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Jassa (Crustacea: Amphipoda): a new morphological and molecular assessment of the genus

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Abstract

The amphipod genus *Jassa* Leach, 1814 now comprises 24 species that occur in temperate regions of both hemispheres on solid substrates from the lower intertidal zone to 500 m depth. The propensity for some species to form dense colonies in water intake structures and offshore platforms has brought them to attention as an unwanted pest. Based on the examination of ~25,000 specimens from ~1,100 museum and private collections, it is evident that some species of *Jassa* have been transported by human vectors since at least the 19th century and now occur widely. Their colonial, tube-living habit enables such transport, and collection records document them on ships, buoys and portable water systems as well as on natural movable substrates such as logs, drift algae and larger crustaceans. Because *Jassa* can be so readily found, but species discrimination has had a problematic history, the purpose of this monograph is to assist researchers to identify species through illustrations, descriptions, keys and habitat summaries. Seven species which were named in the 19th century but whose names have lapsed are placed in the context of currently known species. Two new species, *J. laurieae* **n. sp.** and *J. kimi* **n. sp.** are described, and *J. monodon* (Heller, 1866) and *J. valida* (Dana, 1853) are resurrected. *Jassa mendozai* Winfield *et al.*, 2021 is submerged under *J. valida,* and *J. cadetta* Krapp *et al.*, 2008 and *J. trinacriae* Krapp *et al.*, 2010 are submerged under *J. slatteryi* Conlan, 1990. Morphological differences are related to current understanding of growth, behaviour and ecology. CO1 analysis suggests a Southern Hemisphere origin with diversification northward and an evolutionary direction toward greater physiological plasticity, leading to success in long distance transport and establishment in exotic locations. Correct identification of *Jassa* world-wide will facilitate further research on this ecologically important genus and will allow for differentiation of indigenous from exotic introductions.

Key words: *Jassa*, Amphipoda, Ischyrocerini, revision, dispersal, CO1

Introduction

The colonial, tube-living amphipod genus *Jassa* Leach, 1814, is a frequently encountered genus because of its widespread distribution in temperate and cold oceans and the propensity for some species to dominate fouling communities in large numbers on rocky coasts and on man-made structures (Conlan 1989, 1990; Franz 1989; Krone *et al.* 2013; Beermann 2014). Once thought to be monospecific but highly variable (Sexton & Reid 1951), Conlan (1989, 1990) used observations of sex- and age-invariant characters along with mating behaviour and the growth of sexually dimorphic body parts to recognize 19 species within the genus. Since then, five additional species have been described: *J. kjetilanna* Vader & Krapp, 2005*, J. cadetta* Krapp *et al.*, 2008, *J. trinacriae* Krapp *et al.*, 2010, *Jassa* sp. of Krapp *et al.*, 2010 and *J. mendozai* Winfield *et al.*, 2021.

Despite improved descriptions and identifications, there has been some residual confusion in the literature caused by the variable sexual dimorphism of the males and sequences/barcodes/MOTUs that did not correspond with morphological identifications (e.g., Pilgrim & Darling 2010; Lobo *et al.* 2017). Sexual dimorphism occurs in the second antennae and second gnathopods, and these obvious but variable body parts have been the source of taxonomic confusion (Conlan 1989, 1990). In most species, the male's second antennae become stouter with body size and the long filter setae on the peduncle and flagellum become sparser and shorter. Some species also develop plumose setae on the antenna's distal parts. More obvious is the enlargement of the male's second gnathopod which is incised to form a thumb-like structure on the posterior part of the propodus. These thumbed males are not all alike: they are divisible into minor and major forms, and these two forms appear to occur in each species. Minor males have smaller thumbs than major males of the same body length. In some species, minor forms also have a pronounced tooth on the inner side of the dactyl that fits into the palm. Major males tend to have a larger body size and lack this tooth, although the dactyl can be expanded proximally.

Seminal studies on the sexual behaviour of *J. marmorata* Holmes, 1905 greatly enhanced the understanding of why there was so much variation in characters that had previously been relied on for taxonomic distinction (Borowsky 1983, 1985; Clark 1997; Clark & Caudill 2001; Kurdziel & Knowles 2002). This understanding was the key for disentangling taxonomy from sexual behaviour and a summary is given here as a basis for recognizing species distinctions in this paper.

Thumbing in male *Jassa* occurs only at a terminal molt. Females never produce a thumb. While thumbless males can be physiologically mature if old enough, only thumbed males are sexually active. Thumbless males tend to evict receptive females from their tubes while thumbed males attend the females, copulating with them after they molt (Borowsky 1983, 1985). Receptive females are less tolerant of thumbless than thumbed males around their tubes. Therefore, the thumb appears to function as a label that enables females to distinguish male intentions. The thumb also appears to signal dominance to thumbless males, as thumbed males win agonistic contests with thumbless males, even if the thumbed male is smaller than the thumbless male. Receptive females can mate multiple times and with multiple males after molting, suggesting that *Jassa* may exhibit cryptic female choice (Clark & Caudill 2001; Dennenmoser & Thiel 2015). At least in an experimental situation, there is evidence that males are unaware of female receptivity until they touch them. Since the second antennae are used in both male-male and male-female interactions (Borowsky 1985; Clark 1997; pers. obs.), this may explain the sexual changes in antenna 2 setation noted above, which are presumably adaptations for chemosensation on the female's cuticle.

The major-minor dimorphism in thumbed males is also reflected in different behaviours (Clark 1997). Major males fight, display and attempt to evict other males that are attending receptive females. Minor forms never fight with major forms or display and attempt to evict them, although they may occasionally display and attempt to evict other minors. Both forms succeed in mating if they are alone with a female. When together with other males, like-morph males have greater success in mating than if they are with unlike morphs. Major males have as much variance in mating success as minor males, indicating that major forms do not monopolize females, at least in experimental conditions. Minors succeed in mating even when they are out-numbered by majors. Indeed, the reverse is also true: majors do not dominate minors in mating success. When they are out-numbered by minors, they have less success in mating than if they are alone with the female.

Major and minor morphs are not genetically determined but are significantly affected by diet quality (Kurdziel & Knowles 2002). Experimentally, majors can be produced only on a high protein diet, and a natural population of *J. marmorata* at Stony Brook Harbor, New York, predominated in major relative to minor forms three months after the spring phytoplankton bloom. The rest of the year, minors predominated, and in late fall they averaged half the body length of the spring minors. Cultured males that eventually molt to the major form take longer to grow and molt more times than minor forms, which become sexually active sooner. Predominance of minor forms in winter was also observed for *J. marmorata* and *J. herdmani* (Walker, 1893) in Helgoland, Germany (Beermann 2014). It is not known whether minors survive longer than majors once they reach their terminal thumbing molt but minimal investment in developing secondary sexual traits selects for an extended lifespan in other species (Hooper *et al.* 2018).

Over 300 papers focussing on or peripherally encountering *Jassa* have been published since the taxonomic revision by Conlan (1989, 1990). *Jassa* can be widely encountered and experimented with in the laboratory or in the field (Borowsky 1985; Clancy 1997; Clark 1997; Tisch 1997; Clark & Caudill 2001; Kurdziel & Knowles 2002; Karez & Ludynia 2003; Armsby & Tisch 2006; Havermans *et al.* 2007; Beermann & Franke 2012; Beermann & Boos 2015). It is an economically important group because of its fouling ability (Dixon & Moore 1997; Bunker 2004; Moshchenko & Zvyagintsev 2004, 2010; Beermann & Franke 2011; Bloecher *et al.* 2013; Krone *et al.* 2013; Fernandez-Gonzalez *et al.* 2014), it can transmit parasites to native and cultivated fish (Yasumoto & Nagasawa 1996; Laskowski & Zdzitowiecki 2017), it can inhibit, overgrow, displace and prey on other species (Sebens 1985; Franz & Mohamed 1989; Zintzen *et al.* 2006, 2008; Kerckhof *et al.* 2010 a, b; Duchêne 2012; Suwandy 2012; Beermann 2014; Valentine *et al.* 2016), and it is able to be transported and successfully introduced as an exotic (Inglis *et al.* 2006a ,b, c, 2008), where it can impact native species (Suwandy 2012). Consequently, it has been integral to the calculation of pollution indices as at least some of its species are considered to be insensitive to pollution, unlike other amphipods (Bellan 1980; Gray *et al.* 1990; Dauvin & Ruellet 2007; Dauvin *et al.* 2016; de-la-Ossa-Carretero & Dauvin 2010). As a positive influence, it reduces epiphyte fouling of macroalgae and seagrasses (Duffy 1990), it consumes excess organics released from fish farms (Gonzalez-Silvera *et al.* 2015) and it provides a food resource for gray whales (Dailey *et al.* 2000), fish (Blankley 1982; Bennett *et al.* 1983; Brawley & Fei 1987; Pulfrich & Griffiths 1988; Wilber *et al.* 2003; Norderhaug *et al.* 2005; De Troch *et al.* 2013; Reubens *et al.* 2010, 2013, 2014a, b; Wada *et al.* 2010; Stenberg *et al.* 2015; Choi *et al.* 2017; Ventura *et al.* 2017; Şensurat-Genç *et al.* 2019) and invertebrates (McCain 1968; Sebens 1985; Genzano 2005; Donahue *et al.* 2009; Di Camillo *et al.* 2013; Caplins & Turbeville 2010). Correct identification is essential for behavioural, conservation, ecological, genetic, taxonomic and phyletic studies and for identifying introductions and their impacts (e.g., Borowsky 1985; Karez & Ludynia 2003; Krapp *et al.* 2008, 2010; Pilgrim & Darling 2010; Lobo *et al.* 2017). The purpose of this paper is to stimulate additional study on other species in the genus by assisting workers to identify the species morphologically and molecularly and to recognize their intra-specific variability. Specifically, this study:

1. provides new data on the distribution and habitat of the species;
2. provides diagnoses, enhanced illustrations and a key to the species;
3. submerges three species, presents two new species and resurrects two others which had been named in the 19th century but largely forgotten;
4. presents new data on the proportions and size relationships of minor to major form thumbed males;
5. searches the history of lapsed species;
6. examines the functional morphology of characters that characterize the genus and species;
7. based on the mitochondrial cytochrome oxidase subunit 1 (CO1) gene, assigns published barcodes to accepted species, presents new barcodes for two holotypes and a neotype and provides a phylogenetic hypothesis for the evolution of the genus.

Material and methods

Distribution

Collections were borrowed from institutions and private lenders (Table 1). Each collection was microscopically examined, specimens identified to species using the key and descriptions in Conlan (1990), and their numbers recorded by sex, rough developmental stage (adult, subadult, juvenile) and maturity (thumbed if male, brood plates setose if female). Collection records are available from the Canadian Museum of Nature (CMN). Species distributions were mapped based on these collections as well as on non-validated records in OBIS (Ocean Biogeographic Information System, obis.org), with dubious records filtered out. Post-1990 literature, which assumes that the authors were aware of the new species described by Conlan (1990), was also consulted extensively, with intensive effort to capture the more recent literature from 2010 to 2020. Distributions in OBIS and the literature were considered to be non-validated and were mapped with a different symbol to collections where the specimen had been examined. 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) while coordinates obtained from the internet were in other formats, these were converted to dms using the website https://www.fcc.gov/media/radio/dms-decimal.

TABLE 1. Acronyms for institutions that provided specimens, with their former names in brackets as used in Conlan (1990). Loans from private collectors follow.

Acronym	Institution
AM	Australian Museum, Sydney, New South Wales, Australia
BM	Bishop Museum, Honolulu, Hawai'i, USA (formerly BPBM, Bernice P. Bishop Museum)
CAS	California Academy of Sciences, Steinhardt Aquarium, Golden Gate Park, San Franciso, California, USA
CBG	Centre for Biodiversity Genomics, University of Guelph, Guelph, Ontario, Canada
CMN	Canadian Museum of Nature, Ottawa, Ontario, Canada (formerly NMNS, National Museum of Natural Sciences)
CMNZ	Canterbury Museum, Christchurch, New Zealand
MARBK	Marine Amphipod Resources Bank of Korea, Dankook University, The Republic of Korea
MCVR	Museo di Storia Naturale, Verona, Italy
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
MNRJ	Museu Nacional de Rio de Janeiro, Brazil
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))
NHMLA	Natural History Museum Los Angeles County, Los Angeles, California, USA (formerly LACM, Los Angeles County Natural History Museum and AHF, The Allan Hancock Foundation)
NHMW	Naturhistorisches Museum, Wien, Austria
NMCC	National Museums of Canada Collections, Ottawa, Ontario, Canada
NMNH	Smithsonian National Museum of Natural History, Washington, DC, USA (formerly USNM, National Museum of Natural History, Smithsonian Institution)
NMS	National Museum of Scotland, Edinburgh, Scotland, UK (formerly RSME, the Royal Scottish Museum, Edinburgh)
NRM	Naturhistoriska Riksmuseet, Stockholm, Sweden
NSMT	National Museum of Nature and Science, Tsukuba, Ibaraki 305-0005, Japan
RBCM	Royal British Columbia Museum, Victoria, British Columbia, Canada

......continued on the next page

TABLE 1. (Continued)

Acronym	Institution
SAM	South Australian Museum, Adelaide, Australia
SNM	Statens Naturhistoriske Museum, København, Denmark (formerly ZMUC, Zoologisk Museum, København, Denmark)
TAMU	Texas A & M University, College Station, Texas, USA
TSZ	Tromsø Museum, Tromsø, Norway
UAMN	University of Alaska Museum of the North, Fairbanks, Alaska, USA (formerly UAM, University of Alaska Museum)
UCT	Iziko South African Museum, Cape Town, South Africa (collection formerly at UCT, the University of Cape Town)
UiB	Universitetsmuseet i Bergen, Bergen, Norway (formerly ZMUB, Zoologisk Museum, Universitetet i Bergen)
UiO	Naturhistorisk Museum, Universitetet i Oslo, Norway (formerly ZMUO, Zoological Museum, University of Oslo)
VIMS	Virginia Institute of Marine Science, Gloucester Point, Virginia, USA
ZIN	Zoological Institute of Russian Academy of Sciences, St. Petersburg, Russia
ZMH	Centrum für Naturkunde, Universität Hamburg, Germany (formerly ZMUH, Zoologisches Institut und Zoologisches Museum, Universität Hamburg, Federal Republic of Germany)
ZUEC	Museu de Zoologia da Universidade Estadual de Campinas "Adão José Cardoso", Brazil
F. Costa	University of Minho, Campus de Gualtar, 4710-057 Braga, Portugal
G. Diviacco	Istituto di Anatomia Comparata dell' Università di Genova, Genoa, Italy
E. Gonzalez	Departamento de Biologia Marina, Facultad de Ciencias del Mar, Universidad Católica del Norte, P.O. Box 117 Coquimbo, Chile
J.S. Hong	Korea Ocean Research and Development Institute, Yeong Dong, Seoul, The Republic of Korea
S.-I. Ishimaru	Zoological Institute, Faculty of Science, Hokkaido University, Sapporo, Japan
Y.-H. Kim	Department of Life Sciences, Dankook University, Cheonan, The Republic of Korea
G. Krapp-Schickel	Forschungsinstitut Museum A. Koenig, Adenauerallee 160, 53113 Bonn, Germany
M. Ledoyer	Station Marine d′Endoume CNRS, Marseille, France
Y. Wakabara	Instituto Oceanográfico, Universidade de São Paulo, Brazil

Habitat

Habitat data were compiled from collection data of material examined as well as from the literature where there was a fair likelihood that the species identifications were correct. This largely required limitation to literature that had been published after the revision by Conlan (1990), though older literature was included if the true identification of the species could be discerned from the illustrations, descriptions and collecting data given, e.g., Stebbing (1888), Barnard (1969), Bousfield (1952, 1956a, b, 1958, 1962, 1973), Bousfield & Leim (1959), Bousfield & Laubitz (1972), and the CMN collections data base.

Most species had compact ranges within a single hemisphere and oceanic coast while four species were trans-hemispheric. The distributions of these four species (*J. marmorata*, *J. slatteryi* Conlan, 1990, *J. morinoi* Conlan, 1990 and *J. valida* Dana (1853)) were examined further, both in natural and artificial habitats to determine a putative indigenous range. The indigenous range was considered to be that where they occurred frequently and on remote, exposed coasts that were less subject to human visitation and modification than harbours, though they could occur there as well.

Habitat use by these species was also examined relative to habitat use by the local species of *Jassa*. This was based on a latitudinal transect on the Pacific coast of North America where collections were focussed on natural vs artificial habitats and substrate choice was documented. The collections were made in the summers of 1986–1987 at 122 locations spanning southeastern Alaska to southern California. Natural collections were at low tide or by scuba diving while artificial habitats were shallow subtidally from floating docks.

To examine habitat partitioning in an artificial habitat, two of the four trans-hemispheric species (*J. marmorata* and *J. slatteryi*) were followed over a year (Sep. 2009–Sep. 2010) amongst four algal groups (*Ulva*, *Chaetomorpha*, *Gigartina* and *Polysiphonia*) on three floating docks in an Australian harbour (Adelaide). The two *Jassa* species were considered introduced, as they were only known from a few harbours along the southern Australian coast and were not found on its extensive exposed coasts. The three floating docks were each randomly sampled at 5 locations along their lengths, with each of four algal groups sampled at each location. This amounted to 60 (i.e., 3 x 5 x 4) samples taken at ~4 week intervals. All individuals were extracted from the algae, identified and counted relative to algal dry weight.

Taxonomy

Species differentiation and illustration. Methods for species differentiation are described in Conlan (1990). For species described after Conlan (1990) (*Jassa kjetilanna*, *J. cadetta* and *J. trinacriae*), types were borrowed, keyed through Conlan (1990) and compared with descriptions and illustrations of other species of *Jassa*. Types of *J. mendozai* were not accessible due to closure of the collections during the COVID-19 pandemic but the type had been well illustrated by Winfield *et al*. (2021), enabling close comparison with other species. The World Register of Marine Species was considered the authority for classification. A key to the world species was developed based on all species known. Descriptions of the full body are given for new taxa while previously described taxa are given shorter diagnoses based on key character states. Full descriptions are given in Conlan (1990). 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. Body length was determined on the dorsal surface of the straightened animal from the tip of the rostrum to the base of the telson. Length variation about the mean is reported as standard deviation. 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. Those plates that also appeared in Conlan (1989, 1990) were inked using Rapidograph technical pens. All illustrations were made by artist Susan Laurie-Bourque in consultation with the first 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; JV or JUV, juvenile; SUBAD, subadult; LFT, left; RT, right; INT, intersex. Scale bars are 0.1 mm, based on eyepiece micrometer measurements. Non-digital photographs were scanned at high resolution. Adobe Photoshop was used to clean the scans and to increase contrast but manipulation was minimal in order to maintain scientific content. 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.

Thumbless males and females with asetose brood plates were termed juveniles and thumbed males and females with setose brood plates were termed adults. If the cuticle inside the propodus of a male was thumbed, or if the female had large, asetose brood plates and the female was about to molt, it was termed subadult as both situations indicated that the next molt would be adult. In some species, large juvenile males had small expansions in the distal half of the palm, which are herein called "pre-thumbs".

Minor vs major form males. When a single population held sufficient males of variable thumb lengths, these (and occasionally other body parts that appeared to sexually differ in development) were measured and graphed relative to body length. Measures were based on eyepiece micrometer lengths and then converted to mm using a stage micrometer.

In some species, small thumbed males also had toothed dactyls with the tooth fitting into the palm while large thumbed males did not. Coincident with dactyl toothing was a difference in the point of origin in the thumb: in the distal part of the propodus if the dactyl was toothed and in the proximal part of the propodus if the dactyl was not toothed. Those with a toothed dactyl and distally originating thumb were called minor forms and the others major forms. The criterion of thumb origin was then applied to other species where the dactyl did not tooth, so that minor forms were defined as all thumbed males where the thumb arose in the distal half of the propodus and majors where the thumb arose in the proximal half of the propodus. An objective measure of "thumb origin" was, therefore, the length of the propodus to the position of the thumb origin (measured by a straight line along the anterior of the propodus from the dactyl insertion to a bisecting line perpendicular to the thumb origin), divided by the full length of the propodus (measured by a straight line along the anterior of the propodus from the dactyl insertion to the carpus). Thumbed males were termed minor form if this proportion was < 0.5 and major form if the proportion was > 0.5.

Drawings of representative males in each category were made to illustrate their different morphologies. Thumb length was the longest straight-line length through the thumb from the palmar incision to the thumb tip. Thumb width, only measured on *J. marmorata*, was the longest straight-line width of the thumb, which occurred in the central part of the thumb. Females of some species were also measured for propodus length to compare with males.

Temporal variability. Within-population variability of male thumb length was determined for as many species as possible where there were sufficient specimens for analysis. A population of *Jassa staudei* Conlan, 1990 was also available in sufficient numbers for study of temporal variability of morphology. This species had colonized the walls of two 1.6 m^3 outdoor pressure head tanks, through which the seawater for the aquarium system at Friday Harbor Laboratories, Washington, USA moved at rapid pace. The seawater intake was at ~10 m depth. Collections at near-monthly intervals were made by Craig Staude (Friday Harbor Laboratories) beginning in Sept. 1984. Over a 28 month period, 18 collections held sufficient males for plotting thumb length relative to body length. All collections were preserved in 70% ethanol and sent to the Canadian Museum of Nature, where they were identified and measured for body, gnathopod 2 propodus and thumb length as described above.

Statistical analysis. Graphs and statistical analyses were constructed using SigmaPlot 14 (Systat Software, Inc.). Variables were regressed on body length and fitted to a linear regression if all assumptions were met (normal distribution, constant variance, and 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. Independence of the 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.

Difference in the gnathopod 2 thumb or propodus length and pereopod 3 basis width between sexes and age groups was determined for specimens from the same source population and within the same body length range by ANOVA if the data were normally distributed or by the non-parametric Kruskal-Wallis test on ranks if the data were not normally distributed. Normality was tested by the Shapiro-Wilk method. Pairwise comparisons were made by the Holm-Sidak method if the data were normally distributed with equal variance and, if not, by the non-parametric Dunn's test.

Functional morphology

Observations on functional morphology were made on live animals in aquaria and in the field at Helgoland, Germany (*J. falcata* (Montagu, 1808), *J. herdmani* and *J. marmorata*), Audrassalas, France (*J. falcata*), New York Aquarium and Jamaica Bay, New York (*J. marmorata*), Friday Harbour Laboratories, Washington (*J. staudei*) and Moss Landing Marine Laboratories, California (*J. slatteryi* and *J. marmorata*). Animals in aquaria were maintained in running seawater and provided with substrates (hydroids and macroalgae) on which to build tubes. When individuals were separated, they were kept in individual dishes surrounded by mesh to enable access to fresh seawater but to prevent escape. Interaction of specific appendages and their setae and spines were evaluated microscopically with a dissecting microscope and low lighting with substrate provided.

DNA analysis

DNA extraction and CO1 amplification. DNA was extracted from one or two pereopods of *J.valida* and *J. kimi* **n. sp.** using the QIAmp DNA Mini Kit (Qiagen) according to the manufacturer's protocols with a modification of the last step, eluting the DNA with only 100 µl of elution buffer. In order to provide the DNA barcode of this new

TABLE 2. Data on systematic position, accession numbers (BOLD Process ID), Barcode index numbers (BIN) and CO1-5P sequence lengths (Seq. Length) of the species sequences used in this work. Highest posterior density (95% HPD) of the calibration point (species included in the monophyletic clade) used with relative reference.

Family	Genus	Species	BOLD Process ID	BIN	CO1-5P Seq. Length	95% HPD Calibration points and Reference
Ischyroceridae	*Jassa*	*Jassa valida*	BMFVF056-19	BOLD:ACH7340	651	
		Jassa marmorata	GBCMA1758-09	BOLD:AAA3311	1434	
		Jassa slatteryi	ZPC084-13	BOLD:AAC2037	658	
		Jassa falcata	SWEMA861-15	BOLD:AAU2334	661	
		Jassa kimi **n. sp.**	JASSA152-19	BOLD:ADT6684	589	
		Jassa morinoi	BCAMP234-08	BOLD:AAW9144	650	
		Jassa pusilla	BNSA317-14	BOLD:ACP9511	658	
		Jassa laurieae **n. sp.**	FCCOM498-11	BOLD:ACG5178	659	
		Jassa herdmani	BNSA104-12	BOLD:AAX8442	658	
		Jassa staudei	GBCMA1649-09	BOLD:AAB3295	1434	
Ischyroceridae	*Hemijassa*	*Hemijassa goniamera*	AWIAM156-09	BOLD:AAG7166	650	
	Ericthonius	*Ericthonius difformis*	SWEMA643-15	BOLD:ACV6420	658	
		Ericthonius brasiliensis	GBCMA4967-13	BOLD:ACH6329	710	
		Ericthonius punctatus	BNSA022-12	BOLD:ABW2100	658	
Caprellidae	*Caprella*	*Caprella equilibra*	SERCI472-14	BOLD:ACM2452	658	
	Paracaprella	*Paracaprella pusilla*	GBCM1849-14	BOLD:ACQ1205	656	
Aoridae	*Grandidierella*	*Grandidierella japonica*	GBCMA5599-13	BOLD:ACI2381	607	
Gammaridae	*Gammarus*	*Gammarus balcanicus*	GBCMA11492-16		549	1.3–2.6Ma; Mamos *et al.* 2016
	Gammarus	*Gammarus balcanicus*	GBCMA11354-16	BOLD:ADD3923	549	
Pontogammaridae	*Jugogammarus*	*Jugogammarus kusceri*	GBCMA12786-16		656	9–83 Ma; Copilaş-Ciocianu *et al.* 2019
	Niphargogammarus	*Niphargogammarus aequimanus*	GBCMA12809-16		656	
Eulimnogammaridae	*Ommatogammarus*	*Ommatogammarus albinus*	GBCMA1865-09		405	17–27Ma; Mamos *et al.* 2016
	Eulimnogammarus	*Eulimnogammarus viridulus*	GBCMA0147-06		501	
Acanthogammaridae	*Diplacanthus*	*Diplacanthus brevispinus*	GBCMA0133-06	BOLD:AAJ3888	633	

genus, the Folmer fragment of the mitochondrial cytochrome oxidase subunit 1 gene (CO1) was amplified using the universal primers LCO1490/HCO2198 (Folmer *et al.* 1994; Table 2). Each reaction consisted of 0.2 mM dNTPs, 0.5 µM of forward and reverse primers, 10 x PCR-buffer, 0.02U/µl Hotmaster Taq (5Prime), 3 µl of template DNA, and water to make the mix to the final 25 µl. PCR thermal cycling conditions consisted of an initial denaturation at 94 °C for 2 min, followed by 36 cycles of 94 °C for 20 s, primer annealing at 42 °C for 20 s, extension at 65 °C for 1 min, and lastly a final extension at 65 °C for 15 mins. The PCR product quality was assessed in a 2% agarose gel. Then, sequencing was performed at a contract sequencing facility (EUROFINS, Germany).

Sequences and phylogenetic analyses. The CO1 sequences of all other *Jassa* species present in BOLD and Genbank were retrieved (Table 2) as well as sequences of species of the same family (Ischyroceridae), closely related families (i.e. Caprellidae and Aoridae) and distantly related families (e.g. Gammaridae) for outgroup comparison. Despite being clearly *Jassa* species, two BINs (BOLD:ACG5178 and BOLD:AAV1495) present in BOLD were not considered in this work because of their morphological uncertainty. An additional search (BLASTN) on Genbank was done in order to implement some other genes in the analyses (i.e. ITS region, 16S, 18S and 28S). This was successful only for the three species *J. falcata, J. slatteryi* and *J. marmorata* (corresponding accession numbers respectively: DQ378017.1, AB295408.1 and KJ193731.1). *Jassa falcata* and *J. slatteryi* featured the complete18s gene whereas only a fragment of the same gene was available for *J. marmorata*. The CO1 sequences were checked and aligned in MEGA X (Kumar *et al.* 2018). Overall and pairwise distances between *Jassa* species and the closely related *Hemijassa goniamera* (Walker, 1903) were conducted using the Kimura 2-parameter model (Kimura 1980) and 1,000 bootstrap in MEGA X.

Phylogenetic relationships among the *Jassa* species were reconstructed, using only unique haplotypes, with maximum likelihood (ML) and Bayesian inference (BI) of the CO1 gene and time calibrating the latter. The ML was inferred with PhyML (Guindon *et al.* 2010) using 1,000 bootstraps for the branch support. The best substitution (GTR+I+G) model was tested with the SMS routine in PhyML with Bayesian Information Criterion (BIC; Lefort *et al.* (2017). The time calibrated BI phylogeny was reconstructed in BEAST 2.5.2 (Drummond & Bouckaert 2014) on XSEDE. The GTR model of evolution with a proportion of invariant (I) and gamma shape parameter (G), found using bModelTest (Bouckaert & Drummond 2017), and the birth-death speciation model were set as priors. In order to calibrate the phylogeny, two methods were used — one based on the CO1 mutation rate and another on calibration points. For the first method, a strict clock with rates ranging from 0.7 and 1.7% Ma^{-1} and a starting value of 1.2% as proposed by Copilaş-Ciocianu *et al.* (2019) was applied. For the calibration point method, three calibration points were chosen from the literature, one based on fossil records (Copilaş-Ciocianu *et al.* 2019) and two based on geological events (Mamos *et al.* 2016). Three runs of 300,000,000 iterations of Markov chain Monte Carlo (MCMC) sampled every 1,000 iterations were performed. All runs were examined using Tracer v 1.7.1 (Rambaut *et al.* 2018) and all sampled parameters achieved sufficient sample sizes (ESS>200). Tree files were combined using LogCombiner 1.8.4 on XSEDE (Drummond & Bouckaert 2014), with 30% of burn-in. The maximum clade credibility tree was generated using TreeAnnotator (Drummond & Bouckaert 2014) on XSEDE. All the XSEDE analyses were performed on the CIPRES Science Gateway (Miller *et al.* 2010).

Results

Distribution

About 25,000 specimens were examined from nearly 1,100 collections from which 24 species were recognized (Figs 1–12). One or more species of *Jassa* were found mentioned or more thoroughly treated in 338 publications, most of which were post-Conlan (1990) (Supplementary Table S1). A survey of the most recent literature (241 papers published over 2010–2019) found that the majority (134 papers) concerned species in the NE Atlantic and its seas (Fig. 13). The species most commonly identified was *J. marmorata* (54 papers), followed by *J. herdmani* (25) and *J. falcata* (20). Another 25 publications about this region did not identify the species or gave suspected misidentifications. Much behind the NE Atlantic region was literature concerning the NW Pacific (32 papers), followed by the SW Atlantic (17), NE Pacific (16), NW Atlantic (15) and SE Atlantic (15). *Jassa marmorata* and *J. slatteryi* were the most frequently treated; other species received little or no attention. Regions with the least attention to *Jassa* were in the South Pacific, Indian Ocean and Southern Ocean, where *Jassa* appeared in only 2–6 publications over this 10-year period.

Based on these collections and literature sources, the most polar ranges found were for *J. pusilla* (Sars, 1894) at Hammerfest, Norway (71°N) (Fig. 9) and in the Ross Sea, Antarctica (74.7°S) for *J. thurstoni* Conlan, 1990 (Fig. 12). The most tropical records were for *J. marmorata* and *J. morinoi* Conlan, 1990 in the northern hemisphere in Banjul, The Gambia (13°N) (Figs 1, 2, 5 and 6) and for *J. marmorata* in the southern hemisphere at Cañete, Peru (13°S) (Fig. 2). Four of the 24 species crossed the tropics to span the temperate regions of both hemispheres (Figs 1–8) while the other 20 species were only known from one hemisphere (12 species exclusively in the Northern Hemisphere (Figs 9–10) and 8 species in the Southern Hemisphere (Figs 11–12)).

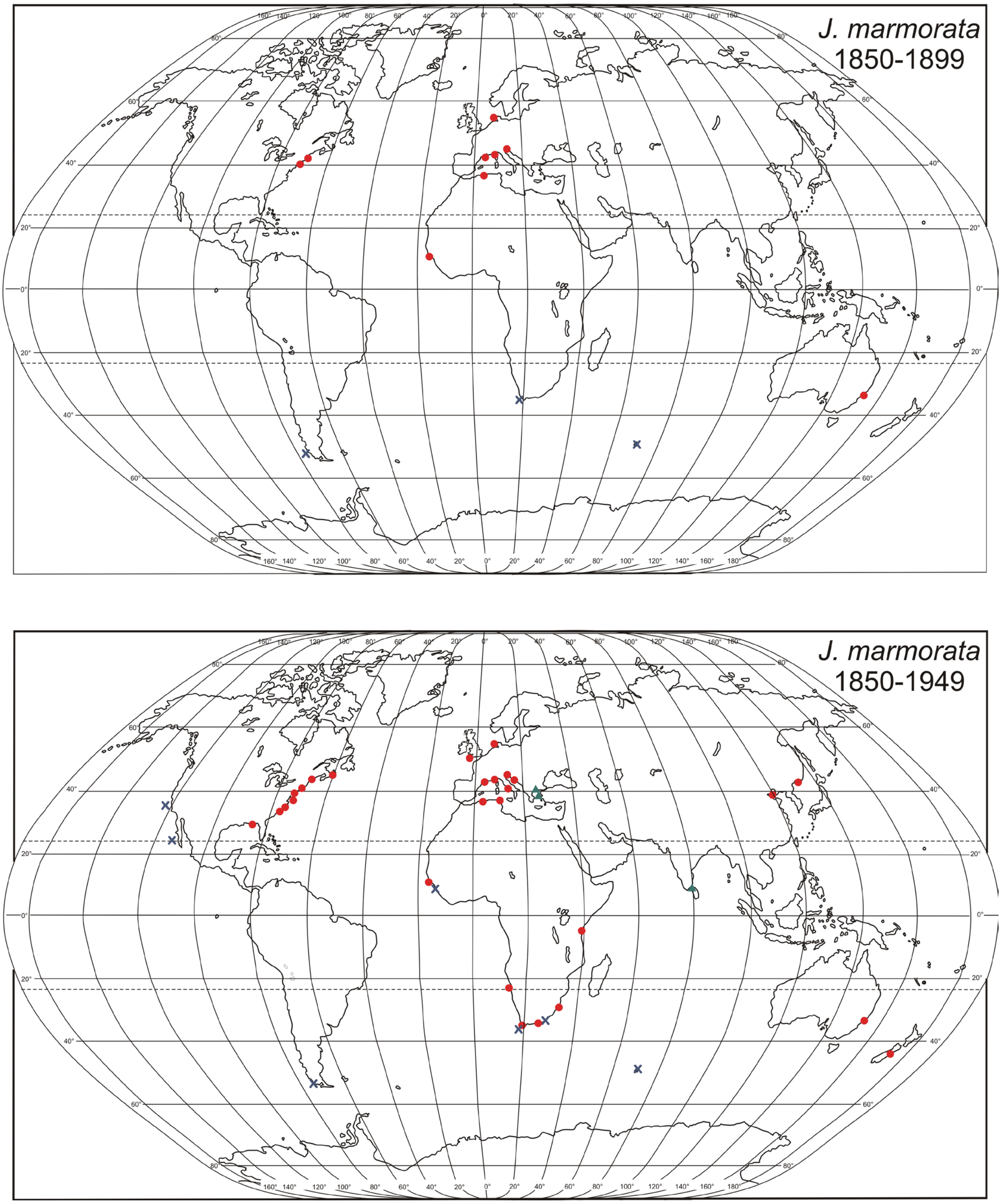

FIGURE 1. Progressive discovery of *Jassa marmorata* from 1850 to 1949. Red dot: identification confirmed by specimen examination; green triangle: literature record (Supplementary Table S1) with identification not confirmed but judged likely to be this species; blue x: suspected or known to be on the hull or interior of a boat or ship.

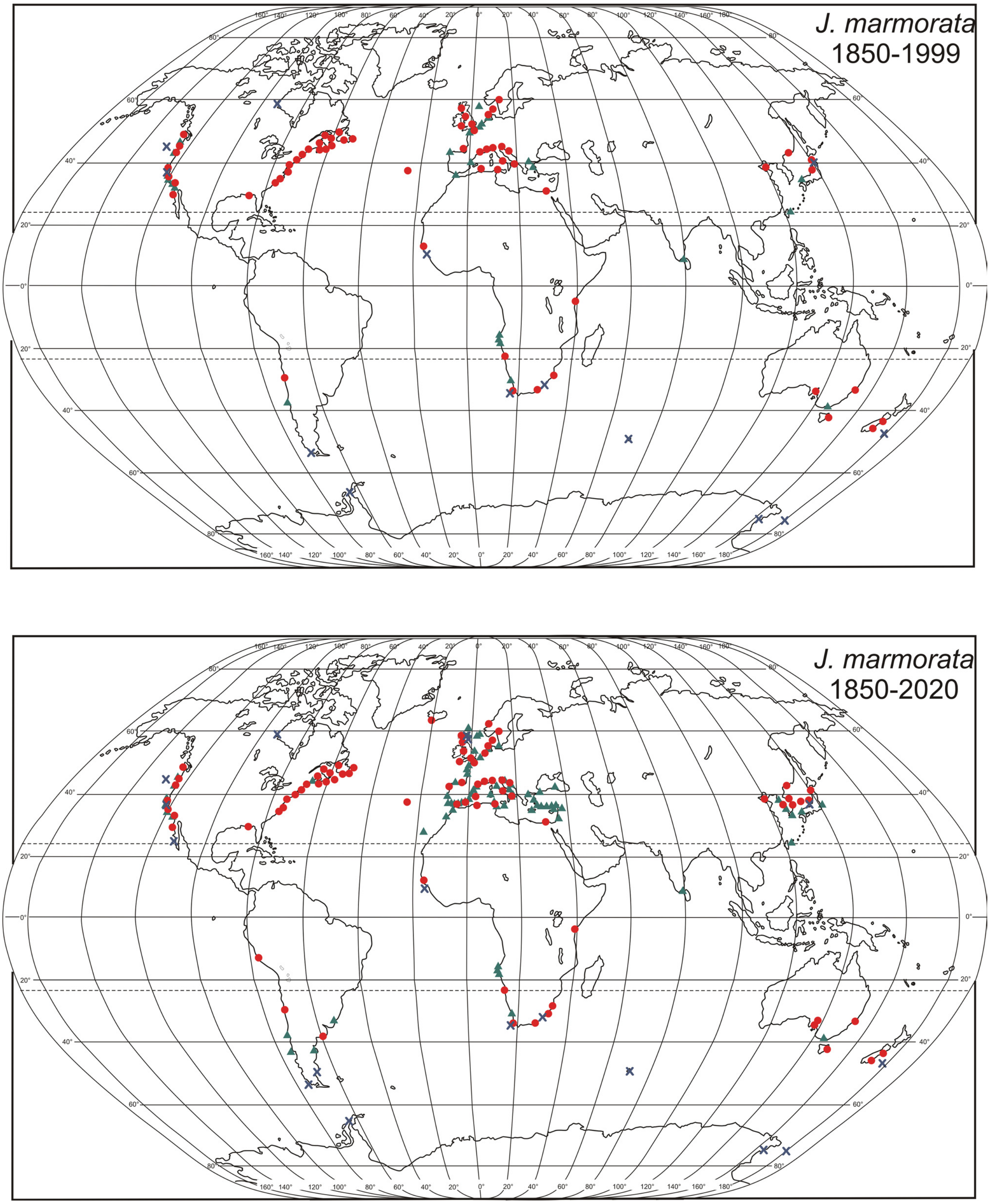

FIGURE 2. Progressive discovery of *Jassa marmorata* from 1850 to 2020. Red dot: identification confirmed by specimen examination; green triangle: literature record (Supplementary Table S1) with identification not confirmed but judged likely to be this species; blue x: suspected or known to be on the hull or interior of a boat or ship.

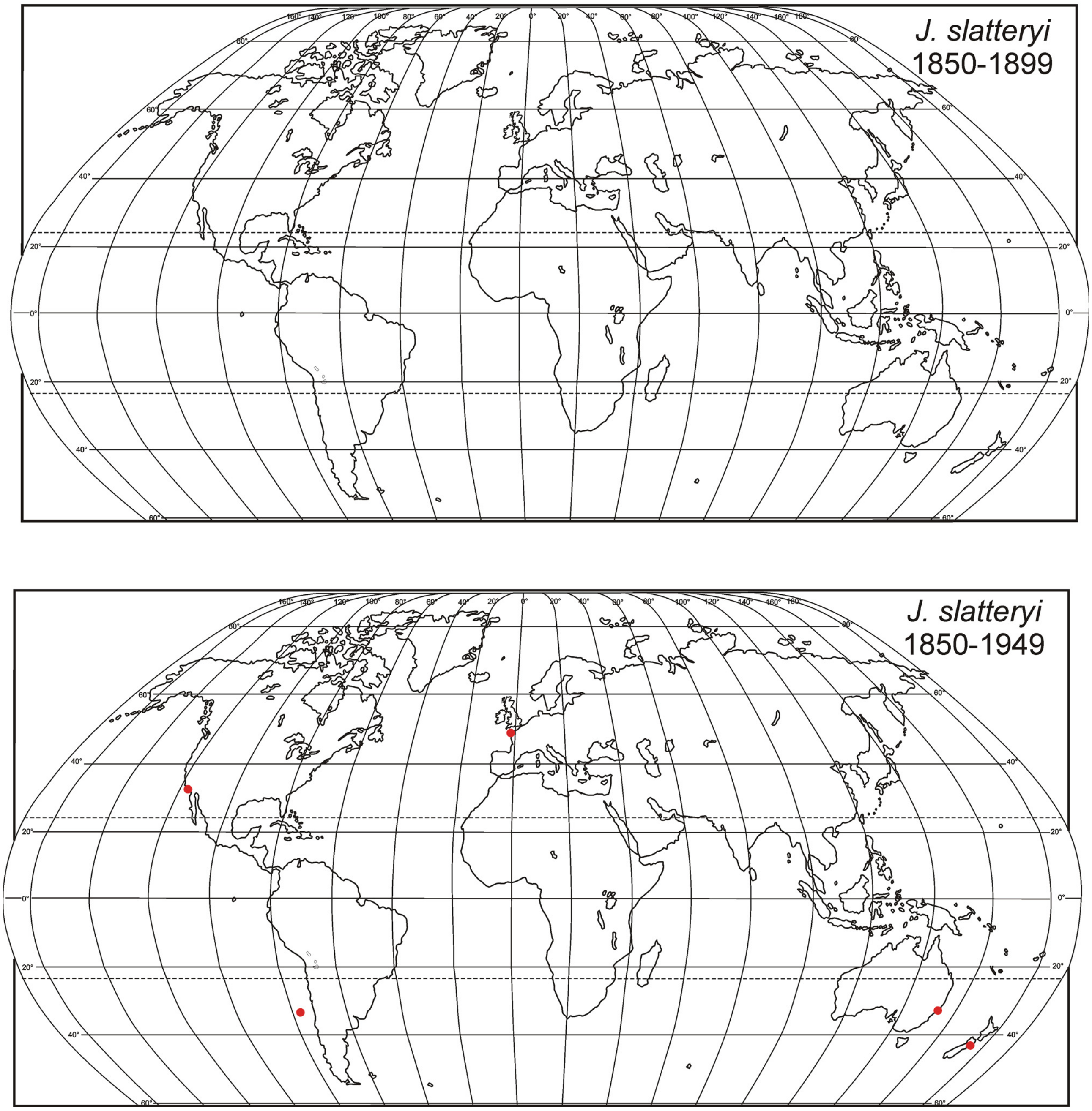

FIGURE 3. Progressive discovery of *Jassa slatteryi* from 1850 to 1949. Red dot: identification confirmed by specimen examination; green triangle: literature record (Supplementary Table S1) with identification not confirmed but judged likely to be this species; blue x: suspected or known to be on the hull or interior of a boat or ship.

Transhemispheric species. The collection data showed that *Jassa marmorata* (Figs 1–2), *J. slatteryi* (Figs 3–4), *J. morinoi* (Figs 5–6) and *J. valida* Dana (1853) (Figs 7–8) have had historically lengthy records in both hemispheres. *Jassa marmorata* is the most widespread and frequently encountered. It was already being found in the 19th century in numerous parts of the world: Atlantic North America and Europe, Pacific South America, the Mediterranean Sea, Atlantic Africa, South Africa, Kerguelen Island and eastern Australia. Collections during the first half of the 20th century yielded many more confirmed records of *J. marmorata* in the North Atlantic but relatively few locations elsewhere. *Jassa marmorata* also was found on the coasts of more countries: the Pacific USA, England, China, Russia, South Africa, Tanzania, and New Zealand (Fig. 1). In the second half of the 20th century, collections along the Pacific coast of North America yielded *J. marmorata* from British Columbia to Baja California (Fig. 2). On the Atlantic coast of North America, additional records from both natural and artificial habitats showed a range from Newfoundland to the

Gulf coast of Florida (Supplementary Tables S2 and S3). In Europe, confirmed records showed *J. marmorata* ranging from southern Norway to the Mediterranean Sea. *Jassa marmorata* was also being found on ships as far away as Antarctica. In the 21st century, collections and literature records showed *J. marmorata* as far north as Iceland, on Atlantic islands far from continents, and more widely in South America, the Mediterranean Sea, Asia and Australia (Supplementary Tables S4–S7). Although common on artificial substrates in Europe (Supplementary Table S5) and elsewhere (Supplementary Table S7), collection records also showed it in seemingly natural habitats (Supplementary Tables S4 and S6). However, locations for these "natural" habitats were often close to cities and towns and so could have been influenced by human proximity. In most cases, collection records were not precise enough to detail how undisturbed the sampling site was.

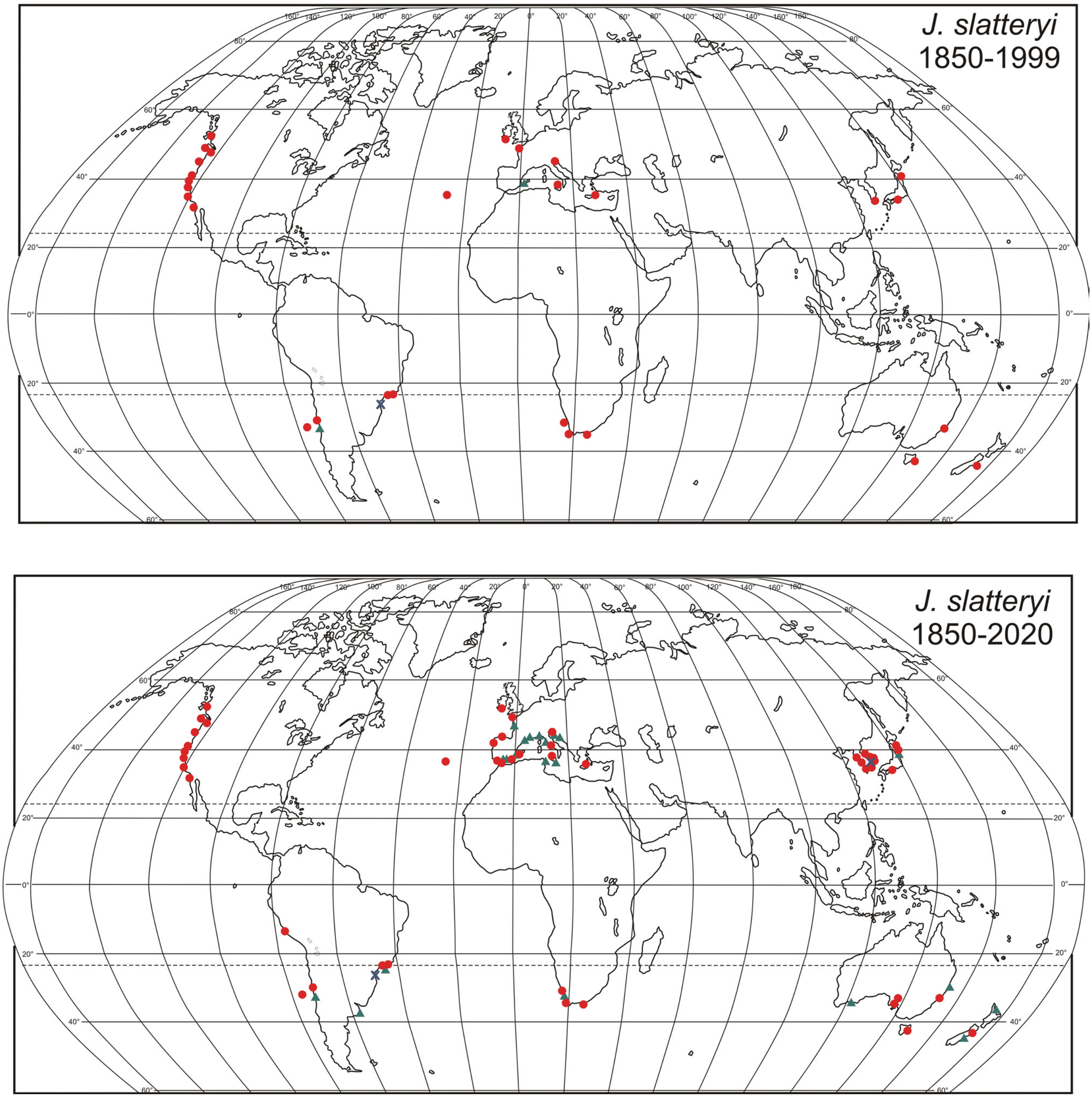

FIGURE 4. Progressive discovery of *Jassa slatteryi* from 1850 to 2020. Red dot: identification confirmed by specimen examination; green triangle: literature record (Supplementary Table S1) with identification not confirmed but judged likely to be this species; blue x: suspected or known to be on the hull or interior of a boat or ship.

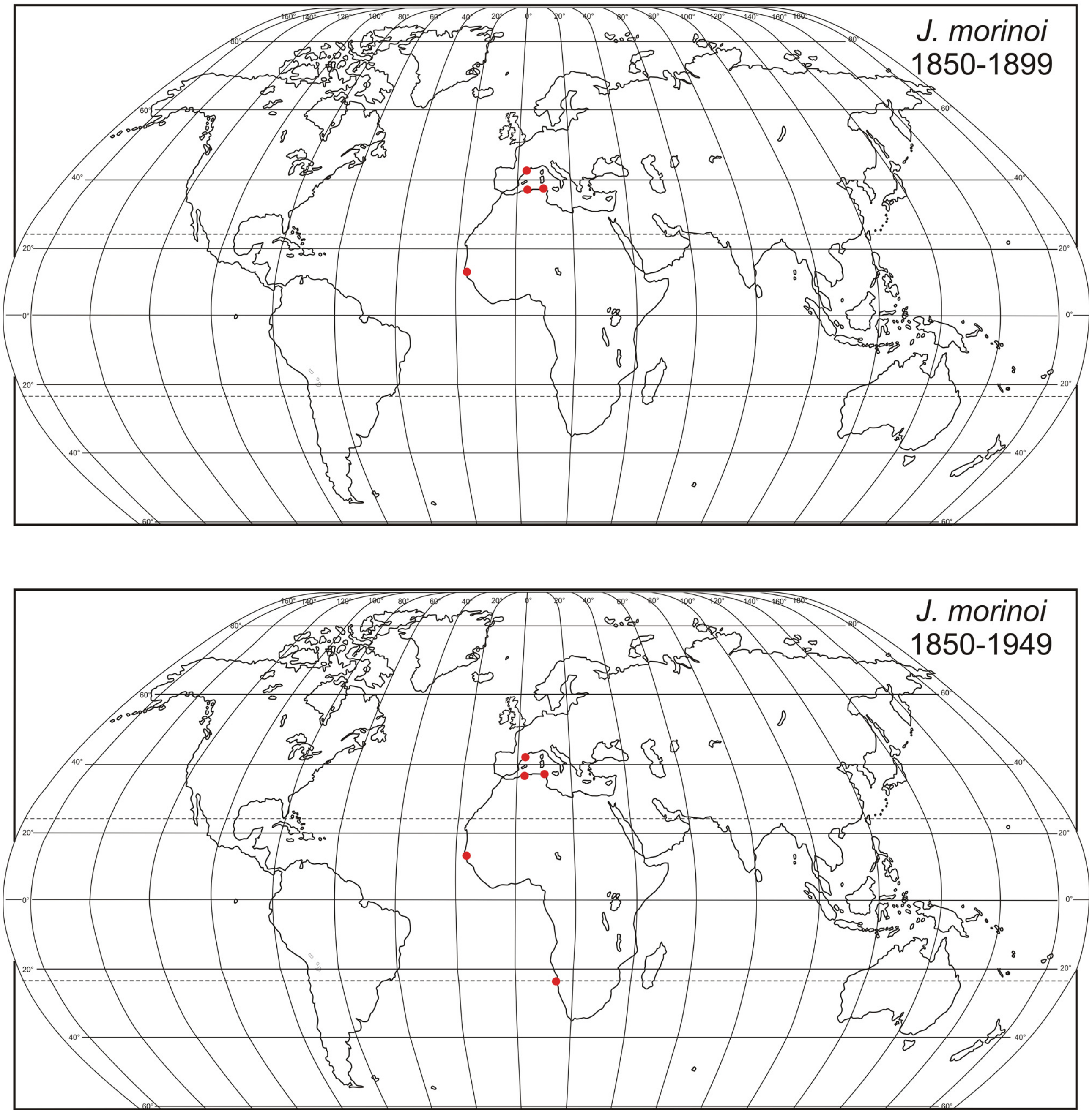

FIGURE 5. Progressive discovery of *Jassa morinoi* from 1850 to 1949. Red dot: identification confirmed by specimen examination; green triangle: literature record (Supplementary Table S1) with identification not confirmed but judged likely to be this species; blue x: suspected or known to be on the hull or interior of a boat or ship.

Jassa slatteryi has similarly been found on the coasts of most continents but has not been verified to be on the Atlantic coast of North America, where *J. marmorata* and *J. valida* dominate[1] (Figs 3–4). First collection records known are for Isla Robinson Crusoe (formerly Masatiera), Chile (1916; NRM 190); Concarneau, France (1923; MNHN Am 2656); Port Jackson, Australia (~1922; AM P.5869); Lyttelton Harbour, New Zealand (1928; NHM C38/42 2737-1928.12.1:46; also SNM); and in San Diego harbour, USA (1948; NMNH 218558) (Table 3). In the second half of the 20th century, *J. slatteryi* was found more widely on the Pacific coast of North America, from central British Columbia to southern California in both natural (remote) and human influenced locations (Supplementary Tables S8–S10). Confirmed presence was also recorded for mainland Chile, Brazil, Ireland, Italy, South Africa, The Republic of Korea, Japan and Tasmania (Australia). For 2000–2018, there were additional literature reports of *J.*

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[1] Schwindt *et al.* (2020) reported *J. slatteryi* on the SW Atlantic coast from an unknown literature source but this has not been verified and may instead have been *J. valida* which was unknown at that time.

slatteryi on the coasts of Argentina and The Republic of Korea. *Jassa slatteryi* was found in a second harbour in New Zealand (Inglis *et al.* 2006b) after previously being found in Lyttelton (Table 3; Inglis *et al.* 2008). Like *J. marmorata*, it was found on human-modified substrates in Europe and elsewhere (Supplementary Tables S5 and S7) as well as in seemingly natural locations (Supplementary Tables S4 and S6).

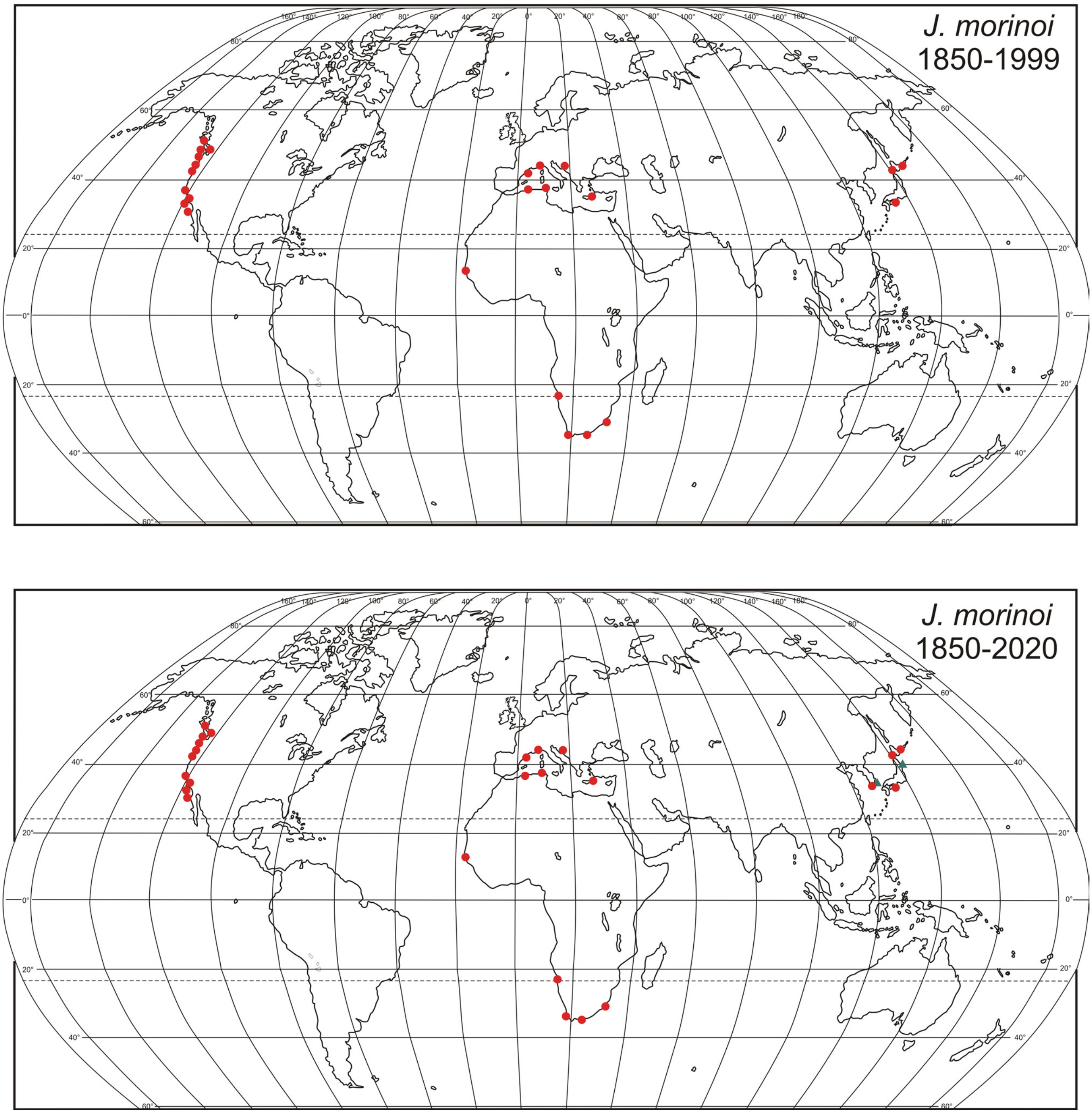
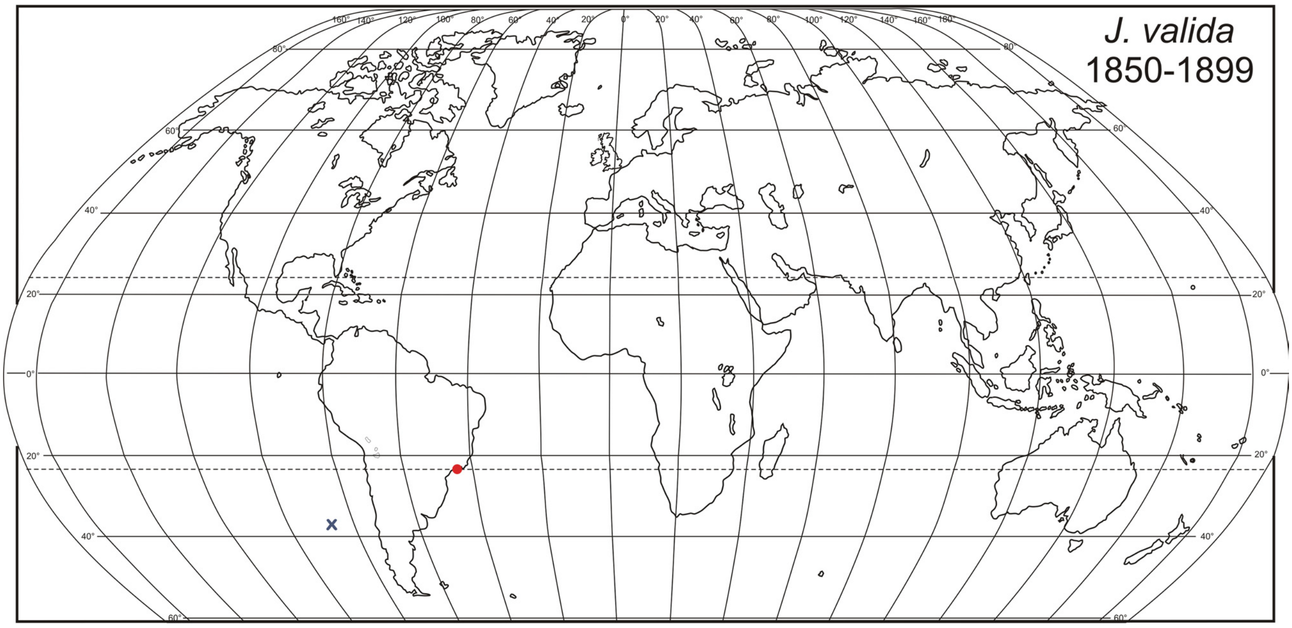


FIGURE 6. Progressive discovery of *Jassa morinoi* from 1850 to 2020. Red dot: identification confirmed by specimen examination; green triangle: literature record (Supplementary Table S1) with identification not confirmed but judged likely to be this species; blue x: suspected or known to be on the hull or interior of a boat or ship.

The third transhemispheric species, *Jassa morinoi*, is first known from the collections of Edouard Chevreux in 1885 in the Mediterranean Sea and in 1890 at Dakar, Senegal (Figs 5–6; Table 3). No further collections in the first half of the 20th century revealed *J. morinoi* but in the second half, it was found extensively along the Pacific coast of North America from British Columbia to California, more widely in the Mediterranean Sea, and on the coast of South Africa in both artificial and seemingly natural locations (Supplementary Tables S4–S9). Additional collections in 2000–2019 revealed *J. morinoi* in The Republic of Korea and other parts of Japan. *Jassa morinoi* has a more limited world distribution than *J. marmorata* and *J. slatteryi*. In the Southern Hemisphere, it is only confirmed from parts of the African coast[2]. In the Northern Hemisphere, it has never been found on the Atlantic coasts of North America[3] or Europe.



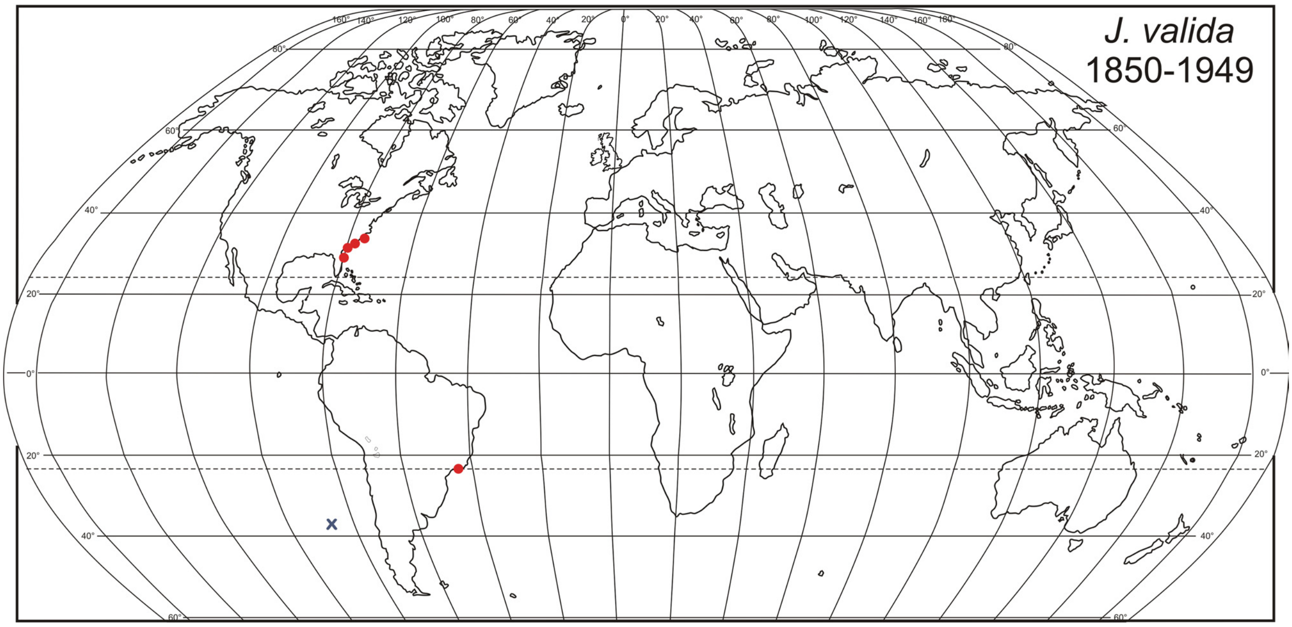


FIGURE 7. Progressive discovery of *Jassa valida* from 1850 to 1949. Red dot: identification confirmed by specimen examination or by identical haplotypes to examined specimens; green triangle: literature record (Supplementary Table S1) with identification not confirmed but judged likely to be this species; blue x: suspected or known to be on the hull or interior of a boat or ship.

The fourth trans-hemispheric species, *J. valida*, has the most limited trans-hemispheric range of the four (Figs 7–8). It is known mainly from the Atlantic coast of the Americas, but there is a ship-based record far off the coast of

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[2] One record of "*J. morinoi*" in South America was found in OBIS but the identification is not confirmed and its collection location (from sand at Paracuru, State of Ceará, Brazil) would place it as an outlier in an unusual habitat (sand) at a more tropical location (3° S) than has been confirmed for any species of *Jassa*. Therefore, it has not been mapped.

[3] An unconfirmed record of "*J. morinoi*" from soft sediment in the Gulf of Mexico is suspected to be mis-identified and is actually ship contamination by *J. valida*. For further information, see the Remarks for *J. valida* in the Taxonomy section.

Chile and identical haplotypes have been found on the coast of South Africa and the French Frigate Shoals, part of the northwestern Hawaiian Islands (Plaisance *et al.* 2011a, b). These latter locations have received extensive shipping for at least two centuries. First described from the coast of Brazil by Dana (1853), recent molecular analysis (Pilgrim and Darling 2010; Desiderato 2020), morphological assessment (LeCroy 2007) and re-examination of U.S. collections recorded in Conlan (1990) revealed it had been collected early in the 20th century on the southern Atlantic and Gulf coasts of the U.S. but not recognized as this species. Morphologically similar to *J. marmorata*, re-examination of "*J. marmorata*" collections mainly at CMN and NMNH revealed that the two species have distinct distributions, with the transition occurring around North Carolina (Supplementary Tables S2 and S3). Specimens to the south are more likely to be *J. valida*, which is not known to occur further north. Conversely, *J. marmorata* largely (but not entirely) disappears south of this transition point but is the only species known northwards to Newfoundland. Both species have been collected from seemingly natural locations on the North American coast as well as on artificial substrates in harbours, such as buoys, docks, and settling plates. References to "*J. marmorata*" in the southwestern Gulf of Mexico by Winfield *et al.* (2021) and more widely in the Gulf of Mexico by LeCroy *et al.* (2009) and repeated by Paz-Ríos & Ardisson (2013) and OBIS[4] may instead pertain to *J. valida.*

Collection records suggest that shipping has been a historic mechanism for the dispersal of *Jassa*. *Jassa marmorata*, *J. slatteryi* and *J. valida* have all been collected from or close to ships far out to sea, where such coastal species would not normally occur without a hard substrate to attach their tubes to. The first confirmed record of *J. marmorata* is from the screw of the H.M.S. *Challenger* (Dec. 1873) off South Africa (Table 3) (NHM, station 142). Another scraping from the ship's screw at Kerguelen Island in Jan. 1874 was also confirmed to be *J. marmorata* (NHM, station 149). These two collections indicate that *J. marmorata* was able to survive the *Challenger*'*s* epic journey, potentially originating in the ship's home port of Portsmouth, England where it departed in Dec. 1872 (Murray & Thomson 1895). Indeed, Stebbing (1888) suspected that the H.M.S. *Challenger* was transporting *Jassa*: "There is the possibility, as I have elsewhere suggested, that these creatures may have travelled out from our own waters along with the vessel to the southern latitudes at which they were captured." (Stebbing 1888, p. 1135). *Jassa valida* was also picked up at sea off the coast of Chile by H.M.S. *Challenger* (NHM, station 302), though there is no indication that it was attached to the ship's screw as was *J. marmorata*.

Other museum collections support Stebbing's suggestion that shipping was dispersing *Jassa* widely as early as the 19th century. Fifteen specimens of *J. marmorata* were collected in Smyth Channel, Chile by Wilhelm Michaelsen in 1893 (ZMH K-26608), possibly where they were fouling the Swedish ship. Schellenberg (1926) noted that "*Iassa falcata*" had been collected from the hull of the *Gauss* in the Atlantic Ocean during the German Southpolar Expedition of 1901–1903 (specimens not seen). *Jassa marmorata* was confirmed from a scrape of an un-named ship bottom in 1894 (location unknown but likely USA; NMNH 34225), from a boat bottom in Monterey Bay, California (1931, NMNH 120848), and from a ship in the Danish Atlantide Expedition at Bathurst, Gambia (1945, stn 155; SNM and RSME 1959.61.149). *Jassa marmorata* was collected in 1937 from the U.S.L.H. Tender *Cypress* situated off Ft. Pierce, Florida (NMNH 142577)[5]. An unconfirmed species of *Jassa* was collected in the Bay of Biscay plankton under the name of *J. pulchella* (Stebbing and Fowler 1904) and suspected by Sexton and Reid (1951) to have 'put to sea' on a floating object (possibly the ship's hull). However, *Jassa* is known to naturally swim into the plankton, despite being mostly benthic (Havermans *et al.* 2007; Fernandez-Gonzalez *et al.* 2014).

More recently, *J. marmorata* has been found fouling ships in South Africa (1951; UCT DBN 131P), Japan (1988; H. Morino loan), Brazil (1985; NMNS IZ1985-095) and Australia (Lewis *et al.* 2006). The intended destination for this latter vessel, a barge fouled by *J. marmorata* in Tasmania, was the subantarctic Macquarie Island, which is home to *J. alonsoae* and *J. justi* Conlan, 1990 (Fig. 11). Recognizing the potential hazard to Macquarie Island of *J. marmorata* and other species fouling the barge, a management decision was subsequently made not to deploy the barge (Lewis *et al.* 2006). Two collections of *J. slatteryi* showed evidence of rafting: (1) along with *J. marmorata*, on a raft floating out at sea, near Guayacán, La Herradura Bay, Chile in 1984 (E. González loan); and (2) on the screw of a ship anchored in Samcheon-po bay on the south coast of The Republic of Korea (Lim & Park 2006). This is close to a previous record of *J. slatteryi* (then called *J. falcata*) on settling plates in Deukryang Bay, The Republic of Korea (Hong 1983). Jeong *et al.* (2006, 2007 and 2012) found *J. slatteryi* to be abundant in an eelgrass bed at nearby Gwangyang Bay, The Republic of Korea, which is a heavily industrialized part of the coast.

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[4] Despite exact location coordinates given in OBIS for the coast of Mexico, the source for these records, which is LeCroy *et al.* (2009) is for collecting locations no further south than the U.S. Therefore, these exact coordinates should not be used.

[5] Since *J. valida* was not recognized at the time of identification by Conlan (1990), and this species is now known from Florida more so than *J. marmorata*, the correct identification may be *J. valida*.

Seawater systems on ships may also be a source of sample contamination if they are inhabited by *Jassa*. This could lead to erroneous conclusions on its distribution and habitat. Ship-based sample contamination by *J. marmorata* living in the German research vessel *Polarstern*'s seawater system are confirmed for two deepwater Arctic transects (Sirenko *et al.* 2004). This species was erroneously reported at 26 of 30 soft sediment stations at 1018–4478 m depth (Kröncke 1994) and 16 of the 17 stations at 560–4411 m depth (Kröncke 1998) (also listed in OBIS). By contrast, other amphipods occurred in ≤ 7 of the 30 stations (Kröncke 1994) and ≤ 4 of the 17 stations (Kröncke 1998). The depth, location and sediment type are well beyond that known for *J. marmorata* (Table 4). Another sample (P. Shaw loan P1327-7-6a) finding *J. marmorata* at 1580 m depth on the Axial Seamount, Juan de Fuca Ridge (Pacific coast, off Oregon) is likely contamination by the submersible *Pisces* or its mother ship (P. Shaw, pers. comm.). A report of *J. valida* (described as a new species but synonymized herein) from soft sediments at 456–3295 m depth by Winfield *et al.* (2021) is also possibly ship contamination. Further discussion is presented in the Remarks for *J. valida* in the Taxonomy section.

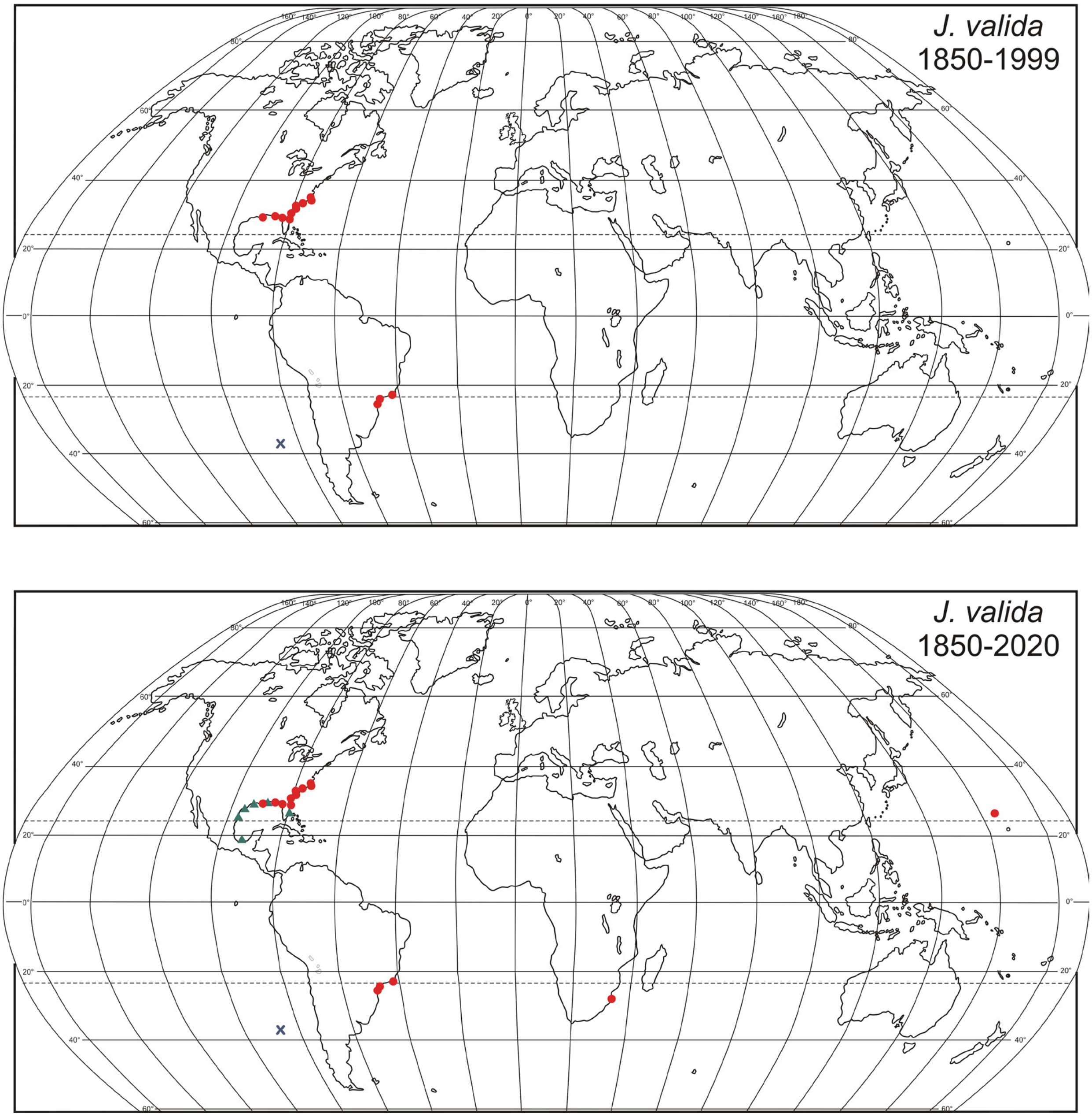

FIGURE 8. Progressive discovery of *Jassa valida* from 1850 to 2020. Red dot: identification confirmed by specimen examination or by identical haplotypes to examined specimens; green triangle: literature record (Supplementary Table S1) with identification not confirmed but judged likely to be this species; blue x: suspected or known to be on the hull or interior of a boat or ship.

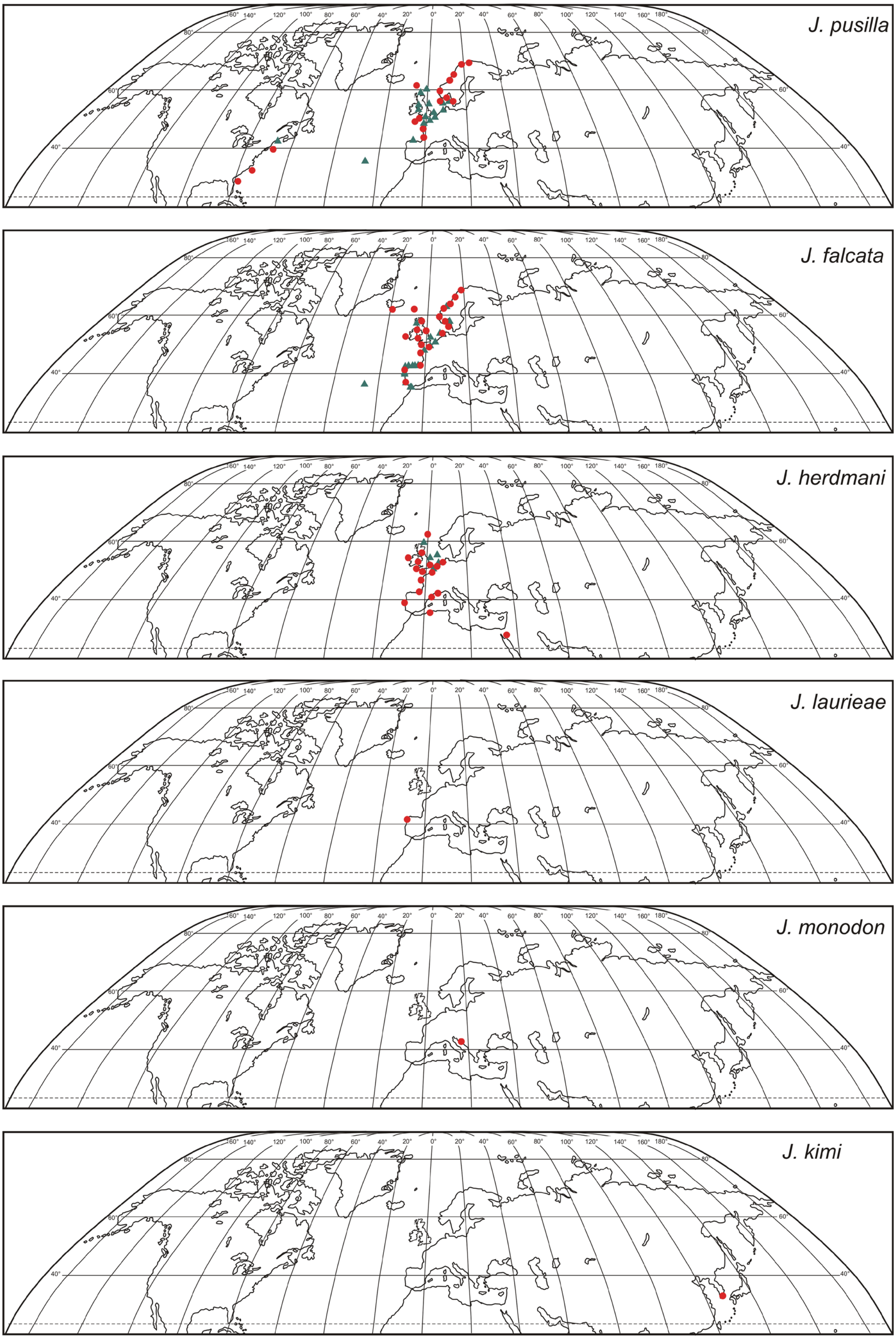

FIGURE 9. Records of Northern Hemisphere species of *Jassa* that were found in the eastern and/or western North Atlantic and seas, along with *J. kimi* in the western Pacific. Red dot: identification confirmed by specimen examination; green triangle: literature record (Supplementary Table S1) with identification not confirmed but judged likely to be this species; blue x: suspected or known to be on the hull or interior of a boat or ship.

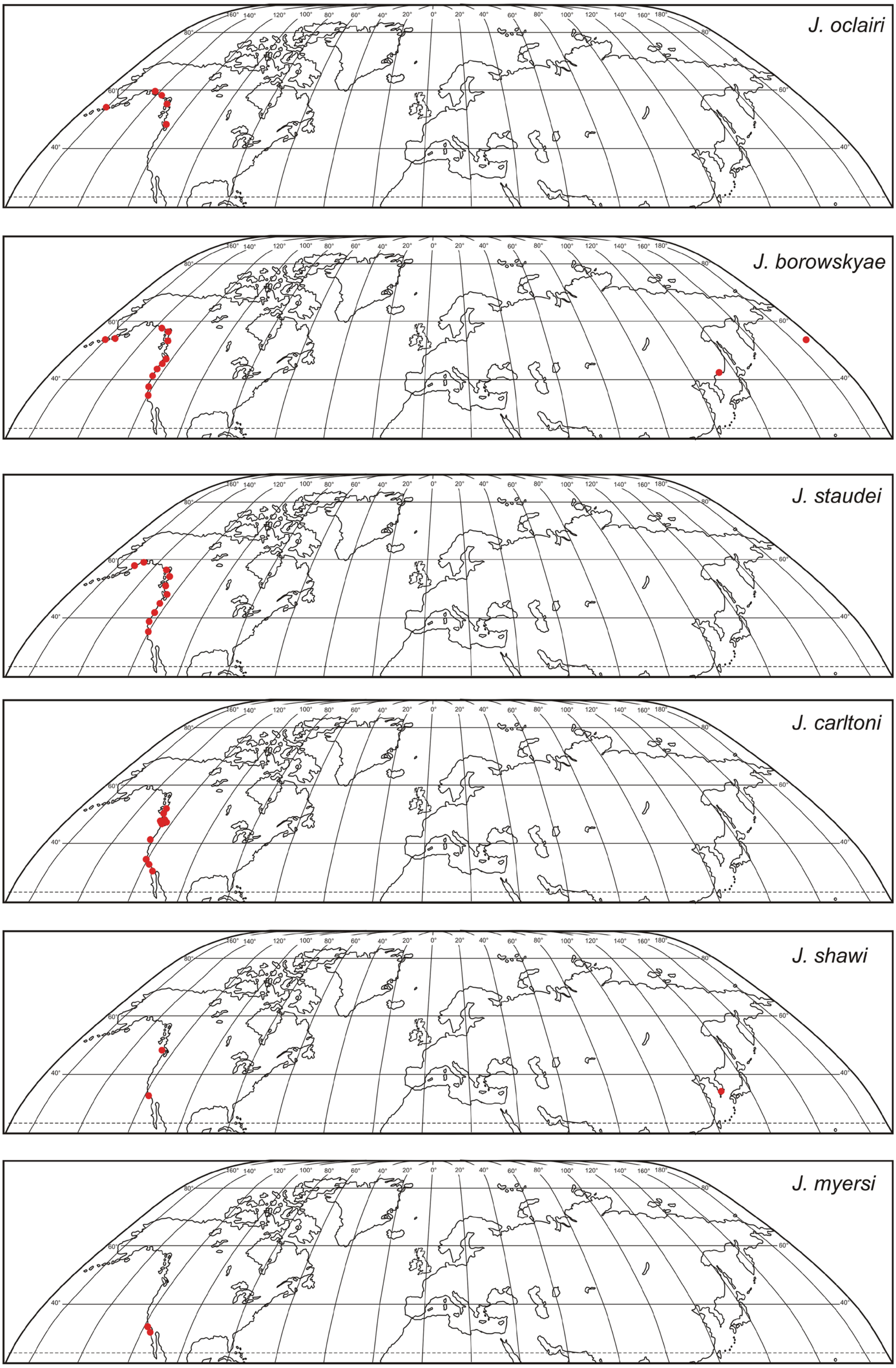

FIGURE 10. Records of Northern Hemisphere species of *Jassa* that were found in the eastern and/or western North Pacific and seas. Red dot: identification confirmed by specimen examination; green triangle: literature record (Supplementary Table S1) with identification not confirmed but judged likely to be this species; blue x: suspected or known to be on the hull or interior of a boat or ship.

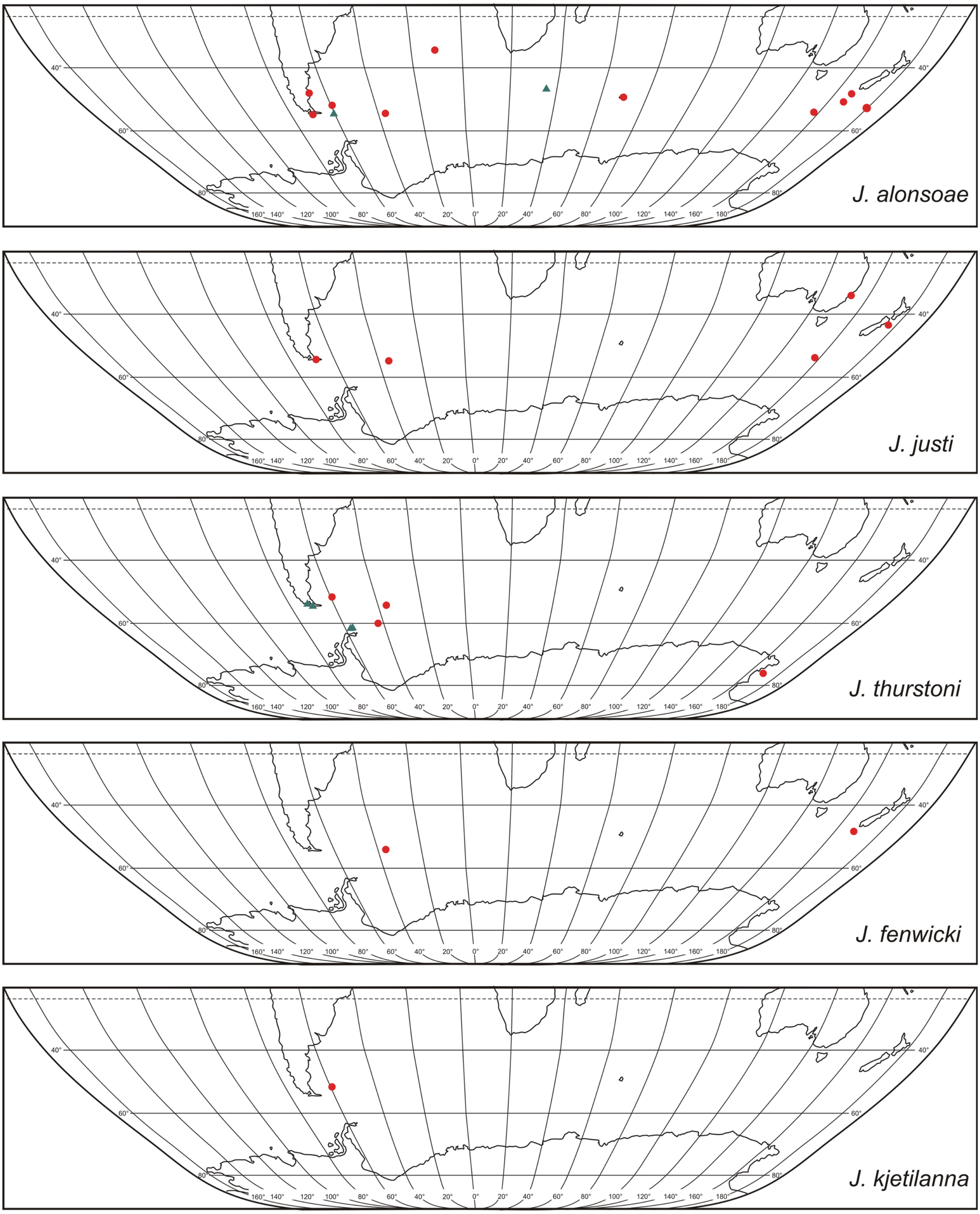

FIGURE 11. Records of Southern Hemisphere species of *Jassa*. Red dot: identification confirmed by specimen examination; green dot: literature record (Supplementary Table S1) with identification not confirmed but judged likely to be this species; blue x: suspected or known to be on the hull or interior of a boat or ship.

