



## A revision of the genus *Paracallisoma* Chevreux, 1903 (Crustacea: Amphipoda: Scopelocheiridae: Paracallisominae) with a redescription of the type species of the genus *Paracallisoma* and the description of two new genera and two new species from the Atlantic Ocean

TAMMY HORTON<sup>1</sup> & MICHAEL H. THURSTON

National Oceanography Centre, Southampton, European Way, Southampton SO14 3ZH, UK.

<sup>1</sup>Corresponding author. E-mail: [tammy.horton@noc.ac.uk](mailto:tammy.horton@noc.ac.uk)

### Abstract

The genus *Paracallisoma* (Crustacea: Amphipoda) is revised and the type species, *Paracallisoma alberti* is redescribed based on holotype material supplemented with new material from the region of the type locality. This revision results in the establishment of two new genera, *Pseudocallisoma* **gen. nov.** and *Haptocallisoma* **gen. nov.**, and the description of a new species of *Haptocallisoma* and a new species of *Paracallisoma* from the North Atlantic Ocean. An account of all known species within the three genera is given and updated keys to the genera and species are provided.

**Key words:** Amphipoda, Atlantic, bathyal, abyssal, necrophage, new species, *Haptocallisoma*, *Paracallisoma*, *Pseudocallisoma*

### Introduction

The family Scopelocheiridae was established by Lowry & Stoddart (1997) with taxa characterised by a 7/4 setal-tooth arrangement on the outer plate of maxilla 1 and strongly reduced gnathopod 1 dactyl, generally shrouded in setae. Subsequently the family has received little attention. *Anisocallisoma*, (*A. armigera*) and *Paracallisoma spinipoda* were described by Hendrycks & Conlan (2003) and Vinogradov (2004) added *Scopelocheiropsis sublitoralis*. Kaim-Malka (2003) reported on the biology and life cycle of *Scopelocheirus hopei* Costa, 1851. Kilgallen & Lowry (2015) in a review of the family separated scopelocheirid species into two subfamilies, Scopelocheirinae and Paracallisominae, based on mandibular structure, a columnar triturative molar in the former and a non-setose flap or no molar at all in the latter. Diagnoses of all known genera within the family were given, together with the description of two new genera, *Austrocallisoma* and *Tayabasa*, and three new species from Australian waters (Kilgallen & Lowry 2015).

The scopelocheirids are scavenging lysianassoid amphipods found from shelf to trench depths. Scopelocheirines occur mainly at shelf and upper slope depths and are specialist scavengers with *Aroui* Chevreux, 1911 in particular and *Scopelocheirus* Bate, 1857 to a lesser extent associated with spatangoid echinoids (Lowry & Stoddart 1989). *Scopelocheirus* is also attracted to baited traps (Kaim-Malka 2003; unpublished observations). Paracallisomines occur through a much wider depth range, from the upper slope (Ledoyer 1986; Vinogradov 2004) to hadal depths (Dahl 1959; Blankenship *et al.* 2006). Some species appear to be at least partially bathy- or abyssopelagic (Birstein & Vinogradov 1958; Hendrycks & Conlan 2003). Some species of the new genus *Pseudocallisoma* are known to be important food items for seabirds (Vermeer & Devito 1988), suggesting either that they are not wholly benthic and make extensive migrations up through the water column, or that carcasses become buoyant after death and float to the sea surface to be collected by seabirds. Little is known of the feeding habits of paracallisomines but they have been reported frequently from baited traps in the deep sea (Ingram & Hessler 1983; Thurston 1990; Horton *et al.* 2013).

*Eucallisoma* J.L. Barnard, 1961 is characterised by an expanded basal article on gnathopod 1 which appears glandular and may have some special function related to this. Barnard (1961) stated that the genus is related to others that are believed to be semiparasites on salps or medusae, and that gnathopod 1 may function as special secretory organs for paralysis, or digestion or for secretion of toxic waste products.

Most of the specimens used in this study have been taken in baited traps deployed in the deep sea. Baited traps and cameras have been used extensively in Institute of Oceanographic Sciences and National Oceanography Centre investigations for more than thirty years and have captured or photographed large numbers of amphipods (Thurston 1979, 1990; Lampitt *et al.* 1983; Horton 2004, 2005; Diffenthal & Horton 2007; Horton & Thurston 2009, 2011, 2013, 2014; Horton *et al.* 2013). The method is valuable in providing large numbers of specimens for taxonomic and population studies of this important, yet largely underappreciated component of the deep-sea fauna.

## Methods

This study is based primarily on material collected using baited traps but material from other sources has been used. Most material was collected within two metres of the sea floor using a variety of free-fall devices. Specimens were found in bait recovered from deployments of an experimental fish trap (TRAP B), a baited benthic camera system (BSNACK), in purpose-designed amphipod traps (AmphT, TAmph, AMPHITRAP, DEMAR, VET) and in simple auxiliary traps attached to benthic landers or placed on the seafloor by Remotely Operated Vehicle. In addition, specimens have been caught in various towed gears; benthic nets (BN 2.4, BN 1.5/5C, BN 1.5/3M), supra-benthic nets (SBN) attached to bottom nets, and single and multiple rectangular mid-water trawls (RMT 8, RMT 1+8M). Material was fixed in 4% formaldehyde and transferred to 80% Industrial Denatured Alcohol for sorting and storage.

Sorting, initial observation and dissection were undertaken using Wild M5 or Leica™ MZ 7.5 stereomicroscopes. Dissected parts were mounted in polyvinyl-lactophenol stained with lignin pink. Illustrations were prepared using Wild M20 or Olympus™ BX51 compound microscopes. Illustrations of *Haptocallisoma lemarete*, *Paracallisoma idioxenos*, and *Pseudocallisoma coecum* were hand-inked many years ago, prior to the advent of digital-inking technology; those of *H. abyssi* and *P. alberti* were scanned and inked digitally using Adobe® Illustrator® and a WACOM™ digitiser tablet (Coleman 2003). Type material of both new species has been deposited at the Natural History Museum, London (NHMUK). Additional material is held in the Australian Museum, Sydney (AM); Canadian Museum of Nature, Ottawa, Canada (CNMC); Discovery Collections, National Oceanography Centre, Southampton; Musée Océanographique Monaco (MOM); Swedish Museum of Natural History, Stockholm (SMNH); United States National Museum of Natural History, Smithsonian Institution, Washington DC, (USNM); Zoological Museum, Hamburg (ZMH).

Setal and mouthpart classifications follow Watling (1989) and Lowry & Stoddart (1992, 1993, 1995). Measurements of inner and outer plates of maxilla 2 and the relative lengths and proportions of gnathopods and pereopods follow Horton & Thurston (2014). Use of the terms ‘acute’ and ‘transverse’ relative to the palm of gnathopod 2 follows Poore & Lowry (1997) where ‘acute’ describes the condition in which the included angle between the longitudinal axis of the propodus and the palm is less than 90° and ‘transverse’ the condition in which this angle approximates to 90°.

Some of the taxa examined show modifications of the propodus of pereopods 3–7. The term ‘prehensile’ is used where the propodus is expanded to a greater or lesser degree forming a palm against which the dactylus can close. The palm thus formed is lined with setae noticeably stouter than those on the corresponding margin of the carpus. The following abbreviations have been used: A, antenna; C, cephalon; E, epimeron; Ep, epistome; G, gnathopod; L, lower lip; Md, mandible; Mx, maxilla; Mxp, maxilliped; P, pereopod; T, telson; U, uropod; l, left; r, right; x, female; y, male. Bold type in descriptions refer to diagnostic character states.

## Systematics

### Superfamily Lysianassoidea Dana, 1849

### Family Scopelocheiridae Lowry & Stoddart, 1997

### Subfamily Paracallisominae Kilgallen & Lowry, 2015

**Diagnosis.** Mandible a non-setose flap or occasionally absent (*Scopelocheiropsis sublitoralis*).

**Remarks.** The subfamily Paracallisominae can be distinguished from the Scopelocheirinae by the possession of a non-columnar, non-triturative molar that has been reduced to a non-setose, conical structure (the molar appears absent in *Scopelocheiropsis sublitoralis*). In their revision of the family Scopelocheiridae, Kilgallen & Lowry (2015) noted that ‘there is still a large knowledge gap in the diversity of deep-sea scopelocheirids’. This paper is an initial attempt to redress this knowledge gap by redefining the genus *Paracallisoma*, describing two new genera, allocating known species among these genera, and describing two new species belonging to this complex.

**Included genera.** The Paracallisominae contains nine genera: *Anisocallisoma* Hendrycks & Conlan, 2003; *Austrocallisoma* Kilgallen & Lowry, 2015; *Bathycallisoma* Dahl, 1959; *Eucallisoma* J.L. Barnard, 1961; *Haptocallisoma* **gen. nov.**; *Paracallisoma* Chevreux, 1903; *Pseudocallisoma* **gen. nov.**; *Scopelocheiropsis* Schellenberg, 1926; *Tayabasa* Kilgallen & Lowry, 2015.

### Key to the genera of Paracallisominae

1. Gnathopod 1, basis expanded (glandular?) . . . . . 2
- Gnathopod 1, basis ordinary . . . . . 4
2. Maxilla 1, inner plate fully setose along medial margin . . . . . 3
- Maxilla 1, inner plate with only 1 pappose apical seta . . . . . *Anisocallisoma*
3. Maxilliped palp article 4 vestigial; posteroventral lobe of pereopod 4 coxa strongly narrowed, subacute . . . . . *Tayabasa*
- Maxilliped palp article 4 well developed; posteroventral lobe of pereopod 4 coxa broad, subquadrate . . . . . *Eucallisoma*
4. Pereopods 3 to 7 or only pereopods 3 and 4 strongly prehensile . . . . . 5
- Pereopods 3 to 7 not prehensile. . . . . 6
5. Pereopods 3 and 4 prehensile; gnathopod 1 elongate, slender, longer than gnathopod 2; pereopods 3 and 4 carpus strongly compressed, shorter than wide; pereopod 5 basis subrectangular . . . . . *Scopelocheiropsis*
- Pereopods 3 to 7 prehensile; gnathopod 1 not elongate, robust, subequal to gnathopod 2; pereopods 3 and 4 carpus longer than wide; pereopod 5 basis suboval. . . . . *Haptocallisoma* **gen. nov.**
6. Coxae 1 and 2 tapering distally. . . . . 7
- Coxae 1 and 2 subrectangular, not tapering distally . . . . . 8
7. Maxilla 1 palp 2-articulate, maxilliped palp article 4 well developed . . . . . *Pseudocallisoma* **gen. nov.**
- Maxilla 1 palp 1-articulate, maxilliped palp article 4 absent . . . . . *Austrocallisoma*
8. Pereopod 5 basis subcircular; gnathopod 1 propodus strongly tapering. . . . . *Bathycallisoma*
- Pereopod 5 basis pyriform; gnathopod 1 propodus subrectangular . . . . . *Paracallisoma*

### *Paracallisoma* Chevreux, 1903 *sensu stricto*

*Paracallisoma* Chevreux 1903: 84.—Schellenberg 1926a: 257.—Chevreux 1935: 39.—Gurjanova 1962: 308.—Hurley 1963: 60.—J.L. Barnard 1969: 305 (key), 354.—Barnard & Karaman 1991: 454 (key), 510.—Hendrycks & Conlan 2003: 2322.

**Type species.** *Paracallisoma alberti* Chevreux, 1903, original designation.

**Diagnosis.** Eyes absent, or present, lacking ommatidea, red-pigmented, pigment lost in alcohol. Mandible, left *lacinia mobilis* a stemmed, distally asymmetrically expanded, serrate blade; incisor ordinary, molar an acute conical structure; palp attached level with molar. Lower lip, lobes separate, sub-triangular. Maxilla 1, outer plate broad with eleven setal teeth in simple 7/4 arrangement, inner plate strongly setose medially, palp 2-articulate, article 2 large, slender, rectangular. Maxilla 2 inner and outer plates subequal in width, inner plate slightly shorter than or subequal in length to outer plate. Maxilliped, inner plate almost straight apically, palp strongly exceeding outer plate, dactyl well developed. Gnathopod 1 simple, coxa large, subrectangular (not tapered), slightly shorter than coxa 2; basis linear; ischium long; propodus longer than or subequal to carpus; dactyl vestigial, shrouded in setae. Gnathopod 2 subchelate, coxa large, subrectangular (not tapered), propodus shorter than carpus, ordinary. **Pereopods 3–7 robust but not prehensile.** Pereopods 3 and 4, carpus longer than wide. **Pereopod 5 basis weakly expanded proximally, widening distally with strong posterodistal lobe.** Uropod 1 peduncle normal, rami 0.7 x peduncle. **Telson with apices incised.**

**Remarks.** The species in this genus can be linked by the possession of a pyriform pereopod 5 basis and robust, but not prehensile, pereopods 3–7. The distolateral, subapical notch with robust seta on each telson lobe is typical.

**Included species.** *Paracallisoma sensu stricto* currently includes three species: *P. alberti* Chevreux, 1903; *P. idioxenos* **sp. nov.**; *P. zivianii* (Kilgallen & Lowry, 2015).

## Removals:

- P. abyssi* Oldevig, 1959 (to *Haptocallisoma gen.nov.*)  
*P. coecum* (Holmes, 1908); (to *Pseudocallisoma gen.nov.*)  
*P. platepistomum* Andres, 1977; (to *Pseudocallisoma gen.nov.*)  
*P. spinipoda* Hendrycks & Conlan, 2003 (to *Haptocallisoma gen.nov.*)  
*P. woolgoolga* (Kilgallen & Lowry, 2015) (to *Haptocallisoma gen.nov.*)

## *Paracallisoma alberti* Chevreux, 1903

Figs 1–5

*Paracallisoma alberti* Chevreux 1903: 84, figs 2, 3.—Stebbing 1906: 719.—Chevreux 1935: 39, pl. 1, fig. 3, pl. 9, fig. 2, pl. 16, fig. 5 (in part).—Birstein & Vinogradov 1955: 223, 279 (in part).—Schellenberg 1955: 191 (in part).—J.L. Barnard 1958: 97 (list).—Belloc 1960: 4.—Birstein & Vinogradov 1960: 176, fig. 5, 233, fig. 33 (in part).—Andres 1977: 60—Desbruyères, Geistdorfer, Ingram, Khripoudoff & Lagardère 1985: 236, fig. 1, 237.—Thurston 1990: 262 (in part, part = *P. idioxenos*).—Barnard & Karaman 1991: 511 (in part).—Palerud & Vader 1991: 41 (in part).—Lopes, Marques & Bellan-Santini 1993: 209, table 1.—Dauvin & Bellan-Santini 2002: 316 (table 1).—Horton 2006: 20, table 2.—Horton, Thurston & Duffy 2013: 355, table 2.

Not *Paracallisoma alberti*.—Schellenberg 1926a: 258, fig. 11.—Birstein & Vinogradov 1962: 34.—Lowry & Bullock 1976: 102.—De Broyer & Jażdżewski 1993: 73. (= *Paracallisoma* sp. De Broyer, Lowry, Jażdżewski & Robert 2007).

Not *Paracallisoma alberti*.—Lampitt, Merrett, & Thurston 1983: 76, table 1(= *P. idioxenos*). —Thurston 1990: 266. (part = *P. idioxenos*, part = *P. alberti* s.s.).

Not *Paracallisoma alberti*.—Birstein & Vinogradov 1958: 228.—Birstein & Vinogradov 1960: 176, fig. 5, 233, fig. 33.—Gurjanova 1962: 309, fig. 102.—Nagata 1963: 1.—Birstein & Vinogradov 1970: table 1, table 3.—Hatch 1983: 194, 195, table 3.—Nysewander 1983: 328, table 7.—Hatch 2013: 275 (= *P. coecum*).

Not *Paracallisoma alberti*.—Birstein & Vinogradov 1964: 161; Not *Paracallisoma* aff. *alberti*.—Treude, Janßen, Queisser & Witte 2002: 1284, table 2. (= *Paracallisoma* sp.).

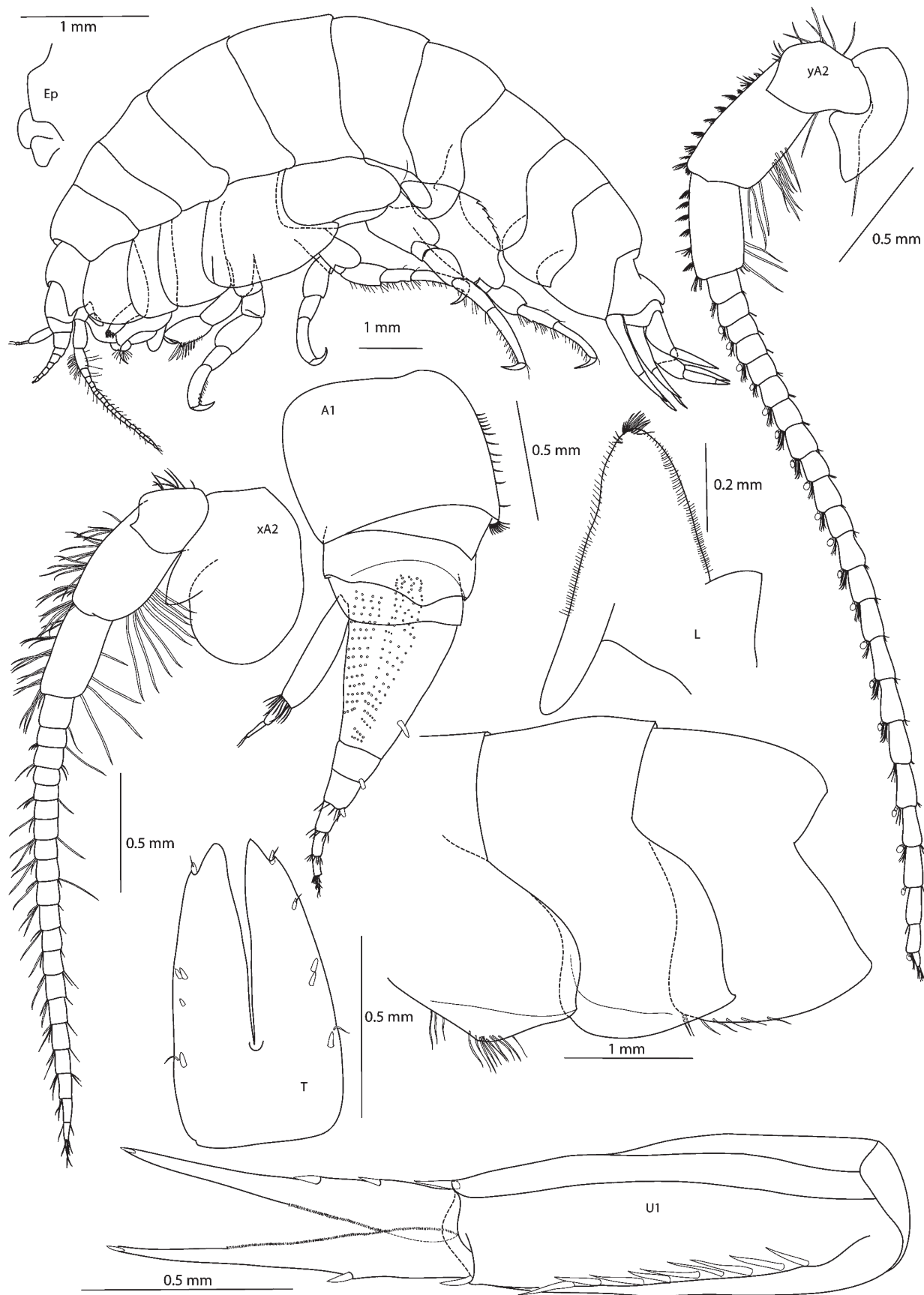
**Type material. Syntypes**—one female, 13mm, *Princesse-Alice* station 532, 26–27 June 1895, 37°52'N 24°42.75'W, trap on seafloor, 2178 m; three females, *Princesse-Alice* station 730, 3–5 August 1896, 37°58'N 26°13.25'W, trap on seafloor, muddy sand, 2660 m; five males, nine females, *Princesse-Alice* station 792, 29 June–1 July 1897, 32°32.16'N 17°04.42'W, trap on seafloor, blackish grey ooze to fine sand, 2480 m. All syntypes are held at the Musée Océanographique Monaco. The co-ordinates given here are those reported in Chevreux (1935) rather than in the original publication (Chevreux 1903), which used the Paris, not the Greenwich meridian for calculating longitude. The syntypes were not examined as part of this study but are figured in Kilgallen & Lowry (2015).

**Material examined.** Faroe-Shetland Channel. Station 57060#1, 11–13 August 2002, 61°39.16' N, 01°13.97' W, DEMAR, 1611m, one adult female 14.5 mm (dissected carcass and four slides (NHMUK 2015. 2825)), seven adult males, three juveniles (NHMUK 2015. 2827–2836).

Cape Verde Basin. Station 53509#3, 3 September 1995, 29°13.07'N 43°08.50'W to 29°17.49'N 43°06.14'W, RMT8M-3, 2880–3025 m (227–407 m above bottom), one specimen.

Mid Atlantic Ridge. Station 54106#2, 21 August 1997, 37°07.5'N 32°22.0'W to 37°04.5'N 32°22.0'W, RMT8-2, 2542–2619 m. Station JC011/079, 5 August 2007, 53°56.44'N 36°11.56'W, DEMAR, 2564 m, four specimens. Station JC011/098, 9–11 August 2007, 54°04.08'N 34°09.43'W, DEMAR, 2500 m, 23 specimens. JC011/114, 12–13 August 2007, 54°02.31'N 34°09.60'W, DEMAR, 2453 m, five specimens. Station JC037/013, 8–10 August 2009, 49°02.00'N 27°43.44'W, AMPHITRAP, 2501 m, 59 specimens. Station JC037/052, 25–27 August 2009, 53°59.32'N 36°08.12'W, AMPHITRAP, 2570 m, 14 specimens. Station JC037/060, 27–30 August 2009, 53°58.46'N 36°06.12'W, AMPHITRAP, 2340 m, six specimens. Station JC037/076, 31 August–1 September 2009, 53°58.94'N 34°02.94'W, AMPHITRAP, 2552 m, eight specimens. Station JC048/008, 2–6 June 2010, 53°59.32'N 36°08.07'W, AMPHITRAP, 2628 m, eight specimens. Station JC048/020, 8–9 June 2010, 54°03.95'N 34°09.12'W, AMPHITRAP, 2505 m, eight specimens. Station JC048/032, 16–19 June 2010, 48°47.34'N 28°38.45'W, AMPHITRAP, 2448 m, 1886 specimens. Station JC048/046, 23–26 June, 49°02.01'N, 27°43.44'W, AMPHITRAP, 2507 m, 784 specimens.

