Zoosyst. Evol. 91 (2) 2015, 215–246 | DOI 10.3897/zse.91.5715

PENSOFT

museum für naturkunde

Stenothoids living with or on other animals (Crustacea, Amphipoda)

Traudl Krapp-Schickel[1], Wim Vader[2]

1 *Zoologisches Forschungsmuseum Alexander Koenig, Adenauerallee 160, D-53113 Bonn*

2 *Tromsø Museum, N-9037 Tromsø, Norway*

http://zoobank.org/89B46F52-BA36-41A9-9D7F-B635CAF052C1

Corresponding author: *Traudl Krapp-Schickel* (traudl.krapp@uni-bonn.de)

Received 22 July 2015
Accepted 26 August 2015
Published 2 October 2015

Academic editor:
Michael Ohl

Abstract

This paper describes new or little known species of Stenothoidae, collected from sea anemones, bivalves or hermit crabs. A key to world *Stenula* species is provided.

Key Words

Taxonomy
Amphipoda
Stenothoidae
new species
revalidated species
associations with other animals

Introduction

Associations between amphipods and other animals are probably not all that rare, but few have been recorded hitherto, mainly because collection methods earlier were too crude. With the advance of Scuba-diving, new associations are being discovered at a rapid pace. The present paper adds a few more examples from the family Stenothoidae.

Material and methods

All specimens in alcohol were studied under a Reichert and Wild M5 dissecting microscope, then drawn from preparations (dissected and stored in glycerine or Faure's medium) under a Wild M20 microscope. The pencil drawings were partly inked by hand, and partly with the software Adobe Illustrator CS 3, using a Wacom A4 drawing board. The material is lodged at the Museums of Verona (MVR, Italy), Copenhagen (ZMUC, Denmark), Smithsonian Washington (USNM, USA), see detailed indications at the descriptions.

Abbreviations

A1, 2, antennae 1, 2; art, article; Cx, coxa; Ep, epimeral plate; Gn 1, 2, gnathopods 1, 2; Md, mandible; Mx1, 2, maxillae 1, 2; Mxp, maxilliped; P 3–7, peraeopods 3–7; U 1–3, uropods 1–3.

In this paper the following terms are applied (see also Krapp-Schickel 2011: 1–2): tooth: non-articulated pointed ectodermal structure; spine: stout, articulated structure (synonymous with "robust seta"); seta: slender, flexible articulated structure.

Systematics

Stenothoidae Boeck, 1871
Stenothoinae Boeck, 1871

Genus *Stenothoe* Dana, 1852

Type species. *Stenothoe valida* Dana, 1852

The diagnosis of this genus is summarized, it shows few eminent features: Md palp lacking totally, P 5 basis linear, P 6–7 basis widened, T laminar. The genus contains many apparently free-living species and others that are living in symbiosis with other marine invertebrates; these latter in many cases show greatly diminished sexual dimorphism.

Stenothoe species are mainly found in the Atlantic and Mediterranean, while few are living in the Pacific, in the region of Australia-New Zealand or in the Indian Ocean (Krapp-Schickel 2015). There remains the strong suspicion that e.g. members living near Australia or in the Indian Ocean are not closely related to those from the Atlantic Ocean (urosome segments tend to lose their clear articulation in the former), but as the easier visible appendages such as legs or antennae match the generic definition, plus the fact that both have lost the Md palp (most probably an independent evolution), also these species are treated in the same genus *Stenothoe*, for the time being. Here we have examples of these different groups:

Stenothoe bartholomea sp. n.

http://zoobank.org/54165FFC-8D4D-4299-A613-6C12FCC1147C
Figures 1–5
Vader 1983: 146 sub *Stenothoe* n.sp.

Holotype. female ov. 3 mm, Florida, Monroe County, Cross Key: from *Bartholomea annulata* (Lesueur, 1817), 4/10/1971, J. Thomas coll. Slide MVRCr 7716, 7717.

Additional material. one female front part, slide MVRCr 7718; several hundreds, same locality, same date, in alcohol, deposited at MVRCr.

Type locality. Florida, Monroe County, Cross Key.

Etymology. after the host anemone *Bartholomea annulata* (Lesueur, 1817), from where it was collected.

Diagnosis. Sexual dimorphism lacking. Gn 1 and Gn 2 propodus similar in shape, propodus hind margin rounded, in Gn 2 without clear palmar corner. P 6, 7 basis posterodistal corner lengthened and rounded; merus posterodistally widened and lengthened, reaching half length of carpus. U3 peduncle < ramus. T with or without submarginal spines and marginal setae.

Description.

Length 2.5 – 3 mm.

Head. Eyes round, medium. Mouthparts: Md with acute hook on the place where a palp would have inserted; molar absent, incisor and lacinia mobilis strong, spine row present. Mx 1 palp with 2 arts, Mx 2 plates sitting upon each other. Mxp IP small, OP vanishing. Antennae: subequal, A1 flagellum about 15 arts, A2 flagellum about 10 arts.

Peraeon. Gn 1 basis about 3 times as long as wide, merus triangular, distally rounded and beset with spines, nearly reaching end of carpus; carpus triangular; propodus somewhat wider and clearly longer than carpus, anteriorly beset with long setae; palm well defined by a group of spines and palmar corner. Cx 2 tongue-shaped, posteriorly excavate. Gn 2 basis 3 –3.5 times longer than wide, rectangular; merus rectangular-trapezium-shaped, distally pointed, carpus triangular, distally with stiff short and long pectinate setae, propodus oval, posterior margin regularly rounded, palm defined by some robust spines but palmar corner lacking, with one or more small triangular elevations.

Peraeopods: Cx 3 rectangular, distal margin not much longer than proximal one. Cx 4 triangular, clearly wider than long. P 3, 4 similar, slender, dactylus longer than half propodus. P 5 basis rectolinear. P 6, 7 basis with posterior margin rounded, postero-distal lobe well developed; merus lengthened and widened, reaching about half length of carpus; propodus > carpus, dactylus > half of propodus.

Pleon. U 1 peduncle > subequal rami, all beset with a few spines. U 2 peduncle > longer than unequal rami; U 3 peduncle about 3 times as long as wide, peduncle < ramus, ramus art 1 < art 2, with few short spines.

Telson with or without pair of submarginal spines and small marginal setae.

Remarks. In Krapp-Schickel 2015 a key is offered for *Stenothoe* species world-wide, grouped after geographical regions. Among these species this new one is one of only two with a regularly rounded Gn 2 male propodus, lacking excavations, deep incisions or prominent elevations. The other one is *S. tergestina* (Nebeski, 1881), frequently found in the Mediterranean, free-living in algae.

Distribution. Florida, Atlantic Ocean.

Ecology. living with and on the sea-anemone *Bartholomea annulata* (Lesueur, 1817).

Stenothoe miersii (Haswell, 1879)

Figures 6, 7
Montagua Miersii Haswell, 1879: 323, pl. 24, fig. 4.
Montagua longicornis Haswell, 1879: 323, pl. 24, fig. 5.
Stenothoe miersi. —Stebbing 1906: 200 (in part). —Stebbing 1910: 637 (in part). Lowry and Stoddart 2003: 260. —Krapp-Schickel 2009: 873–875.
Stenothoe ?miersii. —J.L. Barnard 1974: 120, figs 75–76.
Stenothoe valida. —Sheard 1937: 21 (=*S. miersii*, but confused with other species).
not *Montaguana miersii*. —Chilton 1883: 79 (part =*S. moe*, J.L Barnard 1972).
not *Montagua miersii*. —Chilton, 1884: 1043 (part =*S. moe*, J.L Barnard 1972).
not *Probolium miersii*. —Thomson and Chilton 1886: 150 (=*S. valida*).

Type locality. Port Jackson, New South Wales, Australia.

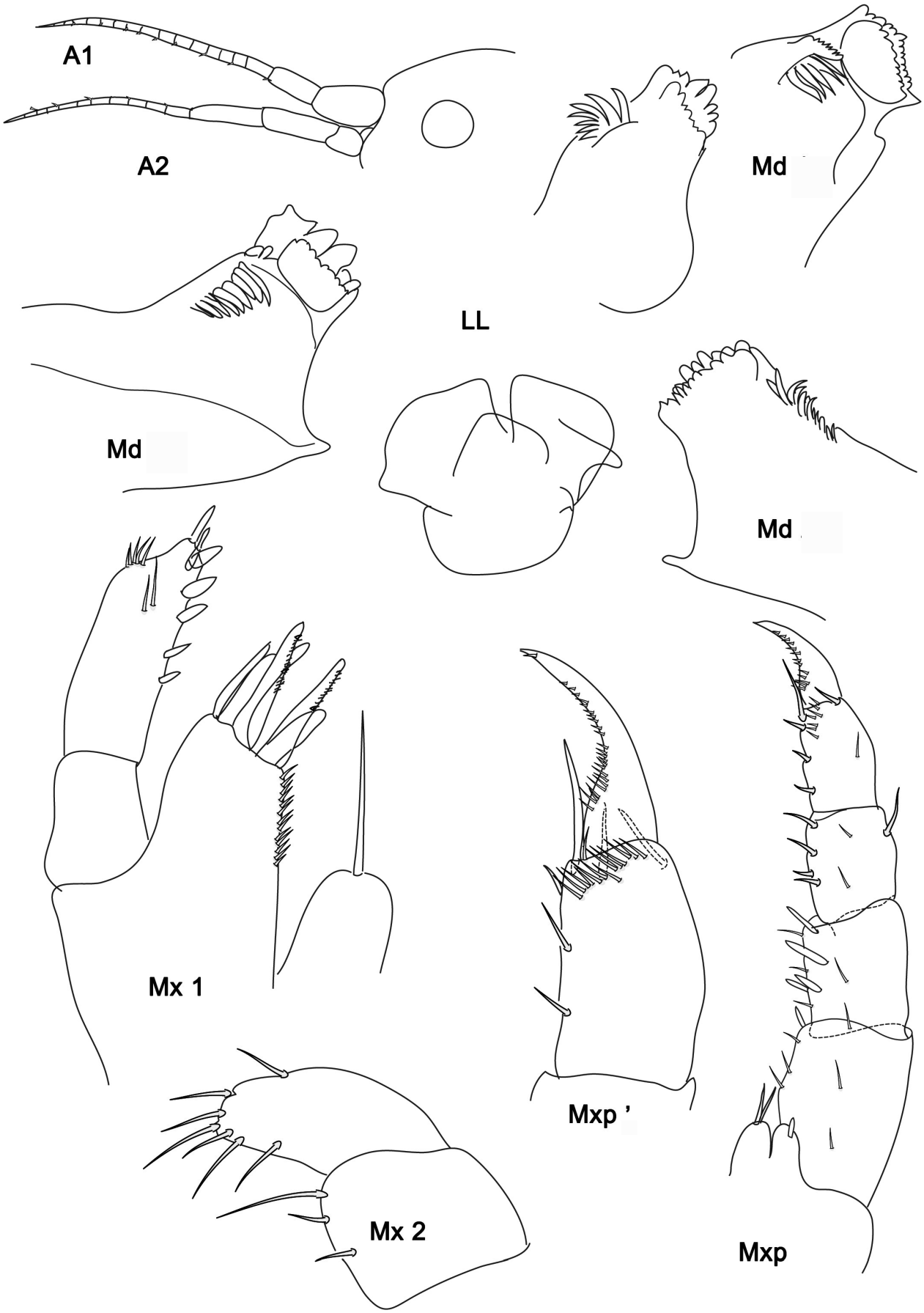

Figure 1. *Stenothoe bartholomea* sp. n. female 3 mm holotype. **A1, 2** antennae; **Md** mandibles from both sides; **LL** lower lip; **Mx1, 2** maxillae 1, 2; **Mxp** maxilliped; **Mxp’** maxilliped dactylus and propodus enlarged.

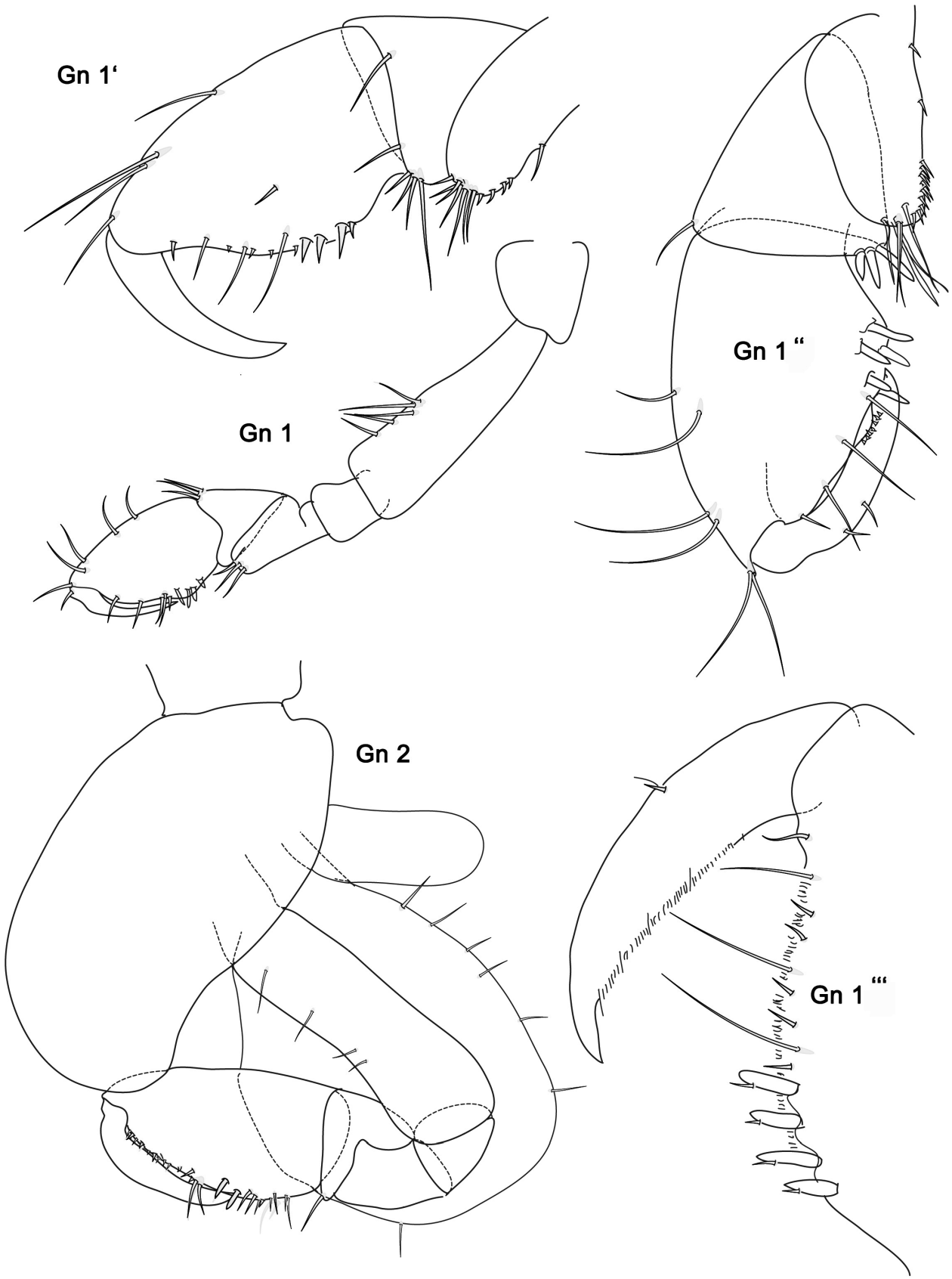

Figure 2. *Stenothoe bartholomea* sp. n. female 3 mm holotype. **Gn 1** gnathopod 1; **Gn 1’, Gn 1 ‘’, Gn 1 ‘’’** palm and dactylus enlarged; gnathopod 1 dactylus and propodus enlarged; **Gn 2** gnathopod 2.

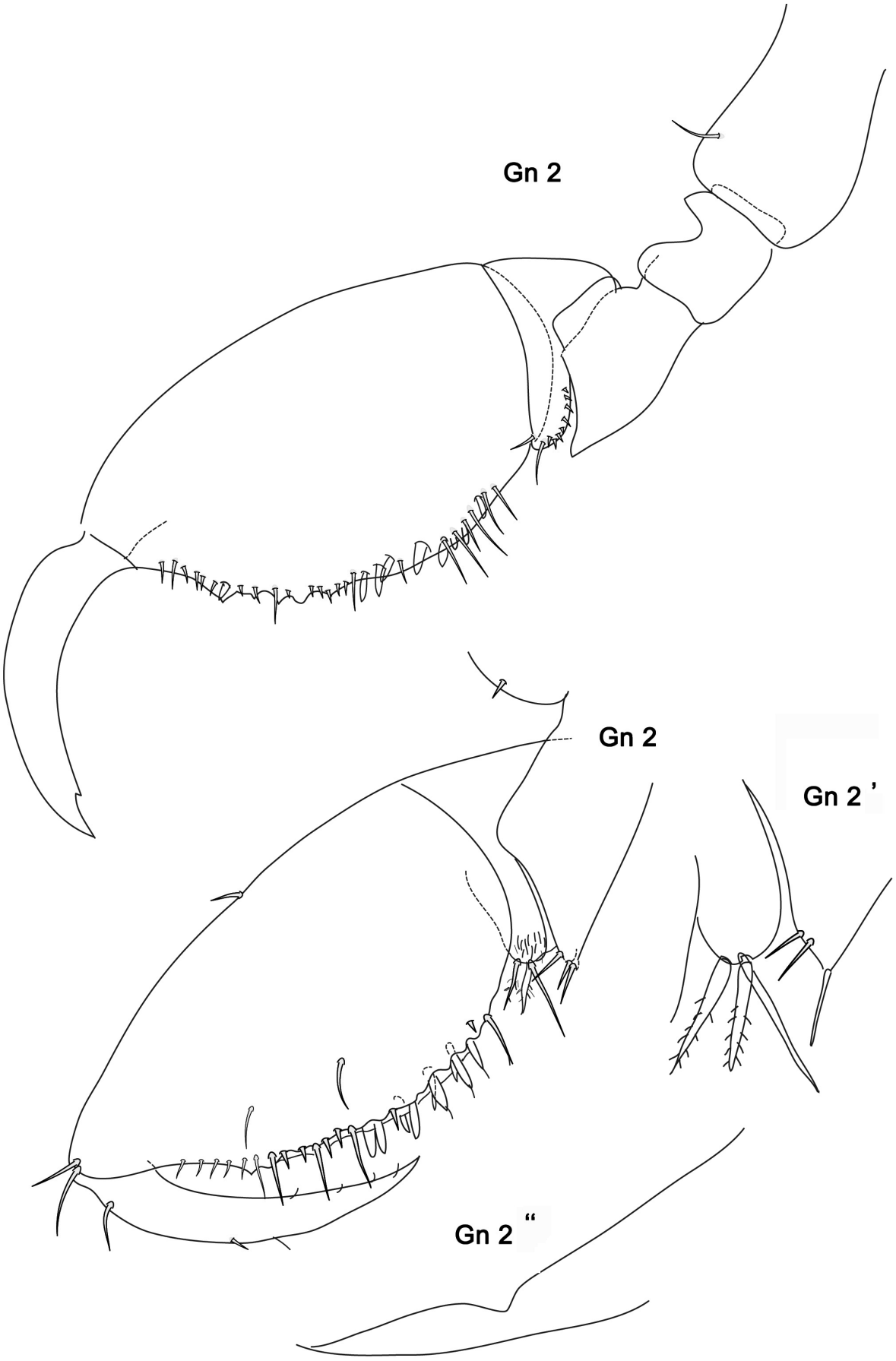

Figure 3. *Stenothoe bartholomea* sp. n. female 3 mm holotype. **Gn 2, Gn 2’, Gn 2’’** gnathopod 2 from both sides and tip of carpus + merus resp. palmar corner enlarged.

