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## New genera for species of *Jassa* Leach (Crustacea: Amphipoda) and their relationship to a revised Ischyrocerini

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**NEW GENERA FOR SPECIES OF *JASSA* LEACH (CRUSTACEA: AMPHIPODA) AND THEIR RELATIONSHIP TO A REVISED ISCHYROCERINI**
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## Table of Contents



## Abstract


Four Southern Hemisphere and one Northern Hemisphere species of *Jassa* (Crustacea: Amphipoda: Ischyrocerini) are removed from this genus. The south temperate *Jassa barnardi* Stephensen, 1949 is synonymized with *Ventojassa frequens* (Chilton, 1883). The south temperate and subantarctic *Jassa multidentata* Schellenberg, 1931 and *Jassa wandeli* Chevreux, 1906 are transferred to *Pleojassa* **n. gen.**, with the addition of *P. lowryi* **n. sp.,** *P. moorei* **n. sp.** and *P. orientalis* **n. sp.** *Hemijassa* Walker, 1907 is resurrected for the Antarctic *Jassa goniamera* Walker, 1903. The Northern Hemisphere *Jassa ocia* (Bate, 1862) is transferred to *Plumulojassa* **n. gen.** and shown to range throughout the temperate coasts of the northeastern Atlantic and its eastern seas. Placed in context of the other genera of the Ischyrocerini Stebbing, 1899, *Jassa*, *Pleojassa*, *Hemijassa* and *Plumulojassa* join *Parajassa* Stebbing, 1899 in having a unique uropod 3 morphology. Characteristics of the uropod 3 and other appendages are used to revise four other genera of the Ischyrocerini. *Ischyrocerus* Krøyer, 1838 now becomes a temperate to polar genus, with *Neoischyrocerus* Conlan, 1995 embracing tropical species of *Ischyrocerus* and all members of *Coxischyrocerus* Just, 2009 and *Tropischyrocerus* Just, 2009. A new diagnosis and illustrated key to the 18 genera of Ischyrocerini is given.



**Key words:** Ischyrocerini, *Ventojassa*, *Hemijassa*, *Plumulojassa*, *Ischyrocerus*, *Neoischyrocerus*, *Coxischyrocerus*, *Tropischyrocerus*


## Introduction

In an analysis of the world species of *Jassa* Leach, 1814, Conlan (1989, 1990) revised the genus to contain 19 species, showing why there had been previous systematic confusion. Based on observations of mating behaviour by Borowsky (1983, 1985) and morphological variation during growth, Conlan (1989) suggested that a generic characteristic of the genus is that males do not become sexually active until their last molt. At this time, they produce a thumb-like protuberance on their second gnathopods which is used for signalling dominance and sexual intent. Coincident with thumb production is enlargement and altered setation of the second antennae and reduction in size of the bases of the third and fourth pereopods which hold the tube-spinning glands. At this time, the thumbed males abandon a tubicolous life style, wandering in search of receptive females, which they guard until the female molts and can release her eggs for fertilization. Small males with shorter than predicted thumbs, termed 'minor forms', may act as sneaks relative to the large-thumbed, 'major form' males.

On the basis of these observations, it was evident that some species of *Jassa* did not display these changes and did not possess other character states typical of the 19 species and so should be transferred to other genera. Accordingly, Conlan (1995) transferred *Jassa lilipuna* J.L. Barnard, 1970 to the new genus *Neoischyrocerus* Conlan, 1995 and *Jassa socia* Myers, 1989 to *Ischyrocerus* Krøyer, 1838. The purpose of this paper is to assign the remaining species that lack the generic characters for *Jassa* to extant or new genera. *Jassa barnardi* Stephensen, 1949 is synonymized with *Ventojassa frequens* (Chilton, 1883). *Jassa multidentata* Schellenberg, 1931 and *Jassa wandeli* Chevreux, 1906 are transferred to *Pleojassa* **n. gen.**, with the addition of *P. lowryi* **n. sp.**, *P. moorei* **n. sp.** and *P. orientalis* **n. sp.** *Jassa goniamera* Walker, 1903 is transferred to *Hemijassa* Walker, 1907 and *J. ocia* (Bate, 1862) is transferred to *Plumulojassa* **n. gen.** Finally, these genera are placed within the larger context of the tribe Ischyrocerini Stebbing, 1899 and a new diagnosis and illustrated key is given.

## Material and methods

Methods for species differentiation are described in Conlan (1990). As many specimens as possible were borrowed from museums and private lenders and compared with their type specimens. Loan sources are given in Table 1. Collection records are available from the Canadian Museum of Nature (CMN). The World Register of Marine Species, (marinespecies.org) was considered the authority for classification. Species distributions were mapped based on the collections examined and on literature sources where identifications were considered to be correct, as well as on non-validated records in OBIS (Ocean Biogeographic Information System, obis.org), with dubious records filtered out. Those distributions that were based on specimen identification were given a different map symbol than distributions in OBIS and the literature, which were considered to be non-validated. OBIS and literature sourcing continued to the end of August 2020 in order to cover the time period 1990–2019, with additions of early 2020 information. Location coordinates in the text are given in the format provided by the institution. If the true collecting coordinates were not provided, the rough location is given as an approximate value. Since most of the coordinates for older collections were in degrees, minutes and seconds (dms), coordinates obtained from the internet in other formats were converted to dms using the website https://www.fcc.gov/media/radio/dms-decimal.

The taxa are described in a similar format to Conlan (1990) to aid comparison to the genus *Jassa* and its species. Descriptions of the full body are given, as well as shorter diagnoses based on key character states. Variation was examined on as many specimens as possible to aid identification of growth stages. Variation in sexually variable appendages (the second gnathopod and antenna 2) was graphed where sufficient specimens from the same collection (assuming a single population) were available. For consistency of description with Conlan (1990) and referring to the considerations of d'Udekem d'Acoz (2010) and Krapp-Schickel (2011), the following terminology was applied in the descriptions: seta = slender, flexible articulated structure; spine = robust, inflexible articulated structure (synonymous with 'robust seta'); tooth = non-articulated, pointed ectodermal structure.

Species illustrations were taken from specimens in alcohol and from body parts slide mounted in polyvinyl lactophenol stained with lignin pink. Slide mounts were examined under oil immersion if necessary. The plates were completed by first drawing from the specimens to be illustrated from the preserved whole body and from microscope slides of body parts using camera lucida and microscopes (Wild M5, Olympus SZX16 stereoscopes and Leitz compound microscope). All details were checked for correctness and distortion. The resulting pencil drawing was computer scanned and digitally "inked" using the vector based drawing software CorelDraw X3. The new line drawing was then exported into Adobe Photoshop CS6 for the addition of labels and digital sharpening of the reduced plate, resulting in grayscale 600 dpi tiff files. All illustrations were made by artist Susan Laurie-Bourque in consultation with the author. Abbreviations in the illustrations are: A, antenna; UL, upper lip; MD, mandible; LL, lower lip; MX, maxilla; MXPD, maxilliped; GN, gnathopod; P, pereopod; PL, pleopod; U, uropod; T, telson; LFT, left; RT, right. Scale bars are 0.1 mm, based on eyepiece micrometer measurements.

**TABLE 1.** Acronyms for institutions that provided specimens, with their former names in brackets as used in Conlan (1990).

| Acronym | Institution |
|---|---|
| AM | Australian Museum, Sydney, New South Wales, Australia |
| AuM | Auckland Museum, New Zealand |
| CEAMARC | The Collaborative East Antarctic Marine Census for the Census of Antarctic Marine Life |
| CMN | Canadian Museum of Nature, Ottawa, Ontario, Canada (formerly NMNS, National Museum of Natural Sciences) |
| CMNZ | Canterbury Museum, Christchurch, New Zealand |
| MfN | Museum für Naturkunde, Leibniz-Institut für Evolutions- und Biodiversitätsforschung an der Humboldt-Universität zu Berlin, Berlin, Germany |
| MNHN | Muséum national d'Histoire naturelle, Paris, France |
| MNZTPT | Museum of New Zealand / Te Papa Tongarewa, Wellington, New Zealand (formerly NMNZ, National Museum of New Zealand) |
| NHM | Natural History Museum, London, London, England, UK (formerly BMNH, British Museum (Natural History)) |
| NHMW | Naturhistorisches Museum, Wien, Austria |
| NIWA | National Institute of Water and Atmospheric Research Auckland, New Zealand |
| NRM | Naturhistoriska Riksmuseet, Stockholm, Sweden |
| RBINS | Royal Belgian Institute of Natural Sciences |
| SNM | Statens Naturhistoriske Museum, København, Denmark (formerly ZMUC, Zoologisk Museum, København, Denmark) |
| UCT | Iziko South African Museum, Cape Town, South Africa (collection formerly at UCT, the University of Cape Town) |
| UiO | Naturhistorisk Museum, Universitetet i Oslo, Norway (formerly ZMUO, Zoological Museum, University of Oslo) |
| ZMH | Centrum für Naturkunde, Universität Hamburg, Germany (formerly ZMUH, Zoologisches Institut und Zoologisches Museum, Universitlit Hamburg, Federal Republic of Germany) |
| ZMUO | Zoological Museum, University of Oslo, Oslo, Norway |

Individuals observed by scanning electron microscopy were cleaned by sonification, critical point dried (SAMDRI PVT-3) and gold coated. The critical point drying procedure was exchange of ethanol with $CO_2$ until full saturation with liquid $CO_2$, heating the $CO_2$ to a critical temperature of 31°C and a critical pressure of 1100 psi, heating to the cut out point of 44 °C, and finally reduction of heat and pressure to ambient.

Size variation of appendages that appeared to change with body length and sex was measured by eyepiece micrometer and then converted to mm using a stage micrometer. Unlike *Jassa*, the sexual state of the males could not be determined as males of these species did not produce a morphological indicator of adulthood. Individuals with obvious male secondary sexual characters that appeared to be well developed were termed male. Such characters were those that differed from the adult female or from small, presumably juvenile individuals. This could include shorter filter setae and addition of plumose setae to the distal part of antenna 2, enlarged gnathopod 2 propodus and (rarely) presence of a thumb on the posterior margin, and more sinuous dactyl than in the female. Females were considered to be adult if their brood plates were setose. Unsexable individuals or ones with incompletely modified secondary sexual characters were termed juvenile.

Body length was determined on the dorsal surface of the uncurved animal from the tip of the rostrum to the base of the telson. Thumb length was the longest straight-line length through the thumb from the palmar incision to the thumb tip. Propodus length was measured along the anterior margin from carpus to dactyl insertion. Antenna 2 article 5 length was also measured for species that appeared to vary sexually. For placement of the genera within the Ischyrocerini Stebbing, 1899, a table of characters was created from literature descriptions and illustrations. All species of the Ischyrocerini were examined for intra-generic variation. Particular attention was given to the large genus *Ischyrocerus* Krøyer, 1838 as tropical members appeared morphologically closer to members of *Neoischyrocerus* Conlan, 1995, *Coxischyrocerus* Just, 2009 and *Tropischyrocerus* Just, 2009 and these latter three genera did not appear to be morphologically separate.

Graphs and statistical analyses were constructed using SigmaPlot 14 (Systat Software, Inc.). The variables were regressed on body length and fitted to a linear regression if all assumptions were met (normal distribution, constant variance, independent residuals). All analyses were performed at a 95% confidence level. Normality was tested by the Shapiro-Wilk method. Constant variance was tested by computing the Spearman rank correlation between the absolute values of the residuals and the observed value of the dependent variable. When the correlation was significant, the constant variance assumption was violated. Independent residuals was tested by the Durbin-Watson statistic. This is a measure of serial correlation between the residuals. Durbin Watson statistic values deviating by ±0.5 or more from 2.0 (non-correlation) indicated serial correlation.

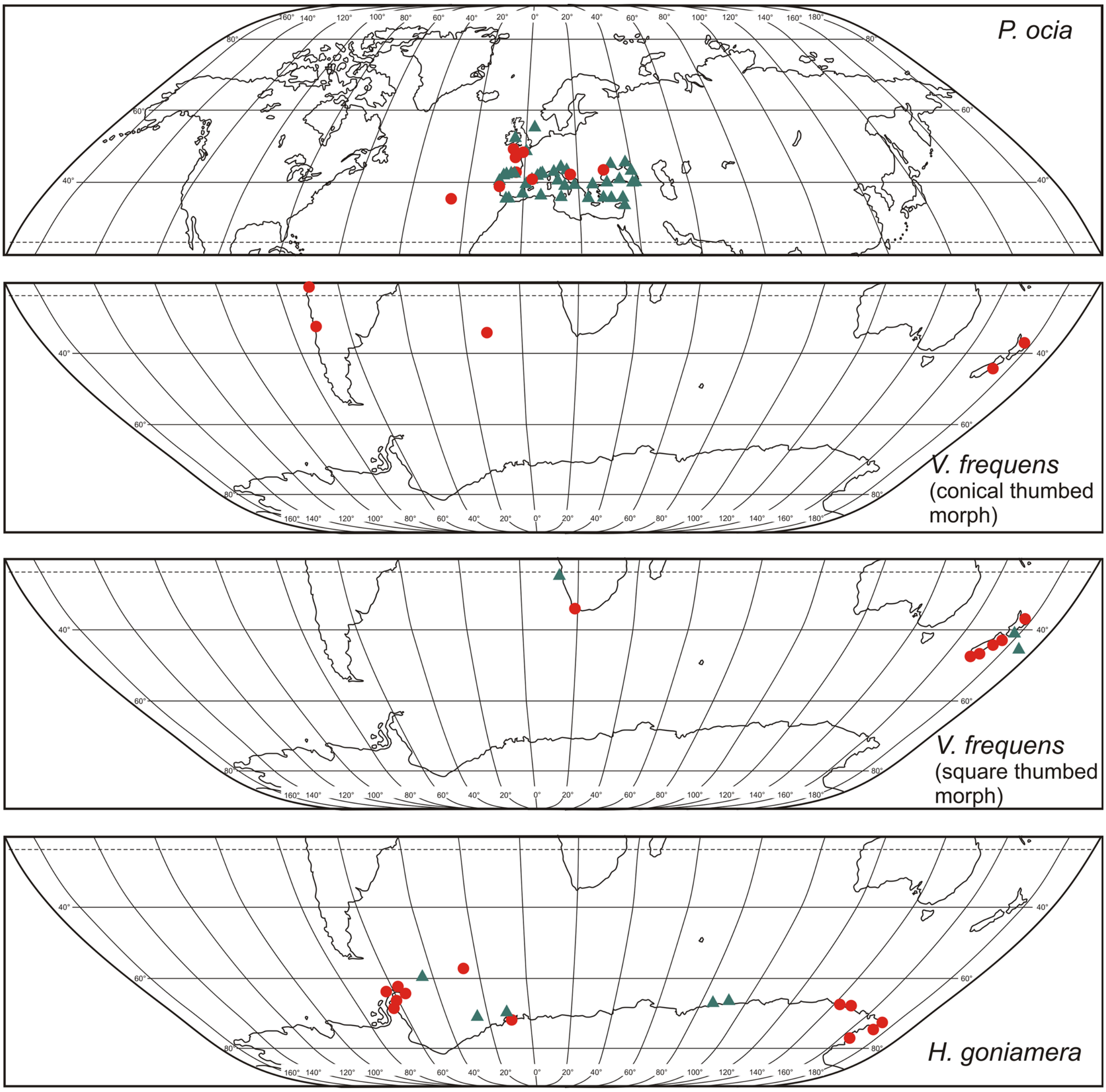



**FIGURE 1.** Distribution records of *Plumulojassa ocia*, *Ventojassa frequens* and *Hemijassa goniamera*. Red dot: identification confirmed by specimen examination; green triangle: literature record (Supplementary Table S1) with identification not confirmed but judged likely to be this species.

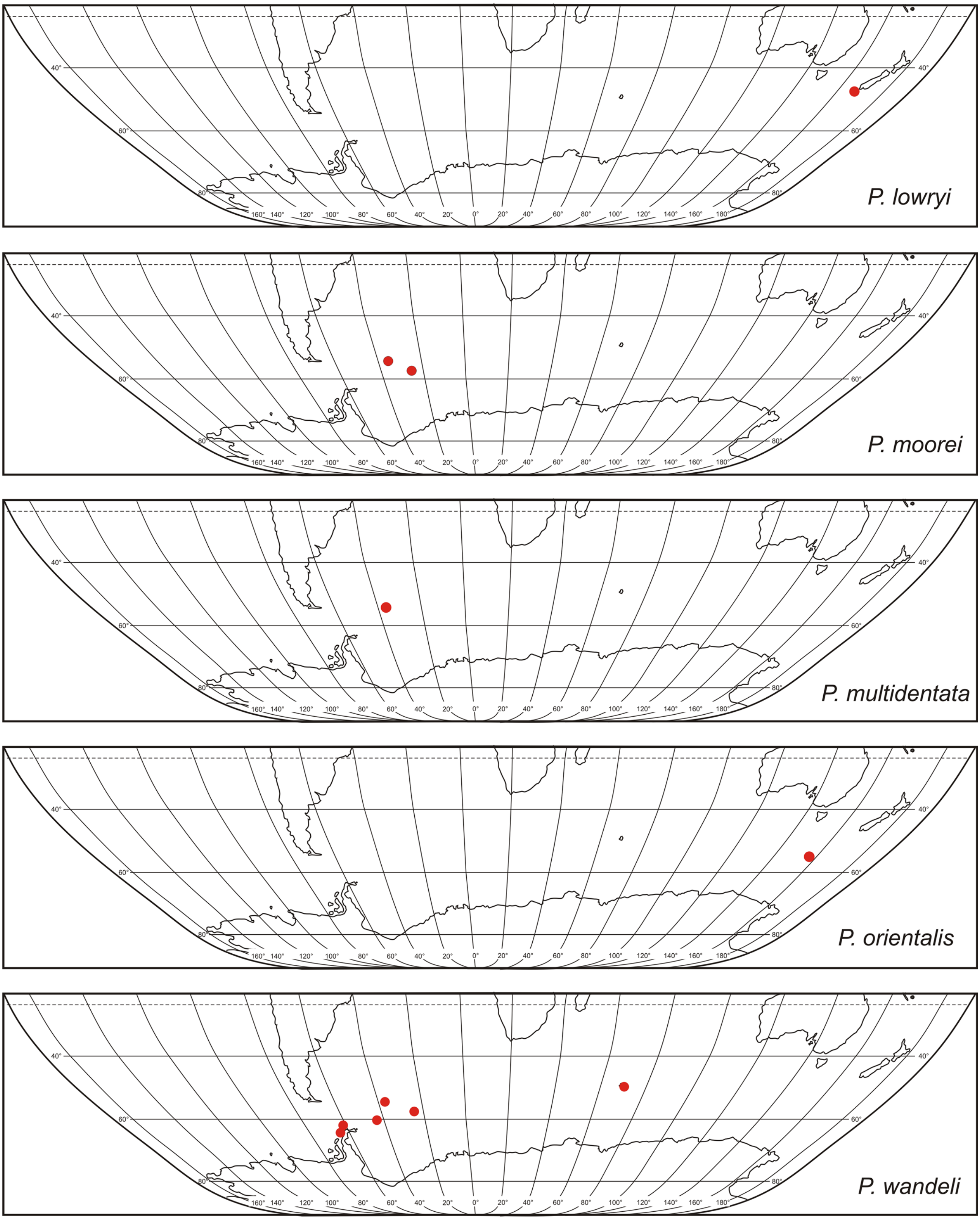



**FIGURE 2.** Distribution records of *Pleojassa moorei, P. lowryi, P. wandeli, P. multidentata, and P. orientalis.* Red dot: identification confirmed by specimen examination; green triangle: literature record (Supplementary Table S1) with identification not confirmed but judged likely to be this species.

**TABLE 2.** Earliest collection records for specimens examined in this paper or in the literature if identification is likely correct**.** Species are abbreviated by the first three letters of their names**.** Suggested status: I = indigenous; N = non-indigenous**.**

| Region | Species | Suggested Status | Earliest collection record | Location | Collection/Literature source |
|---|---|---|---|---|---|
| Atlantic Europe | OCI | I | before 1862 | Ilfracombe, U.K., Gosse, coll. | Bate (1862) |
| Mediterranean and Black Seas | OCI | I | 1865 | Lesina (Hvar), Croatia, C. Heller, coll. | NHMW 20620 |
| Atlantic Africa | FRE (cubic humbed) | I | 1953 or earlier | Lüderitz Bay, Namibia, A. Schellenberg, coll. | Schellenberg (1953) |
| | OCI | I | 14 Aug. 1888 | Pico-Faial Channel, Azores, E. Chevreux, coll. | MNHN Am. 2660 |
| Pacific South America | FRE (conical humbed) | I | 1931 or earlier | Valparaiso, Chile, A. Schellenberg, coll. | NRM 3786 |
| New Zealand | FRE (conical thumbed) | I | 1883 or earlier | Lyttelton Harbour, New Zealand, C. Chilton, coll. | CMNZ 2015.149.84 |
| | FRE (cubic thumbed) | I | 1884 or earlier | Lyttelton Harbour, New Zealand, C. Chilton, coll. | CMNZ 2015.149.575-604 (part) |
| | LOW | I | 21 Nov. 1976 | Rima Islet, The Snares, New Zealand (48°07′S, 166° 36′E), G. D. Fenwick, coll. | AM P.34948, P.37922, P.37923 |
| Southern Hemisphere islands (20–40°S) | FRE (conical thumbed) | I | 30 Jan. 1926 | Tristan da Cunha, R. R. S. Discovery station 4 | K. H. Barnard (1932) |
| Southern Hemisphere islands (40–60°S and 0–180°E) | ORI | I | 23 Dec. 1977 | Station MA-147, S.E. corner of Gorilla Head Rock, Macquarie I. (54°29′S, 158°58′E) | AM P.43955 |
| | WAN | I | 13 Feb. 1966 | S. baie du Morbihan, Port-Douzième, Kerguelen Island, J. C. Hureau, coll. | D. Bellan-Santini loan |
| Southern Hemisphere islands (40–60°S and 0–180°W) | GON | I | 13 Nov. 1908 | Visokoi I., South Sandwich Islands (56°42′S, 27°12′W), C. A. Larsen, coll. | UiO F2968 |
| | MOO | I | 1882–1883 | South Georgia (54°15′S, 36°45′W), Deutsch Polar Commision | ZMH K-28907 |
| | MUL | I | 1883 | Station 7813, Moltke Hafen, Royal Bucht, South Georgia (54°30′58″S, 36°0′45″W), Deutsche Polar Commission, K. von den Steinen, coll. | ZMH 33618 ex K-8028 |
| | WAN | I | 31 Aug. 1883 | South Georgia (54°15′S, 36°45′W), Deutsch Polar Expedition, K. von den Steinen, coll. | ZMH K-8021 |
| Southern Hemisphere (>60°S and 0–180°E) | GON | I | 10, 14 and 26 Nov. 1899 | Cape Adare, McMurdo Sound, Ross Sea (71°17′S, 170°14′E), Southern Cross Expedition | NHM 1902:11:5:6-10 |
| Southern Hemisphere (>60°S and 0–180°W) | GON | I | 16 Jan. 1902 | Graham Region SE of Seymour I. (64°20′S, 56°38′W), Svenska Sydpolarexp. 1901–1903, No. 5. | NRM 3679 |
| | WAN | I | 1 Nov. 1909 | Petermann I. (65.17°S, 64.14°W) | MNHN Am. 2628 |

## Results

**Species distributions.** *Plumulojassa ocia* (Bate, 1862) was found extensively along the Atlantic coast of Europe and the Irish, North, Mediterranean and Black Seas to as far west as the Azores (Fig. 1). It was first documented by Bate (1862) from the UK and subsequent collections found it more widely on European coasts (Table 2). It is still frequently noted in systematic and ecological literature (Supplementary Table S1). The other species were found solely in the Southern Hemisphere (Figs 1 and 2). Many of these were also found in the 19th or early 20th century collections, reflecting the efforts of European south polar expeditions. *Ventojassa frequens* (Chilton, 1883), *Hemijassa goniamera* (Walker, 1903) and *Pleojassa wandeli* (Chevreux, 1906) have now been found over a wide longitudinal range while the other *Pleojassa* species are known from only a single to a few locations. The distribution maps suggest that *Hemijassa goniamera* and *Pleojassa wandeli* are polar while the other Southern Hemisphere species are cold temperate. None of the species is known from <20° latitude.

**Habitat.** Table 3 gives a summary of the collection information available for each species, supplemented with data from the literature. The number of specimens available for examination ranged from three (*P. orientalis*) to ~1550 (*P. moorei*). The number of collections available for study ranged from one for *P. orientalis* to 56 for *P. wandeli*. Inorganic substrates ranged from sand to bedrock. While the Southern Hemisphere species were mostly found in isolated locations, *P. ocia* is known from European coasts, and its greater variety of substrates, which includes anthropogenic substrates, reflects the greater availability of information for this species. It has been found on numerous species of macroalgae, in and on sea cucumbers, and in mussel, vermetid and sabelariid reefs, sponges and ascidians, from the low intertidal zone to 200 m depth. Algal substrates were typical also for the Southern Hemisphere species, along with hydroids, bryozoans and sponges. Most species were found on exposed coasts in the low intertidal zone to subtidally. *Hemijassa goniamera*, *P. moorei* and *P. orientalis* were found only subtidally, with *H. goniamera* ranging to at least 584 m depth. From the collections available for study, ovigerous females were only found in autumn and winter samples of *P. ocia*. For the Southern Hemisphere species, ovigerous females of *P. wandeli* were found in most seasons. Eggs of *P. moorei* at Signy Island (South Orkney Islands) were at an early stage of development in austral summer (Thurston 1974b). Little information was available for the other Southern Hemisphere species. The Antarctic and subantarctic *Hemijassa goniamera* was by far the largest species in this study, with females mature between 13.8 and 20.0 mm body length. *Pleojassa wandeli* and *P. multidentata*, also polar and subpolar, were found ovigerous to nearly 10 mm body length. Subantarctic *P. moorei* and the more temperate *P. lowryi*, *V. frequens* and *P. ocia* were much smaller, the females being 2–5 mm in length when mature.

## Taxonomy

### Transferral of *Jassa ocia* to *Plumulojassa* n. gen. and creation of a neotype for *P. ocia*

### Genus *Plumulojassa* n. gen.

**Description of male.** Maximum body length 4.1 mm.

*Head lobe*: triangular, apically acute.

*Antenna 1*: accessory flagellum 1 article.

*Antenna 2*: slightly stouter than antenna 1 but hardly longer, filter setae somewhat shorter, never with plumose setae; flagellum with at least the last two articles bearing posteriorly curved spines, first article considerably longer than any of the following articles.

*Maxilla 1*: inner plate bearing a few short, fine setae; palp without setae at the base of article 1, article 2 with 1 row of facial setae.

*Gnathopod 1*: coxa rectangular; propodus defined by 3 spines (medial-lateral-medial), these mid-distant along the palm; dactyl not facially striated.

*Gnathopod 2*: with a gill; coxa deeper posteriorly; basis, anterolateral and anteromedial margins clothed in long plumose setae; carpus less than 1/4 propodus length; propodus, palm with a broad, bifid or trifid hinge tooth, defined by two narrow, apically acute teeth, these reaching nearly to the depth of the hinge tooth, thus giving the palm a transverse appearance; dactyl shorter than the propodus, inner margin slightly sinuous, tip reaching beyond the posterior defining tooth; dactyl, cusps reduced to small buttons interspersed with a few short setae.

*Pereopod 3*: coxa deepest at the centre; basis not slenderer in larger males, margins convex; merus overlapping the carpus, anterior margin bearing a series of single plumose setae; propodus not posteriorly spinose.

*Pereopods 5–7*: at least one basis posterodistally produced, anterior margin with a few short setae and no spines; merus not posteriorly spinose; carpus bearing 2 spines at the posterodistal angle on pereopod 5 and sometimes also on pereopod 6; spines lacking on pereopod 7; propodus not markedly expanded anteriorly; dactyl without facial striations, posterior (outer) margin not cusped distally, anterior (inner) margin bearing a seta only at the unguis.

*Pleopods*: rami long, length > depth of the pleon, each with 2 coupling hooks**.**

*Urosome*: segment 1 bearing a pair of setae dorsally.

*Uropod 3*: peduncle mid-ventrally setose, without mid-dorsal spines or mid-ventral setae, but with a crown of spines dorsomedially at the insertion of the rami, and a small cluster of setae distolaterally; outer ramus not setose mid-dorsally, tipped by a basally immersed, dorsally recurved spine, a single seta at the spine's point of immersion and a dorsal cluster of minute cusps proximal to the spine, none of these cusps particularly larger than the other; inner ramus with a single apical spine**.**

*Telson*: dorsolateral cusps accompanied by setae (1 long, single and 2 short, plumose) but without spines.

**Description of adult female.** Body length at maturity 2.4–4.0 mm**.** Character states as in the male except as follows.

*Brood plates*: broad, setae abundant, hook-tipped.

*Antenna* 2: posterior filter setae long, not shorter in larger individuals.

*Gnathopod 1*: basis not flanged, without plumose setae.

*Gnathopod 2*: propodus much larger and different in shape from the propodus of gnathopod 1 but differing only in the following respects from the large male: size slightly smaller, hinge tooth bifid, distal palmar tooth more central, proximal tooth little more than an acute expansion, bearing a large, single medial defining spine; dactyl, inner margin straight, tip apposing the defining spine.

**Type species.** *Podocerus ocius* Bate, 1862 (monotypy).

**Etymology.** The name refers to the abundant plumose setae on the anterior legs, particularly gnathopod 2, which makes this genus unmistakable among the *Jassa*-like genera, even at young stages.

## *Plumulojassa ocia* (Bate, 1862) new combination

(Figs 3–7)

*Podocerus ocius* Bate, 1862, 257, Plate 44, Fig. 5; Bate & Westwood, 1863, 450, 451; Heller, 1866, 45; Czerniavski, 1868, 83–84, Plate 6, Fig. 35; Della Valle, 1893, 448, 449, Plate 14, Figs 11–27; Walker, 1895, 444.

*Jassa ocius*: Stebbing, 1906, 655, 656.

*Jassa ocia*: Chevreux & Fage, 1925, 347, 348, Fig. 355; Gurjanova, 1951, 909, 910, Fig. 630; J. L. Barnard, 1958, 85; Lincoln, 1979, 554, Figs 266 g–j; Myers, 1989, 435–436, Fig. 297.

*Podocerus dentex* Czerniavski, 1868, 84, Plate VI, Fig. 35; Sexton & Reid, 1951, 56–57.

**Description of male.** Neotype (here designated)**.** Length 3.5 mm**.**

*Antenna 2*: overlapped by antenna 1 to the end of article 5; article 5, simple setae as long as those of the female; flagellum 4 articles, the last as long as the penultimate; article 1 71% of flagellum length**.**

*Mandible*: palp articles 2 and 3 without dorsal fringe of setae; raker spines 2 right, 3 left**.**

*Gnathopod 1*: coxal margins, anterior 100% of dorsal length, ventral margin shallowly concave; basis flanged both anteriorly and posteriorly, anterior margin fringed with long plumose setae laterally and medially, posterior margin with a few plumose setae throughout its length; carpus, length 45% of propodus length, posterior lobe 58% of anterior margin length, anterodistal setal cluster long, 67% of anterior margin length; propodus, palm convex, with 3 central defining spines**.**

*Gnathopod 2*: coxal margins, anterior 24% and posterior 59% of ventral length, ventral margin convex; carpus less than 1/4 propodus length, posterior lobe with a cluster of setae; propodus, anterior margin with a few individual plumose setae proximally (setae about 1/2 the width of the basis), palm and lateral face clothed in long plumose setae, palm with 2 defining teeth, each bearing plumose setae proximally but not apically, neither accompanied by a defining spine, defining teeth 14% (distal) and 17% (proximal) of propodus length**.**

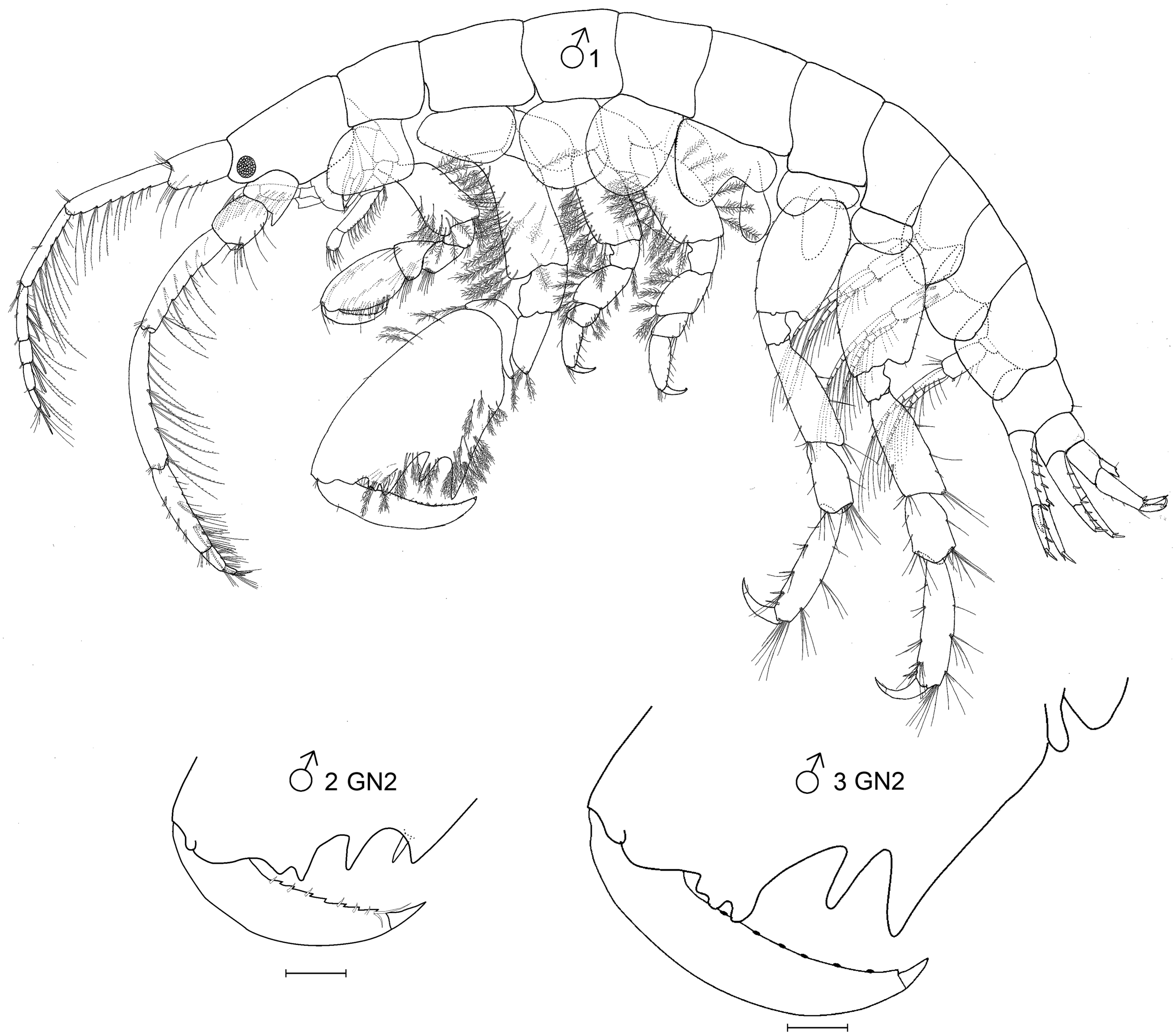



**FIGURE 3.** *Plumulojassa ocia* (Bate, 1862). Neotype, male 1, 3.5 mm. West side of St. Warna's Cove, St. Agnes, Scilly Isles, Cornwall, England, 1 August 1973, P. Parslow, coll., NHM 1987:514. Male 2, 3.0 mm and male 3, 3.7 mm, Le Croisic, France, date unknown, E. Chevreux, coll., MNHN Am. 2664. Setae are omitted from the gnathopod 2 profiles of males 2 and 3. All views lateral. Scale 0.1 mm.

*Pereopod 3*: coxa deepest at the centre; basis not slenderer in larger males, margins convex; merus, setae 1/2 article width, article width maximally 75% of length; carpus 45% overlapped by the merus; propodus, width 57% of length.

*Pereopod 5*: missing

*Pereopods 6–7*: basis posterodistally produced, anterior margin with a few short setae and no spines; merus not posteriorly spinose.

*Uropod 1*: peduncle, posteroventral spinous process underlying 36% of the inner ramus, inner and outer rami with 0 and 2 mid-dorsal spines respectively, terminating in a fringe of cusps ventral to the apical spine group.

*Uropod 2*: peduncle, posteroventral spinous process underlying 5% of the inner ramus.

*Uropod 3*: inner ramus without spines mid-dorsally.

**Condition.** Without right antenna 2, left pereopods 5–7 and right pereopod 5. Remaining right appendages, telson and mouthparts slide mounted. Remaining left appendages with the carcass. Figure 3 shows right pereopods 6–7.