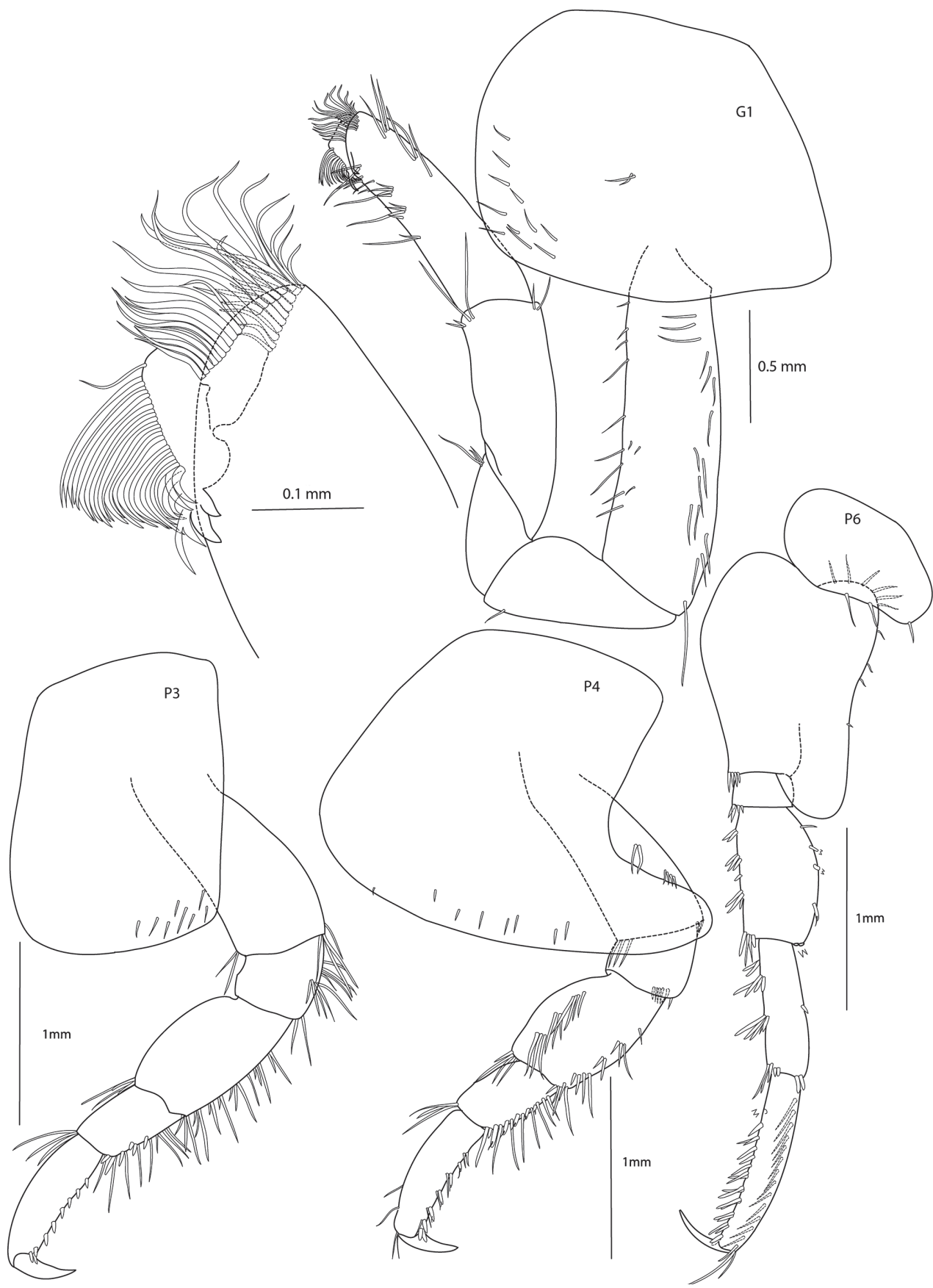




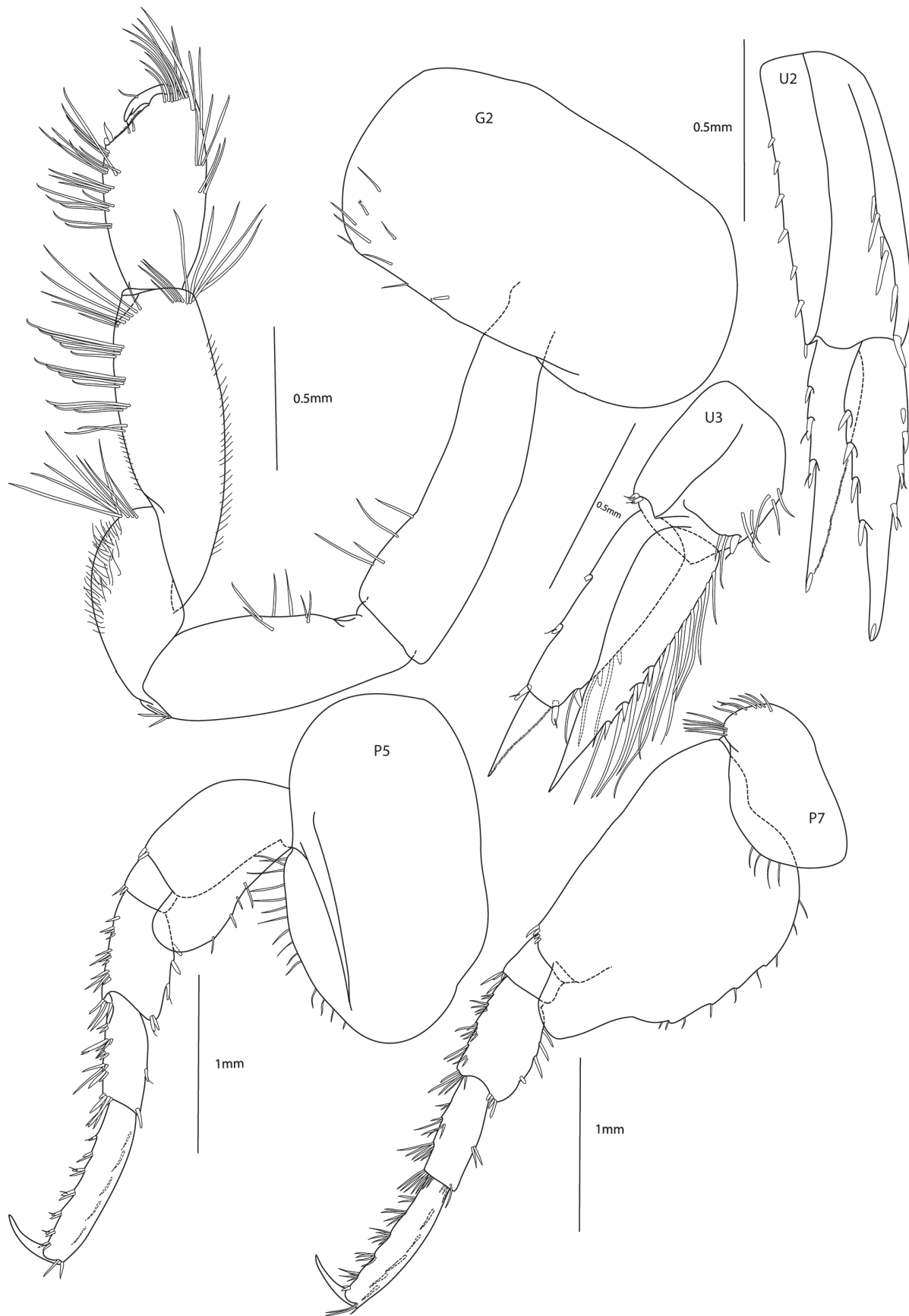
**FIGURE 1.** *Paracallisoma alberti* Chevreux, 1903. Adult female, 14.5 mm, Faroe-Shetland Channel, 1611 m; habitus, antennae, epistome and upper lip, lower lip (half), pleosome, uropod 1, telson. Adult male, Faroe-Shetland Channel, 1611 m; antenna 2.



**FIGURE 2.** *Paracallisoma alberti* Chevreux, 1903. Adult female, 14.5 mm, Faroe-Shetland Channel, 1611 m; mouthparts.



**FIGURE 3.** *Paracallisoma alberti* Chevreux, 1903. Adult female, 14.5 mm, Faroe-Shetland Channel, 1611 m; gnathopod 1, pereopods 3, 4 and 6.



**FIGURE 4.** *Paracallisoma alberti* Chevreux, 1903. Adult female, 14.5 mm, Faroe-Shetland Channel, 1611 m; gnathopod 2, pereopods 5, 7, uropods 2 and 3.



Iberian Basin, Sedlo Seamount. Station 56319#1, (Meteor cruise M60/1, operation #696) 23 November 2003, 40°11.43'N, 26°33.99'W, DEMAR, 2655 m, 24 specimens. Station 56354#1, (Meteor cruise M60/1, operation #735), 29 November 2003, 39°50.17'N, 26°17.82'W, DEMAR, 2876 m, twelve specimens.

Norwegian Sea. Midnatssol Exploration Well, Station TL/280807/010#2, 28 August 2007, 64°09.93'N 05°16.75'E, ROV-deployed trap, 928 m, 19 specimens. Haklang Exploration Well, Station TL/171008/031#1, 17 October 2008, 67°02.81'N 07°03.53'E, ROV-deployed trap, 1248 m, one specimen.

**Description.** Based on adult female, 14.5 mm, Faroe-Shetland Channel, Station 57060#1, 1611 m.

*Head* exposed, deeper than long, lateral cephalic lobe large, narrow, subacute; rostrum absent; *eyes* pigmented, lacking ommatidia, pigment lost in alcohol. *Antenna 1* short, length 0.1 x body; peduncular article 1 short, length 0.73 x breadth, without posterodistal spine or lobe; peduncular article 2 short, 0.25 x article 1; peduncular article 3 short, 0.25 x article 1; flagellum seven-articulate, without posterodistal setae, calceoli absent; accessory flagellum long, 0.6 x primary flagellum, 3-articulate, article 1 long, 4.0 x article 2, forming partial cap over callynophore. *Antenna 2*: length 1.5 x antenna 1; peduncle without brush setae; peduncular article 1 greatly enlarged, not covering article 2; weakly geniculate between peduncular articles 3–4, article 3 short, 0.5 x article 4; peduncular articles 4 and 5 not enlarged; flagellum well-developed, 21 articulate, calceoli absent.

*Mouthpart bundle* subquadrate. *Epistome and upper lip*, interantennal carina notched proximally; epistome produced, rounded, dominant; upper lip slightly produced and rounded. *Mandible* incisors symmetrical, large, with convex margins, left and right accessory setal rows with simple robust setae; left *lacinia mobilis* a smooth stemmed, distally asymmetrically expanded blade; molar an acute conical structure, mandibular palp attached midway; article 1 short, length 0.65 x breadth, without setae; article 2 slender, length 4.2 x breadth, with 17 distolateral A2-setae; article 3 slender, blade-like, with 14 D3 setae along distal two thirds of the margin, and three E3 setae. *Maxilla 1* inner plate triangular, with ten pappose setae; outer plate setal teeth, outer row with ST1-7 large, slender, ST1 bifurcate apically, ST2 four-cuspidate, ST3 three-cuspidate, ST4-5 five-cuspidate, ST6-7 six-cuspidate, inner row with STA-D slender, STA one-cuspidate, STB three-cuspidate, STC four-cuspidate, STD three-cuspidate distally; palp large, two-articulate, article 1 short, article 2 with six terminal robust setae, robust flag seta and one subterminal seta; *Maxilla 2* inner plate broad, tapering distally, with 18 pappose setae in subparallel medial setal row, with terminal robust setae; outer plate slightly longer than inner with apicomedial dentate and plumose setae. *Maxilliped* inner plate large, subrectangular, slightly emarginate distally with three apical nodular setae, oblique facial setal row strong with 15 pappose setae reaching apical margin, two marginal pappose setae; outer plate medium size, subrectangular with eleven apical plumose setae, with eight small nodular setae medially and two longer robust setae on the distomedial corner; palp large, 4-articulate, article 2 broad, length 2.2 x breadth, 1.8 x article 3; article 3 long, slender, length 2.2 x breadth; dactylus well-developed, with one sub-terminal seta, unguis present.

*Gnathopod 1* simple; coxa large, as long as coxa 2, subquadrate; basis long, slender, length 3.4 x breadth, anterior margin smooth, with simple setae; ischium long, length 1.7 x breadth, anterior margin smooth with one seta posterodistally; merus, posterior margin with a few simple setae distally; carpus subrectangular, long, length 3 x breadth, subequal to propodus; propodus large, margins subparallel, posterior margin with a few groups of simple, slender setae, apex with numerous distally pappose robust setae; dactylus, anterior margin shrouded in pappose setae, posterior margin with one small tooth. *Gnathopod 2* subchelate; coxa large, subequal in size to coxa 3; ischium, length 3.0 x breadth; carpus long, length 3.0 x breadth, posterior margin straight; propodus subtriangular, expanded distally, length twice breadth, posterior margin with five groups of slender robust setae, apically with row of distally plumose setae decreasing in size towards palm; palm acute, with very slightly concave serrate margin; dactylus inserted close to anterodistal corner of propodus, curved strongly and reaching only halfway across palm, palm corner with tooth. *Pereopod 3* coxa large, subrectangular; basis robust, sinuous and slightly expanded distally; merus slightly expanded anteriorly; propodus posterior margin with six robust setae and two distal locking setae; dactylus short, curved. *Pereopod 4* as pereopod 3 except coxa wider than deep with well-developed but narrow posterior lobe, ventral and posterior margins confluent, width 1.3 x depth, apex narrowly rounded; propodus posterior margin with six robust setae, five simple setae and one pair of distal locking robust setae. *Pereopod 5* coxa posteriorly lobate with a lateral ridge, 14–15 simple setae along posterodistal margin; basis weakly expanded proximally, widening distally with strong posterodistal lobe extending to 0.3 x length of merus, posterior margin concave with four short robust setae, posterodistal lobe anterior margin with two robust seta distally; merus slightly expanded posteriorly with robust setae on both posterior and anterior margins; propodus

long, length 5.2 x breadth, anterior margin with one single and five pairs of robust setae and one pair of distal locking setae, posterior margin with five long slender simple setae; dactylus slender, curved. *Pereopod 6* coxa small, weakly lobate posteriorly; basis anterior margin smooth, slightly convex with four short robust setae anterodistally, posteroproximal margin expanded rounded, forming lobe with six simple setae on margin, posterior margin slightly concave with four short simple marginal setae, rounded posterodistal lobe extending beyond ischium; merus weakly expanded posteriorly; propodus long, length 5.7 x breadth, anterior margin with eleven pairs/single robust setae and one pair of distal locking setae, posterior margin with 14 long slender simple setae; dactylus slender, curved. *Pereopod 7* coxa small, postero-lobate with four simple slender setae on posteroventral margin and twelve simple setae on anterior margin; basis anterior margin straight with five short robust setae distally, proximal posterior margin expanded, convex with nine short simple setae along margin, excavate posterodistally with a round posterodistal lobe extending beyond ischium; merus weakly expanded posteriorly; propodus long, length 4.7 x breadth, anterior margin with five groups of robust setae, and one pair of distal locking setae, posterior margin with five long slender simple setae; dactylus long, slender, slightly curved.

*Pleonites 1–3* dorsally smooth. *Epimeron 1* anterior margin straight, posteriorly rounded with minute tooth. *Epimeron 2* anterior margin sinuous, rounded; posterior margin convex, posteroventral corner with small tooth. *Epimeron 3* posteroventral corner produced, subrectangular, ventral margin with seven robust setae.

*Gills* on pereopods 2–7. *Brood plates* on pereopods 2–5.

*Urosomite 1* concave anteriorly with a rounded smooth boss posteriorly. *Uropod 1* peduncle long, 1.2 x inner ramus, with one apicolateral robust seta, one apicomедial robust seta, and nine dorsomedial setae; rami subequal; inner ramus, with one medial robust seta, and a microsetose lateral margin; outer ramus, with two lateral robust setae and a microsetose medial margin. *Uropod 2* peduncle long, as long as inner ramus, with one apicolateral robust seta, one apicomедial robust seta, five dorsomedial setae, and six dorsolateral robust setae; inner ramus, length 1.2 x outer ramus, with four medial robust setae and four lateral robust setae; outer ramus, with three lateral robust setae and a microsetose medial margin. *Uropod 3* peduncle short, length 0.6 x inner ramus, with two apicolateral robust setae, one apicomедial robust seta and two simple setae, and five slender simple medial setae; inner ramus, with four medial robust setae and twelve medial slender plumose setae; outer ramus, two-articulate, article 2 short (0.41 x article 1), with a microsetose medial margin; article 1 with four medial robust setae and three slender plumose setae, and three lateral robust setae.

*Telson* weakly tapering, length 1.8 x breadth, cleft 67%, with four robust setae per lobe, distal margins incised with subapical notch and one small immersed seta per lobe

**Sexual dimorphism.** Male antenna twice as long as antenna 1, 23-articulate, with brush setae, stronger callinophore with more profuse aesthetascs, calceoli present on both antennae.

**Remarks.** *Paracallisoma alberti*, the type species of the genus is redescribed here in full using new material. These specimens indicate that the species has eyes (Fig. 5). In common with many other deep-sea lysianassoids, the eyes show no macroscopic structure and the red pigment found is highly labile in alcohol (Thurston 1974; Thurston & Bett 1993; Horton & Thurston 2014).

It should be noted that there is an ontogenetic change, with the gnathopod 2 dactyl: palm ratio, which decreases with increasing body length.

Separation of this Atlantic species from the Pacific species *Paracallisoma coecum* (Holmes, 1908) has been discussed in the literature. Schellenberg, (1926a) placed the Pacific species *P. coecum* (Holmes, 1908) in synonymy with *P. alberti* (Chevreux, 1903). This view was followed by Birstein & Vinogradov (1955, 1958, 1960, 1962, 1964, 1970) and Gurjanova (1962) although the latter did note several differences between her Bering Sea specimens and the drawings of Chevreux (1903). Hurley (1963) and Barnard (1964) retained *P. coecum* as a distinct species pending a re-examination of Atlantic material. The description of *Paracallisoma platelistomum* Andres, 1977, a species closely related to *P. coecum* made it clear, even without further Atlantic material, that the two species were distinct. Examination of material of both species and the description of new species of *Paracallisoma* have allowed us not only to distinguish easily between the two species, but warranted the erection of a new genus for the more slender and largely pelagic ‘paracallisomas’.

**Depth range.** 928–3025 m. The species has been captured in mid-water nets at least 200 m above the sea floor (this study).



**FIGURE 5.** *Paracallisoma alberti* Chevreux, 1903. Adult female, Sedlo Seamount, Azores, 2655 m; fresh specimen, showing ocular patches.

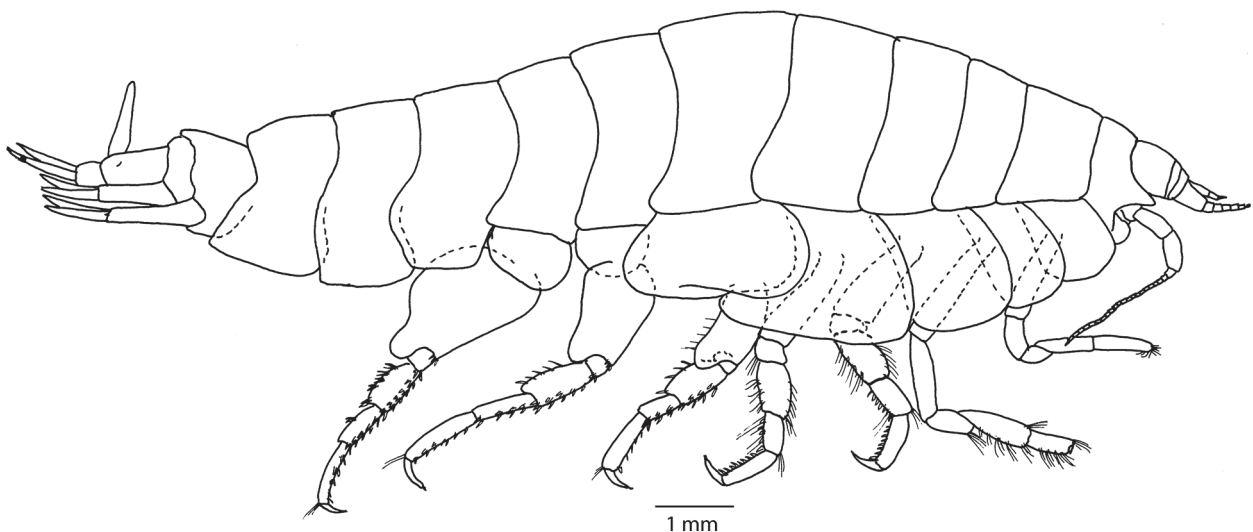
**Distribution.** *P. alberti* is known from the North East Atlantic in the Madeiran and Iberian Basins at depths of 2178–2660 m (Chevreux 1903), the Porcupine Seabight (Lampitt *et al.* 1983), the Bay of Biscay (Chevreux 1935; Desbruyères *et al.* 1985), the Faroe-Shetland Channel at 1396–1661 m (Horton 2006) and the Mid-Atlantic Ridge at 2340–2628 m (Horton *et al.* 2013).

***Paracallisoma idioxenos* sp. nov.**

Figs 6–8

Not *Paracallisoma alberti*—Lampitt *et al.* 1983: 76, table 1.—Thurston 1990: 266.

**Material examined. Holotype**—Pre-adult female, 15.4 mm; carcass and seven slides, (NHMUK 2015.2853), Station 52216#5, 23–25 June 1985, 48°50.02'N 16°29.51'W, AmphT, 4842 m.