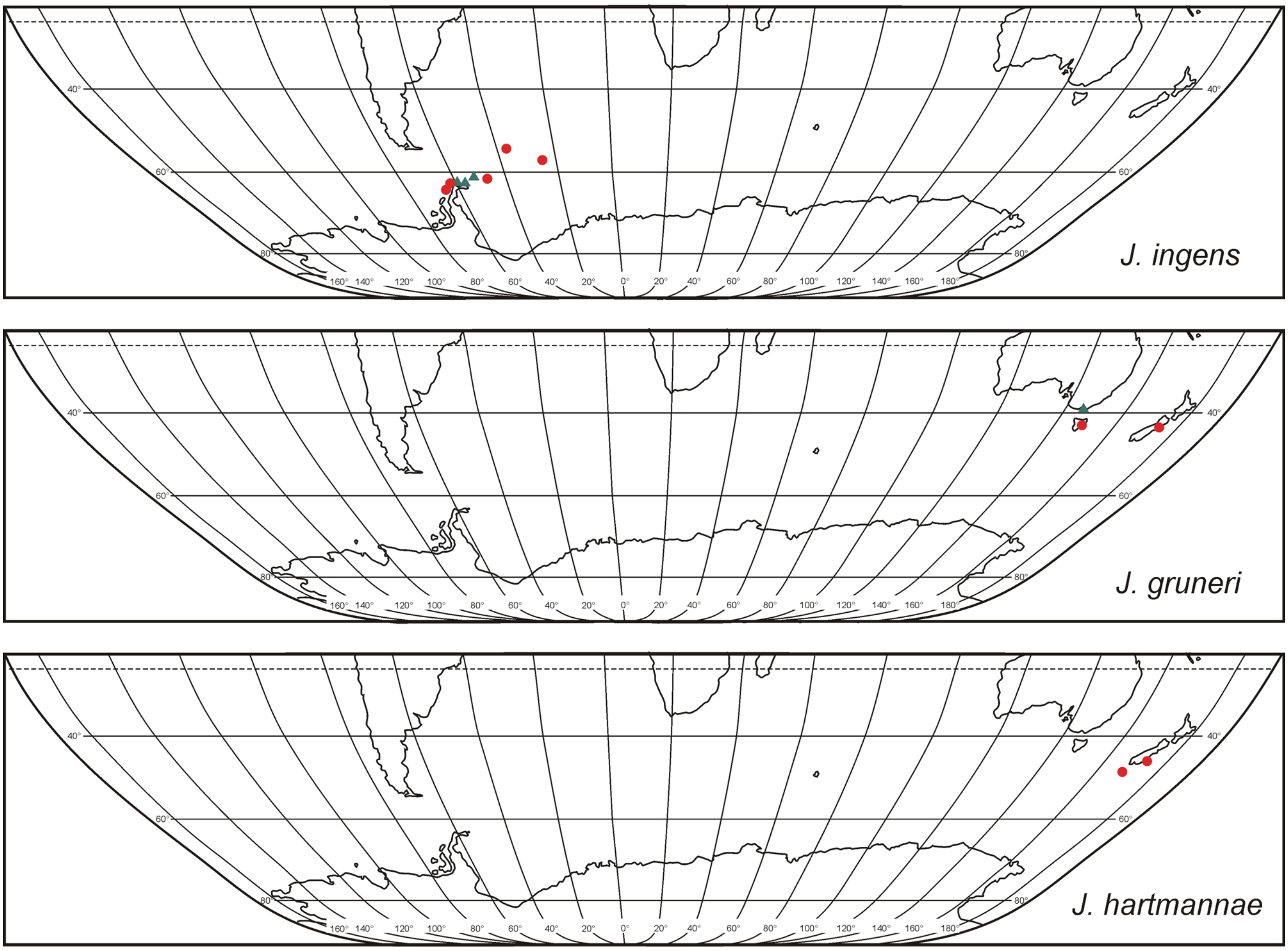

FIGURE 12. Records of Southern Hemisphere species of *Jassa* (continued). Red dot: identification confirmed by specimen examination; green dot: literature record (Supplementary Table S1) with identification not confirmed but judged likely to be this species; blue x: suspected or known to be on the hull or interior of a boat or ship.

Land-based seawater systems have turned up *J. marmorata* in the Steinhart Aquarium, San Francisco, California (CAS 79-1-33), the Pacific Environment Institute, Vancouver, British Columbia (NMNS) and the marine stations at Helgoland, Germany (Beermann & Franke 2012) and Millport, UK (Dixon & Moore 1997). *J. staudei* has been found living in the aquaria pressure head tank at Friday Harbor Laboratories, Washington (NMNS 1986-057, W-8) and in the Fisheries and Oceans Canada seawater holding tanks, Vancouver, British Columbia (NMNS IZ1987-002, 87-5), and *J. borowskyae* Conlan, 1990 in the seawater holding tanks for Hatfield Marine Science Center, Oregon (NMNS 1986-057, O-9).

North Atlantic and Mediterranean species. In addition to the widespread *J. marmorata*, *J. slatteryi* and *J. morinoi*, collection and literature records have found five other species on European coasts: *J. pusilla*, *J. falcata*, *J. herdmani*, *J. laurieae* **n. sp.** and *J. monodon* (Heller, 1866) (Fig. 9). *Jassa pusilla* has been confirmed on the Northeastern Atlantic coast from northern Norway to northern Spain and west to the Faroe Islands (Conlan 1990). It has also been confirmed on the Northwestern Atlantic coast from Newport, Rhode Island (41.5°N, 71.3°W) to Cape Hatteras, North Carolina. The oldest collection records known are for 1883 on the Atlantic coast of North America and 1874 on the Atlantic coast of Europe. It has only been found subtidally (8–505 m) and only on natural substrates (Table 4). The other European species, *J. falcata, J. herdmani, J. laurieae* and *J. monodon* appear to be restricted there. *Jassa falcata* and *J. herdmani* are fully Northeastern Atlantic in distribution and range into the western part of the Mediterranean Sea. *Jassa falcata* ranges into Iceland and northern Scandinavia while *J. herdmani* is not known in either of these regions. *Jassa laurieae* is only known from the Northeastern Atlantic and *J. monodon* is only known from the eastern part of the Mediterranean Sea (Adriatic).

Jassa falcata and *J. herdmani* have been found on a variety of natural and artificial substrates from the low intertidal zone to 30–40 m depth (Table 4). *Jassa falcata* is the first species of *Jassa* found, dating back to at least 1808 when it was described by Montagu (1808). It has been validated from Tromsø, Norway (69.6°N, 18.9°E) to Peniche, Portugal (39.4°N, 9.4°W) and as far west as Vestmannaeyjar, Iceland (63°25′ 0″ N, 20°17′ 0″ W) (Conlan 1990). An unconfirmed record of '*Jassa* cf. *falcata'* by Izquierdo & Guerra-Garcia (2011) would place *J. falcata* just into the entrance to the Mediterranean Sea at Torreguadiaro, Spain (36.3°N, 5.3°W). Although there are many literature references to *J. falcata* further into the Mediterranean Sea and in many other locations around the world, these identifications were made prior to or, if later, possibly without the knowledge of the revision of *Jassa* by Conlan (1990). Thus, literature references to *J. falcata* can be suspect because of its problematic taxonomic history before and after Sexton and Reid's (1951) merger of all species to "*J. falcata*".

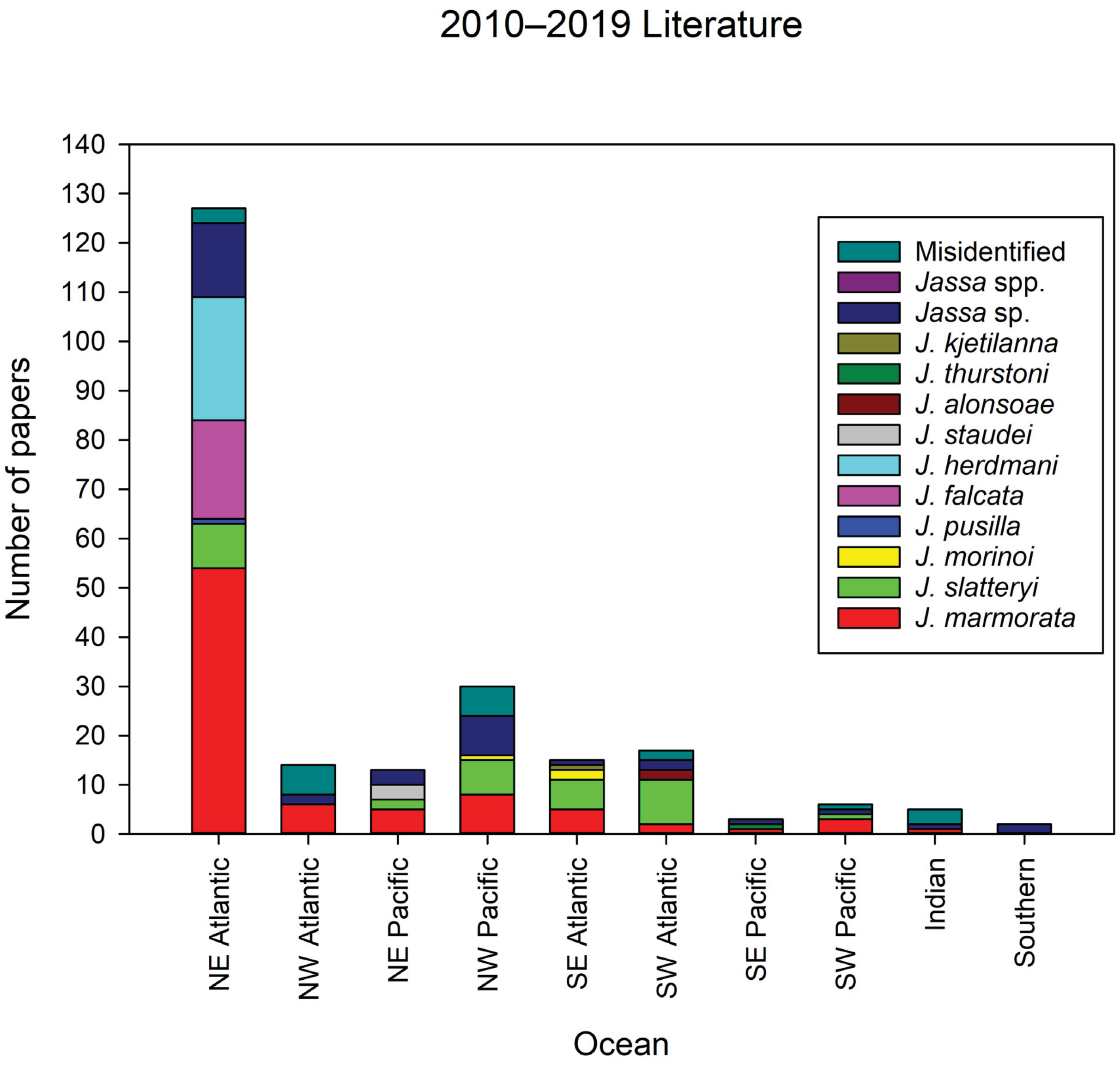

FIGURE 13. Number of papers published in 2010–2019 that mentioned or focussed on *Jassa*.

Jassa herdmani has a more southerly range than *J. pusilla* and *J. falcata*. It has been confirmed from the Isle of Man (54.1°N, 4.7°W) to Cherchell, Algeria (36.6°N, 2.2°E) (Conlan 1990). It was first found in 1888 by W.O. Walker and described by Walker (1893). All three species have been found together in museum collections (Table 5).

Jassa laurieae was first identified as *J. pusilla* by Lobo *et al.* (2017) but molecular analysis of the CO1 gene indicated that these two species were not the same. Morphological examination for this paper showed differences also, supporting the molecular evaluation that these were two distinct species. *Jassa laurieae* is only known from Portugal.

Jassa monodon (Heller, 1866) was first described by Heller (1866) from a collection in the Adriatic Sea at Lesina (now the island of Hvar, Croatia) (43.2°N, 16.4°E). Krapp-Schickel (1974) examined the holotype and determined

ABLE 3. Earliest collection records for specimens examined in this paper and in Conlan (1990). Species names are abbreviated by their first three letters. Suggested status: I = indigenous; N = non-indigenous; C = cryptogenic.

Region	Species	Suggested Status	Earliest collection record	Location	Collection/Literature source
Atlantic North America	MAR	I	15 Sept. 1883	Iron buoy, off Gay Head, Vineyard Sound, Massachusetts, USA, USFC	NMNH
	PUS	I	1883	North of Cape Hatteras (36°41′15″N, 74°39′50″W), Station 2012, U.S. Fisheries Commission, Steamer *Albatross*)	NMNH 6335
	VAL	I	25 Jan. 1935	St. Augustine, Florida	NMNH 132978
Atlantic Europe	MAR	N	1893	Helgoland, Germany	MfN, ZMB 8816
	SLA	N	30 Nov. 1923	Concarneau, France	MNHN Am. 2656
	PUS	I	1874	183-220 m depth, Bergen, Norway	NRM 5444
	FAL	I	On or before 1808	Dredge of *Sertularia* and algae, Torcross, South Devon, England, G. Montagu, coll. (50°13′N, 3°40′W)	NHM, type no. 603a
	HER	I	24 July 1888	Puffin I., Anglesey, Wales, W.O. Walker, coll.	NHM 1925.9.8: 1725-1726
	LAU	I	23 Sept. 2010	Praia Norte, Viana do Castelo, Portugal, P. Gomes, coll. (41.6938, -8.85118)	CMN A2019.0061
Mediterranean and Black Seas	MAR	N	1890	Trieste, Italy	NHMW 20611, Pesta: 277
	SLA	N	~1952	Sampieri, Sicily, W. Wieser, coll.	MCVR
	MOR	N	1885	Cherchell, Algeria, E. Chevreux, coll.	MHNP Am. 2772
	HER	I	1885	Cherchell, Algeria, E. Chevreux, coll.	MNHN Am. 2772
	MON	I	1865	Lesina (now Hvar, Croatia)	NHMW 20619 and 20621
Pacific North America	MAR	N	7 June 1931	#23, from boat bottom, Hopkins Marine Station, Monterey Bay, California, USA, G. E. MacGinitie, coll.	NMNH 120848
	SLA	I	30 Dec. 1948	From cable crossing structure and/or buoy, San Diego harbor, California, T. E. Bowman, coll.	NMNH 218558
	MOR	I	May-July 1909	Ucluelet, Vancouver I., British Columbia, Canada, C. H. Young & W. Spreadborough, coll.	NMNS 1909-2, 1916

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TABLE 3. (Continued)

Region	Species	Suggested Status	Earliest collection record	Location	Collection/Literature source
	VAL	N	2007	From stacked PVC layers deployed over 1 year (2006-2007), French Frigate Shoals, NW Hawaiian Islands (23.771196, -166.147746), L. Plaisance, coll.	GenBank HM466379 - 85 (7 specimens)
	OCL	I	6 July 1969	Intertidal zone, Izembek Lagoon, Aleutian Islands, Alaska, N. Powell, coll. (55°18.9′N, 162°45.5′W)	NMNS 1969-319
	BOR	I	12 June 1945	Echachets, Clayoquot Sound, Vancouver I., British Columbia	NMNH 172360
	STA	I	May 1909	Ucluelet, Vancouver I., British Columbia, C. H. Young & W. Spreadborough, coll.	NMNS Cat. 923
	CAR	I	6 Aug. 1955	Scraping of floating docks and pilings, rocks, mudflat at low tide, Browning Passage, Tofino, Vancouver I., British Columbia, E. L. Bousfield, coll.	NMNS 1955-104, P2
	SHA	I	11-13 Nov. 1962	Scraping of calcareous sponge under ledge in surge channel, La Jolla, California, J.L. Barnard, coll. (32°50′N, 116°30′W)	NHMLA, 45-W-5
	MYE	I	29 Dec. 1948	On rocky reef with loose rock and gravel, SW shore of Smugglers Cove, Santa Cruz I., California	NHMLA, 1660
Asia and Pacific Russia	MAR	N	Sept. 1934	Petrov I., Sea of Japan	NMNH 137739
	SLA	C	2 Apr. 1976	Tanabe Bay, Wakayama Pref., Japan, H. Morino, coll. (33°41′N, 135°22′E)	CMN A2020.0036
	MOR	C	17 March 1971	On *Sargassum microcanthum* at Bansho-no-hana Pt., Tanabe Bay, Wakayama Pref., Japan, H. Morino, coll. (33°42′N, 135°30′E)	H. Morino loan
	BOR	C	28 March 1984	5 m depth, in *Zostera marina* community, Vitiaz Inlet, Peter the Great Bay, Sea of Japan, P. Fedorov, coll.	ZIL
	KIM	I	23 June 2011	Impo Port, Yeosu-Si, The Republic of Korea, S.-S. Hong, coll.	Y.-H. Kim loan
	SHA	I	23 June 2011	Impo, The Republic of Korea, Y.-H. Kim, coll.	Y.-H. Kim loan
Atlantic South America	MAR	N	29 Nov. 2016	Mar del Plata Port, Argentina	C. Rumbold/J. Beermann

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TABLE 3. (Continued)

Region	Species	Suggested Status	Earliest collection record	Location	Collection/Literature source
	SLA	N	31 Jan. 1964	19 m, near Ubatuba, Brazil (23°30′S, 45°06′W), Y. Wakabara, coll.	Y. Wakabara loan 274 15(3)IX
	VAL	N	Between 1838 and 1842	Dredge in the harbour, Rio de Janeiro, Brazil (collected during the United States Exploring Expedition led by Charles Wilkes, 1838-1842).	Dana (1853)
	ALO	I	6 Dec. 1892	No. 153, on kelp, Ushuaia Bay, Tierra del Fuego, Argentina (54°49′S, 68°16′W), Michelsen, coll.	ZMH K-10724
	JUS	I	5 Feb. 1970	Isla Navarino, Banco de las Tacas, Chile (55°05′S, 67°40′W), J. Markham, coll.	NMNS 70-218, 27897
Atlantic Africa	MAR	N	5 Feb. 1890	In algae at Pt. Bélair, *Melita* Station 313, Dakar, Senegal, E. Chevreux, coll.	MNHN Am. 2769
	SLA	N	2 Mar. 1951	Langebaan Lagoon, South Africa, C. Griffiths, coll.	UCT LB 248Y
	MOR	N	1 Mar. 1890	Intertidal zone, along the large dam, *Melita* Station 334, Dakar, Senegal, E. Chevreux, coll.	MNHN Am. 2767
Indian Africa	MAR	N	18 Dec. 1873	Offshore: on the screw of H.M.S. *Challenger*, Stn. 142 (~128 km SE of Cape Town, South Africa) (35°4′S, 18°37′E)	NHM 89.5.15.138
	MAR	N	27 July 1972[1]	Onshore: From weeds, Scottburgh, South Africa, C. Griffiths, coll.	UCT NA 244F
	MOR	N	27 July 1972	From weeds, Scottburgh, South Africa, C. Griffiths, coll.	UCT NA 244F
	VAL	N	2019	From brown mussel beds (*Pema pema*) on outer coast pier stanchions adjacent to Durban Port, South Africa (-29.866461, 31.048315), F. MacKay, coll.	
Pacific South America	MAR	N	22 Nov. 1984	Offshore: on a raft floating out to sea, Guayacán, la Herradura Bay, Coquimbo, Chile, E. González, coll.	CMN 1989-069
	SLA	N	6 Dec. 1916	20-25 m, Cumberland Bay, Robinson Crusoe Island, Chile (33.6414°S, 78.8461°W), K. Bäckström, coll.	NRM 190, S.P.E. 53
	VAL	N	28 Dec. 1875	Offshore: at the water surface, H.M.S. *Challenger*, Stn. 302 (~650 km west of Isla Grande de Chiloé, Chile) (42°43′S, 82°11′W)	NHM

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TABLE 3. (Continued)

Region	Species	Suggested Status	Earliest collection record	Location	Collection/Literature source
Australia	MAR	N	1881	Port Jackson, Australia, H.M.S. *Alert* expedition, R. Coppinger, coll. (and see Supplementary data for *J. australis*)	NHM 1881: 31
	SLA	N	~1922	Balmoral, Port Jackson, New South Wales, T. Whitelegge, coll.	AM P.5869
	JUS	I	31 Oct. 1974	Upper *Zostera* zone, Careel Bay, Pittwater, New South Wales, P. Hutchings, coll.	AM P.20891
	GRU	I	8 Nov. 1978	3-5 m, Hobart Harbour, Tasmania, G. Edgar, coll.	
New Zealand	MAR	N	28 Mar. 1928	Lyttelton, South Island, C. Chilton, coll.	SNM
	SLA	N	28 Mar. 1928	Lyttelton, South Island, C. Chilton, coll.	SNM
	JUS	I	2 Nov. 1973	3-4 m, on *Caulerpa brownii*, St. Kilda Rocks, Kaikoura, South Island, G.D. Fenwick, coll.	AM P.25954
	HAR	I	25 Jan. 1968	Intertidal, formalin wash of algae, stn. E973 (JLB NZ-8), Saint Clair, Dunedin, South Island	NMNH 149461
	GRU	I	Unknown but collected by Chilton (1884)	Lyttelton harbour	CMNZ 2015.149.575...604
Southern Hemisphere islands (20-40°S)	ALO	I	24 Oct. 1937	0 m, stn. 13e, Tristan da Cunha, E. Sivertsen, coll., Norwegian Scientific Expedition	UiO F 3922
Southern Hemisphere islands (40-60°S and 0-180°E)	MAR	N	21 Jan. 1874	*Challenger* station 149E, dredge, 55 m, Greenland Harbour, Kerguelen Islands	NHM
	ALO	I	Dec. 1910	Kerguelen Islands, Kapt. Ring	UiO F 2971
	JUS	I	1911-1914	Siftings from kelp, Macquarie I. (54°30′S, 158°57′E), Australasian Antarctic Expedition	AM P.18414
	FEN	I	21 Jan. 1977	0-2 m, amongst red algae, Punui Bay, The Snares (48°07′S, 166°38′E), G.D. Fenwick, coll.	AM P.34951
	HAR	I	6 Jan. 1977	1.5 m, stn. SA-3492, from *Lessonia variegata* holdfast, Senecio Pool, The Snares (48°07′S, 166°38′E), G.D. Fenwick, coll.	AM P.34950

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TABLE 3. (Continued)

Region	Species	Suggested Status	Earliest collection record	Location	Collection/Literature source
Southern Hemisphere islands (40-60°S and 0-180°W)	ALO	I	31 August 1883	South Georgia (54°15′S, 36°45′W), Deutsch Polar Expedition, K. von den Steinen, coll.	ZMH K-8021
	JUS	I	1931	South Georgia (54°15′S, 36°45′W), Swedish Antarctic Expedition	H. Gruner loan 22.958
	THU	I	19 April 1902	160 m, No. 17, Shag Rock bank, between South Georgia and the Falkland Islands (53°34′S, 43°3′W), Svenska Sydpolarexp. 1901-1903	NRM 3685
	FEN	I	9 May 1902	1-2 m, amongst algae, Cumberland Bay, South Georgia (54.2333°S, 36.4667°W), Najviken Håpning	NRM 3015
	KJE	I	20 Oct. 2003	On the crab *Paralomis granulosa* caught in a bait trap at 30 m, Choiseul Sound, East Falkland (58-59°S, 52°W), W. Vader, coll.	TSZ 19054
	ING	I	16 Jan. 1884	Moltke Harbour, Royal Bay, South Georgia (54°30′58″S, 36°0′45″W), Deutsche Polarstation 1882-1883, K. von den Steinen, coll.	ZMH K-8017A
Southern Hemisphere islands (>60°S) and Antarctica	THU	I	23 Jan. 1903	Flagon (Flagstaff?) Point, Ross Sea, Antarctica, *Discovery* Expedition	NHM 1907.6.6 414-15
	ING	I	13 Jan. 1928	75 m, No. 133, Deception I., South Shetland Islands (62°57′S, 60°38′W), O. Olstad, coll.	UiO F2966a

[1] An earlier record does not indicate whether *J. marmorata* was collected onshore or from a ship: NHM 1909.2.1:95-100. Zanzibar. C. Crossland, coll. 1901. Also listed in OBIS is a collection of *J. marmorata* in September, 1916 at Port Shepstone, Natal but this identification has not been confirmed.

TABLE 4. Collection data for each species of *Jassa* gathered from specimens examined in this study and in Conlan (1990), with supplementary data from literature reports where the identification is likely correct. OBIS records of depth range are included except where errors are suspected. Species names are abbreviated by their first three letters. Biota used by *Jassa* as substrate are identified to genus for brevity. LI = low intertidal. Extreme depths, where ship contamination is suspected, are excluded.

Distribution	Species	No. specimens examined	No. collections examined	Substrate		Coast	
				Inorganic	Organic	Exposed	Protected
Trans-hemispheric	MAR	~9,000	362	Bedrock, sand and pebble beach, oyster reef, fish farm, floating dock, tire, settling plate, mussel spat collector, aquaculture cage, aquarium tank, aquarium intake and excurrent pipes, power plant intake pipe, ship's seawater intake, ship's screw, ship bottom, ballast water, raft, rope, driftwood, oil & gas platform, sea buoy, tide gauge, wind turbine foundation, submerged cable, aquaculture cage, submarine light, piling	Algae and seagrasses: *Asparagopsis, Bryocladia, Caulerpa, Ceramium, Chondrus*, *Cladophora, Codium*, *Corallina*, Corallinaceae, *Cymodocea*, *Delesseria, Dictyota, Ellisolandia, Enteromorpha*, *Gigartina*, *Gracilaria*, *Hypnea*, *Laminaria, Phyllophora, Polysiphonia*, *Sargassum*, *Rugulopteryx, Ulva*, unidentified driftweed, eelgrass, filamentous algae, kelp holdfast; barnacle: *Perforatus;* bryozoan: *Bowerbankia*, *Bugula*, *Calyptotheca,* unidentified bryozoan; gorgonian: *Paramuricea;* hydroid: *Ectopleura*, *Tubularia*; mussel: *Brachidontes, Mytilus,* unidentified Mytilidae; polychaete: *Hydroides, Polydora* tube, *Sabellaria alveolata* reef; sponge: *Isodictya* fingers	X	X
	SLA	~1500	82	Bedrock, boulder, stone, shell, woody debris, sandy shore surf zone, cave, breakwater, raft, floating dock, wharf, shackle, chain, rope, settling plate, netting, ship/boat bottom, ship's screw, sea buoy, piling, aquaculture cage, cable crossing structure	Algae and seagrasses: *Chorda*, *Corallina*, *Cymodocea*, *Cystoseira*, *Dichotomaria*, *Dictyopteris, Fucus*, *Gigartina*, *Phyllospadix*, *Polysiphonia*, *Sargassum, Ulva*, *Zostera*, unidentified driftweed, filamentous red algae, kelp holdfast; ascidian; bryozoan: *Biflustra grandicella*; hydroid; mollusc: blue mussel, *Crassoster gigas*, slipper limpet bed; sponge: *Mycale*	X	X
	MOR	~1000	58	Bedrock, boulders, shell, gravel beach, surf exposed beach	Algae and seagrasses: *Chorda, Corallina, Cystoseira, Egregia, Eisenia*, *Laminaria* holdfast*; Macrocystis* stipe and holdfast, *Phyllospadix*, *Rhodymenia*, *Sargassum*, *Zostera*, epiphytic algae, fucoids, kelp, unidentified algae, unidentified eelgrass; ascidian; polychaete tube; sponge	X	X
	VAL	730	35	Bedrock, jetty, piling, buoy, floating fish cage, suspended shell, oyster basket, ship's hull, settling plate	Algae and seagrasses: *Sargassum,* unidentified algae; sternum of the spiny lobster *Palinurus*	X	X

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TABLE 4. (Continued)

Distribution	Species	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
					J	F	M	A	M	J	J	A	S	O	N	D		
Trans-hemispheric	MAR	2–27	12–38	+0.5 –33[1]	X x	X	X x	X	X x	X	X	X	X x	X x	X	X x	2.1–9.5	Borowsky (1985); Franz (1989); d'Udekem d'Acoz (1993); Krapp-Schickel (1993); Coleman (1994); Clark (1997); Dixon & Moore (1997); Conradi & López-González (1999); Relini *et al.* (2000); Clark & Caudill (2001); Valério-Berardo & Flynn (2002); Karez & Ludynia (2003); Moshchenko & Zvyagintsev (2004, 2010); Sirenko *et al.* (2004); Alonso de Pina (2005); Armsby & Tisch (2006); Inglis *et al.* (2006a); Scinto *et al.* (2007); Gittenberger *et al.* (2010); Guerra-García *et al.* (2010); Piola & Conwell (2010); Switzer (2010); Beermann & Franke (2011); González *et al.* (2011); Pacios *et al.* (2011); Guerra-García *et al.* (2012); Beermann & Purz (2013); Di Camillo *et al.* (2013); Fernandez-Gonzalez *et al.* (2014); McCollin & Brown (2014); Gutow *et al.* (2015); Mülayim *et al.* (2015a, b); Ponti *et al.* (2016); Davoult *et al.* (2017); Fernandez-Gonzalez & Sanchez-Jerez (2017); Jak & Glorius (2017); Fofonoff *et al.* (2018); Bonifazi (2019); Hamdy *et al.* (2019); Khammassi *et al.* (2019); Mangano *et al.* (2019); Marchini *et al.* (2019); Navarro-Barranco *et al.* (2019); Sedano *et al.* (2020a, b)
	SLA	8–22	31–34	LI–27	X	X	X x	X	X x	X	X	X	X x	X x	X	X	1.8–9	Yu *et al.* (2002, 2009); Sano *et al.* (2003); Tanaka & Leite (2004); Inglis *et al.* (2006b, c, 2008); Lim & Park (2006); Jeong *et al.* (2007, 2012); Flynn & Valério-Berardo (2009); Haupt *et al.* (2012); Costa *et al.* (2015); Navarro-Barranco *et al.* (2015); Gouillieux (2017); Fernandez-Gonzalez & Sanchez-Jerez (2017); Sigueira *et al.* (2017); Bonifazi *et al.* (2018); Bueno & Leite (2019); Jacobucci *et al.* (2019); Machado *et al.* (2019)
	MOR	9–15	30–34	LI–11	x		X	X	X	X	X	X				X	2.0–5.9	Barnard (1969) as *J. falcata* thick form; Lim *et al.* (2008); Kodama *et al.* (2017, 2020)
	VAL	14-17	16-34	0-17	X	X	X	X	X	X		X				X	2.5-6.1	Thomson (1883); LeCroy (2007); Winfield *et al.* (2021)

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TABLE 4. (Continued)

Distribution	Species	No. specimens examined	No. collections examined	Substrate		Coast	
				Inorganic	Organic	Exposed	Protected
North Atlantic and Mediterranean Sea	PUS	~450	53	Bedrock, rocks, sand, muddy sand	Algae and seagrasses: *Cystoseira*, *Saccorhiza* bulbs, *Sargassum*, unidentified filamentous algae, red algae, coralline algae; carapace of the crab *Mamaia*; hydroid: *Eudendrium*, *Thuiaria*; polychaete tubes; sea fan: *Plumarella*; sponge	X	
	FAL	~4000	111	Bedrock, float, aquaculture cage, settling plate, wind turbine foundation	Algae and seagrasses: *Ascophyllum*, *Ceramium*, *Corallina, Delesseria, Ellisolandia, Fucus, Gelidium*, *Halidrys*, *Laminaria, Lithothamnion*, *Mastocarpus*, *Palmaria, Phyllophora, Phymatolithon, Polysiphonia*, *Ptilota, Saccharina, Sargassum,* unidentified kelp holdfasts and coralline algae; bryozoan	X	X
	HER	657	43	Bedrock, ship bottom, oil & gas platform, wind turbine foundation, buoy, floating wood, settling plate, fish farm, aquaculture cage, raft, shipwreck	Algae and seagrasses: *Cladophora; Laminaria*; unidentified filamentous algae; hydroid: *Tubularia*; sponge	X	X
	LAU	2	2	Bedrock	Algae and seagrasses: unidentified	X	
	MON	2	2				
North Pacific	OCL	~400	13	Bedrock, boulder	Algae and seagrasses: unidentified kelp holdfast	X	
	BOR	~1000	56	Bedrock, boulder, rock spit, water engineering structure, aquarium wall	Algae and seagrasses: *Phyllospadix*, unidentified eelgrass, red and brown filamentous algae, kelp holdfast, laminarian, red algae, unidentified algae; unidentified corallinid and pelvetiid algae; ascidian; bryozoan; hydroid;	X	X
	STA	~5500	127	Bedrock, boulder, rocky spit, settling block, floating dock, tire, rope, aquarium wall, oyster culture trays	Algae and seagrasses: *Enteromorpha*, *Laminaria*, *Phyllospadix, Sargassum*, *Ulva*, unidentified eelgrass, red filamentous algae, kelp holdfast, red algae; bryozoan; hydroid; mollusk shell, *Crassostrea*; sponge; ascidian	X	X
	CAR	375	39	Bedrock, boulders, stones, pebbles, surf exposed beach, log float, piling, floating dock	Algae and seagrasses: coralline algae, *Egregia* holdfast*, Enteromorpha, Fucus, Gigartina, Gymnogongrus, Hedophyllum* holdfast, *Phyllospadix* roots, *Sargassum*, *Ulva*, *Zostera*, unidentified algae; filamentous bryozoan; hydroid; polychaete tube; shell; sponge; colonial ascidian; woody debris	X	X

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TABLE 4. (Continued)

Distribution	Species	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
					J	F	M	A	M	J	J	A	S	O	N	D		
North Atlantic and Mediterranean Sea	PUS	9.3		8-505[2]			X			X							2.8-4.8	Viejo (1999)
	FAL	8-18	High	LI-40	X	X	X	X	X	X	X	X	X	X	X	X	3.2-11.7	Dixon & Moore (1997); Pavia *et al.* (1999); Norderhaug *et al.* (2002); Jørgensen & Christie (2003); Karez & Ludynia (2003); Norderhaug (2004); Strong *et al.* (2009); Beermann & Franke (2011); Eilertsen *et al.* (2011); Leblanc *et al.* (2011); Guerra-García *et al.* (2012); Beermann & Purz (2013); Bloecher *et al.* (2013); Hinojosa-Arango *et al.* (2013); Schaal *et al.* (2016); Jak & Glorius (2017)
	HER	5–18	30.5–35.5	LI–32[3]	X	X	X	X	X	X	X	X	X	X	X	X	3.3–9.7	d'Udekem d'Acoz (1993); Zintzen *et al.* (2006, 2008); Havermans *et al.* (2007); Beermann & Franke (2011); Beermann & Purz (2013); Beermann (2014); Jak & Glorius (2017); Coolen *et al.* (2018, 2019); Luttikhuizen *et al.* (2019); Almeida & Coolen (2020); Dauvin *et al.* (2020)
	LAU			LI														
	MON																	
North Pacific	OCL	11	27.6	LI–11						X	X	X	X				6.2–11.8	
	BOR	9–17	31–34	LI–20			X			X	X	X				X	3.2–7.7	
	STA	9–18	15–34	LI–82	X	X	X	X	X	X	X	X	X	X	X	X	3.9–10.8	Switzer (2010)
	CAR	11–17	21–32+	LI				X	X	X	X	X			X	X	1.8–4.0	

.......*continued on the next page*

TABLE 4. (Continued)

Distribution	Species	No. specimens examined	No. collections examined	Substrate		Coast	
				Inorganic	Organic	Exposed	Protected
	SHA	5	2	Bedrock, settling block	Calcareous sponge	X	X
	MYE	166	12	Bedrock, boulder	Algae and seagrasses: *Amaroucium*, *Egregia* stipe and holdfast, *Phyllospadix* roots, unidentified corallinid and pelvetiid algae; ascidian; sponge	X	
	KIM	1	1	Breakwater			X
Southern Hemisphere	ALO	513	43		Algae and seagrasses: *Macrocystis*, unidentified filamentous algae, kelp holdfast; spider crab	X	X
	JUS	78	7	Bedrock	Algae and seagrasses: unidentified eelgrass, filamentous algae, kelp holdfast; bryozoan; sponge; ascidian	X	
	THU	13	8		Algae and seagrasses: drifting and benthic kelp *Macrocystis pyrifera*	X	
	FEN	2	2		Algae and seagrasses: unidentified red algae	X	
	KJE	25	1		Crab: carapace of *Paralomis*	X	
	ING	142	39	Bedrock	Algae and seagrasses: *Ascoseira, Desmarestia, Iophon*/*Phyllophora*, kelp holdfast, *Lithothamnia,* unidentified filamentous algae; bryozoan; hydroid; sponge	X	X
	GRU	13	2				X
	HAR	16	2	Bedrock	Algae and seagrasses: heavy turf algae, kelp holdfast		

......*continued on the next page*

TABLE 4. (Continued)

Distribution	Species	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
					J	F	M	A	M	J	J	A	S	O	N	D		
	SHA	~13	~30	LI–1						X					X		2.9–6.8	
	MYE			LI						X				X		X	3.1–5.8	Barnard (1969) as *J. falcata* thin form
	KIM			4–6														
Southern Hemisphere	ALO			LI–150	x	x	x			x		x		x	x	x	3.4–12.8	Adami & Gordillo (1999); Schejter *et al.* (2016)
	JUS			3–14	x												5.5–8.3	
	THU			7–160	x				x								5.9–6.5	Wichmann *et al.* (2012)
	FEN			0–2													7.4	
	KJE			20–35			x							x			5.0	Vader and Krapp (2005)
	ING			1–75[4]								x	x				15.1–24.1	Thurston (1974)
	GRU			3–5													3.2	
	HAR			LI–2	x												3.1–4.5	

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[1] Riera *et al.* (2014) collected "*Jassa marmorata*" from 150 m depth at Tenerife but did not indicate that they had considered the possibility that these specimens are J. *slatteryi* which resembles their photographs and description and is also widespread. This depth would considerably extend the depth range known for either of these species. Cartes & Sorbe (1999) recorded two specimens of "*J. marmorata*" from 501-506 m on the Catalan slope off Barcelona, Spain. They were rare, found in 1of 20 samples. Identification is unconfirmed. Some unconfirmed OBIS records are suspected ship contamination and mis-identifications

[2] some unconfirmed OBIS records give a minimum depth of 0 m

[3] unconfirmed OBIS records: 0-34 m

[4] unconfirmed OBIS records: 1-342 m

TABLE 5. Instances where congeners were found in the same collection. Species names are abbreviated by their first three letters.

Distri-bution		Trans-hemispheric				North Atlantic and inland seas					North Pacific and inland seas							Southern Hemisphere							
	Species	MAR	SLA	MOR	VAL	PUS	FAL	HER	LAU	MON	OCL	BOR	STA	CAR	SHA	MYE	KIM	ALO	JUS	THU	FEN	KJE	ING	GRU	HAR
Trans-hemispheric	MAR	—																							
	SLA	X	—																						
	MOR	X	X	—																					
	VAL	X	X		—																				
North Atlantic	PUS					—																			
	FAL	X				X	—																		
	HER	X	X	X		X	X	—																	
	LAU								—																
	MON									—															
North Pacific	OCL										—														
	BOR		X	X								—													
	STA	X	X	X							X	X	—												
	CAR			X									X	—											
	SHA														—										
	MYE															—									
	KIM																—								
Southern Hemisphere	ALO																	—							
	JUS																		—						
	THU																			—					
	FEN																	X			—				
	KJE																					—			
	ING																						—		
	GRU																							—	
	HAR																								—

that it was *Jassa falcata* but re-examination of the holotype for this study by one of us (KC) indicates that this specimen is not *Jassa falcata*. Therefore, *Jassa monodon* stands as a valid species. Furthermore, Heller's (1866) *Podocerus pulchellus* is also *Jassa monodon*.

North Pacific species. Seven species of *Jassa* are restricted to the North Pacific (Figs 9–10) while the widespread *J. marmorata*, *J. slatteryi* and *J. morinoi* also occur there (Figs 1–6). Of the seven restricted species, *J. kimi* **n. sp.** is only known from The Republic of Korea. Among the six other North Pacific species, *J. borowskyae* and *J. shawi* Conlan, 1990 are known from both the eastern and western sides while *J. oclairi* Conlan, 1990, *J. staudei*, *J. carltoni* and *J. myersi* Conlan, 1990 are only known from the eastern side. *Jassa oclairi* is a northern species, known only from British Columbia to the Alaskan Aleutian Islands. *Jassa borowskyae* also occurs in the Aleutians but ranges farther south to California. *Jassa staudei* and *J. carltoni* Conlan, 1990 range from British Columbia to California. *Jassa shaw*i may have a similar range but there are too few specimens to confirm this. *Jassa myersi* is only known from California. *Jassa staudei* has been found in the same collections as *J. oclairi* and *J. borowskyae*, as well as with the three transhemispheric species *J. marmorata*, *J. slatteryi* and *J. morinoi* (Table 5). *Jassa carltoni*, *J. staudei* and *J. morinoi* have also been found together. The lesser-known species *J. kimi*, *J. myersi* and *J. shawi* have not been found with other species of *Jassa*. These and *J. oclairi* have only been found on natural substrates and their epibiota while the better known species have been found on both natural and artificial substrates (Table 4). They have all been found in the low intertidal zone, with *J. staudei* known to the greatest depth (82 m) and the greatest salinity range (15–34 psu).

The earliest collection record for North Pacific species was for *J. morinoi* and *J. staudei* in 1909 at the remote village of Ucluelet on Vancouver Island, British Columbia, Canada (Table 3). The others were similarly first found in remote locations. Only *J. marmorata* also occurs on the Atlantic coast of North America, where it has been known there since 1883. The first record of *J. marmorata* on the Pacific coast of North America was in 1931, where it was found on a boat bottom in Monterey Bay, California. All other known records for *J. marmorata* on the Pacific coast of North America are from human-modified locations (Supplementary Table S9).

Southern Hemisphere species. In addition to the four trans-hemispheric species, eight species of *Jassa* appear to be restricted to the Southern Hemisphere: *Jassa alonsoae* Conlan, 1990, *J. justi*, *J. thurstoni*, *J. fenwicki* Conlan, 1990, *J. kjetilanna* Vader & Krapp, 2005, *J. ingens* (Pfeffer, 1888), *J. gruneri* Conlan, 1990 and *J. hartmannae* Conlan, 1990 (Figs 11–12). *Jassa alonsoae*, *J. justi*, *J. thurstoni* and *J. fenwicki* have been found over a broad longitudinal range (90°W–180°E) while *J. kjetilanna*, *J. ingens, J. gruneri* and *J. hartmannae* are known only more locally. *Jassa thurstoni* and *J. ingens* have been found in the Antarctic while the other Southern Hemisphere species are known only from north of 60°S. *Jassa alonsoae* and *J. justi* range the farthest north, reaching 35°S. *Jassa alonsoae* and *J. ingens* have been the most frequently collected (Table 4). *Jassa justi*, *J. thurstoni*, *J. kjetilanna* and *J. gruneri* have only been found subtidally; the others range into the low intertidal zone. The deepest known collection is for *J. thurstoni* at 160 m. *Jassa alonsoae* and *J. kjetilanna* have been found on crabs. Other substrates for the Southern Hemisphere species are sponges, bryozoans, ascidians, macroalgae, and eelgrass.

Collection records indicate that *J. alonsoae* was the first of the Southern Hemisphere species to be collected, found on South Georgia in 1883 by K. von den Steinen as part of the First International Polar Year, 1882–1883 (Table 3). It was not recognized as a species distinct from the European *J. falcata* until described by Conlan (1990), although Sexton & Reid (1951) had earlier noted a distinctive "Large Polar Form" of *J. falcata*. Soon after, *J. ingens* was collected in South Georgia as part of the same expedition. *Jassa justi*, *J. thurstoni* and *J. fenwicki* have also been collected on South Georgia but only *J. alonsoe* and *J. fenwicki* have been found together in the same museum collection (Table 5). While *J. ingens* was recognized as a distinct species by Pfeffer (1888) (as *Podocerus ingens*), the others were lumped under "*J. falcata*" until being recognized as distinct by Conlan (1990). The most recently described is *J. kjetilanna* by Vader & Krapp (2005).

Habitat

Collection and literature data. Table 4 summarizes collection information for the specimens of *Jassa* examined for this study and for Conlan (1990), along with additional data found in the literature. The number of specimens examined ranged from ~9,000 for *J. marmorata* to 1 for *J. kimi*. Generally, more specimens were available for species found in the North Atlantic and North Pacific. *Jassa marmorata* occurred in the largest number of collections (362) and also was recorded in more of the literature than other species. The collecting data indicated that most or all species occurred on hard substrates among a variety of macroalgae and seagrasses, as well as hydroids, bryozoans, sponges, mussels, polychaete tubes and ascidians in well circulated waters of moderate to high salinity. *Jassa valida, J. pusilla*, *J. alonsoae* and *J. kjetilanna* were also collected on the carapaces of decapod crustaceans, a mobile hard substrate. *Jassa marmorata* was found on the most varied substrates, many of which were artificial (buoys, floating docks, cables, lights, tires, ropes, aquaria, aquaculture cages, settling plates, oil & gas platforms, and a ship's screw, hull or ballast).

All species were found on exposed coasts while fewer were found on protected coasts. *Jassa marmorata* was found in the greatest temperature (2–26.5 °C) and salinity (12–38 psu) range but the Antarctic *J. ingens* and *J. thurstoni* may have been inhabiting colder waters. Depth data indicate that many species occurred in the low intertidal to the shallow subtidal zone. The maximum depth record (excluding extremes considered to be ship contamination) was 505 m for *J. pusilla*, which was never recorded intertidally.

For species that were well sampled (>100 specimens in >10 collections), adult females of many species were found ovigerous in both summer and winter. *Jassa oclairi* was found ovigerous only in summer and *J. ingens* only in austral winter. *Jassa ingens* was considerably larger than any of the other species, females being ovigerous at 15.1–24.1 mm body length. Female *J. falcata, J. oclairi, J. staudei* and *J. alonsoae* had maximum length at maturity of 10–12 mm while the remainder were smaller at maturity. Many of the species reached maturity at 2–3 mm body length. Females of all species showed a substantial range in body length at maturity (generally 40–60% of maximal body length). *Jassa slatteryi* showed the greatest range (91% of maximal body length) and *J. ingens* the least (31%).

Trans-hemispheric species in natural vs artificial habitats. Collection data for the four trans-hemispheric species showed that *J. marmorata* occurred in nearly 99% of the 70 natural habitats sampled on the coast of the NW Atlantic but fewer (38%) of the natural habitats sampled in the NE Atlantic and Mediterranean coasts (Table 6). It was entirely absent from the 41 natural habitats sampled on the NE Pacific coast. Too few putatively natural coasts were sampled elsewhere (*n* = 6), though it was present at four of the six locations (Tasman Sea, Sea of Japan and the South African coast) (Supplementary Table S6). By comparison, *J. marmorata* was found at >50% of the artificial habitats sampled on all coasts and as much as 94% of the 33 artificial habitats sampled on the NE Atlantic and Mediterranean coasts (Table 7). Exact locations of the samples are given in Supplementary Tables S2–S9.

TABLE 6. Summary of Supplementary Tables S2, S4, S6 and S8 showing the percentage of collections where each of the four trans-hemispheric species were found in a natural habitat. Species names are abbreviated by their first three letters.

Species	NW Atlantic	NE Atlantic and Mediterranean	NE Pacific	Elsewhere
Number of collections	70	21	41	6
MAR	98.6	38.1	0	66.7
SLA	0	47.6	26.8	33.3
MOR	0	19.0	85.4	33.3
VAL	2.9	0	0	0

TABLE 7. Summary of Supplementary Tables S3, S5, S7 and S9 showing the percentage of collections where each of the four trans-hemispheric species were found in an artificial habitat. Species names are abbreviated by their first three letters.

Species	NW Atlantic	NE Atlantic and Mediterranean	NE Pacific	Elsewhere
Number of collections	32	33	35	25
MAR	53.1	93.9	60.0	64.0
SLA	0	6.1	42.9	20.0
MOR	0	0	5.7	8.0
VAL	50.0	0	0	24.0

Jassa slatteryi did not dominate natural habitats on any coast as did *J. marmorata* on the Atlantic coasts of Canada and USA and was entirely absent from any of the 70 natural or 32 artificial sites sampled on that coast (Tables 6 and 7). Despite being absent on the NW Atlantic coast, it did occur on NE Atlantic coasts, though mostly in the Mediterranean

Sea at 10 of the 21 putatively natural sites sampled and at two of the 33 artificial sites sampled (a pier on the coast of Ireland and in a Venice lagoon) (Supplementary Tables S4 and S5). On the NE Pacific coast, it was found at 43% of the 35 artifical sites sampled, all of which were harbours in California (Supplementary Table S9). At natural sites on the NE Pacific coast it was found much more widely, from California to British Columbia (Supplementary Table S8). Elsewhere, *J. slatteryi* was found at two of the six natural sites sampled (coasts of Australia and Japan) and five of the 25 artifical sites (aquaculture structure, settling plate, ship bottom, raft and floating dock on the coasts of Japan, Korea, Brazil, Chile and Australia) (Supplementary Tables S6 and S7).

Jassa morinoi dominated the 41 natural habitats sampled on the NE Pacific coast, occurring in 85% of the samples from British Columbia to California (Tables 6 and 7 and Supplementary Tables S8 and S9). It was infrequently found in artificial habitats on this coast (two of 35 sites sampled) (Table 7 and Supplementary Table S9). Like *J. slatteryi*, it was never found along the NW coast of the Atlantic in either natural or artificial habitats, but unlike *J. slatteryi*, it also did not occur on NE Atlantic coasts. Elsewhere, it was found in one of the six putatively natural sites sampled (Bansho-no-hana Pt., Japan) and at two of the 25 artificial sites sampled (in macroalgae beneath buoys in Japan and along a dyke in Dakar, Senegal) (Supplementary Tables S6 and S7).

Jassa valida is best known from the NW and SW coasts of the Atlantic, where it has been found in both natural and artificial situations, though more often in the latter (Tables 6 and 7). Natural habitats in the NW Atlantic were surf swept rocks in North Carolina and on seaweed offshore of Georgia (Supplementary Table S2). Artificial habitats are pilings, jettys, buoys and settling plates from North Carolina to Florida in the NW Atlantic (Supplementary Table S3). In the SW Atlantic, it has only been found on the coast of Brazil from a ship's hull and from settling plates (Supplementary Table S7), though no natural habitats on this coast have yet been sampled (Supplementary Table S6). Substrate information for other locations was not available.

TABLE 8. Summary of Supplementary Table S10 showing differential substrate use in six natural NE Pacific locations where multiple species of *Jassa* were co-habiting. Species names are abbreviated by their first three letters. Two species found on the same substrate are linked by 'and', while two species found farther apart on the same type of substrate are linked by 'or'.

Co-ordinates	Location	Habitat	Substrate					
			Bryozoan	Colonial ascidian	Hydroid	Macroalgae	Seagrass	Sponge
48°50.4′N, 125°12.5′W	British Columbia: Vancouver Island: Seppings Island	Bedrock on exposed coast	CAR			CAR or MOR		CAR
48°50.2′N, 125°08.5′W	British Columbia: Vancouver Island: Barkley Sound: Brady's Beach	Bedrock tidepool on exposed coast		CAR	STA			
44°29′N, 124°05′W	Oregon: Seal Rocks	Bedrock on exposed coast		BOR		STA and BOR	SLA and BOR	
43°20′N, 124°23′W	Oregon: Sunset Bay	Bedrock on exposed to semi-protected coast				STA or CAR	MOR	
41°45′N, 124°11′W	California: Crescent City: outer harbor	Rock spit on exposed coast	STA and BOR		STA and BOR	BOR		
35°27′N, 120°54′W	California: Cayucos	Bedrock on exposed coast					SLA or BOR	

TABLE 9. Summary of Supplementary Table S10 showing differential substrate use in four artificial NE Pacific locations where multiple species of *Jassa* were co-habiting. Species names are abbreviated by their first three letters. Two species found on the same substrate are linked by 'and', while two species found farther apart on the same type of substrate are linked by 'or'.

Co-ordinates	Location	Habitat	Substrate						
			Bryozoan	Colonial ascidian	Wood	Hydroid	Macroalgae	Seagrass	Sponge
48°50.2′N, 125°08.0′W	British Columbia: Vancouver Island: Barkley Sound: Bamfield Marine Sciences Centre	Floating dock				MAR	STA		
48°25′N, 123°20′W	British Columbia: Vancouver Island: Victoria harbour	Floating dock				MAR and STA	MAR and STA		
37°29.5′N, 122°30′W	California: Pillar Point Harbor	Floating dock				MAR and SLA			
35°22′N, 120°52′W	California: Morro Bay marina	Floating dock			STA and SLA		SLA		

Habitat overlap of trans-hemispheric species with local species. Sampling of various substrates along the NE Pacific coast found six natural and four artificial sites where two or more species of *Jassa* co-occurred (Tables 8 and 9; Supplementary Table S10). In the natural habitats, two species could be found occupying the same substrate at the same time or individually but on the same type of substrate. For example, the trans-hemispheric *J. slatteryi* was found in the same kind of seagrass (*Phyllospadix*) as the local *J. borowskyae* on exposed bedrock at Cayucos, California but not in close proximity, while in seagrass on exposed coast at Seal Rocks, Oregon, it was found at the same sub-station, in close proximity to *J. borowskyae*. The trans-hemispheric *J. morinoi* occupied various macroalgae as did the local *J. carltoni* on an exposed coast at Seppings Island, British Columbia but not with *J. carltoni* in seagrass on a semi-protected coast at Sunset Bay, Oregon. Two local species could also be found co-habiting a substrate: *J. staudei* and *J. borowskyae* in macroalgae at Seal Rocks, Oregon and in hydroids and bryozoans on an exposed coast at Crescent City, California. The local species occupied a greater variety of substrates (each on four types, and collectively bryozoans, colonial ascidians, hydroids, macroalgae, seagrasses or sponges) while the trans-hemispheric *J. slatteryi* and *J. morinoi* were only found on macroalgae or seagrasses at these sites. The macroalgae occupied, although not fully identified, were also varied (Supplementary Table S10).

At the four artificial habitats where two species co-occurred, two of which were in British Columbia and two in California, the species makeup and substrate variation was much more limited than at the natural sites (Table 9). At the British Columbia sites, the trans-hemispheric *J. marmorata* co-occurred with the local *J. staudei* either together or individually on hydroids and macroalgae. In one California site (Pillar Point Harbor), the trans-hemispheric *J. marmorata* and *J. slatteryi* co-occupied hydroids. In the other California site (Morro Bay marina), the trans-hemispheric *J. slatteryi* co-occurred on a floating dock with the local *J. staudei* and separately on macroalgae.

Habitat overlap of two trans-hemispheric species in an exotic location. Year-long sampling of a floating dock at West Beach, Adelaide, Australia found *J. marmorata* and *J. slatteryi* co-habiting macroalgae with tubicolous tanaids and corophiid amphipods. These two species exceeded 200 individuals (g algal dry wt.)$^{-1}$ at the time of first sampling in Oct. 2009 (austral spring), due to a predominance of hatchlings along with a few adults and larger juveniles (Fig. 14). All age groups disappeared in Nov. 2009 when the surface water temperature had risen from <16°C to 24°C in one month. They remained absent for the duration of austral summer, only re-appearing in May 2010 when the water temperature had declined below 21°C. They remained present over the austral autumn and winter while the water temperature ranged from 17 to 12°C. Those found in austral autumn were large juveniles and they remained in small numbers throughout austral winter until the cessation of sampling in Sept. 2010.

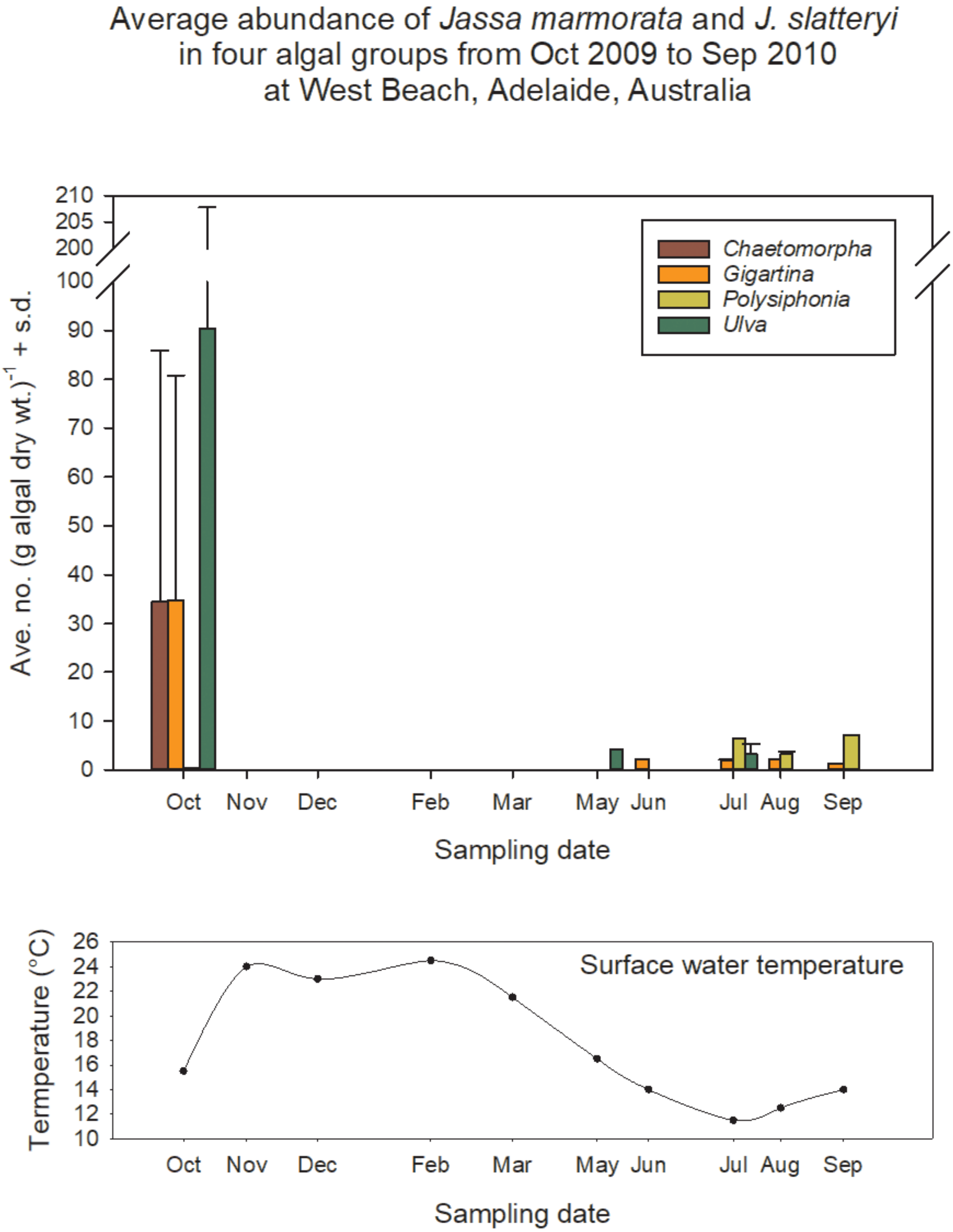

FIGURE 14. Combined average abundance of *Jassa marmorata* and *J. slattery* in four algal groups sampled randomly on three floating docks at West Beach, Adelaide, Australia from October 2009 to September 2010. Surface water temperature at the docks varied from 12 °C in austral winter to 25 °C in austral summer. Neither species was found at temperatures >21°C.

Specific targeting of four macroalgal groups that occurred year-round on the docks showed that all four were colonized by *J. marmorata* and *J. slatteryi*, though the preference varied. In austral spring when hatchlings were numerous, *Ulva* was most highly colonized followed by *Chaetomorpha* and *Gigartina*. Barely any individuals were found on *Polysiphonia*. However, during the austral autumn and winter, when large juveniles predominated, the algae of choice were *Gigartina*, *Polysiphonia* and *Ulva* while *Chaetomorpha* was not colonized.

Taxonomy

Family Ischyroceridae Stebbing, 1899b

Tribe Ischyrocerini Stebbing, 1899b

Genus *Jassa* Leach, 1814

Lusyta Nardo, 1847b, p. 20.
Cratophium Dana, 1852b, p. 309.
Macleayia Haswell, 1880, p. 32.
Bruzeliella Norman, 1905, p. 83.

Description of adult male. Body length at maturity 2–24 mm.

Head lobe: oval or squared, but with dorsal angle more acute and ventral angle more broadly rounded.

Antenna 1: accessory flagellum 2-articled, second minute, only second setose.

Antenna 2: stouter and longer than antenna 1, bearing finely pectinate "filter setae" on peduncular articles 3–5 and shorter, pectinate "brush setae" on flagellum, in many species these being interspersed with feathery plumose setae on distal part of peduncular article 5 and proximal part of flagellum; flagellum with at least 2 of its distal articles bearing posteriorly curved spines, first article considerably longer than any of the distal articles.

Mandible: at least 1 molar with 1 seta and 1 lateral flake.

Maxilla 1: inner plate bearing a few short fine setae, palp with 1 or more rows of setae.

Gnathopod 1: coxa rectangular, often anterodistally produced; propodus, palm defined by 3 spines that are usually arranged in medial-lateral-medial sequence.

Gnathopod 2: coxa deeper posteriorly, with 1 gill; basis, setae, when present, simple or short and plumose, and located on the anterolateral flange only; carpus less than 0.25 of length of propodus; propodus with triangular, shallowly bifid tooth directly posterior to dactyl hinge and larger thumb incised anteriorly to palmar defining spines (or associated setae if spines absent), inner margin of thumb not setose, outer margin with 3-4 discrete clusters; dactyl shorter than propodus, extending beyond the thumb to rest against the thumb's posterior margin when closed, inner margin expanded at location of hinge tooth or more centrally and acutely as a tooth into palmar incision, dactyl cusps reduced to small buttons interspersed with a few short setae.

Pereopods 3 and 4: coxa 3 usually deepest posterior of centre; coxa 4 deepest centrally; basis, margins convex, or anterior margin straight or shallowly concave in large specimens; merus anterodistally produced to half to fully overlap the carpus, anterior margin bearing numerous setae in clusters or singly; propodus not posteriorly spinose.

Pereopods 5–7: basis of at least one of peraeopods 5–7 posterodistally produced; merus and carpus, posterior margin not spinose; propodus variably expanded; dactyl, posterior (outer) margin not cusped distally, anterior (inner) margin bearing 1 seta at the unguis or short setae along its length.

Pleopods: well developed, with 2 peduncular coupling hooks each in most species, but more in large species.

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

Uropod 1: peduncle usually extended ventrally as a spinous process under the rami.

Uropod 2: ventral spinous process short or absent.

Uropod 3: peduncle finely setose ventrally, but without spines middorsally, and with a crown of spines around the dorsodistal margin and a cluster of setae distolaterally; outer ramus not setose mid-dorsally, tipped by a basally immersed, dorsally recurved spine, 2 large cusps, and many additional minute cusps; inner ramus tipped by 1 single short spine which is not recurved and not accompanied by cusps.

Telson: each corner with 1 pair of button-like cusps accompanied by 1 long pectinate seta and 1 or 2 short plumose setae, but without spines.

Description of adult female. Body length at maturity 2–21 mm. Character states as in the male except as follows.

Brood plates: broad, setae abundant, tips hooked.

Antenna 2: peduncle, posterior filter setae long.

Gnathopod 2: propodus much larger and different in shape from the propodus of gnathopod 1, palm concave or sinuous, without a thumb, defining spines not lost with age; dactyl fitting into a depression between the palmar angle and spines.

Peraeopod 3: basis broadly expanded, margins convex, not straight or concave.

Variation. Antenna 2 may develop plumose setae on article 5 and the flagellum when individuals are approaching maturity, though small individuals that appear to be otherwise adult may not develop plumosity. This occurs in both sexes. The mandibular palp article 2 may bear a row of setae on the dorsal margin in a few species. The maxilla 1 may bear a cluster of setae at its base though most species lack these setae. A key character is the presence or absence and length of a single or cluster of setae on the anterodistal margin of the carpus at the junction of the propodus in gnathopod 1. If present, these setae may be slightly medial or lateral. The bases of gnathopods 1 and 2 may or may not possess a row of setae and the presence and length of these setae is a key character for species definition. The propodus of gnathopod 2 may have a concave or sinuous palm in the juveniles and adult females. Large subadult males may have a small thumb, termed a “pre-thumb” at the location where the much larger thumb will appear at the last molt. Small subadults of the same species do not exhibit a pre-thumb. At the terminal molt, the thumb may be long or short, sinuous or straight, incised, acute or squared at the tip. “Major form males” have larger thumbs than “minor forms”, but being at the terminal molt, a minor form does not transition into a major form. The minor form may have a tooth on the dactyl that fits into the palmar incision. In the major form, the dactyl is expanded on its inner margin close to the hinge. Most terminal molt species lose their palmar defining spines that are present in the juvenile; the female always retains these spines. For all species the number of spines defining the gnathopod palms may be occasionally 2 or 4 rather than the usual 3. The bases of pereopods 3 and 4 are wide with convex margins in juveniles and females but the bases are slenderer in the thumbed male. In a few species the propodus of pereopods 5–7 may be prehensile. The peduncular spinous process of uropod 1 is absent in some species. The number of major cusps adjacent to the recurved spine that tips the third uropod outer ramus may be rarely 3 or 4 rather than 2. The inner ramus bears extra spines mid-dorsally in some species. Unless noted otherwise, these interspecific differences apply to both sexes and all ages of a species.

Species treatments. The key characters of the 24 species are presented following, with the species grouped by commonality of distribution: trans-hemispheric (Table 10 and Figs 15–36), North Atlantic (Table 11 and Figs 37–59), North Pacific (Table 12 and Figs 60–87) and Southern Hemisphere (Table 13 and Figs 88–104). Key characters are not affected by age or gender and so can be used for the identification of most specimens, with the possible exception of hatchlings. Some additional gender and age-specific characters are added to assist with identification. Following the species treatments is a key to all 24 species. While the distributional format is aimed to simplify regional identifications, the key should be checked in case the specimen is a new species or a new introduction.

Trans-hemispheric species

TABLE 10. Key character states of trans-hemispheric species. X indicates the presence of the first character state described while — indicates the alternative character state given in italics. S and L indicate length. ? indicates that the state is unknown. Character states apply to both sexes and juveniles unless indicated otherwise.

Character	*J. marmorata* (Figs 15-21)	*J. slatteryi* (Figs 22-27)	*J. morinoi* (Figs 28-30)	*J. valida* (Figs 31-36)
Antenna 2, large subadult and thumbed male, posterior margin of article 5 and flagellum bearing plumose setae in addition to the usual finely pectinate filter setae (e.g., Fig. 42) *or without plumose setae* (e.g., Fig. 48)	X	X	—	—
Antenna 2, large subadult and adult female, posterior margin of article 5 and flagellum bearing plumose setae in addition to the usual finely pectinate filter setae (e.g., Fig. 15) *or without plumose setae* (e.g., Fig. 37)	X	X	—	—
Mandibular palp, margin of article 2 with a fringe of setae dorsally (e.g., Fig. 47) *or without a fringe* (e.g., Fig. 41)	—	—	—	—
Maxilla 1 with a seta or cluster of setae at the base of palp article 1 (Fig. 101) *or without seta(e)* (e.g., Fig. 36)	—	—	—	—
Gnathopod 1, basis, anterolateral margin with a fringe of spine-like setae (e.g., Fig. 95) *or without spine-like setae* (e.g., Fig. 31)	—	—	—	—
Gnathopod 1, carpus, with a seta or cluster of setae at the anterodistal junction of the propodus which may be slightly lateral or medial (e.g., Fig. 22) *or without seta(e)* (e.g., Fig. 37)	X	X	X	X
Gnathopod 1, carpus, seta(e) at the anterodistal junction of the propodus moderately long (L, length ≥25% of anterior margin length) (e.g., Fig. 22) or short (S, length <25% of anterior margin length) (e.g., Fig. 15) *or without seta(e)* (e.g., Fig. 37)	S	L	L	S
Gnathopod 2, basis with a fringe of setae on the anterolateral margin (e.g., Fig. 15) *or fringe absent (minute setae may be present but are too small to be described as an obvious fringe)* (e.g., Fig. 54)	X	X	X	X
Gnathopod 2, basis, if setal fringe present, setae relatively long (L, length ≥40% basis width) (Fig. 15) or short (S, length mostly <40% basis width) (e.g., Fig. 28) *or fringe absent (minute setae may be present but are too small to be described as an obvious fringe)* (e.g., Fig. 48)	L	S	S	S
Gnathopod 2, propodus, setae on the anteroproximal margin long (L, setal length ≥ maximal basis width) (Fig. 67) or short to absent (S, setal length < maximal basis width) (e.g., Figs 15, 42)	S	S	S	S
Gnathopod 2, propodus, setae on the anterior margin plumose (Fig. 62) *or simple* (e.g., 28)	—	—	—	—
Gnathopod 2, female propodus, palm concave, palmar angle pronounced (acute, right angled or bulbous) (e.g., Figs 44, 52) *or palmar angle shallow, giving the palm a sinuous appearance* (e.g., Fig. 100)	X	X[10]	X	X
Pereopods 5-7, propodus, anterior margin expanded for grasping (e.g., Fig. 95) *or not expanded for grasping* (e.g., Fig. 48)	—	—	—	—
Uropod 1, peduncular spinous process that extends ventrally from the peduncle and underlies the rami, moderately long (L, length = at least 25-50% the length of the longest ramus) (e.g., Fig. 42) or very short (S, length ≤10% of the length of the longest ramus, in which case it may not be visible) (e.g., Fig. 83)	L	L	L	L
Uropod 3, inner ramus with 1-2 mid-dorsal spines in addition to the usual spine at the tip (e.g., Fig. 42) *or without dorsal spines* (e.g., Fig. 48)	—	—	—	—
Telson, tip with a seta or cluster of setae extending between the third uropods (in addition to the usual upright setae at each side) (e.g., Fig. 31) *or without setae at the tip*[11] (e.g., Fig. 22)	—	—	X	X

[10] Female *J. slatteryi*: the palmar angle may appear more distant from the defining spines (Fig. 26) than in most other North Atlantic species (e.g., Fig. 15) but the palm is still more concave than in species that have sinuous palms (e.g., Fig. 95)

[11] These setae are visible when the animal is on its side, the abdomen is grasped with forceps in one hand, and the third uropods are depressed downwards with a fine needle in the other hand. This brings the telson into view.

***Jassa marmorata* Holmes, 1905**
(Table 10, Figs 15–21)

Synonyms: see Conlan (1990).

Diagnosis.

Both sexes:

Mandibular palp: article 2, dorsal margin without a fringe of setae.

Maxilla 1: without a seta or setal cluster at the base of the palp article 1.

Gnathopod 1: basis, anterolateral margin with a few short setae along its length; carpus with a (usually) single or a small cluster of short setae at the anterodistal junction of the propodus (setae <25% of anterior margin length and slightly lateral).

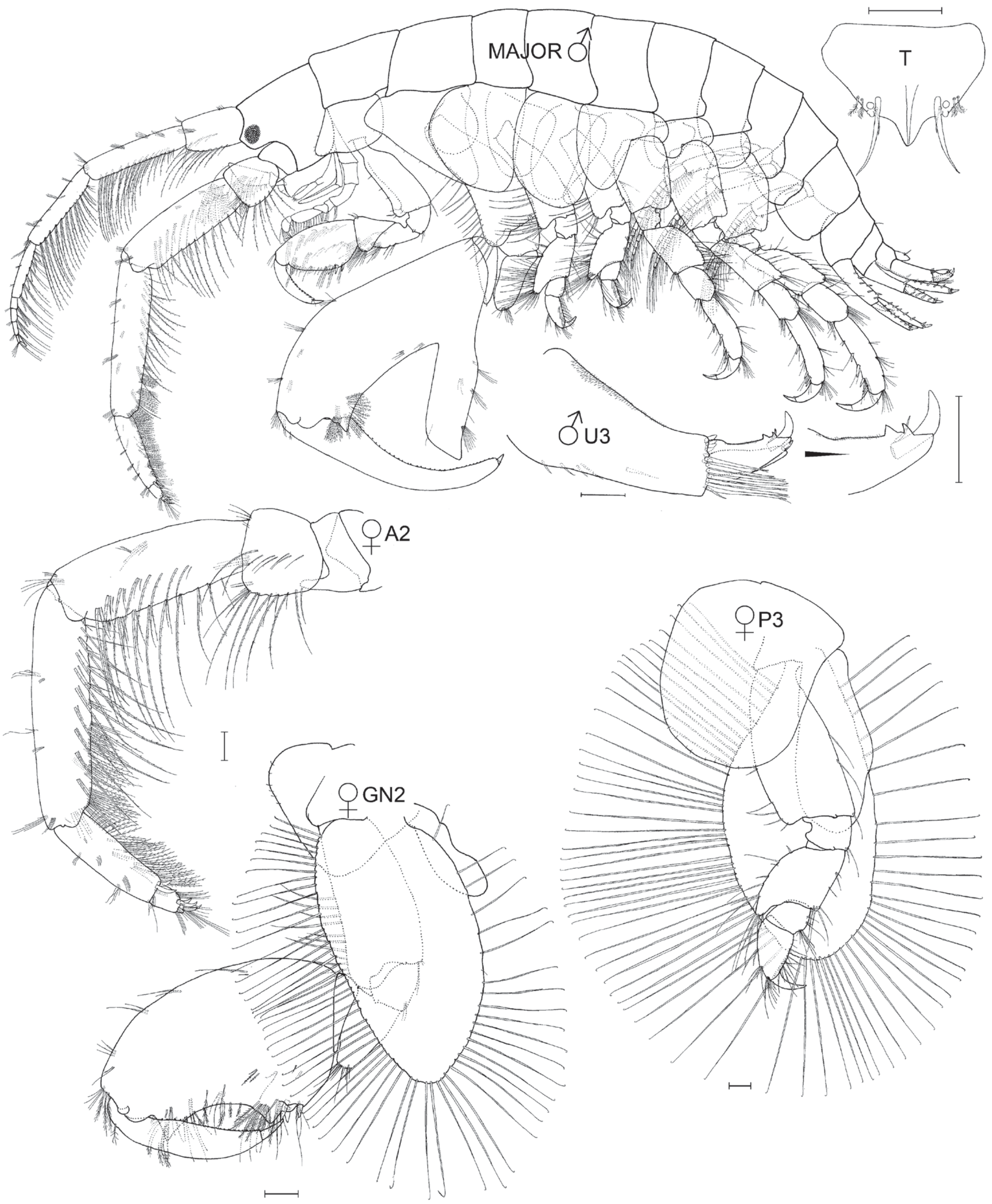

FIGURE 15. *Jassa marmorata* Holmes, 1905. Neotype, adult male, major form, 6.7 mm, NMCC 1987-1067; adult female, 5.3 mm. Barren Islands Marina, Jamaica Bay Wildlife Refuge, Brooklyn, New York (40°35′N, 73°55′W), early July 1984, B. Borowsky, coll., among hydroids and *Ulva* on submerged docks at the marina, IZ 1984-112 (CMN). Lateral views: whole body, pereopod 3 and uropod 3; dorsal view: telson; other views medial. Scale 0.1 mm. Illustration after Conlan (1990).

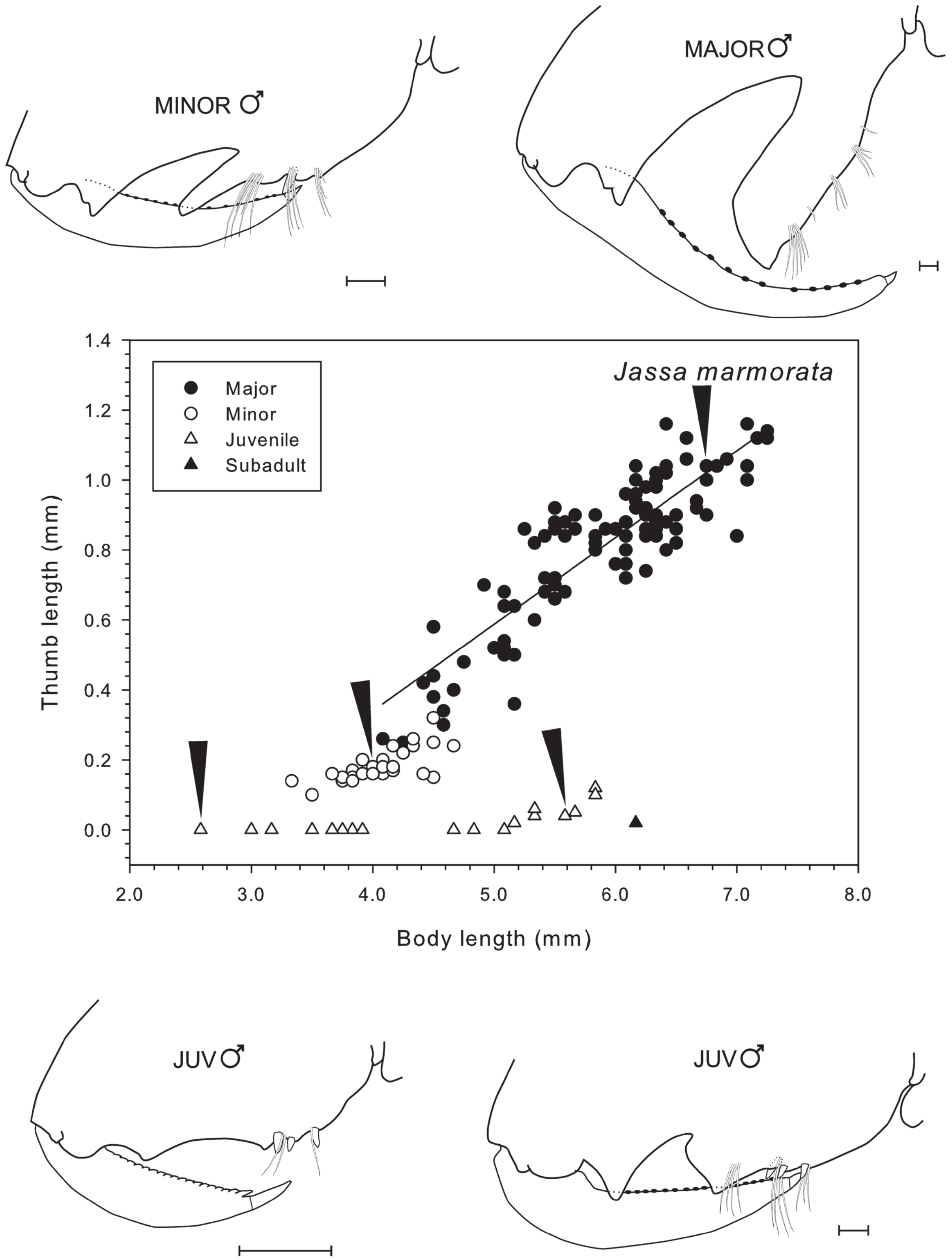

FIGURE 16. *Jassa marmorata* Holmes, 1905. Variation in thumb length relative to body length in males in a single population (Barren Islands Marina, Jamaica Bay Wildlife Refuge, Brooklyn, New York (40°35′N, 73°55′W), early July 1984, B. Borowsky, coll., among hydroids and *Ulva* on submerged docks at the marina, IZ 1984-112 (CMN). Arrows refer to the associated gnathopod illustrations. Setae omitted except for those around the thumb and spines in order to landmark position changes with growth. All views lateral. Scale 0.1 mm. Linear regression assumptions passed for the major form male. Linear regression statistics: Major form, thumb length = -0.652 + 0.248 body length, $r^2 = 0.765$, $n = 103$. Illustration after Conlan (1990).

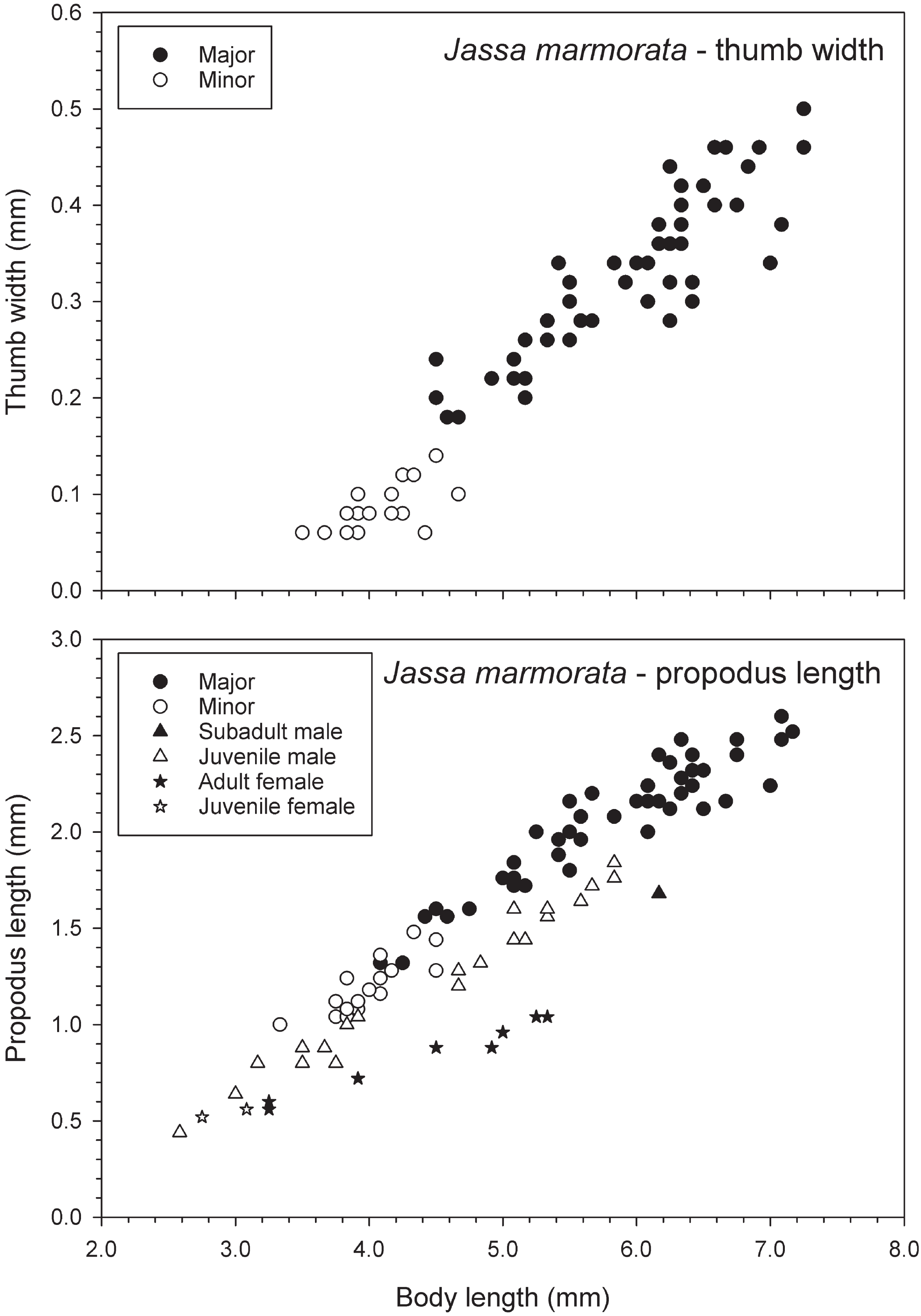

FIGURE 17. *Jassa marmorata* Holmes, 1905. Variation in thumb width and gnathopod 2 propodus length relative to body length in males and females in a single population (Barren Islands Marina, Jamaica Bay Wildlife Refuge, Brooklyn, New York (40°35′N, 73°55′W), early July 1984, B. Borowsky, coll., among hydroids and *Ulva* on submerged docks at the marina, IZ 1984-112 (CMN). Linear regression assumptions failed for all plots.

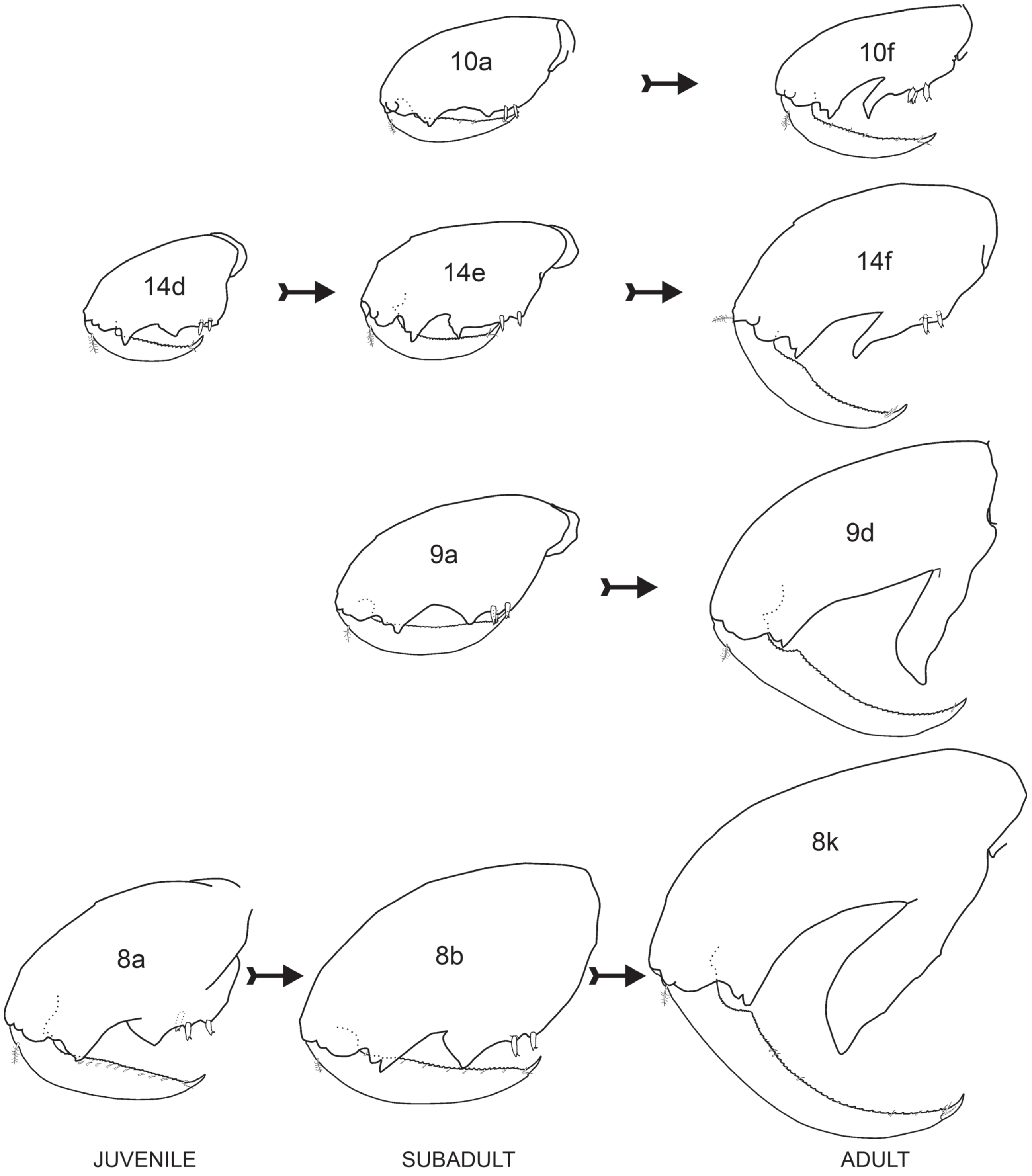

FIGURE 18. *Jassa marmorata* Holmes, 1905. Transformation of the propodus and dactyl of gnathopod 2 of four males as they moulted from non-thumbed to the final thumbed morphology. Most setae are not shown in order to enhance clarity. Adaptation of illustrations in Sexton and Reid (1951) with their figure numbers. First row: Plate 16, Specimen 10, J.30 a, male F_1 of Broad-Form female J.CCLXII, 1 July 1929, before (10 a) and after (10f) moulting. Second row: Plate 21, Specimen 14(2), male J.11, F_1 of J.CXLI, moult Feb. 10, 1929 (14d), moult Feb. 23, 1929 (14e) and dead May 1, 1929 (14f). Third row: Plate 15, Specimen 9, male J.30a (b) F_1 of Broad-Form female J.CCLXII, moult July 6, 1929 (9a) and dead August 24, 1929 (9d). Fourth row: Plates 13 and 14, Specimen 8, male J.17e, F1 of Broad-Form pair J.CLXXIV, moult May 18, 1929 (8a), moult June 1, 1929 (8b) and as it emerged from its moult on June 1, 1929 (8k).

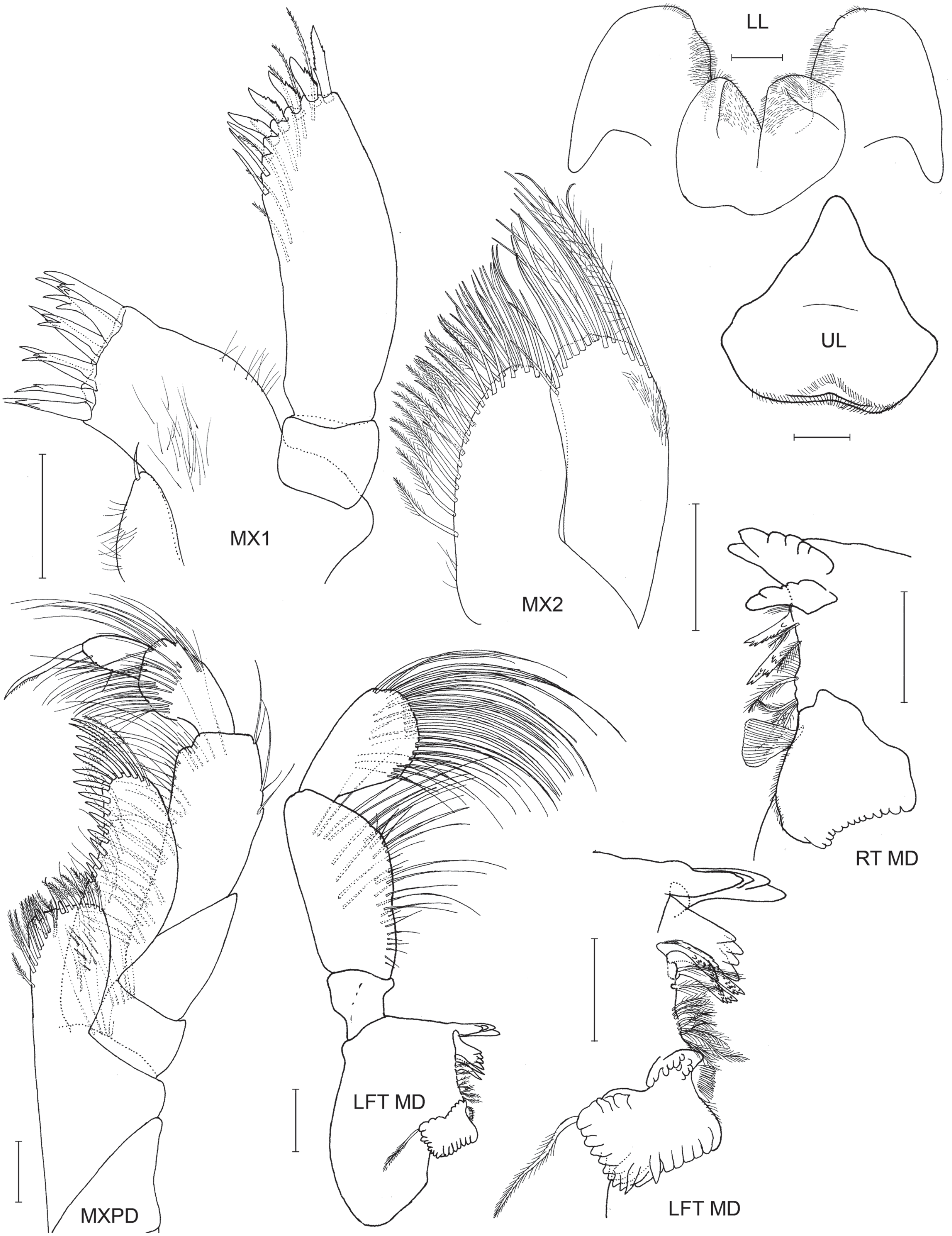

FIGURE 19. *Jassa marmorata* Holmes, 1905. Neotype, adult male, major form, 6.7 mm, NMCC 1987-1067, Barren Islands Marina, New York, IZ 1984-112 (CMN). Mouthparts. Frontal view: upper lip; lateral view: maxilla 2; other views medial. Scale 0.1 mm.

Gnathopod 2: basis with a row of closely spaced setae along the anterolateral margin (at least some setal lengths >40% of the basis width); carpus and propodus, setae on the anterior margin short and simple (setal length < basis width).

Pereopods 5–7: propodus not expanded anteriorly.

Uropod 1: ventral peduncular spinous process underlying about 1/3 of the longest ramus.

Uropod 3: inner ramus without spines mid-dorsally (with only the single apical spine).

Telson: tip without apical setae (only the usual short setae at each dorsolateral cusp).