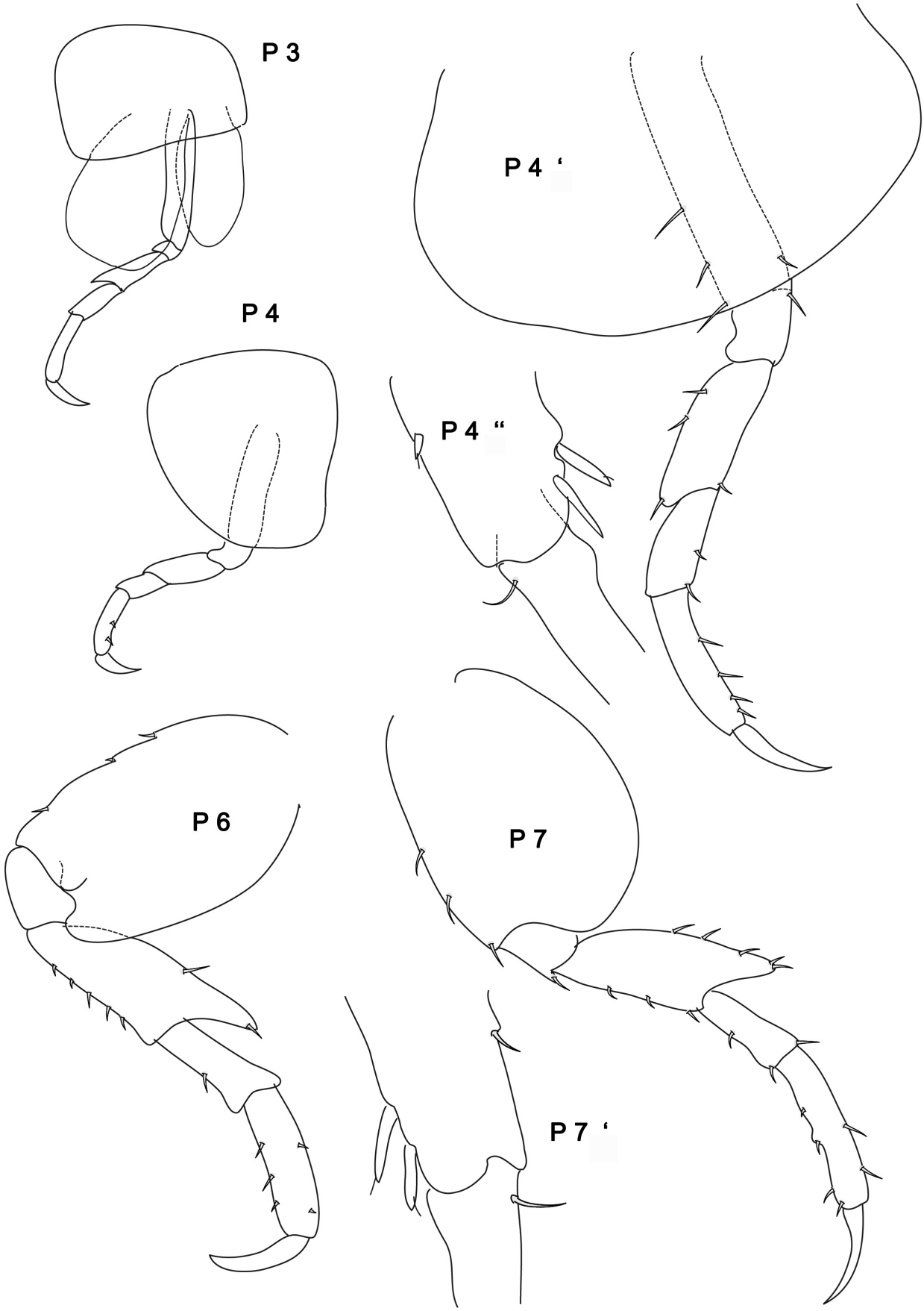

Figure 4. *Stenothoe bartholomea* sp. n. female 3 mm holotype. **P 3–4, P 6–7** peraeopod 3–4; peraeopod 6–7; **P 4’, P 4’’** entire leg with coxa resp. distal end of propodus **P 4** enlarged; **P 7’** distal end of propodus **P 7** enlarged.

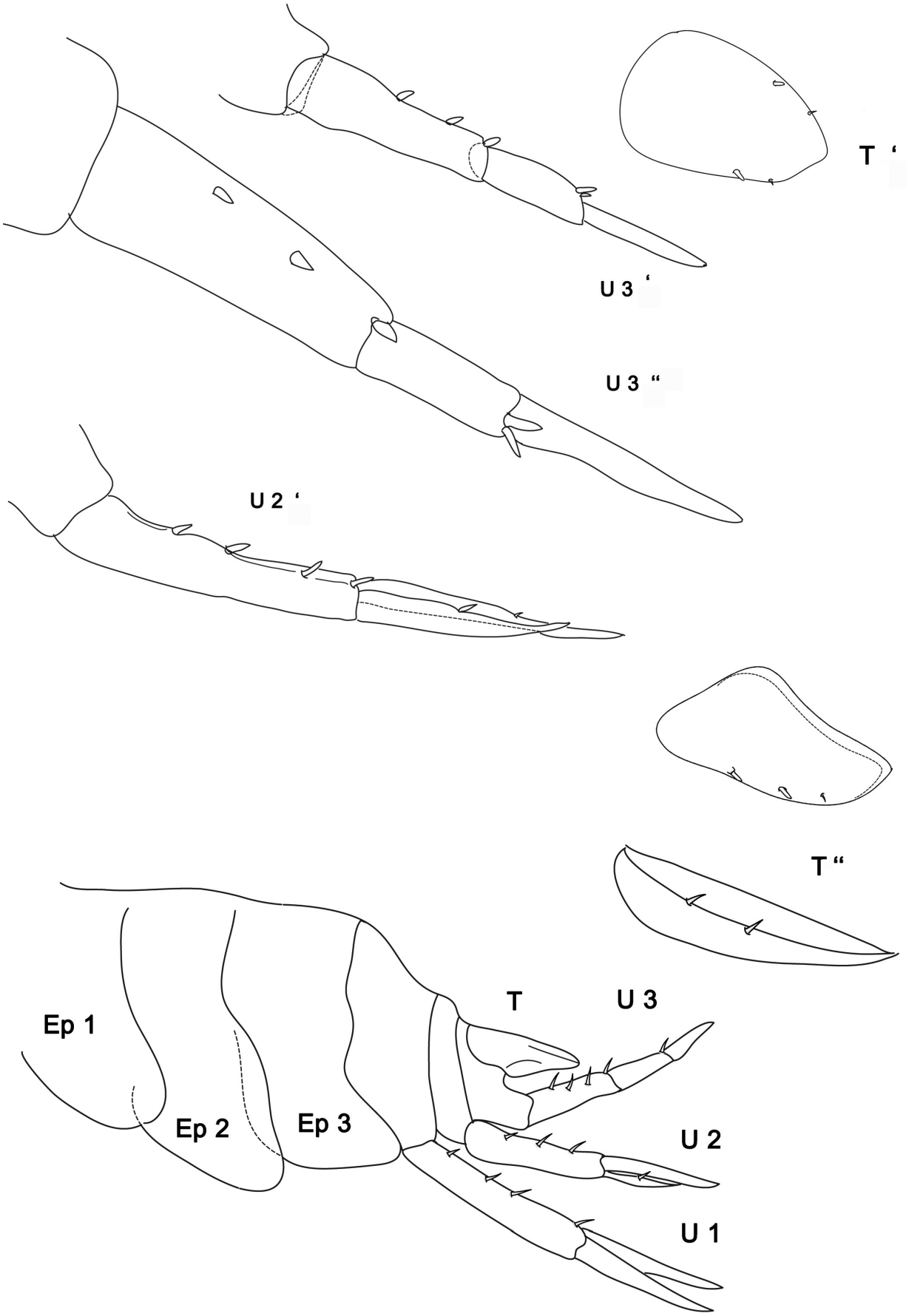

Figure 5. *Stenothoe bartholomea* sp. n. female 3 mm holotype. **Ep 1, 2, 3** epimeral plates 1–3. **U 1, 2, 3** uropod 1, 2, 3; **U 2'** uropod 2 enlarged; **U 3', U 3''** uropod 3 in two enlargements. **T', T''** telson enlarged in different positions.

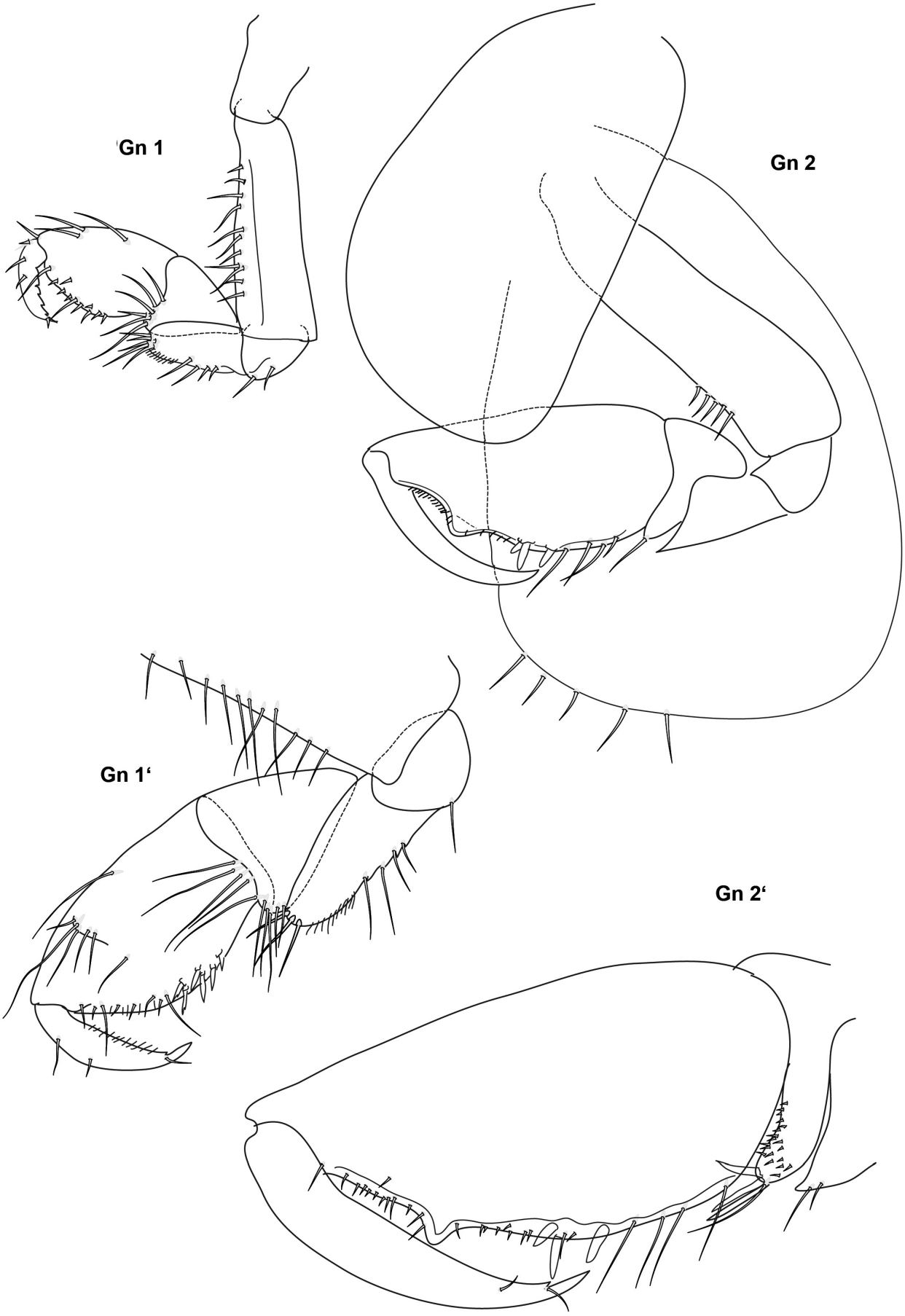

Figure 6. *Stenothoe miersii* (Haswell, 1879) male 3 mm; **Gn 1, 2** gnathopod 1, 2; **Gn 1', Gn 2'** gnathopods distally enlarged.

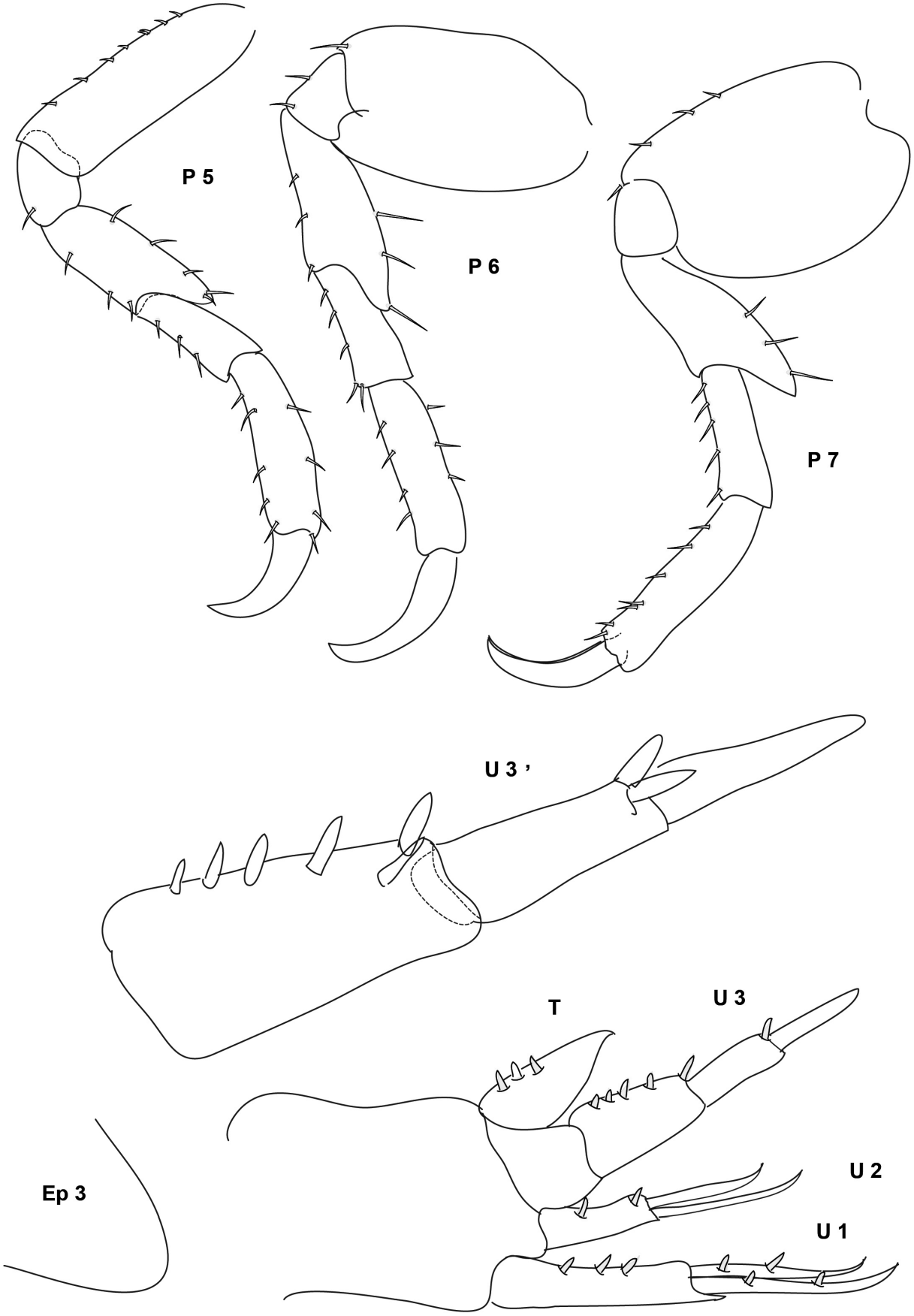

Figure 7. *Stenothoe miersii* (Haswell, 1879) male 3 mm; **P 5–7** peraeopod 5–7; **U 1–3** uropod 1–3; **U 3’** third uropod enlarged; **Ep 3** third epimeral plate; **T** telson.

Material examined. 1 spec. from Bermagui (400 km S of Port Jackson, Australia), 8/6/1989, Wim Vader collected on a hermit crab in shallow water. Stored at the Australian Museum (AM xxx) Sydney.

Remarks. In Haswell (1879) two species of *Montagua* were described from Port Jackson, Sydney: *M. miersii*, directly followed by *M. longicornis*. It appears that the first was the female, the latter the male of the same species, belonging to *Stenothoe*. J.L. Barnard (1974) described four species of *Stenothoe* from Australia. One of these he called *S.* ?*miersi*, doubting about the synonymy, as no type material is available. Barnard's description matches the different populations around most of the Australian coastline, also the Lizard Island specimens (Krapp-Schickel 2009: 873–875), and again the illustrations given here of a female.

Ecology. It may well be that this specimen lived among the encrusting hydroids and bryozoans growing on top of the hermit-crab-shell and thus had no direct association with the crab; it was the only *Stenothoe* specimen found among many hermit crabs.