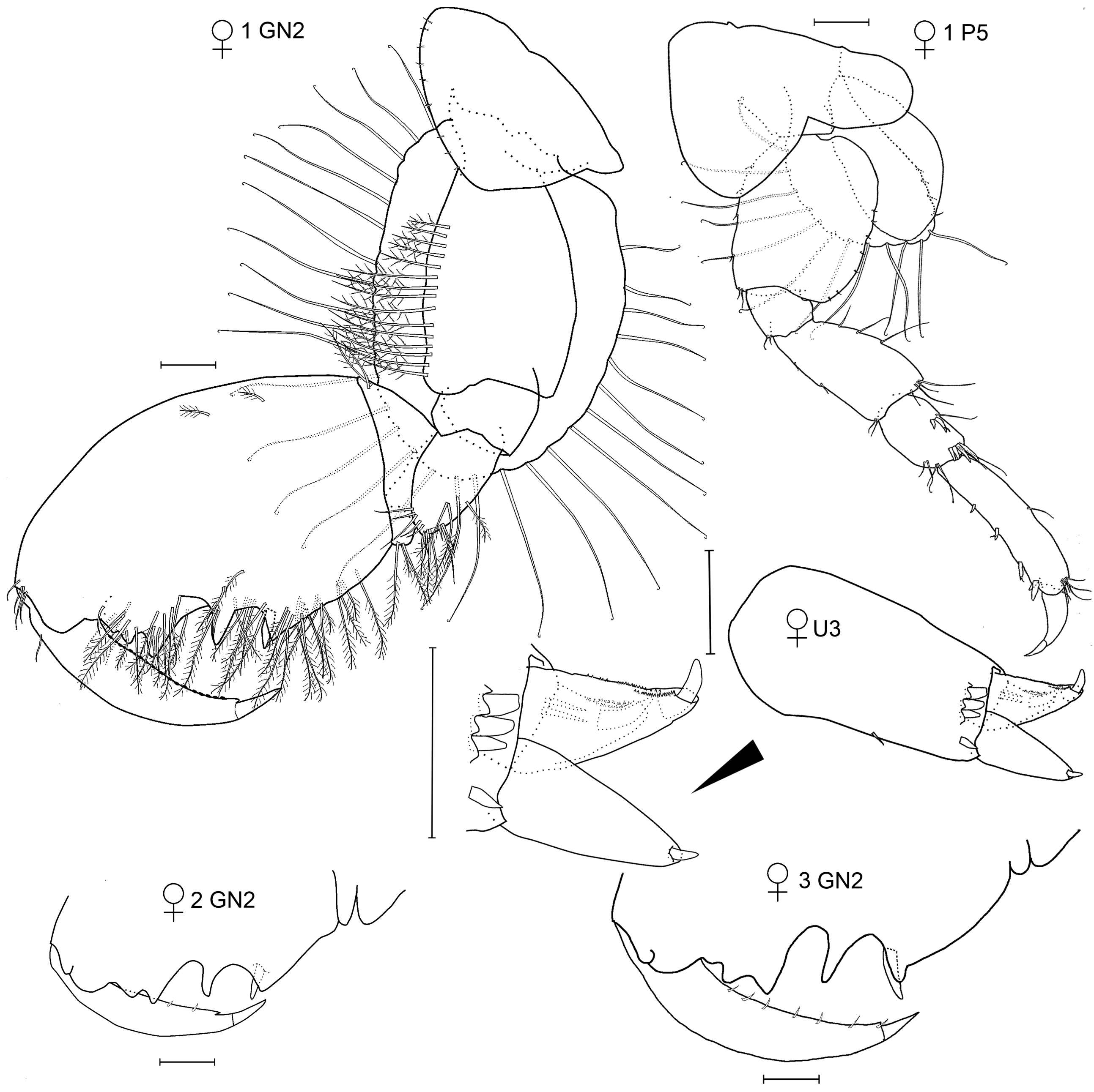



**FIGURE 4.** *Plumulojassa ocia* (Bate, 1862). Female 1, 3.75 mm. Intertidal, in *Corallina elongata*, Peniche, Portugal, 8 October 1979, J. C. Marques, coll., CMN A2019.0055. Female 2, 3.5 mm and female 3, 4.0 mm, Le Croisic, France, date unknown, E. Chevreux, coll., MNHN Am. 2664. Setae are omitted from the gnathopod 2 profiles of females 2 and 3. Lateral views: all gnathopods 2 and pereopod 5; medial view: uropod 3. Scale 0.1 mm.

**Description of adult female.** (Not type; MNHN Am. 2664, France: Loire-Atlantique: Le Croisic, E. Chevreux, coll.**)**. Length 3.5 mm**.** Character states as in the male except as follows.

*Antenna 2*: article 5 without plumose setae distally**.**

*Gnathopod 1*: coxa, ventral margin straight**.**

*Gnathopod 2*: coxal margins, anterior 27% and posterior 87% of ventral length, ventral margin convex; propodus, hinge tooth pronounced, palmar setae densely plumose throughout, so much so as to nearly obscure the shape of the palm.

**Condition.** Ovigerous. Without right antenna 2 and left pereopods 6 and 7**.** Remaining right appendages slide mounted**.** Remaining left appendages with the carcass.

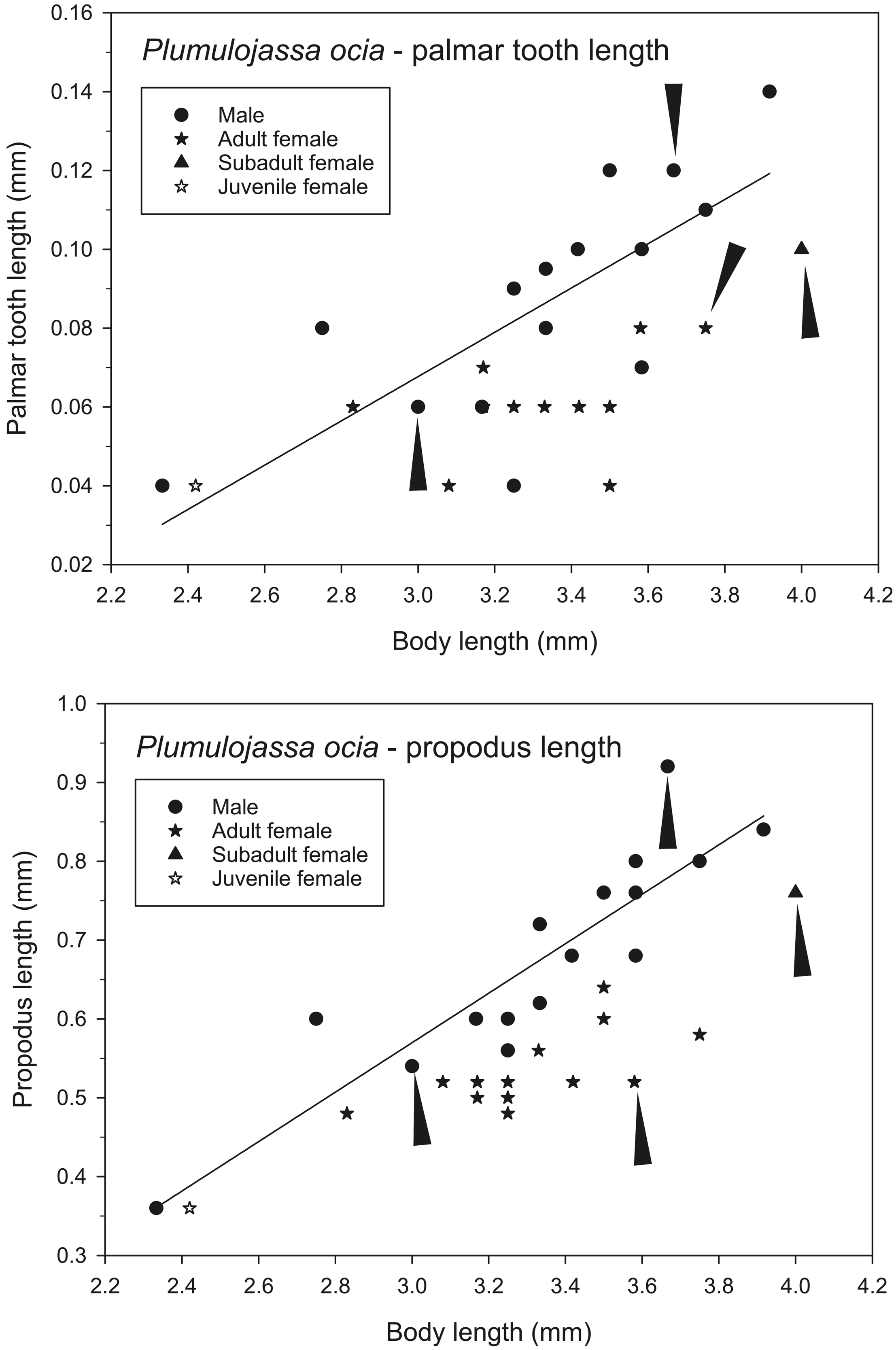



**FIGURE 5.** *Plumulojassa ocia* (Bate, 1862). Variation in gnathopod 2 palmar tooth length and propodus length relative to body length in males and females from a single population (Le Croisic, France, date unknown, E. Chevreux, coll., MNHN Am. 2664). Second gnathopod profiles illustrated in Figs 3 and 4 are indicated by an arrow. Linear regression assumptions passed for the male. Linear regression statistics: male, palmar tooth length = -0.101 + 0.056 x body length, $r^2 = 0.756$, $n = 17$; male propodus length = -0.371 + 0.314 x body length, $r^2 = 0.800$, $n = 17$.

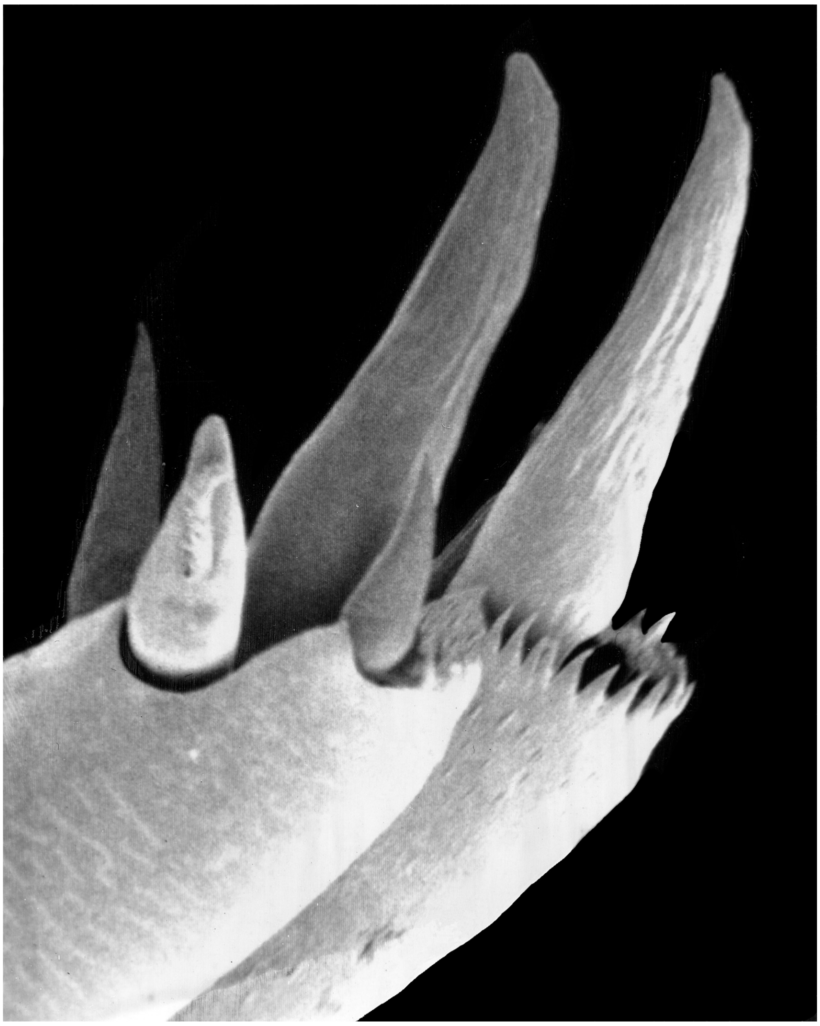


**FIGURE 6.** *Plumulojassa ocia* (Bate, 1862). Le Croisic, France, date unknown, E. Chevreux, coll., MNHN Am. 2664. Tip of right uropod 1 inner and outer rami, showing the fringe of cusps on the apex of the outer ramus. X5000.

**Variation.** Maximum body length: male 4.1 mm, female 4.0 mm**.** Sexual dimorphism in *Plumulojassa ocia* occurs in the density of plumosity and slight difference in shape of the gnathopod 2 propodus**.** The female's and small male's gnathopod 1 and pereopod 3–4 bases are not plumose, the coxae are somewhat deeper and less divergent, and the gnathopod 2 is somewhat smaller than the large male's**.** Both sexes possess a tooth in the central part of the palm of gnathopod 2**.** This tooth is analogous in position to the thumb in *Jassa* because it is distal of the palmar defining spine**.** However, there is no evidence of the palmar tooth appearing at the last molt as in *Jassa***.** Small *P. ocia* also have a palmar tooth (Figs 3 and 5)**.** The second tooth apparent in large males is not analogous to the thumb in *Jassa* because it is just a projection at the palmar defining spine**.** This projection is less pronounced in females and small males than in large males (Figs 3 and 4)**.** Females have a generally smaller palmar tooth than males of the same body length (Fig. 5)**.** Large males lose their palmar defining spine and the dactyl's inner margin becomes slightly sinuous (Fig. 3)**.**

**Type material examined.** Neotype, ♂, NHM 1987:514, west side of St. Warna's Cove, St. Agnes, Scilly Isles, Cornwall, England (49°50′N, 6°20′W), 1 August 1973, extreme low water spring, R. Parslow, coll.

**Other material examined.** U.K.: Jersey, Channel Isles, collector and date unknown 1 ♂ (NHM).

France: Le Croisic, in sponges (*Halicondria*), date unknown, E. Chevreux, coll., 8 ♂♂, 17 ♀♀, 13 juveniles (MNHN Am. 2664); Le Croisic, in sponges (*Halicondria*), station 214, E. Chevreux, coll., 3 ♂♂, 1 juvenile (MNHN Am. 2663); Banyuls, Pêche au feu No. 3, 5 Aug. 1909, 2 juveniles (MNHN Am. 2669); Port de Cette (Sète), date unknown, E. Chevreux, coll., 1 ♂, 1 juvenile (MNHN Am. 2667); Cette (Sète), in algae, 8 May 1897, E. Chevreux, coll., 1 ♂ (MNHN Am. 2662); Cette (Sète), Feb. 1897, E. Chevreux, coll., 6 ♀♀ (MNHN Am. 2653); Guéthary, date unknown, E. Chevreux, coll., 1 ♂, 2 ♀♀ (MNHN Am. 2666); Île-de-Bréhat, date unknown, E. Chevreux, coll., 1 ♀, 2 juveniles (MNHN Am. 2668); Port-Vendres, 1892, E. Chevreux, coll. (MNHN Am. 2665); Port-Vendres, 1892, E. Chevreux, coll., 1 ♂, 1 juvenile (MNHN Am. 2665).

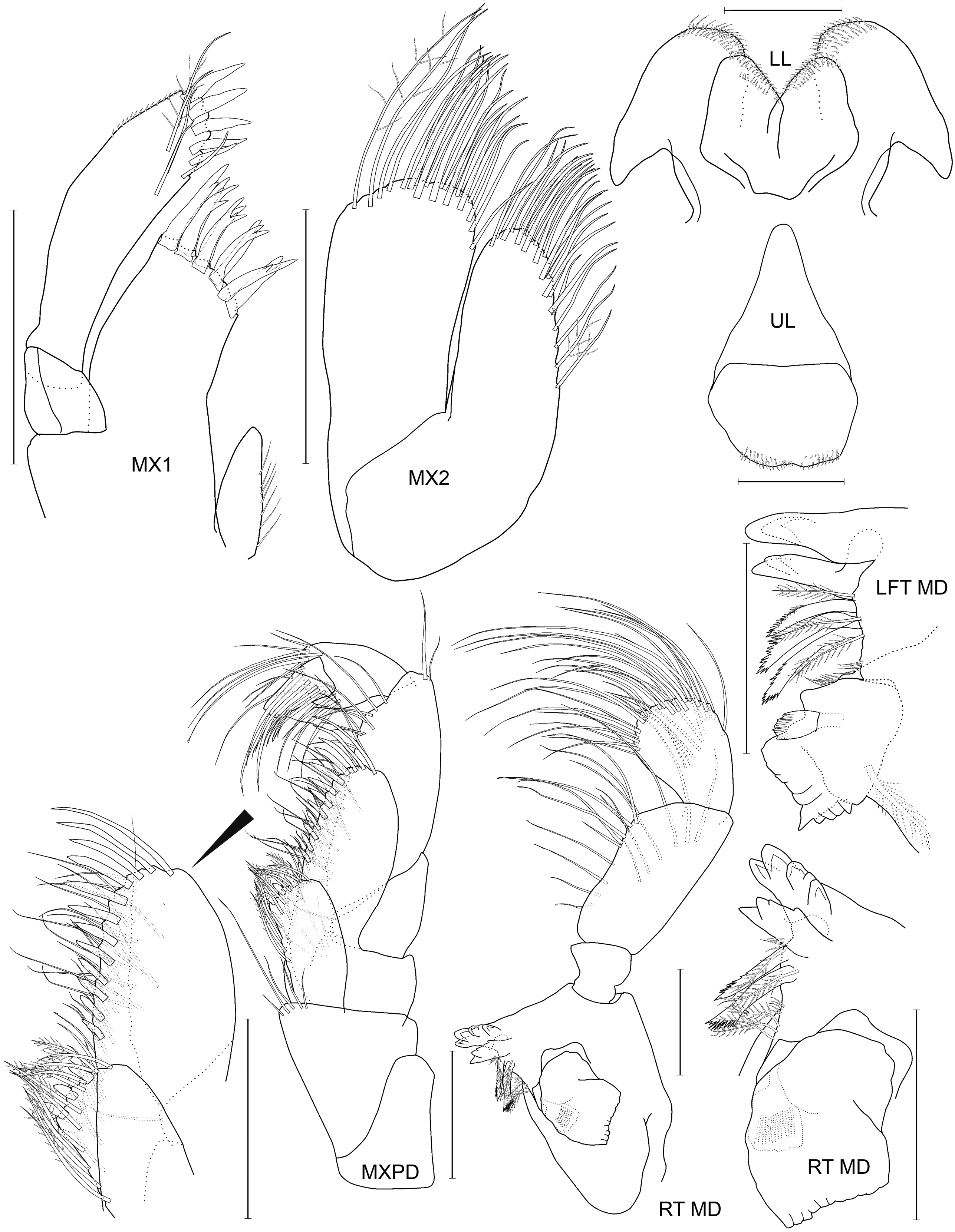



**FIGURE 7.** *Plumulojassa ocia* (Bate, 1862). Female 1, 3.75 mm. Intertidal, in *Corallina elongata*, Peniche, Portugal, 8 October 1979, J. C. Marques, coll., CMN A2019.0055. Mouthparts. Frontal view: upper lip; lateral view: maxilla 1 and left mandible; other views medial. Scale 0.1 mm.

**TABLE 3.** Collection data for specimens examined in this study and in Conlan (1990), with supplementary data from literature reports where the identification is likely correct. Species are abbreviated by the first three letters of their names. LI = low intertidal**.** For *H. goniamera*, which was mostly collected by bottom trawl, the average of the start and end of the trawl depth is given**.** Female information is lacking for *V. frequens* morphs and the number of specimens examined pertains to the males only, since small adult females and juveniles could not be separated into morphs**.**

| Distribution | Species | No. specimens examined | No. collections examined | Substrate | | Coast | | Temperature range (°C) | Salinity range (psu) | Depth range (m) | Months female ovigerous (X = Northern Hemisphere; x = Southern Hemisphere ) | | | | | | | | | | | | Female body length at maturity (mm) | Supplementary habitat reports from the literature |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | Inorganic | Organic | Exposed | Protected | | | | J | F | M | A | M | J | J | A | S | O | N | D | | |
| North Atlantic and Mediterranean Sea | OCI | 77 | 16 | Rocks, seawall, hydrotechnical structures, hydrocarbon extraction platforms, acropod, cubes, fine sand, muddy sand and vermetid tubes, shell debris, pan scrubbers | Algae and seagrass: *Asparagopsis armata, Corallina elongata*, *C. officinalis*, *Cystoseira barbata, Gellidium pusillum*, *Laminaria hyperborea (*and *L. saccharina)* holdfast, *Posidonia oceanica*, *Zostera* spp., unidentified algae; echinoderm: surface and coelomic fluid of sea cucumbers *Stichopus regalis, Holothuria stellati, Cucumaria planci*; mollusk: mussel, *Brachidontes pharaonis*, *Mytilus galloprovincialis*, vermetid reef; polychaete: *Sabellaria alveolata* and *S. spinulosa* reef; sponge: *Halicondria; Ircinia fasciculata;* unidentified sponge debris; tunicate: *Botryllus schlosseri* | X | X | | | LI–200 | X | X | | | | | | X | | | | | 2.4–4.0 | Walker (1895); Chevreux (1900); Chevreux & Fage (1925); Jones (1948); Ruffo (1958); Bellan-Santini & Leyoyer (1973); Vader (1978); Lincoln (1979); Moore (1984); Koukouras *et al.* (1985); Arresti *et al.* (1986); Alexeev (1991); Sezgin *et al.* (2001); Sorbe *et al.* (2002); Kitsos & Koukouras (2003); Surugiu & Giurgiu (2006); Ersoy Karaçuha *et al.* (2009); Grimes (2009); Gozler *et al.* (2010); Uzunova (2011); Guerra-García *et al.* (2012); Fiorentino *et al.* 2012; Sezgin & Çil (2013); Bakir & Kataðan (2014); Bertocci *et al.* (2017); Çinar *et al.* (2017); Plicanti *et al.* (2017); Trayanova (2017); Gravina *et al.* (2018); Bonifazi *et al.* (2019); Sedano *et al.* (2020a,b) |

| Distribution | Species | No. specimens examined | No. collections examined | Substrate | | Coast | | Temperature range (°C) | Salinity range (psu) | Depth range (m) | Months female ovigerous (X = Northern Hemisphere; x = Southern Hemisphere ) | | | | | | | | | | | | Female body length at maturity (mm) | Supplementary habitat reports from the literature |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | Inorganic | Organic | Exposed | Protected | | | | J | F | M | A | M | J | J | A | S | O | N | D | | |
| SoutSouthern Hemisphere | FRE (coni-cal thumb-ed) | 65 | 12 | bedrock | Algae: *Macrocystis* | x | x | | | LI–43 | | | | | | | | | | | | | 3.0–4.0 | K. H. Barnard (1932); Stephensen (1949) |
| | FRE (cubic thumb-ed) | 14 | 9 | | Algae: *Caulerpa brownii*, *Codium* sp., *Cystophora torulosa*, unidentified green algae | | x | | | LI–7 | | | | | | | | | | | | | | |
| | GON | 76 | 15 | | Bryozoans, hydroids, sponges, alcyonarians | x | | | | 30–584[1] | | x | | | | | | | | | | | 13.8–20.0 | Bellan-Santini (1972); Dauby *et al.* (2001); Keil *et al.* (2008); De Broyer *et al.* (2009) |
| | LOW | 197 | 2 | | Unidentified algae and barnacles in *Durvillea* zone | x | | | | 7 | | | | | | | | | | | x | | 2.5–5.1 | |
| | MOO | ~1550 | 40 | Bedrock, boulders, gravel, sand | Algae: *Ascoseira mirabilis*, *Desmarestia anceps*, *D. chordalis*, *Phyllogigas grandifolius*, *Iophon/Phyllophora*; *Lithothamnia,* Rhodophyceae; bryozoan: unidentified; sponge: unidentified | x | | ≤2 | | 2–10 (pos-sible max 20) | | | x | x | | x | | | | | | | 2.9–4.5 | Thurston (1974b) |
| | MUL | 42 | 8 | | Algae: *Macrocystis* | x | | | | LI–15 | x | | | | | | | x | | | | | 6.0–9.1 | De Broyer *et al.* (2009) |
| | ORI | 3 | 1 | | Algae: *Durvillea antarctica* holdfast | x | | | | 8 | | | | | | | | | | | | x | 9.8 | |
| | WAN | ~286 | 56 | Bedrock, boulders, gravel, stones, sand | Algae: *Ascoseira mirabilis*, *Desmarestia anceps*, *D. chordalis*, *Phyllogigas grandifolius*, *Iophon/Phyllophora*; *Lithothamnia*, Rhodophyceae; bryozoan: unidentified; sponge: unidentified | x | x | ≤2 | | LI–31 | | x | x | | | | | x | | | x | | 5.9–9.7 | Chevreux (1913); Bellan-Santini & Ledoyer (1973, 1974); Thurston (1974a,b); De Broyer *et al.* (2009) |

[1] One collection from a vertical haul that covered an extreme depth range of 0-1828 m is excluded as the depth at which *H. goniamera* was present is unknown

Portugal: Pico-Faial Channel, Azores (38°31′19″N, 30°54′45″W), 130 m, 14 Aug. 1888, E. Chevreux, coll., Hirondelle station 226, 1 ♀ (MNHN Am. 2660); Peniche, on *Corallina elongata* from infralittoral fringe to 14 m, 8 Oct. 1979, J. C. Marques, coll., 2 ♂♂, 2 ♀♀ (CMN A2019.0055).

Romania: Agigea, dredge amongst algae, 11 m, 4 Jan. 1936, S. Carausu, coll., 2 ♀♀ (MNHN Am. 2663).

Croatia: Hvar (Lesina), 1865, C. Heller, coll., 2 ♀♀ (NHMW 20620).

**Remarks.** The propodus of gnathopod 2 is densely plumose at all sizes and in both sexes**.** This, along with the near lack of overlap of the merus over the carpus of pereopods 3–4 instantly distinguish *P. ocia* from any species of *Jassa***.** *Plumulojassa ocia* is synonymous with *Jassa dentex* (Czerniavski, 1868)**.** This was recognized by Della Valle (1893) and Sowinski (1897) but Stebbing (1906) recognized *J. dentex* as separate**.** Sexton & Reid (1951) explained Stebbing's taxonomic confusion which was based on his mis-interpretation of illustrations made by Walker (1893)**.** Chevreux & Fage (1925) and others followed Stebbing (1906) uncritically, despite Walker (1910) having pointed out that the original species description referred to the distinctive double toothing on the second gnathopod in *P. ocia***.** Stebbing (1906), followed by Stephensen (1942) also considered that *J. dentex* was synonymous with *Podocerus odontonyx* Sars, 1894 (now synonymous with *J. pusilla* (Sars, 1894) (see Conlan 1990))**.** However, it is unmistakably *Plumulojassa ocia* (Fig. 33D)**.** *Plumulojassa ocia* is so distinctive that literature records are probably taxonomically correct and so are included in maps and habitat information (Fig. 1, Table 3, Supplementary Table S1).

According to Joan Ellis (NHM), "I have not found the type(s) of this species, nor any evidence that it was ever in the NHM collection, in spite of Bate's (1862) indication to the contrary**.** Also, in 1895 A. O. Walker (Ann. Mag. Nat. Hist. (6) 15:473) stated that the specimen was not in the collection that Bate presented to the Museum**.** I suppose one must assume that the type material of *Jassa ocia* is lost." (personal communication, 31 July 1984). This species has been widely collected (Table 3) but long confused as a species of *Jassa* (Supplementary Table S1). In order to assist future researchers with correct identification, a neotype is erected herein from material from Cornwall, England, which was located as close as possible to the type location (Ilfracombe, Devon, England). This neotype is fully described and illustrated and is housed at the NHM, fulfilling all subsections of ICZN Article 75.3, Qualifying Conditions for erection of a Neotype (https://code.iczn.org/types-in-the-species-group/article-75-neotypes/?frame=1).

## Transferral of *Jassa barnardi* to *Ventojassa frequens* and description of the type species of *V. frequens*

### *Ventojassa frequens* (Chilton, 1883)

(Figs 8–16)

*Podocerus frequens* Chilton, 1883, 85, Plate III, Fig. 2; Thomson & Chilton, 1886, 143; Shaw & Poore, 2016, 37–38
*Podocerus latipes* Chilton, 1884, 258, Plate XIX, Fig. 2; Thomson & Chilton, 1886, 143; Shaw & Poore, 2016, 38
*Jassa frequens* (Chilton), Stebbing, 1906, 656; Chilton, 1921, 227, Fig. 4; Schellenberg, 1931, 253; 1953, 119–120, Fig. 6; J. L. Barnard, 1958, 85
*Jassa pusilla*: K. H. Barnard, 1932, 242–243
*Jassa barnardi* Stephensen, 1949, 50–52, Figs 21, 22; J. L. Barnard, 1958, 84
*Ventojassa frequens* (Chilton), J. L. Barnard, 1972, 135–137, Figs 74–75; Griffiths, 1975, 138, 140; Gonzalez, 1991, 58

**Description of male.** Type: based on CMNZ 2015.149.86 (Fig. 8)**.** (*Character states for the two males in Figs 10 and 11 added in brackets and italics if the appendage is obscured in the type)***.** Length 4.0 *(3.6, 3.3)* mm**.**

*Antenna 1*: accessory flagellum 2 articles (right), 3 articles (left)**.**

*Antenna 2*: similar in length and width to antenna 1, with filter setae in the male as long as in the juvenile and female; flagellum 7 articles, the last as long as the second last, article 1 25% of full length, articles 5–7 posterodistally spinose**.**

*Mouthparts* obscured *(Mandible: articles 2 and 3 with a dorsal fringe of setae; raker spines, 4 right, 2 left. Maxilla 1: inner plate bearing a few short, fine setae; palp without setae at the base of article 1, article 2 with 1 row of facial setae distally)***.**

*Gnathopod 1*: coxae to propodus obscured *(coxa rectangular, coxal margins, anterior 70% of dorsal length, ventral margin gradually rounded; basis, anterior margin without a fringe of setae laterally, with only a few setae at the anterodistal junction with the ischium, with 1 long seta on the posterior margin; carpus, length 90% of propodus length, posterior lobe 60% of anterior margin length, anterodistal setal cluster short, 5% of the anterior margin length; propodus, palm convex, defined by 1 spine)*; dactyl cusped distally, without facial striations**.**

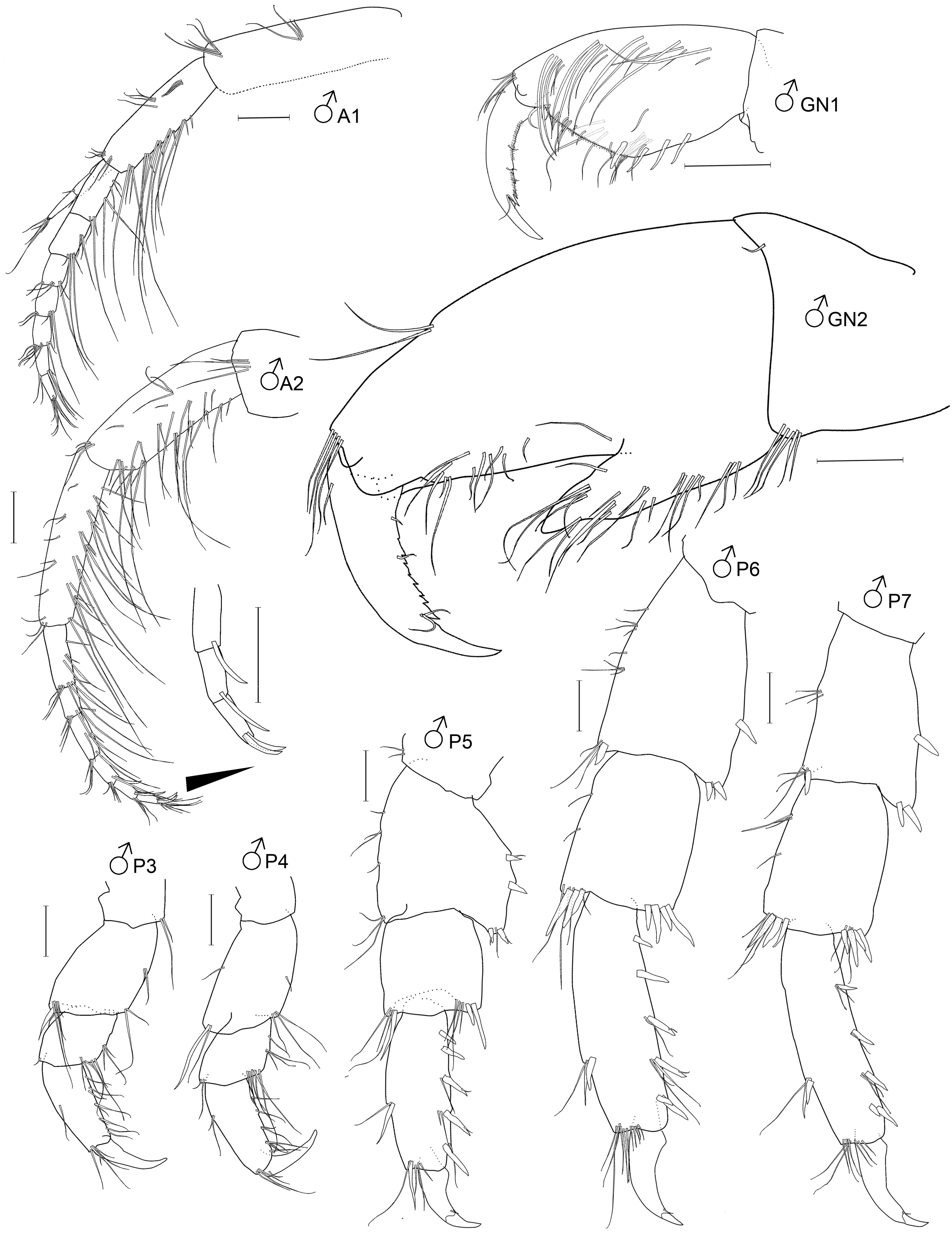



**FIGURE 8.** *Ventojassa frequens* (Chilton, 1883). Type, adult male, 4.0 mm, CMNZ 2015.149.86, Lyttelton Harbour, New Zealand, date unknown, Charles Chilton, coll. Drawings taken from the mount of the whole animal. Only portions of appendages that were clearly visible could be drawn. Setae obscured on the posterior of antenna 1 peduncle article 2 and gnathopod 1 carpus. Scale 0.1 mm.

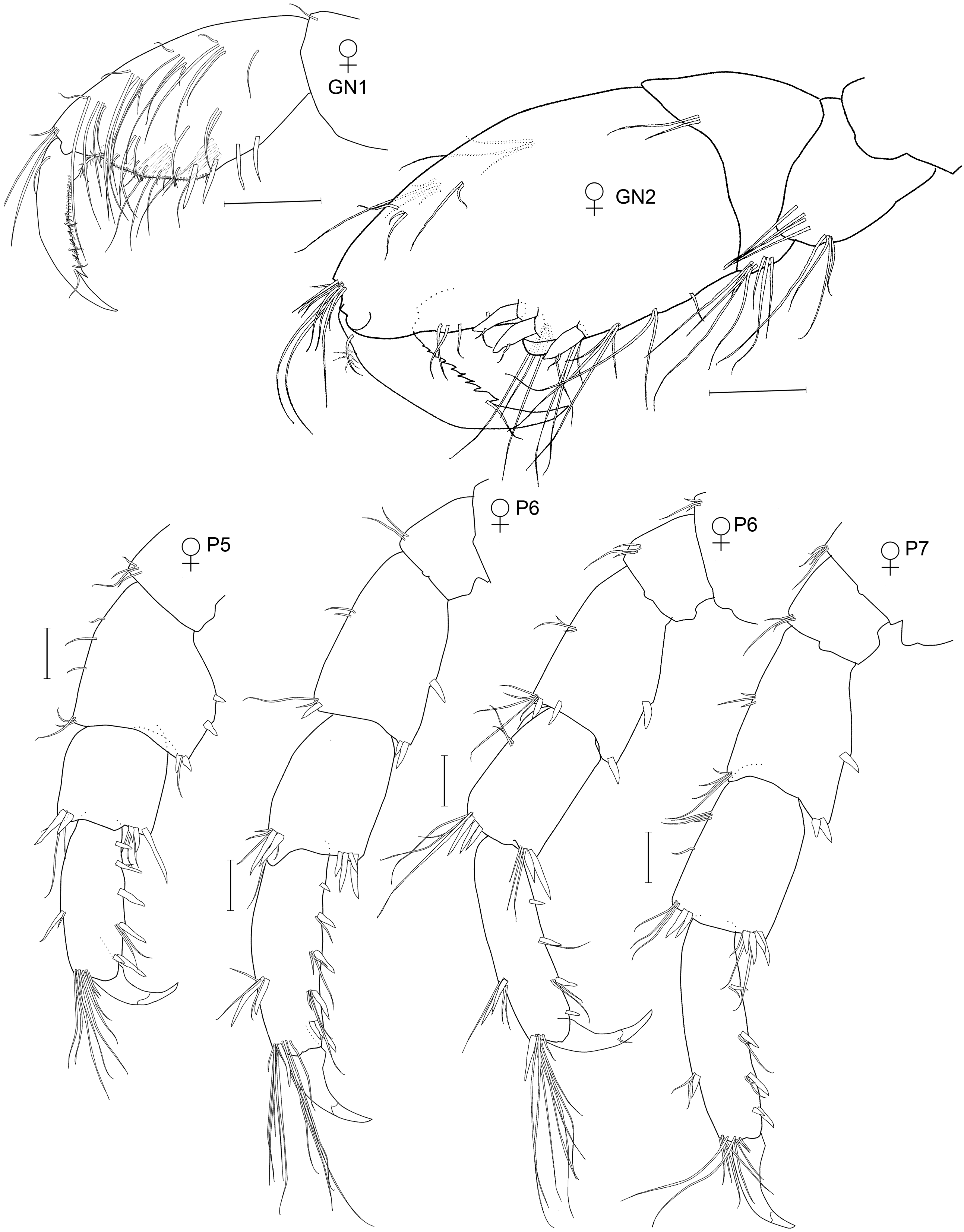



**FIGURE 9.** *Ventojassa frequens* (Chilton, 1883). Type, adult female, 4.0 mm, CMNZ 2015.149.85, Lyttelton Harbour, New Zealand, date unknown, Charles Chilton, coll. Drawings taken from the mount of the whole animal. Only portions of appendages that were clearly visible could be drawn. Scale 0.1 mm.