Thumbed male:

Antenna 2: large individuals with plumose setae on the flagellum and peduncular article 5.

Gnathopod 2: propodus, palmar defining spines not produced on a ledge, present in small thumbed males but absent in large thumbed males. In minor males, the thumb is distally acute, short relative to body length and located on the distal half of the propodus. The dactyl is not centrally toothed. In major males, the thumb is distally squared, longer relative to body length and on the proximal half of the propodus. The dactyl is expanded close to the junction with the propodus but is not centrally toothed.

Adult female:

Antenna 2: large animals with plumose setae on the flagellum and peduncular article 5.

Gnathopod 2: propodus, palm concave, palmar defining angle acute.

Remarks. *Jassa marmorata* has often been mis-identified as *J. falcata* in the past (Conlan 1990). Sexton and Reid (1951) studied the development of *J. falcata* and their *J. falcata* "broad form" is in fact *J. marmorata*. The transformation of four males from non-thumbed to thumbed state in aquarium cultured specimens is reproduced in Fig. 18 from Sexton and Reid's (1951) plates. This shows that some subadult males have a small "pre-thumb" in the palm of gnathopod 2 (Figs 8a, b, 14 d, e and 18) while others do not (Figs 9a, 10a and 18). The appearance of a pre-thumb appears to occur only in larger juveniles (Fig. 16). Fig. 18 also shows that while the palmar defining spines are retained in small thumbed males, they are lost in large thumbed males.

Sexton and Reid (1951) produced intersexes with a short, narrow thumb and small, setose brood plates by inbreeding siblings generated by a pair collected in the wild. Although the intersexes mated with female siblings, the offspring did not survive to maturity. Two intersexes and an ovigerous female were also found in NMNH 148787, 3–38, taken in a dredge at 18–27 m over sandy, weedy bottom inside the northern point of entrance to Magdalena Bay, Lower California, on July 18, 1938. Both intersexes had all the distinguishing features of *J. marmorata* but short thumbs on the second gnathopods and a toothed dactyl similar to that in minor forms of *J. falcata* and *J. staudei*.

Jassa marmorata is morphologically similar to *J. valida* and the two overlap in distribution at the junction of their ranges in North Carolina, which is a biogeographic break for many species (Pappalardo *et al.* 2015). Distributions listed in OBIS for *J. marmorata* for the coasts of the US south of North Carolina, including the Gulf of Mexico require confirmation because they may be for mis-identified *J. valida*. A similar southerly range into the Gulf of Mexico and on the coasts of Cuba and the Bahamas listed by Conlan (1990) may also be for *J. valida*, not *J. marmorata*. It is possible that some or all records of *J. marmorata* on the coasts of Uruguay and Argentina described by Alonso de Pina (2005) are unrecognized *J. valida*, since *J. valida* is already known from this coast. The most dependable character to distinguish the two species of any size is the lack of apical setae on the telson of *J. marmorata* and presence in *J. valida*. However, viewing this character requires moving the third uropods out of the way of the telson (this can be done by holding the animal on its side and bending the uropods downwards with a fine needle). It also requires that the usual pair of setae at the the telson knobs, which project dorso-distally, are not confused with the apical setae, which project distally. The other diagnostic characters of *J. marmorata*, which are easier to view, can be used for adult and subadult specimens.

Due to the availability of a large number of specimens from the neotype population (162 adult and juvenile males measured for Fig. 16), there were 10 major form and 17 minor form males that overlapped in body length (4.08–4.67 mm) for comparison of thumb length relative to body length. A Kruskal-Wallis test indicated that thumb length was significantly longer in the major than minor forms of this size range ($H_{KW} = 4.017$, $p < 0.001$; median thumb length 0.39 vs 0.22 mm, respectively). The thumbs also appeared wider in major than minor forms (Fig. 17) although there were insufficient specimens with a common range of body length to test this. The second gnathopod propodus length was significantly greater in major form adult males (mean 1.812 ± 0.245 mm) than juvenile males (1.533 ± 0.200 mm) of the same body length range (4.08–5.83 mm) (*t*-test, $t = 3.458$, $p = 0.001$, $n = 27$ major forms and 12 juveniles) (Fig. 17). Similarly, the juvenile males had a significantly longer propodus than the adult females of the same body length range (3.25–5.33 mm) ($H_{KW} = 2.195$, $p < 0.05$, median 1.20 mm for juvenile males, $n = 15$ and 0.88 mm for adult females, $n = 8$) (Fig. 17).

The SEM image of the telson (Fig. 20) shows paired short plumose setae to either side of the telson nubs and associated long, erect seta dorsal to each nub. The nub magnifications show that the nubs are actually cusped and the erect setae are ringed at their tips by rows of scales. Presumably, the erect setae have a sensory function, perhaps for position within the tube and the cusped nubs may assist with gaining a purchase within the tube. Possibly the plumose setae are mechanoreceptive as well (Kauffmann 1994).

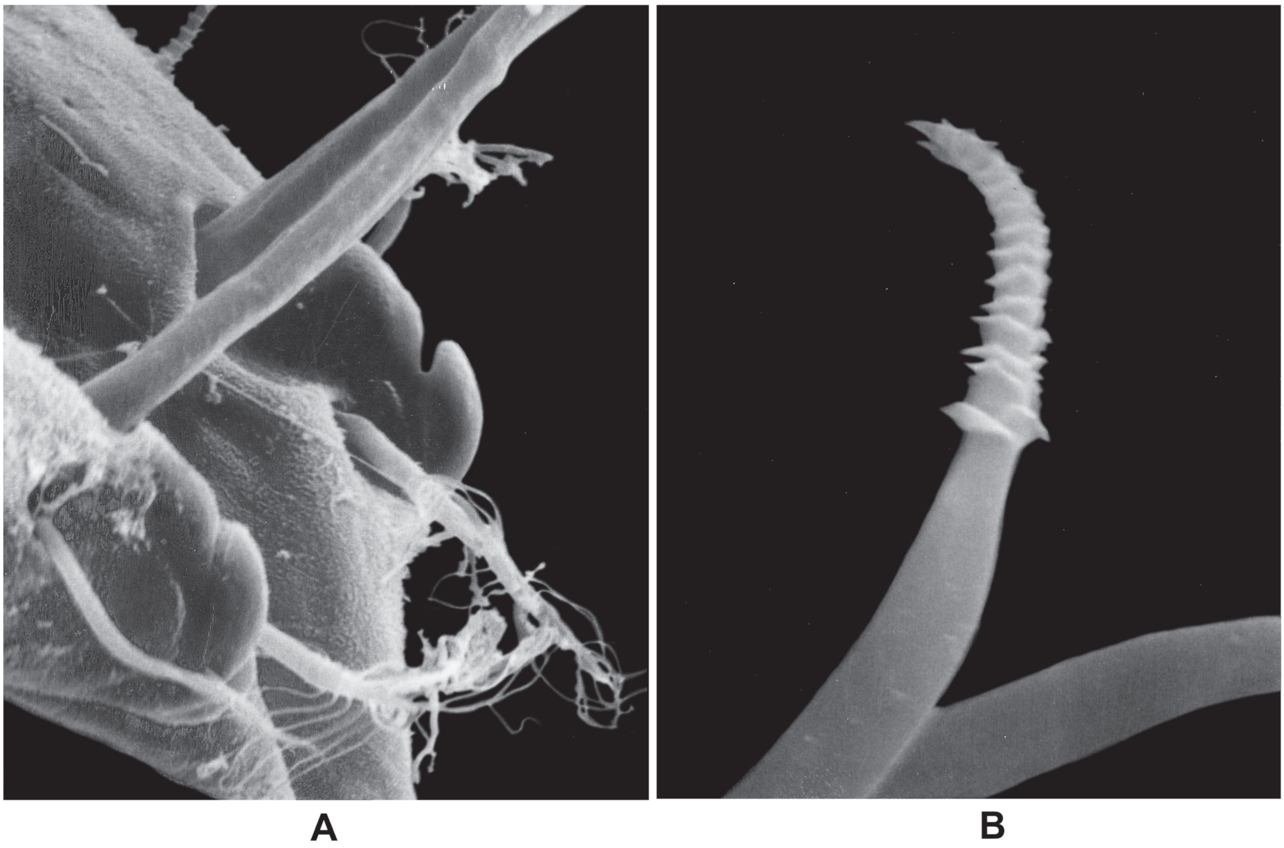

FIGURE 20. *Jassa marmorata* Holmes, 1905. Adult male, 6.8 mm. Barren Islands Marina, New York, IZ 1984-112 (CMN). Telson. A, cusps and associated setae. B, tip of erect seta arising proximally to each cusp. x2000.

Only two specimens of the ~25,000 specimens of *Jassa* examined were found to be densely coated in epibionts (Fig. 21). All other specimens appeared to be clean or with much smaller and sparser epibionts. However, specimens collected in Helgoland Harbour (Germany) often were coated with epibionts. Both of the densely coated specimens were large, major form thumbed males and the epibionts were algal in appearance (green *Enteromorpha*-like algae or filamentous as in Fig. 21). The specimen bearing a green algal coat (found among algae on a floating dock in Adelaide, Australia) was so densely covered that it was barely recognizable. The specimen shown in Fig. 21 was from a fouling community on a natural gas platform in Morecambe Bay, UK In both specimens, the epibionts were concentrated on the anterior of the body, coating the dorsum and second gnathopods. This pattern suggests that the animals were partially tubicolous during the time of infestation. Movement within the tube may have prevented epibiont accumulation on the posterior part of the body. The cleaning action of the first gnathopods may have prevented epibiont growth on body parts within reach, such as the antennae. That epibiont growth was able to establish in such quantity on these males suggests that the males had not molted for some time, and that they were senescent and not able to prevent epibiont settlement.

There are four corrections to Conlan (1990): (1) Sexton and Reid (1951) Plate 12, 5a–5f should be added to p. 2053; (2) specimens from Crooke's Point, New York (p. 2054) are from Staten Island, New York, not the Hudson River (S. Grabe, pers. comm., date not recorded); (3) *J. marmorata* is not yet known from Alaska; an Alaskan specimen attributed to *J. marmorata* in Conlan (1990) and repeated by Fofonoff *et al.* (2019) is actually the indigenous *J.*

staudei (specimen re-examined May 23, 2018); (4) Conlan (1990) did not recognize that "*J. marmorata*" in the Gulf of Mexico and on the US Atlantic coast from Florida to North Carolina were more likely to be *J. valida* than *J. marmorata*, although the two species could overlap in range (Figs 1, 2, 7, 8). Therefore, the identification of specimens from these coasts are suspect. This has been rectified for collections at the Canadian Museum of Nature (CMN) but not elsewhere (see Remarks section for *J. valida*). Similarly, "*J. marmorata*" found in the southwestern Gulf of Mexico with *J. valida* by Winfield *et al*. (2021) are possibly also *J. valida* as the specimens they reported were very small (2.36 ± 0.38 mm body length, *n* = 5) and therefore likely difficult to view the diagnostic terminal seta(e) on the telson that denotes the identification as *J. valida* (Supplementary Data File S1). It was not possible to borrow the specimens to confirm the identification as the museum collections were closed due to the COVID-19 pandemic.

FIGURE 21. *Jassa marmorata* Holmes, 1905. Adult male, 6.6 mm, coated with epibionts. Morecambe Bay, Irish Sea, England, UK, 19 May, 1986, P. G. Moore, coll., fouling natural gas platform, level D, CPP1, IZ1986-092 (CMN).

A loan that came after Conlan (1990) is a sample of *J. marmorata* in a collection taken at 13 m depth on a shell-muddy-sand substrate offshore of São Paulo, Brazil in 1963. This is the earliest known collection of *J. marmorata* on the Atlantic coast of South America (Table 3). It is possible that this sample was contaminated by *J. marmorata* fouling the ship. A scraping of a small ship in 1985 in this area found *J. marmorata* on the hull.

A study of amphipods inhabiting the moderately polluted Newport Bay in 1954 (now part of Los Angeles) found "*J. falcata*" in small numbers compared to the large populations on pilings in Los Angeles Harbor (Barnard and Reish 1959). Although not seen, these specimens may be *J. marmorata*, since it has been found exclusively on other human-modified habitats on the Pacific coast of North America (this study and Fofonoff 2019). *Jassa marmorata* has been collected in California as far back as 1931 (Table 3).

Jassa slatteryi **Conlan, 1990**
(Table 10, Figs 22–27)

J. cadetta Krapp *et al*., 2008, pp. 337–345, figs. 4–7
J. trinacriae Krapp *et al.*, 2010, pp. 85–100, figs. 5–7

Diagnosis.

Both sexes:

Mandibular palp: article 2, dorsal margin without a fringe of setae.

Maxilla 1: without a seta or setal cluster at the base of the palp article 1.

Gnathopod 1: basis, anterolateral margin without a row of short setae along its length; carpus with a single or group of long setae at the anterodistal junction of the propodus, (seta(e) ≥50% the length of the anterior margin length and slightly medial).

Gnathopod 2: basis with a row of setae along the anterolateral margin (length of most setae <40% of the basis width); carpus and propodus, setae on the anterior margin short and simple (setal length < basis width).

Pereopods 5–7: propodus not expanded anteriorly.

Uropod 1: ventral peduncular spinous process underlying about ¼ of the longest ramus.

Uropod 3: inner ramus without spines mid-dorsally (with only the single apical spine).

Telson: tip without apical setae (only the usual short setae at each dorsolateral cusp).

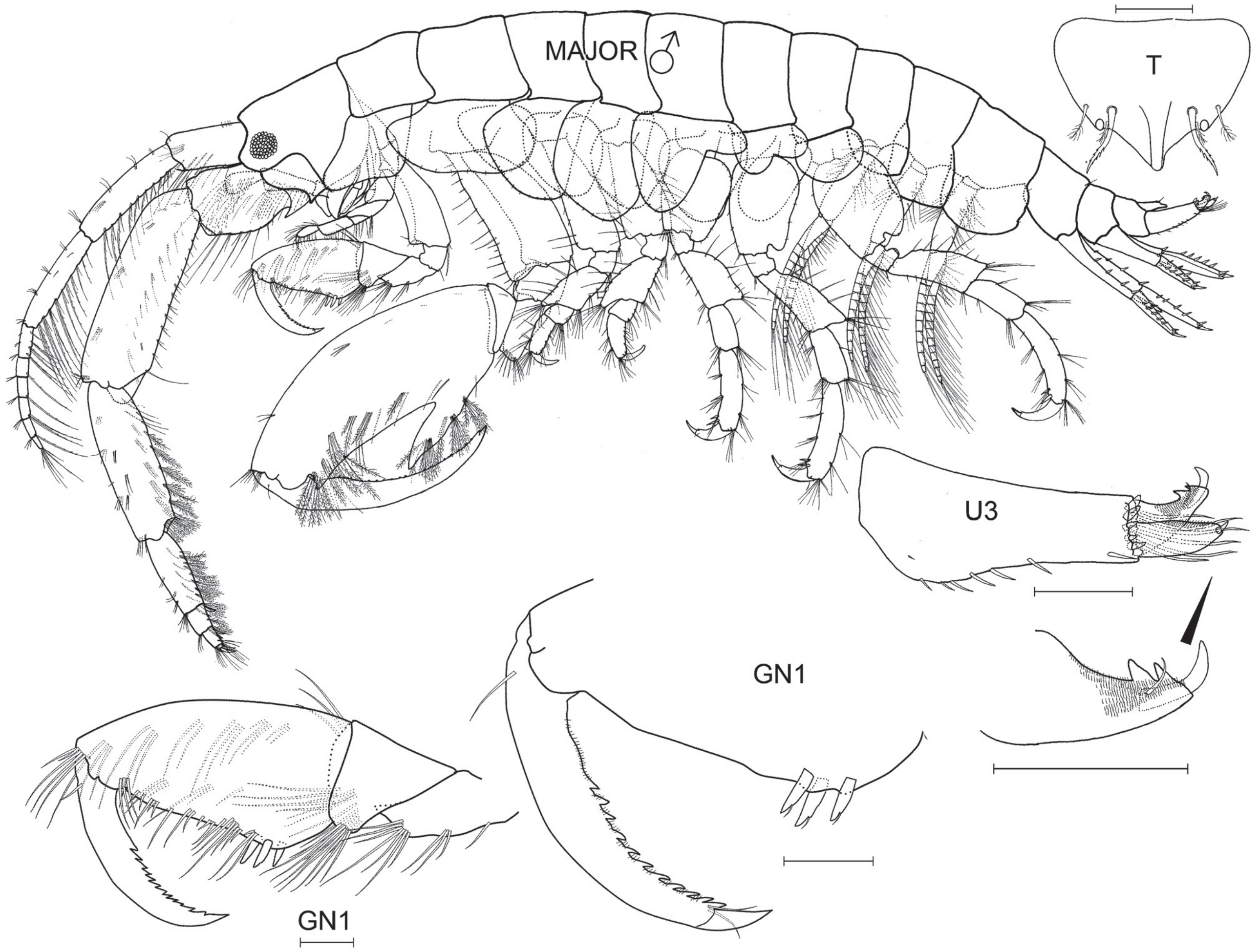

FIGURE 22. *Jassa slatteryi* Conlan, 1990. Holotype, adult male, major form, 5.1 mm, NMCC 1987-1068. Moss Landing Harbor, California (36°48'00.7"N, 121°47'13.9"W), 4 July 1986, K. E. Conlan, coll., station C9, scraping of the bottom of a row boat just below water level, IZ 1986-057 (CMN). Lateral view: whole body and gnathopod 1; dorsal view: telson; other views medial. Scale 0.1 mm. Illustration after Conlan (1990).

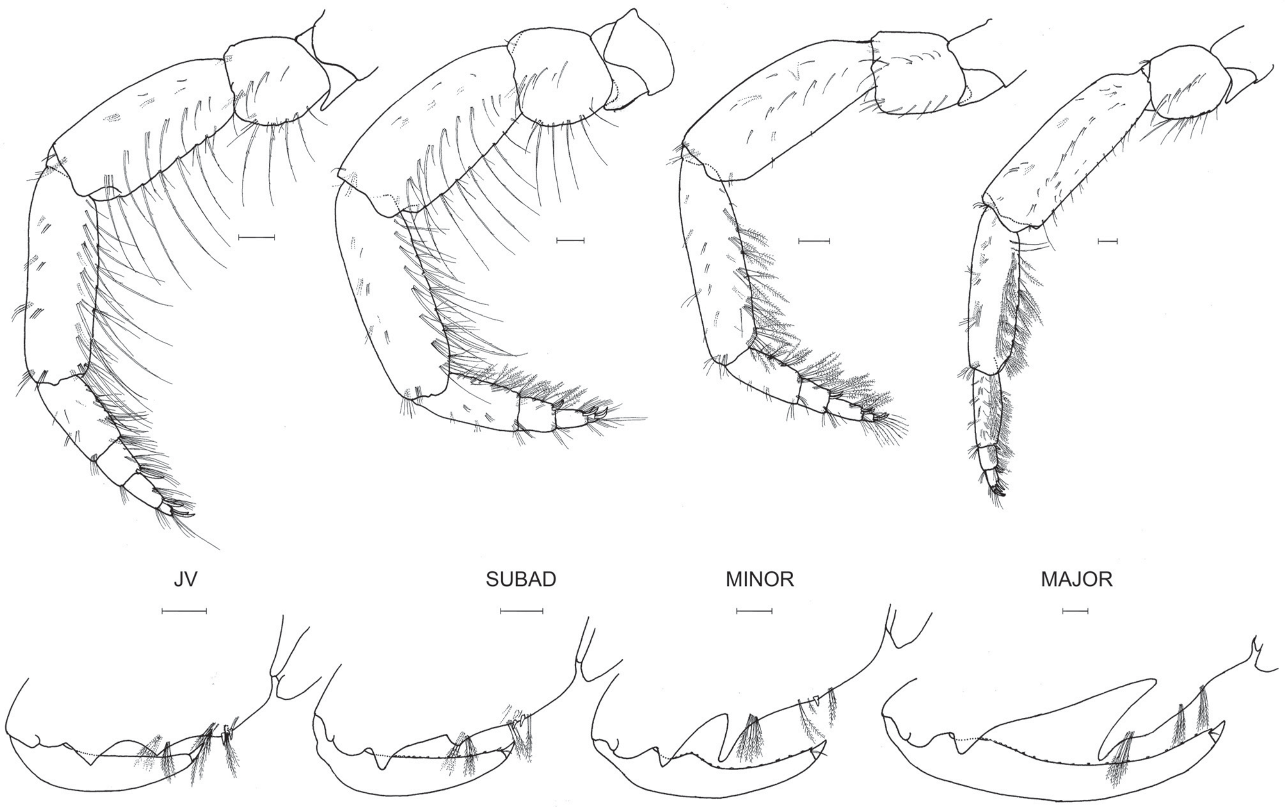

FIGURE 23. *Jassa slatteryi* Conlan, 1990. Paratype, juvenile male, 2.7 mm; paratype, subadult male, 4.5 mm; paratype, minor form male, 3.5 mm; holotype, major form male, 5.1 mm. Moss Landing Harbor, California (36°48’00.7″N, 121°47’13.9″W), 4 July 1986, K. E. Conlan, coll., station C9, scraping of the bottom of a row boat just below water level, IZ 1986-057 (CMN). Setae omitted except for those around the thumb and spines in order to landmark position changes with growth. Lateral view: second gnathopods; medial view: second antennae. Scale 0.1 mm. Illustration after Conlan (1990).

Thumbed male:

Antenna 2: large individuals with plumose setae on the flagellum and peduncular article 5.

Gnathopod 2: propodus, palmar defining spines not produced on a ledge, present in small thumbed males but absent in large thumbed males. In minor males, the thumb is distally acute, short relative to body length and located on the distal half of the propodus. The dactyl is not centrally toothed. In major males, the thumb is distally acute, longer relative to body length and on the proximal half of the propodus. The dactyl is expanded close to the junction with the propodus but is not centrally toothed.

Adult female:

Antenna 2: large animals with plumose setae on the flagellum and peduncular article 5.

Gnathopod 2: propodus, palm shallowly concave, palmar defining angle acute.

Remarks. Smaller males and females lack the plumose setae on the distal parts of the antenna 2. The long filter setae on antenna 2 are absent or much shorter in the thumbed males than the females or juveniles. Large subadult males have some plumose setae on the flagellum but retain the long setae typical of juveniles and females on the peduncle (Figs 22–23).

The long seta on the anterodistal margin of the gnathopod 1 carpus is usually visible, extending upright or away from the propodus. However, it may also lay flat against the medial face of the propodus, so it is necessary to check for its presence using a fine needle inserted into a rod for grasping or with needle-nosed forceps. Presence of this long seta (or setal cluster), along with lack of apical setae on the telson are key distinguishing characters for *J. slatteryi* of any size or sex, except from *J. carltoni*, which also has these character states. Differences from *J. carltoni* are more in the shape of the gnathopod 1 palm (straighter in *J. slatteryi* and concave in *J. carltoni*), the density of setae on the anterior margin of the basis of gnathopod 2 (more setae in *J. slatteryi* than *J. carltoni*) and in the shape and spination of the gnathopod 2 propodus: slenderer in the female of *J. slatteryi* with the defining spines tightly

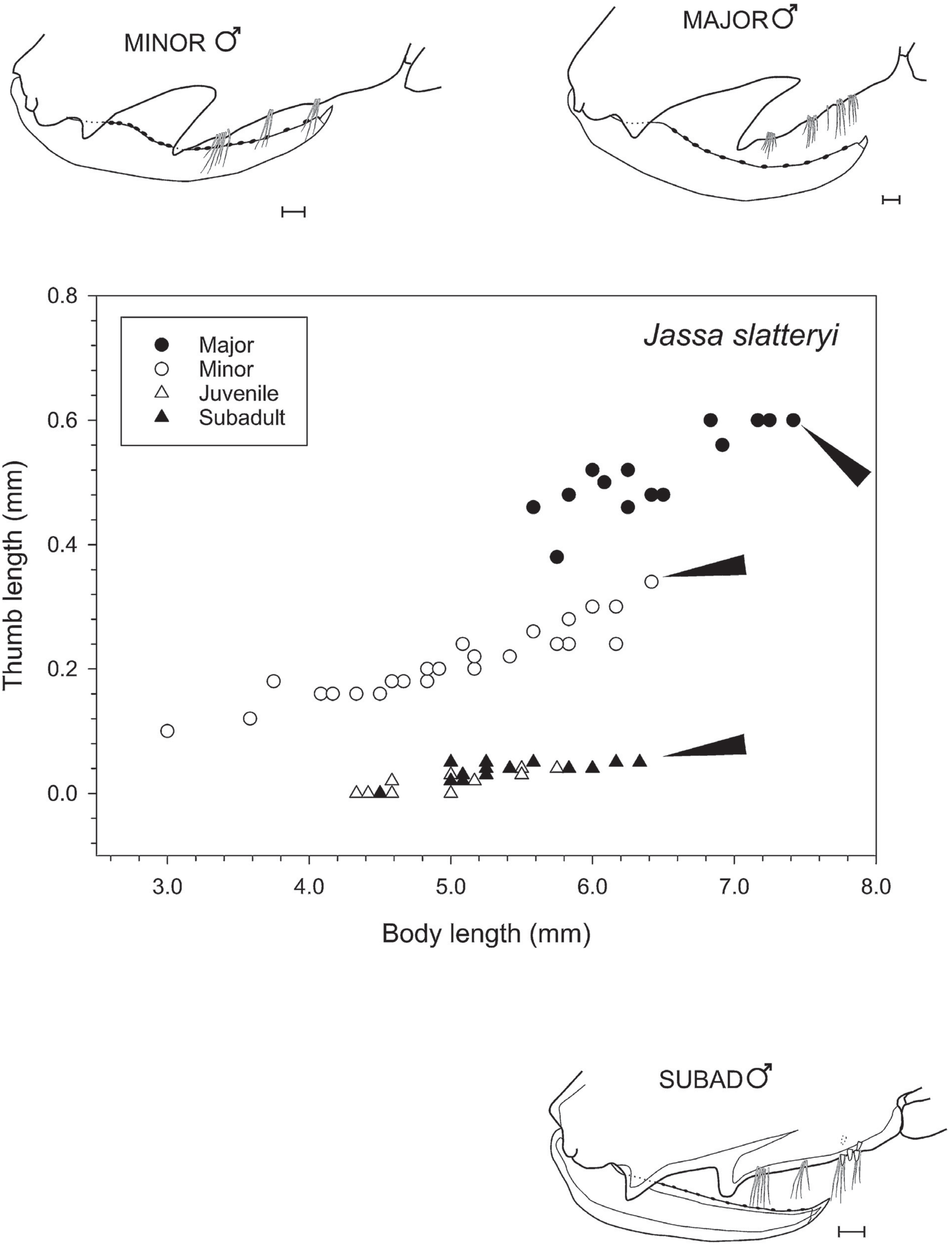

FIGURE 24. *Jassa slatteryi* Conlan, 1990. Variation in thumb length relative to body length in a single population of males on a settling plate from Deukryang Bay, The Republic of Korea, May–July 1981, J.S. Hong, coll., A2020.0035 (CMN). Arrows refer to the associated gnathopod illustrations. The subadult male had a thumb visible inside the cuticle, indicating that it would molt next into a thumbed adult. Setae omitted except for those around the thumb and spines in order to landmark position changes with growth. All views lateral. Scale 0.1 mm. Linear regression assumptions failed for all plots. Illustration after Conlan (1990).

clustered and the major form male's thumb always acute at the tip and not curved posteriorly, while in *J. carltoni* the female's defining spines are more dispersed and the major form male's thumb is more rounded at the tip and curved posteriorly. While *J. slatteryi* has been found on many coasts, *J. carltoni* is only known from the Pacific coast of North America. *Jassa slatteryi* also occurs on the Pacific coast of North America, however, though it has not been found in the same collections as *J. carltoni*.

A subset of the specimens described by Hong (1983) as *J. falcata* were lent for analysis for this study. They had been collected in Deukryang Bay, The Republic of Korea from a settling plate. Major forms ranged from 5.5 to 7.2 mm in body length while minor forms were 3.0–6.2 mm (Fig. 24). Thumb length was less relative to body size in minor forms than major forms. A plot of propodus length to body length for the same males, with addition of females from the Deukryang Bay population showed a longer propodus length relative to body length for the adult males than for the females, juvenile and subadult males (Fig. 25). For the adult males that overlapped in body length (5.58–6.41 mm), propodus length did not significantly differ between major and minor form (ANOVA, $F = 0.211$, $p = 0.654$, $df = 14$; major form propodus length 1.863 ± 0.122 mm, $n = 7$; minor form propodus length 1.830 ± 1.51 mm, $n = 8$).

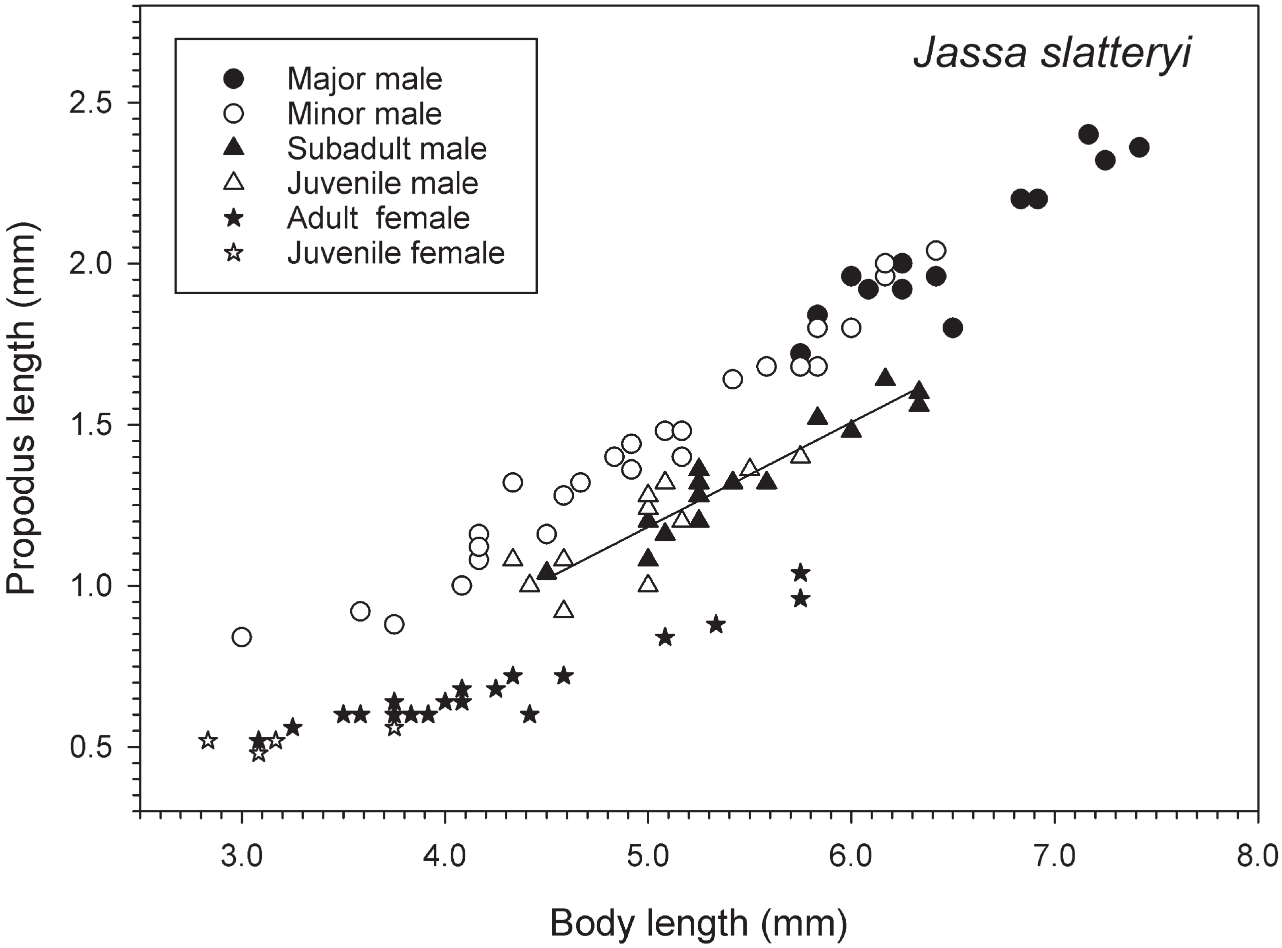

FIGURE 25. *Jassa slatteryi* Conlan, 1990. Variation in gnathopod 2 propodus length relative to body length in a single population of males and females on a settling plate from Deukryang Bay, The Republic of Korea, May–July 1981, J.S. Hong, coll., A2020.0035 (CMN). Linear regression assumptions passed for the subadult male. Linear regression statistics: subadult male, Gn2 propodus length = -0.435 + 0.324 x body length, $r^2 = 0.916$, $n = 15$.

Lim and Park (2006) redescribed and illustrated a minor form of *J. slatteryi* from a collection taken from the screw of a ship in Samcheon-po bay on the south coast of The Republic of Korea. Rumbold *et al.* (2015a) examined *J. slatteryi* from Argentina both morphologically and with the CO1 gene, comparing it with *J. marmorata* and *J. staudei*. They also provided a photograph of live pigmentation of a subadult male and photographs of various body parts of a minor form thumbed male. Their Fig. 3I is the tip of the maxilliped palp, not the mandible as stated. Pilgrim & Darling (2010) found *J. slatteryi, J. marmorata* and *J. staudei* to be unique based on the CO1 gene. A loan of *J. slatteryi* that was obtained after Conlan (1990) was of three samples at 11–24 m depth offshore of Rio de Janeiro and Ubatuba, Brazil in 1964–1966. This is the earliest known collection of *J. slatteryi* on the Atlantic coast of South America (Table 3).

Conlan (1990) cited in error that *J. slatteryi* occurred in the Galapagos Islands, Ecuador, based on identification of 7 major form males, 3 adult females and 1 juvenile borrowed from the Swedish Museum of Natural History. The collection location was Cumberland Bay, Masatiera, but this is located in Robinson Crusoe Island, Chile (formerly Más a Tierra). The reference by Rumbold *et al.* (2015a) to *J. slatteryi* occurring in the Galapagos Islands is therefore also in error. Some other location errors in Conlan (1990) were also found when collections were re-examined for this paper as some specimens of "*J. slatteryi*" on the Pacific North American coast were unrecognized *J. morinoi* or *J. carltoni*. Corrected distributions indicate that both *J. slatteryi* and *J. morinoi* are indeed trans-hemispheric (Figs 3–6) yet also occur at remote locations along the Pacific North American coast, particularly in British Columbia. *Jassa carltoni* is only known from the Pacific coast of North America and is now known from British Columbia (Fig. 10; update of Conlan 1990).

Intersexes, having characteristics of both females (setose brood plates) and males (penial papillae and thumbed second gnathopods) were found in Santa Ynez, Eureka Harbor, and Morro Bay, California, Tanabe Bay, Japan and Adelaide, Australia (Fig. 26). The intersexes had small thumbs which could differ in size between right and left gnathopod.

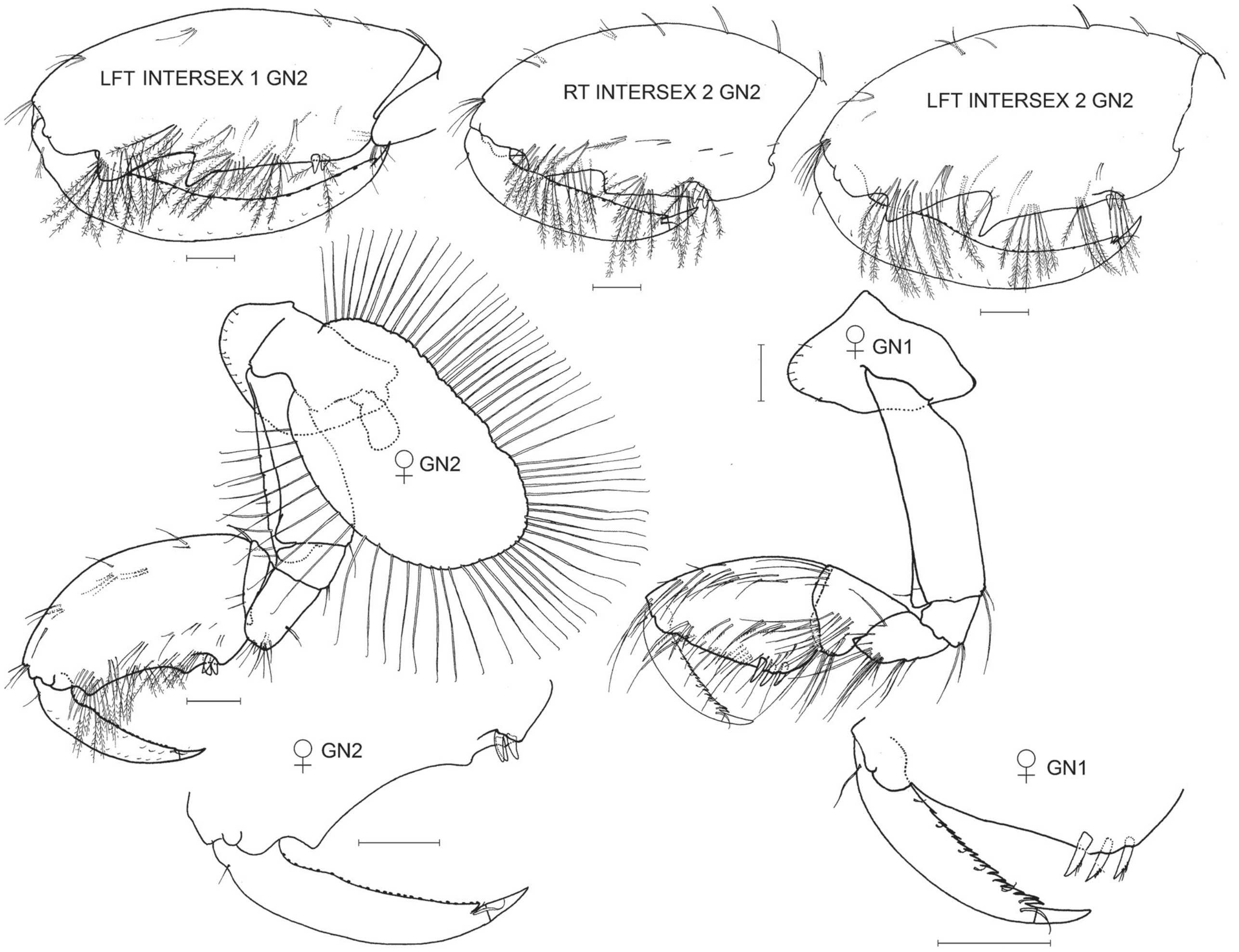

FIGURE 26. *Jassa slatteryi* Conlan, 1990. Intersex 1, 4.6 mm; intersex 2, 5.6 mm. Tanabe Bay, Wakayama Prefecture, Japan (33°41′N, 135°22′E), 2 Apr. 1976, H. Morino, coll., no habitat data, A2020.0036 (CMN). Allotype, adult female, 4.1 mm, NMCC 1987-1069. Moss Landing Harbor, California (36°48'00.7″N, 121°47'13.9″W), 4 July 1986, K. E. Conlan, coll., station C9, scraping of the bottom of a row boat just below water level, IZ 1986-057 (CMN). Lateral views: intersex 1 and 2 left gnathopod 2; other views medial. Scale 0.1 mm.

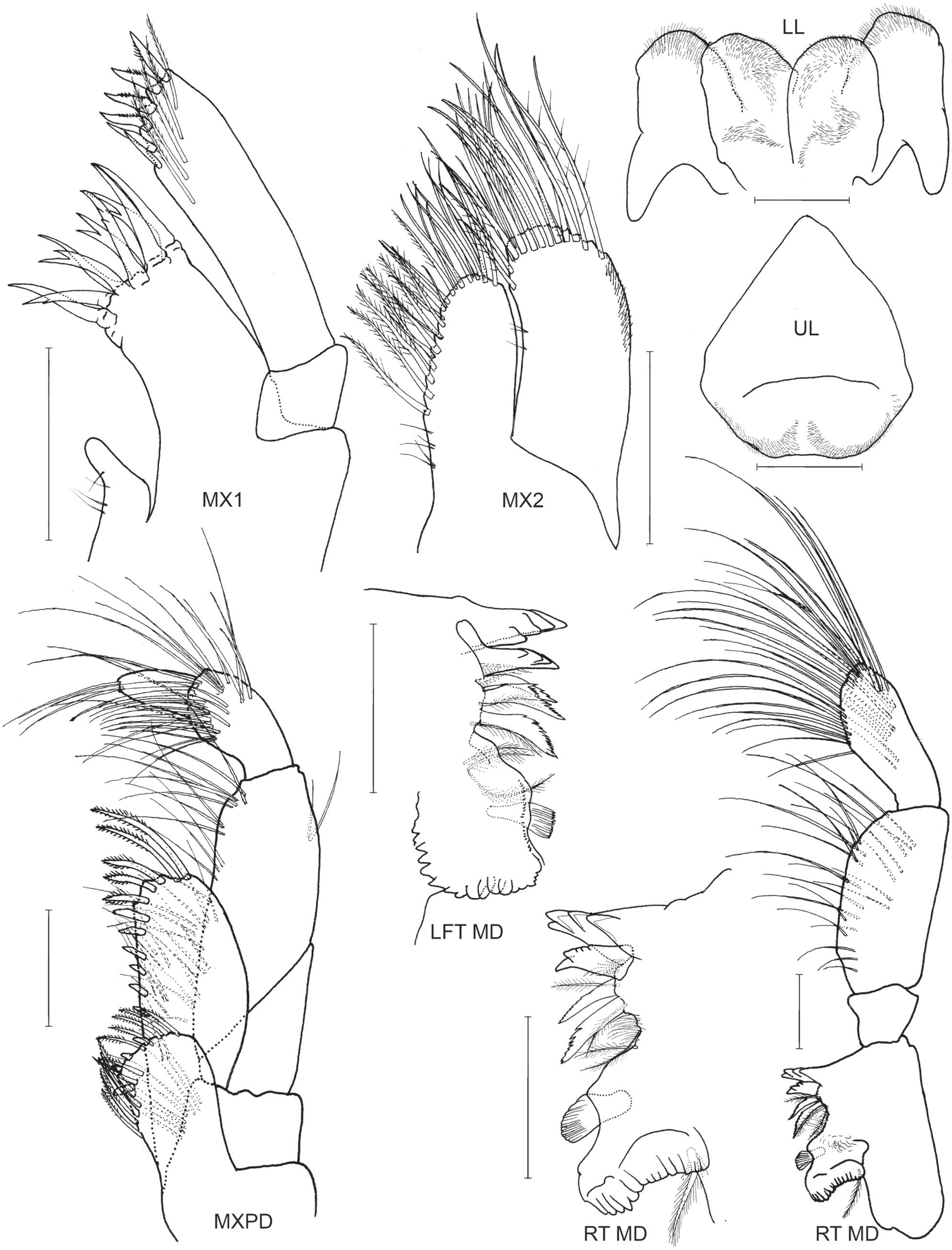

FIGURE 27. *Jassa slatteryi* Conlan, 1990. Holotype, adult male, major form, 5.1 mm, NMCC 1987-1068. Moss Landing Harbor, California (36°48’00.7″N, 121°47’13.9″W), 4 July 1986, K. E. Conlan, coll., station C9, scraping of the bottom of a row boat just below water level, IZ 1986-057 (CMN). Mouthparts. Frontal view: upper lip; lateral view: maxilla 1; other views medial. Scale 0.1 mm.

Two species described after the revision by Conlan (1990) are submerged under *J. slatteryi*: *J. cadetta* Krapp *et al*., 2008 and *J. trinacriae* Krapp *et al.*, 2010. *Jassa cadetta* was described by Krapp *et al.* (2008) based on specimens collected in algae at shallow depth in the Venice Lagoon, Malamocco, Italy (~45°22′18″N, 12°20′15″E). These had a different karyotype and morphology than *J. marmorata*, which was also found there, and therefore was designated a new species. The possibility that *J.cadetta* could be *J. slatteryi* was not considered by the authors, but examination of the types lent by the Museo Civico di Storia Naturale di Verona, Italy showed that their morphology was unmistakeably that of *J. slatteryi* (Supplementary data file S2). Both *J. marmorata* and *J. slatteryi* are common inhabitants of fouling communities in populated areas such as Venice Lagoon (Table 4).

Jassa trinacriae was described based on specimens collected at Grotta Conza, Sicily (~38°11′14″N, 13°16′57″E), at the northern end of the Conca d'Oro, a cave of about 90 m length, 175 m above sea level, and 1 km distant from the sea. Presumably the specimens were in saline water as *Jassa* is not known from fresh water (Table 4). Additional specimens collected in 1952 from Sampieri, Sicily were also ascribed to this species by Krapp *et al*. (2010). A loan of these individuals from the same museum as for *J. cadetta* allowed confirmation that all specimens were clearly *J. slatteryi* (Supplementary data file S3). Therefore, *J. trinacriae* is submerged. These specimens are the earliest collection known for the Mediterranean, since the record for Rovinj, Croatia noted in Conlan (1990) had no collection date (Table 3). Navarro-Barranco *et al.* (2015), Fernandez-Leborans *et al.* (2016), Fernandez-Gonzalez & Sanchez-Jerez (2017) and Bonifazi *et al.* (2018) document other Mediterranean locations where *J. slatteryi* has been confirmed.

Krapp *et al.* (2010) also described a *Jassa* sp. from a thermal spring in Fordongianus, Sardinia where the water was 45 °C (54–58 °C at the origin of the spring). Angelone *et al.* (2005) reported an electrical conductivity of 1,547 µS cm^{-1}, pH 8.40 and Eh 259 mV in this spring, which is in range of that found in seawater. Fordongianus is about 20 km east of the Sardinian west coast. This specimen was also borrowed from the Museo civico di Storia Naturale di Verona, Italy and examined (Supplementary data file S4). Its immature appearance and small size (2.2 mm length) suggest that it is a hatchling. If indeed a species of *Jassa*, this would be the warmest water recorded (Table 4). The specimen was slide mounted and therefore could not be manipulated to view all body parts. Conclusive determination would require specimens at a more advanced age.

Jassa morinoi **Conlan, 1990**

(Table 10, Figs 28–30)

Diagnosis.

Both sexes:

Mandibular palp: article 2, dorsal margin without a fringe of setae.

Maxilla 1: without a seta or setal cluster at the base of the palp article 1.

Gnathopod 1: basis, anterolateral margin with a few short setae at the distal angle; carpus with a single or small cluster of long setae at the anterodistal junction of the propodus (setae ≥50% the length of the anterior margin length and slightly medial).

Gnathopod 2: basis with about 5–10 widely spaced, short setae along the anterolateral margin (length of most setae <40% of the basis width); carpus and propodus, setae on the anterior margin short and simple (setal length < basis width).

Pereopods 5–7: propodus not expanded anteriorly.

Uropod 1: ventral peduncular spinous process underlying about 1/3 of the longest ramus.

Uropod 3: inner ramus without spines mid-dorsally (with only the single apical spine).

Telson: tip with apical setae in addition to the usual short setae at each dorsolateral cusp.

Thumbed male:

Antenna 2: without plumose setae on the flagellum and peduncular article 5.

Gnathopod 2: propodus, palmar defining spines pronounced and produced on a ledge in large minor form males. Palmar defining spines absent in major form males. Thumb distally acute in both minor and major males and sinuous in major males. The dactyl is proximally expanded but not centrally toothed in minor forms.

Adult female:

Antenna 2: without plumose setae on the flagellum and peduncular article 5.

Gnathopod 2: propodus, palm concave, palmar defining angle acute.

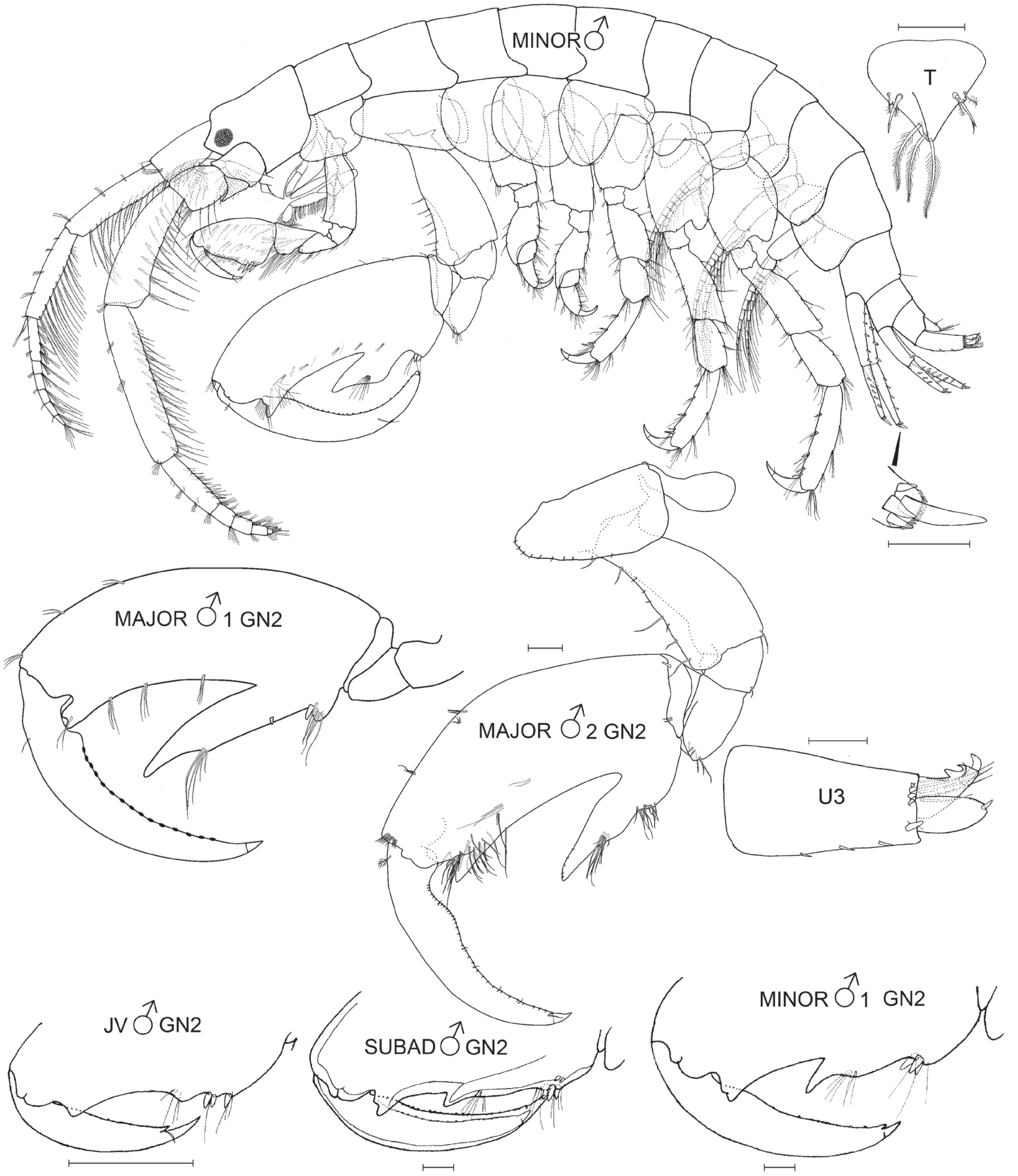

FIGURE 28. *Jassa morinoi* Conlan, 1990. Holotype, adult male, minor form, 5.6 mm, NSMT-Cr 26015 (C-33-1-1); paratype, minor form male 1, 4.7 mm, NSMT-Cr 26018 (C033-1-4). Bansho-no-hana Point, Tanabe Bay, Wakayama Prefecture, Japan (~33°42′N, 135°20′E), 17 March 1971, H. Morino, coll., low intertidal zone, on *Sargassum microcanthum*. Major form male 1, ~5–6 mm, western Crete, date unknown, G. Krapp Schickel, coll., 1 m+ depth, Schwanune and *Corallina*, NHMW 7622. Major form male 2, 3.75 mm, Stillwater Cove, Carmel Bay, California, June 1985, P. N. Slattery, coll., 35 ft. depth, rock and coralline bottom, IZ1989-024 (CMN). Subadult male, 4.2 mm, with larger thumb showing inside, and juvenile male, 3.5 mm, south end of Long Beach, Vancouver I., British Columbia, 6 July, 1970, E. L. Bousfield, coll., low intertidal zone, exposed coast, bedrock, kelp, *Phyllospadix* and fucoids, 1970-152, station P702 (CMN). Setae omitted on the gnathopod 2 profiles except for those around the thumb and spines in order to landmark position changes with growth. Lateral views: whole body and all second gnathopods; dorsal view: telson; medial view: uropod 3. Appendages are of the holotype unless noted otherwise. Scale 0.1 mm. Illustration after Conlan (1990).

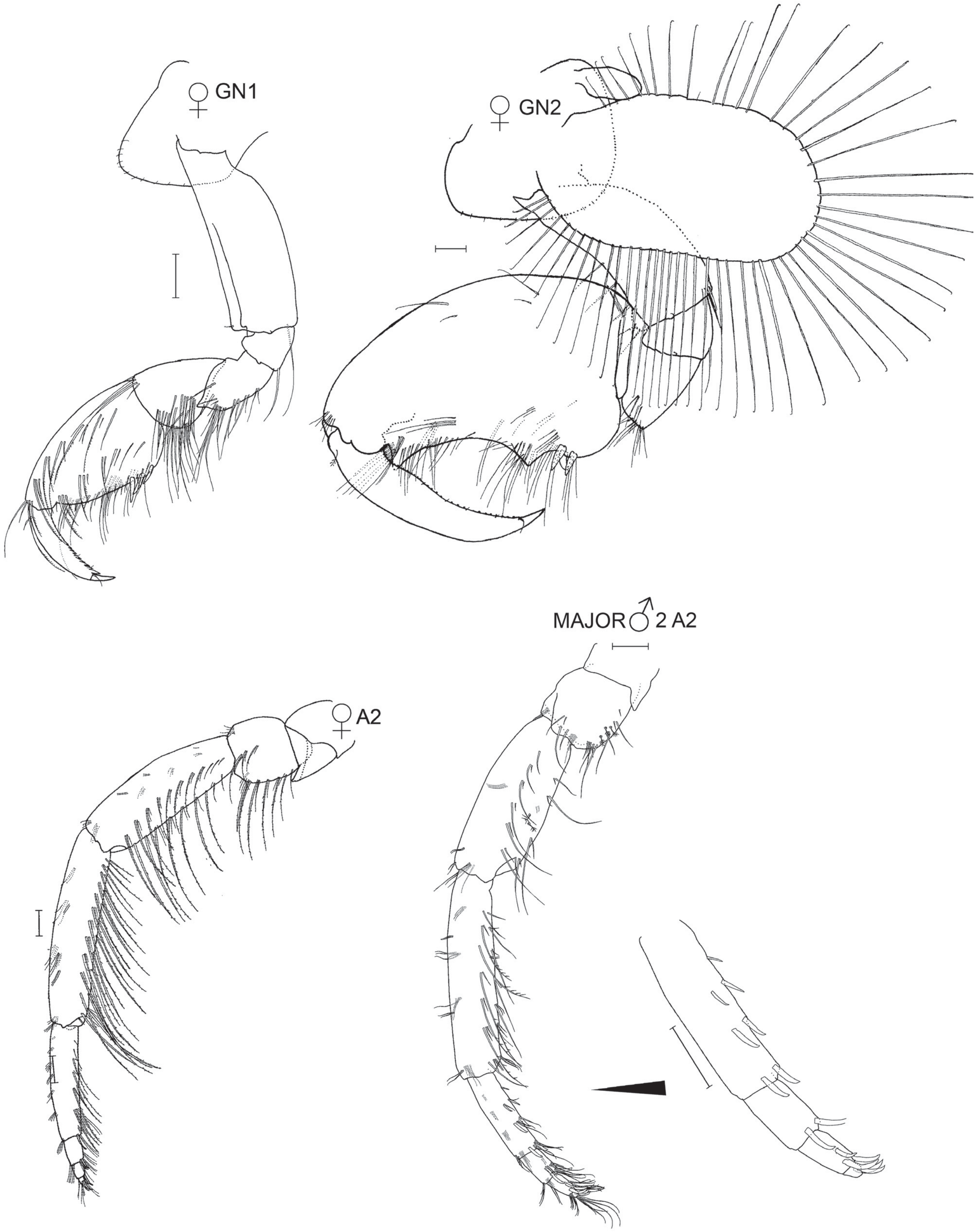

FIGURE 29. *Jassa morinoi* Conlan, 1990. Allotype, adult female, 5.8 mm, NSMT-Cr 26016 (C-33-1-2). Bansho-no-hana Point, Tanabe Bay, Wakayama Prefecture, Japan (~33°42′N, 135°20′E), 17 March 1971, H. Morino, coll., low intertidal zone, on *Sargassum microcanthum*. Major form male 2, 3.75 mm, Stillwater Cove, Carmel Bay, California, June 1985, P. N. Slattery, coll., 35 ft. depth, rock and coralline bottom, IZ1989-024 (CMN). All views medial. Scale 0.1 mm.

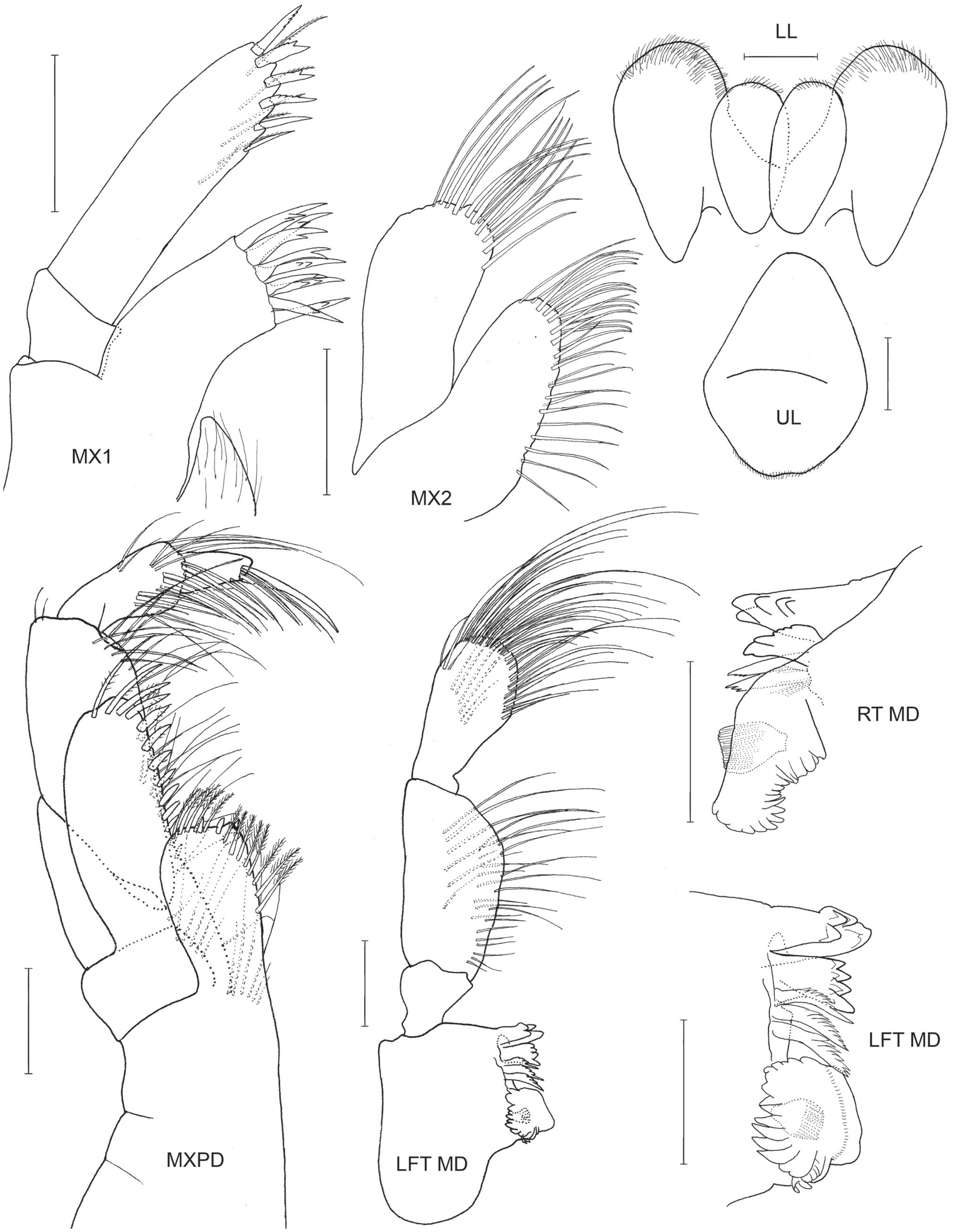

FIGURE 30. *Jassa morinoi* Conlan, 1990. Holotype, adult male, major form, 5.6 mm, NSMT-Cr 26015 (C-33-1-1). Bansho-no-hana Point, Tanabe Bay, Wakayama Prefecture, Japan (~33°42′N, 135°20′E), 17 March 1971, H. Morino, coll., low intertidal zone, on *Sargassum microcanthum*. Mouthparts. Frontal view: upper lip; other views medial. Scale 0.1 mm.

Remarks. *Jassa morinoi, J. valida* and *J. monodon* are unique among the species of *Jassa* in having a seta or group of setae at the tip of the telson which extend between the third uropods as a horizontal extension of the body. This apical seta or setae can be most easily seen when the third uropods are held downward. The apical setae should not be confused with the usual upright seta or setae that accompany each telson knob on each lateral edge in every species of *Jassa*. The three species can be told apart by the length (if present) or absence of the diagnostic seta or cluster of setae at the anterodistal junction of the carpus and propodus of gnathopod 1. This seta or setal cluster is slightly medial in *J. morinoi* and *J. valida* and absent in *J. monodon*. Care must be taken to twist the gnathopod 1 to check for this seta on the medial face of the propodus as it may lay flat against the propodus and therefore be obscured from view. This seta or setal cluster is long in *J. morinoi* (length as great as the width of the gnathopod 1 basis) but much shorter in *J. valida*, to the extent that it may not be visible at low magnification (length << the width of the gnathopod 1 basis).

Jassa morinoi can also be confused with *J. slatteryi* as both can co-occur in collections and both have the long seta(e) at the anterodistal junction of the carpus and propodus of gnathopod 1. The key character separating these species at any age or sex is the presence of the apical seta or setae on the telson in *J. morinoi* and absence in *J. slatteryi*.

Jassa morinoi has been found widely, dating as far back as 1885 in the Mediterranean Sea (Table 3). An illustration of two specimens of *Jassa* (named "*J. falcata*") by Ledoyer (1986), collected from Madagascar (Thomassin st. 270, microatolls of Sarodrano, 23°30′30″S, 43°44′00″E) and Thomassin st. 263, microatolls of Songoritelo, 23°14′S, 43°37′E) shows key features that suggest that the specimens are *J. morinoi* (telson tip with long setae, gnathopod 2 basis with sparse setae, male antenna 2 flagellum not plumose). However, the long seta(e) at the junction of carpus and propodus of gnathopod 1 is not shown or described, leaving the identification suggestive but not certain. *Jassa morinoi* is known from neighbouring South Africa.

The earliest collection record for *J. morinoi* on the coast of Pacific North America is 1909 near the (then) remote village of Ucluelet on British Columbia's exposed outer coast of Vancouver Island. It may be indigenous on the Pacific North American coast because it has been found frequently on exposed coasts away from harbours. For this study, it is known from 38 Pacific North American collections, ranging from Athlone Island, British Columbia (52°N) to Santa Catalina Island, California (33°N). Some "*J. slatteryi*" listed in Conlan (1990), from Pacific North America were found to be mis-identified and were actually *J. morinoi*. However, re-examination of the entire NMNS/CMN collection of "*J. slatteryi*" found that *J. slatteryi* does indeed occur on this coast and the two species can be found mixed together in aggregate collections. The re-examination of the NMNS/CMN collection also revealed that some of the major form males previously thought to be *J. slatteryi* were actually *J. morinoi*. Illustrations of some of these newly found major forms have been added to Fig. 28 along with the minor form male previously thought to be a major form in Conlan (1990). Therefore, like most of the other species of *Jassa*, the major form of *J. morinoi* can lose its palmar defining spines, although this does not always happen, as shown in Fig. 28.

A first discovery of "*J. morinoi*" in the southwestern Gulf of Mexico by Winfield *et al*. (2021) is questionable as it is more likely *J. valida* (Supplementary Data File S1). It is apparent from their identification criteria that they were not aware of the key character that separates the species (setal length at the anterodistal junction of carpus and propodus). Winfield *et al*. (2021) were also identifying relatively small specimens (3.03 ± 0.46 mm body length, $n = 3$) which may have been difficult to manipulate in order to view this seta. It was not possible to borrow the specimens to confirm the identification as the museum collections were closed due to the COVID-19 pandemic.

Specimens of *J. morinoi* noted in Conlan (1990) as lent by Dr. H. Morino, Ibaraki University, Japan, have been recently transferred to the National Museum of Nature and Science, Tsukuba, Japan. This includes the type specimens (Morino 2019).

Jassa valida (Dana, 1853)

(Table 10, Figs 31–36)

Cratophium validum Dana, 1853, pp. 841–843, plate 56, fig. 2

Podocerus validus (Dana, 1853): Bate (1862), p. 253, plate XLIII, fig. 9; Stebbing (1888), pp. 1135–1136, plate CXXXVIII. B; not *Jassa pulchella* Leach (1814): Stebbing (1906), p. 654

Jassa sp. A: LeCroy (2007), pp. 565, 567, fig. 486.

Jassa mendozai Winfield *et al*., 2021

Diagnosis.

Both sexes:

Mandibular palp: article 2, dorsal margin without a fringe of setae.

Maxilla 1: without a seta or setal cluster at the base of the palp article 1.

Gnathopod 1: basis, anterolateral margin with one distal and a few very short setae proximally; carpus with a single short, slightly medial seta at the anterodistal junction of the propodus (setal length <20% of the length of the anterior margin of the carpus).

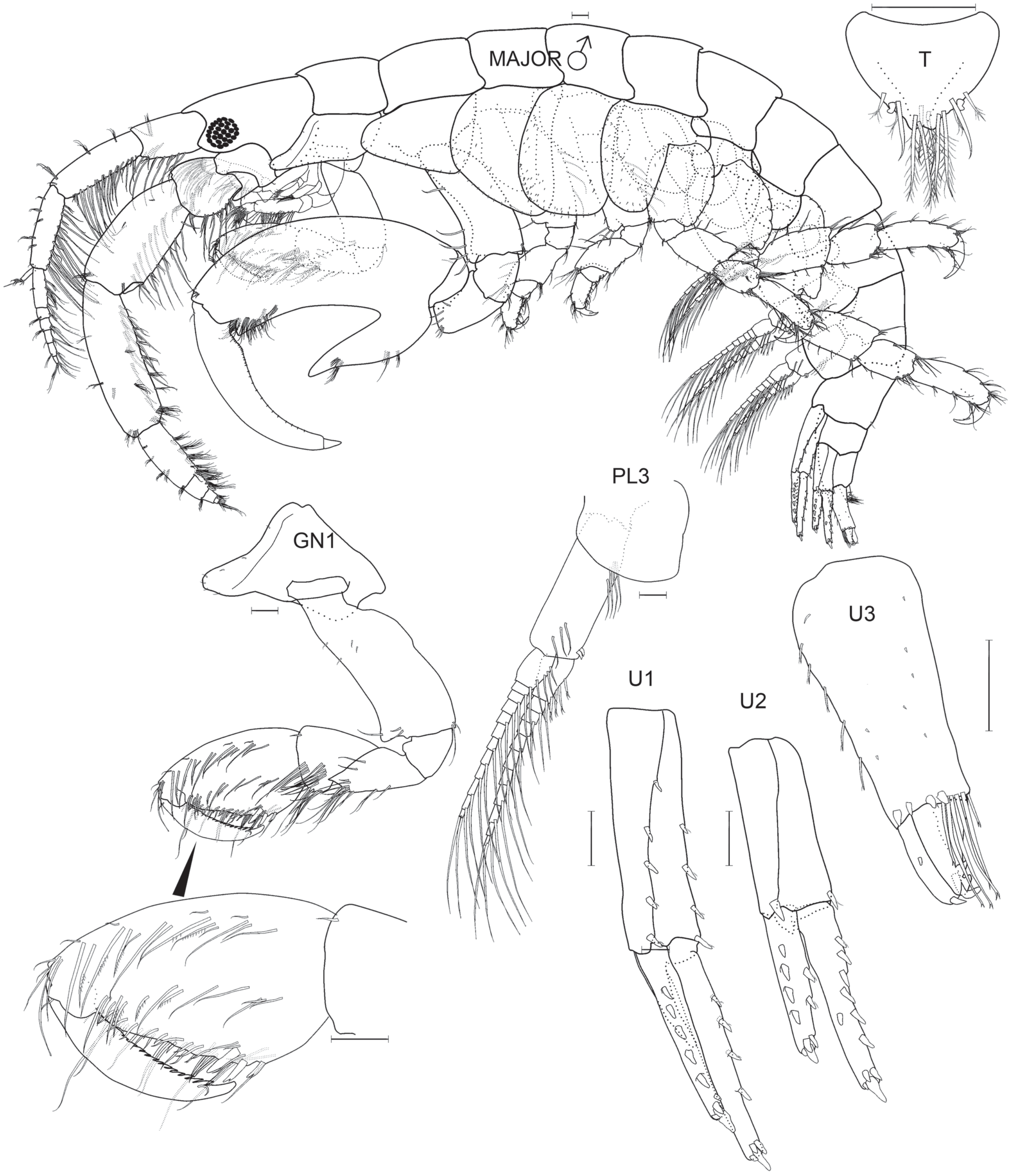

FIGURE 31. *Jassa valida* (Dana, 1853). Neotype, adult male, major form, 5.5 mm, JSIAH327. Babitonga, Brazil (26.239°S, 48.647°W), 5 Sept. 2017, A. Desiderato, coll., from settling plate, 1.5 m depth (MNRJcarcino 029820, accession no. BMFVF063-19). Lateral views: whole body, pleopod 3 and uropods; dorsal view: telson; medial view: gnathopod 1. Scale 0.1 mm.

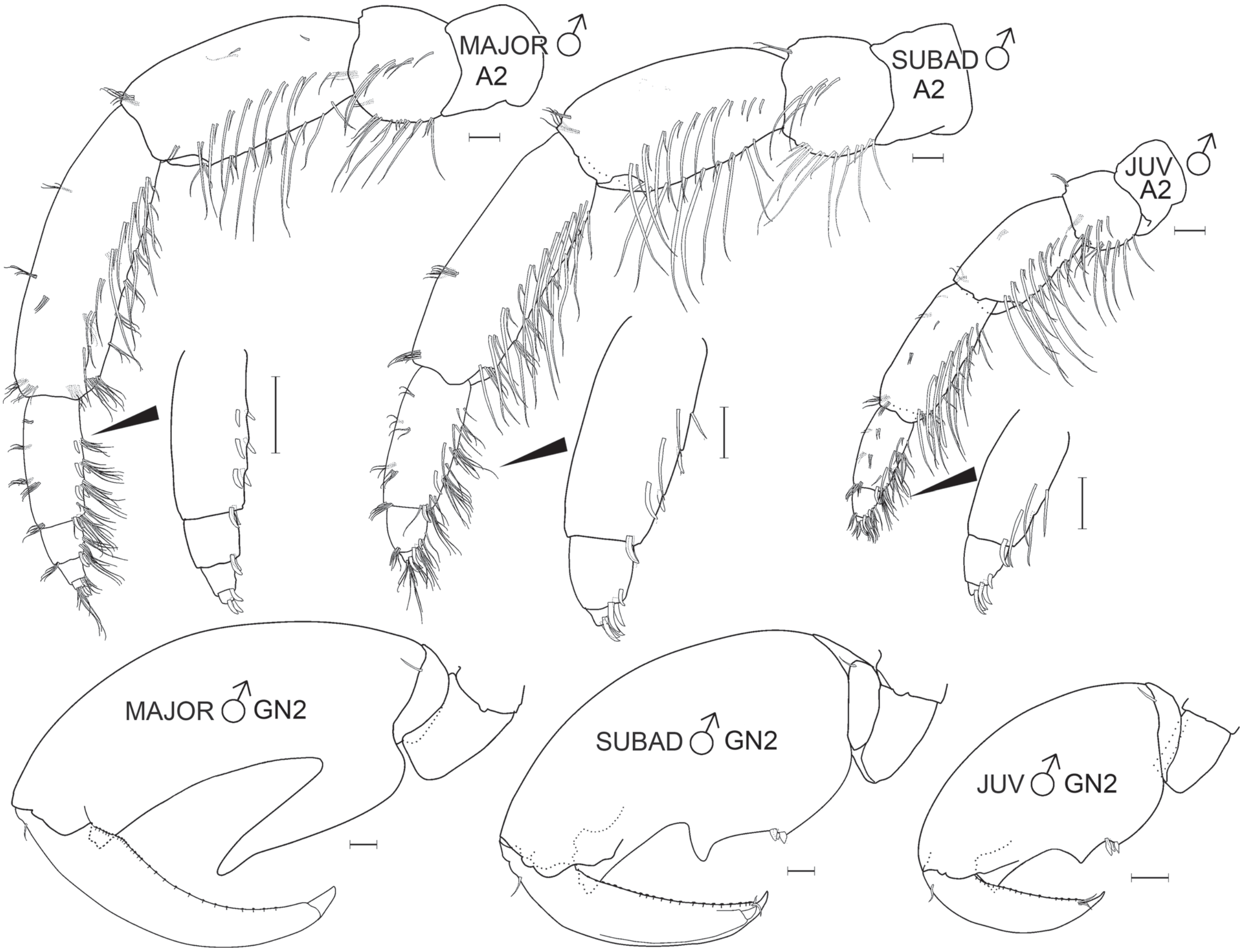

FIGURE 32. *Jassa valida* (Dana, 1853). Comparison of the antenna 2 and gnathopod 2 between the neotype, adult male, major form, 5.5 mm, JSIAH327 (MNRJcarcino 029820, accession no. BMFVF063-19), subadult male, 5.6 mm, JSIAH323 (ZUEC CRU 4342, accession no. BMFVF064-19) and juvenile male, 3.3 mm, JSIAH330 (ZUEC CRU 4341, accession no. BMFVF063-19), Babitonga, Brazil (26.239°S, 48.647°W), 5 Sept. 2017, A. Desiderato, coll., from settling plate. Setae on the enlargement of the antenna 2 flagellum omitted to show spination; setae of the gnathopod 2 propodus omitted to show palm shape. All views medial. Scale 0.1 mm.

Gnathopod 2: basis with a few setae along the anterolateral margin but without long filter setae (most setal lengths ≤ 40% of the basis width); carpus and propodus, setae on the anterior margin short and simple (setal length << basis width).

Pereopods 5–7: propodus not expanded anteriorly.

Uropod 1: ventral peduncular spinous process underlying about 1/2 of the longest ramus.

Uropod 3: inner ramus without spines mid-dorsally (with only the single apical spine).

Telson: tip with apical setae in addition to the usual short setae at each dorsolateral cusp.

Thumbed male:

Antenna 2: without plumose setae on the flagellum and peduncular article 5.

Gnathopod 2: propodus, palmar defining spines absent except in small males. Thumb distally acute in major and minor males. Dactyl expansion low, shallowly expanded proximally.

Adult female:

Antenna 2: without plumose setae on the flagellum and peduncular article 5.

Gnathopod 2: propodus, palm concave, palmar defining angle acute.

Description of the adult male, major form. Neotype (here designated). Length 5.5 mm.

Antenna 1: overlaps antenna 2 to about ½ peduncular article 5.

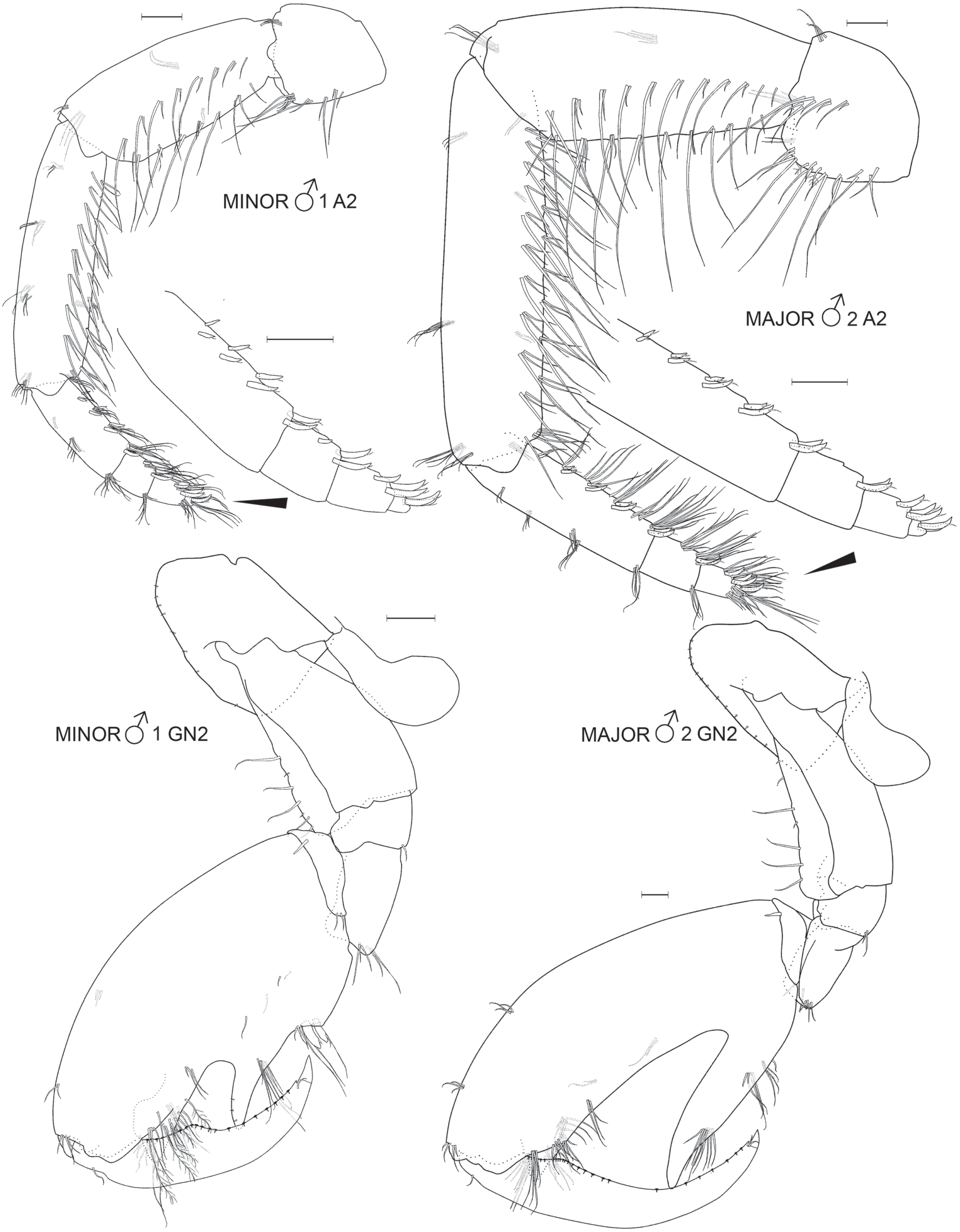

FIGURE 33. *Jassa valida* (Dana, 1853). Adult male 1, minor form, 3.5 mm and adult male 2, major form, 4.8 mm, Radio Island jetty, North Carolina, U.S.A., 6 April 1975, E. L. Bousfield, coll., station C12, IZ1975-93 (CMN). All views medial. Scale 0.1 mm.

Antenna 2: article 5, posterior margin bearing short setae, these shorter than in the juvenile; flagellum 4 articles, article 1 65% of full flagellum length, posterior margin with pairs of spines on each article, 4 pairs on article 1 and 1 pair for each article thereafter at the posterodistal junction with the following article.

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

Maxilla 1: palp without setae at based of article 1, article 2 with 1 row of facial setae.

Gnathopod 1: coxa strongly produced anterodistally, anterior margin 77% of dorsal length, ventral margin shallowly rippled; basis, anterior margin without a fringe of short, spine-like setae, posterior margin with 1 single cluster at junction of ischium; carpus, posterior lobe 37% of anterior margin length, with a single short seta medially at the anterodistal junction with the propodus; propodus, palm straight; dactyl cusped along most of posterior margin, without facial striations.

Gnathopod 2: coxal margins, anterior 39% and posterior 54% of ventral length, ventral margin straight; gill moderately large; basis, anterolateral flange with 5 widely spaced, relatively short setae (setal length ≤ 50% width of basis), palmar setae concentrated in hinge tooth area, thumb 39% of propodus length, distally acute, posterior margin shallowly concave, giving a conical appearance overall, defining setae closely approximated, not accompanied by spines; dactyl, inner margin shallowly expanded at the location of hinge tooth.

Pereopod 3: coxa, greatest depth posteriorly; basis, anterior margin shallowly concave; merus, anterior marginal setal clusters well separated, with 1 or 2 setae in middle clusters, setal length about 65% of article width; article width 60% of length; carpus fully overlapped by merus; propodus, width 55% of length.

Pereopod 4: coxa nearly rectangular, deeper than wide, ventrally convex; other articles as for pereopod 3.

Pereopods 5–7: propodus not expanded anteriorly, dactyl without fringe of setae along anterior margin, without facial striations.

Pleopods: with 2 peduncular coupling hooks.

Uropod 1: peduncle, posteroventral spinous process underlying 41% of inner ramus, inner and outer rami with 4 and 5 mid-dorsal spines, respectively, not terminating in a fringe of cusps ventral to apical spine group.

Uropod 2: peduncle, posteroventral spinous process underlying 15% of inner ramus.

Uropod 3: outer ramus with 2 sequential cusps proximal to the basally immersed, dorsally recurved spine and single seta originating at insertion of recurved spine; inner ramus with only single apical spine.

Telson: with 5 long, plumose setae at the apex in addition to the usual pair of short setae and single long seta at each lateral knob.

Condition. Without right antenna 1 and pereopods 5–7. Other right appendages, left antenna 1, pereopods 5–7 and uropod 3, telson and mouthparts slide mounted. Tip of right gnathopod 2 thumb and dactyl damaged, shapes drawn from the left gnathopod 2.

Description of the adult female. (Same location as for neotype, BBwB3). Length 3.6 mm. Character states as in the male except as follows.

Antenna 2: article 5, filter setae longer than in the neotype, as long and as dense as the filter setae on article 4.

Gnathopod 1: coxa, not as anteriorly produced as in the neotype, ventral margin relatively straight.

Gnathopod 2: coxal margins, anterior 51% and posterior 86% of ventral length, ventral margin straight; propodus, hinge tooth pronounced, palmar setae moderately dense throughout but not so dense as to obscure the palm's shape, palmar angle acute, distal, but close to defining spines; dactyl, inner margin slightly expanded at the hinge tooth, tip reaching the palmar defining spines.

Telson: with 2 apical setae.

Condition. Brood plates setose, ovigerous. Without right pereopods 5–7, part of left antenna 2 and left pereopods 6–7. Other right appendages, left pereopod 5 and uropod 3, telson and mouthparts slide mounted.

Variation. Females and juvenile and subadult males have long filter setae on the posterior margin of antenna 2 peduncle article 5 while these shorten in thumbed males. The spination of the flagellum also varies, increasing in number on the flagellum article 1 in thumbed males, with a pair of spines on each additional flagellum article. In females and juvenile males, flagellum article 1 has a single distal pair on this article, followed by single pairs on successive articles. Subadult and minor form males are intermediate between the juveniles and thumbed males with more pairs of spines on flagellum article 1 than juveniles but fewer than the major form thumbed male. Subadult males also show a "pre-thumb" on the second gnathopod propodus distal to the palmar defining spines at the location of the palmar defining angle in the juveniles. Major form thumbed males lose the defining spines while minor forms retain them. The dactyl is also centrally expanded into the palm in minor forms. The number of setae on the gnathopod 2 basis varies from 5–6 but they are always widely spaced. The bases of pereopods 3 and 4, which hold the tube spinning glands are expanded in the females and juveniles but more slender in the thumbed males. The uropod 3 outer ramus can have 3 cusps proximal to the dorsally recurved spine rather than the usual 2. The number of apical setae on the telson varies from 1 to 5.

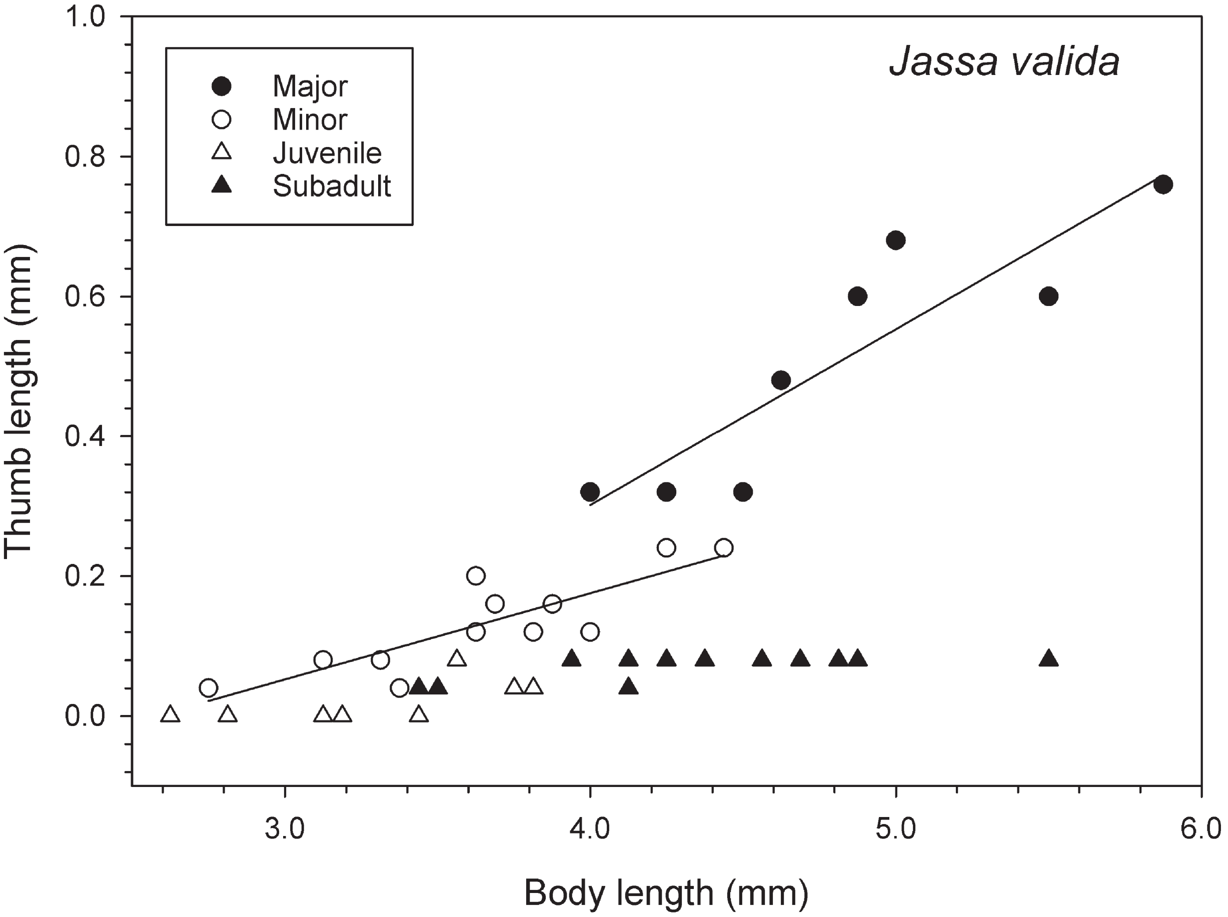

FIGURE 34. *Jassa valida* (Dana, 1853). Variation in thumb length relative to body length in a single population of males at Radio Island, Beaufort, North Carolina, 31 March 1975, McGovern, coll., IZ 1975-93 (CMN). Linear regression assumptions passed for the adult major form and minor form males. Linear regression statistics: Major form, thumb length = -0.704 + 0.252 body length, $r^2 = 0.802$, $n = 8$; minor form, thumb length = -0.317 + 0.123 body length, $r^2 = 0.713$, $n = 12$.

Type material. Neotype: major form male, JSIAH327, (Museu Nacional de Rio de Janeiro), catalogue no. MNRJcarcino 029820, accession no. BMFVF063-19, Brazil: Santa Catarina: Babitonga (26.239°S, 48.647°W), 5 Sept. 2017, from settling plate, 1.5 m depth, A. Desiderato, collector.

Adult female, 3.6 mm, BBwB3, (Museu Nacional de Rio de Janeiro), catalogue no. MNRJcarcino 029821, Babitonga, Brazil (26.239°S, 48.647°W), 5 Sept. 2017, from settling plate, 1.5 m depth, A. Desiderato, collector.

Juvenile male, 3.3 mm, JSIAH330, (Museu de Zoologia da Universidade Estadual de Campinas "Adão José Cardoso") catalogue no. ZUEC CRU 4341, accession no. BMFVF063-19, Babitonga, Brazil (26.239°S, 48.647°W), 5 Sept. 2017, from settling plate, 1.5 m depth, A. Desiderato, collector.

Subadult male, 5.6 mm, JSIAH323, (Museu de Zoologia da Universidade Estadual de Campinas "Adão José Cardoso") catalogue no. ZUEC CRU 4342, accession no. BMFVF064-19, Babitonga, Brazil (26.239°S, 48.647°W), 5 Sept. 2017, from settling plate, 1.5 m depth, A. Desiderato, collector.

Other material examined. 562 specimens from Brazil (Cananeia (25.008°S, 47.923°W and 25°02′S, 47°56′W), Babitonga (26.239°S, 48.647°W), Paranaguà (25.517°S, 48.501°W), Pontal do Sul (25.559°S, 48.341°W), Antonina (25.435°S, 48.705°W), Guaratuba (25.873°S, 48.579°W), Guaraqueçaba (25.435°S, 48.705°W), Sao Paulo region (23°48′S, 48°34′W), west of Chile (*Challenger* station 302 (42°43′S, 82°11′W)); Mississippi: Gulf coast; Florida: St. Andrews Bay, Panacea, Fort Myers, off Panama City, St. Augustine; Georgia: Jekyll I.; North Carolina: Beaufort, Radio I., Fort Macon, Morehead City (CMN, NHM, L. Pequegnat, Y. Wakabara).