Genera *Metopa* Boeck, 1871 and *Stenula* Barnard, 1962

Lincoln 1979 has synonymized *Stenothoides latipes* Chevreux & Fage, 1925, with *Metopa rubrovittata* Sars, 1883 and transferred both to the genus *Stenula*, a genus coined by Barnard 1962.

Members of *Metopa* are mainly distributed in the Atlantic and Arctic, only very few are living outside. They can be divided into three groups by looking at their Gn 1 palmar corner:

L Gn 1 locking, palmar corner 120°, propodus widened
SI simple, Gn 1 palmar corner absent, propodus hind margin straight
N normal, Gn 1 palmar corner 150–160°, propodus hind margin rounded

a) Atlantic Ocean and Arctic:

M. abyssalis Stephensen, 1931 ..... N
M. aequicornis Sars, 1879 ..... N
M. affinis Boeck, 1871 ..... SI/N
M. alderi (Bate, 1857) ..... N
M. boeckii Sars, 1892 ..... N
M. borealis Sars, 1883 ..... SI
M. bruzelii (Goës, 1866) ..... SI
M. clypeata (Krøyer, 1842) ..... SI
M. cristata Gurjanova, 1955 L
M. eupraxiae Krapp-Schickel, 2009 L
M. gigas Just, 2013 ..... SI
M. glacialis Krøyer, 1842 L
M. groenlandica Hansen, 1888 L
M. hearni Dunbar, 1954 ..... N
M. invalida Sars, 1892 ..... SI.
M. latimana Hansen, 1888 ..... N
M. leptocarpa Sars, 1883 ..... L (Md palp lacking?)
M. longicornis Boeck, 1871 ..... SI
M. longirama Dunbar, 1942 ..... SI
M. normani Hoek, 1889 ..... N
M. norvegica (Liljeborg, 1851) L
M. palmata Sars, 1895 ..... SI
M. propinqua Sars, 1892 ..... SI
M. pusilla Sars, 1892 ..... SI
M. quadrangula Reibisch, 1905 ..... SI
M. robusta Sars, 1892 ..... SI
M. rubrovittata Sars, 1883 ..... N
M. samsiluna J.L. Barnard, 1966 ..... N
M. sinuata Sars, 1892 ..... N
M. solsbergi Schneider, 1884 ..... N
M. spinicoxa Shoemaker, 1955 ..... N
M. submajuscula Gurjanova, 1948 L
M. spitzbergensis Brüggen, 1907 ..... SI
M. tenuimana Sars, 1892 ..... SI
M. wiesei Gurjanova, 1933 ..... SI

b) Pacific Ocean:

M. abyssi Pirlot, 1933 Pacific ..... N
M. angustimana Gurjanova, 1948 ..... SI
M. bulychevae Gurjanova, 1955 L
M. cistella J.L. Barnard, 1969 ..... SI
M. colliei Gurjanova, 1948 L
M. dawsoni J.L. Barnard, 1962 ..... SI
M. exigua Krapp-Schickel, 2009 ..... N
M. japonica Gurjanova, 1952 L
M. kobjakovae Gurjanova, 1955 L
M. koreana Gurjanova, 1952 ..... SI
M. layi Gurjanova, 1948 ..... N
M. majuscula Gurjanova, 1948 L
M. mirifica Gurjanova, 1952 L
M. samsiluna JL Barnard, 1966 L
M. timonovi Gurjanova, 1955 L
M. torbeni Krapp-Schickel, 2009 ..... SI
M. uschakovi Gurjanova, 1948 ..... N

Many authors have cited *Metopa rubrovittata*: Sars 1883: 90, 1895: 255, Reibisch 1905: 31, Chevreux and Fage 1925: 125, Stephensen 1929: 5, 1931: 189, 1938: 175, Schellenberg 1942: 120, Gurjanova 1951: 432, Oldevig 1959: 44, Moore 1984: 26. None of them gives illustrations of the mouthparts, only Lincoln 1979: 192 found a very short uniarticulate mandible palp in his material from the British coasts which he then called *Stenula rubrovittata* (Sars), confirmed by Vader (see Lincoln op. cit., p. 180) for a specimen from the Norwegian west coast, but we have no information about the mouthparts of the Norwegian material called *Metopa rubrovittata* collected by Sars.

Chevreux 1900 erected a new genus *Stenothoides* for stenothoid species with present, but reduced mandibular palp.

J.L. Barnard 1962 coined a new genus *Stenula* leaving the species with rectilinear basis of P 6 in *Stenothoides* and splitting those species which have P 6 basis widened (see Chevreux and Fage 1925: 130, Gurjanova 1938: 279 and 1951: 445). His diagnosis for *Stenula* is the following:

P 5 basis slender; P 6, 7 basis broad; Md palp with 1 article; Mx1 palp with 1 article.

Barnard 1962 included 10 species in *Stenula*: *S. angusta* (Shoemaker), *S. arctica* (Gurjanova), *S. bassarginensis* (Gurjanova), *S. beringiensis* (Gurjanova), *S. carinatus* (Gurjanova), *S. latipes* (Chevreux & Fage) (type), *S. modosa* J.L. Barnard, 1962, *S. ratmanovi* (Gurjanova), *S. serripes* (Gurjanova), *S. ussuriensis* (Gurjanova), nota bene 7 of 10 species described by Gurjanova from the Arctic Sea.

Just 1980: 52 transferred *Metopa nordmanni* Stephensen, 1931 to *Stenula*.

In the European register of marine species Bellan-Santini and Costello 2001 cited 15 *Stenula* species: the ten above specified by Barnard 1962, plus *S. alexanderi* Tzvetkova & Golikov, 1990, *S. nordmanni* (Stephensen, 1931), *S. peltata* (where they mistakenly cited Della Valle 1893 as author instead of Smith 1874) and – following Lincoln 1979 – they placed *Stenothoides latipes* Chevreux & Fage, 1925 in junior synonymy with *S. rubrovittata* (Sars, 1892), which according to them therefore should be the actual type at the moment. We do not think this is correct, as *Stenothoides latipes* remains in any case the type.

S. carinatus (Gurjanova) was transferred to *Metopa* and renamed *M. eupraxiae* sp. n. by Krapp-Schickel 2009b.

Thus at the beginning of this study 14 species belong to *Stenula*. Judging from the illustrations of the mandible in Tandberg 2011: fig. 25, *M. invalida* Sars, 1892 from N. Norway has to be added as 15th species. These species are mainly living in the far north region (N-Atlantic, N-Pacific, Arctic), only two of them were described by J.L. Barnard from California.

Tandberg & Vader could demonstrate in Tandberg (2011), that the character of Gn 2 palmar corner present/absent does not bring any clear results in a cladistic analysis. E.g. *Metopa clypeata* (the type species) or *M. palmata*, both with strongly rectangular palmar corner, strangely enough are not grouped together with *M. alderi* = *M. spectabilis* or *M. norvegica*, probably because of the strong allometry, which shows their members with very different palmar corners depending on age. It might therefore be more helpful to look at the shape of Gn 1, which shows normally much less allometry and which can be basic (the type of *Stenula* plus several other members of this genus and a lot of *Metopa*, with the carpus shorter than or equal to the propodus) or elongated (type of *Metopa* and some other *Stenula*, with Gn 1 simple and carpus, often also propodus, much lengthened and narrow).

Tandberg 2011 cites in her thesis at the beginning a letter from G.O. Sars to Sparre-Schneider, writing „I have advanced to the supposedly most difficult of all amphipod-families: *Stenothoidae*“. There is no doubt that there is a great difference between having a fully developed mandibular palp (*Metopa*) or none (*Stenothoe*), but the genus *Stenula*, as presently conceived, gathers all transitions, and is with high probability heterogeneous.

There are also various transitions within the maxillae, having two (*Stenothoe*) or one (*Metopa*, *Stenula*) articles in Mx1 palp, where often one cannot clearly decide if and where an articulation is present; while the Mx2 plates may sit in tandem-position (many *Metopa* like *M. affinis*, *aequicornis*, *groenlandica*, *glacialis*, *clypeata*) or riding position (in some *Stenothoe* and *Stenula*), with all steps in-between.

In three species we have no information about the mandible palp at all: *S. rubrovittata*, *S. modosa*, *S. peltata*. The following have a short stump, about as long as the width of the mandible-incisor: *S. angusta*, *S. bassarginensis*, *S. ratmanovi*. All other species have a uniarticulate mandible palp which is clearly longer than the mandible-incisor: *S. alexanderi*, *S. arctica*, *S. beringiensis*, *S. incola*, *S. serripes*, *S. ussuriensis*, and also *Metopa derjugini* Gurjanova, 1948, which is therefore here also transferred to *Stenula* (see above). Just 1980: 52 looked at the mandible of *Metopa nordmanni* using the type specimen, and found again a uniarticulate palp longer than the mandible-incisor (also illustrated by Tzvetkova and Golikov 1990), while Shoemaker 1955: 127 found material from Point Barrow with strikingly similar legs but different antennae (A1>A2), a two-jointed Mx1 palp and a 3-articulated mandible palp. Although he cites *Metopa nordmanni* Stephensen, 1931 in the synonymy-list, his species belongs to *Proboloides* and thus is a different animal with nearly identical body but different mouthparts, an observation which can be made rather frequently within Stenothoidae.

Stenula species could also be divided by the ratios of articles in Gn 1, having propodus subequal to carpus, or clearly much longer resp. clearly shorter. The first group is formed by the majority: *S. beringiensis*, *S. derjugini*, *S. incola*, *S. latipes*, *S. modosa*, *S. peltata*, *S. ratmanovi*, *S. serripes*; propodus is longer than carpus in *S. angusta*; propodus is shorter than carpus in *S. arctica*, *S. bassarginensis*, *S. nordmanni*, *S. ussuriensis* and also

S. alexanderi (this species is very aberrant also in the shape of Gn 1 dactylus).

It is the great help of a cladistic analysis that one can test the states of many characters together, and if a group of characters is changing together, it is more probable that a naturally related clade is found. But in the above listed species there are A1 subequal A2 or much different, Gn 1 propodus simple, rounded or with strong palmar corner, Gn 1 carpus short or extremely lengthened, Gn 2 propodus regularly rounded or deeply excavated, P 6, 7 strongly rounded or with widened but parallel margins, telson spinose or naked. And even using more than 60 characters as in the very exhaustive phylogenetic analysis of Tandberg & Vader (Tandberg 2011), there remains the big danger that the character states are not homologous. As an example, several analyses bring *Stenula incola* J.L. Barnard, 1969 from the intertidal of California always closely together with *Stenula serripes* Gurjanova, 1955: both show a one-articulate mandibular palp of medium length, Gn 2 with a well defined palmar corner, P

7 basis about as wide as long and P 7 merus very much lengthened and widened, and they are thus „very similar" after the coded characters. But their biogeography, Gn 1 and P 6 are obviously quite different, and they are most probably not closely related at all.

At the moment there is nothing else to do than to continue „making order" within this complicated family of Stenothoidae in describing as completely as possible its single members.

First we tried to find material of *Metopa rubrovittata* Sars from the northern North Atlantic (type loc. Christiansund and Finnmark) for comparing it with material of *Stenula latipes* (Chevreux & Fage) from the English Channel (type loc. Saint Vaast la Hougue, see Chevreux 1908: 42, 1925: 130).

Metopa rubrovittata Sars, 1883

Figures 8–9, 10B, C

Sars 1883: 90, t. 4, fig. 2, 2a; 1892: 255, pl. 89, fig. 2; Reibisch 1905: 31; Chevreux and Fage 1925: 127, fig., 125; Stephensen 1929: 5; Stephensen 1931: 189; Stephensen 1938: 175; Schellenberg 1942: 120, fig. 98; Gurjanova 1951: 432, fig. 276; Oldevig 1959: 44.

Type locality. Christiansund (W Norway) and Vadsø (Finnmark)

Material examined.

–7 spec. in alcohol, 2 on slide: Surtsey (Vestmannaeyjar) off Iceland, 63.30 N, -20.60 W. NA 30 m 18/8/1971 leg. Sigurdsson, det. J. Just. ZMUC-CRU–4464.

–1 spec. 20/8/1971 same locality as above, ZMUC-CRU–4465.

– 4 spec. North Sea without date, 4 spec., 57.266667 N 5.5 E. ZMUC-CRU–4467.

Discussion. It seemed strange that the sharp eye of Chevreux would have overlooked the synonymy between *M. rubrovittata* (cited by him in the same work Chevreux and Fage 1925: 127, fig. 125) and his newly erected *Stenothoides latipes* (loc. cit.: 129, fig. 127, 128), later transferred to *Stenula* and finally synonymized as *Stenula rubrovittata* (Sars, 1883) by Lincoln 1979. But until now really nobody had looked at the mouthparts of *M. rubrovittata*, an often cited species, which nevertheless is rarely found in Museum collections.

In fact, the studied material shows a classical mandible palp of *Metopa* species with 3 articles, though it has to be admitted that it was quite a difficult task to see always the articulations. But nevertheless, already the length of the mandible palp is very different in the material from the Channel (cf. Fig. 8 with Fig. 10B, C), thus it can be confirmed that Chevreux was right: both *Metopa rubrovittata* Sars, 1883 as well as *Stenula latipes* (Chevreux & Fage, 1925) do exist, and they show extremely similar body morphology, colour pattern and even ecological niche, only the mouthparts are somewhat different. Thus, *Metopa rubrovittata* Sars, 1892 is herewith revalidated and *Stenothoides latipes* (Chevreux & Fage, 1925) remains the type species of *Stenula*. It is not clear what the geographical distribution of the two species is, as all the numerous citations cannot be judged without examining their mandible.

For control Jean-Claude Sorbe sent us material from the Bay of Biscay, and the single specimen he had collected affirms this decision.

Stenula latipes (Chevreux & Fage, 1925)

Fig. 10A

Chevreux and Fage 1925: 130, fig. 127–129.

Type locality. Grandcamp-les-Bains (Calvados), on the shell of *Eupagurus bernhardus* (L.); very common in a dredge of 20m depth in Saint-Vaast-la-Hougue. English Channel. Chevreux and Fage 1925: 11 specified that the shell from which the amphipod was collected was *Buccinum undatum* inhabited by the hermit crab.

Material examined. 1 spec. 3 mm, Survey OXYBENT 9 STN OB9–B–TS04; 43.8175 N, 2.042 W; Bay of Biscay, Capbreton Canyon; 500–510 m; 22/06/1999; coll. Sorbe.

4 spec. Denmark, Anholt (Kattegat) without date, 17,5 fathoms = 31,5 m. ZMUC-CRU–4466.

?Stenula peltata (Smith, 1872)

Figures 11–13

Smith 1872 in: Smith and Harger 1872: 29, pl. 3, fig. 5–8; Della Valle 1893: 570; Stebbing 1906: 194–195.

? synonymous to Gurjanova 1948: 310 *S. ratmanovi*

Type locality. St. George's Banks, 55 m depth. Near Cultivator Shoal.

Material examined. one specimen USNM 35636, 41.5557 N, 68.1641 W, NA, 30 fathoms, sandy bottom, 29/8/1872.

As the original paper is not easily accessible and as there is some confusion about the authors, I repeat herewith the type-description by Smith:

Description.

Female. Eyes round and nearly white in alcohol. Antennulae (=A1) considerably shorter than epimera of the 4th segment (Cx 4); first article of the peduncle stout, subequal to head, the second shorter, the third very short and similar to the arts of the flagellum; flagellum scarcely longer than the peduncle, with 8 arts. Antennae (=A 2) slightly longer than antennulae; peduncle art 4, 5 about equal in length; flagellum subequal to flagellum of antennulae. Cx 2 (fig. 5) nearly ovate, twice as high as broad; Cx 3 somewhat rectangular, not wider than the second but considerably deeper; Cx 4 (fig. 6) very large, slightly deeper than Cx 3 and 1/3–1/4 longer than deep, being about as long as the first five segments of the thorax, the inferior margin regularly curved and the posterior convex in outline. Gn 1 (fig. 7) small and slender; merus

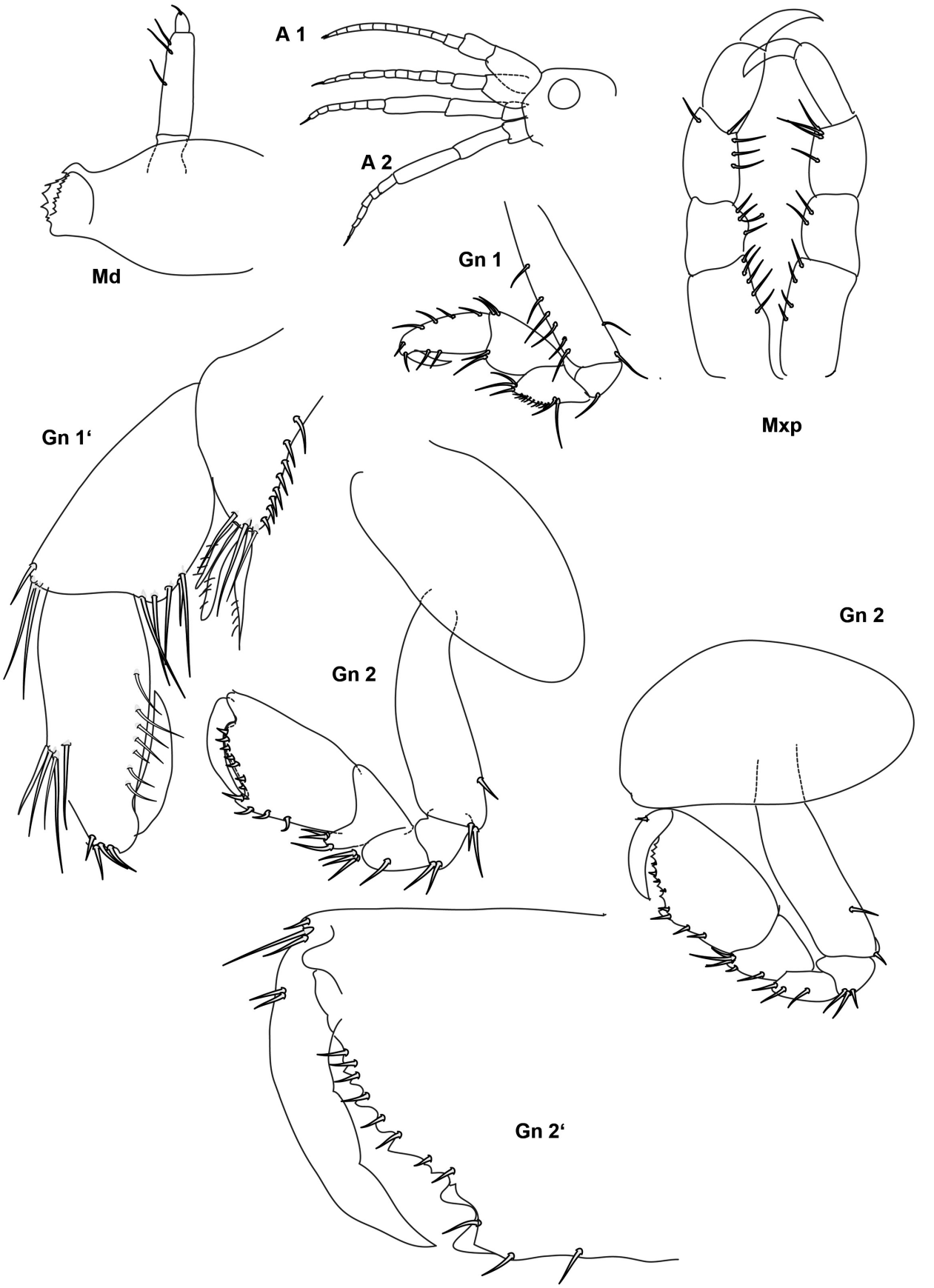

Figure 8. *Metopa rubrovittata* Sars, 1883 male 3 mm; **Md** mandible; **Mxp** maxilliped; **A 1, 2** antenna 1, 2; **Gn 1, 2** gnathopod 1, 2; **Gn 1', Gn 2'** gnathopod 1, 2 distally enlarged.