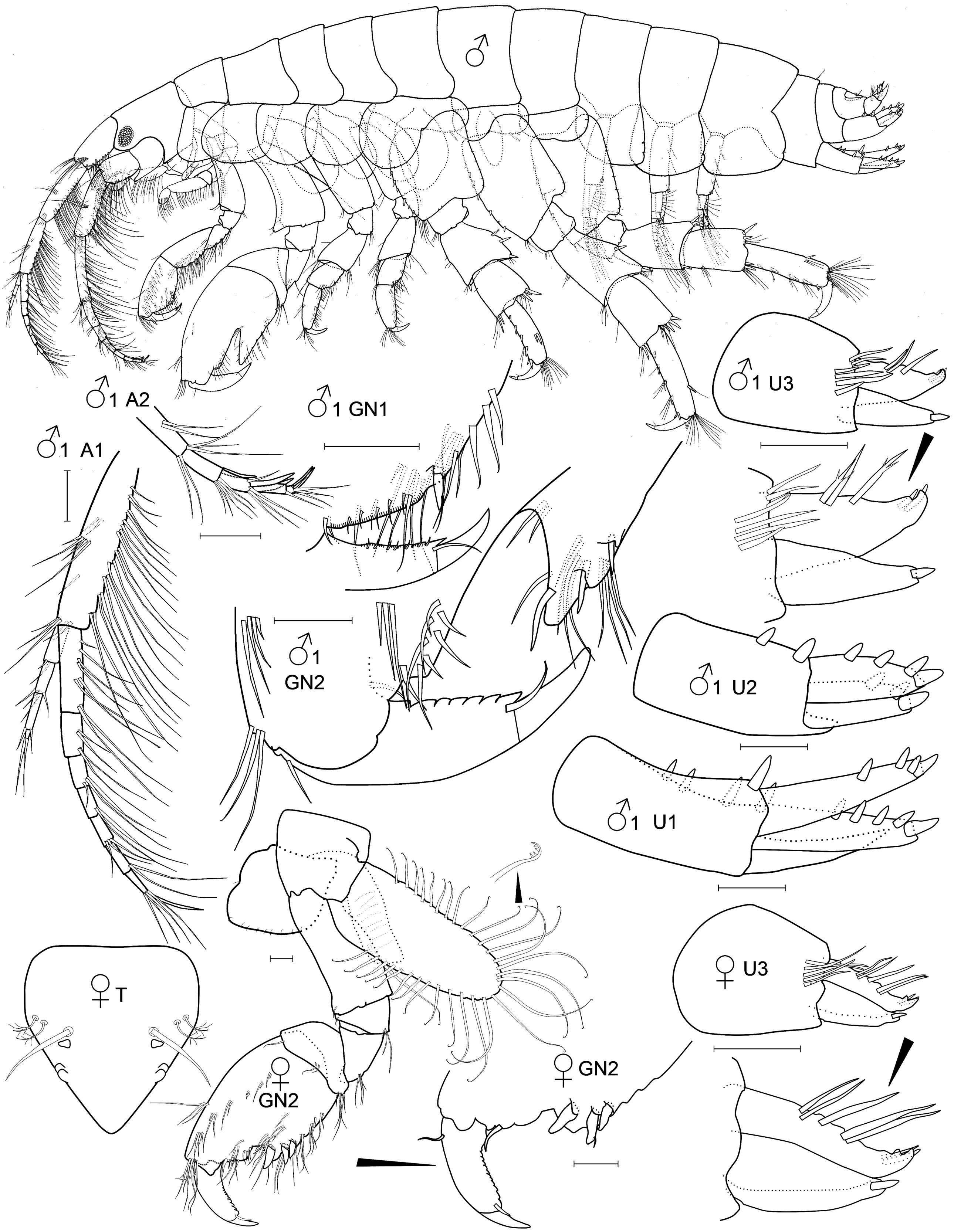



**FIGURE 10.** *Ventojassa frequens* (Chilton, 1883). Male, 3.6 mm, male 1, 3.3 mm, and adult female, 4.0 mm, Nightingale Island, Tristan da Cunha, 8 February 1938, E. Sivertsen, coll., ZMUO F3934a, station no. 114. Lateral views: whole body and antenna 1; dorsal view: telson; other views medial. Scale 0.1 mm.

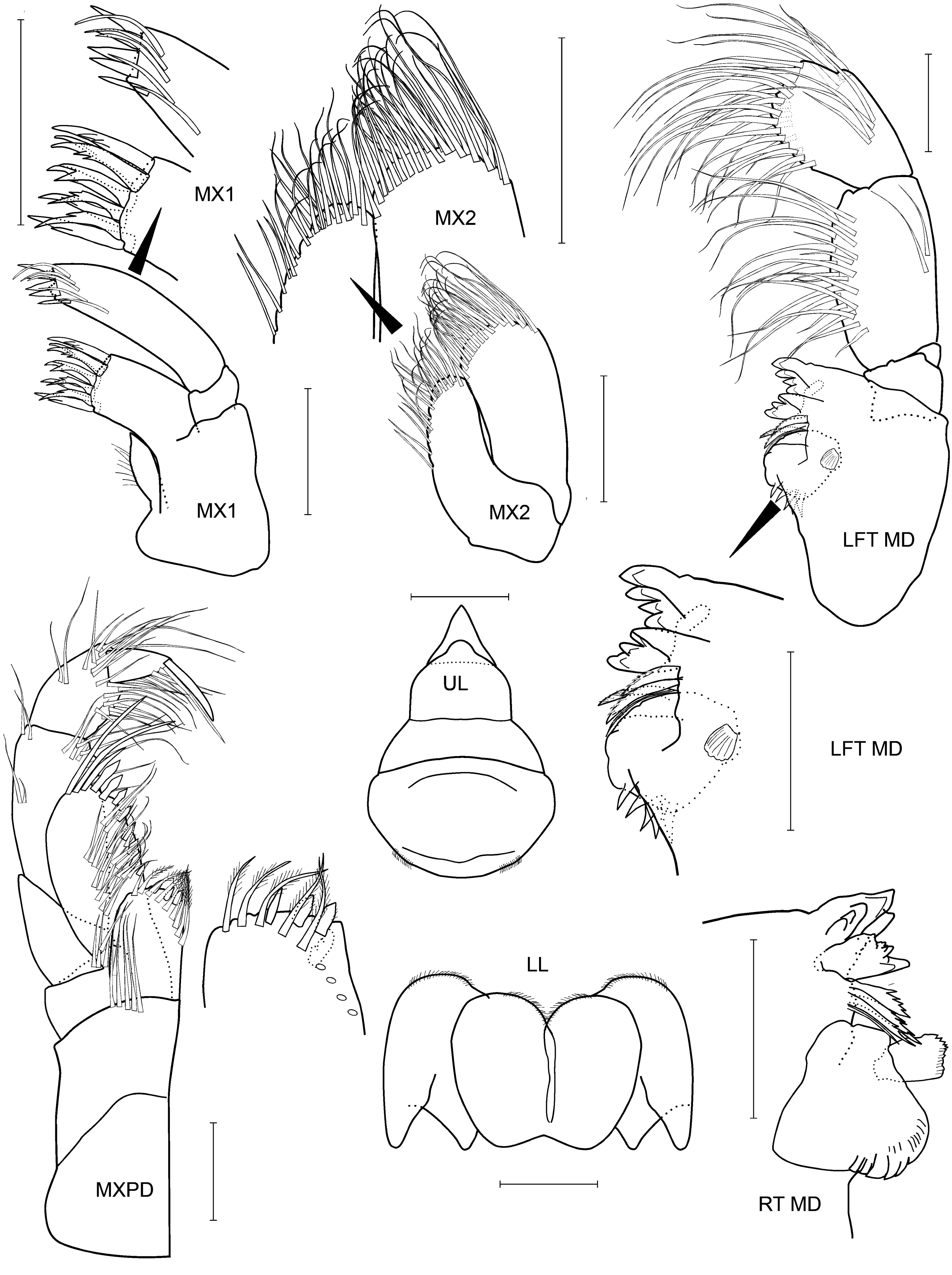



**FIGURE 11.** *Ventojassa frequens* (Chilton, 1883). Male 1, 3.3 mm, Nightingale Island, Tristan da Cunha, 8 February 1938, E. Sivertsen, coll., ZMUO F3934a, station no. 114. Mouthparts. Frontal view: upper lip; lateral views: maxillae 1 and 2, left mandible; other views medial. Scale 0.1 mm.

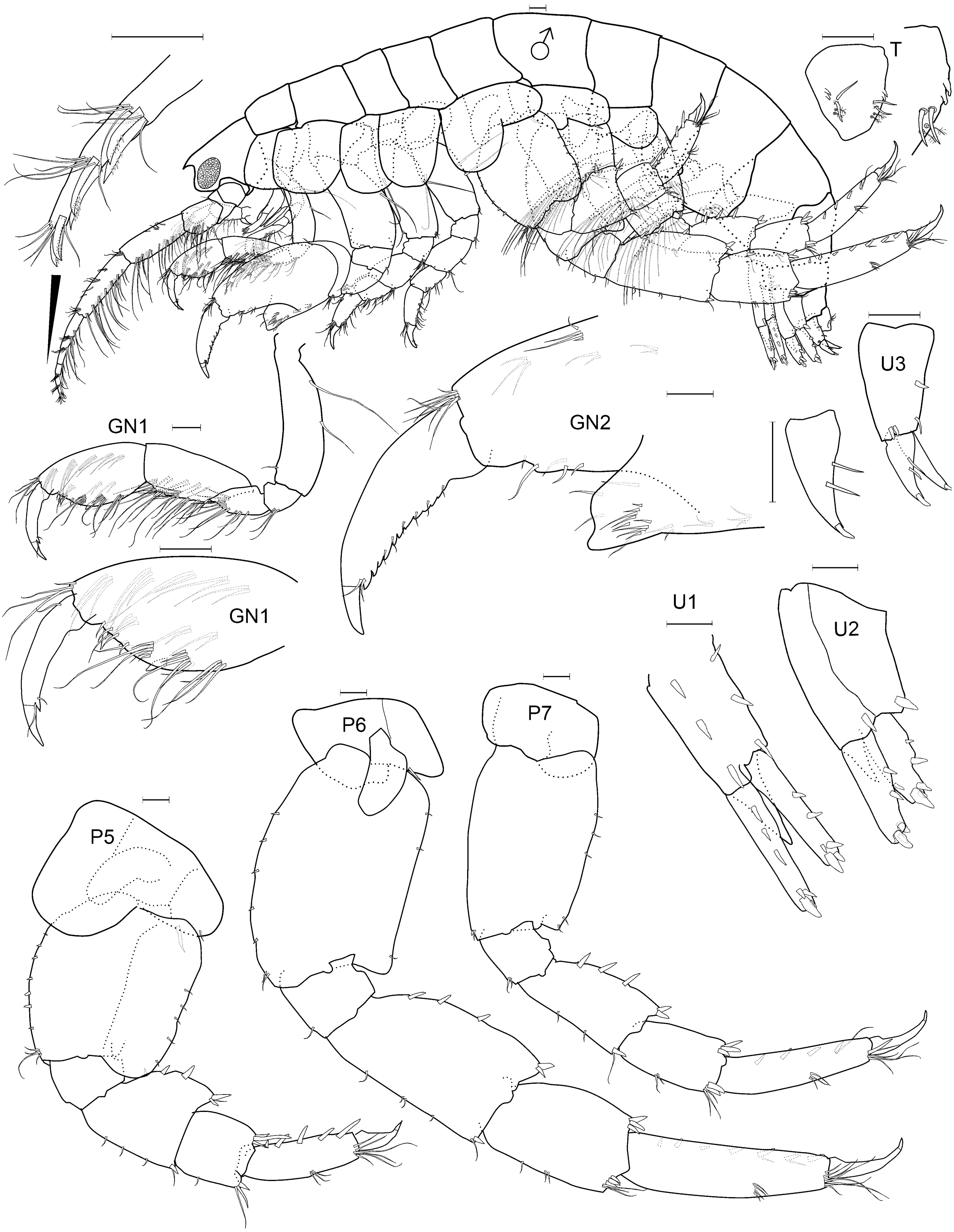



**FIGURE 12.** *Ventojassa frequens* (Chilton, 1883). Male, 4.5 mm. St. Kilda Rocks, Kaikoura, New Zealand (42.45°S, 173.7°E), 8 November 1973, G. D. Fenwick, coll., AM P.25948. On the green alga *Caulerpa brownii* (C. Agardh) Endlicher at 3 m depth. Lateral views: whole body, gnathopods 1 and 2, pereopod 5 and uropod 3; dorsal view: telson; other views medial. Scale 0.1 mm.

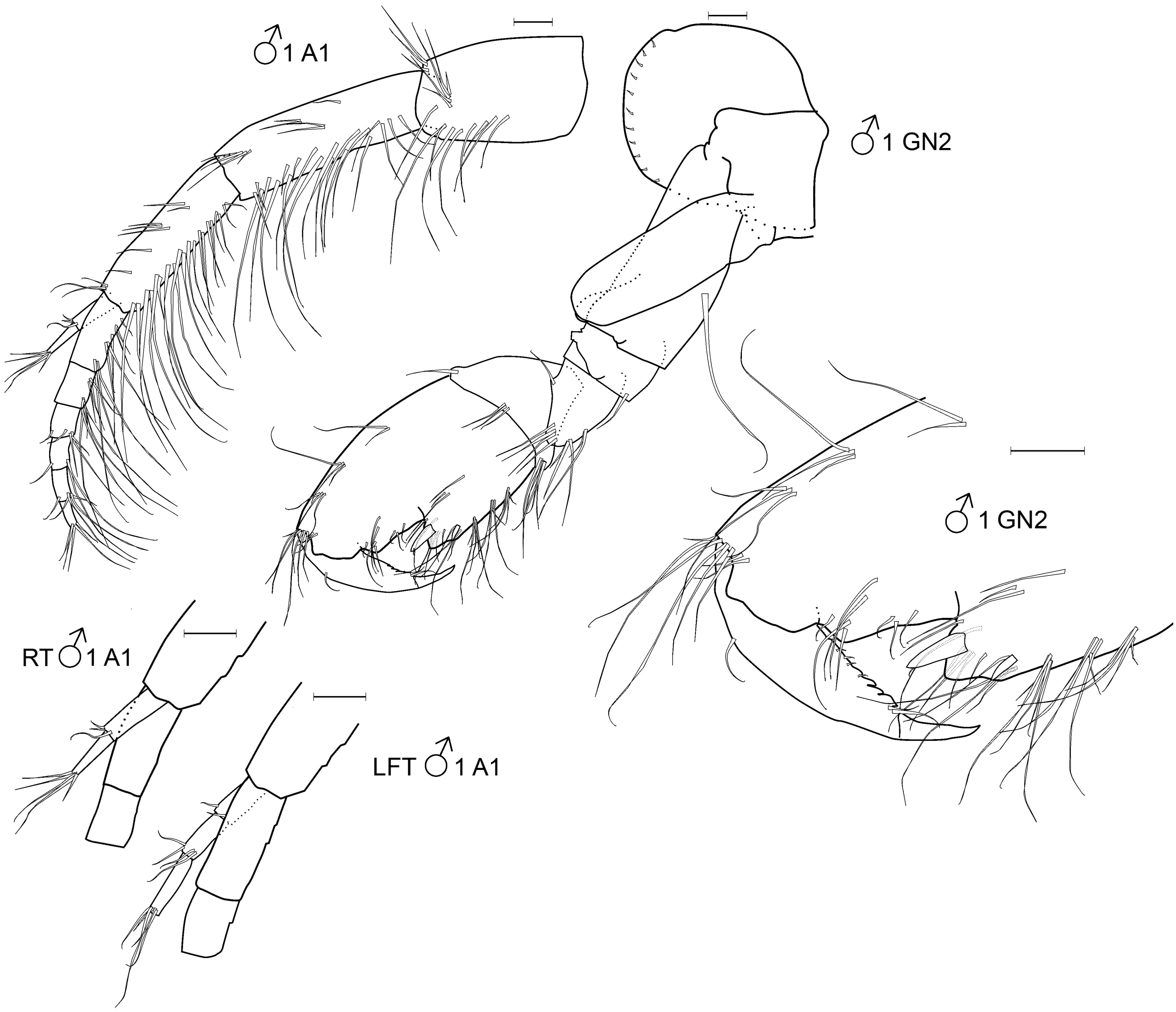



**FIGURE 13.** *Ventojassa frequens* (Chilton, 1883). Male 1, 4.0 mm. St. Kilda Rocks, Kaikoura, New Zealand (42.45°S, 173.7°E), 8 November 1973, G. D. Fenwick, coll., AM P.25948. On the green alga *Caulerpa brownii* (C. Agardh) Endlicher at 3 m depth. Lateral view: full antenna 1 and left antenna flagellum; other views medial. Scale 0.1 mm.

*Gnathopod 2: (with a gill)*; coxae to antero-proximal part of propodus obscured *(coxa not deeper posteriorly, coxal margins, anterior 100% and posterior 100% of ventral length, ventral margin gradually rounded; basis, anterolateral flange without a row of long, simple filter setae; carpus, anterior margin 50% the length of the propodus anterior margin, posterior lobe with a cluster of short distal setae; propodus, anterior margin with only a few distal clusters of short setae (setae about 20% of basis width));* propodus without hinge teeth, palm sparsely setose throughout, without a palmar defining spine, thumb conical in shape, 20% the length of the propodus and carpus combined; dactyl shorter than propodus, not expanded near the hinge, tip apposing the thumb tip, inner margin cusped**.**

*Pereopod 3*: coxa and basis obscured *(coxa deepest centrally; basis wider than the gnathopod 1 basis, anterior margin shallowly convex);* merus, anterior margin with one seta midway and cluster of setae distally, article width 70% of length; carpus barely 20% overlapped by merus; propodus width 47% of length, not posteriorly spinose**.**

*Pereopods 5–7*: proximally obscured *(robust, basis, merus, carpus and propodus all bearing spines singly or in clusters; at least one basis posterodistally produced)*; propodus not strongly expanded anteriorly; dactyl not facially serrated, posterior (outer) margin not cusped distally, anterior (inner) margin setose only at the junction of the unguis**.**

*Pleopods*: each with 2 coupling hooks *(rami short, ≤ depth of the pleon)***.**

*Urosome*: segment 1 with pair of dorsally erect setae**.**

*Uropod 1*: obscured *(posteroventral spinous process underlying 83% of the inner ramus, inner and outer rami with 2 mid-dorsal spines, outer ramus with 3 mid-dorsal spines, inner ramus with 1, in addition to the distal spine group)***.**

*Uropod 2*: obscured *(peduncle, posteroventral spinous process underlying 25% of the inner ramus)***.**

*Uropod 3*: partially obscured *(peduncle not mid-ventrally setose, without mid-dorsal spines, without spines at the insertion of the rami, but with a cluster of setae distolaterally);* outer ramus with 2 erect setae mid-dorsally *(and tipped by 2 small, straight spines distolaterally and adjacent small cusp; inner ramus not mid-dorsally spinose or setose, with a single apical spine)***.**

*Telson*: partially obscured, with a pair of strong cusps dorsolaterally *(and a single cusp at each dorsal apex, accompanied by a strong, erect seta and pair of small plumose setae).*

**Condition.** Whole body slide mounted; missing one pereopod 7.

**Description of adult female.** Type: based on CMNZ 2015.149.85 (Fig. 9)**.** Descriptions of characters not visible in the type are in brackets and italics and based on the adult female in Fig. 10**.** Length 3.8 *(4.0)* mm**.** Character states as in the male except as follows.

*Brood plates*: obscured *(relatively slender, setae well separated, abundant, hook-tipped*)**.**

*Antennae 1 and 2*: similar in length, article 5 without plumose setae, simple filter setae as long as those of the male**.**

*Gnathopod 2*: propodus without a hinge tooth, palm 40% of the posterior margin, setae not so dense as to obscure the palm's shape, defined by 3 medial spines.

**Condition.** Whole body slide mounted**.** Without right antenna 2 and pereopods 5–7, left pereopods 5 and 7.

**Variation.** Maximum body length: male 4.5 mm, female 4.5 mm**.** There is some variation in the number of accessory flagellum articles on antenna 1**.** There can be 2 or 3 articles and this can also vary between right and left sides of an animal (Fig. 13)**.** The females and small males can have 3 palmar defining spines on the propodus of gnathopod 2 rather than 2**.** The number of erect setae on the outer ramus of uropod 3 varies from 1 to 5**.**

**Type material examined**. Type, conical thumbed ♂, CMNZ 2015.149.86, Lyttelton Harbour, New Zealand, date unknown, Charles Chilton, coll**.** Type, adult ♀♀, CMNZ 2015.149.85 and 84, Lyttelton Harbour, New Zealand, date unknown, Charles Chilton, coll.

**Other material examined**. New Zealand: Lyttelton Harbour, date unknown but possibly 1883 or earlier, C. Chilton, coll., 3 conical thumbed ♂♂, 2 cubic thumbed ♂♂, 18 adult ♀♀, 5 juveniles (CMNZ 2015.149.575...604); Lyttelton, 28 Mar. 1928, 1 conical thumbed ♂, 5 adult ♀♀ (SNM); Brighton, Otago, New Zealand, Jan. 1890, C. Chilton, coll., 1 cubic thumbed ♂ (CMNZ 2015.149.2161); Stewart I., date unknown, H. B. Kirk, coll., 1 adult ♀ (CMNZ 2015.149.2116); Huaroa Point, Whangaparaoa Peninsula, Auckland Province, New Zealand (36.595°S, 174.836°E), 16 Feb. 1968, J. L. Barnard, coll., NIWA station E979, JLB NZ-14, low water level, on heavy stand of algae, including *Cystophora torulosa* and bases of dying *Codium* sp., 1 cubic thumbed ♂ (NIWA 7825), 1 adult ♀ (NIWA 7835), 1 cubic thumbed ♂ (NIWA 7839); St. Kilda Rocks, Kaikoura (42.42°S, 173.7°E), 8 Nov. 1973, G. D. Fenwick, coll., 3–4 m depth on *Caulerpa brownii* and green algae, 8 cubic thumbed ♂♂ (AM P.25948) and ~50 specimens (MNZTPT CR.007823); Fraser Rocks, Tapeka, Bay of Islands, Northland, 15 Nov. 1995, 0–1 m, collector unknown, 31 conical thumbed ♂♂, 43 adult ♀♀, 23 juveniles (AuM MA134534).

Tristan da Cunha: type series for *Jassa barnardi* Stephensen, 1949: Norwegian Scientific Expedition, E. Sivertsen, coll., Nightingale station 113, 8 Feb. 1938, 19 conical thumbed ♂♂, 37 adult ♀♀, 56 juveniles (SNM), Nightingale station 114, 8 Feb. 1938, 0 m, 6 conical thumbed ♂♂, 21 adult ♀♀, 7 juveniles (UiO F3934) and 1 conical thumbed ♂, 1 adult ♀ (CMNC 1994–0444), Inaccessible station 154, 25 Feb. 1938, 40 m, 1 conical thumbed ♂, 1 adult ♀, 10 juveniles (UiO F3898), Inaccessible station 156, 29 Feb. 1938, 5–8 m, 3 adult ♀♀ (UiO F3897), station unknown, 30 Dec. 1939, 1 juvenile (SNM).

Chile: Caleta Bruna, date unknown, collector unknown., 1 conical thumbed ♂, 1 adult ♀, 1 juvenile (MNHN Am. 2649); Valparaiso, collector and date unknown, 1 conical thumbed ♂, 8 adult ♀♀, 2 juveniles (NRM 3786).

South Africa: False Bay, date unknown, C. Griffiths, coll., station FAL 604G, 1 cubic thumbed ♂, 1 juvenile ♂ (UCT).

**Remarks**. *Ventojassa frequens* does not exhibit sexual dimorphism in the antenna 2 but does in the gnathopod 2 and enlargement of pereopods 5 and 6 relative to 7**.** The pereopod enlargement is particularly pronounced in large females though large males show this enlargement to a lesser extent**.**

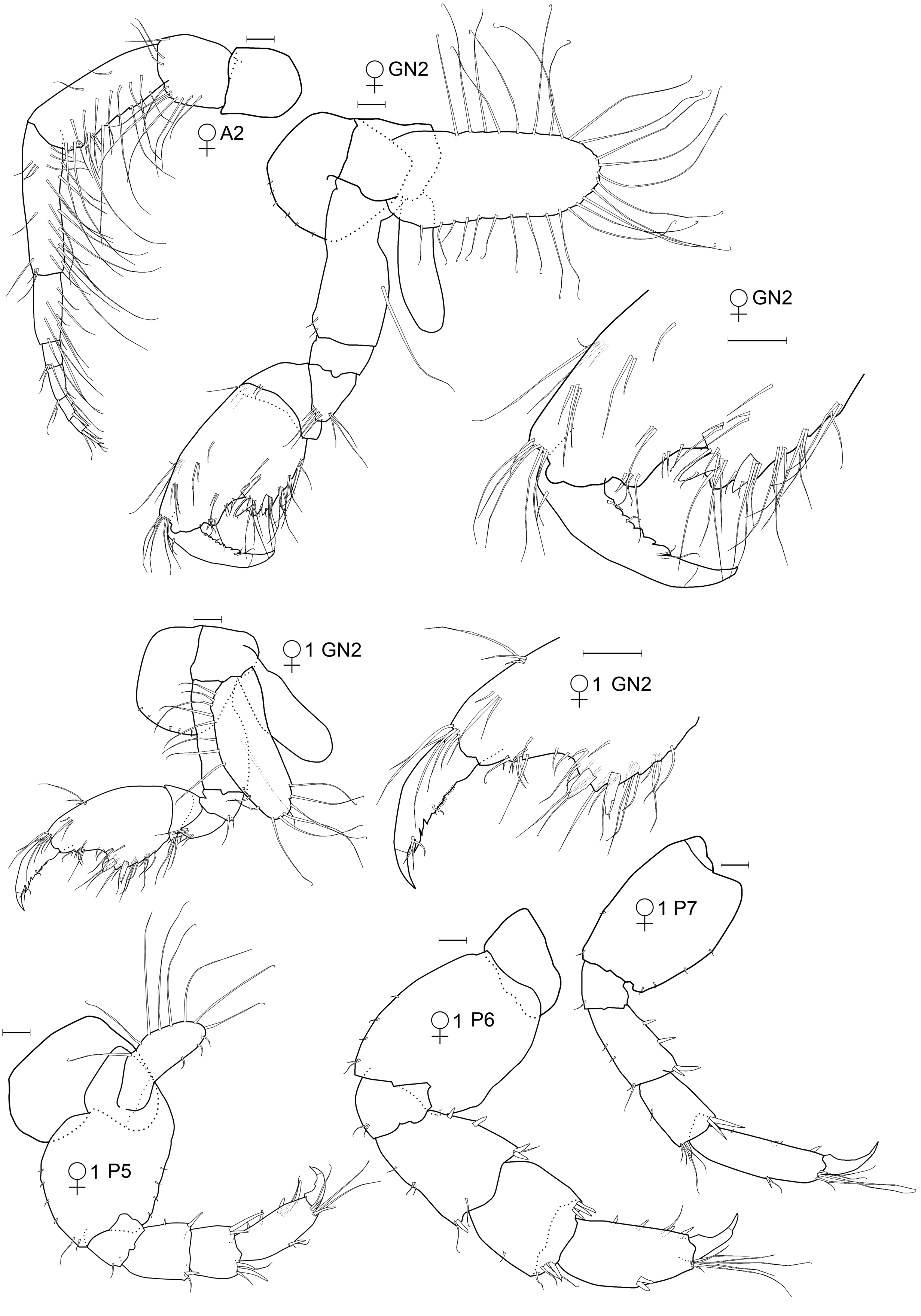



**FIGURE 14.** *Ventojassa frequens* (Chilton, 1883). Adult female, 3.0 mm and adult female 1, 3.5 mm. St. Kilda Rocks, Kaikoura, New Zealand (42.45°S, 173.7°E), 8 November 1973, G. D. Fenwick, coll., AM P.25948. On the green alga *Caulerpa brownii* (C. Agardh) Endlicher at 3 m depth. All views medial. Scale 0.1 mm.

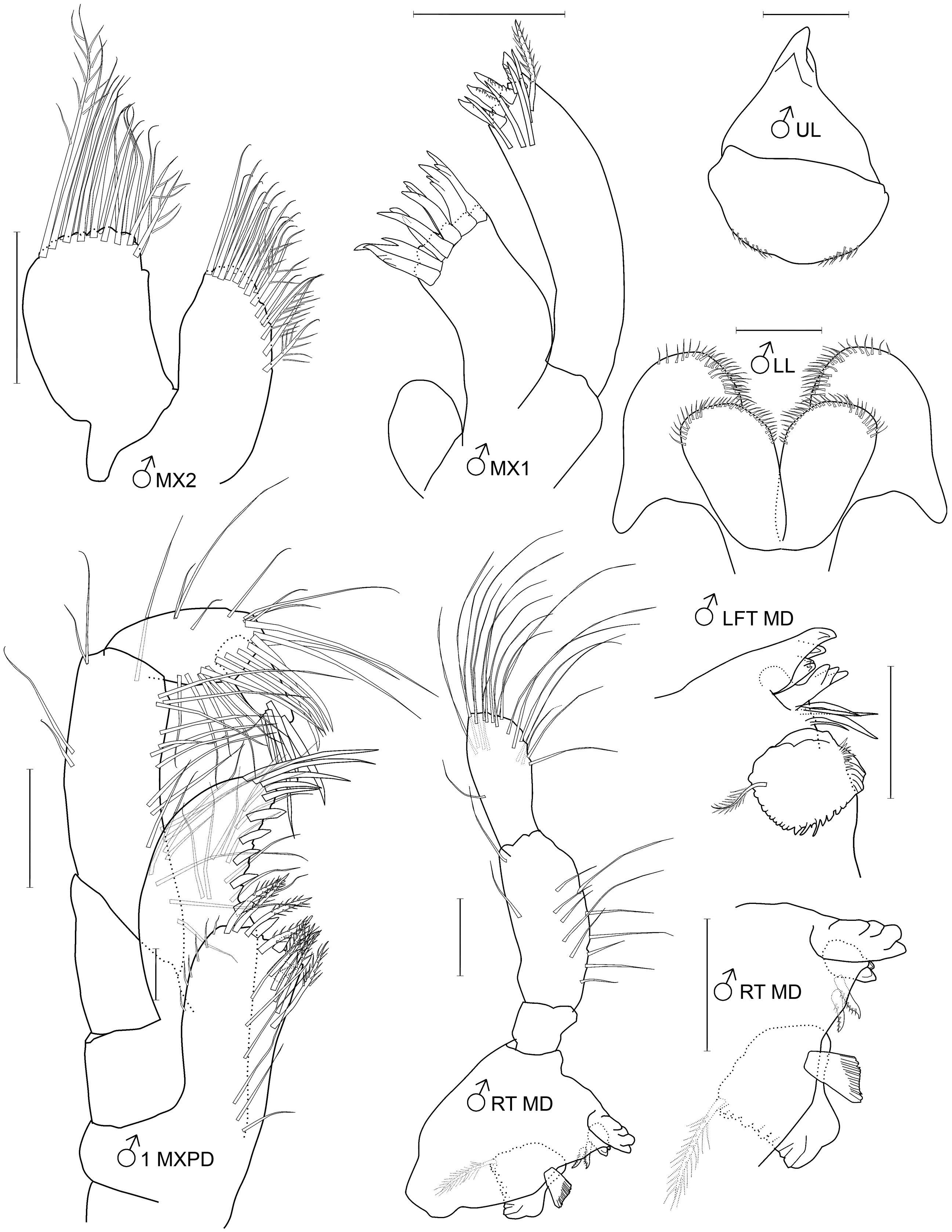
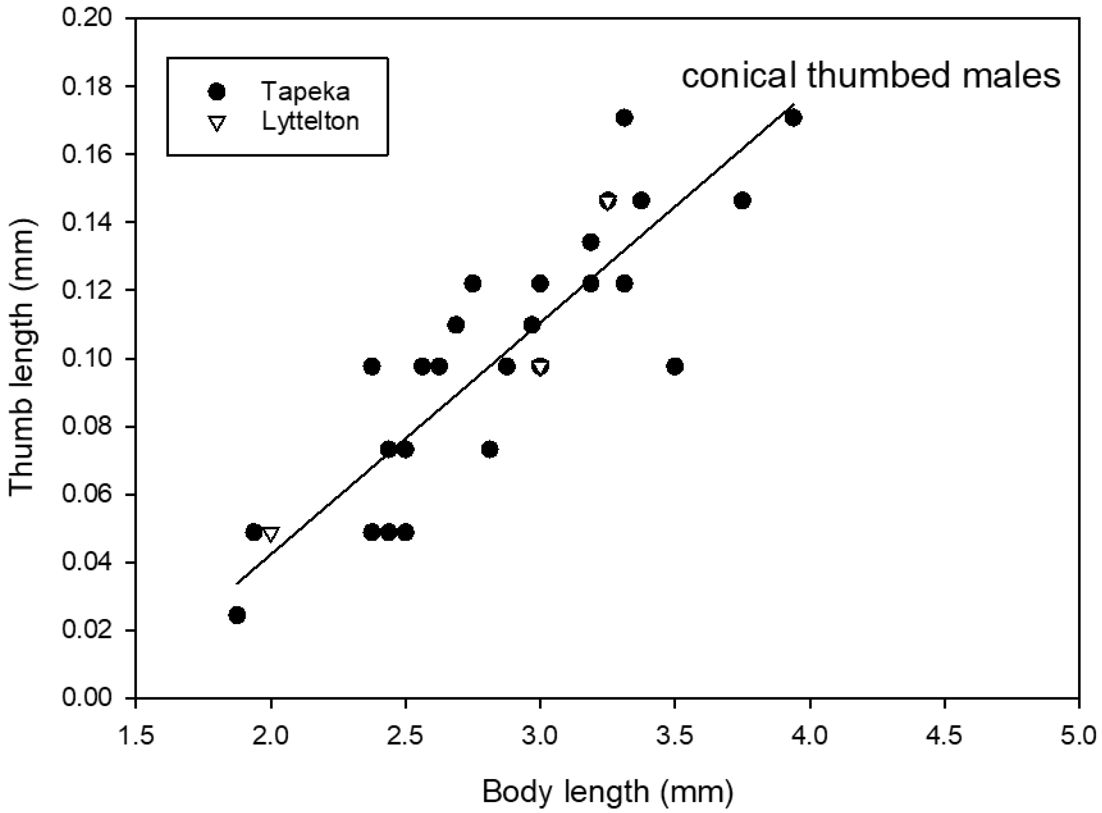



**FIGURE 15.** *Ventojassa frequens* (Chilton, 1883)**.** Male, 4.5 mm and male 1, 4.0 mm**.** St. Kilda Rocks, Kaikoura, New Zealand (42.45°S, 173.7°E), 8 November 1973, G. D. Fenwick, coll., AM P.25948**.** On the green alga *Caulerpa brownii* (C. Agardh) Endlicher at 3 m depth. Mouthparts**.** Frontal view: upper lip; lateral views: maxilla 1 and right mandible; other views medial**.** Scale 0.1 mm.



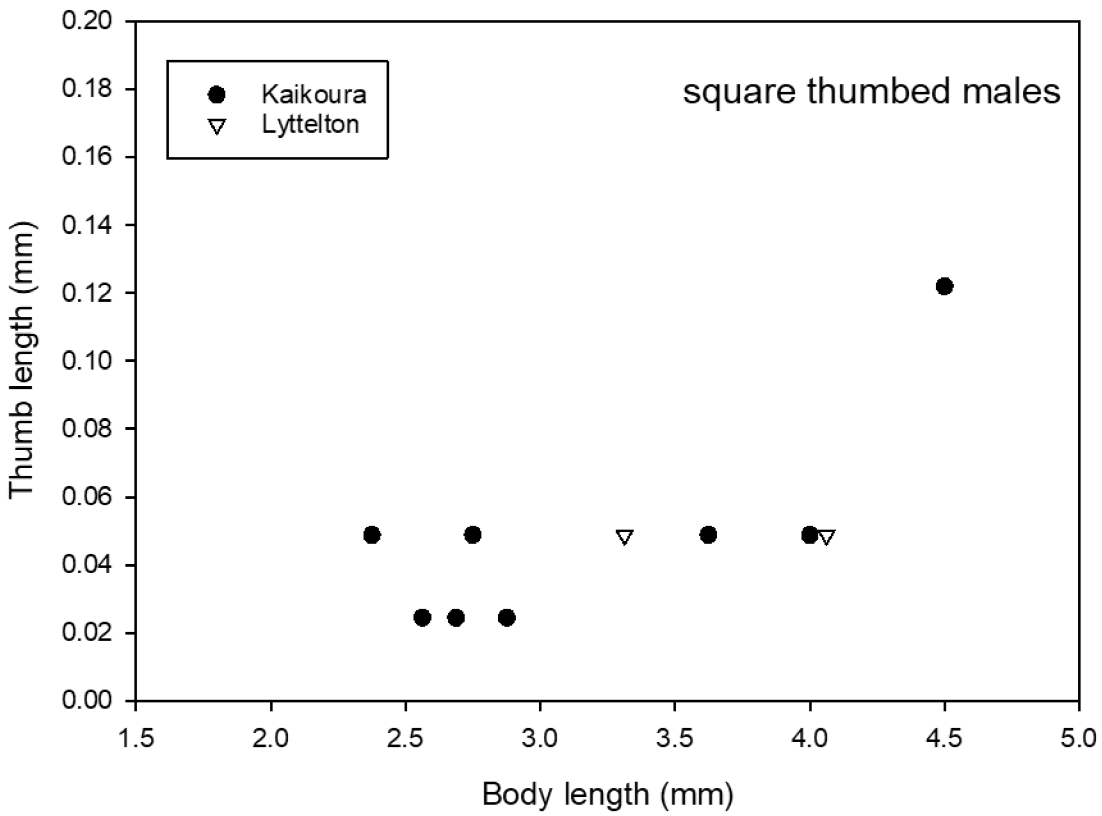




**FIGURE 16.** *Ventojassa frequens* (Chilton, 1883). Comparison of thumb length relative to body length for the conical and cubic thumbed males from Chilton's collection at Lyttelton, N.Z. and two collections at Tapeka and Kaikoura, N.Z. about 100 years later. Linear regression assumptions passed for the conical thumbed males at Tapeka. Linear regression statistics: male, thumb length = -0.094 + 0.068 x body length, $r^2 = 0.754$, $n = 31$.