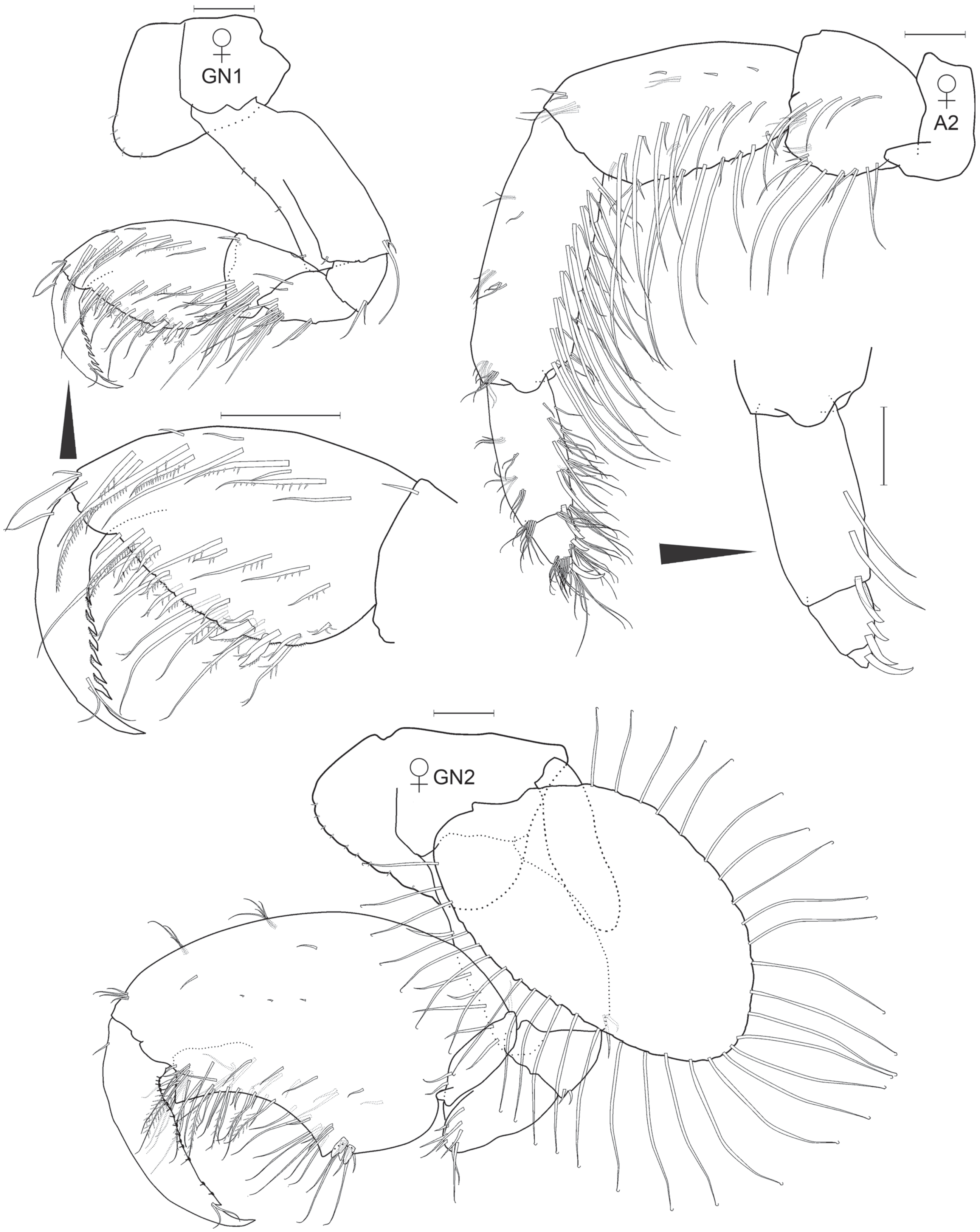

FIGURE 35. *Jassa valida* (Dana, 1853). Adult female, 3.6 mm, BBwB3, Babitonga, Brazil (26.239°S, 48.647°W), 5 Sept. 2017, A. Desiderato, coll., from settling plate (MNRJcarcino 029821). All views medial. Scale 0.1 mm.

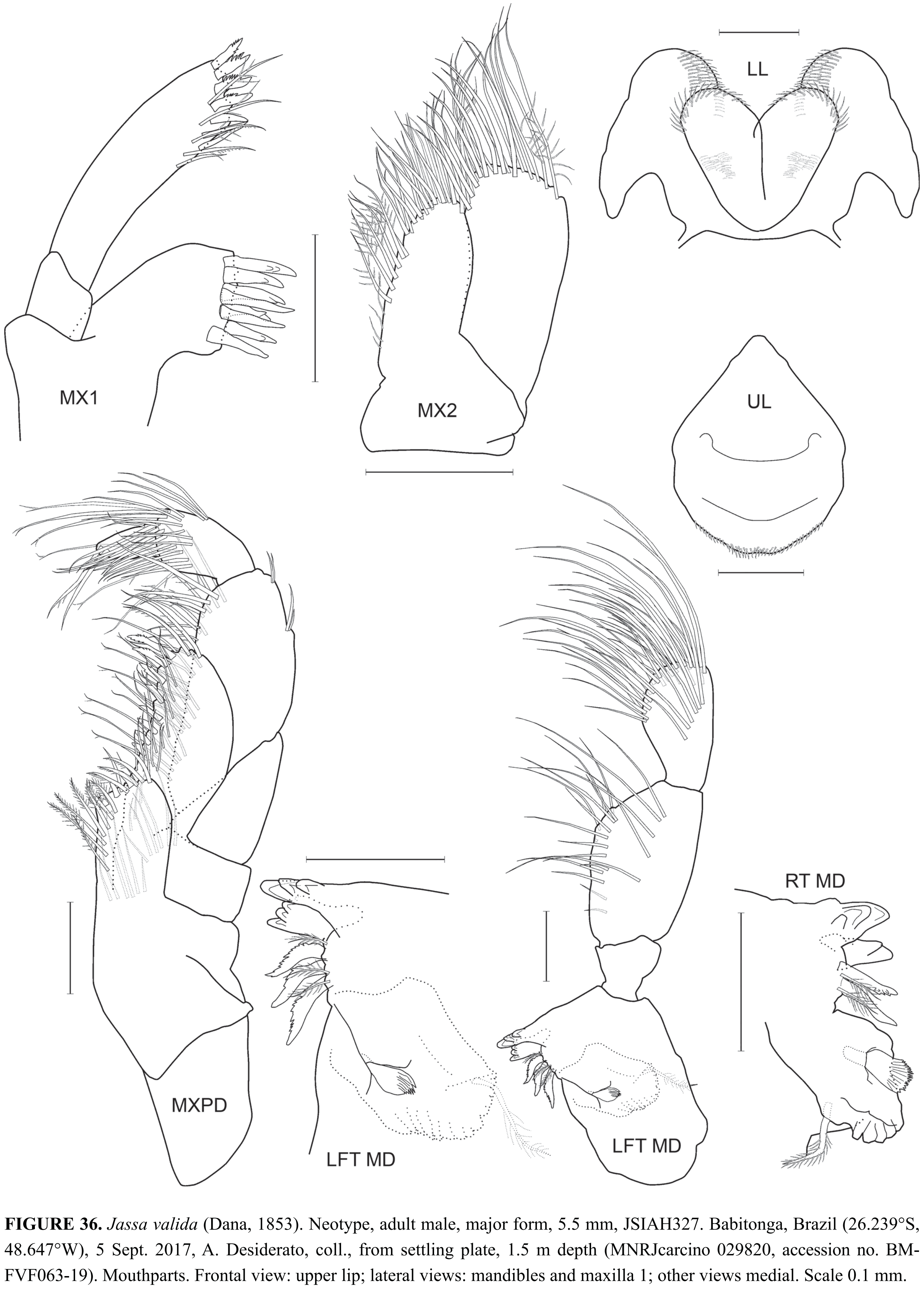

FIGURE 36. *Jassa valida* (Dana, 1853). Neotype, adult male, major form, 5.5 mm, JSIAH327. Babitonga, Brazil (26.239°S, 48.647°W), 5 Sept. 2017, A. Desiderato, coll., from settling plate, 1.5 m depth (MNRJcarcino 029820, accession no. BM-FVF063-19). Mouthparts. Frontal view: upper lip; lateral views: mandibles and maxilla 1; other views medial. Scale 0.1 mm.

Remarks. *Jassa valida* was first described from a dredge collection in the harbour of Rio de Janeiro, Brazil during the United States Exploring Expedition led by Charles Wilkes (1838–1842) (Fig. 7). Dana (1853) originally named it *Cratophium validum* but it was subsequently transferred to *Podocerus validus* and then synonymized with *Jassa pulchella* (now *J. falcata*) (Stebbing 1906). As noted in Conlan (1990), the type specimens have been lost (confirmed absent from the collection of the Smithsonian Institution, National Museum of Natural History, 13 May 2019 by Karen Reed, Museum Specialist, Department of Invertebrate Zoology).

Dana's (1853) illustrations of the adult male and female show three characteristics that, in combination, are unique to *J. valida*: apical telson setae, conical thumb and a short, medial seta at the anterodistal junction of carpus and propodus on gnathopod 1. *Jassa valida* shows the typical divergence of major and minor form thumbed males (Fig. 34) with the major forms having a much longer thumb than minors of the same body size but little overlap of the two in the population sampled. Subadult males with a thumbed cuticle visible inside the existing cuticle, had a small "pre-thumb".

Thomson (1883) recorded *J. valida* in the harbour of Rio de Janeiro living in "...great numbers hiding among the hairs which line the sutures on the thoracic sterna of the common cray-fish (*Palinurus*)...". Most of these were females. Stebbing (1888) illustrated an adult male specimen collected off the coast of Chile at the ocean surface during the *Challenger* Expedition (station 302, 42°43′S, 82°11′W, 28 Dec. 1875). He showed (and described) apical setae on the telson, widely spaced setae on the basis of gnathopod 2 and a conical thumb, all key characters of *J. valida*. Further examination of this specimen for this study showed that the diagnostic seta on the carpus of gnathopod 1 was short and medial, another key character that identifies *J. valida*. Although this Chilean location is far from the type locality of Rio de Janeiro, it is possible that the *Challenger* was colonized by *J. valida* while the ship was previously in port in Valparaiso in Nov. 1875. Prior to that, the *Challenger* had been in Japan. *Jassa valida* is not currently known from either of these locations, though. Stebbing (1888) further mentioned that another specimen, which also appeared to be this species had been collected at the ocean surface and labelled "Philippines, off Tablas". This specimen was not figured or described and since the identification is unclear, it has not been mapped. Its collection would have been around Nov. 1874 prior to the *Challenger* sailing northward to Hong Kong.

Specimens collected from settling plates at seven localities along the Brazilian coast in 2017 by one of us (AD) were found to be morphologically identical to *Jassa valida*. CO1 analysis further established them as being identical to a haplotype from Charleston Harbor, South Carolina, which was distinguished by Pilgrim and Darling (2010) as distinct from *J. marmorata*. This extended the known range of *J. valida* from Brazil to the U.S. Atlantic coast. Morphologically identical specimens illustrated by LeCroy (2007) as *Jassa* sp. A extended the North American range of *J. valida* into the northern Gulf of Mexico. A recent collection in the southwestern Gulf of Mexico by Winfield *et al.* (2021), and reported as a new species (*J. mendozai*) is unmistakeably *J. valida* (Supplementary Data File S1). Finally, morphological re-examination by one of us (KC) of 338 lots in the international collection of the Canadian Museum of Nature (CMN), comprising about 5,700 specimens of species that could co-occur with or be confused with *J. valida* (*J. marmorata, J. slatteryi* and *J. morinoi)* showed that it had been mis-identified by Conlan (1990) as *J. marmorata*. The re-examination showed that Atlantic North American collections from North Carolina to Florida and into the Gulf of Mexico were more likely to be *J. valida* than *J. marmorata*, although the latter could be found there infrequently (Fig. 8). The northerly range of *J. valida* ended at Beaufort, North Carolina; any specimens northwards, from Virginia to Newfoundland, were exclusively *J. marmorata* (Fig. 2). Therefore, records of "*J. marmorata*" in OBIS for South Carolina, Georgia, Florida and into the Gulf of Mexico should be considered to require confirmation as they may pertain to mis-identified *J. valida*. Collections in the Smithsonian Institution (NMNH) that were examined for Conlan (1990) were unfortunately not available for re-examination as this might have extended the range of *J. valida* into Cuba and the Bahamas. Where unpublished notes for Conlan (1990) described morphologies that are indicative of *J. valida*, these localities have been included in the maps and habitat data.

Records of "*J. marmorata*" in the four quadrants of the Gulf of Mexico by LeCroy *et al.* (2009) and Paz-Ríos & Ardisson (2013) (and also listed in OBIS) may pertain to *J. valida*, though their stated wide distribution is based on literature for the U.S. Gulf and Atlantic coasts, not Mexico. A mention of "*Jassa falcata*" collected from Laguna Madre, Mexico (western Gulf of Mexico) by Raz-Guzmán & Soto (2017) is possibly *J. valida*.

The *J. valida* collected by Winfield *et al.* (2021) from soft sediments at 456–3295 m depth in the southwestern Gulf of Mexico very possibly were not naturally at such great depth but were ship contaminants. No species of *Jassa* has been confirmed to exist at such great depth and *Jassa* is known to contaminate seawater systems in ships and aquaria (see the Distribution section for transhemispheric species). As a tube-liver on shallow-water solid substrates, *J.*

valida does not have the morphology for deep living, such as eye and coxal reduction, longer and slenderer pereopods and weaker sexual selection of the second gnathopod than in shallower species (Kodama & Kawamura 2019). A similar mis-interpretation of deep-sea collections by Kröncke (1994, 1998) is reported by Sirenko (2004). Although the authors stated that a filter, placed midway along the length of the ship's seawater system prevented individuals from reaching the sample sediments as they were sieved, this does not obviate the possibility that there was no pre-existing colony of *Jassa* living in the system. Inshore individuals could have accessed the ship's seawater system while the ship was docked and established colonies there long prior to the cruise. Small hatchlings could have passed through the intercepting filter, allowing for individuals to establish colonies beyond the filter. Small numbers of individuals (29 *J. valida* and reported as a new species, along with five reported as "*J. marmorata*" and three as *J. morinoi*" from 19 of 129 stations) could then have been dislodged over the 14 days of the cruise and been captured while the sediment samples were being sieved.

In South America, Alonso de Pina (2005) noted first records of *J. marmorata* on the coasts of Uruguay and Argentina but it has not been confirmed whether these were unrecognized *J. valida*. An effort to borrow these specimens was unsuccessful. In a comparative study of the amphipod fauna in *Sargassum* on two Itanhaém shores of Brazil, the "*J. falcata*" referred to by Wakabara *et al.* (1983) is likely *J. valida.* A specimen collected near Sao Paulo, Brazil for another study and lent by Y. Wakabara was *J. valida*. It has also been found with *J. slatteryi* in a scraping of the hull of a small ship in Brazil. Re-examination of CMN collections from the Pacific coasts of North and South America, Europe, Asia and Australasia did not yield *J. valida.* However, individuals sequenced from Durban, South Africa in 2019 (F. MacKay, coll.) and the French Frigate Shoals, northern Hawaiian Islands in 2007 (Plaisance *et al.* 2011a, b) that are identical haplotypes to Brazilian and U.S. specimens suggest that *J. valida* is more widespread than currently recognized.

Jassa valida has been found among algae on non-natural substrates such as buoys, pilings, jetties, settling plates and offshore fish cages as well as on natural substrates such as rocks and floating *Sargassum* (Table 4). These are typical habitats for any species of *Jassa*, but the CMN collections suggest that there can be habitat partitioning. On the Atlantic coast of North America, where its range overlaps with *J. marmorata* and *J. pusilla*, the three species may segregate by water mass (Table 4). While *J. valida* and *J. marmorata* can both be found in shallow subtidal waters, *J. pusilla* occurs substantially deeper. A site-specific colonization study offshore of Panama City, Florida by Pequegnat and Pequegnat (1968) yielded "*J. falcata*" on submerged buoys at an inshore location 3.2 km (2 mi) from the coast and an offshore location 17.7 km (11 mi) from the coast. Examination of specimens lent from this study yielded only *J. valida* inshore and only *J. marmorata* offshore. The inshore location is not bathed by cooler offshore bottom water that the offshore location receives. This suggests that despite the range overlap, the two species do not co-occur in the same water mass. *Jassa valida* has been found mixed with *J. marmorata* in only two of the CMN collections, both from North Carolina, which is the southern end of the range of *J. marmorata* (Fig. 2) and the northern end of the range of *J. valida* (Fig. 8).

Jassa valida is consistently recognizable from *J. marmorata* and *J. slatteryi* by having the terminal setae on the telson at any age and in both sexes (which *J. marmorata* and *J. slatteryi* always lack) (Table 10). *Jassa morinoi* and *J. monodon* also possess the terminal telson setae, but neither of these species have been found on the eastern coasts of North or South America. The presence, length and origin of the seta (or small cluster of setae) at the anterodistal junction of the gnathopod 1 carpus with the propodus is a useful character as it is present regardless of sex or age. In *J. valida* and *J. marmorata*, this seta (or small cluster of setae) is short, but differs in location. In *J. valida* it is slightly medial (Fig. 31) while in *J. marmorata*, it is slightly lateral (Fig. 15). In *J. slatteryi* and *J. morinoi* this seta is long (Figs 22 and 29) while in *J. monodon* this seta is absent. The shorter and less dense setation on the basis of gnathopod 2 distinguish *J. valida* from *J. marmorata* and *J. monodon*, though not *J. slatteryi* and *J. morinoi*. *Jassa valida* never develops plumose setae on the distal end of antenna 2 as it ages and the pointed apex of the terminal male's thumb distinguishes it from larger specimens of *J. marmorata*. The multiple spines on the antenna 2 of thumbed males of *J. valida* is distinctive although limited to this demographic. *Jassa marmorata* and *J. monodon* can achieve a greater size than *J. valida*, *J. slatteryi* and *J. morinoi* but summer specimens of *J. marmorata* can be as small so this is not a useful character trait. LeCroy (2007) also noted differences in living pigmentation between *J. valida* and *J. marmorata* but preservation can remove the pigmentation patterns.

North Atlantic and Mediterranean species

TABLE 11. Key character states of locally distributed North Atlantic species. Trans-hemispheric species (Table 10) may occur there as well. X indicates the presence of the first character state described while — indicates the alternative character state given in italics. S and L indicate length. ? indicates that the state is unknown. Character states apply to both sexes and juveniles unless indicated otherwise.

Character	*J. pusilla* (Figs 37-41)	*J. falcata* (Figs 42-47)	*J. herdmani* (Figs 48-53)	*J. laurieae* (Figs 54-55)	*J. monodon* (Figs 56-59)
Antenna 2, large subadult and thumbed male, posterior margin of article 5 and flagellum bearing plumose setae in addition to the usual finely pectinate filter setae (e.g., Fig. 42) *or without plumose setae* (e.g., Fig. 48)	—	X	—	X	—
Antenna 2, large subadult and adult female, posterior margin of article 5 and flagellum bearing plumose setae in addition to the usual finely pectinate filter setae (e.g., Fig. 15) *or without plumose setae* (e.g., Fig. 37)	—	X	—	?	?
Mandibular palp, margin of article 2 with a fringe of setae dorsally (e.g., Fig. 47) *or without a fringe* (e.g., Fig. 41)	—	X	X	—	—
Maxilla 1 with a seta or cluster of setae at the base of palp article 1 (Fig. 101) *or without seta(e)* (e.g., Fig. 36)	—	—	—	—	?
Gnathopod 1, basis, anterolateral margin with a fringe of spine-like setae (e.g., Fig. 95) *or without spine-like setae* (e.g., Fig. 31)	—	—	—	—	—
Gnathopod 1, carpus, with a seta or cluster of setae at the anterodistal junction of the propodus which may be slightly lateral or medial (e.g., Fig. 22) *or without seta(e)* (e.g., Fig. 37)	—	—	—	—	—
Gnathopod 1, carpus, seta(e) at the anterodistal junction of the propodus moderately long (L, length ≥25% of anterior margin length) (e.g., Fig. 22) or short (S, length <25% of anterior margin length) (e.g., Fig. 15) *or without seta(e)* (e.g., Fig. 37)	—	—	—	—	—
Gnathopod 2, basis with a fringe of setae on the anterolateral margin (e.g., Fig. 15) *or fringe absent (minute setae may be present but are too small to be described as an obvious fringe)* (e.g., Fig. 54)	—	—	—	—	X
Gnathopod 2, basis, if setal fringe present, setae relatively long (L, length ≥40% basis width) (Fig. 15) or short (S, length mostly <40% basis width) (e.g., Fig. 28) *or fringe absent (minute setae may be present but are too small to be described as an obvious fringe)* (e.g., Fig. 48)	—	—	—	—	S
Gnathopod 2, propodus, setae on the anteroproximal margin long (L, setal length ≥ maximal basis width) (Fig. 67) or short to absent (S, setal length < maximal basis width) (e.g., Figs 15, 42)	S	S	S	S	S
Gnathopod 2, propodus, setae on the anterior margin plumose (Fig. 62) *or simple* (e.g., 28)	—	—	—	—	—
Gnathopod 2, female propodus, palm concave, palmar angle pronounced (acute, right angled or bulbous) (e.g., Figs 44, 52) *or palmar angle shallow, giving the palm a sinuous appearance* (e.g., Fig. 100)	X	X[12]	X	?	?
Pereopods 5-7, propodus, anterior margin expanded for grasping (e.g., Fig. 95) *or not expanded for grasping* (e.g., Fig. 48)	—	—	—	—	—
Uropod 1, peduncular spinous process that extends ventrally from the peduncle and underlies the rami, moderately long (L, length = at least 25-50% the length of the longest ramus) (e.g., Fig. 42) or very short (S, length ≤10% of the length of the longest ramus, in which case it may not be visible) (e.g., Fig. 83)	L	L	L	?	L
Uropod 3, inner ramus with 1-2 mid-dorsal spines in addition to the usual spine at the tip (e.g., Fig. 42) *or without dorsal spines* (e.g., Fig. 48)	—	X	—	?	—
Telson, tip with a seta or cluster of setae extending between the third uropods (in addition to the usual upright setae at each side) (e.g., Fig. 31) *or without setae at the tip*[13] (e.g., Fig. 22)	—	—	—	?	X

...continued on the next page

TABLE 11. (Continued)

Character	*J. pusilla* (Figs 37-41)	*J. falcata* (Figs 42-47)	*J. herdmani* (Figs 48-52)	*J. laurieae* (Figs 54-55)	*J. monodon* (Figs 56-59)

[12] Female *J. falcata*: the palmar angle may appear more distant from the defining spines (Fig. 44) than in most other North Atlantic species but the palm is still more concave than in species that have sinuous palms (e.g., Fig. 93)

[13] These setae are visible when the animal is on its side, the abdomen is grasped with forceps in one hand, and the third uropods are depressed downwards with a fine needle in the other hand. This brings the telson into view.

Jassa pusilla (Sars, 1894)

(Table 11, Figs 37–41)

Synonyms: see Conlan (1990).

Diagnosis.

Both sexes:

Mandibular palp: article 2, dorsal margin without a fringe of setae.

Maxilla 1: without a seta or setal cluster at the base of the palp article 1.

Gnathopod 1: basis, anterolateral margin with a few very short setae; carpus without a single or small cluster of setae at the anterodistal junction of the propodus.

Gnathopod 2: basis with a few minute setae along the anterolateral margin but without long filter setae (most setal lengths <10% of the basis width); carpus and propodus, setae on the anterior margin short and simple (setal length < basis width).

Pereopods 5–7: propodus not expanded anteriorly.

Uropod 1: ventral peduncular spinous process underlying about 1/4 of the longest ramus.

Uropod 3: inner ramus without spines mid-dorsally (with only the single apical spine).

Telson: tip without apical setae, only the usual short setae at each dorsolateral cusp.

Thumbed male:

Antenna 2: without plumose setae on the flagellum and peduncular article 5.

Gnathopod 2: propodus, palmar defining spines absent except in small males. Thumb distally acute or squared in minor males and indented in major males. Dactyl expansion variable, centrally toothed or shallowly expanded proximally.

Adult female:

Antenna 2: without plumose setae on the flagellum and peduncular article 5.

Gnathopod 2: propodus, palm concave, palmar defining angle acute.

Remarks. The shape of the male second gnathopod is highly variable but Fig. 39 shows how shapes can grade within a series, this being a single collection made by G. O. Sars from Risör, Norway. Juvenile males that approach the size of the thumbed males have pre-thumbs that are small relative to minor and major forms (Figs 39A, B and 40). The pre-thumb is located in the distal half of the palm. Those juveniles that are about to molt into a thumbed stage (showing a thumbed cuticle under the juvenile cuticle) are termed subadult in Fig. 40. These have small pre-thumbs as well. Minor forms are interpreted as being those that have thumbs that are also in the distal half of the palm (as in minor forms of other species) but that have a larger and longer thumb and never show a thumbed cuticle inside (i.e., will not molt again) (Figs 38 and 39C–E). Minor forms also have centrally toothed dactyls (Figs 39C–E). Major form males have longer thumbs that are apically indented at the tip. Their thumbs originate in the proximal half of the propodus (Figs 38 and 39F–J). The dactyl expansion is shallow and proximal in most major forms (Fig. 39J) but is centrally toothed in some (Fig. 39G). Sars originally named the major form *Podocerus pusillus* and the minor form *Podocerus odontonyx* (Fig. 38) (see Conlan 1990). Fig. 39B is interpreted as being juvenile because no thumbed cuticle was visible internally, its pre-thumb is short relative to body length (Fig. 40) and its dactyl is not centrally toothed as in the minor forms (Figs 39C–E). None of the specimens termed juvenile and subadult in Fig. 40 had centrally toothed dactyls.

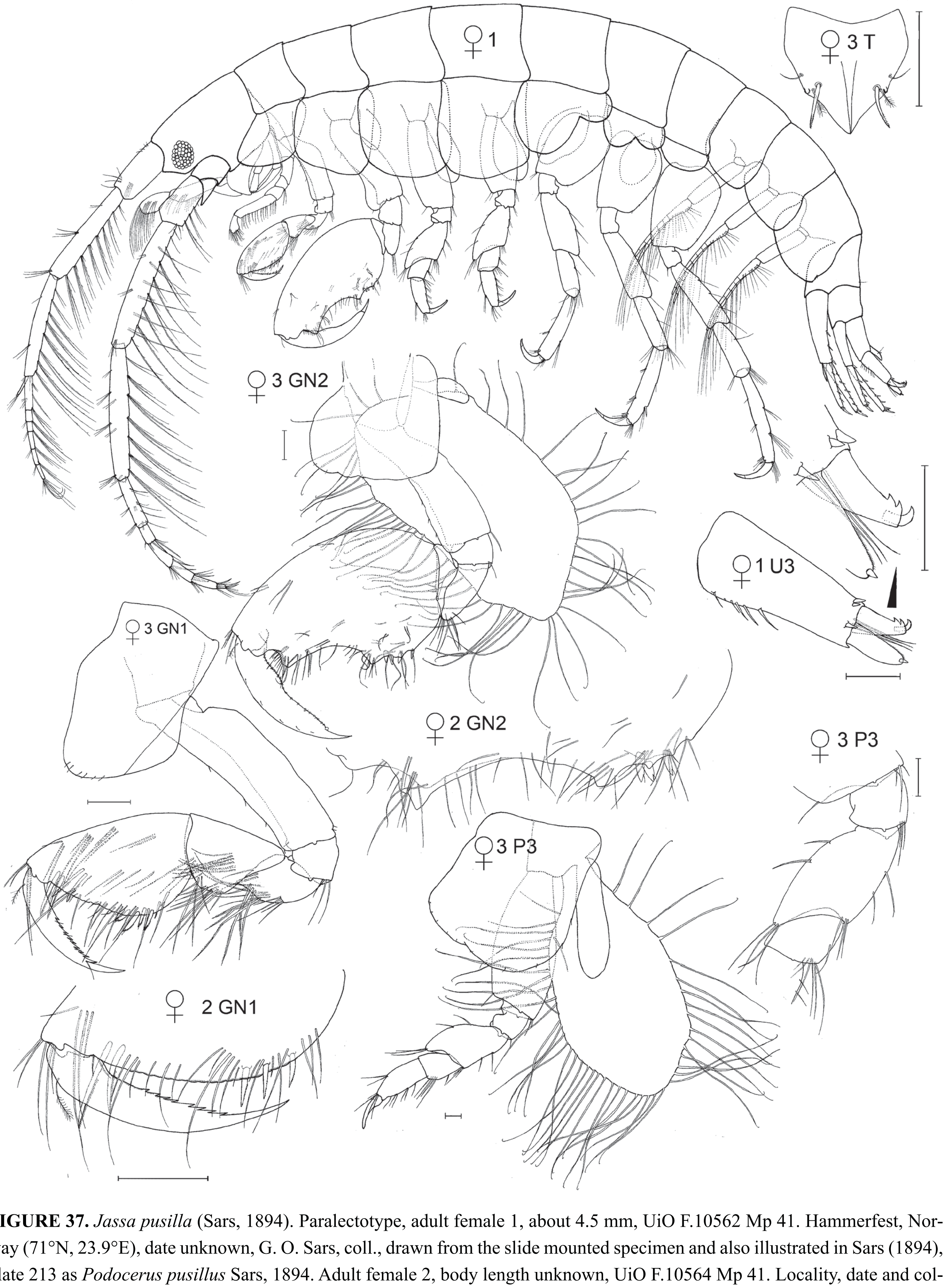

FIGURE 37. *Jassa pusilla* (Sars, 1894). Paralectotype, adult female 1, about 4.5 mm, UiO F.10562 Mp 41. Hammerfest, Norway (71°N, 23.9°E), date unknown, G. O. Sars, coll., drawn from the slide mounted specimen and also illustrated in Sars (1894), plate 213 as *Podocerus pusillus* Sars, 1894. Adult female 2, body length unknown, UiO F.10564 Mp 41. Locality, date and collector unknown, illustrated in Sars (1894), plate 213 as *Podocerus pusillus* Sars, 1894. Adult female 3, 4.7 mm, UiO F.13359. Risör, Norway (approx. 59°N, 9°E), date unknown, G. O. Sars, coll. Lateral view: whole body, gnathopods 1 and 2 and pereopod 3; dorsal view: telson; medial view: uropod 3. Scale 0.1 mm. Illustration after Conlan (1990).

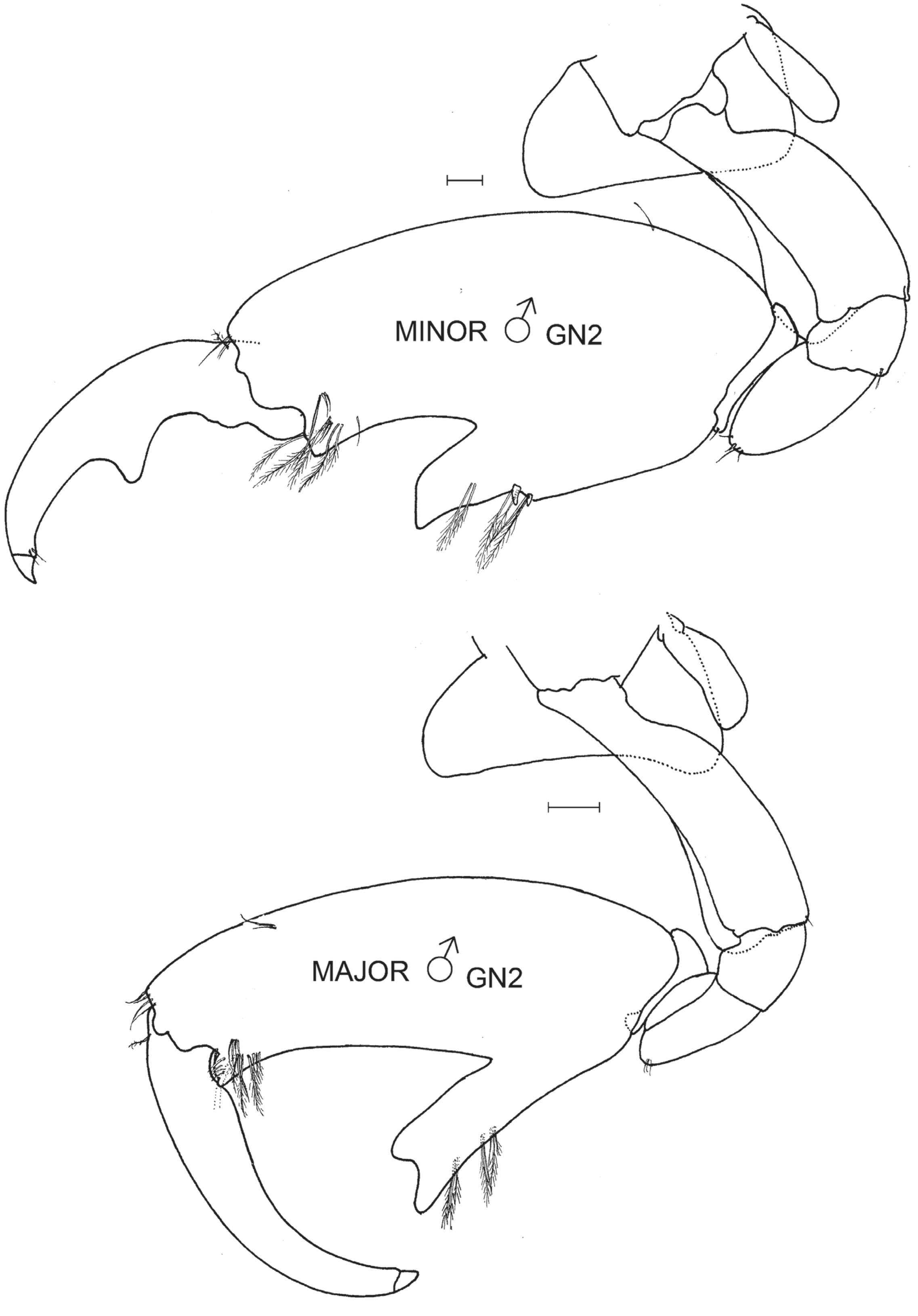

FIGURE 38. *Jassa pusilla* (Sars, 1894). Adult male gnathopod 2, minor form, body length unknown, UiO F. 10565 Mp 41. Same location and collector, drawn from the slide mounted specimen and also illustrated in Sars (1894), plate 213 (lectotype of *Podocerus odontonyx* Sars, 1894, submerged by Conlan (1990)). Adult male gnathopod 2, major form, body length unknown, UiO F. 10563 Mp 41. Hammerfest, Norway (71°N, 23.9°E), date unknown, G. O. Sars, coll., drawn from the slide mounted specimen and also illustrated in Sars (1894), plate 213 (lectotype of *Podocerus pusillus* Sars, 1894, transferred to *Jassa pusilla* by Stebbing, 1906). Medial views. Scale 0.1 mm.

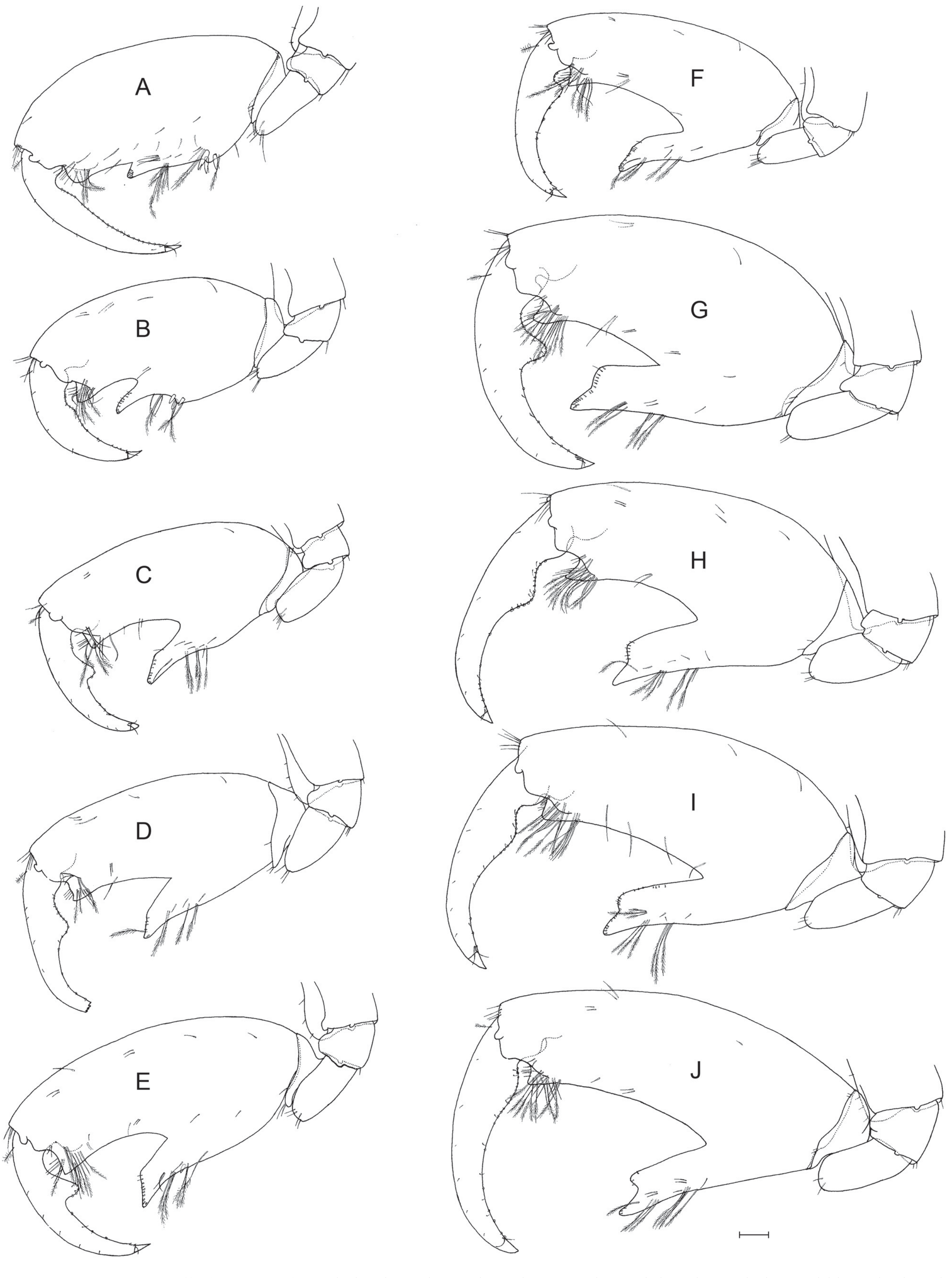

FIGURE 39. *Jassa pusilla* (Sars, 1894). Variation in male gnathopod 2 propodus and dactyl morphology within a single collection made by G. O. Sars at Risör, Norway (~ 59°N, 9°E), date unknown, G. O. Sars, coll., UiO F. 13359. Body and thumb lengths of each specimen are shown in **FIGURE 40.** All views medial. Scale 0.1 mm.

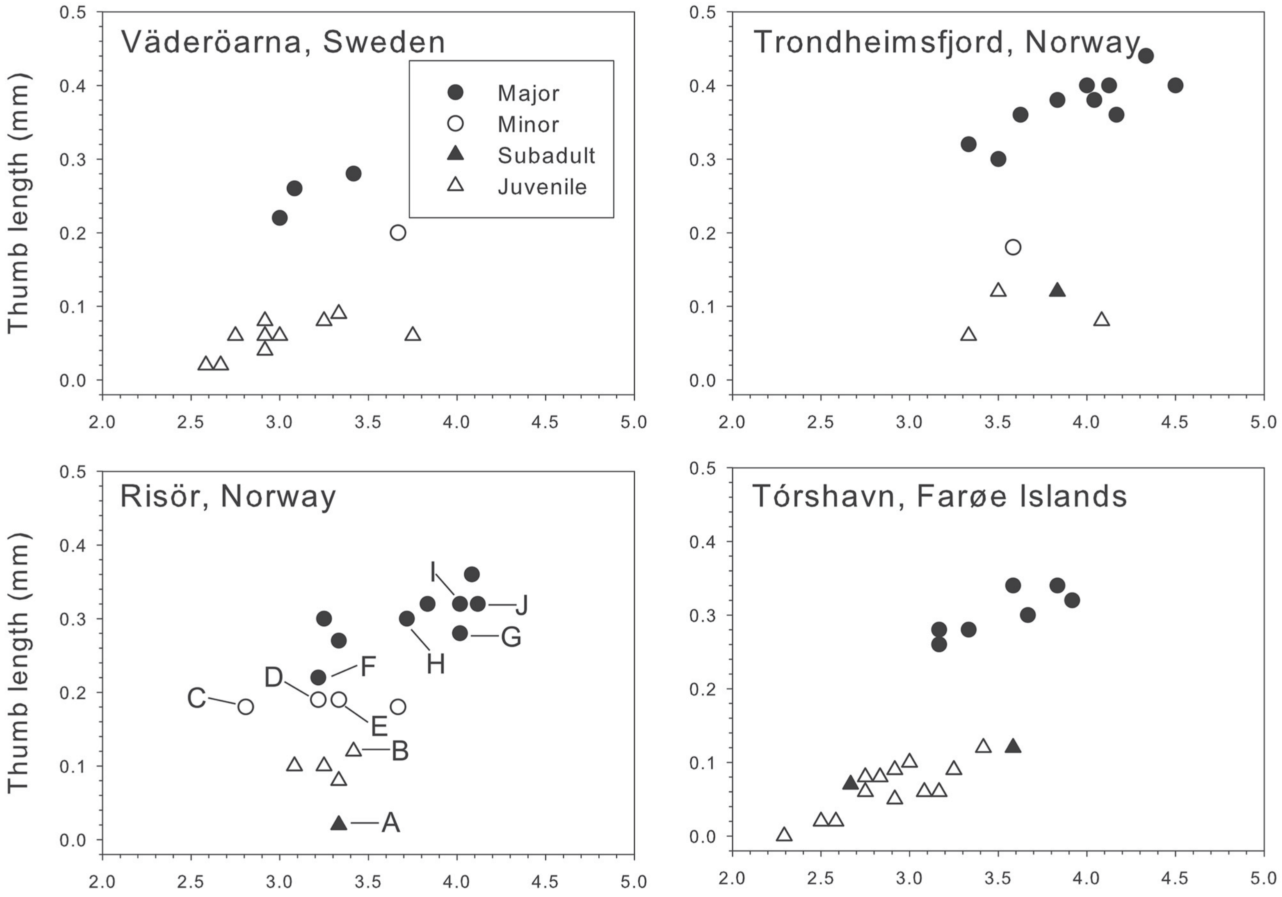

FIGURE 40. *Jassa pusilla* (Sars, 1894). Variation in male gnathopod 2 propodus length relative to body length in four populations. Väderöarna, Sweden (~ 58.57°N, 11.06°E), NRM 5427. Trondheimsfjord, Norway (~ 63.43°N, 10.39°E), date unknown, G. O. Sars, coll, UiO F. 13352. Risör, Norway (~ 59°N, 9°E), date unknown, G. O. Sars, coll., UiO F. 13359. Tórshavn, Farøe Islands (60°55′N, 8°56′W) station 69L.9,33, Michael Pars^n Sd. Jenson (UiO). Letters on the Risör graph pertain to the illustrations in **FIGURE** 39. Linear regression assumptions failed for all plots.

Four populations sampled in Väderöarna, Sweden, Trondheimsfjord, Norway, Risör, Norway and Tórshavn, Farøe Islands showed a similar relationship between thumb length and body length, with the juveniles having pre-thumbs and the minor forms being rare (Fig. 40). *Jassa pusilla* is a small species, with the minor forms 2.8–3.8 mm in body length and the major forms 3.0–4.5 mm in these four populations.

The record of *J. pusilla* from samples along the coast of Portugal by Lobo *et al.* (2017) is in error, and is the new species *J. laurieae*. The three collections of *J. pusilla* from deep water offshore of the Atlantic U.S. coast (NMNH 6335, 33530, and 106781) (Fig. 9) morphologically resembled this species, not either of the other two species from this coast (*J. valida* and *J. marmorata*), which occur shallower. *Jassa pusilla* is a smaller species with delicate, never plumose antennae, lacking the typical long setae along the basis of gnathopod 2 that the other two possess, and also lacking the diagnostic antero-medial seta on the gnathopod 1 carpus at the junction of the propodus. The minor form thumbed male of *Jassa pusilla* has a strong tooth on the inner margin of the dactyl, which the minor forms of the other two species lack. One of the specimens from NMNH 6335 was a 3 mm long minor form thumbed male with a strong tooth on the dactyl, its propodus closely resembling that in Figs 38 and 39E. Another thumbed male (NMNH 33530) closely resembled Fig. 39B. The other specimens were female or juvenile. These three collections are the only ones known from the western North Atlantic.

FIGURE 41. *Jassa pusilla* (Sars, 1894). Adult female 3 from FIGURE 37, 4.7 mm,, UiO F.13359. Risör, Norway (~ 59°N, 9°E), date unknown, G. O. Sars, coll. Mouthparts. Frontal view: upper lip; lateral views: maxilla 1 and right and left mandibles; other views medial. Scale 0.1 mm.

Jassa falcata (Montagu, 1808)

(Table 11, Figs 42–47)

Synonyms: see Conlan (1990).

Diagnosis.

Both sexes:

Mandibular palp: article 2, dorsal margin with a fringe of setae.

Maxilla 1: without a seta or setal cluster at the base of the palp article 1.

Gnathopod 1: basis, anterolateral margin with a few very short setae; carpus without a single or small cluster of setae at the anterodistal junction of the propodus.

Gnathopod 2: basis with a few minute setae along the anterolateral margin but without long filter setae (setal lengths <20% of the basis width); carpus and propodus, setae on the anterior margin short and simple (setal length < basis width).

Pereopods 5–7: propodus not expanded anteriorly.

Uropod 1: ventral peduncular spinous process underlying about 1/2 of the longest ramus.

Uropod 3: inner ramus with 1–2 spines mid-dorsally in addition to the usual single apical spine.

Telson: tip without apical setae, only the usual short setae at each dorsolateral cusp.

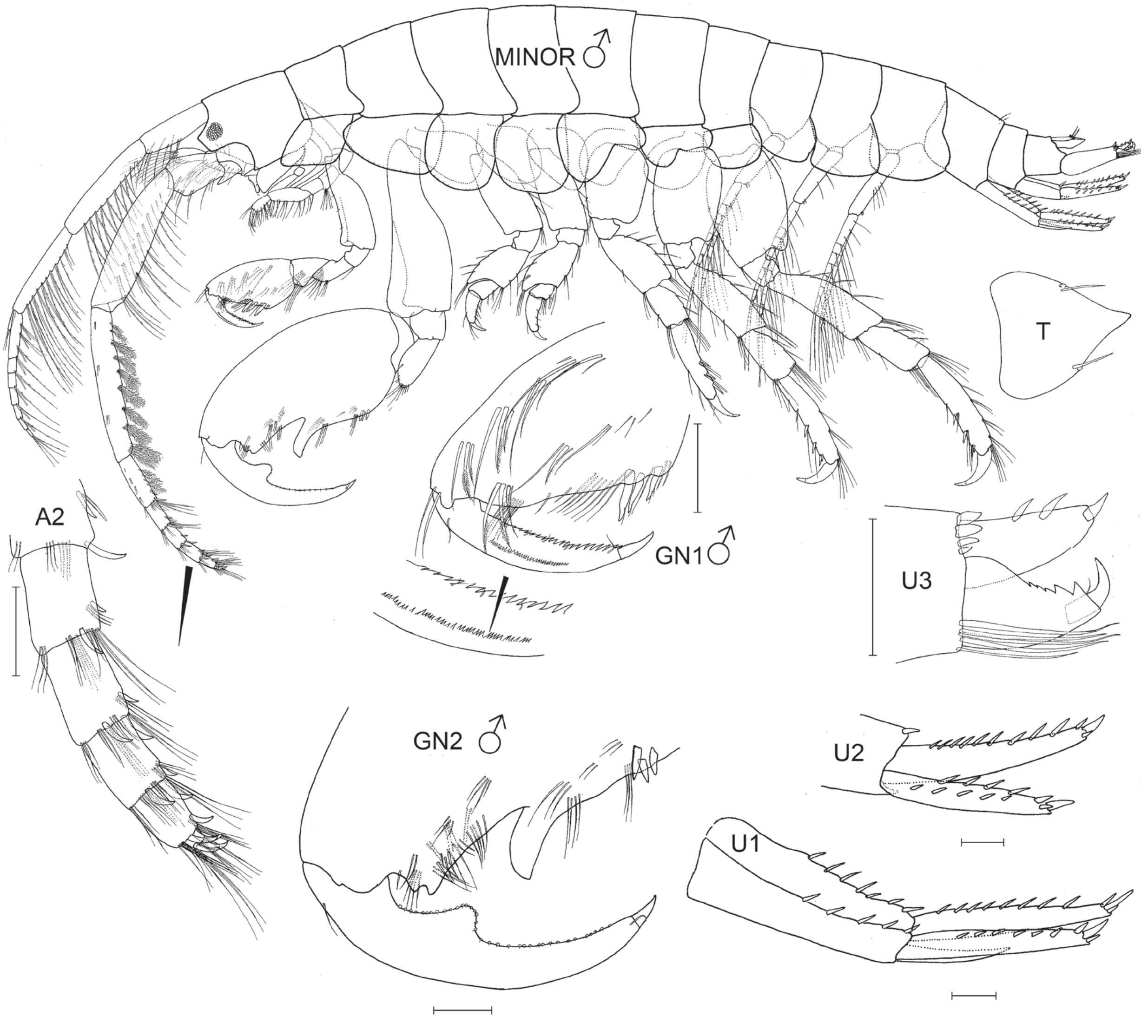

FIGURE 42. *Jassa falcata* (Montagu, 1808), type species for the genus *Jassa*. Holotype, adult male, minor form, 6.3 mm. Torcross, South Devon, England, date unknown, collector unknown, NHM 603a. Lateral views: whole body and right uropods 1-3; dorsal view: telson; other views medial. Scale 0.1 mm. Illustration after Conlan (1990).

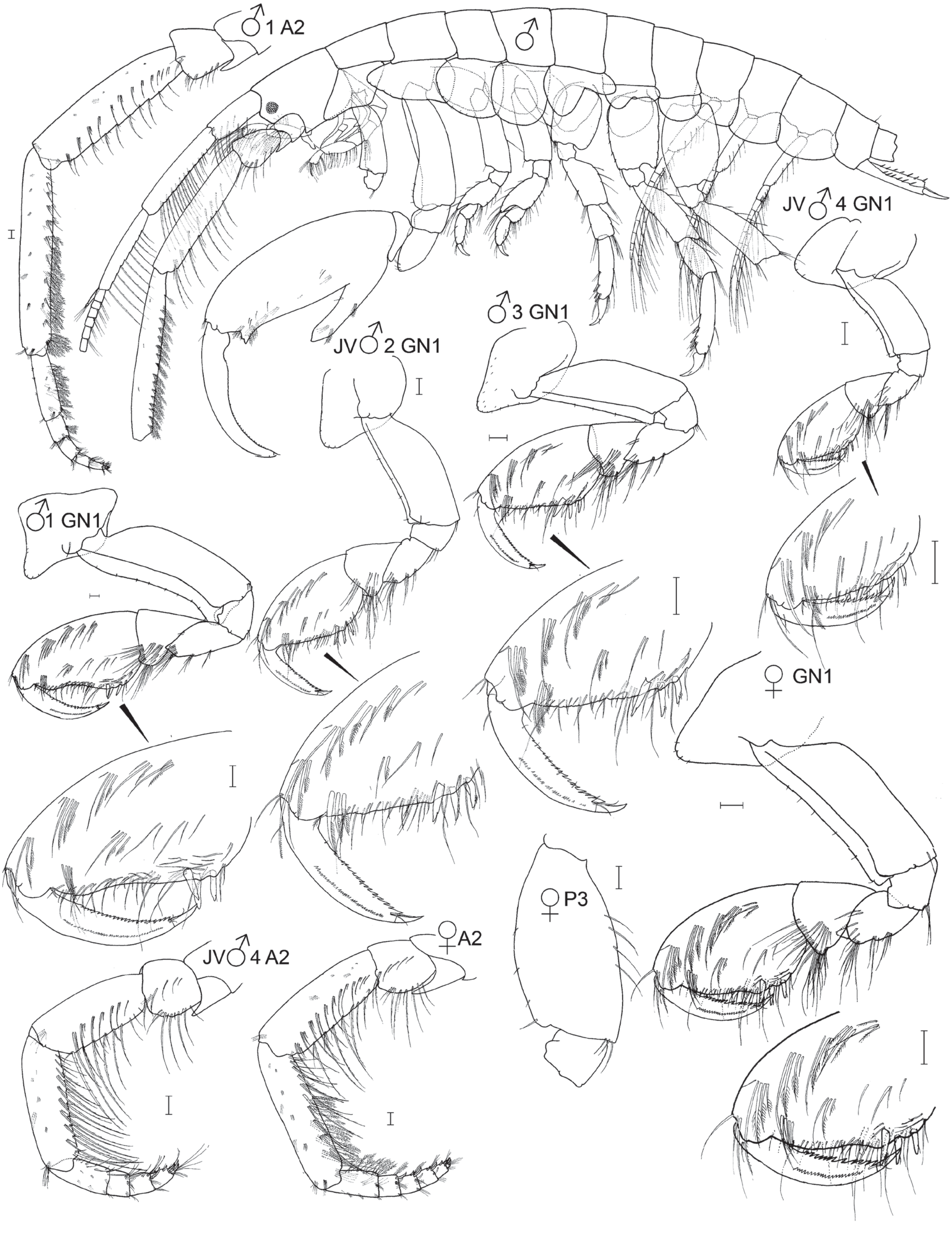

FIGURE 43. *Jassa falcata* (Montagu, 1808). Adult male, major form, 5.7 mm, lectotype for the series 296a-296g of *Jassa pulchella* Leach, 1814. Devon, England, date unknown, collector unknown, NHM 296e. The tip of the thumb on gnathopod 2 was probably damaged while the animal was alive; other damage was probably incurred while it was dry mounted. Adult male 1, major form, 11.0 mm; juvenile male 2, 7.0 mm; adult male 3, major form, 6.5 mm; juvenile male 4, 4.5 mm; and adult female, 7.0 mm. Stoer Bay, Sutherland, Scotland, 22 October 1937, D. M. Reid, coll., very abundant on the floats of coastal salmon nets (SNM). Lateral view: whole body; other views medial. Appendages are of the lectotype unless indicated otherwise. Scale 0.1 mm. Illustration after Conlan (1990).

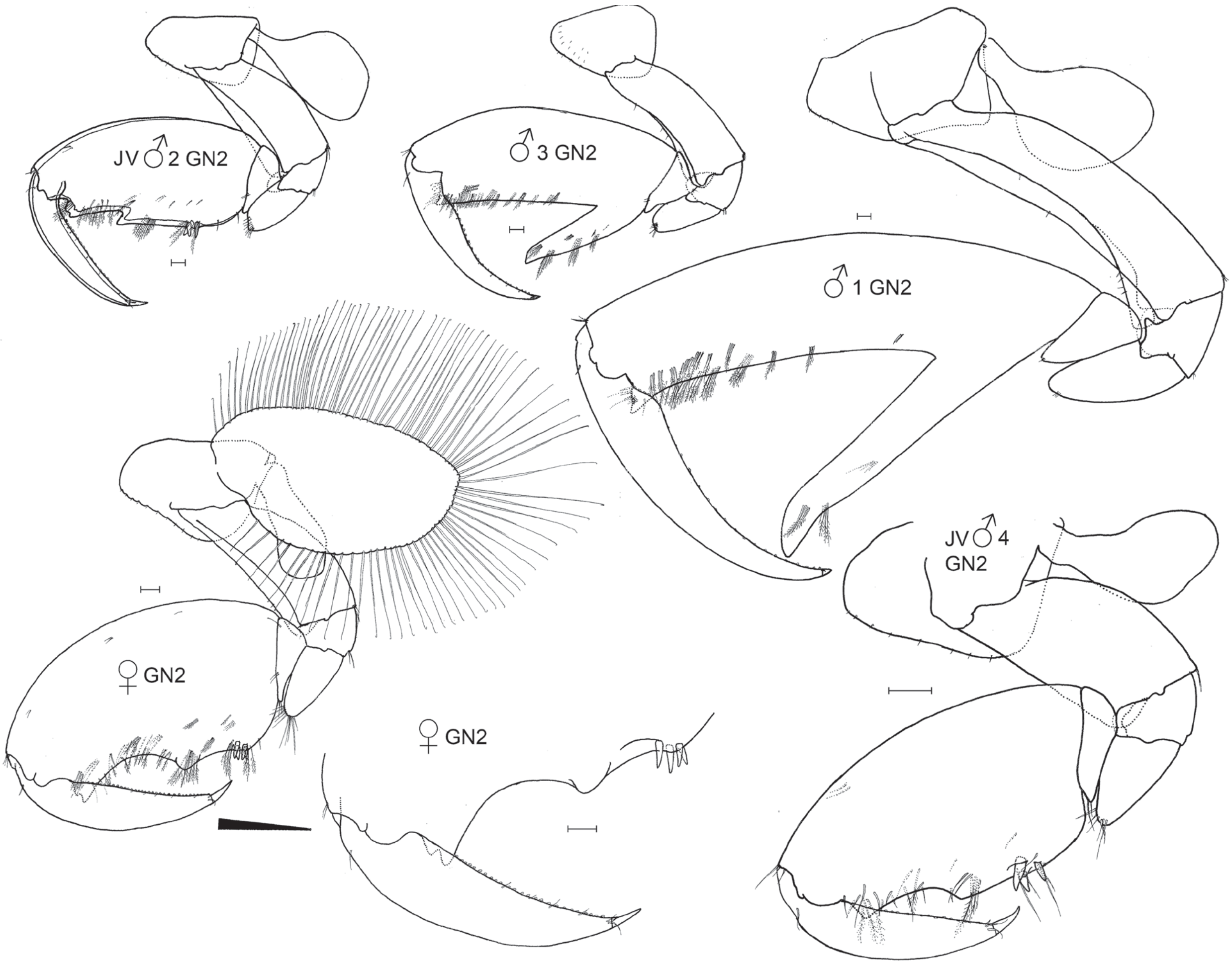

FIGURE 44. *Jassa falcata* (Montagu, 1808). Adult male 1, major form, 11.0 mm; juvenile male 2, 7.0 mm; adult male 3, major form, 6.5 mm; juvenile male 4, 4.5 mm; and adult female, 7.0 mm. Stoer Bay, Sutherland, Scotland, 22 October 1937, D. M. Reid, coll., very abundant on the floats of coastal salmon nets (SNM). Developing new cuticle is visible inside the propodus and dactyl of the juvenile male 2 gnathopod 2, not yet at the terminal molt as the new cuticle lacks a thumb. All views medial. Scale 0.1 mm.

Thumbed male:

Antenna 2: with plumose setae on the flagellum and peduncular article 5.

Gnathopod 2: propodus, palmar defining spines absent except in small males. Thumb distally acute or squared in minor males and squared in major males. Dactyl centrally toothed in minor forms and shallowly expanded proximally in major forms.

Adult female:

Antenna 2: with plumose setae on the flagellum and peduncular article 5.

Gnathopod 2: propodus, palm concave, palmar defining angle bulbous, distal to and fairly distant from the defining spines.

The basis of pereopod 3, which holds the tube spinning gland, was also measured as the width appeared to be greater in the females and juvenile males than in the adult males (Fig. 46b). Basis width was measured at the widest part of the basis which tended to be in the central part. The same individuals as for Gn2 propodus length were measured, with the addition of 6 additional adult males for which propodus length was lacking. Fig. 46b suggests that basis width was greater in the females and juvenile males (which included one subadult male) than in the adult males. Pairwise comparisons by Dunn's Method showed a significant difference between major form adult males ($n = 20$) and juvenile males ($n = 8$) ($Q = 2.905$, $p<0.05$). Differences of adult females from both adult and juvenile males were not significant ($Q = 1.913$ and 0.454, respectively), although Fig. 46b suggests a transitional difference.

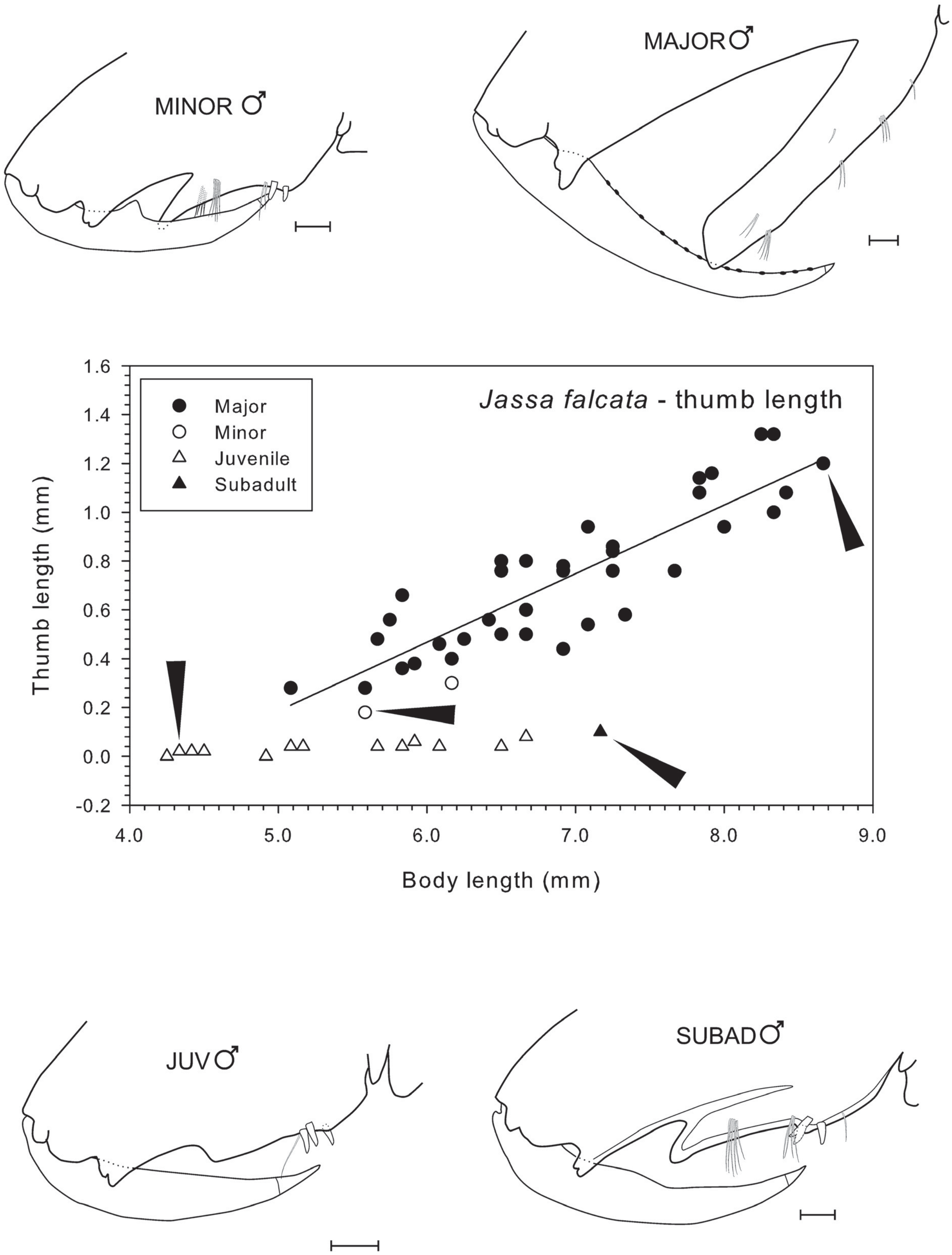

FIGURE 45. *Jassa falcata* (Montagu, 1808). Variation in thumb length relative to body length in males in a single collection at Audrassalas, Pas-de-Calais, France, 1 July 1985, K. E. Conlan, coll., in tubes and and actively walking over *Ceramium rubrum* (mainly) and *Polysiphonia*, even though out of contact with seawater at low tide, IZ 1985-093 (CMN). Arrows refer to the associated gnathopod illustrations. The subadult male had a thumb visible inside the cuticle, indicating that it would molt next into a thumbed adult. Setae omitted except for those around the thumb and spines in order to landmark position changes with growth. All views lateral. Scale 0.1 mm. Linear regression assumptions passed for the adult major form male. Linear regression statistics: Major form, thumb length = -1.219 + 0.281 body length, $r^2 = 0.773$, $n = 38$. Illustration after Conlan (1990).

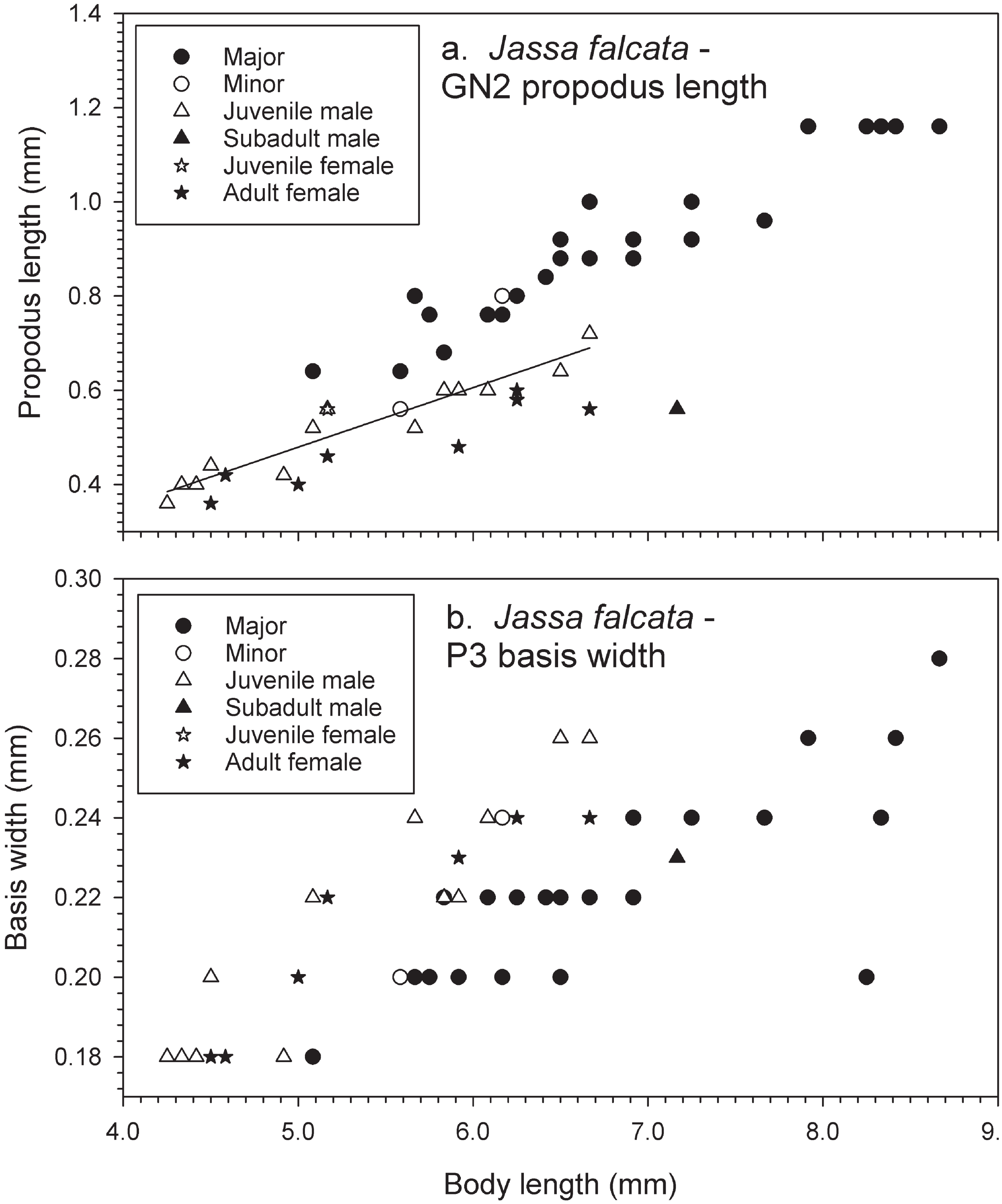

FIGURE 46. *Jassa falcata* (Montagu, 1808). Variation in gnathopod 2 propodus length and pereopod 3 basis width in males and females from a population at Audrassalas, Pas-de-Calais, France (1 July 1985, K. E. Conlan, coll., in tubes and and actively walking over *Ceramium rubrum* (mainly) and *Polysiphonia*, even though out of contact with seawater at low tide, IZ 1985-093 (CMN). Linear regression assumptions passed for the juvenile male. Linear regression statistics: juvenile male, propodus length = -0.152 + 0.126 x body length, $r^2 = 0.916$, $n = 13$.

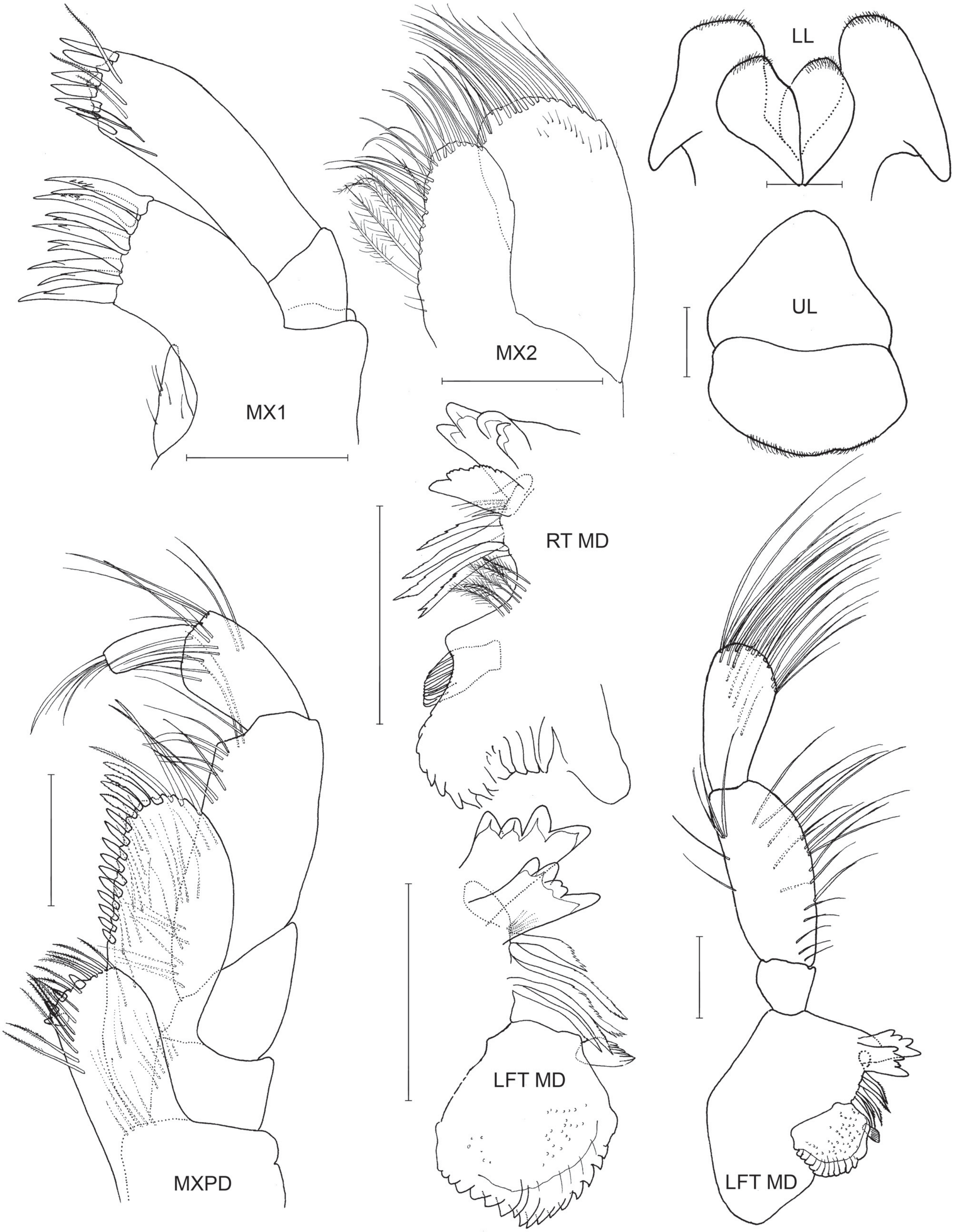

FIGURE 47. *Jassa falcata* (Montagu, 1808). Holotype, adult male, minor form, 6.3 mm. Mouthparts. Frontal view: upper lip; lateral views: maxilla 1; other views medial. Scale 0.1 mm. Illustration after Conlan (1990).

Because of the large variation in male thumb morphology in *Jassa* as well as the synonymy of previously recognized species to *J. falcata* by Sexton and Reid (1951), many references to *J. falcata* in the literature are mis-identifications. Conlan (1990) lists corrected identifications for those specimens that could be obtained. The specimens noted in Lobo *et al.* (2017) as being *J. falcata* are confirmed as this species (specimens examined 4 March 2019). So too are the specimens described by Walker (1911) (NHM).

Remarks. Minor forms have a distinct tooth on the inner surface of the dactyl which inserts into the palmar incision on the propodus (Figs 42 and 45). In major forms, the thumb is long and the propodus deeply incised (Figs 43–45). The dactyl lacks the obvious tooth of the minor form, though it is expanded proximally. These differences are so great that this lead Leach (1814) to describe the major form as *J. pulchella*; Montagu (1808) had based his description of *J. falcata* on a minor form male. Walker (1911) was of the opinion that both forms occurred within the species.

A plot of thumb length vs body length for a population sampled in summer at Audrassalas, France (Fig. 45) shows the shorter thumb length and dactyl toothing in the minor form and the very long thumb of the major form. Comparing mean thumb length between the minor form group ($n = 2$) and the major form group of the body length range (5.6–6.2 mm, $n = 10$) found that the differences were not great enough to exclude the possibility that the differences were due to random sampling variability (ANOVA, $F = 4.289$, $p = 0.065$). Minor forms were rare in this population and were uncommon in other collections also, despite~4,000 specimens having been examined (Table 4).

A plot of gnathopod 2 propodus length for the same population (Fig. 46a) showed a significant difference between the major form adult male ($n = 14$), juvenile (including subadult) male ($n = 8$) and adult females ($n = 5$) within the body length range where each overlapped (5.08–6.67 mm) (ANOVA, $F = 22.112$, $p < 0.001$). Adult males had a significantly longer propodus than adult females (*t*-test, $t = 5.631$, $p < 0.001$) or juveniles ($t = 5.107$, $p < 0.001$). Propodus length for major form adult males averaged 0.794 ± 0.104 mm while for juvenile males it averaged 0.595 ± 0.0657 mm. Adult females had an average propodus length of 0.536 ± 0.0623 mm which was not significantly different from the juvenile males ($t = 1.175$, $p = 0.251$).

Jassa herdmani **Walker, 1893**

(Table 11, Figs 48–53)

Synonyms: see Conlan (1990).

Diagnosis.

Both sexes:

Mandibular palp: article 2, dorsal margin with a fringe of setae.

Maxilla 1: without a seta or setal cluster at the base of the palp article 1.

Gnathopod 1: basis, anterolateral margin with a few very short setae; carpus without a single or small cluster of setae at the anterodistal junction of the propodus.

Gnathopod 2: basis with a few minute setae along the anterolateral margin but without long filter setae (setal lengths <20% of the basis width); carpus and propodus, setae on the anterior margin short and simple (setal length < basis width).

Pereopods 5–7: propodus not expanded anteriorly.

Uropod 1: ventral peduncular spinous process underlying about 40% of the longest ramus.

Uropod 3: inner ramus without spines mid-dorsally (with only the single apical spine).

Telson: tip without apical setae, only the usual short setae at each dorsolateral cusp.

Thumbed male:

Antenna 2: without plumose setae on the flagellum and peduncular article 5.

Gnathopod 2: propodus, palmar defining spines absent except in small males. Thumb distally acute or squared in minor males and squared in major males. Dactyl centrally toothed in minor forms and shallowly expanded proximally in major forms.

Adult female:

Antenna 2: without plumose setae on the flagellum and peduncular article 5.

Gnathopod 2: propodus, palm concave, palmar defining angle acute, distal to but close to the defining spines.

Remarks. The neotype (Fig. 48), which was erected by Conlan (1990), is a minor form male with short thumb and toothed dactyl, corresponding with "The specimen originally described as *P. herdmani*, taken by Professor

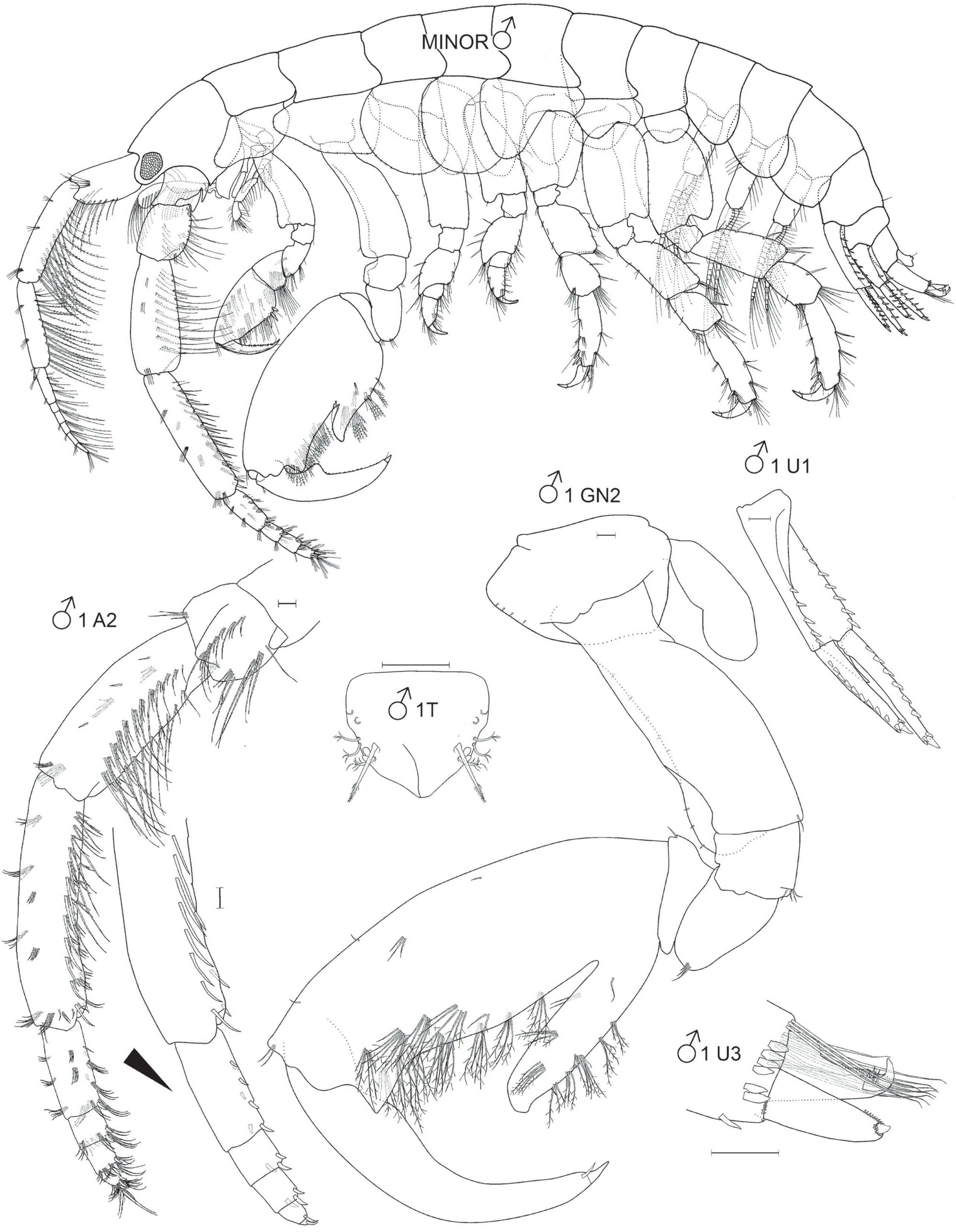

FIGURE 48. *Jassa herdmani* (Walker, 1893). Neotype, adult male, minor form, 6.0 mm, NHM 1925.9.8: 1686. Port Erin breakwater, Isle of Man, England, November 1892, A. O. Walker, coll. Adult male 1, major form, 7.9 mm, 1 m below water surface on steel frame used to hold settling plates, Langstone Harbour, Plymouth, England, 26 March 1986, R. J. Trott, coll., IZ1986-041 (CMN). Lateral view: whole body; dorsal view: telson; other views medial. Scale 0.1 mm. Illustration after Conlan (1990).

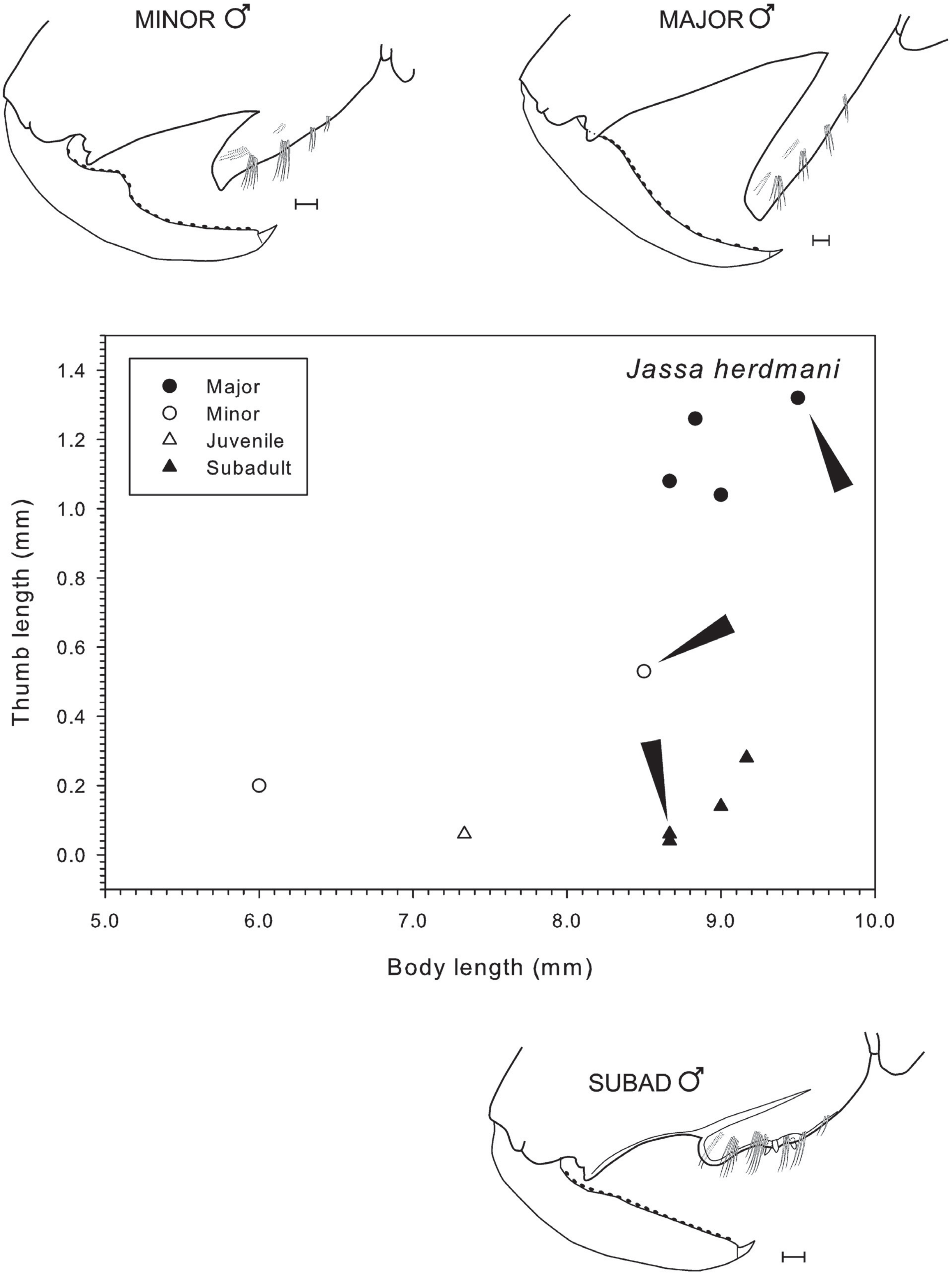

FIGURE 49. *Jassa herdmani* (Walker, 1893). Variation in thumb length relative to body length in males from Plymouth Sound, England, 14 April 1937, D. M. Reid, coll., from a buoy (SNM). Arrows refer to the associated gnathopod illustrations. The subadult male had a thumb visible inside the cuticle, indicating that it would molt next into a thumbed adult. Setae omitted except for those around the thumb and spines in order to landmark position changes with growth. All views lateral. Scale 0.1 mm. Linear regression assumptions failed for all plots. Illustration after Conlan (1990).

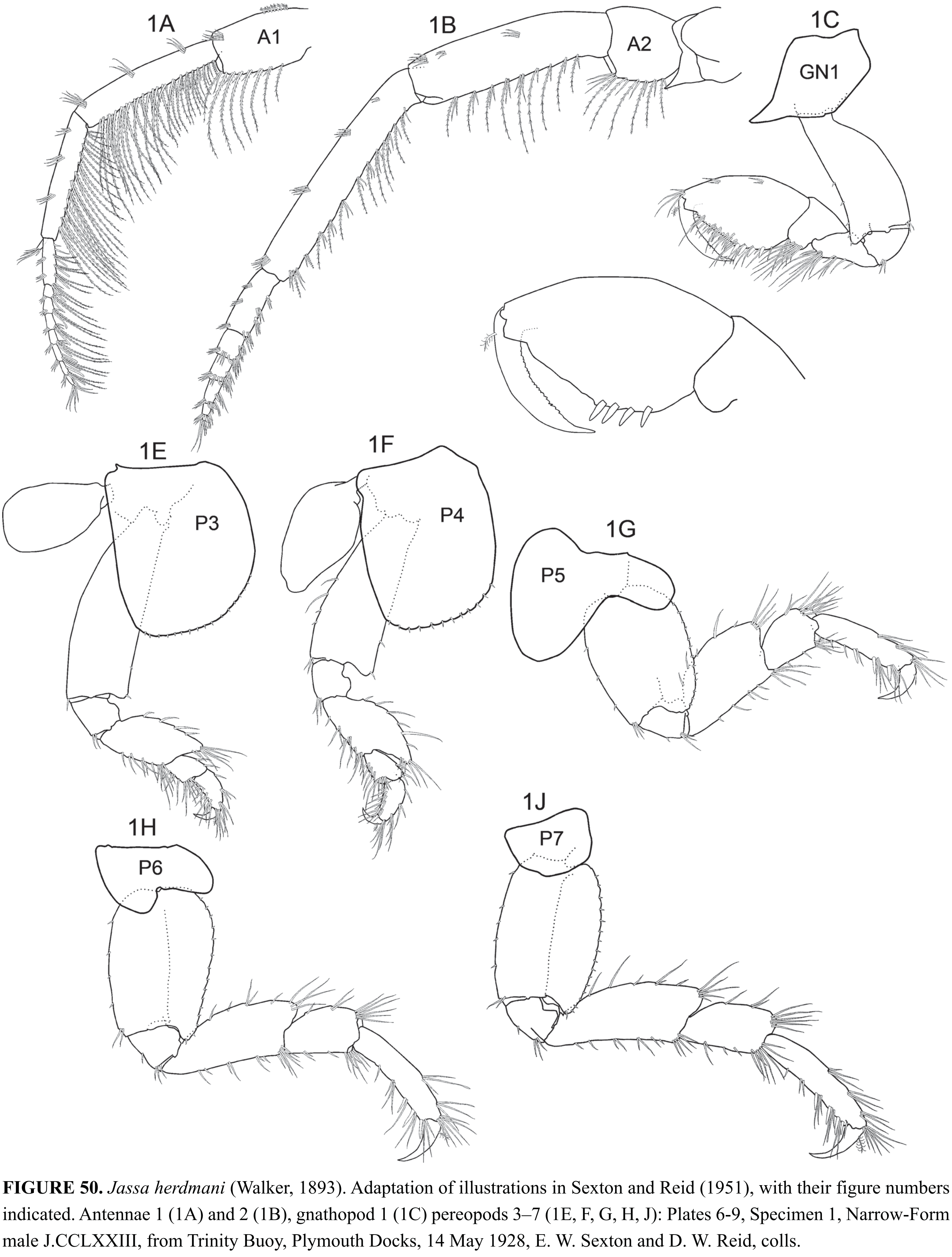

FIGURE 50. *Jassa herdmani* (Walker, 1893). Adaptation of illustrations in Sexton and Reid (1951), with their figure numbers indicated. Antennae 1 (1A) and 2 (1B), gnathopod 1 (1C) pereopods 3–7 (1E, F, G, H, J): Plates 6-9, Specimen 1, Narrow-Form male J.CCLXXIII, from Trinity Buoy, Plymouth Docks, 14 May 1928, E. W. Sexton and D. W. Reid, colls.