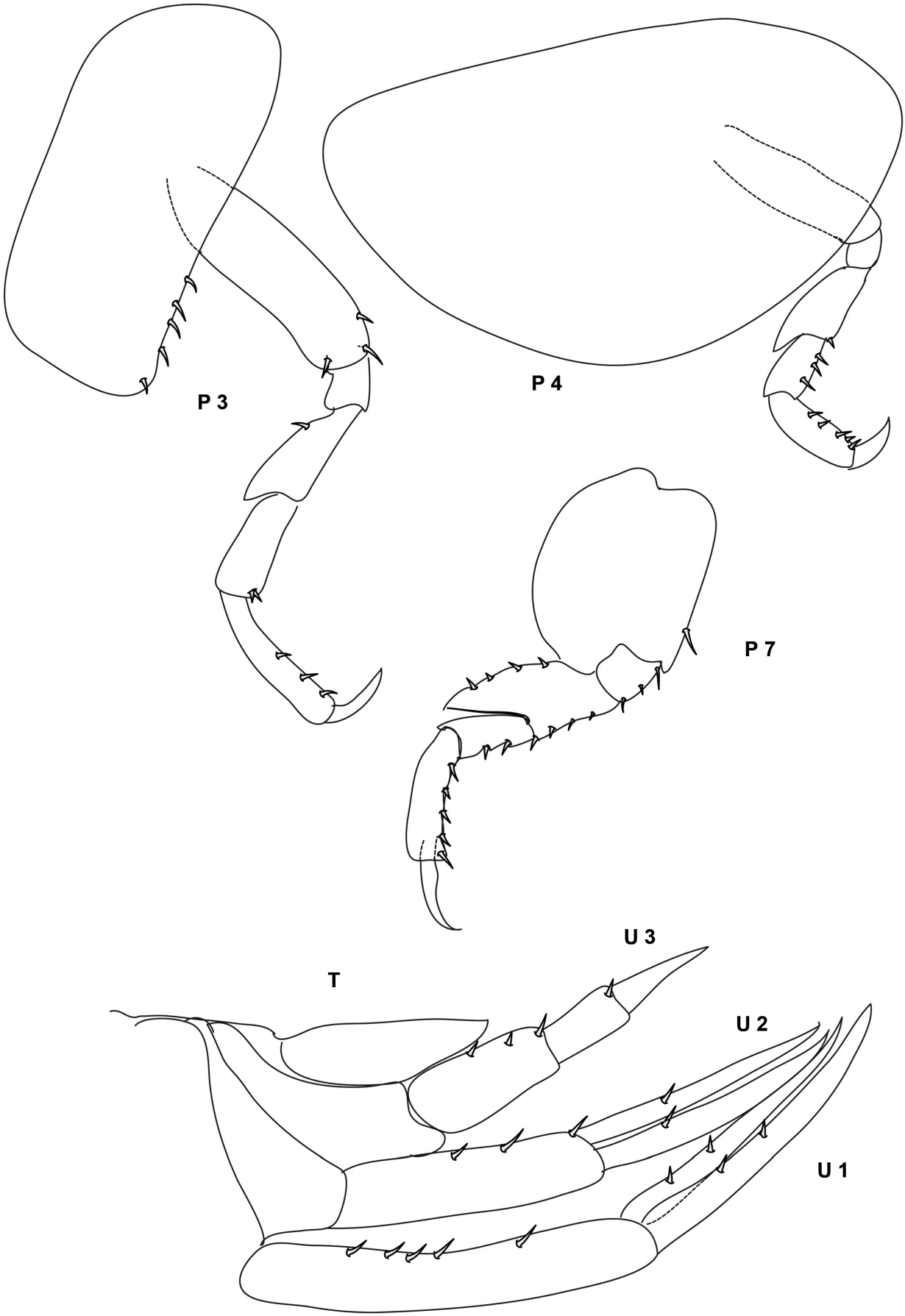

Figure 9. *Metopa rubrovittata* Sars, 1883 male 3 mm; **P 3, 4, 7** peraeopod 3, 4, 7; **U 1–3** uropod 1–3; **T** telson.

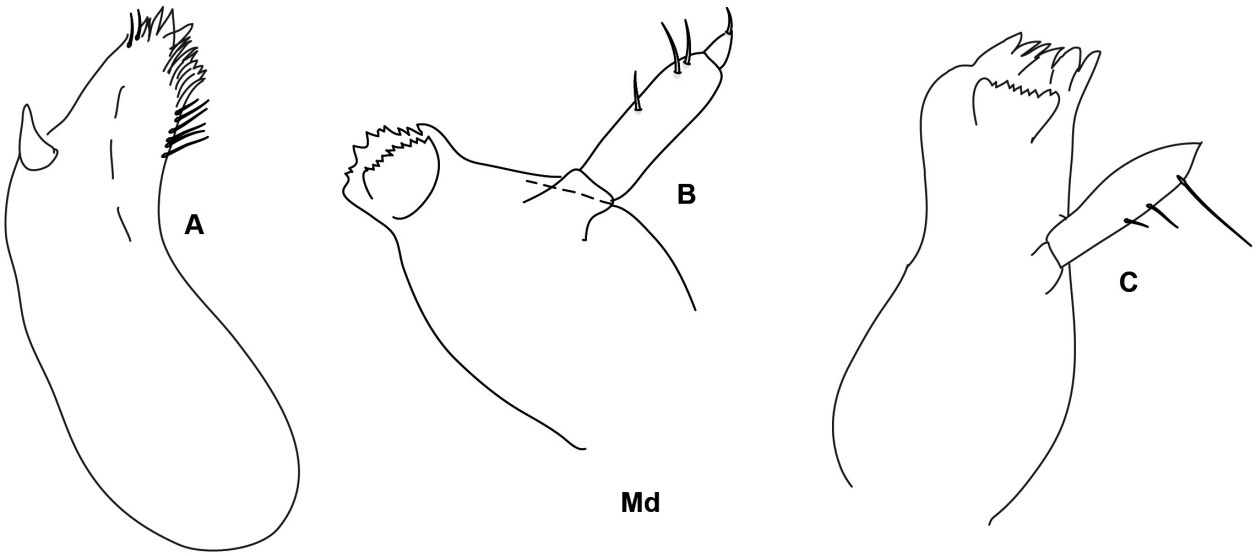

Figure 10. *Stenula latipes* Chevreux & Fage, 1925: **Md A** mandible A; *Metopa rubrovittata* Sars, 1892: **Md B, C** mandible B, C.

triangular and distally broader than the carpus, which is not quite twice as long as broad and has the lateral margins parallel; propodus narrower but slightly longer than the carpus and narrowed distally; dactylus about half as long as the propodus. Gn 2 (Fig. 5) stouter; merus short triangular, carpus much broader than long and only slightly produced beneath the propodus; propodus about as long as the breadth of Cx 2, nearly twice as long as broad; palmar margin (Fig. 8) convex in outline, slightly oblique, with an acute lobe and a spine at the posterior angle, within which the top of the dactylus closes. P 4, 5 slender and nearly naked, P 5 basis slender, four times as long as broad, not wider than the merus. P 6, 7 slightly shorter than P 5, basis posteriorly dilated and squamiform in both pairs, but broader in P 7. U 3 ramus slightly longer than the peduncle.

Length of largest specimen, from front of head to tip of telson, about 6 mm.

The mandibles are without palp or molar tubercles, and in all other characters the species agrees with the genus *Stenothoe* as restricted by Boeck, but it seems to be very distinct from either of the European species.

Discussion. The hint after the original description, that this species should belong to *Stenothoe* as it has no mandible palp, was not convincing: no *Stenothoe* is described from the region off Massachusetts or Connecticut, nor from the entire Atlantic, with gnathopods similar to the ones illustrated.

The incomplete illustrations of *S. ratmanovi* (Gurjanova, 1948) are very similar to what little we know about ?*Stenothoe peltata*, and the two species may well be synonymous, in spite of the large geographic distance between the type localities. In that case the older name *Stenula peltata* (Smith, 1874) would become the valid name of the taxon.

We hoped to get more information by studying the single type specimen (see Fig. 11, 12) and illustrate here all what we could see; but there were no mouthparts except the maxilliped, and we still don't know anything about the shape of the mandibular palp.

A sample in the collections of the Smithsonian Inst. (Washington) raised new hope to shed light in this situation: there could exist a *Stenula* sp. from the coelenteron of *Haliactis arctica.* Will this be *S. peltata*?

Stenula pugilla sp. n.

http://zoobank.org/F3F651B1-E8C4-430E-8184-219956DFE464
Figures 14–18
Vader 1983: 146, sub *Stenothoe* sp.

Holotype. male 3 mm in alcohol; USNM 1241824; M/v"John N.Cobb", cruise 43, sta. 45, Project Chariot Cruise, Vessel John N Cobb R/V; Chukchi Sea: 67°31'N, 167°12'W coll. Spark. 27 fm = 49 m depth, 19/8/1959. Gear dredge. From coelenteron of *Haliactis arctica* T. Bowman Acc.No.234238.

Additional material. male, female on 2 slides, both 3 mm.

Type locality. Chukchi Sea, Arctic. From coelenteron of *Haliactis arctica.*

Etymology. the epitheton should remind on the shape of the propodus Gn 2, which looks somewhat like a small fist, in Latin „pugilla"; it is used as noun in apposition.

Description.

Length 3 mm.

Head. Eyes round, normal. Mouthparts: Md with very short palp, length about half of width of incisor. Mx 1

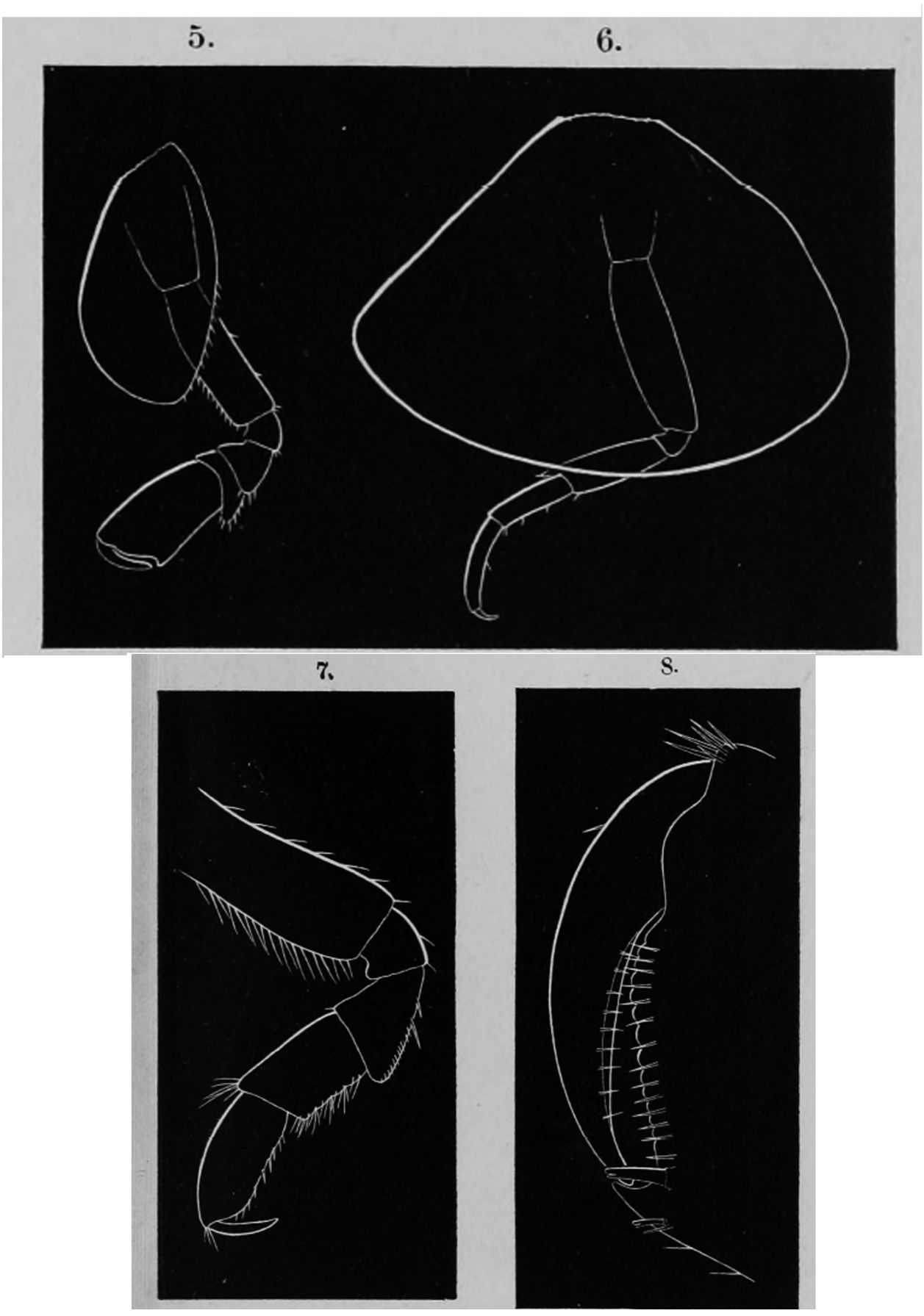

Figure 11. *Stenula peltata* (Smith, 1872): original illustrations of **5** gnathopod 2; **6** ? peraeopod 4; **7** gnathopod 1; **8** dactylus and propodus of gnathopod 2 distally.

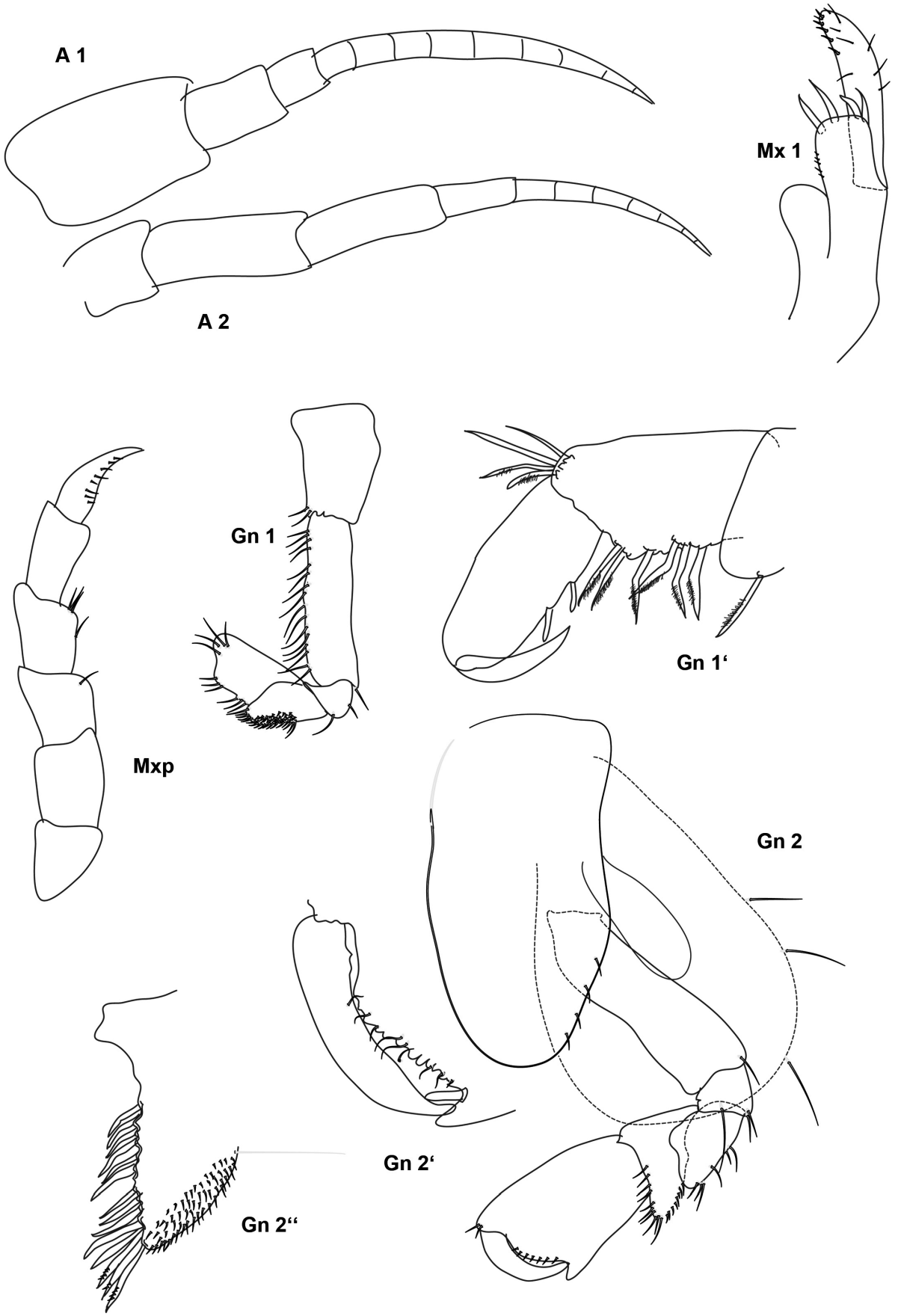

Figure 12. *Stenula peltata* (Smith, 1872): illustration of the single type specimen; **A 1, 2** antenna 1, 2; **Mx 1** maxilla 1; **Mxp** maxilliped; **Gn 1** gnathopod 1 without propodus and dactylus; **Gn 1'** dactylus, propodus and carpus enlarged; **Gn 2** gnathopod 2; **Gn 2'** dactylus and propodus enlarged; **Gn 2''** gnathopod 2 tip of carpus enlarged.