**FIGURE 6.** *Paracallisoma idioxenos* sp. nov. Holotype, pre-adult female, 15.4 mm, habitus.

**Allotype**—Adult male, 11.0 mm (NHMUK 2015.2854), station data as above.

**Paratypes**—20 specimens (NHMUK 2015.2855-2864), station data as above.

**Additional material.** Porcupine Seabight and Porcupine Abyssal Plain, Station 9756#8, 13–15 April 1978, 49°53.6'N 13°57.9'W, TRAP B, 3852 m, one specimen. Station 50812#1, 3 August 1980, 49°45.4'N 14°10.3'W, BN1.5/3M, 4080–4100 m, one specimen. Station 50909, 10–11 November 1980, 49°53.83'N 14°00.36'W, TAmph, 3918 m, one specimen. Station 52403#20, 8–9 December 1986, 49°10.9'N 16°16.7'W, AmphT, 4850 m, one specimen. Station 52701#1, 16–21 May 1991, 48°48.2'N 16°24.9'W, BSNACK, 4840 m, one specimen. Station 52701#35, 22–23 May 1991, 48°48.5'N 16°23.6'W, DEMAR, 4843 m, 29 specimens. Station 52806, 2–3 August 1992, 50°11.8'N 14°41.1'W, Aberdeen pop-up fish trap, 3976 m, one specimen. Station 13077#4, 14–18 March 1997, 48°55.82'N 16°35.25'W, trap on NIOZ Lander, 4844 m, one specimen. Station 13077#35, 19–23 March 1997, 48°58.10'N 16°24.93'W, trap on NIOZ Lander, 4845 m, one specimen. Station 13077#71, 24–27 March 1997, 48°50.01'N 16°17.97'W, traps on NIOZ Lander, 4840 m, eight specimens. Station 13077#92, 27–28 March 1997, 48°49.50'N 16°20.97'W; DEMAR, 4844 m, twelve specimens. Station 13078#3 29–31 March 1997, 48°46.99'N 16°22.09'W; DEMAR, 4842 m, one specimen. Station 13078#14, 1–2 April 1997, 48°55.12'N 16°25.06'W; DEMAR, 4845 m, seven specimens. Station 13078#22, 3 April 1997, 48°43.02'N 16°38.18'W; DEMAR, 4842 m, one specimen. Station 13200#31, 7 July 1997, 48°48.79'N 16°23.43'W; DEMAR, 4842 m, six specimens. Station 13200#42, 13–15 July 1997, 48°54.81'N 16°34.93'W; DEMAR, 4844 m, 34 specimens. Station 13200#55, 16 July 1997, 48°49.02'N 16°21.59'W; DEMAR, 4844 m, two specimens.

Iberian Margin. Station 15741#1, 4–5 August 2005, 39°34.95'N 10°16.50'W, Trap, 4286 m, one specimen. Station 56839#1, 4–5 May 2006, 38°06.59'N 09°58.18'W, Trap, 4445 m, two specimens. Station 56847#1, 7–8 May 2006, 39°35.50'N 10°19.00'W, Trap, 4403 m, five specimens.

**Description.** Holotype, pre-adult female, 15.4 mm. *Head* exposed, deeper than long, lateral cephalic lobe large, narrow, subacute; rostrum absent. *Eyes* apparently absent in preserved material. *Antenna 1* short, length 0.12 x body; peduncular article 1 short, length 0.95 x breadth, without posterodistal spine or lobe; peduncular article 2 short, 0.28 x article 1; peduncular article 3 short, 0.14 x article 1; flagellum 5-articulate, without posterodistal setae, calceoli absent, accessory flagellum long, 0.61 x primary flagellum, 3-articulate, article 1 long, 3.5 x article 2, forming partial cap over callynophore. *Antenna 2* 2.1 x antenna 1; peduncle without brush setae; peduncular article 1 greatly enlarged, not covering article 2; weakly geniculate between peduncular articles 3–4, article 3 short, 0.7 x article 4; peduncular articles 4 and 5 not enlarged; flagellum well developed, 21-articulate, calceoli absent. *Mouthpart bundle* subquadrate. *Epistome and upper lip* separate; epistome produced, rounded; upper lip not produced, slightly rounded. *Mandible* incisors symmetrical, large, with convex margins; left *lacinia mobilis* a stemmed asymmetric blade; accessory setal rows without distal setal tuft, each with three robust simple setae; molar an acute conical structure, mandibular palp attached midway; article 1 short, length 0.65 x breadth, without setae; article 2 slender, length 4.2 x breadth, with 15 submarginal posterodistal A2-setae; article 3 slender, blade-like, with 18 D3 setae along distal two thirds of the margin, and three E3 setae. *Maxilla 1* inner plate tapering distally, inner margin fully setose, with eleven pappose setae; outer plate broad with eleven setal teeth in 7/4 arrangement; outer row with ST1 large, slender, four-cuspidate, ST2–7 large, slender, ST2 four-cuspidate, ST3 six-cuspidate, ST4 six-cuspidate, ST5 five-cuspidate, ST6 seven-cuspidate, ST7, seven-cuspidate, inner row with STA–D slender, STA bifurcate, STB weakly one-cuspidate, STC four-cuspidate, STD three-cuspidate distally; palp large, 2-articulate, article 1 short, article 2 with seven terminal robust setae, one robust flag seta present on distolateral corner and one subterminal seta. *Maxilla 2* inner plate broad, tapering distally, with 21 pappose setae, with terminal robust setae; outer plate slightly longer than inner with apicomedial dentate and plumose setae. *Maxilliped* inner plate large, subrectangular, slightly emarginate distally with four apical nodular setae, oblique facial setal row strong with 14 pappose setae and a submarginal row of four pappose setae; outer plate medium size, subrectangular with ten apical plumose setae, with ten small nodular setae medially and two longer robust setae on the distomedial corner; palp large, four-articulate, article 2 broad, length 1.8 x breadth, 1.8 x article 3; article 3 long, slender, length 2.2 x breadth; dactylus well-developed, with one sub-terminal seta, unguis present.

*Gnathopod 1* simple; coxa large, slightly shorter than coxa 2, basis long, slender, length 3.6 x breadth, anterior margin smooth, with simple setae; ischium length 1.6 x breadth, anterior margin smooth with one seta posterodistally; merus, posterior margin with a few simple setae distally; carpus subrectangular, long, length three x breadth, subequal to propodus; propodus large, margins subparallel, posterior margin with a few groups of simple, slender setae, apex densely furnished with pappose robust setae; dactylus minute, complex, covered in



sensory setae, posterior margin with one small tooth. *Gnathopod 2* subchelate; coxa large, subequal in size to coxa 3; ischium long, length 3.0 x breadth; carpus long, length 3.1 x breadth, posterior margin straight; propodus subrectangular, margins sub-parallel, not expanded distally, long, length 2.1 x breadth, posterior margin with five groups of slender robust setae, apically with row of distally plumose setae decreasing in size towards palm; palm acute, straight, with serrate margin; dactylus inserted near middle of distal margin of propodus, curved, and reaching almost to palmar angle, corner defined by two teeth. *Pereopod 3* coxa large, subrectangular; basis robust, sinuous and slightly expanded distally; merus slightly expanded anteriorly; propodus posterior margin with eight robust setae and two distal locking setae; dactylus short, slightly curved. *Pereopod 4* as pereopod 3 except coxa wider than deep with well-developed posteroventral lobe, subacutely produced, posterior and ventral margins confluent, breadth 1.4 x depth. *Pereopod 5* coxa very large, posterior lobate with a lateral ridge, eleven simple setae along ventral margin; basis weakly expanded proximally, widening distally with strong posterodistal lobe extending to 0.3 x length of merus, posterior margin concave with six short robust setae, anterior margin with two robust seta distally; merus weakly expanded posteriorly with robust setae on posterior and anterior margins; propodus long, length 4.4 x breadth, anterior margin with five groups of one or two robust setae and one pair of distal locking setae, posterior margin with 4–5 simple setae; dactylus slightly curved. *Pereopod 6* coxa small, weakly lobate posteriorly; basis anterior margin smooth, strongly convex with four short robust setae anterodistally, posteroproximal margin expanded, rounded, forming lobe with five simple setae on margin, posterior margin slightly concave with three short simple marginal setae, narrowly rounded posterodistal lobe reaching merus; merus weakly expanded posteriorly; propodus long, longer than propodus of pereopods 5 and 7, length 5.5 x breadth, anterior margin with six groups of one or two robust setae and one pair of distal locking setae, posterior margin with ten–eleven slender simple setae; dactylus slightly curved. *Pereopod 7* coxa small, lobate posteriorly with five simple slender setae on posteroventral margin and about ten simple setae on anterior margin; basis anterior margin slightly sinuous with five short robust setae anterodistally, proximal posterior margin broadly expanded, rounded, convex with six short simple setae along margin, excavate posterodistally with a round posterodistal lobe extending to 0.25 x merus; merus weakly expanded posteriorly; propodus long, length 3.3 x breadth, anterior margin with four pairs of robust setae, and one pair of distal locking setae, posterior margin with four slender simple setae; dactylus slightly curved.

*Pleonites 1–3* dorsally smooth. *Epimeron 1* anterior margin setose, slightly concave, lateral face with angled ridge; posteriorly rounded, with a slight posteroventral tooth. *Epimeron 2* anterior margin sinuous, rounded; lateral face with angled ridge, posterior margin convex, posteroventral corner with small tooth. *Epimeron 3* posteroventral corner with small tooth, ventral margin with 15 small robust setae.

*Gills* on pereopods 2–7. *Brood plates* on pereopods 2–5.

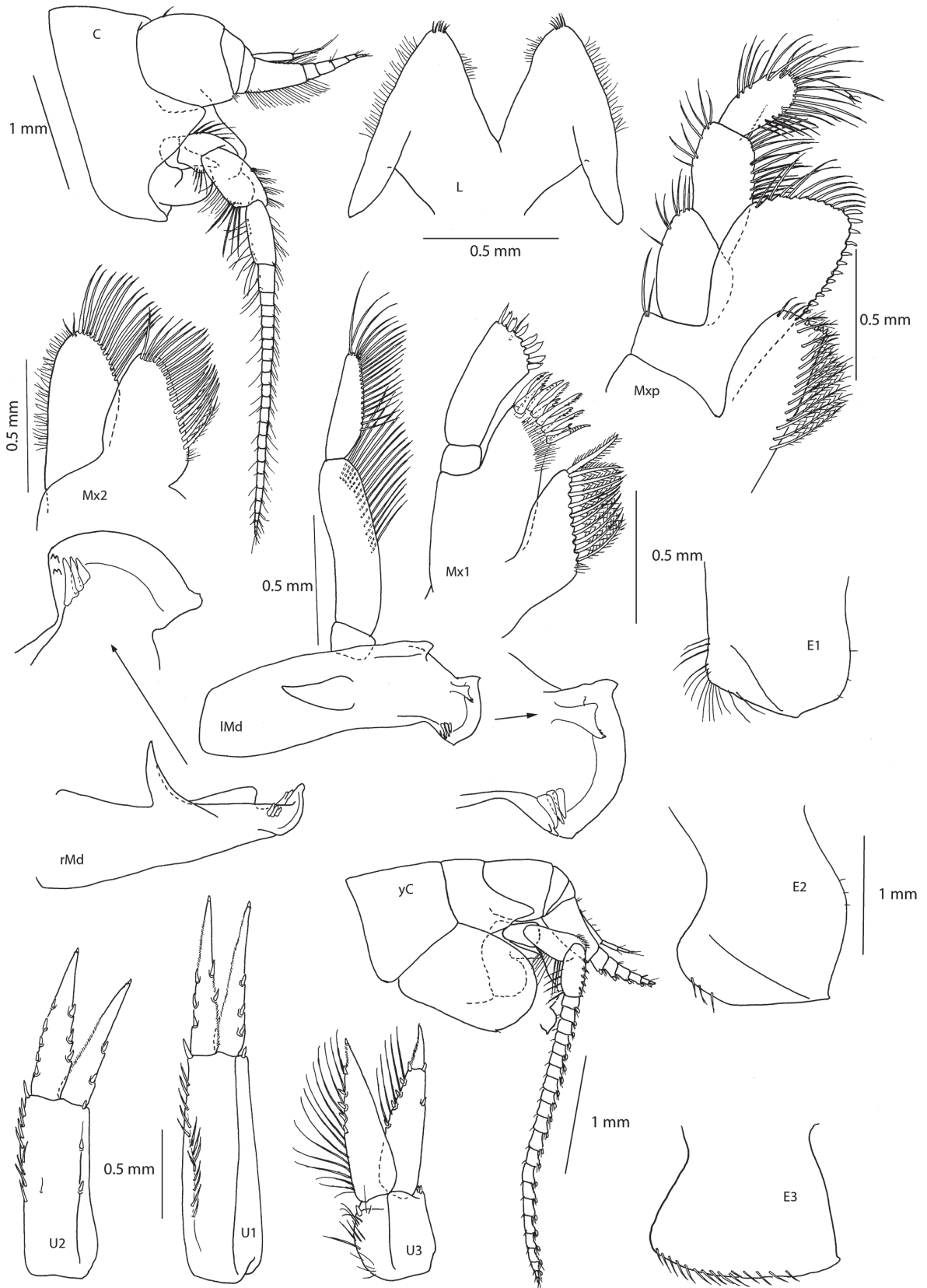
*Urosomite 1* concave anteriorly with a rounded smooth boss posteriorly. *Uropod 1* peduncle long, 1.46 x inner ramus length, with one apicolateral robust seta, one apicomедial robust seta, and 14 dorsomedial setae; rami subequal; inner ramus, with three medial and two lateral robust setae, and a microsetose lateral margin; outer ramus, with three lateral robust setae and a microsetose medial margin. *Uropod 2* peduncle long, 1.2 x inner ramus, with one apicolateral robust seta, one apicomедial robust seta, ten dorsomedial setae, and two dorsolateral robust setae; inner ramus, length 1.1 x outer ramus, with five medial robust setae and three lateral robust setae; outer ramus, with two lateral robust setae and a microsetose medial margin. *Uropod 3* peduncle short, with two apicolateral robust setae, one apicomедial robust seta and two simple setae, and five slender simple medial setae; inner ramus slightly shorter than outer, with four medial robust setae and 14 medial slender plumose setae; outer ramus, 2-articulate, article 2 short, with a microsetose medial margin; article 1, medial margin with six medial robust setae and six slender plumose setae, and one lateral slender robust seta.

*Telson* sub-triangular, length 1.6 x breadth, deeply cleft (68%), with two lateral robust setae per lobe, distal margins incised with subapical notch and one small immersed seta per lobe.

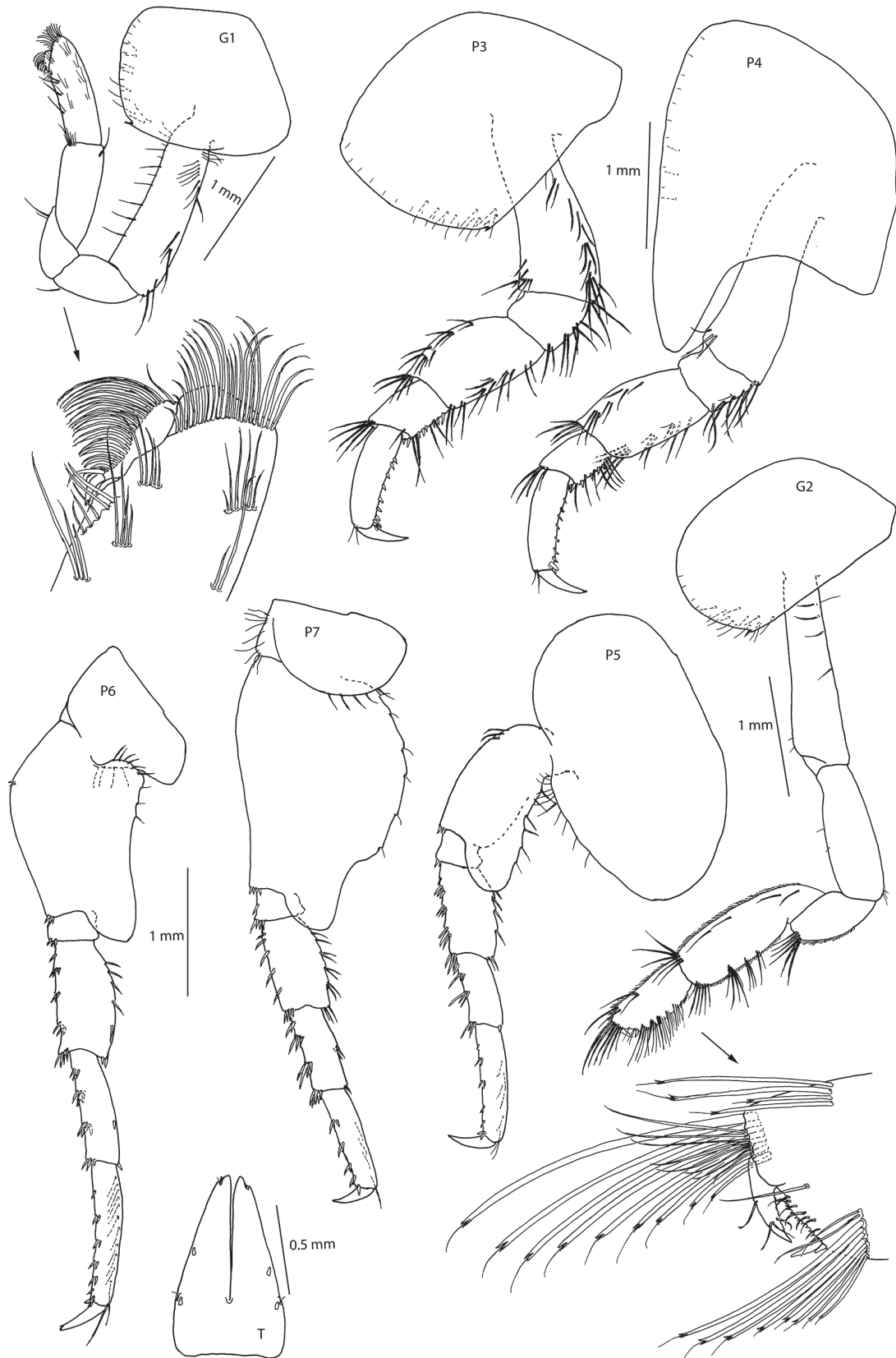
**Sexual dimorphism.** Male antenna 2 length 2.1 x antenna 1, 24-articulate, with brush setae, calceoli present on both antennae, lateral cephalic lobe narrower than in female.

**Etymology.** Derived from the Greek, *idioxenos*— friend, in honour of the friendship between the authors and Roger Bamber, dedicatee of the special issue in which this paper appears.





**FIGURE 7.** *Paracallisoma idioxenos* sp. nov. Holotype, pre-adult female, 15.4 mm, head, antennae, mouthparts, epimera and uropods. Allotype, adult male, 11 mm, head and antennae.



**FIGURE 8.** *Paracallisoma idioxenos* sp. nov. Holotype, pre-adult female, 15.4 mm, gnathopods, pereopods and telson.

**Remarks.** *Paracallisoma idioxenos* sp. nov. is very closely allied to *Paracallisoma alberti* Chevreux, 1903, and has been recorded as this species in recent literature (Lampitt *et al.* 1983; Thurston 1990). The differences are subtle and were only recognised when material of *P. alberti* from the region of the type locality was obtained for study. The species can be distinguished by the variation in the insertion of the gnathopod 2 dactylus and the shape of the propodus: in the type species *P. alberti*, the dactyl is inserted at the anterodistal angle of article 6, and does not reach the palmar corner (only reaching about halfway down the palm) and the propodus is broadened distally. However, in *P. idioxenos* the dactylus is inserted around the middle of the apex of article 6 and nearly reaches the palmar corner, and the margins of the propodus are subparallel. The new species has a more nearly triangular telson with narrower lobes than does *P. alberti* and among subtle differences in setation has more dorsomedial robust setae on the peduncles of uropods 1 and 2 (14 and ten respectively compared to nine and five).

**Depth range.** 3852–4850 m.

**Distribution.** North-east Atlantic Ocean. Porcupine Seabight (3852–4850 m), Iberian Margin (4286–4445 m).

### *Paracallisoma zivianii* Kilgallen & Lowry, 2015

*Paracallisoma zivianii* Kilgallen & Lowry, 2015: 29.

**Type material. Holotype**—male, 12.0 mm, AM P.69091, east of Flynn Reef, Queensland, Australia (16°37.82'S 146°23.08'E), 1000 m, baited trap, 7–8 June 1993, collected by J.K. Lowry, P. Freewater & W. Vader, RV *Sunbird* [QLD-950/SEAS].

**Paratype**—one specimen, 10.8 mm, AM P.69092, east of Flynn Reef, Queensland, Australia (16°37.82'S 146°23.08'E), 1000 m, baited trap, 6–7 June 1993, collected by J.K. Lowry, P. Freewater & W. Vader, RV *Sunbird* [QLD-931/SEAS].

**Remarks.** This species is most similar to *P. alberti*. It differs from both *P. alberti* and *P. idioxenos* in the shape of the gnathopod 2 palm, which is transverse. It also differs in the length of the dactyl of gnathopod 2 which is as long as the palm but shorter in the other two species. The latter character must be used with caution as it is an ontogenetic character for both species, with smaller specimens having relatively longer dactyli.

