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New species and host associations of commensal leucothoid amphipods from coral reefs in Florida and Belize (Crustacea:Amphipoda)

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Abstract

Six new amphipod species in the genus *Leucothoe* from the tropical western Atlantic Ocean are described and illustrated. Extensive field collecting and specialized underwater collecting techniques have documented 43 new invertebrate host records for these new taxa. Four of these new species inhabit interior canals of sponges; *Leucothoe barana* n.sp., *Leucothoe garifunae* n.sp., *Leucothoe saron* n.sp., and *Leucothoe ubouhu* n.sp. A remarkable new species, *Leucothoe flammosa* n.sp., nestles in the gills of seven species of bivalve mollusks. A single species, *Leucothoe wuriti* n.sp., appears restricted to the branchial chamber of two species of solitary ascidians. Detailed illustrations and scanning electron microscopy enables comparison of ultrastructure details. More precise taxonomic character morphologies are also presented thus allowing improved taxonomic precision within the family Leucothoidae.

Key words: Amphipods, commensal, eusocial, coral reefs, marine biodiversity, sponges, tunicates, ascidians, *Gari'funa*

Introduction

In 2000 Jim Lowry *et al.* proposed merging the families Anamixidae and Leucothoidae. The revised Leucothoidae (*sensu lato*) is now comprised of 122 species in six genera. This includes 33 former anamixid species in *Anamixis* Stebbing, 1897 (19 spp.); *Nepanamixis* Thomas, 1997a (4 spp.); and *Paranamixis* Schellenberg, 1938 (10 spp.); and 89 leucothoid species, *Leucothoe* Leach, 1814a (86 spp.); *Leucothoella* Schellenberg, 1928b (2 spp.); and *Paraleucothoe* Stebbing, 1899 (1 sp.).

Species in the former anamixid genera differ from other leucothoids in exhibiting radical sexual dimorphism, eusocial population structure, and tropic to warm temperate distributions. Species in *Leucothoe* and *Leucothoella* exhibit minor sexual dimorphism, and tropic to polar distributions. Thiel (1999, 2000) has reported extended parental care of young in several *Leucothoe* taxa. One of the more derived leucothoid genera, *Paraleucothoe novaehollandiae*, Haswell, 1879a, an endocommensal of the stalked ascidian *Pyura stolonifera* Heller, 1878 (*Paraleucothoe flindersi* Stebbing, 1888 and *Paraleucothoe brevidigitata*, Miers, 1884) has moderately developed sexually dimorphic characters, and a temperate to cold temperate distribution (Dalby, 1996).

While leucothoids are frequently reported as associates of sessile invertebrates such as sponges, ascidians, and bivalve mollusks, little specific host information has been documented. The works of Thomas (1997a) in the marine tropics and Vader (1984a,b) in Norwegian waters are exceptions. Prior to the discovery by Thomas and Barnard (1983) of a radical transformation where “leucomorph” males (Leucothoidae: *Leucothoides*) transform into “anamorph” hypermales (Anamixidae) these stages were treated as separate families. Thomas (1997a) documented four leucomorph species with their anamorph counterparts; however, many “orphan” species remain to be associated with their anamorph counterparts. Confirmation of these unassociated species can only be accomplished by collection of both stages inside their invertebrate host or by molecular genetic techniques.

With their distinct morphology and common occurrence in shallow coastal marine environments, leucothoid amphipods drew the attention of early naturalists, resulting in some of the earliest recorded amphipod descriptions. However, taxonomists of the 1700’s lacked the sophisticated taxonomic tools and equipment widely available today. Thus many early descriptive efforts lacked diagnostic figures and text descriptions. One product of this study is a revised list of diagnostic taxonomic characters for the Leucothoidae (Table 1).

TABLE 1. Diagnostic taxonomic characters of Leucothoidae examined in this study.

Structure:	Diagnostic characters
1. Head:	Anteroventral margin; presence and shape of mid-ventral keel.
2. Antennae:	Length and proportion; length ratio of A1 to A2; length ratio of A1 and A2 to body.
3. Coxa 1:	Shape; setation.
4. Coxa 4:	Anterior margin – excavate vs. tapered.
5. Gnathopod 1:	Articles 2, 5, and 6 – medial and lateral setal arrangements and ornamentation; article 5 – dentition.
6. Gnathopod 2:	Articles 2, 5, and 6 – medial and lateral setal arrangements and ornamentation; article 5 – dentition and number, placement, and length of mediofacial setal rows; article 6 – length, serration, setal arrangements, and ornamentation.
7. Mouthparts:	Maxilliped – inner and outer plates, palp setal arrangements and ornamentation; maxillae 1 and 2—setal arrangements and ornamentation; Upper and lower lips—setal arrangements.
8. Pereopods 5–7:	Article 2—width to length ratio, ornamentation.
9. Uropods 1–3:	Length ratios to each other, spination; length ratios of rami to peduncle.
10. Epimera 1–3:	Setal arrangements; E3—shape of posteroventral margin.
11. Telson:	Length to width ratio; terminal ornamentation.

Leucothoids are of scientific interest for their unusual ecology as commensal inhabitants of sessile invertebrates such as sponges, sea squirts, and bivalves. Obligate commensal species have evolved highly characteristic and unusual morphologies and feeding strategies due to their way of life, including eusocial structure, a condition once thought limited to insects and naked mole rats. Duffy first documented eusocial behavior in marine sponge-inhabiting snapping shrimp (1996, 2003). Thomas documented eusociality, communal living,

and “nest guarding” in highly derived tropical leucothoids (1979, 1997a). Because of their cryptic lifestyle and need for specialized collecting methods, leucothoid diversity is greatly underrepresented in museum collections. Specialized in-situ underwater collecting techniques pioneered by the authors are beginning to reveal the vast extent of leucothoid diversity (Thomas, 1997b, Thomas and Klebba, 2006).

Ongoing field and lab studies by the authors and colleagues suggest that potentially hundreds of new species remain to be discovered and described. While leucothoid amphipods offer interesting avenues of investigation including host associations, distribution and behavior patterns, eusocial structure, and extended parental care, their wider use by investigators is constrained by taxonomic confusion within the group. This taxonomic constraint is addressed by workers in marine invertebrate groups that encounter specimens of *Leucothoe* in their studies, declaring that the “...genus is in urgent need of taxonomic revision” (Morton, 1980). Many cryptic species groups exist in the Leucothoidae, a situation clearly illustrated by our current research, which has revealed at least 13 distinct new species formerly attributable to the *Leucothoe spinicarpa* (Abildgaard, 1789) “complex,” a common taxonomic dumping ground for poorly resolved *Leucothoe* species.

Materials and methods

Using SCUBA and specialized underwater collecting techniques amphipods were collected *in-situ* from marine sponges, bivalves, and ascidians throughout southeast Florida, the Florida Keys, and the western Caribbean Sea (Belize). Specimens were captured directly from their host either with a modified squirt bottle, or by isolating hosts and substrata underwater in plastic bags and coercing the amphipods from the host using a small amount of alcohol or formalin in the lab.

Specimens were either fixed in 2% buffered formalin or preserved in 70% ethanol. Prior to observation, specimens were gently cleaned with small sable hair brushes and transferred to glycerin for dissection, illustration, and analysis. For SEM analysis, specimens were rehydrated to distilled water (three fluid changes for 10 minutes each), soaked in a dilute surfactant for 15 minutes (two drops of Tween 80 in 100 ml of water), briefly sonicated (10 seconds) to remove accumulated surface debris, and re-rinsed in distilled water (three fluid changes for 10 minutes each). Specimens were then fixed in salt water buffered osmium tetroxide (equal parts, under fume hood) for two and a half hours, dehydrated in a graded alcohol series, transferred to acetone (three fluid changes for 10 minutes each), soaked in Hexamethyldisilazane Reagent (HMDS) for 15 minutes, air-dried overnight, and sputter coated with palladium for scanning electron microscopy (SEM). The preparation protocol was modified from Felgenhauer (1987) using a more finely graded alcohol series (5%, 10%, 15%, 25%, 35%, 50%, 60%, 70%, 75%, 80%, 85%, 90%, 95%, and 100%) to prevent distortion and shrinkage. Photographs were taken with an ISI-DS-130 dual state scanning electron microscope.

Results

Analysis of collections from southeastern Florida, the Florida Keys, and the western Caribbean Sea (Belize) revealed 11 new amphipod species in the family Leucothoidae of which six new species are fully described and illustrated. Two recently described species, *Leucothoe ashleyae* and *Leucothoe kensleyi* (Thomas & Klebba, 2006), and are also treated in this analysis. Additionally, we have confirmed another three undescribed species that require further analysis prior to formal descriptions but are detailed here for comparative purposes (Figure 25, Table 4). New morphological information regarding *Leucothoe urospinosa* Serejo, 1998 is also presented (Figure 26). Figures 23–24 provide comparative differences in diagnostic characters among species treated herein.

TABLE 2. Invertebrate hosts of *Leucothoe* amphipods; F–Florida, B–Belize.

Invertebrate hosts of <i>Leucothoe</i> amphipods	With commensals	Without commensals	Not sampled
Sponges:			
<i>Agelas conifera</i> (Schmidt, 1870)	B		F
<i>Agelas dispar</i> Duchassaing and Michelotti, 1864	B		F
<i>Agelas sceptrum</i> Lamarck, 1815		F	B
<i>Aiolochoxia crassa</i> (Hyatt, 1875)	B		F
<i>Amphimedon compressa</i> Duchassaing and Michelotti, 1864	B		F
<i>Amphimedon erina</i> de Laubenfels, 1936b	B		F
<i>Anthosigmella varians</i> (Duchassaing and Michelotti, 1864)		B	F
<i>Aplysina fistularis</i> (Pallas, 1766)		F	B
<i>Aplysina lacunosa</i> (Pallas, 1766)		B	F
<i>Callyspongia plicifera</i> (Lamarck, 1814)		B	F
<i>Callyspongia vaginalis</i> (Lamarck, 1814)	F,B		
<i>Cinachyra</i> sp. Sollas, 1886		B	F
<i>Geodia neptuni</i> Sollas, 1886b		B	F
<i>Haliclona mucifibrosa</i> de Weerd et al., 1991		B	F
<i>Holopsamma helwigii</i> de Laubenfels, 1936a	F	B	
<i>Hyrtilos</i> sp. Duchassaing and Michelotti, 1864	B		F
<i>Iotrochota birotulata</i> (Higgin, 1877)	B	F	
<i>Ircinia felix</i> (Duchassaing and Michelotti, 1864)		B	F
<i>Ircinia strobilina</i> Lamarck, 1816		B	F
<i>Leucetta imberbis</i> (Duchassaing and Michelotti, 1864)	B		F
<i>Leucosolenia</i> sp. Bowerbank, 1864	B		F
<i>Lissodendoryx isodictyalis</i> (Carter, 1882)	B		F
<i>Monanchora arbuscula</i> (de Laubenfels, 1953)	B		F
<i>Mycale laxissima</i> (Duchassaing and Michelotti, 1864)		B	F
<i>Niphates digitalis</i> (Lamarck, 1814)	F,B		
<i>Niphates erecta</i> Duchassaing and Michelotti, 1864	B		F
<i>Sphaciospongia vesparium</i> (Lamarck, 1814)	F	B	
<i>Spongia officinalis</i> subsp. <i>obliqua</i> Duchassaing and Michelotti, 1864	B		F
<i>Spongia</i> sp. Linnaeus, 1759	B		F
<i>Svenzea zeai</i> (Alvarez et al., 1998)	B		F
<i>Tedania ignis</i> (Duchassaing and Michelotti, 1864)	F,B		
<i>Verongia aurea</i> Hyatt, 1875		F	B
<i>Xestospongia muta</i> (Schmidt, 1870)		B	F
Mollusks:			
<i>Americardia media</i> Linnaeus, 1758	B		F
<i>Anadara notabilis</i> (Roding, 1798)	F		B
<i>Dendostrea frons</i> (Linnaeus, 1758)	B		F
<i>Laevicardium laevigatum</i> Linnaeus, 1758	F		B
<i>Lima scabra</i> Born, 1778	F,B		
<i>Lithophaga antillarum</i> Orbigny, 1846	B		F
<i>Lucina pennsylvanica</i> Linnaeus, 1758	B		F
<i>Mytilopsis leucopheata</i> Conrad, 1831	B		F
Ascidians:			
<i>Ascidia curvata</i> (Traustedt, 1882)	F,B		
<i>Phallusia [Ascidia] nigra</i> Savigny, 1816	F,B		

Ongoing studies in the region by the authors continue to reveal a high rate of species discovery and additional host data. All species are inquilines, associated with single or multiple host species, including sponges, bivalves, and ascidians. Host species that contained leucothoids at one location often lacked leucothoids in other locations, while many seemingly suitable sponge species analyzed contained no amphipods. Some sponge species contained high numbers of amphipods (>100), while other sponges housed only one or two individuals per sponge. Table 2 documents leucothoids and their hosts collected in Florida and Belize. Two species, *L. ashleyae* and *L. kensleyi*, exhibit an interesting reciprocal distribution pattern in the same sponge host in the western Caribbean Sea, southeastern Florida, and the Florida Keys.

Names of four of the new species are derived from the Gari'funa language of Central America. The Gari'funa, also known as Caribs, or Black Caribs, are of mixed African and Carib Indian descent, originating on St. Vincent Island in the Lesser Antilles, and later settling in other areas including Central America. Gari'funa descendants comprise approximately eight percent of the population of Belize and have a strong heritage and cultural presence in the Stann Creek District of Belize, where much of our research was conducted.

Figure Legend.—Figures with lower case letters to the left of each caption = paratype; Capital letters in figures refer to the following appendages; A = antennae, Cx = coxae, E = epimera, Hd = head, LL = lower lip, Md = mandible, N = gnathopod, P = pereopod, T = telson, U = uropod, UL = upper lip, X = maxillae. Capital letters to the right of each caption refer to the following; L = left, R = right. Lower case letters to the left of capital letters refer to the following adjectives; l = lateral, m = medial, x = magnified. Numbers to the right of capital letters refer to specific structures.

Specimens are deposited in the Yale Peabody Museum (YPM).

***Leucothoe barana* n.sp.**

Figures 1–3; 7a–b

Holotype. Male “A,” 10.17 mm, YPM38640: JDT Bel 03/12B—16Dec03; Co Cat Kay, Pelican Cays, Belize; N 16°39.527' x W 88°12.032'; patch reef, in the sponge *Amphimedon compressa*, 1–15m; J.D. Thomas and K.N. Klebba, collectors.

Paratypes. Female “B,” 8.27 mm, YPM38641: JDT Bel 03/12B—16Dec03; Co Cat Kay, Pelican Cays, Belize; N 16°39.527' x W 88°12.032'; patch reef, in the sponge *Amphimedon compressa*, 1–15m; J.D. Thomas and K.N. Klebba, collectors.

Other material examined. YPM38642: 24April04; North Pine Channel, Big Pine Key, Florida, U.S.A., N 24°40.000' x W 81°21.044'; seagrass bed, in the loggerhead sponge *Sphaciospongia vesparium*; J.D. Thomas and K.N. Klebba, collectors; JDT Bel 03/9D—12Dec03; Carrie Bow Caye, Belize; N 16°48.136' x W 88°04.723'; patch reef, in the sponge *Amphimedon compressa*; J.D. Thomas and K.N. Klebba, collectors.

Diagnosis. Head: anterior margin with sharp projection; mid-ventral keel pronounced, anterior margin vertical, projecting anteroventrally as sharp point. Maxilliped: apical lobes of inner plate each with three stout, toothed, conate setae; anterolateral margins of outer plate with numerous serrate setae; palp article 1 apical and apicolateral margins with approximately 10 serrate setae, article 4 anteromedial margin with dense covering of short pubescent setae. Coxae 1–4: anterior and ventral margins with series of sharp cusps. Gnathopod 1: basis with slightly expanded posterior margin; anterior margin with nine medium setae. Gnathopod 2: propodus with secondary row of nine mediofacial setae. Pereopods 5–7: bases narrow, posterior margins serrate.

Description of male holotype “A”. Ratios of antennae 1 and 2, 0.33 and 0.28 X body length; relative lengths of antennae 1 and 2, 1.00:0.88, flagellae 13 and 7-segmented. Anterior margin of head with small upturned angular projection; mid-ventral keel pronounced, anterior margin vertical, projecting anteroventrally as a sharp point, ventral margin straight. Coxae 1–4, width ratios 1.00:1.45:1.15:1.55; coxae 5–6 bilobed; coxa 7 reduced, ovate.

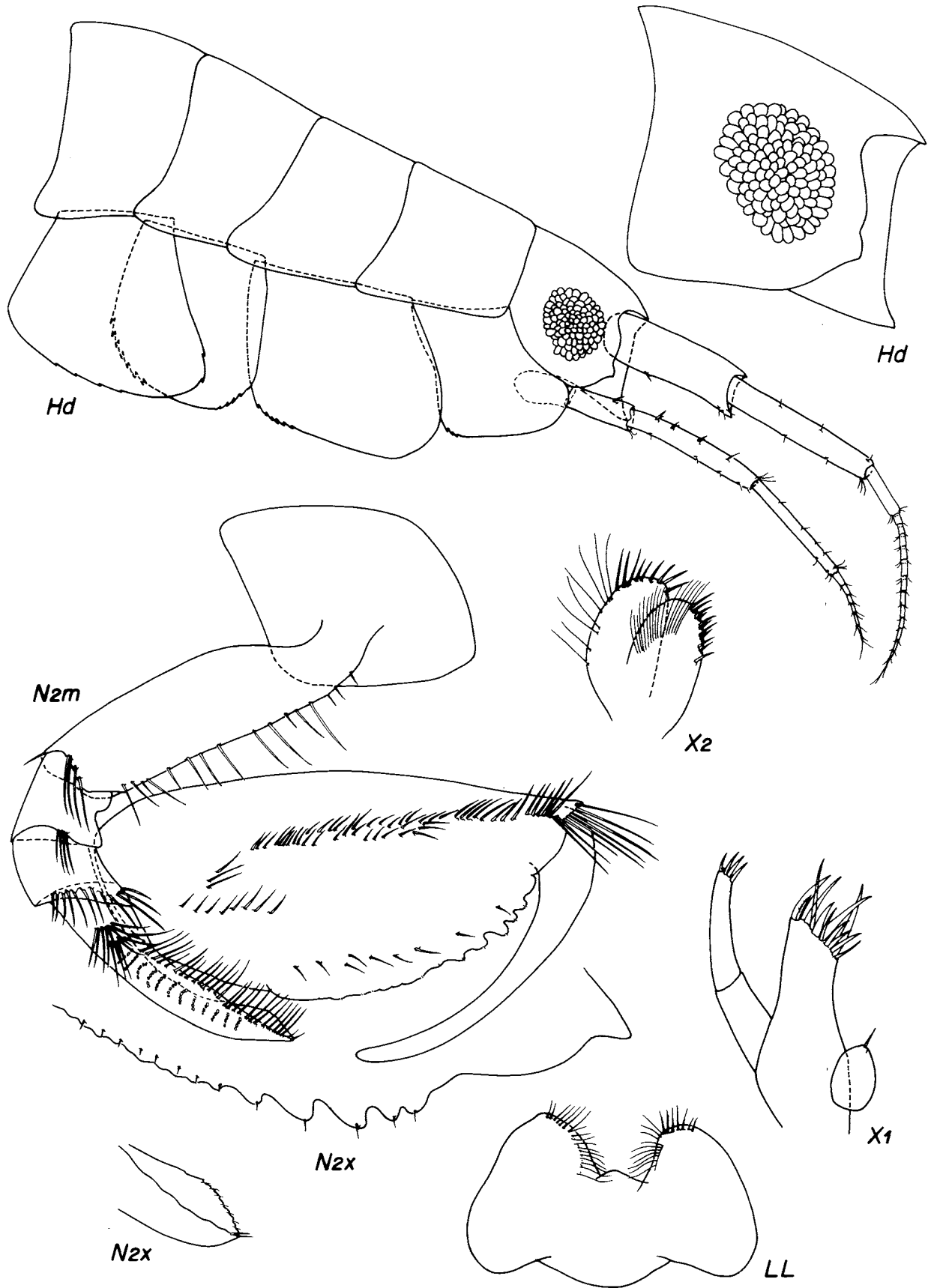


FIGURE 1. *Leucothoe barana* n.sp., male holotype "A," 10.17 mm.

