

# Leucothoid and Maerid Amphipods (Crustacea) from deep regions of the North Atlantic

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**Abstract** From amphipod collections from the deep Norwegian Sea, three species are here redescribed: *Maera loveni* (Bruzeliuss 1859) (Maeridae), *Leucothoe* aff. *spini-carpa* (Abildgaard, 1789) and *L. uschakovi* Gurjanova, 1951 (Leucothoidae). A key to all Atlantic and Mediterranean *Leucothoe* species (males only) is provided.

**Keywords** Amphipoda · Leucothoidae · Maeridae · Atlantic Ocean

## Abbreviations

A 1, 2	Antenna 1, 2
Acc	Accessory
Art	Article
Cx 1–7	Coxa 1–7
Ep 1–3	Epimera or epimeral plates
Flag	Flagellum
Gn 1, 2	Gnathopod 1, 2
IP	Inner plate
Md	Mandible
Mx 1, 2	Maxilla 1, 2
Mxp	Maxilliped
OP	Outer plate
P 3–7	Peraeopod 3–7
Ped	Peduncle

Pl 1–3	Pleonite 1–3
Pn	Peraeonite
T	Telson
U 1–3	Uropod 1–3
Us 1–3	Urosomites 1–3
Tooth	Non-articulated pointed ectodermal structure
Spine	Stout, articulated structure (synonymous to “robust seta”)
Seta	Slender, flexible articulated structure

## Introduction

The amphipod fauna of the deep Norwegian Sea is as yet very insufficiently known. Most of our knowledge still rests on the data from the Norske Nordhavs Expedition (Sars 1885) and the Danish Ingolf Expedition (Stephensen 1923, 1925, 1931, 1944). In recent years, much marine material has been collected during the BioFar and BioIce programmes, but the amphipod collections from these programmes have not yet been worked out. In addition, Norwegian marine biologists, primarily Torleiv Brattegard, the late Torleif Holthe and Jon Arne Snelli, have during the 1970s and 1980s brought together large collections of marine animals from the continental slope and abyssal plain of the Norwegian Sea; this material rests in the collections of the Zoological Museum, Bergen.

In the year 2009, Vader and Tandberg, with financial support from the Norwegian Academy of Sciences, organized an International Amphipod Workshop in Skibotn, N. Norway, where part of these collections, that is material from deeper than 1,000 m, was sorted and in many cases preliminarily identified. In 2011, the present authors, again

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with support from the Norwegian Academy of Sciences, got the opportunity to describe the Maeridae and Leucothoidae from this material in more detail, and we present here the results of this study.

## Material and methods

Samples were taken mainly by RP bottom sledge. The amphipods were fixed using 3–5 % formalin, then washed, preserved in 70 % alcohol and sorted under a dissecting microscope. Slides were prepared with glycerine and/or Faure's medium. Pencil drawings were done using various compound microscopes with camera lucida; the transfer or "inking" was done by hand as well as using the program Adobe Illustrator.

All examined material is deposited at the Crustacean collection of the Zoological Museum, Bergen.

## Systematics

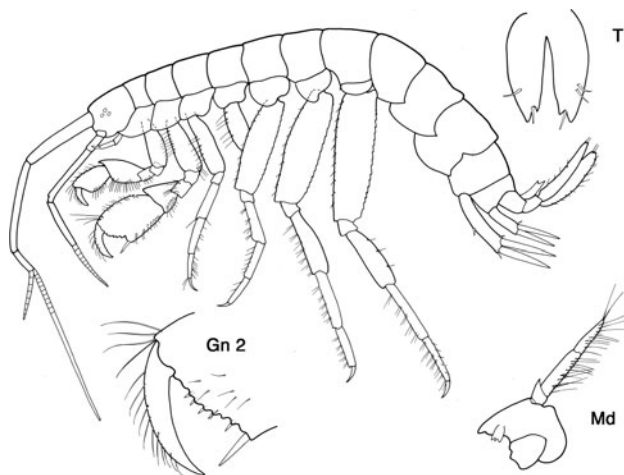
Family Maeridae Krapp-Schickel, 2008

*Maera loveni* (Bruzelius, 1859) (Figs. 1, 2)

*Gammarus loveni* Bruzélius 1859: 59

*Maera loveni* Bate 1862: 193; Norman 1869: 416; Sars 1895: 519, pl. 182; Stebbing 1906: 438; Shoemaker 1930: 116; Schellenberg 1942: 44; Gurjanova 1951: 757–758, fig. 526; Lincoln 1979: 286, fig. 133; Krapp-Schickel and Jarrett, 2000: 34, fig. 4.

*Maera tenera* G.O. Sars, 1885 (cf. also Stephensen 1940: 311 who already proposed this synonymy)



**Fig. 1** *Maera loveni* (Bruzélius, 1859): habitus; Gn 2 gnathopod 2; Md mandible, T telson

*Maera prionochira* von der Brüggén 1907: 230, Figs. 5, 6, 7 (figure captions are most probably switched: what is labelled as Gn 1 is the normal Gn 2, and what is labelled as Gn 2 must be an anomaly. But Ep 3 and T shape are matching).

*Type locality* Bohuslän, Koster Islands, Gullmarfjord, "locis profundioribus".

*Material examined* 1 male 34 mm, 83.06.03.2, 1.220 m depth, 60°12,1'N, 06° 37,5'W 1983 3/VI.

*Diagnosis* Largest member of the *Maera* sensu stricto—group; diagnostic differences are the very little visible ommatidia of the small eyes, long flagellum in A 1, the anteriorly acutely lengthened Cx 1, the long spine on the palmar corner of Gn 2, the posterodistal corner of Ep 1–3 with upturned acute tooth, and the asymmetrically incised lobes in the telson with one spine inserted on the inside.

Redescription (using the original one by Bruzélius, completed by the allometric differences of the present specimen):

*Body* Uncommonly elongate and narrow, back completely smooth. [Length of type material 20 mm, up to 37 mm after Shoemaker 1930: 334; in the present specimen 34 mm].