**Depth range.** 963–1000 m.

**Distribution.** *Australia*—east of Flynn Reef, Queensland, to north-east of Coffs Harbour, New South Wales.

### *Haptocallisoma* gen. nov.

*Scopelocheirus*.—Oldevig 1959: 16.—Barnard & Karaman 1991: 528 (in part, part *Scopelocheirus*)

*Paracallisoma*.—Hendrycks & Conlan 2003: 2322.—Kilgallen & Lowry 2015: 20 (in part, part *Paracallisoma*)

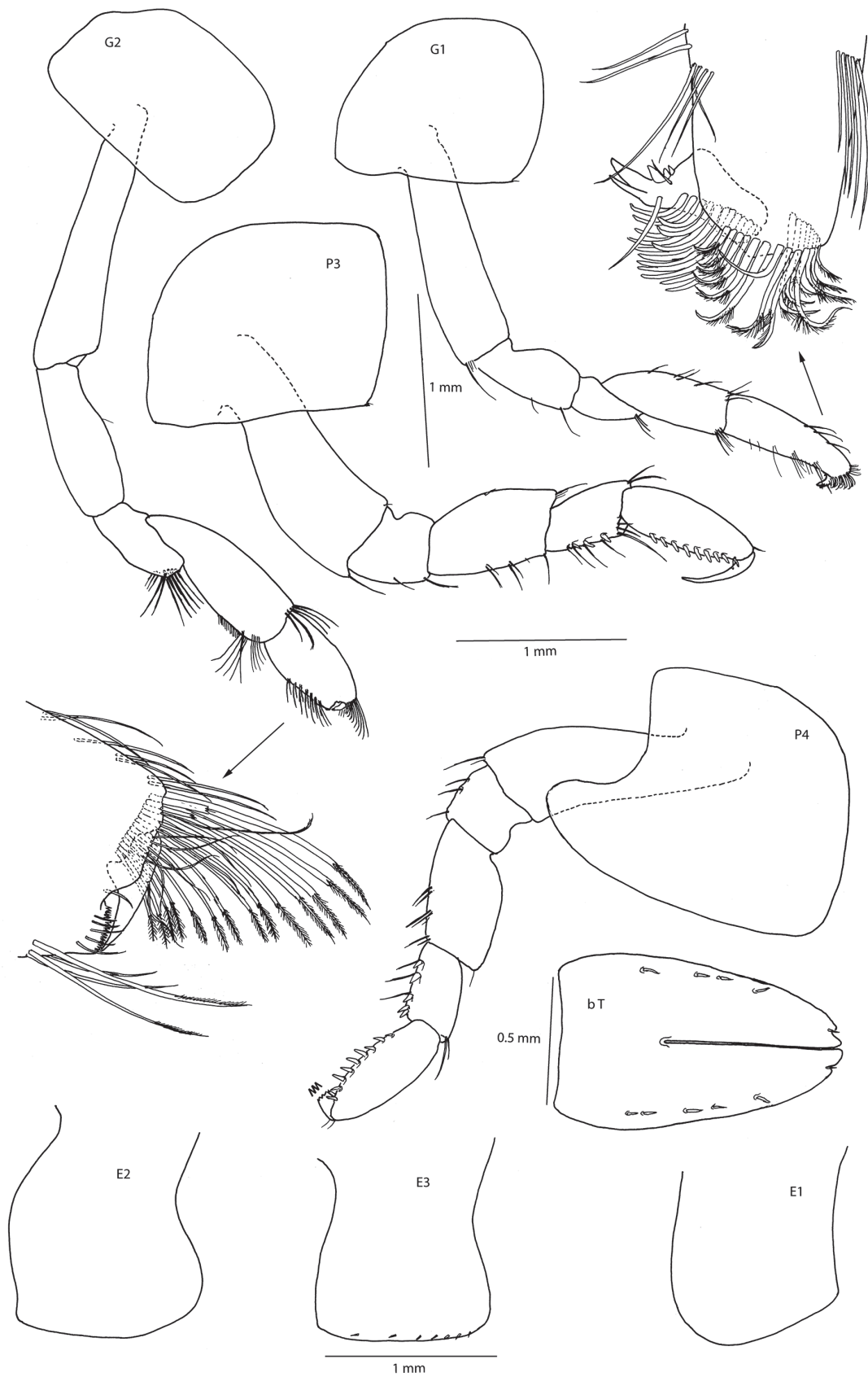
**Type species.** *Scopelocheirus abyssi* Oldevig, 1959.

**Diagnosis.** Mandible, incisor ordinary; left *lacinia mobilis* present, a stemmed, distally asymmetrically expanded, non-serrate blade; left and right setal row each with three robust setae, molar simple, conical, acute; palp attached level with molar. Lower lip, lobes widely separated. Maxilla 1, inner plate strongly setose medially; outer plate with eleven robust setae, in simple 7/4 arrangement; palp two-articulate, **article 2 large, expanded distally**. Maxilla 2, inner plate with oblique row of mediofacial pappose setae. Maxilliped well developed, **inner plate emarginate distally**, palp four-articulate. **Coxae 1 and 2 large, broad, subrectangular**. Gnathopod 1 simple, propodus longer than carpus, dactylus shrouded in setae. Gnathopod 2 subchelate, propodus shorter than carpus. **Pereopods 3 to 7 prehensile (on P7 poorly developed)**. Pereopods 3 and 4 carpus longer than wide. **Pereopod 5, basis suboval**. Uropod 1 peduncle normal, rami variable. Telson with apices incised.

**Etymology.** From the Greek, *hapto*—to join, fasten to, lay hold of or grasp; in reference to the prehensile pereopods 3–7 of the species in this genus added to the common stem of the subfamily ‘-callisoma’.

**Remarks.** This new genus is characterized by the prehensile pereopods 3 to 7, the suboval basis of pereopod 5, and the large distally expanded article 2 of maxilla 1.

**Included species.** *Haptocallisoma abyssi* (Oldevig, 1959) **comb. nov.**; *H. lemarete* **sp. nov.**; *H. spinipoda* (Hendrycks & Conlan, 2003) **comb. nov.**; *H. woolagooga* (Kilgallen & Lowry, 2015) **comb. nov.**



**FIGURE 9.** *Haptocallisoma abyssi* (Oldevig, 1959) **comb. nov.** Lectotype, immature female, ~13 mm, Swedish Deep, 3200 m, gnathopods, pereopods 3, 4, epimera. Syntype specimen b, sex unknown, ~12 mm, telson.



**FIGURE 10.** *Haptocallisoma abyssi* (Oldevig, 1959) **comb. nov.**. Syntype specimens, 12–13 mm, Swedish Deep, 3200 m. Specimen d, sex unknown, head. Specimen c, immature female, ~13 mm, antennae. Specimen a, immature female, ~12 mm, mouthparts: mandible palps, article 3 lost.



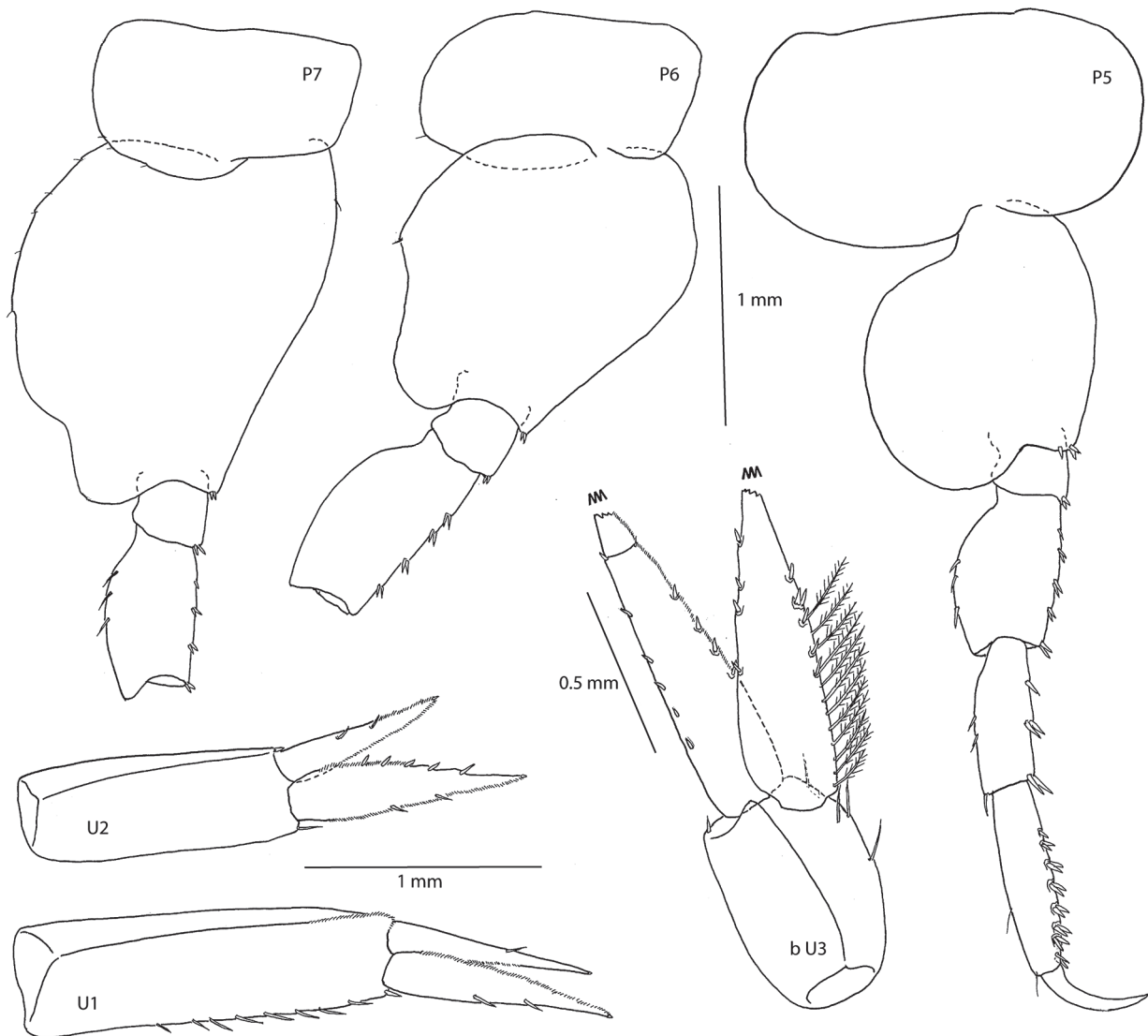
*Haptocallisoma abyssi* (Oldevig, 1959) comb. nov.

Figs 9–14

*Scopelocheirus abyssi* Oldevig 1959: 16, figs 1–3.—Barnard & Karaman 1991: 528.—Vinogradov, Vereschchaka & Vinogradov 1996: 8.—Brandt 1997: 1540 (table 2).

*Paracallisoma abyssi*.—Horton 2006: 20, table 2.—Horton, Thurston & Duffy 2013: 354.—Kilgallen & Lowry 2015: 22.

**Type material.** Lectotype and 23 paralectotype specimens, maximum length about 15 mm, Swedish Museum of Natural History, Stockholm, “Svenska Djupet” 77°39′N. 01°17′O. 3200 m, Biloculina-lera, bottent. –1°, 4. 27.7 1898. Svenska Spetsb.-Exp.” The material is in poor condition and no specimen is complete. A female specimen about 12 mm long and thought to be that used by Oldevig for his description is selected here as a lectotype. The dissected carcass of the lectotype is registered under Amphipoda Type no. 2343 with three slides of dissected parts under Amphipoda Type no. 5356, 5357 and 5362. The carcasses of paralectotype specimens ‘a–e’ are registered under Amphipoda Type no. 5351–5355 with associated slides registered under Amphipoda Type no. 5358–5361.



**FIGURE 11.** *Haptocallisoma abyssi* (Oldevig, 1959) comb. nov.. Lectotype, immature female, ~13 mm, Swedish Deep, 3200m, pereopods 5, 6, 7, uropods 1 and 2. Uropod 3 illustrated from syntype specimen b, sex unknown, ~12 mm.

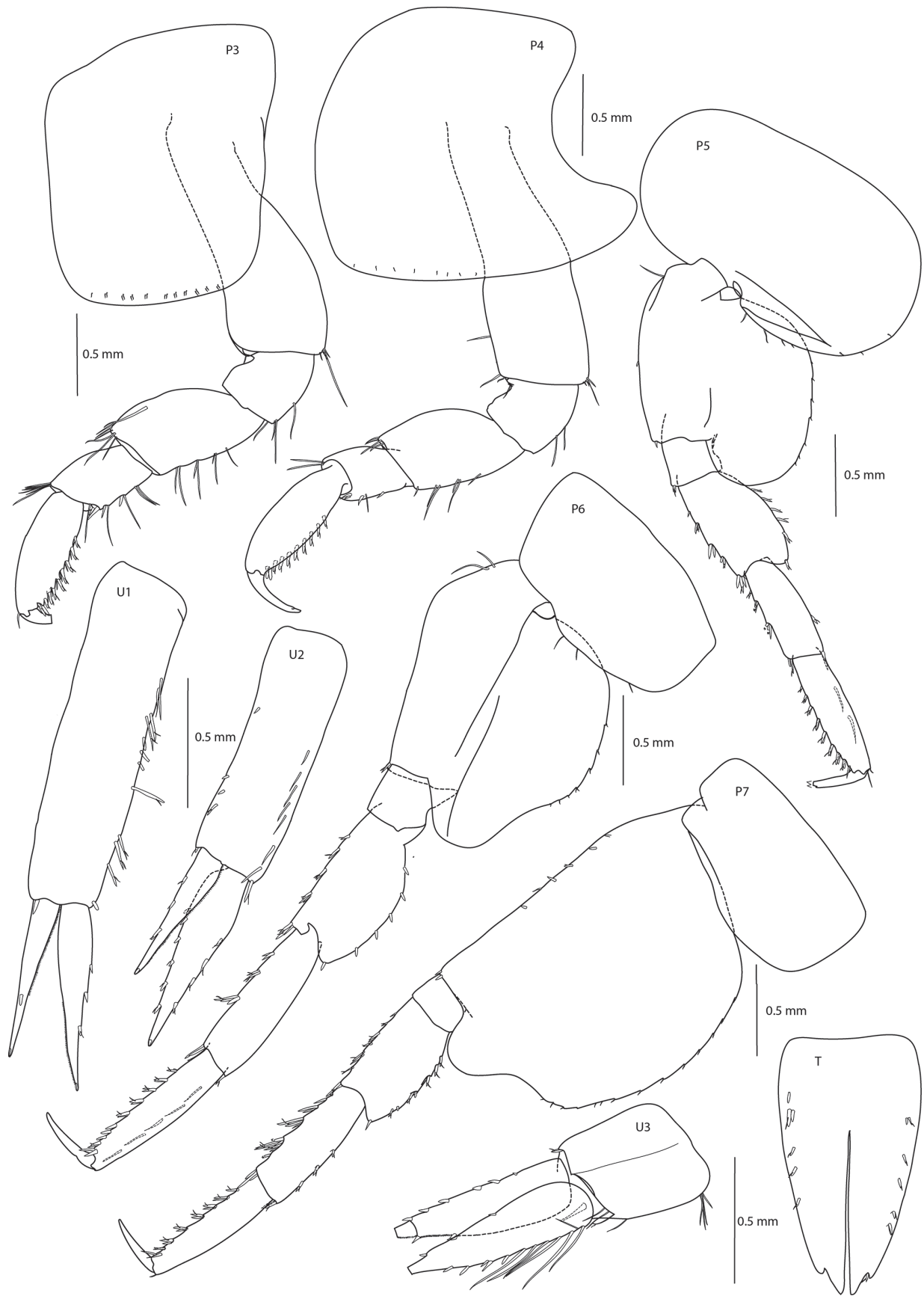
**Material examined.** Type series: Greenland Sea, Boreas Basin. Swedish Spitzbergen Expedition, “Swedish Deep”, 27 July 1898, 77°39′N 01°17′E, 3200 m, lectotype and 23 paralectotype specimens.



**FIGURE 12.** *Haptocallisoma abyssi* (Oldevig, 1959) **comb. nov.** Adult female, 13.9 mm, Norwegian basin, 1611 m, habitus, head, gnathopods, pleosome and urosome. Adult male, 13.6 mm, Norwegian basin, 1611 m, head, antennae.



**FIGURE 13.** *Haptocallisoma abyssi* (Oldevig, 1959) **comb. nov.**. Adult female, 13.9 mm, Norwegian basin, 1611 m, mouthparts.



**FIGURE 14.** *Haptocallisoma abyssi* (Oldevig, 1959) **comb. nov.**. Adult female, 13.9 mm, Norwegian basin, 1611 m, pereopods, uropods and telson.

**Additional material.** Faroe-Shetland Channel. Station 57060#1, 11–13 August 2002, 61°39.16' N, 01°13.97' W, DEMAR, 1611 m, one adult female 13.9 mm (dissected carcass and four slides (NHMUK 2015. 2837)), one adult male 13.6 mm (one slide NHMUK 2015. 2838), four females, one immature male and four juveniles (NHMUK 2015. 2839–2847). Station 53979#1, 16–17 August 1996, 61°28.72' 02°47.66' W, fish trap, 1396 m, two specimens.

Norwegian Sea. Midnatssol Exploration Well, Station TL/280807/010#2, 28–29 August 2007, 64°09.93' N 05°16.75' E, ROV-deployed trap, 928 m, 42 specimens. Haklang Exploration Well, Station TL/171008/031#1, 17 October 2008, 67°02.81' N 07°03.53' E, ROV-deployed trap, 1248 m, one specimen. Gro Exploration Well, Station LE/090609/005#1, 9–10 June 2009, 66°08.88' N 03°56.41' W, ROV-deployed trap, 1380 m, three specimens.

**Description.** Based on lectotype, immature female, ~12 mm (G1–2, P3–7, E1–3, U1–2); paralectotype 'a', immature female, ~12 mm (A2, L, Md, Mx1–2, Mxp); paralectotype 'b', sex unknown, ~12 mm (U3, T); paralectotype 'c', immature female, ~13 mm (A1); paralectotype 'd', sex unknown, ~12 mm (C).

*Head* exposed, deeper than long, lateral cephalic lobe small, subacute; rostrum very short; interantennal carina sinuous proximally, not notched. *Antenna 1* short, 0.12 x body; peduncle article 1 short, length 0.9 x breadth, without posterodistal spine or lobe; peduncular article 2 short, 0.23 x article 1; peduncle article 3 short, 0.16 x article 1; flagellum 8-articulate, calynophore present, two-field; accessory flagellum long, 0.68 x primary flagellum, 3-articulate, article 1 long, 3.4 x article 2. *Antenna 2* length 3 x antenna 1; peduncle article 1 greatly enlarged, not covering article 2; weakly geniculate between peduncle articles 3–4, article 3 short 0.4 x article 4; peduncle articles 4 and 5 not enlarged; flagellum well developed, 35-articulate, calceoli absent.

*Mouthpart bundle* subquadrate. *Epistome and upper lip* separate; epistome straight; upper lip not produced, slightly rounded. *Mandible* incisors symmetrical, large, with slightly convex margins; left *lacinia mobilis* incomplete (distal part broken), right lacking; accessory setal rows each with three robust simple setae; molar a conical structure; palp article 1 short, length 0.75 x breadth, without setae; article 2 slender, length five x breadth, with 12–14 submarginal distolateral A2-setae; article 3 missing. *Maxilla 1* inner plate tapering distally, inner margin fully setose, with twelve pappose setae; outer plate broad with eleven setal teeth in 7/4 arrangement; outer row with ST1–2 large, slender, without cusps, ST3 two-cuspidate, ST4–5 three-cuspidate, ST6 two-cuspidate, ST7 without cusps, inner row with STA–C slender, without cusps, STD three-cuspidate terminally; palp large, two-articulate, article 1 short, article 2 widening distally with seven terminal robust setae, flag seta and one subterminal seta; *Maxilla 2* inner plate broad, tapering, with twelve pappose setae in oblique mediofacial setal row, with terminal spines and setae; outer plate slightly longer than inner with apicomedial spines and setae. *Maxilliped* inner plate large, subrectangular, emarginate distally with three apical nodular setae, with one apicomedial seta, oblique facial setal row strong with eleven pappose setae; outer plate medium size, broadly rounded with twelve apical plumose setae, with 15 medial small nodular setae and two longer robust setae at the distomedial corner; palp large, 4-articulate, article 2 longest, slender, length 2.4 x breadth, 1.8 x article 3; article 3 long, slender, length 2.2 x breadth; dactylus well-developed, with 3 sub-terminal setae.

*Gnathopod 1* simple; coxa broad, as long as coxa 2, basis long, slender, length 3.5 x breadth, anterior margin smooth, without setae; ischium length twice breadth, anterior margin smooth, posterior margin with a few simple setae; merus, posterior margin with a few simple setae distally; carpus subrectangular, long, length 2.8 x breadth; propodus as long as carpus, tapering distally, posterior margin with six groups of simple, slender setae, apex with numerous distal robust pappose setae; dactylus posterior margin with three small teeth. *Gnathopod 2* minutely subchelate; coxa large, narrower than coxa 3; carpus long, length 2.8 x breadth; propodus suboval, slightly narrowing distally, short, 0.68 x carpus, length twice breadth, posterior margin with seven groups of slender robust setae, apically with row of distally plumose setae decreasing in size towards palm; palm transverse indented medially with convex serrate margin distally; dactylus reaching corner of palm, posterior margin smooth. *Pereopod 3* prehensile; coxa large, broad, subrectangular; basis robust, sinuous and slightly expanded distally; merus slightly expanded anteriorly; propodus posterior margin with eight robust setae and two distal locking setae; dactylus long, slender and curved to close along palm of propodus. *Pereopod 4* prehensile; as pereopod 3 except coxa width 1.2 x depth, with well-developed narrowly rounded posterior lobe. *Pereopod 5* coxa posterior lobate; basis widely expanded, posterior margin and posterodistal lobe broadly rounded, extending to distal margin of ischium; merus expanded posteriorly with robust setae on anterior and posterior margins; carpus shorter than propodus; propodus long, length 3.9 x breadth, anterior margin with one single and six pairs of robust setae and one pair of locking setae; dactylus long, 0.55 x propodus, curved to close against palm of propodus. *Pereopod 6* coxa small, posterior



lobate; basis anterior margin, convex and rounded, lacking robust setae, proximal posterior margin expanded, rounded, convex, with one short simple seta at angle proximal to excavate distal posterior margin, round posterodistal lobe not extending to merus; merus 1.2 x merus of pereopod 5; distal articles lost. *Pereopod 7* (weakly prehensile); coxa small, posterior lobate; basis anterior margin convex with one short slender seta proximally, posterior margin broadly expanded, rounded, convex with five short simple setae along margin, excavate distally with a short, rounded, posterodistal lobe not extending to merus; merus weakly expanded posteriorly; distal articles lost.

