*Cribrinopsis fernaldi* Siebert & Spaulding, 1976	Kodiak, Alaska	F	Stevens & Anderson 1999
		Fishes		
Oxylebius pictus Gill, 1862	*Urticina lofotensis* (Danielssen, 1890) and *U. piscivora* (Sebens & Laakso, 1978)	Vancouver Island, Canada	F	Elliott 1984, 1992

anemone *Tealia* sp., but these bright amphipods were also observed on different marine invertebrates (mainly echinoderms), so likely not specific to sea anemones. It is believed that the bright colouration of *C. lineatus* is aposematic, and their tissue may contain distasteful chemical compounds (e.g., terpenes) which deter predators such as fish from feeding on them (after Bousfield & Hendrycks 1994, 1995). Shimek (2004) suggested that *Chromopleustes* spp. may sequester poisonous saponins from sea cucumbers.

The colouration of different anemone-associated species is unusually conspicuous, and most studies associate this as a warning (aposematic) colour, since they can also be poisonous by feeding on the host tissues with cnidocysts (e.g., Merilaita & Ruxton 2007; Merilaita & Kelley 2018). Presently, we do not yet have such data for *Pleusymtes actiniae* sp. nov., and, in fact, such studies are extremely rare for anemone-associated crustaceans. However, even if the described conspicuous colouration is not a warning/aposematic signal, and the species does not feed on host tissues, it can be perceived as disruptive. This disruptive colouration can conceal the silhouette of an amphipod against the background of anemone tentacles, which is also very characteristic of anemone-associated species (e.g., Azofeifa-Solano *et al*. 2014; Krapp-Schickel *et al*. 2015). Here we emphasize once again that whatever the result of further research, the colouration of this species is unusually conspicuous (bright) compared to other known species of the genus *Pleusymtes* from the Arctic and other regions (see above). Moreover, other known symbiotic species of the family Pleustidae are also very brightly coloured compared to their free-living relatives (e.g., Marin & Sinelnikov 2016; Kodama *et al*. 2020). Based on the striking colouration of *Pleusymtes actiniae* sp. nov. and in-situ underwater observations which revealed that the amphipods were restricted to the host *U. eques*, we believe that the species is most likely an obligate associate of the anemone. Further research involving more intensive and widespread collecting is required to confirm the definitive nature of this relationship.

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