Chilton recognized two male morphs based on the male's thumb shape and the expansion of the pereopods 5 and 6 (especially pereopod 6): conical thumb with "stout" pereopods 5 and 6 in his then named *Podocerus frequens* Chilton, 1883 and cubic thumb with "much expanded" pereopods 5 and 6 in his then named *Podocerus latipes* Chilton, 1884. However, Chilton (1884) had reservations about the two forms being different species, stating that *Podocerus latipes* "...may prove to be only a variety of *P. frequens*." Chilton (1921) added some collecting information for these specimens, stating that they were fairly common in Lyttelton Harbour at the roots of *Macrocystis* and other seaweeds above low-water level. Chilton (1921) also pointed out that Stebbing (1906) had synonymized the two species as *Jassa frequens* (Chilton, 1883), regarding the cubic thumbed morph illustrated by Chilton (1884) to be the male and seemingly ignoring the conical thumbed male illustrated earlier by Chilton (1883).

Chilton's type material listed in Shaw & Poore (2016) were kindly lent by the Canterbury Museum along with material from other locations listed above. The single male specimen that Chilton (1883) illustrated in his type description and Plate III, Fig. 2 was of a very small conical thumb (his Fig. 2b) and this drawing does not correspond with the long conical thumb borne by the male slide mounted and designated type CMNZ 2015.149.86 (Fig. 8). Chilton (1883) did note in his new species description that "The process on the propodos of second gnathopoda of male varies in size in different specimens, and is often longer and more distinct than shown in fig. 2b." The other two type slides CMNZ 2015.149.84 and 85 are whole body mounts of adult females, but neither corresponds with Chilton's (1883) Fig. 2, either. Chilton's label on CMNZ 2015.149.84 states that the specimen is a male but it is actually an adult female with setose brood plates.

Chilton (1921) also illustrated the cubic thumbed type of male gnathopod 2 in Fig. 4A, p. 228 and this drawing matches the slide mounted male gnathopod 2 on Chilton's slide CMNZ 2015.149.2161 from Brighton, Otago, New Zealand, collected Jan. 1890. Chilton's (1921) Figs 4B, C correspond to dissected appendages of a female from Stewart Island, collected by H. B. Kirk (CMNZ 2015. 149.2116). Chilton's (1921) Fig. 4D appears to be a pereopod 5 (not 6 as stated in the figure caption) but does not exactly match the pereopods on either of these slide mounts, showing fewer spines on the anterior margin of the basis.

*Jassa barnardi* Stephensen, 1949 from Tierra del Fuego (type shown in Figs 10 and 11) is clearly the same as Chilton's conical thumbed male (type male shown in Fig. 8). It has the same slender antennae, slender propodus of gnathopod 1, conical thumb on the propodus of gnathopod 2, minimal overlap of the merus over the carpus on pereopods 3 and 4 and wide merus and carpus on pereopods 5–7 with strong spination on the posterior margins. The same features of the urosome, not visible on Chilton's slide mount of the type is evident in his un-mounted specimens preserved in alcohol (CMNZ 2015.149.575...604). This forces its synonymy under *Ventojassa frequens*.

Additional illustrations of specimens from more recent collections are given here for comparison (Figs 12–15). Fig. 16 shows a graph of thumb length relative to body length in the conical thumbed and cubic thumbed males. The majority of specimens were taken from recent collections in New Zealand but they correspond well with specimens from Chilton's collection. The contrast between the two morphs is shown in the much longer thumb in the conical thumbed males compared to the cubic thumbed males of the same body length. Within the longer conical thumbed group, there is no marked transition in thumb length, suggesting that thumb production occurs gradually over several molts rather than at the terminal molt as in *Jassa* (Conlan, 1989). For the cubic thumbed group, the largest specimen showed a longer thumb than the others, but more specimens are needed to determine variation.

Chilton's two morphs may indeed be separate species, but this requires DNA analysis as no non-sexually dimorphic characters could be found that separated the two morphs. While large males could be distinguished based on thumb morphology (conical vs cubic), and large females found with the cubic thumbed males had grossly enlarged pereopods 5 and 6 while large females found with conical thumbed males had less enlarged pereopods 5 and 6, smaller females and thumbless males could not be assigned to the two morphs. In addition, the two morphs appeared to co-occur, as evidenced by Chilton's collection from Lyttelton, New Zealand (CMNZ 2015.149.575...604), which contained 3 conical thumbed males and 2 cubic thumbed males, as well as adult females with a range of moderately to grossly enlarged pereopods 5 and 6. There was also a juvenile *Jassa gruneri* Conlan, 1990 mixed in. One of the two cubic thumbed males in this collection is the one likely used by Chilton (1884) to illustrate the second gnathopod of the male *Podocerus latipes* in his type description, as this appendage had been torn off from the right side and the left gnathopod 2 corresponded with his Plate XIX, Fig. 2b.

K. H. Barnard (1932) illustrated a conical thumbed male gnathopod 2 of a specimen named "*Jassa pusilla*" captured at Tristan da Cunha 30 Jan. 1926 at 40–46 m on a R. S. S. *Discovery* expedition. Stephensen (1949) noted that this was the same as his new species *Jassa barnardi* (herein transferred to *V. frequens* as stated above). He listed additional specimens to those examined for this study collected at Tristan da Cunha, Nightingale and Inaccessible Islands at 0–40 m depth. The specimens listed by Schellenberg (1931) from Valparaiso and Iquique, Chile (just south of Caleta Bruna) were possibly those examined for this paper and listed above. Schellenberg (1953) illustrated a cubic thumbed male gnathopod 2 and the urosome of a female from Lüderitz bay, Namibia (not seen). In his New Zealand study, J. L. Barnard (1972) collected *V. frequens* from washes of mixed species of low intertidal algae at stations in Dunedin, Lyttelton, Kaikoura, Wellington, and Leigh in addition to the cubic thumbed morph he illustrated from Huaroa Point and examined for this paper. These have not been seen but are likely to be the same cubic thumbed morph as otherwise, J. L. Barnard would likely have remarked on the difference. Additional unexamined collections of *V. frequens* from the Bay of Islands, Waitemata Harbour, Leigh, Hahei, and the Chatham Islands, New Zealand (0–12 m depth) are held at the Auckland Museum (AuM). Griffiths (1975) recorded two collections of *V. frequens* from False Bay, South Africa. No station number was given, so it could not be determined whether either of these corresponded to a single False Bay collection (station FAL 604G) that was lent by Griffiths for this study. This collection held a cubic thumbed morph.

There are eight species of *Ventojassa* currently known (ordered by date of description and collection location): *V. ventosa* (J.L. Barnard, 1962) from California, *V. crenulata* Ledoyer, 1979 from Madagascar, *V. dentipalma* Kim & Kim, 1991 from Korea, *V. helenae* Vader & Myers, 1996 and *V. zebra* Vader & Myers, 1996 from Australia, *V. beagle* Alonso, 2012 from Argentina and *V. palauensis* Myers, 2013 from Palau. Of these, *V. frequens* may be closest to the Australian *V. helenae* and *V. zebra* which share the broad merus and carpus on pereopod 5. However, *V. frequens* has a narrower palm of gnathopod 1, a different ornamentation of the palm of gnathopod 2, pereopod 5 is without stridulating ridges, and pereopod 6 is more spinose and (especially in larger males and females) markedly stouter than pereopod 7. Common to other species of *Ventojassa*, *V. frequens* has a strongly produced interramal spinous process underlying the rami of uropods 1 and 2 but this is almost as long as the rami, where in other species it is typically shorter.

## Transferral of *Jassa goniamera* to *Hemijassa* Walker, 1907 and redescription of the genus

### Genus *Hemijassa* Walker, 1907.

*Hemijassa* Walker, 1907, 38.

**Description of male.** Maximum body length 22 mm.

*Head lobe*: squared, angles acute.

*Antenna 1*: accessory flagellum 2 articles, the second minute, only the second article setose.

*Antenna 2*: stouter and longer than antenna 1, the filter setae progressively shorter; flagellum with all but the first article bearing spines on the posterior margin, first article considerably longer than any of the following articles.

*Maxilla 1*: inner plate bearing a few short, fine setae; palp without setae at the base of article 1; article 2 with many scattered rows of facial setae distally.

*Gnathopod 1*: coxa rectangular; propodus, palm defined by 4 spines located proximally of centre; dactyl not facially striated.

*Gnathopod 2*: with a gill; coxa not deeper posteriorly; basis, filter setae simple or finely barbed and located on the anterolateral flange only; carpus less than 1/4 propodus length; propodus with a pronunced conical, multiply incised tooth below the dactyl hinge, and a larger acute thumb with 3 minute palmar defining spines at its tip, thumb setose on both inner and outer margins; dactyl shorter than the propodus, inner margin not expanded, tip resting on the tip of the thumb or between the thumb's anterior margin and the palm; dactyl cusps reduced to small buttons interspersed with a few short setae.

*Pereopods 3 and 4*: coxae rectangular; basis, margins more parallel than convex; merus slightly overlapping the carpus, anterior margin bearing discrete clusters of setae; propodus not posteriorly spinose.

*Pereopods 5–7*: at least one basis posterodistally produced, anterior margin with a few short setae; merus and carpus, posterior margin not spinose; dactyl without facial serrations, posterior (outer) margin not cusped distally, anterior (inner) margin bearing a row of setae along its length.

*Pleopods*: rami long, length > depth of the pleon, each with >2 coupling hooks.

*Urosome*: segment 1 bearing a pair of erect setae dorsally.

*Uropod 3*: peduncle mid-ventrally setose and spinose, without spines mid-dorsally, with a ventral row of short setae, with a crown of spines dorsomedially at the insertion of the rami and a cluster of setae distolaterally; outer ramus not setose mid-dorsally, tipped by a basally immersed, dorsally recurved spine and minute serrations dorsally, but without cusps; inner ramus with a single apical spine.

*Telson*: each corner with a pair of dorsolateral cusps and accompanying setae (1 long, simple and 2 short, plumose) but without spines.

**Description of adult female.** Maximum body length 20 mm. Character states as in the male except as follows.

*Brood plates*: broad, setae abundant, hook-tipped.

*Antenna 2*: peduncle, posterior filter setae long, not shorter in larger individuals.

*Gnathopod 2*: propodus and dactyl much larger and different in shape from that of the male.

*Pereopods 3 and 4*: basis slender as in the male.

**Type species.** *Jassa goniamera* Walker, 1903 (monotypy).

**Remarks.** Walker (1903) first suggested the genus name but decided to place his new species (*goniamera*) under *Jassa*. Walker (1907) transferred *J. goniamera* to *Hemijassa* after it was pointed out by other taxonomists that it did not fit in *Jassa*, *Ischyrocerus* or *Bruzeliella* Norman, 1905 (the latter synonymized by Walker 1911 under *Jassa*) based on characteristics of the antennal accessory flagellum and uropod 3. However, taxonomists appear to have disregarded the transfer of *J. goniamera* to *Hemijassa* and continued to assign *H. goniamera* to *Jassa*, as *J. goniamera*, *J. falcata* (Montagu, 1808), *J. ingens* Pfeffer, 1888 or *J. wandeli* (Bellan-Santini 1972; Thurston 1974b; Lowry & Bullock 1976). Sexton & Reid (1951) erroneously submerged the genus and species under *Jassa falcata*. *Hemijassa* is formally re-erected here as *H. goniamera* is clearly not a species of *Jassa*, as noted by Conlan (1989, 1990). In *Hemijassa*, gnathopod 2 morphology is unlike that of *Jassa*. The "thumb" is at, rather than distal to, the palmar defining spines, and occurs in both sexes. The "thumb" in *Hemijassa* could be considered homologous to the ledge that develops at the defining spines in *Jassa morinoi* Conlan, 1990 and *J. ingens*, and thus bears no homology to the *Jassa* thumb at all. There is no evidence of a transformational increase in thumb length relative to body length as occurs in *Jassa*. The lack of sexual difference in the shape of the bases of pereopods 3 and 4 is also suggestive of a different sexual life style. In *Jassa*, the pereopod 3 and 4 bases are broadly convex in non-thumbed males and females but slender in thumbed males. This difference corresponds with abandonment of a tubicolous lifestyle in *Jassa* once the males develop a thumb and a roving behaviour in search of receptive females to mate with (Borowsky, 1985).

## *Hemijassa goniamera* (Walker, 1903)

(Figs 17–21)

*Jassa goniamera* Walker, 1903, 61, 62, Plate 11, Figs 98–107 (part, according to Thurston (1974b), specimens less than 5 mm long are *Parajassa georgiana*); Stebbing, 1906, 739; Schellenberg, 1931, 253; Nicholls, 1938, 128; Stephensen, 1947, 73, Fig. 24; J. L. Barnard, 1958, 85; Lowry & Bullock, 1976, 75; Thurston, 1974b, 100.
*Hemijassa goniamera* Walker, 1907, 38.
*Jassa falcata*: ?Chilton, 1912, 511; not Schellenberg, 1926, 383; Sexton & Reid, 1951, 72, 75, 77–78, 81–83, 85, 86; Bellan-Santini, 1972, 191.
*Jassa ingens*: K. H. Barnard, 1932, 242 Fig. 151C (in part).

**Description of male.** Lectotype (here designated): Length 18.3 mm.

*Antenna 2*: overlapped by antenna 1 to midway along article 5; article 5, posterior marginal setae very short and simple, minute compared with those of the female; flagellum 8 articles, the last 1/2 the size of the second last, article 1 46% of full length.

*Mandible*: palp articles 2 and 3 with a dorsal fringe of setae; raker spines 6 right, 8 left.

*Gnathopod 1*: coxal margins, anterior 72% of dorsal length, ventral margin straight; basis, anterior margin with a fringe of long setae laterally, posterior margin with many setae also, which are just as long and wide ranging as on the anterior margin, but more scattered; carpus, length 64% of propodus length, posterior lobe 47% of anterior margin length, anterodistal setal cluster short, 25% of the anterior margin length; propodus, palm convex; dactyl cusped along the full length, without facial striations.

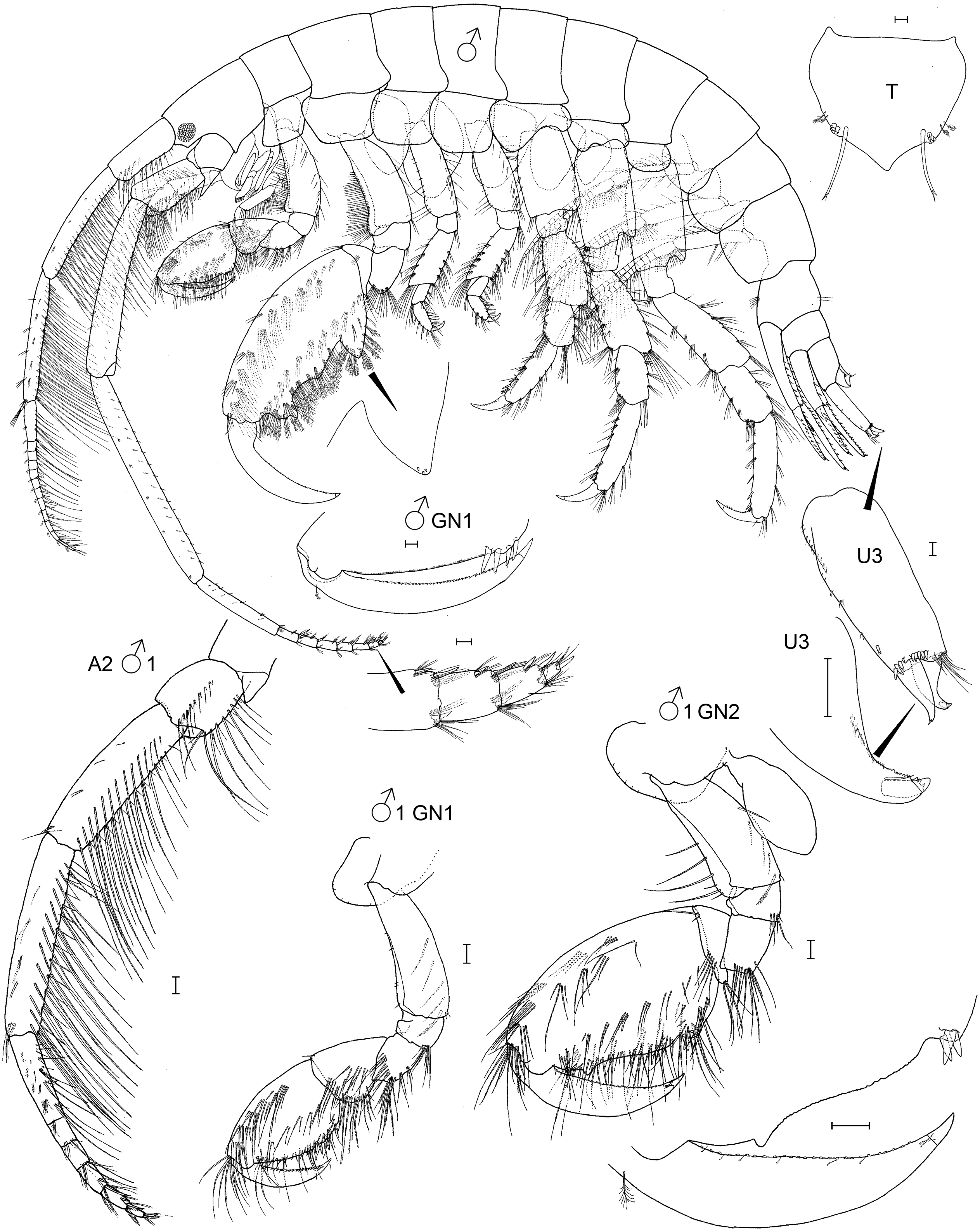



**FIGURE 17.** *Hemijassa goniamera* (Walker, 1903). Lectotype, male, 18.3 mm, and paralectotype, male 1, 6.1 mm, Cape Adare, McMurdo Sound, Ross Sea, Antarctica, 10, 14 and 26 November 1899, Southern Cross Expedition, NHM 1987:515. Lateral view: whole body; dorsal view: telson; other views medial. Scale 0.1 mm.

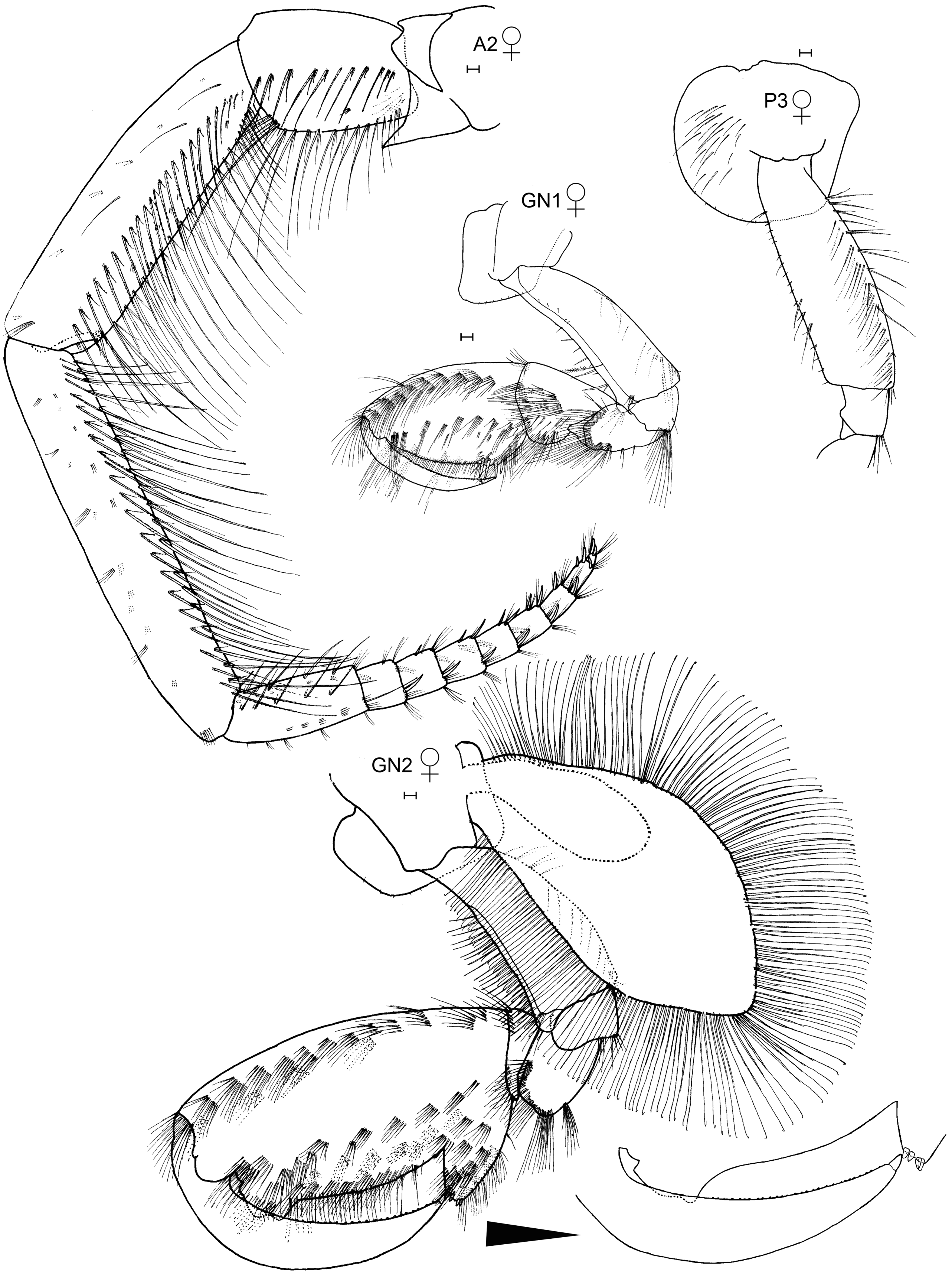



**FIGURE 18.** *Hemijassa goniamera* (Walker, 1903)**.** Paralectotype, adult female, 19.9 mm, Cape Adare, McMurdo Sound, Ross Sea, Antarctica, 10, 14 and 26 November 1899, Southern Cross Expedition, NHM 1987:515**.** All views medial**.** Scale 0.1 mm.

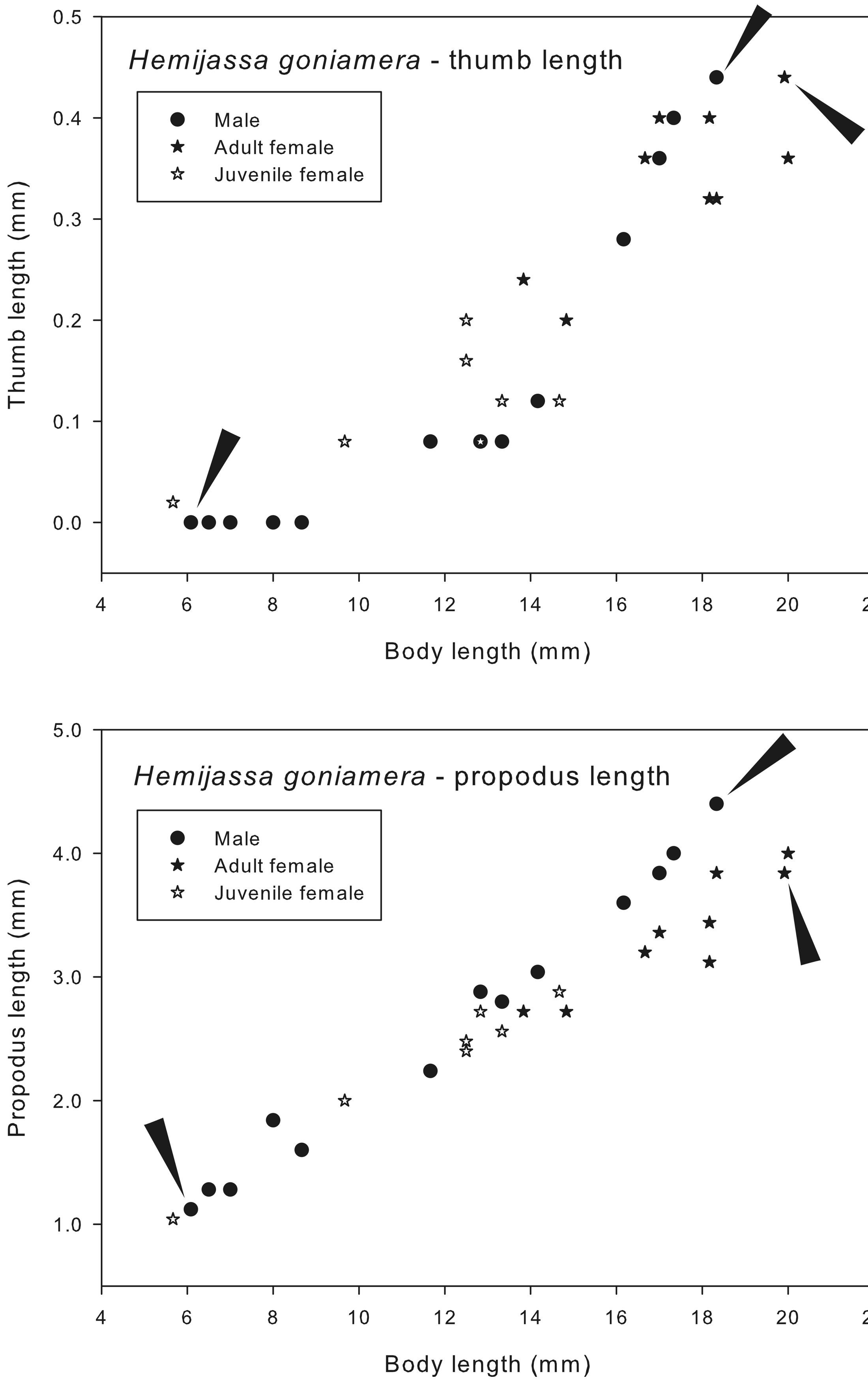



**FIGURE 19.** *Hemijassa goniamera* (Walker, 1903)**.** Variation in gnathopod 2 thumb length and propodus length relative to body length in males and females from a single population (Cape Adare, McMurdo Sound, Ross Sea, Antarctica, 10, 14 and 26 November 1899, Southern Cross Expedition, NHM 1987:515)**.** Types illustrated in Figs 17 and 18 are indicated by an arrow.

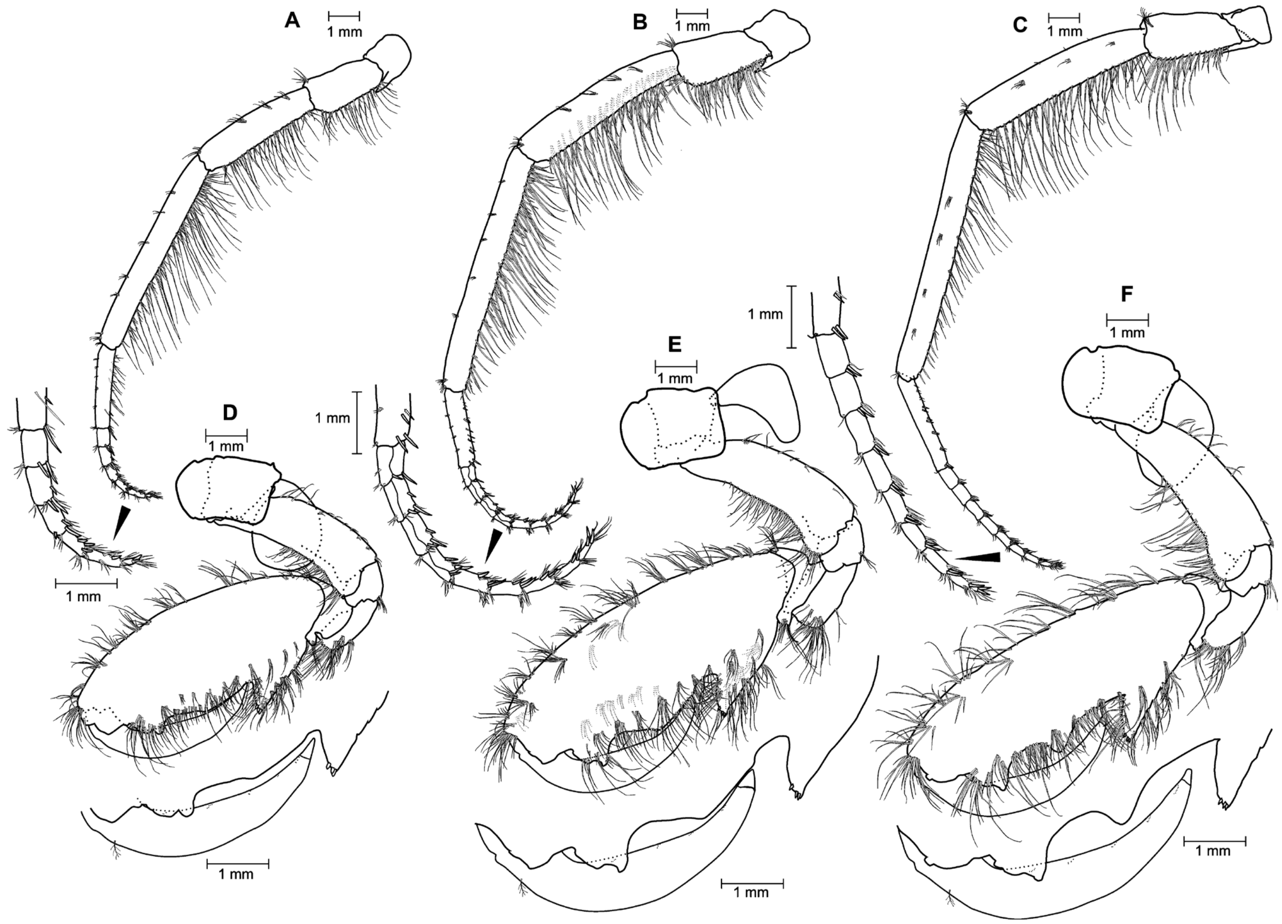



**FIGURE 20.** *Hemijassa goniamera* (Walker, 1903)**.** Variation in setation of antenna 2 and shape of the gnathopod 2 palm in three males**.** A, D: male, 22 mm, Weddell Sea off Kapp Norvegia, Polarstern EASIZ II Expedition (Ant. XV/3), Stn. 049, IG28520, 30 January 1998, Agassiz trawl beginning at 246 m depth, 70.0145°S, 10.00806°W, C. De Broyer and Y. Scailteur, coll. (RBINS)**.** B, E: male, 21 mm, Weddell Sea off Kapp Norvegia, Polarstern EASIZ II Expedition (Ant. XV/3), Stn. 062, IG28252, 31 January 1998, Agassiz trawl beginning at 248 m depth, 70.01461°S, 10.00794°W, C. De Broyer and Y. Scailteur, coll. (RBINS)**.** C, F: male, 22 mm, Stn. 062**.** IG28252. All views lateral**.** Scale 1 mm**.**

*Gnathopod 2*: coxal margins, anterior 87% and posterior 100% of ventral length, ventral margin straight; basis, anterolateral flange with a row of long, simple filter setae (setae about 1/2 article width); carpus, posterior lobe with a cluster of distal setae; propodus, anterior margin with a series of clusters of short setae (setae about 1/2 basis width)**.**

*Pereopod 3*: basis narrower than the gnathopod 1 basis, anterior margin shallowly concave; merus, anterior margin with a row of setae along its length, article width 45% of length; carpus barely 10% overlapped by merus; propodus width 40% of length.

*Pereopods 5–7*: basis posterodistally produced, anterior margin with a few short setae; merus and carpus, posterior margin not spinose**.**

*Uropod 1*: peduncle, posteroventral spinous process underlying 41% of the inner ramus, inner and outer rami with 12 and 13 mid-dorsal spines respectively, not terminating in a fringe of cusps ventral to the apical spine group**.**

*Uropod 2*: peduncle, posteroventral spinous process underlying 25% of the inner ramus**.**

*Uropod 3*: inner ramus not mid-dorsally spinose.

**Condition.** Left antenna 1, tip of flagellum missing, without left pereopod 7**.** Right appendages, telson and mouthparts slide mounted.

**Description of adult female.** Paralectotype: Length 19.9 mm**.** As in the genus description.

**Condition.** With all appendages**.** Right appendages, telson and mouthparts slide mounted.

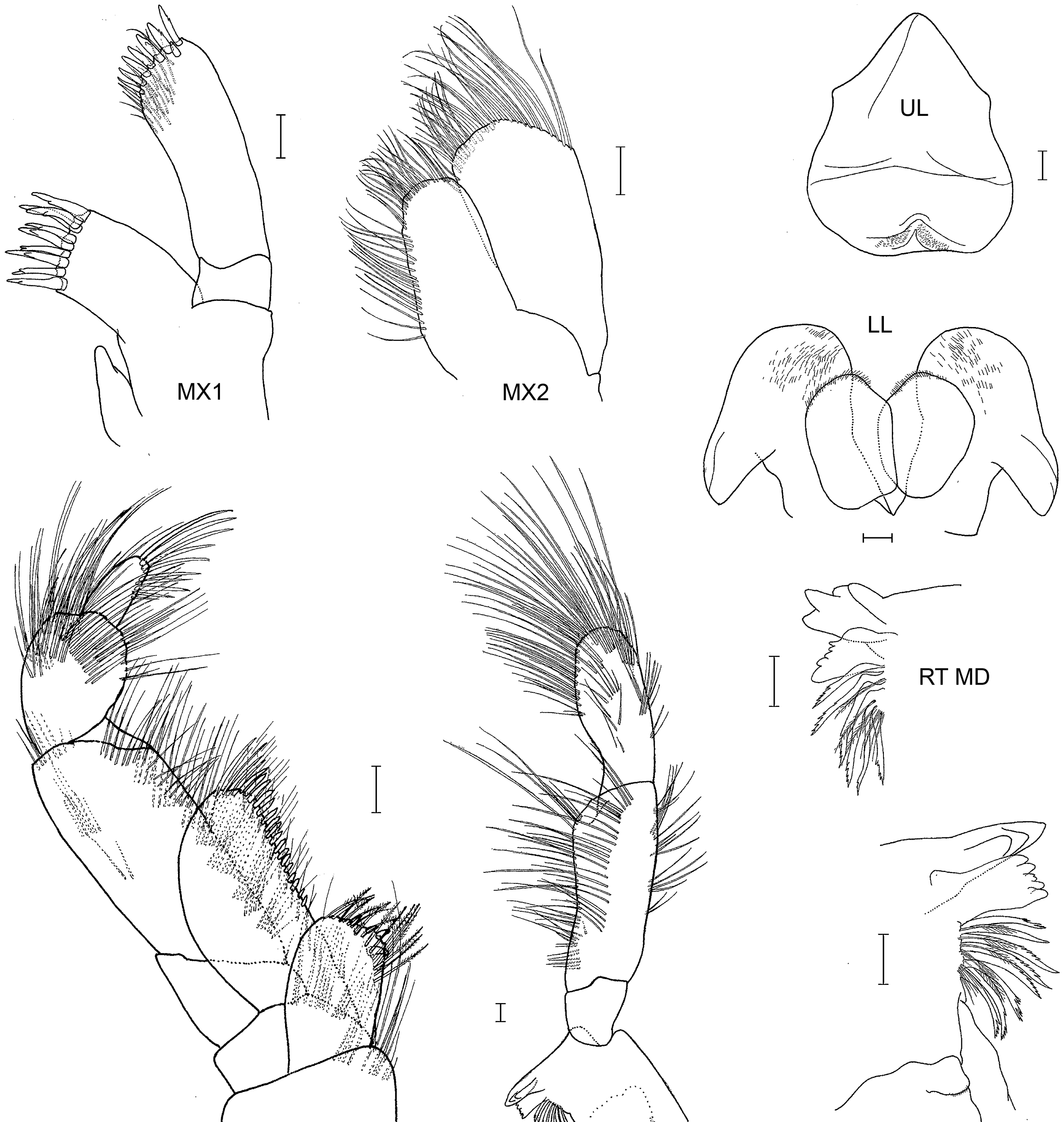



**FIGURE 21.** *Hemijassa goniamera* (Walker, 1903)**.** Lectotype, male, 18.3 mm, Cape Adare, McMurdo Sound, Ross Sea, Antarctica, 10, 14 and 26 November 1899, Southern Cross Expedition, NHM 1987:515**.** Mouthparts**.** Frontal view: upper lip; lateral view: left mandible with palp; other views medial**.** Scale 0.1 mm.

**Variation.** Maximum body length: male 22 mm, female 20 mm**.** *Hemijassa goniamera* exhibits sexual dimorphism in the antenna 2 and gnathopod 2. The antenna 2 development appears to be much like that in species of *Jassa*, with antennae long with short filter setae in large males compared to females and small males (Figs 17, 18 and 20)**.** The palm of gnathopod 2 is sinuous in small males, but with a ledge or tooth in large males (Fig. 20)**.** In females the palm remains sinuous at all sizes (Fig. 18).

**Type material examined.** Lectotype, ♂, NHM 1987:515, Cape Adare, McMurdo Sound, Ross Sea, Antarctica (71°17′S, 170°14′E), "Southern Cross" Expedition, 5 November 1902**.** Paralectotypes, 5 ♂♂, 9 adult ♀♀, 6 small (juvenile?) males and 10 juvenile females, NHM 1902.11.5:6–10 (part), same location.

**Other material examined.** South Sandwich Islands: Visokoi I., 13 Nov. 1908, 60–100 m, C. A. Larsen, coll., 1 ♀ (UiO F2968).

South Shetland Islands, Antarctica: off Cape Bowles, Clarence I., 23 Feb. 1927, ‘Discovery’ station 170, 342 m, 5 ♂♂, 8 ♀♀ (NHM 1936:11.2:2411–2426 (part)); Bransfield Strait, 2 Mar. 1927, ‘Discovery’ station 175, 200 m, 1 ♂ (NHM 1936.11.2: 2411–2428 (part).

Graham Region, Antarctica: Seymour I. (64°20′S, 56°38′W), 16 Jan. 1902, 150 m, Svenska Sydpolarexp. 1901–1903, No. 5, 3 juveniles (SNM) and 10 juveniles (NRM 3679); SW of Snow Hill I., (64°36′S, 57°42′W), 20 Jan. 1902, 125 m, Svenska Sydpolarexp. 1901–1903, No. 6, 1 ♂, 1 ♀, 1 juvenile (NRM 3680).