*Pleonites 1–3* smooth dorsally. *Epimeron 1* rounded posteriorly; anterior margin slightly concave. *Epimeron 2* anterior margin sinuous, anterior corner rounded; posterior margin convex, posteroventral corner slightly produced. *Epimeron 3* subquadrate, posterior margin slightly convex, posteroventral corner not produced, ventral margin with seven small robust setae.

*Gills* on pereopods 2–7. *Brood plates* on pereopods 2–5.

*Uropod 1* peduncle long, with one apicomedial robust seta and eight dorsomedial setae; inner ramus 0.61 x peduncle, with two medial robust setae and microsetose lateral margin; outer ramus 0.91 x inner ramus, with one lateral robust seta and microsetose medial margin. *Uropod 2* peduncle long, with just one apicomedial robust seta; inner ramus 0.88 x peduncle, with two medial robust setae and five lateral robust setae; outer ramus, 0.75 x inner ramus, with two lateral robust setae and a microsetose medial and distolateral margins. *Uropod 3* peduncle short, length 1.5 x breadth, with one apicolateral seta and four medial setae; inner ramus apex lost, at least 1.5 x peduncle, with six medial robust setae and twelve medial slender plumose setae and four lateral robust setae; outer ramus apex lost, at least 1.5 x peduncle, two-articulate; article 1 with four medial robust setae and a microsetose medial margin and six lateral robust setae. *Telson* longer than broad, slightly tapering, length 1.6 x breadth, cleft 64%, with 4/5 robust setae on each lobe, distal margins shallowly incised, with one small immersed seta.

**Additional description.** Adult female 13.9 mm and adult male 13.6 mm from Faroe-Shetland Channel, Station 57060#1, 11–13 August 2002, 61°39.16' N, 01°13.97' W, DEMAR, 1611m, DTI SEA4 cruise.

*Mandible* as in lectotype except left *lacinia mobilis* a stemmed asymmetric blade, accessory setal row with two robust setae; palp article 2 with 16 submarginal distolateral A2-setae; article 3 slender, blade-like, with 18 D3 setae along distal two thirds of the margin, and three E3 setae.

*Gnathopod 2* as in lectotype except dactyl (damaged) not reaching palm edge, with denticulate posterodistal margin, three subterminal setae.

*Pereopod 5* prehensile; anterior margin with one robust seta distally, posterior margin with eight short robust setae; merus with six robust setae on posterior margin and five groups of robust setae on anterior margin; propodus long, length 4.2 x breadth, anterior margin with eight pairs of robust setae and one pair of distal locking setae, posterior margin with two slender setae; dactylus long, slender, tip broken. *Pereopod 6* prehensile; basis anterior margin rounded proximally with two long simple setae, posterior margin with seven short simple setae along margin, round posterodistal lobe extending to merus; propodus long, length 4.2 x breadth, anterior margin with five pairs of robust setae, five single robust setae and a pair of locking setae, posterior margin with five slender setae; dactylus long, slender, almost straight. *Pereopod 7* basis anterior margin straight with five short robust setae, posterior margin with twelve short simple setae along margin; propodus long, length 4.3 x breadth, anterior margin with one single and six pairs of robust setae and one pair of distal locking setae; dactylus long, slender, almost straight.

*Urosomite 1* concave before low rounded boss. *Uropod 1* peduncle very long, 1.85 x inner ramus, with one apicolateral robust seta, one apicomedial robust seta, and 14 dorsomedial setae; inner ramus, 0.54 x peduncle, with three medial robust setae, and a microsetose lateral margin; outer ramus 0.9 x inner ramus, with one dorsolateral robust seta and a microsetose medial margin. *Uropod 2* peduncle long, 1.32 x inner ramus, with one apicolateral robust seta, one apicomedial robust seta, seven dorsomedial setae, and four dorsolateral robust setae; inner ramus, 0.8 x peduncle, with four medial robust setae and six lateral robust setae; outer ramus, 0.7 x inner ramus, with three lateral robust setae and a microsetose medial margin. *Uropod 3* peduncle short, length and breadth subequal, with one apicolateral robust seta, one apicomedial robust seta, one distoventral robust seta, and seven slender simple medial setae; inner ramus, tip lost, at least 1.7 x peduncle, longer than article 1 of outer ramus with five medial robust setae, six medial slender plumose setae and three lateral robust setae; outer ramus, 2-articulate, article 2 tip lost, article 1 at least 1.6 x peduncle with four medial robust setae, six lateral robust setae and a microsetose distomedial margin.

**Sexual dimorphism.** *Male antenna 1* short, length 0.12 x body; peduncle article 1 short, length 0.7 times breadth, with 16 short plumose setules on posterior margin; peduncle article 2 short, 0.45 x article 1; peduncle article 3 short, 0.25 x article 1; flagellum 8-articulate, with posterodistal setae; callynophore strong, two field; accessory flagellum long, 0.73 x primary flagellum, 4-articulate, Article 1 long, 4.0 x article 2. *Male antenna 2* length four x antenna 1; peduncle with brush setae; peduncle article 1 greatly enlarged, not covering article 2; weakly geniculate between peduncle articles 4–5, article 3 short, 0.7 x article 4; peduncle articles 4 and 5 not enlarged; flagellum well developed, 41-articulate; calceoli present.

**Remarks.** The original description of this species is very short with only pereopod 6, pereopod 7, and telson illustrated (Oldevig 1959). A lectotype has been selected from Oldevig's material and the species is redescribed and re-illustrated using this specimen, others from the type series, and new material from the Faroe-Shetland Channel. The characteristic prehensile pereopods 3–7 and the broadly expanded basis of pereopod 5 justify the inclusion of *H. abyssi* in the new genus *Haptocallisoma*.

**Depth range.** 1611–3200 m.

**Distribution.** Boreas Basin between Greenland and Svalbard, Faroe-Shetland Channel.

***Haptocallisoma lemarete* sp. nov.**

Figs 15–18

sp. nov. aff. *Paracallisoma* Thurston 1979: 56.

aff. *Paracallisoma* Lampitt, Merrett & Thurston 1983: 76, table 1.

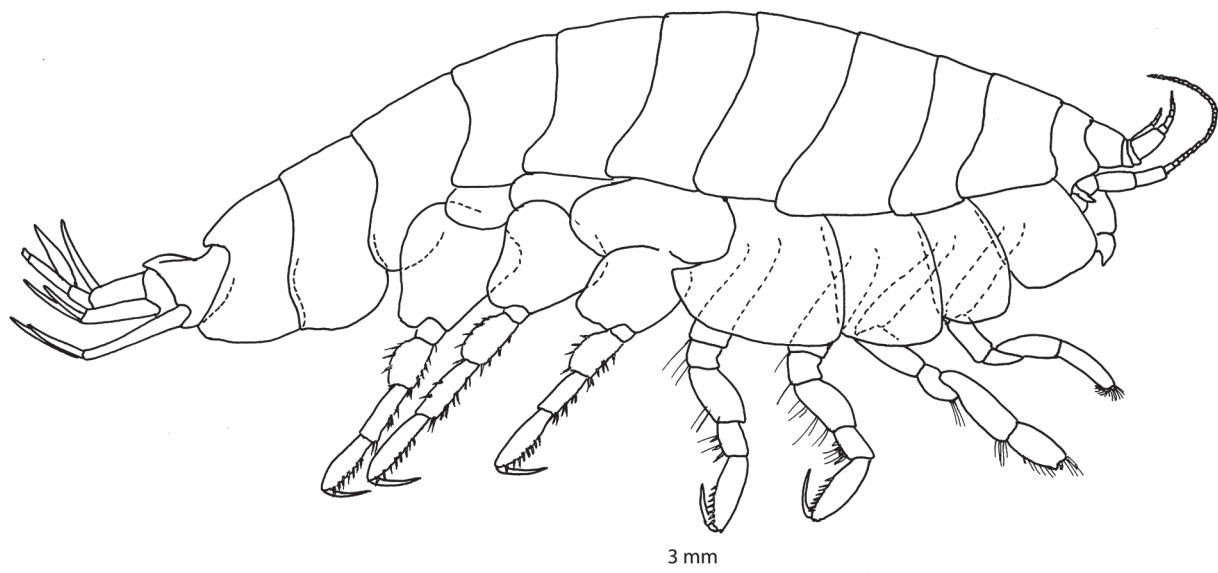
*Scopelocheirus* group gen. nov. Thurston 1990: 262–263, tables 3 & 4.

*Paracallisoma* sp. nov. 1 Duffy, Horton & Billett 2012: 4865.

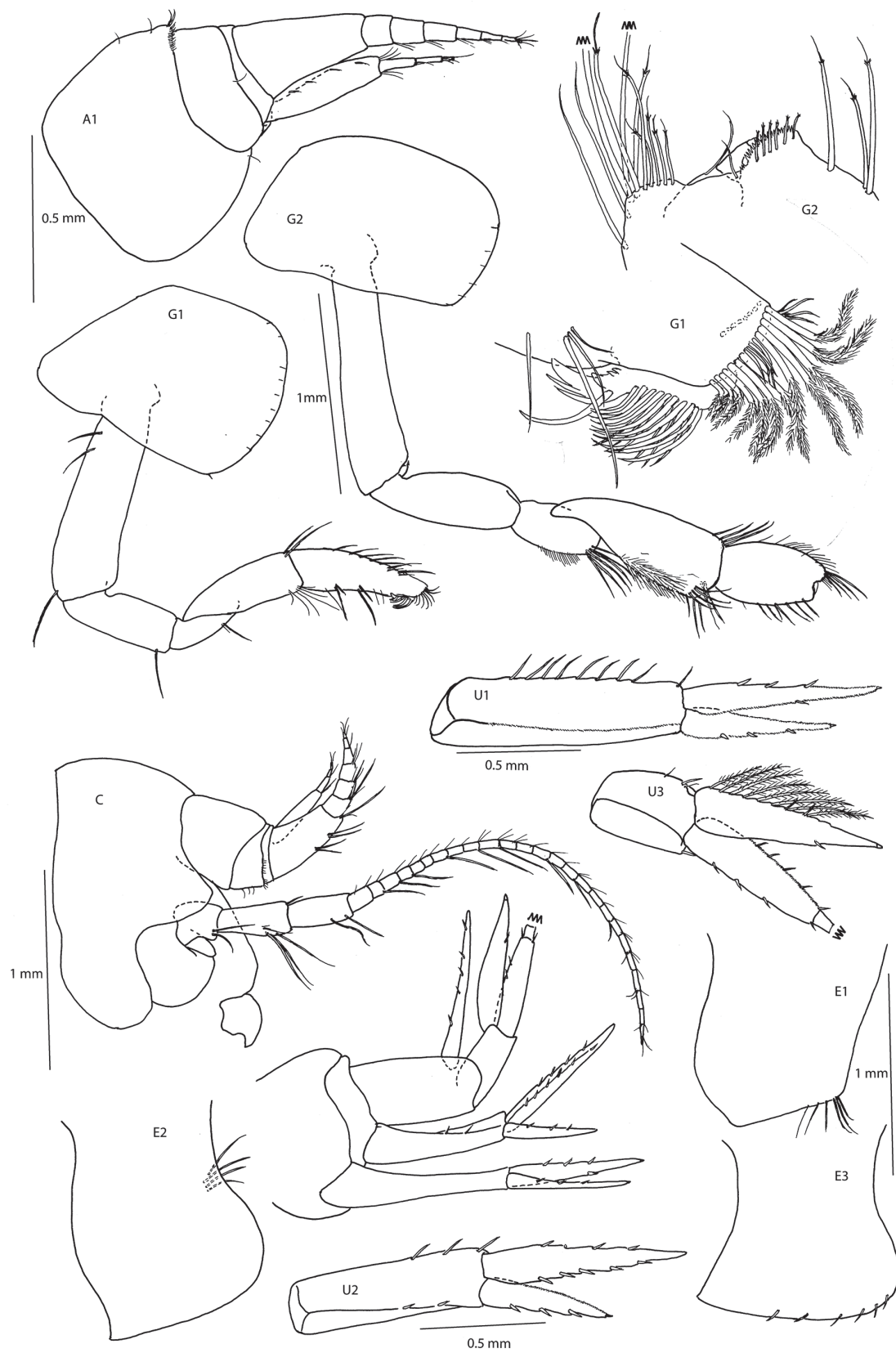
*Paracallisoma* sp. 4 Horton, Thurston & Duffy 2013: 354–356.

**Type material. Holotype**—Adult female, 10.6 mm (dissected carcass and seven slides NHMUK. 2848), Station 9131#18, 21 November 1976, 20°07.7'N 21°32.9'W to 20°09.1'N 21°40.4'W, RMT8, 3760–3920 m (100–250 metres above bottom (mab)).

**Paratypes**—Station 9131#18, 21 November 1976, 20°07.7'N 21°32.9'W to 20°09.1'N 21°40.4'W, RMT8, 3760–3920 m (100–250 mab), four specimens (NHMUK 2015. 2849–2852).



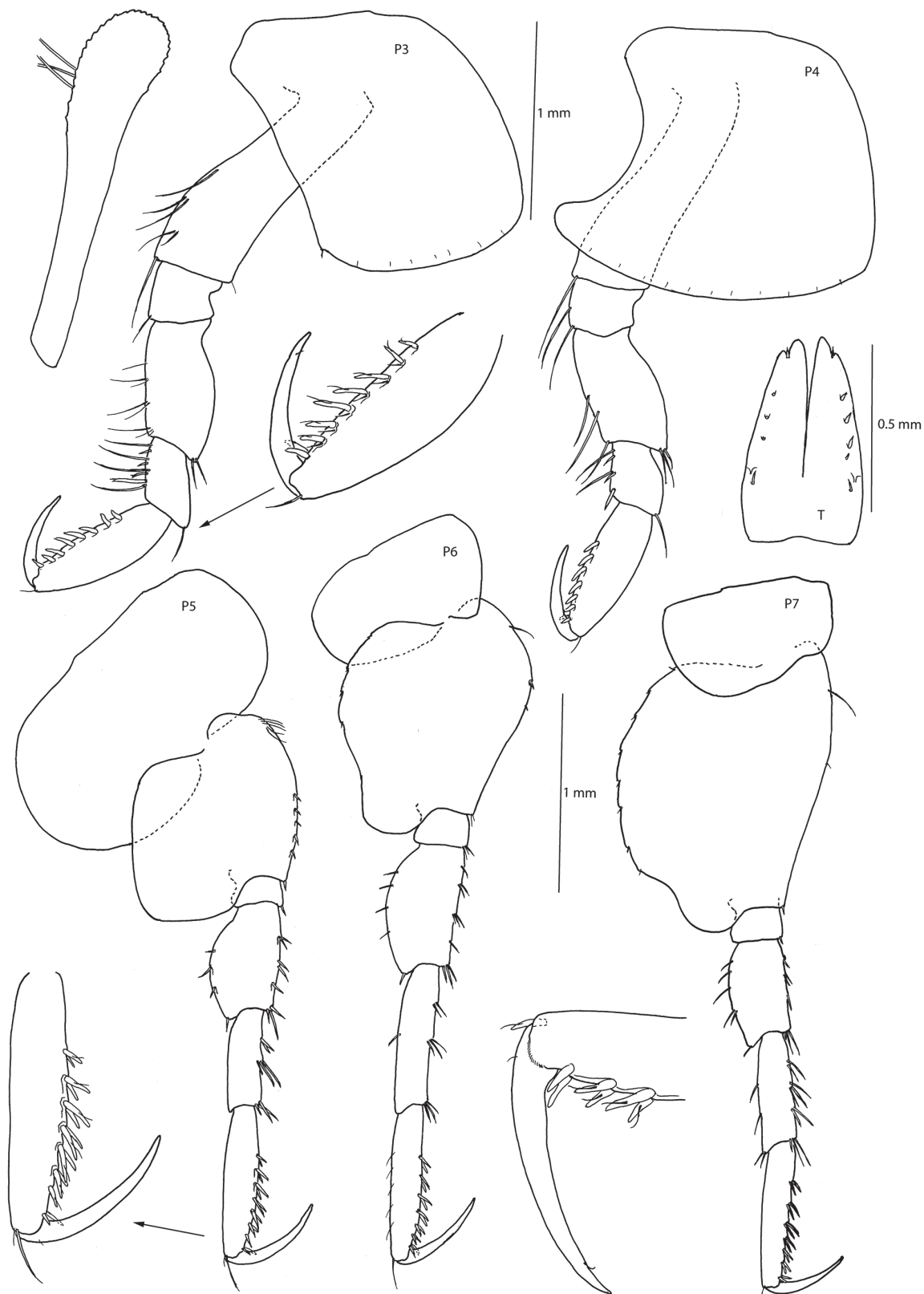
**FIGURE 15.** *Haptocallisoma lemarete* sp. nov. Holotype, adult female, 10.6 mm, habitus.



**FIGURE 16.** *Haptocallisoma lemarete* sp. nov. Holotype, adult female, 10.6 mm, head, antennae, gnathopods, epimeres, urosome, uropods.



FIGURE 17. *Haptocallisoma lemarete* sp. nov. Holotype, adult female, 10.6 mm, mouthparts.



**FIGURE 18.** *Haptocallisoma lemarete* sp. nov. Holotype, adult female, 10.6 mm, pereopods, telson.

**Additional material**—Cape Verde Basin. Station 9131#12, 20 November 1976, 20°07.0'N 21°26.0'W to 20°06.6'N 21°25.1'W, BN1.5/5C, 3856–3861 m, one specimen. Station 9131#19, 21–22 November 1976, 20°14.4'N 21°47.0'W to 20°23.8'N 21°49.4'W, RMT8, 3500–3760 m (250–500 mab), two specimens. Station



9541#18, 18 April 1977, 20°18.5'N 21°41.2'W to 20°20.8'N 21°53.0'W, RMT8, 3970–4020 m (0–20 mab), two specimens. Station 9541#19, 18–19 April 1977, 20°19.7'N 21°51.3'W to 20°18.4'N 21°40.5'W, RMT8, 3970–4040 m (0–20 mab), one specimen. Station 9541#22, 20 April 1977, 20°08.9'N 21°25.0'W to 20°12.5'N 21°37.7'W, RMT8, 3740–3870 m (20–100 mab), one specimen. Station 9541#24, 21 April 1977, 20°20.1'N 21°45.0'W to 20°25.4'N 21°56.3'W, RMT8, 3520–3940 m (100–500 mab), three specimens. Station 12600#44, 9–10 October 1993, 21°05.2'N 31°06.6'W, DEMAR, 4540 m, two specimens. Station 12600#60, 14 October 1993, 21°05.1'N 31°12.9'W, DEMAR, 4569 m, two specimens.

Horseshoe Abyssal Plain. Station 9629#1, 27–28 October 1977, 35°47.4'N 13°12.5'W, Trap B, 4855 m, two specimens.

Porcupine Seabight and Abyssal Plain. Station 9756#8, 49°53.6'N 13°57.9'W, Trap B, 13–15 April 1978, 3852 m, one specimen. Station 50909, 10–11 November 1980, 49°53.83'N 14°00.36'W, TAMph, 3918 m, one specimen. Station 52806, 2–3 August 1992, 50°11.8'N 14°41.1'W, Fish Trap, 3976 m, one specimen. Station 53201#25, 14–15 April 1994, 48°49.1'N 16°31.0'W, DEMAR, 4844 m, six specimens. Station 13077#4, 14–18 March 1997, 48°55.82'N 16°35.25'W, NIOZ Lander trap, 4844 m, 68 specimens. Station 13077#35, 19–23 March 1997, 48°50.10'N 16°24.93'W, NIOZ Lander trap, 4845 m, 60 specimens. Station 13077#71, 24–27 March 1997, 48°50.01'N 16°17.97'W, NIOZ Lander trap, 4840 m, 51 specimens. Station 13077#92, 27–28 March 1997, 48°49.50'N 16°20.97'W, DEMAR, 4844 m, 110 specimens. Station 13078#3, 29–31 March 1997, 48°46.99'N 16°22.09'W, DEMAR, 4842 m, two specimens. Station 13078#14, 1–2 April 1997, 48°55.12'N 16°25.06'W, DEMAR, 4845 m, 59 specimens. Station 13078#22, 3 April 1997, 48°43.02'N 16°38.18'W, DEMAR, 4842 m, 82 specimens. Station 13200#31, 11 July 1997, 48°48.79'N 16°23.43'W, DEMAR, 4842 m, 130 specimens. Station 13200#42, 13–15 July 1997, 48°54.81'N 16°34.93'W, DEMAR, 4844 m, 195 specimens. Station 13200#55, 16 July 1997, 48°49.02'N 16°21.59'W, DEMAR, 4844 m, 129 specimens.

Demerara Abyssal Plain. N.O. *Jean Charcot*, Cruise DEMERABY, haul Na04, 24 September 1980, 10°21.1'N 46°44.0'W, Trap, 4850 m, one specimen.

Madeira Abyssal Plain. Station 12174#20, 18–23 August 1990, 31°07.6'N 21°10.0'W, BATHYSNACK, 4941 m, three specimens.

Iberian Margin. Station 15734#1, 1–2 August 2005, 39°29.78'N 09°47.89'W, Trap, 3600 m, four specimens. Station 15741#1, 4–5 August 2005, 39°34.95'N 10°16.50'W, Trap, 4286 m, 42 specimens. Station 56837#1, 2–3 May 2006, 38°21.67'N 09°53.00'W, Trap, 4230 m, ten specimens. Station 56839#1, 4–5 May 2006, 38°06.59'N 09°58.18'W, Trap, 4445 m, twelve specimens. Station 56847#1, 7–8 May 2006, 39°35.50'N 10°19.00'W, Trap, 4403 m, 75 specimens. Station JC010/094, 11–13 June 2007, 39°29.90'N 09°56.20'W, Trap, 3400 m, one specimen.

Mid-Atlantic Ridge. Station JC011/098, 9–10 October 2007, 54°04.08'N 34°09.43'W, DEMAR, 2500 m, four specimens.