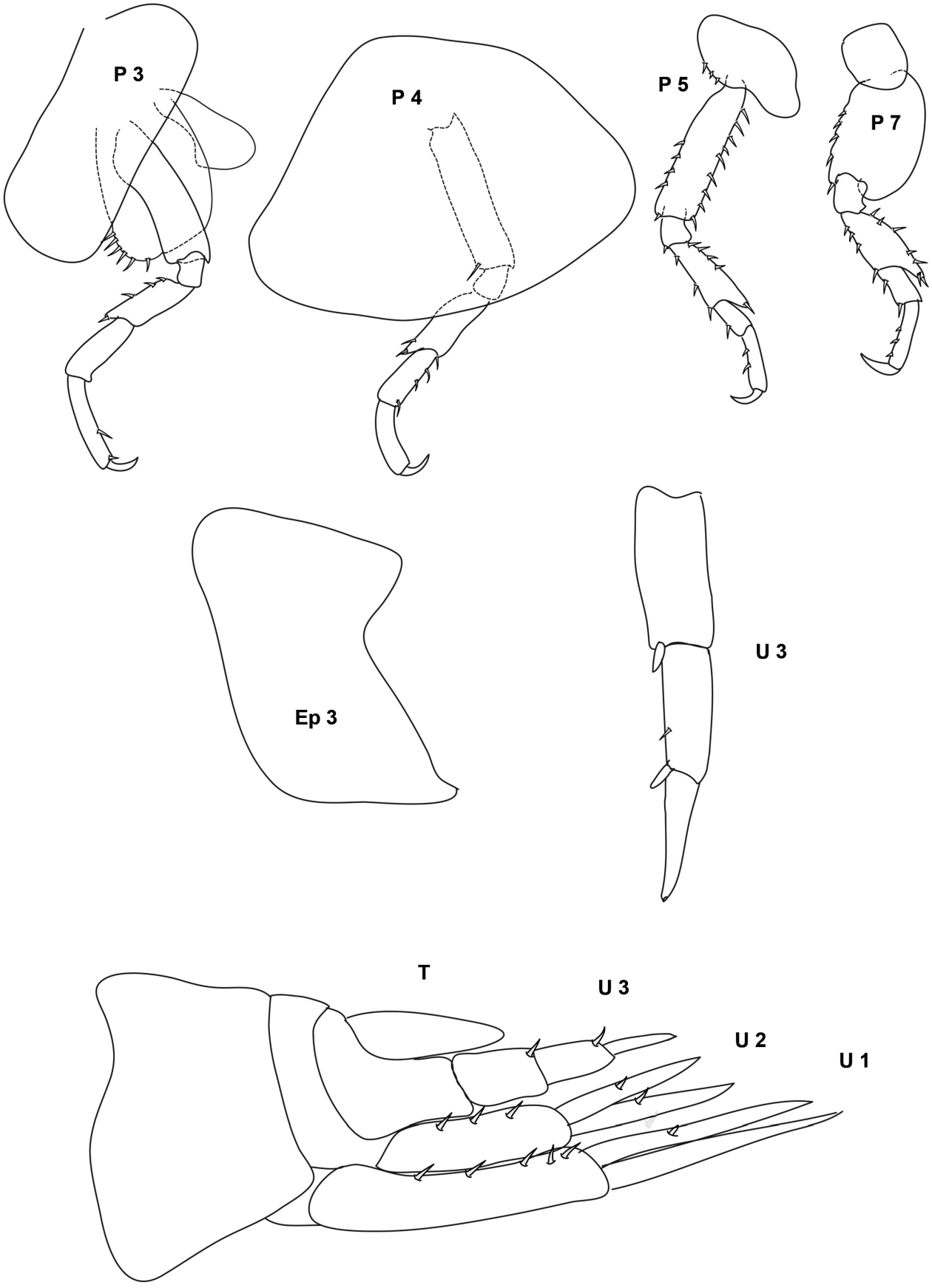

Figure 13. *Stenula peltata* (Smith, 1872): illustration of the single type specimen; **P 3, 4 5, 7** peraeopod 3, 4, 5, 7; **Ep 3** third epimeral plate; **U 1, 2, 3** uropod 1, 2, 3; **T** telson.

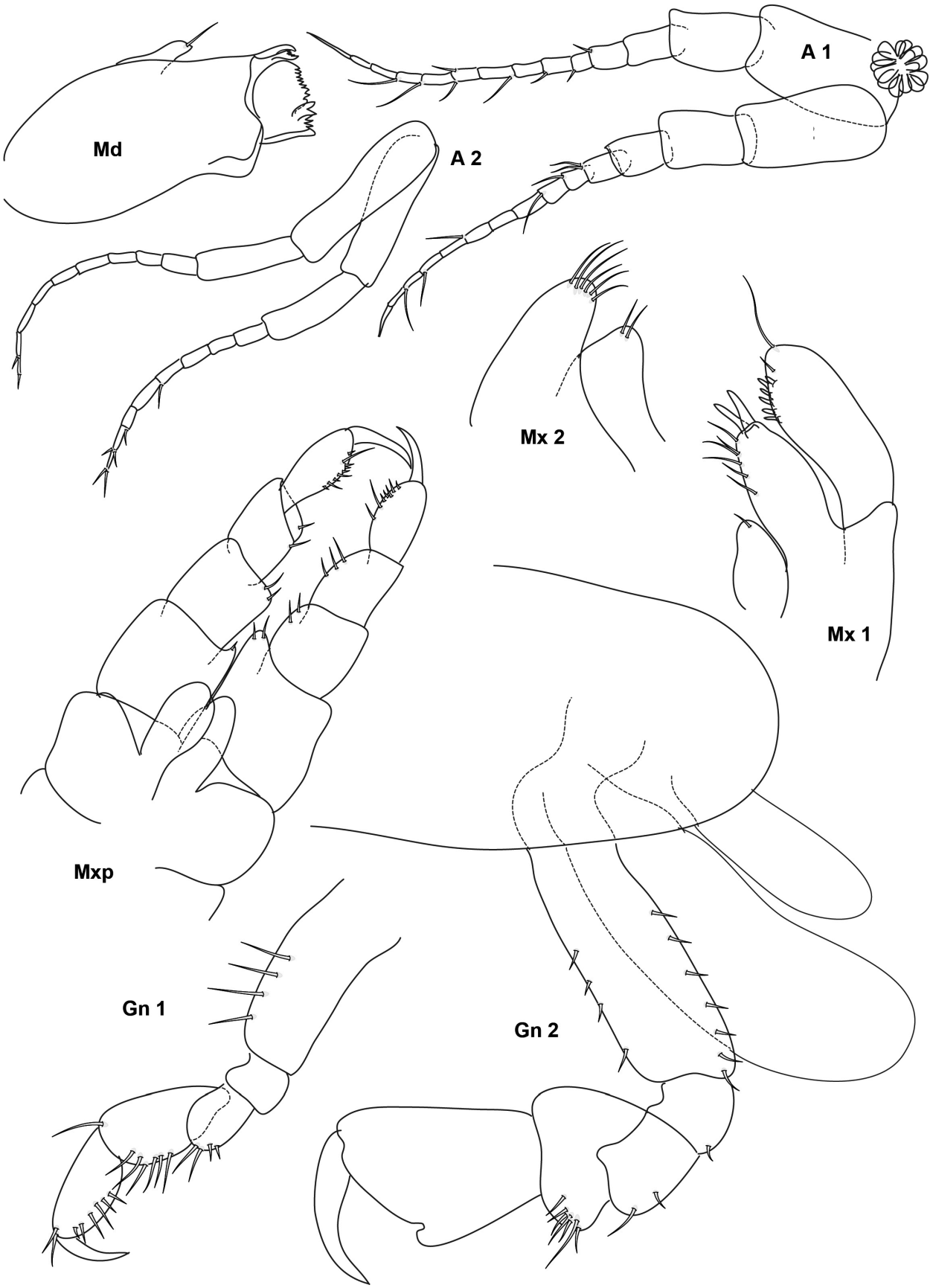

Figure 14. *Stenula pugilla* sp. n. female 3 mm: **A 1, 2** antenna 1, 2; **Md** mandible; **Mx 1, 2** maxilla 1, 2; **Mxp** maxilliped; **Gn 1, 2** gnathopod 1, 2.

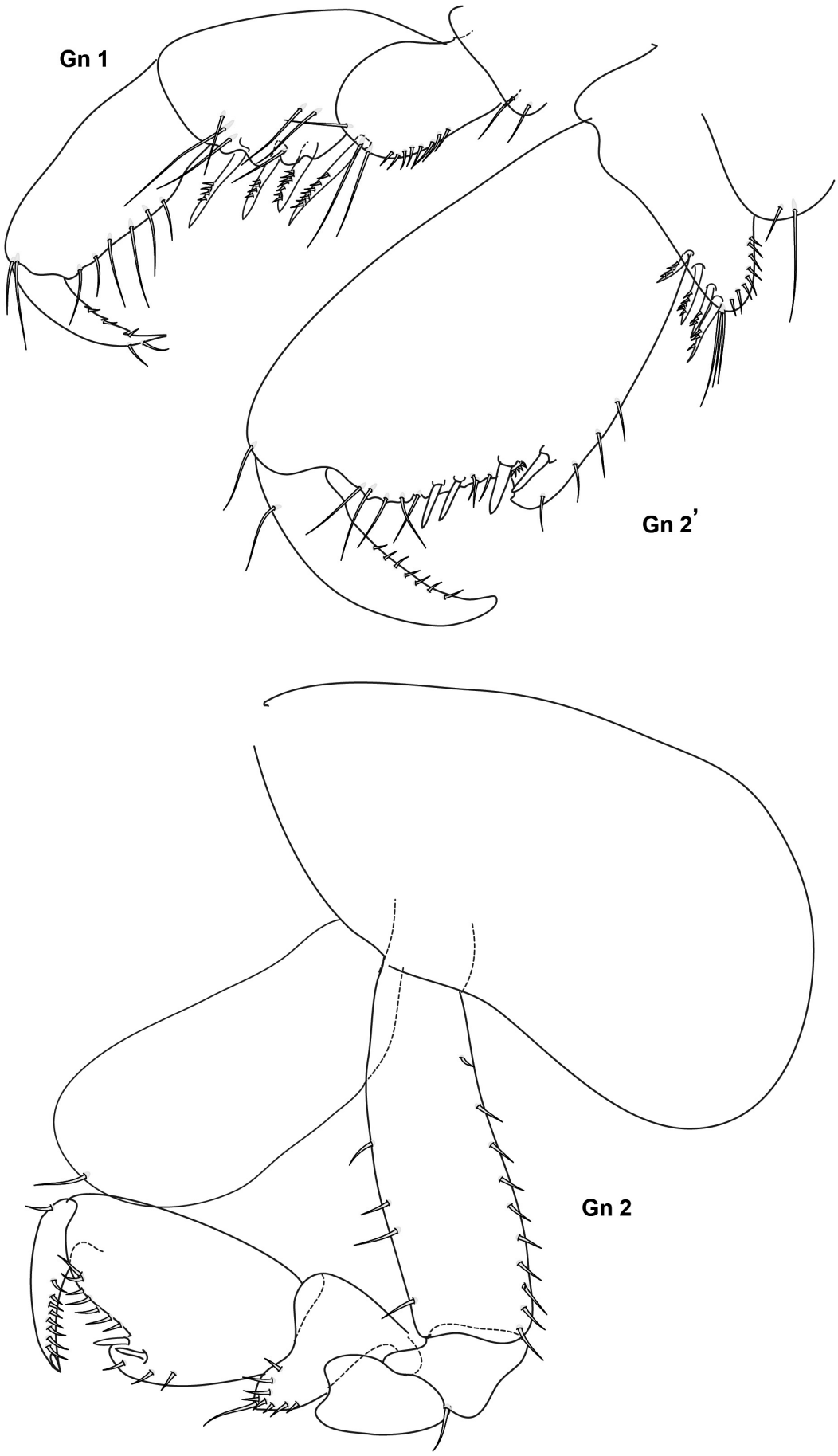

Figure 15. *Stenula pugilla* sp. n. female 3 mm: **Gn 1** gnathopod 1 distal arts; **Gn 2** gnathopod 2; **Gn 2'** gnathopod 2 distally enlarged.

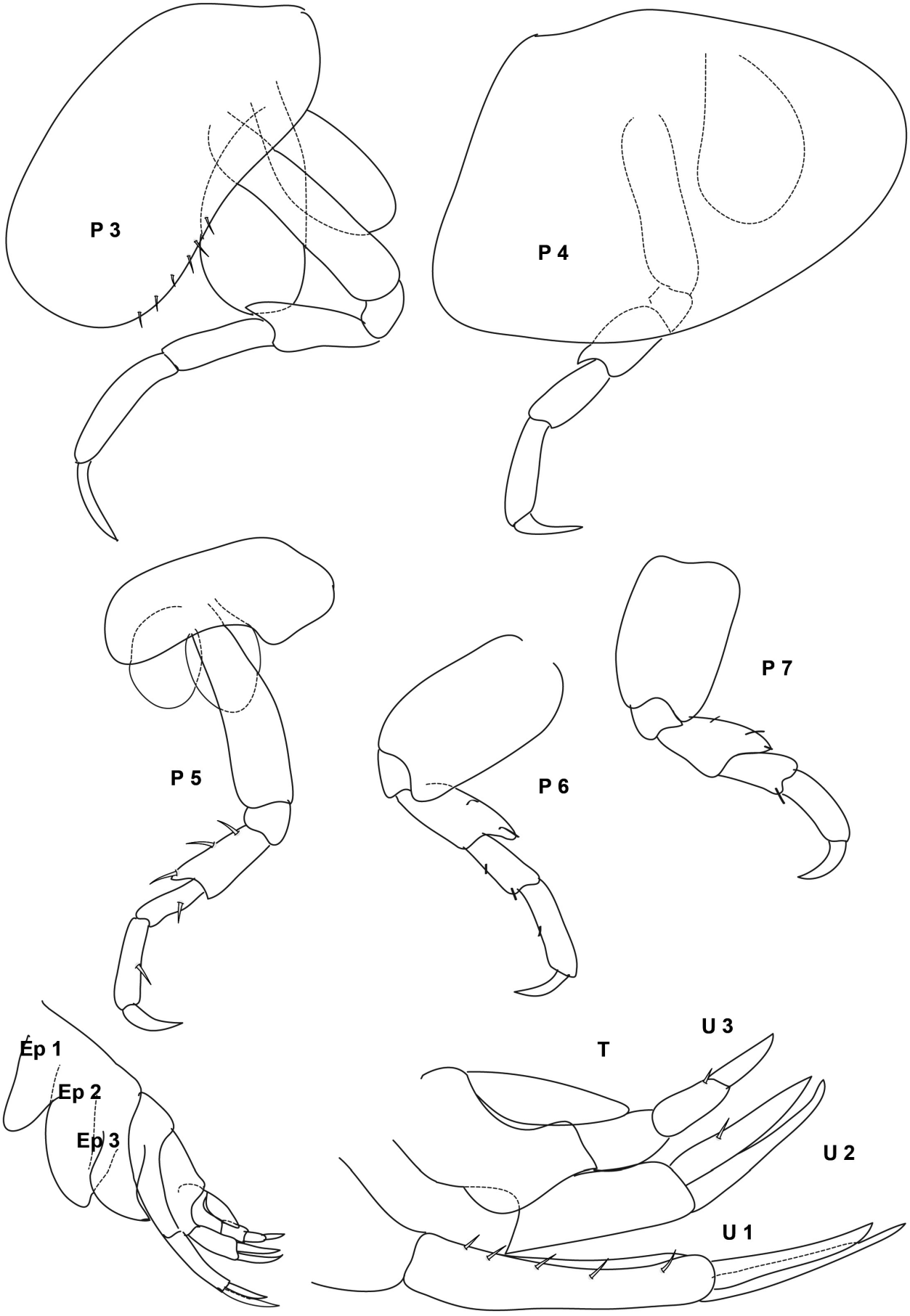

Figure 16. *Stenula pugilla* sp. n. female 3 mm: **P 3–7** peraeopod 3–7; **Ep 1–3** epimeral plate 1–3; **U 1–3** uropod 1–3; **T** telson.