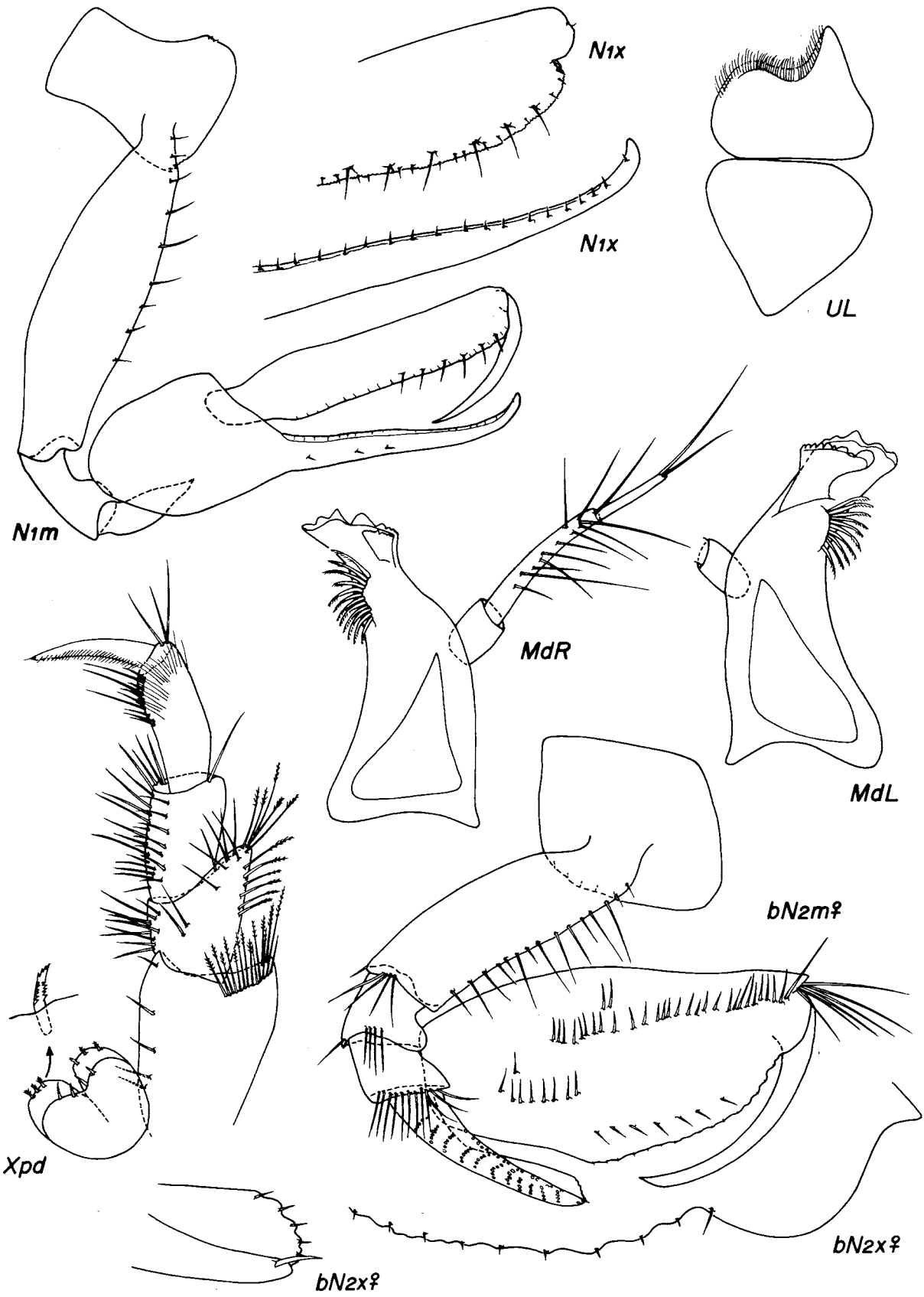


FIGURE 2. *Leucothoe barana* n.sp. male holotype "A," 10.17 mm; female paratype "B," 8.27 mm.

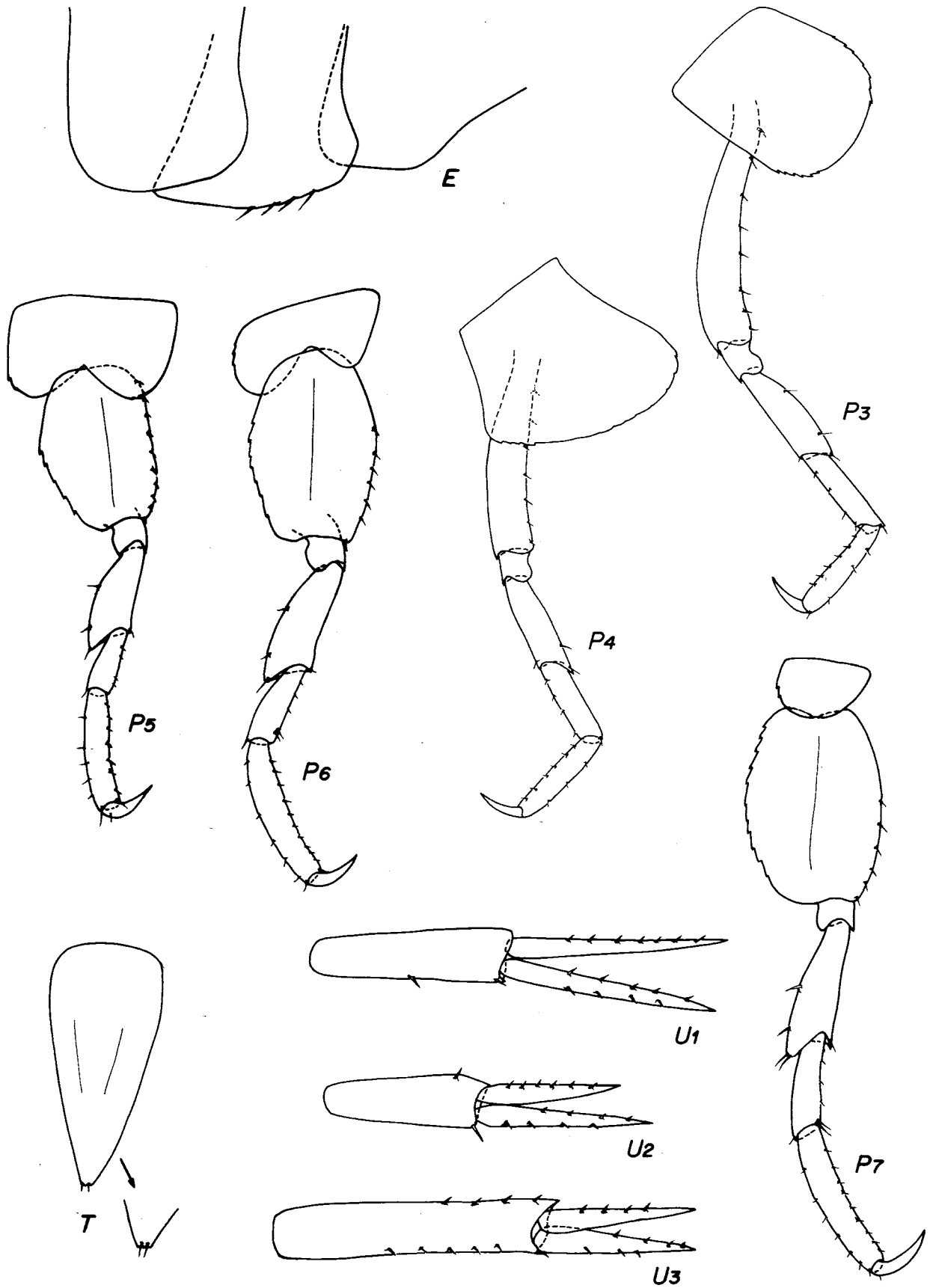


FIGURE 3. *Leucothoe barana* n.sp. male holotype "A," 10.17 mm.

Upper lip asymmetrically lobate, anterior margin setose. Mandibles lacking molar; palp 3-articulate, ratio of articles 1–3, 1.00:2.89:1.56; article 2 with 12–13 posterior and one apical seta; article 3 with two apical setae; incisors strongly dentate. Left mandible, lacinia mobilis large, strongly toothed; 10 raker spines. Right mandible, lacinia mobilis a small flake; 12 raker spines. Lower lip, inner lobes fused; outer lobes with moderate gape, anterior margins continually setose. Maxilla 1, palp 2-articulate with four apical setae; outer plate with 12 spines. Maxilla 2, inner plate with 11 stout medial marginal and 17 long facial setae; outer plate with nine stout apical and eight lateral marginal setae. Maxilliped, inner and outer plates reduced; inner plate fused, apical lobes each with three stout, toothed, conate setae; outer plate, anterolateral margins with numerous serrate setae; palp 3-articulate; palp article 1 apical and apicolateral margins with approximately 10 serrate setae, article 4 anteromedial margin with dense covering of short pubescent setae.

Gnathopod 1, anteroventral margin produced, serrate, ventral margin straight, posteroventral margin rounded with three serrations; basis linear, anterior margin with nine medium setae, posterior margin slightly inflated, setae lacking; carpal lobe thin, geniculate, LW 5, anterior margin deeply grooved with numerous short plumose setae, each margin bordered by four rows of denticles, lateral margin with three short setae; propodus, posterior margin finely serrate, lateral margin with 14 short submarginal and five-six long thick setae set in basal incision; dactyl long, with linear striations, reaching 0.47 of propodus. Gnathopod 2, coxa subquadrate, LW 1.11, anterior, ventral, and posterior margins straight, smooth, posteroventral corner with six serrations; basis linear, anterior margin with mix of 17 short to medium length setae, posterior margin bare; carpal lobe distally rounded, weakly dentate, reaching 0.53 of propodus, medial margin setose; propodus, palm convex with five blunt projections near insertion of dactyl, medial posterior margin with nine short submarginal setae, primary mediofacial setal row reaching 0.77 of propodus, secondary mediofacial row with eight linear and three oblique setae; dactyl strong, recurved, reaching 0.67 of propodus.

Pereopod 3, coxa narrow, LW 1.25, anterior margin straight, anteroventral margin with five serrations, ventrally rounded, posteroventral margin with seven serrations. Pereopod 4, coxa anterior margin slightly produced with two serrations, ventral margin slightly convex with four midventral serrations, posterior margin straight, smooth. Pereopods 5–7, coxae 5–6 bilobed; coxa 7 small, ventrally convex; pereopods 5–7 bases narrow, LW 1.47:1.45:1.44, posterior margins serrate.

Epimera 1–3, ventral setae 0:4:0, respectively; epimera 3, posteroventral margin broadly rounded. Uropods 1–3, relative lengths 1.00:0.77:1.01; relative lengths of peduncles 1–3, 1.00:0.79:1.24. Uropod 1, peduncle 0.92 X rami length, with zero medial and two lateral marginal setae; outer ramus 0.84 X inner ramus; inner ramus with seven medial and zero lateral marginal setae; outer ramus with five medial and four lateral marginal setae. Uropod 2 shortened, peduncle 0.92 X rami length, with two apical spines; outer ramus 0.83 X inner ramus; inner ramus with four medial and three lateral marginal setae; outer ramus with zero medial and six lateral marginal setae. Uropod 3, peduncle 1.40 X rami length, with six medial and four lateral marginal setae; outer ramus subequal to inner ramus; inner ramus with three medial and four lateral marginal setae; outer ramus with zero medial and four lateral marginal setae. Telson, LW 2.21, apical margin tridentate with two apical setae.

Description of female paratype “B”. Similar to male in all aspects except gnathopod 2, margin of palm with only slight projections.

Etymology. Gari’ funa term for “sea.”

Relationship. *Leucothoe barana* most closely resembles *Leucothoe kensleyi* in the angular projection on the head and the narrow bases of pereopods 5–7, but is further distinguished by the large projecting mid-ventral keel, and serrate margins of coxae 1–4. *Leucothoe barana* resembles *Leucothoe ashleyi*, *L. kensleyi*, and *Leucothoe ubouhu* n.sp.in having a secondary row of mediofacial setae on male gnathopod 2. However, *L. barana* exhibits a higher setal count (eight setae) in the secondary mediofacial row, while the other species generally have four or less setae.

Ecology. In Belize, *Leucothoe barana* inhabits the interior canals of the sponges *Amphimedon compressa*, *Calyx podatypa*, *Iotrochota birotulata*, *Leucetta imberbis*, *Niphates erecta*, *Svenzea zeai*, and *Tedania ignis*. In the Florida Keys, it was collected from the Loggerhead sponge, *Spheciospongia vesparium*.

Distribution. Western Atlantic, Belize to the Florida Keys, 1–15 meters.

***Leucothoe flammosa* n.sp.**

Figures 4–6; 7c–d

Leucothoe spinicarpa :Ortiz, 1975:8.

Holotype. Male “A,” 5.44 mm, YPM38643: Sta.—26Jun01; Key West Florida, U.S.A.; N 24°33'32.0" x W 81°48'35.14"; patch reef, in branchial chamber of the Rough File Clam, *Lima scabra*, 1–3m; J.D. Thomas and K.N. Klebba, collectors.

Paratypes. Female “B,” 4.30 mm, YPM38644: Sta.—26Jun01; Key West, Florida, U.S.A.; N 24°33'32.0" x W 81°48'35.14"; patch reef, in branchial chamber of the Rough File Clam, *Lima scabra*, 1–3m; J.D. Thomas and K.N. Klebba, collectors.

Other material examined. YPM38645: JDT Bel03–7a—4Mar03; Co Cat Cay, Pelican Cays, Belize; N 16°39.527' x W 88°12.032'; mangrove lagoon, in *Lima scabra*, 3m; J.D. Thomas and K.N. Klebba, collectors.

Diagnosis. Antennae 1 and 2: shortened. Maxilliped: inner plate with numerous facial setae. Gnathopod 1: basis, anterior margin expanded proximally, with five short setae, posterior margin with five subproximal setae, carpus posterior margin with dense brush of 17 long setae; propodus robust, dactyl a short nail. Gnathopod 2: palm oblique, with numerous submarginal facial setae. Pereopods 5–7: narrow bases. Uropod 3: inner rami lacking setae.

Description of male holotype “A”. Ratios of antennae 1 and 2, 0.21 and 0.16 X body length; relative lengths of antenna 1 and 2, 1.00:0.78, flagella 4 and 3-segmented. Anterior margin of head rounded; mid-ventral keel reduced, anterior margin apically sharp, ventral margin straight. Coxae 1–4, width ratios 1.00:0.96:1.06:1.54; coxae 5–6 bilobed; coxa 7 reduced, ovate.

Upper lip asymmetrically lobate, anterior margin setose. Mandibles lacking molar; palp 3-articulate; ratio of articles 1–3, 1.00:2.56:1.22; article 2 thickened with nine anterior setae; article 3 with two apical setae; incisors serrate, anterior margin straight. Left mandible, lacinia mobilis large, toothed; 11 raker spines. Right mandible, lacinia mobilis a small flake; 11 raker spines. Lower lip, inner lobes fused; outer lobes with moderate gape, anterior margins continually setose, dense covering of facial setae. Maxilla 1, palp 2-articulate with four apical setae; outer plate with 10 spines. Maxilla 2, inner plate with few sparse marginal, two long, stout apical and 12 lateral setae; outer plate with three stout and numerous thin apical setae, facial margin sparsely setose. Maxilliped, inner and outer plates reduces; inner plate fused, apical lobes notched with numerous facial setae; outer plate anterolateral margins with numerous setae; palp 3-articulate; palp article 1 apical and apicolateral margins with approximately 10 setae; article 4 with dense covering of short, pubescent setae.

Gnathopod 1, coxa subquadrate, anteroventral margin smooth with one submarginal seta, ventral margin straight, posteroventral margin rounded; basis proximally thickened, anteroproximal margin produced, anterior margin with five short setae, posterior margin with five subproximal setae; carpal lobe, thickened, LW 2.17, anterior margin grooved with 10 short setae, lacking lateral ornamentation, midposterior margin with five short setae, posterior margin with dense brush of 17 long setae; propodus, posterior margin smooth, lateral margin with 13 short submarginal setae; dactyl reduced, nail-like, reaching 0.18 of propodus. Gnathopod 2, coxa quadrate, LW 0.76, anterior margin straight, anteroventral margin with one seta, ventral margin slightly rounded, posterior margin smooth; basis linear, anterior margin with seven widely spaced short setae, posterior margin bare; carpal lobe curved, lacking ornamentation, apical margin slightly constricted and tridentate, reaching 0.60 of propodus, medial margin setose; propodus, palm oblique, linear, produced as thin blade with short embedded setae, posterior margin with dense tuft of submarginal setae; primary mediofacial

setal row reaching 0.61 of propodus, lacking secondary mediofacial row; dactyl smooth, curved, reaching 0.55 of propodus.

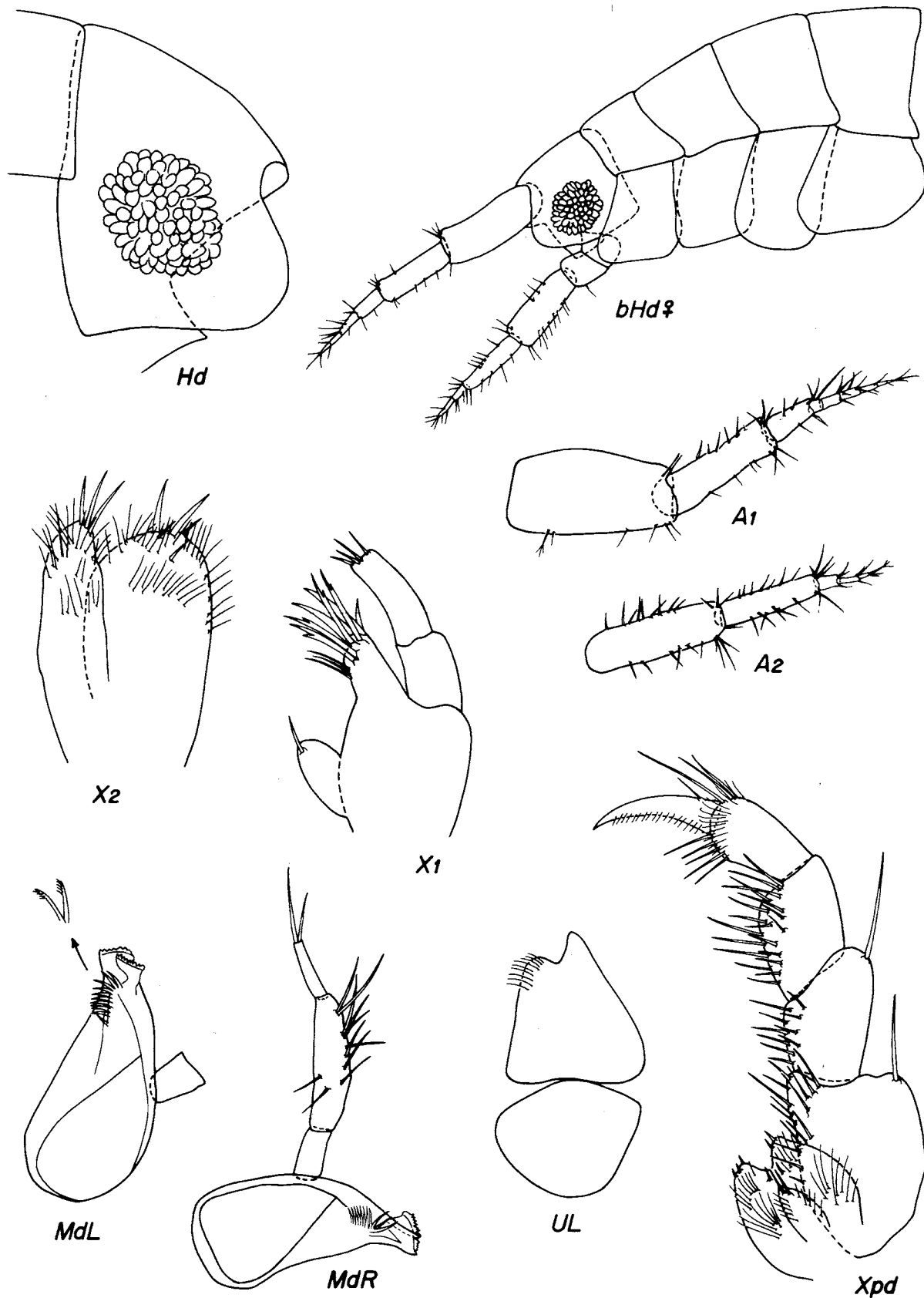


FIGURE 4. *Leucothoe flammosa* n.sp. male holotype "A," 5.44 mm; female paratype "B," 4.30 mm.