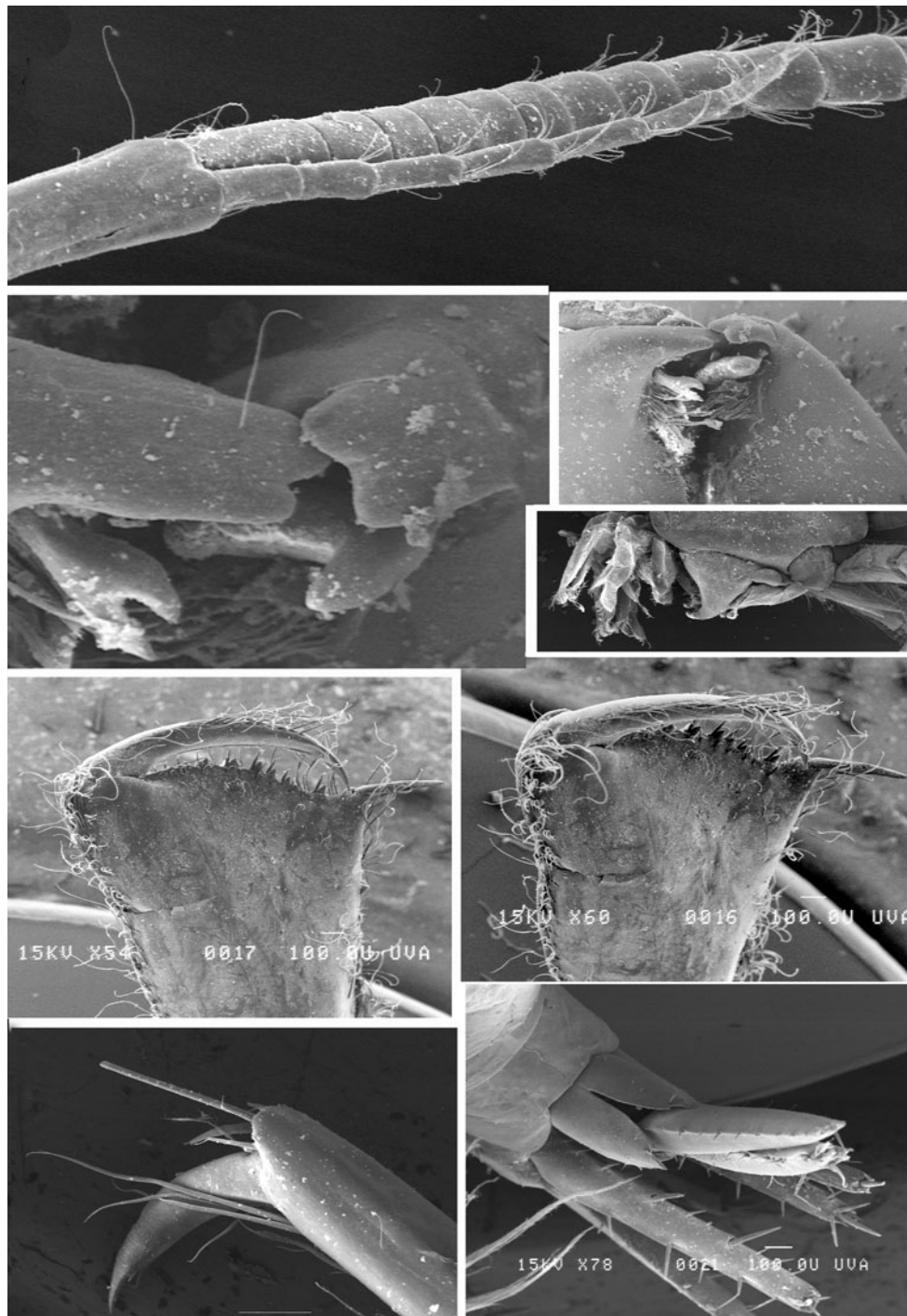
*Head* Lateral cephalic lobe regularly rounded, antero-distal corner acute. Eyes small [with scattered ommatidia, which are pale and scarcely visible in alcohol].

A1 reaching segment 4 of the abdomen, about twice as long as A 2, regularly beset with short setae; peduncle art 1 long and narrow, but thicker and shorter than art 2; [art 3 about 1/3 length of art 2]; flagellum with about 30 arts, acc. flag. with 7–8 arts.

A 2 ped art 3 much shorter and somewhat thicker than art 4, art 4 subequal art 5 [here art 4 > art 5], art 4 longer than end of A 1 peduncle art 1; art 5 does not reach the end of A 1 ped art 2 [does reach it here]; flagellum somewhat shorter than peduncle art 5 [here subequal], consists of 10–12 arts [here 13].

*Mouthparts* Mandibles strong, with high molar; palp with 3 arts, the second the longest, art 1 the shortest and with tooth-shaped prolongation. Mx1 IP narrow, distally with 3–4 plumose setae; [OP with bifurcate robust spines]; Mx 2 lobes elongate, densely beset with long marginal setae [partly plumose; on IP also facial setae]. Mxp IP reaches about half of palp art 2, distally with dense setae; OP (=ischium) reaches about 1/3 of palp art 2 (=carpus), along inner margin strong spines which are toothed on one side, distally with setae; art 2 of the palp is the longest and is also densely beset with spines and setae. UL rounded, LL divided into large rounded lobes with short processes anterodistally.

*Peraeon* Coxal plates short, Cx 1, 2 smaller than Cx 3, 4 [here clearly the opposite]. Cx 1 anterodistal corner acutely produced, all other coxae rounded.



**Fig. 2** *Maera loveni* (Bruzeliuss, 1859): SEM pictures. *Upper half* first antenna with accessory flagellum. Directly underneath: mouthpart-details (on *left* and *right* side the two mandibles working together, on *right* side an overview of the mouthpart bundle, laterally

seen). *Lower half*: second gnathopod in two different positions. *Lowest left*: dactylus and propodus of pereopod 7. *Lowest right*: telson and uropods seen from dorsally

*Gn 1* much smaller than *Gn 2* Carpus subequal to propodus [here longer], anterodistal corner acute, posterior margin rounded; anterior margin almost without setae, a number of oblique rows of densely long setae along the posterior margin; [propodus distally widening, posterior margin regularly

rounded]; also facial setae on both sides. Dactylus strong, outer margin with long and fine setae, but no spines.

*Gn 2 carpus [triangular]* Much smaller than propodus, on posterior margin very dense setae; propodus almost

rectangular, proximal part somewhat narrower than distal one. Palm slightly convex, with 7–8 small acute humps beset with shorter spines and longer setae; palmar corner with a strong, straight and acute spine, posterior margin with dense short setae.

*P 3 somewhat longer than P 4* Subsimilar: basis long and narrow, ischium short, merus, carpus and propodus gradually shorter; dactylus short [robust].

*P 5–7 uncommonly narrow bases (in the type material of 20 mm)* Distally narrowing [in our specimen of 34 mm bases not so narrow], [anterior margin beset with short setae, posterior margin finely serrated; in P 5 basis proximally rounded, in P 6, 7 basis with posteroproximal lobe]; dactyli strong, convex and acute.

*Pleon* Ep 1, 2, 3 all with small upturned sharp tooth on posterodistal corner.

U 1 peduncle longer than subequal rami and reaching somewhat further than U 2, with one strong spine along half of anterior margin and two spines distally; rami beset with short spines along the margins and distally; U 2 peduncle shorter than subequal rami, U 3 reaching much further than U 1, 2, rami flattened, subequal in length, margins with shorter, distal end with longer setae and fine spines.

Telson deeply cleft, but not quite to the basis, lobes diverging, distally narrowing and with short V-shaped incision [inner arm of this “V” much shorter], beset with one strong spine [which is subequal or somewhat longer than outer arm of incision].

No sexual differences observed; the female has only slightly shorter appendages.

*Colour* Pale.

*Distribution* North Atlantic, American and European coasts; Arctic Ocean; Greenland; Iceland; European coasts from northern Norway to British Isles. Depth range as yet only known from 6 to 400 m. Now down to 1,220 m.