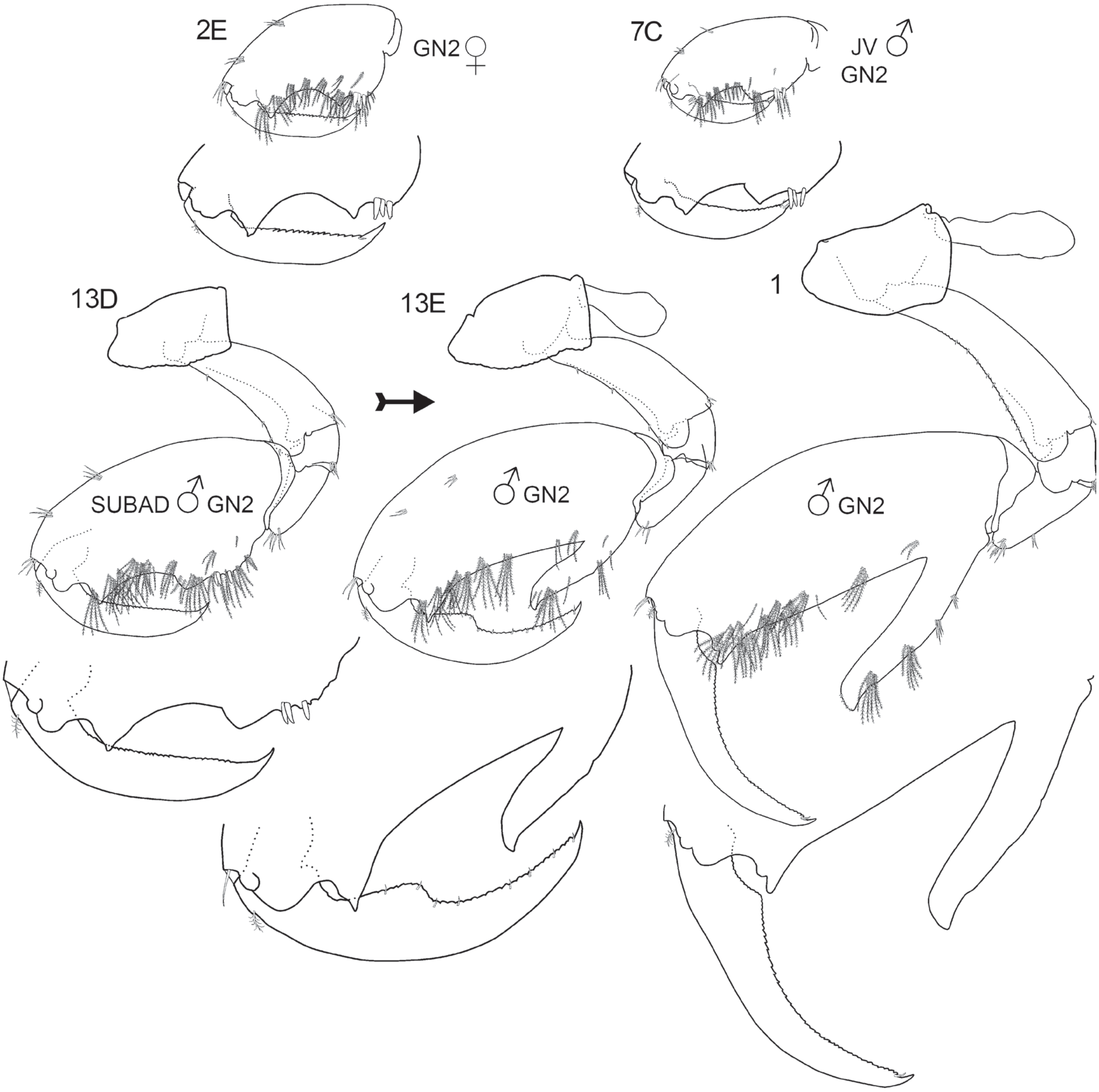

FIGURE 51. *Jassa herdmani* (Walker, 1893). Adaptation of illustrations in Sexton and Reid (1951), with their figure numbers indicated. Adult female gnathopod 2: Plate 10, Specimen 2, Narrow-Form female J.CXLIV (2E), dredging from a buoy at the entrance to Plymouth Docks, 23 August 1928, E. W. Sexton and D. W. Reid, colls. Juvenile male gnathopod 2: Plate 12, Specimen 7, Narrow-Form male, cut-across stage, J.5 (1): F_1 of female J.CXLIV (7C). Transformation of non-thumbed (13D) to thumbed (13E) gnathopod 2: Plate 19, Specimen 13 (2), Male K. B. 11, from a scrape of a buoy moored outside the [Plymouth] Breakwater, 3 May 1930, E. W. Sexton and D. W. Reid, colls. Adult male gnathopod 2, major form: Plate 7, Specimen 1, Narrow-Form male J.CCLXXIII, from Trinity Buoy, Plymouth Docks, 14 May 1928, E. W. Sexton and D. W. Reid, colls.

Herdman from a Compound Ascidian off the Island of Bute...” (Walker 1911, p. 71). *Jassa herdmani* naturally co-occurs with *J. falcata* and *J. marmorata* but the three species differ in microhabitat selection, life cycle, reproduction and temperature adaptation (Beermann & Franke 2012; Beermann & Purz 2013). The identity of the three species can be easily confused, especially when small (Sexton & Reid 1951; Conlan 1990). Conlan (1990) outlines how these can be distinguished on the basis of the antenna 2 plumosity, gnathopod 1 and 2 shape and setation and uropod 3 inner ramus spination.

Fig. 49 shows the thumb length relationships among specimens collected later by D.M. Reid from Plymouth Harbour on April 14, 1937. Although the collection was small, different morphologies of the minor and major form adult male are evident and the subadult male has a small pre-thumb before it molts into a (probably major form) thumbed male, judging by its large body length. Sexton and Reid (1951) called this pre-thumbed stage of the subadult male the "cut-across stage". Reproductions of Sexton and Reid's (1951) figures that are confirmed *J. herdmani* are shown in Figs 50 and 51. These specimens were collected in Plymouth Harbour at various dates between 1928 and 1930 and kept in aquaria, where changes in their morphologies were recorded as they molted. The transformation of the subadult male 13D to major form thumbed male 13E (their labels) is shown in Fig. 51. They mistook these specimens as *J. falcata*, calling them the ″Narrow Form" of *J. falcata.* The females of the two species also differ subtly, with the palmar angle of the gnathopod 2 propodus more bulbous and farther from the defining spines in *J. falcata* (Fig. 44) than in *J. herdmani* (Figs 51, 52).

The dactyl toothing appears to vary with thumb length. In the minor form with short, distal thumb (Figs 48 and 49), the dactyl tooth is pronounced. In the major form with longer, more proximal thumb (Fig. 51, specimen 13E), the dactyl tooth is shallower and more proximal. In the large major form with a long, proximal thumb (Figs 48, 49 and 51, specimen 1), the dactyl is expanded proximally, rather than more centrally toothed. One of the key features for *J. herdmani* is the cluster of setae on the dorsal margin of the mandibular palp article 2. This is shown in Fig. 53.

One specimen noted in Lobo *et al.* (2017) as being *Jassa* sp. is *J. herdmani* (specimen examined 4 March 2019). This is likely the *Jassa* sp. in their Fig. 2 that matches other specimens of *J. herdmani* from the North Sea in their CO1-5P sequence.

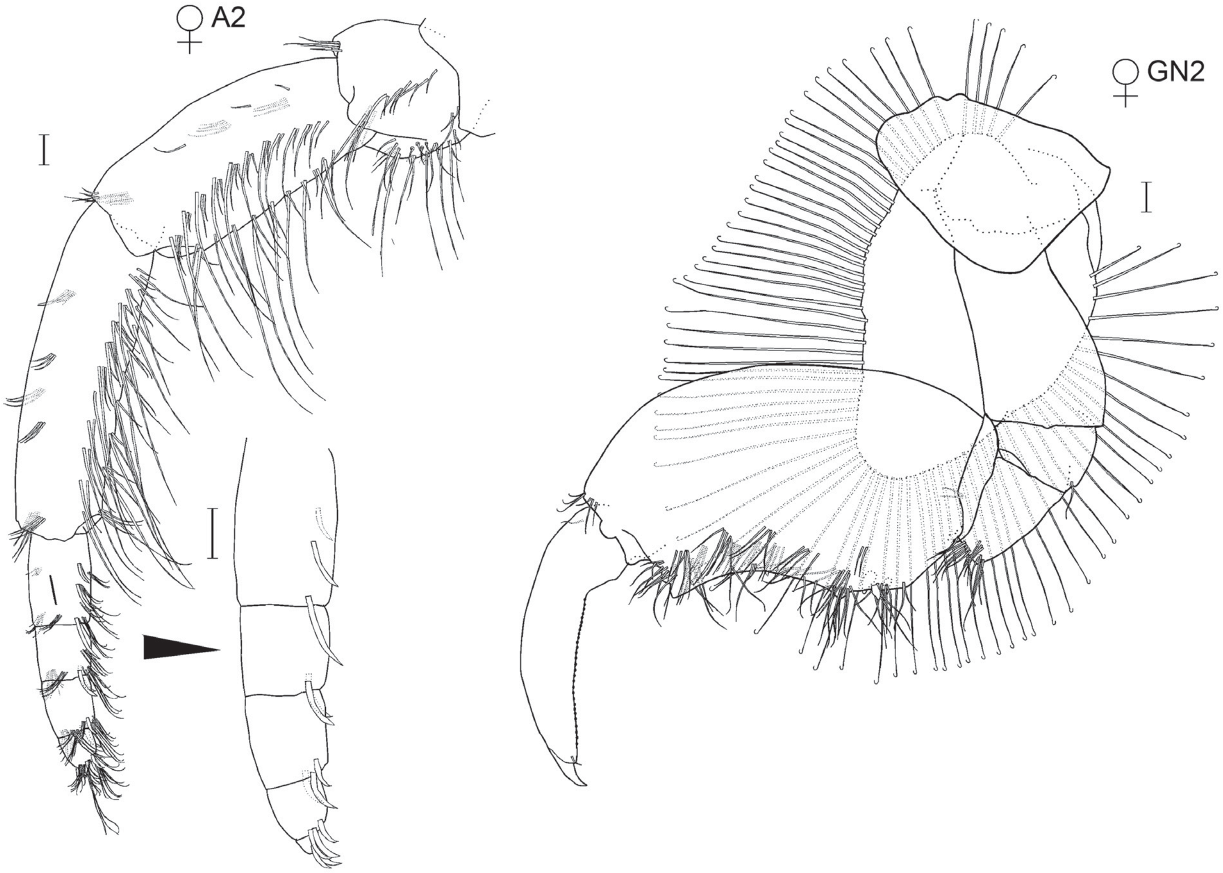

FIGURE 52. *Jassa herdmani* (Walker, 1893). Adult female, 7.2 mm, 1 m below water surface on steel frame used to hold settling plates, Langstone Harbour, Plymouth, England, 26 March 1986, R. J. Trott, coll., IZ1986-041 (CMN). Lateral view: whole body; dorsal view: telson; other views medial. Scale 0.1 mm.

The finding of a single juvenile female in coral rubble at Aqaba, Jordan by Lyons and Myers (1991) (identification confirmed) places the range of *J. herdmani* far outside the northeast Atlantic coast and western Mediterranean Sea where it has most often been collected (Fig. 9). This suggests that *J. herdmani* may have a propensity for exotic dispersal similar to *J. marmorata, J. slatteryi* and *J. morinoi.* It commonly fouls offshore structures in the North Sea (oil and gas platforms, wind turbines and shipwrecks) (Coolen *et al.* 2018; Luttikhuizen *et al.* 2019) which are thought to supply extended shallow, hard substrate and it has been collected on buoys (Sexton and Reid 1951) and boat bottoms as far back as 1890 (NHM 1925.9.8:1602). The Suez Canal is a transportation route for many exotic species, resulting in the eastern Mediterranean having many more introductions than the western Mediterranean (Galil *et al.* 2015). Lyons and Myers (1991) suggest that *J. herdmani* may be on the Atlantic coast of central Africa as well. This is based on literature reports that have not been confirmed by examination of specimens. Possibly these reports refer to *J. marmorata* or *J. morinoi* which are confirmed there (Figs 1, 2, 5 and 6).

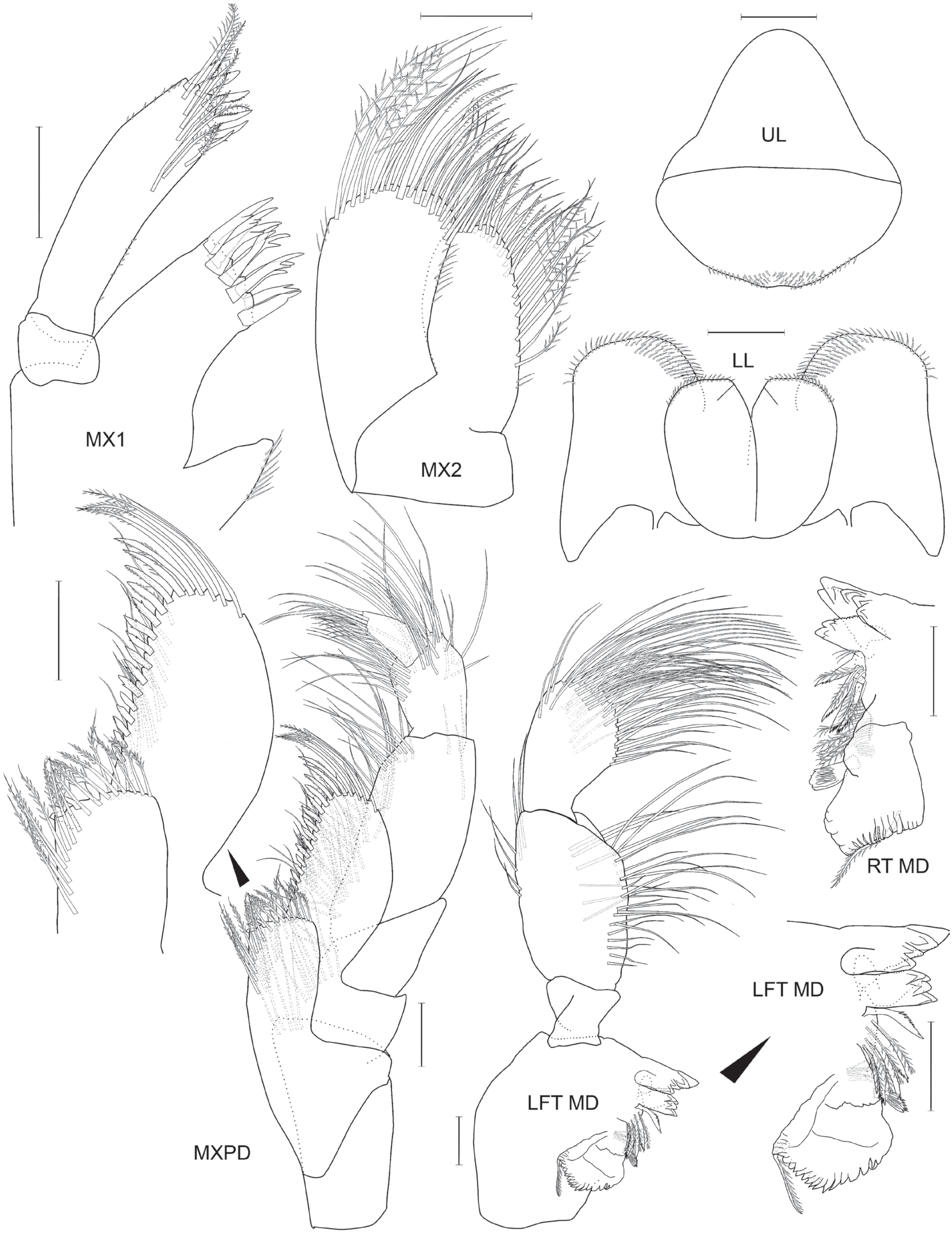

FIGURE 53. *Jassa herdmani* (Walker, 1893). Adult male 1, major form, 7.9 mm, 1 m below water surface on steel frame used to hold settling plates, Langstone Harbour, Plymouth, England, 26 March 1986, R. J. Trott, coll., IZ1986-041 (CMN). Mouthparts. Lateral views: maxilla 1 and maxilla 2; frontal view: upper lip; other views medial. Scale 0.1 mm.

Jassa laurieae n. sp.

(Table 11, Figs 54, 55)

Diagnosis.

Male:

Mandibular palp: article 2, dorsal margin without a fringe of setae.

Maxilla 1: without a seta or setal cluster at the base of the palp article 1.

Gnathopod 1: basis, anterolateral margin with a few minute setae along its length; carpus without a single or cluster of short setae at the anterodistal junction of the propodus.

Gnathopod 2: basis without a row of long setae along the anterolateral margin (setae minute, << basis width); carpus and propodus, setae on the anterior margin minute (setal length << basis width).

Pereopods 5–7: missing.

Uropods: missing.

Telson: missing.

Thumbed male:

Antenna 2: large individuals with plumose setae on the flagellum and peduncular article 5.

Gnathopod 2: propodus, palmar defining spines not produced on a ledge, absent in large thumbed males (state for small thumbed males unknown). Minor males unknown. Major males, thumb distally rounded and on the proximal half of the propodus. Dactyl expanded close to the junction with the propodus but not centrally toothed.

Adult female: Unknown.

Description.

Male, holotype. Length ~4.7 mm.

Antenna 1: each article with long filter setae on the posterior margin; accessory flagellum 2 articles, the second minute; flagellum 4 articles, each bearing aesthetascs.

Antenna 2: stouter than antenna 1 and overlapped by antenna 1 to 2/3 the length of article 5; distal part of article 4 and full length of article 5 and flagellum bearing plumose setae on the posterior margin in addition to filter setae which are about the same length; flagellum 4 articles, article 1, 50% of flagellum length, article 4, 40% as long as article 3, flagellum articles 2–4 bearing curved spines posterodistally.

Mandible: palp articles 2 and 3 without dorsal fringe of setae; raker spines 1 right, 4 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.

Gnathopod 1: coxa produced forward, coxal margins, anterior 175% of dorsal length, ventral margin straight; basis flanged anteriorly, anterior margin without a fringe of long setae (all setae minute), posterior margin without setae; carpus, posterior lobe 45% of anterior margin length, without an anterodistal setal cluster; propodus, palm convex, defined by 3 spines (medial-lateral-medial), these mid-distant along the palm; dactyl facially striated.

Gnathopod 2: coxa rounded, coxal margins, anterior 26% and posterior 38% of ventral length, ventral margin convex; gill present; carpus, posterior lobe with a cluster of setae; propodus, anterior margin with only a few minute setae proximally (setae << the width of the basis), palm with a few plumose setae at the dactyl hinge, defined by a long, straight thumb that is rounded at the tip, without palmar defining spines, thumb length 35% of propodus length.

Pereopod 3: coxa deepest posteriorly; basis, margins convex; merus, setae 1/2 article width, article width maximally 65% of length; carpus nearly 100% overlapped by the merus; propodus not posteriorly spinose.

Pereopod 4: coxa nearly rectangular, deeper than wide, ventrally convex; other articles as for pereopod 3.

Pereopods 5–6: missing.

Pereopod 7: coxa-ischium missing, distal articles slender, propodus not distally expanded, with small spines only anterodistally at the junction of the dactyl; dactyl, posterior (outer) margin not cusped distally, anterior (inner) margin bearing a seta only at the unguis.

Pleopods: missing.

Uropods: missing.

Telson: missing.

Condition. Mouthparts, right antennae 1 and 2, gnathopod 1, left gnathopod 2, and right pereopods 3 and 4 slide mounted. Whole body with left antenna 2 and gnathopod 1, right gnathopod 2 (coxa to merus) and left pereopod 4 in 70% ethanol. Missing posterior portion of the body from pereon segment 4 onwards, which had been removed for CO1 analysis.

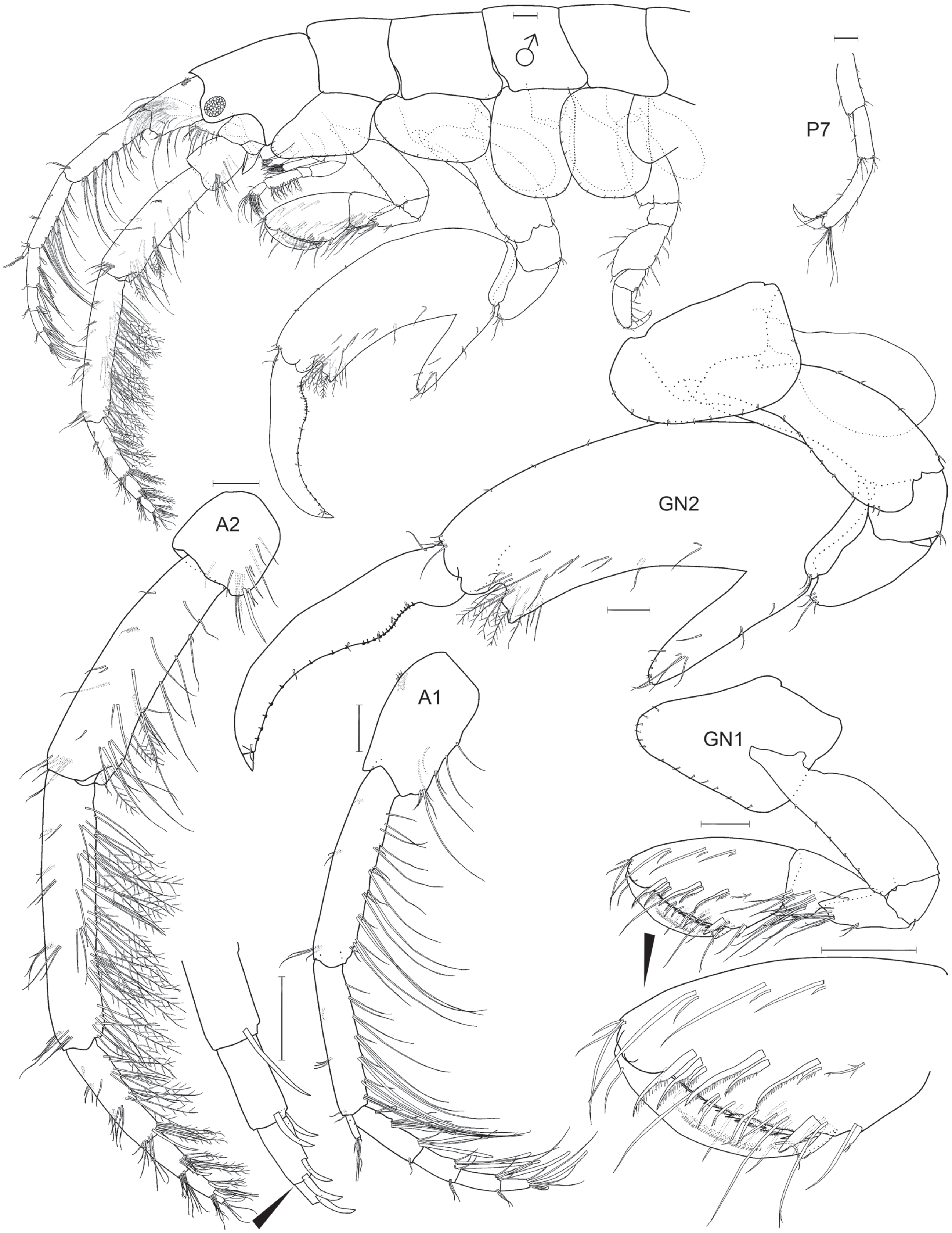

FIGURE 54. *Jassa laurieae* **n. sp.** Holotype, adult male, major form, ~4.7 mm, CMNC 2019-1385. Praia Norte, Viana do Castelo, Portugal (41.6938, -8.85118), 23 September 2010, P. Gomes, coll., from macroalgae (A2019-0061, SFC 29-003, barcode index no. AAY5420) (CMN). Lateral view: whole body and left gnathopod 2; other views medial. Scale 0.1 mm.

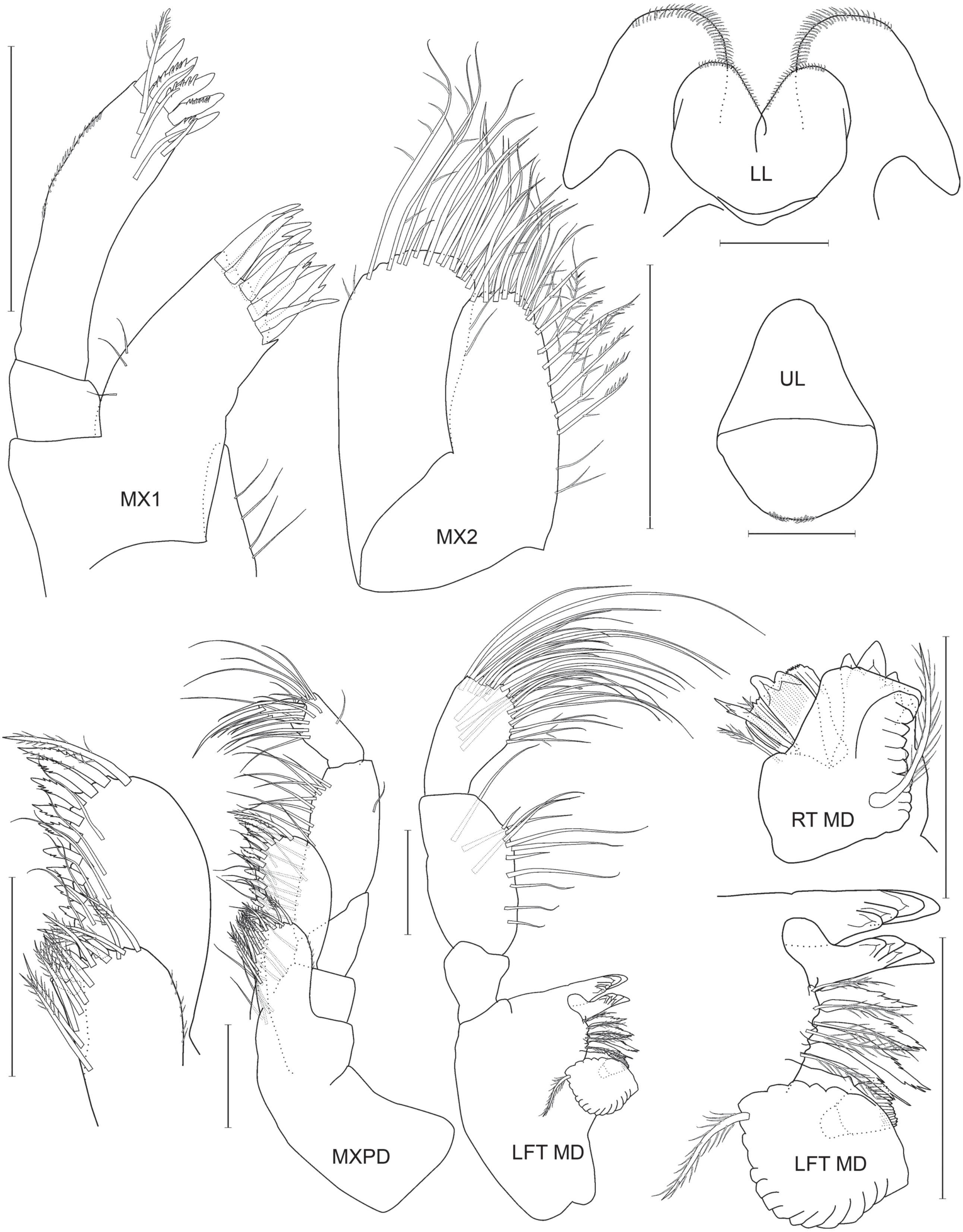

FIGURE 55. *Jassa laurieae* **n. sp.** Holotype, adult male, major form, ~4.7 mm, CMNC 2019-1385. Praia Norte, Viana do Castelo, Portugal (41.6938, -8.85118), 23 September 2010, P. Gomes, coll., from macroalgae (A2019-0061, SFC 29-003, barcode index no. AAY5420) (CMN). Mouthparts. Frontal view: upper lip; lateral view: maxilla 1; other views medial. Scale 0.1 mm.

Variation. Maximum body length: male ~4.8 mm.

Type material examined. Holotype, male, ~4.7 mm, from macroalgae at Praia Norte, Viana do Castelo, Portugal (41.6938, -8.85118), Pedro Gomes, collector, 23 September 2010, Specimen ID SFC 29-003, Process ID FCCOM341-11. Donated by Filipe Costa, University of Minho, Portugal, to the Canadian Museum of Nature (CMN A2019.0061, catalogue no. CMNC 2019-1385). Paratype, male, ~4.8 mm, same location, date and collector, Specimen ID SFC 29-002, Process ID FCCOM340-11 (catalogue no. CMNC 2019-1386).

Etymology. Named in honour of artist Susan Laurie-Bourque who skillfully illustrated all the plates for this paper, Conlan (1990; in press), and many earlier taxonomic treatments.

Remarks. *Jassa laurieae* is only known from the holotype and paratype specimens which are both major form adult males. Both specimens had the posterior portions of their body removed for CO1 analysis, with the results published in Lobo *et al.* (2017). Body length has been estimated based on the expected length of the remaining body using *J. kimi* as a model, which is similarly sized. The actual body portion available for study was 1.8 mm long for the holotype and 1.2 mm long for the paratype. Lobo *et al.* (2017) considered *J. laurieae* to be a Portuguese variant of *J. pusilla*, but the CO1 analyses revealed that both the holotype and paratype were genetically similar and clearly distinct from North Sea specimens of *J. pusilla* as well as from Portuguese and North Sea *J. falcata*, *J. herdmani* and *J. marmorata*, and from U.S. *J. staudei*.

Jassa laurieae is only known from the Atlantic coast of Portugal, where it may be found with *J. falcata*, *J. pusilla* and *J. herdmani* (Fig. 9). Morphologically, the major form males of *J. laurieae* and *J. falcata* are similar in appearance at the anterior end, with plumose setae on antenna 2, minute setae on the anterior bases of gnathopods 1 and 2, absence of a seta or cluster of setae on the anterodistal margin of the gnathopod 1 carpus at the junction of the propodus, and relatively long thumb with rounded tip. The two differ in that *J. laurieae* lacks the dorsal fringe of setae on article 2 of the mandibular palp which both *J. falcata* and *J. herdmani* consistently possess in both sexes and all ages. *Jassa falcata* is also distinctive in having 1–2 spines midway along the inner ramus of uropod 3, but the state for *J. laurieae* is unknown. Large major form *J. falcata* have a very long thumb which is more squared at the tip than in *J. laurieae* but there are too few specimens of the latter to determine variation.

Jassa laurieae is less similar in appearance to congener *J. pusilla* than to *J. falcata* in the major form male, although the females and juveniles may prove to be more similar. Major form males of *J. pusilla* develop an indent at the tip of the thumb and never have plumose setae on the antenna 2. Both species are similar in lacking the dorsal setal cluster on article 2 of the mandibular palp and lack of a seta or setal cluster on the anterodistal junction of the carpus with the propodus on gnathopod 1. They are also similar in their small body length, while *J. falcata* achieves a greater length. Until more specimens of *J. laurieae* are found, these two species are currently only distinguishable by the major form male. Additional distinguishing characters may occur on the posterior region of the body, though.

Jassa herdmani bears the distinguishing setal fringe on article 2 of the mandibular palp (any age, both sexes), and this serves to easily separate it from *J. laurieae*. Major form males of *J. herdmani* do not bear plumose setae on antenna 2 and achieve greater body size.

***Jassa monodon* (Heller, 1866)**

(Table 11, Figs 56–59)

Podocerus monodon Heller, 1866, pp. 45–46, plate IV, figs. 4, 5; not *J. falcata*: Krapp-Schickel (1974), p. 344.

Diagnosis.

Mandibular palp: article 2, dorsal margin without a fringe of setae.

Maxilla 1: state unknown.

Gnathopod 1: basis, anterolateral margin without a setal fringe along its length; carpus without a seta or cluster of setae at the anterodistal junction of the propodus.

Gnathopod 2: basis with 5–7 widely spaced setae along the anterolateral margin (setal length 1/2 to 2/3 the width of the basis); carpus and propodus, setae on the anterior margin short and simple (setal length < basis width).

Pereopods 5–7: propodus not expanded anteriorly.

Uropod 1: ventral peduncular spinous process underlying about 1/3 of the longest ramus.

Uropod 3: inner ramus without spines mid-dorsally (with only the single apical spine).

FIGURE 56. *Jassa monodon* (Heller, 1866). Holotype, subadult male, 5 mm, CR 20619. Lesina (Hvar, Croatia), 1865, C. Heller, coll. (NHMW). Left side of body with magnification of the left second gnathopod. Photographs by Peter Dworschak (NHMW) with adjustments by S. Laurie-Bourque.

FIGURE 57. *Jassa monodon* (Heller, 1866). Holotype, subadult male, 5 mm, CR 20619. Lesina (Hvar, Croatia), 1865, C. Heller, coll. (NHMW). Right side of body with magnifications of the right antennae 1 and 2, left pereopod 3 or 4, right or left pereopod 7 and third uropods and telson as viewed from the right side. Photographs of the appendage magnifications by K.E. Conlan (CMN). Photograph of uropod magnification by Peter Dworschak (NHMW). Photograph adjustments by S. Laurie-Bourque.

FIGURE 58. *Jassa monodon* (Heller, 1866). Adult male, major form, length unknown, CR 20621. Lesina (Hvar, Croatia), 1865, C. Heller, coll. (NHMW). Left side of body with magnification of the left second gnathopod. Photographs by Peter Dworschak (NHMW) with adjustments by S. Laurie-Bourque.

FIGURE 59. *Jassa monodon* (Heller, 1866). Adult male, major form, length unknown, CR 20621. Lesina (Hvar, Croatia), 1865, C. Heller, coll. (NHMW). Right side of body with magnification of the right second gnathopod. Photographs by Peter Dworschak (NHMW) with adjustments by S. Laurie-Bourque.

Telson: tip with 1–2 apical setae in addition to the usual short setae at each dorsolateral cusp.

Condition. Without left gnathopod 1, right pereopods 5–7 and left pereopod 5. Right antennae 1 and 2, left pereopods 3, 4 and 7 broken from the animal but present in the vial.

Thumbed male:

Antenna 2: missing (subadult, peduncular article 5 with long filter setae; flagellum with short brush setae (not plumose setae)).

Gnathopod 2: propodus, palmar defining spines absent in the major form, thumb long, more than half the length of the propodus and distally acute. Dactyl expanded close to the junction with the propodus but not centrally toothed. Minor form unknown.

Condition. Without right and left antennae 1 and 2 and pereopods 5–7.

Adult female: unknown.

Remarks. *Jassa monodon* was first described by Heller (1866) as *Podocerus monodon*, based on a subadult male specimen collected at Lesina (Hvar, Croatia). No information on depth or substrate was given. This specimen is in the crustacean collection of the Naturhistorisches Museum Wien (NHMW 20619) and was examined by one of us (KC) in November 2018. Krapp-Schickel (1974) had previously examined this specimen and called it a female *Jassa falcata*. A second specimen of *Jassa monodon* (NHMW 20621) was also found in Heller's collection from Lesina and named *Podocerus pulchellus* in Heller (1866) and Krapp-Schickel (1974). This specimen is a major form thumbed male. These are the only two specimens known for this species. Due to their type status and fragility, the specimens could not be measured for body length or dissected for line drawing. Heller (1866) recorded the length of the holotype subadult male as 5 mm. The length of the major form adult male was not recorded.

Jassa monodon has a unique combination of diagnostic characters (Table 11). Other species that currently occur in the vicinity of the type locality for *Jassa monodon* are *J. marmorata*, *J. slatteryi* and *J. morinoi* (Figs 1–6, 9). The European *J. pusilla* and *J. falcata* are not known to occur in the Mediterranean Sea. The European *J. herdmani* has been found in the western part of the Mediterranean Sea but not as far east as the Adriatic, where *J. monodon* was collected. Tables 10 and 11 show the key distinguishing characters for these species.

Possibly the "*Podocerus falcatus*" described from Trieste, Italy by Nebeski (1880) was *J. monodon* mixed with *J. marmorata*. In interpreting this study, Sexton and Reid (1951) suggested that Nebeski (1880) was dealing with both a "Broad-form" and a ″Narrow-form". Conlan (1990) identified Sexton and Reid's Broad-form as *J. marmorata* and their Narrow-form as being *J. falcata* or *J. herdmani*, but did not know of *J. monodon*'s characteristics at the time. Both *J. marmorata* and *J. monodon* were known from the vicinity of Trieste in the 19th century (Table 3, Figs 1 and 9).

North Pacific species

Jassa kimi n. sp.

(Table 12, Figs 60–61)

Diagnosis.

Male:

Mandibular palp: article 2, dorsal margin without a fringe of setae.

Maxilla 1: without a seta or setal cluster at the base of the palp article 1.

Gnathopod 1: basis, anterolateral margin with a few minute setae along its length; carpus with a single short medial seta at the anterodistal junction of the propodus.

Gnathopod 2: basis without a row of long setae along the anterolateral margin (setae minute, << basis width); carpus and propodus, setae on the anterior margin minute (setal length << basis width).

Pereopods 5–7: propodus not expanded anteriorly.

Uropod 1: ventral peduncular spinous process underlying about 1/3 of the longest ramus.

Uropod 3: inner ramus without spines mid-dorsally (with only the single apical spine).

Telson: tip without apical setae in addition to the usual short setae at each dorsolateral cusp.

Thumbed male:

Antenna 2: without plumose setae on the flagellum and peduncular article 5.

Gnathopod 2: propodus, palmar defining spines not produced on a ledge, minute in large thumbed male (state for small thumbed males unknown). Minor male unknown. Major male, thumb distally rounded with posterior corner more acute than the anterior corner, incised well into the proximal half of the propodus. Dactyl expanded close to the junction with the propodus but not centrally toothed.

TABLE 12. Key character states of locally distributed North Pacific species. Trans-hemispheric species (Table 10) may occur there as well. X indicates the presence of the first character state described while — indicates the alternative character state given in italics. S and L indicate length. ? indicates that the state is unknown. Character states apply to both sexes and all ages unless indicated otherwise.

Character	*J. kimi* (Figs 60-61)	*J. oclairi* (Figs 62-64)	*J. borowskyae* (Figs 65-66)	*J. staudei* (Figs 67-77)	*J. carltoni* (Figs 78-82)	*J. shawi* (Figs 83-84)	*J. myersi* (Figs 85-87)
Antenna 2, large subadult and thumbed male, posterior margin of article 5 and flagellum bearing plumose setae in addition to the usual finely pectinate filter setae (e.g., Fig. 65) *or without plumose setae* (e.g., Fig. 60)	—	X[14]	X	X	—	—	—
Antenna 2, large subadult and adult female, posterior margin of article 5 and flagellum bearing plumose setae in addition to the usual finely pectinate filter setae (e.g., Fig. 65) *or without plumose setae* (e.g., Fig. 81)	?	X	X	X	—	—	—
Mandibular palp, margin of article 2 with a fringe of setae dorsally (Fig. 64) *or without a fringe* (e.g., Fig. 66)	—	X	—	—	—	—	—
Maxilla 1 with a seta or cluster of setae at the base of palp article 1 (Fig. 101) *or without seta(e)* (e.g., Fig. 61)	—	—	—	—	—	—	—
Gnathopod 1, basis, anterolateral margin with a fringe of spine-like setae (e.g., Fig. 88) *or without spine-like setae* (e.g., Fig. 83)	—	—	—	—	—	—	—
Gnathopod 1, carpus, with a seta or cluster of setae at the anterodistal junction of the propodus which may be slightly lateral or medial (e.g., Fig. 65) *or without seta(e)* (e.g., Fig. 67)	X	X	X	—	X	X	X
Gnathopod 1, carpus, seta(e) at the anterodistal junction of the propodus moderately long (L, length ≥25% of anterior margin length) (e.g., Fig. 81) or short (S, length <25% of anterior margin length) (e.g., Fig. 83) *or without seta(e)* (Fig. 68)	S	L	L	—	L	S	L
Gnathopod 2, basis with a fringe of setae on the anterolateral margin (e.g., Fig. 67) *or fringe absent* (Fig. 83) *(minute setae may be present but are too small to be described as an obvious fringe)* (e.g., Fig. 60)	—	X	X	X	X	—	X[15]
Gnathopod 2, basis, if setal fringe present, setae relatively long (L, length ≥40% basis width) (e.g., Fig. 62) or short (S, length mostly <40% basis width) (e.g., Fig. 28) *or fringe absent* (Fig. 83) *(minute setae may be present but are too small to be described as an obvious fringe)* (e.g., Fig. 60)	—	L	L	L	S	—	S
Gnathopod 2, propodus, setae on the anteroproximal margin long (L, setal length ≥ maximal basis width) (Fig. 67) or short to absent (S, setal length < maximal basis width) (e.g., Fig. 78, Fig. 83)	S	S	S	L	S	S	S

......*continued on the next page*

TABLE 12. (Continued)

Character	*J. kimi* (Figs 60-61)	*J. oclairi* (Figs 62-64)	*J. borowskyae* (Figs 65-66)	*J. staudei* (Figs 67-77)	*J. carltoni* (Figs 78-82)	*J. shawi* (Figs 83-84)	*J. myersi* (Figs 85-87)
Gnathopod 2, propodus, setae on the anterior margin plumose (Fig. 62) *or simple* (e.g., Fig. 85)	—	X	—	—	—	—	—
Gnathopod 2, female propodus, palm concave, palmar angle pronounced (acute, right angled or bulbous) (e.g., Fig. 83) *or palmar angle shallow, giving the palm a sinuous appearance* (e.g., Fig. 85)	?	X	X	X	X	X	—
Pereopods 5-7, propodus, anterior margin expanded for grasping (e.g., Fig. 95) *or not expanded for grasping* (e.g., Fig. 60)	—	—	—	—	—	—	—
Uropod 1, peduncular spinous process that extends ventrally from the peduncle and underlies the rami, moderately long (L, length = at least 25-50% the length of the longest ramus) (e.g., Fig. 78) or very short (S, length ≤10% of the length of the longest ramus, in which case it may not be visible) (e.g., Fig. 65)	L	L	S	L	L	S	S
Uropod 3, inner ramus with 1-2 mid-dorsal spines in addition to the usual spine at the tip (e.g., Fig. 42) *or without dorsal spines* (e.g., Fig. 60)	—	—	—	—	—	—	—
Telson, tip with a seta or cluster of setae extending between the third uropods (in addition to the usual upright setae at each side) (Fig. 28) *or without setae at the tip*[12] (e.g., Fig. 65)	—	—	—	—	—	—	—

[14] Very large thumbed males may have greatly lengthened second antennae that lack the plumose setae that smaller males possess (Fig. 62)

[15] In *J. myersi*, the setae are sparse, but can be interpreted to be numerous enough to comprise a fringe or not to comprise a fringe. Therefore, in the key to all species, *J. myersi* has been included twice so that it can be keyed out as either having a fringe or not.

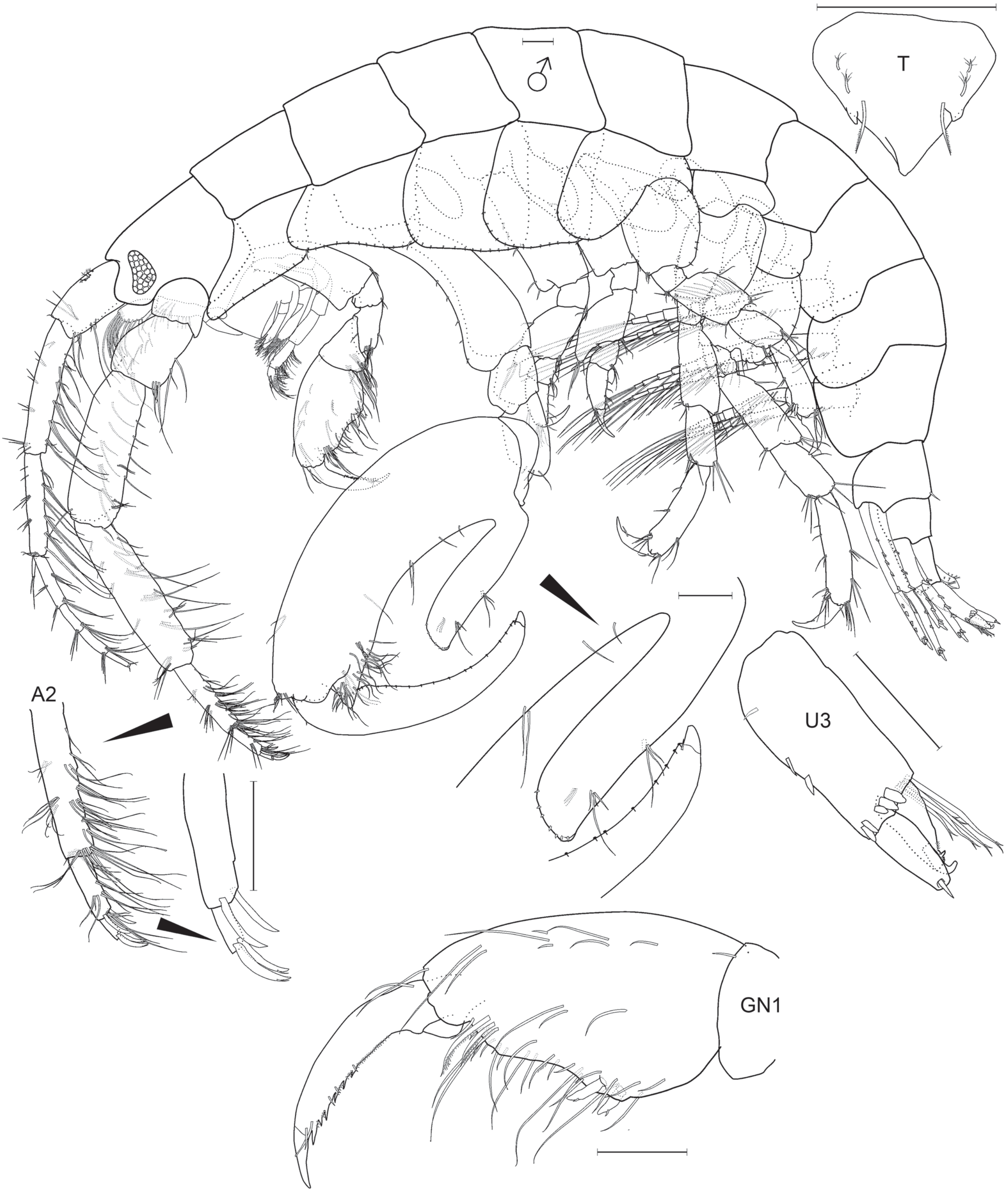

FIGURE 60. *Jassa kimi* **n. sp.** Holotype, adult male, major form, 3.5 mm, DKU-115 (MARBK). Impo Port, Yeosu-Si, The Republic of Korea, 23 June 2011, S.-S. Hong, coll. (MARBK). Lateral view: whole body; dorsal view: telson; medial view: gnathopod 1 and uropod 3. Scale 0.1 mm.

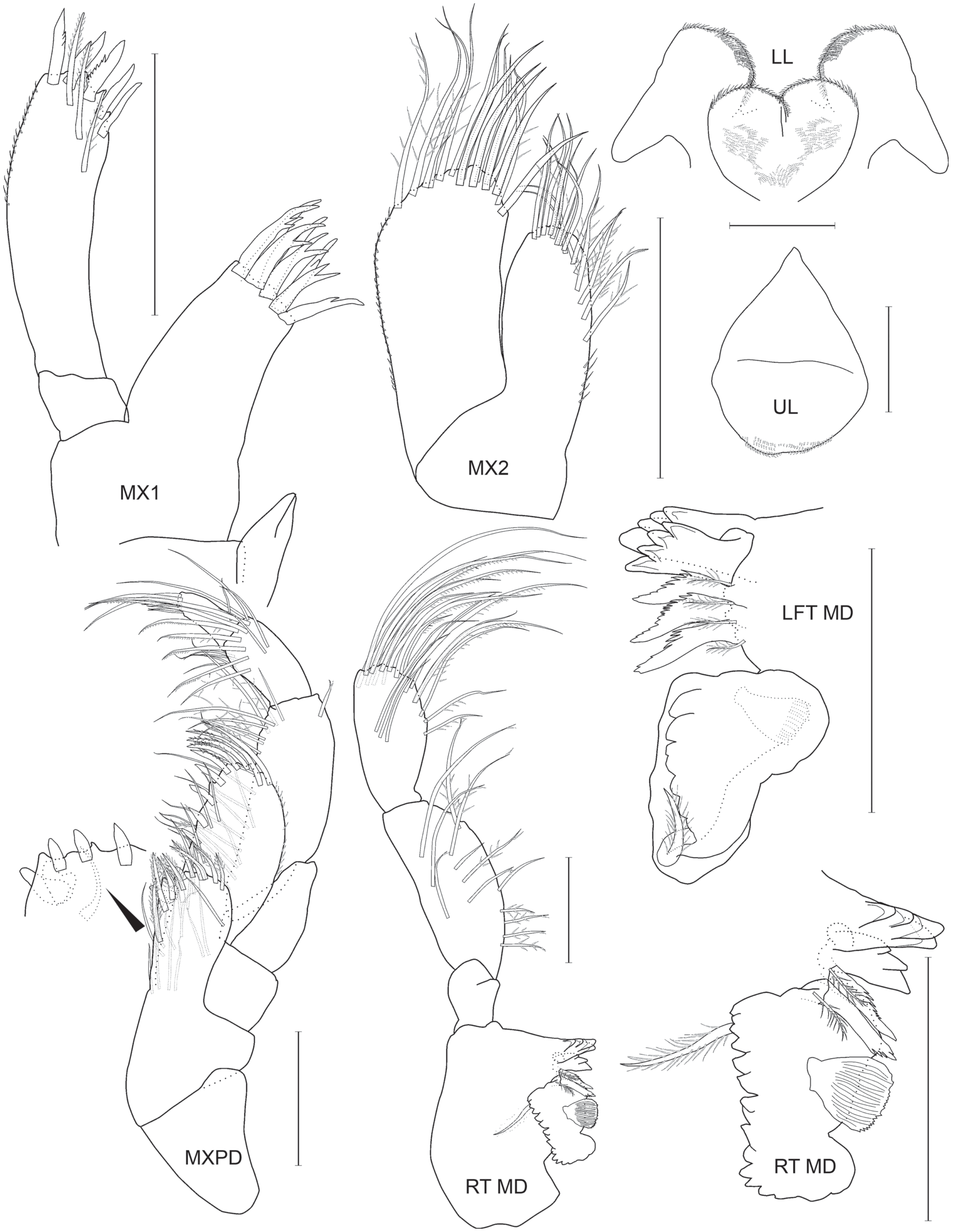

FIGURE 61. *Jassa kimi* **n. sp.** Holotype, adult male, major form, 3.5 mm, DKU-115 (MARBK). Impo Port, Yeosu-Si, The Republic of Korea, 23 June 2011, S.-S. Hong, coll. (MARBK). Mouthparts. Frontal view: upper lip; lateral view: maxilla 1 and right mandible; other views medial. Scale 0.1 mm.

Adult female: Unknown.

Description.

Male, holotype. Length 3.5 mm.

Antenna 1: each article with long filter setae on the posterior margin; accessory flagellum 2 articles, the second minute; flagellum 5 articles, the last minute, bearing aesthetascs.

Antenna 2: stouter than antenna 1 and overlapped by antenna 1 to 2/3 the length of article 5; without plumose setae on the posterior margin of the peduncle and flagellum; flagellum 3 articles, article 1 65% of flagellum length, article 3, 45% as long as article 3, flagellum articles 2 and 3 bearing curved spines posterodistally.

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

Maxilla 1: palp without setae at the base of article 1, article 2 with 1 row of facial setae; inner plate without setae apparent.

Gnathopod 1: coxa produced forward and creased laterally, coxal margins, anterior 60% of dorsal length, ventral margin straight; basis flanged anteriorly, anterior margin without a fringe of long setae (all setae minute), posterior margin without setae; carpus, posterior lobe 40% of anterior margin length, with a single short medial seta at the anterodistal margin; propodus, palm shallowly concave, defined by 2 medial spines, these mid-distant along the palm; dactyl not facially striated.

Gnathopod 2: coxa rectangular, coxal margins, anterior 50% and posterior 40% of ventral length, ventral margin slightly wavy; gill present; carpus, posterior lobe without a cluster of setae; propodus, anterior margin without setae proximally, palm with a few plumose setae at the dactyl hinge, defined by a long, slightly sinuous thumb that is rounded at the anterior tip and more squared at the posterior tip, with 1 short palmar defining spine, thumb length 37% of propodus length.

Pereopod 3: coxa deepest posteriorly; basis, margins shallowly convex; merus, central setae 45% of article width, article width maximally 75% of length; carpus nearly 100% overlapped by the merus; propodus not posteriorly spinose.

Pereopod 4: coxa nearly square; other articles as for pereopod 3.

Pereopod 5–7: distal articles slender, propodus not distally expanded, with small spines only anterodistally at the junction of the dactyl; dactyl, posterior (outer) margin not cusped distally, anterior (inner) margin bearing a seta only at the unguis.

Pleopods: with 2 peduncular coupling hooks.

Uropod 1: peduncle, posteroventral spinous process underlying 37% of the inner ramus, inner and outer rami with 2 and 4 mid-dorsal spines respectively, not terminating in a fringe of cusps ventral to apical spine group.

Uropod 2: peduncle, posteroventral spinous process absent.

Uropod 3: outer ramus with 1 larger cusp proximal to the basally immersed, dorsally recurved spine and minute cusps around it; inner ramus without a spine mid-dorsally.

Telson: tip without apical setae in addition to the single long seta and pair of short plumose setae at each dorsolateral cusp.

Condition. Mouthparts, left antenna 1, right antenna 2, left gnathopod 1, right gnathopod 2, pereopods 3–7, pleopods 1–3 and uropods 1–3, left uropod 3 and telson slide mounted. Right antenna 1 article 1, left antenna 2, right gnathopod 1 coxa-ischium, left gnathopod 2, pereopod 5, pleopods and uropods 1 and 2 with the whole body. Missing remainder of right antenna 1 and gnathopod 1 and left pereopods 4, 6 and 7.

Type material examined. Holotype, male, 3.5 mm, from a light trap at 4–6 m depth near a breakwater at Impo Port, Yeosu-Si, The Republic of Korea, 34°35′47″N, 127°48′17″E, S.-S. Hong, collector, 23 June 2011. catalogue number: MARBK-115; deposit institution : Marine Amphipoda Resources Bank of Korea (MARBK), Cheonan, South Korea.

Etymology. Named in honour of Young-Hyo Kim, who has considerably expanded our knowledge of the biodiversity of Korean amphipods.

Remarks. Numerous combinations of non-sexually dimorphic characters serve to distinguish *J. kimi* from all other species of *Jassa*. *Jassa kimi* lacks the fringe of setae on the anterior margin of the gnathopod 2 basis which is distinctive in numerous North Pacific species of *Jassa* (*J. borowskyae*, *J. carltoni*, *J. oclairi*, *J. staudei*, *J. marmorata*, *J. slatteryi*, and *J. morinoi*). From the other North Pacific species that also lack this fringe (*J. myersi* and *J. shawi*), it can be distinguished by having only a very short seta on the carpus of gnathopod 1 at the anterodistal junction of the propodus (long seta in *J. myersi* but short in *J. shawi*). From *J. shawi* it can be distinguished by the length of the peduncular process underlying the rami of uropod 1. In *J. kimi*, this process is about one third the length of the longer inner ramus, which is typical of most species of *Jassa*. In *J. shawi*, this process is extremely short, appearing absent unless viewed microscopically.

When compared with Northern Hemisphere species that are restricted to the Atlantic and adjoining seas (*J. falcata*, *J. herdmani*, *J. laurieae*, *J. monodon* and *J. pusilla*), the absence of a setal fringe on gnathopod 2 can be readily used as a distinguishing character as all lack this fringe. These species bear other character states that are not shared with *J. kimi*. *Jassa falcata* and *J. herdmani* possess an extra fringe of setae on the second article of the mandibular palp which is directed dorsally, which *J. kimi* does not possess. *Jassa monodon* has a distinctive cluster of setae at the apex of the telson, which *J. kimi* lacks. *Jassa laurieae* and *J. pusilla* lack the carpal seta on gnathopod 1 that *J. kimi* possesses. The male dimorphism also differs. *Jassa kimi* does not bear plumose setae on antenna 2 while *J. laurieae* does. The thumb shape of the major male distinguishes *J. kimi* from *J. pusilla*: very long and slightly sinous in *J. kimi* with a squared end, while in *J. pusilla* the thumb is shorter and the tip incised.

For Southern Hemisphere species, the fringe of spine-like setae along the anterior margin of the basis of gnathopod 1, long carpal seta(e) on gnathopod 1 and/or the prehensile pereopods 5–7 will separate *J. kimi* from *J. alonsoae*, *J. fenwicki*, *J. hartmannae*, *J. ingens*, *J. justi*, *J. kjetilanna* and *J. thurstoni*. That leaves *J. gruneri*, which is less easy to compare as the thumbed male is unknown for *J. gruneri* but known for *J. kimi* and the female and juvenile are known for *J. gruneri* but unknown for *J. kimi*. When the female and juvenile male of *J. kimi* are found, it is likely that the palm of the gnathopod 2 will be concave, which is a characteristic of most Northern Hemisphere species of *Jassa*, while females and juvenile males of Southern Hemisphere species typically have sinuous palms (as does *J. gruneri*). Other characteristics may also distinguish these species: e.g., fewer articles in the antenna 2 flagellum in *J. kimi* than *J. gruneri* and generally more slender and elongated mouthparts in *J. kimi* than *J. gruneri*.

Jassa oclairi **Conlan, 1990**

(Table 12, Figs 62–64)

Diagnosis.

Both sexes:

Mandibular palp: article 2, dorsal margin with a fringe of setae.

Maxilla 1: without a seta or setal cluster at the base of the palp article 1.

Gnathopod 1: basis, anterolateral margin with only a few short setae distally; carpus with a single or small cluster of long setae at the anterodistal junction of the propodus (setae 40-50% of anterior margin length and slightly lateral).

Gnathopod 2: basis with a row of long plumose setae along the anterolateral margin (setae 75% of article width); carpus and propodus, setae on the anterior margin short and plumose (setal length < basis width).

Pereopods 5–7: propodus not expanded anteriorly.

Uropod 1: ventral peduncular spinous process underlying about 1/3 of the longest ramus.

Uropod 3: inner ramus without spines mid-dorsally (with only the single apical spine).

Telson: tip without apical setae (only the usual short setae at each dorsolateral cusp).

Thumbed male:

Antenna 2: large individuals nearly asetose, without plumose setae on the flagellum and peduncular article 5 (which are present in smaller males).

Gnathopod 2: propodus, palmar defining spines not produced on a ledge, present in small thumbed males but absent in large thumbed males. In minor males, the thumb is distally squared, short relative to body length and located on the distal half of the propodus. The dactyl is centrally toothed on the inner margin. In the major form male, the thumb is distally squared, and originates more centrally on the propodus. The dactyl is expanded close to the junction with the propodus but is not centrally toothed.

Adult female:

Antenna 2: with abundant plumose setae on the flagellum and peduncular article 5.

Gnathopod 2: propodus, palm concave, palmar defining angle acute.

Remarks. Only one major form male was available for study. Although larger in body size than the minor form adult males, its thumb was relatively short (Fig. 63). However, its second antennae were substantially longer than in the juvenile or female and lacked their plumosity on the peduncle article 5 and flagellum. This is the largest of the Northern Hemisphere species of *Jassa* and also the most plumose, with plumose setae occurring on the antennae 1 and 2, gnathopod 2 and pereopods 5–7. It is only known from Alaska and northern British Columbia (Fig. 10). This

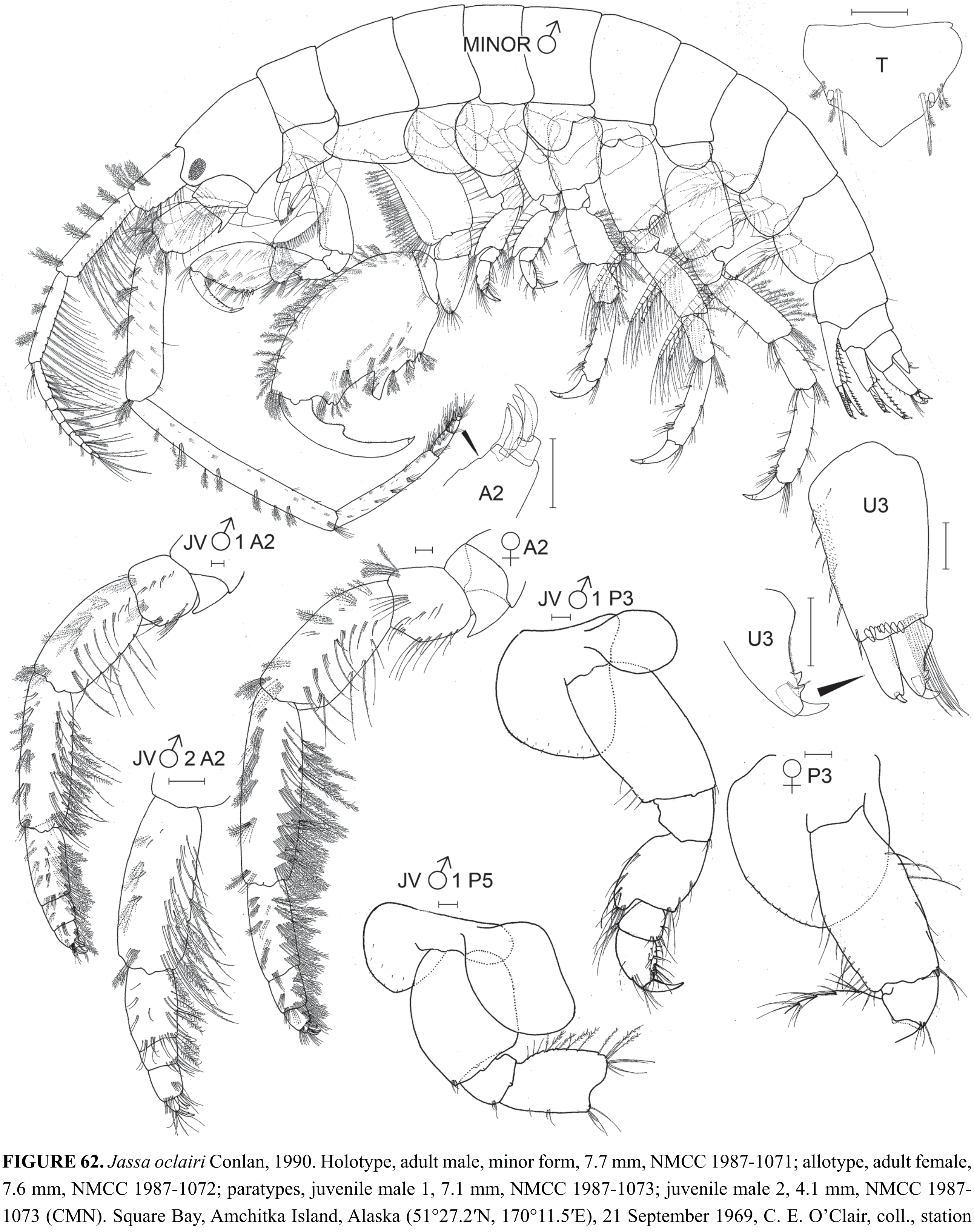

FIGURE 62. *Jassa oclairi* Conlan, 1990. Holotype, adult male, minor form, 7.7 mm, NMCC 1987-1071; allotype, adult female, 7.6 mm, NMCC 1987-1072; paratypes, juvenile male 1, 7.1 mm, NMCC 1987-1073; juvenile male 2, 4.1 mm, NMCC 1987-1073 (CMN). Square Bay, Amchitka Island, Alaska (51°27.2′N, 170°11.5′E), 21 September 1969, C. E. O'Clair, coll., station CT 02069, amongst kelp community dominated by *Laminaria longipes* on exposed rocky shore in the intertidal zone below MLLW, 1976-30 (CMN). Lateral view: whole body; dorsal view: telson; other views medial. Appendages are of the holotype unless noted otherwise. Scale 0.1 mm. Illustration after Conlan (1990).

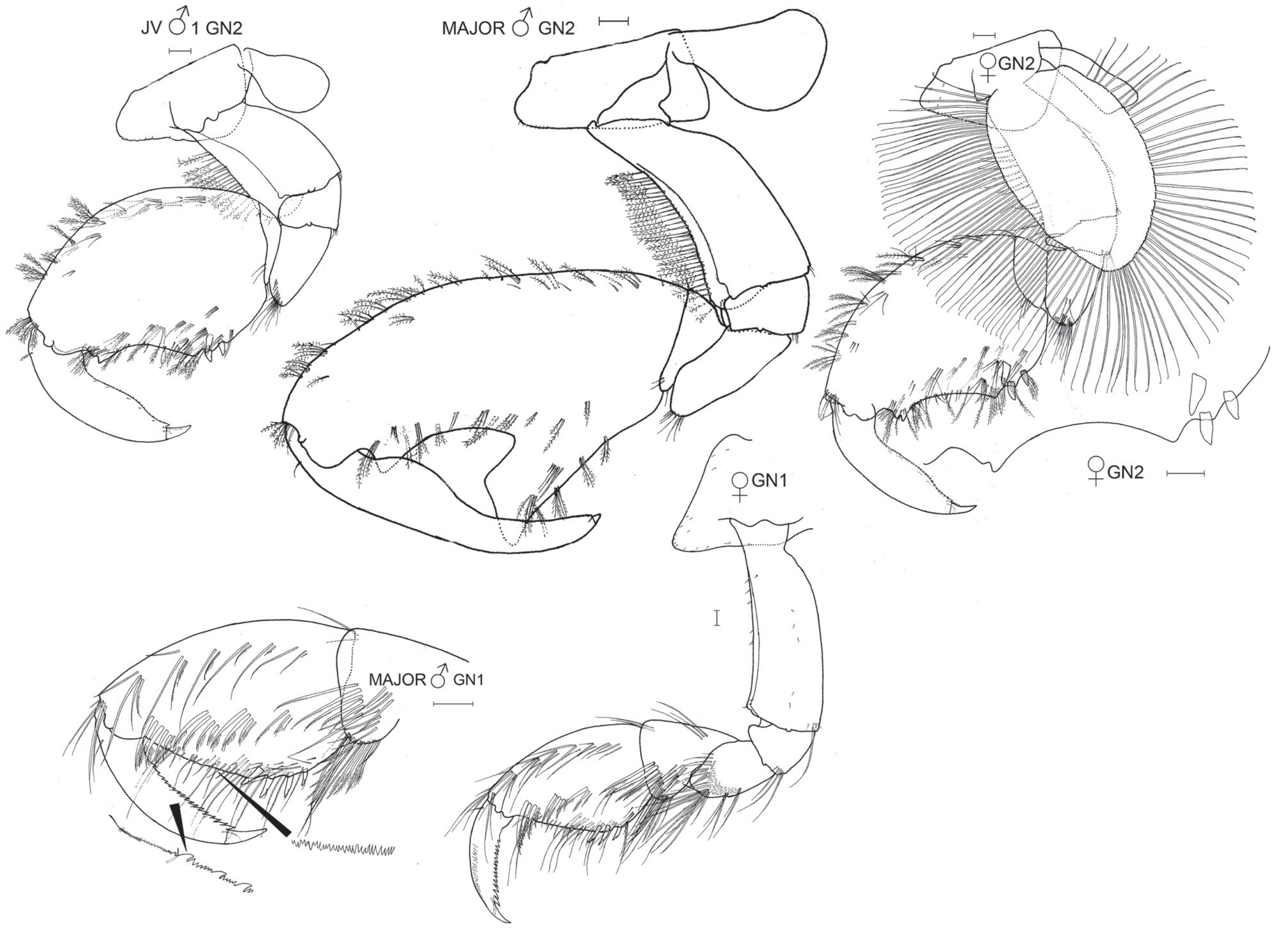

FIGURE 63. *Jassa oclairi* Conlan, 1990. Allotype, adult female, 7.6 mm; paratype, juvenile male 1, 7.1 mm; adult male, major form, 11.6 mm. Snipe Bay, Baranof Island, Alaska (56°25′N, 134°57′W), 8 July 1975, no further collection data (University of Alaska). All views medial. Scale 0.1 mm.

is the only Pacific species known to have the dorsal fringe of setae on article 2 of the mandibular palp. It shares this character state with the European *J. falcata* and *J. herdmani*. All other species lack this fringe. This is the only Pacific species known to have the dorsal fringe of setae on article 2 of the mandibular palp. It shares this character state with the European *J. falcata* and *J. herdmani*. All other species lack this fringe.

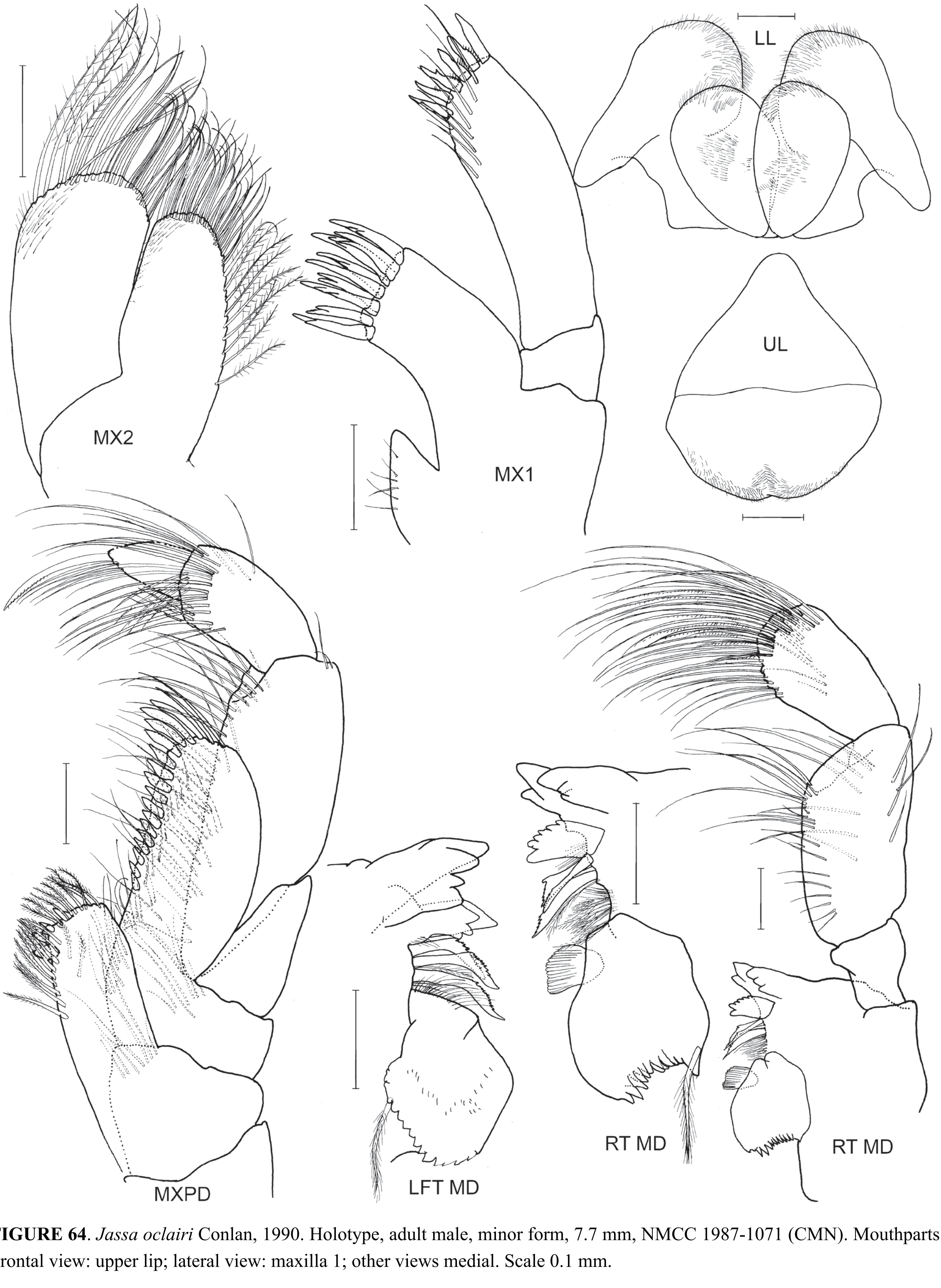

FIGURE 64. *Jassa oclairi* Conlan, 1990. Holotype, adult male, minor form, 7.7 mm, NMCC 1987-1071 (CMN). Mouthparts. Frontal view: upper lip; lateral view: maxilla 1; other views medial. Scale 0.1 mm.

Jassa borowskyae Conlan, 1990

(Table 12, Figs 65–66)

Diagnosis.

Both sexes:

Mandibular palp: article 2, dorsal margin without a fringe of setae.

Maxilla 1: without a seta or setal cluster at the base of the palp article 1.

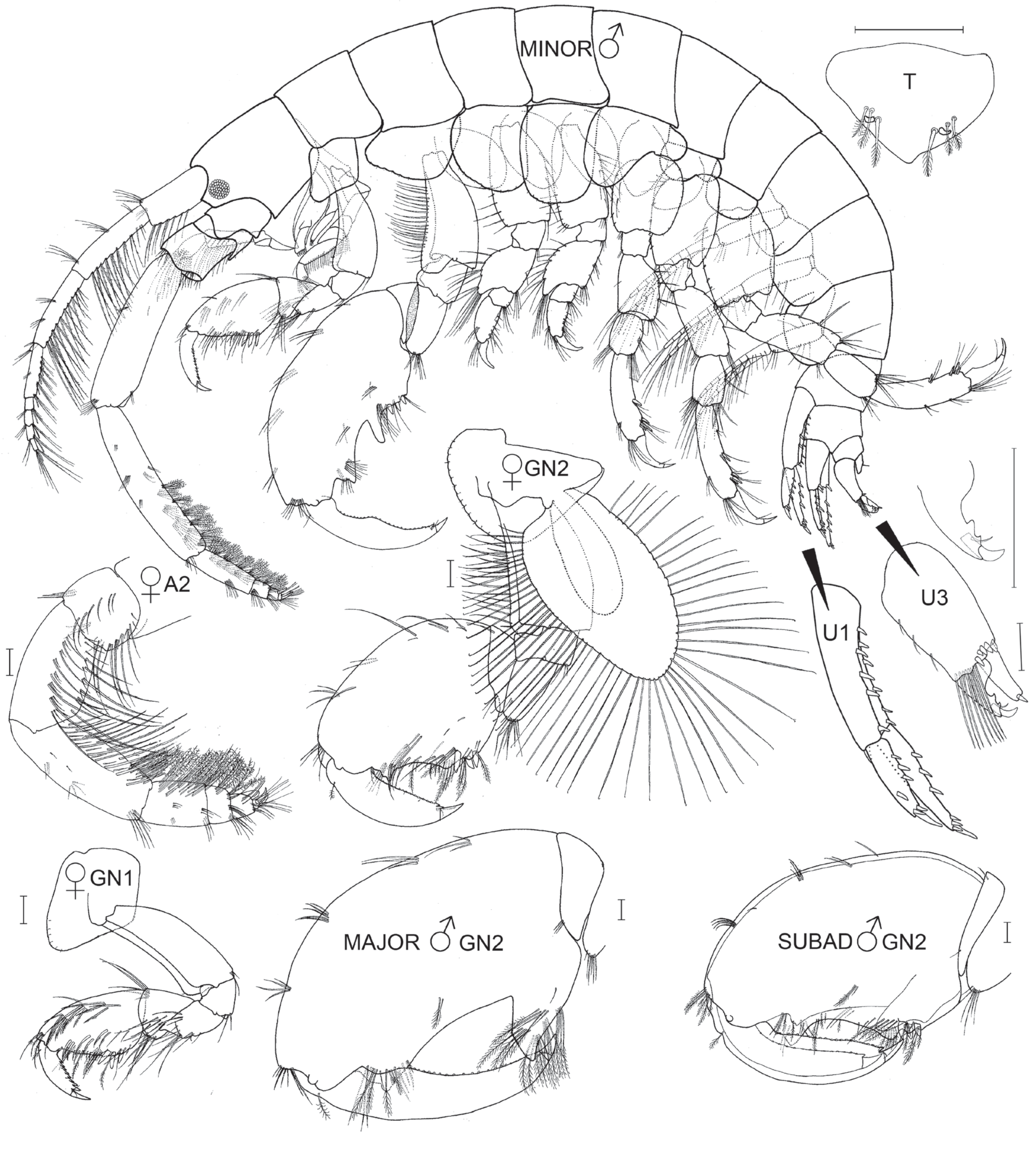

FIGURE 65. *Jassa borowskyae* Conlan, 1990. Holotype, adult male, minor form, 4.5 mm, NMCC 1987-1064; allotype, adult female, 5.0 mm, NMCC 1987-1065. Brady's Beach, Barkley Sound, Vancouver Island, British Columbia, 26 June 1976, E. L. Bousfield, coll., station B5, scrapes of boulders embedded in sand, *Phyllospadix*, kelp, brown algae, at low water, 1976-157 (CMN). Subadult male, 4.3 mm; adult male, major form, 5.0 mm. Point Grenville, Washington, 22 July 1966, E. L. Bousfield, coll., station W22, scrapes of boulders embedded in sand at low water, 1966-211 (CMN). Lateral views: whole body and uropods; dorsal view: telson; other views medial. Appendages are of the holotype unless noted otherwise. Scale 0.1 mm. Illustration after Conlan (1990).

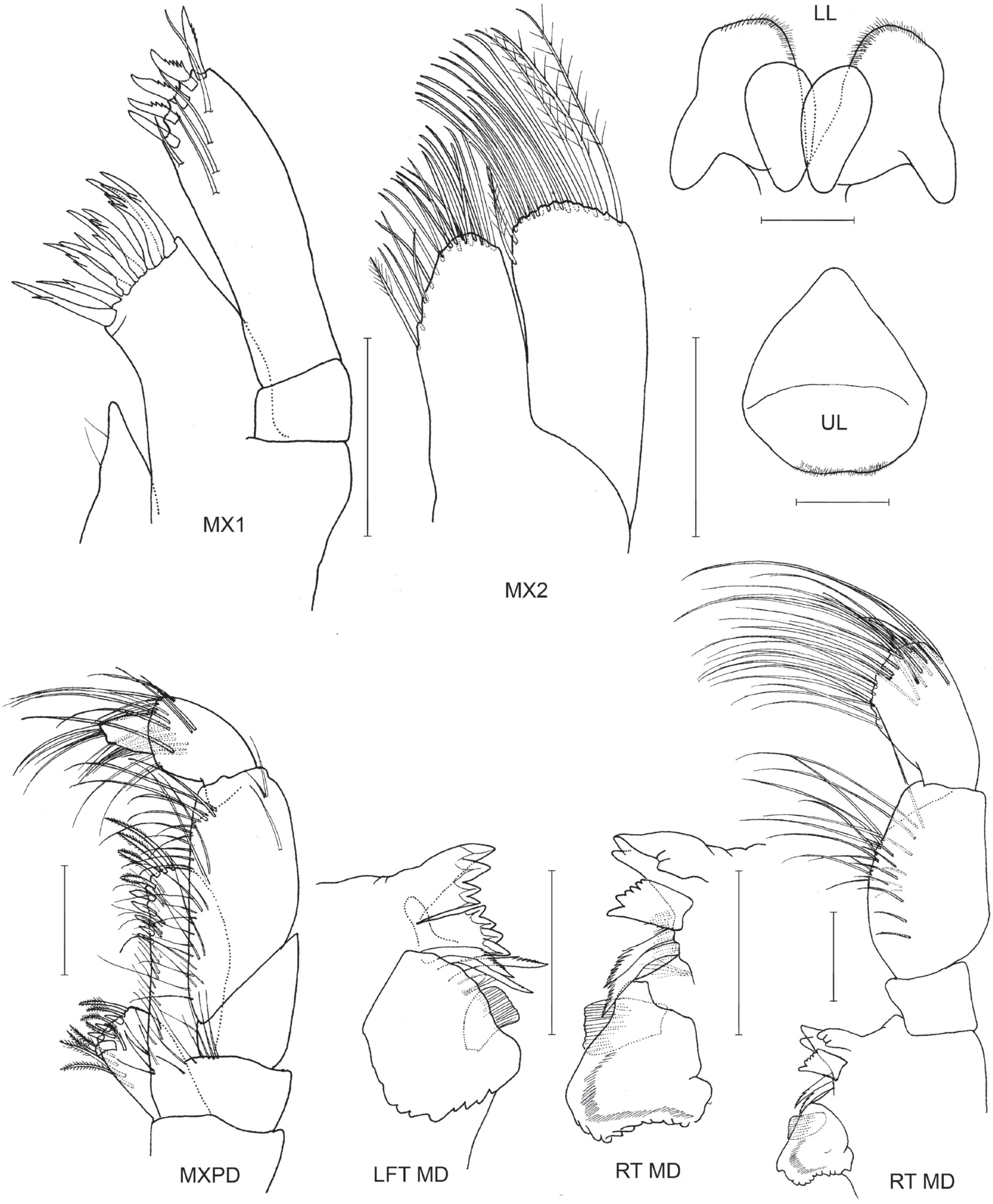

FIGURE 66. *Jassa borowskyae* Conlan, 1990. Holotype, adult male, minor form, 4.5 mm, NMCC 1987-1064. Brady's Beach, Barkley Sound, Vancouver Island, British Columbia, 26 June 1976, E. L. Bousfield, coll., station B5, scrapes of boulders embedded in sand, *Phyllospadix*, kelp, brown algae, at low water, 1976-157 (CMN). Mouthparts. Frontal view: upper lip; lateral views: maxillae 1 and 2 and maxilliped; other views medial. Scale 0.1 mm.

Gnathopod 1: basis, anterolateral margin without a row of short setae along its length; carpus with a single or small cluster of long setae at the anterodistal junction of the propodus (setae 95% of anterior margin length and slightly lateral).

Gnathopod 2: basis with a row of setae along the anterolateral margin (setae >50% of basis width); carpus and propodus, setae on the anterior margin short and simple (setal length < basis width).

Pereopods 5–7: propodus not expanded anteriorly.

Uropod 1: ventral peduncular spinous process very short, underlying only 10% of the longest ramus.

Uropod 3: inner ramus without spines mid-dorsally (with only the single apical spine).

Telson: tip without apical setae (only the usual short setae at each dorsolateral cusp).

Thumbed male:

Antenna 2: large individuals with plumose setae on the flagellum and peduncular article 5 and lacking long filter setae.

Gnathopod 2: propodus, palmar defining spines not produced on a ledge, present in small thumbed males but absent in large thumbed males. In minor males, the thumb is distally acute, short relative to body length and located on the distal half of the propodus. The dactyl is not strongly centrally toothed. In major males, the thumb is distally squared, longer relative to body length and on the proximal half of the propodus. The dactyl is expanded close to the junction with the propodus but is not centrally toothed.

Adult female:

Antenna 2: large animals with plumose setae on the flagellum and peduncular article 5.

Gnathopod 2: propodus, palm concave, palmar defining angle acute.

Remarks. *Jassa borowskyae* shares the abbreviated process on uropod 1 with two other Northeastern Pacific species, *J. myersi* and *J. shawi* while all other species of *Jassa* have a well developed peduncular process that is 25% to 50% the length of the longest ramus. However, these latter two species lack the diagnostic dense setal fringe on the basis of gnathopod 2 that *J. borowskyae* possesses. Many more minor than major form adult males were found in the collections of *J. borowskyae* available for study but there were not enough specimens from a single population to plot the relationship of thumb length or propodus length to body length.

Jassa staudei Conlan, 1990

(Table 12, Figs 67–77)

Diagnosis.

Both sexes:

Mandibular palp: article 2, dorsal margin without a fringe of setae.

Maxilla 1: without a seta or setal cluster at the base of the palp article 1.

Gnathopod 1: basis, anterolateral margin without a row of short setae along its length; carpus without a single or small cluster of setae at the anterodistal junction of the propodus.

Gnathopod 2: basis with a row of long setae along the anterolateral margin (setae length 100% of basis width); carpus and propodus, setae on the anterior margin long and simple (some setal lengths ≥ basis width).

Pereopods 5–7: propodus not expanded anteriorly.

Uropod 1: ventral peduncular spinous process underlying 35-40% of the longest ramus.

Uropod 3: inner ramus without spines mid-dorsally (with only the single apical spine).

Telson: tip without apical setae (only the usual short setae at each dorsolateral cusp).

Thumbed male:

Antenna 2: large individuals with plumose setae on the flagellum and peduncular article 5 and lacking long filter setae.

Gnathopod 2: propodus, palmar defining spines not produced on a ledge, present in small thumbed males but absent in large thumbed males. In minor males, the thumb is distally squared, short relative to body length and located on the distal half of the propodus. The dactyl is strongly centrally toothed. In major males, the thumb is distally squared, longer relative to body length and on the proximal half of the propodus. The dactyl is expanded close to the junction with the propodus but is not centrally toothed.

Adult female:

Antenna 2: large animals with plumose setae on the flagellum and peduncular article 5.

Gnathopod 2: propodus, palm concave, palmar defining angle acute.

Remarks. Conlan (1990) noted that *J. staudei* has longer setae along the anteroproximal margin of the second gnathopod propodus than any other species. This is a key feature of the species as it is invariate (occurring in both sexes and at all ages). Another key feature is the lack of a single or cluster of setae at the junction of the carpus and propodus of gnathopod 1 (also an invariate character state). Other characteristics of the species are the plumose setae that appear on the antenna 2 peduncle article 5 and flagellum in larger males and females, the long, dense setae on the anterior margin of the gnathopod 2 basis, the well-developed peduncular spinous process on uropod 1, and the characteristics of the maxilla 1, mandibular palp and uropod 1 as noted above. All these characters combined will serve to distinguish this speci es from congeners on the Pacific coast of North America, whether native or introduced.

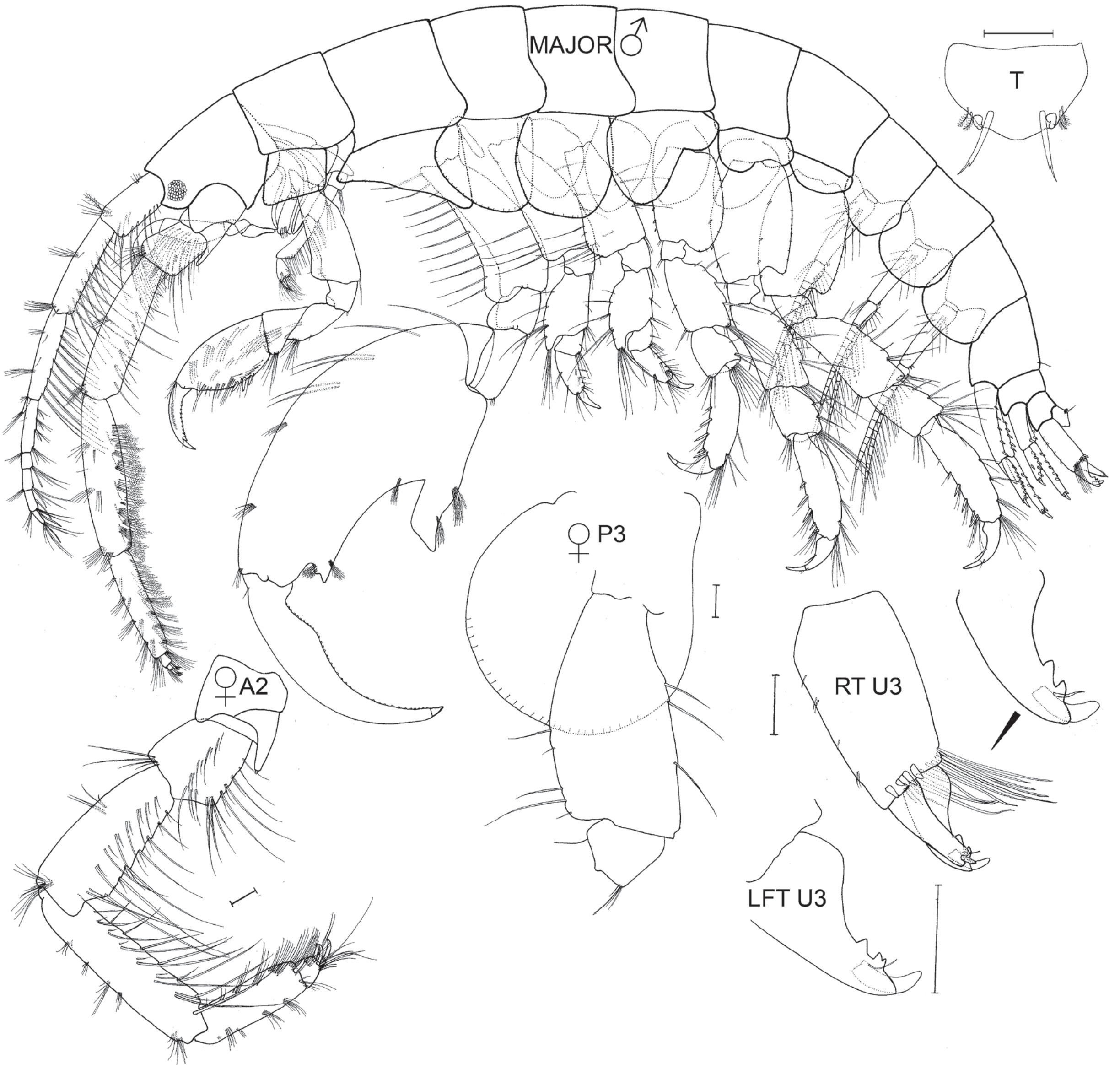

FIGURE 67. *Jassa staudei* Conlan, 1990. Holotype, adult male, major form, 6.0 mm, NMCC 1987-1074; allotype, adult female, 5.5 mm, NMCC 1987-1075. North side of Wouwer Island, Broken Group, Barkley Sound, Vancouver Island, British Columbia (48°51.06′N, 125°21.08′W), 27 June 1976, E. L. Bousfield, coll., station B7, dip net collection at low water, amongst *Phyllospadix* Hooker (1840), kelp, sponges and under rock, 1976-157 (CMN). Lateral view: whole body; dorsal view: telson; other views medial. Appendages are of the holotype unless noted otherwise. Scale 0.1 mm. Illustration after Conlan (1990).

In a population of *J. staudei* collected inside the pressure head tank for the aquaria at Friday Harbor Laboratories, Washington, minor forms were rare compared to major forms (Table 14, Figs 69–72). Sampled near-monthly from June 1985 to Feb. 1987 (Figs 70–72), major forms achieved a greater body length than minor forms on average and always had longer thumbs relative to body length than the minor forms (Table 14). Average major form body length was 8.5 ± 1.1 mm (*n* = 276), with a range of 4.8–10.7 mm. The smallest major form was found in December 1985 (4.8 mm) and largest in October 1986 (10.7 mm). Only 19 minor forms were found over the 18 samplings, giving an overall ratio for minor to major of 0.069:1. Average minor form body length was 5.7 ± 0.8 mm. The smallest minor form was found in September 1985 (3.8 mm) and the largest in June and July 1986 (6.6 mm). Juvenile males were found in all samplings with a maximum body length of 9.0 mm found in October 1986. However, large juveniles close to this size were found in most of the other collections as well.

Minor forms were also rare in four geographically varying populations collected in June along the western coast of North America (Fig. 73). Average body length of major form males was greatest at the protected location (Friday Harbor, Washington: 8.69 ± 1.31 mm). Among the three other locations, which were on exposed Pacific coasts, average body length increased southwards, from Wouwer Island, British Columbia (4.93 ± 0.57 mm) to Pt. Delgada, California (5.86 ± 0.50 mm) to Albion Cove, California (7.92 ± 0.82 mm).