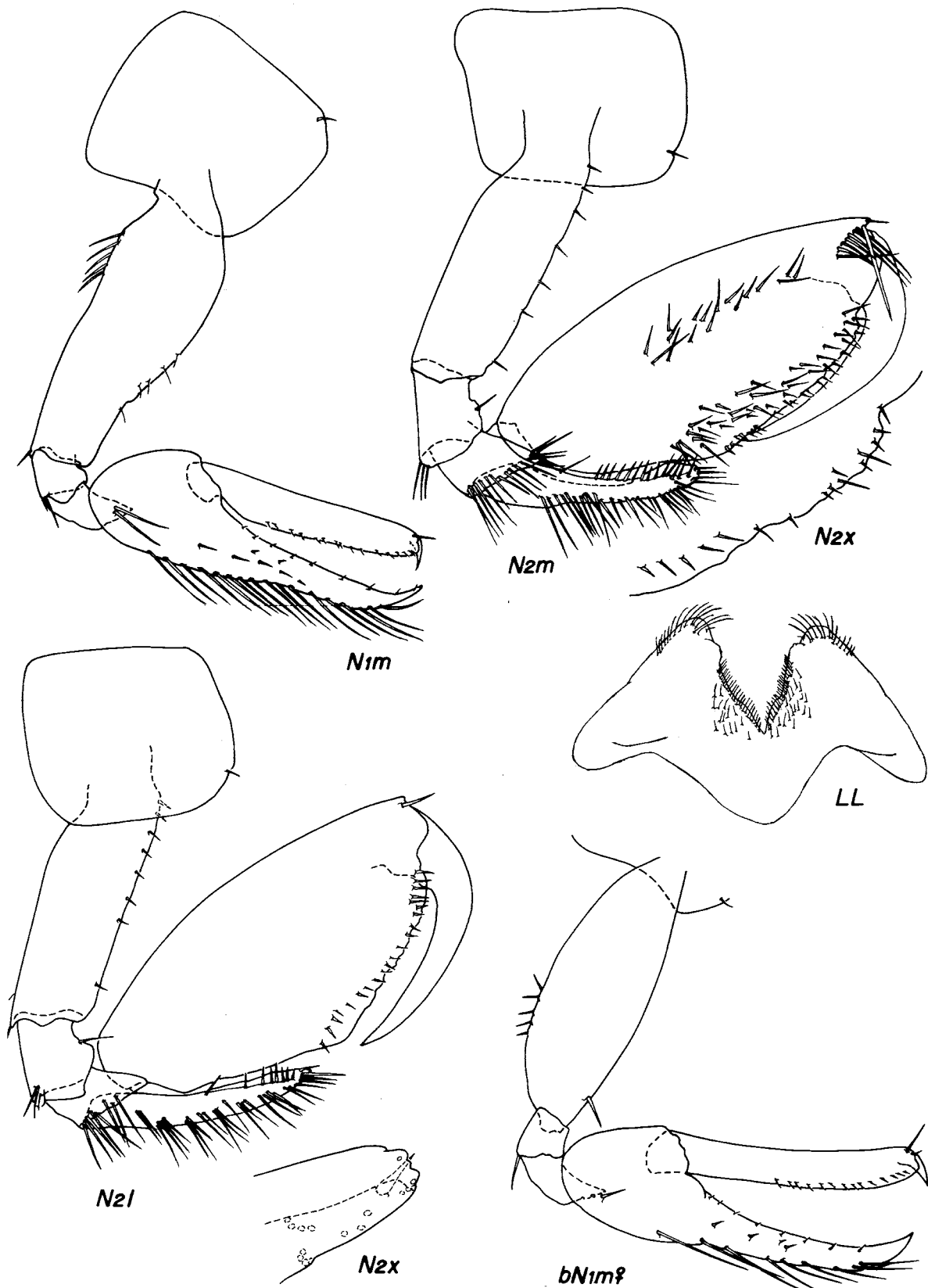


FIGURE 5. *Leucothoe flammosa* n.sp. male holotype "A," 5.44 mm; female paratype "B," 4.30 mm.

Pereopod 3, coxa quadrate, LW 1.16, anterior, ventral and posterior margins straight. Pereopod 4, coxa anterior margin straight, ventrally rounded, posterior margin straight. Pereopods 5–7, coxae 5–6 bilobed; coxa 7 small, ventrally convex; pereopods 5–7 bases narrow, LW, 1.33:1.22:1.55, posterior margins smooth.

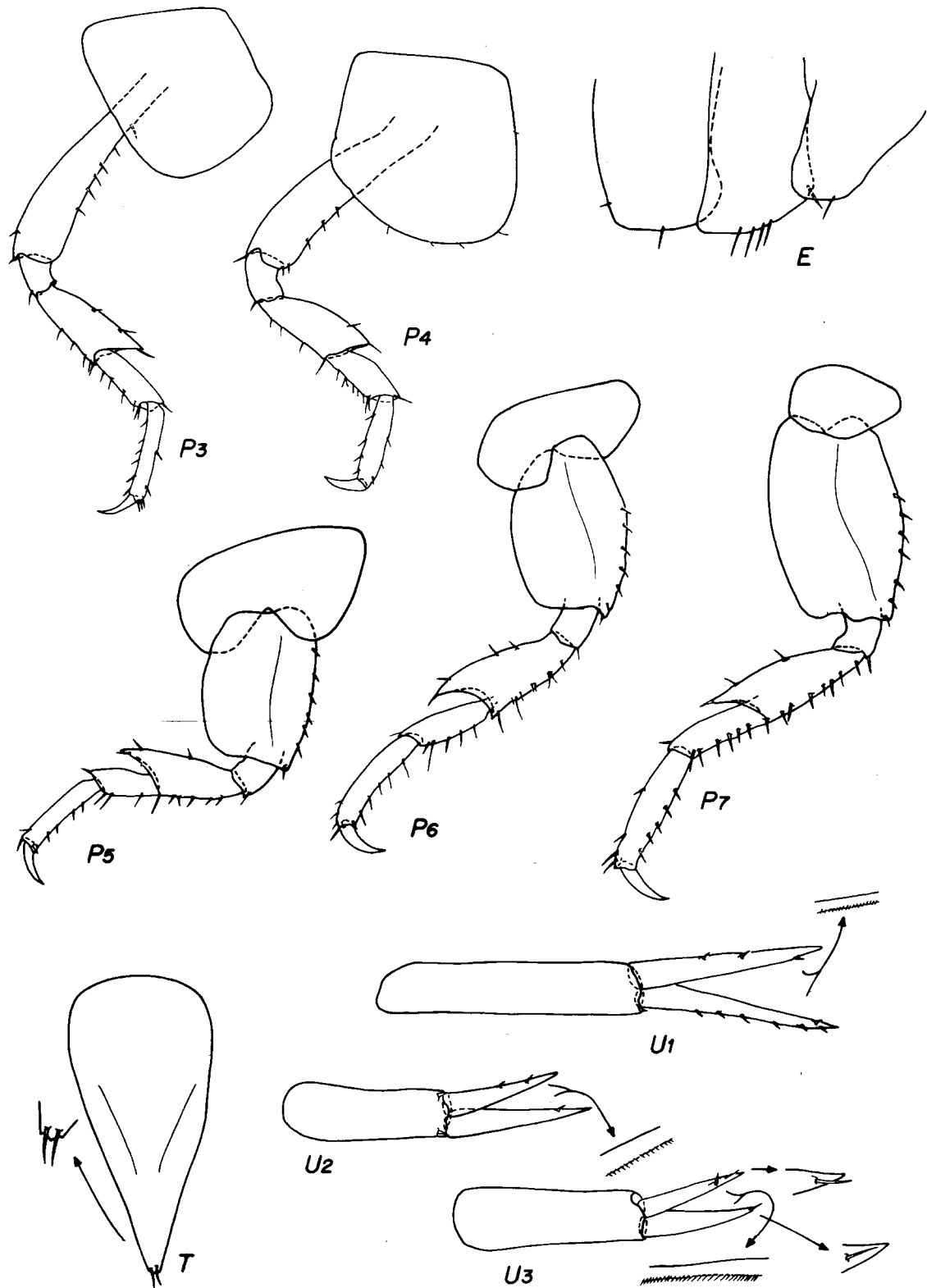


FIGURE 6. *Leucothoe flammosa* n.sp. male holotype "A," 5.44 mm.

Epimera 1–3, ventral setae, 1:5:1, respectively; epimera 2, ventral margin tapering anteriorly; epimera 3, posteroventral margin subquadrate with single posterior seta. Uropods 1–3, margins finely serrate; relative lengths 1.00:0.70:0.66; relative lengths of peduncles 1–3, 1.00:0.61:0.73. Uropod 1, peduncle 1.47 X rami length, with four medial and zero lateral marginal setae; outer ramus 0.94 X inner ramus; inner ramus with one medial and five lateral marginal setae; outer ramus with one medial and two lateral marginal setae. Uro-

pod 2 shortened, peduncle 1.13 X rami length, with one medial and one lateral apical seta; outer ramus 0.80 X inner ramus; inner ramus with one medial and zero lateral marginal setae; outer ramus with zero medial and four lateral marginal setae. Uropod 3, peduncle 1.78 X rami length, lacking setae, outer ramus 0.89 X inner ramus, inner ramus with zero marginal and one apical seta, outer ramus with one apical and one subapical seta. Telson LW 2.22, apical margin tridentate bearing two apical setae.



FIGURE 7. *Leucothoe barana* n.sp.: A. male gnathopod 1 carpus, medial, 1.73kx; B. male Gnathopod 2, medial, 127x. *Leucothoe flammosa* n.sp.: C. male gnathopod 1, medial, 173x; D. female gnathopod 2, medial, 173x.

Description of female paratype “B”. Similar to male in all aspects except gnathopod 1 basis, anterior margin straight, not expanded proximally, with a single subdistal seta, posterior margin slightly convex with five mid-marginal setae; carpus with fewer posterior setae (nine versus 17); propodus scimitar-shaped, gnathopod 2 propodus with single line of mediofacial setae.

Etymology. Latin, “flammosa” meaning “fiery red”, referring to the numerous protruding red mantle extensions of its bivalve host, the rough file clam, *Lima scabra*.

Relationship. *L. flammosa* is distinguished from all other *Leucothoe* species in having shortened antennae, bearing facial setae on the inner plate of the maxilliped, lower lip outer lobes with dense covering of facial setae, gnathopod 1 propodus with tufts of long setae on the posterior margin, and gnathopod 2 with a weak, obliquely dentate palm.

Ecology. *Leucothoe flammosa* has only been recorded from the mantle cavities of bivalve mollusks, where it inhabits the inner folds of the gills. In Florida it has been collected from the Rough File Clam, *Lima scabra* and the Eared Ark, *Anadara notabilis*. In Belize, *L. flammosa* is commonly found in *Lima scabra* and less frequently in other bivalves including *Americardia media*, *Dendostrea frons*, *Lithophaga antillarum*, *Lucina pennsylvanica*, and *Mytilopsis leucopheata*. Additional sampling in Florida waters will probably expand the list of known host associates for this species.

Prior reports of leucothoid amphipods from the mantle cavities of bivalves include Ortiz (1975) who reported “*L. spinicarpa*” from the mantle cavities of the bivalves *Lima scabra* and *Atrina rigida* (Lightfoot, 1786) in Cuban waters, and Morton (1980) who reported a probable specimen of *Leucothoe* from *Pholadomya candida* Sowerby 1823 in waters off Key West, Florida. While these reports are most likely *L. flammosa*, no specimens were saved for further studies. Because *L. flammosa* is only known from the mantle cavities of bivalves, it is likely that these reports were indeed *L. flammosa*.

Distribution. Western Atlantic, Belize to Florida, 1–20 meters.

Leucothoe garifunae n.sp.

Figures 8–10; 14a–b

Holotype. Male “A,” 5.17 mm, YPM38646: JDT Bel—03/08A, 10Dec03; Spruce Cay, south of Wee Wee Cay, Belize; N 16°44.119' x W 88°08.544'; patch reef, in the sponge *Iotrochota birotulata*, 3m; J.D. Thomas and K.N. Klebba, collectors.

Paratypes. Female “B,” 5.94 mm, YPM38647: JDT Bel 03/08A—10Dec03; Spruce Cay, south of Wee Wee Key, Belize; N 16°44.119' x W 88°08.544'; patch reef, in the sponge *Iotrochota birotulata*, 3m; J.D. Thomas and K.N. Klebba, collectors.

Other material examined. YPM38648: 20May98; Boynton Beach, Florida, U.S.A; N 26°29.029' W 80°04.002'; inlet, in *Holopsamma helwigii*, 1–4m; Martin Thiel, collector.

Diagnosis. Head: anterior margin with angular projection. Mid-ventral keel: steep, projecting beyond head margin. Gnathopod 2: anterior margin of basis with 30–40 long setae; propodus, primary mediofacial setal row reaching 0.87 of propodus, inner margin of palm with linear row of numerous short submarginal setae. Telson: apically rounded.

Description of male holotype “A”. Ratios of antennae 1 and 2, 0.31 and 0.28 X body length; relative lengths of antennae 1 and 2, 1.00:0.90, flagella 18 and 8-segmented. Mid-anterior margin of head with angular projection; mid-ventral keel pronounced, anterior margin oblique, antero-ventral margin sharp, ventral margin convex. Coxae 1–4, width ratios 1.00:1.22:1.00:1.65; coxae 5–6 bilobed; coxa 7 reduced, ovate.

Upper lip asymmetrically lobate, non-lobate margin setose. Mandibles lacking molar; palp 3-articulate, ratio of articles 1–3, 1.00:2.90:2.00; article 2 with 15 posterior setae; article 3 with two apical setae; incisors weakly dentate. Left mandible, lacinia mobilis large, toothed; 11 raker spines. Right mandible, lacinia mobilis

a small flake; 11 raker spines. Lower lip, inner lobes fused; outer lobes with moderate gape, anterior margins continually setose. Maxilla 1, palp 2-articulate with four apical setae, outer plate with eight spines. Maxilla 2, inner plate with five stout medial setae, apical margin with numerous small setae and 11 short facial setae; outer plate with three long stout apicomedial setae, remaining apical and lateral margins with row of facial setae. Maxilliped, inner and outer plates reduced; inner plate fused, apical lobes with three apical and several long setae; outer plate with few marginal setae; palp 3-articulate, palp article 1 apical and apicolateral margins with several setae; article 4 anteromedial margin with dense covering of short pubescent setae.

Gnathopod 1, coxa anteroventral corner produced with 2 small notches, ventral margin smooth, posteroventral margin quadrate; basis linear, anterior margin with nine widely spaced short setae, posterior margin lacking setae; carpal lobe, LW 4.86, anterior margin with thin groove, lined with numerous bristle-like setae, mid-posterior margin with three short setae; propodus, posterior margin finely dentate, lateral margin with five stout setae, medial margin with numerous alternating short and medium length setae; dactyl long, reaching 0.41 of propodus. Gnathopod 2, coxa sub-rectangular, LW 1.05, anterior margin straight, ventral margin slightly produced, quadrate, with numerous short submarginal setae, posterior margin straight, remainder of coxa with numerous short scattered facial setae (not illustrated); basis linear, anterior margin with 35–40 long setae, posterior margin lacking setae; carpal lobe, distal margin transverse with four large serrations, reaching 0.61 of propodus, medial margin setose, followed by a brush of baleen-like, flattened setae; propodus, palm obliquely convex with two small medial projections near insertion of dactyl, medial posterior margin with 30–40 short submarginal setae with secondary tufts of three and four setae respectively, primary mediofacial setal row reaching 0.87 of propodus, secondary mediofacial row lacking; dactyl strong, recurved, reaching 0.70 of propodus.

Pereopod 3, coxa narrow, LW 1.41, anterior margin straight, smooth, ventral margin convex, posterior margin rounded, smooth; pereopod 4, coxa anterior margin straight, ventral margin rounded, posterior margin tapered. Pereopods 5–7 coxae 5–6 bilobed; coxa 7 small, ventrally convex; pereopods 5–7 bases of normal proportions, LW 1.23:1.24:1.22, posterior margins smooth.

Epimera 1–3, lacking ventral setae; epimera 3, posteroventral margin broadly truncate. Uropods 1–3, relative lengths 1.00:0.75:0.91; relative lengths of peduncles 1–3, 1.00:0.78:1.35. Uropod 1, peduncle 1.14 X rami length, with zero medial and four lateral marginal setae; outer ramus 0.73 X inner ramus; inner ramus with zero medial and six lateral marginal setae; outer ramus with five medial and six lateral marginal setae. Uropod 2 shortened, peduncle 0.71 X rami length, with single distomedial spine; outer ramus 0.68 X inner ramus; inner ramus with four medial and five lateral marginal setae; outer ramus with zero marginal and one midapical seta. Uropod 3, peduncle subequal to rami in length, with zero medial and six lateral marginal setae; outer ramus subequal to inner ramus; inner ramus with three medial and four lateral marginal setae; outer ramus with three medial and five lateral marginal setae. Telson, LW 2.60, apical margin evenly rounded with two apical setae.

Description of female paratype “B”. Similar to male in all aspects except gnathopod 2, carpal lobe lacking thick, blunt apical seta: propodus, medial margin of palm with 12 longer setae versus 30+ shorter setae in males.

Etymology. Named in honor of the Gari’funa culture of Central America.

Relationship. *Leucothoe garifunae* resembles *Leucothoe barana* in the angle of the head and the prominent mid-ventral keel. However, *L. garifunae* is readily distinguished by differences in gnathopod 2, including the setose anterior margin of the basis, the long wiry setal tufts on the medial carpal surface, and the more numerous row of postero-marginal setae on the propodus. *L. garifunae* also differs from *L. barana* in having smooth posterior margins on pereopods 5–7 and in the rounded versus tridentate condition of the telson.

Ecology. Inhabits the interior canals of the sponges *Iotrochota birotulata*, *Pseudoceratina crassa*, and *Leucetta imperbis* in Belize, and *Holopsamma helwigii* in Florida.

Distribution. Western Atlantic, Belize to Florida, 1–4 meters.

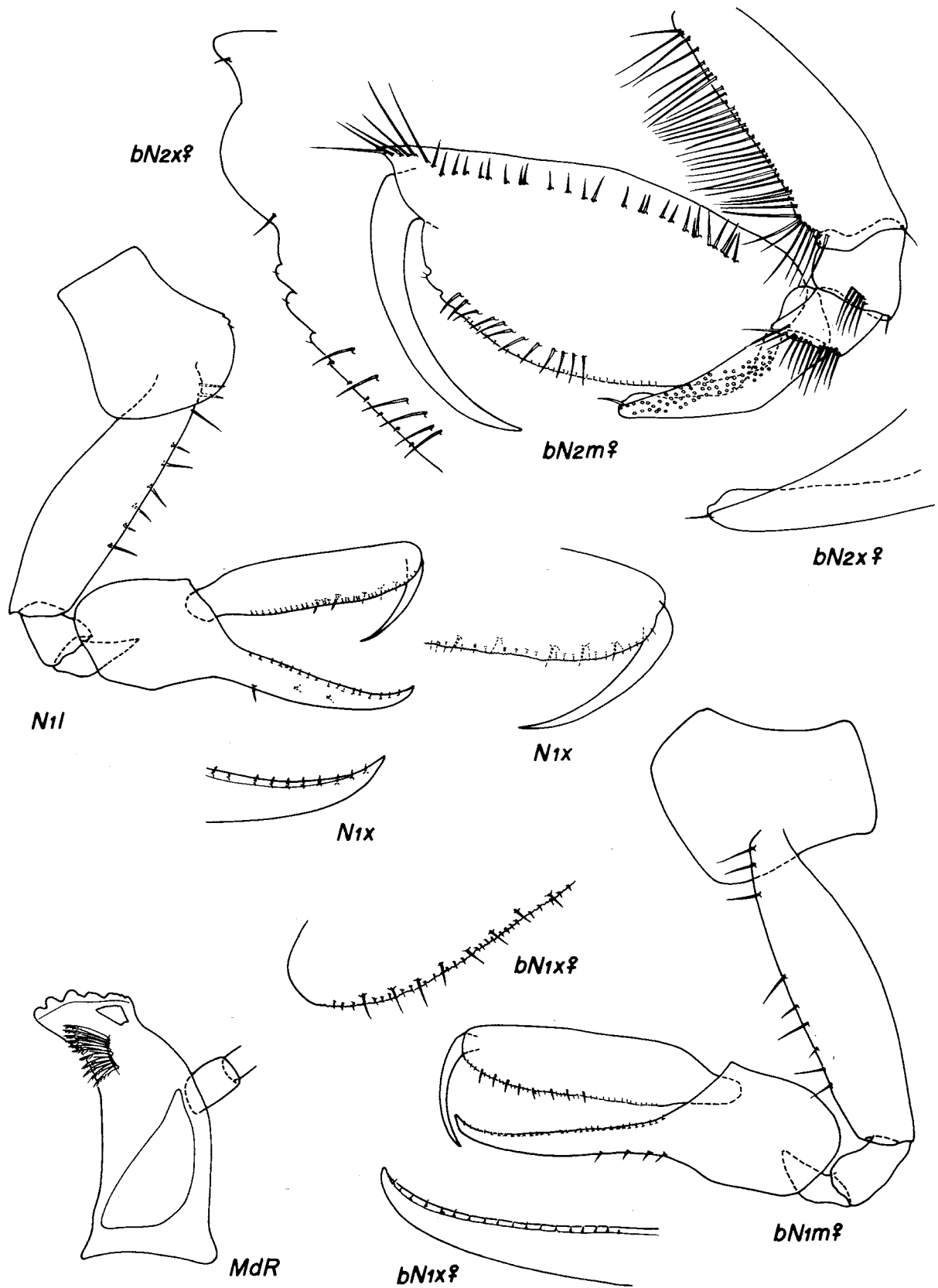


FIGURE 9. *Leucothoe garifunae* n.sp. male holotype "A," 5.17 mm; female paratype "B," 5.94 mm.