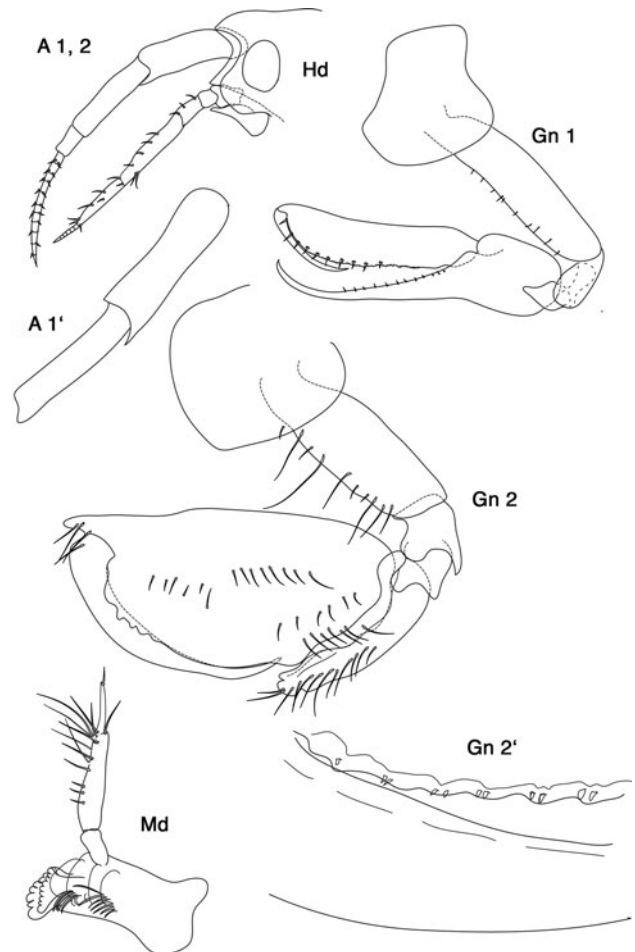
For a key to all 12 *Maera* species worldwide (*M. anoculata*, *M. danae*, *M. edwardsi*, *M. fusca*, *M. grossimana*, *M. hiron-dellei*, *M. loveni*, *M. pachytelson*, *M. schieckei*, *M. similis*, *M. sodalis*, *M. tinkerenensis*) see Krapp-Schickel and Jarrett 2000: 29.

Leucothoidae Dana, 1852

*Leucothoe* aff. *spinicarpa* (Abildgaard, 1789) (Figs. 3, 4)

Krapp-Schickel 1989; Krapp-Schickel and Menioui 2005, 64–66; Crowe 2006: 57–68.

*Material examined* 1 ? fem. 6 mm, 4 immatures 4–5 mm, 1,542–1,560 m depth, 62°28.1'N, 14° 13.4'W, Stn 83.06.06.1, 1983 6/VI.



**Fig. 3** *Leucothoe* aff. *spinicarpa* (Abildgaard, 1789): A 1, 2 antenna 1, 2; A 1' first antenna peduncle article 1, 2 enlarged. Hd head. Gn 1, 2, Gn 2' parts of dactylus and propodus enlarged. Md mandible

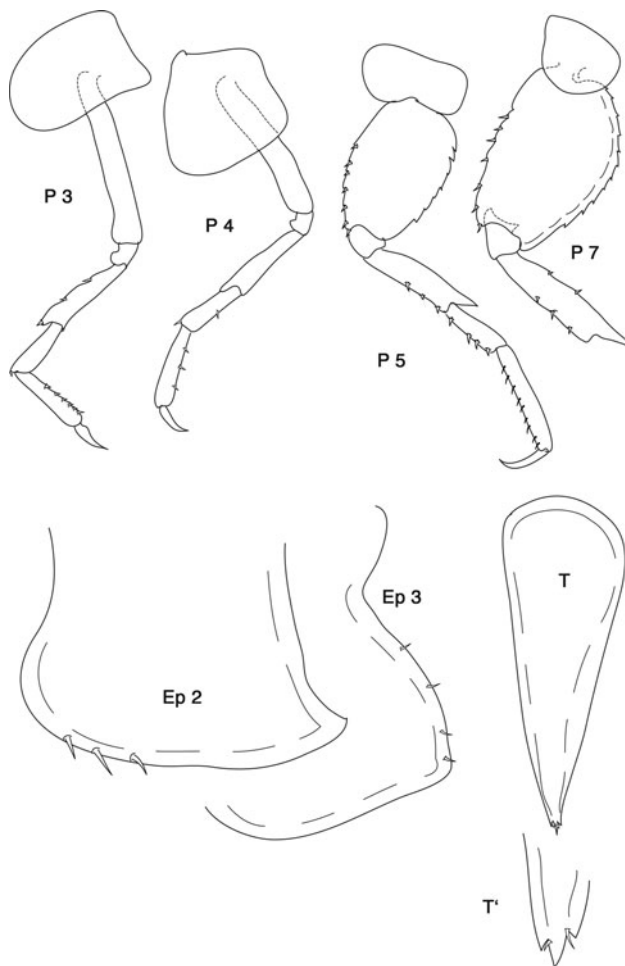
*Diagnosis* Eyes oval. Mandibular palp long and narrow, art 3 half length of art 2. Cx 1 inferior margin smooth, about as long as wide. Gn 1 carpus distal part about 6× longer than wide, dactylus reaching about 0.3× of propodus length. P 3, 4 with very narrow basis, P 5–7 basis ovally broadened, with regularly rounded hind margin, ratio length to width 2.5: 4 or 3.5: 5. Ep 2 posterodistally with upturned tip, Ep 3 distoposterior corner with right angle, blunt, anterior corner lacking setae.

*Description* Length 4–6 mm.

*Head* Anterior margin rounded, anterodistal margin rectangular with rounded corner. Mid-cephalic keel with acute projection. Rostrum small.

*Eyes oval* Antenna 1 one-third of body length, flagellum 11-articulate, peduncle art 1 width proximally less than twice article 2, disto-inferiorly with acute tooth, length art 1 subequal art 2, art 3 about 1/3 of art 2, acc. flagellum not seen.





**Fig. 4** *Leucothoe* aff. *spinicarpa* (Abildgaard, 1789): P 3–7 pereopods. Ep 2, 3 = epimeral plates 2, 3. T telson, T' distal end of telson enlarged

Antenna 2 one-third of body length, subequal in length to antenna 1, peduncle art 4 > art 5, flagellum 6 arts.

**Mouthparts** Mandibles lacking molars, palp 3-articulate, ratio of articles 1–3 is about 1: 2.8: 1.4, art 2 with 8–9 long lateral and 1 distal setae, art 3 with 1 distal seta, incisors strongly dentate.

**Peraeon** Cx 1–4 relative widths 1.0: 1.2: 0.8: 1.

Cx 1 smooth, length and width subequal; anterior margin smooth, excavate, anterodistal margin produced, anterodistal corner about 120°, distal margin regularly rounded, smooth, posterior margin excavate, facial setae absent.

Gn 1 basis not inflated, with small tiny setae on anterior margin; ischium smooth; carpus distal part linear, length about 6× width; propodus straight, palm dentate with 9 short spines; dactylus smooth, reaching about 0.3× propodus length.

Cx 2 about as long as wide, subquadrangular, much wider than Cx 3, distally smooth; anterior margin straight, anterodistal corner rectangular, inferior margin rounded, posterior margin straight, facial setae absent.

Gn 2 basis slightly inflated, on anterior margin 10 setae of different length; carpus nearly reaching half propodus length, curved, distally truncate, densely setose; propodus distally with tooth-shaped prolongation, palm convex with many low humps, with 22 mediofacial setal rows, with a few submarginal setae, proximally near dactylus end widening with clear corner of about 120°; dactylus curved, both margins smooth, bare, reaching somewhat more than half of propodus length.

Cx 3 length > width, smooth, bare, anterior and posterior margin straight, distally rounded, facial setae absent.

Cx 4 wider than long, smooth, bare, anterior margin somewhat convex, distal margin scarcely rounded, posterior margin shorter than anterior one, excavate, facial setae absent.

P 3, 4 basis very narrow, about the width of merus and up to 6–7× the width of basis; dactylus reaching nearly half length of propodus, posterior margins with short and thin spines.