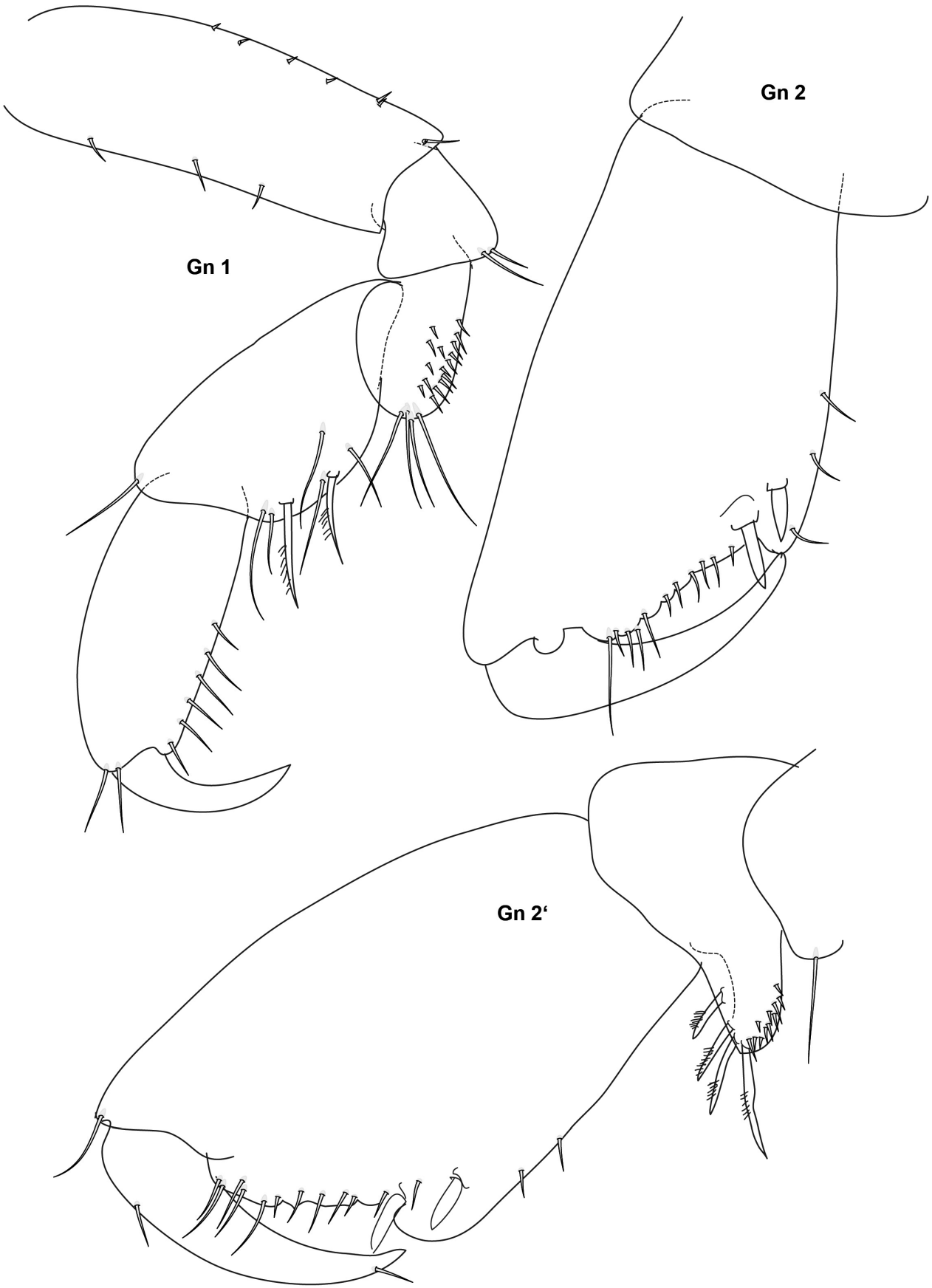

Figure 17. *Stenula pugilla* sp. n. male 3 mm: **Gn 1** gnathopod 1; **Gn 2, Gn 2’** gnathopod 2 from both sides.

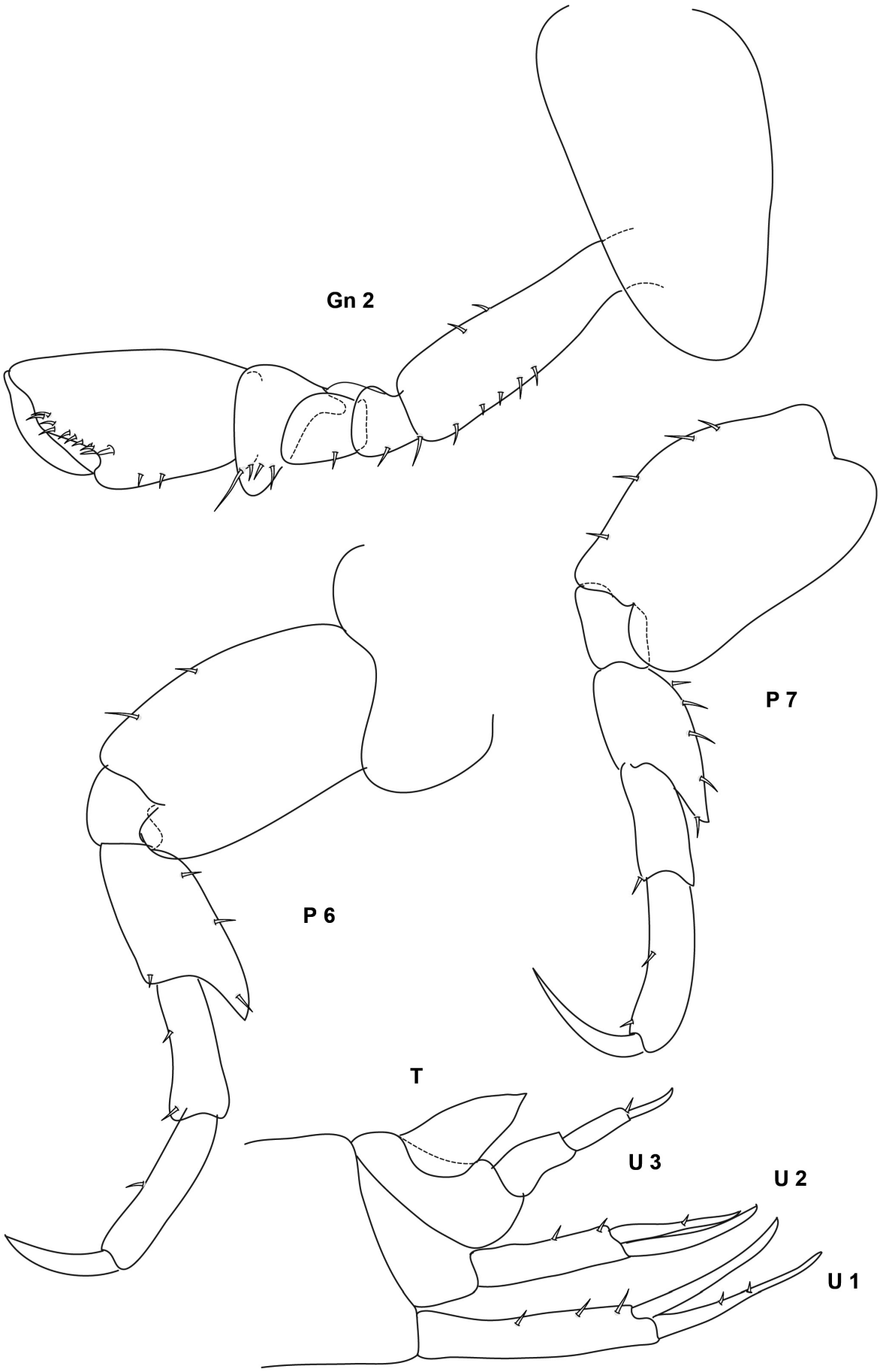

Figure 18. *Stenula pugilla* sp. n. male 3 mm: **Gn 2** gnathopod 2; **P 6, 7** peraeopod 6, 7; **U 1–3** uropod 1–3; **T** telson.

palp with one art, Mx 2 plates in tandem – position. Antennae: subequal, A 1 and A 2 flagellum about 10–12 arts. Mxp length of inner plate about half length of ischium, outer plate about 1/3–1/2 of merus.

Peraeon. Gn 1 basis on anterior margin setose, merus with short stiff setae, carpus with long setae and pectinate spines, propodus hind margin setose, somewhat rounded to nearly straight.

Cx 2 tongue-shaped. Gn 2 male and female basis on both margins beset with setae; merus rectangular, naked, carpus triangular, with stiff setae posterodistally, propodus medially widest with setose palm, defined by thumb-shaped protrusion.

Peraeopods: Cx 3 narrow, distally rounded, posteriorly with some setae; Cx 4 distally about 3× wider than Cx 3. P 3 dactylus clearly longer than in other peraeopods; P 3–7 merus somewhat widened and not much lengthened; P 6, 7 basis widened, with parallel margins.

Pleon. U 1 peduncle spinose, > slightly unequal rami; U 2 rami subequal; U 3 peduncle = ramus art 1 = ramus art 2.

Telson naked, triangular.

Female: subsimilar to male.

Remarks. The note ‚from the coelenteron of *Haliactis*' on the label of this sample may as well just have meant that the sea anemones had contracted on collection.

Discussion. Within the above discussed criteria of dividing *Stenula* species into groups, the new species belongs to the majority having Gn 1 propodus subequal to carpus (together with *S. solsbergi*, see below, here transferred to *Stenula*) and to the few members having a very short stump of mandible palp. The shape of Gn 2 palm male and female defined by a thumb-like hump is unique and quite helpful in identifying this species.

Stenula solsbergi (Schneider, 1884)

Figures 19, 20

Metopa solsbergi Schneider, 1884: 71; Sars 1892: 266, t. 94; Lincoln 1979: 186, fig. 84.

Material examined. one specimen, 3 mm, from the vicinity of Tromsø, N Norway (without date), collected together with *Chlamys*. The material was dredged in an area with much *Metridium*.

Type locality. Malangenfjord, Norway; 18 m depth.

Vader 1983 reported already *Metopa solsbergi* from the North Atlantic: Elmhirst 1925 found this species present on *Metridium senile* L. on pier piling in western Scotland, Fenwick and Steele 1983 off the coast of Newfoundland, Canada, again on *Metridium*.

This seems to be the very first time that the mouthparts were checked, and a reduced, uniarticulate mandibular palp could be illustrated, moving also this species to *Stenula*.

At the end of our study, we now know 16 members of the genus *Stenula*, as *S. invalida*, *S. solsbergi* and *S. pugilla* sp. n. are added, *S. arctica* given in synonymy with *S. nordmanni*, *S. latipes* revived and *S. rubrovittata* put back into *Metopa*:

S. alexanderi Tzvetkova & Golikov, 1990; Siberia
S. angusta (Shoemaker, 1955); Alaska, N Pacific
S. bassarginensis (Gurjanova, 1948); Arctic
S. beringiensis (Gurjanova, 1948); Bering Sea, N Pacific
S. derjugini (Gurjanova, 1948); Bering Sea, N Pacific
S. incola J.L. Barnard, 1969; California, Pacific
S. invalida (Sars, 1892); Atlantic
S. latipes (Chevreux & Fage, 1925) (type); Atlantic
S. modosa J.L. Barnard, 1962; California, Pacific
S. nordmanni (Stephensen, 1931); Greenland, ?SW-North Sea (fide Schellenberg 1942: 120) ?
(syn. with *S. arctica* (Gurjanova, 1951); Arctic)
?*S. peltata* (Smith, 1872); Atlantic (generic allocation doubtful)
S. pugilla sp. n.; Chukchi Sea, Alaska
S. ratmanovi (Gurjanova, 1948) (could be junior synonym of *S. peltata*)
S. serripes (Gurjanova, 1955); Kurile Isl., NE Pacific
S. solsbergi (Schneider, 1884); N. Norway, N. Atlantic
S. ussuriensis (Gurjanova, 1948); Japan Sea, NE Pacific

Key to world *Stenula* s. l.

The amphipod genus *Stenula* is probably not a monophyletic entity (cf. Tandberg and Vader 2011, this paper), and it is at present not possible to decide which taxa belong to it. In this key we have therefore cast our nets widely, and we include all species in the *Metopa-Stenula* complex with a uniarticulate mandible palp. This palp is very short in what we might call ‚typical *Stenula*', a bit longer, but still shorter than the incisor of the mandible, in a number of other species, also traditionally placed in *Stenula*, and still a bit longer, but clearly uniarticulate, in a few *Metopa* species: *M. hearni*, *M. palmata* and *M. sinuata*. Just's (1980) „*Stenula* sp." is in our opinion identical with *M. sinuata*, as that author himself already suspected.

The task has been made more difficult by several factors: many species have only been partly illustrated, and at least for the species *S. angusta*, *S. invalida*, *S. modosa* and ?*S. peltata*, as well as possibly some of Gurjanova's species, males are still unknown.

We treat here the 16 *Stenula* species mentioned above, plus three species which are closely related, but until now still left unchanged in *Metopa*:

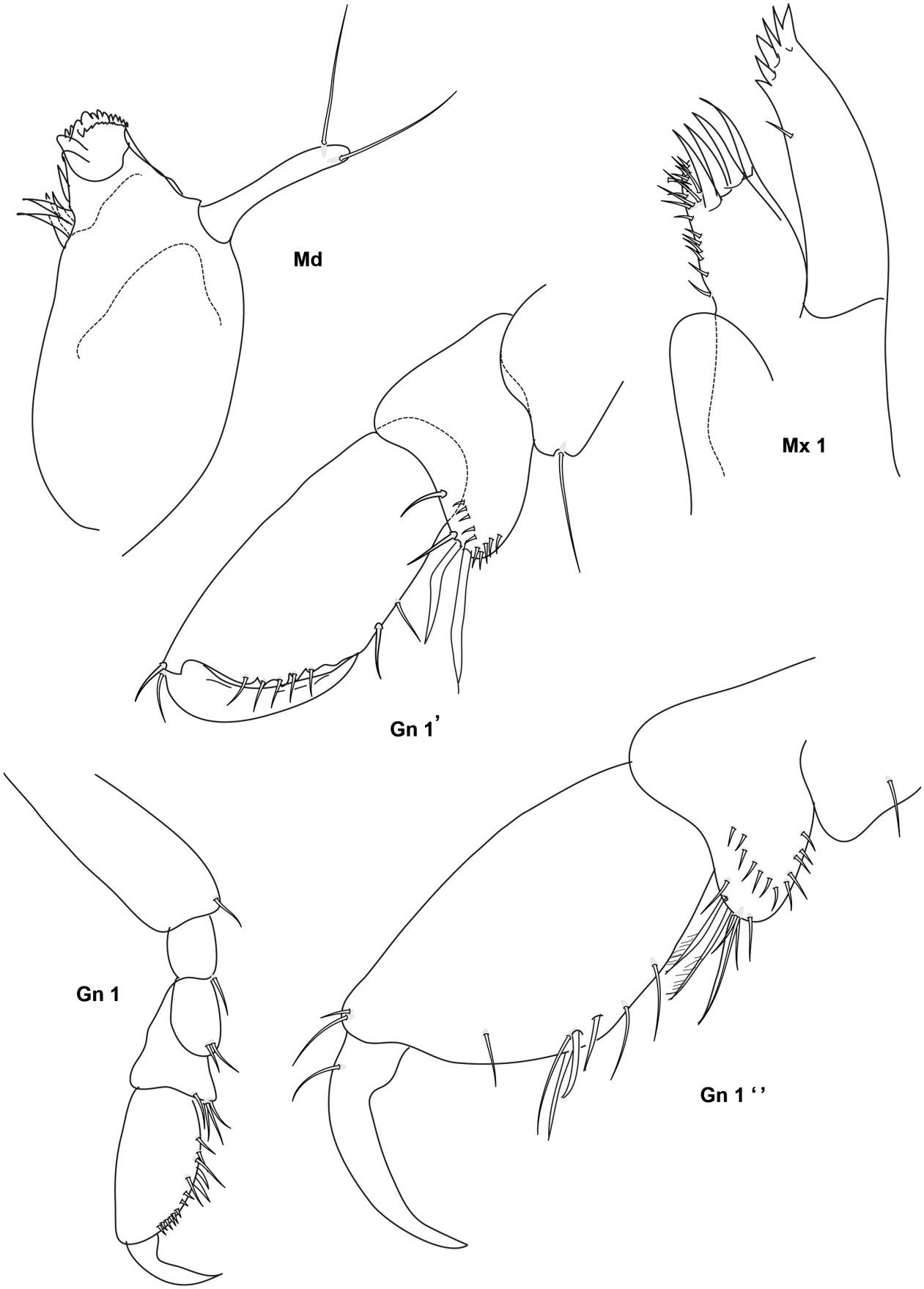

Figure 19. *Stenula solsbergi* (Schneider, 1884): **Md** mandible; **Mx 1** maxilla 1; **Gn 1** gnathopod 1; **Gn 1’, Gn 1 ‘’** gnathopod 1 right and left distally enlarged.

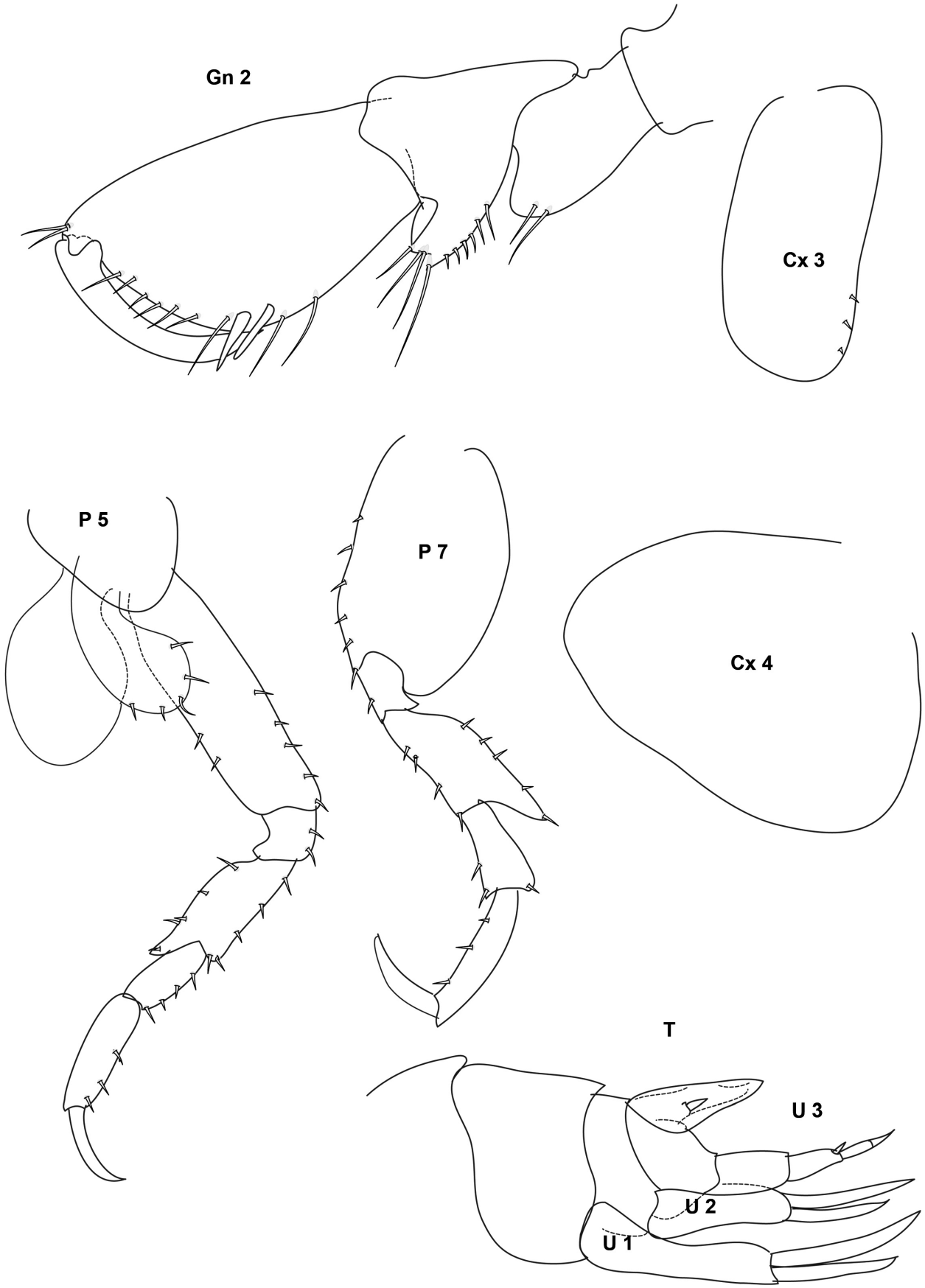

Figure 20. *Stenula solsbergi* (Schneider, 1884): **Gn 2** gnathopod 2; **Cx 3, 4** coxa 3, 4; **P 5, 7** peraeopod 5, 7; **U 1–3** uropod 1–3; **T** telson.