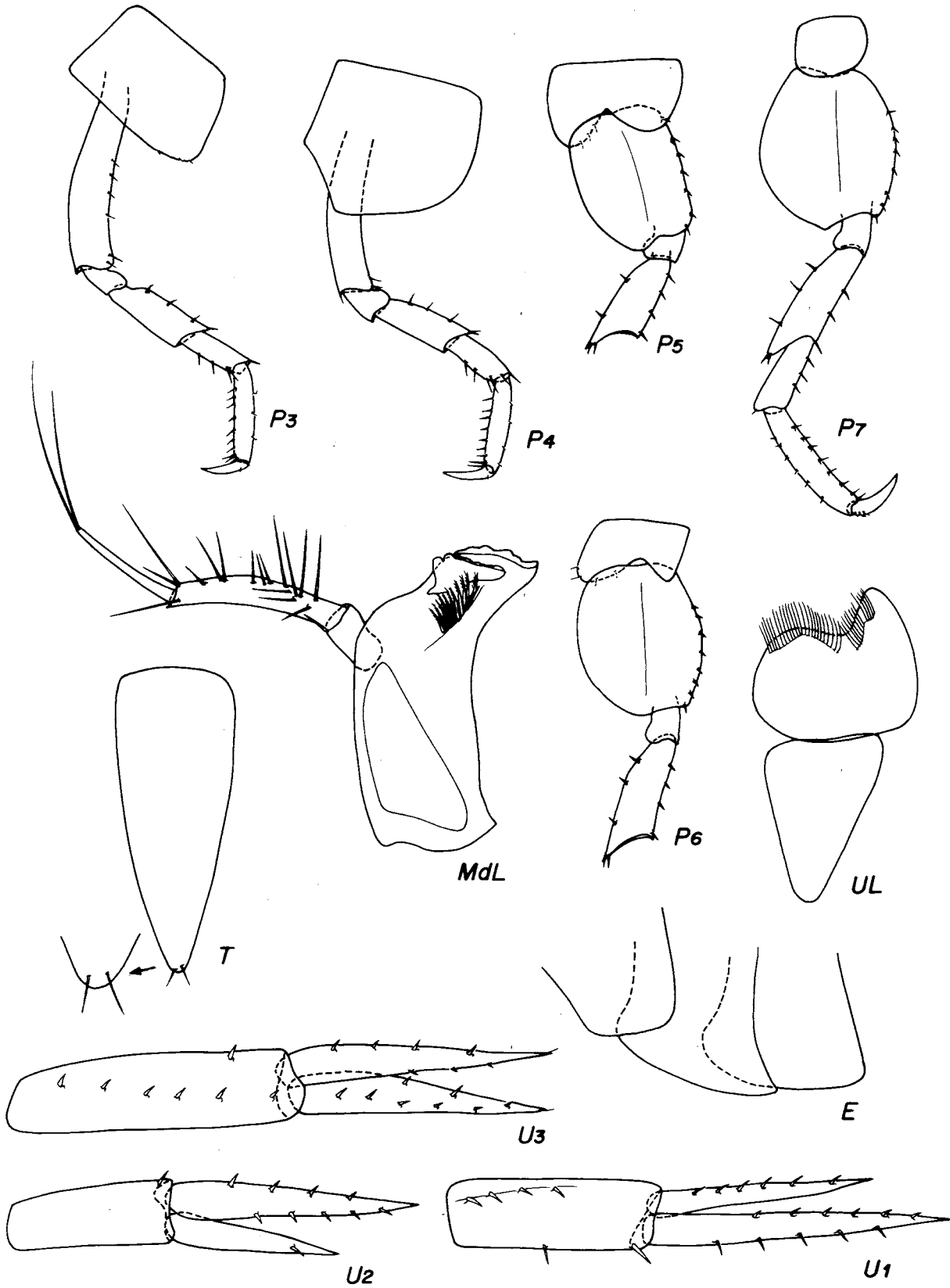


FIGURE 10. *Leucothoe garifunae* n.sp. male holotype "A," 5.17 mm.

***Leucothoe saron* n.sp.**

Figures 11–13; 14c–d

Holotype. Male “A,” 6.72 mm, YPM38649: JDT Bel 03/02A—5Dec03; Carrie Bow Caye; N 16°48.136' x W 88°04.723'; patch reef, rubble bottom, in the sponge *Pseudoceratina crassa*, 10m; J.D. Thomas and K.N. Klebba, collectors.

Paratypes. Female “B,” 6.85mm, YPM38650: JDT Bel 03/02A, 5Dec03; Carrie Bow Caye; N 16°48.136' x W 88°04.723'; patch reef, rubble bottom, in the sponge *Pseudoceratina crassa*, 10m; J.D. Thomas and K.N. Klebba, collectors.

Diagnosis. Gnathopod 2: distomedial margins of articles 2 and 3 each with long brush of recurved setae. Coxa 3: narrow. Epimera 1–3: ventral margins with four, three and two anteroventral setae.

Description of male holotype “A,” Ratios of antennae 1 and 2, 0.39 and 0.29 X body length; relative lengths of antenna 1 and 2, 1.00:0.76, flagella 11 and 7-segmented, respectively. Anterior margin of head rounded; midventral keel anterior margin sinuous, ventral margin broadly rounded. Coxae 1–4, width ratios 1.00:1.27:0.87:1.30; coxae 5–6 bilobed; coxa 7 reduced, ovate.

Upper lip asymmetrically lobate, anterior margin setose. Mandibles lacking molar; palp 3-articulate, ratio of articles 1–3, 1.00:3.22:3.11; article 2 with five anterior, two posterior, and two apical setae; article 3 with two apical setae; incisors strongly toothed. Left mandible, lacinia mobilis large, toothed; 11 raker spines. Right mandible, lacinia mobilis a small flake; 12 raker spines. Lower lip, inner lobes fused; outer lobes with moderate gape, anterior margins continually setose. Maxilla 1, palp 2-articulate, with five apical setae; outer plate with eight spines and row of subapical setae. Maxilla 2, inner plate with eight stout medial setae and oblique row of thin lateral setae; outer plate with four stout apical setae and row of submarginal lateral setae. Maxilliped, inner and outer plates reduced; inner plate fused, apical lobes each with three serrate setae; outer plate, anterolateral margin with few setae; palp 3-articulate; palp article 1 apical and apicolateral margins with several serrate setae; article 4 anteromedial margin with dense covering of short pubescent setae.

Gnathopod 1, coxa anteroventral margin produced, ventral margin straight, posterior margin slightly produced; basis linear, anterior margin with four short setae, posterior margin bare; carpal lobe, LW 7.33, anterior margin deeply grooved, margins tuberculate, with 13 short setae; propodus, posterior margin finely denticulate with seven submarginal setae interspersed with numerous short setae, lateral margin bare; dactyl long, with linear striations, reaching 0.50 of propodus. Gnathopod 2, coxa subrectangular, LW 1.08, anterior, ventral, and posterior margins slightly rounded; basis linear, anterior margin with 13 short setae, posterior margin lacking setae; distal margin of articles 2 and 3 with a brush of long recurved setae, the latter reaching midway along carpus; carpal lobe expanded distally, apical margin obliquely serrate, reaching 0.68 along propodus; propodus, palm convex with one strong process near insertion of dactyl, remainder of palm evenly rounded with numerous short subapical setae, primary mediofacial setal row reaching 0.66 of propodus, secondary mediofacial row lacking; dactyl strongly recurved with numerous linear striations, reaching 0.68 of propodus.

Pereopod 3, coxa narrow, LW 1.33, anterior margin rounded, ventral margin convex, posterior margin straight. Pereopod 4, coxa anterior margin straight, ventral margin produced, posterior margin slightly excavate. Pereopods 5–7, coxae 5–6 bilobed; coxa 7 small, ventrally convex; pereopods 5–7 bases slightly expanded, LW 1.26:1.15:1.14, posterior margins smooth.

Epimera 1–3, ventral setae 4:3:2, respectively; epimera 3, posteroventral margin rounded. Uropods 1–3, relative lengths 1.00:0.71:0.87; relative lengths of peduncles 1–3, 1.00:0.69:1.00. Uropod 1, peduncle 0.92 X rami length, with one medial and three lateral setae; outer ramus subequal to inner ramus; inner ramus with nine medial and zero lateral setae; outer ramus with seven stout medial and five lateral setae. Uropod 2 shortened, peduncle 0.89 X rami length; outer ramus 0.77 X inner ramus; inner ramus with nine medial and four lateral setae; outer ramus with five medial and three lateral setae. Uropod 3, peduncle 1.28 X rami length; outer ramus 0.93 X inner ramus; inner ramus with one medial and four lateral setae; outer ramus with one medial and four lateral setae. Telson LW 1.68, apical margin tridentate bearing two apical setae.

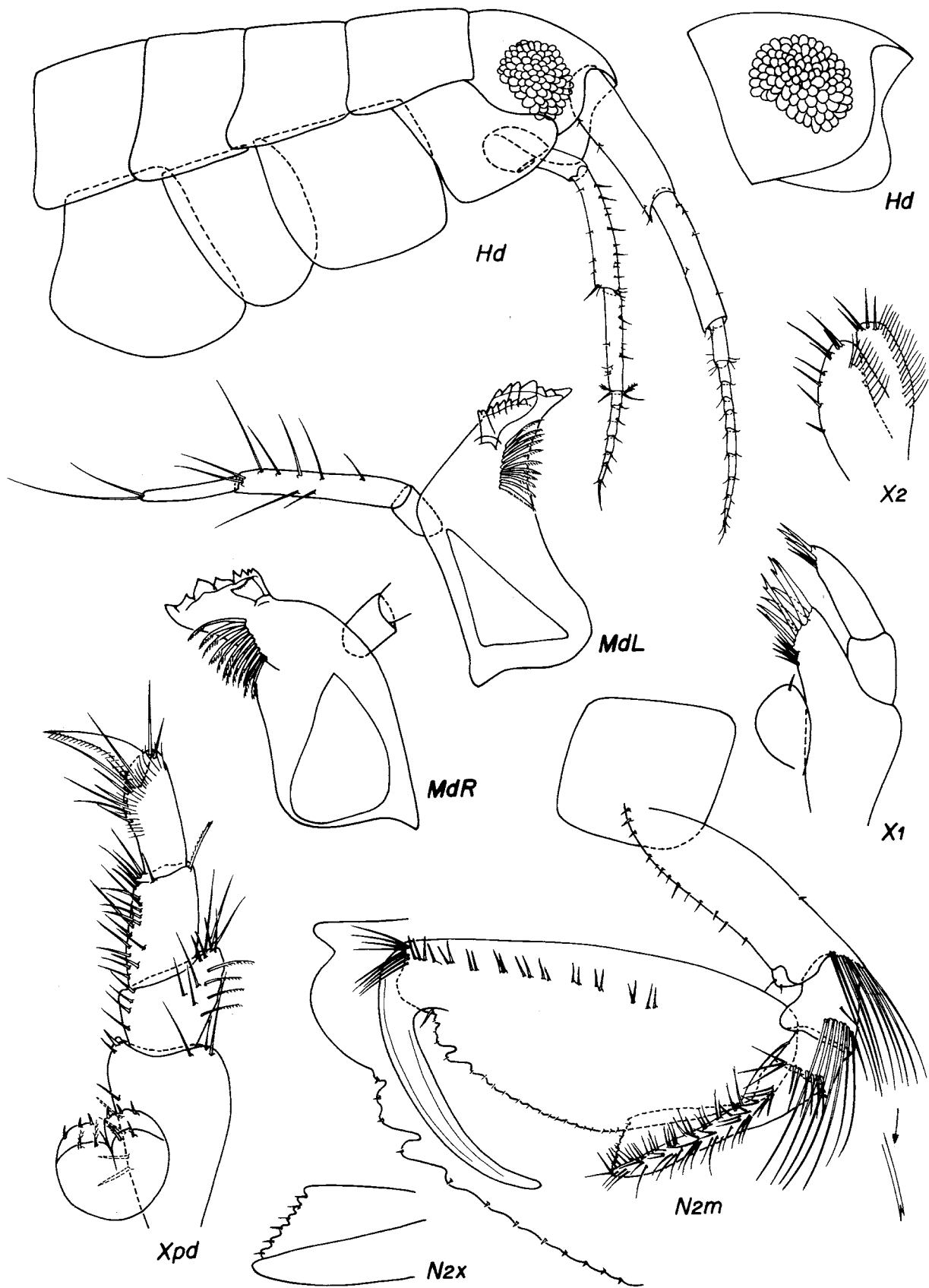


FIGURE 11. *Leucothoe saron* n.sp. male holotype "A," 6.72 mm.

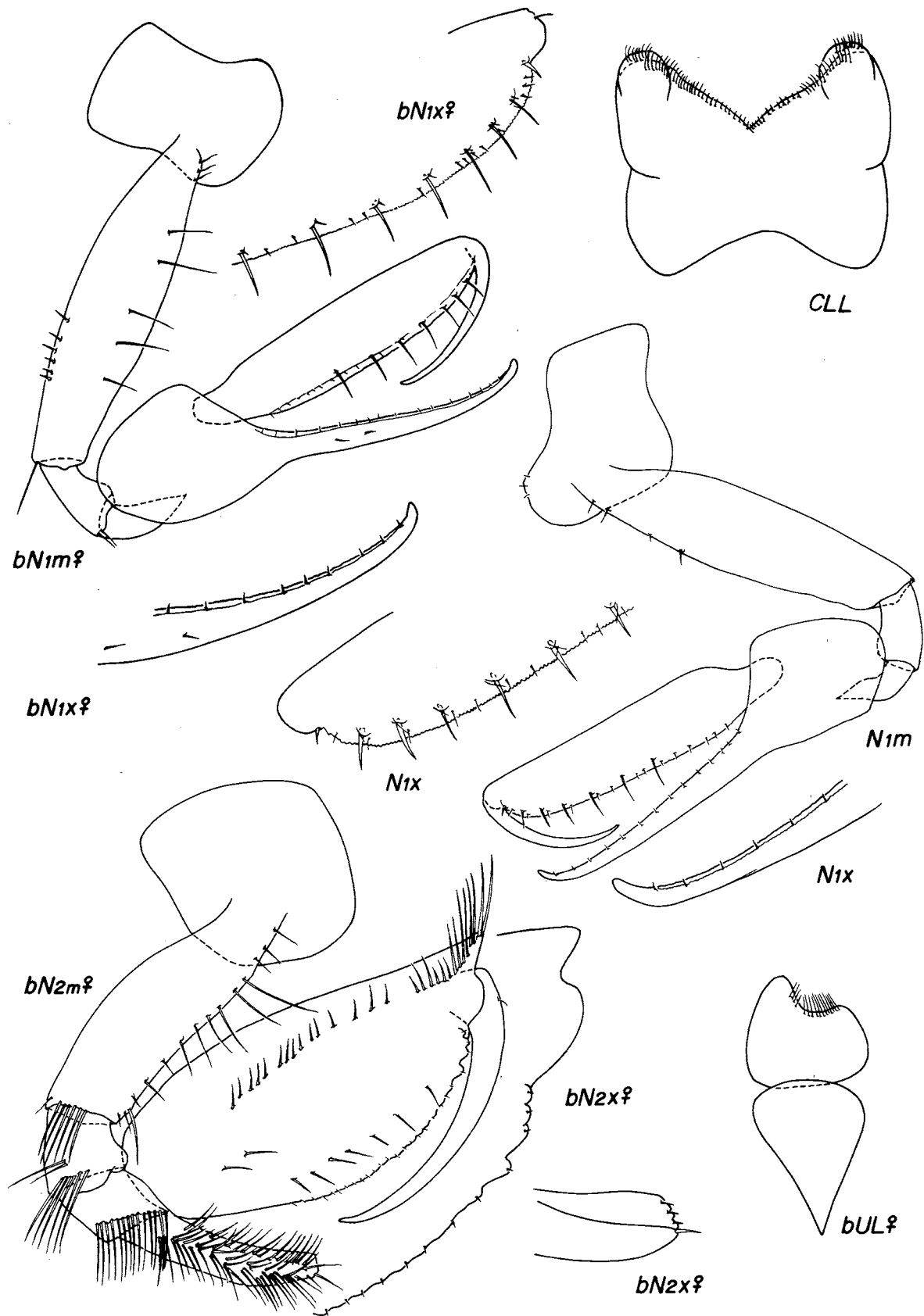


FIGURE 12. *Leucothoe saron* n.sp. male holotype "A," 6.72 mm; female paratype "B," 6.85 mm.

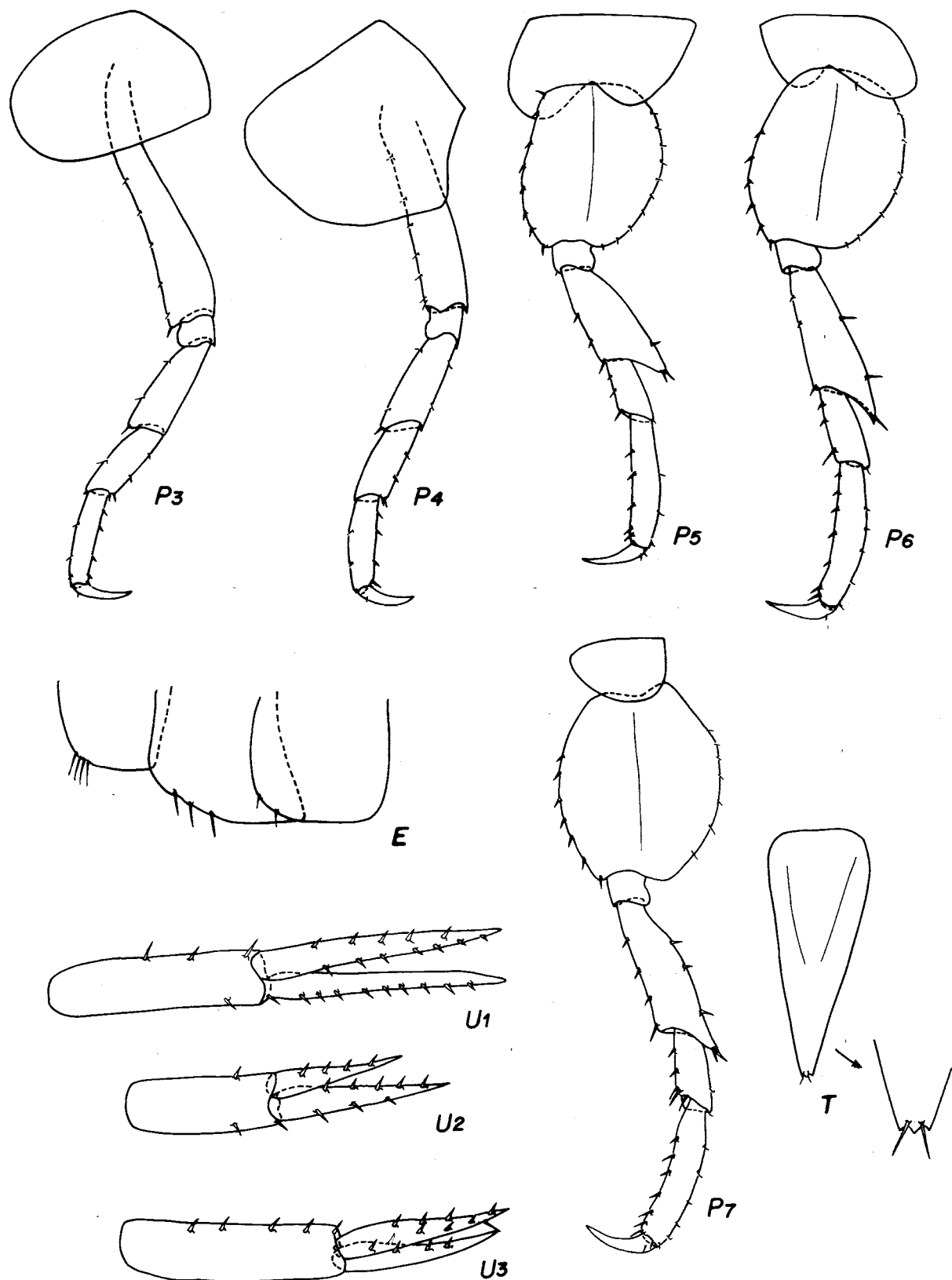


FIGURE 13. *Leucothoe saron* n.sp. male holotype "A," 6.72 mm.