Ross Sea, Antarctica: Coulman I., 13 Dec. 1902, 183 m, 1 ♂, 1 ♀ (NHM 1907.6.6:410–415); Flagon Pt., Winter Quarters Bay, McMurdo Sound, 23 Jan. 1903, ‘Discovery’ Expedition, 1 ♂, 1 ♀, 1 juvenile (NHM 1907.6.6.414–415); Flagon Pt., Winter Quarters Bay, McMurdo Sound, 17 Jan. 1903, ‘Discovery’ Expedition, 3 ♀♀ (NHM 1907.6.6:410–415).

Weddell Sea, Antarctica: Cap Norvegia, (71°2′S, 12°W), 17 Feb. 1930, Norvegia Expedition, Riiser-Larsen, 1 ♀ (UiO); off Kapp Norvegia (70.0145°S, 10.00806°W), 30 Jan. 1998, Agassiz trawl beginning at 246 m, C. deBroyer and Y. Scailteur, coll., Polarstern EASIZ II Expedition (Ant XV/3), 1 ♂ (RBINS IG28520); off Kapp Norvegia (70.01461°S, 10.00794°W), 31 Jan. 1998, Agassiz trawl beginning at 248 m, C. deBroyer and Y. Scailteur, coll., Polarstern EASIZ II Expedition (Ant XV/3), 2 ♂♂ (RBINS IG28252).

Commonwealth Bay, Antarctica: 21 Dec. 1913, 10–120 m, Australasian Antarctic Expedition, 1 ♂ (AM P.18415).

Terre Adélie, Antarctica: Archipel de Pointe Géologie, 2 Jan.1965, 110–130m, fond à bryozoaires, hydraires, spongiaires et alcyonaires, P.M. Arnaud, coll., station TA-D102 (D. Bellan-Santini loan).

**Remarks.** Schellenberg (1926) may have recorded *H. goniamera* at Gauss-Station (Kaiser Wilhelm II Land) during the Deutsche Südpolar-Expedition 1901–1903, collected on August 12, 1902 and named it *Jassa falcata*. Other specimens listed as “*J. falcata”* may have been *P. wandeli*, judging by their size and collection location. One collection of “*J. falcata*” from Terre Adélie, Antarctica and listed in Bellan-Santini (1972) was examined and found to be *H. goniamera*. It is likely that the other three collections listed therein (not seen) are also *H. goniamera*, judging by the size of the specimens (7–17 mm) and depth of collection (15–140 m).

*Hemijassa goniamera* is only known subtidally and can be found clinging to bryozoans and hydroids (Dauby *et al.* 2001). Trace metal levels are relatively low in *H. goniamera* and well within the range of other Antarctic amphipods (Keil *et al.* 2008).

## Transferral of *Jassa wandeli* and *J. multidentata* to *Pleojassa* n. gen. with addition of *P. moorei* n. sp., *P. lowryi* n. sp. and *P. orientalis* n. sp.

### Genus *Pleojassa* n. gen.

**Description of male.** Maximum body length 10.8 mm.

*Head lobe*: squared, dorsal angle more acute, lower angle lobe more rounded.

*Antenna 1*: accessory flagellum 2 articles, the second minute, setose only distally.

*Antenna 2*: stouter and longer than antenna 1, setation variable, filter setae shorter and sparser in larger individuals, flagellum spination variable, first article considerably longer than following articles.

*Maxilla 1*: inner plate bearing a few short, fine setae; palp without setae at the base of article 1, article 2 with 1 row of facial setae.

*Gnathopod 1*: coxa rectangular; carpus, anterior margin length < propodus length; propodus, palm defined by 1–2 medial defining spines, this central or slightly proximal of centre; dactyl facially striated.

*Gnathopod 2*: without a gill; coxa not deeper posteriorly; basis without filter setae; carpus a quarter of propodus length or less, lobe apically setose; propodus without anteroproximal setae, hinge tooth rectangular cuboid or conical, shallowly or deeply bifid, or multiply incised, palm concave to the single medial defining spine, there produced or not into a short “hook” or long thumb; dactyl shorter than the propodus, variably expanded at the hinge tooth, tip apposing the defining spine, or if thumb present, its posterior margin, cusps reduced and interspersed with short setae.

*Pereopod 3*: coxa deepest centrally or slightly posterior of centre; basis a little slenderer in larger individuals;

merus, anterior margin bearing well-spaced single or clustered setae; carpus, overlap by merus variable; propodus not posteriorly spinose.

*Pereopods 5–7*: basis variably posterodistally produced or not produced, anterior margin spinose or setose; merus not posterodistally spinose; carpus with a cluster of spines posterodistally at least on pereopod 5; propodus not strongly expanded anteriorly; dactyl not facially serrated, posterior (outer) margin not cusped distally, anterior (inner) margin, setation variable.

*Pleopods*: rami very short, length ≤ depth of the pleon, each with 2 coupling hooks.

*Urosome*: segment 1 with dorsal pair of erect setae.

*Uropod 3*: peduncle mid-ventrally setose, without mid-dorsal spines, but with a crown of spines dorsomedially at the insertion of the rami and a cluster of setae distolaterally; outer ramus not setose mid-dorsally, tipped by a basally immersed, dorsally recurved spine and associated seta and serrations, cusps variable, but never as on *Jassa*; inner ramus with or without a spine or spines mid-dorsally in addition to the single apical spine.

*Telson*: each dorsolateral corner with a pair of cusps accompanied by setae (2 long, simple, and 2 short, plumose) but not spines.

**Description of adult female.** Maximum body length 9.8 mm. Character states as in the male except as follows.

*Brood plates*: broad, setae well separated, abundant, at least some hook-tipped.

*Antenna 2*: peduncle, posterior filter setae long, not shorter in larger individuals.

*Gnathopod 2*: propodus much larger and different in shape from propodus of gnathopod 1, palm concave, defined by a single medial spine and without a thumb; dactyl tip apposing the defining angle and spine, dactyl cusps strong.

*Pereopod 3*: basis somewhat broader than in the male.

**Variation.** Antenna 2 peduncular setal change appears to be similar to that of *Jassa*, with the male's setae shorter in larger specimens and the female's remaining long. Male gnathopod 2 thumbing is not homologous, however, because the thumb develops at the palmar defining spine rather than distal to it. Consequently the thumb's setation pattern is quite different.

**Type species.** *Jassa wandeli* Chevreux, 1906.

**Included species.** *Pleojassa wandeli* (Chevreux, 1906), *P. multidentata* (Schellenberg, 1931), *P. moorei* **n. sp.,** *P. lowryi* **n. sp.** and *P. orientalis* **n. sp.**

**Remarks.** Distinguishing features from *Jassa* are a single spine defining the palm of gnathopod 2, and hence different thumb setation, closure of the second gnathopod's dactyl at, rather than distal to, the defining spine, lack of a gnathopod 2 gill, reduced pleopods and lack of a double cusp on the uropod 3 outer ramus.

The males of *P. wandeli* and *P. multidentata* produce a long thumb if sufficiently larger than the adult female and thus would superficially appear to be a *Jassa*. Thumb development appears from specimens to be a progressive transformation, not at a terminal molt, however (although this has not been tested experimentally as it has for *Jassa*). Males of *P. orientalis* probably also produce a thumb as this species closely resembles *P. multidentata*. *Pleojassa moorei* and *P. lowryi* are not known to produce thumbs in the males and sufficient specimens were available to find males of similar or larger size than adult females to indicate that the males were adult as well. However, the five species resemble each other in characters that are conservative within *Jassa*, such as the tendency toward setal reduction in the antenna 2 of the male compared to the female, and in similar morphologies of the mouthparts, gnathopod 1, female gnathopod 2, female brood plates and third uropod hooking.

## Key to World species of *Pleojassa* (both sexes)

1 Uropod 1, posteroventral peduncular spinous process nearly as long as the outer ramus. Gnathopod 1, carpus without a seta at the anterodistal junction of the propodus. Female gnathopod 2, palmar setae not densely plumose (Fig. 22) ............... ........................................................................................ *P. moorei* **n.sp.**

\- Uropod 1, posteroventral peduncular spinous process ½ to ¾ the length of the outer ramus. Gnathopod 1, carpus with or without a single seta or cluster of setae at the anterodistal junction of the propodus. Female gnathopod 2, palm bearing abundant plumose setae (Figs 27 and 28) .................................................................... 2

2 Pereopods 3 and 4, carpus nearly fully overlapped by the merus (Fig. 25). Female body size at maturity 2.5–5.1 mm. Gnathopod 2, propodus, palm densely plumose in both sexes; larger male ~3 mm body length or more, palm defined by a small hook but not by a thumb (Fig. 25) ........................................................... .*P. lowryi* **n.sp.**

- Pereopods 3 and 4, carpus 1/2 to 3/4 overlapped by the merus (Figs 27–29). Female body size at maturity 5.9–9.8 mm. Gnathopod 2, propodus, only the female palm densely plumose; larger male ~6 mm body length or more, palm defined by a thumb (Fig. 30) . . . . . . . . . . 3

3 Female gnathopod 2, propodus, dactylar hinge tooth shallow (Fig. 33). Antenna 2, large male and female, posterior margin of article 5 and flagellum plumose (Fig. 33) . . . . . . . . . . *P. wandeli* (Chevreux, 1906)

- Female gnathopod 2, propodus, dactylar hinge tooth deep (Figs 27 and 28). Antenna 2, adult female and comparably sized male, posterior margin of article 5 and flagellum not plumose (Figs 27 and 28). . . . . . . . . . 4

4 Gnathopod 1, carpus with a single or cluster of setae at the anterodistal junction of the propodus (Fig. 27). Known only from South Georgia (Fig. 2) . . . . . . . . . . *P. multidentata* (Schellenberg, 1931)

- Gnathopod 1, carpus without a single or cluster of setae at the anterodistal junction of the propodus (Fig. 28). Known only from Macquarie Island (Fig. 2) . . . . . . . . . . *P. orientalis* **n. sp.**

***Pleojassa moorei* n. sp.**
(Figs 22–24)

**Description of male.** Holotype: Length 4.0 mm.

*Antenna 1*: missing. (*Male, 3.4 mm, not type, CMN IZ1989-013, antenna 2 overlapped by antenna 1 to midway along article 5*).

*Antenna 2*: article 5 bearing a few simple setae only, these about as long as those of the female; flagellum 3 articles, article 1 75% of full flagellum length.

*Mandible*: palp articles 2 and 3 without a dorsal fringe of setae; raker spines 3 right, 4 left.

*Gnathopod 1*: coxal margins, anterior 92% of dorsal length; ventral margin straight; basis, anterior and posterior margins each with a single seta distally; carpus, length 80% of propodus length, posterior lobe 47% of anterior margin length, without an anterodistal setal cluster; propodus, palm convex, one defining spine slightly proximal of centre.

*Gnathopod 2*: coxal margins, anterior 65% and posterior 61% of ventral length, ventral margin sinuous; carpus 1/4 the length of propodus; propodus with 2 hinge teeth, palm sparsely setose throughout, defined by a single spine, this not associated with a discrete thumb-like extension from the palm.

*Pereopod 3*: basis slender, anterior margin shallowly convex; merus, anterior margin setose only distally, article width two thirds of length; carpus a third overlapped by the merus; propodus width 44% of length.

*Pereopods 5–7*: slender, setae and spines sparse, basis not posterodistally produced, anterior margin with a few short setae; merus, posterior margin not spinose.

*Uropod 1*: peduncle, posteroventral spinous process underlying 88% of the inner ramus, inner and outer rami with 1 and 3 mid-dorsal spines respectively.

*Uropod 2*: peduncle, posteroventral spinous process underlying 21% of the inner ramus.

*Uropod 3*: inner ramus not mid-dorsally spinose.

**Condition.** Without antennae 1, right antenna 2 or left pereopod 3. Remaining right appendages, telson and mouthparts slide mounted. Remaining left appendages with the carcass.

**Description of adult female.** Allotype: Length 4.25 mm. Character states as in the male except as follows.

*Antenna 2*: only slightly longer than antenna 1, article 5 without plumose setae, simple filter setae about twice the length of those of the comparably sized male.

*Gnathopod 2*: propodus without a hinge tooth, palm 40% of the posterior margin, setae not so dense as to obscure the palm's shape.

**Condition.** Without antennae 1 and right pereopod 6. Right antenna 2 and gnathopod 2 slide mounted. Other appendages with the carcass.

**Variation.** Maximum body length: male 4.0 mm, female 4.5 mm. Examination of 8 males and 8 females from the type collection showed no variation in the antenna 1 accessory flagellum with consistently 3 articles. No thumb is produced on the propodus of gnathopod 2 to indicate the sexual state of males as in *Jassa* (Borowsky, 1985). However, there is some indication of adulthood in the larger antenna 2 and propodus of the gnathopod 2 as well as a longer palm and more pronounced hinge tooth in the male than in the female of similar body length (Figs 22 and 23).

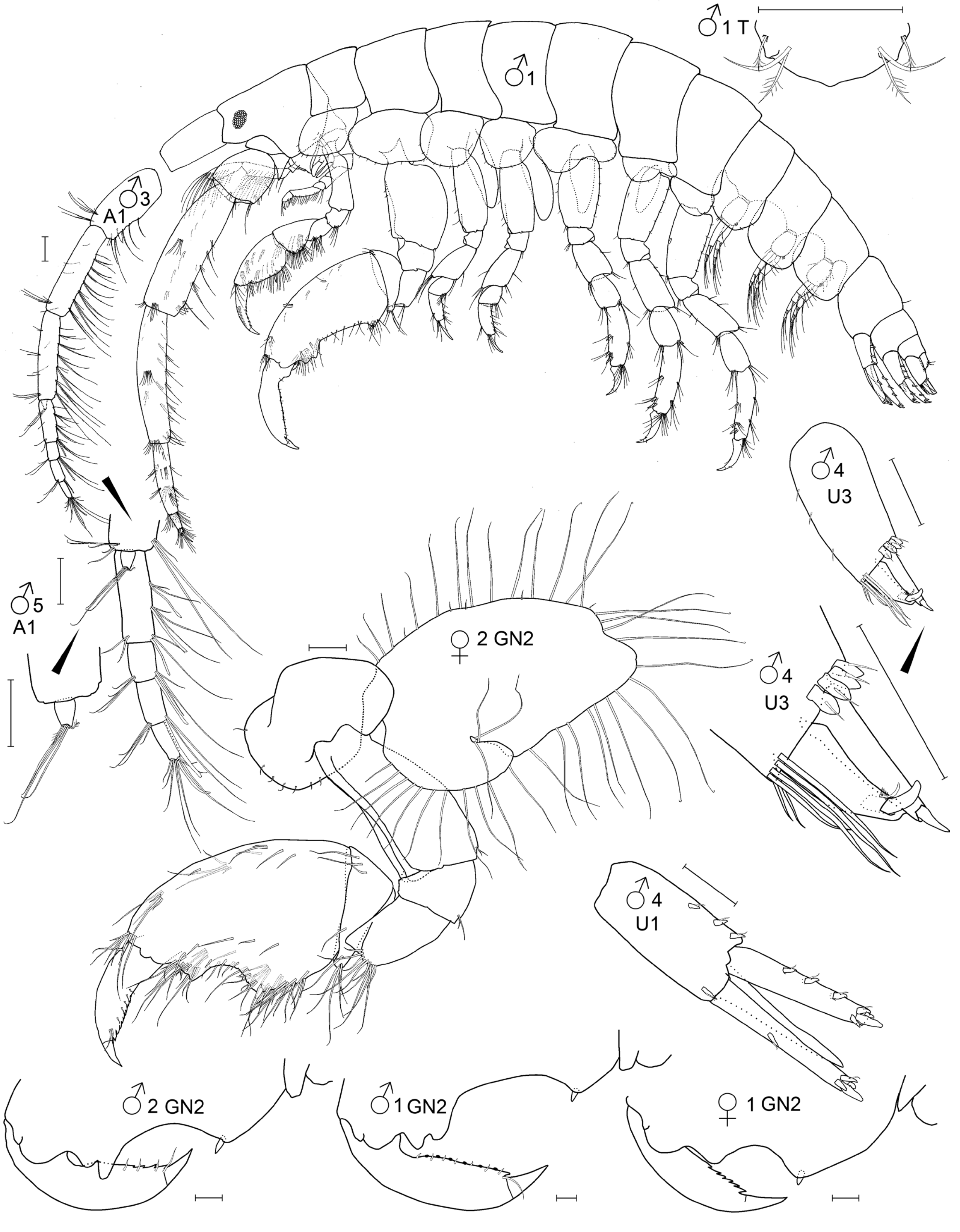



**FIGURE 22.** *Pleojassa moorei* **n. sp.** Holotype, male 1, 4.0 mm (NHM 1987:511), allotype, female 1 (NHM 1987:512), 4.25 mm and paratype, male 2, 3.25 mm**.** Billie Rocks, Signy Island, South Orkney Islands, 4 March 1965, M. H. Thurston, coll., NHM 1969:768:ca. 430, station no. 13(244)**.** Male 3, 3.4 mm, male 4, 3.6 mm, male 5, 3.4 mm, and female 2, 4.2 mm, Billie Rocks, Signy Island, South Orkney Islands, 3 March 1965, M. H. Thurston, coll., CMN IZ1989-013, 1969:771:ca 260 (pt.), station no. 16(333)**.** Most setae are omitted from the gnathopod 2 profiles**.** Lateral views: whole body, male 3 antenna 1, uropod 3 and gnathopod 2 profiles; dorsal view: uropod 1 and telson; medial views: male 5 antenna 1 and female 2 gnathopod 2**.** Scale 0.1 mm.

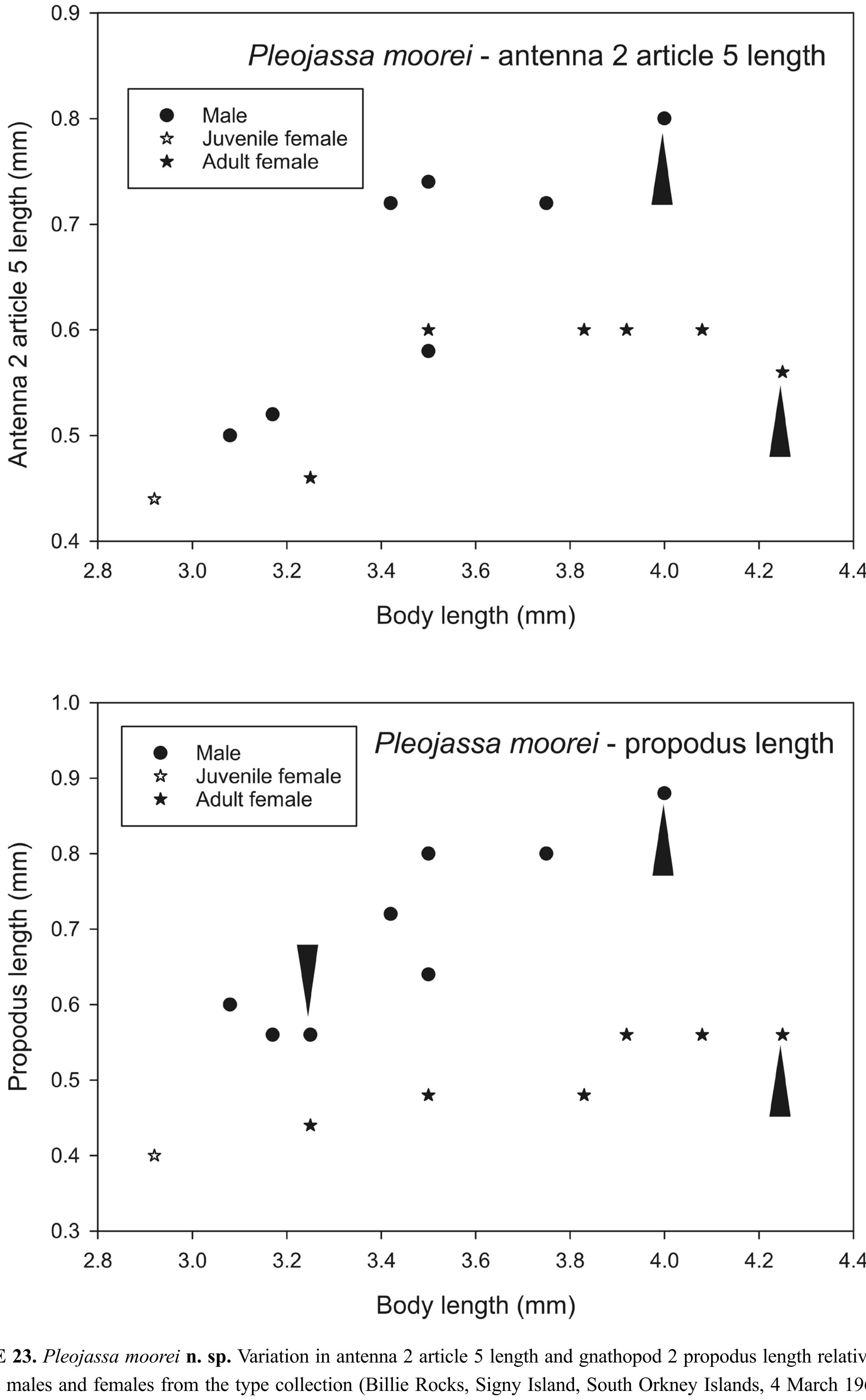



**FIGURE 23.** *Pleojassa moorei* **n. sp.** Variation in antenna 2 article 5 length and gnathopod 2 propodus length relative to body length in males and females from the type collection (Billie Rocks, Signy Island, South Orkney Islands, 4 March 1965, M. H. Thurston, coll., NHM 1969:768:ca. 430, station no. 13(244)). Specimens illustrated in **FIGURE 22** are indicated by an arrow. Regression assumptions failed for all plots**.**

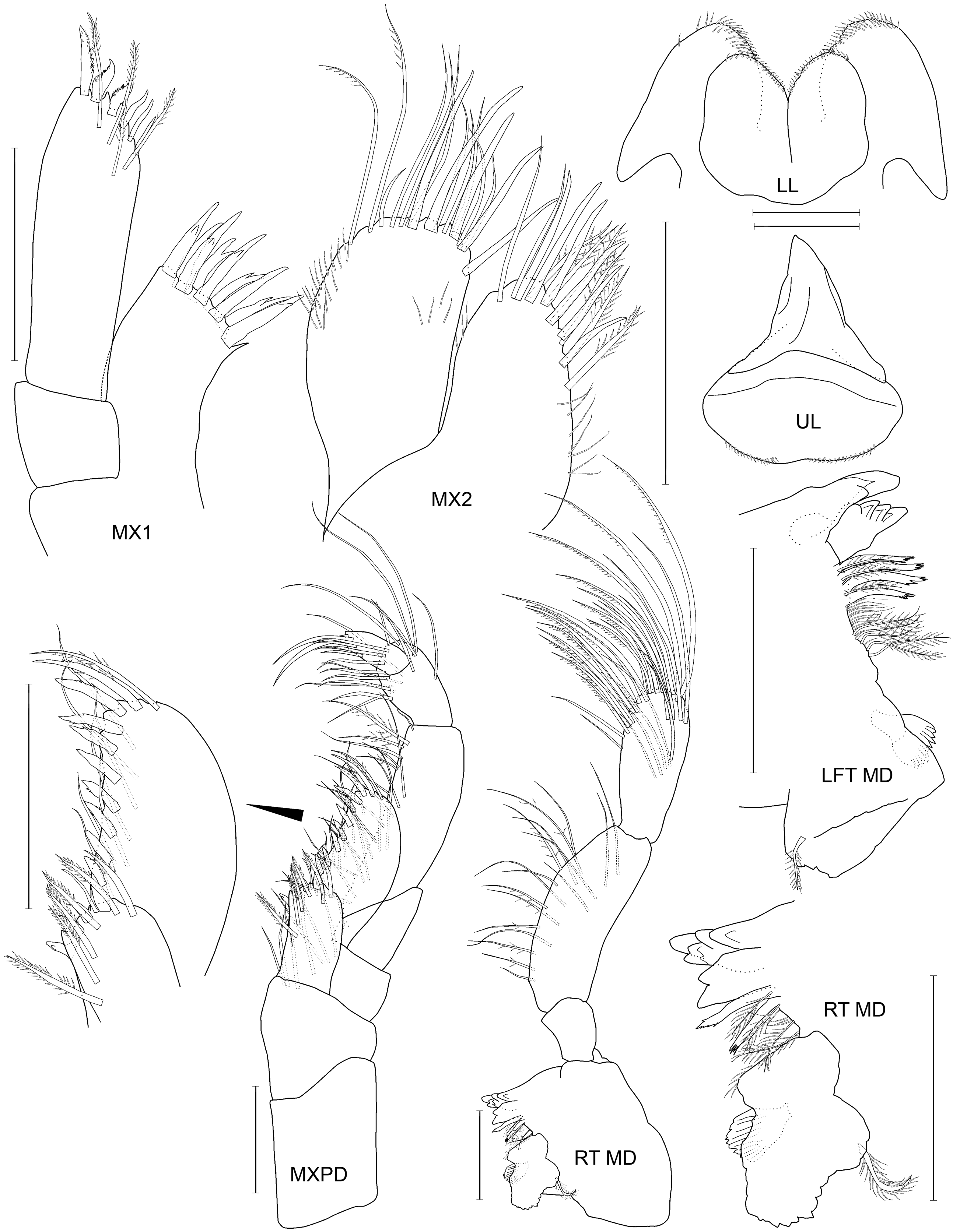



**FIGURE 24.** *Pleojassa moorei* **n. sp.** Male 4, 3.6 mm, Billie Rocks, Signy Island, South Orkney Islands, 3 March 1965, M. H. Thurston, coll., CMN IZ1989-013, 1969:771:ca 260 (pt.), station no. 16(333)**.** Mouthparts**.** Frontal view: upper lip; lateral view: maxilla 1; other views medial**.** Scale 0.1 mm.

**TABLE 4.** Morphological differences between *Pleojassa moorei* and *P. lowryi***.** Character states apply to both sexes unless expressly stated.

| Body part | Character | Character state | |
|---|---|---|---|
| | | *P. moorei* | *P. lowryi* |
| Body length at maturity (mm) | ♀ range | 2.9 – 4.2 | 2.7 – 5.1 |
| | ♂ maximum | 4.0 | 5.3 |
| Antennae 1 & 2 | Shape | Slenderer, longer | Stouter, shorter |
| | Setation | Sparsely setose | Densely setose |
| Antenna 2 | Difference between small and large individuals | Longer in large individuals, setae sparser and shorter (♂ only) | Plumose setae on posterodistal margin of article 5 and posterior margin of flagellum (both sexes) |
| Gnathopod 1 | Basis, medial margin, spination | Not spinose | Spinose along most of length |
| | Carpus, anterodistal setae, presence | Absent | Present, short |
| | Propodus, palm shape | Broader, convex | Slenderer, nearly straight |
| Gnathopod 2 | Carpus, length relative to propodus | ¼ | < ¼ |
| | Propodus, ♀, palm, length in relation to posterior margin | < ½ | > ½ |
| | Propodus, palm setation, abundance | Sparse | Dense |
| posteroventral | Propodus, palm setation, type | Simple | Plumose |
| | Propodus, adult ♂, hinge tooth, shape | Split in two | Shallowly bifid |
| | Propodus, adult ♂, palmar defining angle, shape | Not produced | Produced into a hook |
| Pereopods 3 & 4 | Length of propodus overlapped by the carpus | ½ | ¾ |
| Pereopods 5–7 | Basis, shape | Slender | Stout |
| | Setation, abundance | Sparse | Moderately dense |
| | Spination, abundance | Sparse | Moderately dense |
| Uropod 1 | Posteroventral peduncular spinous process, length relative to outer ramus | Equal | ¾ |

**Type material examined.** Holotype, ♂, Billie Rocks, Signy Island, South Orkney Islands (60°43′S, 45°38′W), 4 March 1965, M. H. Thurston, coll., 3.1–3.4 m depth, diver collection of *Lithothamnia*, *Desmarestia anceps*, *D. chordalis*, *Ascoseira mirabilis*, Rhodophyceae, Porifera, and Polyzoa off solid rock inclined at 65° (NHM, registration no. 1987:511, station no. 13(244))**.** Allotype, ♀, same location (NHM, registration no. 1987:512)**.** Paratypes, ~200 specimens, same location (NHM, registration no. 1969:768 (pt.)).

**Other material examined.** (excluded from type series): South Georgia: no. 10427, (54°30′58″S, 36°0′45″W), K. von den Steinen, coll., 16 January 1884, 1 juvenile (ZMH K-28907).

South Orkney Islands: 38 collections from Billie Rocks, Berntsen Point, Outer Islet and Paal Harbour, Signy Island, Dec.–July 1964 and Feb.–Mar. 1965, ~1350 specimens (NHM stations 9–12, 15–26, 30, 32–35, 40, 46–49, 54).

**Etymology.** In appreciation of Dr. Geoff Moore's contributions to our knowledge of the systematics, ecology and behaviour of amphipods and of his assistance in locating specimens for this study.

**Remarks.** Table 4 summarizes obvious differences between *P. moorei* and *P. lowryi***.** Thurston (1974b) collected 2,912 specimens at 29 stations on Signy Island and named this species *Jassa falcata* form 3**.** The additional collections examined here were split collections from the same station.

***Pleojassa lowryi* n. sp.**
(Figs 25 and 26)

**Description of male.** Holotype: Length 5.3 mm**.** Without antenna 1**.** *(Paratype, male, 3.8 mm, antenna 2 overlapped by antenna 1 to the end of article 5)***.**

*Antenna 2*: article 5 and flagellum, posterior margin bearing abundant plumose setae, simple filter setae interspersed, these sparser and shorter than in the female; flagellum 3 articles, article 1 86% of full flagellum length**.**

*Mandible*: palp articles 2 and 3 without a dorsal fringe of setae; raker spines 4 right, 6 left**.**

*Gnathopod 1*: coxal margins, anterior 112% of dorsal length; ventral margin straight; basis, antero-medial margin with a row of short, spine-like setae, antero-lateral and posterior margins setose only distally; carpus, length 60% of propodus length, posterior lobe 42% of anterior margin length, setal cluster short, 16% of the anterior margin length; propodus, palm nearly straight, one defining spine slightly proximal of centre**.**

*Gnathopod 2*: coxal margins, anterior 48% and posterior 70% of ventral length; ventral margin shallowly concave; carpus less than a quarter the length of the propodus; propodus, hinge tooth conical, shallowly bifid, palm densely plumose throughout, defined by a single minute spine at the end of a short hook-like protuberance**.**

*Pereopod 3*: basis slender, anterior margin shallowly convex; merus, anterior margin setose centrally and distally, central setae less than 1/4 article width, article width 73% of length; carpus three quarters to fully overlapped by the merus; propodus width 58% of length**.**

*Pereopods 5–7*: stout, basis of pereopod 6 and 7 posterodistally produced, anterior margin of each basis spinose; merus bearing spines along its posterior margin**.**

*Uropod 1*: peduncle, posteroventral spinous process underlying 39% of the inner ramus, inner and outer rami with 3 and 5 mid-dorsal spines respectively**.**

*Uropod 2*: peduncle, posteroventral spinous process underlying 17% of the inner ramus**.**

*Uropod 3*: inner ramus with 1 spine mid-dorsally.

**Condition.** Without antennae 1, right antenna 2, right pereopods 5 and 6, and both pereopods 7**.** Remaining right appendages (or left appendage when right lacking), telson, and mouthparts slide mounted**.** Other left appendages with the carcass.

**Description of adult female.** Allotype: Length 5.1 mm**.** Character states as in the male except as follows.

*Antenna 1*: overlapping antenna 2 to the end of article 5; article 5, posterior margin with long filter setae and a few plumose setae distally; flagellum, posterior margin with a few plumose setae proximally and brush setae distally**.**

*Gnathopod 2*: propodus without a hinge tooth, palm 58% the length of the posterior margin, setae plumose, so abundant as to obscure the palm's shape.

**Condition.** Without left pereopod 7.

**Variation.** Maximum body length: male 5.3 mm, female 5.1 mm**.** Males of comparable body length to adult females have abundant plumose setae on the posterior margin of the second antennal article 5 and flagellum. Small males and juvenile females lack plumose setae on antenna 2 but bear long filter setae. The palm of gnathopod 2 is abundantly plumose in both adult females and comparably sized males and less so in small males and females. There is no evidence of thumb production in males of similar body length to adult females. There is some divergence in the gnathopod 2 propodus length between the sexes, with a greater length achieved by males than females of similar body length (Fig. 26).

**Type material examined**. Holotype, ♂, Rima Islet, The Snares, New Zealand (48°07′S, 166°36′E), in a crevice in the *Durvillea* zone, barnacles encrusted with sponge, 21 Nov. 1976, G. D. Fenwick, coll. (AM P.34948, collection event SA-3417). Allotype, ♀, same location (AM P.37922). Paratypes, 5 adult ♂♂, 25 adult ♀♀, and 163 juveniles, same location (AM P.37923).

**Other material examined.** Alert Stack, The Snares, New Zealand (48°07′ S, 166°36′E), from algae below the *Durvillea* zone to 7m depth, 20 Dec. 1976, G. D. Fenwick, coll., 2 juveniles (AM P.34949, collection event SA-3456).

**Etymology**. In gratitude to Dr. Jim Lowry (Australian Museum) for assistance in locating Southern Hemisphere material.

**Remarks.** The spination on the anterior margin of the basis of gnathopod 1 is not homologous with that of the Southern Hemisphere *Jassa alonsoae* Conlan, 1990, *J. justi* Conlan, 1990, *J. fenwicki* Conlan, 1990 and *J. hartmannae* Conlan, 1990 because it is medial instead of lateral. Readily recognizable differences between *Pleojassa lowryi* and *P. moorei* are listed in Table 4.

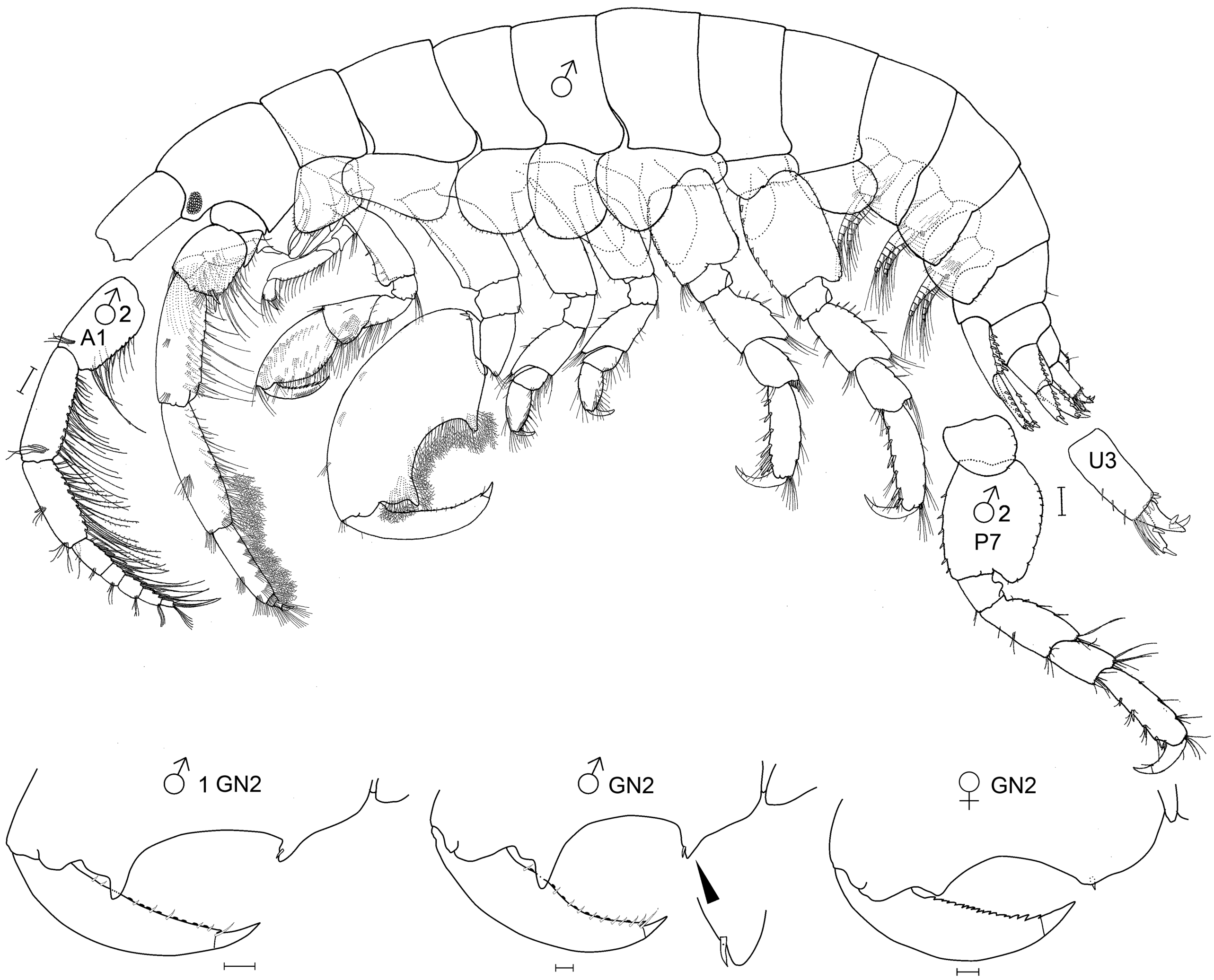



**FIGURE 25.** *Pleojassa lowryi* n. **sp.** Holotype, male, 5.3 mm, allotype, female, 4.6 mm and paratypes, male 1, 2.9 mm and male 2, 4.3 mm. Rima Islet, The Snares, New Zealand, 21 November 1976, G. D. Fenwick, coll., AM P.34948, station no. SA-3417. Setae are omitted from the second gnathopod profiles. All views lateral. Scale 0.1 mm.