Cx 5–7 facial setae absent.

P 5–7 similar, bases length: width ratio about 1.4–1.6, anterior margins with slight serrations and small weak spines, posterior margins strongly serrate.

**Pleon** Ep 1 posteroventral corner rounded. Ep 2 with spines on distal margin, posteroventral corner acutely produced. Ep 3 posteroventral corner blunt and rectangular, distally bare, but some short spines on posterior margin.

U 1–3 relative lengths 1.0: 0.8: 1.1.

**Telson** Ratio length: width about 3, tip tridentate because of two indentations near distal end, with a short seta inserted in each one.

**Remarks** These specimens undoubtedly belong to the “*spinicarpa*”-group.

We started out with the supposition that material of more than 1,500 m depth cannot be *L. spinicarpa* which primarily is a shallow water species. Sars (1891) writes “30–150 fathoms”, while Lincoln (1979) records the species as “occasionally intertidally, down to 600 m”. Our material contains no specimens with signs of sexual maturity, and we know extremely little about the life span, variability or allometry in *L. spinicarpa*. The species has been redescribed by Krapp and Menioui (Krapp-Schickel and Menioui 2005) and by Crowe (2006) on the basis of topotypical material; Crowe also designed a male neotype of 13 mm, deposited in the Zoological Museum of Oslo.

*L. spinicarpa* (Abildgaard, 1789) is one of the earliest amphipods to be formally described, and the description is correspondingly vague. Shortly after also the species *L. articulosa* Montagu, *L. denticulata* A. Costa and *L. antarctica* Pfeffer were described, all morphologically quite

similar to *L. spinicarpa* and all for a long time synonymized with that species. *L. denticulata* was re-established and fully described by Krapp-Schickel and Menioui (2005), and the redescription of *L. antarctica* is in preparation, but a modern redescription of *L. articulosa*, also revived by Krapp-Schickel and Menioui (loc. cit.), is still lacking.

Sars (1890–1895) revised the species and described *L. spinicarpa* from Norway, synonymizing *L. articulosa* (type locality S-Devonshire, type material also lost) with it. But in his illustration on pl. 101 (sub male *L. articulosa* of 16 mm), Ep 3 has a small but well-defined posterodistal tooth-shaped tip, which is still more acutely illustrated in the drawing of *L. articulosa* by Bate and Westwood 1863 Fig. 3, while Lincoln 1979 describes Ep 3 in his material (sub *L. spinicarpa*) as “quadrate OR with minute blunt tooth”; in the illustration of the neotype, Ep 3 is posterodistally rectangular.

Crowe (2006) specified several characters useful for comparison within the “*spinicarpa*-group”: the number of flagellum articles on the antenna 1 and 2; the anterior setation of the basis and the mediofacial setae on the propodus of gnathopod 2; the propodus and dactylus length of pereopods 3–7; the shape and setation of epimera 3 and the telson.

Our material (4–6 mm) is not fully mature, and therefore a number of these characters cannot be applied here, for example the antennar articles. The deepwater specimens deviate in a few points from Crowe’s redescription of *L. spinicarpa*: Gn 2 carpus is distally rounded (as in females and juveniles of *L. spinicarpa*, but differing from adult males). Ep 1 lacks anterodistal setae in our material, and the mediofacial row (or 2 shorter rows?) of setae on the propodus of Gn 2 has a quite different shape than in Crowe’s material.

As our material does not contain obvious males and none of the specimens seems to be fully adult, we refrain from describing a new species and design our material as *L. aff. spinicarpa*.

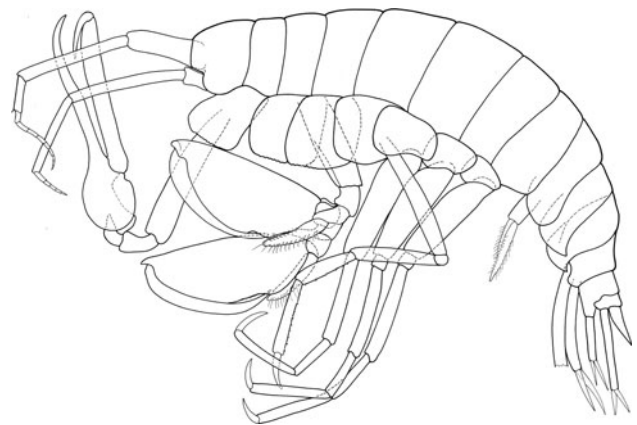
*Leucothoe ushakovi* Gurjanova, 1951 (Figs. 5, 6, 7)

Gurjanova 1951: 487–488, fig. 320 A, B

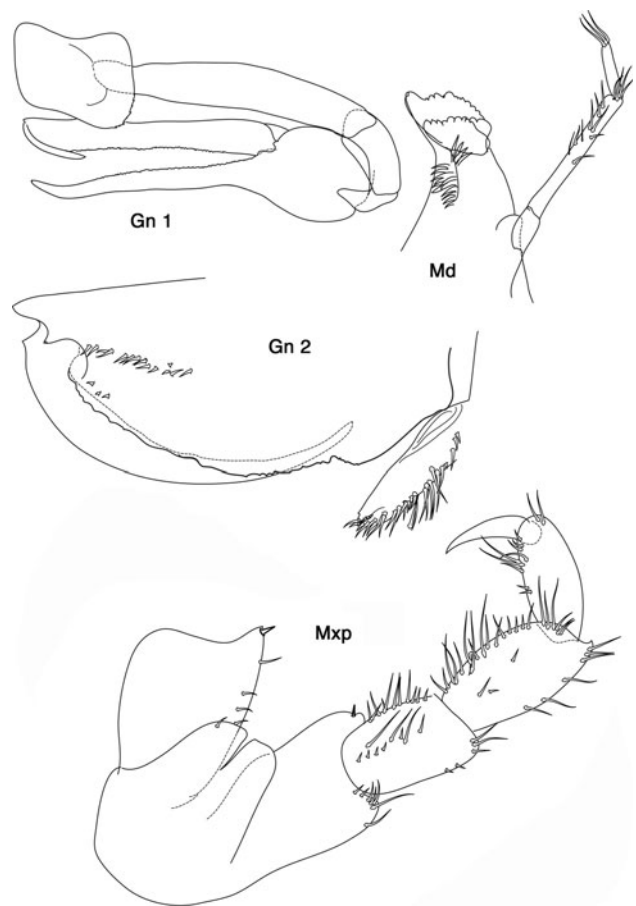
**Material examined** 10 specimens of 8–27 mm length, 3,892 m depth, 65° 39,9’N, 04° 35,8’W, Stn 83.06.09.1, 1983 9/VI.

**Type locality** Greenland Sea.

**Diagnosis** Eyes apparently absent in fixed material. Mandibular palp long and narrow, art 3 up to 2.5× shorter than art 2. Cx 1 inferior margin weakly serrate, ratio length: width in large animals up to 2. Gn 1 carpus distal part about 10× longer than wide, dactylus reaching 0.25× of propodus length. P 3–7 with very narrow and similar basis, ratio length to width up to 4 in P 5–7, up to 7–8 in P 3, 4. Ep 2, 3 posterodistally with upturned tooth. U 1–3 peduncle always longer than rami.