Description of female paratype "B". Similar to male except gnathopod 1, basis, anterior margin of basis with five long setae (versus short setae), posterodistal margin with group of six short setae (versus no poste-

rior setae in holotype “A”); gnathopod 2, basis anterior margin with 15 long setae (versus 13 short setae in male); distomedial setal tufts on articles 2 and 3 reduced in length, carpal lobe, apically rounded with three small serrations; propodus, medifacial setal row with more setae than found in male. Medial surface of propodus with two setae in secondary row, and row of seven submarginal posterior setae on palm.

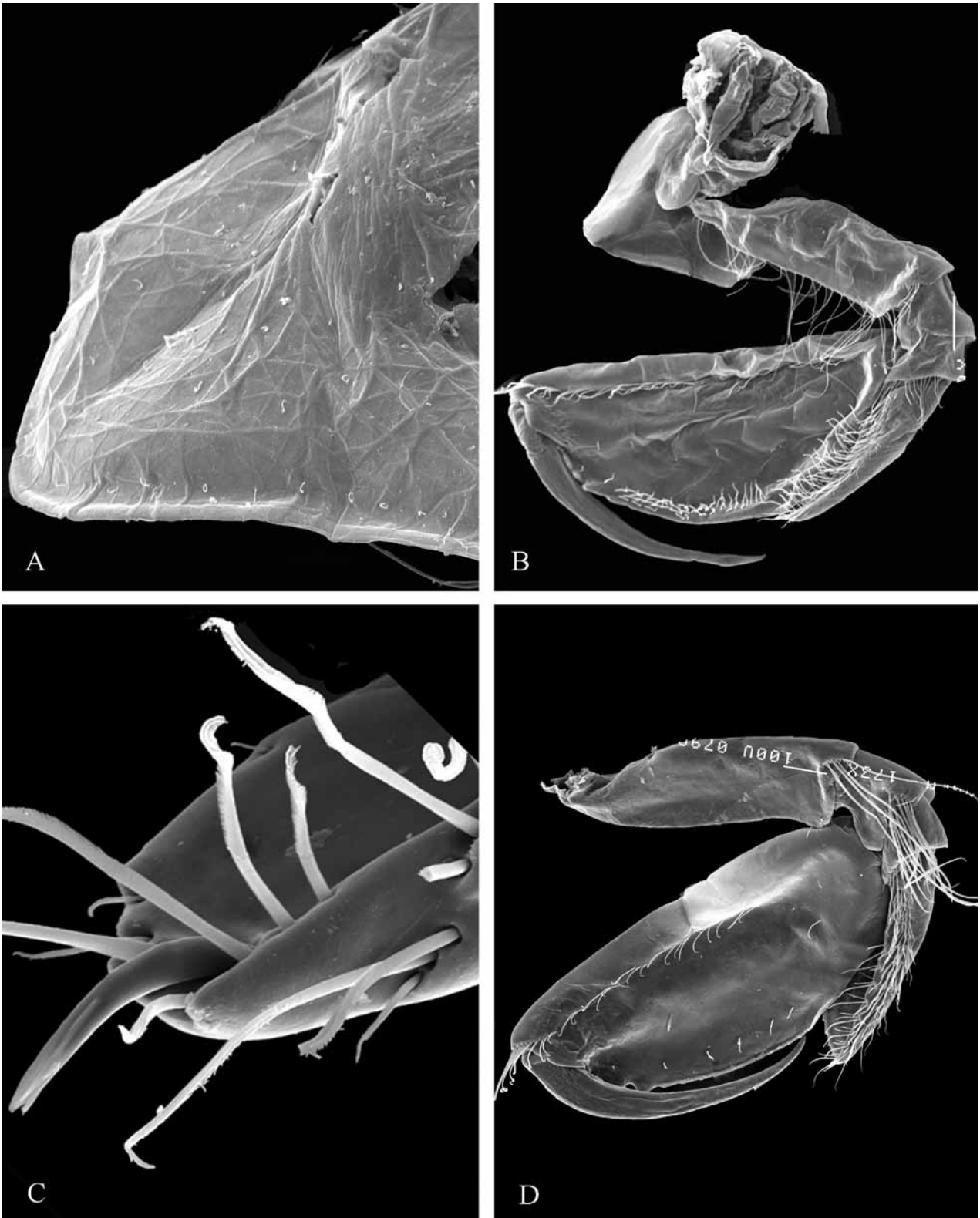


FIGURE 14. *Leucothoe garifunae* n.sp.: A. male coxa 2 setal pattern, lateral, 345x; B. male gnathopod 2, medial, 127x. *Leucothoe saron* n.sp.: C. female gnathopod 2 carpal lobe, medial, 1.73kx; D. male gnathopod 2, medial, 173x.

Etymology. Greek for “broom,” referring to the broom-like row of submarginal setae on the posterior margin of articles 2 and 3 of the second gnathopod.

Relationship. Males of *Leucothoe saron* are distinguished from all other Western Atlantic species by the broom-like tufts of setae on articles 2 and 3 of the second gnathopod. In other features *L. saron* resembles many other Western Atlantic species of *Leucothoe* in the rounded anterior margin of the head, ovate bases of pereopods 5–7, and the general morphology of gnathopod 1. *L. saron* resembles *L. ubouhu* in the distal margin of the carpus of gnathopod 2 in males.

Ecology. Known from the sponges *Agelas dispar*, *Pseudoceratina crassa*, and *Iotrochota birotulata*.

Distribution. Western Atlantic, Belize, hard bottom patch reef areas, 1–10 meters.

Leucothoe ubouhu n.sp.

Figures 15–18; 22a–b

Holotype. Male holotype “A,” 9.03 mm, YPM38656: JDT Bel 03/12A—6Dec03; Co Cat Cay, Pelican Cays, Belize; N 16°39.527' x W 88°12.032'; patch reef, in the sponge *Spongia officinalis* subsp. *obliqua*, 1–15m; J.D. Thomas and K.N. Klebba, collectors.

Paratypes. Female paratype “B,” 7.78 mm, YPM38657: JDT Bel 03/12A—16Dec03; Co Cat Cay, Pelican Cays, Belize; N 16°39.527' x W 88°12.032'; patch reef, in the sponge *Spongia officinalis* subsp. *obliqua*, 1–15m; J.D. Thomas and K.N. Klebba, collectors.

Other material examined. YPM38658: 20June78; Loggerhead Key, Florida, U.S.A.; French Wreck; N 24° 37.957 x W 82°56.012'; host unknown, 3–15m; J.D. Thomas, collector.

Diagnosis. Head: anterior margin angular, anteroventral margin with slight concavity. Gnathopod 1: basis, anterior margin with 7 short setae, propodus, posteromedial margin with three short submarginal setae, dactyl elongate. Gnathopod 2: propodus, medifacial setal row reaching 0.66 of propodus, secondary medifacial row with four setae, medial surface of palm with row of seven submarginal setae. Mandible: palp article 2 with 16–17 setae.

Description of male holotype “A”. Ratios of antennae 1 and 2, 0.38 and 0.29 X body length; relative lengths of antennae 1 and 2, 1.00:0.78, flagella 14 and 7-segmented. Anterior margin of head angular, anteroventral margin with slight concavity; mid-ventral keel, anterior margin vertical, slightly exceeding anterior margin of head, ventral margin broadly rounded. Coxae 1–4, width ratios 1.00:1.28:0.96:1.52; coxae 5–6 bilobed; coxa 7 reduced, ovate.

Upper lip asymmetrically lobate, anterior margin setose. Mandibles, lacking molar; palp 3-articulate, ratio of articles 1–3, 1.00:3.30:1.20; article 2 with 10 anterior, two posterior, and four apical setae; article 3 with two apical setae; incisors strongly toothed. Left mandible, lacinia mobilis large, strongly toothed; 11 raker spines. Right mandible, lacinia mobilis a small flake; 14 raker spines. Lower lip, inner lobes fused; outer lobes with wide gape, anterior margin intermittently setose. Maxilla 1, palp 2-articulate with four apical setae; outer plate with seven spines and four basal setae. Maxilla 2, inner plate with 10 medial marginal and 10–11 facial setae; outer plate with four apical and 11 lateral setae. Maxilliped, inner and outer plates reduced; inner plates fused, apical lobes each with three stout spine-setae, apicomедial margin with projection; outer plate with four apicolateral setae; palp 3-articulate; palp article 1 apical and apicolateral margins with approximately 14 serrate setae; article 4 anteromedial margin with dense covering of short pubescent setae.

Gnathopod 1, coxa anteroventral margin produced with two small serrations, ventral margin straight, posteroventral margin rounded; basis slightly expanded, anterior margin with seven short setae, posterior margin setae lacking; carpal lobe, thin, geniculate, LW 7.33, anterior margin grooved with widely spaced short setae, each margin bordered by six-seven rows of denticles, lateral margin with three short setae; propodus, posterior margin serrate, lateral margin with eight long and 12–13 short setae; dactyl long, smooth, recurved, reaching

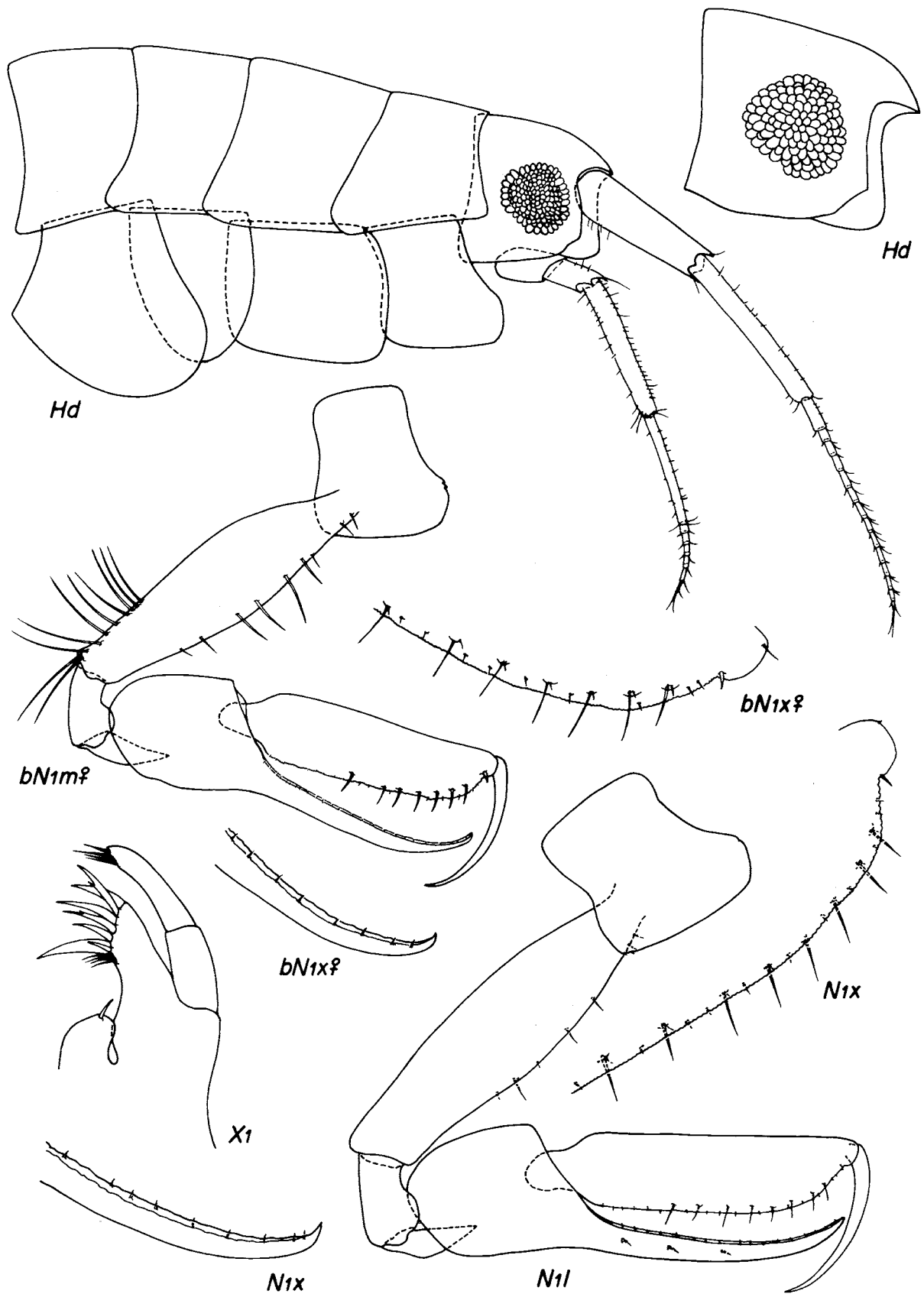


FIGURE 15. *Leucothoe ubouhu* n.sp. male holotype "A," 9.03 mm; female paratype "B," 7.78 mm.

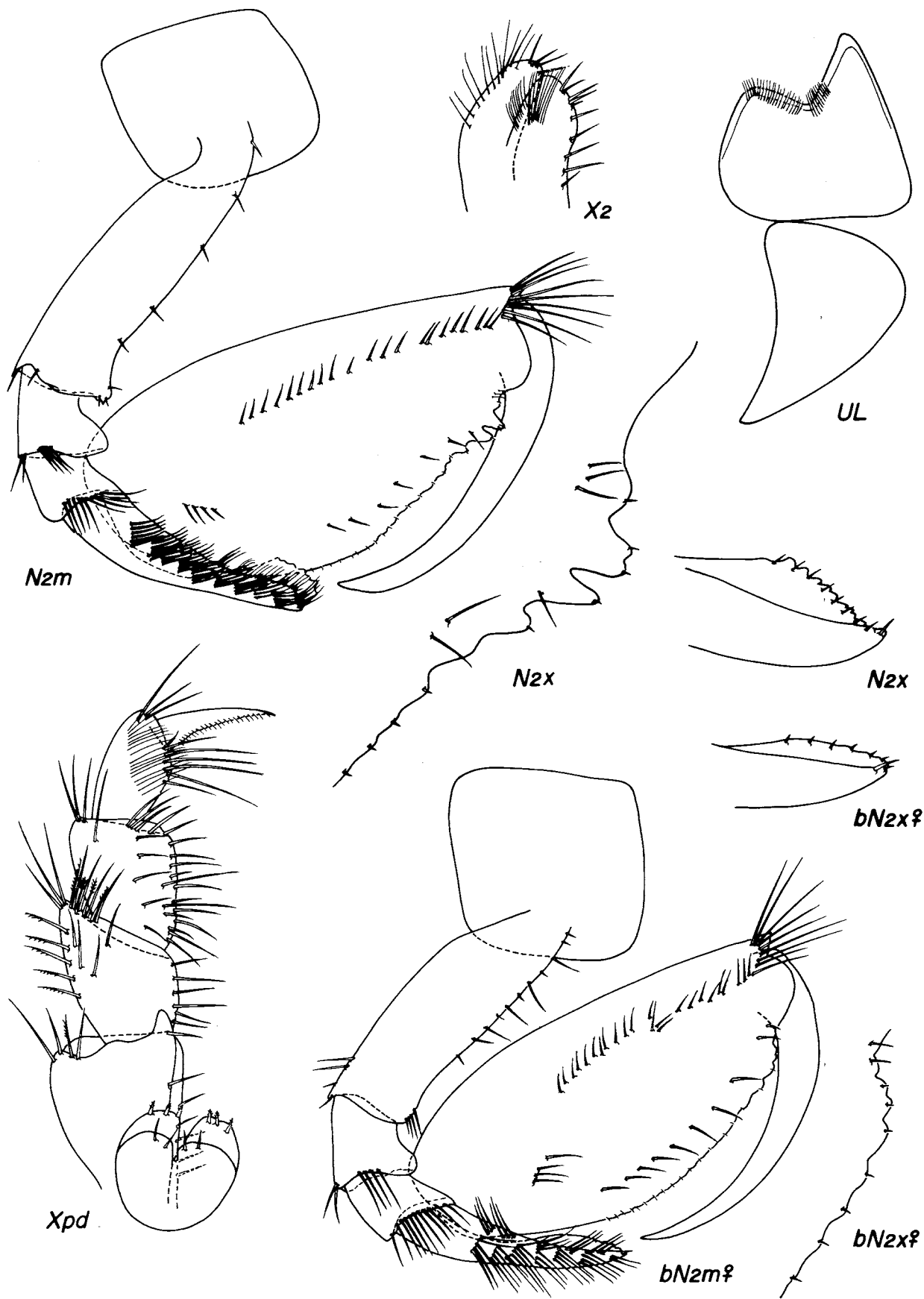


FIGURE 16. *Leucothoe ubouhu* n.sp. male holotype "A," 9.03 mm; female paratype "B," 7.78 mm.

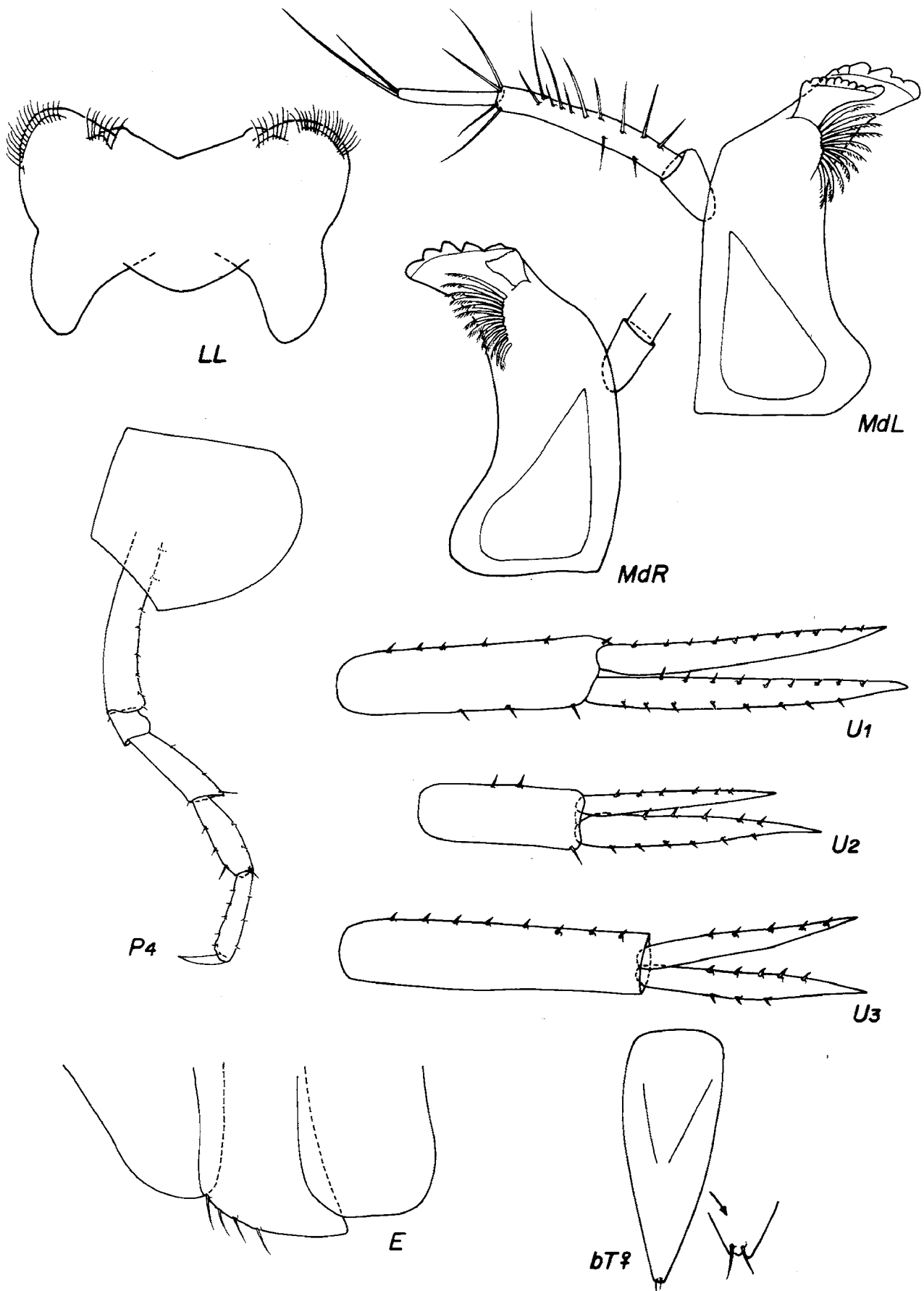


FIGURE 17. *Leucothoe ubouhu* n.sp. male holotype "A," 9.03 mm; female paratype "B," 7.78 mm.