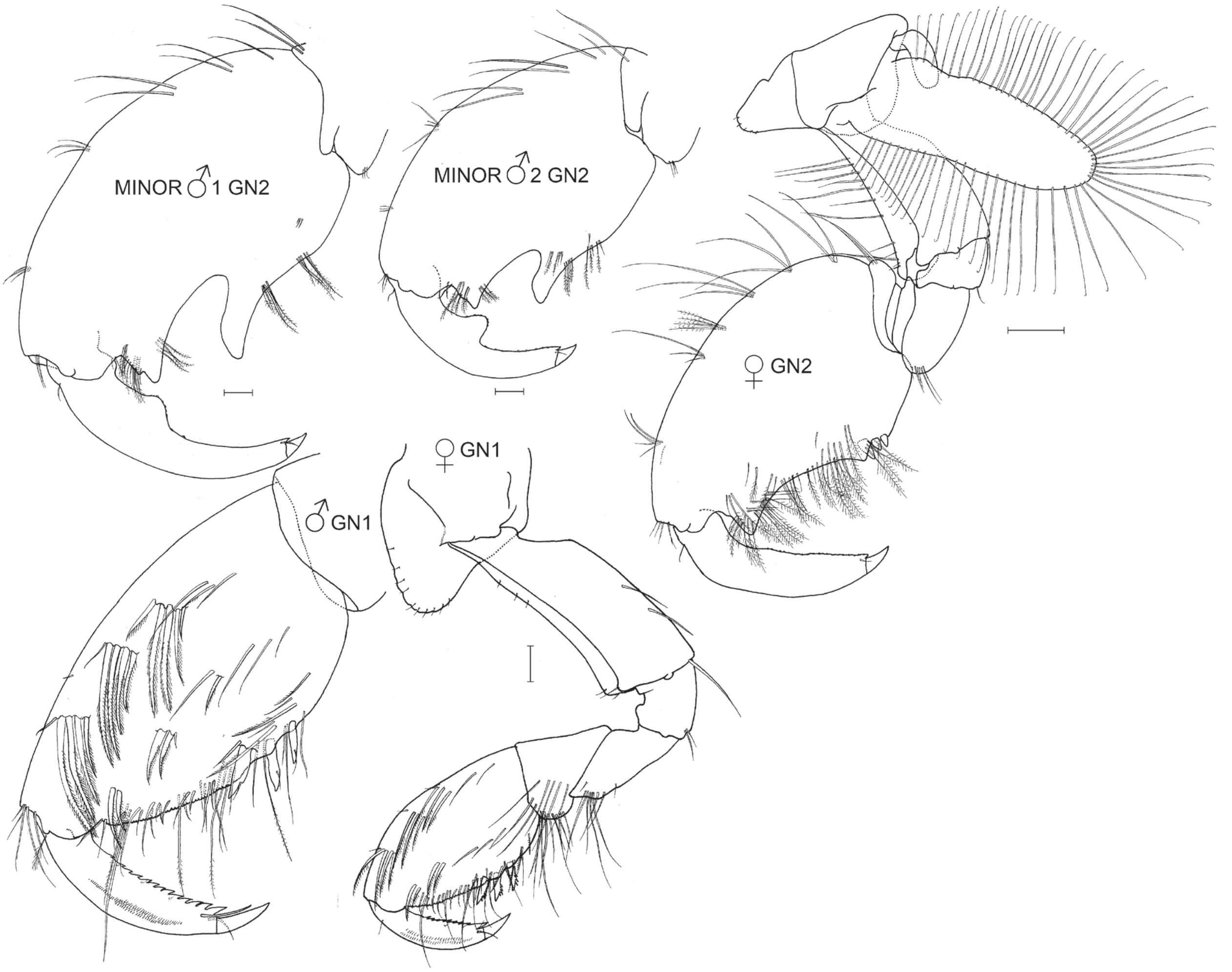

FIGURE 68. *Jassa staudei* Conlan, 1990. Holotype, adult male, major form, 6.0 mm, NMCC 1987-1074; allotype, adult female, 5.5 mm, NMCC 1987-1075; paratype, adult male 1, minor form, 5.1 mm, NMCC 1987-1076. Adult male 2, minor form, 4.2 mm, Edward King Island, British Columbia, 10 July 1976, E. L. Bousfield, coll., station B28, dip net collection at low water, amongst *Phyllospadix*, kelp, sponges and under rock, 1976-157 (CMN). All views medial. Appendages are of the holotype unless noted otherwise. Scale 0.1 mm.

TABLE 14. Summary of the time series graphs for male *J. staudei* (Figs. 69–72). Collections were made by Craig Staude from 23 June 1985 to 23 Feb. 1987 from the pressure head tanks for the marine lab aquaria at Friday Harbor Laboratories, Washington.

	Major form		Minor form		Juvenile	
	Body length (mm)	Thumb length (mm)	Body length (mm)	Thumb length (mm)	Body length (mm)	Thumb length (mm)
Average	8.5	0.9	5.7	0.2	6.9	0.0
Standard deviation	1.1	0.2	0.8	0.1	1.3	0.0
Minimum	4.8	0.2	3.8	0.1	2.3	0.0
Maximum	10.7	1.4	6.6	0.3	9.0	0.0
n	276	276	19	19	270	270

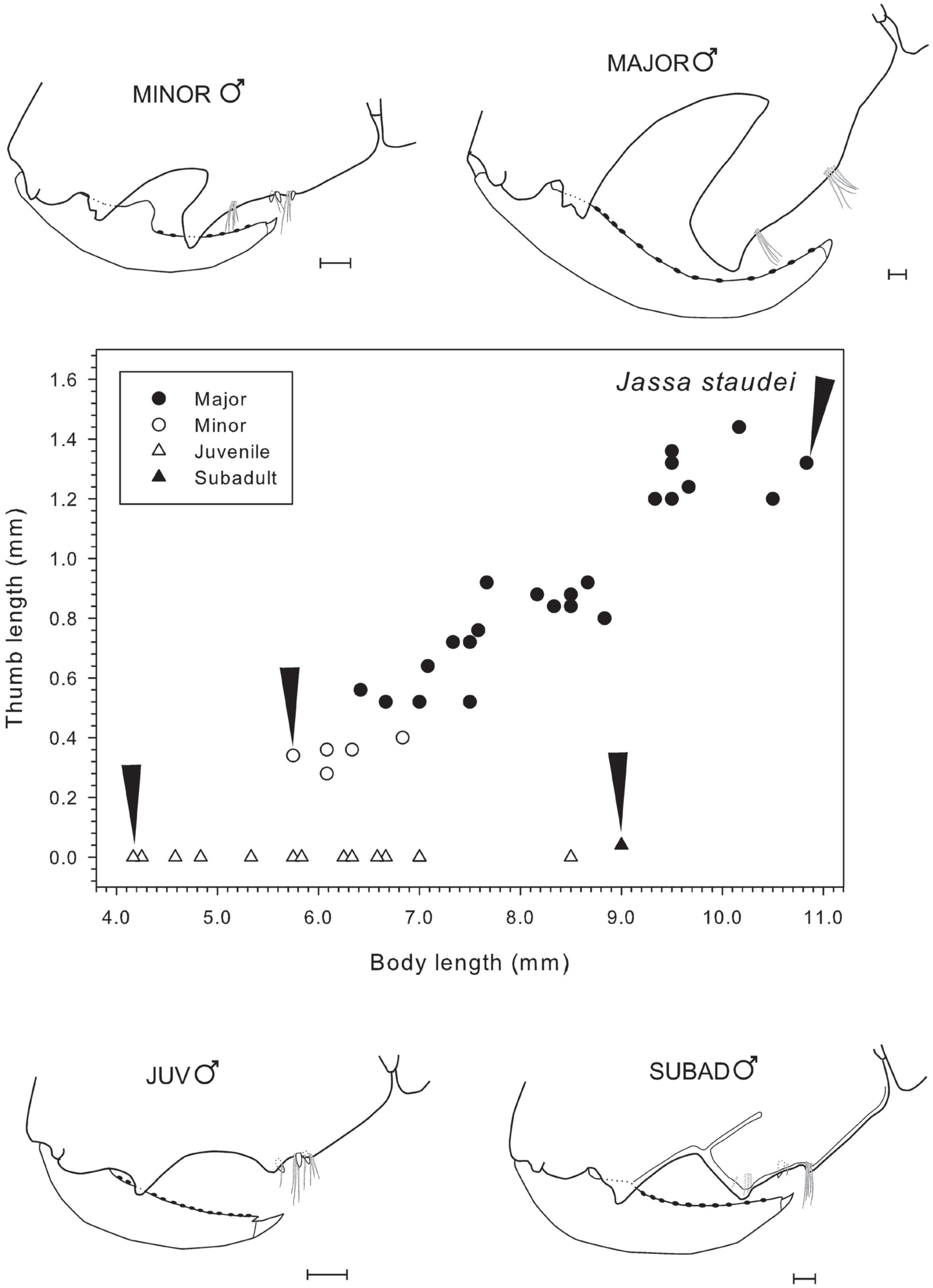

FIGURE 69. *Jassa staudei* Conlan, 1990. Variation in thumb length relative to body length in males living inside the east pressure head tank at Friday Harbor Laboratories, San Juan Island, Washington, 2 October 1984, C. Staude, coll., IZ1984-175 (CMN). Arrows refer to the associated gnathopod illustrations. The subadult male had a thumb visible inside the cuticle, indicating that it would molt next into a thumbed adult. Setae omitted except for those around the thumb and spines in order to landmark position changes with growth. All views lateral. Scale 0.1 mm. Linear regression assumptions failed for all plots. Illustration after Conlan (1990).

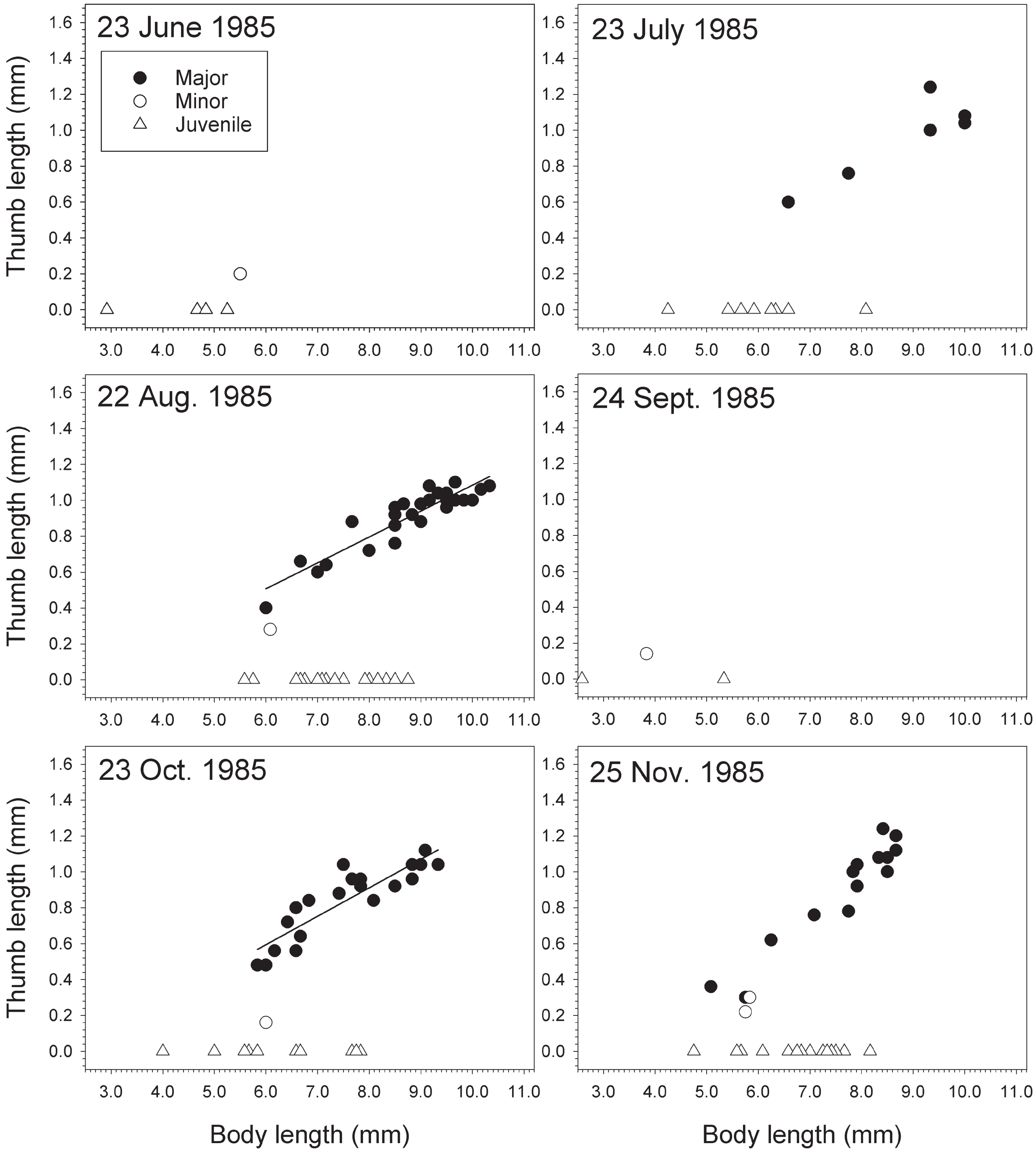

FIGURE 70. *Jassa staudei* Conlan, 1990. Variation in thumb length relative to body length in males from populations collected in June–Nov. 1985 from the east pressure head tank at Friday Harbor Laboratories, San Juan Island, Washington, C. Staude, coll., IZ1984-175 (CMN). Linear regression assumptions passed for the adult major form males on 22 Aug. and 23 Oct. 1985. Linear regression statistics: 22 Aug. 1985: Major form, thumb length = -0.359 + 0.144 x body length, r^2 = 0.842, *n* = 27; 23 Oct. 1985: Major form, thumb length = -0.355 + 0.158 x body length, r^2 = 0.784, *n* = 20. Subadult males (those with a thumbed cuticle visible inside the propodus) were not differentiated from juveniles.

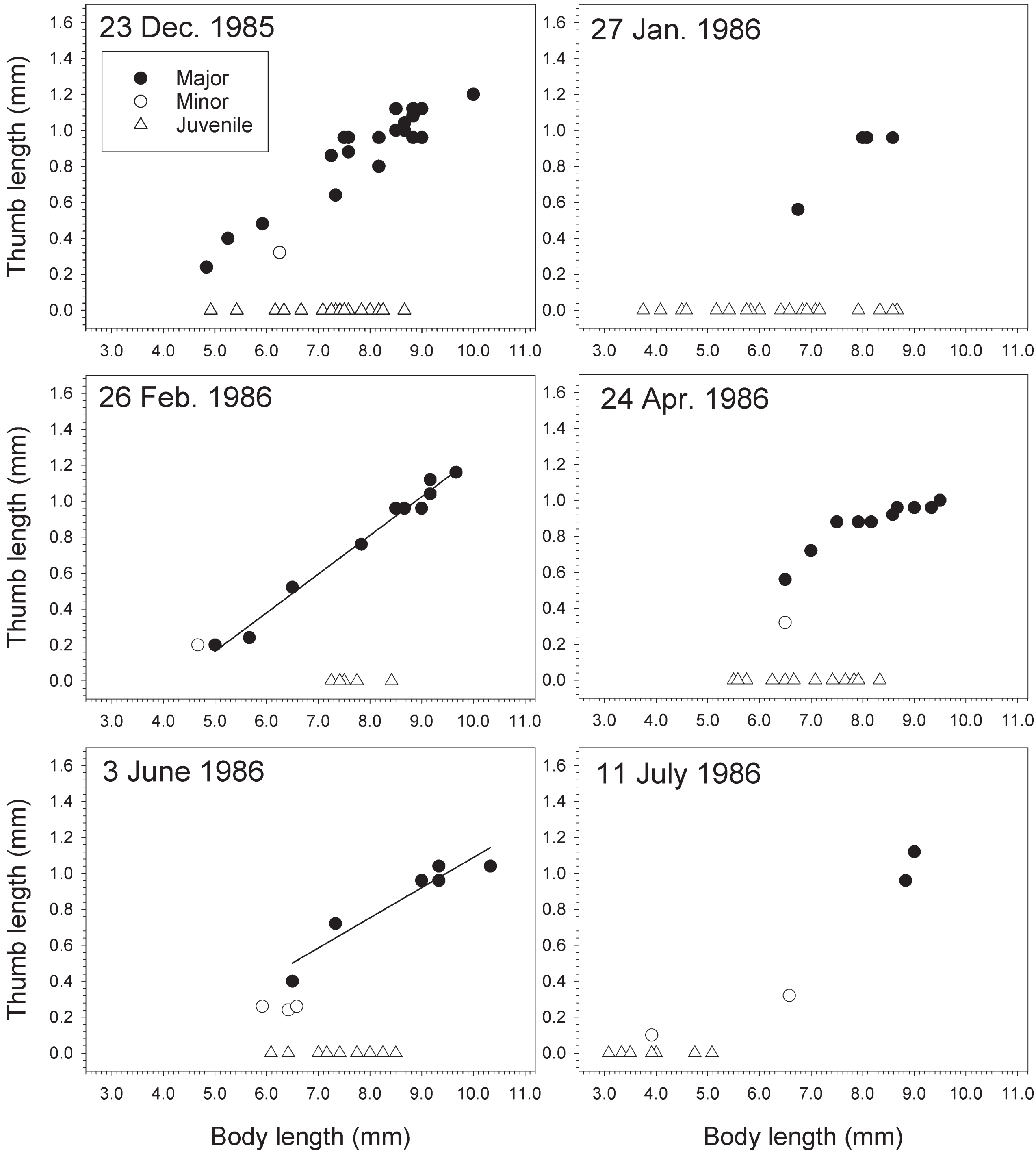

FIGURE 71. *Jassa staudei* Conlan, 1990. Variation in thumb length relative to body length in males from populations collected in Dec. 1985–July 1986 from the east (Dec.–Feb.) or west (Apr.–July) pressure head tank at Friday Harbor Laboratories, San Juan Island, Washington, C. Staude, coll., IZ1984-175 (CMN). Linear regression assumptions passed for the adult major form males on 26 Feb. and 3 June 1986. Linear regression statistics: 26 Feb. 1986: Major form, thumb length = -0.910 + 0.215 x body length, $r^2 = 0.985$, $n = 10$; 3 June 1986: Major form, thumb length = -0.587 + 0.168 x body length, $r^2 = 0.893$, $n = 7$. Subadult males (those with a thumbed cuticle visible inside the propodus) were not differentiated from juveniles.

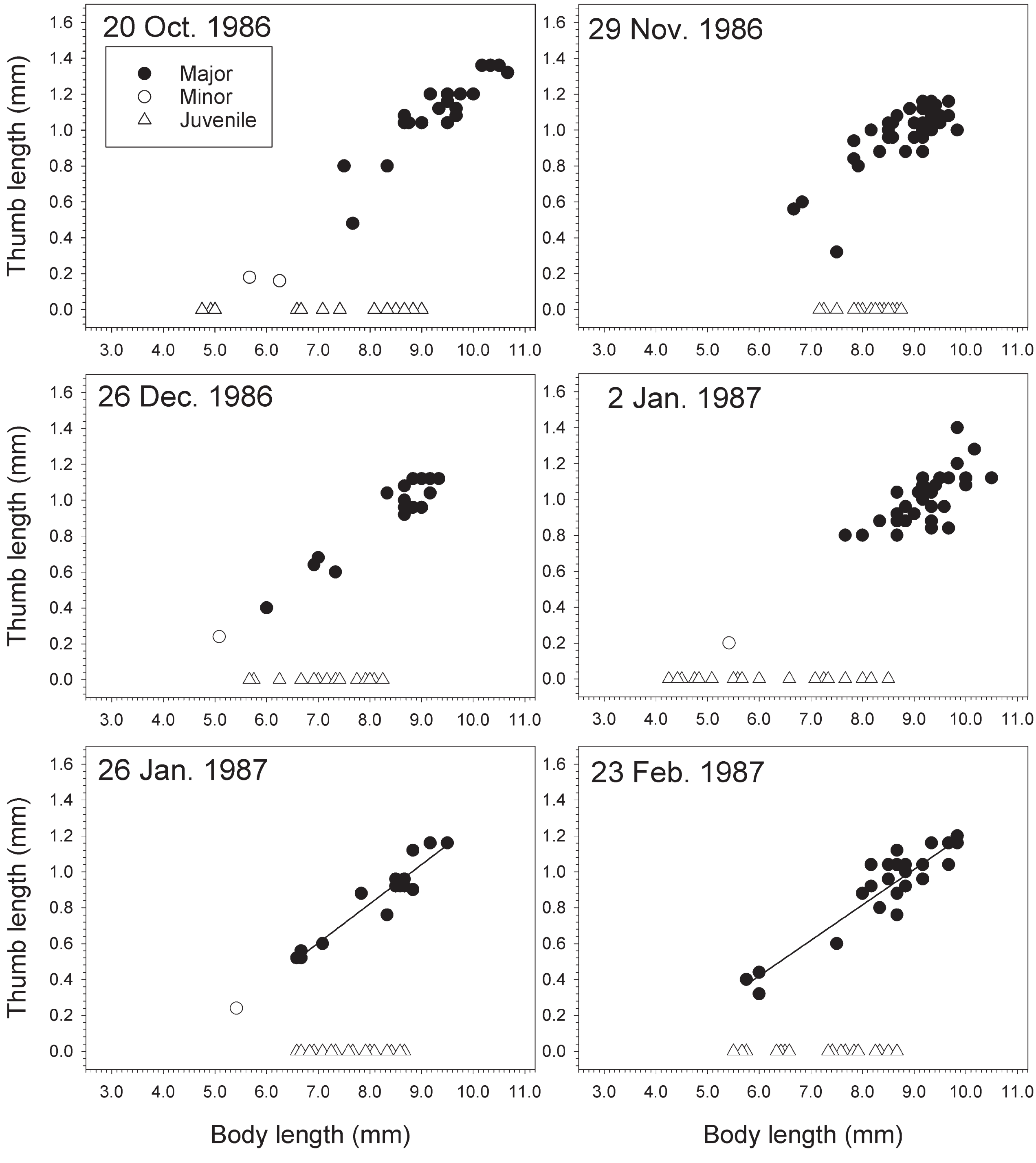

FIGURE 72. *Jassa staudei* Conlan, 1990. Variation in thumb length relative to body length in males from populations collected in Oct. 1986–Feb. 1987 from the west pressure head tank at Friday Harbor Laboratories, San Juan Island, Washington, C. Staude, coll., IZ1984-175 (CMN). Linear regression assumptions passed for the adult major form males on 26 Jan. and 23 Feb. 1987. Linear regression statistics: 26 Jan. 1987: Major form, thumb length = -0.926 + 0.219 x body length, $r^2 = 0.906$, $n = 15$; 23 Feb. 1987: Major form, thumb length = -0.766 + 0.198 x body length, $r^2 = 0.843$, $n = 26$. Subadult males (those with a thumbed cuticle visible inside the propodus) were not differentiated from juveniles.

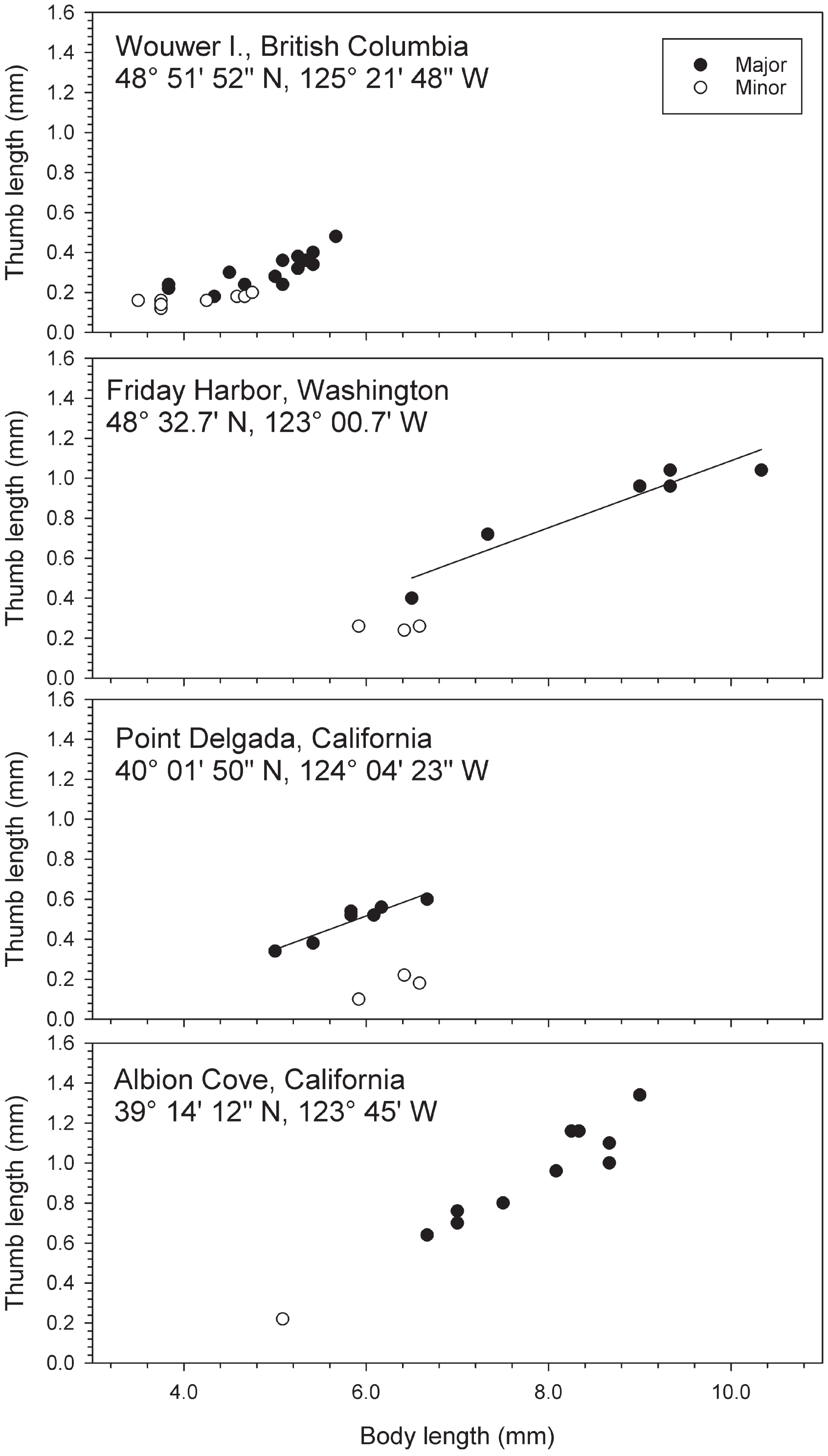

FIGURE 73. *Jassa staudei* Conlan, 1990. Variation in thumb length relative to body length in thumbed males from four populations collected in June on the Pacific coast of North America, ordered by latitude. West side of Wouwer Island, British Columbia, 27 June 1976, E. L. Bousfield, coll., station B7, low water collection, bedrock, *Phyllospadix*, kelp, sponges, ~12 °C, ~32+ psu, 1976-157 (CMN). Friday Harbor Laboratories, San Juan Island, Washington, west pressure head tank for marine lab aquaria, 3 June 1986, C. Staude, coll., IZ1984-175 (CMN). Shelter Cove, Point Delgada, California: 5 June 1986, P. Shaw, coll., formalin wash of open coast shallow subtidal algae and bryozoans (*Aglaophenia* Lamouroux, 1812), >33psu, rocky coast, strong surge. Albion Cove, California, 29 June 1978, J.R. Chess, coll., airlift pump of fouling community on rock substrate, 20 m depth, IZ1986-071 (CMN). Linear regression assumptions passed for the adult major form males at Friday Harbor and Point Delgada. Linear regression statistics: Friday Harbor: Major form, thumb length = -0.587+ 0.168 x body length, $r^2 = 0.893$, $n = 7$; Point Delgada: Major form, thumb length = -0.489 + 0.168 x body length, $r^2 = 0.885$, $n = 8$.

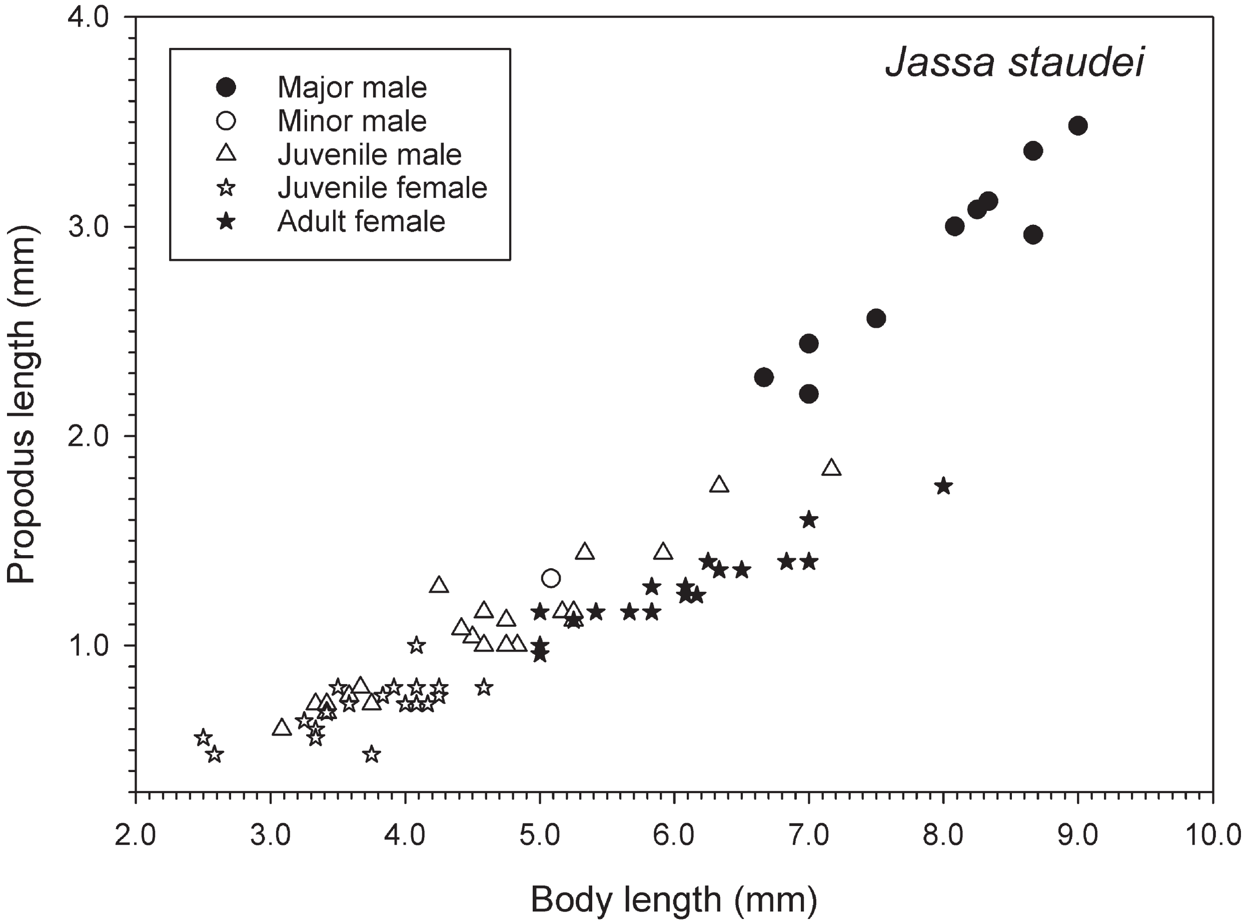

FIGURE 74. *Jassa staudei* Conlan, 1990. Variation in gnathopod 2 propodus length relative to body length in adult and juvenile males and females in a population from Albion Cove, California, 29 June 1978, J.R. Chess, coll., airlift pump of fouling community on rock substrate, 20 m depth, IZ1986-071 (CMN). Linear regression assumptions failed for all plots.

The Albion Cove population was also assessed for length of the gnathopod 2 propodus relative to body length (Fig. 74). For the four groups that were sufficiently numerous to measure, the relationship of propodus to body length appeared to be isometric for females and allometric for males. However, the data failed one or more assumptions of normality, constant variance or independence of residuals and so regressions were not applied. Adult major form males (n = 10) were considerably greater in body length (7.92 ± 0.82 mm, n = 10), than adult females (6.07 ± 0.79 mm, n = 19) and had a longer propodus as well (2.85 ± 0.45 mm vs 1.28 ± 0.19 mm). Of the 23 juvenile males measured, only one overlapped the major form adult males in body length (7.17 mm) but its propodus length (1.84 mm) was shorter than any of the major form adults that were of similar size (propodus length 2.31 ± 0.12 mm, body length 6.89 ± 0.19 mm, n = 3). For the females, there was no overlap in body length between juveniles and adults. However, for juvenile females and juvenile males, propodus length was similar among small sized individuals of both sexes but diverged in larger juveniles with a longer propodus in the males than females. However, the differences in the median propodus length between the juvenile males (n = 8) and adult females (n = 19) that overlapped in body length (5.0–8.0 mm) were not great enough to exclude the possibility that the difference was due to random sampling variability (ANOVA, F = 3.651, p = 0.068, *power* = 0.332).

Fig. 76 shows magnifications of the second antenna flagellum in an adult female (A, B) and a subadult male (C, D). For suspension feeding, the second antennae are splayed out ~90°to either side of the body and the antennal setae spread widely. Along with the splayed first antennae, this provides a near 180°wide net for the capture of drifting particles. The curved spines at the flagellum tip (A) and scaled setae (B) are adaptations for deposited (spines) and suspended (scales) food capture. Fig. 76B shows that the scales cover the anterior length of the filter setae and wrap around the setae only partially, so the posterior length is bare. Possibly this arrangement improves capture of small particles which are then scraped by the medial setae of the first and second gnathopods, mandibular palps and

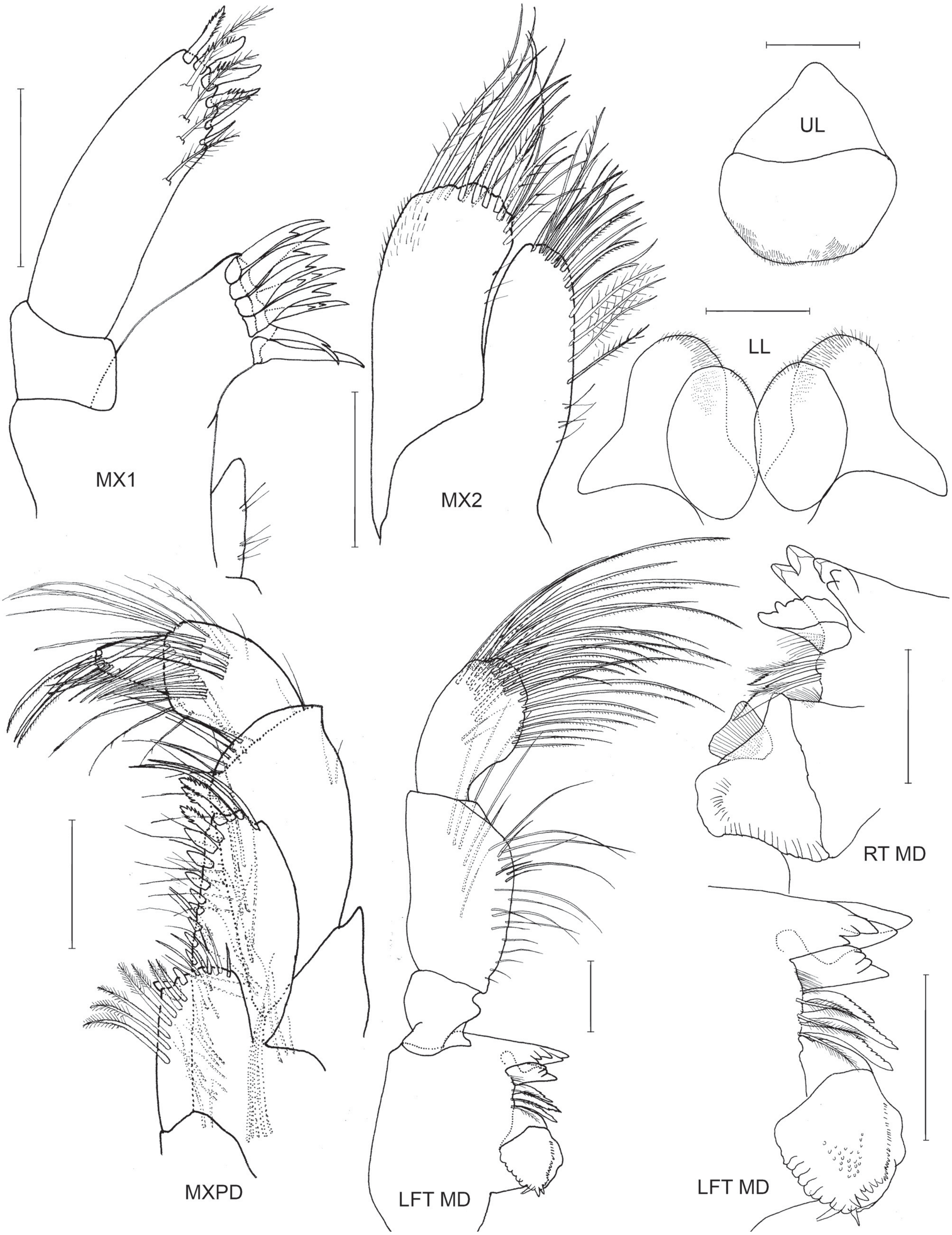

FIGURE 75. *Jassa staudei* Conlan, 1990. Holotype, adult male, major form, 6.0 mm, NMCC 1987-1074. North side of Wouwer Island, Broken Group, Barkley Sound, Vancouver Island, British Columbia (48°51.06′N, 125°21.08′W), 27 June 1976, E. L. Bousfield, coll., station B7, dip net collection at low water, amongst *Phyllospadix* Hooker (1840), kelp, sponges and under rock, 1976-157 (CMN). Mouthparts. Frontal view: upper lip; lateral view: maxilla 1; other views medial. Scale 0.1 mm.

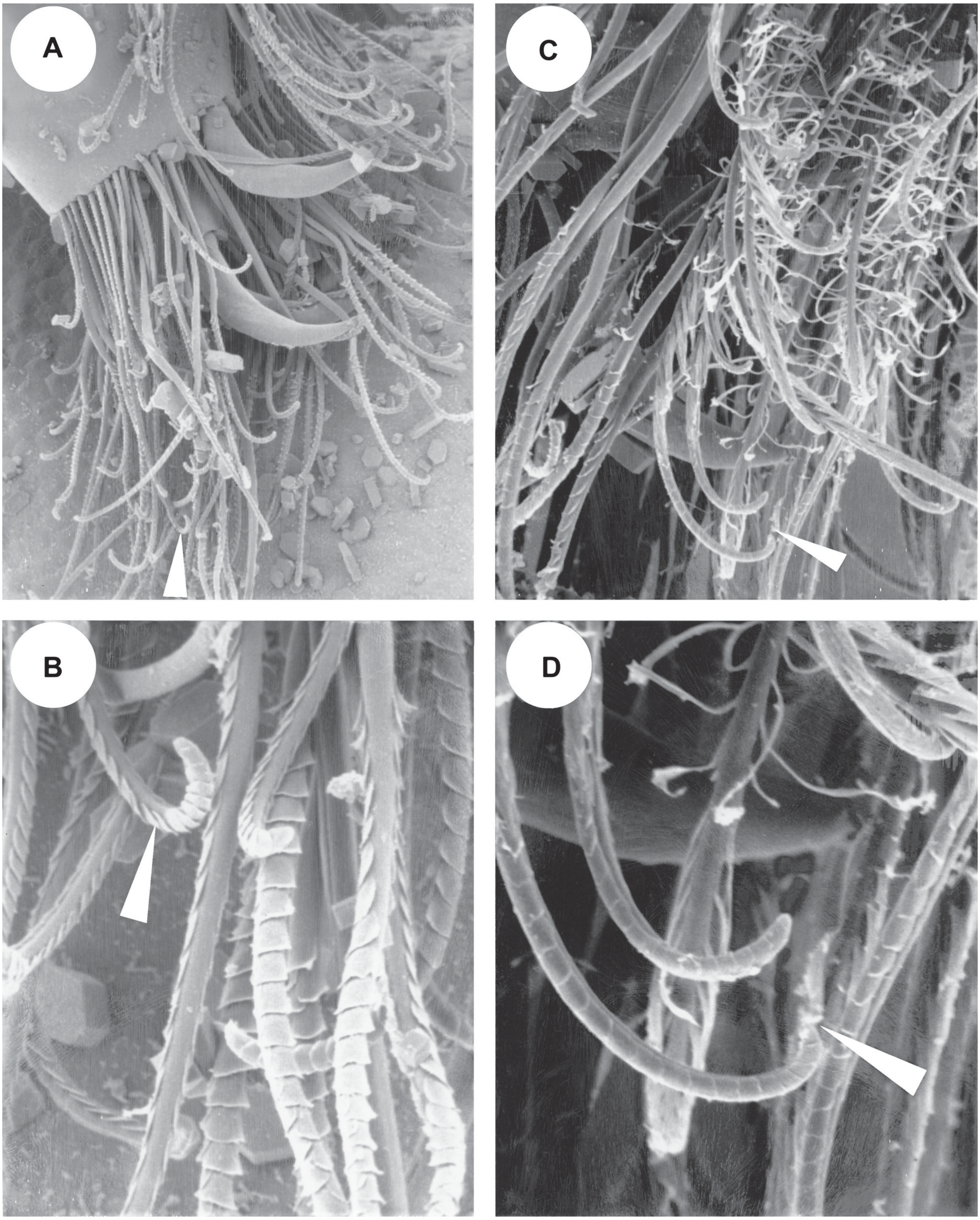

FIGURE 76. *Jassa staudei* Conlan, 1990. East pressure head tank at Friday Harbor Laboratories, San Juan Island, Washington, 26 Dec. 1986, C. Staude, coll., IZ1984-175 (CMN). Antenna 2, tip of flagellum. A, adult female, 9.0 mm; B, magnification of A, arrow showing the same seta as in A; C, subadult male, 7.5 mm; D, magnification of C, arrow showing the same seta as in C. A and C x1200; B and D x4700.

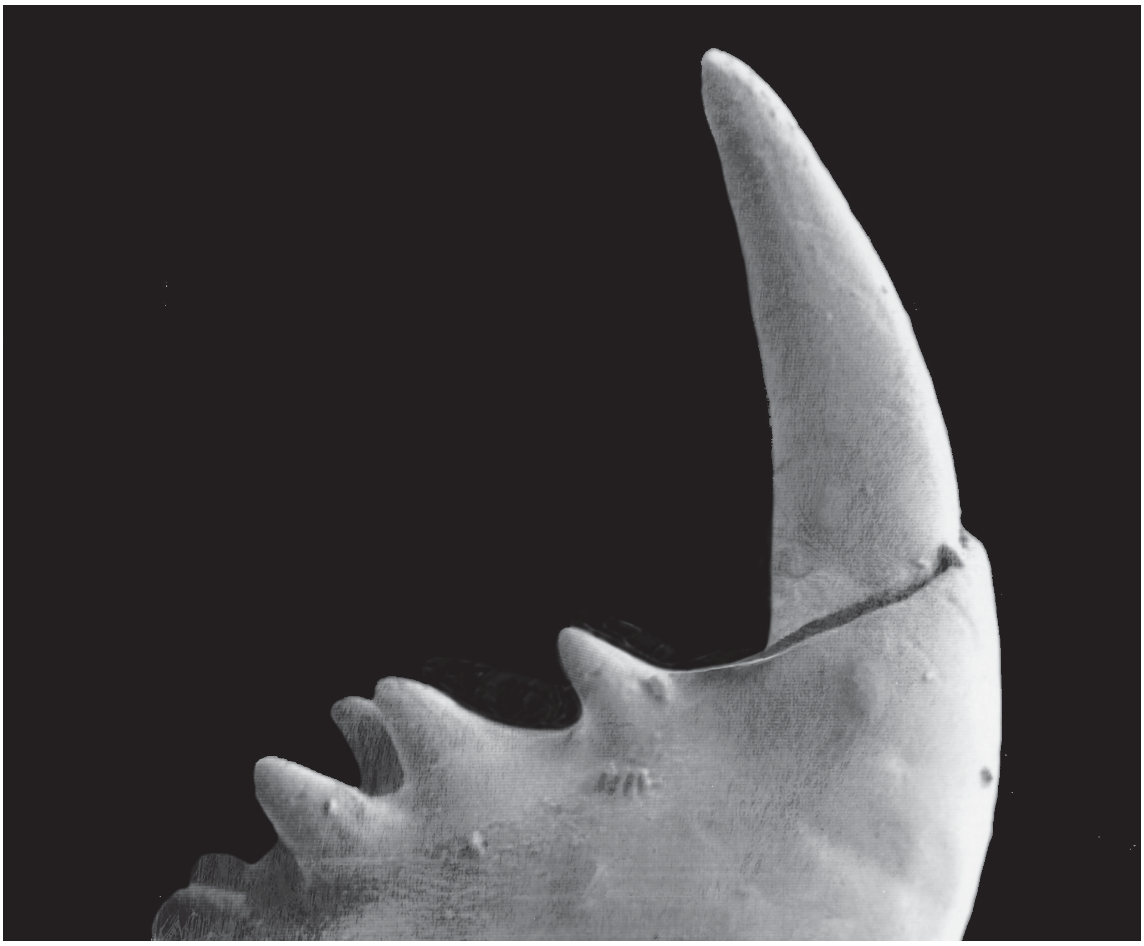

FIGURE 77. *Jassa staudei* Conlan, 1990. Adult male, major form, 9.0 mm. East pressure head tank at Friday Harbor Laboratories, San Juan Island, Washington, 26 Dec. 1986, C. Staude, coll, IZ1984-175 (CMN). Uropod 3, tip of outer ramus. x1200.

maxilliped palps. The antennal setae are also used to capture particles on the uropods, when the urosome is bent under the body toward the head (pers. obs. on *J. marmorata*). The plumose setae typical of larger individuals of both sexes are visible in the subadult male (Fig. 76C, D). The tip of the plumose seta, visible in Fig. 76D, has unextended plumes, giving the tip a bulbous appearance. The function of these plumose setae is presumably for sexual sensing since it occurs in adults and subadults but not juveniles. Plumosity can be dense in some species (e.g., in *J. staudei, J. falcata, J. slatteryi, J. oclairi, J. borowskyae*), though in all species there is a modification of setation on the posterior part of the antenna 2 flagellum at least in the adult males.

Fig. 77 shows an unusual cusping at the tip of the third uropod outer ramus with four cusps rather than the usual two proximal to the basally immersed, dorsally recurved spine.

Piola & Conwell (2010) (repeated by Marchini & Cardeccia 2017) reported *J. staudei* fouling a fishing boat docked in New Zealand (location not given). It had been identified by NIWA's Marine Invasives Taxonomic Service (MITS) but this identification has not been confirmed. If it is correct, this would be the first instance of *J. staudei* having been found outside the North Pacific. The point of origin of the fishing boat was not indicated. The study embraced fishing boats only from Australia/New Zealand, the Northwest Pacific, and the South Pacific. If the fouling species was *J. staudei*, it would have been likely that the fishing boat was from *J. staudei*'s home region, the Northwest Pacific. However, the two boats sampled from this region recorded no fouling. *Jassa staudei* is not known from either of the other two regions. It is possible that the specimen(s) were mis-identified and were more likely *J. marmorata* or *J. slatteryi*, which have been confirmed present in New Zealand since 1928 (Table 3). *Jassa marmorata* was found fouling two other fishing boats in the study. Marchini & Cardeccia (2017) cited Inglis *et al.* (2008) as finding *J. staudei* in the Port of Timaru, New Zealand. Inglis *et al.* (2008) were referring to *J. slatteryi*, however; no mention of *J. staudei* could be found.

Jassa carltoni **Conlan, 1990**

(Table 12, Figs 78–82)

Diagnosis.

Both sexes:

Mandibular palp: article 2, dorsal margin without a fringe of setae.

Maxilla 1: without a seta or setal cluster at the base of the palp article 1.

Gnathopod 1: basis, anterolateral margin with a few short setae along its length; carpus with a (usually) single or a small cluster of long setae at the anterodistal junction of the propodus (setae 65-70% of anterior margin length and slightly medial).

Gnathopod 2: basis with a few moderately long setae on the anterodistal margin (most setal lengths <40% of the basis width); carpus and propodus, setae on the anterior margin short and simple (setal length < basis width).

Pereopods 5–7: propodus not expanded anteriorly.

Uropod 1: ventral peduncular spinous process underlying about 1/3 of the longest ramus.

Uropod 3: inner ramus without spines mid-dorsally (with only the single apical spine).

Telson: tip without apical setae (only the usual short setae at each dorsolateral cusp).

Thumbed male:

Antenna 2: without plumose setae on peduncular article 5 and flagellum.

Gnathopod 2: propodus large and stout, palmar defining spines not produced on a ledge, spines lost in large thumbed males. Major form: thumb about 30% the length of the propodus and curved posterodistally, dactyl sinuous, expanded proximally. Minor form: thumb about 15% the length of the propodus, dactyl expanded more distally than in the major form, into the palmar incision between the thumb and the proximal tooth.

Adult female:

Antenna 2: without plumose setae on peduncular article 5 and flagellum.

Gnathopod 2: propodus, palm concave, palmar defining angle acute, palmar defining spines relatively widely spaced.

Remarks. Conlan (1990) first recognized *Jassa carltoni* as a new species in Californian collections described by Barnard (1969) as "*Jassa falcata"*. The largest specimens available were chosen as the type lot (Fig. 78). However, the holotype, a major form male, appears to have a damaged thumb, as the tip is short and apically indented compared to the major form paratype (Fig. 79). The minor form paratype (Fig. 79) has a similarly shaped but shorter thumb with the dactyl expanded into the palmar incision. Additional specimens from British Columbia are figured in order to show the morphology of an undamaged major form male as well as a subadult male that had an obvious thumb inside the cuticle. Plots of thumb and propodus length on gnathopod 2 for specimens from a single population show that the major form thumbed male has a substantially longer thumb and gnathopod 2 propodus length than the minor form thumbed male (Figs 79, 80). Propodus length of adult females is also much less than for major form males but more similar to minor form and subadult males. However there were insufficient specimens of similar body length for statistical comparison.

Jassa carltoni most resembles *J. slatteryi*, both of which occur on the Pacific coast of North America. Although both have a 4-articled flagellum on antenna 2, the flagellum is slenderer in *Jassa carltoni* than in *J. slatteryi* and unlike *J. slatteryi*, it does not become plumose in large thumbed males. The palm of gnathopod 1 is convex while in *J. slatteryi* it is straight or shallowly concave. Both males and females of *J. carltoni* have a sparser setation on the anterior margin of the basis and a wider propodus on gnathopod 2 (maximal width ~65% of maximal length) than for *J. slatteryi* (maximal width ~50% of maximal length). The thumb shape also differs: tip rounded and curved posteriorly in major form males of *J. carltoni* and tip acute and not curved posteriorly in major form males of *J. slatteryi*. In minor form males of *J. carltoni*, the thumb is shorter and more acute than in the major forms, and more closely resembles *J. slatteryi*. The shape differences in the gnathopod 1 palm still hold, though.

Many (but not all) of the locations for *J. slatteryi* noted by Conlan (1990) for British Columbia are actually for *J. carltoni*, as this latter species was not recognized at that time to occur outside of California. It was only through recent molecular analysis that *J. carltoni* was discovered to occur also in British Columbia. Subsequent re-examination of collections found *J. carltoni* also in Oregon. A "*J. slatteryi"* noted by Conlan (1990) from Alaska (University of Alaska loan, Latouche T1, M75, 5 Sept. 1975) may also be *J. carltoni* but this specimen was no longer available for study and so is omitted from the distribution map. Given the similarity in environmental conditions between southeastern Alaska and British Columbia, it is likely that *J. carltoni* ranges northwards at least into southeastern Alaska. *Jassa carltoni* has not been found outside of the Pacific coast of North America, however.

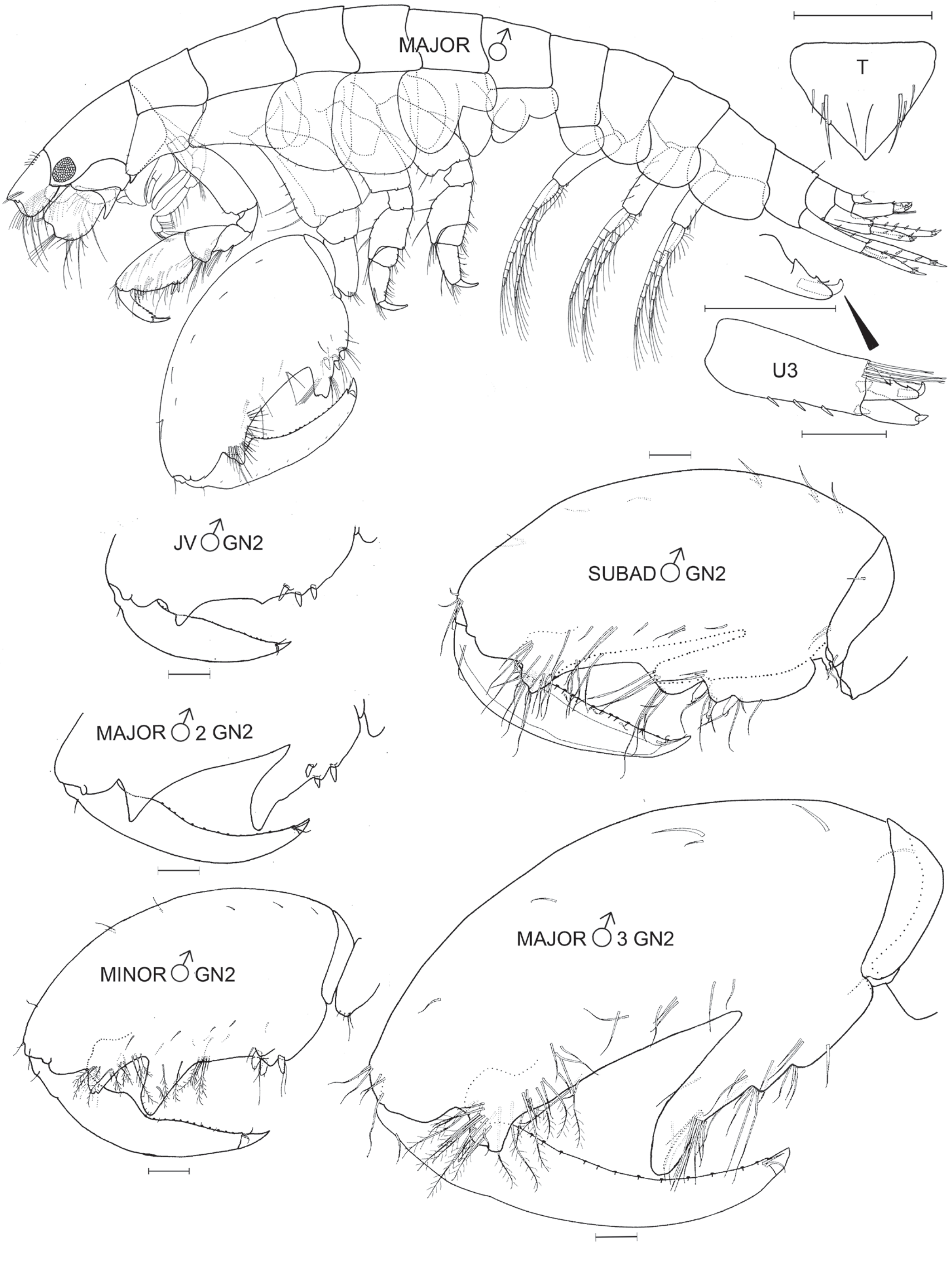

FIGURE 78. *Jassa carltoni* Conlan, 1990. Holotype, adult male, major form, 3.0 mm, Corona del Mar, California, J. L. Barnard, coll., 9–11 December 1962, station 46-K-1, wash of 1/6 liter of ascidians and soft polychaete tubes collected at low tide (NHMLA 62-132.1). Paratype, juvenile male, 1.7 mm, La Jolla, California, 11–13 Nov. 1962, J. L. Barnard, coll., station 45-R-1, no further collection data, 62-135.1 (NHMLA); subadult male, 4.0 mm, Cable Beach, Vancouver Island, British Columbia, 14 July 1972, D. Kittle, coll., station 342, 1973-128 (CMN); paratype, adult male, minor form, 2.8 mm, La Jolla, California, 11–13 Nov. 1962, J. L. Barnard, coll., station 45-W-5, scraping of calcareous sponge under ledge in surge channel at low tide, 62-134.1 (NHMLA); paratype, adult male 2, major form, 2.9 mm, Hazard Canyon Reef, Montana de Oro State Park, St. Louis Obispo County, California, 1–9 Dec. 1961, J. L. Barnard, coll., station 42-T-5, wash of *Egregia* holdfasts collected at low tide, 61-100.2 (NHMLA); adult male 3, major form, 4.0 mm, Sarita Bay, Vancouver Island, British Columbia, 2 July 1976, E. L. Bousfield, coll., station B13, 1976-157, bedrock, muddy sand, eelgrass, algae and fine gravel subtidally, hand and dip net collection at low tide, ~14 °C, 26 psu (CMN). Lateral view: whole body and gnathopod 2 views; dorsal view: telson; other views medial. Setae omitted from the juvenile male and major male 2 second gnathopods. Scale 0.1 mm. Illustration after Conlan (1990).

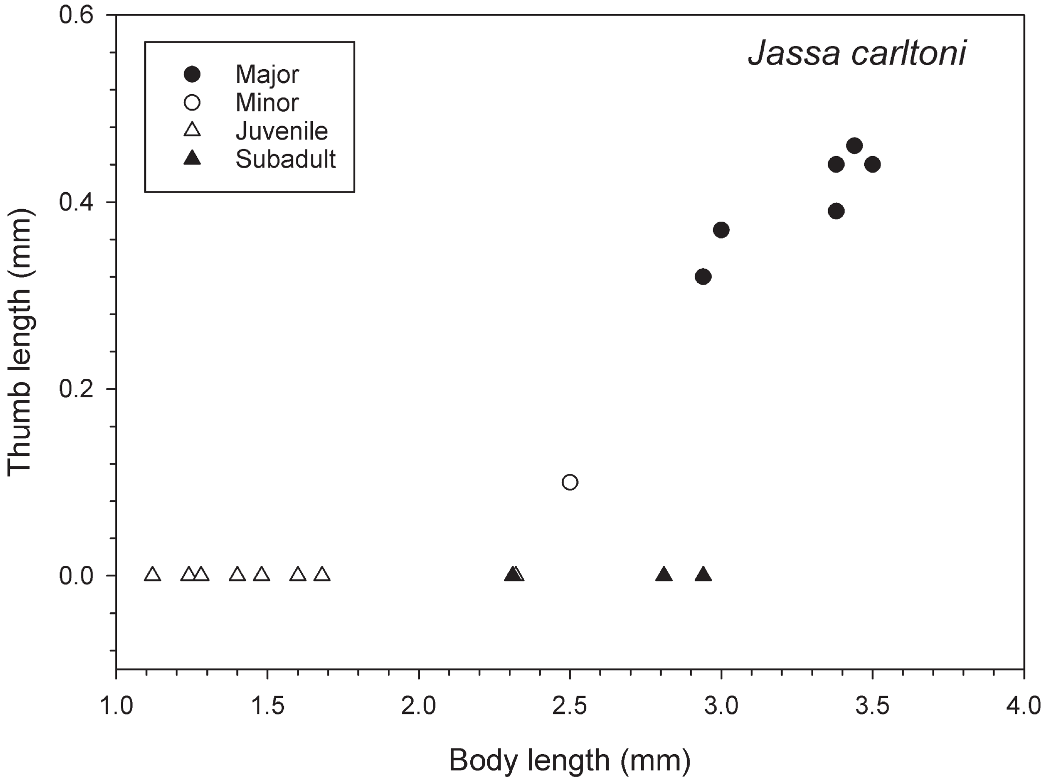

FIGURE 79. *Jassa carltoni* Conlan, 1990. Variation in thumb length relative to body length in males in a single collection at Wizard Islet, Vancouver Island, British Columbia, July 1972, D. Kittle, coll., station 712, NMNS 73-128 (CMN). Linear regression assumptions failed for all plots.

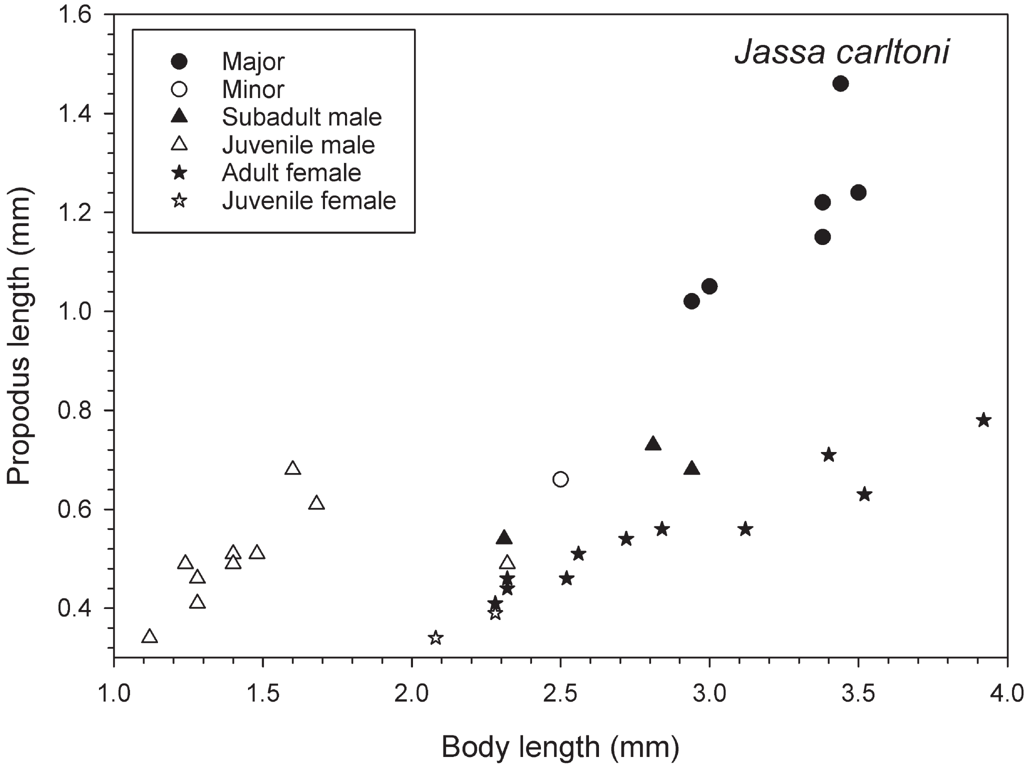

FIGURE 80. *Jassa carltoni* Conlan, 1990. Variation in gnathopod 2 propodus length relative to body length in males and females in a single collection at Wizard Islet, Vancouver Island, British Columbia, July 1972, D. Kittle, coll., station 712, NMNS 73-128 (CMN). Linear regression assumptions failed for all plots.

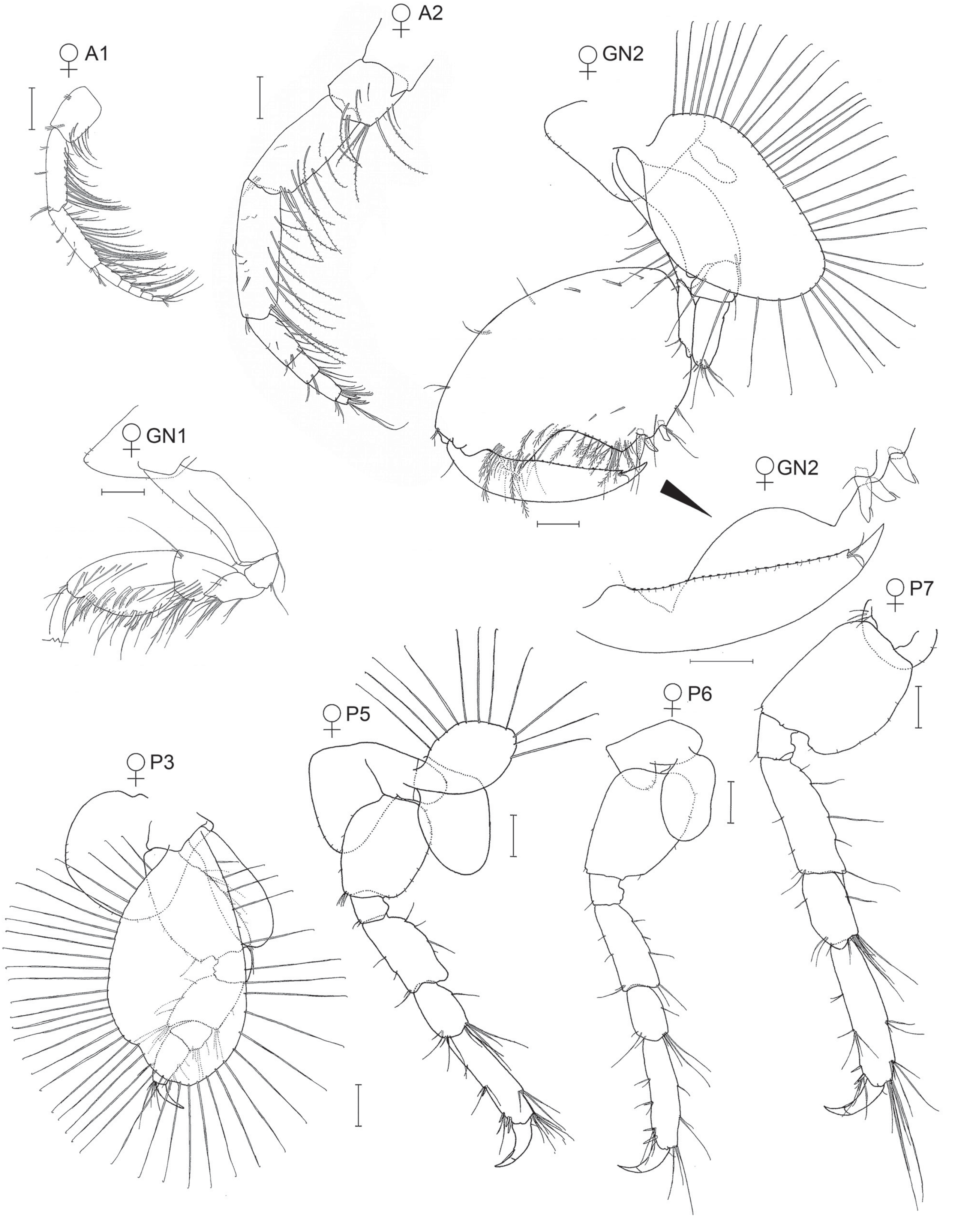

FIGURE 81. *Jassa carltoni* Conlan, 1990. Allotype, adult female, 2.8 mm, 62-132.2 (NHMLA). Corona del Mar, California, J. L. Barnard, coll., 9–11 December 1962, station 46-K-1, wash of 1/6 liter of ascidians and soft polychaete tubes collected at low tide. Scale 0.1 mm. Illustration after Conlan (1990).

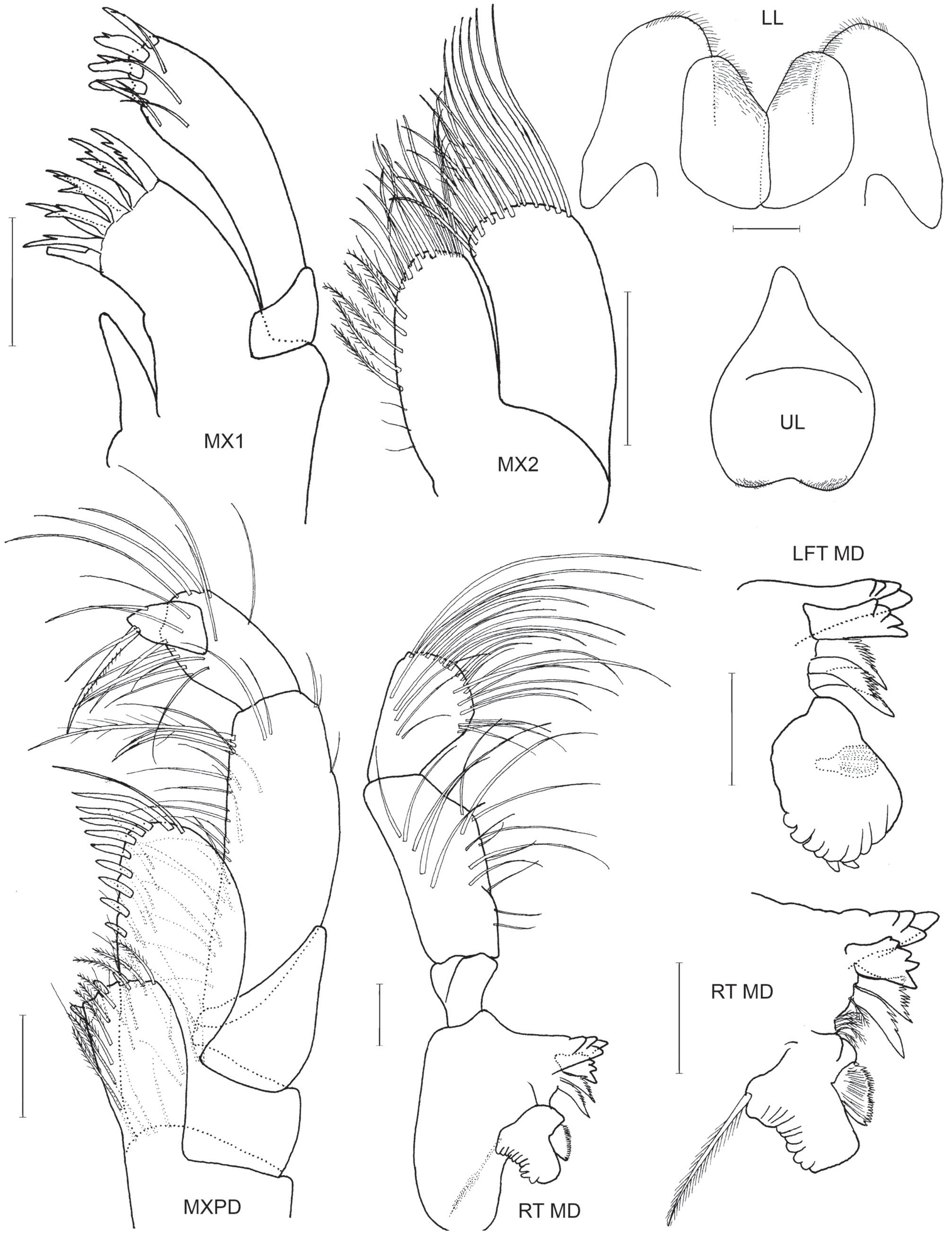

FIGURE 82. *Jassa carltoni* Conlan, 1990. Holotype, adult male, major form, 3.0 mm, 62-132.1 (NHMLA). Corona del Mar, California, J. L. Barnard, coll., 9–11 December 1962, station 46-K-1, wash of 1/6 liter of ascidians and soft polychaete tubes collected at low tide. Mouthparts. Frontal view: upper lip; lateral view: maxilla 1; other views medial. Scale 0.1 mm.

Jassa shawi Conlan, 1990

(Table 12, Figs 83–84)

Diagnosis.

Both sexes:

Mandibular palp: article 2, dorsal margin without a fringe of setae.

Maxilla 1: without a seta or setal cluster at the base of the palp article 1.

Gnathopod 1: basis, anterolateral margin with one short seta at distal angle; carpus with a short seta medially, at the anterodistal junction of the propodus (seta length <15% of the carpus length).

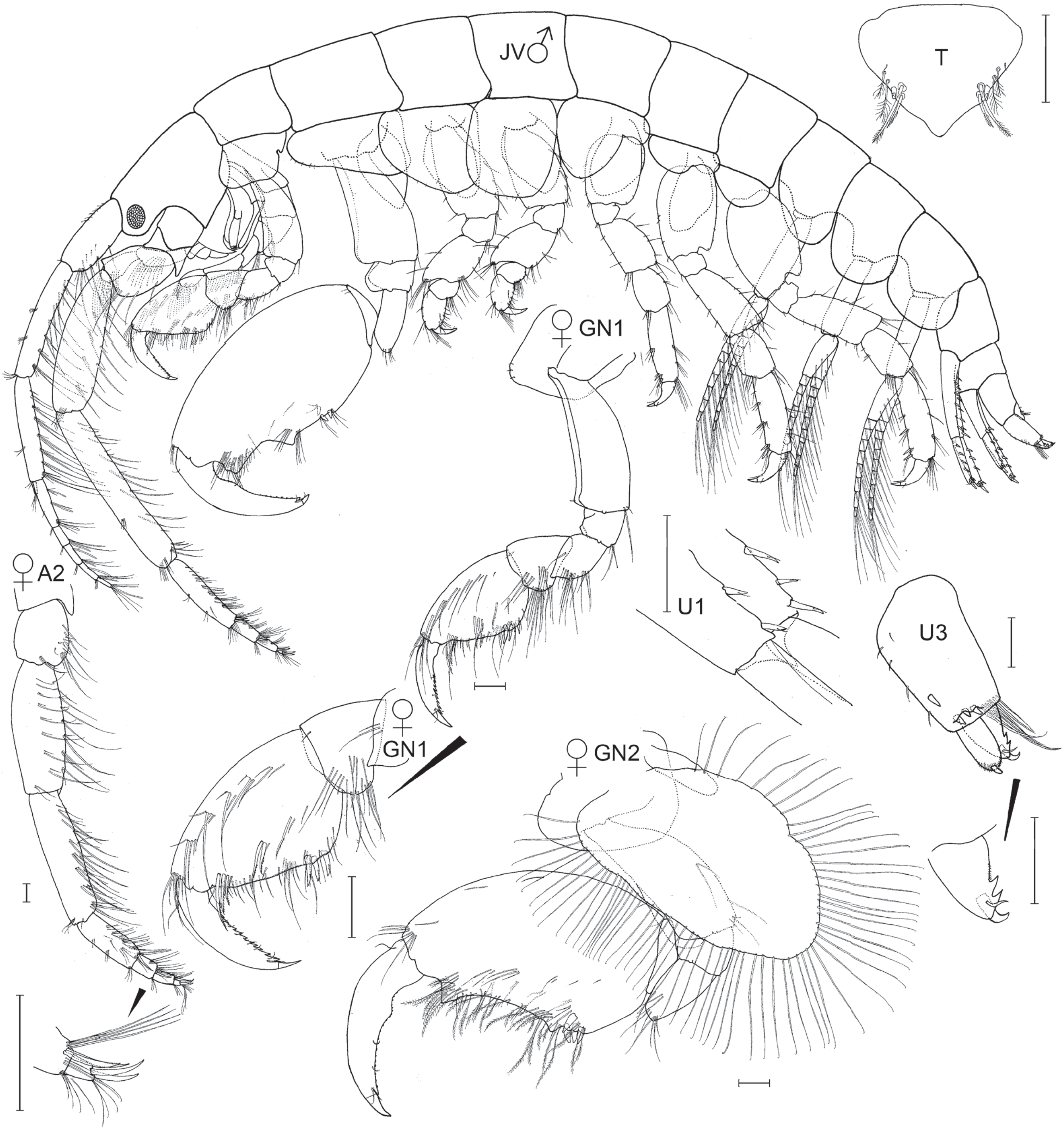

FIGURE 83. *Jassa shawi* Conlan, 1990. Holotype, juvenile male, 6.8 mm, NMCC 1987-1133; allotype, adult female, ovigerous, 5.6 mm, NMCC 1987-1134 (CMN). Bamfield Marine Sciences Centre, Barkley Sound, Vancouver Island, British Columbia, 24 June 1976, E. L. Bousfield, coll., station B1, on settling blocks suspended from floating dock at the water's surface, 1976-157 (CMN). Lateral view: whole body; dorsal views: uropod 1 magnification, telson; other views medial. Appendages are of the holotype unless noted otherwise. Scale 0.1 mm. Illustration after Conlan (1990).

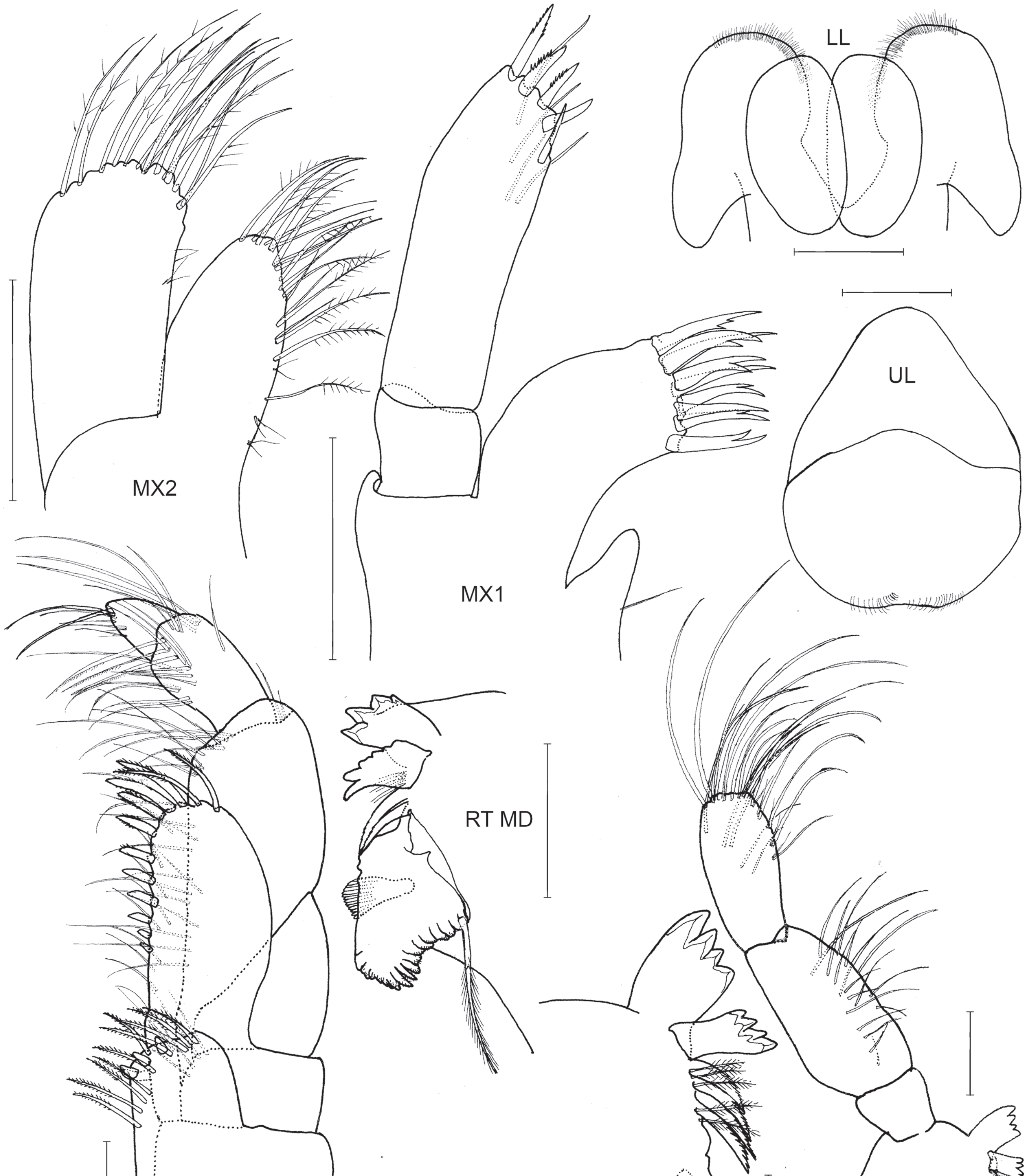

FIGURE 84. *Jassa shawi* Conlan, 1990. Holotype, juvenile male, 6.8 mm, NMCC 1987-1133. Bamfield Marine Sciences Centre, Barkley Sound, Vancouver Island, British Columbia, 24 June 1976, E. L. Bousfield, coll., station B1, on settling blocks suspended from floating dock at the water's surface, 1976-157 (CMN). Mouthparts. Frontal view: upper lip; lateral view: maxilla 2; other views medial. Scale 0.1 mm.

Gnathopod 2: basis without a row of setae along the anterolateral margin; carpus and propodus, setae on the anterior margin short and simple (setal length < basis width).

Pereopods 5–7: propodus not expanded anteriorly.

Uropod 1: ventral peduncular spinous process very short, underlying only about 10% of the longest ramus.

Uropod 3: inner ramus without spines mid-dorsally (with only the single apical spine).

Telson: tip without apical setae (only the usual short setae at each dorsolateral cusp).

Thumbed male: unknown.

Adult female:

Antenna 2: without plumose setae on the flagellum and peduncular article 5.

Gnathopod 2: propodus, palm concave, palmar defining angle acute.

Remarks. Conlan (1990) was in error about the absence of a seta at the anterodistal junction of carpus with the propodus on gnathopod 1. There is one present slightly medially (Fig. 83). The seta is short and difficult to see but present in both sexes. Only 2 subadult males, 2 adult females and 1 immature were available for study so variation and the appearance of the thumbed adult male could not be determined.

Jassa myersi **Conlan, 1990**

(Table 12, Figs 85–87)

Diagnosis.

Both sexes:

Mandibular palp: article 2, dorsal margin without a fringe of setae.

Maxilla 1: without a seta or setal cluster at the base of the palp article 1.

Gnathopod 1: basis, anterolateral margin with a few short setae along its length; carpus with a single or small cluster of relatively long setae at the anterodistal junction of the propodus (setal length about 1/3 the length of the anterior margin length).

Gnathopod 2: basis with only a few short setae along the anterolateral margin (setal lengths <20% of the basis width); carpus and propodus, setae on the anterior margin short and simple (setal length < basis width).

Pereopods 5–7: propodus not expanded anteriorly.

Uropod 1: ventral peduncular spinous process very short, underlying about 6% of the longest ramus.

Uropod 3: inner ramus without spines mid-dorsally (with only the single apical spine).

Telson: tip without apical setae (only the usual short setae at each dorsolateral cusp).

Thumbed male:

Antenna 2: without plumose setae on the flagellum and peduncular article 5.

Gnathopod 2: propodus, palmar defining spines not produced on a ledge.

Adult female:

Antenna 2: without plumose setae on the flagellum and peduncular article 5.

Gnathopod 2: propodus, palm sinuous, palmar defining angle shallowly rounded and towards the centre of the palm (not close to the palmar defining spines).

Remarks. This is the only Northern Hemisphere species that has a sinuous palm on the propodus of gnathopod 2. It also has a variably fringed basis, leading to mixed interpretation of whether a fringe of setae is present or absent. It shares with *J. borowskyae* and *J. shawi* a reduced peduncular process underlying the rami of uropod 1. Among the 166 specimens available for study, there were only 8 thumbed males. These all had very short thumbs and palmar defining spines proximal to the base of the thumb. The thumbed males had shorter setae on the antenna 2 than the females (Fig. 85) but none had plumose setae as develops in thumbed males of some other species of *Jassa*. This may signify that *J. myersi* does not develop plumose setae but the sample size is small. However, none had slenderized bases of pereopods 3–4 which is typical of large thumbed males. Conlan (1990) suggested, therefore, that these males were not at maximal size for the species. A plot of gnathopod 2 propodus length relative to body length shows an apparent greater size for males than females (Fig. 87). Analysis of variance on adult females ($n = 4$) and juvenile males ($n = 6$) that overlapped in body length (3.5–4.5 mm) found that the differences in mean propodus length was not sufficiently great to exclude the possibility that the difference was due to random sampling variability ($F = 1.041^{-15}$, $p = 1.0$).

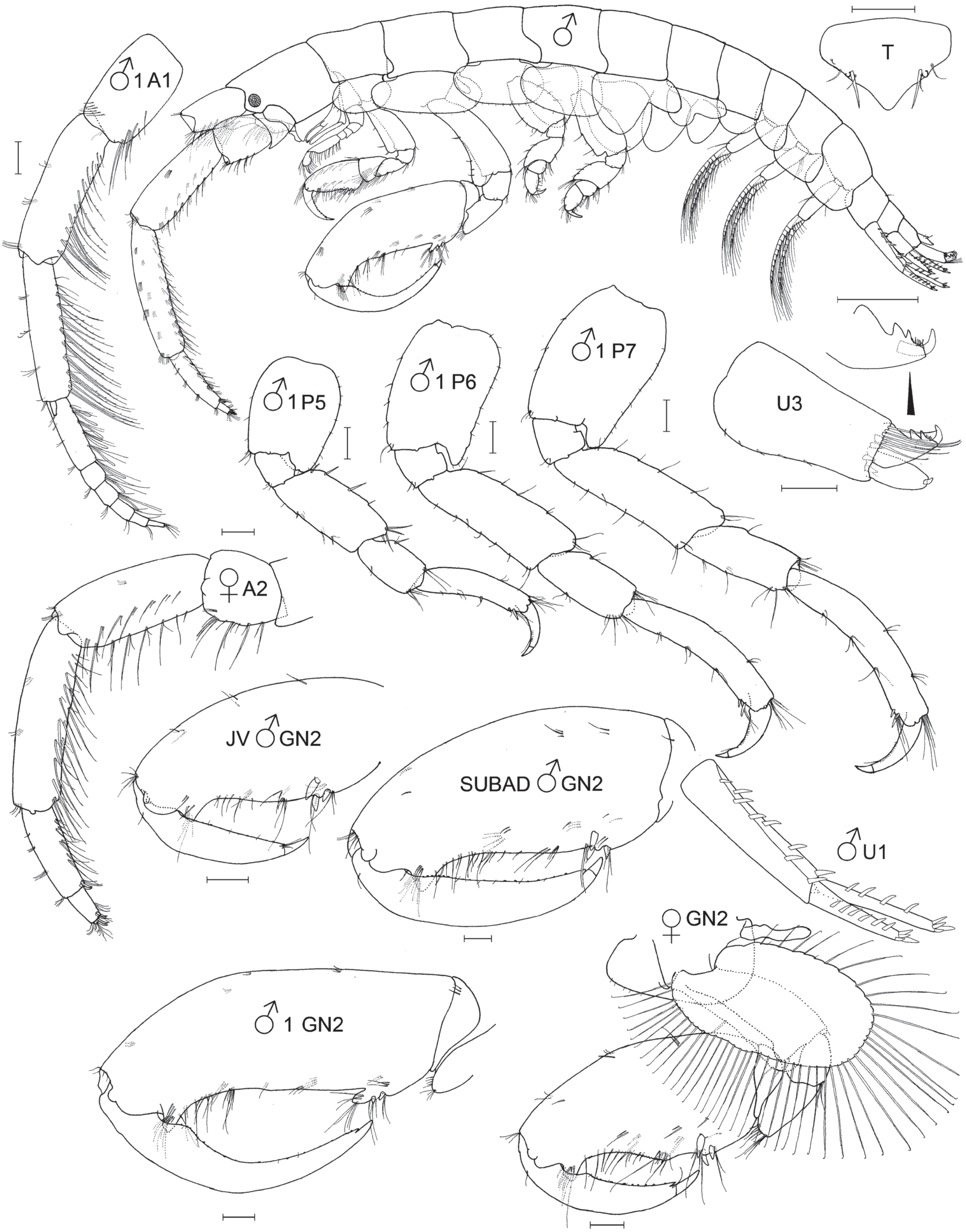

FIGURE 85. *Jassa myersi* Conlan, 1990. Holotype, adult male, 5.8 mm, NHMLA 61-125.1; allotype, adult female, 4.4 mm, NHMLA 125.2; paratype, juvenile male, 3.7 mm, NHMLA 125.3. Coal Oil Point, Goleta, California, 2 July 1961, J. L. Barnard, coll., station 39-H-2, on rock surfaces in *Phyllospadix* zone, low intertidal zone. Adult male 1, 4.5 mm and subadult male, 5.1 mm, Coal Oil Point, Goleta, California, 2 July 1961, J. L Barnard, coll., station 39-K-1, on rock surfaces in *Phyllospadix* zone, low intertidal zone (NHMLA). Lateral views: whole body and uropods; dorsal view: telson; other views medial. Appendages are of the holotype unless noted otherwise. Scale 0.1 mm. Illustration after Conlan (1990).

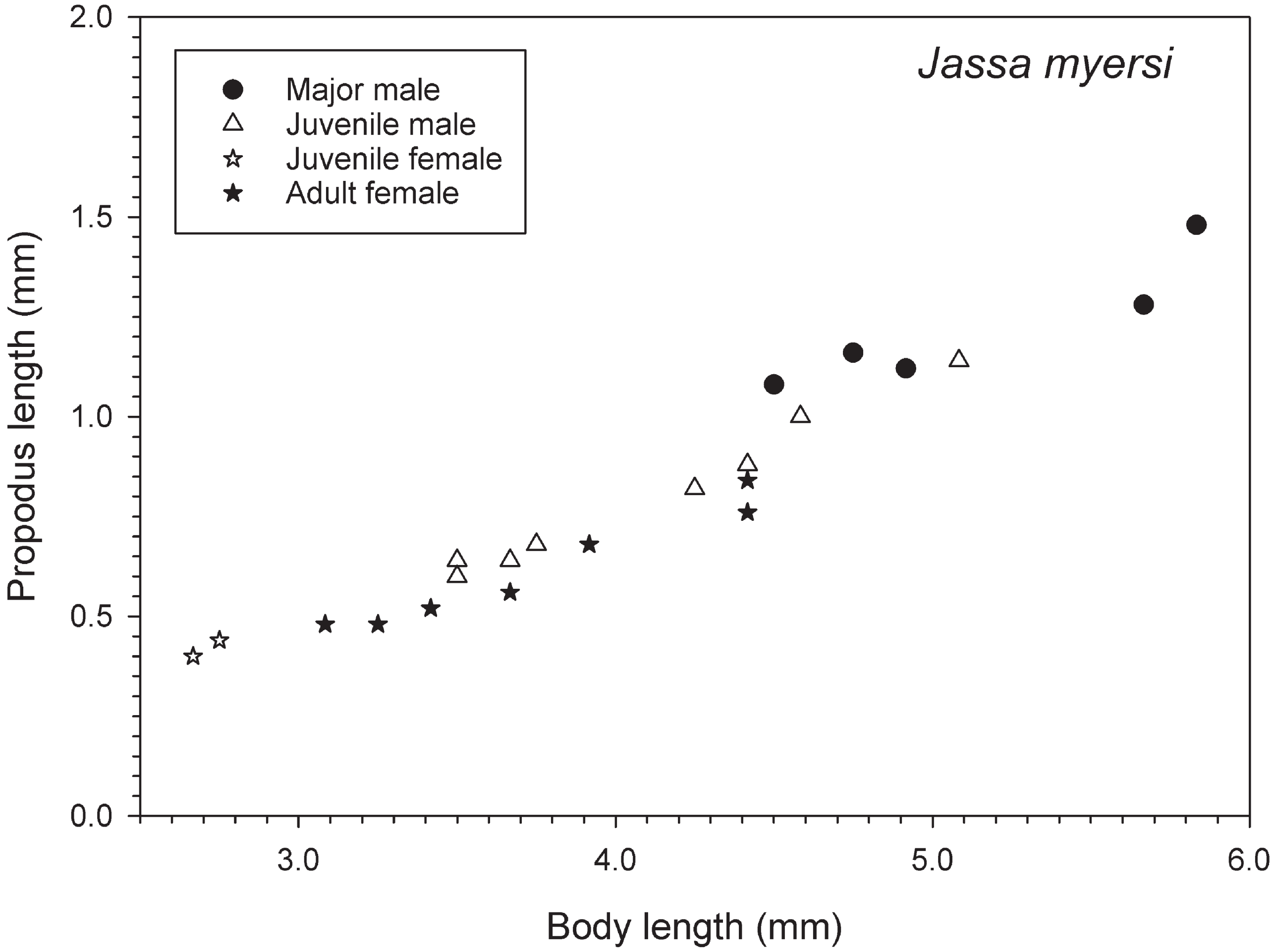

FIGURE 86. *Jassa myersi* Conlan, 1990. Variation in gnathopod 2 propodus length relative to body length in males and females from a single population. Coal Oil Point, Goleta, California, 2 July 1961, J. L. Barnard, coll., stations 39-H-1, 39-H-2 and 39-K-1, on rock surfaces in *Phyllospadix* zone, low intertidal zone (NHMLA). Linear regression assumptions failed for all plots.