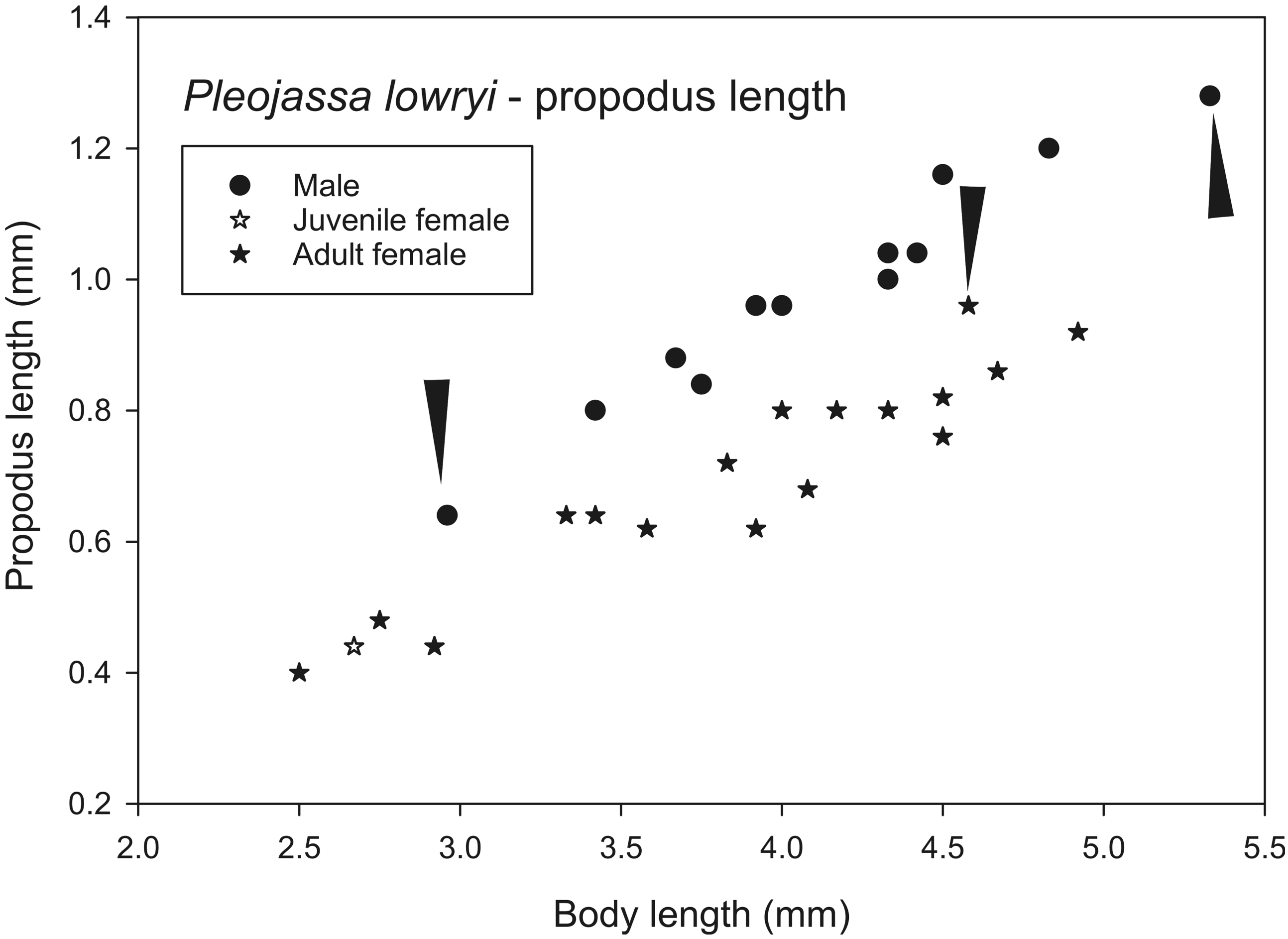



**FIGURE 26.** *Pleojassa lowryi* **n. sp.** Variation in gnathopod 2 propodus length relative to body length in males and females from the type collection (Rima Islet, The Snares, New Zealand, 21 November 1976, G. D. Fenwick, coll., Am P.34948, station no. SA-3417). Second gnathopods illustrated in **FIGURE** 25 are indicated by an arrow. Regression assumptions failed for all plots.

***Pleojassa multidentata*** **(Schellenberg, 1931)**
(Fig. 27)

*Jassa multidentata* Schellenberg, 1931, 251–253, Fig. 131; J. L. Barnard, 1958, 85; Lowry & Bullock, 1976, 75.

**Description of male.** (Not type; MfN 22.962, South Georgia, Swedish Antarctic Expedition): Length 8.0 mm.

*Antenna 2*: overlapped by antenna 1 to midway along article 5; antenna 2, article 5 bearing simple setae only, these less than half the length of those of the female; flagellum 3 articles, article 1 86% of full flagellum length.

*Mandible*: palp articles 2 and 3 without a dorsal fringe of setae; raker spines 4 right, 6 left.

*Gnathopod 1*: coxal margins, anterior 110% of dorsal length, ventral margin shallowly concave; basis, anterior and posterior margins not setose; carpus, length 75% of propodus length, posterior lobe 49% of anterior margin length, anterodistal setal cluster short, 18% of the anterior margin; propodus, palm convex, defining spine central.

*Gnathopod 2*: coxal margins, anterior 30% and posterior 72% of ventral length, ventral margin convex and slightly sinuous; carpus less than 1/4 the length of propodus, posterior lobe with a short distal seta; propodus, hinge tooth large, conical, not bifid, palmar setae sparse throughout, thumb 30% of article length, distally squared, tip with a minute defining spine, both inner and outer margins setose, posterior margin straight.

*Pereopod 3*: coxa, greatest depth posterior of centre; basis, anterior margin shallowly concave; merus, anterior margin with 2 clusters of setae, these setae shorter than article width, article width 95% of length; carpus 49% overlapped by the merus; propodus, width 36% of length.

*Pereopods 5–7*: setae and spines moderately abundant, basis posterodistally produced, anterior margin spinose; merus, posterior margin not spinose.

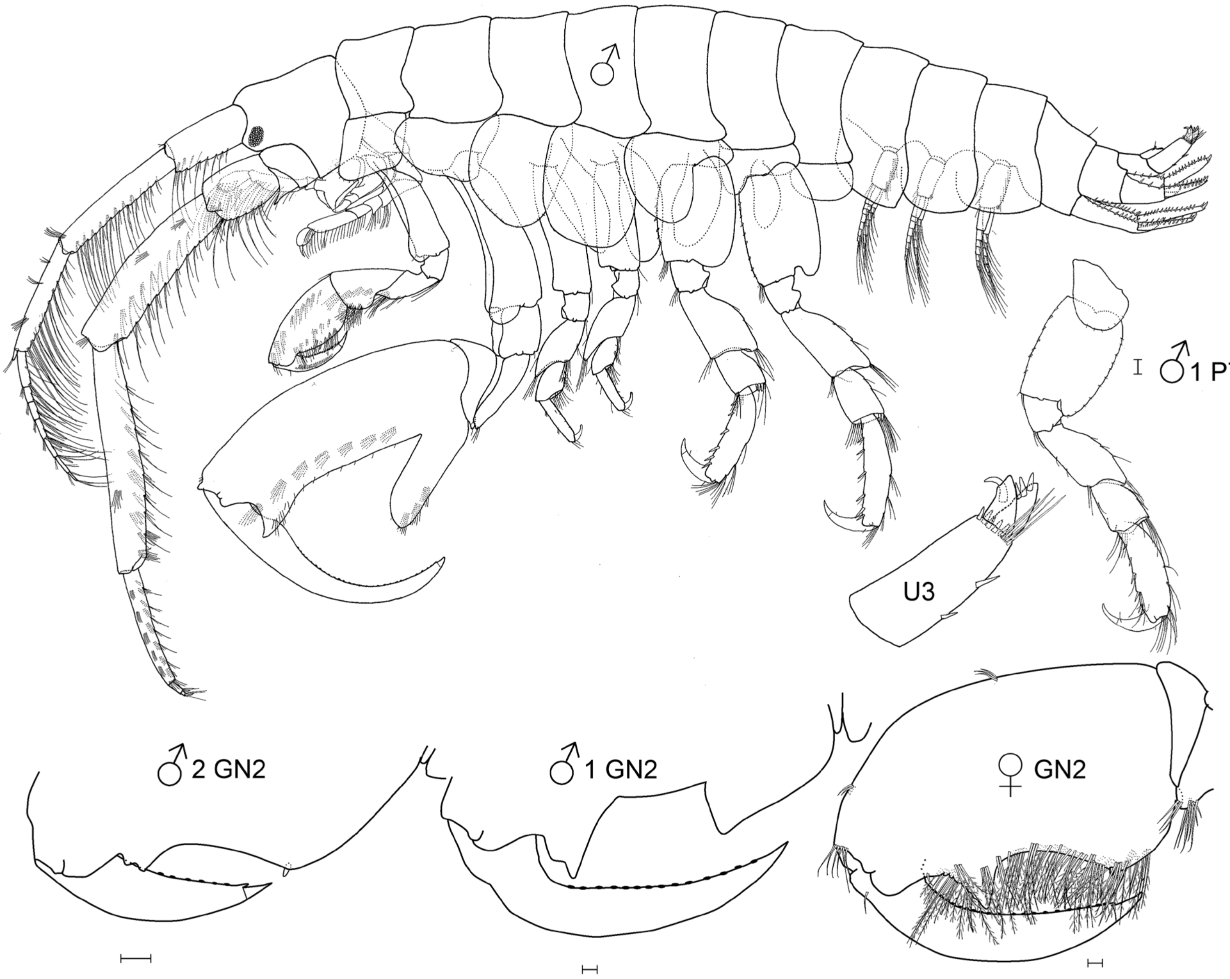



**FIGURE 27.** *Pleojassa multidentata* (Schellenberg, 1931). Male, 8.0 mm and male 1, 7.4 mm. South Georgia, Swedish Antarctic Expedition (1901–1903), collection date and collector unknown, MfN 22.962. Male 2, paralectotype, 3.7 mm and adult female, lectotype, 7.7 mm. South Georgia, 1883, Deutsche Polar Commission, K. von den Steinen, coll., ZMH K-8028. Setae are omitted from the gnathopod 2 profiles of the male 1 and male 2. All views lateral. Scale 0.1 mm.

*Uropod 1*: peduncle, posteroventral spinous process underlying 38% of the inner ramus, inner and outer rami with 14 and 17 mid-dorsal spines respectively.

*Uropod 2*: peduncle, posteroventral spinous process underlying 27% of the inner ramus.

*Uropod 3*: inner ramus with two spines mid-dorsally.

**Condition.** Previously dried. Without left antennae 1 and 2 flagella, right and left pereopod 7, and right uropod 1 outer ramus. Right appendages, both uropods 1, telson, and mouthparts slide mounted.

**Description of adult female.** Lectotype (here designated): Length 7.7 mm. Character states as in the male except as follows.

*Antenna 2*: article 5 without plumose setae.

*Gnathopod 2*: propodus, hinge tooth pronounced, anterior margin crenulated, palmar setae dense throughout, sufficiently so to obscure the palm's shape.

**Condition.** Ovigerous. Previously dried. Without left pereopods 3, 6 and 7, and right pereopods 4–7.

**Variation.** Maximum body length: male 8.0 mm, female 9.1 mm. The number of antennal articles is constant over body length and sex. Larger males show a shortening of the second antennal setae and a change in the shape of the second gnathopod palm (Fig. 27). The dactyl's inner margin also changes shape from evenly convex to proximally expanded and sinuous.

**Type material examined.** Lectotype, ♀ (ZMH K-8028) and paralectotypes (ZMH, K-33618, K-33620, K-33622, K033623, K-33625, K-33631 and K-33632, all from K-8028), station 7813, Moltke Hafen, Royal Bucht, South Georgia (54°30′58″S, 36°0′45″W), 1883, Deutsche Polar Commision, K. von den Steinen, coll.

**Other material examined.** South Georgia: Moltke-Hafen (54°30′58″S, 36°0′45″W), Deutsche Polar Commission, 2 August 1899, 1 ♀, 1 juvenile (ZMH K-8019); specific location not given, Deutsche Polar Commission, K. von den Steinen, coll., 16 January 1884, 2 ♀♀, 4 juveniles (ZMH K-8021); stn. 7804, low ebb, K. von den Steinen, coll., 16 January 1884, Deutsche Polar Commission, K. von den Steinen, coll., 5 juveniles (ZMH K-8017A); Jason Hafen, station 19 (54°14′S, 36°31′W), 10–15 m depth, small stones, 23 April 1902, 1 juvenile (NRM 3676); Kochtopfbucht, Grytviken, station 35 (54°22′S, 36°28′W), 2–8 m depth, the inside edge of the *Macrocystis* formation, stone bottom, 12 June 1902, 1 juvenile (NRM 3677); mouth of the Moraine Fjord, 5 m depth, stone bottom, 15 January 1902, 1 ♀ (NRM 3678); specific location not given, Swedish Antarctic Expedition of 1901–1903, 1 ♂, 4 ♀♀, 13 juveniles (MfN 22.962).

**Remarks.** In his type description of *Jassa multidentata*, Schellenberg (1931) notes having examined specimens from the Swedish Museum of Natural History (collected in 1902, during the Swedish Antarctic Expedition of 1901–1903 from four locations in South Georgia), and from the Hamburg Museum (from South Georgia, but locations and collection dates not specified). Specimens examined for this study are listed above**.** The type designation is limited to the Hamburg material, selecting the 7.7 mm adult female of K-8028 as lectotype. Pertinent additional information on this sample was provided by H. Petersen, ZMH, 15 January 1988: "The material from K-8028 = Jassa multidentata Schellenberg, 1931 is, however, originally derived from the sample K-8017 = Jassa ingens Pfeffer**.** Since Schellenberg was also at the disposal of the material from the German Station in South Georgia (in 1882-1883) with the compiled Amphipod material from Pfeffer, we are assuming that Schellenberg has presented the material from Jassa ingens to Pfeffer only for comparison**.** It is presumed that Schellenberg separated from this sample - which also had been revised earlier by Chilton - Specimen which belonged to Jassa multidentata. It would be advisable to point that this location is not mentioned in the original description from Schellenberg (1931)**.** By this, we are presuming that the material has really been presented to Schellenberg during the time of determination."

*Pleojassa multidentata* differs from *P. orientalis* in the shape of the gnathopod 2 palm (both sexes) (Figs 27 and 28), and by possessing a cluster of short setae at the anterodistal margin of the carpus of gnathopod 1, which is absent in *P. orientalis***.** *Pleojassa multidentata* is only known from South Georgia while *P. orientalis* is only known from Macquarie Island (Fig. 2).

### *Pleojassa orientalis* n. sp.

(Fig. 28)

**Description of adult female.** Holotype: Length 9.8 mm**.**

*Antenna 2*: overlapped by antenna 1 to the end of article 5; article 5, posterior margin bearing long simple setae only, without plumose setae; flagellum 3 articles, article 1 89% of the full flagellum length**.**

*Mandible*: palp articles 2 and 3 without a dorsal fringe of setae; raker spines, number not measured**.**

*Gnathopod 1*: coxal margins, anterior 140% of dorsal length; ventral margin shallowly convex; basis, anterior margin with a few short setae distally, posterior margin not setose; carpus, length 75% of propodus length, posterior lobe 59% of anterior margin length, without an anterodistal setal cluster; propodus, palm convex, with two defining spines slightly proximal of centre**.**

*Gnathopod 2*: coxal margins, anterior 44% and posterior 73% of ventral length; ventral margin shallowly concave; carpus less than 1/4 the length of propodus; propodus, hinge tooth large and conical, not anteriorly bifid, palmar setae plumose, distributed throughout the palm, but not so dense as to obscure the palm's shape, palmar angle acute, with a single, minute spine at its corner; dactyl, inner margin slightly sinuous**.**

*Pereopod 3*: coxa, greatest depth posterior of centre; basis, anterior margin shallowly convex; merus, anterior marginal setae in well separated clusters, central setae, length 1/2 or less the article width, article width 72% of length; carpus 42% overlapped by merus; propodus, width 48% of length**.**

*Pereopods 5–7*: setae and spines moderately abundant, basis posterodistally produced, anterior margin spinose; merus, posterior margin not spinose**.**

*Uropod 1*: peduncle, posteroventral spinous process underlying 52% of the inner ramus, inner and outer rami with 10 and 6 mid-dorsal spines respectively**.**

*Uropod 2*: peduncle, posteroventral spinous process underlying 42% of the inner ramus**.**

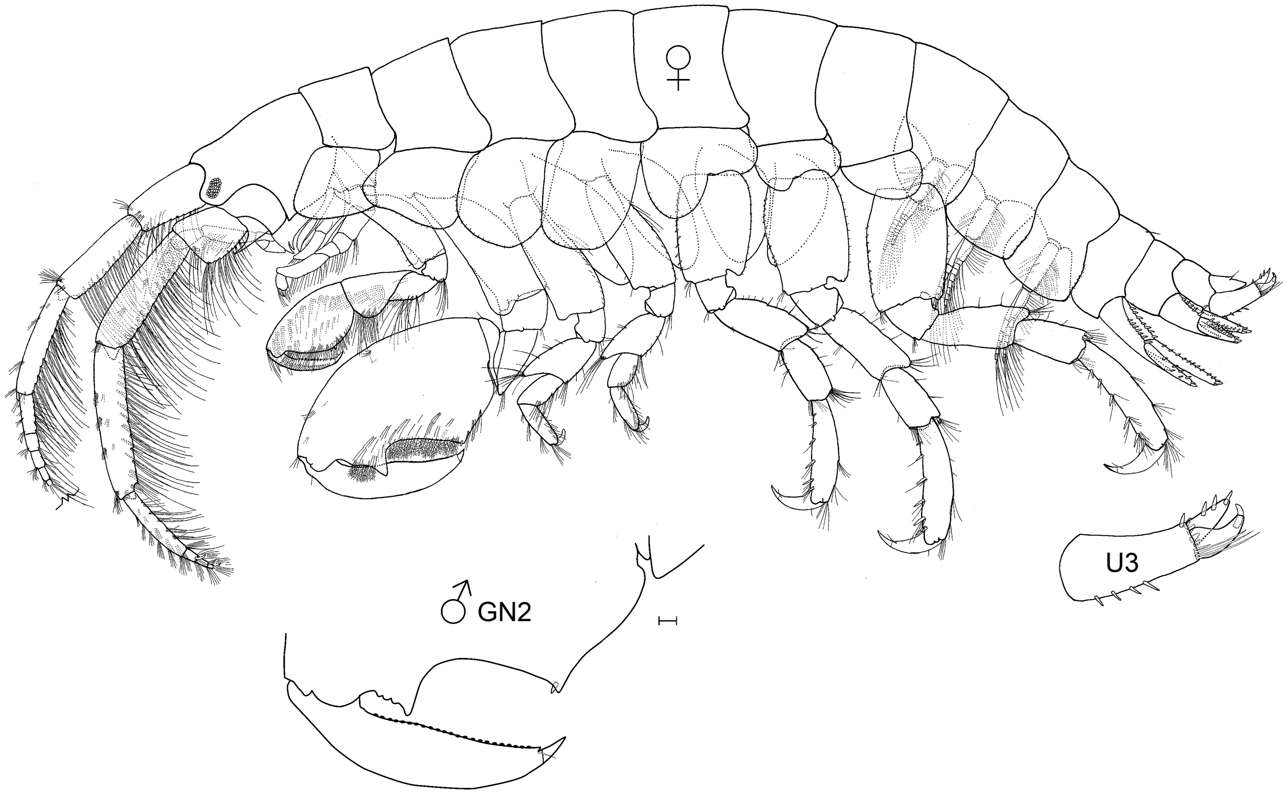



**FIGURE 28.** *Pleojassa orientalis* **n. sp.** Holotype, adult female, 9.8 mm and male, paratype, ~6.5 mm (full length estimated from comparison with the female as body posterior to segment 4 missing)**.** Southeast corner of Gorilla Head Rock, Macquarie Island, Australia (54°29′S, 158°58′E), 23 December 1977, J. K. Lowry, coll., AM P.34955, station no. MA-147**.** Setae are omitted from the male gnathopod 2 profile**.** All views lateral**.** Scale 0.1 mm.

*Uropod 3*: inner ramus with 2 spines mid-dorsally.

**Condition.** Without left pereopod 5 and right pereopod 6**.** Flagellum of right antenna 1 lacking terminal article(s)**.** Right appendages, left pereopod 6, and telson slide mounted.

**Description of male.** Allotype: Length approximately 6.5 mm; head to end of segment 6, 3.9 mm**.** Character states as in the female except as follows.

*Antenna 2*: article 5, filter setae half or less the length of those in the female, interspersed with plumose setae**.**

*Gnathopod 2*: as in the female, but palm less densely setose and dactyl inner margin straight.

**Condition.** Without body segments posterior of segment 6, antennae 1 flagella, left antenna 2 distal flagellum, right antenna 2, left pereopods 5–7, and right pereopods 5 and 7.

**Variation.** Maximum body length: male unknown, female 9.8 mm**.** The male is 2/3 the body length of the adult female holotype (judging by relative difference in head length)**.** This suggests that this male may not yet be mature, so it cannot be assumed that larger males lack a thumb as illustrated for the smaller male**.** Due to lack of material, sexual variation and growth is not well known and only can be inferred from congeners**.** Judging by its close resemblance to *P. multidentata*, in which the male is known to grow a thumb, this development is probably similar in *P. orientalis***.** The small male bears plumose setae on the antenna 2 while the adult female lacks plumose setae**.** However, as in *P. wandeli*, larger females may have plumose setae.

**Type material examined.** Holotype, ♀, ovigerous (AM), type no. P.34955, station no. MA-147, Macquarie Island: Gorilla Head Rock, southeast corner (54º29′S, 158º58′E), 23 December 1977, in a small *Durvillea antarctica* holdfast, 8 m**.** Allotype, small (juvenile?) ♂ (AM), type no. P.37924, same location**.** Paratype, juvenile ♀ (AM), type no. P.37925, same location**.**

**Etymology.** In reference to the eastern location of the species relative to *P. multidentata*.

**Remarks.** *Pleojassa orientalis* differs from *P. multidentata* in the shape of the gnathopod 2 palm (both sexes) (Figs 27 and 28), and in lacking a cluster of short setae at the anterodistal margin of the carpus of gnathopod 1, which is present in *P. multidentata*. *Pleojassa orientalis* may prove to be a geographic variant of *P. multidentata*, given the wide longitudinal range that Southern Hemisphere species can have (Figs 1 and 2). They are given separate species status herein because these morphological differences are key characters for distinguishing species in *Jassa* (Conlan *et al.*, in press) and this may be the same case in *Pleojassa* and other relatives of *Jassa*.

### *Pleojassa wandeli* (Chevreux, 1906) new combination
(Figs 29–34)

*Jassa wandeli* Chevreux, 1906, 94–99, Figs 54–56; 1913, 181, Fig. 61; J. L. Barnard, 1958, 85.
*Jassa falcata*: Sexton & Reid, 1951, 73–74; (form 1) Thurston, 1974a, 46–47: 1974b, 101–102; Lowry & Bullock, 1976, 73.

**Description of male.** (Not type; Billie Rocks, Signy Island, South Orkney Islands, 5 March 1965, M. H. Thurston, coll. (NHM 1969:735:39 station 10 (95))**.** Length 9.8 mm**.**

*Antenna 2*: overlapped by antenna 1 to midway along article 5; article 5 and flagellum, posterior margin covered in a mass of plumose setae; simple setae absent; flagellum 3 articles, the last half the length of the second; article 1 87% of full flagellum length**.**

*Mandible*: palp articles 2 and 3 without a dorsal fringe of setae; raker spines 4 right, 5 left**.**

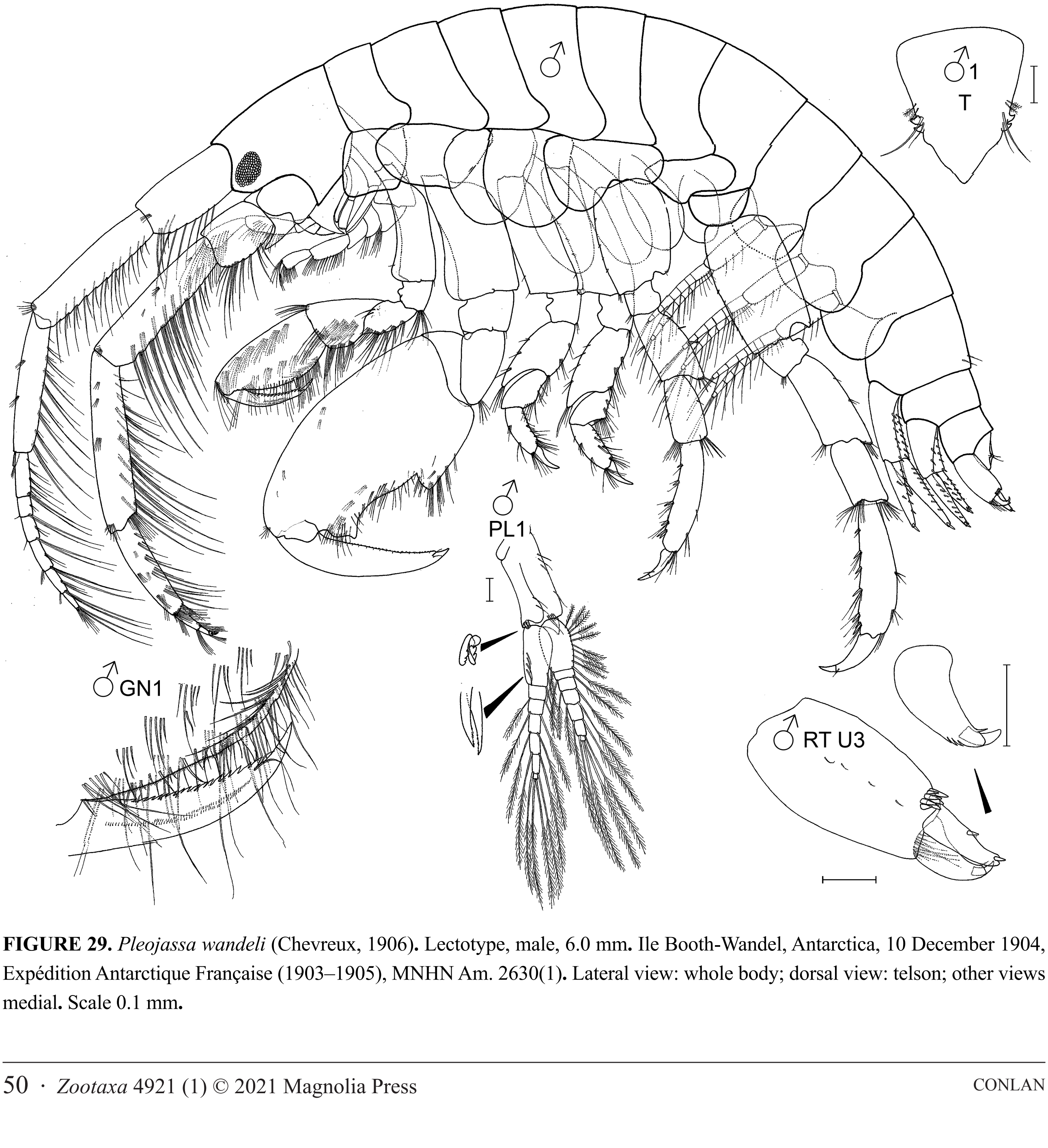



**FIGURE 29.** *Pleojassa wandeli* (Chevreux, 1906)**.** Lectotype, male, 6.0 mm**.** Ile Booth-Wandel, Antarctica, 10 December 1904, Expédition Antarctique Française (1903–1905), MNHN Am. 2630(1)**.** Lateral view: whole body; dorsal view: telson; other views medial**.** Scale 0.1 mm**.**

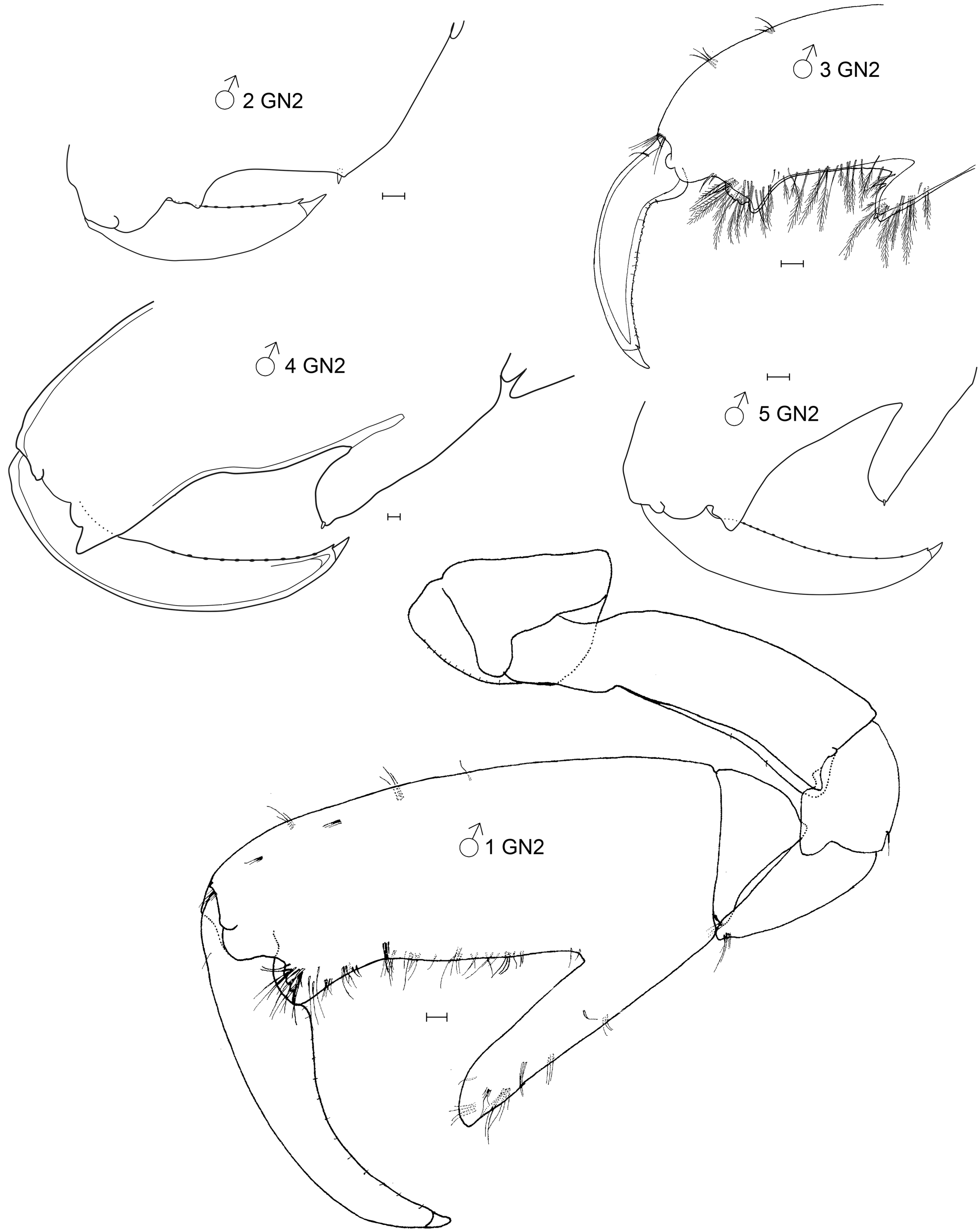



**FIGURE 30.** *Pleojassa wandeli* (Chevreux, 1906)**.** Variation in the male gnathopod 2 propodus and dactyl, with the palmar defining spine as a landmark**.** Note the internal thumbed cuticle in males 3 and 4**.** Male 1, 9.8 mm and male 3, 6.3 mm, Billie Rocks, Signy Island, South Orkney Islands, 5 March 1965, M. H. Thurston, coll., NHM 1969:735:39, station no. 10(95)**.** Male 2, 4.0 mm, Berntsen Point, Signy Island, South Orkney Islands, 21 April 1964, M. H. Thurston, coll., NHM 1969:752:15, station no. 33 (1427) pt**.** Male 4, 9.3 mm, Ile Petermann, 565, Pourquoi pas? Antarctica 1908–1910, 2e Miss. Charcot 1912, 16 Nov. 1909, MNHN Am. 2627**.** Male 5, 6.6 mm, Kerguelen Island, Antarctica (49.30°S, 69.30°E), 13 Feb. 1966, D. Bellan-Santini loan**.** Lateral views: males 2, 4 and 5 (setae omitted); medial views: males 1 and 3**.** Scale 0.1 mm.

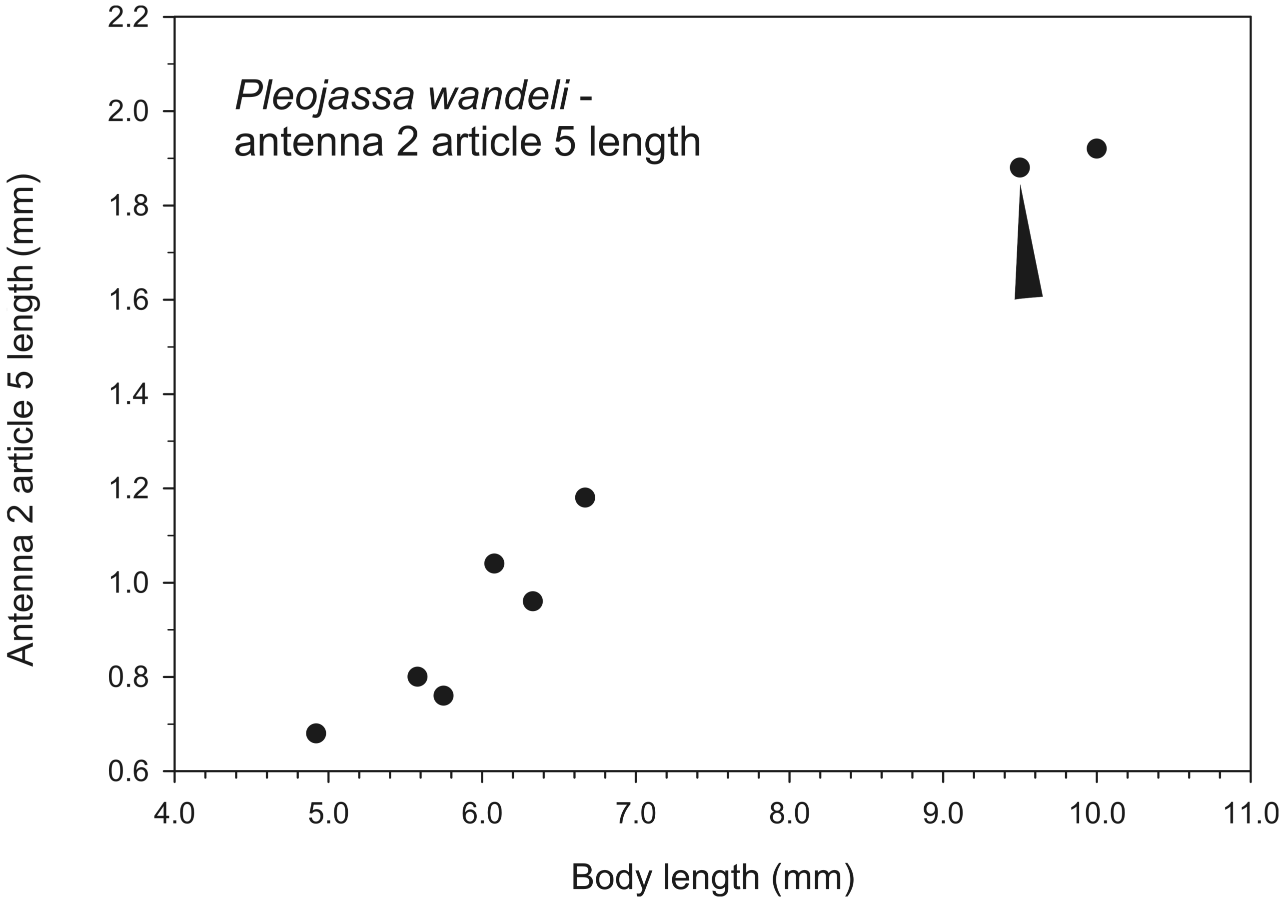



**FIGURE 31.** *Pleojassa wandeli* (Chevreux, 1906)**.** Variation in antenna 2 article 5 length relative to body length in males from a single population (Billie Rocks, Signy Island, South Orkney Islands, 5 March 1965, M. H. Thurston, coll., NHM 1969:735:39, station no. 10(95))**.** The male 1 illustrated in **FIGURE** 30 is indicated by an arrow**.** Linear regression assumptions failed for this plot**.**

*Gnathopod 1*: coxal margins, anterior 113% of dorsal length; ventral margin straight; basis, anterior margins with a few fine setae spaced along their length, posterior margin with a single distal seta; carpus, length 65% of propodus length, posterior lobe 50% of anterior margin length, anterodistal setal cluster short, 39% of the anterior margin length; propodus, palm convex, with one defining spine slightly proximal of centre**.**

*Gnathopod 2*: coxal margins, anterior 21% and posterior 83% of ventral length, ventral margin straight; carpus less than a quarter the length of the propodus, posterior lobe without a distal seta; propodus, palm, hinge tooth rectangular cuboid, shallowly bifid centrally, setae sparse but spread throughout the palm, thumb 36% of propodus length, distally squared, posterior margin straight, with clusters of setae subapically, and 3 groups posteriorly, and with 1 minute defining spine at its tip**.**

*Pereopod 3*: coxa, greatest depth at the centre; basis, anterior margin straight; merus, anterior marginal setae in discrete, well spaced clusters, about a third the article width, article width 61% of length; carpus 44% overlapped by the merus; propodus, width 56% of length**.**

*Pereopods 5–7*: setae and spines moderately abundant, basis posterodistally produced, anterior margin spinose; merus, posterior margin not spinose**.**

*Uropod 1*: peduncle, posteroventral spinous process underlying 38% of the inner ramus, inner and outer rami with 7 and 13 mid-dorsal spines respectively**.**

*Uropod 2*: peduncle, posteroventral spinous process underlying 10% of the inner ramus**.**

*Uropod 3*: inner ramus with 2 dorso-medial spines.