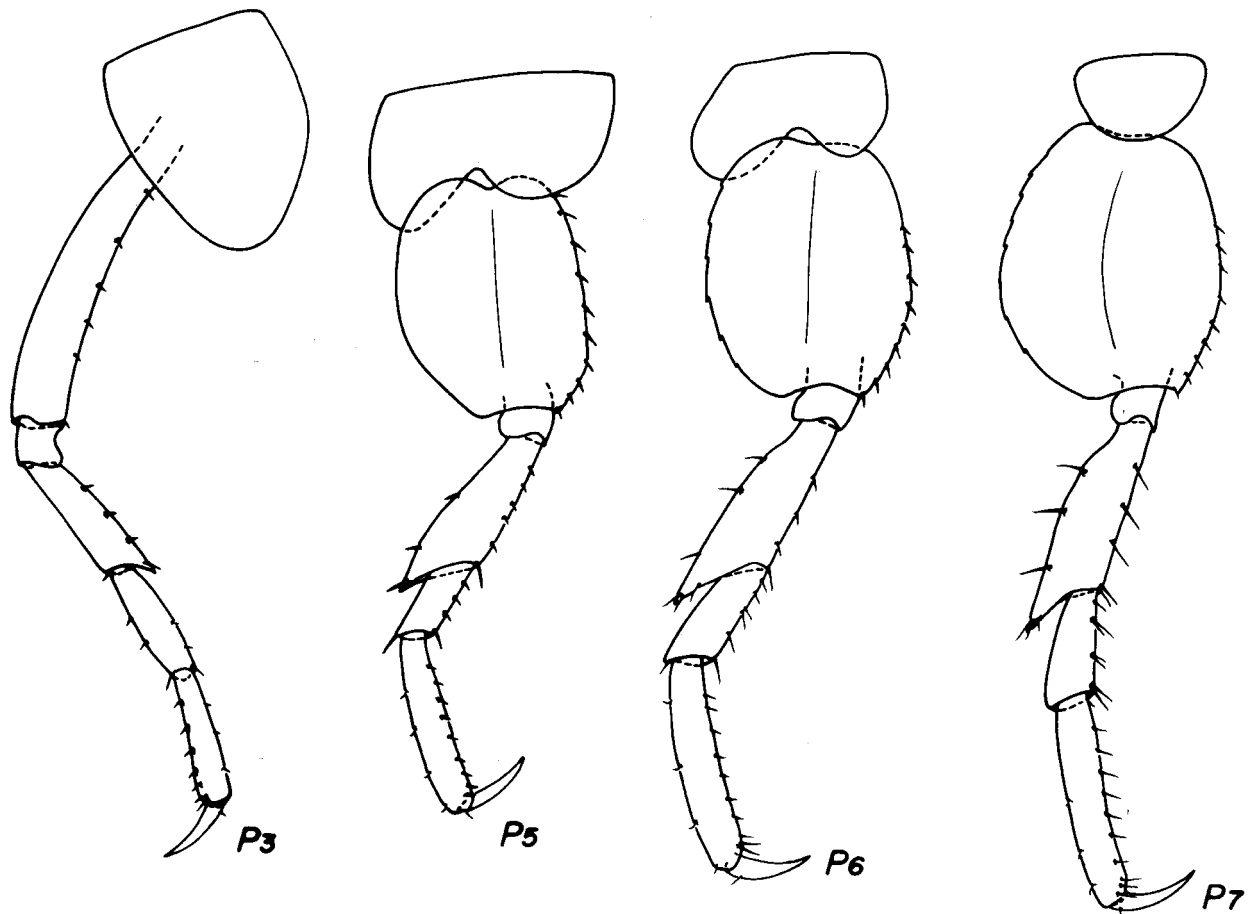


FIGURE 18. *Leucothoe ubouhu* n.sp. male holotype "A," 9.03 mm.

0.51 of propodus. Gnathopod 2, coxa elongate, LW 0.88, anterior, ventral, and posterior margins smooth, posteroventral corner lacking serrations; basis linear, anterior margin with six short setae, posterior margin bare; carpal lobe distal margin slightly expanded and oblique, strongly serrate with approximately 10 serrations, with short apical setae, reaching 0.52 of propodus, medial margin setose; propodus, palm linear with three strong projections near insertion of dactyl, medial margin with seven submarginal setae, primary mediofacial setal row reaching 0.66 of propodus, secondary mediofacial row with four setae; dactyl long, recurved, reaching 0.52 of propodus.

Pereopod 3, coxa reduced, tongue-shaped, LW 1.18, anterior margin straight, ventral margin convex, posterior margin rounded. Pereopod 4, coxa anterior margin rounded, ventral margin convex, tapering posteriorly, posterior margin excavate. Pereopods 5–7, coxa 5–6 bilobed; coxa 7 small, ventrally convex; pereopods 5–7 bases, LW 1.26:1.24:1.22, posterior margin of pereopod 5 smooth, posterior margins of pereopods 6–7 minutely serrate.

Epimera 1–3, ventral setae 0:4:0, respectively; epimera 3, posteroventral margin broadly rounded. Uropods 1–3, relative lengths 1.00:0.71:0.92; relative lengths of peduncles 1–3, 1.00:0.60:1.16. Uropods 1–3, medial margins of outer rami lacking setae. Uropod 1, peduncle 0.92 X rami length, with three medial and six lateral marginal setae; outer ramus 0.96 X inner ramus; inner ramus with eight medial and nine lateral marginal setae; outer ramus with 11 lateral marginal setae. Uropod 2 shortened, peduncle 0.96 X rami, with one medial apical seta and two lateral marginal setae; outer ramus 0.81 X inner ramus length, inner ramus with six medial and five lateral marginal setae; outer ramus with six lateral marginal setae. Uropod 3, peduncle 1.40 X rami length, with one apicomedial and nine lateral marginal setae; outer ramus reaching 0.97 of inner ramus; inner ramus with three medial and five lateral marginal setae; outer ramus with five lateral marginal setae. Telson LW 2.59, apical margin tridentate with two apical setae.

Description of female paratype “B”. Similar to male in all aspects except the following: Gnathopod 1, basis, posterior margin with slight proximal inflation, posterodistal margin with 10 long setae, anterior margin with nine; gnathopod 2, carpus, distally oblique, with six to eight apical setae; basis, anterior margin with 11 scattered long and short setae, anteroventral corner with tuft of four short setae, posterodistal margin with three setae.

Etymology. Gari’ funa term for “island.”

Relationship. *Leucothoe ubouhu* most closely resembles *Leucothoe barana* in the angular margin of the head. The oblique margin of the carpus on gnathopod 2 and the extremely long dactyl of gnathopod 1 of *L. ubouhu* resembles *Leucothoe saron*. Females of *L. ubouhu* are distinct among Western Atlantic species in having a tuft of numerous long posterodistal setae on basis of gnathopod 1.

Ecology. In Belize, *L. ubouhu* was found in the sponges *Cliona [Anthosigmella] varians*, *Hyrtios* sp., *Lisodendoryx isodictyalis*, *Mycale laxissima*, and *Spongia officinalis* subsp. *obliqua*. The host is unknown in Florida.

Distribution. Western Atlantic, Belize to Florida, 2–15 meters.

Leucothoe wuriti n.sp.

Figures 19–21; 22c–d

Leucothoe spinicarpa :Ortiz: 1975:10, Figure 5.

Holotype. Male “A,” 6.84 mm, YPM38659: JDT Bel 03/03-7b—4Mar03; Co Cat Cay, Pelican Cays, Belize; N 16°39.527' x W 88°12.032'; mangrove lagoon, in the tunicate *Phallusia nigra*, 3m; J.D. Thomas and K.N. Klebba, collectors.

Paratypes. Female “B,” 5.70 mm, YPM38660: JDT Bel 03/03-7b—4Mar03; Cat Cay, Pelican Keys, Belize; N 16°39.527' x W 88°12.032'; mangrove lagoon, in the tunicate *Phallusia nigra* on mangrove roots, 3m; J.D. Thomas and K.N. Klebba, collectors.

Other material examined. YPM38661: 8May76; Big Pine Key, Florida, U.S.A, Newfound Harbor Marine Institute, canal; N 24°40.000' x W 81°21.044'; in the tunicate *Phallusia nigra* from fouling communities, 1–3m; J.D. Thomas collector.

Diagnosis. Mandibular palp: article 2 with 18 setae. Coxae: coxa 1 bell-shaped, anteroventral and posteroventral margins produced, proximal margins constricted, anterior margin with a long facial seta, coxa 3 narrow, coxa 4 posteromedial margin excavate. Gnathopod 1: basis, anterior margin with 5 short setae; carpus, posterior margin with six short setae. Gnathopod 2: propodus, mediofacial row of feeding setae displaced to midline, reaching 0.92 of propodus. Pereopods: pereopods 3–4 bases with both anterior and posterior setae; pereopods 5–7, bases narrow, posteroventral margin of bases tapering ventrally.

Description of male holotype “A”. Ratios of antennae 1 and 2, 0.27 and 0.23 X body length; relative lengths of antennae 1 and 2, 1.00:0.85, flagella 10 and four-segmented. Anterior margin of head rounded; mid-ventral keel, anterior margin straight, vertical, with rounded anteroventral projection. Coxae 1–4, width ratios 1.00:0.89:0.71:1.11; coxae 5–6 bilobed; coxa 7 reduced, ovate.

Upper lip asymmetrically lobate, all margins setose. Mandibles lacking molar; palp 3-articulate, ratio of articles 1–3, 1.00:3.56:1.56; article 2 with 18 posterior setae; article 3 with two apical setae; incisors strongly dentate. Left mandible, lacinia mobilis large, strongly toothed; 12 raker spines. Right mandible, lacinia mobilis a small flake; 10 raker spines. Lower lip, inner lobes fused; outer lobes with broad gape, anterior margin continually setose. Maxilla 1, palp 2-articulate with four apical setae; outer plate with nine spines. Maxilla 2, inner plate with eight thickened medial, six apicomarginal and two submarginal facial setae; outer plate with three stout apical and 15 lateral marginal setae. Maxilliped, inner and outer plates reduced; inner plate fused, apical lobes each with 3 setae; outer plate anterolateral margin with few setae; palp 3-articulate, palp article 1, lateral margin with plumose setae; article 4 anteromedial margin with dense covering of short pubescent setae.

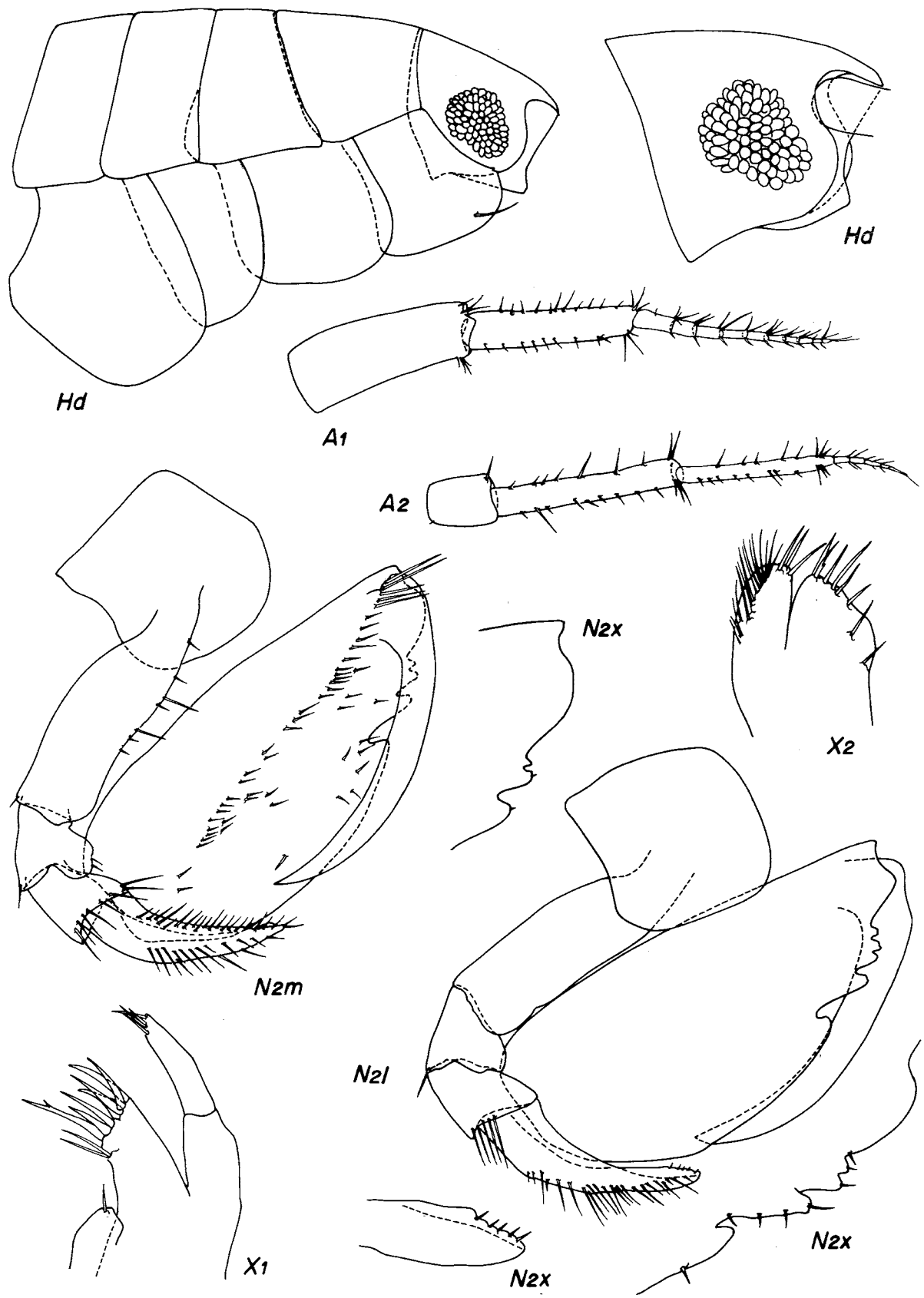


FIGURE 19. *Leucothoe wuriti* n.sp. male holotype "A," 6.84 mm.

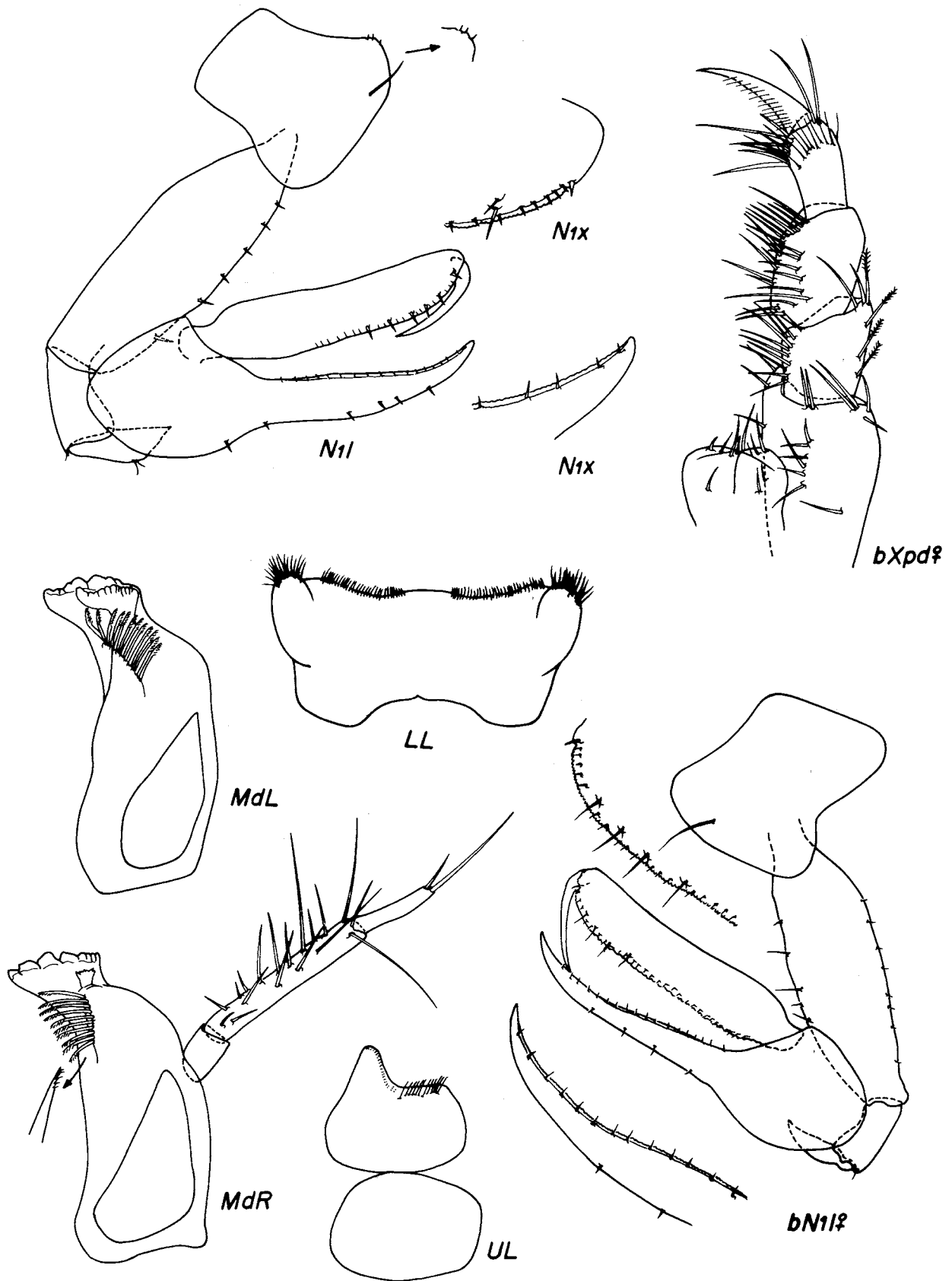


FIGURE 20. *Leucothoe wuriti* n.sp. male holotype "A," 6.84 mm; female paratype "B," 5.70 mm.