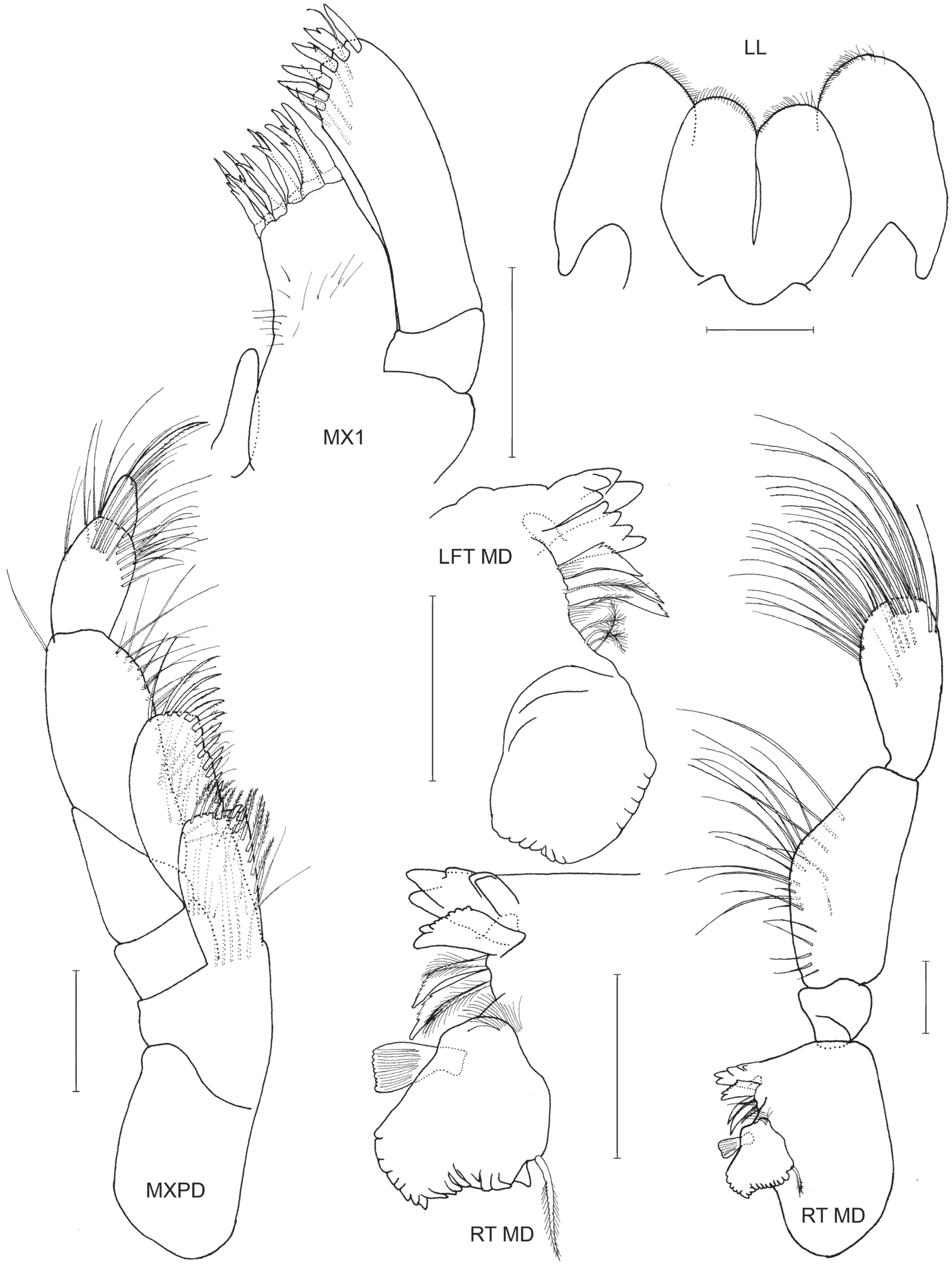

FIGURE 87. *Jassa myersi* Conlan, 1990. Holotype, adult male, 5.8 mm, NHMLA 61-125.1. Coal Oil Point, Goleta, California, 2 July 1961, J. L. Barnard, coll., station 39-H-2, on rock surfaces in *Phyllospadix* zone, low intertidal zone (NHMLA). Mouthparts. All views medial. Scale 0.1 mm.

Southern Hemisphere species

TABLE 13. Key character states of locally distributed Southern Hemisphere species. Trans-hemispheric species (Table 10) may occur there as well. X indicates the presence of the first character state described while — indicates the alternative character state given in italics. S and L indicate length. ? indicates that the state is unknown. Character states apply to both sexes and juveniles unless indicated otherwise.

Character	*J. alonsoae* (Fig. 88)	*J. justi* (Fig. 92)	*J. thurstoni* (Figs 93-94)	*J. fenwicki* (Fig. 95)	*J. kjetilanna* (Figs 96-98)	*J. ingens* (Figs 99-101)	*J. gruneri* (Figs 102-103)	*J. hartmannae* (Fig. 104)
Antenna 2, large subadult and thumbed male, posterior margin of article 5 and flagellum bearing plumose setae in addition to the usual finely pectinate filter setae (e.g., Fig. 95) *or without plumose setae* (e.g., Fig. 92)	—	—	—	X	—	—	—	—
Antenna 2, large subadult and adult female, posterior margin of article 5 and flagellum bearing plumose setae in addition to the usual finely pectinate filter setae (e.g., Fig. 15) *or without plumose setae* (e.g., Fig. 97)	—	—	—	?[17]	—	—	—	—
Mandibular palp, margin of article 2 with a fringe of setae dorsally (e.g., Fig. 53) *or without a fringe* (e.g., Fig. 94)	—	—	—	—	—	—	—	—
Maxilla 1 with a seta or cluster of setae at the base of palp article 1 (Fig. 101) *or without seta(e)* (Fig. 94)	—	—	—	—	—	X	—	—
Gnathopod 1, basis, anterolateral margin with a fringe of spine-like setae (e.g., Fig. 88) *or without spine-like setae* (e.g., Fig. 102)	X	X	—	X	—	X	—	X
Gnathopod 1, carpus, with a seta or cluster of setae at the anterodistal junction of the propodus which may be slightly lateral or medial (e.g., Fig. 99) *or without seta(e)* (e.g., Fig. 102)	X	—	X	—	X	X	—	—
Gnathopod 1, carpus, seta(e) at the anterodistal junction of the propodus moderately long (L, length ≥25% of anterior margin length) (e.g., Fig. 88) or short (S, length <25% of anterior margin length) (e.g., Fig. 96) *or without seta(e)* (e.g., Fig. 102)	L	—	L	—	S	L	—	—
Gnathopod 2, basis with a fringe of setae on the anterolateral margin (e.g., Fig. 88) *or fringe absent (minute setae may be present but are too small to be described as an obvious fringe)* (Fig. 93)	X	X	—	X	X	X	X[18]	X
Gnathopod 2, basis, if setal fringe present, setae relatively long (L, length ≥40% basis width) (e.g., Fig. 88) or short (S, length mostly <40% basis width) (e.g., Fig. 92) *or fringe absent (minute setae may be present but are too small to be described as an obvious fringe)* (Fig. 93)	L	S[18]	—	S[19]	S	X	L	S
Gnathopod 2, propodus, setae on the anteroproximal margin long (L, setal length ≥ maximal basis width) (Fig. 67) or short to absent (S, setal length < maximal basis width) (e.g., Fig. 95)	S	S	S	S	S	S	S	S
Gnathopod 2, propodus, setae on the anterior margin plumose (Fig. 62) *or simple* (e.g., Fig. 95)	—	—	—	—	—	—	—	—

...continued on the next page

TABLE 13. (Continued)

Character	*J. alonsoae* (Fig. 88)	*J. justi* (Fig. 92)	*J. thurstoni* (Figs 93-94)	*J. fenwicki* (Fig. 95)	*J. kjetilanna* (Figs 96-98)	*J. kjetilanna* (Figs 96-98)	*J. gruneri* (Figs 102-103)	*J. hartmannae* (Fig. 104)
Gnathopod 2, female propodus, palm concave, palmar angle pronounced (acute, right angled or bulbous) (e.g., Fig. 104) *or palmar angle shallow, giving the palm a sinuous appearance* (e.g., Fig. 95)	—	X	—	—	—	X	—	X
Pereopods 5-7, propodus, anterior margin expanded for grasping (e.g., Fig. 95) *or not expanded for grasping* (e.g., Fig. 93)	—	—	—	X	—	X	—	—
Uropod 1, peduncular spinous process that extends ventrally from the peduncle and underlies the rami, moderately long (L, length = at least 25-50% the length of the longest ramus) (e.g., Fig. 88) or very short (S, length ≤10% of the length of the longest ramus, in which case it may not be visible) (e.g., Fig. 83)	L	L	L	L	L	L	L	L
Uropod 3, inner ramus with 1-2 mid-dorsal spines in addition to the usual spine at the tip (e.g., Fig. 42) *or without dorsal spines* (e.g., Fig. 93)	—	—	—	—	—	—	—	—
Telson, tip with a seta or cluster of setae extending between the third uropods (in addition to the usual upright setae at each side) (e.g., Fig. 31) *or without setae at the tip*[16] (e.g., Fig. 96)	—	—	—	—	—	—	—	—

[16] These setae are visible when the animal is on its side, the abdomen is grasped with forceps in one hand, and the third uropods are depressed downwards with a fine needle in the other hand. This brings the telson into view.

[17] The state for the adult female is unknown. In other species of *Jassa*, if large males develop plumose setae, the large females do as well. This suggests, therefore, that adult females of *J. fenwicki* develop plumose setae.

[18] *J. justi*: although short, the setae are numerous and closely spaced.

[19] *J. fenwicki*: similar to *J. justi*, the setae are short and closely spaced.

Jassa alonsoae Conlan, 1990

(Table 13, Figs 88–91)

Diagnosis.

Both sexes:

Mandibular palp: article 2, dorsal margin without a fringe of setae.

Maxilla 1: without a seta or setal cluster at the base of the palp article 1.

Gnathopod 1: basis, anterolateral margin with a row of short setae along its length; carpus with a cluster of moderately long setae at the anterodistal junction of the propodus (setal length about 1/3 the length of the anterior margin).

Gnathopod 2: basis with a row of setae along the anterolateral margin (at least some setal lengths >40% of the basis width); carpus and propodus, setae on the anterior margin short and simple (setal length < basis width).

Pereopods 5–7: propodus not expanded anteriorly.

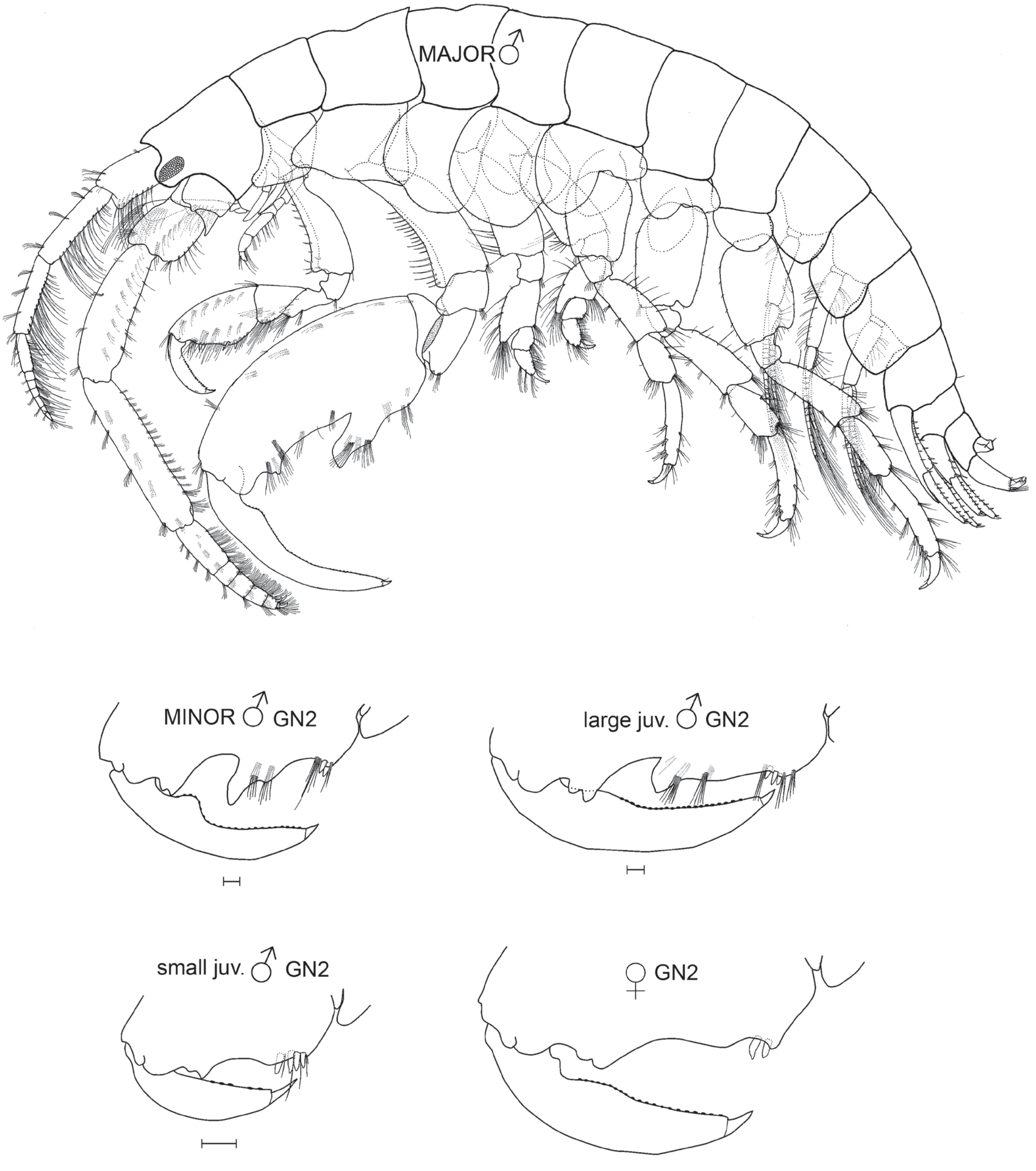

FIGURE 88. *Jassa alonsoae* Conlan, 1990. Holotype, adult male, major form, 11.1 mm, ZMH K-33619; allotype, female, 9.8 mm, ZMH K-33635; paratype, adult male, minor form, 9.3 mm; paratype, large juvenile male, 12.8 mm; paratype, small juvenile male, 4.6 mm. South Georgia (54°30’58″S, 36°0’45″W), 16 January 1884, Deutsche Polar Commission, K. von den Steinen, coll., station 7804 (ZMH K-8017A). All views lateral. Setae omitted from the gnathopod 2 profiles except for those around the thumb and spines of the males in order to landmark position changes with growth. Scale 0.1 mm. Illustration after Conlan (1990).

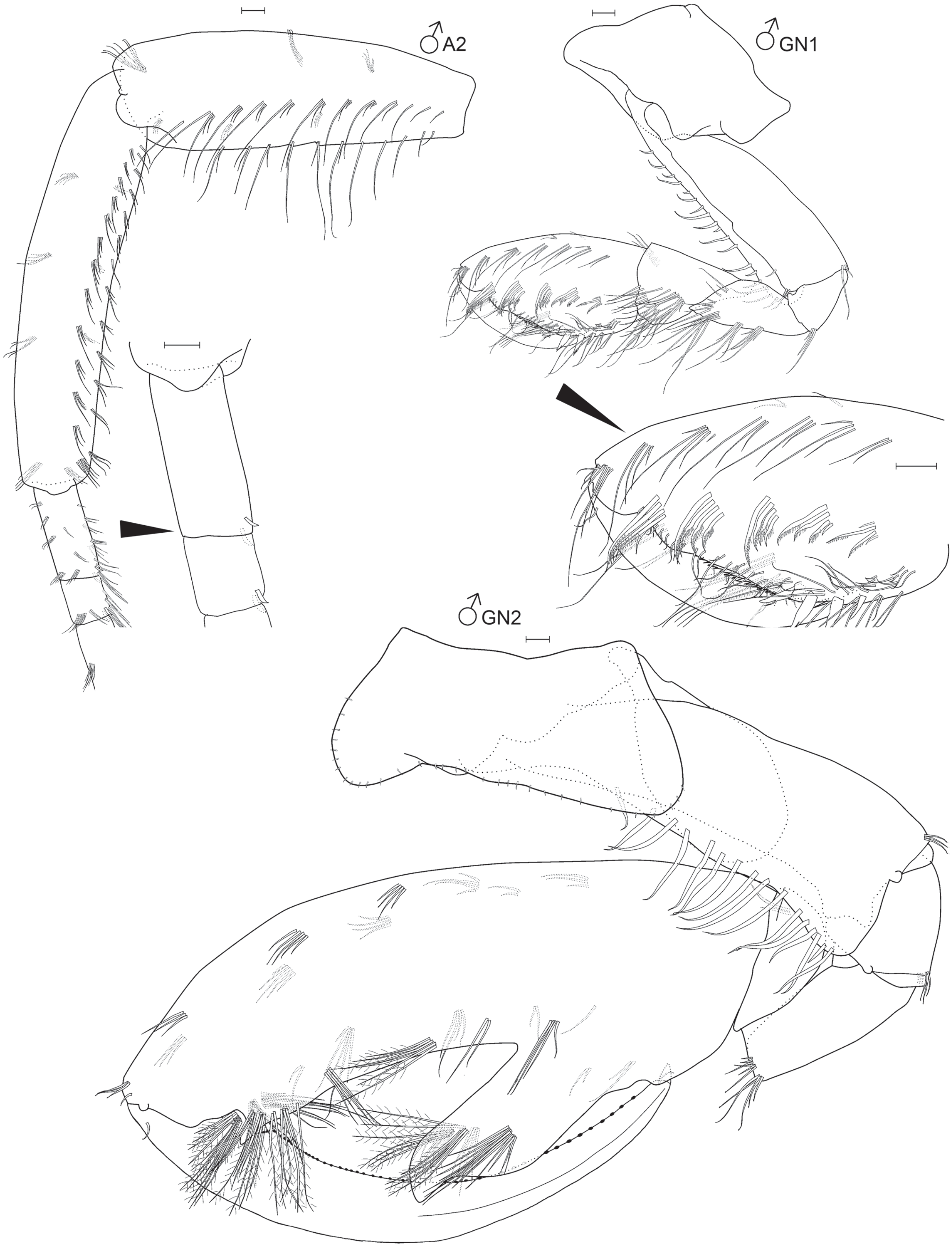

FIGURE 89. *Jassa alonsoae* Conlan, 1990. Adult male, 10.0 mm. Puerto Deseado, Santa Cruz, Argentina, 26 October, 1981, G.M. Alonso, coll., A2020.0028 (CMN). Lateral view: gnathopod 2; other views medial. Scale 0.1 mm.

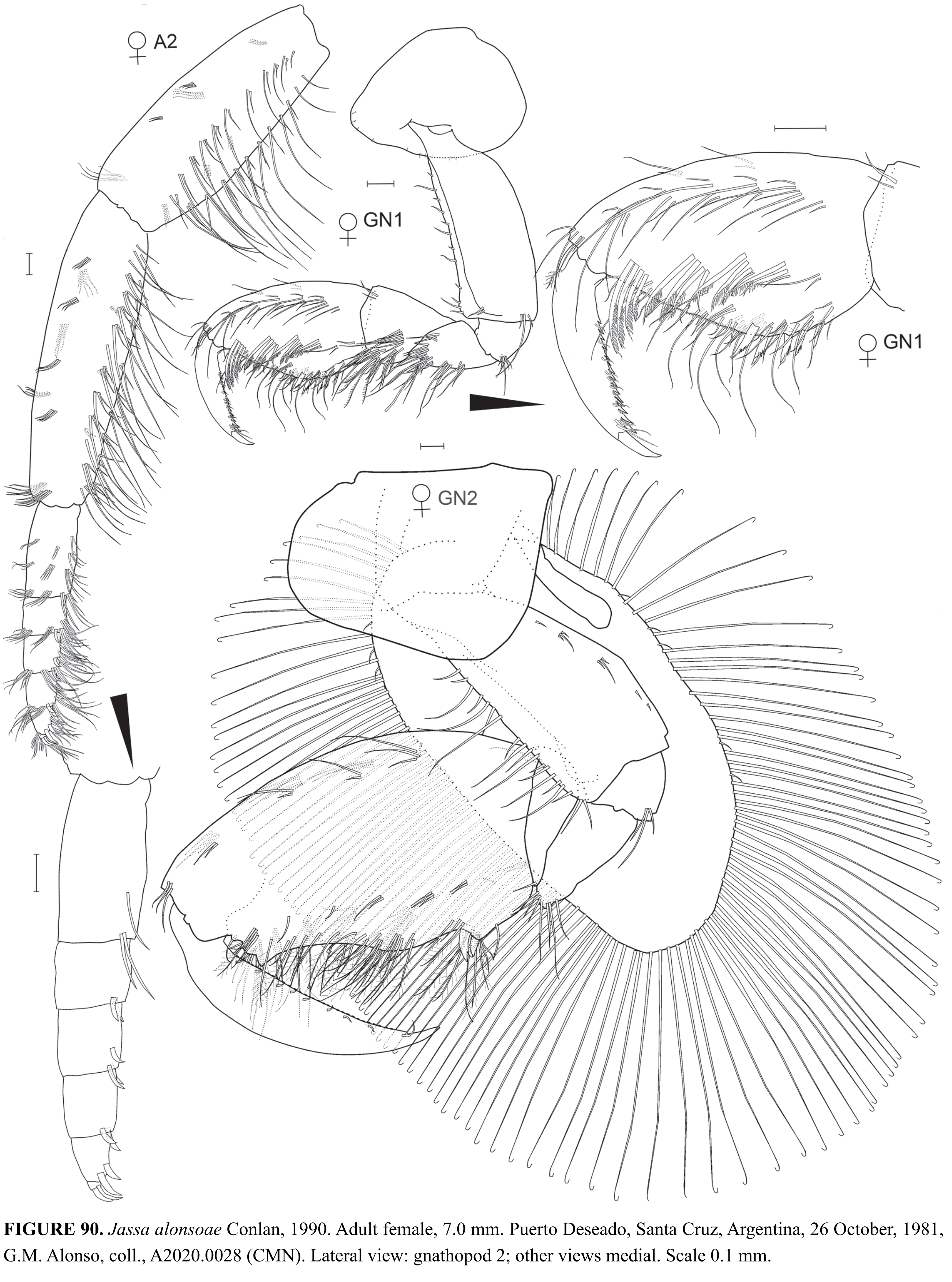

FIGURE 90. *Jassa alonsoae* Conlan, 1990. Adult female, 7.0 mm. Puerto Deseado, Santa Cruz, Argentina, 26 October, 1981, G.M. Alonso, coll., A2020.0028 (CMN). Lateral view: gnathopod 2; other views medial. Scale 0.1 mm.

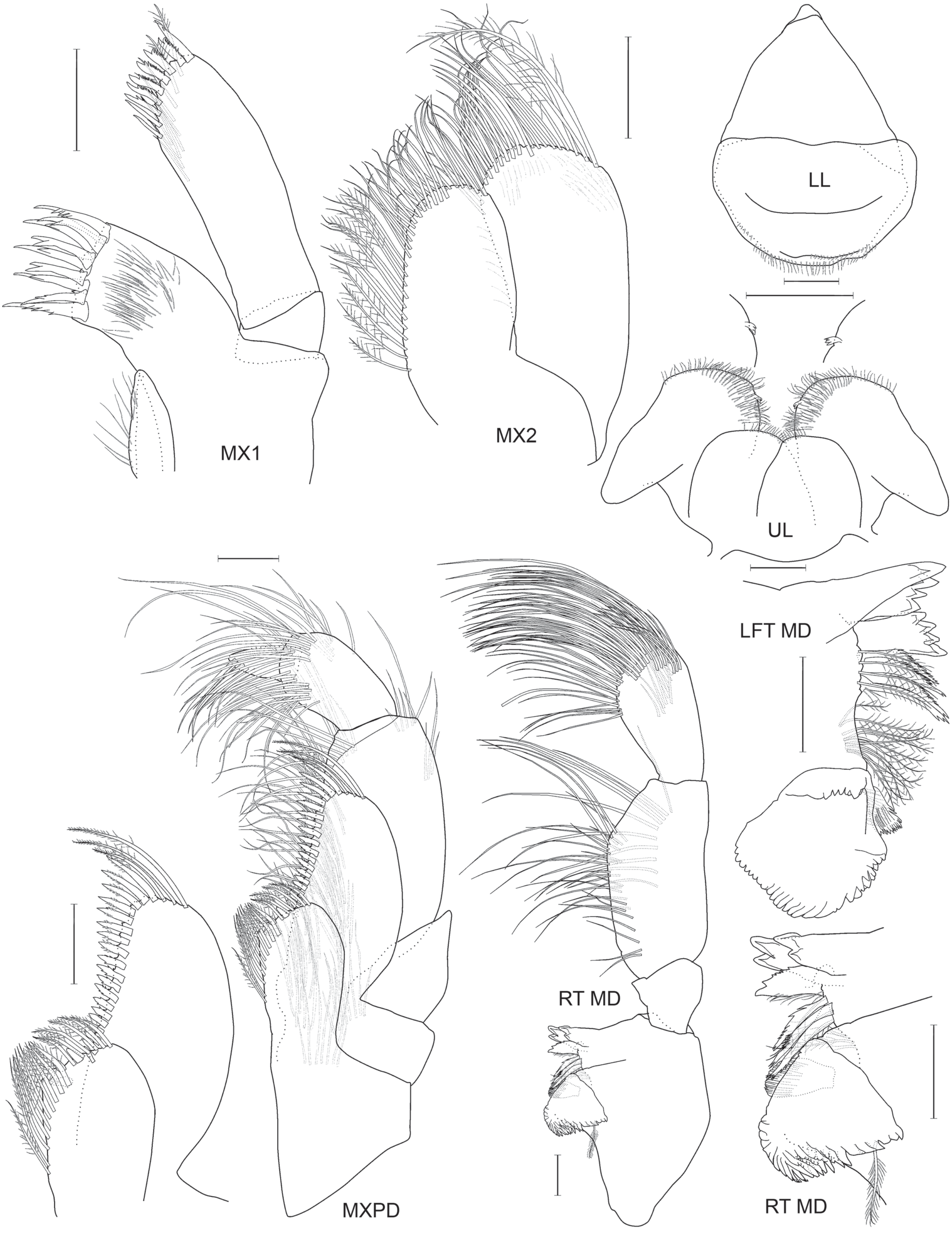

FIGURE 91. *Jassa alonsoae* Conlan, 1990. Adult male, 10.0 mm. Puerto Deseado, Santa Cruz, Argentina, 26 October, 1981, G.M. Alonso, coll., A2020.0028 (CMN). Mouthparts. Frontal view: upper lip; other views medial. Scale 0.1 mm.

Uropod 1: ventral peduncular spinous process underlying about 1/3 of the longest ramus.

Uropod 3: inner ramus without spines mid-dorsally (with only the single apical spine).

Telson: tip without apical setae (only the usual short setae at each dorsolateral cusp).

Thumbed male:

Antenna 2: without plumose setae on the flagellum and peduncular article 5.

Gnathopod 2: propodus, palmar defining spines not produced on a ledge, present in small thumbed males but absent in large thumbed males. In major males, the thumb is distally squared, the posterior margin sinuous. The dactyl is expanded close to the junction with the propodus but is not centrally toothed. Minor form males have a short, squared thumb and a dactyl tooth. Subadult males have a small prethumb.

Adult female:

Antenna 2: large animals without plumose setae on the flagellum and peduncular article 5.

Gnathopod 2: propodus, palm sinuous.

Remarks. *Jassa alonsoae*, *J. justi, J. fenwicki*, *J. ingens* and *J. hartmannae* have a fringe of setae along the anterior margin of gnathopod 1 which may be robust and spine-like (Figs 88–90, 92, 95, 99 and 104). *Jassa alonsoae* differs from the others in having long setae on the basis of gnathopod 2 while the others have short setae similar to the basis of gnathopod 1. The row of setae on the gnathopod 1 basis is a distinctive character, which is only known for these Southern Hemisphere species. However, it is difficult to see on small animals and in *J. ingens* the setae do not run the full length in all animals (Fig. 99). The other Southern Hemisphere species (*J. thurstoni*, *J. kjetilanna* and *J. gruneri*) seem to lack this fringe although there can be minute setae present (Figs 93, 96 and 102). The sinuous shape of the female's gnathopod 2 palm is a feature of several (but not all) Southern Hemisphere species also (*J. alonsoae, J. thurstoni, J. fenwicki, J. kjetilanna, J. ingens and J. gruneri*) (Figs 88, 90, 93, 95, 97, 100 and 102). However, it is not unique to the Southern Hemisphere as the other two Southern Hemisphere species, *J. justi* and *J. hartmannae* have shallowly concave palms (Figs 92 and 104) and the Northern Hemisphere *J. myersi* has a sinuous palm (Fig. 85). The other Northern Hemisphere species (and the transhemispheric species) have more clearly concave palms.

Jassa alonsoae has been found more frequently than the other Southern Hemisphere species (Fig. 11). It has a wide longitudinal range but has not been found south of 60°S. Specimens described by Stephensen (1949) as "*Jassa pulchella" w*ere examined (SNM) and are *J. alonsoae*. Conlan (1990) noted other mis-identifications. Monod (1926) mentioned a collection of "*J. falcata*" from the carapace of the spider crab *Eurypodius latreilli* in the Strait of Magellan. Although these specimens have not been seen, they may be *Jassa alonsoae* as this species has been collected in this area and it was found on spider crabs in a Falkland Island collection (AM P.31689). Monod's illustration of the female gnathopod 2 resembles that of *J. alonsoae*. Stebbing's (1888) "*Podocerus falcatus"* from Greenland Harbour, Kerguelen Island (*Challenger* station 149E) may also be *J. alonsoae*. Its sinuous gnathopod 2 palm suggests an indigenous Southern Hemisphere species and *J. alonsoae* is the only species known from Kerguelen Island (Fig. 11). It is figured by Stebbing (1888) on Plate CXIX along with a female collected off the ship's screw at *Challenger* station 142, off South Africa. Examination of this female (NHM) found that it is not *J. alonsoae* but *J. marmorata*. A description of the *Challenger* stations at http://www.19thcenturyscience.org/HMSC/HMSC-INDEX/index-linked.htm indicates that there was a second collection of *Jassa* at Kerguelen Island (*Challenger* station 149) but this was from the ship's screw "after leaving the Cape". Examination of this collection found it to be also *Jassa marmorata*, indicating that this species was travelling with the ship.

Jassa justi **Conlan, 1990**

(Table 13, Fig. 92)

Diagnosis.

Both sexes:

Mandibular palp: article 2, dorsal margin without a fringe of setae.

Maxilla 1: without a seta or setal cluster at the base of the palp article 1.

Gnathopod 1: basis, anterolateral margin with a fringe of short, spine-like setae; carpus without a single or cluster of setae at the anterodistal junction of the propodus.

Gnathopod 2: basis with a row of short, spine-like setae along the anterolateral margin; carpus and propodus, setae on the anterior margin short and simple (setal lengths < 20% of the basis width).

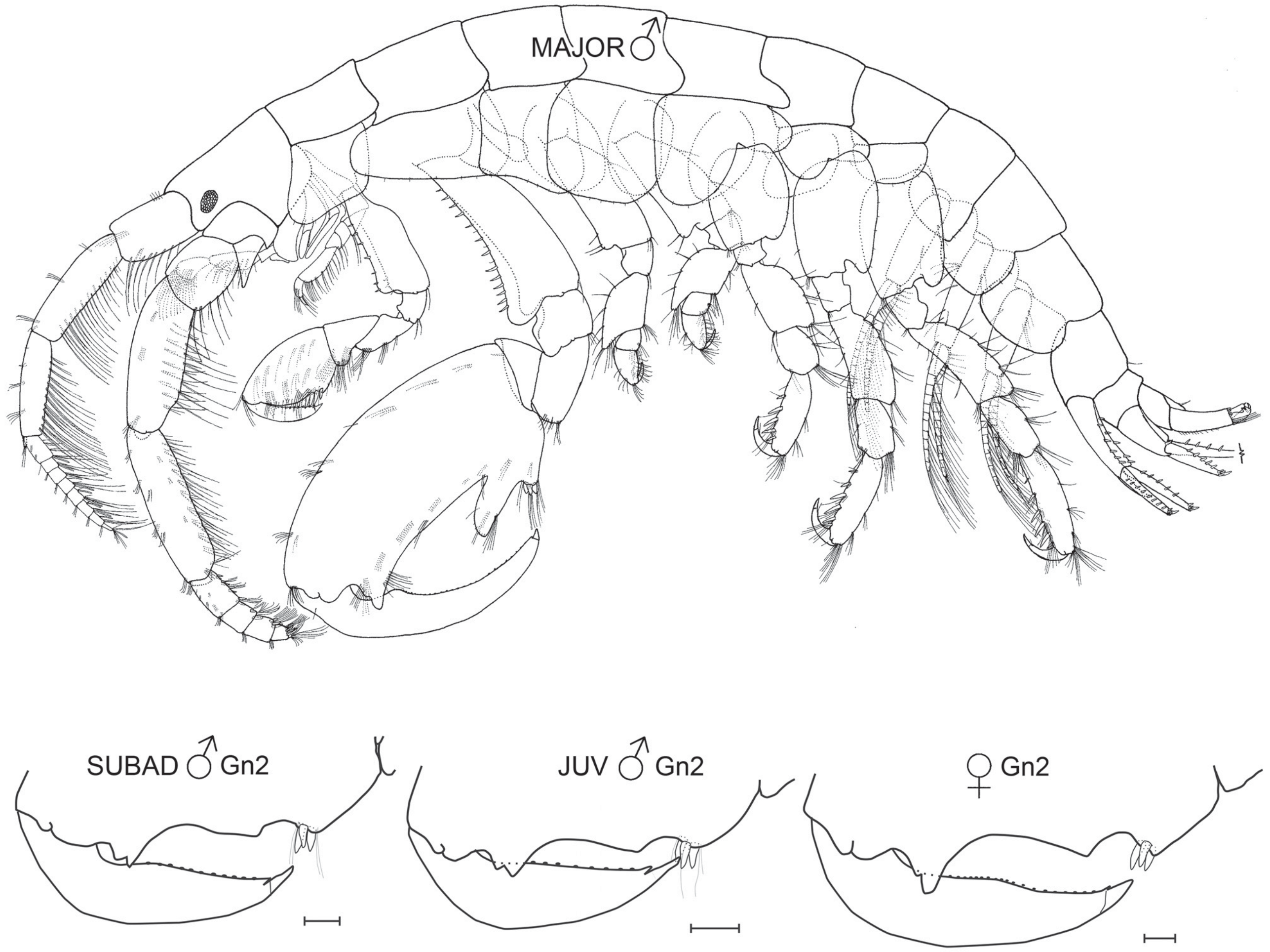

FIGURE 92. *Jassa justi* Conlan, 1990. Holotype, adult male, major form, 8.5 mm, AM P34953; allotype, female, 6.9 mm, AM P37920; paratypes, subadult male, 5.4 mm and juvenile male 4.2 mm, AM P37921. Garden Bay, Macquarie Island (54°29′S, 158°58′E), 20 November 1977, J. K. Lowry and D. S. Horning, colls., station MA-10, among mixed red and green algae on rocky bottom, -3 m (AM). All views lateral. Setae omitted from the gnathopod 2 profiles except for those around the thumb and spines of the males in order to landmark position changes with growth. Scale 0.1 mm. Illustration after Conlan (1990).

Pereopods 5–7: propodus not expanded anteriorly.

Uropod 1: ventral peduncular spinous process underlying about 1/2 of the longest ramus.

Uropod 3: inner ramus without spines mid-dorsally (with only the single apical spine).

Telson: tip without apical setae (only the usual short setae at each dorsolateral cusp).

Thumbed male:

Antenna 2: without plumose setae on the flagellum and peduncular article 5.

Gnathopod 2: propodus, palmar defining spines produced on a ledge; dactyl expanded close to the junction with the propodus but not centrally toothed.

Adult female:

Antenna 2: without plumose setae on the flagellum and peduncular article 5.

Gnathopod 2: propodus, palm concave, dactyl fitting into a depression between the palm and the defining spines.

Remarks. *Jassa justi* shares with *Jassa alonsoae*, *J. fenwicki, J. ingens* and *J. hartmannae* the fringe of spine-like setae along the anterolateral margin of gnathopod 1. Gnathopod 2 sports a similar fringe. The proximal origin of the thumb in the holotype male suggests that it is a major form, in which case the pronounced palmar defining spines may be typical of all thumbed males, rather than being lost in larger major forms. This retention of the palmar defining spines by major form thumbed males would be similar to *J. ingens* (Fig. 99), while in most species the spines are lost.

Jassa hartmannae and *J. kjetilanna* may also retain their spines as they are similarly produced but sample size is small. There were no minor form males of *J. justi* available for study. Like *J. fenwicki* and *J. ingens*, the propodus spines on pereopods 5–7 are pronounced, though the propodus is differently shaped and not expanded.

Jassa thurstoni Conlan, 1990

(Table 13, Figs 93–94)

Diagnosis.

Both sexes:

Mandibular palp: article 2, dorsal margin without a fringe of setae.

Maxilla 1: without a seta or setal cluster at the base of the palp article 1.

Gnathopod 1: basis, anterolateral margin with only a single short seta distally; carpus with a small cluster of moderately long setae at the anterodistal junction of the propodus (setae 25% of anterior margin length).

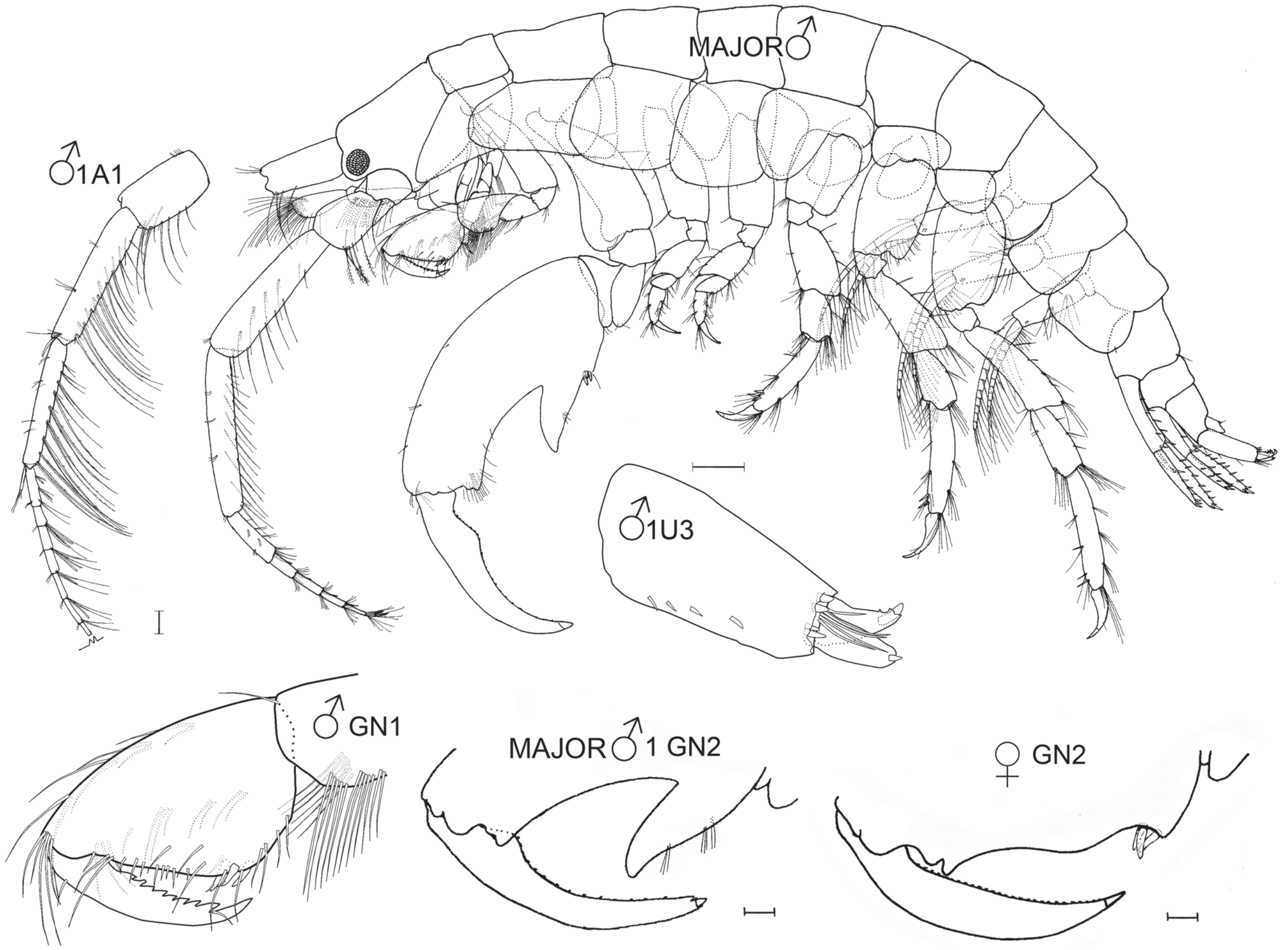

FIGURE 93. *Jassa thurstoni* Conlan, 1990. Holotype, adult male, major form, 5.9 mm, NHM 1969:761:2. Paal Harbour, Signy Island, South Orkney Islands (60°43′S, 45°36′W), 5 February 1965, M. H. Thurston, coll., station 44 (1218). Anchor dredge over mud at 20–25 m depth (NHM). Adult male 1, major form, paratype, 6.0 mm, NMCC-1082. Observation Bluff, Outer Islet, Signy Island, South Orkney Islands (60°42′30″S, 45°35′10″W), 14 September 1965, M. H. Thurston, coll., station 52 (2085), Agassiz trawl over gravel and sand, sand with some rock, algae on rocks, 20 m depth, NHM 1969:763:1 donated to CMN, accession no. IZ 1989-013. Adult female, paratype, 6.5 mm, NHM 1969:762:3. Berntsen Point–Bare Rock, Signy Island, South Orkney Islands (60°42′10″S, 45°35′30″W), 16 October 1964, M. H. Thurston, coll., station 50 (AT 76). Agassiz trawl over gravel and sand, some rocks with *Desmarestia anceps* and *Phyllogigas grandifolius*, 5–10 m depth (NHM). Lateral view: whole body, antenna 1 and gnathopod magnifications; medial view: uropod 3. Setae omitted from the gnathopod 2 profiles except for those around the thumb and spines of the male 1 in order to landmark position changes with growth. Scale 0.1 mm. Illustration after Conlan (1990).

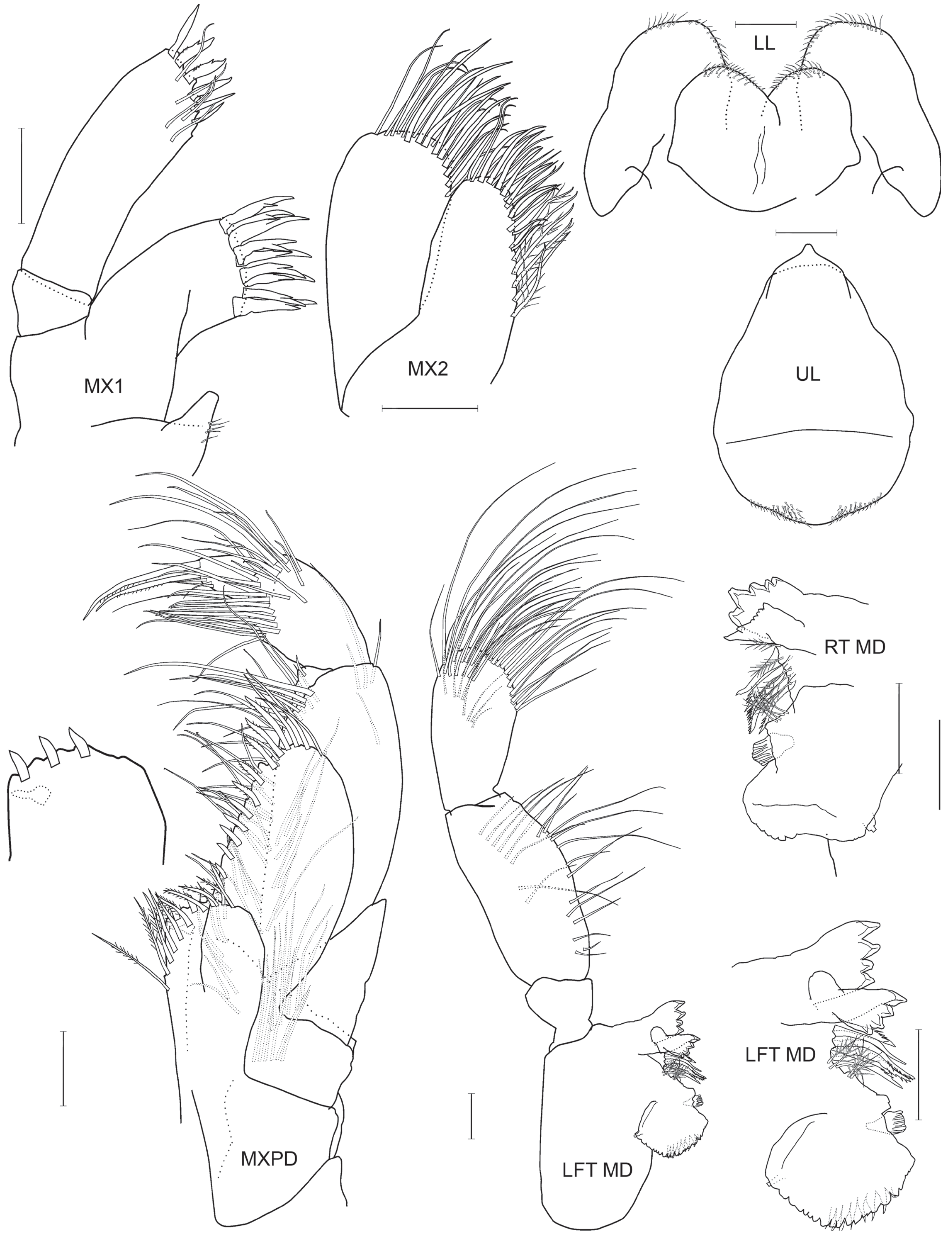

FIGURE 94. *Jassa thurstoni* Conlan, 1990. Adult male 1, major form, paratype, 6.0 mm, NMCC-1082. Observation Bluff, Outer Islet, Signy Island, South Orkney Islands (60°42′30″S, 45°35′10″W), 14 September 1965, M. H. Thurston, coll., station 52 (2085), Agassiz trawl over gravel and sand, sand with some rock, algae on rocks, 20 m depth, NHM 1969:763:1. IZ 1989-013 (CMN). Mouthparts. Frontal view: upper lip; lateral view: maxilla 1; other views medial. Scale 0.1 mm.

Gnathopod 2: basis with only a few minute setae along the anterolateral margin (setal lengths <20% of the basis width); carpus and propodus, setae on the anterior margin short and simple (setal length < basis width).

Pereopods 5–7: propodus not expanded anteriorly.

Uropod 1: ventral peduncular spinous process underlying about 1/2 of the longest ramus.

Uropod 3: inner ramus without spines mid-dorsally (with only the single apical spine).

Telson: tip without apical setae (only the usual short setae at each dorsolateral cusp).

Thumbed male:

Antenna 2: without plumose setae on the flagellum and peduncular article 5.

Gnathopod 2: propodus, palmar defining spines not produced on a ledge; dactyl expanded close to the junction with the propodus but not centrally toothed.

Adult female:

Antenna 2: without plumose setae on the flagellum and peduncular article 5.

Gnathopod 2: propodus, palm sinuous; dactyl, inner margin evenly curved, tip fitting into depression between palmar angle and defining spines.

Remarks. Only two thumbed males of *J. thurstoni* were available for study, both of which were major forms. Therefore, the appearance of the minor form is unknown. *Jassa thurstoni* is morphologically similar to *J. kjetilanna* and both have been collected in the Falkland Islands. A comparison of the two species is given in the Remarks for *J. kjetilanna*.

Compared to the Southern Hemisphere *J. fenwicki* and *J. ingens*, *Jassa thurstoni* has a slender antenna 2 without brush or plumose setae on the flagellum and the pereopods 5–7 are not modified for grasping. It also lacks the fringe of spine-like setae along the anterolateral margin of gnathopod 1, which is typical of the Southern Hemisphere species *J. alonsoae*, *J. fenwicki*, *J. hartmannae*, *J. ingens* and *J. justi*. Another Southern Hemisphere species that lacks the fringe, *J. gruneri*, differs from *J. thurstoni* in lacking a seta or cluster of setae at the anterodistal junction of the gnathopod 1 carpus with the propodus, while *J. thurstoni* possesses a setal cluster there. *Jassa gruneri* also possesses a short fringe of relatively long setae on the basis of gnathopod 2 while *J. thurstoni* lacks this fringe. *Jassa thurstoni* is only known from the Antarctic and sub-Antarctic islands while *J. gruneri* is only known from Tasmania (Figs 11–12).

***Jassa fenwicki* Conlan, 1990**

(Table 13, Fig. 95)

Diagnosis.

Mandibular palp: article 2, dorsal margin without a fringe of setae.

Maxilla 1: without a seta or setal cluster at the base of the palp article 1.

Gnathopod 1: basis, anterolateral margin with a fringe of short, spine-like setae; carpus without a single or cluster of setae at the anterodistal junction of the propodus.

Gnathopod 2: basis with a row of short, spine-like setae along the anterolateral margin; carpus and propodus, setae on the anterior margin short and simple (setal lengths <20% of the basis width).

Pereopods 5–7: propodus expanded anteroproximally, spines strong and along nearly its full length.

Uropod 1: ventral peduncular spinous process underlying about 1/2 of the longest ramus.

Uropod 3: inner ramus without spines mid-dorsally (with only the single apical spine).

Telson: tip without apical setae (only the usual short setae at each dorsolateral cusp).

Thumbed male:

Antenna 2: with plumose setae on the flagellum and peduncular article 5.

Gnathopod 2: propodus, palmar defining spines absent, the thumb distally squared and originating proximally. The dactyl is strongly expanded close to the junction with the propodus.

Subadult female:

Antenna 2: not plumose on the flagellum and peduncular article 5 (but see Remarks).

Gnathopod 2: propodus, palm sinuous.

Adult female: unknown

Remarks. Only one thumbed male, one subadult female and two juveniles are known from two collections in disparate locations (Cumberland Bay, South Georgia (54°14′S, 36°28′W), and The Snares, New Zealand (48°01′S, 166°32′E)). In both collections *J. fenwicki* was mixed with *J. alonsoae*. The appearance of the minor form male and the adult female are unknown. However, the combination of the spine-like fringes on gnathopods 1 and 2, lack of a seta on the gnathopod 1 carpus-propodus anterior junction and the proximally expanded and strongly spinous propodus of pereopods 5–7 are distinctive. Although the subadult female lacked plumose setae on the antenna 2 peduncular article 5, larger individuals may develop them. All other species of *Jassa* that develop plumose setae in the larger male also develop them in the larger female. It can be reasonably assumed that since the subadult female has a sinuous palm of gnathopod 2, an adult female would as well.

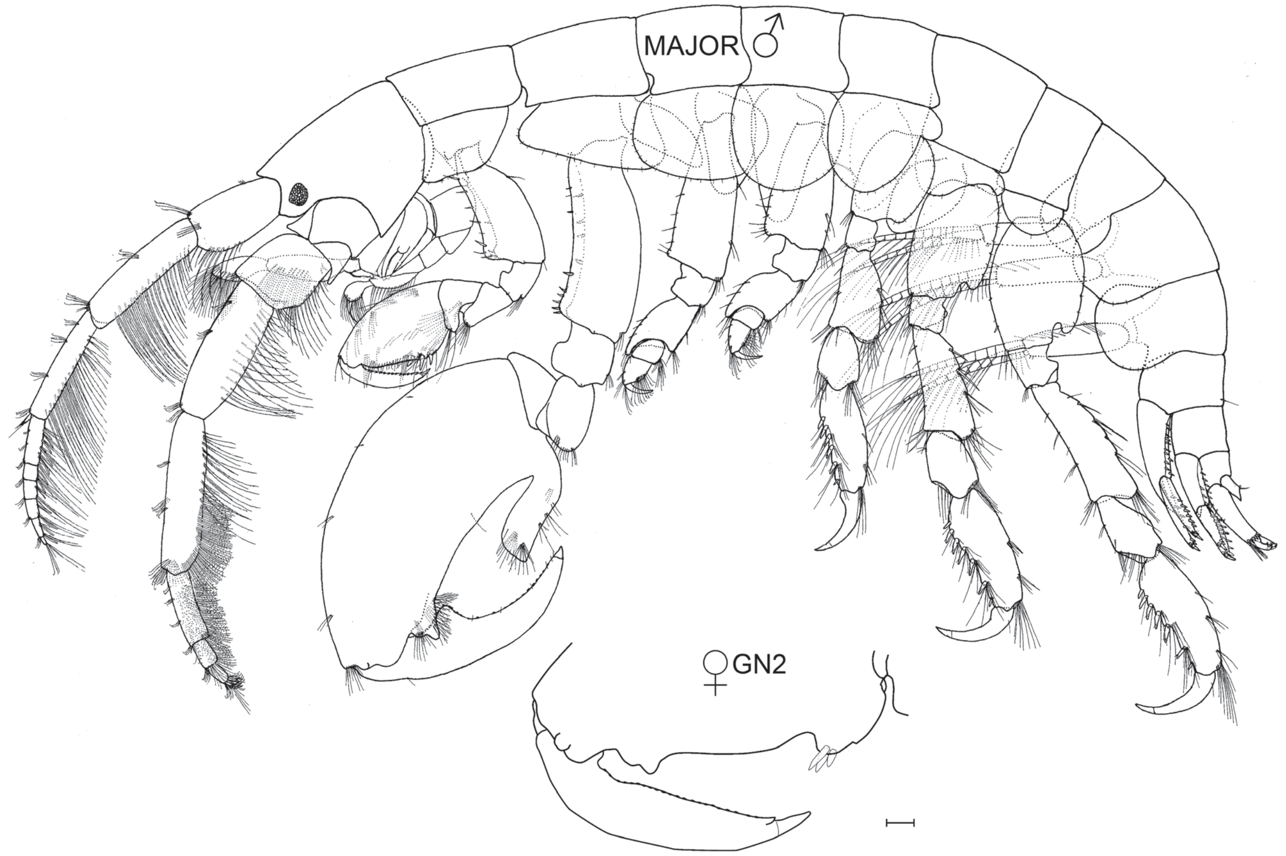

FIGURE 95. *Jassa fenwicki* Conlan, 1990. Holotype, adult male, major form, 7.4 mm, AM P34951. Punui Bay, The Snares Islands, New Zealand (48°01′ S, 166°32′ E), 21 January 1977, G. D. Fenwick, coll. (AM). Allotype, subadult female, Cumberland Bay, South Georgia (54°14′ S, 36°28′ W), 9 May 1902, among algae, 1–2 m depth, type no. 3946 from lot no. 3015 (NRM). All views lateral. Setae omitted from the female gnathopod 2 profile. Scale 0.1 mm. Illustration after Conlan (1990).

Jassa kjetilanna Vader & Krapp, 2005

(Table 13, Figs 96–98)

Diagnosis.

Both sexes:

Mandibular palp: article 2, dorsal margin without a fringe of setae.

Maxilla 1: without a seta or setal cluster at the base of the palp article 1.

Gnathopod 1: basis, anterolateral margin with a few short setae along its length; carpus with a very short seta at the anterodistal junction of the propodus (seta about 10% of anterior margin length and slightly lateral).

Gnathopod 2: basis with a row of short setae along the anterolateral margin (setal lengths <10% of the basis width); carpus and propodus, setae on the anterior margin short and simple (setal length < basis width).

Pereopods 5–7: propodus not expanded anteriorly.

Uropod 1: ventral peduncular spinous process underlying about 1/3 of the longest ramus.

Uropod 3: inner ramus without spines mid-dorsally (with only the single apical spine).

Telson: tip without apical setae (only the usual short setae at each dorsolateral cusp).

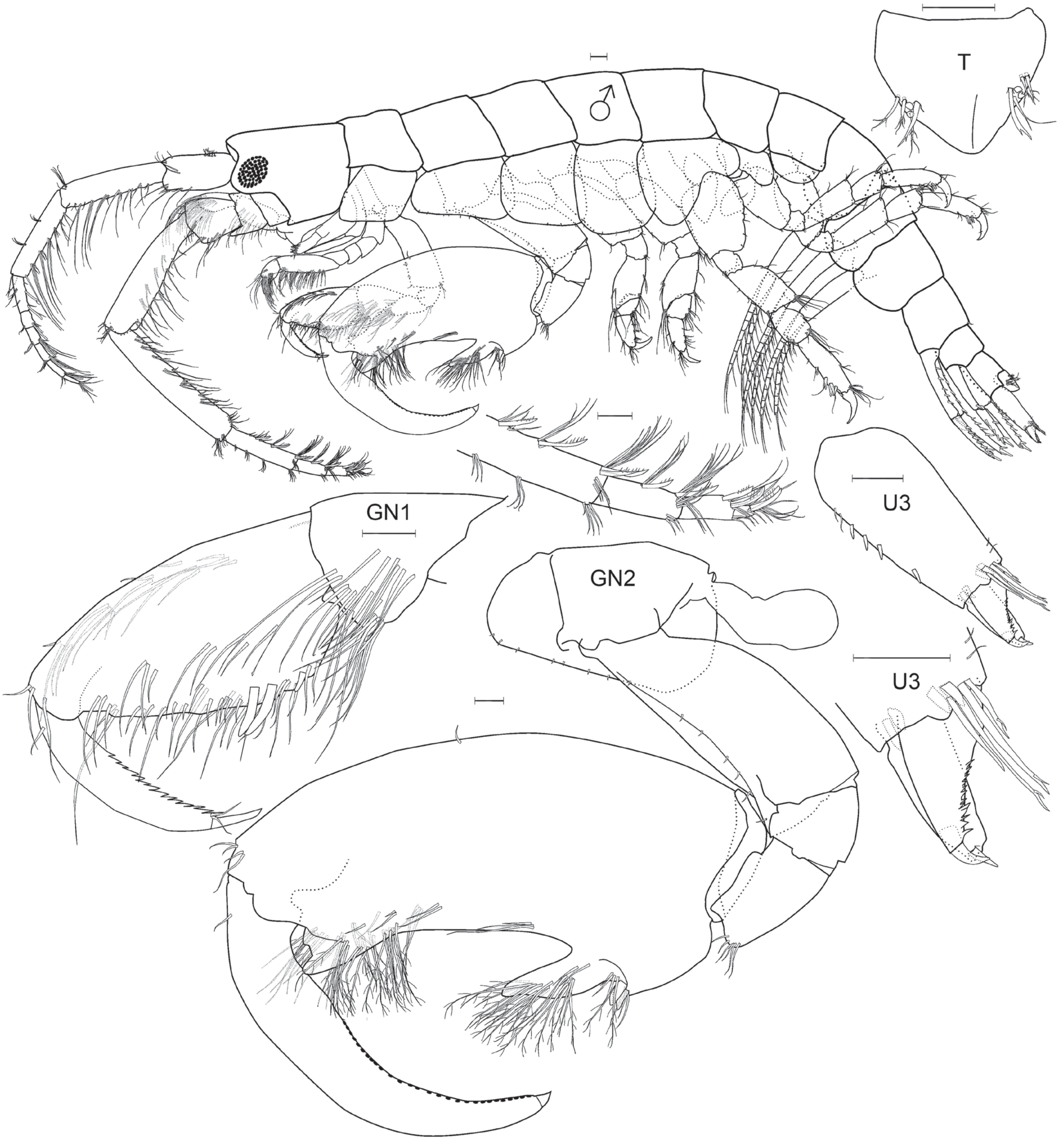

FIGURE 96. *Jassa kjetilanna* Vader and Krapp, 2005. Adult male, major form, 6.5 mm. Choiseul Sound, East Falkland, 29 October 2003, A. and W. Vader, coll., from the lithodid crab *Paralomis granulosa* (Hombron & Jacquinot, 1846) at 20–30 m depth (TSZ Cr 19054). Lateral view: whole body and uropod 3; dorsal view: telson; other views medial. Scale 0.1 mm.

Thumbed male:

Antenna 2: without plumose setae on the flagellum and peduncular article 5.

Gnathopod 2: propodus, palmar defining spines produced on a ledge in both small and large thumbed males. In minor males, the thumb is distally acute, short relative to body length and located on the distal half of the propodus. The dactyl is not centrally toothed. In major males, the thumb is also acute, relatively short, and on the proximal half of the propodus. The dactyl is shallowly expanded close to the junction with the propodus but is not centrally toothed.

Adult female:

Antenna 2: without plumose setae on the flagellum and peduncular article 5.

Gnathopod 2: propodus, palm sinuous; dactyl, inner margin evenly curved, tip fitting into depression between palmar angle and defining spines.

Remarks. Known only from the Falkland Islands, this species bears the characteristics of the genus *Jassa* (antennal setation, strong mandibular palp, gnathopod 2 palm defined by a cluster of spines, terminal male's thumb produced distally to the spines; pereopod 3 and 4 merus anteriorly produced over the carpus).

Specimens collected on 29 October 2003 by A. and W. Vader from the lithodid crab *Paralomis granulosa* (Hombron & Jacquinot, 1846) at 20–30 m depth in Choiseul Sound, East Falkland, were borrowed from Tromsø Museum, Norway (TSV Cr 19054). The collection consisted of 3 major form thumbed males, 3 subadult (or near-subadult non-thumbed males), 5 adult females (2 ovigerous) and 14 juveniles. Representatives of each group were illustrated (Figs 96–98). Although Vader & Krapp (2005) thoroughly illustrated the types, which were also collected from Choiseul Sound, there was some minor disagreement between the types and the specimens examined, as follows.

Maxilla 2: The inner ramus is an extension of the base, not segmented as illustrated by Vader & Krapp (2005).

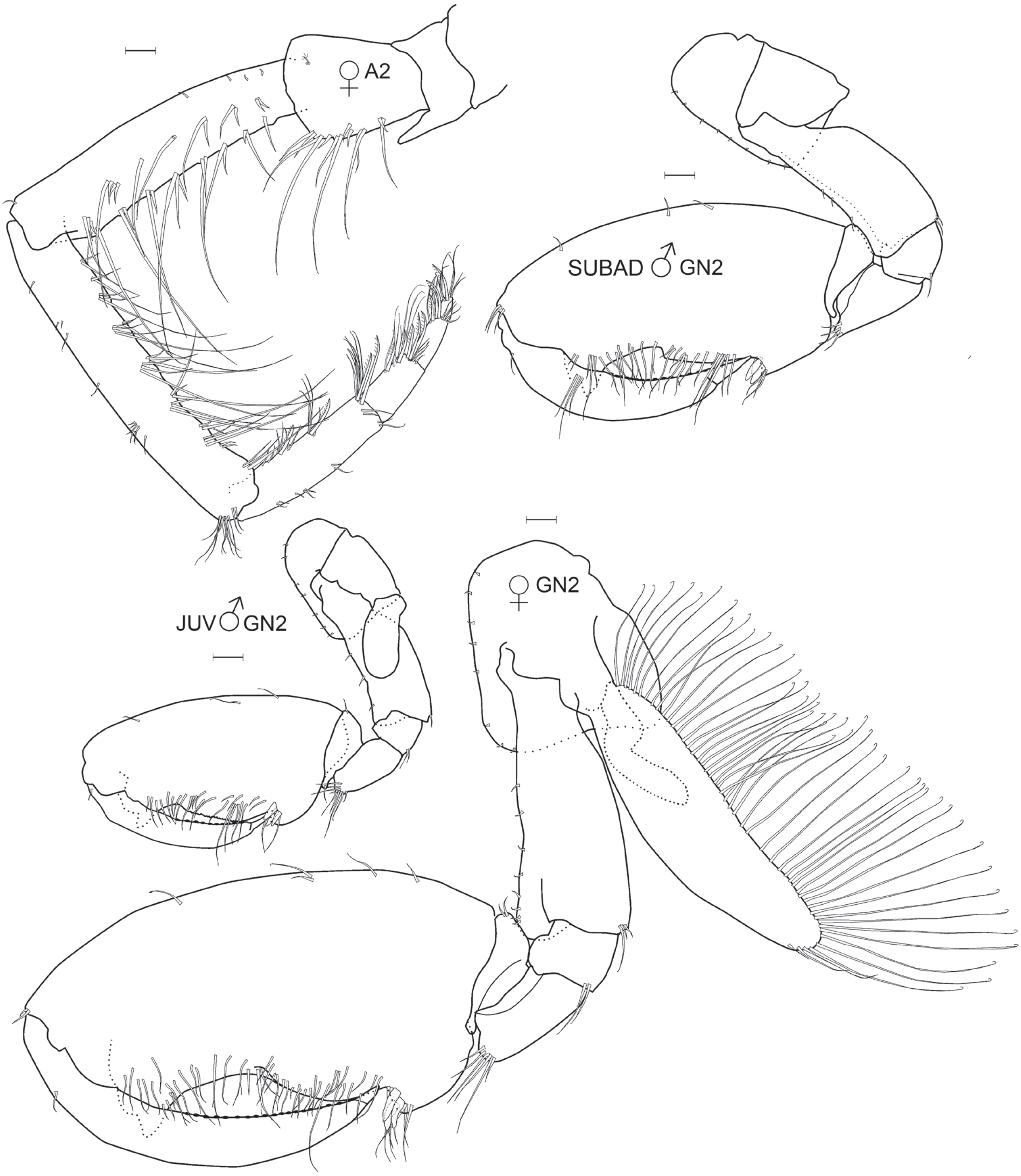

FIGURE 97. *Jassa kjetilanna* Vader and Krapp, 2005. Adult female, 5.0 mm; subadult male, 5.0 mm; juvenile male, 3.5 mm. Choiseul Sound, East Falkland, 29 October 2003, A. and W. Vader, coll., from the lithodid crab *Paralomis granulosa* (Hombron & Jacquinot, 1846) at 20–30 m depth (TSZ Cr 19054). All views medial. Scale 0.1 mm.

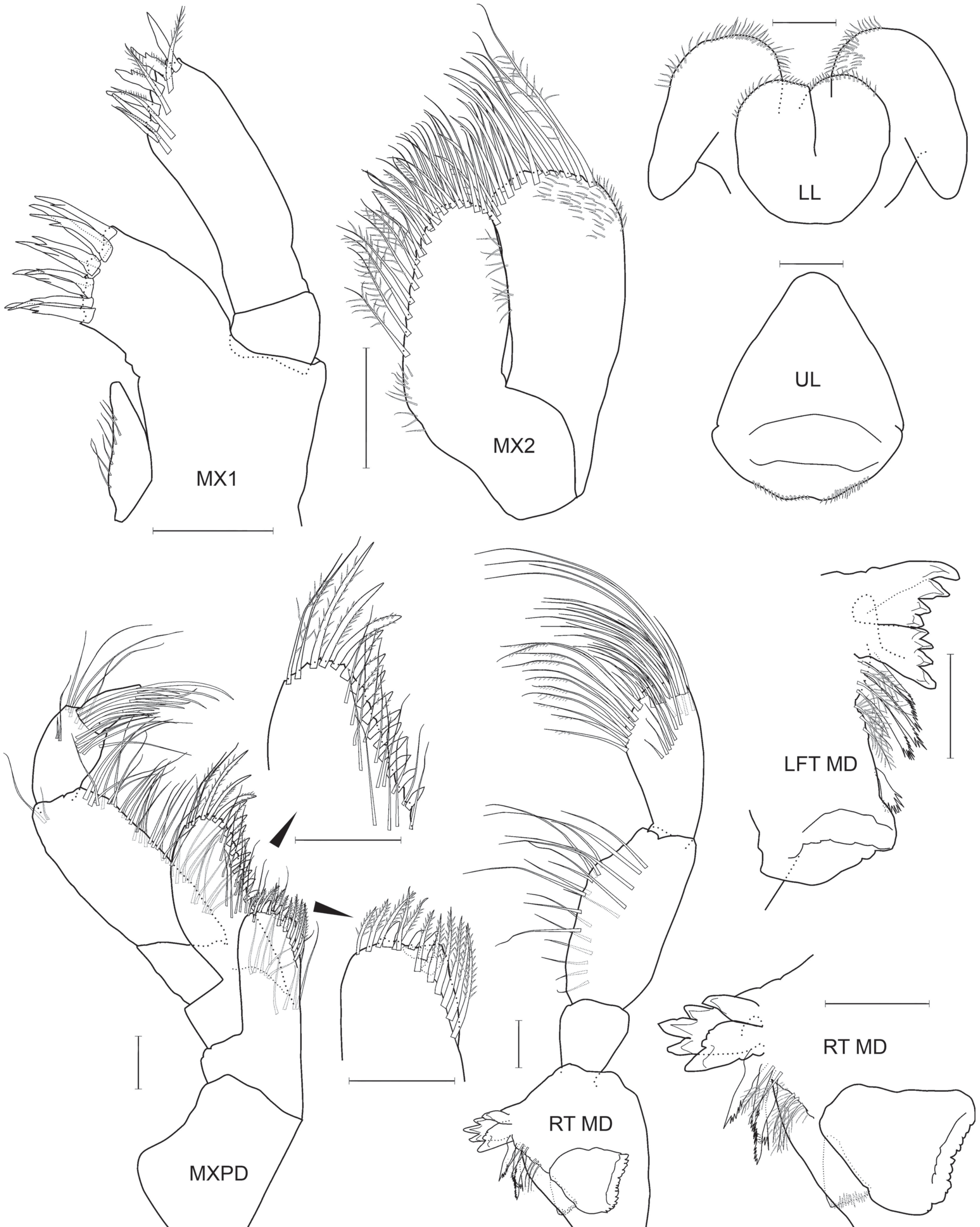

FIGURE 98. *Jassa kjetilanna* Vader and Krapp, 2005. Adult male, major form, 6.5 mm. Choiseul Sound, East Falkland, 29 October 2003, A. and W. Vader, coll., from the lithodid crab *Paralomis granulosa* (Hombron & Jacquinot, 1846) at 20–30 m depth (TSZ Cr 19054). Mouthparts. Frontal view: upper lip; lateral view: maxillae 1 and 2; other views medial. Scale 0.1 mm.

Gnathopod 1: The cluster of setae at the anterodistal junction of the carpus and propodus, stated as present in Vader & Krapp's (2005) description but absent in the specimens they illustrated, are confirmed present in the specimens examined herein (single, slightly lateral seta in the specimens examined).

Gnathopod 2: Subadult males have a small 'pre-thumb' (Fig. 97), but the juvenile male gnathopod 2 illustrated by Vader & Krapp (2005) has too large a thumb to be subadult. Instead, it is likely a 'minor form' adult. The larger thumbed gnathopod 2 illustrated by Vader & Krapp (2005) is not 'hyperadult', but resembles that of a 'major form' adult male (Conlan 1990).

Uropod 1: The interramal spine that projects underneath the rami is not lateral as illustrated.

Uropod 3: The apparent lack of the characteristic pair of cusps proximal to the curved embedded spine at the tip of the outer ramus were present in the specimens examined herein.

No conclusions could be drawn on the variation of thumb size relative to body size as only three thumbed males were available for measurement. In comparison with other Southern Hemisphere species of *Jassa*, Vader & Krapp (2005) considered the relationship of *J. kjetilanna* to *J. thurstoni* and *J. alonsoae* due to their co-occurrence in the Falkland Islands. *Jassa alonsoae* has many morphological features that are not shared with *J. kjetilanna*, but *J. thurstoni* is more similar if intraspecific variation is taken into consideration. It requires the use of sex- and age-invariant characters to differentiate species of *Jassa* because their morphology varies so much with age, size and sex. Using only key characters, *J. kjetilanna* and *J. thurstoni* are separable by the length of the seta or setal cluster on the carpus at the anterodistal junction of the propodus. This is minute in *kjetilanna* (length ~10% of the anterior margin of the carpus) and easily overlooked, but longer in *J. thurstoni* (~25% of the length of the carpus). This setal length is invariant in other species of *Jassa*, so the length difference between *J. kjetilanna* and *J. thurstoni* is considered significant enough to indicate that these species are morphologically distinct. There are also shape and size differences: slender, long antennae in *J. thurstoni*, shorter, stouter antennae in *J. kjetilanna*; anteriorly produced coxa 1 in *J. thurstoni* adult male and less produced coxa 1 in *J. kjetilanna*; differently shaped thumbs in the adult males with tendency to pronunciation of the defining spines in *J. kjetilannna* and loss in *J. thurstoni*; and similarly sized pereopods 5–7 in *J. kjetilanna* with relatively strong spines at the anterodistal end of the propodus compared to increasingly longer pereopods 5–7 in *J. thurstoni* with slender, seta-like spines anterodistally on the propodus.

Jassa ingens **Pfeffer, 1888**

(Table 13, Figs 99–101)

Synonyms: see Conlan (1990).

Diagnosis.

Both sexes:

Mandibular palp: article 2, dorsal margin without a fringe of setae.

Maxilla 1: with a small cluster of setae at the base of the palp article 1.

Gnathopod 1: basis, anterolateral margin with a few to a full row of short setae along its length which may be slender or spine-like; carpus with a single or small cluster of setae at the anterodistal junction of the propodus (setae about 1/3 of anterior margin length and slightly lateral and medial).

Gnathopod 2: basis with a row of small setae along the anterolateral margin (setal lengths <10% of the basis width); carpus and propodus, setae on the anterior margin short and simple (setal length < basis width).

Pereopods 5–7: propodus expanded anteriorly.

Uropod 1: ventral peduncular spinous process underlying about 40% of the longest ramus.

Uropod 3: inner ramus without spines mid-dorsally (with only the single apical spine).

Telson: tip without apical setae (only the usual short setae at each dorsolateral cusp).

Thumbed male:

Antenna 2: large individuals without plumose setae on the flagellum and peduncular article 5.

Gnathopod 2: propodus, palmar defining spines produced on a ledge, present in both small and large thumbed males.

Adult female:

Antenna 2: without plumose setae on the flagellum and peduncular article 5.

Gnathopod 2: propodus, palm sinuous.

Remarks. All of the thumbed males available for study had relatively short thumbs with the palmar defining spines present and produced on a ledge, suggesting that these spines are not lost even in the largest animals. The antenna 2 setae are long in small juveniles but shorten drastically in the adult males. The expanded propodus of pereopods 5–7 is distinctive, even in the young. This is the largest species known for the genus, with body length at maturity in the specimens available 19.6–24.1 mm for the adult (thumbed) males and 15.3–20.8 mm for the adult females.

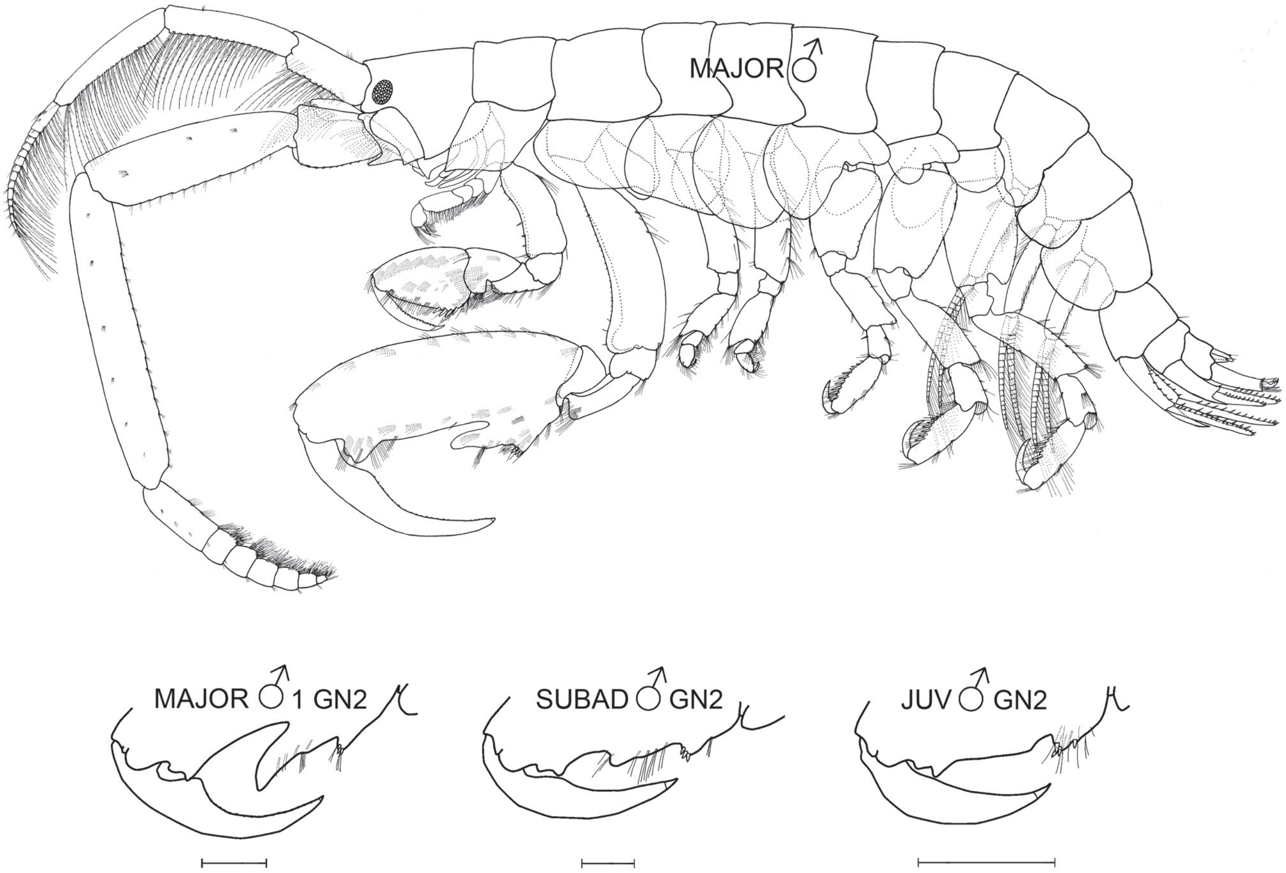

FIGURE 99. *Jassa ingens* (Pfeffer, 1888). Whole body: lectotype, adult male, major form, 22.1 mm, ZMH K-8017. Moltke-Hafen, Royal Bucht, South Georgia (54°30′58″S, 36°0′45″W), 16 Januarly 1884, Deutsche Polarstation 1882/83, K. Von den Steinen, coll. (ZMH). Adult male 1, major form, 20.3 mm and juvenile male, 10.6 mm, NHM 1969:705:9. Billie Rocks, Signy Island, South Orkney Islands (60°42′S, 45°36′W), 5 March 1965, M. H. Thurston, coll., station 10 (97). SCUBA collection on vertical creviced rock with *Lithothamnia*, *Desmarestia anceps*, *Ascoseira mirabilis*, *Iophon*/*Phyllophora*, Porifera, Polyzoa, 1.9–2.2 m depth, IZ 1989-013 (CMN). Subadult male, 19.9 mm, NHM 1969:713:4. Billie Rocks, Signy Island, South Orkney Islands (60°42′S, 45°36′W), 27 February 1965, M. H. Thurston, coll., station 20 (512), SCUBA collection on rock inclined at 45–50°with overlying boulders and sand in crevices. *Lithothamnia*, *Desmarestia anceps*, Rhodophyceae, Polyzoa, 7.4–7.7 m depth (NHM). All views lateral. Setae omitted from the gnathopod 2 profiles except for those around the thumb and spines of the males in order to landmark position changes with growth. Scale 1 mm. Illustration after Conlan (1990).

FIGURE 100. *Jassa ingens* (Pfeffer, 1888). Adult male, major form, 20.3 mm, NHM 1969:705:9. Billie Rocks, Signy Island, South Orkney Islands (60°42′S, 45°36′W), 5 March 1965, M. H. Thurston, coll., station 10 (97). SCUBA collection on vertical creviced rock with *Lithothamnia*, *Desmarestia anceps*, *Ascoseira mirabilis*, *Iophon*/*Phyllophora*, Porifera, Polyzoa, 1.9–2.2 m depth, IZ 1989-013 (CMN). Adult female, 19.2 mm, NHM 723:7, Factory Cove–Berntsen Point, Signy Island, South Orkney Islands (60°42′S, 45°36′W), 15 April 1964, M. H. Thurston, coll., station 46 (1929). Agassiz trawl close inshore over boulder slopes with *Desmarestia anceps*, *Phyllogigas grandifolius* and Rhodophyceae dominant, 6–14 m depth, IZ 1989-013 (CMN). Lateral view: male uropod 3; medial views: female gnathopod 2 and uropod 3. Scale 0.1 mm.

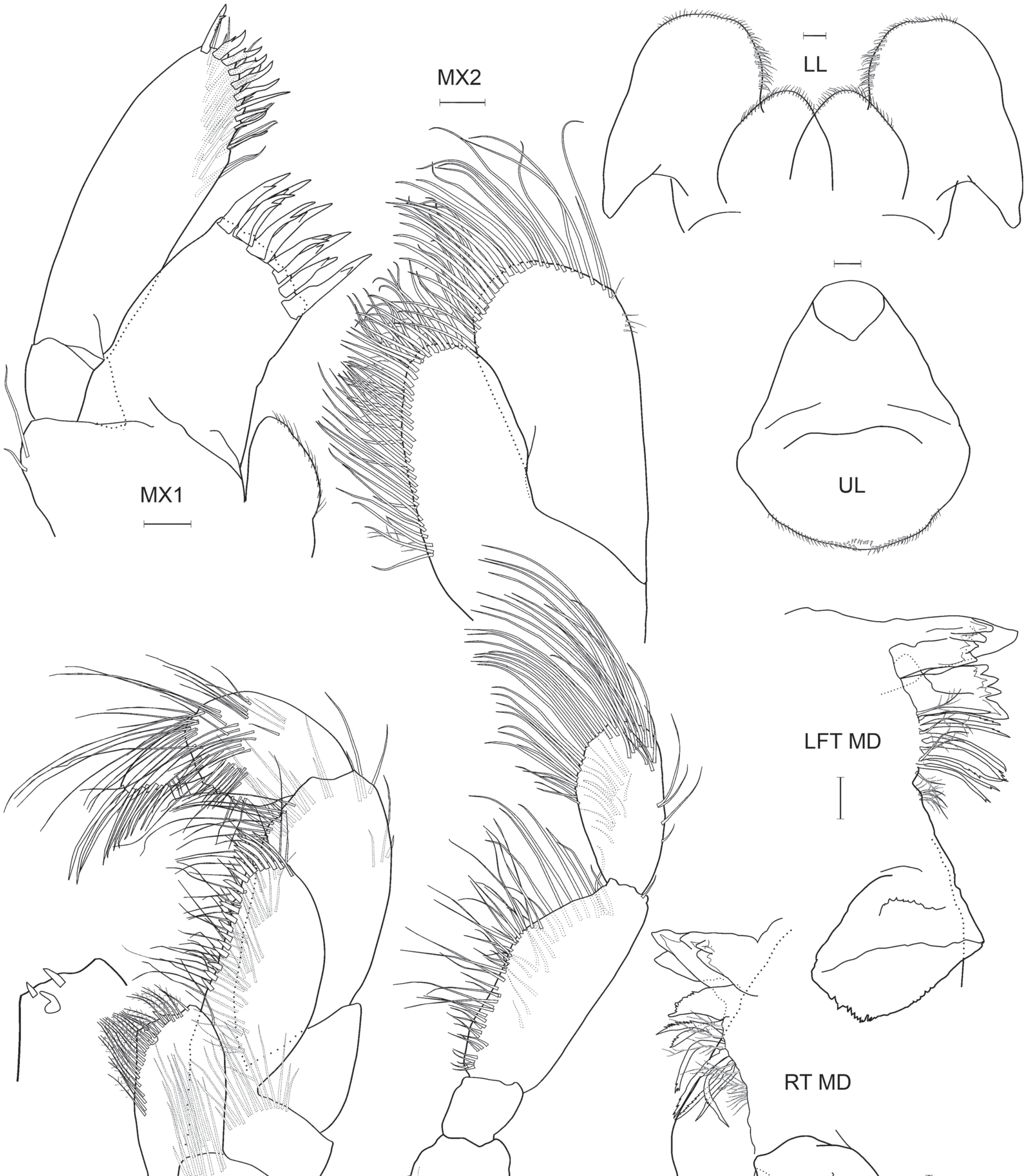

FIGURE 101. *Jassa ingens* (Pfeffer, 1888). Adult male, major form, 20.3 mm, NHM 1969:705:9. Billie Rocks, Signy Island, South Orkney Islands (60°42′S, 45°36′W), 5 March 1965, M. H. Thurston, coll., station 10 (97). SCUBA collection on vertical creviced rock with *Lithothamnia*, *Desmarestia anceps*, *Ascoseira mirabilis*, *Iophon*/*Phyllophora*, Porifera, Polyzoa, 1.9–2.2 m depth, IZ 1989-013 (CMN). Mouthparts. Frontal view: upper lip; other views medial. Scale 0.1 mm.

Jassa gruneri Conlan, 1990

(Table 13, Figs 102–103)

Diagnosis.

Both sexes:

Mandibular palp: article 2, dorsal margin without a fringe of setae.

Maxilla 1: without a cluster of setae at the base of the palp article 1.

Gnathopod 1: basis, anterolateral margin with only a few short setae distally; carpus without a single or small cluster of short setae at the anterodistal junction of the propodus.

Gnathopod 2: basis with a few or a full row of setae along the anterolateral margin (setal lengths 50% of the basis width); carpus and propodus, setae on the anterior margin short and simple (setal length < basis width).

Pereopods 5–7: propodus not expanded anteriorly.

Uropod 1: ventral peduncular spinous process underlying about 40% of the longest ramus.

Uropod 3: inner ramus without spines mid-dorsally (with only the single apical spine).

Telson: tip without apical setae (only the usual short setae at each dorsolateral cusp).

Thumbed male: unknown.

Adult female:

Antenna 2: without plumose setae on the flagellum and peduncular article 5.

Gnathopod 2: propodus, palm sinuous.

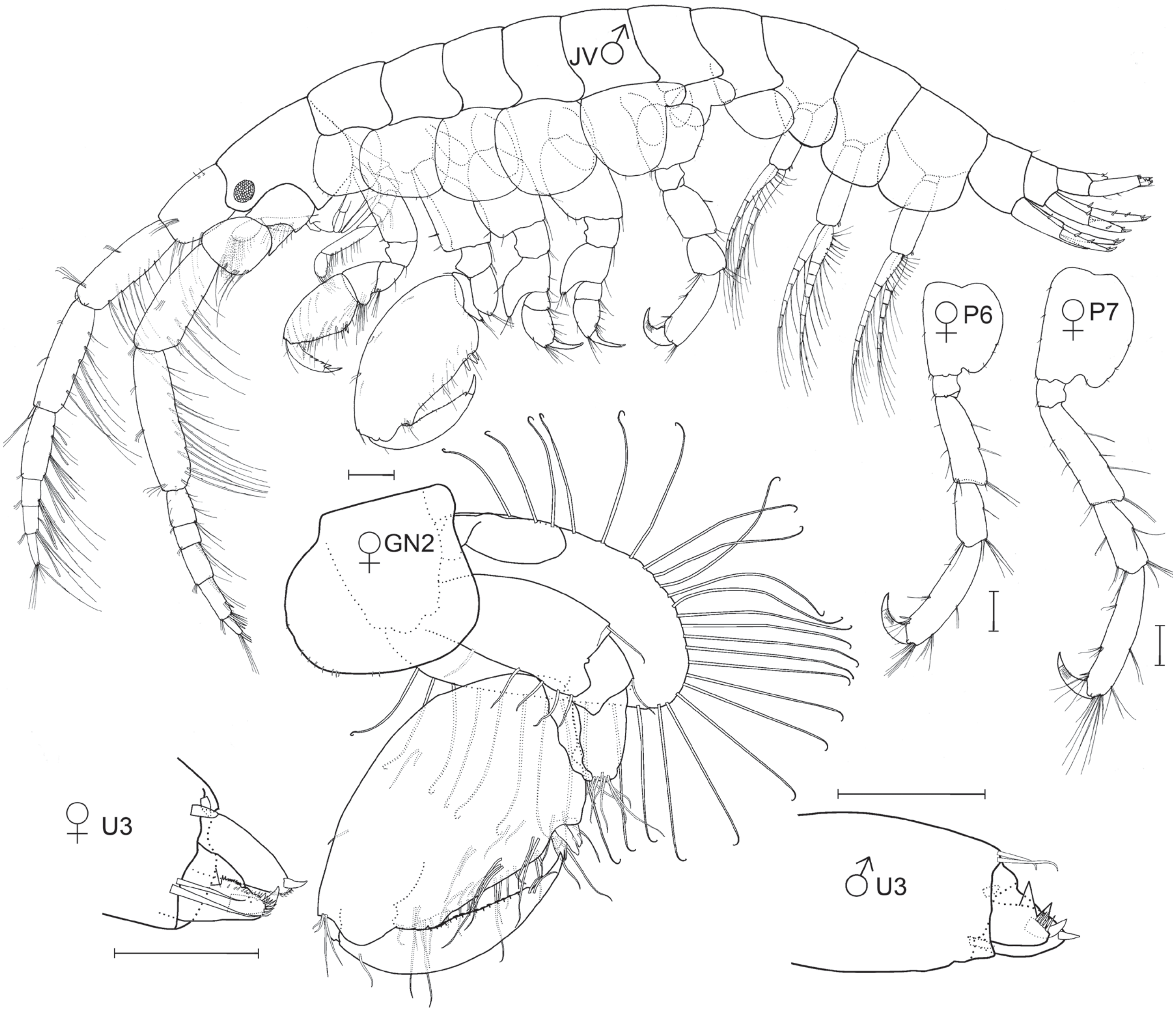

FIGURE 102. *Jassa gruneri* Conlan, 1990. Holotype, juvenile male, 2.1 mm, NMCC 1987-1077; allotype, adult female, 3.2 mm, NMCC 1987-1078. Hobart Harbour, Tasmania (42°50′S, 147°20′E), 8 November 1978, G. Edgar, coll., SCUBA, algal washes, 3–5 m depth, 1978-287 (CMN). Lateral views. Scale 0.1 mm. Illustration after Conlan (1990).