**Fig. 5** *Leucothoe ushakovi* Gurjanova 1951: habitus

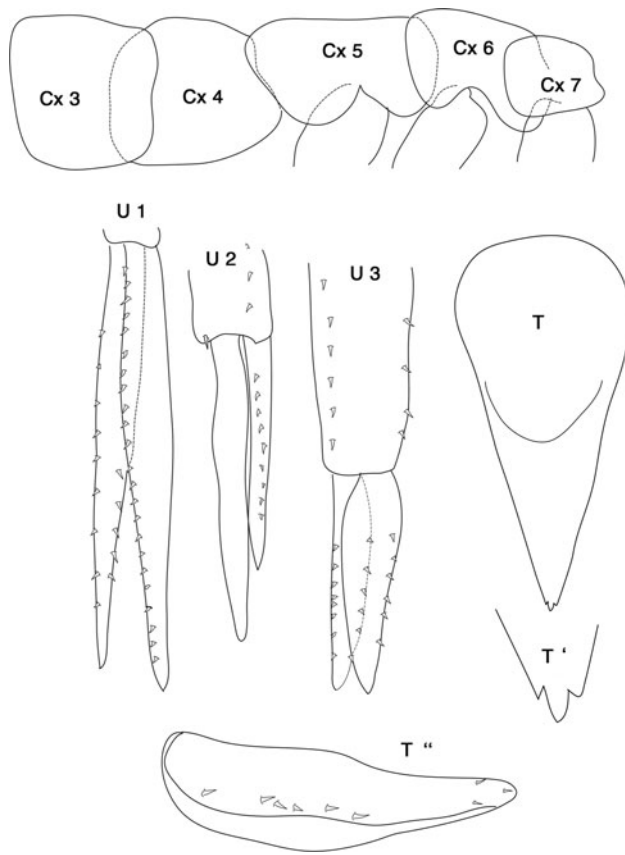


**Fig. 6** *Leucothoe ushakovi* Gurjanova 1951: Gn 1, 2 gnathopod 1, 2; Md mandible, Mxp maxilliped

**Redescription** Length up to 34 mm.

**Head** Anterior margin rounded, anterodistal margin rectangular with rounded corner. Ventral cephalic keel antero-ventral margin without projection. Rostrum acute, small.

Eyes apparently absent in fixed material.



**Fig. 7** *Leucothoe ushakovi* Gurjanova 1951: Cx 3–7 = coxal plates; U 1–3 = uropods; T telson, T' and T'' enlargement of telson distally and laterally

Antenna 1 one-third of body length, flag 6–15 articulate, ped art 1 width proximally about twice art 2, length art 1 < art 2, art 3 half length art 2, acc. flag with 1 small art.

Antenna 2 one-third of body length, subequal in length with A 1, ped art 4 > art 5, flag 6–10 arts.

**Mouthparts** Mandibles lacking molars, palp 3-articulate, ratio of articles 1–3 is about 2: 6.5: 2.7 or 1.8: 6.2: 3, art 2 with 8–9 long lateral and 3 distal setae, art 3 with 2–3 distal setae, incisors strongly dentate; left mandible lacinia mobilis large, strongly toothed, with 16 raker spines; right mandible lacinia mobilis small, with 16 raker spines.

Lower lip inner lobes fused, bare; outer lobes with small gap.

Mx 1 palp with 2 arts, with 2 distal setae; outer plate with distal spines and setae, inner plate naked. Mx 2 inner plate with many thin marginal and a few facial setae; outer plate with few distal setae. Mxp inner plates fused, distal margin with a v-shaped indentation; outer plate triangular, reaching 0.3× palp art 1, with one subdistal spine; palp with 4 arts, art 2 and art 3 with marginal and facial setae, dactylus < art 3.

*Peraeon* Cx 1–4 relative widths 1.0: 1.3: 1.3: 1.5.

Cx 1 smooth, in smaller specimens ratio length to width about 11: 8, in larger ones up to 2: 1; anterior margin smooth, anterodistal margin produced, rounded, distal margin straight, with some dentations, posterior margin excavate, facial setae absent.

Gn 1 basis scarcely inflated, naked; ischium with posterior setae; carpus distal part linear, length about 10× width, proximal margin finely serrated; propodus straight, palm dentate with 10 short setae; dactylus smooth, reaching 0.25× propodus length.

Cx 2 about as long as wide, subquadrangular, wider than Cx 3, distally weakly dentate; anterior margin straight, anterodistally rectangular, inferior margin straight, posterior margin straight, facial setae absent.

Gn 2 basis slightly inflated, naked; carpus 0.3× propodus length, curved, distally truncate, densely setose; propodus distally with tooth-shaped prolongation, posterior margin smooth, with 1 mediofacial setal row, with a few submarginal setae, palm convex and dentate, proximally near dactylus end widening with angle of about 120°; dactylus curved, outer margin smooth, bare, inner margin with rounded humps, reaching 0.75× propodus length.

Cx 3 length subequal width, anterodistal corner overriding distal face of Cx 2, smooth, bare, anterior margin straight, anterodistal corner rounded, facial setae absent.

Cx 4 wider than long, smooth, bare, anterior margin somewhat convex, distal margin evenly rounded, posterior margin excavate, facial setae absent.

P 3, 4 basis very narrow, about the width of merus and up to 7–8× the width of basis; dactylus reaching 1/3 of propodus, posterior margins with short and thin spines.

Cx 5–7 facial setae absent.

P 5–7 very similar, bases length: width ratio about 4, anterior margins with very slight serrations and small weak spines, posterior margins smooth.

**Pleon** Ep 1 with 1 spine on inferior margin, Ep 2, 3 bare. Ep 1 posteroventral corner rounded, Ep 2, 3 posteroventral corner acutely produced.

U 1–3 relative lengths 1.0: 0.8: 1.1. U 1 peduncle nearly twice the outer ramus which is about 0.9× of inner ramus length. U 2 peduncle > inner ramus length, outer ramus length 0.8× inner ramus length. U 3 peduncle about twice inner ramus length, outer and inner ramus length subequal. U 1–3 margins of peduncle, inner and outer rami all with short spines.

**Telson** Twice as long as wide, apex with very small V-shaped excavation in the acute tip, with submarginal short spines.

No sexual differences observed.

**Colour** In alcohol somewhat yellowish, body semi-transparent.

**Distribution** Greenland Sea at the depth of 3,000 m (2 specimens, types). Norwegian Sea at 65°N and 04° W, 3,892 m depth (presently studied material)

**Remarks** Gurjanova (1951) reports about the type material that “Gn1 propodus is longer than basal article”, which is not the case in our material, obviously due to the propodus growing allometrically. About the telson, she described that the lateral margins are “completely smooth”, which was the case in some of the presently studied specimens, while others had some submarginal small spines.

### Remarks on the genus *Leucothoe*

The amphipod genus *Leucothoe* is extremely easy to recognize as such, but its many species are differentiated from each other by only subtle characters, and this has traditionally led to a whole-sale lumping of many species under just a few names, esp. sub *Leucothoe spinicarpa* (Abildgaard, 1789). In the last years, it has become clear that the genus, with many of its species living commensally inside sponges, ascidians and even bivalve mollusks, is a very speciose one, and especially in the Pacific Ocean, there are still large numbers of as yet undescribed species (cf White and Reimer 2012a, b, c). The present identification key, which is based exclusively on the literature, is therefore restricted to the *Leucothoe* species of the somewhat better known Atlantic Ocean, although also in this area, there is no doubt still a considerable number of as yet undescribed species to be discovered (cf. Thomas and Klebba 2007).

As the genus *Leucothoe* shows both sexual differences and in many species a considerable allometry, the present key is only suitable for adult male specimens.