**Description.** Holotype, adult female, 10.6 mm.

*Head* exposed, deeper than long, lateral cephalic lobe short, rounded; rostrum absent. *Antenna 1* short, length 0.14 x body; peduncle article 1 short, length 0.83 x breadth; peduncle article 2 short, 0.3 x article 1; peduncle article 3 short, 0.1 x article 1; flagellum seven-articulate, callynophore two-field; accessory flagellum long, 0.7 x primary flagellum, three-articulate, article 1 long, 3.7 x article 2. *Antenna 2* length 2.9 x antenna 1; peduncle article 1 greatly enlarged, not covering article 2; article 3 short, 0.6 x article 4; peduncle articles 4 and 5 not enlarged; flagellum well-developed, 26-articulate, long slender setae on some articles. No brush setae, calceoli absent.

*Mouthpart bundle* subquadrate; interantennal carina sinuous, not notched proximally. *Epistome and upper lip* separate; epistome produced, rounded; upper lip rounded. *Lower lip* broadly gaping rounded outer lobes, apically setose. *Mandible* incisors symmetrical, large, with convex margins; left *lacinia mobilis* a stemmed asymmetric blade; accessory setal row with three simple robust setae; molar an acute conical structure, mandibular palp attached midway; article 1 short, length 0.75 x breadth, without setae; article 2 slender, length 4.7 x breadth, with eleven submarginal posterodistal A2-setae; article 3 slender, blade-like, with 13 D3 setae along distal two thirds of the margin, and three E3 setae. *Maxilla 1* inner plate tapering, inner margin fully setose, with ten pappose setae; outer plate with eleven setal teeth in a simple 7/4 arrangement, outer row with ST1–7 large, slender, ST1–2 without cusps, ST3 four-cuspidate, ST4 five-cuspidate, ST5 four-cuspidate, ST6 three-cuspidate, ST7 three-cuspidate, inner row with STA–D slender, STA without cusps, STB–D one-cuspidate; palp large, strongly broadened distally, two-articulate, article 1 short, article 2 with six terminal robust setae, a robust flag seta and one subterminal seta;

*Maxilla 2* inner plate broad, tapering distally, with 15 pappose setae in oblique mediofacial setal row, with terminal robust pectinate setae; outer plate longer than inner with apicomедial dentate and plumose setae. *Maxilliped* inner plate large, subrectangular, with three apical nodular setae and one medial seta, two apical pappose setae near the lateral corner, oblique facial setal row strong with ten pappose setae reaching apical margin; outer plate medium size, oval with seven apical plumose setae, twelve small nodular setae medially and two longer robust setae on the distomedial corner; palp large, four-articulate, article 2, length 2.7 x breadth, 1.9 x article 3; article 3 long, slender, length 1.4 x breadth; dactylus well-developed, with three sub-terminal setae.

*Gnathopod 1* simple; coxa large, broad, as long as coxa 2, subquadrate, anterior margin straight; basis long, slender, length 3.2 x breadth, anterior margin smooth; ischium long, length twice breadth, anterior margin smooth with one seta posterodistally; merus, posterior margin with two simple setae distally; carpus subrectangular, long, length 2.5 x breadth; propodus just longer than carpus, tapering, posterior and anterior margins with a few groups of simple, slender setae, apex with numerous distally pappose robust setae; dactylus minute, posterior margin with three small teeth. *Gnathopod 2* minutely subchelate; coxa large, subequal in size to coxa 3; ischium, length three x breadth; carpus long, length 2.6 x breadth, posterior margin straight; propodus subrectangular, long, length 1.7 x breadth, posterior margin with groups of slender robust setae, apically with row of slender setae decreasing in size towards palm; palm transverse, convex, serrate; dactylus inserted at centre of propodus apex, curved and not reaching palm corner, corner lacking robust setae. *Pereopod 3* prehensile; coxa large, subrectangular; basis robust, sinuous and slightly expanded distally, with five simple setae on posterior margin and one anterodistally; merus slightly expanded anteriorly; carpus shorter than propodus; propodus posterior margin with seven robust setae and two distal locking setae; dactylus long, 0.5 x propodus, curved to close along palm of propodus. *Pereopod 4* as in pereopod 3 except coxa width 1.18 x depth, posterior lobe, weakly produced, narrowly rounded, posterior margin sloping anteriorly, propodus posterior margin with six robust setae, and two distal locking setae. *Pereopod 5* prehensile; coxa posterior lobate; basis widely expanded, subquadrate, posterior margin straight, posterodistal lobe truncate, extending to distal margin of ischium; merus expanded posteriorly with robust setae on both posterior and anterior margins; carpus shorter than propodus; propodus long, length 4.4 x breadth, anterior margin with one single and five pairs of robust setae and one pair of locking setae; dactylus long 0.6 x propodus, slender, curved to close along palm of propodus. *Pereopod 6* prehensile; coxa small, posterior lobate; basis anterior margin, convex and rounded with one long and two short robust setae, proximal posterior margin expanded, rounded, convex with three short simple setae along margin, slightly excavate distally with a round posterodistal lobe, not extending to merus; merus expanded posteriorly with robust setae on anterior and posterior margins, longer than merus of pereopod 5; carpus long, 0.9 x propodus; propodus long, length 5.5 x breadth, anterior margin with six pairs of robust setae and one pair of distal locking setae, posterior margin with five long slender simple setae; dactylus long, slender, curved to close along palm of propodus. *Pereopod 7* weakly prehensile; coxa small, posterior lobate; basis anterior margin convex with one slender seta proximally and one short robust seta distally, posterior margin broadly expanded, rounded, convex with eight short simple setae along margin, excavate distally with a short, rounded, posterodistal lobe not extending to merus; merus expanded posteriorly; carpus shorter than propodus; propodus long, length five x breadth, anterior margin with six groups of robust setae, and a pair of distal locking setae; dactylus long, slender, curved to close along propodus.

*Gills* on pereopods 2–7. *Brood plates* on pereopods 2–5.

*Pleonites 1–3* dorsally smooth. *Epimeron 1* convex, rounded posteriorly; anterior margin slightly concave, posterodistal angle obtuse. *Epimeron 2* anterior margin sinuous, rounded; posterior margin convex, posteroventral corner slightly produced. *Epimeron 3* anterior margin sinuous, rounded, posteroventral corner produced, subacute, ventral margin with seven small robust setae.

*Urosomite 1* with a lateral ridge and a slight posterodorsal carina. *Uropod 1* peduncle long, with one apicolateral robust seta, one apicomедial robust seta and nine dorsomedial setae; inner ramus length 0.8 x peduncle, with three medial robust setae, one lateral robust seta and microsetose lateral and distomedial margins; outer ramus length 0.75 x inner ramus, with three lateral robust setae and microsetose lateral and medial margins. *Uropod 2* peduncle long, with one apicomедial robust seta, three dorsomedial setae, and two dorsolateral robust setae; inner ramus as long as peduncle, with four medial robust setae and five lateral robust setae; outer ramus short, 0.54 x inner ramus, with three lateral robust setae and a microsetose medial margin. *Uropod 3* peduncle short, length 1.4 x breadth, with one apicolateral seta, one apicomедial robust seta and two simple setae; inner ramus length 1.9 x peduncle, with two medial robust setae and eight medial slender plumose setae; outer ramus,

length at least 1.5 x peduncle, two-articulate; article 1 with five medial robust setae, with a microsetose medial margin and four lateral robust setae, article 2 tip lost.

*Telson* longer than broad, slightly tapering distally, length 1.7 x breadth, cleft 68%, with 4/5 robust setae on each lobe, distal margins incised with subapical notch and one small immersed seta.

**Sexual dimorphism.** Male, 10.7 mm, from Station 13200#42. Antenna 2 elongate, as long as pereon, 44-articulate, with brush setae, stronger callynophore, with more profuse aesthetascs; calceoli present on both antennae. Head lobes marginally acute in male, apex just sharper than in female. About 21 plumose setae on uropod 3 medial margin.

**Etymology.** Derived from the Greek, *Lema*, *-tos* (n)—temper of mind, will, courage, audacity; and the Greek, *arete* (f)—excellence, goodness, virtue; with reference to the motto on the coat of arms granted to the name ‘Bamber’ depicting two red chevrons between four black fleurs-de-lis on a silver shield, the crest being a red bulls head. The motto, “*Fortis et egregious*” translates as “Bold and excellent”, terms which can certainly be used to describe our long-standing friend and colleague Roger Bamber.

**Remarks.** This species can be distinguished from others in the genus by the quadrate expansion of the basis of pereopod five which is truncate distally.

**Depth range.** 2500–4850 m. Most records are at abyssal or lower slope depths.

**Distribution.** North Atlantic Ocean between the Demerara Abyssal Plain and the Mid-Atlantic Ridge at 54°N.

### ***Haptocallisoma spinipoda* (Hendrycks & Conlan, 2003) comb. nov.**

*Paracallisoma spinipoda* Hendrycks & Conlan 2003: 2322, figs 8–9.

**Type material. Holotype**—adult male, 10 mm, (appendages on one slide) (CMNC 2002–0029), Station 216, cup #1, North-east Pacific off Point Conception, California, United States 34°47.94’N, 123°03.80’W, 3450 m, 24/06/1992.

**Paratype.** juvenile, sex unknown, 5.0 mm, CMNC 2002–0030, Station 621, cup #1, 34°50.88’N, 122°58.68’W, 4000 m, date unknown.

**Remarks.** *Haptocallisoma spinipoda* belongs in the new genus *Haptocallisoma* on account of the broadly expanded pereopod 5 basis and prehensile pereopods 3–7. The species can be distinguished from *H. abyssi* by differences in the shape of epimeron 3 (produced, with a concave posterior margin versus not produced and with a convex posterior margin in *H. abyssi*), differences in the shape of the telson (in *H. spinipoda*, the lobes are slightly divergent distally, whereas they are closely appressed in *H. abyssi*), and minor differences in setation of the mouthparts. The subrectangular pereopod 5 basis in *H. lemarette* sp. nov. differs markedly from the broadly rounded structure found in *H. spinipoda*. *H. spinipoda* is the first species in this genus to be described from the Pacific Ocean.

**Depth range.** 3450–4000 m.

**Distribution.** North-east Pacific off Point Conception, California, United States 34°47.94’N, 123°03.80’W.

### ***Haptocallisoma woolgoolga* (Kilgallen & Lowry, 2015) comb. nov.**

*Paracallisoma woolgoolga* Kilgallen & Lowry, 2015

**Type material. Holotype**—female, 10.0 mm, AM P.69088, north-east of Coffs Harbour, New South Wales, Australia (30°10.88’S 153°32.22’E), 1000 m, baited trap, 12–13 August 1993, Collected by P.B. Berents, R.T. Springthorpe & W. Vader, MV *Cheryl Lee* [NSW-877].

**Paratypes**—one male, 7.5 mm, AM P.69089; many specimens, 7.0–9.3 mm, AM P.69090, with same collection details as holotype.

**Remarks.** *Haptocallisoma woolgoolga* (Kilgallen & Lowry, 2015) is morphologically very close to other species in the genus *H. spinipoda*, *H. abyssi*, and *H. lemarette* sp. nov. It can be distinguished from *H. spinipoda* by the gnathopod 2 palm (slightly concave in *H. spinipoda*, straight in *H. woolgoolga*); the shape of the pereopod 5 basis (evenly rounded in *H. spinipoda*, with a slight excavation along the posteroventral margin in *H. woolgoolga*);

and the shape of the epimeron 2 posteroventral corner (producing a small tooth in *H. spinipoda*, subquadrate in *H. woolgoolga*). In addition, in *H. woolgoolga* the pereopod 6 basis posterior lobe is much less distinctly excavate relative to that of *H. spinipoda*. *H. woolgoolga* can be distinguished from *H. abyssi* by the pereopod 5 basis (broadly rounded in *H. abyssi*, versus slightly excavate along the posteroventral margin in *H. woolgoolga*), more strongly expanded and prehensile pereopod 3 propod in *H. abyssi* and by characters of the telson. The pereopod 6 basis is also less strongly excavate posteriorly in *H. woolgoolga*. *Haptocallisoma woolgoolga* can be distinguished from *H. lemarete* **sp. nov.** by characters of the telson, the pereopod 5 basis lobe (straight margin and truncate posterodistal edge in *H. lemarete* **sp. nov.**), and the more strongly expanded and prehensile pereopod 3 propod in *H. lemarete* **sp. nov.** The pereopod 6 basis is also less strongly posteriorly excavate in *H. woolgoolga*.

**Depth range.** 200–1942 m.

**Distribution.** *Australia*—east of Mooloolaba, Queensland, to south of Tasmania.

### Key to the species of *Haptocallisoma*

1. Pereopod 5 basis subrectangular, posterodistal lobe truncate . . . . . *Haptocallisoma lemarete* **sp. nov.**  
Pereopod 5 basis subcircular, posterodistal lobe broadly rounded . . . . . 2
2. Pereopod 3 propodus subparallel sided and weakly prehensile . . . . . *Haptocallisoma woolgoolga*  
Pereopod 3 propodus expanded and strongly prehensile . . . . . 3
3. Telson lobes divergent distally, with a strong subapical notch; epimeron 3 posteroventral corner produced . . . . . *Haptocallisoma spinipoda*  
Telson lobes closely appressed, with a weak, subapical notch; epimeron 3 subquadrate, not produced . . . . . *Haptocallisoma abyssi*

### *Pseudocallisoma* **gen. nov.**

*Paracallisoma*—Dahl, 1959: 220.—Gurjanova 1962: 308.—Hurley 1963: 60.—Barnard 1964: 319, 1969: 305.—Barnard & Karaman 1991: 510.

**Type species.** *Scopelocheirus coecus* Holmes, 1908, by original designation.

**Diagnosis.** Mandible, left lacinia mobilis a stemmed, distally asymmetrically expanded non-serrate blade; incisor ordinary; molar simple, small, subconical; palp attached slightly proximal to molar. Maxilla 1 inner plate strongly setose medially; **palp 2-articulate**, large. Maxilla 2 inner plate broader than outer, inner and outer plates subequal in length. Maxilliped inner and outer plates well developed, palp strongly exceeding outer plate, **dactyl well developed**. **Gnathopod 1 coxa tapering**, slightly shortened and partly covered by coxa 2, basis broad, without glandular material, carpus longer than propodus, dactyl vestigial, shrouded in setae. **Gnathopod 2 coxa tapering**, propodus much shorter than carpus, minutely subchelate. **Pereopods 3–7 distal articles slender**. **Uropod 1 peduncle elongate, rami less than 0.6 x peduncle length**. Telson elongate, **apices not incised**.

**Etymology.** From the Greek, *pseudos*—lie, added to the common stem of the subfamily ‘-callisoma’, in reference to historic problems in differentiating the type species of the genus *Paracallisoma* and the new genus *Pseudocallisoma*.

**Remarks.** This new genus is characterised by tapered coxae 1 and 2, slender pereopods 5 to 7 and the elongate peduncle of uropod 1, with the rami less than 0.6 times its length. *Austrocallisoma* (Kilgallen & Lowry, 2015) is very similar to *Pseudocallisoma* in possessing tapered coxae 1 and 2 and slender pereopods 3–7 but can be distinguished by the 1-articulate maxilla 1 palp and absence of maxilliped palp article 4.

**Included species.** *Pseudocallisoma coecum* (Holmes, 1908) **comb. nov.**; *P. platepistomum* (Andres, 1977) **comb. nov.**

### *Pseudocallisoma coecum* (Holmes, 1908) **comb. nov.**

Figs 19–21

*Scopelocheirus coecus* Holmes 1908: 500, figs 10–12.—Shoemaker 1945: 186 (in part, part ?*P. platepistomum*).—J.L. Barnard 1954: 54, figs 4, 5.—Gurjanova 1951: 241 (key).



*Paracallisoma coecum*.—Hurley 1963: 61, fig. 18.—Andres 1977, 60.—Barnard & Karaman 1991: 511.—Thurston 2001: 685 (table 2).

*Paracallisoma coecus*.—J.L. Barnard 1958: 97 (list).—J.L. Barnard 1964: 319, fig. 3.—Brusca 1967a: 384, 385, table 4.—Brusca 1967b: 450.—Childress & Nygaard 1974: 228, table 1(physiology).—Childress 1975: 788 (table 1a) (physiology).—Quetin, Ross & Uchio 1980: table 1(physiology).—Smith & Baldwin 1982: 292 (table 3).—Austin 1985: 601.—Vermeer & Devito 1988: 65, 67, table 2 (ecology).—Ikeda 2013: 342 (table 1).

*Paracallisoma alberti*.—Birstein & Vinogradov 1955: 223, 279 (in part).—Birstein & Vinogradov 1958: 228.—Birstein & Vinogradov 1960: 176, fig. 5, 233, fig. 33.—Gurjanova 1962: 309, fig. 102.—Nagata 1963: 1.—Birstein & Vinogradov 1970: table 1, table 3.—Hatch 1983: 194, 195, table 3 (ecology).—Nysewander 1983: 328, table 7 (ecology).—Sanger & Ainley 1988: 182 (ecology).—Hatch 2013: 275 (ecology).

Not *Paracallisoma coecum* = *Paracallisoma platepistomum*.—Shoemaker 1945:186.

**Material examined. Holotype**—female, 20.8 mm, specimen and four slides, USNM, 38538. Bureau of Fisheries, Station 4405, 1196–1287 m, off San Clemente Island, California, 09 April 1904.

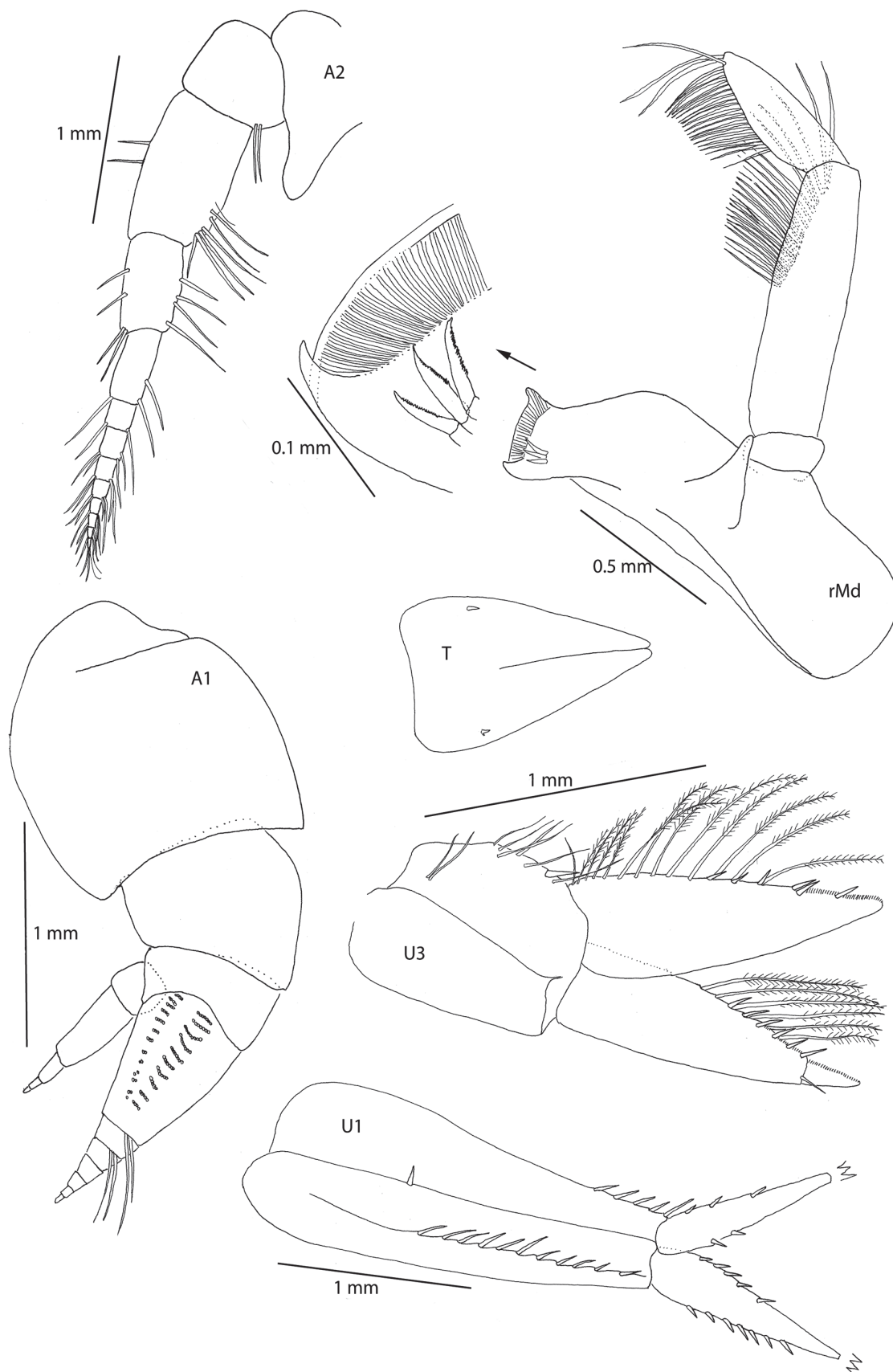
**Description.** Holotype, female, 20.8 mm USNM, 38538.

*Antenna 1* peduncle article 1 short, length 0.9 x breadth, without posterodistal spine or lobe; peduncle article 2 short, 0.5 x article 1; peduncle article 3 short, 0.26 x article 1; flagellum seven-articulate, without posterodistal setae, callynophore present, calceoli absent; accessory flagellum long, 0.63 x primary flagellum, five-articulate, article 1 short, 0.6 x article 2. *Antenna 2* length 1.2 x antenna 1; peduncle without brush setae; peduncle article 1 greatly enlarged, not covering article 2; article 3 short, 0.6 x article 4; peduncle articles 4 and 5 not enlarged; flagellum well-developed, nine-articulate, calceoli absent.