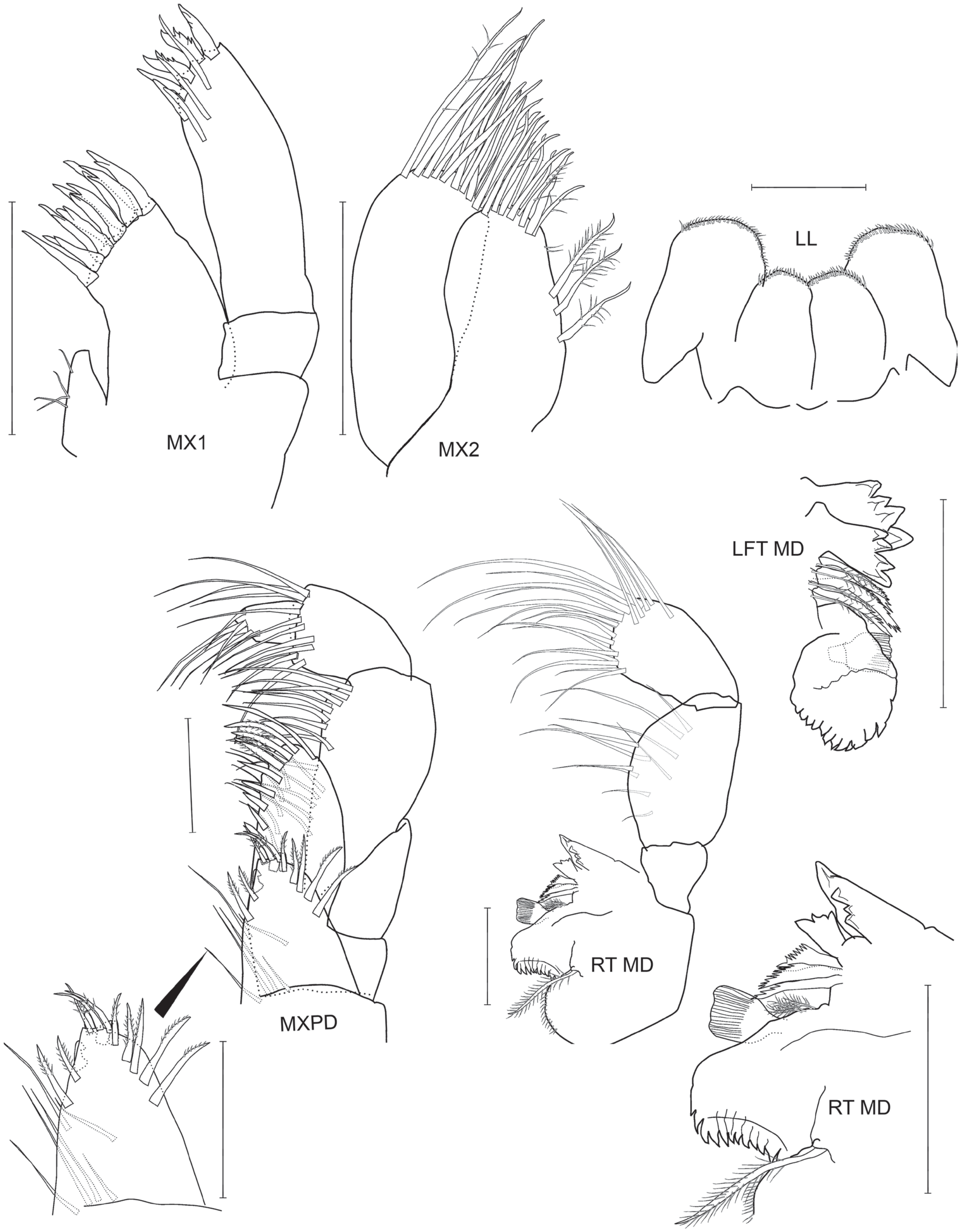

FIGURE 103. *Jassa gruneri* Conlan, 1990. Holotype, juvenile male, 2.1 mm, NMCC 1987-1077. Hobart Harbour, Tasmania (42°50′S, 147°20′E), 8 November 1978, G. Edgar, coll., SCUBA, algal washes, 3–5 m depth, 1978-287 (CMN). Mouthparts. Lateral view: maxilla 1; other views medial. Scale 0.1 mm.

Remarks. This is a small-bodied species with the juvenile male holotype 2.1 mm and the adult female allotype 3.2 mm (Conlan 1990). It is part of the Southern Hemisphere sinuous-palmed group, keying closest to *J. thurstoni*. *Jassa gruneri* differs in the lack of a seta on the carpus of gnathopod 1 at the anterodistal junction of the propodus (present in *J. thurstoni*) and in the presence of a row of setae on the basis of gnathopod 2 (absent in *J. thurstoni*). This row is more pronounced in the female allotype than the juvenile male holotype (Fig. 102). Currently it is only known from Tasmania and New Zealand. The New Zealand specimen (Fig. 12) is a juvenile male and was found in a collection in Lyttelton harbour described by Chilton (1884). In this same collection is a specimen used by Chilton to describe his new species *Podocerus latipes* Chilton, 1884, which was synonymized by Stebbing (1906) under *Jassa frequens* (Chilton, 1883) and later transfered to *Ventojassa* (Conlan 2021).

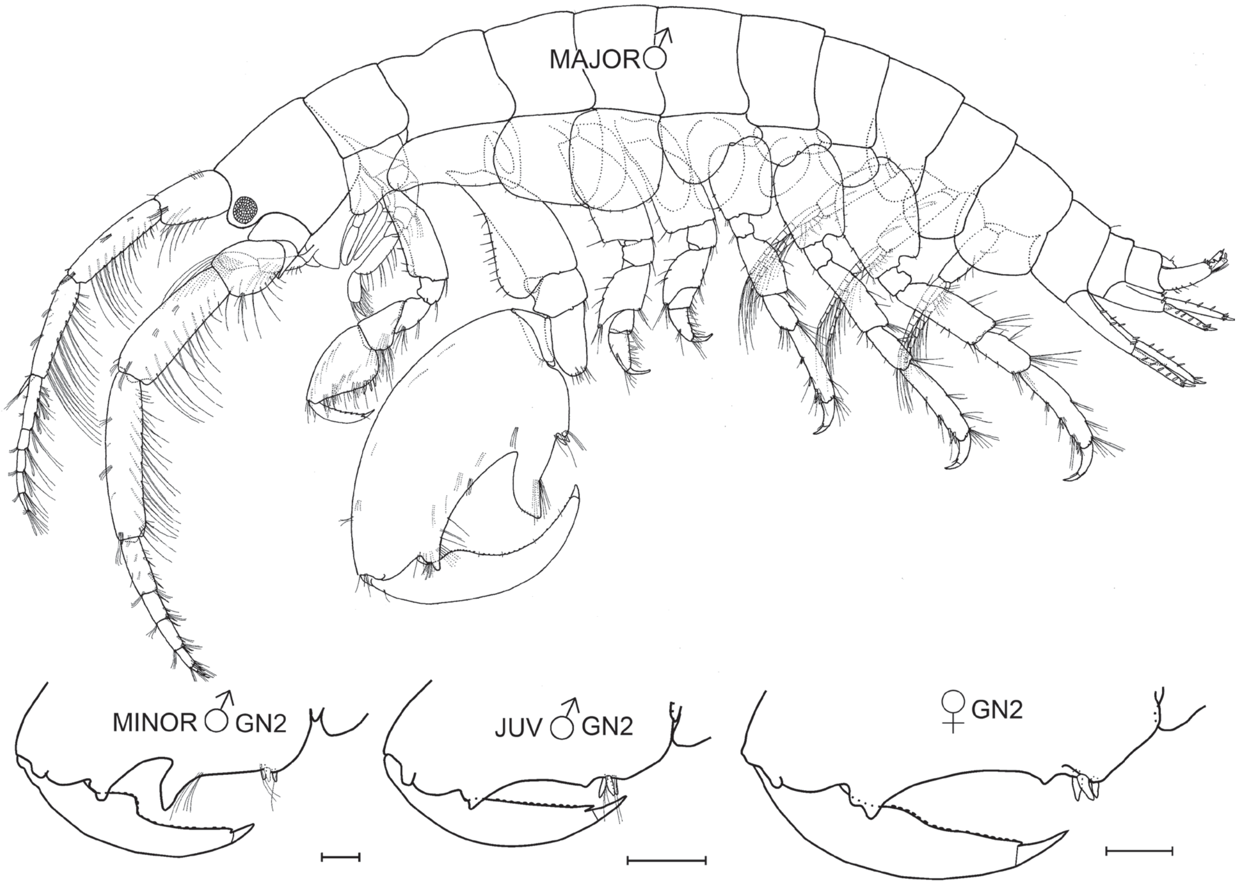

FIGURE 104. *Jassa hartmannae* Conlan, 1990. Holotype, adult male, major form, 4.5 mm, AM P34950. Senecio Pool, The Snares, New Zealand (48°07′S, 166°38′E), 6 January 1977, G. D. Fenwick, coll., from *Lessonia variegata* holdfast, 1.5 m depth (AM). Allotype, adult female, NMNH 235008; paratypes, adult male, minor form, 3.1 mm and juvenile male, 1.8 mm, NMNH 235009, St. Clair, Dunedin, New Zealand (45°50′S, 17°20′E), 25 January 1968, J. L. Barnard, coll., station E973 (J. L. Barnard station NZ-8), formalin wash of algae, especially of pterocladians or streblocladians, heavy turf (*Gelidium-Bostrychia*) and several specimens of *Pyura* sp. (NMNH). Setae omitted on the gnathopod 2 profiles except for those around the thumb and spines of the males in order to landmark position changes with growth. All views lateral. Scale 0.1 mm. Illustration after Conlan (1990).

Jassa hartmannae Conlan, 1990

(Table 13, Fig. 104)

Diagnosis.

Both sexes:

Mandibular palp: article 2, dorsal margin without a fringe of setae.

Maxilla 1: without a cluster of setae at the base of the palp article 1.

Gnathopod 1: basis, anterolateral margin with a row of short setae along its length which may be slender or spine-like; carpus without a single or small cluster of short setae at the anterodistal junction of the propodus.

Gnathopod 2: basis with a row of short setae along the anterolateral margin (setal lengths ≤25% of the basis width); carpus and propodus, setae on the anterior margin short and simple (setal length < basis width).

Pereopods 5–7: propodus not expanded anteriorly.

Uropod 1: ventral peduncular spinous process underlying about 50% of the longest ramus.

Uropod 3: inner ramus without spines mid-dorsally (with only the single apical spine).

Telson: tip without apical setae (only the usual short setae at each dorsolateral cusp).

Thumbed male:

Antenna 2: large individuals without plumose setae on the flagellum and peduncular article 5.

Gnathopod 2: propodus, palmar defining spines produced on a ledge, present in both small and large thumbed males.

Adult female:

Antenna 2: without plumose setae on the flagellum and peduncular article 5.

Gnathopod 2: propodus, palm shallowly concave.

Remarks. There is an error in the key to species in Conlan (1990) (though the description is correct). The gnathopod 1 carpus lacks a seta or setae at the anterodistal junction with the propodus. There are only 16 specimens known so far from two collections listed in Conlan (1990), both from New Zealand. Four of these are thumbed males (three major form and one minor form). All males possessed palmar defining spines, suggesting that they may not lose them even if major form. *Jassa hartmannae* most closely resembles *J. justi* but they differ in the stonger spination of the propodus of pereopods 5–7, stouter antenna 2 and spinier basis of gnathopod 2 in *J. justi* than *J. hartmannae* (Figs 92, 104). *Jassa justi* also achieves twice the body length of *J. hartmannae*.

Lapsed species

Seven names are listed in the World Register of Marine Species (Horton *et al.* 2020) as accepted species of *Jassa*, but types have not been found to determine how these relate morphologically to the above species. Following is a summary of what is known about each.

Jassa algensis **(Nardo, 1847a)**

Originally named *Cancer algensis* by Stefano Chiereghin in an unpublished manuscript, this species, from the Venice lagoon, was mentioned in two publications by Nardo in 1847. Nardo (1847a, p. 132) described "...*Cancer algensis*, Chiereghin, sp.60, fig. 76–79, which has the peculiarity of weaving a garment shaped like a cornucopia on the leaves of the zostera within which it is hidden like the larvae of the Friganee. This was believed by Leach a *Podocerus*, but should be regarded as a new genus that we named *Lusyta*, next to *Atylus*, Leach, and *Carapus*, Say." (translated from Italian). Nardo (1847b) gave a short Latin description of *Lusyta algensis* which is of no help in deciphering whether this species is in the genus *Jassa*. Nardo (1869) illustrated *Lusyta algensis*, showing two figures of its tubes which appeared to be attached to a substrate (one figure life-sized and one enlarged), and two figures of the full body (one figure life-sized and one enlarged). The illustrations are small, but some features are evident.

Tubes: the two tubes shown are conical, not cylindrical, and curved. The tubes appear to be open only at one end, with the open head end being 2.5x the width of the closed tail end. The two tubes overlap each other at about 90° with the head of each tube farthest from the other head. The length of the tube in the life-sized illustration is about 7 mm.

Body length: the length of the full body in the life-sized illustration is about 6 mm.

Antennae 1 and 2: are both slender and about the same length.

Gnathopods: the illustration of the full body (enlarged) shows the two gnathopods to be no larger than the pereopods.

Illustration of other features, such as the morphology of the third uropod were too small to assist with determining taxonomic status. Nardo's description of *Lusyta algensis* sheds further light by stating that "The first two feet are large, equal..." (*I primi due piedi sono grossetti, eguali…*).

Stebbing (1906) listed *Lusyta* Nardo, 1847a and *L. algensis* Nardo, 1847a under the title "Gammarideorum genera dubia et species dubiae." Two features of the illustrations and description in Nardo (1869) suggest that *Lusyta algensis* is not *Jassa*: the equally sized gnathopods, and the appearance of the tube. In *Jassa*, the second gnathopod is so enlarged compared to the first (even in the female and juvenile) that this should be evident both in the description and in the drawings made by Nardo (1869). The tubes are not *Jassa*-like. *Jassa* builds a cylindrical tube which is open at both ends, not a curved, conical tube that is open only at one end. Therefore, it is unlikely that Nardo's *Lusyta algensis* is in fact *Jassa* at all. To confirm this is not possible, unfortunately, as most of the Nardo collection has been lost and what is left has no labels (pers. comm. with Roberta Salmaso, Museo Civico di Storia Naturale, Verona, 17 July 2018).

***Jassa australis* (Haswell, 1879)**

Haswell (1879) collected this species from Port Jackson, Australia and named it *Podocerus australis*. According to H. Stoddart of the Australian Museum, "the original material of Haswell's *Podocerus australis* is missing and the 'species' was never collected/recorded again under this name." (H. Stoddart (AM), personal communication, 6 November 1984). J.L. Barnard (1974) further elaborated on Haswell's material, indicating that the Australian Museum held four specimens of Haswell's collection G.5386 under the name *Podocerus australis*, but these specimens were actually *Icilius*. This was reiterated by H. Stoddart (AM): "the material referred to in this entry (G. 5386) is *Icilius australis*, which remains *Icilius australis*." (H. Stoddart (AM), personal communication, 6 November 1984).

The British Museum holds specimens (not type) identified as *P. australis*, Haswell, 1879 by E.J. Miers (NHM 1881:31) that were collected at Port Jackson by Dr. R. Coppinger, aboard H.M.S. *Alert*. These specimens were examined and found to be *J. marmorata*. 1881 is the earliest record of *J. marmorata* in Australia (Table 3). Thus it is possible that Haswell's illustrated specimens were *J. marmorata* as well, though *J. slatteryi* has also been found in Port Jackson (Table 3). *Jassa justi* has also been found in Australia but is not known from Port Jackson (Conlan 1990). Haswell's figure of *P. australis* shows a male with large, distally acute thumb (posterior margin of the propodus incised for 75% of its length). Large *J. marmorata* have a long thumb that is squared distally; smaller thumbed males have distally acute thumbs. Large thumbed *J. slatteryi* have distally acute thumbs but the incision is not as great as shown by Haswell (1879). Since there is no type specimen for Haswell's *P. australis*, the name has never been subsequently used, and there is no formal link from *P. australis* to the genus *Jassa*, the name *Jassa australis* (Haswell, 1879) should be listed as *nomen dubium*.

***Jassa calcaratus* (Rathke, 1843)**

In documenting the fauna of Norway, Rathke (1843) described and figured a new species which he had collected from seaweed at Kristiansund, Norway. Named *Podocerus calcaratus*, his illustration of the male's long-thumbed gnathopod 2 indicates that it is probably *Jassa falcata*. Rathke (1843) indicated that *P. calcaratus* was close to, but different from *P. pulchellus* (now *Jassa falcata*) but did not state why. Bate (1862) disagreed and synonymized *P. calcaratus* under *P. pulchellus* (now *Jassa falcata*). Sars (1894) listed *P. calcaratus* as a synonym of *P. falcatus* (now *Jassa falcata)*, saying that "The *P. calcaratus* of Rathke is undoubtedly the adult male of this species..." One large male specimen, collected at Tromsø, Norway, and identified as *Podocerus calcaratus* by Danielsen, (not type), was lent by the Zoological Museum, Bergen, Norway (ZMUB 2832) for this study. The vial held a secondary label, *Jassa pulchella*. This specimen was clearly a major form male *J. falcata*. Although the whereabouts of the type specimens are unknown, it is clear from Rathke's (1843) description, illustrations and collection location that his *P. calcaratus* is indeed *J. falcata* (Montagu, 1808). Therefore, *J. calcaratus* is synonymized with *J. falcata*.

***Jassa californicus* (Boeck, 1871)**

The Norwegian scientist Axel Boeck (1871) described seven new species from a collection made in the San Francisco area of California and sent to him for taxonomic assessment and deposition in Norway by a Professor Esmark. One of these was *Podocerus californicus*, based on two female specimens. Stebbing (1906) recognized this species as *Jassa californica*. Conlan (1990) noted that the whereabouts of the type specimens was unknown. As a further effort to locate these specimens, The Natural History Museum, Oslo, Norway, which is the repository for Boeck's collection, was contacted but the reply was, "...we have not any *Podocerus californicus* Boeck, 1871 in our collection, and I don't know where you can find it — if it exists..." (Åse Ingvild Wilhelmsen, 8 June 2018). It is possible that these specimens could have been any of the species indigenous to the California coast but named much later: *J. slatteryi* (Figs 3–4), *J. morinoi* (Figs 5–6), *J. borowskyae*, *J. staudei*, *J. carltoni*, *J. shawi* or *J. myersi* (Fig. 10). It is possible also that it could have been *J. marmorata* which would place its introduction to this area much earlier than is currently known.

Jassa orientalis (Dana, 1852a)

Dana (1852a) originally named this species *Gammarus orientalis*, changing it to *Cratophium orientale* the following year (Dana 1853). Dana (1853) based his description of this species on a single specimen captured "From the sea, off the eastern entrance of the Straits of Sunda. Collected, March 4, 1842." This was during the United States Exploring Expedition led by Charles Wilkes (1838–1842). Bate (1862) transferred it to the genus *Podocerus*. Della Valle (1893) synonymized it with *P. falcatus* (now *Jassa falcata*). As noted in Conlan (1990), the type specimens were lost (confirmed absent from the collection of the Smithsonian Institution, National Museum of Natural History, 13 May 2019 by Karen Reed, Museum Specialist, Department of Invertebrate Zoology). Dana's (1853) Plate 56, Fig. 3, showing the whole body and gnathopod 2 of a female or non-thumbed male, indicate that the specimen is indeed a *Jassa*, but the species cannot be determined from the description and illustration.

Since *Jassa* as a genus is not known from Indonesia, it is possible that this specimen was a species of *Jassa* that had been displaced from one of Wilkes' six ships, all of which may have been fouled by *Jassa*, as occurred in the *Challenger* Expedition (see Results: Distribution). The ships used by the Wilkes expedition departed from Hampton Roads, Virginia in 1838 (Philbrick 2004). *Jassa marmorata* has been known from this coast since 1883 (Table 3) and currently it is the only species of *Jassa* known from the Virginia coast (Figs 1–2), suggesting that the ships were fouled by this species and subsequently dispersed to temperate coasts of South America, Australia and the Pacific U.S. that were visited by the Wilkes expedition. Therefore, it is possible that *Cratophium orientale* is synonymous with *Jassa marmorata* but the loss of the type specimens cannot make this unequivocal.

Jassa spinipes (Johnston, 1829)

Named *Gammarus spinipes* by Johnston (1829), this British species was "...found among *Sertulariae* taken from a fishing boat, so that it probably inhabits deep water.″No further locality information was given. Johnston described the second gnathopod: "...the palm much dilated, armed with a single claw, and beneath with a conical spine, much like a claw. Between these there is a triangular process." In his remarks, Johnston stated that "I cannot refer it to any described species. It surely cannot be the *Jassa pulchella* of Dr. Leach." This is because, "...in *Jassa pulchella* the inferior antennae are the longest, and are said to be leg-shaped, a form which those of *Gamm. spinipes* have not, if I have a correct idea of what is meant by that term." Johnston (1829) provided no illustrations for his new species description and the whereabouts of his type is unknown. This comparison of *G. spinipes* to *J. pulchella* is perhaps the reason why it appears in WoRMS as *J. spinipes*.

In their comprehensive publications on the British Amphipoda, Bate (1862) and Bate & Westwood (1863, 1868) did not mention a species named *spinipes*, either of the genera *Gammarus*, *Podocerus* or *Jassa*. Stebbing (1906) mentioned *G. spinipes* in his addendum, only giving the reference for Johnston (1829). Lincoln (1979) did not mention either *G. spinipes* or *J. spinipes* in his updated treatment of the British Amphipoda. The reason for the transfer of *G. spinipes* to *Jassa* is not given in WoRMS and appears to be unjustified, given Johnston's short description and lack of a type.

Jassa variegatus (Leach, 1814)

Stebbing (1899a) compared Leach's (1814) descriptions of the genera *Podocerus* and *Jassa*, collected from Devon, England, demonstrating that the two genera were valid, while previously, it had been thought that the two were the same. This study initiated the transfer of species to each genus, with *Podocerus variegatus* Leach, 1814 being the type for the genus *Podocerus*. Conlan (1990) examined the syntypes NHM 295b and 285d of *Podocerus variegatus* and found them to be indeed in the genus *Podocerus. Jassa pulchella* Leach, 1814 erected by Leach as the type for the genus *Jassa* (NHM 296a–g; lectotype: 296e), is now *J. falcata* (Montagu, 1808) (holotype: NHM 603a). A second species of *Jassa* described by Leach (1814), *J. pelagica,* was transferred by Stebbing (1899a) to *Parajassa*.

Stebbing (1899a) documented the taxonomic confusion surrounding these three species over the 85 years between Leach's publication and his own. Conlan (1990) mis-interpreted Stebbing (1899a) in thinking that there werestill specimens of Leach's type series for *P. variegatus* that contained *Jassa*. However, this appears to be not the case, since *P. variegatus* and *P. pelagica* had their types validated by Conlan (1990) along with the type species for the genera *Podocerus* and *Jassa*. Therefore, the name *J. variegatus* is invalid (it is actually *P. variegatus*).

Key to the world species of *Jassa* (both sexes)[6]

1 Gnathopod 2, basis, at least the distal part of the anterolateral margin bearing a fringe of setae (at least some setal lengths 20–40% or more of the maximal basis width) (e.g., Figs 15, 28, 78, 88 and 102) (fringe also present in juveniles but may be less pronounced than in adults...e.g., see Fig. 102) 2

\- Gnathopod 2, basis, setae short, minute or absent (setal lengths <20% of the maximal basis width) (e.g., Figs 37, 85, 95 and 104). 13

2 Gnathopod 2, propodus, anteroproximal margin with a row of long setae (setal length ≥ the maximal basis width). Gnathopod 1, carpus without a seta or cluster of setae at the anterodistal junction of the propodus (Figs 67 and 68) . . . *J. staudei* Conlan, 1990

\- Gnathopod 2, propodus, setae on the anteroproximal margin short or absent (setal length <65% of the maximal basis width). Gnathopod 1, carpus, seta(e) at the anterodistal junction of the propodus present or absent (may be slightly medial or lateral and as long as the carpus or very short) (e.g., Figs 15, 22, 65 and 88–90) 3

3 Gnathopod 2, female, palm sinuous (e.g., Figs 88, 97 and 102). 4

\- Gnathopod 2, female, palm concave (e.g., Figs 15, 26, 29 and 65). 6

4 Gnathopod 1, basis, anterior margin with a row of spine-like setae; carpus, anterodistal margin with a single or cluster of setae at the junction of the propodus (Figs 88–90) . . . . . . *J. alonsoae* Conlan, 1990

\- Gnathopod 1, basis, anterior margin without a row of spine-like setae (Figs 85 and 102) 5

5 Gnathopod 1, carpus, anterodistal margin with a seta or cluster of setae at the anterodistal junction of the propodus (seta(e) ~40% the length of the carpus) (Fig. 85) . . . . . . *J. myersi* Conlan, 1990[7]

\- Gnathopod 1, carpus, anterodistal margin without a seta or cluster of setae at the junction of the propodus (Fig. 102) . . . . . . *J. gruneri* Conlan, 1990

6 Uropod 1, peduncular spinous process that extends ventrally from the peduncle and underlies the rami very short (≤10% of the length of the longest ramus) (Fig. 65) . . . . . . *J. borowskyae* Conlan, 1990

\- Uropod 1, peduncular spinous process that extends ventrally from the peduncle and underlies the rami at least 25% to 50% the length of the longest ramus (e.g., Figs 42, 88 and 99) 7

7 Gnathopod 1, carpus with a seta or cluster of setae at the anterodistal junction of the propodus (seta or setal cluster may be slightly lateral or medial and short or as long as the carpus) (e.g., Figs 15, 22, 29, 31, 62 and 81) 8

\- Gnathopod 1, carpus without a seta or cluster of setae at the anterodistal junction of the propodus . . . *J. monodon* (Heller, 1866)

8 Gnathopod 1, carpus, seta or cluster of setae at the anterodistal junction of the propodus short (length <25% of the length of the carpus) and slightly medial or lateral (Figs 15 and 31). 9

\- Gnathopod 1, carpus, seta or cluster of setae at the anterodistal junction of the propodus long (length 25–50% of the length of the carpus or longer) and slightly medial or lateral (Figs 22, 29, 62 and 81). 10

9 Telson, tip bearing a seta or setae extending between the third uropods (these setae are in addition to the usual upright setae at each lateral cusp and are visible when the uropods are pressed downwards and away from the telson). Antenna 2, thumbed males and adult females of any size without plumose setae on the posterior margin of article 5 and the flagellum (though setae may look finely pectinate). Gnathopod 2, propodus of major form thumbed male, thumb conical, tip acute, spine or spine group on the posterior margin at the origin of the thumb absent (character states differ in the minor form) (Figs 31–33) . . . . . . *J. valida* (Dana, 1853)

\- Telson, tip without apical setae (though the usual upright setae at each lateral cusp are present). Antenna 2, large thumbed males and adult females, with dense plumose setae on the posterior margin of article 2 and the flagellum. Gnathopod 2, propodus of major form thumbed male, thumb wide, tip squared, spine or spine group on the posterior margin at the origin of the thumb absent (character states differ in the minor form) (Figs 15–16). . . . . . . *J. marmorata* Holmes, 1905

10 Gnathopod 2, basis and propodus, anterior marginal setae abundant and plumose (Figs 62–63). Mandibular palp, article 2, with a fringe of setae on the dorsal margin (Fig. 64) . . . . . . *J. oclairi* Conlan, 1990

\- Gnathopod 2, basis and propodus, anterior marginal setae sparse and simple (Figs 22, 28 and 78). Mandibular palp, article 2, without a fringe of setae on the dorsal margin (Figs 27, 30 and 82) 11

11 Telson, tip bearing apical seta or setae in addition to the usual upright seta or setae at each lateral cusp (Fig. 28) . . . . . . *J. morinoi* Conlan, 1990

\- Telson, tip without apical setae, only with the usual upright seta or setae at each lateral cusp (Figs 22 and 78) 12

12 Antenna 2, large thumbed male and large adult female, peduncular article 5 and flagellum, posterior margin bearing dense plumose setae (Figs 22 and 23). Gnathopod 2, propodus of major form male, thumb tip acute; spine or spine group on the posterior margin at the origin of the thumb absent (although present in small thumbed males) (Figs 22 and 23). Gnathopod 1, female propodus, palm straight to shallowly concave. Gnathopod 2, female propodus, maximum width about 50% of maximum length, palmar angle not close to the defining spines; spines tightly clustered (Fig. 26) . . . . . . *J. slatteryi* Conlan, 1990

\- Antenna 2, thumbed male and large adult female, peduncular article 5 and flagellum setae not plumose (though may be microscopically pectinate) (Fig. 81). Gnathopod 2, propodus of major form male, thumb tip angled posteriorly, spine or spine group on the posterior margin at the origin of the thumb present (Fig. 78). Gnathopod 1, female propodus, palm convex. Gnathopod 2, female propodus, maximum width about 65% of maximum length, palmar angle close to the defining spines; spines sequential

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[6] This key is limited by incomplete knowledge of *J. kimi*, *J. laurieae*, *J. monodon* and *J. shawi*. Sufficient information for *J. kimi*, *J. monodon* and *J. shawi* allow for their inclusion but *Jassa laurieae* has been excluded because its characteristics are unknown posterior of pereon segment 4. See Table 11 and Remarks section for *J. laurieae* for distinguishing character states.

[7] *J. myersi* appears twice in the key because the setal fringe on the anterolateral margin of the basis of gnathopod 2 can be interpreted as being present or absent due to the sparseness of the setae on some individuals

(Fig. 81) . . . . *J. carltoni* Conlan, 1990

13 Uropod 1, peduncular spinous process that extends ventrally from the peduncle and underlies the rami short (<10% of the length of the longest ramus) (e.g., Figs 65 and 83). Only known from the Northeastern Pacific. 14

\- Uropod 1, peduncular spinous process that extends ventrally from the peduncle and underlies the rami at least 25% to 50% the length of the longest ramus) (e.g., Figs 42, 88 and 99). Not known from the Northeastern Pacific 15

14 Gnathopod 1, carpus, seta or setal cluster at the anterodistal junction of the propodus about 35% of the length of the carpus. Gnathopod 2, female propodus, palm sinuous (Fig. 85) . . . . *J. myersi* Conlan, 1990

\- Gnathopod 1, carpus, seta or setal cluster at the anterodistal junction of the propodus minute (<15% of the length of the carpus) and slightly medial. Gnathopod 2, female propodus, palm concave, palmar defining angle acute and close to the defining spines (Fig. 83) . . . . *J. shawi* Conlan, 1990

15 Pereopods 5–7, anterior margin of the propodus, spines strong and spine row extending half or more of its full length, propodus expanded or not expanded for grasping (Figs 92, 95 and 99). 16

\- Pereopods 5–7, anterior margin of the propodus, spines mostly on the distal half, propodus not expanded for grasping (e.g., Figs 42, 48, 93 and 96). 18

16 Gnathopod 1, carpus, seta or setal cluster at the anterodistal junction of the propodus about 1/3 the length of the carpus and slightly lateral and medial. Body length at maturity 15–25 mm (thumbed males and females with setose brood plates) (Fig. 99) . . . . *J. ingens* (Pfeffer, 1888)

\- Gnathopod 1, carpus without a seta or setal cluster at the anterodistal junction of the propodus. Body length at maturity 5–9 mm (thumbed males and females with setose brood plates) (Figs 92 and 95) 17

17 Pereopods 5–7, anterior margin of the propodus expanded proximally for grasping. Antenna 2, thumbed male, posterior margin of article 5 and flagellum densely clothed in plumose setae. Gnathopod 2, female, palm of the propodus sinuous (Fig. 95) . . . . *J. fenwicki* Conlan, 1990

\- Pereopods 5–7, anterior margin of the propodus not expanded proximally for grasping. Antenna 2, thumbed male, posterior margin of article 5 and flagellum without plumose setae (though setae are minutely barbed). Gnathopod 2, female, palm of the propodus with a distinct ledge distal of the palmar defining spines (Fig. 92) . . . . *J. justi* Conlan, 1990

18 Gnathopod 1, carpus with a seta or setal cluster at the anterodistal junction of the propodus (length about 25% of the carpus length) (Fig. 93) . . . . *J. thurstoni* Conlan, 1990

\- Gnathopod 1, carpus without a short seta or setal cluster at the anterodistal junction of the propodus (e.g., Figs 42–43), or if seta present, length <15% of the carpus length (e.g., Figs 60 and 96). 19

19 Mandibular palp, article 2 with a fringe of setae on the dorsal margin (Figs 47 and 53) 20

\- Mandibular palp, article 2 without a fringe of setae on the dorsal margin (Figs 41, 61 and 98) 21

20 Uropod 3, inner ramus bearing 1 or 2 spines centrally in addition to the usual spine at the tip (Fig. 42). Antenna 2, large adult male and female, posterior margin of peduncular article 5 and flagellum article 1 bearing dense plumose setae (Figs 42–43) (these absent in small juveniles). Gnathopod 2, female propodus, palmar angle bulbous, distant from the defining spines (Fig. 44). . . . . *J. falcata* (Montagu, 1808)

\- Uropod 3, inner ramus without central spines (only the usual spine at the tip) (Fig. 48). Antenna 2, large adult male and female, posterior margin of peduncular article 5 and flagellum article 1 without plumose setae (Fig. 48) (although setae may be minutely barbed) (Fig. 50). Gnathopod 2, female propodus, palmar angle acute, close to the defining spines (Figs 51 and 52) . . . . *J. herdmani* (Walker, 1893)

21 Gnathopods 1 and 2, basis, anterior margin bearing a fringe of setae or spines (Fig. 104) . . . . *J. hartmannae* Conlan, 1990

\- Gnathopods 1 and 2, basis, anterior margin without an obvious fringe of setae or spines (setae minute or restricted distally (Figs 37, 60 and 96) 22

22 Gnathopod 2, female, palm sinuous (Fig. 97). Gnathopod 2, propodus of the major form thumbed male, thumb short with acute tip, spine or spine group on the posterior margin at the origin of the thumb on a ledge (Fig. 96). Southern Hemisphere . . . . *J. kjetilanna* Vader and Krapp, 2005

\- Gnathopod 2, female, palm concave (Fig. 37). Gnathopod 2, propodus of the major form thumbed male, thumb long with rounded or incised tip, spine or spine group on the posterior margin at the origin of the thumb residual or absent (Figs 39 and 60). Northern Hemisphere 23

23 Antenna 2 markedly larger than antenna 1, width up to 2x the width of antenna 1 in the thumbed male. Gnathopod 2, propodus of the major form thumbed male, thumb tip not incised (Fig. 60). North Pacific . . . . *J. kimi* **n. sp.**

\- Antenna 2 not markedly larger than antenna 1, width up to 1.5x the width of antenna 1 in the thumbed male. Gnathopod 2, propodus of the major form thumbed male, thumb tip incised (Figs 37–39). North Atlantic. . . . . *J. pusilla* (Sars, 1894)

Functional morphology

Live animal observations on *J. marmorata*, *J. slatteryi, J. falcata* and *J. herdmani* demonstrated the flexibility of the animals and the uses of various appendages and setae (Supplementary Table S11). For example, the first gnathopods could reach sufficiently to clean most of the head, using the medial setae on the propodus, and they were also essential for cleaning the antennae. The carpus, propodus and dactyl could be twisted to function as a plate for the maxillipeds, which then scraped particles from the medial setae for processing by the buccal mass. The setal cluster at the anterodistal junction of the carpus with the propodus, consistently long, short or absent in the

24 species and therefore useful for species identification, appeared to rub the maxillipeds and other mouthparts as well as the anterior medial margin of gnathopod 2. Thus, the setal cluster appeared to have a feeding and cleaning function in conjunction with the medial setae on the propodus. The sequential operation of the buccal appendages was also elucidated, with the upper lip moving in synchrony with the mandible and the maxilla 1 with the maxilliped. While the antenna 2 could provide the same function as antenna 1 in suspension feeding, it also was used as a prod to collect detritus as well as a fighting appendage. Assessment of tube occupation showed that pereopods 3–4 secreted the tube matrix, pereopods 5–7 and the uropods provided purchase, and the pleopods created a posterior to anterior current. Individuals were able to swim by taking a streamlined position with antennae stretched anteriorly but quickly returned to a substrate when released in the water. When *J. slatteryi* and *J. marmorata* were provided with a choice of the green alga *Ulva*, a hydroid or a glass surface for residence, almost all adult females, juvenile females and juvenile males constructed a tube within two days of introduction to a glass bowl and hydroids were the preferred substrate for both species (Supplementary Table S12). No individuals built tubes on the glass surface. Tube appearance was also found to differ with the substrate (Fig. 105), being sewn together among hydroids (Fig. 105a), elongated on a hard substrate (Fig. 105b) or compacted in dense colonies (Figs 105c–e).

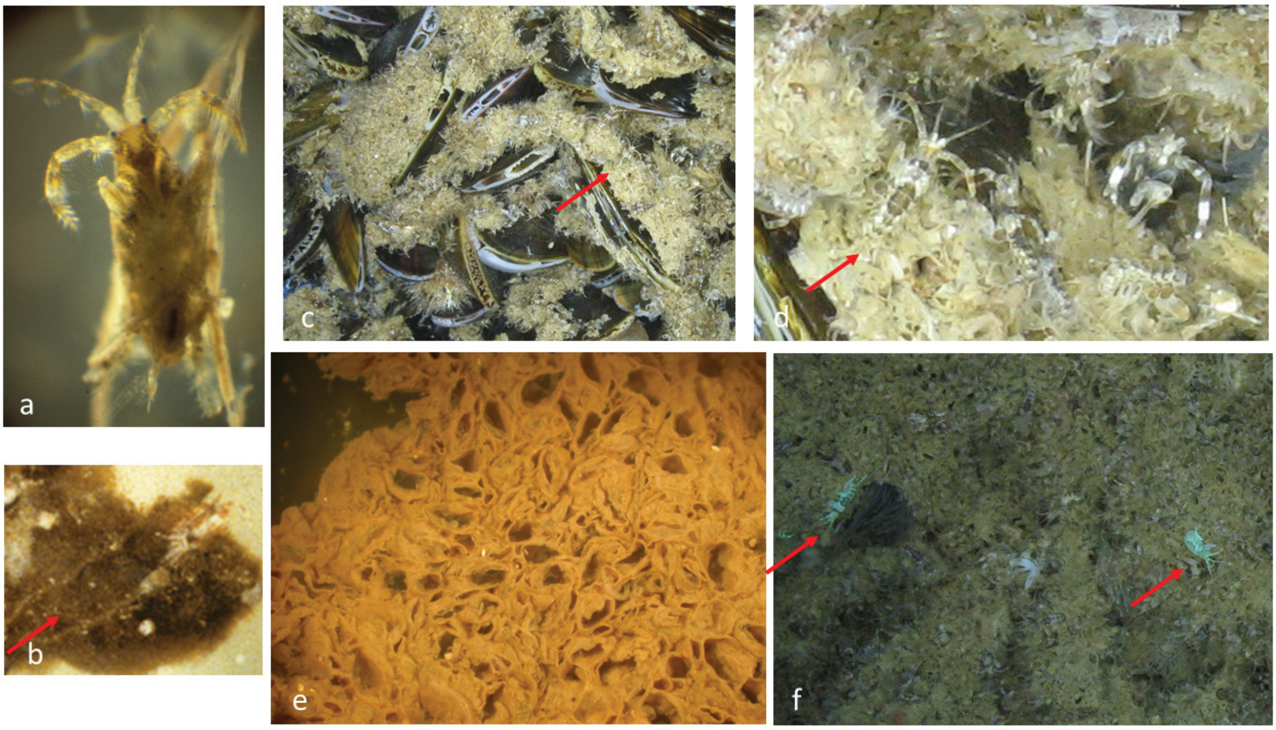

FIGURE 105. Various tube configurations constructed by *Jassa.* (a) a single tube amongst hydroids constructed by *J. marmorata,* Nahant, Massachusetts, USA; (b) view through aquarium glass showing a tube built horizontally by *J. staudei* inside a diatom mass, Friday Harbor, Washington, USA; (c) dense clusters of tubes coating mussels on an offshore platform in the North Sea built by *J. herdmani;* (d) close-up of (c), with the arrows indicating the same individual in both images; (e) dense packing of individual tubes of *J. herdmani*, Helgoland, Germany; (f) two turquoise coloured individuals of *J. herdmani* (arrows) on the dense tube mass, same location as for (c). Images of *J. marmorata* and *J. staudei* by K. E. Conlan. Images of *J. herdmani* by J. Beermann.

Cryptic colouration was variable (Fig. 106), with hatchlings being clear (Fig. 106a) and juveniles more pigmented (Fig. 106b) but not as fully as adults (Figs 106c–l). Colouration varied from chocolate brown to red, depending on the substrate colour, and certain consistencies in patterns were found in the species observed (*J. borowskyae, J. staudei, J. marmorata, J. carltoni, J. falcata* and *J. herdmani*). The brown banding was widest on the dorsum of segments 3 and 4 (Figs 106c, e) and the antennae were banded brown/orange and white (Figs 106d, f–l). The larger second gnathopods also had dark-light patterns (Figs 106f–l) while the smaller legs were less pigmented (Figs 106h–l). In the *J. staudei* and *J. marmorata* major males photographed, the mottled pattern on the second gnathopods was similar (Figs 106f, g, i); so too were the eye-like patterns on the dorsum of segment 2 (visible in *J. staudei*, Fig. 106e), which also occured in *J. marmorata* and *J. falcata* (not shown). While the second antennal flagella of *J.*

staudei and *J. marmorata* were only brown banded on segment 1 (Figs 106f, i, k), in *J. falcata* and *J. herdmani*, all segments were banded to give a candy-cane pattern (Fig. 106h, j, l). The wing-shaped pigmentation on the dorsum (visible in *J. borowskyae*, Fig. 106c) was intraspecifically variable, though it has been observed in some specimens of *J. marmorata* and *J. falcata*. The lateral extensions on the dorsum of segment 4 in the photographed juvenile *J. carltoni* (Fig. 106b) have also been seen in juvenile *J. marmorata*. The stronger pigmentation on the dorsum of segment 5 in the photographed *J. borowskyae* (Fig. 106c) has also been seen in *J. slatteryi* (not shown). A few individuals of *J. falcata* collected from Audrassalas, France and *J. herdmani* from Helgoland, Germany were bright turquoise (Fig. 105f). The individuals did not appear to behave any differently from the brown and white mottled individuals.

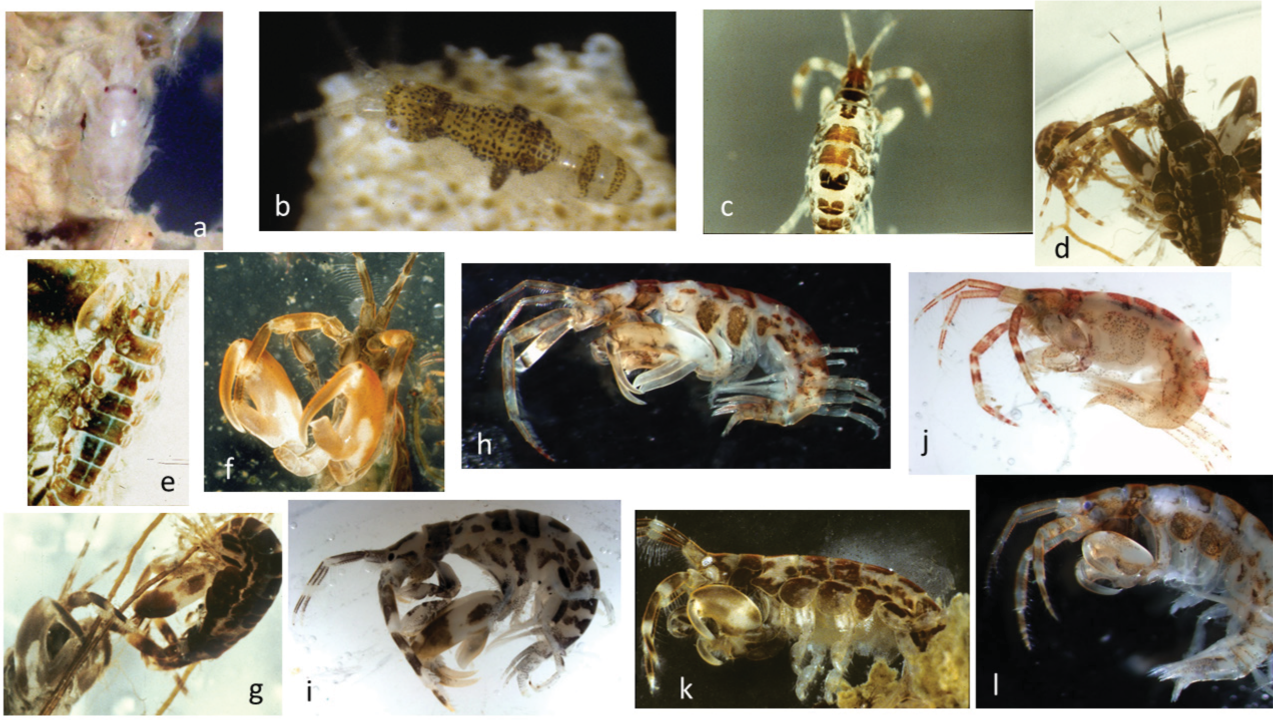

FIGURE 106. (a)–(e), dorsal views of pigment patterns in (a) *J. herdmani* hatchling, (b) *J. carltoni* juvenile, (c) *J. borowskyae* adult female, (d) *J. marmorata* major form thumbed male, (e) *J. staudei* major form thumbed male; (f)–(g), views of major form thumbed male gnathopod 2 in *J. staudei* (f) and *J. marmorata* (g); (h)–(l), lateral views of (h) *J. falcata* major form thumbed male, (i) *J. marmorata* major form thumbed male, (j) *J. falcata* adult female, (k) *J. staudei* adult female and (l) *J. herdmani* adult female. Collecting locations: *J. herdmani*, *J. falcata* and *J. marmorata* in (i) from Helgoland, Germany; *J. carltoni* from Seppings I., British Columbia, Canada; *J. borowskyae* from Oregon, U.S.A.; *J. marmorata* in (d) from Nahant, Massachusetts, USA; *J. staudei* from Friday Harbor, Washington, USA Images of *J. carltoni*, *J. borowskyae*, *J. staudei* and *J. marmorata* in (d) by K. E. Conlan. Images of *J. herdmani*, *J. falcata* and *J. marmorata* in (i) by J. Beermann.

DNA analysis

The CO1 fragment was amplified or retrieved from 10 out of the 24 currently known *Jassa* species. The overall mean distance was 0.21 (0.01 SE) with and without *Hemijassa goniamera*, exemplifying the generally high genetic divergence within the genus. Excluding *H. goniamera*, which as expected displayed a higher average distance (0.242), the highest distances were found between *J. slatteryi* and *J. herdmani* as well as between *J. morinoi* and *J. falcata* (0.257 and 0.252 respectively), with the latter being the one with highest average distance (0.233; Table 15). In contrast, the lowest average distance was found in *J. marmorata* (0.181) which also displayed the lowest pairwise distances with *J. valida, J. slatteryi* and *J. kimi* (0.142, 0.152 and 0.154, respectively; Table 15).

The CO1 gene revealed high saturation in the genus *Jassa*, resulting in long branches and low resolution. Nonetheless, both analyses confirmed the basal position of *H. goniamera* as a sister taxon to the genus *Jassa*, which was otherwise monophyletic (Fig. 107). Despite the fact that the ML did not retrieve good support for the nodes belonging to *Jassa* (not shown), both phylogenies displayed a similar topology, clearly dividing the genus into two main clades that were supported by the BI (100–99% posterior probability). One clade was composed of the primarily European and North Atlantic species (*J. herdmani*, *J. falcata*, *J. pusilla* and *J. laurieae*) whereas the other clade comprised Pacific (*J. kimi* and *J. staudei*) and trans-hemispheric species (*J. marmorata*, *J. slatteryi*, *J. morinoi* and *J. valida*).

TABLE 15. Estimates of evolutionary divergence between sequences. The number of base substitutions per site between sequences are shown. Standard error estimates are shown above the diagonal. In the diagonal and in bold are the average between-species distance of each species, excluding *H. goniamera* for *Jassa* species. In the first column and line are the distances of the *Jassa* species from *H. goniamera*. Species names in the column headers are abbreviated by their first three letters.

	GON	PUS	MOR	LAU	STA	HER
H. goniamera	**0.242**	0.022	0.022	0.025	0.020	0.025
J. pusilla	0.245	**0.228**	0.019	0.022	0.020	0.022
J. morinoi	0.241	0.208	**0.197**	0.020	0.018	0.023
J. laurieae	0.260	0.227	0.201	**0.214**	0.021	0.022
J. staudei	0.225	0.214	0.180	0.215	**0.195**	0.022
J. herdmani	0.279	0.246	0.241	0.224	0.225	**0.216**
J. kimi	0.237	0.246	0.189	0.222	0.181	0.235
J. valida	0.236	0.230	0.168	0.211	0.182	0.240
J. slatteryi	0.228	0.225	0.162	0.211	0.162	0.257
J. marmorata	0.223	0.210	0.156	0.197	0.160	0.231
J. falcata	0.244	0.241	0.252	0.218	0.236	0.238

continued.

	KIM	VAL	SLA	MAR	FAL
H. goniamera	0.022	0.022	0.021	0.020	0.024
J. pusilla	0.021	0.021	0.021	0.019	0.023
J. morinoi	0.018	0.018	0.018	0.018	0.023
J. laurieae	0.020	0.020	0.020	0.020	0.022
J. staudei	0.018	0.018	0.018	0.017	0.022
J. herdmani	0.022	0.022	0.023	0.022	0.022
J. kimi	**0.205**	0.018	0.019	0.016	0.021
J. valida	0.186	**0.196**	0.018	0.016	0.022
J. slatteryi	0.207	0.168	**0.196**	0.016	0.020
J. marmorata	0.154	0.142	0.152	**0.181**	0.022
J. falcata	0.226	0.238	0.215	0.227	**0.233**

Discussion

Distribution and habitat

The distributions mapped in Figs 1–12 reflect the 1099 collections examined morphologically (Table 4) with the addition of literature published after the revision by Conlan (1990). That the assignments by Conlan (1990) are valid, has been substantiated by subsequent analyses of the CO1 gene for 10 species so far (Pilgrim and Darling 2010; Lobo *et al.* 2017; this study). The CO1 analyses also identified errors in Conlan (1990) and indicated that there were more undescribed species. As a consequence of the molecular and morphological analyses, *J. kimi* and *J. laurieae* are newly described, *J. valida* and *J. monodon* are resurrected, *J. cadetta* and *J. trinacriae* are synonymized with *J. slatteryi*, *J.*

mendozai is synonymized with *J. valida* and the North American distributions of *J. marmorata*, *J. slatteryi*, *J. morinoi*, *J. valida* and *J. carltoni* have been clarified.

Our understanding of the world distribution of *Jassa* suffers from uneven specimen collection and availability, as well as incomplete habitat characterization. The Northern Hemisphere was more intensively sampled than the Southern Hemisphere, with the coasts of Europe receiving particularly extensive effort. Many of the collections were at low tide or subtidally from floating docks rather than deeper. However, extremely deep collections are suspect as *Jassa* is able to colonize aquaria and water pipes and so deep water ship-based collections can be contaminated by dislodged individuals residing in the ship's seawater system, giving an erroneous interpretation of depth of origin (Sirenko *et al.* 2004). Data on maximum body lengths, temperature tolerance and timing of egg production are similarly biased by the preponderance of summer collecting. Substrate characterization for each species was difficult using collection data if the specimens had come from bulk collections.

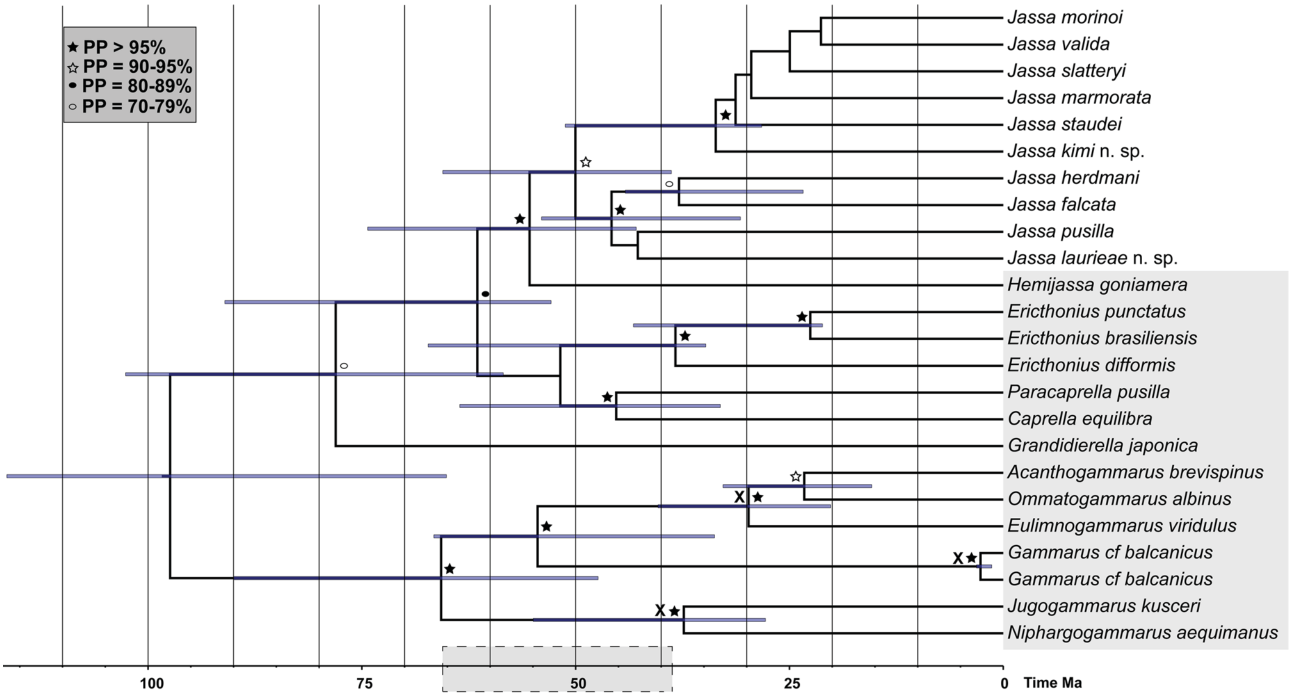

FIGURE 107. Time calibrated bayesian phylogram of *Jassa* species and outgroups (grey box on the right). Posterior probabilities (PP) are shown by black stars > 95%, empty stars = 90–95%, black circles = 80–89% and empty circles = 70–79%; not shown if < 70%) and blue bars indicate the 95% HPD interval of clade age (not shown if PP < 70%). Grey box with dashed borders show the putative time-range of the emergence of the *Jassa* clades. Calibration nodes are marked with X.

Despite the uneven sampling, this study has demonstrated that there is considerable habitat and distribution information available for *Jassa*, both in historical collections and in the literature. These data suggest that *Jassa* is a coastal marine genus whose species can be found living in self-built tubes on hard substrates from low water level to as deep as 500 m (Table 4). Most species have been found on cold temperate, high salinity coasts, with the broadest range documented for *J. marmorata* (2–27 °C, 12–38 PSU). Lower temperature tolerance is likely for the more polar *J. ingens* and *J. thurstoni*, though. Many species have been found on surf exposed coasts, living on bedrock or amongst algae, hydroids, sponges, ascidians or in polychaete tubes. Some have been found on mobile natural substrata such as driftwood, unattached algae, crab carapaces and turtle shells (also Chilton 1911; Monod 1926; Domènech *et al.* 2015; Moore & Eastman 2015). Many species have also been found in harbours and on artificial substrates such as docks, buoys, ship and recreational boat hulls, shipwrecks, nets, aquaria and offshore platforms (Diviacco 1979; Coleman 1994; Zintzen *et al.* 2006, 2008; Beermann & Franke 2011; McCollin & Brown 2014; Fernandez-Leborans *et al.* 2016; Martínez-Laiz *et al.* 2019).

The intensive and long duration collecting in Europe (and later in North America) likely well define *Jassa*'s northerly limits. These appear to be controlled by major current patterns. For example, the cold Labrador Current appears to limit the northerly range of *J. marmorata* on the Atlantic coast of North America to about 50 °N and the warm Gulf Stream limits its southerly range there. Likewise, the European species are limited in their northerly range by the northward extent of the Gulf Stream and so can reach >70 °N. Ranges of some species close to the tropics are likely aided by cool currents, such as the Canary and Humboldt Currents that bring cold water upwelling to the western coasts of Africa and South America, respectively. The wide longitudinal range of some Southern Hemisphere species is undoubtedly due to the powerful Southern Ocean current. Most of these species have a temperate range, with only *J. ingens* appearing to be limited to the Antarctic and sub-Antarctic islands. *Jassa ingens* is by far the largest bodied of the species, suggesting that its physiology, which may require highly oxygenated cold water may be a limitation to its distribution. Although no species of *Jassa* is known in the high Arctic, climate change may enable greater penetration. Live *J. marmorata* were found on the hull of a ship at the Port of Churchill, Manitoba (58.5°N) in 2010–2011 which is the most active port in Arctic Canada (Chan *et al.* 2015). This is well outside the currently known range for this species in Canada (Fig. 2). In Europe, *J. marmorata* has been found as far north as Grindavik, Iceland (63.8°N). Barnes *et al.* (2009) have identified *J. alonsoae* as a candidate for range shifting into the Antarctic; other Southern Hemisphere species may also be found there in future. Detection of range shifts due to changes in environmental conditions will require consideration of vector activity and availability of suitable habitat outside the native range (Nall *et al.* 2015).

The maps and supplementary habitat data also suggest that 20 of the species have compact ranges within an ocean basin, many of which occur on a continuous stretch of coast. These can be considered to be indigenous. None of these species crosses the tropics, which seems to be a natural barrier to these primarily cool and cold water species. Beermann *et al.* (2020) have demonstrated conclusively that *J. marmorata* and *J. slatteryi* have crossed the tropics through ship transport. The trans-hemispheric distributions of *J. morinoi* and *J. valida* suggest that they have as well. A fifth, *J. staudei*, was reported by Piola & Conwell (2010) from way beyond its home range (North Pacific) in New Zealand, but this identification is questionable. *Jassa marmorata*, *J. slatteryi* and *J. valida* have all been recorded from ships as early as the Challenger Expedition of 1872–1876 which collected *J. marmorata* on the ship's screw far from its home port in England (Supplementary Table S7). Aquaculture organisms, such as oysters can be a vector for introduction as well, as they supply a solid substrate for attachment and attached *Jassa* may survive cleaning and translocation (Haupt *et al.* 2012). *Jassa* may also be introduced accidentally along with macroalgal packaging for fish bait (Haska *et al.* 2012). Apart from ships, recreational boats and translocation of commercial aquaculture and bait organisms as potential transport vectors, less mobile coastal structures such as semi-submersible rigs, docks, nets, buoys and platforms can become mobile and raft *Jassa*, such as when storms dislodge these structures and generate rafting marine debris (Wanless *et al.* 2010). In an extreme case, the 2011 Japanese earthquake and tsunami distributed Japanese coastal debris across the Pacific to North America, carrying with it living, reproductive *Jassa* and 288 other living taxa (Carlton *et al.* 2017, 2019; Miller *et al.* 2018, 2019a, b; Clarke Murray *et al.* 2019). Indeed, rafting *J. marmorata* were thought to have sustained Japanese fish for four years that were marooned live inside a derelict Japanese boat hold that had dislodged after the tsunami and drifted across the Pacific to Oregon (Craig *et al.* 2018). Rafting on natural substrates such as drift algae is also a vehicle for dispersal and enables transport across biogeographic barriers (Wichmann *et al.* 2012). Free drifting is also a potential dispersal agent, since *Jassa* is quick to recruit to new substrates (Franz & Mohamed 1989; Tanaka & Leite 2004; Ros *et al.* 2020), survives drifting (Havermans *et al.* 2007) and can also go into the plankton (Macquart-Moulin 1968; Jørgensen & Christie 2003). Effective dispersal is also assisted by high fecundities, year-round reproduction and short generation times (Nair & Anger 1979; Jeong *et al.* 2007; Flynn & Valério-Berardo 2009; Flynn *et al.* 2011; Beermann & Purz 2013; Beermann 2014). Thus, only a few individuals are needed for successful colonization and production of a dense population in a short time (Beermann 2014; Luttikhuizen *et al.* 2019). The degree of colonization by *Jassa* can undergo strong seasonal variation depending on the responsible ecological parameters (reproduction, sex ratio, occurrence of juveniles) (Jeong *et al.* 2006; Beermann 2014). The placement of aquaculture nets, offshore wind turbines and oil drilling platforms further supplies solid substrate to *Jassa* where previously soft benthos would have been inhospitable (Jak & Glorius 2017; Glarou *et al.* 2020). This can result in skewed communities of selected populations on offshore structures that are an order of magnitude denser than on the mainland (Krone *et al.* 2013).

Further examination of the trans-hemispheric species suggest possible centres of origin. *Jassa marmorata* is likely indigenous to the Atlantic coasts of Canada and USA (Beermann *et al.* 2020). Here, it is the sole species of *Jassa* north of North Carolina where it can be found on natural, relatively pristine exposed coast as well as in bays and harbours on human modified substrates such as docks, pilings and ships. The transition to dominance by *J. valida* south of the biogeographic break at Cape Hatteras, North Carolina is likely due to the warming influence of the Gulf Stream. There were too few collections to indicate whether *J. valida* is indigenous to the Atlantic coasts of North America or South America, or elsewhere. *Jassa slatteryi* and *J. morinoi* may be both indigenous to the Northeastern Pacific as they can both be found on exposed, isolated coasts there. This is more compelling for *J. morinoi* which was found at more that 85% of the 41 collection sites and in much fewer artificial habitats there or elsewhere. *Jassa slatteryi* has been found much more widely than *J. morinoi*, suggesting that it has been more successful than *J. morinoi* at establishing exotic populations or that it has a longer history of introductions. More collecting in possible other centres of origin, such as the coasts of Asia, Russia and South America will assist our understanding of the origins and dispersal mechanisms of these species. The first dates of discovery of the trans-hemispheric species (Table 3) sets the earliest known date in which these were found in a suspected exotic location but they could have been living there well before that. This is especially true of areas that were not intensively collected in the 1800's, such as North America, but possibly less true of areas such as the UK and western Europe that have a 200+ year history of natural history collecting. Thus, the absence of *J. marmorata* and *J. slatteryi* from the UK prior to 1900 (Figs 1 and 3) may have been a true absence though they could have been mis-identified as the indigenous *J. falcata* and *J. herdmani*. The first collection records in Table 3 depend on early collections that were available for study. The effort to re-discover the types for those with lapsed names revealed that early descriptions and illustrations did not reach today's standards, leading to inconclusive decisions on the true identification. Loss of early collections also hindered tracing species distributions and movements.

The assessment of species overlaps, which examined precise substrate occupation by trans-hemispheric and local species of *Jassa* found the trans-hemispheric *J. marmorata* only in harbours in the NE Pacific, indicating that it had been introduced there. In harbours where indigenous species were also present, it could be found occupying the same substrate, which was either hydroids or macroalgae. Substrate use was much more varied on natural exposed coasts, embracing ascidians, bryozoans, seagrasses, sponges, hydroids and a variety of macroalgae. As in the harbours, more than one species could be found on the same substrate, but these species were indigenous (*J. staudei*, *J. borowskyae*, *J. morinoi* and *J. carltoni*) or at least cryptogenic (*J. slatteryi*). Several other species of *Jassa* have been found to coexist on small spatial scales (e.g. Beermann 2014; Griffiths *et al.* 2011; Fernandez-Gonzalez & Sanchez-Jerez 2017), yet to segregate behaviourally (Karez & Ludynia 2003; Beermann & Boos 2015). In addition, small differences in the species' life histories may favor ecological coexistence mediated by 'intermediate disturbance' mechanisms (Beermann & Purz 2013; Roxburgh *et al.* 2004).

The year-long record of two introduced species (*J. marmorata* and *J. slatteryi*) in an exotic location (Australia), found that both species occupied the same algal substrates, though their presence in shallow water appeared to relate to temperature as they disappeared when surface summer water temperature exceeded ~16 °C, possibly descending to cooler deeper water. In addition to temperature, space competition may have been a factor in their disappearance as they shared their substrates with numerous corophiid amphipods and tanaids which remained year-round. Unpublished data indicate that most of these cohabitants are introduced as well. Resident invertebrate predators were not obvious but fish predation may have affected abundances also, especially in austral spring when the hatchlings were released. Scinto *et al.* (2007) found a similar disappearance of *J. marmorata* in summer's high water temperatures at Portofino, Italy, though the tolerance of this population was greater than in Australia as it was still present at ≤26.5 °C. This temperature was also a threshold for *Jassa* in the East China Sea (Lin *et al.* 2017). In the South Australian study, there was no obvious algal preference as all four species were colonized, though in fall/winter the two *Jassa* species were not found on *Chaetomorpha* but more frequently on *Polysiphonia* and *Gigartina*. The South Australian coast around Adelaide is dominated by soft sediment and mangroves where *Jassa* does not occur, but most of the harbours have both species of *Jassa* on their floating docks (unpubl. obs.). Marinas are a hub for non-indigenous species, with the mobile boating visits effective vectors for spread (Ulman *et al.* 2017; Martínez-Laiz *et al.* 2019; Peters *et al.* 2019). The close association of *Jassa* with algae, hydroids, bryozoans and molluscs also means that these substrates can act as vectors for introduction (Guerra-García *et al.* 2012; Davoult *et al.* 2017). The Australian coast further south is exposed bedrock which may provide a more hospitable habitat than the mangroves, though *J. marmorata* typically prefers protected over exposed sites (Clancy 1997; Conradi *et al.* 2000; Karez & Ludynia 2003) and *J. slatteryi* achieves high abundances in seagrass beds (Jeong *et al.* 2006, 2007).

Algal preferences have been found in other studies, with fine branching red algae chosen over broader bladed red algae (Karez & Ludynia 2003; Norderhaug 2004; Eilertsen *et al.* 2011), though lab choice experiments do not always replicate field observations (Karez & Ludynia 2003). Conspecifics are also known to partition algae that they cohabit, with *J. marmorata* preferring the algal interior over the periphery (Beermann & Boos 2015). An algal canopy can provide greater access to passing detritus but the understory can be more stable year-round when the canopy seasonally sloughs (Kodama *et al.* 2020). This explains the differential distribution of *J. morinoi* in *Sargassum*. For *J. falcata*, its distribution in a kelp bed is related to its preference for degraded over fresh kelp, the former having a C:N ratio and phlorotannin content reduced by bacteria (Norderhaug *et al.* 2003), which increases the ability to use the carbon and increases palatability.

Morphological analysis and function

The 24 species of *Jassa* differ morphologically in many parts of their bodies, though some parts are more conservative than others. Some of the variable characters can be related to sexual behaviour while conservative characters relate to lifestyle, such as food gathering and tubicoly. For other morphologies, the function is difficult to estimate.

Morphologies related to feeding

All species of *Jassa* have first and second antennae clothed in pairs of long, finely pectinate setae. Observations of living animals (Supplementary Table S11) showed that these setal pairs are spread at roughly 90° to each other, with a resultant 180°coverage for water filtration. *Jassa* species are generally unselective suspension feeders but at least some species are able to also subdue large prey and even conspecifics (Nagle 1968; Dixon & Moore 1997; Armsby & Tisch 2006). Individuals within a population can be trophically plastic depending on source material (Mavraki *et al.* 2019). *Jassa falcata* will also consume old fecal pellets in a laboratory situation (Dixon & Moore 1997). In some species also, the filter feeding is complemented by grazing macroalgae and epiphytes in the tube's direct vicinity (Jeong *et al.* 2004, 2007, 2012; Sano *et al.* 2003). Accordingly, laboratory cultures of *Jassa* are most successful when fed a mixed diet of algal detritus and small planktonic prey (i.e. *Artemia* nauplii, rotifers; Nair & Anger 1979; Havermans *et al.* 2007; Beermann & Purz 2013). Enriched terrestrial-derived diets associated with aquaculture can also sustain *Jassa*, and the enriched fatty acids are transferred to the eggs (Gonzalez-Silvera *et al.* 2015; White 2017).

While there is little apparent variation among the species in the first antennae, the second antennae differ both among the species and among the sexes (see Morphologies related to mating). Live animal observation indicates that in addition to forming a net for filter feeding, the second antennae are also used as prods, both to gather detritus and in agonistic interactions. All species of *Jassa* have pairs of posteriorly curved spines on the distal articles of the flagellum, and these spines are probably essential for these purposes. Less obvious is the purpose of the plumose setae on the distal parts of antennae 2. Not all species develop this plumosity, but in those species that do (Tables 10–13), it occurs in both sexes and only at or just before maturity. The plumosity would therefore seem to have a sexual function, perhaps to demonstrate and detect maturity either by tactile or chemosensory means or both. Thiel (2011) considered that the plumosity in large male *J. slatteryi* aided them to locate the female but did not consider the use by the female, since large females also develop plumosity. However, small thumbed males and small ovigerous females do not always have plumose setae on their antennae, suggesting that plumosity is not a prerequisite to reproduction.

The mouthparts of the 24 species of *Jassa* are highly conservative, indicating a similar diet. The mandibular palps of all species have facial setae on the lateral side which would brush against the medial row of setae on the antennae. The European *J. falcata* and *J. herdmani*, and the NE Pacific *J. oclairi* have an additional fringe of setae which is on the dorsal margin of the mandibular palps and slightly medial (Tables 11 and 12). Both sets of setae likely have a cleaning function. Live animals frequently clean their antennae and head with their mandibular palps and gnathopods. The propodus of gnathopod 1 bears numerous groups of pectinate setae on its medial face and the live animal observations show how it can be twisted to form a plate for the maxillipeds to feed from (Supplementary Table S11). These setae aid food grasping but may also be used as chemosensors to evaluate food quality as in lysianassids (Kaufmann 1994). Additional setation was also noted on the maxilla 1 at the base of the palp in *J. ingens* but this was the only species that had this feature (Table 13). Possibly this added setation relates to this species' much greater size than for other *Jassa* species. Diet may also differ in such a highly seasonal environment as the Antarctic. Small setae on the dorsum, termed microtrichs, were extensively studied by Steele & Steele (1997, 1999) in *J. marmorata* (as *J. falcata*) and other amphipods. They are stucturally similar to chemosensory sensilla in insects, suggesting use in feeding.

Morphologies related to tubicoly

The morphology of pereopods 3 and 4 is conservative among the species, as these appendages are used for tube building, with the spinning glands in the basis and the "amphipod silk" excreted from the dactyl tips (Moore &

Eastman 2015; Neretin *et al.* 2017). Basis width does vary among the sexes, though (see the section "Morphologies related to mating"). Individuals usually sit at the opening of their self-constructed tubes feeding and continuously improving the tubes with amphipod silk and deliberately incorporated detritus (Ulrich *et al.* 1995; Dixon & Moore 1997). The tubes are attached to nearly all kinds of hard substrata—from natural rocky and biogenic surfaces (e.g., algae, bivalves, hydrozoans, crabs and other *Jassa* tubes) to artificial substrata. The tubes can differ in appearance depending on the substratum and population density (Fig. 105). Especially on "disturbed", i.e. anthropogenic substrata (e.g. harbor walls, sea signs, submerged ropes, ship hulls, fish cages and offshore constructions), some species such as *J. marmorata*, *J. herdmani* and *J. slatteryi* can reach remarkably high densities of up to 1.45 x 10^6 individuals m^{-2} (Zintzen *et al.* 2006; Scinto *et al.* 2007; Beermann & Franke 2011; Krone *et al.* 2013; Coolen *et al.* 2018; Haberlin 2018). A single steel platform in the North Sea was estimated to be covered by >320 x 10^6 individuals of *Jassa* spp., with their tubes weighing 832 kg (Krone *et al* 2013). Addition of protective scour substrates to the wind farms can increase the background macrofaunal biomass by 24x (Coolen *et al.* 2019). The massive increase in biomass is a boon to fish predators (Derweduwen *et al.* 2016). Future large-scale wind farming in the North Sea will have a measurable impact on pelagic primary production through the effects of *Jassa* and other filter feeders settled on the wind turbines' sub-sea platforms (Slavik *et al.* 2019). *Jassa* can also respond positively to organic matter accumulation and an enhanced hydrodynamic regime created by such artificial enclosures as fish farms by increasing densities under and near the nets (Dauvin *et al.* 2020). The resulting dense fouling mats have a significant impact on their surroundings, covering aquaculture facilities, plugging seawater systems, and overgrowing other sessile organisms (Sebens 1985; Beermann & Franke 2012; Fernandez-Gonzalez 2014, 2016; examples in this text). The tubes also provide substrate for clinging species, such as the alien *Caprella mutica* in the North Sea (Schückel *et al.* 2010). In dense populations (Fig. 105b), minimum tube spacing is defined by second antennal length (which can be used agonistically) or by the distance to which an animal is prepared to extend out of its tube to interact with its neighbour. If this does not achieve spacing, then distancing is enforced by the gnathopods. When attached to hard substrata, where one end of the tube is attached and the tube extends perpendicularly, the animals do not have the luxury of turning around and feeding at both ends as they do on biotic substrata (Fig. 105a, c, d).

Another conservative part of the body, which is crucial for tube aeration, as well as swimming, is the three pairs of pleopods. These are well developed compared to some confamilials (Conlan 2021), with long setae extending from them and the peduncles are held together by two coupling hooks. In the tube, the pleopods produce a posteroanterior current (Dixon & Moore 1997). Somewhat less conservative are the adaptations for grasping the tube. The posterior pereopods 5–7 splay outwards from the body and are used to grasp the tube's interior along with the uropods. Most species have similarly shaped pereopods 5–7 that increasingly lengthen posteriorly. They are moderately setose but only spinose on the posterior margin of the propodus and usually only distally. However, in the Southern Hemisphere species *J. fenwicki* and *J. ingens*, the propodus is expanded for grasping and the spines are large and extend the full length of the propodus. *Jassa justi* also shows this strong spination, but the propodus is not expanded. Presumably these species live in conditions where strong grasping ability is favoured, such as in strong currents and wave exposure or they may associate with crustacean hosts that could dislodge them while grooming. Crab-associated isaeid amphipods have similarly prehensile pereopods (Vader & Tandberg 2015).

Regarding the urosome area, all species have an easily overlooked pair of setae on the dorsum of urosome segment 1 which presumably senses the proximity of the tube's interior. Almost all species also have a spinous process that extends under the uropod 1 rami, but in the Pacific *J. borowskyae*, *J. shawi* and *J. myersi* this is much reduced in length (Table 12). While this spinous process may aid in grasping the tube, it also can provide a cleaning function for the antennae setae when the urosome is tucked under the body and combs the antennal setae (Supplementary Table S11). Other posterior characters that show some variability are the additional spines on the uropod 3 inner ramus in *J. falcata* and the additional setae at the tip of the telson which extend between the two uropod 3 peduncles in *J. valida*, *J. morinoi* and *J. monodon*. These may have some sensory function. Other features of the uropods and telson (spination, setation and cusping) are conservative and the morphology of the uropod 3 outer ramus has been used as a defining feature of the genus (Conlan 1990; Barnard and Karaman 1991). Another easily overlooked character that likely has a sensory function is the small cluster of short setae on the dorsum of antenna 1 peduncular article 1. This is present in *Jassa* as well as the sister group *Hemijassa* Walker, 1907.

Morphologies related to species recognition

All species of *Jassa* have aesthetascs on the first antennae which function in chemosensation (Kaufmann 1994).

Characters with less obvious function but that may function in species recognition are the length and position of the seta on the gnathopod 1 carpus at the margin of the propodus, and the setal fringe along the basis of gnathopods 1 and 2, which can be long and dense or sparse to minute, simple or plumose. Live animal observation gave no indication of function, though it was noted that the gnathopod 1 carpus seta brushed against the maxillipeds and the gnathopod 2 basis setae provided a lateral fringe for the propodus when it was held in the groove in the basis created by the lateral and medial flanges. These characters were key to distinguishing the species (see the Key to species), as were the state of plumosity of antenna 2, the length of the uropod 1 peduncular spinous process, and the presence/absence of apical setae on the telson, the additional setal fringe on the mandibular palp and the extra spines on the uropod 2 inner ramus. These characters all have the common characteristic of being conservative within a species, not differing between the sexes or between adults and juveniles, but differing among the species. Such would be features that could signal species distinctiveness to other species of *Jassa* as well as to the taxonomist.

Morphologies related to mating

The obvious key character for mating is the development of the thumb on the propodus of gnathopod 2 in males at their last molt, which happens in all species of *Jassa*. Thumb size and position varies within and between species. The graphs presented for as many species as there were sufficient specimens for, indicate that each species is similar in having small minor form thumbed males that are small also in body length, that co-occur with large bodied, major form thumbed males with much longer thumbs. Whether a male becomes a minor or major form has been demonstrated to be caused by diet during growth (Kurdziel & Knowles 2002) and these forms differ in mating behaviour (Kurdziel & Knowles 2002) and possibly also in longevity (Hooper *et al.* 2018). This study has revealed that of the 24 species known, the major form of *J. falcata* can produce the longest thumb (Fig. 44), which is so different in appearance from the minor form (Fig. 42) to have been initially named *J. pulchella* Leach, 1814 (Conlan 1990). *Jassa marmorata* could be considered to develop the most massive thumb in major forms (Fig. 15), though *J. staudei* can be similarly massive (Fig. 69). The species with the smallest thumb known is *J. myersi* (Fig. 85), but further collecting may reveal specimens with longer thumbs than are currently known as sample size was small (Table 4). Minor forms of some species (e.g*., J. falcata*, *J. hartmannae*, *J. herdmani*, *J. oclairi*, *J. pusilla* and *J. staudei*) also have a pronounced tooth on the dactyl which fits into the space between the thumb and palm. This may make the thumb less obvious, which may be advantageous to a sneaker mating strategy. This toothing may be found in all species if enough minor forms are examined, and appears to be homologous with the dactyl expansion in major forms which is closer to the dactyl hinge. Although thumb production is considered to be a terminal molt phenomenon, many species have a small “prethumb” prior to thumb production and the long thumb can often be seen inside the cuticle of the prethumbed male (e.g., Figs 24, 28, 45, 49, 65, 69 and 78). These individuals have been termed subadults in this study. Clark (1997) used a different method for separating major from minor males in *J. marmorata*, deeming majors as those with a thumb tip >0.4 mm distant (perpendicular) from the palm and minors at a perpendicular distance <0.4 mm. This criterion produced a similar relationship to body length as the method used in this study and previously (Conlan 1989, 1990), with minors smaller and having little overlap in body length with the majors (compare Clark 1997 with Fig. 16 in this study).

The study of geographic and temporal variation of size and proportion of minor to major form thumbed males in *J. staudei* showed average body length increasing southwards on the Pacific northeast coast in exposed locations, but the largest average body length was in a protected location. This may relate to food availability and/or temperature differences. Within the protected location at Friday Harbor Laboratories, Washington, minors and majors were present year round in contrast to *J. marmorata* on the Atlantic northwest, where majors disappeared from August to April (Clark 1997). A winter increase in average body length seen in different populations of *J. marmorata* on the Atlantic northwest (Franz 1989; Clark 1997) was also not visible in the *J. staudei* population. This could relate to the greater seasonality of water temperature at these locations (3–26 °C min.-max. SST on the Atlantic northwest; (Franz 1989) compared to 7.5–11.0 °C mean monthly SST on the Pacific northeast (Deysher 1984)). Since the development of minor forms is diet related, these species-specific differences may not hold if the populations are living in similar conditions. *Jassa marmorata* now occurs in harbours on the Pacific northeast, and given its wide powers of dispersal and establishment, it may be able to displace native *Jassa* species there, though in Europe, the native European *J. falcata* and *J. herdmani* seem able to co-exist (Beermann 2014). The observed coexistence in the North Sea seems to be facilitated by the high flexibility and reproductive output of *J. marmorata*, compensating for possible competitive advantages of the two native species acquired through adaptation to their native habitat (Beermann & Purz 2013; Beermann & Boos 2015).

This study has also shown that juvenile males diverge from females by enlarging the gnathopod 2 propodus, reducing the setation of antenna 2 and narrowing the basis of pereopods 3 and 4. The use of the thumb as a signalling device has been well studied (see Introduction). The reduced setation of antenna 2 and narrowing of the pereopod 3 and 4 bases, which hold the tube spinning glands probably relates to abandonment of tubicoly in favor of roving and attending receptive females.

Unusual morphologies

Intersexing was found in one among hundreds of thousands of specimens of *J. herdmani* examined from the North Sea and from some specimens of *J. slatteryi* from California, Japan and Australia (see Remarks for *J. slatteryi*). Possible causes of intersexing in crustaceans are hermaphroditism, environmental sex determination, parasitism, genetic aberration and endocrine-disrupting pollutants (Sudo & Azeta 1996; Short *et al.* 2012; Rumbold *et al.* 2015b). Intersexing was induced in *J. marmorata* (as *J. falcata* broad form) in the laboratory by inbreeding (Sexton & Reid 1951).

Reduced antennae and modified appendages may result from loss or damage at a previous instar and regrowth following. Moore (1973) noted several deformed appendages in a single female of *J. falcata* from a kelp holdfast on the NE coast of the UK.

The turquoise blue colour noted in some individuals of *J. falcata* and *J. herdmani* may be similar to that found in cambarid crustaceans. This has been found to have a genetic basis (Fitzpatrick 1987). Such colouration was not found in other species though opportunity to study live animals was relatively limited.

Specimens either live or preserved in collections were rarely found coated with epibionts larger than small parasites. This rarity indicates that *Jassa* are effective at cleaning their cuticles. That both the epibiont covered individuals (Fig. 21 and see Remarks for *J. marmorata*) were thumbed and therefore at their terminal molt suggests that they had not molted recently and were likely close to the end of their lives. Both individuals were *J. marmorata*, which was collected and examined more widely than other species (Table 4). Such a phenomenon may occur in other species but their relative paucity in collections would limit the likelihood of their being found. However, *J. marmorata* occurs in such a diversity of habitats and locations that it may be more prone to abnormalities than other species as a consequence.

Crypsis

The mottled pigmentation pattern on the integument of the various species of *Jassa* in Fig. 106 suggest consistencies among the species, though variability in pattern is also visible. The broken pattern would be adaptive to life on substrates such as algae, hydroids and bryozoans, which would form a variable pattern in which to blend in the photic zone. There were no obvious pattern differences between the six species examined, though increasing pigmentation was notable from hatchling to adult. Like in caprellids, tanaids, isopods and more distantly related arthropods (but not in the amphipod *Gammarus*), the pigment is an ommochrome, principally xanthommatin (Needham 1970). Through their tubicolous lives, the anterior body from antennae to the posterior of segment 2 would be most visible to competitors and predators during body extension. Crypsis would be favoured especially among roving males when the whole body is outside the protective tube. High habitat complexity would provide opportunity for crypsis, explaining the observed preference for hydroids over *Ulva* of *J. slatteryi* and *J. marmorata* (Supplementary Table S12). Other factors, such as seasonality, competition, predator preference and substrate architecture, palatability, protective ability and food value can influence substrate selection by amphipods also (Stoner 1980; Hacker & Steneck 1990; Holmlund *et al.* 1990; Norderhaug 2004).

DNA analysis and an evolutionary hypothesis for *Jassa*

The CO1 analysis depended on suitably stored material and public sequences and so it necessarily focussed on Northern Hemisphere species that were readily accessible or fresh. Two clades were identified from the 10 species analysed (Fig. 107): an older group which comprised species largely only found in the eastern Atlantic, and a younger group comprising species mostly from the western Atlantic and eastern Pacific (with only secondary distributions attributable to human mediation). This split ranged between 38 and 68 Ma after the opening of the Atlantic Ocean (Ellis and Stoker 2014). A similar evolutonary split has been recently demonstrated for crangonyctid amphipods (Copilaş-Ciocianu *et al.* 2019), although only deepening the divergence of the already segregated lineages in these ones. Additional analyses using more loci and species could substantiate the importance of this geological event for the speciation of marine amphipods.

On the western Atlantic coast, free movement to the Pacific may have been possible to as late as 3–3.5 Ma when the Central American Seaway fully closed (O'Dea *et al.* 2007). With closure came reduced upwelling and a 3-fold reduction in seawater temperature variation (O'Dea *et al.* 2007). Before full closure, shallow marine basins connected Caribbean-Pacific waters (Farris *et al.* 2011), but large-scale ocean flow between the Atlantic and Pacific through the Central American Seaway may have ended by 13–15 Ma (Montes *et al.* 2015). *Jassa* as a group is largely a cold to cool-temperate genus, suggesting that trans-oceanic interchange may have required this cooler seaway rather than the later shallow Caribbean basins. *Jassa valida* has the southerly-most range on the North Atlantic coast, ranging into the Guf of Mexico, but is not yet known from the Caribbean.

The eastern Atlantic clade comprised the European species *J. pusilla*, *J. falcata*, *J. herdmani* and *J. laurieae*. Of these, the Scandinavian deep-water *J. pusilla* is trans-Atlantic, potentially connected to the North American Atlantic coast by the Greenland current which underlays the Gulf Stream (Sheldon *et al.* 2016). The collection data suggest that the species in this clade are relatively stenothermal and stenohaline (Table 4). None of these are trans-hemispheric, suggesting that they are not prone to, or do not survive human-mediated transport. Ranging little further south than 40 °N, they are the more northerly ranging of the two clades, with *J. pusilla* and *J. falcata* occurring well north of 60 °N on the Scandinavian coast (Fig. 9). *Jassa falcata* has a life history that is better adapted to low temperatures than *J. marmorata* in the North Sea (Beermann & Purz 2013).

The other clade comprised the Pacific species, *J. kimi* and *J. staudei* and the four trans-hemispheric species. All four trans-hemispheric species (*J. marmorata*, *J. slatteryi*, *J. morinoi* and *J. valida*) occur in numerous oceans (Figs 1–8). The collection data suggest, however, that human-mediated dispersal of these species was occurring well back into the 19th century. Using presence in natural, remote locations as a criterion of nativity would suggest that *Jassa marmorata* is indigenous to the northwestern Atlantic (Supplementary Table S2) while *J. slatteryi* and *J. morinoi* are indigenous to the northeastern Pacific (Supplementary Table S8). This agrees with Pilgrim & Darling (2010) who found as much genetic variability in *J. slatteryi* as in the indigenous eastern Pacific *J. staudei*, thereby suggesting nativity in this area. *Jassa valida* may be indigenous to the northwestern or southwestern Atlantic where it has been found most frequently or indigenous elsewhere and undercollected. The presence of *J. marmorata* on the Pacific North American coast appears to be a result of human introduction as it was only found in human-modified locations (Supplementary Table S9). This is substantiated by Pilgrim & Darling (2010), who found low genetic diversity of *J. marmorata* from the Pacific North American coast compared to the indigenous *J. slatteryi* and *J. staudei*. Although widely collected on European coasts as well, many of the collections of *J. marmorata* appear to have come from artificial substrates or locations adjacent to cities, harbours and aquaculture facilities (Supplementary Tables S4 and S5). Collections elsewhere in the world also suggest human mediation (Supplementary Tables S6 and S7). That *J. marmorata* can survive ship transport was demonstrated for the short distance by Carlton & Hodder (1995) for a hull-fouled ship sailing from Yaquina Bay, Oregon to San Francisco Bay, California. The long distance transport of *J. marmorata* on the screw of the HMS Challenger was much earlier noted by Stebbing (1888). While *J. marmorata* has apparently succeeded in being introduced to harbours in the native range of *J. slatteryi* and *J. morinoi*, the same cannot be said for the opposite. *Jassa marmorata* has also been found more widely than *J. slatteryi* (Figs 1–4). This is not likely an artifact of preferential recognition, as the maps are based on post-1990 identifications, where *J. marmorata* and *J. slatteryi* could be identified using Conlan (1990) or post-1990 literature. Prior to that, identifications were largely to *J. falcata*, as a result of the work of Sexton and Reid (1951). *Jassa slatteryi* has a demonstrated propensity for quickly dispersing and colonizing new substrates (Ros *et al.* 2020), a trait that is clearly also held by *J. marmorata*. A key to the added success of *J. marmorata* may be in its high reproductive output and long life (>1 yr in laboratory conditions) (Beermann & Purz 2013). Its different genetic makeup (at least to *J. slatteryi*) may also be significant. *Jassa marmorata* ($2n = 12$) has two more chromosomes than *J. slatteryi* ($2n = 10$) (Coleman 1994; Libertini *et al.* 2000; Krapp *et al.* 2008; *J. slatteryi* identified as *J. cadetta*). It also has a different karyotype morphology (22 vs 20 chromosome arms) and a different chromosome location of 18S-5.8S-28S ribosomal cistrons.

Although the habitat data are biased towards those species that are widely collected, the suggestion from Fig. 107 and Table 4 is that the evolutionary direction in at least the Northern Hemisphere species of *Jassa* was toward greater physiological plasticity, leading to success in long distance transport and establishment in exotic locations. Addition of Southern Hemisphere species may indicate other significant events that split the genus between the hemispheres, as well as pointing to a centre of origin for *Jassa*. The sister species in the analysis, *Hemijassa go-*

niamera is a cold polar species, as are other sister species that were previously thought to be in the genus *Jassa* but have been recently moved to a new genus (Conlan 2021). Possibly, therefore, *Jassa* originated in cold regions of the Southern Hemisphere. Significantly, although currently known in the Antarctic (*J. ingens* and *J. thurstoni*), no species of *Jassa* is known in the High Arctic[8].

Conclusions

Currently, 24 species of *Jassa* are valid with another seven names lapsed due to loss of types. Of the 24 species, five are known only in the North Atlantic, seven in the North Pacific, eight in the Southern Hemisphere and four are trans-hemispheric. Of the trans-hemispheric species, two are thought to be indigenous to the Northeastern Pacific and two are indigenous to the western Atlantic and all four are introduced elsewhere. Two of the 24 species are newly described (*J. lauriae* **n. sp.** and *J. kimi* **n. sp.**) while two others are resurrected (*J. valida* and *J. monodon*). Two previously described species (*J. cadetta* and *J. trinacriae*) are submerged under *J. slatteryi* and *J. mendozai* is submerged under *J. valida*. Diagnoses, full illustrations and distribution maps are given for each species along with a key and summaries of distinguishing characters. Habitat data and live animal observations are given to assist the understanding of species differences and how these evolved. Habitat range is low intertidal or shallow subtidal to 500 m in moderate to high salinities and no species is known from the Arctic or from the tropics. Rare documentation of *J. marmorata* and *J. valida* in depths as great as 4478 m is considered to be ship contamination as *Jassa* spp. are known to colonize ship and aquarium seawater systems from whence dislodged individuals can be captured in samples during sieving operations.

CO1 analyses of 10 of the species showed two lineages in the Northern Hemisphere and suggest a south polar origin with subsequent diversification from the Atlantic to the Pacific. Historical records suggest that human-mediated dispersal was occurring by ship transport as far back as the 1800's, but only four of the 24 species appear to have succeeded in establishing populations outside of their home ranges. However, even those species that appear limited to a home range have been found on artificial substrates and their propensity for forming dense colonies has drawn attention to the genus as a fouler that can modify habitats and interfere with human operations. As *Jassa* can be readily encountered in most temperate to polar oceans and therefore has appeared in numerous publications on numerous topics, it is important to be certain of species identifications, especially knowing that some species are prone to human-mediated dispersal and therefore may not have been expected. The added illustrations in this monograph compared to Conlan (1990) will hopefully assist future scientists to correctly identify new collections, clarify identifications in the older literature, update museum collections, find *Jassa* in more locations and perhaps discover more species.

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[8] Reports of *J. marmorata* in the Arctic by Kröncke (1994, 1998) at 560-4478 m depth are due to contamination of samples by colonies living in the ship's seawater system (Sirenko *et al.* 2004).

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