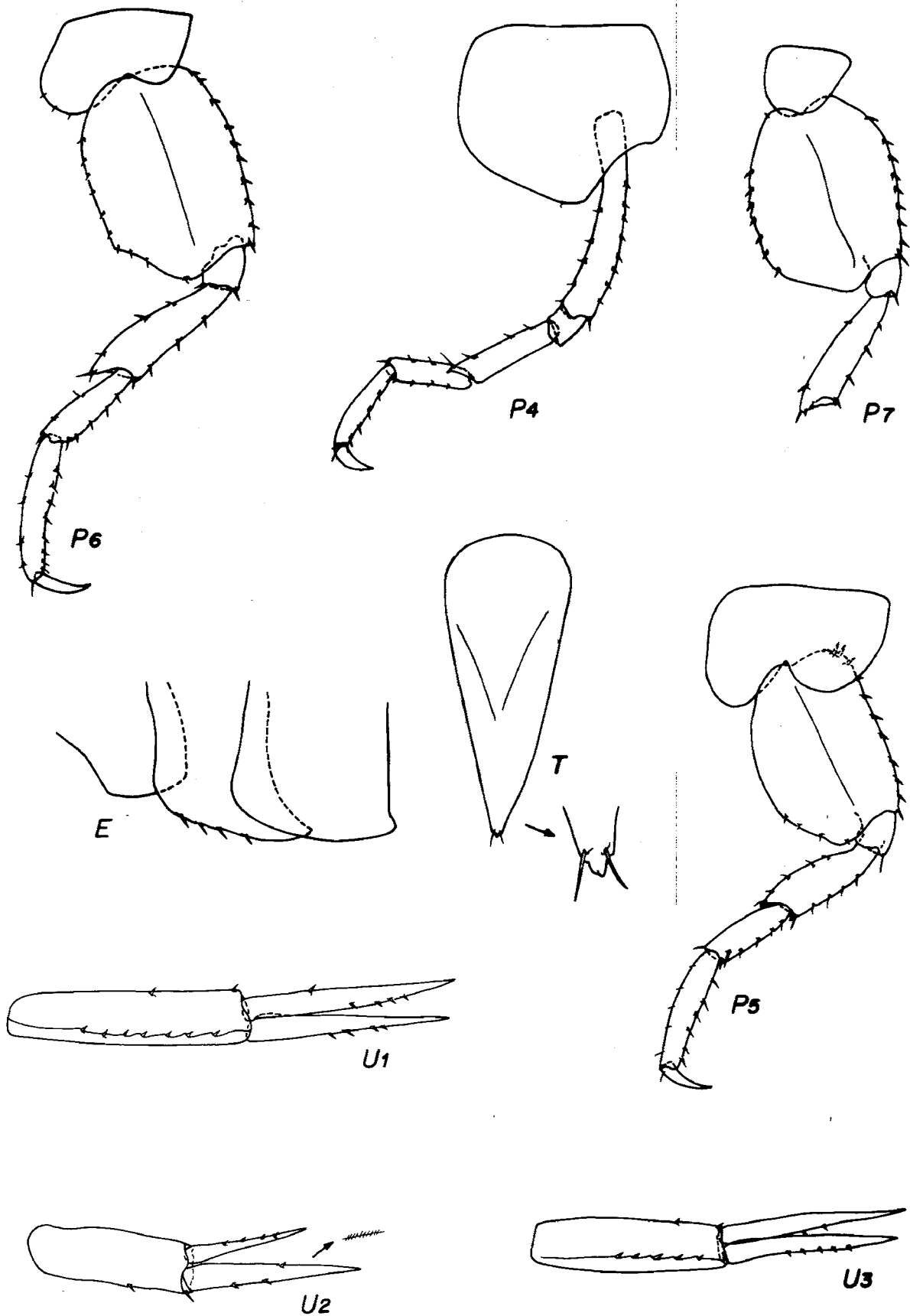


FIGURE 21. *Leucothoe wuriti* n.sp. male holotype "A," 6.84 mm.

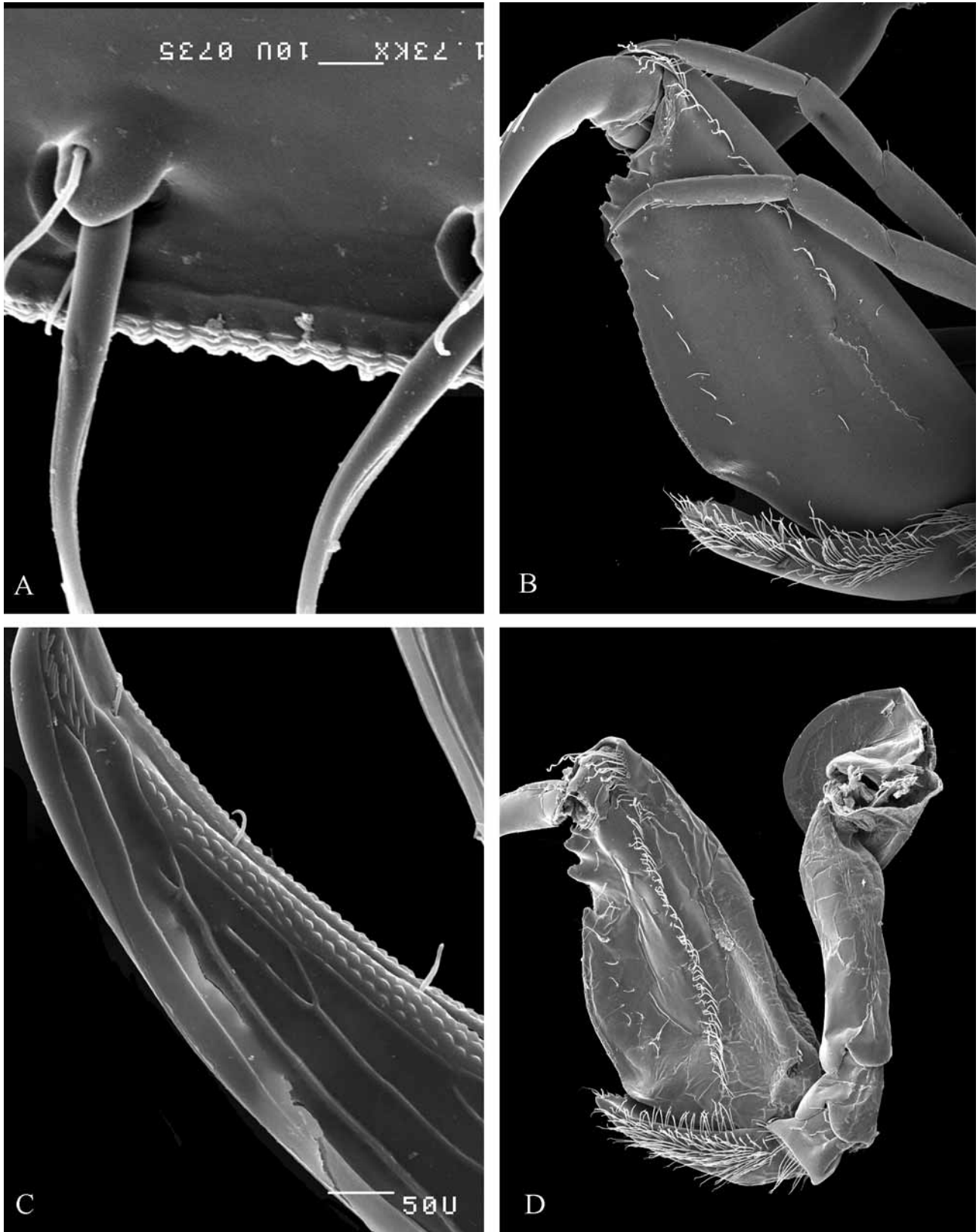


FIGURE 22. *Leucothoe ubouhu* n.sp.: A. male gnathopod 1, lateral, 1.74kx; B. male gnathopod 2, medial, 69x. *Leucothoe wuriti* n.sp.: C. male gnathopod 1 carpus, medial, 1268x; D. male gnathopod 2, medial, 69x.

Gnathopod 1, coxa anteroventral margin slightly produced, with three short setae and one large anterior submarginal seta, ventral margin rounded, posterior margin produced; basis linear, anterior margin with six

short setae, posterior margin with tuft of four short setae; carpal lobe thick, LW 5.57, posterior margin with six short setae, anterior margin grooved, bordered by paired rows of denticles, bearing ca 17 short setae; propodus, posterior margin serrate, lateral margin with six stout setae and assorted array of shorter setae; dactyl long, reaching 0.36 of propodus. Gnathopod 2, coxa subrectangular; LW 0.97, anterior and ventral margins rounded, posterior margin slightly excavate; basis linear, anterior margin with seven medium setae, posterior margin lacking setae; carpal lobe, lateral margin smooth, recurved, apical margin oblique, with seven serrations, bearing setae, reaching 0.59 propodus; propodus, palm, distal margin with one major and two minor projections, remainder of palm smooth, rounded, primary mediofacial row of feeding setae displaced to midline, reaching 0.92 of propodus, secondary mediofacial row lacking; dactyl thick, recurved, reaching 0.77 of propodus.

Pereopod 3, coxa narrow, LW 1.55, anterior margin rounded, ventral margin convex, posterior margin straight. Pereopod 4, coxa anterior margin straight, ventral margin rounded, posteromedial margin excavate. Pereopods 3 and 4 bases with both anterior and posterior setae. Pereopods 5–7, coxa 5–6 bilobed; coxa 7 small, ventrally convex; pereopods 5–7, posteroventral margin of bases tapering, bases narrow, length to width ratios 1.48:1.45:1.50, posterior margin of pereopods 5 and 6 bases smooth, posterior margin of pereopod 7 with small serrations.

Epimera 1–3, ventral setae, 0:4:0, respectively; epimera 3, posteroventral margin rounded, minutely produced. Uropods 1–3, relative lengths 1.00:0.59:0.82; relative lengths of peduncles 1–3, 1.00:0.59:0.82. Uropods 1–3, medial margins of outer rami lacking setae. Uropod 1, peduncle 1.15 X rami length, with two medial and seven lateral marginal setae; outer ramus 0.94 X inner ramus; inner ramus with one medial and four lateral marginal setae; outer ramus with four lateral marginal setae. Uropod 2 shortened, peduncle 0.95 X rami length, with two medial and two lateral marginal setae; outer ramus 0.75 X inner ramus; inner ramus with two medial and one lateral marginal setae, medial margin finely serrate; outer ramus with four lateral marginal setae. Uropod 3, peduncle 1.06 X rami length, with one medial and five lateral marginal setae; outer ramus 0.97 X inner ramus; inner ramus with two lateral marginal setae; outer ramus with zero medial and five lateral marginal setae. Telson LW 2.35, apical margin tridentate bearing two apical setae.

Description of female paratype “B”. Similar to male in all aspects except gnathopod 1, basis, posterior margin with eight short setae (versus no posterior setae in male); carpus narrow, length 6.42 X width.

Etymology. Gari’funa for “black” referring to the tunic color of its common ascidian host, *Phallusia nigra*.

Relationship. The elongate, displaced row of mediofacial setae on the propodus of gnathopod 2 in *L. wuriti* distinguishes it from all other *Leucothoe* species in the region. *L. wuriti* resembles *L. garifunae* and *L. ubouhu* in the numerous setae on mandibular palp article 2, with 18, 16, and 17 setae, respectively.

Remarks. *Leucothoe wuriti* exhibits a distinctive dorsal red “checkerback” color pattern on metosome segments 4–7. This color pattern is repeated on the lateral margins of somites 1–7 as small lateral spots and blotches and extends ventrally to the coxae and bases of appendages. Antennae 1 and 2 have distinctive red bands.

Ecology. In Florida, *L. wuriti* is known only from branchial chamber of the large, black, solitary ascidian, *Phallusia* (formerly *Ascidia*) *nigra*. Specimens can be collected *in-situ* by gently squeezing the base of the tunicate and capturing the amphipods from the water column as they are expelled from the siphons. In Belize, *L. wuriti* has been collected from both *Phallusia nigra* and *Ascidia curvata*, a translucent solitary ascidian. In his 1975 paper Ortiz also reported *L. spinicarpa* from *Ascidia nigra* in Cuban waters. While no specimens of this amphipod are available for examination, the distinct color pattern drawn by Ortiz matches the checkerback pattern of *L. wuriti* indicating this report is almost certainly that of *L. wuriti*.

Distribution. Western Atlantic, Belize to Florida, 2–15 meters.

TABLE 3. *Leucothoe* species in invertebrate hosts. F–Florida, B–Belize; Subscripts represent abundance of each species in each sponge – 1 – Scarce, 2 – Common, 3 – Abundant.

Host species	<i>L. ashleyae</i>	<i>L. barana</i> n.sp	<i>L. flammosa</i> n.sp	<i>L. garifunae</i> n.sp	<i>L. kensleyi</i>
Sponges:					
<i>Agelas dispar</i>					
<i>Aiolochoiria crassa</i>	B ₂			B ₁	B ₁
<i>Anthosigmella varians</i>					
<i>Amphimedon compressa</i>	B ₂	B ₂			B ₁
<i>Callyspongia vaginalis</i>	F ₁ , B ₃				F ₃ , B ₁
<i>Haliclona mucifibrosa</i>	B ₂				
<i>Holopsamma helwigii</i>				F ₂	
<i>Hyrtilos</i> sp.					
<i>Iotrochota birotulata</i>	B ₃	B ₁		B ₂	B ₁
<i>Leucetta imberbis</i>		B ₁		B ₂	
<i>Leucosolenia</i> sp.				B ₂	
<i>Lissodendoryx isodictyalis</i>					
<i>Mycale laxissima</i>	B ₁				
<i>Niphates digitalis</i>	F ₁ , B ₃				
<i>Niphates erecta</i>	B ₁	B ₁			
<i>Spheciospongia vesparium</i>		F ₁			
<i>Spongia officinalis</i> subsp. <i>obliqua</i>					
<i>Spongia</i> sp.					
<i>Svenzea zeai</i>		B ₁			
<i>Tedania ignis</i>	B ₂	B ₁			
Mollusks:					
<i>Americardia media</i>			B ₁		
<i>Anadara notabilis</i>			F ₁		
<i>Dendostrea frons</i>			B ₁		
<i>Lima scabra</i>			F ₃ , B ₃		
<i>Lithophaga antillarum</i>			B ₁		
<i>Lucina pennsylvanica</i>			B ₁		
<i>Mytilopsis leucopheata</i>			B ₁		
Ascidians:					
<i>Ascidia curvata</i>					
<i>Phallusia [Ascidia] nigra</i>					

continued.

Host species	<i>L. saron</i> n.sp	<i>L. ubouhu</i> n.sp	<i>L. urospinosa</i>	<i>L. wuriti</i> n.sp
Sponges:				
<i>Agelas dispar</i>	B ₁			
<i>Aiolochoiria crassa</i>	B ₃			
<i>Anthosigmella varians</i>		B ₃		

<i>Amphimedon compressa</i>		
<i>Callyspongia vaginalis</i>		
<i>Haliclona mucifibrosa</i>		
<i>Holopsamma helwigii</i>		
<i>Hyrtios</i> sp.		B ₁
<i>Iotrochota birotulata</i>	B ₂	
<i>Leucetta imberbis</i>		
<i>Leucosolenia</i> sp.		
<i>Lissodendoryx isodictyalis</i>		B ₁
<i>Mycale laxissima</i>		B ₁
<i>Niphates digitalis</i>		
<i>Niphates erecta</i>		
<i>Sphaciospongia vesparium</i>		F ₁
<i>Spongia officinalis</i> subsp. <i>obliqua</i>		B ₂
<i>Spongia</i> sp.		B ₁
<i>Svenzea zeai</i>		
<i>Tedania ignis</i>		B ₃
Mollusks:		
<i>Americardia media</i>		
<i>Anadara notabilis</i>		
<i>Dendostrea frons</i>		
<i>Lima scabra</i>		
<i>Lithophaga antillarum</i>		
<i>Lucina pennsylvanica</i>		
<i>Mytilopsis leucopheata</i>		
Ascidians:		
<i>Ascidia curvata</i>		B ₃
<i>Phallusia [Ascidia] nigra</i>		F ₂ , B ₂

Discussion

Commensal amphipods typically inhabit a single host species and rarely occur in multiple host species of the same class. However, our research shows leucothoids exhibit both broad and restricted host association relationships. Presumably, commensal amphipods utilize internal host cavities as access to food resources and possible protection from predators. The respiratory/feeding current flows generated by sponges, ascidians, and bivalve mollusks provide a reliable source of fine particulate matter (Thomas, 1997b). In leucothoids the head, antennae, maxillipeds, and gnathopods are all highly modified as a filter feeding mechanism to trap and process food particles from host-generated currents. The inner canals of sponges provide a protective breeding habitat for amphipods, where adults provide extended parental care of juveniles until they reach sexual maturity (Thiel, 1995). Thiel (2000) also noted both adult and juvenile “*Leucothoe spongicola*” and “*Leucothoe ascidicola*” amphipods (termed for their host associations) in Florida left their host sponges and ascidians, respectively, after a reproductive peak in August, returning in September.

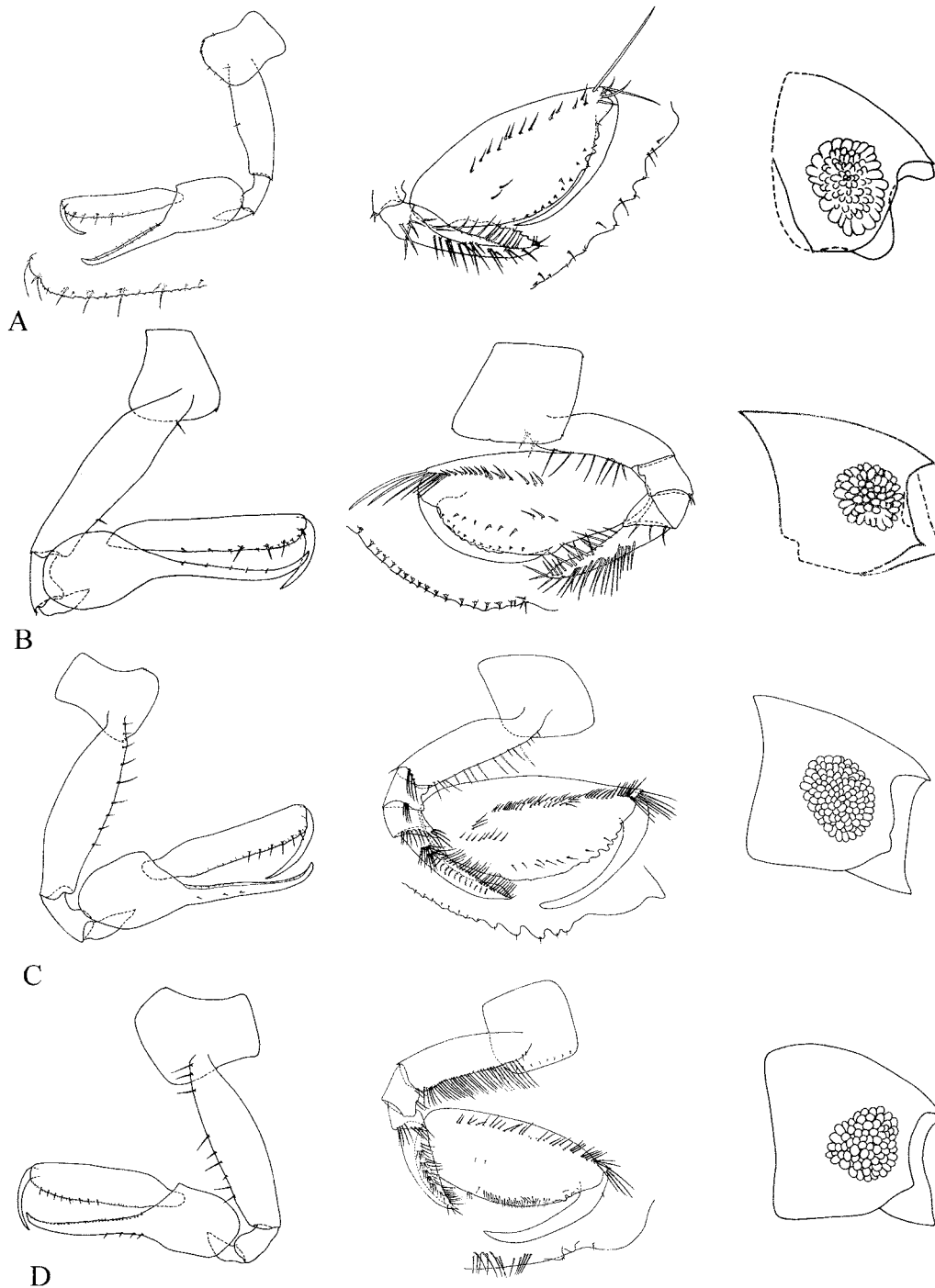


FIGURE 23. Comparison of (left to right) the gnathopod 1, gnathopod 2, and head of four new leucothoid species; Row A: *Leucothoe ashleyae*; Row B: *Leucothoe kensleyi*; Row C: *Leucothoe barana* n.sp.; Row D: *Leucothoe garifunae* n.sp.