1 Coxa 4 distal margin clearly sinuous; N. Norway, 4 mm ..... *M. sinuata* Sars, 1892
– Coxa 4 distal margin regularly convex or almost straight 2
2 Gn 1 propodus and carpus very long and slender, dactylus broad and heavily setose; Gn 2 rectipalmate 3
– Gnathopods not as above 4
3 Gn 1 propodus < carpus, palm concave, dactylus length to width > 2; N. Norway, 5 mm..... *M. palmata* Sars, 1892 (see note 1)
– Gn 1 propodus > carpus, palm convex, dactylus length to width = 3:2; Laptev Sea, 3.8 mm..... *S. alexanderi* Tzvetkova & Golikov, 1990 (see note 2)
4 P 6 –7 basis and merus posteriorly serrated, hind margin of basis proximally with acute tooth; Kurile Islands, NE Pacific, 7 mm..... *S. serripes* (Gurjanova, 1955)
– P 6 –7 basis not serrated nor with tooth 5
5 Gn 2 propodus in male with deep U-shaped excavation 6
– Gn 2 propodus in male not with deep U-shaped excavation 7
6 Gn 2 propodus palm in male semicircularly excavated near distal corner, rest of palm much longer than width of excavation; Japan Sea, 4 mm ..... *S. ussuriensis* (Gurjanova, 1948)
– Gn 2 propodus palm in male deeply and irregularly excavated, rest of palm shorter than width of excavation. Japan Sea, 5 mm..... *S. bassarginensis* (Gurjanova, 1948)
7 Gn 2 propodus male palm clearly irregular, defined by strong tooth..... 8
– Gn 2 propodus in male smooth or slightly crenulate, convex or straight 9
8 Telson with 3 pairs of spines; Kamchatka, NE. Pacific, 3.5 mm..... *S. beringiensis* (Gurjanova, 1948)
– Telson naked or with small setules; California, 2 mm..... *S. incola* Barnard, 1969
9 Gn 2 propodus palmar corner prominent, shaped like a finger-tip; Chukchi Sea, 3 mm ..... *S. pugilla* Krapp-Schickel & Vader, 2015
– Gn 2 propodus palmar corner blunt or with acute tooth 10
10 Gn 1 carpus unusually long, up to 3 × longer than wide; eyes very large..... 11
– Gn 1 carpus clearly not as long; eyes normal 12
11 Gn 1 dactylus not reaching half length of propodus; A1 clearly shorter than A2; P 6–7 basis with rounded hind margin; W. Greenland, 5 mm ..... *S. nordmanni* (Stephensen, 1931) (= *S. arctica* (Gurjanova , 1951) (see note 3)
– Gn 1 dactylus reaching half length of propodus. A1 and 2 subequal; P 6–7 basis with straight hind margin; California, 2 mm..... *S. modosa* Barnard, 1962
12 Telson with 2 pairs of spines; Bering Sea, 4 mm. ..... *S. derjugini* (Gurjanova, 1948)
– Telson naked..... 13
13 Gn 1 carpus clearly shorter than propodus 14
– Gn 1 carpus subequal to propodus 15
14 P 7 very broad, posterior margin convex; mandiblepalp long, but unarticulated; Canada, 3–4 mm ..... *M. hearni* (Dunbar, 1954)
– P 7 basis slender, posterior margin rather straight; mandible-palp shor, Point Barrow, Alaska, 3 mm. ..... *S. angusta* (Shoemaker, 1955)
15 P 6–7 posterior tip on merus reaches halfway of less along carpus 16
– P 6–7 posterior lobe on merus reaches clearly further than halfways along carpus 17
16 Gn 2 propodus length:width = 3. P 7 basis broad, length = 2 width.; N. Norway, 4 mm..... *S. invalida* (Sars, 1892)
– Gn 2 propodus l:w = 2; P7 basis less wide, l< 2w, N. Norway, 7 mm..... *S. solsbergi* (Sp. Schneider, 1884)
17 We have been unable to find reliable differences between *Stenula latipes* (Chevreux & Fage, 1925), a species associated with hermit crabs in W. Europe, and *S. ratmanovi* (Gurjanova, 1948), an only partly described species from Kamchatka in the northern Pacific. Moreover, the illustrations of this latter species and those of *Stenothoe peltata* (Smith, 1874) from Georges Banks, NW Atlantic, are, as far as they go, practically identical.

Notes

1) This is the type species of Norman's (1902) short-lived genus *Sthenometopa*.
2) Probably not a *Stenula*, to be transferred to *Metopa* or *Sthenometopa*.
3) In transferring *Metopa nordmanni* to *Stenula*, Just (1980) apparently overlooked the fact that this species is clearly identical to *Stenula arctica* (Gurjanova, 1951).

Table 1. Associations of Stenothoidae with larger marine invertebrates.

Amphipods	Hosts	Reference
on Sea anemones		
Parametopella antholobae Krapp-Schickel & Vader, 2009	*Antholoba achates* (Drayton, 1846)	Krapp-Schickel and Vader 2009
Stenothoe barrowensis Shoemaker, 1955 Point Barrow, Alaska	unidentified	Shoemaker 1955; Vader 1983
Stenothoe bartholomea Krapp-Schickel & Vader, 2015 Florida Keys	*Bartholomea annulata* (Lesueur, 1817)	this paper, Vader 1983 (as *Stenothoe* sp. n.)
Stenothoe boloceropsis Krapp-Schickel, Häussermann & Vader, 2015 Chiloe Island, Chile	*Boloceropsis platei* McMurrich, 1904	Krapp-Schickel et al. 2015
Stenothoe brevicornis G. O. Sars, 1883 N. Norway, Newfoundland, Canada Stellwagen Bank, Canada	*Actinostola callosa* (Verrill, 1882) *Liponema multicornis* (Verrill, 1880)	Vader and Krapp-Schickel 1996 Fenwick and Steele 1983 Auster et al. 2011
Stenula pugilla Krapp-Schickel & Vader, 2015 Chukchi Sea	*Haliactis arctica* Carlgren, 1921	this paper (see also Vader 1983, as *Stenothoe* sp.)
Stenula solsbergi (Sp. Schneider, 1884) W.Scotland Newfoundland, Canada	*Metridium senile* (L., 1767)	(as *Metopa solsbergi*) Elmhirst 1925 Fenwick and Steele 1983
Other large coelenterates		
Metopa bruzelii (Goes, 1866) Newfoundland, Canada	*Primnoa resedaeformis* (Gunnerus, 1763)	Buhl-Mortensen and Mortensen 2004, 2005
Proboloides calcarata G. O. Sars, 1883 Newfoundland, Canada	*Primnoa resedaeformis*	Buhl-Mortensen and Mortensen 2004, 2005
Stenothoe minuta Holmes, 1905 N. Carolina, USA	*Astrangia danae* Milne-Edwards & Haime, 1849	Pearse 1947
Stenothoe valida Dana, 1853 Barbados, W.Indies	*Millepora complanata* Lamarck, 1816	Lewis 1992
Stenula nordmanni (Stephensen, 1931) Newfoundland, Canada	*Gersemia* sp.	Fenwick and Steele 1983 (as *S. arctica*)
Torometopa sp. Antarctic	*Primnoella* sp.	De Broyer et al. 2003?
Hydromedusae		
Metopa alderi (Sp. Bate, 1857) E. Scotland Norfolk, England Bohuslän, Sweden N Norway	*Tima bairdii* (Johnston, 1933)	Evans and Ashworth 1909 Hamond 1967 Dahl 1946; Hansson 1971 Vader 1972
Metopa borealis G. O. Sars, 1883 W. Scotland	*Phialidium* sp.	Elmhirst 1925
Ascidians		
Malvinometopa porcellana (K. H. Barnard, 1932) Falkland islands	'pharynx of large ascidian'	K.H.Barnard 1932 (as *Metopoides p.*)
Metopa groenlandica Hansen, 1888 Maine, USA W. Greenland	*Pyura ovifera* (Linnaeus, 1767) *Boltenia* sp., various ascidians	Blake 1929 (as *M. hirsutimana*) Stephensen and Thorson 1936 Tandberg and Vader 2009
Stenothoe eduardi Krapp-Schickel, 1976 Napoli, Mediterranean	on and in ascidians (*Microcosmos*)	Krapp-Schickel 1976
Stenothoe marina Sp. Bate, 1857 Norway	"inside ascidians"	G. O. Sars 1892, Vader 1984
Stenothoe minuta Holmes, 1905 N. Carolina W. France	*Styela plicata* (Lesueur, 1823)	Pearse 1947 Pirlot 1933 Toulmond and Truchot 1964) (as *Microstenothoe ascidiae* Pirlot)
Stenothoe valida Dana, 1853 E. Greenland	*Boltenia* sp.?	Stephensen and Thorson 1936
Torometopa paralellocheir (Stebbing, 1888) Falkland Islands	'branchial sac of simple ascidian'	Stebbing 1920 (as *Metopoides* p.)
Bivalves		
Metopa alderi (Sp. Bate, 1857) Svalbard	*Musculus discors* (Linnaeus, 1767), *M. niger* (JE Gray, 1824)	Tandberg et al. 2010

Amphipods	Hosts	Reference
Metopa glacialis (Krøyer, 1842) N. Brunswick, Canada Bear Island Svalbard Korea W. Greenland	*Musculus discors* (Linnaeus, 1767) *M. koreanus* Ockelmann, 1980 *M. laevigatus* (JE Gray, 1824)	Shoemaker 1955 Vader and Beehler 1983 Tandberg, Vader and Berge 2010 Ockelmann 1980 Just 1983
Metopa groenlandica Hansen, 1888, E. Greenland	*Pandora glacialis* Leach, 1819	Stephensen and Thorson 1936
Hermit crabs		
Metopa rubrovittata G. O. Sars, 1883 N.W. Europe	*Pagurus bernhardus* Linnaeus, 1758	many authors
Metopelloides micropalpa Shoemaker, 1930 St Laurent estuary, Canada	*Pagurus pubescens* Krøyer, 1838	Besner 1976
M. paguri Marin & Sinelnikov, 2012 Russian coast Japan Sea	*Pagurus pectinatus* (Stimpson, 1858) & *Elassochirus cavimanus* (Miers, 1879)	Marin and Sinelnikov 2012
Stenula latipes (Chevreux & Fage, 1925) W. France Ireland England	*Pagurus bernhardus* (L., 1758)	Chevreux and Fage 1925, many later authors, ?Giard 1908 (as *Metopa rubrovittata*) McGrath 1978 Lincoln 1979
Spider crabs		
Stenothoe symbiotica Shoemaker, 1956 Florida, USA Florida, USA	'large spider crab' *Stenocionops spinimana* (Rathbun, 1892)	Shoemaker 1956 Thomas and Cairns 1984

A short survey of associations between stenothoids and larger marine invertebrates (Table 1).

Table 1 lists the associations between stenothoid amphipods and other marine invertebrates known to us, with the exception of those reported from sponges, hydroids or bryozoans. These latter are excluded because in most cases it is unclear what the exact niche of the amphipods is: usually the labels say only ‚among hydroids and bryozoans' or ‚found together with sponges'. Among the others the associates of various large coelenterates and also those found in ascidians generally do not seem to be obligate symbionts. Although now and then found in large numbers (e.g. *Metopa bruzelii* and *Proboloides calcarata* on gorgonians), the same species are also regularly found apparently free-living.

The situation is different for the associates of mollusks (all *Metopa* species) and those on sea anemones (mostly *Stenothoe* and *Stenula* species). Practically all these species appear to be obligate associates of only a single or in some cases a few hosts, and they have never been found free-living (for a possible exception see Blain and Gagnon 2014, who claim to have found numbers of *Stenothoe brevicornis* on the alga *Desmarestia viridis*). The amphipod associates of sea anemones always live on the column of the host or among the tentacles (Elmhirst 1925, Krapp-Schickel and Vader 2009, Krapp-Schickel et al. 2015; Vader 1983, Vader and Krapp-Schickel 1996), with the possible exception of *Stenula pugilla*, found according to the label ‚in the coelenteron of *Haliactis arctica*' (this paper). At least *Stenothoe brevicornis*, somewhat surprisingly, feeds to a large extent on host tissue (Moore et al. 1994), contrary to earlier assumptions (Vader 1983). Large numbers of amphipods are usually found on a single host, and ovigerous females are commonly present. Interestingly, sexual dimorphism is in most cases much less developed in the associates of sea anemones than in related free living stenothoids (see also Vader 1983).

In contradistinction to the case with sea anemones, all the stenothoid associates of bivalve mollusks are *Metopa* species. Once more the associations seem to be obligate ones, the amphipods are rarely found free-living (and never leave their hosts in laboratory observations) and they are confined to a single host or, in the case of *Metopa glacialis*, to a series of closely related host species. A partial exception is *Metopa alderi*, usually an associate of large hydroids and hydromedusae, that recently was found in *Musculus* spp in N. Spitsbergen (Tandberg et al. 2010b). The data on mollusk-associated stenothoids have recently been reviewed by Tandberg et al. (2010a): the amphipods live inside the host and feed on that part of the ingested material that the host does not consume itself. In addition, the stenothoid symbionts of bivalves seem to exhibit territoriality as well as extended parental care: invariably only a single pair of adults is present within a single host, often together with several cohorts of juveniles.

In the case of the single, quite aberrant *Stenothoe* species that lives on a spider crab, *S. symbiotica* Shoemaker, 1956, its biology is as yet completely unknown, but also this association appears to be an obligate and probably species-specific one; the species has never been collected elsewhere and it has clearly prehensile peraeopods. Also the amphipod associates of hermit crabs and their tenanted mollusk shells are of unknown biology. *Metopelloides paguri* Marin & Sinelnikov, 2012 and *M. micropalpa* (Shoemaker, 1930) have slightly but clearly prehensile posterior peraeopods, and may therefore well be direct associates of their host hermit crabs (Vader 1983b). But the somewhat mysterious pair of *Metopa rubrovittata* Sars and *Stenula latipes* (Chevreux & Fage) do not have prehensile peraeopods (even though the posterior legs

carry maybe more spines than is usual in *Metopa* species?) and many authors have associated these species primarily with the *Hydractinia*-cover of the tenanted gastropod shells rather than with the hermit crabs themselves, although without any proof. These two species occupy the same niche, and slightly different, but possibly overlapping distributions, and have the exactly identical, quite special coloration pattern, but according to present classifications they have to be placed in different genera. Also the species associated with hermit crabs seem to be largely obligate symbionts, although possibly occurring on a larger range of hosts.

Acknowledgements

We are grateful to Dr. Chad Walter of the Smithsonian Institution, Washington DC, who after thirty years refound the unidentified sample that contained *Stenula pugilla*, and lent it to us. We thank prof. R.T. Barrett, Tromsø for linguistic assistance, as well as Dr. Oliver Coleman, Naturkunde Museum Berlin, for constructive criticism.

References

Auster PJ, Heinonen KB, Watling L, Parrish-Kuhn C, Heupel E, Lindholm J (2011) A rare deepwater anemone and its associates in the Stellwagen Bank National Marine Sanctuary (Gulf of Maine, northwest Atlantic). Marine Biodiversity Records 4: 19. doi: 10.1017/s1755267211000200

Barnard JL (1962) Benthic marine Amphipoda of southern California: 3) Families Amphilochidae, Leucothoidae, Stenothoidae, Argissidae, Hyalidae. Pacific Naturalist 3(1/2/3): 1–163.

Barnard JL (1966) Benthic Amphipoda of Monterey Bay, California. Proceedings of the US National Museum 119(3541): 1–41. doi: 10.5479/si.00963801.119-3541.1

Barnard JL (1969) Gammaridean Amphipoda of the Rocky Intertidal of California: Monterey Bay to La Jolla. US National Museum Bull. 258: 1–230.

Barnard JL (1972) Gammaridean Amphipoda of Australia, Part I. Smithsonian Contributions to Zoology 103: 1–333.

Barnard JL (1974) Gammaridean Amphipoda of Australia, Part 2. Smithsonian Contributions to Zoology 139: 1–148.

Barnard KH (1916) Contributions to the Crustacean Fauna of South Africa. 5. The Amphipoda. Annals of the South African Museum 15: 105–302. doi: 10.5962/bhl.title.10646

Barnard KH (1932) Amphipoda. Discovery Reports 5: 1–326.

Bate CS (1857) A synopsis of the British edriophthalmous Crustacea. Annals and Magazine of Natural History (ser 2) 19: 135–152.

Bellan-Santini D, Costello MJ (comps.) (2001) Amphipoda. In: Costello MJ, Emblow CS, White R (Eds) European Register of Marine Species. A check-list of the marine species in Europe and a bibliography of guides to their identification. Patrimoines naturels 50: 295–308.

Besner A (1976) Structure écologique annuelle des associations d'amphipodes gammaridiens dans l'hyperbenthos et l'endobenthos d'un fond vaseux circalittoral de l'estuaire maritime du Saint Laurent en 1970 et 1971. PhD Thesis, Univ. of Montreal, Montreal, 119 pp.

Blain C, Gagnon P (2014) Canopy-forming seaweeds in urchin-dominated systems in eastern Canada: Structuring forces or simple prey for grazers? PLoS ONE 9(5): e98204. doi: 10.1371/journal.pone.0098204

Blake CH (1929) Crustacea. New Crustacea from the Mount Desert region. Biological Survey of the Mount Desert Region 3: 8–34.

Boeck A (1871) Crustacea Amphipoda Borealia et Arctica. Forhandlinger i Videnskabs-Selkabet i Christiania 1870: 83–280.

Brüggen E von der (1907) Amphipoda. Zoologische Ergebnisse der russischen Expeditionen nach Spitzbergen. Annuaire du Musee Zoologique Academie Imperiale des Sciences de St. Petersbourg 11: 214–244.