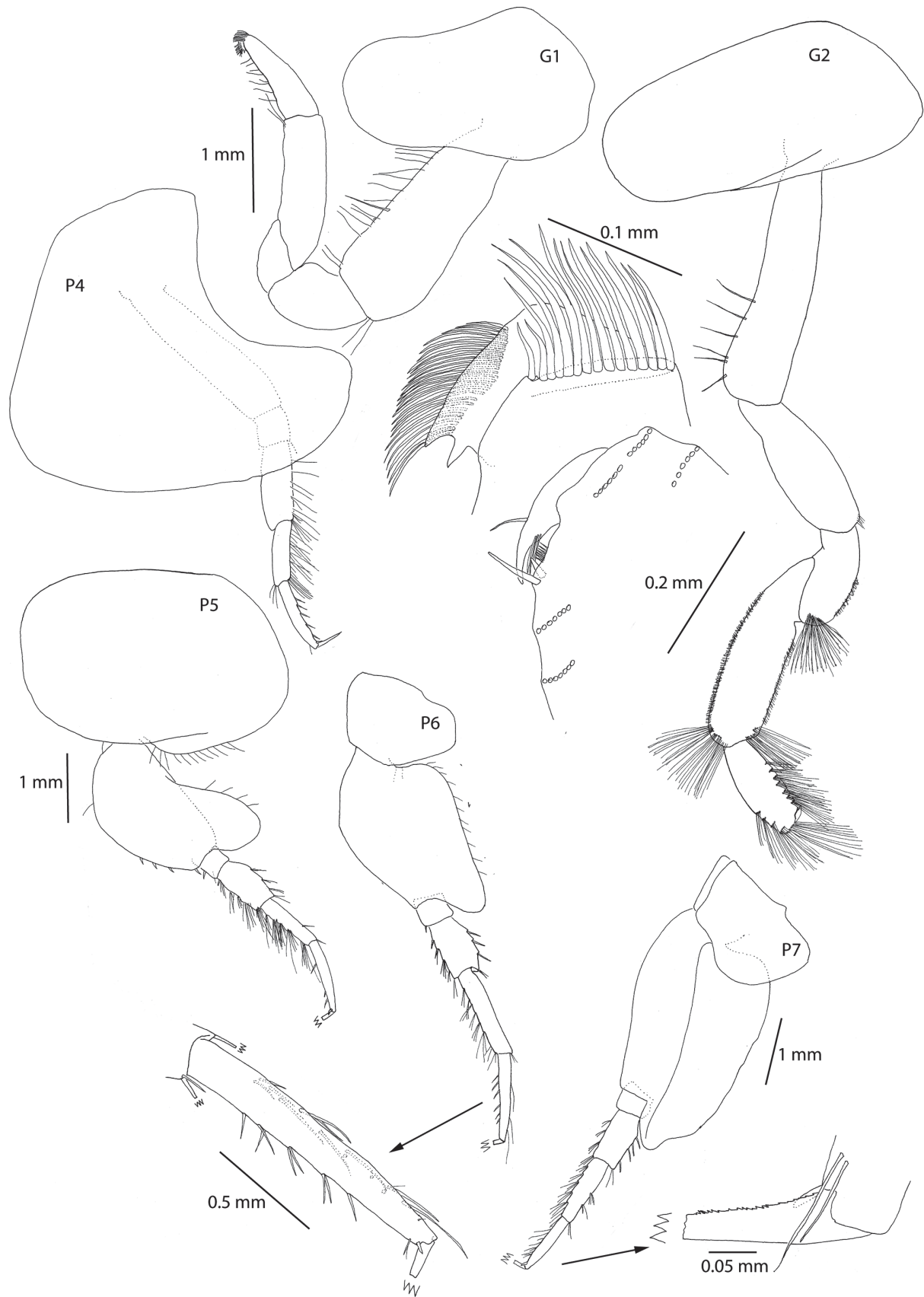
*Mouthpart bundle*—*Right mandible* incisor symmetrical, large, slightly convex margin with tooth-like projection at either end; *lacinia* absent; accessory setal row with three robust setae, lacking distal setal tuft; molar an acute conical structure, mandibular palp attached midway; article 1 short, length 0.64 x breadth, without setae; article 2 slender, length 3.25 x breadth, with 24 submarginal posterodistal A2-setae; article 3 slender, oval, with 19 D3 setae along distal two thirds of the margin, and 3 E3 setae.

*Gnathopod 1* simple; coxa large, shorter than coxa 2, tapering, rounded distally, anterior margin slightly concave; basis long, expanded distally, length 2.7 x breadth, anterior margin smooth, with 14 simple setae; ischium short, length 1.2 x breadth, anterior margin smooth; merus, posterior margin without distal setae; carpus subrectangular, long, length 3.3 x breadth, longer than propodus; propodus tapering distally, posterior margin with a few groups of simple, slender setae, apex with numerous distally pappose robust setae; dactylus minute, complex, covered in sensory setae. *Gnathopod 2* subchelate; coxa large, tapering slightly; ischium long, length 2.8 x breadth; carpus long, length 3.75 x breadth, posterior margin straight; propodus subrectangular, narrow, length 2.4 x breadth with numerous pappose robust setae distally; posterior margin with seven groups of slender robust setae, apically with row of distally plumose setae; palm very short, acute, with short setules, palmar corner with one long and one short robust seta; dactylus inserted in anterior third of propodus apex, curved, just longer than palm, posterior margin with three setae. *Pereopods* simple. *Pereopod 3* missing. *Pereopod 4* coxa wider than deep, posterior lobe well-developed, broadly rounded, posterior margin sloping anteriorly, breadth 1.1 x depth; basis slender, straight; merus not expanded anteriorly; carpus slender, posterior margin strongly setose; propodus slender, posterior margin with five robust setae and two distal locking setae; dactylus long, straight. *Pereopod 5* coxa large, deep, width 1.4 x depth weakly lobate posteriorly with a lateral ridge, twelve simple setae along posterodistal margin; basis weakly expanded proximally, strongly widening distally, posterodistal lobe large, reaching a quarter of the way along the merus, anterior margin with four robust setae distally; merus very slightly expanded posteriorly with robust setae on both posterior and anterior margins; carpus slender, posterior margin strongly setose; propodus very long, slender, tapering, length 6.3 x breadth, anterior margin with three robust setae and one pair of distal locking setae; dactylus slender, tip broken. *Pereopod 6* coxa small, not lobate posteriorly; basis anterior margin evenly convex, posterior margin expanded, straight, with eleven simple setae, rounded posterodistal lobe reaching merus; merus as in pereopod 5; carpus 1.1 x propodus; propodus very long, tapering, length 7.4 x breadth, anterior margin with nine robust setae and one pair of distal locking setae, posterior margin with 13 long slender simple setae; dactylus, slender, tip broken. *Pereopod 7* coxa small, posterior lobate; basis, anterior margin weakly convex, proximal posterior margin expanded, rounded, convex, then sloping slightly anteriorly and excavate posterodistally, posterodistal lobe narrow, reaching almost halfway along merus; merus anterior and posterior margins subparallel; carpus 1.07 x propodus; propodus long, slender, length 6.1 x breadth, anterior margin with seven groups of robust setae, and one pair of distal locking setae; dactylus, slender, tip broken.

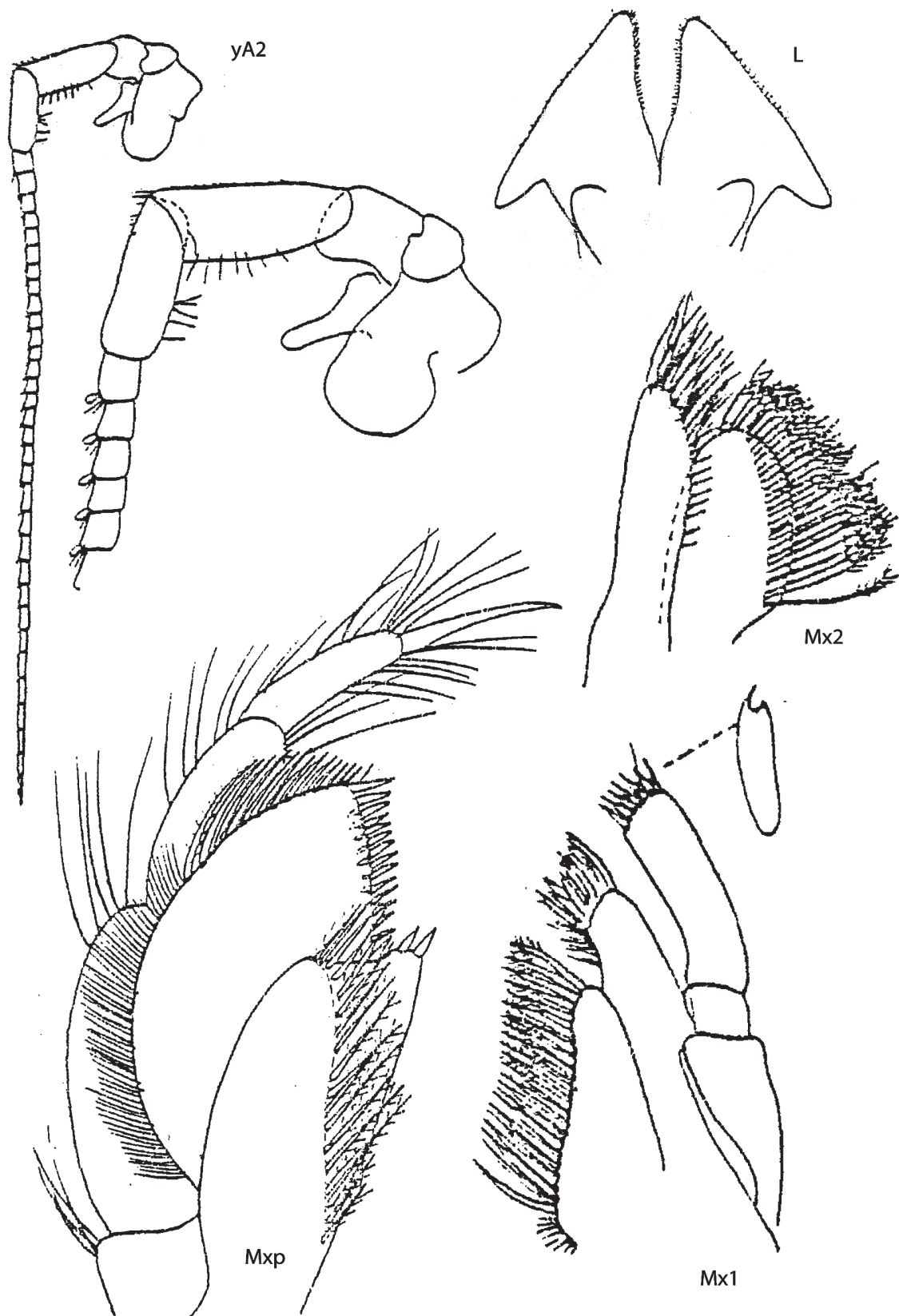




**FIGURE 19.** *Pseudocallisoma coecum* (Holmes, 1908). Holotype, Pacific Ocean, off California, 1196–1287 m, 20.8 mm, antennae, uropods 1, 3, telson, right mandible.



**FIGURE 20.** *Pseudocallisoma coecum* (Holmes, 1908). Holotype, Pacific Ocean, off California, 1196–1287 m, 20.8 mm, gnathopods, pereopods 4–7.



**FIGURE 21.** *Pseudocallisoma coecum* (Holmes, 1908). Figures from Barnard (1954), male, 15 mm, Velero IV specimen, Pacific Ocean, off California, antenna 2, lower lip, maxilliped, maxilla 1 and maxilla 2.

Gills on pereopods 2–7. Brood plates on pereopods 2–5.

*Uropod 1* peduncle long, 1.9 x inner ramus, with five lateral robust setae, one dorsal robust seta, and eleven dorsomedial robust setae; rami subequal; inner ramus, with seven medial robust setae, and five lateral robust setae; outer ramus, with three lateral robust setae and 2 medial robust setae. *Uropod 2* missing. *Uropod 3* peduncle short, length 0.8 x inner ramus, with one apicolateral robust seta, one simple seta, two dorsal slender simple setae, and five medial slender simple setae; inner ramus, with six medial robust setae and 13 medial slender plumose setae, with a microsetose distomedial margin; outer ramus, 2-articulate, article 2 short, with a microsetose distomedial margin; article 1 with six medial robust setae, six slender plumose setae, and one robust seta apicolaterally.

*Telson* longer than broad, slender and strongly tapering distally, length 1.65 x breadth, cleft 62%, with a pair of dorsolateral robust setae, lobes subacute, lacking apical incision.

**Supplementary description from Barnard (1954) illustrations & material.** *Head* exposed, deeper than long, lateral cephalic lobe large, narrow, subacute; rostrum absent; *eyes* apparently absent. *Maxilla 1* inner plate tapering distally, inner margin fully setose, with >20 pappose setae; outer plate narrow with eleven setal teeth in 7/4 arrangement; palp large, two-articulate, article 1 short, article 2 narrow, with six terminal robust setae, one robust flag seta; *Maxilla 2* inner plate broad, rounded apically, with pappose setae in oblique mediofacial setal row; outer plate slightly longer than inner. *Maxilliped* inner plate large, subrectangular, emarginate distally with three apical nodular setae, oblique facial setal row strong with 16 pappose setae; outer plate medium size, subrectangular with apical plumose setae and small nodular setae medially; palp large, 4-articulate, article 2 broad, article 3 long, slender, length 3.3 x breadth; dactylus well-developed.

**Remarks.** *Pseudocallisoma coecum* (Holmes, 1908), the type species of this genus is described here from the holotype, a carcass and slides in poor condition supplemented by the material figured by Barnard (1954). *Pseudocallisoma coecum*, originally placed in *Scopelocheirus* by Holmes (1908), and then *Paracallisoma* by Schellenberg (1926a), is known from the Pacific Ocean at depths down to 4023 m. A single male specimen was illustrated by Barnard (1954) from bathypelagic material collected by the *Velero IV* off the coast of California. The male differs only in the longer second antennae which are about three times as long as in the female and with the presence of calceoli on both antennae (Barnard 1954). A juvenile specimen (6 mm) was figured by Barnard (1964), and differs in the less setose mouthparts, the outer plate of the maxilliped having only four lateral setae instead of 14. *Pseudocallisoma coecum* has also been recorded frequently at high northern latitudes in the Pacific under the name *Paracallisoma alberti* by Birstein and Vinogradov (1955, 1958, 1960, 1962, 1964, 1970) and Gurjanova (1962). This species is closely related to *P. platepistomum* (see remarks section for *P. platepistomum*).

**Depth range.** 500–4023 m (Holmes 1908; Shoemaker 1945; Barnard 1964; Brusca 1967; Childress & Nygaard 1974). Records from hauls fished with open nets (e.g. 0–9000 m, Birstein and Vinogradov (1958)) are uninformative and have been excluded. Although the shallowest depth of occurrence for net-caught material is ca. 500 m, this species is reported as a constituent of seabird stomach contents (Hatch 1983, 2013; Nysewander 1983; Vermeer & Devito 1988; Sanger & Ainley 1988). *P. coecum* has been found in stomach contents of six widely divergent species of seabird (Sanger & Ainley 1988) and forms an important part of the diet of two storm petrel species (Vermeer & Devito 1988). Storm petrels do not dive and feed by picking food items from the surface while airborne. *P. coecum* is positively buoyant and may have to swim to stay down (Childress & Nygaard 1974) but it seems improbable that the storm petrel diet consists entirely of dead or moribund individuals.

**Distribution.** *Pacific Ocean*: off San Clemente Island, California, United States (Holmes 1908); Pacific City, Oregon, United States (from the stomach of a duck\*) (Shoemaker 1945); San Nicolas Basin and off Santa Barbara Island, California, United States (Barnard 1954); outer Santa Barbara Passage, California, United States (Hurley 1963); off Kamchatka, Russia (Shoemaker 1945; Gurjanova 1962); Gulf of Alaska (Barnard 1964); Kuril-Kamchatka Trench (Birstein & Vinogradov 1958); near the Tenji Seamount, south-south-west of the Aleutian Trench (Birstein & Vinogradov 1958); near the Makarov Seamount (Birstein & Vinogradov 1960); Japan Trench (Nagata 1963) (from Kilgallen & Lowry 2015). [\*This material was collected from the stomach of a storm petrel, not a duck.]

### ***Pseudocallisoma platepistomum* (Andres, 1977) comb. nov.**

*Paracallisoma platepistomum* Andres, 1977: 60–64, figs 3, 4.—Andres & Lott 1977: 62.—Barnard & Karaman 1991: 511.  
*Scopelocheirus coecus*:—Shoemaker 1945: 186 (in part, part *Pseudocallisoma coecum*).

**Type material. Holotype**—female, 28 mm, Zoological Museum Hamburg, (K 30455), *Meteor* Station 3/24, 11 March 1966, 42°26.8'N 14°49.0'W to 42°40.9'N 14°49.2'W, Agassiz trawl, 5325 m.

**Material examined.** Iberian Basin. Station 7406#33, 6 October 1970, 39°49.9' N 20°13.1' W to 39°44.2' N 20°20.4' W, RMT8, 990–1250 m, one specimen. Station 7478#1, 6 November 1970, 40°10.8' N 19°58.9' W to 40°04.1' N 19°55.0' W, RMT8, 1460–2000 m, one specimen (NHMUK 2015. 2865).

Nares Basin. Bermuda Oceanographic Expedition Net 1105, 25 July 1931, 32°12' N 64°36' W, metre net, 1463 m (Shoemaker 1945).

Cape Verde Basin. Station 7089#5, 12 November 1969, 17°50' N 25°29' W, RMT8, 700–790 m, one specimen. Station 7089#55, 22 November 1969, 17°28' N 24°50' W, RMT90, 2000–1300(–0), two specimens.

Biscay Basin. Station 8508#3, 13 April 1974, 44°29.0' N 12°29.9' W to 44°21.0' N 12°31.5' W, RMT8, 1000–1250 m, one specimen.

**Diagnosis.** Rostrum present, very short. Epistome straight with small, rounded process ventrally. **Antenna 1, peduncle article 1 stout, conspicuously shorter than broad.** Gnathopod 1, coxa 1 posterior margin weakly convex; dactylus, complex shrouded in setae. Gnathopod 2, oblique and palm acute, straight, bearing small, tooth-like setae and lateral and medial submarginal setae. Coxa 4 posterodistal lobe large, relatively slender and narrowly rounded. Pereopod 6, basis posterior margin weakly sinuous, rounded distal lobe extending 30% along merus. Epimeron 2 and 3 weakly toothed posteroventrally. Uropod 3, outer ramus article 2 short, 0.11 x article 1. Telson, each lobe with three short submarginal setae.

**Remarks.** *Pseudocallisoma platelistomum* can be distinguished from *P. coecum* in the following features: antenna 1, peduncle article 1 much broader than long, length 0.65 x width (vs. nearly as broad as long, length 0.9 x width); gnathopod 1, coxa posterior margin convex (vs. concave), setation of complex dactylus only rising from distal margin of basal part (vs. hood-shaped protuberance above unguis densely setose); gnathopod 2, straight palm with small, tooth-like setae and lateral/medial submarginal setules (vs. sinuous, row of setules); coxa 4, posterodistal lobe large, narrowly rounded (vs. stout, broadly rounded); pereopod 6, basis posterior margin slightly concave (vs. straight); uropod 3, outer ramus article 2 very short, length 0.11 x article 1 (vs. 0.23 x); telson with three small robust setae laterally (vs. one basal robust seta). As both species in the genus appear to be meso- and bathypelagic, the specimen recorded from 5325 m (Andres 1977) may have been caught in midwater during deployment/recovery of the net rather than the seafloor.

**Depth range.** 790–2000 (5325) m (Shoemaker 1945, Andres 1977).

**Distribution.** *North Atlantic Ocean:* Iberian Basin (Andres 1977); off Bermuda (Shoemaker 1945), Cape Verde Basin, Biscay Basin.

## Acknowledgements

We thank the crew and scientists on board the many cruises for help in collecting the samples. In particular we are grateful to those who operated the baited traps and dealt with samples at sea and to Grant Duffy, Steven Lawler, Morena Aloisi, Raeanne Miller, Zoë Gutteridge, and Jenna Ashford for sorting and counting of material, and to Andy Gates, Dan Jones, and Kerstin Kroeger of the SERPENT project, for collecting samples during survey visits to oil exploration sites at Midnatssol, Gro & Haklang. Specimens used in this study were collected during projects supported by NERC Grant NE/C51297X/1, the HERMIONE project (grant agreement no. 226354) part of the EC's Seventh Framework Programme (FP7/2007–2013); and the Atlantic Frontier Environmental Network (AFEN). We are also grateful to the following curators for organising loans of type and other material in their care: Jan Walker and Elizabeth Nelson (Smithsonian Institution, Washington D.C.), Karin Sindemark Kronstedt (Swedish Museum of Natural History, Stockholm). We thank Ed Hendrycks and an anonymous reviewer for helpful suggestions which improved the manuscript. The authors would like to thank The Natural Environment Research Council (NERC) and BP for providing funding to Tammy Horton.

## References

Andres, H.G. (1977) Gammaridea (Crustacea, Amphipoda) aus dem Iberischen Tiefseebecken Auswertung des Materials der Fahrten 3 und 15 von F.S. "Meteor". *Meteor Forschungs-Ergebnisse Reihe D*, 25, 54–67.