**Condition.** Without the left pereopod 5**.** Right appendages, telson and mouthparts slide mounted**.** Remaining appendages with the carcass.

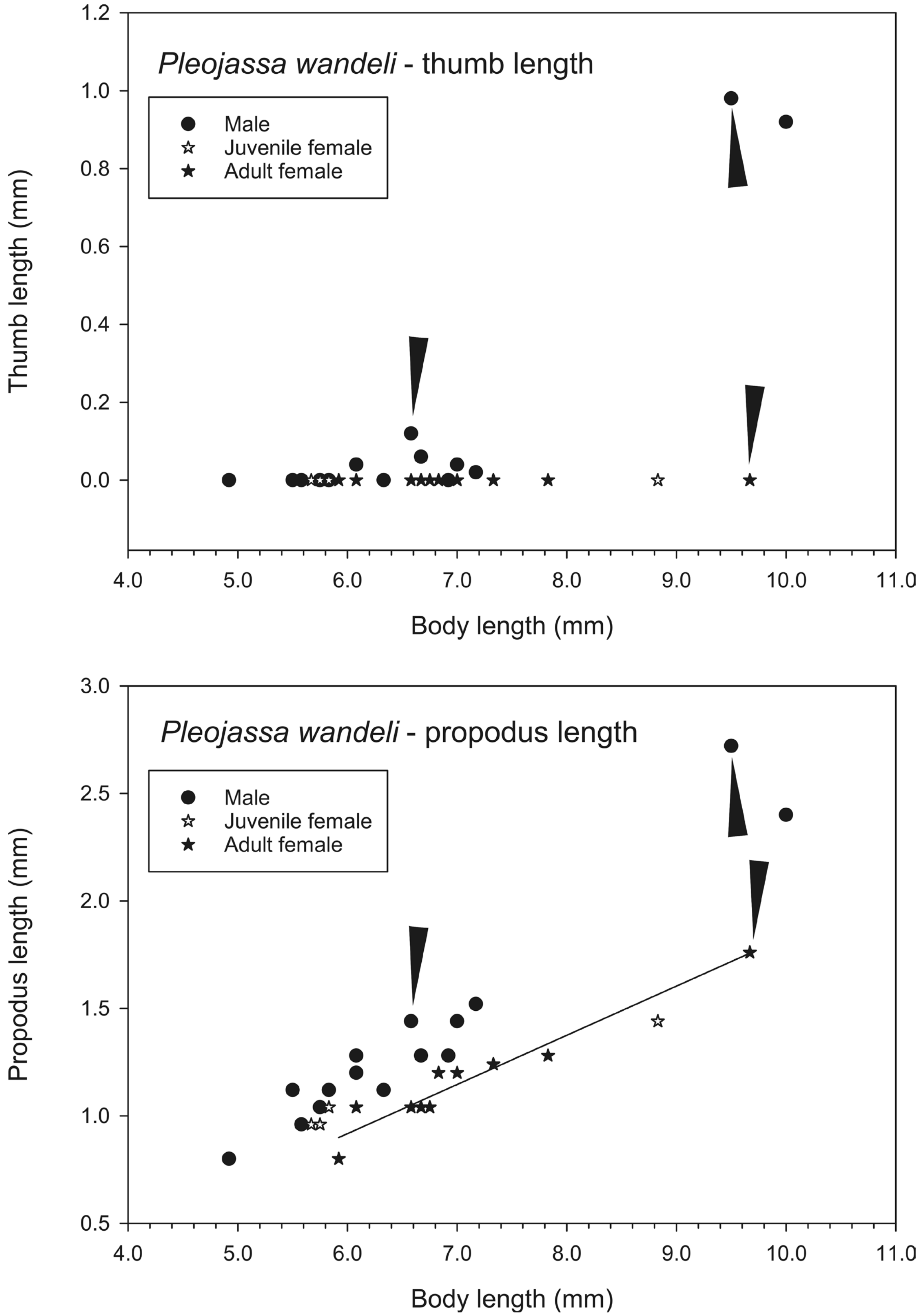



**FIGURE 32.** *Pleojassa wandeli* (Chevreux, 1906)**.** Variation in gnathopod 2 thumb length and propodus length relative to body length in males and females from a single population (Billie Rocks, Signy Island, South Orkney Islands, 5 March 1965, M. H. Thurston, coll., NHM 1969:735:39, station no. 10(95))**.** The male 1 and male 3 illustrated in **FIGURE 30** and the female illustrated in **FIGURE 33** are indicated by an arrow**.** Linear regression assumptions passed for the adult female**.** Linear regression statistics: Adult female, thumb length = -0.455 + 0.229 x body length, $r^2$ = 0.932, *n* = 11**.**

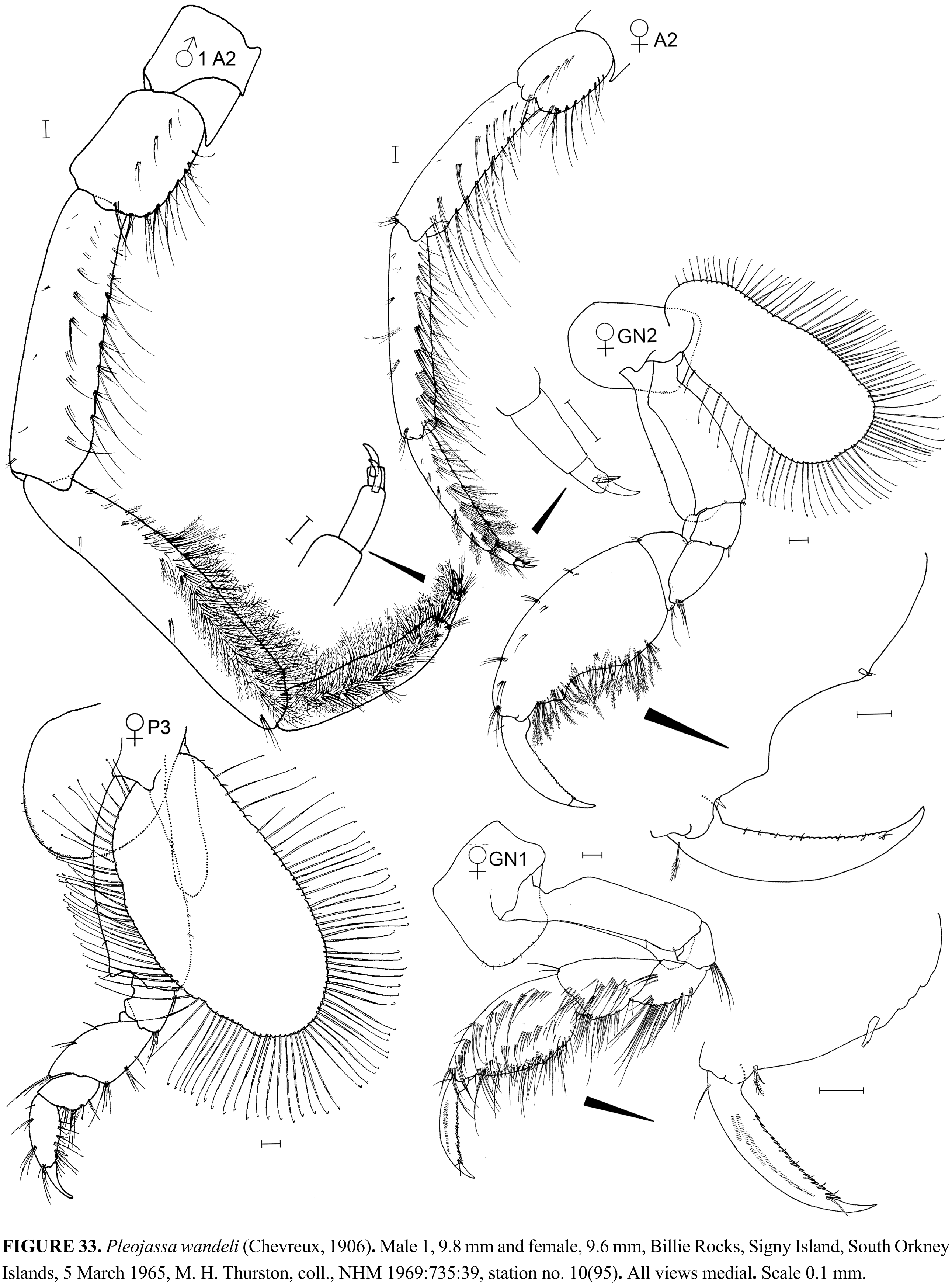



**FIGURE 33.** *Pleojassa wandeli* (Chevreux, 1906)**.** Male 1, 9.8 mm and female, 9.6 mm, Billie Rocks, Signy Island, South Orkney Islands, 5 March 1965, M. H. Thurston, coll., NHM 1969:735:39, station no. 10(95)**.** All views medial**.** Scale 0.1 mm.

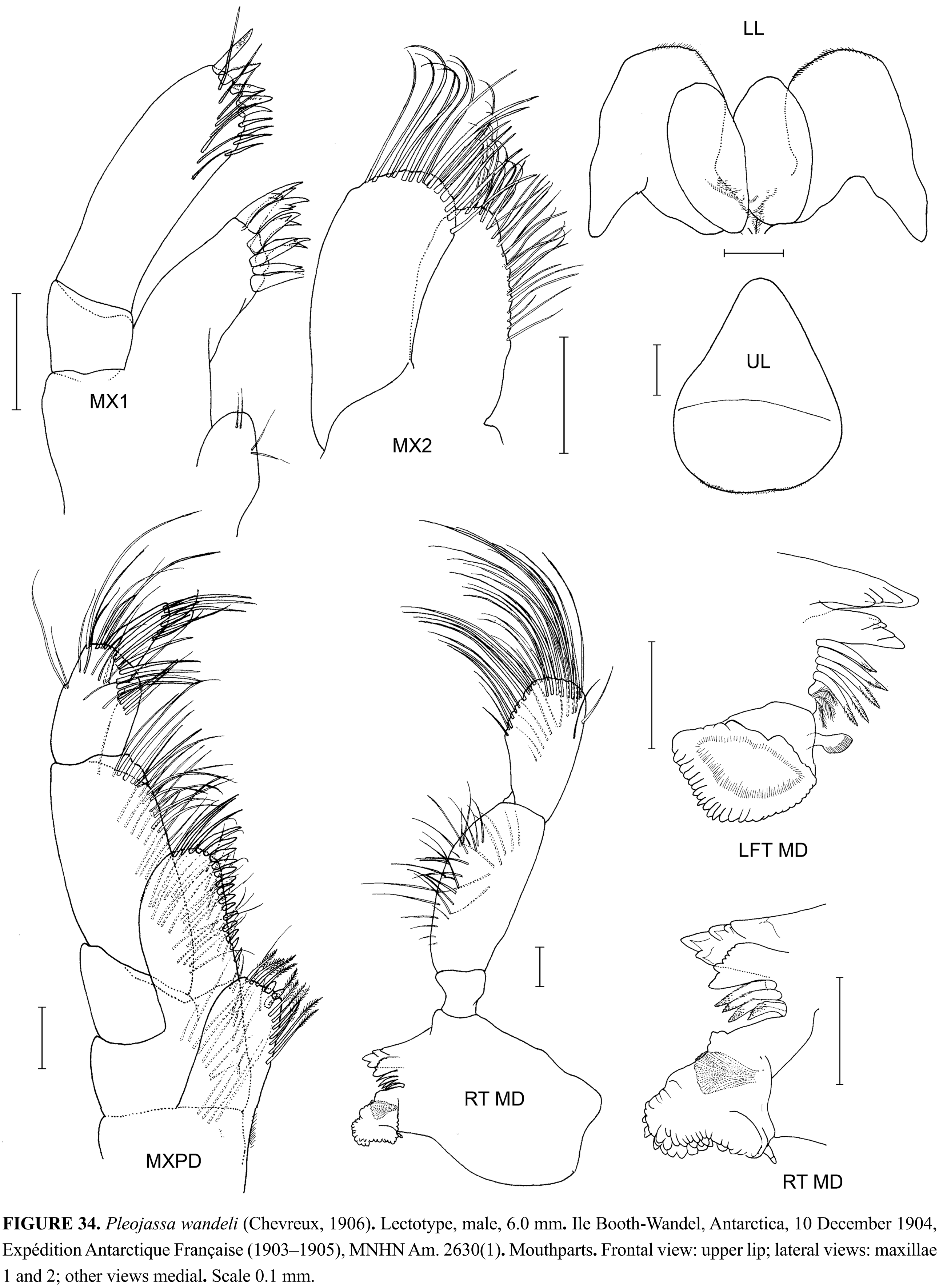



**FIGURE 34.** *Pleojassa wandeli* (Chevreux, 1906)**.** Lectotype, male, 6.0 mm**.** Ile Booth-Wandel, Antarctica, 10 December 1904, Expédition Antarctique Française (1903–1905), MNHN Am. 2630(1)**.** Mouthparts**.** Frontal view: upper lip; lateral views: maxillae 1 and 2; other views medial**.** Scale 0.1 mm.

**Description of adult female.** (Not type; same location as for the male). Length 9.6 mm. Character states as in the male except as follows.

*Antenna 2*: article 5, posterior margin with long simple setae mainly, but interspersed with a few plumose setae.

*Gnathopod 2*: coxal margins, anterior 56% and posterior 94% of ventral length, ventral margin convex; propodus, hinge tooth strongly pronounced, palmar setae densely plumose throughout, so much so as to nearly obscure the shape of the palm.

**Condition.** With all appendages. Right appendages, telson, and mouthparts slide mounted. Left appendages with the carcass.

**Variation.** Maximum body length: male 10.8 mm, female 9.7 mm. In small individuals of both sexes, the filter setae on antenna 2 are long and plumose setae are absent. In the adult female, these long filter setae are also present along with some plumose setae on the flagellum (Fig. 33). In larger males, with or without thumbs, the filter setae are shorter and mixed with dense plumose setae. In the specimens available, plumose setae were evident at ≥5.5 mm body length. Males of a single population appeared to show a linear increase in antenna 2 article 5 length with body length (Fig. 31).

Large males have long thumbs on the propodus of gnathopod 2 but unlike *Jassa*, development may be gradual over more than one molt (Conlan, 1989). This is indicated in the short thumbed male in Fig. 30, where a somewhat longer thumb was visible inside the cuticle. In *Jassa*, a thumb that is visible within the cuticle is always much longer than the subadult's small "pre-thumb" (Conlan *et al.* in press). The thumb develops at the location of the single palmar defining spine. This spine, though small, can be seen at the tip of the thumb, even on some long-thumbed specimens. In the population graphed, the gnathopod 2 propodus was longer in the males than females of the same length (Fig. 32) and the relationship to body length appears to be linear in both sexes (although lack of mid-sized specimens in the males caused failure of the Durbin-Watson statistic for independent residuals and the Constant Variance Test using Spearman rank correlations). The shape of the gnathopod 2 dactyl margin also varies. In females of all sizes and in small males, the inner margin is straight. In males with a long thumb, the dactyl is curved and proximally produced (Fig. 30).

**Type material examined.** Lectotype (here designated), ♂, Ile Booth-Wandel, Antarctica, 10 December 1904, Mission Charcot, among sponges at low tide, Expédition Antarctique Française (1903–1905) (MNHN, catalogue no. Am. 2630(1)). Paralectotypes, 1 ♀, 13 juveniles, same location.

**Other material examined.** (excluded from type series): South Georgia: Royal Bucht, Moltke Hafen (54°15′S, 36°0′45″W), 31 Aug. 1883, K. von den Steinen, coll., Deutsche Polar Commision 1882–1883, 1 juvenile (ZMH K-32085 ex 22473).

South Sandwich Group: Visokoi I. (56°42′S, 27°12′W), 13 Nov. 1908, C. A. Larsen, coll., 18–31 m depth, 1 ♀ (MfN), 1 juvenile (UiO F2973).

Petermann I.: Pourquoi Pas?, Antarctica 1908–1910, 2$^{e}$ Mission Charcot 1912, 1 Nov. 1909, 1 ♂, 1 ♀ (MNHN Am. 2628); Pourquoi Pas?, Antarctica 1908–1910, 2$^{e}$ Mission Charcot 1912, 16 Nov. 1909, M. le Dr. Liouville, coll., 6 ♂♂, 2 ♀♀ (MNHN Am. 2627).

South Shetland Islands: Deception I. (62°57′S, 60°38′W), 17 Dec. 1927, C. Olstad, coll., 25 m depth, Norvegia Expedition No. 58, ~15 individuals, not sexed (UiO F2970),

Kerguelen I.: S. baie du Morbihan, Port-Douzième, *Durvillea antarctica* holdfast, 13 Feb. 1966, J. C. Hureau, coll., littoral (D. Bellan-Santini loan), 1 ♂.

South Orkney Islands: 46 collections from Billie Rocks, Berntsen Point, Elephant Flats, and Factory Cove, Signy Island, Dec., Apr. and June 1964 and Feb.–Apr. 1965, ~230 specimens, M. H. Thurston, coll. (NHM stations 1, 3, 4, 10, 13, 15–20, 22–26, 29, 30, 32, 33, 35, 46, 49 and 51).

**Remarks.** *Pleojassa wandeli* resembles *P. multidentata* in thumb development and overall appearance. The latter can be distinguished by the shorter seta at the anterodistal junction of the carpus and propodus of gnathopod 1, lack of antenna 2 plumosity in the adult, denser plumosity of the gnathopod 2 palm in the female and juvenile, more pronounced hinge tooth, and pronounced uropod 2 peduncular process.

Chevreux (1913) listed an additional specimen collected on Petermann Island at Port-Circoncision, 10 Oct. 1909, collected at 6 m depth from algae. This has not been seen but the other two collections listed were examined (listed above), which includes the long thumbed male illustrated by Chevreux (1913). A smaller male from Petermann Island (collected 16 Nov. 1909), showing an internal thumbed cuticle is illustrated in Fig. 30. Schellenberg (1926) may have been describing *P. wandeli* when he listed "*Jassa falcata"* from Kerguelen Island, collected in January 1902 during the Deutsche Südpolar-Expedition 1901–1903. Although not seen, these specimens are within the size range and location known for *P. wandeli* (females adult at 7–9.5 mm). This would make the first known collection of *P. wandeli* from Kerguelen Island much earlier than the 1966 collection of "*Jassa falcata*" lent by D. Bellan-Santini and confirmed to be *P. wandeli* (Table 2). Additional collections of "*Jassa falcata*" from Kerguelen and Crozet Islands reported by Bellan-Santini & Ledoyer (1973, 1974) are likely *P. wandeli* as well. No other species of *Pleojassa*, *Hemijassa* or *Jassa* are known from these islands. This would also expand the known range of *P. wandeli* to the Crozet Islands. Thurston (1974b) collected 572 specimens at Signy Island, naming them "*Jassa falcata* form 1". Many of these were examined for this study and are confirmed *P. wandeli*. Thurston (1974a) noted that his "*Jassa falcata*" from Deception Island (62.98°S 60.65°W), Hope Bay (63.3833°S, 56.9833°W), Port Lockroy (64.8252°S, 63.4945°W) and the Argentine Islands (65.25°S, 64.27°W) agreed with Chevreux' (1906) description and figures of *Pleojassa wandeli*. Kim *et al.* (2014) found *P. wandeli* in a scuba collection at 20–30 m depth in Marian Cove, King George Island (62°12′06.48″S, 58°44′03.14″W). They included a photograph of the left lateral side of a live animal, showing the dorsum, coxae, antennae and distal part of the gnathopods pigmented dark brown. There was a contrasting reduced or lack of pigmentation around the edges of the articles, on the proximal parts of the gnathopods, and on the pereopods.

## Generic relationships within the Ischyrocerini

With the addition of *Plumulojassa*, *Hemijassa,* and *Pleojassa* to the Ischyrocerini and the consideration of new characters, the Ischyrocerini is herein modified from earlier diagnoses by Myers & Lowry (2003), Souza-Filho & Serejo (2014) and Just (2017). Additions to the latter are highlighted in bold. Characteristics of the component genera are detailed in Supplementary Table S2. Generic changes to *Neoischyrocerus* (Supplementary Table S3) and *Ischyrocerus* (Supplementary Table S4) are also made. Finally, an illustrated key is given to all the known genera of the Ischyrocerini to place the new genera in the context of the larger tribe.

## Tribe Ischyrocerini Krøyer, 1838

Supplementary Table S2

**Type genus.** *Ischyrocerus* Krøyer, 1838

**Diagnosis (with changes from Just (2017) in bold).**

*Antennae*: slender, antenna 1 with accessory flagellum (occasionally vestigial).

*Mandible*: palp with 3 articles, **the third expanded distally (occasionally similar in shape to the second)**.

*Coxae 1–4*: **progressively deepening, subrectangular to oval** (occasionally coxa 1 much smaller than and mostly obscured by coxa 2 and differing in shape), margins entire.

*Gnathopod 1*: carpus shorter than the propodus (occasionally longer), propodus oval to weakly subchelate.

*Gnathopod 2*: propodus in adult male (**and occasionally in the female**) moderately to strongly enlarged compared to gnathopod 1, of varying shape (**occasionally hardly modified**).

***Pereopods 3–4*: merus moderately to fully overlapping the carpus anteriorly, dactyl shorter than the carpus (occasionally longer).**

*Pereopods 5–7*: of similar form, increasing in length backwards (**occasionally 6 larger than 5 and 7**).

*Urosomites*: 1–3 free.

*Uropods 1 and 2*: peduncle without distoventral corona **of spines**, with 2 subequal rami **with or without an underlying peduncular spinous process (occasionally uropod 2 outer ramus modified**).

*Uropod 3*: peduncle long (**occasionally short**), broad proximally, narrow distally, biramous (**occasionally uniramous), outer ramus terminating in cusps and/or spine(s**).

*Telson*: entire, **with one to many dorsally or apically projecting setae or spines**.

**Component genera.** *Jassa* Leach, 1814; *Ischyrocerus* Krøyer, 1838; *Paradryope* Stebbing, 1888; *Microjassa* Stebbing, 1899; *Parajassa* Stebbing, 1899; ***Hemijassa* Walker, 1907**; *Isaeopsis* K.H. Barnard, 1916; *Pseudischyrocerus* Schellenberg, 1931; *Bathyphotis* Stephensen, 1944; *Ventojassa* J.L. Barnard, 1970; *Neoischyrocerus* Conlan, 1995; *Scutischyrocerus* Myers, 1995; *Ruffojassa* Vader & Myers, 1996; *Veronajassa* Vader & Myers, 1996; *Alatajassa* Conlan, 2007; *Myersius* Souza-Filho & Serejo, 2014; ***Pleojassa* n. gen.; *Plumulojassa* n. gen.**

## Changes to *Ischyrocerus* and *Neoischyrocerus*

*Ischyrocerus* is primarily a cold water, Northern Hemisphere genus, captured from deep trawls (Stephensen 1944; Gurjanova 1951) as far north as the high Arctic, but also found in the intertidal and shallow subtidal zone (J.L. Barnard 1962). It has been extensively found in the Southern Hemisphere as well, though mostly in warmer waters (Myers 1995, 1997; Just 2009). This large genus requires revision and may prove to be less cosmopolitan than previously thought by J.L. Barnard & Karaman (1991).

Three genera have been created for warm water *Ischyrocerus*-like species: *Neoischyrocerus* Conlan, 1995 (4 species), *Coxischyrocerus* Just, 2009 (2 species) and *Tropischyrocerus* Just, 2009 (2 species). These genera embrace species in which the male develops an enormously lengthened and pendulous gnathopod 2 (about 200–300% the length of gnathopod 1) with an anteriorly rounded ischium and a very long propodus with the palm nearly the full length of the propodus, and the proximal end of the palm marked by a bulge next to the carpus (the S. Californian *N. claustris* (J.L. Barnard, 1969), *N. chinipa* (J.L. Barnard, 1979) from the Galapagos and Pacific Panama, *N. vidali* Ortiz & Lalana, 2002 from the Cuban Caribbean, *C. inexpectatus* (Ruffo, 1959) from the Mediterranean Sea and *T. socia* (Myers, 1989) from Bora Bora), a tooth-like projection (e.g., *N. lilipuna* (J.L. Barnard, 1970) from Hawaii and *T. pugilus* Just, 2009 from Australia), or with neither (e.g., *C. rhombocoxus* Just, 2009 from Australia). The dactyl may be the full length of the propodus or shorter, the length growth related. By comparison, the female's gnathopods are similarly sized with the second only slightly larger than the first. Other commonalities are antennae with long filtering setae that are not pediform or sexually dimorphic, a 2-articulate accessory flagellum with the second article minute, pereopods 3 and 4 with little overlap of the merus over the carpus, a well developed peduncular spinous process under the rami of uropod 1, a spiny peduncle of uropod 3 with the outer ramus bearing a row of minute cusps and the inner ramus tipped by a small spine, and the telson with a pair of strong, dorsally projecting spines.

The difficulty with these genera is where species cross the generic boundaries. Examples are: enlarged coxa 2 relative to coxa 1 in the adult male (*C. rhombocoxus* and *N. claustris*), similar gnathopod propodus appearance as noted above, and similar female gnathopod palms (convex in all species in the three genera except for *T. pugilus*), pereopod 3 and 4 propodus posteriorly spinose (*N. lilipuna*, *N. vidali*, *T. socia* and *C. inexpectatus)*. The generic-level differences among the genera therefore recede into issues of sexual variation (e.g., enlargement of coxa 2 relative to coxa 1 that was used to define *Coxischyrocerus* but also occurs in *Neoischyrocerus*, or the modified pereopod 5 basis shape in adult males of *C. rhombocoxus* and *C. inexpectatus*).

Therefore, *Coxischyrocerus* Just, 2009 and *Tropischyrocerus* Just, 2009 are herein merged into the senior genus *Neoischyrocerus* Conlan, 1995. Myers (1995, 1997) noted the need for diminutive Indo-Pacific species placed at that time in *Ischyrocerus* or *Jassa* to be placed in their own genus and these are also included, as noted below.

## Genus *Neoischyrocerus* n. comb.

Supplementary Table S3

**Type species.** *N. claustris* J.L. Barnard, 1969

**Diagnosis. (with differences from *Ischyrocerus* in bold).** Body length at maturity **1–2 mm (usually), rarely 4–6 mm. Tropical and warm temperate** distribution, collected from algae, sponges, corals or from a spiny lobster, **0–16 m, 9–40°N and 5–34°S.**

*Pereon*: dorsally smooth (most species), ridged or carinate (some species)**.**

*Antenna 1*: accessory flagellum 2 articles (second minute), projecting forward or flush with the flagellum; antennae 1 and 2 peduncles **subequal** in width or antenna 2, **10% wider** (based on comparison of antenna 1 peduncle article 2 with antenna 2 peduncle article 4), peduncular setae and setal pattern similar to antenna 1, or slightly shorter, **not plumose.**

*Gnathopod 2, adult male*: **190–350%** the length of gnathopod 1, **basis and propodus especially elongate**; coxa 1, **60–110%** the depth of coxa 2; basis **concave or sinuous**; ischium anteriorly rounded; propodus often slender (posterior length **180–400%** of central width), **palm nearly the full length of the propodus, often with a bulge or tooth defining it proximally at the junction of the carpus (sometimes palm continuous with the carpus), sometimes centrally toothed instead and with shallow bulge or teeth at the junction of the dactyl**; **dactyl half or nearly the full length** of the propodus**.**

*Gnathopod 2, juvenile male*: shorter than the adult male gnathopod 2, palm bearing 1–2 strong spines about midway along the length of the propodus, dactyl ending at the spines**.**

*Gnathopod 2, female*: only slightly larger than gnathopod 1, palm of the propodus convex (usually) or shallowly concave (rarely)**.**

*Pereopods 3 and 4*: propodus, posterior margin bearing **spines or setae**; coxa 4, posterior margin **straight, not shallowly concave.**

*Pereopod 5, male*: similar to but shorter than pereopods 6 and 7 or **variously modified with posteriorly concave basis or posteriorly expanded and spinose merus.**

*Uropod 1*: peduncle with short ventrodistal spinous process underlying the rami, length **~15–35%** of the outer ramus length**.**

*Uropod 3*: peduncle bearing 1–2 rows of spines dorsally, ending in a single spine at the distal margin, but **without a corona of spines** around the margin or setae; rami **without spines mid-dorsally**, outer ramus subequal to or shorter than the inner and bearing **3–8** minute dorsal cusps apically, **without (rarely with) a small apical straight spine**.

**Component species (with transferred species in bold).** ***Ischyrocerus longimanus*** **(Haswell, 1879)** (Australia); ***I. parvus*** **Stout, 1913** (California); ***I. carinatus*** **K.H. Barnard, 1916** (South Africa); ***I. gorgoniae*** **K.H. Barnard, 1940** (South Africa); ***I. ctenophorus*** **Schellenberg, 1953** (South Africa); ***Coxischyrocerus inexpectatus*** **(Ruffo, 1959)** (Mediterranean, Red Sea?); *N. claustris* J.L. Barnard, 1969 (California); *N. lilipuna* J.L. Barnard, 1970 (Hawaii); ***I. oahu*** **J.L. Barnard, 1970** (Hawaii); ***I. oahu oahu*** **J.L. Barnard, 1970** (Hawaii); *N. chinipa* J.L. Barnard, 1979 (Galapagos Islands and Panama); ***I. oahu armatus*** **Ledoyer, 1979** (Madagascar); ***Tropischyrocerus socia*** **(Myers, 1989)** (Bora Bora); ***I. mediodens*** **Myers, 1995** (Papua New Guinea); ***I. parma*** **Myers, 1995** (Papua New Guinea); ***I. apiensis*** **Myers, 1997** (Samoa); *N. vidali* Ortiz & Lalana, 2002 (Cuba); ***C. rhombocoxus*** **Just, 2009** (Australia); ***T. pugilus*** **Just, 2009** (Australia).

**Remarks.** Species of *Ischyrocerus* were transferred to *Neoischyrocerus* if they demonstrated at least one key character (grossly enlarged and pendulous male gnathopod 2 similar in shape to that of others in the genus; dactyls with comb-like striae as noted in J.L. Barnard (1970), Conlan (1995) and Ortiz & Lalana (2002); similar spination on uropod 3)**.** Presence or absence of these striae were not mentioned by other authors, therefore questioning as to whether this character had been looked for**.** Mouthpart characteristics were not widely described, but may be useful for generic definition, especially the clavate vs slenderer shape of the mandibular palp and the presence/absence of a long apical seta on the maxilla 1 inner plate.

**Excluded but uncertain generic status**. *Ischyrocerus kapu* J.L. Barnard, 1970 from Hawaii. The author based the generic assignment on a single male specimen. He noted its resemblance to *N. lilipuna* but also considered that it should be in a new genus. On balance, though, he assigned it to *Ischyrocerus* but noted that this was based on limited information because the specimen lacked antennae and pereopods and the female was also unknown. The male's gnathopod 2 is unusual in having a long conical extension of the merus underneath the propodus, a feature that is not known for either *Ischyrocerus* or *Neoischyrocerus*. Myers (1995) stated that *I. kapu* is congeneric with other species being transferred to *Neoischyrocerus*. The male's propodus is wider than in other members of *Neoischyrocerus*, but its uropod 3 resembles other species of *Neoischyrocerus* rather than *Ischyrocerus*. Further material demonstrating the species' complete morphology is required before it can be confidently transferred to *Neoischyrocerus* or to a new genus.

### Genus *Ischyrocerus* n. comb.

Supplementary Table S4

**Type species.** *Ischyrocerus anguipes* Krøyer, 1838

**Diagnosis (with differences from *Neoischyrocerus* in bold).** Body length at maturity **2–18 mm**, though **most species are >5 mm** long at adulthood**.** Primarily known from the Northern Hemisphere in **cold temperate to polar waters from 32°N** (La Jolla, California; J.L. Barnard 1969) **to 81°N** in the Arctic Ocean (Stephensen 1944), collected from algae, hydroids, crabs or substrate unknown, **1 to ~2000 m. Widely known in Europe but not in the Southern Hemisphere, although one species was found at 42°S off of Chile (J.L. Barnard 1964).**

*Pereon*: dorsally smooth (most species), ridged or carinate (some species)**.**

*Antenna 1*: accessory flagellum 2 articles (second minute), flush with the flagellum or rarely projecting forward; antenna 2 peduncle article 4, **115–170%** wider than antenna 1 peduncle article 2 (or rarely equal width), setae and setal pattern similar to antenna 1 or setae shorter, **occasionally plumose.**

*Gnathopod 2, adult male*: **100–220%** the length of gnathopod 1, **basis usually not especially elongate, propodus elongate and slender or short and broad (rarely similar to gnathopod 1)**; coxa 1 **70–140%** the depth of coxa 2; **basis concave or straight**; ischium anteriorly rounded or straight; **propodus variably shaped, slender or broad** (posterior length **120–290%** of central width), **palm only on the distal portion of the propodus or nearly the full length of the propodus, without a bulge or tooth defining it proximally at the junction of the carpus, palm variously toothed**; dactyl **33–75%** the length of the propodus**.**

*Gnathopod 2, juvenile male*: shorter than the adult male gnathopod 2, palm bearing 1–2 strong spines about midway along the length of the propodus, dactyl ending at the spines**.**

*Gnathopod 2, female*: only slightly larger than gnathopod 1, palm of the propodus convex or concave**.**

*Pereopods 3 and 4*: propodus, posterior margin bearing setae but **not spines; c**oxa 4, posterior margin **straight to shallowly concave.**

*Pereopod 5, male*: similar to but shorter than pereopods 6 and 7 or basis posteriorly concave; **merus not differing.**

*Uropod 1*: peduncle with short ventrodistal spinous process underlying the rami, length **~25–50%** of the outer ramus length**.**

*Uropod 3*: peduncle bearing **0–2 rows** of spines dorsally, **ending in a corona of spines** at the distal margin (**rarely a single seta or single spine)**; rami with 0–1 spines (outer), 0–4 spines (inner), outer ramus subequal to a third shorter than the inner and bearing **0–9** cusps, **occasionally with 1–2 apical spines that are straight or dorsally recurved**.

**Component species.** *Ischyrocerus anguipes* Krøyer, 1838 (N. Europe and Arctic Ocean); *I. latipes* Krøyer, 1842 (Arctic Ocean); *I. minutus* Liljeborg, 1851 (N. Europe); *I. megacheir* (Boeck, 1871) (40°N–80°N, Atlantic to Arctic Ocean); *I. brevicornis* (Sars, 1879) (E. Greenland, Arctic Ocean); *I. tuberculatus* (Hoek, 1882) (Barents Sea, 71°N–77°N); *I. tenuicornis* (Sars, 1885) (N. Europe); *I. nanoides* (Hansen, 1887) (Arctic, Baffin Bay and W Greenland, 61°N –81°N); *I. megalops* Sars, 1894 (N. Europe); *I. commensalis* Chevreux, 1900 (E. Atlantic Canada and Saguenay Fjord); *I. brusilovi* Gurjanova, 1933 (Russian waters); *I. enigmaticus* Gurjanova, 1934 (Kara Sea, 78°58′N); *I. cristatus* Gurjanova, 1938 (Sea of Japan); *I. elongatus* Gurjanova, 1938 (Sea of Japan); *I. rhodomelae* Gurjanova, 1938 (Sea of Japan); *I. serratus* Gurjanova, 1938 (Sea of Japan); *I. hanseni* Stephensen, 1944 (64°N, between Iceland and Greenland); *I. albanovi* Gurjanova, 1946 (Arctic Ocean); *I. laptevi* Gurjanova, 1946 (Arctic Ocean); *I. chamissoi* Gurjanova, 1951 (Russian waters); *I. dezhnevi* Gurjanova, 1951 (Russian waters); *I. krascheninnikovi* Gurjanova, 1951 (Russian waters); *I. stephenseni* Gurjanova, 1951 (Russian waters); *I. pelagops* J.L. Barnard, 1962 (California); *I. hortator* J.L. Barnard, 1964 (off Chile); *I. malacus* J.L. Barnard, 1964 (California); *I. gurjanovae* Kudrjaschov, 1975 (Kurile Islands); *I. tzvetkovae* Kudrjaschov, 1975 (Kurile Islands); *I. fractus* King & Holmes, 2004 (Ireland).

**Remarks.** Species were retained in *Ischyrocerus* if they lacked the key characters noted above for *Neoischyrocerus* in the appearance of the male gnathopod 2, pereopod dactyls or uropod 3 spination pattern**.** *Ischyrocerus fractus* is the only species known in this genus where the male's gnathopod 2 propodus is very little different from the female's**.** It is also the smallest known at adulthood for this genus (2 mm).

**Excluded, but uncertain generic status.** *Ischyrocerus camptonyx* Thurston, 1974b from subantarctic Signy Island is not *Ischyrocerus*. It is possibly an undescribed species of *Jassa* or synonymous with *J. alonsoae*, in which case Thurston's name would take precedence. *Jassa thurstoni* Conlan, 1990 (called *J. falcata* form 2 by Thurston) and *Pleojassa moorei* n. sp. (called *J. falcata* form 3) are also known from Thurston's collections there. For *I. camptonyx*, hallmarks of the genus *Jassa,* rather than *Ischyrocerus* are the spines at the tip of the antenna 2, the sinuous palmed gnathopod 2, the strong overlap of the merus over the carpus on pereopods 3 and 4, the typical *Jassa*-like uropod 3 with long peduncle lacking mid-dorsal spines (but with a corona of spines around the distal margin), a lateral setal brush and the strong hooked spines at the tip of the outer ramus, and the telson with a long seta at each corner rather than a spine. However, Thurston describes the uropod outer ramus "with three stout hooked spines dorsally near apex and a minute comb with five-six teeth laterally", which does not correspond to his illustration and are not *Jassa*-like. Possibly, though, his description could be interpreted differently. One of the three spines may be the apically immersed, dorsally recurved spine typical of *Jassa*, the other two spines are cusps, and the five–six teeth are minute dorsal cusps proximal to the two large ones. If so, then this also speaks of *I. camptonyx* as being a *Jassa*, either its own species or synonymous with *J. alonsoae*. It is not a *Pleojassa*, even though the male's second-gnathopod resembles that of *P. moorei*, because this genus lacks a gill on gnathopod 2 while *I. camptonyx* possesses one. Thurston considered that the few males available for study were juvenile because they all lacked a thumb as in *Jassa*. However, some of these specimens were larger than the adult, ovigerous females. The female allotype was 4.5 mm and the male holotype was 5.5 mm. This suggests that the male holotype is actually an adult that will not produce a thumb, in which case it is not *Jassa*. Therefore, until the range of variation can be assessed in Thurston's specimens, this species should remain in *Ischyrocerus* with a question as to its proper generic placement.