Brunel P, Bosse L, Lamarche G (1998) Catalogue of the marine invertebrates of the estuary and Gulf of St. Lawrence. Canadian Special Publication of Fisheries and Aquatic Sciences, 126–405.

Buhl-Mortensen L, Mortensen PB (2004) Crustaceans associated with the deep-water gorgonian corals *Paragorgia arborea* (L., 1758) and *Primnoa resedaeformis* (Gunnerus, 1763). Journal of Natural History 38: 1233–1247. doi: 10.1080/0022293031000155205

Buhl-Mortensen L, Mortensen PB (2005) Distribution and diversity of species associated with deep-sea gorgonian corals off Atlantic Canada. In: Freiwald A, Roberts JM (Eds) Cold-water corals and ecosystems. Springer Verlag, Berlin-Heidelberg, 849–879. doi: 10.1007/3-540-27673-4_44

Chevreux E (1908) Sur les commensaux de Bernard l'Hermite. Bulletin de la Société Zoologique de France 14: 183–189.

Chevreux E, Fage L (1925) Amphipodes. Faune de France 9: 1–488.

Chilton C (1883) XIV – Addition to the Sessile-eyed Crustacea of New Zealand. Transactions of the NZ Institute 15: 249–255.

Chilton C (1884) Notes on a few Australian Edriophthalmata. Proceedings of the Linnean Society of New South Wales 9(4): 1–10.

Dahl E (1946) Notes on some amphipods from the Gullmar Fiord. Arkiv for Zoologi 38A(8): 1–8.

Dana JD (1852) Conspectus crustaceorum quae in orbis terrarum circumnavigatione, Carolo Wilkes e classe Rei publicae Faederatae Duce, lexit et descripsit Jacobis D. Dana. Pars III [Amphipoda Nr 1]. Proceedings of the American Academy of Arts and Sciences 2: 201–220.

De Broyer C, Chapelle G, Duchesne PA, Munn R, Nyssen F, Scailteur Y, Van Roozendael F, Dauby P (2003) Structural and ecofunctional biodiversity of the amphipod crustacean benthic taxocoenoses in the Southern Ocean. Marine Biota and Global Change 1: 1– 51.

Della Valle A (1893) Gammarini. Fauna und Flora des Golfes von Neapel und der angrenzenden Meeresgebiete, 948 pp.

Dunbar MJ (1954) The amphipod Crustacea of Ungava Bay, Canadian eastern Arctic. Journal of the Fisheries Research Board of Canada 11: 709–798. doi: 10.1139/f54-044

Elmhirst R (1925) I. Associations between the amphipod genus *Metopa* and coelenterates. Part I. Scottish Naturalist 155: 149–150.

Evans W, Ashworth JW (1909) Some medusae and ctenophores from the Firth of Forth. Proceedings of the Royal Physical Society of Edinburgh 17: 300–311.

Fenwick GD, Steele DH (1983) Amphipods of Placentia Bay, Newfoundland. Memorial University Newfoundland, Occasional Papers in Biology 7: 1–22.

Giard A (1908) Un amphipode mimétique des hydraires: *Metopa rubrovittata* G. O. Sars. Feuilles des Jeunes Naturalistes 31: 214.

Goës A (1866) Crustacea Amphipoda Maris Spetsbergiam alluentis, cum speciebus aliis arcticis enumerat. Ofversigt av Kongelige Vetenskabs Akademiens Forhandlingar 1865: 517–536.

Gosner KL (1971) Guide to identification of marine and estuarine invertebrates: Cape Hatteras to the Bay of Fundy. John Wiley & Sons, 693 pp.

Gurjanova E (1933) Zur Amphipodenfauna des Karischen Meeres. Zoologischer Anzeiger 103: 119–128.

Gurjanova E (1938) (Amphipoda, Gammaroidea of Siaukhu Bay and Sudzukhe Bay (Japan Sea)). Reports of the Japan Sea Hydrobiological Expedition of the Zoological Institute of the Academy of Sciences USSR in 1934, 1: 241–404. [In Russian]

Gurjanova E (1948) Amphipoda Tixogo Okeana II. Stenothoidae dal'Nevostochyx Morei, Notebook of the Academician Sergei Aleksevich Zernov (Hydrobiologist), 287–325.

Gurjanova E (1951) Amphipoda - Gammaridea. Akademii Nauk, Bokoplavy morej SSSR, Moscow, 1031 pp.

Gurjanova E (1952) Novye vidy bokoplavov (Amphipoda, Gammaridea) iz dal'nevostochnyx morei. Akademii Nauk SSSR. Trudy Zoologicheskogo Instituta 12: 171–195.

Gurjanova E (1955) Novye vidy bokoplavov (Amphipoda Gammaridea) iz severnoi chasti Tixogo (=Tikhogo) Okeana. Zoological Institute Ak. Nauk SSSR 18: 166–218.

Hamond R (1967) The Amphipoda of Norfolk. Cahiers de Biologie Marine 8: 113–152.

Hansen HJ (1888) Malacostraca marina Groenlandiae occidentalis. Oversigt over det vestlige Grønlands fauna af Malakostrake Havkrepsdyr. Videnskabelige Meddelelser fra Dansk Naturhistorisk Forening, Kjøbenhavn 1887: 5–226.

Hansson HG (1971) Några fynd av atlantiska faunaelement i Bohuslän efter höststormarna i 969. Fauna och Flora, Uppsala 66: 118–120.

Haswell WA (1879) On some additional new genera and species of amphipodous crustaceans. Proceedings of the Linnean Society New South Wales 4/5: 319–350.

Hoek PPC (1889) Crustacea Neerlandica. Tijdschrift der Nederlandsche Dierkundige Vereeniging ser. 2, 2: 170–234.

Just J (1980) Amphipoda (Crustacea) of the Thule area, northwest Greenland: faunistics and taxonomy. Meddelelser Om Grønland Bioscience 2: 1–61.

Just J (1983) *Anonyx affinis* (Crus., Amphipoda; Lysianassidae), commensal in the bivalve *Musculus laevigatus*, with notes on *Metopa glacialis* (Amphipoda: Stenothoidae). Astarte 12: 69–74.

Just J (2013) *Metopa gigas*, sp. n. from southern Greenland, a giant among congeners (Crustacea, Amphipoda. Stenothoidae). Zootaxa 3641(3): 289–295. doi: 10.11646/zootaxa.3641.3.8

Krapp-Schickel G (1976) Die Gattung *Stenothoe* (Crustacea; Amphipoda) im Mittelmeer. Bijdragen tot de Dierkunde 46: 1–34.

Krapp-Schickel T (2009) New and poorly described stenothoids (Crustacea, Amphipoda) from the Pacific Ocean. Memoirs of the Museum of Victoria 66: 95–116.

Krapp-Schickel T (2009) Stenothoidae. In: Lowry JK, Myers AA (Eds) Benthic Amphipoda (Crustacea: Peracarida) of the Great Barrier Reef, Australia. Zootaxa 2260: 872–879.

Krapp-Schickel T (2011) New antarctic stenothoids sensu lato (Amphipoda, Crustacea). European Journal of Taxonomy 1: 1–17. doi: 10.5852/ejt.2011.2

Krapp-Schickel T (2013) On the Austral-Antarctic stenothoids *Proboloides*, *Metopoides*, *Torometopa* and *Scaphodactylus* (Crustacea: Amphipoda). Part 2: group of *Proboloides*, *Scaphodactylus*, *Torometopa* with two new genera (Stenothoidae, Amphipoda). Zoosystematics and Evolution 86: 11–45.

Krapp-Schickel T (2015) Minute but constant morphological differences within members of Stenothoidae: The *Stenothoe gallensis* – group with four new members, keys to *Stenothoe* world-wide, a new species of *Parametopa* and *Sudanea* n. gen. (Crustacea, Amphipoda). Journal of Natural History. doi: 10.1080/00222933.2015.1021873

Krapp-Schickel T, Häussermann V, Vader W (2015) A new *Stenothoe* species (Crustacea: Amphipoda: Stenothoidae) living on *Boloceropsis platei* (Anthozoa: Actiniaria) from Chilean Patagonia. Helgoland Marine Research 69: 213–220.

Krapp-Schickel T, Vader W (2009) A new *Parametopella* species (Crustacea: Amphipoda: Stenothoidae) from *Antholoba achates* (Anthozoa: Actiniaria) from Coquimbo, Chile (with remarks on *Parametopa alaskensis* (Holmes)). Journal of the Marine Biological Association UK 89: 1281–1287. doi: 10.1017/S0025315409000484

Krøyer H (1842) Nye nordiske Slaegter og Arter af Amfipodernes Orden, henhørende til Familien *Gammarina*. (Foreløbigt Uddrag af et større Arbejde). Naturhistorisk Tidsskrift 4: 141–166.

Lesueur CA (1817) Observations on several species of the genus „*Actinia*"; illustrated by figures. Journal of Academy Sciences of Philadelphia 1: 149–154, 169–189.

Lewis JB (1992) Abundance, distribution and behavior of a commensal amphipod *Stenothoe valida* Dana on the hydrocoral *Millepora complanata* Lamarck. Bulletin of Marine Science 51: 245–249.

Liljeborg V (1851) Bidrag till Norra Rysslands och Norriges fauna, samlade under en vetenskaplig Resa i dessa Lander 1848, Kongliga Svenska Vetenskaps-Akademiens Handlingar (series 3) 2: 233–341.

Lincoln RJ (1979) British marine Amphipoda: Gammaridea. British Museum, London, 658 pp.

Lowry JK, Stoddart H (2003) Zoological catalogue of Australia 19.2B. Environment Australia, 373 pp.

Marin I, Sinelnikov S (2012) *Metopelloides paguri* sp. nov., a new species of symbiotic stenothoid amphipod (Crustacea: Amphipoda: Stenothoidae) associated with sublittoral hermit crabs from the Russian coasts of the Sea of Japan. Zootaxa 3244: 59–67.

McGinitie GE (1955) Distribution and ecology of the marine invertebrates of Point Barrow, Alaska. Smithsonian Miscellaneous Collections 139–9: 1–201.

McGrath D (1978) *Stenula latipes* (Chevreux et Fage) (Crustacea: Amphipoda) associated with the hermit crab *Pagurus bernhardus* (L.), new to the British fauna. Irish Naturalist Journal 19: 196–197.

Moore PG (1984) The fauna of the Clyde Sea area. Crustacea: Amphipoda. Occasional Publications 2: 1–84.

Moore PG, Rainbow PS, Vader W (1994) On the feeding and comparative biology of iron in coelenterate-associated gammaridean Amphipoda (Crustacea) from N.Norway. Journal of Experimental Marine Biology and Ecology 178: 205–231. doi: 10.1016/0022-0981(94)90037-X

Nebeski O (1881) Beitraege zur Kenntniss der Amphipoden der Adria. Arbeiten aus dem Zoologischen Institute der Universität Wien und der Zoologischen Station Triest 3(2): 1–52.

Ockelmann KW (1983) Descriptions of mytilid species and definition of the Dacrydiinae n. subfam. (Mytilacea-Bivalvia). Ophelia 22: 81–123. doi: 10.1080/00785326.1983.10427225

Oldevig H (1959) Arctic, subarctic and Scandinavian Amphipods in the collections of the Swedish Natural History Museum Stockholm. Meddelanden from Goteborgs Musei Zool. Avdelning, Vetenskaps-Vitterhets-Samhalles Handlingar (6B) 8(2): 5–132.

Pearse AS (1947) On the occurrence of ectoconsortes on marine animals at Beaufort, N. C. The Journal of Parasitology 33: 453–458. doi: 10.2307/3273324

Pirlot JM (1933a) Les Amphipodes de l'expedition du Siboga. Deuxieme partie. Les amphipodes gammarides II. – Les amphipodes de la mer profonde. 1. Siboga Expedition, Monographie 33c: 115–167.

Pirlot JM (1933b) Un nouvel amphipode ascidicole. Bulletin de l'Institut Océanographique 633: 1–6.

Reibisch J (1905) Faunistisch-biologische Untersuchungen über Amphipoden der Nordsee. Wissenschaftliche Meeresuntersuchungen, herausgegeben von der Kommission zur Untersuchung der deutschen Meere in Kiel und der Biologischen Anstalt auf Helgoland. Neue Folge 8: 147–236.

Sars GO (1879) Crustacea et Pycnogonida nova in itinere 2do et 3tio expeditionis Norvegicae anno 1877 & 78 collecta. (Prodromus descriptionis). Archiv for Mathematik og Naturvidenskab 4: 427–476.

Sars GO (1883) Oversigt af Norges Crustaceer med forelobige Bemaerkninger over de nye eller mindre bekjendte Arter. I. Forhandlinger Videnskaps-selskaps i Christiania 18: 124.

Sars GO (1890–1895) An account of the Crustacea of Norway. 1,2 vols. Alb. Cammermeyers Forlag, Christiania and Copenhagen, 1, 711 pp.

Schellenberg A (1942) Flohkrebse oder Amphipoda. Krebstiere oder Crustacea. In: Tierwelt Deutschlands und der angrenzenden Meeresteile. F. Dahl. Jena, Gustav Fischer 4: 252.

Schneider JS (1884) Undersøgelser af dyrelivet i de arktiske fjorde. II. Crustacea og Pycnogonida indsamlede i Kvaenangsfjorden 1881. Tromsø Museum Aarshefter 7: 47–134.

Sheard K (1937) A catalogue of Australian Gammaridea. Transactions and Proceedings of the Royal Society of South Australia 61: 17–29.

Shoemaker CR (1955) Amphipoda collected at the Arctic Laboratory, Office of Naval Research, Point Barrow, Alaska, by G.E. MacGinitie. Smithsonian Miscellaneous Collections 128(1): 1–78

Shoemaker CR (1956) A new genus and two new species of amphipods from Dry Tortugas, Florida. Journal of the Washington Academy of Sciences 46: 61–64.

Smith SI (1874) Notes on some of the species enumerated. In: Smith SI, Harger O (Eds) Report on the Dredging in the Region of St. George's Banks, in 1872. Transactions of the Connecticut Academy of Arts and Sciences 3: 1–57.

Stebbing TRR (1906) Amphipoda, I. Gammaridea. Das Tierreich 21: 1–806. [Abb. 1–127]

Stebbing TRR (1910) V. Amphipoda. Scientific results of the trawling expedition of H.M.C.S. „Thetis". Memoir Australian Museum 4(2): 565–658.

Stebbing TRR (1920) Crustacea from the Falkland Islands collected by Mr Rupert Vallentin, F. L. S. Part III. Proceedings of the Zoological Society of London (1919): 327–340.

Stephensen K (1929) Marine Crustacea Amphipoda. Zoology of the Faroes 23: 1–40.

Stephensen K (1931) The Danish Ingolf-Expedition III (11), Crustacea Malacostraca VII (Amphipoda III), 179–290.

Stephensen K (1938) Amphipoda, Tanaidacea and Pycnogonida. Senkkenbergiana 20(3/4): 236–264.

Stephensen K, Thorson G (1936) On the amphipod *Metopa groenlandica* H. J. Hansen found in the mantle cavity of the lamellibranchiate *Pandora glacialis* Leach in East Greenland. Meddelelser om Grønland 118–4: 1–7.

Tandberg AHS (2011) Studies on the amphipod genus *Metopa* (Stenothoidae): Taxonomy, Ecology, Phylogeny. A dissertation for the degree of Philosophiae Doctor, University of Tromsø, 48 + 36 + 25+ 94 + 2 + 11 + 36 pp.

Tandberg AHS, Schander C, Pleijel F (2010) First record of the association between the amphipod *Metopa alderi* and the bivalve *Musculus*. Marine Biodiversity Records 3, e 5, 2 pp. doi: 10.1007/s00300-010-0833-9

Tandberg AHS, Vader W (2009) A redescripiton of *Metopa* species (Amphipoda, Stenothoidae) based on the type material. 1. Zoological Museum, Copenhagen (ZMUC). Zootaxa 2093: 1–36.

Tandberg AHS, Vader W, Berge J (2010) Studies on the association of *Metopa glacialis* (Amphipoda, Crustacea) and *Musculus discors* (Mollusca, Mytilidae). Polar Biology 33: 1407–1418.

Thomas JD, Cairns KD (1984) Discovery of a majid host for the commensal amphipod *Stenothoe symbiotica* Shoemaker, 1956. Bulletin of Marine Science 34: 484–485.

Thomson GM, Chilton C (1886) Critical list of the Crustacea Malacostraca of NZ. Transactions and Proceedings of the NZ Institute 18: 141–159.

Toulmond A, Truchot JP (1964) Inventaire de la faune marine de Roscoff. Amphipodes-Cumacés. Travaux du Station Biologique de Roscoff, Supplément, 1–42.

Tzvetkova NL, Golikov AA (1990) (Fauna, ecology and role in ecosystems of amphipods (Amphipoda, Gammaridea) at the New Siberian shoals and adjacent waters of the Laptev Sea.) Issledovaniya Fauny Morei 37(45): 258–343. [In Russian]

Vader W (1972) Associations between gammarid and caprellid amphipods and medusae. Sarsia 50: 51–56.

Vader W (1983a) Associations between amphipods (Crustacea: Amphipoda) and sea anemones (Anthozoa, Actiniaria). Memoirs of the Australian Museum 18: 141–153. doi: 10.3853/j.0067-1967.18.1984.380

Vader W (1983b) Prehensile pereopods in gammaridean Amphipoda. Sarsia 68: 139–148.

Vader W (1984) Notes on Norwegian marine amphipods 8. Amphipods found in association with sponges and tunicates. Fauna Norvegica, Ser. A 5: 16–21.

Vader W, Beehler CL (1983) *Metopa glacialis* (Krøyer) (Stenothoidae) in the Barents and Beaufort Seas, and its association with the lamellibranchs *Musculus niger* (Gray) and *M. discors* (Linnaeus) s. l. Astarte 12 (1979): 57–61.

Vader W, Krapp-Schickel G (1996) Redescription and biology of *Stenothoe brevicornis* Sars (Amphipoda: Crustacea), an obligate associate of the sea anemone *Actinostola callosa* (Verrill). Journal of Natural History 30: 51–66. doi: 10.1080/00222939600770041

Vader W, Tandberg AHS (2013) A survey of amphipods associated with molluscs. Crustaceana 86: 1038–1049. doi: 10.1163/15685403-00003210

Vader W, Tandberg AHS (2015) Amphipods as associates of other Crustacea, a survey. Journal of Crustacean Biology. doi: 10.1163/1937240X-00002343

Watling L (1976) *Parametopella inquilinus*, new species from Delaware Bay oyster beds (Amphipoda: Stenothoidae). Proceedings of the Biological Society of Washington 88: 429–432.