Recent authors, for example Thomas and Klebba 2007, have discovered a series of new and most interesting character traits, of use in the identification of *Leucothoe* species, such as the exact form of the mid-ventral keel and the size and placement of the various rows of setae on the Gn2 propodus. We have unfortunately been unable in most cases to use these characters, as they were not shown in earlier illustrations of other species.

The taxa in the *spinicarpa* group of species are only now being properly diagnosed and their differences catalogued, and as yet there are, for example, no modern descriptions of *L. articulosa* (Montagu, 1804) and of *L. miersi* Stebbing, 1888 (by most authors still synonymized with *L. spinicarpa*). In addition, we have included both *L. occidentalis* Reid, 1951 and *L. serraticarpa* Della Valle, 1893 twice in the key, as the two modern descriptions of these taxa differ in some respect from each other.

We hope that the present key may be a contribution to the further unravelling of the relationships among Atlantic *Leucothoe* species.

### Identification key to Atlantic *Leucothoe* species (adult males only)

NB We have omitted those taxa considered by White (2011) in her monograph as unidentifiable or ‘probably not valid’. *Leucothoe campi* Mateus & Mateus, 1986 and *L. spinulosa* Chevreux, 1919–20, though probably valid species, are not well enough described to be included in the key. All Atlantic records of *L. furina* (Savigny, 1816) are suspect (cf White 2011), while White’s Atlantic report of *L. acanthopus* Schellenberg, 1928 rests on a geographic error: the Dahlak Archipelago is in the Red Sea.

1. --- Eyes absent or rudimentary..... 2  
 --- Eyes well-developed ..... 6

2. --- Eyes composed of a few translucent ocelli. Gn 1 not extremely slender, propodus 2/3 of carpus.....

..... *Leucothoe cathalae* FRUTOS & SORBE, 2012

..... Biscaya 4 mm

- Eyes completely absent. Gn 1 very slender, propodus 3/4 of carpus ..... 3

3. --- Rostrum well-developed, covering 3/4 of A 1 peduncle art. 1.



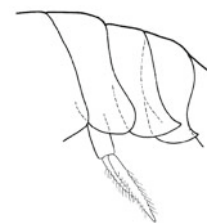
Telson short, as broad as long.....*Leucothoe rostrata* CHEVREUX, 1908

Azores, deep sea 3.5 mm

(NB. Only 3 females known)

- Rostrum short, covering less than half of A 1 peduncle art. 1. Telson slender, at least 2 x as long as broad..... 4

4. --- Very large animals, up to 34 mm. (Cx 1 almost 2 x as long as broad. Ep 3 with well-developed posterodistal tooth).....



..... *Leucothoe uschakovi* GURJANOVA, 1951

Greenland Sea (deep) 34 mm

- Moderately large animals, 5 - 12 mm..... 5



5. --- Animal up to 12 mm. Gn 1-2 basis with anterior margin smooth. P

5 basis with posterior margin smooth.....

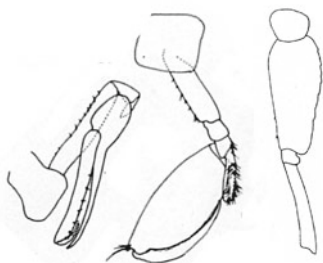
..... *Leucothoe ayrtonia* BELLAN-SANTINI, 1997

Barbados Trench 12 mm

(NB. Only one specimen known)

--- Animal up to 5 mm. Gn 1-2 basis with anterior margin setose. P 5

basis with posterior margin serrate.



*Leucothoe atosi* BELLAN-SANTINI, 2007

Mid-Atlantic Ridge (37°N), 5 mm

(NB. No adult males known)

6. --- Gnathopod 1 dactylus short (<1/5 propodus).....

7



--- Gnathopod 1 dactylus long (1/4 propodus or longer).....

16



7. --- A 1 peduncle art. 1 greatly swollen.....

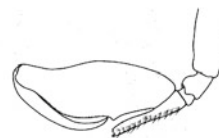
8

--- A 1 peduncle art.1 not swollen.....

9

8. --- P 3-7 dactylus very slender, > 5 x as long as broad. Gn 2 propodus

about 3 x as long as broad, palm defined by a protuberance.....



*Leucothoe oboa* KARAMAN, 1976

Mediterranean, 3 - 5 mm

--- P 3-7 dactylus less slender, < 4 x as long as broad. Gn 2 propodus  
about 2 x as long as broad, palm not defined by a protuberance.....

*Leucothoe pachycera* DELLA VALLE, 1893

Mediterranean, 3 - 4 mm

9. --- Ep 3 posterodistal corner rounded or rectangular....

10



--- Ep 3 posterodistal corner clearly acute or with a small or large  
tooth.....

14

10. --- Gn 1 carpus densely setose. An associate of bivalve mollusks.....

..... *Leucothoe flammosa* THOMAS & KLEBBA, 2007

Caribbean, 5 mm

--- Gn 1 carpus not densely setose.....

11

11. --- Gn 1 carpus saw-edged by triangular teeth, with a row of strong  
setae.....

*Leucothoe cheiriserra* SEREJO, 1998

Brazil, 3 mm

--- Gn 1 carpus not like this.....

12

12. --- Mandible palp art. 3 long, 2/3 of art. 2.....



*Leucothoe venetiaram* GIORDANI SOIKA, 1950

Mediterranean, 3 mm

--- Mandible palp art. 3 short, &lt; 1/3 of art. 2..... 13



13. --- A 1 flagellum with 3-5 arts, Gn 1 propodus palm smooth, Gn 2 basis anterior margin setose, carpus distally truncate, T length > 2x width.....

***Leucothoe lihue*** BARNARD, 1970

(s. Serejo, 1998). Brazil, 3 mm

--- A 1 flagellum with 6-10 arts, Gn 1 propodus palm dentate, Gn 2 basis bare, carpus distally tapering, T length < 2x width.....

***Leucothoe minima*** SCHELLENBERG, 1925

W. Africa, 2 - 3 mm

14. --- Cx 4 anterior margin with anterodistal tooth (or at least clearly angular).



Gn 1 carpus with very fine denticulations. Ep 3 posterodistally with deep sinus and strong tooth.....

***Leucothoe lilljeborgii*** BOECK, 1861

Norway, 4 - 5 mm

--- Cx 4 anterior margin rounded. Gn 1 carpus with clear denticulations. Ep 3 posterodistally with round sinus and moderate tooth..... 15

15. --- Telson slender, > 2 x as long as broad, with acute tip.



Gn 2 carpus not tapering apically, with bifid tip.....

***Leucothoe incisa*** ROBERTSON, 1892

Scotland 5 - 7 mm

--- Telson wider, < 2 x as long as broad, with rounded tip.



Gn 2 carpus apically tapering, with acute tip.....

***Leucothoe occulta*** KRAPP-SCHICKEL, 1975

Mediterranean 5 - 8 mm

**16. (coming from 6: Gn 2 dactylus longer than 1/4 propodus)**

--- Ep 3 posterodistal corner rounded or rectangular..... 17

(NB. see also 33a, or illustration for 9)

--- Ep 3 posterodistal corner acute, or with small or large tooth.... 35

17. --- Gn 2 propodus palm smooth, or with minor serrations or crenulations..... 18

-- Gn 2 propodus palm with sizeable protuberances..... 30

(NB. In case of doubt, try both options)

18. --- Gn 2 propodus with conspicuous distal cap-like projection.....