**Uncertain status of *Ischyrocerus anguipes* in the Southern Hemisphere.** Sars' (1894) excellent illustrations of *I. anguipes* may have resulted in some mis-identifications by early workers in the Southern Hemisphere. Alternatively, their identifications were correct and *I. anguipes* was being introduced by shipping if the specimens came from ports. K.H. Barnard's (1916) "*I. anguipes*" could have been a species of *Neoischyrocerus*, however, as the specimens were 3 mm and the male's second gnathopod propodus was 3.5 x longer than wide with the dactyl nearly the full length of the propodus, which is typical of adult male *Neoischyrocerus.*

Schellenberg's (1953) "*I. anguipes*" from Lüderitzbucht, Namibia was a 4.8 mm male which he stated differed from K.H. Barnard's (1916) "*I. anguipes*" in its gnathopod 2 morphology. "The metacarpus of the 2nd gnathopod is shaped in the same way but stronger and exhibits a spination like on the first gnathopod. The palm is evenly finely corrugated (or: "wavy") along its almost entire length." (*Der fast gleich geformte, aber stärkere Metacarpus des 2. Gnathopoden zeigt die Bestachelung wie am 1. Gnathopoden. Die Palma ist fast in ihrer ganzen Länge gleichmäßig fein gewellt.*) (translated from German to English by Jan Beermann, Alfred Wegener Institute, Bremerhaven, Germany). The similarly shaped gnathopods 1 and 2 suggest that this specimen was a female or juvenile, or an adult male of a different species, as adult male *I. anguipes* have a gnathopod 2 that is more than twice the length of gnathopod 1, with a concave, rather than convex palm. Schellenberg illustrated the uropod 3 outer ramus as 5-cusped, terminating in a basally immersed, dorsally recurved spine similar to *Jassa*. The corona of spines at the peduncle's distal margin is typical of *Ischyrocerus* and *Jassa*.

"*I. anguipes*" captured off the coast of Ceylon in ~150 m depth were briefly described by Walker (1904) but not illustrated. One male and one ovigerous female were 2.5 mm long. The male's gnathopod 2 was similar to that of *I. anguipes*, but this could also be *Neoischyrocerus* which has similarly shaped, though more pendulous second gnathopods with the dactyl in the largest males nearly the full length of the propodus.

Chilton (1921) described "*I anguipes*" from Lyttelton, New Zealand which were up to 6 mm long, saying that they closely resembled Sars' (1894) illustrations of that species. His description was minimal, however, and he provided no illustrations.

## Key to genera of the Ischyrocerini

1 Urosome 1 bearing 3 dorsal teeth or cusps (Fig. 35a) . . . . . . . . . . . . *Bathyphotis* Stephensen, 1944

– Urosome 1 without dorsal teeth although there may be a pair of short setae (Fig. 35b) . . . . . . . . . . . . 2

2 Pereopods 5–7, ischium posteriorly winged (Fig. 35c). Uropod 3 uniramous, ramus ending in a cluster of spines (Fig. 35e) . . . . . . . . . . . . *Alatajassa* Conlan, 2007

– Pereopods 5–7, ischium not posteriorly winged (Fig. 35d). Uropod 3 biramous (Fig. 35f) . . . . . . . . . . . . 3

3 Pereopods 3–4, propodus prehensile (Fig. 35g) . . . . . . . . . . . . *Isaeopsis* K.H. Barnard, 1916

– Pereopods 3–4, propodus rectangular or oval and not expanded distally (Fig. 35h) . . . . . . . . . . . . 4

4 Coxa 4 posteriorly excavate (Fig. 35i) . . . . . . . . . . . . 5

– Coxa 4 not posteriorly excavate (though it may be shallowly concave) (Fig. 35j) . . . . . . . . . . . . 7

5 Gnathopod 1, carpus longer than the propodus (carpus:propodus length ~125%). Gnathopod 2, female, propodus massive, length ~175% the length of the propodus of gnathopod 1, palm toothed (Fig. 35k) . . . . . . . . . . . . *Veronajassa* Vader and Myers, 1996

– Gnathopod 1, carpus subequal to or shorter than the propodus (carpus: propodus length ~45–95%). Gnathopod 2, female, propodus not massive, length ~125% the length of the propodus of gnathopod 1, palm not toothed (Fig. 35l) . . . . . . . . . . . . 6

6 Eyes absent. Maxilla 1, inner plate with a long apical seta (Fig. 36a). Coxa 1 more than half the depth of coxae 2–4. Gnathopod 1, carpus length ~95% the length of the propodus; propodus, palm shallowly excavate (Figs 36c, d). . . . . . . . . . . . *Myersius* Souza-Filho & Serejo, 2014

– Eyes present. Maxilla 1, inner plate without a long apical seta (Fig. 36b). Coxa 1 ≤ half the depth of coxae 2–4. Gnathopod 1, carpus length ~45–50% the length of the propodus; propodus, palm convex (Figs 36e, f). . . . . . . . . . . . *Microjassa* Stebbing, 1899

7 Gnathopod 1, carpus ~100% the length of the propodus. Pereopods 3 and 4, dactyl ~175% the length of the propodus (Fig. 36g). . . . . . . . . . . . *Scutischyrocerus* Myers, 1995

– Gnathopod 1, carpus shorter than the propodus. Pereopods 3 and 4, dactyl ≤90% the length of the propodus (Fig. 36h). . . . . . . . 8
8 Uropod 3 with a cluster of distolateral setae beside the outer ramus (Fig. 36i). *Jassa* group . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 9
– Uropod 3 without a cluster of distolateral setae beside the outer ramus Fig. 36j) . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 13
9 Antenna 1, accessory flagellum absent or scale-like (Fig. 37a) . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . *Parajassa* Stebbing, 1899
– Antenna 1, accessory flagellum 2 articles, the second minute (Fig. 37b) . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 10
10 Gnathopods and pereopods 3–4 clothed in abundant, long plumose setae (Fig. 3). Gnathopod 2, either sex, propodus, palm bearing a central tooth and a second tooth at the palmar angle, with or without a single large spine at the palmar angle (Fig. 37c) . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . *Plumulojassa* **n. gen.**
– Gnathopods and pereopods 3–4, setae simple or finely pectinate except in the palm of the male gnathopod 2 where the setae may be plumose (Figs 17, 22, 25 and 27– 29). Gnathopod 2, either sex, propodus, palm sinuous, concave or with a pronounced thumb defining the palm proximally, spines if present grouped in triplicate or if single, very small (Figs 37d–f) . . . . . . . . . . . . . . . . . . 11
11 Gnathopods 1 and 2, propodus, palm defined by 1 spine. Gnathopod 2 without a gill. Pereopod 5, carpus with a cluster of spines posterodistally. Pleopods, rami very short, length ≤ depth of the pleon (Figs 22–28). . . . . . . . . . . . . . . . . . . . . . . *Pleojassa* **n. gen.**
– Gnathopods 1 and 2, propodus, palm defined by multiple spines (usually 3–4). Gnathopod 2 with a gill. Pereopod 5, carpus not spinose posterodistally. Pleopods, rami long, length > depth of the pleon (Fig. 17) . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 12
12 Gnathopod 2, propodus, both sexes producing a thumb at adulthood, palmar defining spines, if present, at the thumb tip (Fig. 37e), juvenile palm sinuous, without a thumb; pereopods 3 and 4, carpus <25% overlapped by the merus; uropod 3, outer ramus with many minute cusps proximal of the dorsally recurved terminal spine but without additional larger cusps (Figs 17–21) . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . *Hemijassa* Walker, 1907
– Gnathopod 2, propodus, only the male producing a thumb at adulthood, palmar defining spines, if present, proximal of the thumb tip (Fig. 37f), juvenile palm concave or sinuous, without a thumb; pereopods 3 and 4, carpus 80–100% overlapped by the merus; uropod 3, outer ramus with 2 (usually) larger cusps in addition to minute cusps proximal of the dorsally recurved terminal spine (Figs 35b,d,f,h, 36 h,i and 37f) . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . *Jassa* Leach, 1814
13 Uropods 1, 2 and/or 3, peduncle with lateral row of setae (Fig. 37g). . . . . . . . . . . . . . . . . . . . . *Ruffojassa* Vader and Myers, 1996[1]
– Uropods 1, 2 and/or 3, peduncle without a lateral row of setae . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 14
14 Antenna 1, accessory flagellum 3–4 articles, the last minute. Uropod 3, outer ramus with one to several medial setae projecting dorsally (Fig. 37h) . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . *Ventojassa* J. L. Barnard, 1970
– Antenna 1, accessory flagellum 1–2 articles, the last minute. Uropod 3, outer ramus without medial setae projecting dorsally . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 15
15 Gnathopod 1, carpus longer than the propodus (carpus ~120% of the propodus length). Known only from subantarctic islands and Brazil, 44–1058 m . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . *Pseudischyrocerus* Schellenberg, 1931
– Gnathopod 1, carpus shorter than the propodus (carpus ~50–95% of the propodus length). Various locations and depths. . . . . . 16
16 Mandibular palp, article 3 slender, ventrally convex and broadest centrally, tip acute (Fig. 37i). Antennae 1 and 2, length ≥85% of the body length (headlobe to end of uropods), antenna 2 not stouter than antenna 1. Pereopods 3 and 4, merus not overlapping the carpus anteriorly. Uropod 2, outer ramus, length 65% of the inner ramus. . . . . . . . . . . . . . . . . . . . . . . *Paradryope* Stebbing, 1888[2]
– Mandibular palp, article 3 broad distally, end rounded (Fig. 37j). Antennae 1 and 2, length ≤65% of the body length (headlobe to end of uropods), antenna 2 stouter than or similar to antenna 1. Pereopods 3 and 4, merus overlapping 10–100% of the carpus. Uropod 2, outer ramus, length 75–80% of the inner ramus . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 17
17 Adult male gnathopod 2 grossly lengthened and pendulate, length 190–350% of the length of gnathopod 1, propodus slender, length 180–400% of its width at the centre, dactyl 50–100% of the length of the propodus (Figs 38a-c). Uropod 3 with 1–2 rows of mid-dorsal spines but without a corona of multiple spines on the distal margin (Fig. 38d). Warm temperate and tropical, Northern and Southern Hemisphere, known from 9–40°N and 5–34°S, 0–16 m depth.. . . . . . . . . . . . . . . . . . *Neoischyrocerus* Conlan, 1995
– Adult male gnathopod 2 variable in length but not pendulate, length 100–220% of the length of gnathopod 1, propodus variably slender or stout, length 120–290% of its width at the centre, dactyl 33–75% of the length of the propodus (Figs 38e-g). Uropod 3

1 J.L. Barnard's (1962) California *Parajassa angularis* and Moore's (1985) New Zealand *R. andromedae* do not agree with Vader & Myers' definition of *Ruffojassa* (lacking accessory flagellum, telson not cusped).

2 There is an error in the original description by Stebbing (1888) for *Paradryope*. The illustrations of the whole animal and gnathopods were made aboard ship at the time of collection. The drawing of the whole animal on Plate CXXIII shows gnathopod 2 larger than and differently shaped than gnathopod 1, with a sculptured palm while gnathopod 1 has an evenly convex palm. The magnifications of the gnathopods on this same plate are erroneously reverse-labelled, with the sculptured-palmed and larger gnathopod erroneously labelled gnathopod 1. The Ischyrocerini typically all have a larger gnathopod 2 than gnathopod 1 with various degrees of modification of the palm of gnathopod 2 in the male (and sometimes female). Stebbing (1888) noted that he wrote the description of *Paradryope* in the laboratory, years after these illustrations were made aboard ship. Most of the specimen had been lost, with only fragments of the antennae and pereopods remaining, so his description was based mainly on the ship-board illustration. This would explain why he carried through the ship-board labelling error to his description, as he no longer had the full specimen to check against the illustration. This error was carried through by J.L. Barnard & Karaman (1991). Stebbing also noted that there was nothing in the appearance of *Paradryope* "to enhance the probability of its having actually come from so great a depth" (4200 m). This is the only specimen known in this genus. It was collected at the Challenger Expedition Station 241, North Pacific, east of Yokohama (35°41′N, 157°42′E), June 23, 1875.

with 1–2 rows of mid-dorsal spines and a corona of numerous spines on the distal margin[3] (Fig. 38h). Cold temperate and polar, primarily Northern Hemisphere, known from 36–81°N and 42°S, 1–2000 m depth . . . . . . . . . . . . . . . *Ischyrocerus* Krøyer, 1838

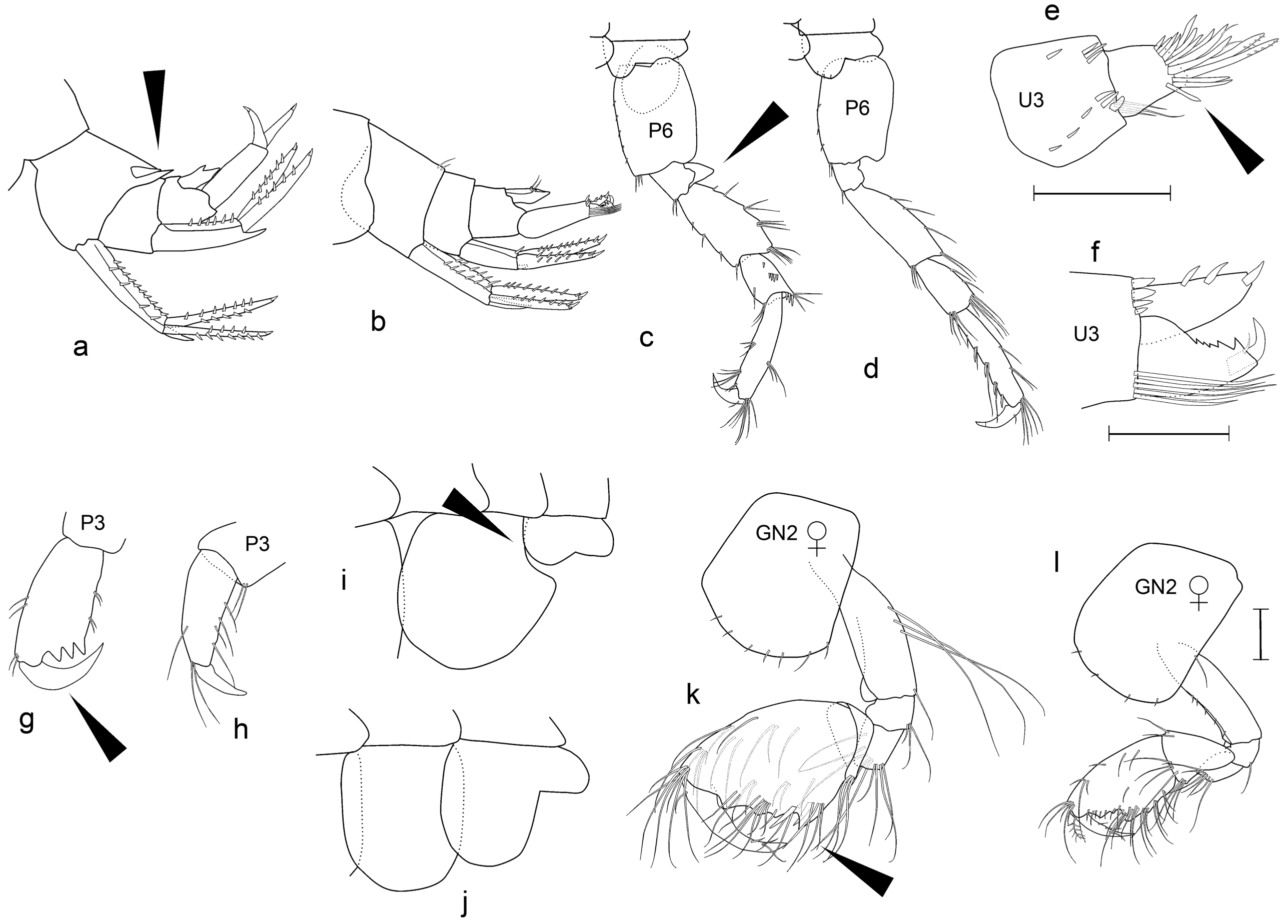



**FIGURE 35.** a. *Bathyphotis tridentata* after Stephensen (1944); b. *Jassa falcata* from Conlan *et al.* (in press); c. *Alatajassa similis* after Conlan (2007); d. *Jassa falcata* from Conlan *et al.* (in press); e. *Alatajassa similis* after Conlan (2007); f. *Jassa falcata* from Conlan *et al.* (in press); g. *Isaeopsis tenax* after K.H. Barnard (1916); h. *Jassa falcata* from Conlan *et al.* (in press); i. *Microjassa bahamensis* after Conlan (1995); j. *Neoischyrocerus lilipuna* after Conlan (1995); k. *Veronajassa neptunea* after Vader and Myers (1996); l. *Myersius denticaudatus* after Souza-Filho and Serejo (2014). Scale 0.1 mm.

## Discussion

Conlan (1989, 1990) and Conlan *et al.* (in press) have shown that the location and timing of thumbing in male *Jassa* is a highly conservative characteristic of this genus, indicating that six species that thumbed differently should be transferred out of the genus. In *Jassa*, the thumb is always developed at the last molt and always distal to the palmar defining spines on the propodus of gnathopod 2. *Jassa* now consists of 24 species (Conlan *et al.* in press), an increase of five from the 19 described by Conlan (1990). Recipient genera for the transferred species are the existing genera *Ventojassa* and *Hemijassa* and the new genera *Pleojassa* and *Plumulojassa*. *Jassa barnardi* was found to be synonymous with *Ventojassa frequens* and is transferred herein. Examination of the type series for *V. frequens* and other specimens in the Chilton collection found two adult male gnathopod morphs ("*frequens*" and "*latipes*") but no consistent differences among the juveniles and females that could be associated with the males. Consequently, these differences were noted but not taxonomically assigned. *Ventojassa* comprises eight temperate and tropical species, which are known from both hemispheres. *Jassa goniamera* was transferred to *Hemijassa*, a genus that is only known from the Antarctic and subantarctic islands. *Jassa wandeli* and *J. multidentata* were transferred to the new genus *Pleojassa* and the new species *P. lowryi*, *P. moorei* and *P. orientalis* were added. *Pleojassa* is a cold temper-

3 *Ischyrocerus fractus* is unusual in lacking this corona but the male's gnathopod 2 is similarly shaped and not enlarged relative to gnathopod 1. This species is only known from Ireland.

ate to polar Southern Hemisphere genus. Finally, *Jassa ocia* was transferred to the new genus *Plumulojassa***.** It is only known from the northeastern Atlantic and its eastern seas and has been often found in ecological studies as it is readily collected at shallow depth**.** *Hemijassa goniamera* shows close relatedness to *Jassa* spp. in a CO1 analysis (Conlan *et al.* in press). *Pleojassa* has not been analysed yet, but the similar sexual modification of *P. wandeli* and *P. multidentata* to species of *Jassa* suggest that species of *Pleojassa* may be more closely related to *Jassa* than are species of *Hemijassa*. *Pleojassa* and *Hemijassa* are confined to the Southern Hemisphere while *Jassa* radiated in both hemispheres.

Most of the species treated herein have been known since the 19th century (Table 2). The relatively compact distribution of *P. ocia* in the Northeastern Atlantic and associated seas suggests that it has not been dispersed by human means except possibly locally**.** In a survey of the biota of Portuguese marinas vs nearby natural shore, it was found only on the latter (Afonso *et al.* 2020)**.** The widespread distribution of the Southern Hemisphere species is a consequence of the strong Antarctic Circumpolar Current**.** Figures 1 and 2 show some latitudinal differentiation with *H. goniamera* and *P. wandeli* on the coast of Antarctica and its subantarctic islands and *V. frequens* much more temperate. *Pleojassa lowryi*, *P. moorei*, *P. multidentata* and *P. orientalis* may be intermediate in range but records are sparse.

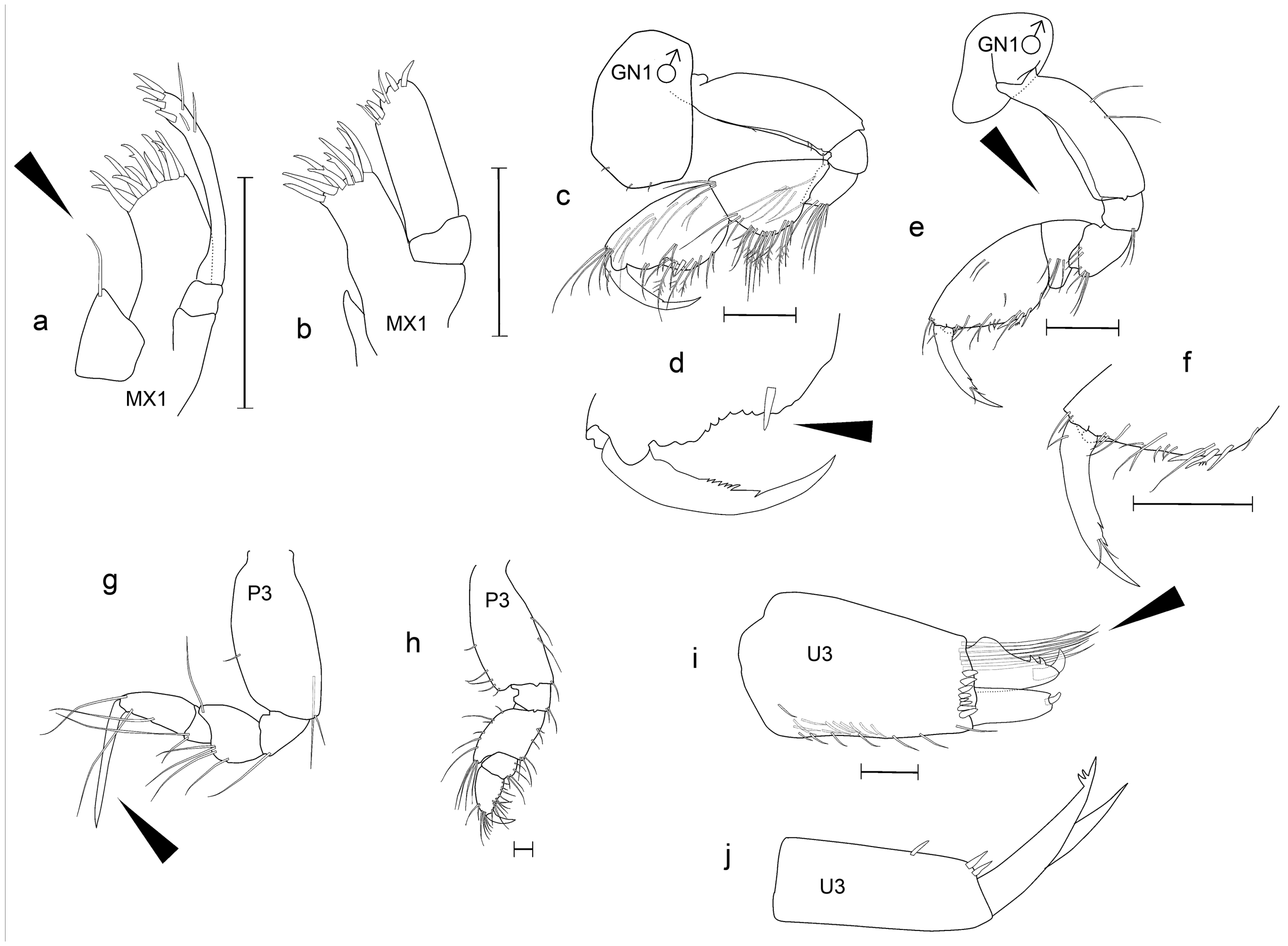



**FIGURE 36.** a. *Myersius denticaudatus* after Souza-Filho and Serejo (2014); b. *Microjassa cumbrensis* after Conlan (1995); c. *Myersius denticaudatus* after Souza-Filho and Serejo (2014); d**.** magnification of c (palm only); e. *Microjassa floridensis* after Conlan (1995); f. magnification of e (palm only); g. *Scutischyrocerus scutatus* after Myers (1995); h. *Jassa marmorata* from Conlan *et al.* (in press); i. *Jassa oclairi* from Conlan *et al.* (in press); j. *Pseudischyrocerus denticaudata* after Schellenberg (1931)**.** Scale 0.1 mm.

Collection data indicate that solid substrates and attached algae and hydroids are typical for these species (Table 3)**.** Being a coastal species in a highly populated region of the world, *P. ocia* has been more frequently encountered than the Southern Hemisphere species (Table 3, Supplementary Table S1)**.** It is known from a variety of substrates, both inorganic and organic, even on the surface and coelomic fluid of sea cucumbers (Ruffo 1958)**.** Scipione *et al.*

(2017) found *P. ocia* apparently favouring extremely low pH on Ischia, Italy (pH 7.3–6.9) caused by natural $CO_2$ venting**.** In the Mediterranean Sea, it prefers *Sabellaria alveolata* reefs over more open, hard substrate (Plicanti *et al.* 2017; Bonifazi *et al.* 2019)**.** It also favours high current areas, sheltering within mussel beds (Kitsos & Koukouras 2003). It will colonize manufactured hard substrates and associate with introduced species, though (Fiorentino *et al.* 2012; Çinar *et al.* 2017; Sedano *et al.* 2020a,b)**.** It is not pollution tolerant, however**.** Varigin (2017) found that *P. ocia* had disappeared from the coastal fouling community of Odessa Bay (Black Sea) in 2016**.** The change was attributed to large scale eutrophication which favoured mussels and barnacles over a more diverse community 40 years ago. Although benthic, it has also been found in the plankton at night (Macquart-Moulin 1968; Vereshchaka & Anokhina, 2014).

Like *Jassa*, the species treated here are probably plankton and bottom detritus feeders as they have similar antennal structure with long setae and spines on the antenna 2 flagellum**.** Dauby *et al.* (2001) examined *H. goniamera* and found crustacean remains (probably copepods) and diatoms in its stomach. Like *Jassa ingens*, this is a large Antarctic species, with males found to 22 mm body length**.** It is also the deepest living of the species studied here (collected from 30–541 m depth). Females have been found ovigerous at various times of the year and egg brooding is likely a long process in cold water**.** The finding of female *P. moorei* brooding eggs at an early stage of development in austral summer by Thurston (1974b) suggests that it synchronizes reproduction to the highly pulsed polar plankton bloom, which is typical of other Antarctic plankton feeding species (unpub. data).

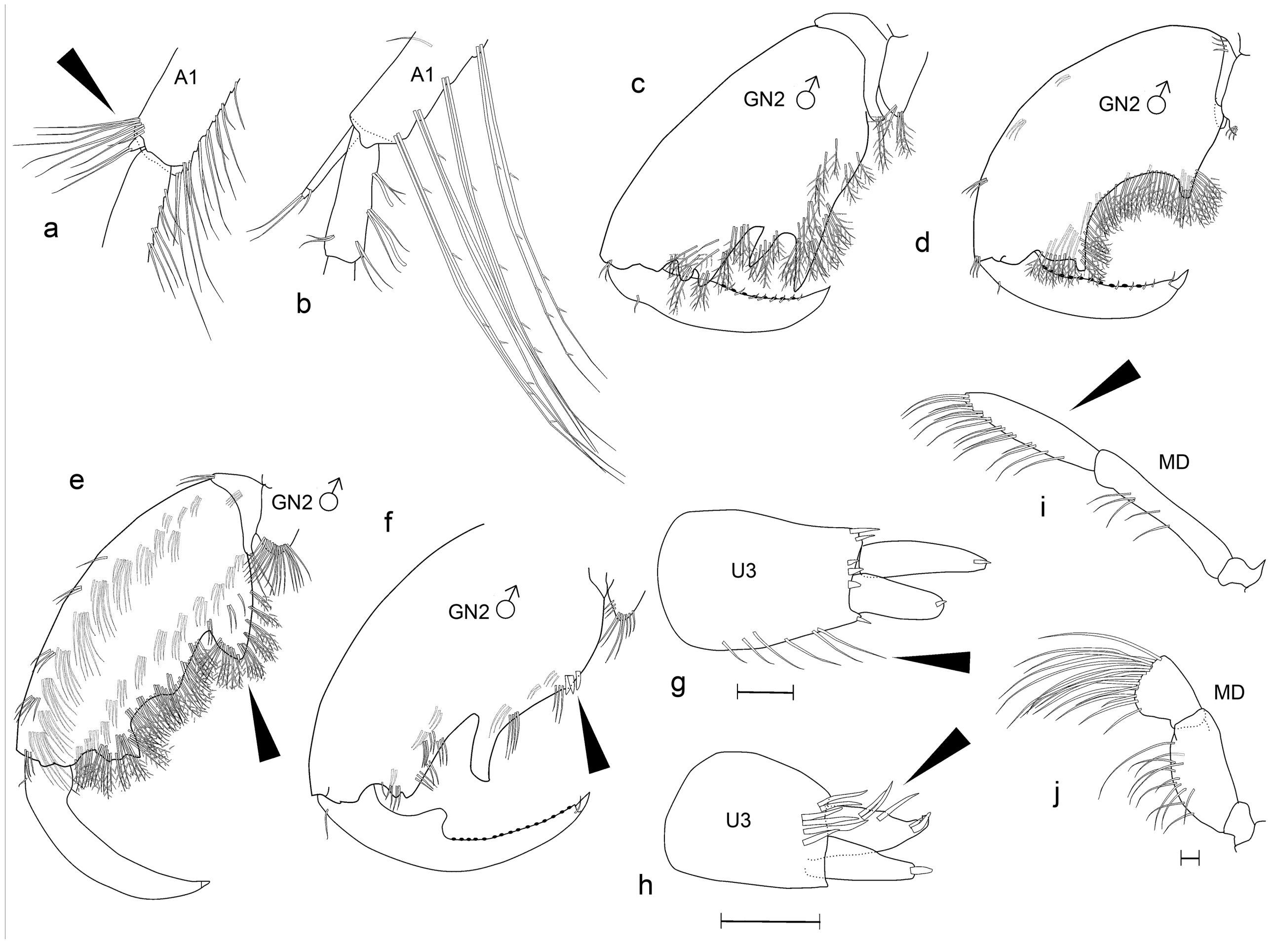



**FIGURE 37.** a. *Parajassa pelagica* after Sars (1894); b. *Jassa thurstoni* from Conlan *et al.* (in press); c. *Plumulojassa ocia* from **FIGURE** 3; d. *Pleojassa lowryi* from **FIGURE** 25; e. *Hemijassa goniamera* from **FIGURE** 17; f. *Jassa falcata* from Conlan *et al.* (in press); g. *Ruffojassa festa* after Vader and Myers (1996); h. *Ventojassa frequens* from **FIGURE** 10; i. *Paradryope orguion* after Stebbing (1888); j. *Neoischyrocerus lilipuna* after Conlan (1995)**.** Scale 0.1 mm.

Placement of the new genera into the Ischyrocerini relied on characters that had been described and/or figured for all the genera**.** This became problematic, because many of the characters that were found to be conservative for the new genera and therefore useful for generic definition were overlooked in literature descriptions and illustrations**.** Such conservative characters were: antenna 2 flagellum distally spinose or not; presence/absence of a gill on gnathopod 2; brood plate setae hook-tipped or not; pleopods reduced or full length; presence/absence of a pair of setae on the dorsum of urosome 1. However, some conservative characters were noted by most authors, particularly the number of articles in the antenna 1 accessory flagellum and the morphology of the uropod 3. Examination of the full Ischyrocerini showed that *Plumulojassa*, *Hemijassa*, *Pleojassa* and *Jassa* shared a distinctive uropod 3 that defined them as the "*Jassa* group". These genera lacked mid-dorsal spines on the peduncle, bore a cluster of distally projecting setae beside the outer ramus, and had a distinctive spine on the outer ramus tip, which was deeply immersed and curved dorsally. *Ischyrocerus* was by far the largest genus in the Ischyrocerini, and Myers (1995, 1997) had noted the need for a revision. Examination of variation within the tropical members of *Ischyrocerus* revealed inconsistencies within the genera *Coxischyrocerus* and *Tropischyrocerus,* leading to synonymy with the senior genus *Neoischyrocerus.* Uropod 3 spination patterns as well as characters of the male gnathopod 2 revealed consistent differences between *Neoischyrocerus* and *Ischyrocerus*, leading to re-definition of *Ischyrocerus* as a cold temperate/polar group and *Neoischyrocerus* as tropical/warm temperate. Collecting information indicates that *Ischyrocerus* has a far greater depth range than *Neoischyrocerus*, suggesting a physiological difference that confines them to separate water masses. Although these taxonomic rearrangements have not yet been tested genetically, past morphological revision of *Jassa* by Conlan (1990) has been borne out by CO1 analyses (Conlan *et al.* in press), giving support that this revision may have a genetic basis.

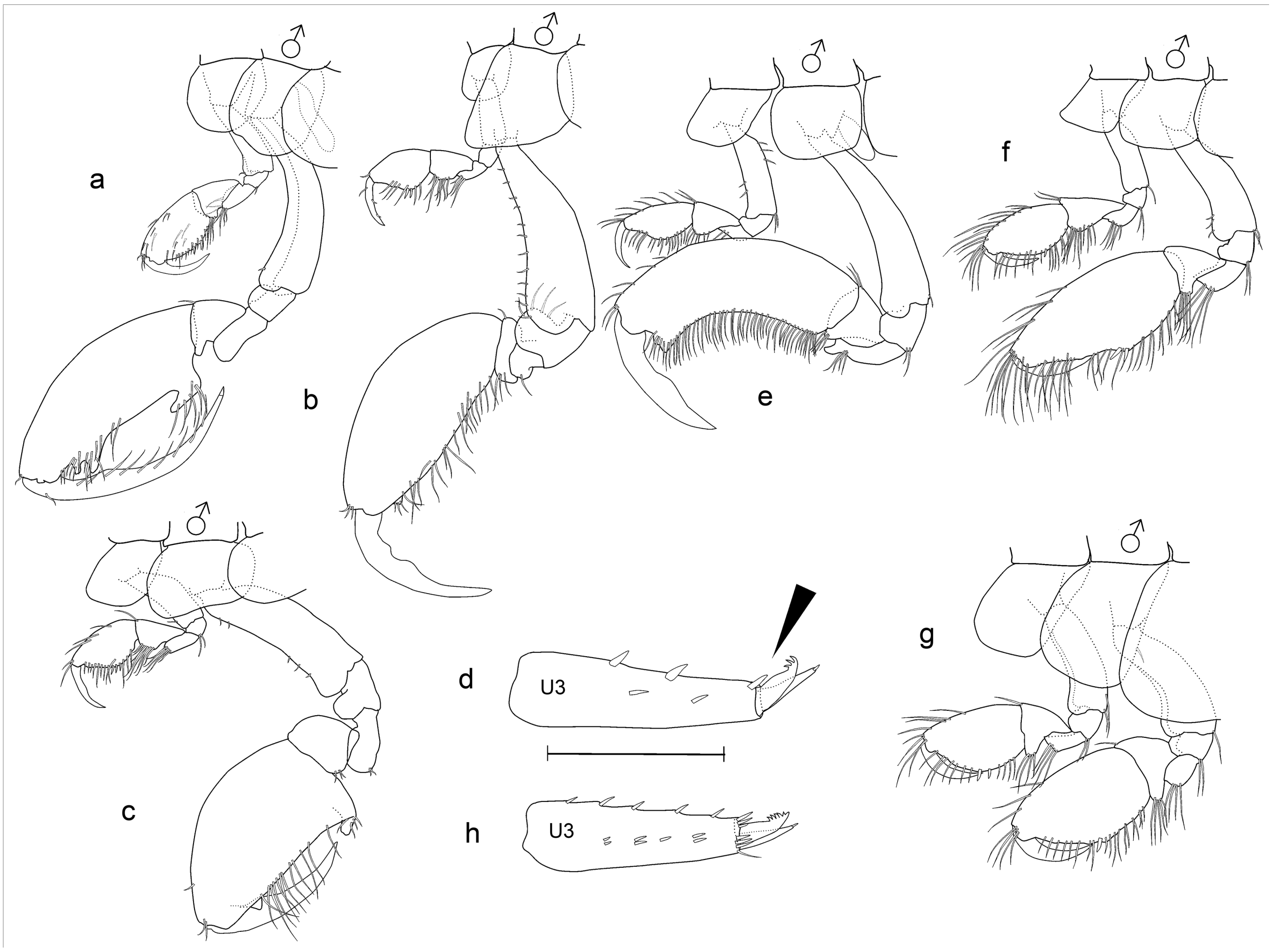



**FIGURE 38.** a. *Neoischyrocerus lilipuna* after Conlan (1995); b. *Coxischyrocerus rhombocoxus* after Just (2009); c. *Tropischyrocerus pugilus* after Just (2009); d. *Neoischyrocerus claustris* after Conlan (1995); e. *Ischyrocerus anguipes* after Sars (1894); f. *Ischyrocerus megacheir* after Sars (1894); g. *Ischyrocerus megalops* after Sars (1894); h. *Ischyrocerus anguipes* after Sars (1894)**.** Scale 0.1 mm.

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This work resulted from a study of the genus *Jassa* published in 1990. The institutions and individuals acknowledged therein were essential to the success of this work as well. In particular, I am indebted to Susan Laurie-Bourque who ably constructed the line drawings and maps, and Val Tait who alerted me to new specimens to examine. Essential support was also provided by Jan Beermann, Ed Hendrycks and Joel Grice. The Canadian Museum of Nature, Carleton University and the University of Ottawa (Ottawa, Canada) provided financial and logistical support. To all I give hearfelt thanks.

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