In southeastern Florida and the Florida Keys, *Leucothoe ashleyae* is found in small numbers only in the tube sponge, *Callyspongia vaginalis*, while *Leucothoe kensleyi* inhabits 14 sponge species, including *C. vaginalis* (Crowe, 2001). Conversely, *Leucothoe kensleyi* is rarely encountered in Belize sponges, while *Leucothoe ashleyae* is relatively common, inhabiting nine different sponge species, including *C. vaginalis*. While *C. vaginalis* exhibits several different growth forms in its range, only the form encrusted with sponge zooanthids, *Parazoanthus parasiticus* (Duchassaing and Michelotti, 1860), contains amphipods, despite abundant sampling efforts of other *C. vaginalis* growth forms. *In-situ* observations of *C. vaginalis* show the amphipods

inhabiting the inner canal walls of the sponge, heads and antennae protruding into the large central spongo-coel. In this position the amphipods trap food particles on setal tufts lining the medial surface of the carpal lobes of the second gnathopods (Thomas, 2004).

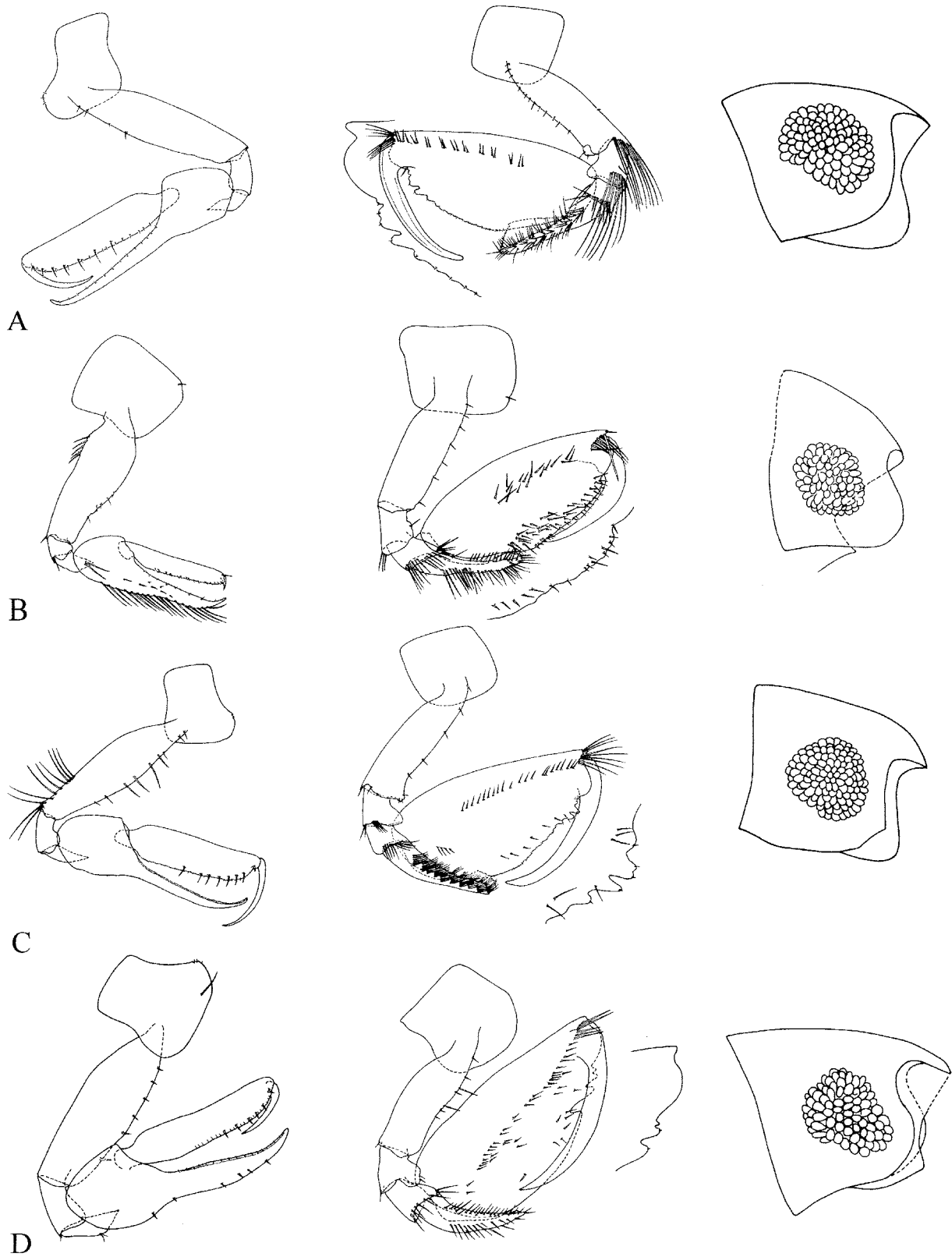


FIGURE 24. Comparison of (left to right) the gnathopod 1, gnathopod 2, and head of four new leucothoid species; Row A: *Leucothoe saron* n.sp. ; Row B: *Leucothoe flammosa* n.sp.; Row C: *Leucothoe ubouhu* n.sp.; Row D: *Leucothoe wuriti* n.sp.

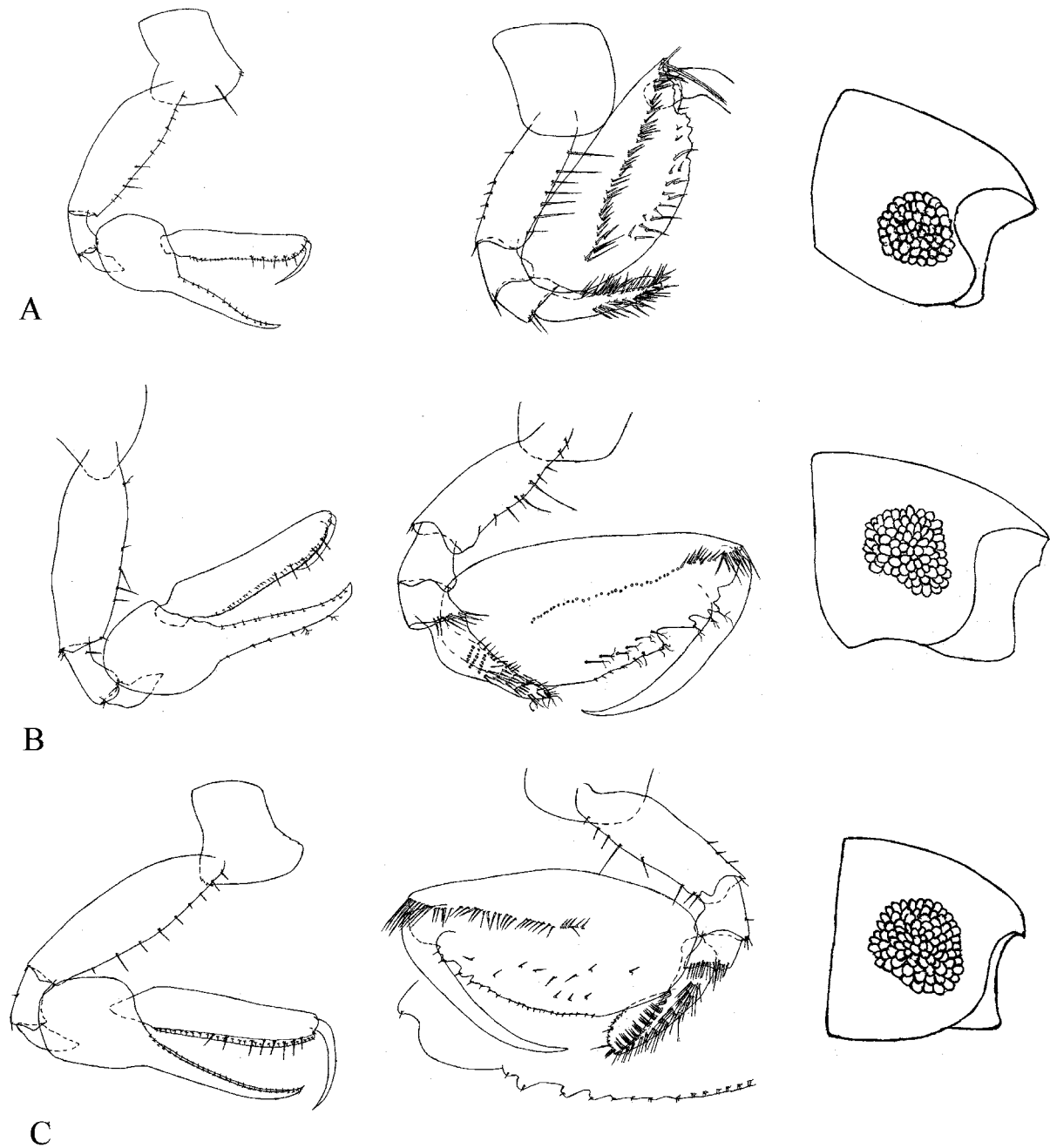


FIGURE 25. Comparison of (left to right) the gnathopod 1, gnathopod 2, and head of three new leucothoid species; Row A: *Leucothoe* n.sp. A; Row B: *Leucothoe* n.sp. B; Row C: *Leucothoe* n.sp. C.

A major factor in host selection in leucothoids may be the interior size and morphology of canal openings of the host. Henkel and Pawlik (2005) reported that commensal abundance increased with internal surface area of the sponge, apparently as the potential volume of food availability increases with the size of the sponge. However, Crowe (2001) found that 12 of 14 sponge species showed no relationship between host volume and abundance of commensal leucothoids, suggesting size variations in canals had a greater affect on sizes of resident amphipods than on their numbers. The thin-walled tubular morphology of *C. vaginalis* restricts the depth and size of interior canals in the walls resulting in smaller habitat openings than found in most other sponge hosts. In our study, two of the smaller species commonly found in our study, *L. ashleyae* and *L. kensleyi*, are abundant in the small canals of *C. vaginalis*. In her study of commensal colomastigid

amphipods, LeCroy (1995) noted that sponge volume controlled the presence of *Colomastix* amphipods, but found no relationship between host size and commensal amphipod numbers. Thiel (1999) also failed to find a relationship between host size and number of amphipods, while Frith (1976) documented more commensals in larger branched or fistulose sponges than in flatter, unbranched sponges. Larger sponges may be preferred amphipod hosts because: 1) they are bigger ecological targets; 2) have more internal space and thus increased current flow potential and food availability and; 3) have been available for colonization for a longer time. (Gage, 1966; Dalby, 1996).

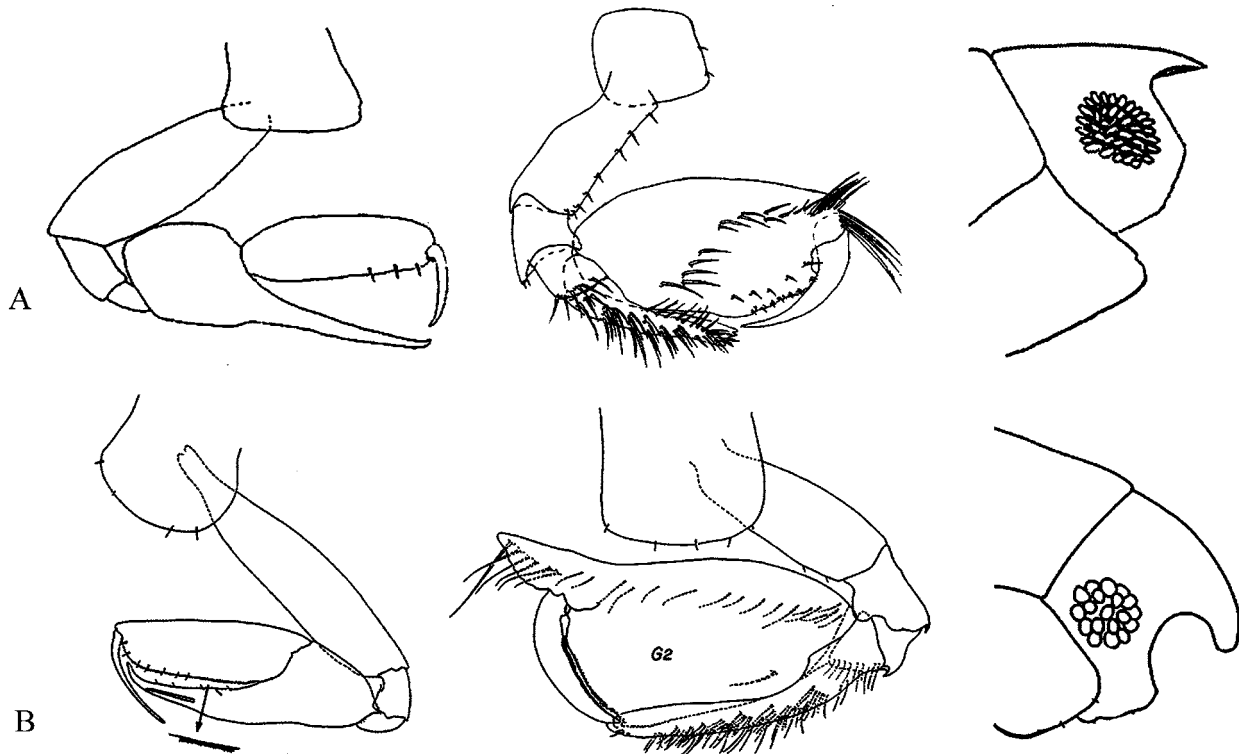


FIGURE 26. Comparison of (left to right) the gnathopods 1, 2; and head of two leucothoid species. Row A: *Leucothoe urospinosa* Serejo, 1998; Row B: *Leucothoe laurensi* Thomas and Ortiz, 1995.

TABLE 4. Morphological comparison of three undescribed cryptic *Leucothoe* species.

Species	<i>Leucothoe</i> n.sp. A	<i>Leucothoe</i> n.sp. B	<i>Leucothoe</i> n.sp. C
Head angle	rounded	rounded	rounded
Cephalic keel	rounded	subquadrate, slight projection	rounded
Coxa 4, posterior margin	excavate	excavate	excavate
Gnathopod 1, palm	serrate, with 4–5 spines	serrate, with 8–9 spines	serrate, with 5 spines
Gnathopod 1, basis	8 short anterior setae	9 short anterior setae	11 short anterior setae
Gnathopod 2, palm	crenulate, with 3 large projections	crenulate, with 2 large projections	crenulate, with 3 large projections
Gnathopod 2, carpus	truncate, serrate	rounded, flared, serrate	rounded, serrate

Many sponges produce chemically active secondary metabolites that may deter sponge predators and thereby increase survivability of any associates (Duffy & Paul, 1992; Chanas *et al.*, 1996; Chanas & Pawlik, 1997; Marin *et al.*, 1998) suggesting amphipods may select their hosts based on chemical deterrents (Meroz & Ilan, 1995). Variations in distribution densities may also effect host selection. Williams *et al.* (1992) maintain that hosts with different symbiotic compositions are also genetically distinct. In Australia the stalked tunicate

Pyura stolonifera (Heller, 1978) exhibits brown and yellow growth forms. Dalby (1996) reported the amphipod *Paraluciothoe novaehollandiae* from both forms but found that yellow morphs favored nemertean symbionts and deterred copepod symbionts, while the brown morphs did the opposite.

In our study some of the most commonly collected sponge species (*C. vaginalis*, *Tedania ignis*, and *Pseudoceratina crassa*) were host to leucothoid amphipods in over 90% of collections. Similarly, of 179 individual sponges sampled, Henkel and Pawlik (2005) found the three most abundant species (*C. vaginalis*, *Niphates digitalis*, and *Callyspongia plicifera*) often hosted brittlestars, which commonly co-occur with leucothoid commensals.

Further examination of potential commensal-host interactions and habitats will reveal more about the ecology, life histories, and phylogeny of these amphipods. In particular, leucothoids exhibit several highly variable character states, and certain morphological structures appear to provide more taxonomic value than others, e.g., gnathopod 2 has 10 characters (Table 1) that are each equally as important as the single character of head shape. Additional ecological investigations will lead to a better understanding of commensal-host interactions and may provide the key to the function, development, and taxonomic usefulness of many characters.

With the exception of *Leucothoe kensleyi*, all leucothoid species with narrow bases on pereopods 5–7 are reported from deep waters (2000 m). *Leucothoe laurensi* (Thomas & Ortiz, 1995) has a terminal blade-like extension on the gnathopod 2 propodus, possibly increasing the mediofacial surface area for food collection. Differences in lengths of mandibular palps in *Leucothoe* species also suggest different feeding methods or habitats. Different character states provide important information about each species, allowing functional relationships and phylogenies to be examined.

Leucothoe ashleyae shares the characters of a rounded head margin and serration patterns on gnathopods 1 and 2 with *L. cheiriserra*, *L. leptosa*, and *L. basilobata* (all described by Serejo, 1998). However, all four species exhibit variations in other character states, e.g. gnathopod 2 basis shape, posterior margin of coxa 4, and the anteroventral margin of epimeron 3.

Leucothoe flammosa shares no diagnostic characters with any other known *Leucothoe* species. It has unique patterns and types of setae not found on other species. Behavior studies by the first author of *L. flammosa* suggest these unusual morphologies are adaptations to clearing the body and appendages of increased mucus loads encountered in the mantle cavities of its bivalve hosts.

Leucothoe barana, *L. ashleyae*, *L. kensleyi*, and *L. ubouhu* all have a secondary row of mediofacial setae on the second gnathopods. The head angle and prominent mid-ventral keel of *L. garifunae* resembles that of *L. barana*, and *L. ubouhu*, but is otherwise distinct from all other known *Leucothoe* species. *L. ubouhu* has a quadrate head angle similar to *L. barana*, *L. garifunae*, and an elongate dactyl similar to *L. saron*.

Leucothoe saron and *Leucothoe wuriti* have rounded head margins, similar shapes of coxae 1–4, and broad second articles of pereopods 5–7 shared by many known *Leucothoe* species. However, *L. saron* is distinguished by the medial tufts of setae on articles 2 and 3 of gnathopod 2, while *L. wuriti* is distinguished by its displaced row of mediofacial setae on gnathopod 2 and the tapered bases of pereopods 5–7. While our research illustrates the taxonomic importance of these characters they were rarely incorporated in previous species descriptions adding to the taxonomic confusion within the Leucothoidae.

The distribution of *Leucothoe urospinosa* Serejo, 1998, originally described from Brazil now extends to Belize and Florida. Serejo (1998) placed it in the "*L. spinicarpa* group VI" of Ledoyer (1978) because of its long gnathopod 2 dactyl, the rounded anteroventral corner of epimeron 3, and the denticulate palm of gnathopod 2. *L. urospinosa* is distinguished by short, subequal antennae, a prominent rostrum, and spine groupings on the ramus of uropod 1. A character omitted in the original description and figures of *L. urospinosa*, and noted from these collections, is the ventral displacement of the mediofacial setal row on article 6 of gnathopod 2, (Figure 26).

Another Caribbean leucothoid species, *Leucothoe laurensi* Thomas and Ortiz, 1995, described from Cuba ranges from Brazil to Florida, U.S.A. has an unusual terminal blade-like extension on the gnathopod 2 propodus (Figure 26). In this character *L. laurensi* closely resembles *Leucothoe euryonyx* (= *Leucothoe quadrimana* Ruffo, 1966; Ruffo and Krapp-Schickel, 1967; Krapp-Schickel, 1975b; and *Leucothoe dentitelson* Chevreux, 1925).

The continued development of more detailed and precise taxonomic characters has resolved some of the confusion within the *L. spinicarpa* species "complex" in southeast Florida and the western Caribbean Sea. The *L. spinicarpa* species "complex," long assumed to be a globally distributed species is actually a convenient taxonomic dumping ground for poorly resolved taxa and will eventually reveal both numerous distinct taxa and synonymies. The confusion surrounding a single founding species in leucothoids exemplifies the taxonomic challenges of the family. This research suggests the level of undocumented diversity of leucothoid amphipods is extremely high. The authors believe this scenario of cryptic species discovery will be repeated frequently as investigators refine taxonomic and ecological studies in the Leucothoidae.

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