- Andres, H.G. & Lott, N. (1977) Verzeichnis der Typen aus der Sammlung Crustacea des Zoologischen Instituts und Zoologischen Museums der Universität Hamburg. Amphipoda, Gammaridea. *Mitteilungen aus dem Hamburgischen Zoologischen Museum und Institut*, 74, 53–64.
- Austin, W.C. (Eds) (1985) *An Annotated Checklist of Marine Invertebrates in the Cold Temperate Northeast Pacific*. 3 ed. Cowichan, B.C., Khoyatan Marine Laboratory, 682 pp.
- Barnard, J.L. (1954) Four species of bathypelagic Gammaridea (Amphipoda) from California. *Allan Hancock Foundation Publications, Occasional Paper*, 13, 52–69.
- Barnard, J.L. (1958) Index to the families, genera, and species of the gammaridean Amphipoda (Crustacea). *Allan Hancock Foundation Publications, Occasional Paper*, 19, 1–145.
- Barnard, J.L. (1961) Gammaridean Amphipoda from depths of 400 to 6000 meters. *Galathea Report*, 5, 23–128.
- Barnard, J.L. (1964) Some bathyal Pacific Amphipoda collected by the U.S.S. Albatross. *Pacific Science*, 18 (3), 315–335.
- Barnard, J.L. (1969) The families and genera of marine gammaridean Amphipoda. *Bulletin of the United States National Museum*, 271, 1–535.
- Barnard, J.L. & Karaman, G.S. (1991) The families and genera of marine gammaridean Amphipoda (except marine gammaroids). *Records of the Australian Museum*, Supplement 13, 1–866.  
<http://dx.doi.org/10.3853/j.0812-7387.13.1991.91>  
<http://dx.doi.org/10.3853/j.0812-7387.13.1991.367>
- Bate, C.S. (1857) A synopsis of the British Edriophthalmous Crustacea. *Annals and Magazine of Natural History*, Series 2, 19, 135–152.
- Belloc, G. (1960) Catalogue des types d'amphipodes du Musée Océanographique de Monaco. *Bulletin de l'Institut Océanographique, Monaco*, 57, 1–28.
- Birstein, I.A. & Vinogradov, M.E. (1955) Pelagicheskie gammaridy (Amphipoda–Gammaridea) Kurilo-Kamchatskoi Vpadiny. [Pelagic gammarids (Amphipoda–Gammaridea) of the Kurile–Kamchatka Trench]. *Trudy Instituta Okeanologii*, 12, 210–287.
- Birstein, I.A. & Vinogradov, M.E. (1958) Pelagicheskie gammaridy (Amphipoda–Gammaridea) severo-zapadnoi chasti Tikhogo Okeana. [Pelagic gammarids of the north-west parts of the Pacific Ocean]. *Trudy Instituta Okeanologii*, 27, 219–257.
- Birstein I.A. & Vinogradov, M.E. (1960) Pelagicheskie gammaridy (Amphipoda–Gammaridea) tropicheskoi chasti Tikhogo Okeana. [Pelagic gammarids from the tropical Pacific Ocean]. *Trudy Instituta Okeanologii*, 34, 165–241.
- Birstein I.A. & Vinogradov, M.E. (1962) Pelagicheskie gammaridy (Amphipoda–Gammaridea) sobrannye sovetkoi antarkticheskoi ekspeditsiei na dizel'-elektrokhode "Ob" k iugu ot 40° iu. *Issledovaniia Fauny Morei*, 1(IX), 36–57. Translation [Pelagic Gammaridea (Amphipoda) collected by the Soviet Antarctic Expedition on the M/V "Ob", south of 40°S. *Studies of marine fauna I* (IX), Biological Reports of the Soviet Antarctic Expedition (1955-1958), 1, 33–56, 1966].
- Birstein I.A. & Vinogradov, M.E. (1964) Pelagicheskie gammaridy (Amphipoda–Gammaridea) severnoi chasti Indiiskogo Okeana [Pelagic gammarid amphipods of the northern part of the Indian Ocean]. *Trudy Instituta Okeanologii*, 65, 152–195.
- Birstein, I.A. & Vinogradov, M.E. (1970) O faune pelagicheskikh gammarid Kurilo-Kamchatskogo raiona Tikhogo Okeana. *Trudy Instituta Okeanologii*, 86, 401–419. Translation [On the fauna of the pelagic gammarids of the Kurile–Kamchatka region of the Pacific Ocean. In: Bogorov, V.G. (Eds), *Fauna of the Kurile–Kamchatka Trench and its environment*. Israel Program for Scientific Translations, Jerusalem, pp. 419–438. (1972)].
- Blankenship, L.E., Yyanos, A.A., Cadien, D.B. & Levin, L.A. (2006) Vertical zonation patterns of scavenging amphipods from the hadal zone of the Tonga and Kermadec Trenches. *Deep-Sea Research Part I—Oceanographic Research Papers*, 53 (1), 48–61.  
<http://dx.doi.org/10.1016/j.dsr.2005.09.006>
- Brandt, A. (1997) Biodiversity of peracarid crustaceans (Malacostraca) from the shelf down to the deep Arctic Ocean. *Biodiversity and Conservation*, 6(11), 1533–1556.  
<http://dx.doi.org/10.1023/A:1018318604032>
- Brusca, G.J. (1967a) The ecology of pelagic Amphipoda, I. Species accounts, vertical zonation and migration of Amphipoda from the waters off southern California. *Pacific Science*, 21 (3), 382–393.
- Brusca, G.J. (1967b) The ecology of pelagic Amphipoda, II. Observations on the reproductive cycles of several pelagic amphipods from the waters off southern California. *Pacific Science*, 21 (4), 449–456.
- Chevreaux, E. (1903) Note préliminaire sur les amphipodes de la famille des Lysianassidae recueillis par la *Princesse-Alice* dans les eaux profondes de l'Atlantique et de la Méditerranée. *Bulletin de la Société Zoologique de France*, 28, 81–97.
- Chevreaux, E. (1911) Campagnes de la Melita: Les Amphipodes d'Algérie et de Tunisie. *Mémoires de la Société Zoologique de France*, 23, 145–285.
- Chevreaux, E. (1935) Amphipodes provenant des Campagnes scientifiques du Prince Albert I<sup>er</sup> de Monaco. *Résultats des Campagnes Scientifiques accomplies par le Prince Albert I<sup>er</sup> de Monaco*, 90, 214 pp.
- Childress, J.J. (1975) The respiratory rates of midwater crustaceans as a function of depth of occurrence and relation to the oxygen minimum layer off Southern California. *Comparative Biochemistry and Physiology*, 50A, 787–799.  
[http://dx.doi.org/10.1016/0300-9629\(75\)90146-2](http://dx.doi.org/10.1016/0300-9629(75)90146-2)
- Childress, J.J. & Nygaard, M. (1974) Chemical composition and buoyancy of midwater crustaceans as function of depth of

- occurrence off Southern California. *Marine Biology*, 27, 225–238.  
<http://dx.doi.org/10.1007/BF00391948>
- Coleman, C.O. (2003) “Digital inking”: How to make perfect line drawings on computers. *Organisms Diversity & Evolution*, 3, Electronic Supplement 14, 1–14.
- Costa, A. (1851) Amphipoda, pp. 44–46, fig. 2. In: Hope, F.G. *Catalogo dei crostacei italiani e di moltri altri del Mediterraneo*. Napoli, Azzolino, 48pp.
- Dahl, E. (1959) Amphipoda from depths exceeding 6000 meters. *Galathea Report*, 1, 211–241.
- Dana, J.D. (1849) Synopsis of the genera of Gammaracea. *American Journal of Science and Arts*, Series 2, 8, 135–140.
- Dauvin, J-C. & Bellan-Santini, D. (2002) Les crustacés amphipodes Gammaridea benthiques des côtes françaises métropolitaines: Bilan des connaissances. *Crustaceana*, 75, 299–340.  
<http://dx.doi.org/10.1163/156854002760095408>
- De Broyer, C. & Jazdzewski, K. (1993) Contribution to the marine biodiversity inventory. A checklist of the Amphipoda (Crustacea) of the Southern Ocean. *Documents de Travail de l'Institut Royal des Sciences Naturelles de Belgique*, 73, 1–154.
- De Broyer, C., Lowry, J., Jazdzewski, K. & Robert, H. (2007) Catalogue of the Gammaridean and Corophiidean Amphipoda (Crustacea) of the Southern Ocean with distribution and ecological data. In: De Broyer, C. (Eds.) *Census of Antarctic Marine Life: Synopsis of the Amphipoda of the Southern Ocean*, Vol. 1. *Bulletin de l'Institut Royal des Sciences Naturelles de Belgique, Biologie*, Bruxelles, 77 (suppl. 1), pp. 325.
- Desbruyères, D., Geistdorfer, P., Ingram, C.L., Khripoudoff, A. & Lagardère, J.P. (1985) Répartition des populations de l'épibenthos carnivore. In: Laubier, L. & Monniot, C. (Eds.). *Peuplements Profonds du Golfe de Gascogne*. IFREMER, Paris, pp. 233–251.
- Diffenthal, M. & Horton, T. (2007) *Stephonyx arabiensis* (Crustacea: Amphipoda: Lysianassoidea: Uristidae), a new deep-water scavenger species from the Indian Ocean, with a key to the genus *Stephonyx*. *Zootaxa*, 1665, 31–41.
- Duffy, G.A., Horton, T. & Billett, D.S.M. (2012) Deep-sea scavenging amphipod assemblages from the submarine canyons of the Western Iberian Peninsula. *Biogeosciences*, 9, 4861–4869.  
<http://dx.doi.org/10.5194/bg-9-4861-2012>
- Gurjanova, E.F. (1951) Amphipods of the seas of the USSR and surrounding waters (Amphipoda-Gammaridea). *Akademiya Nauk SSSR, Opredeliteli po Faune SSSR*, 41, 1–1029. [In Russian]
- Gurjanova, E.F. (1962) Amphipods of the northern part of the Pacific Ocean (Amphipoda-Gammaridea). Part 1. *Akademiya Nauk SSSR, Opredeliteli po Faune SSSR*, 74, 1–440. [In Russian]
- Hatch, S.A. (1983) Storm-petrels (*Oceanodroma* spp.). In: Baird P.A. & Gould P.J. (Eds.). *The breeding biology and feeding ecology of marine birds in the Gulf of Alaska. Final Report, Outer Continental Shelf Environmental Assessment Program Research Unit*, 341, 171–206.
- Hatch, S.A. (2013) Kittiwake diets and chick production signal a 2008 regime shift in the Northeast Pacific. *Marine Ecology Progress Series*, 477, 271–284.  
<http://dx.doi.org/10.3354/meps10161>
- Hendrycks, E.A. & Conlan, K.E. (2003) New and unusual abyssal gammaridean Amphipoda from the north-east Pacific. *Journal of Natural History*, 37, 2303–2368.  
<http://dx.doi.org/10.1080/00222930210138926>
- Holmes, S.J. (1908) The Amphipoda collected by the U.S. Bureau of Fisheries steamer "Albatross" off the west coast of North America, in 1903 and 1904, with descriptions of a new family and several new genera and species. *Proceedings of the United States National Museum*, 35, 489–543.  
<http://dx.doi.org/10.5479/si.00963801.35-1654.489>
- Horton, T. (2004) Revision of the amphipod genus *Valettopsis* Holmes, 1908 (Crustacea: Lysianassoidea), with the addition of three new species. *Journal of Natural History*, 38, 1735–1755. Available from: <http://www.tandfonline.com/doi/full/10.1080/0022293031000156259#abstract> (Accessed 3 Aug. 2015)
- Horton, T. (2005) A new amphipod species from the Indian Ocean (Crustacea: Amphipoda: Lysianassoidea: Podopronidae). *Zootaxa*, 861, 1–11.
- Horton, T. (2006) Deep-sea scavenging amphipods from the Faroe-Shetland Channel. *Porcupine Marine Natural History Society Newsletter*, 19, 17–20.
- Horton, T. & Thurston, M. (2009) *Hirondellea sindhusagar* (Crustacea: Amphipoda: Lysianassoidea), a new deepwater scavenger species from the Indian Ocean, with a key to the genus *Hirondellea*. *Zootaxa* 2096, 433–441. In: Brökeland, W. & George, K.H. (Eds.) (2009) Deep-sea taxonomy— a contribution to our knowledge of biodiversity. *Zootaxa*, 2096, 1–488.
- Horton, T. & Thurston, M. (2011) *Centromedon zoe* (Crustacea: Amphipoda: Lysianassoidea), a new deep-water scavenger species from the North Atlantic, with a key to the genus *Centromedon*. *Zootaxa*, 2869, 54–62.
- Horton, T. & Thurston, M. (2013) *Hirondellea namarensis* (Crustacea: Amphipoda: Lysianassoidea: Hirondelleidae), a new deep-water scavenger species from the Mid-Atlantic Ridge. *Marine Biology Research*, 9, 554–562.  
<http://dx.doi.org/10.1080/17451000.2012.749994>
- Horton, T. & Thurston, M. (2014) A revision of the bathyal & abyssal necrophage genus *Cyclocaris* Stebbing, 1888 (Crustacea: Amphipoda: Cyclocaridae) with the addition of two new species from the Atlantic Ocean. *Zootaxa*, 3796 (3), 507–527.

<http://dx.doi.org/10.11646/zootaxa.3796.3.6>

- Horton, T., Thurston, M.H. & Duffy, G.A. (2013) Community composition of scavenging amphipods at bathyal depths on the Mid-Atlantic Ridge. *Deep-Sea Research II*, 98, 352–359.  
<http://dx.doi.org/10.1016/j.dsr2.2013.01.032>
- Hurley, D.E. (1963) Amphipoda of the family Lysianassidae from the west coast of North and Central America. *Allan Hancock Foundation Publications, Occasional Paper*, 25, 1–160.
- Ingram, C.L. & Hessler, R.R. (1983) Distribution and behaviour of scavenging amphipods from the central North Pacific. *Deep-Sea Research*, 30, 683–706.  
[http://dx.doi.org/10.1016/0198-0149\(83\)90017-1](http://dx.doi.org/10.1016/0198-0149(83)90017-1)
- Ikeda, T. (2013) Metabolism and chemical composition of marine pelagic amphipods: synthesis toward a global bathymetric model. *Journal of Oceanography*, 69(3), 339–355.  
<http://dx.doi.org/10.1007/s10872-013-0177-5>
- Kaim-Malka, R.A. (2003) Biology and life cycle of *Scopelocheirus hopei* (A. Costa, 1851), a scavenging amphipod from the continental slope of the Mediterranean. *Journal of Natural History*, 37, 2547–2578.  
<http://dx.doi.org/10.1080/00222930210155693>
- Kilgallen, N.M. & Lowry, J.K. (2015) A review of the scopelocheirid amphipods (Crustacea, Amphipoda, Lysianassoidea), with the description of new taxa from Australian waters. *Zoosystematics and Evolution*, 91(1), 1–43.  
<http://dx.doi.org/10.3897/zse.91.8440>
- Lampitt, R.S., Merrett, N.R. & Thurston, M.H. (1983) Inter-relations of necrophagous amphipods, a fish predator, and tidal currents in the deep sea. *Marine Biology*, 74, 73–78.  
<http://dx.doi.org/10.1007/BF00394277>
- Ledoyer, M. (1986) Crustacés Amphipodes Gammariens. Familles des Haustoriidae à Vitjazianidae. *Faune de Madagascar*, 59, 599–1112.
- Lopes, M.F.R., Marques, J.C. & Bellan-Santini, D. (1993). The benthic amphipod fauna of the Azores (Portugal): an up-to-date annotated list of species, and some biogeographic considerations. *Crustaceana*, 65 (2), 204–217.  
<http://dx.doi.org/10.1163/156854093X00568>
- Lowry, J.K. & Bullock, S. (1976) Catalogue of the marine gammaridean Amphipoda of the Southern Ocean. *Royal Society of New Zealand Bulletin*, 16, 1–187.
- Lowry, J.K. & Stoddart, H.E. (1989) The scopelocheirid genus *Aroui* (Crustacea: Amphipoda: Lysianassoidea) with notes on the association between scopelocheirid amphipods, cassinid gastropods and spatangoid echinoids. *Records of the Australian Museum*, 41, 111–120.  
<http://dx.doi.org/10.3853/j.0067-1975.41.1989.139>
- Lowry, J.K. & Stoddart, H.E. (1992) A revision of the genus *Ichnopus* (Crustacea: Amphipoda: Lysianassoidea: Uristidae). *Records of the Australian Museum*, 44, 185–245.  
<http://dx.doi.org/10.3853/j.0067-1975.44.1992.32>
- Lowry, J.K. & Stoddart, H.E. (1993) Crustacea Amphipoda: Lysianassoids from Philippine and Indonesian waters. *Mémoires du Muséum National d'Histoire Naturelle, Series A, Zoology*, 156, 55–109.
- Lowry, J.K. & Stoddart, H.E. (1995) New lysianassoid genera and species from south-eastern Australia (Crustacea: Amphipoda). *Records of the Australian Museum*, 47, 7–25.  
<http://dx.doi.org/10.3853/j.0067-1975.47.1995.5>
- Lowry, J.K. & Stoddart, H.E. (1997) Amphipoda Crustacea IV. Families Aristiidae, Cyphocarididae, Endeavouridae, Lysianassidae, Scopelocheiridae, Uristidae. *Memoirs of the Hourglass Cruises*, 10, 1–148.
- Nagata, K. (1963) Two new gammaridean amphipods (Crustacea) collected by the second cruise of the Japanese expedition of deep sea. *Publications of the Seto Marine Biological Laboratory*, 11 (1), 1–5.
- Nysewander, D.R. (1983) Black-legged Kittiwake (*Rissa tridactyla*). In: Baird P.A. & Gould, P.J. (Eds.), *The breeding biology and feeding ecology of marine birds in the Gulf of Alaska. Final Report, Outer Continental Shelf Environmental Assessment Program Research Unit*, 341, 295–348.
- Oldevig, H. (1959) Arctic, subarctic and Scandinavian amphipods in the collections of the Swedish Natural History Museum in Stockholm. *Göteborgs Kungliga Vetenskaps-och Vitterhets-Samhälles Handlingar Series B.*, 8, 1–132.
- Palerud, R. & Vader, W. (1991) Marine Amphipoda Gammaridea in north-east Atlantic and Norwegian Arctic. *Tromsø, Naturvitenskap*, 68, 1–97.
- Poore, A.G.B. & Lowry, J.K. (1997) New amphipod amphipods from Port Jackson, New South Wales, Australia (Crustacea: Amphipoda: Amphipodidae). *Invertebrate Taxonomy*, 11, 897–941.  
<http://dx.doi.org/10.1071/IT95045>
- Quetin, L.B., Ross, R.M. & Uchio, K. (1980) Metabolic characteristics of midwater zooplankton: Ammonia excretion, O:N ratios, and the effect of starvation. *Marine Biology*, 59, 201–209.  
<http://dx.doi.org/10.1007/BF00404742>
- Sanger, G.A. & Ainley, D. (1988) Review of the distribution and feeding ecology of seabirds in the oceanic subarctic North Pacific Ocean. In: Nemoto, T. & Percy, W.G. (Eds.), *The Biology of the Subarctic Pacific*. (Proceedings of the Japan—United States of America seminar on the biology of the micronekton of the Subarctic Pacific.) Part 2. *Bulletin of the Ocean Research Institute, University of Tokyo*, 26 (2), 161–186.

- Schellenberg, A. (1926a) Die Gammariden der Deutschen Südpolar-Expedition 1901–1903. *Deutsche Südpolar-Expedition*, 18, 235–414.
- Schellenberg, A. (1926b) Amphipoda 3: Die Gammariden der Deutschen Tiefsee-Expedition. *Wissenschaftliche Ergebnisse der Deutschen Tiefsee-Expedition auf dem Dampfer "Valdivia" 1898–1899*, 23, 193–243.
- Schellenberg, A. (1955) Amphipoda. *Reports of the Swedish Deep-Sea Expedition, Zoology*, 2(14), 182–195.
- Shoemaker, C. (1945) The Amphipoda of the Bermuda Oceanographic Expeditions, 1929–1931. *Zoologica, Scientific Contributions of the New York Zoological Society*, 30, 185–266.
- Smith, K.L. & Baldwin, R.J. (1982) Scavenging deep-sea amphipods: effects of food odor on oxygen consumption and a proposed metabolic strategy. *Marine Biology*, 68, 287–298.  
<http://dx.doi.org/10.1007/BF00409595>
- Stebbing, T.R.R. (1906) Amphipoda. I. Gammaridea. *Das Tierreich*, 21, 1–806.
- Thurston, M.H. (1974) The Crustacea Amphipoda of Signy Island, South Orkney Islands. *British Antarctic Survey Scientific Reports*, 71, 133 pp.
- Thurston, M.H. (1979) Scavenging abyssal amphipods from the north-east Atlantic Ocean. *Marine Biology*, 51, 55–68.  
<http://dx.doi.org/10.1007/BF00389031>
- Thurston, M.H. (1990) Abyssal necrophagous amphipods (Crustacea: Amphipoda) in the northeast and tropical Atlantic Ocean. *Progress in Oceanography*, 24, 257–274.  
[http://dx.doi.org/10.1016/0079-6611\(90\)90036-2](http://dx.doi.org/10.1016/0079-6611(90)90036-2)
- Thurston, M.H. (2001) Pelagic amphipods. In: Jazdzewski K., Baldinger A., Coleman C.O., De Broyer C., Gable M.F. & Plaiti W. (Eds.), Proceedings of the Xth International Colloquium on Amphipoda, Heraklion, Crete, Greece, 16–21 April 2000. *Polskie Archiwum Hydrobiologii*, 682–694.
- Thurston, M.H. & Bett, B.J. (1993) Eyelessness in marine gammaridean Amphipoda (Crustacea): geographical, bathymetric and taxonomic considerations. *Journal of Natural History*, 27 (4), 861–881.  
<http://dx.doi.org/10.1080/00222939300770531>
- Treude, T., Janßen, F., Queisser, W. & Witte, U. (2002) Metabolism and decompression tolerance of scavenging lysianassoid deep-sea amphipods. *Deep Sea Research Part I: Oceanographic Research Papers*, 49 (7), 1281–1289.  
[http://dx.doi.org/10.1016/S0967-0637\(02\)00023-7](http://dx.doi.org/10.1016/S0967-0637(02)00023-7)
- Vermeer, K. & Devito, K. (1988) The importance of *Paracallisoma coecus* and myctophid fishes to nesting fork-tailed and Leach's storm-petrels in the Queen Charlotte Islands, British Columbia. *Journal of Plankton Research*, 10 (1), 63–75.  
<http://dx.doi.org/10.1093/plankt/10.1.63>
- Vinogradov, G.M. (2004) Near-bottom and pelagic gammaridean amphipods in the western Indian Ocean. *Annals of the South African Museum* 112, 39–88.
- Vinogradov, M.E., Vereschchaka, A.L. & Vinogradov, G.M. (1996) Visual observations from DSRV "Mir" in location of the Russian submarine "Komsomolet" wreck. *Deep-Sea Newsletter*, 24, 7–8.
- Watling, L. (1989) A classification system for crustacean setae based on the homology concept. In: Felgenhauer, B.E., Watling, L. & Thistle, A.B. (Eds.), *Functional Morphology of Feeding and Grooming in Crustacea. Crustacean Issues* 6, Balkema, Rotterdam, pp. 15–27.