***Leucothoe laurensi*** THOMAS & ORTIZ, 1995

Caribbean, 2 - 3 mm

--- Gn 2 propodus without cap-like distal projection (but may be produced distally) ..... 19

19. --- Lateral cephalic lobes angular or with a prominent corner..... 20

-- Lateral cephalic lobes evenly rounded..... 24

20. --- Gn 2 propodus palm with a row of small spines, no crenulations.

(P 5-7 basis not much expanded, almost twice as long as broad).....

***Leucothoe kensleyi*** THOMAS & KLEBBA, 2006

Caribbean, 3 mm

-- Gn 2 propodus palm without a row of small spines, but with several crenulations..... 21

21. --- Gn 2 basis with dense fringe of long setae. (Cx 2-4 and hind margin basis of P 5-7 smooth.)

***Leucothoe garifunae* THOMAS & KLEBBA, 2007**

Caribbean, 5 mm

--Gn 2 with fewer and shorter setae..... 22

22. --- Cx 2 with anterodistal corner very acute.....

***Leucothoe hortapugai* WINFIELD, ORTIZ & CHAZARO- OLVERA,**

2009 Gulf of Mexico, 7 mm

--- Cx 2 with anterodistal corner rounded..... 23

23. --- P 5 - 7 basis  $l : b = 5 : 3$ .....

***Leucothoe barana* THOMAS & KLEBBA, 2007**

Caribbean, 10 mm

--- P 5 - 7 basis  $l : b = 4 : 3$  (otherwise extremely similar to the former).....

***Leucothoe ortizi* WINFIELD & ALVAREZ, 2009**

Gulf of Mexico, 6.9 mm

24. --- Gn 1 dactylus not more than  $\frac{1}{4}$  of propodus.....(see sketches in

option 6) ..... 25

--- Gn 1 dactylus more than  $\frac{1}{3}$  of propodus..... 26

25. ---Md palp art. 3 much shorter ( $\frac{1}{3}$ ) than art. 2 (see sketch in option

12). Large species..... ***Leucothoe miersi* STEBBING, 1888**

S. Africa, 12 mm

-- Md palp art. 3  $\frac{2}{3}$  as long as art. 2 (see sketch in option 12). Small species..... ***Leucothoe venetiarum* GIORDANI-SOIKA, 1950**

Mediterranean, 3 mm

26. --- Eyes rounded oval. Cx 1 anterodistal corner angular.



***Leucothoe spinicarpa* (ABILDGAARD, 1789)**

NW Europe 10 - 19 mm

-- Eyes roundish or irregularly squarish. Cx 1 anterodistal corner rounded..... 27

27. --- Gn 2 carpus distally with (a few small) spines. Eyes large, covering  $\frac{1}{2}$  of head depth.....

***Leucothoe occidentalis* REID, 1951**

W. Africa 5 - 7 mm

(NB Material from Morocco by Krapp-Schickel & Menioui, 2005; only female known)

-- Gn 2 carpus without spines. Eyes moderate, covering  $\frac{1}{3}$  of head depth..... 28

28. --- Telson very slender ( $l : b = 3.5 : 1$ ), tip acute, without setae. Gn 2 propodus with wavy, irregular crenulations....

***Leucothoe articulosa* (MONTAGU, 1804)**

W. Europe, 6 - 13 mm

(NB. No good modern redescription of this species exists)

-- Telson slender ( $l : b = 2.5 : 1$ ), tip subacute, with two or three setules.

..... 29

29. --- Gn 2 propodus palm with regular blunt serrations, stronger

proximally. Gn 1 carpal lobe without elevated anterodorsal projection.....

***Leucothoe denticulata* COSTA, 1851**

Mediterranean, 5 - 15 mm

--- Gn 2 propodus palm with regular acute serrations only proximally.

Gn 1 carpal lobe with elevated anterodorsal projection.....

***Leucothoe hendrickxi* WINFIELD & ALVAREZ, 2009**

Gulf of Mexico, 7 mm

**30. (coming from 17: Gn 2 propodus palm with sizeable protuberances)**

--- Md palp art. 3 clearly longer than  $\frac{2}{3}$  art 2..... 31

--- Md palp art. 3 clearly shorter than  $\frac{2}{3}$  art 2..... 32

31. --- Gn 2 propodus palm with 6 high and narrow comb-like protuberances. Telson slender ( $l : b = 2 : 1$ ), with emarginate tip.....

***Leucothoe ctenochir* K. H. BARNARD, 1925**

S. Africa, 5 mm

--- Gn 2 propodus palm with 4 proximal rounded low protuberances.

Telson broad (l : b=5 : 3), with rounded tip.....

***Leucothoe basilobata* SEREJO, 1998**

Brazil, 3 mm

32. --- Md palp art. 3 very short, 1/5 of art. 2. (Uropods with clearly unequal rami, in U 1 - 2 with finely serrate margins) .....

***Leucothoe urospinosa* SEREJO, 1998**

Brazil, 4 mm

-- Md palp art. 3 ca 1/2 of art. 2..... 33

33. --- Gn 2 with dense tufts of long setae on arts 2 and 3.....

***Leucothoe saron* THOMAS & KLEBBA, 2007**

Caribbean, 6 - 7 mm

-- Gn 2 without dense tufts of long setae on arts 2 and 3 (shorter setae may be present) ..... 34

34. --- Gn 1 with very long dactylus (ca 1/2 propodus). Lateral cephalic lobes angular.....***Leucothoe ubouhu* THOMAS & KLEBBA, 2007**

Caribbean, 4 - 5 mm

--- Gn 1 with shorter dactylus (ca 1/4 propodus). Cephalic lateral lobes rounded.....***Leucothoe ashleyi* THOMAS & KLEBBA, 2006**

Caribbean, 3 - 4 mm

**35. (coming from 16: Ep 3 posterodistal corner acute, or with small or large tooth)**

--- Gn 2 propodus palm smooth, or denticulate or crenulate.... 36

--- Gn 2 propodus with sizeable protuberances..... 42

(NB. When in doubt, try both options)

36. --- Ep 3 posterodistal corner with small notch only. (P 3 propodus with 3 strong distal spines, Gn 2 propodus slender, 2.5 x as long as broad).....

***Leucothoe leptosa* SEREJO, 1998**

Brazil, 3 mm

-- Ep 3 posterodistally with small or larger tooth..... 37

37. --- Ep 3 with very small posterodistal tooth, without any clear

sinus..... 38



--- Ep 3 with small or moderate posterodistal tooth, demarcated above by a sinus..... 39



38. --Basis Gn 2 with a dense fringe of long setae. Antennae 'normal', with slender peduncles. P 5 - 7 dactyli normal. Live animals vividly red or yellowish..... ***Leucothoe richiardi* LESSONA, 1865**

Mediterranean, 6 - 8 mm

--- Basis Gn 2 with only scattered setae. Antennae short, with robust peduncles. P 5 - 7 dactyli long and slender. Live animals almost transparent..... ***Leucothoe euryonyx* WALKER, 1901**

W. Africa, 2.5 - 3 mm

39. --- Cx 4 with long posterodistal lobe.



P 5 - 7 dactyli very long and slender. (Gn 1 carpus densely serrate. Cx 1 with angular corners) .....

***Leucothoe serraticarpa* DELLA VALLE, 1893**

Mediterranean, 5 - 9 mm

-- Cx 4 without long posterodistal lobe. P 5 - 7 dactyli normal or short..... 40

40. --- P 5 - 7 basis not much expanded (l : b=3 : 2). (Gn 2 propodus

palm with proximal square excavation, corresponding to a bump on

dactylus, carpus distally acute) ..... ***Leucothoe procera* SP. BATE,**

1857

Great Britain, 17 mm



--- P 5 - 7 basis almost as broad as long..... 41

41. --- A 1 clearly longer than A 2. Cx 6 - 7 and basis P 6 - 7 with many long setae.....

*Leucothoe prope serraticarpa* s. KRAPP-SCHICKEL & MENIOUI, 2005

Morocco, 14 mm

--- A 1 subequal to A 2. Cx 6 - 7 and basis P 6 - 7 with only few setae.....

*Leucothoe brunonis* KRAPP-SCHICKEL & MENIOUI, 2005

Morocco, 6 - 8 mm

42. ---Antennae very long (flagellum A 1 >30 arts). Gn2 propodus palm with 3 tall narrow protuberances. Ep 3 posterodistally with deep sinus above tooth.....*Leucothoe dolichoceras* K. H.BARNARD, 1916

S. Africa, 12 mm

-- Antennae normal (flagellum A 1 about 10 arts). Gn 2 propodus palm with a few irregular low protuberances. Ep 3 posterodistally with inconspicuous blunt tooth, without a sinus above.....

*Leucothoe wuriti* THOMAS & KLEBBA, 2007

Caribbean, 6 - 7 mm

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## References

- Abildgaard PC (1789) Zoologia Danica seu animalium Daniae et Norvegiae rariorum ac minus notorum. Descriptiones et Historia. Havniae, N. Möller et filius
- Bate CS (1862) Catalogue of the specimens of Amphipodous Crustacea in the collections of the British Museum. Taylor & Francis, London
- Bate CS, Westwood JO (1863) History of the British sessile-eyed Crustacea. John van Voorst, London
- Bruzeliuss RM (1859) Bidrag til kännedomen om Skandinaviens Amphipoda Gammaridea. Kongl Svensk Vetensk-Akad Handl New Series 3:1–104
- Crowe SE (2006) A redescription of *Leucothoe spinicarpa* (Abildgaard, 1789) based on material from the North Atlantic (Amphipoda, Leucothoidae). Zootaxa 1170:57–68
- Dana JD (1852) Conspectus crustaceorum quae in orbis terrarum circumnavigatione, Carolo Wilkes e classe Reipublicae Faederate Duce, lexit et descripsit Jacobus D. Dana. Pars III (Amphipoda 1). Proc Am Acad Arts Sci 2:201–220
- Della Valle A (1893) Gammarini del Golfo di Napoli. Fauna Flora Golf Neapel 20:1–948
- Gurjanova E (1951) Amphipoda Gammaridea from the seas of the USSR and vicinity. Opredeliteli Faune SSSR Zool Inst Akad Nauk SSSR 41:1–1029 (In Russian)
- Krapp-Schickel G (1989) Family Leucothoidae. In: Ruffo S, et al. (eds) The Amphipoda of the Mediterranean. Part 2 Gammaridea (Haustoriidae to Lysianassidae). Mém Inst Océan Monaco 13, pp 443–459
- Krapp-Schickel T (2008) What has happened with the *Maera*-clade (Crustacea, Amphipoda) during the last decades? Boll Mus Civ Stor Natur Verona Botanica Zoologia: 3–32
- Krapp-Schickel T, Jarrett NE (2000) The amphipod family Melitidae on the Pacific coast of North America. Part II. The *Maera-Ceradocus* complex. Amphipacifica 2(4):23–61
- Krapp-Schickel T, Menioui M (2005) *Leucothoe* species from Moroccan Atlantic coasts with redefinition of some species within the *Leucothoe spinicarpa* clade. Boll Mus Civ Stor Natur Verona Botanica-Zoologia 29:63–83
- Lincoln RJ (1979) British marine Amphipoda: Gammaridea. British Museum, London
- Mateus A, Mateus E (1986) Campagne de la 'Calypso' dans le Golfe de Guinée et aux Iles Principe, São Tomé et Annobon (1956). Amphipodes récoltés à bord de la 'Calypso'. Anais Fac Ciénc Porto 66:125–223
- Montagu G (1804) Description of several marine animals found on the south coast of Devonshire. Trans Linn Soc London 7:61–85
- Norman AM (1869) Shetland final dredging report—Part II. On the Crustacea, Tunicata, Polyzoa, Echinodermata, Actinozoa, Hydrozoa & Porifera. Rep thirty-eighth Meeting Brit Ass Adv Sci 38:113–141
- Reid DM (1951) Report on the Amphipoda (Gammaridea and Caprellidea) of the coast of tropical West Africa. Atlantide Rep 2:189–291
- Sars GO (1885) Zoology. Crustacea I. Norweg N-Atl Exped 1876–1878 6:1–280
- Sars GO (1890–95) Amphipoda. An account of the Crustacea of Norway with short descriptions and figures of all the species I. Alb. Cammermeyer, Christiania & Copenhagen
- Schellenberg A (1942) Krebstiere oder Crustacea IV. Flohkrebse oder Amphipoda. Die Tierwelt Deutschlands 40:1–252
- Shoemaker CR (1930) The Amphipoda of the Cheticamp expedition of 1917. Contr Can Biol Fish 5:221–359
- Stebbing TRR (1888) Report on the Amphipoda collected by H.M.S. Challenger during the years 1873–1876. Rep Sci Res Voyage H.M.S. Challenger 1873–76. Zool 29:1–1737
- Stebbing TRR (1906) Amphipoda I. Gammaridea. Das Tierreich 21:1–806
- Stephensen K (1923) Crustacea Malacostraca. V. (Amphipoda I). Dan Ingolf-Exped 3:1–100
- Stephensen K (1925) Crustacea Malacostraca. VI. (Amphipoda II). Dan Ingolf-Exped 3:101–178
- Stephensen K (1931) Crustacea Malacostraca. VII. (Amphipoda III). Dan Ingolf-Exped 3:179–290
- Stephensen K (1940) The Amphipoda of N Norway and Spitzbergen with adjacent waters. Tromsø Mus Skr 3(1):279–362
- Stephensen K (1944) Crustacea Malacostraca. VIII. (Amphipoda IV). Dan Ingolf-Exped 3(13):1–51
- Thomas JD, Klebba KN (2007) New species and host associations of commensal leucothoid amphipods from coral reefs in Florida and Belize. Zootaxa 1494:1–44

- von der Brüggen E (1907) Amphipoda. Zoologische Ergebnisse der russischen Expeditionen nach Spitzbergen. Ann Mus Zool Acad Imp Sci St Petersburg 11:214–244
- White KN (2011) A taxonomic review of the Leucothoidae (Crustacea: Amphipoda). Zootaxa 3078:1–113
- White KN, Reimer JD (2012a) Commensal Leucothoidae (Crustacea, Amphipoda) of the Ryukyu Archipelago, Japan. Part I: ascidian dwellers. ZooKeys 163:13–55
- White KN, Reimer JD (2012b) Commensal Leucothoidae (Crustacea, Amphipoda) of the Ryukyu Archipelago, Japan. Part II: sponge-dwellers. ZooKeys 166:1–58
- White KN, Reimer JD (2012c) Commensal Leucothoidae (Crustacea, Amphipoda) of the Ryukyu Archipelago, Japan. Part III. coral-rubble. ZooKeys 173:11–50